Ovary structure and anatomy in the Heliconiaceae and Musaceae (Zingiberales)

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Ovary anatomy and organography was investigated in five species of *Heliconia* (Heliconiaceae) and three species of *Musa* (Musaceae). The ovaries of both genera may be longitudinally divided into three regions: sublocular, locular, and prolongation. The prolongation is the elongated closure of the top of the locules. The proportions of these regions differ between genera and to a lesser extent among species within a genus. In general, *Heliconia* has a larger sublocular region while the prolongation is larger in *Musa*. These differences are correlated with the occurrence of gynopleural nectaries in the sublocular region of the Heliconiaceae and in the prolongation of the Musaceae. Anatomical and organographic details are related to our knowledge of the development of the ovary and fruit. Many anatomical differences between the genera are correlated with the functions of these regions in the fruit. The structure and homology of the placental trichomes of the Musaceae are discussed, and I conclude that they are not homologous to the arils of the other Zingiberales.

Key words: plant morphology, plant anatomy, nectaries, monocotyledons.

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L'auteur a étudié l'anatomie de l'ovaire et l'organographie chez cinq espèces d'*Heliconia* (Heliconiaceae) et trois espèces de *Musa* (Musaceae). Dans les deux genres, les ovaires peuvent être divisés longitudinalement en trois régions : sub-loculaire, loculaire et prolongation. La prolongation est la fermeture allongée de la partie supérieure des locules. Les proportions de ces régions diffèrent entre les genres et à un moindre degré entre les espèces du même genre. En général, le genre *Heliconia* montre une grande région sub-loculaire alors que la prolongation est prononçée dans le genre *Musa*. Ces différences sont corrélées avec la présence de nectaires gynopleurals dans la région sub-loculaire chez les Heliconiaceae, et dans celle de la prolongation chez les Musaceae. L'auteur pense que les détails anatomiques et organographiques sont reliés au développement de l'ovaire et du fruit. Plusieurs différences anatomiques entre les genres sont corrélées avec les fonctions de ces régions du fruit. L'auteur discute la structure et l'homologie des trichomes placentaires des Musaceae et, en conclusion, ils ne seraient pas homologues avec les arilles des autres Zingiberales.

Mots clés : morphologie végétale, anatomie végétale, nectaires, monocotylédones.

[Traduit par la rédaction]

Introduction

The Zingiberales are a natural order of monocotyledons consisting of eight families (Musaceae, Helliconiaceae, Strelitziaceae, Lowiaceae, Zingiberaceae, Costaceae, Cannaceae, and Marantaceae). Based on taxonomic history (Bentham and Hooker 1883; Petersen 1889; Schumann 1900, 1902, 1904; Winkler 1930; Loesener 1930; Hutchinson 1934, 1959; Nakai 1941; Tomlinson 1962) and overall similarity, the order may be divided into two informal groups of families. These are the banana group, consisting of the four families Musaceae, Heliconiaceae, Strelitziaceae, and Lowiaceae, and the ginger group, consisting of the remaining four families. Although there is a growing consensus that the ginger group is monophyletic, the status of the banana group is equivocal (Dahlgren and Rasmussen 1983; Kress 1990).

The Zingiberales are characterized by epigynous flowers with five or fewer stamens. Of the two informal subdivisions of the order, the banana group has retained the greater number of primitive features in its flowers. The flowers of this group have either six (*Ravenala madagascariensis* (Strelitziaceae), some *Musa* spp. and most *Ensete* spp. (Musaceae)), or more commonly, five polliniferous stamens. In the latter case, the sixth stamen is either suppressed or, in the Heliconiaceae, is represented by a staminode (Andersson 1985; Kress 1984; Kirchoff 1991). In contrast, the families of the ginger group possess at most one functional stamen. In the Marantaceae and Cannaceae, the number of androecial members that produce pollen is reduced to half of one anther (Kirchoff 1991). The remaining androecial members are petaloid staminodes, which have become variously modified to play roles in attracting floral visitors.

The plants of the banana group have diverse habits that range from trees to small herbs. In contrast, floral structure is relatively uniform. The flowers are generally zygomorphic, with epigynous, trilocular ovaries, axile placentation, and many ovules per locule. The Heliconiaceae are an exception to this rule with one basally inserted ovule per locule, and *Musa* subg. *Pallidimusa* was reported to have a unilocular ovary with parietal placentation (Nakai 1948). Septal nectaries were reported in all of the families of the banana group (Dahlgren et al. 1985; Pai and Tilak 1965; Schumann 1900; Schmid 1985), although my own investigations showed that they are lacking from the Lowiaceae (Kirchoff 1988*b*).

The monogeneric Heliconiaceae (*Heliconia*) have the largest number of species in the banana group. All members of this family are herbs with sympodial rhizomes and erect, unbranched, aerial stems. There are three growth habits in the Heliconiaceae (musoid, zingiberoid, cannoid), which differ mainly in the positions of the leaves and the length of the petiole and sheath (Andersson 1985; Kress 1984). Leaf and bract arrangements are distichous throughout. The inflorescence is a terminal thyrse with distichous bracts subtending bracteate cincinni. One of the most notable features of the family are the brightly colored inflorescence bracts that play a role in attracting hummingbird pollinators (Kress 1986).

The Musaceae consist of two genera, *Musa* and *Ensete*. Both genera have large leaves with overlapping leaf bases that form a conspicuous pseudostem. Both the leaves and inflorescence

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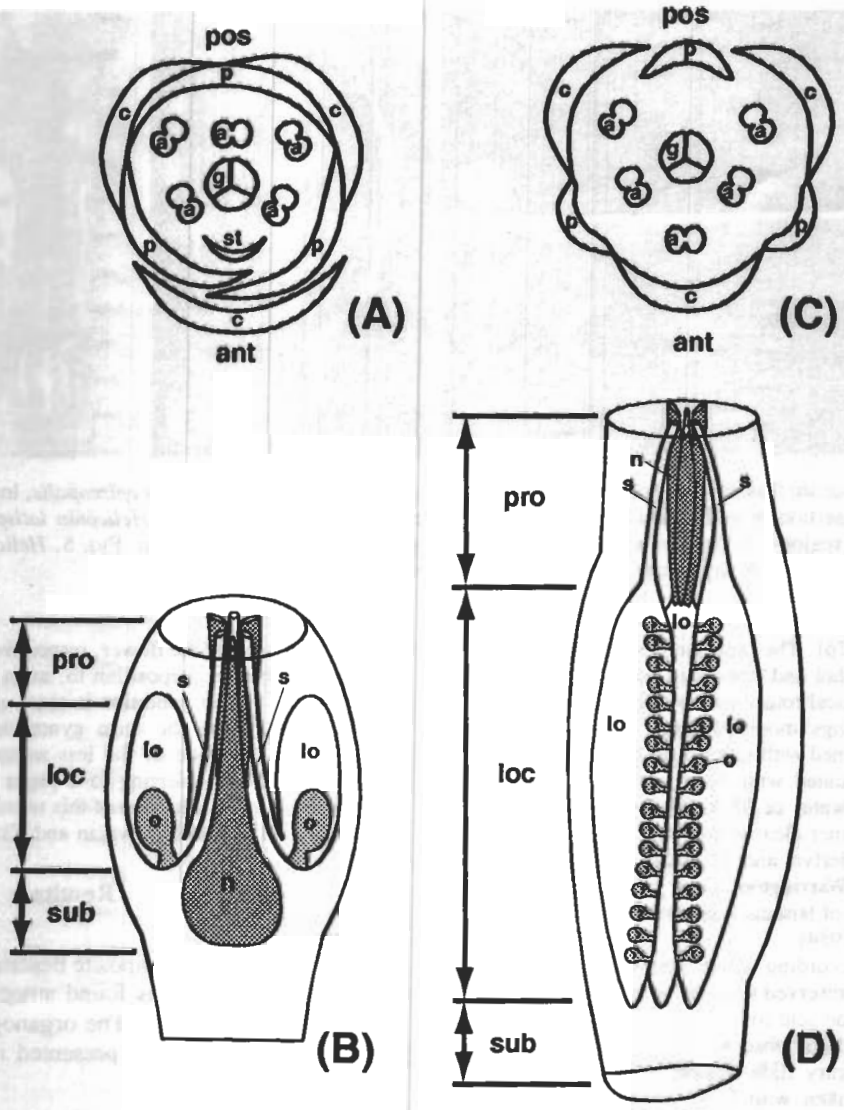


FIG. 1. Freehand diagrams of flower and ovary structure. (A) Heliconiaceae, floral diagram. (B) Heliconiaceae, ovary structure. (C) Musaceae, floral diagram. (D) Musaceae, ovary structure. *a*, androecial member; *ant*, anterior; *c*, sepal; *g*, gynoecium; *lo*, locule; *loc*, locular region; *n*, nectary; *o*, ovule; *p*, petal; *pos*, posterior; *pro*, prolongation; *s*, stylar canal; *st*, staminode; *sub*, sublocular region.

bracts are spirally arranged (Skutch 1927). In *Musa*, renewal shoots are produced from leaf-opposed buds (Fisher 1978), whereas *Ensete* is monocarpic. The inflorescence is a terminal thyrse that protrudes from the center of the overlapping leaf bases. The flowers are bone in hands, which are highly modified, condensed cincinni (Fahn 1953). Dahlgren et al. (1985) stated that the flowers are subtended by recurved, hyaline bracts, but I have not observed these in any of the species known to me.

The flowers of the Musaceae are generally monecious, although hermaphroditic flowers have been reported in *Musa velutina* (Simmonds 1966; Nur 1976), *Musa acuminata* ssp. *banksii*, *Musa schizocarpa* (Simmonds 1966), and *Ensete* spp. (Cheesman 1947). This condition is not found consistently in the latter genus.

The purposes of this study were (*i*) to collect data on floral structure and anatomy for a phylogenetic analysis of the order, (*ii*) to gain a better understanding of nectary structure and evolution in the order, and (*iii*) to provide the requisite anatomical background for detailed studies of floral development.

Material and methods

Mature flowers of the Heliconiaceae and Musaceae were collected at Lyon and Waimea arboreta, Oahu, Hawaii, and from the Duke University Greenhouses, Durham, N.C. Only female flowers of *Musa* were investigated in this study. The following species were studied: (*i*) Heliconiaceae: *Heliconia episcopalis* Vell. (Waimea accession No. 78P284, voucher: Lau 2710 at BISH); *Heliconia indica* Lam. (Waimea accession No. 79P1202, voucher: Kirchoff 87-109 at BISH), *Heliconia latispatha* Benth. (Waimea accession No. 74P1142, voucher: Kirchoff 87-107 at BISH), *Helilconia psittacorum* L. f. (Waimea accession No. 76P779 and 75P1181, voucher: Kirchoff 87-111 at BISH), *Heliconia clinophylla* R. R. Smith (Duke Greenhouse, unaccessioned); (*ii*) Musaceae: *Musa velutina* H. Wendl. & Drude (Lyon unaccessioned, voucher: Kirchoff 88-144 at BISH); *Musa ornata* Roxburgh (Waimea accession No. 77P550, voucher: Kirchoff 87-116 at BISH); *Musa* cv. Go Sai Yung (Waimea accession No. 82P86, voucher: Kirchoff 87-117 at BISH).

