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ORIGINAL ARTICLE

Inflorescence and flower development in the Hedychieae (Zingiberaceae): *Hedychium coccineum* Smith

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Abstract The inflorescence of *Hedychium coccineum* Smith is thyrse, and the primary bracts are initiated in a spiral phyllotactic pattern on the sides of the inflorescence dome. Cincinnus primordia are initiated on the flank of the inflorescence apex, in the axils of primary bracts. This primordium subsequently develops a bract and a floral primordium. Then, the floral primordium enlarges, flattens apically, and becomes rounded. Sepals are initiated sequentially from the rounded corner of the primordium ring sepal initiation, and the floral primordium continues to enlarge and produces a ring primordium. Later, this ring primordium separates three common primordia surrounding a central cavity. The adaxial common primordium is the first separation. This primordium produces the posterior petal and the fertile stamen. The remaining two common primordia separate and produce respectively a petal and a petaloid, the inner androecial member. As the flower enlarges, the cavity of the floral cup becomes a rounded–triangular apex; these apices are the sites of outer androecial primordium initiation. The abaxial outer androecial member slightly forms before the two adaxial members develop. But this primordium ceases growth soon after initiation, while the two posterior primordia continue growth to produce the lateral petaloid staminodes. During this stage, gynoecial initiates in the floral cup and continues to grow until extending beyond the labellum.

Keywords Floral initiation · Labellum · Lateral staminode · Petaloid anther

The Zingiberaceae are one of the eight families of the order Zingiberales in monocotyledons. This family is distributed in tropical and subtropical areas and has 53 genera and over 1,377 species. On the basis of vegetative and floral characteristics, the currently accepted classification of the Zingiberaceae (Petersen 1889; Schumann 1904; Holttum 1950; Burtt and Smith 1972; Smith 1981; Larsen et al. 1998) divides the family into four tribes (Hedychieae , Alpinieae, Zingibereae and Globbeae). Recent molecular data have been used to explore the phylogenetic relationships. On the basis of molecular data, a realignment of the genera of the Zingiberaceae into four subfamilies (Kress et al. 2002): the Siphonochiloideae (the genus Siphonochilus only), the Tamijioideae (the single genus Tamijia), the Alpinioideae (most of the former Alpinieae), and the Zingiberoideae (including the former tribes Hedychieae, Zingibereae, and Globbeae).The flowers of Zingiberaceae consists of five parts, including sepal, petal, lateral petaloid staminodes, labellum, fertile stamen, and gynoecium. But in these four tribes of Zingiberaceae, the floral structure is different from

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each other. For example, the ovary is unilocular in all members of the Globbeae but trilocular in the other three tribes with some exceptions (e.g., unilocular in *Tamijia* and partially unilocular in *Caulokaempfeira*, *Paracautleya*, *Scaphochlamys*, *Siphonochilus*, and *Riedelia*; Larsen et al. 1998; Sakai and Nagamasu 2000). The lateral staminodes are developed in Hedychieae, Globbeae, and Zingibereae and generally absent in the Alpinieae (but all five staminodes are absent in the *Rhynchanthus*). In *Siphonochilus* (Hedychieae) and *Zingiber* (Zingibereae), the lateral staminodes fuse to a central labellum, which is the same pattern with that in a then report in a small genus *Tamijia* (Alpinieae) in Borneo (Sakai and Nagamasu 2000).

The study on the flower development can provide important information for research on the relationship of each group (Tucker 1992; Endress 1994). The flowers of the Zingiberales have strongly modified androecia. Evolution of the androecial number in the Zingiberales is 6→5→1→1/2. With the reduced number of the androecial member, the number of petaloid organs is increase subsequently. The recognized phylogenetic analyses of the Zingiberales supported that only the ginger group is monophyletic, but the banana group is not. The banana group is polyphyletic. Musaceae is at the base of the phylogenetic tree. Lowiaceae and Strelitziaceae form a clade, paraphyletic to Heliconiaceae. According to the number of the androecial member, Zingiberales can be divided into two groups: one is the banana group, which has five (or six) androecial members and the ginger group that has only one (or 1/2) androecial member. The banana group involves four families, that is, Musaceae, Strelitziaceae, Lowiaceae, and Heliconiaceae; plants of the former three families possess five fertile stamen, and the sixth androecium was usually considered missing, but in Heliconiaceae, the sixth androecium developed to a staminode (Kress 1990). In the ginger group, which is a monophyletic group (Kress 1990), the Costaceae possess a fertile stamen with filamentary appendage, the rest five staminodial members united and developed to the labellum (Kirchoff 1988). The Cannaceae and Marantaceae possess only one fertile thecae (Kress 1990). The Cannaceae has three or four specialized staminodes (Kirchoff 1991). The outer androecial members of Marantaceae form one or two petaloid staminodes; the inner androecial members form a fertile stamen with one theca and two staminodes (Kirchoff 1983; Kunze 1984). However, there has been some controversy over the development of androecial members in Zingiberales, especially in Zingiberaceae.

