Floral Anatomy of Chelyocarpus, Cryosophila, and Itaya (Palmae)

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This paper presents the floral anatomy of the *Chelyocarpus* alliance to accompany a current assessment of the group including the description of a new genus (Moore, 1972). Although reports of floral anatomy in palms are few, those completed have been valuable in determining functions of floral organs and relationships among genera, and have provided new information on floral structure in angiosperms (Uhl and Moore, 1971). As the accompanying paper (Moore, 1972) explains, the genera considered here are of special interest because they may form a primitive alliance within the palms, and because two species, *Chelyocarpus dianuerus* and *C. ulei* possess floral plans that are unique in the family.

Materials and Methods

Material examined consisted of flowers at or near anthesis, fixed in formalin-acetic acid-ethanol in the field or garden, and subsequently stored in glycerine alcohol (10% glycerine, 70% ethanol). At least 25 flowers of each collection were cleared, and six or more were sectioned serially, stained, and filmed as described in previous reports (Uhl, 1966; 1969a & b). The reader is referred to the accompanying paper (Moore, 1972) for full descriptions and illustrations of the flowers; only brief descriptions, dimensions of floral organs, and collection numbers are included in this paper.

Descriptions

CHELYOCARPUS (Fig. 1–7).

Chelyocarpus ulei is described from *Moore and Salazar 9494*. Flowers, each 4–5 mm. long and 2 by 4 mm. wide, have two broadly ovate sepals, 2 mm. long by 2 mm. wide, which are distinct or slightly joined at the base forming a shallow cup around two distinct ovate petals of about the same size. The androecium consists of seven (five–eight) stamens in a distinctive arrangement. One stamen is opposite and sheathed by each sepal and the others form two rows of two to three stamens each, one row opposite each petal (Fig. 6). The flower is thus wider along the axis of petal insertion. Filaments of the stamens (Fig. 3a, b) are 2.5 mm. long, ventrally expanded, and tightly encase the lower two-thirds of two (three, four) carpels. Each carpel is 1.5 mm. long with a wide ovarian part 1.0 mm. long which narrows abruptly to a short wide style 0.5 mm. long (Fig. 4). The style is slightly reflexed and ends in a slanted, distal stigmatic opening (Fig. 7). The single ovule (Fig. 7) is borne in a locule occupying two-thirds the height of the ovarian part of the carpel and terminated by a large locular canal. The locular canal and inner ventral surface of the locule are lined by a glandular epithelium. Stigmatoid tissue consisting of large uniseriate one- to three-celled trichomes with large basal cells is borne on the margins and adjacent outer surfaces of the style. The tissues of the
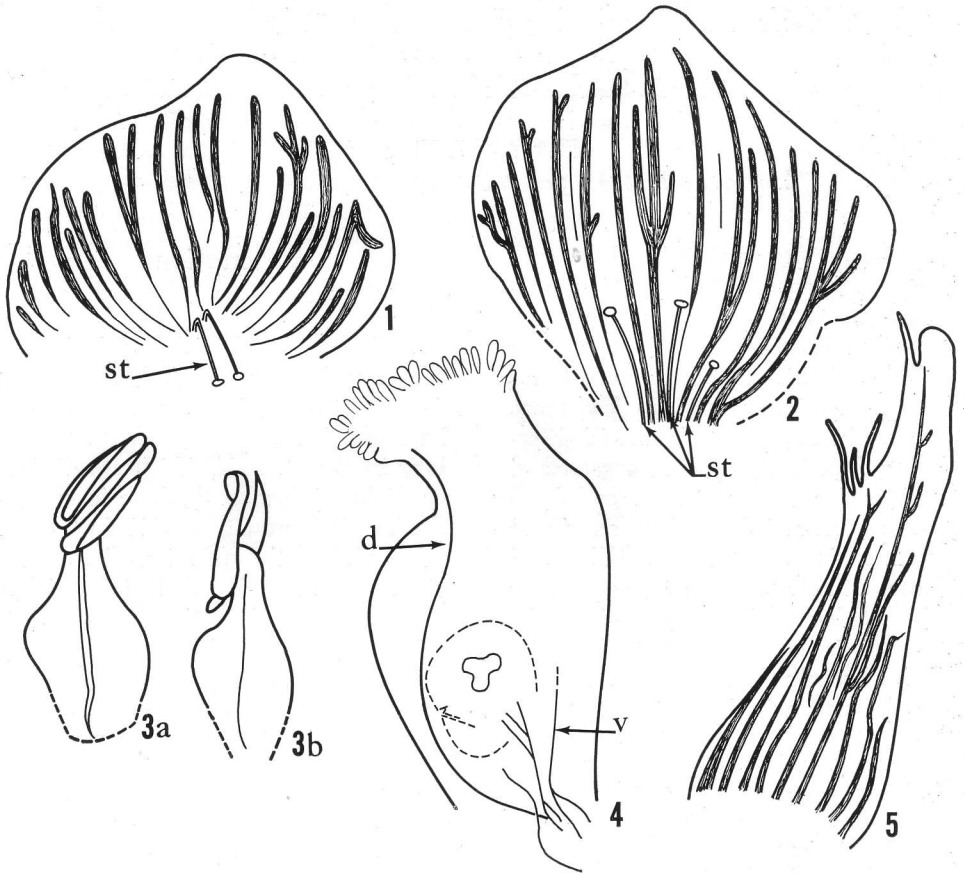
1–5. *Chelyocarpus ulei*. 1, sepal, × 10; 2, petal, × 10; 3, stamen: a, ventral view; b, lateral view, × 8; 4, carpel, × 25; 5, subtending bract, × 10. Details: *d*, dorsal bundle; *st*, stamen trace; *v*, ventral bundle.

style and extreme distal part of the ovary are more mature than the basal part of the carpel. Large tanniniferous cells are scattered in the style (Fig. 7) but are rare below.

