



Floral development in *Biancaea decapetala* and *Albizia julibrissin* (Fabaceae: Caesalpinioideae), and its systematic significance

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ABSTRACT: This study investigates the floral morphology and development of two legume species from the subfamily Caesalpinioideae, *Biancaea decapetala* (a caesalpinoid), and *Albizia julibrissin* (a mimosoid), using scanning electron microscopy. The floral organ initiation in *A. julibrissin* involved the helical orientation of sepals' formation, simultaneous initiation of petals, and formation of the ring meristem in place of stamens. Whereas in *B. decapetala*, organ whorls grow unidirectionally, from abaxial to adaxial, a characteristic found in the subfamily Papilionoideae. However, the floral development sequence in *B. decapetala* differs from papilionaceous flowers, as it lacks petal specialization and features a fused staminal tube. While fused sepal tube, free stamens, and short style were observed in flowers of *B. decapetala*; fused petals, fused staminal tube, and long style occurred in flowers of *A. julibrissin*. The petal aestivation is valvate in *A. julibrissin*, compared to ascending cochleate in *B. decapetala*. The observations during the initiation and developmental stages of floral whorls are essential to unravel the functional specificity of appendages. *A. julibrissin* belongs to the Mimosoid clade, which was until recently placed outside the Caesalpinioideae subfamily (of which *B. decapetala* was always been a part of) due to its floral architecture. There has been significant number of discussions and deliberations in the botanical community about the placement of this clade in the subfamily. Understanding of floral development in the subfamily and comparison of caesalpinoids with mimosoids can be crucial in evaluating the phylogenetic placement of the mimosoid clade. While most changes in the developmental sequence may appear subtle and minute, these are imperative for the remarkable disparity in the floral morphology of legumes.

KEY WORDS: Floral ontogeny, legumes, morphogenesis, primordia, scanning electron microscopy, unidirectional initiation.

INTRODUCTION

The family Fabaceae is one of the largest groups of flowering plants, with *ca.* 770 genera and 19,500 species (<http://www.mobot.org/MOBOT/Research/APweb/>). The family displays a high disparity of morphological, chemical, and ecological features, besides having a large number of economically important taxa (Lewis and Rico Arce, 2005; Lewis *et al.*, 2013; LPWG, 2013, 2017). Besides the importance of legumes in food security, they also help in soil amelioration and are thought to reverse the adverse impact of climate change. Several tree species in the family provide quality timber and minor forest produce of commercial value (Yahara *et al.*, 2013). The family displays evolutionary diversification due to diverse morphological, physiological, and ecological characteristics (LPWG, 2017). Fabaceae are further classified into six sub-families based on morphological and molecular data: (i) Caesalpinioideae (including mimosoid clade), (ii) Cercidoideae, (iii) Detarioideae, (iv) Dialioideae, (v) Duparquetioideae, and (vi) Papilionoideae (LPWG, 2017). The traditionally known sub-family Mimosoideae has been merged in Caesalpinioideae as a separate clade (LPWG, 2017). Systematic affinities of the mimosoid clade in

Caesalpinioideae have been controversial and have not been fully resolved, and require a formal tribal and/or clade-based classification (LPWG, 2017). *Biancaea* Tod. is a genus native to South and South-East Asia, comprising seven species (Choo, 2021). The genus was recently carved out from *Caesalpinia* (Roth) Alston (Gagnon *et al.*, 2016; LPWG, 2017). *Biancaea decapetala* (Roth) O. Deg. is an evergreen shrub with copious prickles and is native to East and South-East Asia (Wyatt and Lipow, 2021). The species has been widely cultivated and has now naturalized in Africa, Europe, North and South America (Broome *et al.*, 2007; ILDIS, 2014). The genus *Albizia* Durazz. belonging to the mimosoid clade has 120-140 species and shows a wide distribution in tropical regions of the world (Lewis and Rico Arce, 2005; LPWG, 2017). *Albizia julibrissin* Durazz. is a tree native to regions spanning from the Caucasus and Iran to Asia Minor, Central to East China, and Japan (Weber, 2003). It bears pink-colored flowers in the form of tomentose terminal panicles (Wyatt and Lipow, 2021).

The floral organization holds significant taxonomic and evolutionary significance (Tucker, 2003; Endress, 2011). Usually, an angiosperm flower comprises four whorls: calyx, corolla, androecium and gynoecium,



which demonstrate diversity in their number, arrangement, color, pattern and form (Khodaverdi *et al.*, 2014). Studies have been carried out to document key developmental stages of floral organs, providing crucial information to understand the origin of flower diversity in legumes (Thomson *et al.*, 2017). Generally, in flowers of Fabaceae, sepals, petals, and outer and inner stamen primordia develop unidirectionally from the distal end to the proximal end, with acropetal or mixed acropetal order of primordia initiation in vertical succession on floral meristem, resulting in symmetrical flowers (Tucker, 2003). At subsequent stages, bilateral symmetry is seen and a specialized structure of floral organs is formed. In the tribes, Ingeae and Acacieae, species having multiple carpels and many stamens are most commonly observed. The polycarpelly phenomenon in the subfamily Papilionoideae is seen with multiple stamens in *Swartzia* (Torke and Mansano, 2009; Pinto *et al.*, 2012; Paulino *et al.*, 2014) and *Aldina diplogyne* (Stergios and Aymard, 2008). Similarly, multiple stamens are also found in Caesalpinioideae, especially in the mimosoid clade. Since floral biology is a key feature in the establishment of angiosperm phylogeny, understanding their ontogeny through comparative studies also becomes important (Tucker and Douglas, 1994; LPWG, 2013, 2017). Besides, the study of reproductive whorls has proved to be of tremendous taxonomic value (Classen-Bockhoff, 2000; Vrijdaghs *et al.*, 2005). A lot of work has been carried out on floral ontogeny in legumes and the data generated has been useful in compiling the legume phylogenetic framework (Tucker, 1984, 1987, 1988a,b, 1989, 1990, 1991, 1993, 1996, 1998, 2003; Ramírez-Domenech and Tucker, 1990; Tucker and Kantz, 2001; Klitgaard, 1999; Prenner, 2004a,b,c,d,e; 2011, 2013; Prenner and Cardoso, 2017; Torke and Mansano, 2009; Wojciechowski *et al.*, 2004; Marazzi and Endress, 2008; Prenner and Klitgaard, 2008; Movafeghi *et al.*, 2010, 2011; Naghiloo *et al.*, 2010, 2012; Khodaverdi *et al.*, 2014; Prenner *et al.*, 2015; Falcao *et al.*, 2020; Rather *et al.*, 2021). Although the subfamily Papilionoideae has received extensive research on floral development, other sub-families, such as Caesalpinioideae, despite displaying diversity in floral architecture and form, have been understudied in comparison.

