

Fluorescent nectar in non-flying mammal-pollinated plants – observations and considerations in some Asparagaceae

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Abstract

Background and aims – Fluorescence is the emission of light by a fluorophore that has absorbed light of shorter wavelengths. While the role of fluorescence in visual communication has been documented in some animals (budgerigars, gelatinous zooplankton), it is controversially discussed in plants. Floral nectar fluorescence has been mainly found in flowers pollinated by bees. It has been suggested as direct visual cue by which bees can evaluate the available quantity of nectar, thus being important for pollination and foraging efficiency. However, this function has been questioned, since fluorescence is said to be obscured by floral reflections due to low quantum efficiency. The aim of this study was to examine the nectar of plants pollinated by non-flying mammals, namely *Eucomis regia*, *Massonia grandiflora*, *M. echinata*, and *M. pustulata* (Asparagaceae) from South Africa.

Material and methods – To detect possible fluorescence in flowers, the plants were illuminated in a darkened room under UV light and photographed with a camera equipped with a UV/IR cut filter (transmitting at 400–700 nm).

Key results – Within the inflorescences, the nectar of all species showed blue to bluish fluorescence and UV absorption. Separated nectar also fluoresced.

Conclusion – As fluorescence in flowers occurs not only in bee-pollinated plants but also in plants pollinated by wind, and by nocturnal or crepuscular pollinators (non-flying mammals, bats, moths) for which floral scent is an important attractant, floral fluorescence seems to have no adaptive value for the attraction of flower visitors. We discuss the potential role of fluorescence in flowers as just a by-product of compounds that might have other functions such as visual attraction by reflection (or UV absorbance), protection of genetic material in pollen from UV induced damage, or as a floral filter causing nectar to be bitter, repelling ineffective pollinators but not effective ones.

Keywords

Asparagaceae, fluorescence, nectar, UV absorption, non-flying mammals, pollination

INTRODUCTION

Communication between animals as well as between plants and animals operates mainly via olfactory and visual channels (Stevens 2013). Colour is an important visual cue and communication based on colour depends on the animals' sensory capacities. Colour vision is the capability to discriminate between different wavelengths

of the visible spectrum independently of light intensity (brightness) (Jacobs 1993). To be able to perceive colour, light-sensitive visual pigments with at least two different spectral sensitivities are necessary. Humans can perceive light from about 380 (violet) to 750 nanometre (red) wavelengths and different animals' visual capacities reach from 280 (ultraviolet) to 800 nm (red), depending on the photoreceptors' sensitivities, pre-receptor filters and the

associated neural processing (Li et al. 2008; Osorio and Vorobyev 2008). Only few species are able to perceive colours beyond this range, i.e. in the near-infrared (Meuthen et al. 2012).

Fluorescence is a phenomenon that occurs when light of shorter wavelength (e.g. UV, blue, blue-green) is absorbed by a fluorophore (e.g. a carotenoid) and subsequently some of the absorbed energy is emitted as light of longer wavelength (e.g. blue, green, yellow, or red fluorescence) (Marshall and Johnsen 2017; Van der Kooi et al. 2019). Fluorescence occurs in animals and plants. However, its biological implication is rarely documented. In animals, fluorescence is important as a mate choice signal for budgerigars (Arnold et al. 2002) and possibly in jumping spiders (Lim et al. 2007) and gelatinous zooplankton uses fluorescence for prey capture (Haddock and Dunn 2015). In plants, fluorescence is found in different tissues and organs such as leaves, wood, bark, fruits, and flowers; however, its ecological significance in visual communication is controversial (Lagorio et al. 2015).

