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The genus *Amorphophallus* Blume (Araceae): phylogenetic studies and evolutionary patterns

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Author contributions

Publ. 1: CC acquired the necessary and extensive plant material, in large parts made accessible through the research collection from WH. Study design and lab experiments - isolation of the DNA, primer design, DNA amplification and sequencing, followed by editing of the sequences - were done by CC. Preliminary analyses were carried out by AA and CC. Final data analysis was carried out by SB. CC and WH wrote the first draft of the manuscript, the final manuscript was written by all authors.

Publ. 2: This chapter is based on crossing experiments from three previous publications (Claudel & Galloway, 2012; Claudel et al., 2013; Claudel & Mangelsdorff, 2014) as well as newly performed crosses. In total, 62 crosses were performed by CC. Additionally, the data of other hybridisers, Alan Galloway and Steve Jackson in particular, was compiled and evaluated by CC, with special emphasis on the taxonomic relationship between the crossing partners and the viability of the progeny. The manuscript was written by CC.

Publ. 3: This publication was conceived and designed by CC. Extensive photographic material was provided by CC and WH and compiled by CC. Photographic material, specifically depicting the petiolar patterns, was prepared by CC. MS identified and circumscribed the mimicked lichen types. CC made the analyses and wrote the first draft of the manuscript. The final version of the manuscript was written by CC, MS, SL-Y and WH.

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Publ. 5: This Publ. was conceived and designed by CC. The literature was compiled and screened by CC. CC wrote the first draft of the manuscript. CC and SL-Y wrote the final version of the manuscript.

Publ. 6: CC and AA initiated the project and carried out pilot measurements. CC collected the data. OL and DS analysed the data. CC and SL-Y wrote the first draft of the manuscript. CC, OL, DL, SLY and AA wrote the final manuscript.

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Abstract

The genus *Amorphophallus* (ca. 237 species) is one of the largest genera of the Araceae and morphologically very diverse. The high species number and the high morphological variation make the understanding of the evolutionary history of the genus challenging. Therefore, in Publ. 1, a new molecular phylogenetic analysis using nuclear (ITS1) and plastid (*rbcL* and *matK*) sequences based on 157 species is conducted and the resulting phylogenetic tree is used to delimit four subgenera. Moreover, several morphological and biochemical characters, some of which are related to mimicry, are explored in the phylogenetic context, demonstrating the congruence between molecular and some morphological and biochemical traits. However, several species complexes are difficult to resolve. Subsequently, the species boundaries are explored in Publ. 2 through the creation of artificial hybrids. As for the traits related to mimicry, at least two types of mimicry are encountered in several *Amorphophallus* species. One is a unique type of defensive colouration, petiolar lichen mimicry, providing the fleshy petiole the look of an old woody stem. Lichen mimicry in *Amorphophallus* has been previously described; however, in a few species only. Therefore, in Publ. 3, defensive colouration is explored in 138 *Amorphophallus* species, with an emphasis on lichen-like patterns. Mimicry of specific lichen types is identified in 69% of the investigated *Amorphophallus* species and the results are discussed in the context of the phylogenetic analysis. Deceit flowers, more precisely oviposition-site mimicry, is the second type of mimicry. The inflorescences mimic substrates, usually decomposing organic matter, which are used by Coleoptera and Diptera for feeding or breeding. *Amorphophallus* species are assumed to have specialised plant-pollinator interactions, involving specific pollinators, which in turn have contributed to the species richness of the genus. However, the available information about *Amorphophallus* pollinators is scarce; moreover, several reports are anecdotal. Therefore, the observations on visitors and pollinators in *Amorphophallus* are compiled, reviewed and discussed and the specificity of the plant-pollinator interaction is explored in Publ. 4. The key element of oviposition-site mimicry are the scent compounds. In previous investigations, the scent compounds of 92 *Amorphophallus* species have been identified and categorised to explore the evolution of floral odours in *Amorphophallus*. However, only few distinct evolutionary trends could be identified. One possible cause that has not been previously discussed, is intraspecific odour polymorphism. Consequently, the emitted scent compounds in *Amorphophallus* and the subjective odour classifications are reviewed and screened for odour polymorphism in Publ. 5. Significant odour polymorphism is identifiable in some *Amorphophallus* species, underlining the necessity for more investigations assessing the intraspecific variation of emitted scent compounds. Publ. 6 addresses thermogenesis, a floral temperature increase assumed to enhance scent volatilisation

during anthesis. The floral temperature of 80 *Amorphophallus* species has been measured and the resulting temperature curves have been used to explore and discuss the impact of thermogenesis on the evolution of the genus. The temperature curves show an unprecedented variation within the genus; moreover, the functionality of thermogenesis remains contentious, calling for further investigations. Lastly, using 36 *Amorphophallus* species, a phylogenomic study is conducted in Publ. 7, investigating the interrelationship between the main clades and providing a timeline for the evolution of the genus. For the first time, a phylogenetic hypothesis is presented that resolves the interrelationship between the African and the Asian clades. In a final chapter, the morphological variation is discussed in regard to the molecular phylogeny and evolutionary constraints. Moreover, further aspects of defensive colouration, odour polymorphism, thermogenesis and the plant-pollinator interaction are discussed.

Introduction to the Araceae

The oldest phylogenetic lineages of angiosperms comprise the ANA grade (Amborellales Melikyan et al., Nymphaeales Salisb. ex Bercht. & J. Presl, Austrobaileyales Takht. ex Reveal), the Chloranthales Mart., the magnoliids and the monocots (Chase et al., 2016; Cole et al., 2019; Li et al., 2019). The basalmost orders of the monocots are the Acorales Mart. and the Alismatales R. Br. ex Bercht. & J. Presl; and the largest taxon within the latter is the Araceae Juss. (Christenhusz & Byng, 2016; Cole et al., 2019; Li et al., 2019).

To date, the Araceae comprise 150 genera and ca. 4,599 species (Boyce & Croat, 2023) and form the fourth largest family of monocots. However, the family is estimated to comprise over 8,000 species (Boyce & Croat, 2023). Most species occur in the Palaeotropics and the Neotropics, South America and Asia in particular, but also in Africa (Mayo et al., 1997).

The inflorescence is the most distinctive feature of the family, consisting of a fleshy axis, the spadix, bearing the flowers. The flowers are usually reduced to carpels or stamens and are spirally arranged on the spadix, which is subtended or partially enclosed by a modified leaf, the spathe. The combination of a spathe and a spadix gives the visual impression of a large single bloom; moreover, the spathe can be distinctly coloured, probably mainly serving the purpose of pollinator attraction (Mayo et al., 1997). Furthermore, the spathe can simultaneously serve as landing platform or as a trap, depending on the type of plant-pollinator interaction (Bröderbauer et al., 2012). Most *Amorphophallus* species have simple floral chambers (Bröderbauer et al., 2012) and the visitors or pollinators are usually not trapped (van der Pijl, 1937; Grimm, 2009; Punekar & Kumaran, 2010; Chaturvedi, 2017; Sites, 2017; Moretto et al., 2019; Chai & Wong, 2019). That said, in some cases, floral trap characteristics, such as the slippery and sometimes overhanging spathe, as well as the broadened appendix base, were identified as means of temporary pollinator trapping until pollen shedding (van der Pijl, 1937; Sivadasan & Sabu, 1989; Beath, 1996; Chai & Wong, 2019; Moretto et al., 2019).

Araceae flowers are either bisexual or unisexual. If bisexual, the flowers are uniformly arranged on the spadix. If the flowers are unisexual, the spadix bears pistillate (female) flowers on its basal part and staminate (male) flowers above them (Mayo et al., 1997). All Araceae are protogynous, and when the pollen is released by the staminate flowers, the pistillate flowers are no longer receptive. The floral zones may be flanked by sterile zones or by sterile flowers, pistillodes or staminodes. In several genera, the distal part of the spadix consists of a sterile appendix which can serve multiple purposes that are not mutually exclusive, such as landing

area for potential pollinators, scent volatilisation or thermogenesis (Vogel, 1963, 1990; Mayo et al., 1997).

The Araceae, or more colloquially the arum family or aroids, show exceptional variation in leaf morphology, leaf venation, stem and root modifications as well as in the features of their underground storage organs, which are usually rhizomes or tubers (Mayo et al., 1997; Boyce & Wong, 2019; Croat & Ortiz, 2020). These features represent adaptations to the wide variety of habitats occupied by Araceae, ranging from aquatic (floating, submerged, emerged or rheophytic) via terrestrial or lithophytic to epiphytic; mostly in tropical regions but also extending to subtropical regions and to temperate zones (Mayo et al., 1997; Cabrera et al., 2008; Boyce & Wong, 2019; Croat & Ortiz, 2020).

Wolffia globosa (Roxb.) Hartog & Plas and the famous *Amorphophallus titanum* (Becc.) Becc. ex Arcang. represent two extremes of the morphological and anatomical diversity within the aroids. One extreme is the smallest angiosperm, *Wolffia*, a hydrophyte whose floating thalli are less than 1 mm in length (Beigel, 2020). At the other end of the scale is the species *Amorphophallus titanum*, known as the "Titan Arum" (Bown, 1988), which has the largest unbranched inflorescence known, reaching well over 3 m in height, rarely up to 3,70 m (McPherson & Hetterscheid, 2011; Gibson, 2018; POWO, 2024a). Moreover, *A. titanum* produces the largest and heaviest non-woody tubers of the plant kingdom, weighing up to 150 kg (Claudel et al., 2017).

This morphological diversity obscures the taxonomic relationship of the Araceae to other plant families, a topic that has been extensively discussed in the past, for example with respect to Arecaceae Bercht. & J. Presl, Cyclanthaceae Poit. ex A. Rich., Pandanaceae R. Br., Typhaceae Juss., Asparagaceae-Nolinoideae Eb. Fisch. & Mwachala; Acoraceae Martinov, and Alismatales (see Mayo et al., 1997 and references herein). However, with the advent of molecular tools, i.e., the polymerase-chain-reaction (PCR) (Saiki et al., 1988), new data resources became available. In particular, the analysis of restriction fragment length polymorphisms (RFLP), amplified fragment length polymorphisms (AFLP), and the comparison of homologuos DNA sequences provided new approaches (Patwardhan et al., 2014). Consequently, the affiliation of the Araceae to the Alismatales could be established based on molecular markers (French et al., 1995; Cabrera et al., 2008; Cusimano et al., 2011; Nauheimer et al., 2012; Chase et al., 2016; Li et al., 2019; Tippery et al., 2021; Haigh et al., 2023; Zhao et al., 2023).

The Araceae can be subdivided into three major lineages representing eight subfamilies. The three major lineages are defined as proto-aroids, lemnoids, and eu-aroids or true Araceae (Cusimano et al., 2011; Low et al., 2020). The proto-aroids consist of the two basalmost subfamilies within the Araceae: the Gymnostachyoideae Bogner & Nicolson and the Orontioideae Mayo, Bogner, & Boyce. The former is represented by the monotypic genus *Gymnostachys* R.Br. that grows exclusively in western Australia, whereas the latter contains three small genera, *Lysichiton* Schott, *Orontium* L. and *Symplocarpus* Salisb. The genus *Orontium* is monotypic, whereas *Lysichiton* contains two species, and *Symplocarpus* five species (Boyce & Croat, 2023). The members of the Orontioideae are not found in tropical biomes but occur in the Northern hemisphere in eastern Asia, western North America and eastern North America (Nauheimer et al., 2012; Lee et al., 2019).

The second lineage, the lemnoids, includes plants with an extremely reduced Bauplan, basically consisting of small and free-floating thalli (Landolt, 1986). In extreme cases, such as the above-mentioned *Wolffia globosa*, the whole plant measures less than 1 mm (Beigel, 2020). Vegetative propagation is dominant in lemnoids and even if flowers develop, they are extremely reduced, often consisting of one single pistil and/or one stamen (Landolt, 1986). These extremely reduced dimensions obscured the relationship to other plant taxa and the lemnoids were previously considered to form a family of their own, the Lemnaceae (Mayo et al., 1997). However, with the advent of molecular tools it was demonstrated that the lemnoids are nested within the Araceae, and consequently they have been assigned the rank of a subfamily, the Lemnoideae (French et al., 1995; Cabrera et al., 2008; Cusimano et al., 2011; Nauheimer et al., 2012). Similar to the Gymnostachyoideae and the Orontioideae, the Lemnoideae are a small subfamily containing only five genera with a total of 37 or 38 species (Boyce & Croat, 2023; Sree et al., 2016). However, despite the low species number and the extremely reduced Bauplan, they have the widest geographic distribution of all Araceae (Landolt, 1986; Sree et al., 2016). Moreover, they have the fastest vegetative reproduction rates (Sree et al., 2016). The inclusion of Lemnoideae within Araceae has not remained undisputed. The proto-aroids and the lemnoids are considered phylogenetically and morphologically distinct from Araceae by some authors (Tippery et al., 2021). Consequently, it has been proposed to restore the Lemnaceae and the Orontiaceae family, the latter encompassing the Gymnostachyoideae and the Orontioideae (Tippery et al., 2021). However, this proposal has been rejected by other authors (Haigh et al., 2023).

The third main lineage, the eu-aroids or the true Araceae represent the vast majority of the aroid species (~99%) (Boyce & Croat, 2023; Cusimano et al., 2011; Low et al., 2020). Of these, some 95% occur in the tropics (Cabrera et al., 2008). The eu-aroids are subdivided into five

subfamilies, the Pothoideae Engl., the Monsteroideae Engl., the Lasioideae Engl., the Zamioculcadoideae Bogner & Hesse, and the Aroideae Arnott. The main characteristic of the three relatively early divergent phylogenetic lineages, the Pothoideae, the Monsteroideae and the Lasioideae, are bisexual flowers (Mayo et al., 1997; Cusimano et al., 2011; Nauheimer et al., 2012). These are highly reduced and spirally arranged on the spadix. In between these lineages and the Aroideae, in the "transition zone" (Cusimano et al., 2011), are the genus *Stylochaeton* Lepr. and the Zamioculcadoideae. The latter consists of the genera *Gonatopus* Hook.f. ex Engl. (five species) and *Zamioculcas* Schott (monotypic) (Mayo et al., 1997). The phylogenetic placement of these three genera has been consistently considered a challenge, as they present an array of morphological characters that is unique amongst the Araceae (Mayo et al., 1997; Bogner & Hesse, 2005; Cusimano et al., 2011). Particularly, perigoniate flowers and pinnatisect leaves are characteristic of the Zamioculcadoideae (Bogner & Hesse, 2005). This led Bogner and Hesse (2005) to conclude that the Zamioculcadoideae form an "… ancient group of aroids, which has no close relationship to any other living genus …". In contrast, the flowers of the Aroideae, the last of the five subfamilies of the eu-aroids, are unisexual, forming a pistillate flower zone with an adjacent staminate flower zone (Mayo et al., 1997; Cusimano et al., 2011).

The progression of life forms within the Araceae is somewhat mirrored by the eight Araceae subfamilies. Most members of several families within the Alismatales live in aquatic environments, some completely submerged and Nauheimer et al. (2012) concluded that water-associated life forms within the Araceae represent the plesiomorphic character state. Indeed, most proto-aroids (*Orontium*, *Lysichiton*, *Symplocarpus*) are aquatics or helophytes. Similarly, the Lemnoideae are all free-floating hydrophytes. In contrast, the eu-aroids include all the lush subtropical and tropical herbs, climbers, rhizomatous and tuberous geophytes, displaying an unrivalled morphological diversity as well as various life forms, ranging from aquatic to terrestrial and epiphytic (Mayo et al., 1997; Croat & Ortiz, 2020).

This plasticity is reflected by aroids that are commonly cultivated as houseplants. These include: members of the genus *Anthurium* Schott, which are cultivated for their ornamental inflorescences (Croat & Ortiz, 2020); the very popular *Monstera deliciosa* Liebm., which is "… one of the most instantly recognizable plant images of the world …" (Mayo et al., 1997); other foliage plants, such as philodendrons; and genera such as *Anubias* Schott, *Bucephalandra* Schott. and *Cryptocoryne* Fisch. ex Wydler, which are grown in the majority of freshwater aquariums worldwide. Last but not least is the famous *Amorphophallus titanum*, the corpse flower, which is cultivated in botanic gardens worldwide for its equally compelling attraction

as a spectacular foul-smelling inflorescence (Lobin et al., 2007; Kite & Hetterscheid, 1997, 2017).

It is no coincidence that the occurrence of “monstrous” generic names and synonyms is comparatively high in the aroid family (Nicolson, 1987; Genaust, 2013). In the case of *Monstera*, it has not been reported if the name chosen by Adanson (1763) refers to the fenestrate leaves or the abundant growth of the plant. However, several generic names explicitly refer to the foul smell or mythological creatures associated with snakes and dragons. These include amongst others *Dracontium* Blume ex Decne. (dragon, snake); *Gorgonidium* Schott (gorgon); *Typhonium* Schott (*Typhṓn*, the mythological creature with countless dragon and snake heads); *Hydrosme* Schott (refering to the mythological Hydra in combination with foul smell); and *Pythonium* Schott (derived from greek “python”, dragon, snake) (Nicolson, 1987; Genaust, 2013). Significantly, the two last generic names represent synonyms of the genus *Amorphophallus*, another form of monstrosity which, referring to Schott's illustration (1858a) “approaches pornography” according to Nicolson (1987) (Fig. 1).

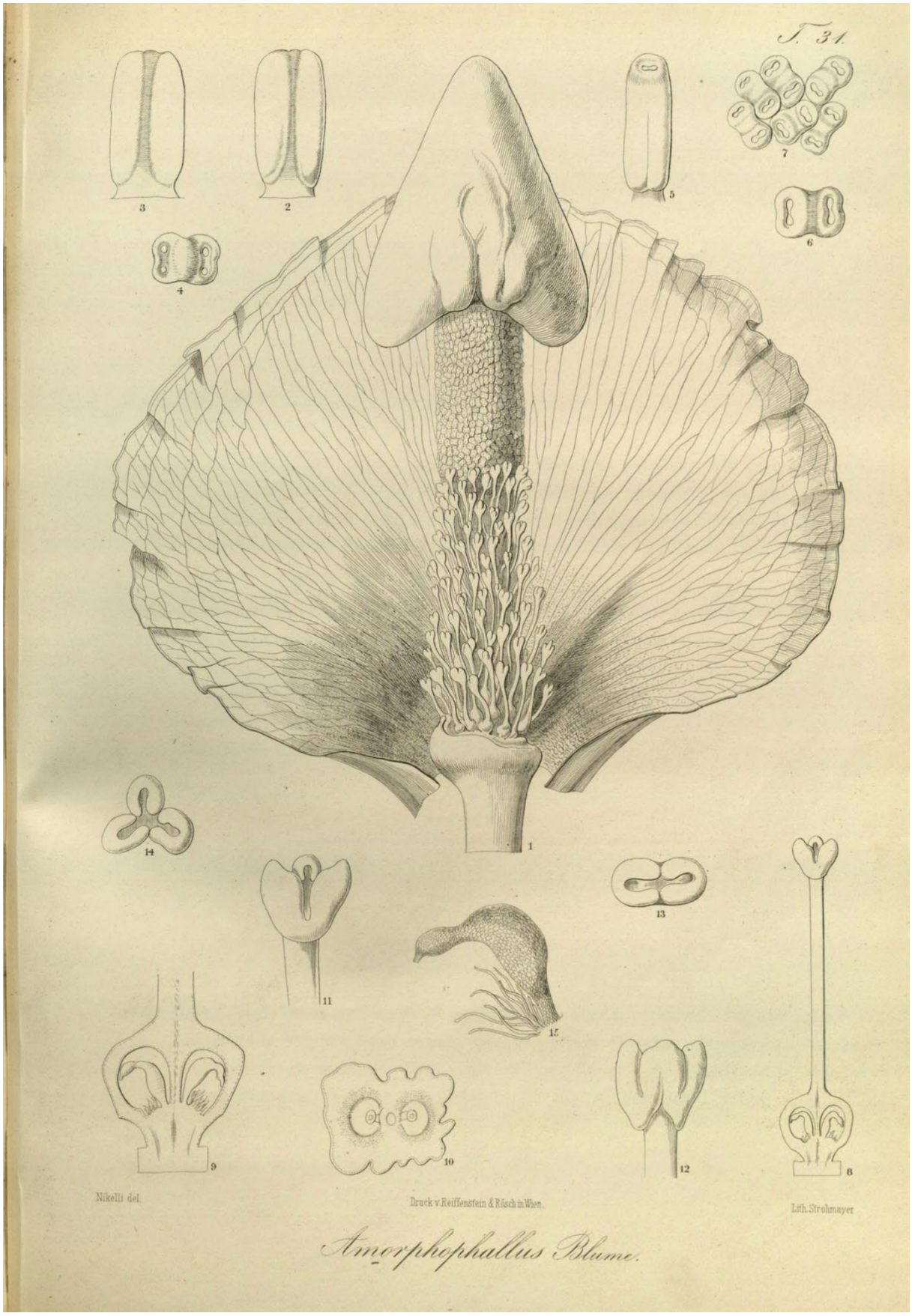

Figure 1. The illustration of *Amorphophallus campanulatus* Blume (now a synonym of *A. paeoniifolius* (Dennst.) Nicolson) in the Genera Aroidearum Exposita (Schott, 1858a).

Introduction to *Amorphophallus*

Amorphophallus plants are perennial geophytes, consisting of an underground tuber or rarely a rhizome storing carbohydrates, usually bearing a single compound leaf during each growing season (Hetterscheid & Ittenbach, 1996). The leaf increases in size with each growing season until the plant reaches maturity. The tubers are variable in form, size and weight. They can be depressed-globose, broadly to thinly elongate, slightly branched in the lower parts, form a chain of tubers or be rhizomatous (Hetterscheid & Ittenbach, 1996). One aspect that is particularly well suited to exemplify morphological flexibility in *Amorphophallus* is plant size and weight. In this regard, the two extremes of the genus are *A. obscurus* Hett. & M. Sizemore and *A. titanum*. The leaves of *A. obscurus* reach a height of ca. 6 cm (Hetterscheid & van der Ham, 2001) whereas the leaves of *A. titanum* reach "the size of a small tree, up to 7 m tall" (POWO, 2024a). In other words, *A. titanum* is more than a hundred times taller than *A. obscurus*. The tuber weight varies between a few grams in the smallest species and up to 150 kilograms in *A. titanum* (Claudel et al., 2017).

The tubers accumulate different starchy carbohydrates, e.g., glucomannan, which are used for nutritional and/or industrial purposes. In particular, *A. albus* P. Y. Liu & J. F. Chen, *A. konjac* K. Koch, *A. muelleri* Bl. and *A. paeoniifolius* are of commercial interest as they generate high glucomannan contents and have a long history of selection and breeding (Srzednicki & Borompichaichartkul, 2020). In addition to the tubers, the leaves of some species are sold on local food markets in Asia (Sookchaloem et al., 2016). However, they need to be processed carefully, as most *Amorphophallus* species contain calcium oxalate, accumulated in all tissues as raphide crystals, which may cause very unpleasant sensations (Mayo et al., 1997; Prychid et al., 2008).

The *Amorphophallus* leaf is composed of a petiole and a compound tripartite lamina (Hetterscheid & Ittenbach, 1996; Mayo et al., 1997; Sookchaloem et al., 2016). It consists of one anterior and two posterior divisions or leaflets (Mayo et al., 1997; Sookchaloem et al., 2016) that are usually more or less equal in size and appearance. The three main divisions of the lamina can be further divided into leaflets of second or even third order in some species (Sookchaloem et al., 2016). Once fully unfolded, the lamina gives the plant an umbrella-like appearance (Hetterscheid & Ittenbach, 1996). The vernation of the bud is a defining trait of the genus, in that all parts of a newly developing leaf are pointing upwards (Hetterscheid & Ittenbach, 1996; Mayo et al., 1997). Similarly, the size of the peduncle, which bears the inflorescence, varies considerably among the species, in dwarf and giant species alike (Hetterscheid & Ittenbach,

1996). For example, in dwarf species, such as *A*. *obscurus* and allies (Claudel et al., 2017) the inflorescence is partly buried in the soil and no peduncle is visible, whereas in *A*. *pulchellus* Hett. & Schuit. and its close relatives, the height of the peduncle exceeds the vegetative plant parts. At the other end of the scale, the two giants of the genus, *A*. *gigas* Teijsm. & Binnend. and *A*. *titanum*, present the largest inflorescences of the genus; *A*. *titanum* on a short peduncle and *A*. *gigas* on a peduncle that reaches up to 3.5 meters high (Hetterscheid, 1994; Hetterscheid & Ittenbach, 1996; Hejnowicz & Barthlott, 2005; McPherson & Hetterscheid, 2011; POWO, 2024a).

Naturally, variation is more pronounced in the inflorescences than in the vegetative parts (Fig. 2). The *Amorphophallus* inflorescence consists of a spadix surrounded by a spathe (Fig. 2 A-G) The spathe is triangular or ovate, often cymbiform or campanulate, more rarely funnel-shaped (Hetterscheid & Ittenbach, 1996) (Fig. 2 A-E). It can be constricted (Fig. 2 F & G), and is, at least in its upper part, usually tightly wrapped around the spadix during inflorescence development. It unfolds at anthesis, allowing the potential pollinators to access the flowers. If strongly constricted, the spathe is divided into an upper limb and a base (kettle) (Fig. 2 F & G), which forms a chamber or a trap (van der Pijl, 1937; Beath, 1996; Mayo et al., 1997; Bröderbauer et al., 2012).

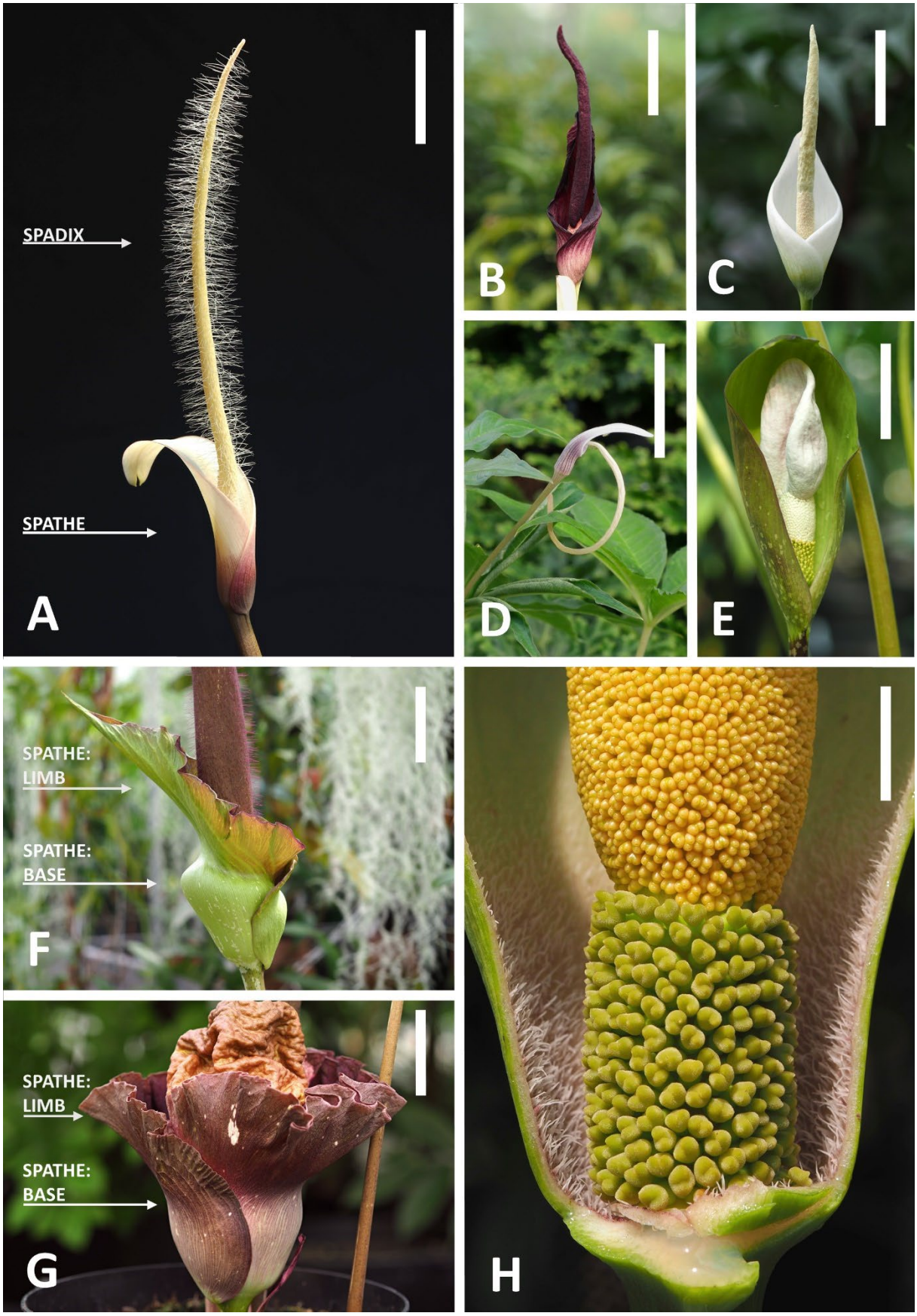

Figure 2. A-H: Floral diversity in *Amorphophallus*. A: *A. natolii* Hett., Wistuba, Amoroso, Medecilo & Claudel. B: *A. julaihii* Ipor, Tawan & P.C.Boyce. C: *A. josefbogneri* Hett. D: *A. pulchellus*. E: *A. thaiensis* (S. Y. Hu) Hett. F: *A. laoticus* Hett. G: *A. bangkokensis* Gagnep. H: *A. johnsonii* N. E. Br. Scale bars: A-G = 5 cm. H = 1 cm. Photographs: Cyrille Claudel.

However, complex traps for pollinators are not common in *Amorphophallus* (Bröderbauer et al., 2012). The tissue surrounding the insertion of the spadix, the spathe base, is occasionally specialised as a food tissue (van der Pijl, 1937), or is covered with hair-like papillae in African species (Ittenbach, 2003), e.g., in *A. johnsonii* (Fig. 2 H). The spadix is divided into three zones, the pistillate zone at the bottom, followed by the staminate zone above it, and finally on top, the sterile appendix (Mayo et al., 1997) (Fig. 3 A & B). These zones can be directly adjacent to, or separated by a sterile zone, or occasionally by staminodes, serving as food bodies that attract pollinators (Sivadasan & Sabu, 1989; Hetterscheid & Ittenbach, 1996). The appendix is assumed to be derived from fused sterile staminate flowers and to represent a synstaminodium (Bogner et al., 1985; McPherson & Hetterscheid, 2011; Hetterscheid et al., 2012). It serves as a platform for landing or departing insects (Gibernau et al., 2004), which are attracted by the scent, the warmth, or both (Knoll, 1926; Meeuse & Raskin, 1988; Vogel, 1990; Seymour et al., 2003a; Angioy et al., 2004). The appendix varies considerably in form and colour (Fig. 2 A-G), ranging from slender to conical, elongate to irregularly folded, or nearly spherical, and coloured white to yellow, green, red, brown, grey or black, and in various shades, from pale to dark (Hetterscheid & Ittenbach, 1996; Ittenbach, 2003; Yuzammi et al., 2017). Terminal appendices are not a universal feature of the family, but occur mainly in the tribes *Areae*, *Arisaemateae*, *Colocasieae*, *Schismatoglottideae*, *Thomsonieae* and *Zomicarpeae* (Mayo et al., 1997). The main function of the appendix appears to be the release and volatilisation of scent compounds (Vogel, 1963, 1990).

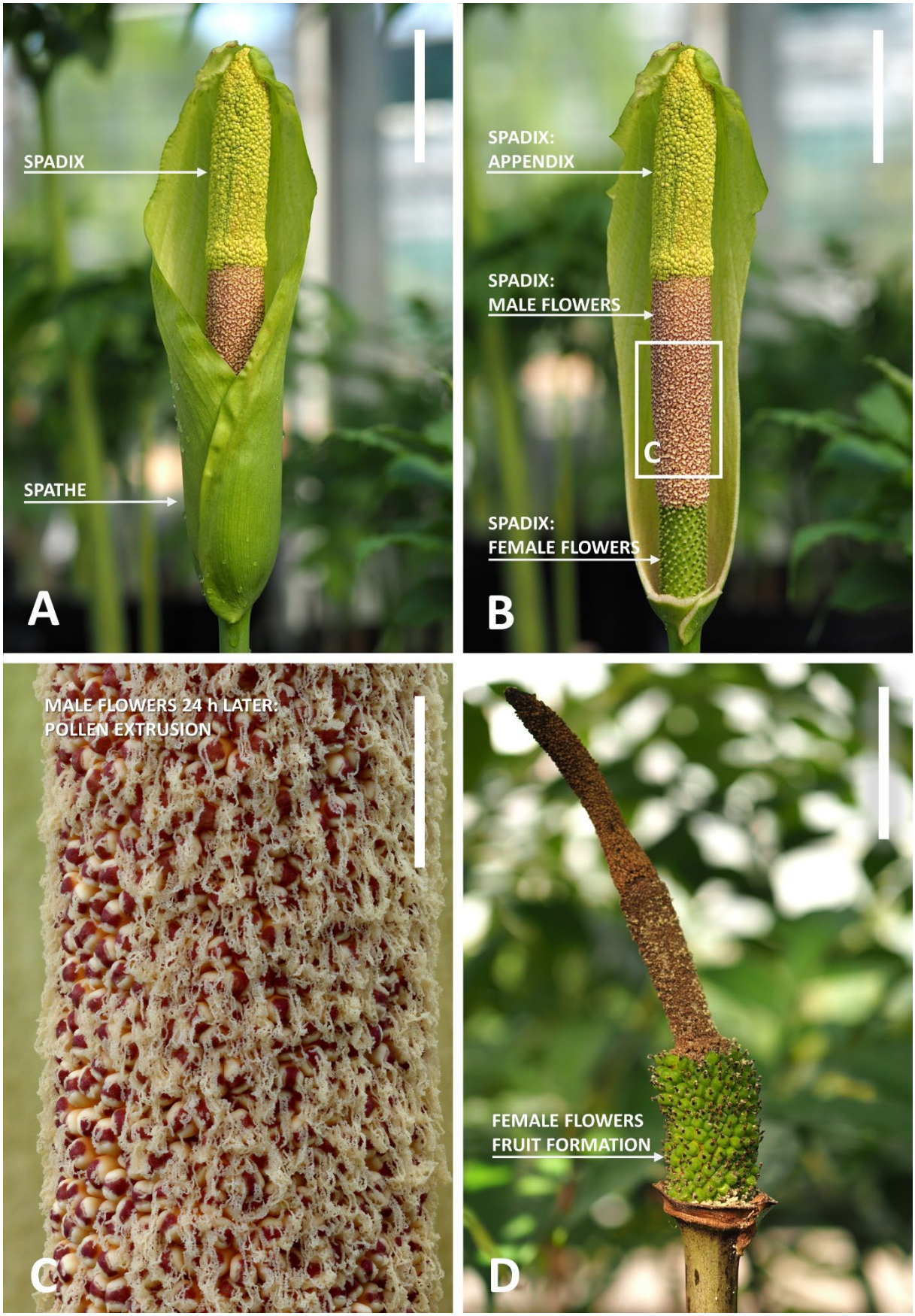

Figure 3. A-D: *Amorphophallus napalensis* (Wall.) Bogner & Mayo. A: Inflorescence on day 1 of anthesis. B: Same inflorescence cut open, showing the female flowers (green) and the male floral zone (beige). The distal yellowish-green element is the appendix. C: Pollen extrusion on day two of anthesis. D: Development of berries after fecundation. Scale bars: A, B & D = 5 cm. C = 1 cm. Photographs: Cyrille Claudel.

As in all other Araceae, the inflorescence is protogynous (Mayo et al., 1997). On the first day of anthesis, the female flowers are receptive. Pollen is released only after female receptivity has ended, usually on day two of anthesis, and self-pollination is thus prevented (Mayo et al., 1997; Hesse, 2006). The pollen is released through slits or pores, in powder or strands (Ulrich et al., 2017) (Fig. 3 C). If successfully pollinated, the inflorescence will develop into an infructescence (Fig. 3 D), consisting of many brightly coloured berries borne on a peduncle (Hetterscheid & Ittenbach, 1996; McPherson & Hetterscheid, 2011) (Figs. 4 & 5). The berries contain either one or several seeds (Hetterscheid & Ittenbach, 1996). The colour of the berries can be white, green, yellow, orange, red, purple or blue, depending on the species or on the phylogenetic unit, suggesting birds as their major dispersal agents (Singh & Gadgil, 1995; Hetterscheid, 1994; Hetterscheid & Ittenbach, 1996; Sedayu et al., 2010; Rambey et al., 2022; Low, 2024) (Fig. 4 A-D).

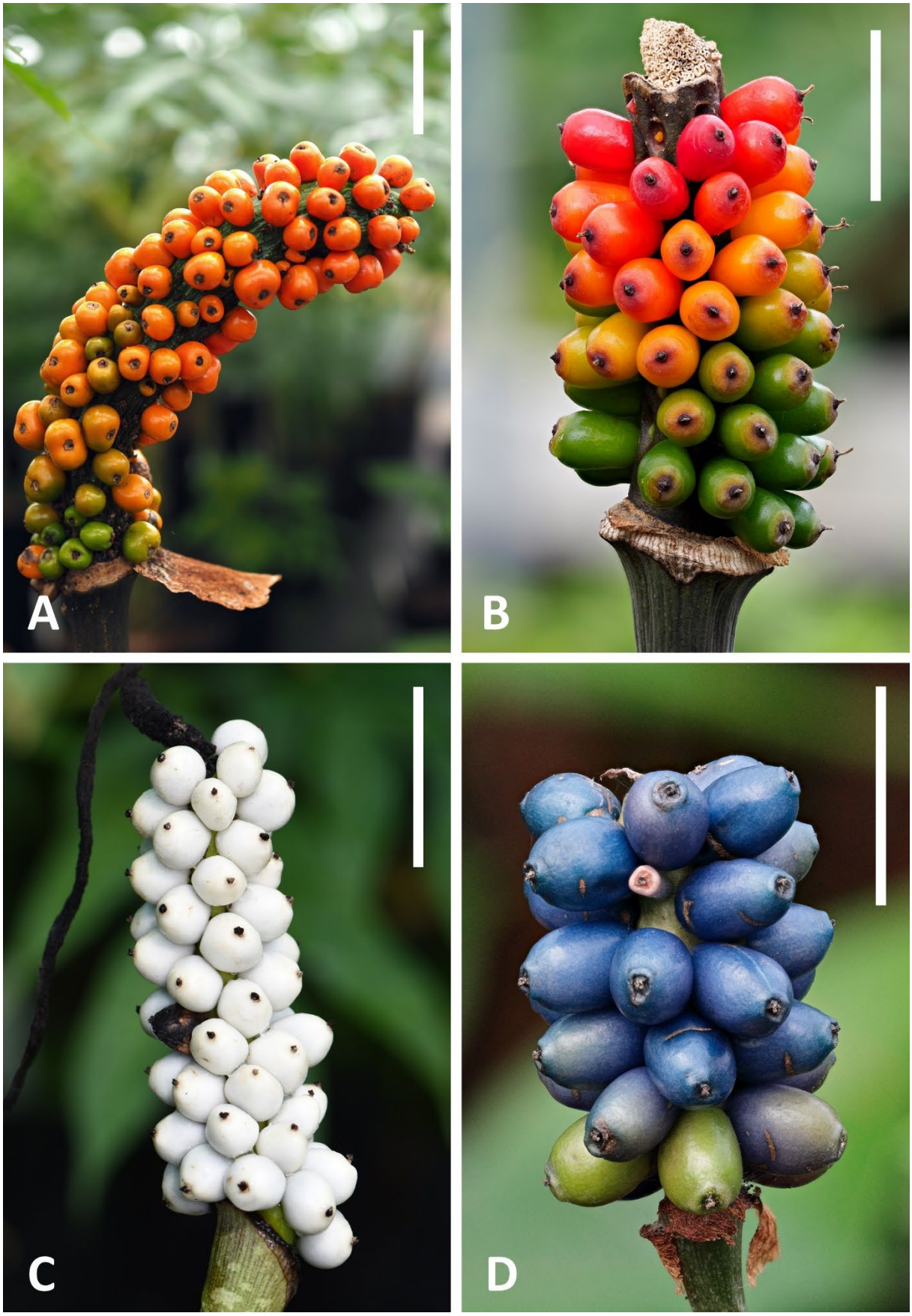

Figure 4. A-D: The most frequent fruit colours in *Amorphophallus* represented by some selected species. A: Orange berries in *A. konjac*. B: Red berries in *A. barbatus* A. Galloway & Ongsakul. C: White berries in *A. aberrans* Hett. D: Blue berries in *A. brevipetiolatus* A. Galloway, Ongsakul & Petra Schmidt. Scale bars = 5 cm. Photographs: A, B & D Cyrille Claudel. C Steve Jackson.

It is noteworthy to point out that no other genus within the Araceae displays such a diversity of berry colours (Sedayu et al., 2010). This, in conjunction with birds as main dispersal agents, might have significantly contributed to the wide palaeotropical distribution of the genus, ranging from West Africa to Japan and from China to Australia (Hetterscheid & Ittenbach, 1996). Moreover, it is interesting to note that *Amorphophallus* is the only genus within the eu-aroids that comprises species with blue berries. In fact, the only other species within the whole aroid family that bears deep blue berries is the sole representative of the Gymnostachyoideae, *Gymnostachys anceps* R. Br. (Mayo et al., 1997). However, the blue colour might represent a transitional stage as ripe fruits are also reported to be blue-black (PlantNET, 2023). Similarly, the most extensive study, investigating fruit ripening, dispersal and germination of *Gymnostachys anceps*, exclusively observed fruits with a "purplish black" colour and not a single blue fruit (Shaw, 1997). In contrast, the berry colour of several *Amorphophallus* species ranges from deep to bright blue when fully ripe (Fig. 4 D; Fig. 5 A-D). Others, such as *A. kiusianus* (Makino) Makino, turn bright pink before eventually turning dark blue (Fig. 5 D). It has been hypothesised that the blue berries are eaten and distributed by a particular group of birds (Hetterscheid & Ittenbach, 1996; Sedayu et al., 2010). However, until today no specific observations have been reported. Moreover, it remains to be investigated if the different shades of blue across (Fig. 4 D; Fig. 5 A-D) and within species (Fig. 5 A & B) possibly correlate with specific bird species.

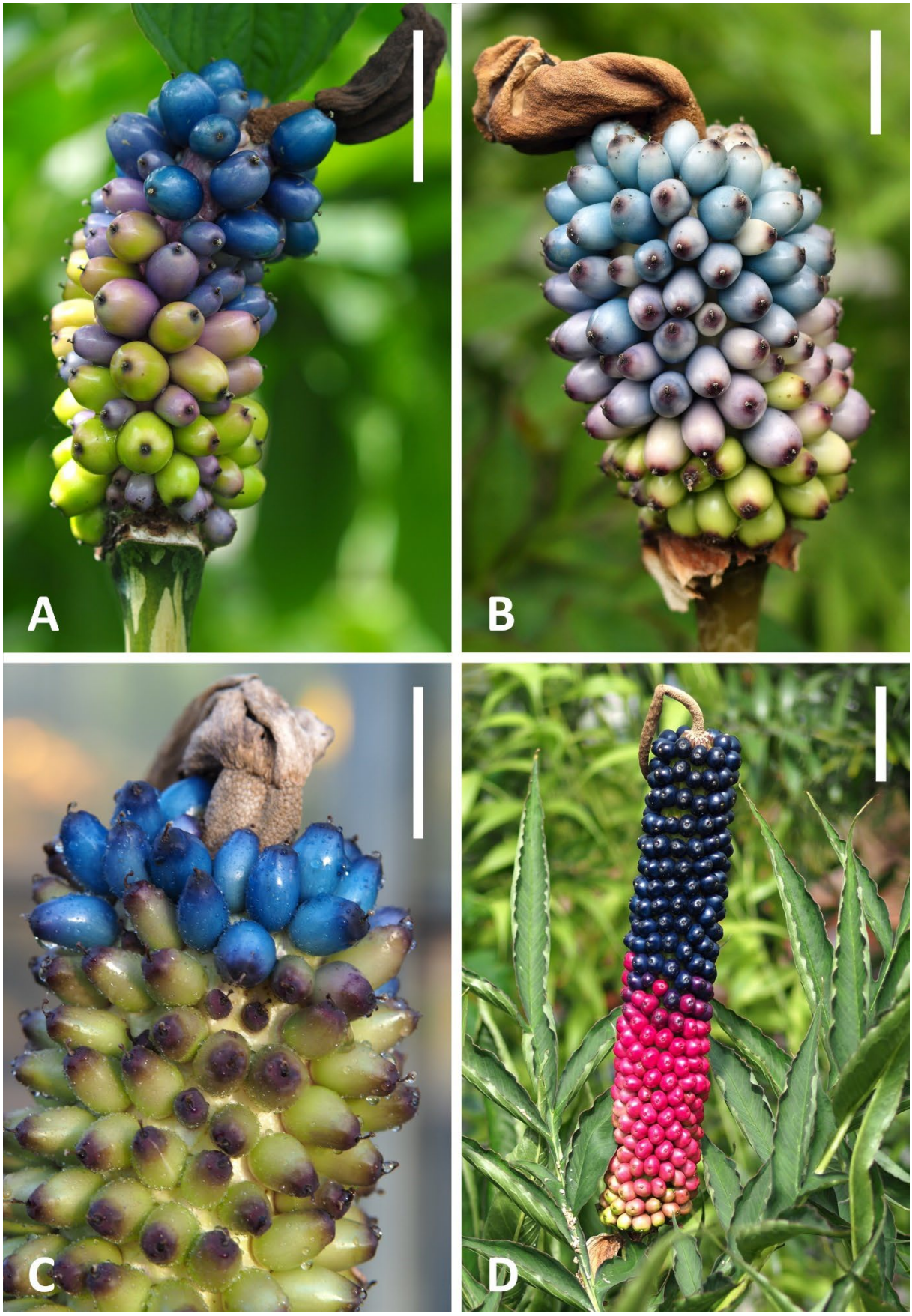

Figure 5. A-D: Blue fruit colours in *Amorphophallus*. The shades of blue differ between species and within species. A & B: two individuals of *A. yunnanensis* showing a distinctly different shade of blue. C: The berries have a very bright shade of blue in *A. thaiensis*. D: In contrast, the berries of *A. kiusianus* change from green to bright pink and from pink to dark blue when ripening. Scale bars: A, B, C & D = 5 cm. Photographs: Cyrille Claudel.

Taxonomy: Part I

The first description of a plant species later known under the generic name *Amorphophallus* dates back to the year 1692 (van Rheede, 1692). In his monumental Hortus Malabaricus, van Rheede (1692) portrayed and named two species, "Mulenschena" and "Schena". Mulenschena refers to the "spinescent projections" (mullen = with spines) whereas Schena (= cormous plant) refers to the tuber present in both species (Suresh et al., 1983). Thus, both plants are tuberous, one with a rough and one with a smooth petiole. In the following decades and centuries, the two species portrayed by van Rheede (1692) were named and described under not less than 33 synonyms or illegitimate names, including different generic names (WCSP, 2024) and finally, more than three centuries later, synonymised under *Amorphophallus paeoniifolius* (Dennst.) Nicolson (Nicolson, 1977).

However, only six years later, Suresh et al. (1983) re-established a second variety of *A. paeoniifolius*, formerly described as *A. campanulatus* var. *blumei* (Prain, 1903). Using floral and vegetative characters, Suresh et al. (1983) distinguished "the cultivated and the wild elements" and assigned the varietal name to what they considered the cultivated element, *A. paeoniifolius* var. *campanulatus* (Decne.) Sivad. Thus, more than 300 years and 33 synonyms later (WCSP, 2024), van Rheede's original Mulenschena and Schena became *A. paeoniifolius* var. *paeoniifolius* and *A. paeoniifolius* var. *campanulatus*, respectively. However, Hetterscheid and Ittenbach (1996) objected that "… no correlation between any of these characters [i.e., those supposed to separate the varieties] has been found on a large scale" and that variation in *A. paeoniifolius* was mainly due to two factors, namely a wide geographical distribution, and a long history as a crop plant. Hetterscheid (2012) even speculated that "it may even turn out that it is a domesticated, rather than a natural species". This exemplifies some taxonomic ambiguities associated with *Amorphophallus* in general and the morphological variability of *A. paeoniifolius* in particular.

The generic name itself, *Amorphophallus*, emerged comparatively late. It was first mentioned by Blume in a letter, addressed to the Governor-General of the Dutch Gold Coast and published in the Bataviaasche Courant on 23 Nov 1825. However, the generic name constituted a nomen nudum and it took almost another decade until the plant was validly published as *Amorphophallus campanulatus* Blume ex Decne. (Blume, 1834). In 1837, Blume published the first suprageneric and infrageneric classification of *Amorphophallus* based on nine species, integrating the genus in the tribe Thomsonieae Blume and presenting the first three sections, *Candarum* (Reich.) Bl. (nom. illeg.), *Adenophallus* Bl. and *Leiophallus* Bl. (Blume, 1837; Hetterscheid, 2020).

However, as soon as the generic name *Amorphophallus* was validly published, it was threatened to be merged into other genera (Nicolson et al., 1984). Martius (1831) had investigated the flower morphology of some Aroideae and established a new genus, *Pythion* (Martius, 1831) based on a species later recognized as a synonym of *Amorphophallus campanulatus* Blume ex Decne. More importantly, Wallich (1830) erected the genus *Thomsonia*, which differed from *Amorphophallus* in the appearance of the appendix, i.e., smooth in *Amorphophallus* and "tuberculate" in *Thomsonia* (Bogner et al., 1985). Although this was known to Blume, he judged the appearance of the smooth appendix important enough to consider *Amorphophallus* separate from *Thomsonia*. Consequently, both genera should have been merged into *Thomsonia* according to the priority rule (Turland et al., 2018). However, Nicolson et al. (1984) proposed to conserve the "well-known name *Amorphophallus*" against *Thomsonia* and three years later the proposal was unanimously recommended by the Permanent Nomenclature Committee (Brummitt, 1987).

Schott (1856) rearranged the genus *Amorphophallus* and restricted the usage of the name *Amorphophallus* to one of the three sections proposed by Blume (1837), notably sect. *Candarum*, and raised the other two sections to generic rank as *Brachyspatha* Schott and *Conophallus* Schott. In the following years (1857, 1858a, 1858b, 1860) Schott expanded his concept and included further species in *Amorphophallus*, also publishing additional closely related genera *Corynophallus*, *Hansalia*, *Hydrosme*, *Rhaphiophallus* and *Synantherias*.

Shortly afterwards, Engler started to investigate the Araceae. His classification system (1879) was founded on "evolutionary connections" (Mayo & Bogner, 2013) which led to a different understanding of the evolutionary history and, consequently, the classification of Araceae. Most of the genera closely related to *Amorphophallus* proposed by Schott (1857, 1858a, 1858b, 1860) were reduced to *Amorphophallus* by Engler. However, Engler used these taxa as framework for his sectional classification of the genus *Amorphophallus*. Only two of the genera described by Schott were kept by Engler, *Hydrosme* and *Plesmonium* Schott. Finally, Brown (1901) reduced *Hydrosme* to *Amorphophallus*, stating that the only separating character (funicle adnate or not adnate to the body of the ovule), is "… surely too slight and unimportant a difference to form a genus upon, especially where all other parts of the inflorescence are in such a variable and unstable condition among the various species …". The decision was later followed by Engler (1911) in his monograph of the Araceae-Lasioideae. The monograph by Engler (1911) still represents the most recent complete revision of the genus, encompassing 78 *Amorphophallus* species arranged in 11 sections as well as eight additional *Amorphophallus* species, then published under their generic synonyms *Plesmonium*, *Pseudodracontium* N. E. Br. and *Thomsonia*. However, several of these species were later synonymised or assigned the rank of subspecies (e.g., Nicolson, 1977; Bogner et al., 1985;

Hetterscheid & Serebryanyi, 1994; Hetterscheid & Ittenbach, 1996; Ittenbach, 2003), melting the original 86 *Amorphophallus* species (Engler, 1911) down to 62 recognised species today (POWO, 2024b).

When Engler published his first monographic treatment of the Araceae (1879), the genus *Amorphophallus* had not yet aroused particular interest, either from the public or from the scientific community. However, the situation changed with the discovery of *A. titanum*. According to Watson (1889), *A. titanum* is the most impressive plant, at least in the Araceae. "Compared with it, the *Rafflesia*, *Victoria regia* and *Aristolochia Goldiana*, all giants among flowers, are small and almost commonplace". Watson was assistant curator at the Royal Botanic Gardens, Kew, England. He had the privilege to raise the first *A. titanum* plant in the western world to flowering. The plant had been donated as a small seedling by the Florence Botanic Gardens, more precisely by Marquis Bardo Corsi Salviati from Sesto, Italy, in 1879 (Watson, 1889; Giordano et al., 2013). The Marquis in turn had received the seeds from his friend Dr. Odoardo Beccari, the discoverer of this "wonderful plant" (Hooker, 1891). On the sixth of August 1878, the "botanist, explorer and traveler Odoardo Beccari" discovered this extraordinary plant at Ajer Mantjoer on Sumatra (Gandawijaja et al., 1983). Beccari instantly knew he had made a spectacular discovery. "It is a gigantic Aroid, which can only be compared with the *Godwinia* discovered by Seemann in Nicaragua" (Anonymous, 1878; Beccari, 1878a). The plant Beccari was referring to was *Dracontium gigas* (Seem.) Engl., a species that had been discovered by Seemann in Nicaragua, a decade before Beccari made his discovery. At that time, *Dracontium gigas* was considered the "largest Aroid, both in leaf and flower" (Seemann, 1869).

However, Beccari had not yet seen the inflorescence of his extraordinary finding and tentatively assigned the name *Conophallus titanum*. He sent the first description to his friend, the Marchese Bardo Corsi Salviati, entrusting him to publish the description in the *Bullettino della Reale Società Toscana di Orticoltura*. The task was carried out by Emanuele Orazio Fenzi, at that time secretary of the Reale Società Toscana di Orticoltura, of which he later became president (Tomassoli, 1996). Shortly before Beccari's first account was printed, a second letter from Beccari arrived, announcing that he had finally found the inflorescence of the extraordinary plant (Beccari, 1878b). A full account of Beccari's report was transmitted by Fenzi to *The Gardeners' Chronicle* in England. Printed a few months later, on the 9 of November 1878 (Anonymous, 1878), the publication of *Conophallus titanum* aroused considerable interest. In the following year, Arcangeli (1879) formally transferred *Conophallus titanum* to the genus *Amorphophallus*.

Shortly after the plant had flowered at Kew in 1889, Beccari (1889a) wrote a letter to William Thiselton-Dyer, the director of the Royal Botanic Gardens, Kew. In the letter, he wrote that the Kew plant was the last surviving one of all the tubers and seeds he had originally sent from Sumatra. The tubers of *A. titanum* that he had originally sent from Sumatra had rotted and perished in Marseille, as they were not released by the customs in time (Beccari, 1889a). The seeds that Becarii had sent to the Marquis Corsi, had germinated well and reached respectable sizes, and were subsequently sent to other European gardens (Beccari, 1889b). However, they all died in the following years, except the one tuber sent to Kew (Beccari, 1889b). Nonetheless, this one "wonderful plant" (Hooker, 1891), unrivalled by any other plant in "size and magnificence" (Watson, 1889) was enough to raise an enormous attention worldwide and is considered to be "the greatest superstar of the botanical world" since then (Bown, 2010, p. 230).

The art of deception

The “superstar of the botanical world” (Bown, 2010, p. 230) is very inconspicuous in its natural habitat. Beccari (1889b) summarised the events around the discovery, description and flowering of *Amorphophallus titanum*. He explicitly pointed out that one could be tempted to believe that *A. titanum* was discovered in the remotest and wildest parts of Sumatra, however, the very opposite was true. It grew in the immediate surroundings of the village Beccari was living in, in the most frequented and accessible area. Beccari had been investigating the spot for several days without noticing anything extraordinary. However, after a few days, he suddenly found himself in front of a plant that appeared to be a lichen-covered tree trunk. On closer examination, he realized that the lamina of the “tree” belonged to an aroid and that he had been fooled for several days by this large petiole covered with lichen-like spots and its resemblance to a tree trunk. Beccari, an excellent observer, immediately recognized the potential protective function and postulated that the lichen mimicry served the purpose of anti-herbivory in two ways. Firstly, by disguising the plant as a tree amongst other trees, and secondly by pretending to possess a lichen-covered tree bark and to be consequently inedible.

Extracts of Beccari's original account (1878a) were translated and his discovery was presented to the English speaking audience in *The Gardeners'* Chronicle in 1878 (Anonymous, 1878). Remarkably, the English translation of Beccari’s original letter contains a minor but significant difference when compared to the original letter published in the *Bullettino della Reale Società Toscana di Orticoltura*. The original description of the petiole provided by Beccari in the *Bullettino* (1878a), reads as follows: “… di color verde e con fitte e piccole macchie quasi orbicolari, *bianche come le macchie prodotte dai licheni sulla scorza liscia di un albero*.” The translated version of the species’ description published in *The Gardeners' Chronicle* is identical in all parts, except for the second part of the above sentence. It starts identically: “… of a green colour, with numerous small, nearly orbicular dots, of a white colour” (Anonymous, 1878). However, the second part is missing. It could be translated as: “*white as the spots produced by lichens on the smooth bark of a tree*.” Moreover, Beccari (1889b) also accurately discussed the elaborate floral mimicry in carrion mimics, such as *A. titanum*, pointing out the blood-like colouration (“tinta sanguigna”) of the spathe as well as the cadaverous scent (“odore cadaverico”) emitted by the inflorescence, serving the purpose of attracting deceived pollinators.

Thus, Beccari (1878a; 1889b) was the first who explicitly discussed lichen mimicry on the petiole of *A. titanum* and its putative function. Surprisingly, this phenomenon remained widely

unnoticed for more than a century. Eventually, Barthlott (1995) wrote a publication about plant mimicry, where he stated that a few large *Amorphophallus* species are covered with dots, blotches and crust-like spots, imitating patterns of lichens and/or algae on a woody stem. These patterns were assumed to serve as protection against herbivory or physical damage (Barthlott, 1995; Hejnowicz & Barthlott, 2005). However, beyond that, this particular form of defensive colouration still remains unstudied.

Taxonomy: Part II

In the 1980s, Wilbert Hetterscheid started to work on a revision of *Amorphophallus*. At that time the species number in *Amorphophallus* had risen to ca. 100 (Bogner et al., 1985). The cooperation with some avid plant explorers such as Mary Sizemore and the late Alan Galloway, to name the most outstanding, was crucial for this project. For many years Sizemore and Galloway contributed new material to Hetterscheid's ongoing research. This led to the description of many new species and other scientific contributions in the following years (e.g., Hetterscheid & Ittenbach, 1996; Kite & Hetterscheid, 1997; Hetterscheid & Serebryanyi, 1994; Hetterscheid & van der Ham, 2001; Hetterscheid, 2003; Li & Hetterscheid, 2010). In 1996, Hetterscheid and Ittenbach (1996) stated that the species number had risen to ca. 170. Only seven years later, the species number had risen again to ca. 185 (Ittenbach, 2003) and in 2010, it reached 200 (Sedayu et al., 2010). To date, ca. 237 species are accepted (Boyce & Croat, 2023). Of these, no less than 22 species have been described in the past five years (Galloway et al., 2019a, b, c; Hetterscheid et al., 2020; Yuzammi & Hetterscheid, 2020; Bustamante et al., 2020, 2021; Tamayo et al., 2021; Bulawin et al., 2022; Calaramo et al., 2022; Fischer et al., 2022; Naive et al., 2022; 2024; Serebryanyi et al., 2023). Moreover, many more species can be expected to be described in the future, considering that many parts of the tropics are still under-collected (Prance et al., 2000; Sosef et al., 2017; Croat, 2019).

Grob et al. (2002, 2004) were the first to use molecular markers exploring the phylogeny of the genus *Amorphophallus*. Grob et al. (2002) investigated 46 *Amorphophallus* and two *Pseudodracontium* species and used several chloroplast markers (*rbc*L = ribulose 1,5 bisphosphate carboxylase large subunit, *mat*K = maturase K, the *trn*L = transfer RNA lysin gene including its intron, and the *trn*L-*trn*F intergenic spacer; *trn*F = transfer RNA phenylalanine) as well as a single-copy nuclear marker (*FLORICAULA/LEAFY* second intron, *FLint2*) (Grob et al., 2004) to investigate the phylogeny of the genus. Grob et al. (2002) inferred five main clades and discussed these clades in relation to Engler's classification (1911). The clades 4 and 5 form a clade with no support in Grob et al. (2002) but a well-supported clade in Grob et al. (2004), indicating a subgeneric delineation into four subgroups (Grob et al., 2004). Clade 1 contains all the African and Malagasy species; and the monophyly of this clade is supported by the characteristic life cycle, involving the simultaneous development of a leaf and an inflorescence (Grob et al., 2002). In contrast, clade 2 was found to be "morphologically highly heterogeneous" (Grob et al., 2002). Moreover, Grob et al. (2002) explicitly stated that not a single morphological diagnostic character or a character combination could be found to morphologically circumscribe and delimit clade 2 and clade 3. Clade 4 is characterized by an insertion of 12 base pairs

within *mat*K. As for clade 5, Grob et al. (2002) found that the genus *Pseudodracontium* is nested within *Amorphophallus*, requiring the reduction of *Pseudodracontium* to *Amorphophallus*. All in all, Grob et al. (2002) demonstrated that the sectional classification of Engler (1911) could no longer be maintained and that the morphological circumscription of several of the main clades is seriously hampered by the morphological heterogeneity expressed in these clades (Grob et al., 2002). Lastly, the evolutionary geographical origin of the genus, Africa or Asia, remained unresolved (Grob et al., 2002).

Shortly afterwards, van der Ham et al. (2005) explored the pollen morphology of the 46 *Amorphophallus* and two *Pseudodracontium* species in the phylogenetic context, using the phylogenetic tree presented by Grob et al. (2004). Despite the high variability of pollen characters, van der Ham et al. (2005) found some discrepancies between morphological and molecular characters. Although smaller phylogenetic subunits were found to share a similar pollen morphology, the monophyly of the genus could not be supported by pollen characters (van der Ham et al., 2005). Nor could any of the main clades inferred by Grob et al. (2004) be supported by pollen characters (van der Ham et al., 2005), suggesting that the morphological heterogeneity (Grob et al., 2002) extends to the pollen morphology. Lastly, some species were shown to be polymorphic (van der Ham et al., 2005).

The next step towards comprehension of the phylogeny of the genus *Amorphophallus* was taken by Sedayu et al. (2010). They used the sequences previously generated by Grob et al. (2002, 2004) and increased the sampling size up to 69 *Amorphophallus* and two *Pseudodracontium* species. The molecular markers *trn*L, *rbc*L and *FLint2* were combined and several analyses, such as maximum parsimony and Bayesian analysis were conducted (Sedayu et al., 2010). Sedayu et al. (2010) inferred four main clades, largely similar to those inferred by Grob et al. (2004) but differently arranged. The four clades were found to reflect the overall biogeographic distribution of the genus and were designated as African clade, Continental Asian Clade I (CA I), Continental Asian Clade II (CA II), and South East Asian Clade (SEA). However, in the 50% majority rule consensus tree from the Bayesian analysis, only the SEA Clade was substantially supported (0.96 Bayesian posterior probability) (Sedayu et al., 2010). Furthermore, the morphological character evolution of 70 characters was investigated (Sedayu et al., 2010). Out of these 70, five characters that correlated well with the molecular phylogeny were discussed, namely: 1. Growth cycle, which is specific to the African clade and had already been discussed by Grob et al. (2002). 2. Stylar length, another feature that delimits the African clade (sessile stigma) from the Asian clades (style present). 3. Pollen release by connective rupturing in a small group of Asian species (ca. 3 species) as opposed to pollen release directly from the pores.

4. Leaf lamina, being either divided into three segments of approximately the same size as opposed to the anterior leaf segment being distinctly less developed than the two posterior segments. This feature apparently evolved three times, once in each of the three Asian clades. 5. Berry colour, which is particularly diverse in the genus *Amorphophallus* and needs to be studied and discussed more closely. The African clade and the CA II clade contain only species with orange or red berries. Orange or red berries are also the dominant colour in the SEA clade, with some exceptions, notably green berries at full maturity in *A. sumawongii* (Bogner) Bogner & Mayo and dirty pinkish-brownish berries in *A. polyanthus* Hett. & M. Sizemore (Sedayu et al., 2010). In contrast, the berry colour ranges from white via yellow, orange and red to blue in the CA I clade (Sedayu et al., 2010). The clade containing the species with blue berries is of particular interest as it unites a larger group of species (12 species in Sedayu et al., 2010) that is otherwise "morphologically highly heterogeneous" (Grob et al., 2002). The inflorescence morphology of these species is very variable, leading Sedayu et al. (2010) to conclude that this clade could not be inferred based on inflorescence morphology alone. Moreover, the "great morphological flexibility in *Amorphophallus*" is assumed to have been derived from adaptations to different pollinators (Sedayu et al., 2010).

Finally, using gas chromatography-mass spectrometry (GC-MS), Kite and Hetterscheid (1997, 2017) identified the scent compounds emitted by 92 *Amorphophallus* species and investigated the occurrence of major scent classes and evolutionary trends in the phylogenetic context, using the majority-rule consensus tree resulting from the Bayesian analysis presented in Publ. 1. Similar to previous studies (Grob et al., 2002; Sedayu et al., 2010), several evolutionary trends could be identified in several smaller clades (Kite & Hetterscheid, 2017). Two clades in particular, each from a different subgenus, were found to be characterised by the emission of benzenoid compounds or aromatic hydrocarbons (Kite & Hetterscheid, 2017). However, the majority of *Amorphophallus* species were found to mainly emit dimethyl oligosulphides, a scent class that is characteristic of the decomposition of various organic matters, including vegetables rich in sulphur, carrion, dung, cadavers and cancerous wounds (Ollerton & Raguso, 2006; Shirasu et al., 2010; Jürgens et al., 2013). *Amorphophallus* species that emit dimethyl oligosulphides were found to be scattered across the four subgenera and to represent the ancestral state of odour emission in *Amorphophallus* (Kite & Hetterscheid, 2017). In addition, some scent types were found to have a high degree of plasticity, evidenced by sister species emitting unrelated scent compounds (Kite & Hetterscheid, 2017). As with floral morphology (Sedayu et al., 2010), the interspecific variation is assumed to be driven by specialised plant-pollinator interactions and pollinator resource partitioning (Kite & Hetterscheid, 2017). The morphological –

or in this context biochemical - flexibility in *Amorphophallus* apparently extends to the emitted floral scent compounds.

Deception & pollinators

Scent compounds that mimic substrates used by Coleoptera and Diptera for feeding, mating and breeding are the key factor of deceptive floral mimicry systems, i.e. oviposition-site mimicry (Jürgens et al., 2006; Vereecken & McNeil, 2010; Urru et al., 2011; Jürgens et al., 2013; Jürgens & Shuttleworth, 2016; Johnson & Schiestl, 2016). Scent mimicry is prominent within *Amorphophallus* and many species olfactorily mimic decomposing organic material such as carrion, various excrements, fermenting fruits, and mushrooms (Kite & Hetterscheid, 1997, 2017). Some *Amorphophallus* species, such as *A. gigas*, *A. konjac*, *A. paeoniifolius* and *A. titanum* are accordingly referred to as carrion or corpse flowers (Teijsmann & Binnendijk, 1862; Hetterscheid, 1994; Barthlott et al., 2009; Lamprecht & Seymour, 2010; Chen et al., 2015; Jürgens & Shuttleworth, 2016; Raman et al., 2017) or as dung mimics, such as *A. aphyllus* (Claudel et al., 2017) (Fig. 6 A-D).

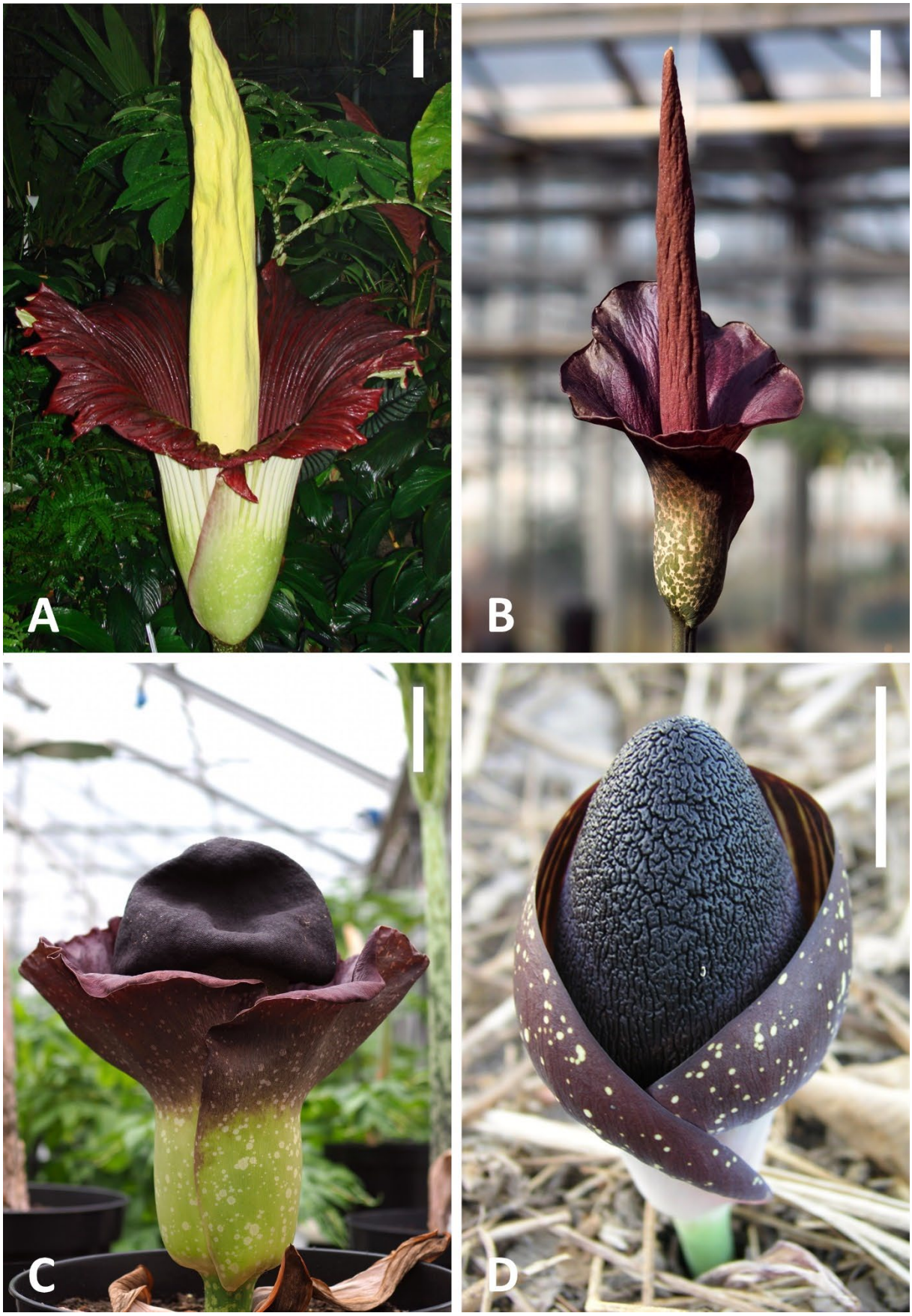

Figure 6. A-D: Carrion and dung mimicry. A: *Amorphophallus titanum*, the iconic carrion flower. B: Inflorescence of *A. konjac*, another carrion mimic. C: *Amorphophallus paeoniifolius*, the type species of the genus. D: Dung mimicry in *A. aphyllus* (Hook.) Hutch. (Claudel et al., 2017). Scale bars = 10 cm. Photographs: A Steve Jackson. B, C & D Cyrille Claudel.

Moreover, the appendix of some *Amorphophallus* species is more or less densely covered with hair-like staminodes (Hetterscheid et al., 2012) (Fig. 7 A-D). Hair-like staminodes may contribute to the visual appearance of mammal skin (Hetterscheid et al., 2012). However, *A. natolii* (Fig. 2 A; Fig. 7 A) emits a woody odour which does not fit into the carrion scheme. The odour is reminiscent of freshly cut wood (Hetterscheid et al., 2012), accompanied by a slight fungal odour (personal observation). Similar to some *Arisaema* species (Vogel & Martens, 2000), it is conceivable that *A. natolii* mimics hairy fungi, for example *Syzygites* sp. or *Phycomyces* sp., possibly attracting hairy fungus beetles (Mycetophagidae) or fungus gnats (Mycetophilidae). The hair-like staminodes might also represent a physical obstacle to landing insects, which in the attempt to land might drop down into the kettle of the inflorescence. Lastly, Beccari (1889b) noticed and described the blood-like colouration ("tinta sanguigna") of the inside of the spathe of *A. titanum* (Fig. 6 A), indicating that the olfactory mimicry ("odore cadaverico") is supported visually. These features suggest that *Amorphophallus* species exploit several senses of insect visitors and pollinators. That said, the knowledge about insect visitors and pollinators in *Amorphophallus* is limited, especially considering the size and wide geographical distribution of the genus. Moreover, the plant-pollinator interaction is unknown for most *Amorphophallus* species. According to Moretto et al. (2019), three Scarabaeoidea families are most frequently cited as pollinators of *Amorphophallus*. The Dynastidae, more precisely the genus *Peltonotus* in India and Southeast Asia; the Hybosoridae, particularly the genus *Phaeochrous* in Southeast Asia and Africa; and the copro-necrophagous Scarabaeidae in Southeast Asia and India (van der Pijl, 1937; Bogner, 1976; Sivadasan & Sabu, 1989; Hetterscheid & Ittenbach, 1996; Giordano, 1999; Jung, 2006; Grimm, 2009; Punekar & Kumaran, 2010; Chaturvedi, 2017; Sites, 2017; Moretto et al., 2019; Chai & Wong, 2019; Wong et al., 2022). However, in several cases, a multitude of arthropod visitors, including ants, bees, cockroaches and spiders, were observed to be attracted by *Amorphophallus* inflorescences (van der Pijl, 1937; Hetterscheid, 1994; Giordano, 1999; Jung, 2006: Punekar & Kumaran, 2010; Chen et al., 2015; Chaturvedi, 2017; Moretto et al., 2019; Chai & Wong, 2019; Wong et al., 2022). Moreover, flies as well as stingless bees have also been observed acting as pollinators (Gombocz, 1936; Bogner, 1976; Hetterscheid, 1994; Giordano, 1999; Punekar & Kumaran, 2010; Chai & Wong, 2019; Wong et al., 2022).

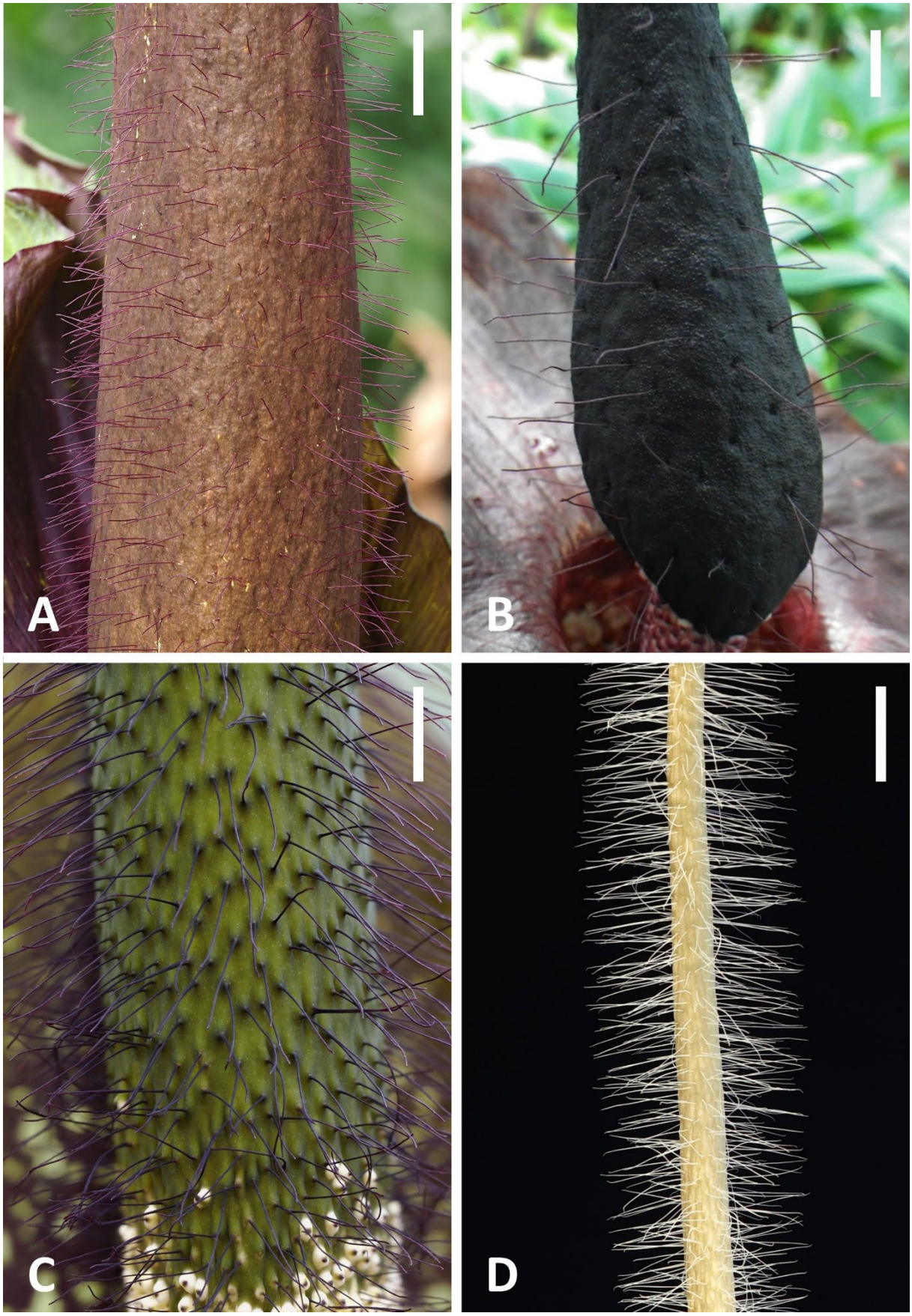

Figure 7. A-D: Appendices with hair-like staminodes: A: *Amorphophallus laoticus*. B: *Amorphophallus cirrifer* Stapf. C: *Amorphophallus pilosus* Hett. D. *Amorphophallus natolii*. Scale bars = 10 cm. Photographs: A., C. Steve Jackson. B., D & E. Cyrille Claudel.

Thermogenesis in the Araceae

Another feature associated with oviposition-site mimicry and pollinator attraction is thermogenesis (Johnson & Schiestl, 2016). Thermogenesis, the ability to produce warmth in floral organs, is one of the most peculiar features of many Araceae (Bay, 1995; Mayo et al., 1997; Seymour & Schultze-Motel, 1997; Gibernau et al., 2005; Seymour, 2010; Kakishima et al., 2011). In fact, the Araceae have the highest number of thermogenic genera and species and are the most investigated family in this respect (Grant et al., 2010; Seymour, 2010). The main, but not mutually exclusive, functions attributed to thermogenesis in Araceae are identified as improved scent volatilisation during stigma receptivity and heat reward for insect pollinators, either as a direct reward or as part of providing a shelter or heated floral chamber as a mating place (e.g., Dormer, 1960; Mayo et al., 1997; Meeuse & Raskin, 1988; Skubatz et al., 1990; Kite et al., 1998; Albre et al., 2003; Seymour et al., 2003a, 2003b; Ivancic et al., 2004; Seymour et al., 2009a, 2009b; Kakishima et al., 2011).

In the Araceae, thermogenesis is usually restricted to the male flowers, staminodes and/or the appendix (Meeuse & Raskin, 1988; Skubatz et al., 1990; Bay, 1995; Mayo et al., 1997; Albre et al., 2003; Seymour et al., 2003a, 2003b; Ivancic et al., 2004, 2005, 2008; Chouteau et al., 2007; Seymour et al., 2009a, 2009b). Only *Taccarum ulei* Engl. & K. Krause is known to elevate the temperature in the female flowers (Maia et al., 2013). Apparently, thermogenesis occurs only in plants that are pollinated by insects (Seymour et al., 2004).

However, the assigned functionalities of thermogenesis in aroids have long been debated. One of the earliest investigators of thermogenesis in aroids was Leick (1915). Considering that some aroids heat up strongly without producing a noticeable scent, whereas others smell strongly without being thermogenic, he rejected the idea of thermogenesis essentially serving the purpose of odour volatilisation (Leick, 1915). Instead, he advocated the idea of heat reward for insects. A decade later, Knoll (1926) came to the opposite conclusion, stating that the main function of thermogenesis is the volatilisation of the odoriferous compounds.

Furthermore, scented artificial inflorescences were shown to attract insects whereas heated but not scented artificial inflorescences did not attract insects, suggesting that heat does not have a relevant function, at least not as attractant (Knoll, 1926; Dormer, 1960; Meeuse & Raskin, 1988; Kite et al., 1998). In contrast, heat was found to increase the attractiveness of *Helicodicerus muscivorus* (L.f.) Engl. inflorescences (Angioy et al., 2004). Moreover, it had been proposed that heat encourages insects to stay longer in the inflorescence, thus ensuring pollination

(Moodie, 1976). However, heat might also increase the mobility of pollinating insects, ensuring pollen transport to other inflorescences (Ivancic et al., 2005). Thus, depending on the study, heat has been proposed to serve as attractant; or to retain the floral visitor, or to increase its mobility, pushing it to leave the inflorescence; three contrasting purposes designed for pollinators. Another proposal is that radiating warmth fits very well into the imagery of carrion, dung, and decomposition and thus supports this type of mimicry in Araceae (Moodie, 1976; Meeuse & Raskin, 1988). More precisely, it has been proposed that thermogenesis contributes to multisensory mimicry in *Helicodicerus* and *Typhonium* (Angioy et al., 2004; Rands, 2021). Lastly, thermogenesis has also been associated with huge inflorescences, such as in *A. titanum* (Barthlott et al., 2009).

Assuming that thermogenesis primarily serves pollinator attraction or pollinator reward, or both, and given the peculiarity and the energetic costs of this feature, enhanced fruit set might be expected compared to related non-thermogenic species. In fact, fruit set has been rarely considered in *Amorphophallus* and the few studies that examined fruit set in other aroids often came to opposite or mixed conclusions. A high fruit set has been documented in the thermogenic aroid *Helicodiceros muscivorus* (L. f.) Engl. (Seymour et al., 2003a; Gibernau & Seymour, 2014) whereas a very low fruit set was reported for *Alocasia macrorrhizos* (L.) G. Don (Ivancic et al., 2005). In the latter study, 59 individuals from several populations of *Alocasia macrorrhizos* were sampled *in situ* and the thermogenic behaviour, among others, was investigated. Temperature elevations exceeding ambient temperature by up to 25.6°C were recorded (Ivancic et al., 2005), which are some of the highest ever recorded in the plant kingdom. However, despite intense odour production and temperature increase, the seed set observed was extremely low (Ivancic et al., 2005). Likewise, Gibernau et al. (2010) investigated a population of *Anaphyllopsis americana* (Engler) A. Hay in French Guiana. Thermogenic activity in the inflorescences of this species is of exceptional duration, lasting up to 30 days (Gibernau et al., 2010). However, despite the long duration of the floral and thermogenic cycle, the fruit set was low, suggesting an "inefficient pollination system" (Gibernau et al., 2010).

Another proposed function of thermogenesis is to prevent freezing in *Symplocarpus foetidus* Salisb. (Knutson, 1974, 1979), which is capable of regulating and maintaining elevated temperatures for weeks in a cold environment (Knutson, 1974, 1979; Seymour, 2004; Seymour et al., 2009c; Kozen, 2013). However, despite these outstanding thermogenic abilities, apparently only few insects are attracted (Seymour & Blaylock, 1999). In a survey of 195 *Symplocarpus* inflorescences only 11 invertebrates were found, namely "six spiders, one isopod, two

lepidopteran larvae, one hemipteran, and one collembolan, none of which seemed particularly good pollen vectors" (Seymour & Blaylock, 1999). Similarly, Barriault et al. (2021) investigated the pollination biology and the reproductive success of *Symplocarpus foetidus* during two consecutive years (2008 and 2009) and concluded that many different insect types visit the inflorescences and that fruit sets were relatively low. Subsequently, Seymour et al. (2009c) investigated thermogenesis in *Symplocarpus renifolius* Schott ex Tzvelev and came to the conclusion that it provides the optimal temperature for pollen tube growth after germination.

Other suggested functions of thermogenesis in Araceae include infrared radiation and the formation of carbon dioxide (CO_2) (Moodie, 1976; Korotkova & Barthlott, 2009; Vereecken & McNeil, 2010). Moreover, it has been suggested that thermogenesis may promote pollen dispersal through desiccation of the anthers or the pollen, or that it may play a role in pollen maturation (Bemadinger-Stabentheiner & Stabentheiner, 1995; Gibernau & Barabé, 2000; Gibernau et al., 2000; Kozen, 2013). In contrast, Seymour et al. (2009a) rejected the idea of thermogenesis as a side-effect of pollen production. That said, none of these suggestions has been tested in depth.

The varied patterns, differences in cycle duration and temperature intensity, and contradictory observations and statements make it challenging to identify a specific purpose, let alone a single function, of thermogenesis in aroids. It has been stated that: "… the spatial and temporal patterns observed are so varied that there seems to be no general rule for thermogenesis in Araceae inflorescences" (Kakishima et al., 2011).

Thermogenesis in *Amorphophallus*

Investigations or reports on thermogenesis in *Amorphophallus* cover only eight *Amorphophallus* species; moreover, different methodological approaches, i.e. respirometry, temperature measurements and thermal imaging have been used (van der Pijl, 1937; Skubatz et al., 1990; Prakash & Nayar, 2000; Lamprecht et al., 2002; Barthlott et al., 2009; Korotkova & Barthlott, 2009; Kakishima et al., 2011; Lamprecht & Seymour, 2010; Shirasu et al., 2010; Handayani et al., 2020). In *Amorphophallus*, the main thermogenic zones are the appendix and the male flower zone (van der Pijl, 1937; Prakash & Nayar, 2000; Lamprecht et al., 2002; Barthlott et al., 2009; Korotkova & Barthlott, 2009; Kakishima et al., 2011; Lamprecht & Seymour, 2010; Shirasu et al., 2010, Handayani et al., 2020). The best investigated thermogenic *Amorphophallus* species is *A. titanum* (Barthlott et al., 2009; Korotkova & Barthlott, 2009; Lamprecht & Seymour, 2010; Shirasu et al., 2010), the "flagship species for Botanic Gardens" (Lobin et al., 2007). The spathe in this species is inwardly dark-coloured and the inflorescence can exceed more than three meters height (McPherson & Hetterscheid, 2011; Lobin et al., 2007; Gibson, 2018; POWO, 2024a). During anthesis, a powerful stench reminiscent of carrion or dung is released (Kite & Hetterscheid, 1997, 2017; Shirasu et al., 2010; Raman et al., 2017), which is sustained by the generation of heat, reaching up to 12.6°C above ambient temperature in the appendix (Lamprecht & Seymour, 2010) and up to 10°C above ambient temperature in the male floral zone (Korotkova & Barthlott, 2009). Consequently, it has been proposed that thermogenesis in *Amorphophallus titanum* serves scent volatilisation, forming vertical scent updrafts to the canopy for pollinator attraction (Barthlott et al., 2009). Moreover, thermogenesis offers a functional explanation for the large inflorescences of carrion mimicking species, according to Barthlott et al. (2009).

However, temperature increase varied between the investigated *Amorphophallus* species. *Amorphophallus titanum*, *A. muelleri* (van der Pijl, 1937) and *A. paeoniifolius* (Prakash & Nayar, 2000; Lamprecht et al., 2002; Lamprecht & Seymour, 2010; Handayani et al., 2020) showed a significant temperature increase. In contrast, only a moderate temperature increase could be observed in *A. bulbifer* (Roxb.) Blume, *A. forbesii* Engl. & Gehrm. (Skubatz et al., 1990) and *A. konjac* (Skubatz et al., 1990; Lamprecht & Seymour, 2010) whereas no temperature increase at all was found in *A. gigas* (Teijsmann & Binnendijk, 1862; Kakishima et al., 2011) and *A. variabilis* Bl (van der Pijl, 1937). Remarkably, the two giants of the genus, *A. gigas* and *A. titanum* show opposite behaviour with regard to temperature increase. While the appendix of *A. titanum* reaches 12.6°C above ambient temperature (Lamprecht & Seymour, 2010), no temperature elevation at all could be observed in that of *A. gigas* (Teijsmann &

Binnendijk, 1862; Kakishima et al., 2011). This is noteworthy given that *Amorphophallus titanum* and *A. gigas* represent the largest and tallest species of the genus (Hetterscheid & Ittenbach, 1996); both are closely related (Publ. 1), sympatric, and considered to be carrion mimics (Hetterscheid, 1994). If thermogenesis was associated with carrion mimicry, plant size and/or low population densities (Barthlott et al., 2009; Seymour, 2010), then it remains to be elucidated why *A. titanum* displays a high temperature elevation (Barthlott et al., 2009; Lamprecht & Seymour, 2010) whereas *A. gigas* remains cool (Teijsmann & Binnendijk, 1862; Kakishima et al., 2011).

Low temperature increases despite high respiration rates have been explained by heat loss through evaporative cooling (Gibernau et al., 2005; Lamprecht & Seymour, 2010; Seymour, 2010). Lamprecht and Seymour (2010) investigated the thermogenic activity of *A. konjac*, a comparatively large species (Hetterscheid & Ittenbach, 1996), by means of temperature measurements and respirometry. The authors recorded a low temperature increase in the appendix despite strong respiration rates (Lamprecht & Seymour, 2010). Moreover, they observed the formation of liquid droplets on the appendix and argued that a large surface area leads to higher evaporation and consequently stronger evaporative cooling, thus accounting for the low temperature elevation despite the high respiration rates (Lamprecht & Seymour, 2010). However, this explanation is not wholly convincing. In the same publication, the authors reported a temperature elevation of 12.6°C above ambient temperature in the appendix of *A. titanum* (Lamprecht & Seymour, 2010). Considering that the appendix of *A. titanum* is significantly larger than the appendix of *A. konjac*, it seems doubtful that passive evaporative cooling in relation to surface area alone can account for the difference in temperature elevation between the two species. However, respiration was only estimated but not measured in *A. titanum* (Lamprecht & Seymour, 2010) making it impossible to compare the respiration rates and the potential heat loss in both species.

Referring to the investigations in *A. titanum* (Barthlott et al., 2009) and *A. johnsonii* (Beath, 1996), Seymour (2010) hypothesised that the combination of large inflorescences and enhanced scent volatilisation through thermogenesis may help to overcome long distances between individuals in *Amorphophallus* species with low population densities. However, the effectiveness of scent updrafts to the canopy for pollinator attraction (Barthlott et al., 2009) were never actually tested, which is mandatory, considering that it implies a vertical scent dispersal and not a horizontal spread, necessary to overcome long distances. Furthermore, thermogenesis was never actually substantiated in *A. johnsonii* (Beath, 1996). Lastly, except for a few subsequently

published studies (Yuzammi et al., 2014; Yuzammi & Hadiah, 2018; Yudaputra et al., 2021) the population densities and dynamics of most *Amorphophallus* species are unknown. Therefore, the role of thermogenesis on the population level remains purely speculative.

Despite the thermogenic property and the different types of sophisticated deceit in *Amorphophallus* inflorescences, the attraction of a multitude of different insects and other arthropods suggests an unspecialised plant-pollinator interaction. Similarly, odour emission in *Amorphophallus* does not seem to indicate a close relationship to a specific pollinator but rather to a whole group of pollinators, mostly copro-necrophagous insects. However, this is in disagreement with the idea of a strongly constrained floral morphology/biochemistry, evolutionarily driven by specialised plant-pollinator interactions. (Sedayu et al., 2010; Kite & Hetterscheid, 2017). Therefore, assuming that species-specific and specialised plant-pollinator interactions are not the primary evolutionary drivers of speciation in *Amorphophallus*, the question arises how this morphologically highly diverse genus became the largest genus in the Araceae with a palaeotropical distribution (Boyce & Croat, 2023).

Objectives

The aim of the present work is to provide a deeper understanding of the genus *Amorphophallus* on several levels. The first objective is to generate a phylogenetic hypothesis for the evolution of the genus *Amorphophallus* based on molecular markers (Publ. 1). The latest attempts to infer the phylogeny of the genus included 48 species (46 *Amorphophallus* and two *Pseudodracontium* species) (Grob et al., 2002, 2004) and 71 species (69 *Amorphophallus* and two *Pseudodracontium* species) (Sedayu et al., 2010). Moreover, these and other studies found several of the main clades to be morphologically highly heterogeneous, which presents a challenge to our understanding of the evolutionary history of the genus (Grob et al., 2002; van der Ham et al., 2005; Sedayu et al., 2010). The high occurrence of homoplasious characters and the disagreements between the morphological and molecular approaches (Grob et al., 2002; van der Ham et al., 2005; Sedayu et al., 2010) made a more extensive analysis necessary, the more so as some 237 species have been described by now (Boyce & Croat, 2023). Therefore, relying on previous investigations (Grob et al., 2002, 2004; Sedayu et al., 2010), the species sampling is significantly increased in the present investigation and another molecular marker is incorporated. The present matrix contains 157 *Amorphophallus* species. Moreover, an additional molecular marker, the internal transcribed spacer 1 (ITS1) is included and the resulting phylogenetic tree serves as a framework for further phylogenetic investigations.

The unexpectedly close relationship between some species in the phylogenetic tree (Publ. 1), suggests that some species might be of hybrid origin. Therefore, artificial hybrids were created in order to explore if hybridisation of sympatric or allopatric *Amorphophallus* species can lead to fertile hybrid progeny (Publ. 2).

In Publ. 3, the phylogenetic tree from Publ. 1 is used to explore the occurrence of defensive (anti-herbivory) colouration, more specifically petiolar mimicry of old tree trunks, within the genus *Amorphophallus*. These patterns resemble lichens or cyanobacteria in form and colour, sometimes even in structure. Petiolar lichen mimicry in a few *Amorphophallus* species has been described by some authors (Beccari, 1878a, 1889b; Barthlott, 1995; Hejnowicz & Barthlott, 2005). However, the occurrence of petiolar mimicry types across larger parts of the genus has never been explored. Consequently, the complete available living material, representing some 100 species, as well as photographic material from 136 species is investigated and categorized. The results are discussed in the evolutionary context.

Previous studies suggested that specialised plant-pollinator interactions led to species-specific evolutionarily constrained floral morphologies (Sedayu et al., 2010; Kite & Hetterscheid, 1997, 2017). However, several *Amorphophallus* species are known to display a variable floral morphology (Jung, 2006; own observation). Moreover, several *Amorphophallus* species are known to attract a multitude of different insects and other arthropods (van der Pijl, 1937; Bogner, 1976; Sivadasan & Sabu, 1989; Giordano, 1999; Jung, 2006: Punekar & Kumaran, 2010; Chen et al., 2015; Chaturvedi, 2017; Chai & Wong, 2019; Moretto et al., 2019; Wong et al., 2022). As this contradicts the idea of an evolutionary constrained plant-pollinator interaction, the data about floral visitors and pollinators are summarised, reviewed, and discussed in Publ. 4.

Similarly, the scent compounds emitted by 92 *Amorphophallus* species revealed few evolutionary trends when investigated in the phylogenetic context (Kite & Hetterscheid, 2017). Some evolutionary trends were assumed to be indicative of either divergent or convergent evolutionary processes driven by specific pollinators and hence leading to an evolutionarily constrained inflorescence morphology (Kite & Hetterscheid, 2017). However, as far as it is known, the plant-pollinator interaction does not appear to be highly specialised (Giordano, 1999; Jung, 2006: Punekar & Kumaran, 2010; Chen et al., 2015; Chaturvedi, 2017; Chai & Wong, 2019; Moretto et al., 2019; Wong et al., 2022). Moreover, if intraspecific scent variation exceeds interspecific variation, tracing of evolutionary trends based on the quantity of emitted scent compounds might be challenged. Therefore, odour polymorphism and its putative function in some deceptive *Amorphophallus* species is reviewed and discussed in Publ. 5.

Intensified scent volatilisation has been proposed to be one main function of thermogenesis in *Amorphophallus*. However, few studies actually investigated the functions of thermogenesis in *Amorphophallus* and many questions remain unanswered (Skubatz et al., 1990, Barthlott et al., 2009; Lamprecht & Seymour, 2010) or have not been asked yet. Therefore, Publ. 6 is dedicated to the investigation of thermogenesis in the genus *Amorphophallus*. Absence or presence of thermogenesis is documented in 80 *Amorphophallus* species and explored within the phylogenetic context. Moreover, the association between selected morphological traits and thermogenesis is tested.

All previous studies found that several morphological, palynological or olfactory characters are variable, heterogeneous or “flexible”, making it difficult or even impossible to characterise larger phylogenetic units based on these characters alone (Grob et al., 2002; van der Ham et al., 2005; Sedayu et al., 2010; Kite & Hetterscheid, 2017). Moreover, at least some species exhibit palynological, floral, morphological and odour polymorphism (van der Ham et al., 2005; Jung,

2006; Sedayu et al., 2010; Kite & Hetterscheid, 2017; Publ. 5). Conversely, the interrelationship of the four large subgeneric clades remained unresolved or poorly supported in all previous studies (Grob et al., 2002, 2004; van der Ham et al., 2005; Sedayu et al., 2010; Publ. 1). These findings and the high species diversity of the genus *Amorphophallus* point towards rapid radiation. Therefore, a phylogenomic study including 36 *Amorphophallus* species is conducted in Publ. 7 to resolve the relationships between the four subgenera of the genus *Amorphophallus* and to provide a timeline for the evolution of the genus.

The final discussion is dedicated to additional aspects of the present investigations. The species sampling from Publ. 1 is discussed with regard to species delimitations and natural hybridisation. Moreover, morphological, floral and olfactory interspecific variation and intraspecific polymorphism are discussed in the context of their putative functionality.

Publ. 1: Large-scale phylogenetic analysis of *Amorphophallus* (Araceae) derived from nuclear and plastid sequences reveals new subgeneric delineation

Claudel C, Buerki S, Chatrou L, Antonelli A, Alvarez N, Hetterscheid W. 2017. *Botanical Journal of the Linnean Society* 184: 32–45.

Author contributions: CC acquired the necessary and extensive plant material, in large parts made accessible through the research collection from WH. Study design and lab experiments - isolation of the DNA, primer design, DNA amplification and sequencing, followed by editing of the sequences - were done by CC. Preliminary analyses were carried out by AA and CC. Final data analysis was carried out by SB. CC and WH wrote the first draft of the manuscript, the final manuscript was written by all authors.

Botanical Journal of the Linnean Society, 2017, **184**, 32–45. With 3 figures.

Large-scale phylogenetic analysis of *Amorphophallus* (Araceae) derived from nuclear and plastid sequences reveals new subgeneric delineation

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Remarkably little is known about the evolution of the emblematic genus *Amorphophallus*. To shed new light on phylogenetic relationships between species of *Amorphophallus* and test its current classification, the first well-sampled molecular phylogenetic analysis is presented here, comprising 157 species for which we generate nuclear (*ITS1*) and plastid (*rbcL* and *matK*) sequences. Our combined plastid and nuclear maximum likelihood and Bayesian inferences provide a solid backbone for subgeneric delineation in supporting the existence of four major clades. These latter clades are here formally recognized as subgenera (two of which are new): *Amorphophallus*, *Metandrium*, *Scutandrium* and *Afrophallus*. Each subgenus is discussed based on selected morphological features and additional traits (e.g. distribution). Finally, our results strongly support the inclusion of the genus *Pseudodracontium* in *Amorphophallus* and the required taxonomic changes are proposed here. In addition to clarifying species relationships in *Amorphophallus* and proposing a new infrageneric classification, this study provides a baseline for researchers working on the evolution and biogeography of Araceae and more broadly on the tropical flora, especially in Southeast Asia.

ADDITIONAL KEYWORDS: *Afrophallus* – *Amorphophallus* – Araceae – Bayesian inference – classification – maximum likelihood – *Metandrium* – *Pseudodracontium* – *Scutandrium*.

INTRODUCTION

Amorphophallus Blume ex Decne. (Araceae) comprises mainly lowland plants, growing in the tropical and subtropical zones of the Palaeotropics from West Africa to the Pacific Islands and Japan (Mayo, Bogner & Boyce, 1997). The centre of diversity is in Southeast Asia, which is home to *c.* 70% of the estimated 219 species (Boyce & Croat, 2011).

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Amorphophallus outranks all other aroid genera in morphological diversity (Hetterscheid & Ittenbach, 1996). Almost every plant organ shows remarkable variation, but plant size is probably the most obvious variable character. The smallest species, *A. pusillus* Hett. & Serebr. and *A. ongsakulii* Hett. & A.Galloway, have a spathe of no more than 3 cm long, whereas the giant of the genus, *A. titanum* (Becc.) Becc. ex Arcang. has a spathe reaching >2 m in length. Tuber size varies from 1 cm to >1 m in diameter and tuber weight varies from 1 g in the smallest species to 150 kg in *A. titanum*.

There is an equally wide variation in leaf size (2 cm–5 m in length and 3 cm–7 m in lamina diameter) and architecture, petiole patterning, shape of the appendix, shape and distribution of staminodes and other characters.

The basically tripartite leaf evokes the image of a sapling tree in many species: the single stem of the leaf is topped by a horizontal decompound lamina. The leaflets often have drip-tips, thus 'disguising' the plants among numerous young seedling trees in the immediate surroundings. In addition, the petiole surface of many species is covered with dots, blotches, warts and crust-like spots, seemingly imitating patterns of lichen and/or algae on a woody stem. Inflorescence may be solitary, simultaneous with or directly preceding or rarely emerging directly after leaf development or leaf senescence.

Taxonomic history

Blume (1837) presented the first suprageneric and infrageneric classification of *Amorphophallus*, treating it as part of the new tribe Thomsonieae. Brown (1882) proposed the genus *Pseudodracontium* N.E.Br., distinct from *Amorphophallus*. *Pseudodracontium* was taxonomically revised by Serebryanyi (1995). Engler (1911) presented the most recent comprehensive classification of *Amorphophallus*, but he recognized a number of closely related genera separate from *Amorphophallus*, viz. *Thomsonia* Wall., *Plesmonium* Schott, *Pseudodracontium*, *Anchomanes* Schott and *Pseudohydrosme* Engl., these genera being accommodated in tribe Amorphophalleae. *Thomsonia* and *Plesmonium* were subsequently included in *Amorphophallus* and *Anchomanes* and *Pseudohydrosme* were transferred to other tribes (Bogner, Mayo & Sivadasan, 1985). Hetterscheid (1994) presented arguments for the reduction of *Pseudodracontium* to *Amorphophallus* and Hetterscheid & Claudel (2012) formalized this step, resulting in Thomsonieae now being monogeneric. The last attempt to resurrect a genus earlier subsumed in *Amorphophallus* was made by Ying (1991), who published two new combinations of Taiwanese *Amorphophallus* spp. in the long defunct genus *Hydrosme* Schott. This taxonomic decision has not been accepted by taxonomists (Hetterscheid & Peng, 1995) and is not followed in recent treatments of *Amorphophallus* in the *Flora of Thailand* (Hetterscheid, 2012) or the *Flora of China* (Li & Hetterscheid, 2010). The monophyly of Thomsonieae was already presumed by Hetterscheid (1994, see also Serebryanyi, 1995: 218) based on morphological characters that are (nearly) unique in Araceae. This tribal monophyly has since been confirmed in all molecular phylogenetic analyses (Grob *et al.*, 2002; Grob, Gravendeel & Eurlings, 2004; Cabrera *et al.*, 2008; Sedayu *et al.*, 2010; Cusimano *et al.*, 2011). The monophyly of *Amorphophallus* has, however, not been corroborated by phylogenetic analyses so far. Molecular phylogenetic studies of Thomsonieae (Grob *et al.*, 2002, 2004; Sedayu *et al.*, 2010) have shown conclusively that *Pseudodracontium* is nested in *Amorphophallus*, thus providing phylogenetic support for the taxonomic decision of Hetterscheid & Claudel (2012).

Despite these changes and new combinations at the generic level, the subgeneric classification of *Amorphophallus* remained intact; ten out of the 11 sections accepted by Engler (1911) are still recognized and have not been revised since. The only change in the subgeneric classification has been presented by Sivadasan (1989) who merged section *Synantherias* with section *Rhaphiophallus* (Schott) Engl., both characterized by the presence of neuter flowers. This decision was followed by Jaleel *et al.* (2011) who presented a revision of the Indian species of section *Rhaphiophallus*.

The first phylogenetic analysis of Araceae based on molecular markers (Cabrera *et al.*, 2008) placed tribe Thomsonieae (*Amorphophallus* + *Pseudodracontium* still being regarded as separate genera at that time) as sister to Caladieae. This relationship was later confirmed by further molecular studies of the family (Cusimano *et al.*, 2011; Nauheimer, Metzler & Renner, 2012; Henriquez *et al.*, 2014). The first analyses of species-level relationships in *Amorphophallus* were based on limited sampling (*c.* 30% of species diversity) (Grob *et al.*, 2002, 2004; Sedayu *et al.*, 2010) and revealed a small number of well-supported clades, the relationships among which were unresolved.

This study expands the taxonomic sampling included in a previous molecular phylogenetic analysis from 69 species (Sedayu *et al.*, 2010) to 157 species, representing 70% of the known species diversity in the genus. We analyse DNA sequence data from nuclear (*ITS1*) and plastid (*rbcL* and *matK*) genomes with the following specific aims: (1) to validate the position of *Amorphophallus* within Araceae; (2) to test its monophyly with respect to *Pseudodracontium* and (3) to propose a new subgeneric classification.