Specimens were fixed and stored in formalin – acetic acid – alcohol (FAA) (Berlyn and Miksche 1976). Dehydration was carried out following one of two protocols, either through a *n*-butyl or *t*-butyl alcohol series (Berlyn and Miksche 1976) or with 2,2-dimethoxypro-

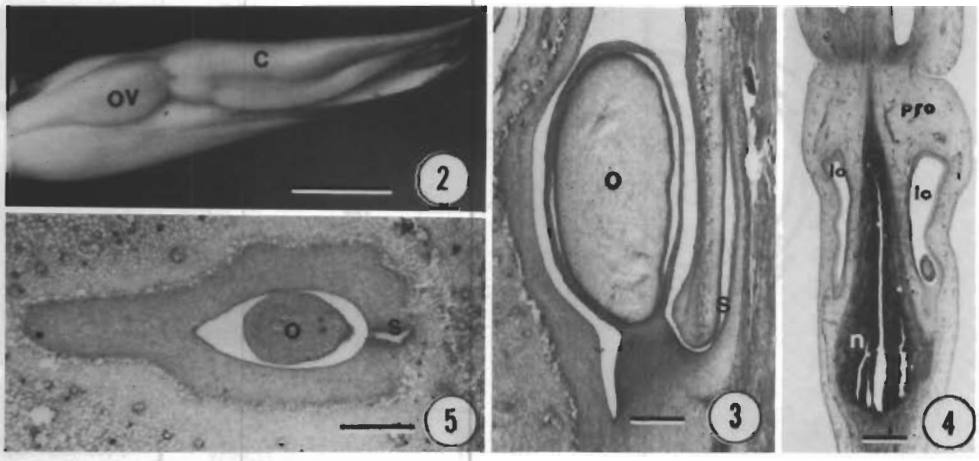


FIG. 2. *Heliconia indica*, mature flower. *c*, calyx; *ov*, ovary. Scale bar = 10 mm. FIG. 3. *Heliconia episcopalis*, longitudinal section showing insertion of ovule (*o*) and insertion of stylar canal (*s*) into locule. Scale bar = 0.25 mm. FIG. 4. *Heliconia latispatha*, longitudinal section of flower with three distinct regions. *lo*, locule; *n*, nectary; *pro*, prolongation. Scale bar = 1.0 mm. FIG. 5. *Heliconia indica*, cross section though base of locule with insertion of stylar canal (*s*). *o*, ovule. Scale bar = 0.5 mm.

pane (Postek and Tucker 1976). The specimens were transferred to 100% *n*-butyl or *t*-butyl alcohol and embedded in paraffin. Sections were cut on an American Optical rotary microtome at 10–12 μm and mounted on slides using Bissings' modified Haupt's adhesive (Bissing 1974). The sections were stained with safranin and fast green (Berlyn and Miksche 1976) and mounted with Permount. Additional fixed material was transferred to water or 95% EtOH and freehand sectioned. The sections were either cleared and observed unstained, or stained in toluidine blue (Berlyn and Miksche 1976). Aqua-poly mount (Polysciences, Inc., Warrington, Penn.) was used to mount these sections. The presence of tannins was verified by staining with 1% ferric chloride (Gahan 1984).

Clearings were prepared according to indications given by O'Brien and McCully (1981). FAA-preserved sections were washed in water, followed by full strength lactic acid for 1 to many days. The cleared sections were left unmounted and observed under an Olympus SZH stereo microscope on temporary slide mounts.

Photomicrographs were taken with Leitz Ortholux II and Wild M5A photomicroscopes using Kodak Technical Pan film.

Measurements were made from median longitudinal sections of the ovaries using a vernier caliper calibrated in millimetres. Measurements were taken from flowers as close to anthesis as possible. Only a few measurements per species were possible owing to the difficulty in collecting sufficient ovaries at the correct stage.

The vascular pattern presented for the Heliconiaceae is based on detailed investigations of *H. indica*, *H. episcopalis*, and *H. clinophylla*. The vasculature of *H. latispatha* and *H. psittacorum* was not investigated in detail. The vasculature of the Musaceae was not investigated in this study.

Terminology

Much of the terminology used in describing the sides of a flower refers to the relation of the flower to the axis on which it is borne. In the highly modified cincinni of the Heliconiaceae (Lane 1955) and Musaceae (Fahn 1953) it is difficult to determine the position of this axis and it is beyond the scope of this paper to do so. Consequently, my designation of the median, anterior, and posterior regions of the flowers are somewhat arbitrary. For the purposes of this paper the median plane of the flower bisects the flower pedicel and the main axis of the flower and passes through the free sepal (Heliconiaceae) or petal (Musaceae) (Fig. 1). I refer to the side of the ovary adjacent to the free sepal (Heliconiaceae) or away from the free petal (Musaceae) as anterior, while the opposite side of the flower is the posterior side (Fig. 1). Anterolateral and posterolateral refer to the lateral regions of the ovary, just off the median plane, on the anterior and posterior sides of the flower, respectively. When I use anatomical terms jointed by the preposition to, as in rectangular to cuboidal, I mean that the former condition is more common while the latter is less common. I use the term gynopleural nectaries (Smets and Cresens 1988) in place of the less accurate term septal nectaries, except where I am referring to a paper that uses the latter term. Justifications for the adoption of this terminology are given in Smets and Cresens (1988) and Newman and Kirchoff (1992).

Results

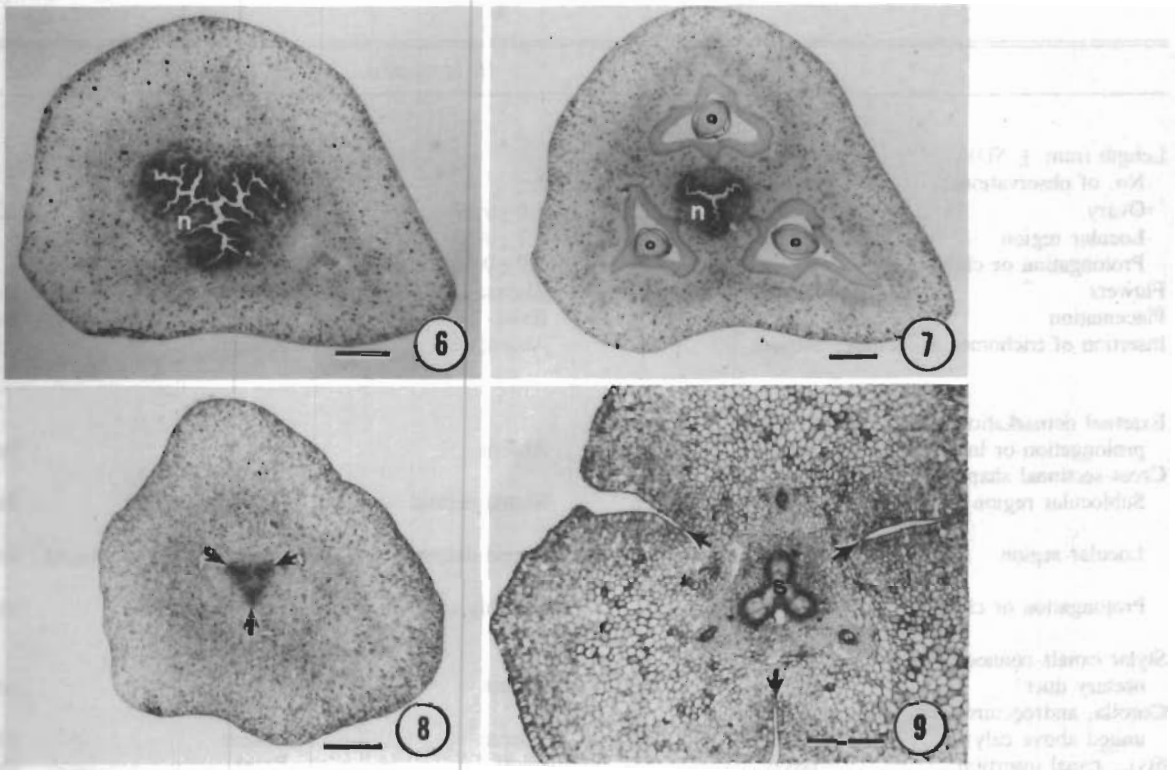
Heliconiaceae

The following is a composite description that includes all of the significant variations found among the *Heliconia* species investigated in the study. The organography and histology of the individual species are presented in Table 1.

Organography

The flowers of the Heliconiaceae are bisexual and zygomorphic (Figs. 1A, 2). The two trimerous perianth whorls are united at the base into a short floral tubes. At the top of this tube the median sepal becomes free from the other perianth members, while the remaining members are united into a lip through the adnation of the sepals to the petals (Fig. 1A). The androecium consists of six androecial members arranged in two whorls. There are five pollen-bearing stamens and a single staminode, inserted opposite the free sepal. The ovary is inferior and trilocular wth one basally inserted anatropous ovule per locule (Fig. 3). Gynopleural nectaries are present beginning below and extending through the locular region of the ovary.

In most of the species of *Heliconia* investigated in this study the ovary may be longitudinally divided into three distinct regions (Figs. 1B, 4). The central and most prominent region is that containing the three locules (locular region). Below this is the sublocular region, which varies from extremely short to more than half of the length of the locules. In the later case, the sublocular region contains the major portion of the nectary (Fig. 4, *n*). Above the locules, the ovary is closed by a cap of tissue. In some species, this closure is elongated into a prolongation. In these species the main distinction between the locular region and the prolongation is the lack of locules in the



FIGS. 6–9. *Heliconia indica*, cross sections. Fig. 6. Sublocular region. *n*, nectary. Scale bar = 1.0 mm. Fig. 7. Locular region. *n*, nectary; *o*, ovule. Scale bar = 1.0 mm. Fig. 8. Prolongation. Arrows point to nectary ducts. Scale bar = 1.0 mm. Fig. 9. Style showing exit of nectary ducts (arrows) and triradiate stylar canal (*s*). Scale bar = 0.25 mm.

latter. There may or may not be an external difference indicating the presence of the prolongation. The length of the ovary ranges from 5.5 to 15.3 mm (Table 1).

Stylar canals arise from the base of the locules, just above and toward the central axis from the insertion of the ovules (Figs. 1B, 3, 5, *s*). They traverse the locular region and the prolongation as three separate canals, located just interior to the locules. The canals either enter the style directly or, just below the insertion of the style, they fuse to form a single triradiate canal that enters the style. In one species (*H. episcopalis*) there is a solid column of tissue uniting the petals, androecium and style above the attachment of the sepals. The stylar canals traverse this tissue and enter the style.