Regarding flowers, different visual and olfactory floral signals attract animals that visit flowers to satisfy their needs (mostly food: mainly sugar-containing nectar, also pollen) and thereby transfer pollen (Schiestl and Johnson 2013; Wester and Lunau 2017). Visual floral signals include shape and colour including patterns (Leonard and Papaj 2011) mainly of petals, but also other floral organs. The importance of visual signals varies depending on the visual capacities and preferences of the different animal pollinator groups. For instance, bees have a trichromatic visual system based on three types of photoreceptors with sensitivity peaks at 340 nm (UV), 430 nm (blue), and 540 nm (green). They exhibit innate preferences for colours dominated by short wavelengths. Birds are tetrachromatic: with an additional red photoreceptor, they are sensitive in the red, green, blue, and additionally violet or ultraviolet range of wavelengths. Some flies and butterflies possess multiple (up to 16) different types of photoreceptors, perceiving wavelengths in the UV to red (Kelber and Osorio 2010; Song and Lee 2018). Bats are nocturnal dichromats with the ability of colour vision (UV and red) during twilight (Müller et al. 2009). Non-flying mammals, that pollinate flowers (Wester 2010; Wester et al. 2019), such as rodents and elephant-shrews, are mostly nocturnal or crepuscular (Skinner and Chimimba 2005). As dichromats, they are sensitive in the green and blue, or alternatively the ultraviolet range of wavelengths (Jacobs et al. 2001; Thüs et al. 2020).

Concerning flowers, fluorescence occurs in different floral organs such as petals (Cruden 1972; Gandía-Herrero et al. 2005a; Ono et al. 2006), filaments and anthers (Ashman et al. 2000), pollen (Roschina 2012; Mori et al. 2018), stigmas (Thien et al. 1995) as well as nectar (Frey-Wyssling and Agthe 1950; Thorp et al. 1975), and appears mostly blue, green, and yellow, but also purple, pink, red, and other colours (Thorp et al. 1975; Hagler and Buchman 1993; Thien et al. 1995; Mori et al. 2018). Fluorescent

compounds were identified as phenolics (flavonoids and other compounds) (nectar, petals, pollen), carotenoids, and azulene (pollen) as well as betalains (petals) (Scogin 1979; Hagler and Buchmann 1993; Gandía-Herrero et al. 2005b; Ono et al. 2006; Roshchina 2012; Mori et al. 2018).

Usually, floral nectar is a transparent liquid, but occasionally it is coloured and attracts attention by colouration or potentially gloss (Kugler 1955, 1956; Sandvik and Totland 2003; Hansen et al. 2006, 2007; Aldasoro et al. 2008; Zhang et al. 2012; Mione and Argeo Diaz 2020). However, Thorp et al. (1975) detected fluorescent nectar (in combination with UV absorption) in several plant species of different families. The colour of the fluorescence was described as yellow, blue, and blue-green. They proposed that fluorescent nectar is a direct visual cue for bees to evaluate the quantity of available nectar, thus being important for pollination and foraging efficiency (see also Davies et al. 2005). Additionally, fluorescent patterns of petals, stamens, and stigmas are suggested to play a role in pollinator attraction (Thien et al. 1995; Ashman et al. 2000; Gandía-Herrero et al. 2005a). However, the ecological relevance of floral fluorescence as an attractant for pollinators has been questioned (Cruden 1972). Due to the low fluorescence quantum efficiency (the ratio of photons absorbed to the number of photons emitted) of floral fluorescent pigments, the fluorescence is said to be obscured by floral reflections (Kevan 1976; Iriel and Lagorio 2010a, 2010b). However, honeybees were reported to respond positively to visual cues in fluorescent nectar (Thorp in Thien et al. 1995; see also Thorp et al. 1976). Mori et al. (2018) conducted choice experiments with honeybees and fluorescent hydroxycinnamoyl derivatives, isolated on filter paper from pollen and anthers of some plant species. They showed that the bees perceived and were attracted to the fluorescent compounds and suggested that fluorescence from pollen and anthers may serve as attractant for pollinators. However, there seems to be no clear experimental evidence showing that floral fluorescence attracts pollinators. Mori et al. (2023) found that bees were attracted to bee-pollinated *Camellia rusticana* Honda (Theaceae) flowers but not to flowers of the related, bird-pollinated *C. japonica* L. Attraction of bees to *C. rusticana* flowers has been explained by the red petals reflecting additionally in UV and by the blue fluorescence of anthers, while *C. japonica* has been interpreted to be inconspicuous to bees due to lacking UV reflection and blue fluorescence. The authors also assumed that birds might be repelled by the blue fluorescence. The fact that bees prefer red UV-reflecting flowers over red UV-non-reflecting ones has been shown for neotropical orchid bees, and it was also shown that hummingbirds have no preference for any of these colours (Lunau et al. 2011). However, it is unknown whether the fluorescence in *C. rusticana* anthers contributes to bee attraction and bird repellence, especially as the anthers' fluorescence is mainly covered by non-fluorescent pollen grains (Mori et al. 2023; fig. 1). Kurup et al. (2013) presented attraction

