

## FLORAL ONTOGENY OF TWO *JATROPHA SPECIES* (EUPHORBIACEAE S.S.) AND ITS SYSTEMATIC IMPLICATIONS

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### Abstract

Floral ontogeny of *Jatropha multifida* L. and *Jatropha integerrima* Jacq. (Euphorbiaceae) was studied using scanning electron microscopy (SEM). These two species possess unisexual male flowers and bisexual (with unfunctional staminodes) female flowers. In both male and female flowers, five sepal primordia arise in a 2/5 sequence on the periphery of the floral apex and initiate anticlockwise or clockwise in different floral buds. Five petal primordia initiate simultaneously alternate to sepals. Dicyclic stamens (obdiplostemony) arise in both male and female flowers. In *J. multifida*, five outer stamen primordia arise first simultaneously and then three inner stamens initiate simultaneously. However, in *J. integerrima*, ten stamen primordia arranged in two whorls initiate simultaneously. While the ovary is absent in the male flowers, in the female flowers, three carpel primordia appear simultaneously. With further development of the ovary the stamens degenerate in the female flowers, whereas in the male flowers, the stamens grow normally. Ancestral state reconstruction using MacClade indicates that stamen simultaneous vs. non-simultaneous initiation supports the phylogenetic analysis based on nuclear ribosomal DNA ITS sequence.

**Key words:** Floral ontogeny, *Jatropha multifida*, *Jatropha integerrima*, Systematic implications.

### Introduction

The genus *Jatropha* belongs to the subfamily Crotonoideae – Euphorbiaceae s.s. and consists of approximately 175 species (Li & Gilbert, 2008). *Jatropha* plants are broadly distributed in Central America, Africa and Asia. There are five species cultivated in China, viz., *Jatropha curcas*, *Jatropha podagrica* Hook, *Jatropha gossypifolia*, *Jatropha multifida*, and *Jatropha integerrima* Jacq. Dehgan & Webster (1979) established an infrageneric classification of the genus based on their morphological diversity. Two subgenera (subgen. *Jatropha* and subgen. *Curcas*), 10 sections and 10 subsections were recognized to encompass the 175 species. *Jatropha multifida* and *J. podagrica* were placed into section *Peltatae* subgenus *Jatropha* (Dehgan & Webster, 1979). This classification is now widely accepted (Hemming & Radcliffe-Smith, 1987; Dehgan, 2012). Recently, a phylogenetic study of seven prominently distributed species (*J. curcas*, *J. glandulifera*, *J. gossypifolia*, *J. integerrima*, *J. multifida*, *J. podagrica* and *J. tanjorensis*) was conducted (Pamidiamarri *et al.*, 2009a, b), which showed that *J. multifida* and *J. podagrica*, and *J. curcas* and *J. integerrima*, respectively, were sister to each other, based on RAPD and AFLP evidences (Pamidiamarri *et al.*, 2009a). However, ITS of nrDNA indicated that *J. podagrica* was sister to *J. curcas* (Pamidiamarri *et al.*, 2009b).

Floral ontogenetic data can often provide valuable data for phylogenetic study (Endress, 1994; Sun *et al.*, 1998). Singh (2005) has studied the floral ontogeny of the male flower of *J. gossypifolia* with particular reference to obdiplostemony. In our previous study, the floral ontogeny of three species in *Jatropha*, viz. *J. curcas*, *J. podagrica* and *J. gossypifolia*, was investigated, in which stamen initiation and anther arrangement pattern were revealed to have certain systematic or phylogenetic implication (Liu *et al.*, 2008).

In this paper, the floral ontogeny of *J. multifida* and *J. integerrima* was studied using scanning electron microscopy (SEM). We describe and compare the floral ontogeny of male and female flowers of the two species, as well as compare the floral ontogeny with that of other species of *Jatropha* and discuss the related systematic implications.

### Materials and Methods

Floral buds of *J. multifida* and *J. integerrima* at different developmental stages were collected from Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (XTBG, CAS). The voucher specimens (Liu Huanfang 001, 040) were deposited in Herbarium of South China Botanical Garden (IBSC), CAS.

For SEM observation, floral buds were fixed in FAA (90 parts 70% ethyl alcohol: 5 parts glacial acetic acid: 5 parts 40% formaldehyde). Bracts and larger floral organs were removed under a dissecting microscope; all floral buds were dehydrated in an alcohol series (75%, 85%, 95%, 100%, 100%) and transferred to isoamyl acetate. The materials were critical point dried with CO<sub>2</sub>, mounted on stubs, gold-coated in the JFC-1600 Auto Fine Coater (JEOL, Tokyo, Japan), and observed under a JSM-6360LV SEM (JEOL) operated at 10 kV.

