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Comparative pollen morphology with respect to different functional groups of pollinators in Araceae

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Abstract

Araceae are overwhelmingly diverse, particularly with respect to their highly specialized inflorescences and flowering cycles. Their diversification began in the Early Cretaceous and led to a cosmopolitan distribution with the highest diversity in the tropics of America and Asia. However, until today the Araceae family remains surprisingly understudied. Their morphological diversity has often been associated with their diverse plant-pollinator interactions. This thesis aims to compare the pollen morphology with respect to different functional groups of pollinators in different Araceae species. Pollen ornamentation was investigated by Scanning Electron Microscopy (SEM) to determine potential correlations with different functional groups of pollinators. In addition, inflorescence morphology, pollen structure, and pollination biology of *Dracontium pittieri* were studied in detail in the field in Costa Rica. The present thesis demonstrates genus-specific ornamentation characteristics of pollen in *Anthurium*, *Syngonium,* and *Philodendron.* For *Anthurium*, we found Euglossini and Cecidomyiidae associated with reticulate pollen ornamentation. In *Syngonium* echinate pollen ornamentation was found in all investigated species suggesting a specialized plant-bug pollination system. In *Philodendron* psilate pollen structure was found correlating with a beetle pollination system. The lack of ornamentation in *Philodendron* is substituted by the presence of pollenkitt. For *D. pittieri,* we found an imperfect trap mechanism that is based on a specialized carrion-mimicry system. The coloration and construction of the spathe are adapted to trapping visiting insects. The epidermis surface of the chamber is slippery and contributed greatly to the trapping of insects. *D. pittieri* emits a strong, fetid scent that attracts beetles of the Histeridae family as pollinators. The investigation of pollen ornamentation supports the hypothesis of a specialized beetle pollination system in *D. pittieri*. The present study shows that ornamentation of pollen may give valuable insights into pollination biology, but that more aspects have to be considered to understand the complex processes behind pant-pollinator interactions.

Keywords: Araceae, pollen, pollination, plant-pollinator interaction, trap flowers, carrion-mimicry system.

Zusammenfassung

Die Familie der Araceae weist eine erstaunliche Vielfalt auf, vor allem im Hinblick auf den Bau der Blütenstände und den Blühverlauf. Ihre Diversifizierung begann in der frühen Kreidezeit und führte zu einer kosmopolitischen Verbreitung mit der größten Diversität in den Tropen Amerikas und Asiens. Doch bis heute ist die Familie der Araceae erstaunlich wenig erforscht. Ihre morphologische Diversität wird häufig mit den vielfältigen Interaktionen zwischen Pflanzen und Bestäubern in Verbindung gebracht. Ziel dieser Arbeit ist es, die Pollenmorphologie verschiedener Araceae-Arten im Hinblick auf unterschiedliche Bestäubergruppen zu vergleichen. Die Oberflächenstruktur des Pollens wurde mittels Rasterelektronenmikroskopie (REM) untersucht, um eine Korrelation mit jeweiligen Bestäubergruppen zu ermitteln. Zusätzlich wurden die Blütenstandsmorphologie, die Pollenstruktur und die Bestäubungsbiologie von *Dracontium pittieri* im Detail untersucht. Dazu wurden Feldbeobachtungen zur Interaktion zwischen *D. pittieri* und Blütenbesuchern in Costa Rica durchgeführt. Die vorliegende Arbeit zeigt gattungsspezifische Oberflächenstrukturen von Pollen bei *Anthurium*, *Syngonium* und *Philodendron*.

In *Anthurium* wurden Bestäuber aus der Familie Euglossini und Cecidomyiidae in Kombination mit einer retikulaten Oberflächenstruktur des Pollens in Verbindung gefunden. In *Syngonium* wurden für alle untersuchten Arten eine echinate Oberflächenstruktur vorgefunden, die möglicherweise auf eine spezialisierte Wanzen-Bestäubung hinweisen. In *Philodendron* wurde eine psilate Oberflächenstruktur des Pollens vorgefunden, die in Verbindung zur Käferbestäubung steht. Das Fehlen weiterer Oberflächenstrukturen in *Philodendron* wird mit der Produktion von Pollenkitt substituiert. Bei *D. pittieri* wurde eine imperfekte Fallenkonstruktion und ein spezialisiertes Aas-Mimikry System gefunden. Die Färbung und die Form der Spatha sind an das Fangen von besuchenden Insekten angepasst. Die Epidermis der Kammer ist rutschig und trägt zum Fangen von Insekten bei. *D. pittieri* emittiert einen starken, aasigen Geruch, der Käfer aus der Familie der Histeridae als Bestäuber anlockt. Die Untersuchung der Oberflächenstruktur des Pollens gibt weiteren Einblick in die Bestäubungsbiologie, dennoch müssen weitere Aspekte berücksichtigt werden, um die komplexen Prozesse hinter den Interaktionen von Pflanzen und Bestäubern zu verstehen.

Schlagwörter: Araceae, Pollen, Bestäubung, Pflanzen-Bestäuber Interaktion, Kesselfallenblume, Aas-Mimikry System.

1. Introduction

Angiosperms, also referred to as flowering plants, are the largest and most diverse group within the plant kingdom. They are represented by more than 300,000 species, which is around 80 percent of all currently known plants on Earth (Ulrich *et al.*, 2013). Their vast diversification has often been linked to adaptations to different insect pollinators, which play a dominant role in the reproductive biology of flowering plants (Bernhardt, 2000). Beetle pollination also known as cantharophily is likely one of the oldest pollination systems together with pollination by flies, moths, trips, and true bugs (Sivadasan and Sabu, 1989). Biotic pollination systems may have evolved from ancestrally antagonistic systems (Pellmyr and Thien, 1986). Insects may have acted as florivores that used flowers primarily as feeding and mating sites. Subsequently, more specialized pollination interactions have evolved and led to the astonishing diversity of today's angiosperms. The idea of an evolutionary shift from an antagonistic origin to a specialized mutualistic pollination system appears intuitive, but evidence is scarce and uncertain. A recent study by Etl *et al.,* (2022) presents such a transition from florivory to a pollination mutualism in *Syngonium hastiferum* (Araceae) and bugs of the family Miridae. Etl *et al.,* (2022) showed that a shift from an antagonistic to a mutualistic relationship was accompanied by changes in floral traits such as thermogenesis, scent release, and pollen morphology (Etl *et al.*, 2022).

The Araceae are monophyletic and sister group to the rest of the monocot order Alismatales (Petersen *et al.*, 2016). They comprise around 130 genera with approximately 6000 species. Their diversification began in the Early Cretaceous and led to highly specialized inflorescences and pollination mechanisms (Ulrich *et al.*, 2013). As hypothesized by Mayo *et al.,* (1997), early Araceae have probably first occurred in wet habitats with Laurasia as a center of distribution. Later, their distribution extended towards Africa, South America, Asia, and Australia. Today, they have a cosmopolitan distribution with highest diversity in the tropics of America and Asia. They show a broad variety of life forms including epiphytes, hemi epiphytes, terrestrial herbs, and even free-floating aquatics. Until today, the Araceae remain surprisingly understudied and are poorly represented in herbaria (Mayo *et al.,* 1997). General knowledge about the family appears rather incomplete and new genera and species are still regularly found and described. Therefore, the Araceae classification must be considered as an ongoing progress. Mayo *et al.,* (1997) presented a phylogenetic framework of Araceae and proposed eight subfamilies: I) Gymnostachydoidae, II) Orontioideae, III) Lemnoidae, IV) Pothoideae, V) Monsteroidae, VI) Lasioideae, VII)

Zamioculcadoidae and VIII) Aroideae. This classification is supported by more recent molecular phylogenetic analyses (Cabrera *et al.*, 2008).

In spite of their species richness and their diversity of lifeforms, all Araceae share a characteristic feature: The typical inflorescence of a spadix bearing numerous flowers, which is surrounded by a bract also referred to as spathe. Due to their diverse pollination systems, inflorescence forms, and widespread deceptive trapping mechanisms, the Araceae are a suitable research subject for the study plant-pollinator interactions and pollinator shifts. This work focuses on a detailed comparative analysis of inflorescence and floral morphology, pollen structure, scent emission patterns, and pollination behavior in several Araceae species (from the genera *Philodendron, Syngonium, Anthurium*, and *Dracontium*) with different functional groups of pollinators.

The studied species of *Philodendron* and *Syngonium* belong to the subfamily Aroideae. The Aroideae consist of 72 genera and at least 2670 species , which are characterized by having only unisexual flowers (Boyce and Sin Yeng, 2012). The female flowers are usually located in the basal part of the spadix and the male flowers usually in the apical part. Occasionally, they are separated by sterile flowers that are involved in the functioning of the trapping mechanisms. These so-called floral traps are among the most sophisticated devices that have evolved in the context of pollination (Bröderbauer *et al.,* 2012). Modification of floral organs and the evolution of novel organs have enabled the vast adaptations to different functional groups of pollinators (e.g., flies, beetles). The floral traps are characterized by the formation of a chamber enclosing reproductive organs and potential pollination rewards. The chamber often shows different adaptations for trapping including slippery surfaces of the epidermis, elongated sterile flowers or the constriction of the spathe. Additionally, some species produce wax platelets or emit strong scent (Bröderbauer *et al.,* 2013). Based on these trapping devices, different types of floral traps can be distinguished (Bröderbauer *et al.,* 2012). As members of the Araceae family, Aroideae show a clearly separated flowering of female and male phase (Boyce and Sin Yeng, 2012). During the female phase, pollinators are arrested for a distinct period of time and can only escape once pollen is released during the male phase. How these diverse and complex traps have evolved remains still unknown (Bröderbauer *et al.,* 2012).

The genus *Anthurium* belong to the subfamily Pothoideae. The Pothoideae is the second largest subfamily consisting of approximately more than 1000 described species (Boyce and Croat, 2018). Members of Pothoideae are recognized by bisexual flowers and a simple spathe not enclosing the spadix (Mayo *et al.*,1997). The flowering sequence can last several weeks, with a female phase usually shorter than the male phase (Mayo *et al.*,1997). Floral odors and floral traits are diverse

among species. The general floral morphology is less elaborate offering exposed rewards for floral visitors including pollen, stigmatic fluids, floral tissues, or floral scent (Jiménez *et al.*, 2019). A great diversity of pollination systems exists in this subfamily ranging from bee-pollination, over curculionid-pollinated species, to unique vertebrate pollination systems (Gibernau, 2011).

The genus *Dracontium* belongs to the subfamily Lasioideae, which consists of ten genera (Mayo *et al.*,1997). Members of Lasioideae have bisexual flowers and the spathe surrounds the spadix forming a chamber around the flowers. The anthesis usually last for several days. Pollination systems involve Diptera and Coleoptera are characterized by involving trap mechanism (Bröderbauer *et al.,* 2012).

In order to understand the morphological diversity of flowers, their interactions with their respective insect pollinators must be understood. Generally, an important distinction can be drawn between floral advertisements and floral rewards. Among advertisement traits, olfactory and visual cues play a crucial role in the attraction of pollinators. In Araceae, attraction of pollinators to inflorescence is mainly mediated by floral scents varying highly among taxa (Milet-Pinheiro *et al.*, 2017). In species pollinated by male euglossini bees (Schwerdtfeger *et al.,* 2002; Hentrich *et al.,* 2010) or cyclocephaline scarabs (Gottsberge *et al.*, 2013; Maia *et al.*, 2013), usually a pleasant and sweet scent is emitted to attract pollinators from distance. These pleasant flowery scents often contain substances as geraniol or citronellol and are the most common to attract a variety of insects. Some specialized bee pollinated systems use scent mimicking insect pheromones, particularly sexual hormones to attract their pollinators. Other specialized species pollinated by flies or coprophagous scarabs often emit unpleasant carrion- and dung-like scent usually consisting of amines, ammonia, and indoles (Jürgens *et al*., 2006). These often come along with deception of flies or beetles and are found in many Araceae (Jürgens and Shuttleworth, 2015). Even though the scent itself does generally not function as a reward for the visiting insect, it guides the way to the actual rewards, which is pollen, nectar or more rarely food bodies in Araceae (Endress, 2001). Pollen appears to be an extremely nutritious and valuable reward containing highly important proteins, carbohydrates, and sugars for the visiting insects. Therefore, pollen diversification appears to be strongly correlated with pollination types in Araceae, as proposed by some authors (Chartier *et al*., 2014).

The pollen of Araceae is highly diverse, particularly in pollen wall structure. A possible correlation between ornamentation and pollination syndromes in Araceae was first postulates by Grayum (1986). Sannier *et al.*, (2009) found a clear correlation between psilate pollen wall structure with beetle pollination and echinate pollen with fly pollination in Araceae. It was suggested that the

lack of pollen ornamentation in beetle pollinated species is substituted by a secretion on the stigma and/or the inner spathe surface that may play the same role as pollenkitt (Hesse, 2000). Pollen as a food reward for pollinating insects might appear to be a waste of important resources, but even the most specialized insect cannot groom its body completely clean and cannot avoid pollen adhering to its body surface and making it an effective pollinator. Differences in mouth parts, leg structure, and sensory capacities of pollinating insects may provide important background information to interpret the morphology and evolution of flowers (Conner, 1997).

Besides pollen, other common floral rewards in Araceae are stigmatic exudates, floral tissues, heat, and providing sites for oviposition, rendezvous, refuge, or mating (Bernhardt, 2000). But observation of pollinators and pollination rewards of Araceae have only been documented in about 6% of all known species, mostly representing the bisexual genera *Anthurium*, *Monstera,* and *Spathiphyllum* (Díaz Jiménez *et al.*, 2019). Currently, detailed studies are very limited. A recent study in a species with unisexual flowers, *Syngonium hastiferum,* has shown that spiny pollen is related to plant bug pollination while related *Syngonium* species with smooth pollen are pollinated by scarab beetles (Etl *et al.*, 2022). Within the genus *Syngonium* there are three distinct pollen morphologies known so far (spiny, smooth, and warty), most probably referring to different pollination strategies. Also, in other species-rich genera like *Amorphophallus,* reports indicate a broad diversity of pollinators. The most common assumed pollinators in *Amorphophallus* belong to three beetle families Dynastinae, Hybosoridae, Scarabidae (Sivadasan and Sabu, 1989). However, other observations involving smaller beetles e.g., Nitidulidae or Staphilinidae exist (Punekar and Kumaran, 2010) and flies of the families Calliphoridae and Muscidae have been reported as pollinators as well (Chen *et al.*, 2015). Recently, stingless bees have been repeatedly observed on different *Amorphophallus* species in different tropical regions across Asia (Claudel and Lev-Yadun, 2021). Interestingly, several different pollen morphologies were found for *Amorphophallus* species (Ulrich *et al.*, 2017) supporting the hypothesizes of a correlation between pollination specialization and pollen morphology. But so far, only beetle-pollinated species have been studied.

It becomes evident that pollination systems in Araceae are still poorly understood. Therefore, the behavior of the visiting insects must be studied as well as the floral traits of the plants. This thesis aims to understand more about the evolutionary processes behind the diversification of the angiosperm family Araceae with regard to the shift from antagonistic to mutualistic interactions and by focusing on floral and pollen morphological adaptations (including trapping mechanisms), scent emission patterns, and pollinator behavior in different Araceae species from the genera

Syngonium, *Philodendron*, and *Anthurium.* I hypothesized I) that pollination by different groups of pollinators is reflected in differences in pollen morphology and morphological adaptation of inflorescences. In addition, I focused on *Dracontium pittieri*. The genus *Dracontium* has a Neotropical distribution but shows similarities to the paleotropical genus *Amorphophallus*. The former genus is currently recognized with 23 species and represents the most species-rich tuberous genus within Araceae, but surprisingly very little is known about its pollinations systems. *Dracontium pittieri* emits a strong fetid scent at anthesis and flowers are dark purplish in color similar to carrion-mimicking Araceae like *Amorphophallus* (Kite and Hetterschieid, 1997; Benbow *et al.*, 2015), but actual pollinators remain unknown (Zhu and Croat, 2004). *D. pittieri* provides an interesting case for investigating a specialized insect pollination system with deceptive mechanism. I hypothesized that II) *D. pittieri* is specialized on beetle pollination and uses a specific scent pattern to attract pollinators, III) that its pollen structure is psilate combined with pollenkitt, and IV) that its carrion-mimicry system also involves trapping devices to imprison its pollinators.

2. Material and Methods

2.1 Study areas

The field work for this study was conducted from February until April 2023 during the dry season in Costa Rica, Central America. Its neighboring countries are Nicaragua in the north and Panama in the southeast and it is surrounded by the Caribbean Sea in the east and the Pacific Ocean in the west. The field work was conducted at The Tropical Research Station La Gamba and at adjacent trails of the Piedras Blancas National Park.

Figure 1: Location of Tropical Research Station La Gamba and the Piedras Blancas National Park. ©Tropical Field Station La Gamba.

2.2 Tropical Research Station La Gamba

The Tropical Research Station La Gamba (N 8°42.61', W 83°12.97') was established in 1993 and is associated with the "Rainforest of the Austrians" ("Regenwald der Österreicher"). The station is situated near the Pacific coast of southern Costa Rica in the province of Puntarenas and the Golfo Dulce region. It is part of the ecoregion Isthmian-Pacific Moist Forest region (Corrales *et al.,* 2015). It belongs to the small community of La Gamba and is 4 km off the Pan-American Highway and only 51 km from the Panamanian border. The station consists of a botanical garden and is surrounded by primary lowland rainforest of the Piedras Blancas National Park, secondary

rainforests, and agricultural areas. The Tropical Research Station is at an altitude of 77 m asl. The annual mean precipitation is about 6000 mm and the mean temperature of 28.3°C with 33° during day and 24° during the night (Hofhansl *et al.*, 2019).

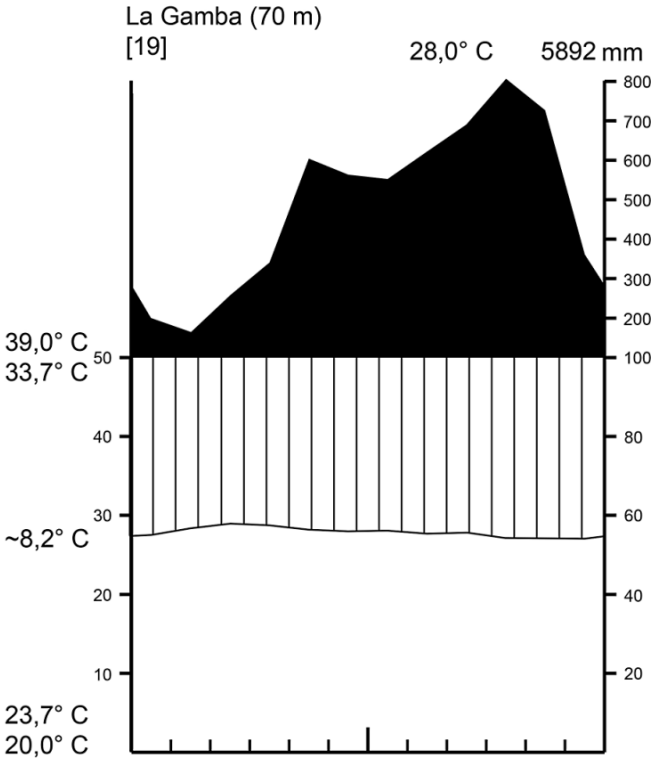

Figure 2: Climate diagram of Tropical Research Station La Gamba (Weissenhofer and Huber, 2008).

2.3 National Park Piedras Blancas

The Tropical Research Station La Gamba lies at the eastern edge of the Piedras Blancas National Park, which is one of the last remaining primary lowland tropical rainforests in Central America. It is part of the Osa Conservation Area. The National Park borders in the south on the Golfo Dulce and in the northwest on the Rio Esquinas. It is home to more than 3,000 vascular plant species and a vast diversity of animals. It is accounted as the most diverse forest in Central America and even one of the richest forests in the world. However, hunting and deforestation was a serious problem in the past, especially in the 1980s. In 1991, the Viennese musician Prof. Michael Schnitzler bought large areas of the forest using funds from the Austrian public. These areas were saved from destruction and the forests became famous as the “Rainforest of the Austrians”. On the opposite

side of the Golfe Dulce, the Corcovado National Park is located. Both National Parks are connected by a series of other protected areas.

