More than fruity scents: floral biology, scent and spectral reflectance of twelve Annonaceae species

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Abstract

The pantropical family Annonaceae possesses a broad array of floral phenotypes and pollination specialisations. Being the most species-rich lineage in the magnoliids, Annonaceae are a major flowering plant component of tropical rainforests, and are important in the plant-pollinator network of this biome. Insects such as beetles, flies, bees, cockroaches and thrips have been reported as their pollinators. Although there has been considerable effort to assess their interactions with pollinators, attempts to characterise the visual and olfactory communication channels between them are scarce. Here, we report the floral phenology and characterise the spectral reflectance and odour of 12 Annonaceae species from five genera, viz. *Meiogyne*, *Monoon*, *Polyalthia*, *Pseuduvaria*, and *Uvaria*. *Pseuduvaria* species are either monoecious or dioecious while the four genera produce hermaphroditic flowers. The *Meiogyne* species are likely pollinated by small beetles; the *Polyalthia* and *Pseuduvaria* species are likely pollinated by both beetles and flies; and the *Uvaria* species is likely pollinated by both beetles and bees. All species produce flowers that are not reflective in the 300–350 nm UV spectrum, and have various spectral reflectance profile across the remaining UV and visible spectra. We detected diverse floral volatiles across all the species assessed. The flowers of the small beetle-pollinated species, including *Meiogyne* species and *Polyalthia xanthocarpa*, emitted mostly branched-chain esters, including isobutyl acetate and isoamyl acetate. The *Pseuduvaria* species emitted scent reminiscent of rotten fruit, largely consisting of 2,3-butanediol, a common by-product in yeast fermentation. The flowers of *Uvaria concava*, which were visited by both bees and beetles, released mainly straight-chain esters, including methyl hexanoate and methyl (*Z*)-4-octenoate. A corrugated inner petal outgrowth was observed in *Meiogyne* and *Pseuduvaria*; this functions as a food body reward in *Meiogyne*, but as a nectary gland for *Pseuduvaria*. This study provides insights into how Annonaceae flowers attract different guilds of pollinators.

Introduction

The pantropical family Annonaceae is an early-divergent angiosperm lineage of trees and lianas, comprising *ca*. 2500 species from 110 genera (Couvreur et al., 2019). Annonaceae species are one of the major components of tropical lowland to lower montane rainforests (Sosef et al., 2017). Almost all Annonaceae species possess a basic floral architecture of one whorl of three sepals, two whorls of three petals, numerous spirally arranged stamens and often free carpels (van Heusden, 1992). These flowers are largely pollinated by small beetle pollinators from Curculionidae, Nitidulidae, Staphylinidae and Chrysomelidae (Gottsberger, 2012; Saunders, 2012). Because beetle pollinators spend considerable time in the flowers and can often inflict damage to floral tissues, Annonaceae flowers have evolved protective structures like fleshy corolla and shield-like stamen connectives (Gottsberger, 1999). These adaptations are particularly pronounced in Neotropical species that are pollinated by large scarab beetles from Cetoniinae, Dynastinae, Rutelinae and Trichiinae (Gottsberger, 1999). While small beetles pollinate the majority of Annonaceae species, some are reported to be pollinated by thrips (Gottsberger, 1999) or small flies (Silberbauer-Gottsberger et al., 2003), and more rarely, flowers can be pollinated by bees (Teichert et al., 2009) or cockroaches (Nagamitsu et al., 1997). Pollinators are often rewarded with pollen, stigmatic exudates, floral nectar and thickened nutritious floral tissues (Gottsberger and Webber, 2018; Saunders, 2020). The floral chamber created by the corolla often additionally serves as tryst sites, and more rarely as oviposition sites (Saunders, 2020). Highly specialised pollination systems have been previously identified in Annonaceae, such as floral mimicry of fruits (Goodrich and Jürgens, 2018, and references therein), fermentation substrates (Goodrich et al., 2006), mushrooms (Teichert et al., 2012) and aerial litter (Liu et al., 2024). Other derived pollination strategies, including private channel communication with beetles (Maia et al., 2012) and euglossine bees (Teichert et al., 2009) have also been reported. Among these floral specialisations, mimicry of fruits was proposed to be the ancestral condition for the family (Johnson and Schiestl, 2016), and was likely pervasive, as around half of the recorded species emit fruity floral aromas (Goodrich, 2012).

How flowers achieve specialised pollination is a research interest for pollination ecologists. In particular, visual and olfactory cues have been recognised for their roles in mediating these interactions (Schaefer and Ruxton, 2011). Annonaceae flowers display diverse combinations of colour and odour, which might have enabled the evolution of specialisation in pollinators.

Strong floral fragrance is often noticeable in Annonaceae flowers. Based on a review by Goodrich (2012), there appears to be a myriad of floral odour reported in the family based on textual description. Although delineation of the chemical components of floral aromas is rare for Annonaceae, volatiles from over 12 chemical classes have been reported so far (Goodrich, 2012). The type of pollination adaptation seems to be associated with molecules of specific classes. For instance, proposed fruit mimics appear to be associated with aliphatic esters (Jürgens, 2000; Johnson and Schiestl, 2016); flowers mimicking fermenting substates reportedly emit fermentation by-products, including short-chain alcohols and ketones (Goodrich et al., 2006); and monoterpenoids are associated with aerial litter mimics (Liu et al., 2024) and flowers pollinated by Euglossines bees (Teichert et al., 2009).

Floral coloration is also diverse within the family, and is more frequently documented in the literature. Floral colours, including yellow, red, pink, green, orange, white and dark maroon or indigo flowers have been recorded in Annonaceae (van Heusden, 1992). It has been reported that colour can shape the choice decision of one of the major pollinating beetle family Nitidulidae (Döring et al., 2012; Vuts et al., 2022), highlighting the importance of floral visual cues. Surprisingly, virtually no attempt has been made to characterise Annonaceae floral colour based on spectral reflectance with only one exception (Liu et al., 2024). Given the diversity of pollination strategies, floral colour is an overlooked area which can potentially help elucidate how Annonaceae flowers interact with their pollinators.

Previous studies have revealed that Annonaceae species in Australia display a variety of floral adaptations to small beetle, fly or bee pollinators (Silberbauer-Gottsberger et al., 2003). For instance, *Meiogyne* and *Polyalthia* (as *Haplostichanthus*), both generally with yellowish corolla, are reportedly pollinated by small beetles from the family Nitidulidae and Curculionidae, respectively. *Pseuduvaria* is reportedly pollinated by flies, and *Uvaria* is reportedly pollinated by stingless bees. The aim of the current study is to characterise the phenotypic adaptations for various types of pollination systems in Annonaceae. We selected 12 species from the genera *Meiogyne*, *Monoon*, *Polyalthia*, *Pseudvaria* and *Uvaria* in Australia. These systems offer arenas for studying specialised bee pollination and potential floral mimicry of fruit and fermenting substrates. Their floral biology, floral spectral reflectance and floral odour are characterised here, laying a foundation for the future study of floral traits and pollination ecology of specialised pollination systems. Furthermore, magnoliids including Annonaceae preserve many architectural elements of ancestral

angiosperm flowers (Sauquet et al., 2017). Characterisation of the pollination strategies employed by early-divergent angiosperms like magnoliids may therefore offer insights into the pollination system of the ancestral flower.

Materials and methods

Study species and study sites

We examined three *Meiogyne* Miq. species (*Meiogyne cylindrocarpa* (Burck) Heusden, *Meiogyne trichocarpa* (Jessup) D.C.Thomas & R.M.K. Saunders, *Meiogyne stenopetala* (F.Muell.) Heusden), one *Monoon* Miq. species (*Monoon patinatum* (Jessup) B.Xue & R.M.K.Saunders), two *Polyalthia* Blume species, (*Polyalthia hispida* B.Xue & R.M.K.Saunders, *Polyalthia xanthocarpa* B.Xue & R.M.K.Saunders), four *Pseuduvaria* Miq. species (*Pseuduvaria hylandii* Jessup, *Pseuduvaria glabrescens* (Jessup) Y.C.F.Su & R.M.K.Saunders, *Pseuduvaria mulgraveana* Jessup, *Pseuduvaria villosa* Jessup) and two *Uvaria* species (*Uvaria concava* Teijsm. & Binn. and *Uvaria rufa* Blume) (See Table 1 for detailed information on the studied plants. Observations were conducted in the wild for individuals of *Me. stenopetala* in Mount Tamborine in 2013 (permit number: WITK08297010). All other observations were made on cultivated individuals at various sites: Gardens by the Bay, Singapore, in 2018; Garry and Nada Sankowsky Arboretum, Tolga, Australia, in 2019 and 2023; Cairns Botanic Gardens, Australia, in 2023; and Graham Wood Arboretum, Wondecla, Australia, in 2023 (see Table 1 for details).

