



PRINCIPES

Journal of The Palm Society

July, 1972
Vol. 16, No. 3

THE PALM SOCIETY

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JOURNAL OF THE PALM SOCIETY

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Cover Picture

Chelyocarpus dianeurus is a little known but botanically interesting and horticulturally promising fan palm here seen in the rainforest near Buenaventura, Colombia. Photo by M. V. Parthasarathy.

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An illustrated quarterly devoted to information about palms and published in January, April, July and October by The Palm Society, Inc.

Subscription price is \$6.00 per year to libraries and institutions. Membership dues of \$10.00 per year include a subscription to the Journal. Single copies are \$1.50 each. The business office is located at **1320 S. Venetian Way, Miami, Florida 33139**. Changes of address, undeliverable copies, orders for subscriptions, and membership dues are to be sent to the business office.

Second class postage paid at Miami, Florida and at additional mailing offices.

Mailed at Lawrence, Kansas
October 18, 1972

Chelyocarpus and its Allies Cryosophila and Itaya (Palmae)

HAROLD E. MOORE, JR.

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Two handsome fan palms of the subfamily Coryphoideae have been growing for many years in the garden of the Museu Emilio Goeldi at Belém, Pará, Brazil, where they have been known as *Chelyocarpus ulei* and *Tessmanniophoenix chuco* or *Tessmanniodoxa chuco*. Seed of the latter was introduced into the United States by Mr. Stanley Kiem in 1961 and of *C. ulei* by the writer in 1967. There are, in addition, two other related palms in Colombia and Peru. The four together are of particular interest to the grower because of their ornamental potential and to the botanist because they have characteristics that place them among the most primitive of palms. There has, however, been some uncertainty as to the correct generic disposition of *Tessmanniodoxa chuco* and of an undescribed palm from Peru. Crucial to a solution of generic problems has been the identity of the palm described in 1847 by Martius as *Thrinax? chuco*. Recently specimens in flower and fruit from the general region from which *Thrinax chuco* was described have become available. The problem may now be resolved with some confidence and the Peruvian palm is described as a new genus, *Itaya*.

A Brief History of *Thrinax chuco*

Alcide Dessalines d'Orbigny, a French explorer and scientist, travelled widely in South America during the years 1826 to 1833. An account of these travels—*Voyage dans l'Amérique méridionale*—was published in seven volumes of text

and two of plates. Volume 7 part 3 of this work was an account of the palms collected by d'Orbigny prepared by C. F. P. von Martius. Known alternatively and more familiarly as *Palmetum Orbignianum*, this study of the palms appeared in several fascicles over a period from 1842 to 1847 except for one plate published earlier (see Stafleu, 1967). It included, among many others, a fan palm, *Thrinax? chuco*, collected in 1832 (see Urban, 1906) near a Brazilian fort, Principe da Beira, on the banks of the Guaporé or Iténes River which separates Bolivia and Brazil.

Martius' description appears to have been based on a drawing and actual material of leaf and fruit (*d'Orbigny no. 32*). There are fragments of a leaf in the Martius herbarium now at the Jardin Botanique National de Belgique, Bruxelles, Belgium, though three fruits mentioned by Martius have not been located there nor has material been found at Paris. The description of the material available is very detailed, but unfortunately neither inflorescence nor flowers were described and these are vital for a definitive generic placement of this palm as Martius noted. That it was not a *Thrinax* has been assumed for a long time, and it has been placed variously in *Trithrinax*, *Acanthorrhiza*, *Tessmanniophoenix*, and most recently in *Tessmanniodoxa*.

The transfers of *Thrinax chuco* to *Trithrinax* by Walpers in 1849 and to *Acanthorrhiza* by Drude in 1882 were made without further knowledge of the

palm as was Burret's assignment of it to *Tessmanniophoenix* in 1928. In 1934, however, Burret published photographs of *Chelyocarpus ulei* and *Tessmanniophoenix chuco* taken by Captain H. A. Johnstone in the botanic garden at the Museu Goeldi where they appear to have been brought as seed by Professor Huber from much the same region where Ule had collected *Chelyocarpus ulei*. Burret also published supplementary notes on flowers, fruits, and inflorescences of these plants from specimens provided by Captain Johnstone. Burret visited Brazil himself in 1937-38, when he saw living material at Belém. He thereafter decided that the genus *Tessmanniophoenix*, founded on *T. longibracteata*, was the same as *Chelyocarpus* so he provided a new name, *Tessmanniodoxa*, for *Tessmanniophoenix* or *Thrinax chuco* which he considered generically distinct by reason of the smooth rather than corky-tessellate surface of the mature fruit.

There the matter rested until 1960 when, with Ing. Adolfo Salazar C. and Dr. Earl E. Smith, I collected two fan palms in Peru. An attempt to identify these palms initiated a reexamination of

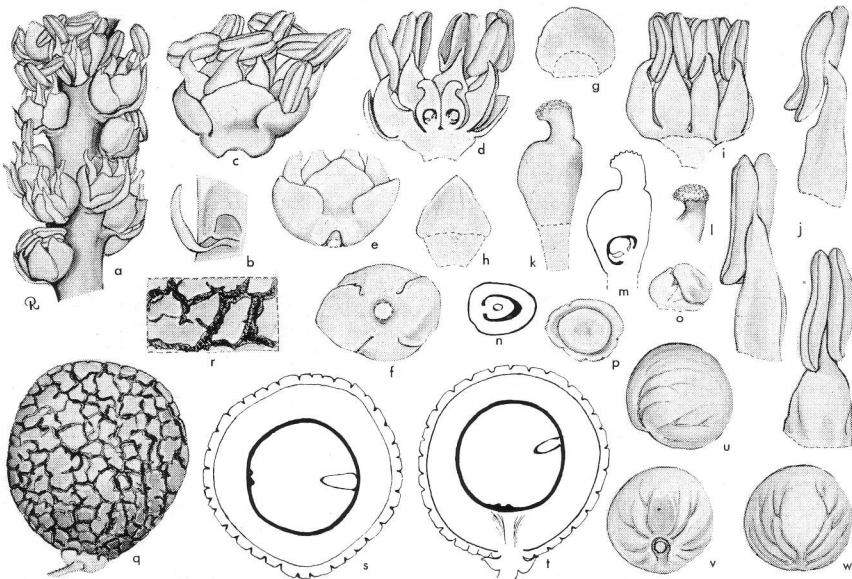
the whole problem and attempts to obtain complete material of *Thrinax chuco* from its type locality. Dr. Ghillean T. Prance and his colleagues have recently collected ample specimens in flower and fruit of a palm that agrees in every detail with Martius' description of *Thrinax chuco* from known locations on the Rio Madeira downriver from its junction with the Guaporé on which Principe da Beira lies. There seems little doubt now that the cultivated material is correctly identified with *Thrinax chuco* but comparisons with *Chelyocarpus ulei* and with another palm from Colombia that Burret also placed in *Tessmanniodoxa* suggest that all belong to *Chelyocarpus*, which in turn is amply distinct from the Peruvian palm here called *Itaya*.

These genera, with *Cryosophila*, form an alliance characterized by a distinctive leaf-blade. Their relationships to other apocarpous genera of the coryphoid palms (Coryphoideae) and the principal differences between them may be brought out in a partial synoptic key and in descriptions and comments to follow.

1. Carpels 3-1, distinct (apocarpous genera).
2. Perianth uniseriate, lobed; primary inflorescence branches subtended by persistent tubular bracts sheathing the bases, a prophyll usually present on the peduncular base of at least the lower branches; carpel 1. _____ *Coccothrinax, Thrinax, Zombia*
2. Perianth biseriate, the sepals and petals clearly distinguishable in separate whorls; subtending bracts various but a prophyll seldom present on the peduncular base of inflorescence branches (but see *Chelyocarpus chuco*); carpels 1-3.
3. Carpels approximate apically, with styles as wide as or wider than ovary, the gynoeceum essentially top-shaped, stigmas short and incurved, erect, or recurved; stamen-filaments or staminodes short and adnate to the petals, anthers included. _____ *Liberbaileya, Maxburretia, Rhapsis*
3. Carpels with styles conspicuously narrower than the ovary, the gynoeceum never top-shaped; stamen-filaments distinct or connate but not markedly adnate to the petals, anthers usually exerted.
4. Flowers with an elongate pseudopedicellate base equalling or exceeding the petals, these reflexed at anthesis; flowers near the base of the rachillae perfect, those near the apex staminate; leaves regularly divided into 1-ribbed acute segments, a short palman (undivided portion) present; carpel 1. _____ *Schippia*
4. Flowers lacking a pseudopedicellate base, the petals erect or spreading but not reflexed at anthesis; flowers essentially uniform in an inflorescence; leaves variously divided.

5. Leaves regularly divided part way to the base into 1-ribbed or more rarely 2-3-ribbed segments with acute or briefly bifid or briefly toothed apices throughout; stamens always 6. *Chamaerops*, *Rhapidophyllum*, *Trachycarpus*, *Trithrinax*
 5. Leaves divided at the center beyond the middle or nearly to the base into 2 halves, each half divided laterally into more or less cuneate, 2-several-ribbed segments, these again shallowly to deeply divided into acute or briefly bifid 1-ribbed segments; stamens 6-24.
 6. Stamens 6, the flat filaments connate half their length or more; styles elongate, exerted; root-spines present on the trunk. *Cryosophila*
 6. Stamens 6 or more, the filaments distinct or united briefly at the base for less than half their length; styles not exerted; root-spines not present on trunk.
 7. Petals 2, 3, or 4, distinct, imbricate; sepals 2, 3, or 4, distinct or briefly connate; stamens (5-) 6 or (7-) 8; carpels (1-) 2 or 3 (4-); embryo lateral; petioles not split basally in the leaf-sheath; sheath remaining closed. *Chelyocarpus*
 7. Petals 3, connate half their length; sepals 3, connate basally; stamens 18-24; carpel 1; embryo subbasal; petiole split basally in the leaf-sheath; sheath splitting opposite the petiole. *Itaya*
1. Carpels 3, connate by their styles or the gynoecium entirely syncarpous (non-apocarpous genera).

Chelyocarpus



1. *Chelyocarpus ulei*. a, portion of rachilla $\times 2$; b, bracteole and floral scar $\times 4$; c, flower $\times 4$; d, flower in vertical section $\times 4$; e, f, perianth in lateral and bottom views $\times 4$; g, sepal $\times 4$; h, petal $\times 4$; i, flower, perianth, removed $\times 4$; j, stamens in three views $\times 8$; k, pistil $\times 4$; l, stigma $\times 4$; m, pistil in vertical section $\times 4$; n, ovary in cross-section $\times 4$; o, p, ovule in lateral and top views $\times 8$; q, fruit $\times 1$; r, surface of fruit $\times 2$; s, fruit in cross-section $\times 1$; t, fruit in vertical section $\times 1$; u, v, w, seed in lateral, antirapheal, and rapheal views $\times 1$. a-p from material of Moore & Salazar 9494, q-w from material of Moore 9548, both preserved in liquid.

Chelyocarpus Dammer, Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 7: 395. 15 Jan. 1920.

Type: *C. ulei* Dammer

Tessmanniophoenix Burret, *op. cit.* 10: 397. 1 Dec. 1928.

Lectotype: *T. longibracteata* Burret, (*vide* Burret, *op. cit.* 15: 337. 1941).

Tessmanniodoxa Burret, *op. cit.* 15: 336. 30 Mar. 1941.

Lectotype: *T. chuco* (Martius) Burret (*vide* Moore, *Gentes Herbarum* 9: 273. 1963).

Solitary, unarmed, hermaphroditic palms of moderate size, the trunk naked except for fibrous residual sheaths below the crown.

Leaves numerous in a spreading crown, induplicate palmate, flabelliform; sheath fibrous, densely appressed-villous when young, not splitting opposite the petiole, with prominent fibrous ligule on each side of petiole at apex, this disintegrating into loose fibers in age; petiole elongate, unarmed, not splitting basally in sheath, rounded below and channelled above basally becoming biconvex and rhombic in section with obtuse margins distally, terminating adaxially in a small, deltoid, elevated hastula plicately grooved dorsally, and in a narrow deltoid margin abaxially; rachis not developed; blade flat, thin, divided centrally well beyond the middle or nearly to the base, each half divided into paired or irregularly grouped 1-ribbed segments (*C. chuco*), or divided to the base into elongate-cuneate many-ribbed segments, these again divided into several acute or very briefly bifid 1-ribbed segments.

Inflorescences several, interfoliar, pendulous; peduncle flattened, bearing a prophyll and at intervals 2 (-3) tomentose sterile bracts with tubular bases

and cochleariform blades; rachis flattened, with several recurved, once-branched, flattened primary branches basally adnate to the rachis, each subtended by a prominent fertile bract similar to those on the peduncle but progressively smaller and at least the lower branches bearing a membranous prophyll (*C. chuco*), or bearing only simple rachillae, or the lower rachillae sometimes fasciate or subfasciculate on short branches but the fertile bracts, except sometimes for an open one subtending the whole rachis, small and not like those on the peduncle; rachillae usually adnate for some distance above an acute, sometimes elongate subtending bract.

Flowers perfect, at least in *C. ulei* strongly scented, borne singly in a spiral along the rachillae, each sessile or on a very short pedicel subtended by a small to prominent acute bract; sepals 2 or 3 and distinct or briefly connate basally, or 4, distinct, and slightly imbricate; petals 2, 3, or 4, distinct, imbricate; stamens 5, 6, 7, 8, or 9, one opposite each sepal, remainder opposite petals, the filaments erect, distinct, fleshy, thick and broad below and more or less abruptly narrowed to a subulate tip, anthers dorsifixed at the middle, laterally dehiscent by longitudinal slits, exerted at anthesis, bifid at apex and base; carpels 3 or 2, rarely 1 or 4, only one usually developing into a fruit, style short, somewhat recurved, stigma papillate, ovule hemianatropous, attached adaxially at the base, an aril present and basally fused to the locular wall.

Fruit globose with excentrically apical stigmatic residue; epicarp smooth or coarsely corky-tessellate; mesocarp thick, dry; endocarp membranous: seed not adherent to the pericarp, globose; hilum basal, round; raphe slightly impressed the length of the seed and with ascending branches; endosperm homogeneous; em-

bryo below or above the middle opposite the raphe; germination remote-tubular; seedling with one scale leaf and bifid eophyll.

Distribution and ecology: three species of Amazonian Bolivia, Brazil, Peru, and of western Colombia, at low elevations in areas of high rainfall.

Chromosome complement: $n=18$ (cf. Read & Moore, 1967).

Anatomical features: central vascular bundles of petiole with a single phloem strand (Parthasarathy, 1968). For foliar and floral anatomy see Uhl, 1972a & b.

Chelyocarpus was initially set apart because of the corky-tessellate surface of the fruit of the type-species which so resembled a turtle's carapace as to suggest the generic name. Dammer commented on the dimerous or two-parted perianth of *C. ulei* but lacking flowers thought his material perhaps atypical. More complete collections, however, have shown that the perianth is normally dimerous in the species. Although the tessellate fruit is unusual it is not unique in palms. Dransfield (1970) has noted the occurrence of corky-warted fruits in three undescribed species of *Licuala*, a genus otherwise with smooth fruits, and similar fruit surfaces have evolved independently in several genera. A difference in fruit alone does not seem of sufficient importance to outweigh striking resemblances to two other species which Burret assigned first to *Tessmanniophoenix* and then to *Tessmanniodoxa*. Companion studies of floral anatomy and leaf anatomy (Uhl, 1972a & b) bolster the resemblances.

All three species have similar habit; the leaf-blade is deeply divided centrally, then variously divided and segmented laterally, while the densely appressed-villous sheath does not split opposite the petiole nor does the petiole split basally in the sheath; central vascular bundles of the petiole have single phloem strands;

inflorescences are similar in nature of bracts and flattened axes with much adnation, though one is more branched than the others; flowers follow a basic pattern though with some interesting variation—the normal dimerous and tetramerous (four-parted) state of two species is unique among the palms so far as I am aware; fruits and seeds are similar except for the tessellate fruit coat of *C. ulei*. I have, therefore, transferred both species of *Tessmanniodoxa* to *Chelyocarpus*.

Chelyocarpus chuco differs from the remaining species in a series of characteristics listed in the key to species. It might be argued that *Tessmanniodoxa*, restricted to its lectotype-species (*T. chuco*), deserves subgeneric or even generic rank. I consider it merely to represent the basic pattern from which *C. dianeurus* and *C. ulei* diverge in having a less complex inflorescence, flowers readily derived from a trimerous state by multiplication of parts or by reduction, and leaves with an indument of trichomes and deep lateral lobing. It is particularly interesting to note that these species correlate with three of nine refugia—Madeira-Tapajós (7), East Peruvian (6), Chocó (1)—postulated by Haffer (1969) as regions where rainforest persisted during drier epochs of the Pleistocene.

