

OVARY STRUCTURE IN THE COSTACEAE (ZINGIBERALES)

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The morphology and histology of the ovary is investigated in four species representing the four genera of the family Costaceae. Only one species of *Costus* has been investigated prior to this study. The present study identifies new characters and confirms or corrects those previously reported for all four genera. Aspects of ovary structure studied include the general topography and histology of the ovary, paths of the stylar canals, the prolongation of the ovary above the locules, the presence of a vascular plexus at the top of the ovary, and the position and structure of the floral nectary. These characters contribute to a broader data base for phylogenetic analysis of the Zingiberales.

Introduction

The Costaceae are monocotyledons belonging to the order Zingiberales. The Zingiberales are a natural order consisting of the eight families Zingiberaceae, Costaceae, Marantaceae, Cannaceae, Lowiaceae, Musaceae, Heliconiaceae, and Strelitziaceae (Nakai 1941; Tomlinson 1962; Takhtajan 1969, 1980). Within this group, the Costaceae and Zingiberaceae are sister taxa (Dahlgren and Rasmussen 1983; Kress 1990). The Costaceae are characterized by spiral monostichous phyllotaxy, closed leaf sheaths, a nectary gland in the top of the ovary, and the lack of aromatic compounds. The Zingiberaceae are characterized by distichous phyllotaxy, open leaf sheaths, epigynous glands in the flower, and the possession of aromatic compounds.

The four genera of the Costaceae (*Costus*, *Monocostus*, *Dimerocostus*, and *Tapeinocheilas*) are found in tropical and subtropical areas throughout the Old and New World—in rain forests and other moist, shady sites. The 20 species of *Tapeinocheilas* occur mostly in Indonesia, New Guinea, and Australia (Queensland) (Maas 1972, 1977). The monotypic genus *Monocostus* is restricted to the Huallaga River region in central Peru (Maas 1972, 1977). *Dimerocostus* has two species and occurs from Central America to central Bolivia (Maas 1972, 1977). *Costus*, the largest genus, with 125–175 species, has a pantropical distribution. Maas (1972, 1977) separates *Costus* into the subgenera *Costus* and *Cadalvena*.

Schumann (1904) was the first to recognize the four genera *Costus*, *Monocostus*, *Dimerocostus*, and *Tapeinocheilas* as the subfamily Costoideae of the Zingiberaceae. This treatment held until Nakai (1941) separated the Costoideae from the remainder of the Zingiberaceae as the family Costaceae. Tomlinson's (1956, 1962) studies of the morphology and anatomy of the Zingiberaceae (*sensu lato*) support this separation.

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Aside from work on the single species *Costus speciosus* (Brown 1938; Rao et al. 1954; Pai 1966; Van Heel 1988), the majority of information on ovary structure in the Costaceae comes from taxonomic work on this family (Maas 1972, 1976, 1977, 1979, 1985). The data on internal and external ovary structure that can be extracted from Maas's work are sparse, as befits taxonomic treatments. Nevertheless, these articles serve as a source of basic ovary characters such as the number of locules and the presence of septal nectaries.

The purpose of the present study is to investigate ovary structure to identify new structural characters that can be used in phylogenetic analyses. We have also attempted to confirm the literature data on the structure of the ovary in the Costaceae. Increased knowledge of ovary structure in the Costaceae will broaden the data base used in analysis of evolutionary relationships in this family. In his taxonomic review of the Zingiberaceae (*sensu lato*), Panchaksharappa (1962) pointed out the necessity for examining the remaining three genera of the Costoideae for possession of the same features as *Costus* and stated that such results would go a long way in the taxonomic evaluation of the family.

Material and methods

Mature flowers of the Costaceae were collected from Lyon and Waimea Arboreta, Oahu, Hawaii: *Costus dubius* (Afz.) K. Schuman (Waimea accession no. 82P837), *Tapeinocheilas ananassae* K. Schuman (Waimea accession no. 74P753, voucher: Kirchoff 88-140 at BISH), *Dimerocostus strobilaceus* O. Kuntze ssp. *strobilaceus* (Lyon accession no. 78.1074, voucher: Kirchoff 88-148 at BISH), *Monocostus uniflorus* (Poegg. ex O.G. Petersen) Maas (Waimea accession no. 76P641, voucher: Kirchoff 87-110 at BISH). Anatomical data were collected from five to seven ovaries of each species.

Specimens were fixed and stored in FAA (Berlyn and Miksche 1976). Sections were prepared using standard paraffin techniques (Berlyn and Miksche 1976) with the following additions. To remove tannins, the ovaries were soaked in

Stockwell's bleach (Johansen 1940) for 5–15 d and rinsed in Sorensen's phosphate buffer, pH 7.2, prior to dehydration. Dehydration was either with a t-butyl alcohol series (Berlyn and Miksche 1976) or with 2,2-dimethoxypropane (Postek and Tucker 1976). There was no noticeable difference in the specimen using either method of dehydration. The specimens were then transferred to 100% t-butyl alcohol and embedded in paraffin. Sections were cut on an American Optical rotary microtome or a Reichert 2040 Autocut microtome at 10–20 μm and mounted on slides using Bissing's modified Haupt's adhesive (Bissing 1974). The sections were stained with safranin-fast green (Berlyn and Miksche 1976), dewaxed using ClearRite III in place of xylene, and mounted with Permount. Photomicrographs were taken with Leitz Ortholux II and Wild M5A photomicroscopes.

Longitudinal measurements of the following portions of the ovary were made: the distance from pedicel to perianth attachment, the length of the locules, the length of the prolongation above the locules, and the length of the secretory tissue of the nectary (table 1). These measurements were made using one of three procedures. (1) Sagittal sections of whole ovaries were measured using calipers. (2) Longitudinal sections mounted on slides were measured using an ocular micrometer on an Olympus SZH stereomicroscope. (3) Longitudinal distances were calculated from serial cross sections counting the number of serial sections on slides and multiplying by the section thickness. Means and standard deviations were calculated.

The median plane of the flower bisects the inflorescence axis, the flower pedicel, and the main axis of the flower. We refer to the side of the ovary away from the inflorescence axis as abaxial (or anterior) and the side adjacent to the inflorescence axis as adaxial (or posterior). Anterolateral and posterolateral refer to the lateral regions of the flower, just off the median plane, on the anterior and posterior sides of the flower, respectively. We use the term "carpel" only in a descriptive sense.

Results

HABIT AND MORPHOLOGY OF COSTACEAE (FIGS. 1, 2)

The Costaceae are herbaceous monocotyledons with sympodial rhizomes, well-developed aerial shoots, terete stems that are often helically twisted, and usually unbranched aerial shoots; *Tapeinocheilas* and some *Costus* spp. have branched shoots. The leaves are arranged in spiral monostichous phyllotaxy. Each leaf consists of a closed tubular sheath and an entire, lanceolate, or oblanceolate to linear lamina with an acumi-

nate apex. A ligule is present at the junction of the sheath and blade.

The inflorescence is an ovoid to cylindrical spike or thyrses with bracts and flowers arranged in a spiral monostichous or fibonacci helix. The inflorescence is terminal on the end of a leafy (*Dimerocostus*, some *Costus* spp.) or separate leafless shoot (*Tapeinocheilas*, some *Costus* spp.), or the flowers are borne in the axils of foliage leaves (*Monocostus*). In *Dimerocostus* the shoot/inflorescence apex continues to grow past the inflorescence, frequently producing a second inflorescence on the same shoot (fig. 1).

The flowers of the Costaceae are bisexual and zygomorphic (figs. 1, 2). The sepals are greenish and fused into a synsepalous, trilobate calyx. The lobes are generally triangular to deltoid, and acuminate. In *Tapeinocheilas* the calyx is coriaceous; in the other three genera it is herbaceous. In all of the genera, the petals are longer than the sepals and fused basally but become free where exerted above the calyx. The medial member of the corolla is often longer than the laterals. All members of the androecial whorls but one, the medial member of the inner whorl, are represented by petaloid staminodes and are fused to form a conspicuous, often three-lobed, labellum. The labellum is white or conspicuously colored. The size and texture of the labellum varies across the family from relatively small and callose to large and delicate (fig. 1). The single polleniferous stamen is the median member of the inner whorl and is inserted opposite the labellum. The filament is petaloid and fleshy with the anther attached on the adaxial surface, near the apex. The ovary is inferior with numerous ovules on axile placentas. The ovules are anatropous and crassinucellate. The long, slender style is clasped between the thecae of the anther.

