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# Floral vasculature and ontogeny in *Canna indica*

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The identity of the labellum is a hot point in Zingiberales, which has long been discussed by many authors. In this study, floral vasculature and ontogeny of *Canna indica* (Cannaceae) was observed by LM and SEM in order to ascertain the identity of the labellum and the functional stamen of this species and provide evidence for the homologies of the floral organs in Zingiberales. The results indicate that the labellum of *C. indica* have incorporated two androecial members from both outer and inner whorls, rather than three, one or half member, as previously suggested by morphologists of Cannaceae flowers. The two labellum traces are here interpreted as: one from the outer androecial whorl (diverging from the carpellary dorsal bundle), while the other from the inner androecial whorl (diverging from the parietal bundle). The functional stamen also incorporates two androecial bundles, the same as the labellum: one trace from the carpellary dorsal bundle, and the other (the petaloid appendage) from the parietal bundle. In addition, the origin of the vascular system in the androecium of Zingiberales and its systematic significance are discussed.

The eight families recognised within the order Zingiberales are traditionally divided into two groups based on stamen number: the monophyletic ginger families with one fertile stamen (Marantaceae, Cannaceae, Zingiberaceae, Costaceae) and the paraphyletic banana families with five (occasionally six) fertile stamens (Heliconiaceae, Strelitziaceae, Musaceae, Lowiaceae) (Tomlinson 1962, Kirchoff 1991, Kress 1990, Kress et al. 2001, Kirchoff et al. 2009). The main evolutionary line of Zingiberales follows a decreasing androecium number [(6)5→1→1/2] with a simultaneously increasing number of petaloid floral organ members.

*Canna*, the single genus within Cannaceae, has a neotropical distribution, with approximately 10 species native to the West Indian Islands and to the area between the southern USA and northern Argentina (Dahlgren et al. 1985, Mass Van de Kamer and Mass 2008). The flower of Cannaceae is asymmetrical (Fig. 1). The perianth has three sepals and three petals. The petals, androecium and style are fused into a floral tube, 1.5 cm long. The androecium is composed of two trimerous whorls. The inner whorl contains the functional stamen, which is reduced to one theca with a petaloid appendage, the labellum and inner staminode. There is only one (occasionally two) petaloid staminode(s) in the outer whorl. The ovary is inferior and tri-locular (Fig. 2–3). Each locule contains two series of anatropous ovules per locule (Pai 1965, Kirchoff 1983b).

Several morphologists have claimed that the stamen of *Canna* belongs to the inner androecial whorl (Eichler 1875, Rao and Donde 1955, Pai 1963, Kirchoff 1983b). Costerus (1916, 1917) suggested that the anther and petaloid appendage are members of different whorls. The labellum is a common structure in Zingiberales, but its source is complicated. Thompson (1933) determined that the labellum of Cannaceae arose from a fusion of primordia numbers 8, 13 and 16, which are components of different whorls. Comparing the labellum in *Canna* with the hooded staminode (which encloses the style and stigma before pollination) of Marantaceae, Pai (1963) suggested that the former was of unitary constitution, but illustrated these descriptions with diagrams only. Kirchoff (1983b) reported work on floral organogenesis in *C. indica* and stated that the labellum is composed of an inner androecial member. The images of different phases that were provided in that study are insufficient, and most are unrecognisable because of the printing technology used. The views of stamen origin(s) and labellum of *C. indica* are therefore controversial. We pursued the present study to obtain a better understanding of the homologies of the floral organs.

## Material and methods

### Plant material

Young flowers and inflorescences of *Canna indica* were collected at the South China Botanical Garden, Chinese Academy of Sciences. Material was preserved in FAA (70% ethanol, 5% formalin, 5% acetic acid) for 48 h and transferred into 70% ethanol for preservation. Observations were

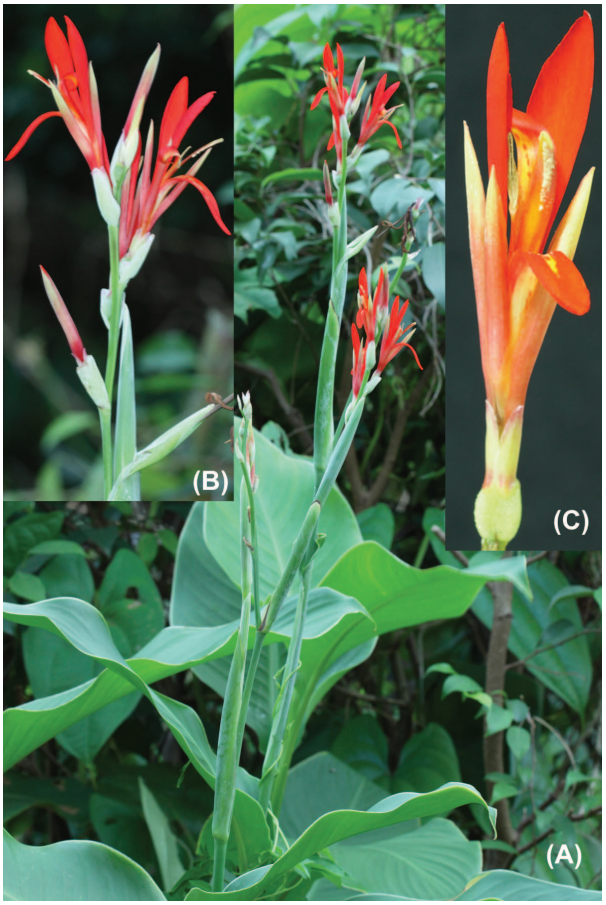


Figure 1. *Canna indica*. (A) habit, (B) inflorescence, (C) flower.

made either in the field or in the lab on material fixed in formalin–acetic acid–alcohol.