When one assesses the characteristics of *Chelyocarpus*, it becomes evident that it must be considered among the most primitive of palm genera, sharing this honor with *Trithrinax*, also South American but apparently representing a separate cluster of interrelated genera. *Chelyocarpus chuco*, as also *Trithrinax*, comes close to what might in some ways be considered a palm prototype so far as inflorescence, flowers, and fruit are concerned—trimerous perianth whorls, hexamerous androecium, trimerous gynoecium, and continuous growth in the development of fruit (see Murray, 1971).

Within *Chelyocarpus* there is apparent simplification of the inflorescence and there are modifications of the flower which suggest directions of evolution toward connation and reduction in the perianth, elaboration of the androecium, and reduction of the gynoecium found in the related genus *Itaya* and in the more specialized *Thrinax* alliance.

Primitive though it may be, *Chelyocarpus* seems clearly to have close affinities with two genera of more specialized nature—*Cryosophila* and *Itaya*. The deep central division of the leaf and lateral lobing are unusual among apocarpous genera and there are striking resemblances in the inflorescence, in flowers, and in fruit. *Cryosophila* exhibits floral specialization probably related to pollination while retaining a hexamerous androecium and trimerous gynoecium. *Itaya* is most advanced of the three in floral structure and in having two phloem strands in central vascular bundles of the petiole. Preliminary studies of the late metaxylem in the stems of *Chelyocarpus*, *Cryosophila*, and *Itaya*

show the presence of simple perforation plates and often a characteristic ligule in vessels of *Itaya* as opposed to the more generalized compound perforation plates (scalariform) in *Chelyocarpus* and in *Cryosophila albida* a mixture of vessels having either scalariform perforation plates with 1–5 (often only 1–2) bars or simple perforation plates and no ligules (Larry Klotz, personal communication).

Before leaving this small group, some notes on the division of the leaf may complement observations made by Dransfield (1970) on unusual leaf-division in *Licuala* and *Rhapis*. In *Chelyocarpus* and allies, the leaf-blade is split deeply or nearly to the base along one side of the continuing nerve presumed to represent the midnerve of the central pinna of an induplicate leaf. Division is thereby nearly equal, for each of the central lobes will have half a segment at its inner margin but one has a marginal nerve while the other lacks marginal thickening.

Key to Species

1. Perianth trimerous with 3 sepals and 3 petals; stamens 6; carpels 3; fruit not corky-tessellate, the seed with embryo above the middle; inflorescence with several recurved once-branched primary branches, each subtended by a prominent bract and at least the lower branches bearing a membranous prophyll on the peduncular portion; leaf-blade green below, divided nearly to the base at center but the lateral divisions not deeply divided (Fig. 12Ba). Eastern Bolivia, western Brazil. *C. chuco*
1. Perianth dimerous or tetramerous with 2 or 4 sepals and 2 or 4 petals; stamens 5–9; carpels usually 2; fruit and seed various; inflorescences with a prophyll and usually 2 prominent sterile bracts below the terminal rachis, this sometimes subtended by an open fourth bract, lacking prominently bracteate primary branches bearing prophylls, the rachillae all simple or the basal ones fasciate or subfasciculate on short branches; leaf-blades silvery below, divided centrally to below the middle or nearly to the base, then divided to the base laterally into elongate-cuneate many-ribbed segments, these again divided into 1-ribbed segments (Fig. 12Aa, 13Ba).
2. Perianth tetramerous with 4 distinct sepals and 4 petals; bracts below the flowers much shorter than the perianth; fruit with smooth epicarp, the seed with embryo below the middle; inflorescence rachis and rachillae glabrous; leaf divided to within 15–18 (or rarely 3–5?) cm. of the base at center. Western Colombia. *C. dianeurus*
2. Perianth dimerous with 2 usually distinct or rarely briefly connate sepals and 2 petals; bracts below the flowers equalling or exceeding the perianth; fruit corky-tessellate, the seed with embryo above the middle; inflorescence rachis and rachillae floccose-tomentose at least at anthesis; leaf divided to within 1–2 cm. of the base at center. Western Brazil, eastern Peru. *C. ulei*



2. *Chelyocarpus chuco* cultivated at Museu Goeldi, Belém, Brazil. Note the pale infructescence on plant at upper right. Photo by S. Kiem.



3. Fruits of *Chelyocarpus chuco*. Photo by S. Kiem.

Chelyocarpus chuco (Martius) H. E. Moore, *tr. nov.* (Fig. 2-3, 12B).

Thrinax? *chuco* Martius, *Palmetum Orbignianum* 45, t. VIII, fig. 1 & T. XXV B, 1847.

Type: *d'Orbigny* 32 (BR).

Triptrinax chuco (Martius) Walpers, *Annales Botanices Systematicae* 1: 1005. 1849.

Acanthorrhiza chuco (Martius) Drude in Martius, *Flora Brasiliensis* 3(2): 554. 1 Mai 1882; Beccari, *Webbia* 2: 241. 1907.

Tessmanniophoenix chuco (Martius) Burret, *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem* 10: 400. 1 Dec. 1928.

Tessmanniodoxa chuco (Martius) Burret, *op. cit.* 15: 337. 30 Mar. 1941. Trunk to 5 m. high or more, slender.

Leaves 10-22 in a crown; sheath more than 3 dm. long, pale (golden?) appressed-villous; petiole elongate, to ca. 1.8 m. long (*teste* Martius), ca. 2 cm.

wide basally, 1 cm. wide apically, with brown furfuraceous scales at first, becoming glabrate; hastula deltoid or truncate-deltoid, 1.5-2.5 cm. long, 2-3 cm. wide at base; blade thin, green, to 1.05 m. long at center, 1.8 m. across, divided centrally to within 1.5-2 cm. of the base, divided laterally one-fourth to nearly three-fourths to the base into 15-24 lanceolate 1-ribbed segments on each side, these mostly grouped in pairs toward the margins or irregularly toward the center, the ultimate segments to 50 cm. long, 2.5-6 cm. wide, each with a midrib, 2-3 lateral secondary and several finer tertiary nerves on each side more prominent below than above, flexuous cross-veinlets prominent on both surfaces when dry, proximal segments often conspicuously narrowed and "shouldered" toward the acute or very briefly bifid apex, lower surface of blade green but paler than upper surface, very densely beset with minute, shining, translucent dots.

Inflorescences 3-4 (*teste* Martius), to more than 5.5 dm. long; sterile bracts 2 (or more?), densely light brown floccose-lepidote outside, glabrous within, ca. 21 cm. long; branches 5-7, each

subtended by a fertile bract similar to the peduncular bracts but progressively smaller, the lowermost branches bearing a membranous prophyll to 12 cm. long, upper branches with incomplete prophylls or prophyll lacking, main axis and branches more or less flattened, branches mostly curved with flattened base to ca. 18 cm. long, 1.3 cm. wide in fruit, fertile portion to ca. 20 cm. long; rachillae to 8 cm. long, subtended by narrowly triangular, membranous, tomentum-tipped bracts to 15–17 mm. long on lowermost branches, shorter above, shortly adnate above the bract and with a short sterile base.

Flowers sessile or briefly pedicellate, borne singly in a spiral on the rachillae, bracts short; perianth 2–2.5 mm. long, creamy white, erect at anthesis; sepals 3, connate for ca. 0.5 mm., 2.0–2.5 mm. long, lobes deltoid; petals 3, about as long as the sepals, distinct, imbricate; stamens 6, filaments broad and thick basally, subulate above, anthers exerted and spreading from the narrow mouth of the perianth; carpels 3.

Fruit globose or depressed-globose, with persistent thickened perianth, 1.6–2.0 cm. wide, 1.6–1.8 cm. high; epicarp not tessellate; mesocarp rather thin; endocarp membranous; seed brown, depressed-globose, ca. 1.6 m. wide, 1.4 cm. high; embryo above the middle.

Vernacular names: *Carnaubinha* fide Prance *et al.*; *chuco* in Itonama, *huechichaho* in Baures, *iriai* in Cayuvava, *sava* in Itênès, *choinan* in Pacaguara, fide d'Orbigny.

Distribution and ecology: Bolivia and Brazil along banks of rivers, larger in forests than along the banks (fide d'Orbigny), flowering November (Prance *et al.*) to January (d'Orbigny), fruiting April (d'Orbigny) to July (Prance *et al.*).

Specimens examined:

BOLIVIA. STATE OF PANDO: west bank

of Río Madeira opposite Abunã in forest on terra firme, 9 July 1968, G. T. Prance, E. Forero, L. F. Coelho, J. F. Ramos & L. G. Farias 5708 (BH). BRAZIL. Region of Forte Príncipe da Beira, Rio Guaporé, 1832, d'Orbigny 32 (Hb. Mart, BR, holotype). TERRITORY OF RONDÔNIA: basin of Río Madeira; east bank of Río Madeira between Abunã and Penha Colorado, varzea forest, 20 Nov. 1968, G. T. Prance, W. A. Rodrigues, J. F. Ramos & L. G. Farias 8717 (BH). CULTIVATED. Botanical Garden, Museu Emilio Goeldi, Belém, Pará, Brazil: 8 Nov. 1946, L. H. Bailey 324 (BH); photographs only, 1961, Stanley Kiem s. n. (BH); 1 June 1963, Museu Goeldi 349. R-8 (BH); 1966, Cavalcante s. n. (BH); 20 Mar. 1967, H. E. Moore, Jr. 9549 (BH).

Chelyocarpus chuco stands somewhat by itself in the genus as noted earlier. The presence of a prophyll on some primary branches is unusual in the alliance, for such have not been observed in *Cryosophila* nor in *Itaya*. The less deeply lobed leaf with its green under-surface further sets the species apart from others in *Chelyocarpus*, from *Itaya*, and from most in *Cryosophila*.

Chelyocarpus dianeurus (Burret) H. E. Moore, *tr. nov.* (Fig. 4, 5, 13B).

Tessmanniophoenix dianeura Burret, Notizblatt des Botanischen Garten und Museums zu Berlin-Dahlem 11: 499. 11 Jul. 1932; Dugand, Revista de la Academia Colombiana de Ciencias 8:387. 1951.

Type: Archer 2199 (US).

Tessmanniodoxa dianeura (Burret) Burret, Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 15: 337. 30 Mar. 1941. Trunk gray, to ca. 5 m. high or more, 6–9 cm. in diam.

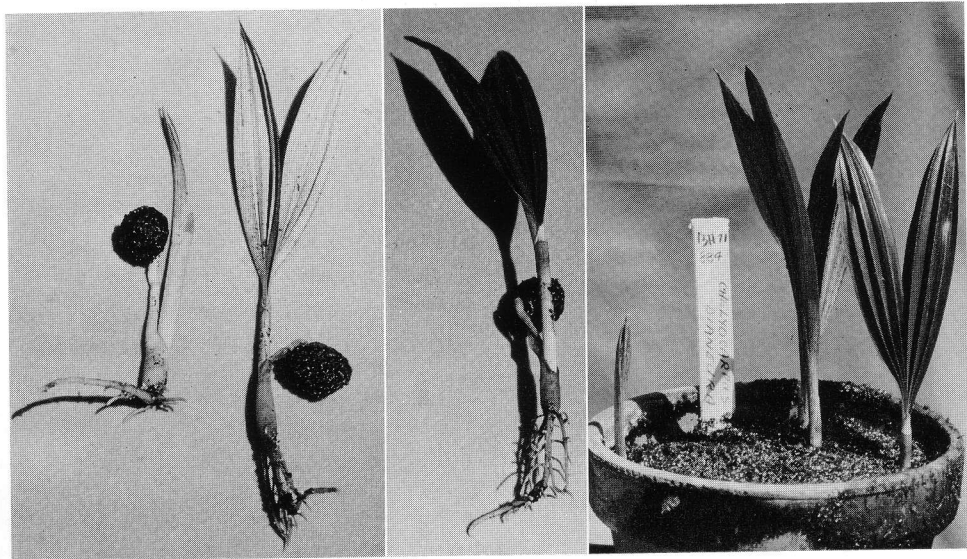
Leaves ca. 10 or more; sheaths to ca. 3 dm. long, brown-fibrous-margined, the inner ones densely golden appressed-villous; petiole as long as the blade or longer, 1–1.3 m. long, ca. 1.5 cm. wide at base and apex, brown furfuraceous-



4. *Chelyocarpus dianeurus* leaf, the central segments brought together in order to hold the blade (Moore, Parthasarathy & Orjuela 9458). Photo by M. V. Parthasarathy.

lepidote becoming glabrate; hastula deltoid with incurved margins, ca. 2 cm. high, 2 cm. wide; blade green and shining above, silvery below, 0.65–1.12 m. long, to 1.2 m. across, divided centrally to within 15–18 (or 3–5 fide Dugand) cm. of the base, divided laterally to or nearly to the base into 5–7 elongate-cuneate many-ribbed segments 1.2 m. long, 7–25 cm. wide, each again divided into 3–6 acute 1-ribbed segments 8–24 cm. long, 2–4.5 cm. wide, these with the midrib prominent below, the midrib, a lateral nerve on each side, and numerous oblique cross-veinlets evident above, lower surface covered with a continuous layer of thin white membranous scales, these rubbing off on contact.

Inflorescences several among the leaves, to ca. 8 dm. long; peduncle ca. 5 dm. long, flattened at base, brown-tomentose when protected, bearing a prophyll inserted ca. 21 cm. above the base and 2 sterile bracts at intervals of ca. 14 and 10 cm. respectively, these



5. Seedlings of *Chelyocarpus dianeurus* to show remote-tubular germination, single scale leaf, and bifid eophyll. From Moore & Gutiérrez 9999 cultivated at Cornell University.

(fide Burret) to 25 cm. long, oblong-lanceolate, densely dull gray-white-tomentose outside; rachis ca. 35 cm. long with ca. 50 simple rachillae, the lowest to 16 cm. long, upper shorter, each subtended by a small fertile bract.

Flowers sessile or on a low tubercle, subtended by a short bract; perianth 2.5 mm. high; sepals 4, ovate or nearly semiorbicular, slightly imbricate, rounded at apex; petals 4, longer than the sepals, ovate-oblong or oblong, rounded; stamens 8 (-9), filaments flattened, broad basally, narrowed above, nearly filiform at the anthers, these oblong; carpels 2 or rarely 1.

Fruit greenish or probably yellowish or whitish at full maturity, globose or subglobose, 1.8-2.0 cm. wide, 1.7-2.0 cm. high; epicarp not tessellate; mesocarp whitish, ca. 1.5-2 mm. thick when fresh; seed depressed-globose, ca. 1.6 cm. wide, 1.3 cm. high, the seed coat thickened and slightly intruded on either side of the hilum; embryo in lower third; germination remote-tubular with 1 scale leaf and bifid eophyll.

Vernacular name: *noli* fide Archer, but this name is elsewhere applied to *Elaeis oleifera* fide Dugand; *quitasol* but this name also used for *Mauritia* (cf. Dugand) and probably other fan palms.

Distribution and ecology: western Colombia at elevations near sea level as an undergrowth palm in low rainforest, usually on slopes.

Uses: according to Archer, local Amerindians make pillows from the indument of sheath and petiole base.

Specimens examined:

COLOMBIA. DEPT. CHOCÓ: headwaters of the Río Tutunendo, east of Quibdó, May, 1931, *W. A. Archer 2199* (US, holotype). DEPT. VALLE: Buenaventura, 23 May 1926, *O. F. Cook 132* (US); 26 May 1926, *O. F. Cook 146* (US); 29 May 1926, *O. F. Cook 158* (US); forests in concession of Cartón Colombia, Baja Calima region, north of Buenaventura,

0-50 m. alt., 10 Feb. 1967, *H. E. Moore, Jr., M. V. Parthasarathy & Pablo Orjuela 9458* (BH, CALI); forested slopes in Cartón Colombia concession, near Río San Joaquín, Baja Calima region, north of Buenaventura, alt. 0-50 m., 24 Nov. 1971, *H. E. Moore, Jr. & M. Gutiérrez 9999* (BH, CALI). Another collection cited by Dugand has not been seen—Dept. Valle: Río Calima, La Trojita, 5-50 m. alt., 19 Feb.-10 Mar. 1944, *J. Cuatrecasas 16702* (COL).

Fresh flowers of other species of *Chelyocarpus* have been available for study but for *C. dianeurus* only those of the type have been seen. These are blackened and leave much to be desired in the way of analysis. Fruits collected in late November, 1971, and distributed through the seed bank of The Palm Society were greenish and perhaps had not achieved their fully mature color but seeds began to germinate at Cornell University in late March, 1972.

Chelyocarpus dianeurus and *C. ulei* are very similar in aspect but are clearly different in flower and fruit. The normally tetramerous flowers readily distinguish *C. dianeurus* from all other palms.

