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WHY THE ORCHIDS HAVE MONO-SYMMETRIC FLOWERS? A POLLINATION PERSPECTIVE

Sourav Mukherjee and Suresh D Jagtap[1]

Biology Department, Takalkar Institute, Pune- 411 041, Maharashtra, India
[1]Interactive Research School for Health Affairs (IRSHA), Bharati Vidyapeeth, Pune- 411 041, Maharashtra, India

Abstract

The flowers of family Orchidaceae are mono-symmetric and show a great level of specialization in pollination mechanism. Zygomorphy is perceived to be an added advantage for pollination. It is also thought that pollinator driven selection pressure might have evolved zygomorphy over ancestral actinomorphy in both Eudicots and Monocots. The floral contour of orchids often helps in guiding its pollinators to accomplish pollination, without reward-wastage or pollen robbing. The present communication gives a glimpse of orchid floral morphology in relation to their pollination mechanism.

Introduction

THE FAMILY Orchidaceae is considered as one of the largest plant families, with recent documentation suggesting 693 genera encompassing about 29,481 species worldwide (POWO, 2025; WFO, 2023). The orchid flowers have a unique trait where the male part of the flower comprises only one stamen and is fused with female parts of the flower to form a structure called column. Pollens lay at distal end of the column as discrete masses (pollinia) (Pal *et al.*, 2019) (Fig. 1A-B). Diandrae orchid genera have two fertile stamens placed sub terminally on the sides of column. Besides this, the orchid flowers possess the labellum or the median petal. This part of the perianth is more complex, larger or smaller, and often more strongly marked than other floral parts (Rudall and Bateman, 2002) (Fig. 1A-B).

Hence, in orchid flowers, there is only a single mirror-plane and no axis of symmetry (Rudall and Bateman, 2002). The labellum is developmentally uppermost member and spatially the lowermost, due to the 180° torsion of the subtending pedicel and/or ovary, in the majority of orchid flowers, the phenomenon known as resupination (Rudall and Bateman, 2002).

What is Zygomorphy?

Floral symmetry is actually the repeated pattern in structural units as assessed in relation to the principal axis of the flower, which is considered as the vector (= line) passing from the centre of the receptacle (Neal *et al.*, 1998). Although there is different types of symmetry in angiosperm flowers (Fig. 2): a) poly-symmetric flowers have more than one plane of symmetry and are called radially symmetrical or actinomorphic; b) disymmetric flowers have two planes of symmetry and are called bilaterally bi-symmetrical, as in *Dicentra*; c) mono-symmetric flowers possess only one plane of symmetry as Orchidaceae members, and are called zygomorphic or bilaterally symmetrical flowers; and d) asymmetrical flowers which do not have any plane of symmetry (Neal *et al.*, 1998; Rudall and Bateman, 2002). The medial zygomorphy bilateral symmetry is observed in orchids, which is perceived as right and left identical.

Evolution of Zygomorphy

Zygomorphy is often considered as homoplastic trait, a trait that shows independent evolution (Bukhari *et al.*, 2017; Sargent, 2004) and has evolved independently at least 38 times (Zhang *et al.*, 2010), 70 times (Citerne *et al.*, 2010), or 199 times (Reyes *et al.*, 2016) in the evolutionary history of angiosperms and is known to occur in at least 110 families and 32 orders (Stephens *et al.*, 2024). It occurs prominently in Asteraceae, Fabaceae,

Fig. 1 A-B. Orchid flowers.