MATERIAL AND METHODS

Sampling

Fresh material from all available extant *Amorphophallus* spp. was sampled (see Appendix for sampled material). Our material derives from well-curated collections at botanical gardens (notably Leiden BG, the former Wageningen BG in the Netherlands and Hamburg BG in Germany), complemented by additional fresh or freshly conserved leaf material from collaborators. Herbarium or spirit specimens for all the

taxa used in this study are deposited at the Leiden (L) branch of the National Herbarium of the Netherlands or Herbarium Hamburgense (HBG).

Marker and sequence sampling

Initially four molecular markers were chosen, based on previously sequenced loci for Araceae and expected amount of phylogenetic information. These were the internal transcribed spacer 1 (*ITS1*), the second intron of the *Floricaula/Leafy* gene (*FLint2*), the entire ribulose-bisphosphate carboxylase gene (*rbcL*) gene and the partial maturase K gene (*matK*). In case of the *FLint2*, *rbcL* and *matK* genes, previous studies (Batista, 2008; Grob *et al.*, 2002, 2004; Sedayu *et al.*, 2010) had successfully applied these loci, providing a set of 72 *FLint2* and *rbcL* sequences and 49 *matK* sequences for *Amorphophallus* and related taxa. *ITS1* from 152 *Amorphophallus* spp. and one species of the former genus *Pseudodracontium* was sequenced and concatenated with the data from the *FLint2* intron, *rbcL* and *matK* sequences already available and one *rbcL* and *matK* sequence each representing the genera *Anchomanes* Schott, *Gonatopus* Engl. and *Hapaline* Schott as outgroup taxa. One sequence of *Amorphophallus lanceolatus* (Serebr.) Hett. & Claudel was included as representative for the '*Pseudodracontium*' species alliance. One sequence was estimated to be sufficient as this group is morphologically homogeneous (Serebryanyi, 1995). Because several individuals used in the previous studies from Grob *et al.* (2002, 2004) and Sedayu *et al.* (2010) were no longer available, we replaced them with other genotypes of the same species. However, on the basis of the available plastid sequences, genetic differentiation within *Amorphophallus* is low and does not allow to discriminate between closely related species, e.g. *rbcL* sequences are identical in *A. variabilis* Bl. (GenBank accession AF497103), *A. sagittarius* Steen. (GenBank accession AF497097) and *A. decus-silvae* Backer & Alderw. (GenBank accession AF497071). However, one exception is known. Sedayu *et al.* (2010) analysed the *rbcL* gene of a second accession (GenBank accession DQ012488) of *A. galbra* F.M.Bailey from Papua New Guinea and compared it to an accession (GenBank accession AF497075) previously sampled by Grob *et al.* (2004) from Australia. Two DNA substitutions are located at the beginning of the sequence. However, as Sedayu *et al.* (2010) stated: 'The sequences are derived from plants with conspicuously different vegetative morphologies…it suggests that *A. galbra* needs further taxonomic revision and perhaps a redefinition of its species boundaries'. The same applies to the *matK* sequences, for which infraspecific variability equals zero. Furthermore, it was taken care that genotypes chosen as substitutes originated from the same geographic location whenever possible. For a detailed list of the examined material and the sequences used from GenBank, see Appendix.

The phylogenetic utility of *FLint2* at lower taxonomic levels

Amorphophallus has been demonstrated by Grob *et al.* (2004). However, due to dinucleotide tandem repeats and repeated regions, sequencing and aligning of *FLint2* might be problematic and, as indicated by Grob *et al.* (2004) in the case of *A. napiger* Gagn., different alleles containing different phylogenetic information can be present in different individuals of one species. Grob *et al.* (2004) stated that it is unclear if those variants represent paralogous loci, partial homologues, pseudogenes or normal allelic polymorphisms. They state that this occurred only in one of 46 *Amorphophallus* spp. and so we initially decided to include this marker in our analysis.

DNA extraction, amplification, purification and cycle sequencing

Total genomic DNA was extracted from fresh or silica gel-dried leaf material using the Analytik Jena innuPREP Plant DNA Kit (Analytik Jena AG). Initial ITS amplification was performed using the primer pair described by Käss & Wink (1997) and modified following Beyra Matos & Lavin (1999). Based on the first sequences more specific primers were designed. Available *FLint2*, *rbcL* and *matK* sequences (Grob *et al.*, 2004; Sedayu *et al.*, 2010) were used to design new primer pairs. Amplification of *ITS1* and *FLint2* were performed in a total reaction volume of 35 µL containing 2 mM $MgCl_2$, 1× buffer, 4% DMSO, 200 µM DNTPs, 10 µM forward primer, 10 µM reverse primer, 1–2 U Thermo-Start Taq DNA Polymerase (Thermo Scientific, Germany), *c.* 20 ng genomic DNA and distilled H_2O to volume. For amplifications of *rbcL* and *matK*, DMSO was replaced by a BSA solution at 0.5 µg/µL final concentration. The newly designed primer pairs used were: ITS 1AF 5′-GAGGAAGGAGAAGTCGTAACA-3′, ITS 2AR 5′-ACTTGCGTTCAAAGATTCGAT-3′; FLintF 5′-CTCTTCCACCTCTACGACCAGTG-3′, FLintR 5′-CATCTTGGGCTTGTTGATGTAGC-3′; RBCL1F 5′-ATGTCACCACAAACAGAAAC-3′, RBCL3R 5′-GGTAGTCATGCATTACGATAG-3′, RBCL2F 5′-TACTGCAGGTACGTGTGAAG-3′, RBCL4R 5′-GAATTACTGAATTACGCAAGC-3′; MATK3F 5′-GTATCAGATATACTAATACCC-3′, MATK4R 5′-GACCAAATCGATCAATAATAT-3′. All amplifications were performed in type T personal and T gradient thermocyclers (Biometra, Göttingen, Germany) using the following programmes for the different loci: *FLint2* and *ITS1* – 7 min initial

denaturation at 95 °C; 15 s at 64 °C, 30 s at 72 °C, 2 min at 95 °C, 15 s at 64 °C, 30 s at 72 °C, 2 min at 95 °C, 15 s at 64 °C, 30 s at 72 °C followed by 38 cycles of 30 s at 95 °C, 15 s at 63 °C and 30 s at 72 °C plus 1 s more at each following cycle followed by a final extension of 5 min at 72 °C; *rbcL* and *matK* – 10 min initial denaturation at 95 °C; 15 s at 51 °C, 45 s at 72 °C, 2 min at 95 °C, 15 s at 51 °C, 45 s at 72 °C followed by 32 cycles of 30 s at 95 °C, 15 s at 50 °C and 45 s at 72 °C plus 1 s more at each following cycle followed by a final extension of 5 min at 72 °C. The resulting *FLint2* PCR products were purified using a gel extraction procedure. The stained bands were excised under UV light and put in a tube containing 250 µL of HPLC purified water (Carl Roth, Karlsruhe, Germany). After diffusion of the PCR product into the water, the remaining agarose was removed and an alcohol precipitation was performed. The PCR products from *ITS1*, *rbcL* and *matK* were not purified, but directly sequenced. Cycle sequencing was performed using the Prism Big Dye Terminator Cycle Sequencing-Ready-Reaction kit (Applied Biosystems, Darmstadt, Germany). The reaction volume of 20 µL included 0.6 mM primer, 6.5 µL buffer and 1.5 µL dye reaction mix and 0.5–1.0 µL (*c.* 40 ng DNA) PCR product. DMSO (1 µL for *ITS1* and *FLint2*) or BSA (0.5 µg/µL for *rbcL* and *matK*) was added. Cycle sequencing programme for *FLint2* and *ITS1* was: 2 min at 96 °C followed by 32 cycles for 30 s at 96 °C, 3 min at 63 °C plus 1 s at each cycle with a final extension of 5 min at 72 °C. For *rbcL* and *matK*: 2 min at 96 °C followed by 30 cycles of 30 s at 96 °C, 15 s at 50 °C, 3 min at 63 °C plus 1 s at each cycle with a final extension of 5 min at 72 °C. Purification of the sequencing products was done by ethanol precipitation. The purified sequence reaction was run on an ABI Prism 377 automated sequencer (Applied Biosystems, Darmstadt, Germany).

Alignment

Raw sequences were examined and assembled using Sequencher version 4.8 (Gene Codes, Ann Arbor, MI, USA). Sequences were aligned using the clustalX algorithm (Thompson *et al.*, 1997) as implemented in BioEdit (Hall, 1999), using default settings. The alignment was checked and corrected manually. Manual correction was straightforward for *rbcL* and *matK* and needed care for *ITS1* and especially *Flint2*. The sequences of the four regions were trimmed and concatenated into one matrix.

Phylogenetic inference

Single-gene and partitioned phylogenetic inferences were carried out employing both maximum likelihood (ML) and Bayesian Markov chain Monte Carlo (MCMC) analyses. In the case of the partitioned analyses, the data set was divided into two partitions representing the nuclear and plastid genomes and each partition was allowed to have partition-specific model parameters. Phylogenetic analyses were performed at the CIPRES portal in San Diego, California, USA (http://www.phylo.org/, last accessed on 5 April 2017 Miller, Pfeiffer & Schwartz, 2010).

ML analyses were performed using RAxML v. 8.1.11 (Stamatakis, 2006; Stamatakis, Hoover & Rougemont, 2008) with a 1000 rapid bootstrap analysis followed by the search of the best-scoring ML tree in a single run. The default model, GTRCAT, was used for all partitions as advised by the authors of the software. The Bayesian MCMC analyses were performed in MrBayes v.3.2 (Ronquist *et al.*, 2012) after the best-fit model for each DNA region had been estimated using MrModeltest (Nylander, 2004) under the Akaike information criterion (the GTR + G + I model was inferred for all partitions). We checked for possible incongruences [Bayesian posterior probability (BPP) > 0.9 and bootstrap support (BS) > 75%] before concatenating the nuclear rDNA and plastid data into a single analysis. The alignments of *ITS*, *FLint2* and combined plastid markers were analysed with MrBayes, with analysis parameters as indicated below. The resulting maximum clade credibility trees were inspected visually for well-supported incongruence (using the same criteria as above). These were absent, which justified the concatenation of the nuclear rDNA and plastid data. Four Metropolis-coupled Markov chains with an incremental heating temperature of 0.2 were run for 10 h on the CIPRES portal (yielding 13 416 000 generations) and sampled every 1000th generation. Each analysis was repeated twice starting with random trees. The MCMC sampling was considered sufficient when the effective sampling size (ESS) was >200 and trace files for all parameters reached stationarity and converged, as verified in Tracer v1.4 (Rambaut & Drummond, 2007). After a burn-in period of 25% per run (corresponding to the recommended approach by the MrBayes tutorial), the remaining trees were used to construct a half-compatible maximum credibility tree (i.e. majority-rule consensus from MrBayes) and its associated BPPs.

As shown by several empirical and theoretical studies (see Alfaro & Holder, 2006 for a review) BPPs have the tendency to overestimate node support. On the other hand, due to the way BPPs are defined (Ronquist *et al.*, 2012), these values better reflect sections of the DNA sequences supporting specific phylogenetic relationships compared to the classical bootstrap approach (see, e.g. Buerki *et al*, 2012). In this regard, BPPs are well adapted to organisms exhibiting slow rates of mutation, which is the case here and in many other Araceae (e.g. *Arum* L.; Espindola *et al.*, 2010) and

monocots in general (e.g. *Pandanus* Parkinson; Buerki *et al.*, 2012). In this context, we consider nodes with BPPs ≥ 0.95 highly supported, but those might have quite low BS values compared to other studies (usually *c*. 75% or higher).

RESULTS

FLint2 issue and exclusion

For *FLint2* a specific primer pair with a high melting temperature was designed based on the sequences from Grob *et al.* (2004) and Sedayu *et al.* (2010). Highly specific amplification products were yielded. However, no sequences could be obtained from 24 taxa. These taxa clearly exhibited an overlap of two sequences, probably representing two different alleles; Grob *et al.* (2004) found two sequences only in the case of *A. napiger* and *Filarum manserichense* Nicolson. These exhibited different phylogenetic information. We assume that the 24 taxa which did not yield a readable sequence are either heterozygous or that two paralogous loci were amplified. Given the risk of amplifying paralogous copies across our sampled taxa and the dramatic consequences this may cause to the assessment of among-taxa relationships, we decided to exclude *FLint2* entirely from the analysis.

DNA sequencing

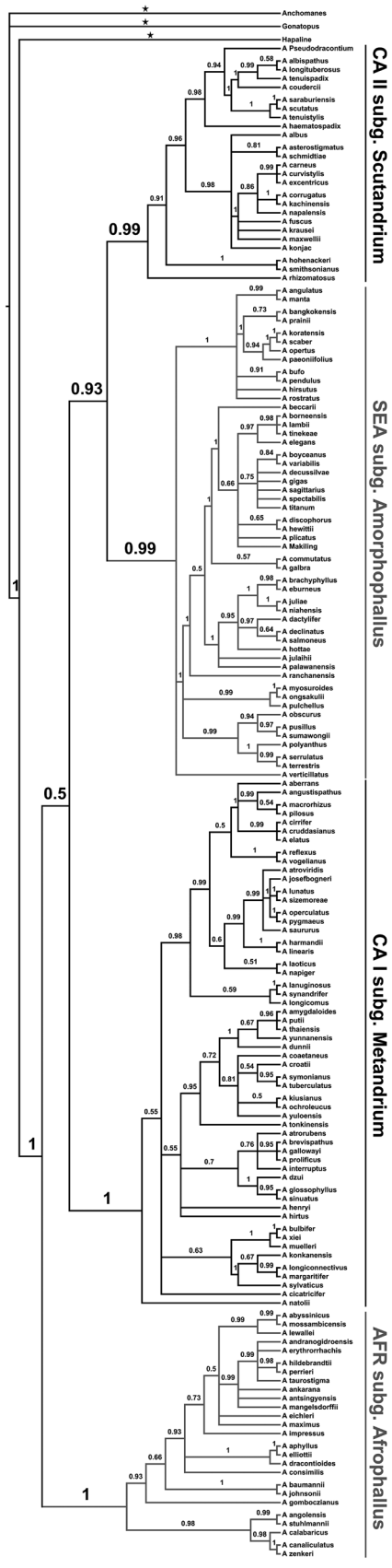
ITS1 could be sequenced in nearly all taxa, with the exception of *A. macrorhizus* Craib, for which only the second half of the sequence could be obtained. After trimming, the sequence length varied between 353 (*A. vogelianus* Hett. & H.Billenst.) and 406 [*A. bangkokensis* Gagn., *A. paeoniifolius* (Dennst.) Nicolson] base pairs (bp). With the exception of *A. paeoniifolius*, the spacer proved to be homogeneous for all individuals of one species each, which were investigated to test the homogeneity of the ITS sequences (data not shown). As for *rbcL* and *matK* all samples yielded sequences, with a final sequence length of 1364 bp for *rbcL* and 735 bp for the partial *matK* sequence (741 in the case of *A. haematospadix* Hook.f.) after trimming. Thus, the final alignment, trimmed and including gaps, consisted of 2610 characters and included *ITS1* (505 bp), *rbcL* (1364 bp) and partial *matK* (741 bp). Of 2610 characters, 1995 were constant, 258 variable characters were potentially parsimony uninformative and 357 characters were potentially parsimony informative. *ITS1* contained 160 (45%), *rbcL* 101 (28%) and *matK* 96 (27%) of the 357 potentially parsimony-informative characters. For the outgroup taxa, only the plastid markers were included into the alignment as *ITS1* proved unalignable with confidence.

Phylogenetic inference

Although differing in the level of phylogenetic resolution provided by each DNA region individually, single-gene nuclear and plastid phylogenetic trees were congruent (i.e. there is no incongruence supported with a BPP > 0.9 and/or a BS > 75%). The Bayesian single-gene phylogenetic trees are provided in Supporting Information to allow readers to further inspect species relationships and phylogenetic resolution provided by nuclear and plastid DNA regions (Figs S1, S2). In addition to supporting congruence between the nuclear and plastid DNA sequences, the separate analyses also demonstrated that species represented by different DNA accessions were retrieved in the same phylogenetic positions (therefore, suggesting species monophyly). These preliminary analyses supported the concatenation of the nuclear and plastid DNA regions into a combined DNA matrix.

The combined partitioned phylogenetic trees generated by the Bayesian and the RAxML analyses were largely congruent in their topologies especially with respect to the definition of the four main clades (see Fig. 1). The Southeast Asia clade (SEA clade, see Sedayu *et al.*, 2010) is strongly supported with a value of 0.99 BPP in the Bayesian analysis and a BS of 76% in the RAxML analysis; the continental Asia clade II (CA-II clade, see Sedayu *et al.*, 2010) has a support value of 0.99 BPP (BS: 78%); the continental Asia clade I (CA-I clade, see Sedayu *et al.*, 2010) is fully supported with a value 1 BPP (BS: 90%) and the African clade (AFR clade, see Sedayu *et al.*, 2010) with 1 BPP (BS: 90%). In the RAxML phylogenetic tree, the CA-II clade (BS: 78%) and African clade (BS: 90%) are inferred sister with no support (BS: 46%). These two together link to the SEA clade (BS: 76%) again with no support (BS: 30%) to finally link to the last group, the CA-I clade (BS: 90) with a support of 100% BS for the whole genus. In the Bayesian analysis, the SEA (BPP: 0.99) and CA-II (BPP: 0.99) clades are sister with their common node being supported by a value of 0.93 BPP. They are linked at the next node by the CA-I clade (BPP: 1.0) with no node support of 0.50 BPP. The next node of the entire backbone links these three clades to the African clade (BPP: 1.0) with a support of 1.0 BPP for the whole genus.

Both phylogenetic trees support the monophyly of *Amorphophallus* with the highest possible score (BPP: 1.0; BS: 100%). As the topologies are largely congruent except for the higher level relationships, which are especially poorly resolved in the RAxML analysis, only the Bayesian half-compatible maximum credibility tree (majority-rule consensus tree) will be presented (Fig. 1) and discussed further with reference to the bootstrap values of the RAxML analysis. For better illustration, two of the four major clades each, of the partitioned Bayesian tree are presented separately in Figures 2 and 3.



DISCUSSION

We compare our results with the most recent molecular phylogenetic analysis of *Amorphophallus* by Sedayu *et al.* (2010), especially with regard to the four major clades and the position of the *Pseudodracontium* group. Our results strongly confirm that *Pseudodracontium* belongs to *Amorphophallus*. Sedayu *et al.* (2010) also recognized four major clades in *Amorphophallus*. The recognized clades were the African clade (AFR) containing African species; the Southeast Asian (SEA) clade containing a majority of species from the Southeast Asian insular regions (Indonesia, Philippines, eastern Malaysia); the continental Asia II (CA-II) clade containing mainly species from the Asian mainland (India, southern China, Myanmar, Thailand and Indochina) and the continental Asia I (CA-I) clade containing species distributed in the same geographical region as those from CA-II. The present study recovers all four clades from Sedayu *et al.* (2010). However, three species of the CA-II clade, *A. rhizomatosus* Hett., *A. hohenackeri* (Schott) Engl. & Gehrm. and *A. smithsonianus* Sivad., are not clearly resolved in the RAxML analysis. The two latter are discussed more closely below. The position of *A. rhizomatosus* as sister to the CA-II plus the African clade in the RAxML analysis can be explained by early-diverging nature of this species, showing fewer derived characters than the remaining species, with its rhizome, the simple inflorescence, without a kettle, and a plain whitish spathe (Hetterscheid & Ittenbach, 1996). However, the position of *A. rhizomatosus* is well resolved in the Bayesian analysis.

The backbone of the Bayesian phylogeny, linking these four well-supported clades together, is less strong. Clades SEA and CA-II are linked at the next node with CA-I with no node support of 0.50 BPP. The next higher level node of the entire backbone links these three clades to the African clade with a support of 1 BPP for the whole genus. This is a different pattern from the backbone based on maximum parsimony in Sedayu *et al.* (2010), where the CA-I and CA-II clades form a sister group pair, linked at their base with SEA and the highest level node adding the AFR clade. Although the four major clades are supported by both algorithms/approaches, the relationships between clades remain poorly supported and would require further molecular investigations. Moreover, the Bayesian analysis of Sedayu *et al.* (2010) yielded low resolution for the

Figure 1. Bayesian majority-rule consensus tree of *Amorphophallus* based on plastid and nuclear DNA regions. Outgroup taxa indicated with a star above the branch. BPP values above the branches. BPP values of the four major subclades and their internal nodes are highlighted. Two of the four major subclades are further presented separately for better illustration (Figs 2, 3). BPP, Bayesian posterior probability.

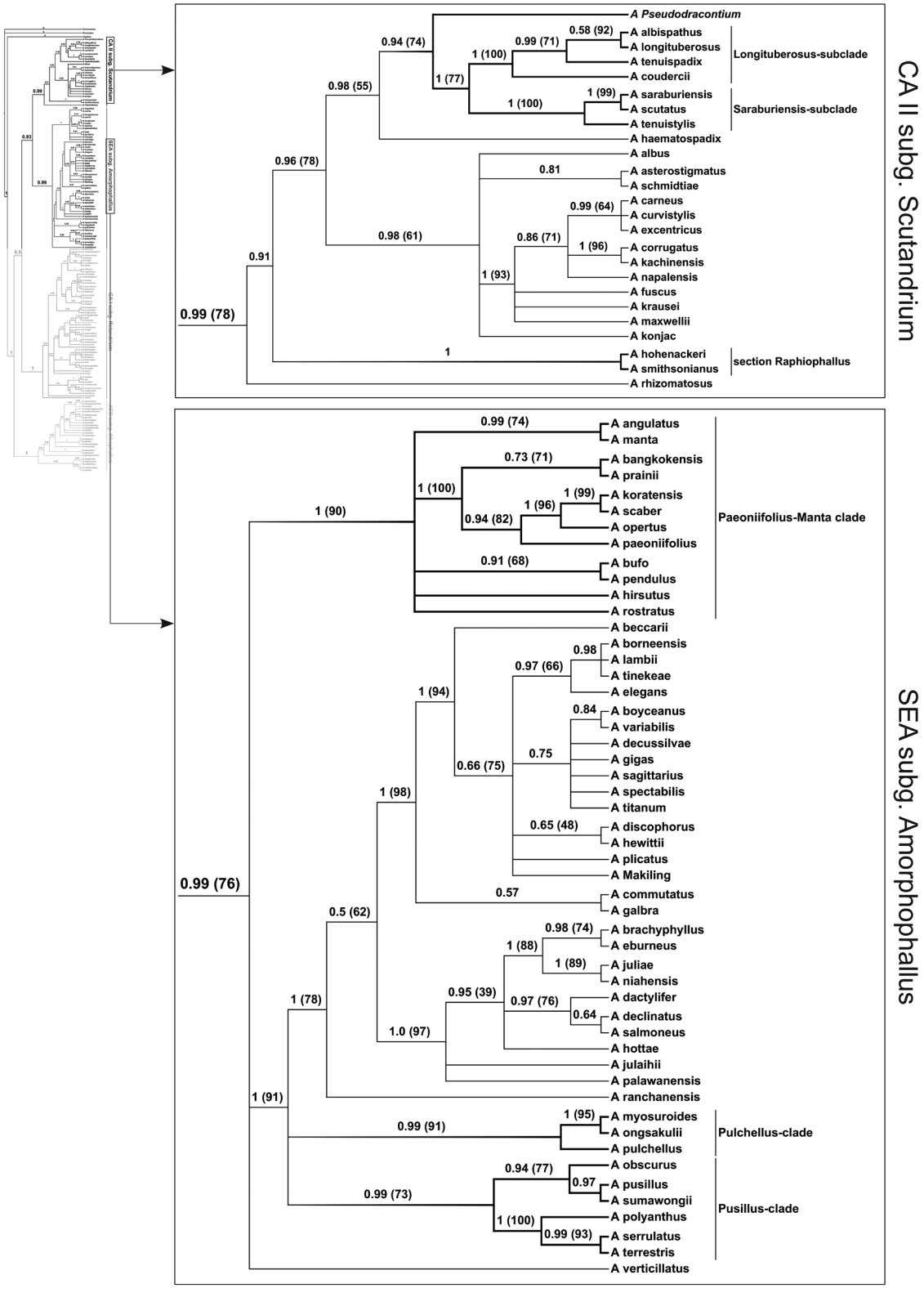


Figure 2. Close-up of the majority-rule consensus from the Bayesian analysis of *Amorphophallus* showing the CA-II subgenus *Scutandrium* and the SEA subgenus *Amorphophallus* clade. Clades referred to in the text are highlighted and indicated with a parenthesis. BPP values are given above the branches. Identical clades retrieved from the RAxML analysis are indicated with BS values in parentheses behind the BPP values. BPP, Bayesian posterior probability; BS, bootstrap support.

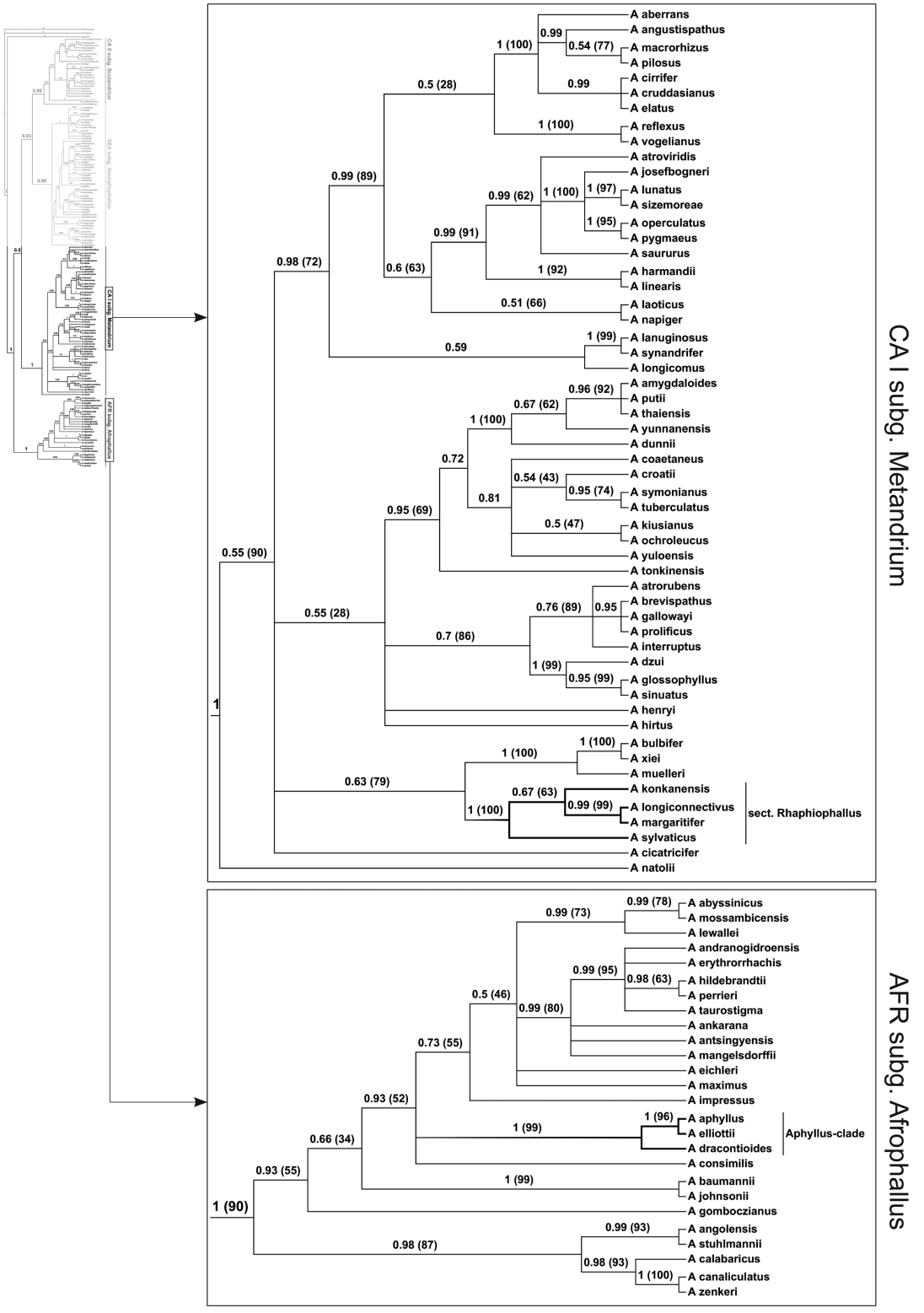


Figure 3. Close-up of the majority-rule consensus from the Bayesian analysis of *Amorphophallus* showing the CA-I subgenus *Metandrium* and the AFR subgenus *Afrophallus* clade. Clades referred to in the text are highlighted and indicated with a parenthesis. BPP values are given above the branches. Identical clades retrieved from the RAxML analysis are indicated with BS values in parentheses behind the BPP values. BPP, Bayesian posterior probability; BS, bootstrap support.

relationships among these four groups. The genus *Amorphophallus* is supported with 0.99 BPP, but the next higher level comprises the CA-I (BPP: 0.63) and the CA-II (BPP: 0.76) groups with the SEA (BPP: 0.96) and the Africa (BPP: 0.87) group forming a polytomy in between. In the RAxML analysis the monophyly of the genus *Amorphophallus* is supported with BS of 100%, but the structure of phylogenetic relations among the four major clades differs from the Bayesian analysis and is poorly or not supported as mentioned above.

All in all, the greatly increased number of species of the present analysis compared to that of Sedayu *et al.* (2010) leaves the major internal structure of the phylogeny intact, with the exception of the backbone. The relationships among these four subgroups were not at all resolved in previous studies and unfortunately still remain unclear in some points. Further investigations at a deeper phylogenetic level are required to solve this problem. Although a thorough revision of the sectional taxonomy and nomenclature of *Amorphophallus* is pending, it is too complex and extensive to be satisfactorily treated here. An exception is made for section *Rhaphiophallus* for reasons given below (see under subgenus *Metandrium* Stapf). However, the Bayesian phylogenetic tree presented here (Fig. 1) is the most extensive and accurate phylogenetic hypothesis proposed so far and the opportunity is used to formally name the four major clades.

In addition, a few relevant observations in the morphological and biological context of these four clades are made below, with special emphasis on some selected clades within these four groups, such as the *Paeoniifolius-Manta* clade (Fig. 2), the *Pulchellus* and *Pusillus* clade (Fig. 2), section *Rhaphiophallus* (Figs 2, 3), the *Pseudodracontium* group (Fig. 2) and the *Aphyllus* clade (Fig. 3).

Infrageneric taxonomy and subgeneric classification of *Amorphophallus*

The history of infrageneric classification and nomenclature of *Amorphophallus* is complex except for the rank of subgenus. Only one subgenus has ever been established, *Metandrium* (Stapf, 1924), with the type species *A. cirrifer* Stapf. In our analysis *A. cirrifer* is a member of the CA-I clade, which therefore should carry the name *Metandrium* at the subgeneric rank. Distribution: India and continental Southeast Asia (Burma, Thailand, Laos, Cambodia, Vietnam and southern and eastern China) to southern Japan [*A. kiusianus* (Makino) Makino], the Philippines (*A. natolii* Hett., A.Wistuba, V.B.Amoroso, M.Medecilo & C.Claudel) and Indonesia (*A. muelleri* Bl.).

The autonymic subgenus *Amorphophallus* is automatically typified by *A. paeoniifolius* (Dennst.) Nicolson, the type species of the genus. In consequence, the SEA clade, to which this species belongs is named *Amorphophallus* at the subgeneric level. Distribution: all over Southeast Asia, from India eastwards via continental Southeast Asia and Indonesia to the Philippines and Australia (*A. galbra*).

This leaves the African and CA-II clade to be given a new name. In the case of the CA-II clade this is *Amorphophallus* subgenus *Scutandrium* Hett. & Claudel, subgen. nov. Type species (chosen here): *Amorphophallus krausei* Engl. (Type: *Shaik Mokim s.n.*, CAL, holotype). Diagnosis: Tuber globose, subglobose, elongate or rarely a rhizome (*A. rhizomatosus*); leaf solitary, or rarely more (*A. rhizomatosus*); inflorescence solitary, appearing every second year alternating with solitary leaf in next year (excluding *A. rhizomatosus*: leaf + inflorescence simultaneous) spathe erect, rarely constricted, base inside smooth or verrucate; spadix shorter than or as long as spathe, rarely longer; staminodes (when present) broadly shield-like; styles short, rarely very long (*A. maxwellii* Hett.); berries red or orange. The name derives from the shield-like staminodes on many species of this subgenus. Distribution: southern India and continental Southeast Asia (Burma, Thailand, Laos, Cambodia, Vietnam and southern China).

In the case of the African clade the new name is *Amorphophallus* subgenus *Afrophallus* Hett. & Claudel, subg. nov. Type species (chosen here): *Amorphophallus abyssinicus* (A.Rich.) N.E.Br. (Type: *Quartin Dillon*, P, holotype, P00083579). Diagnosis: tuber depressed to disciform, rarely globose; inflorescence and leaf appearing in same season, simultaneous or the leaf soon following the inflorescence; spathe erect often strongly constricted, base inside smooth, verrucate or with hair-like papillae; spadix shorter than spathe or longer; staminodes absent; styles absent or short (rarely long: *A. gallaensis*); berries orange or red. Distribution: tropical and subtropical Africa and Madagascar. The name *Afrophallus* refers to the exclusive occurrence of this subgenus in Africa (including Madagascar). No species of any of the other three subgenera occur in Africa.

Subgenus *Amorphophallus*: the *Paeoniifolius-Manta* clade

The *Paeoniifolius-Manta* clade (Fig. 2), of which 12 species are analysed in this study, has jumped from a basal position in the CA-I clade in Sedayu *et al.* (2010) to a similar position in the SEA clade in this study. Its position in Sedayu *et al.* (2010) was unsupported, whereas in this study it is positioned to create the highest level node of the entire SEA clade (BPP: 1.0; BS: 90%; Fig. 2). In Sedayu *et al.* (2010) only four species of this clade were sampled, *A. paeoniifolius* (Asia to W. Africa), *A. pendulus* Bogn. & Mayo (eastern

Malaysia, Borneo), *A. hirsutus* Teijsm. & Binnend. (Sumatra, Andamans) and *A. bangkokensis* (central Thailand). To these we have added *A. manta* Hett. & Ittenbach (Sumatra, western Malaysia), *A. angulatus* Hett. & A.Vogel (eastern Malaysia), *A. prainii* Hook f. (southern Thailand, western Malaysia, Sumatra), *A. rostratus* Hett. (Philippines), *A. bufo* Ridl. (western Malaysia), *A. opertus* Hett. (central Thailand), *A. scaber* Serebryanyi & Hett. (eastern Thailand, Vietnam) and *A. koratensis* Gagn. (central Thailand).

The content of this clade as recovered in this study was unexpected considering the gross morphology of the species. Notably the inclusion of *A. rostratus* is remarkable from morphological and geographical points of view, given its origin in the Philippines, whereas all other species show a much more western distribution. Looking more closely to morphological detail, the characters differing between *A. rostratus* and other closely related species from the Philippines (notably *A. dactylifer* Hett., *A. declinatus* Hett. and *A. adamsensis* L.M.Magtoto *et al*.), do seem to fit the most common habit found in the *Paeoniifolius-Manta* clade, notably the red-leafed seedling leaves (shared with *A. manta*, *A. angulatus*, *A. pendulus* and *A. hirsutus*) and the lack of offset development on the tuber (shared with *A. manta*, *A. angulatus*, *A. pendulus*, *A. bufo* and *A. hirsutus*). Further internal structure of the *Paeoniifolius-Manta* clade shows a supported subclade of *A. paeoniifolius*, *A. prainii*, *A. koratensis*, *A. opertus* and *A. scaber* with full support (100 BPP). These species share a sessile inflorescence with thick, leathery spathes, strongly stretching peduncles when fruiting, tubers with thick annulated root scars and short to long rhizomatous offsets (with the exception of *A. prainii*). With the exception of *A. prainii* and *A. bangkokensis* (forming their own subclade), all possess strongly verrucate petioles. *Amorphophallus hirsutus*, fitting this group well from a morphological point of view, is not included. Its inflorescence morphology is nearly 100% identical to that of *A. paeoniifolius* and *A. bangkokensis*. It shares the smooth petiole with *A. prainii* and *A. bangkokensis*. However, its most peculiar feature, unique in the genus, is the upper part of the appendix suddenly narrowed to a stump-like, truncate top covered with short, stiff bristle-like hairs. Its place in the present phylogenetic analysis and its peculiar mixture of characters may indicate its origin from a fairly recent hybridization event involving at least either *A. paeoniifolius* or *A. bangkokensis* and *A. prainii*.

Subgenus *Amorphophallus*: *Pulchellus*- and *Pusillus*-clades

Two clades with uniquely dwarf species are found in subgenus *Amorphophallus*, the *Pulchellus*-clade (named after *A. pulchellus* Hett. & Schuit.) and the *Pusillus*-clade (named after *A. pusillus*, see also Sedayu *et al.*, 2010) (Fig. 2). Both are strongly supported with values 0.99 BPP (BS: 91%) and 0.99 BPP (BS: 73%), respectively. The *Pulchellus*-clade, containing *A. pulchellus*, *A. myosuroides* Hett. & A.Galloway, *A. ongsakulii* and *A. claudelii* A.Galloway & A.Ongsakul (the latter not included in our analysis), was not analysed by Sedayu *et al.* (2010). All four species are from Laos and were discovered and described recently (Hetterscheid, 2006; Hetterscheid & Claudel, 2013, Galloway, 2015). At the time of the work by Sedayu *et al.* (2010), no material of this group was available. Their monophyly as shown in this paper is also supported by non-molecular characters such as their unique fruiting behaviour (fruiting pedunculus bending over to the soil after fertilization) and the fact they possess real synflorescences (otherwise only found in the *Pseudodracontium*-clade). The *Pusillus*-clade [*A. pusillus*, *A. terrestris* Hett. & C.Claudel, *A. obscurus* Hett. & M.Sizemore, *A. polyanthus* Hett. & M.Sizemore, *A. serrulatus* and *A. sumawongii* (Bogn.) Bogn.] was already included in subgenus *Amorphophallus* by Sedayu *et al*. with only *A. pusillus* and *A. sumawongii* being analysed. Its monophyly is also strongly supported by non-molecular characters including: their unique inconspicuously brownish-reddish speckled inflorescence colour; the inflorescences held partly under the soil surface; and their infructescences held close to the soil surface with fruits being dryish, with an inconspicuously darker and paler grey-coloured, warty surface. It seems that species in both these clades have developed a pollination and dispersal strategy different from that in all other *Amorphophallus* spp. (with the possible exception of *A. harmandii* Engl. & Gehrm.). Their life cycle seems to fit small ecological niches bound to the soil surface and seems much less directed towards pollinators and dispersers living in higher altitudes (such as actively flying beetles, flies and birds).

Only *A. sumawongii* from the *Pusillus*-clade seems to deviate from the other clade members. It looks much more like an 'average' *Amorphophallus* in size and behaviour with the exception of its fruits being green, dry and warty, maturing in only 2 weeks and dropping easily at the slightest touch of the fruiting head or peduncle. It thus seems not to make use of birds as a dispersal vector, unlike the other members of the clade. Another peculiar character of this species is its sterile appendix entirely composed of rod-like staminodes, their stamen-like morphology largely intact but for the lack of functional thecae. The morphology of the species initially led authors to believe it was related to either *A. napalensis* (Wall.) Bogner & Mayo (Bogner, 1976, in publishing the new species *Thomsonia sumawongii* Bogn., suggested this relationship) or to the *Pseudodracontium*-clade (see discussion in Grob *et al.*, 2002: 464).

SUBGENUS *METANDRIUM*: IS *AMORPHOPHALLUS* SECTION *RHAPHIOPHALLUS* DEFUNCT?

The taxonomic history of *A.* section *Rhaphiophallus* was provided by Hetterscheid, Yadav & Patil (1994) and Jaleel *et al.* (2011). In both papers the authors suggested the taxonomic reality of this section to be strongly supported by morphological characters. However, in all molecular studies of *Amorphophallus* to date (Grob *et al.*, 2002, 2004; Sedayu *et al.*, 2010) including the present one, the species group putatively composing section *Rhaphiophallus* was shown to be polyphyletic, consisting of two independent groups. One containing *A. hohenackeri* and *A. smithsonianus* found in the subgenus *Scutandrium* in the present analysis (Fig. 2). The other containing *A. sylvaticus* (Roxb.) Kunth, *A. konkanensis* Hett., Yadav & Patil, *A. margaritifer* (Roxb.) Kunth and *A. longiconnectivus* Bogn. found in subgenus *Metandrium* in the present analysis (Fig. 3). This result was known to Jaleel *et al.* in 2011, but, although their paper also incorporated a molecular approach, the authors left the taxonomic status of the section undiscussed.

A remarkable discrepancy between molecular and morphological phylogenetic results like this cannot be ignored. A first step in such a re-evaluation is always to look more closely at the nature and phylogenetic value of the morphological traits involved (see Stuessy, Mayer & Hörandl, 2003 for a new and thorough explanation of morphological analysis in phylogenetic frameworks). Engler (1911) knew of three species belonging to section *Rhaphiophallus*: *A. hohenackeri* (type species of section *Rhaphiophallus*), *A. sylvaticus* (type species of section *Synantherias*) and *Plesmonium margaritiferum* Schott (type species of *Plesmonium* = *A. margaritifer*). Section *Rhaphiophallus* was recognized based on the possession of flattened 'neuter flowers' between the female zone on the spadix and male zone and the presence of a short style. Section *Synantherias* was also based on such a sterile zone but lacking a style (a wrong observation because the species clearly has a short style). Both sections were part of *Amorphophallus* based on the possession of a fully sterile appendix. *Plesmonium* was maintained by Engler on the basis of the fertile male zone extending to the tip of the spadix (= lacking a sterile appendix) and the possession of large, pearlike sterile structures between female and male zones. Barnes & Fisher (1939) described a further species (*A. mysorensis* E.Barnes & C.E.C.Fisch.) from this species alliance, associating it with *A. sylvaticus* based on sharing a sterile appendix and the globose neuter flowers. Bogner (1985) and Bogner *et al.* (1985) considered the lack of a sterile appendix in *Plesmonium margaritiferum* an irrelevant difference with *Amorphophallus* and subsequentially merged the former into the latter. This was followed by Sivadasan (1989) when he described the new species *A. smithsonianus* and merged sections *Synantherias* and *Rhaphiophallus* under the latter, the name with nomenclatural priority. Since then section *Rhaphiophallus* has been maintained (see above). The last remaining morphological support for the section is the sterile organs between female and male zone. Hetterscheid *et al.* (1994) challenged this point arguing that the sole remaining 'unique' character is in fact not unique in *Amorphophallus* and could thus not be used without a relevant phylogenetic analysis of the entire genus. However, no alternative was presented.

Palynological data (Van der Ham *et al.*, 1998) represent an addition to the present molecular results. Three of the species in subgenus *Metandrium* possess pollen grains with a smooth (psilate) exine, whereas one (*A. sylvaticus*) has a warty (verrucate) exine of a unique subtype in *Amorphophallus*. This clade of four species forms the sister group to three species [*A. bulbifer* (Roxb.) Bl., *A. muelleri* and *A. xiei* H.Li & Dao] and this clade receives BPP support value of 1 (100 RAxML). The three species mentioned form their own small clade with equal support. Two of these three species also possess pollen with psilate exines; for *A. xiei* the character is unknown. Pollen grains of the two species in subgenus *Scutandrium* are fossulate (*A. hohenackeri*) or striate (a unique variant of this with scabrate ridges, otherwise unknown in Araceae). Section *Rhaphiophallus* in its present sense would thus show a strange mixture of pollen exine types. Tuber and leaf characters may also support the split as suggested from molecular phylogenetic trees.

SUBGENUS *SCUTANDRIUM*: *PSEUDODRACONTIUM* AND *AMORPHOPHALLUS*

The nesting of the *Pseudodracontium* group in the genus *Amorphophallus* (Fig. 2) is again confirmed (Hetterscheid & Claudel, 2012). The clade containing the *Pseudodracontium* group is well supported (BPP: 0.94; BS: 74%; Fig. 2). Its position in the present molecular phylogenetic analysis as sister to a clade consisting of two smaller clades (*Longituberosus* subclade and the *Saraburiensis* subclade) creates a larger clade in which especially the chemistry of the volatile parts of the scent is interesting. Scents of 92 species have been chemically analysed over the years (Kite & Hetterscheid, 1997; Kite *et al.*, 1998; Hetterscheid & Kite, in press). Whereas scents composed of oligomethyl oligosulphides dominate in a majority of *Amorphophallus* spp., creating a rather upsetting gaseous/sewage-like smell, all four species of the *Longituberosus* clade produce a strong anise scent. The major component of this scent is 4-methoxyphenetyl alcohol, otherwise known as anise oil. The only other occurrence of this component in *Amorphophallus* is as a trace element in the scent of a number of former

Pseudodracontium spp. The dominant chemicals in the former *Pseudodracontium* spp. are again the oligomethyl oligosulphides. Additionally, there is the remarkable scent of the species of the *Saraburiensis*-clade, which is strongly cheesy. This is brought about by a frequent compound in their smell, isocaproic acid. The strongly different smells in this clade are exactly paralleled by inflorescence morphology differences. Sister taxon to the clade consisting of the former *Pseudodracontium*, *Longituberosus* and *Saraburiensis* clade, is *A. haematospadix*. This species has a unique banana-like scent, consisting of ethyl acetate and isoamyl acetate. Since the clade including *A. haematospadix* receives strong support in the Bayesian analysis (0.98 BPP, 55 BS), there is enough evidence to support the inclusion of the former genus *Pseudodracontium* in this position. Other evidence is that all members of the clade starting from *Pseudodracontium* encompass elongate tubers. This forms a distinct synapomorphy. In contrast *A. haematospadix* has a globose/depressed globose tuber, which represents the plesiomorphic state with the sister clade to the *Haematospadix-Pseudodracontium* clade containing only species with (depressed-)globose tubers.

Subgenus *Afrophallus*: *Aphyllus* clade

As described by Hetterscheid & Ittenbach (1996) and Sedayu *et al.* (2010) the most prominent apomorphy of subgenus *Afrophallus* (Fig. 3) is the unique seasonal cycle of the genus. Each year, both flowering/fruiting and leafing occurs in mature tubers. This specific growing cycle supports the molecular-based monophyly of subgenus *Afrophallus*.

Nested in subgenus *Afrophallus* is a clade consisting of three species from western Africa displaying a unique and highly derived inflorescence type, *A. aphyllus* (Hook.) Hutch., *A. elliottii* Hook.f. and *A. dracontioides* (Engl.) N.E.Br. They form the most strongly supported clade in *Afrophallus*, named the *Aphyllus* clade here.

Most eye-catching in all three species are the swollen, ovate, thick-walled appendices, with a blackish surface, densely reticulated with fissures in between. The appendix surface may be broadly flattened or raised. In two species (*A. elliottii* and *A. dracontioides*) the spathe is strongly hooded, hiding the spadix from sight, but in *A. aphyllus*, the spathe is cup-shaped, exposing the appendix. When in flower the latter species resembles strongly mammalian dung. All three smell strongly of mammalian dung and *A. aphyllus* is known to attract flies (B. Suchy, pers. comm.). All three species grow in grassy savannah with occasional bushes and small deciduous trees. The species flower late in the dry season with their inflorescences well exposed. After pollination the leaf development starts alongside the development of the grassy vegetation surrounding the plants and reveal another unique feature: all three species possess narrowly lanceolate leaflets which resemble grass and thus hide the plants from sight in the vast grassy areas. After fertilization the peduncle elongates dramatically, transforming the sessile inflorescence to a long pedunculate infructescence and exposing the fruiting head with bright red berries among and above the grass, most probably in order to attract birds for dispersal of the seeds.

Fly attraction and pollination are also supported by the echinate pollen, which is rare in *Amorphophallus* and confined to subgenus *Afrophallus*. In subgenus *Afrophallus* three echinate pollen types are found of which the three species mentioned here, share one unique subtype (Van der Ham et al., 1998, 2000, 2005; 'subtype a' with short, unstoreyed, basally connected spines). Echinate pollen is often associated with fly pollination in Araceae (Gibernau, 2003; Punekar & Kumaran, 2010) and the types here point to the carrion variety (sapromyophily; Proctor, Yeo & Lack, 1996).

CONCLUSIONS

In this study we have provided support for the monophyly of the genus *Amorphophallus*, comprising *Pseudodracontium*. By including nearly three quarters of extant *Amorphophallus* species, we confirm previous subgeneric clade delineation with stronger support than previously obtained and name four subgenera. In addition, we also establish strongly supported clades at the within-subgenus level. Our study sets the grounds for future studies aiming at investigating the morphological evolution and historical biogeography of this spectacular genus.

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REFERENCES

Alfaro ME, Holder MT. 2006. The posterior and the prior in Bayesian phylogenetics. *Annual Review of Ecology, Evolution, and Systematics* **37:** 19–42.

Barnes E, Fisher CEC. 1939. New or little-known plants from southern India: XI. *Bulletin of Miscellaneous Information (Royal Botanic Gardens, Kew)* **1939:** 659–662.

Batista ARS. 2008. *Filogenia do complexo Caladieae-Zomicarpeae (Araceae) baseada em sequências do DNA plastidial*. MSc. Thesis, Universidade Católica de Brasília.

Beyra Matos A, Lavin M. 1999. Monograph of *Pictetia* (Leguminosae-Papilionoideae) and review of the Aeschynomeneae. *Systematic Botany Monographs* **56:** 1–93.

Blume CL. 1837. *Amorphophallus*. *Rumphia* **1:** 138–149.

Bogner J. 1976. Eine neue *Thomsonia*-Art (Araceae) aus Thailand. *Plant Systematics and Evolution* **125:** 15–20.

Bogner J. 1985. One new name and five new combinations in Araceae. *Aroideana* **8:** 73–79.

Bogner J, Mayo SJ, Sivadasan M. 1985. New species and changing concepts in *Amorphophallus*. *Aroideana* **8:** 15–25.

Boyce PC, Croat TB. 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.

Brown NE. 1882. Four new genera of Aroideae. *Journal of Botany, New Series* **11:** 193–197.

Buerki S, Callmander MW, Devey DS, Chappell L, Gallaher T, Munzinger J, Haevermans T, Forest F. 2012. Straightening out the screw-pines: a first step in understanding phylogenetic relationships within Pandanaceae. *Taxon* **61:** 1010–1020.

Cabrera LI, Salazar GA, Chase MW, Mayo SJ, Bogner J, Dávila P. 2008. Phylogenetic relationships of aroids and duckweeds (Araceae) inferred from coding and noncoding plastid DNA. *American Journal of Botany* **95:** 1153–1165.

Cusimano N, Bogner J, Mayo SJ, Boyce PC, Wong SY, Hesse M, Hetterscheid WL, Keating RC, French JC. 2011. Relationships within the Araceae: comparison of morphological patterns with molecular phylogenies. *American Journal of Botany* **98:** 654–668.

Engler A. 1911. Araceae Lasioideae. In: Engler A, ed.*Das Pflanzenreich IV,* 23C (Heft **48**). Leipzig: W. Engelmann, 1–130.

Espindola A, Buerki S, Bedalov M, Küpfer P, Alvarez N. 2010. New insights into the phylogenetics and biogeography of *Arum* (Araceae): unravelling its evolutionary history. *Botanical Journal of the Linnean Society* **163:** 14–32.

Galloway A. 2015. Three new *Amorphophallus* species from Laos. *Aroideana* **38:** 3–7.

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

Grob GB, Gravendeel B, Eurlings MC. 2004. Potential phylogenetic utility of the nuclear FLORICAULA/LEAFY second intron: comparison with three chloroplast DNA regions in *Amorphophallus* (Araceae). *Molecular Phylogenetics and Evolution* **30:** 13–23.

Grob GBJ, Gravendeel B, Eurlings MCM, Hetterscheid WLA. 2002. Phylogeny of the tribe Thomsoniae (Araceae) based on chloroplast *matK* and *trnL* intron sequences. *Systematic Botany* **27:** 453–467.

Hall TA. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41:** 95–98.

Henriquez CL, Arias T, Pires JC, Croat TB, Schaal BA. 2014. Phylogenomics of the plant family Araceae. *Molecular Phylogenetics and Evolution* **75:** 91–102.

Hetterscheid WLA. 1994. Preliminary taxonomy and morphology of *Amorphophallus* Blume ex Decaisne (Araceae). In: Serebryanyi MM, ed. *Proceedings Moscow Aroid Conference*, 35–48.

Hetterscheid WLA. 2006. Notes on the genus *Amorphophallus* (Araceae) 15. New species from SE Asia. *Aroideana* **29:** 53–79.

Hetterscheid WLA. 2012. *Amorphophallus*. In: Boyce PC, Sookchaloem D, Hetterscheid WLA, Gusman G, Jacobsen N, Idei T, Nguyen VD, eds. *Araceae. Flora of Thailand 11*. Bangkok: The Forest Herbarium, 218–232.

Hetterscheid WLA, Claudel C. 2012. The end of *Pseudodracontium* N.E. Br. *Aroideana* **35:** 40–46.

Hetterscheid WLA, Claudel C. 2013. Three new species of *Amorphophallus* (Araceae) from Indochina. *Aroideana* **36:** 87–92.

Hetterscheid WLA, Ittenbach S. 1996. Everything you always wanted to know about *Amorphophallus*, but were afraid to stick your nose into. *Aroideana* **19:** 7–131.

Hetterscheid WLA, Kite G. in press. Phylogenetic trends in the evolution of inflorescence odours in *Amorphophallus*. *Phytochemistry*.

Hetterscheid WLA, Peng C-I. 1995. Notes on the genus *Amorphophallus* (Araceae) IV. Revision of the species in Taiwan. *Botanical Bulletin of Academia Sinica* **36:** 101–112.

Hetterscheid WLA, Yadav SR, Patil KS. 1994. Notes on the genus *Amorphophallus* (Araceae). 5. *Amorphophallus konkanensis*, a new species from India, and taxonomic reflections on *Amorphophallus* section *Rhaphiophallus*. *Blumea* **39:** 289–294.

Jaleel VA, Sivadasan M, Alfarhan AH, Thomas J, Alatar AA. 2011. Revision of *Amorphophallus* Blume ex Decne. sect. *Rhaphiophallus* (Schott) Engl. (Araceae) in India. *Bangladesh Journal of Plant Taxonomy* **18:** 1–26.

Käss E, Wink M. 1997. Phylogenetic relationships in the Papilionoideae (family Leguminosae) based on nucleotide sequences of cpDNA (*rbcL*) and ncDNA (ITS 1 and 2). *Molecular Phylogenetics and Evolution* **8:** 65–88.

Kite GC, Hetterscheid WLA. 1997. Inflorescense odours of *Amorphophallus* and *Pseudodracontium* (Araceae). *Phytochemistry* **46:** 71–75.

Kite, GC, Hetterscheid WLA, Lewis MJ, Boyce PC, Ollerton J, Cocklin E, Diaz A, Simmonds MSJ.

1998. Inflorescence odours and pollinators of *Arum* and *Amorphophallus* (Araceae). In: Owens SJ, Rudall PJ, eds. *Reproductive biology*. Kew: Royal Botanic Gardens, 295–315.

Li H, Hetterscheid WLA. 2010. *Amorphophallus*. In: *Flora of China, Vol. 23*. Beijing: MBG Press and Science Press, 23–33.

Mayo SJ, Bogner J, Boyce PC. 1997. *The genera of Araceae*. Kew: Royal Botanic Gardens.

Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), 14 November 2010, New Orleans, LA. Piscataway: IEEE.

Nauheimer L, Metzler D, Renner SS. 2012. Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. *The New Phytologist* **195:** 938–950.

Nylander JAA. 2004. *MrModeltest, 2nd edn*. Uppsala: Evolutionary Biology Centre, Uppsala University.

Proctor M, Yeo P, Lack A. 1996. *The natural history of pollination*. London: Harper Collins Publishers.

Punekar SA, Kumaran KPN. 2010. Pollen morphology and pollination ecology of *Amorphophallus* species from north Western Ghats and Konkan region of India. *Flora* **205:** 326–336.

Rambaut A, Drummond AJ. 2007. *Tracer v1.4*. Available at: http://evolve.zoo.ox.ac.uk/software.html

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61:** 539–542.

Sedayu A, Eurlings MCM, Gravendeel B, Hetterscheid WLA. 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.

Serebryanyi MM. 1995. A taxonomic revision of *Pseudodracontium* (Araceae – Aroideae Thomsonieae). *Blumea* **40:** 217–235.

Sivadasan M. 1989. *Amorphophallus smithsonianus* (Araceae), a new species from India, and a note on *A.* sect. *Synantherias*. *Willdenowia* **18:** 435–440.

Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics (Oxford, England)* **22:** 2688–2690.

Stamatakis A, Hoover P, Rougemont J. 2008. A rapid bootstrap algorithm for the RAxML Web servers. *Systematic Biology* **57:** 758–771.

Stapf O. 1924. *Amorphophallus cirrifer*. *Botanical Magazine* **149:** t. 9000.

Stuessy TF, Mayer V, Hörandl E. 2003. *Deep morphology. Toward a renaissance of morphology in plant systematics. Regnum Vegetabile 141*. Königstein: Koeltz Scientific Books.

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG. 1997. The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* **25:** 4876–4882.

Van der Ham RWJM, Hetterscheid WLA, van Heuven BJ. 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 RWJM, Hetterscheid WLA, van Heuven BJ, Star W. 2000. Exine architecture in echinate pollen of *Amorphophallus* (Araceae) in relation to taxonomy. In: Harley MM, Morton CM, Blackmore S, eds. *Pollen and spores: morphology and biology*. Kew: Royal Botanic Gardens, 241–248.

Van der Ham RWJM, Grob G, Hetterscheid WLA, Star W, van Heuven BJ. 2005. Notes on the genus *Amorphophallus* (Araceae) - 13. Evolution of pollen ornamentation and ultrastructure in *Amorphophallus* and *Pseudodracontium*. *Grana* **44:** 252–265.

Ying S-S. 1991. Miscellaneous notes on the flora of Taiwan (14). 174: some correct names of genus *Amorphophallus* in Taiwan (Araceae). *Memoirs of the College of Agriculture, National Taiwan University* **31:** 31.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Bayesian majority-rule consensus tree of *Amorphophallus* based on nuclear DNA (*ITS1*). BPP values above the branches. BPP values of the four major subclades, their internal nodes and mentioned clades are highlighted. The outgroup consists of two African species, *A. calabaricus* and *A. stuhlmannii*.

Figure S2. Bayesian majority-rule consensus tree of *Amorphophallus* based on plastid DNA (*rbcL* and *matK*). BPP values above the branches. BPP values of the four major subclades, their internal nodes and mentioned clades are highlighted. Like in the combined analysis, the outgroup consist of the genera *Anchomanes*, *Gonatopus* and *Hapaline*.

Appendix. List of material used. GenBank accession numbers beginning with A indicate species examined by Grob *et al.* (2002, 2004). Accessions beginning with D indicate species examined by Sedayu *et al.* (2010). One accession number starting with E indicates species examined by Batista (2008). All other numbers starting with K indicate species examined by the first author.

Publ. 2: Hybridization in *Amorphophallus*

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Author contribution: This chapter is based on crossing experiments from three previous publications (Claudel & Galloway, 2012; Claudel et al., 2013; Claudel & Mangelsdorff, 2014) as well as newly performed crosses. In total, 62 crosses were performed by CC. Additionally, the data of other hybridisers, Alan Galloway and Steve Jackson in particular, was compiled and evaluated by CC, with special emphasis on the taxonomic relationship between the crossing partners and the viability of the progeny. The manuscript was written by CC.

(ranging from 58.8% to 52.1%). However, the results of these studies also indicated that the individual species is the main factor determining the KGM content and the quality of the KGM flour and that the growing conditions are a secondary factor that can be optimized to maximize the KGM yield.

2.6 Hybrids

2.6.1 Hybridization in *Amorphophallus*

During the phylogenetic investigations of the genus *Amorphophallus* on a larger scale (Claudel et al., 2017), a negligible but intriguing phenomenon constantly reproduced in most analyses: four species of the subg. *Scutandrium* Hett. & Claudel paired in an unexpected combination. The first two species, *A. konjac* K. Koch and *A. maxwellii* Hett., are tall and large. The plants easily exceed one meter height and are characterized by an equally large inflorescence, both with a dark maroon spathe (Hetterscheid and Ittenbach, 1996). In contrast, the other two species which are 'morphologically very similar' (Hetterscheid and Ittenbach, 1996) are distinctly smaller and the inflorescences bear light-coloured spathes. The spathe is whitish to pale green outside and faintly maroonish inside in the case of *A. krausei* Engl; and greenish outside and whitish inside in the case of *A. albus* P. Y. Liu & J. F. Chen. Based on the morphological similarity between the two species pairs, *A. konjac* was expected to be closely related to *A. maxwellii* and *A. albus* was expected to pair with *A. krausei*. Instead, *A. konjac* paired with *A. albus* and *A. maxwellii* with *A. krausei.*

This result was too intriguing to be ignored and, as a consequence different accessions of *A. albus* and *A. konjac* were sequenced in order to validate or disprove the result. However, it persisted and the question arose if hybridization events possibly influenced the result. It first seemed unlikely, however, taking into consideration that several *Amorphophallus* species, (i.e., *A. paeoniifolius* (Dennst.) Nicolson, *A. albus* and *A. konjac*) have a long breeding history in Asia (Hetterscheid and Ittenbach, 1996; Zheng et al., 2013; Liu et al., 2015) it did not seem impossible. Moreover, Zhang et al. (1998) reported the successful hybridization of several *Amorphophallus* species, amongst others hybridization between *A. albus* and *A. konjac*. It therefore seemed suddenly not only possible but even likely that these species might have been hybridized in the past.

Thus, the first author (Claudel et al., 2017) decided to reproduce the cross between the aforementioned species in order to investigate the placement of the progeny within the phylogenetic analysis. This was the starting point of further attempts to cross as many different *Amorphophallus* species as possible and to explore the limits of hybridization within the genus. Thanks to Mr. John Tan, an avid plantsman from Singapore, the author received the necessary support to raise many hundred plants of hybrid origin. Moreover, several *Amorphophallus* enthusiasts around the world, from Australia to Indonesia, from the US to Europe joined the informal project and started to hybridize species and consequently reported the outcome. The overall aim of the project was to create new hybrids of ornamental value, with desirable traits, such as increased hardiness and robustness and/or decreased odour properties (Claudel and Galloway, 2012). Therefore, the limits of hybridization within the genus had to be explored in order to improve or to combine specific traits from different species and to increase the overall vigour.

Although the ornamental value was in the foreground instead of crop traits, such as tuber growth or glucomannan content, a short comment should be made concerning

species with agricultural importance. These essentially include six species from three different subgenera, namely *A. albus* and *A. konjac*, *A. paeoniifolius* and *A. bulbifer* Blume, *A. muelleri* Blume and *A. xiei* H. Li & Z. L. Dao.

Amorphophallus albus and *A. konjac* belong to the subgenus *Scutandrium* and both have 2n = 26 chromosomes which is considered to be the basic chromosome number in the genus (Shete et al., 2015). As previously mentioned these two species are compatible and the hybrids show signs of hybrid vigour (Claudel et al., 2013). Moreover, the resulting F1-generation is fertile and the hybrids can either be crossed one with each other or back-crossed with one of the parents (personal observation). This opens up endless opportunities for breeding programs of suitable crop plants. Overcoming the poor disease resistance of *A. konjac* (Zheng et al., 2013) could be a possible outcome. Moreover, the study from Zheng et al. (2013) concerning *A. konjac* revealed that the genetic 'variation between wild and cultivar genotypes' is very small. Yin et al. (2019) come to the same conclusion concerning the genetic variation within *A. albus*. In other words, it seems that the *Amorphophallus* species have a long history of cultivation but not necessarily a long breeding history.

Amorphophallus paeoniifolius from the subgenus *Amorphophallus* is the species with the widest distribution, possibly due to their use as starchy crop plant (Hetterscheid & Ittenbach, 1996). It belongs to a small clade (Claudel et al., 2017) together with *A. prainii* Hook f. and a few other species which are characterized by 2n = 28 chromosomes (Chauhan & Brandham, 1985). Although widely planted, the aberrant chromosome number limits the potential in terms of hybridization as only few species can be used as crossing partners.

Even more limited in this context are the three species *A. bulbifer*, *A. muelleri* and *A. xiei* from the subgenus *Metandrium* Stapf. The chromosome number for *A. xiei* has not been investigated; however, *A. xiei* is so similar to *A. bulbifer* that its species identity has been questioned by Li and Hetterscheid (2010). *Amorphophallus bulbifer* and *A. muelleri* are triploids characterized by the chromosome number 2n = 39 (Ramachandran, 1977; Chauhan and Brandham, 1985; Patil, 1995; Shete et al., 2015) and it has been discussed if the chromosome number in these two species is based on allotriploidy or autoploidy (Chauhan and Brandham, 1985; Patil, 1995; Shete et al., 2015). Both species seemingly exclusively rely on the formation of epiphyllar bulbils and apomictic seed formation for propagation (more precisely: agamospermy). This is underlined by the investigation of Patil (1995) who states that the: 'autopolyploid nature in *A. bulbifer* (2n = 39) is supported by the lowest pollen fertility 5.69% and apomictic seed formation...' Thus, these species seemingly cannot be used for generative propagation, neither for hybridization nor for selections based on breeding.

However, Kuruvilla et al. (1989) reported 2n = 26 for *A. bulbifer*. Possibly some populations from *A. bulbifer* and *A. muelleri* are true diploids which could be used for breeding experiments. This finding would fit with the concept that apomixis in plants is facultative (Savidan, 2000), in other words that if sexual reproduction has not been observed, than the observation has just not been rigorous enough. Moreover, although the pollen fertility is very low (Patil, 1995) the pollen nevertheless is fertile. These points deserve closer attention as these species are of economic value (Zhao et al., 2009, 2010; Zhang et al., 2010) and breeding programs could give rise to new high-performance cultivars. It is noteworthy to add that Tjio (1948) reports 2n = 39 for *A. rivieri* Dur., a synonym of *A. konjac*. Either the plant was not correctly identified and was in fact a specimen of *A. bulbifer* or *A. muelleri*, or further triploid specimens occur within other species.

However, at the starting point the focus was set on the ornamental value and the feasibility of a cross. As a result, nearly 250 crosses worldwide were performed, of which 47 were successful and yielded viable seeds (Claudel and Galloway, 2012; Claudel et al., 2013; Claudel and Mangelsdorff, 2014). Some outstanding specimens from a few

crosses were named and subsequently released, namely: *Amorphophallus* 'Kiat Tan' (*A. lewallei* Malaisse & Bamps x *A. maximus* (Engl.)), *Amorphophallus* 'Mary Sizemore' and *Amorphophallus* 'Meister Eckhardt' (both *A. albus* x *A. konjac*), *Amorphophallus* 'Heine' (*A. lewallei* x *A. richardsiae* Ittenb.), *Amorphophallus* 'Blue Nightspot' (*A. glaucophyllus* Hett. & Serebr. x *A. lacourii* Linden & Andre) and *Amorphophallus* 'Majda' (*A. pulchellus* Hett. & Schuit. x *A. myosuroides* Hett. & A. Galloway) (Claudel, 2019; Galloway, 2019). Besides exhibiting good growing properties and beautiful foliage or inflorescences it was required that these could not be mistaken for the true species. These cultivars represent a trial balloon and will demonstrate if *Amorphophallus* cultivars of hybrid origin will find their niche and spread in collections.

The perhaps most amazing cross was performed by Ralph Mangelsdorff in 2002 (Claudel et al., 2012). It involved two very different crossing partners in terms of absolute size. The seed parent was *A. variabilis* Bl. which usually hardly exceeds 1.20 meter height (Hetterscheid and Ittenbach, 1996) and has a long peduncled but otherwise rather small and inconspicuous inflorescence. The pollen parent however was *A. titanum* (Becc.) Becc. ex Arcangeli, the most striking species of the genus with leaves up to six meters high and sessile, very large inflorescences exceeding 3 meter height (McPherson and Hetterscheid, 2011). Only a few seeds fully developed (Claudel et al., 2012) and only one seedling reached flowering stage. The plant displayed perfectly intermediate character traits and was very showy at that. It was named *Amorphophallus* 'John Tan' (Claudel et al., 2012) in honour of Mr. Tan and represents therefore the first named *Amorphophallus* cultivar of hybrid origin. Moreover, used as pollen parent, it also is the 'father' of the first *Amorphophallus* hybrid involving three *Amorphophallus* species (Claudel et al., 2012).

Since 2014 the interest in hybridization amongst enthusiasts seemingly declined. Considering that one cross can yield a few to a few hundred seeds and that it takes, species-dependant, three to seven years to raise the hybrids until maturity, it becomes apparent that it is a task which requires time, space and efforts, especially if larger species are involved. Moreover, it requires close observation of the plants, as *Amorphophallus* species, like all aroids are protogynous (Boyce and Wong, 2012) which in most cases imply a short time frame for successful pollination. As a general rule, the 'female phase', the phase characterized by receptive stigmas, starts and ends on day one of anthesis, whereas the 'male phase', characterized by pollen release, occurs on day two. That said, the female phase does not necessarily last the whole day but can end after a period of six hours only (personal observation). In contrast to that, some species are characterized by an extended female phase which lasts up to five days (personal observation) such as for example *A. antsingyensis* Bogner, Hett. & Ittenb., *A. gigas* Teijsm. & Binnend., *A. henryi* N. E. Br., *A. konjac*, *A. lambii* Mayo & Widjaja, *A. natolii* Hett. et al. and *A. variabilis*. Either way, the pollen needs to be applied to the stigmas when these are receptive which is often indicated by a sticky fluid on the stigma surface. Applying pollen either requires a plant which flowered in the preceding days and serves as pollen donator or stored pollen, dried and frozen or refrigerated (Claudel & Galloway, 2012).

Fresh pollen is naturally the best choice and is ideally applied on the day of release as it is assumed to be short-lived and to deteriorate within a few days at room temperature (Harrington, 1970; Zhang et al., 1998; Barabé et al., 2008). However, it can be gently dried using silica gel (Claudel and Galloway, 2012) and either be refrigerated at 4°C–8°C or frozen at –20°C or comparable temperatures. As stated in Claudel et al. (2013) and Claudel and Mangelsdorff (2014), eight out of 25 successful crosses were performed using frozen pollen; in one case the pollen had been stored for more than two years. Moreover, in the new series of crosses (see Appendix 2.I) 16 out of 37 successful crosses have been performed using

either refrigerated or frozen pollen. This demonstrates the usefulness of refrigerated/frozen pollen and it shows the potential of a pollen bank. A pollen bank would not only ease the task in hybridization attempts but even more in ex-situ conservation projects as it would allow, for example, self-pollination of single specimens using stored pollen from former inflorescences. However, except for the fact that *Amorphophallus* pollen is storable under the aforementioned conditions, many questions remain to be addressed and investigated. For example the impact of cooling versus freezing on the longevity of the pollen. Another area to be investigated is the decrease of viability over time under different cooling or freezing regimes. Furthermore, the effects of further freezing regimes including −80°C and cryogenic cooling on viability also need to be investigated. Lastly, the question whether the different kinds of pollen (Van der Ham et al., 1998, 2005; Ulrich et al., 2017) within the genus *Amorphophallus* respond differently to the suggested or other treatments should also be addressed.

It is a fortunate and interesting development that the Toronto Zoo (Ontario, Canada) has started to address these questions (personal communication, Paul Gellatly, curatorial gardener). Although a zoo, the Toronto Zoo also maintains a growing *Amorphophallus* collection, including a dozen specimens of *A. titanum*. Fortunately, the Toronto Zoo has a strong focus on conservation genetics and ex-situ conservation projects and houses the facilities to properly store genetic material. In 2018 the first specimen of *A. titanum* flowered and aroused considerable attention. It was decided to collect the pollen for conservation purposes, namely pollinating future *A. titanum* inflorescences. The pollen has been collected and stored in various ways to determine the viability of long term pollen storage. It has been frozen and stored in −80°C, as well as cryogenically preserved. The Zoo is currently in the process of viability testing in order to determine if these approaches constitute a practicable long term pollen storage solution.

Despite the work it entails, nearly 250 further pollination attempts (see Appendices 2.I and 2.II) have been performed in the meantime by the most arduous hybridizers, namely Alan Galloway from the US and Steve Jackson from Australia. It is worthwhile pointing out that it was A. Galloway who introduced many *Amorphophallus* species to science over the last two decades. Moreover, he is a most skilled grower. Both facts combined have opened up many hybridization options.

On the other side of the globe, Steve Jackson has created the first hybrids involving species such as *A. decus-silvae* Backer & Alderw. and *A. gigas*, two of the tallest and most spectacular species of the genus. The cultivation of these species is not exactly easy and although S. Jackson has been supported by a favourable climate, the fact that he kept these species in cultivation for decades speaks for itself.

Except for five pollinations performed by the first author and not taking into account pollinations which involved several attempts, 229 further hybridizations attempts were carried out by A. Galloway and S. Jackson. Out of a total of 234 hybridizations attempts 37 were successful and yielded viable seeds (see Appendix 2.I). However, the overall fitness of the progeny can strongly differ. In general, two categories can be observed. The first one includes hybrids showing signs of hybrid vigour acquired through heterosis. Heterosis can be defined as 'The physiological vigour of an organism as manifested in its rapidity of growth, its height and general robustness, is positively correlated with the degree of dissimilarity in the gametes by whose union the organism was formed …' (Shull, 1948). In other words, the hybridogenic *Amorphophallus* progeny is more robust and produces larger leaves and inflorescences than its corresponding parents. The second category is the outbreeding depression (not to be confounded with the inbreeding depression). The hybrids display a loss of fitness, are more vulnerable to diseases and disturbances and

have weaker growing and flowering properties than their corresponding parents (Leimu and Fischer, 2010; Barmentlo et al., 2018). This is due to biochemical and/or physiological incompatibilities between the crossing partners. The crossing partners are genetically too distant and the selective advantage of adapted gene complexes of the involved species is disrupted through hybridization (Wikipedia, 2019). One of the markers, indicating the limitation of hybridization in *Amorphophallus* is albinism (Claudel et al., 2013). Albinism in the progeny of a given *Amorphophallus* cross can be displayed at two levels. One is the number of seedlings affected and the second is the degree of albinism that a single seedling expresses. In the best case only a few seedlings show slight signs of chlorophyll-free leaf tissue which may eventually slowly turn green after the leaf unfolds. In the worst case all the seedlings are completely devoid of chlorophyll and will die as soon as the stored nutrients are consumed.

This raises the question how closely related two crossing partners need to be if 'optimal outcrossing distance' (Schierup and Christiansen, 1996) or hybrid vigour is the goal or on the opposite, how distantly related they can possibly be if not improvement but pure survival at any cost is the aim. Unfortunately there is no specific answer to this question. It must be taken into consideration that effects based on inbreeding depression, outbreeding depression or heterosis play a role even between different populations of a given single species (Leimu and Fischer, 2010; Barmentlo et al., 2018). Predicting which effect might dominate would require a precise knowledge about the genetics of each crossing partner. Besides this limitation it must be also taken into consideration that the presented hybridization attempts are arbitrary, mainly for two reasons. Firstly, the involved species are selected based on traits judged desirable by the hybridizers. Second, the opportunities to hybridize depend on the cultivated species.

However, some concluding observations can be made. Out of nearly 500 hybridization attempts a total of 84 yielded viable seeds, especially crosses between closely related species are often successful. As insignificant as this might seem, it demonstrates that *Amorphophallus* species hybridize readily which suggests that interspecific hybridization barriers are not pronounced in many species. This could be accounted for by adaptive radiation. *Amorphophallus* is a comparatively young genus (Nauheimer et al., 2012) within the Araceae. However, with an estimated 219 species (Boyce and Croat, 2011) it exhibits a high species diversity growing in the (sub)tropical zones of the palaeotropics, outranking all other aroid genera in morphological diversity (Hetterscheid and Ittenbach,1996; Claudel et al., 2017). For example, the genus encompasses an exceptionally high diversity in berry colour, ranging from white, green, and yellow, orange, red to blue and purple. This is a characteristic trait indicating seed dispersal through birds (Claudel et al., 2017) which might have played a major role in the wide distribution of the genus. Last but not least, many closely related species have similar or even identical nuclear and plastid sequences (Claudel et al., 2017). Although speculative, all facts combined – high species and morphological diversity acquired in a short period of time, palaeotropical distribution pattern, birds as dispersal vector and finally, similar genetic sequences – suggest adaptive radiation.

Additionally, six out of the 37 successful crosses involve three different species and one cross even involves four species (see Appendix 2.II). The latter consists of a hybrid between two Malagasy species as pollen acceptor (*A. taurostigma* x *A. ankarana*) crossed with a hybrid between two African species as pollen donor (*A. lewallei* x *A. impressus*). Nine of the successful crosses even involve species from different subgenera. For example *A. variabilis* crossed with *A. maximus* involves *A. variabilis*, a species from South East Asia from the subgenus *Amorphophallus* and *A. maximus* an African species from the subgenus *Afrophallus* Hett. & Claudel.

Simply put, the boundaries of hybridization within *Amorphophallus* are not yet reached, there is still a lot of potential to be uncovered and many questions remain to be answered.

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Appendix 2.I Successful *Amorphophallus* Hybridizations

Pollen Acceptor	Pollen Donor	Pollen Used	Hybridizer	Result
(*A. decus-silvae* Backer & Alderw. x *A. variabilis* Bl.)	(*A. decus-silvae* Backer & Alderw. x *A. variabilis* Bl.)	Refrigerated	S. Jackson	Success
(*A. lewallei* Malaisse & Bamps x *A. impressus* Ittenb.)	*A. henryi* N. E. Br.	Refrigerated	S. Jackson	Success, three species + subgeneric cross
(*A. lewallei* Malaisse & Bamps x *A. impressus* Ittenb.)	(*A. impressus* Ittenb. x *A. taurostigma* Ittenb. & Hett 'White Veins')	Fresh	S. Jackson	Success, three species
(*A. taurostigma* Ittenb. & Hett x *A. ankarana* Hett.)	(*A. lewallei* Malaisse & Bamps x *A. impressus* Ittenb.)	Fresh	S. Jackson	Success, four species
(*A. variabilis* Bl. x *A. decus-silvae* Backer & Alderw.)	*A. longituberosus* (Engl.) Engl. & Gehrm.	Fresh	S. Jackson	Success, three species + subgeneric cross
A. decus-silvae Backer & Alderw.	*A. borneensis* (Engl.) Engl. & Gehrm.	Refrigerated	S. Jackson	Success
A. decus-silvae Backer & Alderw.	*A. henryi* N. E. Br.	Fresh	S. Jackson	Success, subgeneric cross
A. discophorus Backer & Alderw.	*A. galbra* F.M. Bailey	Refrigerated	S. Jackson	Success
A. galbra F.M. Bailey	(*A. variabilis* Bl. x *A. decus-silvae* Backer & Alderw.)	Fresh	S. Jackson	Success
A. henryi N. E. Br.	(*A. lewallei* Malaisse & Bamps x *A. impressus* Ittenb.)	Fresh	S. Jackson	Success, three species + subgeneric cross
A. henryi N. E. Br.	*A. laoticus* Hett.	Fresh	S. Jackson	Success
A. hewittii Alderw.	(*A. decus-silvae* Backer & Alderw. x *A. variabilis* Bl.)	Fresh	S. Jackson	Success, three species

(*Continued*)

Pollen Acceptor	Pollen Donor	Pollen Used	Hybridizer	Result
A. impressus Ittenb. AGA-1158-01	*A. maximus* (Engl.) N. E. Br. AGA-0240-01	Refrigerated	A. Galloway	Success
A. konjac K. Koch AGA-1266-01	*A. albus* P.Y. Liu & J.F. Chen	Frozen	A. Galloway	Success
A. konjac K. Koch AGA-1797-01	*A. albispathus* Hett.	Frozen	A. Galloway	Success
A. konjac K. Koch AGA-1798-01	*A. crispifolius* A. Galloway, A. Ongsakul, & P. Schmidt	Frozen	A. Galloway	Success
A. konjac K. Koch AGA-1798-01	*A. kachinensis* Engl. & Gehrm. AGA-2500-01	Fresh	A. Galloway	Success
A. laoticus Hett.	(*A. lewallei* Malaisse & Bamps x *A. impressus* Ittenb.)	Refrigerated	S. Jackson	Success, three species + subgeneric cross
A. lewallei Malaisse & Bamps	*A. antsingyensis* Bogner, Hett. & Ittenb.	Fresh	C. Claudel	Success
A. lewallei Malaisse & Bamps	*A. gomboczianus* Pic. Serm.	Fresh	C. Claudel	Success
A. longiconnectivus Bogn. AGA-0891-01	*A. schmidtiae* Hett. & A. Galloway AGA-2188-01	Frozen	A. Galloway	Success
A. maximus (Engl.) N. E. Br.	*A. variabilis* Bl.	Fresh	S. Jackson	Success, subgeneric cross
A. natolii Hett.et al.	*A. variabilis* Bl.	Refrigerated	S. Jackson	Success, subgeneric cross
A. ochroleucus Hett. & V.D. Nguyen	*A. dunnii* Tutch	Fresh	S. Jackson	Success
A. ongsakulii Hett. & A. Galloway AGA-1534-01	*A. myosuroides* Hett. & A. Galloway AGA-1756-01	Fresh	A. Galloway	Success
A. operculatus (ined.)	*A. sizemoreae* Hett.	Refrigerated	S. Jackson	Success
A. pulchellus Hett. & Schuit. AGA-2342-01	*A. ongsakulii* Hett. & A. Galloway	Fresh	A. Galloway	Success
A. richardsiae Ittenb. AGA-1920-01	*A. mossambicensis* (Schott ex Garcke) N. E. Br. AGA-0900-01	Refrigerated	A. Galloway	Success
A. thaiensis S.-Y. Hu AGA-2236-01	*A. putii* Gagn. AGA-0832-01	Fresh	A. Galloway	Success
A. variabilis Bl.	*A. natolii* Hett. et al.	Frozen	S. Jackson	Success (x2), subgeneric cross
A. variabilis Bl.	(*A. variabilis* Bl. x *A. decus-silvae* Backer & Alderw.)	Fresh	S. Jackson	Success
A. variabilis Bl.	*A. lambii* Mayo & Widjaja	Refrigerated	S. Jackson	Success
A. variabilis Bl.	*A. maximus* (Engl.) N. E. Br.	Fresh	S. Jackson	Success
A. variabilis Bl. 'Slukas Dark Giant'	(*A. variabilis* Bl. x *A. decus-silvae* Backer & Alderw.)	Fresh	S. Jackson	Success

(*Continued*)

Pollen Acceptor	Pollen Donor	Pollen Used	Hybridizer	Result
A. variabilis Bl. 'Slukas Dark Giant'	*A. dracontioides* (Engl.) N. E. Br.	Frozen	S. Jackson	Success
A. variabilis Bl. 'Slukas Dark Giant'	*A. hewittii* Alderw.	Fresh	S. Jackson	Success
A. yunnanensis Engl.	*A. dunnii* Tutch.	Fresh	S. Jackson	Success

Appendix 2.II Failed *Amorphophallus* Hybridizations

Pollen Acceptor	Pollen Donor	Pollen	Hybridizer	Result
(*A. decus-silvae* Backer & Alderw. x *A. variabilis* Bl.)	*A. henryi* N. E. Br.	Refrigerated	S. Jackson	Failed (x2)
(*A. decus-silvae* Backer & Alderw. x *A. variabilis* Bl.)	*A. dracontioides* (Engl.) N. E. Br.	Frozen	S. Jackson	Failed
(*A. decus-silvae* Backer & Alderw. x *A. variabilis* Bl.)	*A. laoticus* Hett.	Refrigerated	S. Jackson	Failed
(*A. decus-silvae* Backer & Alderw. x *A. variabilis* Bl.)	*A. longituberosus* (Engl.) Engl. & Gehrm.	Frozen	S. Jackson	Failed
(*A. decus-silvae* Backer & Alderw. x *A. variabilis* Bl.)	*A. taurostigma* Ittenb. & Hett 'White Veins'	Fresh	S. Jackson	Failed
(*A. decus-silvae* Backer & Alderw. x *A. variabilis* Bl.)	*A. laoticus* Hett.	Frozen	S. Jackson	Failed
(*A. excentricus* Hett. x A. krausei Engl.)	*A. scutatus* Hett. & T.C. Chapman	Refrigerated	S. Jackson	Failed
(*A. impressus* Ittenb. x *A. taurostigma* 'White Veins')	*A. elatus* Ridl.	Frozen	S. Jackson	Failed
(*A. lewallei* Malaisse & Bamps x *A. impressus* Ittenb.)	*A. rostratus* Hett.	Fresh	S. Jackson	Failed
(*A. lewallei* Malaisse & Bamps x *A. impressus* Ittenb.)	*A. laoticus* Hett.	Fresh	S. Jackson	Failed
(*A. maximus* (Engl.) N. E. Br. x *A. variabilis* Bl.)	*A. natolii* Hett.et al.	Refrigerated	S. Jackson	Failed
(*A. ongsakulii* Hett. & A. Galloway x *A. myosuroides* Hett. & A. Galloway	*A. titanum* (Becc.) Becc. ex Arcangeli	Frozen	A. Galloway	Failed
(*A. variabilis* Bl. x *A. borneensis* (Engl.) Engl. & Gehrm.) AGA-2729-09	*A. maxwellii* Hett.	Frozen	A. Galloway	Failed
(*A. variabilis* Bl. x *A. decus-silvae* Backer & Alderw.)	*A. laoticus* Hett.	Refrigerated	S. Jackson	Failed
(A. variabilis Bl. x A. *decus-silvae* Backer & Alderw.)	*A. natolii* Hett. et al.	Frozen	S. Jackson	Failed (x2)
(*A. variabilis* Bl. x *A. decus-silvae* Backer & Alderw.)	(*A. lewallei* Malaisse & Bamps x *A. impressus* Ittenb.)	Frozen	S. Jackson	Failed
(*A. variabilis* Bl. x *A. decus-silvae* Backer & Alderw.)	*A. discophorus* Backer & Alderw.	Refrigerated	S. Jackson	Failed
(*A. variabilis* Bl. x *A. decus-silvae* Backer & Alderw.)	*A. rostratus* Hett.	Refrigerated	S. Jackson	Failed

(*Continued*)

Pollen Acceptor	Pollen Donor	Pollen	Hybridizer	Result
(*A. variabilis* Bl. x *A. decus-silvae* Backer & Alderw.)	*A. taurostigma* Ittenb. & Hett 'White Veins'	Refrigerated	S. Jackson	Failed
A. albus P.Y.Liu & J.F.Chen	*A. cirrifer* Stapf	Refrigerated	A. Galloway	Failed
A. albus P.Y. Liu & J.F. Chen	*A. maxwellii* Hett.	Refrigerated	A. Galloway	Failed
A. albus P.Y. Liu & J.F. Chen	*A. natolii* Hett. et al.	Frozen	S. Jackson	Failed
A. amygdaloides Hett. & M. Sizemore AGA-1047-03	*A. brevipetiolatus* A. Galloway, A. Ongsakul, & P. Schmidt AGA-1570-03	Frozen	A. Galloway	Failed
A. amygdaloides Hett. & M. Sizemore AGA-1047-03	*A. muelleri* Bl.	Fresh	A. Galloway	Failed
A. asterostigmatus Bogn. & Hett. AGA-1964-01	(*A. decus-silvae* Backer & Alderw. x *A. variabilis* Bl.) AGA-2461-11	Frozen	A. Galloway	Failed
A. atrorubens Hett. & M. Sizemore AGA-1214-01	*A. maxwellii* Hett.	Refrigerated	A. Galloway	Failed
A. atroviridis Hett. AGA-1046-01	*A. maxwellii* Hett. AGA-1177-01	Refrigerated	A. Galloway	Failed
A. bangkokensis Gagn.	*A. rostratus* Hett.	Refrigerated	S. Jackson	Failed
A. barbatus A. Galloway & A. Ongsakul	*A. laoticus* Hett.	Fresh	C. Claudel	Failed
A. barbatus A. Galloway & A. Ongsakul AGA-2309-01	*A. titanum* (Becc.) Becc. ex Arcangeli	Frozen	A. Galloway	Failed
A. borneensis (Engl.) Engl. & Gehrm.	(*A. decus-silvae* Backer & Alderw. x *A. variabilis* Bl.)	Refrigerated	S. Jackson	Failed
A. borneensis (Engl.) Engl. & Gehrm.	*A. interruptus* Engl. & Gehrm.	Refrigerated	S. Jackson	Failed
A. borneensis (Engl.) Engl. & Gehrm.	*A. titanum* (Becc.) Becc. ex Arcangeli	Frozen	S. Jackson	Failed
A. boyceanus Hett.	*A. gomboczianus* Pic. Serm.	Frozen	S. Jackson	Failed
A. boyceanus Hett.	*A. scutatus* Hett. & T.C. Chapman	Refrigerated	S. Jackson	Failed
A. boyceanus Hett.	*A. tuberculatus* Hett. & V.D. Nguyen.	Refrigerated	S. Jackson	Failed
A. cicatricifer Ridl.	(*A. lewallei* Malaisse & Bamps x *A. impressus* Ittenb.)	Refrigerated	S. Jackson	Failed
A. cicatricifer Ridl.	(*A. lewallei* Malaisse & Bamps x *A. impressus* Ittenb.)	Refrigerated	S. Jackson	Failed
A. cicatricifer Ridl.	*A. sizemoreae* Hett.	Fresh	S. Jackson	Failed
A. coaetaneus Liu & Wie	(*A. excentricus* Hett. x *A. krausei* Engl.)	Frozen	S. Jackson	Failed
A. coaetaneus Liu & Wie AGA-1800-01	*A. kachinensis* Engl. & Gehrm. AGA-1815-01	Frozen	A. Galloway	Failed
A. crispifolius A. Galloway, A. Ongsakul, & P. Schmidt AGA-1753-01	*A. laoticus* Hett. AGA-2025-01	Refrigerated	A. Galloway	Failed
A. croatii Hett. & A. Galloway	*A. aberrans* Hett.	Refrigerated	S. Jackson	failed
A. croatii Hett. & A. Galloway	*A. titanum* (Becc.) Becc. ex Arcangeli	Fresh	S. Jackson	Failed
A. dactylifer Hett.	*A. rostratus* Hett.	Refrigerated	S. Jackson	Failed
A. dactylifer Hett.	*A. rostratus* Hett.	Frozen	S. Jackson	Failed

(*Continued*)

Pollen Acceptor	Pollen Donor	Pollen	Hybridizer	Result
A. dactylifer Hett.	*A. rostratus* Hett.	Frozen	S. Jackson	Failed
A. declinatus Hett. AGA-2169-01	*A. gallowayi* Hett. AGA-2008-02	Fresh	A. Galloway	Failed
A. decus-silvae Backer & Alderw.	*A. laoticus* Hett.	Fresh	S. Jackson	Failed
A. decus-silvae Backer & Alderw.	*A. titanum* (Becc.) Becc. ex Arcangeli	Refrigerated	S. Jackson	Failed
A. decus-silvae Backer & Alderw. x *A. variabilis* Bl.)	*A. titanum* (Becc.) Becc. ex Arcangeli	Frozen	S. Jackson	Failed
A. discophorus Backer & Alderw.	*A. laoticus* Hett.	Fresh	S. Jackson	Failed
A. dracontioides (Engl.) N. E. Br. (Engl.) N. E. Br.	(*A. decus-silvae* Backer & Alderw. x *A. variabilis* Bl.)	Refrigerated	S. Jackson	Failed
A. dracontioides (Engl.) N. E. Br. (Engl.) N. E. Br.	A. *decus-silvae* Backer & Alderw.	Refrigerated	S. Jackson	Failed
A. dracontioides (Engl.) N. E. Br. (Engl.) N. E. Br.	*A. discophorus* Backer & Alderw.	Refrigerated	S. Jackson	Failed
A. dunnii Tutch.	*A. ochroleucus* Hett. & V.D. Nguyen	Fresh	S. Jackson	Failed (3x)
A. dunnii Tutch.	*A. coaetaneus* Liu & Wie	Frozen	S. Jackson	Failed
A. excentricus Hett.	*A. dactylifer* Hett.	Frozen	S. Jackson	Failed
A. galbra F.M. Bailey	*A. variabilis* Bl. 'Slukas Dark Giant'	Frozen	S. Jackson	Failed
A. galbra F.M. Bailey	(*A. variabilis* Bl. x *A. decus-silvae* Backer & Alderw.)	Fresh	S. Jackson	Failed
A. gallowayi Hett.	*A. variabilis* Bl. 'Slukas Dark Giant'	Refrigerated	S. Jackson	Failed
A. gallowayi Hett. AGA-2008-02	*A. barbatus* A. Galloway & A. Ongsakul AGA-2309-01	Frozen	A. Galloway	Failed
A. gallowayi Hett. AGA-2202-01	*A. myosuroides* Hett. & A. Galloway AGA-1756-01	Refrigerated	A. Galloway	Failed
A. henryi N. E. Br.	(*A. variabilis* Bl. x *A. decus-silvae* Backer & Alderw.)	Fresh	S. Jackson	Failed
A. henryi N. E. Br.	*A. bangkokensis* Gagn.	Fresh	S. Jackson	Failed
A. henryi N. E. Br.	*A. laoticus* Hett.	Refrigerated	S. Jackson	Failed
A. henryi N. E. Br.	*A. rostratus* Hfett.	Frozen	S. Jackson	Failed
A. hirsutus Teijsm. & Binnend.	*A. bangkokensis* Gagn.	Refrigerated	S. Jackson	Failed
A. hirtus N. E. Br.	*A. rostratus* Hett.	Frozen	S. Jackson	Failed
A. hirtus N. E. Br. AGA-2228-01	*A. maxwellii* Hett.	Frozen	A. Galloway	Failed
A. hirtus N. E. Br. AGA-2228-01	A. sp. #579 AGA-2176	Frozen	A. Galloway	Failed
A. impressus Ittenb. AGA-1158-01	*A. maxwellii* Hett. AGA-1200-01	Refrigerated	A. Galloway	Failed
A. interruptus Engl. & Gehrm.	*A. natolii* Hett. et al.	Frozen	S. Jackson	Failed
A. interruptus Engl. & Gehrm.	A. spec. 'Pseudodracontium group'	Refrigerated	S. Jackson	Failed
A. kachinensis Engl. & Gehrm. AGA-2500-01	*A. maxwellii* Hett.	Frozen	A. Galloway	Failed
A. khammouanensis A. Galloway AGA-2198-01	*A. konjac* K. Koch AGA-2535-01	Frozen	A. Galloway	Failed

(*Continued*)

Pollen Acceptor	Pollen Donor	Pollen	Hybridizer	Result
A. khammouanensis A. Galloway AGA-2290-04	*A. kachinensis* Engl. & Gehrm. AGA-1815-01	Frozen	A. Galloway	Failed
A. khammouanensis A. Galloway AGA-2290-05	*A. yunnanensis* Engl. AGA-2506-01	Fresh	A. Galloway	Failed
A. konjac K. Koch	*A. opertus* Hett.	Refrigerated	S. Jackson	Failed
A. konjac K. Koch	*A. titanum* (Becc.) Becc. ex Arcangeli	Refrigerated	S. Jackson	Failed
A. konjac K. Koch AGA-1469-01	*A. pygmaeus* Hett.	Frozen	A. Galloway	Failed
A. konjac K. Koch AGA-1797-01	*A. atrorubens* Hett. & M. Sizemore AGA-1214-01	Frozen	A. Galloway	Failed
A. konjac K. Koch AGA-1798-01	*A. gallowayi* Hett.	Frozen	A. Galloway	Failed
A. konjac K. Koch AGA-1798-01	*A. krausei* Engl.	Frozen	A. Galloway	Failed
A. konjac K. Koch AGA-1798-01	*A. ochroleucus* Hett. & V.D. Nguyen AGA-0886-01	Fresh	A. Galloway	Failed
A. konjac K. Koch AGA-1947-01	*A. longituberosus* (Engl.) Engl. & Gehrm.	Frozen	A. Galloway	Failed
A. krausei Engl. AGA-0283-01	*A. hirtus* N. E. Br. AGA-2228-01	Fresh	A. Galloway	Failed
A. krausei Engl. AGA-2619-01	*A. maxwellii* Hett.	Frozen	A. Galloway	Failed
A. lambii Mayo & Widjaja	*A. opertus* Hett.	Refrigerated	S. Jackson	Failed
A. laoticus Hett.	*A. bangkokensis* Gagn.	Fresh	S. Jackson	Failed (x3)
A. laoticus Hett.	(*A. variabilis* Bl. x *A. decus-silvae* Backer & Alderw.)	Fresh	S. Jackson	Failed
A. laoticus Hett.	*A. decus-silvae* Backer & Alderw.	Refrigerated	S. Jackson	Failed
A. laoticus Hett.	*A. haematospadix* Hook. f.	Refrigerated	S. Jackson	Failed
A. laoticus Hett.	*A. henryi* N. E. Br.	Refrigerated	S. Jackson	Failed
A. laoticus Hett.	*A. henryi* N. E. Br.	Refrigerated	S. Jackson	Failed
A. laoticus Hett.	*A. hirtus* N. E. Br.	Refrigerated	S. Jackson	Failed
A. laoticus Hett.	*A. konjac* K. Koch	Refrigerated	S. Jackson	Failed
A. laoticus Hett.	*A. paeoniifolius* (Dennst.) Nicolson	Fresh	S. Jackson	Failed
A. laoticus Hett.	(*A. lewallei* Malaisse & Bamps x *A. impressus* Ittenb.)	Fresh	S. Jackson	Failed
A. laoticus Hett. AGA-1750-01	*A. dzui* Hett.	Frozen	A. Galloway	Failed
A. laoticus Hett. AGA-2025-01	*A. maxwellii* Hett. AGA-1200-01	Fresh	A. Galloway	Failed
A. longituberosus (Engl.) Engl. & Gehrm.	*A. variabilis* Bl. x *A. decus-silvae* Backer & Alderw.	Fresh	S. Jackson	Failed (x2)
A. longituberosus (Engl.) Engl. & Gehrm.	*A. borneensis* (Engl.) Engl. & Gehrm.	Frozen	S. Jackson	Failed
A. longituberosus (Engl.) Engl. & Gehrm.	*A. decus-silvae* Backer & Alderw.	Refrigerated	S. Jackson	Failed
A. longituberosus (Engl.) Engl. & Gehrm.	*A. dracontioides* (Engl.) N. E. Br.	Frozen	S. Jackson	Failed
A. longituberosus (Engl.) Engl. & Gehrm.	*A. laoticus* Hett.	Fresh	S. Jackson	Failed

(*Continued*)

Pollen Acceptor	Pollen Donor	Pollen	Hybridizer	Result
A. longituberosus (Engl.) Engl. & Gehrm.	*A. variabilis* Bl.	Refrigerated	S. Jackson	Failed
A. maxwellii Hett.	(*A. impressus* Ittenb. x *A. taurostigma* Ittenb. & Hett 'White Veins')	Refrigerated	S. Jackson	Failed
A. maxwellii Hett.	*A. henryi* N. E. Br.	Fresh	S. Jackson	Failed
A. maxwellii Hett. AGA-1177-01	*A. konjac* K. Koch AGA-2545-01	Refrigerated	A. Galloway	Failed
A. mossambicensis (Schott ex Garcke) N. E. Br. AGA-0900-01	*A. maximus* (Engl.) N. E. Br. AGA-0240-01	Refrigerated	A. Galloway	Failed
A. muelleri Bl.	*A. rostratus* Hett.	Fresh	C. Claudel	Failed
A. myosuroides Hett. & A. Galloway	*A. haematospadix* Hook. f.	Fresh	S. Jackson	Failed
A. myosuroides Hett. & A. Galloway	*A. pygmaeus* Hett.	Fresh	S. Jackson	Failed
A. myosuroides Hett. & A. Galloway AGA-1756-01	*A. ongsakulii* Hett. & A. Galloway AGA-1534-01	Refrigerated	A. Galloway	Failed (x2)
A. myosuroides Hett. & A. Galloway AGA-1756-01	(*A. variabilis* Bl. x *A. decus-silvae* Backer & Alderw.) AGA-2642-03	Frozen	A. Galloway	Failed
A. myosuroides Hett. & A. Galloway AGA-1756-01	*A. gallowayi* Hett. AGA-2008-02	Refrigerated	A. Galloway	Failed
A. myosuroides Hett. & A. Galloway AGA-1756-01	*A. julaihii* Ipor, Tawan & P.C. Boyce AGA-2811-01	Refrigerated	A. Galloway	Failed
A. myosuroides Hett. & A. Galloway AGA-1756-01	*A. obscurus* Hett. & M. Sizemore	Refrigerated	A. Galloway	Failed
A. myosuroides Hett. & A. Galloway AGA-1756-01	*A. saururus* Hett. AGA-0176-01	Fresh	A. Galloway	Failed
A. natolii Hett. et al.	*A. sizemoreae* Hett.	Refrigerated	S. Jackson	Failed (x3)
A. natolii Hett. et al.	*A. hirtus* N. E. Br.	Frozen	S. Jackson	Failed (x2)
A. natolii Hett.et al.	*A. titanum* (Becc.) Becc. ex Arcangeli	Refrigerated	S. Jackson	Failed (x2)
A. natolii Hett. et al.	*A. aberrans* Hett.	Refrigerated	S. Jackson	Failed
A. natolii Hett. et al.	*A. cicatricifer* Ridl.	Refrigerated	S. Jackson	Failed
A. natolii Hett. et al.	*A. hirtus* N. E. Br.	Refrigerated	S. Jackson	Failed
A. natolii Hett. et al.	*A. pygmaeus* Hett.	Frozen	S. Jackson	Failed
A. natolii Hett. et al.	*A. rostratus* Hett.	Frozen	S. Jackson	Failed
A. natolii Hett. et al.	*A. sizemoreae* Hett.	Frozen	S. Jackson	Failed
A. natolii Hett. et al.	*A. tuberculatus* Hett. & V.D. Nguyen.	Frozen	S. Jackson	Failed
A. natolii Hett. et al.	*A. variabilis* Bl. 'Slukas Dark Giant'	Refrigerated	S. Jackson	Failed
A. natolii Hett. et al.	*A. variabilis* Bl. 'Slukas Dark Giant'	Frozen	S. Jackson	Failed
A. natolii Hett. et al.	(*A. variabilis* Bl. x *A. decus-silvae* Backer & Alderw.)	Refrigerated	S. Jackson	Failed
A. natolii Hett. et al. AGA-2376-01	*A. maxwellii* Hett. AGA-1980-05	Frozen	A. Galloway	Failed

(*Continued*)

Pollen Acceptor	Pollen Donor	Pollen	Hybridizer	Result
A. obscurus Hett. & M. Sizemore	(*A. variabilis* Bl. x A. *decus-silvae* Backer & Alderw.)	Frozen	S. Jackson	Failed
A. obscurus Hett. & M. Sizemore	*A. decus-silvae* Backer & Alderw.	Refrigerated	S. Jackson	Failed
A. obscurus Hett. & M. Sizemore	*A. rostratus* Hett.	Refrigerated	S. Jackson	Failed
A. obscurus Hett. & M. Sizemore	*A. variabilis* Bl.	Refrigerated	S. Jackson	Failed
A. obscurus Hett. & M. Sizemore AGA-2032-01	*A. myosuroides* Hett. & A. Galloway	Fresh	A. Galloway	Failed
A. ongsakulii Hett. & A. Galloway AGA-1534-01	(*A. decus-silvae* Backer & Alderw. x *A. variabilis* Bl.)	Refrigerated	S. Jackson	Failed
A. ongsakulii Hett. & A. Galloway AGA-1534-01	*A. gallowayi* Hett. AGA-1754-01	Fresh	A. Galloway	Failed
A. ongsakulii Hett. & A. Galloway AGA-1534-01	*A. saururus* Hett. AGA-0176-01	Frozen	A. Galloway	Failed
A. ongsakulii Hett. & A. Galloway AGA-1534-01	*A. titanum* (Becc.) Becc. ex Arcangeli	Frozen	A. Galloway	Failed
A. ongsakulii Hett. & A. Galloway AGA-2007-01	*A. obscurus* Hett. & M. Sizemore	Fresh	A. Galloway	Failed
A. operculatus (ined.)	*A. interruptus* Engl. & Gehrm.	Refrigerated	S. Jackson	Failed
A. operculatus (ined.)	*A. variabilis* Bl.	Refrigerated	S. Jackson	Failed
A. ravenii V. D. Nguyen & Hett. AGA-2179-01	*A. rostratus* Hett. AGA-2166-01	Frozen	A. Galloway	Failed
A. reflexus Hett. & A. Galloway AGA-1069-01	*A. urceolatus* ined. AGA-2414-06	Fresh	A. Galloway	Failed
A. rostratus Hett.	*A. laoticus* Hett.	Refrigerated	S. Jackson	Failed (x2)
A. rostratus Hett.	*A. dactylifer* Hett.	Refrigerated	S. Jackson	Failed
A. rostratus Hett.	*A. laoticus* Hett.	Fresh	S. Jackson	Failed
A. saururus Hett. AGA-0176-01	*A. myosuroides* Hett. & A. Galloway AGA-1756-01	Refrigerated	A. Galloway	Failed (x2)
A. saururus Hett. AGA-0176-01	*A. maxwellii* Hett.	Frozen	A. Galloway	Failed
A. saururus Hett. AGA-0238-01	*A. urceolatus* ined. AGA-2414-05	Fresh	A. Galloway	Failed
A. scutatus Hett. & T.C. Chapman	*A. laoticus* Hett.	Fresh	S. Jackson	Failed
A. sizemoreae Hett.	*A. boyceanus* Hett.	Fresh	S. Jackson	Failed (x2)
A. sizemoreae Hett.	(*A. decus-silvae* Backer & Alderw. x *A. variabilis* Bl.)	Refrigerated	S. Jackson	Failed
A. sizemoreae Hett.	(*A. gigas* Teijsm. & Binnend. x *A. decus-silvae* Backer & Alderw.)	Refrigerated	S. Jackson	Failed
A. sizemoreae Hett.	*A. gallowayi* Hett.	Frozen	S. Jackson	Failed
A. sizemoreae Hett.	*A. operculatus* (ined.)	Frozen	S. Jackson	Failed
A. sizemoreae Hett.	*A. operculatus* (ined.)	Refrigerated	S. Jackson	Failed
A. sizemoreae Hett. AGA-1016-01	*A. declinatus* Hett. AGA-2169-01	Frozen	A. Galloway	Failed
A. sp. #587 AGA-2494-02	*A. konjac* K. Koch AGA-0095-01	Frozen	A. Galloway	Failed

(*Continued*)

Pollen Acceptor	Pollen Donor	Pollen	Hybridizer	Result
A. sp. #587 AGA-2494-03	*A. ferruginosus* A. Galloway AGA-2283-01	Frozen	A. Galloway	Failed
A. sp. #587 AGA-2494-09	*A. hirtus* N. E. Br. AGA-2228-01	Fresh	A. Galloway	Failed
A. taurostigma Ittenb. & Hett 'White Veins'	(*A. variabilis* Bl. x A. *decus-silvae* Backer & Alderw.)	Refrigerated	S. Jackson	Failed
A. thaiensis S.-Y. Hu	*A. laoticus* Hett.	Frozen	S. Jackson	Failed
A. thaiensis S.-Y. Hu	*A. titanum* (Becc.) Becc. ex Arcangeli	Refrigerated	S. Jackson	Failed
A. thaiensis S.-Y. Hu	*A. titanum* (Becc.) Becc. ex Arcangeli	Fresh	S. Jackson	Failed
A. thaiensis S.-Y. Hu AGA-1928-01	*A. maxwellii* Hett.	Frozen	A. Galloway	Failed (x2)
A. thaiensis S.-Y. Hu AGA-1928-01	*A. brevipetiolatus* A. Galloway, A. Ongsakul, & P. Schmidt AGA-1570-03	Frozen	A. Galloway	Failed
A. thaiensis S.-Y. Hu AGA-1928-01	*A. titanum* (Becc.) Becc. ex Arcangeli	Frozen	A. Galloway	Failed
A. tuberculatus Hett. & V.D. Nguyen.	*A. natolii* Hett. et al.	Frozen	S. Jackson	Failed
A. variabilis Bl.	*A. titanum* (Becc.) Becc. ex Arcangeli	Frozen	S. Jackson	Failed (x6)
A. variabilis Bl.	*A. cicatricifer* Ridl.	Refrigerated	S. Jackson	Failed
A. variabilis Bl.	*A. laoticus* Hett.	Frozen	S. Jackson	Failed
A. variabilis Bl.	*A. longituberosus* (Engl.) Engl. & Gehrm.	Frozen	S. Jackson	Failed
A. variabilis Bl.	*A. longituberosus* (Engl.) Engl. & Gehrm.	Frozen	S. Jackson	Failed
A. variabilis Bl.	*A. natolii* Hett. et al.	Refrigerated	S. Jackson	Failed
A. variabilis Bl.	*A. sumawongii* (Bogn.) Bogn..	Refrigerated	S. Jackson	Failed
A. variabilis Bl.	*A. thaiensis* S.-Y. Hu	Frozen	S. Jackson	Failed
A. variabilis Bl.	*A. tinekeae* Hett. & A. Voge AGA-2522-01	Frozen	A. Galloway	Failed
A. variabilis Bl. 'Slukas Dark Giant'	*A. dracontioides* (Engl.) N. E. Br.	Refrigerated	S. Jackson	Failed
A. variabilis Bl. 'Slukas Dark Giant'	*A. hirtus* N. E. Br.	Refrigerated	S. Jackson	Failed
A. variabilis Bl. 'Slukas Dark Giant'	*A. natolii* Hett. et al.	Fresh	S. Jackson	Failed
A. variabilis Bl. 'Slukas Dark Giant'	*A. titanum* (Becc.) Becc. ex Arcangeli	Refrigerated	S. Jackson	Failed
A. variabilis Bl. AGA-1245-01	*A. crispifolius* A. Galloway, A. Ongsakul, & P. Schmidt AGA-1753-01	Refrigerated	A. Galloway	Failed
A. variabilis Bl. AGA-1246-01	*A. barbatus* A. Galloway & A. Ongsakul AGA-2309-01	Frozen	A. Galloway	Failed
A. variabilis Bl. AGA-1246-01	*A. maxwellii* Hett. AGA-1200-01	Fresh	A. Galloway	Failed
A. verticillatus Hett.	*A. coaetaneus* Liu & Wie	Fresh	S. Jackson	Failed
A. verticillatus Hett.	*A. dracontioides* (Engl.) N. E. Br.	Fresh	S. Jackson	Failed
A. verticillatus Hett.	*A. longituberosus* (Engl.) Engl. & Gehrm.	Frozen	S. Jackson	Failed

(*Continued*)

Pollen Acceptor	Pollen Donor	Pollen	Hybridizer	Result
A. verticillatus Hett.	*A. natolii* Hett. et al.	Refrigerated	S. Jackson	Failed
A. verticillatus Hett.	*A. natolii* Hett. et al.	Refrigerated	S. Jackson	Failed
A. yuloensis H. Li	*A. cicatricifer* Ridl.	Refrigerated	S. Jackson	Failed
A. yuloensis H. Li	*A. tuberculatus* Hett. & V.D. Nguyen.	Fresh	C. Claudel	Failed
A. yunnanensis Engl.	*A. ochroleucus* Hett. & V.D. Nguyen	Frozen	S. Jackson	Failed

References

Anil, S. R., Beevy, S. S. & Siril, E. A. 2013. Karyosystematic studies in *Amorphophallus* Blume ex decne. *J. Root Crops*, 39(2), 39–50.