Chelyocarpus ulei Dammer, Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 7: 395. 15 Jan. 1920; Burret, *op. cit.* 10: 395. 1 Dec. 1928, *op. cit.* 12: 151. 31 Dec. 1934; Macbride, Field Museum of Natural History, Botanical Series 13: 331. 1960. (Fig. 1, 6-12A). Type: *Ule 5885* (B).

Tessmanniophoenix longibracteata Burret, Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 10: 398. 1 Dec. 1928; *op. cit.* 11: 315. 30 Mar. 1932; Macbride, Field Museum of Natural History, Botanical Series 13: 332. 1960.

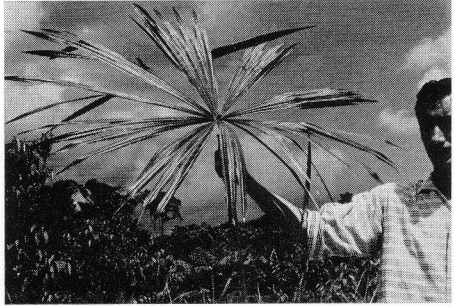
Type: *Weberbauer 6765* (B, destroyed, F, lectotype).



6. *Chelyocarpus ulei* with inflorescence in forest at Aucayacu, Peru (Moore & Salazar 9494).

Trunk gray, to ca. 9 m. high, 7.5 cm. in diam., more or less prominently ringed with obscure scars.

Leaves 10–15; sheath ca. 4.5 dm. long, densely pale-brown appressed-villous; petiole to 1.35 m. long, 1.5 cm. wide, brown furfuraceous-lepidote becoming glabrate; hastula deltoid with incurved margins, 1–2 cm. long, 1.5 cm. wide; blade green above, silvery below, 0.65–1.2 m. long, 1.3–1.4 m. wide, divided centrally to within 1–3 cm. of the base, laterally divided into 5–7 (–8) elongate-cuneate many-ribbed segments 0.35–1.2 m. long, 6.8–35 cm. wide, each again divided into 3–8 acute or very briefly bifid 1-ribbed segments 8–21 cm. long, 2.5–5.8 cm. wide, the segments with midrib, 3 lateral secondary nerves and many tertiary nerves on each side prominent below, flexuous cross-veinlets numerous and prominent above, lower



7. Leaf of *Chelyocarpus ulei* held by Ing. Salazar near Aguaytía, Peru (Moore, Salazar & Smith 8379).

surface with a continuous layer of pale membranous scales.

Inflorescences pendulous, pale yellow at anthesis, to 1.13 m. long; peduncle flattened, brown-tomentose or becoming glabrate, bearing an ancipitous, brown-tomentose-margined prophyll to 3 dm. long inserted ca. 8 cm. above the base, 2 brown-tomentose sterile bracts ca. 3 dm. long and 2.8 dm. long inserted ca. 1.8 dm. and 1.3 dm. higher respectively, and a fourth open sterile bract ca. 1.5 dm. long at base of rachis; rachis to 4.6 dm. long, flattened, pale-brown floccose-tomentose at anthesis; rachillae floccose-tomentose, slender, numerous, to ca. 1.9 dm. long, each subtended by a very narrowly triangular membranous fertile bract, the lowest to ca. 8.5 cm. long, rachillae variously adnate to rachis above when simple or the lower ones subfasciculate or fasciate on very short branches.

Flowers pale yellow or creamy turning black, scented of fishmeal or burning rubber, 4–5 mm. long, each subtended by a linear bract usually as long as or longer than the flower; sepals 2, ca. 3 mm. long; petals 2, distinct, ca. 2.5 mm. long; stamens 5–8 often 7, most filaments broad and thick basally, tapered to the exerted anthers; carpels 2, ca. 1.5 mm. long, included.



8. Inflorescence of *Chelyocarpus ulei* with prophyll and two sterile bracts (Moore & Salazar 9494).



9. Another inflorescence of *Chelyocarpus ulei* from the same tree as Fig. 8 but flowers at full anthesis.

Fruit globose, ca. 2.5 cm. in diam. when fresh, 1.8–2.1 cm. in diam. when dry, brown, corky-tessellate; mesocarp dry, whitish, ca. 5 mm. thick; seed globose, ca. 13 mm. high, 14 mm. wide; embryo above the middle.

Vernacular names: *uchpapanga* fide Burret (1928).

Distribution and ecology: eastern Peru, western Brazil, in rainforest at 200–550 m. alt.

Chromosome complement: $n=18$ (Read & Moore, 1967).

Specimens examined:

BRASIL, near Belém, Rio Juruá Miry, Sept. 1901, *Ule* 5885 (B). PERU. DEPT. LORETO: Prov. Coronel Portillo; on wooded slopes 6–8 kms. beyond Aguatía on road to San Alejandro (Tingo Maria-Pucallpa highway), alt. ca. 300 m., 29 Apr. 1960, *H. E. Moore, Jr., Adolfo Salazar C. & Earl E. Smith* 8379 (BH, USM). DEPT. HUANUCO: Río Pozuzo, 200–300 m., 1909–1914, *A. Weberbauer* 6765

(B, holotype of *Tessmanniophoenix longibracteata*, destroyed, F, lectotype). Prov. Leoncio Prado; Distr. Crespo Castillo, bosque humedo tropical, Aucayacu, alt. ca. 500 m., 10 Mar. and 6 May 1964, *E. Vasquez A. s. n.* (BH); 5 Sept. 1967, *A. Salazar C.* 401 (BH); Campamento de UTCF, Aucayacu, 1 Mar. 1967, *H. E. Moore, Jr. & A. Salazar C.* 9494 (BH, USM). CULTIVATED. Botanic Garden, Museu Emilio Goeldi, Belém, Pará, Brazil: 22 Aug. 1912, *J. Huber* 12179 (BH, photo); 8 Nov. 1946, *L. H. Bailey* 326 (BH); 1 June 1963, *Museu Goeldi* 329.0–6 (BH); 20 Mar. 1967, *H. E. Moore, Jr.* 9548 (BH).

The type of *Chelyocarpus ulei*, first associated with *Acanthorrhiza chuco* (Dammer, 1907), had a leaf smaller than usual for the genus. It may have been taken from a juvenile plant (the petiole was described as 5–7 mm. wide and 3 mm. thick—I have seen none less than 1.5 cm. wide) but appears to have been destroyed. Two inflorescences and fruits from the type, however, are still extant



10. A fruit cluster of *Chelyocarpus ulei* from cultivation at Museu Goeldi, Belém, Brazil. Note the tessellate fruit from which the genus gets its name (Moore 9548).

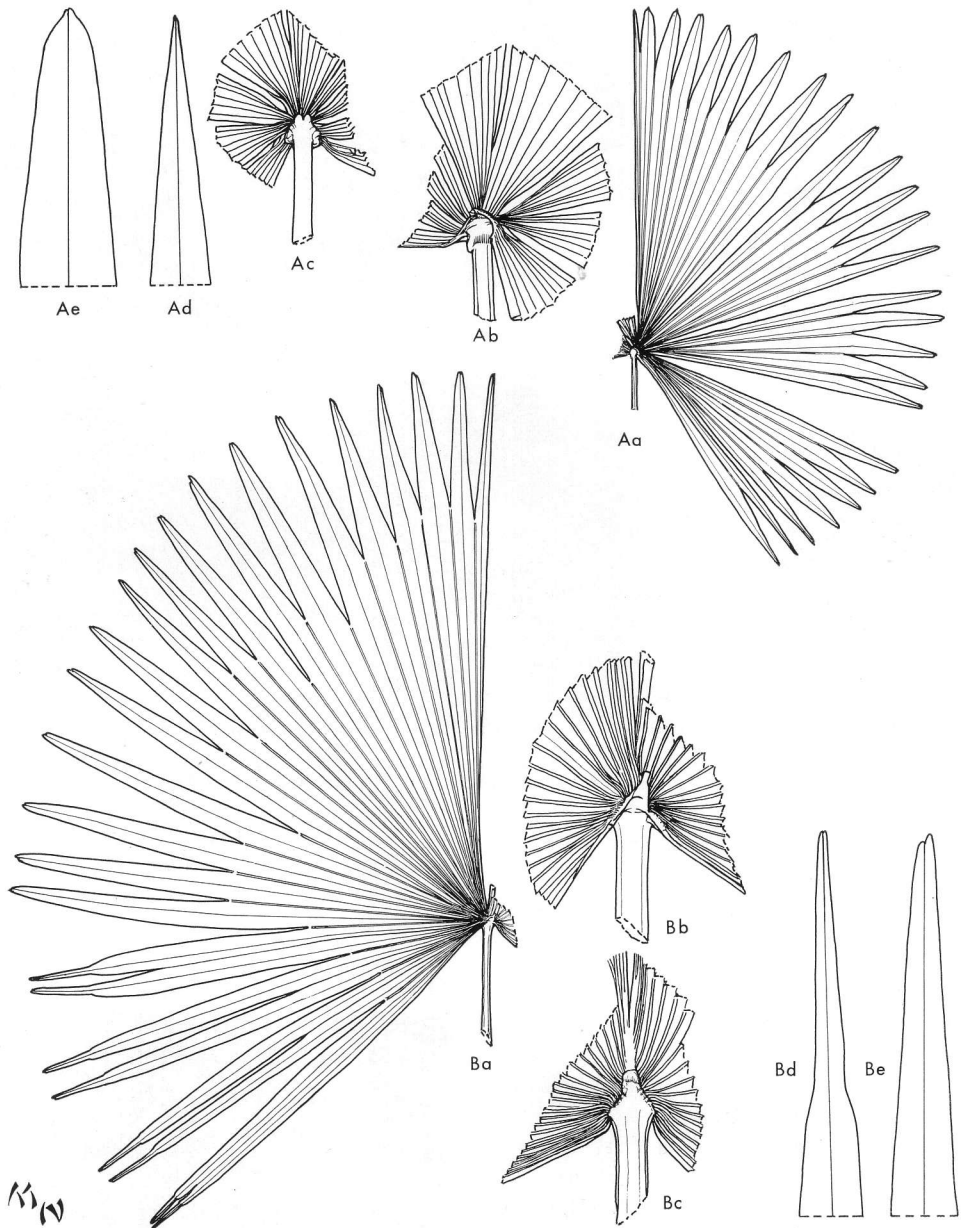
at Berlin and through the kindness of Prof. Dr. Eva Potzta were located and forwarded on loan. I have compared these with other materials cited here and find no difference. The fruits match recent materials from Peru and the tomentum and prominent stubs of bracts below the floral scars of the type are similar to those on Peruvian materials of comparable condition.

Tessmanniophoenix was first distinguished from *Chelyocarpus* because of its supposedly smooth fruit (Burret, 1928, 1934), but Burret later (1941) associated its lectotype, *T. longibracteata* from Peru, with *Chelyocarpus*. He neither transferred *T. longibracteata* as a species nor clearly indicated its identity with *C. ulei*. The implicit association with the last can now be made explicit

and because the holotype of *T. longibracteata*, once at Berlin, has been destroyed, I have designated an isotype at the Field Museum of Natural History as lectotype.

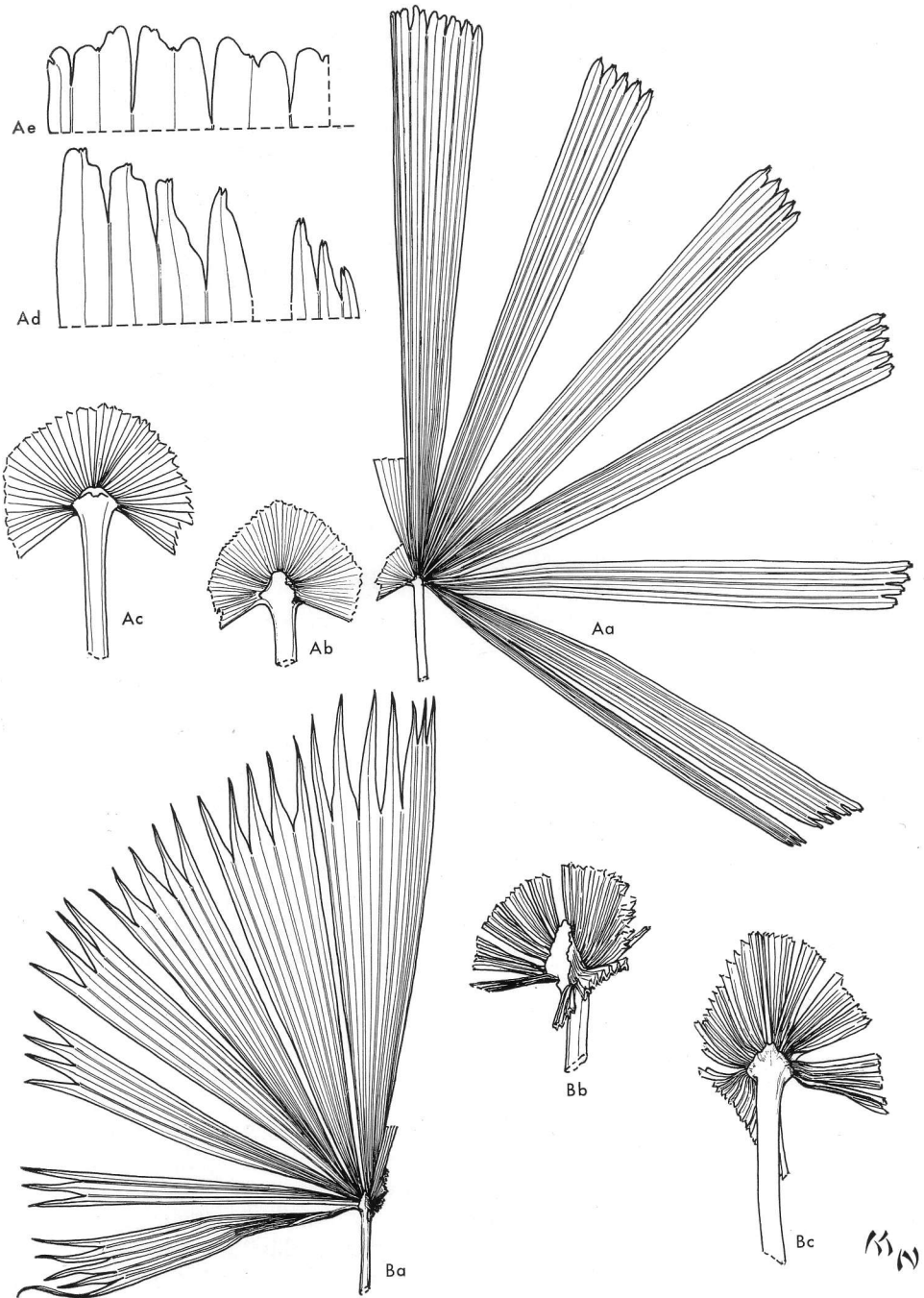


11. A young plant of *Chelyocarpus ulei* about five years old cultivated at Cornell University from seed of Moore 9548.



12. Leaves of *Chelyocarpus*. A, *C. ulei*: Aa, blade with one half cut away $\times 1/15$; Ab, hastula $\times 1/3$; Ac, dorsal crest $\times 1/3$; Ad, Ae, tips of segments $\times 1/3$. From Moore 9548 (BH). B, *C. chuco*: Ba, blade with one half cut away $\times 1/15$; Bb, hastula $\times 1/3$; Bc, dorsal crest $\times 1/3$; Bd, Be, tips of segments $\times 1/3$. From Moore 9549 (BH).

13. Leaves of *Chelyocarpus* and *Itaya*. A, *Itaya amicomum*: Aa, blade with one half cut away $\times 1/15$; Ab, hastula $\times 1/3$; Ac, dorsal crest $\times 1/3$; Ad, tips of segments at base of leaf $\times 1/3$; Ae, tips of



segments at center of leaf $\times 1/3$. From Moore, Salazar & Gutiérrez 9509 (BH). B, *Chelyocarpus dianeurus*: Ba, blade with one half cut away $\times 1/15$; Bb, hastula $\times 1/3$; Bc, dorsal crest $\times 1/3$. From Moore & Gutiérrez 9999 (BH).

Plants of *Chelyocarpus ulei* cultivated at the Museu Goeldi may, in fact, have come from a Peruvian source rather than from Brazil. I have seen a photograph of a specimen (*Huber 12179*) made at the garden there in 1912 and labelled with the manuscript name "*Acanthorrhiza ucalina*" which seems to be *C. ulei*.

Chelyocarpus ulei is apparently unique among palms in its usually dimerous perianth. Exceptional flowers do occur, as Burret noted, with five or six perianth parts. Stamens may also vary as may carpels. The normal pattern, however, is one of a stamen opposite each sepal, two or three opposite each petal. The development of the corky-tessellate fruit coat has not been worked out but it probably follows much the pattern for *Johannesteijsmannia* studied by Dransfield (1970). The prominent bracts subtending the flowers are also distinctive.

DOUBTFUL SPECIES

Chelyocarpus wallisii Burret, Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 10: 396. 1 Dec. 1928.
T.: *Wallis* s. n. (B, seeds only, destroyed).

