

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

Bruce K. Kirchoff

Abstract: Flower organogenesis in *Hedychium gardnerianum* and *Hedychium coronarium* begins with the sequential formation of the sepals on a rounded-triangular apex. Growth in three regions of the apex, inside the sepals, produces three common petal – inner androecial primordia. Intercalary growth below and between these primordia produces a floral cup, the site of gynoecial formation. The common primordia separate to form petals and inner androecial members. After separation, the anterior inner androecial members fuse to form the labellum. The posterior member forms the polleniferous stamen. Up to this point in development, the flowers of *H. coronarium* are slightly ahead of those of *H. gardnerianum*. However, in *H. gardnerianum*, initiation of the two thecae of the stamen occurs immediately following the separation of the common primordia, while thecae formation in *H. coronarium* is slightly delayed. These results show that the relative timing of developmental events can vary even over a short developmental period. Formation of the outer androecium takes place at the apices of a triangle formed by the inner androecial members. The anterior outer androecial member aborts soon after formation, whereas the posterior outer androecial members form the two petaloid staminodes that are found on the lateral sides of the labellum in the mature flower.

Key words: flower development, flower structure, inflorescence, stamen, Zingiberaceae, *Hedychium*.

Résumé : Chez l'*Hedychium gardnerianum* et l'*Hedychium coronarium*, l'organogénèse commence avec la formation séquentielle des sépales et d'un apex triangulaire arrondi. La croissance dans trois régions de l'apex, en dedans des sépales, produit trois primordiums pétale – androcée interne communs. La croissance intercalaire sous et entre ces primordiums produit le réceptacle, site de formation du gynécée. Les primordiums communs se séparent pour former les pétales et les membres de l'androcée interne. Après la séparation, les membres de l'androcée interne antérieur se fusionnent pour former le labelle. Le membre postérieur forme l'étamine pollinifère. Jusqu'à cette étape du développement, les fleurs de l'*H. coronarium* sont légèrement en avance sur celles de l'*H. gardnerianum*. Cependant, chez l'*H. gardnerianum*, l'initiation des deux thèques de l'étamine se fait immédiatement à la suite de la séparation des primordiums communs, alors que la formation des thèques est légèrement retardée chez l'*H. coronarium*. Ces résultats montrent que la chronologie relative des étapes du développement peut varier, même au cours de courtes périodes du développement. La formation de l'androcée externe a lieu aux apex des triangles formés par les membres de l'androcée interne. Le membre antérieur de l'androcée externe avorte tôt après sa formation, alors que les membres postérieurs de l'androcée externe forment les staminodes pétaloïdes qu'on retrouve sur les côtés latéraux du labelle, chez les fleurs adultes.

Mots clés : développement floral, structure de la fleur, inflorescence, étamine, Zingiberaceae, *Hedychium*.

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Introduction

The Zingiberaceae are one of eight families of monocotyledons that make up the order Zingiberales. Four of these families form the monophyletic ginger group containing the Marantaceae, Cannaceae, Costaceae, and Zingiberaceae (Dahlgren and Rasmussen 1983; Kirchoff 1988a; Kress 1990). The relationships of the remaining four families (Musaceae, Strelitziaceae, Heliconiaceae, and Lowiaceae) are less certain (Kress 1990; Kirchoff and Kunze 1995). I will refer to this latter group as the banana group.

Within the ginger group, the Zingiberaceae are the sister group of the Costaceae. Kress (1990) unites these families based on three synapomorphies: sepals fused at least at the base, staminodes variously fused for most of their length,

and possession of nuclear endosperm. The possession of petaloid staminodes in the place of stamen is a synapomorphy of the ginger group as a whole. The autapomorphies of the Zingiberaceae include the possession of aromatic compounds, and the presence of epigynous nectaries (Rao 1963; Panchaksharappa 1962). The Costaceae are typified by the apomorphies spiral monostichous phyllotaxy, closed leaf sheaths, and highly modified gynopleural nectaries (Panchaksharappa 1962; Kirchoff and Rutishauser 1990; Newman and Kirchoff 1992).

The Zingiberaceae is composed of four tribes that are erected mainly on the basis of flower structure (Smith 1981). The Hedychieae, the subject of this paper, are characterized by stems where the plane of distichy of the leaves is parallel to the rhizome; petaloid lateral staminodes that are free from the labellum; and a trilocular ovary with axial placentation, or a unilocular ovary with basal or free columnar placentation (Holtum 1950). The Globbeae have petaloid lateral staminodes that are free from the labellum, a bow-like filament, and a unilocular ovary with parietal placentae. The Zingibereae

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B.K. Kirchoff. Department of Biology, University of North Carolina at Greensboro, Greensboro, NC 27412, U.S.A.
e-mail: kirchoff@goodall.uncg.edu

Table 1. Species investigated.

Species	Collector—voucher	Deposited	Accession No.
<i>Hedychium coronarium</i> Koenig	—	—	Lyon 67.1051
	Kirchoff 84-12	FTG	FTG 78-333
<i>Hedychium gardnerianum</i> Sheppard ex Ker-Gawler	Kaplan K517	FTG	FTG X.14-39
	—	—	Waimea 83P-779
	—	—	Lyon 67-1053

Note: FTG, Fairchild Tropical Garden, Miami, Fla., U.S.A.; Lyon, Lyon Arboretum, Oahu, Hawaii, U.S.A.; Waimea, Waimea Arboretum, Oahu, Hawaii, U.S.A.

have stems with the plane of distichy of the leaves parallel to rhizome, petaloid lateral staminodes that are fused to labellum, and a trilobular ovary with axial placentation. In the Alpineae the stems have their plane of distichy perpendicular to the rhizome; the lateral staminodes are very small, never petaloid and sometimes missing altogether; and the ovary is trilobular with axial placentae or unilobular with free central placentation.

Like other families of the ginger group, the Zingiberaceae have flowers with strongly modified androecia. Plants in this family have a single pollen-bearing stamen and four petaloid staminodes that are united in various ways in the different tribes. In the Hedychieae the most common interpretation of these fusions is that of Eichler (1884). According to this interpretation, two staminodes are fused to form a large compound labellum (or lip), two other androecial members form the lateral staminodes, and the fifth androecial member is missing.

This paper presents the structure and development of the inflorescence and flowers of two species of the Hedychieae: *Hedychium gardnerianum* and *Hedychium coronarium*. The objectives are to (i) evaluate Eichler's (1884) interpretation of the androecium, (ii) gain an indication of developmental variability within the genus, and (iii) provide data on flower development for a study of the evolution of developmental patterns in the Zingiberales.

Materials and methods

Young inflorescence buds of *H. gardnerianum* Sheppard ex Ker-Gawler and *H. coronarium* Koenig were collected from Fairchild Tropical Garden, Miami, Florida, and from the Harold H. Lyon Arboretum and Waimea Arboretum, Oahu, Hawaii. Voucher and (or) accession data are given in Table 1.

Inflorescence and flower development were studied with the epi-illumination, light microscopy technique of Sattler (1968), Posluszny et al. (1980), and Charlton et al. (1989). Living material was fixed in formalin—acetic acid—alcohol (FAA) (Berlyn and Miksche 1976), dehydrated to 100% ethanol, and stained for several days in Fast Green (Johansen 1940; Charlton et al. 1989). Destaining was carried out in 100% ethanol for a period of 2 days to several weeks. Photographs were taken with Kodak Technical Pan Film on a Leitz Ortholux 2 photomicroscope equipped with an Ultropak illuminator. Exposure time was regulated by varying the film speed set at the camera between ISO 300 and 400. The film was developed in Dektol for 3 min at 68°C to give maximum contrast (Eastman Kodak Company 1983).

Flower buds for paraffin sectioning were washed in tertiary butyl alcohol (TBA) or EtOH to remove the fixative, dehydrated through a TBA series or with 2,2-dimethoxypropane, and prepared for sectioning using standard paraffin technique (Berlyn and Miksche

1976). Some specimens were pretreated with ethylenediamine (Carlquist 1982) in an attempt to remove the hardening effects of long storage in fixative. I found little benefit to this procedure. Sections were cut at 4–5 µm on a Reichert–Jung 2040 Autocut microtome and mounted on slides using Bissing's modified Haupt's adhesive (Bissing 1974). The sections were dewaxed using Clear-Rite III in place of xylene. Staining was carried out with tannic acid and ferric chloride followed by safranin and Fast Green (Berlyn and Miksche 1976). Permount was used as the final mounting medium. Photographs were taken with Kodak Technical Pan Film on a Leitz Ortholux 2 photomicroscope. I regulated exposure time by varying the film speed set at the camera between ISO 150 and 250. The film was developed in Kodak HC-110 dilution B for 8 min at 68°C (Eastman Kodak Company 1983).

