Pollination Chamber Types in Annonaceae and Their Evolutionary Significance: Postprint

Authors: Cheng Mei, Xu Fengxia

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Abstract

Coevolution of floral structure and pollinators is a key driver of the successful evolution of flowering plants, and the pollination chamber represents a prominent floral structure in Annonaceae. Due to the high diversity in petal size, whorl number, petal count per whorl, and fusion patterns among petals within this family, pollination chamber morphology is also highly diverse. Detailed floral structures have been documented for 68 of the 107 genera in Annonaceae. This study classifies the pollination chambers of these 68 genera into three categories—open, semi-closed, and closed—based on their degree of closure during anthesis. Specifically, 24 genera feature open pollination chambers, 38 genera feature semi-closed chambers, and 26 genera feature closed chambers. Approximately 17 genera exhibit two or three chamber types. Distinct correspondence exists between pollination chamber types and pollinators: bees and flies primarily pollinate plants with open chambers or those with relatively spacious chambers among semi-closed and closed types, whereas thrips mainly pollinate plants with semi-closed and closed chambers. The Paleotropics and Neotropics constitute the primary distribution centers for Annonaceae. While species richness is highest in the Paleotropics, both pollination chamber types and pollinators are relatively uniform there; in contrast, the Neotropics harbor fewer species but exhibit high diversity in both chamber types and pollinators. Previous research indicates that Africa represents the evolutionary origin of Annonaceae, with open-type chambers predominantly distributed in tropical Africa, commonly occurring in early-diverging genera across tribes, and exclusively pollinated by small beetles, thus representing a relatively primitive chamber type. Semi-closed chambers are distributed across tropical Africa, tropical Asia, and tropical America, while closed chambers are primarily restricted to tropical Asia; these two types are associated with more diverse pollinator assemblages and represent the more derived pollination chamber types within Annonaceae.

Full Text

Preamble

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Classification of Pollination Chamber Types and Their Evolutionary Significance in Annonaceae

Mei Cheng[1,2,3], Fengxia Xu[1,3*]
[1] Key Laboratory of Plant Resources Conservation and Sustainable Utilization, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China
[2] University of Chinese Academy of Sciences, Beijing 100049, China
[3] Guangdong Provincial Key Laboratory of Digital Botanical Garden, Guangzhou 510650, China

Abstract

The co-evolution of floral structures with pollinators represents a critical factor underlying the evolutionary success of flowering plants. In Annonaceae, the pollination chamber constitutes a distinctive floral feature. Due to high diversity in petal size, whorl number, petals per whorl, and fusion patterns among petals, pollination chamber morphology exhibits remarkable variation across the family. Among the 107 genera in Annonaceae, detailed floral structures have been reported for 68 genera. This study classifies the pollination chambers of these 68 genera into three categories—open type, partially closed type, and tightly closed type—based on their closure status during anthesis. Specifically, 24 genera possess open-type chambers, 38 have partially closed chambers, and 26 exhibit tightly closed chambers, with approximately 17 genera featuring two or three chamber types. Different pollination chamber types show specific correlations with pollinator guilds: bees and flies primarily pollinate plants with open chambers or those with larger chamber spaces in the partially and tightly closed categories, while thrips mainly pollinate species with partially closed and tightly closed chambers. The paleotropics and neotropics constitute the primary distribution centers for Annonaceae. Although species richness is highest in the paleotropics, both pollination chamber types and pollinator assemblages remain relatively uniform there. Conversely, the neotropics harbor fewer species but exhibit high diversity in both chamber types and pollinators. Previous research indicates Africa as the origin center of Annonaceae. Open-type chambers predominantly occur in tropical Africa, commonly appearing in early-divergent genera across all tribes, and are exclusively pollinated by small beetles, representing the ancestral chamber type. Partially closed chambers are distributed across tropical Africa, tropical Asia, and tropical America, while tightly closed chambers are mainly confined to tropical Asia. Both latter types are associated with more diverse pollinator assemblages and represent more derived conditions within the family.

Keywords: Annonaceae, pollination chamber, type, pollination, evolution

1. Overview of Annonaceae

Annonaceae represents a relatively derived and species-rich family within the basal angiosperm order Magnoliales. According to the phylogenetic framework of Guo et al. (2017), the family comprises four subfamilies, 107 genera, and over 2,400 species. The four subfamilies are Anaxagoreoideae, Ambavioideae, Annonoideae, and Malmeoideae. Annonaceae exhibits a pantropical distribution and constitutes a major component of tropical floras worldwide (Kessler, 1993).