### Light microscopy

For paraffin sectioning, flowers of different stages were dehydrated for successive 30 min periods in 80%, 90%,


Figure 2. Dissected mature flower of *Canna indica*. C = calyx, P = petal, S = staminode, L = labellum, FS = functional stamen, G = gynaecium.

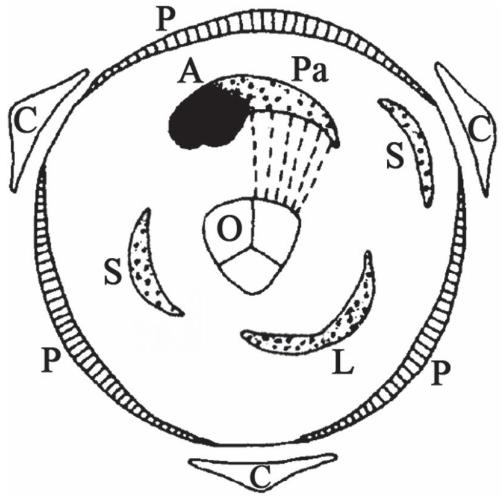


Figure 3. Floral diagram of *Canna indica*. C = calyx, P = petal, A = anther, Pa = petaloid appendage, S = staminode, L = labellum, O = tri-locular inferior ovary. Adapted from Kress 1990.

100%, and 100% ethanol and were then embedded in paraffin. Both transverse and longitudinal serial sections (7–10 µm) were cut using a microtome and mounted on slides. These sections were stained with Safranine T (50% ethanol) and fast green (95% ethanol). Photomicrographs were taken using a Zeiss Axiophoto microscope equipped with a 5-megapixel QImaging digital camera.

### Scanning electron microscopy

Floral buds were dissected in 70% ethanol and then dehydrated using an ethanol series to absolute ethanol. The material was then critical-point-dried using a JFD-310 lyophilization apparatus, mounted onto scanning electron microscope (SEM) stubs using double-sided adhesive tape and coated with platinum using a JFC-1600 coater. The dried material was examined using a SEM JSM-6360 cold field emission at 20 kV.

## Results

### Floral vasculature

The pedicel is sub-rotund in transverse section and consists of epidermis, cortex and vascular tissue. The vascular tissue region contains an outer ring of 16–19 large bundles and a central region with 10–15 bundles (Plate 1). In the sub-locular region, the bundles of the inner ring converge into 8–10 large bundles (Plate 2). The remaining bundles of the inner ring converge into the ovary axis and become the placental bundles in the locular region. The ovary of *Canna indica* has axile placentation with three locules. In the locular region, the three carpellary dorsal bundles and the three parietal bundles are distinct from the other bundles in location and size. The carpellary dorsal bundle is located in the median of each carpel. The three parietal bundles are notably large and stand opposite the septa in the ovary wall. Among the three bundles, the adaxial parietal bundle (a2) is the largest

while the lateral (a3) is the smallest (Plate 3). The placental bundles are arranged in three groups with two traces each in the ovary locule and bear small branches to the ovules (Plate 4).

The three carpellary dorsal and three parietal bundles undergo a progressive change upwards through the flower. The abaxial parietal bundle (a1) divides into four discrete strands (Plate 9, 10). The daughter strands of the a1 bundle gradually spread further apart (Plate 11–14). Of these four strands, the outer branch becomes the midrib of the abaxial petal, and the two side strands of the inner three strands also enter the petal, becoming the lateral strands (Plate 15–18). The middle strand of the inner three strands further divides into two strands, which enter the labellum (Plate 15–22). The adaxial parietal bundle (a2) divides into three traces (Plate 14). The outer branch develops into the midrib of the adaxial petal, and the other two branches first divide into four and then into six strands. The outer two strands enter the adaxial petal as its lateral strands, and the remaining parts travel upwards to the petaloid portion of the functional stamen (Plate 15–22). The lateral parietal bundle (a3) divides into two traces (Plate 17). The outer branch becomes the midrib of the lateral petal, and the inner branch enters the inner-whorl staminode (Plate 18–24).

The abaxial carpellary dorsal bundle (d1) divides into three strands (Plate 11). The inner branch enters the style (Plate 12–13), and the branch near a1 gradually moves into the abaxial petal and becomes its lateral strand (Plate 14–15). Slightly higher, the third branch divides into two traces (Plate 16–17). The outer trace enters the abaxial outer-whorl staminode and disappears rapidly at the floral base (Plate 18–20). The inner trace becomes the lateral strand of the labellum (Plate 17–24). The adaxial carpellary dorsal

