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REVIEW ARTICLE

Pollen, anther, stamen, and androecium mimicry

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ABSTRACT

Floral colours represent a highly diverse communication signal mainly involved in flower visitors' attraction and guidance, but also flower discrimination, filtering non-pollinators and discouraging floral antagonists. The divergent visual systems and colour preferences of flower visitors, as well as the necessity of cues for flower detection and discrimination, foster the diversity of floral colours and colour patterns. Despite the bewildering diversity of floral colour patterns, a recurrent component is a yellow UV-absorbing floral centre, and it is still not clear why this pattern is so frequent in angiosperms. The pollen, anther, stamen, and androecium mimicry (PASAM) hypothesis suggests that the system composed of the flowers possessing such yellow UV-absorbing floral reproductive structures, the flowers displaying central yellow UV-absorbing structures as floral guides, and the pollen-collecting, as well as pollen-eating, flower visitors responding to such signals constitute the world's most speciose mimicry system. In this review, we call the attention of researchers to some hypothetical PASAM systems around the globe, presenting some fascinating examples that illustrate their huge diversity. We will also present new and published data on pollen-eating and pollen-collecting pollinators' responses to PASAM structures supporting the PASAM hypothesis and will discuss how widespread these systems are around the globe. Ultimately, our goal is to promote the idea that PASAM is a plausible first approach to understanding floral colour patterns in angiosperms.

INTRODUCTION

Flower colours are the main advertisement for many pollinators from different taxa (Lunau & Maier 1995; van der Kooi *et al.* 2019a). Different colour vision systems, colour discrimination capabilities, colour preferences as well as the necessity of divergent cues for flower detection by pollinators have been proposed to explain the huge diversity of flower colours (Kay 1976; Chittka & Menzel 1992; Lunau & Maier 1995; Kevan *et al.* 1996; Cooley *et al.* 2008; Reverté *et al.* 2016; Hoyle *et al.* 2018). Flower colour diversity may also have evolved in response to processes besides pollinator attraction, such as colour discrimination, filtering non-pollinators and discouraging floral antagonists (Lunau *et al.* 2011; Soper Gorden & Adler 2016; Garcia *et al.* 2020). Interestingly, flowers and inflorescences of animal-pollinated plants rarely present one single colour, but a colour pattern consisting of one large peripheral component and one or multiple small central components made up of some floral organs such as a disc, style, stamens, protuberances and/or colour patches on the petals (Jones & Buchmann 1974; Dafni & Giurfa 1999; Hempel de Ibarra *et al.* 2015; Narbona *et al.* 2021). The absence of colour pattern has been found to correlate with ornithophilous as compared to melittophilous flowers (Papiorek *et al.* 2016). Such colour patterns not only increase the diversity of visual advertisements, but also fulfil additional functions such as guiding potential pollinators towards the floral resources, distracting floral antagonists from pollen (Lunau 2000; Fairnie *et al.* 2022) and protecting pollen by absorbing ultraviolet light (Koski & Ashman 2015a,b). Despite floral colours having been extensively studied in pollination ecology and evolution (van der Kooi *et al.* 2019a), little is known about such colour patterns. Most studies mention only the main colour of flowers and the functional role of stamens, styles and floral guide colours have been considered independently of each other.

In general, floral colours and colour patterns attract floral visitors, which undertake pollination while they consume diverse floral resources, such as nectar, fatty oils, resin, perfume or pollen. Pollinators can even be deceived by such advertisements in flowers that do not offer any floral reward (Whitehead *et al.* 2018; Shrestha *et al.* 2020). Specifically, pollen and pollen-bearing organs play a decisive role in attracting pollen-eating and pollen-collecting flower visitors because they both signal and feed them (Lunau 2000). Pollen-eating pollinators, such as flies (Holloway 1976; Haslett 1989; Brodie *et al.* 2015), some bats (Herrera & Martínez Del Río 1998), some beetles (Johnson & Nicolson 2001), micropterigid moths (van der Pijl 1960), and heliconiid butterflies (Gilbert 1972), take up pollen directly using their mouthparts. On the other hand, pollen-collecting pollinators, such as masarid wasps (Cess & Cess 1989; Müller 1996) and bees (Thorp 2000; Portman *et al.* 2019), achieve pollen harvesting, grooming, and transport, performing stereotyped behaviour associated with specialized structures (e.g. bristles on mouthparts or legs for pollen harvesting; pollen combs or bristles on legs for pollen grooming; crop, scopa, or corbiculae for pollen transport). Both pollen-eating and pollen-collecting animals strongly respond to visual, olfactory, gustatory, and tactile floral cues from pollen grains and pollen-bearing anthers and stamens (Gack 1981; Wacht *et al.* 1996; Lunau 2000; Heuschen *et al.* 2005; Pohl *et al.* 2008; Ruedenauer *et al.* 2020, 2021; Figs 1 and 2).

Visual cues play the most important role in indicating the presence and access to floral resources for pollen-eating and -collecting flower visitors. Flowers pollinated by pollen-eating and pollen-collecting animals often display floral colour patterns (Lunau 2007). Surprisingly, the colour combination within the attractive structure is not random and often obeys two rules. The first is an increase in colour spectral purity from the peripheral to the central colour within the attractive structure, forming a positive centripetal spectral purity gradient (Lunau 1992b; Lunau *et al.* 1996; Heuschen *et al.* 2005). Such a pattern would guide bee pollinators to the right position to perform pollination while searching for floral resources (Lunau 1990; Lunau *et al.* 2009; Fig. 1E–H) and pollen transfer

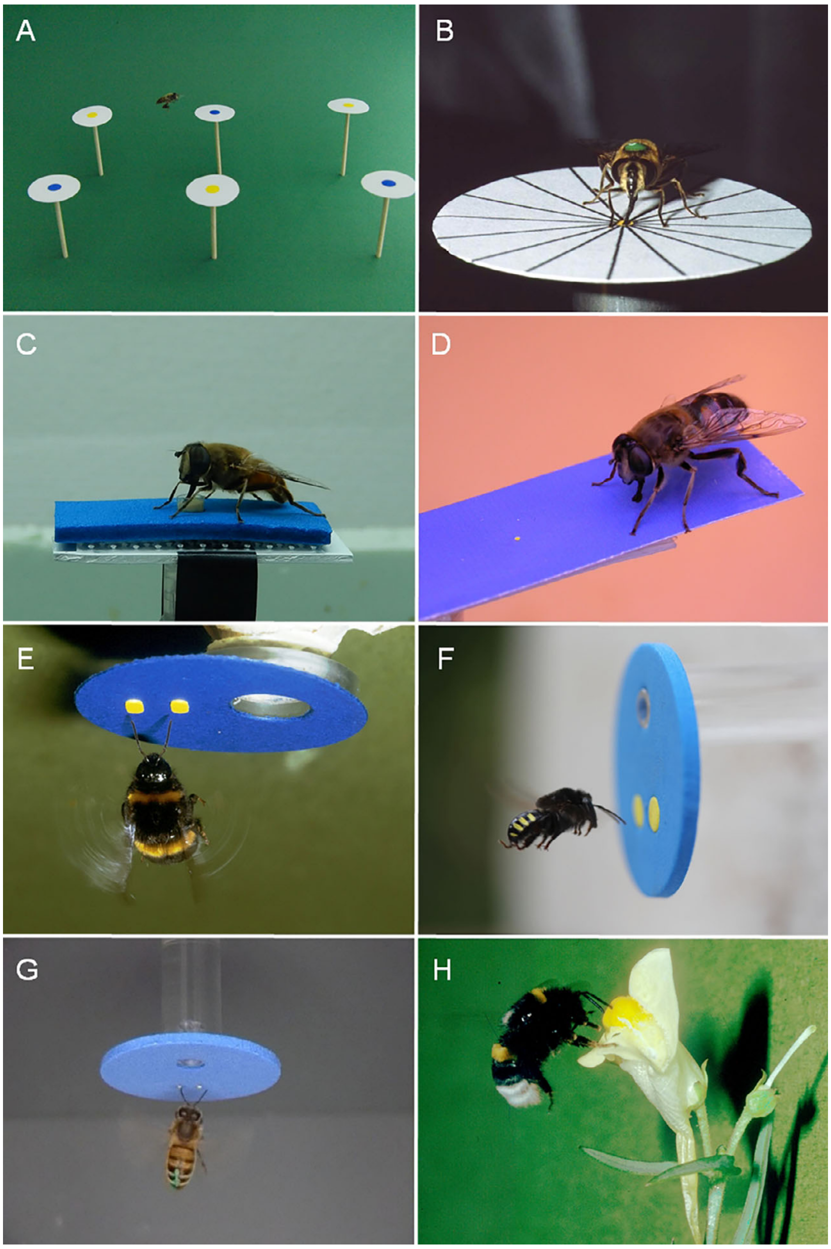

Fig. 1. Bees and flies responding to stamen-imitating structures of artificial and real flowers in laboratory conditions. A: *Eristalis tenax* hoverfly can be trained to visit artificial flowers with either blue- or yellow-coloured guides. B: *Eristalis tenax* hoverfly is guided by black line guides towards a yellow colour patch where it shows proboscis reflex. C: Visually guided proboscis extension of *Eristalis tenax* towards yellow UV-absorbing real pollen. D: Proboscis reaction of *Eristalis tenax* towards a yellow UV-absorbing colour spot <1 mm in diameter. E: *Bombus terrestis* worker choosing between yellow UV-absorbing unscented colour spot and whole emitting pollen odour. F: *Melipona quadrifasciata* worker showing antennal reaction at an anther dummy. G: *Apis mellifera* worker exhibiting antennal reaction at a 0.7-mm sized anther dummy. H: Naive *Bombus lucorum* worker showing antennal reaction at the lower lip of *Linaria vulgaris*.

Fig. 2. Bee and fly responses to PASAM. A: Western honeybee antennates and lands on the anther mimicking stigma of a crocus flower. B: *Bombus pratorum* worker approaches the stamen mimicking colour patch of *Rhododendron* sp. and ignores the real stamens. C: *Rhingia* sp. hoverfly extends its proboscis towards the anther mimics. D: and it finally finds the slit entrance to the nectar holder of *Rhododendron* sp. E: Muscoid fly touches the heads of the staminodes of *Parnassia palustris* with its proboscis. F: *Eristalis* sp. hoverfly eats pollen presented in the narrow floral tube surrounded by stamen mimics of *Myosotis palustris*. G: *Osmia cornuta* female visits the cone-shaped corona of a *Narcissus pseudonarcissus* flower. H: *Bombus pascuorum* worker exhibiting antennal reaction at the androecium mimicking stigmas of a *Begonia* flower.

