



---

**Pollen flower classification now and then: Vogel (1978)  
revisited**

Journal:	<i>Plant Biology</i>
Manuscript ID	Draft
Wiley - Manuscript type:	Research Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Melo, Lilian; Uppsala Universitet, Department of Ecology and Genetics Vasconcelos, Thais; University of Michigan-Ann Arbor, Department of Ecology and Evolutionary Biology Brito, Vinícius; Universidade Federal de Uberlândia, Instituto de Biologia
Keyword:	ambophily, androecium, buzz pollination, floral traits, pollination syndrome, stamen

SCHOLARONE™  
Manuscripts

1                   **Pollen flower classification now and then: Vogel (1978) revisited**

2

3                   Melo L.R.F. <sup>1,2\*</sup>, Vasconcelos T.<sup>3</sup>, & Brito V.L.G.<sup>4</sup>

4                   <sup>1</sup>Postgraduate Program in Ecology, Conservation and Biodiversity - Institute of Biology, Federal University of  
5                   Uberlândia, Uberlândia, Minas Gerais, Brazil.

6                   <sup>2</sup> Department of Ecology and Genetics, Evolutionary Biology Centre, Uppsala University, 752 36 Uppsala, Sweden.

7                   <sup>3</sup> Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA.

8                   <sup>4</sup> Institute of Biology, Federal University of Uberlândia, Uberlândia, Minas Gerais, Brazil.

9  
10                   \*Corresponding author: [lilian.melo@ebc.uu.se](mailto:lilian.melo@ebc.uu.se); +46 736517729

11  
12                   Short title: Pollen flower classification

13                   Key message of the paper: A new classification of pollen flowers has been proposed in a more objective way that  
14                   allows these flowers to be recognized and compared based on their morphological traits.

15

16

17

18                   **Abstract**

- 19                   • “Pollen flower” describes flowers that present pollen as the only resource  
20                   available for their pollinators. Such flowers are mainly pollinated by bees and  
21                   present a series of morphological and functional adaptations, especially in their  
22                   male reproductive organs, related to their tight interaction with pollinators. In  
23                   1978, these adaptations led the botanist Stefan Vogel to classify pollen flowers  
24                   into three types: *Magnolian*, *Papaver* and *Solanum*. However, Vogel’s  
25                   classification was based on limited access to data from that time and, for that  
26                   reason, it did not encompass all the variability of floral traits and ecological  
27                   interactions that pollen flowers are currently known to present.
- 28                   • In this study, we revisit the pollen flower classification of Vogel to assess whether  
29                   it can still accurately describe the currently known diversity of pollen flowers or  
30                   whether a new classification is needed.
- 31                   • Pollen flowers were identified in 75 of the 420 angiosperm families recognized  
32                   in the APG IV. Analyses of their floral morphospace identified three functional  
33                   groups that are different from the original categorization proposed by Vogel and  
34                   are here named poricidal type, inconspicuous type, and brush-blossom type.
- 35                   • We propose a new classification that is more objective and allows pollen flowers  
36                   to be compared using only their morphology rather than the type of pollinator  
37                   that visits them.

38                   Key-words: ambophily, androecium, buzz pollination, floral traits, pollination syndrome,  
39                   stamen.

## Introduction

Despite their high variability in flower morphology, all angiosperm species produce pollen grains as the male gamete carriers during their sexual reproduction. Pollen grains may also attract and can be directly consumed by pollinators creating an evolutionary dilemma: pollen is needed as both a nutritive resource for pollinators and for plant reproduction (Westerkamp 1996; Luo *et al.* 2008). Such dilemma is deeper in flowers that offer only or mainly pollen as a reward for pollinators. The botanist Stefan Vogel (1978) called these flowers “pollen flowers”, in contrast to other flowers that offer, for example, nectar, oil, or resin as reward to pollinators. In his own words

“... these are flowers which offer a surplus of pollen as the only reward to their insect visitors, instead of nectar or other substances”.

Although the evolutionary transitions between pollen flowers and those that have other types of floral resources have been discussed since the beginning of the 19<sup>th</sup> century (Stäger 1092; Beutler 1953) it was in this seminal paper that Vogel firstly described their evolutionary trends, presenting a classification based on both floral morphology and potential pollinators. He described the morphological traits of pollen flowers, especially of the male reproductive organs, based on presumed floral adaptations to interaction with pollinators, especially bees. He classified all variability of pollen flowers in three basic floral types called: *Magnolian*, *Papaver*, and *Solanum*.

According to Vogel, the *Magnolian* type would represent the most “ancestral” pollen flower. The high amount of pollen in this group is related to primary polyandry, inherited from anemophilous ancestors. This assumption was also shared by contemporaneous botanists such as Cronquist (1968), who believed that an androecium

63 with many stamens was more “primitive” than those observed in oligandric flowers. The  
64 main representatives of this floral type are found in the orders Magnoliales and  
65 Nymphaeales and the pollen grains, released by small stamens, are directly eaten by  
66 beetles, which are also the main pollinators of this flower type. The *Papaver* type is also  
67 polyandric. In such flowers, pollen is predominantly used by female bees not to be  
68 directly eaten but to feed their offspring and, for this reason, this type was considered  
69 a specialization within the melittophily syndrome. Polyandric families such as  
70 Papaveraceae and Ranunculaceae represent this floral type, in addition to members of  
71 Ochnaceae, Dilleniaceae, and Cistaceae. Finally, the *Solanum* type comprised all  
72 oligandric, and often zygomorphic, pollen flowers. This type was considered strictly  
73 melittophilous and floral visitors have a morphological match with flowers during the  
74 visit. Pollen is released in small portions like a cloud, from the mechanical vibratory  
75 movements produced by the bees. Still according to Vogel (Vogel 1978), although some  
76 of these oligandric pollen flowers, such as Primulales, Melastomataceae, and  
77 Commelinales, probably never had nectaries, many ancestral representatives of the  
78 *Solanum* type are derived from oligandric nectar flowers, which sometimes still show a  
79 rudimentary and non-functional nectary.

80 Over the past years, there have been significant advancements in our  
81 understanding of floral trait evolution and plant-pollinator interactions (Hetherington-  
82 Rauth & Johnson 2020; Phillips *et al.* 2020; Mackin *et al.* 2021). However, it is surprising  
83 to note that there has been limited exploration regarding pollen flower classification  
84 since Vogel's seminal research, which is now more than four decades old. Vogel  
85 mentioned 37 flowering plant families to exemplify his pollen flower types and their

interaction with pollinators. Though this shows an extensive knowledge of the subject given the information accessibility of that time, it is noteworthy that his categorization was based on the angiosperm classification systems contemporary to his time (e.g., (Cronquist 1981; Takhtajan 1980). Furthermore, Vogel emphasized an evolutionary hierarchy between his three floral types (from the most 'primitive' - *Magnolian*, to the most 'modern' or 'derived' - *Solanum*) which is no longer coherent with our current understanding of the evolutionary history of floral traits. Several environmental conditions can impact the evolution of floral traits (Mackin *et al.* 2021; Trunschke *et al.* 2021) and, given that different traits are under different selective pressures (Melo *et al.* 2021; Kriebel *et al.* 2022), we cannot generalize whole clades as being more or less evolved. Moreover, there is little information about the distribution of pollen flowers in modern phylogenies, which precludes our understanding of whether different pollen flower types evolved sequentially, as proposed by Vogel, or independently, appearing several times in different clades.

In this study, we revisit Vogel's seminal work on the classification of pollen flowers with three specific aims: 1) to review which angiosperms families have species with pollen flowers in the current classification of the Angiosperm Phylogeny Group IV (APG IV); 2) to analyse the phylogenetic distribution of pollen flowers in modern family-level angiosperm phylogenies to understand how they might have evolved and; 3) to analyse whether the floral types coined by Vogel have statistical support, based on our current knowledge of pollen flower biology.

## Methods

### *Angiosperm families with pollen flowers*

To compile a comprehensive list of flowering plant families that present species with pollen flowers, published data was reviewed by searching papers published from 1978 until 2022. We used the Angiosperm Phylogeny Group IV - henceforward APG IV (Chase *et al.* 2016) classification, which recognizes 64 orders and about 416 families, as a reference for our search, using each family name as a search term until all 416 families were covered. The review was performed using mainly two platforms: the Angiosperm Phylogeny website (Stevens 2016), and Google Scholar. In addition, taxonomical publications with species descriptions and herbarium photos available online (nybg.org) and, Re flora (reflora.jbrj.gov.br) were consulted to confirm some morphological traits. Family names cited before 2016, including those in Vogel (1978), required synonymization because taxonomic classification has changed over time and some families or genera have been split or merged into other groups (Stevens 2016).

### *Trait data scoring*

From each of the plant families sampled, the following three floral traits were recovered from Vogel's original work: (1) type of anther dehiscence (poricidal or longitudinal), (2) pollen release (shed, exposed or small portions) and (3) number of stamens (polyandric or oligandric). Pollinator's type and behaviour, criteria investigated by Vogel, was not included in the analysis because they are extrinsic factors not directly linked to floral morphology. We did, however, take note of primary pollinators (bees, beetles, or others) and their interactions with the flower when this information was available (Table SI-1).

With this information gathered, we selected additional traits that are currently known to influence the behaviour of pollinators in pollen flowers and could improve floral type classification. The new traits annotated were: (1) stamen dimorphism (Vogel 1978; Vallejo-Marin *et al.* 2009), (2) isolated or grouped flowers (Krick & Ackerman 2015; Costa *et al.* 2017; Timerman & Barrett 2018), (3) floral display as “shooting-star”, “brush-blossom” or none (Russell *et al.* 2016), (4) reduced petals (Matthews & Endress 2006), (5) colour contrasting stamen in relation to the petal colour (Lunau *et al.* 2017; Dellinger *et al.* 2021; Melo *et al.* 2021), (6) radial or zygomorphic floral symmetry (Stebbins 1974; Marazzi *et al.* 2007; Vallejo-Marín *et al.* 2010), (7) diurnal or nocturnal anthesis (Cordeiro *et al.* 2021), and (8) other floral resources (e.g., thermogenesis and oil offered by glands) (Silberbauer-Gottsberger *et al.* 2001). These new floral traits were selected based on their morphological relevance and functional importance during flower-pollinator interaction (Stebbins 1951; Sargent 2004; Endress 2011; Paterno *et al.* 2020) - Table SI-2.

To perform a statistical revaluation of the pollen flower types described by Vogel (1978), we compared three morphospaces. The first one included only the three floral traits and angiosperm families mentioned by Vogel (Vogel 1978). The second uses only the three floral traits mentioned by Vogel but includes both the original families cited by him plus those recovered as having pollen flowers in our literature review. Finally, the third morphospace includes all families (original Vogel plus our review) and uses eight additional floral traits that were found to be relevant to pollen flower pollination along our review. By comparing the three morphospaces, our goal was to discuss how adding new possibilities of trait combinations could cluster new pollen-flower groups.

The scoring was performed at the family level, i.e., the attributed value refers to the existence of at least one species or genus with those traits in that family - as listed in - Table SI-1. For example, although we know that not all Fabaceae species have pollen flowers, the family was included in our list because some genera and species within this family have pollen flowers. In fact, in the case of Fabaceae, there are two clearly distinct types of pollen flowers within the family, which here are called Fabaceae 1 (e.g., *Acacia* sp. and *Swartzia* sp.) and Fabaceae 2 (e.g., *Cassia* sp., *Chamaecrista* sp. and *Senna* sp.). With the exception of Fabaceae where at least two types of pollen flowers are clearly present, all other families were represented by a single data point.

#### *Morphospaces and Cluster Analysis*

To visualize how families are distributed in the morphospace, we performed non-metric multidimensional scaling (NMDS) based on floral traits considering the Euclidean distances between data points, using the *metaMDS* function of the *vegan* package (Oksanen *et al.* 2022) to find a stable solution. We used several random starts and the *geom\_jitter* function of the *ggplot2* package (Wickham 2016), which adds a small amount of random variation to the location of each point, for visualization.

Subsequently, to assess whether there was statistical support for clustering of families in the morphospace, a *k*-means cluster analysis was performed based on the family scores on the NMDS1 and NMDS2 axis of the morphospace. *K*-mean clustering is a simple non-supervised algorithm that estimates the best position of the centroid for each previously defined *k* clusters on the morphospace by minimizing the distances between the centroid and the data points (Frades & Matthiesen 2010). At the end of the process, a given data point (family) is ascribed to its nearest centroid, defining the



clusters. To search for the optimal cluster number, we used a gap statistic which compares the total intracluster variation for different values of  $k$  (in our case from 2 to 10) with their expected values under a null reference distribution generated by Monte Carlo simulations (Tibshirani *et al.* 2001). The gap statistic is computed using the function *clusGap* from the *cluster* package (Maechler *et al.* 2022). The optimal number of clusters is the one with highest gap statistic which can be assessed using the function *fviz\_gap\_stat* from the package *factoextra* (Kassambara & Mundt 2020). All analyses were performed in the R environment (Core Team 2020).

### *Phylogenetic distribution of pollen flowers*

We used the family-level phylogeny of seed plants made by (Qian & Zhang 2014) to visualize the distribution of families with different pollen flower types over the angiosperm phylogeny. This phylogeny included 425 families of angiosperms – (12 gymnosperms families were removed) and was chosen because it is appropriate for phylogenetic analyses of functional traits at the family-level, being the closest family-level phylogeny to the current classification (APG IV) used to review families with pollen flowers. We indicated the presence of the different flower pollen types in this family-level phylogeny using iTOL - Interactive Tree of Life (Letunic & Bork 2021).

## **Results**

### *Pollen flower types based on morphological traits*

Vogel's original work described species or genera of pollen flowers in 38 botanical families belonging to 19 angiosperm orders, of which eight belonged to the *Magnolian* type, 11 to the *Papaver* type and 18 to the *Solanum* type. In our review, 130

works were analysed, including books and papers and we identified 78 families presenting pollen flowers and belonging to 28 angiosperm orders (Table SI-1). The 40 newly recognized families encompass species with pollen flowers in at least one of their genera. The families Corsiaceae, Rhabdodrendaceae, Clethraceae, Calceolariaceae, and Hydnoraceae present species with pollen flowers, but they were removed from subsequent analyses due to limited morphological data.

We identified a clear clustering in the morphospace built using the original three floral traits and 38 families of pollen flowers proposed in Vogel's original work (Figure 1A). However, when all 73 families with pollen flowers are analysed for these traits, an overlap between clusters is observed, showing that the original traits do not allow a clear distinction between the pollen flower types proposed by Vogel when current pollen flower diversity is considered (Figure 1B). Finally, when analysing the morphospace containing all 73 families and adding the eight additional floral traits, we recover three clusters, suggesting three floral types (Figure 1C). These new clusters, however, do not coincide with Vogel's original types in terms of traits nor taxonomic representation at the family level.