The mimosoid clade has been a topic of extensive discussions and deliberations among botanists for its placement within the family. Despite obvious morphological differences in flowers, they have been placed within Caesalpinioideae. This has raised further questions about their recent phylogenetic placement, and is scrutinized by several legume experts. The present study attempts to provide ontogenetic data for *A. julibrissin*, a mimosoid, and *B. decapetala*, a true caesalpinoid as two contrasting members of the subfamily Caesalpinioideae using microscopic observations. A detailed understanding of floral development in the

subfamily and their comparison may be key in evaluating the phylogenetic placement of the mimosoid clade.

MATERIALS AND METHODS

Floral buds of *Biancaea decapetala* and *Albizia julibrissin* at several developmental stages were collected (from bud initiation to flower anthesis) from various locations in China and voucher specimens were prepared and stored in the Herbarium of the College of Life Sciences of Northwest A & F University (WUK 10254 and WUK 10548, respectively). The samples were dissected to study floral biology in detail. Samples were fixed with FAA (formaldehyde, glacial acetic acid, 70% ethanol; 5:5:90 v/v) and subsequently stored in 70% ethanol (Johansen, 1940). The materials were dehydrated in an ascending acetone series, followed by critical point drying (E-3000, Quorum Technologies, UK) (Adit *et al.*, 2022). After sputter-coating the mounted stubs with gold (JFC-1600 Autofine coater, Jeol, Japan), micromorphological observations were taken under the scanning electron microscope (Hitachi S-3400, Japan). Terminologies were adapted from Tucker (1984, 1998) to describe the floral development in the present study.

RESULTS

Floral morphogenesis and development in *Biancaea decapetala*

The inflorescence of *B. decapetala* is a raceme (Fig. 1A) containing around five to eighteen monoclinal flowers with bilateral symmetry (Figs. 1B, C). The mature flowers contain five sepals connected at the base (Fig. 1D) along with a distinct yellow-colored standard petal with a reddish-purple spot at the center and white indumentum at the abaxial side (Fig. 1E). The lateral petals and the glabrous abaxial petals were oblong and yellow in color. Both lateral and abaxial petals were longer than the standard (Fig. 1F, G). The androecial whorl consists of 10 stamens; the anthers and the upper portion of the filament were red, while the lower portion of the filaments was white. The gynoecium is represented by a solitary, green carpel (Figs. 1H, I). The carpel is ~1.5 mm longer than the stamen. The ovary is superior and unilocular with multiple ovules in marginal placentation. The style is solid in nature. The dry-type stigma is cup-shaped with a densely papillate surface.

The floral meristems initiate in acropetal order across the inflorescence. The floral meristem is subtended by an elliptical bract. Whorl development is mixed acropetal, with an early arising of the carpel. The whorls appear in the following sequence: sepals, petals, carpel, outer stamens, and inner stamens. The sepals are initiated in a unidirectional order; adaxial and lateral sepals appeared first (Fig. 2A), followed by abaxial ones (Fig. 2B). The formation of the sepals was followed by the appearance

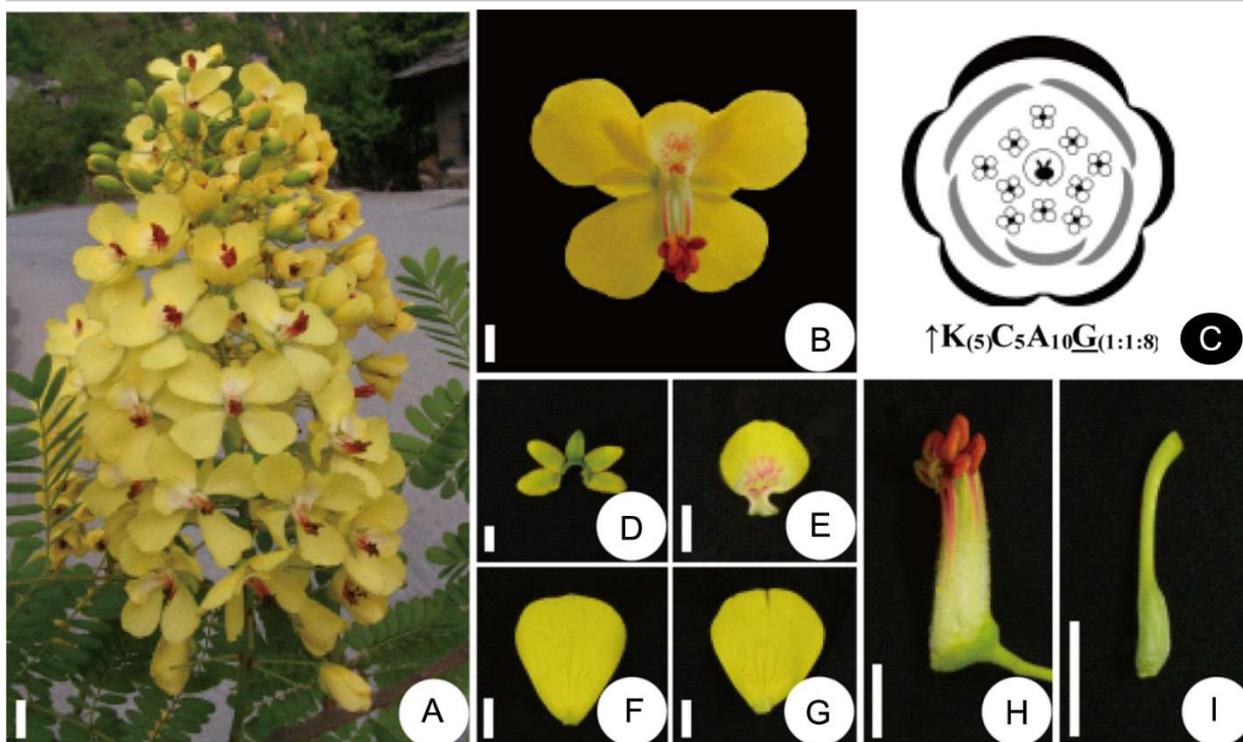


Fig. 1 Floral biology of *Biancaea decapetala* represented by **A**. inflorescence, **B**. flower, **C**. floral diagram and floral formula, **D**. sepals, **E**. standard petal, **F**. lateral petal, **G**. abaxial petal, **H**. stamens and **I**. pistil. Scale: A = 1 cm; B–I = 5 mm.