Acanthorrhiza wallisii H. Wendland ex Regel, Gartenflora 28: 163, t. 977, fig. 2 1872 ('*Acanthorrhiza*') *nomen nudum*; Drude in Martius, Flora Brasiliensis 3(2): 554. 1 Mai 1882 *nomen nudum*; Beccari, Webbia 2: 242. 1907 *nomen nudum*.

Tessmanniophoenix wallisii Burret, Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 10: 397. 1928 *nomen provisorium*.

This species was based on five seeds once in the herbarium at Berlin and thought to have been collected by Wallis

in Colombia or Ecuador. Burret associated these seeds with a palm figured in very stylized fashion without description or diagnostic details in 1872 under the name *Acanthorrhiza wallisii*, which must be taken as a *nomen nudum*. The later description of the seeds, though sufficient to validate the name *Chelyocarpus wallisii*, is not sufficient to associate the name clearly with any species of the genus and the seeds themselves were lost during World War II. The name should therefore be ignored now and in the future.

Cryosophila

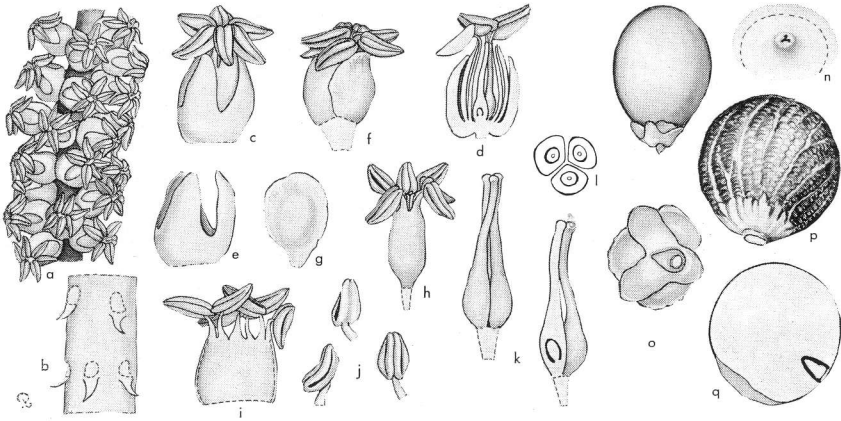
Cryosophila Blume, Rumphia 2: 53. 1838-39 ('1836'). (Fig. 14).
Type: *Corypha nana* Humboldt, Bonpland & Kunth.

Acanthorrhiza H. Wendland, Gartenflora 18: 241. July. 1869.
Type: *A. aculeata* (Liebmann) H. Wendland.

Solitary, hermaphroditic palms of moderate size, the trunk armed with often branched root-spines, slender, prickly stilt roots sometimes developed.

Leaves numerous in a spreading crown, induplicate palmate, flabelliform; sheath fibrous, densely floccose-tomentose, splitting opposite the petiole and persisting as fibrous margins on the bases of petioles and at length fraying into slender elongate fibers at the apex; petiole elongate, unarmed, rounded below, channelled above and with margins sharp throughout their length, terminating adaxially in a small, deltoid, elevated hastula dorsally plicately grooved, and abaxially in a narrow margin; rachis not developed; blade flat, thin, divided centrally to or nearly to the base (except in *C. williamsii*?), each half deeply divided into elongate-cuneate many-ribbed segments, these

Cryosophila



14. *Cryosophila argentea* (a-l) and *C. nana* (m-q). a, portion of rachilla $\times 2$; b, portion of rachilla showing floral scars and bracteoles $\times 4$; c, flower $\times 4$; d, flower in vertical section $\times 4$; e, calyx $\times 4$; f, flower, calyx removed $\times 4$; g, petal $\times 4$; h, androecium $\times 4$; i, androecium expanded, interior view $\times 4$; j, anthers in three views $\times 4$; k, gynoecium, external view (left) and in vertical section (right) $\times 8$; l, carpels in cross-section $\times 8$; m, fruit $\times 1$; n, apex of fruit $\times 8$; o, base of fruit $\times 4$; p, seed $\times 2$; q, seed in vertical section $\times 2$. a-l from material of *Read 689* preserved in liquid, m-q from dried material of *McVaugh 900*.

again divided into 2 or more acute or briefly bifid 1-ribbed segments.

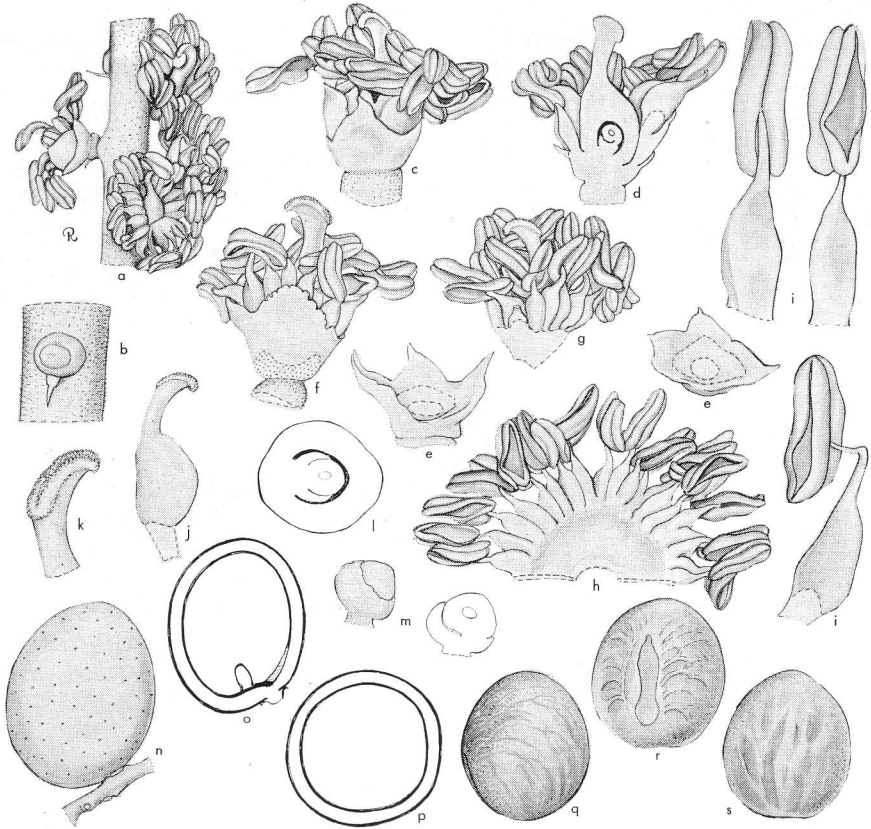
Inflorescences interfoliar, arcuate or pendulous; peduncle bearing a prophyll near the base and at intervals 4 (or more?) tomentose sterile bracts with tubular base and cochleariform blade; rachis somewhat angled, with several to many recurved, once-branched primary branches, only the lower or all (in *C. guagara*) subtended by prominent fertile bracts like those of the peduncle but progressively smaller, or the upper ones with reduced bracts only, primary branches usually with obvious, not or only slightly adnate, peduncular base and rachis, but rarely (*C. cookii*) the peduncle and rachis not evident and rachillae fastigiately grouped along the rachis; rachillae little or not adnate above an acute subtending bract.

Flowers perfect, borne singly in a spiral along the rachillae on brief pedicels each subtended by a small, acute bract;

sepals 3, narrowly ovate to deltoid, briefly connate basally; petals 3, imbricate, rounded at apex, scarcely longer than sepals; stamens 6, filaments flat, connate basally in a tube one-half their length or more, then distinct and strap-shaped or subulate, anthers exerted and spreading at an angle of 90° , dorsifixed near the base, briefly bifid at base and apex, dehiscent laterally by longitudinal slits; carpels 3, distinct, only one usually developing into a fruit, styles elongate, exerted, stigma scarcely expanded, ovule campylotropous with a small aril on the funicle, inserted adaxially at the base.

Fruit white at maturity, with terminal stigmatic residue; epicarp smooth; mesocarp somewhat fleshy; endocarp membranous; seed globose, not adherent to the endocarp, with round basal hilum, raphe-branches impressed, ascending and anastomosing from the base; endosperm homogeneous with slight intrusion of

Itaya



15. *Itaya amicornum*. a, portion of rachilla $\times 2$; b, pedicel and bract $\times 4$; c, flower $\times 4$; d, flower in vertical section $\times 4$; e, calyx $\times 4$; f, flower, calyx removed $\times 4$; g, flower, perianth removed $\times 4$; h, androecium expanded, interior view $\times 4$; i, stamens in three views $\times 8$; j, pistil $\times 4$; k, stigma $\times 8$; l, ovary in cross-section $\times 8$; m, ovule in lateral view and vertical section $\times 8$; n, fruit $\times 1$; o, fruit in vertical section $\times 1$; p, fruit in cross-section $\times 1$; q, r, seed in lateral, rapheal, and antirapheal views $\times 1$. a-m from material of Moore, Salazar & Gutiérrez 9509, n-s from material of Gutiérrez 1940, both preserved in liquid.

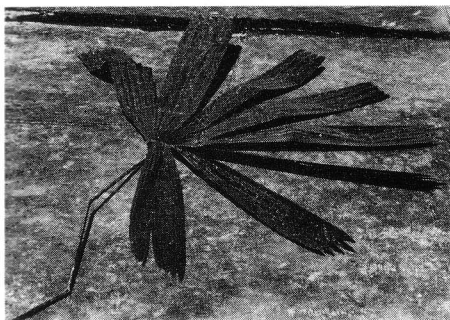
seed coat adaxially at the base, embryo lateral at or below the middle.

Distribution and ecology: eight or fewer species of western Mexico to northern Colombia at moderate to low elevations in dry woods (*C. nana*) to rainforest.

Anatomical features: central vascular bundles of petiole with a single phloem strand (Parthasarathy, 1968). See Tomlinson (1961) and Uhl (1972b)

for vegetative anatomy, and Uhl (1972a) for floral anatomy.

The species of *Cryosophila* are eight or fewer and in need of detailed study in the field. Most herbarium material is completely inadequate for drawing distinctions among species such as have been drawn among those of *Chelyocarpus*, though admittedly the genus is more uniform. A generic description is included here to complete the trio



16. A leaf of *Itaya amicornum* removed from plant press for photography after folding (Moore, Salazar & Smith 8447).



17. An inflorescence of *Itaya amicornum*. Note split petiole base immediately at left of tape measure and bracts of another inflorescence at left. The pinnate leaf in the background is from a *Scheelea* (Moore, Salazar & Gutiérrez 9509).

composing the *Chelyocarpus* alliance. Habit, leaf, inflorescence, flowers, and fruit have been illustrated photographically by Allen (1953) and Bartlett (1935). The root-spines on the trunk are unique among palms and the androecium is distinctive. A possibly specialized mode of pollination is suggested by the arrangement of anthers at anthesis. In general, *Cryosophila* seems to be more advanced than *Chelyocarpus*, less so than *Itaya*.

Itaya H. E. Moore, *gen. nov.*

Palma solitaria hermaphrodita foliis induplicatis flabelliformibus ad 3/4 bipartitis lateraliter in 4-7 segmenta elongato-cuneata partitis. Inflorescentiae interfoliatae bracteis sterilibus 5 ramis 6-7. Flores bisexuales sepalis 3 et petalis 3 ad medium connatis, staminibus 18-24, carpello 1. Fructus stigmatibus terminalibus, seminis endospermio homogoneo embryo prope basin sito.

Solitary, unarmed, hermaphroditic palms of moderate size, the trunks with smooth cortex (drying roughened), naked except for fibrous residual sheaths below the crown.

Leaves numerous in a spreading crown, induplicately palmate, flabelliform; sheaths short, split opposite the petiole

and persisting as fibrous margins on the bases of the petioles and at length fraying into slender elongate fibers at the apex; petioles elongate, unarmed, the bases prominently split, more or less long-persistent in a latticework effect below the crown, rounded below and channelled above, basally becoming bi-convex and rhomboid in section distally with obtuse margins, terminating adaxially in a small, deltoid, elevated hastula basally plicately grooved, and abaxially in a narrow deltoid margin; rachis not developed; blade flat, thin, three-fourths orbicular in outline, the segments circumscribing an arc of about 270°, divided about three-fourths to the base at the middle, each half again deeply divided into several (4-7) elongate-cuneate, 4-7-ribbed segments, these very shallowly divided apically into briefly bifid 1-ribbed segments.

Inflorescences several, interfoliar, elongate, arcuate; peduncle terete, bearing a bicarinate abaxially split prophyll and ca. 5 chartaceous, persistent, and at length marcescent sterile bracts with tubular bases and inflated acute apices split on one side; primary branches

6-7, each subtended by a persistent and at length marcescent fertile bract similar to the sterile bracts but progressively smaller and the uppermost scarcely tubular at the base, branches more or less flattened, adnate to the rachis often nearly to the succeeding bract, the lower branches again twice- to once-branched, the upper ones once-branched into slender slightly sinuous rachillae, each rachilla subtended by a linear acute bract.

Flowers perfect, borne singly in a spiral along the rachillae, each on a very short pedicel subtended by a small acute bract; sepals 3, connate in an acutely 3-lobed cupular calyx; petals 3, connate about half their length in a 3-lobed corolla, the lobes rounded and erect at anthesis, probably valvate in bud, stamens 18-24, one or two opposite each sepal, remainder opposite petals, filaments connate basally in a fleshy tube less than half their length, slightly adnate to corolla basally, fleshy and more or less subulate above, anthers oblong in outline, dorsifixed at the middle, versatile, laterally dehiscent by longitudinal slits, exerted at anthesis, bifid at apex and base, carpel 1, excentrically ovoid, narrowed to a slender curved style and oblique papillose stigma, ovule hemianatropous, attached adaxially at the base, the short funicle bearing a prominent oblique aril.

Fruit oblong-ovoid or subglobose with excentrically apical stigmatic residue; epicarp minutely granular-roughened and irregularly beset with minute perforations; exocarp ca. 0.5 mm. thick with sclerosomes; mesocarp ca. 1 mm. thick, white, dry, with anastomosing fibers; endocarp not discrete: seed oblong-ovoid; hilum ellipsoid, subbasal, raphe-branches ascending-spreading; endosperm homogeneous; embryo excentrically basal; germination not known; seedling with undivided, elliptic eophylls.

Type: *Itaya amicorum* H. E. Moore.

Distribution: Peru, in seasonal rain-forest at low elevations.

Chromosome complement: unknown.

Anatomical features:

Central vascular bundles of the petiole with two phloem strands; late metaxylem elements with simple perforation plates and often a characteristic ligule (Larry Klotz, personal communication).

Foliar and floral anatomy—see Uhl, 1972a & b.

Itaya amicorum H. E. Moore, *sp. nov.*
(Fig. 13A, 15-17).

Caulis ad 5 m. altus foliis 12-20 ad 1.25 m. longis 2 m. latis. Inflorescentia ad 1.25 m. longa. Flores 3 mm. alti. Fructus 2.4 cm. longus.

Trunk to 5 m. high, 9 cm. in diam., gray.

Leaves ca. 12-20, spreading from ascending petioles; sheath ca. 5 dm. long, densely light-brown floccose-tomentose; petiole ca. 2.6 m. long above sheath, brown-furfuraceous basally, minutely deciduous-floccose distally, 1.3-1.4 cm. wide, 7 mm. thick at apex; hastula ca. 1 cm. high, 1.5 cm. wide; blades to 1.25 m. long at middle, 2 m. wide, segments 4-7 on each side, to 1.25 m. long, 9-20 cm. wide at apex, again divided 1-7 cm. deep into segments 0.5-3 cm. wide and bifid to 3-10 mm., upper surface glossy when dry with numerous prominent cross-veinlets, lower surface densely appressed white-tomentose, the principal nerves conspicuously elevated, tomentose or glabrescent, secondary nerves few, not elevated, cross-veinlets evident.

Inflorescence to 1.25 m. long or more, creamy white with brownish bracts at anthesis; peduncle to 2.3 cm. wide near base; prophyll (on a smaller inflorescence) ca. 14 cm. or more long, 2.5 cm. wide, peduncular bracts to ca. 6 dm.

long, 5 cm. wide, split ca. 10 cm. from apex, upper bracts ca. 10 cm. long, all densely pale-brown floccose-tomentose at first, outside fibers longitudinal and dense, inner fibers obliquely transverse, the bracts at length fraying into masses of longitudinal fibers; lower branches to 5 dm. long, pale puberulous, rachillae to 12 cm. or more long, puberulous.

Flowers ca. 3 mm. high when dry, sepals 1.5–2 mm. high, petals ca. 2 mm. high, stamens and style exserted.

Fruit (from *Gutiérrez R. 194*) said to be whitish when ripe, 2.4 cm. long, 2.2 cm. in diam. when fresh but perhaps not completely mature; seed 1.8 mm. high, 1.5–1.6 mm. wide and broad.