An attenuate bract (Fig. 5), 5 mm. long, subtends each flower and is vascularized by eight (7–14) traces from outer bundles of the rachilla. One or two of the larger traces is a vascular bundle and the others are fibrous strands. The vascular supply to the base of each flower is seven to eight large and about seven smaller bundles derived from

bundles of the rachilla. These bundles branch and the branches unite in a circular complex at the base of the floral organs. Fibrous sheaths are absent from bundles of the floral axis, stamen, and carpellary supplies, but are present on traces to sepals and petals (Fig. 1, 2, 6).

All perianth traces arise from the vascular complex opposite the appropriate organ. Each sepal receives 12 (10–20) traces and each petal 10–12 traces. No fusion of petal and stamen traces was observed. Sepal and petal
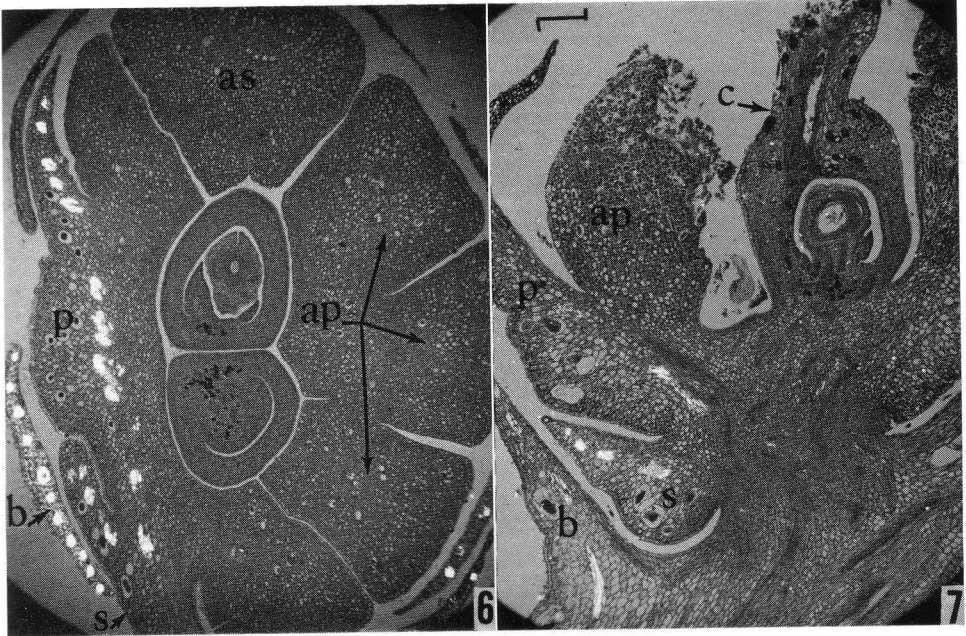
6–7. *Chelyocarpus ulei.* 6, oblique transection of flower slightly below the middle; 7, longisection of flower. Details: *ap*, antipetalous stamen; *as*, antisepalous stamen; *b*, subtending bract; *c*, carpel; *p*, petal; *s*, sepal. For magnifications, scale, Fig. 7, equals 0.2 mm.

traces are in adaxial rows and many branch. Branching of traces is variable, even in perianth segments of the same flower.

The arrangement of the stamens, one opposite each sepal and one to several opposite each petal, is reflected in the vascular system. The traces to the antisepalous stamens are bundles adjacent to or near the mid-bundles of the corresponding sepals (Fig. 1), and traces to antipetalous stamens branch from close to petal traces (Fig. 2). Although both one- and two-trace stamens occur, one trace per stamen is somewhat more common in the collection examined. When a stamen has two traces, each may arise from a separate part of the stelar complex, or a single bundle may branch near or in the base of the filament. Figure 1 shows the origin of two traces to an antisepalous stamen, and Fig. 3a,

a trace branched in the lower part of a filament.

A complex of 3–5 bundles enters the base of each carpel. Just below the locule, this supply separates into a dorsal, two ventral, several short lateral bundles (Fig. 4), and 3–4 large strands which enter the funiculus. The ovular supply divides into 5–6 strands which can be seen in Fig. 6 in the base of the funiculus and outer integument. The vascular supply of the carpel is less mature than those of many palm carpels (Uhl and Moore, 1971), and only the dorsal and bases of ventral and lateral bundles can be discerned in cleared material (Fig. 4). In sections, however, a ring of ca. 30 procambial strands can be observed around the locule.

The hemianatropous ovule is attached to the ventral face of the carpel (Fig. 6) and the micropyle faces dorsally (Fig. 4, 6, 7). The nucellus is 3–4 cells thick

and surrounded by two integuments which are free for about one-third the length of the ovule. The outer integument forms the micropyle and is ca. 6 cells wide. The inner integument consists of 2 (–3) cell layers with an inner layer of very large cells which appear tapetal. A large aril, reaching about half the height of the ovule, surrounds the funiculus. The aril is very shallow on the ventral side of the funiculus (Fig. 4, 6, 7) and is not vascularized.