In these new clusters, we found that the vast majority of pollen flowers analysed are bisexual, presenting gynoecium and androecium in the same flower. The first group of pollen flowers is composed of plant families that present flowers with anthers with longitudinal dehiscence, shed or exposed pollen grains, radial symmetry, many stamens (polyandric) and commonly brush-blossom floral display. This group, which we call the "brush-blossom type" (Figure 2A) includes families such as Myrtaceae, Lythraceae, Papaveraceae, Magnoliaceae, Nymphaeaceae, among others (Table SI-3). The second

group is composed of families that also have flowers with anthers with longitudinal dehiscence. However, in this group, their flowers are mostly grouped, small and with reduced petals and few stamens (oligandric). The families Araceae, Canellaceae, Cyperaceae, Ruppiaceae, among others, belong to this group (Table SI-3), which we call the “inconspicuous type” (Figure 2B). The last group comprises families that mostly have anthers with poricidal dehiscence and the pollen grains being released through small portions. In addition, they often have few stamens (oligandric), which contrast with the petal’s colours, radial symmetry, and a shooting-star floral display (Vallejo-Marin & Russell 2024). We call this the “poricidal type” (Figure 2C). This group includes families such as Melastomataceae, Primulaceae, Commelinaceae, Iridaceae, Ochnaceae, Solanaceae and Fabaceae 2 (Table SI-3).

#### *Distribution of pollen flowers in the angiosperm phylogeny*

A visualization of the phylogenetic distribution of pollen flowers over the angiosperm phylogeny suggests that there is no single origin for any of the pollen flower types recognized in our analyses. They have probably arisen several times independently, under different pressures and environmental contexts. The brush-blossom type is more common within the ANA grade, the Magnoliids and Monocots clades. The poricidal type, on the other hand, is represented by families in several clades throughout the phylogeny, from Magnoliids to Asterids. Finally, the inconspicuous type also has a more restricted distribution to clades of early diversification within flowering plants (Figure 3).

## **Discussion**

The three pollen flower types originally proposed by Vogel do not comprise all the morphological diversity of pollen flowers currently known. By including new information on floral diversity and updated angiosperm classification, our results recovered 40 additional families with pollen flowers than what had been described in Vogel's 1978 seminal work. This means a significant increase in the number of families and potentially morphological diversity of pollen flowers, which also allowed us to refine the interpretation of floral types based on their shared morphology. Our results show that, considering recent data on floral traits linked to interaction with pollinators, pollen flowers are better classified in three new functional types. These previously unveiled morphological combinations, together with the pollination systems that they may be associated with, is likely to facilitate our understanding of the ecology and evolution of pollen flowers.

#### *The role of pollination biology studies in understanding pollen flower classification*

Pollination syndromes and floral biology had been debated long before the first studies on pollen flowers (Stäger 1092; Vogel 1954; Werth 1956; van der Pijl 1961; Faegri & van Der Pijl 1966) and the types proposed by Vogel were important for understanding the interaction between these flowers and their pollinators. However, Vogel grouped families that are very morphologically distinct together based mainly on the fact that they tend to be pollinated by similar functional group of pollinators (e.g., he classified Araceae and Magnoliaceae flowers as *Magnolian* type due to beetle pollination), rather than classifying them in terms of individual floral traits, which in turn can be easily measured and compared. Including information about the pollination biology in this type of categorization may be impractical because, despite the conserved floral morphology within species, floral visitors can be diverse and vary with location (Lefebvre

et al. 2018; Dellinger et al. 2021). However, information on pollination biology can be used *a posteriori* to interpret morphological groupings, as exemplified by analyses of pollination syndromes (Ollerton et al. 2009).

Currently, some plant-pollinator interactions in pollen flowers are already well known and described (e.g., Melastomataceae and bees (Konzmann et al. 2020; Bochorny et al. 2021; Passos et al. 2022; Valadão-Mendes et al. 2022). However, others need more studies and observations, such as plants that show ambophily, as some flowers in Cyperaceae. This family is characteristically anemophilous, but there are some reports of species adapted to entomophily as well. For example, reproductive tests indicated that *Rhynchospora ciliata* is self-incompatible and that ambophily enhances its reproductive success (Costa & Machado 2012). Ambophily, i.e., plants that are pollinated either by biotic or abiotic vectors (Culley et al. 2002), are not addressed by Vogel in his work. However, in our literature review we identified at least 10 families with flowers that offer only pollen as floral resource for insect pollinators that may also spread their pollen through wind (e.g., Cyperaceae and Ranunculaceae) or water (Hydrocharitaceae and Ruppiaceae) (Tanaka et al. 2004; Duan et al. 2009; Costa et al. 2017), all of which belong to the inconspicuous type as described here. As stated earlier, information about the pollination systems of these families is still scarce and further investigations are needed. It is also necessary to understand whether these ambophilous examples are truly adapted to two pollination modes, or whether they are mainly adapted to aquatic ecosystems (Taylor et al. 2018), or to wind, like some anemophilous systems (Tanaka et al. 2004), and only opportunistically use insects as vectors. In addition, some plants, like some of the families mentioned above

(Cyperaceae and Hydrocharitaceae), can act in more than one pollination mode and thus ensure greater reproductive success (Tanaka *et al.* 2004; Costa & Machado 2012; Costa *et al.* 2017).

#### *A new perspective on the diversity of pollen flowers*

Vogel's classification leaves little room for trait combinations that do not strictly follow one of his originally proposed pollen flower types. Therefore, families or clusters that have unpredicted trait combinations are not classifiable in his system. For example, the genus *Dalechampia* (Euphorbiaceae) has species with both poricidal anthers and polyandry and belongs to our newly categorized brush-blossom type, but it does not fit into any of Vogel's original floral types (Armbruster *et al.* 2013). Although we also found three functional clusters of pollen flowers, our classification is perhaps more flexible because the new clusters include previously unclassifiable families. Also, the new classification is more objective, and the plants can be compared depending on their morphological traits, and not directly on the type of pollinator that visits them.

When we compare both classifications, our brush-blossom type brings together eight families of the *Papaver* type and six families of the *Magnolian* type of Vogel's (1978). In addition to these, nine new families containing a set of specific traits of this group are presented (Table SI-3). It is interesting to note that this group includes two of the families that named two of Vogel's three original floral types, namely Papaveraceae and Magnoliaceae. The fact that they belong to the same group in our new classification highlights the similarities in their floral traits. Flowers of the brush-blossom type usually have large and striking petals. The stamens are many, sometimes contrasting with the petals, and are often highlighted in a brush-blossom display, which favours the contact

of floral visitors with the anthers with longitudinal dehiscence. Thus, we suggest that this group has the most morphologically generalist pollen flowers - sensu (Ollerton *et al.* 2011), as they are attractive (considering their colours, shapes, and sizes) to different pollinator groups, and the pollen grains are completely available. For the flowers analysed from these families, visits from beetles, bees, flies, thrips, and other small insects were reported in the literature (Endress 1986; Bhunia *et al.* 2012; Erbar 2014).

According to our newly proposed classification, the inconspicuous type is not very representative for the families originally presented by Vogel. Only three families cited by Vogel were classified within this group (Philydraceae, formerly *Solanum* type, and Araceae and Pandanaceae, formerly *Magnolian* type). None of the other 18 families belonging to this group were considered by Vogel's seminal paper, including Juncaginaceae, Piperaceae, Poaceae, Zosteraceae, among others (Table SI-3). It is worth to mention that they were not considered at the time of Vogel's work perhaps because they were seen only as anemophilous flowers. However, some more recent studies have proposed that the floral structures do offer resources and allow legitimate interactions with animal pollinators in Cyperaceae, Poaceae and Trimeniaceae (Bernhardt *et al.* 2003; Wolowski & Freitas 2015; Costa *et al.* 2017). The main morphological traits of the flowers of this cluster are related to the pollination systems in which these pollen flowers are involved. For example, although many of these flowers have reduced petals (thus being comparatively less attractive to animal pollinators than other pollen flower types), longitudinal dehiscence may leave pollen grains more exposed to visitors and easily accessible during the plant-pollinator interaction (Costa *et al.* 2017). The studies reviewed reported visits by beetles, flies, hoverflies, bees, some small insects and even

vertebrates in flowers of this group, such as the pollination of *Freycinetia reineckeii* (Pandanaceae) by flying foxes (Pteropidae – flying foxes) (Cox 1990).

There are 28 families in the poricidal type, including 18 families that belonged to Vogel's *Solanum* type; two families, classified as *Papaver* type (Begoniaceae and Ericaceae) and seven new families included by our review (Asphodelaceae, Euphorbiaceae, Iridaceae, Mayacaceae, Pittosporaceae, Pontederiaceae and Tecophilaeaceae). Most families, unlike those in the other two groups, bear anthers with poricidal dehiscence. In this way, pollen is not easily accessible and is released in small portions like a cloud by mechanical vibratory movements of bees (De Luca & Vallejo-Marín 2013). This interaction is known as *buzz pollination* and occurs in species from 65 angiosperm families (De Luca & Vallejo-Marín 2013; Vallejo-Marín 2019). Vogel presented the *Solanum* type as being the most specialized (i.e. strictly 'melittophilous') and, in fact, poricidal anthers may exclude some visitors (e.g. pollen eating beetles and flies), which corroborates a more specialized interaction (De Luca & Vallejo-Marín 2013).

In addition, poricidal anthers combined with stamen dimorphism, another common trait in families of this group, can help increase the efficiency of pollen transfer by releasing pollen into specific areas of the pollinator's body called "safe sites" (Vallejo-Marín & Russell 2024; Koch *et al.* 2017). Heteranthery occur in 16 families of angiosperms (Vallejo-Marín *et al.* 2010), 12 of which present pollen flowers (Aizoaceae, Commelinaceae, Tecophilaeaceae, Dilleniaceae, Malvaceae, Bixaceae, Fabaceae 2 (*Cassia*, *Senna* and *Chamaecrista*), Lythraceae, Malpighiaceae, Melastomataceae, Lecythidaceae, and Solanaceae). As one set of stamens offer pollen grains as a food source for bees while the other produce pollen for pollination, the presence of two



stamen sets of different morphologies within the same flower has been interpreted as a functional division of labour (Luo *et al.* 2008; Vallejo-Marin *et al.* 2009). The two sets of stamens can be distinct in their colour, for instance when one set present colour contrast in relation to the petal, while the other set has a cryptic colour, such as *Microlicia cordata* (Melastomataceae) (Velloso *et al.* 2018). In other cases, the difference in size between the sets of stamens may be more relevant than the colour contrast - as seen in (Brito *et al.* 2021; Melo *et al.* 2021). The division of labour between the two sets of stamens further reinforces the presence of a well-specialized plant-pollinator relationship (Dellinger *et al.* 2019; Telles *et al.* 2020; Nunes *et al.* 2021).

The floral traits associated with the poricidal type are seen as an evolutionary convergence to the “solanoid” floral form which has been pointed out several times in the past by Delpino (1868) and cited in (Vallejo-Marin & Russell 2024; Macior 1964; Faegri 1986; Harder & Barclay 1994). Some common traits of these flowers are reflected petals, prominent stamen cone, poricidal anthers and absence of nectar (Endress 1994; Matthews & Endress 2002). Flowers that have reflected petals often present a shooting-star display, which strongly highlight their stamens at the front of the flower. Even though these flowers have few stamens, these are prominent to floral visitors (Harder & Barclay 1994). The evolution of poricidal dehiscent anthers likely had a significant impact on the ability of different types of pollinators to remove pollen (Buchmann 1983; De Luca & Vallejo-Marin 2013; Pereira Nunes & Vallejo-Marin 2022). Although pollen release by vibration is not associated with a single type of floral morphology (Buchmann 1983), some floral morphologies, such as “solanoid” or “*Solanum type*”, appear to have evolved specifically in response to pollen collection by vibrating bees and represents an adaptative peak for *buzz-pollinated* plants (Vallejo-Marin & Russell 2024; Faegri & van

Der Pijl 1966; Vogel 1978; Harder & Barclay 1994; Matthews & Endress 2002; De Luca & Vallejo-Marin 2013). In his work, Vogel (1978) focuses on pollination by deceit, and the flowers belonging to this group are those that present the morphology that best allows the flower to “deceive” the pollinator [e.g. ref]. In that way, the poricidal type is perhaps the closest representation of the more classic view of pollen flower in the context originally proposed by Vogel.

During our review, we noticed that *buzz pollination* occurs in families that do not belong to the poricidal type. Thus, this pollination mode is not exclusive to plants with poricidal anthers. Bees may also perform vibratory movements to collect pollen in some plants with longitudinal opening anther, such as the flowers of the genus *Swartzia* (Fabaceae 1) that are visited by carpenter bees (*Xylocopa*) (Lopes & Machado 1996; Pinheiro *et al.* 2018; Basso-Alves *et al.* 2022). Other authors, including Vogel himself, also mention the use of vibration in the pollination of other species with non-poricidal anthers (Buchmann 1985; de Oliveira & Sazima 1990; Fidalgo *et al.* 2009; Nevard *et al.* 2021).

#### *Pollen flowers in the angiosperm phylogeny*

The brush-blossom flowers are common in early-diverging angiosperm families, such as those of the ANA grade, Magnoliids and Chloranthales. They can be also found in families of the order Ranunculales, as well as in Myrtales and Caryophyllales. Although most prevalent in these groups, this type of flower has likely arisen multiple times throughout evolutionary history of flowering plants. Many families within the brush-blossom type are classified as *Magnolian* type according to the classification proposed by Vogel (1978). In his work, he suggested that these flowers probably predated nectar

flowers and could be the oldest pollen flowers in the evolutionary history of angiosperms. Interestingly, a recent reconstruction of the flower of the most recent common ancestor of all extant angiosperms bears a remarkable resemblance to the flowers found in the brush-blossom type (Sauquet *et al.* 2017), potentially supporting Vogel's idea.

Families belonging to the poricidal type are not present among the early-diverging angiosperm families. The diversification of these flowers is probably influenced by several biotic and abiotic factors in their respective habitats (*e.g.*, pollinators, temperature) and the emergence of important innovations (traits flexibility) that may have facilitated the adaptation and diversification of these plants as suggested by (Onstein 2020). The inconspicuous type families tend to appear earlier on the phylogeny. They can be found in the clades Canellales, Piperales, Pandanales, Poales and Ranunculales. Its emergence is less frequent and concentrated in clades that share a common origin. This indicates that they form a more conserved group within the evolutionary history of pollen flowers. It is important to note that most of the families mentioned in this category were not included in Vogel's work and were only recognized for having pollen flowers after our study.

## Conclusion

Vogel's work in 1978 was undoubtedly significant for classifying flower types based on their interactions with pollinators. However, we find that his original classification is insufficient considering our current understanding of the vast diversity of pollen flowers. Attempting to fit all recognized pollen flowers into the existing floral types of *Magnolian*, *Papaver*, and *Solanum* would be impractical and insufficient. In our

research, we present a new perspective on the classification of pollen flowers. Rather than relying mainly on pollinator interaction, we advocate the analysis of individual morphological traits, spanning the full spectrum of known pollen flower diversity. By expanding the sampling of floral morphological traits, we can reach a wider range of combinations between these characters. In conclusion, our research suggests a move away from Vogel's classification and encourages a more inclusive and comprehensive classification of pollen flowers based on morphological traits.