Table 1. Plant species and collection localities in South Africa.

Plant species	Locality
<i>Eucomis regia</i>	Farm Fairfield, Western Cape, Overberg, 14 km NW of Napier; elevation 250 m, collected in September 2009
<i>Massonia echinata</i>	Oorlogskloof Nature Reserve, Northern Cape, Bokkeveld, south of Nieuwoudtville; elevation about 700 m, collected in September 2015
<i>Massonia grandiflora</i>	Near the Kliphuis campsite at the Pakhuis pass, Western Cape, northern Cederberg; elevation 740 m, collected in September 2017
<i>Massonia pustulata</i>	Napier, Western Cape, Overberg; elevation 250 m, collected in August 2014

of insects by fluorescent rims of prey catching traps that evolved from leaves in carnivorous pitcher plants. Masking the fluorescence of the traps' rim (by coating them with the acetone extract of non-fluorescent pitcher zone) resulted in a reduction in prey capture. However, the role of fluorescence in attracting insects has been questioned as the acetone extract may have changed the rim tissue not only by removing fluorescence (Jansen 2017).

In the only study examining nectar of more than hundred plant species, fluorescence has been detected mainly in bee-pollinated species, but not in plants pollinated by butterflies, moths, or birds (Thorp et al. 1975). However, almost no data are available for plants pollinated by other animal groups (except a study of a bird-pollinated *Aloe* L., Asphodelaceae, with fluorescent nectar, that was also visited by bees, Hagler and Buchmann 1993).

The aim of our study is to examine nectar for potential fluorescence of plants pollinated by non-flying mammals, namely four species of South African Asparagaceae, the Pineapple lily *Eucomis regia* (L.) L'Hér. subsp. *regia* (Fig. 1A) and three Hedgehog lilies of the genus *Massonia* Houtt. (Fig. 1C, E, G). *Eucomis regia* and *M. grandiflora* Lindl. are pollinated by mice and elephant-shrews (Namaqua Rock Mouse *Micaelamys namaquensis* (A. Smith, 1834), Four-striped Field Mouse *Rhabdomys pumilio* (Sparrman, 1784), Pygmy mouse *Mus minutoides* A. Smith, 1834, Cape Rock Elephant-shrew *Elephantulus edwardii* (A. Smith, 1839), Wester et al. 2019; Verreaux's Mouse *Myomyscus verreauxii* (A. Smith, 1834), *Micaelamys namaquensis*, *E. edwardii*; Wester et al. 2024). *Massonia echinata* L.f. has been shown to be visited and most probably pollinated by elephant-shrews (*E. edwardii*, Flasch et al. 2016) and *Massonia pustulata* Jacq. by mice (Petra Wester, unpubl. data). We discuss our findings in the context of the relevance of fluorescent nectar as a potential attractant for flower visitors and consider alternative explanations.