STRUCTURE OF THE OVARY (FIGS. 3–13)

The ovary may be divided into three relatively distinct regions based on the longitudinal position of the locules (figs. 3a, 4a, 5a, 6a). The central and most prominent region contains the locules and is referred to as the locular region. Below this is the sublocular region, which is short and closes the locules from below. The third region, the area above the locules, is termed the prolongation. Normally an inferior ovary is closed above the locules with a small cap of tissue. In some genera of Costaceae, this cap is extended into a prolonged closure. A main distinction between the locular and prolongation regions is the lack of locules in the latter. There may or may not be an external indication of the presence of the prolongation. A vascular plexus occurs in the vascular zone of the prolongation, and a floral nectary is present near the top of the ovary in the central axis of the flower.

Table 1

OVARY STRUCTURE AND HISTOLOGY IN INDIVIDUAL SPECIES

	<i>Monocostus uniflorus</i>	<i>Tapinocheilas ananassae</i>	<i>Dimerocostus strobilaceus</i>	<i>Costus dubius</i>
N	6	7	5	7
Organography:				
Length of (mm \pm SD):				
Ovary	14.2 \pm .92	11.9 \pm 1.11	21.3 \pm 1.65	8.9 \pm 1.17
Locular region	9.7 \pm .82	8.8 \pm 1.14	1.17 \pm 1.41	7.0 \pm .92
Prolongation	2.2 \pm .27	2.1 \pm .31	7.5 \pm .77	1.4 \pm .47
Nectary	2.7 \pm .15	3.5 \pm .47	5.9 \pm 1.42	2.7 \pm .74
Cross-sectional shape of:				
Sublocular region	Round to oval	Oval and slightly biwinged	Circular	Oval
Locular region	Proximally, oval; distally, rounded triangular	Rounded triangular with pronounced wings	Rounded triangular and slightly biwinged	Rounded rectangular
Prolongation	Rounded triangular	Rounded triangular, wings less pronounced	Rounded triangular to oval and slightly biwinged	Oval to round
Ovary symmetry	Bilateral	Bilateral	Bilateral	Radial
Aerenchyma abaxial to central axis in distal portion of locular region	Small amount	Present	Present	NA
No. of locules	2	2	2	3
Longitudinal extent of ovules	Below insertion of stylar canal	Below insertion of stylar canal	Below insertion of stylar canal	Above and below insertion of stylar canal
No. of rows of ovules/locule	2	2	4	4
Stylar canal insertion	Lateral	Lateral	Apical	Lateral
No. of stylar canals in proximal prolongation	2	2	2	3
No. of stylar canals in distal prolongation	1	2	2	3
Stylar canals fuse	Below perianth	In style	Below perianth	Below perianth
Nectary placement	Between locules and in prolongation	Between locules and in prolongation	In prolongation	Between locules and in prolongation
Secretory tissue	Smoothly rounded lobes	Highly convoluted finger-like projections	Highly convoluted finger-like projections	Smoothly rounded lobes
No. of nectary ducts in prolongation ...	1	2	1	2
Histology, sublocular region:				
Epidermis:				
Cell shape	Cuboidal to rectangular	Cuboidal	Cuboidal	Rectangular to cuboidal
Outer wall	Thickened	Not thickened	Not thickened	Not thickened
Trichomes	Absent	Multicellular, uniseriate	Unicellular	Absent
Hypodermis	Present	Absent	Present	Present
No. of cell layers	1	NA	3	3
Cell shape	Columnar	NA	Isodiametric	Columnar
Vascular zone:				
Ground tissue	Isodiametric parenchyma cells	Isodiametric parenchyma cells	Isodiametric parenchyma cells	Aerenchyma
Bundles arranged	One ring with additional bundles in center	Irregularly arranged	One ring with additional bundles in center	One ring with additional bundles in center

Table 1 (Continued)

	<i>Monocostus uniflorus</i>	<i>Tapeinocheilas ananassae</i>	<i>Dimerocostus strobilaceus</i>	<i>Costus dubius</i>
Histology, locular region:				
Epidermis:				
Cell shape	Cuboidal to rectangular	Cuboidal	Cuboidal	Rectangular to cuboidal
Outer wall	Thickened	Not thickened	Not thickened	Not thickened
Trichomes	Absent	Multicellular, uniseriate	Unicellular	Absent
Hypodermis	Present	Present in upper half of region	Present	Present, differs proximally and distally
No. of cell layers	1	5-10	2-4	Proximally, 2; distally, 4
Cell shape	Proximally, columnar; distally, very thin and long columnar	Isodiametric	Proximally, isodiametric; distally, columnar	Proximally, columnar; distally, isodiametric
Vascular zone:				
Ground tissue	Isodiametric parenchyma cells	Isodiametric parenchyma cells	Isodiametric parenchyma cells	Aerenchyma
Ground tissue cell layers	8-16	10-20 adaxially; 15-20 abaxially	15-20	NA
No. of isodiametric parenchyma cell layers adjacent to locule epithelium	1	2	2-3	1-2
Locule epithelium	Cuboidal to rectangular	Cuboidal to squamous	Cuboidal	Rectangular to cuboidal
Stylar canal epithelium	Cuboidal to columnar	Cuboidal	Columnar	Cuboidal
Nectary	Present at this level	Present at this level	Absent at this level	Present at this level
No. of layers of isodiametric parenchyma cells surrounding nectary	1-2	4-8	NA	2-8
Duct epithelium	Rectangular	Cuboidal	NA	Rectangular
Duct walls facing lumen	Not thickened	Thickened	NA	Thickened
Secretory epithelium	Columnar	Cuboidal to columnar	NA	Columnar
Central axis:				
Proximally	Isodiametric parenchyma interspersed with vasculature	Isodiametric parenchyma interspersed with vasculature	Isodiametric parenchyma and aerenchyma; vasculature arranged in band between locules	Isodiametric parenchyma interspersed with vasculature
Distally	Nectary present	Nectary present	Nectary absent; vasculature in center of axis	Nectary present
Prolongation:				
Epidermis:				
Cell shape	Cuboidal	Cuboidal	Cuboidal	Rectangular
Outer wall	Thickened	Not thickened	Not thickened	Not thickened
Trichomes	Absent	Multicellular, uniseriate	Unicellular	Unicellular
Hypodermis	Present	Present	Present	Present
No. of cell layers	1	5-10	2-4	2-4
Cell shape	Columnar	Isodiametric	Columnar	Isodiametric
Vascular zone:				
Differs proximally and distally	No	No	No	Yes
Ground tissue layers	3-8	10-20 abaxially; 20-40 adaxially	40-50	Proximally, 30; distally, 6-10 in <i>c1</i> , 20 in <i>c2</i> ^a

Table 1 (Continued)

	<i>Monocostus uniflorus</i>	<i>Tapeinocheilas ananassae</i>	<i>Dimerocostus strobilaceus</i>	<i>Costus dubius</i>
No. of rings of vascular bundles in addition to scattered bundles present	2	2	1	3; location differs proximally and distally ^a
Stylar canal epithelium	Cuboidal	Cuboidal	Cuboidal to columnar	Cuboidal
Stylar canal surrounded by	Parenchyma	Sclerified cells	Sclerified cells	Parenchyma
Nectary:				
No. of layers of isodiametric parenchyma cells surrounding nectary	1-2	2-5	4-5	Absent
Aerenchyma external to parenchyma	Present	Present	Present	Absent
Duct epithelium	Cuboidal	Cuboidal to columnar	Cuboidal	Proximally, cuboidal; distally, rectangular
Duct walls facing lumen	Thickened	Not thickened	Not thickened	Thickened
Secretory epithelium	Columnar	Columnar	Cuboidal to mostly columnar	Columnar
Outer wall of secretory epithelium ..	Not thickened	Thickened	Not thickened	Not thickened

Note. Order of characters is the same as in the General Description. Characters that are uniform across all four species are not included in the table. NA, not applicable.
^a See text for fuller explanation.