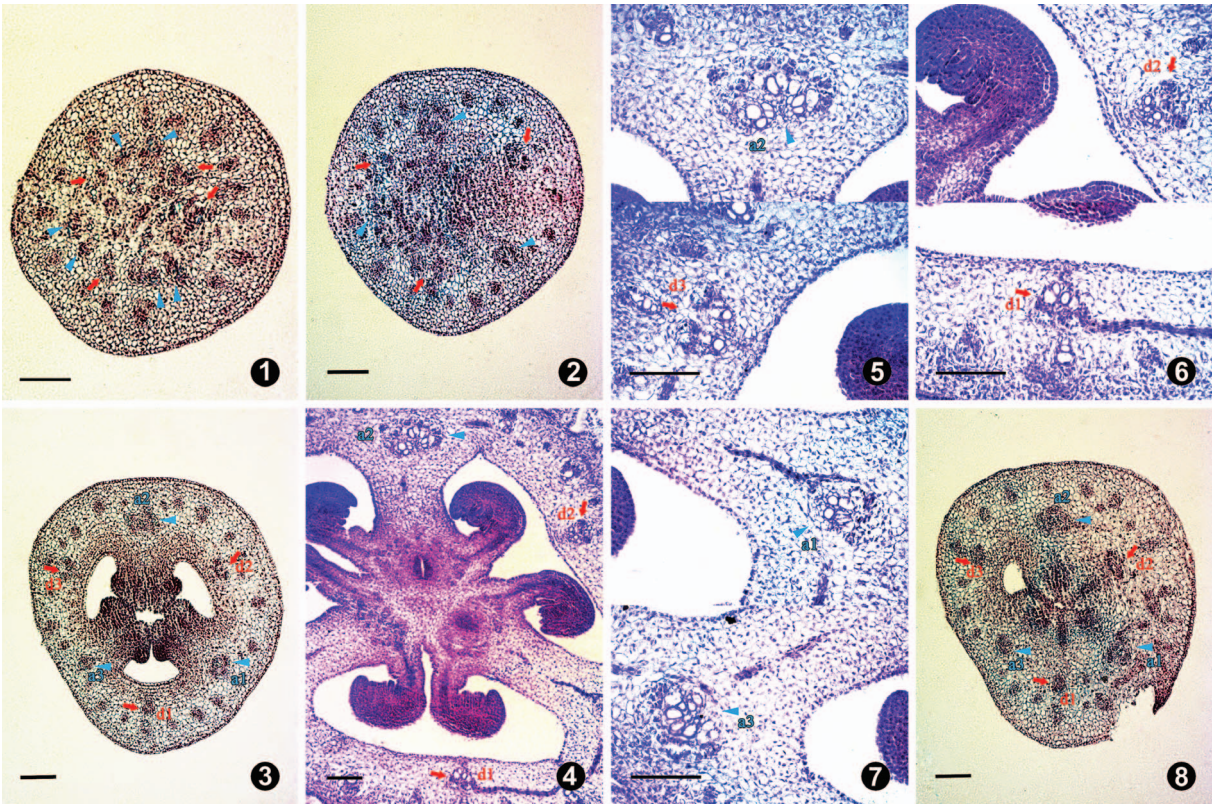


Plate 1–24. Floral vasculature in *Canna indica*. The adaxial side is upward. All plates are in transverse section. Arrow (↑), carpellary dorsal bundle; arrow head (△), parietal bundle. (1) the pedicel showing an outer ring and a central region of vascular bundles, (2) the sub-locular region, with the bundles of the inner ring, converges into 8–10 large bundles, (3) the locular region, showing the ovuliferous zone, parietal bundle (a1, a2, a3), and carpellary dorsal bundle (d1, d2, d3), (4) the placental bundles are arranged in three groups with two traces each in the ovary locule and bear small branches to the ovules, (5)–(7) enlargement of plate (4), showing the adaxial parietal bundle a2 (5); the abaxial carpellary dorsal bundle d1 (6); the adaxial carpellary dorsal bundle d2 (7), (8) the top of the locular region, showing parietal bundles and locules, (9)–(10) the abaxial parietal bundle a1 divides into three strands, (11) the abaxial carpellary dorsal bundle d1 divides into three strands, (12)–(13) the inner branch of the abaxial parietal bundle d1 enters the style, (14) the daughter strands of a1 spread further apart, (15) the adaxial parietal bundle a2 divides into three traces, (16) the outer branch of a2 developes into the midrib of the adaxial petal, (17) the branch of d1 near a1, which gradually moves into the abaxial petal and becomes its lateral strand, (18) a3 divides into two traces, (19) the inner branch of d2 enters the style, and the outer branch becomes the midrib of the lateral outer whorl staminode, (20) the outer branch of the two traces of the third branch of d1 enters the abaxial outer whorl staminode, (21) d3 divides into two bundles, (22) the inner branch of d3 moves close to one bundle of a2, (22)–(23) the outer branch of d3 enters the adaxial outer whorl staminode, (24) the style departs from the petaloid appendage of the functional stamen (FS), and the inner branch of d3 enters the anther of the FS. Abbreviations: labellum (L), style (Sty), inner staminode (IS), adaxial outer whorl staminode (S2), lateral outer whorl staminode (S3). Scale bars = 100 μm.