Additional buds were washed and dehydrated in EtOH, pre-stained in Fast Green (Johansen 1940), embedded in JB-4 Plus, and sectioned at 2.5–4 µm on a Reichert–Jung 2040 Autocut microtome (Berlyn and Miksche 1976). The sections were mounted directly on slides, dried, and observed under the microscope.

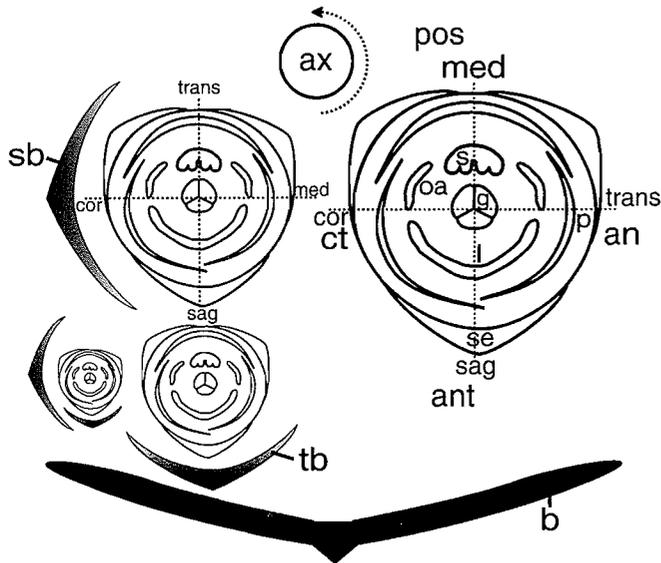
Terminology

I follow Troll (1964) and Weberling (1989) for typological inflorescence terminology and, where appropriate, Kunze (1986) in modifying this terminology to fit the inflorescences of the Zingiberales. According to this terminology, an inflorescence is a modified shoot system that serves the formation of flowers (Troll 1964). Thus, "inflorescence" is a general term that applies to any arrangement of flowers. A florescence is an indeterminate, terminal-flowering unit of an inflorescence. If the florescence terminates the main axis of the plant it is called the main florescence, and a florescence that occurs on a lateral axis is a colflorescence. Florescences may be composed of single lateral flowers or, as in the Zingiberaceae, of branched lateral elements termed partial florescences. The partial florescences of the Zingiberaceae are cincinni. Since each florescence consists of more than one flower, it is a polytelic (many flowered) axis. A synflorescence is an inflorescence that consists of a system of florescences. A polytelic synflorescence is an indeterminate inflorescence consisting of main and colflorescences, the colflorescences often arranged in branching units that repeat the structure of the inflorescence as a whole (paracladia). The inflorescence of the Zingiberaceae is a polytelic synflorescence whose florescence system is usually represented by a single main florescence (Kunze 1985).

"Thyrse" is a descriptive term that refers to an inflorescence with a single main axis and cymose lateral branches. The inflorescence of *Hedychium* is a Thyrse.

The elements of a branch system are numbered according to their position within the ramification. The primary (or first order) axis arises from the axil of a cataphyll, bears foliage leaves, and terminates in an inflorescence. The bracts born directly on this axis are the primary (or main) bracts (Fig. 1, b). Primary bracts subtend cincinni that terminate in primary flowers, the first flowers of the cincinni. Secondary bracts are born on the axes that terminate in

Fig. 1. Diagram of cincinnus and flower structure in *Hedychium*. Flowers are formed successively as the cincinnus develops. Note that the flowers all have the same orientation. The stamen of each flower is oriented toward the inflorescence axis (*ax*), not the axis of next lower order as in most cincinni. *an*, anodic side of flower; *ant*, anterior side of flower; *b*, primary (main) bract; *cor*, coronal plane; *ct*, cathodic side of flower; *g*, gynoeceium; *l*, labellum; *med*, median plane; *oa*, outer androecial member (lateral petaloid staminode); *p*, petal; *pos*, posterior side of flower; *s*, stamen; *sag*, sagittal plane; *sb*, secondary bract; *se*, sepal; *tb*, tertiary bract; *trans*, transverse plane. Arrow indicates direction of rise of the phyllotactic helix.



primary flowers (Fig. 1, *sb*). Secondary bracts subtend secondary flowers, the second flowers of the cincinni. This numbering scheme can be continued to tertiary and higher order bracts and flowers of the cincinnus (Fig. 1).

Since the secondary, tertiary, etc. bracts are the first phyllomes on each branch of the cincinnus, they are also prophylls (first leaves). I use this term to refer to a bract of a cincinnus when its position within the ramification is not important. The prophylls of the cincinni have been incorrectly termed bracteoles in some taxonomic treatments of the Zingiberaceae. A bracteole is a sterile bract that occurs immediately below a terminal flower. The prophylls of the cincinni are fertile. I refer to the apex that arises in the axil of a prophyll as a cincinnus apex because it continues the growth of the cincinnus by producing a fertile bract (prophyll) and terminal flower.

The median plane of the flower bisects the flower and the axis that bears it (Eichler 1875; Kunze 1985) (Fig. 1, *med*). The transverse plane bisects the flower at right angles to the median plane (Fig. 1, *trans*). Organs that lie in or close to the median plane are termed medial and those in the transverse plane are transversal (Weberling 1989).

The terms median and transverse specify the orientation of the flowers relative to the axes that bear them. In most inflorescences these planes will always have the same relationship to the internal parts of the flower. That is, if the median plane of the first flower bisects the single anther of the flower, the median plane of every other flower will also bisect the single anther of these flowers. This is not true in *Hedychium*. All of the flowers of *Hedychium* are initiated so that the stamen backs on the main inflorescence axis, not on the axis that bears the flower (Fig. 1). In this situation the median

planes of the odd-numbered flowers (first, third, etc.) bisect the anthers of these flowers, whereas the median planes of the even-numbered flowers (second, fourth, etc.) run between the staminodes and the labellum of these flowers (Fig. 1). Application of these terms requires identifying the anther as medial in some flowers and transversal in others. To avoid this problem, I will use the term coronal for the plane that separates the staminodes from the labellum (Fig. 1, *cor*) and the term sagittal for the plane that bisects the stamen (Fig. 1, *sag*), no matter what the orientation of these flowers with respect to the rest of the inflorescence. These terms are appropriate because they are defined with reference to the internal form of the organ(ism), not to the attachment of this organ(ism) to some external structure. In humans, the coronal plane is the plane that runs through the coronal suture and separates the frontal and parietal lobes of the brain. The sagittal plane is a vertical plane through the body of a bilaterally symmetrical organism, separating the body into right and left halves.

In *Hedychium* the anterior (or abaxial) side of the flower is the side away from the primary inflorescence axis (Fig. 1, *ant*). The posterior (or adaxial) side is adjacent to this axis (Fig. 1, *pos*). The anodic side of the flower is the coronal side that lies in the direction of the rise of the phyllotactic helix (Fig. 1, *an*). The cathodic side lies opposite the direction of phyllotactic rise (Fig. 1, *ct*).

Unless otherwise noted, the anterior side of the flower is always at the bottom of the photographs in polar views of floral buds and in cross sections. Although cincinni of both handedness occur, the secondary bract is always shown to the left in polar views of *H. gardnerianum* and to the right in polar views of *H. coronarium*.

Results

Organography

Hedychium gardnerianum and *H. coronarium* are medium-sized plants with shoots to 3 m, distichous leaves, and terminal inflorescences (Fig. 2). The leaves are divided into a sheath, petiole, and blade. The blades may reach 40 cm. The sheaths are open for most of their length but have tubular bases. Each inflorescence consists of a single terminal (main) florescence. Coflorescences do not occur in this genus. The inflorescence bears a series of spirally arranged primary bracts that subtend partial florescences composed of cincinni. Each cincinnus bears one or two flowers in *H. gardnerianum* and two to six flowers in *H. coronarium*.