Phenology

To assess floral ontology, 10 flowers for each species were tagged and observed for seven consecutive days. Observations were made daily to assess the duration of the pistillate and staminate phase. Stigmatic peroxidase activity has been widely used as a gauge for stigma receptivity (Dafni and Maués, 1998). However, the stigmas of some species, especially *Meiogyne* spp., displayed peroxidase activity even during bud stage based on our preliminary assessment with Peroxtesmo KO paper (MacheryNagel, Düren, Germany). The onset of stigmatic receptivity was therefore defined by stigmatic exudate secretion, while the end of stigmatic receptivity was determined by the abscission of stigmas. Staminate activity was similarly determined by anther dehiscence and the abscission of petals. A pistillate phase is defined here as the period that the flower has only the pistillate function, and likewise a

staminate phase is defined as the period that the flower only exhibits the staminate function. An overlap phase describes the period that the flower has both the pistillate and staminate functions, while an interim phase refers to the non-receptive period between the pistillate and staminate phase. Floral thermogenesis was assessed using a handheld digital thermometer every two hours throughout the day in the floral chamber, with additional readings *ca.* 10 cm away from the flower to measure ambient temperature.

Floral visitors

Floral visitors were recorded during the entire observation period. A representative number of floral visitors were collected and either preserved in 50% isopropanol for identification or frozen at -20°C and silica-dried for inspection of pollen deposition under a dissecting microscope. Probable pollinators were assessed by these criteria: 1) visitation to flowers of both sexes or sexual phases; 2) contact with floral sexual organs; and 3) presence of pollen grains on visitors in pistillate-phase flowers. Since the pistillate phase precedes the staminate phase, the presence of these pollen-laden insects provide evidence for inter-floral transfer of pollen grains.

Spectral reflectance of the petals

Pollinators often access Annonaceae floral reproductive organs via apical and basal apertures created by the inner petals (Saunders, 2012). For genera with similar colour and morphology between the inner and outer petals, namely *Meiogyne*, *Monoon*, *Polyalthia* and *Uvaria*, petal spectral reflectance was represented by that of the inner petals. The abaxial surface of the inner petals was measured for genera with drooping inner petals, viz. *Meiogyne*, *Monoon* and *Polyalthia*, whereas the adaxial surface of the inner petals were measured for *Uvaria*, which has spreading inner petals. *Pseuduvaria* has varying coloration among different parts of the petals, and therefore three perianth areas were measured: outer petal adaxial surface, inner petal abaxial surface, and inner petal gland. Differences between sexes and sexual phases were not assessed due to logistic constraints. Spectral reflectance of the flowers at 300–700 nm was measured using an Ocean Optics FLAME-S-UV-VIS-ES spectrometer (Dunedin, FL, USA), a DH-mini UV-VIS-NIR light source and an R200-7-UV-VIS probe positioned at 45°. For each species, individual flowers (n=1–8) selected randomly from one to five biologically distinct individuals were used as replicates.

Floral odour

To sample the floral volatiles, up to 10 intact flowers were enclosed in a “Toppits” oven bag for each sample. To control for ambient contaminants, an empty bag was likewise sampled. Two slits were made in the headspace bag, with one end connecting to a charcoal cartridge (ORBO 32, Supelco, USA), supplying filtered air, and the other connected to a PAS 500 air pump (Spectrex, USA). Floral volatiles were collected in a Porapak-Q cartridge (ORBO 1103, 50/80, Supelco, USA) at a flow rate of 100 m/min for 4 h. The porapak-Q cartridge was then sealed and transported to the laboratory at The University of Hong Kong. The floral volatiles then were eluted in 1 ml hexane (HPLC-grade, Sigma-Aldrich, USA). The eluents were then concentrated to 200 µl by nitrogen blowdown. For each species, technical replicates were made. The internal standard toluene was added to each sample at 34.68 ng/µl.

Gas Chromatography-Mass Spectrometry was performed on an Agilent 6890N/5973 gas chromatograph-mass selective detector to characterise floral headspace. For each sample, 1 µl eluent was injected into the inlet at 230 °C for 1 min, and then injected into a DB-WAX column (30 m × 0.25 mm, 0.25 µm thick film; J&W) in splitless mode. Helium was supplied at a flow rate of 1 ml/min as the carrier gas. Oven temperatures were held at 60 °C for 3 min, followed by a ramp up to 250 °C at 10 °C/min, and finally held for 7 min. Peaks were manually integrated and identified tentatively using the Wiley and National Institute of Standards and Technology mass spectral libraries (NIST, USA; 2020), with an 85% quality threshold. Compound identities were verified by published standardised retention index values or by co-injecting with commercially available standards. Molecules were quantified with the internal standard toluene (see also Kantsa et al., 2018). The relative abundance of each molecule was calculated. Volatiles recovered in the ambient control sample were excluded in other samples.

Results

The floral biology of the studied species is summarised in Table 1. Most species assessed displayed strong levels of protogyny and none were thermogenic. All *Meiogyne*, *Monoon*, *Polyalthia* and *Uvaria* species assessed here bear hermaphroditic flowers, whereas the *Pseuduvaria* species bear unisexual flowers (*Ps. hylandii* and *Ps. glabrescens*) or a combination of staminate and hermaphroditic flowers (*Ps. mulgraveana*).

Floral biology and pollinator activities—*Meiogyne* species

The three *Meiogyne* species (Fig. 1a–c) produced yellow flowers with longitudinally grooved basal outgrowths on the adaxial surface of the inner petals (Fig. 1c, Fig. 2a, c) and emitted a banana-like scent. Their pistillate phase lasted two days, while the duration of staminate phase differs among species (1–3 days) (Table 1). They exhibited a short overlap between the pistillate and staminate phases that lasts *ca.* 0–5 hours. Small beetles were frequently observed visiting the flowers of *Me. cylindrocarpa* (Curculionidae and Nitidulidae), *Me. trichocarpa* (Curculionidae and Nitidulidae), and *Me. stenopetala* (Nitidulidae and Staphylinidae) in both staminate and pistillate phase, during which they contacted the stamens and stigmas. Pollen-laden curculionid beetles from the tribe Ochyromerini and pollen-laden nitidulid beetles from the subfamily nitidulinae observed in pistillate-phase flowers were likely the pollinators of both *Me. cylindrocarpa* and *Me. trichocarpa*. The staphylinid beetles from the subfamily Omaliinae and the nitidulid beetles from the subfamily Epuraeinae were likely the pollinators of *Me. stenopetala.* These floral pollinators consumed pollen grains on the flowers where the beetles also sought shelter and copulated. Stigmas of all three *Meiogyne* species produced a thin film of stigmatic exudate, which became more copious towards the end of the pistillate phase. Consumption of stigmatic exudate was invariably observed in curculionid, nitidulid and staphylinid beetle visitors. Consumption of floral tissues, specifically petals and stigmas, were observed, primarily by curculionid beetles, and less frequently by nitidulid and staphylinid beetles, leaving gnaw marks on the floral tissues of the three *Meiogyne* species. However, consumption of the inner petal corrugation was particularly pronounced compared to the surrounding floral tissues (Fig. 2). Nectar secretion was not observed on the inner petal corrugation of *Me. cylindrocarpa*, *Me. trichocarpa* and *Me. stenopetala*, thus they likely functioned as a food body reward for the floral visitors.

Floral biology and pollinator activities—*Polyalthia* species

Polyalthia xanthocarpa (Fig. 1f) exhibited a 2–3-day pistillate phase followed by a 1-day staminate phase (Table 1). The transition between pistillate and staminate phase was not observed directly and could have occurred at night: it is therefore unclear whether an interim or overlap phase was present. As with *Meiogyne*, *Po. xanthocarpa* bore yellow flowers with a banana-like odour (Fig. 1f) and were visited by curculionid beetles that accessed the floral sexual organs in both the staminate and pistillate phases (Table 1). Pollen grains were not observed on the limited number of pistillate-phase visiting beetles, however. The curculionid beetles were observed to consume pollen and utilise the flower for shelter. Secretion of

stigmatic exudate in *Po. xanthocarpa* was weak and the consumption of stigmatic exudate was not observed. In contrast, *Polyalthia hispida* bore yellow flowers without detectable odour (Fig. 1e). Its anthesis comprised a three-day pistillate phase followed by a two-day staminate phase. No floral visitors were observed.

Floral biology and pollinator activities—*Uvaria* species

Uvaria concava bore flowers with red petals and emitted a fruity odour (Fig. 1k). It had a 2–3-day pistillate phase, followed by a prolonged overlap phase (1–2 days), in which stigmas remained attached to the ovaries as the anthers dehisce. The drying and abscission of stigmas usually occurred one day after the overlap phase and were sometimes synchronised with petal abscission. In most flower, petal abscission occurred two days after the staminate function initiated. Because of the variation in the timing of stigma drying, the duration of staminate phase varied between 0–1 day. Nitidulid beetles (subfamily Nitidulinae) were the primary floral visitors observed: they accessed the floral sexual organs and were present throughout anthesis. They were probable pollinators since pollen-laden individuals were found in pistillate-phase flowers. We observed the visitation of a single honeybee (*Apis* sp.) during the overlap phase; although the bee contacted the floral sexual organs while collecting pollen, we failed to capture it and were unable to assess pollen deposition.