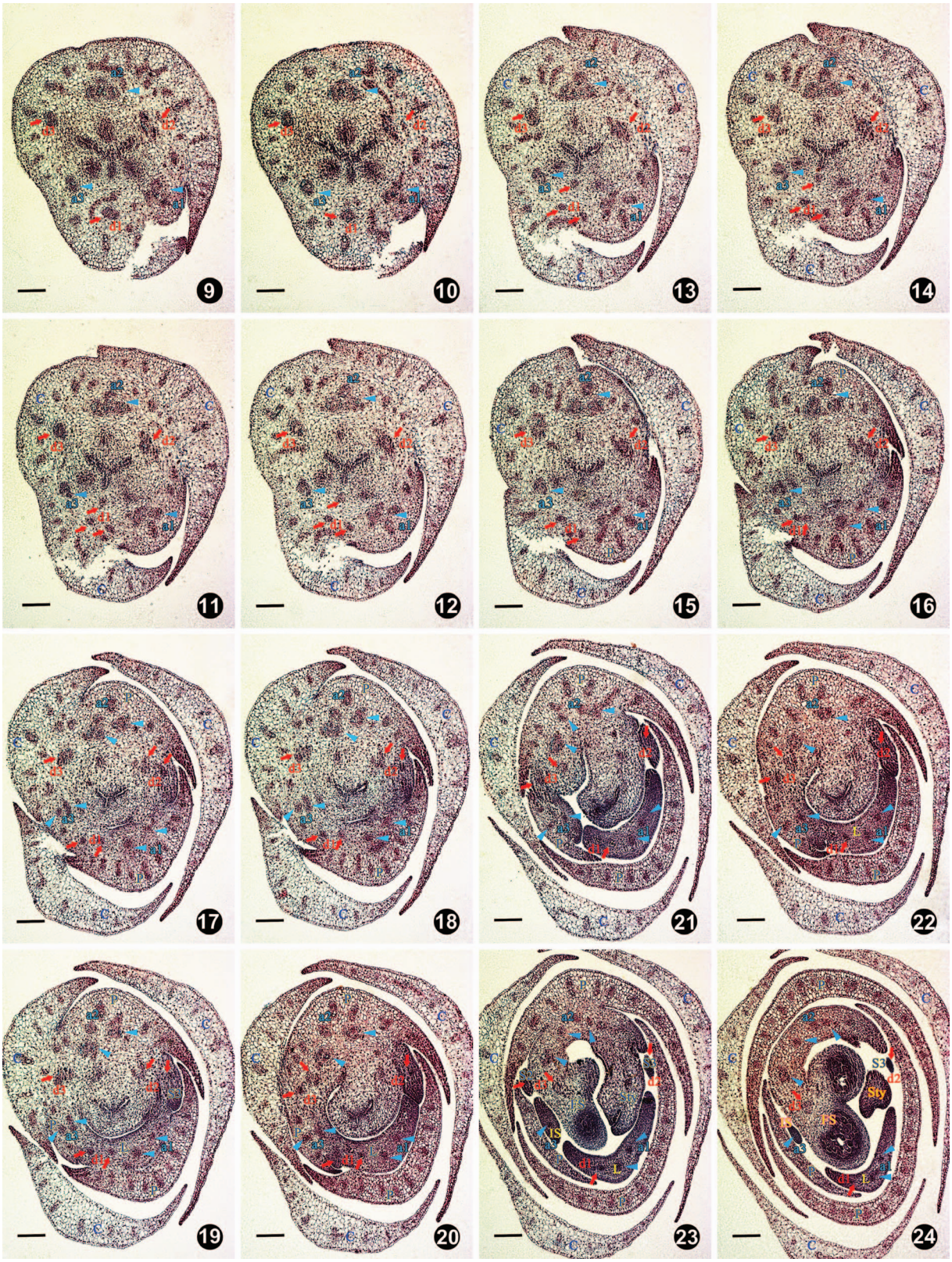


Plate 1–24. (Continued).

bundle (d2) divides into two bundles, and the inner branch enters the style (Plate 16–20). The outer branch becomes the midrib of the lateral outer-whorl staminode (Plate 16–24). The adaxial carpellary dorsal bundle (d3) divides into two strands; the outer branch is smaller than the inner branch (Plate 20). The outer branch enters the adaxial outer-whorl staminode, and the inner branch moves into the anther of the functional stamen (Plate 21–24).

### Floral ontogeny

A protuberance on the side of the inflorescence primordium produces a bract. Each bract on the inflorescence axis produces a laterally elongated primordium in its axil, which gives rise to a pair of flowers. The larger of these flowers is produced directly from this primordium, while the smaller arises in the axil of a bractlet produced on the side of the primordium (Fig. 4A–B).

Early floral development proceeds from a truncate floral apex. Three calyx primordia are initiated sequentially at the three sides of the floral apex. The lateral calyx appears first, followed by the abaxial calyx and the adaxial calyx (Fig. 4D–E).

The petals and androecial members arise from a ring primordium. The ring primordium develops by intercalary growth, producing a slight depression (floral cup). Three common primordia are initiated on the ring primordium. The adaxial common primordium is initiated first (Fig. 4C). The common primordium widens and separates into the stamen and petal because of the formation of two growth centres. The stamen primordium is first apparent in the region that will produce the anther and is obvious again in the region of the petaloid appendage. A double-stamen primordium emerges in this manner. One primordium gives rise to the petaloid appendage while the other produces the anther (Fig. 4D–E). The abaxial primordium is initiated next. Cell divisions of the common primordium give rise to two growth centers that produce the labellum on the interior edge and the petal on the outer edge (Fig. 4E–F). Subsequently, the lateral common primordium divides into two primordia that will form the lateral petal and the inner staminode (Fig. 4F). The inner staminode was smaller than the petal when it initiated and longer than the petal until blooming (Fig. 4F–L, 5A).

Outer androecial members are subsequently initiated on the remaining areas of the common primordium that are not occupied by the inner androecial members. The order of formation of the outer androecial whorl is abaxial outer staminode, adaxial outer staminode and lateral outer staminode. The lateral outer staminode can develop into a mature organ. The other two outer staminodes are initiated and usually aborted during early development (Fig. 5D, G). In a small number of flowers, the primordium of the abaxial staminode grows very slowly or stops growing after initiation and then disappears (Fig. 5E, H). Occasionally, both the adaxial and abaxial staminodes can develop into mature floral organs (Fig. 5F, I).

