Floral Structure in the Neotropical Palms Chelyocarpus Dammer, Cryosophila Blume and Itaya H. E. Moore (Arecaceae)

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Floral structure in the neotropical palms Chelyocarpus Dammer, Cryosophila Blume and Itaya H. E. Moore (Arecaceae)

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Abstract

CASTAÑO, F., M. CRÈVECOEUR, J.-C. PINTAUD & F. W. STAUFFER (2011). Floral structure in the neotropical palms Chelyocarpus Dammer, Cryosophila Blume and Itaya H. E. Moore (Arecaceae). *Candollea* 66: 65-79. In English, English and French abstracts.

Floral morphology and anatomy in the neotropical palm genera *Chelyocarpus* Dammer, *Cryosophila* Blume and *Itaya* H. E. Moore *(Arecaceae: Coryphoideae, Cryosophileae)* are studied in detail and the implications for the establishment of an alliance formed by the three genera, as suggested by previous researchers, are discussed. All taxa are characterized by the presence of hermaphrodite flowers, congenitally united imbricate sepals, imbricate petals, carpels basally ascidiate, but apically plicate, and crassinucellar and bitegmic ovules with a funicular aril. Most of these floral character states are also shared with other members of *Cryosophileae* and do not support the establishment of an alliance. The combination of an uniseriate perianth, basally united filaments and a partially syncarpous gynoecium in the endemic Peruvian palm *Chelyocarpus repens* F. Kahn & K. Mejia does not correspond with the diagnostic characters proposed for *Chelyocarpus* and is not found elsewhere in *Cryosophileae*.

Key-words

ARECACEAE – Chelyocarpus – Cryosophila – Itaya – Neotropics – Morphology – Anatomy

Résumé

CASTAÑO, F., M. CRÈVECOEUR, J.-C. PINTAUD & F. W. STAUFFER (2011). Structure florale chez les palmiers néotropicaux Chelyocarpus Dammer, Cryosophila Blume et Itaya H. E. Moore (Arecaceae). *Candollea* 66: 65-79. En anglais, résumés français et anglais.

La morphologie et l'anatomie florale des genres de palmiers néotropicaux *Chelyocarpus* Dammer, *Cryosophila* Blume et *Itaya* H. E. Moore *(Arecaceae: Coryphoideae, Cryosophileae)* sont étudiées en détail. Ces taxons sont caractérisés par la présence de fleurs hermaphrodites, ayant des sépales et pétales imbriqués et congénitalement unies, des carpelles ascidiés à la base, mais plissées au niveau apical et des ovules crassinucellaires, bitégumentés munis d'arille funiculaire. Ces caractères floraux sont pour la plupart partagés avec d'autres membres des *Cryosophileae* et ne justifie donc pas l'établissement d'une alliance. La combinaison d'un périanthe unisérié, de filaments soudés à la base et d'un gynécée partiellement syncarpique chez l'espèce endémique péruvienne *Chelyocarpus repens* ne correspond pas aux caractères diagnostiques proposés pour *Chelyocarpus* et n'a été retrouvée nulle part ailleurs chez les *Cryosophileae*.

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Introduction

The understanding of flowers is a central theme for the phylogenetic reconstruction of the angiosperms at all levels (Endress, 1994) and of particular interest because of its usefulness in circumscribing taxonomic entities. In the case of the palms, contributions on the floral structure are relatively scant. In fact, reproductive structures of only 4% of the nearly 2600 palm species have been studied in detail (Stauffer & al., 2002). Most of these contributions have already proved to be highly valuable in determining specific functions of organs and establishing relationships among genera and tribes (Uhl & Moore, 1971; Uhl & Dransfield, 1987; Dransfield & Uhl, 1998).

Although the subfamily *Coryphoideae* possesses a high concentration of putatively unspecialized traits, including apocarpous gynoecia only found in *Nypa* Steck *(Nypoideae)* (Uhl & Dransfield, 1987; Dransfield & al., 1990), relatively few efforts have been made so far to study their floral structure. Floral morphology and anatomy, with emphasis in the vasculature patterns were studied for the first time in *Coryphoideae* by Morrow (1965), who analyzed 27 genera and inferred affinities and evolutionary patterns within the group. Floral morphology and anatomy in the *Trachycarpeae* have been studied in detail in the Asian genus *Rhapis* L. f. *(Rhapidinae)* by Uhl & al. (1969) and Giddey & al. (2008), and more recently the floral structure and development have been studied in *Licuala* Thunb. *(Livistoninae)* (Stauffer & al., 2009), and *Sabal* Adans. (Castaño & al., 2009).