In order to investigate the systematic significance of floral ontogenetic features in these species, stamen initiation was mapped onto a phylogenetic tree of the genus *Jatropha* that was reconstructed based on ITS sequences and was chosen here because of the relatively high support value of the tree (Pamidiamarri *et al.*, 2009b). The ancestral states were reconstructed from unordered characters with the software MacClade 4.06 (Maddison & Maddison, 2003).

## Results

### Floral ontogeny of *J. multifida*

**Male flower:** The male flower is initiated as a circular primordium preceded by two sequentially formed lateral bracteoles (Figs. 1A and 1B). Five sepal primordia arise in a 2/5 sequence on the periphery of the floral apex and initiate anticlockwise or clockwise in different floral buds of the same species (Figs. 1C, 1D and 1E). The first sepal primordium arises in a non-medial abaxial position, relative to the inflorescence meristem, and the second one in a medial adaxial position (Fig. 1C). The third sepal primordium is initiated abaxially, close to the first sepal primordium and then the two remaining sepal primordia are initiated in lateral positions (Figs. 1D and 1E). The first sepal primordium is quite large by the time the fifth one appears. Five petal primordia are initiated simultaneously inside the sepals and alternate with the sepals (Figs. 1F and 1G). Five outer stamen primordia are initiated in an antipetalous position (Figs. 1H and 1I). Subsequently, three inner stamen primordia initiate in an antisepalous position (Fig. 2A). Nevertheless, the stamens are the same size at maturity. Each young stamen first becomes two-lobed (Fig. 2B) and then four microsporangia are formed (Fig. 2C). The mature anthers are all arched outward (Figs. 2C and 2D), and five nectaries are positioned alternate to outer stamens (Fig. 2D).

**Female flower:** The female flower possesses five sepal primordia that develop in an anticlockwise or clockwise spiral sequence (Figs. 2E and 2F). The petal primordia arise simultaneously and alternate with the sepals (Fig. 2G). Five outer stamen primordia initiate in an antipetalous position (Fig. 2H). Subsequently, three inner stamen primordia initiate in an antisepalous position (Fig. 2I). Shortly after all stamens are visible, the center of the flower primordium becomes dome-shaped, and differentiation of the gynoecium commences (Fig. 3A). At this time, the eight stamens appear to be in one whorl despite their different sizes. Then three carpel primordia become visible, and the tricarpellary nature of the gynoecium becomes evident (Figs. 3B and 3C). With the development, stamens stop developing and are aborted (Figs. 3D 3E and 3F). The ovary has 3 locules and 3 styles, and each stigma is bifid (Fig. 3G). Traces of the aborted stamens can still be seen in the mature female flower (Figs. 3F and 3G). Meanwhile, as the female flower matures, five nectaries are positioned alternate to outer stamens (Figs. 3F and 3G). In our research of 40 samples, 90% of female flowers have three stigmas and locules, and 10% of female flowers have only two stigmas and locules (Figs. 3H and 3I).

### Floral ontogeny of *J. integerrima*

**Male flower:** The development of the five sepals and five petals is the same as that in *J. multifida*. However, in *J. integerrima*, ten stamen primordia, arranged in two whorls, are initiated simultaneously (Fig. 4A). Five outer stamens are positioned in an antipetalous position and five inner stamens are positioned in an antisepalous position (Fig. 4B). Each young stamen first becomes two-lobed (Fig. 4C) and then four microsporangia appear (Fig. 4D). An outer whorl of 5 anthers arch inward and an inner

whorl of 5 anthers arch outward (Fig. 4D). Successively, the outer whorl of anthers become introrse (Fig. 4E). At anthesis, the outer whorl of anthers bow down instead of remaining upright (Figs. 4F and 4G).

**Female flower:** The initiation and development of five sepals and petals is the same as that in the female flowers of *J. multifida*. Ten stamen primordia arranged in two whorls initiate simultaneously (Fig. 4H). Five outer stamens are in an antipetalous position and five inner stamens are in an antisepalous position (Fig. 4I). Three carpel primordia become visible following the appearance of the stamen (Figs. 4I and 4J). Later the ovary has 3 locules and 3 styles, and each stigma is bifid (Fig. 4K). The development of the ovary and stamens is the same as that in *J. multifida*. In our research of 40 samples, 95% of female flowers have three locules and 5% of female flowers have four locules (Fig. 4L).