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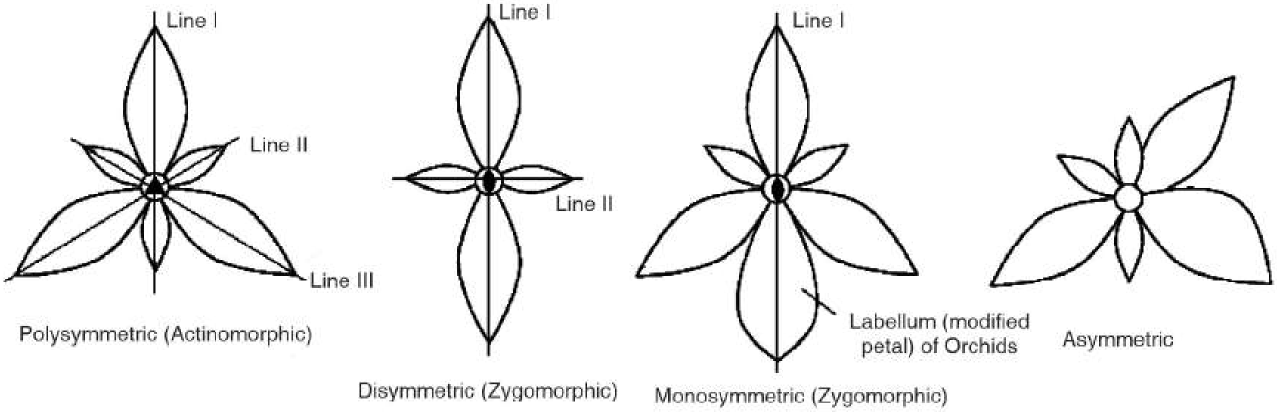

Fig. 2. Types of symmetry in flowers (modified from Rudall and Bateman, 2002).

and Lamiaceae, in dicots and Zingeberaceae and Orchidaceae, in monocots (Hileman, 2014; Zhang *et al.*, 2010). Earliest fossil flowers were actinomorphic and zygomorphy might have first appeared about 30-40 million years later (cf. Bukhari *et al.*, 2017). This key feature is often considered to be one of the most vital forces operating for speciation in angiosperms and causes their subsequent diversification (Zhang *et al.*, 2010). The single symmetry axis in these flowers might have originated from an unequal distribution of organs at maturity and/or superimposition of secondary identities on the basal sepal, petals, or stamen identities (Citerne *et al.*, 2010). There are fundamental three patterns of the zygomorphy, with respect to petals, termed commonly as 2:3, 4:1, and 0:5 (Donoghue *et al.*, 1998), all the three patterns are found mainly in dicots. These patterns depict the upper (inner, adaxial; which are near the main axis) and lower (outer, abaxial; which are distant from the main axis) petal arrangements. When the two adaxial petals are differentiated from the three abaxial ones, it is a 2:3 pattern, which is suggested to be a most common form of zygomorphy (Donoghue *et al.*, 1998). During resupination, at least in case of genus *Rhododendron*, the 2:3 pattern is changed to 3:2, indicating thereby that three adaxial petals (one medial and two lateral) and two abaxial petals and the medial abaxial petal of the mature flower occupied atypical adaxial position, before resupination (Donoghue *et al.*, 1998). This pattern may also be found even in those orchids which show resupination.

Zygomorphic flowers might be better adapted for pollination as compared to their counterparts (or the actinomorphic flowers) and have several advantages over actinomorphy (Neal *et al.*, 1998), which are summarized in Table 1. Floral traits are often specifically adapted to the available primary pollinators, and one can simply understand the relation between zygomorphy and pollination. The pollination strategies, of orchids are complex and often employ sexual deceit and other forms of deception (Pal *et al.*, 2019). However, the putative relationship between zygomorphy and its pollination mechanism is not much explored, in orchids. The present communication is an attempt to understand the significance and evolution of zygomorphic flowers in orchids with respect to their pollination mechanism.

Material and Methods

The literature survey and the data collection for the present communication were primarily from the standard websites. In order to procure pertinent literature without having any author bias, combinations of keywords like *Orchids, Orchidaceae, Zygomorphy, Zygomorphic flower* were incorporated with *Pollination,* and *Evolution* in Google Scholar, Science Direct, Elsevier, Pubmed Central, and BMC. Peer reviewed journal articles, theses, and abstracts, were in the inclusion criteria for the literature search. Language bias was not incorporated in order to obtain maximum information available.

Results and Discussion

Zygomorphy has long been associated with specific morphological adaptations that are thought to enhance the efficiency of pollination by particular types of pollinators (Rudall and Bateman, 2004). The pollination ecology of these flowers is specialized, more precise, advanced, and nevertheless, advantageous over the radially symmetrical flowers (Yoder *et al.*, 2020). Due to trimerous pattern in monocots, complete radial symmetry is commonly observed. Amongst the monocots, distinct bilateral symmetry is often found exclusively in Asparagales, some Commelinids, Zingiberales *etc.* (Rudall and Bateman, 2004). Most obvious and prominent zygomorphic flowers are found in the family Orchidaceae, which are highly species-rich group with predominantly showy and insect-pollinated flowers (Rudall and Bateman, 2004). Zygomorphy in monocots is slightly

Table 1. Zygomorphy and its role in enhancing pollination efficiency.