of petal primordia (Fig. 2C). The petals were initiated in unidirectional order, concurrent with carpel formation, from the abaxial to the adaxial side in the following sequence: two abaxial primordium, followed by two lateral primordia, and finally, the adaxial primordium. The outer stamens also initiate in unidirectional order; first, stamen primordium arose at the abaxial position, followed by two lateral primordia and then two abaxial primordia (Fig. 2F). The inner stamen whorl arose alternating to the outer stamen primordia (Fig. 2H). The carpel initiation was precocious; it appeared as a protuberance at the center of the floral meristem before the emergence of stamen primordia (Fig. 2D).

The abaxial bract elongates to cover the floral meristem. Petals attain bilateral symmetry and all five developing petals do-not differ in size. The abaxial petals covered the lateral ones and the adaxial ones (Fig. 2K); the abaxial and lateral petals grew faster than the standard. While petals reflex outward, stamens and pistils turn inward, forming the unique pseudo-butterfly morphology of the flower (Fig. 2K). The stamens begin differentiating prior to the petals (Figs. 2I–K). The outer whorl of the stamen elongated faster than the inner ones (Fig. 2L). At the end of development, both whorls occupied the same circumference. The base of filaments bears simple trichomes (Fig. 3A). Anthers present rimose dehiscence, an apical appendage (Fig. 3B) and tricolpate pollen grains (Fig. 3C). The carpel cleft arose adaxially after all floral organs were initiated, forming the marginal suture (Figs.

3D–F). The ovules began to initiate while the carpel margins are still open and un-fused (Fig. 3G); this was followed by the closure of the carpel cleft (Fig. 3H) and differentiation of style and stigma (Figs. 3I–M). The carpel bears simple trichomes (Figs. 3H–J). The stigma was crateriform (Fig. 3K), with papillose edges (Figs. 3L, M). Ovule primordium became hemispheric during initiation, with the open carpel (Fig. 4A). Subsequently, the inner and outer integuments were formed (Figs. 4B, C); the outer integument grew to cover the nucellus and inner integument (Figs. 4D–H) revealing the anatropous ovule (Fig. 4I).

Floral morphogenesis and development in *Albizia julibrissin*

The inflorescence of *A. julibrissin* is a cephalic pseudanthium containing up to nine bisexual flowers with radial symmetry (Fig. 5A). Sepals are born on the paraxial end of the pedicel (Fig. 5B). The corolla tube is white, while anthers are numerous, having long and pink filaments. The reproductive whorls appeared above the perianth. The ovary is superior, unilocular, with multiple ovules in marginal placentation. The long and slender style is solid in nature. The dry-type stigma is minute and cup-shaped.

Whorl development is mixed acropetal with an early arising of the carpel. The whorls appear in the following sequence: sepals, petals, carpel and stamens. The adaxial sepals were the first to be differentiated, followed by