#### Acknowledgements

We thank Anselmo Nogueira, Agnes Dellinger, Lucas Bacci, Thuane Bochorony, Marcelo Monge, and Ana Flávia Versiane as well as one anonymous reviewer for their feedback helping us to improve your manuscript substantially. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brazil (CAPES) – Finance Code 001 to LRFM. Fundação de Amparo à Pesquisa do Estado de Minas Gerais [grant RED-00253-16 and RED-00039-23] and Conselho Nacional de Desenvolvimento Científico e Tecnológico [grants 308107/2021-7, 423939/2021-1, 401843/2022-0 and 350145/2022-9 to VLGB].

## References

- Armbruster W.S., Lee J., Edwards M.E., Baldwin B.G. (2013) Floral paedomorphy leads to secondary specialization in pollination of Madagascar *Dalechampia* (Euphorbiaceae). *Evolution* **67**:1196–1203.
- Basso-Alves J.P., da Silva R.F., Coimbra G., Leitão S.G., de Rezende C.M., Bizzo H.R., Freitas L., Paulino J.V., Mansano V. de F. (2022) Heteromorphic stamens are differentially attractive in *Swartzia* (Fabaceae) (F.X. Picó, Ed.). *AoB PLANTS* **14** [online] URL: <https://academic.oup.com/aobpla/article/doi/10.1093/aobpla/plac041/6694830>
- Bernhardt P., Sage T., Weston P., Azuma H., Lam M., Thien L.B., Bruhl J. (2003) The pollination of *Trimenia moorei* (Trimeniaceae): Floral volatiles, insect/wind pollen vectors and stigmatic self-incompatibility in a basal angiosperm. *Annals of Botany* **92**:445–458.
- Beutler R. (1953) Nectar. *Bee World* **34**:106–116. [online] URL: <https://www.tandfonline.com/doi/full/10.1080/0005772X.1953.11094798> (accessed 1 July 2022).
- Bhunia, Debasis; Mondal A.K. (2012) STUDIES ON PRODUCTION, MORPHOLOGY AND FREE AMINO ACIDS OF POLLEN OF FOUR MEMBERS IN THE GENUS NYMPHAEA L. (NYMPHAEACEAE). *IJSN* **3**:705–7018.
- Bochorny T., Bacci L.F., Dellinger A.S., Michelangeli F.A., Goldenberg R., Brito V.L.G. (2021) Connective appendages in *Huberia bradeana* (Melastomataceae) affect pollen release during buzz pollination. *Plant Biology:plb*.13244. [online] URL: <https://onlinelibrary.wiley.com/doi/10.1111/plb.13244>
- de Brito V.L.G., Leite F.B., Telles F.J., Jorge L.R., Sazima M. (2021) The attractive role of floral elements in heterantherous species without pronounced stamen differences. *Arthropod-Plant Interactions* **15**:23–31. [online] URL: <http://link.springer.com/10.1007/s11829-020-09794-1>
- Buchmann S.L. (1983) Buzz pollination in angiosperms. *Handbook of Experimental Pollination Biology*:73–113.
- Buchmann S.L. (1985) Bees Use Vibration to Aid Pollen Collection from Non-Poricidal Flowers Author ( s ): Stephen L . Buchmann Reviewed work ( s ): Source : Journal of the Kansas Entomological Society , Vol . 58 , No . 3 ( Jul . , 1985 ) , pp . 517-525 Published by : Allen Pres. Journal of the Kansas Entomological Society **58**:517–525.
- Chase M.W., Christenhusz M.J.M., Fay M.F., Byng J.W., Judd W.S., Soltis D.E., Mabberley D.J., Sennikov A.N., Soltis P.S., Stevens P.F., Briggs B., Brockington S., Chautems A., Clark J.C., Conran J., Haston E., Möller M., Moore M., Olmstead R., Perret M., Skog L., Smith J., Tank D., Vorontsova M., Weber A. (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* **181**:1–20. [online] URL: <https://academic.oup.com/botlinnean/article-lookup/doi/10.1111/boj.12385>
- Cordeiro G.D., Liporoni R., Caetano C.A., Krug C., Martínez-Martínez C.A., Martins H.O.J., Cardoso R.K.O.A., Araujo F.F., Araújo P.C.S., Oliveira R., Schlindwein C., Warrant E.J., Dötterl S., Alves-Dos-Santos I. (2021) Nocturnal Bees as Crop Pollinators. [online] URL: <https://doi.org/10.3390/agronomy11051014>
- Core Team (2020) R Core Team (2020). [online] URL: <http://www.r-project.org/index.html>
- Costa, A.C.G. & Machado I.C. (2012) Flowering dynamics and pollination system of the sedge *Rhynchospora ciliata* (Vahl) Kükenth (Cyperaceae): does ambophily enhance its reproductive success? *Plant Biology* **14**:865–1010. [online] URL: <https://onlinelibrary.wiley.com/doi/10.1111/j.1438-8677.2012.00574.x>
- Costa A.C.G., Thomas W.W., Machado I.C. (2017) Comparative floral biology of *Rhynchospora ciliata* (Vahl) Kükenth and *R. pubera* (Vahl) Boeckeler (Cyperaceae): the role of white involucral bracts in attracting pollinating insects. *Plant Species Biology* **32**:403–411. [online] URL: <https://esj-journals.onlinelibrary.wiley.com/doi/10.1111/1442-1984.12173>
- Cox P.A. (1990) Pollination and the Evolution of Breeding Systems in Pandanaceae. *Annals of the Missouri Botanical Garden* **77**:816. [online] URL: <https://www.jstor.org/stable/2399673?origin=crossref>
- Cronquist A. (1981) An integrated system of classification of flowering plants. Columbia university press
- Culley T.M., Weller S.G., Sakai A.K. (2002) The evolution of wind pollination in angiosperms. *Trends in Ecology & Evolution* **17**:361–369. [online] URL: <https://linkinghub.elsevier.com/retrieve/pii/S0169534702025405>

- De A., Fidalgo O., De A., Kleinert M.P., Fidalgo A.D.O. (2009) Reproductive biology of six Brazilian Myrtaceae: is there a syndrome associated with buzz-pollination? Reproductive biology of six Brazilian Myrtaceae: is there a syndrome associated with buzz-pollination? *New Zealand Journal of Botany* **47**:355–365. [online] URL: <https://www.tandfonline.com/action/journalInformation?journalCode=tnzb20>
- Dellinger A.S., Artuso S., Margoth Fernández-Fernández D., Schönenberger J. (2021) BRIEF COMMUNICATION Stamen dimorphism in bird-pollinated flowers: Investigating alternative hypotheses on the evolution of heteranthery.
- Dellinger A.S., Chartier M., Fernández-Fernández D., Penneys D.S., Alvear M., Almeda F., Michelangeli F.A., Staedler Y., Armbruster W.S., Schönenberger J. (2019) Beyond buzz-pollination – departures from an adaptive plateau lead to new pollination syndromes. *New Phytologist* **221**:1136–1149.
- Dellinger A.S., Pérez-Barrales R., Michelangeli F.A., Penneys D.S., Fernández-Fernández D.M., Schönenberger J. (2021) *Low bee visitation rates explain pollinator shifts to vertebrates in tropical mountains.*
- Duan Y.W., Zhang T.F., He Y.P., Liu J.Q. (2009) Insect and wind pollination of an alpine biennial *Aconitum gymandrum* (Ranunculaceae). *Plant Biology* **11**:796–802. [online] URL: <https://onlinelibrary.wiley.com/doi/10.1111/j.1438-8677.2009.00195.x>
- Endress P.K. (1986) Reproductive structures and phylogenetic significance of extant primitive Angiosperms. *Plant Systematics and Evolution* **152**:1–28.
- Endress P.K. (1994) Floral structure and evolution of primitive angiosperms: Recent advances. *Plant Systematics and Evolution* **192**:79–97.
- Endress P.K. (2011) Evolutionary diversification of the flowers in angiosperms. *American Journal of Botany* **98**:370–396.
- Erbar C. (2014) Nectar secretion and nectaries in basal angiosperms, magnoliids and non-core eudicots and a comparison with core eudicots. *Plant Diversity and Evolution* **131**:63–143. [online] URL: [http://www.schweizerbart.de/papers/pde/detail/131/82442/Nectar\\_secretion\\_and\\_nectaries\\_in\\_basal\\_angiosperm?af=crossref](http://www.schweizerbart.de/papers/pde/detail/131/82442/Nectar_secretion_and_nectaries_in_basal_angiosperm?af=crossref)
- Faegri, K., Van Der Pijl L. (1966) *The principles of pollination ecology*, Pergamon P. New York, NY, USA.
- Faegri K. (1986) The solanoid flower. *Transactions of the Botanical Society of Edinburgh* **45**:51–59.
- Frades I., Matthiesen R. (2010) Overview on Techniques in Cluster Analysis. In: pp 81–107. [online] URL: [http://link.springer.com/10.1007/978-1-60327-194-3\\_5](http://link.springer.com/10.1007/978-1-60327-194-3_5)
- Harder L.D., Barclay R.M.R. (1994) The Functional Significance of Poricidal Anthers and Buzz Pollination: Controlled Pollen Removal From Dodecatheon. *Functional Ecology* **8**:509.
- Hetherington-Rauth M.C., Johnson M.T.J. (2020) Floral Trait Evolution of Angiosperms on Pacific Islands. *The American Naturalist* **196**:87–100. [online] URL: <https://www.journals.uchicago.edu/doi/10.1086/709018>
- Jari Oksanen [aut, cre], Gavin L. Simpson [aut], F. Guillaume Blanchet [aut], Roeland Kindt [aut], Pierre Legendre [aut], Peter R. Minchin [aut], R.B. O’Hara [aut], Peter Solymos [aut], M. Henry H. Stevens [aut], Eduard Szoecs [aut], Helene Wagner [aut], J.W. [aut] (2022) Package ‘vegan.’
- Kassambara, A. and Mundt F. (2020) Factoextra: Extract and Visualize the Results of Multivariate Data Analyses. R Package Version 107 [online] URL: <https://cran.r-project.org/package=factoextra>
- Koch L., Lunau K., Wester P. (2017) To be on the safe site – Ungroomed spots on the bee’s body and their importance for pollination. *PLoS ONE* **12**:1–16.
- Konzmann S., Hilgendorf F., Niester C., Rech A.R., Lunau K. (2020) Morphological specialization of heterantherous *Rhynchanthera grandiflora* (Melastomataceae) accommodates pollinator diversity. *Plant Biology* **22**:583–590.
- Krick J., Ackerman J.D. (2015) Adding ecology to particle capture models: Numerical simulations of capture on a moving cylinder in crossflow. *Journal of Theoretical Biology* **368**:13–26.

- Kriebel R., Drew B.T., González-Gallegos J.G., Celep F., Antar G.M., Floriano J., Pastore B., Uría R., Sytsma K.J. (2022) *Stigma shape shifting in sages (Salvia: Lamiaceae): hummingbirds guided the evolution of New World floral features*. [online] URL: <https://academic.oup.com/botlinnean/article/199/1/428/6463651>
- Lefebvre V., Villemant C., Fontaine C., Daugeron C. (2018) Altitudinal, temporal and trophic partitioning of flower-visitors in Alpine communities. *Scientific Reports* **8**:4706. [online] URL: <https://www.nature.com/articles/s41598-018-23210-y>
- Letunic I., Bork P. (2021) Interactive Tree Of Life (iTOL) v5: an online tool for phylogenetic tree display and annotation. *Nucleic Acids Research* **49**:W293–W296. [online] URL: <https://academic.oup.com/nar/article/49/W1/W293/6246398>
- Lopes, Ariadna Valentina De F. E; Machado I.C. (1996) Biologia floral de *Swartzia pickelii* Killip ex Ducke (Leguminosae-Papilionoideae) e sua polinização por *Eulaema* spp. (Apidae-Euglossini). *Brazilian Journal of Botany* **19**:17–24.
- De Luca P.A., Vallejo-Marín M. (2013) What's the “buzz” about? The ecology and evolutionary significance of buzz-pollination. *Current Opinion in Plant Biology* **16**:429–435.
- Lunau K., Konzmann S., Winter L., Kamphausen V., Ren Z.X. (2017) Pollen and stamen mimicry: the alpine flora as a case study. *Arthropod-Plant Interactions* **11**:427–447.
- Luo Z., Zhang D., Renner S.S. (2008) Why two kinds of stamens in buzz-pollinated flowers? Experimental support for Darwin's division-of-labour hypothesis. *Functional Ecology* **22**:794–800.
- Macior L.W. (1964) AN EXPERIMENTAL STUDY OF THE FLORAL ECOLOGY OF DODECATHEON MEADIA. *American Journal of Botany* **51**:96–108. [online] URL: <https://onlinelibrary.wiley.com/doi/full/10.1002/j.1537-2197.1964.tb06605.x> (accessed 2 July 2022).
- Mackin C.R., Peña J.F., Blanco M.A., Balfour N.J., Castellanos M.C. (2021) Rapid evolution of a floral trait following acquisition of novel pollinators (I. Bartomeus, Ed.). *Journal of Ecology* **109**:2234–2246. [online] URL: <https://onlinelibrary.wiley.com/doi/10.1111/1365-2745.13636> (accessed 26 June 2022).
- Maechler M, Rousseeuw P, Struyf A, Hubert M H.K. (2022) cluster: Cluster Analysis Basics and Extensions. R package version 213 [online] URL: <https://cran.r-project.org/package=cluster>.
- Marazzi B., Conti E., Endress P.K. (2007) Diversity in Anthers and Stigmas in the Buzz - Pollinated Genus *Senna* (Leguminosae, Cassiinae). *International Journal of Plant Sciences* **168**:371–391. [online] URL: <http://www.jstor.org/stable/10.1086/512105>. Accessed:
- Matthews M.L., Endress P.K. (2002) Comparative floral structure and systematics in Oxalidales (Oxalidaceae, Connaraceae, Brunelliaceae, Cephalotaceae, Cunoniaceae, Elaeocarpaceae, Tremandraceae). *Botanical Journal of the Linnean Society* **140**:321–381.
- Matthews M.L., Endress P.K. (2006) Floral structure and systematics in four orders of rosids, including a broad survey of floral mucilage cells. *Plant Systematics and Evolution* **260**:199–221. [online] URL: <https://link.springer.com/10.1007/s00606-006-0443-8>
- Melo L.R.F., Vasconcelos T., Reginato M., Paula A., Caetano S., Lourenço V., Brito G. De (2021) Evolution of stamen dimetrisism in Melastomataceae, a large radiation of pollen flowers. *Perspectives in Plant Ecology, Evolution and Systematics* **48**:125589. [online] URL: <https://doi.org/10.1016/j.ppees.2021.125589>
- Nevard L., Russell A.L., Foord K., Vallejo-Marín M. (2021) Transmission of bee-like vibrations in buzz-pollinated plants with different stamen architectures. *Scientific Reports* **11**:13541. [online] URL: <https://www.nature.com/articles/s41598-021-93029-7>
- Nunes C.E.P., Nevard L., Montealegre-Z F., Vallejo-Marín M. (2021) Variation in the natural frequency of stamens in six morphologically diverse, buzz-pollinated, heterantherous *Solanum* taxa and its relationship to bee vibrations. *Botanical Journal of the Linnean Society* **197**:541–553. [online] URL: <https://academic.oup.com/botlinnean/article/197/4/541/6325391>



