

Ontogeny and glandular features of *Alexa grandiflora* flowers offer evolutionary insights into the *Angylocalyx* clade: a Papilionoideae (Leguminosae) lineage with non-papilionaceous corolla

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Abstract

Alexa grandiflora Ducke is a papilionoid legume tree native to the Brazilian Amazon Forest. It belongs to the early-diverging Angylocalyx clade within the subfamily Papilionoideae, which is characterized by keel flowers, with some genera having flowers other than typical papilionaceous ones. This study describes the floral organography, organogenesis, and secretory structures of *A. grandiflora* and compares its floral morphology with that of three species from different genera within the Angylocalyx clade to deepen the understanding of the clade's floral structure and, by extension, the broader Papilionoideae subfamily. To conduct the study, floral buds and flowers from *A. grandiflora* were collected and processed for surface and anatomical studies, and flowers from herbarium specimens of *Castanospermum australe*, *Xanthocercis madagascariensis* and *Angylocalyx oligophyllus* to elucidate the clade's floral evolution and its implications for Papilionoideae diversity. Floral buds and flowers of *A. grandiflora* were analyzed using surface and anatomical techniques, while herbarium specimens of the comparative taxa were examined via scanning electron microscopy. In *A. grandiflora*, the apical meristem of the racemose inflorescence primary axis produces first-order bracts acropetally in a helical order. Sepal initiation is unidirectional, petal initiation is simultaneous, with the adaxial petal growing faster than the others. Antesepalous stamens appear simultaneously and concurrently with the carpel, while antepetalous stamens emerge simultaneously. Floral secretion of nectar, terpenes, and oleoresin supports phyllostomid bat pollination in *Alexa* species, consistent with the previously proposed association between intense nectar and terpene production and chiropterophily in the genus. Comparative analysis reveals that the Angylocalyx clade shares key floral traits, including a gamosepalous calyx, an enlarged adaxial petal, and similarly shaped lateral and abaxial petals. However, variations are observed in the type of inflorescence and in the level of insertion of the filament in the anther, highlighting the floral diversity within the clade.

Introduction

Papilionoideae stands out as it includes about two-thirds of all genera and species within the family Leguminosae (LPWG 2017; 2023). It occurs in different plant formations, ranging from tropical and subtropical zones to temperate regions worldwide (Lewis et al. 2005). This subfamily comprises approximately 503 genera and around 14,000 species distributed across 28 tribes. It represents a highly diverse group with significant ecological, economic, and ecosystemic importance (LPWG 2017; 2023).

With the advent of molecular phylogenies, several studies (Cai et al. 2024; Cardoso et al. 2012; Choi et al. 2022; LPWG 2017) have positioned the Angylocalyx clade (or Angylocalyceae tribe) along with the Dipterygeae and Amburaneae tribes, within the so-called “ADA clade”. This clade represents the earliest or one of the two earliest branching lineages of the Papilionoideae subfamily. However, the relationship between the ADA clade, the Swartzioideae clade, and the large clade comprising the remaining Papilionoideae is unclear, varying on different phylogenies (Cai et al. 2024; Cardoso et al. 2012; Choi et al. 2022; LPWG 2017).

Within the ADA, the Angylocalyx clade is the sister group to Amburaneae + Dipterygeae (Cai et al. 2024; Choi et al. 2022) and includes the following genera: *Xanthocercis* Baill (3 species), *Angylocalyx* Taub. (7 species), *Castanospermum* A. Cunn. ex Hook. (monotypic), and *Alexa* Moq. (10 species), comprising a total of 21 species (Dumaz-le-Grand 1953; Maesen 1997; POWO 2024; Ramírez 1995; Silva et al. *in prep*; Yakovlev 1972).

The Angylocalyx clade is strongly characterized by a vertebrate floral syndrome, which can be ornitophilous in *Alexa*, *Castanospermum*, and *Angylocalyx* or chiropterophilous in *Alexa*, featuring an enlarged calyx and hypanthium, thickened petals white, red or orange, and a distinct floral morphology of papilionaceous flowers typical of Papilionoideae. The adaxial petal is typically larger than the others (two abaxial and two lateral), undifferentiated or highly reduced. Additionally, the gynoeceum is exserted. An exception is the small white flowers of *Xanthocercis*, which have been reported to be pollinated by insects, mainly bees (Burrows et al. 2018; Foden and Potter 2005; Ramírez 1995; Silva et al., 2023).

Morphological differences among the inflorescences and flowers of the Angylocalyx clade's genera are notable. *Xanthocercis* is distinguished by a paniculate inflorescence with numerous short secondary racemes and small flowers with thin lanceolate petals. In contrast, the other genera (*Alexa*, *Castanospermum* and *Angylocalyx*) have cauliflorous racemose inflorescences or terminal racemes (*Alexa*) (Lewis et al. 2005). Floral differences are primarily concentrated in the size of the floral structures, which are larger in *Castanospermum* and *Alexa*, in relation *Xanthocercis* and *Angylocalyx*. Additionally, the arrangement and color of the petals at anthesis varies in *Angylocalyx* and *Castanospermum*, the adaxial petal is reflexed, and the other petals form a pseudo tube, while in *Alexa* and *Xanthocercis*, the petals do not form a pseudo tube (Dumaz-le-Grand, 1953; Maesen, 1997; Ramírez, 1995; Silva et al. *in prep*).

The flowers of representants within the Angylocalyx clade exhibit moderately zygomorphic symmetry in *Alexa* and *Xanthocercis* and strongly zygomorphic symmetry in *Castanospermum* and *Angylocalyx*. Adaxial petal is larger than the others, while the remaining four petals (two lateral and two abaxial) are morphologically similar. Also share features such as a pronounced hypanthium (Ramírez 1995).

Most *Alexa* species are distinguished by having large flowers with a persistent, leathery to woody gamosepalous calyx, white, usually fleshy petals— the lateral and abaxial petals poorly differentiated—ten relatively undifferentiated, essentially free stamens, and large, compressed, dehiscent woody pods with a velutinous indumentum. Other characteristics include imparipinnate leaves, velutinous racemes, and discoid seeds (Ramírez 1995; Silva 2024). *Alexa grandiflora* Ducke stands out for its wide geographical distribution and common floral morphological characteristics among the *Alexa* species. These include an enlarged hypanthium and five calyx lobes, similar petals with only the adaxial petal being larger, and a stipitate ovary. Another important point is the diversity of secretory structures in *Alexa grandiflora*, since this diversity (presence of glands in the leaves, petiole, base of the floral pedicel, calyx and flowers) is not common in early lineages of Papilionoideae. Studies of the floral secretory structures of the species are important to understand the floral mechanisms of pollination, in addition to adding knowledge to the taxonomy of the group. These invariant characteristics make *A. grandiflora* a model species for floral studies within the genus, as it represents the most common traits of the group and therefore represents a good model to be the focus of study (Silva et al. 2023).