2.4 Esquinas Rainforest Lodge, La Gamba

The Esquinas Rainforest Lodge is located in the National Park Piedras Blancas and adjacent to the Tropical Research Station La Gamba (walking distance of approximately ten min.). The lodge offers a variety of eco-tours through the National Park, including diverse hiking and birdwatching trails. Some of these trails were study sites for the work presented here, namely the Bird Trail, the Manakin Trail, and the Riverbed Trail (Fig. 3). The Riverbed Trail is a short loop hiking trail through an approximately 30-year-old secondary lowland rainforest and is connected to the Manakin Trail. The Bird Trail runs through an abandoned cocoa plantation and connects the botanical garden of the Tropical Research Station and the Esquinas lodge.

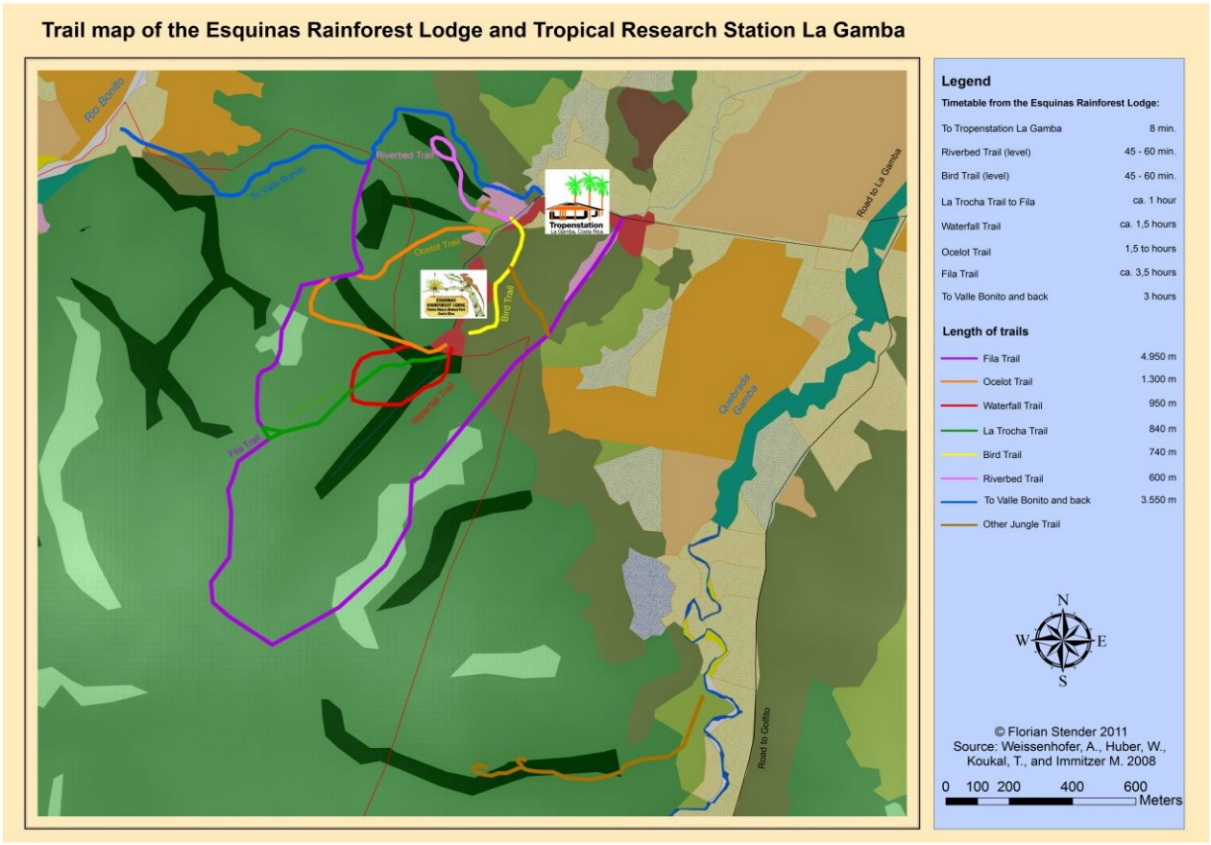

Figure 3: Trail map of Esquinas Rainforest Lodge and Tropical Research Station La Gamba (Weissenhofer *et al.,* 2008).

2.5 Studied plant species

2.5.1 *Anthurium*

Four species of the genus *Anthurium* were investigated. *Anthurium* is the largest genus of the Araceae family counting more than 1000 species. It belongs to the subfamily Pothoideae and is native to the Americas. Most species are epiphytes and their inflorescences are supported by a widely open spathe and bear numerous bisexual flowers along their spadix (Díaz Jiménez *et al.*, 2019). Individual flowers are protogynous.

Anthurium acutangulum, C. Koch, 1853. *A. acutangulum* occurs in wet tropical forests from Panama to Honduras, from sea level up to 900m asl. The bisexual flowers are arranged in several spirals around the spadix.

Anthurium hacumense, Engler, 1898. *A. hacumense* is native to the Neotropics and mostly found in lowland rainforests. It usually has a remarkably long inflorescence peduncle, and the spadix is violet colored.

Anthurium ravenii, Croat and Baker, 1983. *A. ravenii* occurs from Honduras to the Pacific slope of Ecuador usually occurring in tropical wet and premontane forests. The inflorescence is erect-spreading and the spathe often greenish-white colored.

Anthurium hoffmannii, Schott, 1858. *A. hoffmanni* is native to Costa Rica and Panama. The inflorescence has a characteristic creamy white spadix.

2.5.2 *Syngonium*

Three species of *Syngonium* were investigated. *Syngonium* belongs to the subfamily of Aroideae and comprises 39 species. *Syngonium* is native to tropical rainforests in Central and South America, southern Mexico, and the West Indies. Its main center of diversity is in Costa Rica and Panama. The inflorescence usually occurs solitary to multiple at a time, mainly formed at the top of the main shoot.

Syngonium macrophyllum, Engler 1920. *S. macrophyllum* ranges from Central to South America. It is most common below 700 m sea level. Usually, four to eight inflorescences grow per axil.

Syngonium podophyllum, Schott 1851. *S. podophyllum* is the most common and most widespread species native to Latin America ranging from Mexico to Bolivia. It may produce six to eleven inflorescences per plant.

Syngonium hastiferum, Standley and Williams 1982. *S. hastiferum* is endemic to the Golfo Dulce Region in Costa Rica. It grows in tropical wet rain forests. The inflorescence is usually erect at anthesis and there are up to five per axil.

2.5.3 *Philodendron*

Three species of *Philodendron* were investigated. The genus comprises 616 species and belongs together with *Anthurium* to the most poorly studied genera in Araceae. It belongs to the subfamily Aroideae and is restricted to the New World occurring from northern Mexico to southern Uruguay (Mayo *et al.*, 1997). It shows highly diverse growth forms including epiphytes, hemi-epiphytes and terrestrial species. The inflorescence can occur solitary or in multiples at a time. The flowers are unisexual.

Philodendron grandipes, K. Krause, 1913. *P. grandipes* is native from southeast Nicaragua to Ecuador. The inflorescence is erect and there are usually two to four per axil.

Philodendron microstictum, Standl and William, 1952. *P. microstictum* is native to Costa Rica. The inflorescence is spreading and solitary.

Philodendron tripartitum, Schott, 1829. *P. tripartitum* is native from Mexico to tropical America. The inflorescence usually grows solitary.

2.5.4 *Dracontium*

Dracontium is recognized with 23 species and is restricted to the New World. It represents the most species-rich tuberous genus within Araceae (Zhu and Croat, 2004) and belongs to the subfamily of Lasioideae. Its distribution is restricted to the New World ranging from Central to South America including southern Mexico and the West Indies. Life forms are highly diverse and range from terrestrial, epiphytic, hemiepiphytic to free floating aquatics. One species of *Dracontium* was studied in this thesis.

Dracontium pittieri, Engl, 1989. *D. pittieri* is endemic to the Pacific slope in the province of Puntarenas in Costa Rica. It represents the largest species in the genus *Dracontium* (Zhu and Croat, 2004). The inflorescence appears solitary, and the flowers are unisexual.

2.6 Observation of flower visitors and scent emission intensity in *D. pittieri*

The female phase of anthesis of one individual of *D. pittieri* was studied for three days close to the Bird Trail at the Esquinas Lodge. It was observed daily in the following intervals: 05:00-09:00 a.m., 09:00-12:00 a.m., 12:00-05:00 p.m. and 05:00-08:00 p.m. Scent emission was tested by the human nose and ranked in its intensity in a scale from 0-3, whereas 0 indicates no scent, 2 an intermediate scent intensity, and 3 the strongest scent intensity. During each observation interval, the scent was described every 15 mins. After multiple observation rounds, the interval of 08:30-12:30 a.m. was found to be the only time of scent emission and, accordingly, additional observation rounds where performed only during this interval. Videos and pictures of flower visitors were taken using Olympus Tough TG6 camera. No simultaneous collection was performed to avoid disturbance in visitors' behavior. During all observations, neither mosquito repellent nor sunscreen was applied to avoid any influence of artificial volatile compounds.

The male phase of anthesis of two individuals of *D. pittieri* was observed. One individual was intensively studied for 14 days and the second individual for four days at the Bird Trail of the Esquinas Lodge. The intervals of observations were from 05:00-09:00 a.m., 09:00-12:00 a.m., 12:00-05:00 p.m. and 05:00-08:00 p.m. All observations were conducted from 0.50 m distance and at the height of the inflorescence using a ladder to compensate for the height difference. After multiple observations intervals, of the observations were restricted to the interval of 09:00-12:00 a.m. as only then any scent was perceivable. Scent emission intensity was assessed the same way as during the female phase.

During female and male phase, all insects hovering in a proximity of 40 cm to the spathe or touching the inside or outside of the spathe, as well as touching the spadix were counted as flower visitors. The behavior was studied with special focus on their interest in the spadix.

2.7 Collection of flower visitors in *D. pittieri*

After observing the behavior of the different flower visitors, individual insects were caught with either a landing net or directly with transparent plastic containers. If collected by landing net, insects were then transferred into containers as well. Later, white paper cones were used to catch

specific flower visitors. These cones were arranged inside the spathe with the opening aligned with the opening of spathe (see Fig. 4). Insects caught with the cone were prevented to touch any reproductive organs of *D. pittieri*. These insects were transferred into a plastic container as well. Afterwards the collected insects were labelled including information about plant ID, the time and date of the day, flowering phase of plant, and location. The labels were put inside the tubes. These were directly frozen at -18°C in a freezer at the Tropical Research Station of La Gamba.

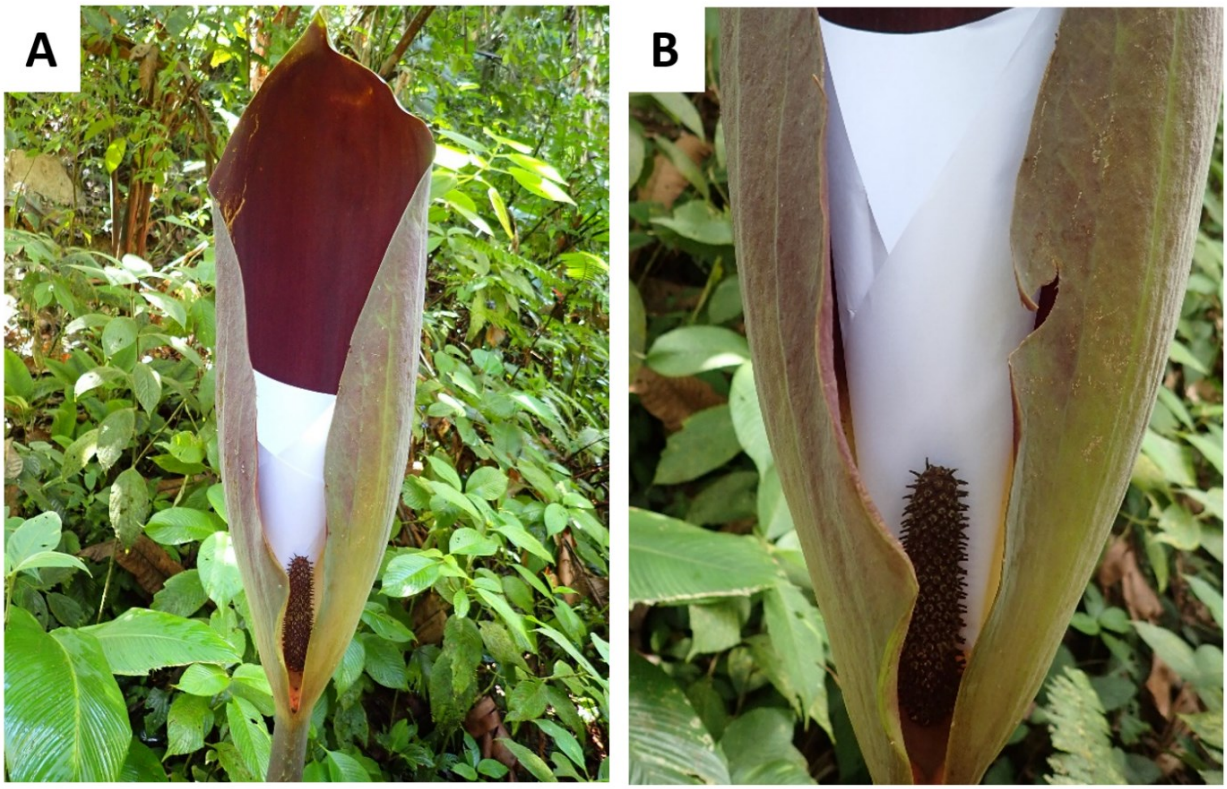

Figure 4: Collection of flower visitors using a white paper cone in *D. pittieri*. **A**, Overview of spathe chamber and spadix. **B**, Close-up of paper cone behind spadix; insects would fall into the paper cone without coming in contact with the spadix.

2.8 Mounting of flower visitors

First, frozen insects were thawed for 5-10 min. Afterwards, a single insect pin (Ento Sphinx, Pardubice, Czech Republic, Number 0.5 and 1) was inserted into the thorax and fixed upon a Styrofoam board with a suitable label next to it. Wings, legs, and antennas were positioned by using tweezers and additional insect pins. In some cases, characteristic features such as genitals were prepared. Mounted insects were air dried for one to three days and additional pins were removed before transferring the samples into a sealed insect collection box. The insect collection

box was stored inside the air-conditioned laboratory of the Tropical Research Station La Gamba and later sent to the University of Vienna.

2.9 Floral scent collection

For scent extraction, the interval of 11:45-12:45 a.m. was chosen in accordance with maximum scent emission intensity and flower visitor abundance. As a preparatory step, polyethylene bags (Toppits® “Bratschlauch 3m”, Germany) with a size of 35 cm were produced. For this purpose, one end of the bag was sealed with a soldering rod. Afterwards, the bag was placed around the upper third of the spathe and kept open on the lower side to guarantee air circulation and to prevent heat stress for the plant. The bag was adjusted to the shape of the plant (Fig. 5A). For scent sampling, adsorbent tubes (quartz glass tube: inner diameter 2 mm, length 25 mm) filled with 1.5 mg of adsorbent Tenax TA (mesh 60-80, Supelco, Germany) were used. A small hole (>0.5 cm) was cut into the upper part of the bag. The tube led on the one side into the bag through the hole and on the other side to a silicone tube that was connected to a vacuum pump (G12/01EB, Gardner Denver, Germany) (Fig. 5A). The vacuum pump was immediately turned on and simultaneously a timer was set. The vacuum pump sucked the volatile organic compounds of the plant for 60 min with a flow rate of 200 ml per minute. Afterwards, the scent trap was removed, and the adsorbent tube covered with a rubber protection to prevent contamination. The tube was stored in the laboratory of the Tropical Research Station La Gamba at room temperature until further usage. A modified method was used to avoid heat stress on the plant. Instead of using the polyethylene bag, the vacuum devise including the tube was positioned in the uppermost third of the spathe without a polyethylene bag (Fig. 5B).

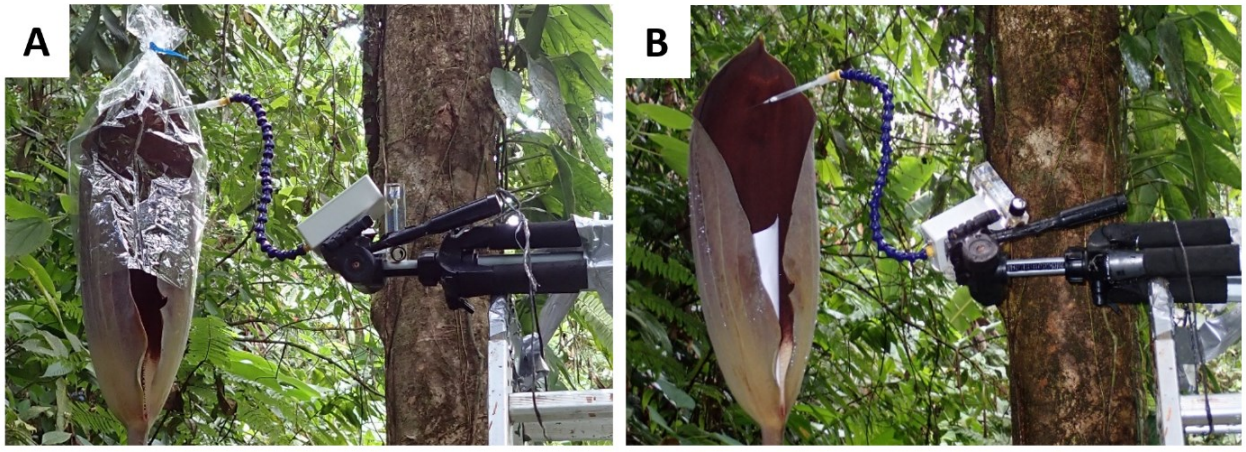

Figure 5: Collection of floral scent during the male phase of anthesis of *D. pittieri.* **A**, using a polyethylene bag. **B**, without using a polyethylene bag.

2.10 Synthesis of scent eluates

The adsorbent tube was placed into a conical vial to begin with the eluation. A syringe was attached to the scent trap and 0.5 ml acetone was added as a solvent. Afterwards, it was sucked up and released 20 times using a syringe. Then, another 1.0 ml of acetone was added, and this procedure was repeated. At all times, it was ensured that the tip of the scent trap was immersed in the liquid of the conical vial. Afterwards, the whole eluate of 1.5 ml was filled into the conical vial using the syringe. The eluate was labelled according to its date and the duration of the collection (Tab. 1). It was stored at room temperature at the laboratory of the Tropical Research Station La Gamba.

2.11 Bioassay experiments

Bioassay experiments were performed with eluated scents from the scent collection experiments (Tab. 1). The experiments were adjusted to the fast evaporation of the compounds. The experiments were conducted from 11:00-12:00 a.m., the period that marked the time with the strongest scent release and highest abundance of flower visitors in *D. pittieri*. They were conducted in proximity of other *D. pittieri* individuals (ca. 75 m, 100 m and 150 m). Only one of these three individuals was in its male phase, all other individuals were not emitting any scent. By choosing this location, it was assumed that flower visitors do exist in the area and that the environmental conditions would be suitable for the occurrence of *D. pittieri*. For each experiment, one sample and one negative control were exposed at approximately 2 m height. The scent compounds were applied on white paper cone, which was placed in a flask. A negative control consisting of a paper cone without scent was placed nearby the scented cone.

Table 1: List of collected floral scents of *D. pittieri* obtained during the male phase with information regarding date, time, solvent type and amount, duration of collection and date of performed bioassay experiment.