Annonaceae species typically possess bisexual flowers with protogynous dichogamy, showing clear differentiation between sepals and petals. The perianth usually consists of two whorls (rarely one), with three petals per whorl, and distinct differentiation between inner and outer whorls. The pollination chamber represents a characteristic structural feature distinguishing Annonaceae from other families. First proposed for Annonaceae by Gottsberger (1970), the pollination chamber refers to a spatial structure formed when petals contract or converge toward the flower center during anthesis. Similar pollination chamber structures also occur in Myristicaceae (Armstrong & Drummond, 1986), Dipterocarpaceae (Momose et al., 1998), and Araceae (Young, 1986) among extant angiosperms (Roubik et al., 2005). Compared with the relatively conservative morphological structures in these other families, Annonaceae exhibits exceptionally high diversity in pollination chamber morphology (Saunders, 2010).

2. Current Status and Significance of Pollination Chamber Classification

Petal size, whorl number, petals per whorl, fusion patterns, and floral movements collectively determine pollination chamber morphogenesis (Li et al., 2016). These traits show high diversity in Annonaceae, representing the primary cause of variation in pollination chamber morphology. Such diversity reflects the broader floral morphological diversity within the family, and classifying these complex structures constitutes an essential prerequisite for studying pollination chamber evolution. Research specifically addressing pollination chamber classification remains scarce. The only existing classification was proposed by Saunders (2010), who divided Annonaceae pollination chambers into types 0–VII based on differences in petal shape, fusion position, and fusion pattern. Type 0 represents flowers where petals fully expand without forming a pollination chamber during anthesis. Type I comprises chambers formed by nearly erect petals with slightly touching margins. Type II features chambers created by basal constriction of petals around reproductive organs. Type III consists of chambers formed by apically aggregated inner petals. Type IV comprises chambers formed by boat-shaped inner petals with fused margins. Type V includes bowl-shaped corollas with apical openings. Type VI features chambers formed by imbricate inner petals with small basal openings, sometimes with outer petals spreading outward. Type VII consists of tubular corollas formed by basally fused or free petals. Additionally, Shao (2017) investigated floral structural characteristics and pollination biology across 10 genera and 12 species, suggesting a co-evolutionary relationship between pollination chambers and pollinators.

While Saunders' classification is detailed and comprehensive, the inherently complex and diverse floral structures in Annonaceae result in ambiguous boundaries between categories, with obvious morphological overlaps among types. Moreover, the eight types are scattered across various genera, making the system difficult to apply in morphological descriptions or evolutionary studies of Annonaceae pollination chambers. Therefore, reclassifying Annonaceae pollination chambers to establish clearly delimited, more generalizable, and comprehensible categories is necessary.

Based on available literature, detailed floral morphological descriptions exist for 68 of the 107 genera in Annonaceae (Tables 1, 2, 3). This study analyzes pollination chamber morphology across these 68 genera and classifies them into three categories: open type, partially closed type, and tightly closed type. We reveal correlations between pollination chamber types and both pollinators and geographic distribution, and explore evolutionary patterns in Annonaceae pollination chambers. These findings provide new data for investigating floral structural diversity and evolution in the family and offer valuable references for taxonomic, systematic, and pollination biological studies.

The specific criteria for the three pollination chamber types are as follows:

(1) Open-type pollination chamber: Petals are free and spread outward during anthesis, fully exposing reproductive organs without forming any spatial structure—equivalent to Saunders' Type 0. Among the 68 reported genera, 24 possess open-type chambers (Table 1). These plants typically have relatively large, conspicuous flowers in red, purple, purple-brown, or brown colors. Floral scent is either absent or resembles mushrooms, musk, decaying matter, or feces, with no obvious thermogenesis (Gottsberger et al., 2003; Gottsberger, 2012). Examples include *Uvaria grandiflora* Roxb. (Plate I: A) and *U. macrophylla* Roxb. (Plate I: B).

(2) Partially closed pollination chamber: Petals form a partially open spatial structure through basal constriction or apical convergence toward the flower center. Most species develop a small pollinator entrance (pollination pore) at the petal base. Because the chamber is not tightly sealed, pollinators can freely enter and exit even when the pore is partially obscured by petals. This category corresponds to Saunders' Types I, II, IV, V, VI, and VII, as well as Type III in the genus *Pseuduvaria*. Among the 68 reported genera, 38 possess partially closed chambers (Table 2). These species typically have one or two whorls of fleshy, thickened petals in white, yellow, green, or red colors. During anthesis, they emit strong fruity or pungent odors, often accompanied by thermogenesis (Gottsberger et al., 2003; Gottsberger, 2012; Saunders, 2012).

Examples include *Anaxagorea javanica* Blume (Plate I: C), *Desmos filipes* (Ridl.) Ridl. (Plate I: D, with one outer petal removed), *Miliusa chunii* W.T. Wang (Plate I: E), *Polyalthia lauii* Merr. (Plate I: F), and *Pseuduvaria trimera* W. G. Craib (Plate I: G).