**Stamen initiation:** Stamen initiation occurs simultaneously between whorls in *J. integerrima*, which is similar to that in *J. gossypifolia*, *J. podagrica* and *J. curcas* (Liu et al., 2008). This is not the case in *J. multifida*. How stamen initiation occurs in *J. tanjorensis* and *J. glandulifera* remains unknown. Stamen initiation occurs non-simultaneously (personal research) in outgroup *Croton argyranthemus* (Pamidiamarri et al., 2009b) (Fig. 5).

Parsimony reconstruction suggests that the ancestor of the clade *Jatropha* was characterized by non-simultaneous stamen initiation. The ancestor of one clade in *Jatropha* (including *J. integerrima*, *J. gossypifolia*, *J. podagrica* and *J. curcas*) was characterized by simultaneous stamen initiation, and the ancestor of the other clade (including *J. tanjorensis*, *J. multifida* and *J. glandulifera*) was characterized by non-simultaneous stamen initiation.

## Discussion

*Jatropha multifida* and *J. integerrima* possess unisexual male flowers and bisexual (with unfunctional staminodes) female flowers with pentamerous calyx and corolla. The androecium of male flowers contains 8 (*J. multifida*) or 10 (*J. integerrima*) stamens with basally connate filaments and elongated anthers. In general, the gynoecium in female flowers contains three carpels that are connate at their base and 8 (*J. multifida*) or 10 (*J. integerrima*) staminodes.

Based on our results, formation of flowers in *J. multifida* and *J. integerrima* can occur in two modes. In male flowers, there is no emergence of female organs during development. In female flowers, bisexual elements are present but the androecium degenerates in later development. This development pattern is the same as that observed in *J. curcas*, *J. podagrica* and *J. gossypifolia*, as reported in our previous study (Liu et al., 2008). Both sex organ primordia appear in the early developmental stages and selective developmental arrest of preformed organ primordia is the most common method for generating unisexual flowers (Delong et al., 1993; Grant et al., 1994). We found that female flowers conform to this pattern in these five *Jatropha* species but they are regarded as bisexual (with unfunctional staminodes) flowers.