(Koch *et al.* 2017). The second is the display of a yellow and UV-absorbing colour of central floral structures, resembling the widespread natural colour of pollen grains, which has so far been called pollen, anther, stamen, or androecium mimicry (PASAM) (Heuschen *et al.* 2005; Lunau 2007; Lunau *et al.* 2017; Fig. 2). Syrphid flies of the genus *Eristalis* innately respond with the extension of the proboscis towards yellow and UV-absorbing colours (Lunau & Wach 1994; Lunau 2014; An *et al.* 2018) and are guided by pollen and anther mimicking colour patches (Dinkel & Lunau 2001; Wiegel & Lunau 2023; Fig. 1A–D). Despite PASAM being phylogenetically and geographically pervasive, it has been poorly considered in the literature. Moreover, there is much confusing literature involving terms related to PASAM as well as floral colour patterns in general.

The PASAM hypothesis suggests that the mimicry system composed of the pollen and pollen-bearing stamens (as models), the yellow UV-absorbing mimicking structures (as mimics), and the pollen-collecting as well as pollen-eating flower visitors responding to such signals (as operators or signal receivers), constitute the world's most speciose mimicry system. In this review we call the attention of researchers to some hypothetical PASAM systems and address some open topics related to PASAM, such as (i) PASAM as true mimicry case; (ii) delimitation between PASAM and other colour patterns; (iii) pollen-eating and pollen-collecting bees' and flies' responses to PASAM; (iv) diversity, functions, and complexity of PASAM structures; and (v) PASAM representing a universal code globally. To access these topics, we will explore examples of PASAM around the world, and pollen-eating and pollen-collecting pollinators' responses to PASAM structures based on original and published information. We then discuss how widespread these systems are throughout the world, presenting evidence of the PASAM hypothesis. We also present a glossary clarifying the definition of PASAM and the main terms related to flower colour patterns.

TERMINOLOGY OF FLORAL COLOUR PATTERNS

In general, there are two ways to describe floral colour patterns, by flower-based and by flower visitor-based terms. Flower-based terms are descriptive and valid without any knowledge of the responses of flower visitors. Such flower-based terms include floral structures such as pollen, anthers, stamens, and staminodes, floral colour patterns, UV bull's eyes (Silberglied 1979), as well as its reflectance properties such as yellow and UV-absorbing, etc. By contrast, flower visitor-based terms are interpretative and require knowledge about the flower visitors' response to the flower structures, their colour patterns and colour properties. Flower visitor-based terms include mimicry, deception, flower guide, nectar guide, pollen guide, false anther, and fake pollen. Therefore, while flower-based terms are handled unambiguously, flower visitor-based terms are ambiguous. For example, even when we make careful observations of flower visitors, we will never know what kind, and which amount of reward the flower visitors expected to find when they decided to visit a given flower, thus whether they were totally satisfied, fobbed off with another reward, partly or completely deceived. Problems like this have hampered classification of the phenomena concerning the interaction between colour-patterned flowers and their visitors, and different authors have used deviant denominations for flower visitor-based terms, particularly for mimicry and related phenomena (Osche 1983; Vogel 1993; Bernhardt 1996; Lunau 2000; Ruxton & Schaefer 2011; Johnson & Schiestl 2016). Therefore, a clear definition is necessary to avoid misunderstandings. We provide relevant terms related to floral colour patterns in an attempt to find distinct, non-overlapping definitions among them in Table S1. Such definitions do not require flower visitors' observations and assessment of their behaviour *a priori* and should always be treated as hypotheses to be further tested. At the same time, these clear definitions could replace the bewildering diversity of descriptions found in the literature (Table 1).

POLLEN, ANTHER, STAMEN AND ANDROECIUM MIMICRY: TRUE MIMICRY OR NOT?

Pollen, anther, stamen and androecium mimicry are fundamentally dependent on how researchers define mimicry. Mimicry systems are based on a model displaying a signal that is copied by the mimic such that the signal receiver cannot or not fully discriminate between model and mimic, ultimately exerting positive selection pressure on the mimic (de Jager & Anderson 2019). Moreover, the similarity between model and mimic is regarded as Batesian mimicry if the model is rewarding and the mimic is rewarding less or not rewarding and is regarded as Mullerian mimicry if both the model and the mimic are rewarding (Roy & Widmer 1999). If the differences in reward between the model and mimic are small or if one flower visitor can take up the mimic's reward, but another does not, then the delimitation between Batesian and Mullerian mimicry becomes blurred. Therefore, a critical parameter evidencing any mimicry system is the response of the signal receiver to the mimic, which must be identical to the response to the model. On the other hand, the concept of sensory exploitation is based on the imitation of a generalized signal but assumes that the signal receiver responds differently to each signal (*i.e.* the original signal and its signal copy) in different contexts. Originally, the concept of sensory exploitation assumes that male animals exploit a sensory bias in females for distinct signals in the context of courtship and mating (Arnqvist 2006). Similarly, flowers might exploit sensory bias in pollinators (*e.g.* Pohl *et al.* 2008; Schaefer & Ruxton 2009; Schiestl & Johnson 2013; Koski 2020). For example, hoverflies and bees respond differently to close-range signals but show sensory bias in favour of colour signals resembling the colour of pollen and anthers. Inexperienced and flower-naïve bumblebees make the first contact with flowers using their antennas at the floral guide of high spectral purity surpassing the spectral purity of the corolla (Lunau *et al.* 1996, 2006). The antennal response is a general feature in landing bees (Evangelista *et al.* 2010; Reber *et al.* 2016); even the antennal position is modified to accomplish contact with floral guides in landing bumblebees (Pohl & Lunau 2007). Syrphid flies cannot touch surfaces due to their short antennas; the innate proboscis reflex of the hoverfly *Eristalis tenax* towards yellow and UV-absorbing floral guides is exhibited by naïve flies and cannot be conditioned towards colours other than yellow (An *et al.* 2018; Lunau *et al.* 2018).

As in many other mimicry systems, little is known about the response of pollen-eating and pollen-collecting flower visitors towards the mimic and the model in PASAM systems. The response of naïve individuals to anther imitation dummies has been investigated only for very few species, such as the syrphid fly *Eristalis pertinax*, the bumblebees *Bombus terrestris* and *B. lucorum* and the honeybee *Apis mellifera* (Lunau 1991, 1992a; Wacht *et al.* 1996, 2000; Heuschen *et al.* 2005; Pohl *et al.* 2008; Figs 1 and 2). Experiments in laboratory conditions show that naïve and non-trained hoverflies and bumblebees innately respond to anther dummies (Lunau 2000, 2007; Fig. 1). *Eristalis tenax* hoverflies can be trained to land or not to land on artificial flowers presenting a yellow colour patch (An *et al.* 2018; Fig. 1A). After landing, even naïve hoverflies approach central yellow colour spots (Dinkel & Lunau 2001; Fig. 1B) and innately extend their proboscis towards yellow colours of natural pollen (An *et al.* 2018; Fig. 1C). This proboscis reflex towards yellow spots can be elicited even towards spots smaller than 0.5 mm (Lunau 2021a; Fig. 1D). When approaching artificial flowers, naïve and non-trained bumblebees, *Bombus terrestris*, innately target visual signals of anthers, but the colour contrast and the superior spectral purity (perceived as stronger saturation) of the colour spots are responsible for the antenna reaction (Lunau 2007; Fig. 1E) rather than the yellow UV-absorbing hue. Experienced stingless bees, e.g. *Melipona quadrifasciata*, show similar antenna reactions at anther dummies (Lunau 2021b; Fig. 1F). Even experienced Western honeybees, *Apis mellifera*, exhibit the antenna reaction at small-sized floral guides (Lunau *et al.* 2009; Fig. 1G). Naïve bumblebees, *Bombus terrestris*, exhibit the antenna reaction also at anther mimics of *Linaria vulgaris* (Lunau 1992a; Fig. 1H). Similarly, pollen-eating and pollen-collecting pollinators also respond to yellow floral structures in natural systems. Western honeybees

Table 1. List of PASM types described in flowering plant species and their original denomination.