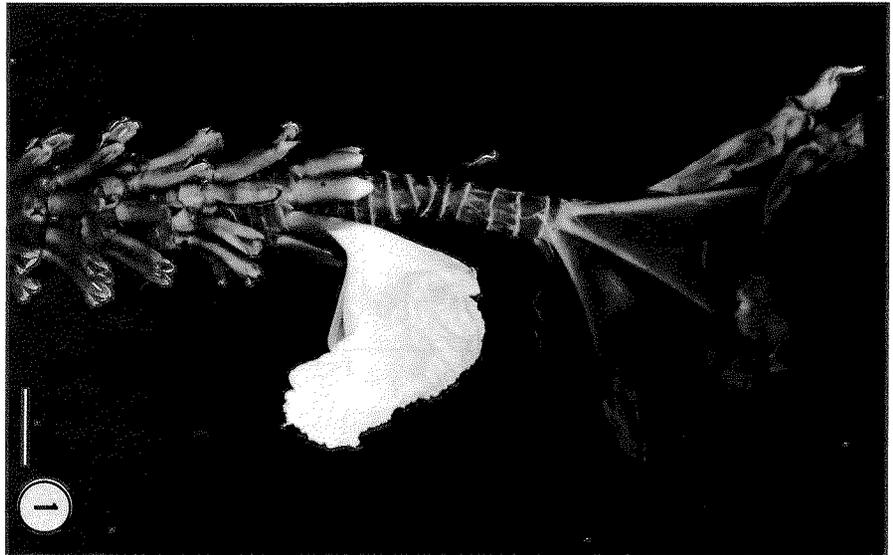


Fig. 1 *Dimerocostus strobilaceus*. Shoot growing past the inflorescence. One flower is open near the apex of the inflorescence. Bar = 4 cm.

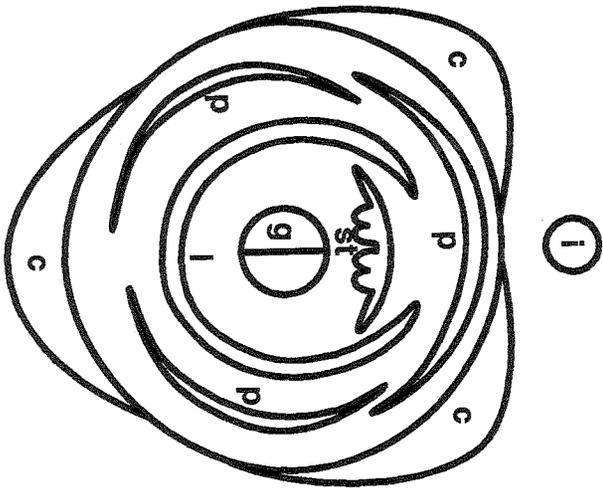


Fig. 2 Floral diagram of a representative of the Costaceae with a bilocular ovary. *l* = inflorescence axis; *c* = synsepalous calyx; *p* = petals; *l* = labellum; *st* = stamen; *g* = gynoecium.

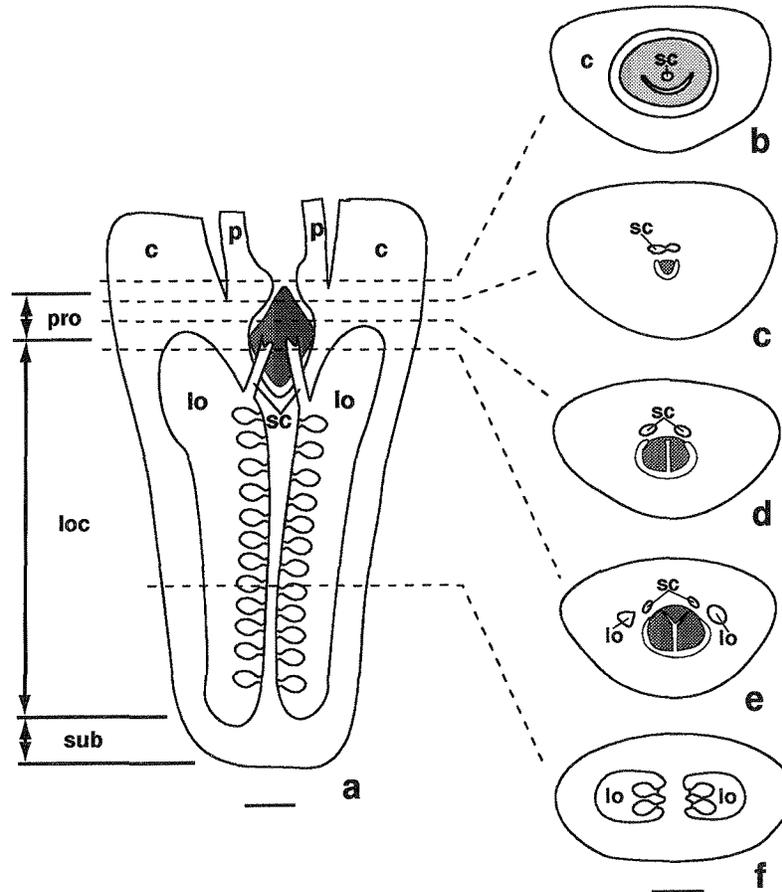


Fig. 3 Diagrams of mature ovary of *Monocostus uniflorus*. *a*, Longitudinal diagram of the ovary. The three regions of the ovary are the sublocular (*sub*), locular (*loc*), and prolongation (*pro*). The nectary (shaded) lies between the tops of the locules (*lo*) and in the prolongation. *c* = synsepalous calyx; *p* = petals; *sc* = stylar canals (truncated; see *b–e* for their course); bar = 1.57 mm. *b–f*, Cross sections of the ovary at the levels indicated in *a*. Bar = 1.1 mm. *b*, Perianth attachment. *c* = synsepalous calyx; lightly shaded area = corolla and style; *sc* = stylar canal; curved slit = nectary pore at top of ovary. *c*, Distal portion of the prolongation. Shaded area = nectary tissue. Two stylar canals (*sc*) are present on the adaxial side of nectary. *d*, Proximal portion of the prolongation. Shaded area = nectary tissue. Two stylar canals (*sc*) are present on the adaxial side of nectary. *e*, Top of locules showing empty locules (*lo*) and two stylar canals (*sc*). Shaded area = nectary tissue. *f*, Mid-locular region with two rows of ovules per locule (*lo*).

The ovaries of the Costaceae investigated in this study vary in size (table 1). The distance from the attachment of the pedicel to the attachment of the perianth ranges from 8.9 to 21.3 mm. Variations also occur in the length of locules, prolongation, and nectary (table 1).

The ovary is either bilaterally symmetrical and bilocular (*Monocostus uniflorus*, *Tapeinocheilas ananassae*, *Dimerocostus strobilaceus*; figs. 3–5) or radially symmetrical and trilocular (*Costus dubius*; fig. 6). In the distal portion of the locular region of *T. ananassae* and *D. strobilaceus* there is an aerenchymatous region present abaxial to the central axis in the position where the third locule would appear (figs. 7, 8). The comparable region of aerenchyma in *M. uniflorus* is small and confluent with the circumlocular aerenchymatous region (fig. 9, *ae*). Ovules are borne on axile placentas with two (*M. uniflorus*, *T. ananassae*; fig. 9) or four (*D. strobilaceus*, *C. dubius*; fig. 10)

rows of ovules per locule. Ovules occur below (*M. uniflorus*, *T. ananassae*, *D. strobilaceus*) or both above and below (*C. dubius*) the insertion of the stylar canals (figs. 3–6). Stylar canals rise from the locules just below and lateral to each locular apex (*M. uniflorus*, *T. ananassae*, *C. dubius*; figs. 3*a*, 4*a*, 6*a*) or at the apex of each locule (*D. strobilaceus*; fig. 5*a*). In the proximal portion of the prolongation, there are two or three stylar canals. When two are present they traverse the ovary on the adaxial side of the nectary (*M. uniflorus*, *T. ananassae*, *D. strobilaceus*; figs. 3*d*, 4*d*, 5*d*). When three stylar canals are present they occur near the center of the central axis, between the lobes of nectary tissue (*C. dubius*; fig. 6*d*). In the distal portion of the prolongation, there are one (*M. uniflorus*; fig. 3*c*), two (*T. ananassae*, fig. 4*c*; *D. strobilaceus*, fig. 5*c*), or three (*C. dubius*; fig. 6*c*) stylar canals occurring near the center of the central axis. When multiple stylar canals are