(3) Tightly closed pollination chamber: During anthesis, petals tightly aggregate toward the flower center or become extremely constricted at the base, forming an enclosed space. At certain floral stages, the pollination pore becomes blocked by outer petals, completely isolating the interior from the exterior environment, preventing any insect movement during this period. This corresponds to Saunders' Type III and Type II chambers in *Artabotrys* and some *Polyalthia* species (e.g., *P. obliqua* Hook. f. & Thomson) (Shao, 2017). Among the 68 reported genera, 26 possess tightly closed chambers (Table 3). These plants show clear differentiation between inner and outer petal whorls (e.g., *Mitrephora*, *Goniothalamus*, *Annona*) (Plate I: I, J, L) or have only a single petal whorl (*Dasymaschalon*) (Plate I: K). Petals are fleshy and thickened, ranging from white, yellow, cream, green, to brown colors, with pronounced thermogenesis during anthesis (Gottsberger, 2012; Saunders, 2012).

3. Functions of the Pollination Chamber

The pollination chamber plays a crucial role in attracting pollinators and enhancing pollination efficiency. Documented functions include:

1. **Attracting and retaining pollinators:** Annonaceae petals produce odors during anthesis and facilitate scent dispersal through thermogenesis, helping pollinators locate flowers. Additionally, many beetles and thrips are photophobic, and the dark chamber provides a warm, secure refuge. Pollinators aggregate, mate, and oviposit within chambers while feeding on fleshy petals, pollen, stigmatic exudates, and nectar (Gottsberger, 1999, 2012). Consequently, pollinators may remain inside chambers for hours to days, only departing after anthers dehisce and they become covered in pollen (Gottsberger, 1989).

2. **Selecting effective pollinators:** Specific floral morphologies and food rewards restrict access to insects with small body sizes, such as beetles and thrips, that can pass through the narrow pollination pores. This selective filtering mechanism excludes "ineffective" pollinators, ensuring pollination efficiency while preventing resource waste and damage to reproductive organs (Gottsberger, 1999).

3. **Enhancing pollination efficiency through pollen discounting and pollinator trapping:** Pollen discounting refers to the phenomenon where most pollen released during the male phase falls within the pollination chamber, allowing subsequent pollinators to collect additional pollen and thereby increasing pollen transfer while minimizing waste (Saunders, 2010; Gottsberger, 2012). Pollinator traps are floral structures that temporarily detain insects until pollination is completed (Lau et al., 2017). In

some Annonaceae species, the initially closed pollination chamber opens its outer petals during the pre-female phase to expose the pollinator entrance, then closes again to trap pollinators inside until anthers dehisce and petals abscise, releasing pollen-laden insects (Gottsberger & Webber, 2018).

4. **Mechanical protection:** Fleshy, thickened petals provide varying degrees of coverage over reproductive organs, protecting them from herbivory and ensuring integrity of both male and female structures (Shao, 2017).

4. Relationships Between Pollination Chamber Types, Pollinators, and Geographic Distribution

4.1 Pollination Chamber Types and Plant Systematics

Among the 68 reported genera, 24 possess open-type chambers (Table 1), 38 have partially closed chambers (Table 2), and 26 exhibit tightly closed chambers (Table 3), with 17 genera featuring two or three chamber types. Based on the phylogeny of Guo et al. (2017), Annonaceae comprises four subfamilies and 15 tribes. The most ancestral subfamily, Anaxagoreoideae, contains all three chamber types. Within subfamily Ambavioideae, the three chamber types have evolved independently across genera, with early-divergent *Tetrameranthus* and *Lettowianthus* both possessing open-type chambers (Van Heusden, 1992; Saunders, 2010, 2012), while the remaining seven genera show scattered distribution of all three types. Within subfamily Annonoideae, tribe Bocageeae includes the earliest-divergent genus *Mkilua* with open-type chambers, and its sister tribe Guatterieae also possesses open-type chambers. In more derived tribes (Annoneae, Monodoreae, Uvarieae), the earliest-divergent genera within each tribe contain open-type chambers (Figure 1). The more recently derived subfamily Malmeoideae comprises eight tribes and 48 genera, but exhibits low phylogenetic support and lacks comprehensive floral morphological data. In the well-studied tribe Miliuseae, all three chamber types occur, though open-type chambers are rare, with partially closed and tightly closed types predominating (Van Heusden, 1992, 1997; Saunders, 2010; Gottsberger, 2012). Thus, classification into open, partially closed, and tightly closed types reveals evolutionary patterns correlated with the family' s phylogeny. While Saunders' eight-type system also shows that open-type chambers (Type 0) occur in early-divergent lineages, the remaining seven types (I–VII) are too complex to intuitively reveal evolutionary patterns or their correlation with phylogeny based solely on morphological criteria.