Uvaria rufa flowers bore orange petals with tints of red and green (Fig. 1l). The flower emitted a fruity odour and had a one-day pistillate phase, followed by a one-day interim phase and a four-day staminate phase. Only one unidentified fly was observed, which visited during the interim phase. It is unclear whether pollen grains were deposited onto this fly visitor.

Floral biology and pollinator activities—*Pseuduvaria*

Pseuduvaria species (Fig. 1g–j) displayed an array of sexual systems (Table 1). *Pseuduvaria hylandii* was assessed to be dioecious, while *Ps. mulgraveana* and *Ps. glabrescens* were assessed to be structurally andromonoecious, in which the same individuals bear staminate flowers that lack carpels, as well as bisexual flowers with a few stamens. *Pseuduvaria hylandii* had prolonged anthesis for both pistillate and staminate flowers (> 6 days), but we were unable to assess the anthesis duration (and floral phenology) for *Ps. glabrescens* due to logistic limitations. Anthesis in staminate flowers of *Ps. mulgraveana* lasts two days, whereas in hermaphroditic flowers the pistillate phase lasts for two days, followed immediately by

petal abscission, with anthers dehiscing two days after petal abscission. We were only able to assess one staminate individual of *Ps. villosa* and were therefore unable to determine its sexual system.

The flowers of all four *Pseuduvaria* species possessed white outer petals (Fig. 1g–j). They also possessed white to reddish inner petals with dark maroon inner petal glands on their adaxial surface (fig. 2d). These flowers emitted a strong fermentation odour that resembled rotten fruits. They had a mitriform corolla, with large basal apertures that allowed larger insects to access the floral chamber. The inner petals were apically connivent and the three pairs of glands on the inner petals form a platform in the floral chamber (Fig. 1h, Fig. 2d–f). Nectar secretion was observed on the inner petal glands and surrounding dark red petal tissues of the four *Pseuduvaria* species (Fig. 2e). Drosophilid flies and nitidulid beetles were observed to be the primary floral visitors of *Ps. glabrescens*, *Ps. hylandii* and *Ps. mulgraveana* (Table 1). These insects were observed accessing the floral chamber and consuming nectar, often positioning themselves underneath the sexual organs to access the nectary. Pollen grains were observed to be deposited either onto the back of the insects (Fig. 2f), or onto the inner petal glands where the pollen grains were then picked up secondarily by the flies and beetles on their legs. The drosophilid flies and nitidulid beetles were observed moving across the stigmas and stamens with their legs touching the sexual organs, which may assist pollen transfer. Some drosophilid flies are large enough to brush the back of their thorax or abdomen against the sexual organs, which may additionally deposit pollen grains onto the stigmas. Both drosophilid flies and nitidulid beetles were observed to access the sexual organs of pistillate and staminate flowers for *Ps. glabrescens*, *Ps. hylandii* and *Ps. mulgraveana*. While pollen grains were observed on the drosophilid flies and nitidulid beetles found in pistillate-phase flowers of *Ps. hylandii*, pollen deposition was observed only on nitidulid beetles from pistillate-phase flowers of *Ps. glabrescens* and *Ps. mulgraveana*. Other dipteran visitors, namely lauxaniid and neriid flies, were also observed in *Ps. hylandii*, but they are too large to access the floral chamber and thus unlikely to be pollinators. Unfortunately, we failed to observe any floral visitors for *Ps. villosa*, though it has similar floral colour and odour to the other *Pseuduvaria* species (Fig. 1j).

Floral biology and pollinator activities—*Monoon*

Monoon patinatum produced flowers with greenish petals (Fig. 1d). Only two staphylinid beetle visitors from the subfamily Tachyporinae were observed during the pistillate phase (Table 1). Pollen grains were not observed on their bodies.

Floral Colour

Various types of floral coloration were observed in the studied species, including red (*Uvaria concava*), orange (*U. rufa*), yellow (*Meiogyne cylindrocarpa*, *Me. trichocarpa*, *Me. stenopetala*, *Polyalthia hispida* and *Po. xanthocarpa*), green (*Monoon patinatum*), and a mixtue of white and maroon (*Pseuduvaria hylandii*, *Ps. glabrescens*, *Ps. mulgraveana* and *Ps. villosa*). The spectral reflectance of the petals of 12 Annonaceae species is shown in Fig. 3. The petals of all species are not UV-reflective from 300–350 nm; most of the reflectance was observed in the visible spectrum (400–700 nm). Note that while yellow-flowered species possess similar coloration to human perception, their spectral reflectance can be quite varied, highlighting the importance of quantification of reflective spectra.

Floral Odour

The floral headspace composition of 11 Annonaceae species is summarised in Table 2. We detected a total of 97 volatiles from seven classes of compounds. We did not detect any major volatiles in the headspace of *Polyalthia hispida* against the ambient air control, and therefore did not present the headspace data here.

Aliphatic ester was the most abundant class of volatiles in *Meiogyne cylindrocarpa*, *Me. trichocarpa*, *Me. stenopetala*, *Polyalthia xanthocarpa*, *Uvaria concava* and *U. rufa*. The headspaces of all *Meiogyne* species and *Po. xanthocarpa* contained a varying degree of esters, including isobutyl acetate (*Me. cylindrocarpa*: 7.87 ± 2.16%; *Me. trichocarpa*: 11.86 ± 4.37%; *Me. stenopetala*: 56.71 ± 1.5%) and isoamyl acetate (*Me. cylindrocarpa*: 79.58 ± 7.65%; *Me. trichocarpa*: 84.07 ± 4.01%; *Me. stenopetala*: 28.17 ± 4.13%; *Po. xanthocarpa*: 99.28 ± 0.02%). For *U. concava*, the floral headspaces were dominated by two esters, namely methyl-(*Z*)-4-octenoate (25.36 ± 0.32%), and methyl hexanoate (54.69 ± 0.32%), while for *U. rufa*, the most abundant volatiles were hexyl acetate (21.27 ± 0.25%), butyl acetate (20.65 ± 0.21%), and ethyl octanoate (20.04 ± 0.22%). In *Meiogyne* and *Polyalthia*, branched-chain aliphatic esters dominated the floral odour, while in *Uvaria*, the floral odours primarily consisted of straight-chain the aliphatic esters. For *Monoon patinatum*, the headspace mainly comprised the monoterpenes β-ocimene (45.50 ± 0.61%) and allo-ocimene (11.89 ± 0.59%),

and 2-methyl-butanoic acid (16.48 ± 0.53%). The oxygenated aliphatic compound was the most abundant volatile class for *Pseuduvaria hylandii*, *Ps. glabrescens*, *Ps. mulgraveana* and *Ps. villosa*, consisting of the molecule 2,3-butanediol (84.83–96.98% of the headspaces).

Discussion

Floral phenology

Most species assessed in this study exhibited a 3–5 day anthesis period and none exhibited circadian trapping, a time-dependent trapping mechanism in which pollinators are trapped and released in accordance to the insects' peak circadian activities (Lau et al., 2017). The duration of anthesis for most species in the current study is similar to the typical non-trapping Annonaceae species (≥ 2 days) (Pang and Saunders, 2014; Lau et al., 2017). As the family is self-compatible (Pang and Saunders, 2014), temporal separation of sexual phases is an important adaptation to reduce autogamy. An interim phase was observed in *Uvaria rufa*, during which the stigmas are no longer receptive and anther dehiscence has not begun, potentially offering additional assurance to prevent autogamy (Pang and Saunders, 2014). However, in some of the other species, including *Meiogyne* spp. and *U. concava*, an overlap phase was observed, during which carpels and stamens are simultaneously functional within a flower. This overlap phase could offer reproductive assurance by autogamy when pollinator availability is scarce. It was previously reported that *U. concava* was pollinated by stingless bees (Meliponinae) in its natural population (50 km from our site of study) (Silberbauer-Gottsber et al., 2003). Because bee visitors to Annonaceae often collect pollen only as a food reward, and seldom visit pistillate-phase flowers, the overlap phase has been suggested to be essential for bee pollination (Gottsberger, 2014). It was, however, reported that meliponine visitors also collect stigmatic exudate as a reward (Silberbauer-Gottsberger et al., 2013), suggesting the flower offers reward to the meliponine visitors even during pistillate phase. The role of the prolonged overlap phase for *U. concava* is therefore contentious.

Floral phenology also played a role in the sexual function of the flower, especially for *Pseuduvaria* species. Previous studies have shown that *Ps. mulgraveana* is structurally andromonoecious (Pang et al., 2013), meaning that staminate flowers and bisexual flowers are borne on the same plant. The stamens of bisexual flowers, however, release functional pollen grains only after petal abscission (Pang et al., 2013), rendering the plant functionally monoecious, which is corroborated by our observations.