Vernacular name: *falso bombonaje*, *sacha bombonaje* (fide Gutiérrez R.)

Specimens examined:

PERU. DEPT. LORETO: Prov. Maynas; in forest on trail to Omaguas beyond landing on Río Itaya at Varadero de Omaguas, 13 May 1960, *H. E. Moore, Jr., Adolfo Salazar C. & Earl E. Smith 8447* (BH, USM); Río Itaya, Fundo Ciudadilla, alt. 150 m., 17 Feb. 1965, *Abelardo Gutiérrez Ruíz 194 AGR* (BH); Río Itaya, on Varadero de Omaguas from Fundo Ciudadilla, about 2 1/2 hours by 40 H. P. speedboat from Iquitos, 150 m. alt., 5 Mar. 1967, *H. E. Moore, Jr., A. Salazar C. & A. Gutiérrez R. 9509* (BH, holotype, USM, isotype).

I have taken the name for this genus from the river near which it grows and the epithet from the spirit of the program under which I first encountered it and for my associates in Peru.

Itaya appears to be most closely related to *Chelyocarpus* and *Cryosophila* with which it has been contrasted in the key. It is, however, more specialized than either in the connation and adnation of sepals and petals, in its numerous stamens, in its unicarpellate gynoecium, and in the presence of two phloem strands in central vascular bundles of the petiole. The split in the petiole base

has been commented upon for *Thrinax* by Read (1967). It is an immediately recognizable field difference but one which often cannot be discerned from herbarium material which usually lacks leaf bases. In this feature, *Chelyocarpus* and *Cryosophila* are to *Itaya* as *Coccothrinax* and *Zombia* are to *Thrinax*.

Four fruits near maturity were obtained and forwarded for study by Ing. Gutiérrez R. to whom special thanks are due. They have an epicarp which is marked by numerous apparently natural openings but which is never fractured as in *Chelyocarpus ulei*.

Itaya amicum is thus far known only from the type locality. It is a promising horticultural subject on account of its large and handsome leaves much resembling those of some *Licuala* species, its moderate stature, and its creamy-white inflorescences and flowers. As yet, the species has not been introduced into cultivation.

ACKNOWLEDGMENTS

I first encountered *Chelyocarpus ulei* and *Itaya amicum* during the course of a reconnaissance survey of palms in eastern Peru with Ing. Adolfo Salazar C., then with the Programa Co-operativa para el Desarrollo Forestal del Perú, and Dr. Earl E. Smith, then Forestry Adviser, Agricultural Division, United States Operation Mission to Peru, International Cooperation Administration. The reconnaissance was sponsored by the Agriculture Division, USOM/PERU, ICA. A second field encounter with these two genera in 1967 and subsequent work has been supported largely by National Science Foundation grants GB-3528, GB-7758, and GB-20348X. I am indebted to the John Simon Guggenheim Memorial Foundation for the privilege of studying the type of *Thrinax chuco* in 1955. I am also indebted to Dr. A. Lowalree at Bruxelles, to Dr. Alicia Lourteig at Paris, and

Dr. Eva Potzta at Berlin for their assistance in searching for types.

Ing. Flavio Bazan, then Director General of the Servicio Forestal y de Caza of the Ministerio de Agricultura for Peru, and my project companions organized a memorable field experience in 1960. Ing. Bazan and Ing. Salazar, now Dean of the Facultad de Ciencias Forestales, Universidad Agraria, La Molina, Peru, and personnel of the Servicio Forestal greatly facilitated field work in 1967. My indebtedness to my Peruvian friends is expressed in a small way in the epithet used in *Itaya*.

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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

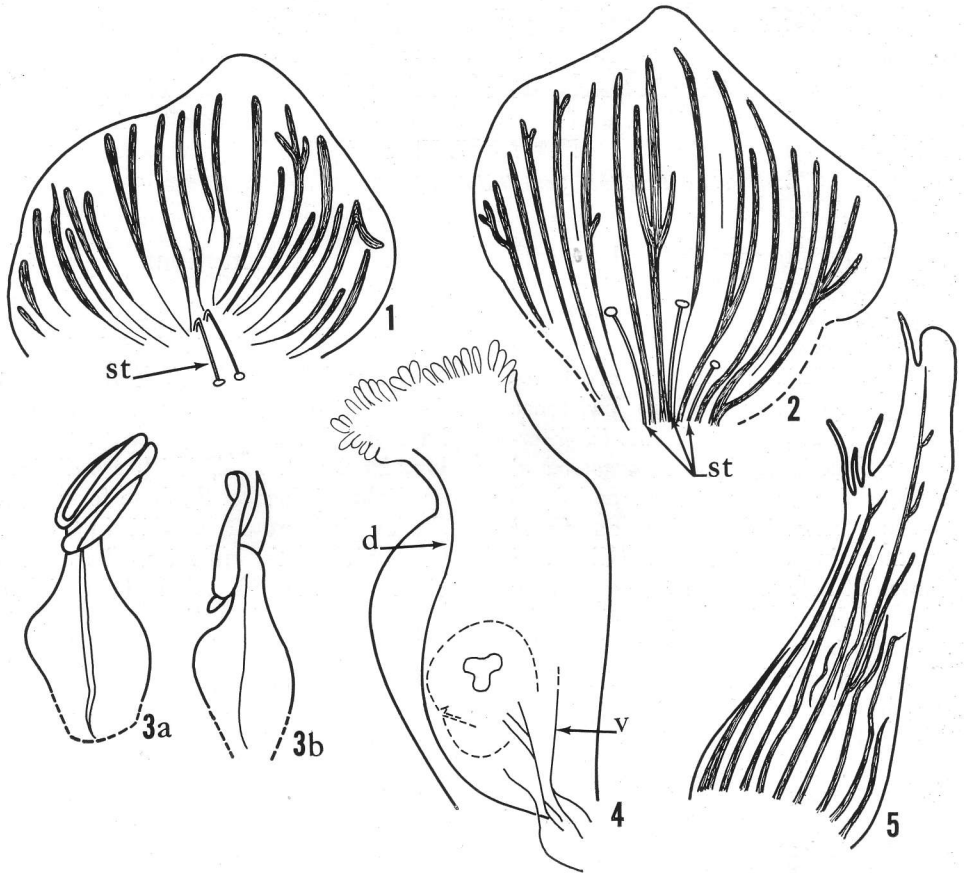
Material examined consisted of flowers at or near anthesis, fixed in formalin-acetic acid-ethanol in the field or garden, and subsequently stored in glycerine alcohol (10% glycerine, 70% ethanol). At least 25 flowers of each collection were cleared, and six or more were sectioned serially, stained, and 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

* From work supported by National Science Foundation Grant GB-20348X, H. E. Moore, Jr. principal investigator.



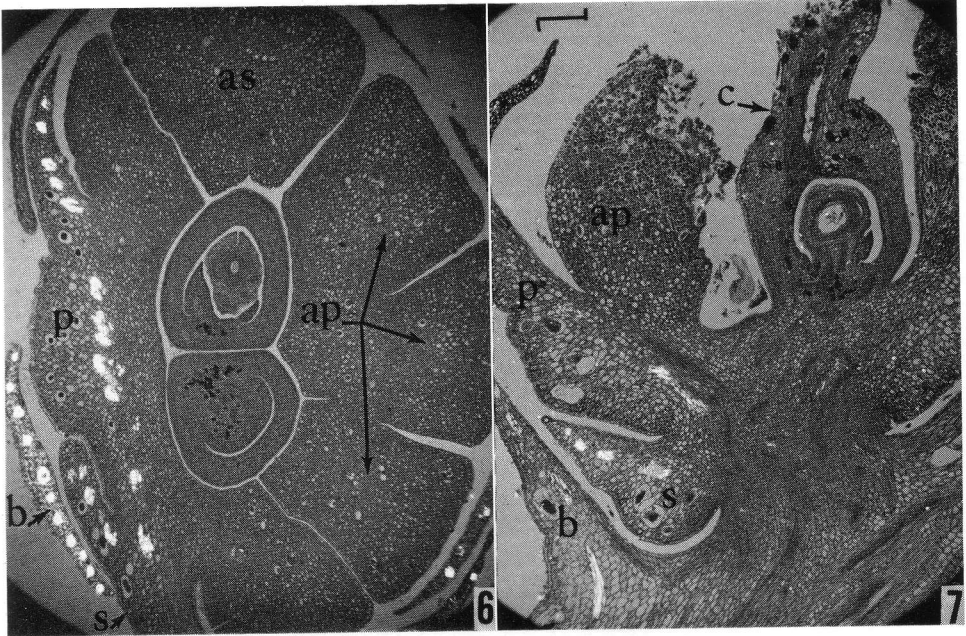
1-5. *Chelyocarpus ulei*. 1, sepal, $\times 10$; 2, petal, $\times 10$; 3, stamen: a, ventral view; b, lateral view, $\times 8$; 4, carpel, $\times 25$; 5, subtending bract, $\times 10$. Details: *d*, dorsal bundle; *st*, stamen trace; *v*, ventral bundle.

style and extreme distal part of the ovary are more mature than the basal part of the carpel. Large tanniferous 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.

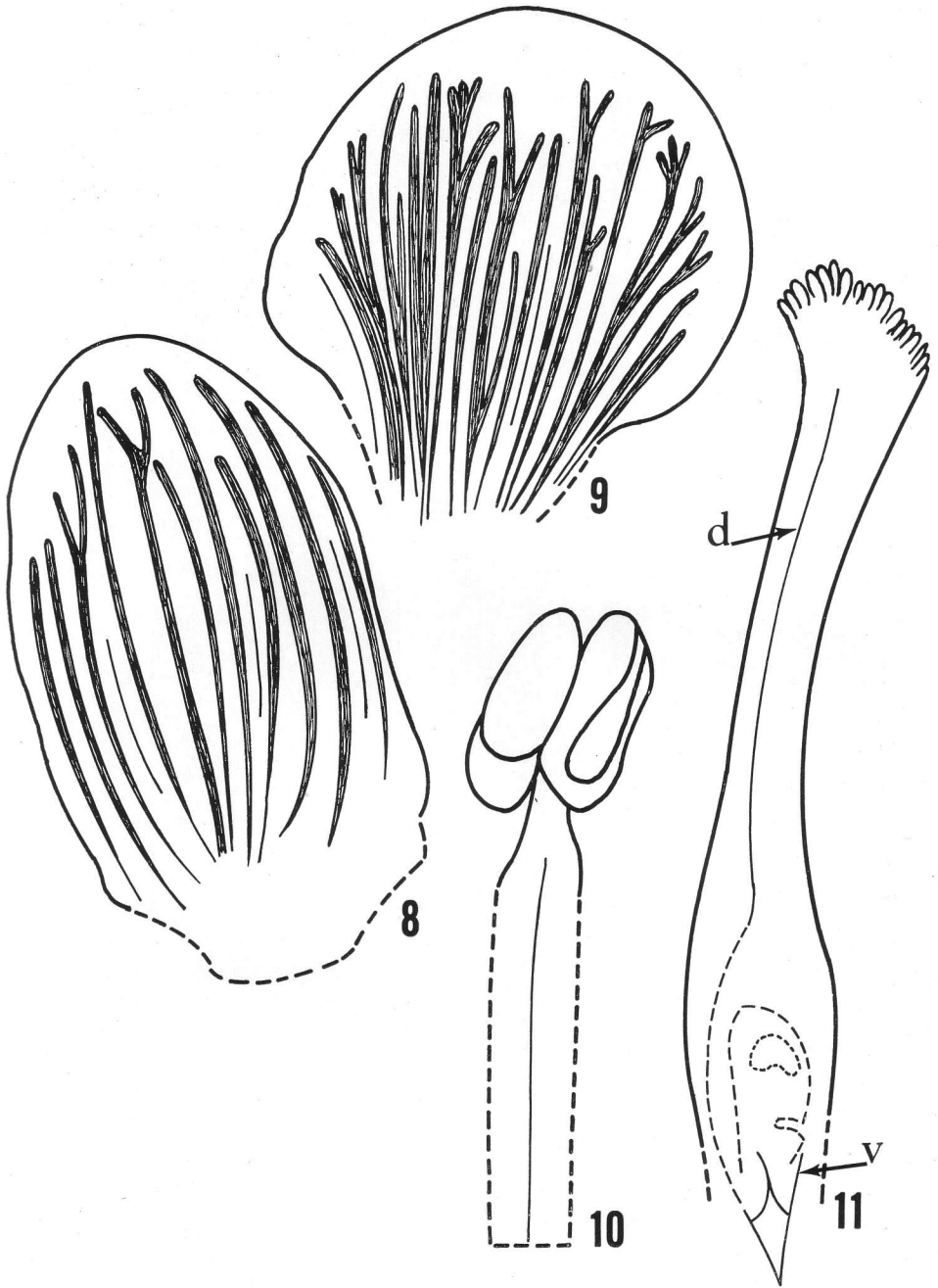
Flowers of *C. chuco* appear more stable in number of parts with three sepals, three petals, six stamens, and three carpels present in all examined. Sepals and petals are similar in shape and size to those of the other two species—ovate and ca. 2 mm. long. Sepals are connate for one-third their length,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

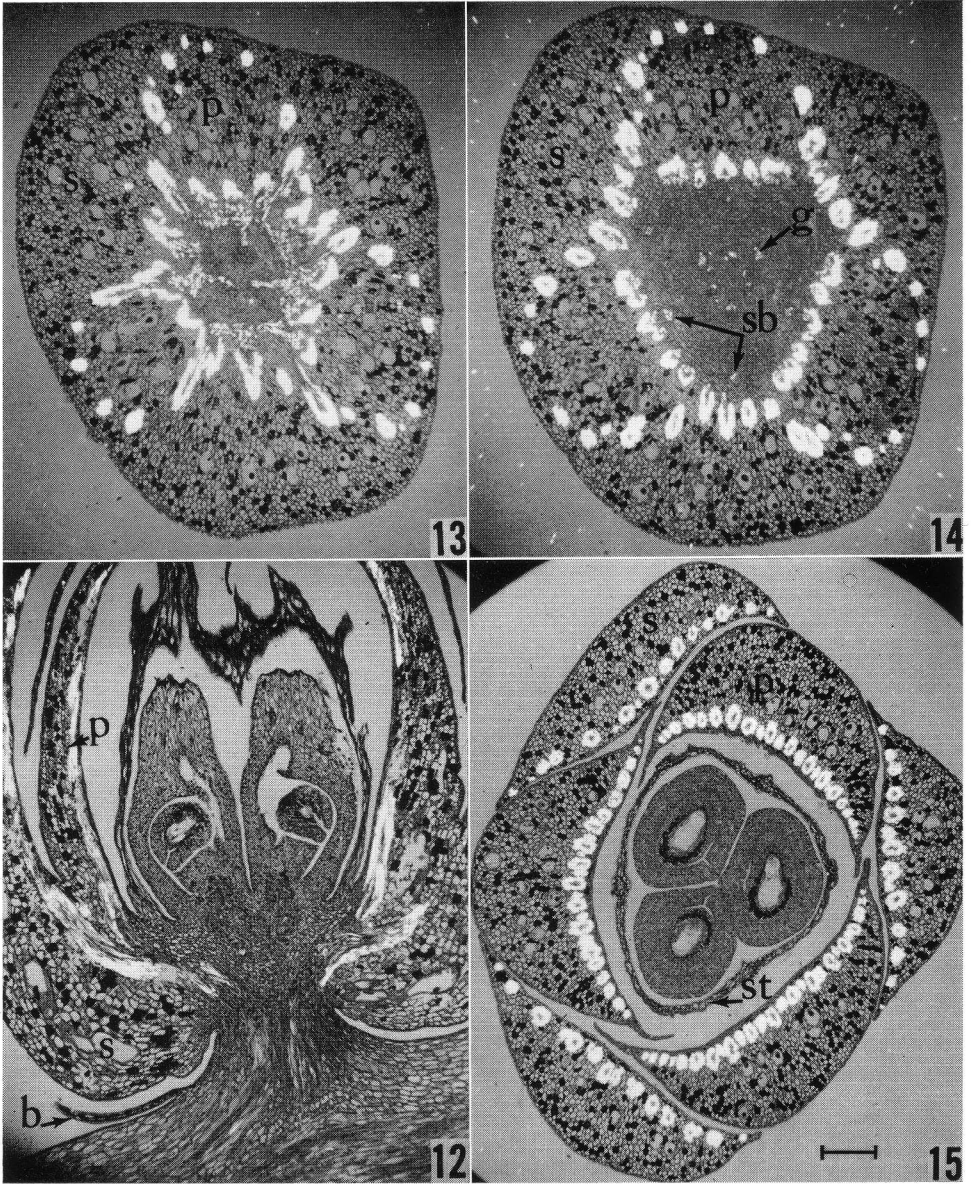
CRYOSOPHILA (Fig. 8-15).