MATERIAL AND METHODS

Flowering plants of three species of *Massonia* and one of *Eucomis* L'Hér., all Hyacintheae of the Asparagaceae subfamily Scilloideae (previously Hyacinthaceae subfam. Hyacinthoideae), that have been collected in South

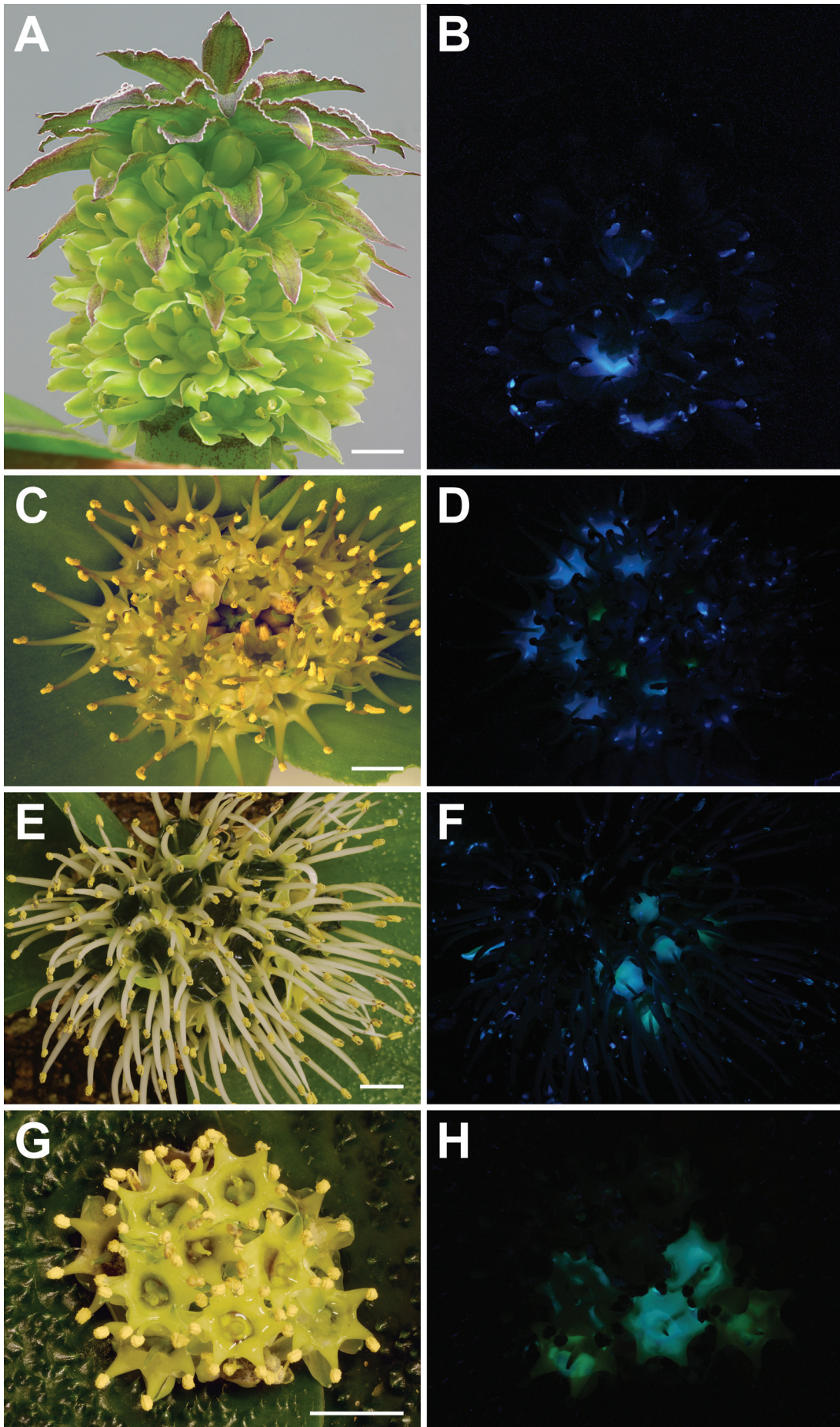
Africa (Table 1) and cultivated in the greenhouses of the Botanical Garden of the Heinrich-Heine-University, Düsseldorf (Germany), were studied in the afternoons of January (*M. echinata*, *M. pustulata*), February (*M. grandiflora*), and March (*E. regia*) 2018.