Inner petal corrugation and glands

Inner petal outgrowth was observed in *Meiogyne* spp. and *Pseuduvaria* spp. in the current study. This outgrowth has independently evolved in around 20 genera, including *Annona* L., *Alphonsea* Hook.f. & Thomson, *Asimina* Adans., *Asteranthe* Engl. & Diels, *Duguetia* A.St.-Hil., *Maasia* Mols, Kessler & Rogstad, *Meiogyne* Miq., *Miliusa* Lesch. ex A.DC., *Orophea* Blume, *Porcelia* Ruiz & Pav., *Pseuduvaria* Miq., *Sapranthus* Seem., *Stenanona* Standl., *Tetrameranthus* R.E.Fr., *Tridimeris* Baill., *Uvaria* L., *Wangia* X.Guo & R.M.K.Saunders, and *Xylopia* L. (van Heusden, 1992; Schatz and Maas, 2010; Xue et al., 2017). In *Pseuduvaria*, the inner petal outgrowth has been reported to be a nectary gland (Silberbauer-Gottsberger et al., 2003). In the current study, the four *Pseuduvaria* species also possessed this floral tissue, which invariably functioned as nectary, corroborating the previous study. Likewise, all three *Meiogyne* species assessed in our study possessed weakly folded to longitudinally grooved basal growths on the adaxial surface of the inner petals. Although this structure has previously been interpreted as a gland (van Heusden, 1992, 1994), histological studies have failed to identify secretory ducts or hairs (Xue et al., 2021). The inner petal corrugation may potentially offer tactile cues for the floral mimicry of aerial litter in *Meiogyne heteropetala* (Liu et al., 2024), but the role of this tissue remains enigmatic for most *Meiogyne* species. Our observations indicate that pollinators preferentially consume the inner petals over other floral structures (Fig. 2), suggesting that the corrugation likely functions as a food body in *Me. cylindrocarpa*, *Me. trichocarpa* and *Me. stenopetala*. In Annonaceae, specialised nutritious petal tissues are common in species that are pollinated by scarab beetles in the neotropics, including *Annona*, *Cymbopetalum*, *Duguetia*, and *Malmea* species (Gottsberger and Webber, 2018). Among these lineages with specialised food body, there is potential convergence in tissue structure. The inner petal corrugation of these species is anatomically similar to those found in *Meiogyne*, lacking secretory openings, ducts or trichromes, and comprising a mixture of cells full of starch granules and cells enriched with tannins (Gottsberger and Webber, 2018; Xue et al., 2021).

Exploitation of pollinators associated with fruits

The fruity floral aromas and beetle pollination of Annonaceae have led some authors to propose some Annonaceae flowers mimic fruits (Johnson and Schiestl, 2016; Goodrich and Jürgens, 2018). In particular, fruit mimicry has been postulated in *Anaxagorea*, *Annona*, *Artabotrys*, *Duguetia* and *Xylopia* and is likely to be prevalent in the Annonaceae (Johnson

and Schiestl, 2016; Goodrich and Jürgens, 2018; Chen et al., 2020). These flowers are pollinated by small beetles such as Curculionidae, Nitidulidae and Staphylinidae that are known to use fruits as a food source or oviposition site (Phelan and Lin, 1991; Racette et al., 1992; Frank and Thomas, 1999; Mutinelli et al., 2015). Previous studies have recorded small-beetle visitors in *Polyalthia xanthocarpa* flowers (as "*Haplostichanthus* spec. ("Cape tribulation")"; Morawetz, 1988), and curculionid beetles have been observed visiting the flowers in Cape Tribulation, Australia (pers. comm., Dr David Tng). For *Meiogyne*, nitidulid and curculionid beetles have been reported to be the pollinators of *Me. cylindrocarpa* in tropical rainforests in West Malesia (Momose, 2005; Roubik et al, 2005). Beetles from these families were also observed in the current study.

In this study, floral aromas resembling ripe fruits were recorded in *Me. cylindrocarpa*, *Me. trichocarpa*, *Me. stenopetala*, *Po. xanthocarpa*. Small beetle pollinators (families Nitidulidae, Curculionidae and Staphylinidae) were observed as floral visitor of *Me. cylindrocarpa*, *Me. trichocarpa*, *Me. stenopetala* and *Po. xanthocarpa* (Table 1). Their floral odour resembled strong banana-like scent to human perception, and is largely composed of either isoamyl acetate or isobutyl acetate (Table 2). These two molecules have been reported in various fruits, including banana (Jordán et al., 2001), papaya (Katague and Kirch, 1965), pear (Zhang et al., 2023) and wild soursop (Pino et al., 2002), and is implicated as the semiochemicals of Curculionidae and Nitidulidae (Rochat et al., 2000; Torto et al., 2007). The spectral reflectance of *Meiogyne* species, especially *Me. cylindrocarpa* and *Me. trichocarpa*, exhibited low UV reflectance, with stronger reflectance from 500–700 nm (Fig. 3). The UV-absorbing yellow spectral profile is a characteristic for pollen (Dötterl et al., 2014) and was also reported in fruits such as bananas (Xie et al., 2018). Some nitidulid and curculionid beetles are known to associate with fruits (Phelan and Lin, 1991; Racette et al., 1992; Mutinelli et al., 2015), and nitidulidae has previously been demonstrated to be attracted to various shade of yellow (Döring et al., 2012; Vuts et al., 2022). The current evidence suggests that *Me. cylindrocarpa*, *Me. trichocarpa*, *Me. stenopetala* and *Po. xanthocarpa* likely attract their pollinators at least by exploiting visual and olfactory cues that indicate fruits.

Exploitation of pollinators associated with fermented substrates

Records of floral visitors to *Pseuduvaria* are more comprehensive than for most other Annonaceae genera in Australia. In a previous pollination study on another Australian

Pseuduvaria species, *Ps. froggattii*, it was shown that the flowers are primarily pollinated by drosophilid flies (Silberbauer-Gottsberger et al., 2003). Similarly, *Ps. glabrescens* was previously reported to be visited primarily by small flies (as *Pseuduvaria* spec. ("Davies Creek"); Morawetz, 1988). *Pseuduvaria mulgraveana*, on the other hand, was reported to be pollinated by the nitidulid beetle, *Aethina australis*, and was only infrequently visited by flies. Our observations are largely congruent with these studies: *Ps. hylandii*, *Ps. glabrescens* and *Ps. mulgraveana* were observed to be visited by both nitidulid beetles and drosophilid flies. Pollen deposition on the nitidulid beetles was observed in the pistillate-phase flowers of all three species, while drosophilid flies appeared to be the pollinator only for *Ps. hylandii*. It was previously postulated that flies could pollinate *Ps. villosa*, but floral visitors were not observed in our study.

Floral coloration in the *Pseuduvaria* species varies across different areas of petal tissues (Figs. 1 & 3). The abaxial surface of the inner petals in most species demonstrate largely similar reflectance spectra with the adaxial surface of the outer petals, except for *Ps. hylandii*. In contrast to these areas, the inner petal glands of all four *Pseuduvaria* species studied are burgundy red with generally lower reflectance across all wavelengths. Additionally, all four *Pseuduvaria* species emit an odour reminiscent of rotten fruits. Rotting fruits have been reported to display a reduction in overall reflectance across the visible spectrum under fungal infection (Liu et al., 2020). The contrast between the dark burgundy inner petal gland and the remaining bright floral tissues may have evolved to imitate rotten patches on fruits. Interestingly, in *Pseuduvaria*, nectar secretion is localised in the darkened area (Fig. 2), suggesting there is co-localisation of gustatory cue and visual cue, which may help position the pollinators underneath the reproductive organs and facilitate pollen transfer. The floral odours of all four *Pseuduvaria* species are largely composed of 2,3-butanediol (Table 2), which is a common volatile emitted by yeast and fermenting substrates (Goodrich et al., 2006, 2023). This molecule is one of the major volatiles of *Asimina triloba* (Goodrich et al., 2006), a maroon-petalled floral mimic of fermentation substrates (Goodrich et al., 2023). As with *Ps. glabrescens*, *Ps. hylandii* and *Ps. mulgraveana*, *Asimina triloba* is pollinated by small flies and small beetles (Martin, 2021; Goodrich et al., 2023). This suggests convergence in floral colour and odour between *Asimina* and *Pseuduvaria* for attracting the same pollinator guilds. The four *Pseuduvaria* species may therefore be potential candidates for floral mimics of fermentation substrates.