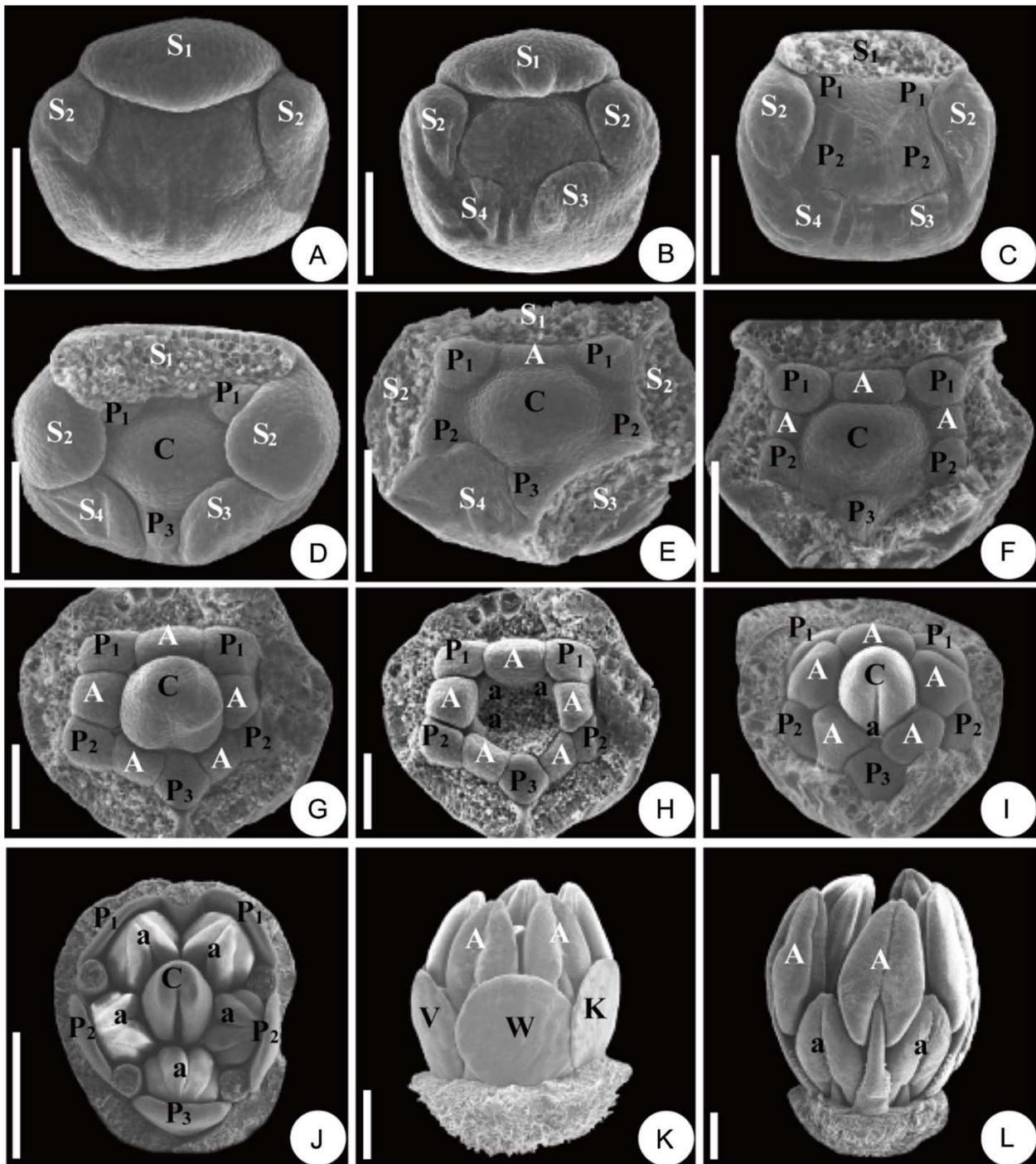


Fig. 2 Scanning electron micrographs of floral bud initiation and development in *Biancaea decapetala* showing: **A**, first three sepals beginning to develop, **B**, two adaxial sepals initiating chronologically, **C**, first four petals beginning to appear, **D**, hemispherical carpel primordia discernible at the center of the bud, **E**, abaxial stamen initiation, **F**, lateral stamen beginning to develop, **G**, two adaxial stamens initiating, **H**, initiation of inner stamen whorl, **I**, outer stamen whorl visible, **J**, filaments and anthers of inner stamen whorl getting differentiated, **K**, imbricate arrangement of petals visible and **L**, filament trichomes start developing. Scale: A–I = 100 μ m, J–L = 500 μ m. Abbreviations: A = outer stamen whorl primordia, a = inner stamen whorl primordia, C = carpel primordium, K = abaxial petal, P = petal primordia, P1–P5 = order of petals based on their initiation (P1 emerging first and P5 last), S = sepal/calyx tube, S1–S5 = order of sepal based on their initiation (S1 emerging first and S5 last), V = standard petal, W = lateral petal.

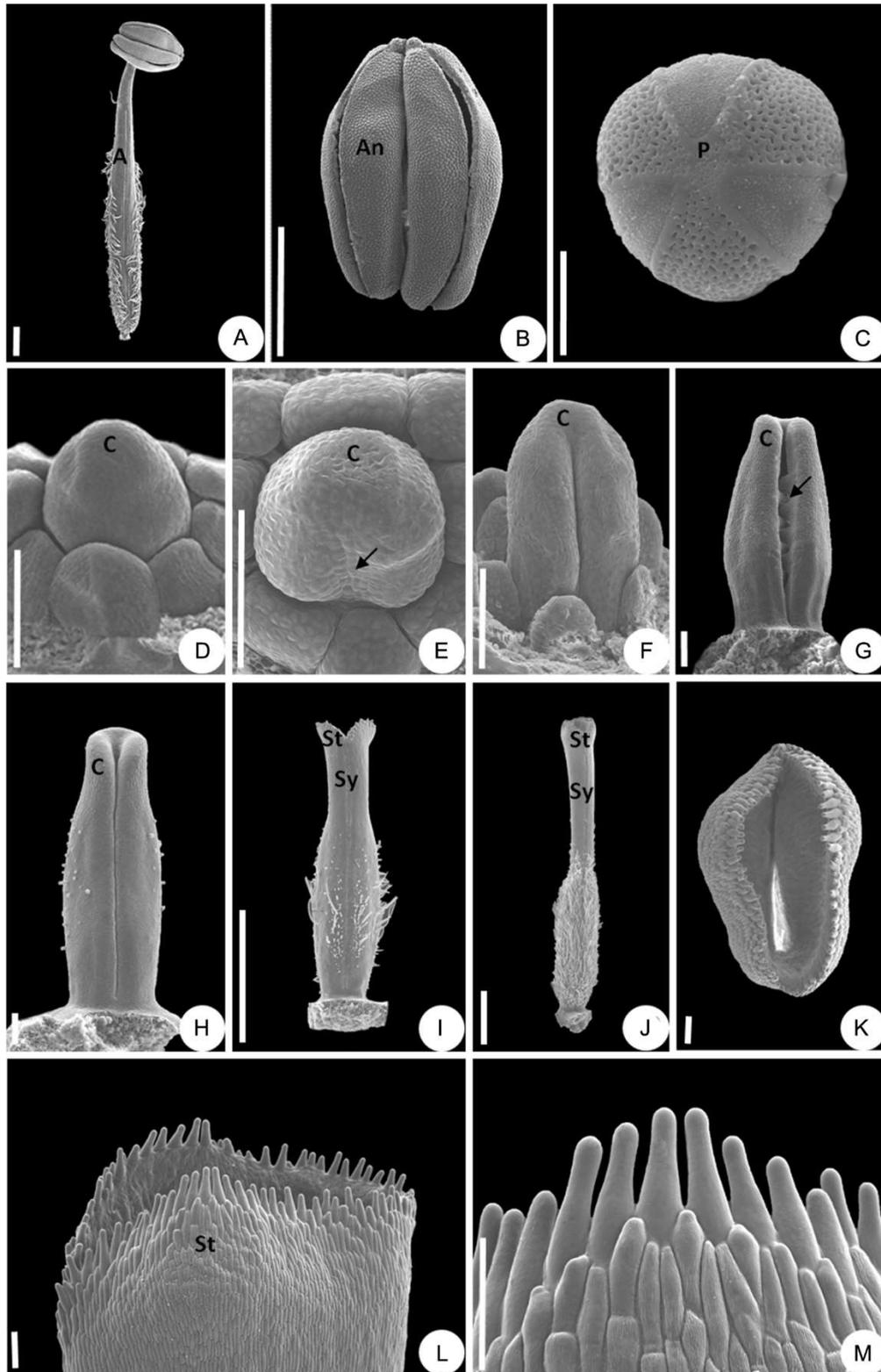


Fig. 3. Scanning electron micrographs of stamen and pistil development in *Biancaea decapetala* showing: **A.** mature stamen with dorsifixed anther and a hairy filament, **B.** longitudinal line of dehiscence visible in a mature anther, **C.** tricolpate pollen grain, **D.** carpel primordium, **E.** ventral suture (arrow) initiating in the carpel primordia, **F.** ventral suture is prominent, **G.** ovules (arrow) start emerging, **H.** ventral suture fused, **I.** differentiation of stigma, style and pubescent ovary, **J.** mature pistil, **K.** top view of the stigma showing funnel shape, **L.** lateral view of stigma and **M.** magnified view of stigma showing papillae arranged in rows. Scale: A–B = 1 mm, C = 15 μ m, D–H = 100 μ m, I–J = 1 mm, K–M = 100 μ m. Abbreviations: A = outer stamens, c = carpel, P = petal primordium, st = stigma, sy = style.