family	species	original denomination	PASM type specification	structure	literature
Asphodelaceae	*Bulbine abyssinica*	False signal of pollen, reward availability	Pollen mimicry	Staminal hairs	Duffy & Johnson (2015)
	Dianella sp.	Pseudanthery, anther mimic	Anther mimicry	Filament sculptures	[#]Bernhardt (1996)
Begoniaceae	*Begonia involucrata*	Intersexual mimicry	Androecium mimicry	Stigmatic lobes	Schemske & Agren (1995)
	Begonia sp.	Pseudanthery, pollen mimic	Androecium mimicry	Stigmatic lobes	[#]Bernhardt (1996)
Bignoniaceae	*Catalpa bignonioides*	*Two anther dummies with anther and filament imitations	Stamen mimicry	Semi-plastic swellings	[#]Osche (1986)
Boraginaceae	*Myosotis palustris*	*Imitation of 5 anthers and filaments	Stamen mimicry	Semi-plastic ring of swellings	[#]Osche (1986)
Commelinaceae	*Coleotrype madagascarica*	*Substituting pollen dummy	Pollen mimicry	Woolly hairs	[#]Vogel (1993)
	Commelina benghalensis	Staminodes provide (or mimic) fertile or sterile pollen	Stamen mimicry	Two types of staminodes not for pollination	Walker-Larsen & Harder (2000)
	Commelina coelestis	Staminodes mimic large amounts of pollen	Stamen mimicry	Staminodes	[#]Hrycan & Davis (2005)
	Tinantia anomala	Staminal trichomes, pollen dummy	Pollen mimicry	Filamental hairs	Simpson *et al*. (1986)
Cucurbitaceae	*Cucurbita pepo*	Imitation stamens	Androecium mimicry	Stigma of female flowers	[#]Lunau (2000)
Ericaceae	*Rhododendron ponticum*	Imitation stamens	Anther mimicry	Floral guides on upper petal	[#]Lunau (2000)
Fabaceae	*Chorizema rhombeum*	Stamen-mimicking structure, anther mimicking colour patch	Anther mimicry	Floral guides on banner petal	[#]Lunau *et al*. (2021)
Gentianaceae	*Gentiana kochiana*	*Semi-plastic anther copy	Anther mimicry	Protuberances on petals	[#]Osche (1983)
Gesneriaceae	*Didymocarpus geitleri*	Anther (pollen) dummy	Anther mimicry	Style	Weber (1989)
	Loxocarous coerulea	*Pollen dummy	Anther mimicry	Basis of filament	[#]Vogel (1993)
Goodeniaceae	*Dampiera linearis*	Stamen-mimicking structure, false stamens	Stamen mimicry	Central floral guide	[#]Lunau *et al*. (2021)
Iridaceae	*Crocus speciosus*	*Full-plastic stamen imitation	Stamen mimicry	Stylodia	[#]Osche (1979)
	Crocus sp.	Stamen-mimicking structure	Stamen mimicry	Style	[#]Lunau *et al*. (2016)
	Dietes grandiflora	*Over-sized signal copies of stamens	Stamen mimicry	Hairy floral guide on outer tepals	Barthlott (1992)
	Iris germanica	Stamen mimics	Androecium mimicry	Beard of protuberances	[#]Lunau (2000)
	Iris germanica	Pollen imitating hairs	Androecium mimicry	Protuberances	[#]Schiestl & Johnson (2016)
	Tritonia laxifolia	Structural stamen mimic	Stamen mimicry	3D structures on petal	Newman *et al*. (2022)
Lentibulariaceae	*Pinguicula alpine*	*Bilobed cushion-like anther imitations	Anther mimicry	Floral guide on floral palate	[#]Osche (1979)
Linderniaceae	*Craterostigma plantagineum*	Plastic false anther, anther dummy	Anther mimicry	Knee of filament	Magin *et al*. (1989)
	Torenia polygonoides	Spotlike anther dummy	Anther mimicry	Colour patch	Magin *et al*. (1989)
Malvaceae	*Sparmannia africana*	Anther and pollen dummies	Pollen mimicry	Filamental swellings	[#]Vogel (1978)
Melastomataceae	*Meriana longifolia*	Anther dummies	Anther mimicry	Connective appendages	[#]Vogel (1978)
	Microlicia cordata	Structure increasing the attractiveness	Anther mimicry	Appendages of staminal filaments	Velloso *et al*. (2018)
Orchidaceae	*Calopogon parviflorus*	Hairs of the crest look like a cluster of dehiscent stamens	Stamen mimicry	Club-shaped hairs on labellum	Robertson (1887)
	Calypso bulbosa	Pollen dummy	Stamen mimicry	Rows of yellow hairs	Boyden (1982)
	Cephalanthera longifolia	Pseudopollen	Pollen mimicry	Papillae on labellum	Dafni & Ivri (1981)
	Cypripedium wardii	Pseudopollen	Pollen mimicry	Floral guides on upper petal	Zheng *et al*. (2021)
	Diuris setacea	Anther-mimicking central floral guide	Anther mimicry	Floral guides on labellum	Lunau *et al*. (2021)
	Eulophia cucullata	Pollen-like nectar guide	Stamen mimicry	Colour patch	[#]Schiestl & Johnson (2016)

Table 1. (Continued)

family	species	original denomination	PASM type specification	structure	literature
	Maxillaria lepidota	Pseudopollen-forming trichomes	Pollen/anther mimicry	Collectable pseudopollen	Davies *et al.* (2013)
	Paphiopedilum barbigerum	Attractive staminode	Anther mimicry	Protuberance on staminode	Shi *et al.* (2009)
	Paphiopedilum micranthum	Mimic the central colour of pollen presentation structures	Anther mimicry	Floral guides on petals	Ma *et al.* (2016)
	Thelymitra crinata	Pollen imitation	Pollen mimicry	Yellow hairs	#Vogel (1978)
	Thelymitra epipactoides	False anther formed by the voluminous column wings	Stamen mimicry	Trichomes of column	Cropper & Calder (1988)
	Thelymitra nuda	Pseudanthery, false anther, pseudopollen	Pollen/anther mimicry	Trichomes on multi-lobed hood	Bernhardt & Burns-Balogh (1986)
Orobanchaceae	*Cistanche phelypæa* subsp. *Llutea*	Fake anther, anther-like swollen folds	Anther mimicry	Swollen folds on petal	Piwowarczyk *et al.* (2016)
	Melampyrum pratense	*Semi-plastic anther dummy	Pollen/anther mimicry	Cushion-like lower lip with ball-shaped hairs	#Osche (1983)
	Orobanche gracilis	*Anther mimic	Anther mimicry	Dumbbell-shaped stigma	#Osche (1983)
Plantaginaceae	*Linaria cymbalaria*	*Semi-plastic anther dummy	Anther mimicry	Mask of lower lip	#Osche 1979
	Polygala vayredae	*Petal with stamen imitating appendages	Stamen mimicry	Appendages of petal tip	#Osche (1986)
Ranunculaceae	*Caltha palustris*	Pollen and stamen mimicry	Stamen mimicry	Central floral guide (UV bull's eye)	#Lunau *et al.* (2017)
Saxifragaceae	*Saxifraga stellaris*	Stamen mimics	Anther mimicry	Two colour patches on each petal	#Lunau (2007)
Theaceae	*Camellia oleifera*	Pseudopollen	Pollen mimicry	Pseudopollen	Yuan *et al.* (2022)

The floral structures described are yellow if not otherwise mentioned. *Translated by the authors; #more examples in the original paper.

antennate and land on the stamen mimicking the stigma of crocus flowers (Lunau *et al.* 2016; Fig. 2A). *Bombus pratorum* bumblebees approach the stamen mimicking the colour patch of *Rhododendron* sp. and ignore the camouflaged real stamens (Mamgain 2022; Fig. 2B); *Rhingia* sp. hoverflies extend their proboscis towards the same stamen mimicking colour patches and finally find the slit entrance to the nectar holder (unpublished; Fig. 2C,D). The yellow colour of anther mimics in *Parnassia palustris* and *Myosotis palustris* elicit the proboscis extension of flies (Lunau 2007; Fig. 2E,F). The corona of *Narcissus pseudonarcissus* and the androecium mimicking stigmas of a *Begonia* flower are targeted by bees (Lunau 2000, 2007; Fig. 2G,H).

So far, PASAM systems have been understood as a way to impede discrimination of flowers in dichogamous, diclinous and heterostylous plants (Pohl *et al.* 2008), replace the signalling function of real pollen (Osche 1983; Lunau 2000) if it is invisibly hidden in the flowers or camouflaged (van der Kooi *et al.* 2019b), exaggerate the signal of real stamens (Velloso *et al.* 2018), and distract the flower visitors from real pollen (Lunau 2000). However, there are very few observations where flower visitors mistake pollen, anthers, or stamen mimics for their real counterparts (Bernhardt 1996). Thereby it is not clear whether these observations have been made with experienced flower visitors, which might have learned to modify their initial response towards the mimic structures, or with naïve flower visitors. Some researchers highlight that flower-visiting bees do not respond with pollen-collection behaviour to pollen, anther, or stamen mimics (Vogel 1978; Bernhardt 1996). As an exception, rarely, bees have been observed performing pollen collection movements on female *Begonia* flowers (Wyatt & Sazima 2011); also buzzing bees are known to buzz pollen-emptied conspicuous stamens (Burkart *et al.* 2014; Russell *et al.* 2017) or *Thelymitra* orchid flowers (Bernhardt & Burns-Balogh 1986). Moreover, it has been found that nectar-seeking flies and bees respond to visual cues of stamens and stamen mimicking structures (Fig. 1). Most importantly, both hoverflies, e.g. *Eristalis tenax*, and bees, e.g. *Bombus terrestris*, *Apis mellifera*, *Osmia cornuta* and *Melipona quadrifasciata*, respond to visual anther dummies (Fig. 2). Taken together, these examples in artificial and natural systems involving pollen-eating and pollen-collecting pollinators and floral structures resembling pollen, anthers, stamens, and entire androecium can be taken as evidence for the PASAM hypothesis that can be further investigated.

DIVERSITY OF POLLEN, ANTHER, STAMEN AND ANDROECIUM AND THEIR MIMICKING STRUCTURES

Models and mimics

Pollen, anther, stamen and androecium visual signalling is a precondition for PASAM (Osche 1983; Lunau 2000) and its striking diversity is illustrated by some meaningful examples in nature (Fig. 3). Stamens represent the sole visual signal of flowers in *Acacia retinodes* (unpublished; Fig. 3A). The secondary multiplication of stamens (dedoublement; Jordan 1883) increases the visual attractiveness of the androecium in many *Hypericum* species (Lunau 2000; Fig. 3B,C). The colour change of stamens in *Rosa multiflora* indicates their visual signalling function (unpublished; Fig. 3D), similar to colour changes of anther mimics (Lunau 1996a; Figs 4E and 5J–L). In older flowers of *Digitalis lutea* where the emptied anthers are