Number	Plant	Date of Collection	Time of Collection	Solvent	Amount	Duration (h)	Notes	Date of Bioassay Experiment
1	*D. pittieri*	05.03.2023	11:45	Acetone	1.5 ml	1	♂, bag	13.03.2023
2	*D. pittieri*	06.03.2023	10:00	Acetone	2.0 ml	2	♂	13.03.2023
3	*D. pittieri*	07.03.2023	10:00	Acetone	1.5 ml	2	♂	13.03.2023
4	*D. pittieri*	08.03.2023	10:00	Acetone	1.5 ml	2	♂	14.03.2023
5	*D. pittieri*	08.03.2023	10:00	Acetone	1.5 ml	1	♂, bag	14.03.2023
6	*D. pittieri*	09.03.2023	10:00	Acetone	1.5 ml	2	♂	14.03.2023
7	*D. pittieri*	10.03.2023	10:00	Acetone	1.5 ml	2	♂	15.03.2023
8	*D. pittieri*	11.03.2023	10:00	Acetone	1.5 ml	2	♂	15.03.2023
9	*D. pittieri*	13.03.2023	10:00	Acetone	1.5 ml	2	♂	21.03.2023
10	*D. pittieri*	27.02.2023	10:00	Acetone	1.5 ml	5 min	♂, bag	21.03.2023

2.12 Plant morphology: Collection of pollen, spadix and spathe

2.12.1 Pollen identification

Pollen of all study species of *Anthurium*, *Syngonium*, *Philodendron,* and *Dracontium* was collected and studied using light microscopy and scanning electron microscopy. The pollen was removed from the spadix by gently shaking it. It was collected in clean paper envelopes and stored in the laboratory at room temperature.

2.12.2 Pollen analysis with light microscope

Pollen grains of all species of *Anthurium*, *Syngonium* and *Philodendron* were prepared for light microscopic analysis using fuchsine stained gelatine (Bosch *et al.*, 2009; Barker and Arceo-Gomez, 2021). The jelly was cut into approximately 3x3x3 mm cubes and swabbed over the pollen sample. Fuchsin jelly swab containing the pollen sample were placed on microscope slides and melted with the aid of a hot plate. Samples were then sealed under a cover glass. A light microscope (LM) Olympus BX50 was used to describe pollen ornamentation at the University of Vienna.

2.12.3 Pollen detection on flower visitors

Insects touching reproductive organs of *D. pittieri* were tested for adhering pollen. Insect bodies were swabbed with fuchsine stained jelly cut into 3x3x3mm cubes (Bosch *et al.*, 2009; Barker and Arceo-Gomez, 2021). The jelly was applied from the top and bottom of the thorax and abdomen, mouth parts, and to the legs of each insect. After samples were prepared as described above (2.12.2) and further used for light microscopic analysis. Identification of pollen grains of *D. pittieri* was done with the aid of a pollen reference constructed for *D. pittieri* as described.

2.12.4 Scanning electron microscopic analysis

For scanning electron microscopy (SEM), dry pollen material was prepared using 2,2-Dimethoxypropane (DMP) and subsequently critical point dried (Halbritter, 1998). First, dry pollen was put into a folded paper and shortly soaked into water (< 2 sec). Then, quickly drained on a filter paper and inserted for 2 sec into a vial containing acidified 2,2-Dimethoxypropane (1 drop 0.2 HCL added to 30 ml DMP) and submerged. After putting to rest for 20 min, the sample was transferred to 100 % acetone for 10 min. Then, the sample was critical point dried (CPD) using a Tousimis Supercritical Autosamdri-815 system. Afterwards, the sample was mounted on aluminum stubs

and sputter-coated with gold using a Bal-Tec SCD 050 sample sputter coater. Subsequently, the sample was investigated using a Jeol-JSM-6390 scanning electron microscope.

2. 12.5 Collection of spadix of *D. pittieri*

An approximately 1 cm large piece of the spadix *D. pittieri* was collected by cutting it using a sterile scalpel and scissors during the male phase of anthesis and air dried and stored in a sealed box. Another 1 cm large piece was stored in 96 % ethanol.

2.12.6 Collection of spathe of *D. pittieri*

Four parts of the spathe of *D. pittieri* were cut for SEM analysis using a sterile scalpel and scissors after the male phase had ended. The first sample was cut at the apical end of the spathe which is colored purplish, the second sample in the middle of the purple area, the third sample in the transition area from purple to white, and the fourth sample in the white area of the spathe (see Fig. 6). All samples were approximately 1x1cm large and cut with a pointy end referring to the growth direction. Samples were air dried and stored within a sealed box using insect pins (Ento Sphinx, Pardubice, Czech Republic, Number 1). Additionally, samples were stored in 96 % ethanol and further analyzed at the University of Vienna.

Figure 6: Illustration of four different areas of the spathe of *D. pittieri*; from which samples were cut and collected for further SEM analysis.

2.12.7 Spathe analysis of *D. pittieri* using SEM

Samples collected in 96 % ethanol were transferred into acetone for 30 min. Afterwards, samples were critical point dried. Combined with the air-dried spathe samples, they were mounted on aluminum stubs, sputter-coated with gold, and then further investigated in a Jeol-JSM-6390 SEM.

3. Results

3.1 Palynological observations

The pollen morphology of ten different genera of Araceae was investigated under LM and SEM. The results are described and illustrated in Figs 7-11. A summary of important pollen characteristics is listed in Table 2.

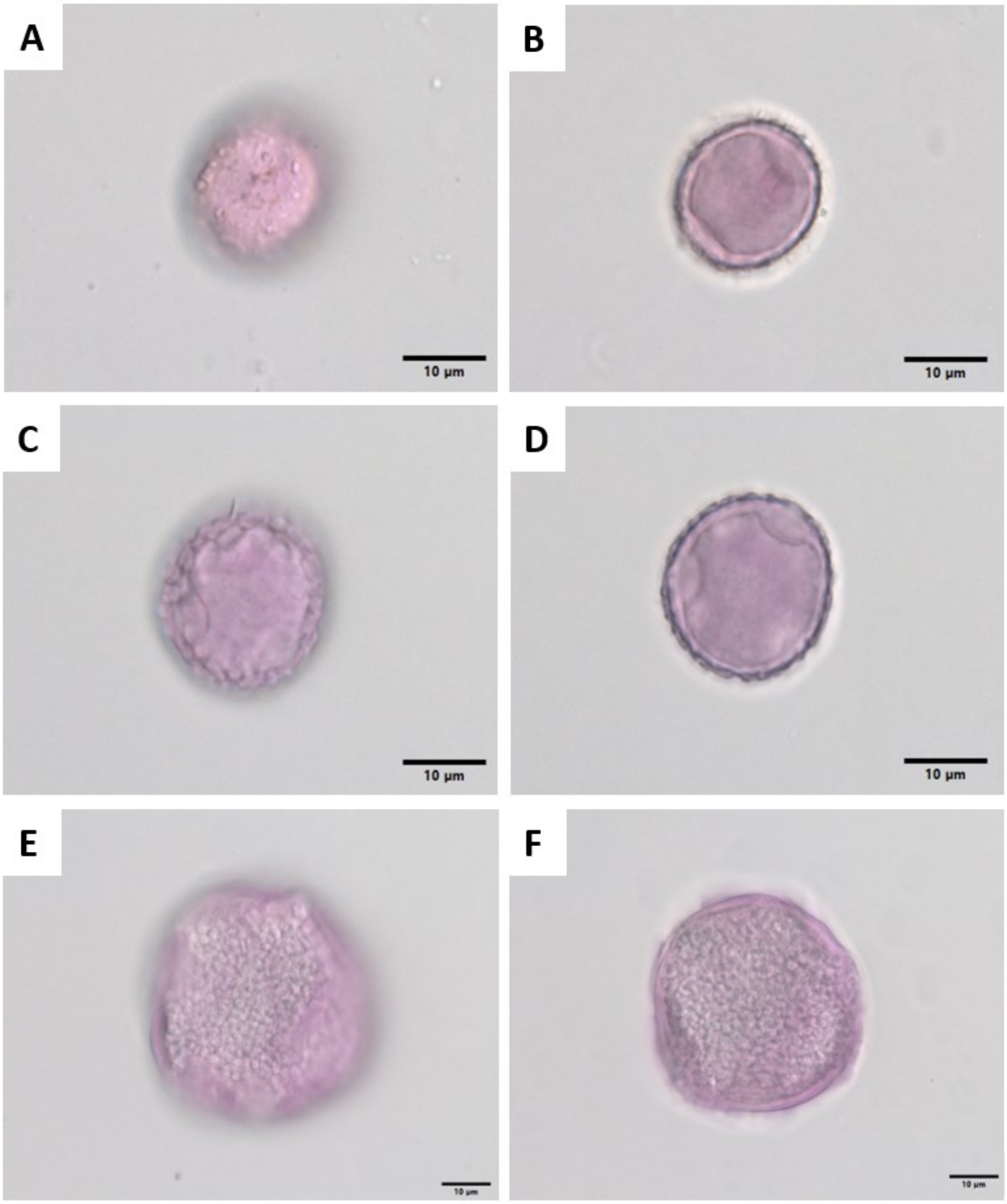

Figure 7: Light microscopic analysis of pollen from different *Anthurium* species. **A-B**, echinate pollen surface typical for *A. acutangulum*, **B**, pollen grain in optical transection, **C-D**, reticulate surface structure of *A. hoffmannii*, **D**, detailed pollen surface in optical transection, **E-F**, reticulate pollen structure of *A. ravenii*, **F**, detailed structure. Scale bars = 10 µm.

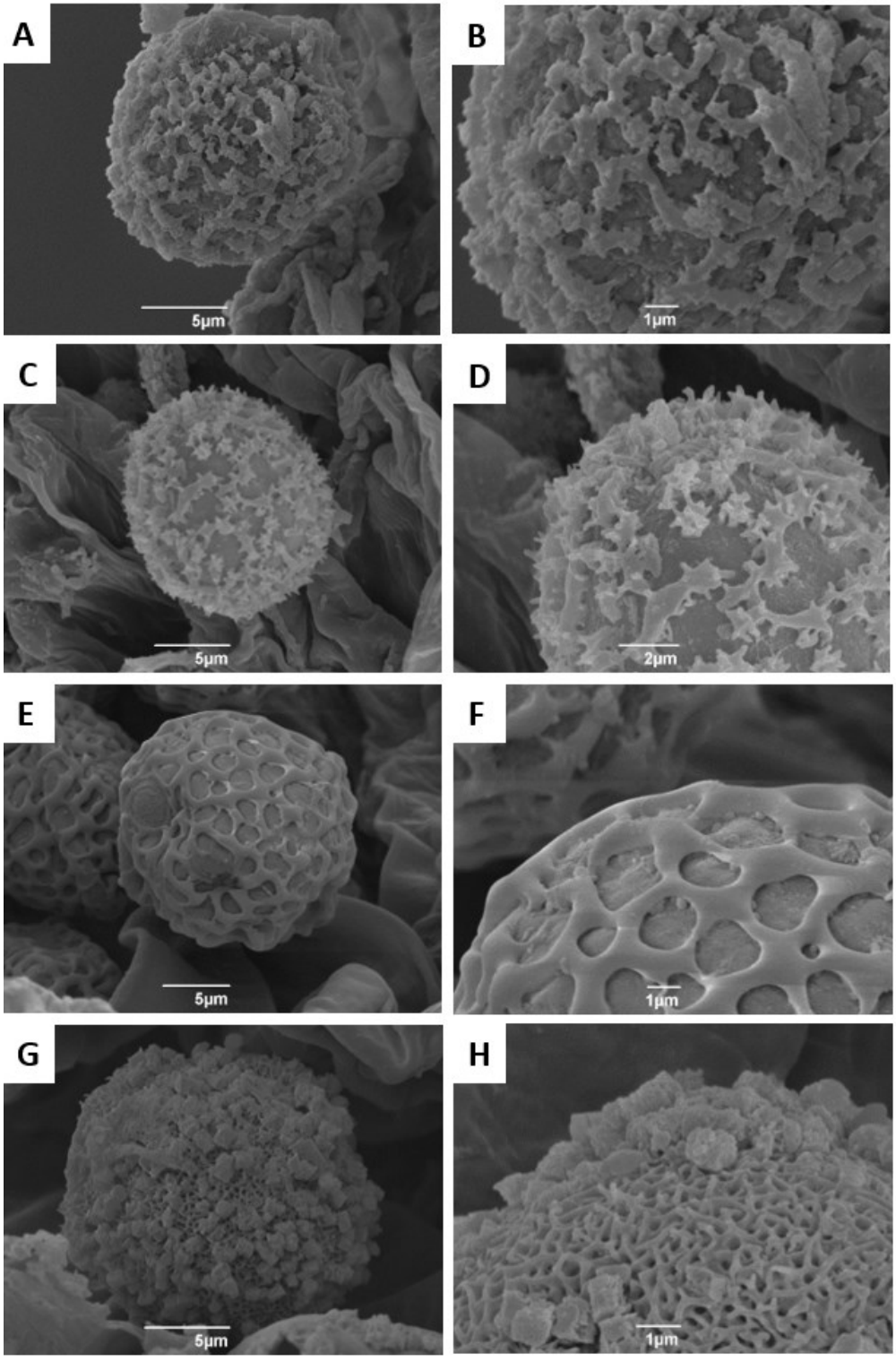

Figure 8: Scanning electron micrographs of different *Anthurium* pollen grains after rehydration. **A-B**, typical reticulate ornamentation of *A. acutangulum*, **B**, detailed view of nanoechinate structure, **C-D**, reticulate and nanoechinate pollen structure of *A. hacumense*, **D**, detailed structure of pollen surface, **E-F**, typical reticulate structure of *A. hoffmannii* with porus, **F**, detailed view, **G-H,** microreticulate ornamentation of *A. ravenii*, **H**, with crystal structures attached. Scale bars = 5 µm (A, C, F, G), 2 µm (D), and 1 µm (B, F, H).

A. acutangulum, Araceae

Shape and size: Pollen unit: **monad**, size of hydrated pollen (LM): **10-12 µm**, size of rehydrated pollen (SEM): **10-12** µm, polarity: **isopolar**, pollen class: **inaperturate**, shape: **spheroidal**. Ornamentation, aperture, and structure: LM ornamentation: **echinate**, SEM ornamentation: **reticulate**, **nanoechinate**, aperture condition: **inaperturate**.

A. hacumense, Araceae

Shape and size: Pollen unit: **monad**, size of hydrated pollen (LM): **not studied,** size of rehydrated pollen (SEM): **10-12 µm**, polarity: **isopolar**, pollen class: **inaperturate**, shape: **spheroidal**. Ornamentation, aperture, and structure: LM ornamentation: **not studied**, SEM ornamentation: **reticulate, nanoechinate,** aperture condition: **inaperturate**.

A. hoffmannii, Araceae

Shape and size: Pollen unit: **monad**, size of hydrated pollen (LM): **20-22 µm**, size of rehydrated pollen (SEM): **10-15 µm**, polarity: **isopolar**, pollen class: **porate**, shape: **spheroidal**. Ornamentation, aperture, and structure: LM ornamentation: **reticulate**, SEM ornamentation: **reticulate**, aperture condition: **porate**, aperture type: **5-porate** (number can vary).

A. ravenii, Araceae

Shape and size: Pollen unit: **monad**, size of hydrated pollen (LM): **40-45 µm**, size of rehydrated pollen (SEM): **20-25 µm**, polarity: **isopolar**, pollen class: **inaperturate,** shape: **spheroidal**. Ornamentation, aperture, and structure: LM ornamentation: **reticulate**, SEM ornamentation: **microreticulate with cubic crystals attached to pollen wall**, aperture condition: **inaperturate**.

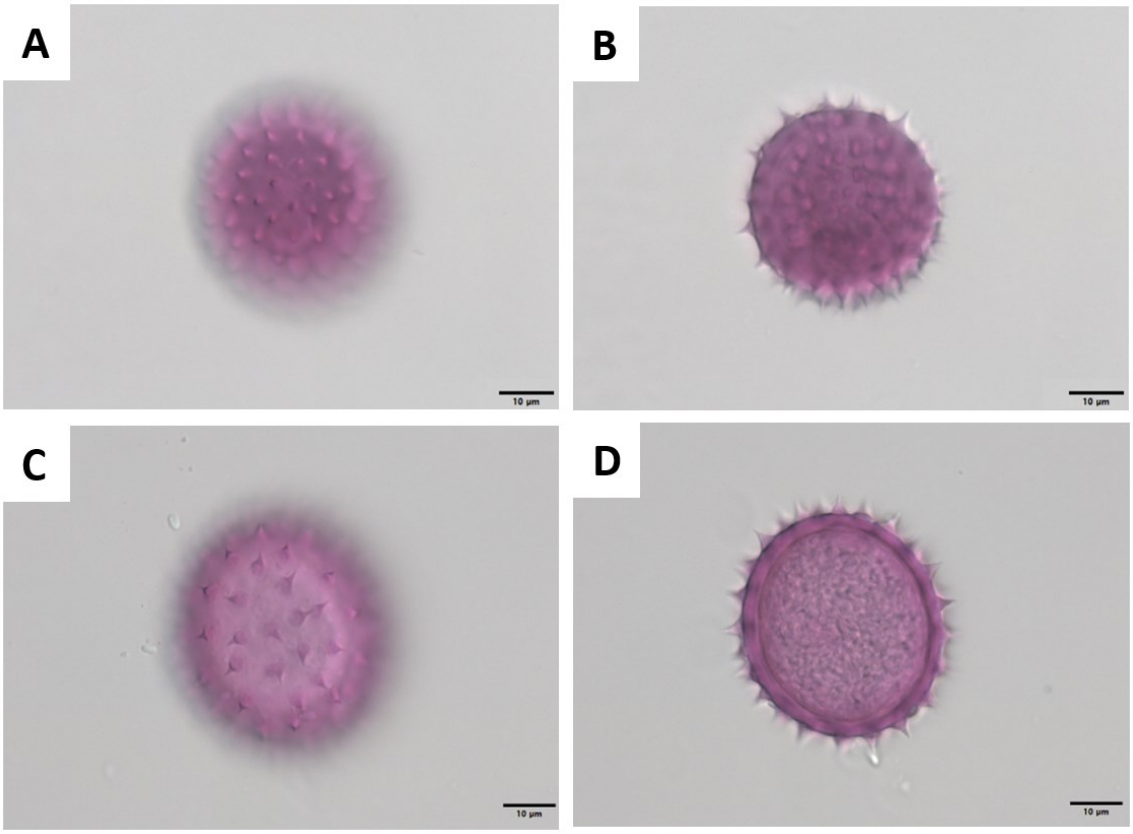

Figure 9: Light microscopic analysis of echinate pollen structure of different *Syngonium* species. **A-B**, pollen surface structure of *S. macrophyllum*, **B**, optical transection of pollen grain, **C-D**, surface structure *of S. podophyllum* and **D**, optical transection of pollen. Scale bars = 10 µm.