4.2 Pollination Chamber Types and Geographic Distribution

Among the 24 genera with open-type chambers, 16 are primarily distributed in Africa, New Guinea, Madagascar, and Malaysia, all belonging to the paleotropical floristic realm according to Takhtajan' s (1986) classification. The remaining eight genera occur in the neotropics (Brazil, Peru, Colombia, Central and South America) and Australia (Table 1).

Of the 38 genera with partially closed chambers, 23 are mainly distributed in the paleotropics (Africa, tropical Asia, Congo, Guinea, Madagascar), while 15 occur in the neotropics (Central and South America, Mexico, Malaysia, Brazil, Peru, Amazon) and Australia (Table 2).

Among the 26 genera with tightly closed chambers, 16 are primarily paleotropical (Africa, tropical Asia, New Guinea), and eight are neotropical (Mexico, Central and South America, Panama, Brazil, Peru, tropical South America). *Pseuduvaria* and *Cymbopetalum* span both realms, with the former occurring in the paleotropics and Australia, and the latter in both paleotropical and neotropical regions (Table 3).

In summary, pollination chamber types correlate with geographic distribution in Annonaceae. Open-type chambers predominantly occur in tropical Africa (accounting for approximately half of all open-type genera) (Table 1), while tightly closed chambers are mainly distributed in tropical Asia (about half of all tightly closed genera) (Table 3). Partially closed chambers show the broadest distribution and highest species richness, occurring in tropical Africa, tropical Asia, and tropical America (Table 2). Additionally, 17 genera possess two or three chamber types, with *Anaxagorea*, *Annona*, *Guatteria*, and *Polyalthia* exhibiting all three types, the first three being primarily neotropical in distribution.

4.3 Pollination Chamber Types and Pollinators

Annonaceae pollinators are diverse, including small beetles, large beetles, thrips, flies, bees, and cockroaches as effective pollinators. Among the 42 genera with known pollinators, small beetles pollinate 32 genera, representing the most important pollinator group across all chamber types. Bees and flies pollinate five and eight genera respectively, primarily in open-type chamber plants. Thrips pollinate eight genera, mainly in partially closed and tightly closed chamber plants. These results demonstrate a correspondence between pollination chamber types and pollinator guilds. In the early-divergent subfamilies Anaxagoreoideae and Ambavioideae, pollination is exclusively by small beetles (except *Tetrameranthus*), while other pollinators appear only in the more derived subfamilies Annonoideae and Malmeoideae. Large beetles primarily pollinate Annonoideae, and cockroaches exclusively pollinate *Uvaria*. Furthermore, pollinator diversity correlates with geographic distribution: paleotropical plants typically have a single pollinator type per genus, mostly small beetles, with occasional large beetles (*Piptostigma*, *Uvariodendron*, *Porcelia*, *Fusaea*) or thrips (*Popowia*, *Trigynaea*, *Bocageopsis*) (Tables 1, 2, 3). In contrast, neotropical plants exhibit higher pollinator diversity, with multiple pollinators even within single genera. For example, *Annona* is pollinated by small beetles, large beetles, and flies (Table 2). Geographic variation in pollinators also occurs within genera: in *Sapranthus*, Central American populations are primarily pollinated by small beetles and bees, whereas northern Mexican populations are mainly pollinated by flies (Van Heusden, 1992).

Summary

Based on pollination chamber morphology during anthesis, Annonaceae pollination chambers are classified into three types: open (24 genera), partially closed (38 genera), and tightly closed (26 genera). Open-type chambers have relatively large, thin petals, while partially closed and tightly closed chambers have smaller, fleshy, thickened petals with pronounced thermogenesis. Different chamber types exert selective effects on pollinators: bees and flies primarily pollinate open-type chambers, while thrips mainly pollinate partially closed and tightly closed chambers. Paleotropical regions harbor the greatest species richness but show relatively uniform chamber types and pollinators, whereas neotropical regions contain fewer species but exhibit high diversity in both chamber types and pollinators. Partially closed chambers are the most species-rich and widely distributed type. Open-type chambers, predominantly distributed in tropical Africa and commonly occurring in early-divergent genera across all tribes, are exclusively pollinated by small beetles and represent the ancestral condition. Partially closed chambers occur in tropical Africa, tropical Asia, and tropical America, while tightly closed chambers are mainly distributed in tropical Asia; both latter types are associated with more diverse pollinators and represent more derived conditions.

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Note: Figure translations are in progress. See original paper for figures.