This study focuses on the neotropical genera *Chelyocarpus* Dammer (4 spp.), *Cryosophila* Blume (10 spp.) and the monotypic *Itaya* H. E. Moore; a palm group called the *"Chelyocarpus* alliance" by Moore (1972) and Uhl (1972a, 1972b). These studies proposed the establishment of the alliance based on their leaves with similar trichome structure and vasculature pattern, whereas flowers present perianth organs with raphide idioblasts in all pieces and vascular bundles always aligned towards their adaxial sides. The androecium was described as highly variable between the genera but similar carpel morphology and anatomy and ovule insertion (hemianatropous) were observed in all taxa. Uhl (1972a, 1972b) supported the establishment of an alliance and identified *Chelyocarpus* as the least specialized genus within the complex, whereas *Itaya* was proposed as the most derived. Her results were of key importance to support further taxonomic assessments of the three genera (Uhl & Dransfield, 1987; Dransfield & al., 2008). All genera of the *"Chelyocarpus alliance"* were assigned to *Coryphoideae,* tribe *Cryosophileae* in the latest palm classification (Dransfield & al., 2005; Dransfield & al., 2008). A first attempt to assess the relationships between *Chelyocarpus, Cryosophila* and *Itaya,* was carried out by Evans (1995) through a cladistic morphological analysis. Meanwhile, morphological and molecular phylogenetic analyses of the whole palm family or selected groups of *Coryphoideae* (i. e. Uhl & al., 1995; Asmussen & al., 2000; Hahn, 2002; Asmussen & al., 2006; Lewis & Zona, 2008; Roncal & al., 2008) have failed to clearly establish the relationships within the tribe and none of them included all the genera of the alliance. More recently, Baker & al. (2009) demonstrated a well supported sister relationship between *Sabal* and the clearly monophyletic tribe *Cryosophileae,* represented in this study by all 10 genera; however, relationships among genera remained poorly resolved.

Chelyocarpus, Cryosophila and *Itaya* have been characterized by a complicated taxonomic history and available collections often do not allow the observation of all the necessary morphological features. These facts have strongly hindered the assessment of their taxonomic relationships with the rest of *Cryosophileae.* The present study has almost doubled the number of taxa with respect to precedent contributions (i.e. Morrow, 1965; Uhl, 1972a,) and has employed modern techniques for palm anatomy. It aims to: 1) identify floral characters that could be critical for the taxonomic differentiation at the generic and specific level, and 2) test whether the floral structure supports the establishment of an alliance, as defined by Moore (1972) and Uhl (1972a, 1972b).

Material and methods

The morphological and anatomical analysis was based on the study of liquid-fixed and fresh flowers as well as herbarium specimens received on loan (Table 1). Samples from living inflorescences of *Chelyocarpus, Cryosophila* and *Itaya* were collected in the Fairchild Tropical Botanical Garden (FTG) and the Montgomery Botanical Center (MBC), between October 31 and November 4 of 2007. Living populations of *Chelyocarpus* and *Itaya* were studied in a visit to the Jenaro Herrera Natural Reserve and the Allpahuayo Mishana National Reserve in Iquitos (Peru) in November of 2007 and 2009. Cultivated individuals of *Cryosophila kalbreyeri* subsp. *cogolloi* R. J. Evans were studied at the Medellín Botanical Garden (Colombia). Additional herbarium material was studied in COL, COAH, FTG, JAUM, HUA, MEDEL and USM during a visit in November of 2007.

Flowers were dissected for morphological study under a stereomicroscope (Wild M3B) at the Conservatory and Botanical Garden of Geneva. Some organs of the dissected specimens were chosen for scanning electron microscopy. They were dehydrated, critical-point-dried and sputter-coated with gold. Micrographs were obtained using a Zeiss DSM 940A scanning electron microscope (Orion 6.60 Imaging System) at the Natural History Museum of Geneva.

Table 1. – Species and samples studied and current geographical distribution (nomenclature and distribution based on Henderson & al., 1995).