A portion of the nectary is located below the locules in all of the species in this study (Fig. 1B). Additional nectariferous tissue occurs in the central axis of the flower in the locular region (Figs. 1B, 4) and in some species persists into the prolongation. The nectary duct is triradiate throughout its length (Figs. 6, 7). The arms of the duct lie in the central axis throughout the ovary. Just below the insertion of the perianth, the nectariferous tissue diminishes, and the three arms of the nectary duct diverge to form three separate ducts (Fig. 8, arrows). These ducts enter the base of the style, then exit at the side of the style a short distance above its insertion (Fig. 9, arrows).

Histology

Sublocular region—Figure 6 shows a cross section through the sublocular region of *H. indica*. Epidermis is simple, of rectangular, cuboidal, isodiametric or columnar cells with an

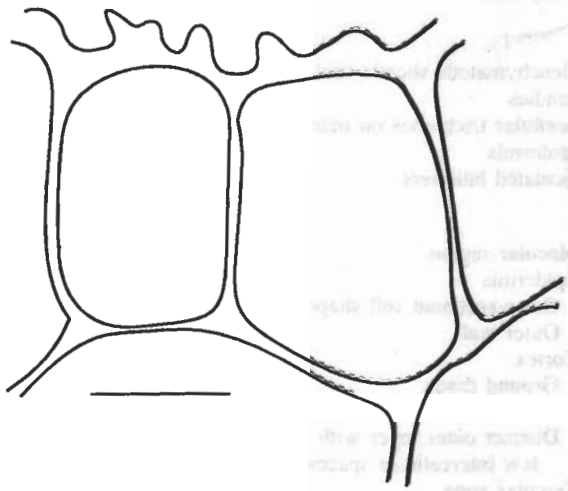


FIG. 10. *Heliconia indica*, camera lucida drawing, cross section of epidermis showing irregular thickening of outer walls. Scale bar = 10 μm.

irregularly thickened outer wall (Fig. 10). Cortex consists of aerenchyma or parenchyma interspersed with many large intercellular spaces; outer one to three layers with few intercellular spaces and distinct from inner layers. Vascular zone is located interior to the cortex, with considerable diversity in composition among species. The general pattern is as follows: ground tissue of isodiametric parenchyma cells, occasionally with fewer intercellular spaces than in cortex; two to five

TABLE 1. Ovary structure and

	H. indica	*H. latispatha*	*H. psittacorum*	*H. episcopalis*
				Organ
Length (mm ± SD)				
No. of observations	3	3	3	2
Ovary	15.3±1.2	8.6±0.17	6.9±0.06	10.3±0.14
Locular region	7.5[a]	4.7±0.19	4.7±0.21	6.3±0.28
Prolongation or closure	6.2[a]	1.9±0.18	0.7±0.30	1.3±0.14
Flowers	Bisexual	Bisexual	Bisexual	Bisexual
Placentation	Basal	Basal	Basal	Basal
Insertion of trichomes in locules	Absent	Absent	Absent	Absent
External demarkation of prolongation or locule closure	Absent	Absent	Absent	Present
Cross-sectional shape of				
Sublocular region	Deltoid	Round-deltoid	Roughly circular	Round-deltoid
Locular region	Round-deltoid to winged	Round-deltoid	Round-deltoid to winged	Irregular
Prolongation or closure	Circular to round-deltoid	Roughly circular	Roughly circular	Three lobed
Stylar canals connected to nectary duct	Absent	Absent	Present	Absent
Corolla, androecium, style united above calyx	Absent	Absent	Absent	Absent
Stylar canal insertion	Basal	Basal	Basal	Basal
Stylar canals fuse below style	Present	Absent	Present	Absent
Nectary secretory tissue				
Below locules	Present	Present	Present	Present
In locular region	Small amount	Small amount	Small amount	Small amount
In prolongation or closure	Small amount	Small amount	Absent	Small amount
Nectary duct	Triradiate dividing into three ducts distally	Triradiate throughout	Triradiate throughout	Triradiate dividing into three ducts distally
Collenchymatous sheaths and bundles	Absent	Absent	Absent	Absent
Unicellular trichomes on outer epidermis	Absent	Absent	Absent	Absent
Articulated laticifers	Absent	Absent	Absent	Absent
				Histo
Sublocular region				
Epidermis				
Cross-sectional cell shape	Rectangular to cuboidal	Rectangular to cuboidal	Cuboidal to isodiametric	Columnar to cuboidal
Outer wall	Irregularly thickened	Irregularly thickened	Irregularly thickened	Irregularly thickened
Cortex				
Ground tissue	Aerenchyma	Aerenchyma	Aerenchyma with thick primary walls	Aerenchyma
Distinct outer layer with few intercellular spaces	Present	Present	Present	Present
Vascular zone				
Cylinders of vascular bundles	3–5 irregular	2–3 irregular	1 distinct, 1 indistinct	2–3 irregular
Scattered vascular bundles	Absent	Absent	Absent	Absent
Aerenchyma surrounding central axis	Absent	Absent	Absent	Absent
Arms of nectary duct branched	Present	Present	Present	Absent
Raphid sacs in vascular zone	Present	Absent	Absent	Present
Tanniniferous idioblast distribution	Throughout ground tissue	Throughout ground tissue	Outer vascular zone	Cortex

anatomy in the individual species

H. clinophylla	*M. velutina*	*M. ornata*	*M.* cv. Go Sai Yung
ography			
3	4	4	3
5.5±0.12	33±2	45±2	57±3
3.3±0.26	21±0.7	34±2	35±3
0.9±0.06	7±0.5	3±0	9±0.8
Bisexual	Unisexual	Unisexual	Unisexual
Basal	Axial	Axial	Axial
Absent	Present on raised portions of placentas and between ovules	Present on raised portions of placentas and between ovules	Present on lower portions of funiculus, raised portions of placentas and between ovules
Absent	Absent	Absent	Absent
Round-deltoid	Rounded triangular or trapezoidal	Rounded triangular or trapezoidal	Pentagonal or rounded triangular
Round-deltoid	Rounded triangular or trapezoidal	Rounded triangular or trapezoidal	Pentagonal or rounded triangular or trapezoidal
Circular to round-deltoid	Rounded triangular or trapezoidal	Rounded triangular or trapezoidal	Pentagonal or rounded triangular or trapezoidal
Absent	Absent	Absent	Absent
Present	Absent	Absent	Absent
Basal	Apial	Apical	Apical
Absent	Absent	Absent	Absent
Present	Absent	Absent	Absent
Present	Only at top of locules	Only at top of locules	Only at top of locules
Present	Present	Present	Present
Triradiate dividing into three ducts distally	Six-armed becoming triradiate distally, 3 separate ducts below style	Six-armed becoming triradiate distally, 3 separate ducts below style	Six-armed becoming triradiate distally, 3 separatae ducts below style
Absent	Present	Present	Present
Absent	Present	Absent	Absent
Absent	Present	Present	Present
logy			
Rectangular	Moderately papillate	Moderately papillate	Slightly convex
Irregularly thickened	Not thickened	Slightly thickened	Not thickened
Parenchyma with large intercellular spaces	Parenchyma with small intercellular spaces	Parenchyma with small intercellular spaces	Parenchyma with small intercellular spaces
Present	Absent	Absent	Absent
1–2, additional bundles near nectary	Absent, but central group present	Absent, but central group present	Absent, but central group present
Absent	Present	Present	Present
Absent	Present	Present	Present
Present	na	na	na
Present	Absent	Present in cortex	Absent
Cortex, vascular zone	Throughout ground tissue	Throughout ground tissue	Throughout ground tissue

