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REVIEW

An overview of the pollination interactions between the ginger family (Zingiberaceae) and insects in Asia

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Abstract. The plant-biotic pollinator interaction is crucial for the survival of both organisms. Insects are recognised as effective biotic pollinators. As there are few specific studies on the pollination of angiosperms, the emphasis of this review is on understanding the pollination process by reviewing the knowledge of the ginger-insect pollinator interaction in Asia. Currently the plant-pollinator interaction of only 5% of Asian species of Zingiberaceae is evaluated. Previous studies indicate that bees, such as, halictid and blue-banded bees are, among the many floral vistors, the most important pollinators of ginger plants in Asia. Knowledge of non-bee pollinators is still scarce. In order to obtain a more detailed understanding of the interrelationship of the pollinators of ginger plants with the morphology of their flowers, floral scent and geographical factors, further research is needed.

INTRODUCTION

Pollination is one of the major interactions that occur between animals and plants in which plants generate new generations while the animals obtain food and other secondary rewards (Simpson & Neff, 1981; Tandon et al., 2016) and is referred to as the plant-pollinator interaction (Nicolson & Wright, 2017). Currently, there are more than a hundred thousand articles on this topic recorded over the last ten years in Science Direct, JSTOR and Google Scholar associated with the keywords plant-animal interactions, pollination and plant-pollinator. In fact, most of these studies are on the factors that influence the interaction rather than on pollinators and floral visitors of a specific species of plant (Field et al., 2012; Brothers & Atwell, 2014; Ling et al., 2020; Phillips et al., 2020). Thus, there are numerous unreported pollinators of angiosperms and new species are continuously being reported for ginger plants.

Keywords used to find articles on ginger plants (Zingiberaceae), e.g. Zingiberaceae-pollinator interaction, ginger and pollinators, and Zingiberaceae and pollinators, only found one to 6000 articles in the above-mentioned academic websites. The online searches indicate that there are very few plant-animal interaction studies focusing exclusively on Zingiberaceae. Therefore, for a better understanding this review focuses on the Zingiberaceae-pollinator interaction in Asian Zingiberaceae. In addition, important fundamental aspects of the plant-biotic pollinator interactions are also presented in order to have a better general understanding of the plant-pollinator interaction.

The plant-pollinator interaction is poorly recorded for Zingiberaceae (common name: gingers), which are better known as a herbal plant and source of food of great medicinal value (Mekuriya & Mekibib, 2018; Zahara et al., 2018). There are approximately 1600 species of ginger in 50 genera in the world (Larsen et al., 1999; Xu & Chang, 2017). Around 1000 species of ginger occur in Asia, especially in the Malaysian region (Larsen et al., 1999). Gingers are perennial flowering herbaceous plants ranging in height from less than 10 cm to 8 m. There are around 20 species that are cultivated for domestic use, such as, *Elettaria cardamomum* (L.) Maton, *Etlingera elatior* (Jack) R.M.Sm. and *Zingiber officinale* Roscoe (Larsen et al., 1999), and most species occur in forests.

They can reproduce asexually by vegetative rhizome propagation and sexually by the transfer of pollen from male to female flowers (Criley, 1995; Binghong et al., 2018). Asexual reproduction commonly occurs naturally in ginger plants and is used to produce large quantities of ginger (Kaufman, 2016), as it is much easier and faster than by sexual reproduction (Campbell & Reece, 2008). However, sexual reproduction can be used to produced new generations of better quality plants, both physically and genetically (Pereira & Coimbra, 2020). *Zingiber neesanum* (J.Graham) Ramamoorthy, *Z. nimmonii* (J.Graham) Dalzell, *Z. spectabile* Griff. are a few examples of gingers produced sexually (Thomas et al., 2016; Rezende et al., 2021).

In general, the 100 million year old plant-pollinator interaction is currently under threat (Nicolson & Wright, 2017). Pesticides, changes in land-use, pathogens, invasive species and climate change threaten the interaction (Spira, 2001; Huang & Giray, 2012; Buchholz & Kowarik, 2019). Similarly, the ginger plants in forested areas are declining in abundance due to anthropogenic activities (Niissalo et al., 2017; Appalasamy et al., 2022). If the pollination of ginger plants is dependent on specific organisms then they are vulnerable to pollinator loss (Spira, 2001). Thus, it is important to understand the processes involved in the plant-pollinator interaction of gingers in order to ensure the conservation of these plants and prevent the extinction of these species in their native habitats.

FLOWER OF ZINGIBERACEAE

Species of Zingiberaceae are distinguishable in the wild by their inflorescences that are morphologically different, with bright flowers located on different parts of the plants. For instance, either on a terminal leafy shoot (e.g. *Alpinia galanga* (L.) Wild., *Globba pendula* Roxb.), terminally on erect stems (e.g. *Plagiostachys albiflora* Ridl.), on the ground (e.g. *Etlingera punicea* (Roxb.) R.M.Sm., *Wurfbainia uliginosa* (J.Koenig) Giseke) or a peduncle (e.g. *Etlingera maingayi* (Baker) R.M.Sm., *Zingiber spectabile*) (Larsen et al., 1999; Appalasamy et al., 2022). In addition, their inflorenscences last for different periods time, for example, those of *Etlingera elatior* for around 24 days (Choon & Ding, 2016) and *Zingiber spectabile* for about two months (Rezende et al., 2021).

Most species of Zingiberaceae have striking flowers with various patterns and range from tiny (e.g. *Globba*) to fairly large (e.g. *Alpinia*) (Larsen et al., 1999; Izlamira et al., 2020). The flowers are hermaphrodite in that each flower contains both male (stamen) and female (pistil) reproductive organs (Fig. 1). According to Larsen et al. (1999), the flowers have a single stamen (male organ) rather than many stamens like flowers of hibiscus and jasmine (Struwe, 2016). In contrast, to the general form the flowers of *Sulettaria polycarpa* (K.Schum.) A.D.Poulsen & M.F.Newman are andromonoecious in which hermaphrodite and staminate (male) flowers are present in the same or different inflorescences of an individual plant (Sakai et al., 1999). However, the male flowers produce nectar and

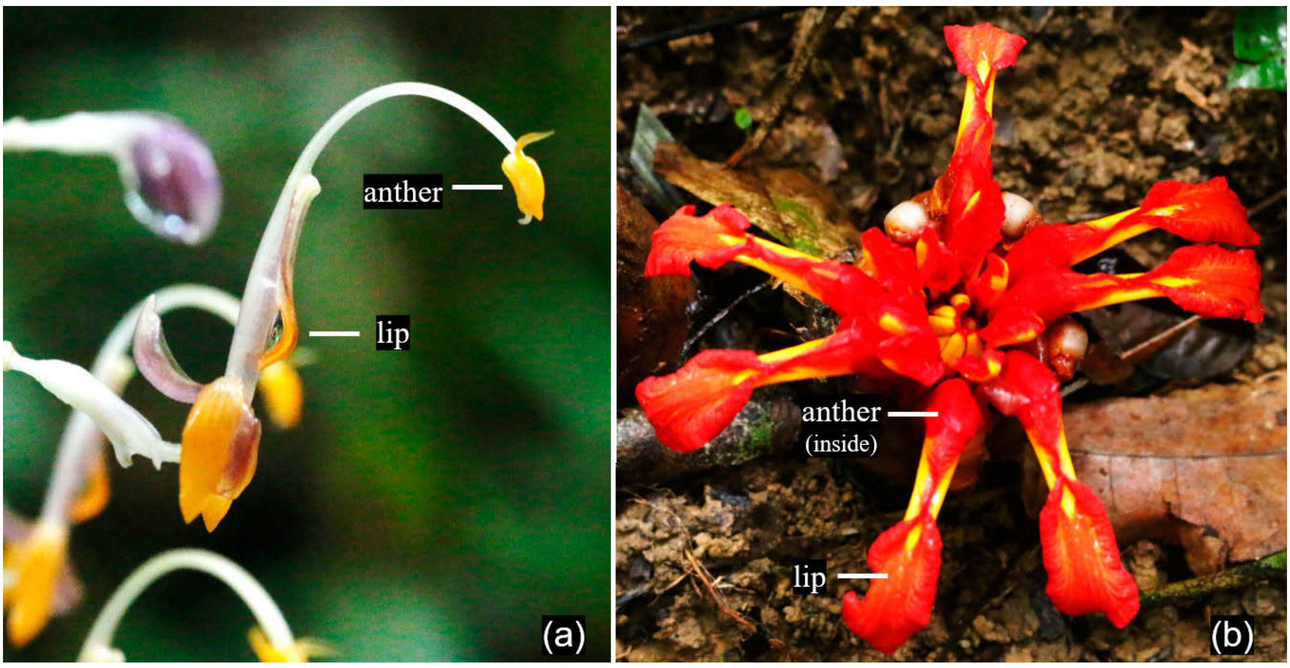

Fig. 1. Location of anther in flowers of ginger (Zingiberaceae). (a) *Globba leucantha* Miq.; (b) *Etlingera punicea* (Roxb.) R.M.Sm.

similar amounts of pollen as hermaphrodite flowers for attracting pollinators (Sakai & Nagamasu, 1998).