Taxa	Sample [origin indicated as (f): fresh material, (p): pickled, liquid-fixed collection, (h): herbarium collection]	Distribution
***Chelyocarpus dianeurus* (Burret) H. E. Moore**	*Cuatrecasas 16702* (h, COL); *Gentry & Monsalve 48371* (h, COL); *Moore & Gutierrez 9999* (h, BH); *s.coll. 10229* (p, K)	Pacific lowlands of Colombia
***Chelyocarpus repens* F. Kahn & K. Mejía**	*Encarnación 1227* (h, G); *Kahn & Mejía 2080* (p, K); *Kahn & Mejía 1725* (h, USM); *Kahn & Mejía 1974* (h, USM); *Kahn & Mejía 2068* (h, P); *Lopez & al. 6152* (h, COAH); *Mejía 153* (h, USM); *Mejía 201* (h, G); *Mejía & Kahn 151* (h, USM); *Plowman & al. 6772* (h, GH); *Tovar & al. 1451* (h, USM)	Peruvian Amazon
***Cryosophila guagara* P. H. Allen**	*Castaño & Stauffer 795* (f, G, MBC)	Southern Costa Rica to adjacent Panama
***Cryosophila kalbreyeri* (Dammer) Dahlgr.**	*Castaño & Stauffer 785* (f, FTG, G); *Bernal & Galeano 399* (h, COL); *Bernal & al. 933* (h, COL); *Cogollo 5110* (h, JAUM); *Cogollo & al. 5114* (h, JAUM); *Evans & Cogollo 247* (h, BH, JAUM); *Killip & Smith* 14412 (h, NY)	SE Panama to NW Colombia
***Cryosophila stauracantha* (Heynh.) R. Evans**	*Castaño & Stauffer 782* (f, FTG, G); *Castaño & Stauffer 794* (f, G, MBC); *Bartlett 11288* (h, MICH); *Evans 204* (h, BH, MICH, MO); *Gentle 4972* (h, LL); *Zona 1077* (p, K)	Extreme SE Mexico to northern Guatemala and Belize
***Cryosophila warscewiczii* (Wendl.) Bartlett**	*Blackmore 36* (p, K); *Castaño & Stauffer 783* (f, FTG, G); *s.coll. 1991-1092* (p, K); *Evans 145* (h, BH, MICH, MO)	Caribbean slopes from southern Nicaragua, Costa Rica, to central Panama
***Itaya amicorum* H. E. Moore**	*Castaño & Stauffer 786* (f, FTG, G); *Henderson 751* (p, AAU); *Fleck 458* (h, USM); *Galeano & Miraña 1654* (h, COL); *Henderson & al. 751* (h, NY); *Henderson & al. 842* (h, COL); *Lopez & al. 5806* (h, COAH); *Moore & al. 9509* (h, BH); *Moore & al. 8446* (h, USM); *Nuñez & al. 16414* (h, USM); *Nuñez & al. 16992* (h, USM); *Vásquez 15834* (h, COL); *Vásquez 7112* (h, P)	Western Amazon region in Colombia, Peru and Brazil

For the anatomical investigations, flowers at or close to anthesis were chosen. The material was dehydrated and embedded in Technovit 7100 [2-hydroxiethyl methacrylate (HEMA)] and sectioned using a rotary microtome (Leitz 1512) at 5-10 µm thickness. The sections were stained with toluidine blue and red ruthenium, and then mounted in Assistent-Histokitt mounting medium. Photos of the anatomical sections were obtained using a microscope Leica DMIRE2 and a camera Leica DC 300F at the Department of Plant Sciences of the University of Geneva. The permanent slides of the microtome sections are deposited at Laboratory of Micromorphology of the Conservatory and Botanical Garden of Geneva.

Results

Shared characters between Chelyocarpus, Cryosophila *and* Itaya

The flowers are hermaphroditic; they are solitary and spirally arranged throughout the rachillae. The sepals are imbricate; they are congenitally united at the base; the petals are imbricate (Fig. 1A, 5B). All the stamens are fertile, attached at the same level, somewhat reflexed and spreading at anthesis; the anthers are exerted, with extrorse dehiscence through a longitudinal stomium (Fig. 3B, 4C, 4D, 6B). The gynoecium is apocarpous (unicarpellate in *Itaya).* All carpels appear fertile at anthesis; they are almost completely ascidiate, but plicate towards the stigmatic region (Fig. 1B, 3F, 4E, 6C). The ovary is globose, but becomes narrow towards the style. The stigma is profusely papillate; characterized by a central slit and two lateral parallel crests. The stigmatic papillae consist of 2-4 cells; they are distributed along the ventral slit but are more profuse in the dorsal ridges and projected upwards in all directions (Fig. 3D, 5E, 6D). The pollen tube transmitting tract (PTTT) is formed superficially in the epidermis of the ventral slits, the latter characterized by the presence of slightly secretory cells; it reaches the ovule by surrounding the funicle. The ovule is crassinucellar and bitegmic; it is inserted at the base at the ventral side of the locule. The funicle is papillate, forming a lateral large-celled secretory aril, which surrounds the ovule laterally and basally, being contiguous to the basal region of the locule (Fig. 1D, 3E, 5D, 6I). The vascularization is more pronounced basally and towards mid-length of each perianth organ. Large raphides are scattered in the floral base.