Regarding the floral morphology of Papilionoideae representatives, it is important to emphasize that papilionaceous flowers represent an important characteristic for the recognition of this subfamily. This floral type has a corolla with five petals: a larger, free upper petal called standard or vexillum. The vexillum covers two equal lateral petals, called wings, and two lower petals, joined at the edges and more internal, surrounded by the wings, called the keel or carina (Tucker 2003a). Most taxa in the subfamily exhibit typical papilionaceous flowers (Tucker 2003a; LPWG 2017). However, exceptions occur, particularly in lineages such as the ADA and Swartzieae clades, which often feature non-papilionaceous corolla, atypical petal aestivation, and lack of stamen fusion (Basso-Alves et al. 2022; Leite et al. 2015; Paulino et al. 2013; Tucker 2003b). These exceptions help to understand the emergence of the papilionaceous flowers shared by the remaining lineages of the subfamily, since the origins of keeled flowers are treated as independent evolutionary events (Prenner 2003; Tucker 2003b; Uluer 2025).

The primary objective of this study is to describe the organography, organogenesis, and glandular structures of the non-papilionaceous flower of *Alexa grandiflora*. Additionally, it seeks to provide information on the floral organography of three other genera within the Angylocalyx clade, contributing to a broader understanding of clade floral morphology and, by extension, the Papilionoideae subfamily. This study hypothesizes that similarities in floral development among species of the Angylocalyx clade may provide morphological evidence supporting the clade's monophyly.

To achieve this, the study addressed the following questions: 1) At what stages of floral development do key transformations occur in the calyx, corolla, androecium, and gynoecium of *Alexa grandiflora*, leading to distinct floral morphology from other genera within the Angylocalyx clade and deviating from the typical papilionaceous flower?, and 2) Where are the sites responsible for secreting noticeably sweet fragrances, nectar, and other exudates located on the floral organs of *Alexa grandiflora*, and how do these secretions contribute to its pollination mechanisms?

Electron micrographs of other representatives of the Angylocalyx clade (*Castanospermum australe* A. Cunn. & C. Fraser, *Xanthocercis madagascariensis* Baill., and *Angylocalyx oligophyllus* Baker f.) were analyzed and compared with the organography and organogenesis of *A. grandiflora*. These findings were further contextualized using studies by Tucker (1993) and Leite et al. (2014; 2015) to discuss related genera. The comparative analysis revealed both shared traits and differences, underscoring potential diagnostic characteristics to the Angylocalyx clade.

Materials and methods

Floral buds in various stages of development and flowers of *Alexa grandiflora* were collected and fixed in FAA 70 (formalin: acetic acid: alcohol; Johansen 1940) or Karnovsky's solution (0.075 mol/L in phosphate buffer, pH 7.2–7.4; Karnovsky 1965) for 24 hours before dissection. *Alexa grandiflora* was collected in the Brazilian Amazon, specifically in the municipality of Marabá, located in the state of Pará. The vouchers were deposited in the herbarium of the Instituto de Pesquisas do Jardim Botânico do Rio de Janeiro (Herbarium RB): *Silva, G.S. 527* (RB01472968) (fig. 1A-C).

The floral materials were dissected using a LEICA MZ75 stereomicroscope (Leica Microsystems, Wetzlar, Germany) and prepared for surface (scanning electron microscopy - SEM) and anatomical observations (light microscopy - LM). In order to compare *A. grandiflora* with other representatives of the Angylocalyx clade, electromicrographs of floral buds of the species *Xanthocercis madagascariensis* (fig. 1D-F), *Angylocalyx oligophyllus* (fig. 1G-I) and *Castanospermum australe* (fig. 1J-L), were taken from exsiccates belonging to the following Vouchers: *Coveny, R. 9946* (MO421756), *Ratovoson, F. 744* (MO61443), *Reistma, J.M.B. 2941* (NY048004), respectively, of the species analyzed, only *C. australe* was previously studied (Tucker, 1993), and the electron micrographs presented here will serve for comparison with *A. grandiflora*, demonstrating similarities and differences in the organography. The buds were obtained from the envelopes of the exsiccates after proper authorization and rehydrated by boiling in water and then immersed in a 5% potassium hydroxide solution for 24 hours and stored in 70% ethanol.

For the surface examination, the dissected materials were dehydrated in ethanolic series, critical point dried in a Bal Tec CPD 030 apparatus (BAL-TEC, Bannockburn, IL, USA), mounted on metal supports, placed on carbon adhesive tape and then coated with palladium-gold in the Emitech K550X Metallizer (Ashford, United Kingdom). This stage was carried out in the Structural Botany Laboratory of the Instituto de Pesquisas do Jardim Botânico do Rio de Janeiro. The observations were made using a JEOL-JSM-6490LV scanning electron microscope (JEOL Ltd., Japan) from the Centro Brasileiro de Pesquisas Físicas (CBPF), at 10, 15, 20, or 30kV, and the electron micrographs were obtained using digital cameras attached to the microscope. The images produced were processed in Adobe Photoshop CS5 (San Jose, California, USA). A modified version of this technique was employed on the samples for gland studies.

Fresh samples of floral organs, collected immediately before flower opening and from newly opened flowers, were stored in sealed glass bottles with silica gel and a paper towel at a low temperature (-18 °C) for seven days, followed by storage at room temperature for ten days (Leite et al. 2019). The samples were then mounted on aluminum stubs with colloidal carbon, coated with gold using a Bal-Tec SCD 050 sputter coater (BAL-TEC, Bannockburn, IL, USA), and observed with a Jeol JSM 6610LV scanning electron microscope (Tokyo, Japan). The images produced were processed using Corel Photo-Paint (Ottawa, Ontario, Canada).

For the anatomical analysis, fixed samples of floral organs were embedded in historesin (Gerrits and Horobin 1991) and sectioned transversely and longitudinally to 2-3 µm thickness using a rotary microtome (Leica RM 2245). The sections were stained with various reagents: 0.05% Toluidine Blue (O'Brien et al. 1964) as a general stain; Sudan IV (Johansen 1940) to detect lipids; Nadi reagent (David and Carde 1964) for terpenes and oleoresins; periodic acid/Schiff reagent (Feder and O'Brien 1968) for neutral polysaccharides; Xylidine Ponceau (Vidal 1970) for proteins; Fehling reagent for reducing sugars (Fehling 1849), and oil red (Jayabalan and Shah 1986) for terpenes. Appropriate controls were performed simultaneously. Images were captured using a light microscope (Leica DM5000 B) equipped with a digital camera (Leica DFC295, Wetzlar, Germany).

The terminology used to describe flower development followed Tucker (1984, 1987; 1997), Klitgaard (1999) and Prenner (2004b). The adaxial side of the flower was considered to be the upper side, close to the axis of the inflorescence, and the abaxial side the lower side, opposite the axis of the inflorescence,

closer to the bract (Tucker 1984). The determination of the type of inflorescence adopted in this work will follow Endress (2010) and the type of ovule, Prakash (1997).