The three gynoecial primordia come into lateral contact to form the style and stigma (Fig. 4M–N). The fusion between primordia is incomplete, allowing flow of nectar from the gynopleural nectarines to the base of the style. The fusion of the lateral conduplication is not complete, forming the stylar canal that connects the stigma to the locules (Fig. 4O). The style is entirely adnate to the petaloid appendage of the functional stamen upon initiation (Fig. 5B). The upper portion of the adnation gradually departs when mature floral organs have developed. The style is adnate to the petaloid appendage for approximately one third of the style length in the florescence (Fig. 5C).

## Discussion

The observations presented here on floral vasculature and ontogeny in *Canna indica* indicate that the labellum and functional stamen incorporate elements of two androecial members each, rather than three, one or half, as suggested by previous studies of Cannaceae (Thompson 1933, Pai 1963, Kirchoff 1983b, Almeida 2013).

In Musaceae (Tilak and Pai 1974), Heliconiaceae (Kirchoff 1992), and Marantaceae (Tilak and Pai 1966, 1968, 1970), the vasculature of the outer androecial whorl derives from the carpellary dorsal bundles and that of the inner whorl from the parietal bundles. In Lowiaceae (Liao et al. 1998) and Strelitziaceae (Tang et al. 2000), the outer whorl derives its vascular supply from the accompanying dorsal bundles and the inner whorl from the parietal bundles. In Cannaceae (Rao and Donde 1955, Pai 1963), the vasculature of the outer androecial whorl derives from the carpellary dorsal bundles or accepts the carpellary dorsal bundles and the parietal bundles simultaneously, and that of the inner whorl derives from the parietal bundles or accepts the parietal bundles and the carpellary dorsal bundles simultaneously. The carpellary dorsal bundles of Zingiberaceae enter the sepals, while those of the Costaceae enter the style (Rao et al. 1954). The vasculature of the inner androecial whorl derives from a vascular complex in Zingiberaceae and Costaceae. The vascular complex derives from parietal bundles in *Curcuma inodora* and *Costus speciosus* (Rao et al. 1954) and from parietal bundles and other vascular bundles in *Alpinia vittata*, *Hedychium coronarium* (Rao et al. 1954, Lin et al. 2007), *Hedychium forrestii* (Zhang et al. 2009) and *Globba racemosa* (Guan et al. 2008) in Zingiberaceae. The inner androecial whorl clearly derives its vascular supply from parietal bundles and the outer whorl from carpellary dorsal bundles in Lowiaceae, Strelitziaceae, Musaceae, Heliconiaceae and Marantaceae. Based on these results, we conclude that the outer androecial whorl derives its vascular supply from the carpellary dorsal bundles and the inner whorl from the parietal bundles in Zingiberales (Liao et al. 1998, 2001, 2005, Tang et al. 2000, 2002, Xie 2002).

Our observations on floral vasculature in *Canna indica* indicate that the labellum incorporates one trace from the carpellary dorsal bundle (constituting one member of the outer androecial whorl) and one trace from the parietal bundle (constituting one member of the inner androecial whorl) (Plate 16–20). The functional stamen also incorporates elements of two androecial members: one trace from the carpellary dorsal bundle (one member of the outer whorl), and the petaloid appendage receives one trace from the parietal bundle (one member of the inner androecial whorl) (Plate 18–24). Costerus (1916, 1917) suggested that the anther and petaloid appendage are associated with different whorls; the anther is a component of the outer whorl, while the petaloid appendage belongs to the inner whorl. Our observations agree with those of Costerus. The functional stamen might have evolved from the adnation of half of the anther of the adaxial outer whorl stamen and half of the filament of the adaxial inner whorl stamen.

Pai (1963) found that the filament of *C. indica* is a flat petaloid structure and that the anther is located on its