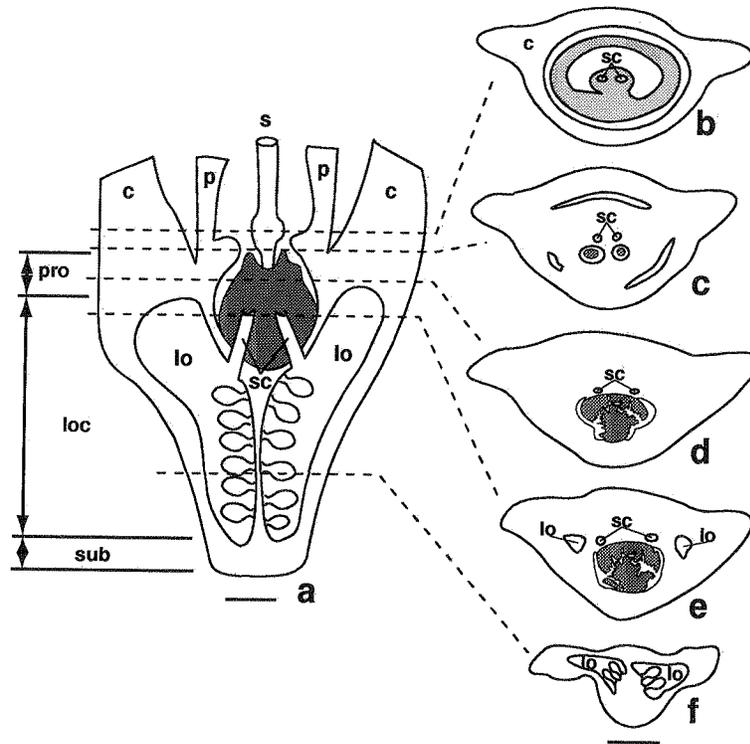


Fig. 4 Diagrams of mature ovary of *Tapeinocheilas ananassae*. *a*, Longitudinal diagram of the ovary. The three regions of the ovary are the sublocular (*sub*), locular (*loc*), and prolongation (*pro*). The nectary (shaded) lies between the tops of the locules (*lo*) and in the prolongation. *c* = synsepalous calyx; *p* = petals; *s* = style (the insertion of the style is distorted to show the opening of the nectary ducts); *sc* = stylar canals (truncated; see *b–e* for their course); bar = 1.85 mm. *b–f*, Cross sections of the ovary at the levels indicated in *a*. Bar = 2.5 mm. *b*, Corolla attachment. *c* = synsepalous calyx; lightly shaded area = corolla and style; *sc* = stylar canals. *c*, Calyx attachment. The tips of the nectary (shaded) are enclosed in the lumen of the nonsecretory nectary ducts. Two stylar canals (*sc*) are present adaxial to the nectary ducts. *d*, Distal portion of the prolongation. Nectary tissue (shaded) partially surrounded by the nectary duct. Two stylar canals (*sc*) present on the adaxial side of nectary. *e*, Top of locules showing empty locules (*lo*) and two stylar canals (*sc*). Shaded area = nectary tissue. *f*, Mid-locular region with two rows of ovules per locule (*lo*).

present, they join to form a single canal below the level of perianth attachment (*M. uniflorus*, *D. strobilaceus*, *C. dubius*) or just above the perianth attachment, in the style (*T. ananassae*). The stylar canal is bilobed (*M. uniflorus*, *T. ananassae*, *D. strobilaceus*) or trilobed (*C. dubius*) in the style, reflecting the number of locules in the ovary.

A nectary occurs between the tops of locules and extends distally into the prolongation (*M. uniflorus*, *T. ananassae*, *C. dubius*; figs. 3*a*, 4*a*, 6*a*) or occurs only in the prolongation (*D. strobilaceus*; fig. 5*a*). The nectary secretory tissue consists of highly convoluted, finger-like projections (*T. ananassae*, *D. strobilaceus*; figs. 11, 12) or is divided into a few smoothly rounded lobes (*M. uniflorus*, *C. dubius*; fig. 13). In *D. strobilaceus* a triradiate canal occupies the central axis in the proximal portion of the prolongation (fig. 21). Near the top of the nectary, tips of the secretory tissue lie in the lumen of the nectary duct(s) (figs. 3*c*, 4*c*, 5*c*, 6*c*, 23). Above the nectary, the duct decreases in size and complexity until it ends in one or two pores (fig. 12). One duct and one pore (*M. uniflorus*, *D. strobilaceus*; figs. 3*a–c*, 5*a–c*,

12) or two ducts and two pores (*T. ananassae*, *C. dubius*; figs. 4*a*, *c*; 6*a*, *c*) occur above the nectary. The nectary duct(s) of the bilocular species lie abaxially to the stylar canals in the central axis (*M. uniflorus*, *T. ananassae*, *D. strobilaceus*; figs. 3*c*, 4*c*, 5*c*); in the trilocular ovary, the two ducts alternate with the stylar canals on the abaxial side of the ovary (*C. dubius*; fig. 6*c*). The pore(s) open at the top of the ovary near the base of the style, on the abaxial side of the style. The corolla tube functions as a nectar reservoir at the base of the perianth.

HISTOLOGY OF THE OVARY (FIGS. 14–26)

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

SUBLOCULAR REGION. Figure 14 shows a cross section through the sublocular region of an *M. uniflorus* ovary. Epidermis simple, of rectangular or cuboidal cells with prominent nuclei; with or

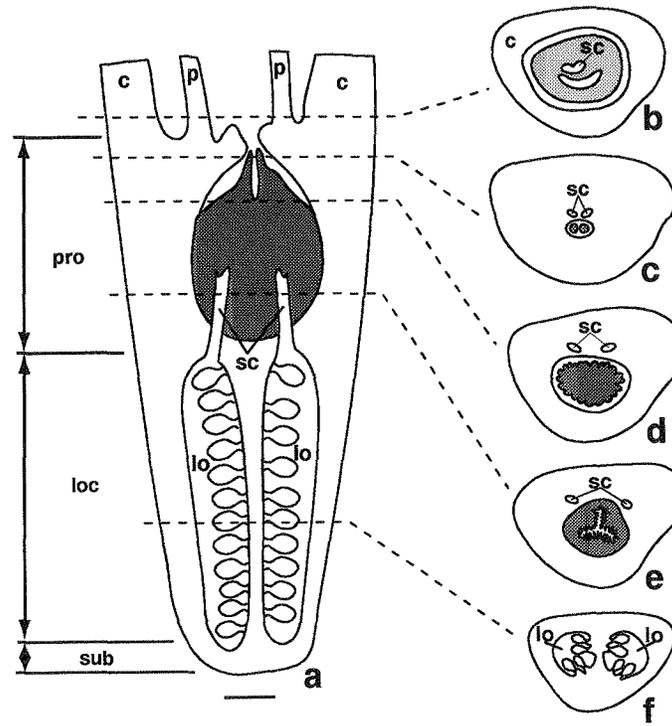


Fig. 5 Diagrams of mature ovary of *Dimerocostus strobilaceus*. *a*, Longitudinal diagram of ovary. The three regions of the ovary are the sublocular (*sub*), locular (*loc*), and prolongation (*pro*). The nectary (shaded) lies in the prolongation. *c* = synsepalous calyx; *p* = petals; *sc* = stylar canals (truncated; see *b-e* for their course); *lo* = locules; bar = 1.96 mm. *b-f*, Cross sections of ovary at the levels indicated in *a*. Bar = 2.28 mm. *b*, Perianth attachment. *c* = synsepalous calyx; lightly shaded area = corolla and style; *sc* = stylar canal; curved slit = nectary pore at top of ovary. *c*, Distal portion of the prolongation. The tips of the nectary are enclosed in the nonsecretory nectary duct. Two stylar canals (*sc*) are present in the central axis. *d*, Mid-prolongation. Nectary tissue (shaded) surrounded by an enlarged, nonsecretory nectary duct. Two stylar canals (*sc*) present on the adaxial side of the nectary. *e*, Proximal portion of the prolongation. Two stylar canals (*sc*) present on adaxial side of the nectary. Shaded area = nectary tissue. *f*, Mid-locular region with four rows of ovules per locule (*lo*).