Results

Alexa grandiflora: Organography of the inflorescences and flowers

The inflorescences are terminal racemose or terminal paniculate with few racemes, erect, congested, rarely axillary, and fasciculate at the base (fig. 2A-B). The primary axis of the inflorescence with 15-30 × 1-4 cm long, elongated, with 10-30 flowers spirally scattered along the axis. It is densely pubescent to velutinous, and cylindrical. Each floral bud is subtended by a bract, oval in shape, pubescent to velvety, with an acute apex; the floral pedicels are cylindrical, pubescent to velvety. Each flower has a pair of lateral bracteoles, acute at the apex, ovate to triangular, pubescent to velvety (fig. 1A). The flowers with 4 × 7 cm long and 1 × 3 cm wide and pedicels with 30–50 mm long, are slightly zygomorphic, monoclinal, and have a campanulate hypanthium (fig. 1A-C, 2A). Hypanthia are leathery, 0.2-0.5 cm, densely pubescent to velvety, dark brown color, pubescent to velvety externally, glabrous internally with a yellow nectary. The calyx is gamosepalous, dark brown, campanulate to tubular, leathery with 3 or 5 lobes, densely pubescent to velvety externally (fig. 3A-B), glabrous internally, with the extrafloral nectary at the base of the pedicel and at the apex of the calyx. The corolla is white, zygomorphic, with five free petals (fig. 3B-D). The largest adaxial petal rounded to spatulate, chartaceous to leathery, thick, densely pubescent externally, glabrous internally, rounded to straight at the apex, with smooth margins (fig. 3E). The lateral petals are symmetrical, narrowly spatulate, chartaceous to leathery, densely pubescent externally, glabrous internally, rounded at the apex, with smooth margins (fig. 3F); abaxial petals spatulate, chartaceous to leathery, densely pubescent externally, glabrous internally, rounded at the apex, with smooth margins (fig. 3G). The androecium is composed of 10 free and straight stamens (fig. 3H). Each stamen consists of a white erect filament and a yellow, elliptic anther, with dorsifixed insertion and longitudinal dehiscence (fig. 3I). The gynoecium is a white to cream, glabrous stipe is straight; the elliptical ovary is densely yellowish-velutinous, slender style, becoming apiculate from the ovary to the stigma and the stigma is acute and glabrous (fig. 3J-L). The nectary is located on the walls and base of the hypanthium (fig. 3).

Alexa grandiflora: Organogenesis of the inflorescences and flowers

The apical meristem of the primary inflorescence axis produces first-order bracts acropetally in helical order (fig. 4A). The transversely elongated floral primordium is subtended by a bract (fig. 4B-4C) which elongates and covers the floral primordium. With the formation of the bract, two lateral bracteoles form and then cover the floral primordium which begins the differentiation of the floral parts (fig. 4D-4F). Floral organ formation is mixed acropetal. The whorls arise in the following sequence: sepals, petals, carpel + antesepalous stamens, and antepetalous stamens (fig. 4A-4C).

Sepal initiation is unidirectional, with the first primordium forming abaxially and in a median position (fig. 4G), followed by the two lateral primordia, and finally by the two adaxial primordia (fig. 4H-4J). At this point in organogenesis, the floral meristem has an elongated form in the dorso ventral axis and the adaxial part of the meristem is considerably elevated concerning the abaxial part where a depression can be observed between the abaxial sepal and the center of the meristem (Fig. 4I-4J). The first abaxial sepal elongates and covers the floral meristem (fig. 4H-4J). Next, the two lateral sepals, initially covered by the abaxial sepal, also grow and cover the floral meristem. Finally, the two adaxial sepals expand more in width and extend in an abaxial direction, completing the coverage of the floral meristem (fig. 4K-4L). Thus, the sepals are imbricated from the beginning of development, with the abaxial sepal being the outermost, followed by the lateral sepals positioned beneath it, and the adaxial sepals innermost of all (fig. 5A-5B). The sepals continue their elongation, but the tissues at the base undergo conation, initiating the gamosepalous calyx (fig. 5B). After sepal elongation the five petal primordia are initiated simultaneously alternate with the sepals (fig. 5C-5E). The circular region of the corolla is elevated, forming a depression at the center of the meristem (fig. 5D-5E).

The five antesepalous stamens emerge simultaneous, concomitantly with the carpel (Figs. 5F-5G). The central carpel primordium is initiated concurrently with the formation of the hypanthium (fig. 5I). At the beginning, an invagination is visible around the carpel, which increases in depth and finally forms a concavity (figs. 5H-I).

Alexa grandiflora: Floral mid and later stages of the development

The adaxial petal primordium grows and curves inwards (fig. 5F-5K). The four remaining petal primordia enlarge slowly at this stage, growing simultaneously while adaxial petal elongation intensifies (fig. 5D-5H). The adaxial petal grows rapidly and remains more evident and thicker than the other petals since the early stages of development (fig. 5J-L, 6A-6C). There is evidence of a common primordia being partitioned between petals and soon-to-be antepetalous stamens (Fig 5I). The primordia of the antesepalous stamens develop simultaneously. Later, the primordia of the antepetalous stamens also develop simultaneously, forming second androecium whorl (Fig 5J-5L). At this point, the calyx is completely united, leaving only remnants of the sepals' lobes evident, which become leathery, providing the main protection for the developing androecium and gynoecium during late floral ontogeny (figs. 6A-6C).

The antesepalous stamens are larger and begin to elongate first. They exhibit a spatial organization where the antesepalous stamens grow toward the carpel, while the antepetalous stamens extend toward the petals (fig. 6D-6F). The elongation of the filaments is concomitant with the differentiation of the anthers (fig. 6D-6E). By the end of androecium development, the stamens are arranged in a single whorl and are completely free from each other (Fig. 6D, 6G-6I). At the final stages of differentiation, the stamens have a cylindrical, glabrous filament, the anthers are bitheca and dorsifixed, with longitudinal dehiscence lines, and stoma can be observed in the connective (fig. 6J-6L).

The adaxial carpel cleft becomes visible after the initiation of all stamens (fig. 5L). The ovules begin to initiate while the carpel margins are still open. The closure of the carpel cleft occurs concomitantly with filament growth. The young carpel grows and begins to curve towards the adaxial side of the flower (fig. 6E, 6H). The carpel forms a stipe while the hypanthium simultaneously becomes evident internally and takes on a cup-shaped form.

***Alexa grandiflora*: floral glands**

Nectar, terpenes, and oleoresin are types of secretions detected in the floral organs of *Alexa grandiflora*. The nectar is secreted by a non-protuberant nectary located in the inner surface of the hypanthium (fig. 7A-C). The nectary is structured, comprising a uniseriate secretory epidermis with stomata and a nectariferous parenchyma composed of multiple layers of amyloiferous and phenolic cells (fig. 7D-G).

Additionally, reducing sugars, indicated by a positive reaction to Fehling reagent, were observed on the surfaces of sepals, petals, filaments, and anthers at various stages of floral development. These sugars are translucent, viscous, and often appear in a crystal-like form (fig. 8C-D, 8G, 8K, 9C, 9E). They are secreted by a one-layered epidermis and subepidermal parenchymatic cells, being released through modified stomata (on sepals, petals, and the connective) or large pores (on the anther epidermis) (figs. 8E-H, 8K, 8M-N; 9C-G, 9I, 9K). At the apices of the sepals and adaxial petal, where exudation is particularly intense, the epidermis ruptures (fig. 8C-E).

Terpenes, which contribute to the floral fragrance, are produced in mesophilic osmophores located on the adaxial side of the sepals, across the petal surfaces, and on both the dorsal and ventral sides of the anther connective in all stamens (figs. 8A-N, 9A-K).