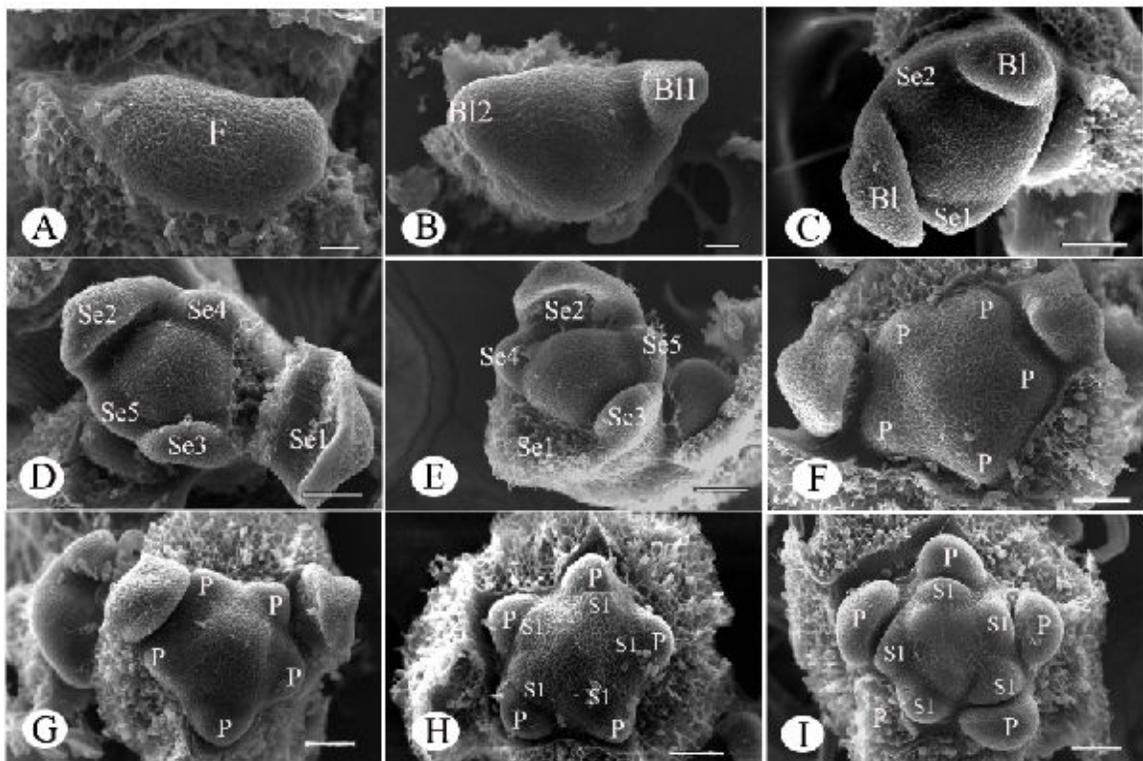


Fig. 1. Early ontogeny of male flower in *J. multifida* L. A, Floral primordium. B, Two sequentially formed bracteoles initiate. C, The first sepal primordium arises in non-median abaxial and the second one in medial adaxial position. D-E, Five sepals are initiated in a spiral pattern, D is anticlockwise and E is clockwise. F-G, Five petal primordia are initiated simultaneously inside the sepals and alternate to sepals. H-I, Five outer stamen primordia are initiated in an antipetalous position. Bl, bracteole; F, floral primordium; P, petal; S, stamen; Se, sepal; Scale bars=50  $\mu$ m C-I, 20  $\mu$ m A and B.

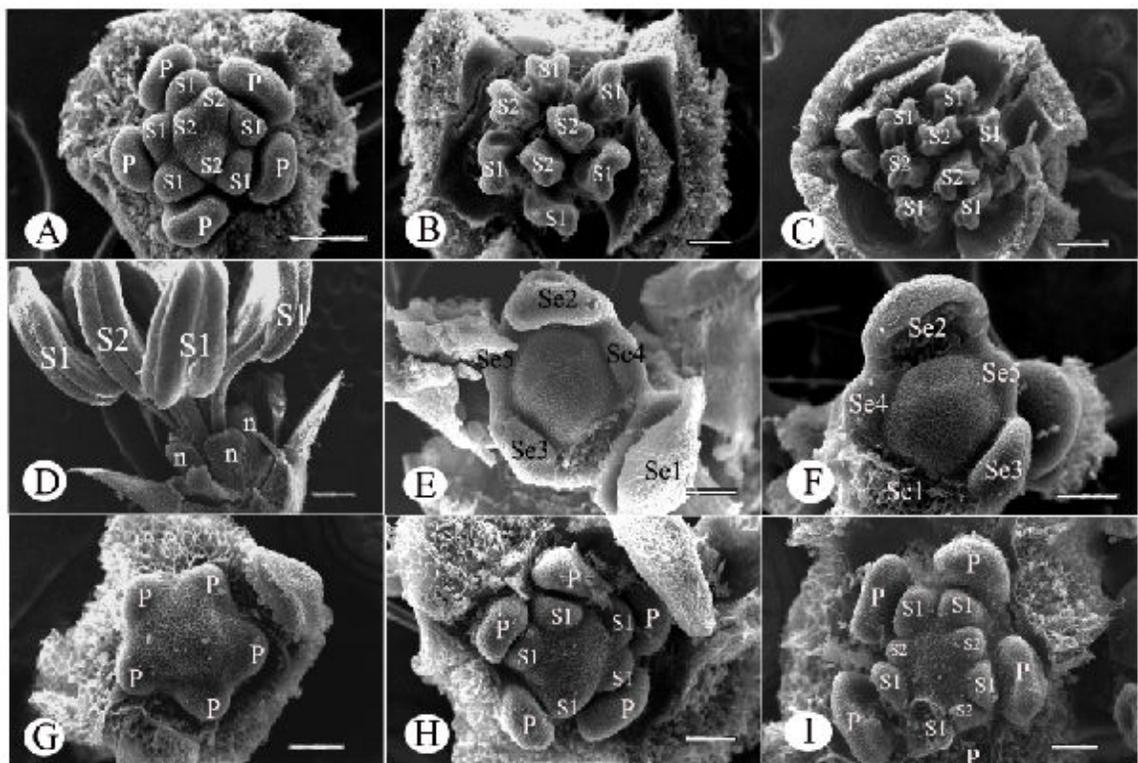


Fig. 2. Late ontogeny of male flower and early ontogeny of female flower in *J. multifida*. A, Three inner stamen primordia initiate in an antisealous position. B, Each young stamen is two-lobed. C, Each mature anther has four microsporangia. D, The mature anthers arch outward and five nectaries are positioned alternate to outer stamens. E-F, Five sepals are initiated in a spiral, E is anticlockwise and F is clockwise. G, Five petal primordia arise simultaneously. H, Five outer stamen primordia initiate in an antipetalous position. I, Three inner stamen primordia initiate in an antisealous position. n, nectary; P, petal; S, stamen; Se, sepal. Scale bars=500  $\mu$ m D, 200  $\mu$ m C, 100  $\mu$ m A and B, 50  $\mu$ m E-I.