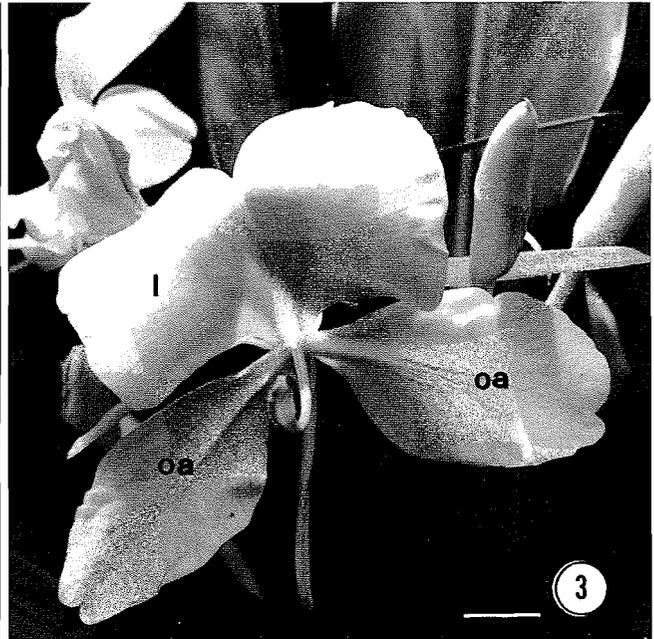
In *H. gardnerianum* the primary inflorescence bracts are most commonly arranged in a 2/7 phyllotactic pattern, but occasionally the direction of the phyllotactic helix changes in the middle of the inflorescence. Additional variations in the 2/7 pattern also occur, especially in the lower regions of the inflorescence, at the transition between the distichously arranged foliage leaves and the spirally arranged bracts. I found both 2/5 and 3/11 patterns in this region. I did not investigate the phyllotaxy of the bracts in *H. coronarium* other than to note that it is spiral.

In both species there is a gradual transition in form between typical foliage leaves and inflorescence bracts. In *H. gardnerianum* there are four sterile bracts at the base of the inflorescence inserted at angles between 1/2 and 2/5. The two sterile bracts in *H. coronarium* are inserted in the plane of distichy of the leaves.

The flowers of both species are constructed according to the typical monocotyledon pattern with organs arranged in whorls of three. The perianth is differentiated into sepals and petals. Of the three petaloid floral members interior to the petals, the labellum lies in the sagittal plane, is bilobate, and

Figs. 4–15. *Hedychium gardnerianum*. Inflorescence and flower development. Fig. 4. Vegetative apex (*v*) bearing distichous young leaves (*le*). *d*, damage. Scale bar = 100 μ m. Fig. 5. Slightly oblique view of young inflorescence apex (*a*) bearing helically arranged bract primordia (*b*). Scale bar = 200 μ m. Fig. 6. Lateral view of same inflorescence apex (*a*) shown in previous figure. *b*, primary

Figs. 2–3. Inflorescence position and flower structure in *Hedychium*. Fig. 2. *Hedychium gardnerianum*. Habit of plants growing at Fairchild Tropical Garden, Miami. The apparent spiral arrangement of the leaves is due to secondary rotation. Scale bar = 20 cm. Fig. 3. *Hedychium coronarium*. Flower structure. *l*, labellum; *oa*, outer androecial member (lateral staminode). Scale bar = 1 cm.



is larger than the others (Figs. 1, 3, *l*). The lateral staminodes are inserted closer to the coronal plane and are unlobed (Fig. 3, *oa*).

Although the labellum is initiated in an abaxial position in both species, the mature flower of *H. coronarium* is resupinate with the labellum oriented adaxially, pointing toward the apex of the inflorescence (Fig. 3). The flower of *H. gardnerianum* is not resupinate.

The ovary is trilocular and inferior. Ovules are numerous and are inserted on axile placentas. Unlike other members of the Zingiberales the apical closure of the locules is not extended into a prolongation. Epigynous nectaries are inserted on top of the ovary, at the base of the style.

Hedychium gardnerianum

Inflorescence development

Just prior to inflorescence formation the vegetative apex is a low, flat dome that initiates leaves in a distichous pattern (Fig. 4). During vegetative growth there are few leaf primordia on the apex. With the transition to inflorescence development the apical region elongates, phyllotaxy begins to change from distichous to spiral, and more phyllome primordia are borne on the apex (Figs. 5, 6). The increased number of phyllomes is associated with a decrease in the insertion size of the phyllome primordia. At initiation, the foliage leaves surround half or more of the apical dome while the bracts occupy only a small percentage of this circumference (cf. Figs. 4, 7).

The apex remains relatively flat topped throughout the transition from vegetative to reproductive growth (Figs. 4, 6, 7).

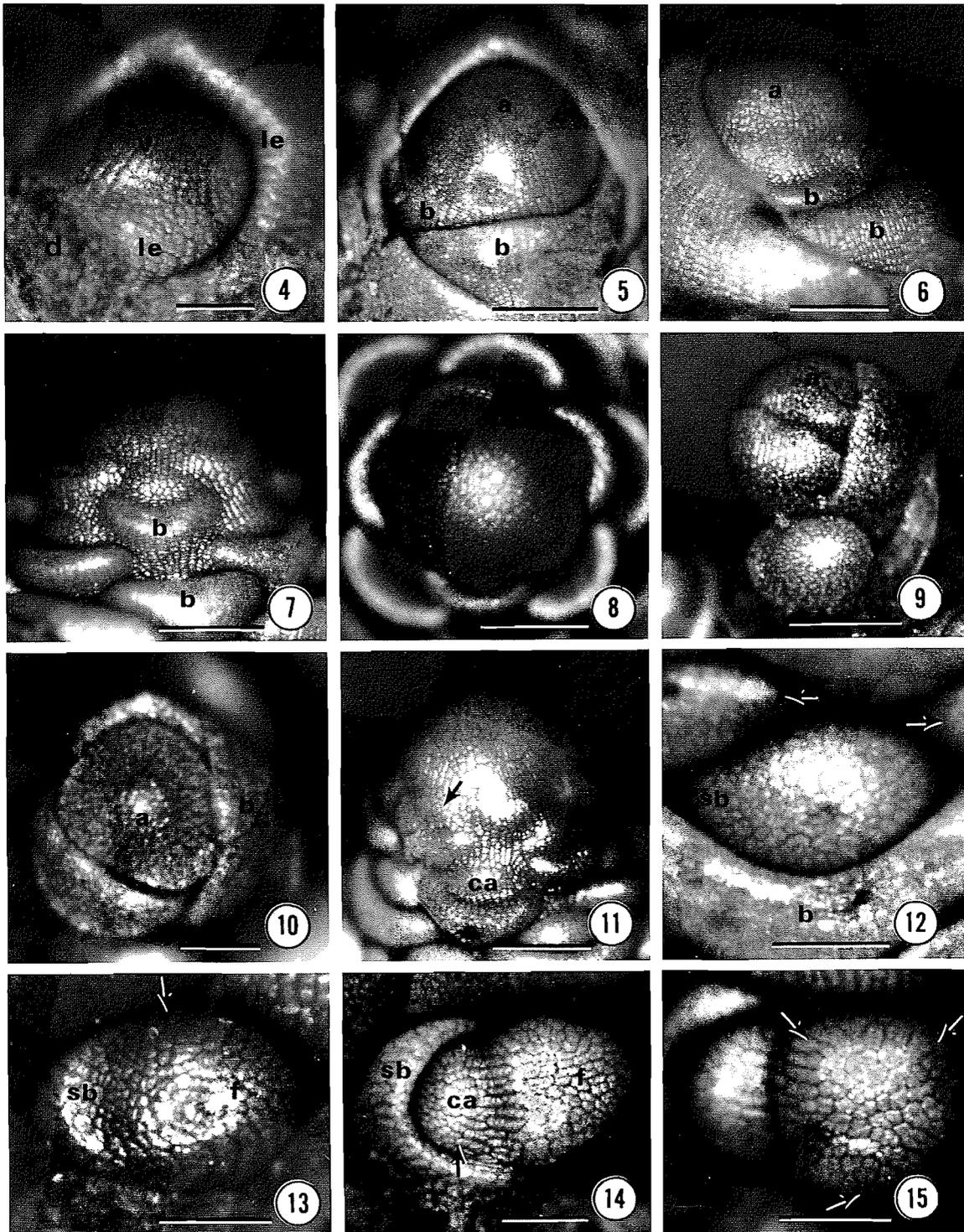
Primary bracts of the inflorescence are initiated on the flanks of the apical dome in a spiral phyllotactic pattern (Figs. 7, 8). Soon after initiation the bract primordia become crescent shaped, the concave side of the crescent opening upward (Fig. 7). Cincinnus primordia are initiated in the axils of the primary bracts (Fig. 7). As the inflorescence ages, the inflorescence apex decreases in size relative to the surrounding bracts and finally ceases growth (Figs. 9, 10). Near the time of its abortion, the apex bears fewer bracts, and the primary bracts and cincinnus buds begin maturation closer to the apical dome than when the apex is most actively producing bracts (cf. Figs. 7, 9).