Hypothesis	Explanation
Pollen position hypothesis	1. Pollinator can approach flower from one direction.
	2. This allows a restricted movement from front to back and on either side.
	3. There are better chances of accurate positioning of the pollen on the pollinator's body (Leppik, 1972; Sargent, 2004).
Reward wastage hypothesis	1. Pollen stealing, wastage are less in bilaterally symmetrical flowers, as the rewards are hidden due to shape of the flower.
	2. Special adaptations are needed to acquire these 'hidden treasure' (Neal *et al.*, 1998), which involves the requirement of a minimum weight or strength of the visitor.
Optical information hypothesis	1. Zygomorphy provides greater possibilities for the transmission of visually mediated information than radial symmetry (Neal *et al.*, 1998).
	2. It demands sophisticated neuronal processing and behavioural versatility on pollinator's part to attract the reward provided by the flower (Neal *et al.*, 1998).
	3. Increased images of floral complexity result in better and increased foraging, more recognition, and better reproductive success (Neal *et al.*, 1998).
Unequal image projection hypothesis	1. Insects tend to memorise and recognise the shape of flower by matching the actual image perceived by the eye with a memorized template, and thus, choice of visitation rely on the overlap between memorized image of the flower and the observed shape (Neal *et al.*, 1998).
	2. The landing of insects (specifically Hymenoptera members) would be enhanced if i) the flowers advertise the colour pattern vertically and ii) nectar guides and labellum (the dissected parts) are on the lower side.
	3. There is a restriction to the approach-flight for the pollinator.
Feeding anther-pollen collection hypothesis	1. Floral parts are better protected in zygomorphy (Dulberger, 1981; Fenster, 1995).
	2. This protects the floral parts during buzz-pollination (Neal *et al.*, 1998; Dulberger, 1981).
	3. Spatial separation of anther and stigma that might prevent unwanted autogamy (Neal *et al.*, 1998), resulting from pollen dust during buzz-pollination.
Protection from rain hypothesis	1. Downward oriented flower capable of protecting its pollens from rain-hit damage (Yu *et al.*, 2021).
	2. The upper lip, which is horizontal, is positioned in such a way that it acts as a 'nectar cover' from rain (Neal *et al.*, 1998).

different in the organization of androecium (Rudall and Bateman, 2004). Specifically in orchids, most often one or more abaxial stamen are present, and there is a subsequent loss of both outer and inner adaxial stamens, and the presence of relatively well-differentiated adaxial petal or the labellum (Rudall and Bateman, 2004). Unless there are some teratological forms, in the majority of orchids, there is one fertile abaxial stamen as in Vanilloideae, Orchidioideae, and Epidendroideae; two as in Cypripedioideae and three as in Apostasioideae, which may be occasionally fused with the stigma.

Does Zygomorphy Facilitate Pollination?

One of the major driving forces for the evolution of zygomorphy is the selection pressure exerted by specific pollinators (Zhang *et al.*, 2010). This shift might have occurred due to an increase in selection pressure by insects and later by the introduction of vertebrate pollinators (cf. Bukhari *et al.*, 2017). Basically, zygomorphy (i) is associated with a greater diversification rate, (ii) facilitates more effective pollination, and (iii) uses fewer pollinators that create more opportunities for reproductive isolation (Yoder *et al.*, 2020). Such pollinator specificity and efficiency of pollination mechanisms could reduce the interspecific competition for pollinators, and increase reproductive fitness or success, either (i) by grouping more sympatric species, or (ii) by a dramatic increase in the success of conspecific pollen transfer and eventual fertilisation process (Alvestegui, 2021). Both lead to viable and effective sustenance of the zygomorphic species, though there were a fewer individuals in an area. This also makes these species more resilient to climatic changes, pollinator availability, or spatial changes in the area, adding to their reproductive success (Alvestegui, 2021). The increased pollinator specificity is often achieved (i) by the orientation of these flowers, which successfully restricts the access of the pollinators visiting it and consistently guides them to a specific direction (Alvestegui, 2021; Neal *et al*., 1998), or (ii) by enhancing cross pollination and by allowing precise control on both pollen export and pollen receipt, both by mediating a close contact between body of pollinator and floral parts (Alvestegui, 2021).