- de Oliveira P.E.A.M., Sazima M. (1990) Pollination biology of two species of *Kielmeyera* (Guttiferae) from Brazilian cerrado vegetation. *Plant Systematics and Evolution* **172**:35–49. [online] URL: <http://link.springer.com/10.1007/BF00937796>
- Ollerton J., Alarcón R., Waser N.M., Price M. V., Watts S., Cranmer L., Hingston A., Peter C.I., Rotenberry J. (2009) A global test of the pollination syndrome hypothesis. *Annals of Botany* **103**:1471–1480. [online] URL: <https://academic.oup.com/aob/article-lookup/doi/10.1093/aob/mcp031>
- Ollerton J., Winfree R., Tarrant S. (2011) How many flowering plants are pollinated by animals? *Oikos* **120**:321–326.
- Onstein R.E. (2020) Darwin's second 'abominable mystery': trait flexibility as the innovation leading to angiosperm diversity. *New Phytologist* **228**:1741–1747. [online] URL: <https://onlinelibrary.wiley.com/doi/10.1111/nph.16294>
- Passos L.S., Telles F.J., Goldenberg R., Amano E., Maia F.R. (2022) What is the role of stamen appendages in the buzz-pollinated *Huberia insignis* (Melastomataceae)? *Flora* **293**:152113. [online] URL: <https://linkinghub.elsevier.com/retrieve/pii/S0367253022001104>
- Paterno G.B., Silveira C.L., Kollmann J., Westoby M., Fonseca C.R. (2020) The maleness of larger angiosperm flowers. *Proceedings of the National Academy of Sciences of the United States of America* **117**:10921–10926.
- Pereira Nunes C.E., Vallejo-Marín M. (2022) How Much Pollen Do Beelike Floral Vibrations Remove from Different Types of Anthers? *International Journal of Plant Sciences* **183**:768–776. [online] URL: <https://www.journals.uchicago.edu/doi/10.1086/722296>
- Phillips R.D., Peakall R., van der Niet T., Johnson S.D. (2020) Niche Perspectives on Plant–Pollinator Interactions. *Trends in Plant Science* **xx**:1–15. [online] URL: <https://doi.org/10.1016/j.tplants.2020.03.009>
- van der Pijl L. (1961) Ecological aspects of flower evolution. II. Zoophilous flower classes. *Evolution* **15**:44–59.
- Pinheiro M., Brito V.L.G. de, Sazima M. (2018) Pollination biology of melittophilous legume tree species in the Atlantic Forest in Southeast Brazil. *Acta Botanica Brasilica* **32**:410–425. [online] URL: [http://www.scielo.br/scielo.php?script=sci\\_arttext&pid=S0102-33062018000300410&lng=en&tling=en](http://www.scielo.br/scielo.php?script=sci_arttext&pid=S0102-33062018000300410&lng=en&tling=en)
- QIAN H., ZHANG J. (2014) Using an updated time-calibrated family-level phylogeny of seed plants to test for non-random patterns of life forms across the phylogeny. *Journal of Systematics and Evolution* **52**:423–430. [online] URL: <https://onlinelibrary.wiley.com/doi/10.1111/jse.12086>
- Russell A.L., Leonard A.S., Gillette H.D., Papaj D.R. (2016) Concealed floral rewards and the role of experience in floral sonication by bees. *Animal Behaviour* **120**:83–91.
- Sargent R.D. (2004) Floral symmetry affects speciation rates in angiosperms. *Proceedings of the Royal Society of London Series B: Biological Sciences* **271**:603–608. [online] URL: <https://royalsocietypublishing.org/doi/10.1098/rspb.2003.2644>
- Sauquet H., Von Balthazar M., Magallón S., Doyle J.A., Endress P.K., Bailes E.J., Barroso De Moraes E., Bull-Hereñu K., Carrive L., Chartier M., Chomicki G., Coiro M., Cornette R., El Ottra J.H., Epicoco C., Foster C.S., Jabbour F., Haevermans A., Haevermans T., Hernández R., Little S.A., Löfstrand S., Luna J.A., Massoni J., Nadot S., Pamperl S., Prieu C., Reyes E., Dos Santos P., Schoonderwoerd K.M., Sontag S., Soulebeau A., Staedler Y., Tschan G.F., Wing-Sze Leung A., Schönenberger J. (2017) The ancestral flower of angiosperms and its early diversification. *Nature Communications* **8** [online] URL: [www.nature.com/naturecommunications](http://www.nature.com/naturecommunications)
- Silberbauer-Gottsberger I., Webber A.C., Küchmeister H., Gottsberger G. (2001) Convergence in beetle-pollinated Central Amazonian Annonaceae, Araceae, Arecaceae, and Cyclanthaceae. *Life Forms and Dynamics in Tropical Forests* **346**:165–183.
- STÄGER R. (1092) Chemischer Nachweis von Nektarien bei Pollenblumen und Anemophilen. *BBZ* **12**:34–43.
- Stebbins G.L. (1951) Natural Selection and the Differentiation of Angiosperm Families. *Society for the Study of Evolution* **5**:299–324. [online] URL: <https://www.jstor.org/stable/2405676>
- Stebbins G.L. (1974) *Flowering Plants: Evolution Above the Species Level* (E. Arnold, Ed.). Harvard University Press,



Cambridge, Mass.

- Stevens P.F. (2016) Angiosperm Phylogeny Website. [online] URL: [www.mobot.org/MOBOT/research/APweb/.7](http://www.mobot.org/MOBOT/research/APweb/.7)
- Takhtajan A.L. (1980) Outline of the classification of flowering plants (magnoliophyta). The Botanical Review **46**:225–359. [online] URL: <http://link.springer.com/10.1007/BF02861558>
- Tanaka N., Uehara K., Murata J. (2004) Correlation between pollen morphology and pollination mechanisms in the Hydrocharitaceae. Journal of Plant Research **117**:265–276.
- Telles F.J., Klunk C.L., Maia F.R. da, De Brito V.L.G., Varassin I.G. (2020) Towards a new understanding of the division of labour in heterantherous flowers: The case of *Pterolepis glomerata* (Melastomataceae). Biological Journal of the Linnean Society **131**:1–11.
- Tibshirani R., Walther G., Hastie T. (2001) Estimating the Number of Clusters in a Data Set Via the Gap Statistic. Journal of the Royal Statistical Society Series B: Statistical Methodology **63**:411–423. [online] URL: <https://academic.oup.com/jrsssb/article/63/2/411/7083348>
- Timerman D., Barrett S.C.H. (2018) Divergent selection on the biomechanical properties of stamens under wind and insect pollination. Proceedings of the Royal Society B: Biological Sciences **285**
- Trunschke J., Lunau K., Pyke G.H., Ren Z.-X., Wang H. (2021) Flower Color Evolution and the Evidence of Pollinator-Mediated Selection. Frontiers in Plant Science **12**:1–20. [online] URL: <https://www.frontiersin.org/articles/10.3389/fpls.2021.617851/full>
- Valadão-Mendes L.B., Rocha I., Meireles D.A.L., Leite F.B., Sazima M., Maruyama P.K., Brito V.L.G. (2022) Flower morphology and plant–bee pollinator interactions are related to stamen dimorphism in Melastomataceae. Plant Biology **24**:240–248. [online] URL: <https://onlinelibrary.wiley.com/doi/10.1111/plb.13359>
- Vallejo-Marin M. (2019) Evolutionary tinkering allows buzz pollinated plants to escape from an adaptive dead-end. New Phytologist **221**:618–620.
- Vallejo-Marin M., Manson J.S., Thomson J.D., Barrett S.C.H. (2009) Division of labour within flowers: Heteranthery, a floral strategy to reconcile contrasting pollen fates. Journal of Evolutionary Biology
- Vallejo-Marin M., Russell A.L. (2024) Harvesting pollen with vibrations: towards an integrative understanding of the proximate and ultimate reasons for buzz pollination. Annals of Botany **133**:379–398. [online] URL: <https://academic.oup.com/aob/article/133/3/379/7468467>
- Vallejo-Marin M., Da Silva E.M., Sargent R.D., Barrett S.C.H. (2010) Trait correlates and functional significance of heteranthery in flowering plants. New Phytologist **188**:418–425. [online] URL: <http://doi.wiley.com/10.1111/j.1469-8137.2010.03430.x>
- Velloso M. de S.C., Brito V.L.G. de, Caetano A.P.S., Romero R. (2018) Anther specializations related to the division of labor in *Microlizia cordata* (Spreng.) Cham. (Melastomataceae). Acta Botanica Brasilica **32**:349–358. [online] URL: [http://www.scielo.br/scielo.php?script=sci\\_arttext&pid=S0102-33062018005004103&lng=en&tling=en](http://www.scielo.br/scielo.php?script=sci_arttext&pid=S0102-33062018005004103&lng=en&tling=en)
- Vogel S. (1954) Blütenbiologische Typen als Elemente der Sippengliederung, dargestellt anhand der Flora Südafrikas. Botanische Studien **1**:1–338.
- Vogel S. (1978) Evolutionary shifts from reward to deception in pollen flowers. The Pollination of Flowers by Insects:89–96.
- Watson, L., and Dallwitz M.. The families of flowering plants: descriptions, illustrations, identification, and information retrieval. Version: 19th May 2024 [online] URL: <https://www.delta-intkey.com/angio/index.htm>
- Werth E. (1956) Bau und Leben der Blumen. Stuttgart: Enke
- Westerkamp C. (1996) Pollen in Bee-Flower Relations Some Considerations on Melittophily\*. Botanica Acta **109**:325–332. [online] URL: <http://doi.wiley.com/10.1111/j.1438-8677.1996.tb00580.x>
- Wickham H. (2016) *Ggplot2: Elegant graphics for data analysis (2nd ed.)*, 2nd edn. Springer International Publishing.

Wolowski M., Freitas L. (2015) An overview on pollination of the Neotropical Poales. *Rodriguesia* **66**:329–336.

### Captions

**Figure 1.** (A) Morphospace is based on three floral traits proposed by Vogel (1978), including the 38 families of pollen flowers he mentioned. (B) Morphospace based on the same three floral traits as in A, but this time including both Vogel's (1978) original families plus 35 new families found to have pollen flowers in our review. (C) Morphospace is based on 11 morphological traits and includes all 73 families. The families included in the three highlighted clusters do not coincide with those present in Vogel's original pollen flower classification (*Magnolian*, *Papaver*, and *Solanum*).

**Figure 2.** The most important floral traits composing each pollen flower group in our reviewed analyses using 11 floral traits in 73 families. The predominance of floral traits **(A)** for the 24 families within the brush-blossom type, **(B)** for the 21 families within the inconspicuous type, and **(C)** for the 28 families within the poricidal type.

**Figure 3.** Families of the three groups of pollen flowers proposed in the new classification, along the Phylogeny of Angiosperm Families (*Qian & Zhang 2014*)- adapted. The illustrations are available in (*Watson & Dallwitz*). Version: 25th July 2023. (Illustrations edited by João Pedro Santos Pereira).

For Peer Review

Melo et al. 2024 – Pollen flower classification now and then

Supplementary information

Table SI 1 – List of species or genera analysed within each family considering traits proposed by Vogel.

Orders	Families	Genus	Species	Author	Vogel type	Dehiscence anthers	Pollen release	Pollinator	Visitors' behaviour	Pollination type	Number of stamens	Reference
Ericales	Actinidiaaceae	<i>Saurauia</i>		Willd.	papaver	poricidal		bees	buzz	biotic	10 to 100	[1]
Caryophyllales	Aizoaceae	<i>Sesuvium</i>	<i>Sesuvium portulacastrum</i>	L.	papaver	longitudinal	exposed	bees	forage	biotic	6 to 120	[2]
Magnoliales	Annonaceae	<i>Annona</i>	<i>Annona squamosa</i>	L.	magnolian	longitudinal	shed	beetles	actively eat	biotic	25 to 100	[3]
Alismatales	Araceae	<i>Philodendron</i>	<i>Philodendron bipinnatifidum</i>	Schott	magnolian	poricidal	shed	beetles	actively eat	biotic	1 to 12	[4]
Austrobaileales	Austrobaileyaceae	<i>Austrobaileya</i>	<i>Austrobaileya scandens</i>	White	new	longitudinal	shed	flies	actively eat	biotic	12 to 25	[5]
Cucurbitales	Begoniaceae	<i>Begonia</i>	<i>Begonia integerrima</i>	Spreng.	papaver	poricidal	small portion	bees	buzz	biotic	4 to 100	[6]
Malvales	Bixaceae	<i>Bixa</i>	<i>Bixa orellana</i>	L.	solanum	poricidal	small portion	bees	buzz	biotic	50 to 150	[7]
Lamiales	Byblidaceae	<i>Byblis</i>	<i>Byblis gigantea</i>	Lindl.	new	poricidal		bees		biotic	5	[8]
Caryophyllales	Cactaceae	<i>Opuntia</i>			papaver		exposed	bees	forage	biotic	15 to 100	[9]
Lamiales	Calceolariaceae	<i>Calceolaria</i>	<i>Calceolaria comulcana</i>	Romero, Bussmann & Puppo	new			bees		biotic		[10]
Canellalles	Canellaceae	<i>Cinnamodendron</i>	<i>Cinnamodendron dinisii</i>	Schwacke	new	longitudinal		bees		biotic		[11]
Canellalles	Canellaceae	<i>Canella</i>			new	longitudinal						[12]
Chloranthales	Chloranthaceae	<i>Chloranthus</i>	<i>Chloranthus serratus</i>	Thunb.	new	longitudinal		thrips		biotic		[13]
Chloranthales	Chloranthaceae	<i>Chloranthus</i>	<i>Chloranthus fortunei</i>	A. Gray	new	longitudinal		thrips		biotic		[13]
Ranunculales	Circaeasteraceae	<i>Circaeaster</i>	<i>Circaeaster agrestis</i>	Maxim.	new	longitudinal				biotic	1 to 2	[14]
Malvales	Cistaceae	<i>Cistus</i>	<i>Cistus salvifolius</i>	L.	papaver	longitudinal	exposed	bees	forage	biotic	3 to 100	[15]
Ericales	Clethraceae	<i>Clethra</i>	<i>Clethra alnifolia</i>	L.	new	longitudinal		bees		biotic	10	[16]
Ericales	Clethraceae	<i>Rariglanda</i>	<i>Rariglanda jerseyensis</i>	Martinez & Choo	new			bees		biotic		[16]
Commelinales	Commelinaceae	<i>Murdannia</i>	<i>Murdannia nudiflora</i>	(L.) Brenan	solanum	poricidal	small portion	bees		biotic	1 to 6	[17]
Commelinales	Commelinaceae	<i>Dichorisandra</i>	<i>Dichorisandra thyrsiflora</i>	J.C.Mikan	solanum	poricidal		bees	buzz	biotic		[18]
Liliales	Corsiaceae	<i>Corsia</i>		Becc.	new	longitudinal		fly/fungi		biotic	6	[19]
Pandanales	Cyclanthaceae	<i>Cyclanthus</i>	<i>Cyclanthus bipartitus</i>	Poit. ex A. Rich.	new	longitudinal		beetles		biotic	10 to 150	[20]
Poales	Cyperaceae	<i>Rhynchospora</i>	<i>Rhynchospora ciliata</i>	(Vahl) Kukenth	new	longitudinal		bees; wind		biotic and abiotic	3 to 22	[21]
Magnoliales	Degeneriaceae	<i>Degeneria</i>		I.W. Bailey & A.C.Sm.	magnolian	longitudinal	shed	beetles		biotic	30 to 50	[12]
Dilleniales	Dilleniaceae	<i>Hibbertia</i>	<i>Hibbertia fasciculata</i>	R.Br. ex DC.	solanum	poricidal	small portion	insects	buzz	biotic	15 to 150	[22]
Dilleniales	Dilleniaceae	<i>Hibbertia</i>	<i>Hibbertia cistiflora</i>	N.A. Wakef	solanum	poricidal		bees	buzz	biotic		[18]
Oxalidales	Elaeocarpaceae	<i>Sloanea</i>		L.	new	poricidal	small portion	bees	buzz	biotic	12 to 100	[23]
Oxalidales	Elaeocarpaceae	<i>Tetratheca</i>		Sm.	solanum	poricidal		bees	buzz	biotic		[18]