Cincinnus development

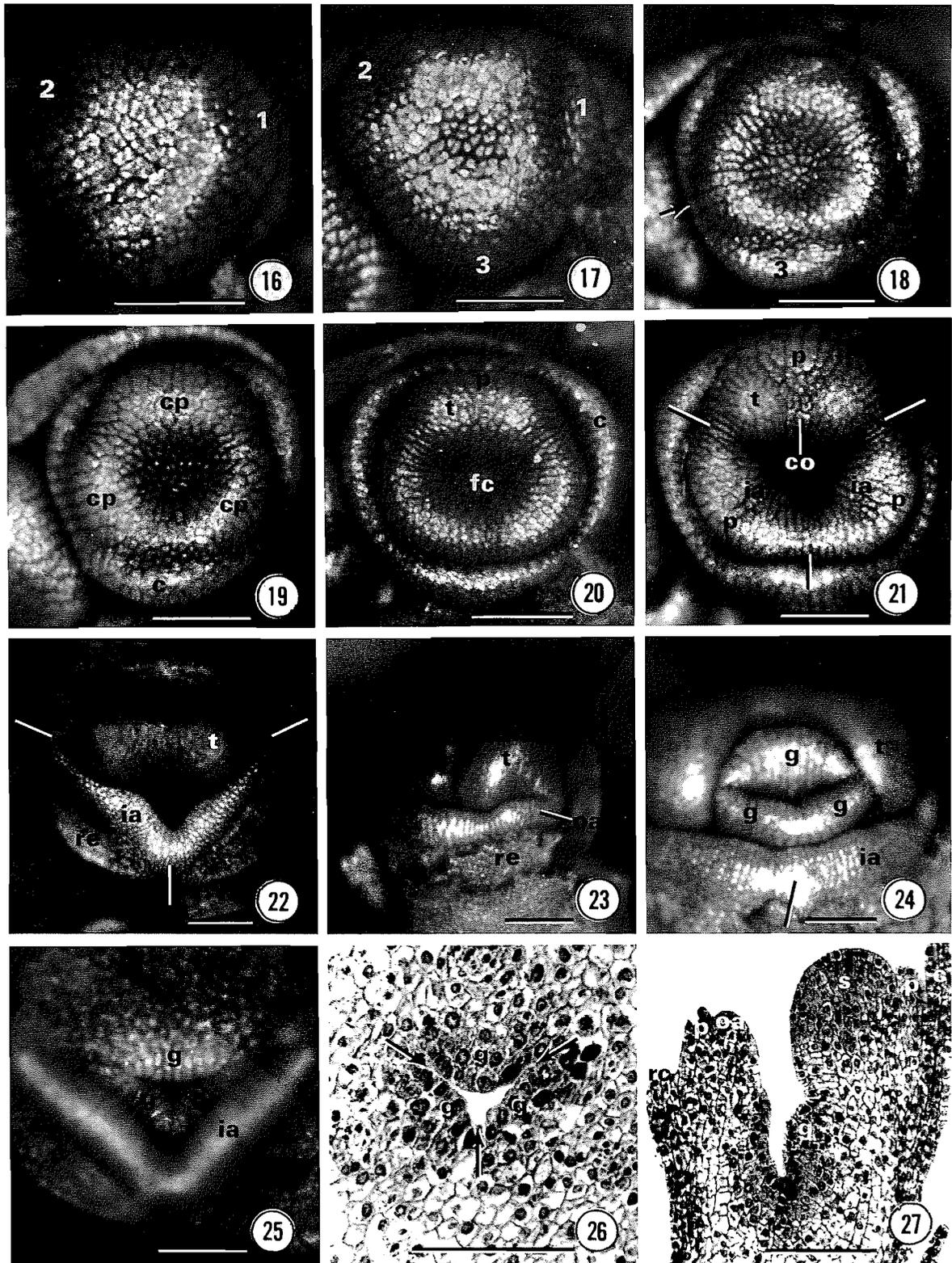
Cincinnus primordia are initiated on the flanks of the inflorescence apex in the axil of a primary bract (Fig. 11, arrow). Following initiation the young cincinnus widens to produce a transversely elongated primordium (Figs. 11, 12). As growth continues the primordium becomes more pointed on one side (Fig. 12, *sb*). This point is the secondary bract at the time of its initiation. At the same stage the margins of the adjacent primary bracts intrude between the cincinnus and the inflorescence axis (Fig. 12, arrows).

The secondary bract is initiated in the transverse plane on either the anodic (in the direction of the rise of the phyllotactic helix) or cathodic (opposite the direction of rise) side of the

bract. Scale bar = 200 μm . Fig. 7. Lateral view of inflorescence apex. *b*, primary bract. Scale bar = 200 μm . Fig. 8. Polar view of inflorescence apex bearing helically arranged bracts. Scale bar = 200 μm . Fig. 9. Lateral view of aborted inflorescence apex (*a*). *b*, primary bract. Scale bar = 200 μm . Fig. 10. Polar view of aborted apex (*a*) shown in previous figure. *b*, primary bract. Scale bar = 100 μm . Fig. 11. Oblique view of inflorescence apex showing initiation of cincinnus primordia (arrow, *ca*). Scale bar = 200 μm . Fig. 12. Cincinnus primordium initiating secondary bract (*sb*). The arrows show the intrusions of adjacent primary bract primordia behind the cincinnus. *b*, primary bract; *sb*, secondary bract. Scale bar = 100 μm . Fig. 13. Young cincinnus showing differentiation of flower (*f*) and formation of the secondary bract (*sb*). The arrow shows the secondary bract extending around the periphery of the cincinnus. Scale bar = 100 μm . Fig. 14. Cincinnus at the stage just preceding tertiary bract (arrow) formation. *ca*, cincinnus apex; *f*, flower; *sb*, secondary bract. Scale bar = 100 μm . Fig. 15. Floral apex showing sites of sepal initiation (arrows). Scale bar = 100 μm .



Figs. 16–27. *Hedychium gardnerianum*. Flower development through gynoecial initiation. Fig. 16. Sepal initiation. 1 and 2, sequentially formed sepals. Scale bar = 100 μm . Fig. 17. Sepal initiation and formation of ring primordium. 1–3, sequentially formed sepals. Scale bar = 100 μm . Fig. 18. Flower primordium showing ring primordium and fusion of sepals into synsepalous calyx (arrow). 3, third formed sepal. Scale bar = 100 μm . Fig. 19. Common primordia (*cp*) surrounding floral cup just prior to perianth – inner androecial formation. *c*, sepal. Scale bar = 100 μm . Fig. 20. Separation of posterior common primordium to form petal (*p*) and fertile stamen. *c*, sepal; *fc*, floral cup; *t*, theca. Scale bar = 100 μm . Fig. 21. Separation of common primordia to form petals (*p*) and inner androecial members (*ia*). The positions of outer androecial initiation are indicated by the three lines. *co*, connective of the fertile stamen; *t*, theca.



Scale bar = 100 μm . Fig. 22. Formation of the outer androecial members (lines). *ia*, inner androecial member; *re*, removed petal; *t*, theca. Scale bar = 100 μm . Fig. 23. Lateral view of flower showing outer androecial member (*oa*). *re*, removed petal; *t*, theca. Scale bar = 200 μm . Fig. 24. Frontal view of same flower as in previous figure. The anterior outer androecial member (line) has ceased growth. *g*, gynoecial primordium forming style; *ia*, inner androecial member; *t*, theca. Scale bar = 100 μm . Fig. 25. Gynoecial initiation (*g*). *ia*, inner androecial member; *rs*, removed fertile stamen. Scale bar = 100 μm . Fig. 26. Cross section showing initiation of three gynoecial primordia (*g*). The arrows show sites of locule formation. Scale bar = 100 μm . Fig. 27. Longitudinal section at gynoecial (*g*) initiation. *c*, sepal; *oa*, outer androecial member; *p*, petal; *rc*, removed sepal; *s*, stamen. Scale bar = 100 μm .

cincinnus apex (Figs. 12, 13, *sb*). Although the bract is initiated in the transverse plane, cell divisions soon begin around the periphery of the cincinnus to produce a tubular bract (Fig. 13, arrow). At later stages, the secondary bract completely surrounds the cincinnus (Figs. 14–19). An axillary bud forms in the axil of the bract and continues the growth of the cincinnus (Fig. 14, *ca*) while the apex of the secondary axis produces a flower (Figs. 13, 14).

Continued growth of the cincinnus follows the same pattern as described above. A new cincinnus apex originates in the axil of a prophyll borne on the next lower order axis. This apex produces a lateral prophyll (Fig. 14, arrow) and terminates in a flower. A new cincinnus apex forms in the axil of this prophyll and continues the growth of the cincinnus. The tertiary bract is always initiated away from the inflorescence axis (Figs. 1, 14), and the quaternary bract is initiated in the transverse plane, on the same side of the cincinnus as the secondary bract (Fig. 1).