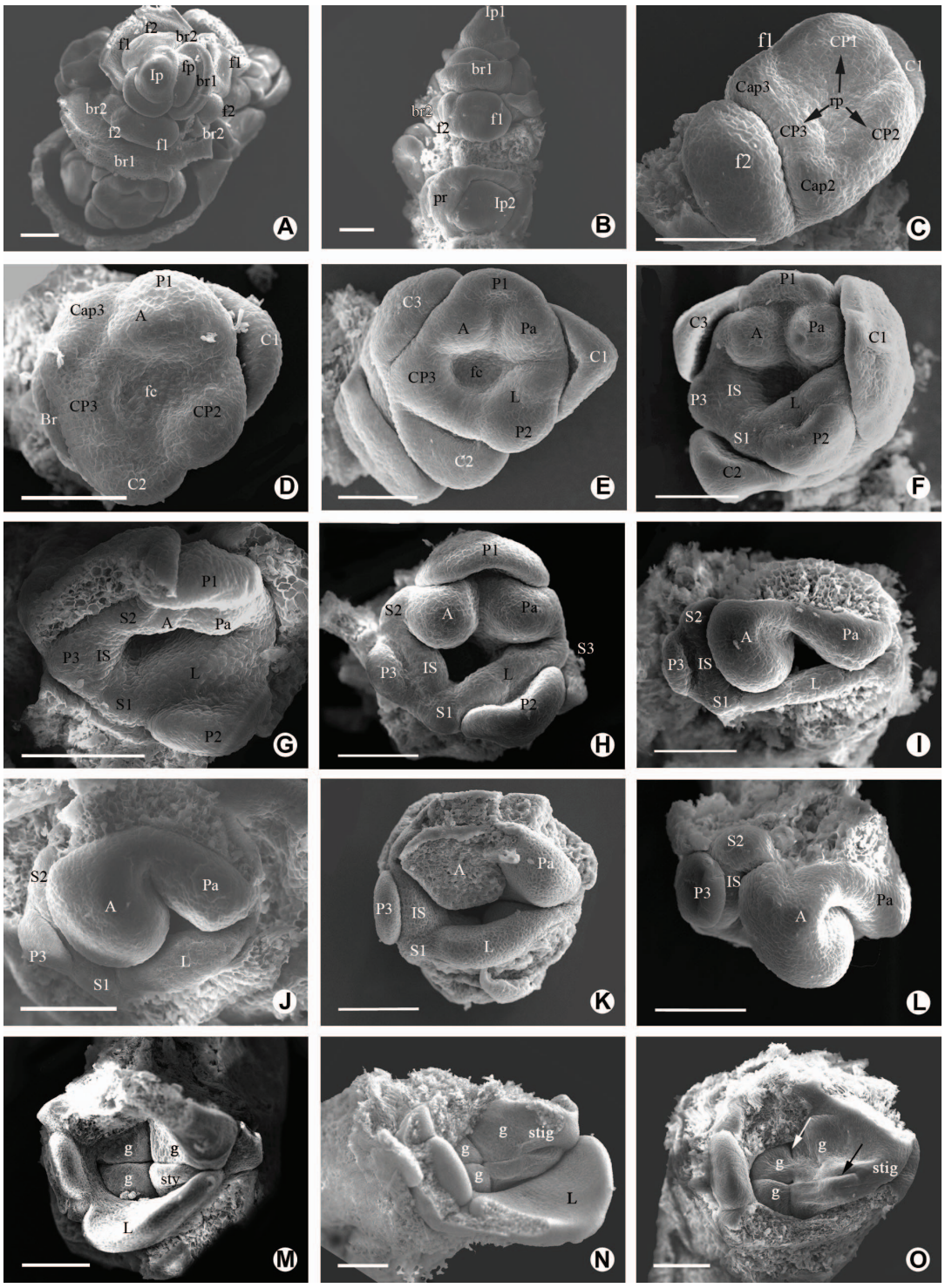


Figure 4. Floral development in *Canna indica.* (A) the sequential formation of flower primordia (fp) and a pair of flowers (f1, f2); inflorescence primordium (Ip), (B) the formation of the inflorescence primordium (Ip2) at the base of the inflorescene; prophyll (pr), (C) the formation of the first calyx (C1) and ring primordium (rp), initiation of the second and third calyx primordia (cap2, cap3), and initiation of the common primordia (cp1, cp2, cp3), (D) the formation of the floral cup (fc) and second calyx (C2) and the initiation of the adaxial petal (P1) and anther (A), (E) formation of the third calyx (C3), the adaxial petal (p1), anther and petaloid appendage and the initiation of the abaxial petal (p2) and labellum, (F) formation of the abaxial petal (p2) and labellum and the initiation of the abaxial outer-whorl staminode (S1), lateral petal (p3) and inner staminode (IS), (G) initiation of the adaxial outer-whorl staminode (S2); the three calyxes have been removed, (H) initiation of the lateral outer-whorl staminode (S3) and the formation of P3 and IS, (I)-(K) the development of anther and petaloid appendage, the anther of (K) has been removed, (L) the lateral petal (P3) is larger than the inner staminode (IS), (M)-(N) the three gynoecial primordia (g) come into lateral contact to form the style (sty) and stigma (stig), (O) fusion between primordia is incomplete (white arrow), allowing flow of nectar from the gynopleural nectaries to the base of the style; fusion of the lateral conduplication is not complete (black arrow), forming the stylar canal that connects the stigma to the locules. Scale bars = 100 μm.