The single flower of most ginger species, such as *Alpinia kwangsiensis* T.L.Wu & S.J.Chen, *Globba schomburgkii* Hook.f. and *Roscoea humeana* Balf.f. & W.W.Sm. has a lifespan of one or less than one day (Li et al., 2001; Zhang et al., 2003; Aswani et al., 2013; Melati et al., 2015; Aswani & Sabu, 2018). The flower of *Boesenbergia longiflora* (Wall.) Kuntze from China, however, has a two-day flowering period, which enables it to avoid self-pollination (Gao et al., 2004). Flowering period (anthesis) of gingers usually lasts from morning to noon and varies between species. There are, however, exceptions, in the occurrence of anthesis, for instance, the flower bud of *Alpinia nieuwenhuizii* Valeton starts to opens at 16.00 h and is fully open at 03:00 h and releases pollen approximately from 13:00 to 14:00 h on the next day (Takano et al., 2005). Therefore, it is concluded that species of ginger differ in lifespan and anthesis. Further studies on the phenology of flowering of more species of Zingiberaceae from around the world are needed for a comprehensive overview of the patterns in their flowering.

Male anthers contain pollen grains for sexual reproduction as shown in the Fig. 1 and are either exposed as in *Globba leucantha* Miq. (Fig. 1a) or hidden as in *Etlingera punicea* (Fig. 1b) and adapted for pollination by particular organisms (unpubl. data). The pollen grains vary in size and shape among species (Saensouk et al., 2015; Moonkaew et al., 2020) and can be used to identify species within a genus, such as *Curcuma* (Saensouk et al., 2015). Pollen grains of *Curcuma* spp. range from 50.5 ± 3.4 µm to 86.9 ± 7.9 µm and are differently shaped, such as, prolate, prolate spheroidal, spheroidal, subprolate and subspheroidal (Saensouk et al., 2015). Variation in shape within a genus is also recorded in *Globba*, where in *G. fecunda* A. Takano & H. Okada and *G. atrosanguinea* Teijsm. & Binn they are oblate whereas those of *G. variabilis* Ridl., *G. hasseltii* Boerl. are spheroidal (Syamsuardi et al., 2010). In general, the pollen shapes are correlated with the type of pollinator in tape grasses (Hydrocharitaceae), fig trees (Moraceae) and naiads (Najadaceae) (Tanaka et al., 2004; Wang et al., 2014). There is, however, little information on the pollen of Zingiberaceae, so there is a need for palynological studies on this family in order to better understand their ecology.

PLANT-POLLINATOR INTERACTIONS IN GENERAL

The basis of the plant-pollinator interaction is the successful pollination of a plant with the help of one or more pollinators while the pollinator(s) receives a reward such as nectar, oil, resins or pollen from the plant (Jones & Jones, 2001). This mutual relationship benefits both organisms.

Pollination occurs naturally aided by animals, water and wind or assisted by a humans. Biotic pollinators play a very important role in ensuring successful pollination (Klein et al., 2003; Chautá-Mellizo et al., 2012; Diego et al., 2021; Ollerton, 2021). Pollination by insects is more common than by other means, for example, kiwifruits and strawberries produce more fruit when pollinated by insects compared to self-pollination or mechanical pollination (Abrol et al., 2019; Sáez et al., 2019). Insects are a dominant group of organisms with the number of species in the world estimated to be five million (Johnson & Triplehorn, 2005; Stork, 2018). Insects are invertebrates with a hard exoskeleton and are easily recognisable in having three body parts (head, thorax, and abdomen) and three pairs of legs, and consume a variety of different foods from plants to other insects and blood of vertebrates (Johnson & Triplehorn, 2005).

There are approximately 350,000 species of vertebrates and invertebrates that are recorded pollinating angiosperms (Ollerton, 2017), but, nevertheless, for many angiosperms in the world the identification of their pollinator and plant-pollinator interactions are unknown (Keys et al., 1995). Examples of previously identified pollinators are bees (e.g. *Apis* spp.), butterflies (e.g. *Leptidea synapis* (Linnaeus)), moths (e.g. *Hadena rivulari* (Fabricius)), beetles (e.g. *Mylabris* sp.), wasps (e.g. *Ceratosolen kaironkensis*), hoverflies (e.g. *Episyrphus balteatus* (De Geer)), sunbirds (e.g. *Nectarinia zeylonica* (Linnaeus)), bats (e.g. *Eonycteris spelaea* (Dobson)), mice (e.g. *Rhabdomys pumilio* (Sparrman)) and lizards (e.g. *Podarcis lilfordi* (Günther)) (Reddi & Bai, 1984; Schemske & Horvitz, 1984; Pettersson, 1991; Weiblen, 2002; Olesen & Valido, 2003; Aswani et al., 2013; Melidonis & Peter, 2015; Pattemore, 2017; Paudel et al., 2017; Doyle et al., 2020; Baqi et al., 2022). Among these, the insects are the most successful pollinators of angiosperms. Honey bees, for instance, are well documented as very efficient pollinators, especially of global crops (Pattemore, 2017). Rader et al. (2016) stress that non-bee insects also play a significant role in global crop pollination.

Entomologists currently group pollinators together, in terms of the group of animals involved, pollination guild or pollination syndrome (Kato et al., 1993; Sakai et al., 1999; Fenster et al., 2004; Solomon Raju et al., 2014). Firstly, the groups of animals involved in pollination are listed in Table 1, with the name for each group ending with suffix '-phily' that referes to a liking for a particular animal (Dictionary.com, 2023). As an example, entomophily, is the combination of the word 'entomology' and suffix '-phily' defines insect pollination. Chiropterophily (bat pollination), mellitophily (bee pollination), ornithophily (bird pollination) and zoophily (vertebrate pollination), etc. Defining pollination in terms of the pollinating agents makes it easier for the general public to understand.

There are designated functional groups or pollination guilds for similar types of pollinators such as the *Amegilla* guild, halictid guild, medium traplining bee guild and syrphid fly guild (Pettersson, 1991; Kato et al., 1993; Sakai et al., 1999; Fenster et al., 2004). These terms are more specific in referring to a distinct group of animals. Finally, pollination syndrome also contributes to the partitioning of pollinators (Wolf & Sowell, 2006). The term pollination syndrome refers to the the characteristics of flowers (traits), which include rewards for the pollinating agent

Table 1. General terms used to define pollination by various pollinating agents.

Group	Pollination by
Cantharophily	beetles
Chiropterophily	bats
Melittophily	bees
Myophily	flies
Ornithophily	birds
Phalaenophily	moths
Psychophily	butterflies
Sphecophily	wasps
Entomophily	insects
Zoophily	vertebrates

(Fenster et al., 2004). For example, "bee" syndrome refers to the flower characteristics that attract bees, which are a zygomorphic structure, bright yellow or blue colour, and nectar and pollen rewards (Hingston & Mc Quillan, 2000).

Furthermore, the success of the plant-pollinator relationship is measured in terms of pollination efficiency (Liu et al., 2020). The effectiveness is quantified in terms of single-visit pollen deposition rate, visitation rate, pollen tube growth, or fruit production per visit (Keys et al., 1995; Eeraerts et al., 2019; Liu et al., 2020). Stavert et al. (2020) stress that pollen tube growth is the most suitable parameter for determining pollinator performance and efficiency and is the most accurate when based on multiple rather than a single pollinator visit.

FLORAL VISITORS VERSUS POLLINATORS

Pollinator is a commonly used term in studies on plant-pollinator interactions, which generates the perception that flowers are only being visited by pollinators and non-pollinators being neglected. In fact, pollinators make up only a part of the floral visitors recorded in studies focused solely on pollinators. With this in mind, floral visitors should be grouped into non-pollinating and pollinating floral visitors, with the general term floral visitors including all the animals visiting a flower.

Floral visitors include any animal that visits flowers, such as, birds, mammals, insects, arachnids, rodents and reptiles (Schemske & Horvitz, 1984; Olesen & Valido, 2003; de Merxem et al., 2009; Melidonis & Peter, 2015; Alves-dos-Santos et al., 2016; Pattemore, 2017; Su et al., 2020). Among the floral visitors there are pollinators, which is based on observing their behaviour (Inouye, 2007; Kamaruddin & Zalipah, 2020). The visitors that do not carry any pollen are not considered to be pollinators, but foragers seeking food (pollen, nectar) (Fumero-Cabán & Meléndez-Ackerman, 2007). In addition, the floral visitors foraging for food are generally referred to as robbers or thieves by pollination ecologists (Zhang et al., 2013).

As flowering plants are visited by many animals during flowering, it is important to identify those that are pollinators. Bees, birds, butterflies and moths are well-known as pollinators thoughout the world (Rader et al., 2016; Wojcik, 2021). According to the Convention on Biological Diversity (2018), the reproduction and genetic diversity of 87.5% of plants is dependent on pollinators. Production of seeds by most species of angiosperms (estimate 260,000 species belonging to 457 families) depends on animal pollinators (Wilson, 1992; Bond, 1994; Wilcock & Neiland, 2002; APG II, 2003; Davies et al., 2004; Ollerton et al., 2011). Hence, the identification of pollinators is vital for the survival and conservation of plants since the interaction between the pollinator and plant is mutualistic.