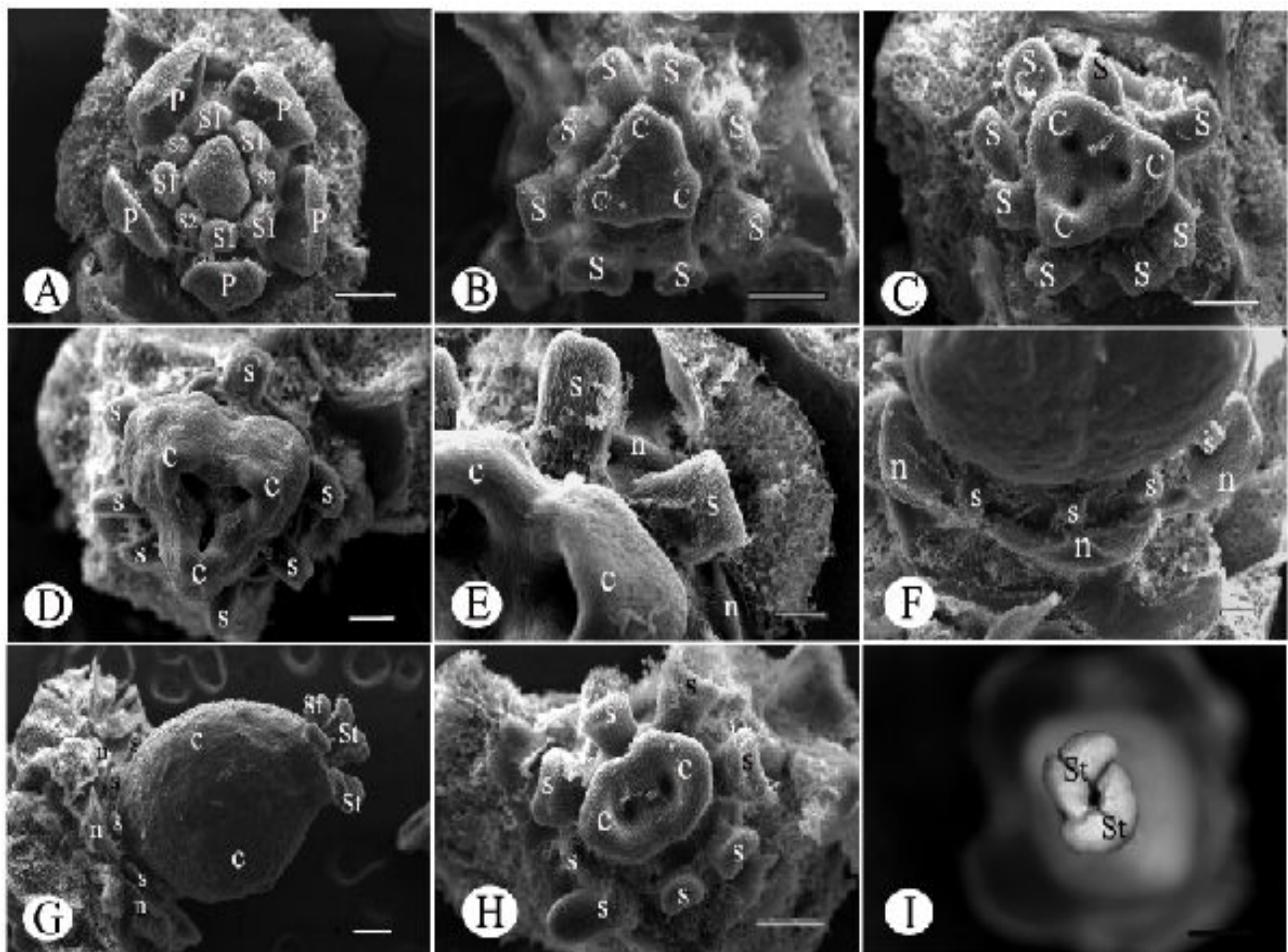


Fig. 3. Late ontogeny of female flower in *J. multifida*. A, The center of the primordium becomes dome-shaped. B-C, Three carpel primordia become visible. D, Fused carpels. E, Carpels close up gradually and stamens stop developing. F, The ovary bulges and the stamens become smaller and degenerate. G, Syncarpous ovary and bifid stigma; five nectaries are positioned alternate to outer stamens. H, Two carpel primordia are initiated. I, Two stigmas and locules. C, carpel; n, nectary; S, stamen; St, stigma. Scale bars=200 $\mu$ m G and I, 100 $\mu$ m A-D, F, H, 50 $\mu$ m E.