Flower development

Flower development begins following the initiation of the secondary bract with the transformation of the cincinnus apex into a floral primordium (Fig. 13). This primordium enlarges, begins to flatten apically, and assumes a rounded, obdeltoid appearance in polar view (Fig. 15). As growth continues the floral primordium becomes flatter and the corners of the deltoid become more pronounced (Fig. 14).

The rounded corners of the floral primordium are the sites of sepal initiation (Fig. 15, arrows). Sepals are initiated in sequential order, beginning with the posterior sepal farthest from the prophyll (Fig. 16). The second sepal forms ca. 120° from the first in a posterior position (Figs. 16, 17). The third sepal forms anteriorly (3 in Figs. 17, 18). Following initiation, the sepals extend their insertion sites around the periphery of the floral primordium until the margins of adjacent sepals become confluent (Fig. 18, arrow). From this stage, intercalary growth below the tips of the sepals produces the majority of the synsepalous calyx. However, the free tips of the sepals do continue to enlarge (Figs. 19–21).

During sepal initiation the whole flower primordium continues to enlarge. The periphery of the flower, interior to the sepals, grows upwards to produce a raised ring of tissue that surrounds a central depression (Figs. 17, 18). This ring primordium is composed of three partially distinct common primordia united below into a cylinder of tissue surrounding a central cavity (Figs. 18, 19). The cylinder with its enclosed central cavity forms the floral cup, the site of gynoecial initiation (Figs. 19, 20, *fc*).

The common primordia become increasingly distinct as the floral primordium enlarges (Figs. 17–19). Each common primordium then divides to produce a petal to the exterior and an inner (antipetalous) androecial member to the interior (Figs. 20, 21). Separation of the three common

primordia is sequential, beginning with the fertile stamen and its associated petal and proceeding in the same direction as sepal initiation (Fig. 21).

The posterior inner androecial member develops into the fertile stamen. The thecae of the stamen are visible from a very early stage of common primordium separation (Fig. 20, *t*). From their earliest appearance the thecae are separated by a sterile connective (Figs. 20, 21). The two anterior inner androecial primordia form the petaloid staminodes that will constitute the labellum (Fig. 21, *ia*).

During the enlargement and separation of the common primordia, the hollow space at the center of the floral cup enlarges and becomes triangular in cross section (Figs. 19–21). This change in shape is caused by the formation of the three dorsio-ventral inner androecial primordia (Fig. 21). As the inner androecial members enlarge they occupy the three sides of the triangle that frame the floral cup (Figs. 21, 22). The three vertices of this triangle are the sites of outer androecial initiation.

The three outer androecial members are initiated at the three locations on the ring primordium left vacant by the formation of the petals and inner androecial members (Fig. 21, lines). The anterior outer androecial member forms slightly before the two posterior members (Figs. 21, 22); however, it ceases growth soon after initiation while the two posterior members continue to grow and eventually produce the lateral, petaloid staminodes (Fig. 23, *oa*). The anterior outer androecial member contributes little or nothing to the formation of the labellum, the organ with which it is most closely associated (Fig. 24, line).

Gynoecial initiation begins with the formation of three gynoecial primordia on the inner margins of the floral cup (Figs. 25–28). The primordia are initiated opposite the petals, below the insertion of androecium (Fig. 27). The posterior primordium is slightly larger than the other two primordia at an early stage of development, suggesting that it is initiated first (Fig. 26). At, or very soon after, initiation the longitudinal extent of the primordia occupies the full depth of the floral cup (Fig. 27).

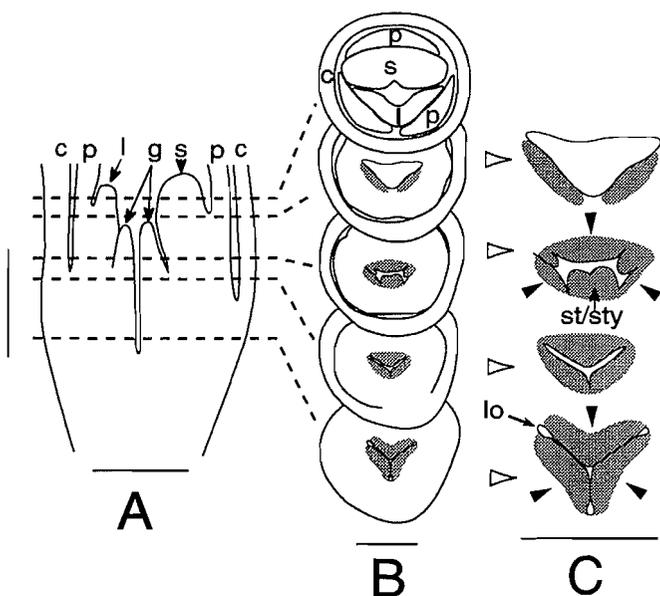
Continued radial growth of the gynoecial primordia produces a trilocular ovary (Figs. 28, 29). The body of the gynoecial primordia (Fig. 28) produces the septa and, through their fusion at the center of the ovary, the central axis of the ovary (Fig. 29, *cx*). The locules arise from an expansion of the spaces between gynoecial primordia (Figs. 28, 29, *lo*).

The style and stigma form from the apical portions of the gynoecial primordia (Fig. 24). The three gynoecial primordia grow upward and fuse along their lateral margins to produce a cylindrical style capped by a trilobed stigma primordium (Fig. 24). The posterior lobe of the stigma is larger than the anterior lobes.

As the ovary enlarges, placenta form from the central axis and protrude into the locules (Fig. 29, *pl*). Each placenta has

Figs. 31–42. *Hedychium coronarium*. Inflorescence and flower development. Fig. 31. Oblique view of inflorescence apex bearing bracts (*b*) and cincinnus primordia (*ca*). The arrow shows the primary bract at time of initiation. Scale bar = 100 μ m. Fig. 32. Older inflorescence apex (*a*) with bracts (*b*) maturing closer to the apex. Scale bar = 100 μ m. Fig. 33. Apical region of old inflorescence showing aborted apex (*as*) surrounded by three cincinni. *sb*, secondary bract. Scale bar = 200 μ m. Fig. 34. Very young flower (*f*) terminating cincinnus axis. The arrow shows the extension of secondary bract around the cincinnus. *ca*, continuing cincinnus apex; *sb*, secondary bract. Scale bar = 100 μ m. Fig. 35. Flattened, obdeltoid floral apex. Scale bar = 100 μ m. Fig. 36. Sequential sepal (1, 2) initiation occurring at the same time as formation of the ring primordium (*rp*). The arrow shows the site of common primordium that will form petal and fertile stamen. Scale bar = 100 μ m. Fig. 37. Separation of first common primordium (*cp*) to form petal (*p*) and

Fig. 28. *Hedychium gardnerianum*. Diagrams of a flower at gynoecial initiation. (A) Reconstruction of a longitudinal section showing the positions of diagrams in (B) and (C). Note that the horizontal and vertical scales are slightly different in this drawing. (B) Tracings of cross sections at the levels indicated in (A). The shaded areas contain smaller, more densely cytoplasmic cells than those in the surrounding regions. (C) Enlargements of shaded regions in (B). The three gynoecial primordia are indicated by arrowheads. The septa form at the positions indicated by these arrowheads. *c*, sepal or synsepalous calyx; *g*, gynoecial primordium; *l*, labellum; *lo*, locule; *p*, petal; *s*, fertile stamen; *st/sty*, stigma–style primordium. Scale bars = 100 μ m.



two ridges, each of which will produce approximately four vertical lines of ovules.

The last floral organs to be initiated are the nectaries. The nectaries form from gynoecial tissue at the base of the style. Their site of initiation and insertion is on the anterior side of the style, just below the fertile stamen (Fig. 30).

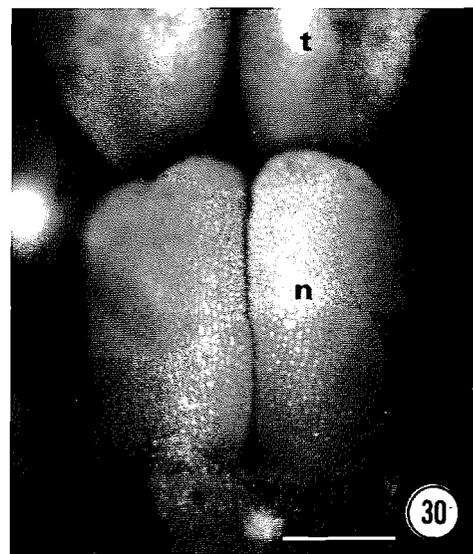
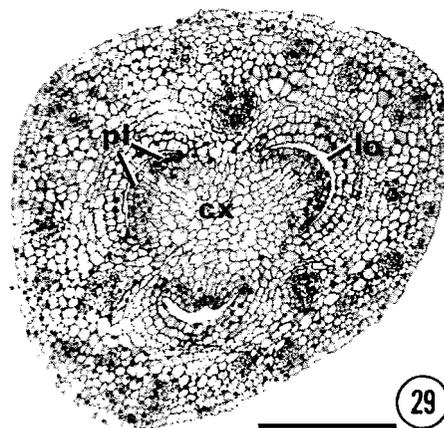
Hedychium coronarium

Inflorescence development

Primary bracts are initiated in a spiral phyllotactic pattern on the sides of the inflorescence dome (Fig. 31, arrow). Soon after initiation the bract primordia become crescent shaped and partially surround the apex (Fig. 31, *b*).