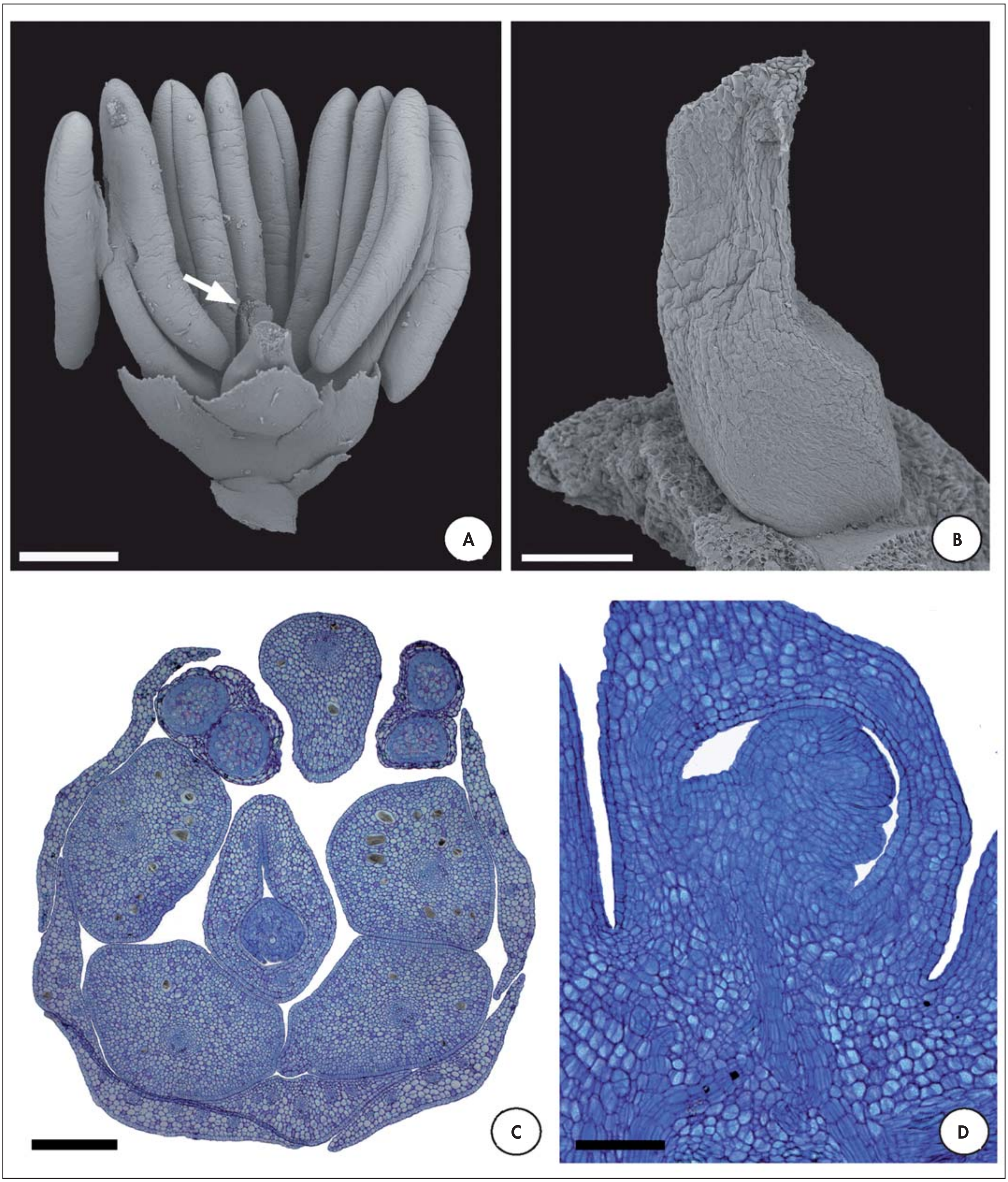

Fig. 1. – *Chelyocarpus dianeurus* (Burret) H. E. Moore. **A.** Flower at anthesis (lateral view), arrow pointing to the gynoecium, scale bar = 600 µm; **B.** Gynoecium at anthesis (lateral view), scale bar = 150 µm; **C.** Transverse section of the flower (level of the ovary), scale bar = 250 µm; **D.** Longitudinal section of a young ovary, scale bar = 100 µm.

Shared characters in Chelyocarpus

The flowers are closely packed on the rachillae. The sepals are ovate and slightly dentate towards the apex. The petals are free; they have approximately the same shape as the sepals (Fig. 1A, 1C). The androecium consists of 4-8 stamens; the filaments are pyriform, fleshy, and more or less circular in transverse section. The anthers are versatile and dorsifixed (Fig. 1A, 3B). The gynoecium consists of one to three carpels. The carpels are urceolate, closely adpressed to the stamens and have their ventral sides facing the center of the flower. The style is short and ovate in cross section (Fig. 1B, 1C, 3C). The stigma is linear and recurved. PTTT is about one cell layer thick (Fig. 3F).

Between five and eight vascular bundles are present in the middle of the floral base. The vascularization of the perianth organs is always close to the adaxial side (Fig. 1C). Each filament is served at the base by 1-3 vascular bundles (depending on the thickness of the filament) but only few conductive cells could be observed towards their tips (Fig. 1C). At least one dorsal vascular bundle was present towards mid-height of the ovary; it continues up to the style and the stigmatic region (Fig. 1C).