Some observations on cleared flowers from the type collection of *Chelyocarpus dianeurus, Archer 2199* (US), and on flowers in young fruit of *Chelyocarpus chuco, Cavalcante s. n.,* can be added. It should be noted that these descriptions are based on a few flowers from herbarium sheets. Flowers of *C. dianeurus* appear somewhat less specialized than those of *C. ulei.* Each flower has four slightly imbricate sepals, briefly, if at all, united basally, and four alternate, distinct petals. Sepals and petals are ovate, and ca. 1.5 mm. long; occasionally one petal is smaller than the other perianth members. Each sepal or petal receives 4–5 traces. There is no definite midvein and the two middle traces are often widely separated. Eight (–9) stamens are usually present, one opposite each perianth part. Traces to the stamens arise slightly above the perianth traces and are large, usually double bundles. The one to three carpels, 1.5 mm. long, resemble carpels of *Itaya* in shape. The single ovule in each carpel, like others of the alliance, appears hemianatropous and has a large aril.

Flowers of *C. chuco* appear more stable in number of parts with three sepals, three petals, six stamens, and three carpels present in all examined. Sepals and petals are similar in shape and size to those of the other two species—ovate and ca. 2 mm. long. Sepals are connate for one-third their length, and petals

are distinct where free. As in *Cryosophila,* traces to floral organs can be distinguished in the solid base of the flower. The number of sepal traces varies from 9–15, and petal traces from 7–9. Filaments of the stamens are basally expanded as are those of the other two species, and most receive one large trace. Three carpels were present in all flowers examined, and one carpel was large with the ovule in early seed formation. The other two carpels were abortive. The ovule appears hemianatropous with a rim of tissue which may represent an aril present basally. *Chelyocarpus chuco* resembles *Cryosophila* in three-parted whorls of sheathing perianth parts which closely encase the gynoecium.

CRYOSOPHILA (Fig. 8–15).

Flowers of *Cryosophila argentea* (*Read 2330 B*), *C.* sp. (*Read 605*), *C. warscewiczii* (*Bailey 558*), and *C.* sp. (Chapman Field, 1971) were examined. No significant differences were observed in the four species. The following description and figures (8–15) are of *C. argentea.* The same collections of *C. argentea* and *C. warscewiczii* were studied by Morrow (1965). His description of calyx and corolla as united for much of their length, of three traces to sepals and petals, and of ovules as anatropous appear incorrect for this genus (see Fig. 8, 9, 12).