Oleoresin is secreted by epidermal and subdermal cells located along the margins of all petals (fig. 8I, J, K). The petal margins are thicker and exhibit a different coloration compared to the rest of the petal (fig. 8A).

***Castanospermum australe*: Organography of the inflorescences and flowers**

Inflorescences are racemose cauliflorous or produced on twigs below the leaves, erect (fig. 2A-B). The primary axis of the inflorescence with 10-15 × 1-2 cm long, elongated, with approximately 10-20 flowers congested in a spiral along the axis, puberulent. Each flower is subtended by a deltoid bract, puberulent, with an acute apex; the floral pedicels are cylindrical, and puberulent. Each flower bears a pair of lateral bracteoles, acute at the apex, ovate to triangular, pubescent (bracteoles caducous, usually evident only in bud). The flowers with 3 × 5 cm long and 1 × 3 cm wide with pedicels 10–25 mm long, slightly zygomorphic, monoclinal and with a campanulate hypanthium, leathery, puberulent externally, glabrous internally. The calyx is gamosepalous, waxy-yellow, campanulate (fig. 10A), leathery with 5 lobes (fig. 10B-C), sparsely covered with small brown hairs externally, glabrous internally. The corolla initially greenish-yellow, then deep orange, zygomorphic, with five free petals. The largest adaxial petal cuneate-obovate (fig 10D), medially reflexed through 90°, strongly emarginate and lobed at the apex, leathery, thick, glabrous internally and externally. Lateral petals symmetrical (fig. 10E), oblong-obovate, cuneate, not auriculate, coriaceous, glabrous internally and externally, with smooth margins; abaxial petals oblong-obovate (fig. 10F), cuneate, not auriculate, coriaceous, glabrous internally and externally, rounded at the apex, with smooth margins. Stamens yellow, turning red, exserted, 10, all free, incurved, about 0.4 × 0.15 cm and can dehisce in the bud stage, anthers yellow, elliptical with dorsifixed insertion, longitudinal dehiscence (fig. 10G-H). The gynoecium has a green stipe, glabrous, style is initially green becoming orange, confluent, slender, incurved, and the stigma acute and glabrous (fig. 10I).

***Xanthocercis madagascariensis*: Organography of the inflorescences and flowers**

Inflorescences are terminal paniculate with many racemes, erect, sparse and bifurcated at the base (fig. 2A-B). The primary axis of the inflorescence is elongated 10-40 × 1-3 cm long, secondary axes of the inflorescence short, 4-15 × 1-2 cm long, with 10-40 flowers scattered spirally along the axis; densely velvety golden-yellow, cylindrical. Each flower is subtended by a bract, oval, velvety, with acute apex; the floral pedicels are cylindrical, pubescent to velvety. Each flower has a pair of lateral bracteoles, acute at the apex, ovate, and velvety. The flowers, with c. 2 × 5 cm long and 1 × 3 cm wide with pedicels 10–25 mm long, pedicellate, slightly zygomorphic, monoclinal, and have a campanulate hypanthium. They are coriaceous, densely velvety, golden yellow, velvety externally, glabrous internally. The calyx is gamosepalous (fig. 11A-B), greenish-brown, campanulate, cartaceous, without lobes, densely pubescent to velvety externally, and glabrous internally. The corolla is white, zygomorphic, with five free petals. The largest adaxial petal is obovate to lanceolate (fig. 11C), cartaceous, thick, thinly pubescent externally, especially along the median, glabrous internally, rounded at the apex, with smooth margins. Lateral petals symmetrical (fig. 11D), narrowly lanceolate, chartaceous, thinly pubescent externally (fig. 11E), especially along the median, glabrous internally, rounded to acute at the apex, with smooth margins; abaxial petals spatulate to lanceolate (fig. 11F), chartaceous, thinly pubescent externally, especially along the median, glabrous internally, rounded to acute at the apex, with smooth margins. Androecium formed by 10 stamens, free, straight filiform, erect white filaments (fig 11G-H), anthers rounded creamy, basifixed, longitudinal dehiscence (fig. 11I). The gynoecium has a white to cream pubescent stipe, the ovary is densely pubescent grayish-green (fig. 11J), elliptical, the stipe glabrous, straight and the stigma acute and glabrous (fig. 11K-L).

***Angylocalyx olygophyllus*: Organography of the inflorescences and flowers**

Inflorescence are racemose cauliflorous or produced on twigs below the leaves, erect (Fig. 2A-B). The primary axis of the inflorescence is elongated 10-15 × 1-2 cm long, with approximately 10-20 flowers congested in a spiral along the axis; puberulent. Each flower is subtended by a deltoid bract, puberulent, with an acute apex; the floral pedicels are cylindrical, and puberulent. Each flower bears a pair of lateral bracteoles, acute at the apex, ovate to triangular, pubescent (bracteoles caducous, usually evident only in bud). The flowers, with c. 3 × 5 cm long and 1 × 3 cm wide with pedicels 10–25 mm long, slightly zygomorphic (fig. 12A-B), monoclinal, and with a campanulate hypanthium, leathery, puberulent externally, glabrous internally. The calyx is gamosepalous (fig. 12A), waxy-yellow, campanulate, leathery with 5 lobes, sparsely covered with small brown hairs externally, glabrous internally, with the formation of a floral nectary at the base of the pedicel. The corolla is initially greenish-yellow, then deep orange, zygomorphic, with five free petals. The largest adaxial petal cuneate-obovate (fig. 12C), medially reflexed through 90°, strongly emarginate and lobed at the apex, leathery, thick, glabrous internally and externally. Lateral petals symmetrical, oblong-obovate (fig. 12D), cuneate, not auriculate, coriaceous, glabrous internally and externally, with smooth margins; abaxial petals oblong-obovate (fig. 12E), cuneate, not auriculate, coriaceous, glabrous internally and externally, rounded at the apex, with smooth margins. Stamens yellow, turning red, exserted (fig. 12F), 10, all free, incurved, about 0.4 × 0.15 cm and can dehisce in the bud stage, anthers yellow, elliptical with dorsifixed insertion, longitudinal dehiscence (fig. 12G). The gynoecium has a green stipe, glabrous, style is initially green becoming orange, confluent, slender, incurved, and the stigma acute and glabrous (fig. 12H-I).

Discussion

Ontogenetic origin of floral features of *Alexa grandiflora*

Alexa grandiflora has racemose inflorescences or paniculate with few secondary racemes; this pattern is evident in most other major clades of Leguminosae in which the racemose pattern is dominant and paniculate or pseudoracemes are also common (Lewis et al. 2005; LPWG 2017; Movafeghi et al. 2011; Tucker 2003a). Considering the species of *Alexa*, most of them, only *A. duckeana* G.S. Silva & Mansano and *A. wachenheimii* Benoist also have paniculates, and it is worth noting that the species *A. imperatricis* (R.H. Schomb.) Baill., *A. surinamensis* Yakovlev and *A. leiopeta* Sandwith have inflorescences with short racemes on the branches and trunk, characterizing cauliflorous inflorescences, unlike the other species which have terminal inflorescences (Silva 2024). In Leguminosae, cauliflory occurs in some lineages, but in practically all subfamilies such as *Cercis* L. (Cercidoideae), *Zygia* P.Browne (Caesalpinoideae), *Cynometra* L. and *Macrolobium* Schreb. (Detarioideae) (Cowan 1953; Ferm *et al.* 2019; Owens 1996; Radosavljevic 2019).