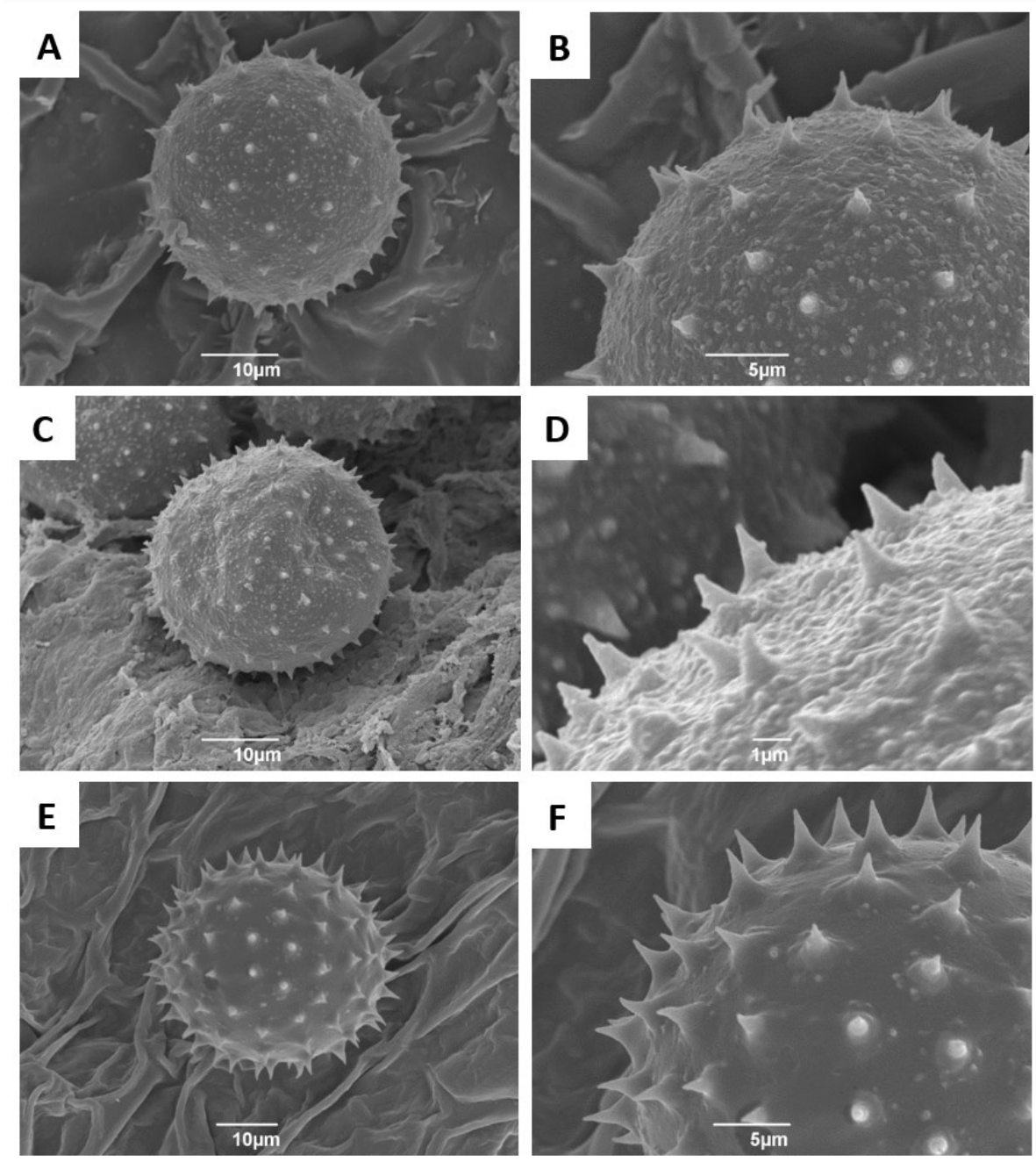

Figure 10: SEM analysis of microechinate and nanoverrucate ornamentation of *Syngonium* species. **A-B,** structure of *S. macrophyllum,* **B**, detailed structure, **C-D**, pollen surface structure of *S. hastiferum*, **D**, close-up of echini*,* **E-F**, pollen ornamentation of *S. podophyllum* and **F**, detailed structure of echini. Scale bars = 10 µm (A, C, E) and 5µm (B, D, F).

S. macrophyllum, Araceae

Shape and size: Pollen unit: **monad**, size of hydrated pollen (LM): **20-25 µm**, size of rehydrated pollen (SEM): **20-25 µm**, polarity: **isopolar**, pollen class: **inaperturate**, shape: **spheroidal**. Ornamentation, aperture, and structure: LM ornamentation: **echinate**, SEM ornamentation: **microechinate, nanoverrucate,** aperture condition: **inaperturate**.

S. hastiferum, Araceae

Shape and size: Pollen unit: **monad**, size of hydrated pollen (LM): **not studied**, size of rehydrated pollen (SEM): **20-25 µm**, polarity: **isopolar**, pollen class: **inaperturate**, shape: **spheroidal**. Ornamentation, aperture, and structure: LM ornamentation: **not studied**, SEM ornamentation: **microechinate, nanoverrucate,** aperture condition: **inaperturate**.

S. podophyllum, Araceae

Shape and size: Pollen unit: **monad**, size of hydrated pollen (LM): **20-25 µm**, size of rehydrated pollen (SEM): **20-25 µm**, polarity: **isopolar**, pollen class: **inaperturate**, shape: **spheroidal**. Ornamentation, aperture, and structure: LM ornamentation: **echinate**, SEM ornamentation: **microechinate, nanoverrucate,** aperture condition: **inaperturate**.

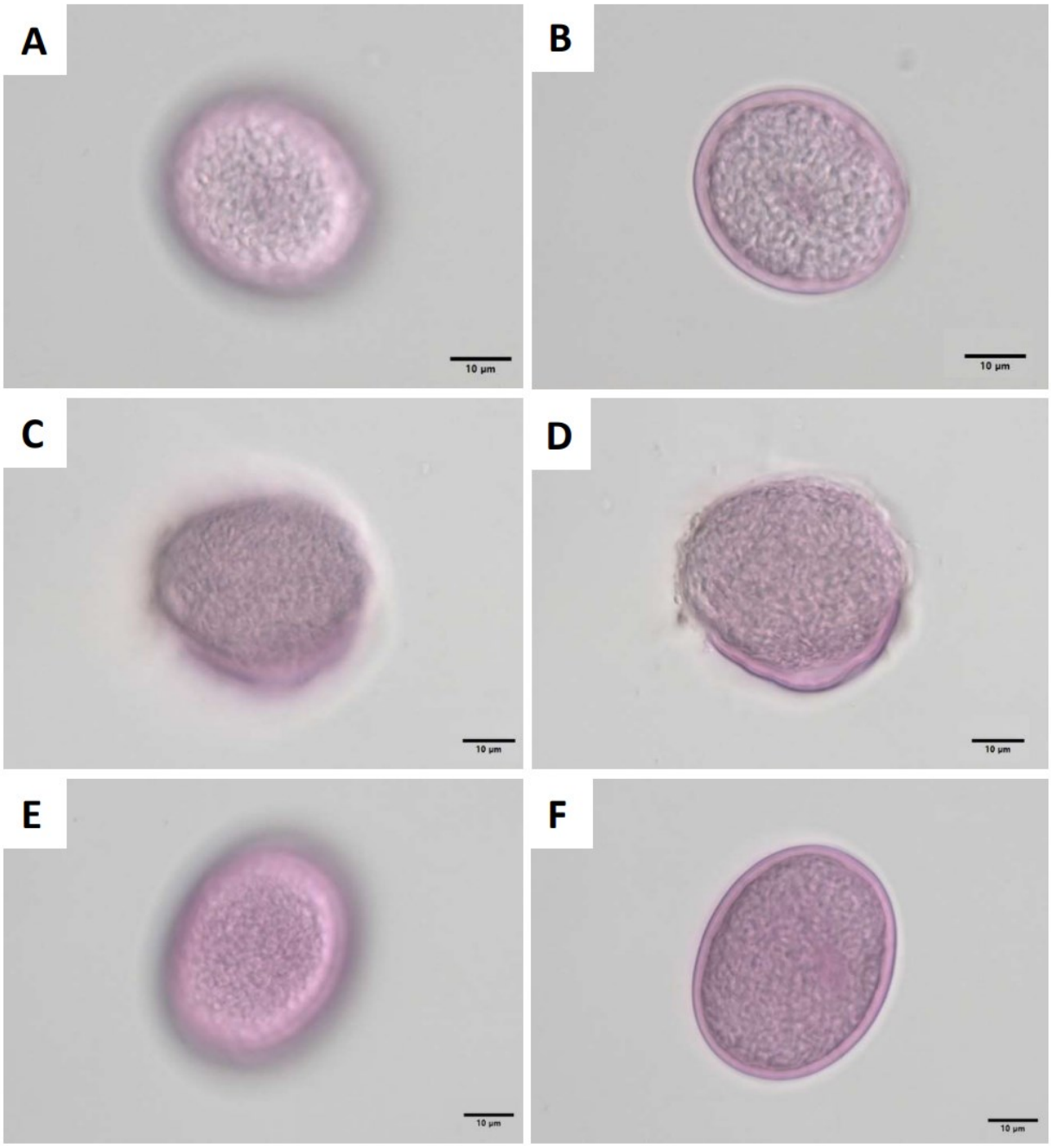

Figure 10: Light microscopic analysis of psilate pollen structure of different *Philodendron* species. **A-B**, ornamentation of surface structure of *P. grandipes*, **B**, optical transection of pollen, **C-D**, surface structure of *P. microstictum*, **D**, pollen grain in optical section, **E-F,** surface structure of *P. tripartitum* and **F,** optical section of pollen grain. Scale bars = 10 µm.

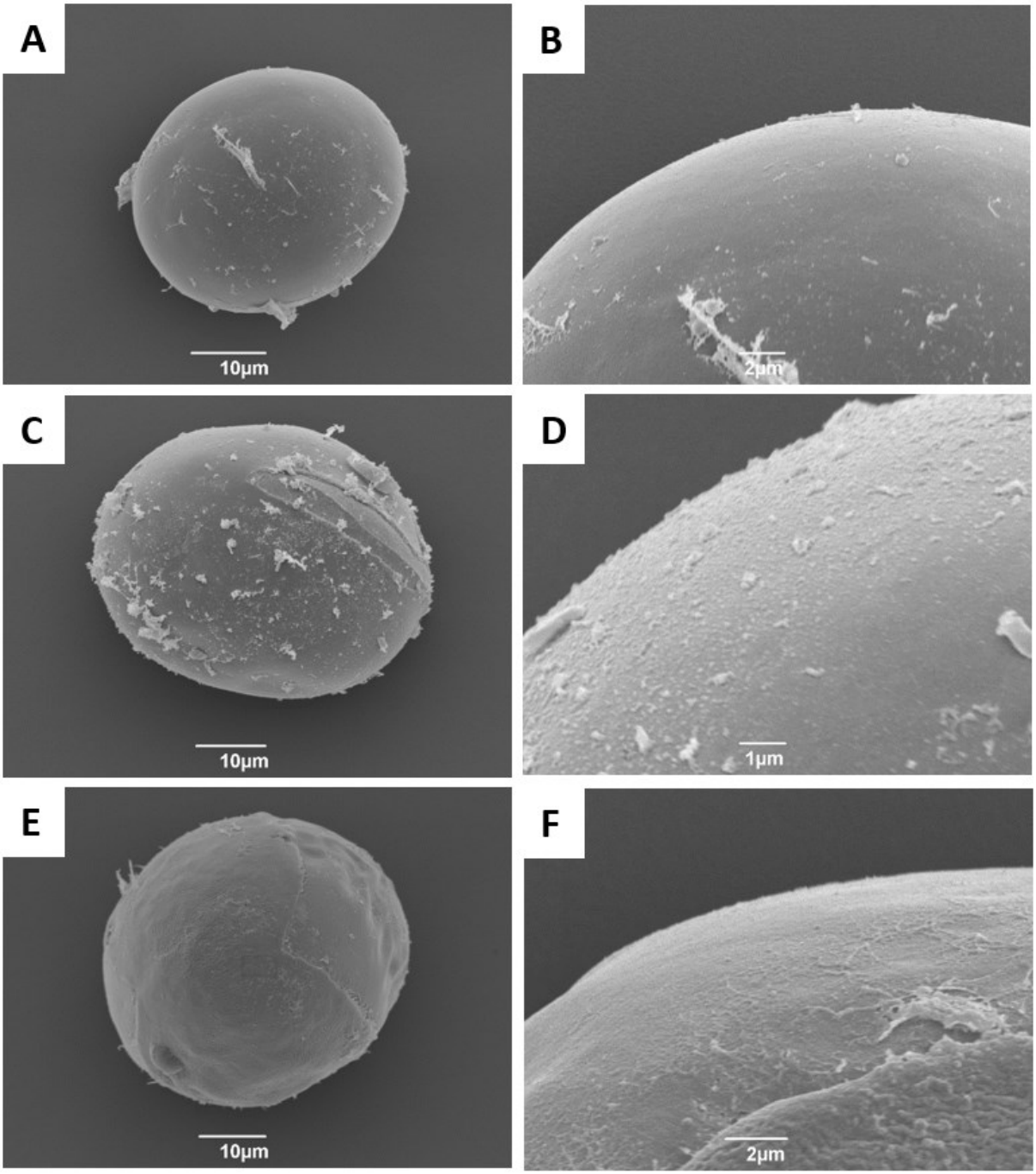

Figure 11: SEM photographs of psilate ornamentation of different *Philodendron* species. **A-B**, ornamentation of *P. grandipes,* **B**, close-up of pollen structure, **C-D** pollen surface of *P. microstictum*, **D**, detailed overview of surface, **E-F**, pollen structure of *P. tripartitum* and **F,** close-up view. Scale bars = 10 µm (A, C, E), 2 µm (B, F) and 1 µm (D).

P. grandipes, Araceae

Shape and size: Pollen unit: **monad**, size of hydrated pollen (LM): **20-25 µm**, size of rehydrated pollen (SEM): **15-20 µm**, polarity: **isopolar**, pollen class: **inaperturate**, shape: **spheroidal**. Ornamentation, aperture, and structure: LM ornamentation: **psilate**, SEM ornamentation: **psilate,** aperture condition: **inaperturate**.

P. microstictum, Araceae

Shape and size: Pollen unit: **monad**, size of hydrated pollen (LM):**35-40 µm**, size of rehydrated pollen (SEM): **30-40 µm**, polarity: **heteropolar**, pollen class: **inaperturate**, shape: **elliptical**. Ornamentation, aperture, and structure: LM ornamentation: **psilate**, SEM ornamentation: **psilate,** aperture condition: **inaperturate**.

P. tripartitum, Araceae

Shape and size: Pollen unit: **monad**, size of hydrated pollen (LM):**30-35 µm**, size of rehydrated pollen (SEM): **30- 35 µm**, polarity: **isopolar**, pollen class: **inaperturate**, shape: **spheroidal**. Ornamentation, aperture, and structure: LM ornamentation: **psilate**, SEM ornamentation: **psilate,** aperture condition: **inaperturate**.

Table 2: Summary of important pollen characteristic of different Araceae species.

Taxon	Pollen size and shape						Aperture and ornamentation			
Species name	Unit	Size (LM) (µm)	Size (SEM) (µm)	Class	Polarity	Shape	Aperture condition	Aperture type	Ornamentation LM	Ornamentation SEM
A. acutangulum	monad	10-12	10-12	inaperturate	isopolar	spheroidal	inaperturate	no aperture	echinate	reticulate, nanoreticulate
A. hoffmannii	monad	20-22	10-15	inaperturate	isopolar	spheroidal	porate	5-porate	reticulate	reticulate
A. ravenii	monad	40-45	20-25	inaperturate	isopolar	spheroidal	inaperturate	no aperture	reticulate	microreticulate with cubic crystals
A. hacumense	monad	-	10-12	inaperturate	isopolar	spheroidal	inaperturate	no aperture	-	reticulate, nanoechinate
P. grandipes	monad	20-25	15-20	inaperturate	isopolar	spheroidal	inaperturate	no aperture	psilate	psilate
P. microstictum	monad	35-40	30-40	inaperturate	heteropolar	elliptical	inaperturate	no aperture	psilate	psilate
P. tripatitum	monad	30-35	30-35	inaperturate	isopolar	spheroidal	inaperturate	no aperture	psilate	psilate
S. macrophyllum	monad	20-25	20-25	inaperturate	isopolar	spheroidal	inaperturate	no aperture	echinate	microechinate, nanoverrucate
S. hastiferum	monad	-	20-25	inaperturate	isopolar	spheroidal	inaperturate	no aperture	-	microechinate, nanoverrucate
S. podophyllum	monad	20-25	20-25	inaperturate	isopolar	spheroidal	inaperturate	no aperture	echinate	microechinate, nanoverrucate

3. 2 Flower visitors, pollinators, and anthesis *of D. pittieri*

3.2.1 Flowering cycle of *D. pittieri*

Anthesis and scent emission of two *D. pittieri* individuals in their natural habitat were investigated. The anthesis of each individual lasted several weeks. For individual 1, 31 sets of flowers (group of neighboring flowers opening simultaneously during the male phase) were counted (see Fig. 12). Photo documentation and scent emission measurements were conducted over 51 days. For individual 2, 16 sets of flowers were counted. Photo documentation and scent emission were performed for 20 days.

During the female phase of anthesis of individual 2, all stigmas were covered with a stigmatic fluid, they appeared white and shiny (Fig. 12A). The style was dark green, and the stigma was 3-lobed. The perianth was colored dark purple and comprised 3-6 tepals per flowers (Fig. 12B). On the third day of the female phase, the translucent sticky liquid of the stigma decreased and slowly dried up (Fig. 12D), completing the female phase on the following day. Subsequently, opened anthers were visible, the spadix showed dehisced anthers on its apical end and masses of excreted pollen (Fig. 12E). During the observation time, a strong scent was perceived by the human nose. The scent was perceived as foul, decaying and carrion-like. Scent emission was perceived from 10:00 a.m., peaking between 11:30 a.m. and 11:45 a.m. and ending at 1:15 p.m. (Fig. 13).

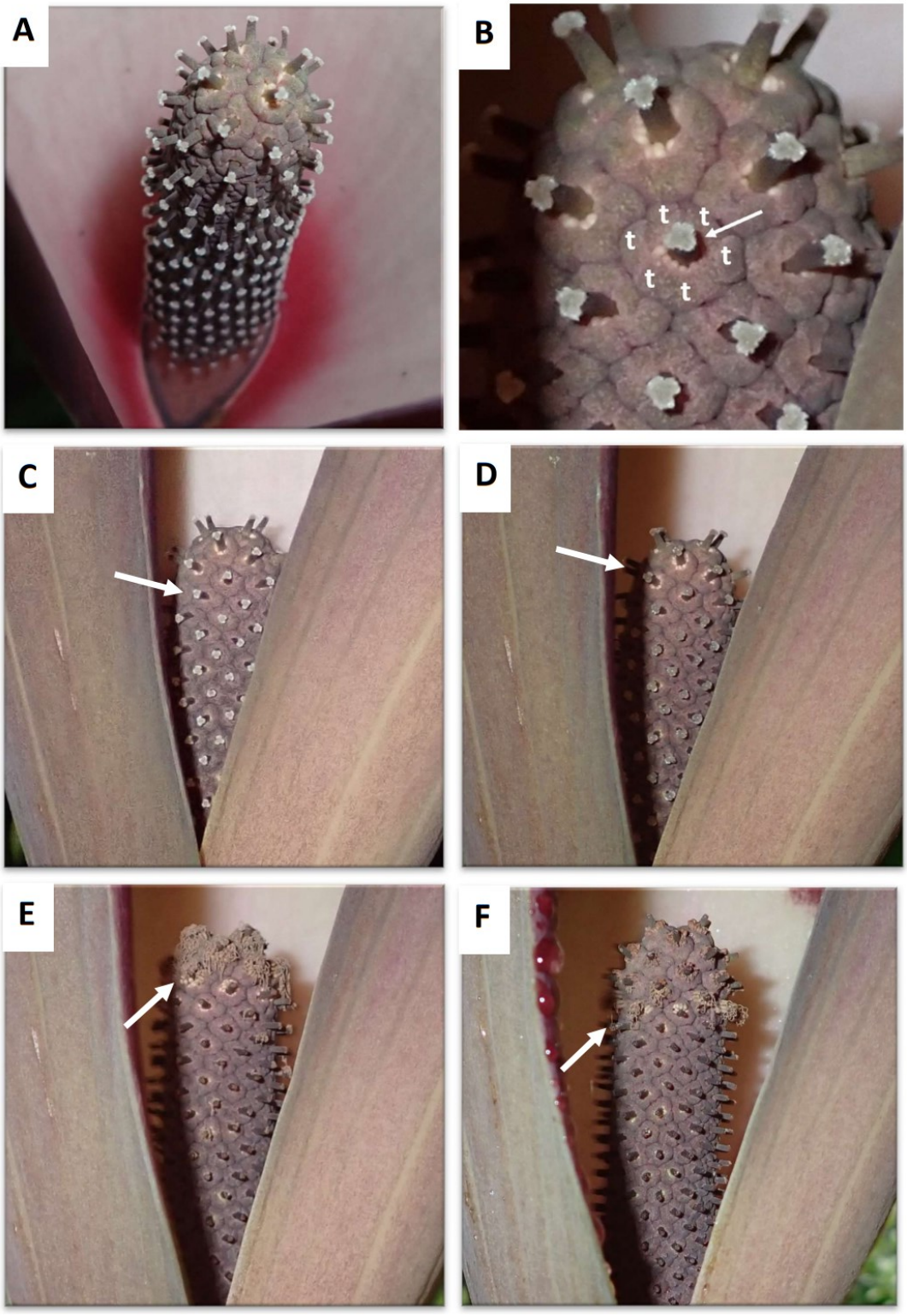

Figure 11: Inflorescence of *D. pittieri* at anthesis. **A-D**, female phase of anthesis. **A**, spadix with stigmas covered with stigmatic fluid. **B**, detail of a female phase inflorescence with receptive stigmas (arrow) surrounded by six tepals (t). **C**, First day, stigmas open and shiny. **D**, Third day, stigmas dried out during transition phase**. E- F**, Male phase of anthesis with sequential opening of anthers starting at the apex of the spadix. **E**, First day, first set of anthers open, offering pollen, and **F**, Second day, a next set of open anthers open with pollen.