Exploitation of bee and beetle pollinators

Uvaria concava was reported to be pollinated by stingless bees in the wild (Silberbauer-Gottsberger et al., 2003) but is here inferred to be pollinated by nitidulid beetles in cultivation (Table 1). This species possesses bright-red petals, reflecting the visible spectrum mostly at 600–700 nm (Fig. 3). However, neither the tribe Meliponini (stingless bees) nor the family Apidae have photoreceptors within this range (van der Kooi et al., 2021). Though the photosensitivity of Nitidulidae is unknown, most coleopteran families with known visual systems are unable to detect this part of the visible spectrum (van der Kooi et al., 2021). It is therefore unclear how floral visual cues assist pollinator attraction in *U. concava*. The floral odour of *U. concava* is largely composed of methyl hexanoate and methyl (*Z*)-4-octenoate. While there is little documentation how meliponine bees and nitidulid beetles respond to these molecules, methyl hexanoate is reported to be a pheromone for male bumblebees (Valterová et al., 2001). Among Annonaceae species that emit esters, branched-chain aliphatic esters are typically produced (Table 2; Jürgens et al, 2000), but *Uvaria* spp. primarily produce straight-chain aliphatic esters instead. Interestingly, the branched-chain aliphatic ester isoamyl acetate (the dominant floral scent component of *Meiogyne* spp. and *Polyalthia xanthocarpa*) is a bee alarm pheromone that reduces foraging in the honeybee species *Apis mellifera* and *Apis cerana* (Gong et al., 2017). Nonetheless, whether this structural change in floral esters contributes to the shift to bee pollination remains to be investigated. Future studies comparing the contrast between spectral reflectance of the petals and reproductive organs as well as colour-based and scent-based bioassays could help assess the role played by visual and olfactory cues in bee-pollinated Annonaceae species.

Conclusions

The basic floral biology, petal spectral reflectance and floral scent of selected species in five Annonaceae genera are characterised here in detail. Our study has identified multiple species that have floral traits resembling fruits (*Meiogyne* spp. and *Po. xanthocarpa*) and fermented substrates (*Meiogyne* spp. and *Po. xanthocarpa*). The specialised floral cues and adaptations identified in this study provide preliminary evidence for potential floral mimicry of fruits and fermented substrates, and offer insights into how floral cues may attract floral visitors. These findings serve as a prelude to future studies on specialised pollination systems, and provide baseline information on floral traits in the pantropical family Annonaceae. Future studies involving the characterisation of colour and odour of co-ocurring fruits and fermenting

substrates would be important to assess whether these species exploit their pollinators through floral mimicry.

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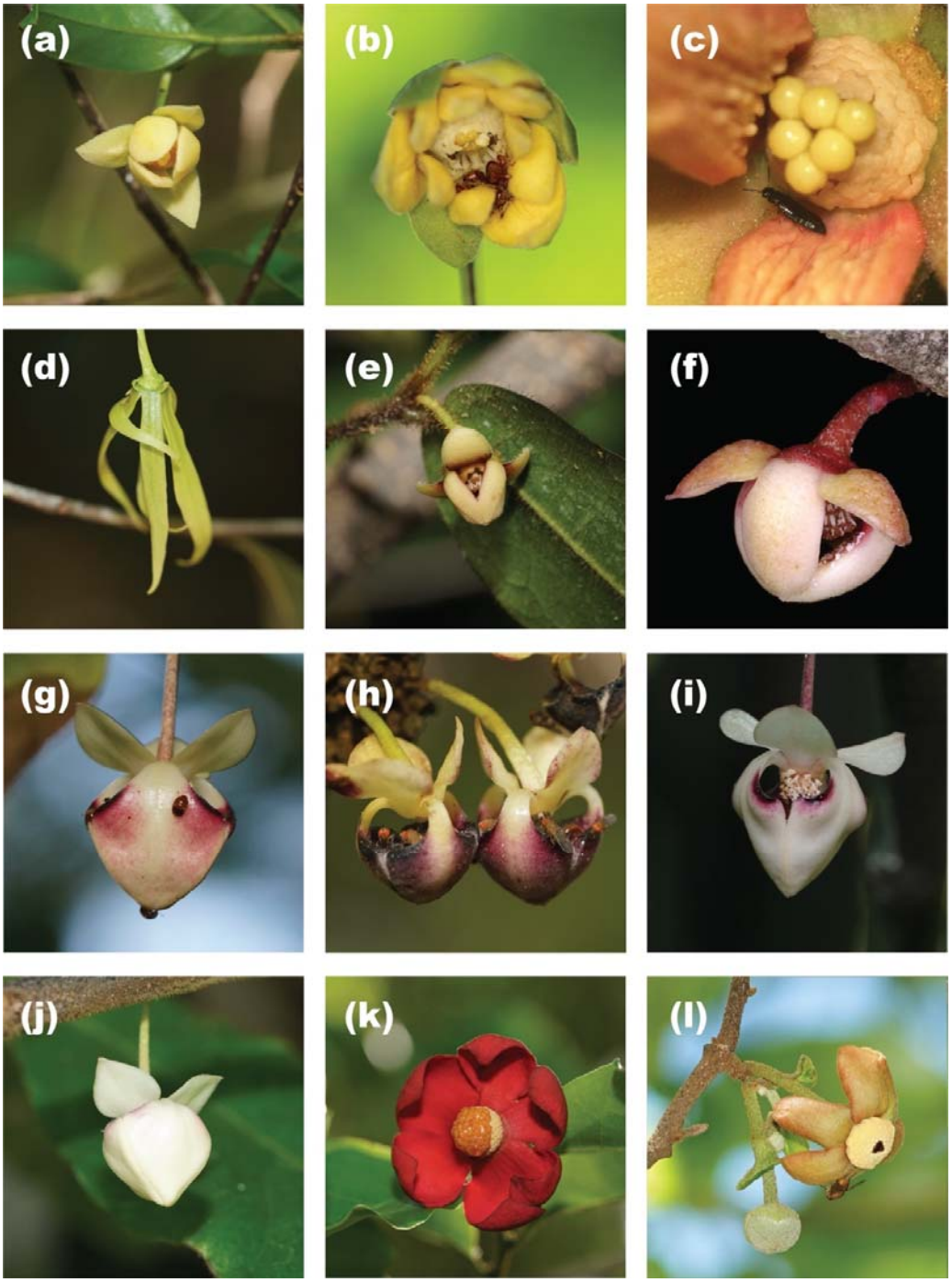

Fig. 1. Flowers of Annonaceae species studied. (a) *Meiogyne cylindrocarpa*. (b) *Meiogyne trichocarpa* with curculionid and nitidulid visitors. (c) *Meiogyne stenopetala* with a staphylinid visitor. (d) *Monoon patinatum*. (e) *Polyalthia hispida*. (f) *Polyalthia xanthocarpa*. (g) *Pseuduvaria glabrescens* with nitidulid visitors. (h) *Pseuduvaria hylandii* with drosophilid visitors. (i) *Pseuduvaria mulgraveana*. (j) *Pseuduvaria villosa*. (k) *Uvaria concava*. (l) *Uvaria rufa* at interim phase with a fly visitor. Photo credit: Photo credits: (a, b, d, e, g–l): Ming-Fai Liu; (c): Chun-Chiu Pang; (f): Garry & Nada Sankowsky.

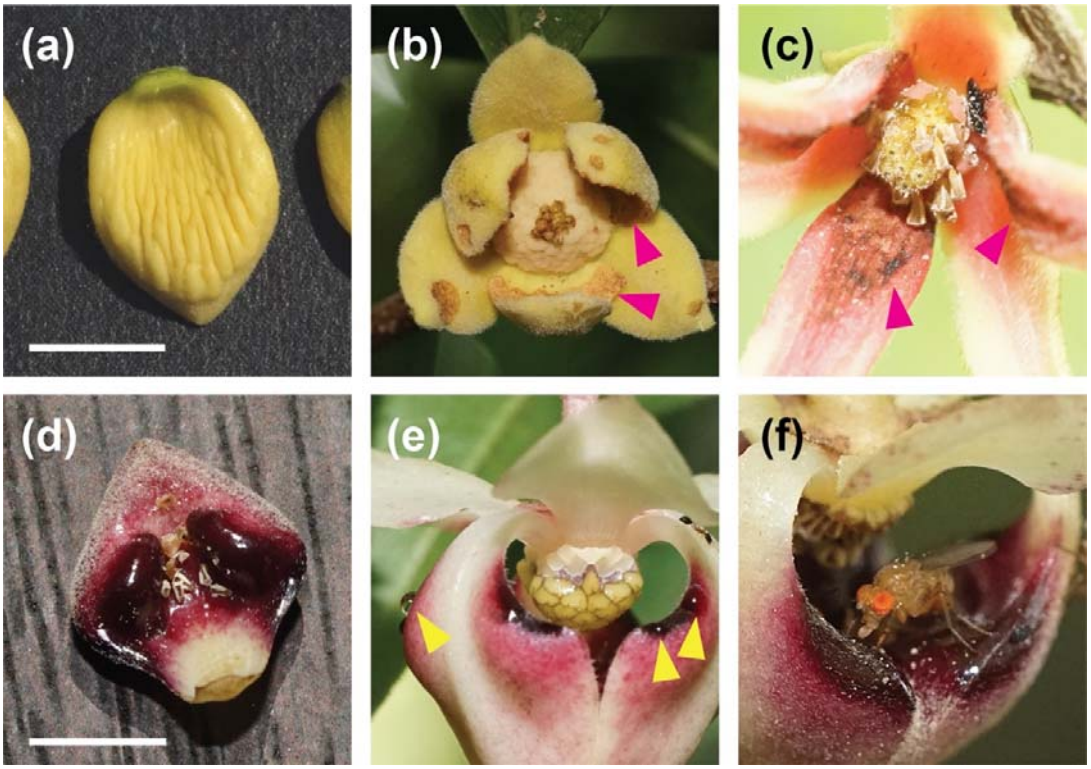

Fig. 2. Inner petal outgrowths. (a) Adaxial surface of inner petal of *Meiogyne cylindrocarpa*. (b) Gnaw marks (magenta arrows) created by curculionid beetles on the inner petals of *Meiogyne trichocarpa*. (c) Gnaw marks (magenta arrows) created by staphylinid beetles on the inner petals of *Meiogyne stenopetala*: longitudinal ridges of the basal corrugation have been gnawed away. (d) Pair of nectary glands on the adaxial surface of the inner petal of *Pseuduvaria hylandii*. (e) Nectar secreted by *Pseuduvaria mulgraveana* (yellow arrows). (f) Drosophilid fly consuming nectar in a *Pseuduvaria hylandii* flower. Photo credit: (a–f): Ming-Fai Liu.