Zygomorphy is associated with fewer pollinator visitations, which may increase the risk of extinction of species, due to pollinator loss, in the restricted area (Yoder *et al*., 2020). However, they share larger proportion of their 'limited' pollinators with other co-occurring (mainly zygomorphic) species, a pattern called floral visitation network, which is highly nested (Yoder *et al*., 2020), indicating thereby a strong correlation between zygomorphy and species richness, which is found in Orchidaceae.

Flowers with monoaxial symmetry often employ manipulative pollination behaviour, like spatial positioning of pollen on the body of pollinator, or by attracting pollinators with greater constancy over a single foraging trip, *etc*. (Yoder *et al*., 2020). To attract a particular pollen vector, orchid flowers often involve and interact with key floral traits like corolla shape, spur length, *etc*. (Alvestegui, 2021). One example of differential spatial positioning of pollen cites as *Epidendrum ibaguense,* which mimic the actinomorphic flowers of *Lantana camara* and *Asclepias curassavica* (Boyden, 1980). These plants strategically place the pollen on head and thorax (*L. camara*), on their legs (*A. curassavica*), and on the proboscis (*E. ibaguense*) of the pollinators. Such a specialized pollinator selection pressure promoted stabilizing selection in zygomorphic flowers which evolved lesser extent in variations in flower size (Lazaro and Totland, 2014). Since these flowers often have fewer pollinators, the mechanical fit between the effective pollinator and flower plays a vital role and reduces the chance to change frequently. Such flowers are ecologically specialized, highly dependent on pollinators and show less variation in floral size (Lazaro and Totland, 2014). Similarly, zygomorphy impedes self-pollen deposition, even though self-compatibility of zygomorphic flowers is more as compared to actinomorphic counterparts (Stephens *et al*., 2024).

The orchids show specialized pollination syndromes, zygomorphic flowers, and often manipulative pollination mechanisms. These characters might have also attributed to the vast diversification of orchids and their eventual speciation process. Various modifications that orchid flowers display in order to get pollinated are:

a. Highly modified labellum in the Cypripedioideae members act as *one way trap* or *Kettle trap* (Bänziger *et al*., 2008; Suetsugu and Fukushima, 2013). The opening in the front side of the labellum is the entry point for the pollinator, which guides the insect to one of the orifices that are formed by the joining of the staminodes, blocking the opening of the labellum at the base. While the pollinator is forced to pass through the stigma and under the anthers, in order to be guided to the basal orifice. In doing so, the pollinator may pick up some pollinia, or, if it has already picked up some pollinia before, pollination is accomplished while crossing the stigma. Usually, it is also estimated that the pollinator does not remain imprisoned in such a trap for more than 10 minutes (Case and Bradford, 2009; Nilsson, 1979), when the pollinator crawls downwards and presses up against stigma. This pressing action ensures the transfer of pollen they might have been carried to the stigmatic surface as well as provides a leverage action to open the exit hole (Case and Bradford, 2009; Nilsson, 1979). While during exit by squeezing through the narrow hole, the pollinator picks up some more pollinarium (Case and Bradford, 2009). Such floral structure provides proper direction to their specific pollinators and increase pollinator specificity (Alvestegui, 2021; Neal *et al*., 1998).

b. Trap-flowers are also found in Epidendroideae subfamily of Orchidaceae. *Trigonidium obtusum* flowers are funnel shaped and with lip that is articulated at the base of the erect column, with incumbent anther and the stigmatic surface is concave. They also employ pseudo copulation methods to attract the male pollinator and trap the same inside the funnel-shaped flowers (Singer, 2002). This can be extrapolated to both pollen position hypothesis and reward wastage hypothesis (Table 1).