This paper presents the structure and the development of the inflorescence and flowers of *Hedychium coccineum*. The objectives are (1) increases some information of the pattern of flower development in the Hedychieae by investigating flower development; (2) search for differences in the timing of developmental events during the organogenetic stages of flower development and gain an indication of developmental variability within the genus; (3) provide data on the flower development for a study of the evolution of developmental patterns in the Zingiberaceae.

Material and methods

Young inflorescence buds of *H. coccineum* were collected from plants growing in the greenhouses of the Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences (CAS). The voucher specimen is deposited in the Herbarium of Xishuangbanna Tropical Botanical Garden and CAS.

Scanning electron micrographs were prepared according to the method described by Green and Linstead (1990). Inflorescence and flower development status were shaped with a mould-cast procedure. Living material of different periods of inflorescence and flowers were dissected and bracts, sepals, etc, were removed. Mixture of silicon rubber base and catalyst in an equal proportion. Once the growing region was exposed, it was quickly covered with the mixture to make a mould and to minimize further drying. If tissue lost turgor, turgidity could be restored by keeping the holder and plant in a moist chamber for several hours. The mould was cured and taken from the apex, riveting it in silicon rubber pedestal. Equal amounts of epoxy cement, resin, and catalyst were mixed, and then were filled the mould. After 12 h, pull the epoxy cast out of the mould so as to restore the floral primordium. Specimen casts were sputter coated with gold and examined in a PHILIP XL30, then scanned by electron microscope (Green et al. 1991). The microscope was operated at 20 kV.

Result

Floral morphology

Hedychium coccineum Smith is a medium-sized plant with pseudostems of 1.5–2 m; leaves, sessile; ligule, 1.2–2.5 cm; leaf blade narrowly linear, glabrous, base subrounded, or attenuated. The bisexual flower has a bilateral symmetry. Spikes are cylindric, usually dense, glabrous, or sparsely villous; bracts oblong, leathery, sparsely pubescent, rarely glabrous, three-flowered, margin involute or rather flat, apex obtuse or acute, and flowers red. The calyx is sparsely pubescent especially at the three-toothed apex. The corolla tube is slightly longer than the calyx; lobes, reflexed and linear; lateral staminodes, lanceolate; the labellum orbicular, approximately

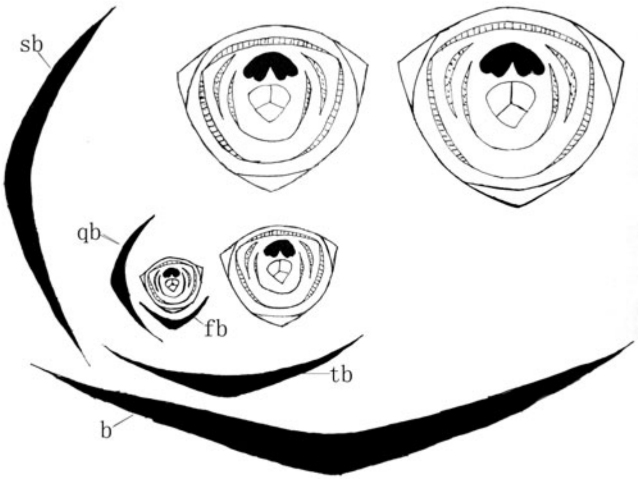

Fig. 1 Diagram of cincinnus and flower structure in *Hedychium coccineum*: *ax* axis, *b* primary bract, *sb* secondary bract, *tb* teriary bract, *qb* quartus bract, *fb* fifthly bract. *a* Apex, *B* bract, *b* primary bract, *ca* cininnus, *rb* removed primary bract, *sb* secondary bract, *tb* teriary bract

2 cm wide or rather small; and the apex, deeply two-cleft (Wu 2007; Fig. 1).