Barabé, D., Lavallée, K. & Gibernau, M. 2008. Pollen viability and germination in some neotropical aroids. *Botany*, 86, 98–102.

Barmentlo, S. H., Meirmans, P. G., Luijten, S. H., Triest, L. & Oostermeijer, J. G. 2018. Outbreeding depression and breeding system evolution in small, remnant populations of *Primula vulgaris*: Consequences for genetic rescue. *Conserv. Genet*., 19(3), 545–554.

Bentham, G. & Hooker, J. D. 1883. *Genera Plantarum*, Vol. 3, Part 2. London, UK: Reeve & Co.

Blume, C. L. 1834. *Amorphophallus*: In J. Decaisne, Description d'un herbier de l'ile de Timor. *Nouv. Ann. Mus. Hist. Nat. III*, 3, 333–501.

Blume, C. L. 1837. *Amorphophallus. Rumphia*, 1, 138–149.

Bogner, J. & Nicolson, D. H. 1991. A revised classification of the Araceae with dichotomous keys. *Willdenowia*, 21, 35–50.

Bogner, J. & Hetterscheid, W. L. A. 1992. Notes on the genus *Amorphophallus* (Araceae). 1. Three new species from tropical Asia. *Blumea*, 36, 467–475.

Bogner, J., Mayo, S. J. & Sivadasan, M. 1985. New and changing concepts in *Amorphophallus*. *Aroideana*, 8(1), 15–25.

Boyce, P. C. & Croat, T. B. 2011 (onwards). The Überlist of Araceae, Totals for Published and Estimated Number of Species in Aroid Genera. http://www.aroid.org/genera/180211uberlist.pdf, last accessed on 28 May 2019.

Boyce, P. C. & Wong, S. Y. 2012. The Araceae of Malesia I: Introduction. *Malay. Nat. J.*, 64, 33–67.

Boyce, P. C., Sookchaloem, D., Hetterscheid, W. L., Gusman, G., Jacobsen, N., Idei, T. & Van Du, N. 2012. *Flora of Thailand*, Vol. 11, Part 2: *Araceae, Acoraceae*. Bangkok, Thailand: Forest Herbarium, National Park, Wildlife and Plant Conservation Department, 325 p.

Brandham, P. E. 1983. Evolution in a stable chromosome system, in: Brandham, P. E. & Bennett, M. D. (eds.), *Kew Chromosome Conference II*. London, UK, pp. 251–260.

Brickell, C. D., Alexander, C., Cubey, J. J., David, J. C., Hoffman, M. H. A., Leslie, A. C., Malécot, V. & Xiaobai, J. 2016. *International Code of Nomenclature for Cultivated Plants*, Vol. 10, pp. 1–184, ed. 9, ISHS, Leuven, Belgium: Scripta Horticulturae.

Brown, N. E. 1882. Four new genera of Aroideae. *J. Bot. New Ser.*, 11, 193–197.

Brown, N. E. 1901. Aroideae, in: Thiselton-Dyer, W.T. (ed.), *Flora of Tropical Africa*, Vol. 8. London, UK: Lovel Reeve & Co.

Cabrera, L. I., Salazar, G. A., Chase, M. W., Mayo, S. J., Bogner, J. & Dávila, P. 2008. Phylogenetic relationships of aroids and duckweeds (Araceae) inferred from coding and noncoding plastid DNA. *Am. J. Bot*., 95(9), 1153–1165.

Chauhan, K. P. S. & Brandham, P. E. 1985. Chromosome and DNA variation in *Amorphophallus* (Araceae). *Kew Bull*., 40(4), 745–758.

Chen, L. –G., Liu, Z. –L. & Zhuo, R.–X. 2005. Synthesis and properties of degradable hydrogels of konjac glucomannan grafted acylic acid for colon-specific drug delivery. *Polymer*, 46, 6274–6281.

Chua, M. 2011. An investigation of the biology and chemistry of the Chinese medicinal plant, *Amorphophallus konjac*. PhD thesis, University of Wolverhampton, Wolverhampton, UK.

Claudel, C., Buerki, S., Chatrou, L. W., Antonelli, A., Alvarez, N. & Hetterscheid, W. 2017. Large-scale phylogenetic analysis of *Amorphophallus* (Araceae) derived from nuclear and plastid sequences reveals new subgeneric delineation. *Bot. J. Linn. Soc*., 184(1), 32–45.

Claudel, C. & Galloway, A. 2012. Hybridization of *Amorphophallus*: State of the art. *Aroideana*., 35, 103–108.

Claudel, C., Galloway, A. & Mangelsdorff, R. 2013. Hybridization of *Amorphophallus*: State of affairs. *Aroideana*., 36, 114–122.

Claudel, C. & Mangelsdorff, R. 2014. Hybridization of *Amorphophallus*: State of the Unions. *Aroideana*, 37, 72–79.

Claudel, C., Mangelsdorff, R. & Hetterscheid, W. L. A. 2012. The first successful hybrid of *Amorphophallus titanum*. *Aroideana*, 35, 81–85.

Claudel, C., Lev-Yadun, S., Hetterscheid, W. L. A. & Schultz, M. 2019. Lichen and cyanobacteria mimicry in huge tree-size *Amorphophallus* petioles results in their masquerade as inedible tree trunks. *Bot. J. Linn. Soc*., 190, 192–214.

Claudel, Cyrille. *Amorphophallus* hybrids, cultivars, 25 May 2019. https://www.amorphophallus-network.org/

Cusimano, N, Bogner, J., Mayo, S. J., Boyce, P. C., Wong, S. Y., Hesse, M., Hetterscheid, W. L. A., Keating, R. C. & French, J. C. 2011. Relationships within the Araceae: Comparisons of morphological patterns with molecular phylogenies. *Am. J. Bot*., 98, 654–668.

Diao, Y., Yang, C., Yan, M., Zheng, X., Jin, S., Wang, Y. & Hu, Z. 2014. De novo transcriptome and small RNA analyses of two *Amorphophallus* species. *PloS One*, 9(4), e95428.

Engler, A. 1876. Vergleichende Untersuchungen über die morphologischen Verhältnisse der Araceae. 1 Theil: Natürliches System der Araceae. *Nov. Act. Ksl. Leop.-Carol.-Deutschen Akad. Naturf*., 39(3), 135–155.

Engler, A. 1879. Araceae, in: de Candolle, A. & de Candolle, C. (eds.), *Monographiae Phanerogamarum*, Vol. 2, pp. 1–681. Paris, France: Sumptibus G. Masson.

Engler, A. 1881. Beiträge zur Kenntnis der Araceae, I. *Bot. Jahrb. Syst*., 1, 179–190.

Engler, A. 1893. Araceae africanae. *Bot. Jahrb. Syst*., 26, 447–466.

Engler, A. (ed.). 1911. Araceae-Lasioideae, in: *Das Pflanzenreich*, IV, 23C (Heft 48). Leipzig, Germany: Wilhelm Engelmann.

Fang, W. & Wu, P. 2004. Variations of Konjac glucomannan (KGM) from *Amorphophallus konjac* and its refined powder in China. *Food Hydrocoll*., 18, 167–170.

Galloway, A. 2019. *Amorphophallus* hybrids, 25 May 2019. https://alangallowaybotanicals.com/

Gholave, A. R., Pawar, K. D., Yadav, S. R., Bapat, V. A. & Jadhav, J. P. 2016. Reconstruction of molecular phylogeny of closely related *Amorphophallus* species of India using plastid DNA marker and fingerprinting approaches. *Physiol. Mol. Biol. Pla*., 23(1), 155–167. doi: 10.1007/s12298-016-0400-0.

Grayum, M. H. 1984. Palynology and phylogeny of the Araceae. Ph.D. dissertation University of Massachusetts. Amherst, MA.

Grayum, M. H. 1990. Evolution and phylogeny of the Araceae. *Ann. Missouri Bot. Gard*., 77, 628–697.

Grob, G. B. J., Gravendeel, B., Eurlings, M. C. M. & Hetterscheid, W. L. A. 2002. Phylogeny of the Tribe *Thomsonieae* (Araceae) based on chloroplast *mat*K and trnL intron sequences. *Syst. Bot*., 27(3), 453–467.

Grob, G. B. J., Gravendeel, B. & Eurlings, M. C. M. 2004. Potential phylogenetic utility of the nuclear *Floricaula/Leafy* second intron: Comparison with three chloroplast DNA regions in *Amorphophallus* (Araceae). *Mol. Phylogenet. Evol*., 30, 13–23.

Harrington, J. F. 1970. Seed and pollen storage for conservation of plant gene resources, in: Frankel, O. H. & Bennett, E. (eds.), *Genetic Resources in Plants: Their Exploration and Conservation*, pp. 501–521. Oxford, UK: Blackwell.

Hawkes, A. D. 1951. Studies in Araceae I. *Loydia*, 14, 98–100.

Hetterscheid, W. L. A. & van der Ham, R. W. J. M. 2001. Notes on the genus *Amorphophallus* (Araceae): 11 New and obsolete species from East Malaysia and continental Southeast Asia. *Blumea*, 46(2), 253–282.

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.

Hetterscheid, W. L. A, Wistuba, A., Amoroso, V., Medecilo, M. & Claudel, C. 2012. *Amorphophallus natolii* (Araceae), a new species from limestone on Palawan, Philippines. *Bot. Stud*., 53, 415–420.

Hetterscheid, W. L. A. & Claudel, C. 2012. The end of *Pseudodracontium*. *Aroideana*, 35, 40–46.

Hetterscheid, W. L. A. 1992(1994). Preliminary taxonomy and morphology of *Amorphophallus* Blume ex Decaisne (Araceae), in: Serebryanyi, M. M. (ed.), *Proceedings of the Moscow Aroid Conference*, pp. 35–48. Moscow, Russia.

Hetterscheid, W. L. A. 2012. *Amorphophallus* in: Boyce, P. C., Sookchaloem, D., Hetterscheid, W. L. A., Gusman, G., Jacobsen, N., Idei, T. & Nguyen, V.D. (eds.), *Araceae. Flora of Thailand* Vol. 11, no. 2. Bangkok, Thailand: The Forest Herbarium.

Hooker, J. D. 1875. *Proteinophallus rivieri*. *Bot. Mag*., 101, t. 6195.

Hooker, J. D. 1894. *Amorphophallus elliottii*. *Bot. Mag*., 55, t. 7394.

Hu, J., Gao, X., Liu, J., Xie, C. & Li, J. 2008. Plant regeneration from petiole callus of *Amorphophallus albus* and analysis of somaclonal variation of regenerated plants by RAPD and ISSR markers. *Bot. Stud*., 49, 189–197.

Jaleel, V. A., Sivadasan, M., Ahmed, H., Alfarhan, A. H., Thomas, J. & Alatar, A. A. 2012. A taxonomic revision of *Amorphophallus* Blume ex Decne. sect. *Conophallus* (Schott) Engl. (Araceae) in India. *Bangladesh J. Plant Taxon*., 19(2), 135–153.

Kite, G. & Hetterscheid, W. L. A. 1997. Inflorescence odours of *Amorphophallus* and *Pseudodracontium* (Araceae). *Phytochemistry*, 46(1), 71–75.

Kite, G. C. & Hetterscheid, W. L. 2017. Phylogenetic trends in the evolution of inflorescence odours in *Amorphophallus*. *Phytochemistry*, 142, 126–142.

Krause, K. 1924. Eine neue Sektion der Gattung *Amorphophallus* Bl. *Notizbl. Bot. Gart. Mus. Berl.-Dahlem*, 9, 37–38.

Kumar, C. S. & Jaleel, V. A. 2009. *Amorphophallus bognerianus* (Araceae), a new species from India. *Aroideana*, 32, 136–141.

Kuntze, O. 1891. *Revisio Generum Plantarum*, Part 2. A. Felix, Leipzig, Germany.

Kuruvilla, K. M., Dutt, B. & Roy, R. P. 1989. Karyomorphological investigations on Aroids of North-eastern Hills. *J. Cytol. Genet*., 24, 13–22.

Leimu, R. & Fischer, M. 2010. Between-population outbreeding affects plant defence. *PLoS ONE*, 5, e12614.

Li, H. & Hetterscheid, W. L. A. 2010. *Amorphophallus*, in: Wu, Z., Raven, P. H. & Deyuan, H. (eds.), *Flora of China*, Vol. 23. Beijing, China: MBG Press and Science Press, pp. 23–33.

Li, J. J., Pei, G. L., Pang, H. X., Bilderbeck, A., Chen, S. S. & Tao, S. H. 2006. A new method for RAPD primers selection based on primer bias in nucleotide sequence data. *J. Biotechnol*., 126, 415–442.

Liu, Y., Li, H., Jarvis, D. & Long, C. 2015. Aroid crops in China. *Aroideana*., 38E, 116–129.

Liu, P. Y. & Chen, J. F. 1984. *Amorphophallus albus. J. Southwest. Agric. Coll*. (Chongqing), 67(1), 1984.

Liu, P. Y. 2004. *Konjac*. Beijing, China: China Agriculture Press.

Liu, S. Y. & Wei, S. J. 1986. *Amorphophallus coaetaneus. Guihaia*, 6, 183.

Long, C. 1998. Ethnobotany of Amorphophallus of China, in: *Current Advances in Araceae Studies: Proceedings of the Sixth International Aroid Conference*, Suppl, Vol. 10, pp. 89–92. Beijing, China: Acta Botanica Yunnanica.

McPherson, S. & Hetterscheid, W. L. A. 2011. *Amorphophallus* in the wild and in cultivation. *Plantsman*., 10, 90–97.

Mekkerdchoo, O., Borompichaichartkul, C., Perrigo, Allison, Srzednicki, G., Prakitchaiwattana, C. & Antonelli, A. 2016. Tracing the evolution and economic potential of konjac glucomannan in *Amorphophallus* species (Araceae) using molecular phylogeny and RAPD markers. *Phytotaxa*, 282(2), 81–106.

Nakai, T. 1948. *Amorphophallus selebicus*: A new giant *Amorphophallus* from Celebes, with some remarks on the bulb of *Amorphophallus titanum*, and photographs of *Amorphophallus selebicus*, *A. titanum*, and *A. decus silvae*. *Bull. Tokyo Sci. Mus*., 22, 1–4.

Nauheimer, L., Metzler, D. & Renner, S. S. 2012. Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. *The New Phytologist*., 195, 938–950.

Nicolson, D. H, Bogner, J., Mayo, S. & Sivadasan, M. 1984. Proposal to amend 723 *Amorphophallus*, add *Thomsonia*, nom. rej. prop. (Araceae). *Taxon*, 33, 740.

Nicolson, D. H. 1977. (429) Proposal to change the typification of 723 *Amorphophallus*, nom. cons. (Araceae). *Taxon*, 26(2, 3), 337–338.

Pan, C., Gichira, A. W. & Chen, J. M. 2015. Genetic variation in wild populations of the tuber crop *Amorphophallus konjac* (Araceae) in central China as revealed by AFLP markers. *Genet. Mol. Res*., 14(4), 18753–18763.

Pan, C., You, Y., Diao, Y., Hu, Z. & Chen, J. 2012. Isolation and characterization of microsatellite loci for the herbaceous tuber crop, *Amorphophallus konjac* (Araceae). *Genet. Mol. Res*., 11(4), 4617–4621.

Patil, K. S. 1995. Cytotaxonomical & Genetical studies in Araceae from Western Ghats of Maharashtra. Ph.D. Thesis. Department of Botany, Shivaji University, Kolhapur, India.

Petersen, G. 1989. Cytology and systematics of Araceae. *Nordic J. Bot*., 9(2), 119–166.

Poerba, Y. S. & Martanti, D. 2008. Genetic variability of *Amorphophallus muelleri* Blume in Java based on random amplified polymorphic DNA. *Biodiversitas*, 9(4), 245–249.

Poerba, Y. S. & Yuzammi, D. 2008. Estimation of genetic variation of *Amorphophallus titanium* Becc. based on random amplified polymorphic DNA. *Biodiversitas*, 9(2), 103–107.

Prain, D. 1893. On the flora of Narcondam and Barren Island. *J. Asiat. Soc. Bengal*, 62(2), 39–86.

Ramachandran, K. 1977. Karyological studies on four South Indian species of *Amorphophallus*. *Cytologia*., 42, 645–652.

Santosa, E., Lian, C. L., Pisooksantivatana, Y. & Sugiyama, N. 2007. Isolation and characterization of polymorphic microsatellite markers in *Amorphophallus paeoniifolius* (Dennst.) Nicolson, Araceae. *Mol. Ecol. Notes*, 7(5), 814–817.

Santosa, E., Lian, C. L., Sugiyama, N., Misra, R. S., Boonkorkaew, P. & Thanomchit, K. 2017. Population structure of elephant foot yams (*Amorphophallus paeoniifolius* (Dennst.) Nicolson) in Asia. *PloS One*, 12(6), e0180000.

Savidan, Y. H. 2000. Apomixis: Genetics and breeding. *Plant Breed. Rev.*, 18, 13–86. doi:10.1002/9780470650158.ch2.

Schierup, M. H. & Christiansen, F. B. 1996. Inbreeding depression and outbreeding depression in plants. *Heredity*., 77(5), 461–468. https://doi.org/10.1038/hdy.1996.172.

Schott, H. W. 1832. Araceae, in: Schott, H.W. & Endlicher, S. (eds.), *Meletemata Botanica*, pp. 16–22. Vienna, Austria: C. Gerold.

Schott, H. W. 1856. *Synopsis Aroidearum*. Vienna, Austria: Mechitarists' Press.

Schott, H. W. 1857. Aroideen-Skizzen. *Oesterr. Bot. Wochenbl*., 7, 261–263.

Schott, H. W. 1858a. *Genera Aroidearum Exposita*. Vienna, Austria: Hölzel.

Schott, H. W. 1858b. Aroideen-Skizzen. *Oesterr. Bot. Zeitschr*., 8, 317–318.

Schott, H. W. 1860. *Prodromus Systematis Aroidearum*. Vienna, Austria: Mechitarists' Press.

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 *trn*L, *rbc*L and LEAFY second intron sequences. *Bot. Stud*., 51, 473–490.

Sheng, D. X. & Teng, J. X. 2008. Analysis of current situation and future trend of konjac industry demand. *China Agricult. Inf*., 7, 39–40.

Shete, C. C., Wadkar, S. S., Gaikwad, N. B. & Patil, K. S. 2015. Cytological studies in some members of *Amorphophallus* from Western Ghats of Maharashtra. *J. Cytol. Genet*., 16(1–2), 17–24.

Shull, G. H. 1948. What Is Heterosis? *Genetics*, 33(5), 439–446.

Sivadasan, M. 1989. *Amorphophallus smithsonianus* (Araceae), a new species from India, and a note on A. sect. *Synantherias*. *Willdenowia*, 18, 435–440.

Stapf, O. 1924. *Amorphophallus cirrifer. Bot. Mag*., 149, t. 9000.

Sugiyama, N., Santosa, E., Lee, O. N., Hikosaka, S. & Nakata, M. 2006. Classification of elephant foot yam (*Amorphophallus paeoniifolius*) cultivars in Java using AFLP markers. *Jap. J. Trop. Agricu*., 50(4), 215–218.

Suresh, C. R., Sivadasan, M. & Manilal, K.S. 1983. A commentary on Rheede's Aroids. *Taxon*, 32(1), 126–132.

Tjio, J. H. 1948. The somatic chromosomes of some tropical plants. *Hereditas*., 34, 135–114.

Ulrich, S., Hesse, M., Weber, M. & Halbritter, H. 2017. *Amorphophallus*: New insights into pollen morphology and the chemical nature of the pollen wall. *Grana*, 56(1), 1–36. doi: 10.1080/00173134.2015.1133699.

van der Ham, R., Grob, G., Hetterscheid, W. L. A., Star, W. & 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. doi: 10.1080/00173130500424417.

van der Ham, R., Hetterscheid, W. L. A. & Van Heuven, B. J. 1998. Notes on the genus *Amorphophallus* – 8: Pollen morphology of *Amorphophallus* and *Pseudodracontium*. *Rev. Paleobot. Palynol*., 103, 95–142. doi:10.1016/S0034-6667(98)00042-6.

Wakabayashi, S. 1955. On the Chromosome of *Amorphophallus konjac*. *Chromosome*, 25(26), 881–885.

Wenbing, C., Chunlin, L. & Jianfu, Z. 2001. Study on genetic diversity of RAPD markers in *Amorphophallus*. *J. Agric. Biotechnol*., 4, 024.

Wikipedia contributors. 2019. "Outbreeding depression" *Wikipedia, The Free Encyclopedia*; 7 May 2019, 14:22 UTC. <https://en.wikipedia.org/w/index.php?title=Outbreeding_depression&oldid=895953627> [accessed 28 May 2019].

Yin, S., Yan, Y., You, L., Chen, Q., Zhou, Y., Chen, K., Li, R., Yang, Z., Man, L. & Gao, Y. (2019). Newly developed genomic SSRs reveal genetic diversity in wild and cultivated *Amorphophallus albus* germplasms. *Plant Mol. Biol. Rep*., 37(4), 365–375.

Ying, S.-S. 1991. Miscellaneous notes on The Flora of Taiwan (14). 174: Some correct names of genus *Amorphophallus* in Taiwan (Araceae). *Mem. Coll. Agric. Nat. Taiw. Univ*., 31(1), 31.

Zhang, D. H., Wang, Q. P. & He, Z. G. 2010. *Amorphophallus muelleri*: A new promising star from low yield crop to quality high yield crop. *Res. Develop. Market*, 2, 013.

Zhang, D. H., Wang, Q. P., Duan, Z. B. & Mi, K. X. 2009. Mechanism of relay multi-seedling release of *Amorphophallus bulbifer* and its application in Southeast Asia. *Res. Develop. Market*., 25, 682–684.

Zhang, D., Wang, Q. & Srzednicki, G. 2010. Mechanism of staggered multiple seedling production from *Amorphophallus bulbifer* and *Amorphophallus muelleri* and its application to cultivation in Southeast Asia. *Trop. Agricu. Develop*., 54(3), 84–90.

Zhang, S. & Liu, Y. 2006. *Small Konjac could be a Big Industry in China New Countryside*. Jianshi, China: Hubei Press.

Zhang, S.-L., Liu, P.-Y., Sun, Y.-M. 1998. Artificial adjustment of flower period and hybridizing techniques of *Amorphophallus konjac*. *Acta Bot. Yunnanica*, X, 62–66.

Zhang, Y. Q., Xie, B. J. & Gan, X. 2005. Advance in the applications of konjac glucomannan and its derivatives. *Carbohyd. Polym*., 60, 27–31.

Zhao, J. 2010. Integrated production of purified konjac flour, King Mongkut's University of Technology Thonburi (PhD thesis). Bangkok, Thailand.

Zhao, J., Zhang, D., Srzednicki, G. Kanlayanarat, S. & Borompichaichartkul, C. 2009. Asexual reproduction of *Amorphophallus bulbifer* by low-cost artificial-induction technique. *Acta Hortic. (ISHS)*, 837, 351–358.

Zhao, J., Zhang, D., Zhao J., Srzednicki, G., Borompichaichartkul, C. & Kanlayanarat, S. 2010. Morphological and growth characteristics of *Amorphophallus muelleri* Blume: A commercially important konjac species. *Acta Hortic. (ISHS)*, 875, 501–508.

Zheng, X., Cheng, P., Ying, D., Yongning, Y., Chaozhu, Y. & Zhongli, H. 2013. Development of microsatellite markers by transcriptome sequencing in two species of *Amorphophallus* (Araceae). *BMC Genom*., 14, 490. https://doi.org/10.1186/1471-2164-14-490.

Zheng, X., Pan, C., Diao, Y., You, Y., Yang, C. & Hu, Z. 2013. Development of microsatellite markers by transcriptome sequencing in two species of *Amorphophallus* (Araceae). *BMC Genom*., 14(1), 490.

Zhong, L., Liu, E., Yang, C., Diao, Y., Harijati, N., Liu, J. & Jin, S. 2018. Gene cloning of a neutral ceramidase from the sphingolipid metabolic pathway based on transcriptome analysis of *Amorphophallus muelleri*. *PloS One*, 13(3), e0194863.

Zhou, Y., Yan, S., Lu, H. X. & Hu G. X. 2004. The cause and control method of konjac soft rot disease. *China Plant Protect*., 24, 17–20

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Mimicry of lichens and cyanobacteria on tree-sized *Amorphophallus* petioles results in their masquerade as inedible tree trunks

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We revisit a case of mimicry in *Amorphophallus* involving visual mimicry of lichens and colonies of cyanobacteria on their tree-trunk sized petioles. We investigate the entire genus for similar defensive coloration types and report a defensive leaf coloration strategy in several *Amorphophallus* spp. that involves mimicry, camouflage and plant-mimicking that results in defensive visual masquerade. We propose that the visual expression of lichen and cyanobacteria mimicry enables the huge and fleshy petioles to look like solid non-edible tree trunks, a classic case of masquerade, probably as defence against herbivores. The results are discussed in a phylogenetic and evolutionary context.

KEYWORDS: Araceae – camouflage – herbivory.

INTRODUCTION

Defensive plant coloration

Part of the diverse defensive arsenal of land plants against herbivores is anti-herbivory coloration and morphology (Lev-Yadun, 2016), including among many tactics mimicry, masquerade and camouflage. Defensive (anti-herbivory) mimicry in plants received little attention in the past, especially in comparison with defensive or aggressive mimicry in animals (Ruxton, Sherratt & Speed, 2004; Lev-Yadun, 2016; Quicke, 2017; Niu, Sun, & Stevens, 2018). Notable exceptions are host resemblance in Australian parasitic mistletoes (Barlow & Wiens, 1977; Canyon & Hill, 1997), host-tree leaf mimicry in the liana *Boquila trifoliolata* (DC.) Decne. (Gianoli & Carrasco-Urra, 2014), background matching leaf colours (Lev-Yadun, 2006, 2016; Niu *et al.*, 2014, 2018) and the proposed Batesian mimicry between two species from New Zealand [the chemically defended leaves of the model *Pseudowintera colorata* (Raoul) Dandy, which is visually mimicked by the leaves of the non-defended *Alseuosmia pusilla* Colenso; Yager, Schaefe & Gould, 2016].

Camouflage, 'potentially the best of all defences' (Lev-Yadun, 2016), enables the organism to become less detectable to a predator by means of crypsis, e.g. by countershading, disruptive coloration and/or background matching (e.g. Cott, 1940; Ruxton *et al.*, 2004; Merilaita & Lind, 2005; Niu & Sun, 2014; Niu *et al.*, 2014, 2018). A special case of background matching in plants consists of sticky trichomes, enabling the plant organism to be covered with small particles of the surrounding soil (Jürgens, 1996; Lev-Yadun, 2006).

The defensive strategy known as masquerade, or camouflage without crypsis, has, until recently, received little scientific attention regarding plants (Lev-Yadun, 2014, 2016; Skelhorn, 2015; Quicke, 2017). Masquerade by animals is a situation when prey, parasite or predator resembles inedible objects such as leaves, twigs, stones, bird-droppings or any

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other relevant and non-appealing object. Thus, unlike crypsis, a masquerading organism is fully visible and detectable, but under false identity. Masquerade in both animals and plants is often not easy to identify and specify because many cases of masquerade fall between crypsis and mimicry (Endler, 1981). For instance, Ruxton *et al.* (2004) brought up the question: when herbivores pass over a stone-mimicking plant, is it a case of crypsis via background matching, or of masquerade? Masquerade is usually considered to operate visually, although there are cases of chemical masquerade e.g. by caterpillars defending against predatory ants (Ruxton, 2009). Likewise, chemical masquerade in plants can consist of mimicking faeces or carrion odours for defence against herbivory (Lev-Yadun, Ne'eman & Shanas, 2009; Lev-Yadun, 2014, 2016). In recent years, studies in animal behaviour have revealed that successful masquerade depends not only on the quality of 'mimicry', but also on the context, i.e. when predators have not experienced the model previously or when the predators have experienced an inedible model (Skelhorn & Ruxton, 2011), or on the size and density of the defending animal (Skelhorn *et al.*, 2011; Skelhorn & Ruxton, 2013).

Various cases initially described as camouflage or other types of defence through mimicry (e.g. Wiens, 1978) were classified later as actual cases of masquerade. Lev-Yadun (2014) reviewed several types of cases of actual masquerade in plants, not defined as such when published, and proposed that there are two different types: (1) non-plant-mimicking defensive masquerade, in which plants look (or smell) like uninteresting objects to herbivores (looking like a stone or an animal, or smelling like droppings, carrion etc.); and (2) plant-mimicking defensive masquerade, in which plants or plant parts do not look appealing to herbivores; by not being green, by looking dead or old, by looking as if they are harbouring insects, already attacked, less nutritious etc. Defensive masquerade by plants may in many cases be non-exclusive, but it serves additional physiological and defensive functions or may operate simultaneously with other defences.

Mimicry of dead leaves is a classic type of masquerade in animals (Skelhorn, 2015; Quicke, 2017). Several related cases of masquerade mixed with camouflage and mimicry that were proposed to be cases of masquerade by Lev-Yadun (2014) were considered for decades to be typical cases of mimicry. These include dry grass mimicry (Wiens, 1978), dry branch mimicry (Wiens, 1978), stone mimicry (Wiens, 1978; Benson, 1982), soil and sand mimicry (Wiens, 1978; Lev-Yadun, 2006), host mimicry by mistletoes (Barlow & Wiens, 1977), mimicry of dead leaves (Stone, 1979; Fadzly *et al.*, 2009, 2016) and fruit mimicry by leaves (Groom, Lamont & Duff, 1994).

After the recognition of the partial overlap on the one hand and distinction on the other between mimicry, crypsis and masquerade (Endler, 1981; Allen & Cooper, 1985; Ruxton *et al.*, 2004; Skelhorn *et al.*, 2010a, b, c), Lev-Yadun (2014) proposed that the above cited cases should be classified not only as cases of mimicry or crypsis, but also as cases of masquerade.

In his review on defensive plant coloration, Lev-Yadun (2016) discussed the problem of conclusions drawn without experiments and pointed out that mimicry or related phenomena have often been described without such data. However, Lev-Yadun (2016) also stressed the need and the importance of accurate documentation of potential (defensive) plant coloration in order to stimulate the developing of better theoretical or experimental concepts.

LICHENS

Lichens are ubiquitous colonizers of a wide variety of substrates, including tree barks, rock and soil, often found forming dense crusts or carpets covering the surfaces they live on. They often form a dense mosaic of pale or dark spots on both tree trunks and twigs. In general, the size of crustose lichen colonies varies between a few mm and 10–20 cm or even more. Thalli of neighbouring lichens are often well delimited by pale or dark thin lines, especially when thalli of different species come into contact after radial expansion.

Tree trunks and branches may be totally covered by lichens, especially in wet habitats such as tropical and temperate rain forests (e.g. Aptroot, 2001). Crustose lichens (i.e. those that cover their substrate as a thin layer or crust) are by far the most dominant group in tropical rainforests. However, most large herbivores except for reindeer and caribou, which feed in winter times on the abundant lichen mats covering the arctic tundra soils, do not feed on lichens as their habitats usually provide enough more nutritious alternatives in the form of herbs and grasses or woody plant foliage.

AMORPHOPHALLUS

Amorphophallus Blume ex Decne. (Araceae) is a genus distributed throughout the Palaeotropics. The genus is divided into four subgenera, namely *Afrophallus* Hett. & Claudel, *Amorphophallus*, *Metandrium* Stapf and *Scutandrium* Hett. & Claudel (Claudel *et al.*, 2017). Its highest species diversity lies in South-East Asia, with 70% of its estimated 219 species (Boyce & Croat, 2011).

Non-plant-mimicking defensive visual masquerade and plant-mimicking defensive visual masquerade have already been reported in *Amorphophallus*, but without being denominated in terms of mimicry. Members of the *aphyllus* clade of subgenus *Afrophallus* possess

'leaflets which resemble grass and thus hide the plants from sight' (Claudel *et al.*, 2017) and as we propose here they constitute a broad case of plant-mimicry by employing morphologies and coloration that function as defensive visual masquerade. Furthermore, *A. aphyllus* (Hook.) Hutch. has an inflorescence that both visually and olfactorily resembles a pile of mammalian dung (Claudel *et al.*, 2017; Kite & Hetterscheid, 2017). This visual resemblance of dung corresponds to a non-plant-mimicking defensive visual masquerade *sensu* Lev-Yadun (2014) and the olfactory resemblance to a chemical non-plant-mimicking masquerade. The dung appearance and odour are likely intended to primarily attract pollinators (Claudel *et al.*, 2017). However, they may also serve as a defensive strategy and deter mammalian herbivores (Lev-Yadun *et al.*, 2009; Urru, Stensmyr & Hansson, 2011).

Amorphophallus spp. have a large underground tuber, which usually bears a single leaf. The leaf is composed of a petiole and a tripartite decompound lamina (Hetterscheid & Ittenbach, 1996; Ittenbach, 2003). The leaf usually lasts for one growing season and is replaced under ideal conditions by a larger leaf in the following growing season until the plant reaches maturity. The mature leaves may be differently coloured from the juvenile ones due to anisophylly, a phenomenon occurring in many aroids (Mayo, Bogner & Boyce, 1997). Although usually not pronounced, anisophylly is distinguishable in some *Amorphophallus* spp. (Claudel *et al.*, 2017; Liu *et al.*, 2017).

In giant *Amorphophallus* spp. such as *A. titanum* (Becc.) Becc. ex Arcangeli and *A. gigas* Teijsm. & Binnend., the petiole of mature leaves reaches heights of up to 6 m (McPherson & Hetterscheid, 2011) and resembles a lichen-covered tree trunk (Hejnowicz & Barthlott, 2005; Lobin *et al.*, 2007; McPherson & Hetterscheid, 2011). Figure 1 illustrates the dimensions of *A. titanum* (Fig. 1A, B), *A. decus-silvae* Backer & Alderw. (Fig. 1C) and *A. hewittii* Alderw. (Fig. 1D) petioles *in situ*. The resemblance to a small tree trunk had already been noted by Barthlott (1995): on the basis of his *in situ* observations of *A. prainii* Hook.f. he stated and illustrated that the diameter of the fleshy, easily damaged *Amorphophallus* petioles correlates with the size of tree saplings growing in the surrounding area. Moreover, Barthlott (1995) observed that the patterns on the petioles of *Amorphophallus* form a perfect imitation of lichens 'including growing zones and overlapping' similar to the lichens on the surrounding trees such as '*Chiodecton mycelioides*, *Dictyonema* and *Lepraria*-species'. Ittenbach (2003) added the observation that the bluish-green downward narrowing coloration on the petiole of *A. gigas* visually matches the typical layer of blue algae [cyanobacteria; Cavalier-Smith, 2002] commonly found on solid structures in humid environments. Again, the pattern leads to the visual impression of a solid tree trunk covered with living organisms, hiding its true nature as a large, fleshy and easily damaged petiole. Furthermore, Ittenbach (2003) also described lichen mimicry on the petiole of *A. taurostigma* Ittenb. & Hett., a Malagasy species.

Hejnowicz & Barthlott (2005) also investigated the mechanical and anatomical properties of the petiole and the cellular basis of the colour pattern in *A. gigas* and *A. titanum*. concluded that the imitation of a solid, lichen-covered tree trunk serves as a protection from herbivory and physical damage. Moreover, they found the coloration and pattern from *A. gigas* to be more complex compared to *A. titanum*, stating: 'The bottom portion of the petiole looks like a tree trunk with fine cracked bark in grey, brownish, and green tones, while in the upper areas, it looks like a young tree stem with whitish lichens'.

We investigate all the available *Amorphophallus* material in order to assess the *Amorphophallus* species that display petiolar mimicry. We categorize the different putative mimicry types and report a unique defensive coloration strategy. Furthermore, we investigate if the different mimicry types reflect in some aspect the phylogeny of *Amorphophallus* and we discuss tree masquerade in an ecological and evolutionary context.

MATERIAL AND METHODS

The Loki Schmidt Botanical Garden of the University of Hamburg houses one of the largest *Amorphophallus* collections, with > 250 living *Amorphophallus* accessions, representing some 100 species. We examined and documented as many living accessions as possible (see Appendix). Leaf material and/or photographs of the petioles have been deposited in the Herbarium Hamburgense (HBG). All photographs made and gathered over the last three decades by the first and the third authors were investigated for petiole patterns and were also deposited in the HBG, notably in the cases of species where leaf material was not available in cultivation or otherwise. Furthermore, photographs taken by other scientists and private collectors were also screened and deposited, notably from (in alphabetical order): Peter Boyce, Malaysia; Willem Eijer, the Netherlands; Alan Galloway, USA; Steve Jackson, Australia; Gijsbert Kortekaas, the Netherlands; David Prehsler, Austria; Mary Sizemore, USA; Elbert Wijaya, Indonesia. Thus, > 20 000 pictures, representing 136 *Amorphophallus* spp., were deposited in HBG. The photographic material represents an extensive documentation for the present investigation and a secure archive for future studies. Specimens

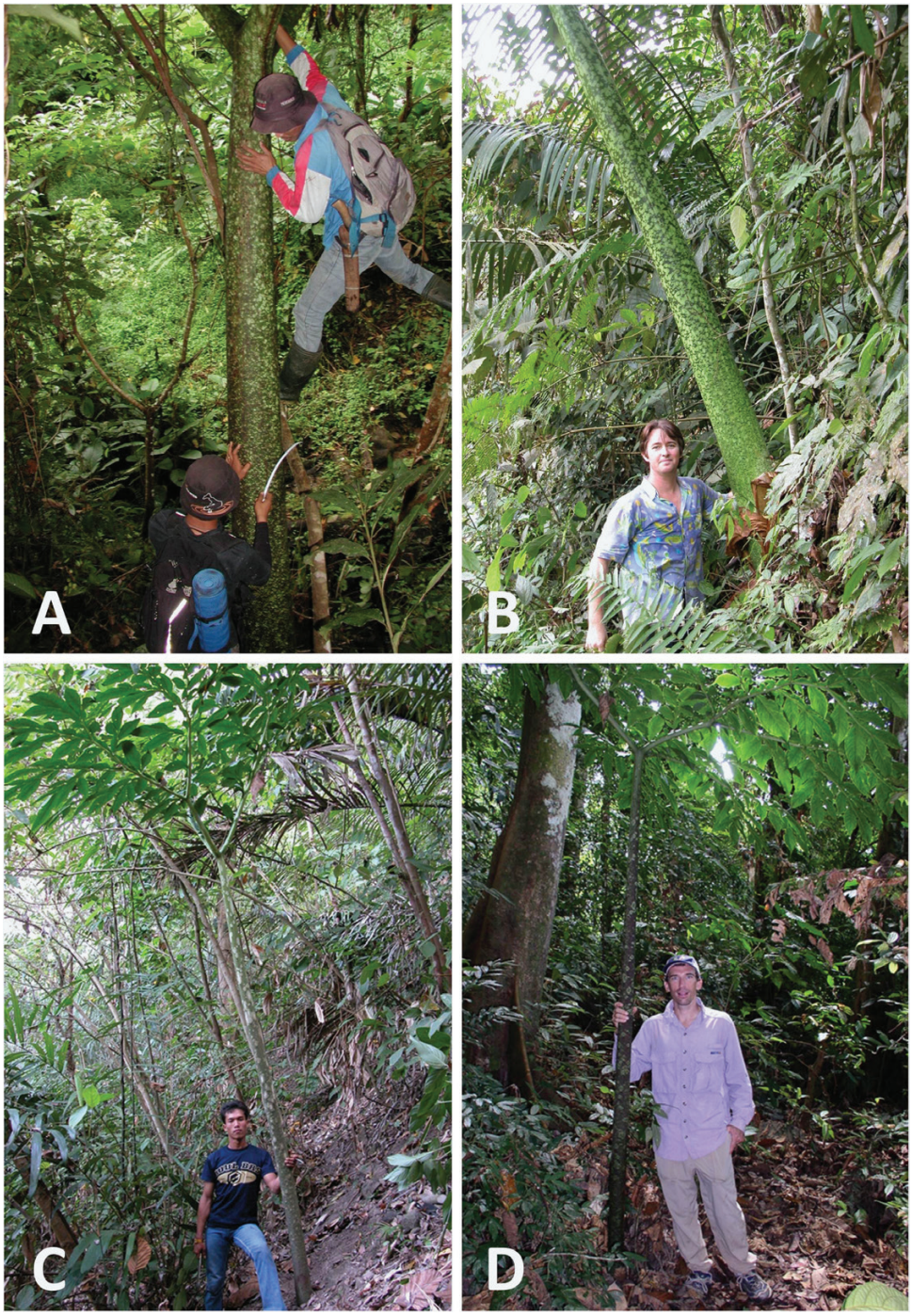

Figure 1. A, B, Giant petioles of *Amorphophallus titanum in situ*. C, Giant petioles of *A. decus-silvae in situ*. D, Giant petioles of *A. hewittii in situ*. Photographs: A, Yuzammi; B, C Troy Davis; D: Peter C. Boyce.

explicitly cited in the Appendix refer to individual plants growing in the Loki Schmidt Botanical Garden, to pictures of these individual plants or to specimens deposited in HBG or at the Naturalis Herbarium in Leiden (L). The remaining species were examined based on photographs only. Individuals of a given species displaying different patterns on the petiole were listed separately (see Appendix). The relevant literature was examined for petiole descriptions and pictures.

Presence or absence of patterns and coloration on the *Amorphophallus* petioles considered as putative mimicry

patterns was investigated. Only petioles exhibiting putative mimicry patterns were taken into account and categorized and coded. The categories are ranked in order of visual complexity and coded as characters from 0 = pattern absent or non-lichenoid, to 5 = most complex pattern type (see Appendix). Characters were plotted on the 50% majority-rule consensus tree of the Bayesian analysis published in Claudel *et al.* (2017) in order to reconstruct ancestral states using parsimony in Mesquite v.3.6 (Maddison & Maddison, 2018). In case a species contained differently patterned specimens, e.g. no pattern and lichenoid pattern, then the mimicry expressing specimen was used for the Mesquite analysis. Moreover, overall growing size is indicated (Figs 5, 6 and Supplementary Material) in addition to the species name using the addenda XS (species not exceeding 20 cm), S (species not exceeding 70 cm), M (species not exceeding 1.20 m), L (species not exceeding 1.70 m), XL (species not exceeding 2.20 m), XXL (species not exceeding 2.70 m) and XXXL (species exceeding 2.70 m). If not stated otherwise, the size information is based on personal observation by the first and the third author.

Species exhibiting no variable coloration at all or non-lichenoid patterns are also listed in the Appendix in order to indicate the total number of species analysed. Species categorized as having a non-lichenoid pattern include different coloration types and patterns; however, these are not taken into consideration in this investigation. The term 'lichenoid' used here refers to patterns generally reminiscent of lichens, but otherwise lacking specific distinguishing features, e.g. ornamentation. In contrast, mimicry refers here to patterns in which lichen thalli display characteristic traits of specific lichen-forming ascomycetes. Visual evaluation and determination of lichenoid and lichen mimicry patterns have been carried out by the eye of a lichenologist (last author). As lichens are living and growing symbiotic entities, we omitted precise size information of the mimicked lichens observed on a particular petiole. Since the size of the *Amorphophallus* petiole increases during the life cycle, precise measurements of the lichen mimicry spots would then be required for all life stages and for every investigated species. Although it would be of interest to document this development in detail for a particular species in a specific context or analysis, it is impossible in the context of the present investigation. Instead, we focused on the visual accuracy of the displayed mimicry with regard to the mimicked organism.

RESULTS

One hundred and thirty-eight species (63% of the species) of *Amorphophallus* were investigated (see Appendix). A few species, including *A. taurostigma*, *A. thaiensis* S.-Y.Hu and *A. variabilis* Bl., include individuals displaying different petiolar coloration types. For example, *A. variabilis* encompasses individuals displaying the cyanobacterial-*Cryptothecia* type and individuals with unicoloured petioles. Therefore, 138 species, representing 152 coloration types, are listed in the Appendix. Out of these 152 coloration types, 48 (31%) are categorized as unicolour, 47 (31%) as non-lichenoid pattern and 57 (38%) as lichenoid or mimicry.

Mimicry of several lichen types and of cyanobacterial colonies was identified on *Amorphophallus* petioles. The identified categories are lichenoid, *Pyrenula* type, *Graphis* type, *Cryptothecia* type, *Coenogonium* type, *Pertusaria* type and cyanobacterial layer type. Some *Amorphophallus* spp. display mimicry that involves several mimicry types on the same petiole. These were categorized accordingly, e.g. as mixed cyanobacterial-*Cryptothecia* type or mixed *Graphis*/*Pyrenula* type (see Appendix), and are listed in both categories. Lichenoid patterns were coded = 1. Two-dimensional single lichen mimicry types were coded = 2. Three-dimensional single lichen mimicry types were coded = 3. Mixed lichen mimicry types were coded = 4. The cyanobacterial layer type combined with *Cryptothecia* type was coded = 5 (see Appendix). The complete analysis is provided in Supplementary Material and two subgenera are presented separately as figures, namely subgenus *Metandrium* (Fig. 5) and subgenus *Amorphophallus* (Fig. 6).

Lichenoid type

Colour patterns of this category are reminiscent of lichens, but without specific features, i.e. *Amorphophallus* petiole patterns consist of mixed pale and/or dark markings of variable sizes and sometimes of irregular shapes. These coloration patterns lack further structures or ornamentation and thus resemble a non-specific, mixed lichen cover. Altogether, they are roughly similar to the patterns exhibited on shaded rainforest trees. Even if non-specific, the patterns can usually be divided into two main lichen groups, namely *Graphis* and *Pyrenula*, and are categorized here (see Appendix) accordingly as, for example, lichenoid-*Graphis* type or lichenoid-*Pyrenula* type.

Amorphophallus spp. expressing a lichenoid pattern are *A. declinatus* Hett., *A. dunnii* Tutch., *A. ferruginosus* A.Galloway (Fig. 3D), *A. galbra* F.M.Bailey, *A. henryi* N.E.Br., *A. hildebrandtii* (Engl.) Engl. & Gehrm., *A. hottae* Bogn. & Hett., *A. koratensis* Gagn., *A. manta*, *A. muelleri* Bl., *A. ochroleucus* Hett. & V.D.Nguyen, *A. paeoniifolius* (Dennst.) Nicolson, *A. putii* Gagn., *A. ranchanensis* Ipor, Tawan, Simon, Meekiong & Fuad, *A. rostratus* Hett., *A. stuhlmannii* (Engl.) Engl. & Gehrm., *A. taurostigma*, *A. thaiensis*,

A. titanum, *A. tuberculatus* Hett. & V.D.Nguyen, *A. variabilis* and *A. yunnanensis* Engl.

PYRENULA TYPE

Pyrenula Ach. is a large, mainly tropical lichen genus. The thalli have an olive to brownish colour, sometimes speckled with numerous, tiny pale dots, often a species-specific feature. The fruit bodies of *Pyrenula* are small (0.2–2.0 mm) and resemble circular blackish warts. Fruit bodies are present only in mature lichen thalli and their presence adds to the often-characteristic external appearance of a particular species.

The *Amorphophallus* petiole pattern, with small, olivaceous marks (0.5–2.0 cm), resembles lichen thalli with scattered dark spots inside these marks that resemble the blackish perithecial fruit bodies of *Pyrenula* or *Anthracothecium* Hampe ex A.Massal. These are usually 0.4–2.0 mm in size (Aptroot, 2012). They are sometimes found with additional fine whitish maculation resembling certain *Pyrenula* spp. including *P. concatervans* (Nyl.) R.C.Harris, *P. quassiaecola* Fée and *P. subcylindrica* Jagadeesh & Upreti. Investigated *Amorphophallus* spp. bearing this type of pattern on their petioles are *A. bulbifer* (Roxb.) Bl., *A. elatus* Ridl., *A. gomboczianus* Pic.Serm., *A. kiusianus* (Makino) Makino, *A. lanuginosus* Hett., *A. laoticus* Hett., *A. macrorhizus* Craib, *A. pilosus* Hett. (Fig. 3C) and *A. prainii*.

GRAPHIS TYPE

The script lichens form a large group of unrelated species that share at least the presence of usually dark coloured, rune-like fruit bodies that evolved several times independently among the lineages of lichen-forming ascomycetes (McLaughlin & Spatafora, 2015). The observed petiole patterns resemble species of *Graphis* Adans., *Phaeographis* Müll.Arg. and other script lichens including *Arthonia* Ach. *Opegrapha* Ach., *Enterographa* Fée of the closely related Arthoniaceae and Opegraphaceae. These lichens are usually pale whitish or greyish, producing the characteristic rune-like fruit bodies in the centre of the thallus.

Patterns of this type of mimicry on the *Amorphophallus* petioles are usually roundish to ellipsoid spots of 0.5–2.0 cm in length, pale whitish, with conspicuous to inconspicuous, dark reticulate or maculate central painting, sometimes strikingly resembling lirellae, the rune- or star-like fruit bodies of the script lichens that usually measure up to 2 mm, but more rarely 5–10 mm in length (Lücking, Archer & Aptroot, 2009). The shape, size and appearance of fertile script lichens are perfectly mimicked by petioles of some *Amorphophallus* spp., including *A. kiusianus* (Makino) Makino (Fig. 3A) and *A. pilosus* (Fig. 3C).

Investigated *Amorphophallus* species bearing *Graphis* type mimicry are: *A. adamsensis* L.M. Magtoto *et al.*, *A. atroviridis* Hett., *A. bufo* Ridl., *A. bulbifer*, *A. croatii* Hett. & A. Galloway, *A. cruddasianus* Prain ex Engl., *A. declinatus*, *A. elatus*, *A. henryi*, *A. kiusianus*, *A. lanuginosus*, *A. laoticus*, *A. longicomus* Hett. & Serebryanyi, *A. macrorhizus*, *A. manta* Hett. & Ittenbach, *A. napiger* Gagn., *A. opertus* Hett., *A. paeoniifolius*, *A. pilosus*, *A. prainii* and *A. yunnanensis*.

CRYPTOTHECIA TYPE

Cryptothecia Stirt. and other lichens of similar appearance such as *Herpothallon* Tobler, *Chiodecton* Ach. and *Dichosporidium* Pat. are relatively large lichens, several centimetres in size, which are common in the tropics. The thalli are usually pale whitish or faintly greenish, usually surrounded by a prothallus that is of a conspicuously different colour, either paler or darker. *Amorphophallus* petioles expressing this type of mimicry bear patterns of relatively large, roundish to ellipsoid marks 1–5 cm long with a conspicuously paler or darker margin and a differently coloured centre. They resemble tree trunks colonized by a variety of tropical rain forest lichen species of genera such as *Cryptothecia*, *Chiodecton*, *Herpothallon* and allies having a ±distinct pale or coloured prothallus surrounding the proper thallus. *Amorphophallus* spp. exhibiting *Cryptothecia* type mimicry include *A. annulifer* Hett., *A. beccarii* Engl., *A. borneensis* (Engl.) Engl. & Gehrm., *A. boyceanus* Hett., *A. bufo*, *A. gigas* (Fig. 2A, B), *A. hewittii* (Fig. 2C), *A. lambii* Mayo & Widjaja, *A. manta*, *A. sagittarius* Steen. and *A. variabilis*.

COENOGONIUM TYPE

Coenogonium Ehrenberg is a widespread and species-rich lichen genus in the tropics, commonly found in the understory of rainforests. *Coenogonium* contains purely crustose species (formerly placed in *Dimerella*; Kauff & Lutzoni, 2002) and peculiar species with a ±console-like growth with half to fully circular thalli raised above the bark surface (*Coenogonium s.s.*). The greenish-yellow coloration, the thalli size of usually 1–5 cm and the three-dimensional, console-like appearance is nearly perfectly mimicked by petioles of *A. dactylifer* Hett. (Fig. 2D). *Amorphophallus dactylifer* is the only species expressing that specific lichen mimicry.

PERTUSARIA TYPE

Pertusaria DC. is a large and widespread genus of crustose lichens. Many *Pertusaria* spp. produce numerous wart-like fruit bodies that may eventually cover large portions of the thallus of the lichen.

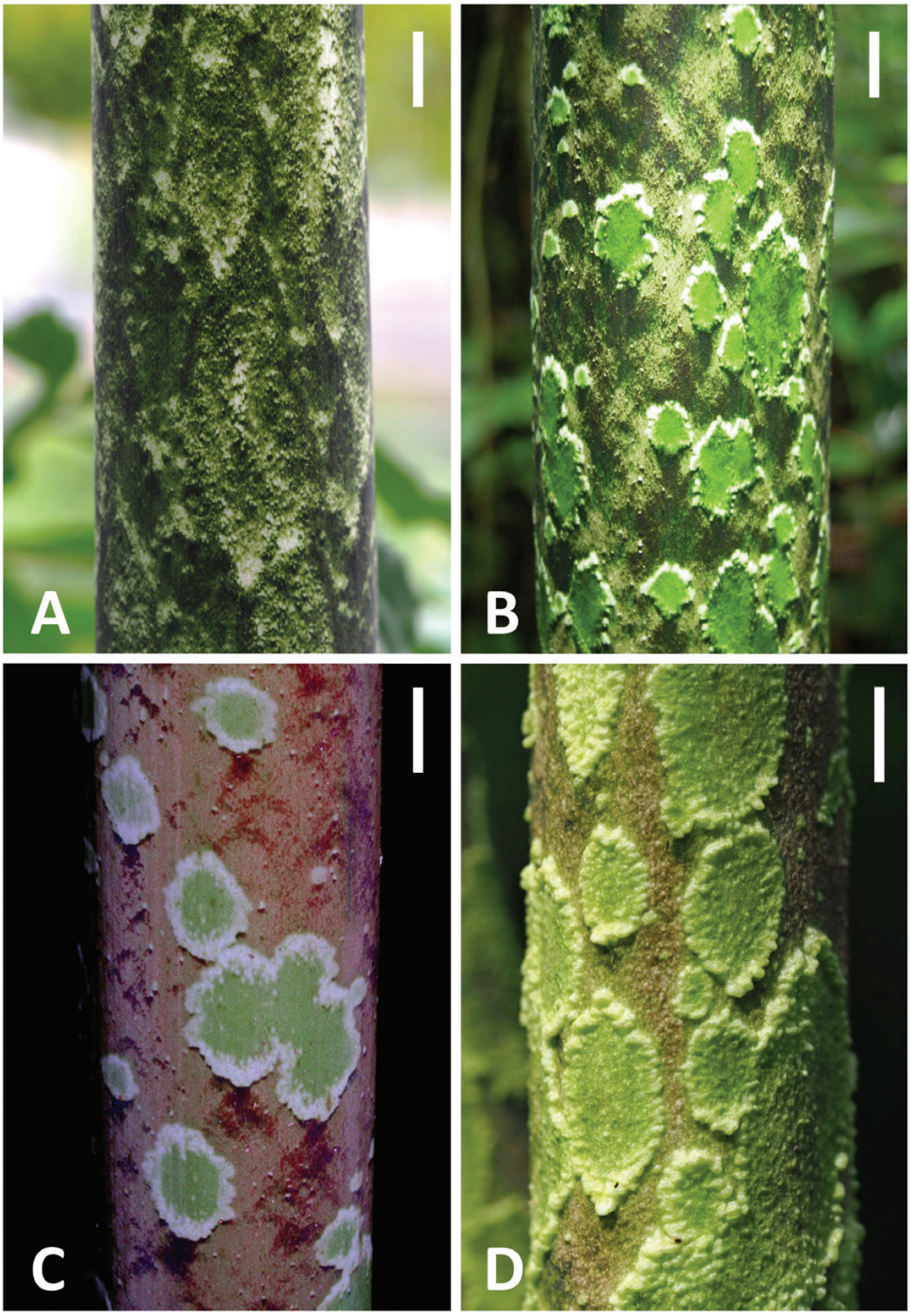

Figure 2. A, B, *Amorphophallus gigas*, cyanobacterial-layer type without and with accompanying lichen mimicry of the *Cryptothecia* type. C, *A. hewittii* displaying *Cryptothecia*-type lichen mimicry on a reddish layer. D, *A. dactylifer* displaying three-dimensional *Coenogonium*-type lichen mimicry. Scale bars = 1 cm. Photographs: A, D, Cyrille Claudel; B, W.L.A. Hetterscheid; C, Peter C. Boyce.

The *Amorphophallus* petiole exhibits a coloration pattern with small, pale whitish marks of pronounced warty to rugose texture, resembling the slightly to distinctly elevated, often almost hemispherical fruit warts of *Pertusaria* spp., which are usually 0.5–1.5(–2.0) mm in size (Archer, 2004). Examples include *P. cicatricosa* Müll.Arg. and *P. thwaitesii* Müll.Arg.

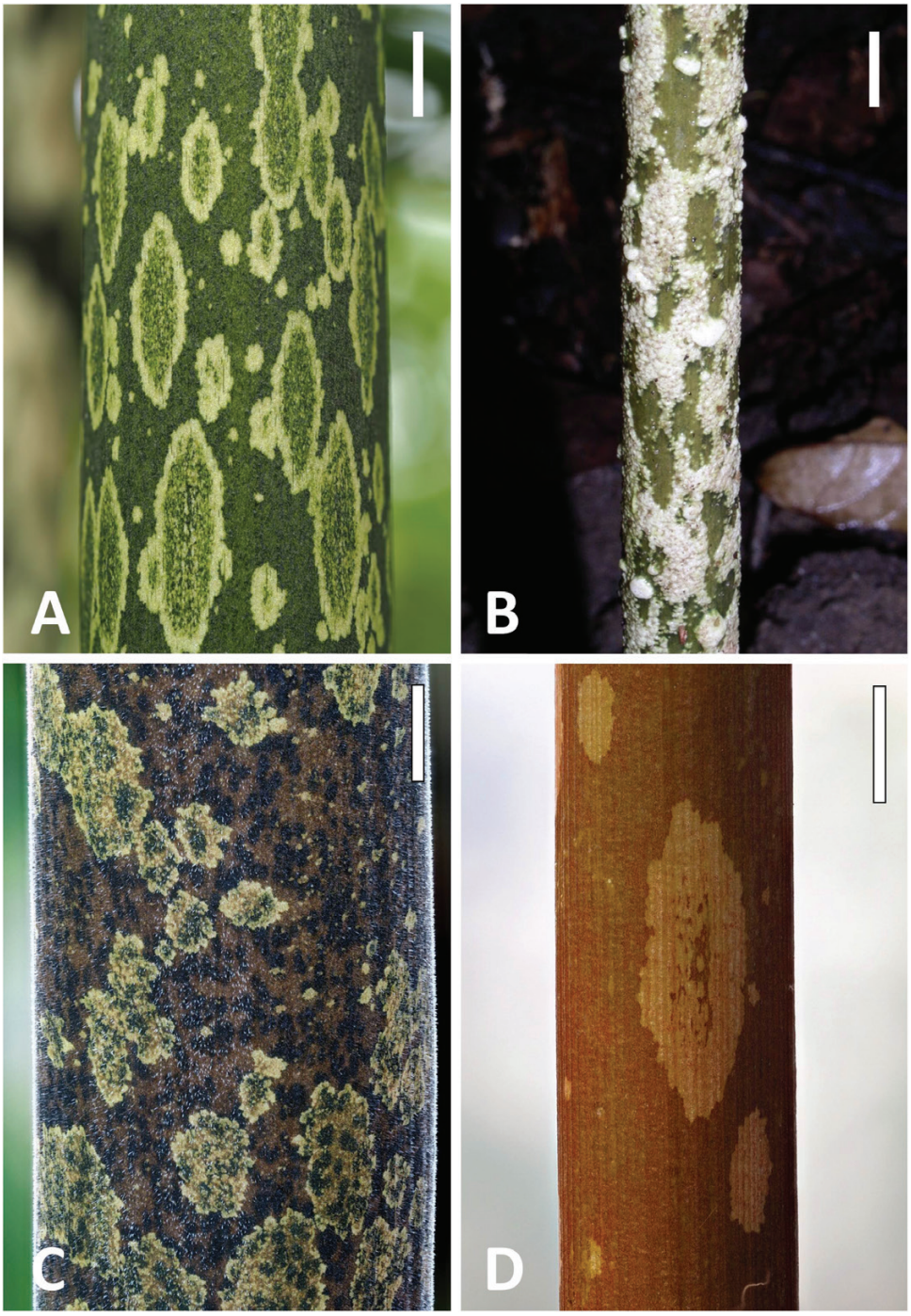

Figure 3. A, *Amorphophallus kiusianus,* displaying *Graphis* mimicry on the petiole. B, *A. infundibuliformis*, displaying *Pertusaria* mimicry. C, *A. pilosus* mixed lichen mimicry on the petiole including the *Pyrenula* type. D, *A. ferruginosus* displaying a simple lichenoid-*Graphis* type pattern. Scale bars = 1 cm. Photographs: Cyrille Claudel.

The verrucose or rugose surface texture of *A. infundibuliformis* Hett., Dearden & A.Vogel in conjunction with a pale coloration, gives a strikingly similar appearance to the real lichens. In addition, the pale spots of *A. infundibuliformis* may mimic the punctiform or capitate soralia, a vegetative propagating structure widespread in species of *Pertusaria* but also found among members of Thelotrematales. Only *A. infundibuliformis* displays this coloration type (Fig. 3B).

Cyanobacterial layer type

Petioles are unevenly coloured, often bluish-green and/or brownish-red. The downward narrowing patterns on the petiole resemble colonies of cyanobacteria; sometimes the patterns are seemingly shaped by seeping water, as if running down the stem of a tree (Fig. 2A–C). The cyanobacterial layer type is usually combined with lichenoid patterns or lichen mimicry in various degrees. In some cases, the cyanobacterial layer imitation is prominent (Fig. 2A), even exclusive, whereas in other cases, the lichenoid pattern or lichen mimicry constitutes the visually dominant part, superimposed on a cyanobacterial imitating layer (Fig. 2B, C). Moreover, as noted by Hejnowicz & Barthlott (2005) for *A. gigas*, the cyanobacterial layer can contain brownish pigmentation, creating the visual illusion of a tree bark shimmering through the cyanobacterial layer. *Amorphophallus* spp. displaying the cyanobacterial layer type include *A. annulifer*, *A. beccarii*, *A. borneensis*, *A. boyceanus*, *A. gigas* (Fig. 2A, B), *A. hewittii* (Fig. 2C), *A. lambii*, *A. sagittarius* and *A. variabilis*.

DISCUSSION

Pitfalls and problems

First of all, we are aware that we cannot provide experimental insight that could back up our observations by actual defence from actual herbivores. Furthermore, we do not have concrete knowledge about mammalian *Amorphophallus*-consuming or trampling herbivores. As a consequence, we know nothing about their visual perception, a crucial component of visual deception. We therefore rely on the assumption that if the displayed lichen mimicry is visually convincing to the eye of a trained lichenologist, then it is likely to deceive any mammalian eye. We therefore only describe the putative defensive anti-herbivory coloration. Despite these shortcomings, we compiled, investigated and deposited all the *Amorphophallus* material we could acquire for the following reasons.

1. The lichen imitations of several species are just too striking to be ignored (Figs 1–4). We are convinced that the accuracy of the visual lichen mimicry and the imitation of lichen-covered young tree saplings are significant enough to deserve a proper documentation and discussion.
2. Depositing all the accessible *Amorphophallus* material provides ample resources for further studies. Other types of camouflage and masquerade elements in this genus wait to be unmasked, such as the grass-like masquerade of the species of the *A. aphyllus* clade or the colour changes in the lamina of *A. bufo* (Liu *et al.*, 2017) during ontogeny.
3. Finally, we follow the arguments made by Lev-Yadun (2016): 'However, these imperfect explanations still allow progress on the issue of defensive plant coloration and may stimulate thinking by other scientists who may first document aspects of plant coloration that have not been documented, and second, develop even better theoretical or experimental ideas than the ones that exist today'.

Lev-Yadun (2016) exposed the problem of inaccuracy and neglect of plant descriptions in the literature regarding plant coloration and colour patterns. This is also true for *Amorphophallus*. The descriptions are often generalized, something that is not surprising, as an accurate description of the complex patterns presents a real challenge. However, recent treatments and descriptions of *Amorphophallus* include drawings, and especially pictures, which provide some relevant information (e.g. Hetterscheid & Peng, 1995; Hetterscheid & Ittenbach, 1996; Hetterscheid, Ittenbach & Bogner, 1999; Ittenbach, 2003; Hetterscheid, 2006; Boyce, Ipor & Hetterscheid, 2010; Hetterscheid & Claudel, 2014; Yuzammi-Kurniawan *et al.*, 2017).

Cyanobacterial layer type

Although *Amorphophallus* petioles displaying the cyanobacterial layer type express variation in the pigmentation and shape of the patterns, the overall phenomenon is basically similar among the species. The coloration and its pattern on the petioles lead to the visual resemblance of tree trunks colonized by cyanobacteria or by similar microorganisms. The appearance of the petiole is often bluish-green and/or brownish-red (Fig. 3A–C). The coloration is often unevenly distributed. It appears to be washed out, slightly blurred or smudgy, as if the cyanobacterial colonies have been shaped by rain and seeping water. In humid habitats, cyanobacteria and lichens are commonly found growing together on tree trunks. Similarly, the cyanobacterial layer mimicry type is usually combined with lichenoid patterns or lichen mimicry of the *Cryptothecia* type in various degrees. Figure 2A, B shows some variation in the pattern and coloration of *A. gigas* petioles. In some cases the mimicry of a cyanobacterial layer type constitutes the main defensive coloration element and is accompanied by few lichen-like patterns (Fig. 2A). In other specimens or species, the cyanobacterial layer is present but only forms a background layer for predominant lichen mimicry (Fig. 2B, C). According to Hejnowicz and Barthlott (2005), who described the cyanobacterial layer type in detail for *A. gigas*, the interspersed brownish pigmentation simulates the tree bark shining through the cyanobacterial

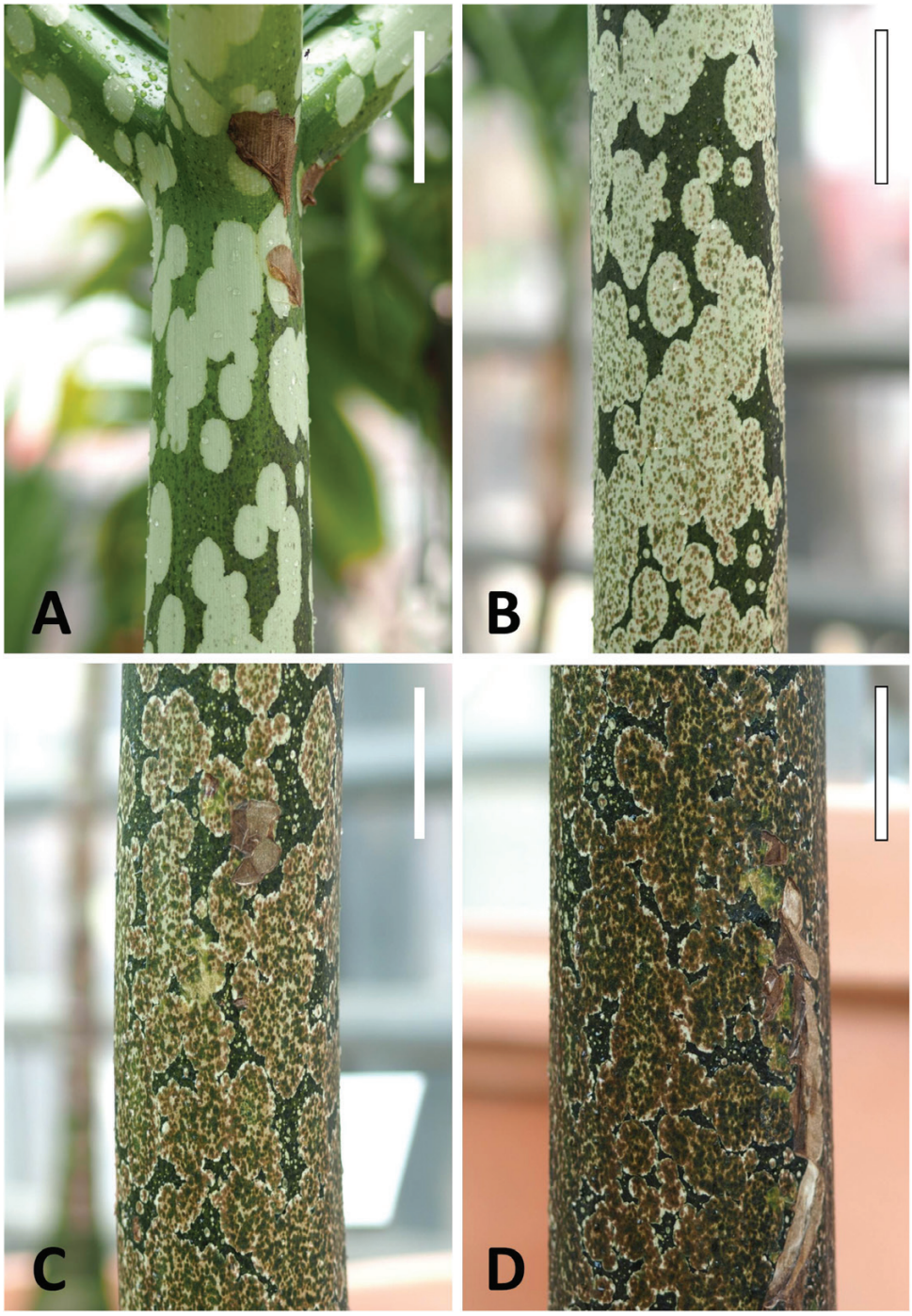

Figure 4. A–D, Petiole from *A. prainii* from top to bottom. A, Highest section of the petiole, lichen imitations are whitish, roundish and spaciously arranged. B–D, The density and complexity, including fruit bodies, increases from top to bottom of the petiole. Scale bars = 5 cm. Photographs: Cyrille Claudel.

layer. This signifies that these *Amorphophallus* spp. mimic tree bark, lichens and cyanobacterial colonies on one petiole. In other words, three unrelated groups of organisms are mimicked on one petiole and result in a very elaborate tree-trunk masquerade.

LICHEN MIMICRY

Some aspects and/or combinations of elements of the displayed visual lichen mimicry are more pronounced in some *Amorphophallus* spp. than in others. For example, the species included in the lichenoid type

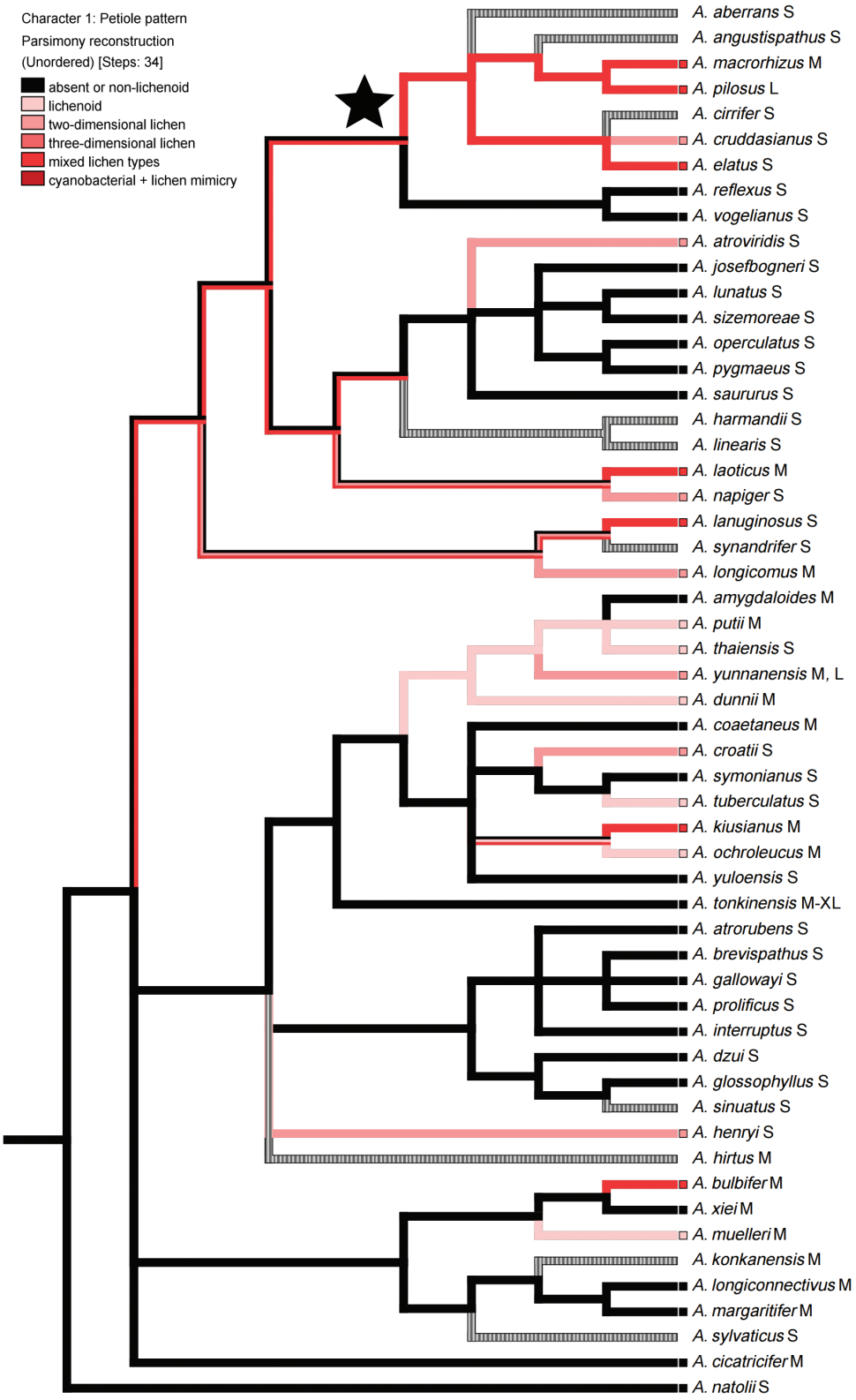

Figure 5. Subgenus *Metandrium*. Petiolar pattern mimicry types ranked in order of complexity ranging from 0 = pattern absent to non-lichenoid to 5 = most complex mimicry type (see Appendix) mapped on the phylogenetic tree reproduced from Claudel *et al.* (2017). Colour legend is provided within the tree. Petiolar pattern of grey shaded clades is not known or lacks

exhibit simple lichen patterns (e.g. *A. ferruginosus*; Fig. 3D), whereas species such as *A. dactylifer* (Fig. 2D) present what looks like an amazingly complex and accurate lichen cover, including the mimicry of three-dimensional thalli. Some *Amorphophallus* spp., including *A. infundibuliformis* (Fig. 3B) and *A. yunnanensis*, exhibit only one lichen mimicry type, whereas other species, including *A. pilosus* and *A. prainii* (Figs 3C, 4A–D) mimic several lichen taxa. In addition, the lichen taxa may be superimposed on the mimicry of a cyanobacterial layer as in, for example, *A. borneensis* and *A. gigas* (Fig. 2A, B). However, the overall phenomenon is basically similar among all the *Amorphophallus* spp. displaying petiolar lichen mimicry, and we therefore describe the lichen mimicry from a general perspective. We do not take into account the patterns displayed on the spathes, peduncles and cataphylls of *Amorphophallus* spp. Nevertheless, we want to clarify that in the majority of cases the displayed pattern type on the spathes, peduncles or cataphylls is similar to that on the petiole, but with different intensities. As a general rule, the most distinct and accurate pattern is displayed on the petiole. The pattern displayed on the peduncle is in most cases less complex than the one on the according petiole. The pattern displayed on the spathes is always less complex than the one on the according petiole. The same applies to the cataphylls, which usually present a similar or a simplified version of the pattern expressed on the petioles. However, there are exceptions – such as some specimens of *A. paeoniifolius* and *A. titanium* – that exhibit lichen patterns on the cataphylls, which are more complex than the patterns presented on the petiole. Moreover, we do not take into account petiolar variability in this investigation. Some of the investigated species, e.g. *A. variabilis* and *A. taurostigma*, contain differently patterned specimens (see Appendix). Petiolar coloration in these species ranges from 'absent' to 'complex mimicry'. This implies that putatively every species contains differently patterned specimens that necessitates further investigations on the species and population level of every species.

Lichens are slow-growing symbiotic entities, and consequently the lichen community will increase in complexity/diversity and density over time and in accordance with the growth of the host sapling. Older saplings will naturally display a denser and more variable lichen cover, giving shelter to an increasing number of lichen species. The petioles of lichen-mimicking *Amorphophallus* spp. develop in perfect accordance with the typical lichen succession on surrounding saplings. Petioles on juvenile *Amorphophallus* plants display less complex lichen cover mimicry, with relatively small lichen colonies. With the increasing size of the following petioles of the maturing plant, the mimicked lichen cover becomes more and more complex and pronounced; the pigmentation becomes more intense and usually darker, thus imitating growth. In some cases it culminates in the introduction of new elements, such as the introduction of fruit bodies of the mimicked lichen, as in the case of *A. prainii* (Fig. 4A–D). Likewise, the *Coenogonium* elements displayed by *A. dactylifer* (Fig. 2D) are nearly even on petioles of juvenile plants and become larger and distinctly three-dimensional on the subsequently larger petioles. Thus, the size, degree and visual intensity of the displayed lichen colonies correlate with the increasing size of the subsequent *Amorphophallus* petioles of maturing plants. A small petiole displays fewer and less intensely coloured lichen colonies than a larger *Amorphophallus* petiole of the same specimen. A similar differentiation can be noticed between the upper and more slender part of a petiole compared to the basal and thicker part of the same petiole. The basal diameter of the petiole in large species is roughly twice as large as the apical diameter (Hejnowicz & Barthlott, 2005), which translates into a denser and more complex lichen cover in the basal part, as illustrated for *A. prainii* in Fig. 4A–D. The increasing complexity of the lichen cover of a subsequently larger *Amorphophallus* petiole is thus underlined by an increasing expansion and differentiation of the lichen colonies from top to bottom of the petiole. This visual representation is in accordance with the lichen cover of the surrounding saplings. The lichen colonies growing in the basal zone of a stem are more compressed and overlapping, and they bear more fruiting bodies since they represent the oldest lichen colonies.

In summary, the petiolar mimicry of *Amorphophallus* is not restricted to the accurate mimicry of lichen taxa; it also mimics the different stages of lichen colonization on growing tree saplings. In other words, different lichen taxa as well as their succession throughout time are mimicked, give a realistic masquerade of tree trunks typical to their habitats.

Several visual signals are sent out by the lichen-mimicking *Amorphophallus* spp. As suggested by Hejnowicz & Barthlott (2005), running animals might want to avoid a collision with what appears to be a hard, solid tree. Moreover, the tree appearance promises to make browsing a useless or unpleasant, if not toxic, experience for several reasons. The hard bark of many trees has a low nutritive value, and lichens themselves are potentially poisonous or

substantial back-up. Star icon identifies the clade containing *A. pilosus* mentioned in text. Full analysis of the genus is provided in Supplementary Material. Addenda behind the species name indicate plant size (see text).

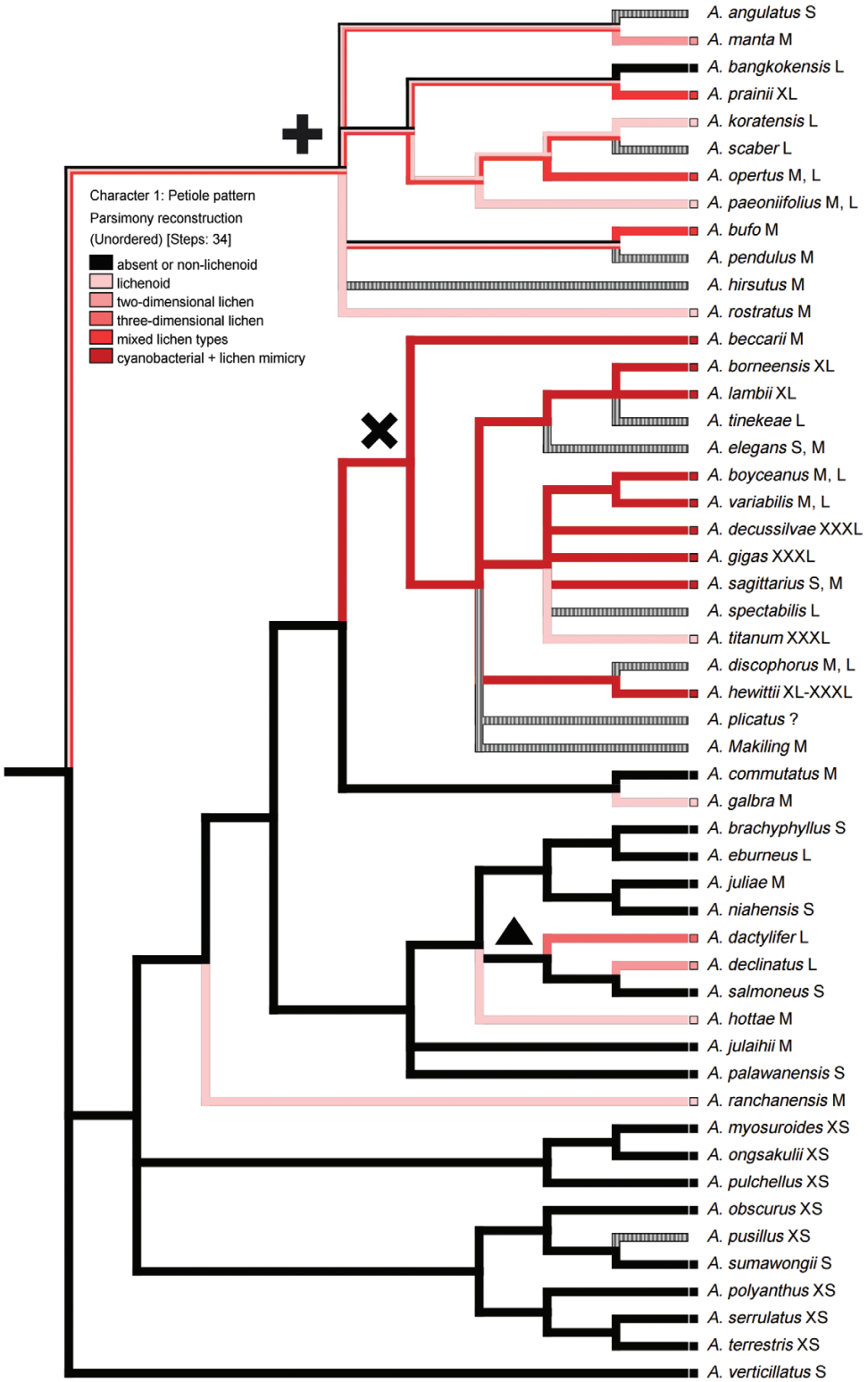

Figure 6. Subgenus *Amorphophallus*. Petiolar pattern mimicry types ranked in order of complexity ranging from 0 = pattern absent to non-lichenoid to 5 = most complex mimicry type (see Appendix) mapped on the phylogenetic tree reproduced from Claudel *et al.* (2017). Colour legend is provided within the tree. Petiolar pattern of grey shaded clades is not known or lacks substantial back-up. Cross icon identifies the *Paeoniifolius-Manta*-clade (see text), tilted cross identifies

at least hard to digest, as they contain significant amounts of secondary metabolites. These may include stictic, norstictic, salacinic, protocetraric, gyrophoric, confluentic and psoromic acids and atranorin; lichen xanthone also occurs in some species of *Graphis*, *Pertusaria* and *Pyrenula* (Archer, 2004; Lücking *et al.*, 2009; Singh & Sinha, 2010).

As if not already complex enough, the defensive coloration works at different distances, similar to the question raised by Ruxton *et al.* (2004) concerning stone-mimicking *Lithops* N.E.Br. A close view of the *Amorphophallus* petiole reveals a stunning case of visual mimicry, which consists of an accurate mimicry of various lichen taxa, and in addition the mimicry of their natural ontogeny and succession along a typical tree trunk. Perceived from a further distance, the *Amorphophallus* leaf with its umbrella-like lamina looks like a lichen-covered sapling, a small tree. The 'trunk' can reach several metres in height for large species and displays a lichen and cyanobacteria cover that is in perfect accordance with the surrounding real tree saplings. The picture is completed by the often-elliptical leaflets of the *Amorphophallus* lamina with their acute to acuminate tips, imitating real leaves on sapling trees. From this perspective, the defensive coloration works as plant-mimicking defensive visual masquerade, as the large, fleshy and easily damaged *Amorphophallus* leaf is perceived as a solid, non-edible woody tree trunk. Last but not least, when perceived from a further distance, the *Amorphophallus* 'tree' disappears by means of camouflage, as it becomes indiscernible, appearing as a tree among many other trees (Fig. 1A–D).

Phylogenetic and evolutionary considerations

Based on the 50% majority-rule consensus tree of the Bayesian analysis presented in Claudel *et al.* (2017) and referenced to in Kite & Hetterscheid (2017), the ancestral state reconstruction reveals that only a few and comparatively simple lichen mimicries are displayed by species of subgenus *Afrophallus* and no species of subgenus *Scutandrium* (see Supplementary Material). Lichen-mimicking *Amorphophallus* spp. in subgenus *Afrophallus* are *A. gomboczianus*, *A. hildebrandtii*, *A. stuhlmannii* and *A. taurostigma.* However, even if the occurrence of mimicry is low in subgenus *Afrophallus*, mimicry is nevertheless displayed in three subgenera of *Amorphophallus*, suggesting that petiolar defensive coloration has played a role in the evolution of the genus from an early stage. However, most cases of mimicry are displayed by species of subgenera *Metandrium* (Fig. 5) and *Amorphophallus* (Fig. 6). The cyanobacterial and lichen mimicry have reached their full potential in the Asian lineages, involving the mimicry of different types and stages of lichen populations, with or without an underlying mimicked cyanobacterial layer on top of the 'tree bark'.

The obvious question is whether the occurrence of lichen mimicry reveals a phylogenetic trend. Kite & Hetterscheid (2017) stated that two phylogenetic trends can be observed with regard to odour types in *Amorphophallus*, ranging from odour types 'mostly occurring in related species to apparently being co-evolved in unrelated species'. The situation is similar in regard to the lichen mimicry discussed here. Lichen-mimicking species are mainly distributed throughout subgenera *Amorphophallus* and *Metandrium*. Some clades contain solely lichen-mimicking species, whereas other clades include lichen-mimicking species and species of different coloration types. For example, subgenus *Amorphophallus* contains a well-supported clade (Fig. 6; triangle icon above the branch) consisting of the Philippine species *A. dactylifer* and the sister species pair of *A. declinatus* and *A. salmoneus* Hett. *Amorphophallus dactylifer* displays one of the most elaborate lichen mimicry cases, involving mimicry of three-dimensional *Coenogonium* colonies (Fig. 2D), whereas *A. declinatus* displays either a lichenoid pattern, or lichen mimicry of the *Graphis* type. In contrast, *A. salmoneus* has a plain green petiole.

Furthermore, the clade (Fig. 5; star icon above the branch) in subgenus *Metandrium*, consisting of *A. reflexus* Hett. & A.Galloway and *A. vogelianus* Hett. & H.Billenst., is sister to the clade containing *A. aberrans* Hett., *A. angustispathus* Hett., *A. macrorhizus*, *A. pilosus*, *A. cirrifer* Stapf, *A. cruddasianus* and *A. elatus* (Claudel *et al.*, 2017). The first two species have unicolorous (*A. reflexus*) or nearly unicolourous (*A. vogelianus*) petioles, whereas the latter display lichenoid patterns or lichen mimicry of the *Graphis* type.

The *Paeoniifolius–Manta*-clade (Fig. 6; cross icon above the branch) of subgenus *Amorphophallus* containing *A. angulatus* Hett. & A.Vogel, *A. bangkokensis* Gagn., *A. bufo*, *A. hirsutus* Teijsm. & Binnend., *A. koratensis*, *A. manta*, *A. opertus*, *A. paeoniifolius*, *A. pendulus* Bogn. & Mayo, *A. prainii*, *A. rostratus* and *A. scaber* Serebryanyi & Hett. (Claudel *et al.*, 2017) contains mainly species that display distinct petiole patterns. Most of these consist of lichenoid patterns or accurate lichen mimicry of the *Graphis* type with the exception of

the clade containing the large Indonesian species (see text) and triangle identifies the clade containing *A. dactylifer* (Fig. 2D) the sole *Coenogonium* mimicking species. Full analysis of the genus is provided in Supplementary Material. Addenda behind the species name indicate plant size (see text).

some specimens of *A. bufo* and *A. manta* that also may display patterns of the *Cryptothecia* type. Some also include blackish dots that may serve as ant mimicry (Liu *et al.*, 2017). However, *A. bangkokensis* displays small dark spots not reminiscent of any lichen on an otherwise brownish petiole, combined with pale stripes. This is a unique character combination in the *Paeoniifolius–Manta* clade and *A. bangkokensis* is the sister species to *A. prainii* that again displays one of the most sophisticated visual lichen mimicry in the genus, a mixed *Graphis–Pyrenula* mimicry.

Similarly, the mimicry of a cyanobacterial layer, with or without accompanying lichens of the *Cryptothecia* type, is a characteristic trait of the whole clade (Fig. 6; tilted cross icon above the branch) of subgenus *Amorphophallus*, which contains mainly Malaysian and Indonesian species such as *A. beccarii*, *A. borneensis*, *A. lambii*, *A. tinekeae* Hett. & A. Vogel, *A. variabilis*, *A. decus-silvae*, *A. gigas*, *A. sagittarius*, *A. titanum*, *A. discophorus* Backer & Alderw. and *A. hewittii* (Claudel *et al.*, 2017). Only *A. titanum* seemingly differs in displaying comparatively simple lichen mimicry on a basically green petiole. Nonetheless, mature plants of *A. titanum* also display a bluish darkening of the basal part of the petiole, which can be interpreted as a visual equivalent of a cyanobacterial layer. Moreover, even if visually relatively simple, the lichenoid patterns are variable. Some *A. titanum* specimens display patterns that match the *Cryptothecia* type, i.e. the characteristical 'lichen' for this clade, whereas other specimens display lichenoid patterns reminiscent of the *Graphis* type. Combined with a conspicuous visual mimicry gradient from top to bottom in both density and complexity of the mimicked lichen, this provides *A. titanum* with a simple but most effective disguise.

Subgenus *Amorphophallus* contains a clade with all the giants of the genus, including *A. decus-silvae*, *A. gigas*, *A. hewittii* and *A. titanum*, and two clades containing all the dwarf species of the genus, including *A. myosuroides* Hett. & A.Galloway, *A. ongsakulii* Hett. & A.Galloway, *A. pulchellus* Hett. & Schuit., *A. obscurus* Hett. & M.Sizemore, *A. polyanthus* Hett. & M.Sizemore, *A. pusillus* Hett. & Serebryanyi., *A. serrulatus* Hett. & A.Galloway, *A. sumawongii* (Bogn.) Bogn. and *A. terrestris* Hett. & C.Claudel. None of the dwarf species reaches > 20 cm in length.

Without analysing each clade in detail, it is clear that the statement in regard to odour types posited by Kite & Hetterscheid (2017) '... odour types in *Amorphophallus* also show a range of phylogenetic trends, from mostly occurring in related species to apparently being co-evolved in unrelated species…' also holds true for petiolar mimicry. There is no obvious pattern from a phylogenetic perspective, except for its predominance in subgenera *Metandrium* and *Amorphophallus*. However, one trait is salient in all the clades that express visual mimicry: plant size. Not every species displaying petiolar mimicry is large; however, every clade containing mimicry-displaying species contains at least one larger growing species. For example, the above-mentioned clade (Fig. 5; star icon above the branch) consisting of *A. aberrans*, *A. angustispathus*, *A. cirrifer*, *A. cruddasianus*, *A. elatus, A. macrorhizus* and *A. pilosus*, contains mostly small-growing species, with petioles rarely exceeding half a metre (*A. aberrans*, *A. angustispathus*, *A. cruddasianus*) or slightly more (*A. cirrifer*, *A. elatus*). However, the petioles of the phylogenetically most recent species of this clade, the sister species *A. macrorhizus* and *A. pilosus*, exceed 1.1 m (Hetterscheid & Ittenbach, 1996) or even 1.5 m (Hetterscheid, 1994), respectively, and both display some of the most visually accurate lichen mimicries.

Similarly, the *Paeoniifolius–Manta* clade (Fig. 6; cross icon above the branch) contains medium-size species such as *A. bufo* (1.0-m petiole, Hetterscheid & Ittenbach, 1996) and large ones such as *A. paeoniifolius* (2.0-m petiole, Hetterscheid & Ittenbach, 1996) and *A. prainii* (2.1-m petiole, Hetterscheid & Ittenbach, 1996), the latter exhibiting one of the most complex lichen mimicries of the entire genus.

Finally, the Malaysian-Indonesian clade (Fig. 6; tilted cross icon above the branch) contains all the species displaying the cyanobacterial layer type, with or without accompanying lichen mimicry. Besides containing predominantly large-growing species, every giant species of the genus is found in this clade, such as *A. borneensis* (2.0-m petiole, Hetterscheid & Ittenbach, 1996), *A. lambii* (2.0-m petiole, Hetterscheid & Ittenbach, 1996), *A. decus-silvae* (3.5-m petiole, Hetterscheid & Ittenbach, 1996), *A. gigas* (4.0-m petiole, Hetterscheid & Ittenbach, 1996) and *A. titanum* (6.0 m petiole, McPherson & Hetterscheid, 2011).

This suggests that petiolar mimicry enables the species to better deceive herbivores via size increase; the tree masquerade becomes more convincing in taller and larger trunk imitations. We propose that petiolar mimicry was one of the factors selecting for larger specimens and, in consequence, led to the evolution of larger and giant species, performing tree masquerade as defence from herbivores. This raises the question: why would small-growing species display petiolar mimicry at all? All types combined, petiole coloration is displayed by 69% of the investigated *Amorphophallus* material. Some species, including *A. henryi*, *A. declinatus* and *A. yunnanensis*, contain differently patterned specimens, ranging from simple lichenoid patterns to accurate two-dimensional lichen mimicry (see Appendix). Considering that these species include small (*A. henryi*) and medium

(*A. yunnanensis*) and large (*A. yunnanensis* and *A. declinatus*) specimens, we assume that petiolar mimicry has evolved from a more general petiolar coloration type, working, for example as disruptive coloration or background matching. In some cases, the coloration and pattern may even fit into both categories. Especially African and Malagasy species, such as *A. taurostigma*, have a petiolar pattern that can be interpreted as lichen mimicry and a background matching pattern. However, only few of the species featuring petiolar mimicry are large species exceeding 2 m in height. Thus, petiolar mimicry alone cannot account for the evolution of giant, tree masquerade-performing species such as *A. titanum*, and additional factors have to be taken into consideration. The leaf height and width of the lamina of *A. titanum* can reach 6 m and more (McPherson & Hetterscheid, 2011), and the construction of the lamina 'relies entirely on turgor pressure for mechanical support' (Hejnowicz & Barthlott, 2005). This makes the lamina vulnerable to external forces such as running animals and strong winds. Furthermore, this type of lamina construction requires continuous access to water (Hejnowicz & Barthlott, 2005). Further abiotic factors such as temperature and the duration as well as the intensity of light also need to be consistent throughout the year as the leaf persists for 9–24 months (Lobin *et al.*, 2007). Only a single leaf per growing season is usually formed in mature plants and the investment in a leaf of such dimensions is huge, despite its lightweight construction (Hejnowicz & Barthlott, 2005). Only tropical lowland rainforests provide the conditions required for the development and evolution of such giant leaves. In such ecologies, the temperature and light regime are almost constant, and water is not a limiting factor. Strong winds are alleviated by the emergent layer or by the canopy layer of the forest, creating an almost windless environment on the forest floor and in the understory layer (Baynton *et al.*, 1965; Zhang *et al.*, 2006). Based on the world map of the Köppen–Geiger climate classification (Peel, Finlayson & McMahon, 2007), only the Malay Archipelago and the Congo Basin provide the necessary climatic conditions for the development of giant *Amorphophallus* leaves. And indeed, every *Amorphophallus* sp. that displays petiolar mimicry and exceeds 2 m in height is confined to the Malay Archipelago. In other words, petiolar mimicry is not restricted to a specific *Amorphophallus* clades or to specific climatic conditions. However, masquerade as a tree trunk based on both large petioles and petiolar mimicry is restricted to specific climatic conditions and is, as far as we know, confined to the Malay Archipelago.

This brings us to the question of the occurrence of tree masquerade-performing *Amorphophallus* spp. in the Congo Basin, as the provided climatic conditions meet the above-mentioned criteria. However, the few *Amorphophallus* spp. (e.g. *A. bequaertii* De Wildeman and *A. calabaricus* subsp. *mayoi* Ittenb.) found nearest to this region are only known from sites not providing tropical lowland rainforest conditions. They were either collected at sites at the border of the tropical rainforest climatic zone, or they were collected at sites at higher elevations, thus not meeting in full the formulated criteria. As for the tropical lowland of the Congo Basin, it is an understudied area with regard to the occurrence of *Amorphophallus* spp.; it should be investigated for tree masquerade-performing *Amorphophallus* spp.

CONCLUSIONS AND PERSPECTIVES

We have provided pictorial support for an intriguing and unique defensive coloration strategy on *Amorphophallus* petioles based on mimicry, i.e. plants expressing defensive visual masquerade and camouflage via lichen and cyanobacterial mimicry. We investigated the occurrence of petiolar mimicry and tree-trunk masquerade in *Amorphophallus* using all available taxa (138 species) and discussed the results in a phylogenetic and evolutionary context. Future studies could include in-depth analyses of defensive coloration strategies of specific species, including the assessment of petiole pattern variation within populations or species, particularly colour polymorphism. Moreover, the assessment of relevant herbivores and their perception and by consequence the design and execution of *in situ* experiments would be desirable. Last but not least, the question whether *Amorphophallus* spp. in the Congo Basin express visual tree-trunk masquerade remains to be answered.

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REFERENCES

Allen JA, **Cooper JM. 1985.** Crypsis and masquerade. *Journal of Biological Education* **19:** 268–270.

Aptroot A. 2001. Lichenized and saprobic fungal biodiversity of a single *Elaeocarpus* tree in Papua New Guinea, with the report of 200 species of ascomycetes associated with one tree. *Fungal Diversity* **6:** 1–11.

Aptroot A. 2012. A world key to the species of *Anthracothecium* and *Pyrenula*. *Lichenologist* **44:** 5–53.

Archer AW. 2004. Pertusariaceae. In: McCarthy PM, Mallett K, eds. *Flora of Australia 56A, Lichens 4*. Melbourne: ABRS/CSIRO Publishing, 116–172.

Barlow BA, **Wiens D. 1977.** Host-parasite resemblance in Australian mistletoes: the case for cryptic mimicry. *Evolution* **31:** 69–84.

Barthlott W. 1995. Mimikry – Nachahmung und Täuschung im Pflanzenreich. *Biologie in unserer Zeit* **25:** 74–82.

Baynton HW, **Biggs WG**, **Hamilton Jr HL**, **Sherr PE**, **Worth JJB. 1965.** Wind structure in and above a tropical forest. *Journal of Applied Meteorology* **4:** 670–675.

Benson L. 1982. *The cacti of the United States and Canada*. Stanford: Stanford University Press.

Boyce PC, **Croat TB. 2011. onwards.** *The Überlist of Araceae*: totals for published and estimated number of species in aroid genera. Available at: http://www.aroid.org/genera/160330uberlist.pdf

Boyce PC, **Ipor IB**, **Hetterscheid WLA. 2010.** A review of the white-flowered *Amorphophallus* (Araceae: Thomsonieae) species in Sarawak. *Gardens' Bulletin* **61:** 249–268.

Canyon DV, **Hill CJ. 1997.** Mistletoe host-resemblance: a study of herbivory, nitrogen and moisture in two Australian mistletoes and their host trees. *Australian Journal of Ecology* **22:** 395–403.

Claudel C, **Buerki S**, **Chatrou L**, **Antonelli A**, **Alvarez N**, **Hetterscheid W. 2017.** Large-scale phylogenetic analysis of *Amorphophallus* (Araceae) derived from nuclear and plastid sequences reveals new subgeneric delineation. *Botanical Journal of the Linnean Society* **184:** 32–45.

Cott HB. 1940. *Adaptive coloration in animals*. London: Methuen & Co. Ltd.

Endler JA. 1981. An overview of the relationships between mimicry and crypsis. *Biological Journal of the Linnean Society* **16:** 25–31.

Fadzly N, **Jack C**, **Schaefer HM**, **Burns KC. 2009.** Ontogenetic colour changes in an insular tree species: signalling to extinct browsing birds? *The New Phytologist* **184:** 495–501.

Fadzly N, **Zuharah WF**, **Mansor A**, **Zakaria R. 2016.** Cryptic coloration of *Macaranga bancana* seedlings: a unique strategy for a pioneer species. *Plant Signaling & Behavior* **11:** e1197466.

Gianoli E, **Carrasco-Urra F. 2014.** Leaf mimicry in a climbing plant protects against herbivory. *Current Biology* **24:** 984–987.