Diagnostic characters for the species of Chelyocarpus

Chelyocarpus dianeurus (Burret) H. E. Moore

The flowers are 2-3 mm long and 1-2 mm wide, sessile. The floral base is very short. The flower subtending bract is very inconspicuous and delicate (Fig. 1A), less than 1 mm long, lanceolate, slightly concave, with the apex rostrate and a sheathing base; it is irregularly dentate. Sepals three or rarely four, approximately 1 mm long and 1 mm broad, fleshy mainly towards their base. When the calyx is tetramerous, one of the sepals is slightly smaller, but similar in shape. Petals three, rarely four, 1 mm long and about 1 mm broad (Fig. 1A, 1C). There are five free stamens, rarely 6-7, up to 2 mm long. The arrangement of the stamens is very irregular with respect to the organs of the perianth, possibly because of their variable number; however, one stamen is normally opposite to each sepal, and the remaining 1-2, each opposite to a petal (Fig. 1C). The anthers are 1-1.5 mm long, conspicuous and very large in comparison with the flower size (Fig. 1A). Although the connective region is thick and prominently developed, the zone that connects the anther to the filament is very short and weak. The tapetum and especially the endothecium are well differentiated, both characterized by large and thin-walled cells. The gynoecium is formed by one or rarely two very short carpels (Fig. 1B). When there is only one carpel, it is closely laterally adpressed by two stamens at each side and the remaining stamen faces the ventral slit. The style is shortly elongate. The ovule is campylotropous; it does not fill all the locule, leaving a reduced empty space. The outer integument has 3-4 cell layers at mid-length of the nucellus, and 1-2 towards the micropyle, whereas the inner integument has 2-3 cell layers throughout the length of the ovule. The micropyle is large, leaving a wide zone where the nucellus is directly exposed to the locule (Fig. 1C-D).

The vascularization of the flower subtending bract could not be observed. Each sepal has 5-6 vascular bundles and each petal has three vascular bundles (Fig. 1C). In the ovarian region the carpel has 4-5 vascular bundles on each side of the ventral slit; another one on the dorsal side. At least one vascular bundle was observed in both, the dorsal and the ventral side of the style. There is one vascular bundle that serves the ovule and ends in the chalaza (Fig. 1D). Some dispersed tannin idioblasts were observed in the flower subtending bract and towards the margins of sepals and petals. A few isolated tannins were present in the androecium, specifically towards the epidermis of the filaments and in the endothecium. There are some raphides in the mesophyll of the petals; they also surround the vascular tissue of each filament (Fig. 1C). Idioblasts (raphides, tannins, etc.) were not observed in the gynoecium.

Chelyocarpus repens F. Kahn & K. Mejia

The flowers are 2.5-3 mm long and 4-5 mm wide (Fig. 2A), they are sessile. Although the flowers are solitary, the variable number of organs in all whorls and the fact that they are very tightly grouped on the rachilla make the interpretation of single flowers difficult. No flower subtending bract could be observed. Only one perianth whorl is present (Fig. 2A). The tepals are basally connate. They are irregular in outline; the free tips are mostly lanceolate to ovoid and dentate. Perianth and androecium are congenitally fused at the base and the perianth is closely adpressed to the androecium for the rest of its length (Fig. 2A). The androecium consists of 4-7 stamens. There is no constant pattern in the position of stamens with respect to the perianth organs. The filaments are 3 mm long and 1.5-2 mm wide at the base. They are congenitally united, forming a fleshy tube that is closely adpressed against the carpels (Fig. 2A). The filaments become free in the upper part. The thecae are short and globose. The mature anther wall is mainly formed by the epidermis and the endothecium. The tapetum is one cell layer thick. The gynoecium consists of one or two carpels of 1-1.2 mm long. When two carpels are present, the ovaries are united at their base (Fig. 2B) but become completely free at the uppermost level of the locules. There is no correlation in the position of the carpels with respect to the organs of the perianth. The styles are completely free, very short and recurved. The ovule is hemianatropous. It fills the locule almost completely. At mid-length of the ovule the outer and the inner integuments are 5-7 and three cell layers thick respectively (Fig. 2B). Towards the micropyle the outer