The flower of *C. argentea* has a short solid base where lower parts of sepals and petals and traces to all floral organs can be recognized (Fig. 13, 14). The three sepals (Fig. 8, 13–15) are lanceolate, 3–5 mm. long and 1.5 mm. wide, and connate for 1.5 mm. basally. The sepals are basally adnate to and closely sheath the slightly imbricate petals (Fig. 12) which are 2 mm. wide and 2.5 mm. long (Fig. 9, 15). At anthesis the sepals and petals form a sheath around the fused linear filaments of the six
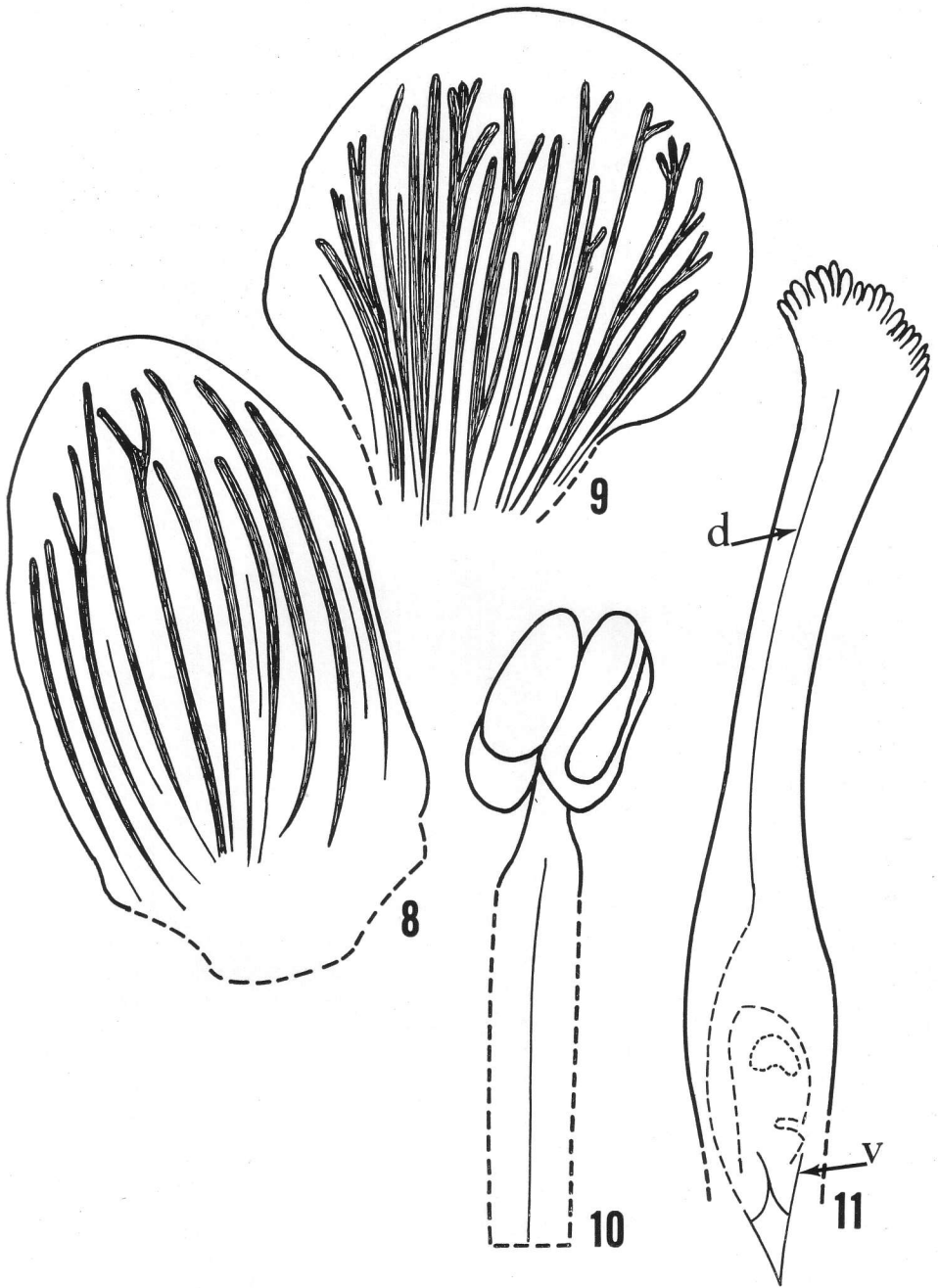
8–11. *Cryosophila argentea.* 8, sepal, × 10; 9, petal, × 10; 10, stamen, × 10; 11, carpel, × 25. Details: *d*, dorsal bundle; *v*, ventral bundle.
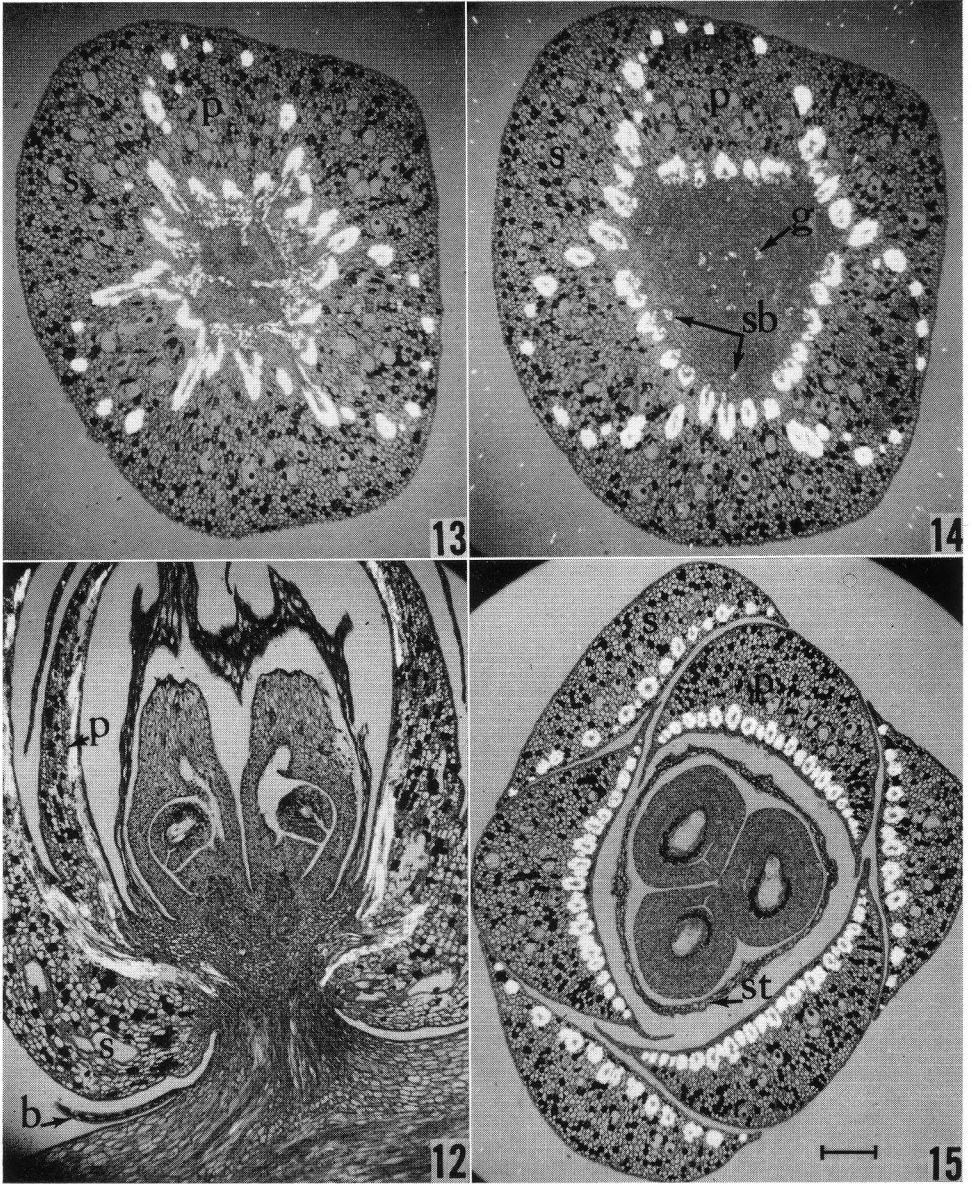
12–15. *Cryosophila argentea.* 12, longisection of flower; 13–15, series of transections through flower. 13, transection through base of flower; 14, transection 120 microns above Fig. 13; 15, transection where floral organs are separate, 400 microns above Fig. 14. Details: *b*, subtending bract; *g*, gynoecial supply in triangular arrangement; *p*, petal; *s*, sepal; *sb*, stamen traces; *st*, fused filaments of stamens. Scale, Fig. 15, equals 0.2 mm.