This has resulted in many studies on the pollinators of specific species of plants, such as, the Orchidaceae (Darwin, 1862; Paulus & Gack, 1990; Singer & Sazima, 2001; van der Niet et al., 2010; Ayasse et al., 2011; Paulus, 2018; Alanís-Méndez, 2019; Ostrowiecka et al., 2019; Zito et al., 2019). However, recent pollination studies on orchids outside Asia have distinguished pollinating from non-pollinating floral visitors (van der Niet et al., 2010; Alanís-Méndez et al., 2019; Ostrowiecka et al., 2019). A study on two Orchids: the Palmer orchid, *Myrmecophila grandiflora* (Lindl.) and Lady of the night, *Brassavola nodosa* (L.) Lindl. in Veracruz, Eastern Mexico revealed that the plants are visited by ants, bees, mosquitoes, moths, and ladybugs. However, only the carpenter bee (*Xylocopa nautlana* Cockerell) and moth (*Scopula* sp.) were pollinators of *M. grandiflora* and *B. nodosa,* respectively (Alanís-Méndez et al., 2019). Similarly, a study on the Broad-leaved marsh orchid, *Dactylorhiza majalis* (Rchb.) P.F.Hunt & Summerh. in North-Eastern Poland revealed that it is pollinated by the Western honey bee, *Apis mellifera* Linnaeus and visited by insects belonging to the orders Diptera, Hymenoptera and Coleoptera (Ostrowiecka et al., 2019). A study on the orchid genus *Schizochilus* in South Africa reports that flies, wasps, skippers, moths, bees and beetles visited the flowers of this orchid, but only flies, bees and wasps pollinated the flower (van der Niet et al., 2010). Summarizing, studies on specific orchids reveal that their flowers are visited by many pollinating and non-pollinating animals, and there is a need to determine the importance of non-pollinating floral visitors.

Floral morphology is a major factor determining which of the floral visitors are potential pollinators. Flower size, form, position of the reproductive organ and shape of the reproduction organ in flowers determines whether an animal can access the anther to collect and transfer pollen onto the stigma (Thompson, 2001; Deschepper et al., 2018; Hernández-Villa et al., 2020). For an example, a study by Deschepper et al. (2018) reveals that the distylous Cowslip, *Primula veris* L. is visited by *Anthophora plumipes* (Pallas) (bee), *Bombus* spp. (bee), *Bombylius major* Linnaeus (bee), *Gonepteryx rhamni* (Linnaeus) (butterfly) and small rove beetles. Variation in the shape of the stigma determines which of these visitors are potential pollinators, with the flowers of Cowslip with a long stigma mostly pollinated by pollen on the proboscis of, e.g., *Bombylius major*, whereas those with a short stigma mostly by pollen on the heads of for, e.g. *Bombus pratorum* (Linnaeus)).

OVERVIEW OF STUDIES ON ZINGIBERACEAE-POLLINATOR INTERACTIONS IN ASIA

The diversity of ginger in most parts of Asia is better known than the Zingiberaceae-pollinator interaction. Publications of Larsen (1996), Larsen et al. (1999), Theilade (1999), Appalasamy et al. (2019, 2020a, b, 2022), Appalasamy & Arumugam (2020) and Izlamira et al. (2020) present detailed accounts of the diversity and distribution of species of ginger in Asia. In addition, recently many new species of ginger have been described in Asia, such as, in the genus *Curcuma* (Maknoi et al., 2019), *Globba* (Sangvirotjanapat et al., 2020) and *Zingiber* (Leong-Škorničková et al., 2014).

On the other hand, there very few publications on the specific pollinators of ginger plants in Asia and even those on non-pollinating floral visitors. Pollinators of ginger plants have been studied in Asian countries like China (Zhang et al., 2003), India (Aswani et al., 2013; Aswani & Sabu, 2018), Indonesia (Kato et al., 1993; Melati et al., 2015), Malaysian Borneo (Sakai et al., 1999; Takano et al., 2005) and Thailand (Kittipanangkul & Ngamriabsakul, 2006). Table 2 lists the pollinator species for 16 genera of ginger in Asia, namely, *Alpinia*, *Amomum*, *Boesenbergia*, *Conamomum*, *Epiamomum*, *Etlingera*, *Globba*, *Hornstedtia*, *Meistera*, *Plagiostachys*, *Roscoea*, *Scaphochlamys*, *Sulettaria*, *Sundamomum*, *Wurfbainia* and *Zingiber*.

A major study on the pollinators of Zingiberaceae in Asia was done in Malaysian Borneo with a total of 34 species of ginger observed at Sabah and Sarawak (Kato, 1996; Sakai et al., 1999; Takano et al., 2005). Takano et al. (2005) focus on one ginger species, *Alpinia nieuwenhuizii* at Sabah while Kato (1996) studied nine species in Sarawak and Sakai et al. (1999) determined the pollinators of 29 species in Sarawak. Other than Malaysian Borneo, pollinators of gingers are recorded for Indonesia. Kato et al. (1993) studied seven species and Melati et al. (2015) one species. Most of the publications report the pollinators of one species of ginger.

Table 2 presents the best examples of Zingiberaceae-pollinator studies in Asia. In summary, 51 species of ginger in Asia are pollinated by 12 groups of pollinators, namely, blue-banded bees, beetles, bumblebees, carpenter bees, halictid bees, honey bees, mining bees, stingless bees, small carpenter bees, wasps, spiderhunters and sunbirds. Table 2 is discussed further in connection with the subtopic 'Pollinators of Zingiberaceae in Asia'.

NON-POLLINATING FLORAL VISITORS OF ZINGIBERACEAE IN ASIA

Most of the pollination studies on Zingiberaceae focus on the pollinators rather than the floral visitors. As mentioned earlier, comprehensive studies on all the floral visitors of Zingiberaceae in Asia are scarce. Nevertheless, the term floral visitor is defined differently in most of the publications. For an example, floral visitors are directly referred to as pollinators of ginger in many studies, such as the floral visitors of *Alpinia nieuwenhuizii* were only counted as visitors if they did touch the sexual organ of the flower (Takano et al., 2005). Although flowers are visited by flies and small bees, these visits failed to fulfil the mentioned floral visitors' criteria. Carpenter bees, *Xylocopa latipes* (Drury) and *Xylocopa collaris alboxantha* are, however, reported as floral visitors and effective pollinators of *A. nieuwenhuizii*.

In spite of the above, there are few studies that separate pollinators and non-pollinators based on the role of the organism. Although the most important study on the pollinators of Zingiberaceae in Asia by Sakai et al. (1999) defines floral visitors similarly to Takano et al. (2005), this author states that significantly fewer non-pollinating floral visitors are recorded for the 29 ginger species studied in Malaysian Borneo. In this study, an halictid bee (*Thrinchostoma afaciatum*) visited *Epiamomum angustipetalum* (S.Sakai & Nagam.) A.D.Poulsen & Škorničk., *Trigona* bee visited *Boesenbergia* aff. *variegata* and an unnamed lepidopteran visited *Hornstedtia* aff. *minor*. *Plagiostachys crocydocalyx* (K.Schum.) B.L.Burtt & R.M Sm. is visited by *Xylocopa* bees and *P. strobilifera* (Baker) Ridl. mainly by unnamed lepidoptera and once by the copper-throated sunbird (*Nectarinia calcostetha* Jardine). The other species of ginger studied were only visited by pollinators.

Another study by Aswani et al. (2013) in India documents that *Etlingera elatior* is visited by ants (*Paratrichina* sp. and *Oecophylla smaragdina* (Fabricius)), butterflies, cockroach, fruit fly (*Drosophila melanogaster* Meigen), greater coucal bird (*Centropus sinensis* (Stephens)), small carpenter bee (*Ceratina* sp.) and spiders. Interestingly, the ants, butterflies and fruit flies are nectar robbers as they collect nectar from stigma without providing a pollination service. Aswani & Sabu (2018) report that in India the butterflies, *Eurema hecabe* (Linnaeus) and *Udaspes folus* (Cramer) visit and collect nectar by inserting their proboscis into the corolla tube of *Globba schomburgkii*. Similarly in China, bumble bees (*Bombus* sp.) collect nectar from *Roscoea humeana* and *R. cautleoides* and unnamed pollen thieves collect pollen grains that are detached from the anthers (Zhang et al., 2010). Thus, these studies indicate that the non-pollinating floral visitors of Asian Zingiberaceae include both insects and birds.

Similarly, pollination studies on species of ginger outside Asia also report non-pollinating floral visitors. Other than insect and birds, a lizard is a non-pollinating floral visitor of *Hornstedtia scottiana* (F.Muell.) K.Schum. in Australia. *Anoles* lizards visit ginger plants for water and food, imbibe the liquid on the inflorescence and eat tiny insects attracted to the liquid. In addition, moths also visit these plants at night and suck liquid from among the bracts at the apex of the inflorescence (Ippolito & Armstrong, 1993). In addition, *Zingiber spectabile* in Brazil is visited by ants, bees, beetles and spittlebugs, similar to the non-pollinating floral vistors of Asian Zingiberaceae (Rezende et al., 2021). Future studies on floral visitors of ginger outside Asia are likely to record more types of non-pollinating floral visitors.

Table 2. Pollinators of Zingiberaceae in Asia. AB – blue-banded bee (*Amegilla* spp.); B – beetle; BB – bumblebee; CB – carpenter bee; HaB – halictid bee (sweat bee); HoB – honey bee; MB – mining bee; SB – stingless bee; SCB – small carpenter bee; W – wasp; SH – spiderhunter (bird); NB – sunbird; * – pollinator unidentified.