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, $\times 10$; 9, petal, $\times 10$; 10, stamen, $\times 10$; 11, carpel, $\times 25$.
 Details: *d*, dorsal bundle; *v*, ventral bundle.



12-15. *Cryosiphila 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.

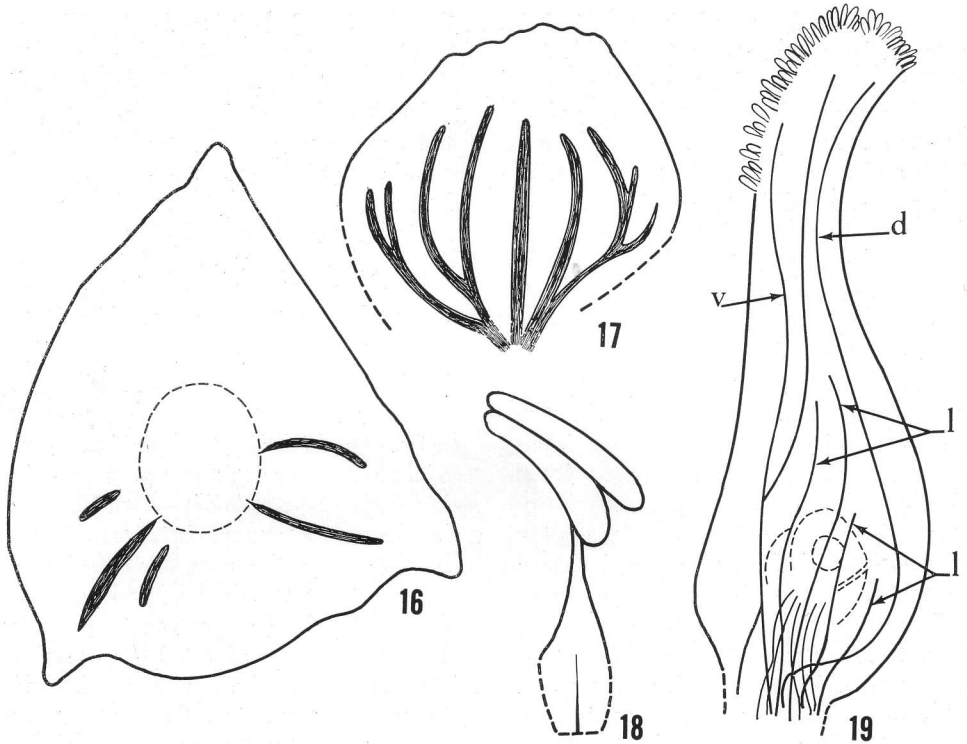
stamens (Fig. 15); and six anthers, 1.5 mm. in length, are exerted forming a radiate pattern on the top of the ovate sepal-petal sheath. The individual carpel is attenuate with an ovarian part 1 mm. high and a tapering style 1.5 mm. long (Fig. 11). No definite stigma is present. The carpel is open distally 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 gynoeceial 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).



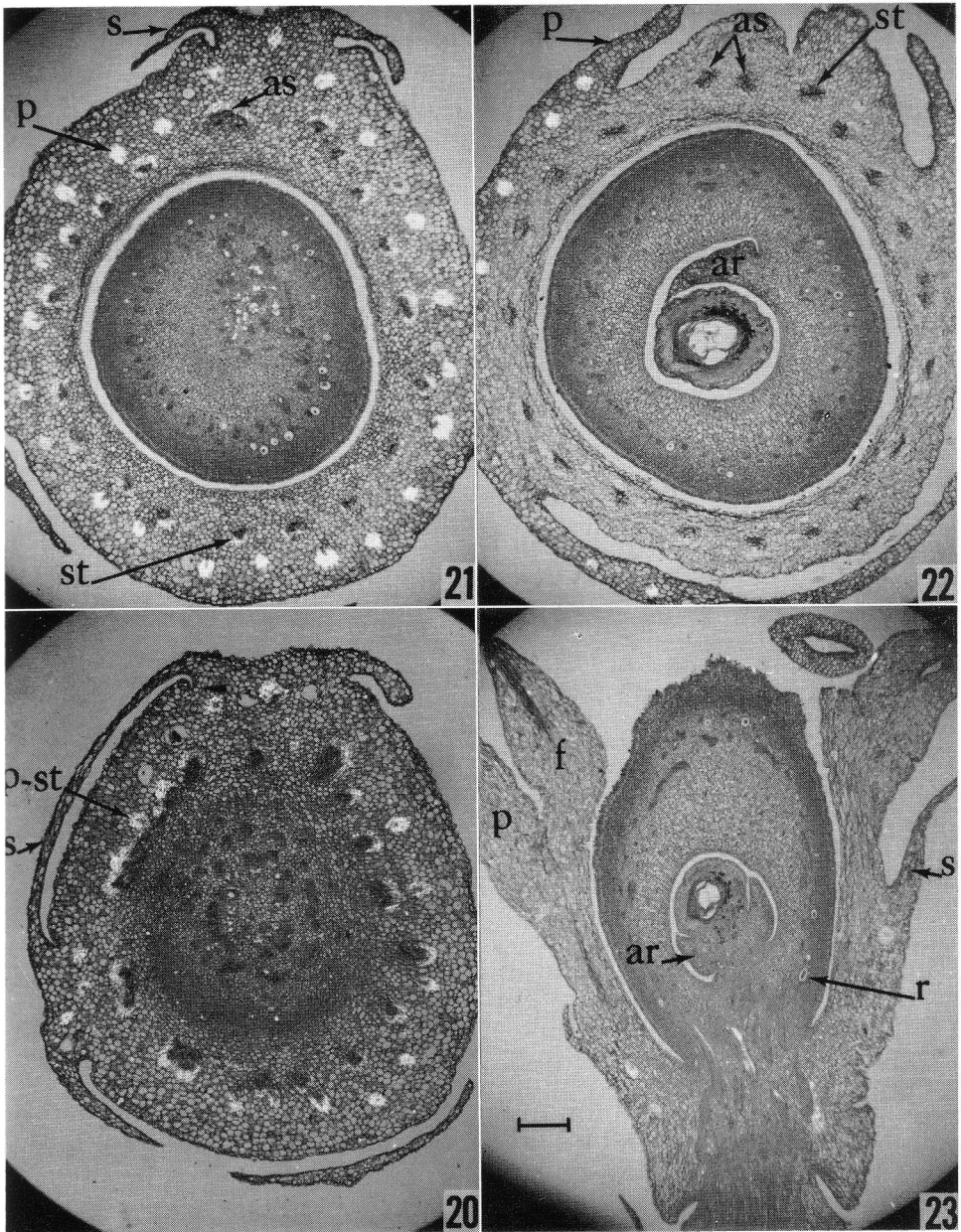
16-19. *Itaya amicornum*. 16, sepals, connate in a triangular sheath, $\times 10$; 17, petal, dotted margins indicate where joined to adjacent petals, $\times 10$; 18, stamen, dotted lines outline connate part of filament, $\times 10$; 19, carpel, $\times 13$. Details: *d*, dorsal bundle; *l*, lateral 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 amicum*. 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 gynoeceal 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 ceroxylid 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 campylotrous, 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 ceroxylid palms where perianth traces are fewer and in a median row. Reduction in number of sepal traces was also found in the ceroxylid 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 tanniferous 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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Leaf Anatomy in the Chelyocarpus Alliance

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The attractive fan-leaves of the *Chelyocarpus* alliance are of the induplicate type and have been described at some length in an accompanying paper (Moore, 1972). For this report, leaves of three species of *Chelyocarpus* and of *Itaya amicorum* were studied anatomically, and some observations were made on cleared leaves of *Cryosophila nana* (Moore 6203) to supplement information on the last genus provided by Tomlinson (1961). Although the diagnostic value of leaf anatomy cannot be assessed until much more information on the family is available, some differences are apparent among the three species of *Chelyocarpus*, and differences of a seemingly greater magnitude characterize *Chelyocarpus*, *Itaya*, and *Cryosophila*. In addition, certain rare or as yet unreported characters and combinations are found in the leaves of the new genus *Itaya*.

Surface preparations, sections, and clearings of major ribs and blade areas were made by techniques described by Tomlinson (1961) and Uhl (1969). To allow easy comparison with information in Tomlinson (1961) and other sources, descriptions are written in a form commonly used for recording anatomical data. A brief summary of leaf morphology in the alliance may be helpful. The large leaf blades are composed of elongate segments which are equivalent to the pinnae of a pinnate leaf. Each segment has a relatively large abaxial rib and is pointed or bifid at

the tip. Segments may be partially united by adaxial (intersegmental) ribs or ridges. Veins may be divided into three main categories: those of the intersegmental ribs, those of the midribs of the segments, and those of the lamina. In the leaves of *Chelyocarpus* and *Cryosophila*, the largest ribs are the adaxial (intersegmental) ridges which occur between individual segments through the undivided portion of the leaf blade. The largest bundles in these leaves also occur in the adaxial intersegmental ridges. In *Itaya*, however, intersegmental ribs are shallow and contain no veins. The midrib of each segment is the largest abaxial ridge in all three genera. Between each midrib and intersegmental rib or segment edge, a number of parallel lateral veins may be recognizable as low ridges on abaxial or occasionally adaxial surfaces of the segments. In all three genera, the lateral veins, which vary in size and number, are situated in an abaxial row, each vein usually in contact with the epidermis or hypodermis. In addition to the longitudinal veins, transverse veins, situated in the central part of the lamina, adaxial to the longitudinal bundles, are distinctive in every taxon described.

Descriptions

CHELYOCARPUS DIANEURUS (Fig. 1-8, 20).

Lamina

Dorsiventral. *Hairs* frequent, restricted to the abaxial surface, usually along small fibrous strands. Each trichome elliptical in longisection, 80 mi-

* From work supported by National Science Foundation Grant GB-20348X, H. E. Moore, Jr., principal investigator.

crons long, about 5 cells long and 2–3 wide, with thick pitted walls (Fig. 6). *Adaxial epidermis* shallow, cells aligned in rows parallel to veins, each cell 1.3–3 times as long as wide, usually longest over veins, end walls at right angles or oblique, outer walls thick and cutinized (Fig. 5). Surface of *cuticle* scalloped. *Abaxial epidermis* shallower than adaxial, cells irregular in size and shape, outer walls rounded to papillose, anticlinal walls not thickened, *cuticle* thin, smooth (Fig. 3, 4, 6). *Stomata* (Fig. 6) abaxial, in 1–2 irregular intercostal series, each stoma with two pairs of lateral subsidiary cells and a large distinctive pair of terminal subsidiary cells; the inner lateral pair colorless and curved around the guard cells, the outer pair curved to elongate; terminal subsidiary cells triangular to six-sided, often club-shaped with thickened wall areas which overarch the guard cells (Fig. 3, 4). *Guard cells* sunken to a level between the epidermis and hypodermis (Fig. 4), 20 microns long, containing silica crystals. Substomatal chambers well developed. *Hypodermis* one row adaxially, absent abaxially, cells slightly larger than epidermal cells with thin-walled, septate fibers in groups of 1–3 alternating with every 1–4 hypodermal cells (Fig. 1). *Chlorenchyma* compact, 1–2 rows of palisade-like layers adaxially, and 3–4 layers of larger isodiametric cells abaxially. Large *raphide sacs* medianly situated in the lamina. *Stigmata* spherical, spinulose, 8.0 microns in diam. in continuous files along veins, walls thicker around each silica body.

Veins

Intersegmental ridges (Fig. 1) prominent adaxially as narrow blunt ribs tapering from 2.5 mm. in height near the base of the leaf and ending where the segments are separate. At about the middle of the leaf, segments are joined

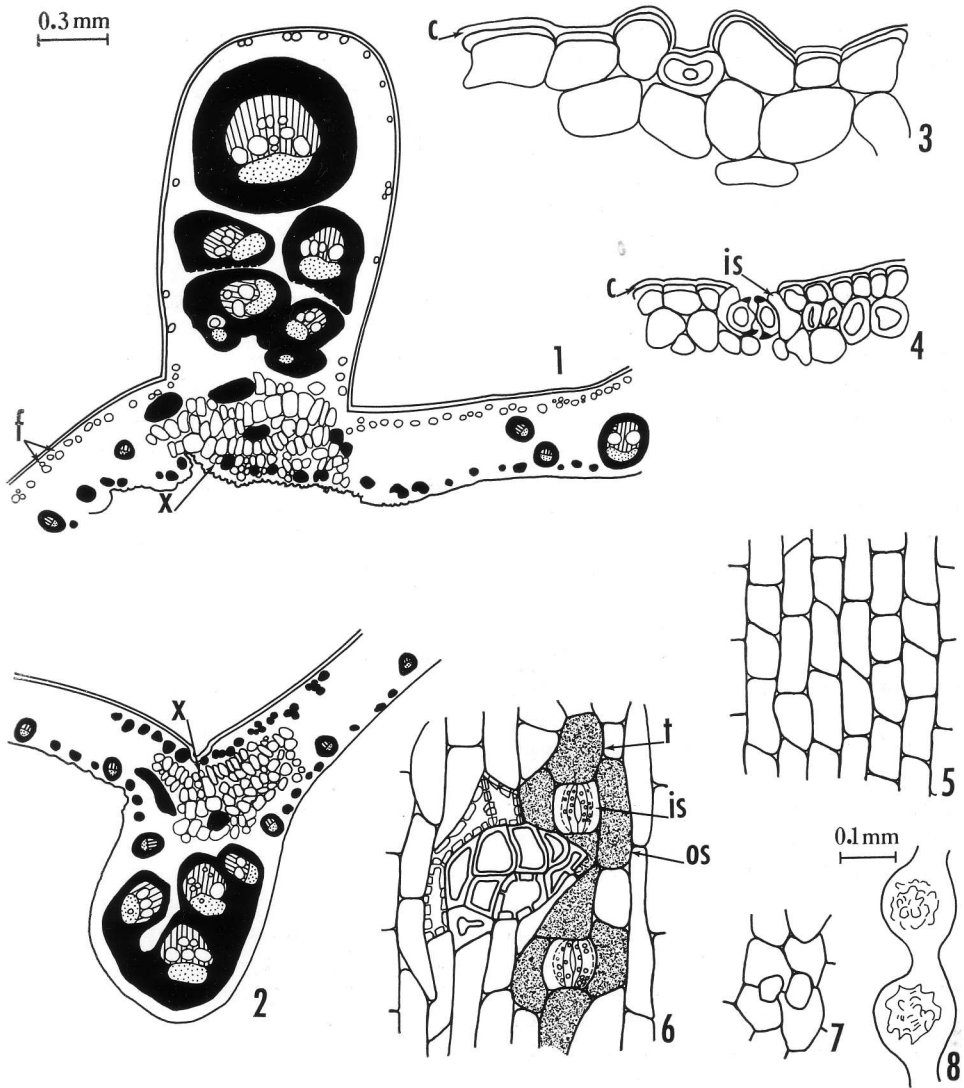
by intersegmental ribs 1.25 mm. high, each rib with a large adaxial (distal) bundle and 3–4 smaller bundles in two lateral rows (Fig. 1). Near the base of the leaf, the larger intersegmental ribs have several (18) additional small vascular bundles and many (–23) small fibrous strands. All veins are oriented with phloem more or less abaxial and have wide sheaths of thick-walled fibers (Fig. 1). Midribs of segments (Fig. 2) form abaxial ridges, 0.5 mm. high where sampled, and have 3 large and 1–2 small vascular bundles with confluent fibrous sheaths. A band of short *expansion cells*, 4 rows wide, is present abaxial to each intersegmental rib, and a similar band adaxial to each midrib (Fig. 1, 2). *Lateral veins* of three types: large and small vascular bundles and alternating strands of 1–6 septate fibers. In a half-segment there are usually 3 large vascular bundles with from 15–22 small veins between each larger pair. The parenchymatous sheath of a vascular bundle usually abuts on the abaxial epidermis. Fibrous sheaths of vascular bundles complete with 1 fibrous layer around xylem and 2–3 around phloem in smaller bundles, and 3–4 around xylem and 2–3 around phloem in larger bundles. Large bundles with 1–3 large vessels and small bundles with ca. 8 xylem elements. Sieve elements large. *Transverse veins* (Fig. 20) sinuous in surface view, extending from the midrib across each half-segment, situated medianly in the lamina, with 3–4 xylem elements and an equally small amount of phloem enclosed in an even fibrous sheath 3–4 layers thick.

Material studied: *Moore and Gutiérrez* 9999.

CHELYOCARPUS ULEI (Fig. 21).