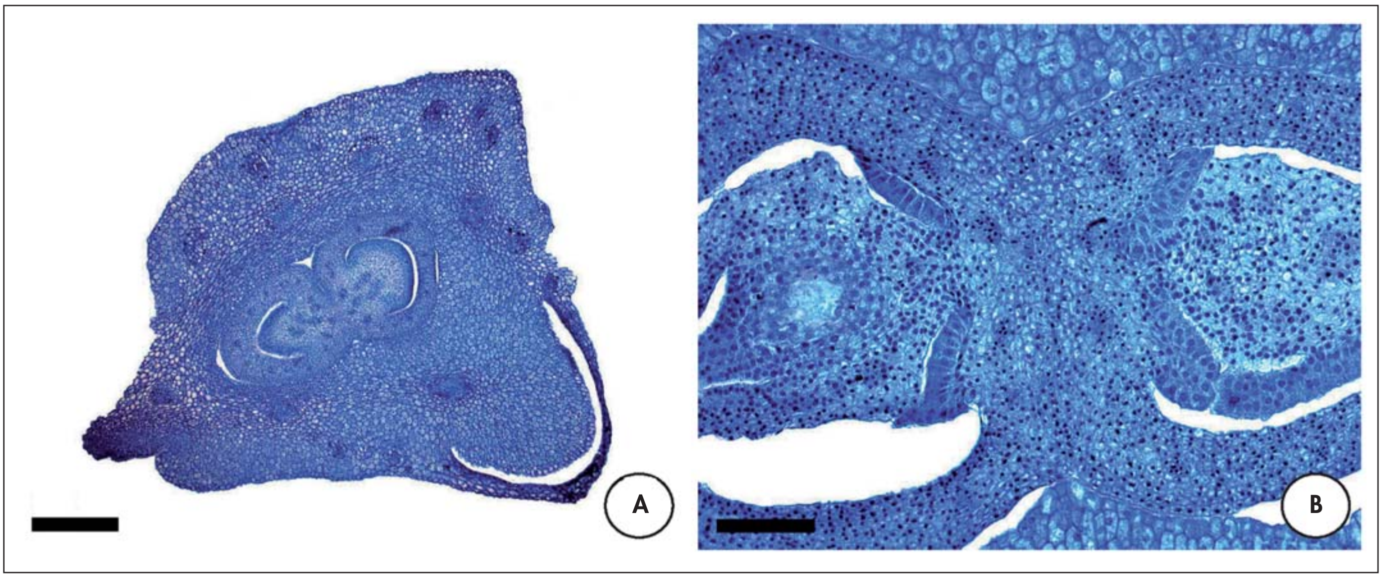

Fig. 2. – *Chelyocarpus repens* F. Kahn & K. Mejia. **A.** Transverse section of the flower (level of the ovary), scale bar = 400 µm; **B.** Transverse section of the ovary, scale bar = 100 µm.

integument is four cell layers thick but the inner one remains invariable. The nucellus is 3-4 cell layers thick. The micropyle is straight.In the floral base it is possible to distinguish a central and an external region. In the central region, there is one vascular bundle per carpel, surrounded by 4-6 bundles externally that will serve each stamen. Additionally, there are a few vascular bundles in the periphery that probably correspond to the perianth vasculature. 3-6 vascular bundles serve each perianth organ where they are still adnate to the androecium. However, in their free portion towards the apex, these bundles tend to disappear. Tannins were not found in the ovary, but are copiously distributed in the style and the stigma, mainly towards the epidermis. Tanniferous cells were also observed upwards near the tip of each perianth organ. Towards the floral base scattered raphides are present.

Chelyocarpus ulei Dammer

The flowers are 4-5 mm long and 2-4 mm wide. They are laterally compressed and more densely grouped towards the rachilla apex; a short pedicel ca. 0.5 mm long supports each flower; the floral base is ca. 1 mm long (Fig. 3A, note the apically fibrous flower subtending bract to the right). The floral subtending bract is 0.4-1.2 cm long, concave, lanceolate, and pilose towards the apex; they are shorter towards the apex of each rachilla. Sepals two, concave, 2 mm long and 2 mm broad, with the margins weakly revolute; the calyx forms a shallow envelope that partially covers the corolla. Petals 2, rarely 3, they are oblong and have approximately the same size as the sepals (Fig. 3A). The androecium consists of 6-8 fertile stamens, which are grouped in two rows of 2-3 antepetalous stamens and the remaining antesepalous (Fig. 3B); the filaments are 2.5-3 mm long, 1-1.5 mm wide at the base, thinner towards the apex, which is slightly twisted. The connective is short and inconspicuous. The anthers are 1.5 mm long. All thecae have more or less the same size (Fig. 3B). The gynoecium is bicarpellate (Fig. 3C) or rarely tricarpellate, 1.5-1.8 mm long. The ovule is hemianatropous and does not fill the locule. Both integuments are three to six cell layers thick towards the micropyle and 3-4 cell layers thick at mid-length of the ovule. It has a zigzag micropyle.

The flower subtending bract has 5-6 vascular bundles. The sepals have 8-9 main vascular bundles and 3-4 procambial strands. There are 10-11 vascular bundles alternating with 5-6 procambial strands in the petals. The filaments have some scattered stomata towards the dorsal side. There are five vascular bundles at the base of each carpel. Two laterals and one dorsal vascular bundle were observed in the style and the stigmatic region. Raphides are present at the base of the calyx and corolla and throughout the filaments; they are however scarcely represented in the walls of the ovary, being more frequent along the style and around the ventral slit but absent in the stigma. Tannin idioblasts are common on the adaxial side of the flower subtending bract and the stigma but rare in the style.

Shared characters in Cryosophila

The flowers are solitary and arranged in a spiral. There is one bract subtending each flower; inserted directly on the rachilla. Sepals three, concave and coriaceus. Petals three, free, concave and broadly ovate (Fig. 4A, 5B). The androecium consists of six stamens; three antesepalous and