No.	Species	Studied region	Pollinators												References
			Insect										Bird		
			AB	B	BB	CB	HaB	HoB	MB	SB	SCB	W	SH	NB	
1.	*Alpinia glabra* Ridl.	Sarawak, Malaysia	/												Sakai et al. (1999)
2.	*Alpinia nieuwenhuizii* Valeton	Sabah, Malaysia				/									Takano et al. (2005)
3.	*Alpinia roxburghii* Sweet, syn. *Alpinia blepharocalyx* K.Schum.	Yunnan province, China				/		/							Zhang et al. (2003)
4.	*Amomum kerbyi* (R.M.Sm.) Škorničk. & Hlavatá syn. *Elettariopsis kerbyi* R.M.Sm.	Sarawak, Malaysia					/								Sakai et al. (1999)
5.	*Amomum* sp. 1, syn. *Elettariopsis* sp. 1	Sarawak, Malaysia	/												Sakai et al. (1999)
6.	*Amomum* sp. 2, syn. *Elettariopsis* sp. 2	Sarawak, Malaysia					/								Sakai et al. (1999)
7.	*Boesenbergia* aff. *variegata*	Sarawak, Malaysia					/								Sakai et al. (1999)
8.	*Boesenbergia burttiana* R.M.Sm.	Sarawak, Malaysia					/								Kato (1996)
9.	*Boesenbergia grandifolia* (Valeton) Merr.	Sarawak, Malaysia					/								Sakai et al. (1999)
10.	*Boesenbergia orbiculata* R.M.Sm.	Sarawak, Malaysia					/								Kato (1996)
11.	*Boesenbergia parva* (Ridl.) Merr.	Sarawak, Malaysia					/								Kato (1996)
12.	*Conamomum cylindrostachys* (K.Schum.) Škorničk. & A.D.Poulsen syn. *Amomum coriaceum* R.M.Sm.	Sarawak, Malaysia					/								Sakai et al. (1999)
13.*	*Epiamomum angustipetalum* (S.Sakai & Nagam.) A.D.Poulsen & Škorničk. syn. *Amomum angustipetalum* S.Sakai & Nagam.	Sarawak, Malaysia													Sakai et al. (1999)
14.	*Epiamomum roseisquamosum* (Nagam. & S.Sakai) A.D.Poulsen & Škorničk. syn. *Amomum roseisquamosum* Nagam. & S.Sakai	Sarawak, Malaysia											/		Sakai et al. (1999)
15.	*Etlingera* aff. *brevilabris*	Sarawak, Malaysia											/		Kato (1996) Sakai et al. (1999)
16.	*Etlingera* aff. *metriocheilos*	Sarawak, Malaysia											/		Sakai et al. (1999)
17.	*Etlingera coccinea* (Blume) S.Sakai & Nagam. syn. *Achasma macrocheilos* Griff.	West Sumatra, Indonesia	/												Kato et al. (1993)
18.	*Etlingera elatior* (Jack) R.M.Sm. syn. *Nicolaia elatior* (Jack) Horan.	Singapore Kerala, India								/				/	Classen (1987) Aswani et al. (2013)
19.	*Etlingera fulgens* (Ridl.) C.K.Lim syn. *Phaeomeria fulgens* (Ridl.) K.Schum.	West Sumatra, Indonesia												/	Kato et al. (1993)
20.	*Etlingera littoralis* (J.Koenig) Giseke	Nakhon Si Thammarat Province, Thailand								/					Kittipanangkul & Ngamriabsakul (2006)
21.	*Etlingera punicea* (Roxb.) R.M.Sm.	Sarawak, Malaysia											/		Sakai et al. (1999)
22.	*Globba aurantiaca* Miq.	West Sumatra, Indonesia	/												Kato et al. (1993)
23.	*Globba brachyanthera* K.Schum.	Sarawak, Malaysia	/												Kato (1996) Sakai et al. (1999)
24.	*Globba leucantha* Miq.	Kelantan, Malaysia									/				Arumugam et al. (2022)
25.	*Globba schomburgkii* Hook.f.	Kerala, India	/												Aswani & Sabu (2018)
26.*	*Hornstedtia* aff. *coninca*	West Sumatra, Indonesia												/	Kato et al. (1993)
27.	*Hornstedtia* aff. *minor*	Sarawak, Malaysia											/		Sakai et al. (1999)
28.	*Hornstedtia leonurus* (J.Koenig) Retz.	Sarawak, Malaysia											/		Sakai et al. (1999)
29.	*Hornstedtia reticulata* (K.Schum.) K.Schum.	Sarawak, Malaysia											/		Sakai et al. (1999)
30.	*Hornstedtia tomentosa* (Blume) Bakh.f.	Sarawak, Malaysia											/		Kato (1996)
31.	*Meistera aculeata* (Roxb.) Škorničk. & M.F.Newman syn. *Amomum aculeatum* Roxb.	West Sumatra, Indonesia	/												Kato et al. (1993)
32.	*Meistera oligantha* (K.Schum.) Škorničk. & M.F.Newman syn. *Amomum oliganthum* K.Schum.	Sarawak, Malaysia	/												Sakai et al. (1999)
33.	*Meistera gyrolophos* (R.M.Sm.) Škorničk. & M.F.Newman syn. *Amomum gyrolophos* R.M.Sm.	Sarawak, Malaysia	/												Kato (1996) Sakai et al. (1999)
34.	*Plagiostachys austrosinensis* T.L.Wu & S.J.Chen	Hainan province, China			/							/			Jia et al. (2015)
35.	*Plagiostachys crocydocalyx* (K.Schum.) B.L.Burtt & R.M Sm.	Sarawak, Malaysia	/												Kato (1996) Sakai et al. (1999)
36.	*Plagiostachys* sp. 1	Sarawak, Malaysia	/												Sakai et al. (1999)
37.	*Plagiostachys strobilifera* (Baker) Ridl.	Sarawak, Malaysia											/		Sakai et al. (1999)
38.	*Roscoea alpina* Royle	Nepal		/											Paudel et al. (2017)
39.	*Roscoea humeana* Balf.f. & W.W.Sm.	Yunnan province, China					/	/							Zhang et al. (2010)
40.	*Roscoea cautleyoides* Gagnep	Yunnan province, China							/						Zhang et al. (2010)
41.	*Scaphochlamys gracilipes* (K.Schum.) S.Sakai & Nagam. syn. *Boesenbergia gracilipes (K.Schum.)* R.M.Sm.	Sarawak, Malaysia					/								Sakai et al. (1999)
42.	*Sulettaria longituba* (Ridl.) A.D.Poulsen & Mathisen syn. *Elettaria longituba* (Ridl.) Holttum	Sarawak, Malaysia					/								Sakai et al. (1999)
43.	*Sulettaria polycarpa* (K.Schum.) A.D.Poulsen & M.F.Newman syn. *Amomum polycarpum* K.Schum.	Sarawak, Malaysia					/								Kato (1996) Sakai et al. (1999)
44.	*Sundamomum calyptratum* (S.Sakai & Nagam.) A.D.Poulsen & M.F.Newman syn. *Amomum calyptratum* S.Sakai & Nagam.	Sarawak, Malaysia	/												Sakai et al. (1999)
45.	*Sundamomum durum* (S.Sakai & Nagam.) A.D.Poulsen & M.F.Newman syn. *Amomum durum* S.Sakai & Nagam.	Sarawak, Malaysia					/								Sakai et al. (1999)
46.	*Sundamomum somniculosum* (S.Sakai & Nagam.) A.D.Poulsen & M.F.Newman syn. *Amomum somniculosum* S.Sakai & Nagam.	Sarawak, Malaysia					/								Sakai et al. (1999)
47.	*Wurfbainia uliginosa* (J.Koenig) Giseke, syn. *Amomum uliginosum* J.Koenig	West Sumatra, Indonesia					/								Kato et al. (1993)
48.	*Zingiber longipedunculatum* Ridl.	Sarawak, Malaysia	/												Sakai et al. (1999)
49.*	*Zingiber officinale* Roscoe	Java, Indonesia													Melati et al. (2015)
50.	*Zingiber puberulum* Ridl.	West Sumatra, Indonesia	/												Kato et al. (1993)
51.*	*Zingiber* sp.	Sarawak, Malaysia													Sakai et al. (1999)

POLLINATORS OF ZINGIBERACEAE IN ASIA

Insects and birds are the two groups recorded pollinating ginger plants in Asia where most pollination is by insects. All the studies listed in Table 2 document diurnal pollinators since anthesis in ginger occurs during daytime.

Blue-banded bees and halictid bees are the major pollinators of Zingiberaceae and make up approximately 30% of those listed in Table 2, in particular *Amegilla pendleburyi* (Cockerell), *A. insularis* (Smith) and *A. zonata* (Linnaeus) of the former group and *Nomia* spp. and *Thrinchostoma afasciatum* Michener of the latter (Kato, 1996). Honey bees, stingless bees, carpenter bees and sunbird pollinate less than three species of ginger. That pollinators other than bees are less recorded may be due to the small area sampled and that only the pollination of approximately 5% of the Asian species of ginger has been evaluated. For other flowering plants, non-bee insect pollinators such as flies and butterflies are recorded (Rader et al., 2016), but for ginger the non-bee insects recorded are mainly non-pollinating floral visitors (Sakai et al., 1999; Aswani et al., 2013). With this in mind, one wonders whether ginger has more non-bee pollinators.

Most of the species of ginger listed in Table 2 are pollinated by one particular pollinator and only four (7.8%) by two different types of pollinators. To be specific, for *Alpinia blepharocalyx* K.Schum. it is carpenter bees (*Xylocopa* spp.) and honey bee (*Apis cerana cerana*), *Etlingera elatior* it is the stingless bee (*Tetragonula irridipennis* (Smith)) and sunbirds *Nectarinia asiatica* (Latham) and *Nectarinia zeylonica* (Linnaeus)) (Zhang et al., 2003; Aswani et al., 2013). The bumblebee *Bombus pyrosoma* Morawitz and Vespidae spp. pollinate *Plagiostachys austrosinensis* T.L.Wu & S.J.Chen and *Roscoea humeana* is visited by the sweat bee (*Lasioglossum* sp.) and honey bee (*Apis* sp.) (Jia et al., 2015; Zhang et al., 2010). The more potential pollinators there are for a plant the more likely it is to be pollinated (Maldonado et al., 2013; Katumo et al., 2022). Consequently, as 92.2% of the species of ginger listed in Table 2 have specific pollinators. Hence, any conservation effort has to bear in mind that the extinction of the specific pollinators will result in unsuccessful pollination and indirectly in a decline in abundance and genetic diversity of a specific species of ginger.