## Melo et al. 2024 – Pollen flower classification now and then

<b>Ericales</b>	Ericaceae	<i>Conostephium</i>		Benth.	new	poricidal		bees	buzz	biotic	8 to 10	[24]
<b>Ericales</b>	Ericaceae	<i>Sprengelia</i>	<i>Sprengelia incarnata</i>	Sm.	new	poricidal		bees	buzz	biotic		[25]
<b>Malpighiales</b>	Euphorbiaceae	<i>Dalechampia</i>			new	poricidal	small portion	bees	buzz	biotic	1 to 1000	[26]
<b>Magnoliales</b>	Eupomatiaceae	<i>Eupomatia</i>	<i>Eupomatia laurina</i>	R.Br.	magnolian	longitudinal	shed	beetles		biotic	25 to 100	[12]
<b>Fabales</b>	Fabaceae	<i>Swartzia</i>	<i>Swartzia apetala</i>	Raddi	solanum	longitudinal		bees	buzz	biotic		[27]
<b>Fabales</b>	Fabaceae	<i>Cassia</i>	<i>Cassia alata</i>	L.	solanum	poricidal		bees	buzz	biotic		[28]
<b>Fabales</b>	Fabaceae	<i>Senna</i>	<i>Senna multijuga</i>	Rich.	new	poricidal	small portion	bees	buzz	biotic		[29]
<b>Fabales</b>	Fabaceae	<i>Chamaecrista</i>	<i>Chamaecrista desvauxii</i>	Collad.	new	poricidal	small portion	bees	buzz	biotic		[30]
<b>Fabales</b>	Fabaceae	<i>Acacia</i>	<i>Acacia retinodes</i>	Schltld.	papaver	longitudinal		bees	buzz	biotic		[31]
<b>Gentianales</b>	Gentianaceae	<i>Exacum</i>	<i>Exacum affine</i>	Balf. f.	solanum	poricidal	small portion	bees	buzz	biotic	4 to 12	[18]
<b>Lamiales</b>	Gesneriaceae	<i>Ramonda</i>	<i>Ramonda myconi</i>	(L.) Rchb.	solanum	poricidal		bees		biotic	2 to 5	[32]
<b>Laurales</b>	Gomortegaceae	<i>Gomortega</i>	<i>Gomortega nitida</i>	Ruiz & Pavon	new	longitudinal		Syrphids		biotic	5 to 10	[33]
<b>Magnoliales</b>	Himantandraceae	<i>Galbulimima</i>	<i>Galbulimima baccata</i>	F.M.Bailey	magnolian	longitudinal		beetles		biotic		[12]
<b>Magnoliales</b>	Himantandraceae	<i>Galbulimima</i>	<i>Galbulimima belgraveana</i>	(F.Muell.) Sprague	magnolian	longitudinal		beetles		biotic		[12]
<b>Piperales</b>	Hydnoraceae	<i>Hydnora</i>	<i>Hydnora africana</i>	Thunb.	new	longitudinal		beetles	actively eat	biotic	3 to 10	[34]
<b>Alismatales</b>	Hydrocharitaceae	<i>Egeria</i>	<i>Egeria densa</i>	Planch.	new	longitudinal		insects		biotic	4 to 100	[35]
<b>Alismatales</b>	Hydrocharitaceae	<i>Blyxa</i>	<i>Blyxa japonica</i>	Maxim. ex Asch. & Gürke	new	longitudinal		insects		biotic		[35]
<b>Alismatales</b>	Hydrocharitaceae	<i>Ottelia</i>	<i>Ottelia alismoides</i>	(L.) Pers.	new	longitudinal		insects		biotic		[35]
<b>Alismatales</b>	Hydrocharitaceae	<i>Stratiotes</i>	<i>Stratiotes aloides</i>	L.	new	longitudinal		insects		biotic		[35]
<b>Alismatales</b>	Hydrocharitaceae	<i>Hydrocharis</i>	<i>Hydrocharis dubia</i>	Backer	new	longitudinal		insects		biotic		[35]
<b>Malpighiales</b>	Hypericaceae	<i>Hypericum</i>	<i>Hypericum roeperianum</i>	G.W.Schimp. ex A. Rich.	papaver		exposed	bees	forage	biotic		[36]
<b>Asparagales</b>	Hypoxidaceae	<i>Hypoxis</i>	<i>Hypoxis camerooniana</i>	Baker	solanum	longitudinal	small portion	bees; flies	buzz	biotic	4 to 6	[37]
<b>Asparagales</b>	Iridaceae	<i>Ixia</i>	<i>Ixia scillaris</i>	L.	new							[38]
<b>Alismatales</b>	Juncaginaceae	<i>Tetroncium</i>		Willd.	new	longitudinal		wind		abiotic	3 to 8	[39]
<b>Ericales</b>	Lecythidaceae	<i>Gustavia</i>	<i>Gustavia augusta</i>	L.	new	poricidal		bees	buzz	biotic	40 to 1000	[40]
<b>Myrtales</b>	Lythraceae	<i>Lagerstroemia</i>	<i>Lagerstroemia indica</i>	L.	solanum	longitudinal	exposed	bees	forage	biotic	4 to 35	[41]
<b>Magnoliales</b>	Magnoliaceae	<i>Liriodendron</i>	<i>Liriodendron chinense</i>	Hemsl.Sarg	magnolian	longitudinal	shed	beetles; bumblebees	actively eat	biotic	50 to 200	[12]
<b>Magnoliales</b>	Magnoliaceae	<i>Liriodendron</i>	<i>Liriodendron tulipifera</i>	L.	magnolian	longitudinal		beetles; bumblebees		biotic		[12]
<b>Magnoliales</b>	Magnoliaceae	<i>Magnolia</i>	<i>Magnolia grandiflora</i>	L.	magnolian	longitudinal		beetles		biotic		[12]
<b>Malpighiales</b>	Malpighiaceae	<i>Hiptage</i>		Gaertn.	solanum			bees		biotic	10	[42]
<b>Malvales</b>	Malvaceae	<i>Apeiba</i>		Aubl.	solanum			bees	buzz	biotic	5 to 100	[43]
<b>Malvales</b>	Malvaceae	<i>Keraudrenia</i>	<i>Keraudrenia velutina</i>	Steetz.	solanum	poricidal		bees	buzz	biotic		[18]
<b>Malvales</b>	Malvaceae	<i>Sparmannia</i>	<i>Sparmannia africana</i>	L.f.	solanum					biotic		[44]
<b>Myrtales</b>	Melastomataceae	<i>Rhynchanthera</i>	<i>Rhynchanthera grandiflora</i>	DC.	new	poricidal	small portion	bees	buzz	biotic	4 to 100	[45]
<b>Myrtales</b>	Melastomataceae	<i>Pleroma</i>	<i>Pleroma raddianum</i>	Triana	solanum	poricidal		bees	buzz	biotic		[46]
<b>Myrtales</b>	Melastomataceae	<i>Osbeckia</i>	<i>Osbeckia wynaadensis</i>	C.B Clarke	solanum	poricidal	small portion	bees	buzz	biotic		[47]
<b>Myrtales</b>	Melastomataceae	<i>Rhexia</i>	<i>Rhexia virginica</i>	L.	solanum	poricidal	small portion	bees	buzz	biotic		[48]
<b>Myrtales</b>	Melastomataceae	<i>Meriania</i>	<i>Meriania longifolia</i>	(Naudin) Cogn.	solanum	poricidal	small portion	bees	buzz	biotic		[49]

Melo et al. 2024 – Pollen flower classification now and then

<b>Myrtales</b>	Melastomataceae	<i>Clidemia</i>	<i>Clidemia capitellata</i>	(Bonpl.) D. Don	new	poricidal	small portion	bees	buzz	biotic		[50]
<b>Myrtales</b>	Melastomataceae	<i>Trembleya</i>	<i>Trembleya laniflora</i>	Cong.	solanum	poricidal	small portion	bees	buzz	biotic		[51]
<b>Myrtales</b>	Melastomataceae	<i>Melastoma</i>	<i>Melastoma malabathricum</i>	L.	solanum	poricidal	small portion	bees	buzz	biotic		[52]
<b>Ranunculales</b>	Menispermaceae			Juss.	new	longitudinal		insects		biotic	1 to 40	[53]
<b>Laurales</b>	Monimiaceae	<i>Wilkiea</i>	<i>Wilkiea huegeliana</i>	(Tul.) A.DC.	new	longitudinal		thrips		biotic	10 to 150	[54]
<b>Magnoliales</b>	Myristicaceae	<i>Myristica</i>		Gronov.	magnolian	longitudinal	shed	beetles	actively eat	biotic	2 to 30	[12]
<b>Ericales</b>	Myrsinaceae	<i>Ardisia</i>	<i>Ardisia elliptica</i>	Thumb.	solanum			bees	buzz	biotic	3 to 6	[55]
<b>Myrtales</b>	Myrtaceae	<i>Eugenia</i>	<i>Eugenia uniflora</i>	L.	new	longitudinal		bees		biotic	4 to 150	[11]
<b>Myrtales</b>	Myrtaceae	<i>Myrcia</i>	<i>Myrcia multiflora</i>	DC.	new	poricidal		bees	buzz	biotic		[56]
<b>Myrtales</b>	Myrtaceae	<i>Gomidesia</i>	<i>Gomidesia schaueriana</i>	O.Berg.	new	poricidal		bees	buzz	biotic		[56]
<b>Myrtales</b>	Myrtaceae	<i>Blepharocalyx</i>	<i>Blepharocalyx salicifolius</i>	(Kunth) O.Berg.	new	poricidal		bees	buzz	biotic		[57]
<b>Nymphaeales</b>	Nymphaeaceae	<i>Nymphaea</i>	<i>Nymphaea pubescens</i>	Willd.	magnolian	longitudinal	shed	insects	actively eat	biotic	40 to 80	[58]
<b>Nymphaeales</b>	Nymphaeaceae	<i>Nymphaea</i>	<i>Nymphaea nouchali</i>	Burm.f.	magnolian	longitudinal	shed	insects	actively eat	biotic	40 to 80	[58]
<b>Nymphaeales</b>	Nymphaeaceae	<i>Nymphaea</i>	<i>Nymphaea stellata</i>	Willd.	magnolian	longitudinal	shed	insects	actively eat	biotic	40 to 80	[58]
<b>Nymphaeales</b>	Nymphaeaceae	<i>Nymphaea</i>	<i>Nymphaea pulchella</i>	DC.	magnolian		shed	bee	actively eat	biotic	40 to 80	[59]
<b>Nymphaeales</b>	Nymphaeaceae	<i>Nymphaea</i>	<i>Nymphaea rubra</i>	Roxb. ex Andrews	magnolian	longitudinal	shed	insects	actively eat	biotic		[58]
<b>Malpighiales</b>	Ochnaceae	<i>Sauvagesia</i>		L.	new	poricidal	small portion	bees	buzz	biotic	10 to 100	[60]
<b>Malpighiales</b>	Ochnaceae	<i>Rhabdophyllum</i>		Tiegh.	new	poricidal		bees	buzz	biotic		[61]
<b>Malpighiales</b>	Ochnaceae	<i>Ouratea</i>		Aulb.	solanum	poricidal		bees	buzz	biotic		[61]
<b>Malpighiales</b>	Ochnaceae	<i>Idertia</i>		Farron	new	poricidal		bees	buzz	biotic		[61]
<b>Malpighiales</b>	Ochnaceae	<i>Campylospermum</i>		Tiegh.	new	poricidal		bees	buzz	biotic		[61]
<b>Malpighiales</b>	Ochnaceae	<i>Luxemburgia</i>		A.St.-Hil.	solanum	poricidal		bees	buzz	biotic		[61]
<b>Malpighiales</b>	Ochnaceae	<i>Philacra</i>		Dwyer	new	poricidal		bees	buzz	biotic		[62]
<b>Pandanales</b>	Pandanaceae	<i>Freycinetia</i>		Gaudich.	new	longitudinal		vertebrate		biotic	10 to 100	[63]
<b>Pandanales</b>	Pandanaceae	<i>Pandanus</i>		Parkinson	new	longitudinal		wind		abiotic		[63]
<b>Pandanales</b>	Pandanaceae	<i>Sararanga</i>		Hemsl.	new	longitudinal		insect		biotic		[63]
<b>Pandanales</b>	Pandanaceae	<i>Scisphila</i>	<i>Sciaphila nana</i>	Blume	new	longitudinal		fly		biotic		[64]
<b>Ranunculales</b>	Papaveraceae				papaver	longitudinal	exposed	bees		biotic	16 to 200	[65]
<b>Ericales</b>	Pentaphragmaceae	<i>Ternstroemia</i>	<i>Ternstroemia laevigata</i>	Wawra	new	longitudinal		bees	buzz	biotic	5	[66]
<b>Commelinales</b>	Philydraceae	<i>Helmholtzia</i>	<i>Helmholtzia acorifolia</i>	F.Muell.	solanum	longitudinal		insects		biotic	1	[67]
<b>Piperales</b>	Piperaceae	<i>Peperomia</i>			new	longitudinal		hoverflies, bees and beetles		biotic	1 to 10	[12]
<b>Poales</b>	Poaceae	<i>Merostachys</i>	<i>Merostachys riedeliana</i>	Rupr. ex Döll	new	longitudinal		insects		biotic		[68]
<b>Alismatales</b>	Posidoniaceae	<i>Posidonia</i>	<i>Posidonia australis</i>	J.D.Hooker	new	longitudinal		water		abiotic	3	[67]
<b>Alismatales</b>	Potamogetonaceae	<i>Althenia</i>	<i>Althenia orientalis</i>	(Tzvelev) Garcia-Mur. & Talavera	new	longitudinal		water		abiotic	4	[69]
<b>Ericales</b>	Primulaceae	<i>Dodecatheon</i>		(L.) ARMast & Reveal	new			bees	buzz	biotic	3 to 9	[32]
<b>Ericales</b>	Primulaceae	<i>Cyclamen</i>		L.	new			bees	buzz	biotic		[70]
<b>Ericales</b>	Myrsinaceae	<i>Lysimachia</i>		L.	new			bees	buzz	biotic		[71]