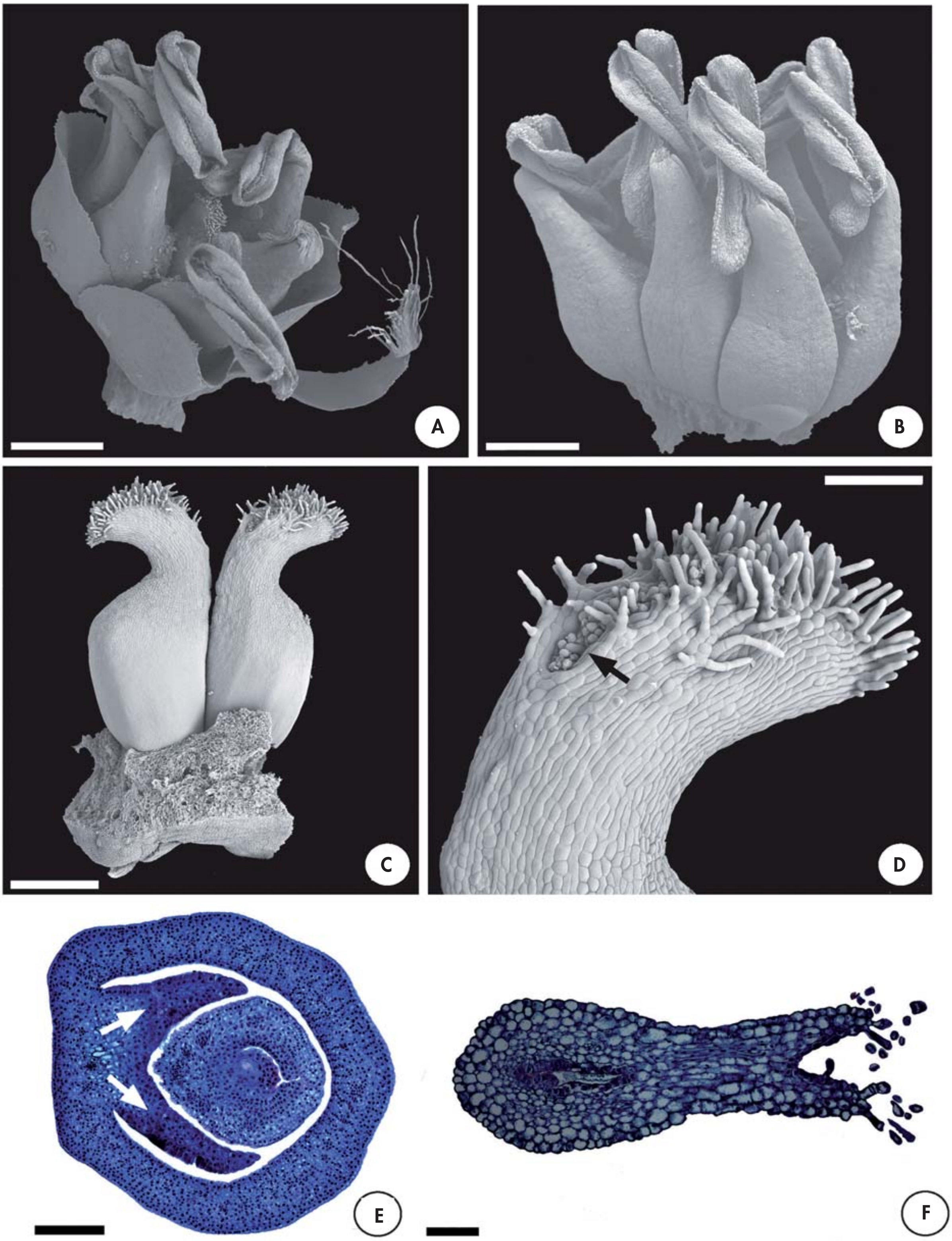

Fig. 3. – *Chelyocarpus ulei* Dammer. **A.** Flower at anthesis (lateral view), scale bar = 800 µm ; **B.** Androecium at anthesis (lateral view), scale bar = 650 µm ; **C.** Gynoecium at anthesis (lateral view), scale bar = 450 µm ; **D.** Detail of stigma (lateral view), arrow pointing to the ventral slit, scale bar = 150 µm ; **E.** Transverse section of the ovary (only one ovary shown), arrows pointing to the funicular aril, scale bar = 150 µm ; **F.** Transverse section of the stigma, scale bar = 100 µm.