Currently, most of the published accounts of the interaction between species of Asian ginger and their pollinators are inadequate. For *Etlingera littoralis* (J.Koenig) Giseke, *E. punicea.*, *Globba leucantha* and *Plagiostachys austrosinensis*, to mention a few, the knowledge is very detailed (Sakai et al., 1999; Kittipanangkul & Ngamriabsakul, 2006; Jia et al., 2015; Arumugam et al., 2022). *Etlingera littoralis* produce at ground level long bright red flowers with yellow margin, slightly away from the main plant, the anther faces the lip (hidden) and stigma extends beyond the tip of the anther (Fig. 2, Chongkraijak et al., 2013). Its pollinator, the stingless bee, *Trigona* sp. walks onto the corolla tube after landing on the lip near the anther to collect pollen and nectar (Kittipanangkul & Ngamriabsakul, 2006). As a result, pollen grains become attached to its hind legs and head, which is then transfered to the stigma when it moves from one flower to another. The position of the anther prevents pollination by well-known pollinators of *Etlingera* spp., birds (Kittipanangkul & Ngamriabsakul, 2006).

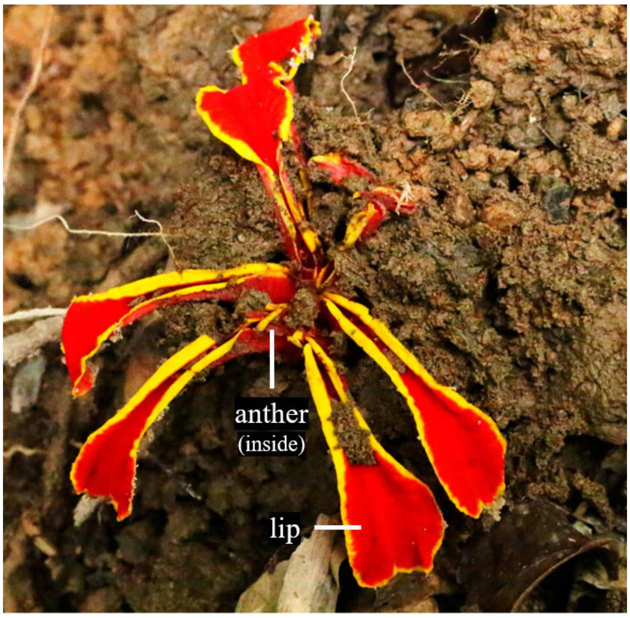

Fig. 2. Flower of *Etlingera littoralis* (J.Koenig) Giseke (Zingiberaceae).

Likewise, in another member of the genus, the lips of the red flower of *E. punicea* have a long bright yellow fringe and tightly rolled sidelobes, and is on the ground away from the plant (Fig. 1b, Larsen et al., 1999). Among its floral visitors, little spiderhunter *Arachnothera longirostra* can pollinate this species of ginger, whereas the tightly rolled sidelobes block the entry of *Amegilla* bees to the floral tube, nectar and honey (Sakai et al., 1999). This is possible because the little spidehunter can access the nectar by inserting its long rostrum into the floral tube of *E. punicea* to suck nectar. This indicates that the floral morphology enables the little spider hunter with a 36mm long rostrum to pollinate *E. punicea*, but not the larger *Amegilla* bee.

In addition, pollinators transfer pollen grains from anther to stigma on different parts of their body parts, viz. head, hind legs, dorsal surface, or rostrum. Carpenter bees, *Xylocopa latipes* and *Xylocopa collaris alboxantha* carry pollen of *Alpinia nieuwenhuizii* on their back (dorsal surface) (Takano et al., 2005), whereas the small carpenter bee *Ceratina ridleyi* Cockerell carries the pollen of *Globba leucantha* on their ventral body parts and legs (Fig. 3, Arumugam et al., 2022). The latter scrape pollen from the anther using their mouthparts while hanging on the anther. The blue banded bee, *Amegilla zonata* (Linnaeus) collect pollen of *Globba schomburgkii* on their dorsal surface when entering a flower (Aswani & Sabu, 2018). Head and hind legs are used by the stingless bee, *Tetragonula irridipennis* (Smith) to transfer pollen grains when visiting flowers of *Etlingera elatior* (Aswani et al., 2013) and *Trigona* sp. the flowers of *E. littoralis* (Kittipanangkul & Ngamriabsakul, 2006).

Fig. 3. Small carpenter bee, *Ceratina ridleyi* Cockerell, the pollinator of *Globba leucantha* Miq. (Zingiberaceae).

Birds and bees carry pollen of Zingiberaceae in similar ways. Birds collect pollen on their beaks while sucking nectar from flowers, with the pollen attaching to the base of the bill and/or just above on the feathers of the forehead. The pollinating birds in Asia are honeyeaters in the case of *Hornstedtia scottiana* (Ippolito & Armstrong, 1993), sunbird *Anthreptes malacensis* (Scopoli) for *Etlingera elatior* (Classen, 1987) and spiderhunters for *Plagiostachys strobilifera* (Baker) Ridl.

FUTURE DIRECTIONS FOR THE RESEARCH ON THE ZINGIBERACEAE-POLLINATOR INTERACTION IN ASIA

The Zingiberaceae-pollinator interaction is poorly explored in Asia, especially in terms of the role floral scent and geographical factors. Previous studies have shown that floral scent plays an essential role in attracting pollinators (Majestic et al., 2009; Whitehead & Peakall, 2009), for example, in Cypress, *Euphorbia cyparissias* L. and *Euphorbia virgultosa* Klokov (Denisow, 2009) and European bellflower, *Campanula bononiensis* L. (Denisow et al., 2014). It increases the likelyhood of pollination by acting attracting foraging pollinators (Wright & Schiesti, 2009). The scent of plants differ greatly in the volatile compounds they contain and specific pollinators are attracted by a particular scent (Takano et al., 2005; Dobson, 2006). There are also general pollinators such as bees attracted by most floral scents (Takano et al., 2005; Bumrungsri et al., 2008). A recent study by Zito et al. (2019) confirm that the mining bee, *Andrena nigroaenea* (Kirby) that pollinates orchids of the genus *Ophyrys* is attracted mainly by Z-9/11-12 alkenes. The floral volatile compound of Zingiberaceae requires further study (Menon & Dan, 2009; Yue et al., 2014; Zhou et al., 2021) as it could greatly add to the understanding of pollination in Zingiberaceae.

The geographical factor is another aspect that could greatly add to the understanding of the Zingiberaceae-pollinator interaction in Asia. Studies indicate that different latitudinal zones (Ollerton et al., 2006), altitude (Warren et al., 1988; Lefebvre et al., 2018), spatial scale and landscape structure (Rader et al., 2011; Saturni et al., 2016) influence pollination. Zingiberaceae mainly occur between 200 m to 500 m above sea level with various spatial distributions (Larsen et al., 1999). Studies on the Zingiberaceae-pollinator interaction in various types of forest, for instance, lowland tropical rainforest, hill dipterocarp forest and limestone forests would provide a clearer picture of pollination in Zingiberaceae.

CONCLUSION

The plant pollinator interaction is the key to the survival of flowering plants. Pollination starts with the visit of a pollinator, followed by pollination and ends in plant reproduction. Many factors enhance the interaction and increase the likelihood of successful pollination. All the criteria involved in pollination vary greatly in angiosperms. The overview of the Zingiberaceae-pollinator interaction in Asia presented indicate that the level of understanding is poor and there is a need for further studies. Understanding the interaction in terms of spatial and temporal factors will help in the conservation of plants and pollinators and ensure the continued survival of both organisms.

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REFERENCES

Abrol D.P., Gorka A.K., Ansari M.J., Al-Ghamdi A. & Al-Kahtani S. 2019: Impact of insect pollinators on yield and fruit quality of strawberry. — *Saudi J. Biol. Sci.* **26**: 527–530.

Alanís-Méndez J.L., Ortiz-Santos L.d.C., Chamorro-Florescano I.A., Pech-Canché J.M. & Limón F. 2019: Pollinators and floral visitors of two orchids in a protected natural area in Tuxpan, Veracruz. — *Ecosist. Recurs. Agropecuar.* **6**: 361–368.

Alves-dos-Santos I., Silva C.I.d., Pinheiro M. & Kleinert A. d.M.P. 2016: Quando um visitante floral é um polinizador? — *Rodriguésia* **67**: 295–307.

Angiosperm Phylogeny Group (APG II) 2003: An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG II. — *Bot. J. Linn. Soc.* **141**: 399–436.

Appalasamy S. & Arumugam N. 2020: Four new records of Zingiberaceae in Gunung Telapak Burok, Berembun Forest Reserve (Fr), Negeri Sembilan. — *IOP Conf. Ser.: Earth Environ. Sci.* **596**: 012059, 6 pp.

Appalasamy S., Arumugam N., Boon J.G. & Aweng E.R. 2019: A short note on wild gingers (Zingiberaceae) in Pulau Pangkor, Perak, peninsular Malaysia. — *Malaysian Forester* **82**: 159–162.

Appalasamy S., Arumugam N., Lam Y. & Nur Azizun R. 2020a: Wild gingers (Zingiberaceae) at Sungai Kangkawat, Imbak canyon conservation area (ICCA), Sabah. — *J. Trop. Biol. Conserv.* **17**: 97–103.