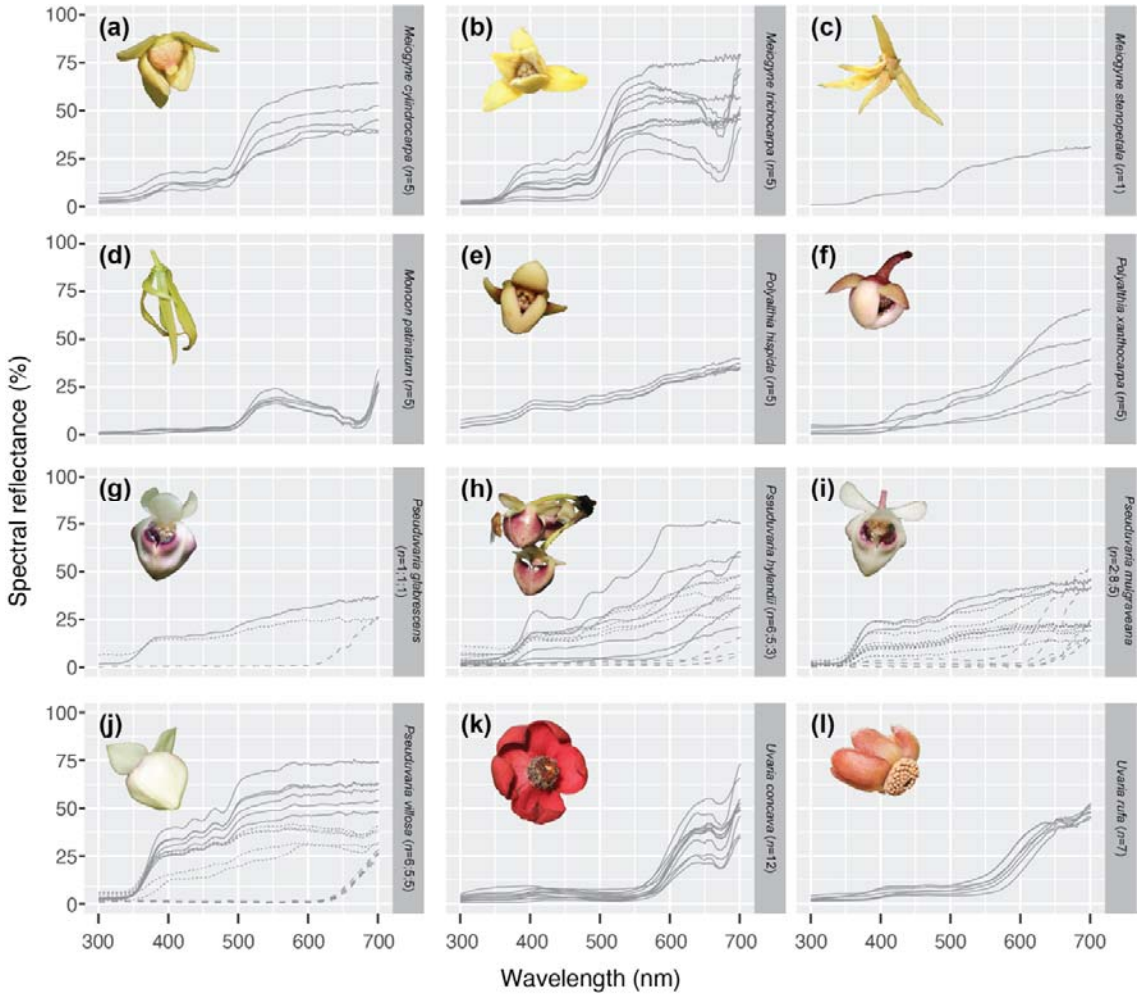

Fig. 3. Spectral reflectance of 12 Annonaceae species. (a) *Meiogyne cylindrocarpa*. (b) *Meiogyne trichocarpa*. (c) *Meiogyne stenopetala*. (d) *Monoon patinatum*. (e) *Polyalthia hispida*. (f) *Polyalthia xanthocarpa*. (g) *Pseuduvaria glabrescens*. (h) *Pseuduvaria hylandii*. (i) *Pseuduvaria mulgraveana*. (j) *Pseuduvaria villosa*. (k) *Uvaria concava*. (l) *Uvaria rufa*. For species with drooping inner petals and no colour differentiation between outer and inner petal whorls, the inner petal abaxial surface was measured (a–f; i.e. *Meiogyne*, *Monoon* and *Polyalthia*). For species with spreading inner petals and no colour differentiation between outer and inner petal whorls, the inner petal adaxial surface (k–l; i.e. *Uvaria*) was measured. For species with dissimilar petal whorls (g–j; i.e. *Pseuduvaria*), three perianth areas were measured (solid line: inner petal abaxial surface; dotted line: outer petal adaxial surface; dashed line: inner petal gland); the sample size (*n*) for these species refer to the sample size for these three perianth areas in the aforementioned order. Photo credits: (a, b, d, e, g–l): Ming-Fai Liu; (c): Chun-Chiu Pang; (f): Garry & Nada Sankowsky.

Table 1. Floral biology of *Meiogyne*, *Monoon*, *Polyalthia*, *Pseuduvaria* and *Uvaria* species. Abbreviations: CBG: Cairns Botanic Gardens, NE Queensland, Australia; GBB: Gardens by the Bay, Singapore; MT: Mt. Tamborine, SE Queensland, Australia; SA: Sankowsky Arboretum, Tolga, NE Queensland, Australia; WA: Graham Wood Arboretum, Wondecla, NE Queensland, Australia; +: present, -: absent, †: presence on both pistillate-phase and staminate-phase flowers, *: contact with reproductive organs, ‡: pistillate-phase visitors were pollen-laden.