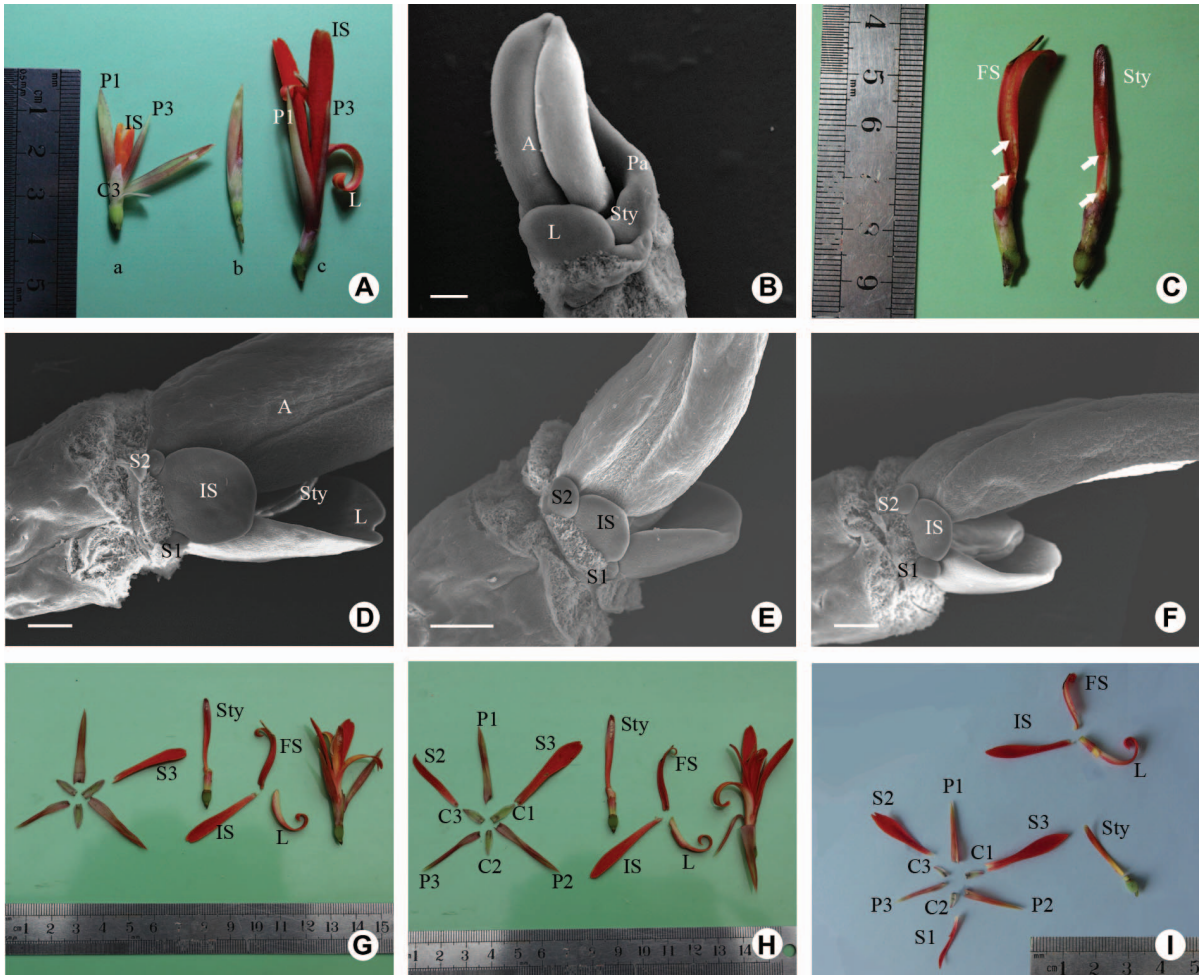


Figure 5. Later stages of floral development in *Canna indica.* (A) a = a dissected flower bud, showing that P3 is longer than the inner staminode (IS), b = flower bud; c = blooming flower, showing that P3 is shorter than IS; (B) the style adnating to the petaloid appendage (Pa); (C) arrows indicate the adnating regions of the style and the petaloid appendage (Pa); (D) the outer staminodes S1 and S2 are aborted; (E) the outer staminode S1 is aborted; (F) the outer staminodes S1 and S2 are normally developed; (G) the mature flower without outer staminodes S1 and S2; (H) the mature flower without outer staminode S1; (I) the mature flower with outer staminodes S1 and S2. Scale bars in (B), (D), (E), (F) = 100 μm.

margin, so he postulated that the reduction of half of the stamen resulted in the loss of half of the anther. However, Pai's hypothesis cannot explain why the adaxial outer whorl staminode disappeared in most of the flowers of *C. indica*. Kirchoff (1983b) concluded from developmental work that the stamen arising as a double primordium was a reflection of asymmetric development, with the anther and petaloid appendage belonging to the inner androecial whorl. Our observations of the floral ontogeny of *C. indica* indicate that the functional stamen initiates as a double primordium, which gradually merges into a structure (Fig. 4E–L); this process is known as the palingenetic process. The double primordium might be part of the adaxial outer whorl androecial member and the adaxial inner whorl member.

Almeida et al. (2013) claimed that the single fertile theca and its petaloid appendage in *C. indica* are derived from half of the primordium of a single stamen, with no contribution from the remaining portion of the stamen, which aborts early in development. Their observation does not agree with ours or with that of Kirchoff (1983b). From our observation, the anther is developing from one of the primordia of the functional stamen (Fig. 4H–L). Almeida et al. (2013) mistook the primordium of the lateral petal or the adaxial outer whorl staminode for the primordium of the anther.

The main pollinators of *Canna indica* belong to a single long-billed hummingbird species (Glinos and Cocucci 2011). The nectar source is located at the base of the style. The pollen is deposited on the abaxial side of the style. The adnation of the style and the petaloid appendage might prevent the pollinators from taking nectary from the adaxial side of the style (Fig. 5C). Kirchoff (1983a) suggested that the flowers of the Cannaceae appear to have evolved as functional units with respect to pollination. The success of pollination depends on the relative sizes of all the attractive parts of the flower, not on the relative sizes of the individual parts. The flower should thus be considered a unit. The number of functional stamens has decreased, but the petaloid filaments have made the flowers of Cannaceae more attractive. This structure may be a successful instance of plant co-evolution with its pollinators.

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## References

Almeida, A. M. R. et al. 2013. Tracking the development of the petaloid fertile stamen in *Canna indica*: insights into the orgin of androecial petaloidy in the Zingiberales. – AOB Plants, doi: 10.1093/aobpla/plt009.

Costerus, J. C. 1916. A fresh investigation into the structure of the flower of *Canna.* – Ann. Jard. Bot. Buitenzorg. Ser. 14: 165–184.