## Melo et al. 2024 – Pollen flower classification now and then

<b>Ranunculales</b>	Ranunculaceae	<i>Anemone</i>	<i>Anemone pavonina</i>	Lam.	papaver	longitudinal		beetles; bees		biotic	15 to 100	[72]
<b>Ranunculales</b>	Ranunculaceae	<i>Thalictrum</i>		L.	papaver	longitudinal		wind, small insects		biotic and abiotic		[73]
<b>Poales</b>	Rapateaceae	<i>Cephalostemon</i>	<i>Cephalostemon riedelia</i>	Körn.	solanum	poricidal	small portion	bees	buzz	biotic	6	[68]
<b>Caryophyllales</b>	Rhabdodendraceae	<i>Rhabdodendron</i>	<i>Rhabdodendron macrophyllum</i>	(Spruce ex Benth.) Huber	new	longitudinal		bees		biotic		[74]
<b>Alismatales</b>	Ruppiaceae	<i>Ruppia</i>		L.	new	longitudinal		water		abiotic	2	[75]
<b>Piperales</b>	Saururaceae	<i>Saururus</i>	<i>Saururus chinensis</i>	(Lour.) Baill.	new	longitudinal		wind and insects		biotic and abiotic	3 to 8	[12]
<b>Alismatales</b>	Scheuchzeriaceae	<i>Scheuchzeria</i>	<i>Scheuchzeria palustris</i>	L.	new	longitudinal		wind		abiotic	6	[69]
<b>Austrobaileyales</b>	Schisandraceae (Illiciaceae)	<i>Illicium</i>	<i>Illicium floridanum</i>	Ellis	new	longitudinal	shed	beetles	actively eat	biotic	4 to 80	[76]
<b>Austrobaileyales</b>	Schisandraceae (Illiciaceae)	<i>Illicium</i>	<i>Illicium micranthum</i>	Dunn.	new	longitudinal	shed	beetles	actively eat	biotic	5 to 80	[76]
<b>Austrobaileyales</b>	Schisandraceae (Illiciaceae)	<i>Illicium</i>	<i>Illicium anisantrum</i>	L.	new	longitudinal	shed	beetles	actively eat	biotic	6 to 80	[76]
<b>Laurales</b>	Siparunaceae	<i>Siparuna</i>	<i>Siparuna guianensis</i>	Aublet	new	longitudinal		flies; gall insects		biotic	2 to 100	[77]
<b>Solanales</b>	Solanaceae	<i>Solanum</i>		L.	solanum	poricidal	small portion	bees	buzz	biotic	5	[78]
<b>Solanales</b>	Solanaceae	<i>Lycianthes</i>		(Dunal) Hassl.	new	poricidal		bees	buzz	biotic		[79]
<b>Dioscoreales</b>	Taccaceae	<i>Tacca</i>		J.R.Forst. & G. Forst.	new	longitudinal		insects		biotic	6	[68]
<b>Asparagales</b>	Tecophilaeaceae	<i>Cyanella</i>		D.Royen	new	poricidal	small portion	bees	buzz	biotic	3 to 6	[80]
<b>Asparagales</b>	Tecophilaeaceae	<i>Conanthera</i>	<i>Conanthera bifolia</i>		new	poricidal		bees	buzz	biotic		[18]
<b>Ericales</b>	Theaceae	<i>Ternstroemia</i>		Mutis ex L.f.	new	longitudinal		bees	buzz	biotic	5 to 100	[81]
<b>Austrobaileyales</b>	Trimeniaceae	<i>Trimenia</i>	<i>Trimenia moorei</i>	Oliv.	new	longitudinal	shed	flies; bees	actively eat	biotic	7 to 23	[82]
<b>Canellalles</b>	Winteraceae	<i>Drimys</i>	<i>Drimys angustifolia</i>	Miers	new	longitudinal	shed	beetles, flies, thrips	actively eat	biotic	15 to 100	[83]; [12]
<b>Alismatales</b>	Zosteraceae	<i>Zostera</i>	<i>Zostera marina</i>	L.	new	longitudinal		water		abiotic	1	[84]

Melo et al. 2024 – Pollen flower classification now and then

Reference

1. J. H. Cane, K. Mackenzie DS. 1993 Honey bees harvest pollen from the porose anthers of cranberries (*Vaccinium macrocarpon*) (Ericaceae). *Am. Bee Journal*, **133**, 293–295.

2. Mary Percival. 1974 *Floral Ecology of Coastal Scrub in Southeast Jamaica*. The Association for Tropical Biology and Conservation. See <http://www.jstor.org/stable/2989824>.

3. Kishore K, Shukla AK, Babu N, Sarangi DN, Patanayak S. 2012 Pollination biology of *Annona squamosa* L. (Annonaceae): Evidence for pollination syndrome. *Sci. Hortic. (Amsterdam)*. **144**, 212–217. (doi:10.1016/j.scienta.2012.07.004)

4. Society CB. 2020 FUNCTION OF OLFACTORY AND VISUAL STIMULI IN POLLINATION OF *LYSICHITON AMERICANUM* ( ARACEAE ) BY A STAPHYLINID BEETLE Author ( s ): Olle Pellmyr and Joseph M . Patt Published by : California Botanical Society Stable URL : <https://www.jstor.org/stable/41424>. **33**, 47–54.

5. Endress PK. 1986 Reproductive structures and phylogenetic significance of extant primitive Angiosperms. *Plant Syst. Evol.* **152**, 1–28. (doi:10.1007/BF00985348)

6. Wyatt GE, Sazima M. 2011 Pollination and reproductive biology of . *J. Pollinat. Ecol.* **6**, 95–107.

7. Nascimento A, Pereira L. 2017 *Bixa orellana* L . ( Bixaceae ): dependência de polinizadores e estratégias de forrageio dos visitantes florais. *Biota Amaz.* **7**, 1–7.

8. Conran JG, Houben A, Lowrie A. 2002 Chromosome numbers in Byblidaceae. *Aust. J. Bot.* **50**, 583. (doi:10.1071/BT02007)

9. Osborn MM, Kevan PG, Lane MA. 1988 Pollination biology of *Opuntia polyacantha* and *Opuntia phaeacantha* (Cactaceae) in southern Colorado. *Plant Syst. Evol.* **159**, 85–94. (doi:10.1007/BF00937427)

10. Romero-Hernández C, Bussmann RW, Puppo P. 2017 New Species of *Calceolaria* (Calceolariaceae) from Northern Peru. *Novon* **25**, 316–321. (doi:10.3417/D-16-00013)

11. Diniz MER, Buschini MLT. 2016 Diversity of flower visitng bees of *Eugenia uniflora* L. (Myrtaceae) in fragments of Atlantic Forest in South Brazil. *Sociobiology* **63**, 982–990. (doi:10.13102/sociobiology.v63i3.982)

12. Erbar C. 2014 Nectar secretion and nectaries in basal angiosperms, magnoliids and non-core eudicots and a comparison with core eudicots. *Plant Divers. Evol.* **131**, 63–143. (doi:10.1127/1869-6155/2014/0131-0075)

13. YI-BO L. 1999 Pollination Ecology of *Chloranthus serratus*(Thunb.) Roem. et Schult. and *Ch. fortunei*(A. Gray) Solms-Laub. (Chloranthaceae). *Ann.*



Melo et al. 2024 – Pollen flower classification now and then

- Bot.* **83**, 489–499. (doi:10.1006/anbo.1998.0845)
14. Adriance S. Foster. 1963 THE MORPHOLOGY AND RELATIONSHIPS OF CIRCAEASTER. *J. Arnold Arbor.* **44**, 299–327.
  15. Nansen C, Korie S. 2000 Determining the time delay of honey bee (*Apis mellifera*) foraging response to hourly pollen release in a typical pollen flower (*Cistus salvifolius*). *J. Apic. Res.* **39**, 93–101. (doi:10.1080/00218839.2000.11101028)
  16. Martínez C, Choo TYS, Allevato D, Nixon KC, Crepet WL, Harbert RS, Daghlán CP. 2016 *Rariglanda jerseyensis*, a new ericalean fossil flower from the Late Cretaceous of New Jersey. *Botany* **94**, 747–758. (doi:10.1139/cjb-2016-0062)
  17. Veena V, Nampy S. 2019 Induced cleistogamy: A strategy for reproductive assurance in *Murdannia nudiflora* (commelinaceae). *Botany* **97**, 547–557. (doi:10.1139/cjb-2019-0007)
  18. Russell AL, Golden RE, Leonard AS, Papaj DR. 2016 Bees learn preferences for plant species that offer only pollen as a reward. *Behav. Ecol.* **27**, 731–740. (doi:10.1093/beheco/arv213)
  19. Mennes CB, Lam VKY, Rudall PJ, Lyon SP, Graham SW, Smets EF, Merckx VSFT. 2015 Ancient Gondwana break-up explains the distribution of the mycoheterotrophic family Corsiaceae (Liliales). *J. Biogeogr.* **42**, 1123–1136. (doi:10.1111/jbi.12486)
  20. Silberbauer-Gottsberger I, Webber AC, Kückmeister H, Gottsberger G. 2001 Convergence in beetle-pollinated Central Amazonian Annonaceae, Araceae, Arecaceae, and Cyclanthaceae. *Life Forms Dyn. Trop. For.* **346**, 165–183.
  21. Costa ACG, Thomas WW, Machado IC. 2017 Comparative floral biology of *Rhynchospora ciliata* (Vahl) Kukenth and *R. pubera* (Vahl) Boeckeler (Cyperaceae): the role of white involucre bracts in attracting pollinating insects. *Plant Species Biol.* **32**, 403–411. (doi:10.1111/1442-1984.12173)
  22. Tucker SC, Bernhardt P. 2000 Floral ontogeny, pattern formation, and evolution in *Hibbertia* and *Adrastaea* (Dilleniaceae). *Am. J. Bot.* **87**, 1915–1936. (doi:10.2307/2656843)
  23. Matthews ML, Endress PK. 2002 Comparative floral structure and systematics in Oxalidales (Oxalidaceae, Connaraceae, Brunelliaceae, Cephalotaceae, Cunoniaceae, Elaeocarpaceae, Tremandraceae). *Bot. J. Linn. Soc.* **140**, 321–381. (doi:10.1046/j.1095-8339.2002.00105.x)
  24. Houston TE, Ladd PG. 2002 Buzz pollination in the Epacridaceae. *Aust. J. Bot.* **50**, 83–91. (doi:10.1071/BT01020)
  25. McQuillan, Karen A; Johnson PB. 2011 Comparative floral presentation and bee-pollination in two *Sprengelia* species (Ericaceae). *Cunninghamia* **12**.
  26. Armbruster WS, Lee J, Edwards ME, Baldwin BG. 2013 Floral pedomorphy leads to secondary specialization in pollination of Madagascar *Dalechampia* (Euphorbiaceae). *Evolution (N. Y.)*. **67**, 1196–1203. (doi:10.1111/evo.12002)

Melo et al. 2024 – Pollen flower classification now and then

27. Moço MC de C, Pinheiro MCB. 1999 Pollination ecology of *Swartzia apetala* Raddi var. *apetala* (leguminosae-papilionoideae). *Brazilian Arch. Biol. Technol.* **42**. (doi:10.1590/s1516-89131999000400006)
28. Zafar, Rashda; Raju A. 2006 Relationships of *Xylocopa* bees with pollen flowers. *Adv. Pollen Spore Res.* **24**, 157–168.
29. Wolowski M, Freitas L. 2010 Sistema reprodutivo e polinização de *Senna multijuga* (Fabaceae) em Mata Atlântica Montana. *Rodriguésia* **61**, 167–179. (doi:10.1590/2175-7860201061202)
30. Nogueira A, Valadão-Mendes LB, El Ottra JHL, Guimarães E, Cardoso-Gustavson P, Quinalha MM, Paulino JV, Rando JG. 2018 Relationship of floral morphology and development with the pattern of bee visitation in a species with pollen-flowers, *Chamaecrista desvauxii* (Fabaceae). *Bot. J. Linn. Soc.* **187**, 137–156. (doi:10.1093/botlinnean/boy008)
31. Bernhardt P, Kenrick J, Knox RB. 1984 Pollination Biology and the Breeding System of *Acacia Retinodes* (Leguminosae: Mimosoideae). *Ann. Missouri Bot. Gard.* **71**, 17. (doi:10.2307/2399054)
32. Harder LD, Barclay RMR. 1994 The Functional Significance of Poricidal Anthers and Buzz Pollination: Controlled Pollen Removal From *Dodecatheon*. *Funct. Ecol.* **8**, 509. (doi:10.2307/2390076)
33. Heo K, Kimoto Y, Riveros M, Tobe H. 2004 Embryology of Gomortegaceae (Laurales): characteristics and character evolution. *J. Plant Res.* **117**. (doi:10.1007/s10265-004-0149-3)
34. Bolin JF, Maass E, Musselman LJ. 2009 Pollination biology of *Hydnora africana* thunb. (Hydnoraceae) in Namibia: Brood-site mimicry with insect imprisonment. *Int. J. Plant Sci.* **170**, 157–163. (doi:10.1086/593047)
35. Tanaka N, Uehara K, Murata J. 2004 Correlation between pollen morphology and pollination mechanisms in the Hydrocharitaceae. *J. Plant Res.* **117**, 265–276. (doi:10.1007/s10265-004-0155-5)
36. Bartoš M, Tropek R, Spitzer L, Padyšáková E, Janšta P, Straka J, Tkoč M, Janeček Š. 2015 Specialization of pollination systems of two co-flowering phenotypically generalized *Hypericum* species (Hypericaceae) in Cameroon. *Arthropod. Plant. Interact.* **9**, 241–252. (doi:10.1007/s11829-015-9378-8)
37. Klomberg Y, Dywou Kouede R, Bartoš M, Mertens JEJ, Tropek R, Fokam EB, Janeček Š. 2019 The role of ultraviolet reflectance and pattern in the pollination system of *Hypoxis camerooniana* (Hypoxidaceae). *AoB Plants* **11**. (doi:10.1093/aobpla/plz057)
38. Goldblatt P, Bernhardt P, Manning JC. 2000 Adaptive Radiation of Pollination Mechanisms in *Ixia* (Iridaceae: Crocoideae). *Ann. Missouri Bot. Gard.* **87**, 564. (doi:10.2307/2666146)
39. Mering S Von. 2013 *Tetroncium* and its only species, *T. magellanicum* ( Juncaginaceae ): distribution, ecology and lectotypification. *Willdenowia* **43**, 13–24. (doi:10.3372/wi.43.43102)