	Meiogyne cylindrocarpa	*Meiogyne trichocarpa*	*Meiogyne stenopetala*	*Monoon patinatum*	*Polyalthia hispida*	*Polyalthia xanthocarpa*	*Pseuduvaria hylandii*	*Pseuduvaria glabrescens*	*Pseuduvaria mulgraveana*	*Pseuduvaria villosa*	*Uvaria concava*	*Uvaria rufa*
Site of study (*n*= individual studied)	SA (*n*=8), GBB (*n*=3), WA (*n*=4)	SA (*n*=8)	SA (*n*=1), WA (*n*=1), MT (*n*=20)	SA (*n*=1)	SA (*n*=2)	SA (*n*=1)	SA (*n*=5)	SA (*n*=1), CBG (*n*=1)	SA (*n*=3)	SA (*n*=1)	SA (*n*=2)	SA (*n*=2)
Habit	treelet/shrub	Treelet	treelet	tree	treelet	treelet	treelet	treelet	treelet	treelet	climber	climber
Flower position	axillary/apical	axillary/apical	axillary/apical	ramiflorous	axillary/apical	axillary/apical/ ramiflorous	cauliflorous	axillary/apical	axillary/apical	ramiflorous	axillary/apical	axillary/apical/ ramiflorous
Sexual system	bisexual flower	bisexual flower	bisexual flower	bisexual flower	bisexual flower	bisexual flower	unisexual flower, dioecious	andromonoecious	andromonoecious	? (only seen staminate treelet)	bisexual flower	bisexual flower
Pistillate phase duration	2d	2d	2d	not assessed	3d	2–3d	>6d	not assessed	2d	not assessed	2–3d	1d
Staminate phase duration	2d	1d	3d	not assessed	2d	1d	>6d	not assessed	2d	not assessed	0–1d	4d
Overlap phase duration	*ca.* 0–3h	*ca.* 5h	*ca.* 1–3h	not assessed	?	?	not applicable	not applicable	-	not assessed	1–2d	-
Interim phase duration	-	-	-	not assessed	?	?	not applicable	not applicable	2d	not assessed	-	1d
Protogyny	+	+	+	not assessed	+	+	not applicable	not applicable	+	not assessed	+	+
Pollinator trapping	-	-	-	-	-	-	-	-	-	-	-	-
Thermogenesis	-	-	-	-	-	-	-	-	-	-	-	-
Floral odour	banana-like	banana-like	banana-like	odorous	odourless	banana-like	rotten fruit	rotten fruit	rotten fruit	rotten fruit	fruity	fruity
Inner petal growth/gland	+, smooth–weakly longitudinally grooved	+, smooth–weakly longitudinally grooved	+, longitudinally grooved	-	-	-	+, smooth & raised	+, smooth & raised	+, smooth & raised	+, smooth & raised	-	-
Inner petal corrugation function	food body	food body	food body	corrugation absent	corrugation absent	corrugation absent	nectary	nectary	nectary	nectary	corrugation absent	corrugation absent
Floral visitors (*n*=total number of floral visitors observed)	*n*=42 (sites: SA+WA) **Coleoptera:** Curculionidae: Ochyromerini (14.3%)†,*,‡ Curculionidae: *Carpophilus* sp. (4.8%)†,* Nitidulidae: Nitidulinae (81%)†,*,‡	*n*=29 **Coleoptera:** Curculionidae: Ochyromerini (17.2%)†,*,‡ Nitidulidae: Nitidulinae (82.8%)†,*,‡	*n*=14 (site: MT+WA) **Coleoptera:** Staphylinidae: Omaliinae (64.3%)†,*,‡ Nitidulidae: Epuraeinae (35.7%)†,*,‡	*n*=2 **Coleoptera:** Staphylinidae: Tachyporinae (100%)*	not observed	*n*=8 **Coleoptera:** Curculionidae: Ochyromerini (100%)†,*	*n*=58 **Diptera:** Drosophilidae: Drosophilinae (60.3%)†,*,‡ Lauxaniidae (3.4%)† Neriidae (3.4%)† **Coleoptera:** Nitidulidae: Nitidulinae (31.0%) †,*,‡ **Hymenoptera:** Formicidae (1.7%)	*n*=19 (site: CBG) **Diptera:** Drosophilidae: Drosophilinae (21%)†,* **Coleoptera:** Nitidulidae: Nitidulinae (79%)†,*,‡	*n*=33 **Diptera:** Drosophilidae: Drosophilinae (21.2%)†,* **Coleoptera:** †,*Nitidulidae: Nitidulinae (72.7%)†,*,‡ **Hymenoptera:** Formicidae (6.1%)	not observed	*n*=13 **Coleoptera:** Nitidulidae: Nitidulinae (92.3%)†,*,‡ **Hymenoptera:** *Apis* sp. (7.7%)†,*	*n*=1 **Diptera:** unknown sp. (100%)

Table 2. Floral scent composition of *Meiogyne*, *Monoon*, *Polyalthia*, *Pseuduvaria* and *Uvaria* species. The average percentage of the relative peak area for each volatile and its standard error are presented below. Italicised molecules were verified by co-injecting with commercially available standards. Unknown molecules were denoted by the top ten most abundant ion fragments, followed by their relative intensity in parentheses. *n* refers to the number of technical replicates performed, followed by the number of individuals the odour was collected from.

	standard retention index (DB-WAX)	Relative content (%)										
		Meiogyne cylindrocarpa (*n*=15;15)	*Meiogyne trichocarpa* (*n*=8;8)	*Meiogyne stenopetala* (*n*=5;2)	*Monoon patinatum* (*n*=3;1)	*Polyalthia xanthocarpa* (*n*=5;1)	*Pseuduvaria hylandii.* (*n*=3;3)	*Pseuduvaria glabrescens* (*n*=4;2)	*Pseuduvaria mulgraveana* (*n*=4;3)	*Pseuduvaria villosa* (*n*=4;1)	*Uvaria concava* (*n*=3;2)	*Uvaria rufa* (*n*=4;2)
Aliphatic hydrocarbon												
1-Tetradecene	1348	—	0.19 ± 0.19	—	—	—	—	—	—	—	—	—
Tetradecane	1401	—	0.33 ± 0.22	—	—	—	—	—	—	—	—	—
Oxygenated Aliphatic Compound												
2,3-Butanediol	1589	—	—	—	—	—	95.97 ± 0.91	84.83 ± 0.80	96.98 ± 0.21	95.32 ± 0.15	—	—
2-Methyl-butanoic acid	1678	—	—	—	16.48 ± 0.53	—	—	—	—	—	—	—
2-Methyl-(*E*)-7-hexadecene	1725	—	—	—	—	—	—	—	—	—	—	0.05 ± 0.00
Ester												
Isobutyl acetate	1014	7.87 ± 2.16	11.86 ± 4.37	56.71 ± 1.50	—	—	—	—	—	—	—	—
Ethyl butanoate	1039	—	—	—	—	—	—	—	—	—	—	7.35 ± 0.38
Butyl acetate	1073	0.22 ± 0.24	—	—	—	—	—	—	—	—	—	20.65 ± 0.21
Isoamyl acetate	1109	79.58 ± 7.65	84.07 ± 4.01	28.17 ± 4.13	—	99.28 ± 0.02	—	—	—	—	—	—
Methyl hexanoate	1191	—	—	—	—	—	—	—	—	—	54.69 ± 0.32	4.70 ± 0.08
Butyl butanoate	1223	—	—	—	—	—	—	—	—	—	—	1.94 ± 0.07
2-methyl-(2*E*)-butenyl acetate	1225	0.82 ± 0.70	—	—	—	—	—	—	—	—	—	—
Ethyl hexanoate	1238	—	—	—	—	—	—	—	—	—	—	12.58 ± 0.29
2-methyl-(2*Z*)-butenyl acetate	1254	1.16 ± 0.70	—	—	—	—	—	—	—	—	—	—
Hexyl acetate	1277	0.07 ± 0.87	—	0.87 ± 0.12	—	—	—	—	—	—	—	21.27 ± 0.25
Isoamyl isovalerate	1316	1.09 ± 0.85	—	—	—	—	—	—	—	—	—	—
Methyl octanoate	1396	—	—	—	—	—	—	—	—	—	4.30 ± 0.29	0.56 ± 0.02
Hexyl butanoate	1423	—	—	—	—	—	—	—	—	—	—	6.38 ± 0.10
Methyl (*Z*)-4-octenoate	1438	—	—	—	—	—	—	—	—	—	25.36 ± 0.32	—

Ethyl octanoate	1442	—	—	—	—	—	—	—	—	—	—	20.04 ± 0.22
Hexyl 2-methylbutanoate	1452	—	—	0.44 ± 0.07	—	—	—	—	—	—	—	—
Octyl acetate	1482	—	—	—	—	—	—	—	—	—	—	1.48 ± 0.06
trans-2-Hexenyl isovalerate	1508	—	—	2.34 ± 0.12	—	—	—	—	—	—	—	—
2,3-Butanediyl diacetate	1530	1.26 ± 1.37	—	0.09 ± 0.05	—	—	—	—	—	—	—	—
linalyl anthranilate	1565	—	0.01 ± 0.01	—	—	—	—	—	—	—	—	—
Hexyl hexanoate	1618	—	—	—	—	—	—	—	—	—	—	0.86 ± 0.02
Octyl butanoate	1625	—	—	—	—	—	—	—	—	—	—	0.66 ± 0.03
Hexyl tiglate	1632	—	—	—	—	—	—	—	—	—	—	0.16 ± 0.02
Ethyl decanoate	1646	—	—	—	—	—	—	—	—	—	—	0.23 ± 0.01
Ethyl trans-4-decenoate	1675	—	—	—	—	—	—	—	—	—	—	0.09 ± 0.00
6-Methyl-4-heptenyl pentanoate	1678	—	—	—	—	—	—	—	—	—	—	0.20 ± 0.00
Ethyl benzoate	1685	—	—	—	—	—	—	—	—	—	—	0.08 ± 0.01
(*E*)-Methylgeranate	1706	—	—	—	—	—	—	—	—	—	—	0.30 ± 0.00
Geranyl 2-methylbutanoate	1735	—	0.03 ± 0.01	—	—	—	—	—	—	—	—	—
Geranyl acetate	1766	1.56 ± 1.97	1.24 ± 0.59	—	—	—	—	—	—	—	—	—
2-Phenylethyl acetate	1835	—	—	0.52 ± 0.01	—	—	—	—	—	—	—	—
Phenylethyl isovalerate	2011	—	—	0.54 ± 0.27	—	—	—	—	—	—	—	—
hexyl benzoate	2098	—	—	—	—	—	—	—	—	—	—	0.05 ± 0.01
Phenylpropanoid												
Methyl eugenol	2026	—	—	—	—	—	—	1.06 ± 0.09	—	—	—	—
Monoterpene												
β-Myrcene	1170	—	0.15 ± 0.11	—	—	—	—	—	—	—	—	—
Limonene	1205	—	1.24 ± 0.61	—	—	—	—	—	—	—	—	—
1,8-cineole	1210	—	0.01 ± 0.01	—	—	—	2.42 ± 1.22	11.78 ± 0.38	—	—	—	—
trans-β-Ocimene	1241	—	0.06 ± 0.04	—	—	—	—	—	—	—	—	—
cis-β-Ocimene	1259	—	0.14 ± 0.10	—	45.50 ± 0.61	—	—	—	—	—	—	—
terpinolene	1283	—	0.05 ± 0.03	—	—	—	—	—	—	—	—	—
allo-Ocimene	1384	—	0.18 ± 0.13	—	11.89 ± 0.59	—	—	—	—	—	—	—
Menthone	1456	—	0.03 ± 0.02	—	—	—	—	—	—	—	1.04 ± 0.07	—
α-Terpineol	1711	—	—	—	—	—	—	—	—	—	—	—
camphor	1532	—	0.02 ± 0.02	—	—	—	—	—	—	—	—	—
menthacamphor	1654	—	0.06 ± 0.04	—	—	—	—	—	—	—	—	—
geranylacetone	1868	—	—	0.18 ± 0.04	3.01 ± 0.12	—	—	—	—	—	—	—