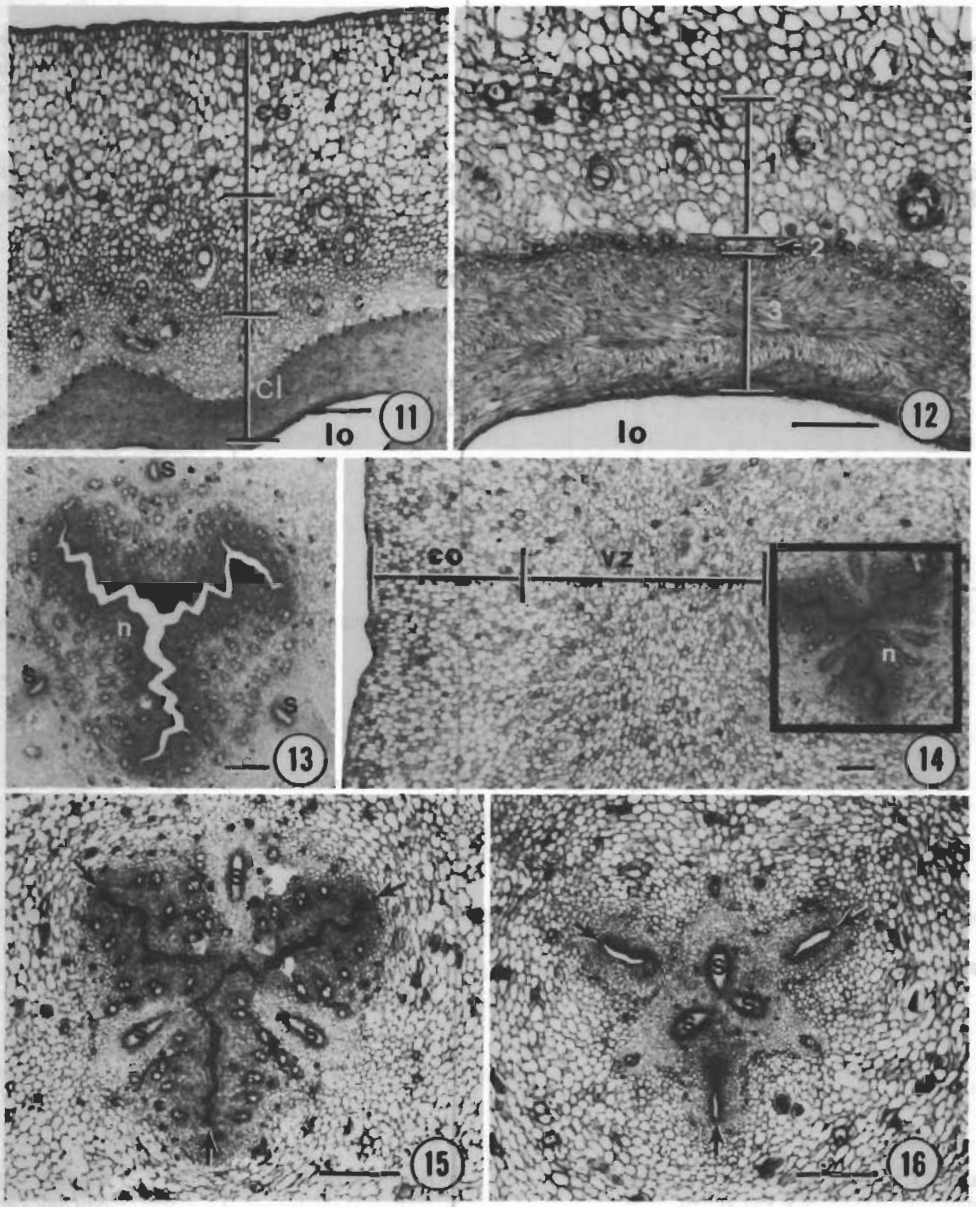
TABLE 1

	H. indica	*H. latispatha*	*H. psittacorum*	*H. episcopalis*
Locular region				
Epidermis				
Cross-sectional cell shape	Rectangular to cuboidal	Rectangular to cuboidal	Columnar to cuboidal	Cuboidal to rectangular
Outer wall	Irregularly thickened	Irregularly thickened	Irregularly thickened	Irregularly thickened
Cortex				
Intercellular spaces in ground tissue	Small	Small	Small	Large
Distinct outer layer with few intercellular spaces	Present	Present	Present	Prsent
Vascular zone				
Ground tissue	Distinct	Distinct	Distinct	Indistinct
Ground tissue of	Parenchyma	Parenchyma	Parenchyma to aerenchyma, cells with thickened walls	Parenchyma
Cylinder(s) of vascular bundles	Absent	Absent	2–3 irregular	1–2
Scattered vascular bundles	Present	Present	Absent	Absent
Circumlocular zone				
No. of distinct layers	3	3	3	3
Ground tissue of	Parenchyma	Parenchyma	Parenchyma	Parenchyma
Circumlocular bundles primarily	Longitudinal	Longitudinal	Longitudinal	Longitudinal
Inverted vascular bundles in central axis	Present	Present	Present	Present
Layer of crystalliferous cells	Discontinuous	Discontinuous	Continuous	2–3, continuous
Distinct endocarp lacking intercellular spaces	Present	Present	Present	Present
Layers of parenchyma surrounding locules	Absent	Absent	Absent	Absent
Locule epithelium cells	Rectangular	Rectangular to cuboidal	Rectangular	Rectangular to cuboidal
Articulated laticifers	Absent	Absent	Absent	Absent
Raphid sac distribution	Cortex, nectary	Cortex, nectary	Cortex, nectary	Cortex, nectary, between vascular bundles
Tanniniferous idioblast distribution	Throughout ground tissue	Throughout ground tissue	Absent	Outermost cortex
Prolongation	Present	Present	Absent	Present, short
Epidermis				
Cross-sectional cell shape	Cuboidal	Cuboidal	na	Cuboidal to columnar
Outer wall	Irregularly thickened	Irregularly thickened	na	Irregularly thickened
Cortex				
Intercellular spaces in ground tissue	Few, small	Small	na	Small
Distinct outer layer with few intercellular spaces	Present	Present	na	Present
Vascular zone				
Vascular plexus	Absent	Absent	na	Present
Perianth vasculature restricted to more or less well defined zone	Present	Present	na	Absent
Anastomoses among bundles of circumlocular zone over tops of locules	Absent	Absent	na	Present as part of plexus
Aerenchyma interior to vascular zone	Absent	Absent	na	Absent
Stylar canal epithelium	Columnar	Columnar	na	Columnar
Raphid sac distribution in ground tissue	Cortex	Cortex, between androecial bundles	na	Cortex
Tanniniferous idioblast distribution	Absent	Absent	na	Infrequent in ground tissue

[a]No. of observations = 1.

(*concluded*)

H. clinophylla	*M. velutina*	*M. ornata*	*M.* cv. Go Sai Yung
Rectangular to cuboidal	Moderately papillate	Moderately papillate	Slightly convex
Irregularly thickened	Not thickened	Slightly thickened	Not thickened
Large	Small	Small	Small
Present	Absent	Absent	Absent
Indistinct	Distinct	Distinct	Distinct
Parenchyma	Parenchyma	Parenchyma	Parenchyma
Absent	Absent	Absent	Absent
Present	Present	Present	Present
3	2	2	2
Parenchyma	Aerenchyma	Aerenchyma	Aerenchyma
Longitudinal	Radial	Radial	Radial
Present	Absent	Absent	Absent
Continuous	Absent	Absent	Absent
Present	Absent	Absent	Absent
Absent	1–3	1–2	ca. 5, cells larger
Rectangular to cuboidal	Rectangular	Rectangular	Cuboidal to rectangular
Absent	Present	Present	Present
Cortex, between vascular bundles	Occasional in vascular zone	Occasional in vascular zone	Occasional in vascular zone
Cortex	Throughout ground tissue	Throughout ground tissue	Throughout ground tissue
Present, very short	Present	Present	Present
Cuboidal to rectangular	Moderately papillate	Moderately papillate	Slightly convex
Irregularly thickened	Not thickened	Slightly thickened	Not thickened
Small	Small	Small	Small
Present	Absent	Absent	Absent
Absent	Absent	Absent	Absent
Present	Absent	Absent	Absent
Present	Absent	Absent	Absent
Absent	Present	Present	Present
Columnar	Rectangular	Rectangular	Rectangular
Cortex, vascular zone ground tissue	Vascular zone	Vascular zone	Vascular zone
Absent	Throughout ground tissue	Throughout ground tissue	Throughout ground tissue



FIGS. 11–16. *Heliconia indica*, cross sections. Fig. 11. Ovary wall in locular region. *cl*, circumlocular zone; *co*, cortex; *lo*, locule; *vz*, vascular zone. Scale bar = 0.25 mm. Fig. 12. Circumlocular zone. 1, outermost layer of parenchyma with embedded vascular bundles; 2, crystalliferous layer; 3, endocarp; *lo*, locule. Scale bar = 0.125 mm. Fig. 13. Nectary (*n*) and stylar canals (*s*) in locular region. Scale bar = 0.25 mm. Fig. 14. Prolongation. An area similar to that in the box is enlarged in Fig. 15. *co*, cortex; *n*, nectary; *vz*, vascular zone. Scale bar = 0.25 mm. Fig. 15. Nectary duct (arrows) and stylar canals (*s*) in proximal portion of prolongation. Enlargement of area similar to that in the box in Fig. 14. Scale bar = 0.25 mm. Fig. 16. Nectary ducts (arrows) and stylar canals (*s*) in distal portion of prolongation. Scale bar = 0.25 mm.

irregular cylinders of collateral vascular bundles, in some species vessel size decreases and number of vessels increases toward the central axis. In *H. psittacorum* the ground tissue is of parenchyma, with smaller cells and fewer intercellular spaces than in the cortex; vascular bundles are in one distinct (outer) and one indistinct (inner) cylinder; outer cylinder bundles are larger than those of the inner, all bundles collateral with normal orientation of xylem and phloem; inner vascular cylinder is adjacent to the nectary tissue that contains smaller, most likely amphicribal bundles. In *H. clinophylla* the ground tissue is of parenchyma with many intercellular spaces; cell size and size of intercellular spaces decreases from cortex to nectary; cell wall thickness increases from cortex to the middle of vascular zone then stabilizes, or decreases slightly to the nectary; there are one to two cylinders of collateral vascular bundles with normal orientation of xylem and phloem, each bundle with a sheath of colorless parenchyma cells, sheath cells opposite the xylem approximately twice the diameter of those opposite the phloem; a number of irregular cylinders of small vascular bundles are located adjacent to the nectary, the number increasing acropetally through the sublocular region. Nectary tissue is of densely cytoplasmic cells surrounding a triradiate nectary duct. The arms of duct are branched or unbranched and lined with a columnar epithelium of densely cytoplasmic cells. Many small vascular bundles are present in the lobes of the nectary. Raphide sacs are absent from outer-

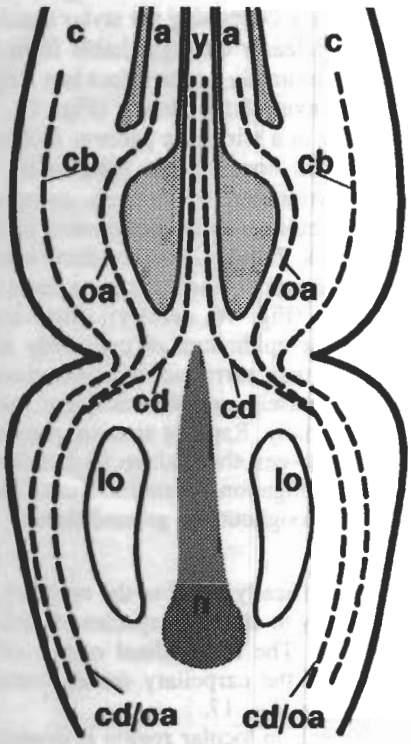


FIG. 17. Longitudinal diagram of *Heliconia* flower showing the path of some of the major vascular strands. *a*, androecial member; *c*, sepal; *cb*, median vascular strand of sepal; *cd*, carpellary dorsal; *cd/oa*, common carpellary dorsal/outer androecial strand; *lo*, locule; *n*, nectary; *oa*, outer androecial strand; *y*, style.

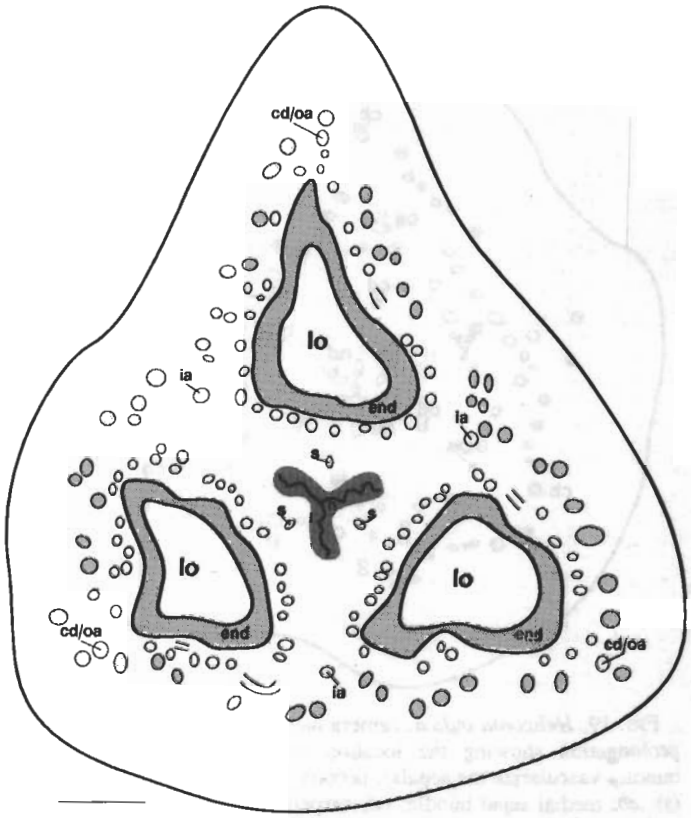


FIG. 18. *Heliconia indica*, camera lucida drawing, cross section of locular region showing the location of the vascular bundles (shaded bundles vascularize the perianth), nectary (*n*) and stylar canals (*s*). *cd/oa*, common carpellary dorsal/outer androecial bundle; *end*, endocarp; *ia*, inner androecial bundle; *lo*, locule. Scale bar = 1 mm.

most cortical layers but present throughout the rest of the cortex, are present or absent from the ground tissue of the vascular zone, and are present in the nectary. Tanniniferous idioblasts are always present, but their distribution varies among species. Starch grains are prevalent in the parenchyma around vascular bundles in *H. psittacorum* and *H. clinophylla*.