To detect possible fluorescence in the flowers of the four species, inflorescences were photographed with a Lumix GH-1 camera (Panasonic, Osaka, Japan) without low-pass filter in front of the sensor (being sensitive additionally for UV and infrared light), mounted on a tripod, in combination with a UV-transmissible Ultra-Achromatic-Takumar 1 : 4.5/85 quartz glass lens (Pentax, Tokyo, Japan) and a UV/IR cut filter (transmitting at 400–700 nm, Baader, Mammendorf, Germany) in a darkened room under UV illumination. Pure UV illumination was achieved by means of a UV torch (UV 365 nm; U301, MTE, Shenzhen, China) in combination with a UV filter (transmitting at 320–380 nm, Baader) in front of the torch. Photographing with the UV/IR cut filter (transmitting in the visible light only) in the dark with UV illumination only allows merely fluorescence (part of the visible light) to be recorded. As reference, standard photos were taken with the same set-up, but under ambient room light (without UV illumination and UV filter). To detect possible ultraviolet patterns in *M. grandiflora* and *M. echinata* inflorescences, photos were taken in combination with the UV filter and under UV illumination. Brightness was adjusted using a white polytetrafluoroethylene (Teflon) disc, reflecting from 300 to 700 nm. Aperture was set manually and exposure time was set automatically.

In the *Massonia* species, nectar was completely removed in half of the flowers per inflorescence. The removed nectar was also examined separately.

RESULTS

In the inflorescences, the nectar of all tested species showed blue to bluish green fluorescence (*E. regia*: Fig. 1B, *M. grandiflora*: Fig. 1D, *M. pustulata*: Fig. 1F, *M. echinata*: Fig. 1H) as well as UV absorption (shown for *M. grandiflora*: Fig. 2A, and *M. echinata*: Fig. 2B). The flowers with nectar removed did not fluoresce (*M. grandiflora*: right floral nectar chambers without fluorescence: Fig. 1D, *M. pustulata*: left floral nectar chambers lacking



◀ **Figure 1.** Inflorescences of *Eucomis regia* (A, B), *Massonia grandiflora* (C, D), *M. pustulata* (E, F), and *M. echinata* (G–H) photographed with a camera being sensitive to UV, visible, and IR light, in combination with a UV-transmissible lens and a UV/IR cut filter (transmitting at 400–700 nm) under ambient room light (A, C, E, G) and the same inflorescences under UV illumination in a darkened room showing blue (B, D) to bluish green (F, H) fluorescent nectar. Note that the fluorescence appears only in the flowers containing nectar (in *E. regia*: nectar clearly visible only in the two middle lower flowers where nectar accumulates in the lower gaps between the filaments and the ovary and is not hidden by other flower parts, in *M. grandiflora*: nectar only in the left flowers of the inflorescence, in *M. pustulata*: nectar only in the right flowers of the inflorescence, in *M. echinata*: nectar only in the lower flowers of the inflorescence) and not in the *Massonia* flowers in which nectar was removed from the floral tubes. The light spots outside the floral tubes are nectar drops at the two tepal tips in the bottom left flower of the *E. regia* inflorescence (A, B) and a tepal coated with nectar on the left side of the *M. pustulata* inflorescence (C, D). Scale bars = 1 cm.

fluorescence: Fig. 1F, *M. echinata*: upper flowers not fluorescing: Fig. 1H) and did not absorb UV in the nectar chamber, formed by the fused anther bases (Fig. 2A, B). Separated nectar also fluoresced.