Groom PK, **Lamont BB**, **Duff HC. 1994.** Self crypsis in *Haeka trifurcata* as an avian granivore deterrent. *Functional Ecology* **8:** 110–117.

Hejnowicz Z, **Barthlott W. 2005.** Structural and mechanical peculiarities of the petioles of giant leaves of *Amorphophallus* (Araceae). *American Journal of Botany* **92:** 391–403.

Hetterscheid WLA. 1994. Notes on the genus *Amorphophallus* (Araceae)—2. New species from tropical Asia. *Blumea* **39:** 237–281.

Hetterscheid WLA. 2006. Notes on the genus *Amorphophallus* (Araceae) 15. New species from SE Asia. *Aroideana* **29:** 53–79.

Hetterscheid WLA, **Claudel C. 2014.** Endemic *Amorphophallus* (Araceae) from Madagascar: a revised key, a new species and molecular phylogeny. *Botanical Studies* **55:** 11.

Hetterscheid WLA, **Ittenbach S. 1996.** Everything you always wanted to know about *Amorphophallus*, but were afraid to stick your nose into. *Aroideana* **19:** 7–131.

Hetterscheid WLA, **Ittenbach S**, **Bogner J. 1999.** Notes on the genus *Amorphophallus* (Araceae) 10. Revision of the endemic *Amorphophallus* species of Madagascar. *Botanische Jahrbücher fur Systematik, Pflanzengeschichte und Pflanzengeographie* **121:** 1–17.

Hetterscheid WLA, **Peng C-I. 1995.** Notes on the genus *Amorphophallus* (Araceae). 4. Revision of the species in Taiwan. *Botanical Bulletin–Academia Sinica* **36:** 101–112.

Ittenbach S. 2003. Revision der afrikanischen Arten der Gattung *Amorphophallus* (Araceae). *Englera* **25:** 2–263.

Jürgens N. 1996. Psammophorous plants and other adaptations to desert ecosystems with high incidence of sandstorms. *Feddes Repertorium* **107:** 345–357.

Kauff F, **Lutzoni F. 2002.** Phylogeny of the gyalectales and ostropales (Ascomycota, Fungi): among and within order relationships based on nuclear ribosomal RNA small and large subunits. *Molecular Phylogenetics and Evolution* **25:** 138–156.

Kite GC, **Hetterscheid WLA. 2017.** Phylogenetic trends in the evolution of inflorescence odours in *Amorphophallus*. *Phytochemistry* **142:** 126–142.

Lev-Yadun S. 2006. Defensive functions of white coloration in coastal and dune plants. *Israel Journal of Plant Sciences* **54:** 317–325.

Lev-Yadun S. 2009. Müllerian and Batesian mimicry rings of white-variegated aposematic spiny and thorny plants: a hypothesis. *Israel Journal of Plant Sciences* **57:** 107–116.

Lev-Yadun S. 2014. Defensive masquerade by plants. *Biological Journal of the Linnean Society* **113:** 1162–1166.

Lev-Yadun S. 2016. *Defensive (anti-herbivory) coloration in land plants. Anti-herbivory plant coloration and morphology*. Zug: Springer.

Lev-Yadun S, **Ne'eman G**, **Shanas U. 2009.** A sheep in wolf's clothing: do carrion and dung odours of flowers not only attract pollinators but also deter herbivores? *BioEssays* **31:** 84–88.

Liu K, **Fadzly N**, **Mansor A**, **Zakaria R**, **Ruppert N**, **Lee CY. 2017.** The dual defensive strategy of *Amorphophallus* throughout its ontogeny. *Plant Signaling & Behavior* **12:** e1371890.

Lobin W, **Neumann M**, **Radscheit M**, **Barthlott W. 2007.** The cultivation of titan arum (*Amorphophallus titanum*) – a flagship species for botanic gardens. *Sibbaldia* **5:** 69–86.

Lücking R, **Archer AW**, **Aptroot A. 2009.** A world-key to the genus *Graphis* (Ostropales: Graphidaceae). *Lichenologist* **41:** 363–452.

Maddison WP, **Maddison DR. 2018.** *Mesquite: a modular system for evolutionary analysis. Version 3.6*. Available at: http://www.mesquiteproject.org

Mayo SJ, **Bogner J**, **Boyce PC. 1997.** *The genera of Araceae*. Kew: Royal Botanic Gardens.

McLaughlin DJ, Spatafora JW, eds. 2015. *The Mycota VII Part B, systematics and evolution*. Berlin, Heidelberg: Springer-Verlag.

McPherson S, **Hetterscheid W. 2011.** *Amorphophallus* in the wild and in cultivation. *Plantsman* **June 2011:** 90–97.

Merilaita S, **Lind J. 2005.** Background-matching and disruptive coloration, and the evolution of cryptic coloration. *Proceedings of the Royal Society of London B* **272:** 665–670.

Niu Y, **Chen G**, **Peng DL**, **Song B**, **Yang Y**, **Li ZM**, **Sun H. 2014.** Grey leaves in an alpine plant: a cryptic colouration to avoid attack? *The New Phytologist* **203:** 953–963.

Niu Y, **Sun H. 2014.** Alpine scree plants benefit from cryptic coloration with limited cost. *Plant Signaling & Behavior* **9:** e29698.

Niu Y, **Sun H**, **Stevens M. 2018.** Plant camouflage: ecology, evolution, and implications. *Trends in Ecology & Evolution* **33:** 608–618.

Peel MC, **Finlayson BL**, **McMahon TA. 2007.** Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences* **11:** 1633–1644.

Quicke DLJ. 2017. *Mimicry, crypsis, masquerade and other adaptive resemblances*. Oxford: Wiley Blackwell.

Ruxton GD. 2009. Non-visual crypsis: a review of the empirical evidence for camouflage to senses other than vision. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **364:** 549–557.

Ruxton GD, **Sherratt TN**, **Speed MP. 2004.** *Avoiding attack. The evolutionary ecology of crypsis, warning signals & mimicry*. Oxford: Oxford University Press.

Singh KP, **Sinha GP. 2010.** *Indian lichens: an annotated checklist*. Kolkata: Botanical Survey of India, Ministry of Environment and Forests.

Skelhorn J. 2015. Masquerade. *Current Biology* **25:** R643–R644.

Skelhorn J, **Rowland HM**, **Delf J**, **Speed MP**, **Ruxton GD. 2011.** Density-dependent predation influences the evolution and behavior of masquerading prey. *Proceedings of the National Academy of Science USA* **108:** 6532–6536.

Skelhorn J, **Rowland HM**, **Ruxton GD. 2010a.** The evolution and ecology of masquerade. *Biological Journal of the Linnean Society* **99:** 1–8.

Skelhorn J, **Rowland HM**, **Speed MP**, **De Wert L**, **Quinn L**, **Delf J**, **Ruxton GD. 2010c.** Size-dependent misclassification of masquerading prey. *Behavioral Ecology* **21:** 1344–1348.

Skelhorn J, **Rowland HM**, **Speed MP**, **Ruxton GD. 2010b.** Masquerade: camouflage without crypsis. *Science* **327:** 51.

Skelhorn J, **Ruxton GD. 2011.** Context-dependent misclassification of masquerading prey. *Evolutionary Ecology* **25:** 751–761.

Skelhorn J, **Ruxton GD. 2013.** Size-dependent microhabitat selection by masquerading prey. *Behavioral Ecology* **24:** 89–97.

Stone BC. 1979. Protective coloration of young leaves in certain Malaysian palms. *Biotropica* **11:** 126.

Urru I, **Stensmyr MC**, **Hansson BS. 2011.** Pollination by brood-site deception. *Phytochemistry* **72:** 1655–1666.

Wiens D. 1978. Mimicry in plants. *Evolutionary Biology* **11:** 365–403.

Yager KG, **Schaefer HM**, **Gould KS. 2016.** Shared leaf shape in *Alseuosmia pusilla* and *Pseudowintera colorata*: a case of Batesian mimicry? *Botany* **94:** 555–564.

Yuzammi Kurniawan A, **Asih NPS**, **Erlinawati I**, **Hetterscheid WLA. 2017.** *The Amorphophallus of Indonesia*. Bogor: LIPI Center for Plant Conservation – Botanic Gardens, Indonesian Institute of Sciences.

Zhang Y, **Song Q**, **Yu G**, **Sun X**, **Dou J. 2006.** Temporal-spatial characteristics of wind in tropical seasonal rainforest in Xishuangbanna of Yunnan Province. *Ying Yong Sheng Tai Xue Bao – The Journal of Applied Ecology* **17:** 11–16.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Supplementary Figure 1. Petiolar pattern mimicry types ranked in order of complexity ranging from 0 = pattern absent to non-lichenoid to 5 = most complex mimicry type (see Appendix) mapped on the Bayesian majority-rule consensus tree reproduced from Claudel *et al.* (2017) with Bayesian posterior probability values below the branches. The four subgenera of the genus *Amorphophallus* are indicated below the branches. Colour legend is provided within the tree. Petiolar pattern of grey shaded clades is not known or lacks substantial back up. Addenda behind the species name indicate plant size (see text).

APPENDIX

Taxon	Voucher	Coloration type	Character state
A. adamsensis L.M.Magtoto *et al*.	Original publication	Graphis type	2
A. albispathus Hett.	HBG 2014-G-42, HBG 2014-G-35, HBG 2014-G-36, HBG 2014-G-37, HBG 2014-G-39, HBG 2009-G-45	non-lichenoid pattern	0
A. albispathus Hett.	HBG 2009-G-44, HBG 2009-G-43	unicolour	0
A. albus Liu & Wei	HBG 2007-G-35, HBG 2009-G-46	non-lichenoid pattern	0
A. amygdaloides Hett. & M.Sizemore	HBG 2009-G-47	non-lichenoid pattern	0
A. andranogidroensis Hett. & Mangelsdorff	HBG 2012-G-3	non-lichenoid pattern	0
A. angolensis (Welw. ex Schott) N.E.Br.	HBG 2016-G-384	unicolour	0
A. ankarana Hett.	HBG 2014-G-50	non-lichenoid pattern	0
A. annulifer Hett.	H.AM 119	cyanobacterial-Cryptothecia type	5
A. antsingyensis Bogner, Hett. & Ittenb.	HBG 2014-G-43	unicolour	0
A. aphyllus (Hook.) Hutch.		non-lichenoid pattern/ masquerade	0
A. arcuspadix A.Galloway, A. Ongsakul, & P.Schmidt	HBG 2014-G-201	unicolour	0
A. asterostigmatus Bogn. & Hett.	HBG 2007-G-55, HBG 2014-G-154, HBG 2014-G-152, HBG 2014-G-155	non-lichenoid pattern	0
A. atrorubens Hett. & M.Sizemore	HBG 2014-G-169	unicolour	0
A. atroviridis Hett.	HBG 2007-G-57, HBG 2007-G-58, HBG 2014-G-179, HBG 2014-G-178	Graphis type	2
A. bangkokensis Gagn.	HBG 2014-G-170	non-lichenoid pattern	0
A. baumannii (Engl.) N.E.Br.	H.AM 1232	unicolour	0
A. beccarii Engl.	H.AM 300	cyanobacterial-Cryptothecia type	5
A. borneensis (Engl.) Engl. & Gehrm.	H.AM 158	cyanobacterial-Cryptothecia type	5
A. boyceanus Hett.	HBG 2012-G-78	cyanobacterial-Cryptothecia type	5
A. brachyphyllus Hett.	HBG 2007-G-61	unicolour	0
A. brevipetiolatus A.Galloway, A.Ongsakul, & P.Schmidt	HBG 2015-G-159, HBG 2015-G-162	unicolour	0
A. brevispathus Gagn.	HBG 2014-G-93	unicolour	0
A. bufo Ridl.		Cryptothecia and/or Graphis type	2
A. bulbifer (Roxb.) Bl.	HBG 2001-G-40, HBG 2007-G-63	mixed Graphis/Pyrenula type	4
A. carneus Ridl.	HBG 2014-G-159	non-lichenoid pattern	0
A. cicatricifer Ridl.	HBG 2014-G-128, HBG 2014-G-134, HBG 2014-G-145	unicolour	0
A. coaetaneus Liu & Wei	HBG 2015-G-163, HBG 2015-G-169	unicolour	0
A. commutatus (Schott) Engl.	HBG 2014-G-167	non-lichenoid pattern	0
A. consimilis Bl.	HBG 2007-G-66, HBG 2014-G-49, HBG 2015-G-172, HBG 2015-G-173	non-lichenoid pattern	0
A. corrugatus N.E.Br.	HBG 2007-G-68	non-lichenoid pattern	0
A. coudercii (Bogn.) Bogn.	H.AM 241	non-lichenoid pattern	0
A. croatii Hett. & A.Galloway	H.AM 1432	Graphis type	2
A. cruddasianus Prain ex Engl.	HBG 2014-G-91, HBG 2016-G-385	Graphis type	2

APPENDIX *Continued*

Taxon	Voucher	Coloration type	Character state
A. curvistylis Hett.	HBG 2014-G-161, HBG 2014-G-162	unicolour	0
A. dactylifer Hett.	HBG 2007-G-69	Coenogonium type	3
A. declinatus Hett.	HBG 2014-G-177	Graphis type	2
A. declinatus Hett.	HBG 2014-G-176	lichenoid-Graphis type	1
A. decus-silvae Backer & Alderw.		cyanobacterial-Cryptothecia type	5
A. dracontioides (Engl.)		non-lichenoid pattern/ masquerade	0
A. dunnii Tutch.	H.AM 001	lichenoid-Graphis type	1
A. dzui Hett.	HBG 2013-G-38	unicolour	0
A. eburneus Bogn.	H.AM 311	unicolour	0
A. eichleri (Engl.) Hook.f.	HBG 2016-G-267	unicolour	0
A. elatus Ridl.	HBG 2015-G-164	mixed Graphis/Pyrenula type	4
A. elliottii Hook.f.	H.AM 1735	non-lichenoid pattern/ masquerade	0
A. excentricus Hett.	HBG 2017-G-90	non-lichenoid pattern	0
A. fallax (Serebryanyi) Hett. & C.Claudel	H.AM 166	non-lichenoid pattern	0
A. ferruginosus A.Galloway	HBG 2013-G-31, HBG 2014-G-200, HBG 2015-G-160	lichenoid-Graphis type	1
A. fuscus Hett.	HBG 2007-G-73, HBG 2014-G-151	non-lichenoid pattern	0
A. galbra F.M.Bailey	HBG 2014-G-164	lichenoid	1
A. gallowayi Hett. (Laos)	H.AM 1431	unicolour	0
A. gigas Teijsm. & Binnend.	HBG 2007-G-74	cyanobacterial-Cryptothecia type	5
A. glossophyllus Hett.	HBG 2014-G-118	unicolour	0
A. gomboczianus Pic. Serm.	HBG 2009-G-61	Pyrenula type	2
A. haematospadix Hook.f.	HBG 2007-G-75, HBG 2014-G-153, HBG 2014-G-150	unicolour	0
A. henryi N.E.Br.	HBG 2007-G-76, HBG 2014-G-83, HBG 2014-G-84, HBG 2014-G-90	Graphis type	2
A. henryi N.E.Br.	HBG 2014-G-81, HBG 2014-G-82, HBG 2014-G-85	lichenoid-Graphis type	1
A. hewittii Alderw.		cyanobacterial-Cryptothecia type	5
A. hildebrandtii (Engl.) Engl. & Gehrm.	HBG 2014-G-55	lichenoid	1
A. hildebrandtii (Engl.) Engl. & Gehrm.	HBG 2009-G-62	lichenoid–sorediate with capitate or punctiform soralia	1
A. hottae Bogn. & Hett.	HBG 2015-G-165, HBG 2015-G-166	lichenoid-Graphis type	1
A. impressus Ittenb.	H.AM 1381	non-lichenoid pattern	0
A. infundibuliformis Hett., Dearden & A.Vogel		Pertusaria type	3
A. interruptus Engl. & Gehrm.	HBG 2007-G-86, HBG 2014-G-127	unicolour	0
A. johnsonii N.E.Br.	HBG 2007-G-87	unicolour	0
A. josefbogneri Hett.	HBG 2014-G-180	unicolour	0
A. julaihii Ipor, Tawan & P.C.Boyce	HBG 2012-G-73	unicolour	0
A. juliae P.C.Boyce & Hett.	HBG 2012-G-71	non-lichenoid pattern	0
A. kienluongensis V.D.Nguyen, Luu & Hett.	HBG 2017-G-88	unicolour	0
A. kiusianus (Makino) Makino	HBG 2007-G-91, HBG 2007-G-92	mixed Graphis/Pyrenula type	4

APPENDIX *Continued*

Taxon	Voucher	Coloration type	Character state
A. konjac K.Koch	HBG 2007-G-95	non-lichenoid pattern	0
A. konjac K.Koch	HBG 2007-G-71, HBG 2007-G-96	non-lichenoid pattern	0
A. koratensis Gagn.	H.AM 1074	lichenoid-Graphis type	1
A. krausei Engl.	HBG 2007-G-100, HBG 2014-G-203	non-lichenoid pattern	0
A. lacourii Linden & Andre	H.AM 245	non-lichenoid pattern	0
A. lambii Mayo & Widjaja	H.AM 1239	cyanobacterial-Cryptothecia type	5
A. lanceolatus (Serebryanyi) Hett. & C.Claudel	H.AM 179	non-lichenoid pattern	0
A. lanuginosus Hett.	HBG 2012-G-74	mixed Graphis/Pyrenula type	4
A. laoticus Hett.	HBG 2014-G-204, HBG 2014-G-206, HBG 2014-G-207, HBG 2014-G-208	mixed Graphis/Pyrenula type	4
A. latifolius (Serebryanyi) Hett. & C.Claudel	H.AM 167	non-lichenoid pattern	0
A. lewallei Malaisse & Bamps	HBG 2007-G-102	unicolour	0
A. longicomus Hett. & Serebryanyi		Graphis type	2
A. longiconnectivus Bogn.	H.AM 1132	non-lichenoid pattern	0
A. longituberosus (Engl.) Engl. & Gehrm.	HBG 2014-G-28, HBG 2014-G-30	non-lichenoid pattern	0
A. lunatus Hett. & M.Sizemore	HBG 2014-G-107, HBG 2014-G-156	non-lichenoid pattern	0
A. macrophyllus (Gagn. ex Serebryanyi) Hett. & C.Claudel	H.AM 178	non-lichenoid pattern	0
A. macrorhizus Craib	H.AM 990	mixed Graphis/Pyrenula type	4
A. mangelsdorffii Bogn.	RMM 550	unicolour	0
A. manta Hett. & Ittenbach		Cryptothecia and/or Graphis type	2
A. margaritifer (Roxb.) Kunth	H.AM 422	non-lichenoid pattern	0
A. maximus (Engl.) N.E.Br.	HBG 2014-G-185	non-lichenoid pattern	0
A. maxwellii Hett.	HBG 2007-G-106	non-lichenoid pattern	0
A. mossambicensis (Schott ex Garcke) N.E.Br.	HBG 2009-G-57, HBG 2014-G-57, HBG 2014-G-44	non-lichenoid pattern	0
A. muelleri Bl.	HBG 2007-G-111	lichenoid-Graphis type	1
A. myosuroides Hett. & A.Galloway	HBG 2013-G-3, HBG 2013-G-91	unicolour	0
A. napalensis (Wall.) Bogner & Mayo	HBG 2007-G-112, HBG 2014-G-146	non-lichenoid pattern	0
A. napiger Gagn.	H.AM 852, H.AM 708	Graphis type	2
A. natolii Hett., A.Wistuba, V.B.Amoroso, M.Medecilo & C.Claudel	HBG 2012-G-57	non-lichenoid pattern	0
A. natolii Hett., A.Wistuba, V.B.Amoroso, M.Medecilo & C.Claudel	HBG 2012-G-55	unicolour	0
A. niahensis P.C.Boyce & Hett.	HBG 2012-G-70	unicolour	0
A. obscurus Hett. & M.Sizemore		unicolour	0
A. ochroleucus Hett. & V.D.Nguyen	HBG 2007-G-113, HBG 2014-G-255, HBG 2015-G-167	lichenoid-Pyrenula type	1
A. ongsakulii Hett. & A.Galloway	HBG 2007-G-114	unicolour	0
A. operculatus (ined.)	HBG 2007-G-115, HBG 2014-G-124	unicolour	0
A. opertus Hett.	H.AM 141	Graphis type	2
A. paeoniifolius (Dennst.) Nicolson	HBG 2007-G-116, HBG 2014-G-160, HBG 2014-G-181, A0-G-8828	lichenoid-Graphis type	1

APPENDIX *Continued*

Taxon	Voucher	Coloration type	Character state
A. palawanensis Bogn. & Hett.	HBG 2014-G-172, HBG 2014-G-173	unicolour	0
A. pilosus Hett.	HBG 2014-G-202	mixed Graphis/Pyrenula type	4
A. polyanthus Hett. & M.Sizemore	HBG 2017-G-89	unicolour	0
A. prainii Hook.f.	HBG 2014-G-147, HBG 2014-G-215	mixed Graphis/Pyrenula type	4
A. prolificus Hett. & A.Galloway	H.AM 1245	unicolour	0
A. pulchellus Hett. & Schuit.	HBG 2014-G-122	unicolour	0
A. putii Gagn.	HAM 972, H.AM 697	lichenoid-Graphis type	1
A. pygmaeus Hett.	HBG 2007-G-121	unicolour	0
A. ranchanensis Ipor, Tawan, Simon, Meekiong & Fuad		lichenoid	1
A. reflexus Hett. & A.Galloway	HBG 2014-G-31	unicolour	0
A. rhizomatosus Hett.		unicolour	0
A. richardsiae Ittenb.	HBG 2007-G-130	non-lichenoid pattern	0
A. rostratus Hett.	HBG 2016-G-268	lichenoid	1
A. sagittarius Steen.		cyanobacterial-Cryptothecia type	5
A. salmoneus Hett.	HBG 2014-G-109, HBG 2014-G-125, HBG 2014-G-165, HBG 2014-G-171	unicolour	0
A. saururus Hett.	HBG 2014-G-174	unicolour	0
A. schmidtiae Hett. & A.Galloway	HBG 2013-G-2, HBG 2013-G-32	unicolour	0
A. scutatus Hett. & T.C.Chapman	HBG 2014-G-89	non-lichenoid pattern	0
A. serrulatus Hett. & A.Galloway	HBG 2017-G-85	unicolour	0
A. sizemoreae Hett.	HBG 2007-G-127, H.AM 985	unicolour	0
A. stuhlmannii (Engl.) Engl. & Gehrm.	H.AM 1215	lichenoid-Graphis type	1
A. sumawongii (Bogn.) Bogn.	HBG 2012-G-16, HBG 2014-G-40	non-lichenoid pattern	0
A. symonianus Hett. & M.Sizemore	HBG 2014-G-96, HBG 2014-G-97, HBG 2014-G-98, HBG 2017-G-81	non-lichenoid pattern	0
A. symonianus Hett. & M.Sizemore	HBG 2014-G-87	unicolour	0
A. taurostigma Ittenb. & Hett.	HBG 2014-G-45	lichenoid-Graphis type	1
A. taurostigma Ittenb. & Hett.	HBG 2014-G-46	non-lichenoid pattern	0
A. taurostigma Ittenb. & Hett.	HBG 2009-G-50	unicolour	0
A. tenuispadix Hett.	HBG 2007-G-136, HBG 2014-G-29	non-lichenoid pattern	0
A. tenuistylis Hett.	HBG 2014-G-149	non-lichenoid pattern	0
A. terrestris Hett. & C.Claudel	HBG 2014-G-254	non-lichenoid pattern	0
A. thaiensis S.-Y.Hu	HBG 2014-G-86	lichenoid-Graphis type	1
A. thaiensis S.-Y.Hu	HBG 2007-G-137, HBG 2014-G-99	non-lichenoid pattern	0
A. titanum (Becc.) Becc. ex Arcangeli	HBG 2017-G-95	lichenoid-cyanobacterial/ Cryptothecia type	1
A. titanum (Becc.) Becc. ex Arcangeli	HBG 2007-G-138, HBG 2017-G-94	lichenoid-cyanobacterial/ Graphis type	1
A. tonkinensis Engl. & Gehrm.	HBG 2017-G-86	non-lichenoid pattern	0
A. tuberculatus Hett. & V.D.Nguyen	HBG 2012-G-75, HBG 2012-G-76	lichenoid-Graphis type	1
A. variabilis Bl.	HBG 2007-G-141, HBG 2007-G-142	cyanobacterial-Cryptothecia type	5
A. variabilis Bl.	HBG 2007-G-140, HBG 2012-G-13, HBG 2014-G-213	lichenoid-Graphis type	1
A. variabilis Bl.	HBG 2007-G-139	unicolour	0
A. verticillatus Hett.	HBG 2007-G-144, HBG 2013-G-1	unicolour	0
A. vogelianus Hett. & H.Billenst.	HBG 2007-G-145, HBG 2014-G-138, HBG 2014-G-139	non-lichenoid pattern	0

APPENDIX *Continued*

Taxon	Voucher	Coloration type	Character state
A. xiei Li & Dao	HBG 2013-G-25	non-lichenoid pattern	0
A. yuloensis H.Li	HBG 2007-G-146, HBG 2013-G-29, HBG 2013-G-30, HBG 2014-G-100, HBG 2014-G-101, HBG 2014-G-102	unicolour	0
A. yunnanensis Engl.	HBG 2007-G-151, HBG 2007-G-153, HBG 2014-G-88, HBG 2014-G-105	Graphis type	2
A. yunnanensis Engl.	HBG 2014-G-79	lichenoid-Graphis type	1

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REVIEW PAPER

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 (Hetterscheid and Ittenbach 1996; Kite and Hetterscheid 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 (Hetterscheid 1994; Hetterscheid and Ittenbach 1996; McPherson and Hetterscheid 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 "carrion, 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. julaihii* 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
A. abyssinicus* subsp. *akeassii Single inflorescence	Ivory Coast: Comoé National Park, savanna parkland of the Lola plaine (Moretto et al. 2019)	**Coleoptera: Scarabaeidae**, *Cleptocaccobius uniseries* ("main pollinator")	**Coleoptera: Aphodiidae**, *Aphodobius zumpti, Mesontoplatys dorsalis, Pseudopharaphodius phalacronothoides, Trichaphodius amplitarsis, Trichaphodius copulates, Trichaphodius flavus, Trichaphodius maldesi*; **Hydrophilidae**, *Sphaeridium* sp.; **Scarabaeidae**, *Caccobius auberti*, *Caccobius ivorensis*, *Cleptocaccobius convexifrons*, *Cleptocaccobius dorbignyi*, *Furconthophagus flaviclava*, *Hyalonthophagus nigroviolaceus*, *Onthophagus lutaticollis*, *Onthophagus tersipennis*, *Sisyphus goryi*; **Staphylinidae sp.**	**Coleoptera: Scarabaeidae**, *Chalconotus suturalis*, *Digitonthophagus fimator*
A. angolensis* subsp. *maculatus Several inflorescences	Gabon: on several unspecified sites (Bogner 1976)	**Coleoptera: Hybosoridae**, *Phaeochrous camerunensis*; **Diptera: Calliphoridae sp.**		
A. barthlottii Single inflorescence	Ivory Coast: Taï National Park, track leading to the Centre de Recherche en Écologie (Moretto et al. 2019)	**Coleoptera: Hydrophilidae**, *Sphaeridium* sp.; **Scarabaeidae**, *Onthophagus liberianus*		
A. bulbifer The number of investigated inflorescences is not specified	India: Karnataka, Anshi National Park (Punekar and Kumaran, 2010)	**Coleoptera: Hybosoridae** (=**Melolonthidae**; probably *Apogonia* sp. according to Moretto et al. 2019); **Nitidulidae**, *Epuraea* sp.	**Diptera: Drosophilidae sp.**	**Coleoptera: Lyctidae**, *Lyctus* sp.
A. commutatus* var. *commutatus 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**, *Epuraea* sp.; **Hymenoptera:** *Trigona* sp. (except Vengurla population)	**Coleoptera:** Rutelinae (=**Rutelidae**, *Anomala* sp. according to Moretto et al. 2019); **Diptera: Drosophilidae sp.; Muscidae**, *Musca domestica*	**Coleoptera: Staphylinidae sp.; Hymenoptera: Formicidae**, *Oecophylla smaragdina,* Dolichoderinae: *Tapinoma* sp.
A. commutatus* var. *anmodensis Single inflorescence	India: Goa, Anmode ghat (Punekar and Kumaran 2010)	**Coleoptera: Scarabaeidae**, *Onthophagus* sp.		
A. commutatus* var. *anshiensis The number of investigated inflorescences is not specified	India: Karnataka, Anshi National Park (Punekar and Kumaran 2010)	**Coleoptera**: **Cantharidae**, *Rhagonycha* sp.; **Cetoniidae**, black beetles**; Scarabaeidae**, *Heliocopris sp*, *Onthophagus* sp.	**Diptera**: **Drosophilidae sp.**	**Hymenoptera**: **Formicidae**, *Oecophylla smaragdina*; **Blaberidae**, Panesthiinae
A. commutatus* var. *wayanadensis 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**, *Epuraea* sp.	**Diptera**: **Drosophilidae**; **Muscidae**, *Musca domestica*; **Hymenoptera:** *Trigona* sp. (only Goa population)	

Table 1 (continued)

Species & inflorescence quantity	Locations & references	Pollinators	Putative pollinators	Visitors
A. gigas Single inflorescence	Indonesia: North Sumatra province, Sipirok (Hetterscheid 1994)	**Coleoptera**: carrion beetles; dung beetles; **Cetoniidae; Staphylinidae**; **Diptera**: **Asilidae**		
A. gomboczianus Several inflorescences	Ethiopia: Sidamo (Gombocz 1936)	**Diptera spp.**		
A. henryi Several populations and several inflorescences	Taiwan: four sampling areas (Jung 2006)	**Coleoptera: Scarabaeidae**, *Onthophagus* sp., *O. argyropygus*, *O. koshunensis*, *O. proletarius*, *O. sauteri*, *O. taurinus*; **Staphylinidae spp.**		**Coleoptera**: **Nitidulidae**; **Scaphidiidae**; **Scarabaeidae**, *Paragymnopleurus* sp.; **Tenebrionidae**; **Diptera**: **Calliphoridae,** *Chrysomyia* spp.; **Drosophilidae,** *Drosophila* spp.; **Sepsidae**, *Sepsis* spp.; **Hemiptera; Homoptera: Aphididae**; **Hymenoptera**: **Formicidae**; **Isoptera**: **Termitidae**, *Odontotermes formosanus*; **Orthoptera**; **Thysanoptera**; **Arachnida**: **Araneae**, **Sparassidae**; **Salticidae**; **Blattoidae**
A. hewittii Several inflorescences	Malaysia: Borneo, Sarawak, Gunung Mulu National Park (Chai and Wong 2019)	**Coleoptera: Hybosoridae**; **Silphidae**, *Diamesus* sp.; **Staphylinidae**, *Creophilus* sp.	**Hymenoptera:** Trigonids	
A. hohenackeri Several inflorescences	India: Kerala, Calicut University campus (Sivadasan and Sabu 1989)	**Coleoptera: Nitidulidae**, *Epuraea motschulskii*		
A. johnsonii Several inflorescences	Ghana: Jachie Sacred Grove (Beath 1996)	**Coleoptera: Hybosoridae**, *Phaeochrous amplus*	**Coleptera: Histeridae**, *Pachycraerus* sp.	**Diptera: Calliphoridae**, *Hemigymnochaeta unicolor;* **Platystomatidae**, *Paryphodes tigrinus*
A. julaihii Several inflorescences	Malaysia: Borneo, Sarawak, Gunung Mulu National Park (Chai and Wong 2019)	**Coleoptera: Staphylinidae**, *Creophilus* sp.		
A. konjac 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, *Achoetandrus rufifacies*, *Aldrichina grahami*, *Chrysomya* spp., *Lucilia* spp.; **Muscidae**; **Sarcophagidae**	
A. konkanensis Not specified, apparently single inflorescence	India: Maharashtra, Sindhudurg district, Kochra (Punekar and Kumaran 2010)	**Coleoptera: Nitidulidae**, *Epuraea* sp.		
A. koratensis Single inflorescence	Thailand: Songkhla, Hat Yai (pers. comm. Sutthinut Soonthornkalump)		**Hymenoptera:** *Tetragonula* sp.	**Hymenoptera: Formicidae**

Table 1 (continued)

Species & inflorescence quantity	Locations & references	Pollinators	Putative pollinators	Visitors
A. muelleri Several inflorescences	Indonesia: Java (van der Pijl 1937)	**Coleoptera: Nitidulidae**		**Coleoptera: Melolonthidae**, *Apogonia destructor*
A. napalensis Several inflorescences at two sites	India: Nagaland, Zunheboto, Lumami village, 880 m. a.s.l.; Mokokchung, Arkong ward. Plot no. 227, 1350 m a.s.l. (Chaturvedi 2017)	**Coleoptera: Scarabaeidae,** *Parastasia* sp. (=**Dynastidae**, *Peltonotus* sp. according to Moretto et al. 2019)		**Diptera: Drosophilidae**, *Drosophila* sp.; **Hymenoptera:** *Trigona* sp.; **Apidae**, *Apis indica*
A. paeoniifolius (1) Several inflorescences, wild occurring and cultivated plants	India: Karnataka, Uttara Kannada district (Singh and Gadgil 1995)	**Coleoptera**: **Rutelidae**, *Adoretus* sp.	**Hymenoptera**: *Melipona* sp. (*Melipona* is now a neotropical genus, probably *Tetragonula* sp.)	Two unidentified insects
A. paeoniifolius (2) Single inflorescence	locality not specified (Giordano 1999)	**Coleoptera**: **Hybosoridae**, *Phaeochrous emarginatus*		
A. paeoniifolius (3) Not specified, apparently single inflorescence	India: Karnataka, Anshi National Park (Punekar and Kumaran 2010)	**Coleoptera**: **Scarabaeidae**, *Heliocopris* sp., *Onthophagus* sp.; **Cetoniidae** Black beetles	**Coleoptera**: **Scarabaeidae**, **Rutelinae** (=**Rutelidae**, *Anomala* sp. according to Moretto et al. 2019)	**Diptera: Calliphoridae; Muscidae,** *Musca domestica*
A. paeoniifolius (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*		
A. paeoniifolius (5) Single inflorescence	Thailand: Nan province, Nan River at Srinan river (Sites 2017)	**Coleoptera**: **Hybosoridae**, *Phaeochrous dissimilis*; **Scarabaeidae**, *Peltonotus nasutus*		
A. prainii Single inflorescence	West Malaysia (Soepadmo 1973)		**Diptera:** „various flies " are mentioned but have not been actually observed	
A. sylvaticus Single inflorescence	India: Maharashtra, Mumbai, Bhandup (Punekar and Kumaran 2010)	**Coloptera: Nitidulidae,** *Epuraea* sp.		
A. titanum (1) Several inflorescences	Sumatra: Fort de Kock (now Bukittinggi) (van der Pijl 1937)	**Coleoptera: Silphidae**, *Diamesus osculans*; **Staphylinidae**, *Creophilus villipennis*		
A. titanum (2) Single inflorescence	Indonesia: North Sumatra province, Sipirok (Hetterscheid 1994)	No insects were observed on the first day of anthesis	**Hymenoptera:** *Trigona* sp. on day two of anthesis	
A. titanum (3) Several inflorescences	Sumatra: (Giordano 1999)	**Coleoptera: Curculionidae**; **Histeridae**; **Hybosoridae**, *Phaeochrous emarginatus*	**Coleoptera: Staphilinidae**; **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
A. variabilis (1) Several inflorescences	Java: Buitenzorg (now Bogor), (Backer 1913)	**Coleoptera: Nitidulidae**	**Staphilinidae**, *Philanthus crassicornis*	
A. variabilis (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 (Blattoidae 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 (Hetterscheid 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* (Hetterscheid 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 (Hetterscheid 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 (Hetterscheid 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* (Hetterscheid 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 Hetterscheid 1997, 2017). Nearly half of the *Amorphophallus* species studied by Kite and Hetterscheid (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 heterogenous. 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 (Hetterscheid 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. Hetterscheid (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* (Staphilinidae) 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; Punekar 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; Punekar and Kumaran 2010). However, other observations rely on observations gathered on behalf of one single inflorescence per *Amorphophallus* species (Soepadmo 1973; Hetterscheid 1994; Giordano 1999; Grimm 2009; Punekar 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* (Punekar 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; Punekar 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. julaihii*. 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; Punekar 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; Punekar 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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References

Backer CA (1913) Het Slangenblad II. Trop Nat 2:177–179

Barthlott W, Lobin W (eds) (1998) *Amorphophallus titanium*—Tropische und Subtropische Pflanzenwelt. Akademie der Wissenschaft und der Literatur in Mainz. Franz Steiner Verlag, Stuttgart

Barthlott W, Szarzynski J, Vlek P, Lobin W, Korotkova N (2009) A torch in the rain forest: thermogenesis of the Titan arum

(*Amorphophallus titanum*). Plant Biol (stuttg) 11:499–505. https://doi.org/10.1111/j.1438-8677.2008.00147.x
Beath DDN (1996) Pollination of *Amorphophallus johnsonii* (Araceae) by carrion beetles (*Phaeochrous amplus*) in a Ghanaian rain forest. J Trop Ecol 12:409–418
Bogner J (1976) *Amorphophallus maculatus*. Der Palmengarten 3:83–86
Boyce PC, Croat TB (2018) The Überlist of Araceae, Totals for Published and Estimated Number of Species in Aroid Genera. Available from:http://www.aroid.org/genera/20201008Uberlist.pdf. Accessed 9 Sept 2021
Bröderbauer D, Diaz A, Weber A (2012) Reconstructing the origin and elaboration of insect–trapping inflorescences in the Araceae. Am J Bot 99:1666–1679. https://doi.org/10.3732/ajb.1200274
Buis RC (2016) The validation of human decomposition fluid as a cadaver–detection dog training aid. Thesis submitted for the degree of Doctor of Philosophy (Science) Centre for Forensic Science University of Technology, Sydney
Bustamante RAA, Mansibang JA, Hetterscheid WLA, Tamayo MN (2020) *Amorphophallus caudatus* (Thomsonieae, Araceae), a new species from Camarines Norte, Luzon island, the Philippines. Nordic J Bot. https://doi.org/10.1111/njb.02982
Chai SK, Wong SY (2019) Five pollination guilds of aroids (Araceae) at Mulu National Park (Sarawak, Malaysian Borneo). Webbia 74:353–371
Chaturvedi SK (2017) Pollinators and visitors of *Amorphophallus napalensis* (Wall.) Bogner and Mayo (Araceae) in Nagaland State, North-East India. Pleione 11:336–340
Chen G, Ma X-K, Jürgens A, Lu J, Liu E-X, Sun W-B, Cai X-H (2015) Mimicking livor mortis: a well-known but unsubstantiated color profile in sapromyiophily. J Chem Ecol 41:808–815. https://doi.org/10.1007/s10886-015-0618-2
Claudel C, Buerki S, Chatrou L, Antonelli A, Alvarez N, Hetterscheid W (2017) Large–scale phylogenetic analysis of *Amorphophallus* (Araceae) derived from nuclear and plastid sequences reveals new subgeneric delineation. Bot J Linn Soc 184:32–45. https://doi.org/10.1093/botlinnean/box013
Delpino F (1889) Sulla Impollinazione Dell'arum Dracunculus. Malpighia III:385–395
Dobson HEM, Bergström G (2000) The ecology and evolution of pollen odors. Plant Syst Evol 222:63–87. https://doi.org/10.1007/BF00984096
Dötterl S, David A, Boland W, Silberbauer-Gottsberger I, Gottsberger G (2012) Evidence for behavioral attractiveness of methoxylated aromatics in a dynastid scarab beetle-pollinated Araceae. J Chem Ecol 38:1539–1543. https://doi.org/10.1007/s10886-012-0210-y
Eltz T (2001) Ecology of stingless bees (Apidae, Meliponini) in lowland dipterocarp forests in Sabah, Malaysia, and an evaluation of logging impact on populations and communities. Dissertation, Julius-Maximilians-Universität Würzburg
Engler A (1920) Araceae-Aroideae und Araceae-Pistioideae. Das Pflanzenreich 23(73):1–274
Faegri K, van der Pijl L (1979) The principles of pollination ecology, 3rd edn. Pergamon Press, London
Fishman MA, Hadany L (2013) Pollinators' mating rendezvous and the evolution of floral advertisement. J Theor Biol 316:99–106. https://doi.org/10.1016/j.jtbi.2012.09.006
Flamini G, Cioni PL, Morelli I (2002) Differences in the fragrances of pollen and different floral parts of male and female flowers of *Laurus nobilis*. J Agric Food Chem 50:4647–4652. https://doi.org/10.1021/jf020269x
Frątczak-Łagiewska K, Grzywacz A, Matuszewski S (2020) Development and validation of forensically useful growth models for Central European population of *Creophilus maxillosus* L. (Coleoptera: Staphylinidae). Int J Legal Med 134:1531–1545. https://doi.org/10.1007/s00414-020-02275-3
Gibernau M (2011) Pollinators and visitors of aroid inflorescences: an addendum. Aroideana 34:70–83
Gibernau M, Chartier M, Barabé D (2010) Recent advances towards an evolutionary comprehension of Araceae pollination. In: Seberg O, Peterson G, Barfod AS, Davis JI (eds) Diversity, phylogeny and evolution in the monocotyledons. Aarhus University Press, Denmark
Giordano C (1999) Observations on *Amorphophallus titanum* (Becc.) Becc.ex Arcangeli in the Forest of Sumatra. Aroideana 22:10–19
Gombocz E (1936) Ein neuer *Amorphophallus*. Ann Hist-Nat Musei Hung 30:1–3
Grimm R (2009) *Peltonotus nasutus* Arrow, 1910 und *Phaeochrous*-Arten als Bestäuber von *Amorphophallus paeoniifolius* (Araceae) in Thailand (Coleoptera: Scarabaeidae). Entomol Z Insektenbörse 119(4):167–168
Hesse M (2006) Reasons and consequences of the lack of a sporopollenin ektexine in Aroideae (Araceae). Flora 201:421–428. https://doi.org/10.1016/j.flora.2005.10.002
Hetterscheid WLA (1994) Sumatran *Amorphophallus* adventures: 20 August–1 September 1993. Aroideana 17:61–77
Hetterscheid WLA (2012) *Amorphophallus*. In: Boyce PC, Sookchaloem D, Hetterscheid WLA, Gusman G, Jacobsen N, Idei T, Nguyen VD (eds) Araceae. Flora of Thailand 11. The Forest Herbarium, Bangkok, pp 218–232
Hetterscheid WLA, Ittenbach S (1996) Everything you always wanted to know about *Amorphophallus*, but were afraid to stick your nose into. Aroideana 19:7–131
Johnson SD, Schiestl FP (2016) Floral mimicry. Oxford University Press, New York
Jürgens A, Shuttleworth A (2016) Carrion and dung mimicry in plants. In: Benbow ME, Tomberlin JK, Tarone AM (eds) Carrion ecology, evolution, and their applications. CRC Press, Boca Raton, pp 361–386
Jürgens A, Dötterl S, Meve U (2006) The chemical nature of fetid floral odours in stapeliads (Apocynaceae–Asclepiadoideae–Ceropegieae). New Phytol 172:452–468. https://doi.org/10.1111/j.1469-8137.2006.01845.x
Jürgens A, Wee S-L, Shuttleworth A, Johnson SD (2013) Chemical mimicry of insect oviposition sites: a global analysis of convergence in angiosperms. Ecol Lett 16:1157–1167. https://doi.org/10.1111/ele.12152
Jung M-J (2006) The Pollination Biology of *Amorphophallus henryi* N. E. Br. Master thesis, National Cheng–Kung University, Taiwan
Kakishima S, Terajima Y, Murata J, Tsukaya H (2011) Infrared thermography and odour composition of the *Amorphophallus gigas* (Araceae) inflorescence: the cooling effect of the odorous liquid. Plant Biol (stuttg) 13:502–507. https://doi.org/10.1111/j.1438-8677.2010.00399.x
Keasar T, Harari AR, Sabatinelli G, Keith D, Dafni A, Shavit O, Zylbertal A, Shmida A (2010) Red anemone guild flowers as focal places for mating and feeding by Levant glaphyrid beetles. Biol J Linn Soc 99:808–817. https://doi.org/10.1111/j.1095-8312.2010.01384.x
Kite GC, Hetterscheid WLA (1997) Inflorescence odours of *Amorphophallus* and *Pseudodracontium* (Araceae). Phytochemistry 46:71–75. https://doi.org/10.1016/S0031-9422(97)00221-5
Kite GC, Hetterscheid WLA (2017) Phylogenetic trends in the evolution of inflorescence odours in *Amorphophallus*. Phytochemistry 142:126–142. https://doi.org/10.1016/j.phytochem.2017.06.006
Kite GC, Hetterscheid WLA, Lewis M, Boyce PC, Ollerton J, Cocklin E, Diaz A, Simmonds MSJ (1998) Inflorescence odours and pollinators of *Arum* and *Amorphophallus* (Araceae). In: Owens S, Rudall P (eds) Reproductive biology in systematics, conservation and economic botany. Kew Publishing, Kew, pp 295–315

Korotkova N, Barthlott W (2009) On the thermogenesis of the Titan arum (*Amorphophallus titanum*). Plant Signal Behav 4:499–505. https://doi.org/10.4161/psb.4.11.9872

Lamprecht I, Seymour RS (2010) Thermologic investigations of three species of *Amorphophallus*. J Therm Anal Calorim 102:127–136. https://doi.org/10.1007/s10973-010-0891-9

Lohonyai Z, Vuts J, Fail J, Tóth M, Imrei Z (2018) Field response of two cetoniin chafers (Coleoptera, scarabaeidae) to floral compounds in ternary and binary combinations. Acta Phytopathol Entomol Hung 53:259–269

Mayo SJ, Bogner J, Boyce PC (1997) The genera of Araceae. Royal Botanic Gardens, Kew

McPherson S, Hetterscheid WLA (2011) *Amorphophallus* in the wild and in cultivation. Plantsman 10:90–97

Michener CD (2007) The bees of the world, 2nd edn. John Hopkins University Press, Baltimore

Moretto P, Cosson B, Krell F-T, Aristophanous M (2019) Pollination of *Amorphophallus barthlottii* and *A. abyssinicus* subsp. *akeassii* (Araceae) by dung beetles (Insecta: Coleoptera: Scarabaeoidea). Cathar La Rev 18:19–36

Ollerton J, Raguso RA (2006) The sweet stench of decay. New Phytol 172:382–385. https://doi.org/10.1111/j.1469-8137.2006.01903.x

Punekar SA, Kumaran KPN (2010) Pollen morphology and pollination ecology of *Amorphophallus* species from North Western Ghats and Konkan region of India. Flora 205:326–336. https://doi.org/10.1016/j.flora.2009.12.024

Raman V, Tabanca N, Demirci B, Khan IA (2017) Studies on the floral anatomy and scent chemistry of titan arum (*Amorphophallus titanum*, Araceae). Turk J Biol 41:63–74. https://doi.org/10.3906/bot-1604-34

Ruprecht UW, Socher SA, Dötterl S (2021) Unexpected occurrence of *Cladosporium* spp. on the inner side of the spathe of the titan arum *Amorphophallus titanum*. Acta Mycol. https://doi.org/10.5586/am.563

Sayyad S, Mulani RM (2016) Endophytic fungal diversity in corms of *Amorphophallus sylvaticus* (Roxb.) Kunth. Int J Eng Res 4:32–34

Shirasu M, Fujioka K, Kakishima S, Nagai S, Tomizawa Y, Tsukaya H, Murata J, Manome Y, Touhara K (2010) Chemical identity of a rotting animal–like odor emitted from the inflorescence of the titan arum (*Amorphophallus titanum*). Biosci Biotechnol Biochem 74:2550–2554. https://doi.org/10.1271/bbb.100692

Singh SN, Gadgil M (1995) Ecology of *Amorphophallus* species in Uttara Kannada District of the Karnataka State, India: implications for conservation. Aroideana 18:5–20

Sites RW (2017) The Aroid Scarab *Peltonotus nasutus* (Coleoptera: Scarabaeidae) in Thailand and its association with *Amorphophallus paeoniifolius* (Araceae). Nat Hist Bull Siam Soc 62:107–109

Sivadasan M, Sabu T (1989) Beetle pollination—cantharophily—in *Amorphophallus hohenackeri* (Araceae). Aroideana 12:32–37

Skubatz H, Nelson TA, Dong AM, Meeuse BJD, Bendich AJ (1990) Infrared thermography of *Arum* lily inflorescences. Planta 182:432–436

Soepadmo E (1973) A short note on *Amorphophallus* cf. prainii Hook.f. Malay Nat J 25:133–134

Tamayo MN, Magtoto LM, Sumalinog MS, Reyes TD, Austria CM (2021) *Amorphophallus calcicolus* (Thomsonieae, Araceae), a new species from the Bohol island, Central Visayas, Philippines. Phytotaxa 489:229–235

Tóth M, Szarukán I, Nagy A, Furlan L, Benvegnù I, Rak Cizej M, Ábri T, Kéki T, Körösi S, Pogonyi A, Toshova T, Velchev D, Atanasova D, Kurtulus A, Kaydan BM, Signori A (2017) European corn borer (*Ostrinia nubilalis* Hbn., Lepidoptera: Crambidae): comparing the performance of a new bisexual lure with that of synthetic sex pheromone in five countries. Pest Manag Sci 73:2504–2508

Trumbo ST, Steiger S (2020) Finding a fresh carcass: bacterially derived volatiles and burying beetle search success. Chemoecology 30:287–296. https://doi.org/10.1101/2020.01.25.919696

Urru I, Stensmyr MC, Hansson BS (2011) Pollination by brood–site deception. Phytochemistry 72:1655–1666. https://doi.org/10.1016/j.phytochem.2011.02.014

van der Pijl L (1937) Biological and physiological observations on the inflorescence of *Amorphophallus*. Recl Trav Bot Néerl 34:57–67

Vereecken NJ, McNeil JN (2010) Cheaters and liars: chemical mimicry at its finest. Can J Zool 88:725–752. https://doi.org/10.1139/Z10-040

Wasserman SL, Itagaki H (2003) The olfactory responses of the antenna and maxillary palp of the fleshfly, *Neobellieria bullata* (Diptera: Sarcophagidae), and their sensitivity to blockage of nitric oxide synthase. J Insect Physiol 49:271–280. https://doi.org/10.1016/S0022-1910(02)00288-3

WCVP (2021) World Checklist of Vascular Plants, version 2.0. Facilitated by the Royal Botanic Gardens, Kew. http://wcvp.science.kew.org/. Accessed 14 Feb 2021.

Wiens D (1978) Mimicry in plants. Evol Biol 11:365–403

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Odor polymorphism in deceptive *Amorphophallus* species - a review

Odor polymorphism in *Amorphophallus*

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ABSTRACT

Some plant lineages, such as Araceae and Orchidaceae, have independently evolved deceptive flowers. These exploit the insect's perception and deceive the insects into believing to have located a suitable opportunity for reproduction. The scent compounds emitted by the flowers are the key signals that dupe the insects, guiding them to the right spots that in turn ensure flower pollination. Most species of the genus *Amorphophallus* of the Araceae emit scent compounds that are characteristic of a deceit, suggesting a specific plant pollinator interaction and according odors. However, only a few clear evolutionary trends in regard to inflorescence odors in *Amorphophallus* could be traced in previous studies – an intriguing result, considered the multitude of characteristic scent compounds expressed in *Amorphophallus* as well as the key function of scent compounds in deceptive floral systems in general. At least two factors could account for this result. (1) The deceptive pollinator-attraction floral system, including the emitted scent compounds, is less specific than assumed. (2) An evolutionary trend cannot be discerned if the intraspecific scent variation (odor polymorphism) exceeds the interspecific odor variation. Therefore, we discuss the potential deceptive function of the emitted scent compounds, in particular those that are related to cadaveric decomposition. Moreover, we review the data about emitted scent compounds in *Amorphophallus* with a focus on putative odor polymorphism. Upon examination, it appears that the emitted scent compounds in *Amorphophallus* are highly mimetic of decomposing organic materials. We show that several species display odor polymorphism, which in turn might constitute an obstacle in the analysis of evolutionary trends. An important odor polymorphism is also indicated by subjective odor perceptions. Odor polymorphism may serve several purposes: it might represent an adaptation to local pollinators or it might assumingly prevent insects from learning to distinguish between a real decomposing substrate and an oviposition-site mimic.

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Introduction

Deceptive flowers

The art of deception is known to be practiced by thousands of plant species for the sake of avoiding herbivory,[1,2] for seed dispersal[3] and for pollination.[4–8] Deceptions by plants are based on visual components, chemical ones, or on both. One of the most complex deceit types is sexual deception in Orchidaceae, which consists of both visual and olfactory mimicry of a specific female insect by a flower.[7–9] Another deceit type that exploits the reproductive instincts of insects is brood-site mimicry or oviposition-site mimicry.

Oviposition site mimicry has independently evolved in several angiosperm plant families such as the Annonaceae, Apocynaceae, Araceae, Orchidaceae and Rafflesiaceae.[10,11] The flowers or inflorescences visually and olfactorily mimic a specific substrate, which constitutes the main food source for saprophagous and copro-necrophagous insects and/or their larvae. The targets are deceived into believing to have located a suitable substrate for feeding, mating and/or breeding. Typical mimicked substrates are: carcasses, carrion, dung, feces, rotting plant material or mushrooms.[10]

The key communications signals in this type of plant-pollinator interaction are the scent compounds.[10,11] Based on chemical mimicry, they are emitted to specifically exploit the insect's perception.[10,11] Moreover, scent compounds have a wide operational range, especially if they are promoted by heat, such as in thermogenic species.[12–14]

In the Araceae, oviposition-site mimicry is found in several genera from the Aroideae subfamily, the genus *Amorphophallus* among others.[15] The plant-pollinator interactions within the Araceae are reported to be based on perception biases and not on co-evolution, the color and odor preferences of the visiting insects, beetles in particular are evolutionary conserved and the plants exploit preexisting preferences.-[5,10,16–19] The evolutionary conservation of preferences for olfactory signals such as methoxylated aromatic hydrocarbons, and by consequence animal perception, can be described as "variation around a theme".[18] The convergence between the scent chemistry of *Amorphophallus*, stapeliads and other brood site deceit flowers is likely to be based on sensory exploitation.[10,20,21]

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However, only few authors investigated and actually tested the evolutionary relationship between innate preferences of pollinating insects and the emitted volatile organic compounds (VOCs) of the pollinated oviposition-site mimics; within one or even across convergent plant lineages.[8,10,16,18,22] Moreover, it has been demonstrated that varied proportions of scent compounds can lead to different signaling functions.[23] Furthermore, we emphasized the necessity to consider the pollinators and the herbivores when investigating the evolution of floral traits. Similarly, because carrion and dung odors are good predictors of three potential dangers to mammalian herbivores, namely pathogenic microbes, proximity of carnivores, and feces-contaminated habitats that present high risks of parasitism, it has been proposed that in addition to pollinator attraction, carrion and dung odors may repel mammalian herbivores.[24]

Amorphophallus

The genus *Amorphophallus* Blume ex Decne comprises some 230 species[25–28] and is the third largest genus in the Araceae family [29,onwards] as well as the largest Araceae genus with a paleotropical distribution. The genus has been delimited into four subgenera, namely the subgenera *Afrophallus* Hett. & Claudel, *Amorphophallus, Metandrium* and *Scutandrium* Hett. & Claudel.[30]

Amorphophallus inflorescences consist of a spadix and a spathe borne on a peduncle.[31] In most species, the spathe is funnel or bowl shaped during anthesis and the spadix is freely accessible to insect visitors or pollinators (Figure 1a, b). More rarely, the spathe is constricted in a lower base (kettle) and an upper limb (Figure 1c). When strongly constricted, the kettle forms a floral chamber or a trap.[32] The spadix has three zones

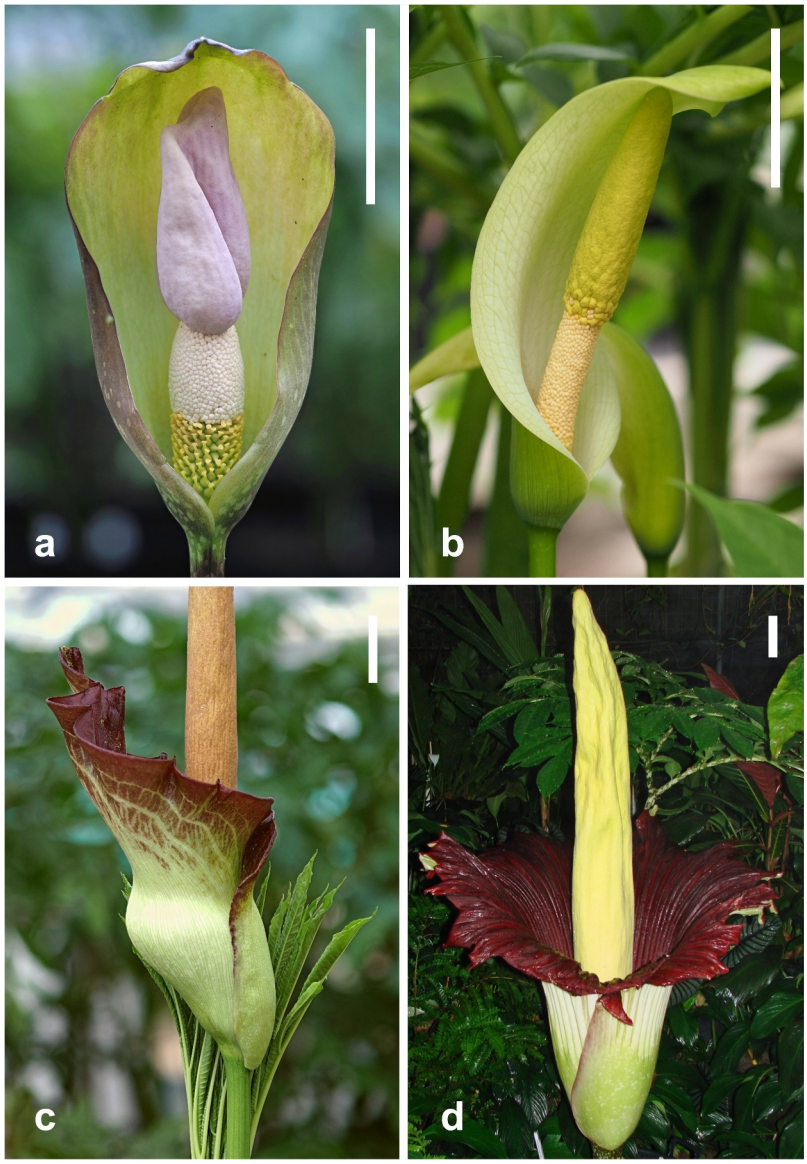

Figure 1. Inflorescences of A: *Amorphophallus thaiensis* and B: *A. albus*, consisting of a spadix surrounded by a spathe. C: spathe separated into a limb and a base forming a floral chamber in *A. angolensis*. The pistillate and the staminate flowers are freely accessible in A & B. D: Inflorescence of the iconic *A. titanum* the largest carrion flower of the genus. Scale bars: A, B & C = 5 cm. D = 10 cm. Photographs: A, B & C = Cyrille Claudel. D = Steve Jackson.

(Figure 1a). The lowermost zone bears the female (pistillate) flowers, and the zone above it bears the male (staminate) flowers. The terminal zone, the appendix, essentially serves for attraction of pollinators through scent emission, sometimes enhanced through heat generation, such as in the iconic *A. titanum* (Figure 1d).[12,13,33] Typical of the Araceae, *Amorphophallus* inflorescences are protogynous and anthesis usually lasts for two days. Stigma receptivity is signaled by the release of VOCs which serve to attract insect visitors and pollinators.

Identification and evolution of scent compounds in *Amorphophallus*

The scent compounds of nearly a hundred species of the genus *Amorphophallus* have been identified[13,34–41] (Supplemental material, Table S1). The scents emitted by *Amorphophallus* species are reminiscent of carrion, various forms of excrements, fish, sewerage, nauseating gases, rancid cheese, fermenting fruit and mushrooms.[34–41] Table S1 lists all the investigated *Amorphophallus* species, the analyzed voucher and sampling time and the identified scent compounds in their relative amount as well as the subjective perception.

Kite and Hetterscheid[37,38] identified the scent compounds of 92 *Amorphophallus* species using GC-MS [gas chromatography–mass spectrometry). They generated seven main categories based on the chemical identity of the defining scent compound per *Amorphophallus* species, mapped these as characters onto the Bayesian consensus tree from [30] and investigated the evolutionary trends of inflorescence odors in *Amorphophallus*. However, the inferred trends provided a heterogeneous picture [38], which is an intriguing result, considering that scent compounds are assumed to be the key elements of deceptive floral systems.[10,11,21,23,42,43]

[38] found that dimethyl oligosulphides are released in species across all four subgenera and are the most common constituents in half of the 92 species studied. Dimethyl oligosulphides are characteristic of the decomposition of various organic matters, ranging from sulfur-rich vegetables, to cancerous wounds and most importantly cadaveric decomposition and carnivore dung.[10,41,44] They are released in various plant lineages and represent well-known attractants for various copro-necrophagous beetles and flies.[45–47] Furthermore, two distantly related *Amorphophallus* clades, comprising a handful of species each, were found to be characterized by the emission of benzenoid compounds, which are considered to be strongly evolutionarily constrained.[38] Moreover, several smaller phylogenetic subunits comprising a few closely related species were identified, such as the *A. aphyllus* group, sharing a similar inflorescence morphology and similar odor types, namely dung odors.[38]

In contrast, other odor types were found to have a high degree of plasticity, evidenced by the observation that some sister species release different scent types.[38] For example, two closely related Asian species with fungal odors, *A. obscurus* and *A. polyanthus* emit chemically very different scent compounds. *Amorphophallus obscurus* releases high proportions of various alcohols, such as isoamyl alcohol whereas *A. polyanthus* mainly emits a ketone, more precisely 2-heptanone. Similarly, *A. ongsakulii* and *A. myosuroides* are characterized by the emission of 90% 2-nonanol and 75% α-ketoisocaproic acid respectively. Consequently, although closely related, both species are placed in two different categories sensu [38]. Moreover, a third closely related species, *A. sumawongii*, is characterized by the emission of dimethyl oligosulphides. However, at least this species is also morphologically different.[38] Lastly, the two African mainland sister species *A. abyssinicus* and *A. mossambicensis* share a similar inflorescence morphology; however, *A. mossambicensis* is a member of the aliphatic esters group and smells of carrion whereas *A. abyssinicus* smells of dung and belongs to the terpenoids and alkanes group.[38]

Beyond that, similarly to previous phylogenetic studies,[48–50] no characters could be identified that would circumscribe larger phylogenetic units. [38],proposed that variation in pollinator taxa is the driving force, leading to the divergence of odor types in some species as well as to the convergence of some odor types in others.

However, besides specific olfactory cues, such a specialized plant-pollinator interaction may also have to rely on an evolutionary constrained inflorescence morphology, discriminating between different insect types. This appears to be unlikely as the spathe of many *Amorphophallus* species forms a funnel- or bowl-like structure (Figure 1), which is easily accessible for a large insect array. Some *Amorphophallus* species, such as *A. ongsakulii* or *A. interruptus* have small and frail inflorescences or a very tight spathe entrance, which excludes pollinators of a larger size. However, beyond that, there seems to be few further discriminatory traits, especially if compared to highly constrained flowers of another deceit type, namely sexual deception in orchids.[7–9] What is more, the apparent olfactory deceit of the majority of *Amorphophallus* species is based on the emission of dimethyl oligosulphides, which is not indicative of a specific plant pollinator interaction as these volatiles attract a wide array of insects searching for decomposing organic matter for feeding, mating or breeding. Unfortunately, the pollinators of *Amorphophallus* species are largely unknown, making it impossible to investigate this putative relationship on a larger scale.[51] Insect pollinators or visitors have been reported for little more than 20 *Amorphophallus* species and roughly a third of these observations rely on a single inflorescence per species.[51] Moreover, most observations suggest an unspecialized plant-pollinator interaction or at least the attraction of a multitude of different insects or other arthropods.[51] Nonetheless, beetles appear to be the main pollinator group in most investigated species.[51,52]

That said, there is another hypothesis possibly accounting for the several trends in *Amorphophallus* inflorescence odors that have not been considered yet, which is intraspecific scent variation or odor polymorphism. Investigations of the scent emissions in the genus *Arum*, another and better studied member of the subfamily Aroideae, revealed that the emitted scent compounds can vary considerably within a single species. Significant differences in the proportion of the emitted scent compounds were detected in *Arum italicum* and *A. maculatum*.[39,53–55] In some cases, the differences in the spectrum of the emitted scent compounds were so significant that they were categorized as chemotypes.[54] Another study investigated the inflorescence morphology, pollinators and scent

compounds in natural hybrids, originating from parental populations from *Arum italicum* and *A. maculatum*.[56] Remarkably, eight scent compounds that were not detected in the floral odor of either parental species were detected in the hybrid offspring.[56] Odor polymorphism has also been documented in the deceptive orchid *Dactylorhiza romana*.[17]

Objectives

The aim of the present review is twofold. (1) Decomposition of organic matter, be it vegetable matter, carrion or dung, appears to represent the dominant deceit type in the genus *Amorphophallus* [e.g., [38]]. In order to ascertain their deceptive function, several of the scent compounds emitted by the model, cadaveric decomposition in particular, are compared to the scent compounds emitted by *Amorphophallus* carrion mimics. (2) Assuming that intraspecific odor polymorphism in *Amorphophallus* is as important as in the genus *Arum*, it is likely to shade putative evolutionary relationships and trends in regard to inflorescence odors. Consequently, the relevant literature is reviewed in regard to odor polymorphism in *Amorphophallus*.

Scent compounds emitted by cadaveric decomposition

Volatile organic compounds (VOCs) released after death are described as the chemistry of death or thanatochemistry.[57] The decomposition of a cadaver is initiated by the degradation of the body through its own enzymatic and chemical reactions, defined as autolysis. The breakdown of four major biological molecule classes during the various stages of decomposition is at the base of the resulting mixture of volatile organic compounds, i.e., the scents of death. The classes are: proteins, nucleic acids, lipids and carbohydrates, and their degradation ultimately leads to VOCs such as diamines, sulfur compounds (dimethyl oligosulphides), phenolic molecules such as indole and skatole, organic acids, alcohols, ketones, aldehydes, esters and ethers, hydrocarbons, nitrogen and oxygenated compounds such as acetone.[57] Conversely, the emitted compounds inform the insects about the nutritive potential of the decomposing organic material, since decomposing lipids will lead to different signals from proteins, etc.[10] However, not only the nutritive composition but also the stage of decomposition is indicated by the emitted volatiles.[10]

Once internal microorganisms take the lead, bloating marks the beginning of putrefaction. The environment and abiotic parameters such as temperature, humidity, and oxygen concentrations can have a strong influence on microorganismal activity, and therefore on decomposition itself. Following [57], autolysis and putrefaction can be subdivided into five general stages; fresh, bloated, active decay, advanced decay and skeletonization. [58] investigated the human decomposition fluid formed during autolysis and corpse putrefaction, in order to identify the most characteristic scent compounds for a cadaver-detection dog-training program. [58], identified 35 VOCs found in 95% of all analyzed samples, among others: dimethyl trisulfide, which after dimethyl disulfide constitutes the most abundant compound across the genus *Amorphophallus*, and pyrazine, the defining volatile compound of *A. preussi*.[38] Furthermore, [58], identified 2-decanone, hexanal, nonanal, phenol and 2-undecanone, all being minor volatile compounds in different *Amorphophallus* species,[38] and also 2-heptanone, the major scent compound in *A. polyanthus*, as well as propionic acid, which is present in *A. gigas*.[36,38,]also identified acetone in 88% of the analyzed samples, a compound also released by *A. borneensis* (8%), *A. commutatus* (11%), *A. erythrrorhachis* (12%), *A. konjac* (2% + 6%), *A. plicatus* (2%), *A. macrorhizus* (3%), *A. henryi* (7%), *A. eburneus* (18%) and *A. tinekeae* (9%).[58]

Similarly, [59],analyzed the profile of VOCs released by pig carcasses during the first 75 hours after death. Dimethyl oligosulphides were identified, notably ethyl acetate, which is the major volatile component of *A. antsingyensis* and *A. consimilis*. Furthermore, 1-propanol and 3-methyl-1-butanol, two of the major volatile compounds for the *Amorphophallus* group defined by high proportions of aliphatic alcohols and ketones[38] were identified. [57],also investigated the decomposition of pig carcasses and recovered 104 volatile organic compounds, amongst them trimethylamine, the defining scent compound of the nitrogen-containing *Amorphophallus* group,[38] together with 4-methylpentanoic acid (isocaproic acid) and butanoic acid, the defining scent compounds of the *Amorphophallus* group defined by high proportions of aliphatic acids.[38] Without comparing every scent compound of the models and the mimics one by one, it becomes apparent that there is a remarkable overlap between the single scent compounds emitted by human decomposition fluid formed during putrefaction, pig carcasses and various *Amorphophallus* species (Table 1). Therefore, referring to the first objective of this review, it is reasonable to assume that the function of these scent compounds is mimicking cadaverous decomposition.

Investigation of odor polymorphism in *Amorphophallus*

Kite and Hetterscheid[37,38] analyzed 15 *Amorphophallus* species twice and four species thrice (Table S1). Some species, such as *A. macrorhizus, A. mossambicensis, A. paeoniifolius* and *A. sumawongii*, yielded more or less similar scent compound spectra in all analyses, although different individuals were investigated and compared. *Amorphophallus consimilis, A. variabilis* and *A. yuloensis* were also analyzed twice and showed similar results. However, similar results should be expected here since clonally propagated plants had been analyzed. The documented variation can obviously at least partly be accounted for by different study methodologies[37,38,40] or because of different sampling times or sample overloads, etc.[38] Particularly, the sampling time seems to be a critical aspect, as the variation in scent composition may strongly vary during anthesis.[13,38,41,55] Thus, whenever possible, a consistent sampling protocol was ensured, minimizing the influence of the sampling time.[38] However, some individuals reveal a broader intraspecific variation or scent polymorphism.

Table 2 shows the *Amorphophallus* species that have been analyzed repeatedly and which show the most significant differences between the analyzed individuals. The three analyses of *A. konjac* also showed significant differences (Table 2; [37,38]). Even more so, if compared to the analysis of *A. konjac* by [34], (Table S1).

Table 1. Scent compounds released by human decomposition fluid, pig carcasses and *Amorphophallus* species. Numbers refer to: **1**) [58], **2**] [59], **3**) [57]. Except for *A. gigas*,[36] all scent compounds emitted by *Amorphophallus* species are retrieved from Kite and Hetterscheid.[37,38] Group defining compounds refer to compounds used by [38],to categorize major scent groups.

Selected VOCs emitted during cadaveric decomposition	ref.	also emitted by the *Amorphophallus* species (rel. % of the total odor composition in descending order)	used as group defining compound[38] of the:
1-phenylethanone (acetophenone)	1	*A. symonianus* (60%), *A. amygdaloides* (60%), *A. cicatricifer* (55%, 39%), *A. pulchellus* (5%), *A. putii* (2%), *A. yuloensis* (11%, 6%)	benzenoid compounds group
1-propanol	2	*A. cirrifer* (16%, 11%), *A. obscurus* (10%), *A. pilosus* (7%)	aliphatic alcohols and ketones group
2-decanone	1	*A. ankarana* (2%)	
2-heptanone	1	*A. polyanthus* (85%, 62%), *A. eichleri* (30%, 25%), *A. ankarana* (3%)	aliphatic alcohols and ketones group
2-undecanone	1	*A. ankarana* (3%)	
3-methyl-1-butanol	2	*A. ankarana* (39%), *A. cirrifer* (36%, 16%), *A. henryi* (30%, 7%), *A. obscurus* (21%), *A. borneensis* (8%), *A. commutatus* (3%), *A. konjac* (3%)	aliphatic alcohols and ketones group
4-methylpentanoic acid	3	*A. elatus* (100%), *A. atroviridis* (98%), *A. linearis* (94%), *A. macrorhizus* (97%, 95%), *A. angustispathus* (50%), *A. saraburiensis* (23%), *A. scutatus* (7%), *A. baumannii* (6%), *A. johnsonii* (4%),	aliphatic acids group
acetone	1	*A. eburneus* (18%), *A. erythrrorhachis* (12%), *A. commutatus* (11%), *A. tinekeae* (9%), *A. borneensis* (8%), *A. henryi* (7%), *A. konjac* (6%, 2%), *A. macrorhizus* (3%), *A. plicatus* (2%)	
butanoic acid	3	*A. taurostigma* (74%), *A. saraburiensis* (4%), *A. scutatus* (4%)	aliphatic acids group
dimethyl oligosulphides	2	identified in varied proportions in **58 out of 92** investigated *Amorphophallus* species	sulfur-containing compounds group
dimethyl trisulfide	1	identified in varied proportions in **47 out of 92** investigated *Amorphophallus* species	sulfur-containing compounds group
ethyl acetate	2	*A. consimilis* (77%, 57%), *A. haematospadix* (65%), *A. annulifer* (60%), *A. antsingyensis* (43%), *A. laoticus* (23%), *A. borneensis* (10%), *A. baumannii* (5%), *A. henryi* (2%)	aliphatic esters group
hexanal	1	*A. pilosus* (3%)	
nonanal	1	*A. elliottii* (3), *A. eburneus* (3%), *A. erythrorrhachis* (2%)	
phenol	1	*A. impressus* (6%)	
propionic acid	1	*A. gigas* (4%)	
pyrazine	1	*A. preussi* (61%)	nitrogen-containing compounds group
trimethylamine	3	*A. brachyphyllus* (85%), *A. eburneus* (64%), *A. tinekeae* (35%), *A. angolensis* (18%), *A. plicatus* (13%), *A. longispathaceus* (4%), *A. konjac* (2%)	nitrogen-containing compounds group

Likewise, a significant variation was detected in the two specimens of *A. scutatus* (Table 2). The scent of the first individual consists of 100% dimethyl oligosulphides, whereas the scent of the second individual contains dimethyl oligosulphides (59%), 1-butanol (12%), 4-methyl-1-pentanol (5%), butanoic acid (4%), S-methyl thioesters (2%), acetic acid (2%), ethylacetate (2%), isocaproic acid (7%), and 2-methylbutanoic acid (2%).[38]

Particularly two of the three analyses of *A. eichleri* are of interest, insofar as the major compound was not the same in analysis one (56% dimethyl disulfide) and in analysis two (30% 2-heptanone) [[38], Table 2]. Therefore, the second individual of *A. eichleri* could be categorized under "alcohols and ketones" group instead of the "sulphur compounds" one.[38]

However, the most remarkable differences are found between the different analyses of *A. titanum*.[13,35,37,38,40,41] The comparison of the results must be done cautiously, as different sampling and analysis methods have been employed. Particularly the methodological approach from [40] differs strongly. Nevertheless, some differences are noteworthy. [37], identified dimethyl disulfide (75%) and trimethyl disulfide (10%) as the major volatile compounds in *A. titanum* and described the scent as gaseous plus urine (Table 2). In a second analysis [38], identified dimethyl disulfide (70%), trimethyl disulfide (25%), tetra disulfide (1%) and S-methyl thioesters (3%) and described the scent as gaseous or as rotting vegetables (Table 2).

[41],identified dimethyl trisulfide as the major component; moreover, they identified various compounds not detected by [38]. Furthermore, [41] closely followed anthesis of *A. titanum* by the human nose, and the scent changed over time from "slight rotten-fruit-like odor" to "yellow-pickled-radish, rotten-egg, rotting-animal-like odour", then "strong rotting-animal-like odor" and finally "rotten-fish and rotten-egg" (Table 2). The scent composition obviously varies strongly during anthesis. Based on the results of[35,41],attempted to objectively describe the scent compounds of *A. titanum* using electronic noses, based on semiconductor-sensors. They compared the odor profile of an *A. titanum* plant grown in Kagoshima with the odor profile of the *A. titanum* plant grown in Tokyo that was previously studied by [41]. [35] described the odor profile from *A. titanum* as "decayed cabbage, garlic and pungent sour".

In contrast, no sign of dimethyl disulfide and dimethyl trisulfide could be detected in the analysis of *A. titanum*.[13] Moreover, the initial carrion smell changed to a weak sweet smell during anthesis. Benzaldehyde, an almond-like smelling compound, was identified as the dominant compound during the ongoing of anthesis.[13] The analyzed plant descended from material cultivated in the Palm Garden in Frankfurt/Main, Germany and had been originally collected near Padang in Indonesia.

Another investigation of the scent chemistry of *A. titanum* was performed by [40]. However, it belonged to another plant source, i.e., Dr. Louis Ricciardiello, New Hampshire, USA. A total of 25 scent compounds were identified in this case, and the resulting odor profiles were again different [[40], Table 2]. No dimethyl- di- or trisulfides were identified. Instead, the three major scent compounds emitted by the appendix were

Table 2. Some selected *Amorphophallus* species which show significant odor polymorphism. Differing scent classes within a species are highlighted in bold. If specified in the original publications, voucher and/or origin are provided. The quantity of the identified scent compounds is presented as in the original publications, either as percentage or as symbol (x; +; -). Percentage numbers are rounded in two cases.[34,40] References are given as numbers and refer to: **1**) [37], **2**) [13], **3**) [41], **4**) [34], **5**) [38], **6**) [40].

species & voucher	chem. category sensu Kite & Hetterscheid	scent compounds per species and individual in % or as given in according reference.									
		isoamyl alcohol	isoamyl acetate	β-pinene	tridecane	α-pinene	camphene	skatole	2-butanol	acetone	butyl acetate
A. henryi HAM 270	alcohols and ketones	30		25	22	16	2	2			
A. henryi 1994–3573	alcohols and ketones	7	18	10	6	2			17	7	6
		1-		phenylethanone	methyl cinnamate	1-phenylethyl acetate					
A. symonianus HAM 924	benzenoid compounds	60	39								
A. symonianus 1998–3421	benzenoid compounds		6	89							
		dimethyl disulfide	dimethyl trisulfide	dimethyl tetrasulphide	2-heptanone	indole	phenylethylalcohol	butyl heptanoate	2-pentanone	α-ketoisocaproic acid	1-butanol
A. eichleri not specified	sulfur compounds	62	15	1	7	2	1				
A. eichleri 1994–7554 (1)	sulfur compounds	56	7	1	25			8			
A. eichleri HAM 007 [2]	**alcohols and ketones?**	23	1		**30**				13	10	6
		dimethyl disulfide	dimethyl trisulfide	dimethyl tetrasulphide	ethanol	2/3-methyl-2-butenal	trimethylamine	3-methyl-1-butanol	acetaldehyle	acetone	2-butanone
A. konjac not specified	sulfur compounds	76	17								
A. konjac 1997–111	sulfur compounds	55	3		9	6	6	3	3	2	2
A. konjac HAM 168	sulfur compounds	40	17	1		3	2	3		6	12
A. konjac China, KBG	sulfur compounds	43	26	2							
		dimethyl disulfide	dimethyl trisulfide	dimethyl tetrasulphide	dimethyl pentasulphide	1-butanol	isocaproic acid	4-methyl-1-pentanol	butanoic acid	ac s-methyl thioester	acetic acid
A. scutatus HAM 589	sulfur compounds	34	61	5							
A. scutatus HAM 590	sulfur compounds	18	29	11	1	12	7	5	4	2	2
		dimethyl disulfide	dimethyl trisulfide	dimethyl tetrasulphide	ac s-methyl thioester	pungent smell	sweet smell	almond like	benzaldehyde	trimethylamine	3-methyl-butanal
A. titanum not specified	sulfur compounds	75	10								
A. titanum 1997–5514	sulfur compounds		25	1	3						
A. titanum Palm Garden	**benzenoid compounds?**					**x**	**x**	**x**	**x**		
A. titanum: gas sample	**nitrogen-containing?**		+							++	+
A. titanum: appendix	**aliphatic acids?**								4		

Table 2. continue

species & voucher	scent compounds per species and individual in % or as given in according reference.													Ref.
	isobutyl acetate	undecane	caryophyllene	ethyl acetate	limonene	3-methyl-2-hexanone								
A. henryi HAM 270														**5**
A. henryi 1994–3573	6	5	2	2	2	1								**5**
A. symonianus HAM 924														**5**
A. symonianus 1998–3421														**5**
	2-hexanone	4-methyl-1-pentanol	2-pentanol											
A. eichleri not specified														**1**
A. eichleri 1994–7554 (1)														**5**
A. eichleri HAM 007 [2]	3	2	2											**5**
	2-methyl-1-butanol	isoamyl alcohol	β-caryophyllene	3-methyl-2-pentanone	4-hydroxy-4-methyl-2-pentanone	n-nonaldehyde	butyl ether	3-methyl-1-pentanol	n-dodecane	2-pentanone	n-tridecane	butyl 2-propenoate		
A. konjac not specified														**1**
A. konjac 1997–111														**5**
A. konjac HAM 168	2													**5**
A. konjac China, KBG	3	6	3	2	2	2	2	2	1	1	1	1		**4**
	ethyl acetate	2-			methylbutanoic acid									
A. scutatus HAM 589														**5**
A. scutatus HAM 590	2	2												**5**
	methyl thiolacetate	acetic acid	isovaleric acid	isovaleric acid	butyric acid	benzylalcohol	γ-butyrolactone	3-hydroxy-2-butanone	2-phenoxyethanol	phenol	4-hydroxy-4-methyl-2-pentanone	nonanal	trimethyl pyrazine	
A. titanum not specified														**1**
A. titanum 1997–5514														**5**
A. titanum Palm Garden														**2**
A. titanum: gas sample	-	+	-											**3**
A. titanum: appendix				**22**	**17**	16	12	6	3	3	3	2	2	**6**

isovaleric acid (21.6%), butyric acid (17.0%) and benzyl alcohol (16.2%) (Table 2). However, the methodological approach followed by [40],differed significantly in that the analyzed tissues were cut off the plant and pre-treated.

Additionally, it should be noted that [60] examined two flowering *A. titanum* individuals. These two plants were the first ones to flower on the European continent and their development was closely followed.[60] One plant was found to be strongly scented whereas the second inflorescence was found to be nearly scentless.[60]

Only the two analyses from Kite and Hetterscheid[37,38] on the one hand, and the two analyses from [41],and [35],on the other, yielded a similar odor profile for *A. titanum*. It was not specified if Kite and Hetterscheid[37,38] repeatedly analyzed the same plant, or two different plants. In any case, if two different plants were analyzed, they are likely to have the same origin since at that time only a few clones of *A. titanum* were shared among different botanical gardens. As for the plants analyzed by [41],and [35], they both originated from one infructescence, harvested in 1993.[61,62] These plants are therefore unequivocally of the same maternal origin and a similar odor profile could be expected.

Therefore, the odor profiles from all analyzed *A. titanum* plants, except from those of the same genetic origin, are markedly different.[13,35,37,38,40,41] Thus, at least in the case of *A. titanum*, the odor profiles of single specimens only partially reflect the genetic and olfactory variability of the species. Moreover, if categorized per major scent compounds, these plants would not be categorized under "sulphur compounds"[37,38] but under benzenoid compounds,[13] nitrogen-containing compounds,[41] and under aliphatic acids.[40] Thus, *A. titanum* could be placed in four different scent categories sensu [38].

The scent experience based on human perception also indicates significant variation in *A. titanum* and in several other species (Table 3). Although subjective, the differences are too important to be ignored. Some species, such as *A. cicatricifer* and *A. fallax*, show slight differences in their odor profiles (Table 3). More important, however, is the perceived odor variation within the subspecies of *A. commutatus*, which range from "rottening meat" to "gaseous and fruity".[63] Likewise, one individual of *A. gigas* was perceived as smelling like "spoiled meat",[61] whereas another has been described as smelling "rotten, fishy and sour".[36] Furthermore, *A. maximus* and *A. mossambicensis* can smell like "rotting meat" or "dung",[37,38] whereas *A. konkanensis* is either reminiscent of "cheese"[38] or of "rottening meat".[63] Furthermore, the scent of *A. sylvaticus* has been described as "rottening" meat by [63],and as "bad vegetables" by [38]. The scent of two specimens of *A. symonianus* has been described as "almond, chemical" by [38]. However, some specimens of *A. symonianus* also smell fruity and strongly cinnamon-like with a pinch of shoe polish (personal observation). Strikingly, the scent of *A. aphyllus*, a species that is known as a dung species par excellence[30,38] has recently been described as "fruity, melon-like, with added alcohol" [Steve Jackson, pers. comm.]. Apparently, the olfactorily deceit in *A. aphyllus* ranges from dung to fermenting fruit.

From carrion to sweet odors

[38],also sampled two individuals of *A. symonianus* that showed a strong difference in the emitted quantities of two aromatic compounds or benzenoids, 1-phenylethylacetate and 1-phenylethanone. The scent of plant one consisted mainly of 1-phenylethanone (60%) and the scent of plant two, of 1-phenylethylacetate (89%) (Table 2). Disregarding the difference in scent composition between the two specimens, the odor is composed of only a few scent compounds.[38] Two questions emerge from these finds. First, how do sweet odor types fit into the variation around a theme revolving around decomposition and decay? Second, is the number of contributing scent compounds indicative of the relationship between the plant and its pollinators? In essence, does a scent composition that comprises exclusively one or two scent compounds indicate a more specialized plant-pollinator interaction than a scent composition that comprises 10–20 scent compounds? One further VOC identified in 95% of all samples of human decomposition fluid was 1-phenylethanone or acetophenone.[58] Acetophenone is the simplest aromatic ketone, and interestingly, the major scent compound of one of the *A. symonianus* individuals. It is also a major scent compound in *A. amygdaloides* and *A. cicatricifer*, and a minor scent compound in *A. pulchellus, A. putii*, and *A. yuloensis*.[38] Although speculative, it is conceivable that these species just mimic an earlier and sweet-scented phase of decomposition and/or target a different pollinator group as suggested by [38].

However, another well-supported clade in the subgenus *Metandrium* contains five species that, except for *A. amygdaloides* (see above), emit a scent that is entirely composed of 1-phenylethyl acetate.[38] The species are *A. dunnii, A. putii, A. thaiensis* and *A. yunnanensis*, and the scent is reported to be generally perceived as fruity, or in the case of *A. dunnii, A. putii* and *A. yunnanensis* as reminiscent of grated carrots.[38] This scent compound cannot be related to cadaveric decomposition and is not reported to be a known attractant otherwise. However, unfortunately the pollinators of all the mentioned species are completely unknown.

Similarly, there is another clade containing sweet-scented species of the subgenus *Scutandrium*, such as *A. albispathus, A. longituberosus* and *A. tenuispadix*, and these species emit anise-like odors almost solely based on 4-methoxyphenethyl alcohol as well as a minor addition of methyl 4-methoxybenzoate.[37,38] It is unclear if and how these scents fit into the theme, as at least 4-methoxyphenethyl alcohol does not seem to be linked to cadaveric decomposition processes. Nonetheless, it is known that methoxylated aromatics in general, and 4-methoxyphenethyl alcohol in particular, are strong attractants to various beetle taxa.[67–69]

Apparently, species that emit benzenoid compounds have little variation if any, in their odor profiles.[38] This suggests an evolutionary trend, linked to a specific pollinator.[38,70] However, it must also be taken into account that only a handful of species, almost exclusively emit either 4-methoxyphenethyl alcohol or 1-phenylethanol derivatives each. Moreover, the species within both clades are closely related and the morphological variation between the species is low in both clades.[71,72] For example, *A. putii* and *A. yunnanensis* from subgenus *Metandrium* are morphologically hardly distinguishable, the

Table 3. *Amorphophallus* species which show significant odor polymorphism based on the subjective human scent perception, with according reference.

species	subjective odor perception as described in according reference	reference
A. aphyllus	dung	[30]
A. aphyllus	fruity, melon-like, with added vodka	[pers. commun. S. Jackson]
A. cicatricifer	gaseous plus fruity	[37]
A. cicatricifer	gaseous, almonds	[38]
A. commutatus	dead meat	[38]
A. commutatus	rottening meat	[63]
A. commutatus var. *anmodensis*	gaseous, fruity	[63]
A. commutatus var. *anshiensis*	gaseous, fruity	[63]
A. commutatus var. *wayanadensis*	rottening meat	[63]
A. fallax	gaseous	[37]
A. fallax [1]	gaseous, sweet	[38]
A. fallax [2]	gaseous, sweet	[38]
A. gigas	spoiled meat	[61]
A. gigas	rotten, fishy, sour	[36]
A. johnsonii	sewerage	[38]
A. johnsonii	carrion	[64]
A. konkanensis	cheese	[38]
A. konkanensis	rottening meat	[63]
A. mossambicensis [1]	carrion	[38]
A. mossambicensis [2]	carrion	[38]
A. mossambicensis [3]	acidic, dung	[38]
A. prainii	gaseous	[37]
A. prainii	rotten meat	Soepadmo, [65]1973
A. sylvaticus	bad vegetables	[38]
A. sylvaticus	rottening meat	[63]
A. symonianus	fruity, cinnamon, shoe polish	(personal obs.]
A. symonianus [1]	almond, chemical	[38]
A. symonianus [2]	almond, chemical	][38]
A. titanum	gaseous plus urine	[37]
A. titanum	gaseous, rotting vegetables	[38]
A. titanum	carrion and weakly sweet	[13]
A. titanum	old fish	[61]
A. titanum	rotting flesh, changing to excrement	[66]
A. titanum	decayed cabbage, garlic and pungent sour	[35]
A. titanum	nearly scentless	[60]
A. titanum	strong scent	[60]
A. titanum: appendix sample	rotting meat	[40]
A. titanum	slight rotten fruit like, yellow pickled radish, rotten egg, rotting animal-like, rotten fish, rotten egg	[41]

main difference being that the appendix in *A. putii* is laterally compressed.[71] Likewise, the overall inflorescence morphology is identical in *A. albispathus, A. longituberosus* and *A. tenuispadix*; the defining characters of the species refer to the leaf architecture, the tuber shape and the pores of the anthers.[71] Moreover, they all occur in Thailand.[71] Consequently, both clades might represent starting points of speciation that putatively exploit another olfactory preference of Coleoptera.

Discussion and conclusions

Obviously, the documented intraspecific variation in odor composition can be partly attributed to differing methodological approaches and/or to different sampling times.[38] However, it might not fully account for the highlighted differences between individuals of several species. Furthermore, although subjective, it appears legitimate to address odor polymorphism, considering the varied odor characterizations in several *Amorphophallus* species.

Most species of two smaller and not closely related clades, the clade containing *A. albispathus, A. longituberosus* and *A. tenuispadix* from subgenus *Scutandrium* and the clade containing *A. putii, A. symonianus* and *A. yunnanensis* from subgenus *Metandrium*, exclusively emit benzenoid compounds, 4-methoxyphenethyl alcohol or 1-phenylethanol derivatives. These species have little or no variation at all in their scent composition. Moreover, except for acetophenone, these benzenoid compounds cannot be related to decomposition.

That said, the majority of *Amorphophallus* species emit more complex odor compositions that can be specifically related to decomposition processes. The emitted scent compounds perfectly mimic their natural decomposing counterparts and some species show a significant odor polymorphism. This particularly applies to *A. titanum*, where practically each analysis yielded a different odor spectrum. A high degree of odor polymorphism, as documented in *A. titanum* may blur the study of evolutionary trends when the intraspecific variation exceeds the interspecific variation in several species. Consequently, although the presented differences are only indicative, they nonetheless demonstrate the need for a more extensive and systematic sampling.

Moreover, odor polymorphism may serve several purposes that need to be addressed. Odor polymorphism might represent an adaptation to local variations in the entomofauna.[73] Consequently, specimens of different geographical origins, ideally covering the full geographic distribution and/or the morphological range, should be investigated, in order to identify the whole odor profile of an *Amorphophallus* species. This would allow investigation of the correlation between scent composition and the local entomofauna. Moreover, if the full

repertoire of emitted scent compounds of each species is known, finer boundaries between species or species groups might be revealed and more subtle evolutionary trends might be detected.

Alternatively, odor polymorphism might prevent insects from learning how to distinguish between the real decomposing substrate and the mimic.[74] Carrion, dung and the like are subjected to several abiotic parameters. Moreover, decomposition processes are strongly influenced by the action of various microorganisms and never smell 100% identical.[57] Consequently, variation in odor composition might in itself be evolutionarily constrained. Under this scenario it would be challenging to trace evolutionary trends based on major scent classes in odor composition, as variation in itself would constitute a trend. Variation would then constitute a form of speciation. Moreover, it might also imply a lower evolutionary constraint of floral traits that are related to the deceptive floral system, leading to increased morphological variation. Although assumptive, the observed intraspecific odor variation is important enough to consider and investigate this phenomenon.

From a functional point of view, it becomes evident that more detailed studies are required in order to better understand the reproductive strategies of *Amorphophallus* species. The visiting and pollinating insects need to be observed and documented. Moreover, when investigating the evolution of floral traits, the necessity not only to consider the pollinators but also the herbivores has been emphasized and in the case of *Amorphophallus*, the putative repellence of mammalian herbivores through carrion or dung odors should be investigated.[24] Similarly, the simultaneous attraction of predators, preying on visiting insects needs to be considered too.[51]

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References

1. Lev-Yadun S. Defensive (anti-herbivory) coloration in land plants. Anti-herbivory plant coloration and morphology. Zug (Switzerland): Springer; 2016.
2. Wiens D. Mimicry in plants. Evol Biol. 1978;11:365–12.
3. Midgley JJ, White JDM, Johnson SD, Bronner GN. Faecal mimicry by seeds ensures dispersal by dung beetles. Nature Plants. 2015;1:15141.
4. Dafni A. Mimicry and deception in pollination. Annu Rev Ecol Syst. 1984;15(1):259–278. doi:10.1146/annurev.es.15.110184.001355.
5. Faegri K, and van der Pijl L. The principles of pollination ecology. 3rd Rev. Oxford, UK: Pergamon Press; 1979.
6. Schaefer HM, Ruxton GD. Deception in plants: mimicry or perceptual exploitation? Trends Ecol Evol. 2009;24(12):676–685. doi:10.1016/j.tree.2009.06.006.
7. Schiestl FP, Ayasse M, Paulus HF, Löfstedt C, Hansson BS, Ibarra F, Francke W. Sex pheromone mimicry in the early spider orchid (Ophrys sphegodes): patterns of hydrocarbons as the key mechanism for pollination by sexual deception. Journal of Comparative Physiology A. 2000;186(6):567–574. doi:10.1007/s003590000112.
8. Schiestl FP. The evolution of floral scent and insect chemical communication. Ecol Lett. 2010;13(5):643–656. doi:10.1111/j.1461-0248.2010.01451.x.
9. Phillips RD, Peakall R. An experimental evaluation of traits that influence the sexual behaviour of pollinators in sexually deceptive orchids. J Evol Biol. 2018;31(11):1732–1742. doi:10.1111/jeb.13370.
10. Jürgens A, Wee S-L, Shuttleworth A, Johnson SD. Chemical mimicry of insect oviposition sites: a global analysis of convergence in angiosperms. Ecol Lett. 2013;16(9):1157–1167. doi:10.1111/ele.12152.
11. Urru I, Stensmyr MC, Hansson BS. Pollination by brood–site deception. Phytochemistry. 2011;72(13):1655–1666. doi:10.1016/j.phytochem.2011.02.014.
12. Barthlott W, Szarzynski J, Vlek P, Lobin W, Korotkova N. A torch in the rain forest: thermogenesis of the Titan arum (*Amorphophallus titanum*). Plant Biology. 2009;11(4):499–505. doi:10.1111/j.1438-8677.2008.00147.x.
13. Lamprecht I, Seymour RS. Thermologic investigations of three species of. Amorphophallus Journal of Thermal Analysis and Calorimetry. 2010;102(1):127–136. doi:10.1007/s10973-010-0891-9.
14. Seymour RS. Scaling of heat production by thermogenic flowers: limits to floral size and maximum rate of respiration. Plant Cell Environ. 2010;33:1474–1485.
15. Gibernau M, Chartier M, Barabé D. Recent advances towards an evolutionary comprehension of Araceae pollination. In Seberg O, Peterson G, Barfod AS, Davis JI, eds. Diversity, phylogeny and evolution in the monocotyledons. Fourth international conference on the comparative biology of the monocotyledons proceedings; Denmark, Aarhus Univ. Press. 2010. 101–104
16. Chittka L, Thomson JD, eds. Cognitive ecology of pollination. Cambridge (UK): Cambridge Univ. Press; 2001.
17. Salzmann C, Schiestl F. Odour and colour polymorphism in the food-deceptive orchid. Dactylorhiza Romana Plant Systematics and Evolution. 2007;267(1–4):37–45. doi:10.1007/s00606-007-0560-z.
18. Schiestl FP, Dötterl S. The evolution of floral scent and olfactory preferences in pollinators: coevolution or pre–existing bias? Evolution. 2012;66–67(7):2042–2055. doi:10.1111/j.1558-5646.2012.01593.x.
19. Sites RW. The aroid scarab *peltonotus nasutus* (Coleoptera: scarabaeidae) in Thailand and its association with *Amorphophallus paeoniifolius* (Araceae). Natural History Bulletin of the Siam Society. 2017;62:107–109.
20. Johnson SD, Jürgens A. Convergent evolution of carrion and faecal scent mimicry in fly–pollinated angiosperm flowers and a stinkhorn fungus. South African Journal of Botany. 2010;76(4):796–807. doi:10.1016/j.sajb.2010.07.012.
21. Jürgens A, Dötterl S, Meve U. The chemical nature of fetid floral odours in stapeliads (Apocynaceae–Asclepiadoideae–Ceropegieae). New Phytologist. 2006;172(3):452–468. doi:10.1111/j.1469-8137.2006.01845.x.

22. Ramirez SR, Eltz T, Fujiwara MK, Gerlach G, Goldman-Huertas B, Tsutsui ND, Pierce NE. Asynchronous diversification in a specialized plant-pollinator mutualism. Science. 2011;333(6050):1742–1746. doi:10.1126/science.1209175.
23. Trumbo ST, Steiger S. Finding a fresh carcass: bacterially derived volatiles and burying beetle search success. Chemoecology. 2020;30(6):287–296. doi:10.1007/s00049-020-00318-0.
24. Lev-Yadun S, Ne'eman G, Shanas U. A sheep in wolf's clothing: do carrion and dung odours of flowers not only attract pollinators but also deter herbivores? BioEssays. 2009;31(1):84–88. doi:10.1002/bies.070191.
25. Bustamante RAA, Mansibang JA, Hetterscheid WLA, Tamayo MN. Amorphophallus caudatus (Thomsonieae, Araceae), a new species from camarines norte, Luzon island, the Philippines. Nordic Journal of Botany. 2020;38(11):e02982. doi:10.1111/njb.02982.
26. Bustamante RAA, Claudel C, Altomonte JCA, Udasco LC Jr., Tamayo MN. *Amorphophallus minimus* (Araceae), a new species from the montane forest of Nueva Ecija, Luzon island, Philippines. Nordic Journal of Botany. 2021;39(8):e03251. doi:10.1111/njb.03251.
27. Tamayo M, Magtot L, Sumalinog JR, Reyes JR, Austria CM. *Amorphophallus calcicolus* (Thomsonieae, Araceae), a new species from the Bohol island, Central Visayas, philippines. Phytotaxa. 2021;489(2):229–235. doi:10.11646/phytotaxa.489.2.12.
28. WCVP. World checklist of vascular plants, version 2.0. facilitated by the royal botanic gardens, kew. Published on the Internet. 2021. Retrieved 14 September 2021. http://wcvp.science.kew.org/
29. Boyce PC, Croat TB. onwards. the überlist of Araceae, totals for published and estimated number of species in Aroid Genera. 2018. Accessed 9 Sept 2021. Available from: http://www.aroid.org/genera/20201008Überlist.pdf
30. Claudel C, Buerki S, Chatrou L, Antonelli A, Alvarez N, Hetterscheid WLA. Large-scale phylogenetic analysis of *Amorphophallus* (Araceae) derived from nuclear and plastid sequences reveals new subgeneric delineation. Botanical Journal of the Linnean Society. 2017;184(1):32–45. doi:10.1093/botlinnean/box013.
31. Mayo SJ, Bogner J, and Boyce PC. The genera of Araceae. Kew: Royal Botanic Gardens, UK; 1997.
32. Bröderbauer D, Diaz A, Weber A. Reconstructing the origin and elaboration of insect–trapping inflorescences in the Araceae. Am J Bot. 2012;99(10):1666–1679. doi:10.3732/ajb.1200274.
33. Skubatz H, Nelson TA, Dong AM, Meeuse BJD, Bendich AJ. Infrared thermography of Arum lily inflorescences. Planta. 1990;182(3):432–436. doi:10.1007/BF02411396.
34. Chen G, Ma X–K, Jürgens A, Lu J, Liu E–X, Sun W–B, Cai X–H. Mimicking livor mortis: a well–known but unsubstantiated color profile in Sapromyiophily. J Chem Ecol. 2015;41(9):808–815. doi:10.1007/s10886-015-0618-2.
35. Fujioka K, Shirasu M, Manome Y, Ito N, Kakishima S, Minami T, Tominaga T, Shimozono F, Iwamoto T, Ikeda K, et al. Objective display and discrimination of floral odors from *Amorphophallus titanum*, bloomed on different dates and at different locations, using an electronic nose. Sensors. 2012;12(2):2152–2161. doi:10.3390/s120202152.
36. Kakishima S, Terajima Y, Murata J, Tsukaya H. Infrared thermography and odour composition of the *Amorphophallus gigas* (Araceae) inflorescence: the cooling effect of the odorous liquid. Plant Biology. 2011;13(3):502–507. doi:10.1111/j.1438-8677.2010.00399.x.
37. Kite GC, Hetterscheid WLA. Inflorescence odours of *Amorphophallus* and *Pseudodracontium* (Araceae). Phytochemistry. 1997;46(1):71–75. doi:10.1016/S0031-9422(97)00221-5.
38. Kite GC, Hetterscheid WLA. Phylogenetic trends in the evolution of inflorescence odours in. Amorphophallus Phytochemistry. 2017;142:126–142. doi:10.1016/j.phytochem.2017.06.006.
39. Kite GC, Hetterscheid WLA, Lewis M, Boyce PC, Ollerton J, Cocklin E, Diaz A, Simmonds MSJ. Inflorescence odours and pollinators of *Arum* and *Amorphophallus* (Araceae). In: Owens S, Rudall P, editors. Reproductive Biology in Systematics, Conservation and Economic Botany. Kew (UK): Kew Publishing; 1998. p. 295–315.
40. Raman V, Tabanca N, Demirci B, Khan IA. Studies on the floral anatomy and scent chemistry of titan arum (*Amorphophallus titanum*, Araceae). Turkish Journal of Botany. 2017;41:63–74. doi:10.3906/bot-1604-34.
41. Shirasu M, Fujioka K, Kakishima S, Nagai S, Tomizawa Y, Tsukaya H, Murata J, Manome Y, Touhara K. Chemical identity of a rotting animal-like odor emitted from the inflorescence of the Titan Arum (*Amorphophallus titanum*). Biosci Biotechnol Biochem. 2010;74(12):2550–2554. doi:10.1271/bbb.100692.
42. Johnson SD, Schiestl FP. Floral mimicry. Oxford (New York): Oxford University Press; 2016.
43. Vereecken NJ, McNeil JN. Cheaters and liars: chemical mimicry at its finest. Can J Zool. 2010;88(7):725–752. doi:10.1139/Z10-040.
44. Ollerton J, Raguso RA. The sweet stench of decay. New Phytologist. 2006;172(3):382–385. doi:10.1111/j.1469-8137.2006.01903.x.
45. Borg-Karlson AK, Englund FO, Unelius CR. Dimethyl oligosulphides, major volatiles released from *Sauromatum guttatum* and Phallus impudicus. Phallus Impudicus. Phytochemistry. 1994;35(2):321–323. doi:10.1016/S0031-9422(00)94756-3.
46. Nilssen AC, Tømmerås BA, Schmid R, Evensen SB. Dimethyl trisulphide is a strong attractant for some calliphorids and a muscid but not for the reindeer oestrids *Hypoderma tarandi* and Cephenemyia trompe. Cephenemyia trompe. Entomologia Experimentalis et Applicata. 1996;79(2):211–218. doi:10.1111/j.1570-7458.1996.tb00828.x.
47. Shankaranarayana ML, Raghavan B, Abraham KO, Natarajan CP, Brodnitz HH. Volatile sulfur compounds in food flavors. C R C Critical Reviews in Food Technology. 1974;4(3):395–435. doi:10.1080/10408397409527163.
48. Grob GBJ, Gravendeel B, Eurlings MCM, Hetterscheid WLA. Phylogeny of the tribe Thomsoniae (Araceae) based on chloroplast *matK* and *trnL* intron sequences. Systematic Botany. 2002;27:453–467.
49. Sedayu A, Eurlings MCM, Gravendeel B, Hetterscheid WLA. Morphological character evolution of *Amorphophallus* (Araceae) based on a combined phylogenetic analysis of *trnL, rbcL* and *LEAFY* second intron sequences. Botanical Studies. 2010;51:473–490.
50. Van Der Ham R, Grob G, Hetterscheid WLA, Star W, van Heuven BJ. Notes on the genus Amorphophallus [Araceae) – 13. Evolution of pollen ornamentation and ultrastructure in Amorphophallus and Pseudodracontium*Pseudodracontium*. Grana. 2005;44(4):252–265. doi:10.1080/00173130500424417.
51. Claudel C. The many elusive pollinators in the genus *Amorphophallus*. Arthropod Plant Interact. 2021. doi:10.1007/s11829-021-09865-x.
52. Moretto P, Cosson B, Krell F–T, Aristophanous M. Pollination of *Amor-phophallus barthlottii* and *A. abyssinicus* subsp. *akeassii* (Araceae) by dung beetles (In-secta: coleoptera: scarabaeoidea). Catharsius La Revue. 2019;18:19–36.
53. Chartier M, Pélozuelo L, Buatois B, Bessière JM, Gibernau M. Geographical variations of odour and pollinators, and test for local adaptation by reciprocal transplant of two European *Arum* species. Funct Ecol. 2013;27(6):1367–1381. doi:10.1111/1365-2435.12122.
54. Gibernau M, Macquart D, Przetak G. Pollination in the genus *Arum* – a review. Aroideana. 2004;27:148–166.
55. Marotz–Clausen G, Jürschik S, Fuchs R, Schäffler I, Sulzer P, Gibernau M, Dötterl S. Incomplete synchrony of inflorescence scent and temperature patterns in *Arum maculatum* L. (Araceae). Phytochemistry. 2018;154:77–84. doi:10.1016/j.phytochem.2018.07.001.