Lamina

Dorsiventral. *Hairs* abaxial only, smaller and fewer than in *C. dianeurus*

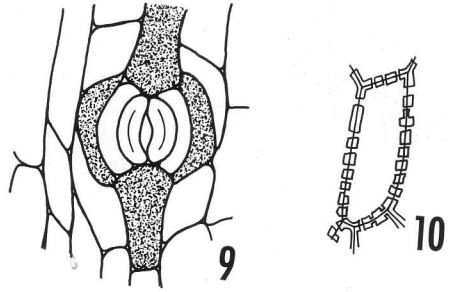


1-8. *Chelyocarpus dianeurus*. 1, transection of intersegmental rib (adaxial surfaces are toward the top of the pages in all sections); 2, transection of the midrib of a segment; 3, longisection of a guard cell and adjacent epidermal and mesophyll cells; 4, transection of a stoma showing guard cells, each with an outer and inner ledge (solid black); 5, surface view of the adaxial epidermis; 6, surface view of abaxial epidermis showing two stomata and a thick-walled trichome; 7, hypodermal cells below guard cells. Scale at upper left shows magnification for Fig. 1-7. 8, stigmata, magnification indicated by adjacent scale. Details: *c*, cuticle; *f*, fibrous strands of adaxial hypodermis; *is*, inner lateral subsidiary cell; *os*, outer lateral subsidiary cell; *ts*, terminal and outer lateral subsidiary cells, stippled.

but structurally similar, 40 microns long, composed of 8–10 thick-walled cells with conspicuous pits. *Adaxial epidermis* shallow, cells longer than wide in parallel rows, end walls at right angles or oblique, outer walls thick and cutinized, anticlinal walls also thick. *Abaxial epidermis* with outer walls round to papillose, cells irregular in size and shape, usually longer over veins. *Cuticle* thin, but thicker over stomatal apparatus. *Stomata* abaxial, intercostal in irregular series; each stoma with two pairs of lateral subsidiary cells, the outer pair larger and curved, the inner smaller pair colorless; terminal subsidiary cells distinctive, raised above epidermal level. *Guard cells* 18 microns long, small outer and inner ledges present, containing small silica bodies. Substomal chambers well developed. *Hypodermis* absent abaxially, adaxially one layer of thin-walled septate fibers alternating with 2–4 large isodiametric cells. *Chlorenchyma* of 1–2 distinct palisade layers adaxial to 2–4 rows of closely aligned mesophyll. Large *raphides* frequent in mid-lamina (Fig. 21). *Stigmata* along bundles as described for *C. dianeurus*, some smaller intercellular stigmata in chlorenchyma.

Veins

Intersegmental ribs largest, adaxial, containing an upper large bundle and about 6 smaller veins arranged as in *C. dianeurus*. *Midribs* abaxial and smaller, 0.5 mm. high in mid-laminas, with 1 large and 3–4 smaller veins, the smallest often a phloem strand only. Bands of *expansion cells* resemble those of *C. dianeurus*. Lateral veins also are like those of *C. dianeurus*. In a segment 4.0 cm. wide there are three larger *lateral veins* in each half-segment and up to 21 smaller parallel veins between each larger pair. The main difference in venation between *C. ulei* and *C. dianeurus* is in transverse veins (cf. Fig. 20, 21).



9–10. *Chelyocarpus chuco*. 9, abaxial leaf surface with stoma, magnification to scale by Fig. 1, 11; 10, thick-walled cell of adaxial epidermis, magnification to scale by Fig. 8.

Transverse veins are 40 microns in diam. and 90 microns apart in *C. ulei* (Fig. 21), and 70 microns in diam. and 450 microns apart in *C. dianeurus* (Fig. 20).

Material examined: *Moore and Salazar 9494*.

CHELYOCARPUS CHUCO (Fig. 9, 10, 22).

Lamina

Dorsiventral. *Hairs* infrequent, flat, scale-like, ca. 80 microns wide, composed of about 8 cells with thick, pitted walls, and a base of 2–3 cells. *Epidermis* shallow on both surfaces, cells longer than wide, end walls transverse to oblique; cells of both surfaces with thick conspicuously pitted walls (Fig. 10), somewhat thinner abaxially, thick *cuticles* extending onto anticlinal walls of both surfaces. Cells of abaxial epidermis longer over veins. *Stomata* (Fig. 9) abaxial, arranged in irregular series intercostally; each stoma with two pairs of lateral subsidiary cells, the inner pair colorless and smaller, terminal subsidiary cells large and distinctive in shape, not elevated above the epidermis; all subsidiary cells more regular in shape than those of the other species. *Guard cells* large, not sunken, both outer and inner ledges evident. *Hypodermis* present both adaxially and abaxially, continuous adaxially with irregularly spaced thin-walled fibers; some-

what discontinuous abaxially, thicker-walled fibers alternating with hypodermal cells. *Chlorenchyma* of 1-2 palisade layers with 3-4 abaxial rows of large isodiametric cells. Raphide sacs present in mid-lamina. *Stigmata* similar to those of *C. dianeurus* and *C. ulei*.

Veins

Intersegmental ribs largest, 2.0 mm. high at the base of the leaf blade, rounded in transection, with 4 large bundles, the uppermost largest, and each bundle with 2 large vessels. *Midribs* abaxial, 1.0 mm. high at the base of the leaf, usually containing one large and a small bundle, sheaths confluent. *Expansion cells* as in *C. dianeurus* and occasionally below folds in the lamina. In segments 3.5 cm. wide, *lateral veins* are of three sizes: about 6 larger laterals extend through each half-segment with 1 strand of intermediate size between 2 large ones and usually 3 smaller bundles between large and intermediate veins. *Transverse veins* (Fig. 22) are large in diam. and extend only short distances between lateral veins. Bundle structure is like that in *C. dianeurus*, but larger bundles more consistently have two large vessels.

Material examined: *Moore 9459*.

ITAYA AMICORUM (Fig. 11-19, 23).

Lamina

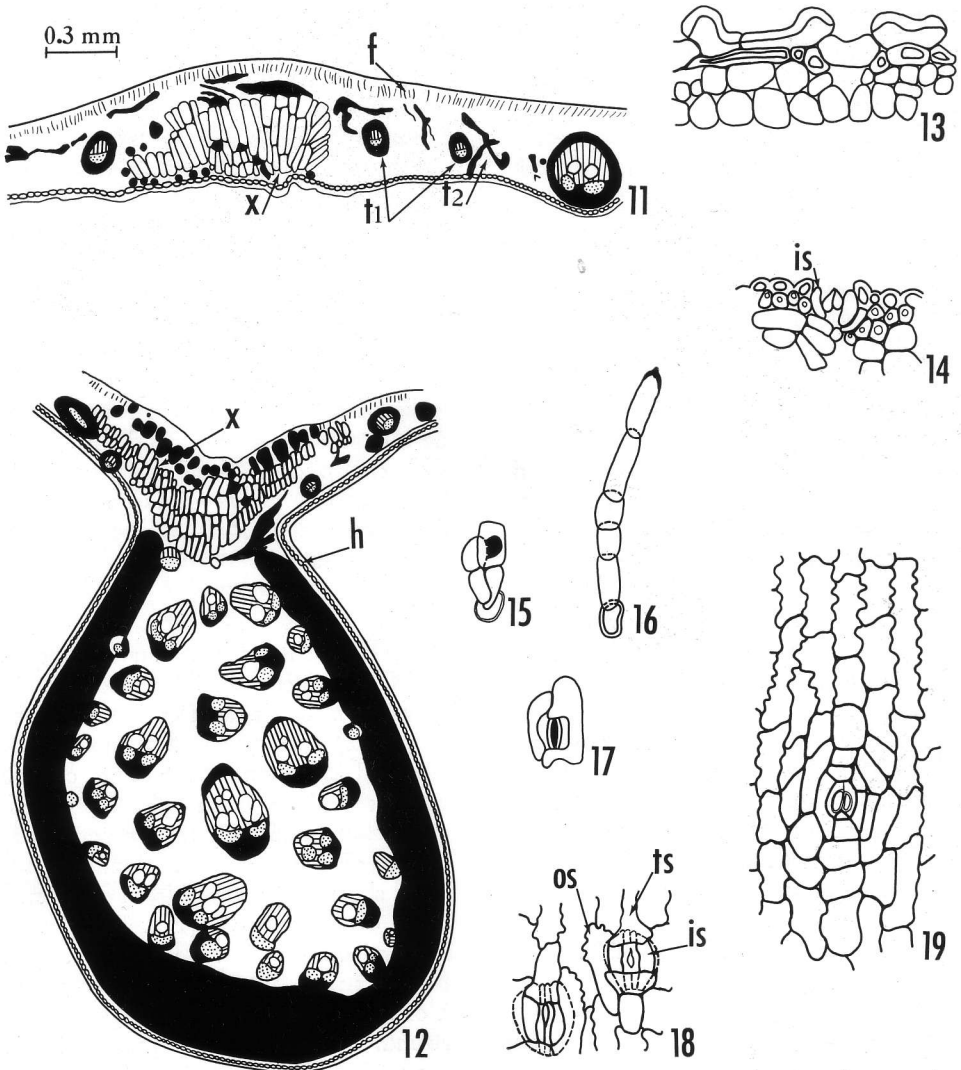
Dorsiventral. *Hairs* of two types were observed: adaxial trichomes of 4 thin-walled cells with a multicellular base (Fig. 15, 19), and abaxial long, uniseriate trichomes usually with a single basal cell (Fig. 16). *Adaxial epidermis* (Fig. 19) shallow, outer walls thick, cells longer than wide, end walls transverse to oblique, all walls conspicuously sinuous in surface view. *Abaxial epidermal cells* (Fig. 18) very shallow, irregular in size and shape, most with sinuous walls

thinner than those of adaxial epidermis. *Stomata* (Fig. 18) abaxial, in intercostal uniseriate files; each stoma with two lateral pairs of curved subsidiary cells, the outer pair and the two terminal subsidiary cells raised above epidermal level, inner subsidiary cells thin-walled and colorless. *Guard cells* 25 microns long, not sunken below epidermal level, but partially covered by large elevated subsidiary cells. Substomatal chambers well developed. *Hypodermis* present on both surfaces and consisting of thick-walled fibers, those of the lower hypodermis thicker-walled and lignified. *Chlorenchyma* 1-2 indistinct palisade layers and 3 layers of large compact mesophyll. *Stigmata* like those described for *Chelyocarpus*.

Veins

Intersegmental ribs shallow, only slightly elevated adaxially, and contain only expansion tissue (Fig. 11). *Midribs* (Fig. 12) large, ca. 2.0 mm. high, elliptical in diam., containing ca. 30 bundles embedded in sclerotic parenchyma surrounded by a wide peripheral sheath of sclerenchyma. Bundles have small sheaths over the phloem and sometimes over the xylem (Fig. 12). Large bundles have 1-4 large vessels and 2 phloem strands; small bundles may have 1 or 2 large vessels and a single phloem strand. *Expansion cells* present below the midrib. *Lateral veins* of two sizes, large bundles with 2 large vessels and 2 phloem strands and small with a single phloem strand and lacking large vessels. Two orders of *transverse veins* are present (Fig. 23): larger vascular bundles 70 microns in diam. extend from the midvein across each half-segment. A system of smaller strands of 1-4 fibers each is evident between larger transverse commissures (Fig. 11, 23).

Material studied: *Moore, Salazar, and Smith 8446*.

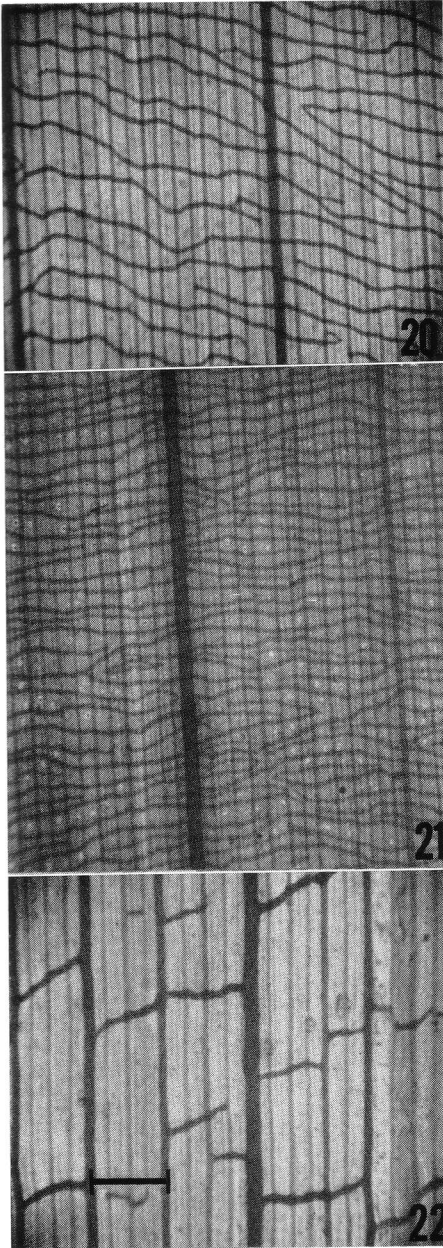


11-19. *Itaya amicomum*. 11, transection through intersegmental rib; 12, transection of midrib; 13, longisection of a stoma and neighboring cells; 14, transection of a stoma; 15, trichome from the adaxial surface; 16, trichome from abaxial surface; 17, hypodermal opening below a guard cell; 18, abaxial surface showing two stomata; 19, adaxial surface with multicellular base of a trichome similar to that in Fig. 15. Details: *h*, fibers of abaxial hypodermis; *t1*, large transverse veins; *t2*, small fibrous transverse veins; other details and shading as in Fig. 1-8; scale indicates magnifications.

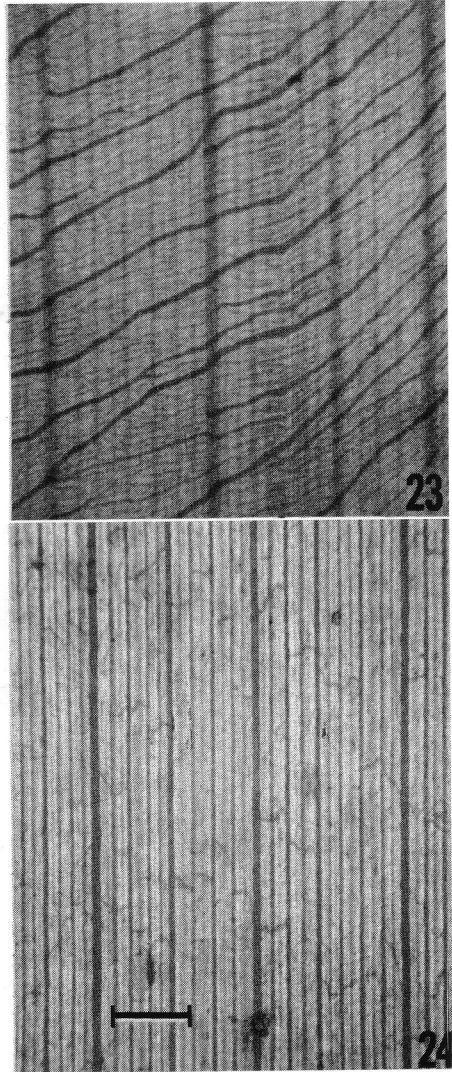
Discussion

Many structural aspects of these leaves fall within a range of characters attributed to palm leaves by Tomlinson (1961). The alliance as a whole may be

characterized as follows: *Laminas* dorsiventral. *Hairs* various. *Epidermal cells* thin-walled or thick-walled, longer than wide, in rows parallel to veins, usually longer over veins. Adaxial cells more



20-22. Cleared sections of *Chelyocarpus* leaf blades to show transverse commissures. 20, *C. dianeurus*; 21, *C. ulei*, open spaces with black centers are raphide sacs; 22, *C. chuco*. Scale equals 2 mm.



23-24. Cleared leaf blades. 23, *Itaya amirorum*, note small transverse veins between large ones; 24, *Cryosophila nana*, only a few very short transverse veins present. Scale equals 2 mm.

regular in size and shape and thicker-walled than abaxial cells. *Stomata* abaxial only, subsidiary cells 6, with two usually distinctive terminal cells and two pairs of lateral subsidiary cells, the terminal and outer lateral pairs overarching the guard cells. *Guard cells* sunken or

Table 1. Summary of anatomical differences in leaves of *Chelyocarpus* alliance.

	<i>Chelyocarpus dianeurus</i>	<i>Chelyocarpus utei</i>	<i>Chelyocarpus chuco</i>	<i>Itaya amicorum</i>	<i>Cryosophila</i> sp. and <i>C. nana</i> (Tomlinson, 1961) <i>C. nana</i> (Moore 6203)
Hairs	abaxial only, thick-walled, elliptical	similar but fewer	abaxial only, thick-walled, scale-like	abaxial thin- walled, long, uniseriate; adaxial short, base large	abaxial only, thin-walled, long, uniseriate
Epidermis	adaxial, thick- walled; abaxial, thin-walled	same	both thick- walled, pitted	sinuous on both surfaces	adaxial, cells uniform, slightly longer than wide. Abaxial, cells rectangular, longer than adaxial and longer over veins
Hypodermis	adaxial only, fibers present	adaxial only, same	adaxial and discontinuous abaxial, fibers present in both	adaxial and abaxial of fibers only except over stomata	adaxial and sometimes abaxial, fibers present
Stomata	intercostal, not in definite files	same	same	intercostal, in single files	intercostal, not in definite files
Guard cells	sunken	sunken	not sunken	slightly sunken	not or slightly sunken
Subsidiary cells	6	6	6	6	6, terminal not distinct

Table 1 Continued.