In Papilionoideae this form of inflorescence is especially concentrated in the first lineages to diverge in the subfamily, in the Angylocalyx clade (*Alexa*, *Castanospermum* and *Angylocalyx*) and the Swartzieae clade (*Bocoa* Aubl., *Swartzia* Schreb., and *Trischidium* Tul.) (Ireland 2007; Lewis et al. 2005; Movafeghi et al. 2011; Prenner 2003, 2013b). Cauliflory is rare in temperate regions but common in tropical forests, with several different sources of development and evolutionary value, such as pollination with birds (Endress 2010; Owens 1996).

Considering the species within other genera of the Angylocalyx clade, terminal racemose inflorescences, racemose cauliflory, and paniculates are observed across various species within this group (fig. 1-2). *Angylocalyx* is characterized by cauliflorous racemose inflorescence, which also occurs in *Castanospermum* and some species of *Alexa*. In *Castanospermum*, the cauliflorous raceme can be short (1-5cm) or long (10-15cm), sometimes has more than one main axis and can be a racemose paniculate with up to 3 racemes. In contrast, *Xanthocercis* is characterized by a paniculate with numerous racemes (Endress 2010; Leite et al. 2022; Lewis et al. 2005; LPWG 2017; Silva et al. 2023). This variation in inflorescence types among species of the genus *Alexa* provides diagnostic characteristics for differentiating the groups. However, this variation also suggests that some groups may have more than one type of inflorescence, not being a synapomorphy for the genus (Polhill 1981).

It is worth noting that *Alexa cowanii* Yakovlev has a racemose inflorescence, but the flowers are arranged in triads, considering a pseudoraceme. The pseudoraceme differs from the common raceme in that it is an inflorescence in which the primary racemose axis produces helical first-order bracts and, in the axil of these bracts, clusters of flowers and their second-order bracts and bracteoles (Lackey 1981; Tucker 1987a,b; Tucker 2006). This pattern can be found in the tribes Abreae, Desmodieae, Millettieae, Phaseoleae and Psoraleae (Teixeira et al. 2009; Tucker 1987a,b; 2003) and so far it is the only case described in the Angylocalyx clade.

The formation of the bract has a notable long plastochrony in relation to the bracteoles in the flower of *A. grandiflora*. Despite being a common feature in most legumes, this variation is more pronounced in *A. grandiflora* compared to other species of legumes (Teixeira et al. 2009; Leite et al. 2014; Prenner et al. 2015). This aspect requires further investigation through comparative analysis within the genus *Alexa* to reach a robust conclusion, but it is clear that the production of a larger structure requires more time. However, the bracts in this genus are consistently larger than the bracteoles, even in species with cauliflorous inflorescences of *Alexa*. This size difference is particularly evident in *A. cowanii*, where the first-order bract is much larger than the second-order bracteoles (Ramírez 1995; Silva et al. *in prep.*).

In *Castanospermum*, the arrangement of the bracts and bracteoles is similar to that found in *Alexa*, but with a shorter plastochrony, where they are initiated by the apex of the inflorescence in helical acropetal succession, with the floral apex being tangentially wide, with the development of two opposite bracteoles, separately (Tucker 1993). The floral whorls in both genera are produced by the floral apex in modified acropetal order: sepals, petals, outer stamens plus carpel, inner stamens. However, key difference lies in the developmental sequence within each whorl. In *Castanospermum*, the order of development is mainly unidirectional. In contrast, *Alexa* exhibits a simultaneous order of within the whorls (except in the calyx which has unidirectional initiation), highlighting distinct patterns of floral organ initiation between the two genera (Tucker 1993; Prenner 2004c).

Table 1. Floral Ontogeny and Morphology in *Alexa grandiflora* and species the Angyocalyx clade, Dipterygeae Clade and Amburaneae clade.

Floral ontogenetic characteristics	Angylocalyx clade		Dipteryx clade			Amburana clade		
	<i>Castanospermum australe</i>	<i>Alexa grandiflora</i>	<i>Dipteryx alata</i>	<i>Taralea oppositifolia</i>	<i>Pterodon pubescens</i>	<i>Amburana cearensis</i>	<i>Myroxylum balsamum</i>	<i>Cordyla pinnata</i>
	Tucker (1993)	This study	Leite et al. (2014)			Leite et al. (2015).	Tucker (1993)	Sinjushin (2018)
Order of sepal initiation	Unidirectional modified (lateral and adaxial sepals together)	Unidirectional (short plastocron on lateral x adaxial)	Unidirectional modified (lateral and adaxial sepals together)	Unidirectional (sometimes reversed)	Bidirectional	Bidirectional	Unidirectional	Unidirectional but two sepals are lacking
Order of petal initiation	Simultaneous	Simultaneous	Simultaneous	Simultaneous	Simultaneous	Bidirectional	Simultaneous	Absence of petal primordia from their initiation.
Order of antesepalous stamens initiation	Unidirectional	Simultaneous	Modified unidirectional	Modified unidirectional	Modified unidirectional	Reversed unidirectional	Unidirectional	The stamens are formed centripetally.
Order of antepetalous stamens initiation	Unidirectional	Simultaneous	Modified unidirectional	Modified unidirectional	Modified unidirectional	Reversed unidirectional	Unidirectional	
Carpel Initiation	Simultaneous to the antesepalous stamens	Simultaneous to the antesepalous stamens	Simultaneous to the antesepalous stamens	Simultaneous to the antesepalous stamens	Simultaneous to the antesepalous stamens	Formed shortly after the initiation of petal primordia	Simultaneous to the antesepalous stamens	Simultaneous to the initiation stamens

The organogeny of the sepals in *Alexa* follows a slightly modified unidirectional pattern common to Papilionoideae (Tucker 1987b) with the first sepal to initiate being the abaxial median one, followed by the two laterals and then by the two adaxial ones. The modification lies in the short plastochrony between lateral and adaxial sepals arising successively (figs 4H-I). A similar pattern is visible in the images of the organogeny of *Castanospermum* presented by Tucker (1993). Although the author cites the development of the calyx as unidirectional, the plates presented shows the lateral and adaxial sepals arising simultaneously (Tucker 1993 Figs. 37 and 38).

Such a pattern was also observed in other taxa of the ADA clade as *Dipteryx* Schreb. (Leite et al. 2014) and *Petaladenium* Ducke (Prenner et al. 2015) where, in this last one, this modification from the usual unidirectional pattern is even stated as a tendency toward bidirectionality where lateral and adaxial sepals arise together and adaxial ones develop faster. Such tendency is also visible in some images of *Castanospermum* presented by Tucker (1993; fig. 40) and in our results for *Alexa*, although in this genus, the development of the adaxial sepals occurs later (fig 4-K-L). In the genera *Taralea* Aubl. and *Dipteryx*, the adaxial sepals develop faster than the lateral ones will be taken a step further with such sepals being the most developed even at anthesis and becoming petaloid (Leite et al. 2014). In genera like *Amburana* Schwacke & Tau and *Pterodon* Vogel (Leite et al. 2014; 2015) the development of the calyx is bidirectional. *Myroxylon* L.f. and *Taralea* presents a common unidirectional pattern with a longer plastochrony between organs arising in the calyx (Leite et al. 2014; Tucker 1993) and *Dussia* Krug & Urb. ex Taub. presents unidirectional development (Prenner 2004b), but no images are presented so we could not observe the plastochrony between its parts development.