56. Chartier M, Liagre S, Weiss–Schneeweiss H, Kolano B, Bessière J-M, Schöneberger J, Gibernau M. Floral traits and pollination ecology of European *Arum* hybrids. Oecologia. 2016;180(2):439–451. doi:10.1007/s00442-015-3498-9.
57. Dekeirsschieter J, Verheggen FJ, Gohy M, Hubrecht F, Bourguignon L, Lognay G G, Haubruge E. Cadaveric volatile organic compounds released by decaying pig carcasses (*Sus domesticus* L.) in different biotopes. Forensic Sci Int. 2009;189(1–3):46–53. doi:10.1016/j.forsciint.2009.03.034.
58. Buis RC. The validation of human decomposition fluid as a cadaver–detection dog training aid. Thesis submitted for the degree of Doctor of Philosophy (Science). Sydney, Australia: Centre for Forensic Science University of Technology. 2016.
59. Armstrong P, Nizio KD, Perrault KA, Forbes SL. Establishing the volatile profile of pig carcasses as analogues for human decomposition during the early post-mortem period. Heliyon. 2016;2(2):70–77. doi:10.1016/j.heliyon.2016.e00070.
60. Winkler H. Einige Bemerkungen über Mangrove-Pflanzen und den *Amorphophallus Titanum* im Hamburger Botanischen Garten. Ber Dtsch Bot Ges. 1931;49:87–102.
61. Hetterscheid. Sumatran *Amorphophallus* adventures: 20 August – 1 September 1993. Aroideana. 1994;17:61–77.
62. Symon JR. *Amorphophallus titanum*: a journey beyond its habitat. Aroideana. 1994;17:18–32.
63. Punekar SA, Kumaran KPN. Pollen morphology and pollination ecology of *Amorphophallus* species from North Western Ghats and Konkan region of India. Flora. 2010;205(5):326–336. doi:10.1016/j.flora.2009.12.024.
64. Beath DDN. Pollination of Amorphophallus johnsonii (Araceae) by carrion beetles (Phaeochrous amplus) in a Ghanaian rain forest. J Tropical Ecology. 1996;12(3):409–418. doi:10.1017/S0266467400009603.
65. Soepadmo E. 1973. A short note on Amorphophallus cf. prainii Hook.f. The Malayan Nature Journal 25: 133–134.
66. Giordano C. Observations on *Amorphophallus titanum* (Becc.) Becc. ex Arcangeli in the Forest of Sumatra. Aroideana. 1999;22:10–19.
67. Dötterl S, David A, Boland W, Silberbauer-Gottsberger I, Gottsberger G. Evidence for behavioral Attractiveness of Methoxylated Aromatics in a Dynastid scarab beetle-pollinated Araceae. J Chem Ecol. 2012;38(12):1539–1543. doi:10.1007/s10886-012-0210-y.
68. Lohonyai Z, Vuts J, Fail J, Tóth M, Imrei Z. Field response of two cetoniin chafers (Coleoptera, scarabaeidae) to floral compounds in ternary and binary combinations. Acta Phytopathologica et Entomologica. 2018;53(2):259–269. doi:10.1556/038.53.2018.016.
69. Tóth M, Szarukán I, Nagy A, Furlan L, Benvegnù I, Rak Cizej M, Ábri T, Kéki T, Körösi S, Pogonyi A, et al. European corn borer (*Ostrinia nubilalis* Hbn., Lepidoptera: crambidae): comparing the performance of a new bisexual lure with that of synthetic sex pheromone in five countries. Pest Manag Sci. 2017;73(12):2504–2508. doi:10.1002/ps.4645.
70. Maia ACD, Gibernau M, Carvalho AT, Gonçalves EG, Schlindwein C. The cowl does not make the monk: scarab beetle pollination of the Neotropical aroid *Taccarum ulei* (Araceae: spathicarpeae). Biological Journal of the Linnean Society. 2013;108(1):22–34. doi:10.1111/j.1095-8312.2012.01985.x.
71. Hetterscheid WLA. Amorphophallus. In: Boyce PC, Sookchaloem D, Hetterscheid WLA, Gusman G, Jacobsen N, Idei T, and Nguyen VD, editors. Araceae. *Flora of Thailand* 11. Bangkok, Thailand: The Forest Herbarium; 2012. p. 218–232.
72. Hetterscheid WLA, Ittenbach S. Everything you always wanted to know about *Amorphophallus*, but were afraid to stick your nose into. Aroideana. 1996;19:7–131.
73. Szenteczki MA, Godschalx AL, Galmán A, Espíndola A, Gibernau M, Alvarez N, Rasmann S. Within–species floral odor variation is maintained by spatial and temporal heterogeneity in pollinator communities. bioRxiv. 2020;2020(9):29.318089. doi:10.1101/2020.09.29.318089.
74. Vázquez V, Barradas I. Deceptive pollination and insects' learning: a delicate balance. J Biol Dyn. 2017;11(1):299–322. doi:10.1080/17513758.2017.1337246.

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Patterns and drivers of heat production in the plant genus *Amorphophallus*

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SUMMARY

Thermogenesis – the ability to generate metabolic heat – is much more common in animals than in plants, but it has been documented in several plant families, most prominently the Araceae. Metabolic heat is produced in floral organs during the flowering time (anthesis), with the hypothesised primary functions being to increase scent volatilisation for pollinator attraction, and/or to provide a heat reward for invertebrate pollinators. Despite in-depth studies on the thermogenesis of single species, no attempts have yet been made to examine plant thermogenesis across an entire clade. Here, we apply time-series clustering algorithms to 119 measurements of the full thermogenic patterns in inflorescences of 80 *Amorphophallus* species. We infer a new time-calibrated phylogeny of this genus and use phylogenetic comparative methods to investigate the evolutionary determinants of thermogenesis. We find striking phenotypic variation across the phylogeny, with heat production in multiple clades reaching up to 15°C, and in one case 21.7°C above ambient temperature. Our results show that the thermogenic capacity is phylogenetically conserved and is also associated with inflorescence thickness. Our study paves the way for further investigations of the eco-evolutionary benefits of thermogenesis in plants.

Keywords: ***Amorphophallus*, pollinator attraction, reward, volatilisation, thermogenesis, phylogeny.**

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INTRODUCTION

Thermogenesis is the ability of an organism to raise its metabolism in order to elevate the temperature of its body or of particular tissues or organs and is characteristic of two major animal groups: mammals and birds. However, metabolic thermogenesis also occurs in plants, albeit rarely. With few exceptions, it is restricted to some gymnosperms and to early lineages of angiosperms. To date, it has been documented in 13 extant families of seed plants (Seymour, 2010). Of these, the best-investigated family, with the highest number of known thermogenic genera and species, is the Araceae, also known as the arum family (Grant et al., 2010; Ivancic et al., 2008; Mayo et al., 1997; Meeuse & Raskin, 1988; Seymour, 2010; Vogel, 1963, 1990).

Like in animals, plant metabolic thermogenesis is based on elevated mitochondrial respiration. Heat is produced through an intense increase in mitochondrial metabolism, during which carbohydrates or lipids are used as substrate by alternative oxidase (AOX) and/or by uncoupling proteins (UCPs) (Grant et al., 2010; Ito–Inaba, 2014; Miller et al., 2011; Onda et al., 2008; Seymour et al., 2015; Vogel, 1963, 1990; Wagner et al., 2008). Some thermogenic

plant species are also thermoregulatory, which enables them to regulate the excess temperature to a certain extent (Nagy et al., 1972; Seymour, 2004; Seymour et al., 1998; Seymour & Matthews, 2006; Seymour & Schultze–Motel, 1998).

Thermogenesis in the Araceae occurs during anthesis and is restricted to floral organs – more specifically, the male flowers and their derivatives, such as staminodes (Ivancic et al., 2008; Kakishima et al., 2011; Skubatz et al., 1990). Except for the genus *Taccarum* Brongn. ex Schott, the female flowers are not known to be thermogenic (Maia et al., 2013). The thermogenic patterns can vary strongly in timing, intensity and cycles (Kakishima et al., 2011). If an appendix (a sterile floral organ) is present, thermogenesis of the appendix and of the male flowers may occur either simultaneously or in an alternating pattern (e.g. Albre et al., 2003; Barabé et al., 2002; Chouteau et al., 2007; Gibernau & Barabé, 2000, 2002; Ivancic et al., 2004, 2005). The thermogenic phase usually lasts 2 days (Skubatz et al., 1990), but in extreme cases can last up to 30 days (Gibernau et al., 2010).

The functions of plant thermogenesis have long been debated and remain a contentious topic. The phenomenon has been associated with the prevention of freezing, spathe unfolding, anther dehiscence, carrion mimicry, infrared radiation, heat reward for pollinators, CO_2 release and the generation of heat for optimal pollen tube growth (Albre et al., 2003; Angioy et al., 2004; Dormer, 1960; Knutson, 1979; Korotkova & Barthlott, 2009; Patiño et al., 2002; Seymour, Yuka, et al., 2009; Vereecken & McNeil, 2010). Yet, the two most common hypotheses associate thermogenesis with (i) improved scent volatilisation during stigma receptivity and (ii) heat reward for insect pollinators. Such reward could be either direct – increasing the body temperature of the visiting insects – or indirect, by providing them with a heated floral chamber that could be used as a shelter, food place or mating site (e.g. Angioy et al., 2004; Bay, 1995; Meeuse & Raskin, 1988; Seymour & Gibernau, 2008; Seymour, Gibernau, & Itoh, 2003; Seymour, White, & Gibernau, 2003; Seymour, White, & Gibernau, 2009; Skubatz et al., 1990; van der Kooi et al., 2019).

Floral biology and thermogenesis in *Amorphophallus*

Amorphophallus Blume ex Decne. is one of the largest genera of the Araceae (Boyce & Croat, 2023). The genus consists of four subgenera: *Afrophallus* Hett. and Claudel, *Amorphophallus*, *Metandrium* Stapf and *Scutandrium* Hett. and Claudel (Claudel et al., 2017) and currently encompasses 237 species (Boyce & Croat, 2023). The genus *Amorphophallus* is widely distributed across the Old World tropics (Africa and Australasia) and is morphologically diverse (Claudel et al., 2017; Hetterscheid & Ittenbach, 1996; Pouchon et al., 2022) (Figure 1).

The inflorescence is protogynous (the female flowers become functional before the male flowers) and consists of a spadix surrounded by a spathe (Figure 2). The spathe is usually triangular or ovate and is more rarely funnel shaped (Hetterscheid & Ittenbach, 1996). It can be separated by a constriction, dividing the spathe into a floral chamber and an upper limb (Hetterscheid & Ittenbach, 1996). The spadix is subdivided into three main zones, with or without sterile delimitations in between (Hetterscheid & Ittenbach, 1996). The lowermost zone bears the female flowers and is adjacent to an intermediate zone that bears the male flowers (generally within the floral chamber), terminating with the final distal sterile zone – the appendix (above the floral chamber). The appendix is considered to be derived from fused staminodes (Mayo et al., 1997) and serves the biosynthesis and volatilisation of the scent compounds (Kite & Hetterscheid, 2017). Moreover, it serves as a landing or departing platform for the attracted insects (Gibernau et al., 2004). In *Amorphophallus*, the reported thermogenic zones are consistently both the male flower zone and the appendix (Korotkova & Barthlott, 2009; Lamprecht & Seymour, 2010; Shirasu et al., 2010; Skubatz et al., 1990).

Some *Amorphophallus* species develop large, dark inflorescences, accompanied by foul smells, and are referred to as *carrion* or *corpse flowers* (Chen et al., 2015; Lamprecht & Seymour, 2010), or more generally, oviposition-site mimics (Johnson & Schiestl, 2016; Jürgens et al., 2006, 2013; Jürgens & Shuttleworth, 2016). Oviposition-site mimicry refers to plant species that deceive and attract beetles and flies, which breed or feed on substrates such as carrion, dung, decaying matter or the like (Johnson & Schiestl, 2016; Jürgens et al., 2006, 2013; Kite et al., 1998; Kite & Hetterscheid, 1997, 2017; Moretto et al., 2019; Urru et al., 2011; Vereecken & McNeil, 2010). Additional features of floral oviposition-site mimicry include floral chambers, floral gigantism and thermogenesis (Johnson & Schiestl, 2016). Copro-necrophagous beetles are assumed to be the main pollinator group in *Amorphophallus* (Moretto et al., 2019). However, knowledge about the species identity of the pollinating invertebrates remains limited for most species in the genus (Claudel, 2021).

The key elements of oviposition-site mimicry are the scent compounds (Jürgens et al., 2013; Jürgens & Shuttleworth, 2016), which are very diverse in the genus and are usually unpleasant to a human nose, ranging from carrion, faeces, urine, dung, fish, sewerage, nauseating gases, rancid cheese to fermenting fruit and mushrooms (Claudel & Lev-Yadun, 2021; Kite & Hetterscheid, 1997, 2017). However, the species of two distantly related *Amorphophallus* clades are characterised by sweet fragrances or benzenoid compounds (Kite & Hetterscheid, 1997, 2017). Kite and Hetterscheid (1997, 2017) categorised 92 *Amorphophallus* species depending on the main emitted scent compounds and benzenoids represent one of seven scent categories *sensu* Kite and Hetterscheid (2017). One clade from the subgenus

Figure 1. Floral diversity within the four subgenera of *Amorphophallus*, exemplified here by some of the species analysed.
(a–c) *Amorphophallus antsingyensis, A. mossambiciensis* and *A. lewallei* from subgenus *Afrophallus*.
(d–g) *A. konjac, A. napalensis, A. longituberosus* and *A. fuscus* from subgenus *Scutandrium*.
(h–j) *A. myosuroides, A. prainii* and *A. bangkokensis* from subgenus *Amorphophallus*.
(k–m) *A. laoticus, A. symonianus* and *A. pilosus* from subgenus *Metandrium*. Scale bars: (a–m) = 10 cm. Photographs: Cyrille Claudel.

Scutandrium is characterised by the emission of 4-methoxyphenethyl alcohol, whereas the other clade from subgenus *Metandrium* is characterised by the emission of 2-phenylethanol derivatives (Kite & Hetterscheid, 1997, 2017). However, although sweetly scented, at least some of these compounds can be related to various stages of cadaveric decomposition (Claudel & Lev-Yadun, 2021).

To date, thermogenesis has been investigated in only 9 out of 237 *Amorphophallus* species (Barthlott et al., 2009; Handayani et al., 2020; Kakishima et al., 2011; Korotkova & Barthlott, 2009; Lamprecht et al., 2002; Lamprecht & Seymour, 2010; Prakash & Nayar, 2000; Shirasu et al., 2010; Skubatz et al., 1990; Teijsmann & Binnendijk, 1862; van der Pijl, 1937; Wagner et al., 1998). It has been proposed that thermogenesis in the appendix serves improved scent volatilisation (Barthlott et al., 2009; Handayani et al., 2020; Korotkova & Barthlott, 2009; Lamprecht & Seymour, 2010; Seymour, 2010), whereas thermogenesis in the male flower zone might also offer heat reward to pollinating insects (Handayani et al., 2020; Korotkova & Barthlott, 2009;

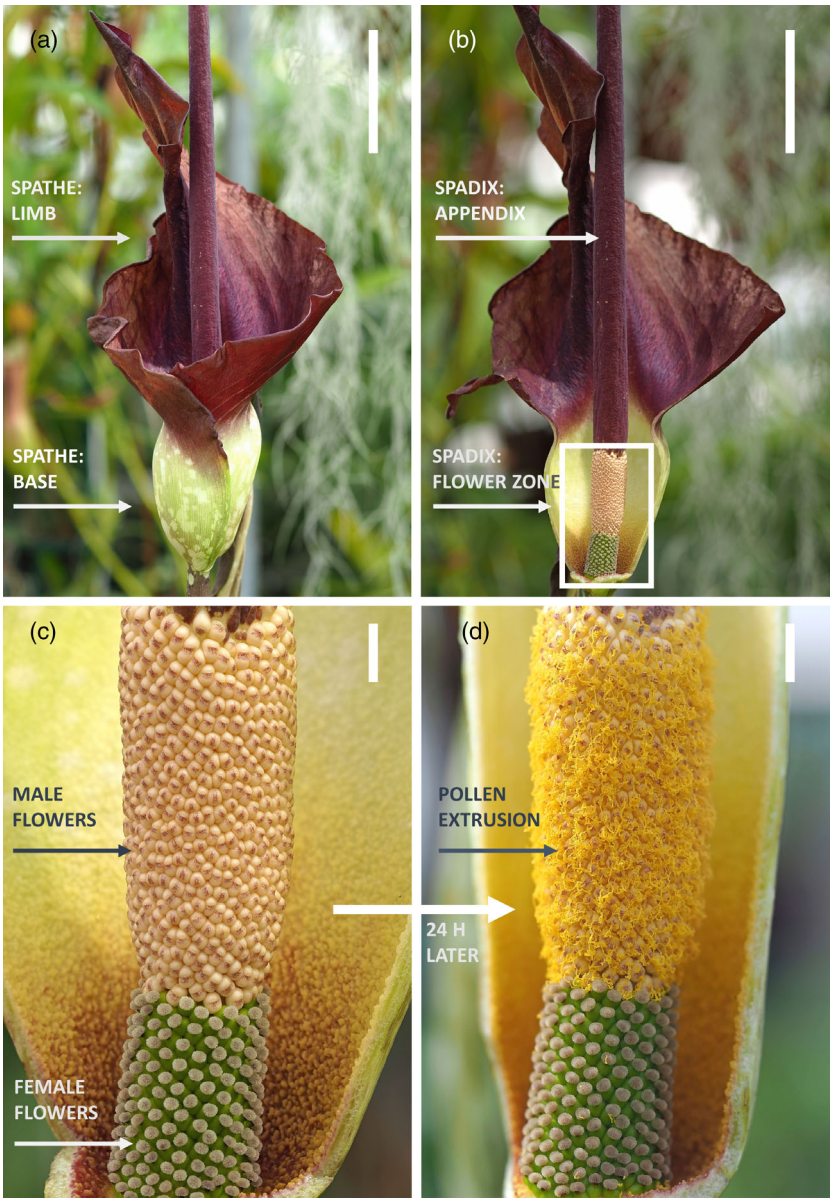


Figure 2. Inflorescences of *Amorphophallus* (here exemplified by *A. declinatus*).
(a) Inflorescence consists of a spadix and a spathe. The spadix has two parts: a limb and a base, the latter forming a floral chamber.
(b) The same inflorescence with the spathe base cut open to show the spadix composed of the appendix (above, outside the floral chamber) and the flower zone (below, within the floral chamber). The main thermogenic floral organs are the appendix and the male flower zone.
(c) First day of anthesis, close-up of the male flower zone (above) and the female flower zone (below).
(d) Second day of anthesis, pollen extrusion. Scale bars: a and b = 10 cm. c and d = 1 cm. Photographs: Cyrille Claudel.

Lamprecht et al., 2002; Seymour, 2010). However, to the best of our knowledge, these functions have never actually been tested. Moreover, although *A. krausei* Engl. (Wagner et al., 1998), *A. muelleri* (van der Pijl, 1937), *A. paeoniifolius* (Handayani et al., 2020; Lamprecht et al., 2002; Lamprecht & Seymour, 2010; Prakash & Nayar, 2000) and *A. titanum* (Barthlott et al., 2009; Korotkova & Barthlott, 2009; Lamprecht & Seymour, 2010; Shirasu et al., 2010) showed a significant temperature increase, only a moderate temperature increase could be observed in *A. bulbifer* (Roxb.) Blume, *A. forbesii* Engl. & Gehrm. (Skubatz et al., 1990) and *A. konjac* (Lamprecht & Seymour, 2010; Skubatz et al., 1990) whereas no temperature increase at all was observed in *A. gigas* (Kakishima et al., 2011; Teijsmann & Binnendijk, 1862) and *A. variabilis* Bl (van der Pijl, 1937).

Our literature compilation indicates that the knowledge of thermogenesis in *Amorphophallus* remains

incomplete and biased towards a single species: *A. titanum*. The lack of thorough data across most *Amorphophallus* species currently hinders our understanding of the patterns and potential role(s) of this fascinating phenomenon in the ecology and the evolution of the group.

Unravelling the evolution of thermogenesis in *Amorphophallus*

Beyond its functional role in particular species, the evolution of thermogenesis remains unexplored in plants. Although thermogenesis has evolved independently in several angiosperm families (Seymour, 2010; Thien et al., 2009), we do not know whether within *Amorphophallus* it originated once or multiple times independently. The physiological and morphological complexity associated with this phenomenon could potentially limit the lability of this trait and result in a high level of phylogenetic conservatism. Furthermore, it is not clear what could be the evolutionary fate of such a complex trait, considering the likely trade-off between the considerable costs of heat production (Lamprecht & Seymour, 2010) and its benefit for reproductive success. If this mechanism is too costly to maintain, a tendency towards the loss of thermogenic capacity across a thermogenic clade could be expected. Alternatively, if thermogenesis represents a cost-effective way to enhance pollination, the evolution of this trait might have positively impacted the diversification rate of heat-producing lineages or evolved multiple times independently within the genus. Besides a putative impact on diversification, given that thermogenesis occurs only in reproductive organs and may play a role in pollination, it could also have influenced the evolution of floral morphology.

The high species richness, large variation in inflorescence size and form, broad geographical distribution, well-documented scent production, reported occurrence of thermogenesis in multiple species and an available multi-locus phylogeny (Claudel et al., 2017), makes the genus *Amorphophallus* a suitable system for studying the evolution of plant thermogenesis. Here we apply quantitative measurements of the thermogenic activity of 80 species along with comparative phylogenetic methods in order to explore the relationship between thermogenesis and morphology in *Amorphophallus*. We ask, address and discuss the following specific questions:

Q1: Is thermogenic capacity an ancestral, phylogenetically conserved trait or did it evolve several times independently?

Q2: Has the evolution of thermogenesis triggered species diversification?

Q3: Is floral morphological evolution associated with the emergence of thermogenic capacity?

Q4: To what extent, can the thermogenic capacity be predicted from morphological traits?

RESULTS

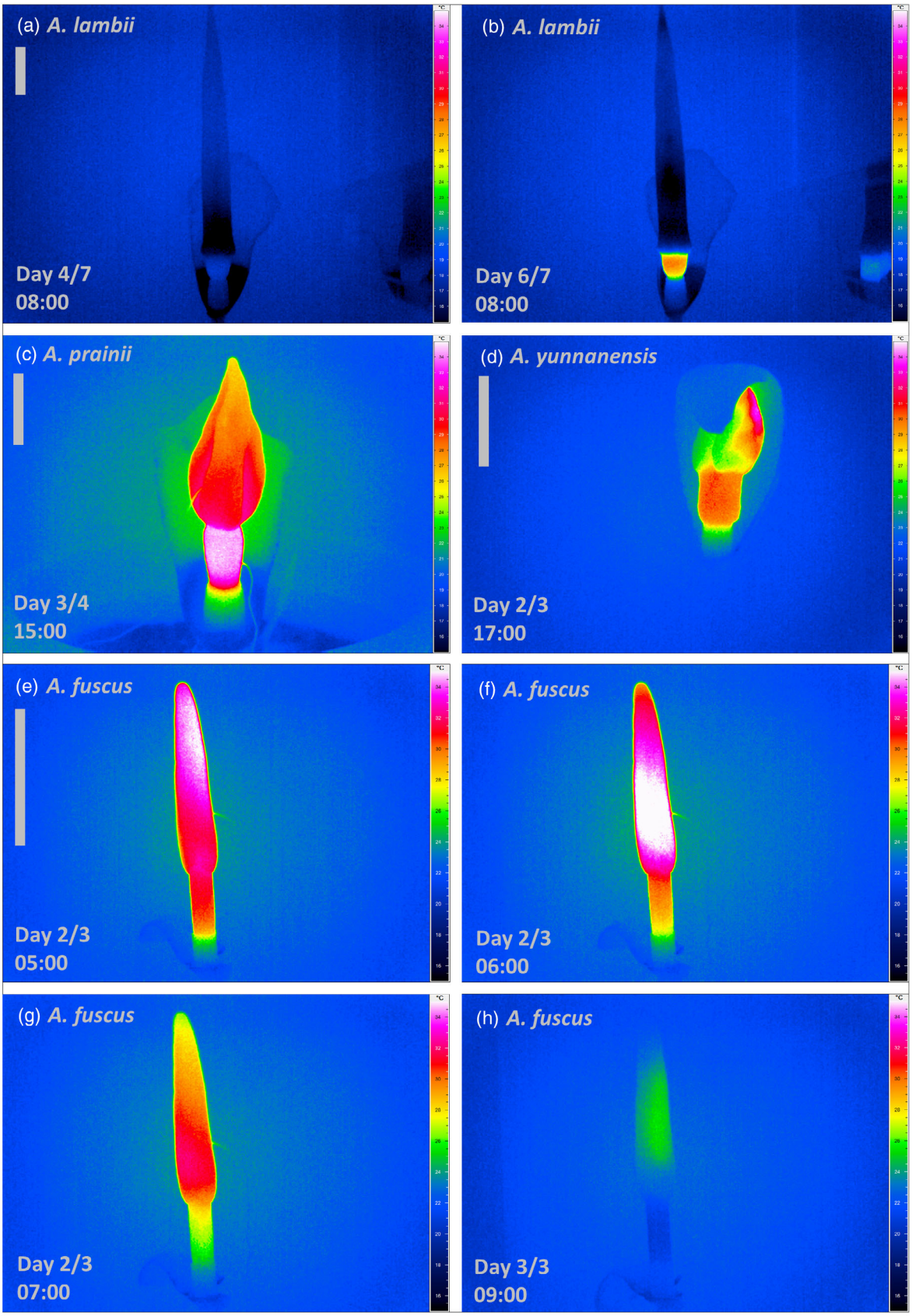
Thermogenic activity

Graphs of the temperature measurements from all 80 species represented by 119 specimens are provided in Data S1, while thermal images from selected species are presented in Figure 3, highlighting key biological aspects of thermogenesis as well as some technical considerations related to thermogenic recordings. Additionally, time-lapse movies based on thermal images were generated for eight selected species representing the four subgenera, namely *A. albispathus*, *A. lewallei*, *A. paeoniifolius*, *A. prainii*, *A. schmidtiae* pattern 1, *A. schmidtiae* pattern 2, *A. tuberculatus*, *A. yunnanensis* (Data S2 embedded movie).

Our measurements show that thermogenesis in *Amorphophallus* is restricted to the male flowers, the staminodes and the appendix. However, the thermogenic pattern of the staminodes and the male zone are largely identical and therefore staminodes are not discussed further. Similarly, the female flowers are not discussed since they did not exhibit temperature increase, except for a few species that had a strong temperature increase in the adjacent male flower zone. In these cases, the observed temperature increase in the female flower zone is due to passive heat transfer.

The beginning of anthesis was usually marked by the beginning of the first thermogenic peak of the appendix, whereas in several species, the end of anthesis was indicated by a decrease in temperature of the male zone (e.g. Figure 4. *A. symonianus*). Cooling of the male zone after pollen extrusion can be attributed to evaporation through

Figure 3. Thermal imaging observations in *Amorphophallus*.
(a) In *A. lambii*, the appendix and the spathe base cool down below ambient temperature. The cooling of the spathe base is remarkable, indicating evaporative cooling, possibly associated with scent emission by the spathe.
(b) Cooling of the spathe base and the appendix is not interrupted by thermogenesis of the male zone.
(c) Thermogenic peak of the male zone preceding the thermogenic peak of the heating-up appendix in *A. prainii*. The adjacent female zone below shows a temperature increase due to some passive heat transfer.
(d) *A. yunnanensis*. Although the overhanging spathe slightly blocks the view, strong temperature differences in the appendix can be observed, probably due to the irregularly folded appendix. In contrast, the male flower zone below is evenly warmed-up.
(e–h) Similarly, in *A. fuscus*, the appendix heats from bottom to top or from top to bottom rather than simultaneously all over. Different local temperature maxima are reached in the appendix, which illustrates the need for a consistent scheme for temperature sensor insertion.
(h) So far, *A. fuscus* is the only *Amorphophallus* species that ends anthesis with a temperature increase of the appendix. Scale bars: a–h = 10 cm. Day numbers are relative to the total duration of anthesis. Photographs: Cyrille Claudel.



the open pores or slits of the anthers. As pollen release generally coincides with the end of the anthesis, this cooling effect is not likely to have impacted the temperature pattern before pollen release. This is supported by the fact that the temperature curve of the male flower zone does not drop below ambient temperature before or during anthesis in nearly all investigated species. There are some exceptions, such as *A. brachyphyllus* and *A. juliae*, which may require specific investigation in future studies.

To illustrate the wide range of thermogenic patterns observed in *Amorphophallus*, eight selected distinctly different temperature curves are shown in Figure 4. These include the species with the highest temperature increase (*A. longituberosus*), and the species with the longest thermogenic activity (*A. schmidtiae*), one species with several peaks of the appendix temperature (*A. fuscus*), one species with several thermogenic peaks exclusively in the male flower zone (*A. vogelianus*), one species displaying thermogenic activity in the appendix only (*A. symonianus*), one species (*A. yunnanensis*) with a strong thermogenic activity of the male zone occurring prior to thermogenesis of the appendix and scent release (personal observation, C.C.), one species (*A. lambii*) with cooling of the appendix, but with a strong thermogenic activity of the male zone. Finally, one species (*A. lewallei*) with a distinct biphasic pattern, starting with a peak of the appendix temperature on the first day of anthesis, followed by a peak of the temperature of the male flower zone on the second day.

The full thermogenic sequence of most species (74/80) lasted approximately 48 h or slightly longer. However, we found several exceptions, such as *A. borneensis*, *A. consimilis*, *A. dracontioides* and *A. lambii* (Figure 4), where anthesis and thermogenesis lasted for about 5–6 days, and *A. schmidtiae* (Figure 4), an extreme case in which the thermogenic activity lasted up to 3 weeks.

In total, 20 species (25%) did not exceed a temperature increase of 1.5°C in the appendix and in the male flowers and we consider these species as 'non-thermogenic'. There were eight species (10%) that we consider 'weakly thermogenic' because they did not exceed ambient temperature by more than 2°C both in the appendix and male zone. Nearly half of the species (36/80 or 45%) exhibited a temperature increase of between 2°C and 10°C in at least one part of the inflorescence and we classify them as 'thermogenic species'. Sixteen species (20%) exceeded ambient temperature by 10°C or more in at least one part of the inflorescence, and these are referred to as 'strongly thermogenic' in the following discussion. Repeated analyses of plants clonally propagated through tuber multiplication showed that the thermogenic pattern is usually similar and reproducible within clones (ramets) of the same genet. Examples included *A. interruptus*, *A. lewallei*, *A. myosuroides*, *A. napalensis*, *A. prainii*, *A. tenuispadix* and *A. thaiensis*. One notable exception was found in *A. schmidtiae*, where the clones exhibited two different thermogenic types. In the first type, thermogenic activity lasted several weeks, even though scent emission was only noticeable by a human nose on the first day of anthesis. In contrast, thermogenesis lasted 2 days in the second type, similar to many other *Amorphophallus* species.

Thermogenic patterns were usually similar between different individuals of a given species, as observed in *A. curvistylis*, *A. myosuroides*, *A. napalensis*, *A. prainii* and *A. tuberculatus*. However, a certain amount of intraspecific variation was found in some of the species. For example, the beginning of anthesis differed between *A. albispathus* HBG 2014-G-37, and *A. albispathus* HBG 2014-G-39 (Data S1). Likewise, the beginning of anthesis and the number of appendix peaks slightly differed between the two documented accessions of *A. albus* (Data S1). These results indicate that thermogenic patterns are largely reproducible under similar conditions, although further investigations may provide a more detailed understanding of intraspecific variation. We cannot exclude that several variables, such as ambient temperature, air humidity, airflow and plant size might influence the thermogenic activity to a minor extent. Consequently, the temperature peaks might be higher under higher ambient temperature and relative humidity, unless the inflorescence is thermoregulated – a factor not directly investigated in our experiments.

Time-series clustering

The cluster dendrogram resulting from the multivariate time-series analyses of appendix and male zone temperature series show that most thermogenic species cluster together, separated from most of the non-thermogenic or weakly thermogenic species (Figure 5). However, our analyses also show that, because thermogenesis is not equal in the different parts of the inflorescence, some thermogenic species fall in fact into the mostly non-thermogenic cluster. For example, in *A. symonianus* and *A. scutatus*, thermogenic activity is high in the male zone but weak in the appendix and they both cluster with species that have low activity in both parts of the inflorescence (Figure 5). However, both *A. coudercii* and *A. lambii* have a high thermogenic activity restricted to the appendix, but while *A. coudercii* clusters with other species that have a high thermogenic activity in the appendix, *A. lambii* stands out among a group of weakly thermogenic species, which may be explained by the unusual cooling of the appendix below room temperature observed in that species. The two dendrograms from the univariate time clustering analyses are broadly similar, both displaying two main clusters, one of species with medium to high-temperature increase and a second of weakly or non-thermogenic species (Figure S1).

In the analysis with intraspecific sampling, replicate individuals cluster together in *A. atroviridis*, *A. bulbifer*, *A.*

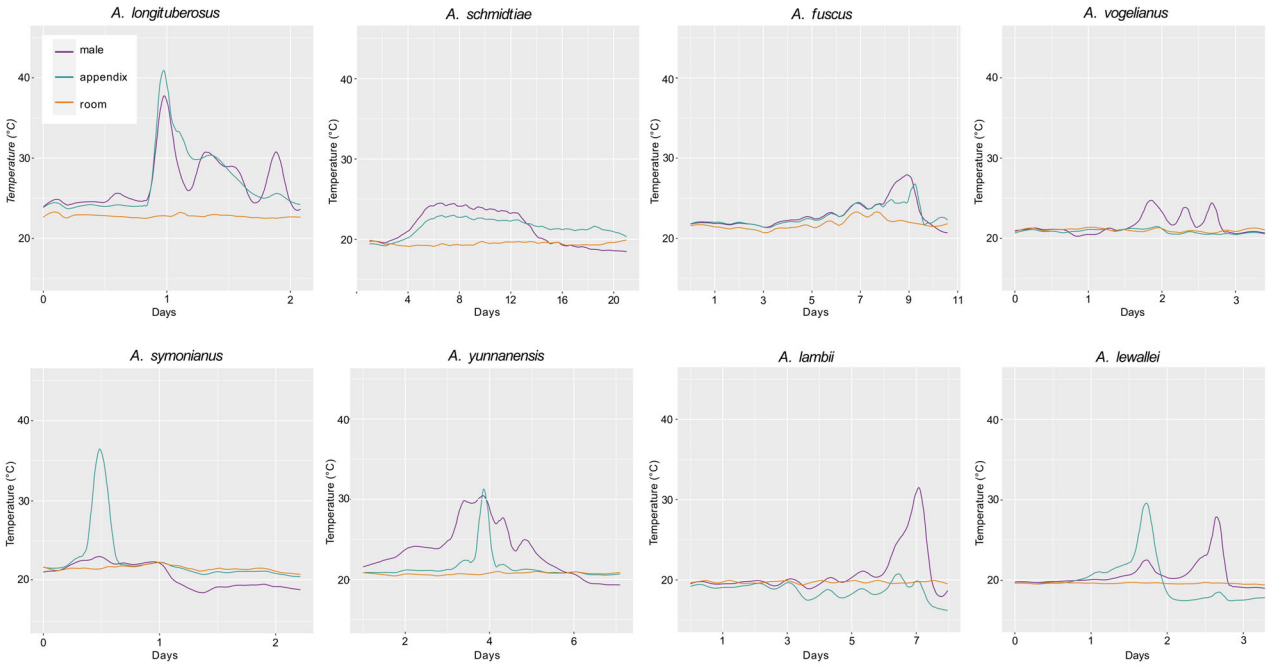


Figure 4. Time series of temperature in the appendix and the male flowers zone measured in eight different species of *Amorphophallus*. For display purpose, raw measurements have been smoothed with a loess function.

interruptus, *A. lewallei, A. myosuroides, A. opertus* and five out of the seven individuals of *A. schmidtiae* (Data S3). For the remaining 14 species with multiple samples, individuals did not form an exclusive cluster, although they often belonged to the same broader cluster.

Time-calibrated phylogeny

The MCMC analyses in BEAST (Bouckaert et al., 2014) converged and all parameters have effective sample size values above 300. The topology of the inferred phylogenetic tree is very similar to the previously recovered one in Claudel et al. (2017), with an improved resolution despite not being fully resolved (Figure 6; Figure S2), with 63% of the nodes have a posterior probability above 0.8 and 55% above 0.9. Hence, although the monophyly of each of the four subgenera is well supported, their relationship with one another remains inconclusive, a result encountered in most previous studies (Claudel et al., 2017; Sedayu et al., 2010) but resolved and discussed in Pouchon et al. (2022).

Models of diversification

The most likely model of diversification selected in the model comparison analysis is a birth-death model with all parameters (λ, μ and net diversification rate) decreasing linearly through time (Figure 6). The pulled speciation rate also decreases through time, from 0.33 at the root, to 0.069 at the tips, with a sharp decrease before 25 MY and a plateau between 25 MY and 10 MY (Figure 6), suggesting that the estimated speciation rate decrease is robust to identifiability issues. In the HiSSE analysis, the best-fit model is the character-independent model (ΔAIC = 2.61, Table S1), indicating that the evolution of thermogenesis is not associated with significant changes in diversification rates across lineages.

Evolution of thermogenesis

Through ancestral state estimation performed on thermogenesis treated either as a binary or continuous trait, thermogenic capacity was inferred to be of a single origin in *Amorphophallus*, present at the origin of the group and subsequently lost in several species belonging to different clades (Figure 7).

Display of peak temperature of the inflorescence during anthesis at the tips of the phylogeny shows that the thermogenic capacity is not a randomly distributed trait: despite missing data, some clades clearly appear to be made up of mostly weakly thermogenic species, and others of mostly of strongly thermogenic species. For example, the subgenus *Amorphophallus* comprises mostly of weakly or non-thermogenic species, such as the Philippine species *A. declinatus*, the Brachyphyllus clade, the Pusillus clade and the Pulchellus clade (Figure 6). In contrast, the subgenus *Metandrium* contains both a clade with weakly or non-thermogenic species (Pygmaeus clade) and a clade of strongly thermogenic species, that is the

phenylethanol scents clade (Figure 6). Finally, the most strongly thermogenic species of the African subgenus *Afrophallus* (*A. mossambicensis* and *A. lewallei*) are sister species, but no reliable trend can be inferred in this clade due to the low number of sampled species. This visual pattern is confirmed by Pagel's lambda estimates ($\lambda = 0.552$ for the appendix' peak temperature, and $\lambda = 0.568$ for the male zone's peak temperature), which indicate a significant amount of phylogenetic signal, although less than expected under Brownian motion evolution (see Figure 8).

Association between thermogenesis and morphological evolution

The overall amount of phylogenetic signal across the morphological dataset is low, as most values of lambda on the phylogeny are below 0.5, except for mean pollen size, spadix length, the ratios of appendix length/spadix length, peduncle length/peduncle diameter (Figure S3). On the cluster dendrogram, lambda values are generally close to zero, except for three traits which have a high lambda on the cluster dendrogram: male zone radius ($\lambda_{dendro} = 0.9620$), peduncle diameter ($\lambda_{dendro} = 0.8639$), spathe length (0.6871) and width ($\lambda_{dendro} = 0.8214$) (Table S2).

Our multiple regression model showed a significant positive correlation between the peak temperature in the appendix and the radius of the male zone (Figure 9; Table S3). The same association was recovered for the peak temperature of the male zone but was not significant. We also found a significant but small negative correlation between the height of the male zone and the peak temperature of the appendix (Figure 9; Table S3).

DISCUSSION

Our study provides an unprecedentedly detailed and consistent recording of thermogenesis for 80 plant species belonging to the Araceae genus *Amorphophallus*. We find substantial evidence of widespread thermogenic activity in the genus, a phenomenon that we report for species in all continents where this plant group occurs, and which is produced by species with vastly different morphologies – from huge to small inflorescences.

Relevance of time-series clustering to the study of thermogenesis

Thermogenesis is a highly complex and dynamic biological phenomenon that challenges attempts to classify thermogenic types. The approach developed here aimed at tackling this complexity in a more statistically and biologically realistic way, by taking into account the full temporal trajectories of temperatures. Our results show that applying time-series clustering to temperature measurements in the inflorescence of thermogenic species is a coherent and powerful approach, which enables a more biologically realistic classification of thermogenic patterns. Indeed, instead of focusing on a single aspect of thermogenesis, that is, the peak of temperature elevation, clustering of the several day long full time series takes into account the full thermogenic pattern of each species. This approach, therefore, integrates the natural complex variation observed in this trait which includes the potentially differential temperature elevation of the different parts of the inflorescence, as well as either their synchronicity or temporal separation and the overall trend in temperature increase throughout anthesis (e.g. linear increase, single or multiple peaks). The time-series clusters identified are therefore different from the groups we would have observed had we classified species based solely on the peak of their temperature elevation (Figure 5). For example, *A. symonianus* and *A. scutatus* are two strongly thermogenic species clusters within a group of species that are mostly weakly thermogenic, yet all of these species share a common characteristic: a net cooling of the male flowers part after pollen release once anthesis has ended (Data S1). Likewise, *A. lambii*, a species with a strong temperature peak in the male zone clusters with species that exhibit only such a small peak, yet all of them share a simultaneous cooling of the appendix. In summary, our analysis of temperature curves revealed that thermogenesis displays great biological variation across *Amorphophallus*, in terms of duration, location in the inflorescence, intensity and shape, a strong indication of the evolutionary flexibility of this trait.

A phylogenetic perspective on thermogenesis

Q1: Is thermogenic capacity an ancestral, phylogenetically conserved trait or did it evolve several times independently?

Ancestral reconstructions of peak temperature at anthesis suggest that the presence of thermogenesis is an ancestral character in *Amorphophallus* and that this capacity has been lost several times in non-sister clades during the long evolutionary history of the group. Despite considerable variation in thermogenic patterns, temperature increase during anthesis still exhibits some degree of phylogenetic conservatism as indicated by Pagel's lambda intermediate values and this is reflected in some clades being made up of mostly strongly thermogenic, or mostly weakly thermogenic species.

Considering that we had temperature data for only half (80/157) of the species included in the *Amorphophallus* phylogeny, the precise sequence of trait shifts (i.e. origin and loss of thermogenic capacity) remains to be confirmed with a more comprehensive species dataset. However, we believe that future analyses will not undermine our main result, which is that the presence of thermogenesis is an ancestral character in *Amorphophallus*. Indeed, our sampling was sufficient to show that thermogenic activity is present across the whole genus (Figure 5)

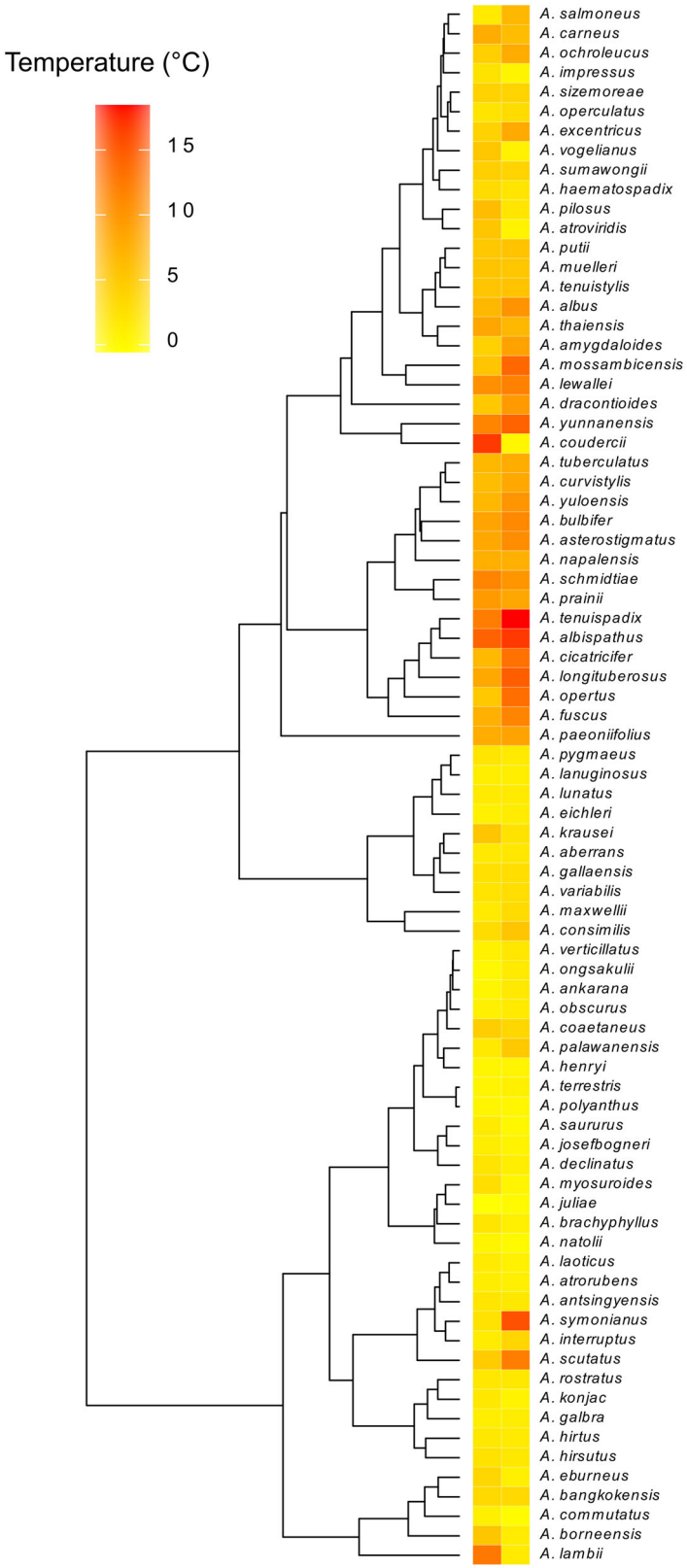


Figure 5. Cluster dendrograms based on multivariate time-series clustering of temperature series obtained from measuring temperature increase above room temperature during anthesis in the male zone and appendix. Coloured squares at the tips represent species' peak temperature in °C.

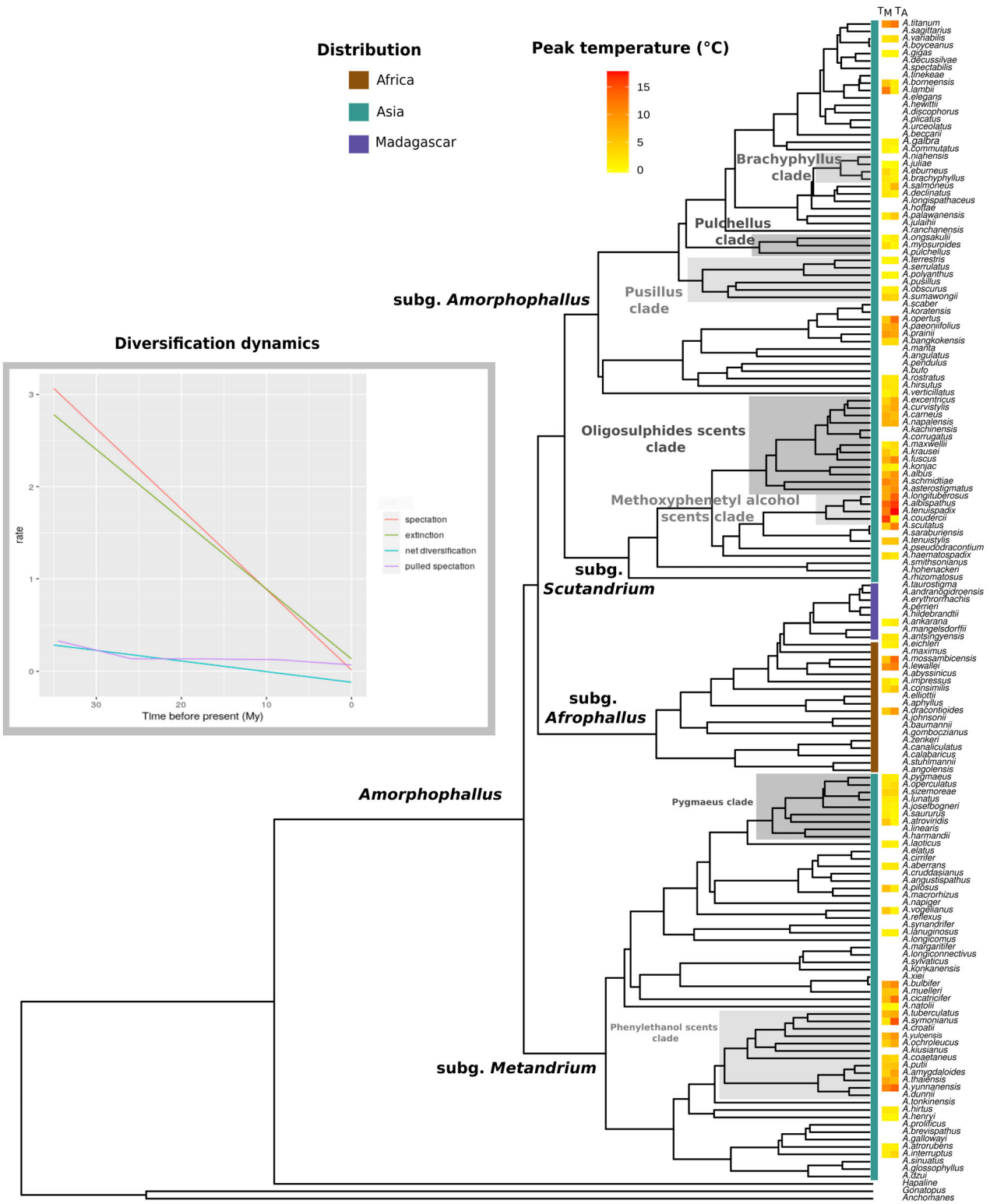


Figure 6. Time-calibrated phylogeny of *Amorphophallus*. Coloured dots at terminals indicate species' broad geographical distribution; followed by coloured squares which indicate the thermogenic activity measured in this study, by showing peak temperature during anthesis in the male zone (left) and the appendix (right) of the inflorescence. Names of subgenera are provided at notes and clades mentioned in the text are delimited with colour-coded boxes. The inset box on the left shows the speciation, extinction and net diversification rate through time inferred under a time variable birth-death model and the pulled speciation rate. Time in millions of years from the present.

and that only 15% of the analysed species did not exhibit significant temperature increase, which indirectly supports the scenario of a single origin early in the evolution of the genus, with subsequent losses, reductions or increases. The exact evolutionary advantage of this trait and its genomic underpinning are beyond the scope of this study and remain to be investigated. A possible scenario could be that once it evolved, the genetic assemblage necessary for a thermogenic capacity was retained throughout the evolutionary history of *Amorphophallus*, and that the observed variation in thermogenic patterns (e.g. duration and intensity of temperature elevation, differences in a location within the inflorescence) is controlled by regulatory mechanisms at the level of gene expression. Under this scenario, genes necessary for thermogenesis may still be present, but not fully expressed, even in non-thermogenic species. Comparative transcriptomic studies of non-thermogenic, weakly thermogenic and strongly thermogenic *Amorphophallus* species would allow us to test this hypothesis and shed light on the genomic underpinning of this complex physiological trait.

Q2: Has the evolution of thermogenesis triggered species diversification?

Results from the two analyses of diversification (Table S1) suggested that the diversification rate of *Amorphophallus* decreased over time. Furthermore, the rejection of a trait-dependent model in favour of a null, trait-independent one, suggests that the evolution of thermogenesis did not significantly impact the diversification rate within the group. This is coherent with our finding that thermogenesis was present at the origin of the group and is not restricted to a certain clade. Hence, thermogenesis, at least within *Amorphophallus*, seems to be decoupled from the rate of diversification, although additional data would be necessary to further test this hypothesis beyond the species included in our analyses. A macroevolutionary analysis across the entire Araceae family could confirm that the evolution of thermogenesis is truly decoupled from the rate of diversification or alternatively show that an effect on species diversification can only be detected over a larger evolutionary timeframe.

Q3: Is morphological evolution primarily linked to thermogenesis or to shared ancestry?

Given the probable occurrence of thermogenesis early in the evolutionary history of *Amorphophallus* and its putatively important ecological role in pollinator attraction, we asked whether this trait has influenced the evolution of inflorescence morphology. If the constraint played by thermogenic capacity on morphological traits were stronger than the effect of shared ancestry, we would expect Pagel's lambda values for morphological traits to be higher on the dendrograms of peak temperature than on the phylogeny. Our findings revealed that three traits (male zone radius, peduncle diameter and spathe width) had very high lambda values on the temperature dendrogram. This suggests that the evolution of inflorescence thickness or width is tightly linked to the thermogenic pattern. Interestingly, the other morphological traits, which appear to have evolved independently of thermogenic capacity, were only weakly conserved phylogenetically. This suggests that the evolution of most floral traits in *Amorphophallus* is highly labile or linked to other factors, such as environmental variables that were not included in our analyses.

Q4: To what extent can individual morphological traits predict the strength of the thermogenic capacity?

The fact that weakly or non-thermogenic species include the smallest species in the genus, bearing inflorescences not exceeding a few centimetres in length (Claudel et al., 2017), hints that thermogenesis may be linked with the evolution of large inflorescences. However, the opposite is also true: some species with the highest recorded temperature elevations, such as *A. albispathus*, are among the smallest species. Finally, some of the largest species, for instance, *A. gigas*, display no temperature elevation at all (Kakishima et al., 2011) and see Claudel et al. (2019) for alternative hypotheses to explain floral gigantism in *Amorphophallus*.

Beyond anecdotal evidence, we formally tested for a possible correlation between overall inflorescence morphology and thermogenic activity in *Amorphophallus*. Our results reject the simplistic view that larger species are more likely to be thermogenic. Instead, we found that temperature increase is mostly associated with the width of the inflorescence as indicated by the positive association between appendix peak temperature and width of the male zone. Similar but non-significant positive associations were found between male zone peak temperature and width, and between the width of the appendix and peak temperature in both the appendix and male zone. We also found a significant, although weak, correlation between the appendix and male zone's height with peak temperature in the male zone and in the appendix, respectively. These results suggest a tendency for thermogenesis to be stronger in species which are shorter but thicker. These traits are characteristic of an overall robustness of the inflorescence, a typical adaptation to beetle pollination (Bernhardt, 2000; Kevan & Baker, 1983). Thick and warm inflorescences may play a role in pollinator attraction or provide a warm shelter for visiting insects, but data on visiting insects and pollinators are too limited to confidently test these hypotheses (Claudel, 2021). The overall weak relationship we found between thermogenic activity and inflorescence morphology suggests that there is no emblematic thermogenic inflorescence and that floral traits cannot be used as a proxy for temperature measurements

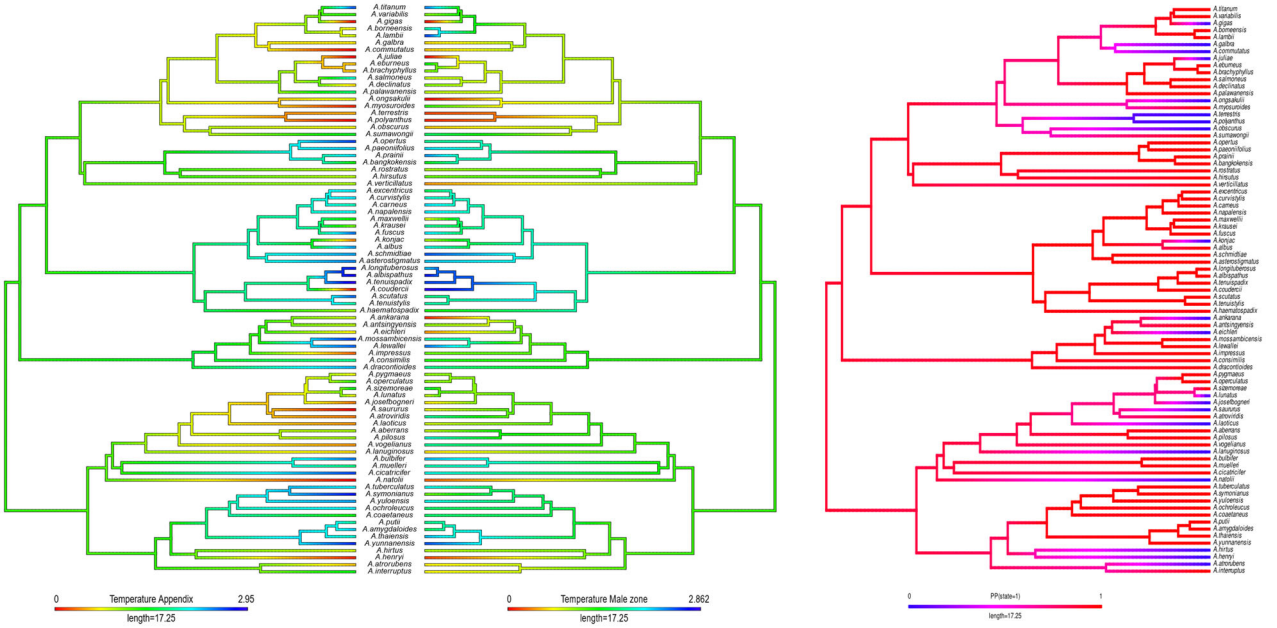


Figure 7. Ancestral state reconstruction of thermogenic activity treated as a continuous character (log peak temperature of the appendix, left; and of the male zone, middle) and as a binary trait (right).

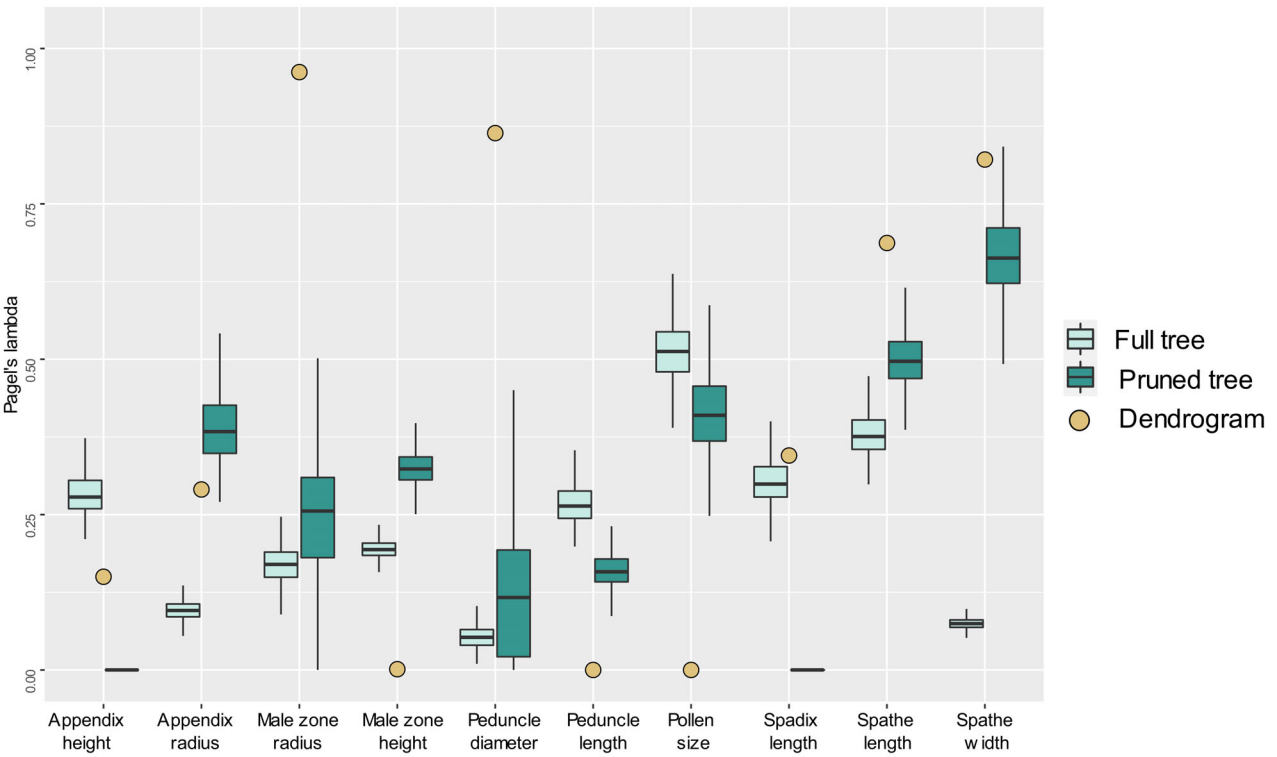


Figure 8. Pagel's lambda values estimated for morphological traits on (1) cluster dendrogram (yellow dots), and (2) a set of 100 trees representing the whole phylogeny (light green), or a pruned phylogeny with the same number of species as cluster dendrogram (dark green).

to reliably predict whether a species is thermogenic. Although we tried to include as many variables as possible in our analyses, we cannot exclude that thermogenic activity may actually have a stronger correlation with other morphological traits such as the number and size of excreting pores.

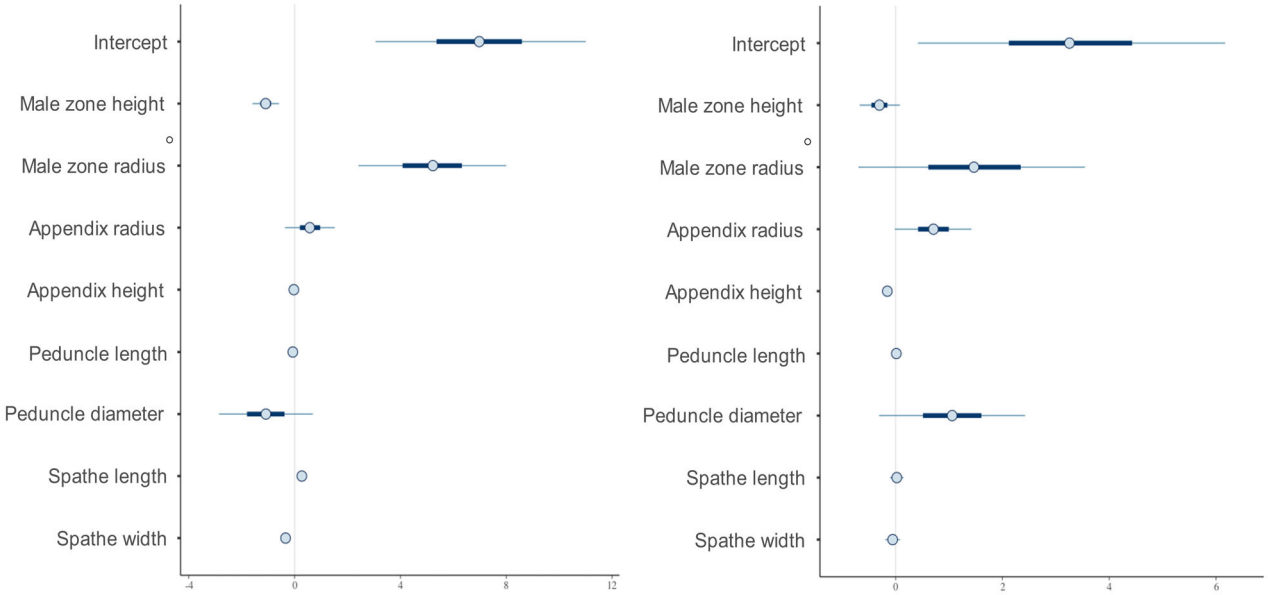


Figure 9. Result of multiple regression between morphological variables and peak temperature in the appendix (left) and in the male zone (right).

Deciphering thermogenesis: future directions

Our findings shed new light on the biology and evolution of metabolic thermogenesis. Despite these advances, the exact function/s of temperature elevation during anthesis remains elusive. For example, the correlation we found between thermogenesis and floral morphology typical of beetle pollination does not shed light on the putative function of temperature elevation in scent emission and pollinator attraction. Thermogenesis could potentially contribute to CO_2 release and thus to the attraction of invertebrate pollinators (Patiño et al., 2002). Indeed, CO_2 detection is widespread in insects (Jones, 2013), which are known to rely on CO_2 gradients for locating suitable food sources (Jones, 2013; Vereecken & McNeil, 2010).

Interestingly, two species groups from the subgenera *Scutandrium* and *Metandrium*, here named in reference to their emitted major scent compounds, the methoxy phenethyl alcohol scents clade and the phenylethanol scents clade (Figure 5), produce sweet, fruity or almond odours based on aromatic hydrocarbons (Kite & Hetterscheid, 2017). These clades comprise mostly thermogenic or strongly thermogenic species, in particular *A. albispathus*, *A. longituberosus* and *A. tenuispadix*, all of which can exceed 15°C above room temperature. One of the greatest temperature elevations recorded in a plant species so far, for example *A. longituberosus* (21.7°C above ambient temperature, Figure 5), is only matched by two other species within the Aroideae (Ivancic et al., 2005; Nagy et al., 1972). However, the putative role of thermogenesis in the volatility of these scent compounds has not been formally tested.

Taken together, the available evidence suggests that rather than playing a fixed and universal role, the function of thermogenesis is likely to vary with the species' ecology, depending for instance on whether a species emits specialised scent compounds or occurs in cooler climates (subtropical regions or high elevation in the tropics). We hypothesise that if such links exist, they are largely loose and non-deterministic, similar to what we found for morphological traits.

A final aspect that deserves closer attention in future studies is the occasional uncoupling of temperature elevation in the appendix and the male flowers zone, in species that heat up only one of the floral organs. A deeper study of such patterns might reveal that the heating of different parts of the inflorescence plays a different role. Thus, the contribution of thermogenesis to pollination success needs to be investigated experimentally for both floral organs independently.

Methodological considerations

Temperature elevation in tissues might not fully quantify total thermogenesis, due to potential heat loss through evaporation or other physical constraints (Gibernau et al., 2005; Lamprecht & Seymour, 2010; Seymour, 2010; Seymour & Schultze–Motel, 1999). Therefore, to quantify thermogenesis, the use of respirometry instead of temperature measurements has been emphasised (Seymour, 2010). It has been argued that (evaporative) heat loss due to the high surface area of the appendix can significantly lower the temperature despite high respiration rates (Lamprecht & Seymour, 2010; Seymour, 2010; Seymour & Schultze–

Motel, 1999). Moreover, it has been argued that evaporation could lead to water droplet formation on the appendix of *A. konjac* (Lamprecht & Seymour, 2010).

However, several points are debatable and should be addressed. It appears unlikely that the droplets described by Lamprecht and Seymour (2010) were actually water. First, the analysed plant was placed under a respiratory hood which can be expected to limit the evaporation. Second, droplet formation on the appendix has been observed in other species too and has been identified as odoriferous secretions (Kakishima et al., 2011; Shirasu et al., 2010; personal observation CC).

Moreover, heat loss is generally not detected in the appendix before anthesis. The cuticle effectively insulates the appendix and prevents evaporative heat loss. Therefore, heat loss through convection/radiation begins only once anthesis and heat production starts. But even then, convection/radiation is probably not the main cause of heat loss. Instead, some of the emitted scent compounds, for example trimethylamine and oligo dimethylsulphides, have a very high vapour pressure. It must therefore be considered that scent volatilisation itself is either the main or at least an important contributor to the evaporative cooling, as the appendix is designed to volatise significant amounts of scent compounds in a short time. It is likely not just a coincidence that species that emit large proportions of the highly volatile trimethylamine are the species that cool below ambient temperature during anthesis, such as *A. brachyphyllus* (appendix) and *A. gigas* (Kakishima et al., 2011). This is more likely to contribute to a temperature decrease than passive evaporation, convection or radiation.

It should also be considered that most *Amorphophallus* species have a short pistillate phase, often less than 12 h. Ample amounts of scent compounds are discharged within a short time and it needs to be investigated if this requires an active, energy-consuming release system, as well as the formation of secretory channels shortly before and during anthesis. The morphological changes preceding and during scent release have been investigated in *Sauromatum venosum*, another thermogenic Aroideae and important morphological changes accompanying anthesis were described by Skubatz et al. (1993, 1995) and Skubatz and Kunkel (1999). Moreover, Terry et al. (2016) studied the relationship between temperature elevation, increased respiration rates and the formation and emission of volatiles in *Macrozamia* Miq. cycad cones. These authors concluded that the energetically expensive synthesis and release of monoterpenes – and not thermogenesis – is at the origin of the respiratory metabolic burst (Terry et al., 2016).

It is therefore reasonable to consider that respiration rates during anthesis could be elevated through metabolic activities, such as the biosynthesis of some scent compounds, the formation of secretory channels, and the release of scent compounds. Consequently, if the temperature elevation is low and the respiration rates are high, it does not forcefully imply a strong heat loss (Lamprecht & Seymour, 2010; Seymour, 2010). Instead, it might signify that other metabolic activities linked to anthesis lead to the elevated respiration rates.

Moreover, the temperature measurements are taken at 2–3 mm depth, and it is unlikely that the tissue loses heat so quickly. Therefore, even if temperature measurements are not fully accurate, they should still represent a valid approximation.

Last but not least, there are potential pitfalls in the comparison of temperature measurements from a multitude of morphologically different species. This is usually 'overcome' by the comparison of mass-specific respiration rates (Seymour, 2010). However, in our case, many flowering events were unique, making it impossible to take the according data without damaging the inflorescence. That said, the case of *A. schmidtiae* demonstrates that the impact of morphology appears to have limits of its own. Plants grown from clonally propagated tubers of *A. schmidtiae* yielded two distinctly different temperature patterns, despite their identical floral morphology and genetics. This phenomenon requires additional research. Nonetheless, it clearly demonstrates that morphology alone cannot account for the varied temperature patterns.

These morphological aspects deserve closer observation and have to be addressed in forthcoming studies. The interplay between metabolism, scent production and release, temperature elevation, thermo-regulation and morphology appears to be more complex than previously assumed. In the meantime, temperature measurements have provided a reliable approximation of thermogenesis in several studies (Seymour et al., 2004; Seymour, Gibernau, & Itoh, 2003) and have been widely used in multiple systems (Hoe et al., 2020; Marotz–Clausen et al., 2018; Prieto & Cascante–Marín, 2017; Sayers et al., 2020; Skubatz et al., 2019). Temperature measurements also present some experimental advantages, such as the possibility of simultaneous individual recording of different floral organs or tissues, and the ease of use, particularly when dealing with large inflorescences. From an ecological perspective, detecting temperature elevation is particularly informative when considering biotic interactions among species, such as heat reward to pollinators. Based on these theoretical and practical considerations, this study does not quantify all the physiological variables involved in thermogenesis and instead uses detailed temperature measurements to approximate thermogenic activity in the plants surveyed. The evolution of thermogenesis in plants remains a hot topic.

CONCLUSIONS

The variation in thermogenic patterns and temperature fluctuation in *Amorphophallus* easily outranks the variation

in any other thermogenic plant group studied so far. Our results indicate that thermogenesis evolved only once early in the evolutionary history of *Amorphophallus* and, despite the loss of this function in several lineages, closely related species tend to display a similar temperature elevation. We also show that thermogenesis is at least partly decoupled from evolutionary success, as it did not influence the rate of species diversification within the genus. Although neither phylogenetic relationships nor thermogenic activity are the primary correlates of floral morphology in *Amorphophallus*, we find that thermogenic capacity is associated to some degree to inflorescence types that are likely adapted to beetle pollination. Yet, the phenomenon is only partly understood and the exact functional role that thermogenesis may have in pollinator attraction remains to be further clarified. Additional measurements and observations are required, particularly concerning the identity and the behaviour of visiting and pollinating insects.

Amorphophallus provides an exciting window into the evolution and natural history of thermogenesis in plants. However, as long as accurate data about species distribution, ecological niche and their pollinators are lacking for most *Amorphophallus* species, the evolution of thermogenesis will remain only partly understood. In addition to increased sampling and temperature measurements under controlled conditions, extensive field observations are also crucially needed to fill the remaining knowledge gaps. Unfortunately, gaining such understanding from natural ecosystems represents a race against time. Indeed, 12 out of the only 16 species assessed by the International Union for Conservation of Nature are threatened or nearly threatened, of which four species are classified under the highest threat category 'Critically Endangered', and two species have too sparse data for being reliably categorised (IUCN v. 2022–2; https://www.iucnredlist.org; accessed in April 2023). Further assessments of the remaining species are urgently needed to guide effective conservation strategies and safeguard the future of these unique and fascinating plants.

MATERIALS AND METHODS

Quantitative measurements of thermogenic activity

We recorded the temperature elevation above room temperature, a proxy for thermogenic activity, of 119 individuals representing 80 *Amorphophallus* species (Data S1) using an Extech SD200 3-channel- or an Extech SDL200 4-channel data logging thermometer (accuracy ±1°C). Fine-wired type K thermocouples of less than 1 mm diameter width were chosen in order to keep the plants as intact as possible. Most measurements took place between 2014 and 2020 in a climatised room in the Institute for Plant Science and Microbiology, Hamburg, Germany, after pilot trials also carried out at the Gothenburg Botanical Garden, Gothenburg, Sweden. Thirty of the measurements were performed in Cairns, Australia, under similar conditions. Most plants were either placed in a shaded and climatised room with largely constant ambient temperature, usually in the range of 20–25°C, or in a shaded office under low-temperature fluctuations. Six plants (*A. gallaensis*, *A. josefbogneri*, *A. ochroleucus*, *A. palawanensis*, *A. pilosus* and *A. thaiensis*) were directly analysed in the greenhouses where it was ensured that no direct sunlight reached the plants. Lastly, two plants (*A. polyanthus* and *A. terrestris*) were analysed within a terrarium under similar conditions as in the greenhouse (~85% humidity) around 20°C. Many investigated plants originate from cultivated material derived from the former research collection from Wilbert Hetterscheid in Leiden, or from the collection from Steve Jackson, a retired horticulturist from Cairns Botanic Gardens, Australia. Although cultivated in botanical gardens, they represent original *in situ* collections. Plants for investigation were chosen opportunistically, depending on the formation of an inflorescence. It must be noted that many flowering events were unique opportunities as several of our studied species rarely flower. This unpredictability in flowering, combined with the complexity and costs of the equipment used, jointly explains why our measurements took 7 years.

The thermocouples were inserted at ~2–3 mm depth in the middle of the pistillate (female) zone, the staminate (male) zone and the lower third of the appendix, usually at their broadest zone. The fourth thermocouple recorded room temperature as a reference. Measurements were taken every 5 min, starting at the onset of anthesis. Additionally, in eight species (Data S2 embedded movie), thermal images were shot using an InfraTec mobileIR E9 thermal camera (accuracy ±2°C). Emissivity was set to 0.98 and one image was taken every 5 min. The spathe of the inflorescence was removed either partially or totally, for visualisation purposes. Thermal imaging served to identify the thermogenic zones and to detect putative spatial dynamics not detectable by the thermocouples. Beyond that, thermal imaging was not used for analytical purposes. In eight selected species *A. albispathus*, *A. lewallei*, *A. paeoniifolius*, *A. prainii*, *A. schmidtiae* pattern 1, *A. schmidtiae* pattern 2, *A. tuberculatus*, *A. yunnanensis*, representing the four subgenera, thermal images were assembled to generate time-lapse movies (Data S2 embedded movie).

Several species were analysed in multiple replicates, either of the same clonally propagated plant or of different individuals of a species, in order to assess both the reproducibility and the variability of the thermogenic patterns within species (Data S1).

Time-series clustering

Thermogenesis is a dynamic phenomenon, and we recorded it as time series, that is temporal measurements of a continuous value (temperature) in the floral organs. Therefore, we used time-series clustering to classify species according to their thermogenic pattern, based on the full length of the temperature series rather than on punctuated events such as maximum temperature or temperature range. We applied shape-based clustering, an approach that aligns the shapes of two time series by warping some of their points along the time axis in order to find the optimal path between them (Aghabozorgi et al., 2015). We performed three different hierarchical clustering analyses, based on the time series of (1) the male zone, (2) the appendix, and (3) the male zone and appendix combined (i.e. multivariate time series). Clustering was performed using the Dynamic Time Warping (DTW) distance implemented in the R package dtwcluster (Sardá-Espinosa, 2019). The analyses were performed on: (i) the complete dataset with 119 time series, including multiple measurements available for 20 species; in some cases, based on clonally propagated plants, in

some cases different specimens of a species; and (ii) a dataset with 80 time series, containing a single individual per species, usually the individual reaching the highest temperature unless its time-series was incomplete due to measurements starting after the onset of thermogenesis or ending too early. Prior to the analysis, all variables were smoothed using the *loess* function in the R package stats.

In order to be used in downstream analyses, the output clusters from the clustering analysis were subsequently converted to dendrograms using the function *as.dendrogram* from the R package stats (version 3.6.2), and exported to the newick format, using the function *as.phylo.dendrogram*, from the R packages ape. Additionally, because the complete temperature time series of the appendix and male zone cannot be used in phylogenetic comparative analyses, we summarised them by computing for each of the 80 species the maximum temperature (later in the text referred to as peak temperature) of the appendix and male zone.

Phylogenetic analyses

We inferred a new time-calibrated molecular phylogeny of *Amorphophallus* including 157 species, that is 67% of the described taxonomic diversity of the genus (Claudel et al., 2017) and three outgroup species from other genera of the Araceae family, *Anchomanes difformis* (Bl.) Engl., *Gonatopus angustus* N.E. Br. and *Hapaline* sp. We used the molecular data from Claudel et al. (2017), which included one nuclear (*ITS1*) and two chloroplast (*rbcL* and *matK*) genes. In contrast to Claudel et al. (2017), who concatenated the three DNA markers and did not estimate divergence times, here we used the partitioned dataset to jointly estimate the tree topology and divergence times in a Bayesian framework using BEAST v2.5.0 (Bouckaert et al., 2014). The alignment was partitioned into nuclear and chloroplast genes, with a GTR + G substitution model for each partition. We applied a birth–death tree prior and an uncorrelated log-normal clock.

In order to produce a time-calibrated phylogeny, we implemented three secondary calibration points using the age estimates of Nauheimer et al. (2012) on the following nodes: (1) crown *Amorphophallus*: 95% HPD (highest posterior density) = 9.76–40.43; (2) *Amorphophallus* + *Hapaline*: 95% HPD = 47.42–68.23 and (3) the root node (node 38 of Nauheimer et al., 2012): 95% HPD = 77.1–97.03. All calibrations were set with a uniform prior to the 95% HPD interval. Convergence of the Markov chains Monte Carlo (MCMC) was assessed in Tracer v1.7.1 (Rambaut et al., 2018). We removed the first 10% of the MCMC samples as a burn-in and produced the maximum clade credibility tree using BEAST plug-in logAnalyser. The phylogeny and traits were visualised using the R package ggtree (Yu et al., 2017).

Diversification rate analyses

We investigated the species diversification dynamic of *Amorphophallus* by testing for constant diversification versus time-varying models. We used RPANDA (Morlon et al., 2016) to fit ten birth–death models, including a pure birth model, constant rate birth–death (BD) and other BD models with λ and/or μ varying exponentially or linearly as a function of time. We selected the best-fit model using AIC. However, because the temporal dynamics of diversification rates has been shown to suffer from unidentifiability issues (Louca & Pennell, 2020), we also estimated the 'pulled speciation rate' on a time grid using the R package castor (Louca & Doebeli, 2018). The pulled speciation rate is fully identifiable and corresponds to the speciation rate under zero extinction and complete sampling, meaning that in the presence of extinction or missing taxa, its value is lower than the speciation rate (Helmstetter et al., 2022) and can be informative or overall rate variation (Louca & Pennell, 2020).

Additionally, we tested whether thermogenesis impacted diversification rates in *Amorphophallus*. We compared character-dependent and character-independent models of diversification using the R package HiSSE (Beaulieu & O'Meara, 2016). We fitted a Hidden State Speciation and Extinction model where speciation and extinction rates are allowed to differ between thermogenic and non-thermogenic species, or due to another, hidden trait. This has been shown to reduce the risk of finding spurious evidence of trait-dependent diversification (Beaulieu & O'Meara, 2016). We compared the HiSSE model against a character-independent model and performed model selection using the AIC criterion.

Evolution of thermogenesis

To explore the evolutionary history of thermogenesis in *Amorphophallus* we performed ancestral state estimation for the 80 species with available temperature data. We carried out two sets of analyses with thermogenesis considered first as a continuous trait (peak temperature during anthesis in °C) and secondly as a binary trait (present/absent). For the latter, given the uncertainty of 1°C in the thermometer, species were coded as thermogenic only if they displayed >1.5°C heating above room temperature during anthesis in at least one of the two heat-producing parts of the inflorescence. All analyses were performed in the R package phytools (Revell, 2012). First, stochastic character mapping was done using the *make.simmap* function with 1000 simulations. Posterior probabilities of each state (thermogenic or not thermogenic) were plotted on the phylogenetic tree using the *densityMap* function. For the two continuous variables (peak temperature in the male part and in the appendix), we used maximum likelihood implemented in the function *contMap* to infer ancestral states at nodes and paint the inferred trait history along the phylogenetic tree.

In addition, we estimated the degree of phylogenetic conservatism of thermogenesis by computing Pagel's lambda (Pagel, 1999) for peak temperature of the male zone and of the appendix using the *phylosig* function in phytools. Departure from the null hypothesis of no phylogenetic signal ($\lambda = 0$) was tested using a Likelihood Ratio Test.

Determinants of thermogenesis

Thermogenesis has been associated with insect pollination (e.g. Seymour & Matthews, 2006). More particularly, beetle pollination has been reported to be characteristic for intensely thermogenic flowers with floral chambers (Bernhardt, 2000). Though most *Amorphophallus* species attract a wide array of arthropods (Claudel, 2021), beetles appear to be their main pollinator group (Moretto et al., 2019). Therefore, to test whether thermogenesis is associated with floral morphological traits, we scored for all species included in the phylogeny a matrix of 10 quantitative variables describing the main elements of the inflorescence (height and radius of the appendix and of the male zone, peduncle length and diameter, spadix length, spathe length) as well as pollen size. Some of these variables, for instance, appendix and male zone parameters are directly related to thermogenesis whereas others are part of the pollination system. For example, beetle pollination is associated with floral chambers and inflorescence robustness (Bernhardt, 2000; Johnson & Schiestl, 2016; Kevan & Baker, 1983), represented here by spathe parameters and peduncle diameter. Moreover, the length of the peduncle might be related to the flight ability of a pollinating insect. Lastly, pollen size is generally associated with biotic and abiotic parameters, such as wind- and insect

pollination as well as the feeding behaviour of the pollinating insects (Ackerman, 2000; Hao et al., 2020). Considering the significant size spread of pollen grains within *Amorphophallus*, ranging from 25 to 90 μm (Punekar & Kumaran, 2010; Ulrich et al., 2017; van der Ham et al., 1998), pollen size might be a significant variable.

To assess whether the evolution of inflorescence size and shape is more tightly linked to thermogenesis or to shared ancestry (Q3), we estimated Pagel's lambda for each of the 10 morphological traits, first on the phylogeny and second on the cluster dendrogram which reflects the degree of closeness in the thermogenic pattern. Tests for the null hypothesis of no phylogenetic signal were performed using a likelihood ratio test. For the analysis on the phylogeny, we took into account phylogenetic uncertainty by computing Pagel's lambda on a set of 1000 phylogenetic trees randomly sampled from the posterior distribution of trees. The larger number of species included in the phylogenetic tree compared to the cluster dendrogram (157 versus 80) hinders a direct comparison of Pagel's lambda values. To address this, we repeated the analysis with the phylogenetic tree pruned to keep only the species included in the cluster dendrogram.

We then built a multivariate regression model to evaluate whether thermogenic activity can be predicted from morphological traits. We used phylogenetic mixed models to model thermogenic activity as a function of morphological traits, using the Bayesian implementation in the R package mcmcglmm (Hadfield, 2010). To account for phylogenetic non-independence, phylogenetic relationships were included as a random variable. Two variables with a high proportion of missing data (pollen size and spadix width) were discarded from the analysis so that in total, the regression included 8 variables and 67 species. We carried out two analyses where the response variable was peak temperature in the appendix and in the male zone, respectively. The glmm analyses were run for 20 million MCMC generations, sampling every 12 000 generations. After discarding a burn-in of 120 000 generations, we checked the convergence of the MCMC chains. It would have been desirable to run a mixed model that also included geography as an explanatory variable, in order to test whether the intensity of thermogenic activity differs significantly between Asian, African and Malagasy species. However, there was insufficient statistical power in our dataset to test this hypothesis, given that only three African species and two species from Madagascar could be included in the phylogeny together with 43 Asian species.

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AUTHOR CONTRIBUTIONS

CC and AA initiated the project and carried out pilot measurements. CC collected the data. OL and DS analysed the data. CC, OL, DL, SLY and AA wrote the manuscript.

CONFLICT OF INTEREST

The authors have declared that no competing interests exist.

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DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are deposited as temperature curves in the supporting information; original measurements are available from the corresponding author upon request.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

Data S1. Time series of appendix and male zone temperatures for the 119 measured individuals representing 80 *Amorphophallus* species. Each time series is represented by two graphs: the first graph displays the temperature measurement and the second graph shows the absolute temperature increase.

Data S2. Time-lapse movies from *A. albispathus*, *A. lewallei*, *A. paeoniifolius*, *A. prainii*, *A. schmidtiae* pattern 1, *A. schmidtiae* pattern 2, *A. tuberculatus*, *A. yunnanensis* are accessible in the embedded movie file.

Data S3. Hierarchical dendrograms obtained from the clustering of the time series of appendix and male zone separately or combined, with 119 individuals (including replicates) or 80 (one individual per species).

Figure S1. The two cluster dendrograms based on the univariate time clustering analyses from the male zone and the appendix are broadly similar. Both display two main clusters, one containing species with medium to high-temperature increase and a second cluster consisting of weakly or non-thermogenic species.

Figure S2. Time calibrated molecular phylogeny of *Amorphophallus* inferred in BEAST. Node labels indicate posterior probabilities. Time in million years is shown in the horizontal axis.

Table S1. Comparison between the Hidden State Speciation and Extinction (HiSSE) and character-independent (CDI2) models of diversification.

Table S2. Values of Pagel's lambda for morphological variables estimated both on the cluster dendrogram of thermogenic activity and on the phylogenetic tree (with all species or pruned to the same tips as the dendrogram).

Table S3. Regression coefficients from the generalised-linear-mixed-model regression between the thermogenic activity of the male zone and appendix parts and morphological variables.

REFERENCES

Ackerman, J.D. (2000) Abiotic pollen and pollination: ecological, functional, and evolutionary perspectives. *Plant Systematics and Evolution*, **222**, 167–185.

Aghabozorgi, S., **Seyed Shirkhorshidi, A.** & **Ying Wah, T.** (2015) Time–series clustering – A decade review. *Information Systems*, **53**, 16–38.

Albre, J., **Quilichini, A.** & **Gibernau, M.** (2003) Pollination ecology of *Arum italicum* (Araceae). *Botanical Journal of the Linnean Society*, **141**, 205–214.

Angioy, A.M., **Stensmyr, M.C.**, **Urru, I.**, **Puliafito, M.**, **Collu, I.** & **Hansson, B.S.** (2004) Function of the heater: the dead horse arum revisited. *Proceedings of the Royal Society B*, **271**, 13–15.

Barabé, D., **Gibernau, M.** & **Forest, F.** (2002) Zonal thermogenetic dynamics of two species of *philodendron* from two different subgenera (Araceae). *Botanical Journal of the Linnean Society*, **139**, 79–86.

Barthlott, W., **Szarzynski, J.**, **Vlek, P.**, **Lobin, W.** & **Korotkova, N.** (2009) A torch in the rain forest: thermogenesis of the Titan arum (*Amorphophallus titanum*). *Plant Biology (Stuttgart)*, **11**, 499–505.

Bay, D. (1995) Thermogenesis in the Aroids. *Aroideana*, **18**, 32–39.

Beaulieu, J.M. & **O'Meara, B.C.** (2016) Detecting hidden diversification shifts in models of trait–dependent speciation and extinction. *Systematic Biology*, **65**, 583–601.

Bernhardt, P. (2000) Convergent evolution and adaptive radiation of beetle–pollinated angiosperms. *Plant Systematics and Evolution*, **222**, 293–320.

Bouckaert, R., **Heled, J.**, **Kühnert, D.**, **Vaughan, T.**, **Wu, C.H.**, **Xie, D.** ***et al.*** (2014) BEAST 2: A software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*, **10**, 1–6.

Boyce, P.C. & **Croat, T.B.** (2023) The Überlist of Araceae, Totals for Published and Estimated Number of Species in Aroid Genera. https://www.researchgate.net/publication/369741356_Uberlist_-_April_2023

Chen, G., **Ma, X.-K.**, **Jürgens, A.**, **Lu, J.**, **Liu, E.–.X.**, **Sun, W.-B.** ***et al.*** (2015) Mimicking livor mortis: a well–known but unsubstantiated color profile in Sapromyiophily. *Journal of Chemical Ecology*, **41**, 808–815.

Chouteau, M., **Barabé, D.** & **Gibernau, M.** (2007) Thermogenesis in *Syngonium* (Araceae). *Canadian Journal of Botany*, **85**, 184–190.

Claudel, C. (2021) The many elusive pollinators in the genus *Amorphophallus*. *Arthropod–Plant Interactions*, **15**, 833–844.

Claudel, C., **Buerki, S.**, **Chatrou, L.**, **Antonelli, A.**, **Alvarez, N.** & **Hetterscheid, W.** (2017) Large–scale phylogenetic analysis of *Amorphophallus* (Araceae) derived from nuclear and plastid sequences reveals new subgeneric delineation. *Botanical Journal of the Linnean Society*, **184**, 32–45.

Claudel, C. & **Lev-Yadun, S.** (2021) Odor polymorphism in deceptive *Amorphophallus* species – a review. *Plant Signaling & Behavior*, **16**, e1991712.

Claudel, C., **Lev-Yadun, S.**, **Hetterscheid, W.L.A.** & **Schultz, M.** (2019) Mimicry of lichens and cyanobacteria on tree–sized *Amorphophallus* petioles results in their masquerade as inedible tree trunks. *Botanical Journal of the Linnean Society*, **190**, 192–214.

Dormer, K.J. (1960) The truth about pollination in *Arum*. *New Phytologist*, **59**, 298–301.

Gibernau, M. & **Barabé, D.** (2000) Thermogenesis in three *philodendron* species (Araceae) of French Guiana. *Canadian Journal of Botany*, **78**, 685–689.

Gibernau, M. & **Barabé, D.** (2002) Pollination ecology of *Philodendron squamiferum* (Araceae). *Canadian Journal of Botany*, **80**, 316–320.

Gibernau, M., **Barabé, D.**, **Moisson, M.** & **Trombe, A.** (2005) Physical constraints on temperature difference in some thermogenic aroid inflorescences. *Annals of Botany*, **96**, 117–125.

Gibernau, M., **Chouteau, M.**, **Lavallée, K.** & **Barabé, D.** (2010) Notes on the phenology, morphometry and floral biology of *Anaphyllopsis americana*. *Aroideana*, **33**, 183–191.

Gibernau, M., **Macquart, D.** & **Przetak, G.** (2004) Pollination in the genus *Arum* – a review. *Aroideana*, **27**, 148–166.

Grant, N.M., **Miller, R.A.**, **Watling, J.R.** & **Robinson, S.A.** (2010) Distribution of thermogenic activity in floral tissues of *Nelumbo nucifera*. *Functional Plant Biology*, **37**, 1085–1095.

Hadfield, J.D. (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R Package. *Journal of Statistical Software*, **33**, 1–22.

Handayani, T., **Yuzammi** & **Hadiah, J.T.** (2020) Inflorescence morphology and development of suweg *Amorphophallus paeoniifolius* (Dennst.) Nicolson. *Biodiversitas*, **21**, 5835–5844.

Hao, K., **Tian, Z.-X.**, **Wang, Z.-C.** & **Huang, S.-Q.** (2020) Pollen grain size associated with pollinator feeding strategy. *Proceedings of the Royal Society B*, **287**, 20201191.

Helmstetter, A.J., **Glemin, S.**, **Käfer, J.**, **Zenil-Ferguson, R.**, **Sauquet, H.**, **de Boer, H.** ***et al.*** (2022) Pulled diversification rates, lineage–through–time plots and modern macroevolutionary modelling. *Systematic Biology*, **71**, 758–773.

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.** & **Wong, S.Y.** (2020) Thermogenesis in four species of *Schismatoglottis* Calyptrata Clade (Schismatoglottideae: Araceae). *Feddes Repertorium*, **131**, 268–277.

Ito–Inaba, Y. (2014) Thermogenesis in skunk cabbage (*Symplocarpus renifolius*): new insights from the ultrastructure and gene expression profiles. *Advances in Horticultural Science*, **28**, 73–78.

Ivancic, A., **Lebot, V.**, **Roupsard, O.**, **Quero–Garcia, J.** & **Okpul, T.** (2004) Thermogenic flowering of taro (*Colocasia esculenta*, Araceae). *Canadian Journal of Botany*, **82**, 1557–1565.

Ivancic, A., **Roupsard, O.**, **Quero–Garcia, J.**, **Lebot, V.**, **Pochyla, V.** & **Okpul, T.** (2005) Thermogenic flowering of the giant taro (*Alocasia macrorrhizos*, Araceae). *Canadian Journal of Botany*, **83**, 647–655.

Ivancic, A., **Roupsard, O.**, **Quero–Garcia, J.**, **Melteras, M.**, **Molisale, T.**, **Tara, S.** ***et al.*** (2008) Thermogenesis and flowering biology of *Colocasia gigantea*, Araceae. *Journal of Plant Research*, **121**, 73–82.

Johnson, S.D. & **Schiestl, F.P.** (2016) *Floral mimicry*. Oxford, New York: Oxford University Press.

Jones, W. (2013) Olfactory Carbon Dioxide detection by insects and other animals. *Molecules and Cells*, **35**, 87–92.

Jürgens, A., **Dötterl, S.** & **Meve, U.** (2006) The chemical nature of fetid floral odours in stapeliads (Apocynaceae–Asclepiadoideae–Ceropegieae). *New Phytologist*, **172**, 452–468.

Jürgens, A. & **Shuttleworth, A.** (2016) Carrion and dung mimicry in plants. In: Benbow, M.E., Tomberlin, J.K. & Tarone, A.M. (Eds.) *Carrion ecology, evolution, and their applications*. Boca Raton: CRC Press, pp. 361–386.

Jürgens, A., **Wee, S.-L.**, **Shuttleworth, A.** & **Johnson, S.D.** (2013) Chemical mimicry of insect oviposition sites: a global analysis of convergence in angiosperms. *Ecology Letters*, **16**, 1157–1167.

Kakishima, S., **Terajima, Y.**, **Murata, J.** & **Tsukaya, H.** (2011) Infrared thermography and odour composition of the *Amorphophallus gigas* (Araceae) inflorescence: the cooling effect of the odorous liquid. *Plant Biology (Stuttgart)*, **13**, 502–507.

Kevan, P.G. & **Baker, H.G.** (1983) Insects as flower visitors and pollinators. *Annual Review of Entomology*, **28**, 407–453.

Kite, G.C. & **Hetterscheid, W.L.A.** (1997) Inflorescence odours of *Amorphophallus* and *Pseudodracontium* (Araceae). *Phytochemistry*, **46**, 71–75.

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.**, **Boyce, P.C.**, **Ollerton, J.**, **Cocklin, E.** ***et al.*** (1998) Inflorescence odours and pollinators of *Arum* and *Amorphophallus* (Araceae). In: Owens, S. & Rudall, P. (Eds.) *Reproductive biology in systematics, conservation and economic botany*. Kew, UK: Kew Publishing, pp. 295–315.

Knutson, R.M. (1979) Plants in heat. *Natural History*, **88**, 42–47.

Korotkova, N. & **Barthlott, W.** (2009) On the thermogenesis of the Titan arum (*Amorphophallus titanum*). *Plant Signaling & Behavior*, **4**, 499–505.

Lamprecht, I., **Schmolz, E.**, **Blanco, L.** & **Romero, C.M.** (2002) Flower ovens: thermal investigations on heat–producing plants. *Thermochimica Acta*, **391**, 107–118.

Lamprecht, I. & **Seymour, R.S.** (2010) Thermologic investigations of three species of *Amorphophallus*. *Journal of Thermal Analysis and Calorimetry*, **102**, 127–136.

Louca, S. & **Doebeli, M.** (2018) Efficient comparative phylogenetics on large trees. *Bioinformatics*, **34**, 1053–1055.

Louca, S. & **Pennell, M.W.** (2020) Extant timetrees are consistent with a myriad of diversification histories. *Nature*, **580**, 502–505.

Maia, A.C.D., **Gibernau, M.**, **Carvalho, A.T.**, **Gonçalves, E.G.** & **Schlindwein, C.** (2013) The cowl does not make the monk: scarab beetle pollination of the Neotropical aroid *Taccarum ulei* (Araceae: Spathicarpeae). *Botanical Journal of the Linnean Society*, **108**, 22–34.

Marotz–Clausen, G., **Jürschik, S.**, **Fuchs, R.**, **Schäffler, I.**, **Sulzer, P.**, **Gibernau, M.** ***et al.*** (2018) Incomplete synchrony of inflorescence scent and temperature patterns in *Arum maculatum* L. (Araceae). *Phytochemistry*, **154**, 77–84.

Mayo, S.J., **Bogner, J.** & **Boyce, P.C.** (1997) *The genera of Araceae*. Kew: Royal Botanic Gardens.

Meeuse, B.J.D. & **Raskin, I.** (1988) Sexual reproduction in the arum lily family, with emphasis on thermogenicity. *Sexual Plant Reproduction*, **1**, 3–15.

Miller, R.E., **Grant, N.M.**, **Giles, L.**, **Ribas–Carbo, M.**, **Berry, J.A.**, **Watling, J.R.** ***et al.*** (2011) In the heat of the night – alternative pathway respiration drives thermogene–sis in *Philodendron bipinnatifidum*. *New Phytologist*, **189**, 1013–1026.

Moretto, P., **Cosson, B.**, **Krell, F.–.T.** & **Aristophanous, M.** (2019) Pollination of *Amorphophallus barthlottii* and *A. abyssinicus* subsp. *akeassii* (Araceae) by dung beetles (Insecta: Coleoptera: Scarabaeoidea). *Catharsius la Revue*, **18**, 19–36.

Morlon, H., **Lewitus, E.**, **Condamine, F.L.**, **Manceau, M.**, **Clavel, J.** & **Drury, J.** (2016) RPANDA: an R package for macroevolutionary analyses on phylogenetic trees. *Methods in Ecology and Evolution*, **7**, 589–597.

Nagy, K.A., **Odell, D.K.** & **Seymour, R.S.** (1972) Temperature regulation by the inflorescence of *Philodendron*. *Science*, **178**, 1195–1197.

Nauheimer, L., **Metzler, D.** & **Renner, S.S.** (2012) Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. *New Phytologist*, **195**, 938–950.

Onda, Y., **Kato, Y.**, **Abe, Y.**, **Ito, T.**, **Morohashi, M.**, **Ito, Y.** ***et al.*** (2008) Functional coexpression of the mitochondrial alternative oxidase and uncoupling protein underlies thermoregulation in the thermogenic florets of skunk cabbage. *Plant Physiology*, **146**, 636–645.

Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877–884.

Patiño, S., **Aalto, T.**, **Edwards, A.A.** & **Grace, J.** (2002) Is *Rafflesia* an endothermic flower? *New Phytologist*, **154**, 429–437.

Pouchon, C., **Gauthier, J.**, **Pitteloud, C.**, **Claudel, C.** & **Alvarez, N.** (2022) Phylogenomic study of *Amorphophallus* (Alismatales; Araceae): when plastid DNA gene sequences help to resolve the backbone subgeneric delineation. *Journal of Systematics and Evolution*, **61**, 64–79.

Prakash, P.S. & **Nayar, N.M.** (2000) Thermogenesis in elephant yam, *Amorphophallus paeoniifolius* (Dennst.) Nicolson (Araceae). *Journal of Root Crops*, **26**, 10–14.

Prieto, D. & **Cascante–Marín, A.** (2017) Pollination by nitidulid beetles in the hemi–epiphytic aroid *Monstera lentii* (Araceae: Monsteroideae). *Flora*, **231**, 57–64.

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.

Rambaut, A., **Drummond, A.J.**, **Xie, D.**, **Baele, G.** & **Suchard, M.A.** (2018) Posterior summarization in Bayesian phylogenetics using tracer 1.7. *Systematic Biology*, **67**, 901–904.

Revell, L.J. (2012) Phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **3**, 217–223.

Sardá–Espinosa, A. (2019) Comparing time–series clustering algorithms in r using the dtwclust package. *The R Journal*, **11**, 22–43.

Sayers, T.D.J., **Steinbauer, M.J.**, **Farnier, K.** & **Miller, R.E.** (2020) Dung mimicry in *Typhonium* (Araceae): explaining floral trait and pollinator divergence in a widespread species complex and a rare sister species. *Botanical Journal of the Linnean Society*, **193**, 375–401.

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.

Seymour, R.S. (2004) Dynamics and precision of thermoregulatory responses of eastern skunk cabbage *Symplocarpus foetidus*. *Plant, Cell & Environment*, **27**, 1014–1022.

Seymour, R.S. (2010) Scaling of heat production by thermogenic flowers: limits to floral size and maximum rate of respiration. *Plant, Cell & Environment*, **33**, 1474–1485.

Seymour, R.S. & **Gibernau, M.** (2008) Respiration of thermogenic inflorescences of *Philodendron melinonii*: natural pattern and responses to experimental temperatures. *Journal of Experimental Botany*, **59**, 1353–1362.

Seymour, R.S., **Gibernau, M.** & **Itoh, K.** (2003) Thermogenesis and respiration of inflorescences of the dead horse arum *Helicodiceros muscivorus*, a pseudo–thermoregulatory aroid associated with fly pollination. *Functional Ecology*, **17**, 886–894.

Seymour, R.S., **Ito, K.**, **Umekawa, Y.**, **Matthews, P.D.G.** & **Pirintsos, S.A.** (2015) The oxygen supply to thermogenic flowers. *Plant, Cell & Environment*, **38**, 827–837.

Seymour, R.S. & **Matthews, P.G.D.** (2006) The role of thermogenesis in the pollination biology of the Amazon waterlily *Victoria amazonica*. *Annals of Botany*, **98**, 1129–1135.

Seymour, R.S. & **Schultze–Motel, P.** (1998) Physiological temperature regulation by flowers of the sacred lotus. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **353**, 935–943.

Seymour, R.S. & **Schultze–Motel, P.** (1999) Respiration, temperature regulation and energetics of thermogenic inflorescences of the dragon lily *Dracunculus vulgaris* (Araceae). *Proceedings of the Royal Society B*, **266**, 1975–1983.

Seymour, R.S., **Schultze–Motel, P.** & **Lamprecht, I.** (1998) Heat production by sacred lotus flowers depends on ambient temperature, not light cycle. *Journal of Experimental Botany*, **49**, 1213–1217.

Seymour, R.S., **Terry, I.** & **Roemer, R.B.** (2004) Respiration and thermogenesis by cones of the Australian cycad *Macrozamia machinii*. *Functional Ecology*, **18**, 925–930.

Seymour, R.S., **White, C.R.** & **Gibernau, M.** (2003) Heat reward for insect pollinators: scarab beetles save energy by making themselves at home inside a warm flower. *Nature*, **426**, 243–244.

Seymour, R.S., **White, C.R.** & **Gibernau, M.** (2009) Endothermy of dynastine scarab beetles (*Cyclocephala colasi*) associated with pollination biology of a thermogenic arum lily (*Philodendron solimoesense*). *Journal of Experimental Biology*, **212**, 2960–2968.

Seymour, R.S., **Yuka, I.**, **Onda, Y.** & **Ito, K.** (2009) Effects of floral thermogenesis on pollen function in Asian skunk cabbage *Symplocarpus renifolius*. *Biology Letters*, **5**, 568–570.

Shirasu, M., **Fujioka, K.**, **Kakishima, S.**, **Nagai, S.**, **Tomizawa, Y.**, **Tsukaya, H.** ***et al.*** (2010) Chemical identity of a rotting animal–like odor emitted from the inflorescence of the titan arum (*Amorphophallus titanum*). *Bioscience, Biotechnology, and Biochemistry*, **74**, 2550–2554.

Skubatz, H., **Calonje, M.** & **Tang, W.** (2019) Thermogenesis in male cones of four cycad species. *Theoretical and Experimental Plant Physiology*, **31**, 287–293.

Skubatz, H. & **Kunkel, D.D.** (1999) Further studies of the glandular tissue of the *Sauromatum guttatum* (Araceae) appendix. *American Journal of Botany*, **86**, 841–854.

Skubatz, H., **Kunkel, D.D.**, **Howald, W.N.**, **Trenkle, R.** & **Mookherjee, B.** (1996) The *Sauromatum guttatum* appendix as an osmophore: excretory pathways, composition of volatiles and attractiveness to insects. *New Phytologist*, **134**, 631–640.

Skubatz, H., **Kunkel, D.D.** & **Meeuse, B.J.D.** (1993) The ultrastructural changes in the appendix of the *Sauromatum guttatum* inflorescence. *Sexual Plant Reproduction*, **6**, 153–170.

Skubatz, H., **Kunkel, D.D.**, **Patt, J.**, **Howald, W.**, **Rothman, T.** & **Meeuse, B.J.D.** (1995) Pathway of terpene excretion by the appendix of *Sauromatum guttatum*. *Proceedings of the National Academy of Sciences of the United States of America*, **92**, 10084–11088.

Skubatz, H., **Nelson, T.A.**, **Dong, A.M.**, **Meeuse, B.J.D.** & **Bendich, A.J.** (1990) Infrared thermography of Arum lily inflorescences. *Planta*, **182**, 432–436.