without a thickened outer cell wall. Trichomes present or absent; when present, unicellular or multicellular. Hypodermis present or absent; when present, one to three layers of isodiametric or columnar cells with few to no intercellular spaces. Vascular zone with ground tissue of isodiametric parenchyma cells or aerenchyma. One outer ring of vascular bundles present with additional bundles scattered throughout the central axis, or vascular bundles irregularly arranged. In *D. strobilaceus* aerenchyma occupies the positions where locules will occur at a higher level. Tanniferous idioblasts absent from epidermis, present elsewhere in ground tissue.

LOCULAR REGION. Figure 15 shows a cross section through the midlocular region of an *M. uniflorus* ovary. Epidermis as in sublocular region. Hypodermis one to 10 layers of columnar or isodiametric cells with few to no intercellular spaces. *Monocostus uniflorus*: proximally, hypodermal cells normally proportioned columnar cells (fig. 18); distally, hypodermal cells very thin and long (fig. 19), the hypodermal cells abaxial to the large vascular bundles slightly smaller (fig. 19, arrow). *Tapeinocheilas ananassae*: hypoder-

mis present only in the upper half of the region (fig. 20). Vascular zone interior to the hypodermis, with considerable diversity in composition among the species. Ground tissue of aerenchyma (fig. 24), or of isodiametric parenchyma cells with occasional intercellular spaces. In the latter case, a layer of aerenchyma surrounds the locules (fig. 15, arrows). Vascular bundles in one ring with additional bundles irregularly arranged. One to three layers of isodiametric parenchyma cells always present directly adjacent to the locules. Locule epithelium simple, of rectangular or cuboidal cells with prominent nuclei. Stylar canals arising laterally or apically from the locules, lined with a densely cytoplasmic, cuboidal, or columnar epithelium. Nectary present or absent at this level with considerable variation in nectary structure among species. When present, surrounded by multiple layers of small, isodiametric parenchyma cells directly adjacent to the nectary. Nectary duct lined with epithelium of cuboidal or rectangular cells; cell walls facing lumen thickened or not thickened. Secretory tissue of isodiametric, densely cytoplasmic cells with few to no intercellular spaces; vascular bundles small and numerous, interspersed with secretory cells. Secre-

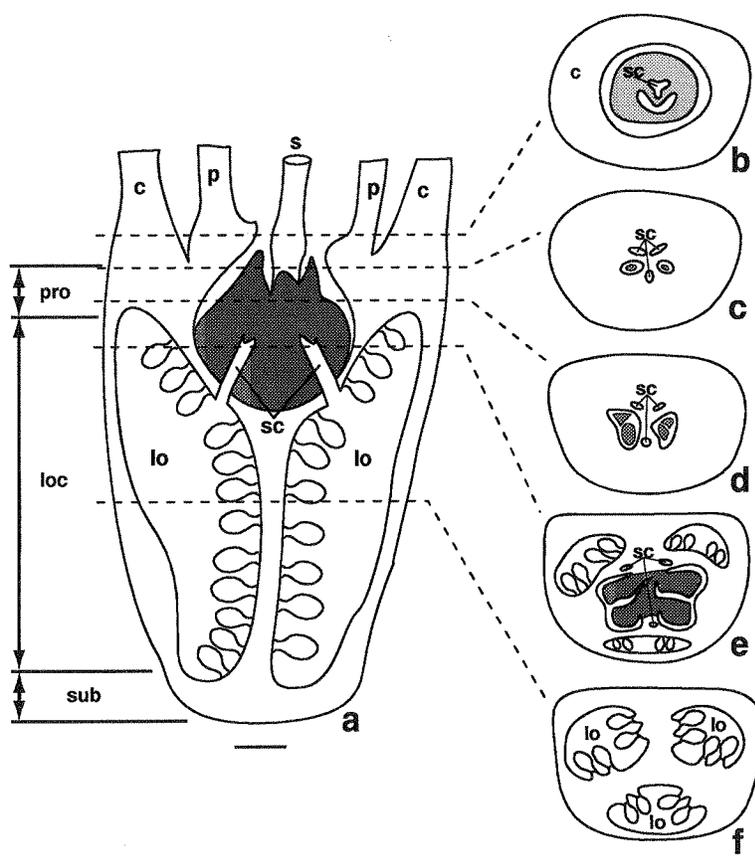
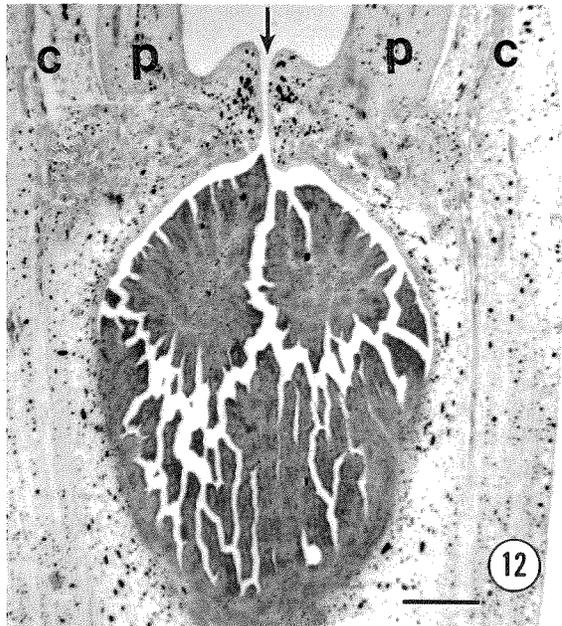
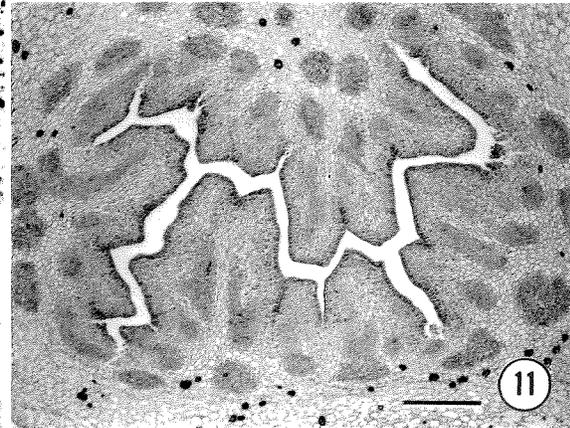
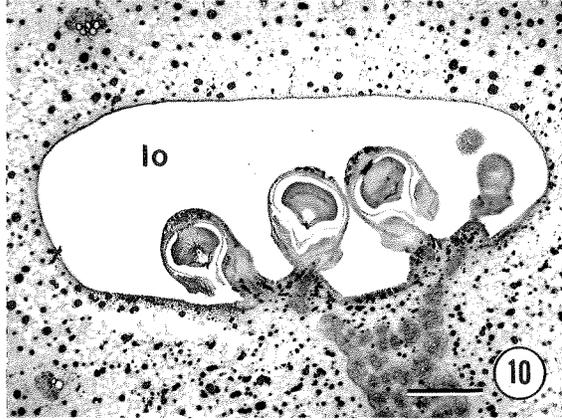
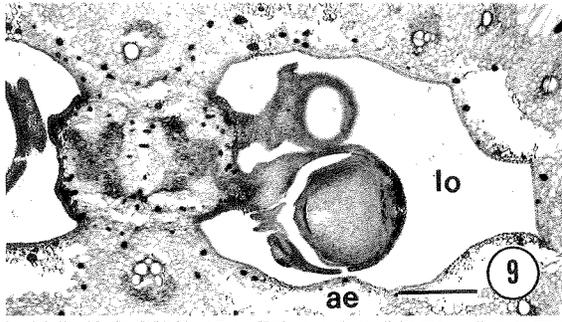
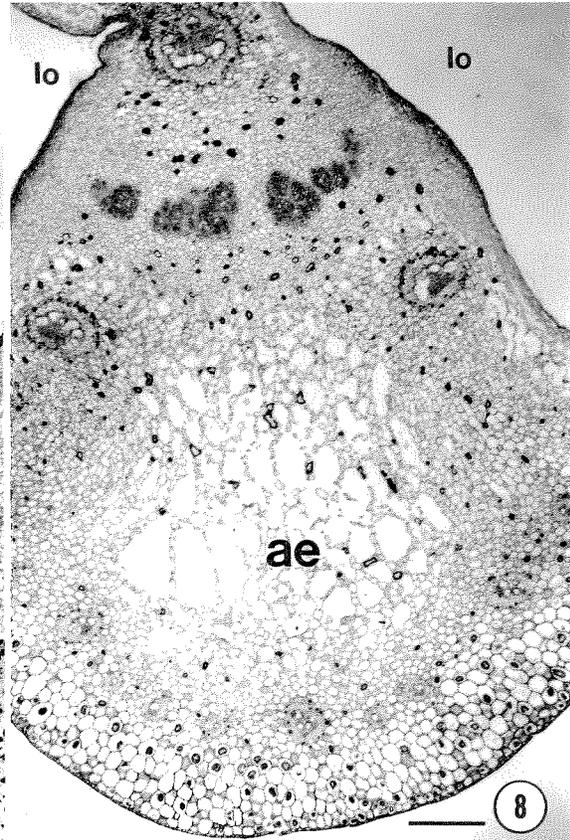
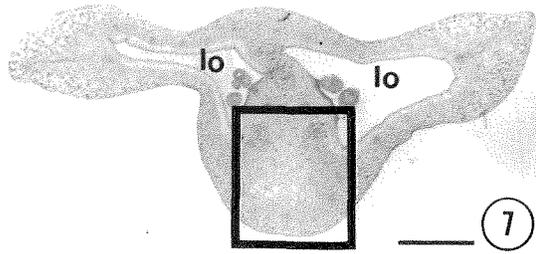