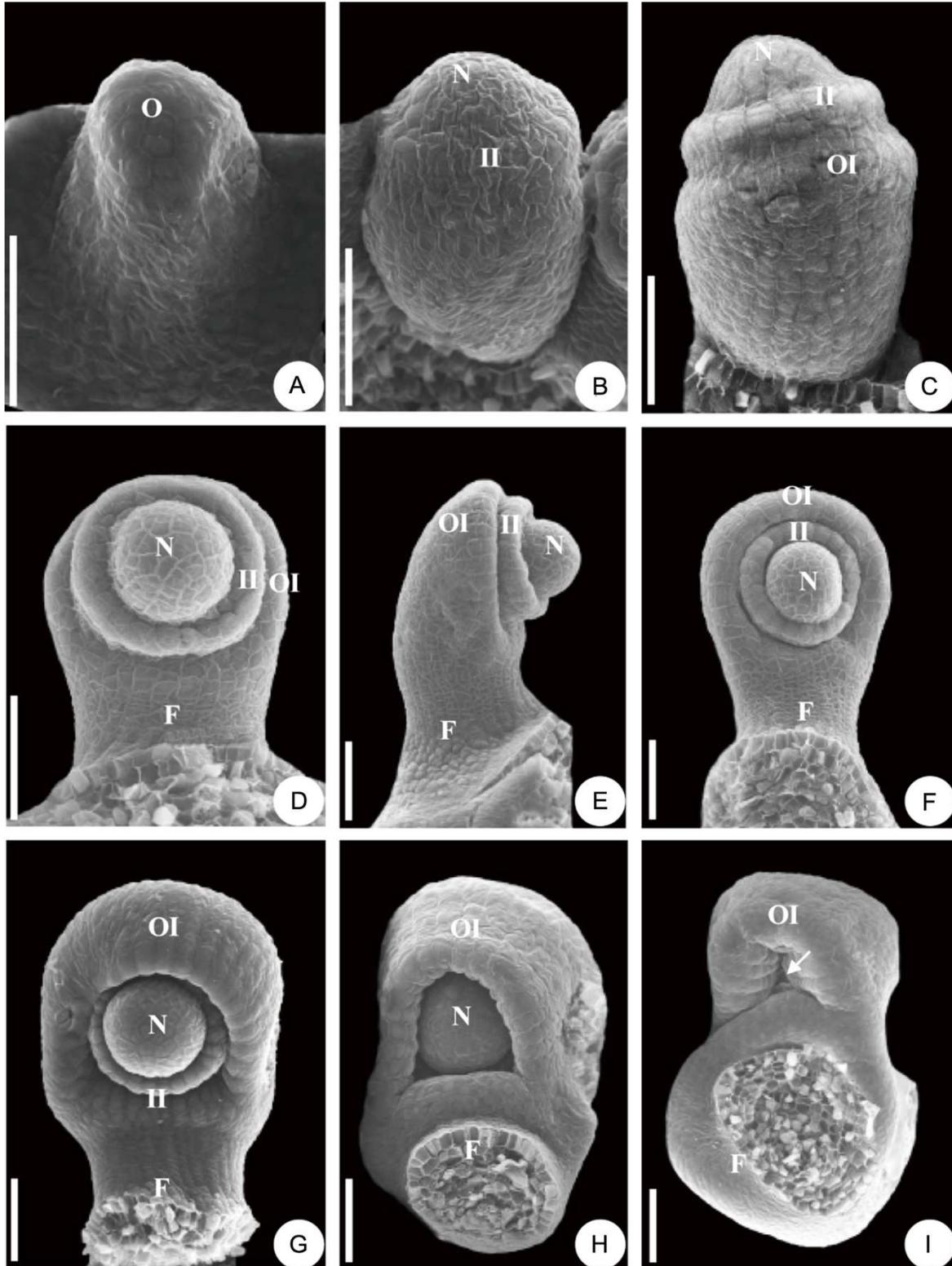


Fig. 4 Scanning electron micrographs of ovule initiation and development in *Biancaea decapetala* showing: **A.** ovule primordium, **B.** differentiation of nucellus and inner integument tissue, **C.** outer integument begins appearing, **D.** inner integument is circular while outer integument is semicircular, **E.** funiculus appears, and bends more than 90°, **F.** outer integument begins to cover inner integument, **G.** progressive development of outer integument, **H.** outer integument completely covers the inner integument and **I.** outer integumentary layer helps in formation of micropyle (arrow). Scale: A–I = 50 μ m. Abbreviations: F = funicle, N = nucellus, O = ovule primordia, OI = outer integument, II = inner integument, C = carpel, P = petal primordium, st = stigma, sy = style.



Fig. 5 Floral biology of *Albizia julibrissin* represented by **A**. inflorescence and **B**. dissected mature flower showing sepals, petals, androecium and gynoecium. Scale: A–B = 1 mm.

lateral sepals, in a spiral manner (Fig. 6A). Petal primordium developed synchronously, once all the sepals were initiated (Fig. 6B). The calyx base gradually unites and bulges at the center (Fig. 6C), simultaneously followed by differentiation of carpel primordium. Subsequently, the trichomatous stamen whorl takes shape and the calyx tube was gradually formed (Figs. 6D, E). The size of sepal and petal primordia were similar (Figs. 6E, F). Carpel primordium continued to develop, forming an abdominal suture and was encircled by the stamen primordia (Fig. 6G). The stamen primordia differentiated into filaments with anther lobes, while the ventral carpel suture was formed (Fig. 6H, I). Due to the continuous development, stamens gradually rose above the carpel (Fig. 6J); the fusion of filament at their base was observed at this stage (Figs. 6K, L). The cup-shaped and crateriform stigma was prominent at maturity (Fig. 6M).