Teijsmann, J.E. & **Binnendijk, S.** (1862) Amorphophallus gigas. *Natuurkundig tijdschrift voor Nederlandsch Indië*, **24**, 329–331.

Terry, L.I., **Roemer, R.B.**, **Booth, D.T.**, **Moore, C.J.** & **Walter, G.H.** (2016) Thermogenic respiratory processes drive theexponential increase of volatile organic compound emissions in Macrozamia cycadcones. *Plant, Cell & Environment*, **39**, 1588–1600.

Thien, L.B., **Bernhardt, P.**, **Devall, M.S.**, **Chen, Z.-D.**, **Luo, Y.-B.**, **Fan, J.-H.** ***et al.*** (2009) Pollination biology of basal angiosperms (ANITA grade). *American Journal of Botany*, **96**, 166–182.

Ulrich, S., **Hesse, M.**, **Weber, M.** & **Halbritter, H.** (2017) *Amorphophallus*: new insights into pollen morphology and the chemical nature of the pollen wall. *Grana*, **56**, 1–36.

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 Kooi, C.J., **Kevan, P.G.** & **Koski, M.H.** (2019) The thermal ecology of flowers. *Annals of Botany*, **124**, 343–353.

van der Pijl, L. (1937) Biological and physiological observations on the inflorescence of *Amorphophallus*. *Recueil des travaux botaniques néerlandais*, **34**, 57–67.

Vereecken, N.J. & **McNeil, J.N.** (2010) Cheaters and liars: chemical mimicry at its finest. *Canadian Journal of Zoology*, **88**, 725–752.

Vogel, S. (1963) Duftdrüsen im Dienste der Bestäubung: über Bau und Funktion der Osmophoren. Akademie der Wissenschaften und der Literatur, Abhandlungen der Mathematisch–Naturwissenschaftlichen Klasse. *Mainz*, **10**, 639–677.

Vogel, S. (1990) The role of scent glands in pollination. On the structure and function of osmophores. English translation of Vogel S. (1963). In: Renner, S. (Ed.) *Duftdrüsen im Dienste der Bestäubung. Über Bau und Funktion des Osmophoren*. Washington, D.C.: Smithsonian Institution Libraries and The National Science Foundation, pp. 44–89.

Wagner, A.M., **Krab, K.**, **Wagner, M.J.** & **Moore, A.L.** (2008) Regulation of thermogenesis in flowering Araceae: the role of the alternative oxidase. *Biochimica et Biophysica Acta*, **1777**, 993–1000.

Wagner, A.M., **Wagner, M.J.** & **Moore, A.L.** (1998) In vivo ubiquinone reduction levels during thermogenesis in Araceae. *Plant Physiology*, **117**, 1501–1506.

Yu, G., **Smith, D.K.**, **Zhu, H.**, **Guan, Y.** & **Lam, T.T.-Y.** (2017) Ggtree: an r package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods in Ecology and Evolution*, **8**, 28–36.

Publ. 7: Phylogenomic study of *Amorphophallus* (Alismatales; Araceae): when plastid DNA gene sequences help to resolve the backbone subgeneric delineation

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Research Article

Phylogenomic study of *Amorphophallus* (Alismatales; Araceae): When plastid DNA gene sequences help to resolve the backbone subgeneric delineation

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Abstract Encompassing ca. 200 species distributed in paleotropical Africa and Asia, *Amorphophallus* is one of the largest genera of Araceae. In spite of the great economic interest in its glucomannan production, only a few studies have attempted to grasp the evolutionary history of this genus. In the current state of knowledge, four main clades, mostly linked to biogeographical delineation, have been identified from phylogenies based on a few genes. However, relationships among and within these clades still remain unclear, due to the rapid radiation that occurred during the early evolutionary history of the genus. Here, we generated genome skimming libraries for 43 specimens from 36 species distributed across the 4 clades, which allowed us to produce a phylogenetic matrix for a set of 71 plastid genes. Our phylogenies confirm the monophyly of these clades but show a new and well-resolved arrangement among these clades. Our analyses therefore provide a new scenario and timeline for the evolution of the main *Amorphophallus* clades, consistent with the morphological characteristics of the clades. The inferred scenario is also in agreement with climate dynamics and the onset of long-distance dispersal by the earliest migratory birds near the Oligocene/Miocene transition around 23 million years ago. Our study provides an up-to-date baseline to understand biogeographic and ecological processes that shaped the current diversity and distribution of *Amorphophallus*, paving the way for larger-scale phylogenomic studies based on plastid and nuclear genomes.

Key words: Alismatales, genome skimming, molecular dating, Oligocene/Miocene dispersion, organelle genomes.

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1 Introduction

The burst of angiosperm diversification in the plant kingdom, presumably triggered by a unique flower innovation and a large array of coevolution processes with pollinators (Hu et al., 2008; Suchan et al., 2015), represents an ideal system for examining how species and traits have evolved. Among Angiosperms, Araceae are one of the most species-rich, morphologically and ecologically diversified of all land-plant families. Displaying highly diverse morphologies ranging from the smallest known Angiosperms in the genus *Wolffia* Horkel ex Schleid., to the largest inflorescence structures in the genus *Amorphophallus* Blume ex Decne. with *A. titanum* (Becc.) Becc. ex Arcang. Araceae encompass ca. 3750 species (Christenhusz & Byng, 2016), most of which have evolved peculiar adaptations to pollinators. Since they arose in the Early Cretaceous ca. 135 millions of years ago (Ma) (Nauheimer et al., 2012), Araceae have undergone multiple radiations into worldwide tropical, temperate, and circum-boreal regions, ranging from aquatic to terrestrial habitats (Mayo et al., 1997), with a particularly large proportion of lineages having evolved lure-and-trap pollination systems (Bröderbauer et al., 2012). Araceae is thus a relevant family to examine how the evolution of pollination traits has triggered diversification of or within lineages.

With ca. 230 described species (Bustamante et al., 2020; Govaerts et al., 2021; Tamayo et al., 2021), *Amorphophallus* Blume ex Decne. is the largest Araceae genus with a paleotropical distribution (Hetterscheid & Ittenbach, 1996; Boyce & Croat, 2011). Its species diversity is only surpassed by the genera *Philodendron* Schott and *Anthurium* Schott (Boyce & Croat, 2011). With an origin estimated ca. 25 Ma

(Nauheimer et al., 2012), its distributional range extends from tropical Africa to India, southeastern China, Southeast Asia, Indonesia, the Philippines, and northern Australia (Hetterscheid & Ittenbach, 1996).

Despite inhabiting a (sub)tropical environment, most *Amorphophallus* species demonstrate a broad ecological tolerance toward a large array of abiotic parameters. For instance, they tolerate varying levels of light intensity, ranging from deep shade (forest floors) to higher levels of irradiation (forest margins or open fields). Moreover, the tuber properties enable them to tolerate drought periods and to occupy small crevices filled with little humus or litter and many *Amorphophallus* species are considered to be pioneering plants (Hetterscheid & Ittenbach, 1996). Morphologically, *Amorphophallus* plants are perennial geophytes that usually consist of an underground tuber, bearing a single compound leaf per growing season. The tubers of some species have a high content of glucomannan, in particular for *A. albus* P.Y.Liu & J.F.Chen, *A. konjac* K. Koch, *A. muelleri* Bl., and *A. paeoniifolius* (Dennst.) Nicolson, a carbohydrate that is used for nutritional or industrial purposes (Yin et al., 2019; Srzednicki & Borompichaichartkul, 2020). Moreover, the leaves of some species are sold as vegetables in local food markets in Asia (Sookchaloem et al., 2016). As in all Araceae, the inflorescence consists of a spadix surrounded by a spathe, borne on a peduncle (e.g., Fig. 1. 1–10). If strongly constricted, the spathe is divided into an upper limb and a base (kettle), forming a chamber or a trap (van der Pijl, 1937; Beath, 1996; Bröderbauer et al., 2012). The spadix is divided into a lower pistillate zone, followed by an upper staminate zone and finally on top, a sterile appendix that serves scent volatilization (Mayo et al., 1997; Kite & Hetterscheid, 2017). Scent volatilization is known to be promoted by heat generation in the appendix, at least in some species (Skubatz et al., 1990; Barthlott et al., 2009; Lamprecht & Seymour, 2010; Shirasu et al., 2010).

The exceptional morphological diversity across the genus is best illustrated by size, which ranges from a few centimeters in dwarf species to several meters in giant species, such as the iconic *A. titanum* (Claudel et al., 2017). Morphological diversity is equally important in inflorescence morphology (Grob et al., 2002; Sedayu et al., 2010), inflorescence odors (Kite & Hetterscheid, 2017; Claudel & Lev-Yadun, 2021), life cycle and berry color (Sedayu et al., 2010), pollen ultrastructure (van der Ham et al., 2005), leaf size and architecture, and petiole patterning with lichen mimicry (Claudel et al., 2017, 2019) (see examples in Fig. 1). In addition, some morphological characters, such as hair-like staminodes (Fig. 1. 13–14), are apparently homoplastic (Hetterscheid, 2012), highly variable (Grob et al., 2002), or

Fig. 1. Examples of morphological diversity within *Amorphophallus* with variations in (1–10) inflorescences for spathe and spadix shape and size, in (6, 10–12) petiole patterning with lichen mimicry, in (13–14) types of staminode with hair-like staminodes, or in (15–18) berry colors. Species: *A. albus* (9), *A. bulbifer* (15), *A. gomboczianus* (7), *A. konjac* (10), *A. laoticus* (12, 13, 16), *A. mossambicensis* (1), *A. muelleri* (6), *A. natolii* (14), *A. ochroleucus* (4), *A. paeoniifolius* (3), *A. sumawongii* (8, 17), *A. taurostigma* (11), *A. verticillatus* (5), *A. yuloensis* (2, 18). Photos were taken by C. Claudel.

polymorphic (van der Ham et al., 2005). The morphological heterogeneity of larger phylogenetic units makes it challenging, if not impossible, to identify morphological synapomorphies (Grob et al., 2002; van der Ham et al., 2005; Sedayu et al., 2010; Claudel et al., 2017). Grob et al. (2002) were the first to explore the phylogeny of *Amorphophallus* using traditional plastid markers (*matK* and *trnL* intron sequences). They inferred 5 main clades based on a sampling of 46 *Amorphophallus* and 2 species of *Pseudodracontium* N.E.Br., the latter genus being subsequently sunk into *Amorphophallus* (Hetterscheid & Claudel, 2012; Claudel et al., 2017). The authors found several main phylogenetic units to be "morphologically highly heterogeneous." When incorporating Floricaula/Leafy second intron (*FLint2*) into the analysis, two out of the five clades were inferred as a single clade in a subsequent investigation (Grob et al., 2004). Subsequently, the resulting strict consensus tree (maximum parsimony [MP] analysis) of the combined data set (*rbcL*, *matK*, *trnL*, and *FLint2*) demonstrated a substantial biogeographic component and was further used to explore the evolution of traits, such as pollen ultrastructure and ornamentation (van der Ham et al., 2005). Pollen morphology was shown to be very variable across the genus; however, no morphological pollen characters were found to support the monophyly of the genus, nor to support any of the four major groups retrieved. Moreover, some species were shown to be polymorphic, indicating that "ectexine features are not necessarily fixed in *Amorphophallus*" (van der Ham et al., 2005).

Based on the work of Grob et al. (2004), Sedayu et al. (2010) expanded the sampling up to 69 species, using *trnL*, *rbcL*, and *Flint2* as molecular markers. Similar to Grob et al. (2004), the resulting phylogenetic trees comprised four major clades that largely reflect the biogeographic distribution of the genus. Consequently, the four clades were named the African (AFR) clade, the Continental Asia I (CA-I) clade, the Continental Asia II (CA-II) clade, and the South East Asia (SEA) clade (Sedayu et al., 2010). However, the interrelationship of the four clades was not resolved in both studies due to unresolved polytomies affecting the basal relationships between these clades (Grob et al., 2004; Sedayu et al., 2010).

In a further attempt to infer the evolutionary history of the genus *Amorphophallus*, Claudel et al. (2017) again expanded the sampling number, investigating a total of 157 *Amorphophallus* species. The internal transcribed spacer 1 (ITS1) was included in the data set whereas *Flint2* was excluded as the latter proved to be too variable (and perhaps paralogous) on a larger scale (Claudel et al., 2017). Again, four major groups were inferred using the plastid and nuclear makers in combined analyses, similar to those inferred by Sedayu et al. (2010) but with a better delineation owing to their extended sampling. This ultimately resulted in the subgeneric delineation of four subgenera, namely *Amorphophallus* (SEA), *Afrophallus* Hett. & Claudel (AFR), *Metandrium* Stapf (CA-I), and *Scutandrium* Hett. & Claudel (CA-II). Claudel et al. (2017) provided a diagnosis for the newly erected subgenera *Afrophallus* and *Scutandrium*; moreover, Claudel et al. (2017) demonstrated the congruence between the molecular approach and the morphology on behalf of smaller phylogenetic units, such as the *Pusillus*, *Pulchellus*, or the *Paeoniifolius-Manta* clades, to name a few. However, when analyzing separately the nuclear and the plastid markers, the relationships among the four subgenera were still partially resolved in the plastid tree, and differed from the nuclear tree with regard to the arrangement of the three Asian subgenera (*Amorphophallus*, *Metandrium*, and *Scutandrium*; see Fig. 3). On the other hand, the four clades were not completely monophyletic within the nuclear tree, which illustrates the limitation of such markers to resolve the evolutionary history of this genus.

Rapid radiation makes it challenging to establish well-resolved phylogenies (Whitfield & Lockhart, 2007), a process that seems to have been at work during the early evolution of *Amorphophallus*. In particular, subgenera *Amorphophallus* and *Metandrium* are morphologically highly diverse, which makes it challenging to identify suitable morphological traits that trace the evolutionary history of the genus. During rapid radiations, the number of DNA substitutions is rather low, leading to little support for phylogenetic inferences and short internodes that reflect shared ancestry (Kong et al., 2021). In the meantime, pervasive introgressions, gene duplications, or incomplete lineage sorting (ILS) where the alleles coalesce before the splitting of species, further complicating the phylogenetic study of such clades and underlying evolutionary questions (Maddison & Knowles, 2006). So far, molecular phylogenies on *Amorphophallus*, which relied on the concatenated analysis of a handful of genes, still leave uncertainties about the initial radiation of the genus by a lack of phylogenetic signal on basal relationships (Grob et al., 2004; Sedayu et al., 2010) or by alternative histories (Claudel et al., 2017), which may be related to ILS and/or gene flow, two processes that are expected during a species′ radiation.

The last decade has seen the rise of high-throughput sequencing, allowing the comparison of multiple loci in a large number of taxa. However, subsequent analyses generally rely on high-quality data, to ensure sufficient levels of depth and coverage, a task that might be costly both economically and computationally (Harrison & Kidner, 2018). In order to decrease costs, recent methodological developments gathering key data from low-coverage sequencing have been proposed (Barrett et al., 2016a; McKain et al., 2018). Genome skimming, consisting of shotgun sequencing of the whole genome at low coverage, allows to target high copy number of certain genomic components, which include chloroplast genomes (cpDNA), mitochondrial genomes (mtDNA), and nuclear ribosomal DNA (nrDNA) repeats (Straub et al., 2012; McKain et al., 2018). This method has been widely used, in both fresh and degraded samples (Trevisan et al., 2019; Alsos et al., 2020; Nevill et al., 2020), for barcoding (Coissac et al., 2016; Bohmann et al., 2020) or phylogenetic applications in both animals (Johri et al., 2020; Tan et al., 2021a, 2021b) and plants (Malé et al., 2014; Barrett et al., 2016b; Givnish et al., 2018; Liu et al., 2018; Pouchon et al., 2018).

Taking benefit of such recent developments, our study uses genome skimming libraries from *Amorphophallus* taxa and available annotated cpDNA genomes to capture plastid DNA genes in order to (i) resolve the phylogenetic positions of the four subgeneric clades of *Amorphophallus*, and (ii) estimate the timing and tempo of *Amorphophallus* diversification.

2 Material and Methods

2.1 Sampling, DNA extraction, and sequencing

Genome skimming libraries were produced for 39 accessions, representing 32 *Amorphophallus* species, plus 2 accessions as outgroup species (see Table S1). Among these accessions, DNA extracts were already collected for 31 *Amorphophallus* samples processed by Claudel et al. (2017), representing 31 species (see Claudel et al., 2017 for voucher number and extraction protocol). The eight remaining accessions were collected newly for this study, including two additional samples of *A. mossambicensis* Klotzsch ex Garcke and one potentially undescribed species *A. spec.* Sabah (Table S1). Lastly, the two outgroup taxa, *Caladium bicolor* (Aiton) Vent. and *Hapaline brownii* Hook.f. were included. Fresh leaf tissues were collected for the new accessions and outgroup taxa in the Hamburg botanical garden (Germany), and in the Vienna botanical garden (Austria) for *A. spec.* Sabah. DNA extractions were performed using the Qiagen plant tissue kit. Additionally, two extraction replicates of the same accessions were also performed for two ingroup species, *A. natolii* Hett. and *A. rhizomatosus* Hett., as quality control to evaluate the efficiency of the following bioinformatic method to capture plastid genes in sequencing libraries. We then produced 43 shotgun libraries, including the two extraction replicates, with a dual indexing strategy following Meyer & Kircher (2010). The library pool was sequenced using an Illumina HiSeq. 2500 protocol (Lausanne Genomic Technologies Facility).

2.2 Data acquisition

Four additional sequencing libraries were retrieved in the European Nucleotide Archive (ENA) for the following *Amorphophallus* species, generated in Liu et al. (2019): *Amorphophallus albus* (SRR7938683), *A. bulbifer* (Roxb.) Blume (SRR7938684), *A. konjac* (SRR7938681), and *A. muelleri* Blume (SRR7938682).

In order to estimate the divergence time of the crown *Amorphophallus* from fossil records available for monocots (Iles et al., 2015), we also completed our outgroup sampling for Alismatales by adding 11 genome skimming libraries generated within the framework of the PhyloAlps project (Alsos et al., 2020), and 38 fully annotated cpDNA available from NCBI GenBank/Refseq (Table S1). Among these, three *Acorus* L. species (Acorales; Acoraceae), sister to all other monocots, were included to root the phylogenies (Nauheimer et al., 2012).

2.3 Plastid gene capture

Plastid genes were captured *in silico* in the genomic libraries by using ORTHOSKIM (Pouchon et al., 2022; https://github.com/cpouchon/ORTHOSKIM) on the GRICAD infrastructure (https://gricad.univ-grenoble-alpes.fr) with 24 cores and 125 GB of RAM.

We first performed global assemblies using the *assembly* mode, using the SPAdes assembler (Bankevich et al., 2012), with the default parameters (i.e., kmer size of 55, minimal kmer coverage ≥3, minimal contig size ≥500 bp). The contigs were next cleaned with *cleaning* mode by using a similarity threshold of 65% and a minimal mapping length of 140 bp. We set the expected taxonomy of contig mapping at the "Embryophyta" level, to exclude all contigs outside of this clade (i.e., contaminants) during this cleaning step.

We next computed a database of references for the cpDNA using the *database* mode with the 38 full cpDNA annotations collected from NCBI Genbank/Refseq and the given seed sequences from the cpDNA genome of *Arabidopsis thaliana* (L.) Heynh. (AP000423). This database consisted of 79 coding genes (CDS) and 4 rRNA non-coding gene sequences.

The capture of cpDNA genes was performed with the *capture* mode for the CDS and rRNA-targeted sequences. Only the exonic regions were targeted for both types of genes. We also set a minimal reference sequence coverage of 50% and a minimal open reading frame (ORF) coverage of 80% to consider the successful capture of CDS sequences.

In order to combine captured CDS and rRNA sequences with those from the full-annotated cpDNA of outgroups in the ORTHOSKIM architecture, we developed a bash script *Annotation_extraction.sh* available at https://github.com/cpouchon/ORTHOSKIM. This script consisted of: (i) extracting all gene sequences from the annotations; (ii) mapping them onto the same seeds used in ORTHOSKIM to keep a standard gene name; and (iii) writing the gene sequences in the same output format. We used this script on the 38 full cpDNA annotations.

2.4 Construction of phylogenetic matrices

In order to estimate the phylogenetic relationships between the four clades and to date the divergence of *Amorphophallus* taxa, two phylogenetic data sets were built: (i) one focusing on ingroup relationships; and (ii) one on outgroup taxa for the dating. For both data sets, a gene-based partitioned alignment was produced using the *alignment* mode in ORTHOSKIM on the same CDS and rRNA gene set, based on the MAFFT algorithm (Katoh & Standley, 2013), and trimmed with trimAl using the heuristic *automated1* algorithm (Capella-Gutiérrez et al., 2009). We filtered out libraries with more than 85% of missing data on the concatenated alignments. The first data set consisted of 45 *Amorphophallus* taxa and a subsampling of 9 Araceae outgroups. The second data set consisted of the same 45 *Amorphophallus* taxa with all 51 Alismatales outgroups.

2.5 Ingroup phylogenetic reconstruction

Phylogenetic reconstructions were performed using maximum likelihood (ML) and Bayesian inference (BI) approaches on the concatenated gene-partitioned alignment. Moreover, we also used a MP approach, as high levels of ILS can mislead the concatenated ML inferences and not MP reconstructions (Kubatko & Degnan, 2007; Mendes & Hahn, 2018). The ML reconstruction was performed in IQ-TREE-2 v.2.1.2 (Minh et al., 2020). We used ModelFinder (Kalyaanamoorthy et al., 2017) to determine the best-fitted model for each partition in IQ-TREE-2 along with 1000 ultra-fast bootstrap (UFBoot) replicates, the SH-like approximate likelihood ratio test to assess branch support under 1000 replicates, and the hill-climbing nearest neighbor interchange (NNI) search option. The BI reconstruction was done in ExaBayes v1.5 (Aberer et al., 2014) using two independent MCMC runs with $4 \times 1\,000\,000$ generations, sampled every 500. Chain convergence was assessed using the *postProcParam* function in

ExaBayes with an expected effective sampling size (ESS) ≥ 200. An extended majority-rule consensus was generated using the *consense* function. MP tree reconstruction was performed in MPBoot v1.1.0 (Hoang et al., 2018) using 1000 UFBoot replicates along with the NNI search option.

2.6 Molecular dating

Molecular dating was performed on the outgroup data set by using BEAST2 v2.6.4 (Bouckaert et al., 2014). For computation purposes, we ran BEAST2 analysis on the plastid concatenated matrix without partition schemes, as performed by Nauheimer et al. (2019) on full plastid genes, by assuming a simple Yule process. We used the GTR + I + G substitution model, estimated by ModelFinder (Kalyaanamoorthy et al., 2017) in IQ-TREE-2 (Minh et al., 2020) with four gamma categories, and an optimized relaxed clock (ORC) especially efficient with long alignments (Douglas et al., 2021). Two parallel MCMC chains with 200 million generations each were run, sampling every 5000th generation. We assessed the convergence of runs with an estimated ESS> 200 using Tracer v.1.7.2 (Rambaut et al., 2018) after removing 25% of samples as burn-in. The resulting trees of different runs were next combined in LogCombiner v.2.6.5 and summarized in a maximum clade credibility tree using TreeAnnotator v.2.6.4 (Bouckaert et al., 2014).

We used a total of nine fossil records (Table 1), available for monocots (Nauheimer et al., 2012; Iles et al., 2015). Our constraint scheme consisted of gamma-distributed priors for all nine fossils, resulting in high probabilities for ages to be close to the minimum constraint (Ho & Phillips, 2009; Nauheimer et al., 2012). The same gamma constraint scheme as used by Nauheimer et al. (2012) was applied to the root in order to estimate the divergence time of Araceae. The offset was set at 123.9 Ma with shape and scale parameters of 2 and 3.07, respectively (see Nauheimer et al., 2012). This allowed the root age to be 5% younger than the earliest monocot pollen *Liliacidites* (125 Ma, Table 1) and 5% older than 138.5 Ma, a median age inferred for the monocot crown group in molecular clock studies (Bell et al., 2010; Smith et al., 2010). For the other calibration points, shape and scale parameters were set at 2 and the offset was adjusted so that the median age could correspond to the minimum boundary age of fossils. The XML input file was generated in BEAUti v.2.6.5.

3 Results

3.1 Sequencing and cpDNA gene capture

DNA sequencing of the shotgun libraries generated on average 6.26 million reads per sample (Fig. S1). We collected 7.05 million reads per sample on average for the additional libraries we used. For the global assemblies, more contigs were assembled for the shotgun libraries produced than for the ones added, resulting in a median of 26 887 and 18 947 contigs, respectively. Nevertheless, cpDNA assemblies were more fragmented in our shotgun libraries in comparison to the additional libraries, resulting in a higher cpDNA contigs number on average (33.23 vs. 9.26), a smaller cpDNA reconstructed size (80 617 vs. 133 857 bp), and a weaker mean coverage (42.62 vs. 173.89), for which the gene capture was efficient (Fig. S1). Differences in

Table 1 Fossil calibration nodes used in divergence time analysis

Fossil taxon	Organ	Node assignment	Node number	Minimum boundary age (Ma)	References
Liliacidites	Pollen	Crown node of monocots	0	125.0	Iles et al. (2015)
Caldesia brandoniana	Fruit, seeds	Stem node of *Caldesia*	13	20.0	Iles et al. (2015)
Aponogeton harryi	Pollen	Stem node of Aponogetonaceae	5	81.13	Iles et al. (2015)
Keratosperma allenbyense	Fruit, seeds	Stem node of Lasioideae	39	48.7	Iles et al. (2015)
Limnobiophyllum scutatum	Vegetative plants	Stem node of Lemnoideae	30	66	Iles et al. (2015)
Araciphyllites tertiarius	Leaves	Stem node of Monstereae	36	47	Iles et al. (2015)
Stratiotes L.	Seeds	Stem node of *Stratiotes*	17	55.9	Iles et al. (2015)
Thalassites parkavonenses	Vegetative plants	Stem node of *Enhalus* + *Halophila* + *Thalassia*	24	47.8	Iles et al. (2015)
Petrocardium cerrejonense	Leaves	Stem node of *Anthurium*	35	55.8	Nauheimer et al. (2012)

References for fossils are given in Nauheimer et al. (2012) and Iles et al. (2015) studies; Ma, millions of years ago.

such statistics were also noted between the extraction replicates, in particular for *A. natolii* AmphSG11, which demonstrates a lower number of reads (Fig. S1).

Concerning plastid gene recovery, the success rate of capture for CDS and rRNA was, respectively, 69.55% and 81.67% for ingroups (including produced and added libraries) and 84.81% and 96.15% for outgroups (Fig. 2). Two genes, *infA* and *petN*, were missing in ingroups, whereas some genes were missing in produced libraries (i.e., *rpl14*, *rpl16*, *rpl36*, *rpoA*, *rps11*, and *rps8*) or captured at a weaker rate, such as *petG* and *petL* (Fig. 2). Overall, we obtained weaker capture rates for the genome skimming libraries we produced than for the ones we added, for both CDS and rRNA genes. Indeed, we captured 72.91% of CDS and 81.39% of rRNA genes in produced libraries vs 89.03% and 95%, respectively, for the additional libraries. Among the extraction duplicates, a lower capture rate was again obtained for the *A. natolii* AmphSG11 library than for its replicate AmphSG43 (62.65% vs. 83.13% of success), which is consistent with its lower sequencing depth (Fig. S1). Fewer differences over capture were found between *A. rhizomatosus* replicates (77.1% vs. 83.13% of success).

3.2 Ingroup phylogenetic reconstructions

To infer the phylogenetic relationships of ingroup taxa, we excluded eight missing or nearly missing genes from the concatenation along with *accD*, *clpP*, *ycf1*, and *ycf2*, for which spurious alignments were produced. The resulting matrix consisted of 71 plastid genes (67 CDS and 4 rRNA), 52 781 bp, with 3310 informative sites, and 26.75% of missing data.

The ML and BI analyses showed fully congruent and well-resolved phylogenetic reconstructions, with 88.23% of nodes supported by UFBoot values ≥ 95% and 94.11% by PP ≥ 0.95 (Fig. 3). The MP tree revealed slightly weaker node supports with 84.31% of nodes supported by UFBoot values ≥ 95% (Fig. S2). In the three analyses, all replicates clustered together and the four main clades were monophyletic (Figs. 3, S2). The basal divergence of *Afrophallus* (AFR) was fully supported with a BPP value of 1.0 and by ML and MP-Ufboot values of 100%. The *Scutandrium* clade (CA-II) next diverged from *Metandrium* (CA-I) and *Amorphophallus* (SEA), which were sisters in the three analyses. These two splits were highly supported with BPP, ML-UFBoot, and MP-UFBoot values of 1.0, 86%, and 98% for the *Scutandrium* split, and 1.0, 98%, and 93% for the split between *Metandrium* and *Amorphophallus* clades (Fig. 3). The only topological difference between the MP, ML, and BI trees concerned the position of *A. natolii* within *Metandrium*. In both ML and BI trees, *A. natolii* is nested within a clade after an earlier split of *A. elatus* Hook.f., *A. laoticus* Hett., and *A. napiger* Gagnep. (Fig. 3). This position is however poorly supported (BPP = 0.65 and ML-UFBoot = 61%). In the MP tree, *A. natolii* appeared sister to the *A. elatus* and *A. napiger* clade (Fig. S2), with no support (MP-UFBoot = 41%).

3.3 Divergence time of *Amorphophallus*

The outgroup data set used to infer divergence time in BEAST2 analyses comprised 53 106 positions, including 27.50% of informative sites and 17.03% of missing data. The resulting phylogenetic tree was highly resolved with 94.73% of nodes fully supported (BPP = 1.00, see Fig. 4). Moreover, concerning the ingroup relationships, we obtained a similar topology between and within the four main clades as for those inferred on the ingroup data set. As stated in the previous analyses, the only topological difference concerned the position of *A. natolii*, appearing sister to the (*A. elatus*, (*A. laoticus*, *A. napiger*)) clade (BPP = 0.86).

All divergence time estimates for each node are given in Table S2 and summarized in Fig. 4. Our analysis estimated the monocot's crown node ca. 128.9 Ma (HPD: 124–137 Ma), in the Early Cretaceous (chronogram given in Fig. 4). The Araceae arising ca. 121.2 Ma (HPD: 105–134 Ma) and beginning to differentiate ca. 94.1 Ma (HPD: 76–114 Ma). The divergence between Butomaceae and Hydrocharitaceae was estimated at 72.7 Ma (HPD: 61–87 Ma) during the Late Cretaceous, more recently than the divergence of Aponogetonaceae and Scheuchzeriaceae ca. 80.7 Ma (HPD: 78–86 Ma). Regarding the other representative monocot families, our estimates dated the crown node of Alismataceae at 41.4 Ma (HPD: 26–60 Ma), Aponogetonaceae at 22.9 Ma (HPD: 12–39 Ma), and Hydrocharitaceae ca. 57.4Ma (HPD: 53–64Ma). Within Araceae, Aroideae appear to have diverged from Calloideae during the Eocene ca. 41.9 Ma (HPD: 33–50Ma) and differentiated near the Eocene/Oligocene transition ca. 34.1 Ma

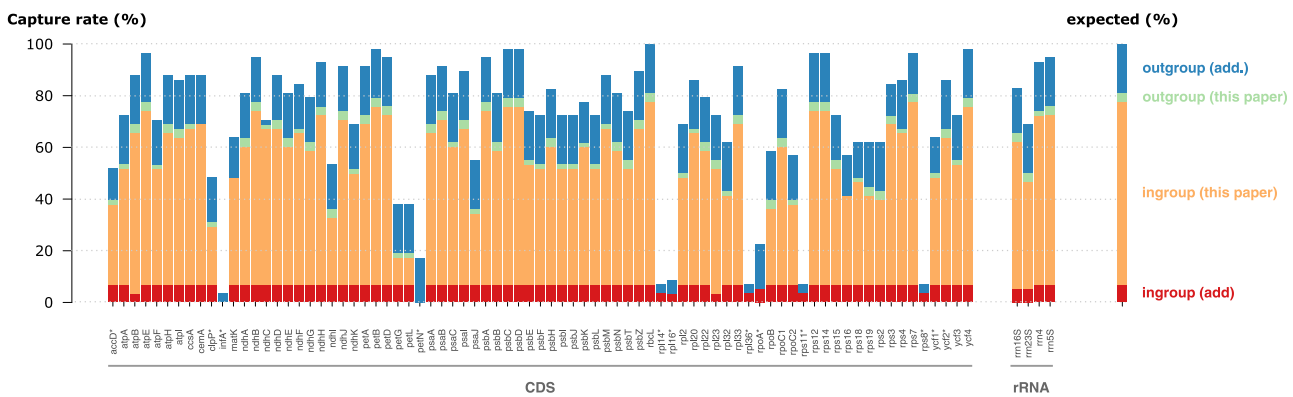

Fig. 2. Chloroplast genes capture within shotgun libraries using the ORTHOSKIM pipeline (Pouchon et al., 2022). Success capture rates are given by plastid genes, for both outgroup and ingroup taxa from produced libraries (in green and orange colors) or collected libraries (in blue and red). Gene excluded for the phylogenetic reconstructions are highlighted with an asterisk.

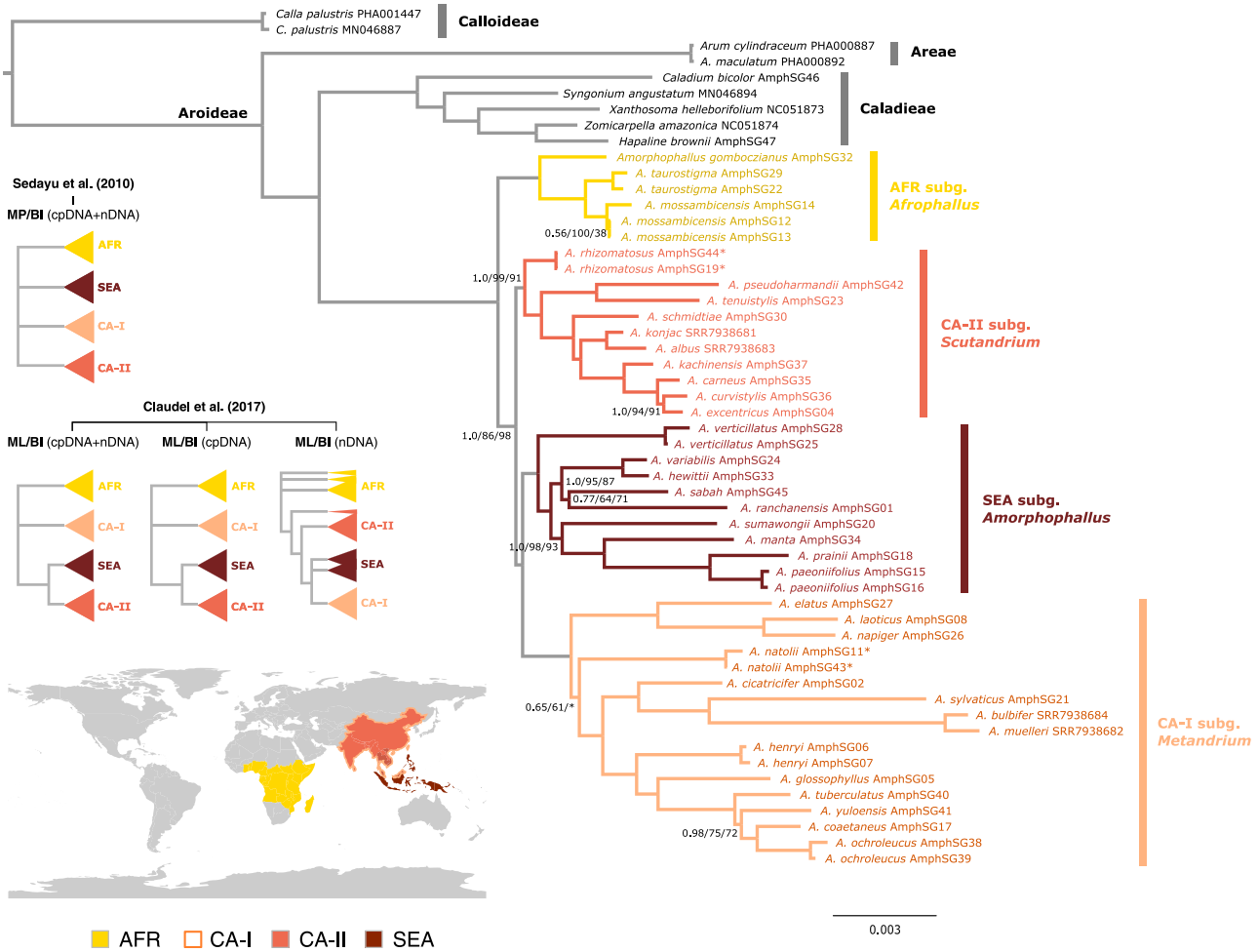

Fig. 3. Majority-rule consensus tree of the Bayesian inference analysis inferred from the concatenation of the 71 plastid genes for *Amorphophallus* subgenera. All nodes have full support, except for those where the specific support value is indicated. Bayesian posterior probability is indicated first, followed by bootstrap support from maximum likelihood (ML) and maximum parsimony (MP) analyses. Subgenera delineation is given according to Sedayu et al. (2010) and Claudel et al. (2017). Extraction replicates of the same Voucher specimens are highlighted by asterisks.

(HPD: 26–43Ma). The monotypic Thomsonieae (encompassing the genus *Amorphophallus*) diverged from Caladieae during the Oligocene at ca. 30.0 Ma (HPD: 23–38 Ma), while the four *Amorphophallus* main clades rapidly evolved in the Oligocene/Miocene transition and started diverging in the Early Miocene. Indeed, the *Amorphophallus* crown node, with *Afrophallus* (AFR) differentiating, is dated to ca. 22.5 Ma (HPD: 17–29 Ma) whereas the *Afrophallus* crown node to ca. 11.4 Ma (HPD: 4–21 Ma). The *Scutandrium* (CA-II) stem and crown nodes were estimated at ca. 20.8 Ma (HPD: 15–27 Ma) and ca. 18.1 Ma (HPD: 12–25 Ma). The *Amorphophallus* (SEA) and *Metandrium* (CA-I) clades diverged at ca. 19.9 Ma (HPD: 15–26 Ma) and began differentiating at ca. 17.3 Ma (HPD: 12–23 Ma) and ca. 17.4 Ma (HPD: 12–23 Ma), respectively.

Finally, without considering the root constraint, the posterior age estimates for seven of eight calibrating nodes were close to their priors: *Aponogeton harryi* (estimated at ca. 80.7 vs. 81.1 Ma constraint), *Araciphyllites tertiarius* (45.8 vs. 47.0 Ma), *Caldesia brandoniana* (21.5 vs. 20.0 Ma), *Keratosperma allenbyense* (50.23 vs. 48.7 Ma), *Limnobiophyllum scutatum* (67.6 vs. 66.0 Ma), *Petrocardium cerrejonense* (54.07 vs. 55.8 Ma), and *Stratiotes* (57.4 vs. 55.9 Ma), while *Thalassites parkavonenses* was estimated ca. 10 Ma younger (Table S2). The posterior age estimate for the root at ca. 128.9 Ma was also close to the *Liliacidites* pollen (125 Ma).

4 Discussion

The plastome phylogeny inferred here, with coding and noncoding cpDNA genes captured in low coverage shotgun libraries, helped us to resolve for the first time phylogenetic hypotheses among *Amorphophallus* subgenera, and to clarify subgeneric delineation. This phylogeny also provided a new timeline for the evolution of *Amorphophallus*. We detail below key points regarding these relationships and dating hereafter.

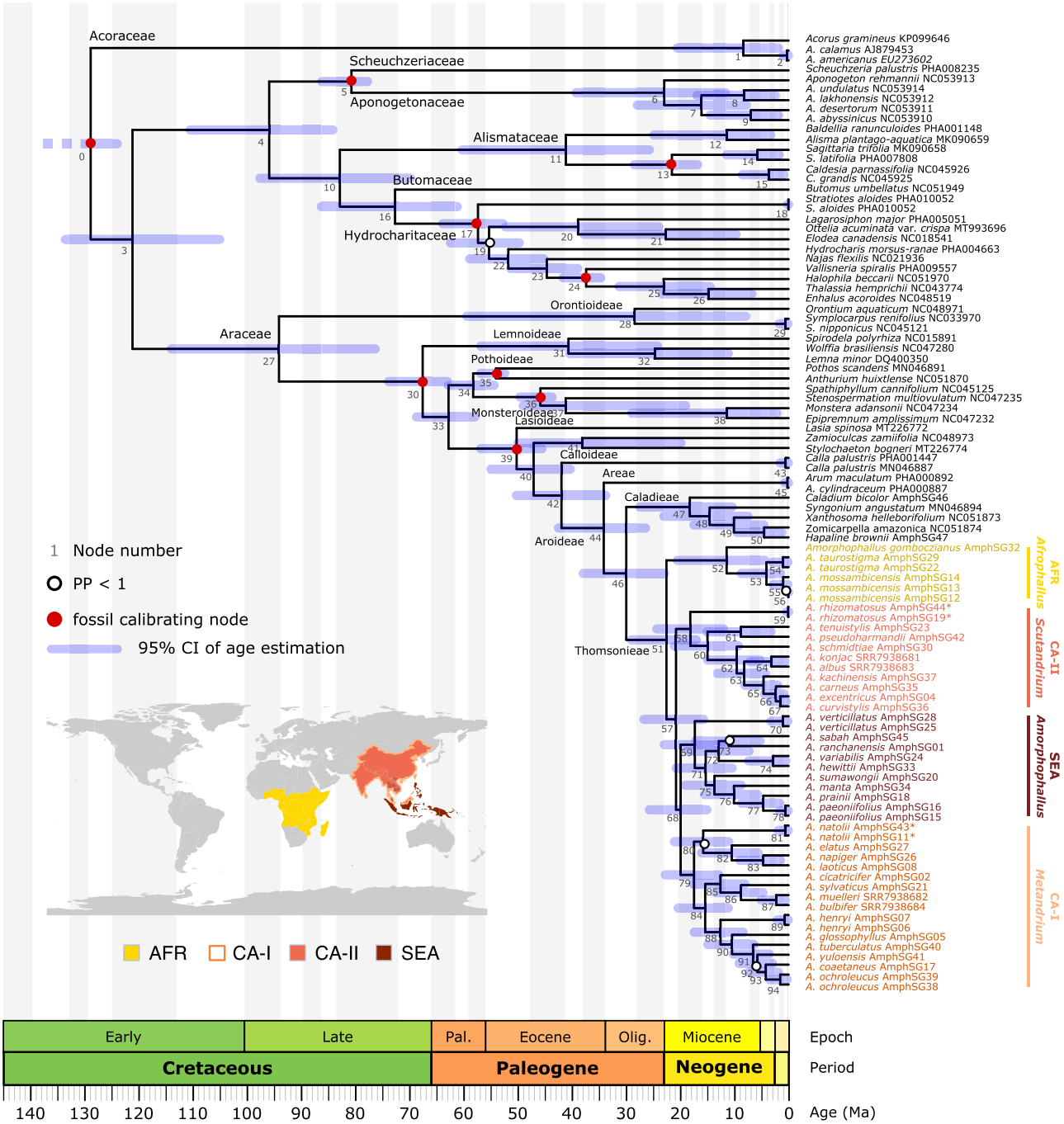

Fig. 4. Time-calibrated maximum clade credibility tree indicating divergence time of *Amorphophallus* radiation from BEAST2 analysis. Blue bars at nodes show 95% confidence intervals. Exact age estimates are shown in Table S2. Black dots with a white center indicate Bayesian posterior probability (BPP) values < 1.0. Red dots indicate fossil calibrating nodes used (see Table 1). Subgenera delineation is given according to Sedayu et al. (2010) and Claudel et al. (2017). Extraction replicates of the same Voucher specimens are highlighted by asterisks.

4.1 Backbone evolution of *Amorphophallus*

Previous phylogenetic works on *Amorphophallus*, based on a handful of genes, failed to resolve the backbone relationships between the four main clades owing to the rapid radiation of these species, providing few informative sites to discriminate internodes and discordant histories (Grob et al., 2002, 2004; Sedayu et al., 2010; Claudel et al., 2017). The fast proliferation of lineages that occur during species' radiations may imply such short durations for speciation that there is not enough time for lineage sorting and/or reproductive isolation to be completed (Pinho & Hey, 2010; Townsend et al., 2012). In such a scenario, high levels of ILS and/or intensive gene flows after secondary contacts of interfertile populations can lead to an "anomaly zone" with a

conflicting signal between gene trees and the species tree (Rosenberg & Tao, 2008; Degnan & Rosenberg, 2009), or for concatenated data between methods (e.g., ML/BI vs. MP trees, see Kubatko & Degnan, 2007; Mendes & Hahn, 2018). In previous studies, topological incongruence was found for the phylogenetic placement of the four subgenera depending on the markers analyzed (nuclear ITS1 vs. plastid *matK-rbcL* trees in Claudel et al., 2017). Moreover, most of the intra and inter subgenera relationships were poorly resolved, as shown by polytomies affecting basal relationships in Sedayu et al. (2010) or in the plastid tree of Claudel et al. (2017). The lack of phylogenetic signal provided by the few markers used could explain such topological discordances. This is concomitant with the short branches delineating the four subgenera highlighted on our plastome trees and the relatively low variability provided by the 71 plastid genes used (i.e., only ~6.3% of informative sites).

Our plastome tree provides a new scenario about the evolution of the main clades of *Amorphophallus*, making sense of the morphology of these species. Despite our cpDNA-based phylogeny is only able, by essence, to infer the evolutionary history of maternally inherited lineages, the very robust supports obtained advocate a strong biological component in the obtained topology. Last, but not least, our plastome topology is also congruent overall regarding the subgenera delineation with the one previously inferred separately based on ITS1, but conflicting with the plastid one inferred on *matK* and *rbcL* only or the combined nuclear-plastid phylogeny (Claudel et al., 2017). Indeed, our plastome tree indicated an early split between the *Afrophallus* (AFR) subgenus and the Asian lineages. This is in agreement with the previous nuclear ITS1 tree while *Afrophallus* was not monophyletic (Claudel et al., 2017). Several morphological traits, such as the life-cycle, stylar length, the shape of the lamina segments, and the absence of staminodes, support this basalmost position within the whole genus (Sedayu et al., 2010; Claudel et al., 2017; Hetterscheid, 2020). Within the Asian clades, our study identifies a further split between the subgenus *Scutandrium* (CA-II) and the subgenera *Amorphophallus* (SEA) and *Metandrium* (CA-I), which are the most derived sister clades. As for the divergence of *Afrophallus*, these splits are also concomitant with the previous nuclear tree but conflict with the plastid tree inferred on *matK-rbcL*, on which *Scutandrium* and *Amorphophallus* clades were sisters (Claudel et al., 2017). This discordance is probably explained by the DNA sampling incompleteness of the *matK* and *rbcL* markers, on which there was likely no sufficient time to accumulate informative sites that allow them to trace back the branching pattern and which can reflect a different topology due to ILS. This is highlighted in our phylogeny by the short branch discriminating *Scutandrium* from the *Metandrium* + *Amorphophallus* clades. The addition of a larger number of plastid loci, for which the lineage sorting could be complete, would thus allow our plastome tree to converge toward a similar topology for the four subgenera to one of the nuclear trees of Claudel et al. (2017), which strengthens our understanding about the evolutionary history of the whole genus.

Several morphological characters support our new subgeneric arrangements, such as the berry color, the plant size, or the overall morphological diversity. Indeed, subgenera *Afrophallus* and *Scutandrium* exclusively contain species with red/orange berries (Claudel et al., 2017), a dominant state in the genus *Amorphophallus* (Sedayu et al., 2010), which seems to be plesiomorphic according to our topology (as well as according to Sedayu et al., 2010). In contrast with these clades, most changes regarding berry color and berry surface are found in subgenera *Amorphophallus* and *Metandrium* (e.g., Fig. 1. 15–18). For example, some species within the subgenus *Amorphophallus* bear greenish- or grayish-colored warty berries, which occur near the ground (Claudel et al., 2017; own observation) and may suggest that animals that move on the forest floor could serve as dispersal agents. Moreover, green-grayish warty berries could also indicate a case of seed camouflage (Lev-Yadun, 2021). However, neither the dispersal agents nor the putative herbivores are known (Claudel et al., 2019). In contrast, green, white, yellow, orange, blue, or red berries, all of which have a smooth surface, are found within subgenus *Metandrium* (Hetterscheid & Ittenbach, 1996; Li & Hetterscheid, 2010; Sedayu et al., 2010; Hetterscheid, 2012; Claudel et al., 2017), suggesting birds as their major dispersal agents (Hetterscheid, 1994; Hetterscheid & Ittenbach, 1996; Singh & Gadgil, 1996; Sedayu et al., 2010).

On the other hand, size and morphological diversity may also be associated with the diversification process across the four subgenera. Indeed, the plant size and morphological diversity are relatively homogeneous within the two basalmost subgenera *Afrophallus* and *Scutandrium* (Hetterscheid & Ittenbach, 1996; Ittenbach, 2003; Hetterscheid, 2012; Claudel et al., 2017). In contrast, all the dwarf species (i.e., the *Pusillus*- and the *Pulchellus*-clade), as well as all the giants of the genus (i.e., *A. borneensis* Engl. & Gehrm., *A. decus-silvae* Backer & Alderw., *A. lambii* S. Mayo & Widjaja, *A. gigas* Teijsm. & Binn., *A. hewittii* Alderw. and *A. titanum*), are included in the subgenus *Amorphophallus* (Claudel et al., 2017). Although the *Pygmaeus*-clade from subgenus *Metandrium* comprises small species (Claudel et al., 2017), differences in plant sizes are less striking within this subgenus. However, the inflorescence morphology is highly heterogeneous in the subgenus *Metandrium* (Grob et al., 2002; Sedayu et al., 2010; Claudel et al., 2017) (e.g., Fig. 1. 4, 6, 13, 14). In contrast to the other Asian clades, the subgenus *Metandrium* has also developed specialized types of staminode, notably hair-like staminodes (e.g., Fig. 1. 13, 14). The exact function of hair-like staminodes is unknown. However, when covering the appendix, hair-like staminodes may possibly contribute to the illusion of a dead hairy mammal in carrion mimicking *Amorphophallus* species (Hetterscheid et al., 2012). Alternatively, hair-like staminodes covering the appendix might impede the successful landing of insect visitors, which might subsequently drop into the basal parts of the spathe. Thus, hair-like staminodes might "help" the insect visitors to leave the appendix and find the spot they are required to visit. Moreover, when situated along the male or the female flowers, hair-like staminodes may play a role in the plant–pollinator interaction, allowing insects of a specific size only to approach the female flowers. However, for the time being, the knowledge about visiting and pollinating insects remains too limited to explore the specific function(s) of hair-like staminodes (Claudel, 2021).

It is noteworthy to add that the increasing complexity of petiolar coloration might also be an indicator of the relationship among the four subgenera (Claudel et al., 2019), starting from relatively simple pattern types in the subgenera *Afrophallus* (e.g., Fig. 1. 11) and *Scutandrium* but reaching highly complex mimicry patterns in the subgenera *Amorphophallus* and *Metandrium* (e.g., Fig. 1. 6, 12).

The distinction of the four subgenera, as shown here and by previous works (Sedayu et al., 2010; Claudel et al., 2017), with the African vs. Asian and Central vs. South East Asian splits, seems to indicate that vicariance events probably shaped the diversification of the genus *Amorphophallus*. However, our plastome tree also reflects a recent increasing complexity for some vegetative and reproductive traits within the most recently diverged *Amorphophallus* and *Metandrium* clades, which may be related to ecological parameters (Claudel et al., 2019). This might suggest that ecological processes probably also acted sequentially with biogeographic processes to drive diversification of these clades, in a "leapfrog" pattern over time, as already shown for some continental or insular plant radiations (Barrabé et al., 2019; Pouchon et al., 2021). However, our knowledge is still limited on the pollination and seed dispersal interactions (with insects and birds, respectively) within the genus to associate such morphological diversity with ecological preferences.

4.2 Delineation within subgenera

Our study provides a fully resolved phylogenetic tree for *Amorphophallus* that clarifies the evolutionary history of both genus and subgenera, and also helps to delineate clades within subgenera by providing new sister species and subclade relationships.

4.2.1 *Afrophallus* (AFR) clade

Two African mainland species (*A. gomboczianus* Pic.Serm and *A. mossambicensis*) and one Malagasy species (*A. taurostigma* Ittenb., Hett. & Bogner) were selected to represent the subgenus *Afrophallus* in the present analysis. Our plastome trees indicated an early divergence of *A. gomboczianus* in contrast to the two other species, as shown in the plastid tree of Claudel et al. (2017). Such relationships support a later evolution of Malagasy species from African mainland species (Sedayu et al., 2010; Claudel et al., 2017).

4.2.2 *Scutandrium* (CA-II) clade

The subgenus *Scutandrium* here shows a similar topology when compared to previous phylogenetic works (Sedayu et al., 2010; Claudel et al., 2017). Indeed, our plastome tree fully supports the basalmost position of *A. rhizomatosus* as found in these studies, indicating that rhizomes constitute a primitive character. The next diverging clade, consisting of *A. tenuistylis* Hett. and *A. pseudoharmandii* Hett. & C. Claudel, a member of the former *Pseudodracontium* genus (Hetterscheid & Claudel, 2012; Claudel et al., 2017), confirmed the previously established relationships (Claudel et al., 2017). Similarly, *A. kachinensis* Engl. & Gehrm., *A. carneus* Ridl., *A. curvistylis* Hett., and *A. excentricus* Hett. also form a well-supported clade (Claudel et al., 2017). The only noticeable difference is that *A. albus* and *A. konjac* are sister species in the present analysis. This is surprising at first sight, considering that *A. albus* is a small-growing species with pale green inflorescences (Fig. 1. 9) and a nauseating smell whereas *A. konjac* is representative of the large and dark-colored carrion flower type (Fig. 1. 10) (Chen et al., 2015; Kite & Hetterscheid, 2017). However, the position of both species differs in Claudel et al. (2017) between the nuclear and the plastid trees. As discussed by Claudel (2020), this result might be attributed to the fact that both species can be easily artificially hybridized and have a long breeding history in Asia.

4.2.3 *Amorphophallus* (SEA) clade

The basal phylogenetic relationships within the subgenus *Amorphophallus* were previously left unresolved due to a polytomy between two main subclades and *A. verticillatus* Hett, another rhizomatous species (Claudel et al., 2017). Our analyses here clarify these relationships by fully supporting an early divergence of *A. verticillatus* Hett., followed by a split between the two main subclades. The relationships within these two subclades are similar to the ones inferred in the plastid tree of Claudel et al. (2017). For example, *A. sumawongii* (Bogner) Bogner & Mayo, nested within the *Pusillus*-subclade, was closer to the *A. variabilis*/*A. ranchanensis* clade than to the *A. manta*/*A. paeoniifolius* clade in the nuclear tree but sister to the *A. manta*/*A. paeoniifolius* clade in the plastid tree (Claudel et al., 2017). Our plastome tree supported such a sister relationship previously inferred on *rbcL-trnL* markers. In this study, *A.* sp. nov. "sabah," a putative new and yet undescribed species is related to *A. ranchanensis* Ipor, A. Simon & Meekiong. It is also noteworthy to point out that *A. manta* Hett. & Ittenb. is confirmed as sister species to the clade comprising *A. prainii* Hook.f. and *A. paeoniifolius* (Claudel et al., 2017).

4.2.4 *Metandrium* (CA-I) clade

Phylogenetic relationships within the subgenus *Metandrium* were poorly resolved in previous works (Sedayu et al., 2010; Claudel et al., 2017). Here, three main subclades were fully supported across our plastome trees and seem to be congruent with the color of the mature berries, which is highly diverse in the subgenus (Sedayu et al., 2010). However, this tentative congruence needs to be tested by increasing the species sampling within the three subclades since our sampling is very limited to reach any solid conclusion on this. Given these caveats, the earliest diverging clade is characterized by species bearing white (*A. laoticus*: see Fig. 1. 16; Hetterscheid, 2006; Claudel CC, pers. obs., 2017), yellow (*A. napiger*: Hetterscheid et al., 2012), or orange to red berries (*A. elatus*, Hetterscheid et al., 2012; Galloway AG, pers. obs., 2011). Referring to Claudel et al. (2017), these three species were nested within a clade composed of species with white to yellow or occasionally green berries; colors found exclusively within this subclade, except for *A. elatus* and *A. macrorhizus* Craib bearing orange to red berries (Hetterscheid et al., 2012; Claudel et al., 2017). Moreover, as found in previous phylogenetic works (Sedayu et al., 2010; Claudel et al., 2017), the two other sister clades are composed of species with red mature berries (i.e., *A. cicatricifer*, *A. bulbifer* and *A. muelleri*: Fig. 1. 15, Hetterscheid et al., 2012; *A. sylvaticus*: Jaleel et al., 2011), an ancestral character of the genus (Sedayu et al., 2010), or blue berries (i.e., *A. henryi* N.E. Br.—*A. ochroleucus* Hett. & V.D.Nguyen clade; Fig. 1. 18), a unique feature of the subgenus *Metandrium* (Sedayu et al., 2010; Claudel et al., 2017). Blue berries are likely to have an adaptive significance as, except for the primitive and distantly related *Gymnostachys anceps* R. Br., they are unique

to the Araceae (Mayo et al., 1997). It has been hypothesized that the distributional range of blue-berried species, representing the northernmost range of the genus, is linked to a particular group of birds, occurring in the same geographical areas (Hetterscheid & Ittenbach, 1996; Sedayu et al., 2010). Therefore, it is conceivable that the putative dispersal agents had a strong impact on the speciation of blue berried *Amorphophallus* species. However, the dispersal agents have not been observed nor reported so far.

Finally, the positioning of *A. natolii* was not congruently dependent on the method (i.e., MP vs. ML/BI) or the data set (i.e., "ingroup" vs. "outgroup") used. In previous studies, this species had a basal position within the *Metandrium* subgenus but was not supported (Claudel et al., 2017). Here, *A. natolii* is placed either at the root of the *A. elatus*—*A. napiger* clade or between this clade and the *A. cicatrifer*—*A. muelleri* clade. This is interesting as this species bears either yellow or orange-red berries (Galloway pers. comm.; own observation). Such discordance could be the result of ILS, hybridization, or gene duplication (Maddison & Knowles, 2006; Degnan & Rosenberg, 2009). Indeed, a somewhat intermediate phylogenetic and morphological position would indicate a hybrid origin of *A. natolii*. However, one might expect chloroplast capture from only one of the two putative parents (Stegemann et al., 2012; Kawabe et al., 2018; Pouchon et al., 2018; Ogishima et al., 2019), instead of admixed plastid genomes, although admixed genomes for instance due to horizontal transfer has been shown on mitochondria (Alvarez et al., 2006; Gandini & Sanchez-Puerta, 2017). On the other hand, short phylogenetic branches, carrying few informative sites, as seen here for *A. natolii*, are more susceptible to homoplasy and ILS (Townsend et al., 2012; Bagley et al., 2020), which can bias both ML and BI analyses in contrast to MP analyses (Kubatko & Degnan, 2007; Mendes & Hahn, 2018). Such discordance between MP and ML/BI trees could thus be strongly explained by ILS.

4.3 Divergence time and dispersal events of *Amorphophallus*

Our dating analysis estimated that *Amorphophallus* arose in the Mid Oligocene at ca. 30 Ma, and started diversifying near the Oligocene/Miocene transition between ca. 22.5 Ma. A previous study focusing on Araceae has estimated the crown *Amorphophallus* divergence in the Late Oligocene ca. 26–24 Ma, which is close to our estimate, while only three species were sampled (Nauheimer et al., 2012). Concerning the other nodes, our overall age estimates were younger than those from the previous dating works on monocots. For example, the crown diversification of monocots was estimated ca. 129.0 vs. 132.4 Ma (Givnish et al., 2018) and 137.5 Ma (Nauheimer et al., 2012); crown Araceae ca. 94.1 vs. 103 (Givnish et al., 2018) and 122 Ma (Nauheimer et al., 2012); or crown Alismataceae 41.14 vs. 65 (Givnish et al., 2018) and 71.5 Ma (Li et al., 2021). However, our posterior age estimates for fossil calibration nodes were consistently closer to their priors than for other studies; for example, for *Caldesia brandoniana* with 21.5 Ma estimate vs. 20.0 Ma (fossil), 58.6 Ma (Givnish et al., 2018), and 36.3 Ma (Li et al., 2021); for *Keratosperma allenbyense* with 50.23 Ma estimate vs. 48.7 (fossil), 90.23 (Nauheimer et al., 2012), and 39.25 Ma (Givnish et al., 2018); or for *Petrocardium cerrejonense* with 54.1 Ma estimate vs. 55.8 (fossil); 31.4 (Givnish et al., 2018), and 64.5 Ma (Nauheimer et al., 2012). This result improves our confidence in the ages estimated here, by confirming the validity of our dating approach.

On the other hand, the spatio-temporal history of the genus *Amorphophallus* highlighted here appears also coherent with the tectonic and climate dynamics from the Eocene to the Miocene, which can explain its current paleotropical distribution in Africa, Continental Asia, and Southeast Asia regions. Indeed, major tectonic and volcanic activities were recorded through this geological period with continental collisions of Eurasian/Indian plates during the Eocene (ca. 50–45 Ma; Pusok & Stegman, 2020), Eurasian/Australian plates during the Early Miocene (ca. 20–15 Ma; Hall, 2013), and African-Arabian/Eurasian plates, initiated with a soft collision during the late Eocene/Oligocene (ca. 40–35 Ma; Darin et al., 2018) and fully connected with a hard collision during the Mid Miocene (ca. 16–13 Ma; Hamon et al., 2013). Climatically, the late Eocene and particularly the Eocene/Oligocene transition (EOT; ca. 34 Ma) experienced an intense global cooling with the onset of Antarctic glaciation, which briefly expanded during the glaciation of the Oligocene/Miocene transition (OMT; ca. 23 Ma), after late Oligocene warming (ca. 27–23 Ma), and intensified after the renewed warm climate and the mid-Miocene climatic optimum (MMCO; ca. 15–13 Ma) with the establishment of a permanent Antarctic ice-sheet (Zachos et al., 2008; Liu et al., 2009; Beddow et al., 2016; Hutchinson et al., 2021). These periods coincided with the emergence of seasonal biomes in Europe and Asia, the aridification of Australian, African, and Asian inlands, and the subsequent contraction of the tropics with tropical forests retreating to lower latitudes (Morley, 2003; Bowen, 2007; Contreras et al., 2013; Fang et al., 2015; Lin et al., 2015; Beasley et al., 2021; Couvreur et al., 2021). Moreover, all above geo-climatic changes, associated with sea level drops, have led to major turnovers of the vegetation (Sun et al., 2015; Pound & Salzmann, 2017; Couvreur et al., 2021), with successful plant dispersal across different paleogeographic regions (Jiang et al., 2019), and the establishment of present-day genera and families in multiple regions, probably pre-adapted to current climates (e.g., Linnemann et al., 2017; Su et al., 2018; Huang et al., 2021; Ling et al., 2021).

Our dating analysis showed that the first split between African and Asian lineages of *Amorphophallus*, also stated in previous phylogenetic works (Claudel et al., 2017), occurred ca. 22.5 Ma, from ancestral lineages emerging ca. 30 Ma. A previous study, based on ancestral area reconstructions of Araceae, showed that such lineages likely evolved in Eurasia (Nauheimer et al., 2012). Proto-*Amorphophallus* lineages, probably pre-adapted to current (sub)tropical conditions, could thus have evolved in Eurasia during the renewal of more favorable conditions after the EOT (ca. 34 Ma) and then successfully dispersed across both the Central Asian and African regions during the OMT cooling (ca. 23 Ma). The OMT, leading to some environmental and ecological changes, had a major impact on the distribution of plant taxa, and probably profoundly affected the evolution of *Amorphophallus* lineages and their current paleotropical distribution. Such a statement needs to be tested by larger-scale biogeographic reconstructions within and outside this group.

Nevertheless, due to the clear geographical distinction of the four subgenera (Claudel et al., 2017), some assumptions about their divergence time can be made here.

Dispersal in both Central Asia and Africa could be explained by overland migrations of tropical forests during such cooling. However, overland migrations are unlikely for the African lineages as the disjunction between Asia and Africa within *Amorphophallus* occurred earlier than the complete land connection between Africa and western Asia with the closure of the Tethys Sea (ca. 14 Ma; Hamon et al., 2013). On the other hand, long-distance dispersal events (LDD) by birds, which seem to be the major dispersal agents of *Amorphophallus* lineages (Hetterscheid, 1994; Hetterscheid & Ittenbach, 1996; Singh & Gadgil, 1996; Sedayu et al., 2010), could explain such dispersal in Africa and Asia. Indeed, some of these geo-climatic changes, forming corridors with the uplifts of mountains or fragmented landscapes by the existence of a myriad of archipelagos, have facilitated bird dispersions along and within latitudinal belts (Nagy, 2020). Moreover, the rise of climatic seasonality during the Oligocene and Miocene changes facilitated behavioral changes in birds with the evolution of long-distance migratory species and lineages (Dufour et al., 2020). Numerous long-dispersal events of plants were recorded between Eurasia and Africa during the Late Oligocene and Early Miocene before the final closure of Arabian/African plates such as in Loranthaceae (Liu et al., 2018), Simaroubaceae (Clayton et al., 2009), Sapindaceae (Buerki et al., 2010), Menispermaceae (Lian et al., 2019), or Urticaceae (Huang et al., 2019). The distance between East Africa and West Asia was thus probably sufficiently close to allow avian migration of *Amorphophallus* through Asia and Africa (Morley, 2003). The further diversification of the subgenus *Amorphophallus* in South East Asia (SEA) ca. 20 Ma, concomitant with the nuclear phylogeny of Claudel et al. (2017), is also coherent with the formation of the Wallacea region and SEA islands during the Early Miocene (20–15 Ma) from the Australia/SEA collision (Hall, 2013). This also brings support for avian dispersion, as zoochory evidence of dispersion was shown within this region and over this period for many plant taxa (Crayn et al., 2015), as in *Goniothalamus* (Thomas et al., 2017). Moreover, the secondary colonization of Madagascar within the African clade is also coherent with intercontinental dispersion from birds, as was shown for Loranthaceae (Liu et al., 2018).

Taken together, our results provided the first insights into the evolutionary history of the *Amorphophallus* genus, with biogeographic and ecological processes, related to climatic and environmental changes during the Late Oligocene and the Early Miocene, which have probably shaped its current diversity and distribution in paleotropical regions. A larger-scale phylogeny, based on plastid, as here, and on nuclear genomes, is however needed to fully understand the morphological and biogeographic diversification of these species and the mechanisms at the origin of their radiation. Last but not least, a better understanding of the ecology of *Amorphophallus* lineages, in particular regarding pollinator interactions (zoochory evidence) and dispersal agents, might trigger our understanding of the importance of long dispersal events in shaping the diversity of the genus.

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References

Aberer AJ, Kobert K, Stamatakis A. 2014. ExaBayes: Massively parallel bayesian tree inference for the whole-genome era. *Molecular Biology and Evolution* 31: 2553–2556.

Alsos IG, Lavergne S, Merkel MKF, Boleda M, Lammers Y, Alberti A, Pouchon C, Denoeud F, Pitelkova I, Puşcaş M, Roquet C, Hurdu BI, Thuiller W, Zimmermann NE, Hollingsworth PM, Coissac E. 2020. The treasure vault can be opened: Large-scale genome skimming works well using herbarium and silica gel dried material. *Plants* 9: 432.

Alvarez N, Benrey B, Hossaert-McKey M, Grill A, McKey D, Galtier N. 2006. Phylogeographic support for horizontal gene transfer involving sympatric bruchid species. *Biology Direct* 1: 21.

Bagley JC, Uribe-Convers S, Carlsen MM, Muchhala N. 2020. Utility of targeted sequence capture for phylogenomics in rapid, recent angiosperm radiations: Neotropical *Burmeistera* bellflowers as a case study. *Molecular Phylogenetics and Evolution* 152: 106769.

Bankevich A, Nurk S, Antipov D, Gurevich AA, Dvorkin M, Kulikov AS, Lesin VM, Nikolenko SI, Pham S, Prjibelski AD, Pyshkin AV, Sirotkin AV, Vyahhi N, Tesler G, Alekseyev MA, Pevzner PA. 2012. SPAdes: A new genome assembly algorithm and its applications to single-cell sequencing. *Journal of Computational Biology* 19: 455–477.

Barrabé L, Lavergne S, Karnadi-Abdelkader G, Drew BT, Birnbaum P, Gâteblé G. 2019. Changing ecological opportunities facilitated the explosive diversification of new Caledonian *Oxera* (Lamiaceae). *Systematic Biology* 68: 460–481.

Barrett CF, Bacon CD, Antonelli A, Cano Á, Hofmann T. 2016a. An introduction to plant phylogenomics with a focus on palms. *Botanical Journal of the Linnean Society* 182: 234–255.

Barrett CF, Baker WJ, Comer JR, Conran JG, Lahmeyer SC, Leebens-Mack JH, Li J, Lim GS, Mayfield-Jones DR, Perez L, Medina J, Pires JC, Santos C, Stevenson DW, Zomlefer WB, Davis JI. 2016b. Plastid genomes reveal support for deep phylogenetic relationships and extensive rate variation among palms and other commelinid monocots. *New Phytologist* 209: 855–870.

Barthlott W, Szarzynski J, Vlek P, Lobin W, Korotkova N. 2009. A torch in the rain forest: Thermogenesis of the Titan arum (*Amorphophallus titanum*). *Plant Biology* 11: 499–505.

Beasley C, Kender S, Giosan L, Bolton CT, Anand P, Leng MJ, Nilsson-Kerr K, Ullmann CV, Hesselbo SP, Littler K. 2021. Evidence of a South Asian proto-monsoon during the Oligocene-Miocene transition. *Paleoceanography and Paleoclimatology* 36: e2021PA004278.

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

Beddow HM, Liebrand D, Sluijs A, Wade BS, Lourens LJ. 2016. Global change across the Oligocene-Miocene transition: High-resolution stable isotope records from IODP Site U1334 (equatorial Pacific Ocean): The OMT at Site U1334. *Paleoceanography* 31: 81–97.

Bell CD, Soltis DE, Soltis PS. 2010. The age and diversification of the angiosperms re-revisited. *American Journal of Botany* 97: 1296–1303.

Bohmann K, Mirarab S, Bafna V, Gilbert MTP. 2020. Beyond DNA barcoding: The unrealized potential of genome skim data in sample identification. *Molecular Ecology* 29: 2521–2534.

Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu CH, Xie D, Suchard MA, Rambaut A, Drummond AJ. 2014. BEAST 2: A software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* 10: e1003537.

Bowen GJ. 2007. When the world turned cold. *Nature* 445: 607–608.

Boyce P, Croat T. 2011 onwards. The Überlist of Araceae, totals for published and estimated number of species in Aroid genera. Available from http://www.aroid.org/genera/18021uberlist.pdf [accessed 1 December 2021].

Bröderbauer D, Diaz A, Weber A. 2012. Reconstructing the origin and elaboration of insect-trapping inflorescences in the Araceae. *American Journal of Botany* 99: 1666–1679.

Buerki S, Forest F, Alvarez N, Nylander JAA, Arrigo N, Sanmartín I. 2010. An evaluation of new parsimony-based versus parametric inference methods in biogeography: A case study using the globally distributed plant family Sapindaceae. *Journal of Biogeography* 38: 531–550.

Bustamante RAA, Mansibang JA, Hetterscheid WLA, Tamayo MN. 2020. *Amorphophallus caudatus* (Thomsonieae, Araceae), a new species from Camarines Norte, Luzon island, the Philippines. *Nordic Journal of Botany* 38: e02982.

Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T. 2009. trimAl: A tool for automated alignment trimming in large-scale phylogenetic analyses. *Bioinformatics* 25: 1972–1973.

Chen G, Ma X, Jürgens A, Lu J, Liu EX, Weibang S, Cai XH. 2015. Mimicking livor mortis: A well-known but unsubstantiated color profile in Sapromyiophily. *Journal of Chemical Ecology* 41: 808–815.

Christenhusz MJM, Byng JW. 2016. The number of known plants species in the world and its annual increase. *Phytotaxa* 261: 201–217.

Claudel C. 2020. Hybrids. In: Srzednicki G, Borompichaichartkul C eds. *Konjac glucomannan production, processing, and functional applications*. Boca Raton, FL: CRC Press, Taylor & Francis Group. 80–97

Claudel C. 2021. The many elusive pollinators in the genus *Amorphophallus*. *Arthropod-Plant Interactions* 15: 833–844.

Claudel C, Buerki S, Chatrou LW, Antonelli A, Alvarez N, Hetterscheid W. 2017. Large-scale phylogenetic analysis of *Amorphophallus* (Araceae) derived from nuclear and plastid sequences reveals new subgeneric delineation. *Botanical Journal of the Linnean Society* 184: 32–45.

Claudel C, Lev-Yadun S. 2021. Odor polymorphism in deceptive *Amorphophallus* species—A review. *Plant Signaling & Behavior* 16: 12.

Claudel C, Lev-Yadun S, Hetterscheid W, Schultz M. 2019. Mimicry of lichens and cyanobacteria on tree-sized *Amorphophallus* petioles results in their masquerade as inedible tree trunks. *Botanical Journal of the Linnean Society* 190: 192–214.

Clayton JW, Soltis PS, Soltis DE. 2009. Recent long-distance dispersal overshadows ancient biogeographical patterns in a pantropical angiosperm family (Simaroubaceae, Sapindales). *Systematic Biology* 58: 395–410.

Coissac E, Hollingsworth PM, Lavergne S, Taberlet P. 2016. From barcodes to genomes: Extending the concept of DNA barcoding. *Molecular Ecology* 25: 1423–1428.

Contreras L, Pross J, Bijl PK, Koutsodendris A, Raine JI, van de Schootbrugge B, Brinkhuis H. 2013. Early to Middle Eocene vegetation dynamics at the Wilkes Land Margin (Antarctica). *Review of Palaeobotany and Palynology* 197: 119–142.

Couvreur TLP, Dauby G, Blach-Overgaard A, Deblauwe V, Dessein S, Droissart V, Hardy OJ, Harris DJ, Janssens SB, Ley AC, Mackinder BA, Sonké B, Sosef MSM, Stévart T, Svenning J, Wieringa JJ, Faye A, Missoup AD, Tolley KA, Nicolas V, Ntie S, Fluteau F, Robin C, Guillocheau F, Barboni D, Sepulchre P. 2021. Tectonics, climate and the diversification of the tropical African terrestrial flora and fauna. *Biological Reviews* 96: 16–51.

Crayn DM, Costion C, Harrington MG. 2015. The Sahul-Sunda floristic exchange: dated molecular phylogenies document Cenozoic intercontinental dispersal dynamics. *Journal of Biogeography* 42: 11–24.

Darin MH, Umhoefer PJ, Thomson SN. 2018. Rapid late Eocene exhumation of the Sivas Basin (Central Anatolia) driven by initial Arabia-Eurasia collision. *Tectonics* 37: 3805–3833.

Degnan JH, Rosenberg NA. 2009. Gene tree discordance, phylogenetic inference and the multispecies coalescent. *Trends in Ecology & Evolution* 24: 332–340.

Douglas J, Zhang R, Bouckaert R. 2021. Adaptive dating and fast proposals: Revisiting the phylogenetic relaxed clock model. *PLoS Computational Biology* 17: e1008322.

Dufour P, Descamps S, Chantepie S, Renaud J, Guéguen M, Schiffers K, Thuiller W, Lavergne S. 2020. Reconstructing the geographic and climatic origins of long-distance bird migrations. *Journal of Biogeography* 47: 155–166.

Fang X, Zan J, Appel E, Lu Y, Song C, Dai S, Tuo S. 2015. An Eocene–Miocene continuous rock magnetic record from the sediments in the Xining Basin, NW China: Indication for Cenozoic persistent drying driven by global cooling and Tibetan Plateau uplift. *Geophysical Journal International* 201: 78–89.

Gandini CL, Sanchez-Puerta MV. 2017. Foreign plastid sequences in plant mitochondria are frequently acquired via mitochondrion-to-mitochondrion horizontal transfer. *Scientific Reports* 7: 43402.

Givnish TJ, Zuluaga A, Spalink D, Soto Gomez M, Lam VKY, Saarela JM, Sass C, Iles WJD, de Sousa DJL, Leebens-Mack J, Chris Pires J, Zomlefer WB, Gandolfo MA, Davis JI, Stevenson DW, dePamphilis C, Specht CD, Graham SW, Barrett cf, Ané C. 2018. Monocot plastid phylogenomics, timeline, net rates of species diversification, the power of multi-gene analyses, and a functional model for the origin of monocots. *American Journal of Botany* 105: 1888–1910.

Govaerts R, Nic Lughadha E, Black N, Turner R, Paton A. 2021. The World Checklist of Vascular Plants, a continuously updated resource for exploring global plant diversity. *Scientific Data* 8: 215.

Grob GBJ, Gravendeel B, Eurlings M, Hetterscheid W. 2002. Phylogeny of the tribe Thomsonieae (Araceae) based on chloroplast matK and trnL intron sequences. *Systematic Botany* 27: 453–467.

Grob GBJ, Gravendeel B, Eurlings MCM. 2004. Potential phylogenetic utility of the nuclear FLORICAULA/LEAFY second intron: Comparison with three chloroplast DNA regions in *Amorphophallus* (Araceae). *Molecular Phylogenetics and Evolution* 30: 13–23.

Hall R. 2013. The palaeogeography of Sundaland and Wallacea since the Late Jurassic. *Journal of Limnology* 72: e1.

Hamon N, Sepulchre P, Lefebvre V, Ramstein G. 2013. The role of eastern Tethys seaway closure in the Middle Miocene Climatic Transition (ca. 14 Ma). *Climate of the Past* 9: 2687–2702.

Harrison N, Kidner CA. 2018. Next-generation sequencing and systematics: What can a billion base pairs of DNA sequence data do for you? *Taxon* 60: 1552–1566.

Hetterscheid W. 1994. Notes on the genus *Amorphophallus* (Araceae)-2. New species from tropical Asia. *Blumea* 39: 237–281.

Hetterscheid W. 2006. Notes on the genus *Amorphophallus* (Araceae) 15. New species from SE Asia. *Aroideana* 29: 53–79.

Hetterscheid W. 2012. Amorphophallus. In: Boyce PC, Sookchaloem D, Hetterscheid W, Gusman G, Jacobsen N, Idei T, Nguyen VD eds. *Flora of Thailand 11*. Bangkok: The Forest Herbarium. Araceae. 218–232.

Hetterscheid W. 2020. Botanical background to *Amorphophallus*. In: Srzednicki G, Borompichaichartkul C eds. *Konjac glucomannan production, processing, and functional applications*. Boca Rato, FL: CRC Press, Taylor & Francis Group. 9–11.

Hetterscheid W, Claudel C. 2012. The end of *Pseudodracontium* N.E. Br. *Aroideana* 35: 40–46.

Hetterscheid W, Ittenbach S. 1996. Everything you always wanted to know about *Amorphophallus*, but were afraid to stick your nose into!!!!! *Aroideana* 19: 7–131.

Hetterscheid W, Wistuba A, Amoroso V, Medecilo M, Claudel C. 2012. *Amorphophallus natolii* (Araceae), a new species from limestone on Palawan, Philippines. *Botanical Studies* 53: 415–420.

Ho SYW, Phillips MJ. 2009. Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence times. *Systematic Biology* 58: 367–380.

Hoang DT, Vinh LS, Flouri T, Stamatakis A, von Haeseler A, Minh BQ. 2018. MPBoot: Fast phylogenetic maximum parsimony tree inference and bootstrap approximation. *BMC Evolutionary Biology* 18: 11.

Hu S, Dilcher DL, Jarzen DM, Winship Taylor D. 2008. Early steps of angiosperm pollinator coevolution. *Proceedings of the National Academy of Sciences* 105: 240–245.

Huang H, Pérez-Pinedo D, Morley RJ, Dupont-Nivet G, Philip A, Win Z, Aung DW, Licht A, Jardine PE, Hoorn C. 2021. At a crossroads: The late Eocene flora of central Myanmar owes its composition to plate collision and tropical climate. *Review of Palaeobotany and Palynology* 291: 104441.

Huang X, Deng T, Moore MJ, Wang H, Li Z, Lin N, Yusupov Z, Tojibaev KS, Wang Y, Sun H. 2019. Tropical Asian Origin, boreotropical migration and long-distance dispersal in Nettles (Urticeae, Urticaceae). *Molecular Phylogenetics and Evolution* 137: 190–199.

Hutchinson DK, Coxall HK, Lunt DJ, Steinthorsdottir M, de Boer AM, Baatsen M, von der Heydt A, Huber M, Kennedy-Asser AT, Kunzmann L, Ladant JB, Lear CH, Moraweck K, Pearson PN, Piga E, Pound MJ, Salzmann U, Scher HD, Sijp WP, Śliwińska KK, Wilson PA, Zhang Z. 2021. The Eocene-Oligocene transition: A review of marine and terrestrial proxy data, models and model-data comparisons. *Climate of the Past* 17: 269–315.

Iles WJD, Smith SY, Gandolfo MA, Graham SW. 2015. Monocot fossils suitable for molecular dating analyses. *Botanical Journal of the Linnean Society* 178: 346–374.

Ittenbach S. 2003. Revision der afrikanischen Arten der Gattung *Amorphophallus* (Araceae). *Englera* 25: 2–263.

Jaleel V, Sivadasan M, Alfarhan A, Thomas J, Alatar A. 2011. Revision of *Amorphophallus* Blume ex Decne. Sect. *Rhaphiophallus* (Schott) Engl.(Araceae) in India. *Bangladesh Journal of Plant Taxonomy* 18: 1–26.

Jiang D, Klaus S, Zhang YP, Hillis DM, Li JT. 2019. Asymmetric biotic interchange across the Bering land bridge between Eurasia and North America. *National Science Review* 6: 739–745.

Johri S, Fellows SR, Solanki J, Busch A, Livingston I, Mora MF, Tiwari A, Cantu VA, Goodman A, Morris MM, Doane MP, Edwards RA, Dinsdale EA. 2020. Mitochondrial genome to aid species delimitation and effective conservation of the Sharpnose Guitarfish (*Glaucostegus granulatus*). *Meta Gene* 24: 100648.

Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS. 2017. ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587–589.

Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780.

Kawabe A, Nukii H, Furihata HY. 2018. Exploring the history of chloroplast capture in *Arabis* using whole chloroplast genome sequencing. *International Journal of Molecular Sciences* 19: 602.

Kite GC, Hetterscheid W. 2017. Phylogenetic trends in the evolution of inflorescence odours in *Amorphophallus*. *Phytochemistry* 142: 126–142.

Kong H, Condamine FL, Yang L, Harris AJ, Feng C, Wen F, Kang M. 2021. Phylogenomic and macroevolutionary evidence for an explosive radiation of a plant genus in the Miocene. *Systematic Biology* 71: 589–609.

Kubatko LS, Degnan JH. 2007. Inconsistency of phylogenetic estimates from concatenated data under coalescence. *Systematic Biology* 56: 17–24.

Lamprecht I, Seymour R. 2010. Thermologic investigations of three species of *Amorphophallus*. *Journal of Thermal Analysis and Calorimetry* 102: 127–136.

Lev-Yadun S. 2021. Avoiding rather than resisting herbivore attacks is often the first line of plant defence. *Biological Journal of the Linnean Society* 134: 775–802.

Li H, Hetterscheid W. 2010. *Amorphophallus*. In: Wu ZY, Raven PH, Hong DY eds. *Flora of China volume 23 Acoraceae through Cyperaceae*. Beijing: Science Press; St. Louis: Missouri Botanical Garden Press. 23: 23–33.

Li ZZ, Lehtonen S, Martins K, Wang QF, Chen JM. 2021. Complete genus-level plastid phylogenomics of Alismataceae with revisited historical biogeography. *Molecular Phylogenetics and Evolution* 166: 107334.

Lian L, Ortiz RDC, Jabbour F, Chen Z, Wang W. 2019. Re-delimitation of *Tinospora* (Menispermaceae): Implications for character evolution and historical biogeography. *Taxon* 68: 905–917.

Lin X, Wyrwoll KH, Chen H, Zhang X, Fu K, Sun M, Yu X, Shen Z. 2015. An active East Asian monsoon at the Oligocene-Miocene boundary: Evidence from the Sikouzi section, Northern China. *The Journal of Geology* 123: 355–367.

Ling CC, Ma FJ, Dong JL, Zhou GH, Wang QJ, Sun BN. 2021. A mid-altitude area in southwestern China experienced a humid subtropical climate with subtle monsoon signatures during the early Oligocene: Evidence from the Ningming flora of Guangxi. *Palaeogeography, Palaeoclimatology, Palaeoecology* 579: 110601.

Linnemann U, Su T, Kunzmann L, Spicer RA, Ding WN, Spicer TEV, Zieger J, Hofmann M, Moraweck K, Gärtner A, Gerdes A, Marko L, Zhang ST, Li SF, Tang H, Huang J, Mulch A, Mosbrugger V, Zhou ZK. 2017. New U-Pb dates show a Paleogene origin for the modern Asian biodiversity hot spots. *Geology* 46: 3–6.

Liu B, Le CT, Barrett RL, Nickrent DL, Chen Z, Lu L, Vidal-Russell R. 2018. Historical biogeography of Loranthaceae (Santalales): Diversification agrees with emergence of tropical forests and radiation of songbirds. *Molecular Phylogenetics and Evolution* 124: 199–212.

Liu E, Yang C, Liu J, Jin S, Harijati N, Hu Z, Diao Y, Zhao L. 2019. Comparative analysis of complete chloroplast genome

sequences of four major *Amorphophallus* species. *Scientific Reports* 9: 809.

Liu Z, Pagani M, Zinniker D, Deconto R, Huber M, Brinkhuis H, Shah SR, Leckie RM, Pearson A. 2009. Global cooling during the eocene-oligocene climate transition. *Science* 323: 1187–1190.

Maddison WP, Knowles LL. 2006. Inferring phylogeny despite incomplete lineage sorting. *Systematic Biology* 55: 21–30.

Malé PJG, Bardon L, Besnard G, Coissac E, Delsuc F, Engel J, Lhuillier E, Scotti-Saintagne C, Tinaut A, Chave J. 2014. Genome skimming by shotgun sequencing helps resolve the phylogeny of a pantropical tree family. *Molecular Ecology Resources* 14: 966–975.

Mayo S, Bogner J, Boyce P. 1997. *The genera of Araceae*. Kew: Royal Botanic Gardens.

McKain MR, Johnson MG, Uribe-Convers S, Eaton D, Yang Y. 2018. Practical considerations for plant phylogenomics. *Applications in Plant Sciences* 6: e1038.

Mendes FK, Hahn MW. 2018. Why concatenation fails near the anomaly zone. *Systematic Biology* 67: 158–169.

Meyer M, Kircher M. 2010. Illumina sequencing library preparation for highly multiplexed target capture and sequencing. *Cold Spring Harbor Protocols* 2010: pdb.prot5448.

Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, Lanfear R. 2020. IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* 37: 1530–1534.

Morley RJ. 2003. Interplate dispersal paths for megathermal angiosperms. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 5–20.

Nagy J. 2020. Biologia Futura: Rapid diversification and behavioural adaptation of birds in response to Oligocene–Miocene climatic conditions. *Biologia Futura* 71: 109–121.

Nauheimer L, Cui L, Clarke C, Crayn DM, Bourke G, Nargar K. 2019. Genome skimming provides well resolved plastid and nuclear phylogenies, showing patterns of deep reticulate evolution in the tropical carnivorous plant genus *Nepenthes* (Caryophyllales). *Australian Systematic Botany* 32(3): 243–254.

Nauheimer L, Metzler D, Renner SS. 2012. Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. *New Phytologist* 195: 938–950.

Nevill PG, Zhong X, Tonti-Filippini J, Byrne M, Hislop M, Thiele K, van Leeuwen S, Boykin LM, Small I. 2020. Large scale genome skimming from herbarium material for accurate plant identification and phylogenomics. *Plant Methods* 16: 1.

Ogishima M, Horie S, Kimura T, Yamashiro T, Dohzono I, Kawaguchi L, Nagano AJ, Maki M. 2019. Frequent chloroplast capture among *Isodon* (Lamiaceae) species in Japan revealed by phylogenies based on variation in chloroplast and nuclear DNA. *Plant Species Biology* 34: 127–137.

Pinho C, Hey J. 2010. Divergence with gene flow: Models and data. *Annual Review of Ecology, Evolution, and Systematics* 41: 215–230.

Pouchon C, Boyer F, Roquet C, Denoeud F, Chave J, Coissac E, Alsos IG, Lavergne S, The PhyloAlps Consortium, The PhyloNorway Consortium, 2022. ORTHOSKIM: *In silico* sequence capture from genomic and transcriptomic libraries for phylogenomic and barcoding applications. *Molecular Ecology Resources* 22: 2018–2037.

Pouchon C, Fernández A, Nassar JM, Boyer F, Aubert S, Lavergne S, Mavárez J. 2018. Phylogenomic analysis of the explosive adaptive radiation of the *Espeletia* complex (Asteraceae) in the Tropical Andes. *Systematic Biology* 67: 1041–1060.

Pouchon C, Lavergne S, Fernández Á, Alberti A, Aubert S, Mavárez J. 2021. Phylogenetic signatures of ecological divergence and leapfrog adaptive radiation in *Espeletia*. *American Journal of Botany* 108: 113–128.

Pound MJ, Salzmann U. 2017. Heterogeneity in global vegetation and terrestrial climate change during the late Eocene to early Oligocene transition. *Scientific Reports* 7: 43386.

Pusok AE, Stegman DR. 2020. The convergence history of India-Eurasia records multiple subduction dynamics processes. *Science Advances* 6: eaaz8681.

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67: 901–904.

Rosenberg NA, Tao R. 2008. Discordance of species trees with their most likely gene trees: The case of five taxa. *Systematic Biology* 57: 131–140.

Sedayu A, Eurlings MCM, Gravendeel B, Hetterscheid W. 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.

Shirasu M, Fujioka K, Kakishima S, Nagai S, Tomizawa Y, Tsukaya H, Murata J, Manome Y, Touhara K. 2010. Chemical identity of a rotting animal-like odor emitted from the inflorescence of the titan arum (*Amorphophallus titanum*). *Bioscience, Biotechnology, and Biochemistry* 74: 2550–2554.

Singh SN, Gadgil M. 1996. Ecology of *Amorphophallus* species in Uttara Kannada District of the Karnataka State, India: Implications for conservation. *Aroideana* 18: 5–20.

Skubatz H, Nelson TA, Dong AM, Meeuse BJD, Bendich AJ. 1990. Infrared thermography of *Arum* lily inflorescences. *Planta* 182: 432–436.

Smith SA, Beaulieu JM, Donoghue MJ. 2010. An uncorrelated relaxed-clock analysis suggests an earlier origin for flowering plants. *Proceedings of the National Academy of Sciences of the United States of America* 107: 5897–5902.

Sookchaloem D, Sungkajanttranon O, Petchsri S, Horadee S, Huayhongthong C, Vanapanich A, Wongsawaddiwattana C. 2016. Leaf blade anatomy characteristics of the genus *Amorphophallus* Blume ex Decne. in Thailand. *Agriculture and Natural Resources* 50: 437–444.

Srzednicki G, Borompichaichartkul C. 2020. *Konjac glucomannan: Production, processing, and functional applications*. Boca Raton: CRC Press.

Stegemann S, Keuthe M, Greiner S, Bock R. 2012. Horizontal transfer of chloroplast genomes between plant species. *Proceedings of the National Academy of Sciences of the United States of America* 109: 2434–2438.

Straub SCK, Parks M, Weitemier K, Fishbein M, Cronn RC, Liston A. 2012. Navigating the tip of the genomic iceberg: Next-generation sequencing for plant systematics. *American Journal of Botany* 99: 349–364.

Su T, Li SF, Tang H, Huang YJ, Li SH, Deng CL, Zhou ZK. 2018. *Hemitrapa* Miki (Lythraceae) from the earliest Oligocene of southeastern Qinghai-Tibetan Plateau and its phytogeographic implications. *Review of Palaeobotany and Palynology* 257: 57–63.

Suchan T, Beauverd M, Trim N, Alvarez N. 2015. Asymmetrical nature of the Trollius-Chiastocheta interaction: Insights into the evolution of nursery pollination systems. *Ecology and Evolution* 5: 4766–4777.

Sun J, Ni X, Bi S, Wu W, Ye J, Meng J, Windley BF. 2015. Synchronous turnover of flora, fauna and climate at the Eocene–Oligocene Boundary in Asia. *Scientific Reports* 4: 7463.

Tamayo MN, Magtoto LM, Melchor S, Sumalinog J, Tomas D, Reyes J, Austria CM. 2021. *Amorphophallus calcicolus* (Thomsonieae, Araceae), a new species from the Bohol island, Central Visayas, Philippines. *Phytotaxa* 489: 229–235.

Tan EYW, Quek ZBR, Neo ML, Fauvelot C, Huang D. 2021a. Genome skimming resolves the giant clam (Bivalvia: Cardiidae: Tridacninae) tree of life. *Coral Reefs* 41: 497–510.

Tan MH, Gan HM, Bracken-Grissom H, Chan TY, Grandjean F, Austin CM. 2021b. More from less: Genome skimming for nuclear markers for animal phylogenomics, a case study using decapod crustaceans. *Journal of Crustacean Biology* 41, ruab09.

Thomas DC, Tang CC, Saunders RMK. 2017. Historical biogeography of *Goniothalamus* and Annonaceae tribe Annoneae: Dispersal-vicariance patterns in tropical Asia and intercontinental tropical disjunctions revisited. *Journal of Biogeography* 44: 2862–2876.

Townsend JP, Su Z, Tekle YI. 2012. Phylogenetic signal and noise: Predicting the power of a data set to resolve phylogeny. *Systematic Biology* 61: 835.

Trevisan B, Alcantara DMC, Machado DJ, Marques FPL, Lahr DJG. 2019. Genome skimming is a low-cost and robust strategy to assemble complete mitochondrial genomes from ethanol preserved specimens in biodiversity studies. *PeerJ* 7: e7543.

van der Ham R, Grob G, Hetterscheid W, Star W, van Heuven BJ. 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.

Whitfield JB, Lockhart PJ. 2007. Deciphering ancient rapid radiations. *Trends in Ecology & Evolution* 22: 258–265.

Yin S, Yan Y, You L, Chen Q, Zhou Y, Chen K, Li R, Yang Z, Man L, Gao Y. 2019. Newly developed genomic SSRs reveal genetic diversity in wild and cultivated *Amorphophallus albus* germplasms. *Plant Molecular Biology Reporter* 37: 365–375.

Zachos JC, Dickens GR, Zeebe RE. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* 451: 279–283.

Supplementary Material

The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse.12910/suppinfo:

Fig. S1. Summary statistics over sequencing effort (reads number), assembled cpDNA contigs number, reconstructed cpDNA size, and mean cpDNA contig coverage for both outgroup and ingroup taxa from produced libraries (in green and orange colors) or collected libraries (in blue and red).

Fig. S2. Inferred maximum-parsimony (MP) tree for *Amorphophallus* subgenera using MPBoot v1.1.0 (Hoang et al., 2018). Bootstrap supports are given for each node using 1000 UFBoot replicates.

Table S1. Voucher and accession numbers of material used.

Table S2. Divergence time estimates using gamma prior distribution and optimised relaxed clock model in BEAST2 analysis.

Final Discussion

Phylogenetic Analysis

The aim of the present work is to provide a deeper understanding of the evolutionary history of the genus *Amorphophallus*. In doing so, several aspects of the biology of the genus were investigated, relying on an extensive living collection, morphological and molecular data and, of course, the available literature. It has been highlighted that every previous investigation into the evolutionary history of the genus *Amorphophallus* encountered the same challenges. First and foremost, the "great morphological flexibility" on the interspecific level (Grob et al., 2002; Sedayu et al., 2010) and "polymorphic" characters on the intraspecific level (van der Ham et al., 2005) made it impossible to reliably reconstruct the evolutionary history of the genus, based on morphological characters alone. Although smaller phylogenetic units could be characterised, species delimitations as well as the circumscription of large subgeneric groups proved challenging, if not impossible (Grob et al., 2002, 2004; van der Ham et al., 2005; Sedayu et al., 2010; Kite & Hetterscheid, 2017). Neither could most molecular investigations satisfyingly delimit the main subgeneric lineages (Grob et al., 2002, 2004; Sedayu et al., 2010). Moreover, the arrangement of the main subgeneric lineages differed from study to study (Grob et al., 2002, 2004; Sedayu et al., 2010; Publ. 1) and some clades remained poorly resolved (Grob et al., 2002, 2004; Sedayu et al., 2010, Publ. 1; Wong et al., 2022).

Publ. 1 represents a considerable step towards an understanding of the evolutionary history of the genus *Amorphophallus*. With 157 species investigated, it is the most extensive phylogenetic study of the genus *Amorphophallus* so far, and one in which the congruence between the molecular phylogeny and several selected morphological and physiological characters could be demonstrated in several clades. Moreover, four subgenera could be formally delimited, representing a first step towards a new subgeneric classification of the genus. However, this investigation also highlights the necessity for further steps, ultimately leading to the revision of the sectional classification of Engler (1911). It is especially desirable to have a higher number of species sampled in order to achieve a better resolution of the phylogenetic tree. Though 157 is a high number of species investigated, it is noteworthy to point out that no less than 22 species have been described in the past five years (Galloway et al., 2019a, b, c; Hetterscheid et al., 2020; Yuzammi & Hetterscheid, 2020; Bustamante et al., 2020, 2021; Tamayo et al., 2021; Bulawin et al., 2022; Fischer et al., 2022; Calaramo et al., 2022; Naive et al., 2022; 2024;

Serebryanyi et al., 2023). This represents an increase of nearly 10% in the number of species in the genus (Boyce & Croat, 2023). If this trend continues, the 157 species investigated in Publ. 1 may soon represent only one half of the species diversity, instead of the original two-thirds (Publ. 1).

As discussed in Publ. 6, the low resolution at species level may be partly due to a rapid radiation of the genus *Amorphophallus*. Moreover, hybridisation may obscure the species delimitation, at least in some cases. Consequently, more molecular data, ideally using genome sequencing technologies, is required to obtain clearer species delimitations. Ideally, the genomic data should rely on chloroplast- and nuclear DNA alike (Johnson et al., 2019).

Hybridisation

As discussed in Publ. 2, the dissimilar species *A. albus* and *A. konjac* repeatedly clustered together in several phylogenetic analyses, indicating a close relationship that is not morphologically supported. Likewise, as discussed in Publ. 1, *A. hirsutus* Teijsm. & Binn. is suspected to be of natural hybrid origin. Similarly, the species complex from the former genus *Pseudodracontium*, now included in *Amorphophallus*, has also been suspected to be of hybrid origin (Hetterscheid & Claudel, 2012). Therefore, the limits of hybridisation have been explored in Publ. 2, demonstrating that, if artificially pollinated, most *Amorphophallus* species readily hybridize (Claudel & Galloway, 2012; Claudel et al., 2013; Claudel & Mangelsdorff, 2014), in some cases even if the parental species belong to different subgenera (Publ. 2). In other cases, the resulting hybrids involved as many as four different *Amorphophallus* species (Publ. 2). Most importantly, the resulting hybrids are fertile (Publ. 2), a prerequisite to successful colonisation of new ecological niches (Chartier et al., 2016).

One artificial hybrid, which is of particular interest in this context, is the first *Amorphophallus* cultivar of hybrid origin, *A.* 'John Tan'. It involves two unlikely crossing partners, *A. variabilis*, a comparatively small species from Indonesia as pollen acceptor and *A. titanum*, the giant of the genus as pollen donor (Claudel et al., 2012). Plants of *A. variabilis* rarely exceed 120 cm in height and produce relatively small inflorescences (Hetterscheid & Ittenbach, 1996), whereas the leaves of *A. titanum* can reach seven meters in height (POWO, 2024a) and the massive inflorescences can exceed three meters, up to 3,70 meters (McPherson & Hetterscheid, 2011; Gibson, 2018; POWO, 2024a). The resulting hybrid, *A.* 'John Tan' proved to be fertile (Claudel et al., 2013). Moreover, Claudel et al. (2012) noted that *A.* 'John Tan' showed a "remarkable

similarity in general appearance to two other *Amorphophallus* giants, namely *A*. *gigas* Teijsm. & Binnend. (Sumatra), and *A*. *decus-silvae* Backer & Alderw. (Java)". Considering that, as far as it is known, the majority of *Amorphophallus* species attract a multitude of arthropod visitors and pollinators (Publ. 4; Publ. 5; Wong et al., 2022), it is reasonable to assume that such a hybrid could not only be fertile (Publ. 2) but potentially attract effective pollinators.

Additionally, this scenario is supported by a recent observation. In 2016, Indra Wirianto, a plant enthusiast from Indonesia, had backcrossed *Amorphophallus* 'John Tan' with its male parent, *A. titanum*. Using *A. titanum* as pollen acceptor, he applied the pollen from *A.* 'John Tan' on July 15 2016 and harvested 26 seeds three months later, on October 13. Indra Wirianto sent a few seeds each to several *Amorphophallus* enthusiasts around the world, including Steve Jackson, a retired horticulturist from the botanical garden Cairns, who gained world-wide recognition for the successful cultivation of otherwise horticulturally challenging *Amorphophallus* species. Accordingly, Steve Jackson was the first to raise a specimen to maturity and almost exactly six years later, on October 5, 2022, the first inflorescence opened (Fig. 8 A). Anthesis started in the evening hours and Steve Jackson noticed up to 20 large beetles buzzing around the inflorescence. The following morning, he and Julia Sumerling, a professional photographer and nature explorer, cut open the spathe to photograph the flowers. They were surprised to discover the large beetles at the bottom of the spathe, crawling over the female flowers (Fig. 8 B & C). The beetles were identified as *Diamesus osculans*, a large carrion beetle with a wide geographical distribution (Sin et al., 2021). Interestingly, *Diamesus osculans* was one of the very first pollinators observed to visit *A. titanum* inflorescences in 1931 in Indonesia (van der Pijl, 1937). Thus, the hybrid created by Indra Wirianto is capable of attracting an effective pollinator on a different continent. It should be noted that the overall appearance of the inflorescence and the plant is more reminiscent of *A. titanum* than of *A. variabilis*, which might be expected, given that it is a backcross with A. *titanum*. However, the overall dimensions appear to be significantly smaller and the maximum leaf height reported so far is around 2 m. Moreover, the plant has already reached flowering size at a tuber weight of only 8 kg. Considering the horticultural value of such a diminutive version of *A. titanum* the plant should be assigned a cultivar status, assuming that it can be propagated vegetatively.

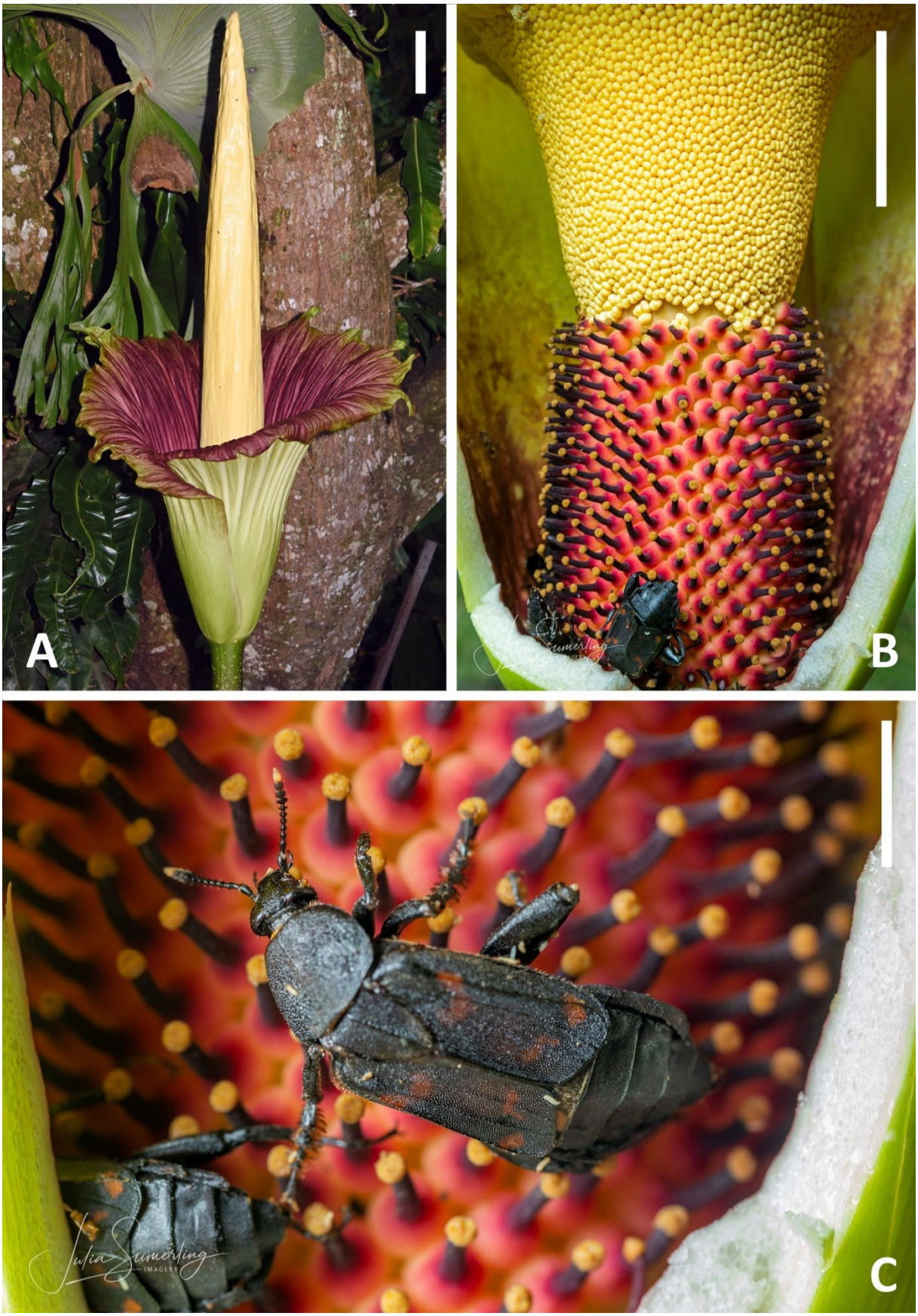

Figure 8. A-C: The first inflorescence of the hybrid between *A. titanum* and *A.* ‚John Tan'. A: Inflorescence on day 1 of anthesis. B: Inflorescence cut open, revealing visiting *Diamesus osculans* beetles. C: Close-up of one *Diamesus osculans* beetle. Scale bars: A = 10 cm. B = 5 cm. C = 1 cm. Photographs: A: with the kind permission of © copyright owner Steve Jackson. B & D: with the kind permission of © copyright owner Julia Sumerling.