In *Cordyla* Lour. (Sinjushin 2018), a taxon with a strongly modified calyx, with three sepals, only three primordia are visible, two of them more adaxial, arising in an annular and peripheral meristematic region, but it is not possible to clearly see if these two superior primordia are remnants of the two lateral or the two adaxial ones, although they seem to be relatively distant from the abaxial primordia to be considered lateral. Other similar discrepancies in calyx development are observed in the Swartzieae clade (Paulino et al. 2013; Tucker 2003b). Such specialized morphology could be a possible extreme variation of the bidirectional organogeny where the two lateral sepals were completely lost.

Such discrepancy in the ADA clade from the usual unidirectional pattern of general Papilionoideae emphasizes that this unidirectional pattern could be a possible synapomorphy of a more internal clade of Papilionoideae. This could also be related to further modifications in whorls internal to the calyx and to the papilionoid corolla formation, since it is widely known that modifications in one whorl commonly influence modifications in internal whorls (De Craene 2018). In agreement with recent reconstructions (Cai et al. 2024) where the papilionoid flower of most of the subfamily would be a synapomorphy of a clade excluding the ADA and Swartzieae and, thus, papilionoid flowers within the ADA clade would be a result of convergent evolution.

The formation and growth of the sepals visualized in *A. grandiflora* is an event not yet described in Leguminosae. In *Castanospermum*, the initiation of the sepals is also unidirectional, but the sepals arch inwards as they grow and extend almost horizontally across the inner part of the flower during organogenesis, where they begin the formation of the calyx tube very early (Prenner 2004c; Tucker 1993), contrary to what was described in the present work

for *Alexa grandiflora*. A similar point between the sister genera is the zonal growth that forms a rather fleshy and thick tube even during early floral development, configuring a ligneous calyx in both species of the genera (Naghiloo et al. 2012; Tucker 1993).

Comparing the initiation of the sepals and the shape of the calyx, for the Dipterygeae and Amburaneae clades significant differences are evident. Among these groups only *Myroxylum balsamum* (L.) Harms has the same order of initiation as *A. grandiflora*, and the hypanthium in most groups is short and only *Castanospermum*, *A. grandiflora* and *Amburana cearensis* (Allemão) A.C.Sm. present a hypanthium that is wide (Leite et al. 2014; 2015; 2022).

The shape of the sepals during floral development in *A. grandiflora* suggests the protective function that the calyx acquires during the flower's organogenesis stages, mainly to protect the reproductive organs. This protection is mainly both biotic factors, such as herbivory, and abiotic factors, including high humidity levels, which can promote the proliferation of fungi and other agents that can damage the floral parts and their reproductive functions (Córdoba and Cocucci 2011; Pennington et al. 2000).

Comparing the calyx of representatives of the Angylocalyx clade, all genera have a gamosepalous calyx with laciniae at the apex (usually five) (figs. 10A-B, 11A-B) in *Xanthocercis* the calyx seems to be more urceolate with a straight calyx apex, which may suggest that the calyx lobes are united or emerge united, but this can be confirmed with a floral ontogeny study of the species (Leite et al. 2022; Marazzi et al. 2019; Vogel 1977).

The simultaneous formation of petals can be found in several groups in Papilionoideae, considering the lineages close to *Alexa grandiflora*, this is quite conserved, (Tab. 1), with the only exception already described for the ADA clade in *Amburana cearensis* where initiation is bidirectional, with the adaxial primordium first initiated in a distinct gap between the two adaxial sepals, the adaxial petal is followed by the two abaxial ones and, finally, the two primordia of the lateral petal are formed, and it is hypothesized that there may be a correlation between petal reduction and this pattern of initiation (Leite et al. 2015; Tucker 1984; 1987; 1994; Tucker 2002a).

Notably, in *A. grandiflora*, the adaxial petal stands out as a key trait in corolla development, since as it grows it overlaps the floral apex and covers the inner parts, becoming robust and hypothetically serving as a protective structure. Although Tucker (1993) states that the order of petal initiation in *Castanospermum* is unidirectional, we can observe in the presented images (Tucker 1993 figs 41-42) no bigger development in the adaxial vertices of the meristem where the author indicates petals regarding the lateral and adaxial ones. Tucker (1993) also states that in some analyzed flowers.

Thus, we consider that *Castanospermum*, like *Alexa* and almost all ADA clade studied genera present simultaneous corolla development. Another peculiarity that links *Alexa* to *Castanospermum*, being a possible synapomorphy, is the extremely early elevation of the annular region supporting the petals, giving the meristem as a whole a concave shape (Present work, figs. 5D-5E; Tucker 1993, figs. 42-43), not seen in other related genera which present, at this stage, convex shapes (Leite et al. 2014; 2015; Prenner et al. 2015; Tucker 1993).

The simultaneous emergence of stamens appears to be exclusive to *Alexa grandiflora* when compared to groups closely related to the ADA clade (Table 1). In contrast, the earlier initiation of the antesepalous stamens compared to the antepetalous can be found in several groups of Papilionoideae. Considering the lineages close to *A. grandiflora*, in *Castanospermum* the antesepalous stamens emerge in close succession (unidirectional) where one stamen in the abaxial position and the two lateral ones emerge, and the two outer adaxial stamens form last, but the plastochrony between them is so short that a tendency toward simultaneous arising cannot be discarded as seen in the images of Tucker (1993, fig. 42). Regarding the beginning of the antepetalous stamens in *Castanospermum*, it is described as beginning with the abaxial pair, followed quickly by the two lateral ones and, lastly, the adaxial stamens (Tucker 1993). This pattern of stamen emergence is different from that described in *Alexa* (the stamens are simultaneous), but the whorl of antesepalous stamens emerging earlier than the antepetalous is the same and common, to almost all Papilionoideae and other legumes as a whole (Prenner 2004a; Prenner 2013a; Tucker 1987b), although rare cases of inversion are known (Mansano et al. 2002).

Another interesting point in the development of the stamens in *Alexa* is the different spatial conformation they acquire throughout development. The receptacle is comparatively wide and the antesepalous stamens grow strongly towards the carpel, achieving, at some points, a 45° inclination on its direction (Fig. 6F). Doing so, they make room for the antepetalous stamens to grow straight between them, and when they are already elongated, they reorganize themselves spatially and stay in the same position, forming a single ring of stamens, but free at the base. A similar strong inclination of the antesepalous stamens toward the carpel, associated with a large receptacle is also seen in *Castanospermum* (Tucker 1993), although not so drastically, contrasting with other genera of ADA clade where the antesepalous stamens grow relatively straight (Leite et al. 2014; 2015; Prenner et al. 2015; Tucker 1993).