	Chelyocarpus dianeurus	Chelyocarpus ulei	Chelyocarpus chuco	Itaya amicorum	Cryosophila sp. and C. nana (Tomlinson, 1961) C. nana (Moore 6203)
Veins					
Intersegmental	adaxial, largest	same	same	adaxial small ridge, no bundles	adaxial, largest
Midrib	abaxial, next largest	same	same	largest, abaxial	abaxial, next largest
Lateral	2 series	same	3 series	2 series	1 series
Buttresses	absent	same	same	same	present
Transverse	from midrib to pinna edge, coarse irregular	same but smaller	large, short	2 series, 1 fibrous, smaller	lacking or rare
Hypodermal openings	1-2 lobed cells	same	same	2-3 lobed cells	4 L-shaped cells
Phloem strands	1	1	1	2	1

not, usually with two ledges, substomatal chambers well developed. *Hypodermis* one layer adaxially of isodiametric cells with interspersed septate fibers or completely fibrous; similar, discontinuous or absent abaxially. *Chlorenchyma* compact, of 1–2 distinct or indistinct palisade layers and 3–4 abaxial layers of large isodiametric cells. *Raphides* frequent in mid-laminas, often large. *Stegmata* in files along veins, spherical, spinulose; smaller silica bodies may be present in mesophyll and guard cells. *Veins* largest in intersegmental ribs or absent (*Itaya*). Midribs of segments abaxial with several large bundles. *Lateral veins* abaxial in laminas, 1–2, or 1–3 sizes. *Transverse veins* median in laminas and thus above longitudinal, distinct in size and course, short and frequently lacking in *Cryosophila*. Larger vascular bundles with 1–4 large vessels, predominately 2 in *C. chuco*, phloem strands 1 or 2, fibrous sheaths usually larger around phloem except in transverse veins where equal. *Expansion cells* in single bands opposite midribs and intersegmental ridges, rarely (*C. chuco*) below other folds in the lamina.

Certain characters in the new genus *Itaya* are noteworthy. The midrib of the induplicate leaf of *Itaya* is structurally like the midribs attributed to reduplicate palms by Tomlinson (1961) in that bundles are enclosed in a central parenchymatic zone surrounded by a sclerenchymatous outer sheath. An unusually large number of bundles is also found in the midrib of *Itaya*. There is only a single band of expansion cells, however, and there are usually two bands lateral to midribs in reduplicate palms. Thus, the large midrib in this genus does not correspond to those described in the family. *Itaya* also differs from the other two genera in the absence of a large vascularized adaxial rib, possessing only a band of expansion cells between segments. This would appear

to be an important character but seems not to have been noted previously, and its significance cannot be assessed at present.

Table 1 summarizes differences in leaf anatomy within the alliance. Only minor differences were found among the three species of *Chelyocarpus*; *C. dianeurus* and *C. ulei* resemble each other closely. Palisade layers are more distinct in *C. ulei* and transverse veins are smaller and more closely spaced than those of *C. dianeurus*. *Chelyocarpus chuco* is unlike the first two species in several respects: type of hair, thicker-walled, pitted epidermal cells, the more constant occurrence of 2 large vessels per bundle, and large, short, transverse commissures.

Characters of a larger magnitude separate the three genera. *Hairs* in *Chelyocarpus* are thick-walled and elliptical or scale-like; those in *Itaya* and *Cryosophila* are thin-walled, relatively long, and uniseriate. *Cryosophila* thus resembles *Itaya* in trichome structure but differs from both other genera in the lack of transverse veins and in the formation of buttresses linking veins to peripheral layers. *Itaya* may be separated from *Chelyocarpus* and *Cryosophila* by a number of characters. These include: epidermal cells with sinuous walls, largely fibrous hypodermal layers, the presence of a second transverse system of fibrous veins, the lack of a vasculated intersegmental rib, the structure of the midrib, the arrangement of stomata in uniseriate files, and the presence of two phloem strands in larger bundles.

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The Carnauba Wax Palm (*Copernicia prunifera*).

III. Exploitation and Plantation Growth

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In Brazil a slow process of exploitation took place which led to the carnauba's present state of incipient domestication. This occurred by first harvesting leaves of wild stands without any regard for the care and maintenance of the tree population, followed by the management or protection of natural stands, and finally with the actual plantation growth of this palm.

Management of Natural Stands

The practice of managing natural carnauba stands began in the second half of the nineteenth century. It involved practices aimed at protecting and preserving, as well as extending, the native stands. Protecting mature trees so that they would provide a continuing source of wax led to the practice of protecting naturally occurring seedlings from being browsed by livestock. This was accomplished by fencing off sections of the grove where young plants were present in any number.

Burning of groves each year at the end of the dry season to control brush and stimulate the growth of herbaceous plants is another practice detrimental to young carnauba palms. It is of no danger to mature plants, as already mentioned, and the fact that livestock could graze on grasses and herbs growing beneath the trees is actually an efficient use of the land.

There have been several attempts to

discourage the practice of burning, as well as other measures to protect the carnauba. The State of Ceará (Dept. Econ. Agr., 1942) recommended that burning be abandoned, and also mentioned regulations in force which made it illegal to destroy a carnauba without permission. The same publication also stated penalties that could be imposed for the damaging practice of early harvest of leaves. This in reference to the official designation of the beginning of the harvest season based on the date of the end of the rainy season.

Harvesting of carnauba leaves is typically associated with three different land and labor systems: (1) harvest by the landowner himself; (2) harvest by a tenant under a special rental agreement; (3) harvest by a sharecropper.

The least common method is that involving harvest by the landowner. Under this arrangement the amount of land is quite small, perhaps no more than a few acres. The work of harvesting the leaves and extracting the wax is often done by the owner and his family, with help on some occasions from hired day labor. Or group labor parties may be organized among a number of small property owners. This involves the owners and some members of their families pooling their labor to harvest the leaves and extract and render the wax of each member's property in turn; the property owner providing food and drink for the duration of his harvest.

The most common method of harvesting carnauba wax is that of the rental agreement. The property owner contracts to rent his land for the sole purpose of harvesting carnauba leaves. A cash rental figure is agreed upon, taking into consideration the number and condition of the palms. Such an arrangement often results in overexploitation, as the renter is interested in deriving as large a profit as possible without much regard for the condition in which the trees are left. The practice is also facilitated by the absence of the landowner who commonly does not reside on the property.

The third system is the traditional sharecropper method common among peasants in northeast Brazil. It is generally associated with large land holdings with extensive areas of native carnauba. The sharecroppers are most often year-long residents on the property, taking part in the carnauba wax harvest as part of the annual cycle of work on a number of crops.

The share of the harvest which a sharecropper could expect for his labors was originally set at two-thirds. More recently this has been reduced to one-third with the advent of higher yields obtained by mechanized wax extraction with the Guarany-Ciclone leaf chopper.

Mechanization of the extracting phase of the wax harvest has led to modification of the systems under discussion. The practice of organizing group labor parties among small property owners has all but disappeared since the bulk of the work has been mechanized. It is now common for the small land owners to contract with the owner of a Guarany-Ciclone, having the harvested leaves processed in return for a portion of the wax obtained. The rental system continues as before, except that now the renter either owns or has access to a machine. On the large plantations, the sharecropper system also continues, although mod-

ified by the introduction of mechanized wax extraction.

Plantations

It is not possible to determine exactly when the planting of carnauba began, since the practice evolved out of the management of natural stands. A visitor to northeast Brazil near the end of the nineteenth century mentions visiting a carnauba "plantation," owned by a German immigrant, which had been in operation for about 40 years. This particular "plantation" was described as being near a river, and may have been only a managed grove (Gissern, 1901).

An account of planting carnauba in upland areas of western Rio Grande do Norte dates back to the 1890s, and by the second decade of the present century cultivation in these areas was said to have developed appreciably (Lins and Andrade, 1960). Since carnauba does not occur naturally in these upland areas, the accounts may represent the first clear-cut examples of cultivation.

These early activities of both managing and cultivating carnauba appear to have been at the initiative of the individual landowners. This is indicated by a Recife, Brazil, newspaper account translated and printed in the *Tropical Agriculturist* (25:814-815, 1905) which exclaims that it is impossible to understand why the state and local governments in the northeast had not undertaken programs to promote carnauba cultivation.

In Ceará, the first published account of planting carnauba dates from 1914, with several reports from the following decade (Souza Pinto, 1928). Additional plantings were also reported in Rio Grande do Norte in the late 1920s (Andrade and Salgado, 1945).

As early as 1924 government programs with regard to the carnauba palm were being discussed. Among the issues were measures to prohibit the cutting of trees,

and measures to encourage cultivation, especially in areas most seriously affected by drought (Bertino, 1936).

The tempo of carnauba planting picked up in the 1930s, mainly in Ceará. By 1939 it was reported that 5 counties combined had a total of 894,000 maturing trees (Chaves, 1939).

The S. C. Johnson & Son, Inc. bought Fazenda Raposa near Fortaleza in 1937, and a year later began a program of planting carnauba. Company records for the period 1938 through 1942 indicate that 196 acres were planted with nearly 83,000 palms. During the same period the Chaves Brothers began planting carnauba on Fazenda Campestre near Pacajus, Ceará. Data on these plantings show that 1,833 acres were planted with an estimated 1,650,000 trees between 1939 and 1950 (Kitzke, 1951, 1952).

Plantation cultivation has increased rapidly since the 1940s and has played an important role in the overall expansion of production which reached 17,000 metric tons in 1967. An idea of the number of planted trees is derived from Bayma (1958) who estimated that every county in Ceará had some carnauba production, and that Ceará and neighboring Piauí combined had over ten million planted trees. It should be mentioned that there is no indication that any selection process was used in gathering seed for the above plantings.

Plantation Practices

The planting of carnauba is traditionally accomplished by placing seeds in small mounds of earth at the onset of the rainy season. The germination rate and success of such plantings is dependent upon adequate rainfall. Research on the germination rate of seeds planted directly in the field indicates that a rate of 60 to 70 percent success can be expected (Prata, 1963). Where germination fails

or seedlings die, replanting is carried out the following year to maintain field capacity.

While a majority of planting is still done by seed directly in the field, experimentation at Fazenda Raposa indicates that planting seeds in nursery beds and subsequently transplanting the most robust seedlings into the field is very effective. The addition of compost into the hole into which the seedling is transplanted provides a good initial source of nutriment and also acts to help store moisture (Kitzke, 1953).

Considerable disagreement exists with regard to the optimal number of plants to the acre. Gomes (1945) mentions densities ranging from 250 to 500 per acre, but favors the lower figure. Bayma (1958) is in general agreement with a figure of 330 per acre. It is interesting to compare these recommended densities with those of Fazenda Raposa and Fazenda Campestre. For the former, the average is 423 per acre, for the latter about 900 per acre.

The use of fertilizer is not common in growing carnauba, nor is irrigation. Mature plants are well adapted to the rainfall regime, and the chief justification for irrigation would be in the event of a drought during the first year or two of a new planting. Of prime concern to the plantation owner is the protection of young plants from damage by browsing animals and fire, and from competition of weeds and brush.

The time interval between planting and first harvesting of carnauba leaves varies somewhat in response to soil and water conditions. The uninformed or impatient planter may begin to harvest leaves when the plants are between four and six years of age. If such measures are followed, they can result in the stunting of the growth of the plant to the degree that average yields may never be achieved.

By postponing the first harvest until the palms are eight to ten years old, they will provide higher yields.

In summary, it can be stated that as far as plantation cultivation is concerned the carnauba palm has considerable promise. Through further improvements in plantation practices and the development of higher yielding strains through seed selection and plant breeding, wax production could be significantly increased without the necessity of expanding present acreage.

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NEWS OF THE SOCIETY

Recent Deaths

Lee Adams and his wife, Mimi, died in a tragic automobile accident in Jacksonville, Florida, on November 16, 1971. Mr. Adams, a native of Jacksonville and former member of The Palm Society, expressed his interest in palms in a series of 20 paintings of selected palm genera commissioned by Dr. Arthur Montgomery for the Fairchild Tropical Garden where they are usually to be seen in the Nell Montgomery Garden House. A more detailed account of the collection and of Mr. and Mrs. Adams by Nixon Smiley is to be found in the Fairchild Tropical Garden Bulletin for January, 1972.

The Secretary has been notified by his sons of the death of Professor Armando Dugand of Baranquilla, Colombia, on December 5, 1971. Professor Dugand had been a member of the society since September, 1956, and was the author of several articles on palms of Colombia.

Seed Bank

Members will be happy to learn that the arrangement whereby seeds are collected at Fairchild Tropical Garden for our Seed Bank has been revised and should result in the availability of even more seeds than ever before to the Seed Bank. Mrs. Wait will locate those seeds she needs to fill your requests, then pass this want list on to the official Garden seed collector. Once the seeds are collected, Mrs. Wait will pick them up, clean them and send them out.

The Palm Society owes a large debt of gratitude to the Garden for all the help it has given and continues to give

us and our members, for the rich variety of palm seeds made available to us, for the help of the Staff who are frequently contacted to answer your questions, and for the use of the research library. We help the Garden too, for when the Seed Bank has seeds the Garden can use, they are shared freely, which results in an even wider dissemination since palms are among the most wanted of the plants distributed by the Garden to its membership annually. The nucleus of the Palm Society was formed by Fairchild Tropical Garden members who were enthusiastic about palms, which explains the close relationship of the two societies.

Albino palm seedlings

Professor Aylthon Brandão Joly of the Universidade de São Paulo, Brazil, recently wrote the Executive Secretary about a naturally occurring albino seedling of *Euterpe edulis* in the tropical rain forest of southeastern Brazil. On returning later to the same spot, he found the seedling again though it was then showing signs of having exhausted the seed's supply of food and was beginning to wither away.

Mrs. Buhler then passed on to the editor her own experience with albino seedlings of her large *Caryota mitis* which seem to come in batches though most of the seedlings are green. These albinos do not survive while the normal seedlings have to be pulled out.

What causes some seedlings to be albino we do not know but on occasion a variegated plant may occur. Such has been reported in *Sabal* and *Chamaedorea*.

LETTERS

EDITOR, PRINCIPES

In the January 1972 issue of *Principes* Vol. 16 there is a letter from Otto Martens to the Lord Howe Board of Control (*sic*). I take issue with some of the statements in the letter, but as an officer of the New South Wales State Government I am unable to reply to the bulk of Mr. Marten's letter.

However, his use of the generic names *Howea* and *Kentia* certainly deserves comment. I think Mr. Martens will agree that there are not four species of *Howea* on the island. His use of *Kentia* is confusing; he is referring presumably to the two *Howea* species which are known in the trade as *Kentia*. I hope he is not referring to either *Hedyscepe* or *Lepidorrhachis* as probably neither will successfully grow under the conditions he describes.

As an ecologist with a deep professional and personal interest in the island (after 12 weeks of field study) I hope the suggestions are ignored. The island is far too important ecologically, phyto-

DEPARTMENT OF AGRICULTURE
NEW SOUTH WALES
ROYAL BOTANIC GARDENS AND
NATIONAL HERBARIUM
SYDNEY, N. S. W. 2000
19 June, 1972

geographically (after all, all the palms are endemic!) and biologically for use of fertiliser and herbicide to increase production of a crop which is less important to the island's economy than the tourist industry.

I suggest to Mr. Martens that before he starts advocating "rejuvenating" natural palm stands he should suggest that research into the effects of such activities be commenced. Is the palm seed so important that Mr. Martens would contemplate initiation of a rather destructive course of action with very little basic data? I doubt it, as only 1000 bushels of seed were collected in 1971-72.

Unfortunately I am unable to debate most of Mr. Martens' comments; I hope that the Lord Howe Island Board of Control will take up the issue.

Yours sincerely,
J. PICKARD
BOTANIST (PLANT ECOLOGIST)

PALM LITERATURE

DEWERS, ROBERT S. & KEETER, TOM L.
Palms for Texas Landscapes. Texas
Agricultural Progress 18(1): 20-22.
Winter 1972.

This article will be of interest to Texans and others who are trying to grow palms on the colder fringes of the subtropics. Included are some cultural tips and a list of palms that have been

successfully established out-of-doors in various parts of the state. Texas Agricultural Progress is a quarterly publication of the Texas Agricultural Experiment Station and the Texas Agricultural Extension Service at Texas A&M University, College Station, Texas.

F. B. ESSIC
L. H. Bailey Hortorium