DISCUSSION

At the example of four Asparagaceae, this study shows that fluorescence of nectar occurs also in non-flying mammal-pollinated plants. We also demonstrate for *M. grandiflora* and *M. echinata* that fluorescence in nectar is accompanied by UV absorption (including that of pollen and filaments), occurring also in *M. pustulata* (not shown) and *E. regia* (Wester et al. 2019: fig. S6b). The combination of UV fluorescence and UV absorption in nectar has been also found by Thorp et al. (1975). UV absorption of pollen has been also documented for *E. regia* (Wester et al. 2019: fig. S6b). UV absorption can be explained by the nature of fluorescence as a requirement for this phenomenon. After the absorption of shorter-wavelength light by a fluorophore, some of the absorbed energy is released as longer-wavelength light (Marshall and Johnsen 2017; Van der Kooi et al. 2019).

Although the mice and elephant-shrews that visit and pollinate the flowers of the four study species (Flasch et al. 2016; Wester et al. 2019, 2024; Petra Wester, unpubl. data), are sensitive in the blue and green wavelengths (Jacobs et al. 2001; Thüs et al. 2020, 2022), the animals are predominantly nocturnal or crepuscular (Rathbun 1979; Perrin 1981; Roxburgh and Perrin 1994; Stuart et al. 2003; Schumann et al. 2005; Skinner and Chimimba 2005; van der Merwe et al. 2012) or, if diurnal, their flower visiting behaviour happens also or predominantly at dusk or dawn (Melidonis and Peter 2015; Petra Wester, unpubl. data). In crepuscular light or in the dark, light including radiation of shorter wavelengths (i.e. UV radiation) is low, thus, fluorescence even weaker and, consequently, most probably irrelevant for the mammals. When light is scarce, scent seems to be more important as an attractant than visual cues, and most rodents and probably elephant-shrews have a well-developed sense of smell (Stoddard 1980; Skinner and Chimimba 2005). Remarkably, plants adapted to non-flying mammal pollinators emit strong floral odours that specifically attract mice and elephant-shrews (Johnson et al. 2011; Wester et al. 2019). These flowers are often covered by the plants' bracts, leaves

or twigs or are cryptically coloured (Wester et al. 2009, 2019; Wester 2010, 2011; Flasch et al. 2016; Kühn et al. 2017; Connolly and Midgley 2020), and this has been interpreted as having evolved to limit the attraction of illegitimate flower visitors, such as bees or birds that might steal nectar or pollen without pollinating (Wester and Lunau 2017; Wester et al. 2019; see also Lunau et al. 2011; Wester et al. 2020). In fact, all plants studied here were heavily visited by non-flying mammals lapping nectar, but not or extremely rarely by insects or birds, despite bees and birds being common visitors to flowers of other species at the study sites (Flasch et al. 2016; Wester et al. 2019, 2024; Petra Wester, unpubl. data). The absence of insect and bird visitors at non-flying mammal-pollinated flowers also supports the improbability of floral fluorescence as an attractant for these animals.

While fluorescence of *E. regia* pollen is not clearly noticeable, or, if existent, at most only weak (Fig. 1B), fluorescent pollen has been detected in the related *Eucomis autumnnalis* (Mill.) Chitt. (Fukui et al. 2017). The latter is a plant with flowers pollinated by spider-hunting wasps (Shuttleworth and Johnson 2009). Behavioural experiments showed that the wasps are attracted by scent rather than visual cues (Shuttleworth and Johnson 2009), a further argument that floral fluorescence most likely is irrelevant as attractant for flower visitors. If *E. regia* pollen shows (weak) fluorescence, this might be phylogenetically constrained and not necessarily of biological importance. Also, other genera (e.g. *Lobelia* L., Campanulaceae and *Salvia* L., Lamiaceae) include species with fluorescent pollen (Fukui et al. 2017) of which some are pollinated by insects and others pollinated by birds (Bertin 1982; Hiraga and Sakai 2007; Wester and Claßen-Bockhoff 2011; Wester et al. 2020).