In Leguminosae this pattern of stamen conformation throughout development found in *A. grandiflora* is like that reported by *Hymenaea verrucosa* Gaertn., a species of the subfamily Detarioideae, where at the beginning of elongation, the filaments of the antepetalous stamens are projected outwards from the circle of the stamen. This projection of the filaments allows contact between the anthers of the antepetalous stamens and the carpel, with the anthers of the antepetalous stamens being pushed outwards, except for the adaxial median anther, which maintains contact with the carpel, but at flower anthesis, the antesepalous and antepetalous stamens are arranged in the same position (Kochanowski et al. 2018).

As for the carpel emerging together with the petals, this is something commonly known in Leguminosae, where in the majority of legumes studied so far using SEM, the carpel appears during the initiation of the petals and the stamens of the outer whorl, which overlap in their initiation times, so the vertical order is modified acropetal, with the exception of the carpel appearing before the antepetalous stamens (Khodarverdi et al. 2014; Mansano et al. 2002; Moço and Mariath 2009; Paulino 2012). This exception is unusual among Eudicots, in which acropetal initiation is the common order (Tucker 1987b; Remizowa, 2019).

In *Castanospermum*, the carpel primordium appears simultaneous with the first antesepalous stamen primordium (slightly different from that seen in *A. grandiflora* on which the carpel arises together with the five antesepalous stamens), as a large radial mound in the center of the flower and still quite short (about 330 µm high) when the carpel cleft becomes visible. A stipe is formed basally by the intercalary or zonate growth of the primordium and the carpel

remains straight and linear, the same shape and position of the carpel in *A. grandiflora* and visualized for other species of the Angylocalyx clade (Tucker 1993). In *A. grandiflora*, the carpel cleft has a lateral expansion before closing completely. Compared to the other groups in the clade, there is a smaller cleft without lateral expansion, which is evident in Leguminosae when the carpel enlarges, and the cleft is produced by extension of the margins (Tucker 1987b).

Floral resources of *Alexa grandiflora* flower

The flower of *A. grandiflora* functions as a highly active secretory system, a trait evident both in the field and through microscopic analysis. This activity is demonstrated by the sweet fragrance emitted and the secretions observed on the surface of all floral organs, ranging from oily exudates to hardened, brittle plates. We propose that all floral organs possess tissues capable of secreting both odor (composed mainly of terpenes) and nectar (composed of reducing sugars). Odor secretion was confirmed through histochemical tests, which detected terpenes in the epidermal and subepidermal layers of sepals, petals, and filaments. Nectar is predominantly produced by cells within the inner portion of the hypanthium and accumulates in the hypanthium cup. Our findings suggest that, in addition to the hypanthial nectary, other floral organs may also secrete nectar. Evidence for this includes 1) Observations of ants walking along the filaments, 2) Crystalline deposits and brittle plates on the surfaces of sepals, petals, filaments, and anthers, and 3) The presence of epidermal layers with modified stomata and subepidermal parenchyma containing cells that test positive for reducing sugars.

A comparison of the hypanthial nectary in *A. grandiflora* with those of other closely related species is currently not feasible, as no information exists regarding the presence of a hypanthial nectary in *C. australe* (see Tucker 1993). Furthermore, the specific stage of hypanthium development during which nectary cells differentiate remains an unresolved aspect in *A. grandiflora* and floral development studies in general. This gap highlights a promising area for further research.

It is important to note that the final form and development of the hypanthium of *A. grandiflora* and *C. australe* are remarkably similar. The hypanthium in *Alexa grandiflora* is notably thick and large, reaching approximately 5 mm in length and 4 mm in width. During organogenesis, it originates with the emergence of the carpel and gradually develops into a tubular to campanulate structure. Similarly, in *Castanospermum australe*, hypanthium development follows a comparable pattern. Initially, the receptacle expands as a circular platform around the base of the carpel. As the floral bud grows to approximately 7–8 mm in height, the receptacle forms a floral cup surrounding the carpel base, positioning it at the bottom of a depression, with the bases of the stamens arranged along the edge (Tucker 1993).

This evidence supports interpreting the flower of *A. grandiflora* as an integrated system for the combined secretion of odor and nectar. The substantial production of nectar and fragrance across the entire flower aligns with the hypothesis of pollination by phyllostomid bats, previously proposed for species of *Alexa* (Ramírez 1995).

Many adaptations associated with large pollinators, such as birds and bats, involve allometric scaling. These adaptations include increased nectar production, larger flower size, thicker petals, an enlarged adaxial petal, and an expanded calyx and hypanthium. These changes in floral structure size, observed in ornithophilic and chiropterophilic flowers compared to related taxa with non-vertebrate pollination, have played a critical role in the evolutionary history of these plants (Córdoba and Cocucci, 2011; Pennington et al., 2000).

The secretion of terpenes in nectar-secreting tissues of various floral organs in *A. grandiflora* (excluding the hypanthium) likely serves to maintain nectar viscosity and reduce evaporation (see Whistler and Smart 1953), as nectar remains exposed for extended periods (pers. obs.). This prolonged exposure after anthesis provides sustenance for patrolling animals, such as ants, which were observed on the sepals, petals, and filaments of *A. grandiflora*. An intriguing interpretation is that the terpenes contribute to the formation of "scented nectar" (Raguso 2004), which could act as a stronger attractant for nectar-seeking animals over long distances (Heinrich 1979).

As terpene secretion involves both epidermal and subepidermal tissues of floral organs in *A. grandiflora*, these secretory sites are classified as mesophilic osmophores, following the definitions of Vogel (1983 1990) and Fahn (1979). In other papilionoid species with non-papilionaceous flowers, such as *Camoensia scandens* (Welw.) J.B. Gillett (Leite et al., 2021), floral fragrance is also produced by mesophilic odor glands. However, in *C. scandens*, these glands are confined to petal margins. The terpenes responsible for fragrance are gradually released through stomata in *A. grandiflora* or via trichomes in *C. scandens*.

Interestingly, various types of floral glands are found in early-branching papilionoids, such as secretory cavities or ducts occurring in the anthers (Leite et al. 2014; Leite et al. 2022; Leite et al. 2025), as well as in the bracteoles, sepals, petals, and ovary (Leite et al. 2014; Leite et al. 2025). Other examples include phenolic cells at the anther apex (Leite et al. 2022), osmophores (present study), and hypanthial nectaries (Tucker 1993; Leite et al. 2014, 2015; Prenner et al. 2015; Sinjushin 2018; Leite et al. 2025; present study).

Expanding the dataset on floral glands in early-branching papilionoid legumes will not only enhance our understanding of floral structure but will also provide a foundation for developing new testable hypotheses. These findings may help explain how similarly functioning, but structurally diverse secretory sites evolve across species, ultimately contributing to the morphological traits that define the papilionoid flower.

Relevance of floral organography for the reproductive biology of the Angylocalyx clade

Considering the species of the other genera of the Angylocalyx the type of inflorescence is closely related to the type of pollinator and the environment in which these lineages are found, the Angylocalyx clade is strongly marked by an ornithophilic floral syndrome in which the calyx and hypanthium are enlarged, this is evident in *Castanospermum* and some species of *Alexa* (a group that has a cauliflorous inflorescence with red petals) (Baker and Baker 1983; Clinch et al. 1972). In *Angylocalyx* the calyx is much smaller in size when compared to the species of *Alexa* and *Castanospermum*, but an increase in the calyx and hypanthium is evident, configuring this ornithophilic syndrome, mainly by hummingbirds (Cardoso et al. 2012; Leppik 1966; Prenner 2009). As for

Xanthocercis, the calyx is also smaller when compared to the species of *Alexa* and *Castanospermum*, but no expansion of the calyx and/or hypanthium is evident.