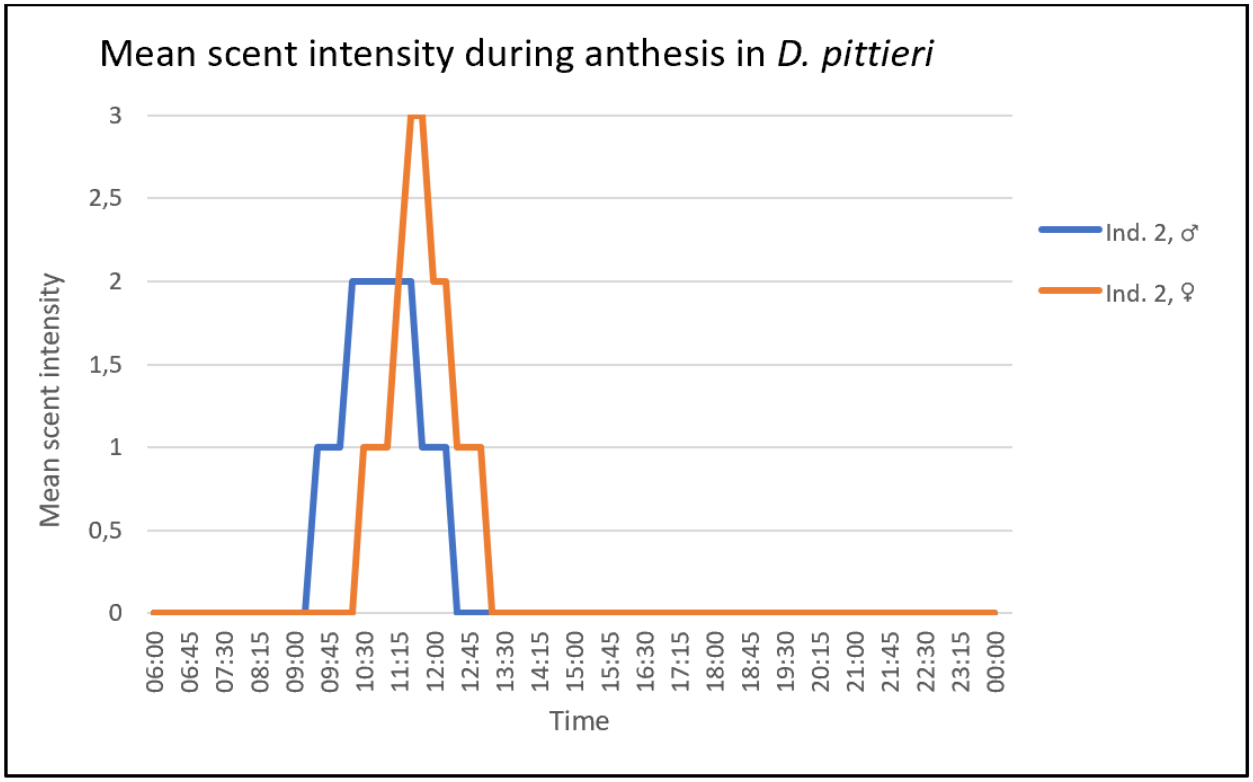

Figure 12: Mean scent emission intensity of *D. pittieri* at flowering phase. Scent tested by the human nose every 15 min during female and male phase for 20 days.

For both individuals in male phase, it was observed that starting from 04:30 a.m., the anthers of mature stamens dehisced along small parts of the spadix. Fig. 14 shows that until 08:00 a.m., the anthers continued to excrete pollen in cohesive strands until the anthers were fully covered. Meanwhile, the flowers above had already wilted, and the flowers below were maturing. By pushing out the anthers and excreting the pollen, the active section of the spadix was colored yellowish-brown, while the other parts of the spadix were dark purple. Fig. 15 shows how the daily male anthesis continued over several day. Every 3rd day another set of flowers entered the male phase offering pollen in cohesive strands (Fig. 15). The anthesis continued from distal to proximal parts of the spadix. During female anthesis, the spathe was closed towards its proximal end. Spathe movement was detected when changing from female to male phase (Fig.16). A longitudinal slit opened towards the proximal end exposing the spadix.

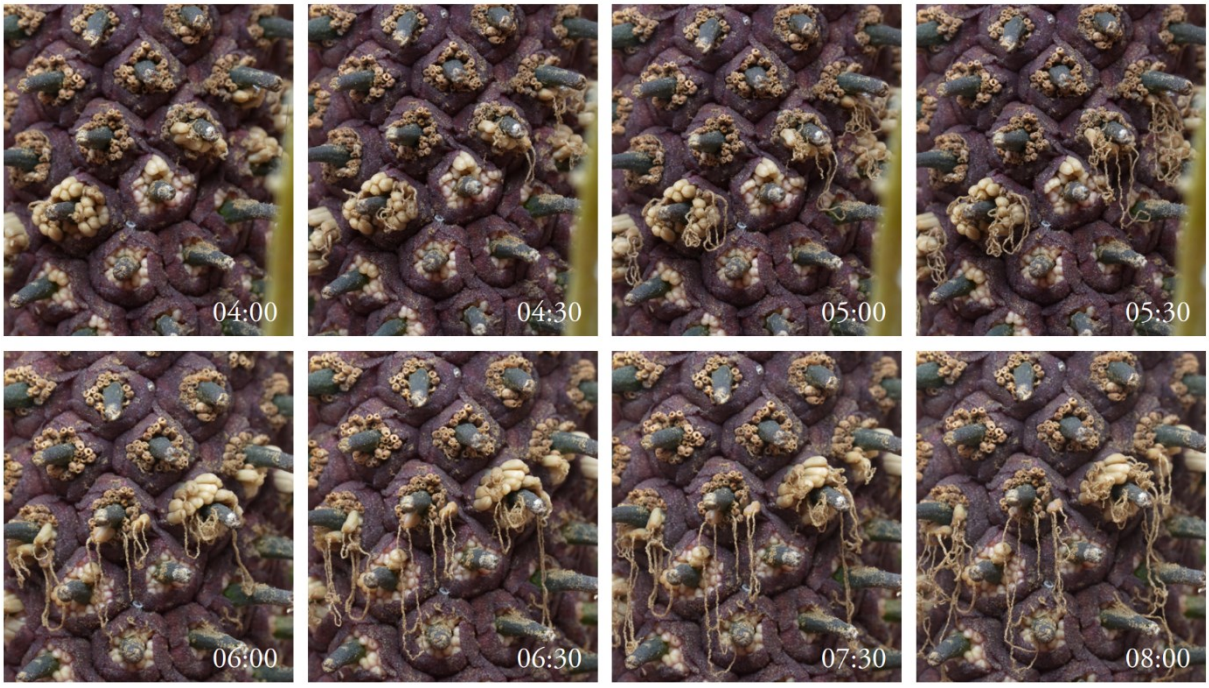

Figure 13: Anther dehiscence and pollen excretion during the male phase of *D. pittieri* between 04:00-08:00 a.m. Anthers excrete pollen in cohesive strands. ©Basil Shu.

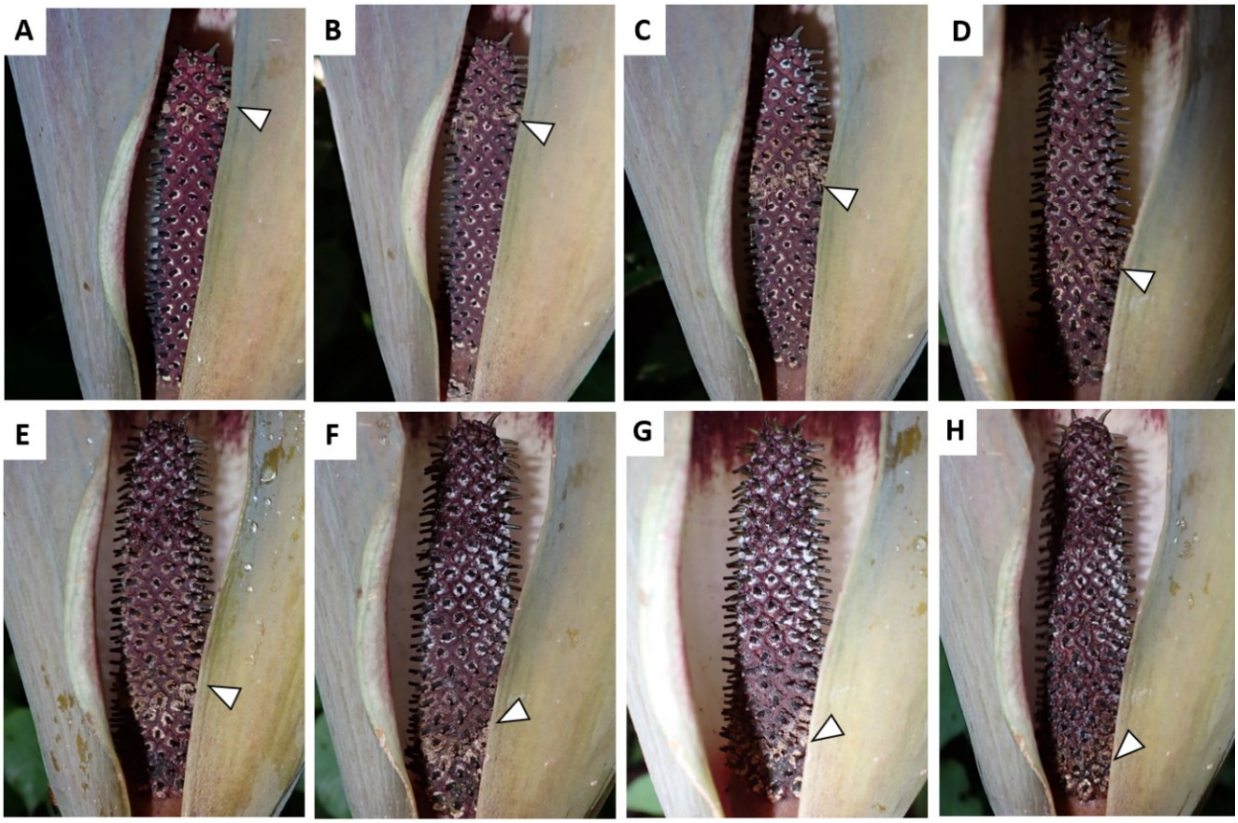

Figure 14: Photographs of male anthesis of *D. pittieri* individual 2. Pollen shedding over 35 days. White arrowheads indicate the dehisced anthers with pollen in cohesive strands. **A- H**, illustrated sequential opening of anthers. **A**, 05/02/23, **B**, 09/02/23, **C**, 19/02/23, **D**, 25/03/23, **E**, 05/03/23, **F**, 10/03/23, **G**, 12/03/23, and **H**, 12/03/23.

Figure 15: Spathe movement of *D. pittieri*. **A**, the base of the spathe remains closed during the female phase of anthesis, and **B**, the base of the spathe opens a narrow slit exposing the spadix during the male phase of anthesis.

As in the female phase, a carrion-like scent was emitted during male phase. Scent emission was perceived from 06:45 a.m. (Ind. 1) and 09:45 a.m. (Ind. 2), peaking between 09:30-10:45 a.m. (Ind. 1) and 10:50-11:15 a.m. (Ind.2) (Fig. 17). The end of scent emission was observed at 01:45 p.m. for individual 1 and 12:30 p.m. for individual 2.

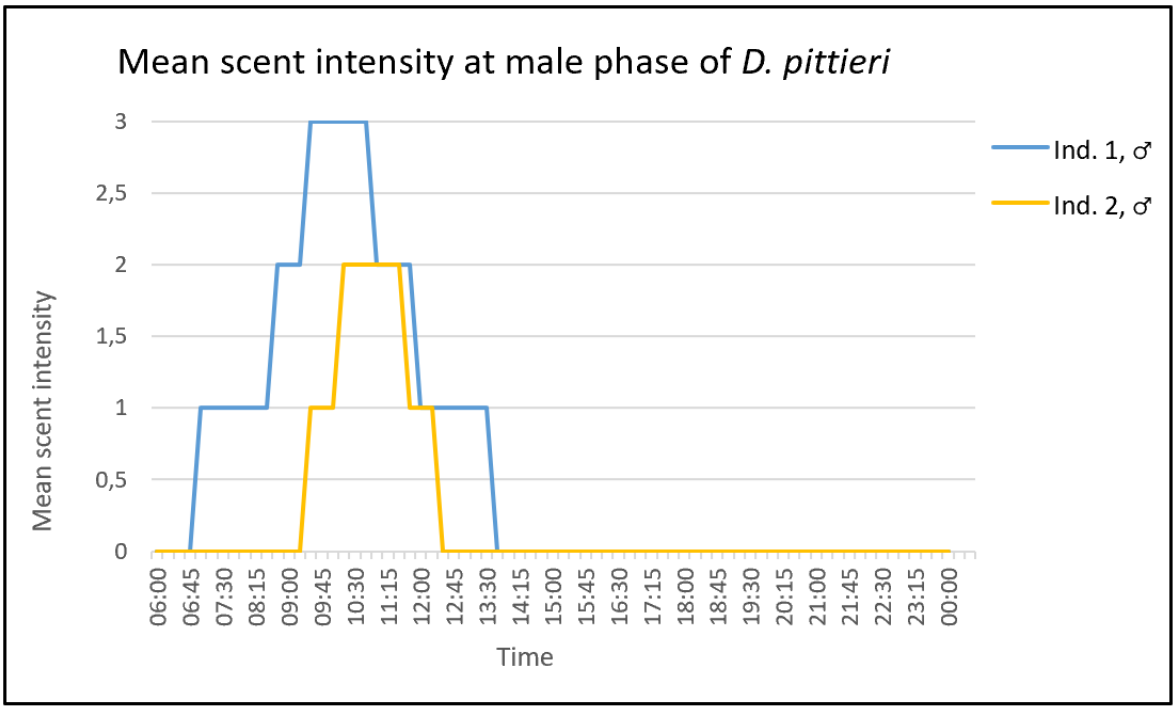

Figure 16: Mean scent emission intensity of two *D. pittieri* individuals at male anthesis. Scent tested by the human nose every 15 min for 25 days for Ind. 1 and for 16 days for Ind. 2.

3.2.2 Flower visitors

Different flower visitors were observed during anthesis and scent emission (Tab. 3). The number of visits and the total number of visitor individuals were positively correlated with scent emission intensity. After the end of the daily scent emission, i.e., after 03:00 p.m. no flower visitors had been observed.

The only visitors touching the spadix were individuals of Cicadellidae, Staphilinidae, and Histeridae (Tab. 3). One individual of Staphilinidae was observed crawling from the outside of the spathe through the proximal end of the spathe into the interior. Inside the spathe, the individual was observed crawling across the spadix touching the open anthers and pollen. After approximately eight minutes the individual attempted to exit via the spathe opening. In addition, an individual of the Cicadellidae was observed climbing around the spadix. The visit lasted longer than 30 sec (Tab. 3). Both the Staphilinidae and the Cicadellidae were not observed feeding on pollen.

Individuals of the Histeridae family were frequent daily visitors to *D. pittieri* (Tab. 3). Their visits occurred only between 10:30- 12:15 a.m., correlating with the scent emission maximum (Fig. 17). Visiting histerid beetles showed two different behaviors for approaching. One way was the direct flight towards the center of the spathe interior, where they crashed into the spathe and then fell into the spathe chamber. The alternative way of approaching was that they were flying around the spathe opening for several rounds. Thereby, the beetles kept a distance of 40-50 cm to the plant. After flying a few circles, the beetles then flew towards the distal spathe opening and dropped into the spathe chamber.

As soon as the beetle had landed inside the chamber by either of the two methods described above, it tried to climb up the inner surface of the spathe but repeatedly fell back into the chamber. The beetle then climbed up the spadix (Fig. 18A). It crawled around the spadix in rounds, thereby touching closed and open flowers. The beetle fed on pollen using their mandibles to wipe over the anthers. When the beetles reached the apex of the spadix, they either tried to fly out of the spathe, or repeatedly wandered around on the spadix and continued to feed on pollen. Once the beetles had arrived at the apical end of the spadix, they were completely covered with yellow pollen. The difficulties to fly out of the spathe starting from the top of the spadix were possibly due to the high amount of pollen clogging their body. In cases where the beetles were not able to fly anymore, they eventually dropped out of the spathe through the slit-like opening at the base of the spathe (Fig. 16). Apart from feeding on the pollen, two histerid beetles were once observed mating on the spadix (Fig. 18E).

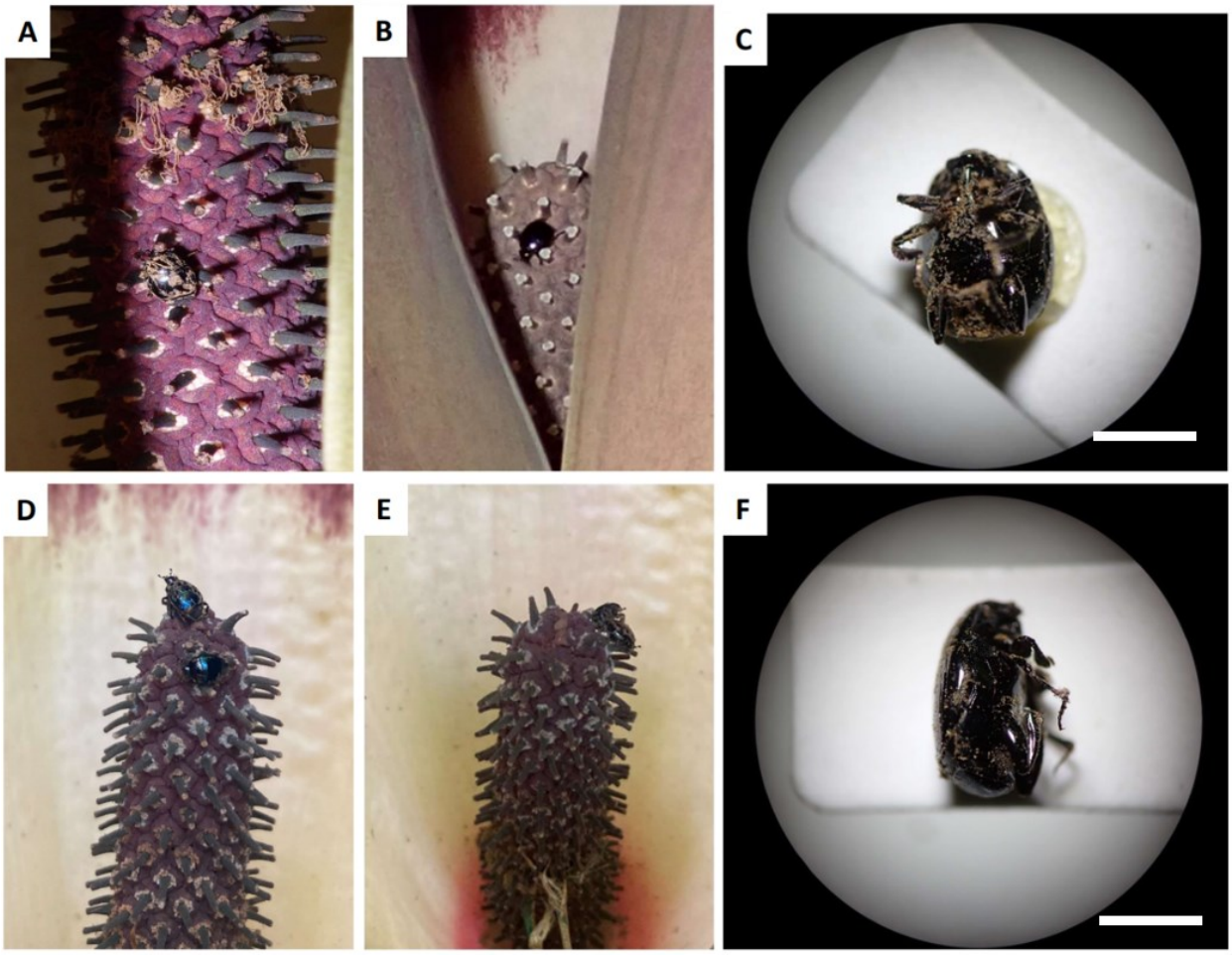

Figure 18: Histerid beetle visiting *D. pittieri* at anthesis. **A**, Histeridae covered with pollen during male anthesis, **B**, Histeridae walking on spadix during female anthesis. Stigmas shiny with stigmatic fluid, **C**, dorsal view of histerid beetle, **D**, two individuals found on spadix, **E**, two individuals copulating, **F**, lateral view of histerid beetle. Scale bars= 0.5 mm.