Stamen initiation in *J. multifida* is different from the other four species in this comparison; its outer whorl of stamens initiate first and the inner whorl of stamens initiate subsequently (centripetal order). In our previous study (Liu *et al.*, 2008), we had thought that stamen initiation in *J. curcas* was non-simultaneous based on the different sizes of the stamens; however, reinvestigation shows that stamen initiation is simultaneous. In *J. integerrima*, *J. curcas*, *J. podagrica* and *J. gossypifolia*, all stamens, arranged in two whorls, initiate simultaneously (summarized in Table 1). The condition in *J. tanjorensis* and *J. glandulifera* remains unknown, though parsimony analysis suggests that it is non-simultaneous. The non-simultaneous condition also occurs in *Croton fuscescens* (De-Paula *et al.*, 2011) and many species in *Euphorbia* (Prenner & Rudall, 2007), *Ricinus*, and several other genera in Euphorbiaceae (Prenner *et al.*, 2008) having numerous stamens. The direction of stamen initiation has systematic and phylogenetic value (Corner, 1946; Wu *et al.*, 2003). Dehgan & Webster (1979) placed *J. multifida*, *J. podagrica*, *J. gossypifolia* and *J. integerrima* in subgenus *Jatropha*, and *J. curcas* in subgenus *Curcas* Pax., according to morphological characters (summarized in Table 1). Pamidiyarri *et al.* (2009a) clustered *J. multifida* with *J. podagrica* based on RAPD and AFLP marker analysis;

these species belong to section *Peltatae* in the system of Dehgan & Webster (1979). However, *J. podagrica* was clustered with *J. curcas* based on nuclear ribosomal DNA ITS sequence analysis (Pamidiyarri *et al.*, 2009b). Stamen initiation supports the classification of Pamidiyarri *et al.* (2009b).

Obdiplostemony is a derived character in the evolution of angiosperms (Takhtajan, 1991), which has been recorded in the orders Cucurbitales, Celastrales, Oxalidales and Zygophyllales (Matthews & Endress, 2002 2004 2005; Sheahan, 2007). Several interpretations have been put forward to explain the formation of obdiplostemony, such as reduction theory, intercalation theory, dedoublement theory and displacement theory (Eckert, 1966; Ronse Decraene & Smets, 1995). Venkata & Ramalakshmi (1968) explained the occurrence of obdiplostemony in Euphorbiaceae by spatial shifts caused by the presence of large antesealous nectaries. The data we present here on *J. multifida* and *J. integerrima* and the data from other species in *Jatropha* (Liu *et al.*, 2008) does not support any interpretation of obdiplostemony put forward so far. The absence of carpels in male flowers may explain why stamens shift to the center of the flower, but does not clarify why the antepetalous stamens are simultaneously or non-simultaneously formed.