Inflorescence development

Spikes were terminal and developed spirally from bottom to top. At initiation, the inflorescence primordia are flat-domed (Fig. 2, 2). During vegetative growth, the first phyllary primordia like a crescent initiate in base of the dome. Then the other phyllary primordial initiate in a distichous pattern (Fig. 2, 3). Primary bracts of the inflorescence are initiated on the flanks of the apical dome in a spiral phyllotactic pattern (Fig. 2, 4). Soon after initiation, the bract primordia become crescent shaped and the concave side of the crescent opens upward. The inflorescence develops gyroidally from the bottom in *H. coccineum* Smith (Fig. 2, 5 and 6).

Cincinnus development

Cincinnus primordia are like ellipsoids and initiated on the flanks of inflorescence apexs in the axil of a primary bract (Fig. 2, 7 and 8). As the cincinnus ages, the young cincinnus widen to produce a transversely elongated primordium (Fig. 2, 9). Following initiation, the primordium becomes more pointed on one side. This point is the secondary bract; at the same time, the first floral primordium is initiated on the other side (Fig. 2, 10). At later stages, the secondary bract completely surrounds the cincinnus (Fig. 2, 11). In the axil of the secondary bract, the primordia continue the growth of the cincinnus, while the apex of the secondary axis produces a flower (Fig. 2, 12). Growth of the cincinnus follows the same pattern as described above. A new cincinnus apex originates in the axil of the secondary bract. This apex produces the tertiary bract and a flower. In the axil of the tertiary bract, a new cincinnus are initiated that produces the quaternary bract and a flower. The bract is always initiated away from the flower but in the same transverse plane (Fig. 2, 13).

Flower development

Flower development begins after the initiation of the secondary bract with the transformation of the cincinnus apex into a floral primordium (Fig. 2, 10). This primordium enlarges, begins to flatten, and assumes a rounded, obdeltoid appearance in polar view (Fig. 2, 11). As growth continues, the floral primordium becomes flatter and the corners of the deltoid become more distinct (Fig. 2, 12; Fig. 3, 14).

The obdeltoid corners of the floral primordium are the sites of sepal initiation (Fig. 2, 10). Sepals are initiated clockwise (Fig. 3, 16). Following initiation, the sepals extend their insertion sites around the periphery of the floral primordium until the margins of the adjacent sepals become confluent (Fig. 3, 15 and 16). From this stage, intercalary growth of the sepals produces the majority of the synsepalous calyx (Fig. 3, 16 and 17).

During sepal initiation, the whole flower primordium continues to enlarge. The periphery of the flower, interior to the sepals, produce a raised ring of tissue that surrounds a central depression (Fig. 3, 15 and 16). This ring primordium is composed of three common primordia united below into a cylinder of tissue surrounding a central cavity (Fig. 3, 15 and 16). The cylinder with its enclosed central cavity forms the floral cup, the site of gynoecial initiation (Fig. 3, 17 and 18).

The common primordia become increasingly distinct as the floral primordium enlarges. First of all, the adaxial common primordium separates from the ring primordium. Then, the two abaxial common primordia begin to separate (Fig. 3, 16). The adaxial common primordium is larger than the two abaxial common primordia (Fig. 3, 17). Each common primordium then produces a petal to the exterior and an inner androecial member to the interior (Fig. 3, 18). Separation of the three common primordia begins with the fertile stamen and its associated petal, and then the abaxial inner androecial members begin to separate (Fig. 3, 19). The adaxial inner androecial member develops into the fertile stamen. During the separation of the common primordia, the thecae of the stamen are visible (Fig. 3, 20; t). The two abaxial inner androecial members are sterile, and then form the petaloid staminodes that will constitute the labellum (Fig. 3, 25; ia).