## Melo et al. 2024 – Pollen flower classification now and then

40. Mori SA, Cornejo X. 2013 Two new species (*Gustavia johnclarkii* and *G. hubbardiorum*) and other contributions to the systematics of *Gustavia* (Lecythidaceae). *Brittonia* **65**, 330–341. (doi:10.1007/s12228-012-9282-9)
41. Odintsova A. 2008 Morphology and vascular anatomy of the flower of *Lagerstroemia indica* L. (Lythraceae) with some phylogenetic implications. *Wulfenia* **15**, 51–62.
42. Davis CC, Anderson WR. 2010 A complete generic phylogeny of Malpighiaceae inferred from nucleotide sequence data and morphology. *Am. J. Bot.* **97**, 2031–2048. (doi:10.3732/ajb.1000146)
43. Brunken U, Muellner AN. 2012 A New Tribal Classification of Grewioideae (Malvaceae) Based on Morphological and Molecular Phylogenetic Evidence. *Syst. Bot.* **37**, 699–711. (doi:10.1600/036364412x648670)
44. Vogel S. 1978 Evolutionary shifts from reward to deception in pollen flowers. *Pollinat. Flowers by Insects.* , 89–96.
45. Konzmann S, Hilgendorf F, Niester C, Rech AR, Lunau K. 2020 Morphological specialization of heterantherous *Rhynchanthera grandiflora* (Melastomataceae) accommodates pollinator diversity. *Plant Biol.* **22**, 583–590. (doi:10.1111/plb.13102)
46. Pereira AC, da Silva JB, Goldenberg R, Melo GAR, Varassin IG. 2011 Flower color change accelerated by bee pollination in *Tibouchina* (Melastomataceae). *Flora Morphol. Distrib. Funct. Ecol. Plants* **206**, 491–497. (doi:10.1016/j.flora.2011.01.004)
47. Simi MS; CN Sunil. 2018 Pollination biology of *Osbeckia wynaadensis* C . B . Clarke ( Melastomataceae ) - an endemic plant in Southern Western Ghats . *Int. J. Plant Reprod. Biol.* **10**, 166–171. (doi:10.14787/ijprb.2018 10.2.)
48. Larson BMH, Barrett SCH. 1999 The ecology of pollen limitation in buzz-pollinated *Rhexia virginica* (Melastomataceae). *J. Ecol.* **87**, 371–381. (doi:10.1046/j.1365-2745.1999.00362.x)
49. Dellinger AS *et al.* 2019 Modularity increases rate of floral evolution and adaptive success for functionally specialized pollination systems. *Commun. Biol.* **2**. (doi:10.1038/s42003-019-0697-7)
50. Melo, Gladys; Machado, Isabel; Luceño M. 1999 Reprodución de tres especies de *Clidemia* (Melastomataceae) en Brasil. *Rev. Biol. Trop.* **47**.
51. Soares NC, Morellato LPC. 2018 Crepuscular pollination and reproductive ecology of *Trembleya laniflora* (Melastomataceae), an endemic species in mountain rupestrian grasslands. *Flora Morphol. Distrib. Funct. Ecol. Plants* **238**, 138–147. (doi:10.1016/j.flora.2016.12.005)
52. Luo Z, Zhang D, Renner SS. 2008 Why two kinds of stamens in buzz-pollinated flowers? Experimental support for Darwin's division-of-labour hypothesis. *Funct. Ecol.* **22**, 794–800. (doi:10.1111/j.1365-2435.2008.01444.x)
53. Kessler PJA. 1993 Menispermaceae. In *Flowering Plants · Dicotyledons*, pp. 402–418. Berlin, Heidelberg: Springer Berlin Heidelberg.

Melo et al. 2024 – Pollen flower classification now and then

(doi:10.1007/978-3-662-02899-5\_48)

54. Williams GA, Adam P, Mound LA. 2001 Thrips (Thysanoptera) pollination in Australian subtropical rainforests, with particular reference to pollination of *Wilkiea huegeliana* (Monimiaceae). *J. Nat. Hist.* **35**, 1–21. (doi:10.1080/002229301447853)

55. Yong GWJ., Soh ZWW., Chui; SX, Chan AAQ., Ascher and JS. 2019 Insect visitors to flowers of cultivated *Ardisia elliptica* Thunb. (Myrsinaceae) and *Memecylon caeruleum* Jack (Melastomataceae) in Singapore. *Nat. SINGAPORE* **12**, 75–80. (doi:10.26107/NIS-2019-0008)

56. De O. Fidalgo A, De M. P. Kleinert A. 2009 Reproductive biology of six Brazilian Myrtaceae: Is there a syndrome associated with buzz-pollination? *New Zeal. J. Bot.* **47**, 355–365. (doi:10.1080/0028825x.2009.9672712)

57. PROENÇA CEB, GIBBS PE. 1994 Reproductive biology of eight sympatric Myrtaceae from Central Brazil. *New Phytol.* **126**, 343–354. (doi:10.1111/j.1469-8137.1994.tb03954.x)

58. Bhunia, Debasis; Mondal AK. 2012 STUDIES ON PRODUCTION, MORPHOLOGY AND FREE AMINO ACIDS OF POLLEN OF FOUR MEMBERS IN THE GENUS NYMPHAEA L. (NYMPHAEACEAE). *IJSN* **3**, 705–7018.

59. Chalegre SL, Domingos-Melo A, de Lima CT, Giulietti AM, Machado IC. 2020 *Nymphaea pulchella* (Nymphaeaceae) and *Trigona spinipes* (Apidae) interaction: From florivory to effective pollination in ponds surrounded by pasture. *Aquat. Bot.* **166**, 103267. (doi:10.1016/j.aquabot.2020.103267)

60. Nadia T de L, Machado IC. 2005 Polinização por vibração e sistema reprodutivo de duas espécies de *Sauvagesia* L. (Ochnaceae). *Rev. Bras. Botânica* **28**, 255–265. (doi:10.1590/s0100-84042005000200006)

61. Schneider J V., Bissiengou P, Amaral M do CE, Tahir A, Fay MF, Thines M, Sosef MSM, Zizka G, Chatrou LW. 2014 Phylogenetics, ancestral state reconstruction, and a new infrafamilial classification of the pantropical Ochnaceae (Medusagynaceae, Ochnaceae s.str., Quiinaceae) based on five DNA regions. *Mol. Phylogenet. Evol.* **78**, 199–214. (doi:10.1016/j.ympev.2014.05.018)

62. Matthews ML, Amaral MDCE, Endress PK. 2012 Comparative floral structure and systematics in Ochnaceae s.l. (Ochnaceae, Quiinaceae and Medusagynaceae; Malpighiales). *Bot. J. Linn. Soc.* **170**, 299–392. (doi:10.1111/j.1095-8339.2012.01299.x)

63. Cox PA. 1990 Pollination and the Evolution of Breeding Systems in Pandanaceae. *Ann. Missouri Bot. Gard.* **77**, 816–840.

64. Funamoto D. 2019 Plant-pollinator interactions in East Asia: A review. *J. Pollinat. Ecol.* **25**, 46–68.

65. Yang S, Chu G, Shi X, Wang S. 2019 Elaborated pollen packaging and dispensing mechanism induced by petal architecture from a Papaveraceae species. *PeerJ* **7**, e7066. (doi:10.7717/peerj.7066)

66. V. BITTRICH; M. C. E.; AMARAL; G. A. R. MELO. 1993 Pollination biology of *Ternstroemia laevigata* and *T. dentata* (Theaceae). *Plant Syst. Evol.*

Melo et al. 2024 – Pollen flower classification now and then

**185**, 1–6.

67. Sinclair E, Krauss S, Anthony J, Hovey R, Kendrick G. 2014 The interaction of environment and genetic diversity within meadows of the seagrass *Posidonia australis* (Posidoniaceae). *Mar. Ecol. Prog. Ser.* **506**, 87–98. (doi:10.3354/meps10812)
68. Wolowski M, Freitas L. 2015 An overview on pollination of the Neotropical Poales. *Rodriguesia* **66**, 329–336. (doi:10.1590/2175-7860201566204)
69. Severova EE, Volkova OA, Demina ON, Fomichev CI, Lock IE, Sokoloff DD. 2020 Diaperturate pollen in submerged aquatic monocots *Althenia orientalis* and *Althenia filiformis* (Potamogetonaceae: Alismatales). *Grana* **59**, 194–202. (doi:10.1080/00173134.2019.1665707)
70. Mast AR, Reveal JL. 2007 Transfer of Dodecatheon to Primula (Primulaceae). *Brittonia* **59**, 79–82. (doi:10.1663/0007-196X(2007)59[79:TODTPP]2.0.CO;2)
71. Anderberg AA, Manns U, Källersjö M. 2007 Phylogeny and floral evolution of the Lysimachieae (Ericales, Myrsinaceae): evidence from *ndhF* sequence data. *Willdenowia* **37**, 407. (doi:10.3372/wi.37.37202)
72. Streinzer M, Roth N, Paulus HF, Spaethe J. 2019 Color preference and spatial distribution of glaphyrid beetles suggest a key role in the maintenance of the color polymorphism in the peacock anemone (*Anemone pavonina*, Ranunculaceae) in Northern Greece. *J. Comp. Physiol. A* **205**, 735–743. (doi:10.1007/s00359-019-01360-2)
73. Wang TN, Clifford MR, Martínez-Gómez J, Johnson JC, Riffell JA, Di Stilio VS. 2019 Scent matters: differential contribution of scent to insect response in flowers with insect vs. wind pollination traits. *Ann. Bot.* **123**, 289–301. (doi:10.1093/aob/mcy131)
74. Prance GT, Nelson BW, Silva MF da, Daly DC. 1984 Projeto Flora Amazônica: eight years of binational botanical expeditions. *Acta Amaz.* **14**, 5–30. (doi:10.1590/1809-43921984145029)
75. Taylor ML, Altrichter KM, Aeilts LB. 2018 Pollen Ontogeny in *Ruppia* (Alismatidae). *Int. J. Plant Sci.* **179**, 217–230. (doi:10.1086/696535)
76. Thien LB, White DA, Yatsu LY. 1983 the Reproductive Biology of a Relict-*Illicium Floridanum* Ellis. *Am. J. Bot.* **70**, 719–727. (doi:10.1002/j.1537-2197.1983.tb12451.x)
77. Renner SS, Schwarzbach AE, Lohmann L. 1997 Phylogenetic position and floral function of *Siparuna* (Siparunaceae: Laurales). *Int. J. Plant Sci.* **158**. (doi:10.1086/297509)
78. Vallejo-Marín M. 2019 Evolutionary tinkering allows buzz pollinated plants to escape from an adaptive dead-end. *New Phytol.* **221**, 618–620. (doi:10.1111/nph.15474)
79. SMITH SD, KNAPP S. 2002 The natural history of reproduction in *Solanum* and *Lycianthes* (Solanaceae) in a subtropical moist forest. *Bull. Nat. Hist.*

Melo et al. 2024 – Pollen flower classification now and then

*Museum. Bot. Ser.* **32**. (doi:10.1017/S0968044602000051)

80. DULBERGER R, ORNDUFF R. 1980 FLORAL MORPHOLOGY AND REPRODUCTIVE BIOLOGY OF FOUR SPECIES OF CYANELLA (TECOPHILAEACEAE). *New Phytol.* **86**, 45–56. (doi:10.1111/j.1469-8137.1980.tb00778.x)

81. Bittrich V, Amaral MCE, Melo GAR. 1993 Pollination biology of *Ternstroemia laevigata* and *T. dentata* (Theaceae). *Plant Syst. Evol.* **185**, 1–6. (doi:10.1007/BF00937716)

82. Bernhardt P, Sage T, Weston P, Azuma H, Lam M, Thien LB, Bruhl J. 2003 The pollination of *Trimenia moorei* (Trimeniaceae): Floral volatiles, insect/wind pollen vectors and stigmatic self-incompatibility in a basal angiosperm. *Ann. Bot.* **92**, 445–458. (doi:10.1093/aob/mcg157)

83. Endress PK. 2010 Flower Structure and Trends of Evolution in Eudicots and Their Major Subclades 1. *Ann. Missouri Bot. Gard.* **97**, 541–583. (doi:10.3417/2009139)

84. Ackerman JD. 1997 Submarine pollination in the marine angiosperm *Zostera marina* (Zosteraceae). II. Pollen transport in flow fields and capture by stigmas. *Am. J. Bot.* **84**, 1110–1119. (doi:10.2307/2446154)

Melo et al. 2024 – Pollen flower classification now and then

Table SI 2 - List of families and traits considered for the cluster analyses.