It is noteworthy to add that the results of a recent study (Wong et al., 2022) could be interpreted as possibly indicative of natural hybridisation events. Using *mat*K, ITS and phytochrome C (PhyC), the authors investigated the molecular phylogeny of the Bornean *Amorphophallus* species, with special focus on *A. hewittii* Alderw. (Wong et al., 2022). The authors presented two phylogenetic trees, one based on the combined *mat*K and ITS dataset and the other on the PhyC dataset. Of particular interest in the present context is Clade B, which contains, among others, all the giant Indonesian species, such as *A. borneensis* Engl. & Gehrm., *A. decus-silvae*, *A. gigas*, *A. hewittii*, *A. lambii* Mayo & Widjaja *A. tinekeae* Hett. & A. Vogel and *A. titanum*. The overall resolution within Clade B is low in both analyses; moreover, the 13 investigated individuals of *A. hewittii* are scattered over the clade, particularly in the combined *mat*K and ITS analysis. The authors conclude that it possibly reflects the "imperfect taxonomy" of *A. hewittii* (Wong et al., 2022). However, the occurrence of natural hybridisation events should also be considered. Although speculative, natural hybridisation in *Amorphophallus* is at least conceivable and more studies on pollen vectors, seed dispersal, reproductive barriers and gene flow are required.

Petiolar mimicry

Another observation that can be made in the *A.* 'John Tan' hybrid concerns the petiolar lichen mimicry. The pattern types displayed on the petioles of the parental species, *A. variabilis* and *A. titanum*, are amongst the most versatile (Publ. 3). They include the lichenoid and the cyanobacterial-*Cryptothecia* pattern type in *A. variabilis* and the *Graphis* type and *Cryptothecia* type in *A. titanum* (Publ. 3). Although the exact petiole patterns of the parental plants of *A.* 'John Tan' are unknown, the complexity of the displayed lichen mimicry (*Graphis* type) on the petiole of *A.* 'John Tan' at least equals the documented petiolar patterns of both parental species (Claudel, 2023). Besides fertility and attractiveness to pollinators, the inheritance and varied expression of such a complex trait may be another factor that is relevant for hybrids for the successful colonisation of new ecological niches (Chartier et al., 2016).

Several species, such as *A. variabilis*, encompass individuals with unicolour petioles as well as individuals with different lichen mimicry types. More precisely, some individuals of *A. variabilis* are devoid of patterns, whereas others display lichenoid and/or cyanobacterial-*Cryptothecia* mimicry pattern types. Moreover, the lichen mimicry pattern types themselves are variable (Publ. 3), suggesting intraspecific colour polymorphism, at least in some species (Publ.

3). Analogous to odour emission and odour polymorphism (Publ. 5), petiolar mimicry must be assumed to exploit the animal's perception. Consequently, variation, i.e. petiolar colour polymorphism, might support the deceit in that it prevents the target from learning to identify and memorise a specific pattern. However, the degree and the frequency within a given species and the putative benefits of intraspecific petiolar colour polymorphism are not known for any *Amorphophallus* species, neither are the specific targets of the deceit known (Publ. 3). It has been suggested that the imitation of a lichen-covered tree trunk might serve as a protection from physical damage by large mammals and herbivory (Hejnowicz & Barthlott, 2005; Publ. 3). As far as the potential physical damage is concerned, it is reasonable to assume that large mammals are the primary targets of the deceit. However, regarding herbivory, the tissues of all *Amorphophallus* species contain needle-shaped raphide crystals, which may cause very unpleasant sensations when masticated (Mayo et al., 1997; Prychid et al., 2008) and it remains to be investigated if *Amorphophallus* species were under the evolutionary pressure of herbivores. Theoretically, the combination of colouration noticeable at close range with defensive raphides may hint at potential aposematism, but this type of potential visual defence has not yet been investigated in *Amorphophallus*.

As stated in Publ. 3, lichen and cyanobacterial mimicry is predominant in the subgenera *Amorphophallus* and *Metandrium*. That said, as with odour polymorphism (Publ. 5), it might be impossible to identify phylogenetic trends based on petiolar colouration, if intraspecific petiolar colour polymorphism is a common feature within the genus. Moreover, exclusively investigating petiolar mimicry types is misleading as other defence types are as effective. Camouflage, "potentially the best of all defences" (Lev-Yadun, 2016) has not been investigated and discussed in Publ. 3. However, camouflage through background matching is likely to play a significant simultaneous role in many *Amorphophallus* species, notably in subgenera *Afrophallus* and *Scutandrium* where petiolar lichen mimicry is rarely encountered (Publ. 3). Instead, many species from subgenus *Afrophallus* and *Scutandrium* display petioles with brownish, reddish or slightly greyish colours, that match the colour of the surrounding soil or rocks, indicating camouflage as a potentially important element of defensive colouration. Moreover, the petioles are sometimes covered with unspecific spots, which possibly serve the purpose of disruptive colouration (personal observation; see also leaf material and/or photographs deposited in the Herbarium Hamburgense HBG for reference).

Ideally, all types of defensive petiole colouration, including colour polymorphism, should be analysed within the phylogenetic context. Future investigations will need to evaluate the occurrence of petiolar mimicry, camouflage and other types of defensive colouration across the whole genus and other related genera to identify more subtle evolutionary trends of petiolar defensive colouration.

One aspect of defensive colouration that has been only briefly mentioned in Publ. 3, is heteroblasty. Heteroblasty occurs in several aroid genera and describes gradual to abrupt changes in successive leaves, depending on endogenous cycles, environmental changes, or maturation (Ray, 1990; Mayo et al., 1997; Croat & Ortiz, 2020). Heteroblasty is rarely reported in *Amorphophallus* (Liu et al., 2017) and it has been exemplified only briefly in Publ. 3 in connection with the increasing complexity of lichen-like patterns on successive petioles of *A. prainii*. Though not strongly pronounced in most *Amorphophallus* species, heteroblasty occurs in varying degrees. Generally, the degree of dissection of the leaf lamina is higher in adult plants than in juvenile ones. Moreover, the petiole colouration pattern is also more complex and more pronounced in adult leaves than in juvenile leaves (Publ. 3; personal observation). More specifically, some species show distinct differences between adult and juvenile leaves. For example, distinct differences can be found in some specimens of *A. maximus* (Engl.) N. E. Br. and *A. impressus*. The lamina of juvenile leaves consists of few simple segments and the petioles are brownish or reddish, becoming gradually darker towards the base, distinctly hairy, and spotted with dark marks. In contrast, the petioles of adult leaves of the same individuals are pale green, without any marks, and completely smooth. Moreover, they bear a highly dissected lamina (personal observation; see also leaf material and/or photographs deposited in the Herbarium Hamburgense HBG for reference). Similarly, seedling plants from some species of the *Paeoniifolius-Manta* clade of subgenus *Amorphophallus* display dramatic changes in leaf pigmentation during maturation from juvenile to adult leaves (Publ. 3). The first leaf is deep red whereas adult leaves are green, with transitional forms in between. Liu et al. (2017) analysed the reflectance curves from juvenile and adult leaves in *A. bufo* Ridl. and concluded that the different leaf forms correspond to camouflage through background matching; juvenile leaves match the background soil whereas adult leaves match the colours of the leaves of the surrounding plants. A similar defensive colouration strategy has been identified and tested in *Pseudopanax crassifolius* (Sol. ex A. Cunn.) K. Koch (Fadzly et al., 2009). Considering that several *Amorphophallus* species show varying degrees of heteroblasty, more studies to document and analyse juvenile and adult *Amorphophallus* leaves in their habitat are required, ultimately testing the adaptive value in terms

of defensive colouration. The relevance of defensive colouration in *Amorphophallus* can hardly be overestimated. Considering that most *Amorphophallus* species, when adult, make only a single leaf per growing season, defensive colouration is probably as important as reproductive success. If the petiole is substantially damaged, the plant is likely to die or at least suffer a serious setback in its development and reproductive success. Consequently, defensive colouration can be expected to have a high adaptive value.

The situation is similar to that hypothesised in regard to odour polymorphism (Publ. 5). The primary function of defensive colouration in *Amorphophallus* is to hide the plant through camouflage, mimicry and/or masquerade. However, within this functional framework, variation of petiolar patterns is likely to increase the adaptive value, as potentially damage-causing herbivores might not recognise or memorise specific patterns. Moreover, variation might enable the species to rapidly colonise and adapt to changing or new environments, which might partly contribute to the observation that "the majority of *Amorphophallus* species seem to be pioneers in disturbed vegetations" (Hetterscheid & Ittenbach, 1996).

Investigating the occurrence of petiolar mimicry in *Amorphophallus* in the phylogenetic context (Publ. 3) has been a first step towards a better understanding of the complexity of defensive colouration types. However, further steps must be made as the investigation of petiolar lichen mimicry (Publ. 3) constitutes only one aspect of defensive colouration. The occurrence of other defensive colouration types, and in particular camouflage, needs to be investigated. Moreover, petiolar colour polymorphism is likely to occur in more species and requires further studies if these variants occur in similar proportions and if they represent adaptations to specific environments or targets. Lastly, leaf heteroblasty in *Amorphophallus* needs to be more extensively documented and investigated.

Pollinators

Recently, floral visitors of three Bornean species, namely *A. hewittii*, *A. eburneus* and *A. julaihii* were documented *in situ* (Wong et al., 2022). Particularly *A. hewittii* is reported to attract a large array of arthropods. Besides a few Coleoptera (Scarabaidae, Staphylinidae, Silphidae) and Diptera (Muscidae) some Formicidae, Blattodea, Lepidoptera and even individuals of Reduviidae as well as Caelifera visited the inflorescence (Wong et al., 2022). Moreover, stingless bees, more precisely *Tetragonula melanocephala*, were observed crawling on the pistillate zone (Wong et al., 2022), again underlining the potential importance of stingless bees as pollinators

of *Amorphophallus* species (Publ. 4). It is noteworthy to add that the floral visitors of *A. hewittii* reported by Wong et al. (2022) differ from those reported by Chai and Wong (2019). The latter identified some Coleoptera (Hybosoridae; *Diamesus* sp.; *Creophilus* sp.) and an unidentified species of stingless bees ("Trigonids") as pollinators of *A. hewittii*. For the ease of comparison, the floral visitors reported by Chai and Wong (2019) and Wong et al. (2022) are summarised in Table 1. Moreover, newly reported floral visitors and pollinators for *A. albus* (Tang et al., 2020), *A. gigas* (Rambey et al., 2021, 2022) and *A. paeoniifolius* (Handayani et al., 2020) are added to Table 1.

Table 1. The *Amorphophallus* species and their (putative) pollinators. The number of inflorescences investigated, together with the location, reference, and categories of pollinators, putative pollinators and visitors to the inflorescences are provided. Modified after Claudel and Lev-Yadun (2021) (Publ. 5), including new entries.

Species & inflorescence quantity	**Location(s) & reference**	**Pollinators**	**Putative pollinators**	**Visitors**
A. albus **(new entry)** 25 inflorescences	China: Sichuan Province, Jinyang Country and Yunnan, Kunming, Botanical Garden (KBG) (Tang et al., 2020)	**Coleoptera: Staphylinidae,** *Atheta* sp. (Jinyang Country)		**Diptera: Calliphoridae**, *Calliphora* sp.; **Muscidae**, *Musca* sp.; **Sarcophagidae**, *Sarcophaga* sp. (KBG)
A. abyssinicus **subsp.** ***akeassii*** single inflorescence	Ivory Coast: Comoé National Park, savanna parkland of the Lola plaine (Moretto et al., 2019)	**Coleoptera: Scarabaeidae**, *Cleptocaccobius uniseries* ("main pollinator")	**Coleoptera: Aphodiidae**, *Aphodobius zumpti, Mesontoplatys dorsalis, Pseudopharaphodius phalacronothoides, Trichaphodius amplitarsis, Trichaphodius copulates, Trichaphodius flavus, Trichaphodius maldesi*; **Hydrophilidae**, *Sphaeridium* sp.; **Scarabaeidae**, *Caccobius auberti*, *Caccobius ivorensis*, *Cleptocaccobius convexifrons*, *Cleptocaccobius dorbignyi*, *Furconthophagus flaviclava*, *Hyalonthophagus nigroviolaceus*, *Onthophagus lutaticollis*, *Onthophagus tersipennis*, *Sisyphus goryi*; **Staphylinidae sp.**	**Coleoptera: Scarabaeidae**, *Chalconotus suturalis*, *Digitonthophagus fimator*
A. angolensis **subsp.** ***maculatus*** several inflorescences	Gabon: on several unspecified sites (Bogner, 1976)	**Coleoptera: Hybosoridae**, *Phaeochrous camerunensis*; **Diptera: Calliphoridae sp.**		
A. barthlottii single inflorescence	Ivory Coast: Taï National Park, track leading to the Centre de Recherche en Écologie (Moretto et al., 2019)	**Coleoptera: Hydrophilidae**, *Sphaeridium* sp.; **Scarabaeidae**, *Onthophagus liberianus*		

Species & inflorescence quantity	Location(s) & reference	Pollinators	Putative pollinators	Visitors
A. bulbifer not specified	India: Karnataka, Anshi National Park (Punekar & Kumaran, 2010)	**Coleoptera: Hybosoridae** (=**Melolonthidae**; probably *Apogonia* sp. according to Moretto et al., 2019); **Nitidulidae**, *Epuraea* sp.	**Diptera: Drosophilidae sp.**	**Coleoptera: Lyctidae**, *Lyctus* sp.
A. commutatus* var. *commutatus several investigated populations but the number of investigated inflorescences is not specified	India: Maharashtra, three localities: Ratnagiri, Vengurla, Goa (Punekar & Kumaran, 2010)	**Coleoptera: Bostrichidae sp.; Nitidulidae**, *Epuraea* sp.; **Hymenoptera:** *Trigona* sp. (except Vengurla population)	**Coleoptera:** Rutelinae (=**Rutelidae**, *Anomala* sp. according to Moretto et al., 2019); **Diptera: Drosophilidae sp.; Muscidae**, *Musca domestica*	**Coleoptera: Staphylinidae sp.; Hymenoptera: Formicidae**, *Oecophylla smaragdina,* Dolichoderinae: *Tapinoma* sp.
A. commutatus* var. *anmodensis single inflorescence	India: Goa, Anmode ghat (Punekar & Kumaran, 2010)	**Coleoptera: Scarabaeidae**, *Onthophagus* sp.		
A. commutatus* var. *anshiensis not specified	India: Karnataka, Anshi National Park (Punekar & Kumaran, 2010)	**Coleoptera**: **Cantharidae**, *Rhagonycha* sp.; **Cetoniidae**, black beetles**; Scarabaeidae**, *Heliocopris sp*, *Onthophagus* sp.	**Diptera**: **Drosophilidae sp.**	**Hymenoptera**: **Formicidae**, *Oecophylla smaragdina*; **Blaberidae**, Panesthiinae
A. commutatus* var. *wayanadensis several investigated populations but the number of investigated inflorescences is not specified	India: Maharashtra, four localities: Mulshi, Ratnagiri, Vengurla, Goa) (Punekar & Kumaran, 2010)	**Coleoptera**: **Nitidulidae**, *Epuraea* sp.	**Diptera**: **Drosophilidae**; **Muscidae**, *Musca domestica*; **Hymenoptera:** *Trigona* sp. (only Goa population)	
A. eburneus (**new entry**) six inflorescences, plus three bagged inflorescences	Malaysia: Borneo, Sarawak, Kuching Division, Padawan, Kg Danu (Wong et al., 2022)	**Coleoptera: Staphylinidae beetles; Diptera: Drosophilidae,** *Colocasiomyia* sp.	**Coleoptera: Scarabaeidae; Hydrophilidae**	**Diptera: Drosophilidae; Syrphidae; unidentified family; Hemiptera: Cicadellidae**
A. gigas (1) single inflorescence	Indonesia: North Sumatra province, Sipirok (Hetterscheid, 1994)	**Coleoptera**: carrion beetles; dung beetles; **Cetoniidae; Staphylinidae**; **Diptera**: **Asilidae**		
A. gigas (2) (**new entry**) single inflorescence	Indonesia: North Sumatra province, North Padang Lawas regency, Halongonan District, Bargottopong Julu Village (Rambey et al., 2021)	**Coleoptera: Chrysomelidae,** *Plagiodera* sp.; **Tenebrionidae,** *Tribolium confusum*; **Diptera:** *Aedes albopictus*; **Muscidae,** *Musca domistica*; **Formicidae:** *Camponutus* sp.; **Lepidoptera: Noctuidae,** *Scania* sp.		

Species & inflorescence quantity	Location(s) & reference	Pollinators	Putative pollinators	Visitors
A. gigas (3) (**new entry**) single inflorescence (only the blooming inflorescence is considered)	Indonesia: North Sumatra province, Sabungan, Sungai Kanan District, (Rambey et al., 2022)		**Coleoptera:** *Sithopilus oryzae;* **Diptera: Anisopodidae** *Sylvicola fenestralis;* **Muscidae,** *Lucilia* sp.; **Formicidae,** *Monomorium minimum*	
A. gomboczianus several inflorescences	Ethiopia: Sidamo (Gombocz, 1936)	**Diptera spp.**		
A. henryi several populations and several inflorescences	Taiwan: four sampling areas (Jung, 2006)	**Coleoptera: Scarabaeidae**, *Onthophagus* sp., *O. argyropygus*, *O. koshunensis*, *O. proletarius*, *O. sauteri*, *O. taurinus*; **Staphylinidae spp.**		**Coleoptera**: **Nitidulidae**; **Scaphidiidae**; **Scarabaeidae**, *Paragymnopleurus* sp.; **Tenebrionidae**; **Diptera**: **Calliphoridae,** *Chrysomyia* spp.; **Drosophilidae,** *Drosophila* spp.; **Sepsidae**, *Sepsis* spp.; **Hemiptera; Homoptera: Aphididae**; **Hymenoptera**: **Formicidae**; **Isoptera**: **Termitidae**, *Odontotermes formosanus***; Orthoptera**; **Thysanoptera**; **Arachnida**: **Araneae**, **Sparassidae**; **Salticidae**; **Blattoidae**
A. hewittii (1) several inflorescences	Malaysia: Borneo, Sarawak, Gunung Mulu National Park (Chai & Wong, 2019)	**Coleoptera: Hybosoridae**; **Silphidae**, *Diamesus* sp.; **Staphylinidae**, *Creophilus* sp.	**Hymenoptera:** Trigonids	
A. hewittii (2) (**new entry**) eight inflorescences, plus one bagged inflorescence	Malaysia: Borneo, Sarawak, Kuching Division, Padawan, Kg Danu (Wong et al., 2022)	**Coleoptera: Silphidae; Cerambycidae; Diptera: Muscidae; Hymenoptera: Apidae,** *Tetragonula melanocephala*	**Coleoptera: Hydrophilidae; Hymenoptera: Formicidae; Lepidoptera**	**Hymenoptera; Diptera: Drosophilidae; Hemiptera: Reduviidae; Orthoptera: Caelifera**
A. hohenackeri several inflorescences	India: Kerala, Calicut University campus (Sivadasan & Sabu, 1989)	**Coleoptera: Nitidulidae**, *Epuraea motschulskii*		
A. johnsonii several inflorescences	Ghana: Jachie Sacred Grove (Beath, 1996)	**Coleoptera: Hybosoridae**, *Phaeochrous amplus*	**Coleptera: Histeridae**, *Pachycraerus* sp.	**Diptera: Calliphoridae**, *Hemigymnochaeta unicolor;* **Platystomatidae**, *Paryphodes tigrinus*
A. julaihii (1) several inflorescences	Malaysia: Borneo, Miri Division, Sarawak, Gunung Mulu National Park (Chai & Wong, 2019)	**Coleoptera: Staphylinidae**, *Creophilus* sp.		

Species & inflorescence quantity	Location(s) & reference	Pollinators	Putative pollinators	Visitors
A. julaihii (2) (**new entry**) two inflorescences plus two bagged inflorescences	Malaysia: Borneo, Miri Division, Sarawak, Gunung Mulu National Park, trail to Deer Cave (Wong et al., 2022)	**Coleoptera: Staphylinidae** (during pistillate anthesis)	**Coleoptera Staphylinidae; Silphidae; Thysanoptera** (during staminate anthesis)	
A. konjac several inflorescences	China: Yunnan, Kunming botanical garden 25.127° N, 102.743° E, 1,788 m. a.s.l.), several inflorescences (Chen et al., 2015)	**Coleoptera: Histeridae**, **Nitidulidae**, **Staphylinidae; Dermaptera**	**Diptera**, **Calliphoridae**, **Calliphoridae** ssp, *Achoetandrus rufifacies*, *Aldrichina grahami*, *Chrysomya* spp. , *Lucilia* spp.; **Muscidae**; **Sarcophagidae**	
A. konkanensis not specified, apparently single inflorescence	India: Maharashtra, Sindhudurg district, Kochra (Punekar & Kumaran, 2010)	**Coleoptera: Nitidulidae**, *Epuraea* sp.		
A. koratensis single inflorescence	Thailand: Songkhla, Hat Yai (pers. comm. Sutthinut Soonthornkalump)		**Hymenoptera:** *Tetragonula* sp.	**Hymenoptera: Formicidae**
A. muelleri several inflorescences	Indonesia: Java (van der Pijl, 1937)	**Coleoptera: Nitidulidae**		**Coleoptera: Melolonthidae**, *Apogonia destructor*
A. napalensis several inflorescences at two sites	India: Nagaland, Zunheboto, Lumami village, 880 m. a.s.l.; Mokokchung, Arkong ward. Plot no. 227, 1,350 m a.s.l. (Chaturvedi, 2017)	**Coleoptera: Scarabaeidae,** *Parastasia* sp. (=**Dynastidae**, *Peltonotus* sp. according to Moretto et al., 2019)		**Diptera: Drosophilidae**, *Drosophila* sp.; **Hymenoptera:** *Trigona* sp.; **Apidae**, *Apis indica*
A. paeoniifolius (1) several inflorescences, both wild and cultivated plants	India: Karnataka, Uttara Kannada district (Singh & Gadgil, 1995)	**Coleoptera**: **Rutelidae**, *Adoretus* sp.	**Hymenoptera**: *Melipona* sp. (*Melipona* is now a neotropical genus so probably *Tetragonula* sp.)	Two unidentified insects
A. paeoniifolius (2) single inflorescence	locality not specified (Giordano, 1999)	**Coleoptera**: **Hybosoridae**, *Phaeochrous emarginatus*		
A. paeoniifolius (3) not specified, apparently single inflorescence	India: Karnataka, Anshi National Park (Punekar & Kumaran, 2010)	**Coleoptera**: **Scarabaeidae**, *Heliocopris* sp., *Onthophagus* sp.; **Cetoniidae** Black beetles	**Coleoptera**: **Scarabaeidae**, **Rutelinae** (=**Rutelidae**, *Anomala* sp. according to Moretto et al., 2019)	**Diptera: Calliphoridae; Muscidae,** *Musca domestica*
A. paeoniifolius (4) single inflorescence	Thailand: Changwat Mae Hong son, 12km NW Soppong (Pangmapa) (Grimm, 2009)	**Coleoptera**: **Hybosoridae**, *Phaeochrous dissimilis*, *Phaeochrous emarginatus*, *Phaeochrous intermedius*; **Scarabaeidae**, *Peltonotus nasutus*		

Species & inflorescence quantity	Location(s) & reference	Pollinators	Putative pollinators	Visitors
A. paeoniifolius (5) single inflorescence	Thailand: Nan province, Nan River at Srinan river (Sites, 2017)	**Coleoptera**: **Hybosoridae**, *Phaeochrous dissimilis*; **Scarabaeidae**, *Peltonotus nasutus*		
A. paeoniifolius (6) (**new entry**) not specified	Indonesia: Bogor Botanic Gardens (Handayani et al., 2020)	**Hymenoptera**: **Apidae**, *Trigona* sp. (*Trigona* is now a neotropical genus, so probably *Tetragonula* sp.)		**Coleoptera**: **Nitidulidae**, *Epuraea-Haptoncurina*; **Diptera**: **Calliphoridae**, *Calliphora vomitoria*; **Muscidae**, *Musca domestica*; **Sarcophagidae**, *Sarcophaga* sp.; **Syrphidae**.
A. prainii single inflorescence	West Malaysia (Soepadmo, 1973)		**Diptera:** „various flies“ are mentioned but have not been actually observed	
A. sylvaticus single inflorescence	India: Maharashtra, Mumbai, Bhandup (Punekar & Kumaran, 2010)	**Coloptera: Nitidulidae,** *Epuraea* sp.		
A. titanum (1) several inflorescences	Sumatra: Fort de Kock (now Bukittinggi) (van der Pijl, 1937)	**Coleoptera: Silphidae**, *Diamesus osculans*; **Staphylinidae**, *Creophilus villipennis*		
A. titanum (2) single inflorescence	Indonesia: North Sumatra province, Sipirok (Hetterscheid, 1994)	No insects were observed on the first day of anthesis	**Hymenoptera:** *Trigona* sp. on day two of anthesis.	
A. titanum (3) several inflorescences	Sumatra: (Giordano, 1999)	**Coleoptera: Curculionidae**; **Histeridae**; **Hybosoridae**, *Phaeochrous emarginatus*	**Coleoptera: Staphilinidae**; **Scarabaeidae**; **Diptera: Calliphoridae**; **Drosophilidae**; **Hymenoptera:** *Trigona geissleri*; *Trigona* sp.	**Coleoptera: Brentidae**, *Hormocerus compressitarsus*; **Arachnida**; **Blattodea**; **Formicidae**
A. variabilis (1) several inflorescences	Java: Buitenzorg (now Bogor), (Backer, 1913)	**Coleoptera: Nitidulidae**	**Staphilinidae**, *Philanthus crassicornis*	
A. variabilis (2) several inflorescences	Java: Bandoeng (now Bandung) (van der Pijl, 1937)	**Coleoptera: Nitidulidae**		

Compared to *A. hewittii*, fewer floral visitors have been reported for *A. eburneus* and *A. julaihii* (Wong et al., 2022; Table 1). Mainly Coleoptera (Staphylinidae; Hydrophilidae), Diptera (Syrphidae; Drosophilidae, *Colocasiomyia*) and some Hemiptera (Cicadellidae) were reported for *A. eburneus*. In contrast, during pistillate anthesis, exclusively Silphidae beetles are reported for *A. julaihii*, whereas Silphidae beetles and Thysanoptera visit the inflorescences during the staminate phase (Wong et al., 2022; Table 1). It could be hypothesised that fewer floral visitors indicate a more specialised plant-pollinator interaction. However, the average fruit set is reported to be significantly higher in *A. hewittii* (82.7%) than in *A. eburneus* (54.1 ± 14.4%) and *A. julaihii* (75.6 ± 11.2%) (Wong et al., 2022). Moreover, only three out of ten *A. eburneus* inflorescences were observed to develop into infructescences (Wong et al., 2022), which suggests low pollination efficiency.

Even more intriguing are the floral visitors and pollinators of *A. paeoniifolius*, reported from Bogor Botanical Gardens, Indonesia. For the first time, the most dominant group of reported floral visitors consists of various Diptera rather than Coleoptera. Moreover, the only reported pollinator is a stingless bee from the genus *Trigona* (Handayani et al., 2020; Table 1). As stated in Publ. 4, the genus *Trigona* is now circumscribed as a neotropical genus (Michener, 2007), therefore the observed stingless bee species is more likely to belong to one of the Asian genera, such as *Tetragonula*. Nevertheless, this observation is remarkable as it confirms the observation made by Singh and Gadgil (1995) who observed stingless bees acting as pollinators in *A. paeoniifolius* in India.

Last but not least, there is no overlap between the reported insect visitors or pollinators of three investigated *A. gigas* inflorescences (Table 1). Whereas carrion and dung beetles are reported as the main pollinators in one case (Hetterscheid, 1994), beetles (*Plagiodera* sp.; *Tribolium confusum*), flies (*Musca domestica*), mosquitos (*Aedes albopictus*), ants (*Camponutus* sp.) and moths (*Scania* sp.) are reported as the main pollinators in another case (Rambey et al., 2021). Lastly, beetles (*Sithopilus oryzae*), mosquitos (*Sylvicola fenestralis*), flies (*Lucilia* sp.) and ants (*Monomorium minimum*) are reported in a third study (Rambey et al., 2022).

All in all, the newly reported observations (Handayani et al., 2020; Rambey et al., 2021, 2022; Tang et al., 2020; Wong et al., 2022) appear to confirm the trend postulated in Publ. 4, describing the attraction of a broad visitor and pollinator group, i.e. copro-necrophagous arthropods and their predators by means of several highly specific scent compounds in varied proportions.

Stingless bees might respond to other olfactory cues, such as fungal components (Publ. 4). However, considering that some neotropical *Trigona* species are obligate necrophages (Camargo & Roubik, 1991), it seems at least possible that some of their Asian counterparts might have developed comparable trophic preferences or dispose of a comparable perception, which could also account for the attraction to some *Amorphophallus* species, *A. titanum* for instance (Hetterscheid, 1994; Giordano, 1999).

It has been proposed that different flowering times, i.e. diurnal or nocturnal anthesis, might contribute to the separation between species or groups of species (Wong et al., 2022). However, this is not wholly convincing. As mentioned by the authors themselves, some specimens of *A. hewittii* showed a shift in the timing of anthesis (Wong et al., 2022). More precisely, the pistillate phase in *A. hewittii* has been reported by Chai and Wong (2019) to start at 17:00 h and be accompanied by the emission of an ammonia-like odour whereas the pistillate phase has been reported by Wong et al. (2022) to start at 11:00 h and to be accompanied by the emission of a rotting meat-like odour. Although the intervals of scent emission are unknown, a strong scent emission from the specimen that started the pistillate phase at 17:00 h has been reported at the beginning of the pistillate phase and on the morning of day 3 (Chai & Wong, 2019). Similarly, the pistillate phase has been reported to last 36 hours in *A. hewittii* by Wong et al. (2022). In other words, the pistillate phase in *A. hewittii* lasts more than 24 hours and scent emission occurs at least in the afternoon and in the morning (Chai & Wong, 2019; Wong et al., 2022). Consequently, at least in *A. hewittii*, cross-pollination is possible at any time. Moreover, as discussed in Publ. 4 & 5, species that mimic carrion and dung odours seem especially designed to attract a multitude of different arthropods that rely on decomposing organic material in their life cycle (Publ. 4 & 5). Therefore, a strictly fixed timing of anthesis does not seem likely, at least not in all species. Similar shifts in timing have been documented in the Araceae genera *Monstera* (Chouteau et al., 2009), *Arum* (Marotz-Clausen et al., 2018), and *Typhonium* (Sayers et al., 2020). According to Sayers et al. (2020), shifts in anthesis time in *Typhonium brownii* Schott can possibly be explained by its wide geographical range and may represent adaptations to different local conditions. However, this was challenged by Sayers et al. (2021) who could not find an association between thermogenic traits and pollinator shifts in two *Typhonium* species. Moreover, shifts in *Arum maculatum* L. occurred within the same population and cannot therefore be due to a wide geographical origin (Marotz-Clausen et al., 2018). Moreover, shifts of anthesis time in *Monstera adansonii* Schott, and in *Monstera deliciosa* occurred among different inflorescences of the same plant (Chouteau et al., 2009).

Shifts in timing might represent a strategy to attract both putative diurnal or nocturnal pollinators. Likewise, if several individuals within a population are flowering, this might keep attracted pollinators within a population. A small shift in timing of anthesis might have significant consequences. Considering that many *Amorphophallus* species readily multiply vegetatively, some populations may originate from one initial seedling and slight variations in anthesis might increase the likelihood of successful pollination within a clonal population. Even if this eventually results in self-pollination, it still represents an advantage, as the fruits are the means of long-distance dispersal, since the berries are eaten by birds (Singh & Gadgil, 1995; Hetterscheid, 1994; Hetterscheid & Ittenbach, 1996; Sedayu et al., 2010; Rambey et al., 2022; Low, 2024).

Odour polymorphism

Odour polymorphism in the genus *Amorphophallus*, together with its putative functionality and the implications for the identification of evolutionary trends, has been discussed in Publ. 5. In the meantime, additional data have been identified. Therefore, the three tables from Publ. 5 are complemented and reproduced here. Further aspects of odour polymorphism, which have not been elaborated in Publ. 5, are also discussed.

Table 2 (Table 1 in Publ. five) lists selected volatile organic compounds (VOCs) that are emitted by several *Amorphophallus* species during anthesis and during cadaveric decomposition of pig carcasses and human decomposition fluid. Carbon dioxide (CO_2) is added to Table 2 as it is one of the compounds released by more than 95% of the analysed human decomposition fluid samples (Buis, 2016). More generally, decomposing organic materials emit elevated amounts of CO_2 due to enzymatic and microbiological activity. Considering that thermogenesis relies on elevated respiration rates (Lamprecht & Seymour, 2010), it can be assumed that all thermogenic *Amorphophallus* species (Skubatz et al., 1990; Barthlott et al., 2009; Lamprecht & Seymour, 2010) emit elevated CO_2 concentrations during anthesis. Carbon dioxide is a known attractant to various insects (Nicolas & Sillans, 1989; Patiño et al., 2002; Vereecken & McNeil, 2010; Jones, 2013). In particular, parasitic and blood sucking insects, and insects feeding or breeding on decomposing organic material, rely on CO_2 gradients to locate a suitable substrate (Nicolas & Sillans, 1989; Patiño et al., 2002; Vereecken & McNeil, 2010; Jones, 2013). Consequently, the release of carbon dioxide might serve as an attractant in oviposition-site mimics and its role as attractant in *Amorphophallus* deserves more attention in the future.

Table 2. Scent compounds released by human decomposition fluid, pig carcasses and *Amorphophallus* species (Kite & Hetterscheid, 1997, 2017; Kakishima et al., 2011). Ref. numbers refer to: **1:** Buis, 2016; **2:** Armstrong et al., 2016; **3:** Dekeirsschieter et al., 2009. Except for *A. gigas* (Kakishima et al., 2011), all scent compounds emitted by *Amorphophallus* species are retrieved from Kite and Hetterscheid (1997, 2017). Group defining compounds refer to the scent categories defined by Kite and Hetterscheid (2017), modified after Claudel and Lev-Yadun (2021) (Publ. 5).

Selected VOCs emitted during cadaveric decomposition	**Ref.**	**also emitted by the *Amorphophallus* species (rel. % of the total odour composition)**	**used as group defining compound of the:**
1-phenylethanone (acetophenone)	1	*A. symonianus* (60%), *A. amygdaloides* (60%), *A. cicatricifer* (55%, 39%), *A. pulchellus* (5%), *A. putii* (2%), *A. yuloensis* (11%, 6%)	benzenoid compounds
1-propanol	2	*A. cirrifer* (16%, 11%), *A. obscurus* (10%), *A. pilosus* (7%)	aliphatic alcohols and ketones
2-decanone	1	*A. ankarana* (2%)	
2-heptanone	1	*A. polyanthus* (85%, 62%), *A. eichleri* (30%, 25%), *A. ankarana* (3%)	aliphatic alcohols and ketones
2-undecanone	1	*A. ankarana* (3%)	
3-methyl-1-butanol	2	*A. ankarana* (39%), *A. cirrifer* (36%, 16%), *A. henryi* (30%, 7%), *A. obscurus* (21%), *A. borneensis* (8%), *A. commutatus* (3%), *A. konjac* (3%)	aliphatic alcohols and ketones
4-methylpentanoic acid	3	*A. elatus* (100%), *A. atroviridis* (98%), *A. linearis* (94%), *A. macrorhizus* (97%, 95%), *A. angustispathus* (50%), *A. saraburiensis* (23%), *A. scutatus* (7%), *A. baumannii* (6%), *A. johnsonii* (4%)	aliphatic acids
acetone	1	*A. eburneus* (18%), *A. erythrrorhachis* (12%), *A. commutatus* (11%), *A. tinekeae* (9%), *A. borneensis* (8%), *A. henryi* (7%), *A. konjac* (6%, 2%), *A. macrorhizus* (3%), *A. plicatus* (2%)	
butanoic acid	3	*A. taurostigma* (74%), *A. saraburiensis* (4%), *A. scutatus* (4%)	aliphatic acids
carbon dioxide	1	**emitted by all thermogenic *Amorphophallus* species**	
dimethyl oligosulphides	2	identified in varied proportions in **58 out of 92** investigated *Amorphophallus* species	sulphur-containing compounds
dimethyl trisulphide	1	identified in varied proportions in **47 out of 92** investigated *Amorphophallus* species	sulphur-containing compounds
ethyl acetate	2	*A. consimilis* (77%, 57%), *A. haematospadix* (65%), *A. annulifer* (60%), *A. antsingyensis* (43%), *A. laoticus* (23%), *A. borneensis* (10%), *A. baumannii* (5%), *A. henryi* (2%)	aliphatic esters
hexanal	1	*A. pilosus* (3%)	
nonanal	1	*A. elliottii* (3), *A. eburneus* (3%), *A. erythrorrhachis* (2%)	
phenol	1	*A. impressus* (6%)	
propionic acid	1	*A. gigas* (4%)	
pyrazine	1	*A. preussi* (61%)	nitrogen-containing compounds
trimethylamine	3	*A. brachyphyllus* (85%), *A. eburneus* (64%), *A. tinekeae* (35%), *A. angolensis* (18%), *A. plicatus* (13%), *A. longispathaceus* (4%), *A. konjac* (2%)	nitrogen-containing compounds

Furthermore, two entries are added to Table 3 (Table 2 in Publ. five). Table 3 lists the scent compounds and their relative amount per species and individual. The new entries are added in bold, namely two individuals each of *A. consimilis* Bl. H.AM 1150 and *A. polyanthus* H.AM 873. These two entries differ insofar as clonally propagated plants of a species were analysed, rather than genetically different individuals (Kite & Hetterscheid, 2017). The variation between the two analyses of clonally propagated material is relatively low compared to the variation between genetically different individuals (Table 3). Moreover, this result can be at least partly explained by methodological aspects, such as different times of day. Nonetheless, the low rate of variation in genetically identical plants is noteworthy.

Lastly, Table 4 (Table 3 in Publ. five) lists *Amorphophallus* species which, based on subjective human scent perception, show significant odour polymorphism. Four additional entries are added in bold, namely *A. eichleri* (Engl.) Hook. f., *A. hewittii*, *A. lambii* and *A. yuloensis* H. Li.

Table 3. Selected *Amorphophallus* species which show significant odour polymorphism. Alternative scent categories are highlighted in bold. New entries are marked in bold and refer to clonally propagated plants; however, analysed at different times of the day. If specified in the original publications, voucher and/or origin are provided. The quantity of the identified scent compounds is presented as in the original publications, either as percentage or as symbol (x ; +; -), indicating the presence and the quantity of a given compound. Percentage numbers are rounded in two cases (Chen et al., 2015; Raman et al., 2017). References are given as numbers and refer to: 1) Kite & Hetterscheid, 1997; 2) Lamprecht & Seymour, 2010; 3) Shirasu et al., 2010; 4) Chen et al., 2015; 5) Kite & Hetterscheid, 2017; 6) Raman et al., 2017. Modified after Claudel and Lev-Yadun (2021) (Publ. 5).

Species, voucher, time & scent category	**Scent compounds per species and individual in % or as provided in according reference**																							**Ref.**
	ethyl acetate	propyl acetate	iso/butyl acetate	methyl acetate	isoamyl acetate	dodecane	tetradecane																	
***A. consimilis* HAM 1150, 09:00-10:30**, aliphatic esters	77	8	5	2	1																			**5**
***A. consimilis* HAM 1150, 13:00-15:00**, aliphatic esters	57	11	10	4	3	7	6																	**5**
	isoamyl alcohol	isoamyl acetate	β-pinene	tridecane	α-pinene	camphene	skatole	2-butanol	acetone	butyl acetate	isobutyl acetate	undecane	caryophyllene	ethyl acetate	limonene	3-methyl-2-hexanone								
A. henryi HAM 270, alcohols and ketones	30		25	22	16	2	2																	**5**
A. henryi 1994-3573, alcohols and ketones	7	18	10	6	2			17	7	6	6	5	2	2	2	1								**5**
	1-phenylethanone	methyl cinnamate	1-phenylethyl acetate																					
A. symonianus HAM 924, benzenoid compounds	60	39																						**5**
A. symonianus 1998-3421, benzenoid compounds		6	89																					**5**
	dimethyl disulphide	dimethyl trisulphide	dimethyl tetrasulphide	2-heptanone	indole	phenylethylalcohol	butyl heptanoate	2-pentanone	α-ketoisocaproic acid	1-butanol	2-hexanone	4-methyl-1-pentanol	2-pentanol											

Species, voucher, time & scent category	Scent compounds per species and individual in % or as provided in according reference																							Ref.
A. eichleri not specified, sulphur compounds	62	15	1	7	2	1																		**1**
A. eichleri 1994-7554, sulphur compounds	56	7	1	25			8																	**5**
A. eichleri HAM 007, **alcohols and ketones**	23	1		**30**				13	10	6	3	2	2											**5**
	dimethyl disulphide	dimethyl trisulphide	dimethyl tetrasulphide	ethanol	2/3-methyl-2-butenal	trimethylamine	3-methyl-1-butanol	acetaldehyle	acetone	2-butanone	2-methyl-1-butanol	isoamyl alcohol	β-caryophyllene	3-methyl-2-pentanone	4-hydroxy-4-methyl- 2-pentanone	n-nonaldehyde	butyl ether	3-methyl-1-pentanol	n-dodecane	2-pentanone	n-tridecane	butyl 2-propenoate		
A. konjac not specified, sulphur compounds	76	17																						**1**
A. konjac 1997-111, sulphur compounds	55	3		9	6	6	3	3	2	2														**5**
A. konjac HAM 168, sulphur compounds	40	17	1		3	2	3		6	12	2													**5**
A. konjac China, KBG, sulphur compounds	43	26	2								3	6	3	2	2	2	2	2	1	1	1	1		**4**
	2-heptanone	hydrocarbons	heptadecene	pentadecane	2-nonanone	2-heptanol																		
***A. polyanthus* HAM 873, 12:30-15:00**, alcohols and ketones	85	10																						**5**
***A. polyanthus* HAM 873, 15:30-17:15**, alcohols and ketones	62		15	15	5	2																		**5**
	dimethyl disulphide	dimethyl trisulphide	dimethyl tetrasulphide	dimethyl pentasulphide	1-butanol	isocaproic acid	4-methyl-1-pentanol	butanoic acid	ac s-methyl thioester	acetic acid	ethyl acetate	2-methylbutanoic acid												
A. scutatus HAM 589, sulphur compounds	34	61	5																					**5**
A. scutatus HAM 590, sulphur compounds	18	29	11	1	12	7	5	4	2	2	2	2												**5**

Species, voucher, time & scent category	Scent compounds per species and individual in % or as provided in according reference																								Ref.
	dimethyl disulphide	dimethyl trisulphide	dimethyl tetrasulphide	ac s-methyl thioester	pungent smell	sweet smell	almond like	benzaldehyde	trimethylamine	3-methyl-butanal	methyl thiolacetate	acetic acid	isovaleric acid	isovaleric acid	butyric acid	benzylalcohol	γ-butyrolactone	3-hydroxy-2-butanone	2-phenoxyethanol	phenol	4-hydroxy-4-methyl-2-pentanone	nonanal	trimethyl pyrazine	
A. titanum not specified, sulphur compounds	75	10																							**1**
A. titanum 1997-5514, sulphur compounds		25	1	3																					**5**
A. titanum Palm Garden, **benzenoid compounds**					**x**	**x**	**x**	**x**																	**2**
A. titanum: gas sample, **nitrogen-containing**		+							++	+	-	+	-												**3**
A. titanum: appendix, **aliphatic acids**								4						**22**	**17**	16	12	6	3	3	3	2	2		**6**

Table 4. *Amorphophallus* species which show significant odour polymorphism based on the subjective human scent perception. New entries in bold. Modified after Claudel and Lev-Yadun (2021).

Species	Subjective odour perception quoted from publication	Ref.
A. aphyllus	dung	Claudel et al., 2017
A. aphyllus	fruity, melon-like, with added vodka	(pers. commun. S. Jackson)
A. cicatricifer	gaseous plus fruity	Kite & Hetterscheid, 1997
A. cicatricifer	gaseous, almonds	Kite & Hetterscheid, 2017
A. commutatus	dead meat	Kite & Hetterscheid, 2017
A. commutatus:	rottening meat	Punekar & Kumaran, 2010
- var. *anmodensis*	gaseous, fruity	Punekar & Kumaran, 2010
- var. *anshiensis*	gaseous, fruity	Punekar & Kumaran, 2010
- var. *wayanadensis*	rottening meat	Punekar & Kumaran, 2010
A. eichleri	**rotting meat, changing to a shrimp-like scent**	Hetterscheid & Ittenbach, 1996
A. eichleri	**rotting meat odour mixed with that of dung**	Kite & Hetterscheid, 1997
A. fallax	gaseous	Kite & Hetterscheid, 1997
A. fallax (1)	gaseous, sweet	Kite & Hetterscheid, 2017
A. fallax (2)	gaseous, sweet	Kite & Hetterscheid, 2017
A. galbra	**sweet**	(pers. commun. S. Jackson)
A. galbra	**reminiscent of a freshly opened tin of paint**	(pers. commun. S. Ferguson)
A. gigas	spoiled meat	Hetterscheid, 1994
A. gigas	rotten, fishy, sour	Kakishima et al., 2011
A. hewittii	**fishy odour**	Kite & Hetterscheid, 2017
A. hewittii	**ammonia-like floral odour**	Chai & Wong, 2019
A. hewittii	**rotting meat-like odour**	Wong et al., 2022
A. johnsonii	sewerage	Kite & Hetterscheid, 2017
A. johnsonii	carrion	Beath, 1996
A. konkanensis	cheese	Kite & Hetterscheid, 2017
A. konkanensis	rottening meat	Punekar & Kumaran, 2010
A. lambii	**urine scent**	Hetterscheid & Ittenbach, 1996
A. lambii	**fishy odour**	Kite & Hetterscheid, 2017
A. mossambicensis (1)	carrion	Kite & Hetterscheid, 2017
A. mossambicensis (2)	carrion	Kite & Hetterscheid, 2017
A. mossambicensis (3)	acidic, dung	Kite & Hetterscheid, 2017
A. prainii	gaseous	Kite & Hetterscheid, 1997
A. prainii	rotten meat	Soepadmo, 1973
A. sylvaticus	bad vegetables	Kite & Hetterscheid, 2017
A. sylvaticus	rottening meat	Punekar & Kumaran, 2010
A. symonianus	fruity, cinnamon, shoe polish	(personal observation)
A. symonianus (1)	almond, chemical	Kite & Hetterscheid, 2017
A. symonianus (2)	almond, chemical	Kite & Hetterscheid, 2017
A. titanum	gaseous plus urine	Kite & Hetterscheid, 1997
A. titanum	gaseous, rotting vegetables	Kite & Hetterscheid, 2017
A. titanum	carrion and weakly sweet	Lamprecht & Seymour, 2010
A. titanum	old fish	Hetterscheid, 1994
A. titanum	rotting flesh, changing to excrement	Giordano, 1999
A. titanum	decayed cabbage, garlic and pungent sour	Fujioka et al., 2012
A. titanum	nearly scentless	Winkler, 1931
A. titanum	strong scent	Winkler, 1931
A. titanum: appendix	rotting meat	Raman et al., 2017
A. titanum	slight rotten fruit like, yellow pickled radish, rotten egg, rotting animal-like, rotten fish, rotten egg	Shirasu et al., 2010
A. yuloensis	**lemon-like scent**	Hetterscheid & Ittenbach, 1996
A. yuloensis	**almond, chemical**	Kite & Hetterscheid, 2017

Furthermore, other aspects of odour polymorphism in *Amorphophallus*, such as the modulation of signals, have not been elaborated in Publ. 5. This particularly concerns one scent class,

namely dimethyl oligosulphides which are the most abundant scent compounds, emitted by the majority of *Amorphophallus* species (Kite & Hetterscheid, 2017). They are therefore assumed to represent the ancestral state of scent emission in the genus *Amorphophallus* (Kite & Hetterscheid, 2017). However, the composition of emitted dimethyl oligosulphides is variable. The ratio between dimethyl mono-, di-, tri-, tetra- and pentasulphides can vary on the inter- and the intraspecific level (Kite & Hetterscheid, 1997, 2017; Shirasu et al., 2010; Chen et al., 2015; Publ. 5). This is noteworthy because some studies found that, depending on the ratio of the emitted dimethyl oligosulphides, the exerted signal on burying beetles of the genus *Nicrophorus* differed (Kalinová et al., 2009; Podskalská et al., 2009; Trumbo & Steiger, 2020). For example, dimethyl disulphides alone may not be sufficient for successful attraction in some insect species (Kalinová et al., 2009). Similarly, dimethyl disulphides combined with dimethyl trisulphides can exert a synergistic effect (Podskalská et al., 2009). Lastly, *Nicrophorus* beetles in search of a breeding place were actually deterred by dimethyl trisulphides alone and the authors proposed that higher levels of dimethyl trisulphides signal more advanced stages of carrion decomposition, indicating a resource that may be too old for successful reproduction and/or may already have been colonized by competitors (Trumbo & Steiger, 2020).

Therefore, even if the emission of dimethyl oligosulphides represented the ancestral state in *Amorphophallus* (Kite & Hetterscheid, 2017), it must be considered that the signaling effect on insects might differ depending on the ratio of the emitted dimethyl oligosulphides. As stated in Publ. 5, *A. julaihii* is one of the few *Amorphophallus* species that apparently attracts exclusively Staphylinidae beetles from the genus *Creophilus* (Chai & Wong, 2019). *Creophilus* beetles are predators that feed on maggots hatched on carrion but not on the carrion itself (Publ. 5). Wong et al. (2022) confirmed the exclusive attraction of Staphylinidae beetles during the pistillate stage of *A. julaihii*; however, they did not determine the genus of the visiting/pollinating beetles. Moreover, Silphidae beetles and Thysanoptera were attracted during staminate anthesis (Wong et al., 2022). Therefore, more observations are needed to confirm if *A. julaihii* specifically and exclusively attracts predatory beetles. Moreover, the scent compounds and their composition emitted by several inflorescences of *A. julaihii* should be identified. That said, it might be beneficial for a plant to exclusively attract predatory insects in search of prey as pollinators, as these are not specifically interested in the mimicked substrate and are less likely to damage the inflorescence.

Another, almost unexplored topic concerns the balance between olfactory repellents and attract-ants. Ramos and Schiestl (2020) investigated the emission of scent compounds in two plant lines of *Brassica rapa* L. during four successive generations; one plant line was continuously

treated with pesticides and molluscicides, whereas the other was not treated and consequently more severely affected by herbivory. Plants grown under a reduced "herbivore load" (Ramos & Schiestl, 2020) expressed a different odour profile, with a significantly higher emission (up to 33.2%) of five out of its thirteen aromatic volatile compounds, designed for pollinator attraction. Ramos and Schiestl (2020) concluded that the "absence of herbivores relaxes the trade-offs between reproduction and defence and allows for rapid evolutionary change of the floral fragrance, likely due to pollinator-mediated selection". Adaptation through selection, "orienting" the odour profile towards the pollinator and away from the herbivore, can apparently occur very fast. Conversely, variable odour profiles of different specimens within a species can be interpreted as a pool of answers to an ever-changing environment with regard to pollinators and predators in particular.

Similarly, a combination of olfactory and visual signals of death and decay, such as a purplish inflorescence enveloped with a nauseating smell and buzzing insects, is likely to repel mammalian herbivores. Dimethyl oligosulphide odours may not only attract copro-necrophagous insects, but are also likely to repel mammalian herbivores. Lev-Yadun et al. (2009) and Lev-Yadun (2021) proposed that carrion and dung odours of various flowers belonging to different taxa, which traditionally have been considered an adaptation for attracting flies and beetles for pollination (Faegri & van der Pijl, 1979; Stensmyr et al., 2002; Jürgens & Shuttleworth, 2016), also have another, overlooked anti-herbivore defensive function. They suggested that such odours may deter mammalian herbivores, especially during the critical period of flowering. This was based on the fact that carrion odour is a good predictor of the proximity of carnivores or of diseased corpses. Similarly, dung odour predicts faeces-contaminated habitats that may present high risks of parasitism and pathogens. The hypothesis that such plant odours may also deter mammalian herbivores (Lev-Yadun et al., 2009), was experimentally supported. Productive grassy plots were avoided by cattle, if the plots were contaminated from time to time by carrion (Lev-Yadun & Gutman, 2013). A similar refraining from faeces-contaminated grass is well known (Michel, 1955; Cooper et al., 2000; Fankhauser et al., 2008). Subsequently, it was proposed that there are good indications for the potential role of faeces and carrion odour mimicry as a defence against herbivory and that these odours are not exclusively employed for the attraction of pollinators (Lev-Yadun et al., 2009; Lev-Yadun, 2017, 2021). Although speculative, the evolutionary success of dimethyl oligosulphides in *Amorphophallus*, which "occur widely in all four subgenera" (Kite & Hetterscheid, 2017) could have been shaped by their functional versatility, acting as both repellent and attractor which in varied proportions can give different signals.

Last but not least, the variation of scent composition during anthesis needs to be assessed, especially in relation to the female and the male flowering phase of the inflorescence. A significant step into this direction has been undertaken by Kang et al. (2023), who detected and identified 422 volatile compounds emitted by an inflorescence of *A. titanum*. The authors of the study found that the volatile profile of *A. titanum* changes during anthesis, with the sulphur containing compounds and aldehydes dominant in the female flowering phase, and the alcohols and hydrocarbons dominant in the male flowering phase (Kang et al., 2023). Similarly, Liu et al. (2023) found that sulphur containing compounds were most abundantly released in the first phase of flowering of *A. titanum*, whereas alcohols and aldehydes were the major emitted compounds in the subsequent phases of anthesis.

In conclusion, the temporal pattern of scent emission of individual inflorescences during anthesis should be studied on a wider scale. Firstly, it is essential to cover the whole period of scent emission, particularly in regard to the female and the male flowering phase. Secondly, it is important to investigate the intraspecific polymorphism. Lastly, it is important to investigate the reproducibility, in order to ascertain if clonally propagated plants release the same or different compounds under different growing or climatic conditions. Moreover, *Amorphophallus* species with distinct features of dung or carrion mimicry could be selected and observed in different habitats, countries or even continents. Assuming that some of the olfactory cues act as universal attractants or repellents, it could be investigated if the same pollinator type is attracted, and if pollination is successful. This could provide an indication of the universal specificity of the emitted scent compounds. Response to scent compounds could be equally tested in other animal groups, particularly mammals, both herbivorous and carnivorous. Herbivores are expected to avoid the plants, while carnivores are expected to be attracted. Lastly, another aspect concerns the putative correlation between scent types and floral colours as floral colours constitute the visual aspect of deception.

Colour polymorphism

Although scent compounds play the key role in pollinator attraction (Jürgens et al., 2013, Publ. 5), mimicry of decomposing organic material is visually supplemented by spathe pigmentation (Chen et al., 2015), which may be “flesh-coloured … resembling carrion” (Mayo et al., 1997), or blood-like (“tinta sanguigna”) (Beccari, 1889b). Kite and Hetterscheid (1997, 2017) and Punekar and Kumaran (2010) recognised two broad evolutionary trends within the genus *Amorphophallus*, associated with two general colour and scent types, i.e., carrion- or dung-smelling

species, commonly with dark brownish or brownish-purple spathes, and “gaseous-smelling” species with pale-coloured inflorescences. However, strictly green or strictly dark-coloured inflorescences are more an exception than a rule and species bearing dark inflorescences and emitting carrion or dung scents often display pale green elements such as a green kettle or a spathe that is dark-coloured on one side but green-coloured on the other side (Fig. 9 A-D). Moreover, despite differences in scent composition, the major scent compounds underlying both odour trends are dimethyl oligosulphides (Kite & Hetterscheid, 1997, 2017). Lastly, considering that dimethyl oligosulphides are characteristic of the decomposition of various organic matters, such as vegetables, carnivore dung, cadavers and even cancerous wounds (Ollerton & Raguso, 2006; Shirasu et al., 2010; Jürgens et al., 2013), both trends appear to be a “variation” around the same theme (Schiestl & Dötterl, 2012).

Figure 9. A-D: Contrasting pale green and dark red elements in several carrion-and dung-mimicking species. A: Inflorescence of *A. henryi*, a dung mimic. B: Inflorescence of *A. laoticus* emitting a smell reminiscent of human faeces. C: Inflorescence of *A. declinatus*, a carrion mimic smelling like rotting meat. D: Inflorescence of *A. rostratus* Hett., another carrion mimic. Scale bars = 10 cm. Photographs: Cyrille Claudel.

Moreover, some *Amorphophallus* species are known to display floral colour polymorphism to a certain extent. One of the most prominent carrion-mimicking species, *A. paeoniifolius*, includes individuals that are dark-coloured and individuals that are basically pale greenish (Fig. 10 A & B). Similarly, the appendix colouration of *A. paeoniifolius* includes shades of grey-yellow, grey-orange, and grey-purple and -brown (Handayani et al., 2020). Likewise, *A. prainii*, a "gaseous" smelling, pale-coloured species (Punekar & Kumaran, 2010; Kite & Hetterscheid, 2017), includes individuals that are whitish, greenish or flesh-coloured (Fig. 10 C, D & E). An even more impressive variation has been documented in *A. henryi*, a dung mimic from Taiwan (Jung, 2006). Populations of *A. henryi* from four selected sampling areas in southwestern Taiwan were investigated; amongst other characteristics, colour variation of the spathe and the appendix was documented (Jung, 2006). Appendix colour ranged from sulphuric yellow to light beige and from reddish-brown to purplish-brown, while colour variation of the spathe, base and limb ranged from pure green to purplish-brown with intermediate shades (Jung, 2006). Moreover, colour polymorphism is not restricted to the spathe. The most prominent carrion species is *A. titanum* (Barthlott et al., 2009; Jürgens & Shuttleworth, 2016; Raman et al., 2017) which displays a spathe that is dark purplish-coloured inside and bright green outside. Spathe colouration is fairly constant in this species, with only slight variation in some individuals (Gandawijaja et al., 1983). However, the appendix shows considerable colour polymorphism, ranging from green (Giordano, 1999) to sulphuric yellow (Fig. 6 A), purplish (Giordano, 1999; personal observation), and dirty greyish (Raman et al., 2017).

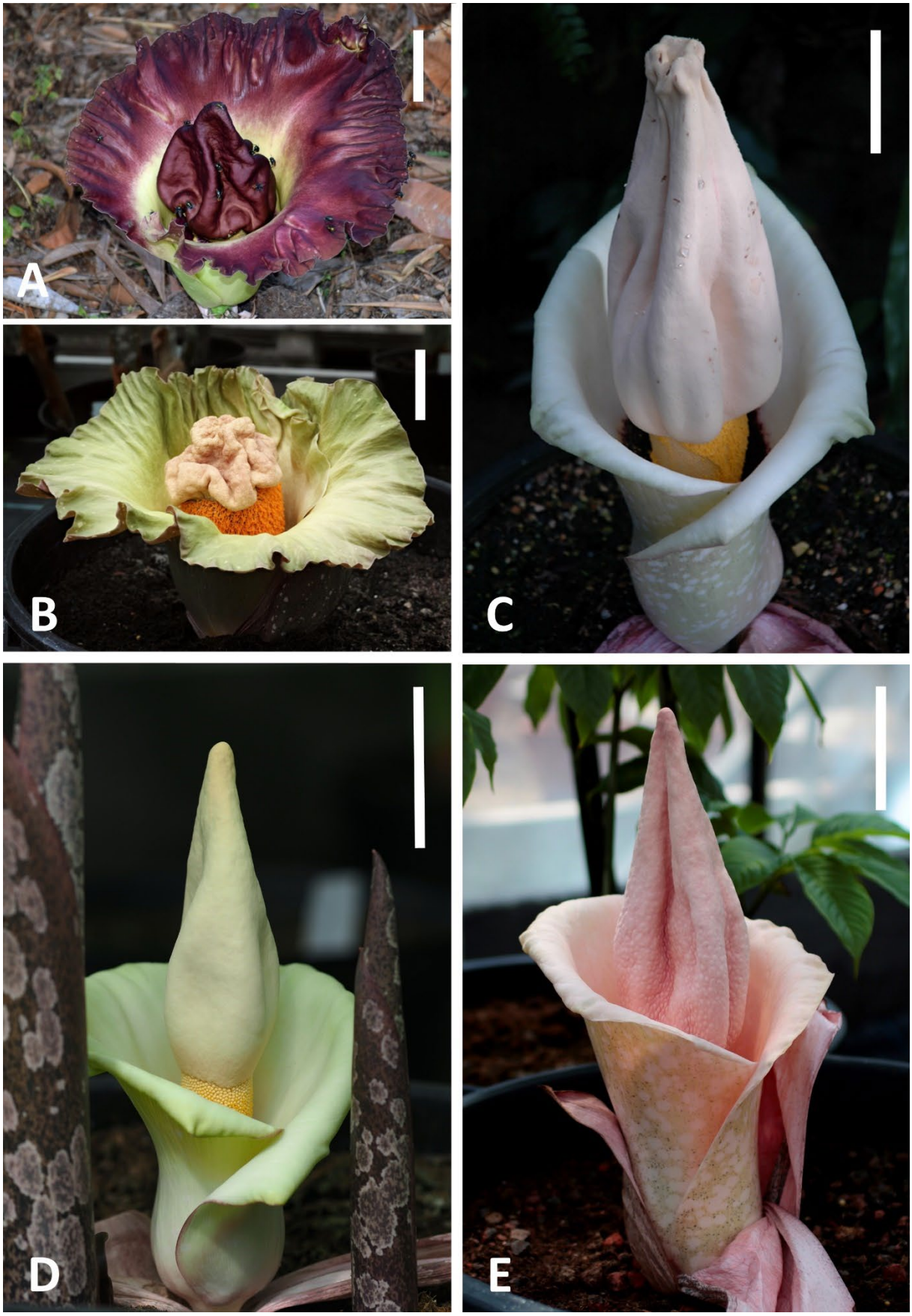

Figure 10. A-D: Colour polymorphism in one species of the dark carrion type associated with carrion or dung odours and one species of the pale coloured type associated with nauseating odours. A & B: Colour polymorphism in inflorescences of *A. paeoniifolius*, a carrion mimicking species. C, D & E: colour polymorphism in three *A. prainii* individuals ranging from whitish, pale greenish to flesh-coloured specimens. Scale bars: A = 5 cm. Scale bars B, C & D = 10 cm. Photographs: Cyrille Claudel.

Versatility and continuity of spathe colouration is also indicated by artificial *Amorphophallus* hybrids. Figure 11 shows two African species, *A*. *lewallei* (Fig. 11 A) and *A*. *mossambicensis* (Fig. 10 B). The former smells like "rotting vegetables" (Kite & Hetterscheid, 2017) and bears a lettuce green spathe (Ittenbach, 2003), whereas the latter represents a typical dark-coloured carrion species with a matching floral odour (Kite & Hetterscheid, 2017). These two plants were cross-pollinated and the hybrid offspring inherited parental traits in various combinations and rearrangements (Fig. 11 C-F). Spathe colour ranged from dark reddish-brown (Fig. 11 C) to green (Fig. 11 D) and various intermediate forms (Fig. 11 E & F). Interestingly, the offspring bearing a pure green spathe also had the darkest appendix (Fig. 11 D). Similar to the observations of Jung (2006), these hybrids further indicate that inflorescence colouration is a continuous character state. Moreover, it should be noted that all hybrids were fertile (personal observation, unpublished data).

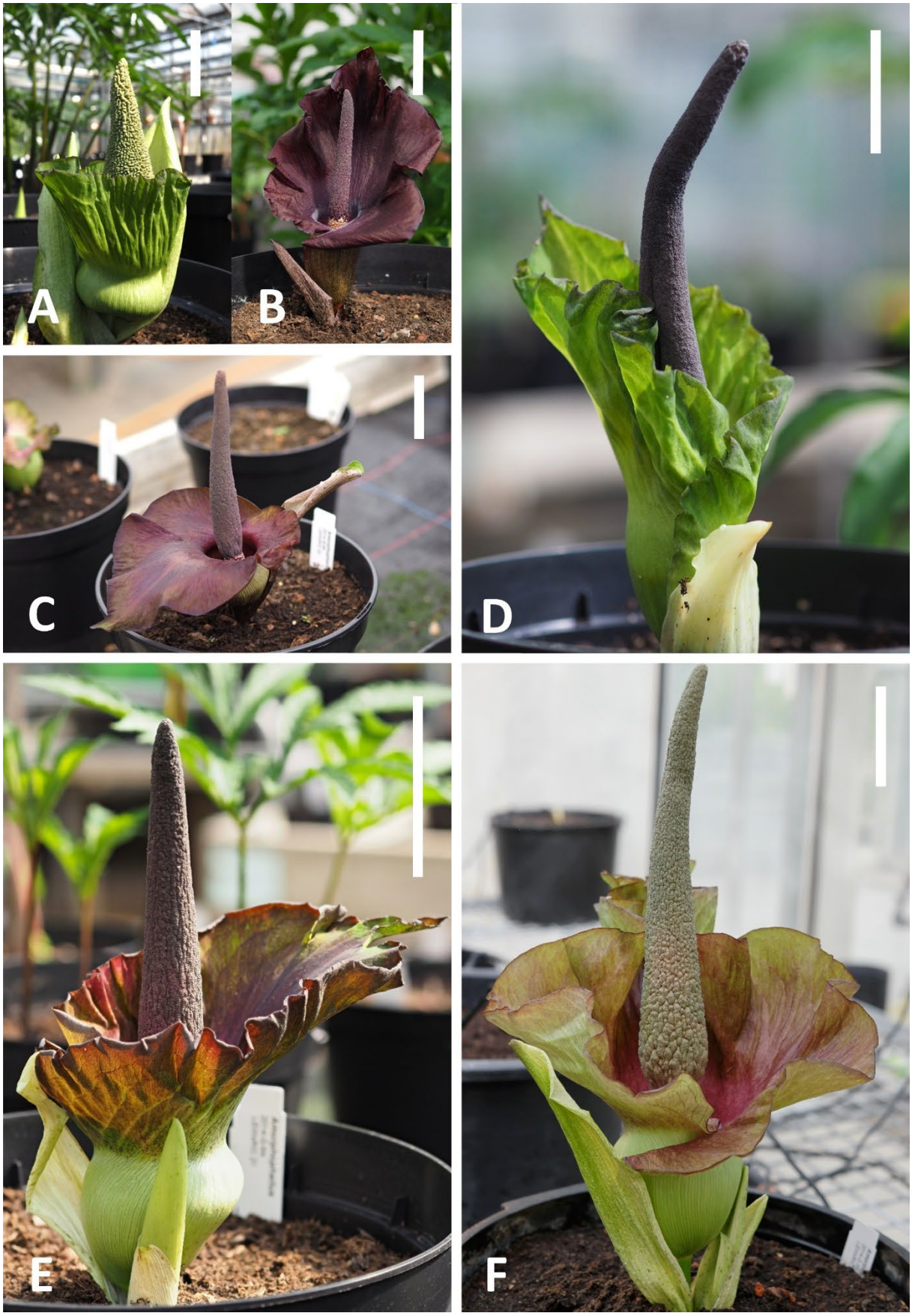

Figure 11. A-F: Colour polymorphism in *Amorphophallus* hybrids. A: *A. lewallei*, a green-coloured species (pollen acceptor). B: *A. mossambicensis* a dark-coloured carrion mimic (pollen donor). C, D, E & F: F1 hybrid plants displaying various intermediate colour combinations. Scale bars = 5 cm. Photographs: Cyrille Claudel.

The question is, how does colour polymorphism fit into the "variation around a theme"? (Schiestl & Dötterl, 2012). The post-mortem hypostasis describes how the hemoglobin sinks within a corpse in the hours following death, leading to livor mortis. The lower part of the corpse shows a purplish discolouration (Goff, 2009), meanwhile the upper part of the corpse becomes accordingly lighter in colour. Subsequently, the corpse turns greenish as hydrogen sulfide and hemoglobin form the greenish sulfhemoglobin (Goff, 2009). Chen et al. (2015) investigated the colouration of inflorescences of *A. konjac*, the red and green pigments in particular. Chen et al. (2015) suggested that the inflorescence of *A. konjac* "mimics different decay phases". Moreover, they demonstrated that the combination of visual and olfactory signals attracted significantly more pollinators than each signal alone.

Like with odours, colour polymorphism possibly represents different phases of cadaveric decomposition. White or whitish, pale greenish or green skin colour, and red, purplish, maroon and their various shades and nuances, all fit into this imagery. Initial stages of decomposition might be represented by sweetly scented species carrying whitish or slightly greenish spathes. The following stages of decomposition might be represented by species carrying more intense greenish or flesh-coloured spathes and emitting gaseous odours. Both stages might include intermediate forms, emitting sweet as well as nauseating scent compounds and carrying spathes with whitish, greenish or flesh-coloured elements. Finally, more advanced stages of decomposition or decay might be gradually represented by what is perceived as the typical carrion-mimicking species, predominantly carrying reddish, brownish, purplish elements, such as *A. konjac* and *A. paeoniifolius*. Similarly, corpses that have died of injuries or have been partly eaten by scavengers might be mimicked by these colour tones, as dark maroon corresponds to the colour of dried blood.

The colour and odour spectrum of *Amorphophallus* species that emit primarily dimethyl oligosulphides seem to be related to different phases of decomposition or different decomposing organic matters. On the one hand, the visual and olfactory clues appear to be very specific in that they indicate different cadaveric phases or substrates; on the other hand, they appear to be very generalised insofar as they all signal one and the same phenomenon, notably the decomposition of organic matter. Although assumptive, it seems as if the two evolutionary trends proposed by Kite and Hetterscheid (1997, 2017) and Punekar and Kumaran (2010) might not give the whole picture. Both trends include exceptions on several levels and instead of a dualistic perception (dark, rotting *versus* pale nauseating) a continuous perception of the phenomenon appears to be more plausible (*from* pale nauseating *to* dark, rotting). Floral characters,

including scent compounds, that are related to oviposition-site deception might display a wider range of polymorphism than other plant taxa as they reflect the variation of their natural counterparts, i.e. decomposing organic material. From a functional perspective, it might be irrelevant if a spathe is green, flesh-coloured, reddish-purplish or all of it, as long as it supports the attraction of insects relying on decomposing organic matter during their life cycle. Therefore, floral polymorphism within a certain functional range can be considered to be a "variation around a theme" (Schiestl & Dötterl, 2012).

Thermogenesis

Methodological considerations

The occurrence of thermogenesis is usually indicated by a temperature raise of the thermogenic floral organ. Therefore, many investigations rely on temperature measurements (Tang, 1987a; Meeuse & Raskin, 1988; Skubatz et al., 1990; Albre et al., 2003; Angioy et al., 2004; Ivancic et al., 2004, 2005, 2008; Chouteau et al., 2007, 2009; Barthlott et al., 2009; Korotkova & Barthlott, 2009; Maia et al., 2013; Wang & Zhang, 2015; Prieto & Cascante-Marín, 2017; Marotz-Clausen et al., 2018; Hoe et al., 2020). However, temperature elevation only reflects the heat excess and not the total heat production, as heat loss through evaporation and/or convection/radiation is not considered (Gibernau et al., 2005; Seymour, 2010). Consequently, respirometry, the measurement of oxygen consumption and/or carbon dioxide (CO_2) production, has been emphasised for the investigation of thermogenesis (Seymour, 2010). However, temperature measurements have been shown to correlate with respiration rates in several studies (Seymour et al., 2003a, 2004) and have been further used in subsequent investigations (Prieto & Cascante-Marín, 2017; Marotz-Clausen et al., 2018; Skubatz et al., 2019; Hoe et al., 2020). In addition, respirometry also has some shortcomings. Firstly, recording respirometry in giant species, such as *A. decus-silvae* Backer & Alderw., *A gigas,* and *A. titanum* represents a technical challenge. Secondly, respirometry does not resolve the spatial distribution of temperature increase, which might be relevant in the context of the plant-pollinator interaction. Last but not least, elevated respiration rates during anthesis can also be caused by the biosynthesis and the release of scent compounds (Terry et al., 2016).

As for the evaporative heat loss during anthesis, the causes and its significance are apparently not well characterised yet. A low temperature increase despite a significant oxygen consumption has been recorded in *A. konjac* and the authors hypothesised that the large surface area of the *A. konjac* appendix was responsible for significant heat loss through high evaporation rates, especially as the second author observed the formation of liquid water running down the

appendix (Lamprecht & Seymour, 2010). However, this seems debatable. In the same study the authors report a temperature excess of 12.6°C in the appendix of *A*. *titanum*, which is the species with the largest appendix in the genus (Hetterscheid & Ittenbach, 1996; Gibson, 2018; POWO, 2024a). This discrepancy has been explained, based on theoretical assumptions, by a much higher heat generation in *A*. *titanum* (Lamprecht & Seymour, 2010). However, it has not actually been tested. Then, the plant of *A*. *konjac* was placed in a greenhouse, and the appendix was covered by a respiratory hood, which can be expected to limit the evaporation and consequently evaporative heat loss. Lastly, odoriferous droplet formation on the appendix during anthesis has been reported in several *Amorphophallus* species (Shirasu et al., 2010; Kakishima et al., 2011; personal observation). It is therefore likely that the liquid found on the appendix of *A*. *konjac* was a secreted odoriferous fluid compound or at least not exclusively water.

Moreover, heat loss through evaporative cooling (Gibernau et al., 2005; Seymour, 2010) has only been considered as a passive phenomenon in relation to the shape and surface area of the thermogenic floral elements and their thermal conductance etc., in other word, the physical properties of the thermogenic organ (Gibernau et al., 2005; Seymour, 2010). However, inflorescences are biological systems that release the scent compounds at a precisely determined moment. Moreover, they can protect themselves from unintended evaporation by means of a cuticle and/or closed stomata/pores. Therefore, heat loss through evaporation is more likely to be linked to scent release, which however, is temporarily determined. The timeframe for stigma receptivity – and therefore pollinator attraction – is short in *Amorphophallus*, often in the range of a few hours only (Hesse, 2006; Chai & Wong, 2019; Claudel, 2020). Consequently, releasing the greatest possible quantity of scent compounds in a short time is likely to be the most important parameter when it comes to evaporative cooling. Vapour pressure and quantity of the emitted scent compound(s) are likely to have a more significant impact on evaporative cooling than passive water evaporation. However, the impact of the scent compounds has never been investigated. Considering that the temperature of the thermogenic floral elements is generally identical with the ambient (room) temperature before anthesis (Claudel et al., 2023; supporting information Data S1), passive heat loss through water evaporation does not appear to be significant. If evaporative cooling was significant at this stage, a noticeable difference between the temperature of the thermogenic floral elements and the ambient temperature should be observed. Instead, evaporative heat loss is generally not detectable in the temperature measurements of the appendix or the male flower zone before anthesis (Claudel et al., 2023; supporting information Data S1). Heat loss in the male flower zone becomes noticeable only after the pores or slits of the anthers have opened to release the pollen; now that the slits or pores are open, passive evaporative cooling may become significant (Claudel et al., 2023; supporting

information Data S1). However, pollen release also implies the ending of anthesis and thermogenesis. Therefore, evaporative cooling of the male flower zone takes place only at the end of anthesis. The situation is different in regard to the appendix. Here, heat loss occurs once scent emission starts, which is consequential, as the emission of scent compounds presupposes a release (mechanism). Therefore, evaporative cooling of the appendix is more likely to be caused by the emitted scent compounds during anthesis.

Amorphophallus species have been shown to emit scent compounds belonging to chemically different scent classes (Kite & Hetterscheid, 1997, 2017; Publ. 5). There is also evidence that the quantity, ratio and volatility of the released scent compounds may differ significantly between species (Kite & Hetterscheid, 1997, 2017) and even between individuals of a given species (Publ. 5). The last point is particularly important as it has been shown that some *Amorphophallus* species display considerable odour polymorphism (Publ. 5). Consequently, if the ratio or the quantity of emitted scent compounds differ significantly between two individuals of a given species, then the impact on evaporative cooling will differ accordingly, due to different vapour pressures. As discussed below, a compound with a high vapour pressure is more likely to contribute to evaporative cooling than a compound with a low vapour pressure. In conclusion, the surface area of the appendix does not appear to be the only critical factor with regard to evaporative cooling.

Moreover, respirometry might in itself have a significant shortcoming. As mentioned above, the time frame for scent emission is short for most *Amorphophallus* species, usually in the range of 12 hours only. It has been shown in the thermogenic Aroideae *Sauromatum venosum*, that the appendix undergoes important morphological modifications and biosynthetic activities shortly before and during anthesis (Skubatz et al., 1993, 1995, 1996; Skubatz & Kunkel, 1999). The endoplasmic reticulum of the appendix tissue fuses with the plasma membrane, forming excretion channels; and newly synthetised scent compounds are transported through these excretory pathways (Skubatz et al., 1993, 1995, 1996; Skubatz & Kunkel, 1999). It has not been investigated to what extent this metabolic burst contributes to the respiration rates in thermogenic aroids. However, it has been investigated in *Macrozamia* Miq. cycad cones (Terry et al., 2016). These authors studied the relationship between temperature elevation, increased respiration and the formation and emission of volatiles, concluding that the energetically expensive synthesis and release of monoterpenes is at the origin of the respiratory metabolic burst (Terry et al., 2016). Consequently, considering the important modifications and biosynthetic activities preceding and during anthesis in *S. venosum* (Skubatz et al., 1993, 1995, 1996; Skubatz & Kunkel, 1999) and the strong scent emissions within a short time in

Amorphophallus (Hesse, 2006; Kite & Hetterscheid, 2017) it is reasonable to assume that the respiration rates during anthesis in *Amorphophallus* might be raised by a comparable metabolic burst, leading to the discrepancy between respiration rates and temperature elevation, discussed by Lamprecht and Seymour (2010). Therefore, more investigations are needed in order to validate the correlation between respirometry and thermogenesis, at least in *Amorphophallus*.

For the purpose of the study from Claudel et al. (2023)/Publ. 6, it would have been useful to quantify the thermogenic tissue (e.g., volume and/or weight). However, firstly, the complexity of the topic was not foreseen. Secondly, access to the inflorescences of many species during anthesis constituted a unique opportunity. Moreover, two temperature patterns could be recorded within one accession from *A. schmidtiae*, challenging the assumption that the temperature patterns are strongly influenced by the morphology. Clonally propagated tubers of *A. schmidtiae* HBG 2013-G-2 switched from one pattern to the other in consecutive years. The first temperature pattern (pattern 1) is unique in the genus in that it lasts up to three weeks, whereas the second pattern (pattern 2) is similar to the temperature patterns of other species of this clade (Claudel et al., 2023; supporting information Data S1 & Data S2 time-lapse movies). Pattern switches occurred exclusively in the accession *A. schmidtiae* HBG 2013-G-2 but not in a second accession, *A. schmidtiae* HBG 2013-G-32. However, the development of *A. schmidtiae* HBG 2013-G-32 could only be followed for a comparatively short period as it was obtained at a late stage of the experiments. It must be emphasised that great care has been taken to follow the development of the tubers, ascertaining that one and the same tuber can occasionally switch from one to another pattern.

The two pattern types of *A. schmidtiae* HBG 2013-G-2 could be the result of a genetic mosaic, leading to one or the other pattern type during tuber formation. However, this has not been tested, and further investigations into this phenomenon are required. Alternatively, this could represent a case of "sex switching", implying functionally male or female plants, similar to *Arisaema* Mart. (Vogel & Martens, 2000; Richardson & Clay, 2001; Srivastava & Banerji, 2012). That said, crossing experiments have not been performed and unlike in *Arisaema* (Srivastava & Banerji, 2012), tuber weight was not indicative of the temperature pattern. The long lasting pattern (pattern 1) was expressed in tubers ranging from 340 g to 3,230 g. Moreover, despite the wide weight range of the tubers, the length of the spadix elements remained nearly constant, differing in the magnitude of ± 1 cm at most.

In any case, tubers of *A. schmidtiae* HBG 2013-G-2 can express two significantly different temperature patterns, despite being morphologically identical. This clearly demonstrates that temperature patterns can be independent from floral morphology.

Last but not least it is noteworthy to point out that in order to sustain such a long thermogenic period, thermogenesis in *A. schmidtiae* might be fuelled by transport of materials stored in the tuber, similar to *Symplocarpus foetidus* (Kozen, 2013). Therefore, it would be necessary to identify the substrate used for thermogenesis for each species; moreover to determine if thermogenesis is fuelled by the tuber, or by substrates stored in the inflorescence, or by both. Last but not least, more knowledge about the regulatory mechanism(s) is required.

Thermogenesis in the phylogenetic frame

Species with a strong temperature increase are scattered across the phylogeny (Publ. 6). The strongest heaters of the genus are species from the subgenus *Scutandrium* Hett. & Claudel, such as *A. albispathus*, *A. longituberosus* and *A. tenuispadix* (16.6°C, 21.7°C and 18.1°C above ambient temperature respectively) (Publ. 6). They are followed by *A. lewallei* (16.3°C above ambient temperature) belonging to the subgenus *Afrophallus* Hett. & Claudel, and *A. symonianus* and *A. yunannensis* (15.1°C and 13.9°C above ambient temperature, respectively) belonging to the subgenus *Metandrium* Stapf (Publ. 6). Except for *A. lewallei*, these species form the two main clusters of strongly thermogenic species, of which one clade is found in the subgenus *Scutandrium* and the other in the subgenus *Metandrium* (Publ. 6). These species are comparatively small (Hetterscheid, 2012) and volatise benzenoid compounds or aromatic hydrocarbons (Kite & Hetterscheid, 1997, 2017; Publ. 5). However, the species in the subgenus *Scutandrium* mainly emit 4-methoxyphenethyl alcohol whereas the species in the subgenus *Metandrium* mainly emit 1-phenylethanol and its derivatives (Kite & Hetterscheid, 1997, 2017).

But not all species with a strong temperature increase release benzenoid compounds. The African species *A. lewallei* displays one of the strongest temperature increases (16.3°C above room temperature), but its major scent compound (86%) is the highly volatile dimethyl disulphide (Kite & Hetterscheid, 2017). Similarly, *A. paeoniifolius* and *A. prainii* belonging to the subgenus *Amorphophallus*, *A. albus* and *A. schmidtiae* belonging to the subgenus *Scutandrium* and *A. bulbifer* belonging to the subgenus *Metandrium* show a significant temperature elevation, but release dimethyl oligosulphides as the main scent compounds (Kite & Hetterscheid, 1997, 2017; Publ. 5). It is interesting to note that two strongly thermogenic species, *A. cicatricifer* Hett. and *A. titanum* (12.8°C and 12.6°C above room temperature, respectively), have been shown to mainly release either dimethyl oligosulphides or benzenoid compounds (Lamprecht

& Seymour, 2010; Kite & Hetterscheid, 1997, 2017; Publ. 5). Beyond that, there is only one species that displays a strong temperature elevation (Publ. 6) but does not release dimethyl oligosulphides or benzenoid compounds as its major scent compounds, namely *A. mossamibicensis* belonging to the subgenus *Afrophallus*, the only strongly thermogenic species (13.6°C above room temperature) that releases aliphatic esters (Kite & Hetterscheid, 1997, 2017). Conversely, many species that release dimethyl oligosulphides do not show a temperature elevation, or only a slight one. For example, the species investigated from the *Pygmaeus* clade, belonging to the subgenus *Metandrium*, are weakly thermogenic or not thermogenic at all (Publ. 6). Similarly, *A. commutatus* (Schott) Engl. and *A. variabilis* from subgenus *Amorphophallus* release dimethyl oligosulphides (Kite & Hetterscheid, 2017) and are weakly thermogenic (Publ. 6). That said, at least all the species investigated that release benzenoid scent compounds are thermogenic or strongly thermogenic in terms of temperature elevation and will be discussed more closely below.

Two species from the *Paeoniifolius* clade (Publ. 1), *A. paeoniifolius* and *A. prainii*, both of which are large plants with geoflorous inflorescences, have strong thermogenic activity in the male flower zone and appendix (Publ. 6). In addition, both species display a long preheating sequence, lasting up to five days in *A. paeoniifolius* (Publ. 6). However, despite of the similarities in thermogenic patterns, *A. paeoniifolius* matches the carrion type with dark inflorescences and rotting meat odours, whereas *A. prainii* has pale-coloured inflorescences accompanied by "gaseous" odours sensu Kite and Hetterscheid (2017). If this represents a switch to different pollinator relationships (Kite & Hetterscheid, 2017), then the temperature pattern itself does not appear to be significant as it is similar between the two species. It is noteworthy to add that the investigation of two *Typhonium* species, another oviposition-site mimic from the Aroideae, yielded similar results. The authors found that divergence in floral scent and morphology is associated with pollinator shifts; however, thermogenic traits are not associated with pollinator shifts (Sayers et al., 2021).

Carrion mimicry

Temperature elevation and scent emission have also been associated with carrion mimicry in *Amorphophallus* (Barthlott et al., 2009) and as part of a highly mimetic tactile system in other aroids (Angioy et al., 2004; Rands, 2021). The insect is deceived into behaving as if it had discovered a fresh and still warm substrate, such as carrion or dung, for feeding or breeding. Indeed, some strongly thermogenic species, such as *A. paeoniifolius* and *A. mossambicensis*, represent typical carrion- or dung mimics with dark coloured inflorescences that emit carrion- or dung-like scents (Kite & Hetterscheid, 2017). The male zone is heated overnight (Claudel et

al., 2023; supporting information Data S1), which, in the case of *A. paeoniifolius* at least, is known to attract large copro-necrophagous beetles amongst others (Publ. 4). However, several species that apparently have distinct visual and olfactory carrion or dung attributes, generate only weak temperature increases. These include *A. declinatus, A. gigas*, *A. henryi*, *A. maxwelii* Hett. and *A. konjac*, all of which display low or no temperature elevations (Claudel et al., 2023; supporting information Data S1). Though it is possible that the low temperature increases are due to heat loss (Gibernau et al., 2005; Lamprecht & Seymour, 2010; Seymour, 2010), it appears to be unlikely, considering some discrepancies. For example, both *A. gigas* and *A. henryi* show no temperature increase but *A. gigas* has a large surface area whereas *A. henryi* has a small and slender appendix (Hetterscheid & Ittenbach, 1996). In contrast, the giant of the genus, *A. titanum*, exceeds ambient temperatures by 10°C to 12.6°C (Barthlott et al., 2009; Korotkova & Barthlott, 2009; Lamprecht & Seymour, 2010), despite having the largest appendix with the largest surface area of any species (Hetterscheid & Ittenbach, 1996). In any case, the fact that temperature elevation is negligibly low or completely absent in several dung- or carrion mimicking species shows that is not a necessary component of dung or carrion mimicry.

Scent volatilisation

As aforementioned, temperature elevation is apparently not specifically associated with a particular scent category *sensu* Kite and Hetterscheid (2017). However, that does not exclude the possibility that the temperature elevations are correlated with the vapour pressure of the scent compounds since a scent compound with low vapour pressure is more likely to benefit from a higher temperature elevation. The two main clusters of strongly thermogenic species are found in subgenus *Scutandrium* and subgenus *Metandrium*. These clusters comprise the species that release sweet, fruity or almond odours based on benzenoid compounds or aromatic hydrocarbons, more precisely 4-methoxyphenethyl alcohol or 1-phenylethanol and its derivatives (Kite & Hetterscheid, 1997, 2017). Therefore, the volatility of benzenoid compounds in comparison to the other scent categories *sensu* Kite and Hetterscheid (2017) is briefly explored. Table 5 lists the vapour pressure of every identified benzenoid compound as well as one representative compound from the six other major scent classes *sensu* Kite and Hetterscheid (2017).

Table 5. Vapour pressure of one representative scent compound per scent category *sensu* Kite and Hetterscheid (2017) and all the identified benzenoid compounds (in hectopascal, in decreasing order). Vapour pressure values measured either at 20°C or 25°C room temperature were retrieved from internet resources (PubChem, 2023; ChemSpider, 2023; Merck, 2023).

Scent category	**Selected compound**	**Vapour pressure in hectopascal**
nitrogen-containing compounds	trimethylamine	1887 at 20°C
aliphatic esters	ethyl acetate	121.32 at 25°C
sulphur compounds	dimethyl disulphide	28 at 20°C
benzenoid compounds	phenylethene	7.14 at 20°C
aliphatic alcohols and ketones	isoamyl alcohol	3 at 20°C
aliphatic acids	isocaproic acid	0.593 at 25°C
benzenoid compounds	1-phenylethanone	0.4 at 20°C
benzenoid compounds	1-phenylethanol	0.1 at 20°C
terpenoids and alkanes	aromadendrene	0.031 at 25°C
benzenoid compounds	1-phenylethyl acetate	0.055 at 20°C
benzenoid compounds	methylcinnamate	0.0149 at 25°C
benzenoid compounds	4-methoxyphenethyl alcohol	0.009 at 25°C

4-Methoxyphenethyl alcohol, here the benzenoid compound with the lowest vapour pressure (0.009 hPa at 25°C), is emitted by the "hottest" species, *A. albispathus*, *A. longituberosus* and *A. tenuispadix*. The only other scent compound with a comparably low vapour pressure is methylcinnamate (0.0149 hPa at 25°C). It is emitted as a major compound by *A. symonianus*, another strongly thermogenic species characterised by 1-phenylethanol and its derivatives (Kite & Hetterscheid, 2017). The next benzenoid compound, 1-phenylethyl acetate, also has a low vapour pressure (0.055 hPa at 20°C). It is the main compound from at least six species (Kite & Hetterscheid, 2017). Two of these (*A. thaiensis*, *A. yunnanensis*) were investigated and showed significant temperature elevations (Publ. 6). As for 1-phenylethanol, it has a low vapour pressure (0.1 hPa at 20°C) and is the main compound emitted by *A. yuloensis* H. Li, another thermogenic species. The last benzenoid compound, phenylethene, has a significantly higher vapour pressure (7.14 hPa at 20°C) than the other benzenoid compounds. However, it is emitted

in limited quantities and is always accompanied by larger quantities of benzenoids with a lower vapour pressure (Kite & Hetterscheid, 2017).

Other non-benzenoid compounds with low vapour pressure include aromadendrene (0.031 at 25°C), which is emitted by *A. impressus*. In contrast to species that release benzenoids with low vapour pressure, *A. impressus* displays only a weak temperature elevation. At least in this case, there seems to be no correlation between low vapour pressure and temperature elevation. Another compound that also has a vapour pressure below 0.1 is isocaproic acid (0.593 at 25°C) from the aliphatic acids category (Kite & Hetterscheid, 2017). Isocaproic acid and α-ketoisocaproic acid are the main compounds emitted by *A. atroviridis* and *A. myosuroides*, respectively. However, both species show either no (*A. atroviridis*) or only a negligible (*A. myosuroides*) temperature elevation of the appendix. Similarly, the species investigated here that emit isoamyl alcohol (3 hPa at 20°C) from the aliphatic alcohols and ketones category (Kite & Hetterscheid, 2017), do not display strong temperature elevation: *A. ankarana* has only a weak temperature elevation in the appendix, whereas *A. henryi* N. E. Br. shows no temperature elevation (Claudel et al., 2023; supporting information Data S1).

Conversely, dimethyl disulphide has a high vapour pressure (28 hPA at 20°C) but as aforementioned, some of the species that release dimethyl oligosulphide as a major scent compound, are amongst the "hottest", displaying high, sometimes even long-lasting, temperatures elevations. Examples of species displaying high temperature elevation accompanied by the emission of dimethyl oligosulphides are, in particular, *A. lewallei*, *A. paeoniifolius*, *A. prainii*, *A. albus*, *A. schmidtiae* and *A. bulbifer*. The two remaining compounds, trimethylamine from the nitrogen-containing compounds category and ethyl acetate from the aliphatic esters category have a significantly higher vapour pressure than all the other compounds (Table 5). Ethyl acetate has a vapour pressure of 121.32 hPA at 25°C. Of all species investigated, only *A. antsingyensis* releases ethyl acetate as a major scent compound while showing only weak temperature elevation. Trimethylamine is the typical compound produced by bacteria during the decomposition of fish (Howgate, 2010a, 2010b). Compared to the other scent compounds, trimethylamine has an extremely high vapour pressure of 1887 hPa at 20°C. Interestingly, two of the species investigated, *A. brachyphyllus* and *A. juliae*, consistently cooled below ambient temperature during anthesis, down to -4.9°C and -1.8°C below ambient respectively (Claudel et al., 2023; supporting information Data S1). These species form a closely related group together with *A. eburneus* Bogner and *A. niahensis* P. C. Boyce & Hett. (Boyce et al., 2010; Claudel et al., 2017). Two of these species, *A. brachyphyllus* and *A. eburneus* are known to release trimethylamine (Kite & Hetterscheid, 1997, 2017) as a major scent compound and *A. juliae* releases a similar odour

(personal observation). Therefore, the cooling effect in *A. brachyphyllus* and *A. juliae* might be caused by the high vapour pressure of trimethylamine. It is noteworthy to point out that the appendix of *A. lambii* displays a temperature decrease during anthesis too, down to 3.5°C below ambient temperature (Claudel et al., 2023; supporting information Data S1). *Amorphophallus lambii* is also reported to have a fishy odour (Kite & Hetterscheid, 2017), which suggests that trimethylamine is also emitted in this species. Closely related to *A. lambii* is *A. hewittii* Alderw. which is also described as having a fishy odour (Kite & Hetterscheid, 2017) or "ammonia-like" (Chai & Wong, 2019). Given that trimethylamine smells fishy at lower concentrations and ammonia-like at higher concentrations (Howgate, 2010a, 2010b), *A. hewittii* is also likely to emit trimethylamine. A strong temperature decrease in the appendix during anthesis can therefore be expected.

In conclusion, the volatilisation of some scent compounds might benefit from increased thermogenesis in some species. However, temperature elevations of the appendix are apparently not generally linked to the volatility of the major scent compounds. Conversely, the emission of scent compounds with high vapour pressure can be expected to decrease the temperature of the appendix during anthesis.

Heat reward

Heat reward for pollinators is the second function most often assigned to thermogenesis, particularly in conjunction with the existence of floral chambers. Heat reward has been proposed to increase the activity of the insects during stigma receptivity, ensuring pollination and preventing its "premature departure" (Moodie, 1976), or heat reward has been proposed to increase the activity of the insect after pollen load, enhancing the insect's departure, particularly after a cooler night (Ivancic et al., 2005). Although both scenarios are plausible, one point remains unresolved. How does the insect know the difference between heat that is meant to make it stay, and heat that is meant to incite departure in search of the next inflorescence? Moreover, since heat is never generated by the female flowers in *Amorphophallus*, the reward is apparently not offered where the pollen needs to be transported to. Therefore, it seems more plausible that heat incites the insect to stay on the inflorescence until pollen release, at least in *Amorphophallus*. Consequently, the signal for leaving would consist in the temperature decrease after anthesis. This could account for the more or less continuous temperature increase of the male flower zone until pollen release in many of the thermogenic *Amorphophallus* species. However, it does not account for the many differences in thermogenic patterns, for instance heating of the male flower zone before anthesis, as in *A. thaiensis* and *A. yunannensis*; or the absence of

thermogenesis in the male flower zone, as in *A. symonianus*; or the long thermogenic episode of the male flower zone in *A. schmidtiae* (pattern 1).

To understand these differences, more knowledge about the pollinating insects and their behaviour is required. However, the knowledge about pollinating insects in *Amorphophallus* is limited (Publ. 4). Members of three Coleoptera families (Dynastidae, Hybosoridae and Scarabaeidae) appear to be the main pollinators (Moretto et al., 2019; Publ. 4). However, the motives of the attracted beetles are apparently different. Beetles using the floral chamber for mating, but not for egg deposition, have been observed in *A. johnsonii*, *A. paeoniifolius*, *A. titanum* and *A. hewittii* (Beath, 1996; Giordano, 1999; Grimm, 2009; Chai & Wong, 2019), whereas mating of beetles has been explicitly excluded in *A. barthlotti* Ittenb. & Lobin and in *A. abyssinicus* (A. Rich.) N. E. Br. (Moretto, 2019). In several species, such as *A. hohenackeri* Engl. & Gehrm., *A. sylvaticus* Kunth, and *A. variabilis*, a food reward has been identified as the bait to retain pollinators until pollen release (van der Pijl, 1937; Sivadasan & Sabu, 1989; Punekar & Kumaran, 2010) whereas no evidence has been found regarding the consumption of floral tissues in *A. hewittii* and *A. julaihii* (Chai & Wong, 2019). Lastly, young larvae have been observed in *A. variabilis* and *A. commutatus* (van der Pijl, 1937; Punekar & Kumaran, 2010), suggesting that mating and egg laying took place in the inflorescences.

The only authors who explicitly refer to floral thermogenesis in *Amorphophallus in situ*, are Teijsmann and Binnendijk (1862) and van der Pijl (1937). Van der Pijl (1937) observed a significant temperature elevation in the inflorescence of *A. muelleri*; however, the behaviour of the visiting and pollinating Nitidulidae left him perplexed as they did not feed on the clear liquid offered by the inflorescence. Moreover, they also visited old and odourless inflorescences in "great numbers" leading the author to wonder "what the real attraction is". In addition, he observed flowering specimens of *A. variabilis* but could not detect a temperature increase (van der Pijl, 1937). In contrast, a short and low temperature elevation (2.6°C) in the appendix of *A. variabilis* could be recorded in the present investigation (Publ. 6). Although small temperature increases can be beneficial to insects (Seymour et al., 2003b; van der Kooi et al., 2019) it is not possible to draw definite conclusions about the impact of such a short and low temperature elevation without specific knowledge about the needs and behaviour of the visiting insects. The heat generated might represent a benefit, but might equally well be "unnecessary" under tropical conditions (Faegri & van der Pijl, 1979).

A heated shelter or place for mating and breeding in a floral chamber represents another form of heat reward. The three closely related African mainland species, *A. impressus*, *A.*

mossambicensis and *A. lewallei*, show an uneven picture in this regard. These species are discussed in more detail as they exemplify some of the challenges encountered in identifying the functionality of thermogenesis. They share an overall similar floral morphology and bear robust inflorescences on a short peduncle with a strongly constricted spathe that forms a floral chamber. The most notable differences are that *A. mossambicensis* represents the carrion type inflorescence (Kite & Hetterscheid, 2017), whereas *A. impressus* and *A. lewallei* are greenish and smell like "rotting vegetables" (Kite & Hetterscheid, 2017).

Thermogenesis in *A. mossambicensis* starts with a strong temperature peak of the appendix in the evening hours (Claudel et al., 2023; supporting information Data S1), assumingly attracting yet unknown nocturnal pollinators. This is followed by less intense but continuous overnight thermogenic activity of the male flowers in the floral chamber until pollen extrusion in the evening hours of day two. Pollen extrusion happens just in time for pollen to be transmitted to another day-one inflorescence, assuming that different specimens follow a similar rhythm. Apparently, in *A. mossambicensis* thermogenesis of the appendix serves scent volatilisation for pollinator attraction, and thermogenesis of the male flowers serves as a heat reward for pollinators staying overnight.

At first view, the temperature pattern in *A. lewallei* is similar (Claudel et al., 2023; supporting information Data S1). However, there are significant differences. The spathe limb starts reflexing during the night preceding anthesis (Fig. 12 A-C). When the appendix reaches its heat peak in the late afternoon of the next day, the upper part of the spathe is completely reflexed and the spadix is freely accessible for flying as well as for crawling insects (Fig. 12 D). The appendix quickly cools down in the evening and the male zone does not provide warmth during the night, a warm shelter is not offered at any time (Fig. 12 E). Furthermore, the appendix cools down below ambient temperature for several hours, dropping to 1.3°C below ambient during the night (Claudel et al., 2023; supporting information Data S1). In parallel to the cooling, an odorous fluid drips from the appendix (personal observation), a phenomenon that has already been documented in several other species, such as *A. gigas* (Kakishima et al., 2011) and *A. titanum* (Shirasu et al., 2010). It has not been investigated if the temperature decrease leads to less efficient scent volatilisation and consequently to the formation of fluid odoriferous compounds or if the release of fluid odoriferous compounds is independent from thermogenic activity. In the following morning, the spathe of *A. lewallei* starts to straighten up and the male flower zone becomes slightly but continuously thermogenic by noon (Fig. 12 F & G; Claudel et al., 2023; supporting information Data S1). The pollen is shed during a strong temperature peak of the male flower zone in the late afternoon, and the spathe is closing again around the spadix (Fig.

12 F- H; personal observation). The spathe's movement continues during the following night so that by the next morning the spathe fully encloses the spadix.

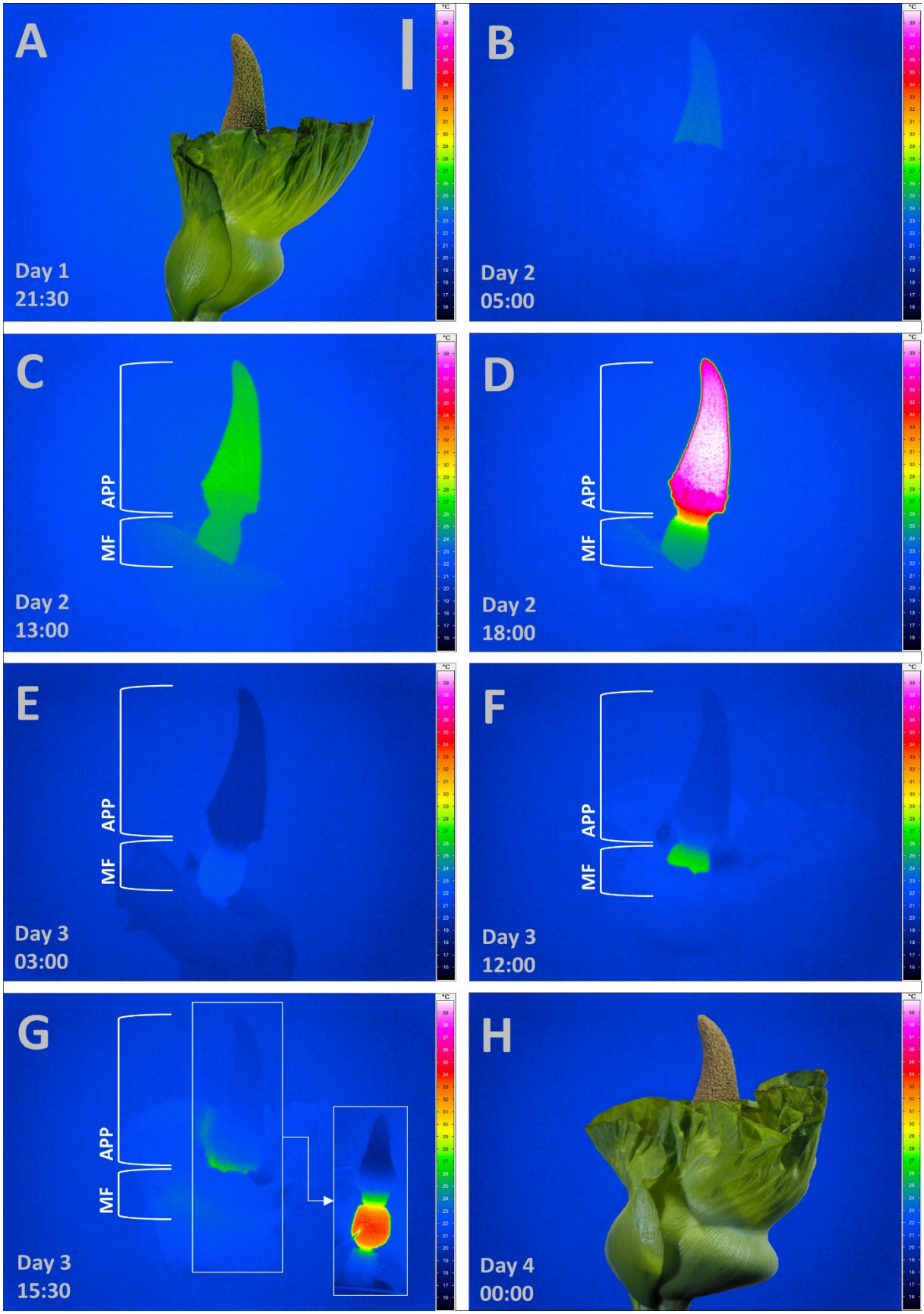

Figure 12. A-H: Biphasic temperature pattern in *A. lewallei*. A-D: Temperature increase of the appendix (APP). E: Thermogenesis of the appendix has ended. F-G: Temperature increase of the male flower zone (MF). A-D: During anthesis the spathe bends downwards, granting putative pollinators access to the flowers. E-H: The spathe flexes back once the male flower zone starts to heat, fully enclosing the spathe after anthesis. Scale bar = 10 cm. Photographs: Cyrille Claudel.

Re-closing of the spathe also occurs in some specimens of *A. paeoniifolius* (personal observation) and *A. titanum* (Giordano, 1999) and is likely to create a specific micro-climate which may be favourable for pollen germination and growth. However, both species have different thermogenic patterns, and the implications for the visiting insects are unknown. The third African species investigated, *A. impressus*, also smells like rotting vegetables (Kite & Hetterscheid, 2017) but again the temperature pattern is different (Claudel et al., 2023; supporting information Data S1). Instead of a pronounced thermogenic peak, the appendix cools down during the night, whereas the male zone heats up slightly during the following day, barely reaching a peak of 2°C above ambient temperature in the evening. There is no evidence of either heat reward or of a heated night shelter. Moreover, the appendix of *A. impressus* also emits odoriferous droplets (personal observation).