Fig. 6 Diagrams of mature ovary of *Costus dubius*. *a*, Longitudinal diagram of the ovary. The three regions of the ovary are the sublocular (*sub*), locular (*loc*), and prolongation (*pro*). The nectary (shaded) lies between the tops of the locules (*lo*) and in the prolongation. *c* = synsepalous calyx; *p* = petals; *s* = style (the insertion of the style is distorted to show the opening of the nectary ducts); *sc* = stylar canals (truncated; see *b-e* for their course); bar = 0.86 mm. *b-f*, Cross sections of ovary at the levels indicated in *a*. Bar = 1.5 mm. *b*, Perianth attachment. *c* = synsepalous calyx; lightly shaded area = corolla and style; curved slit = nectary pores at top of ovary. *c*, Distal portion of the prolongation. The tips of the nectary (shaded) are enclosed in the lumen of the nonsecretory nectary ducts. Three stylar canals (*sc*) present in the central axis. *d*, Proximal portion of the prolongation. Nectary tissue (shaded) surrounded by enlarged nectary ducts. Three stylar canals (*sc*) present near the central axis. *e*, Top of locules with four ovules per locule and three stylar canals (*sc*) present. Shaded area = nectary tissue. *f*, Mid-locular region with four rows of ovules per locule (*lo*).

tory tissue with a simple epithelium of cuboidal or columnar cells with prominent nuclei, distinguishable from underlying cells by shape and very dark staining; outer walls of epithelium facing lumen not thickened. Central axis differs proximally and distally. Proximally, of isodiametric parenchyma interspersed with vasculature, or a mixture of isodiametric parenchyma and aerenchyma, and with vasculature in a dense band between the locules (fig. 22). Distally, nectary present or absent; when absent, vasculature arranged in center of the axis. Tanniferous idioblasts absent from epidermis and epithelia; present throughout ground tissue of other regions. There is a concentration of tanniferous idioblasts surrounding the locules in *C. dubius*.

PROLONGATION. Figure 16 shows a cross section through the prolongation of an *M. uniflorus* ovary. Epidermis simple, of rectangular or cu-

boidal cells with prominent nuclei; with or without a thickened outer cell wall. Trichomes present or absent; when present, unicellular or multicellular. Hypodermis one to 10 layers of columnar or isodiametric cells with few to no intercellular spaces. Vascular zone interior to the hypodermis with considerable diversity in composition among species. Ground tissue of isodiametric parenchyma cells with occasional intercellular spaces. Vascular bundles in one to three rings with additional bundles irregularly arranged; vascular plexus present in inner two-thirds of this zone. *Dimerocostus strobilaceus*: bundle sheaths present in the distal portion of the zone. *Costus dubius*: the vascular zone differs proximally and distally—proximally, the vascular zone consists of ca. 30 layers of isodiametric parenchyma cells (fig. 25, *vz*), vascular bundles arranged in three rings, one ring near the hypodermis and two in the middle of the zone; in the upper part of this region a vas-



cular plexus present among the two inner rings of the zone (fig. 25); distally, ground tissue arranged in two irregular cylinders that can be distinguished by cell size (fig. 26, *c1*, *c2*), the outer cylinder (*c1*) of six to 10 layers of large to medium-sized isodiametric parenchyma cells, large vascular bundles with bundle sheaths arranged in a single ring near the hypodermis; inner cylinder (*c2*) of ca. 20 layers of small isodiametric parenchyma cells, vascular bundles arranged in two rings with a vascular plexus present among the bundles of the rings. Stylar canals lined with densely cytoplasmic, cuboidal, or cuboidal to columnar, epithelium with prominent nuclei. Nectary present, with considerable variation in nectary structure among species. Nectary duct lined with epithelium of cuboidal, columnar, or rectangular cells; cell walls facing lumen may or may not be thickened. Secretory tissue as in locular region. Secretory tissue epithelium of cuboidal or columnar cells; outer walls of epithelium facing lumen may or may not be thickened. *Monocostus uniflorus*, *T. ananassae*, *D. strobilaceus*: nectary surrounded by multiple layers of small, isodiametric parenchyma cells directly adjacent to the nectary. Central axis proximally containing nectary; distally, containing isodiametric parenchyma cells with a small zone of densely cytoplasmic, isodiametric cells surrounding the stylar canals. *Dimerocostus strobilaceus*, *T. ananassae*: stylar canals surrounded by sclerified cells in the distal portion of the central axis (fig. 17). Tanniniferous idioblasts absent from epidermis and epithelia; present throughout ground tissue of remaining regions. A concentration of tanniniferous idioblasts surrounds the stylar canals in all species.

Discussion

Similar patterns of ovary structure exist in the four genera of Costaceae examined in this study. The major portion of the ovary is the locular region, with a small sublocular region below, and a prolongation above the locules. A vascular plexus occurs just below the attachment of the perianth, and a floral nectary is present near the top of the ovary. The placentation is axile (Maas 1972, 1977; Dahlgren et al. 1985).