c. The drop-flowers or fall-through flowers of *Stanhopea* allow its pollinators (mostly Euglossine bees) to brush against the lip base and while coming out, they tend to pick up the viscidia under its scutellum or by depositing pollinia in the stigma. In *S. leitzei* and *S. insignis*, the bee approaches the flower by landing laterally on the hypochile, or on the column foot and get the orchid pollinated (Pansarin and Amaral, 2009).

d. The incompletely unfolded perianth of *Pteroglossaspis ruwenzoriensis* is adapted for getting exclusively pollinated by a beetle (Singer and Cocucci, 1997). The labellum and other perianth parts of *Luisia curtisii* provide a safe and resting place for the beetles that pollinate this orchid (Pedersen *et al*., 2013).

e. Labellum is one of the most common landing platform for insects in orchids like *Encyclia mapuerae* (Krahl *et al*., 2017), *Cranichis candida* (Pansarin *et al*., 2017), *Bonatea cassidea* (Balducci *et al*., 2019), to name a few. Several examples can be cited in this regard.

f. Greater and enhanced efficiency of pollination in orchids are often attributed, along with their bilateral symmetrical flowers, to their compact pollinarium (Johnson and Edwards, 2000). The mass of pollinia gets attached to the body of the pollinators, which ensures successful transfer of pollen.

g. Zygomorphy, along with the formation of pollen aggregate also provide additional advantages to orchids from being pollinated by rain (ombrophily). The aggregated pollen mass and the typical orientation of floral parts (arising due to mono-axial symmetry) pose slight difficulty in removing the pollen grains from these flowers (Lawson and Rands, 2019; Suetsugu, 2019). Exception to this process is observed, however, in *Liparis kumokiri* and *L. loeselii* (Suetsugu, 2019) and *Oeceoclades maculata* (Gonzalez-Dýaz and Ackerman, 1988; Suetsugu, 2019)*, Acampe rigida* (Fan *et al*., 2012), where pollination and eventual seed-set is assisted by raindrops. Again, in (at least) *A. rigida* orchids: i), vertically oriented cup-shaped flowers (related to its zygomorphic nature); ii), a weak anther cap that is easily dislodged by raindrops causing pollinia to bounce upwards; and iii) the intricate stretchable stipe that pulls the pollinia back in a precise way into the stigmatic cavity cause self-pollination (Fan *et al*., 2012).

h. The floral symmetry in orchid flowers is necessary for the pollination by beetles (Peter and Johnson, 2009). Often, flat surface of the flowers, as can be visualized for the labellum in many orchids, assists in the *Rendezvous pollination* by beetles.

i. In *Corybas,* there are domed floral chambers with spur (Han *et al*., 2022). The pollinators (smaller flies) climb up to the flowers to come in contact with the rostellum and pollen-receptive lobes of the stigma. These smaller insects land on the labellum and align themselves facing upwards. Rotation of ovary by 180° indicates that spatial positioning of the floral parts play a crucial role in the mechanism of pollination (Phillips *et al*., 2014). Some insects land and walk before finally positioning their heads towards the dorsal sepals, while opening and closing their genital claspers (Blanco and Barboza, 2005). Their mating behaviour include mounting the flowers' labellum, curling their abdomen under the labellum blades and probing their genital claspers to the labellum appendix.

j. Weak zygomorphy is often said to be associated with bird pollination or ornithophily. *Hexisea imbricata* and *H. bidentata* produce tubular, weak zygomorphic flowers that are pollinated by humming birds (Stpiczyñska *et al*., 2005); *Maxillaria coccinea* also gets pollinated by humming birds and produces diurnal, weakly zygomorphic with backwardly bent (curved) labellum with abundant nectar (Stpiczyñska *et al*., 2004).

k. Orchids, like *Angraecum cadetii* has larger zygomorphic flowers, which are adapted to its pollinator, a cricket (Micheneau *et al*., 2010). The head of the insect and size of opening of the flowers match to a large extent. Similarly, the size of the mouth of the nectar spur (4.3-7.9 mm long) is slightly lesser than that of the head of the orthopteran pollinator, which is 5.8-7.3 mm long. This leads to a very good contact with the pollinia and hence, successful pollen transfer (Micheneau *et al*., 2010). These insects land on these flowers and position towards the dorsal lip of the flower and probe for nectaries. Such a perfect fit of the floral part and the insect body increases pollinator specificity (Lazaro and Totland, 2014).