Appalasamy S., Rathamanalan S., Arsogah S., Harni S., Sam K.K., Amaludin N.A., Geng B.J., Kumaran J.V., Arumugam N. & Subramaniam S. 2020b: Gingers species diversity and distribution along a natural trail of Lojing highlands, Kelantan. — *IOP Conf. Ser.: Earth Environ. Sci.* **549**: 012036, 5 pp.

Appalasamy S., Arumugam N., Zamri N.S.A., Fadhlina A., Kumaran J.V. & Subramaniam S. 2022: First report on wild ginger (Family: Zingiberaceae) species composition with new records in limestone forests of Kelantan, Peninsular Malaysia. — *Trop. Life Sci. Res.* **33**: 33–46.

Arumugam N., Zamri N.S., Kumaran J.V., Nor M.M., Subramaniam S. & Appalasamy S. 2022: First report on pollinating behavior of the small carpenter bee *Ceratina ridleyi* Cockerell (Hymenoptera, Apidae) in *Globba leucantha* var. *bicolor* Holttum (Zingiberaceae). — *J. Hymenopt. Res.* **90**: 173–183.

Aswani K.K. & Sabu M.M. 2018: Reproductive biology of dancing girl ginger, *Globba schomburgkii* (Zingiberaceaeae). — *Int. J. Plant Reprod. Biol.* **10**: 184–188.

Aswani K., Sabu M. & Smisha K.P. 2013: Reproductive biology of *Etlingera elatior* (Jack.) R. M. Sm. ornamental torch ginger. — *Int. J. Plant Anim. Environ. Sci.* **3**: 75–80.

Ayasse M., Stökl J. & Francke W. 2011: Chemical ecology and pollinator-driven speciation in sexually deceptive orchids. — *Phytochemistry* **72**: 1667–1677.

Baqi A., Lim V.C., Yazid H., Khan F.A.A., Lian C.J., Nelson B.R., Seelan J.S.S., Appalasamy S., Mokhtar S.I. & Kumaran J.V. 2022: A review of durian plant-bat pollinator interactions. — *J. Plant Interact.* **17**: 105–126.

Binghong X., Chunyan L., Xinlan X., Bo C., Caixia A., Shiquan L., Xiongyao H., Jian C., Lian L. & Li T. 2018: Studies on collection breeding and application of Zingiberaceae plants wild resources in China. — *J. Plant Sci.* **6**: 179–184.

Bond W.J. 1994: Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. — *Phil. Trans. R. Soc. Lond. (B)* **344**: 83–90.

Brothers A.N. & Atwell J.W. 2014: The role of pollinator-mediated selection in the divergence of floral traits between two closely related plant species. — *Int. J. Plant Sci.* **175**: 287–295.

Buchholz S. & Kowarik I. 2019: Urbanisation modulates plant-pollinator interactions in invasive vs. native plant species. — *Sci. Rep.* **9**: 6375, 9 pp.

Bumrungsri S., Harbit A., Benzie C. & Carmouche K. 2008: The pollination ecology of two species of *Parkia* (Mimosaceae) in southern Thailand. — *J. Trop. Ecol.* **24**: 467–447.

Campbell N.A. & Reece J.B. 2008: *Biology. 8th ed.* Pearson Benjamin Cummings, Frenchs Forest, N.S.W., 1267 pp.

Chautá-Mellizo A., Campbell S.A., Bonilla M.A., Thaler J.S. & Poveda K. 2012: Effects of natural and artificial pollination on fruit and offspring quality. — *Basic Appl. Ecol.* **13**: 524–532.

Chongkraijak W., Ngamnriabsakul C. & Poulsen A.D. 2013: Morphological diversity and distribution of *Etlingera littoralis* (König) Giseke (Zingiberaceae) in Southern Thailand. — *Walailak J. Sci. Tech.* **10**: 643–656.

Choon S.Y. & Ding P. 2016: Growth stages of torch ginger (*Etlingera elatior*) plant. — *Sains Malaysiana* **45**: 507–515.

Classen R. 1987: Morphological adaptations for bird pollination in *Nicolaia elatior* (Jack) Horan (Zingiberaceae). — *Garden's Bull. (Singapore)* **40**: 37–42.

Convention on Biological Diversity 2018: *Review of Pollinators and Pollination Relevant to the Conservation and Sustainable Use of Biodiversity in All Ecosystems, Beyond Their Role in Agriculture and Food Production.* Convention's Subsidiary Body on Scientific, Technical and Technological Advice (SBSTTA). URL: https://www.cbd.int/agro/peer_review_pollinators.pdf

Criley R.A. 1995: Propagation of Zingiberaceae and Heliconiaceae. — *Rev. Brss. Hort. Orn. Campinas* **1**: 14–21.

Darwin C.R. 1862: On the various contrivances by which british and foreign orchids are fertilized by insects, and on the good effects of intercrossing. — *Ann. Mag. Nat. Hist.* **10**: 384–388.

Davies T.J., Barraclough T.G., Chase M.W., Soltis P.S., Soltis D.E. & Savolainen V. 2004: Darwin's abominable mystery: Insights from a supertree of the angiosperms. — *Proc. Natn. Acad. Sci.* **101**: 1904–1909.

de Merxem D.G., Borremans B., de Jäger M.L., Johnson T., Jooste M., Ros P., Zenni R.D., Ellis A.G. & Anderson B. 2009: The importance of flower visitors not predicted by floral syndromes. — *Sth Afr. J. Bot.* **75**: 660–667.

Denisow B. 2009: Pollen production, flowering and insect visits on *Euphorbia cyparissias* L. and *Euphorbia virgultosa* Klok. — *J. Apicult. Res.* **48**: 50–59.

Denisow B., Strzałkowska-Abramek M., Bożek M. & Jeżak A. 2014: Ornamental representatives of the genus *Centaurea* L. as a pollen source for bee friendly gardens. — *J. Apicult. Sci.* **58**: 49–58.

Deschepper P., Brys R. & Jacquemyn H. 2018: The impact of flower morphology and pollinator community composition on pollen transfer in the distylous *Primula veris*. — *Bot. J. Linn. Soc.* **186**: 414–424.

Dictionary.com 2023: *-phily*. URL: https://www.dictionary.com/browse/-phily (last accessed 22 Mar 2023).

Diego C.E.N., Stewart A.B. & Bumrungsri S. 2021: Pollinators necessary for the reproductive success of critically endangered mangrove, *Sonneratia griffithii*. — *Aquatic Bot.* **169**: 103340, 5 pp.

Dobson H.E.M. 2006: Relationship between floral fragrance composition and type of pollinator. In Dudareva N. & Pichersky E. (eds): *Biology of Floral Scent.* CRC Press, Boca Raton, pp. 147–198.

Doyle T., Hawkes W.L.S., Massy R., Powney G.D., Menz M.H.M. & Wotton K.R. 2020: Pollination by hoverflies in the Anthropocene. — *Proc. R. Soc. (B)* **287**: 20200508, 9 pp.

Eeraerts M., Vanderhaegen R., Smagghe G. & Meeus I. 2019: Pollination efficiency and foraging behaviour of honey bees and non-*Apis* bees to sweet cherry. — *Agric. Forest Entomol.* **22**: 75–82.

Fenster C.B., Armbruster W.S., Wilson P., Dudash M.R. & Thomson J.D. 2004: Pollination syndromes and floral specialization. — *Ann. Rev. Ecol. Evol. Syst.* **35**: 375–403.

Field D.L., Pickup M. & Barrett S.C.H. 2012: The influence of pollination intensity on fertilization success, progeny sex ratio, and fitness in a wind-pollinated, dioecious plant. — *Int. J. Plant Sci.* **173**: 184–191.

Fumero-Cabán J.J. & Meléndez-Ackerman E.J. 2007: Relative pollination effectiveness of floral visitors of *Pitcairnia angustifolia* (Bromeliaceae). — *Am. J. Bot.* **94**: 419–424.

Gao J.-Y., Zhang L., Deng X.-B., Ren P.-Y., Kong J.-J. & Li Q.-J. 2004: The floral biology of *Curcumorpha longiflora* (Zingiberaceae): a ginger with two-day flowers. — *Am. J. Bot.* **91**: 289–293.

Hernández-Villa V., Vibrans H., Uscanga-Mortera E. & Aguirre-Jaimes A. 2020: Floral visitors and pollinator dependence are related to floral display size and plant height in native weeds of central Mexico. — *Flora* **262**: 151505, 9 pp.

Hingston A.B. & Mc Quillan P.B. 2000: Are pollination syndromes useful predictors of floral visitors in Tasmania? — *Austral. Ecol.* **25**: 600–609.

Huang Z.Y. & Giray T. 2012: Factors affecting pollinators and pollination. — *Psyche* **2012**: 302409, 3 pp.

Inouye D.W. 2007: Pollinators, role of. In Levin S.A. (ed.): *Encyclopedia of Biodiversity*. *Vol. 6.* Elsevier, Amsterdam, pp. 140–146.

IPPOLITO A. & ARMSTRONG J.E. 1993: Floral biology of *Hornstedtia scottiana* (Zingiberaceae) in a lowland rain forest of Australia. — *Biotropica* **25**: 281–289.

IZLAMIRA R., APPALASAMY S., NIVAARANI A. & NOOR HISHAM M.Z.A. 2020: Zingiberaceae diversity in Ulu Sat Forest Reserve, Kelantan. In Abdullah M.R.C., Abong N.N.D., Jemali N.J.N., Amaludin N.A. & Nordin S.M. (eds): *Ulu Sat Forest: The Heart of Kelantan's Nature Conservation.* Forestry Department of Kelantan, Malaysia, pp. 72–78.