The number of fertile locules varies between two (*Monocostus uniflorus*, *Tapeinocheilas an-*

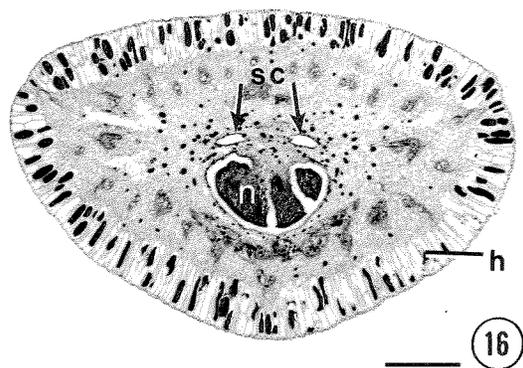
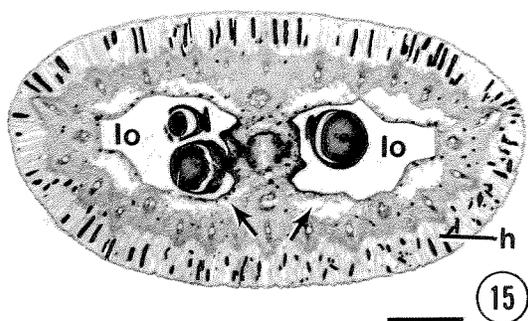
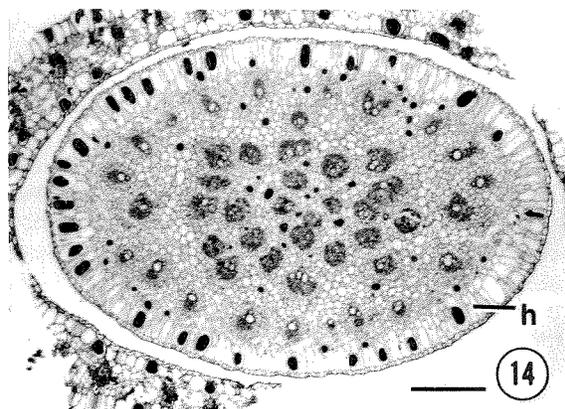
anassae, *Dimerocostus strobilaceus*) and three (*Costus dubius*) and agrees with previous reports (Maas 1972, 1977; Dahlgren et al. 1985). Although *M. uniflorus*, *T. ananassae*, and *D. strobilaceus* are bilocular, the plan of ovary construction is trilocular in these species, although less strongly so in *M. uniflorus* than in the other two species. Evidence for the trilocular plan of construction comes from the presence and distribution of aerenchyma, the position of the locules, the paths of the stylar canals, and a literature report of abnormal bilocular flowers in the Zingiberaceae (Rao 1963).

Aerenchymatous regions occur in *D. strobilaceus* and *T. ananassae* (figs. 7, 8) on the abaxial side of the ovary, in a position corresponding to the third locule in *C. dubius* (fig. 6*f*). In *T. ananassae* (fig. 4*f*) and *D. strobilaceus* (fig. 5*f*) the two existing locules are located on the adaxial side of the ovary, in positions comparable to the two adaxial locules in *Costus*. The comparable region of aerenchyma in *M. uniflorus* is small, occurs only in the distal portion of the ovary, and is confluent with the circumlocular aerenchymatous region.

The path of the stylar canals also supports a trilocular plan of construction. The path of the two stylar canals of all three bilocular species is on the adaxial side of the ovary (figs. 3–5), in a position similar to the two adaxial stylar canals of *C. dubius* (fig. 6). These observations indicate that the “missing” third locule of the bilocular species should be on the abaxial side of the ovary in a position corresponding to the third, abaxial locule of *Costus*.

Further evidence for this interpretation comes from abnormal flowers of *Hedychium coronarium* and *Alpinia mutica* (Zingiberaceae) (Rao 1963; *A. mutica* is cited as *Catimbium muticum*). The normal ovary of both of these species is trilocular. However, Rao (1963) observed abnormal flowers with bilocular ovaries. The loculi of these abnormal flowers are lateral in position with a median septum, as in *M. uniflorus* (fig. 3*f*). This observation suggests a developmental mechanism for the production of bilocular ovaries. A normal trilocular ovary is formed from three conduplicate gynoecial primordia (Van Heel 1988): one anterior and two posterolateral. These pri-

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 Figs. 7–13 Sections of ovaries and nectaries. Tanniniferous idioblasts (black bodies) present throughout. Figs. 7, 8, *Tapeinocheilas ananassae*. Fig. 7, Cross section of the ovary at mid-locular region. *lo* = locules; bar = 1.55 mm. Area in box enlarged in fig. 8. Fig. 8, Enlargement of box in fig. 7 showing aerenchyma (*ae*) abaxial to locules (*lo*). Bar = 3.85 mm. Figs. 9, 10, Cross sections through mid-locular regions of mature ovaries showing rows of ovules per locule. Fig. 9, *Monocostus uniflorus* with two rows of ovules per locule (*lo*). Note the aerenchyma (*ae*) surrounding the locules. Bar = 0.31 mm. Fig. 10, *Dimerocostus strobilaceus* with four rows of ovules per locule (*lo*). Bar = 0.43 mm. Fig. 11, *Tapeinocheilas ananassae*. Cross section of lobes of secretory tissue with finger-like projections that interdigitate. Bar = 0.41 mm. Fig. 12, *Dimerocostus strobilaceus*. Longitudinal section through the nectary in the prolongation. The nectary duct (arrow), which opens at the top of the ovary, is enlarged to surround the distal portion of the nectary. *c* = synsepalous calyx; *p* = petals; bar = 1.2 mm. Fig. 13, *Costus dubius*. Cross section of smooth-surfaced lobes of secretory tissue. Bar = 0.41 mm.



Figs. 14–16 *Monocostus uniflorus*. Cross sections of mature ovary. Tanniferous idioblasts (black bodies) present throughout. Fig. 14, Cross section through the sublocular region. Remnants of the enclosing bract visible surrounding the ovary. *h* = hypodermis; bar = 0.43 mm. Fig. 15, Cross section through mid-locular region. *h* = hypodermis; *lo* = locules; arrows = aerenchyma; bar = 72 μ m. Fig. 16, Cross section through mid-prolongation. *h* = hypodermis; *sc* = styler canals; *n* = nectary; bar = 0.72 mm.

mordia produce three septa: one posterior and two anterolateral (e.g., *C. dubius*; fig. 6f). If the development of the gynoeical primordium on the anterior side of the ovary were aborted, the anterolateral septa would form on the midline and fuse into a single septum with a median orientation (e.g., *M. uniflorus*; fig. 3f).

The number of rows of ovules in each locule

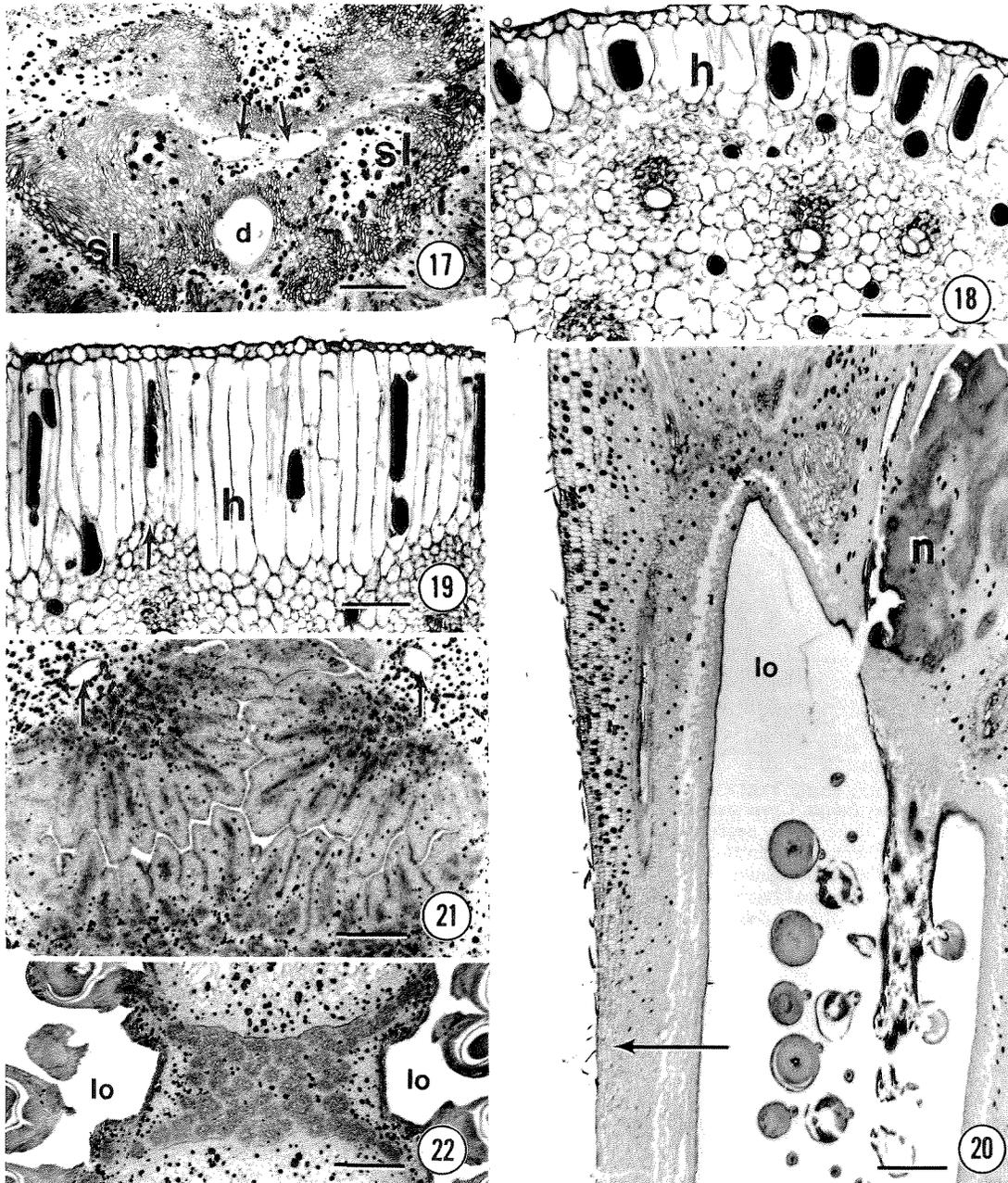
varies among the Costaceae. *D. strobilaceus* and *C. dubius* have four rows of ovules per locule. This report is in partial agreement with Banerji's (1940) report of two to four rows of ovules per locule in *Costus speciosus*. *Monocostus uniflorus* and *T. ananassae* have two rows of ovules per locule. Without additional research, it is not possible to determine whether two or four rows of ovules per locule is the primitive condition for the Costaceae.