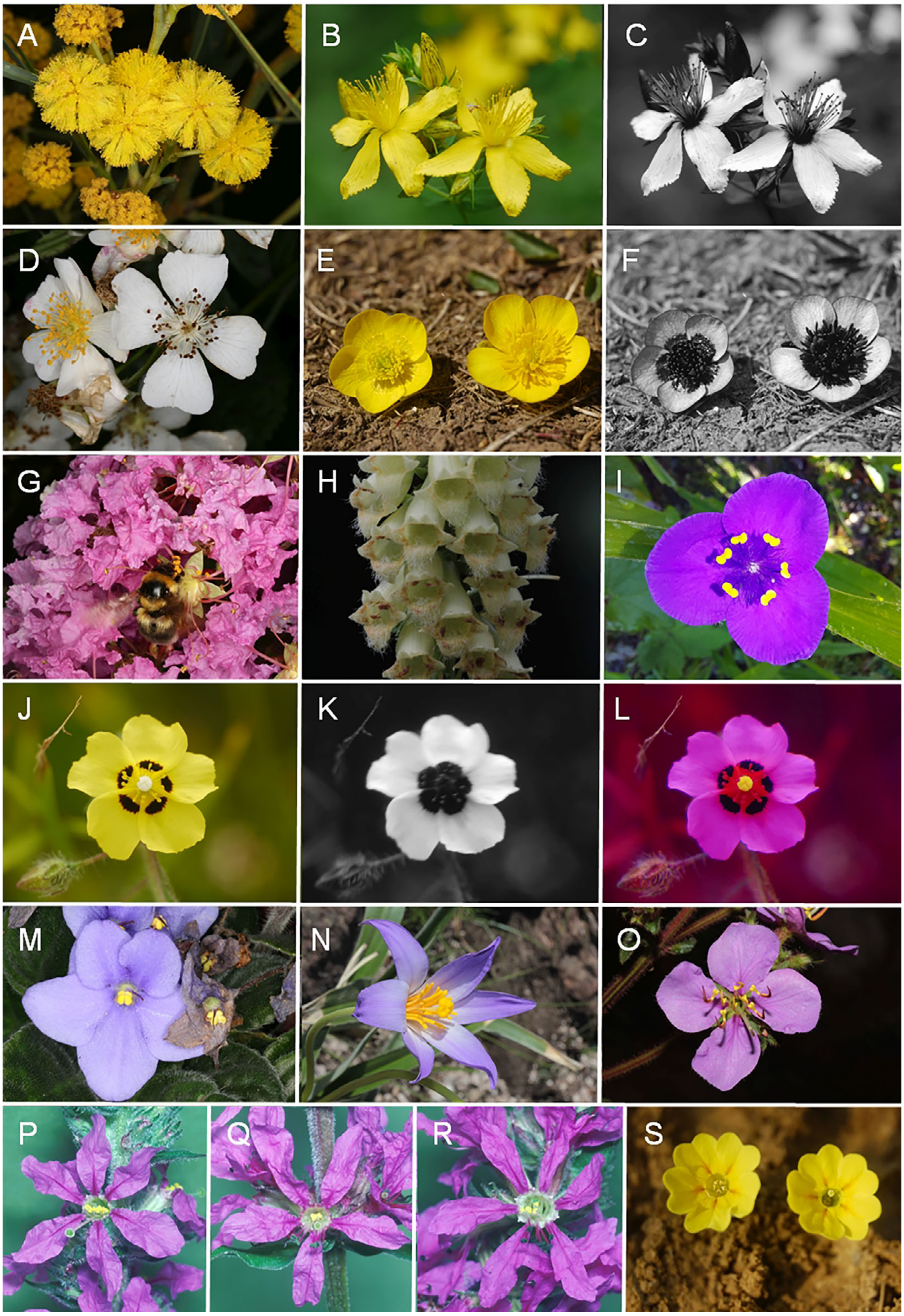

Fig. 3. The signalling function of stamens. A: Stamens as a sole visual signal in *Acacia retinodes* (Fabaceae). B, C: Dedoublement in *Hypericum desetangsii* (Hypericaceae) as shown in the colour photo and UV photo. D: Staminal colour change in *Rosa multiflora* (Rosaceae). E, F: Yellow UV-absorbing androecium and central yellow UV-absorbing colour patch of *Ranunculus* sp. increasing the anther signal, colour photo and UV photo. G: *Lagerstroemia indica* displays showy and camouflaged stamens. H: Signalling with anthers through filamental growth in *Digitalis lutea* I: Broadened connectives in *Tradescantia* sp. J, K, L: Contrasting background for anthers in *Tuberaria guttata* shown in colour, UV, and false colour photos. M: Non-wilting anthers in the protogynous *Saintpaulia ionantha*. N: Stigma simulating anther colour in *Vellozia* sp. O: Stamens with signalling appendages in *Rhexia virginica*. P, Q, R: Uniformity among morphs by pollen colour dimorphism in *Lythrum salicaria*. S: Uniformity among morphs by orange anther mimicking floral guides in pin and thrums of *Primula veris*.

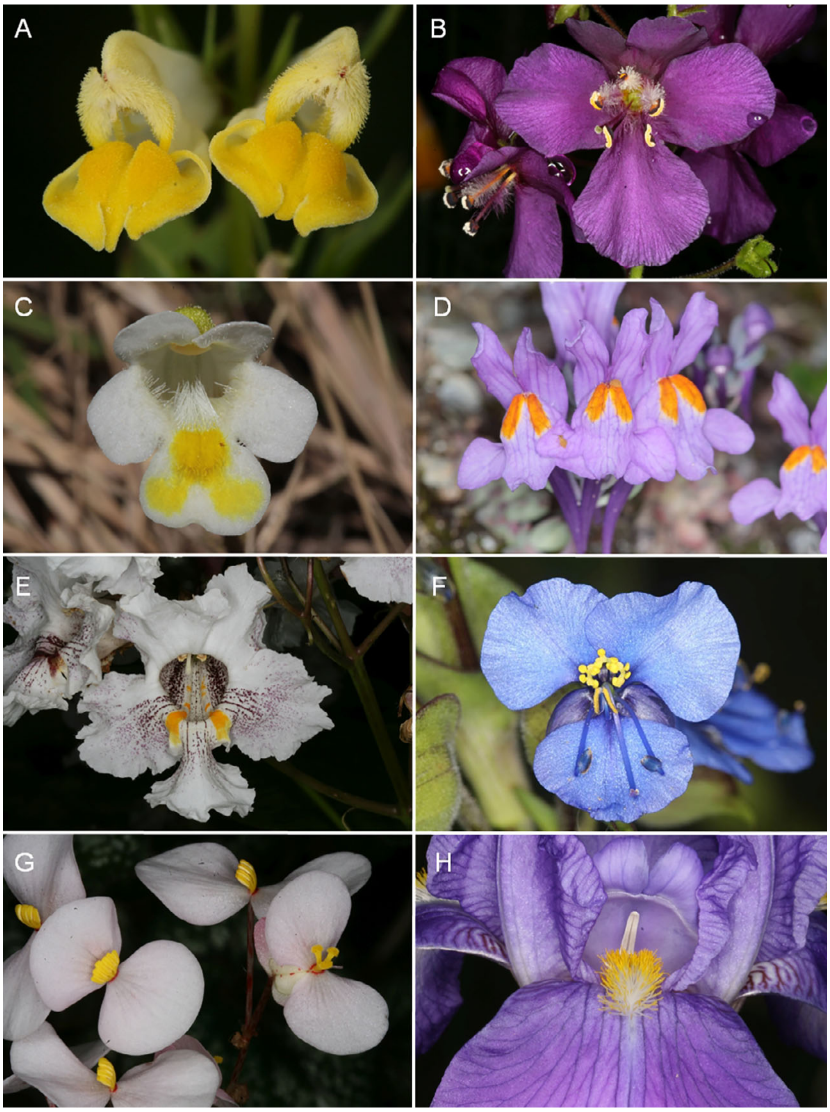

Fig. 4. PASAM examples: A: Pollen mimicry by small spherical protuberances on the lower lip of *Melampyrum pratense*. B: Pollen mimicry by filamental hairs in *Verbascum phoeniceum*. C: Anther mimicry by the stigma of *Pinguicula alpina*. D: Anther mimicry by the lower lip of *Linaria alpina*. E: Stamen mimicry by the semi-plastic floral guides in *Catalpa bignonioides*. F: Stamen mimicry by the three staminodes *in Commelina coelestis*. G: Androecium mimicry by the stigmatic lobes in *Begonia boweri*. H: Androecium mimicry by the beard of protuberances of *Iris germanica*.

displayed as an additional visual signal through filamental growth (Osche 1979; Fig. 3H). The anthers of *Tradescantia* species are visually more conspicuous through broadened connectives (Pellegrini 2017; Fig. 3I) and filament hairs (Tagawa 2023). The anthers of *Tuberaria guttata* are visually more conspicuous through a contrasting background (unpublished; Fig. 3J–L). In the protogynous *Saintpaulia ionantha* flowers, the anthers are non-wilting and thus remain attractive even if emptied (Osche 1979; Fig. 3M). The stigma in *Vellozia* species imitates the colour of the anthers, and together stigma and anthers provide an enlarged conspicuous signal used as a landing platform for bees (Ayensu 1973; Fig. 3N). Stamens with signalling appendages in *Rhexia virginica* are combined with camouflaged other parts of the stamens and thus can direct pollinators to distinct parts of stamens (Larson & Barrett 1999; Fig. 3O). Visual uniformity among the three morphs of the tristylous *Lythrum salicaria* is achieved by pollen colour dimorphism (Darwin 1877), resulting in conspicuous yellow anthers and pollen by short and middle stamens and inconspicuous green anthers and pollen by long stamens (Lunau 1996b; Fig. 3P–R). The visual uniformity among the two morphs of the distylous *Primula veris* is achieved by orange floral guides at the tube opening (Lunau 1996b; Fig. 3S).

Similarly to true pollen, anthers, stamens and androecia, their possible mimicking structures are morphologically diverse and include various structures reflecting the yellow and UV-absorbing colour of such structures (Lunau 1995, 2000, 2007), including three-dimensional mimics ranging from false pollen grains (Davies *et al.* 2013), single anther mimics (Osche 1983) to mimicked bunches of stamens representing an entire androecium (Osche 1983; Fig. 4). Beyond that, there are also mimic organs like staminodes, protuberances in the form, size and colour of real stamens, colour patches, nectar guides, swellings on lower lips, ridges, masks (Osche 1979, 1983), hairy