As the inflorescence ages, the inflorescence apex decreases in size relative to the bracts, and the primary bracts and cincinni begin to mature closer to the apex (Fig. 32). At this

Figs. 29, 30. *Hedychium gardnerianum*. Later stages of flower formation. Fig. 29. Cross section after fusion of gynoecial primordia to form septa and central axis (*cx*) of ovary. *lo*, locule; *pl*, placental ridge. Scale bar = 200 μ m. Fig. 30. Young epigynous nectaries (*n*) at the base of the style. *t*, theca. Scale bar = 200 μ m.

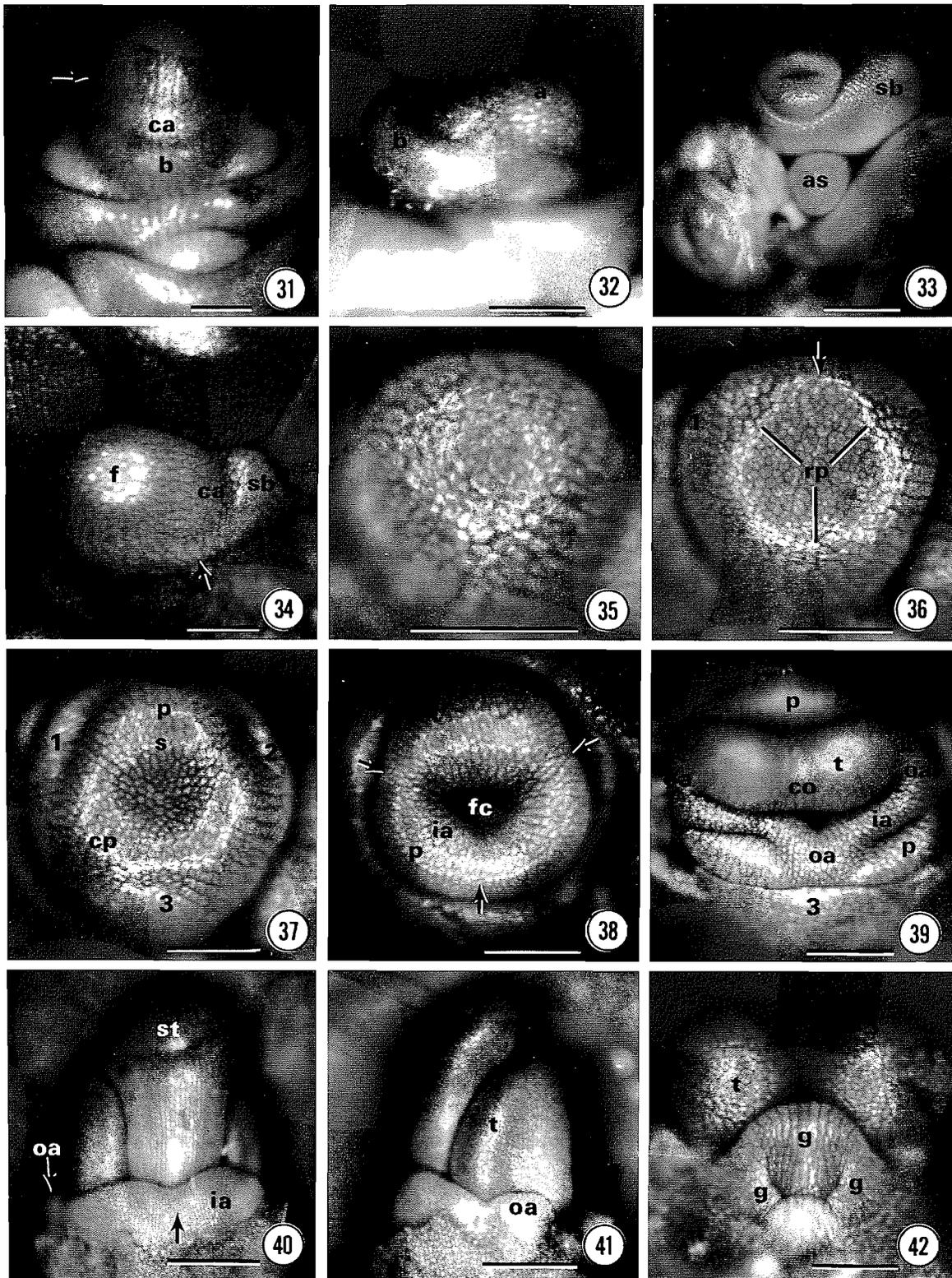


stage, the apex appears displaced slightly to one side. Eventually, the apex ceases meristematic activity and forms a sterile stub at the tip of the inflorescence (Fig. 33, *as*).

Cincinnus development

Cincinnus primordia are initiated on the flanks of the inflorescence apex, in the axils of primary bracts (Fig. 31, *ca*). The cincinnus apex then widens to produce a transversely elongated primordium. This primordium develops a point on one side and initiates a secondary bract in the transverse

fertile stamen (*s*). 1–3 sepals numbered in order of their formation. Scale bar = 100 μ m. Fig. 38. Separation of common primordia to form petals (*p*) and inner androecial members (*ia*). The arrows show the sites of outer androecial formation. *fc*, floral cup. Scale bar = 100 μ m. Fig. 39. Formation of outer androecial members (*oa*). The posterior sepals have been removed. 3, third formed sepal; *co*, stamen connective; *ia*, inner androecial member; *p*, petal; *t*, theca. Scale bar = 100 μ m. Fig. 40. Frontal view of a mid-stage flower showing abortion of anterior outer androecial primordium (arrow). *ia*, inner androecial member; *oa*, posterior outer androecial member; *st*, stigma. Scale bar = 200 μ m. Fig. 41. Lateral view of flower shown in Fig. 40. *oa*, posterior outer androecial member; *t*, theca. Scale bar = 200 μ m. Fig. 42. Gynoecial primordia (*g*) emerging from ovary to form stigma and style. *t*, theca. Scale bar = 100 μ m.



plane (Fig. 34, *sb*). The secondary bract may form on either the anodic or cathodic side of the cincinnus apex. Following its initiation, cell divisions extend the secondary bract around the cincinnus to form a tubular bract (Fig. 34, arrow). An axillary bud forms in the axil of the secondary bract and continues the growth of the cincinnus (Fig. 34, *ca*) while the apex of the cincinnus produces a flower (Fig. 34, *f*).

Continued growth of the cincinnus follows the same pattern described for *H. gardnerianum*. A new cincinnus apex originates in the axil of a prophyll. The new apex produces a prophyll and terminates in a flower. The next cincinnus apex forms in the axil of this prophyll and continues the growth of the cincinnus.

Flower development

There is considerable variability in the pattern of flower development in *H. coronarium*. Preliminary investigation suggests that much of this variability is correlated with the position of the flower in the inflorescence. I will not undertake a full investigation of this variability in this paper. The following description is based on flower development in the central portion of the inflorescence. It does not represent the full range of variability and should not be taken as a full description of flower development in this species.

Flower development begins at the same time as the initiation of the axillary bud that continues the growth of the cincinnus. At this stage the apex of the lower order axis transforms into a floral apex (Fig. 34, *f*). The floral apex enlarges, flattens apically, and takes on a rounded, obdeltoid silhouette in polar view (Fig. 35). The rounded corners of the primordium are the sites of sepal initiation (Figs. 35, 36). Sepals are initiated sequentially, beginning with the posterior sepal farthest from the prophyll (1 in Fig. 36). The second sepal also forms posteriorly, approximately 120° from the first (2 in Fig. 36). The third sepal forms anteriorly (3 in Fig. 37). In some flowers the early formation of the ring primordium partially obscures this sequence, so sepal initiation appears more nearly unidirectional. In the early stages of their growth, the insertions of the sepals extend around the periphery of the floral primordium until the margins of adjacent sepals become confluent (Figs. 37, 38). Intercalary growth below the sepal tips produces the majority of the synsepalous calyx.