The ovule was anatropous and bitegmic (Fig. 7A); the inner integument developed first (Fig. 7B), and gradually the ovule started curving inwards (Fig. 7C). Subsequently, the outer integument surpassed the inner integument's growth and eventually covered it (Figs. 7D–G). However, the integuments did not completely enclose the nucellus, which is left partially exposed (Figs. 7H).

DISCUSSION

Floral characters play a significant role in the delimitation of taxa in Fabaceae (Young and Watson, 1970; Naghiloo *et al.*, 2010; Khodaverdi *et al.*, 2014). The floral ontogeny in *Albizia julibrissin* is in accordance with other members of the mimosoid clade, such as *Mimosa*, with features such as centripetal and simultaneous flower organogenesis (Ramírez-Domenech and Tucker, 1990). On the other hand, in *Biancaea decapetala*, the

unidirectional floral development pattern from the distal axis to the proximal end, is similar to other members of the family (Tucker, 2003). However, uniform development and organ specialization, such as the formation of the staminal tube and specialized petals in the form of butterfly flowers are not seen like Papilionoideae in the species selected in the present study. Tucker (1989) suggests that the growth of floral primordia follows a particular sequence, and distinctions manifest as the development of the tissue progresses. Significant differences in calyx symmetry, petal color, stamen morphology, and stigma size were observed between the two species. In both the species examined here, organ development experiences a time-lapse that helps attain synchrony in organ development. This happens because the initiation of one whorl of organs changes the hormonal balance in the apical meristem to favor the development of subsequent whorls (Tucker, 2003). Key points of comparison in floral development between the two species are provided in Table 1.

The specialization of floral organs observed in the species examined are functionally relevant for pollinator attraction and subsequent reproductive success. Bright-colored standards serve as a means to attract pollinators, while abaxial petals act as protective barriers to the reproductive whorls (Huang *et al.*, 2014). Further, features such as the presence of anatropous ovules with pseudo-integument and fused stamens are also indicative of adaptation to facilitate pollination (Foerste, 1888). Although carpel development in *B. decapetala* is initiated before anthers, the flowers have been reported to be protandrous (Son and Im, 2015), thus promoting cross-pollination. This suggests that carpel maturity is a lengthier process as compared to anther maturity. Additionally, floral rewards such as pollen and nectar presented to the carpenter bees (legitimate pollinators) are