stamens (Fig. 15); and six anthers, 1.5 mm. in length, are exserted forming a radiate pattern on the top of the ovate sepal-petal sheath. The individual carpel is attenuate with an ovarian part 1 mm. high and a tapering style 1.5 mm. long (Fig. 11). No definite stigma is present. The carpel is open distally with upper ventral margins slightly reflexed at anthesis. Short unicellular trichomes are borne along the margins and down the ventral surface for a short distance. A long stylar canal, lined by a single-layered epithelium, extends from the basal locule to the distal opening. The ovule is attached ventrally near the base of the locule and is described as campylotropous since the embryo sac is slightly curved (Fig. 11, 12). The ovule is turned so that the micropyle faces a lateral wall of the locule and is thus pleurotropous. The two integuments are separate for about one-third the length of the ovule. The outer integument, 3–6 cells wide, forms the micropyle and the two-celled inner integument has the inner layer specialized as a tapetum. A chalazal band of tannin is evident (Fig. 15). A short flat aril is present on the funiculus below the micropyle (Fig. 11).

Each flower is subtended by a small bract (Fig. 12), which may reach 0.5 mm. in length, but has no vasculature. Three bundles from the rachilla enter each floral base where they branch, and branches are united in a circular complex (Fig. 13) from which traces to all floral organs arise. Within the flower, fibrous bundle caps are present on sepal and petal traces only. Two to three outer lateral traces for each sepal are the first bundles to branch from the complex (Fig. 13, outermost bundles). Bundles in antipetalous positions divide to form 6–8 central traces to each petal. In contrast to *Chelyocarpus*, two to three outer lateral petal traces are branches of bundles forming the mid and adjacent lateral traces of each sepal. Traces to the stamens arise as branches of, or from a bundle adjacent to, the mid-veins of the three sepals and petals (Fig. 14). Bundles to antisepalous stamens are free below those of antipetalous stamens, indicating a two-whorled arrangement for the stamens.

The derivation of the gynoecial supply can be seen in Fig. 13. Three bundles extend into the center of the flower and branch, and at a higher level the branches form a triangular arrangement (Fig. 14) which divides into three groups of three bundles each, one group supplying each carpel. A dorsal, two ventral bundles, and several immature lateral bundles form the complement of each carpel. Only the dorsal bundle can be distinguished in cleared material (Fig. 11), but a ring of ca. 14 procambial strands around the locule can be seen in transverse sections. One or two large traces to the ovule separate from the ventral bundles at the base of the funiculus (Fig. 11).

Histological features noteworthy in *Cryosophila* are several. Scattered tannin cells are frequent in the outer parts of sepals and petals (Fig. 12–14). As in *Chelyocarpus*, sepal and petal traces are aligned in an adaxial row (Fig. 14, 15). Raphides are abundant in outer parts of sepals and petals, in filaments of stamens, and in the styles of the carpels. The number of traces to sepals and petals and their branching is irregular. Fibrous bundles may branch laterally from major traces, and such branches are more frequent in some species (e.g., *C. argentea*) than in others. Closely aligned fibrous or vascular bundles with large fibrous caps appear to provide a protective "fence" for inner floral organs. Fibrous bundle sheaths in this genus completely surround most bundles (Fig. 14, 15).
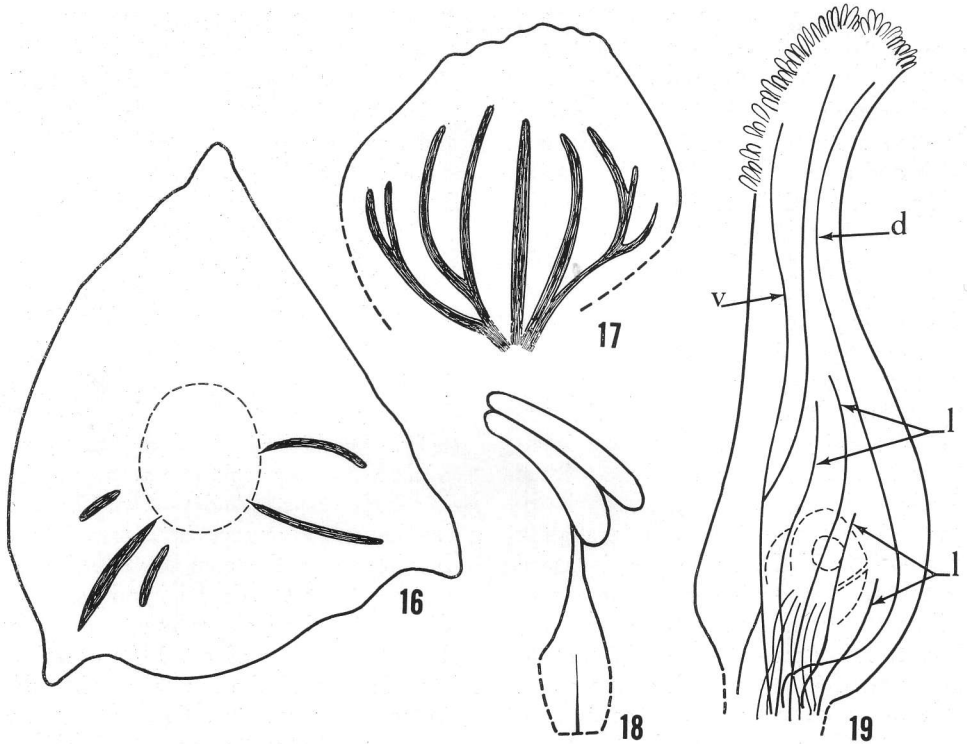
16–19. *Itaya amicorum.* 16, sepals, connate in a triangular sheath, × 10; 17, petal, dotted margins indicate where joined to adjacent petals, × 10; 18, stamen, dotted lines outline connate part of filament, × 10; 19, carpel, × 13. Details: *d*, dorsal bundle; *l*, lateral bundles; *v*, ventral bundle.