The floral primordium continues to enlarge during sepal initiation (Figs. 35–37). As it enlarges, a ring of tissue interior to the sepals expands to produce a ring primordium surrounding a central depression (Figs. 36, 37). During its earliest stages of formation this ring primordium appears composed of an unbroken circle of tissue. At these stages, only the portion of the ring that will produce the fertile stamen and its associated petal can be distinguished from other parts of the ring (Fig. 36, arrow). Later, the ring primordium is clearly composed of three common primordia united below into a cylinder of tissue surrounding a central cavity (Figs. 37, 38). The cylinder with its enclosed central cavity is the floral cup, the site of gynoecial initiation (Fig. 37, 38.)

Each common primordium enlarges and divides to produce a petal to the exterior and an inner androecial member to the interior (Figs. 37, 38). The posterior common primordium is the first to separate (Fig. 37). This primordium

produces the posterior petal and the fertile stamen. The thecae of the stamen are formed slightly after separation of the common primordium (Fig. 39). From an early stage of their growth the thecae are separated by a sterile connective (Fig. 39, *co*).

Separation of the remaining two anterior common primordia is sequential, following the same phyllotactic sequence established by the sepals (Figs. 37, 38). Each of the anterior common primordia produces a petal and a petaloid, inner androecial member (Fig. 39). These two inner androecial members form the labellum (Fig. 40).

As the flower enlarges, the cavity of the floral cup becomes triangular in cross section (Fig. 38). This metamorphosis is caused by the separation of the three common primordia and the formation of the three inner androecial primordia. The three inner androecial members enlarge and occupy three sides of a triangle surrounding the cup. The vertices of this triangle are the sites of outer androecial initiation (Fig. 38, arrows). The anterior outer androecial member forms slightly before the two posterior members (Figs. 38, 39). This primordium ceases growth soon after initiation while the two posterior primordia continue growth to produce the lateral, petaloid staminodes (Figs. 40, 41, *oa*). The anterior outer androecial member contributes little or nothing to the formation of the labellum (Fig. 40, arrow).

Soon after gynoecial initiation three primordia become visible at the top of the ovary (Fig. 42). These primordia are the apical portions of the gynoecial primordia. As in *H. gardnerianum* the gynoecial primordia extend above the ovary and fuse to produce a bilaterally symmetrical style–stigma primordium (Fig. 42). From an early stage of development the posterior lobe of the stigma is larger than the anterior lobes. This condition continues throughout later development (Fig. 40). At later stages of development, the posterior lobe forms a button-like cap on the top of the stigma. Material was not available for a fuller study of gynoecial development in this species.

The nectaries are the last floral organs to be initiated. They form as outgrowths of gynoecial tissue at the base of the style (Fig. 43). They are initiated and borne on the anterior side of the style just below the fertile stamen.

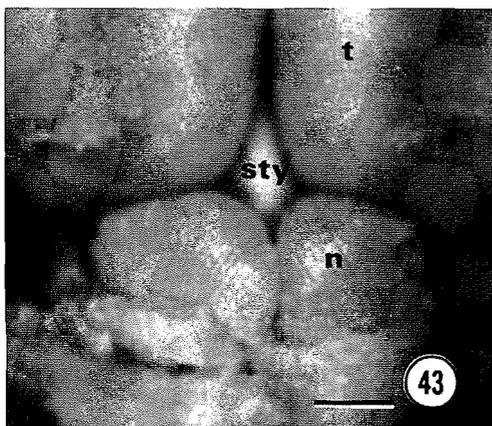
Discussion

For the purposes of this paper, I will restrict my discussion to flower structure and development in *Hedychium*. Where clarity demands, I will refer to other genera but, in general, will keep the discussion narrowly focused on issues relevant to this genus. It is beyond the scope of this paper to review or critique the full history of the interpretation of the flowers of the Zingiberaceae (Brown 1810; Lestiboudois 1829; Payer 1857; Baillon 1876; Eichler 1884; Costerus 1915; Schachner 1924; Loesener 1930; Thompson 1933; among others).

Inflorescence structure

The inflorescence of *Hedychium* is a simple thyrses. It consists of a main axis bearing primary bracts that subtend lateral cincinni with from 1 to 6 flowers per cincinnus (Schumann 1904; Holtum 1950; Smith 1984). Following the typological system of Troll (1964) this type of inflorescence is a polytelic synflorescence (Troll 1964; Kunze 1985;

Fig. 43. Epigynous nectaries (*n*) soon after initiation at the base of the style (*sty*). *t*, theca. Scale bar = 100 μ m.



Weberling 1989). In *Hedychium*, the elaborate branching system of the polytelic synflorescence is reduced to a single main florescence.

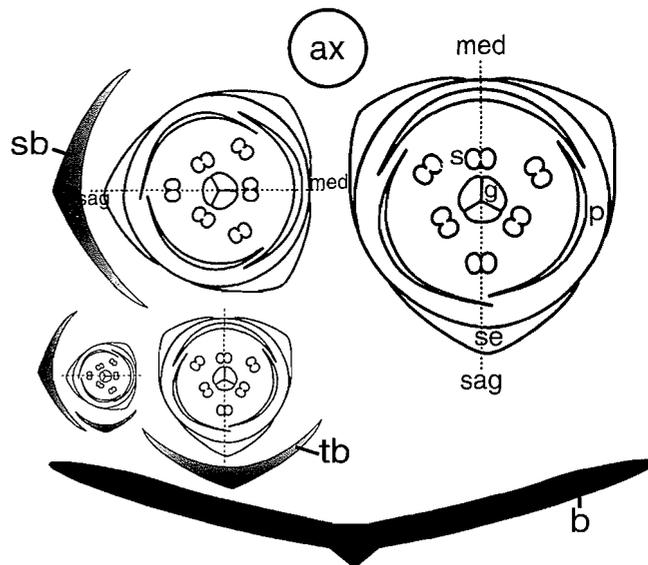
Within the Zingiberaceae, the prophylls of the cincinni are usually tubular (Holtum 1950, p. 72). However, this is not the usual condition for the Hedychieae where it is more common to find prophylls that are open (split) to the base (Holtum 1950, p. 8). Tubular prophylls are more commonly found in the Alpineae. Based on their similarity to the tubular bases of the leaf sheaths, Holtum (1950, p. 8) tentatively suggests that tubular prophylls are primitive in the family.

The developmental evidence presented here demonstrates that the prophylls of both *H. gardnerianum* and *H. coronarium* are initiated in the transverse plane, on the side of the cincinnus primordium. They then extend around the circumference of the cincinnus to produce the tubular prophylls. The fact that the prophylls are not initially formed around the whole circumference suggests, contrary to Holtum (1950), that the tubular condition may be advanced. This supposition is supported by outgroup comparison with the Costaceae, the likely sister group of the Zingiberaceae (Kirchoff 1988a; Kress 1990). In *Costus scaber* the prophyll is initiated in the same position as in *Hedychium* but does not extend as far around the periphery of the cincinnus (Kirchoff 1988b) and remains open at maturity. Thus, by parsimony the ancestor of the Costaceae and Zingiberaceae had open prophylls. Further study of prophyll development in other genera of the Zingiberaceae is necessary to support this interpretation.

In a normal cincinnus all of the flowers are initiated in orientations such that their median and sagittal planes coincide (Fig. 44, broken lines) (Kunze 1985). That is, a single plane cuts the flower in its primary plane of symmetry, bisects the subtending prophyll, and runs through the center of the axis that bears the flower. Since, in these cases, sagittal refers to the same plane as the term median, this term is usually not used. The single plane that bisects the flower and the axis that bears it is referred to as the median plane (Weberling 1989).

In *Hedychium*, by contrast, the median and sagittal planes only coincide in flowers one, three, five, etc., the odd-numbered flowers (Fig. 1). These flowers have the same orientation as their corresponding flowers in normal cin-

Fig. 44. Structure of a typical cincinnus. Flowers are formed successively as the cincinnus develops. All flowers are oriented so that their median plane bisects the lower order axis. The median plane of odd-numbered flowers also bisects the inflorescence axis. *ax*, inflorescence axis; *b*, primary (main) bract; *g*, gynoeceium; *med*, median plane of flower; *p*, petal; *s*, stamen; *sag*, sagittal plane of flower; *sb*, secondary bract; *se*, sepal; *tb*, tertiary bract.



cinni. From their inception, even-numbered flowers have a different orientation with respect to their subtending prophylls and to the axes that bear them. In these flowers the sagittal plane bisects the flower, the primary bract, and the main inflorescence axis, while the median plane bisects the prophyll and the axis that bears the flower (Fig. 1) (see also diagrams in Eichler 1875; Kunze 1985). These changes produce a cincinnus in which the odd-numbered flowers have the same orientation they do in a normal cincinnus, and the even-numbered flowers are initiated with their sagittal planes rotated 90° (cf. Figs. 1, 44). At present, the functional significance of this orientation is unknown, although it probably plays some role in pollination.