During the enlargement and separation of the common primordia, the hollow space at the center of the floral cup enlarges and becomes a rounded–triangular apex (Fig. 3, 18 and 19). The three vertices of this triangle are

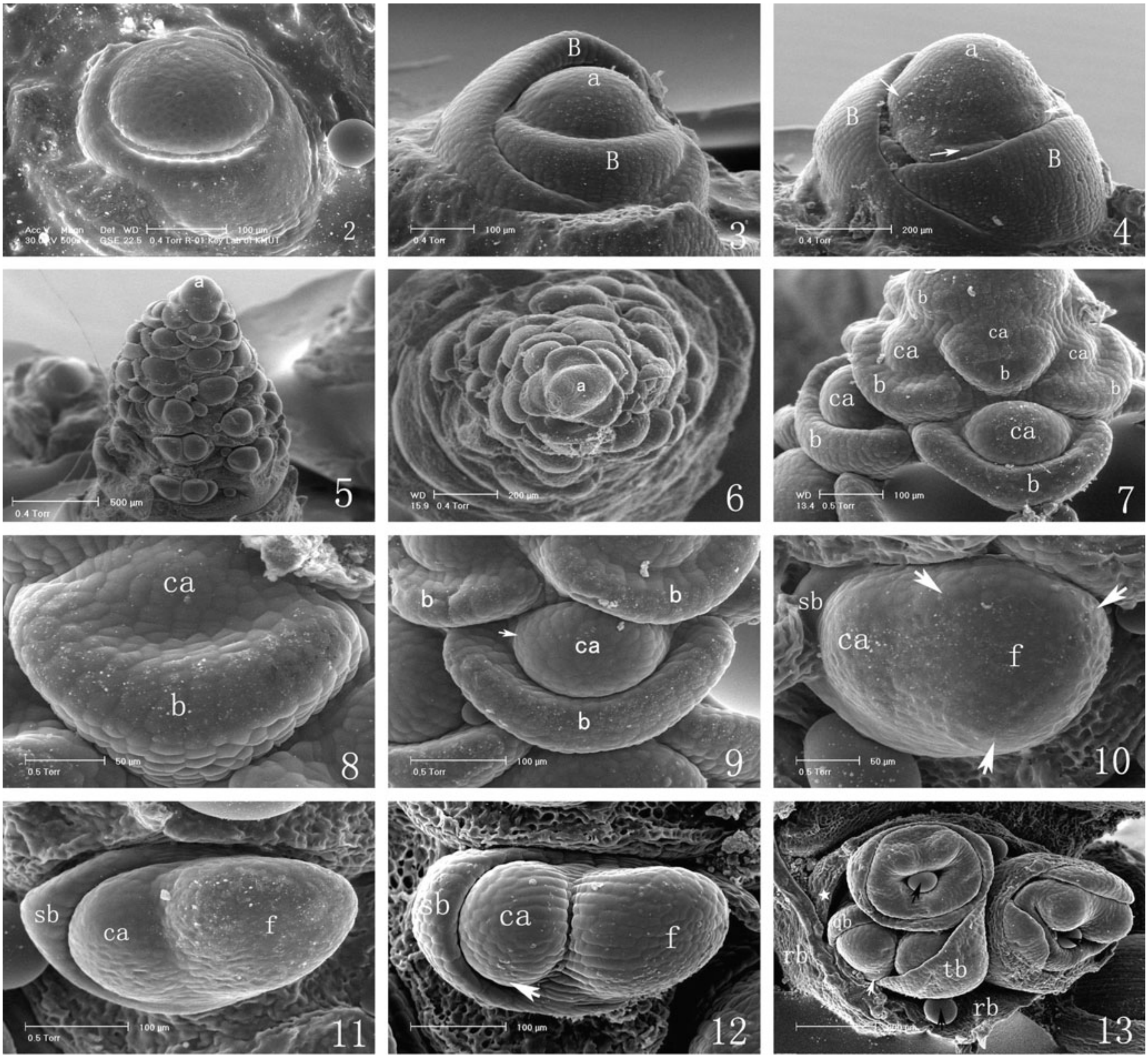

Fig. 2 SEM photomicrographs of inflorenscence development in *H. coccineum* Smith. *2* The transitional stage between vegetative and floral growth and initiation of inflorescence primordia. *3* Lateral view of young inflorescence bearing arranged bract. *4* Initiation of primary bract on the flanks of inflorescence; the *arrow* shows cincinnus primordia. *5* Lateral view of young inflorescence. *6* Polar view of inflorescence with helically arranged young cincinnus primordia and primary bracts. *7* Oblique view of inflorescence apex showing initiation of cincinnus primordia. *8* Farther growth of cincinnus primordia. *9* Cincinnus primordium initiating secondary bract (*arrow*). *10* Young cincinnus showing differentiation of flower and formation of the secondary bracts; the *arrow* shows sites of sepal initiation. *11* Further growth of floral primordium and secondary bract; the first floral primordium begins to flatten apically. *12* Cincinnus at the stage just preceding tertiary bract (*white arrow*) formation. *13* Lateral view of cincinnus. The *star* shows sites of removed secondary bract. The *white arrow* shows sites of fifth bract. The *black arrow* shows air bubble during the mould-cast procedure of the experiment. *cp* Common primordial, *f* flower, *fc* flower cup, *g* gynoecium; *ia* inner androecial member, *oa* outer androecial member, *p* petal, *st* stamen, *t* theca, *sp* sepal. The *black arrows* show the contaminations in the experiments