Costerus, J. C. 1917. Die Uebereninstimmung und der Unterschied in dem Bau der Blumen von *Canna* und derjenigen der Marantaceen. – Ann. Jard. Bot. Buitenzorg. Ser. 15: 59–93.

Dahlgren, R. M. T. et al. 1985. The families of the monocotyledons. Structure evolution and taxonomy. – Springer.

Eichler, A. W. 1875. Blüthendiagramme konstruiert und erlaütert. Vol. 1. – W. Engelmann.

Glinos, E. and Cocucci, A. A. 2011. Pollination biology of *Canna indica* (Cannaceae) with particular reference to the functional morphology of the style. – Plant Syst. Evol. 291: 49–58.

Guan, L.-L. et al. 2008. Flower vascular anatomy of *Globba racemosa*. – Acta Bot. Bor.-Occident. Sin. 128: 2385–2392.

Kirchoff, B. K. 1983a. Allometric growth of the flowers in five genera of the Marantaceae and in *Canna* (Cannaceae). – Bot. Gaz. 144: 110–118.

Kirchoff, B. K. 1983b. Floral organogenesis in five genera of the Marantaceae and in *Canna* (Cannaceae). – Am. J. Bot. 70: 508–523.

Kirchoff, B. K. 1991. Homeosis in the flowers of the Zingiberales. – Am. J. Bot. 78: 833–837.

Kirchoff, B. K. 1992. Ovary structure and anatomy in the Heliconiaceae and Musaceae (Zingiberales). – Can. J. Bot. 70: 2490–2508.

Kirchoff, B. K. et al. 2009. Early floral development of *Heliconia latispatha* (Heliconiaceae), a key taxon for understanding the evolution of flower development in the Zingiberales. – Am. J. Bot. 96: 580–593.

Kress, W. J. 1990. The phylogeny and classification of the Zingiberales. – Ann. Miss. Bot. Gard. 77: 698–721.

Kress, W. J. et al. 2001. Unraveling the evolutionary rediation of the families of the Zingiberales using monphological and molecular evidence. – Syst. Biol. 51: 926–944.

Liao, J.-P. et al. 1998. Studies on vascular system anatomy of the flower of *Orchidantha chinensis* T. L. Wu. – J. Trop. Subtrop. Bot. 6: 275–282.

Liao, J.-P. et al. 2001. Studies on vascular system anatomy of the flower of *Musa coccinea* Andr. – Guihaia 21: 321–325.

Liao, J.-P. et al. 2005. Floral vasculature in *Alpinia hainanensis* in relation to the nature of the labellum in gingers. – Nord. J. Bot. 23: 1–9.

Lin, Z.-M. et al. 2007. Floral vasculature anatomy of *Hedychium coronarium* (Zingiberaceae). – J. Trop. Subtrop. Bot. 15: 23–39.

Maas, H. Van de Kamer and Maas, P. J. M. 2008. The Cannaceae of the world. – Blumea 53: 247–318.

Pai, R. M. 1963. The floral anatomy of *Canna indica* L. – Bull. Bot. Soc. Coll. Sci., Nagpur 4: 13–16, 49–53.

Pai, R. M. 1965. Morphology of the flower in the Cannaceae. – J. Biol. Sci. 8: 4–8.

Rao, V. S. and Donde, N. 1955. The floral anatomy of *Canna flaccida*. – J. Univ. Bombay 24: 1–10.

Rao, V. S. et al. 1954. The floral anatomy of some Scitamineae. Part I. – J. Ind. Bot. Soc. 33: 118–147.

Tang, Y.-J. et al. 2000. Vascular system anatomy of *Strelitzia nicolai* flower. – Bot. Yunnan. 22: 291–297.

Tang, Y.-J. et al. 2002. Studies on vascular system anatomy of the flower of *Alpinia henryi*. – J. Trop. Subtrop. Bot. 10: 27–32.

Thompson, J. M. 1933. Studies in advancing sterility-VI. The theory of Scitaminean flowering. – Hartly Bot. Lab. Publ. No. 11.

Tilak, V. D. and Pai, R. M. 1966. Studies in the floral morphology of the Marantaceae. – Can. J. Bot. 44: 1365–1371.

Tilak, V. D. and Pai, R. M. 1968. Studies in the floral morphology of the Marantaceae-II. Vascular anatomy of the flower in two species of the genus *Phrynium* Willd. – Proc. Ind. Acad. Sci. Sect. B 68: 240–249.

Tilak, V. D. and Pai, R. M. 1970. Studies in the floral morphology of the Marantaceae-III. Vascular anatomy of the flower in some species of the genus *Calathea*. – Marathwada Univ. J. Sci. 2: 31–41.

Tilak, V. D. and Pai, R. M. 1974. The floral anatomy of *Ensete superbum* (Roxb.) Cheesm. – Proc. Ind. Acad. Sci. Sect. 3, 80: 253–261.

Tomlinson, P. B. 1962. Phylogeny of the Scitamineae – morphological and anatomical considerations. – Evolution 16: 192–213.

Xie, Z.-Y. 2002. Floral organogenensis of *Alpinia oxyphylla* Miq., floral vascular system and seed anatomy of inger families and their sytematic significance. – MSc thesis, Chinese Acad. Sci., Guangzhou, China.

Zhang, Z.-G. et al. 2009. Vascular system anatomy of the flower of *Hedychium forrestii* (Zingiberaceae) and its systematic significance. – J. Trop. Subtrop. Bot. 17: 315–320.