Locular region—Figure 7 shows a cross section through the locular region of *H. indica*. Epidermis is of columnar, rectangular, or cuboidal cells with irregularly thickened outer walls (Fig. 10). Cortex consists of ground tissue of loosely or densely packed vacuolate parenchyma cells. Directly under the epidermis the cells are smaller and there are often few or no intercellular spaces. The size of the intercellular spaces increases towards the vascular zone (Fig. 11, *co*). Vascular zone is distinct or indistinct, located between cortex and circumlocular zone; if distinct, it has ground tissue of parenchyma cells (occasionally aerenchyma); if indistinct, vascular bundles occur at the border of the cortex and circumlocular zone. Vascular bundles are irregularly arranged, or arranged into one to three cylinders, are collateral, and most have normal orientation of xylem and phloem. Circumlocular zone is three layered (Figs. 11, *cl*, 12). Outermost (first) layer has ground tissue of parenchyma cells with embedded longitudinal vascular bundles; the vascular bundles are smaller than in the main vascular zone and their xylem poles face the locule, giving bundles in the central axis an inverted orientation. Second layer is a continuous, or discontinuous, layer of crystalliferous parenchyma cells just interior to the vascular bundles; the structure of this layer varies among species (Table 1). Third layer, the endocarp, is adjacent to the locule epithelium and is of densely packed layers of longitudinally and tangentially elongated cells, the layers alternating with each other and discontinuous, with few or no intercellular spaces. The radially elongated cells appear irregular-fusiform in cross section with nuclei visible in many of the cells. Locule epithelium is a single layer of rectangular to cuboidal cells. Septa are composed of vacuolate parenchyma cells with many intercellular spaces present in some species. The septal tissue is aerenchyma at the center of septa in *H. latispatha*. There are three stylar canals, alternating in position with the arms of the nectary duct (Fig. 13, *s*); each canal is lined with a densely cytoplasmic, columnar epidermis. In *H. psittacorum*, stylar canals are connected to the nectary ducts at some level by irregular fissures. Nectary tissue is of densely cytoplasmic cells surrounding a triradiate duct (Fig. 13). The duct is lined with a columnar epithelium of densely cytoplasmic cells, not readily distinguishable from the underlying cells except by shape. The amount of nectary tissue varies among the species. Vascular bundles are small and numerous, interspersed with the secretory tissue. Raphide sacs are present in the cortex, extending into the regions between the vascular bundles in some species, are present in the nectary tissue and absent elsewhere. Their abundance varies greatly among species. Tanniniferous idioblasts are present or absent. When present, they are either restricted to the cortex or found throughout the ground tissue of the locular region (except in the endocarp). In the latter case, highest concentration is usually found in the central axis, surrounding the nectaries.

Prolongation—This region is present or absent as an extended region of tissue closing the locules. There is little

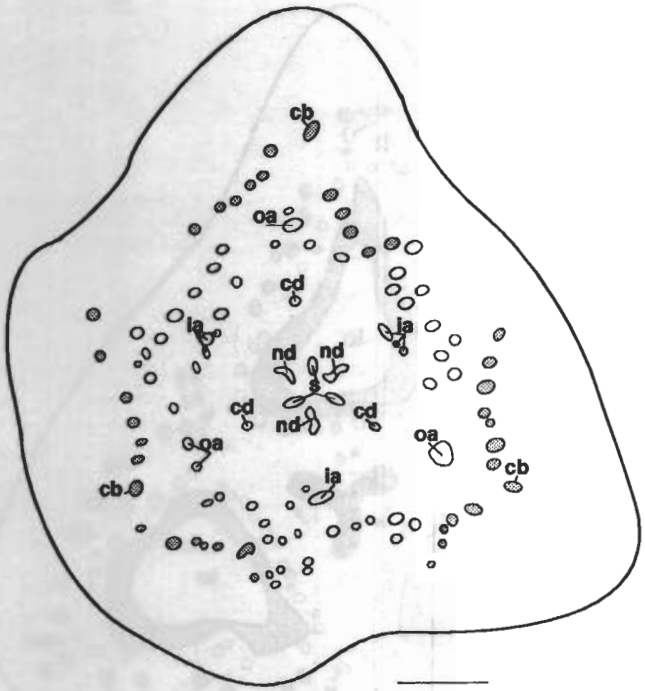


FIG. 19. *Heliconia indica*, camera lucida drawing, cross section of prolongation showing the location of vascular bundles (shaded bundles vascularize the sepals), nectary ducts (*nd*), and stylar canals (*s*). *cb*, medial sepal bundle; *cd*, carpellary dorsal bundle; *ia*, inner androecial bundle; *oa*, outer androecial bundle. Scale bar = 1 mm.

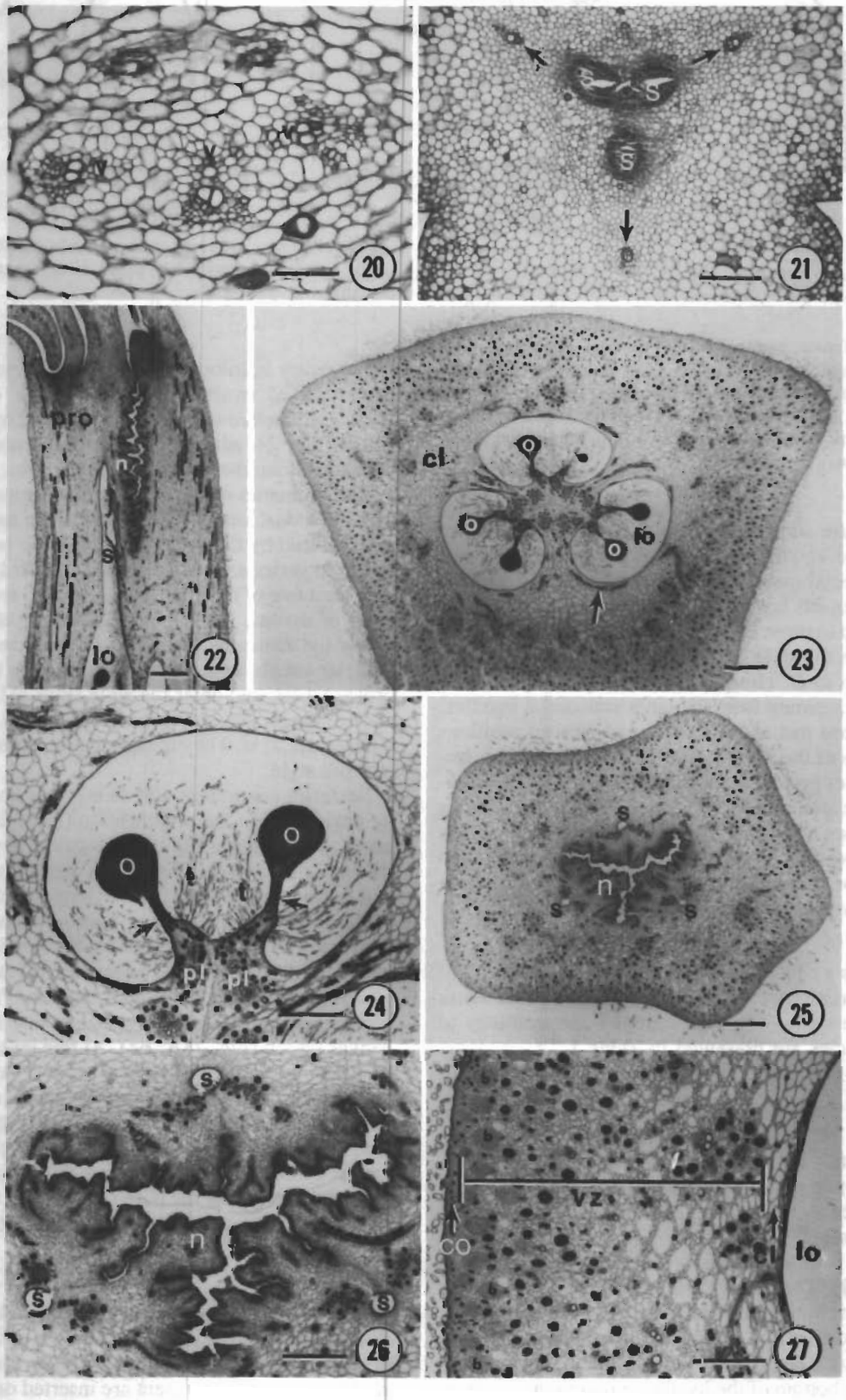
zonation in the prolongation compared with the locular region. Figure 8 shows a cross section through the prolongation of *H. indica*. Epidermis is simple, of cuboidal, rectangular or columnar cells with irregularly thickened outer walls. Cortex (Fig. 14, *co*) consists of ground tissue of vacuolate parenchyma cells, the outermost cells frequently smaller and with fewer intercellular spaces. Vascular zone (Fig. 14, *vz*) has two possible arrangements of tissue: (*i*) an elaborate vascular plexus extending from below the top of the locules to the attachment of the perianth or (*ii*) perianth vasculature roughly arranged into two cylinders, restricted to a more or less well defined zone, with inner androecial and carpellary dorsals/outer androecial bundles located near the central axis; most bundles collateral with normal orientation of xylem and phloem, but androecial bundles often oriented obliquely or bicollateral. In *H. clinophylla* there are numerous anastomoses over the tops of the locules between the bundles of the circumlocular zone. There are three stylar canals; located proximally between the arms of the triradiate nectary duct (Fig. 15, *s*); located distally in the center of the central axis; lined with an epithelium of densely cytoplasmic, columnar cells, or with normal parenchyma cells. The tissue containing the stylar canals consists of smaller cells and is clearly distinguishable from surrounding tissues (Fig. 16). Proximally nectary duct is a single triradiate duct in the central axis of the flower (Fig. 15, arrows), or three separate ducts in a triradiate pattern. In both cases, the lumina are small or nonexistent, lined with a columnar epithelium and surrounded by densely cytoplasmic cells; numerous small vascular bundles are present in the positions of carpellary ventrals. Distally, nectary ducts are the same as proximally or divide to form three separate ducts radially outside the central axis (Fig. 16, arrows); ducts are lined with cuboidal to columnar epithelium of cells only slightly more densely cytoplasmic than surrounding tissue; tissue surrounding ducts is of nondensely cytoplasmic cells; the vasculature is the same as proximally. Raphide sacs are present in the cortex, occasionally between the androecial bundles and in the center of the prolongation. Tanniniferous idioblasts are present or absent throughout the ground tissue.