Fluorescent pollen has been also found in bee-pollinated plant species with keel flowers (e.g. *Crotalaria spectabilis* Roth, *Vigna umbellata* (Thunb.) Ohwi & H. Ohashi, Fabaceae; Fukui et al. 2017) in which the reproductive organs - and thus, pollen - are enclosed by the keel petals and are only exposed during the contact with pollinators that open the flowers (Arroyo 1981; Westerkamp 1997). Thus, this pollen - and its fluorescence - does not play any role in the visual attraction of pollinators.

Fluorescence in flowers occurs also in plants pollinated by other animal groups. In bat-pollinated flowers, fluorescent nectar (*Cheirostemon platanoides* Bonpl., Malvaceae; Scogin 1980) and pollen (*Musa* L., Musaceae;

Fukui et al. 2017) have been detected. Fluorescent pollen and petals have been found in hawkmoth-pollinated flowers (Gandía-Herrero et al. 2005a; Fukui et al. 2017) and fluorescent pollen in plants pollinated by moths, butterflies, and birds (Fukui et al. 2017). Although fluorescence theoretically could be perceived also by insects and other flower visitors such as birds and bats (Müller et al. 2009; Kelber and Osorio 2010), it seems to be irrelevant for their foraging behaviour. Bats are nocturnal, thus floral scent and shape (for echolocation) seem to be more important than colour for finding food (Simon et al. 2011; von Helversen et al. 2000; Jones et al. 2013; Gonzalez-Terrazas et al. 2016). Also, moths and hawkmoths are nocturnal or crepuscular and thus rely predominantly on floral scent to find flowers (Knudsen and Tollsten 1993; Dobson 2006; Riffell et al. 2013). Pollen and other floral parts have been found to be fluorescent even in wind-pollinated plants (e.g. grasses) (Roshchina 2012; Baby et al. 2013; Fukui et al. 2017). In wind-pollinated flowers, attractiveness is insignificant and in general floral display and nectar production did not evolve or were reduced (Faegri and van der Pijl 1979).

Thus, fluorescence in flowers seems to have no significance or adaptive value for increasing visibility or the attraction of flower visitors. This is consistent with the view that fluorescence is obscured by floral reflections due to its low quantum efficiency (Kevan 1976; Iriel and Lagorio 2010a, 2010b). Fluorescence in flowers could be just a by-product of a pigment or other molecule that has other functions such as visual attraction by reflection or UV absorbance (mainly in petals) or protective effects (in anthers and pollen or in nectar). The widespread occurrence of fluorescence in pollen in different families independent of the pollinator group, might suggest a protection of genes from UV induced damage. Fluorescent compounds in pollen might quench harmful UV energy

by transducing the absorbed UV radiation to fluorescence (Rozema et al. 2001) or indirectly by scavenging radicals from reactive oxygen species caused by UV radiation (Mori et al. 2018). Fluorescent substances in nectar are suggested to have antimicrobial properties, keeping microbes from degrading carbohydrates in nectar (Hagler and Buchmann 1993). Fluorescent compounds in nectar might also render carbohydrates less or even non-metabolizable and therefore nutritionally unavailable for non-pollinating flower visitors (Hagler and Buchmann 1993). Fluorescent phenolics are known to impart an unfavourable taste to nectar (e.g. *Aloe littoralis* Baker) for non-pollinators (e.g. honeybees), that is accepted by adapted pollinators (some birds). Phenolics causing nectar to be bitter are also found in other *Aloe* species (e.g. *A. vryheidensis* Groenew.), functioning as a floral filter, repelling ineffective pollinators such as honeybees and sunbirds, but not short-billed generalist nectarivorous birds as effective pollinators (Johnson et al. 2006). The nectar of at least *M. grandiflora* and *M. pustulata* tastes bitter (Wester et al. 2024; Petra Wester, unpubl. data), thus it is possible that phenolics repel insects or sunbirds, but not mammals. One cannot exclude that fluorescent compounds in flowers exhibit multiple functions. However, so far, no convincing evidence exists for visual signalling for pollinators. This is in line with observations of fluorescence in other organisms, being without ecological function. For example, fluorescent porphyrin accumulation in the pelage of some mammals is probably a by-product of physiological processes (Toussaint et al. 2022). Another example is coloured nectar in *Stemona tuberosa* Lour. (Stemonaceae) as a nonadaptive by-product of pigment biosynthesis in other flower parts (Cai et al. 2022).