JIA X.-C., LI J., LU G.-H. & WANG Y.-Q. 2015: The concrete evidence of flexistyly in *Plagiostachys*: pollination biology of a wild ginger on Hainan Island, China. — *Ecol. Evol.* **5**: 5364–5371.

JOHNSON N.F. & TRIPLEHORN C.A. 2005: *Borror and DeLong's Introduction to the Study of Insects. 7th ed.* Tmonson Brooks/Cole, Belmont, 866 pp.

JONES G.D. & JONES S.D. 2001: The uses of pollen and its implication for entomology. — *Neotrop. Entomol.* **30**: 314–349.

KAMARUDDIN F. & ZALIPAH M.N. 2020: Observation of flower visitors to determine their potential role as pollinators of *Ixora coccinae* and *Ruellia simplex*. — *J. Undergrad. Res.* **2**: 61–70.

KATO M. 1996: Plant-pollinator interactions in the understory of a lowland mixed dipterocarp forest in Sarawak. — *Am. J. Bot.* **83**: 732–743.

KATO M., ITINO T. & NAGAMITSU T. 1993: Melittophily and ornithophily of long-tubed flowers in Zingiberaceae and Gesneriaceae in West Sumatra. — *Tropics* **2**: 129–142.

KATUMO D.M, LIANG H., OCHOLA A.C., LV M., WANG Q.-F. & YANG C.-F. 2022: Pollinator diversity benefits natural and agricultural ecosystems, environmental health, and human welfare. — *Plant Div.* **44**: 429–435.

KAUFMAN S. 2016: *Zingiber officinale (Ginger). CABI Compendium.* URL: https://www.cabidigitallibrary.org/doi/10.1079/cabicompendium.57537#sec-36

KEYS R.N., BUCHMANN S.L. & SMITH S.E. 1995: Pollination effectiveness and pollination efficiency of insects foraging *Prosopis velutina* in South-eastern Arizona. — *J. Appl. Ecol.* **32**: 519–527.

KITTIPANANGKUL N. & NGAMRIABSAKUL C. 2006: Pollen and pollinator limitation of seed initiation in *Etlingera littoralis* (J. König) Giseke (Zingiberaceae) in Klong Klai Basin, Khao Nan National Park, Thailand. — *Walailak J. Sci. Tech.* **3**: 207–217.

KLEIN A.-M., STEFFAN-DEWENTER I. & TSCHARNTKE T. 2003: Bee pollination and fruit set of *Coffea arabica* and *C. canephora* (Rubiaceae). — *Am. J. Bot.* **90**: 153–157.

LARSEN K. 1996: A preliminary checklist of the Zingiberaceae of Thailand. — *Thai Forest Bull. (Bot.)* **24**: 35–49.

LARSEN K., IBRAHIM H., KHAW S.H. & SAW L.G. 1999: *Gingers of Peninsular Malaysia and Singapore*. Natural History Publications, Borneo, 135 pp.

LEFEBVRE V., VILLEMANT C., FONTAINE C. & DAUGERON C. 2018: Altitudinal, temporal and trophic partitioning of flower-visitors in Alpine communities. — *Sci. Rep.* **8**: 4706, 12 pp.

LEONG-ŠKORNIČKOVÁ J., THAME A. & CHEW P.T. 2014: Notes on Singapore native Zingiberales I: A new species of *Zingiber* and notes on the identities of two further *Zingiber* taxa. — *Gardens' Bull. (Singapore)* **66**: 153–167.

LI Q.-J., XU Z.-F., KRESS W.J., XIA Y.-M., ZHANG L., DENG X.-B., GAO J.-Y. & BAI Z.-L. 2001: Flexible style that encourages outcrossing. — *Nature* **410**: 432.

LING S.-J., LU T. & REN M.-X. 2020: A novel type of mirror-image flowers caused by lateral bending of the floral tube in a bumblebee-pollinated plant. — *Flora* **272**: 151694, 7 pp.

LIU R., CHEN D., LUO S., XU S., XU H., SHI X. & ZOU Y. 2020: Quantifying pollination efficiency of flower-visiting insects and its application in estimating pollination services for common buckwheat. — *Agric. Ecosyst. Environ.* **301**: 107011, 10 pp.

MAJESTIC C.J., RAGUSO R.A. & ASHMAN T.-L. 2009: The sweet smell of success: Floral scent affects pollinator attraction and seed fitness in *Hesperis matronalis*. — *Funct. Ecol.* **23**: 480–487.

MAKNOI C., RUCHISANSAKUN S. & JENJITTIKUL T. 2019: *Curcuma putii* (Zingiberaceae), a new species from Thailand. — *Ann. Bot. Fenn.* **56**: 351–353.

MALDONADO M.B., LOMÁSCOLO S.B. & VÁZQUEZ D.P. 2013: The importance of pollinator generalization and abundance for the reproductive success of a generalist plant. — *PLoS ONE* **8**(10): e75482, 6 pp.

MEKURIYA W. & MEKIBIB B. 2018: Review on the medicinal values of ginger for human and animal ailments. — *J. Vet. Sci. Technol.* **9**: 519, 5 pp.

MELATI, PALUPI E.R. & BERMAWIE N. 2015: Floral biology of ginger (*Zingiber officinale* Rosc.). — *Int. J. Curr. Res. Biosci. Plant Biol* **2**: 1–10.

MELIDONIS C.A. & PETER C.I. 2015: Diurnal pollination, primarily by a single species of rodent, documented in *Protea foliosa* using modified camera traps. — *Sth Afr. J. Bot.* **97**: 9–15.

MENON A.N. & DAN M. 2009: Chemical composition of essential oils of *Globba* species from South India. — *J. Essen. Oil Res.* **21**: 59–60.

MOONKAEW P., NOPPORNCHAROENKUL N., JENJITTIKUL T. & UMPUNJUN P. 2020: Cytogenetic and pollen identification of genus *Gagnepainia* (Zingiberaceae) in Thailand. — *Comp. Cytogenet.* **14**: 11–25.

NICOLSON S.W. & WRIGHT G.A. 2017: Plant-pollinator interactions and threats to pollination: perspectives from the flower to the landscape. — *Funct. Ecol.* **31**: 22–25.

NIISSALO M.A., LEONG-ŠKORNIČKOVÁ J., KHEW G.S. & WEBB E.L. 2017: Very small relict populations suggest high extinction debt of gingers in primary forest fragments of a tropical city. — *Am. J. Bot.* **104**: 182–189.

OLESEN J.M. & VALIDO A. 2003: Lizards as pollinators and seed dispersers: an island phenomenon. — *Trends Ecol. Evol.* **18**: 177–181.

OLLERTON J. 2017: Pollinator diversity: distribution, ecological function, and conservation. — *Annu. Rev. Ecol. Evol. Syst.* **48**: 353–376.

OLLERTON J. 2021: *Pollinators and Pollination: Nature and Society*. Pelagic Publishing, London, 289 pp.

OLLERTON J., JOHNSON S. & HINGSTON A. 2006: Geographical variation in diversity and specificity of pollination systems. In Ollerton J. & Waser N. (eds): *Plant-Pollinator Interactions: From Specialization to Generalization.* University of Chicago Press, Chicago, pp. 283–308.

OLLERTON J., WINFREE R. & TARRANT S. 2011: How many flowering plants are pollinated by animals? — *Oikos* **120**: 321–326.

OSTROWIECKA B., TAŁAŁAJ I., BRZOSKO E., JERMAKOWICZ E., MIRSKI P., KOSTRO-AMBROZIAK A., MIELCZAREK L., LASOŃ A., KUPRYJANOWICZ J., KOTOWICZ J. & WRÓBLEWSKA A. 2019: Pollinators and visitors of the generalized food-deceptive orchid *Dactylorhiza majalis* in North-Eastern Poland. — *Biologia* **74**: 1247–1257.

PATTEMORE D.E. 2017: Pollination. In Thomas B., Murray B.G. & Murphy D.J. (eds): *Encyclopedia of Applied Plant Sciences*. Academic Press, Oxford, pp. 309–320.

PAUDEL B.R., SHRESTHA M., DYER A.G. & LI Q.-J. 2017: Ginger and the beetle: Evidence of primitive pollination system in a Himalayan endemic alpine ginger (*Roscoea alpina*, Zingiberaceae). — *PLoS ONE* **12**(7): e0180460, 18 pp.

PAULUS H.F. 2018: Pollinators as isolation mechanisms: field observations and field experiments regarding specificity of pollinator attraction in the genus *Ophrys* (Orchidaceae and Insecta, Hymenoptera, Apoidea). — *Entomol. Gen.* **37**: 261–316.

PAULUS H.F. & GACK C. 1990: Pollinators as prepollinating isolation factors: evolution and speciation in *Ophrys* (Orchidaceae). — *Isr. J. Plant Sci.* **39**: 43–79.

PEREIRA A.M. & COIMBRA S. 2020: Corrigendum to: Advances in plant reproduction: from gametes to seeds. — *J. Exp. Bot.* **71**: 6697.

PETTERSSON M.W. 1991: Pollination by a guild of fluctuating moth populations: Option for unspecialization in *Silene vulgaris*. — *J. Ecol.* **79**: 591–604.

PHILLIPS R.D., PEAKALL R., VAN DER NIET T. & JOHNSON S.D. 2020: Niche perspectives on plant-pollinator interactions. — *Trends Plant Sci.* **25**: 779–793.