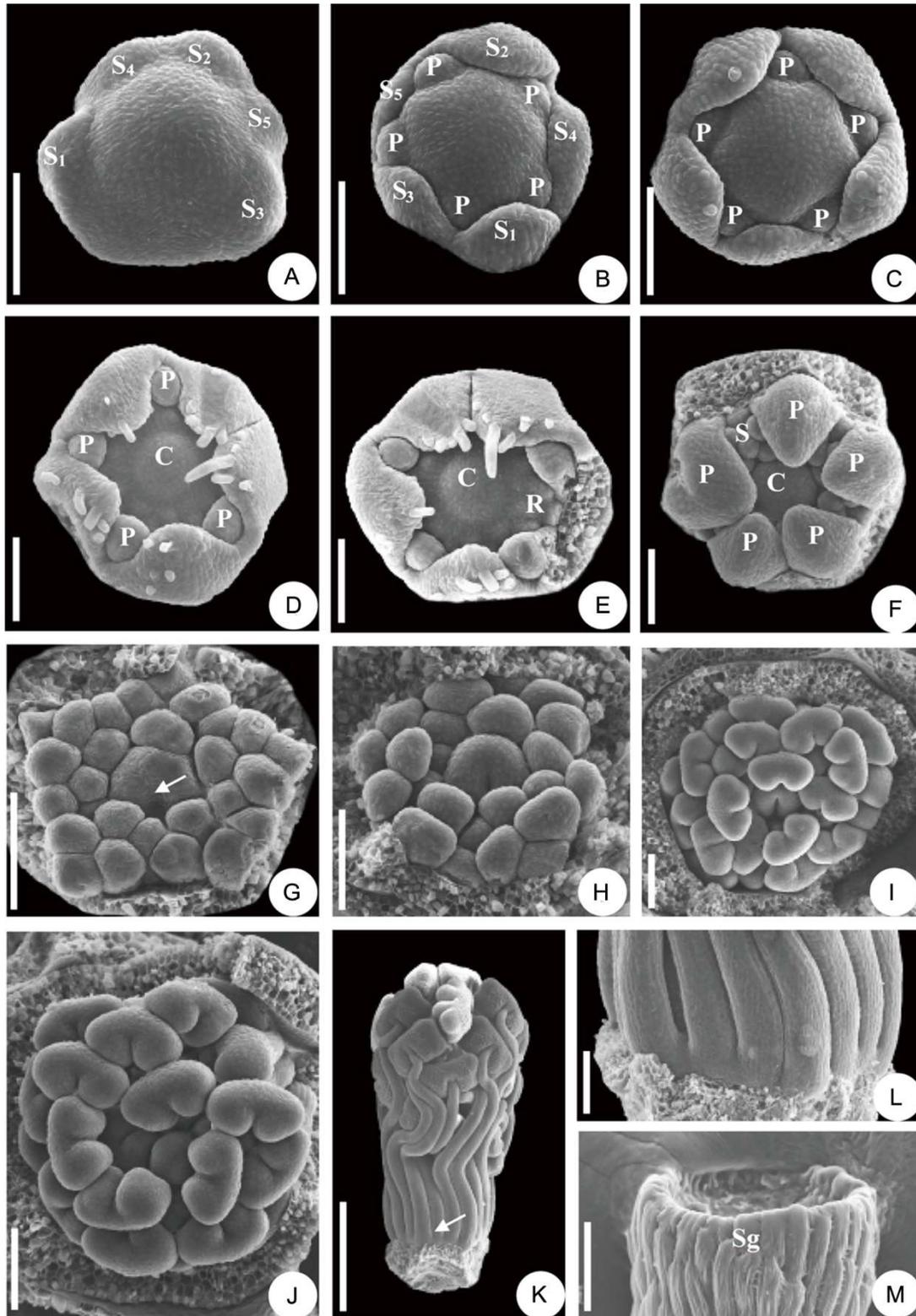


Fig. 6 Scanning electron micrographs of floral bud initiation and development in *Albizia julibrissin* showing **A.** adaxial and lateral sepals beginning to develop, **B.** petals initiating synchronously, **C.** base of sepals gradually uniting, **D.** hemispherical carpel primordium discernible at the center, **E.** meristematic ring appearing, **F.** stamen primordia beginning to develop, **G.** ventral suture of the carpel appearing, **H.** stamen primordia starts differentiating, **I.** differentiation of stamens into filaments and anthers, **J.** stamens covering the carpel, **K.** base of filaments fusing, **L.** magnified view of filament base and **M.** lateral view of stigma. Scale: A–J = 100 μ m, K = 500 μ m, L = 100 μ m, M = 50 μ m. Abbreviations: C = carpel, P = petal primordium, S1–S4 = order of sepal based on their initiation (S1 emerging first and S4 last).

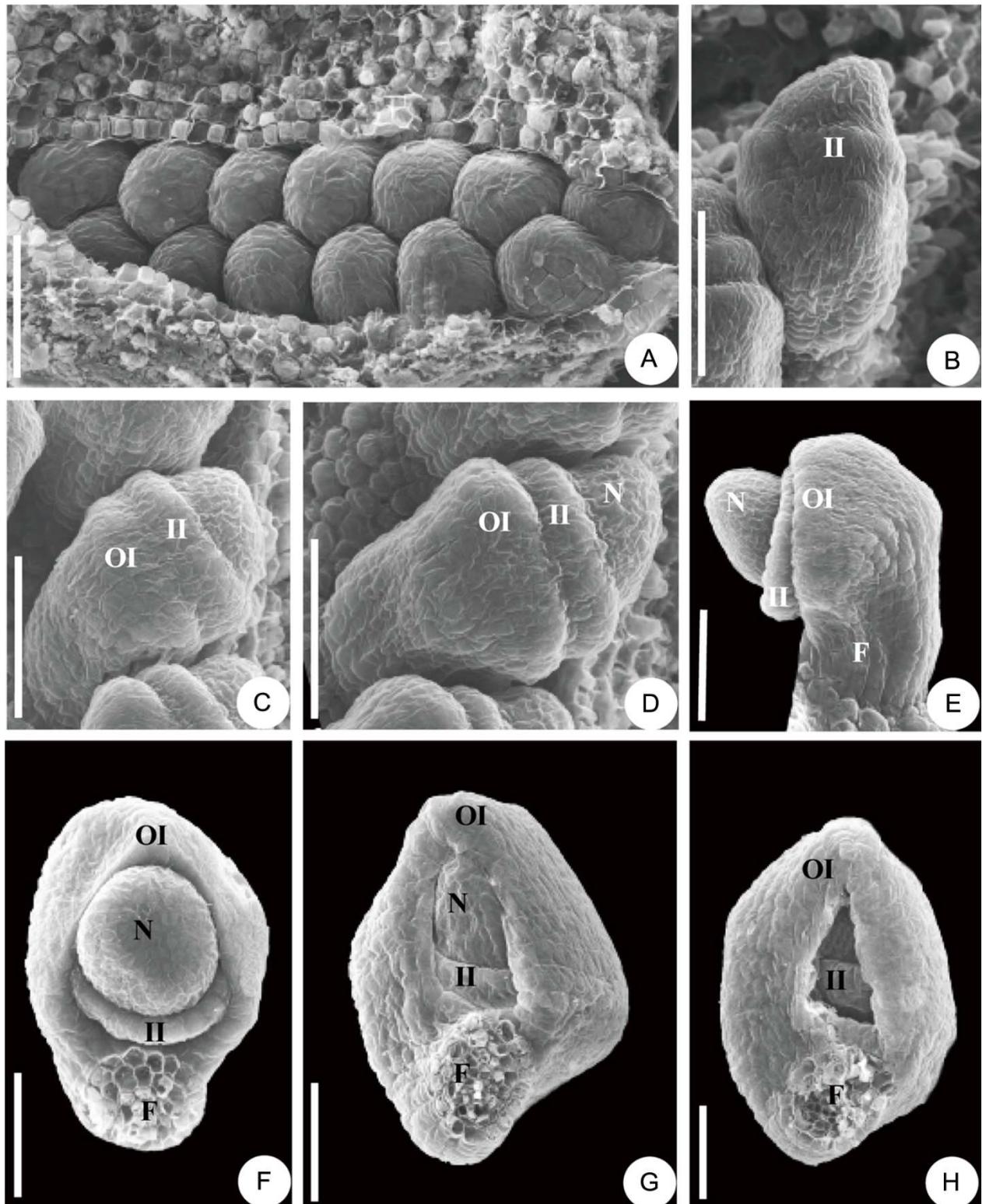


Fig. 7 Scanning electron micrographs of ovule initiation and development in *Albizia julibrissin* showing: **A.** ovule primordium, **B.** differentiation of inner integument tissue, **C.** outer integument beginning to appear **D.** initiating nucellus development, **E.** outer integument gradually covering inner integument, **F.** progressively developing outer integument, **G.** ovule turning nearly 180° and **H.** ovule at maturity. Scale: A–H = 50 μ m. Abbreviations: F = funicle, N = nucellus, OI = outer integument, II = inner integument.

**Table 1.** Comparative floral development information of *Biancaea decapetala* and *Albizia julibrissin* used in the study.