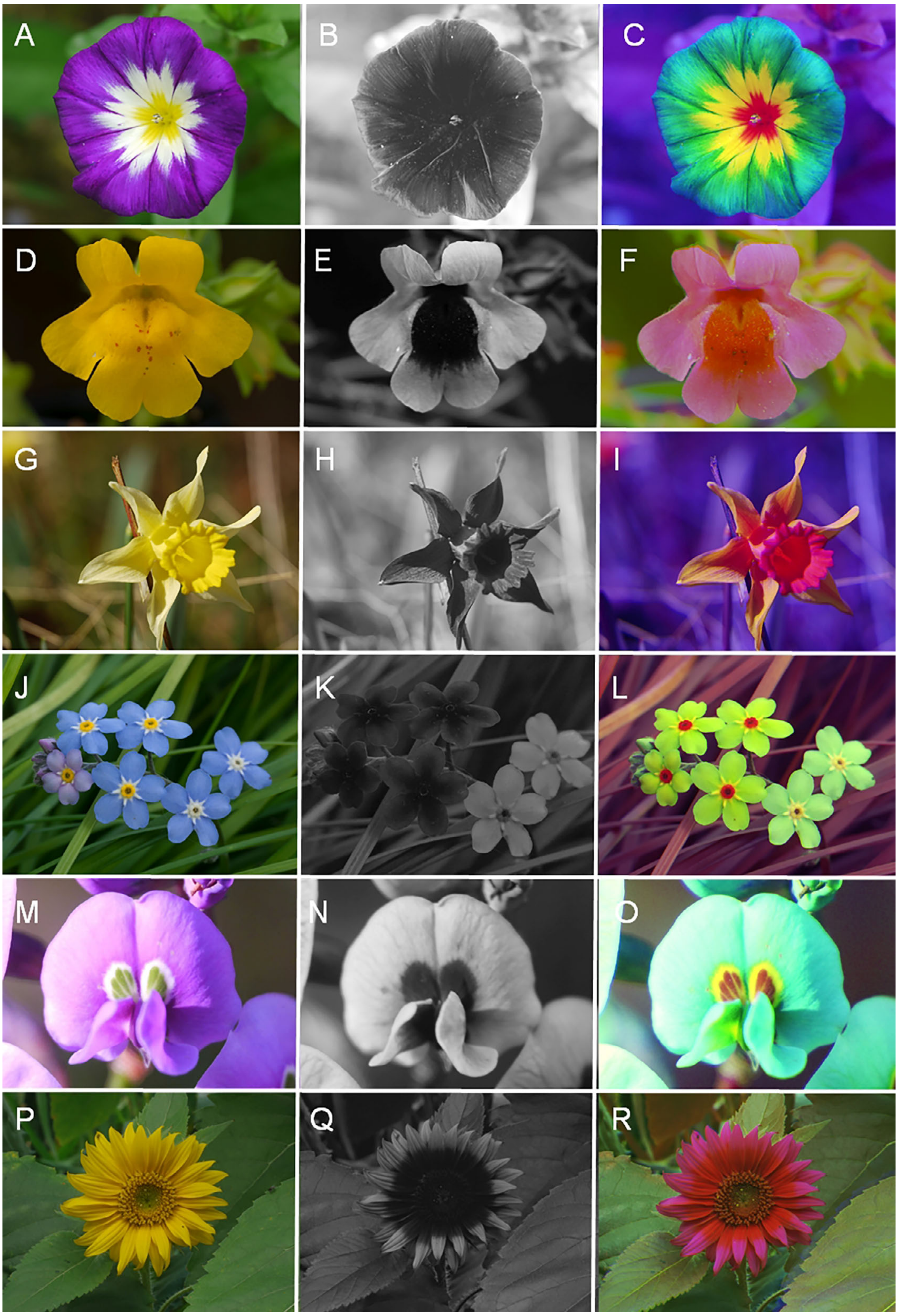

Fig. 5. Colour photos (left), UV photos (middle) and false colour photos (right) in bee view illustrating the conspicuousness of anther mimics for bees in the totally UV-absorbing flower of *Convolvulus tricolour* (A–C), in the UV bull's eye pattern of *Mimulus guttatus* (D–F), in the blue bull's eye pattern of *Narcissus pseudonarcissus* (G–I), in the colour change of *Myosotis arvensis* (J–L), in the human-green anther mimic of *Hardenbergia comptonia* (M–O), and in the inflorescence of *Helianthus annuus* (P–R).

structures or other modifications of filaments or stamens (Magin *et al.* 1989; Lunau 2000), styles (Weber 1989), stigmata, and other flower organs (Duffy & Johnson 2015; Lunau & Wester 2017). Some inflorescences mimic flowers including the androecium by means of different plant organs. For example, *Bougainvillea spectabilis* flowers combine three stamen-mimicking flowers with petal-like bracts; many Asteraceae inflorescences combine yellow and UV-absorbing disk florets mimicking an androecium and differently coloured ray florets mimicking the corolla of a single flower (Vogel 1978; Osche 1979, 1983; Lunau 2000, 2007). Plant-parasitic fungi are known to stimulate host plants to produce pseudoflowers presenting pseudopollen (Ngugi & Scherm 2006). PASAM structures are potentially multimodal signals including visual, olfactory, gustatory and tactile stimuli, but their chemical properties have only rarely been studied (Ruedenauer *et al.* 2017; Wilmsen *et al.* 2017).

Pollen mimicry, as in *Melampyrum pratense* and in *Verbascum phoeniceum*, is characterized by visual and tactile attributes of pollen (Osche 1979; Leins & Erbar 1994; Lunau 2021b; Fig. 4A,B). Typical anther mimicry includes the colour, bilobed form and size of single anthers as in the floral guide of *Pinguicula alpina* (Osche 1979) and the semi-plastic lower lip of *Linaria alpina* (Lunau *et al.* 2017; Fig. 4C,D), whereas stamen mimicry is characterized by imitation of more structures of stamens, such as filaments in *Catalpa bignonioides* and by the three staminodes *in Commelina coelestis* (Osche 1979; Lunau 1992b; Fig. 4E,F). Androecium mimicry comprises the imitation of multiple stamens, as in stigmatic lobes of pistillate *Begonia boweri* flowers and the beard of white filiform protuberances with yellow heads in *Iris germanica* (Osche 1979; Fig. 4G,H).

Response of pollinators

The estimated diversity of PASAM structures for bees and flies might differ from that for humans because of the bees' sensitivity to the ultraviolet range of wavelengths and insensitivity to red light (Chittka 1996; Lunau 2014). Here we provide examples of typical and non-typical PASAM structures in colour photos, UV photos, and false colour photos in bee view (Verhoeven *et al.* 2018; Lunau *et al.* 2021; Fig. 5). From false colour photos in bee view, it is evident that a missing UV bull's eye does not exclude a conspicuous colour pattern resembling stamen mimics; *Convolvulus tricolour* lacks UV patterns but displays a conspicuous bee-visible colour pattern (Lunau 2022; Fig. 5A–C) with a central colour similar to that of a typical UV bull's eye, as in *Mimulus guttatus* (Osche 1983; Fig. 5D–F). The entirely yellow and UV-absorbing flowers like *Narcissus pseudonarcissus* display a bee-visible colour pattern and stamen mimicry due to a blue bull's eye (Lunau & Verhoeven 2017; Fig. 5G–I). Colour changes in anther mimics, for example in *Myosotis arvensis*, highlight the rewarding phase of flowering (Lunau 1996a; Fig. 5J–L). Moreover, also UV-absorbing human-green colours as in the anther mimic of *Hardenbergia comptonia* result in the same bee-green colour as UV-absorbing human-yellow colours (Lunau *et al.* 2021; Fig. 5M–O). Inflorescences like those of sunflowers can display similar colours and UV patterns (Lunau 1992a; Fig. 5P–R) as single flowers.

Simulating pollen and stamens is only one of several functions of PASAM structures. Other functions include guiding pollinators to a place for landing on a flower (Lunau 1996b), guiding pollinators to distinct locations after landing on a flower (Dinkel & Lunau 2001) including nectar holders, distracting pollinators from real stamens (Lunau 2007), increasing the visual similarity between flower morphs and flowering phases (Pohl *et al.* 2008), and facilitating contact with pollen and stigmas through physical manipulation of the pollinators' position, as in *Tritonia securigera* (Fig. 7E; Newman *et al.* 2022). A double function as signal and mechanical fit to pollinating bees has been shown for the staminode of *Jacaranda rugosa* (de Souza Pontes *et al.* 2022). Among zygomorphic flowers, the anther and stamen mimics are mostly displayed in the upper part of the flower in the case of sternotribic pollination (e.g. *Rhododendron* sp.; Fig. 2B–D), whereas the anther and stamen mimics are mostly displayed in the lower part of the flowers in the case of nototribic pollination (e.g. *Iris germanica*; Fig. 4H), indicating the importance of guiding the flower visitors to a distinct landing place on the flowers.

PASAM AS A MULTI-FACETTED PHENOMENON AND BEYOND

Common signals among diverse structures

The enormous diversity of PASAM should not trick researchers into the misinterpretation of all the floral colour patterns displayed by flowers pollinated by pollen-eating and pollen-collecting pollinators. The yellow and UV-absorbing colour is a reliable, but not a sufficient criterion to identify PASAM. A deviant colour is also not a criterion to exclude PASAM. Shape, size and context of structures are helpful to describe hypothetical PASAM, as will be illustrated in the following using known, new as well as converse examples.

Pollen, anther, stamen and androecium mimicking structures may comprise simple colour patches, as on the lower lip of *Euphrasia rostkoviana* (Lunau 2000; Fig. 6A), semi-plastic (half relief) structures, as the protuberances in the upper tube of *Cuphea* sp. (unpublished; Fig. 6B), and full plastic (life-like) stamen mimicking structures, as the flowers of *Bougainvillea spectabilis* combined with bracts simulating petals (Lunau 2007; Fig. 6C). Closely related flowers of the genus *Iris* also present stamen mimicking structures on the hanging perigone leaf of each meranthium, such as simple yellow and UV-absorbing colour spots, hairy colour patches, ridges, crests and beards consisting of numerous protuberances (Osche 1979; Fig. 6D–I). Given the diversity of the yellow UV-absorbing homologous structures on the perigone leaves of congeneric irises, it seems difficult to classify them into different kinds, i.e. it is hard to define these structures either as pollen mimic, anther mimic, stamen mimic, or androecium mimic in different species. The fact that irises offer nectar and deposit small amounts of pollen onto the back of visiting bees poses another difficulty in classifying these structures as nectar guides or stamen mimics. By contrast, the papilionaceous flowers of Fabaceae and Polygalaceae often display anther mimicking structures on different parts of the flowers, including the standard, the wings, as well as yellow and UV-absorbing colour patches on other parts of the flowers seemingly for similar functions (Lunau *et al.* 2021; unpublished; Fig. 6J–Q).