Families	Pollen release							Floral display							
	NMDS	Poricidal 1 Longitudinal 0	Shed	Small portion	Exposed	Polyandric 1 oligandric 0	Stamens dimorphism	Grouped flowers	Shooting star	Brush blossom	Stamen Petal contrast	Reduced petal	Radial symmetry	Nocturnal anthesis	Accessory resources
Actinidiaceae	3	1	0	1	0	1	0	1	0	1	1	0	1	0	0
Aizoaceae	1	0	0	0	1	1	0	0	0	1	0	0	1	0	0
Annonaceae	1	0	1	0	0	1	0	0	0	0	0	0	1	0	1
Araceae	2	1	1	0	0	1	0	1	0	0	0	1	0	1	1
Asphodelaceae	3	1	0	1	0	0	0	1	1	0	1	0	1	0	0
Austrobaileyaceae	1	0	1	0	0	0	0	0	0	1	0	0	1	0	0
Begoniaceae	3	1	0	1	0	1	0	1	1	0	1	0	0	0	0
Bixaceae	3	1	0	1	0	1	0	1	1	1	1	0	1	0	0
Byblidaceae	3	1	0	1	0	0	0	0	0	0	1	0	1	0	0
Cactaceae	1	0	0	0	1	1	0	0	0	1	0	0	1	0	0
Canellaceae	2	0	1	0	0	0	0	1	0	0	0	0	1	0	0
Chloranthaceae	2	0	1	0	0	0	0	1	0	0	0	1	0	1	0
Circaeasteraceae	2	0	0	0	1	0	0	1	0	0	0	1	0	0	0
Cistaceae	1	0	0	0	1	1	0	1	0	1	1	0	1	0	0
Commelinaceae	3	0	0	1	0	0	1	1	0	0	0	0	0	0	0
Cyclanthaceae	2	0	1	0	0	1	0	1	0	0	0	1	0	0	0
Cyperaceae	2	0	0	0	1	0	0	0	1	0	0	1	0	0	0
Degeneriaceae	1	0	1	0	0	1	0	0	0	1	0	0	1	0	0
Dilleniaceae	3	1	0	1	0	0	0	0	0	1	0	0	1	0	0
Elaeocarpaceae	3	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Ericaceae	3	1	0	1	0	0	0	1	1	0	0	0	1	0	0
Euphorbiaceae	3	1	0	1	0	1	0	1	0	0	0	1	0	0	1
Eupomatiaceae	1	0	1	0	0	1	0	0	0	0	0	0	1	0	1
Fabaceae2	3	1	0	1	0	0	1	1	0	0	0	0	1	0	0

Melo et al. 2024 – Pollen flower classification now and then

Fabaceae1	1	0	1	0	0	1	0	1	0	1	0	1	1	0	0
Gentianaceae	3	1	0	1	0	0	0	1	0	0	1	0	1	0	0
Gesneriaceae	3	1	0	1	0	0	0	1	1	0	1	0	1	0	0
Gomortegaceae	2	0	0	0	1	0	0	1	0	0	0	0	1	0	0
Himantandraceae	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0
Hydrocharitaceae	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0
Hypericaceae	1	0	0	0	1	1	0	1	1	1	0	0	1	1	0
Hypoxidaceae	3	0	0	1	0	0	0	1	1	0	0	0	1	0	0
Iridaceae	3	1	0	1	0	0	0	0	1	0	1	0	1	0	0
Juncaginaceae	2	0	0	0	1	0	0	1	0	0	0	1	0	0	0
Lecythidaceae	3	1	0	1	0	1	0	0	0	0	1	0	1	1	0
Lytraceae	1	0	0	0	1	1	1	1	0	1	1	0	1	0	0
Magnoliaceae	1	0	1	0	0	1	0	0	0	1	1	0	1	0	1
Malpighiaceae	3	1	0	1	0	0	1	1	1	0	1	0	0	0	1
Malvaceae	3	1	0	1	0	0	0	1	1	0	1	0	1	0	1
Mayacaceae	3	1	0	1	0	0	0	0	0	0	1	0	1	0	0
Melastomataceae	3	1	0	1	0	0	1	1	0	0	1	0	1	0	1
Menispermaceae	2	0	0	0	1	0	0	1	0	0	0	0	1	0	0
Monimiaceae	1	0	0	0	1	1	0	1	0	0	1	1	1	0	0
Myristicaceae	2	0	1	0	0	1	0	1	0	0	0	0	0	0	0
Myrsinaceae	3	0	0	0	1	0	0	1	1	0	1	0	1	0	0
Myrtaceae	1	1	0	0	1	1	0	1	0	1	0	1	1	0	0
Nymphaeaceae	1	0	1	0	0	1	0	0	0	0	1	0	1	1	1
Ochnaceae	3	1	0	1	0	1	0	1	1	0	0	0	1	0	0
Pandanaceae	2	0	1	0	0	1	0	1	0	0	0	1	0	0	0
Papaveraceae	1	0	0	0	1	1	0	0	0	1	1	0	1	0	0
Pentaphragaceae	1	0	0	0	1	1	0	1	0	0	0	0	1	0	0
Philydraceae	2	0	0	0	1	0	0	0	0	0	0	1	0	0	0



## Melo et al. 2024 – Pollen flower classification now and then

<b>Piperaceae</b>	2	0	1	0	0	1	0	1	0	0	0	1	0	0	0
<b>Pittosporaceae</b>	3	1	0	1	0	0	0	0	0	0	1	0	0	0	0
<b>Poaceae</b>	2	0	0	0	1	0	0	1	0	0	1	0	0	0	0
<b>Pontederiaceae</b>	3	1	0	1	0	0	1	1	0	0	1	0	1	0	0
<b>Posidoniaceae</b>	2	0	1	0	0	0	0	1	0	0	0	1	0	0	0
<b>Potamogetonaceae</b>	2	0	0	0	1	0	0	1	0	0	0	1	0	0	0
<b>Primulaceae</b>	3	1	0	1	0	0	0	0	1	0	0	0	0	0	0
<b>Ranunculaceae</b>	1	0	0	0	1	1	0	0	0	1	1	0	1	0	1
<b>Rapateaceae</b>	3	1	0	1	0	0	0	0	0	0	0	0	1	0	0
<b>Ruppiaceae</b>	2	0	0	0	1	0	0	0	0	0	0	1	0	0	0
<b>Saururaceae</b>	2	0	0	0	1	1	0	1	0	0	0	1	0	0	0
<b>Scheuchzeriaceae</b>	2	0	0	0	1	0	0	1	0	0	0	1	1	0	0
<b>Schisandraceae</b>	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1
<b>Siparunaceae</b>	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0
<b>Solanaceae</b>	3	1	0	1	0	0	0	0	1	0	1	0	1	0	0
<b>Taccaceae</b>	2	0	0	0	1	0	0	1	1	0	0	1	1	0	0
<b>Tecophilaeaceae</b>	3	1	0	1	0	0	0	0	1	0	1	0	1	0	0
<b>Theaceae</b>	1	0	0	0	1	0	0	0	0	1	1	0	1	0	0
<b>Trimeniaceae</b>	1	0	1	0	0	1	0	0	0	0	0	1	1	0	0
<b>Winteraceae</b>	1	0	1	0	0	1	0	0	0	0	1	0	1	0	1
<b>Zosteraceae</b>	2	0	0	0	1	0	0	1	0	0	0	1	0	0	0

Melo et al. 2024 – Pollen flower classification now and then

Table SI 3 – Families in the Vogel classification and families in the proposed new classification to pollen flowers.

Vogel 1978	Magnolian type	Annonaceae; Araceae; Degeneriaceae; Eupomatiaceae; Himantandraceae; Magnoliaceae; Myristicaceae; Nymphaeaceae
	Papaver type	Actinidiaecae; Aizoaceae; Begoniaceae; Cactaceae; Cistaceae; Fabaceae; Hypericaceae; Papaveraceae; Ranunculaceae; Theaceae
	Solanum type	Bixaceae; Byblidaceae; Commelinaceae; Dilleniaceae; Elaeocarpaceae; Fabaceae2; Gentianaceae; Gesneriaceae; Hypoxidaceae; Lecythidaceae; Lytraceae; Malpighiaceae; Malvaceae; Melastomataceae; Myrsinaceae; Ochnaceae; Philydraceae; Primulaceae; Rapateaceae; Solanaceae
Melo et al. (2024)	Brush-blossom type	Aizoaceae; Annonaceae; Austrobaileyaceae; Cactaceae; Cistaceae; Degeneriaceae; Eupomatiaceae; Fabaceae 1 ( <i>Acacia and Swartzia</i> ); Himantandeaceae; Hydrocharitaceae; Hypericaceae; Lytraceae; Magnoliaceae; Monimiaceae; Myrtaceae; Nymphaeaceae; Papaveraceae; Pentaphylaceae; Ranunculaceae; Schisandraceae; Siparunaceae; Theaceae; Trimeniaceae; Winteraceae
	Inconspicuous type	Araceae; Canellaceae; Chloranthaceae; Circaeasteraceae; Cyclanthaceae; Cyperaceae; Gomortegaceae; Juncaginaceae; Menispermaceae; Myristicaceae; Pandanaceae; Philydraceae; Piperaceae; Poaceae; Posidoniaceae; Potamogetonaceae; Ruppiaceae; Saururaceae; Scheuchzeriaceae; Taccaceae; Zosteraceae
	Poricidal type	Actinidiaceae; Asphodelaceae; Begoniaceae; Bixaceae; Byblidaceae; Commelinaceae; Dilleniaceae; Elaeocarpaceae; Ericaceae; Euphorbiaceae; Fabaceae2 ( <i>Cassia, Chamaecrista and Senna</i> ); Gentianaceae; Gesneriaceae; Hypoxidaceae; Iridaceae; Lecythidaceae; Malpighiaceae; Malvaceae; Mayacaceae; Melastomataceae; Myrsinaceae; Ochnaceae; Pittosporaceae; Pontederiaceae; Primulaceae; Rapateaceae; Solanaceae; Tecophilaeaceae



Lilian Melo

PhD in Ecology, Conservation and Biodiversity

Plant Ecology and Evolution - Uppsala University, EBC

Norbyvägen 18 D

752 36 Uppsala

Sweden

August 26, 2024

Christiane Werner and Theo Elzenga

German Society for Plant Sciences and the Royal Botanical Society of the Netherlands

Plant Biology

Dear Editors,

We are pleased to submit our study on the classification of pollen flowers, entitled "Pollen flower classification now and then: Vogel (1978) revisited". Vogel's work in 1978 was undoubtedly significant for classifying flower types based on their interactions with pollinators. However, we have found that his original classification is insufficient in light of our current understanding of the vast diversity of pollen flowers. The results of this study identified 40 additional plant families of pollen flowers that were not previously described in Vogel's 1978 seminal work. This represents a significant increase in the number of families and potentially the morphological diversity of pollen flowers. Furthermore, it has enabled us to refine the interpretation of floral types based on their shared morphology. This study presents a novel perspective on the classification of pollen flowers, suggesting a move away from Vogel's classification and encouraging a more inclusive and comprehensive classification of pollen flowers based on morphological traits. As we near the 50th anniversary of this seminal work, revisiting it is crucial. Today, we have a much better understanding of plant biodiversity globally, and effectively communicating morphological strategies associated with pollen flowers can help us to further study their ecology and evolution.

I confirm that this contribution is original and that it has not been submitted to any other journal.

Please do not hesitate in contacting me if I can be of further assistance.

Lilian Melo

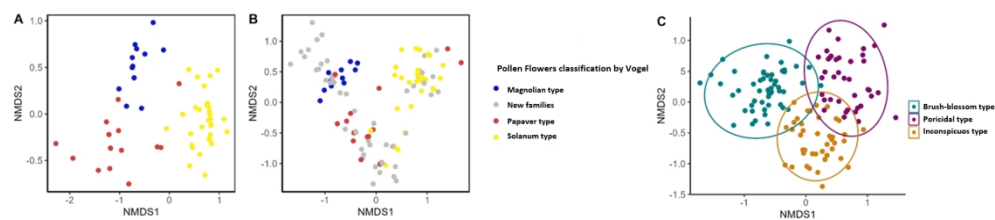


Figure 1. (A) Morphospace is based on three floral traits proposed by Vogel (1978), including the 38 families of pollen flowers he mentioned. (B) Morphospace based on the same three floral traits as in A, but this time including both Vogel’s (1978) original families plus 35 new families found to have pollen flowers in our review. (C) Morphospace is based on 11 morphological traits and includes all 73 families. The families included in the three highlighted clusters do not coincide with those present in Vogel’s original pollen flower classification (Magnolian, Papaver, and Solanum).

487x112mm (96 x 96 DPI)

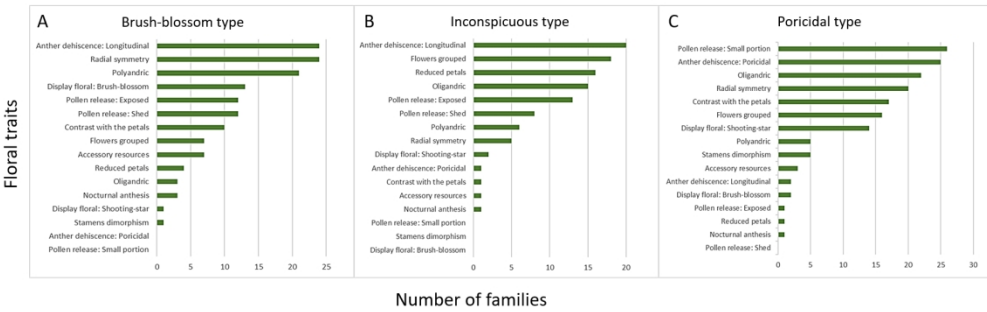


Figure 2. The most important floral traits composing each pollen flower group in our reviewed analyses using 11 floral traits in 73 families. The predominance of floral traits (A) for the 24 families within the brush-blossom type, (B) for the 21 families within the inconspicuous type, and (C) for the 28 families within the poricidal type.

487x154mm (96 x 96 DPI)

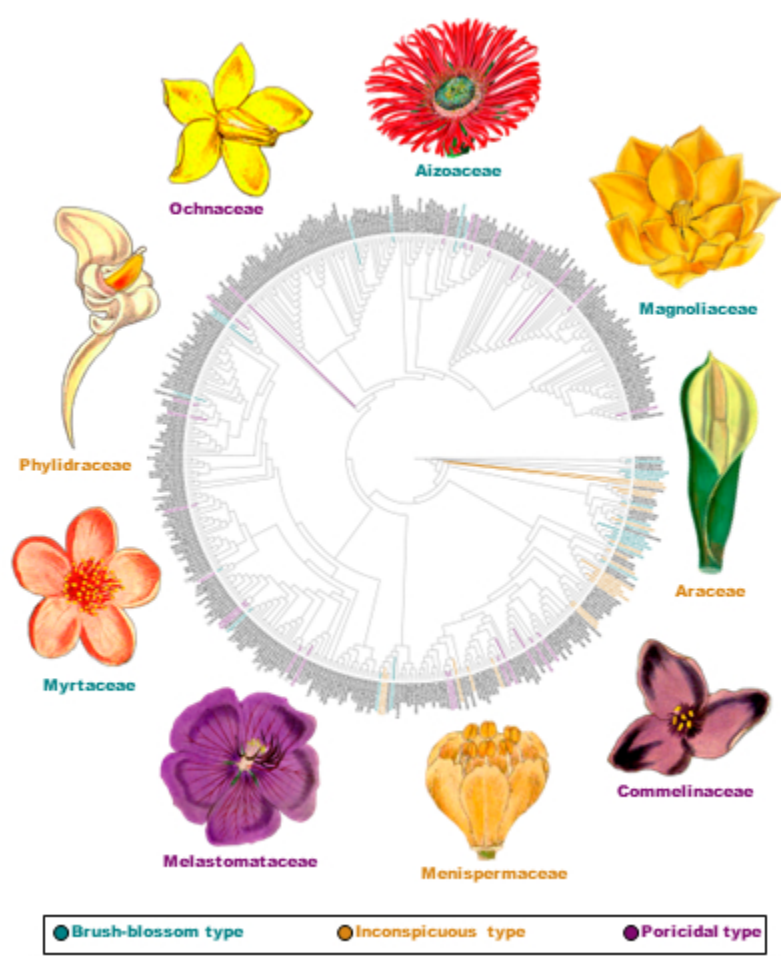


Figure 3. Families of the three groups of pollen flowers proposed in the new classification, along the Phylogeny of Angiosperm Families (Qian & Zhang 2014)- adapted. The illustrations are available in (Watson & Dallwitz). Version: 25th July 2023. (Illustrations edited by João Pedro Santos Pereira).

112x129mm (96 x 96 DPI)