ITAYA (Fig. 16–23).

Material investigated for this new genus consisted of flowers from *Moore, Salazar,* and *Gutiérrez 9509.* Flowers are triangular to funnel-shaped, ca. 6 mm. long, and have a short distinct stalk subtended by a small bract 1.5 mm. long (Fig. 23). Connate sepals form a basal sheath with free tips to 2.5 mm. high, which is adnate to a wide petal-stamen tube that surrounds the large single carpel (Fig. 21–23). The free parts of the ovate petals (Fig. 17) are approximately 3.5 mm. wide and 2.5 mm. high. The filaments of the 19–24 stamens are large, subulate basally, and attenuate distally (Fig. 18). Stamens are inserted with one or two opposite each sepal and ca. six in a row opposite each petal. This arrange-

ment accentuates the triangular shape of the base of the flower. The carpel is asymmetric with a large ovarian part, 2.5 mm. long, which is distally attenuate in a funnel-shaped style 2.5 mm. long (Fig. 19). Branched trichomes cover the margins of the distal opening. The ovarian part of the carpels is covered with short, closely appressed, uniseriate trichomes, 3–4 cells long, and with scattered low hairs, each with a short stalk, 7 cells wide and 4 cells high, and a distal mound-shaped part about 10 cells across.

The bract subtending each flower has no vasculature. The epidermis of the short floral stalk is papillose, and the cortex, ca. eight cells wide, may have some irregularly distributed fibrous bundles unconnected to other strands.
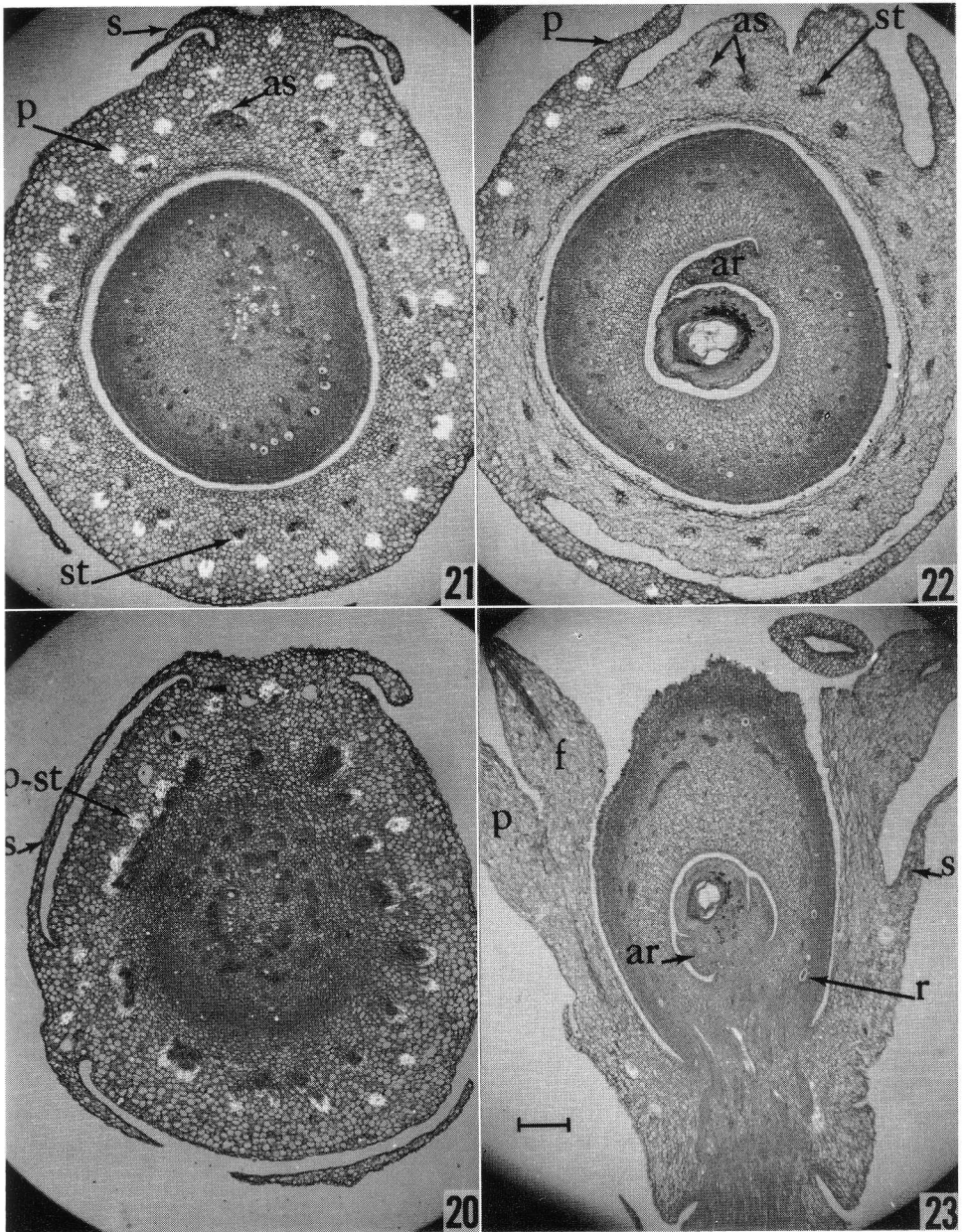
20–23. *Itaya amicorum.* 20–22, series of transections through flower; 20, transection of flower base, sepals partly free; 21, transection 300 microns above Fig. 20, petal and stamen traces mostly separate; 22, transection, 400 microns above Fig. 21, petals partly separate from stamen traces (without fibrous caps); 23, longisection of flower. Details: *ar,* aril; *as,* antisepalous stamen traces, divided in Fig. 22; *f,* filament; *p,* petal; *p–st,* petal–stamen traces partly separated; *r,* raphide sac; *s,* sepal; *st,* stamen trace. Scale, Fig. 23, equals 0.2 mm.