l. In sub-tribe Habenariinae, the pollinarium is either, i), attached to the eyes of the moth (Peter *et al*., 2009; Singer *et al*., 2007); ii), in some cases on the proboscis (Peter *et al*., 2009; Singer, 2001) or very rarely; iii) in their forelegs (Peter *et al*., 2009). The pollinia placed on different body parts of the effective pollinator contact conspecific stigmas and thus favour effective transfer of pollen to the stigma (Xiong *et al*., 2020). Especially in the genus *Habenaria*, pollinia may be attached to various body parts of the pollinator, moth or butterfly, like eyes, heads, and base of proboscis. This strictly depends on the physical match between the nectar spur and the pollinator proboscis length (Xiong *et al.*, 2020). For example, pollinia of *Habenaria limprichtii* attaches on the eyes of their Sphingid pollinators and on the legs of their Noctuid settling moths (Tao *et al.*, 2018; Xiong *et al.*, 2018). This is in favour of pollen position hypothesis. Depending on the body size of the pollinator, the natural selection is found to be disruptive and not strictly directional, along with divergent evolutionary pattern (Xu *et al.*, 2012).

m. Thrips, belonging to Thysanoptera order are primarily pollenivores and behave like supplementary pollinators in orchids, as documented in *Epipactis thunbergii* (Suetsugu *et al.*, 2019). They prefer to carry the dry pollen on their legs, wings, and setae of the abdominal section. The attached pollen grains on these insects are therefore, efficiently dispersed on the stigma while these animals are moving haphazardly inside the flower, rubbing their abdomen on the stigmatic surface, cleansing their body parts with hands, legs, or by wings, or even by some combinatorial mechanisms (Varatharajan *et al.*, 2016). This is in favour of feeding anther-pollen collection hypothesis.

n. It is argued that autogamy is not possible for the orchids (specifically in *Satyrium rupestre*), due to the zygomorphy and reasons like a), the position of the anther and position of stigma and the flowers are non-resupinate; and b), position and shape of rostellum also blocks the passage of pollinia to the stigma; such morphology and structure of these flowers prevent the gravity-driven autogamy (Niet, 2018).

o. The complex structural organisation of orchid flowers, especially, when there is a specific landing platform, the labellum, gives an advantage to the pollinators. Downward vertical orientation might be reducing the chances of landing platform or the chances of landing without touching the reproductive parts like anther or stigma, for approaching pollinator, a phenomenon often termed as illegitimate landings (Ushimaru and Hyodo, 2005).

p. As indicated in Table 1, buzz-pollination may render damage to the floral parts, and thus harm the reproductive fitness of the species (Dulberger, 1981; Neal *et al.*, 1998). The development of pollen-mass or pollinia in orchids, which are in cluster, such damage is partially (if not altogether) alleviated.

Why Orchid Flowers Have Greater Longevity?

Zygomorphic flowers last longer (as compared to their actinomorphic counterparts). Floral longevity is a key feature controlling pollination ecology and balances the flowering cost and the successful pollen transfer or pollen receipt (Stephens *et al.*, 2024). Thus, in general, zygomorphic flowers may tend to live longer to substantially increase their chances of attracting visit by a specific pollinator from a smaller pool of pollinators in the vicinity (Stephens *et al.*, 2024). Orchid flowers live longer than many other flowers, often lasting for more than 10 days.

Molecular dating and phylogenetic analysis revealing the putative origin and evolution of orchid flowers along with the functional ecology of the pollination system in them might throw some more light on this complex (interactive) evolution of the trait of zygomorphy. However, still much needs to be learnt about such a sophisticated pollination mechanism in orchids.

Conclusion

The evolution of zygomorphy from ancestral actinomorphic flowers in angiosperms is often attributed to what is called as a pollinator driven trait. Bilaterally symmetrical orchid flowers are better adapted, last longer, and employ manipulative pollination mechanisms. From the available data, it may be concluded that the floral architecture and shelf life of the flowers are important and these play pivotal role in pollination mechanism in orchids; these characters might have been crucial to their diversification and speciation. Further, unfurling of this aspect with modern tools, phylogenetic analysis, and accurate mechanism of pollination may give a better understanding about these phenomena.

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