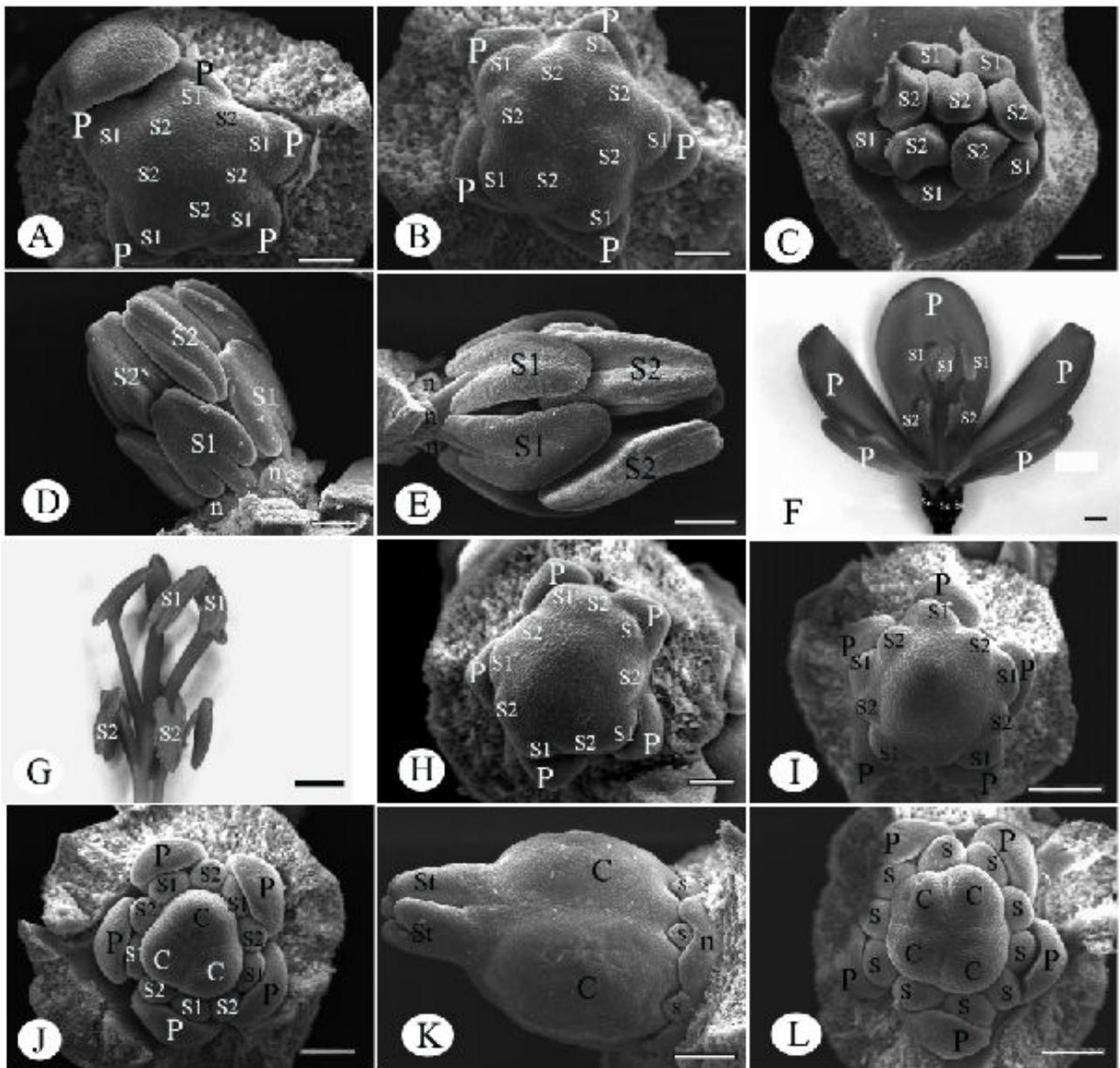


Fig. 4. Ontogeny of male (A-G) and female (H-L) flowers in *J. integerrima* Jacq. A, Ten stamen primordia arranged in two whorls are initiated simultaneously. B, Five outer stamens are positioned in an antipetalous position and five inner stamens positioned in an antisepalous position. C, Each young stamen is two-lobed. D, Each mature anther has four microsporangia. Five outer anthers arch inward and five inner anthers arch outward. E, The outer whorl of anthers become introrse. F, The mature female flower. G, The outer whorl of anthers bow down. H, Ten stamen primordia arranged in two whorls initiate simultaneously. I, Five outer stamens are in an antipetalous position and five inner stamens are in an antisepalous position. J, Three carpel primordia become visible. K, Syncarpous ovary and bifid stigma. L, Four carpel primordia are initiated. C, carpel; n, nectary; P, petal; S, stamen; Se, sepal; St, stigma. Scale bars=500µm E-G, 200µm D and K, 100µm C, I, J, L, 50µm A, B, H.

The pattern of anther arrangement has certain significance in plant evolution (Chen, 1996). The most common pattern is characterized by anthers that all arch inward or outward (Chen, 1996). The mature anthers in *J. multifida* all arch outward, which is similar to what is observed in *J. curcas* and *J. podagrica* (Liu *et al.*, 2008). In *J. integerrima*, the outer whorl of anthers arch inward and the inner whorl of anthers arch outward during development, which is similar to what is observed in *J. gossypifolia* (Liu *et al.*, 2008). However, the outer whorl of anthers in *J. integerrima* bows down when mature (summarized in Table 1). Thus, the pattern of anther arrangement in *J. integerrima* and *J. gossypifolia* is

significantly different. However, we suggest that the pattern of anther arrangement in other *Jatropha* species needs further study because this pattern can change during development. Patterns of anther arrangement are diverse in *Jatropha*. Both whorls of anthers arch inward in *Jatropha lobata* (Prenner *et al.*, 2008). In other genera of Euphorbiaceae, the pattern of anther arrangement is variable: all anthers arch inward in *Astraea lobata* (De-Paula *et al.*, 2011) and *Croton laui* (personal research), but all arch outward in *Ricinus communis* (personal research). More species should be studied to better understand the significance of anther arrangement pattern in this large family.