Vasculature

Except where specifically noted to the contrary, the following descriptions apply to all of the species of *Heliconia* investigated in this study. The longitudinal course of the median sepal bundles and of the carpellary dorsals/outer androecial bundles are shown in Fig. 17.

Perianth vasculature in locular region is organized into one regular cylinder (several irregular cylinders in *H. clinophylla*) of vascular bundles (Fig. 18, shaded bundles). In the prolongation, the bundles are arranged in positions to vascularize the perianth. Bundles vascularizing a sepal are arranged in a single arc outside the petal vasculature (Fig. 19, shaded bundles); the medial bundle of a sepal is radially exterior to the other sepal bundles (Fig. 19, *cb*). Petals receive one central arc of bundles and except in *H. psittacorum* and *H. clinophylla*, two lateral arcs (not depicted in Fig. 19). Except in *H. episcopalis* (see below), few or no anastomoses occur among the main perianth bundles in the mature flower. Anastomoses occur between the perianth bundles and the bundles of the circumlocular region. Stamen and staminode vasculature consists of groups of (1−)3(−4) closely associated vascular strands (Fig. 20, *v*). In the locular region the inner androecial bundles are located outside circumlocular zone, radially exterior to septa but often interior to perianth vasculature (Fig. 18, *ia*). Common carpellary dorsal/outer androecial bundles are located radially outside the circumlocular zone, approximately opposite centerline of the locule (Fig. 18, *cd/oa*). In the prolongation, the common dorsal/outer androecial bundles split to form outer androecial bundles and carpellary dorsals (Fig. 17, *cd*, *oa*). All androecial bundles arch over locules, but not as tightly as carpellary dorsals (see below). Each androecial bundle branches, producing approximately three strands, all of which enter one stamen. Vascular bundles

FIG. 20. *Heliconia indica*, cross section of three closely associated vascular bundles (*v*) constituting an androecial trace. Scale bar = 67 μm. FIG. 21. *Heliconia indica*, cross section of the style showing three carpellary dorsals (arrows) and stylar canals (*s*). Scale bar = 0.125 mm. FIGS. 22–27. *Musa velutina*. Fig. 22. Longitudinal section of the upper locular region and prolongation showing the nectary (*n*) and one stylar canal (*s*). *lo*, locule; *pro*, prolongation. Scale bar = 1.0 mm. Fig. 23. Cross section of the locular region. Arrow points to circumlocular vascular bundle. *cl*, circumlocular zone; *lo*, locule; *o*, ovule. Scale bar = 1.0 mm. Fig. 24. Cross section of a locule showing insertions of trichomes (*t*) on the placentas. Arrows indicate the point of attachment of the funiculus to the placentas. *o*, ovule; *pl*, placental vascular strand. Scale bar = 0.5 mm. Fig. 25. Cross section of the prolongation. *n*, nectary; *s*, stylar canal. Scale bar = 1.0 mm. Fig. 26. Cross section of nectary and stylar canal in the distal prolongation. *n*, nectary; *s*, stylar canal. Scale bar = 0.5 mm. Fig. 27. Cross section of ovary wall in the locular region. The circumlocular zone (*cl*) is small in this photograph. *co*, cortex; *lo*, locule; *vz*, vascular zone. Scale bar = 0.5 mm.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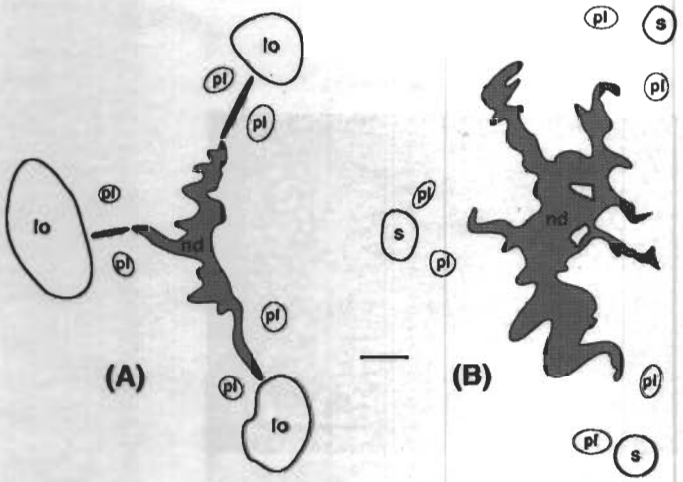

FIG. 28. *Musa velutina*, camera lucida drawings of nectary ducts (*nd*, shaded), placental vascular bundles (*pl*), and stylar canals (*s*). (A) Level of proximal prolongation. The main arms of the duct are opposite the locules. (B) Level more distal in prolongation. Arms of the nectary duct occur opposite the locules and in two of the septa. Scale bar = 0.3 mm.

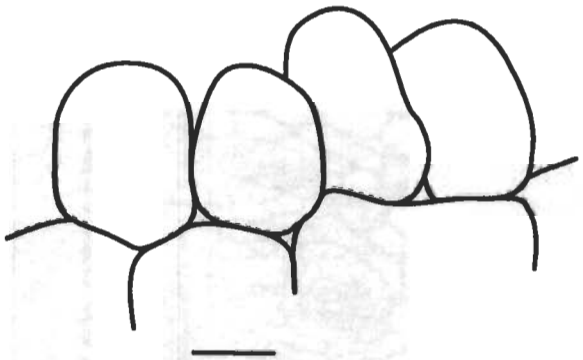

FIG. 29. *Musa velutina*, camera lucida drawing of a cross section of the columnar, moderately papillate epidermal cells. Scale bar = 10 μm.

of the staminode are smaller than those of stamens; in other respects staminode vasculature is identical to vasculature of other outer androecial members. Style vasculature is of three small carpellary dorsals borne on the same radii as the locules (Fig. 21), with two to three vessels per bundle; carpellary ventrals are lacking in the style, but one vessel in the position of a ventral was seen in *H. clinophylla*. In the prolongation the carpellary dorsals separate from the outer androecial bundles, arch strongly inward just above locules and take up positions on the same radius as the stylar canals (Fig. 19, *cd*). The dorsals traverse most of prolongation in this position before entering the style. A vascular plexus is present in some species surrounding the tops of locules and in the prolongation; it may be elaborate, involving most bundles of the prolongation (*H. episcopalis*) or occur just among the bundles of circumlocular zone (*H. clinophylla*).

Musaceae

The following is a composite description that includes all of the significant variations found among the species of *Musa* investigated in the study. The organography and histology of the individual species are presented in Table 1.

Organography

The perianth of *Musa* consists of six members arranged in two whorls (Fig. 1C). Of the six perianth members, three sepals and two petals are adnate at least basally. The median petal is free. The two androecial whorls are constructed on a trimerous plan, but the median stamen of the inner whorl is almost always missing.

Ovary structure is similar in the three species of *Musa* investigated in this study. The ovaries are inferior and vary in size from 33 to 57 mm long. The upper 6–9 mm of this length does not enclose locules and is referred to as the prolongation (Figs. 1D, 22, *pro*). The middle portion of the ovary encloses the locules. At the bottom of the locular region there is a short sublocular region. Both this region and the prolongation intergrade smoothly with the rest of the ovary; their presence cannot be detected from the exterior.

The ovary is trilocular and in the species studied here, has two rows of ovules per locule borne on axile placentae (Fig. 23). Each row of ovules is supplied with its own vascular strand (Fig. 24, *pl*). The locules are almost completely filled with a great number of irregularly dendritic, multicellular, uniseriate trichomes embedded in a mucilaginous gel (Fig. 24, *t*). The individual cells of these trichomes appear collapsed and may be dead by the time the embryo sac is formed. Trichome insertion varies among the species (Table 1) but always occurs in at least two of three closely associated areas: (*i*) between the rows of ovules; (*ii*) on raised portions of the placentas just below the funiculus (Fig. 24); (*iii*) on the funiculus.

Stylar canals arise at the apex of each locule, traverse the prolongation, and enter the style (Figs. 1D, 22, *s*). From the apex of the locules the canals slant inward towards the attachment of the style. They remain distinct throughout their course into the style.

Nectaries are present only in the uppermost part of the locular region and in the prolongation (Figs. 25, 26, *n*). The nectaries arise near the top of the locules, above the insertion of the uppermost ovule. From this point they slant outward to exit between the base of the style and perianth. The position of the nectaries in the upper portion of the prolongation corresponds to the position of the septa in the locular region (compare Figs. 23 and 25). However, the nectary has a more complex structure lower in the prolongation. The nectary duct first becomes apparent opposite the locules, near the top of the locular region (Fig. 28A, *nd*). At this level no part of the nectary duct occurs in the septa. In the proximal portion of the prolongation ducts appear in the septa as well as opposite the locules (Fig. 28B). It is only at the top of the prolongation that the duct is restricted to the septa, as would be expected in a typical gynopleural nectary. Near the top of the prolongation, just below its exit at the base of the style, the single triradiate nectary duct separates into three ducts, which exit at the base of the style.

Histology

Sublocular region—Epidermis is a single layer of cuboidal, slightly convex to moderately papillate cells, outer walls occasionally slightly thickened; unicellular trichomes are present or absent, and when present are inserted on short multicellular pedicles extending slightly above the level of the epidermis. Cortex consists of three to five isodiametric to rectangular parenchyma cell layers immediately interior to the epidermis;

intercellular spaces are small. Vascular zone is immediately interior to the cortex, with ground tissue of vacuolate parenchyma cells, and vascular bundles have large collenchymatous bundle sheaths, usually with only one vessel and several sieve tubes. Collenchymatous bundles are also present, predominating immediately interior to the cortex. Several large vascular bundles with more than one vessel are located between the main vascular region and the central axis. An aerenchyma zone occurs interior to the vascular zone. Central axis contains small parenchyma cells with relatively few intercellular spaces; six to many vascular bundles are found here. Laticifers are articulated and are numerous in the vascular zone, especially surrounding the vascular bundles. Raphide sacs are absent, or present only in the cortex. Tanniniferous idioblasts are present throughout the ground tissue.