Flower structure and development

In recent years, there has been little controversy over flower structure in the Zingiberaceae. What controversy has remained concerns the interpretation of the labellum and nectaries.

The interpretation of the labellum which is supported by this study and is accepted in current taxonomic treatments of the angiosperms (Heywood 1978; Cronquist 1981; Dahlgren et al. 1985) is that of Eichler (1884). Under this interpretation, the labellum is composed of two members of the inner androecial whorl. An outer androecial member is initiated between these two, but does not complete development and does not contribute significantly to the mature labellum. The third member of the inner whorl is the fertile stamen. The other two members of the outer whorl are the two lateral staminodes.

This interpretation was first proposed by Lestiboudois (1829) from a study of *H. coronarium*. Lestiboudois (1829) compared the mature flowers of this species with those

Table 2. Comparison of floral development in *H. gardnerianum* and *H. coronarium*.

Reference stage	Comparison stage in <i>H. gardnerianum</i>	Comparison stage in <i>H. coronarium</i>
Obdeltoid primordium	Domed floral apex (Fig. 15)	Ring primordium forming (Fig. 35)
Two sepals formed	Ring primordium forming (Figs. 16, 17)	Ring primordium present and symmetrical (Fig. 36)
Sepals fused laterally	Ring primordium present (Fig. 18)	Common primordia separating (Figs. 37, 38)
First common primordium separating	Thecae initiation (Fig. 20)	No thecae present (Fig. 38)

of *Canna indica*, which he had previously investigated (Lestiboudois 1823–24). Based on this comparison he formulated the interpretation of the labellum which has generally been supported, with slight modifications by Eichler (1884).

The developmental work presented here further supports this interpretation in *Hedychium*. In both species, two inner and one outer androecial members are initiated on the anterior side of the flower. The two inner androecial members are joined by intercalary growth beneath the primordia, while the outer androecial member ceases growth soon after initiation. The fusion of these two staminodes produces the two-lobed labellum that characterizes this genus.

There has been little previous developmental work on the flowers of the Zingiberaceae. Schachner (1924) undertook the only investigation of flower development in *Hedychium* prior to the present study. Since he was primarily interested in investigating the morphological nature of the labellum, he did not conduct a full developmental study. Rather, he studied only those stages which show the contribution of the inner and outer androecial whorls to the labellum. In *Hedychium*, he found that the labellum is composed of only two members of the inner androecial whorl. These findings support Lestiboudois' (1829) and Eichler's (1884) interpretation of the labellum.

In the Zingiberales, the term labellum has also been applied to floral organs in the Cannaceae, Lowiaceae, and Costaceae. The labellum of the Zingiberaceae is not homotopous and therefore not homologous to the labellum of the Cannaceae or the Lowiaceae. The labellum of the Cannaceae is a single petaloid androecial member (Kirchoff 1983; Kunze 1984). The labellum of the Lowiaceae is a modified petal (Kirchoff and Kunze 1995). In the Costaceae, the labellum is composed of five petaloid androecial members, including the outer androecial member that ceases growth at an early stage in *Hedychium* (Troll 1928; Kirchoff 1988b). The labellum of *Hedychium* is thus homologous to part of the labellum of the Costaceae.

At anthesis the flowers of *H. coronarium* are resupinate. At initiation the labellum is always oriented anteriorly, toward the subtending primary bract (Fig. 1). At anthesis the labellum is posterior, oriented toward the main inflorescence axis (Fig. 3). This reorientation is similar to what occurs in several species of *Orchidantha* (Lowiaceae) (Kirchoff and Kunze 1995). In this genus, the labellum is initiated posteriorly and often rotates to an anterior position, oriented toward the subtending bract and the earth. In neither of these cases

do we have a definitive explanation for the resupination, though it is almost certainly related to pollination.

Flower and inflorescence development are very similar in *H. gardnerianum* and *H. coronarium*. The main differences concern the timing of certain events during floral organogenesis and the shapes of the floral organs during these events. Since I did not investigate the time course of development in either species, I must use a relative time scale to compare developmental events. To do this I 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 instance, the stage at which the common primordia have just been formed and are beginning to separate can be used as a marker against which to view the formation of the synsepalous calyx. In *H. gardnerianum* the synsepalous calyx has already begun to form at this stage (Fig. 19), whereas in *H. coronarium* the sepals remain separate slightly beyond this stage (Fig. 37). In a similar manner I use the stage of sepal formation to investigate the early development of the ring primordium, and the stage at which separation of the posterior common primordium occurs to investigate the formation of the thecae (Table 2). In reviewing these differences (Table 2) please remember that for a given reference stage the flowers of *H. coronarium* may be at one of several stages depending on their position in the inflorescence. The stage listed is only valid for the specific flower referred to in the table.

Up to the stage of thecae initiation in *H. gardnerianum*, the flowers of *H. coronarium* are ahead of those of *H. gardnerianum* (Table 2); however, the thecae are formed relatively earlier in *H. gardnerianum* than in *H. coronarium*. These comparisons show that the relative timing of developmental events can vary even over a short developmental period. The acceleration of development seen in the early stages of development in *H. coronarium* is not maintained throughout organogenesis.

There are two clear differences between the species in primordium shape. First, the ring primordium of *H. coronarium* is more symmetrical than that of *H. gardnerianum*. That of *H. gardnerianum* is shallowly three lobed with slight depressions between the lobes (Figs. 18, 19). That of *H. coronarium* is more evenly formed except for the enlarged portion that will separate into the posterior petal and fertile stamen (Figs. 36, 37). Second, the floral cup remains more open in *H. gardnerianum* than in *H. coronarium*. By the time the outer androecium is present the floral cup of *H. coronarium* is occluded by the thecae and inner androecial members

(Fig. 39). That of *H. gardnerianum* remains open until filled by the gynoeceum (Fig. 22).

Except for the Lowiaceae and Zingiberaceae, all of the families of the Zingiberales possess gynopleural nectaries. Gynopleural nectaries are nectaries that occur either in the septa of the locular region of the ovary, or in homologous regions (Smets and Cresens 1988). In the Zingiberales these nectaries occur both in the septa (Strelitziaceae: Kronstedt and Walles 1986; Marantaceae, Cannaceae: Pai and Tilak 1965) and in regions homologous to the septa but above (Musaceae: Kirchoff 1992; Costaceae: Newman and Kirchoff 1992) or below (Heliconiaceae: Kirchoff 1992) the locules. The Lowiaceae lack all traces of nectaries except for blind sutures at the base of the style (Kirchoff and Kunze 1995). This distribution, and the position of the Costaceae as the sister group of the Zingiberaceae (Kirchoff 1988a; Kress 1990), makes it highly probable that the epigynous nectaries of the Zingiberaceae are derived from gynopleural nectaries.

This hypothesis was first put forward by Brown (1938) and was supported by the work of Rao et al. (1954), Rao and Pai (1959, 1960), and Rao and Gupte (1961). Rao (1963) and Newman and Kirchoff (1992) discuss the hypothesis in more detail. The data presented here demonstrate that the nectaries of *Hedychium* form in an anterolateral position, approximately above the septa. Their existence in this position lends further support to the idea that the epigynous nectaries of the Zingiberaceae are derived from gynopleural nectaries. This paper also confirms Holttum's (1950) statement that the nectaries arise relatively late in flower development.

In many families of the Zingiberales there is an extension of the ovary that lengthens the closure of the locules. In the Lowiaceae and Strelitziaceae this closure is extended into a very long prolongation, several to many times the length of the locules. In these families the prolongation may function to protect the ovary from pollinator damage (Kirchoff and Kunze 1995). This is important in species where the pollinators pull, poke, or manipulate the flowers in their search for nectar (Frost and Frost 1981; Kress and Stone 1993; Kress et al. 1994). In the Heliconiaceae and Musaceae the closure is prolonged, but is usually shorter in length than the locules (Kirchoff 1992). The prolongation bears the nectaries in the Musaceae, whereas it has much less internal differentiation in the Heliconiaceae. In the Costaceae the prolongation bears the highly modified gynopleural nectaries that characterize this family (Newman and Kirchoff 1992).

In the Zingiberaceae, at least part of the protective function provided by the prolongation may be assumed by the nectaries and the floral tube. The epigynous nectaries sit on top of the ovary tightly wrapped in the floral tube (Holttum 1950; Rao 1963; S.W. Newman and B.K. Kirchoff, unpublished). The major portion of the nectar reservoir lies above the nectaries. Pollinators probing for nectar will encounter the nectaries and the sides of the floral tube before they come in contact with the ovary. This arrangement could restrict damage to nonessential parts of the flower while protecting the ovules.

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