Floral colour patterns might also display other mimicry structures, such as pollinators in sexually deceptive flowers (Streinzer

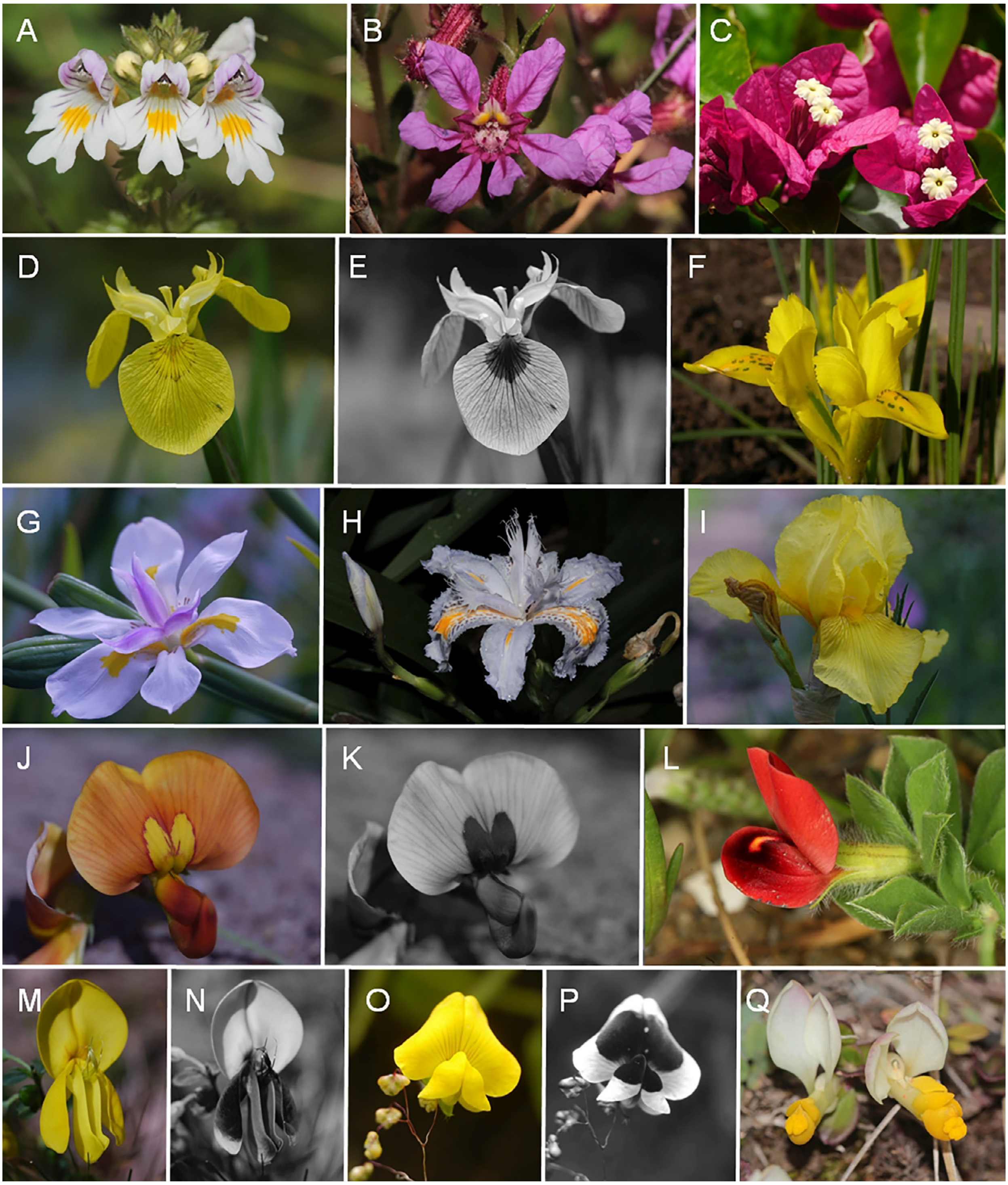

Fig. 6. Diversity of PASAM. Morphological differences among PASAM comprise simple colour patches as in *Euphrasia rostkoviana* (A), semi-plastic structures as the protuberances in the upper tube of *Cuphea* sp. (B) and 3D structures as the flowers of *Bougainvillea spectabilis* (C). The *Iris* flowers with three meranthia often display different stamen mimicking structures on the hanging tepal as simple yellow and UV-absorbing colour patch in *Iris pseudacorus* (D, E), a ridge in *I. danfordiae* (F), a hairy structure in *I. grandiflora* (G), a crested structure in *I. japonica* (H) and a beard in *I. germanica* (I). The papilionaceous flowers display yellow and UV-absorbing anther mimicking structures on different parts of the flowers including the standard in *Colutea orientalis* (J, K), the wings in *Lotus purpureus* (L), wings in *Cytisus scoparius* (M, N), wings and standard in *Scorpiurus vermiculatus* (O, P) and the tip of one petal in *Polygala chamaebuxus* (Q). Black and white photos correspond to UV photos (E, K, N and P).

et al. 2009; Stejskal *et al.* 2015), galls, as in the wild carrot (Polte & Reinhold 2012), glossy nectar (Lunau *et al.* 2021), and aphids, for example for attraction of aphidophagous hoverflies (Cardoso *et al.* 2023), or not involve mimicry (Glover *et al.* 2013). Meaningful investigations of floral guides and colour patterns can omit the mimicry aspect (Leonard & Papaj 2011; Hempel de Ibarra *et al.* 2015, 2022; Richter *et al.* 2023).

Floral guides can also have different functions despite a superficial similarity to PASAM. The beard of the petal tip in *Polygala myrtifola* looks like an androecium-mimicking structure (Fig. 7A) but has been shown to function as a device to open the flowers through the abdomen of *Xylocopa* bees pressing the beard downwards (De Kock *et al.* 2018). The yellow UV-absorbing and translucent window of the two-spurred *Diascia* flowers is thought to serve as an orientation cue for oil-collecting bees (Steiner 1990; Fig. 7B). The so-called beetle marks in some beetle pollinated *Moraea* flowers are often yellow in colour, but seemingly mimic scarab beetles that meet on the flowers and are the main pollinators (Goldblatt *et al.* 2005; Fig. 7C). Large-sized *Aristolochia* trap flowers display a yellow colour patch of unknown role beyond the size of anthers to attract phorid flies (Hipólito *et al.* 2012; Fig. 7D). By displaying salient floral guides, the attention of pollinators can be distracted from differences in reward among conspecific flowers caused by dichogamy, dicliny, heterostyly and emptied pollen resources (Essenberg 2021).

Diclinous flowers

In many plants bearing diclinous flowers, the stigma of the pistillate flowers mimics the stamen of the staminate flowers. In this mimicry system, stamens are the model and stigmas of conspecific flowers are the mimics (Dafni 1984; Dukas 1987; Willson & Ågren 1989; de Avila *et al.* 2017; Russell *et al.* 2020). Nectarless *Begonia* flowers represent a well-known example (Osche 1979; Schemske & Agren 1995; Russell *et al.* 2021; Fig. 2H). In the Cucurbitaceae, the stamens are fused to a column and appear similar to the ring-shaped stigmas of the style, for example in *Bryonia dioica* (Rust *et al.* 2003; unpublished; Fig. 7P). In this case, if both pistillate and staminate flowers offer a reward to floral visitors and the morphology of the stamens is atypical, it is hard to tell which one is the model in a floral mimicry system, given the strong intersexual similarity between them.

Heterostylous flowers

In heterostylous flowers, camouflaged real stamens combined with the display of stamen mimics provide a more uniform signal, since conspicuous real stamens would support the flower visitors' ability to discriminate among the morphs and develop preferences (Barrett 1990; Cawoy *et al.* 2006). Morph preferences by flower visitors would significantly reduce reproductive success, since heterostylous plants require the transfer of pollen between different morphs (Ganders 1979). In this case, there is no specific model, and the similarity of morphs is improved by similar stamen mimicking floral guides that override differences between the morphs caused by stamen length, spatial position of anthers, pollen size and/or amount of pollen (Wolfe & Barrett 1987; Husband & Barret 1992; Alves Dos Santos & Wittmann 2000; Pohl *et al.* 2008). Examples of anther mimicry in heterostylous flowers are the tristylous *Pontederia cordata* and *Eichhornia crassipes* (Lunau 2000, 2007). In the distylous *Primula elatior* and *Primula veris* it has been shown that pin flowers often display anther-mimicking floral guides located where thrum flowers display their real anthers (Fig. 3; Lunau 1996b). In the tristylous *Lythrum salicaria* the signalling uniformity is achieved in a different manner involving similar signals, but not mimicry (Fig. 3P–R). In this case, the three floral morphs each have three levels of anthers and stigma (short, middle, and tall), either occupied by the camouflaged stigma or by pollen-bearing anthers. The short and middle stamens display yellow pollen, whereas the long stamens display camouflaged green pollen. In this way, all three morphs display a conspicuous yellow UV-absorbing signal at the centre of the flower (Fig. 3P–R).

Dichogamous flowers

Similarly, in dichogamous flowers the display of stamen mimics provides a more uniform signal, as compared to the display of real stamens, and this impedes the flower visitors' discrimination between the flowering phase with anthers full of pollen and that with emptied anthers. Preference for a distinct flowering phase would significantly reduce reproductive success. In this case, there is also no specific model, and the similarity of flowering phases is improved by similar anther mimicking floral guides to override differences between the morphs caused by pollen availability (Pohl *et al.* 2008). *Saxifraga* flowers often display yellow and UV-absorbing colour patches on the petals in both flowering phases, in combination with camouflaged and unattractive stamens. However, some *Saxifraga* species, e.g. *Saxifraga rotundifolia* (Fig. 7E) and *Saxifraga signata* (Lunau *et al.* 2020; Fig. 7Q,R), possess complex floral guides, in which it is not evident which part represents an anther mimic. In *Saxifraga rotundifolia*, the multiple red, orange and yellow dots guide pollen-seeking flies towards the centre of the flower, as revealed by experimental simulation of the dot guides, and prolong the handling time on the flowers (Dinkel & Lunau 2001). In the framework of PASAM, the yellow dots are better anther mimics than the red dots, but such differentiation is hard to make due to their function to guide the flower visitors from less to more attractive floral dot guides. The two small protuberances on each petal of *Saxifraga signata* (Fig. 7Q,R) look like anther mimics but have been described as nectar-mimicking structures because of their glossy surface (Lunau *et al.* 2020). The green and glossy floral guides of *Solanum dulcamara* (Fig. 7G; Lunau *et al.* 2020), the glossy yellow staminodes of *Parnassia palustris* (Daumann 1960; Fig. 2E), and the glossy marks on the two upper petals of *Erodium cicutarium* (Aldasoro *et al.* 2000; Fig. 7H) are candidates for a double function as both nectar- and pollen-mimicking structures.