the sites of outer androecial initiation (Fig. 3, 20 and 21; oa). The abaxial outer androecial member ceases growth soon after initiation (Fig. 3, 20, asterisk), while the two adaxial members continue to grow lentamente and eventually produce the lateral, petaloid staminodes (Fig. 3, 24 and 25; oa).

The primordia of the style and stigma are initiated opposite the petals, below the insertion of androecium (Fig. 3, 21; stars). The adaxial primordium is slightly larger than the two adaxial primordia at an early stage of development, suggesting that the adaxial primordium is initiated first (Fig. 3, 21 and 22). Soon after, the primordia

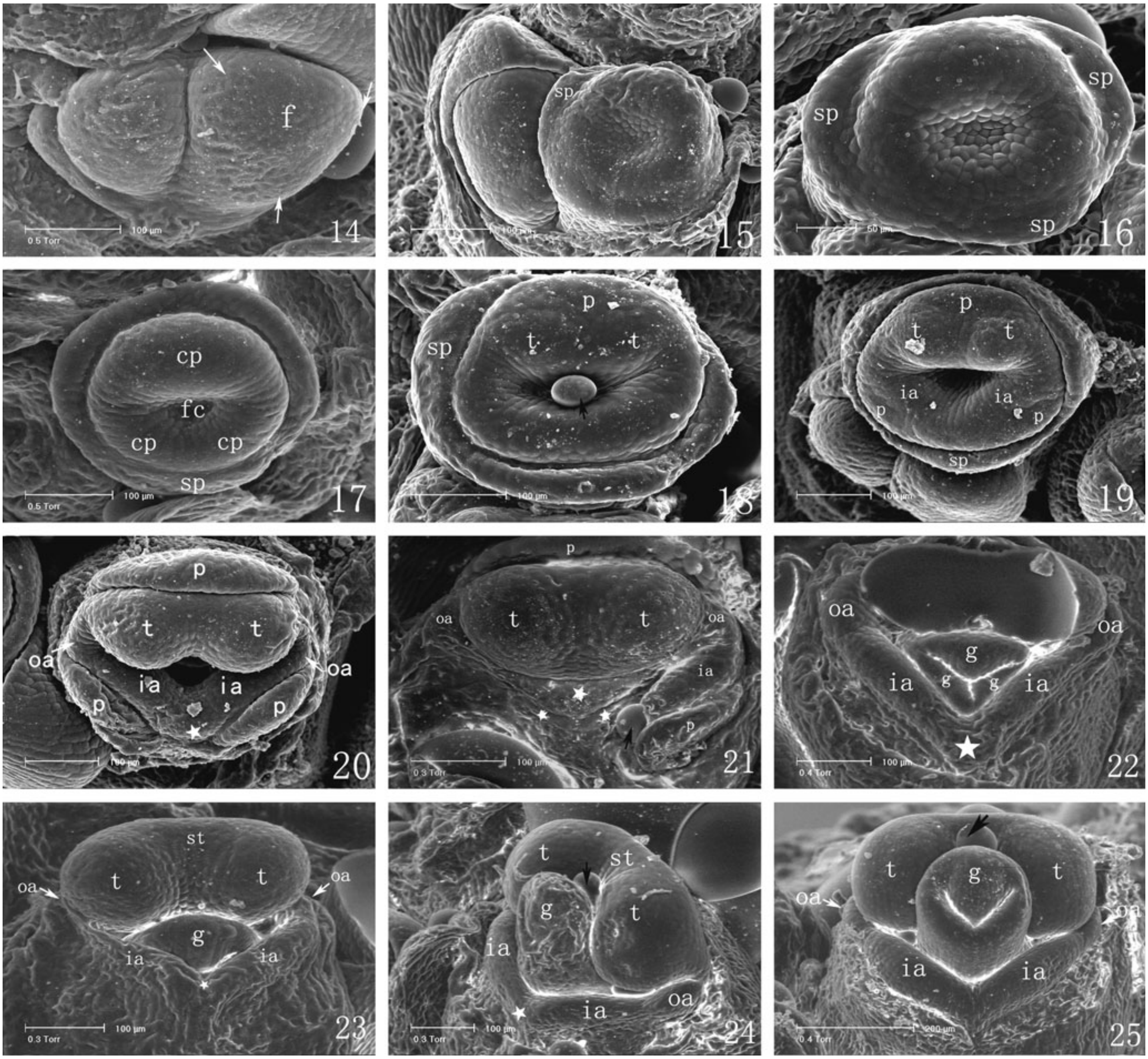

Fig. 3 SEM photomicrographs of flower development in *H. coccineum* Smith. *14* Initial stage of triangular floral primordium. The *white arrow* shows the position of the sepal initiation. *15* Sepal initiation and formation of the ring primordium. *16* Flower primordium showing the ring primordium, forming the floral cup centrally and the fusion of the sepals. *17* Common primordia surrounding the floral cup. *18* Separation of common primordia to form petal and fertile stamen. *19* Separation of anterior common primordium to form abaxial inner androecial members, this is the second flower of cincinnus. *20* Initiation of outer androecial members. The *white arrow* showing the position of outer androecial initiation and the *stars* showing that the outer androecial member disappeared during growth. *21* Formation of outer androecial members and initiation gynoecia. The *stars* show three carpellary primordial. *22–24* Farther development of gynoecia primordia and adaxial outer androecial members. The stars show that the outer androecial member disappeared during growth. *25* Farther growth of gynoecia, producing a cylindrical style

extents longitudinally and occupies the full depth of the floral cup (Fig. 3, 23; g).With continued growth of the gynoecial primordia, the three carpellary primordia grow upward and fuse along their lateral margins to produce a cylindrical style capped by a trilobed stigma primordium (Figs. 3, 24 and 25).

Discussion

Flower structure

The origin and evolution of six androecial members in the Zingiberaceae give rise to much controversy. Lestiboudois