During the female phase of anthesis, histerid beetles landed and crawled around on the outer surface of the spathe. After three to five minutes on the outer surface, beetles then tried to crawl into the spathe but slipped off and fell into the spathe chamber. During the female phase of anthesis, the chamber was not fully opened, it could not be observed if the beetles attempted to climb up the inner surface of the spathe. Fig. 18B shows how histerid beetles were found to climb across the spadix touching the female flowering receptive organs of the spadix. Meanwhile, all stigmas were shiny and sticky, and scent emission was at its maximum.

Up to three histerid beetles could be observed at the same time on the spadix during female phase and visits lasted up to 18 min. During the male phase of anthesis, at least one but never more than two histerid beetles were found daily. Visits lasted a maximum of 35 min.

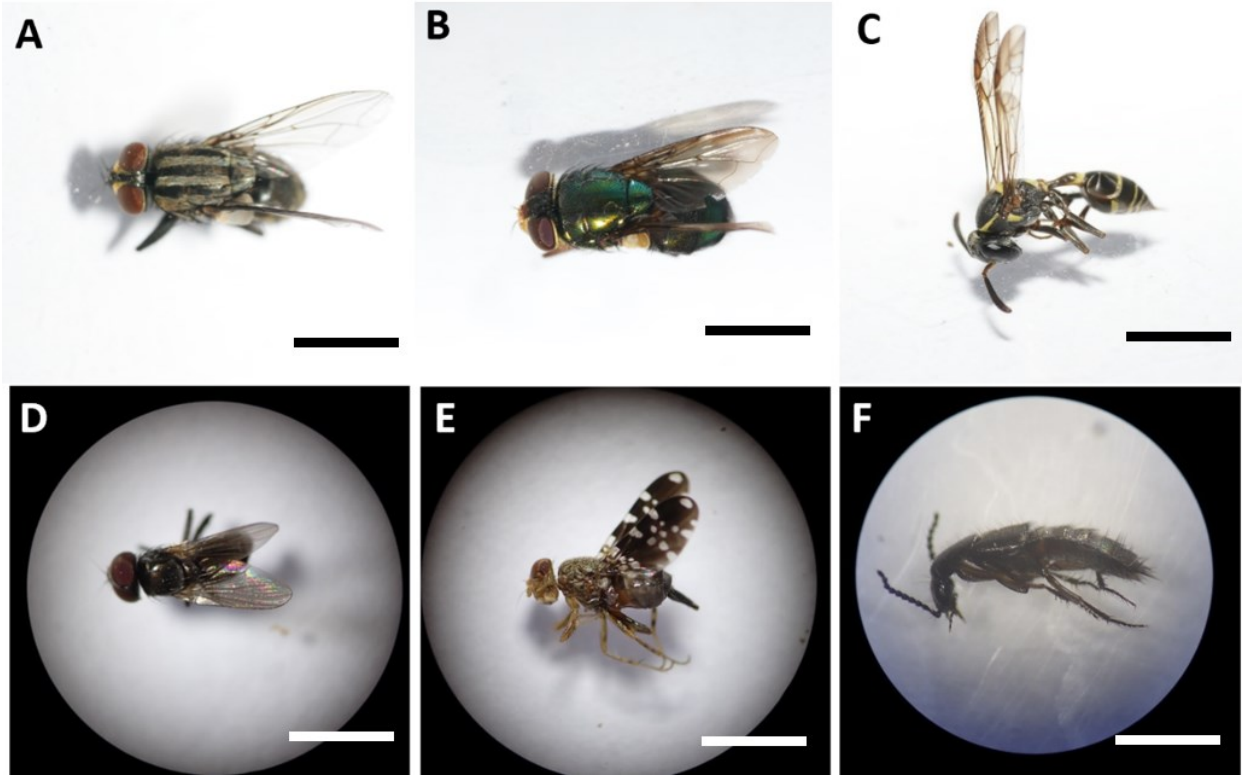

Figure 19: Flower visitors of *D. pittieri* collected at anthesis. **A**, Sarcophagidae, **B**, Syrphidae, **C**, Vespidae, **D**, Calliphoridae, **E**, Ulidiidae, and **F**, Staphilinidae. Scale bars= 0.5 mm.

Other daily visitors of the inflorescence of *D. pittieri* were Calliphoridae, Sarcophagidae, and Syrphidae. They settled on the outside of the spathe. Individuals of Syrphidae and Sarcophagidae were observed on the inside of the spathe, primarily at its distal end, not touching the spadix. Calliphoridae individuals usually spent the complete morning flying around close to the spathe but only rarely landing on it. It has not been observed that they touched more proximal areas of the spathe or the spadix.

Individuals of the family Ulidiidae were frequent visitors approaching in groups of 2-15 individuals. They flew around the opening of the spathe at a distance of approximately 40 cm from the spathe. As scent emission intensity increased, their distance from the spathe decreased and individuals repeatedly sat briefly (<30 sec) on the spathe exterior. Copulations were repeatedly observed (Tab. 3).

Vespidae were found to be irregular flower visitors (Tab. 3). Individuals buzzed around the spathe opening, visits were usually shorter than 30 sec, and in some rare cases, they sat briefly on the spathe exterior. The visits were not regular and lasted only seconds.

Other visitors that had been observed were individuals of Mircropezidae and Plecoptera. Visits had been irregular and short (< 30 sec). They only touched the outside of the spathe and were not

observed inside of the spathe or the spadix (Tab. 3). One individual of Ensifera was observed for several days (eight days). Within that time, the Ensifera remained inside the spathe in the same position and did not show any movements. It did not touch any reproductive organs of *D. pittieri* (Tab. 3).

Table 3: Flower visitors of *D. pittieri* at male anthesis. Morphotypes, frequency, duration and organs that had been touched during visits.

Morphotypes	Frequency	Duration >30sec	Duration <30sec	Spathe	Spadix
Calliphoridae	frequent	x		x	
Cicadellidae	once	x			x
Cicadellidae, Nymph	often	x		x	
Ensifera	once	x		x	
Histeridae	frequent	x			x
Micropezidae	irregular		x	x	
Plecoptera	irregular		x	x	
Sarcophagidae	frequent	x		x	
Staphilinidae	once	x			x
Syrphidae	frequent	x		x	
Ulidiidae	frequent		x	x	
Vespidae	often		x	x	

3.2.3 Potential pollinators

Individuals of Staphilinidae and Histeridae were immediately intercepted after touching the spadix and reproductive organs of *D. pittieri* and tested for adhering pollen. A total of 16 histerid beetles and one Staphilinidae had been analyzed. Pollen was detected on the individuals of Histeridae (n= 11).

Fig. 20A shows a pollen grain taken from *D. pittieri* in SEM to use as a reference for the identification of pollen on insect bodies. Pollen of *D. pittieri* was 20-30 µm in length and the shape was elliptical. Pollen investigated under SEM showed remnants of adhering pollenkitt (Fig. 20A). Pollen was inaperturate and the ornamentation was psilate under SEM.

Using the jelly swab method, no pollen was detected on Staphilinidae, whereas pollen was found on histerid beetles. Fig. 20B shows that further LM analysis detected psilate pollen with a size of 20-25 µm on histerid beetles. Pollen collected on histerid beetles turned out to be identical to pollen directly collected on *D. pittieri* (Fig. 20A). Further investigation of histerid beetles under SEM

demonstrated adhering pollen on different parts of the body (Fig. 20C-F) including pronotum and elytra, leg parts such as tarsus, femur, and tibia (Fig. 20E-F).

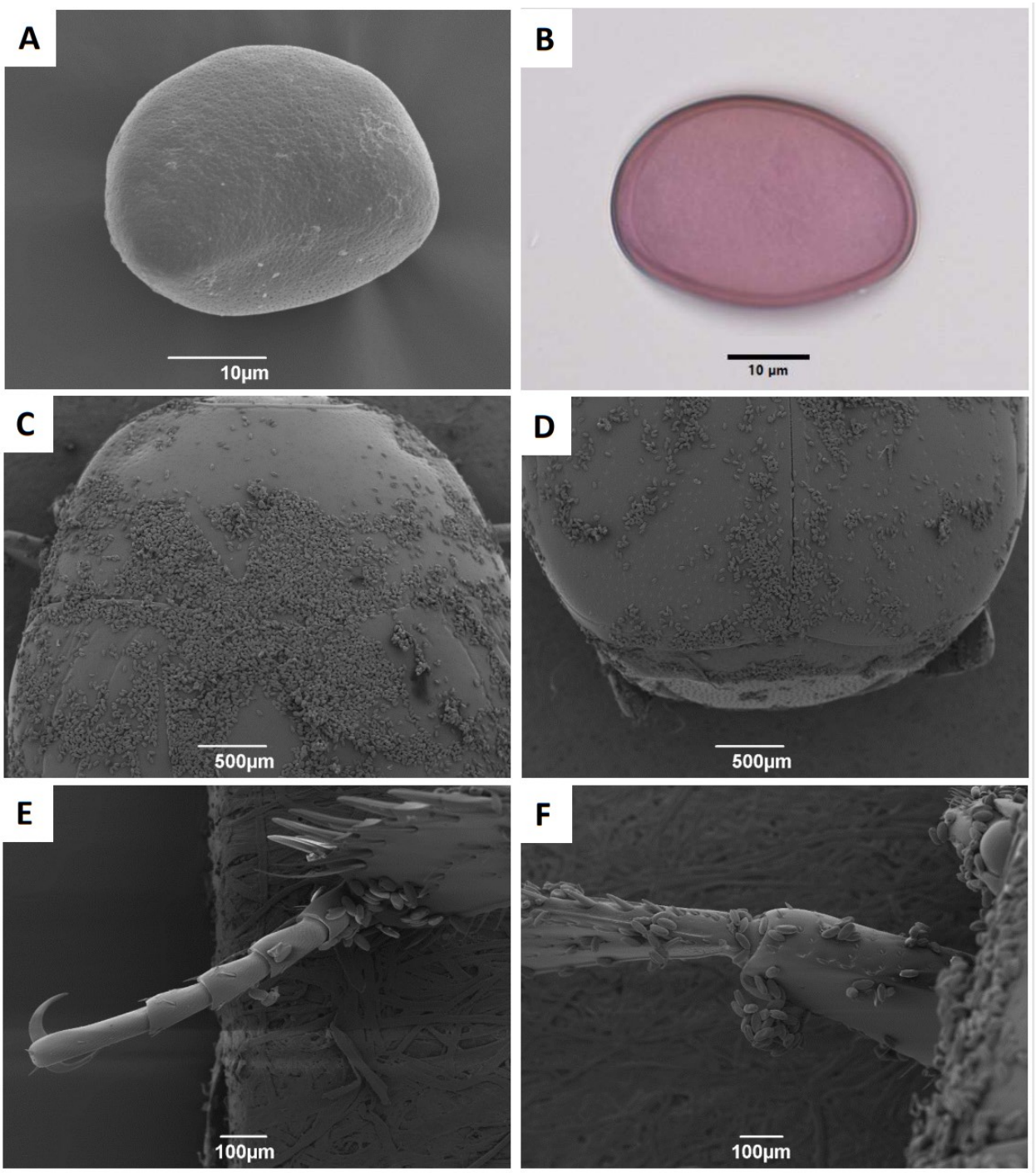

Figure 17: Pollen identification on histerid beetles. **A**, psilate pollen structure using LM, **B**, psilate pollen obtained from *D. pittieri* using SEM, **C-F**, SEM images of different organs covered with psilate pollen grains, **C**, pronotum, **D** elytra, **E**, tibia, femur and cox, **F**, tarsus, and tibia. Scale bars = 500µm (C-D), 100µm (E-F), 10µm (A-B).

3.2.4 Epidermis of spathe

The inner surface of the spathe of *D. pittieri* was dark purple with a transition to white towards the base of the spathe. Generally, the spathe was boat-shaped with a pointed apex and without constriction (Fig. 16). The epidermal structure of the inner surface of the spathe (Fig. 21) indicates a slippery surface functioning in the trapping of pollinators. The epidermis of the spathe was investigated in dried condition using SEM. Four distinct areas were investigated: 1) the distal purple area, 2) the central purple area, 3) the transition from purple to white area, and 4) the white area at the proximal end surrounding the spadix. All areas showed distinctive downward pointing papillate cells (Fig. 21). Area 1 and 2 showed additional wax platelets covering the papillate cells (Fig. 21A-B). The papillate cells in areas 1, 2, and 3 varied in length from 10-25 μm whereas they were longer in area 4 with 20-35 μm. Area 3 marked the transition zone from purple to white and no wax platelets were present in these two lower areas. (Fig. 21C).

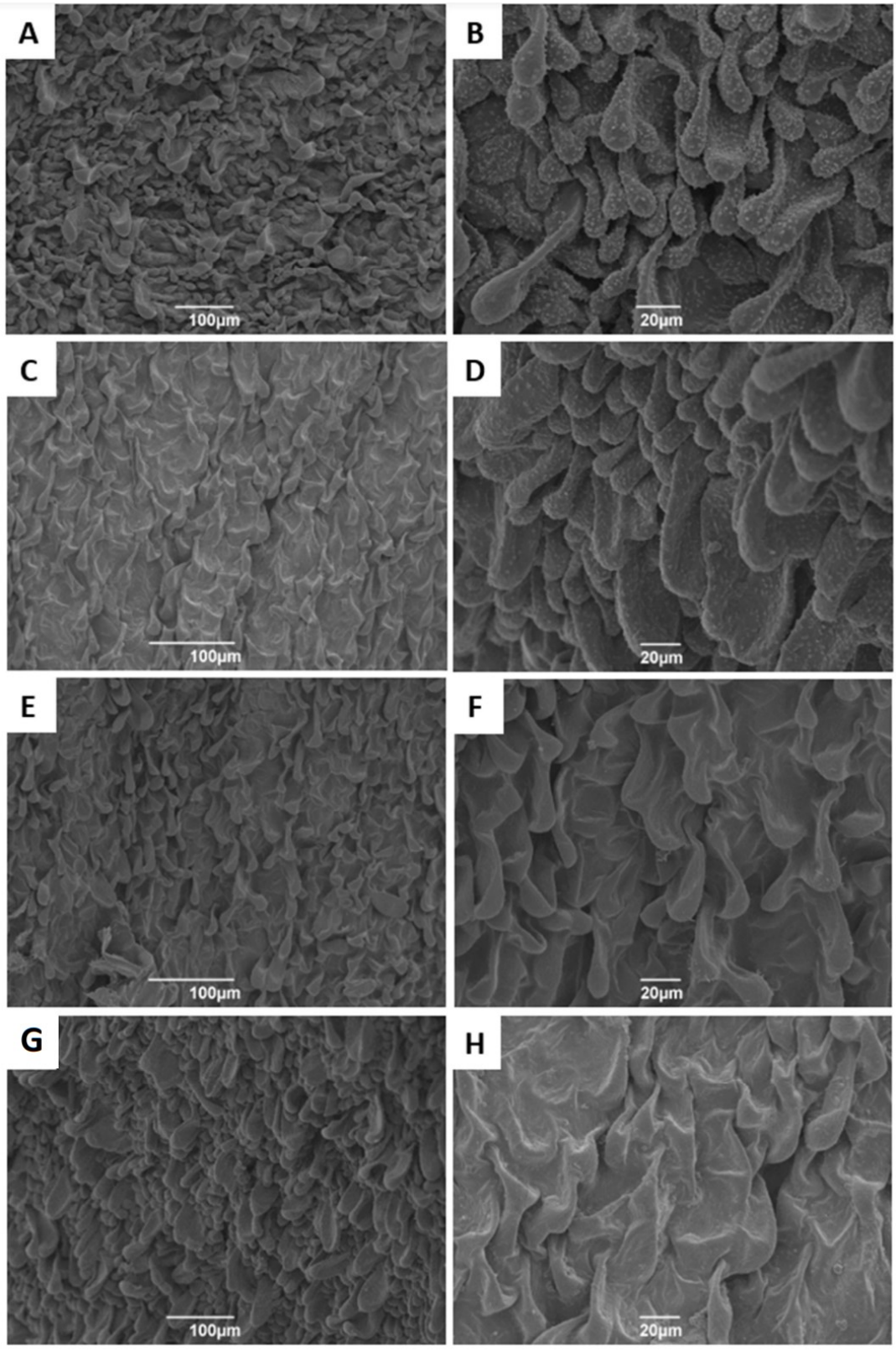

Figure 18: Slippery surfaces with downward pointing papillate cells of four different areas of inner spathe epidermis in *D. pittieri*. **A-B,** distal areas of spathe with wax platelets, **C-D,** central area of spathe with wax platelets, **E-F.** transition zone from purple to white area of spathe, epidermal cells without wax platelets and **F-H,** proximal white area of spathe epidermis without wax platelets. Scale bars = 100µm (A, C, F, G), 20 µm (B, D, E, H).

3.2.5 Bioassay experiment to attract flower visitors

With the prepared eluates of the *D. pittieri* scent, only four fly individuals could be attracted in four experiments. All observed attracted flies belonged to the family Calliphoridae (Tab. 4). With the eluates containing 3.0 ml and 5.0 ml eluate, respectively, one fly could be attracted. With 4.0 ml eluate, two flies could be attracted. In the other experiment, no insects could be attracted. The attracted insects sat on the white paper cones for a short time (<15sec).

Table 4: Occurrence and number of attracted insects to *D. pittieri* eluates within one hour of attraction time.

Date	Attraction Time	Used Volume (ml)	Number of Attracted Insects	Attracted Insect
13.03.2023	11:00-12:00	5.0	1	Calliphoridae
14.03.2023	11:00-12:00	4.5	2	Calliphoridae
15.03.2023	11:00-12:00	3.0	1	Calliphoridae
21.03.2023	11:00-12:00	3.0	0	0

3.2.6 Natural carrion source

A decaying carcass of a coati that was found along the La Bolsa trail, was analyzed for insects. The smell of the carcass was perceived to be similar to the scent emitted by *D. pittieri*. Two different beetles of the Histeridae family were found (Fig. 22).