Flowers with hidden stamens

In many flowers that hide stamens within the corolla (Xiong *et al.* 2019), the visual signalling function of the stamens is replaced by stamen mimics. Stamen mimicry improves the manipulation of the flower visitors' movements at and on the flowers (Lunau 2007). Typical examples are Fabaceae flowers, which display yellow -and UV-absorbing floral guides either on the standard, e.g. *Colutea arborescens* (Lunau 2000; Fig. 6J,K)

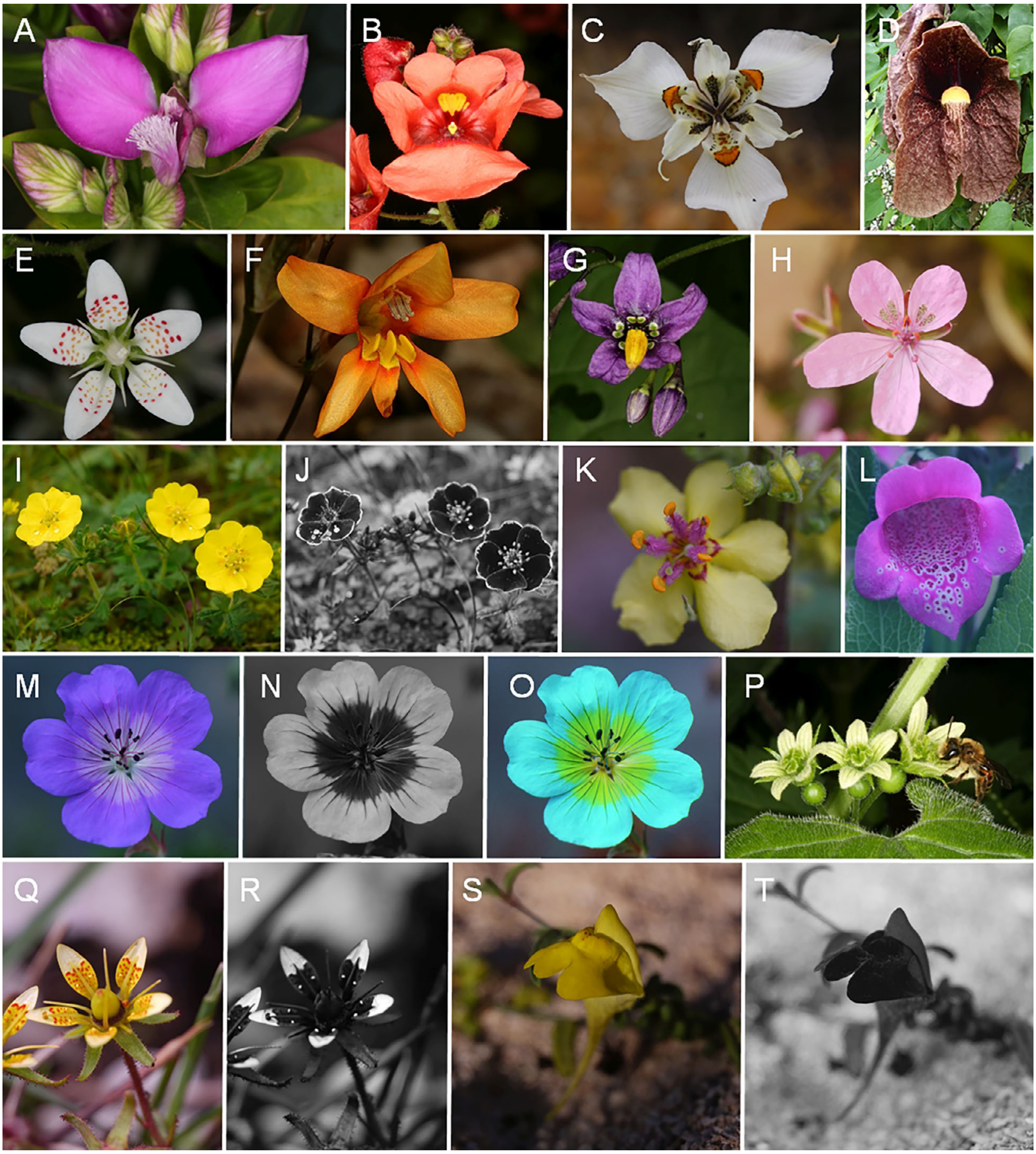

Fig. 7. Critical cases of PASAM. *Polygala myrtifolia* (A); *Diascia* sp. (B); *Moraea cantharophila* (C); *Aristolochia gigantea* (D); *Saxifraga rotundifolia* (E); *Tritonia securigera* (F); *Solanum dulcamara* (G); *Erodium cicutarium* (H); *Potentilla* sp. colour photo (I) and UV photo (J); *Verbascum nigrum* (K); *Digitalis purpurea* (L); *Geranium* sp. colour photo (M), UV photo (N) and false colour photo (O); *Bryonia dioica* (P); *Saxifraga signata* colour photo (Q) and UV photo (R); *Kickxia sagittata* colour photo (S) and UV photo (T).

or on the wings, e.g. *Lotus purpureus* (unpublished; Fig. 6L). Some Fabaceae flowers possess yellow UV-absorbing parts that do not share the form and dimension of anthers, for example, *Cytisus scoparius* and *Scorpiurus vermiculatus*, but share the same guiding function as anther mimics (unpublished; Fig. 6M–P). The gullet flower of *Kickxia sagittata* (Lunau *et al.* 2017; Fig. 7S,T) possesses the typical semi-plastic mask as *Linaria* flowers (Fig. 4D), but without any visual colour pattern, which diminishes a visual function as a floral guide.

Heterantherous flowers

Many flowers that visually display stamens and pollen also display stamen and pollen mimics, enhancing the yellow and

UV-absorbing signalling area or displaying a yellow and UV-absorbing signalling area independent of the presence of pollen (Brito *et al*. 2021). In heterantherous flowers, cryptic or inconspicuous stamens function as pollination stamens, whereas conspicuous pollen-bearing stamens function as attractants and feeding stamens (Müller 1881; Nepi *et al*. 2003; Veena & Nampy 2020) in the context of division of labour of anthers (Papaj *et al*. 2017). In buzz-pollinated flowers with poricidal anthers, pollen cannot provide any signal, but the anthers do (Vallejo-Marin & Russell 2023). The conspicuous appendages of the feeding stamens in heterantherous Melastomataceae flowers represent an example of the signalling feeding stamens as opposed to the cryptic pollination stamens (Melo *et al*. 2022). General visual cues of pollen and stamen signals serve as models in this mimicry system (Lunau & Wester 2017; Velloso *et al*. 2018). *Potentilla* (Fig. 7I,J) and *Ranunculus* (Lunau 2000; Fig. 3E,F) flowers are typical examples displaying a yellow and UV-absorbing androecium and a central yellow and UV-absorbing colour patch, increasing the perceived signal irrespective of the number of open anthers. The yellow and UV-absorbing signalling area also protects the presented pollen against direct UV radiation (Jansen *et al*. 1998; Zhang *et al*. 2015; Peach *et al*. 2020) and UV radiation reflected from the petals towards the anthers (Koski & Ashman 2016). It is well known that the size of the yellow and UV-absorbing signalling area increases with altitude and latitude (Koski & Ashman 2015a,b). In some species, for example in *Caltha palustris*, *Saxifraga aristulata* and some *Potentilla* spp. (unpublished; Fig. 7I,J), the size of the yellow and UV-absorbing area can cover almost the entire petal; in this way, the function of a floral guide is decreased.

Level of scrutiny

Most PASAM lack evidence from observations in the field in terms of if and how the flower visitors respond to the pollen, anther, stamen, and androecium mimicking structures. Indeed, many examples of PASAM have been described only because of the yellow colour and shape of a floral guide or floral organ. UV photos and false colour photos in bee view can provide additional evidence that the relevant structure absorbs UV light, displaying a similar colour as UV-absorbing pollen and anthers. For example, in *Hardenbergia comptonia* the anther mimicking colour patch on the standard is not yellow rather than green, but the false colour photos in bee view indicate that this colour is bee-subjective green as are most pollen and anther mimics (Fig. 5M–O). Moreover, in *Hardenbergia comptonia* the colour patch is framed by a contrasting white UV-absorbing colour which might help to direct the pollinators' attention to the anther mimic. This kind of framing has been described for several anther mimics (Lunau *et al*. 2021).

There are few cases in which anther mimicking structures have been described as displaying a colour other than UV-absorbing yellow. The deep violet dots on the lower lip of *Digitalis purpurea* flowers are human-purple and bee-green (resulting from the absorption of ultraviolet and green light and reflection of blue and red light). In a comparative study, Osche (1983) showed that *Digitalis lutea* (Fig. 3H) displays real anthers at the tube entrance and concluded that the violet spots in *Digitalis purpurea* flowers (Fig. 7L) similarly replace the displayed anthers. Moreover, the yellow and UV-absorbing filament hairs in many *Verbascum* species are replaced by violet filament hairs in *Verbascum nigrum* (Lunau 2022; Fig. 7K). UV-absorbing yellow is the dominant colour among pollen and anthers of bee-pollinated flowering plants; however, some flowers display pollen and anthers of another colour, which could also represent models for mimicry. Furthermore, the yellow and UV-absorbing hue has been described as a key feature for close-range orientation at flowers only in naïve *Eristalis* hoverflies (An *et al*. 2018), whereas bees, including naïve bumblebees and honeybees, use the higher saturation of the colour of pollen and anthers as a key feature for close-range orientation at flowers; consequently, in bee-pollinated flowers, the mimic signal must not necessarily copy the model colour hue but merely its superior bee-subjective saturation (Lunau *et al*. 1996). Thus, other colour combinations of floral colour patches like that of *Geranium* sp. (unpublished; Fig. 7M–O) might function as a floral guide to direct bees towards the centre of the flower by exploiting the same preference for saturated colours that is relevant to trigger the bees' response to anther mimicking structures.

THE PERVASIVENESS OF PASAM

Mimicry systems involve one (automimicry) to many species. Specifically, for the PASAM systems, the fact that most species of flowering plant present stamens with yellow and UV-absorbing anthers or/and yellow and UV-absorbing pollen, being potential models, made estimation of the occurrence of PASAM more complex. Most recent studies indicate PASAM as an exceptional speciose hypothetical mimicry system including many flowering plants displaying conspicuous yellow and UV-absorbing pollen and anthers or mimics besides the signal-receiving flower visitors (Lunau *et al*. 2017). Using reflectance data and UV photos of species pollinated mainly by bees and hummingbirds, Camargo *et al*. (2019) found around 38% of species presenting PASAM in the Neotropical *campo rupestre* in Brazil (40% of the bee-pollinated species and 20% of the hummingbird-pollinated species). It is estimated that up to one-third of the flowering plants in a given flora mimic visual and/or tactile signals of pollen, anthers, stamens, or androecia and interact with many pollen-eating and pollen-collecting flower visitors, such as flies and bees (Lunau 2000; Lunau *et al*. 2017; Lunau & Wester 2017). However, most of the categorization into PASAM signals is accomplished according to the structure and colour pattern of flowers and inflorescences, often without evidence from pollinator behaviour or UV reflection. The proportion of flowering plant species exhibiting one of the various types of PASAM structure ranges from 12% in the tropical flora of Barro Colorado Island in Panama, over 24% in the Mediterranean flora of Crete, 25% in the Yulong Snow Mountains of Yunnan, 28% in the flora of the Alps, 30% in the temperate flora of Germany to 32% in Namaqualand (Fig. 8).