(1829) first proposed the interpretation about the origin and evolution of six androecial members from a study of *H. coronarium*. But the interpretation of labellum that is currently accepted is that of Eichler (1884). They are slight modifications that Lestiboudois (1829) had presented. Based on this interpretation, two inner androecial members are united to form a labellum, the other one form a fertile stamen, two outer androecial members form the two petaloid lateral staminodes, and another one initiated between the two inner androecial members and then ceases growth and contribute only initiation of labellum. The interpretation of the labellum is supported by a developmental work (Schachner 1924; Kirchoff 1997, 1998). Costerus (1915) and Schumann (1904) also support this interpretation in part.

Schumann (1904) proposed that the bilobed labellum of the genera (e.g., *Hedychium, Kaempferia*) consists of two inner androecial members, and the lobeless labellum of the genera (e.g., *Alpinia*, *Amomum*) consists of one outer androecial member.

Costerus (1915) investigate the vascularization of the labellum in a number of genera (*Burbidgea, Curcuma, Amomum, Hornstedtia, Hedychium, Kaempferia,* and *Alpinia*). He concludes that the outer androecial members is represented by the medial vein of the labellum; then, the labellum was composed of two inner androecial members and one outer androecial member.

Tang et al. (2002) studied on the vascular system anatomy of the flower of *Alpinia henryi*. They recognized that the vascular bundles in the pedicel consist of outer ring and the central region (CR). At the locular region, the CR bundles are arranged as three carpellary dorsal bundles, three parietal bundles, and five to seven small placental bundles at the base of prolongation. Outer large branches of the three carpellary dorsal bundles finally enter the calyx. The adaxial parietal bundle splits up into four branches that run up into a functional stamen, while the two abaxial parietal bundles split up respectively into two to three branches going to the labellum. The bundles of the vascular plexus finally enter the petals, the labellum, and the style. So they suggested that (1)the calyx contains not only bundles in three sepals but also in three absent stamens; (2) the labellum represents two absent stamens of the inner whorl of the androecium, and the two glands are of modified gynoplural nectary.

Lin et al. (2007) investigate the floral vasculature anatomy of *H. coronarium*. They supported the interpretation by Gregory (1936) that two lateral appendages were composed of two outer androecial members; the labellum was composed of two inner androecial members and one outer androecial member.