A detailed study on the floral biology of the group should be carried out, which suggests through the morphological and environmental characteristics, the floral syndrome of *Xanthocercis* may be mellitophilous, which may correspond to flowers with zygomorphic symmetry, showy colors (yellow, cream, white), diurnal anthesis and a pleasant smell (Arroyo 1981; Faegri and Van der Pijl 1979; Ferguson and Skvarla 1982).

Probably in *Alexa* the fact that the adaxial petal is robust and differentiated is mainly due to the protection of the internal organs, as can be seen from the initiation of the petals where the adaxial petal overlaps the other petals and protects the internal organs (androecium and gynoecium) and at anthesis this petal, being the largest floral piece, ends up serving as a visual attraction for pollinators, leaving the set of stamens and the gynoecium exposed for pollination (Córdoba and Cocucci 2011; Endress 1996). It is worth noting that, in *Castanospermum*, the adaxial petal is also robust, at anthesis, like that observed in *A. grandiflora*. In organogenesis in both *Alexa* and *Castanospermum* the adaxial petal becomes the largest petal, and the others are similar in size (fig 10E-F) (Tucker 1993).

Compared to other genera in the Angylocalyx clade (*Angylocalyx* and *Xanthocercis*) (figs. 11C-F, 12B-E), the adaxial petals have a completely different thickness to those shown in *A. grandiflora* and *C. australe*, as they are thinner at anthesis. Considering nearby groups, the other representatives of the Angylocalyx clade, the *Myroxylon* is marked by a strongly zygomorphic symmetry, with a distinct adaxial petal, with the other four petals similar and reduced (Arroyo 1981; Bilbao et al. 2021; Cronk and Ojeda 2008; Tucker 2003a).

It is worth noting that the lateral and abaxial petals in all groups of Angylocalyx clade are morphologically similar (figs. 10E-F, 11D-E, 12D-E), almost undifferentiated, with only the lateral petals being larger than the abaxial petals in some cases, but with the same morphology, configuring a non-papilionaceous flower (Polhill 1981; Tucker 2002b). Papilionaceous flowers have often evolved convergently in Leguminosae and other Angiospermae families (Westerkamp 1997). An example can be found in the flowers of *Cercis* (Cercidoideae), which resemble those of most Papilionoideae (Tucker 2002a).

Homoplasies are also observed within Papilionoideae. Pennington et al. (2000) demonstrated that atypical, non-papilionoid flowers in the former tribes Sophoreae, Swartzieae, and Dalbergieae, which possess plesiomorphic traits, are morphologically different and were derived independently from more typical zygomorphic papilionoid flowers. This finding was supported by Lavin et al. (2001), whose outcomes showed that almost actinomorphic flowers evolved independently four times. Thus, actinomorphy is not a plesiomorphy among basal Papilionoideae, as previously suggested (Polhill et al. 1981). However, newer phylogenies are needed to reconstruct the evolution of papilionaceous flowers, as some relationships proposed in earlier works have not been recovered in more recent studies (Choi et al. 2022; LPWG 2017).

Some genera, mainly in the Swartzieae clade (*Swartzia*, *Fairchildia* Britton & Rose, *Cyatostegia* (Benth.) Schery, *Trischidium*, *Candolleodendron* R.S.Cowan, *Bocoa*, *Bobgunnia* J.H.Kirkbr. & Wiersema) and a few in the ADA clade (*Cordyla* and *Mildbraediodendron* Harms), exhibit polystemony resulting from a novel developmental pathway (Basso-Alves et al. 2022; Mansano et al. 2002; Paulino et al. 2013; Tucker 2003b). This includes the ring meristem (except in *Cordyla*) and complete absence of some petal primordia, as seen in *Amburana* (Leite et al., 2015). Additionally, some genera within Swartzieae and ADA clades can also have radially symmetrical flowers (*Cordyla*, *Mildbraediodendron*, *Myrocarpus* Allemão, *Bocoa*) (Pennington et al. 2000; Tucker 2002b).

Regarding the androecium and gynoecium of representatives of the Angylocalyx clade, little variation is perceived, with 10 free, exerted stamens, with anther with longitudinal dehiscence, straight stylus, curved at the apex, the main variation being the insertion of the filament in the anther, which can be dorsifixed (*Alexa* and *Castanospermum*) or basifixed (*Angylocalyx* and *Xanthocercis*) when comparing the genera. In *Castanospermum*, the anthers are dorsifixed (fig. 10G-H), with broad-based filaments tapering strongly distally and near anthesis, the stamens vary in height correlating with the two whorls, but no dorsiventral distinction between the stamens of a flower is noticeable (Tucker 1993). In *Alexa* the anthers are also dorsifixed, but in the other genera of the clade, it is sub-basifixed in *Angylocalyx* (fig. 12F-G) and basifixed in *Xanthocercis* (fig. 11G-L) (Leite et al. 2022; Silva et al. 2023).

The gamosepalous calyx, corolla with the adaxial petal larger than the others, and the lateral and abaxial (free) petals of the same shape and size are the main floral characteristics shared by this clade Angylocalyx. These characteristics differ from the typical corolla of a papilionaceous flower (Lewis et al. 2005, LPWG, 2017). In contrast the shape of the inflorescence and the insertion of the filament in the anther exhibit the most variable characteristics among representatives of the clades.

Conclusion

Our study underscores the importance of ontogenetic research in early-branching papilionoid lineages, providing new insights into the floral development of the Angylocalyx clade and its systematic significance. We elucidate key developmental processes shaping the floral morphology of *A. grandiflora*, revealing that inflorescence development follows an acropetal and helical sequence. Notably, sepal initiation is unidirectional—a common trait among papilionoid species. There is an extended plastochron between the abaxial sepal and the appearance of the two lateral sepals, as well as a distinct pattern of imbrication during growth, setting it apart from other legumes. Petal initiation occurs simultaneously, with the adaxial petal growing significantly larger than the others—a conserved trait across the Angylocalyx clade. This characteristic may have taxonomic significance for the delimitation of species within the genus, since the shape of the petals varies between species and has evolutionary importance.

The clade's defining floral traits include a gamosepalous calyx, an adaxial petal larger than the others, lateral and abaxial petals of similar shape and size, and free stamens. These characteristics differ from species that exhibit papilionaceous floral morphology. The most variable traits among clade members are inflorescence structure and filament insertion patterns, highlighting the morphological diversity within this early-diverging lineage. These findings are crucial for reconstructing floral evolution in Papilionoideae.

As the first comprehensive study of floral ontogeny in *Alexa*, this work significantly advances our understanding of the genus *Alexa* and the Angylocalyx clade. By characterizing these early-branching lineages, we establish a foundation for comparative studies of more derived, species-rich papilionoid groups, particularly those with the highly successful papilionaceous floral morphology.

Declarations

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Competing interests

On behalf of all authors, the corresponding author states that there is no conflict of interest.

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