Twenty to twenty-five immature bundles, some procambial, enter each pedicel from the rachilla. Outer bundles in the flower base are joined in an incomplete vascular complex from which traces to sepals, petals, stamens, and a few bundles to the carpel arise.

Sepals in this genus receive fewer traces than those of *Chelyocarpus* and *Cryosophila* and there is no constant supply. A sepal may have two rather large parallel vascular bundles, only a central vascular bundle, a central and several fibrous bundles, or may lack vasculature (Fig. 16). Frequently a sepal trace branches at about mid-length to produce a lateral petal trace. Each petal receives five or six traces (Fig. 17). The origin of stamen traces is variable, but basically follows the pattern of insertion with traces to antisepalous stamens arising from bundles opposite the sepals and with most antipetalous stamen traces arising as basal branches of petal traces (Fig. 21). One or two antipetalous stamen traces may be derived directly from bundles of the peripheral complex. The bundle to a second antisepalous stamen often branches from the trace to the first (Fig. 21, 22). Traces to stamens are large single bundles which have narrow fibrous caps near their origins and extend only a short distance into the base of each filament.

The inner bundles of the stele of the pedicel and some small branches from the perianth complex enter the base of the carpel where about 12 large bundles form a central ring (Fig. 20) which separates into ovular traces and major bundles of the carpel wall. In cleared material, a dorsal, two ventral bundles, and four pairs of smaller lateral bundles could be distinguished (Fig. 19). Each ventral bundle divides about mid-height and the two branches extend into the style. Additional immature lateral bundles provide ca. 24 strands around the locule (Fig. 21). The ovule is supplied by six large and four to five smaller bundles. Derivation of the ovular supply is variable. Traces to the ovule arise from a ventral complex composed of ventral, lateral, and stelar bundles, but the exact make-up of the complex varies from flower to flower.

The hemianatropous ovule has a large aril (Fig. 19, 23) which is partially adnate to the carpel wall (Fig. 22). Lower parts of the aril have one to two outer layers of large elongate, probably glandular cells. The outer integument, nine cells wide, forms the micropyle and the second layer of the two-celled inner integument is tapetal. The nucellus is three or more cells wide. The micropyle usually points toward the dorsal wall of the locule (Fig. 22), but the ovule is sometimes obliquely oriented so that the micropyle is directly laterally.

Discussion

Studies of floral anatomy support the alliance of *Chelyocarpus*, *Cryosophila*, and *Itaya*, the designation of *Chelyocarpus* as the least specialized and of *Itaya* as the most advanced within the group, and the resemblances of *Itaya* to members of the *Thrinax* alliance.

1. Floral vascular systems of the three genera are alike in that a complex of vascular tissue is formed in the base of the flower and gives rise to perianth, stamen, and most gynoecial traces. The complexes apparently reflect a shortening or suppression of the floral axis so that the insertions of floral organs are closely appressed. In addition, floral organs and their vascular supplies may be adnate in varying degrees (*Cryosophila*, *Itaya*). More elongate floral axes which lack vascular complexes are present in other palm groups as described in *Rhapis* (Uhl, Morrow, and Moore, 1969), *Nannorrhops* (Uhl, 1969a), and some ceroxyloid palms (Uhl, 1969b).