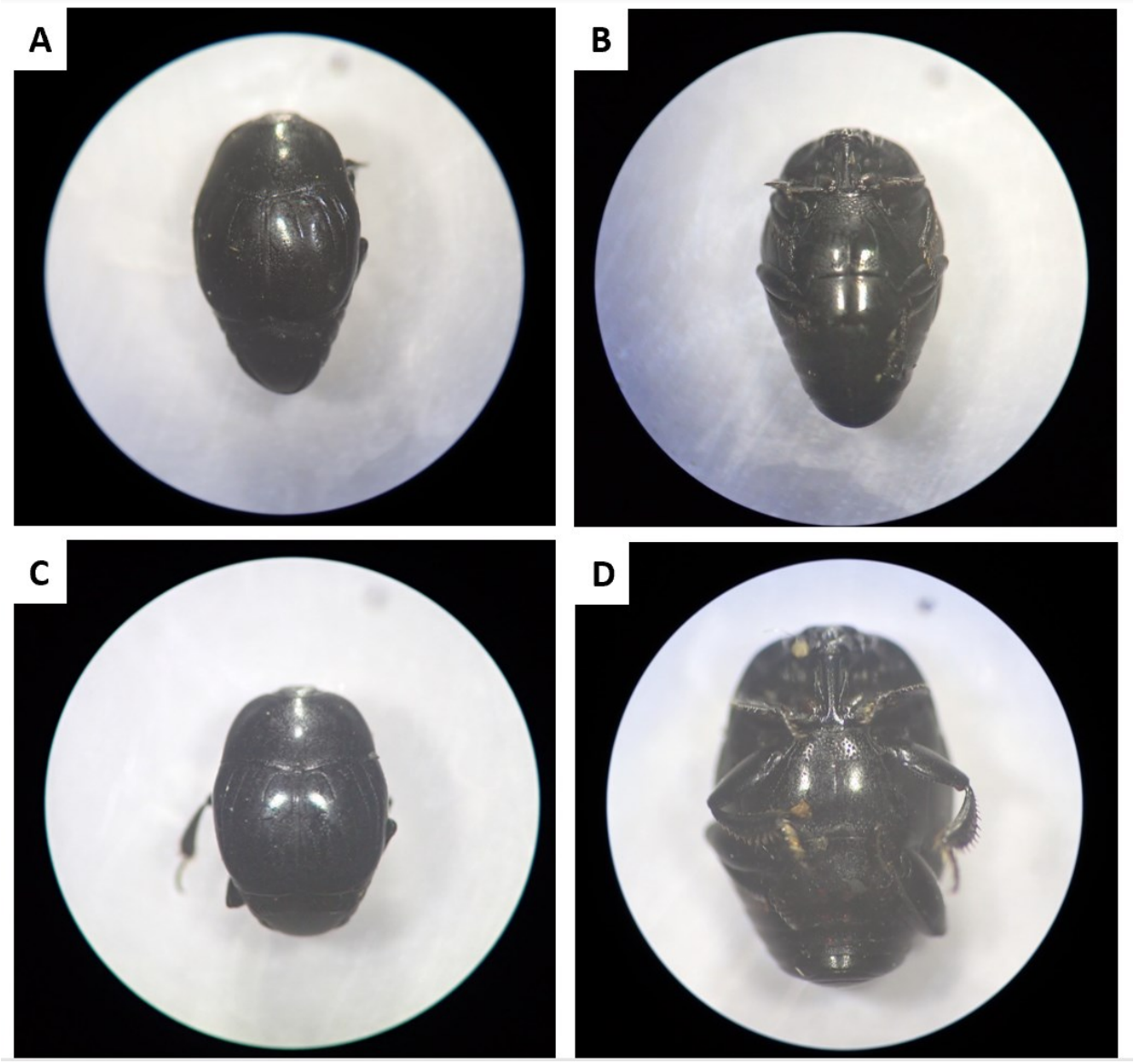

Figure 19: Histeridae beetles found on a carcass of a coati. **A**, individual 1, dorsal view, **B,** individual 2, lateral view, **C**, individual 2, dorsal view and **D**, individual 2, lateral view.

4. Discussion

4.1 Pollination type and pollen ornamentation in Araceae

The high diversity of pollen surface structures in Araceae has often been associated with the diversity in pollination systems (Sannier *et al.*, 2009). The family is described as mostly fly, beetle, and bee pollinated (Sivadasan and Sabu, 1989). The present study confirms our hypothesis that pollen ornamentation of *Anthurium*, *Syngonium*, and *Philodendron* shows genus-specific features. In the following, we compare and discuss the results in the light of earlier studies focused on pollinator types.

Anthurium is morphologically complex and belongs to the subfamily Pothoideae, which is characterized by bisexual flowers (Croat, 1980). So far, a variety of pollinators have been suggested for different species, including Euglossini (Dressler, 1967), flies (Grayum, 1990), and Curculionidae (Mayo *et al*, 1997; Franz, 2007). The studied species of *Anthurium* showed genus-specific ornamentation ranging from non-reticulate to reticulate ornamentation. *A. acutangulum* showed reticulate-nanoechinate ornamentation, in contrast *A. hoffmanni* was described as porate with a reticulate ornamentation. *A. ravenii* showed microreticulate ornamentation with adhering cubic crystals.

In *A. hoffmannii,* the main pollinators are male euglossini bees. According to Steiner (2016), *Euglossa gorgonesis* and *Euglossa flammeae* are the most common flower visitors. Scent emission by *A. hoffmanni* correlates with the activity pattern of euglossini bees starting at 07:00-08:00 a.m. (Steiner, 2016). Bee pollination is restricted to the subfamilies Monsteroideae and Pothoideae. Scent-collecting euglossine bees are the main pollinators in *Anthurium* and *Spathiphyllum* (Hentrich *et al.*, 2010). Euglossini bees visit the inflorescences and get rewarded with scent compounds that are used to attract female conspecifics (Vogel, 1966). Interestingly, also Curculionidae and *Trigona fulviventris* have been reported as pollinators (Steiner, 2016).

In *A. acutangulum* a single morphotype of gall midges (Cecidomyiidae, Cecidomyiinae) is described as the main pollinators (Etl *et al.*, 2022). Etl *et al.,* (2022) found that anthetic *A. acutangulum* inflorescences emit a nocturnal scent reminiscent of a freshly cut cucumber. The gall midges feed on male flowers and get heavily covered with pollen. Cecidomyiidae were found also to be visiting other *Anthurium* species like *A. citrifolium*, *A. ligua*, and *A. triphyllum*, (Schwerdtfeger *et al.*, 2002), all having a similar nocturnal anthesis, but so far their pollen wall structure remain unstudied.

Literature about flower visitors or pollinators is currently missing for *A. ravenii*. However, we found a genus-specific pollen ornamentation type in *Anthurium,* but pollinator groups appear rather species-specific.

When studying *Syngonium macrophyllum*, *S. hastiferum,* and *S. podophyllum*, we found a uniform microechinate-nanoverrucate pollen ornamentation using SEM. We showed that all pollen grains were inaperturate and 20-25 µm large. Inflorescences of *Syngonium* are protogynous with the female phase lasting 1-2 days before male flowers begin to shed their pollen (Croat, 1981). So far, the literature suggests pollination by large scarab beetles belonging to the subfamilies Dynastinae and Rutelinae (Chouteau *et al*, 2007). Usually, the flower visitors enter the chamber during the female phase while the male flowers are not open yet. The spathe then constricts, detaining the visitors for a short period before the male flowers start releasing pollen strands. Literature about pollinators of *S. macrophyllum* and *S. podophyllum* is missing. But interestingly, a recent study revealed a new pollination system for *S. hastiferum* suggesting a novel plant bug pollination system (Etl *et al.*, 2022). Etl *et al.*, (2022) found the plant bug *Neella sp.* nov. of the family Miridae to be the main pollinators in the otherwise beetle pollinated genus *Syngonium*. Miridae are known as widespread florivores among scarab beetle pollinated Araceae such as *S. schottianum*. The latter species is mainly pollinated by nocturnal *Cyclocephalini* scarab beetles and plant bugs occur only as florivores. The pollen structure of *S. schottianum* and *S. hastiferum* appears very different. The pollen surface structure of *S. schottianum* is psilate coated with pollenkitt suitable to adhere on the smooth body of the scarab beetles. In contrast, the pollen surface structure of *S. hastiferum* is echinate without pollenkitt adhering on plant bugs. Furthermore, Etl *et al.*, (2022) speculate that *S. angustatum* with its echinate pollen grains may also be pollinated by plants bugs, but this pollination system remains to be further investigated. Our results of the pollen structure of *S. macrophyllum* and *S. podophyllum* show echinate pollen structure as well. If these species use a plant bug pollination system need to be further tested. Generally, the study of Etl *et al.*, (2022) sheds new light on the pollination biology of the genus *Syngonium,* suggesting that a highly specialized pollination system by scarab beetles may have been replaced with another highly specialized system by plant bugs. This shift may have also been accompanied by a change in pollen morphology. Our results of the pollen of *Philodendron grandipes*, *P. microstictum,* and *P. tripartitum* demonstrated genus-specific features. The ornamentation was characterized as psilate and inaperturate in all species. The pollen size (hydrated condition) varied slightly ranging from 20-25 µm in *P. grandipes*, over 30-35 µm in *P. tripartitum* to 35-40 µm in *P. microstictum*. A psilate pollen surface

structure and a moderate pollen size ranging from 20-40 µm was already suggested for *Philodendron* by Croat (1997).

While studies about pollinators in *P. microstictum* and *P. tripartitum* are missing, dynastine scarab beetles appear to be the main pollinator of *P. grandipes* (Croat *et al.,* 1994). The lack of ornamentation seems to be substituted by the presence of pollenkitt (Hesse, 2000). High amounts of sticky pollenkitt are produced and cover the psilate pollen of *P. grandipes* (Etl *et al.*, 2022). Pollenkitt enables pollen grains of *P. grandipes* to adhere to each other but also to adhere on and insect's body. Pollenkitt in *P. grandipes* covers the psilate surface of the pollen wall enabling the pollen to disperse as strands or clumps (Etl *et al.*, 2022). Gibernau (2011) described beetles of the genus *Cyclocephala* as the main pollinators in *Philodendron*. *Cyclocephala* beetles are known pollinators in *P. anisotomum*, *P, brenesii*, *P. grayumii* and many others, but so far, their pollen wall ornamentation has not been investigated. Our hypothesis that psilate pollen ornamentation correlates with beetles pollination is positively tested in *P. grandipes*.

Overall, we found a high diversity of ornamentation types in pollen grains of Araceae. A correlation between ornamentation type and the pollination system has often been suggested (Punekar and Kumaran, 2010). The underlying idea of this hypothesis is that pollen grains need a vector to reach the receptive organs of other plant individuals (Sannier *et al.*, 2009). The pollen wall may play a crucial role in the efficiency of pollen dispersal (Pacini and Hesse, 2005; Sannier *et al.*, 2009). Grayum (1983) established a correlation between psilate pollen and pollination by beetles and echinate pollen and pollination by flies, respectively. This study demonstrats an association between psilate pollen and beetles in *Philodendron*. The lack of ornamentation in psilate pollen is substitued by the presence of high amounts of pollenkitt. Pollenkitt enables adherence of pollen to insect bodies in *Philodendron*. In contrast, we did not find a correlation between echinate pollen structure and fly pollination. Echinate pollen structure in *Syngonium* appears rather to be asscociated with a novel plant bug pollination system. In *Anthurium*, we found reticulate ornamentation types in all species. Reticulation ranged from nanoreticulate to reticulate but we could find no clear correlation with the different insect groups (Euglossini and Cecidomyiidae) that pollinate different *Anthurium* species.

4.2 Pollination in *D. pittieri*

The pollination biology of *Dracontium* is only known from a few field observations suggesting that the genus is mostly visited by beetles and flies (Zhu, 1995; Zhu and Croat, 2004; Bröderbauer,

2012). To date, the pollinators of *D. pittieri* remained unknown and a clear differentiation of flower visitors and pollinators is missing. Our results cast new light on the pollination system of *D. pittieri*. This study found clear support for the hypothesis that *D. pittieri* has evolved a carrion-mimicking beetle pollination system, in which the beetles get rewarded with pollen. The essentials of this pollination system are here circumscribed via a morphological and palynological approach.

4.2.1 Anthesis and flower visitors

Protogyny is a distinct feature of all members of Araceae (Mayo *et al.*, 1997) and hence also occurs in *D. pittieri*. According to Maia (2018), a separation of female and male flowering phase prevents self-pollination. This study aimed to assess the course of anthesis in *D. pittieri*. Although the number of individuals observed for this work were very few (n=2), we were able to successfully describe the course of anthesis as follows; 1) pre anthetic period, 2) female phase, 3) transition phase, 4) male phase, 5) post anthetic period, and 6) fruit development. We found a clear temporal segregation of female and male phase. The female phase lasted approximately 72 h. During the transition phase, the stigmas completely dried out within 24 h. Subsequently, the male phase of anthesis begun and lasted for several weeks. In Araceae, female and male phase usually do not overlap, except for some cases of self-pollination in *Amorphophallus bulbifer* and *Anthurium bakeri* (Mayo *et al.*, 1997). In *D. pittieri*, the disappearance of the stigmatic fluid during the transition phase indicates that the stigmas are no longer receptive (Zhu and Croat, 2004). The anthesis in *D. pittieri* last several weeks, whereas in other genera like *Amorphophallus,* anthesis usually lasts for two days only (Claudel, 2021). We found that *D. pittieri* emitted a strong fetid scent during both sexual phases. The timing and duration of scent emission differ among species of *Dracontium* (Zhu and Croat, 2004). We found that scent emission in *D. pittieri* was peaking around 11:30-11:45 a.m. and that most floral visits correlated positively with scent emission occurring between 08.30-12.00 a.m.

Our observations of floral visitors allowed us to differentiate between flower visitors and potential pollinators. We found that most flower visitors belonged to the families Calliphoridae, Sarcophagidae, Syrphidae and Ulidiidae. Our observations regarding flower visitors' behavior exclude any of these groups as pollinators since they did not touch the reproductive parts of the inflorescences. Their visits correlated with increasing scent emission. At scent emission maxima, copulation of Ulidiidae flies have been observed but exclusively on the spathe. In contrast, in other aroids genera like *Alocasia,* flies use the spadix as breeding sites (Miyake and Yafuso, 2003) but in *D. pittieri* flies have not been reported touching any reproductive organs at anthesis.

In this study, we describe the novel finding that histerid beetles are the pollinators of *D. pittieri.* The pollinators of *Dracontium* were still unknown (Zhu and Croat, 2004). Croat (1975) suggested a typical-fly pollination syndrome because of the unpleasant scent and trap-like nature of *Dracontium*. Flies and beetles were observed visiting *D. gigas* and blowflies visiting *D. asperum* (Zhu and Croat, 2004). We found two different, so far indetermined species of Histeridae as the only flower visitors touching the reproductive organs of *D. pittieri*. Both species were attracted during the female and the male phase of anthesis. Interestingly, during the female phase up to three individuals were found at the same time, whereas only single individuals appeared during the male phase. It remains unclear if a difference in the scent composition between female and male phase may exist. But we speculate that a stronger or differently composed scent may increase the attractiveness of *D. pittieri* during the female phase to compensate for its shorter anthesis interval and therefore to guarantee pollination. So far, it is known that scent production may vary during anthesis. In *Arum maculatum* it is known that male flowers in contrast to female flowers produce chamber-specific scents to attract pollinators (Marotz-Clausen *et al.*, 2018). To test this hypothesis in *D. pittieri*, we suggest future experiments using gas chromatography mass spectrometry (GC-MS) analysis to quantitatively and qualitatively test the scent compounds.

4.2.2 Pollen structure and beetle pollination

When conducting interception experiments in the field, the visiting histerid beetles were found to be completely covered with pollen. Our analysis with LM and SEM demonstrated that adhering pollen was identical to the reference pollen of *D. pittieri.* Accordingly, the beetles must have brought the pollen along from another flowering individual of *D. pittieri.* On the beetles, pollen was present on pronotum, elytra, and most parts of the legs. We described the pollen grains of *D. pittieri* as psilate and without any ornamentation, which is in accordance with previous studies suggesting that psilate pollen structure in the subfamily of Aroideae is associated with beetle pollination (Chartier *et al.*, 2014). A similar conclusion was reached by Punekar & Kumaran (2010) postulating a relationship between surface structure and ornamentation of pollen and pollen vectors. We found that pollen of *D. pittieri* was produced in strands that stuck easily even on smooth insect bodies such as those of histerid beetles. We observed that the beetles tried to “clean” their body from adhering pollen but were largely unsuccessful. We hypothesize that the lack of ornamentation of *D. pittieri* pollen may be substituted by the production of pollenkitt (see also Hesse, 2000). It seems clear that pollenkitt enables pollen grains of *D. pittieri* to adhere to an insect’s body. However, potential other functions of pollenkitt are not yet fully understood. Hesse (1980) describes pollenkitt as the most adhesive material present on pollen grains. A later study by Pacini

& Hesse (2005) describes various functions of pollenkitt that have to do with pollen adhesion: 1) pollen adhesion to anther for presentation, 2) pollen adhesion to other pollen grains for dispersal, 3) pollen adhesion to animal bodies to facilitate dispersal, and finally, 4) pollen adhesion to stigmas for pollination. So far, our results show that pollenkitt in *D. pittieri* facilitates the adhesion of pollen to anthers for pollen presentation and to insects for pollen dispersal.

In this study, we prepared pollen material for SEM using DMP and critical- point drying technique after Halbritter (1998). With applying this method, most of the pollenkitt was washed off in *D. pittieri* but based on our observations (pollen sticking together in pollen strands, pollen adhering to beetles), it is clear that pollenkitt is present in this species. In *Philodendron,* we were still able to show adhering pollenkitt but in general, we suggest to use other methods for pollenkitt analysis such as the double extraction method described by Dobson (1988).

4.2.3 Trap mechanism

Our results demonstrate that *D. pittieri* uses a carrion-mimicking system offering pollen as a reward for pollinators. In Araceae, deceptive trap blossoms and rewarding chamber blossoms co-occur (Bröderbauer *et al.*, 2012). Deceptive pollination is found in about 32 angiosperm families and has evolved repeatedly (Renner, 2006). Bröderbauer e*t al.,* (2012) identified six types of traps in Araceae highlighting the presence and combinations of trapping devices.

Based on the construction and functioning of the spathe of *D. pittieri,* its trap can be classified in "*Arisarum* type" category according to the classification of functional trap types by Bröderbauer e*t al.,* (2012). In *Arisarum* type traps, the spathe is only convolute at the lower part of the spathe. The spathe has no constriction, and the spadix does not contain any elongated flowers that block the entrance to the proximal part of the spathe. This appears to be the case in *D. pittieri*, where the spathe is erect without constriction and elongated sterile flowers are missing. Interestingly, Bröderbauer e*t al.,* (2012) described *Arisarum* type traps without spathe movements. We found clear evidence for spathe movement during the transition from the female to the male phase of anthesis. While the spathe is still closed at the level of the spadix during the female phase, a slit-like opening is present during the male phase (Fig. 16). Similar movements are found in many aroids (Bröderbauer *et al.,* 2014). In some taxa, spathe movements either serve as protection for developing fruits or they facilitate trapping (Bröderbauer *et al.*, 2012). We speculate that the spathe does not completely open during the very short female phase to guarantee interaction between pollinators and reproductive organs.

While studying *D. pittieri*, we identified the following traits that are relevant for the attraction, deception, and trapping of the pollinators: scent emission at anthesis, spathe coloration, spathe movement, and adaptations of the spathe epidermis are important features of the trapping mechanism. The results demonstrate that *D. pittieri* uses olfactory and visual cues to attract flower visitors. The scent emission acts as an olfactory cue that activates the insect's instinctive behavior. As previously described, the strong fetid scent is emitted during both sexual phases of anthesis and plays a crucial role as olfactory attractant imitating decaying organic material. According to Kite (1998), fetid scent consists of compounds such as sulfides, phenol and indole derivates that potentially mimic the oviposition substrates of visitors such as dung (Diaz and Kite, 2002) or carrion (Stensmyr *et al.*, 2002).

Previous studies state that the precondition for the evolution of a floral trap is most likely a chamber that encloses the sexual floral organs and pollinators (Bröderbauer *et al.*, 2012). By comparing our results for the spathe, we conclude that the spathe facilitates trapping via different aspects. The coloration of the spathe functions as a visual cue. Visual cues include dull coloration or light windows (Bröderbauer *et al.*, 2012). In *D. pittieri* the whole chamber appears fleshy and dark, potentially resembling decaying carrion. The color of the inner (adaxial) surface of the spathe changes from dark purple (distal and central areas) to white towards the proximal areas surrounding the spadix. We hypothesize that the brightly colored areas in the proximal parts of the spathe may help to trap insects in the base of the spathe as they will try to escape from the dark area towards the "light". In general, these visual cues are also found in non-trapping deceptive flowers such as stapeliads and orchids (Meve and Liede, 1994; Jersáková *et al.*, 2006).