In *A. pilosus*, *A. atroviridis* and *A. vogelianus*, belonging to the subgenus *Metandrium*, the temperature elevations of the appendix are either weak or absent. Moreover, the temperature elevation of the male zone differs significantly between the three species. The pattern in *A. vogelianus* is unique insofar as day one of anthesis is characterised by a slight temperature decrease of the male zone, followed by three consecutive thermogenic peaks on days two and three, in the morning and in the late evening (Claudel et al., 2023; supporting information Data S1). A heated shelter seems more plausible in *A. atroviridis* and in *A. pilosus*. Particularly in *A. atroviridis*, the temperature elevation in the male zone is continuous overnight, reaching roughly 5°C above ambient temperature in all three specimens that were analysed (Claudel et al., 2023; supporting information Data S1).

The situation is different in *A. napalensis* belonging to the subgenus *Scutandrium*, a species that occurs at higher elevations in northeast India, Nepal and Bhutan and is one of the few species where detailed observations about pollinators are available (Chaturvedi, 2017). Of the multitude of insects attracted to the inflorescence, only the pollinating beetles stayed overnight (Chaturvedi, 2017), suggesting heat reward in the form of a heated shelter. Closely related species, such as *A. albus*, *A. asterostigmatus* Bogner & Hett., *A. schmidtiae*, *A. curvistylis*, *A. fuscus* and *A. krausei* Engl. share a similar floral morphology (Hetterscheid & Ittenbach, 1996; Hetterscheid, 2012). The appendix more or less equals the spathe in length and the latter is not constricted, forming an easily accessible funnel- or bowl-like structure. The inflorescence is robust and the scent compounds are nauseating, usually based on dimethyl oligosulphides (Kite & Hetterscheid, 1997, 2017), suggesting beetle pollination (Kevan & Baker, 1983; Bernhardt, 2000). Although the temperature patterns of these species are variable, all display significant thermogenesis of the male zone overnight (Claudel et al., 2023; supporting information Data

S1) and all originate from continental Asia, some occurring at higher elevations or in subtropical climates (Hetterscheid & Ittenbach, 1996; Li & Hetterscheid, 2010; Hetterscheid, 2012). Except for the emitted scent compounds, this also applies to the clusters of thermogenic species from subgenus *Scutandrium* and *Metandrium*, which comprise the species that release sweet, fruity or almond odours based on benzenoid compounds or aromatic hydrocarbons, more precisely 4-methoxyphenethyl alcohol or 1-phenylethanol and its derivatives.

Concluding, the main clusters of strongly thermogenic species appear to share a similar floral morphology in terms of overall robustness, i.e., a comparatively short appendix and an easily accessible funnel- or bowl-like spathe etc. (Hetterscheid & Ittenbach, 1996; Li & Hetterscheid, 2010; Hetterscheid, 2012; Publ. 6). Moreover, they all occur in continental Asia (Li & Hetterscheid, 2010; Hetterscheid, 2012; Publ. 1). Heat reward in the form of an overnight heated shelter, putatively designed for pollinating beetles, is conceivable in these three groups. However, observations on pollinators for confirmation of the heat reward hypothesis are lacking for all these species, with the exception of *A. napalensis* (Chaturvedi, 2017).

Thermogenesis in a larger evolutionary frame

Considering the varied temperature patterns in the genus *Amorphophallus*, it is worthwhile to briefly examine the role of metabolic thermogenesis in other plant families. Trying to evaluate the significance of thermogenesis in other plant lineages might contribute to a better understanding of the significance of thermogenesis altogether. Therefore, the 13 plant families where thermogenesis is reported to occur, the *Annonaceae*, *Araceae*, *Arecaceae*, *Aristolochiaceae*, *Cycadaceae*, *Cyclanthaceae*, *Hydnoraceae*, *Magnoliaceae*, *Nelumbonaceae, Nymphaeaceae*, *Rafflesiaceae*, *Schisandraceae*, *Zamiaceae* (Seymour, 2010), are briefly discussed in regard to the number of thermogenic species and the putative functionality of thermogenesis.

The incidence of thermogenesis in seed plants is restricted to gymnosperms and basal lineages of angiosperms. Moreover, the majority of these families, except for four, are small or very small: *Araceae* (3,750 species), *Arecaceae* (2,600 species), *Annonaceae* (2,500 species), *Aristolochiaceae* (500 species), *Magnoliaceae* (294 species), *Cyclanthaceae* (230 species), *Zamiaceae* (230 species), *Cycadaceae* (107 species), *Schisandraceae* (85 species), *Nymphaeaceae* (70 species), *Rafflesiaceae* (25 species), *Hydnoraceae* (18 species), *Nelumbonaceae* (3 species) (Watson & Dallwitz, 1992 onwards; Christenhusz & Byng, 2016).

The oldest of these thermogenic plant lineages are the cycads. Of these, most species studied were shown to be thermogenic (e.g. Tang, 1987a, 1987b; Seymour et al., 2004; Terry et al.,

2004, 2007, 2012, 2016). In particular the male cones were found to be thermogenic, leading to the conclusion that pollen represents the reward whereas the purpose of thermogenesis is scent volatilisation for the attraction of pollinators (Tang, 1987a, 1987b). Moreover, thermogenesis in the female cones, if present, has been proposed to represent a case of auto-mimicry where the female cones mimic the rewarding male cones (Tang, 1987a, 1987b). Additionally, thermogenesis in some *Macrozamia* species has been proposed to serve several purposes, such as increased emission of scent volatiles, mating and breeding stimulation of pollinators, as well as warmth for the subsequent larval development (Terry et al., 2004). In contrast, it has been reported that some volatiles apparently act as a repellent instead of an attractant, if the released amount exceeds a certain threshold (Terry et al., 2007). Considering that floral scents may have originally evolved to deter herbivores, the plant-pollinator interaction in these cycads has been proposed to constitute an intermediate step, described as a "push-pull pollination system" (Terry et al., 2007). Although thermogenesis is widespread in the cycad group, its role is apparently not precisely determined.

Some 60 Arecaceae species have been reported to be thermogenic (Küchmeister et al., 1998; Ervik & Barfod, 1999; Ervik et al., 1999; Silberbauer-Gottsberger et al., 2001; Barfod et al., 2011; Pincebourde et al., 2016). The association of thermogenesis with oviposition-site mimicry has been widely excluded, as Arecaceae do not mimic these substrates; on the contrary, some of them are wind-pollinated (Ervik & Barfod, 1999). Several reports are anecdotal and the extent of thermogenesis in terms of occurrence, duration and temperature elevation is not well documented for many of these species (Ervik & Barfod, 1999). One notable exception is presented by Küchmeister et al. (1998) who report thermogenesis together with odour types and floral visitors from 11 species from the genera *Astrocaryum* G.Mey., *Attalea* Kunth, *Bactris* Jacq. ex Scop., and *Oenocarpus* Mart. However, though the dominant group of the floral visitors are Coleoptera, the "visiting fauna" is highly diverse (Küchmeister et al., 1998; Barfod et al., 2011) and a specific plant-pollinator interaction is not evident. Moreover, it has been observed that thermogenesis in Arecaceae often starts days before actual anthesis (Ervik & Barfod, 1999; Ervik et al., 1999; Silberbauer-Gottsberger et al., 2001; Pincebourde et al., 2016). This might account for the observation of bees and beetles waiting in close proximity for inflorescences to open (Silberbauer-Gottsberger et al., 2001). However, this observation has not been investigated further. Barfod et al. (2011) discussed four putative functions assigned to thermogenesis in palms: 1. Promotion of pollen tube growth. 2. Stimulation of pollinators to leave the inflorescence. 3. Volatilisation of floral scents. 4. Beneficial heat for developing eggs and larvae. However, none of these functions has actually been tested and the functions of thermogenesis in Arecaceae remain cryptic.

As for the Annonaceae family, thermogenesis is predominantly encountered in large flowering species and the heat is generated by the thick petals, using accumulated starch as substrate (Küchmeister et al., 1998; Gottsberger, 2012, 2014; Saunders, 2020). Thermogenesis has been reported to coincide with the flight of dynastid scarab beetles and the identified functions are scent dispersal and heat reward (Küchmeister et al., 1998; Gottsberger, 2012, 2014; Saunders, 2020). Some 58 species have been documented in regard to floral temperature elevations, and thermogenesis is assumed to be widespread in the Annonaceae family (Saunders, 2020). However, not all investigated species are thermogenic. For example, Gottsberger et al. (2011) investigated seven species from five Annonaceae genera. Of these, only two *Uvariodendron* (Engl. & Diels) R.E.Fr. species show a floral temperature increase. Moreover, the temperature increase differs significantly between the genera and species. Küchmeister et al. (1998) report nine thermogenic species from the genera *Anaxagorea* A.St.-Hil., *Duguetia* A.St.-Hil. and *Xylopia* L. with a temperature range from 1,3 °C to 13,2 °C above ambient temperature. All in all, only half of the tested 58 species show an elevated floral temperature (Saunders, 2020 and references therein). More investigations are needed to show to what degree thermogenesis is a prevalent feature of the family or not.

Thermogenesis in Magnoliaceae, more specifically in the genus *Magnolia* L., is reported by several studies (Kikuzawa & Mizui, 1990; Dieringer et al., 1999; Gottsberger et al., 2012; Wang et al., 2013, 2014; Wang & Zang, 2015). The heat is reported to be generated by the petals (Seymour, 2010), by the gynoecium (Wang et al., 2014), or by the petals, the gynoecium and the anthers (Gottsberger et al., 2012). Thermogenesis occurs during both the female and the subsequent male phase (Kikuzawa & Mizui, 1990; Gottsberger et al., 2012; Wang et al., 2014; Wang & Zhang, 2015). The heating pattern consists basically of one temperature peak per floral organ and the peak during the female phase is considered to be a case of auto-mimicry mimicking the pollen-rewarding male phase. Thus, similar to the pattern observed in cycads (Tang, 1987a, 1987b), potential pollinators are attracted during both anthesis phases (Kikuzawa & Mizui, 1990; Gottsberger et al., 2012; Wang et al., 2014; Wang & Zhang, 2015). Moreover, thermogenesis in *Magnolia ovata* (A.St.-Hil.) Spreng was found to coincide with the volatilisation of scent compounds and to provide an “energy reward to beetle visitors” (Seymour, 2010). However, for the time being, only five species of *Magnolia* have been reported to be thermogenic (Kikuzawa & Mizui, 1990; Dieringer et al., 1999; Seymour, 2010; Wang et al., 2013, 2014; Wang & Zang, 2015) and the occurrence of thermogenesis within the Magnoliaceae as a whole is unknown.

The number of reported thermogenic species is even lower in the Cyclanthaceae and Nymphaeaceae. *Cyclanthus bipartitus* Poit. ex A. Rich. and *Asplundia uncinata* Harling are the only reported thermogenic Cyclanthaceae species so far (Silberbauer-Gottsberger et al., 2001; Franz, 2007). In *Asplundia uncinata*, flower weevils (Coleoptera, Derelomini) are the pollinators, using the inflorescences for feeding, mating and oviposition (Franz, 2007). However, pollination under natural conditions appears to be inefficient, leading to high rates of infructescence abortion (Franz, 2007). Moreover, artificial pollination yielded significantly higher seed counts (Franz, 2007).

Likewise, the thermogenic species of the *Nymphaeaceae* comprise two species of the genus *Victoria* Lindl. (Seymour & Matthews, 2006; Schimpf et al., 2017) and a few species of the genus *Nymphaea* L., in particular *N. lotus* L. (Ervik & Knudsen, 2003; Hirthe & Porembski, 2003). In the genus *Victoria*, the sources of heat production are the carpellary appendages and the stamens, providing rewarding heat for pollinating beetles (Seymour & Matthews, 2006). Likewise, heat reward for nocturnal beetle pollinators has also been identified in *N. lotus* (Ervik & Knudsen, 2003). However, a more detailed investigation revealed that the fragrance emitted by *N. lotus* not only attracts nocturnal beetles, but also several bee species (Hirthe & Porembski, 2003). Moreover, the bees were found to be the more effective pollinators (Hirthe & Porembski, 2003), challenging the idea of a close association between thermogenic flowers and beetles in the Nymphaeaceae (Seymour et al., 1998; Ervik & Knudsen, 2003; Seymour & Matthews, 2006).

Thermogenesis in the Aristolochiaceae is even less documented, let alone investigated. It "is likely to occur in flowers of *Aristolochia* and *Asarum*" (González & Pabón-Mora, 2015). However, so far, thermogenesis has been evidenced in only one species (Vogel, 1967, 1990). Vogel (1967, 1990) investigated a structure in an undetermined *Aristolochia* species. He designated the structure as an osmophore disc and noted that its main function consists in the release of scent compounds. Moreover, besides volatising fragrances, the osmophore disc showed a temperature elevation to up to 4°C above ambient temperature. This is the only case where thermogenesis in *Aristolochia* has been actually reported.

In the Schisandraceae, the flowers of a few species of *Illicum*, *Kadsura* and *Schisandra* (Liu et al., 2006; Yuan et al., 2008; Thien et al., 2009) are thermogenic, whereas others are explicitly not thermogenic (Yuan et al., 2007, 2008). However, Thien et al. (2009) reported that in *Illicium floridanum* the highest temperature peak is reached by the pedicel and not by the actual floral

tissue. Moreover, the pedicel still heats during fruit development, thus the function of thermogenesis in *Illicium* remains unclear (Thien et al., 2009).

Furthermore, the thermogenic properties of three parasitic species of the Hydnoraceae have been investigated (Seymour et al., 2009d). Of these, only two were found to be weakly thermogenic and no specific function could be identified (Seymour et al., 2009d). The authors concluded that the role of thermogenesis in this group may be never fully understood (Seymour et al., 2009d).

As for the eudicots, thermogenesis and thermoregulation has been suggested to support pollinator attraction and heat reward in *Nelumbo nucifera* (Seymour & Schultze-Motel, 1997). However, this has been challenged by another study that found that thermogenesis occurs independently in the receptacle, petals and stamens of the flowers (Grant et al., 2010). Consequently, the authors proposed that the function of thermogenesis primarily consists in successful pollen germination or pollen tube growth in *Nelumbo nucifera* (Grant et al., 2010). Similarly, thermogenesis in regard to reproductive success was investigated *in situ* during several years in *Nelumbo lutea* Willd. (Dieringer et al., 2014). Floral characteristics, scent emission, thermogenesis and pollen vectors were investigated, and multitude of arthropod floral visitors was recorded, with Diptera and Coleoptera being the most frequent visitors (Dieringer et al., 2014). However, the authors cautiously concluded that the floral characteristics apparently favour the pollination by beetles and medium-sized bees, such as halictids. Moreover, geitonogamy through intra-floral pollen transfer was also found to contribute to the reproductive success in *Nelumbo lutea* (Dieringer et al., 2014). All in all, a clearly defined functionality of thermogenesis is not discernible.

Lastly, two Rafflesiaceae species were shown to be thermogenic (Patiño et al., 2000, 2002). Patiño et al. (2002) proposed that the main function of thermogenesis in Rafflesiaceae is the formation and release of CO_2 as an attractant for insects, Diptera in particular. In Rafflesiaceae, it is the tissue below the actual flowers, the column, that is the main source of the heat. Like in Arecaceae (Ervik & Barfod, 1999; Pincebourde et al., 2016), thermogenesis occurs not only during anthesis but also prior to anthesis. Moreover, it lasts an exceptionally long time, until and during fruit formation (Patiño et al., 2000, 2002). This exceptionally long thermogenic activity may be related to the fact that Rafflesiaceae are holoparasitic plants (Sofiyanti et al., 2016); the energetic expenses matter less as long as the survival of the host plant is ensured. That said, the aforementioned Hydnoraceae are also holoparasitic but only weakly thermogenic, if at all (Seymour et al., 2009d).

In conclusion, the evolutionary origin, function, and occurrence of thermogenesis among the different plant families is not well investigated and understood. This is underlined by the fact that thermogenic tissues differ across different plant families involving appendixes, columns, cones, discs, female flowers, male flowers, pedicels, petals, receptacles, and carpellary appendages. In many species the exact function is not clearly identifiable. Instead, the assigned function is often based on assumptions. Moreover, as far as it is known, for most reported thermogenic families, only a handful of thermogenic species is known, the exceptions being cycads, the Annonaceae, the Arecaceae, and the Araceae, which have considerably larger numbers of known thermogenic species. However, the floral morphology and the pollinators are very different in these plant lineages. Moreover, the low fruit set documented for some thermogenic aroids challenges the idea of a particularly efficient plant-pollinator interaction in thermogenic species (Ivancic et al., 2005; Gibernau et al., 2010; Barriault et al., 2021).

Furthermore, thermogenesis occurs almost exclusively in early diverging evolutionary lineages, notably in monocots. The only exceptions are the Nelumbonaceae and the Rafflesiaceae. However, the Nelumbonaceae family comprises five genera, four of which are extinct and known only as fossils (Li et al., 2014). The extant genus is *Nelumbo* and the number of recognised extant species ranges from one to three (Li et al., 2014; Lin et al., 2019). As for the Rafflesiaceae, they are estimated to comprise some 25 species, all of which are holoparasites (Christenhusz & Byng, 2016; Sofiyanti et al., 2016). It is reasonable to assume that this implies a low evolutionary constraint for thermogenesis as the host plants, large and fast-growing lianas from the genus *Tetrastigma* (Miq.) Planch., are apparently not impaired much by the energetic costs of the thermogenic parasite. Thus, holoparasites excluded, the only thermogenic dicots are the extant species of the Nelumbonaceae, a basal eudicot lineage (Lin et al., 2019). In other words, thermogenesis has apparently either been abandoned or else did not emerge during the evolution of early angiosperms and does not seem to constitute a successful feature per se. This does not universally exclude or challenge the functionality of thermogenesis. However, it suggests that the role and the impact of thermogenesis will have to be thoroughly tested in each species and that no general functionality can be presupposed.

Considering that the genetic requirements for thermogenesis, i.e., AOX genes and uncoupling proteins, are common in plant tissues, thermogenesis could be considered a highly variable trait that has appeared or has been lost multiple times during evolution. This could imply that there is not one specific functionality of thermogenesis but a multitude of niche functionalities that

might have evolved independently. If indeed it is impossible to identify a general functionality, it follows that the purpose of thermogenesis should be investigated for every single thermogenic species. Conversely, thermogenesis in plants, more specifically in *Amorphophallus*, might be an evolutionary artefact, at least in some groups or species. Or, thermogenesis itself is an evolutionary bye-product of another functionality, the emission of carbon dioxide (CO_2)

Carbon dioxide

The release of CO_2 has not been measured or quantified in Publ. 6. However, it can be assumed that CO_2 is released during thermogenesis as increased metabolic rates, implying oxygen consumption and CO_2 production, are prerequisite to thermogenesis (Wagner et al., 2008; Grant et al., 2010; Seymour, 2010). It therefore seems appropriate to add some considerations concerning the release of CO_2 during thermogenesis. Cellular respiration leads to the formation of CO_2. Similarly, decomposing organic material also emits increased amounts of CO_2 due to enzymatic and microbiological activity etc.; and accordingly, CO_2 is one of the compounds released during corpse decomposition (Buis, 2016). Therefore, an organic food source, dead or alive, is characterised by increased CO_2 concentrations. Consequently, it is probably no coincidence that olfactory CO_2 detection is widespread in animals and most notably in insects (Jones, 2013). In particular, parasitic and blood sucking insects, and insects feeding or breeding on decomposing organic material, rely on CO_2 gradients to locate a suitable substrate (Nicolas & Sillans, 1989; Patiño et al., 2002; Vereecken & McNeil, 2010; Jones, 2013). Therefore, the first evolutionary step towards thermogenesis might have consisted in an increase of CO_2 release for insect attraction. In other words, CO_2 release and not a temperature increase might have been the primary purpose of thermogenesis. The putative role of CO_2 as attractant in thermogenic plants was explicitly noted as early as 1976 (Moodie, 1976). However, it has been neglected since then and only a few investigations even mention it, proposing that it is likely to act as an attractant and anaesthetic, for instance in *Rafflesia* (Patiño et al., 2002).

In some *Amorphophallus* species, spathe unfolding is preceded by a temperature elevation in the appendix and/or the male flower zone, which is referred to as preheating here. Preheating, lasting days prior to anthesis, so far has been documented only once in the Araceae (Seymour et al., 2009a). Seymour et al. (2009a) noted that heating of the male zone in *Arum* occurred up to two days before pollen release. Preheating is documented in several *Amorphophallus* species here, notably in *A. bulbifer*, *A. fuscus*, *A. paeoniifolius*, *A. prainii*, *A. paeoniifolius* (Claudel et al., 2023; supporting information Data S1). Preheating for days prior to anthesis has also been recorded in *Nelumbo nucifera* Gaertn. (Seymour et al., 1998) and in Arecaceae (Ervik & Barfod, 1999; Ervik et al., 1999; Silberbauer-Gottsberger et al., 2001; Pincebourde et al., 2016). An

investigation into the pollination biology of phytelephantoid palms noted that thermogenesis is often more prominent before anthesis and starts at least one week prior to bract splitting (Ervik & Barfod, 1999; Ervik et al., 1999). This phenomenon has been corroborated by Pincebourde et al. (2016) who reported that in the palm *Phytelephas aequatorialis* Spruce, thermogenesis occurs in the bract and the prophyll of the inflorescences several days prior to opening and before pollen and nectar are available, a "puzzling" behaviour (Pincebourde et al., 2016). It was also observed that in the thermogenic *Attalea microcarpa* Mart., many bees and beetles are already waiting on or near the inflorescence before the bract opens (Silberbauer-Gottsberger et al., 2001). Once the bract splits up, bees and beetles invade the inflorescence and the thermogenic male flowers begin to volatise scents reminiscent of orange peel (Silberbauer-Gottsberger et al., 2001).

Preheating adds a new dimension to the event, as it does not fit any of the proposed pollination-related functions for thermogenesis. It occurs days before spathe unfolding and scent release, thus not supporting scent volatilisation or heat reward. Support of pollen tube growth can likewise be excluded as the temperature elevation occurs prior to pollination. Similarly, it seems unlikely to be a prerequisite to pollen maturation as it has been documented only in a few out of 80 *Amorphophallus* species. However, it is conceivable that CO_2 is released as an attractant during preheating.

Although speculative, the emission of CO_2 as an attractant could account for several phenomena of thermogenesis that are otherwise difficult to explain. For example, it could better account for the fact that many strongly thermogenic species are confined to tropical areas. Under this scenario, heat generation would be a consequence and not the purpose of thermogenesis. Moreover, CO_2 as attractant could also explain why in *Amorphophallus* various insect groups are attracted, including beetles, flies, ants, bees (including stingless ones), and cockroaches (van der Pijl, 1937; Sivadasan & Sabu, 1989; Giordano, 1999; Jung, 2006; Punekar & Kumaran, 2010; Chen et al., 2015; Chaturvedi, 2017; Moretto et al., 2019; Chai & Wong, 2019; Wong et al., 2022; Publ. 4). All insects that rely on CO_2 gradients to locate decomposing material for feeding, mating or breeding might be deceived by the emission of CO_2. It is at least conceivable that the beetles mistake the heat producing organs for decomposing organic matter due to the CO_2 emissions, which might account for an observation reported by Seymour and Matthews (2006), stating that beetles consume the major heat-producing organs in *Philodendron*. Similarly, the main source of heat in *Victoria amazonica* (Poepp.) J.C. Sowerby, namely the stylar processes, are consumed by *Cyclocephala hardyi* beetles (Seymour & Matthews, 2006).

Furthermore, CO_2 acting as attractant could explain why both the appendix and the male flower zone are thermogenic. The thermogenic episode of the appendix indicates stigma receptivity whereas the thermogenic episode of the male flower zone indicates pollen extrusion. In addition, the thermogenic activity of both zones more or less overlaps in many thermogenic *Amorphophallus* species. Considering that this leads to more or less continuous CO_2 release during anthesis, the two thermogenic episodes would actually represent a single attraction event that lures the insects deeper into the floral chamber or to the base during anthesis, especially as CO_2 is heavier than oxygen and could accumulate at the base of the inflorescence. This could also account for the lack of complex traps in many *Amorphophallus* species as the insects might be constantly attracted to the inflorescence until pollen release through the continuous release of CO_2. Lastly, it could account for the variation in thermogenic patterns. If indeed the more or less continuous release of CO_2 is a significant factor attracting and retaining pollinators until pollen release, it would lower the evolutionary constraint for a specific temperature pattern. This scenario does not exclude other purposes of thermogenesis, such as scent volatilisation or heat reward as these might have evolved in subsequent evolutionary steps. However, under this scenario, temperature elevation would be a secondary function and not the primary purpose of thermogenesis.

Future experiments, testing the attractiveness of scent compounds or pigmentation of deceptive inflorescences (Chen et al., 2015), might consider including artificial inflorescences that release defined concentrations of CO_2. Temperature elevation does not appear to be generally associated with carrion- or dung mimicry; however, CO_2 release might be a significant factor contributing to oviposition-site mimicry.

Conclusions & outlook

The exceptionally high inter- and intraspecific morphological, biochemical and palynological variation, which is inferred in every study investigating the evolution of the genus *Amorphophallus*, seemingly contradicts the low genetic resolution at the species level. (Brown, 1901; Grob et al., 2002, 2004; van der Ham et al., 2005; Sedayu et al., 2010, Publ. 1; Kite & Hetterscheid, 2017; Wong et al., 2022). Specialised plant-pollinator interactions and resource partitioning have been proposed to be the evolutionary drivers of such morphological variation and species diversity within the genus *Amorphophallus* (Sedayu et al., 2010; Kite & Hetterscheid, 2017). However, as discussed in Publ.s 4 & 5, this is not convincing. On the contrary, the attracted pollinators are deceived, and the deception is based on a "variation around a theme" (Schiestl & Dötterl, 2012). Considering that morphological variation might prevent the duped recipient from recognising and memorising the mimic, it is conceivable that morphological variation itself, within a functional frame or the variation around a theme, is the key element of the deceit. At least, this could account for the high degree of variation in inflorescence morphology, biochemistry and palynology despite a low genetic resolution at the species level. Consequently, the full inter- and intraspecific variation of oviposition-site mimics needs to be assessed to reliably circumscribe the species and to investigate the phylogeny.

A low evolutionary constraint of floral characteristics and defensive colouration, temperature patterns and lichen mimicry in particular, might also favour a rapid adaptation to new habitats and contribute to the species richness of the genus *Amorphophallus*. Pollinators relying on decomposing organic matter are ubiquitous and the inflorescences of most *Amorphophallus* species are available to many different insect types. Similarly, most mammals are likely to be duped by the masquerade of a small tree, as the depicted petiolar lichen types are widely distributed in the tropics and therefore easily recognisable as such.

Lastly, considering the wide distribution of the genus *Amorphophallus* and the exceptional range of fruit colours, seed dispersal appears to be highly effective. This is supported by the observation that many *Amorphophallus* species rapidly colonise areas with disturbed vegetation (Hetterscheid & Ittenbach, 1996). With some 237 species (Boyce & Croat, 2023), *Amorphophallus* is the largest palaeotropical aroid genus. Only the neotropical genera *Anthurium* (1319 species) and *Philodendron* Schott (585 species) comprise more species (Boyce & Croat, 2023). Highly variable deceptive traits, within a functional frame, might be the key factor that has led to the species diversity of the genus *Amorphophallus*.

References

Adanson M. 1763. Familles des Plantes 2: p 578. https://www.biodiversitylibrary.org/item/6958#page/1124/mode/1up

Albre J, Quilichini A, Gibernau M. 2003. Pollination ecology of *Arum italicum* (Araceae). *Botanical Journal of the Linnean Society* 141: 205–214. https://www.aroid.org/gallery/gibernau/2009p/A.%20italicum%20pollination%20-%20Albre%20et%20al%202003.pdf

Angioy A–M, Stensmyr MC, Urru I, Puliafito M, Collu I, Hansson BS. 2004. Function of the heater: the dead horse arum revisited. *Proceedings of the Royal Society of London*, Series B 271 (Suppl.): 13–15. https://royalsocietypublishing.org/doi/10.1098/rsbl.2003.0111

Anonymous. 1878. Another gigantic Aroid. *The gardeners' Chronicle*, n.s, 10: 596. https://www.biodiversitylibrary.org/item/84202#page/614/mode/1up

Arcangeli G. 1879. Sull'*Amorphophallus Titanum* Beccari. *Bullettino della Reale Società Toscana di Orticoltura* 4: 46–51. https://play.google.com/books/reader?id=WSkYIpcNb84C&pg=GBS.PA46&hl=de

Armstrong P, Nizio KD, Perrault KA, Forbes SL. 2016. Establishing the volatile profile of pig carcasses as analogues for human decomposition during the early post-mortem period. *Heliyon* 2: 70–77. https://doi.org/10.1016/j.heliyon.2016.e00070

Backer CA. 1913. Het Slangenblad II. *De Tropische Natuur* 2: 177–179.

Barfod AS, Hagen M, Borchsenius F. 2011. Twenty-five years of progress in understanding pollination mechanisms in palms (Arecaceae). *Annals of Botany* 108: 1503–1516. https://doi.org/10.1093/aob/mcr192

Barriault I, Barabé D, Cloutier L, Pellerin S, Gibernau M. 2021. Pollination ecology of *Symplocarpus foetidus* (Araceae) in a seasonally flooded bog in Québec, Canada. *Botany Letters* 168: 373–383. https://doi.org/10.1080/23818107.2021.1909496

Barthlott W. 1995. Mimikry – Nachahmung und Täuschung im Pflanzenreich. *Biologie in unserer Zeit* 25: 74–82. https://onlinelibrary.wiley.com/doi/10.1002/biuz.19950250203

Barthlott W, Szarzynski J, Vlek P, Lobin W, Korotkova N. 2009. A torch in the rain forest: thermogenesis of the Titan arum (*Amorphophallus titanum*). *Plant Biology* 11: 499–505. https://doi.org/10.1111/j.1438-8677.2008.00147.x

Bay D. 1995. Thermogenesis in the Aroids. *Aroideana* 18: 32–39. https://www.aroid.org/gallery/gibernau/aroideana/0180008.pdf

Beath DDN. 1996. Pollination of *Amorphophallus johnsonii* (Araceae) by carrion beetles (*Phaeochrous amplus*) in a Ghanaian rain forest. *Journal of Tropical Ecology* 12: 409–418. https://www.cambridge.org/core/journals/journal-of-tropical-ecology/article/abs/pollination-

of-amorphophallus-johnsonii-araceae-by-carrion-beetles-phaeochrous-amplus-in-a-ghanaian-rain-forest/DD3CC26903B488A7A1053F1C41D43F6D

Beccari O. 1878a. Una pianta maravigliosa. Letter to Bardo Corsi Salviati in Fenzi, E.O., *Bullettino della Reale Società Toscana di Orticoltura* 3: 270–271. https://play.google.com/books/reader?id=8gEUN_hBTu4C&pg=GBS.PA270&hl=de

Beccari O. 1878b. Il *Conophallus titanum* Beccari. *Bullettino della Reale Società Toscana di Orticoltura* 3: 290–293. https://play.google.com/books/reader?id=8gEUN_hBTu4C&pg=GBS.PA290&hl=de

Beccari O. 1889a. *Amorphophallus titanum*. *The Gardeners' Chronicle* July 20, page 74. https://www.biodiversitylibrary.org/item/83851#page/90/mode/1up

Beccari O. 1889b. Fioritura dell'*Amorphophallus Titanum*. *Bullettino della Reale Società Toscana di Orticoltura*, ser. 2, 4: 250–253. https://play.google.com/books/reader?id=k9enyxLdjbIC&pg=GBS.PA250&hl=de

Beigel H. 2020. Die Kugelige Zwergwasserlinse *Wolffia globosa* (Roxb.) Hartog & Plas – neu in Mitteleuropa. *RegnitzFlora* 10: 38–50. https://www.zobodat.at/pdf/RegnitzFlora_10_0038-0050.pdf

Bermadinger-Stabentheiner E, Stabentheiner A. 1995. Dynamics of thermogenesis and structure of epidermal tissues in inflorescences of *Arum maculatum*. *New Phytologist* 131: 41–50. https://nph.onlinelibrary.wiley.com/doi/abs/10.1111/j.1469-8137.1995.tb03053.x

Bernhardt P. 2000. Convergent evolution and adaptive radiation of beetle-pollinated angiosperms. *Plant Systematics and Evolution* 222: 293–320. https://link.springer.com/article/10.1007/BF00984108

Blume CL. 1825. Letter to the Governor-general. On the flowering of a new species of a new genus of Araceae with a very large inflorescence, obviously *Amorphophallus campanulatus*, in the Botanic Garden, with reference to *Tacca phallifera* RUMPH. *Bataviaasche Courant*, 23 Nov.

Blume CL. 1834. *Amorphophallus*: In J. Decaisne, Description d'un herbier de l'ile de Timor. *Nouvelles annales du Muséum d'histoire naturelle* III 3: 333–501.

Blume CL. 1837. *Amorphophallus*. *Rumphia* 1: 138–149.

Bogner J. 1976. *Amorphophallus maculatus*. *Der Palmengarten* 3: 83–86.

Bogner J, Mayo SJ, Sivadasan M. 1985. New species and changing concepts in *Amorphophallus*. *Aroideana* 8: 15–25.

Bogner J, Hesse M. 2005. Zamioculcadoideae, a new subfamily of Araceae. *Aroideana* 28: 3–20.

Bown D. 1988. Aroids: Plants of the Arum Family. Timber Press, Incorporated, pp 286.

Bown D. 2010. Aroids: Plants of the Arum Family. Second Edition. Timber Press, Incorporated, pp 468.

Boyce PC, Ipor IB, Hetterscheid WLA. 2010. A review of the white-flowered *Amorphophallus* (Araceae: Thomsonieae) species in Sarawak. *Gardens' Bulletin* 61: 249–268. https://www.biodiversitylibrary.org/page/43648398#page/261/mode/1up

Boyce PC, Wong SY. 2019. Borneo and its disproportionately large rheophytic aroid flora. *The Gardens' Bulletin Singapore* 71: 497–524. https://www.nparks.gov.sg/sbg/research/publications/the-gardens%27-bulletin-singapore/-/media/sbg/gardens-bulletin/gbs_71_s2_y2019/71_s2_24_y2019_v71s2_gbs_pg497.pdf

Boyce PC, Croat TB. 2023. The Überlist of Araceae, Totals for Published and Estimated Number of Species in Aroid Genera. https://www.researchgate.net/publication/369741356_Uberlist_-_April_2023

Bröderbauer D, Diaz A, Weber A. 2012. Reconstructing the origin and elaboration of insect–trapping inflorescences in the Araceae. *American Journal of Botany* 99: 1666–1679. https://bsapubs.onlinelibrary.wiley.com/doi/full/10.3732/ajb.1200274

Brown NE. 1901. Order CL Aroideae. in W.T. Thiselton–Dyer (ed.), *Flora of tropical Africa* 8: pp 137–200. https://www.biodiversitylibrary.org/item/132#page/147/mode/1up

Brummitt RK. 1987. Report of the committee for Spermatophyta: 33. *Taxon* 36: 734–739. https://doi.org/10.2307/1221125

Buis RC. 2016. The validation of human decomposition fluid as a cadaver–detection dog training aid. Thesis submitted for the degree of Doctor of Philosophy (Science) Centre for Forensic Science University of Technology, Sydney. https://opus.lib.uts.edu.au/bitstream/10453/62158/7/02whole.pdf

Bulawin NF, Medecilo-Guiang MMP, Alejandro GJD. 2022. *Amorphophallus fontarumii* (Araceae), a new species from Tanay Rizal, Luzon Island, Philippines. *Nordic Journal of Botany*: e03643. https://doi.org/10.1111/njb.03643

Bustamante RAA, Mansibang JA, Hetterscheid WLA, Tamayo MN. 2020. *Amorphophallus caudatus* (Thomsonieae, Araceae), a new species from Camarines Norte, Luzon island, the Philippines. Nordic Journal of Botany 38: https://doi.org/10.1111/njb.02982

Bustamante RAA, Claudel C, Altomonte JCA, Udasco LC Jr, Tamayo MN. 2021. *Amorphophallus minimus* (Araceae), a new species from the montane forest of Nueva Ecija, Luzon island, Philippines. *Nordic Journal of Botany* 39. https://doi.org/10.1111/njb.03251

Cabrera LI, Salazar GA, Chase MW, Mayo SJ, Bogner J, Dávila P. 2008. Phylogenetic relationships of aroids and duckweeds (Araceae) inferred from coding and noncoding plastid DNA. *American Journal of Botany* 95: 1153–1165. https://bsapubs.onlinelibrary.wiley.com/doi/full/10.3732/ajb.0800073

Calaramo MA, Batuyong MAR, Bulawin NF, Alejandro GJD. 2022. Notes on the genus *Amorphophallus* Blume ex Decne. (Araceae) of northwestern Luzon, Philippines, including a new species. *Nordic Journal of Botany* 2022: e03491. https://doi.org/10.1111/njb.03491

Camargo JMF, Roubik DW. 1991. Systematics and bionomics of the apoid obligate necrophages: the *Trigona hypogea* group (Hymenoptera: Apidae; Meliponinae). *Biological Journal of the Linnean Society* 44: 13–39. https://doi.org/10.1111/j.1095-8312.1991.tb00604.x

Chai SK, Wong SY. 2019. Five pollination guilds of aroids (Araceae) at Mulu National Park (Sarawak, Malaysian Borneo). *Webbia* 74: 353–371. https://doi.org/10.1080/00837792.2019.1653425

Chartier M, Liagre S, Weiss–Schneeweiss H, Kolano B, Bessière J-M, Schöneberger J, Gibernau M. 2016. Floral traits and pollination ecology of European *Arum* hybrids. *Oecologia* 180: 439–451. https://link.springer.com/article/10.1007/s00442-015-3498-9

Chase MW, Christenhusz MJM, Fay MF, Byng JW, Judd WS, Soltis DE, Mabberley DJ, Sennikov AN, Soltis PS, Stevens PF. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* 181: 1–20. https://academic.oup.com/botlinnean/article/181/1/1/2416499

Chaturvedi SK. 2017. Pollinators and visitors of *Amorphophallus napalensis* (Wall.) Bogner and Mayo (Araceae) in Nagaland State, North–East India. *Pleione* 11: 336–340. http://pleione.ehsst.org/journals/Pleione112/014%20Pollinators%20and%20visitors%20of%20Amorphophallus%20napalensis%20in%20Nagaland.pdf

ChemSpider. 2023. https://www.chemspider.com/Default.aspx /Accessed 22 September 2023.

Chen G, Ma X-K, Jürgens A, Lu J, Liu E-X, Sun W-B, Cai X-H. 2015. Mimicking livor mortis: a well–known but unsubstantiated color profile in Sapromyiophily. *Journal of Chemical Ecology* 41: 808–815. https://link.springer.com/article/10.1007/s10886-015-0618-2

Chouteau M, Barabé D, Gibernau M. 2007. Thermogenesis in *Syngonium* (Araceae). *Canadian Journal of Botany* 85: 184–190. https://cdnsciencepub.com/doi/abs/10.1139/B07-004

Chouteau M, Barabé D, Gibernau M. 2009. Flowering and thermogenetic cycles in two species of *Monstera* (Araceae). *Bulletin de la société d'histoire naturelle de Toulouse* 145: 5–10. https://www.aroid.org/gallery/gibernau/2009p/Monstera%20-%20Chouteau%20et%20al%202009.pdf

Christenhusz MJM, Byng JW. 2016. The Number of Known Plants Species in the World and Its Annual Increase. *Phytotaxa* 261: 201–217. https://doi.org/10.11646/phytotaxa.261.3.1

Claudel C, Galloway A. 2012. Hybridization of *Amorphophallus*: State of the art. *Aroideana*. 35: 103–108. http://www.aroid.org/aroideana/artpage.php?key=MDM1MDAxNA==I

Claudel C, Mangelsdorff R, Hetterscheid WLA. 2012. The first successful hybrid of *Amorphophallus titanum*. *Aroideana* 35: 81–85. https://www.researchgate.net/publication/267637606_The_first_succesful_hybrid_of_Amorphophallus_titanum

Claudel C, Galloway A, Mangelsdorff R. 2013. Hybridization of *Amorphophallus*: State of affairs. *Aroideana* 36: 114–122. http://www.aroid.org/aroideana/artpage.php?key=MDM2MDAxMA==I

Claudel C, Mangelsdorff R. 2014. Hybridization of *Amorphophallus*: State of the Unions. *Aroideana* 37: 72–79. https://www.aroid.org/aroideana/artpage.php?key=MDM3MDAwOA==K

Claudel C, Buerki S, Chatrou L, Antonelli A, Alvarez N, Hetterscheid WLA. 2017. Large–scale phylogenetic analysis of *Amorphophallus* (Araceae) derived from nuclear and plastid sequences reveals new subgeneric delineation. *Botanical Journal of the Linnean Society* 184: 32–45. https://academic.oup.com/botlinnean/article/184/1/32/3797257

Claudel C. 2020. Publ. „Hybrids“ pages 80–97. In: Konjac Glucomannan Production, Processing, and Functional Applications Edited by George Srzednicki, Chaleeda Borompichaichartkul. Published June 24, 2020 by CRC Press 286 pages – 125 Color & 48 B/W Illustrations. https://doi.org/10.1201/9780429429927

Claudel C, Lev-Yadun S. 2021. Odor polymorphism in deceptive *Amorphophallus* species - a review. *Plant Signaling & Behavior* 16:12, DOI: 10.1080/15592324.2021.1991712 https://doi.org/10.1080/15592324.2021.1991712

Claudel C. 2023. *Amorphophallus* hybrids. Continuously updated. https://www.amorphophallus-network.org/hybrids/variabilis-x-titanum/a-variabilis-x-a-titanum/ Accessed 22 September 2023.

Claudel C, Loiseau O, Silvestro D, Lev-Yadun S, Antonelli A. 2023. Patterns and drivers of heat production in the plant genus *Amorphophallus*. *Plant Journal* 115: 874–894. https://doi.org/10.1111/tpj.16343

Cole TCH, Hilger HH, Stevens P. 2019. Angiosperm phylogeny poster (APP) – Flowering plant systematics. *PeerJ Preprints* 7: e2320v6. https://peerj.com/preprints/2320/

Cooper J, Gordon IJ, Pike AW. 2000. Strategies for the avoidance of faeces by grazing sheep. *Applied Animal Behaviour Science* 69: 15–33. https://doi.org/10.1016/S0168-1591(00)00116-7

Croat TB. 2019. Araceae, a Family with Great Potential. *Annals of the Missouri Botanical Garden* 104: 3–9. https://annals.mobot.org/index.php/annals/article/view/213

Croat TB, Ortiz OO. 2020. Distribution of Araceae and the Diversity of Life Forms. *Acta Societatis Botanicorum Poloniae* 89: 8939. https://pbsociety.org.pl/journals/index.php/asbp/article/view/asbp.8939

Cusimano N, Bogner J, Mayo SJ, Boyce PC, Wong SY, Hesse M, Hetterscheid WLA, Keating RC, French JC. 2011. Relationships within the Araceae: Comparison of morphological patterns with molecular phylogenies. *American Journal of Botany* 98: 1–15. https://bsapubs.onlinelibrary.wiley.com/doi/full/10.3732/ajb.1000158

Dekeirsschieter J, Verheggen FJ, Gohy M, Hubrecht F, Bourguignon L, G Lognay G, Haubruge E. 2009. Cadaveric volatile organic compounds released by decaying pig carcasses (*Sus domesticus* L.) in different biotopes. *Forensic Science International* 189: 46–53. https://doi.org/10.1016/j.forsciint.2009.03.034

Dieringer G, Cabrera LR, Lara M, Loya L, Reyes-Castillo P. 1999. Beetle Pollination and Floral Thermogenicity in *Magnolia tamaulipana* (Magnoliaceae). *International Journal of Plant Sciences* 160: 64–71. https://www.journals.uchicago.edu/doi/10.1086/314099

Dieringer G, Cabrera LR, Mottaleb M. 2014. Ecological relationship between floral thermogenesis and pollination in *Nelumbo lutea* (Nelumbonaceae). *American Journal of Botany* 101: 357–364. https://doi.org/10.3732/ajb.1300370

Dormer KJ. 1960. The truth about pollination in *Arum*. *New Phytologist* 59: 298–301. https://www.aroid.org/gallery/gibernau/1979/The%20truth%20about%20pollination%20-%20Dormer%201960.pdf

Engler A. 1879. Araceae. In: Candolle, A. & C. de, Monographiae Phanerogamarum 2: 1–681. G. Masson, Paris. https://www.biodiversitylibrary.org/item/99440#page/1/mode/1up

Engler A. 1911. Araceae–Lasioideae. In: Engler A, ed. *Das Pflanzenreich IV,* 23C (Heft 48). Leipzig: W. Engelmann, 1–130. https://bibdigital.rjb.csic.es/viewer/9996/?offset=#page=1&viewer=picture&o=bookmark&n=0&q=

Ervik F, Barfod AS. 1999. Thermogenesis in palm inflorescences and its ecological significance. *Acta Botanica Venezuelica* 22:195–212. https://www.researchgate.net/publication/256392296_Thermogenesis_in_palm_inflorescences_and_its_ecological_significance

Ervik F, Tollsten L, Knudsen JT. 1999. Floral scent chemistry and pollination ecology in phytelephantoid palms (Arecaceae). *Plant Systematics and Evolution* 217:279–297. https://link.springer.com/article/10.1007/BF00984371

Ervik F, Knudsen JT. 2003. Water lilies and scarabs: faithful partners for 100 million years? *Biological Journal of the Linnean Society* 80: 539–543. https://doi.org/10.1046/j.1095-8312.2003.00258.x

Fadzly N, Jack C, Schaefer HM, Burns KC. 2009. Ontogenetic colour changes in an insular tree species: signalling to extinct browsing birds?. *New Phytologist* 184: 495–501. https://doi.org/10.1111/j.1469-8137.2009.02926.x

Faegri K, van der Pijl L. 1979. The principles of pollination ecology (3rd Rev. Edn.), Pergamon Press, London.

Fankhauser R, Galeffi C, Suter W. 2008. Dung avoidance as a possible mechanism in competition between wild and domestic ungulates: two experiments with chamois *Rupicapra rupicapra*. *European Journal of Wildlife Research* 54: 88–94. https://link.springer.com/article/10.1007/s10344-007-0115-1

Fischer E, Dumbo B, Dumbo L. 2022. A new species of *Amorphophallus* (Araceae) from Eastern D.R. Congo, and a new record of the genus from Rwanda. *Plant Ecology and Evolution* 155: 333–342. https://doi.org/10.5091/plecevo.93804

Franz NM. 2007. Reproductive trade-offs in a specialized plant/pollinator system involving *Asplundia uncinata* Harling (Cyclanthaceae) and a derelomine flower weevil (Coleoptera: Curculionidae). *Plant Systematics and Evolution* 269: 183–201. https://link.springer.com/article/10.1007/s00606-007-0595-1

French JC, Chung MG, Hur YK. 1995. Chloroplast DNA phylogeny of *Ariflorae*. In: Rudall, P.J., Cribb, P.J., Cutler, D.F., Humphries, C.J. (eds.) Monocotyledons: systematics and evolution. London: Royal Botanic Gardens, Kew, pp. 255–275.

Fujioka K, Shirasu M, Manome Y, Ito N, Kakishima S, Minami T, Tominaga T, Shimozono F, Iwamoto T, Ikeda K, Yamamoto K, Murata J, Tomizawa Y. 2012. Objective display and discrimination of floral odors from *Amorphophallus titanum*, bloomed on different dates and at different locations, using an electronic nose. *Sensors* 12: 2152–2161. https://doi.org/10.3390/s120202152

Galloway A, Luu HT, Malkmus-Hussein B, Prehsler D, Claudel C. 2019b. Three New Species of *Amorphophallus* (Araceae) from Vietnam. *Aroideana* 42: 41–58.

Galloway, A, Malkmus-Hussein B, Prehsler D, Claudel C. 2019c. A new species of *Amorphophallus* (Araceae) from Thailand (Kanchanaburi Province). *Aroideana* 42: 70–75.

Galloway A, Prehsler D, Claudel C. 2019a. Another new miniature *Amorphophallus* (Araceae) species from Laos, the land of dwarf voodoo lilies. *Aroideana* 42: 59–69.

Gandawijaja D, Idris S, Nasution R, Nyman LP, Arditti J. 1983. *Amorphophallus titanum* (Bec.) Bec.: A historical review and some recent observations. *Annals of Botany* 51: 269–278. https://academic.oup.com/aob/article-abstract/51/3/269/174923

Genaust H. 2013. Etymologisches Wörterbuch der botanischen Pflanzennamen. Ausgabe 3, illustriert Springer–Verlag, ISBN 3034892829, 9783034892827 – 704 Seiten

Gibernau M, Barabé D. 2000. Thermogenesis in three *Philodendron* species (Araceae) of French Guiana. *Canadian Journal of Botany* 78: 685–689. https://www.aroid.org/gallery/gibernau/2009p/Thermogenesis%20in%20three%20-%20Gibernau%20%26%20Barab%C3%A9%202000.pdf

Gibernau M, Barabé D, Labat D. 2000. Flowering and pollination of *Philodendron melinonii* (Araceae) in French Guiana. *Plant Biology* 2: 330–333. https://www.aroid.org/gallery/gibernau/2009p/Flowering%20Philo%20melinonii%20-%20Gibernau%20et%20al%202000.pdf

Gibernau M, Macquart D, Przetak G. 2004. Pollination in the genus *Arum* – a review. *Aroideana* 27: 148–166. https://florapix.nl/Arisaema-L/secure/Literature/Gibernau%20et%20al.%202004%20-%20Pollination%20in%20the%20Genus%20Arum%20-%20a%20Review.pdf

Gibernau M, Barabé D, Moisson M, Trombe A. 2005. Physical constraints on temperature difference in some thermogenic aroid inflorescences. *Annals of Botany* 96: 117–125.

Gibernau M, Chouteau M, Lavallée K, Barabé D. 2010. Notes on the phenology, morphometry and floral biology of *Anaphyllopsis americana*. *Aroideana* 33: 183–191. https://www.aroid.org/gallery/gibernau/aroideana/0330007.pdf

Gibernau M, Seymour RS. 2014. Pollination Success of the Corsican *Helicodiceros muscivorus* (Araceae). *Aroideana* 37: 61–71. http://www.aroid.org/gallery/gibernau/aroideana/0370007.pdf

Gibson TC. 2018. Saving giant flowers: Using patterns of blooming in cultivated Titan Arums to promote in situ conservation of wild populations in Sumatra. *Aroideana* 42: 260–270.

Giordano C. 1999. Observations on *Amorphophallus titanum* (Becc.) Becc.ex Arcangeli in the Forest of Sumatra. *Aroideana* 22: 10–19. https://www.aroid.org/gallery/gibernau/aroideana/0220004.pdf

Giordano C, Nardi E, Mosti S. 2013. Lectotypification of C*onophallus titanum* (≡ *Amorphophallus titanum*) (Araceae). *Taxon* 62: 1032–1036. https://onlinelibrary.wiley.com/doi/abs/10.12705/625.9

Goff ML. 2009. Early post-mortem changes and stages of decomposition in exposed cadavers. *Experimental and Applied Acarology* 49: 21–36. https://link.springer.com/article/10.1007/s10493-009-9284-9

Gombocz E. 1936. Ein neuer *Amorphophallus*. *Annales Musei historico–naturalis hungarici*. 30: 1–3. http://publication.nhmus.hu/pdf/annHNHM/Annals_HNHM_1936_Vol_30_b_1.pdf

González F, Pabón-Mora N. 2015. Trickery flowers: the extraordinary chemical mimicry of *Aristolochia* to accomplish deception to its pollinators. *New Phytologist* 206: 10–13. https://doi.org/10.1111/nph.13328

Gottsberger G, Meinke S, Porembski S. 2011. First records of flower biology and pollination in African *Annonaceae*: *Isolona*, *Piptostigma*, *Uvariodendron*, *Monodora* and *Uvariopsis*. *Flora* 206: 498–510. https://www.sciencedirect.com/science/article/abs/pii/S0367253011000077

Gottsberger, G. 2012. How diverse are Annonaceae with regard to pollination? *Botanical Journal of the Linnean Society* 169: 245–261. https://doi.org/10.1111/j.1095-8339.2011.01209.x

Gottsberger G, Silberbauer-Gottsberger I, Seymour RS, Dötterl S. 2012. Pollination ecology of *Magnolia ovata* may explain the overall large flower size of the genus. *Flora - Morphology, Distribution, Functional Ecology of Plants* 207: 107–118. https://doi.org/10.1016/j.flora.2011.11.003

Gottsberger, G. 2014. Evolutionary steps in the reproductive biology of Annonaceae. *Revista Brasileira de Fruticultura* 36: 32–43. https://doi.org/10.1590/S0100-29452014000500004

Grant NM, Miller RA, Watling JR, Robinson SA. 2010. Distribution of thermogenic activity in floral tissues of *Nelumbo nucifera*. *Functional Plant Biology*: 37: 1085–1095. https://doi.org/10.1071/FP10024

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

Grob GBJ, Gravendeel B, Eurlings MCM, Hetterscheid WLA. 2002. Phylogeny of the tribe Thomsoniae (Araceae) based on chloroplast *matK* and *trnL* intron sequences. *Systematic Botany* 27: 453–467.

Grob GB, Gravendeel B, Eurlings MC. 2004. Potential phylogenetic utility of the nuclear FLORICAULA/LEAFY second intron: comparison with three chloroplast DNA regions in *Amorphophallus* (Araceae). *Molecular Phylogenetics and Evolution* 30: 13–23. https://doi.org/10.1016/S1055-7903(03)00183-0

Haigh AL, Gibernau M, Maurin O, Bailey P, Carlsen MM, Hay A, Leempoel K, McGinnie C, Mayo S, Morris S, Pérez-Escobar OA, Wong SY, Zuluaga A, Zuntini AR, Baker WJ, Forest F. 2023. Target sequence data shed new light on the infrafamilial classification of Araceae. *American Journal of Botany* 110(2): e16117. https://doi.org/10.1002/ajb2.16117

Handayani T, Yuzammi Y, Hadiah JT. 2020. Inflorescence morphology and development of suweg (*Amorphophallus paeoniifolius* (Dennst.) Nicolson. *Biodiversitas* 21: 5835–5844. https://smujo.id/biodiv/article/view/7091

Hejnowicz Z, Barthlott W. 2005. Structural and mechanical peculiarities of the petioles of giant leaves of *Amorphophallus* (Araceae). *American Journal of Botany* 92: 391–403. https://bsapubs.onlinelibrary.wiley.com/doi/full/10.3732/ajb.92.3.391

Hesse M. 2006. Reasons and consequences of the lack of a sporopollenin ektexine in Aroideae (Araceae). *Flora* 201: 421–428. https://www.sciencedirect.com/science/article/abs/pii/S0367253006000272?via%3Dihub

Hetterscheid 1994. Sumatran *Amorphophallus* adventures: 20 August – 1 September 1993. *Aroideana* 17: 61–77. http://www.aroid.org/aroideana/artpage.php?key=MDE3MDAwNw==D

Hetterscheid WLA, Serebryanyi MM. 1994. Notes on the genus *Amorphophallus* (Araceae) – 3. Two new species from Vietnam. *Blumea* 39: 283–287. https://repository.naturalis.nl/pub/525235

Hetterscheid WLA, Ittenbach S. 1996. Everything you always wanted to know about *Amorphophallus*, but were afraid to stick your nose into. *Aroideana* 19: 7–131. https://www.researchgate.net/publication/283567478_Everything_you_always_wanted_to_know_about_Amorphophallus_but_were_afraid_to_stick_your_nose_into

Hetterscheid WLA, van der Ham RWJM. 2001. Notes on the genus *Amorphophallus* (Araceae) – 11 New and obsolete species from East Malaysia and continental Southeast Asia. *Blumea* 46: 253–282. https://www.researchgate.net/publication/293528061_Notes_on_the_genus_Amorphophallus_Araceae_-_11_New_and_obsolete_species_from_East_Malaysia_and_continental_Southeast_Asia

Hetterscheid WLA. 2003. Notes on the Genus *Amorphophallus* 12: Three New Species from Tropical Asia. *Aroideana* 26: 113–119. https://www.researchgate.net/profile/Wilbert-Hetterscheid/publication/267641648_Notes_on_the_Genus_Amorphophallus_12_Three_New_Species_from_Tropical_Asia/links/54572b180cf2bccc490f3d88/Notes-on-the-Genus-Amorphophallus-12-Three-New-Species-from-Tropical-Asia.pdf

Hetterscheid WLA. 2012. *Amorphophallus*. In: Boyce PC, Sookchaloem D, Hetterscheid WLA, Gusman G, Jacobsen N, Idei T, Nguyen VD, eds. Araceae. *Flora of Thailand* 11. Bangkok: The Forest Herbarium, 218–232. https://www.researchgate.net/publication/283563815_Flora_of_Thailand_-_Araceae_Acoraceae

Hetterscheid WLA, Claudel C. 2012. The end of *Pseudodracontium* N.E. Br. Aroideana 36: 40–46. https://www.aroid.org/genera/changes/Aroideana0350005.pdf

Hetterscheid WLA, Wistuba A, Amoroso VB, Medecilo MP, Claudel C. 2012. *Amorphophallus natolii* (Araceae), a new species from Limestone on Palawan, Philippines. *Botanical Studies* 53: 415–420. https://ejournal.sinica.edu.tw/bbas/content/2012/3/Bot533-14.pdf

Hetterscheid WLA. 2020. Botanical Background to *Amorphophallus*, Taxonomy. In: Srzednicki G & Borompichaichartkul C. (eds.), Konjac Glucomannan Production, Processing, and Functional Applications. CRC Press, Boca Raton. pp. 9–11. https://doi.org/10.1201/9780429429927

Hetterscheid WLA, Medecilo MP, Callado JRC, Galloway A. 2020. New species of *Amorphophallus* (Araceae) in the Philippines and an updated key. *Blumea* 65: 1–9. https://doi.org/10.3767/blumea.2020.65.01.01

Hirthe G, Porembski S. 2003. Pollination of *Nymphaea lotus* (Nymphaeaceae) by rhinoceros beetles and bees in the northeastern Ivory Coast. *Plant Biology* 5: 670–676. https://doi.org/10.1055/s-2003-44717

Hoe YC, Gibernau M, Wong SY. 2020. Thermogenesis in four species of *Schismatoglottis calyptrata* Clade (Schismatoglottideae: Araceae). *Feddes Repertorium* 131: 268–277. https://ir.unimas.my/id/eprint/32939/1/Thermogenesis%20in%20four%20species%20ofSchismatoglottisCalyptrata%20Clade%20(Schismatoglottideae%20Araceae)_PDF.pdf

Hooker JD. 1891. *Amorphophallus Titanum*, native of Sumatra. *Curtis's Botanical Magazine*, ser. 3, 47: 7153–7175. https://www.biodiversitylibrary.org/item/14245#page/9/mode/1up

Howgate P. 2010a. A critical review of total volatile bases and trimethylamine as indices of freshness of fish. Part 1. Determination. *Electronic Journal of Environmental, Agricultural and Food Chemistry* 9: 29–57.

Howgate P. 2010b. A critical review of total volatile bases and trimethylamine as indices of freshness of fish. Part 2. Formation of the bases, and application in quality assurance. *Electronic Journal of Environmental, Agricultural and Food Chemistry* 9: 58–88.

Ittenbach S. 2003. Revision der afrikanischen Arten der Gattung *Amorphophallus* (Araceae). *Englera* 25: 2–263. https://www.jstor.org/stable/3776772?origin=crossref

Ivancic A, Lebot V, Roupsard O, Quero–Garcia J, Okpul T. 2004. Thermogenic flowering of taro (*Colocasia esculenta*, Araceae). *Canadian Journal of Botany* 82: 1557–1565. https://cdnsciencepub.com/doi/pdf/10.1139/b04-118

Ivancic A, Roupsard O, Quero-Garcia J, Lebot V, Pochyla V, Okpul T. 2005. Thermogenic flowering of the giant taro (*Alocasia macrorrhizos*, Araceae). *Canadian Journal of Botany* 83: 647–655. https://cdnsciencepub.com/doi/10.1139/b05-040

Ivancic A, Roupsard O, Quero-Garcia J, Melteras M, Molisale T, Tara S, Lebot V. 2008. Thermogenesis and flowering biology of *Colocasia gigantea*, Araceae. *Journal of Plant Research* 121: 73–82. https://link.springer.com/article/10.1007/s10265-007-0129-5

Johnson SD, Schiestl FP. 2016. Floral mimicry. Oxford, New York: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198732693.001.0001

Johnson MG, Pokorny L, Dodsworth S, Botigué LR, Cowan RS, Devault A, Eiserhardt WL, Epitawalage N, Forest F, Kim JT, Leebens-Mack JH, Leitch IJ, Maurin O, Soltis DE, Soltis PS, Wong GK, Baker WJ, Wickett NJ. 2019. A Universal Probe Set for Targeted Sequencing of 353 Nuclear Genes from Any Flowering Plant Designed Using k-Medoids Clustering. *Systematic Biology* 68: 594–606. https://academic.oup.com/sysbio/article/68/4/594/5237557?login=false

Jones W. 2013. Olfactory Carbon Dioxide detection by insects and other animals. *Molecules and Cells* 35: 87–92. https://doi.org/10.1007/s10059-013-0035-8

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.

Jürgens A, Dötterl S, Meve U. 2006. The chemical nature of fetid floral odours in stapeliads (Apocynaceae–Asclepiadoideae–Ceropegieae). *New Phytologist* 172: 452–468. https://doi.org/10.1111/j.1469-8137.2006.01845.x

Jürgens A, Wee S-L, Shuttleworth A, Johnson SD. 2013. Chemical mimicry of insect oviposition sites: A global analysis of convergence in angiosperms. *Ecology Letters* 16: 1157–1167. https://doi.org/10.1111/ele.12152

Jürgens A., Shuttleworth A. 2016. Carrion and dung mimicry in plants. In: Benbow ME, Tomberlin JK, Tarone AM, editors. Carrion ecology, evolution, and their applications. Boca Raton: CRC Press, pp. 361–386. https://doi.org/10.1201/b18819

Kakishima S, Terajima Y, Murata J, Tsukaya H. 2011. Infrared thermography and odour composition of the *Amorphophallus gigas* (Araceae) inflorescence: the cooling effect of the odorous liquid. *Plant Biology* 13: 502–507. https://doi.org/10.1111/j.1438-8677.2010.00399.x

Kalinová B, Podskalská H, Růžička J, Hoskovec M. 2009. Irresistible bouquet of death—how are burying beetles (Coleoptera: Silphidae: *Nicrophorus*) attracted by carcasses. *Naturwissenschaften* 96: 889–899. https://link.springer.com/article/10.1007/s00114-009-0545-6

Kang L, Kaur J, Winkeler K, Kubiak D, Hill JE. 2023. How the volatile organic compounds emitted by corpse plant change through flowering. *Scientific Reports* 13, 372. https://doi.org/10.1038/s41598-022-27108-8

Kevan PG, Baker HG. 1983. Insects as flower visitors and pollinators. *Annual Review of Entomology* 28: 407–53. https://www.annualreviews.org/doi/abs/10.1146/annurev.en.28.010183.002203

Kikuzawa K, Mizui N. 1990. Flowering and Fruiting Phenology of *Magnolia hypoleuca*. *Plant Species Biology* 5: 255–261. https://doi.org/10.1111/j.1442-1984.1990.tb00185.x

Kite GC, Hetterscheid WLA. 1997. Inflorescence odours of *Amorphophallus* and *Pseudodracontium* (Araceae). *Phytochemistry* 46: 71–75. https://www.sciencedirect.com/science/article/abs/pii/S0031942297002215?via%3Dihub

Kite GC, Hetterscheid WLA, Lewis M, Boyce PC, Ollerton J, Cocklin E, Diaz A, Simmonds MSJ. 1998. Inflorescence odours and pollinators of *Arum* and *Amorphophallus* (Araceae). In: Owens, S., Rudall, P. (Eds.), Reproductive Biology in Systematics, Conservation and Economic Botany. Kew Publishing, Kew, UK, 295–315. https://www.researchgate.net/publication/261833715_Inflorescence_odours_and_pollinators_of_Arum_and_Amorphophallus_Araceae

Kite GC, Hetterscheid WLA. 2017. Phylogenetic trends in the evolution of inflorescence odours in *Amorphophallus*. *Phytochemistry* 142: 126–142. https://doi.org/10.1016/j.phytochem.2017.06.006

Knoll F. 1926. Die *Arum*–Blütenstande und ihre Besucher. *Abhandlungen der kaiserlich–königlichen zoologisch–botanischen Gesellschaft in Wien* 12: 381–481.

Knutson RM. 1974. Heat production and temperature regulation in eastern skunk cabbage. *Science* 186: 746–747. https://www.science.org/doi/10.1126/science.186.4165.746

Knutson RM. 1979. Plants in heat. *Natural History* 88: 42–47. https://www.aroid.org/gallery/gibernau/1979/Plants%20in%20heat%20-%20Knutson%201979.pdf

Korotkova N, Barthlott W. 2009. On the thermogenesis of the Titan arum (*Amorphophallus titanum*). *Plant Signalling & Behavior* 4: 1096–1098. https://www.tandfonline.com/doi/full/10.4161/psb.4.11.9872

Kozen EN. 2013. The Scent of Eastern Skunk Cabbage, *Symplocarpus foetidus* (Araceae): Qualification of Floral Volatiles and Sex Differences in Floral Scent Composition. Master thesis, Indiana University of Pennsylvania, Indiana.

Küchmeister H, Webber AC, Silberbauer-Gottsberger I, Gottsberger G. 1998. Pollination and its relationship to thermogenesis in species of Arecaceae and Annonaceae of central Amazonia. *Acta Amazonica* 28: 217–245. https://www.scielo.br/j/aa/a/6M9g4Lkw3RwWdSz7wBzFZSS/?format=pdf&lang=pt

Lamprecht I, Schmolz E, Blanco L, Romero CM. 2002. Flower ovens: Thermal investigations on heat-producing plants. *Thermochimica Acta* 391: 107–118. https://www.sciencedirect.com/science/article/abs/pii/S0040603102001685?via%3Dihub

Lamprecht I, Seymour RS. 2010. Thermologic investigations of three species of *Amorphophallus*. *Journal of Thermal Analysis and Calorimetry* 102: 127–136. https://link.springer.com/article/10.1007/s10973-010-0891-9

Landolt E. 1986. The family of Lemnaceae – A monographic study. Vol. 1. Biosystematic Investigations in the Family of Duckweeds (Lemnaceae). *Veröffentlichungen des Geobotanischen Institutes der ETH*, Stiftung Ruebel, Zurich.

Lee JS, Kim S-H, Lee S, Maki M, Otsuka K, Kozhevnikov AE, Kozhevnikova ZV, Wen J, Kim S-C. 2019. New insights into the phylogeny and biogeography of subfamily Orontioideae (Araceae). *Journal of Systematics and Evolution* 57: 616–632. https://onlinelibrary.wiley.com/doi/10.1111/jse.12498

Leick E. 1915. Die Erwärmungstypen der Araceen und ihre blütenbiologische Deutung. *Berichte der Deutschen Botanischen Gesellschaft* 33: 518–536. https://www.zobodat.at/pdf/Ber-Deutschen-Bot-Ges_33_0518-0536.pdf

Lev-Yadun S, Ne'eman G, Shanas U. 2009. A sheep in wolf's clothing: Do carrion and dung odours of flowers not only attract pollinators but also deter herbivores? *BioEssays* 31: 84–88. https://doi.org/10.1002/bies.070191

Lev-Yadun S, Gutman M. 2013. Carrion odor and cattle grazing: evidence for plant defense by carrion odor. *Communicative and Integrative Biology* 6: e26111–3. https://doi.org/10.4161/cib.26111

Lev-Yadun S. 2016. *Defensive (anti-herbivory) coloration in land plants. Anti-herbivory plant coloration and morphology.* Zug: Springer. https://link.springer.com/book/10.1007/978-3-319-42096-7

Lev-Yadun S. 2017. Defensive animal and animal action mimicry by plants. *Israel Journal of Plant Sciences* 64: 179–209. https://brill.com/view/journals/ijps/64/1-2/article-p179_18.xml

Lev-Yadun S. 2021. Avoiding rather than resisting herbivore attacks is often the first line of plant defence. *Biological Journal of the Linnean Society*. 134: 775–802. https://doi.org/10.1093/biolinnean/blab110

Li H, Hetterscheid WLA. 2010. *Amorphophallus*. In: Wu, Z., Raven, P. H. & Deyuan, H. (eds.) Flora of China, Vol. 23. Beijing, China: MBG Press and Science Press, pp. 23–33. http://www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=101404

Li HT, Yi TS, Gao LM, Ma PF, Zhang T, Yang JB, Gitzendanner MA, Fritsch PW, Cai J, Luo Y, Wang H, van der Bank M, Zhang SD, Wang QF, Wang J, Zhang ZR, Fu CN, Yang J, Hollingsworth PM, Chase MW, Soltis DE, Soltis PS, Li DZ. 2019. Origin of angiosperms and the puzzle of the Jurassic gap. *Nature Plants* 5: 461–470. https://www.nature.com/articles/s41477-019-0421-0

Li Y, Svetlana P, Yao J, Li C. 2014. A Review on the Taxonomic, Evolutionary and Phytogeographic Studies of the Lotus Plant (Nelumbonaceae: *Nelumbo*). *Acta Geologica Sinica* 88: 1252–1261. https://doi.org/10.1111/1755-6724.12287

Lin Z, Zhang C, Cao D, Damaris RN, Yang P. 2019. The Latest Studies on Lotus (*Nelumbo nucifera*)-an Emerging Horticultural Model Plant. *International Journal of Molecular Sciences* 20(15): 3680. https://doi.org/10.3390/ijms20153680

Liu D, Zhang P, Liu D, Feng Y, Chi M, Guo Z, Wang X, Zhong J, Sun M. 2023. An Analysis of Volatile Compounds and Study of Release Regularity in the Flower of *Amorphophallus titanum* in Four Periods. *Horticulturae* 9: 487. https://doi.org/10.3390/horticulturae9040487

Liu K, Fadzly N, Mansor A, Zakaria R, Ruppert N, Lee CY. 2017. The dual defensive strategy of *Amorphophallus* throughout its ontogeny. *Plant Signaling & Behavior* 12: e1371890. https://doi.org/10.1080/15592324.2017.1371890

Liu Z, Hao G, Luo Y-B, Thien LB, Rosso SW, Lu A-M, Chen Z-D. 2006. Phylogeny and androecial evolution in Schisandraceae, inferred from sequences of nuclear ribosomal DNA ITS and chloroplast DNA trn L-F regions. *International Journal of Plant Sciences* 167: 539–550. https://aquila.usm.edu/cgi/viewcontent.cgi?article=9729&context=fac_pubs

Lobin W, Neumann M, Radscheit M, Barthlott W. 2007. The cultivation of Titan arum (*Amorphophallus titanum*)—A flagship species for botanic gardens. *Sibbaldia* 5: 69–86. https://doi.org/10.24823/Sibbaldia.2007.8

Low SL, Su T, Spicer TEV, Wu F–X, Deng T, Xing Y–W, Zhou ZK. 2020. Oligocene *Limnobiophyllum* (Araceae) from the central Tibetan Plateau and its evolutionary and palaeoenvironmental implications. *Journal of Systematic Palaeontology* 18: 415–431. https://www.tandfonline.com/doi/full/10.1080/14772019.2019.1611673

Low SL. 2024. Avian frugivory and seed dispersal in *Amorphophallus paeoniifolius and Alocasia odora*. *Tropical Ecology*. https://doi.org/10.1007/s42965-024-00340-1

Maia ACD, Gibernau M, Carvalho AT, Gonçalves EG, Schlindwein C. 2013. The cowl does not make the monk: scarab beetle pollination of the Neotropical aroid *Taccarum ulei* (Araceae: Spathicarpeae). *Biological Journal of the Linnean Society* 108: 22–34. https://doi.org/10.1111/j.1095-8312.2012.01985.x

Marotz–Clausen G, Jürschik S, Fuchs R, Schäffler I, Sulzer P, Gibernau M, Dötterl S. 2018. Incomplete synchrony of inflorescence scent and temperature patterns in *Arum maculatum* L. (Araceae). *Phytochemistry* 154: 77–84. https://doi.org/10.1016/j.phytochem.2018.07.001

Martius CFP. 1831. Über die Art der Befruchtung bei einigen Aroideen und über die Charakteristik mehrerer Gattungen dieser Familie. *Flora oder Allgemeine Botanische Zeitung* 14: 447–464. https://www.biodiversitylibrary.org/item/916#page/35/mode/1up

Mayo SJ, Bogner J, Boyce PC. 1997. *The genera of Araceae*. Royal Botanic Gardens, Kew. https://www.researchgate.net/publication/269552716_The_Genera_of_Araceae

Mayo SJ, Bogner J. 2013. The first evolutionary classification of Araceae: A. Engler's Natural System. In P. Wilkin & S. Mayo (Eds.), Early Events in Monocot Evolution (Systematics Association Special Volume Series). Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9781139002950.011

McPherson S, Hetterscheid WLA. 2011. *Amorphophallus* in the wild and in cultivation. *Plantsman*. June 2011: 90–97. https://www.researchgate.net/publication/283567578_Amorphophallus_in_the_wild_and_in_cultivation

Meeuse BJD, Raskin I. 1988. Sexual reproduction in the arum lily family, with emphasis on thermogenicity. *Sexual Plant Reproduction* 1: 3–15. https://link.springer.com/content/pdf/10.1007/BF00227016.pdf

Merck, 2023. https://www.sigmaaldrich.com/DE/ Accessed 22 September 2023.

Michel JF. 1955. Parasitological significance of bovine grazing behaviour. *Nature* 175: 1088–1089. https://www.nature.com/articles/1751088a0

Michener CD. 2007. The bees of the world, 2nd edn. John Hopkins University Press, Baltimore

Moodie GEE. 1976. Heat production and pollination in Araceae. *Canadian Journal of Botany* 54: 545–546. https://doi.org/10.1139/b76-053

Moretto P, Cosson B, Krell F–T, Aristophanous M. 2019. Pollination of *Amorphophallus barthlottii* and *A. abyssinicus* subsp. *akeassii* (Araceae) by dung beetles (Insecta: Coleoptera: Scarabaeoidea). *Catharsius la Revue* 18: 19–36. https://www.researchgate.net/profile/Philippe-Moretto/publication/332510751_Pollination_of_Amorphophallus_barthlottii_and_A_abyssinicus_subsp_akeassii_Araceae_by_dung_beetles_Insecta_Coleoptera_Scarabaeoidea_Pollinisation_d%27Amorphophallus_barthlottii_et_A_abyssinicus_Araceae_/links/5cb87cdd4585156cd7a1345b/Pollination-of-Amorphophallus-barthlottii-and-A-abyssinicus-subsp-akeassii-Araceae-by-dung-beetles-Insecta-Coleoptera-Scarabaeoidea-Pollinisation-dAmorphophallus-barthlottii-et-A-abyssinicus-Araceae-p.pdf

Naive MAK, Hein KZ, Hetterscheid WLA. 2022. Taxonomic studies of Araceae in Myanmar IV:A new species, a new record and a new synonym for the genus *Amorphophallus*. *Blumea* 67: 123–128. https://doi.org/10.3767/blumea.2022.67.02.05

Naive MAK, Hein KZ, Serebryanyi M, Hetterscheid W. 2024. Taxonomic studies of Araceae in Myanmar VI: *Amorphophallus mirabilis* – a new species and a new record for the genus *Amorphophallus*. *Nordic Journal of Botany* 2024: e04238. https://doi.org/10.1111/njb.04238

Nauheimer L, Metzler D, Renner SS. 2012. Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. *New Phytologist* 195: 938–950. https://nph.onlinelibrary.wiley.com/doi/10.1111/j.1469-8137.2012.04220.x

Nicolas G, Sillans D. 1989. Immediate and latent effects of carbon dioxide on insects. *Annual Review of Entomology* 34: 97–116. https://doi.org/10.1146/annurev.en.34.010189.000525

Nicolson DH. 1977. (429) Proposal to change the typification of 723 *Amorphophallus*, nom. cons. (Araceae). *Taxon* 26: 337–338. https://doi.org/10.2307/1220579

Nicolson DH, Bogner J, Mayo S, Sivadasan M. 1984. Proposal to amend 723 *Amorphophallus*, add *Thomsonia*, nom. rej. prop. (Araceae). *Taxon* 33: 740. https://www.jstor.org/stable/1220801?origin=crossref

Nicolson DH. 1987. Derivation of aroid generic names. *Aroideana* 10: 15–25. https://www.aroid.org/aroideana/artpage.php?key=MDEwMDMwNQ==T

Ollerton J, Raguso RA. 2006. The sweet stench of decay. *New Phytologist* 172: 382–385. https://doi.org/10.1111/j.1469-8137.2006.01903.x

Patiño S, Grace J, Bänziger H. 2000. Endothermy by flowers of *Rhizanthes lowii* (Rafflesiaceae). *Oecologia* 124: 149–155. https://link.springer.com/article/10.1007/s004420050001

Patiño S, Aalto T, Edwards AA, John Grace J. 2002. Is *Rafflesia* an endothermic flower? *New Phytologist* 154: 429–437. https://doi.org/10.1046/j.1469-8137.2002.00396.x

Patwardhan A, Ray S, Roy A. 2014. Molecular Markers in Phylogenetic Studies – A Review. *Journal of Phylogenetics & Evolutionary Biology* 2: 131. https://www.hilarispublisher.com/open-access/molecular-markers-in-phylogenetic-studiesa-review-2329-9002-2-131.pdf

Pincebourde S, Montúfar R, Páez E, Dangles O. 2016. Heat production by an Ecuadorian palm. *Frontiers in Ecology and the Environment* 14: 571–572. https://doi.org/10.1002/fee.1442

PlantNET. 2023. The NSW Plant Information Network System. Royal Botanic Gardens and Domain Trust, Sydney. https://plantnet.rbgsyd.nsw.gov.au/cgi-bin/NSWfl.pl?page=nswfl&lvl=sp&name=Gymnostachys~anceps /Accessed 22 September 2023.

Podskalská H, Růžička J, Hoskovec M, Šálek M. 2009. Use of infochemicals to attract carrion beetles into pitfall traps. *Entomologia Experimentalis et Applicata* 132**:** 59–64. https://doi.org/10.1111/j.1570-7458.2009.00871.x

POWO. 2024a. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:84456-1 /Accessed 12 June 2024.

POWO. 2024b. https://powo.science.kew.org/results?sort=name_asc&page.size=480&q=amorphophallus /Accessed 12 June 2024.

Prain D. 1903. Bengal Plants: a list of the phanerogams, ferns and fern-allies indigenous to, or commonly cultivated in, the Lower provinces and Chittagong Vol. 2 Calcutta, India, pp 1109–1110. https://archive.org/details/in.ernet.dli.2015.47849/page/n453/mode/2up

Prakash PS, Nayar NM. 2000. Thermogenesis in elephant yam, *Amorphophallus paeoniifolius* (Dennst.) Nicolson (Araceae). *Journal of Root Crops* 26: 10–14.

Prance G, Beentje H, Dransfield J, Johns R. 2000. The Tropical Flora Remains Undercollected. *Annals of the Missouri Botanical Garden* 87: 67–71. https://doi.org/10.2307/2666209

Prieto D, Cascante-Marín A. 2017. Pollination by nitidulid beetles in the hemi-epiphytic aroid *Monstera lentii* (Araceae: Monsteroideae). *Flora* 231: 57–64. https://doi.org/10.1016/j.flora.2017.04.010

Prychid CJ, Jabaily RS, Rudall PJ. 2008. Cellular ultrastructure and crystal development in *Amorphophallus* (Araceae). *Annals of Botany* 101: 983–995. https://academic.oup.com/aob/article/101/7/983/133026

PubChem, 2023. https://pubchem.ncbi.nlm.nih.gov/ Accessed 22 September 2023.

Punekar SA, Kumaran KPN. 2010. Pollen morphology and pollination ecology of *Amorphophallus* species from North Western Ghats and Konkan region of India. *Flora* 205: 326–336. https://doi.org/10.1016/j.flora.2009.12.024

Raman V, Tabanca N, Demirci B, Khan IA. 2017. Studies on the floral anatomy and scent chemistry of titan arum (*Amorphophallus titanum*, Araceae). *Turkish Journal of Botany* 41: 63–74. https://doi.org/10.3906/bot-1604-34

Rambey R, Rangkuti AB, Onrizal, Susilowaty A, Wijayanto N, Siregar IZ. 2021. Phenology of the bunga bangkai (*Amorphophallus gigas*) in North Padang Lawas, North Sumatra Province, Indonesia. *IOP Conference Series: Earth and Environmental Science* 782 032019. https://iopscience.iop.org/article/10.1088/1755-1315/782/3/032019/meta

Rambey R, Rahmawaty, Rauf A, Nababan ESM. 2022. Identification of the generative phases of *Amorphophallus gigas* in the Sabungan Village and Langga Payung Village, Sungai Kanan District, North Sumatra Province, Indonesia. *IOP Conference Series: Earth and Environmental Science* 1115 012026. https://iopscience.iop.org/article/10.1088/1755-1315/1115/1/012026

Ramos SE, Schiestl FP. 2020. Evolution of floral fragrance is compromised by herbivory. *Frontiers in Ecology and Evolution* 8:30. https://doi.org/10.3389/fevo.2020.00030

Rands SA. 2021. A commentary on: 'Divergence in floral scent and morphology, but not thermogenic traits, associated with pollinator shift in two brood-site-mimicking *Typhonium* (Araceae) species'. *Annals of Botany* 128: 3. https://doi.org/10.1093/aob/mcab066

Ray TS. 1990. Metamorphosis in the Araceae. *American Journal of Botany* 77:1599–1609. https://doi.org/10.1002/j.1537-2197.1990.tb11400.x

Richardson CR, Clay K. 2001. Sex-ratio variation among *Arisaema* species with different patterns of gender diphasy. *Plant Species Biology* 16: 139–149. https://doi.org/10.1046/j.1442-1984.2001.00058.x

Saiki RK, Gelfand DH, Stoffel S, Scharf SJ, Higuchi R, Horn GT, Mullis KB, Erlich HA. 1988. Primer–directed enzymatic amplification of DNA with a thermostable DNA polymerase. *Science* 239: 487–491. https://www.science.org/doi/10.1126/science.2448875

Saunders RMK. 2020. The evolution of key functional floral traits in the early divergent angiosperm family Annonaceae. *Journal of Systematics and Evolution* 58: 369–392. https://doi.org/10.1111/jse.12645

Sayers TDJ, Steinbauer MJ, Farnier K, Miller RE. 2020. Dung mimicry in *Typhonium* (Araceae): explaining floral trait and pollinator divergence in a widespread species complex and a rare sister species. *Botanical Journal of the Linnean Society* 193: 375–401. https://doi.org/10.1093/botlinnean/boaa021

Sayers TDJ, Johnson KL, Steinbauer MJ, Farnier K, Miller RE. 2021. Divergence in floral scent and morphology, but not thermogenic traits, associated with pollinator shift in two brood-site-mimicking *Typhonium* (Araceae) species. *Annals of Botany* 128: 261–280. https://doi.org/10.1093/aob/mcab044

Schiestl FP, Dötterl S. 2012. The evolution of floral scent and olfactory preferences in pollinators: coevolution or pre–existing bias? *Evolution* 66–67: 2042–2055. https://doi.org/10.1111/j.1558-5646.2012.01593.x

Schimpf NG, Terblanche JS, Smit MF, Matthews PGD. 2017. Respiration, thermogenesis, and thermoregulation of *Victoria cruziana* flowers. *Aquatic Botany* 138: 37–44. https://doi.org/10.1016/j.aquabot.2016.11.014

Schott HW. 1856. Synopsis Aroidearum. Vienna, Austria: Mechitarists' Press. https://www.researchgate.net/publication/281933386_Schott_HW_Synopsis_Aroidearum_complectans_1856

Schott HW. 1857. Aroideen–Skizzen. *Oesterreichisches botanisches Wochenblatt* 7: 261–263. https://www.jstor.org/stable/43793703

Schott HW. 1858a. Genera Aroidearum Exposita. Vienna, Austria: Hölzel. https://www.biodiversitylibrary.org/item/92474#page/2/mode/1up

Schott HW. 1858b. Aroideen–Skizzen. *Oesterreichische botanische Zeitschrift* 8: 317–318. https://www.jstor.org/stable/43803639

Schott HW. 1860. Prodromus Systematis Aroidearum. Vienna, Austria: Mechitarists' Press. https://www.biodiversitylibrary.org/item/1104#page/1/mode/1up

Sedayu A, Eurlings MCM, Gravendeel B, Hetterscheid WLA. 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. https://edepot.wur.nl/175391

Seemann BC. 1869. *Journal of Botany, British and Foreign* 7: 313–315. https://www.biodiversitylibrary.org/item/53384#page/328/mode/1up

Serebryanyi M, Trinh T, Hetterscheid W. 2023. New tuberous Araceae from Binh Thuan Province (South Vietnam). *Blumea* 68: 39–48. https://doi.org/10.3767/blumea.2023.68.01.03.

Seymour RS, Schultze-Motel P. 1997. Heat–producing flowers. *Endeavour* 21: 125–129. https://doi.org/10.1016/S0160-9327(97)80222-0

Seymour RS, Schultze-Motel P, Lamprecht I. 1998. Heat production by sacred lotus flowers depends on ambient temperature, not light cycle. *Journal of Experimental Botany* 49: 1213–1217. https://doi.org/10.1093/jxb/49.324.1213

Seymour RS, Blaylock AJ. 1999. Switching off the heater: influence of ambient temperature on thermoregulation by eastern skunk cabbage *Symplocarpus foetidus*. *Journal of Experimental Botany* 50: 1525–1532. https://doi.org/10.1093/jxb/50.338.1525

Seymour RS, Gibernau M, Itoh K. 2003a. Thermogenesis and respiration of inflorescences of the dead horse arum *Helicodiceros muscivorus*, a pseudo–thermoregulatory aroid associated with fly pollination. *Functional Ecology* 17: 886–894. https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2435.2003.00802.x

Seymour RS, White CR, Gibernau M. 2003b. Heat reward for insect pollinators: scarab beetles save energy by making themselves at home inside a warm flower. *Nature* 426: 243–244.

Seymour RS. 2004. Dynamics and precision of thermoregulatory responses of eastern skunk cabbage *Symplocarpus foetidus*. *Plant, Cell & Environment* 27: 1014–1022. https://doi.org/10.1111/j.1365-3040.2004.01206.x

Seymour RS, Terry I, Roemer RB. 2004. Respiration and thermogenesis by cones of the Australian cycad *Macrozamia machinii*. *Functional Ecology* 18: 925–930. https://doi.org/10.1111/j.0269-8463.2004.00918.x

Seymour RS, Matthews PG. 2006. The role of thermogenesis in the pollination biology of the Amazon waterlily *Victoria amazonica*. *Annals of botany* 98: 1129–1135. https://doi.org/10.1093/aob/mcl201

Seymour RS, Gibernau M. 2008. Respiration of thermogenic inflorescences of *Philodendron melinonii*: natural pattern and responses to experimental temperatures. *Journal of Experimental Botany* 59: 1353–1362. https://doi.org/10.1093/jxb/ern042

Seymour RS, Gibernau M, Pirintsos SA. 2009a. Thermogenesis of three species of *Arum* from Crete. *Plant Cell and Environment* 32: 1467–1476. https://onlinelibrary.wiley.com/doi/10.1111/j.1365-3040.2009.02015.x

Seymour RS, White CR, Gibernau M. 2009b. Endothermy of dynastine scarab beetles (*Cyclocephala colasi*) associated with pollination biology of a thermogenic arum lily (*Philodendron solimoesense*). *Journal of Experimental Biology* 212: 2960–2968. https://doi.org/10.1242/jeb.032763

Seymour RS, Yuka I, Onda Y, Ito K. 2009c. Effects of floral thermogenesis on pollen function in Asian skunk cabbage *Symplocarpus renifolius*. *Biology Letters* 5: 568–570. https://doi.org/10.1098/rsbl.2009.0064

Seymour RS, Maass E, Bolin JF. 2009d. Floral thermogenesis of three species of *Hydnora* (Hydnoraceae) in Africa. *Annals of Botany* 104: 823–832. https://doi.org/10.1093/aob/mcp168

Seymour RS. 2010. Scaling of heat production by thermogenic flowers: limits to floral size and maximum rate of respiration. *Plant, Cell and Environment* 33: 1474–1485. https://doi.org/10.1111/j.1365-3040.2010.02190.x

Seymour RS, Silberbauer-Gottsberger I, Gottsberger G. 2010. Respiration and temperature patterns in thermogenic flowers of *Magnolia ovata* under natural conditions in Brazil. *Functional Plant Biology* 37: 870–878. https://doi.org/10.1071/FP10039

Shaw DE. 1997. *Gymnostachys anceps* R. Br.: Fruit, Germination, and a Discussion of the Possible Means of Dispersal. *Aroideana* 20: 71–78. https://www.aroid.org/gallery/gibernau/aroideana/0200014.pdf

Shirasu M, Fujioka K, Kakishima S, Nagai S, Tomizawa Y, Tsukaya H, Murata J, Manome Y, Touhara K. 2010. Chemical identity of a rotting animal–like odor emitted from the inflorescence of the titan arum (*Amorphophallus titanum*). *Bioscience, Biotechnology, and Biochemistry* 74: 2550–2554. https://doi.org/10.1271/bbb.100692

Silberbauer-Gottsberger I, Webber A, Küchmeister H, Gottsberger G. 2001. Convergence in beetle-pollinated Central Amazonian Annonaceae, Araceae, Arecaceae, and Cyclanthaceae. *Dissertationes Botanica* 346B: 165–183.

Sin S, Khin C, Chhorn S, Yok G, Phak S, Thou S, Phauk S. 2021. First record of the carrion beetle *Diamesus osculans* (Vigors, 1825) in Cambodia. *Cambodian Journal of Natural History* 8–11. http://rupp.edu.kh/cjnh/journal/CJNH-2021-1/CJNH%2021-30%20Sin%20et%20al.pdf

Singh SN, Gadgil M. 1995. Ecology of *Amorphophallus* species in Uttara Kannada District of the Karnataka State, India: implications for conservation. *Aroideana* 18: 5–20. https://www.researchgate.net/publication/277999989_Ecology_of_amorphophallus_species_in_Uttara_Kannada_District_of_the_Karnataka_State_India_implications_for_conservation

Sites RW. 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: 107–109. https://thesiamsociety.org/wp-content/uploads/2020/04/NHBSS_062_11_Sites.pdf

Sivadasan M, Sabu T. 1989. Beetle pollination – cantharophily – in *Amorphophallus hohenackeri* (Araceae). *Aroideana* 12: 32–37. https://www.aroid.org/gallery/gibernau/aroideana/0121411.pdf

Skubatz H, Nelson TA, Dong AM, Meeuse BJD, Bendich AJ. 1990. Infrared thermography of Arum lily inflorescences. *Planta* 182: 432–436. https://link.springer.com/article/10.1007/BF02411396

Skubatz H, Kunkel DD, Meeuse BJD. 1993. The ultrastructural changes in the appendix of the *Sauromatum guttatum* inflorescence. *Sexual Plant Reproduction* 6: 153–170. https://link.springer.com/article/10.1007/BF00228644

Skubatz H, Kunkel DD, Patt J, Howald W, Rothman T, Meeuse BJD. 1995. Pathway of terpene excretion by the appendix of *Sauromatum guttatum*. *Proceedings of the National Academy of Sciences* 92: 10084–1088. https://www.pnas.org/doi/abs/10.1073/pnas.92.22.10084

Skubatz H, Kunkel DD, Howald WN, Trenkle R, Mookherjee B. 1996. The *Sauromatum guttatum* appendix as an osmophore: excretory pathways, composition of volatiles and attractiveness to insects. *New Phytologist* 134: 631–640. https://nph.onlinelibrary.wiley.com/doi/10.1111/j.1469-8137.1996.tb04928.x

Skubatz H, Kunkel DD. 1999. Further studies of the glandular tissue of the *Sauromatum guttatum* (Araceae) appendix. *American Journal of Botany* 86: 841–854. https://www.jstor.org/stable/2656705

Skubatz H, Calonje M, Tang W. 2019. Thermogenesis in male cones of four cycad species. *Theoretical and Experimental Plant Physiology* 31: 287–293. https://doi.org/10.1007/s40626-018-0137-y

Soepadmo E. 1973. A short note on *Amorphophallus* cf. *prainii* Hook.f. *Malayan Nature Journal* 25: 133–134.

Sofiyanti N, Mat-Salleh K, Mahmud K, Mazlan NZ, Hasein MRA, Burslem DFRP. 2016. *Rafflesia parvimaculata* (Rafflesiaceae), a new species of *Rafflesia* from Peninsular Malaysia. *Phytotaxa* 253: 207–213. https://doi.org/10.11646/phytotaxa.253.3.4

Sookchaloem D, Sungkajanttranon O, Petchsri S, Horadee S, Huayhongthong C, Vanapanich A, Wongsawaddiwattana C. 2016. Leaf blade anatomy characteristics of the genus *Amorphophallus* Blume ex Decne. in Thailand. *Agriculture and Natural Resources* 50: 437–444. https://doi.org/10.1016/j.anres.2016.09.002

Sosef MSM, Dauby G, Blach–Overgaard A. et al. 2017. Exploring the floristic diversity of tropical Africa. *BMC Biol* 15: 15. https://doi.org/10.1186/s12915-017-0356-8

Sree K, Bog M, Appenroth K. 2016. Taxonomy of Duckweeds (Lemnaceae), Potential New Crop Plants. *Emirates Journal of Food and Agriculture* 28: 291–302. https://doi.org/10.9755/ejfa.2016-01-038

Srivastava P, Banerji BK. 2012. Gender biasing in *Arisaema* – a unique and rare phenomenon. *Current Science* 102: 189–193. https://www.jstor.org/stable/24083847

Srzednicki G, Borompichaichartkul C. (eds). 2020. Konjac Glucomannan Production, Processing, and Functional Applications Edited by Published June 24, 2020 by CRC Press 286 pages – 125 Color & 48 B/W Illustrations. https://doi.org/10.1201/9780429429927

Stensmyr MC, Urru I, Collu I, Celander M, Hansson BS, Angioy A-M. 2002. Rotting smell of dead–horse arum florets. *Nature* 420: 625–626. https://www.nature.com/articles/420625a

Suresh CR, Sivadasan M, Manilal KS. 1983. A Commentary on Rheede's Aroids. *Taxon* 32: 126–132. https://doi.org/10.2307/1219869

Tamayo M, Magtot L, Sumalinog JR, Reyes JR, Austria CM. 2021. *Amorphophallus calcicolus* (Thomsonieae, Araceae), a new species from the Bohol island, Central Visayas, Philippines. *Phytotaxa* 489: 229–235. http://dx.doi.org/10.11646/phytotaxa.489.2.12

Tang W. 1987a. Heat production in Cycad cones. *Botanical Gazette* 148:165–174. https://www.jstor.org/stable/2995471

Tang W. 1987b. Insect pollination in the cycad *Zamia pumila* (Zamiaceae). *American Journal of Botany* 74: 90–99. https://doi.org/10.1002/j.1537-2197.1987.tb08582.x

Tang R, Li Y, Xu Y, Schinnerl J, Sun W, Gao Chen G. 2020. In-situ and ex situ pollination biology of the four threatened plant species and the significance for conservation. *Biodiversity and Conservation* 29: 381–391. https://doi.org/10.1007/s10531-019-01887-5

Teijsmann JE, Binnendijk S. 1862. *Amorphophallus gigas*. *Natuurkundig tijdschrift voor Nederlandsch Indië /uitgegeven door de Natuurkundige Vereeniging inNederlandsch Indië*. 24: 329–331. https://archive.org/details/natuurkundigtijd24koni/page/328/mode/2up

Terry I, Moore CJ, Walter GH, Forster PI, Roemer RB, Donaldson JD, Machin PJ. 2004. Association of cone thermogenesis and volatiles with pollinator specificity in Macrozamia cycads. *Plant Systematics and Evolution* 243: 233–247. https://link.springer.com/article/10.1007/s00606-003-0087-x

Terry I, Walter GH, Moore C, Roemer R, Hull C. 2007. Odor-mediated push-pull pollination in cycads. *Science* 318(5847):70. https://www.science.org/lookup/doi/10.1126/science.1145147

Terry I, Tang W, Blake AST, Donaldson JS, Rita Singh R, Vovides AP, Jaramillo AC. 2012. Publ. 24 An Overview of Cycad Pollination Studies. In: Stevenson DW, Osborne R, Blake AST (eds). 2012. Proceedings of Cycad 2008: the 8th International Conference on Cycad Biology; Panama City, Panama. New York: New York Botanical Garden Press. https://www.researchgate.net/publication/259667752_An_overview_of_cycad_pollination_studies

Terry I, Roemer RB, Booth DT, Moore CJ, Walter GH. 2016. Thermogenic respiratory processes drive the exponential increase of volatile organic compound emissions in *Macrozamia* cycad cones. *Plant, Cell & Environment* 39: 1588–1600. doi: 10.1111/pce.12730. https://onlinelibrary.wiley.com/doi/abs/10.1111/pce.12730

Thien LB, Bernhardt P, Devall MS, Chen ZD, Luo YB, Fan JH, Yuan LC, Williams JH. 2009. Pollination biology of basal angiosperms (ANITA grade). *American Journal of Botany* 96: 166–182. https://doi.org/10.3732/ajb.0800016

Tippery NP, Les DH, Appenroth KJ, Sree KS, Crawford DJ, Bog M. 2021. Lemnaceae and Orontiaceae are phylogenetically and morphologically distinct from Araceae. *Plants* 10, no. 12: 2639. https://doi.org/10.3390/plants10122639

Tomassoli L. 1996. Fenzi, Emanuele Orazio – in: Dizionario Biografico degli Italiani (Feducci–Ferrerio), Volume 46. Roma: Istituto della Enciclopedia italiana. https://www.treccani.it/enciclopedia/emanuele-orazio-fenzi_%28Dizionario-Biografico%29/

Trumbo ST, Steiger S. 2020. Finding a fresh carcass: bacterially derived volatiles and burying beetle search success. *Chemoecology* 30: 287–296. https://doi.org/10.1007/s00049-020-00318-0

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W–H, Li D–Z, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF (eds.). 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. *Regnum Vegetabile* 159. Glashütten: Koeltz Botanical Books. https://doi.org/10.12705/Code.2018

Ulrich S, Hesse M, Weber M, Halbritter H. 2017. *Amorphophallus*: New insights into pollen morphology and the chemical nature of the pollen wall. *Grana* 56: 1–36. https://doi.org/10.1080/00173134.2015.1133699

Urru I, Stensmyr MC, Hansson BS. 2011. Pollination by brood–site deception. *Phytochemistry* 72: 1655–1666. https://doi.org/10.1016/j.phytochem.2011.02.014

van der Ham R, Grob G, Hetterscheid WLA, Star W, van Heuven BJ. 2005. Notes on the genus *Amorphophallus* (Araceae) – 13. Evolution of pollen ornamentation and ultrastructure in *Amorphophallus* and *Pseudodracontium*. *Grana* 44: 252–265. https://www.tandfonline.com/doi/pdf/10.1080/00173130500424417

van der Kooi CJ, Kevan PG, Koski MH. 2019. The thermal ecology of flowers. *Annals of Botany* 124: 343–353. https://doi.org/10.1093/aob/mcz073

van der Pijl L. 1937. Biological and physiological observations on the inflorescence of *Amorphophallus*. *Recueil des travaux botaniques néerlandais* 34: 57–67. https://natuurtijdschriften.nl/pub/552594

van Rheede HA. 1692. *Hortus Malabaricus* Vol. 11 Amsterdam, pp 34–37. https://www.biodiversitylibrary.org/item/14380#page/44/mode/1up

Vereecken NJ, McNeil JN. 2010. Cheaters and liars: chemical mimicry at its finest. *Canadian Journal of Zoology* 88: 725–752. https://doi.org/10.1139/Z10-040

Vogel S. 1963. Duftdrüsen im Dienste der Bestäubung: über Bau und Funktion der Osmophoren. *Abhandlungen der Mathematisch–Naturwissenschaftlichen Klasse, Akademie der Wissenschaften und der Literatur in Mainz* 1962 10: 639–677.

Vogel S. 1990. The role of scent glands in pollination. On the structure and function of osmophores. English translation of Vogel S. (1963) “Duftdrüsen im Dienste der Bestäubung. Über

Bau und Funktion des Osmophoren". In Renner S. (ed) Smithsonian Institution Libraries and The National Science Foundation, Washington, D.C. 44–89.

Vogel S, Martens J. 2000. A survey of the function of the lethal kettle traps of *Arisaema* (Araceae), with records of pollinating fungus gnats from Nepal. *Botanical Journal of the Linnean Society* 133: 61–100. https://doi.org/10.1006/bojl.1999.0317

Wagner AM, Krab K, Wagner MJ, Moore AL. 2008. Regulation of thermogenesis in flowering Araceae: The role of the alternative oxidase. *Biochimica et Biophysica Acta* 1777: 993–1000. https://doi.org/10.1016/j.bbabio.2008.04.001

Wallich NW. 1830. *Plantae Asiaticae Rariores* 1: pp 83–84. https://www.biodiversitylibrary.org/item/9714#page/193/mode/1up

Wang R, Liu X, Mou S, Xu S, Zhang Z. 2013. Temperature regulation of floral buds and floral thermogenicity in *Magnolia denudata* (Magnoliaceae). *Trees* 27: 1755-1762. https://link.springer.com/article/10.1007/s00468-013-0921-x

Wang R, Xu S, Liu X, Zhang Y, Wang J, Zhang Z. 2014. Thermogenesis, Flowering and the Association with Variation in Floral Odour Attractants in *Magnolia sprengeri* (Magnoliaceae). *PLoS One*. 2014; 9(6): e99356. https://doi.org/10.1371/journal.pone.0099356

Wang R, Zhang Z. 2015. Floral thermogenesis: An adaptive strategy of pollination biology in Magnoliaceae. *Communicative & Integrative Biology* 8: 1 e992746. https://doi.org/10.4161/19420889.2014.992746

Watson W. 1889. *Amorphophallus Titanum*. *Garden and Forest: A Journal of Horticulture, Landscape Art, and Forestry* 11: pp 340–342. https://www.biodiversitylibrary.org/item/107316#page/358/mode/1up

Watson L, Dallwitz MJ. 1992 onwards. The families of flowering plants: descriptions, illustrations, identification, and information retrieval. Version: 11th November 2023. https://www.delta-intkey.com/angio/index.htm

WCSP. 2024. World Checklist of Selected Plant Families. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:60444138-2#synonyms/ Accessed 12 June 2024.

Winkler H. 1931. Einige Bemerkungen über Mangrove-Pflanzen und den *Amorphophallus titanum* im Hamburger Botanischen Garten. *Berichte der Deutschen Botanischen Gesellschaft* 49: 87–102.

Wong SY, Nor Fathiah AR, Hetterscheid WLA. 2022. Phylogeny of *Amorphophallus* (Araceae) on Borneo with notes on the floral biology of three species. *Taiwania* 67: 55–66. https://taiwania.ntu.edu.tw/pdf/tai.2022.67.55.pdf

Yuan L-C, Luo Y-B, Thien LB, Fan J-H, Xu H-L, Chen Z-D. 2007. Pollination of *Schisandra henryi* (Schisandraceae) by female, pollen-eating *Megommata* species (Cecidomyiidae,

Diptera) in south central China. *Annals of Botany* 99: 451–460. https://doi.org/10.1093/aob/mcl287

Yuan L-C, Luo Y-B, Thien LB, Fan J-H, Xu H-L, Chen Z-D . 2008. Pollination of *Kadsura longipedunculata* (Schisandraceae), a monoecious basal angiosperm, by female, pollen-eating *Megommata* sp. (Cecidomyiidae: Diptera) in China. *Biological Journal of the Linnean Society* 93: 523–536. https://doi.org/10.1111/j.1095-8312.2007.00897.x

Yudaputra A, Fijridiyanto IA, Witoni JR, Astuti IP. 2021. The plant expedition of an endangered giant flower *Amorphophallus titanum* in Sumatra. *Warta Kebun Raya* 19: 23–29.

Yuzammi Y, Witono JK, Hetterscheid WLA. 2014. Conservation status of *Amorphophallus discophorus* Backer &Alderw. in Java, Indonesia. *Reinwardtia* 14: 27– 33. https://www.researchgate.net/publication/283567660_Conservation_status_of_Amorphophallus_discophorus_Backer_Alderw_Araceae_in_Java_Indonesia

Yuzammi Y, Kurniawan A, Asih NPS, Erlinawati I, Hetterscheid WLA. 2017. The *Amorphophallus* of Indonesia. Bogor: LIPI Center for Plant Conservation – Botanic Gardens, Indonesian Institute of Sciences.

Yuzammi Y, Hadiah JT. 2018. *Amorphophallus titanum*. The IUCN Red List of Threatened Species 2018: e.T118042834A118043213. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T118042834A118043213.en

Yuzammi Y, Hetterscheid WLA. 2020. A new species of *Amorphophallus* (Araceae-Thomsonieae) from Sulawesi, Indonesia. *Phytotaxa* 461: 6. https://doi.org/10.11646/phytotaxa.461.4.6

Zhao L, Yang YY, Qu XJ, Ma H, Hu Y, Li HT, Yi TS, Li DZ. 2023. Phylotranscriptomic analyses reveal multiple whole-genome duplication events, the history of diversification and adaptations in the Araceae. *Annals of Botany* 131: 199–214. https://doi.org/10.1093/aob/mcac062

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Declaration on oath - Eidesstattliche Erklärung

I hereby declare in lieu of an oath that I have completed the present dissertation independently and without outside help, unless otherwise stated, and that I have not used any further resources and aids others than those indicated. The passages in the work which have been taken from other works, either in wording or in meaning, are always indicated.

Hiermit erkläre ich an Eides statt, daß ich die vorliegende Dissertation, wenn nicht anders angegeben, selbstständig und ohne fremde Hilfe verfasst und keine anderen als die angegebenen Hilfsmittel benutzt habe. Die Stellen der Arbeit, die dem Wortlaut oder dem Sinn nach anderen Werken entnommen wurden, sind in jedem Fall unter Angabe der Quelle kenntlich gemacht.

Hamburg, den 07.05.2024