Floral Characters	<i>Biancaea decapetala</i>	<i>Albizia julibrissin</i>
Inflorescence	Raceme	Capitulum
Symmetry	Bisymmetrical	radial
Bractlet	x	x
Central sepal initiation	Abaxial side	Adaxial side
Hair on sepal	x	x
Calyx lobes /Hypanthium	Hardly has a hypanthium	1/2
Sepal development	Unidirectional	Helical
Petal development	Unidirectional	Synchronous
Stamen type	Adelphic, hairy filament	Coalescence
Base of staminal tube	x	x
Carpel	1	1
Stigma	Funnel-shaped	Funnel-shaped
Style	Erect	Erect, extremely long
Hair on ovary	√	x
Ovary stipitate	Short	Short
Ovule precocity	√	x
Ovule number	8, arrange in two lines	13, arrange in two lines
Ovule type	Bitegmic, anatropous	Bitegmic, anatropous
Floral organ overlaps	x	x
Common primordium	x	x

both associated with the androecium (Phukela *et al.*, 2020). The nectar production, however, peaks when the carpel matures (Son and Im, 2015), suggesting partitioning of resources to engage the pollinator during both floral phases, i.e., male (anther maturity) and female (carpel maturity). In *A. julibrissin*, cross-pollination is also preferred, but by means of late-acting self-incompatibility (Wyatt and Lipow, 2021). Flowers in this species are arranged in capitate heads, with bisexual ones located at the center surrounded by staminate flowers (andromonoecy). The bisexual flowers are observed opening prior to the staminate flowers. Coupled with the fact that stigma is receptive before anther dehiscence, this creates a present protogynous condition in the species (Wyatt and Lipow, 2021).

Caesalpinioideae is a peculiar clade within Fabaceae, especially after recent additions of the Mimosoid group to the subfamily (LPWG, 2017). Notably, there are some striking dissimilarities in the floral ontogeny between Mimosoids and other Caesalpinioids. Mimosoids have an aggregated raceme, radial symmetry of flowers, synchronous organ development, abaxial initiation of median petal, heteromorphic anthers, and non-overlapping (valvate) whorls. In contrast, other Caesalpinioids usually have a lax inflorescence, bilateral symmetry of flowers, successive organ development, adaxial initiation of the median, standard petal, and overlapping whorls (Tucker *et al.*, 1985; Tucker, 2003; De Barros *et al.*, 2017). It has been observed in legumes that single carpel is plesiomorphic conditions; however, Mimosoids with higher carpel number is an obvious exception to the uniform trend in the family (De Craene, 2018). Additionally, androecium whorl in Mimosoids is

also known to have the presence of staminodes; a trait which is usually absent in the sub-families (Venkatesh, 1951; Hopkins, 1986; Tucker, 1988; Endress, 1994; Tucker, 1996, 2003; de Queiroz *et al.*, 1999; Luo *et al.*, 2009; de Barros *et al.*, 2017). As ontogeny is one of the basis for floral diversification among angiosperms, it is likely to play a crucial role in the speciation and delimitation of taxa (Tucker, 2003). According to Tucker (1984, 1997) “a correlation exists between the timing of character expression and the hierarchical level at which it is significant”. Therefore, the order of initiation and position of floral organs are noteworthy and need to be incorporated during the classification of taxa, especially at the subfamily level (Tucker, 2003). Although the legume phylogeny utilizes floral characters for the classification of clades (LPWG, 2017), the present study implores the need to use developmental trends along with the existing floristic data for clade-level segregations.

Floral appendage initiation in angiospermic flowers typically occurs either simultaneous or in a whorled fashion. While unidirectional initiation has long been associated with legumes (Rohrbach, 1870; Frank, 1876; Hartog, 1888, Naghiloo *et al.*, 2010; Prenner, 2013; Khodaverdi *et al.*, 2014; Rather *et al.*, 2021), though it is an uncommon occurrence in Leguminosae. In the present study, helical organogenesis was observed in *A. julibrissin*; while *B. decapetala*, initially exhibited unidirectional organogenesis before transitioning to a helical pattern. This unidirectional organogenesis is generally assumed to be a derived feature in Leguminosae (Polhill and Raven, 1981) and has been reported in papilionoids (Naghiloo *et al.*, 2010; Prenner, 2013; Khodaverdi *et al.*, 2014; Rather *et al.*, 2021). Conversely,



most Caesalpinioids exhibit helical sepal initiation (Tucker, 1984; Derstine and Tucker, 1991; Masoumeh *et al.*, 2013). This trend is not restricted to Leguminosae and has also been observed in other families such as Juglandaceae and Salicaceae (Sattler, 1973), Scrophulariaceae (Singh, 1979), Solanaceae (Mair, 1977), and Labiatae, Plantaginaceae, and Verbenaceae (Lang, 1906). Similarly, a fusion of floral organs during development is also believed to be a derived condition among angiosperms (Stebbins, 1974).

In the present study, *Biancaea decapetala* has racemose inflorescence, whereas *Albizia julibrissin* has capitate heads. Additionally, central sepal initiation is adaxial, and sepal development is helical in *A. julibrissin*, whereas it is unidirectional and abaxial in *B. decapetala*. Another marked difference is that in *A. julibrissin*, the carpel remains open and unfused at the initiation of ovules and fuses later; whereas, in *B. decapetala*, the carpel margins fuse before the ovules appear. The results generated in the present studies agree with the data obtained during the recent molecular studies, although more experiments need to be carried out to clarify taxonomically relevant characters.

The present study investigated the ontogenetic processes involved during flower development in two Caesalpinioid taxa, *Biancaea decapetala*, and *Albizia julibrissin*. The floral initiation and development take place in a sequential manner, and all floral whorls undergo requisite changes in cell/tissue organization. Common primordia formation suggests that multiple factors work together to start the floral initiation process and their subsequent transition from one developmental stage to another. This may also be attributed to energy and resource conservation by the plant during the initial development phases (von Arx, 2013). Although the study shows a resemblance of early ontogenetic features between the two species, there were several variations in the development pattern of ovules during later stages. In *A. julibrissin*, ovule initiation appears to have proceeded earlier, besides showing a distinct fusion of sepals. Further, variability in sepal initiation can be due to the helical pattern of floral development in Caesalpinioids.

Data on phylogenetically relevant characters can provide valuable insights and help in further understanding of legume systematics, especially in the mimosoid clade nested in subfamily Caesalpinioideae. Such studies are also crucial for understanding floral morphogenesis and provide clarity on floral changes in response to biotic/abiotic stress (Takeda *et al.*, 2013; Thomson *et al.*, 2017). It is strongly suggested, that developmental traits must be mapped in a phylogenetic framework, to bring light to evolutionary patterns of flower morphogenesis and development.

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