2. Sepals and petals of the three genera are structurally alike. Ground tissue is parenchymatous with scattered tannins (*Cryosophila*) and raphides (all genera). A row of bundles composed of larger vascular bundles with distinct fibrous sheaths and small fibrous strands, is aligned along the adaxial face of each perianth part. Sepals and petals are similar in *Chelyocarpus* and *Cryosophila*, although in the latter, petals are somewhat different in shape (cf. Fig. 2, 9). It should be noted that the number and branching patterns of the adaxial row of bundles is variable. The perianth is most reduced in *Itaya*, where sepals, and stamen bases are adnate in a flaring tube. Sepals are also more distinct from petals in *Itaya* where sepals are smaller than petals, and sepal vasculature is reduced or lacking. The vascular supply of petals in *Itaya* resembles petal supplies in the other genera except that fewer (five to six) traces are present.

3. Within these genera, the androecium shows more variation than any other floral organ. Two patterns are present. Stamens in *Cryosophila* are arranged in two whorls of three, a lower whorl opposite the sepals, and an upper whorl opposite the petals. In *Chelyocarpus* and *Itaya*, one (–two) stamens are opposite each sepal, and two–six in a row opposite each petal. Vascular supplies show the same arrangement with traces to antisepalous stamens derived as branches of sepal traces or from bundles adjacent to sepal traces in the complex. Bundles of antipetalous stamens are derived as branches of the bundles supplying the opposing petal, or from bundles in the complex adjacent to petal traces. Both one- and two-trace stamens are present in *Chelyocarpus*. *Itaya*, again, shows reduction in that stamen traces are extremely short bundles.

4. Carpels of all genera are unspecialized in shape with ovoid ovarian parts which taper to distally open styles. No definite stigmas are present, but trichomes are borne on and near the margins of the openings. Ventral sutures are closed except distally, although in *Cryosophila* a ventral notch indicating the position of the suture is present above the attachment of the ovule. The dorsal and two ventral bundles of the carpels in all three genera are larger than the lateral bundles which are difficult to follow because of immaturity. Derivation of the ovular supply is from a ventral complex of bundles with some traces direct from the carpellary stele in *Itaya*. Carpels of *Itaya* are larger, have a larger vascular supply, and more mature bundles.

5. Ovules are structurally alike in the three genera. Although the ovule in *Cryosophila* is considered campylotropous, it varies only in a slight curvature of the nucellus from the hemianatropous ovules of the other two genera. All ovules have funicular arils, two integuments that are free for one-third their length, and a two-layered inner integument with a tapetal inner layer. Ovules in *Chelyocarpus* and *Itaya* are crassinucellate. In *Cryosophila*, the nucellus apparently disintegrates early and was not entire in any of the collections examined.

Among the palms that have been studied, floral structure of this group is more like that of *Rhapis* and *Nannorrhops* where sepal and petal traces are many and ventrally aligned, than the ceroxyloid palms where perianth traces are fewer and in a median row. Reduction in number of sepal traces was also found in the ceroxyloid group. The adnation of reduced sepals and petals, more than six stamens with short traces, and the single carpel in *Itaya* seem trends

which are further developed in the flowers of the *Thrinax* alliance as stated in the accompanying paper (Moore, 1972). In the geonomoid group of palms, *Asterogyne* (*Aristeyera*), sepals have a number of traces in a median position, but only a single trace supplies each petal. The characters of the perianth in the geonomoids, however, may be correlated with the submergence of the flowers in pits.

Some suggestions as to the functioning of these flowers can be surmised from their structure. Pollinating agents for the alliance are not known. The open anthers but extreme immaturity of bundles and tissues in the carpels, and anthers protruding from young buds in one collection of *Cryosophila* (*C.* sp.) suggest that these genera are protandrous. A number of structural aspects appear to protect the developing ovules. These are the abundant raphides in sepals, petals, stamen filaments, and carpels; and tannins—particularly the large inclusions in the exposed styles of *Chelyocarpus*, and the scattered tanniniferous cells in the petals and sepals of *Cryosophila*. The fleshy stamen filaments in *Chelyocarpus* and *Itaya* tightly encase the immature lower parts of the carpels. The adaxial row of fibrous or heavily sheathed bundles in sepals and petals, particularly in *Cryosophila*, appears in cleared material like a "stockade" around the stamens and carpels.

Within the alliance, *Chelyocarpus* is perhaps the least specialized in that there is less connation and adnation of floral organs and of vascular supplies. Sepals may be slightly connate basally but other organs are usually free. Occasionally two antipetalous stamens are fused. There is no adnation of sepal and petal traces which arise from separate bundles of a complex. Vascular traces to the stamens usually arise from bundles adjacent to those supplying sepals or petals, and thus they are not branches of the same bundles that form the perianth traces, as in *Cryosophila* and for most stamens in *Itaya*. Variability in the number and branching of sepal and petal traces and in number of perianth parts, of stamens, and of carpels should also be noted for this genus.

Several floral characters cannot yet be assessed with respect to primitiveness or advancement within the palms. These include the vascular supplies of sepals, petals, and stamens, wide or ventrally expanded versus slender filaments, patterns of stamen arrangement within the multistaminate androecia, and some aspects of ovules. Characters that might be considered primitive in this alliance include variation in number of floral parts (*Chelyocarpus*), distinct and similar sepals and petals, carpels of unspecialized form—lacking definite stigmas but with large distally open stylar canals bearing marginal trichomes, and crassinucellate ovules with large funicular arils.

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