Locular region—Figure 23 shows a cross section through the locular region of *M. velutina*. Epidermis is a single layer of slightly convex to moderately papillate cells (Fig. 29), with outer walls occasionally slightly thickened. Unicellular trichomes are present or absent, and when present are inserted on short multicellular pedicles extending slightly above the level of the epidermis. Cortex consists of three to five isodiametric to rectangular parenchyma cell layers immediately interior to the epidermis; intercellular spaces are small. Vascular zone is immediately interior to the cortex (Fig. 27, *vz*); ground tissue is of vacuolate parenchyma cells. The vascular bundles have large collenchymatous bundle sheaths, usually with only one vessel and several sieve tubes. Collenchymatous bundles are also present, predominating immediately interior to the cortex. Several large vascular bundles with more than one vessel occur between the main vascular zone and the circumlocular zone. Circumlocular zone is of two layers, the first of aerenchyma, interior to and intergrading with the vascular zone (Figs. 23, 27, *cl*), and the second of one to five layers of small, often inconspicuous, parenchyma cells immediately adjacent to the locular epidermis. Circumlocular vascular bundles originate from vascular bundles of the vascular zone and run radially around the locules and through the septa, never longitudinally (Fig. 23, arrow). Locule epithelium is of rectangular or cuboidal to rectangular cells. Central axis contains small parenchyma cells with relatively few intercellular spaces and six to eight vascular bundles, six of which (the placental strands) are always closely associated with the locules and produce the vascular supply of the ovules. Laticifers are articulated and numerous in the vascular zone, especially surrounding the vascular bundles. They are of columnar cells arranged in uniseriate, unbranched lines (Fig. 30A), each cell containing some tannin as evidenced by ferric chloride staining. Laticifers are also present and closely associated with the circumlocular vascular bundles. In this region the individual cells are more isodiametric (Fig. 30B) and contain less tannin. Raphide sacs are occasional in the vascular zone. Tanniniferous idioblasts are present throughout the ground tissue.

Prolongation—Figure 25 shows a cross section of the prolongation. Epidermis is a single layer of columnar, slightly convex to moderately papillate cells, with outer walls occasionally slightly thickened. Unicellular trichomes are present or absent, and when present are inserted on short multicellular pedicles extending slightly above the level of the epidermis. Cortex consists of five to seven layers of isodiametric parenchyma cells immediately interior to the epidermis; intercellular spaces are small. Vascular zone is immediately interior to the cortex, with ground tissue of vacuolate parenchyma cells with large intercellular spaces. In the outer region of the zone the vascular bundles have large collenchymatous bundle sheaths, usually with a single vessel and several sieve tubes; collenchymatous bundles predominate immediately below the cortex. There are several large vascular bundles with more than one vessel between the main vascular region and the nectary. An aerenchyma zone occurs interior to and intergrading with the vascular zone. Vascular bundles originate from the vascular strands of the vascular zone and run predominantly longitudinally, although some take a radial course through regions that correspond to septa. These radial bundles contribute to the nectary vasculature. Stylar canals are embedded in ground tissue of isodiametric parenchyma cells with relatively small intercellular spaces (Fig. 26, *s*), with epithelia of rectangular cells. Two placental strands are closely associated with each stylar canal. Nectary structure varies with level in the prolongation (see organography). The nectary duct epithelium is of columnar, moderately papillate, densely cytoplasmic cells. Laticifers are articulated and numerous in the vascular zone, especially surrounding the vascular bundles, and are of columnar cells arranged in uniseriate, unbranched lines. Laticifers are also present and closely associated with the vascular bundles in the aerenchymatous zone and surrounding the nectary, where the individual cells are more isodiametric. Raphide sacs are occasional in the vascular zone, with a higher concentration around the stylar canals in *M. ornata*. Tanniniferous idioblasts are present throughout the ground tissue.

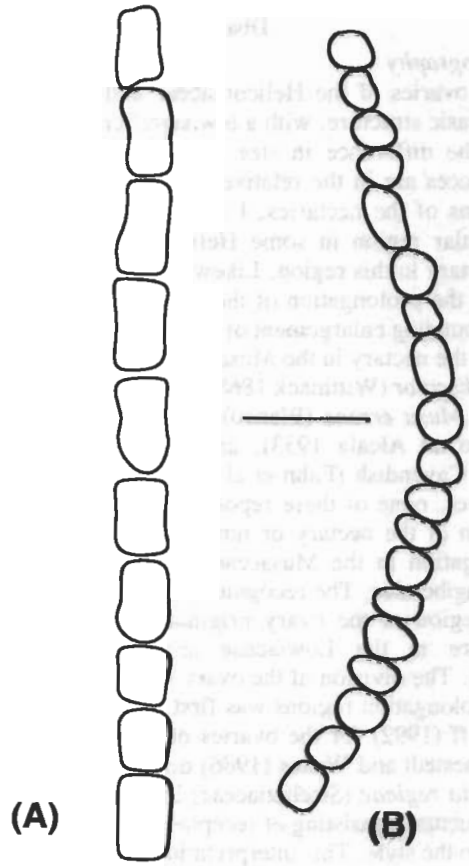

FIG. 30. *Musa velutina*, camera lucida drawings of longitudinal sections of articulated laticifers (A) from the cortex and (B) from the circumlocular zone. Scale bar = 0.1 mm.

Discussion

Organography

The ovaries of the Heliconiaceae and Musaceae share the same basic structure, with a few significant differences. Apart from the difference in size (Table 1), the most significant differences are in the relative sizes of the regions and in the positions of the nectaries. I attribute the enlargement of the sublocular region in some Heliconiaceae to the location of the nectary in this region. Likewise, the placement of the nectary in the prolongation of the Musaceae is correlated with a corresponding enlargement of this region. The epilocular position of the nectary in the Musaceae was previously reported in *Musa discolor* (Wittmack 1868), *Musa textilis* Nee (Thompson 1933), *Musa errans* (Blanco) Teodoro var. *botoan* Teodoro (Juliano ad Alcala 1933), and in *M. acuminata* Colla cv. Dwarf Cavendish (Fahn et al. 1961; Fahn and Kotler 1972). However, none of these reports drew special attention to the position of the nectary or noted the similarities between the prolongation in the Musaceae and that in other families of the Zingiberales. The recognition of the prolongation as a distinct region of the ovary originated from a study of ovary structure in the Lowiaceae and Strelitziaceae (Kirchoff 1988*b*). The division of the ovary into the sublocular, locular, and prolongation regions was first described by Newman and Kirchoff (1992) for the ovaries of the Costaceae.

Kronestedt and Walles (1986) described the prolongation in *Strelitzia reginae* (Strelitziaceae) but identified it as a composite structure consisting of receptacular tissue surrounding and fused to the style. This interpretation is based on an anatomical zonation of the locular region similar to that found in the Heliconiaceae. According to Kronestedt and Walles (1986), the outer portion of the locular region consists of a ring of vascular bundles embedded in parenchyma. They identify this part of the ovary as the receptacle. The inner portion of the ovary, their ovary proper, consists of alternating layers of longitudinally and tangentially elongated cells. The homologous layer in the Heliconiaceae is the endocarp (Humphrey 1896; this study). In the prolongation, there is no distinct demarkation between Kronestedt and Walles' (1986) "style" and "receptacle."

While Kronestedt and Walles' (1986) interpretation may seem plausible for the Strelitziaceae, it does not hold for either the Heliconiaceae or Musaceae. In these families the ovary is a unified structure of which the prolongation is an integral part. This is demonstrated by several lines of evidence. First, the zonation in the ovary of the Heliconiaceae has functional significance. The endocarp of the ovary forms the hard outer covering of the seed (Humphrey 1896; see below). The homologous region in the Musaceae is composed of parenchyma and aerenchyma, and forms both the pulp and the separation zone between the pulp and the peel (Juliano and Alcala 1933; Simmonds 1953). Second, there is a smooth transition in the size of the prolongation in the Heliconiaceae between a simple closure of the locules (*H. psittacorum*) and a distinct prolongation (*H. indica*) (Table 1). Third, there is rarely an external demarkation between the locular region and the prolongation and never a distinct histological difference between the two. Finally, the presence of modified gynopleural nectaries in the prolongation of the Musaceae shows that the prolongation is part of the ovary, not part of the receptacle or style.

The structure of the nectaries differs slightly in the Heliconiaceae and Musaceae. In the Heliconiaceae, the nectaries are strictly gynopleural with the arms of the nectary duct located in, below, or above the septa. Although the development of the nectaries was not investigated, the septal position of the duct(s) suggests that they originate from the noncohesion of the margins of the gynoecial primordia. In fact, Brown (1938) defines septal nectaries based on this noncohesion.

The nectaries of the Musaceae have a more complex structure than those of the Heliconiaceae. In the lower portion of the nectary. The nectary duct appears as a triradiate groove whose arms are located opposite the locules. Slightly higher, three additional grooves, located in the septa, join with the original three to form a six-armed duct. More distally still, the three arms opposite the locules disappear, leaving a triradiate duct whose arms occupy the septa.

In addition to the species of *Musa* investigated in this study, the same nectary morphology has been found in both the male and female flowers of *M. acuminata* cv. Dwarf Cavendish (Fahn et al. 1961; Fahn and Kotler 1972; Fahn and Benouaiche 1979) and in *Ensete superbum* (Roxb.) Cheesm. (Tilak and Pai 1974).

A developmental mechanism for the origin of this type of nectary can be proposed based on studies of gynoecial development in the order (Fahn and Kotler 1972; Kirchoff 1983, 1988*a*; van Heel 1988). A trilocular ovary is normally formed from three conduplicate gynoecial primordia (van Heel 1988), one anterior and two posterolateral. These primordia form three septa, one posterior and two anterolateral (Fig. 1A, *g*). The incomplete fusion of the margins of these primordia produces the ducts of a normal gynopleural nectary. These ducts lie in, radially outside, above, or below the septa (Smets and Cresens 1988). In the formation of normal gynopleural nectaries, other portions of the gynoecial primordia fuse to close the locules and form the tissues of the central axis. Of primary interest here is the fusion of the primordia opposite the locules, in the central axis of the ovary. I suggest that the additional three arms of the nectary duct in *Musa* originate from the noncohesion of the gynoecial primordia in these regions. This would produce a six-armed nectary duct with three arms in the septa and three opposite the locules. Since the ducts opposite the locules only occur in the basal regions of the nectary, the noncoherence of the gynoecial primordia opposite the locules should also occur only here.

The floral histology of the Costaceae was recently investigated by Newman and Kirchoff (1992). The flowers of this family are much more complex than those of either of the families investigated here. Nevertheless, a comparison of ovary anatomy in the Costaceae, Heliconiaceae, and Musaceae can throw considerable light on the origin of the nectaries in these families and in the Zingiberaceae.

The nectaries of the Zingiberaceae consist of epigynous glands inserted directly above the septa on the anterior side of the flower (Rao et al. 1954; Rao and Gupte 1961; Rao and Pai 1959, 1960). Despite their occurrence above the septa, these glands cannot be directly derived from gynopleural nectaries. In normal gynopleural nectaries, the nectary ducts lie on the same radius as the septa, while the secretory tissue alternates with them (Fig. 7). In the Zingiberaceae it is the secretory tissue that lies on the same vertical line as the septa. The ancestral nectaries of the Zingiberaceae should thus have had secretory tissue in the septa and the nectary ducts opposite the locules.