The character "number of rows of ovules per locule" was used by Dahlgren and Rasmussen (1983) in their phylogenetic analysis of the Zingiberales. They report the states of this character as "one row per locule" versus "more than one row per locule." The families with "one row per locule" are listed as the Heliconiaceae and Marantaceae. However, these families have, at most, a single ovule (total) per locule (Marantaceae: Woodson and Schery 1945; Andersson 1981; and Kennedy et al. 1988; Heliconia: Kress 1984). A more adequate coding of this character should include character states for a single ovule, two and four rows of ovules per locule.

The extent of the locules that contain ovules varies among the genera of the Costaceae. In *M. uniflorus*, *T. ananassae*, and *D. strobilaceus* ovules occur only below insertion of the styler canals. In *C. dubius* ovules occur both above and below insertion of these canals. Although it is difficult to account for this difference, the placement of the nectary between the tops of the locules might influence the lower placement of ovules in *T. ananassae* and *M. uniflorus*. However, in *C. dubius* the nectary between the tops of the locules at the same level at which ovules are found. Perhaps factors affecting pollination could help explain the absence of ovules at the tops of the locules in some species.

The styler canals arise from the locules in a lateral position in three species (*C. dubius*, *M. uniflorus*, *T. ananassae*), while in *D. strobilaceus* the canals arise from the apex of the locules. Since the origin of the styler canals is presented here for the first time in the Zingiberales, it is not yet possible to evaluate the usefulness of this character for phylogenetic analysis.

The presence of an apical prolongation of the ovary is an unusual feature of the Costaceae. Unfortunately, the amount of tissue that occurs above the locules and closes an inferior ovary is not usually discussed in the literature. Inferior ovaries of some monocotyledons collected from the greenhouse of the University of North Carolina at Greensboro have only a small amount of tissue in the closure (ca. 1 mm or less). These were Taccaceae (*Tacca* sp.) and unidentified species of Bromeliaceae and Amaryllidaceae. If this length is representative of the common state of this character in monocotyledons, then the 2–3 mm found



Figs. 17-22 Sections of ovaries and nectaries. Fig. 17, *Dimerocostus strobilaceus*. Cross section through the distal portion of the prolongation. Sclerified cells (*sl*) surrounding the nectary duct (*d*) and the two stylar canals (arrows). Bar = 0.57 mm. Figs. 18, 19, *Monocostus uniflorus*. Cross sections of hypodermis (*h*) at different levels in the locular region. Fig. 18, Basal portion of the locular region. *h* = hypodermis; bar = 0.04 mm. Fig. 19, Mid-locular region. The hypodermis (*h*) is of extremely long, columnar parenchyma. Where vascular bundles are very large, the hypodermal cells occurring abaxial to the bundles are slightly smaller (arrow). Bar = 0.13 mm. Fig. 20, *Tapeinocheilas ananassae*. Longitudinal section of ovary showing the distal portion of the locular region. Arrow indicates the approximate level at which the hypodermis becomes distinct. *n* = nectary; *lo* = locules; bar = 0.5 mm. Figs. 21, 22, *Dimerocostus strobilaceus*. Fig. 21, Cross section through the nectary at mid-prolongation. Note the three lobes of highly folded secretory tissue that abut to form a triradiate canal. arrows = stylar canals; bar = 0.57 mm. Fig. 22, Cross section of central axis of ovary in the mid-locular region. The vascular bundles in the central axis are arranged in a band between the locules (*lo*). Bar = 0.57 mm.

in *T. ananassae*, *C. dubius*, and *M. uniflorus* is a considerable deviation from the norm, and the 8 mm prolongation of *D. strobilaceus* is exceptional.

In Dahlgren and Rasmussen's (1983) character

set for phylogenetic analysis of the Zingiberales, they referred to a character termed "hypanthium-like neck" of the ovary (p. 352). Only the Lowiaceae are listed as possessing this character. Although the prolongation in the Costaceae is much

Kress 1990). Brown (1938) was the first to suggest a relationship between the nectaries of *Costus* and those of the Zingiberaceae. This idea was picked up by Rendle (1956) and Cronquist (1968), who state that the epigynous glands of the Zingiberaceae are derived from septal nectaries. Rao (1963) also supports this conclusion based on his studies of floral structure of the Zingiberaceae and of *C. speciosus* (Rao et al. 1954; Rao and Pai 1959, 1960; Rao and Gupte 1961). In *C. speciosus* the nectary ducts do not lie in the septa but opposite the locules. Rao (1963) suggests that the two anterolateral secretory regions (note: Rao is referring to regions of nectary tissue, not nectary ducts) in *C. speciosus* represent the ancestral condition for the epigynous glands of the Zingiberaceae. The epigynous glands of the Zingiberaceae occur on vertical lines corresponding to these two anterolateral regions. However, since the positions of the nectary ducts do not correspond to the septa, the nectaries of *C. speciosus* could not have originated from normal gynopleural nectaries. Thus, the derivation of the nectaries of the Zingiberaceae, and of *C. speciosus*, remains unclear. However, we agree that the origins of these nectaries must be sought in the gynopleural nectaries of the rest of the Zingiberales. The exact mechanism of their origin is all that is lacking.

Floral nectary types in the Zingiberales include gynopleural nectaries (Strelitziaceae, Heliconiaceae, Cannaceae, and Marantaceae), the modified gynopleural nectaries of the Musaceae (Fahn et al. 1961) and Costaceae, and the epigynous glands of the Zingiberaceae. The Lowiaceae lack floral nectaries (Kirchoff 1988b).

In his analysis of the phylogeny of the Zingiberales, Kress (1990) lists septal nectaries as a

variable character that he omitted from his analysis. We hope this article has contributed to the better understanding of the structure of the nectaries in this order and that it will soon be possible to include floral nectary characters for use in a phylogenetic analysis of the order.

This investigation of ovary structure in the Costaceae supports the close relationship among the four genera of the family. The structure and position of the nectary is undoubtedly an autapomorphy of the family. Other characteristics that may be autapomorphies are the presence of a well-differentiated hypodermis and the possession of a nonsecretory lining in portions of the nectary duct. However, the states of these characters must be investigated in the other families of the Zingiberales before a definite conclusion can be reached.

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