RADER R., BARTOMEUS I., GARIBALDI L.A., GARRATT M.P.D., HOWLETT B.G., WINFREE R., CUNNINGHAM S.A., MAYFIELD M.M., ARTHUR A.D. & ANDERSSON G.K.S. 2016: Non-bee insects are important contributors to global crop pollination. — *Proc. Natn. Acad. Sci.* **113**: 146–151.

RADER R., HOWLETT B.G., CUNNINGHAM S.A., WESTCOTT D.A. & EDWARDS W. 2011: Spatial and temporal variation in pollinator effectiveness: do unmanaged insects provide consistent pollination services to mass flowering crops? — *J. Appl. Ecol.* **49**: 126–134.

REDDI C.S. & BAI G.M. 1984: Butterflies and pollination biology. — *Proc. Anim. Sci.* **93**: 391–396.

REZENDE K.M., DOS SANTOS R., DA SILVA A., DA SILVA P.C., CORDEIRO M.H.M. & SILVA C.A. 2021: Aspects of the reproductive biology of *Zingiber spectabile* (Zingiberaceae). — *Physiol. Morphol. Appl. Agric.* **68**: 96–104.

SAENSOUK P., THEERAKULPISUT P., THAMMATHAWORN A, SAENSOUK S., MAKNOI C. & KOHKAEW P. 2015: Pollen morphology of the genus *Curcuma* (Zingiberaceae) in Northeastern Thailand. — *ScienceAsia* **41**: 87–92.

SÁEZ A., NEGRI P., VIEL M. & AIZEN M.A. 2019: Pollination efficiency of artificial and bee pollination practices in kiwifruit. — *Scientia Horticult.* **246**: 1017–1021.

SAKAI S. & NAGAMASU H. 1998: Systematic studies of Bornean Zingiberaceae I. *Amomum* in Lambir Hills, Sarawak. — *Edinburgh J. Bot.* **55**: 45–64.

SAKAI S., KATO M. & INOUE T. 1999: Three pollination guilds and variation in floral characteristics of Bornean gingers (Zingiberaceae and Costaceae). — *Am. J. Bot.* **86**: 646–658.

SANGVIROTJANAPAT S., HỮU ĐĂNG T. & NEWMAN M. 2020: Ten new species of *Globba* section *Globba* from continental South-East Asia. — *Thai Forest Bull. (Bot.)* **48**: 212–233.

SATURNI F.T., JAFFÉ R. & METZGER J.P. 2016: Landscape structure influences bee community and coffee pollination at different spatial scales. — *Agricult. Ecosyst. Environ.* **235**: 1–12.

SCHEMSKE D.W. & HORVITZ C.C. 1984: Variation among floral visitors in pollination ability: A precondition for mutualism specialization. — *Science* **225**: 519–521.

SIMPSON B.B. & NEFF J.L. 1981: Floral rewards: Alternatives to pollen and nectar. — *Ann. Missouri Bot. Garden* **68**: 301–322.

SINGER R.B. & SAZIMA M. 2001: Flower morphology and pollination mechanism in three sympatric goodyerinae orchids from Southeastern Brazil. — *Ann. Bot.* **88**: 989–997.

SOLOMON RAJU A.J., SUVARNA RAJU P. & VENKATA RAMANA K. 2014: Melittophily and malacophily in *Ipomoea pes-caprae* (Convolvulaceae). — *Taprobanica* **6**: 90–99.

SPIRA T. 2001: Plant-pollinator interactions: A threatened mutualism with implications for the ecology and management of rare plants. — *Nature Areas J.* **21**: 78–88.

STAVERT J.R., BAILEY C., KIRKLAND L. & RADER R. 2020: Pollen tube growth from multiple pollinator visits more accurately quantifies pollinator performance and plant reproduction. — *Sci. Rep.* **10**: 16958, 10 pp.

STORK N.E. 2018: How many species of insects and other terrestrial arthropods are there on Earth? — *Annu. Rev. Entomol.* **63**: 31–45.

STRUWE L. 2016: *Field Identification of the 50 Most Common Plant Families in Temperate Regions (Including Agricultural, Horticultural, and Wild Species).* Rutgers University, New Brunswick, NJ, 60 pp.

SU Q., QI L., ZHANG W., YUN Y., ZHAO Y. & PENG Y. 2020: Biodiversity survey of flower-visiting spiders based on literature review and field study. — *Environ. Entomol.* **49**: 673–682.

SYAMSUARDI, MANSYURDIN, NURAINAS & SUSANTI T. 2010: Variasi morfologi polen genus *Globba* (Zingiberaceae) di Sumatra Barat. — *Berkala Penelitian Hayati* **16**: 89–94.

TAKANO A., GISIL J., YUSOFF M. & TACHI T. 2005: Floral and pollinator behaviour of flexistylous Bornean ginger, *Alpinia nieuwenhuizii* (Zingiberaceae). — *Plant Syst. Evol.* **252**: 167–173.

TANAKA N., UEHARA K. & MURATA J. 2004: Correlation between pollen morphology and pollination mechanisms in the Hydrocharitaceae. — *J. Plant Res.* **117**: 265–276.

TANDON V., KUMAR A., RANA C. & RANA A. 2016: Pollination – its type, threats and role in environment conservation. — *Int. J. Curr. Res.* **8**: 35744–35751.

THEILADE I. 1999: A synopsis of the genus *Zingiber* (Zingiberaceae) in Thailand. — *Nordic J. Bot.* **19**: 389–410.

THOMAS G.E., GEETHA K.A., AUGUSTINE L., MAMIYIL S. & THOMAS G. 2016: Analyses between reproductive behavior, genetic diversity and pythium responsiveness in *Zingiber* spp. reveal an adaptive significance for hemiclonality. — *Front. Plant Sci.* **7**: 1913, 13 pp.

THOMPSON J.D. 2001: How do visitation patterns vary among pollinators in relation to floral display and floral design in a generalist pollination system? — *Oecologia* **126**: 386–394.

VAN DER NIET T., JÜRGENS A. & JOHNSON S.D. 2010: Pollinators, floral morphology and scent chemistry in the Southern African orchid genus *Schizochilus*. — *Sth Afr. J. Bot.* **76**: 726–738.

WANG G., CHEN J., LI Z.-B., ZHANG F.-P. & YANG D.-R. 2014: Has pollination mode shaped the evolution of *Ficus* pollen? — *PLoS ONE* **9**(1): e86231, 7 pp.

WARREN S., HARPER K. & BOOTH G. 1988: Elevational distribution of insect pollinators. — *Am. Midland Nat.* **120**: 325–330.

WEIBLEN G.D. 2002: How to be a fig wasp. — *Annu. Rev. Entomol.* **47**: 299–330.

WHITEHEAD M.R. & PEAKALL R. 2009: Integrating floral scent, pollination ecology and population genetics. — *Funct. Ecol.* **23**: 863–874.

WILCOCK C. & NEILAND R. 2002: Pollination failure in plants: why it happens and when it matters. — *Trends Plant Sci.* **7**: 270–277.

WILSON E.O. 1992: *The Diversity of Life*. Harvard University Press, 424 pp.

WOJCIK V. 2021: Pollinators: Their evolution, ecology, management, and conservation. Arthropods. In Ranz R.E.R. (ed.): *Arthropods – Are they Beneficial for Mankind?* IntechOpen, 22 pp

WOLFE L. & SOWELL D. 2006: Do pollination syndromes partition the pollinator community? A test using four sympatric morning glory species. — *Int. J. Plant Sci.* **167**: 1169–1175.

WRIGHT G.A. & SCHIESTL F.P. 2009: The evolution of floral scent: the influence of olfactory learning by insect pollinators on the honest signalling of floral rewards. — *Funct. Ecol.* **23**: 841–851.

Xu Z. & Chang L. 2017: Zingiberaceae. In Xu Z. & Chang L. (eds): *Identification and Control of Common Weeds. Vol. 3*. Springer, Singapore, pp. 909–911.

Yue Y., Yu R. & Fan Y. 2014: Characterization of two monoterpene synthases involved in floral scent formation in *Hedychium coronarium*. — *Planta* **240**: 745–762.

Zahara M., Hasanah M. & Zalianda R. 2018: Identification of Zingiberaceae as medicinal plants in Gunung Cut Village, Aceh Barat Daya, Indonesia. — *J. Trop. Horticult.* **1**: 24–28.

Zhang L., Li Q.-J., Deng X.-B., Ren P.-Y. & Gao J.-Y. 2003: Reproductive biology of *Alpinia blepharocalyx* (Zingiberaceae): another example of flexistyly. — *Plant Syst. Evol.* **241**: 67–76.

Zhang Z.-Q., Kress W.J., Xie W.-J., Ren P.-Y., Gao J.-Y. & Li Q.-J. 2010: Reproductive biology of two Himalayan alpine gingers (*Roscoea* spp., Zingiberaceae) in China: pollination syndrome and compensatory floral mechanisms. — *Plant Biol.* **13**: 582–589.

Zhang Y.-W., Zhao J.-M. & Inouye D.W. 2013: Nectar thieves influence reproductive fitness by altering behaviour of nectar robbers and legitimate pollinators in *Corydalis ambigua* (Fumariaceae). — *J. Ecol.* **102**: 229–237.

Zhou Y., Abbas F., Wang Z., Yu Y., Yue Y., Li X., Yu R. & Fan Y. 2021: HS-SPME-GC-MS and electronic nose reveal differences in the volatile profiles of *Hedychium* flowers. — *Molecules* **26**: 5425, 15 pp.

Zito P., Rosselli S., Bruno M., Maggio A. & Sajeva M. 2019: Floral scent in a sexually deceptive *Ophrys* orchid: from headspace collections to solvent extractions. — *Plant Signal. Behav.* **14**: 1552056, 6 pp.

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