**Table 1. Comparison of androecium characters between seven species of *Jatropha* (classification is based on Dehgan and Webster 1979).**

Subgenus	Section	Species	Stamen initiation	Anther arrangement pattern
Jatropha	<i>Jatropha</i>	<i>J. gossypifolia</i>	simultaneously	Outer whorl arch inward, inner whorl arch outward
		<i>J. tanjorensis</i>	unknown	Unknown
		<i>J. glandulifera</i>	unknown	Unknown
	Peltate	<i>J. podagrica</i>	simultaneously	Arch outward
		<i>J. multifida</i>	non-simultaneously	Arch outward
	Polymorphae	<i>J. integerrima</i>	simultaneously	Outer whorl arch inward but bow down inner whorl arch outward
Curcas	<i>Curcas</i>	<i>J. curcas</i>	simultaneously	arch outward

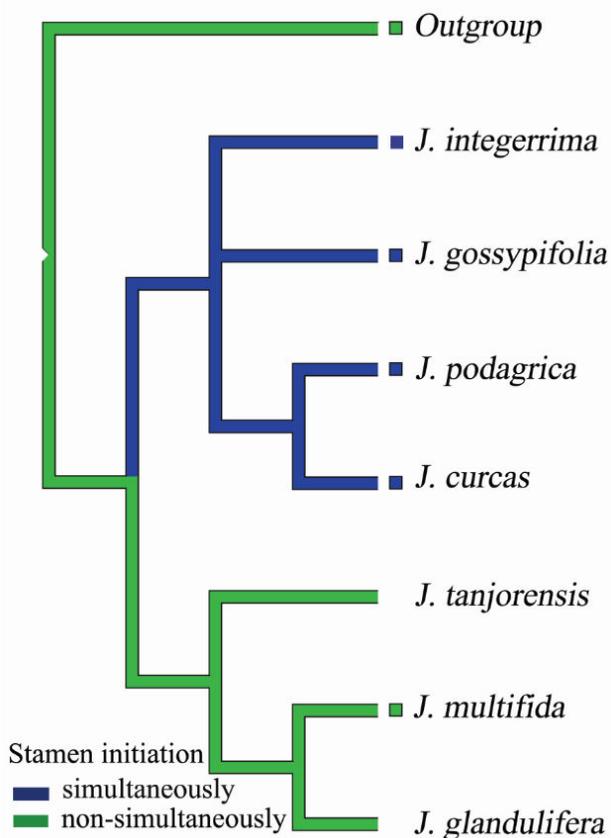


Fig. 5. Phylogeny of *Jatropha* from Pamidiyarri *et al.* (2009b) with stamen initiation mapped and the ancestral states reconstructed with MacClade 4.06. A box (green or blue) following a taxon name reports the state of stamen initiation in the taxon. The absence of a box means data is missing for this taxon.

Floral homologies in Euphorbiaceae are notoriously controversial (Webster, 1994; Prenner & Rudall, 2007; Prenner *et al.*, 2008; De-Paula *et al.*, 2011). In the cyathium of *Euphorbia* and its allies, each flower is widely interpreted as a single stalked stamen or a single naked stalked pistil, whereas some Euphorbiaceae possess perfect flowers (e.g. *Jatropha*) (De-Paula *et al.*, 2011). An androecium of an indefinite number of stamens in many whorls was the primitive condition in Euphorbiaceae (Michaelis, 1924). In contrast, Venkato & Ramalakshmi (1968) suggested that the primitive condition is 10 stamens in two whorls, as in *Jatropha* (Webster, 1994). Dehgan & Schutzman (1994) justified the primitiveness

of *J. curcas* on morphological grounds. However, Webster (1994) thought that an androecium of a single whorl of five or six stamens is most likely to be ancestral within the family. Here we first describe the floral ontogeny in male and female flowers of *Jatropha* and discuss systematic implications. Floral ontogeny in more species of Euphorbiaceae should be studied to test their potential value for systematics and evolutionary analyses.

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