Sesquiterpene												
α-Cubebene	1471	1.11 ± 1.31	—	0.06 ± 0.06	—	—	—	—	—	—	—	—
δ-elemene	1485	1.14 ± 1.36	—	—	—	—	—	—	—	—	—	—
Copaene	1511	—	—	0.83 ± 0.35	—	0.32 ± 0.01	0.26 ± 0.26	1.12 ± 0.05	0.65 ± 0.05	1.05 ± 0.10	—	—
β-bourbonene	1518	1.25 ± 1.45	—	—	—	—	—	—	—	—	—	—
β-Cubebene	1554	1.25 ± 1.50	—	—	—	0.04 ± 0.00	—	—	—	—	—	—
Cyperene	1549	—	—	—	—	—	0.42 ± 0.42	—	—	—	—	—
β-ylangene	1578	1.32 ± 1.57	—	—	—	—	—	—	—	—	—	—
Calarene	1602	1.48 ± 1.60	—	—	—	—	—	—	—	—	—	—
(*E*)-*β*-*caryophyllene*	1608	2.87 ± 1.51	—	—	6.08 ± 0.16	0.14 ± 0.01	—	—	—	—	1.86 ± 0.05	—
γ-elemene	1647	1.42 ± 1.72	—	—	—	—	—	—	—	—	—	—
cis-β-Farnesene	1672	—	0.02 ± 0.01	—	—	—	—	—	—	—	3.39 ± 0.00	—
humulene	1681	2.26 ± 1.70	—	—	2.83 ± 0.27	0.04 ± 0.00	—	—	—	—	—	—
γ-Muurolene	1709	—	—	—	—	0.07 ± 0.00	—	—	—	—	—	—
δ-Selinene	1724	—	—	0.08 ± 0.03	—	—	—	—	—	—	—	—
Germacrene D	1732	1.86 ± 1.83	—	—	3.87 ± 0.14	0.05 ± 0.00	—	—	—	—	0.31 ± 0.16	—
Copaene/ γ-Muurolene	1732	—	—	0.10 ± 0.03	—	—	—	—	—	—	—	—
α-Muurolene	1744	—	—	0.10 ± 0.03	—	—	—	—	—	—	0.79 ± 0.02	—
α-Farnesene	1756	—	—	—	7.40 ± 0.07	—	—	—	—	—	—	0.03 ± 0.00
Bicylogermacrene	1758	1.59 ± 1.91	—	0.10 ± 0.04	—	—	—	—	—	—	—	—
δ-Cadinene	1777	1.65 ± 1.96	—	0.37 ± 0.10	1.83 ± 0.18	0.06 ± 0.00	—	—	—	—	—	0.04 ± 0.01
Cada-1,4-diene	1805	—	—	0.08 ± 0.02	—	—	—	—	—	—	—	—
Miscellaneous Compound												
Naphthalene	1768	—	—	0.06 ± 0.02	1.11 ± 0.09	—	—	—	—	—	0.21 ± 0.11	0.02 ± 0.00
β-Ionene	1872	—	—	—	—	—	—	—	—	—	0.49 ± 0.03	—
Unknown												
43(24), 57(20), 41(14), 56(11), 42(8), 70(7), 55(6), 86(4), 61(3), 69(3)	1176	0.56 ± 0.51	—	0.09 ± 0.06	—	—	—	—	—	—	—	—
57(26), 43(19), 41(12), 56(11), 70(7), 42(7), 71(6), 55(5), 85(4), 86(3)	1201	0.16 ± 0.72	—	1.95 ± 0.54	—	—	—	—	—	—	—	—
57(23), 43(22), 41(13), 56(12), 71(8), 42(6), 85(5), 69(4), 55(4), 68(4)	1244	—	—	1.55 ± 0.33	—	—	—	—	—	—	—	—
57(20), 70(15), 43(14), 85(12),	1299	—	—	1.17 ± 0.34	—	—	—	—	—	—	—	—

41(10), 71(9), 56(7), 55(6), 42(5), 86(3)												
73(29), 57(17), 41(11), 43(11), 56(9), 147(7), 42(5), 32(5), 86(4), 207(3)	1316	—	—	—	—	—	—	0.61 ± 0.21	—	—	—	—
43(24), 67(16), 57(15), 82(12), 41(11), 56(7), 29(4), 42(4), 55(3), 39(3)	1319	—	—	0.37 ± 0.14	—	—	—	—	—	—	—	—
57(19), 43(18), 41(15), 56(11), 105.1(8), 42(7), 119(7), 29(6), 32(6), 86(4)	1344	—	—	—	—	—	0.47 ± 0.24	—	1.09 ± 0.08	1.90 ± 0.10	—	—
43(21), 57(18), 56(15), 41(13), 70(7), 42(6), 55(6), 32(5), 69(4), 86(4)	1381	—	—	0.01 ± 0.01	—	—	—	—	—	—	—	—
43(52), 87(11), 57(9), 70(6), 41(5), 56(5), 42(3), 55(3), 86(3), 45(3)	1387	—	—	2.11 ± 0.46	—	—	0.12 ± 0.06	—	—	—	—	—
57(28), 43(15), 41(13), 56(12), 85(6), 71(6), 42(6), 55(6), 32(4), 86(3)	1405	0.19 ± 0.85	—	0.61 ± 0.15	—	—	0.19 ± 0.10	0.59 ± 0.20	1.12 ± 0.05	1.74 ± 0.07	—	—
57(20), 82(15), 67(14), 41(11), 43(10), 85(9), 56(7), 55(5), 32(4), 42(4)	1475	1.66 ± 1.25	—	0.08 ± 0.08	—	—	0.09 ± 0.05	—	0.17 ± 0.10	—	1.09 ± 0.19	0.02 ± 0.02
57(20), 43(15), 41(15), 56(10), 80(9), 32(8), 29(6), 79.1(6), 42(6), 71(5)	1493	—	—	—	—	—	—	—	—	—	0.48 ± 0.11	—
57(21),43(17),56(12),85(11),41(11),103(9),84(6),42(5),55(5), 32(5)	1499	1.81 ± 1.36	—	0.27 ± 0.05	—	—	—	—	—	—	0.44 ± 0.10	—
57(22), 43(16), 41(16), 56(12), 32(8), 55(7), 42(6), 71(5), 119(5), 69(5)	1510	—	—	—	—	—	—	—	—	—	1.34 ± 0.11	—
57(23), 85(14), 43(14), 41(11), 70(10), 56(8), 71(5), 112(5), 42(5), 55(5)	1555	—	—	0.15 ± 0.08	—	—	0.06 ± 0.06	—	—	—	—	—
111(26), 81(13), 154(12),	1607	0.14 ± 1.73	—	—	—	—	—	—	—	—	3.59 ± 0.07	—

95(10), 112(8), 123(7), 79(7), 41(6), 94(6), 53(5)												
84(15), 57(13), 123(13), 41(12), 43(11), 42(8), 56(8), 81(8), 95(6), 32(6)	1614	—	—	—	—	—	—	—	—	—	—	0.05 ± 0.00
79(16), 108(13), 57(13), 41(12), 43(11), 150(8), 67(8), 56(7), 32(7), 29(6)	1736	—	—	—	—	—	—	—	—	—	0.39 ± 0.02	0.06 ± 0.00
57(19), 43(16), 41(12), 32(11), 56(11), 108(8), 42(6), 45(6), 91(6), 44(5)	1745	—	—	—	—	—	—	—	—	—	0.21 ± 0.12	0.01 ± 0.00
43(16), 57.1(13), 56(11), 41(11), 117.1(10), 84.1(10), 71(8), 55(8), 145.1(7), 69(7)	1821	—	—	—	—	—	—	—	—	—	—	0.15 ± 0.01