This is precisely the situation that Rao (1963) found in *Costus speciosus* (Costaceae). In this species, the proximal portion of the nectary has three regions of secretory tissue in the septa and a triradiate nectary duct the arms of which are opposite the locules. More distally, the nectary ducts become circular in cross section, lie in the septa, and encircle two projections of secretory tissue. Thus, the distal portions of the nectary in this species are in the same positions as the epigynous nectaries of the Zingiberaceae. Rao (1963) suggested that this species represents the ancestral condition of the nectaries of the Zingiberaceae. The problem to date has been how to relate nectary structure in *C. speciosus* to the more normal gynopleural nectaries found in the other Zingiberales, e.g., Strelitziaceae (Kronestedt and Walles 1986), Cannaceae (Pai 1965; Maas and Maas 1988), and Marantaceae (Rao 1975). The structure of the nectary in the Musaceae, and the developmental patterns that most likely produce this structure, provide a potential solution to this problem.

As suggested above, it seems likely that in the proximal portion of the nectary of the Musaceae, the margins of the three gynoecial primordia remain free opposite the locules and fuse in the septa. This produces a triradiate nectary duct whose arms are opposite the locules (Fig. 28A, *nd*). A similar developmental pattern could also produce the proximal portion of the nectary in *C. speciosus*. Thus, a simple change from the normal patterns of gynoecial primordia fusion could produce a condition similar to the ancestral condition of the Zingiberaceae. The development of the distal portion of the nectary in *C. speciosus* was partially investigated by van Heel (1988). He found that the nectary ducts originate from the noncoherence of the margins of the gynoecial primordia in the septa. A detailed anatomical and developmental investigation is needed to determine how the proximal and distal portions of nectary of *C. speciosus* are interrelated.

Histology

The anatomical observations reported here are in agreement with previous work on the histology of the ovary in the Musaceae and Heliconiaceae. Ram et al. (1962) investigated ovary structure and development in *M. acuminata* cv. Pisang lilin and *M. acuminata* ssp. *burmannica*. In both varieties they found that the epidermis was simple and composed of cuboidal cells. Although they refer to the outermost layer of the cortex as a hypodermis, the structure of this layer is very similar to the structure of the outer cortex reported in this paper. Ram et al. (1962) also found a broad vascular region interior to the hypodermis, the outer vascular bundles of which were more fibrous than those found internally. These authors also note the presence of vascular bundles that run at right angles to the axis of the ovary. These bundles are equivalent to the circumlocular bundles described in this paper. Ram et al. (1962) did not mention the presence of an aerenchymatous circumlocular zone, but such a zone is clearly visible in their figures. Adjacent to the locule epidermis they described five to seven layers of isodiametric parenchyma cells, which divide to form the pulp of the fruit. Of the species investigated here, only *M.* cv. Go Sai Yung has an appreciable amount of tissue present in this region. Although one to three layers of cells are present in *M. velutina* and *M. ornata*, the cells of these layers are small and only clearly visible at ca. 400×. These differences are correlated with the fact that the latter two species produce seeds and little pulp, while the former produces abundant pulp and an edible fruit (it is the apple banana of Hawaii).

Juliano and Alcala (1933; *M. errans* var. *botoan*) and Simmonds (1953; *M. acuminata*, *Musa balbisiana*) independently investigated the development of the banana fruit and in the process provided information on the structure of the ovary. Juliano and Alcala (1933) determined that the exocarp consists of the cortex and vascular regions and produces the peel. The endocarp consists primarily of aerenchyma, lacks vascular bundles, and produces the edible portion of the fruit. Simmonds (1953) gave a more complete description of fruit development. Although he drew the line between the exocarp and the endocarp slightly differently than Juliano and Alcala (1933), his conclusions were similar. Simmonds (1953) noted that each locule is surrounded by aerenchymatous tissue that constitutes the innermost portion of the pericarp and develops to form the abscission zone between the peel and the pulp of the fruit. The pulp is produced from the layers of small parenchyma cells that surround the locules. The peel is produced from the outer portions of the ovary.

Thompson (1933; pp. 78–79) described the basic structure of the ovary of *Heliconia bihai* L. but provided little data on its histology or vasculature. In this species, there is a small nectary in the sublocular region that becomes larger through the lower portion of the locular region and then diminishes upwards. The triradiate nectary duct persists into the short closure of the ovary but does not appear to be secretory in this region. Thompson (1933) also described the attachment of the stylar canals at the base of the locules and illustrated these canals connecting to the nectaries at the center of the flower. This connection persists throughout the ovary until the nectary ducts exit at the base of the style. A similar connection is found in the ovaries of *H. psittacorum*. The only anatomical data provided by Thompson (1933) concerned the endocarp, which he described as fibrous.

In *Heliconia* the endocarp functions as the (stony) testa of the seed (Humphrey 1896). After fertilization, the ovule grows to fill the locule while the integuments "remain feebly developed" (Humphrey 1896). The functions of several anatomical structures can be understood in this regard. The most important of these is the endocarp itself. With its alternating layers of radially and longitudinally elongated cells and its lack of intercellular spaces, the sclerification of this layer is all that is required to provide a protective coat for the seed. Surrounding the endocarp is a layer of crystalliferous parenchyma cells. It seems likely that the function of these crystals is to assist in the mechanical separation of the seed (meaning seed plus endocarp) from the exocarp. Although Humphrey (1896) did not report the presence of these crystals, he did mention the presence of thin-walled parenchyma cells surrounding the endocarp. He speculated that the breakup of these cells causes the separation of the seed from the fruit.

Although the seeds of at least some *Musa* species completely fill the locules, the protective layer of the seed is produced from the seed itself, not the endocarp (Humphrey 1896; Friedrich and Strauch 1975).

Vasculature

The vascular pattern described here for the ovaries of the Heliconiaceae was also found in *E. superbum* (Musaceae) (Tilak and Pai 1974). The most notable difference between the species of *Heliconia* described here and *E. superbum* concerns the course of the placental strands. In the Musaceae the pla-

cental strands are the carpellary ventrals that lie in the central axis of the flower. In the Heliconiaceae there are no distinct placental strands in the central axis. Instead, the vasculature of the central axis consists of many small vascular bundles interspersed with the nectary tissue. This difference is correlated with the basal insertion of the ovule in this family, which obviates the need for extended placental strands to supply the ovules.

Friedrich and Strauch (1975) described two arrangements of placental strands in the Musaceae. The *M. acuminata* fruit type has six placental strands (two per locule), each associated with a single row of ovules. This vascular arrangement is also found in *E. superbum* (Tilak and Pai 1974), *M. ornata*, *M. velutina* and *M.* cv. Go Sai Yung (this paper), *M. textilis* (Thompson 1933, p. 62), and *Musa* sp. (Friedrich and Strauch 1975). The second fruit type is the *M. balbisiana* Colla type, which has four irregular rows of ovules per locule (Friedrich and Strauch 1975). From their figures it appears that these four rows are arranged in pairs on a raised placental ridge. Friedrich and Strauch (1975) did not describe the number of placental strands in this fruit type. The only other species I am aware of with the *M. balbisiana* fruit type is *Musa* sp. from Thailand (Friedrich and Strauch 1975).

Aril

The homology of the multicellular trichomes that surround the ovules in the Musaceae has been discussed in the literature. The main point of discussion centers around whether or not the trichomes are homologous to the aril in other Zingiberales. An aril is usually defined as a postfloral outgrowth of the hilum region that more or less covers the seed (van der Pijl 1955). Although Friedrich and Strauch (1975) argued that the trichomes of the Musaceae are homologous to arils, I cannot support this conclusion based on the available evidence. Friedrich and Strauch's (1975) claim is mainly based on the insertion of the trichomes, which these authors describe as on the funiculus.

Wittmack (1868) described the presence of multicellular trichomes around the ovules in *Musa discolor* but did not speculate on their nature. Humphrey (1896) described the arils of many Zingiberales, but after describing the trichomes of the Musaceae concluded that no aril is present in this family. Although he did not spell out his reasons for this conclusion, he noted that there is no trace of the trichomes in the seed. White (1928) and Fahn and Kotler (1972) referred to the trichomes of *Musa* as glandular and described their development from the epithelium of the placental ridges. According to these authors (and to Ram et al. 1962) the trichomes are the source of the mucilaginous gel that fills the locules. These authors also agreed that the trichomes are formed before the ovules. White (1928) concluded that the trichomes form a "structure seemingly [sic] homologous" to the aril of other Zingiberales. Fahn and Kotler (1972) did not speculate on the homology of the trichomes. Simmonds (1953) also mentioned the presence of the trichomes but did not equate them with an aril.

There are several arguments that can be marshalled against White's (1928) and Friedrich and Strauch's (1975) hypothesis that the trichomes are homologous to an aril. The first concerns the time of initiation of the trichomes versus an aril. As noted above, the trichomes are initiated and apparently function before the ovule is formed (White 1928; Fahn and Kotler 1972). By the time the fruit pulp begins to develop, the trichomes have begun to disappear. Only vestiges remain in the mature fruit (Humphrey 1896; Simmonds 1953; Friedrich and Strauch 1975). In contrast, the major portion of the arils of the Zingiberales are formed after fertilization and are only fully represented on the mature seeds (Humphrey 1896; Grootjen and Bouman 1981; Grootjen 1983). Second, the position of the trichomes does not correspond to that of an aril. Although Friedrich and Strauch (1975) and Humphrey (1896) claim that the trichomes are inserted on the funiculus, their insertion is primarily on the placenta, at least for the species investigated in this study (Fig. 24). This insertion can also be seen in some of Friedrich and Strauch's (1975) figures. I distinguish between raised portions of the placentas and the funiculus by the anatomy of these two regions. If the anatomy of the tissue in question is similar to that of the central axis and if it possesses longitudinal vascular strands (i.e., strands that do not immediately vascularize an ovule), I interpret it as part of the placenta. By these criteria some species of *Musa* have raised placental ridges (Fig. 24). In contrast, the funiculi are usually composed of much smaller, more densely staining cells and only contain vascular strands that immediately vascularize ovules. In contrast with the placement of the trichomes in the Musaceae, the aril of the other Zingiberaceae develops from the outer integument and the corresponding position of the raphe (Humphrey 1896; Grootjen and Bouman 1981; Grootjen 1983). These positions do not correspond to any of the insertion points of the trichomes in the Musaceae. Finally, the structure of the trichomes is not similar to any of the arils that have been described in the Zingiberales (Pfeiffer 1891; Humphrey 1896; Grootjen and Bouman 1981; Grootjen 1983). Thus, neither the position, structure, or development of trichomes of the Musaceae support their homology to arils. It is also significant that there are no known intermediates between the normal arils of the Zingiberales and the trichomes of the Musaceae.

Friedrich and Strauch (1975, Table 1) also claim that an aril exists in the Cannaceae and Heliconiaceae (listed as having a "homolog. Gewebe"). However, they do not present any evidence to support these claims. My own observations as well as those of Grootjen and Bouman (1988; Cannaceae) and Humphrey (1896; Cannaceae and Heliconiaceae) indicate that neither of these families possesses arils. In the same table Friedrich and Strauch (1975) also claim that *Costus* (Costaceae) has two rows of ovules. Newman and Kirchoff (1992) have shown that this is not true for *Costus dubius*, which has four rows of ovules per locule.

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