The results presented in this paper clearly support the general interpretation of the labellum as (1) two inner and one outer androecial members initiated on the abaxial side of the flower. The two inner androecial members are joined by intercalary growth and fuse to produce the two-lobed labellum, while the outer androecial member ceases growth soon after initiation. It is not to support the views of

Table 1 Comparison of floral development in four species in Hedychieae

Reference stage	*Scaphochlamys kunstleri* (Kirchoff 1998)	*Hedychium gardnerianum* (Kirchoff 1997)	*Hedychium coronarium* (Kirchoff 1997)	*Hedychium coccineum*
Obdeltoid primordium	Flattened floral apex	Domed floral apex	Ring primordium forming	Domed floral apex
Two sepals formed	Ring primordium forming	Ring primordium forming	Ring primordium present and common primordia separating	Ring primordium present and common primordia separating
Sepals fused laterally	Ring primordium present and common primordia separating	Ring primordium present	Ring primordium present and common primordia separating	Ring primordium present
Three common primordia formed	Posterior (abaxial) primordium larger	Primordia approximately equal size	Primordia approximately equal size	Posterior (abaxial) primordium larger
Common primordia separation	Gynoecial initiation	Floral cup empty	Floral cup empty	Floral cup empty
First common primordium separating	Thecae initiation	Thecae initiation	No thecae present	Thecae initiation
Thecae formation	Stamen connective forms and becomes distinct at stigma initiation	Stamen connective forms and becomes distinct	Stamen connective forms and becomes distinct only slightly later than in *H. gardnerianum*	Stamen connective forms and becomes distinct

Most information of this table comes from Kirchoff (1997, 1998)

Costerus (1915), Tang et al. (2002) and Lin et al. (2007) and support the interpretation of Lestiboudois (1829), Eichler (1884), Rao et al. (1954), Kirchoff (1997) and (1998). (2) The one inner and two outer androecial members are initiated on the adaxial side of the flower. The one inner androecial member forms the functional stamen. The two outer androecial members form the lateral, petaloid staminodes.

Heterochrony

Flower and inflorescence development of *H. coccineum* Smith are very similar to *H. gardenrianum*, *H. coronarium* (Kirchoff 1997), and *Scaphochlamys kunstleri* (Kirchoff 1998). The main differences concern the timing of certain events during floral organogenesis and the shapes of the floral organs during these events. The lack of an absolute time scale against which to judge development in these species means that we must use a relative time scale to compare events. For this reason, we select a stage in the development of a single organ (or organ system) and use this stage as a marker by which to judge other developmental events. For example, the stage of floral primordium initiation can be used as a marker to judge the formation of the ring primordium. In *S. kunstleri*, *H. gardnerianum*, and *H. coccineum*, the ring primordium is still in the process of forming at this stage, whereas in *H. coronarium*, the ring primordium is already present (Table 1). In a similar manner, we use the stage of “two sepals formed” to investigate the development of the ring primordium. The comparison of the developmental events we made shows that their relative timing varies among species, even over short periods. As development proceeds, similarities occur among species. At the stage, two sepals formed and the ring primordium is forming in *S. kunstleri* and *H. gardnerianum*; however, ring primordium is present in *H. coronarium* and *H. coccineum*. At the stage, sepals fused laterally the floral development of *S. kunstleri* and *H. coronarium* that are ahead of those of *H. gardnerianum* and *H. coccineum*. The similarity between *S. kunstleri* and *H. coccineum* at the stage “three common primordia formed” is that their posterior (abaxial) primordium is larger, and the primordium of *H. gardnerianum* and *H. coronarium* is approximately equal in size. The gynoecium forms much earlier in *S. kunstleri* than in the others (reference stages “common primordia separation”). The thecae initiation form is later in *H. coronarium* than in the others (reference stages “first common primordium separating” and “thecae formation”). The rate at which the thecae enlarge determines the stage at which the connective forms and becomes distinct. The three species of *Hedychium* occurs at approximately the stage of “thecae formation.” Although at same stage in *S. kunstleri* the connective forms, the thecae enlarge more slowly, and the connective becomes distinct only at a later stage.

This comparison of floral development shows that their relative timing varies among species, even during short periods. The floral developments may be accelerated over these periods, but the development may be decelerated over the other periods.

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