Pollen, anther, stamen, and androecium mimicking structures are present in all continents and floristic regions, as easily demonstrated by the worldwide distribution of bladderworts, genus *Utricularia*, with *U. purpurea* in North America, *U. longifolia* in South America, *U. striatula* and *U. bisquamata* in Africa, *U. walburgii* in Asia, *U. uniflora* in Australia and *U. vulgaris* in Europe, which all display a yellow contrasting colour mark on the lower lip of the gullet blossom (WCSP 2021).

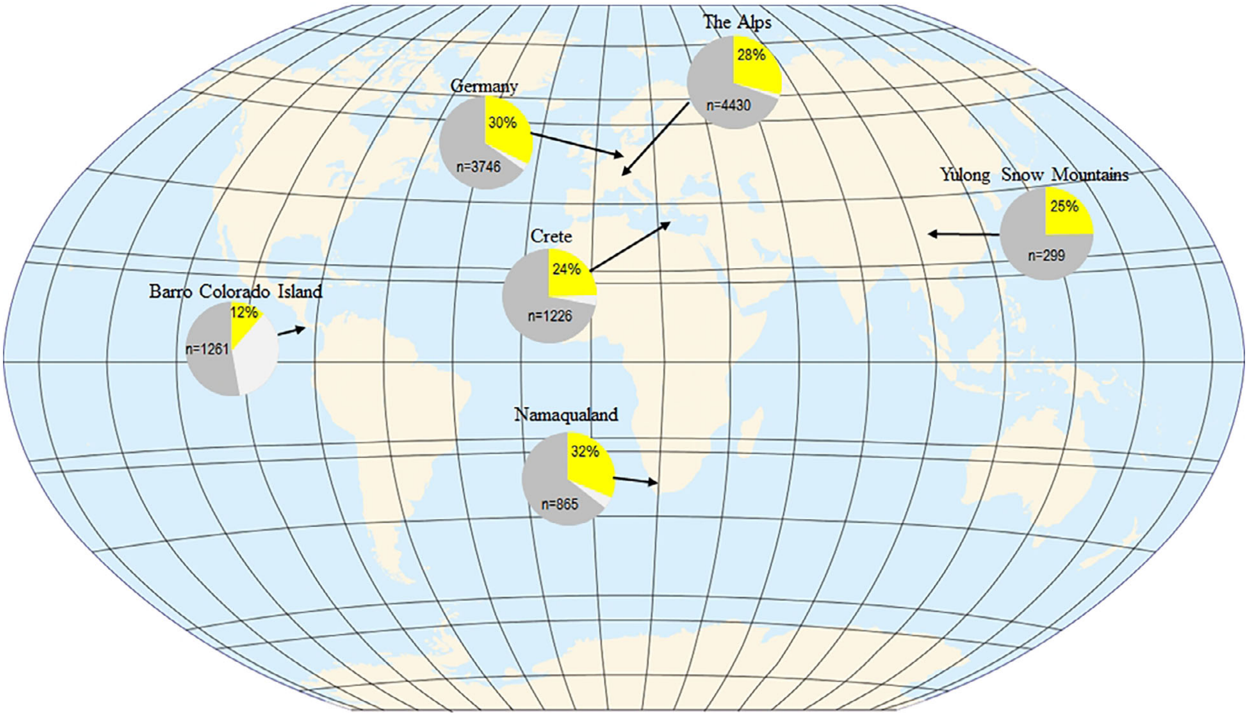

Fig. 8. Frequency of PASAM structures on flowers and inflorescences (labelled yellow) on Barro Colorado Island, in the Serra do Cipo, Brazil, in Germany, on Crete, in the Alps (Lunau *et al*. 2017), in Namaqualand and on the Yulong Snow Mountains. Floral guides, florets of inflorescences, stigmas, 3D structures, staminodes, filamental hairs and other pollen, anther, or stamen-like structures were considered. Species without PASAM structures are labelled dark grey, species in which the presence or absence of pollen imitating structures was not verified are labelled light grey. World map from Wikimedia Commons: Thesevenseas. Unpublished data for Barro Colorado Island analysed from the homepage of the Smithsonian Tropical Research Institute (http://biogeodb.stri.si.edu/bioinformatics/croat/home) (Bedürftig & Lunau unpublished), Germany by Haeupler & Muer (2007) (Weineck & Lunau unpublished), Crete by Fielding & Turland (2005) (Butterwegge & Lunau unpublished) analysing, Namaqualand by Le Roux (2015) (Weber & Lunau unpublished), and Yulong Snow Mountains by an Illustrated Handbook of Common Flowering Plants in Lijiang Alpine Botanical Garden (2017) (Lunau & Ren unpublished).

Also, these structures are present in many phylogenetically unrelated plant families, suggesting that such structures have independently evolved multiple times during angiosperm evolutionary history.

CONCLUSIONS

The survey of pollen, anther, stamen and androecium mimicking signals of flowers and inflorescences shows that the response of pollen-eating and pollen-collecting floral visitors towards these signals has only been tested in a few naïve individuals of a few species of bees and hoverflies. Most cases of PASAM are described only based on similarity in shape, size and colour between pollen, anthers, stamens and androecia with other floral structures and, therefore, should be treated as hypothetical cases to be further tested.

What are the best criteria to identify a floral guide or a floral signalling structure as pollen, anther, stamen, or androecium mimicking signals? It has been exemplified that not all yellow and UV-absorbing floral guides represent pollen, anther, or stamen mimicking signals. Moreover, evidence is presented that other colours of floral guides than UV-absorbing yellow might represent pollen, anther or stamen mimicking signals. One reason for this is that bees and hoverflies might perceive green and UV-absorbing colours as similar compared to yellow and UV-absorbing colours. Another reason is that only some hoverflies are known to innately respond to the yellow and UV-absorbing hue (An *et al*. 2018), whereas bumblebees respond to the higher contrast and higher saturation of the floral signalling structure in question (Lunau *et al*. 1996).

Focusing on the evolution of pollen, anther, stamen and androecium mimicry, Osche (1979, 1983) discussed that visual cues of pollen and anthers represented the very first flower signal, being present in primarily wind-pollinated flowers, due to the protective yellow and UV-absorbing pigments. The improved protection of pollen against UV radiation and wastage through rain and flower-robbing visitors by concealment of stamens in the floral tube might have fostered the evolution of automimicry structures to complement and replace visual pollen signals. This strategy of sensory exploitation of flower visitors through pre-existing signals that already possess a role in the flower visitors' communication signals has been considered widespread among flowering plants, also through chemical signals (Schiestl 2010). Assuming sensory exploitation of an innate preference for pollen signals would also explain the finding that PASAM elicits not only responses in the context of pollen uptake but also any kind of attractive response. One particular aspect of sensory exploitation is that the signal receiver's response is dependent on context; for example, the display of food items on the feathers of argus and peacock pheasants, replacing the mediation of real food during courtship (Blut & Lunau 2015), no longer results in pecking at these signals by the hens but does affect mating decisions.

More research on the response of hoverflies and bees to pollen, anther, stamen or androecium mimicking signals in the field is needed to demonstrate the innate preference for these signals, as well as if and how fast and strong they can be overridden by experience. It is still an open question as to whether PASAM represents a signal mostly directed towards inexperienced flower visitors, or whether the learning of real pollen signals or PASAM signals also plays a role for experienced flower visitors when switching to new food sources. The predominant visual orientation towards PASAM signals is still enigmatic. Bees and hoverflies can taste pollen with their antennae and foreleg tarsi (Ruedenauer *et al.* 2015), and hoverflies can taste pollen with their tarsi and proboscis (Wacht *et al.* 1996, 2000; de Brito Sanchez *et al.* 2014; Ruedenauer *et al.* 2015). Bees can also perceive tactile stimuli via their antennae (Gack 1981). Proline is a common amino acid present in pollenkitt (Linskens & Schrauwen 1969; Mattioli *et al.* 2018) and thus a potential candidate for a universal chemical pollen cue that can be perceived with the antennae of bumblebees (Ruedenauer *et al.* 2019), honeybees (Carter *et al.* 2006; Nicholls *et al.* 2019) and tarsi as well as proboscis of *Eristalis* hoverflies (Wacht *et al.* 1996, 2000). However, proline has never been found in pollen-mimicking structures (Biancucci *et al.* 2015), reinforcing that the visual cue is predominant in the PASAM system as compared to any other chemical cue. In fact, the buzzing behaviour in bumblebees, as shown by flower-naïve individuals (King 1993), can be modified by tactile and chemical cues (Russell *et al.* 2017), but also elicited by an artificial anther reward with chemically inert glass powder (Lunau *et al.* 2015).

Remote sensing of pollen odour plays a role in learned discrimination of pollen types and host plants (Dobson *et al.* 1999; Dobson & Bergström 2000), but pollen odour seems to vary significantly among plants (Dobson *et al.* 1996), preventing innate responses as a consistent cue. It also remains to be studied why pollen, anther, stamen or androecium mimicking signals can direct flower visitors not only to pollen but also to nectar sources (Westerkamp 1996). The staminodes of *Parnassia palustris* have been described as false nectaries and as stamen mimics (Daumann 1960; Lunau 2007); indicating that they can fulfil one of these signalling functions or even both at the same time.

Considering its complexity and the necessity for deep investigation, it is difficult to fit PASAM among the traditional true mimicry cases described in the literature. However, the proportion of species displaying PASAM structures in plant communities from different continents indicates that PASAM is part of a worldwide communication system of bee- and hoverfly-pollinated flowers with their pollinators. Based on this original information, together with actual knowledge about pollen-eating and pollen-collecting bees' and flies' responses to PASAM, we provide support here that PASAM constitutes the world's most speciose mimicry system. The yellow UV-absorbing colour is probably one of the most recurrent visual signals in nature and an example of flower signal standardization which can be observed around the world among many angiosperm species. We here provide the first evidence that PASAM is a worldwide visual signalling strategy to attract, lure, guide, distract, and deceive pollen-eating and pollen-collecting pollinators. From a historical perspective, PASAM was derived from an original pollen signal and functioned to deceive naïve pollen-eating and -collecting flower visitors about the presence, amount and/or location of pollen. The role of a super signal for attraction and guidance of any kind of resource, not only pollen, might be associated with the function of PASAM structures as general floral guides that even experienced pollinators use to find any kind of floral resource.

AUTHOR CONTRIBUTIONS

Klaus Lunau conceived the ideas; all authors wrote the manuscript and contributed critically to the drafts.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Glossary of terms to interpret floral colour patterns.

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