However, further observations and experiments are necessary to clearly evaluate whether flower visitors

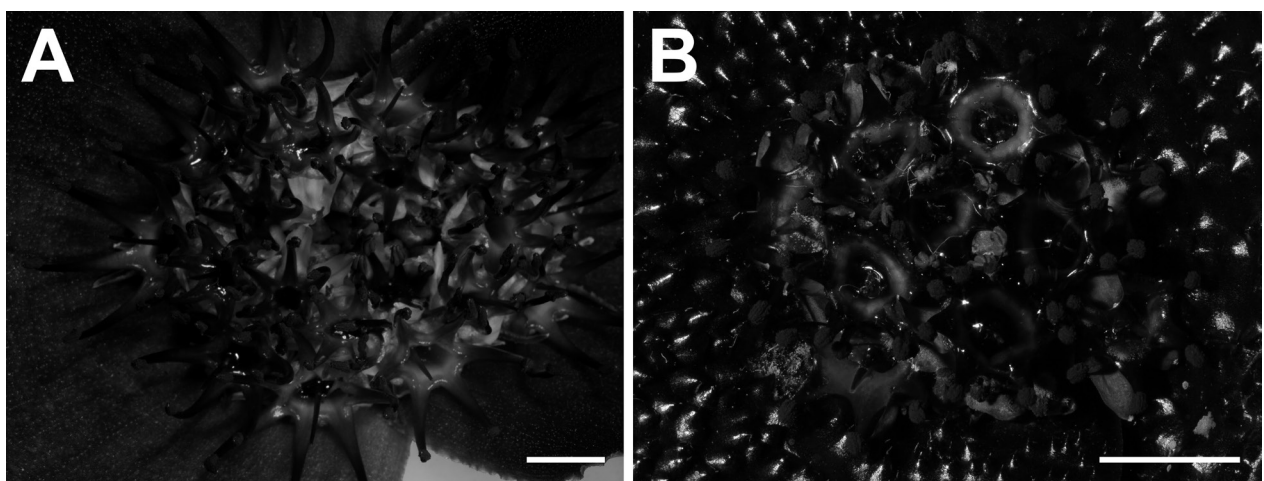


Figure 2. *Massonia* inflorescences, photographed with a camera being sensitive to UV, visible, and IR light, in combination with a UV-transmissible lens and a UV filter (transmitting at 320–380 nm) under UV illumination, showing strong UV absorption (appearing black) of the nectar in flowers of *M. grandiflora* (A, note the glossy nectar only in the left flowers of the inflorescence) and *M. echinata* (B, note the glossy nectar only in the lower flowers of the inflorescence). Compare with Fig. 1C, D, G, H. Scale bars = 1 cm.

are able to perceive floral fluorescence and whether fluorescent nectar or other flower parts play a role in the attraction of flower visitors, independent of other floral cues such as colour, gloss, shape, or scent.

Regarding the examined plant species, further analyses should include a comparison with insect-pollinated conspecifics (nectar fluorescence), measurement of the absorption and emission spectra of the fluorescence as well as chemical analyses of nectar for (fluorescent) secondary compounds (e.g. phenolics). Furthermore, the latter should be tested by bioassays for biological functions (e.g. taste filter, antibiotic function) as an alternative for visual signalling.

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