A further novel finding is that the epidermis of the spathe contributes to the trapping also in *D. pittieri*. This is in line with early observations by Giovanni Arcangeli in the 19th century that already showed trapping of Histeridae on *Dracunculus vulgaris* (Arcangeli G., 1883). In the 20th century Fritz Knoll intensively studied the genus *Arum* (Knoll, 1923). He postulated trapping mechanism of Araceae by describing epidermal structures of the spathe and additional trapping devices such as hairs or oil droplets. For *D. pittieri*, we found downwards pointing papillate cells of the epidermis. Bröderbauer e*t al.,* (2012) found similar structure of downward pointing papillate cells with cuticular folds in *D. asperum*. Furthermore, we found wax platelets on the dark purpled colored areas, whereas the withe areas were without wax platelets. We assume that the co-occurrence of wax platelets and downwards pointing papillate cells appears to reduce the three-dimensional structure of the spathe surface to which insect legs can attach and, therefore, causes insects to slide off the surface and fall into the trap. Additionally, wax platelets can either break off or

stick on the insects' legs. In case of *D. pittieri*, wax platelets appear to contribute to gliding on the distal parts of the spathe. In the white proximal areas, insects are already trapped, and were rather deceived by the white color of the spathe imitating light. Such structures have evolved repeatedly in various context of plant-pollinator interactions (Eigenbrode, 2004; Gaume *et al.*, 2004) and may contribute to trapping in *D. pittieri*.

Thus, *D. pittieri* represents a so-called "imperfect trap", where insects glide down on the epidermis surface and fall into the spathe chamber. Insects are not completely imprisoned inside, because they can either escape by climbing the spadix (during male and female phase) or leaving via the proximal spathe gap (during male phase). The purpose of the trap is to ensure that flower visitors lured to the inflorescence will interact with the reproductive organs of the flower (Bröderbauer *et al.,* 2013). However, when comparing perfect to imperfect traps, pollination success appears higher in cases where pollinators are temporarily imprisoned and trapped. Therefore, Bröderbauer e*t al.,* (2012) concluded that imperfect traps may served as a precursor for perfect traps in the subfamily of Lasioideae, to which also the genus *Dracontium* belongs.

4.2.4 Carrion-mimicry system

This work demonstrated that *D. pittieri* uses a carrion-mimicry system with pollen as a reward for pollinators. Carrion-mimicking systems have evolved many times during angiosperm radiation and are mostly known for Rafflesiaceae (Patiño, Grace and Bänziger, 2000), Apocynaceae (Jürgens and Shuttleworth, 2015), and Araceae (Beath, 1996; Kite *et al.*, 1998). Araceae represent a family with widespread brood-site mimicry including various genera like *Dracunculus*, *Pseudodracontium,* and *Sauromatum* (Kite and Hetterschieid, 1997; Kite *et al.*, 1998; Stensmyr *et al.*, 2002). The probably best known species is *Amorphophallus titanum* (Jürgens and Shuttleworth, 2015).

Floral scents play a crucial role in carrion-mimicry systems (Jürgens and Shuttleworth, 2015). This work demonstrates that *D. pittieri* uses a strong fetid scent to attract pollinators. The scent is reminiscent of carrion and dung that mimics the substrate to which insects belonging to the orders Diptera and Coleoptera are mostly attracted. The scent mimics oviposition-, brood-, or food sites to attract insects. The pollinators of carrion-mimicking Araceae are mainly beetles often including members of the families Scarabaeidae, Staphylinidae, Histeridae and Silphidae (Beath 1996, Kite 1998). The pollinators identified for *D. pittieri* belong to the family Histeridae. We further found other members of Histeridae on a decaying carcass of a coati supporting the hypothesis that *D. pittieri* uses scent that mimics decaying carrion.

Previous studies suggest that besides the scent, these so called sapromyophilious or saprocantharophilous flowers usually present additional visual adaptations to attract pollinators (Jürgens and Shuttleworth, 2015). Typically, the flowers in carrion-mimicking Araceae are dark-brownish or purplish which is also the case in *D. pittieri.* The coloration of the spathe gives the impression of rotting or decaying organic material contributing as a visual cue (Meve and Liede, 1994).
Additionally, pollinating insects in carrion-mimicking systems are often temporarily trapped or held captive inside the spathe (Kite *et al.*, 1998). Often, carrion-mimicking systems are non-rewarding (Diaz and Kite, 2006). In *D. pittieri* we found that pollinators are not temporarily imprisoned, they can escape via the spathe opening. Further, we found that *D. pittieri* produces high amounts of pollen that also functions as a reward for pollinators. Diaz *et al.*, (2006) found a similar rewarding system in *Arum creticum* where *Lasioglossum marginatum* gets rewarded with pollen.
Based on our results, we are confident that *D. pittieri* is pollinated by beetles. We acknowledge that the current investigations rely on a brief period of time and that fruit set has not been observed yet. Therefore, we suggest future investigations to document the activities of histerid beetles on the inflorescence of *D. pittieri* in more detail. Further, fruit set observation and exclusion experiments are suggested to test for the pollination success by histerid beetle.

5. Conclusions

Pollen wall ornamentation can give considerable insights into pollination biology and is methodologically easy to study, but precise correlations to specific pollinator types remain difficult to predict. Based on our findings on *Anthurium*, *Syngonium,* and *Philodendron,* more complex aspects should be considered. This includes investigations on floral morphology, flowering sequence, floral scent, thermogenesis, and floral rewards. Especially, floral scent chemistry and diurnal emission patterns play a key role in the pollination biology of Araceae.

The case study of *D. pittieri* has clearly shown how complex plant-pollinator interactions can be. Floral features promote interaction between plants and pollinators and may lead to highly specialized pollination systems. *D. pittieri* uses a carrion-mimicry system. The key traits of this trapping mechanism involve a protogynous inflorescence, fetid scent emission, slippery surfaces of the spathe epidermis, the coloration and construction of a chamber. All of these traits contribute to the successful pollination of *D. pittieri* by beetles of the family Histeridae. Psilate pollen structure and the presence of adhesive pollenkitt are in line with prior studies postulating a beetle pollination system.

This work adds novel data to the exciting pollination biology of Araceae. With its amazing diversity and almost global distribution, the family is perfectly suited for further analyses of the incredibly diversity of plant-pollinator interaction.

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References

Arcangeli G. (1883) 'Osservazioni sull'impollinazione in alcune Araceae.', *Nuovo Giornale Botanico Italiano*, 15, pp. 72–97.

Barker, D. A. and **Arceo-Gomez, G.** (2021) 'Pollen transport networks reveal highly diverse and temporally stable plant-pollinator interactions in an Appalachian floral community', *AoB PLANTS*, 13(5).

Beath, D. (1996) Pollination of *Amorphophallus johnsonii* (*Araceae*) by Carrion beetles (*Phaeocrous amplus*) in a Ghanaian rainforest. Journal of Tropical Ecology 12, pp. 409-418.

Benbow, M. E., Tomberlin, J. K. and **Tarone, A. M.** (2015) 'Carrion ecology, evolution, and their applications'. CRC press. pp. 381-385

Bernhardt, P. (2000) 'Convergent evolution and adaptive radiation of beetle-pollinated angiosperms'. *Pollen and Pollination*, pp. 293-320.

Bosch, J. *et al.* (2009) 'Plant-pollinator networks: Adding the pollinator's perspective', *Ecology Letters*, 12(5), pp. 309- 419.

Boyce, P. C. and **Croat, T. B.** (2018) 'The Überlist of Araceae, Totals for Published and Estimated Number of Species in Aroid Genera' provided by the Internationaly Aroid Society.

Boyce, P. C. and **Sin Yeng, W.** (2012) 'The Araceae of Malesia I: Introduction', *Malayan Nature Journal*, 64(1), pp. 33–67.

Bröderbauer, D., Diaz, A. and **Weber, A.** (2012) 'Reconstructing the origin and elaboration of insect-trapping inflorescences in the araceae', *American Journal of Botany*, 99(10), pp. 1666–1679.

Bröderbauer, D., Ulrich, S. and **Weber, A.** (2014) 'Adaptations for insect-trapping in brood-site pollinated *Colocasia* (Araceae)', *Plant Biology*, 16(3), pp. 659–668.

Bröderbauer, D., Weber, A. and **Diaz, A.** (2013) 'The design of trapping devices in pollination traps of the genus *Arum* (Araceae) is related to insect type', *Botanical Journal of the Linnean Society*, 172(3), pp. 385–397.

Cabrera, L. I. *et al.* (2008) 'Phylogenetic relationships of aroids and duckweeds (Araceae) inferred from coding and noncoding plastid DNA', *American Journal of Botany*, 95(9), pp. 1153–1165.

Chartier, M., Gibernau, M. and **Renner, S. S.** (2014) 'The evolution of pollinator-plant interaction types in the araceae', *Evolution*, 68(5), pp. 1533–1543.

Chen, G. *et al.* (2015) 'Mimicking Livor Mortis: a Well-Known but Unsubstantiated Color Profile in Sapromyiophily', *Journal of Chemical Ecology 2015 41:9*, 41(9), pp. 808–815.

Chouteau, M., Barabé, D. and **Gibernau, M.** (2007) 'Thermogenesis in *Syngonium* (Araceae)', *Canadian Journal of Botany*, 85(2). pp. 184-190.

Claudel, C. (2021) 'The many elusive pollinators in the genus *Amorphophallus'*, *Arthropod-Plant Interactions*, 15(6), pp. 833–844.

Claudel, C. and **Lev-Yadun, S.** (2021) 'Odor polymorphism in deceptive *Amorphophallus* species - a review', *Plant Signaling & Behavior*, 16(12). p 1991712.

Conner, J. K. (1997) 'The Natural History of Pollination', *Ecology*, 78, pp. 327-329.

Corrales, L., Bouroncle, C. and **Zamora, J. C.** (2015) 'An overview of forest biomes and ecoregions of Central America', in *Climate Change Impacts on Tropical Forests in Central America: An Ecosystem Service Perspective*, pp.17- 38.

Croat, B. (1975) 'A NEW SPECIES OF *DRACONTIUM* (ARACEAE) FROM PANAMA: WITH NOTES ON THE SAPROMYOPHILOUS POLLINATION SYNDROME', , 1(2), pp. 168–171.

Croat, B. (1981) 'A Revision of *Syngonium* (Araceae)', *Annals of the Missouri Botanical Garden*, 68(4), pp. 565–651.

Croat, T. B. (1980) 'Flowering Behavior of the Neotropical Genus *Anthurium* (Araceae)', *American Journal of Botany*, 67(6), pp. 888-904.

Croat, T. B. (1994) 'Taxonomic status of Neotropical Araceae', *Aroideana*, 17(1), pp. 33–60.

Croat, T. B. (1997) 'A revision of *Philodendron* subgenus *Philodendron* (Araceae) for Mexico and Central America', *Annals of the Missouri Botanical Garden*, 84(3), p. 311.

Diaz, A. and **Kite, G. C. (**2002) 'A Comparison of the Pollination Ecology of *Arum Maculatum* and *Arum Italicum* in England', *Collections*, pp. 171-182.

Diaz, A. and **Kite, G. C.** (2006) 'Why be a rewarding trap? The evolution of floral rewards in *Arum* (Araceae), a genus characterized by saprophilous pollination systems', *Biological Journal of the Linnean Society*, 88(2), pp. 257-268.

Díaz Jiménez, P. *et al.* (2019) 'A Review on the Pollination of Aroids with Bisexual Flowers', *Annals of the Missouri Botanical Garden*, 104(1), pp. 83–104.

Dobson, H. E. M. (1988) 'Survey of pollen and pollenkitt lipids - chemical cues to flower visitors?', *American Journal of Botany*, 75(2), pp. 170-182.

Dressler, R. L. (1967) 'Why do euglossine bees visit orchid flowers?', *Atas do simpósio sôbre a biota amazônica*, 5, p. 171.

Eigenbrode, S. D. (2004) 'The effects of plant epicuticular waxy blooms on attachment and effectiveness of predatory insects', *Arthropod Structure and Development*, 33(1), pp.91-102.

Endress, P. K. (2001) 'The Flowers in Extant Basal Angiosperms and Inferences on Ancestral Flowers', 162(5), pp. 1111–1140.

Etl, F. *et al.* (2022) 'Evidence for the recruitment of florivorous plant bugs as pollinators', *Current Biology*, 32(21), pp. 4688-4698.e6.

Franz, N. M. (2007) 'Pollination of *Anthurium* (Araceae) by derelomine flower weevils (Coleoptera: Curculionidae)', *Revista de Biologia Tropical*, 55(1), pp. 269–277.

Gaume, L. *et al.* (2004) 'How do plant waxes cause flies to slide? Experimental tests of wax-based trapping mechanisms in three pitfall carnivorous plants', *Arthropod Structure and Development*, 33(1), pp. 103-111.

Gibernau, M. (2011) 'Pollinators and visitors of aroid inflorescences: an addendum', *Aroideana*, 34, pp. 70-83.

Gottsberger, G., Silberbauer-Gottsberger, I. and **Dötterl, S.** (2013) 'Pollination and floral scent differentiation in species of the *Philodendron bipinnatifidum* complex (Araceae)', *Plant Systematics and Evolution*, 299(4), pp. 793-809.

Grayum, M. H. (1990) 'Evolution and Phylogeny of the Araceae', *Annals of the Missouri Botanical Garden*, 77(4), pp.628- 697.

Halbritter, H. (1998) 'Preparing living pollen material for scanning electron microscopy using 2, 2-dimethoxypropane (DMP) and critical-point drying', *Biotechnic and Histochemistry*, 73(3), pp. 137-143.

Hentrich, H., Kaiser, R. and **Gottsberger, G.** (2010) 'Floral biology and reproductive isolation by floral scent in three sympatric aroid species in French Guiana', *Plant Biology*, 12(4), pp. 587-596.

Hesse, M. (1980) 'Entwicklungsgeschichte und Ultrastruktur von Pollenkitt und Exine bei nahe verwandten entomophilen und anemophilen Angiospermensippen der Alismataceae, Liliaceae, Juncaceae, Cyperaceae, Poaceae und Araceae', *Plant Systematics and Evolution*, 134(3–4), pp. 229-267.

Hesse, M. (2000) 'Plant Systematics and Evolution Pollen wall stratification and pollination', *Plant Syst. Evol*, 222, pp. 1–17.

Hofhansl, F. *et al.* (2019) 'Diversity and composition of tropical forest plant communities in the Golfo Dulce region', *Acta ZooBot Austria*, 156(December), pp. 31–46.

Jersáková, J., Johnson, S. D. and **Kindlmann, P.** (2006) 'Mechanisms and evolution of deceptive pollination in orchids', *Biological Reviews of the Cambridge Philosophical Society*, pp. 219-235.

Jiménez, P. D. *et al.* (2019) 'A review on the pollination of aroids with bisexual flowers', *Annals of the Missouri Botanical Garden*, 104(1), pp. 83–104.

Jürgens, A., Dötterl, S. and **Meve, U.** (2006) 'The chemical nature of fetid floral odours in stapeliads (Apocynaceae-Asclepiadoideae-Ceropegieae)', *New Phytologist*, 172(3), pp. 452–468.

Jürgens, A. and **Shuttleworth, A.** (2015) 'Carrion and dung mimicry in plants', in *Carrion Ecology, Evolution, and Their Applications*, pp. 361-386.

Kite, G. *et al.* (1998) 'Inflorescence odours and pollinators of *Arum* and *Amorphophallus* (Araceae)', *Reproductive biology*, (April 2014), pp. 25-315.

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

Knoll, F. (1923) 'Über die Lückenepidermis der *Arum*-Spatha.', *Plant Systematics and Evolution*, 72, pp. 246–254.

Maia, A. C. D. *et al.* (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(1), pp. 22-34.

Maia, A. C. D. *et al.* (2018) '2-Alkyl-3-methoxypyrazines are potent attractants of florivorous scarabs (Melolonthidae, Cyclocephalini) associated with economically exploitable Neotropical palms (Arecaceae)', *Pest Management Science*, 74(9), pp. 2053-2058.

Marotz-Clausen, G. *et al.* (2018) 'Incomplete synchrony of inflorescence scent and temperature patterns in *Arum maculatum* L. (Araceae)', *Phytochemistry*, 154, pp. 77-84.

Mayo, S. ., Bogner, J. and **Boyce, P**. . **(**1997) 'The genea of Araceae', *The Royal Boatnic Garden Kew*, pp. 33–55.

Meve, U. and **Liede, S**. (1994) 'Floral biology and pollination in stapeliads - new results and a literature review', *Plant Systematics and Evolution*, 192(1–2), pp. 99-116.

Milet-Pinheiro, P. *et al.* (2017) 'Floral scent chemistry and pollination in the Neotropical aroid genus *Xanthosoma* (Araceae)', *Flora: Morphology, Distribution, Functional Ecology of Plants*, 231, pp. 1-10.

Miyake, T. and **Yafuso, M.** (2003) 'Floral scents affect reproductive success in fly-pollinated *Alocasia odora* (Araceae)', *American Journal of Botany*, 90(3), pp. 370-376.

Pacini, E. and **Hesse, M.** (2005) 'Pollenkitt - Its composition, forms and functions', *Flora: Morphology, Distribution, Functional Ecology of Plants*, 200(5), pp. 399-415.

Patiño, S., Grace, J. and **Bänziger, H.** (2000) 'Endothermy by flowers of *Rhizanthes lowii* (Rafflesiaceae)', *Oecologia*, 124(2), pp. 149-155.

Pellmyr, O. and **Thien, L. B.** (1986) 'INSECT REPRODUCTION AND FLORAL FRAGRANCES: KEYS TO THE EVOLUTION OF THE ANGIOSPERMS?', *TAXON*, 35(1), pp. 76–85.

Petersen, G. *et al.* (2016) 'Phylogeny of the Alismatales (Monocotyledons) and the relationship of Acorus (Acorales?)', *Cladistics*, 32(2), pp. 141–159.

Punekar, S. A. and **Kumaran, K. P. N.** (2010) 'Pollen morphology and pollination ecology of *Amorphophallus* species from North Western Ghats and Konkan region of India.', *undefined*, 205(5), pp. 326–336.

Renner (2006) 'Rewardless flowers in the angiosperms and the role ofinsect cognition in their evolution', *Plant-Pollinator Interactions: From Specialization to Generalization*, pp. 124–144.

Sannier, J., Baker, William J, *et al.* (2009) 'A comparative analysis of pollinator type and pollen ornamentation in the Araceae and the Arecaceae, two unrelated families of the monocots', *BMC Research Notes*, 2(1), p. 145.

Schwerdtfeger, M., Gerlach, G. and **Kaiser, R.** (2002) 'Anthecology in the Neotropical Genus *Anthurium* (Araceae): A Preliminary Report', *Selbyana*, 23(2), pp. 258–267.

Sivadasan, M. and **Sabu, T.** (1989) 'Beetle pollination - Cantharophily - in *Amorphophallus hohenackeri* (Araceae)', *Aroideana*, 12(1–4), pp. 32–37.

Steiner, I. (2016) Bestäubungsbiologie von *Anthurium* und *Spathiphyllum* (Araceae) im Südwesten Costa Ricas. PHD, University of Vienna, 2016, pp.1-60.

Stensmyr, M. C. *et al.* (2002) 'Rotting smell of dead-horse arum florets', *Nature*, 420(6916), pp. 625-626.

Ulrich, S. *et al.* (2013) '*Calla palustris* (Araceae): New palynological insights with special regard to its controversial systematic position and to closely related genera', *TAXON*, 62(4), pp. 701–712.

Ulrich, S. *et al.* (2017) '*Amorphophallus*: New insights into pollen morphology and the chemical nature of

the pollen wall', *Grana*, 56(1), pp. 1–36.

Vogel, S. (1966) 'Parfümsammelnde Bienen als Bestäuber von Orchidaceen und Gloxinia', *Österreichische Botanische Zeitschrift*, 113(3/4), pp. 302–361.

Weissenhofer, A. and **Huber, W.** (2008) 'The climate of the Esquinas rainforest', in *Natural and Cultural History of the Golfo Dulce Region, Costa Rica*, (80), pp. 59–62.

Zhu, G. (1995) *Systematics of Dracontium L.(Araceae)*. University of Missouri-Saint Louis.

Zhu, G. and **Croat, T. B.** (2004) 'Revision of *Dracontium* (Araceae)', *Annals of the Missouri Botanical Garden*, 91(4), pp. 593–667.