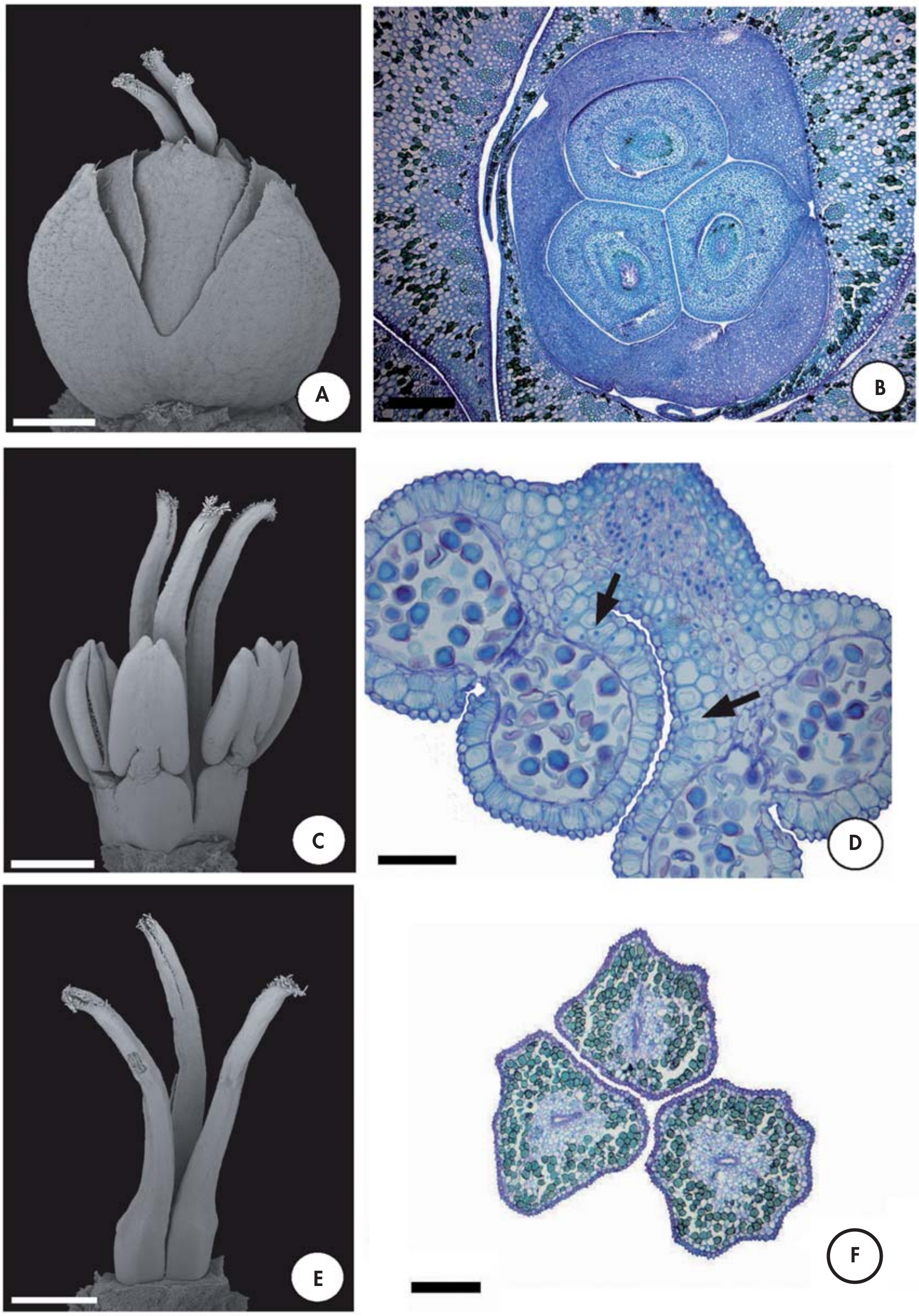

Fig. 4. – *Cryosophila guagara* P. H. Allen. **A.** Flower at anthesis (lateral view), scale bar = 900 µm; **B.** Transverse section of the flower (level of the ovary), scale bar = 300 µm; **C.** Flower at anthesis (lateral view, perianth removed), scale bar = 850 µm; **D.** Transverse section of the anther, arrows pointing to the endothecium, scale bar = 100 µm; **E.** Gynoecium at anthesis (perianth and androecium removed), scale bar = 900 µm; **F.** Transverse section of the style, note abundant tanniferous mesophyll, scale bar = 200 µm.

three antepetalous (Fig. 5C). The filaments are congenitally united at the base, in a very thin, membranous tube, but having their tips free (Fig. 4B, 5B). The anthers are spread at anthesis (Fig. 4C, 5A, 5C). The gynoecium contains three antesepalous, slender bottle-shaped carpels (Fig. 4E). They are largely ascidiate, but plicate towards the distal portion of the elongate style and the stigma (Fig. 5E). There is a minute central protrusion at the base of the flower between the three carpels. The style is cylindrical and angular in cross section (Fig. 4F); the distal part of the style and the stigmas are exerted (Fig. 4A). The stigma is hollow, very short and funnel shaped. The multicellular papillae are mainly distributed on the dorsal side of the two stigmatic crests (Fig. 5E). The pollen tube transmitting tract (PTTT) reaches the ovule by surrounding the funicle directly from the uppermost central region of the locule. The ovule is hemianatropous and does not fill the locule (Fig. 4B, 5D, 5F). The ovule is twisted towards a lateral side of the ovary (Fig. 5F). The funicular aril basally surrounds the ovule (Fig. 5D).

The vascular supply of the flower subtending bract could not be observed. In the perianth, the vascular bundles concentrate towards the adaxial side of each organ (Fig. 4B, 5B). A single vascular bundle serves each stamen (Fig. 4B, 4D). Raphide idioblasts are basally scattered in the calyx and the corolla in very low amounts. Tanniferous cells are scarcely present at the base of the style, becoming very abundant towards the stigma (Fig. 4F). There, tannins fill almost the entire mesophyll. In the ovule, one cell layer in the inner integument is tanniferous (Fig. 4B, 5F).

Diagnostic characters for the species of Cryosophila

Cryosophila guagara P. H. Allen

The flowers are 4-5 mm long and 3-4 mm wide, globose and almost sessile (Fig. 4A). The flower subtending bracts are lanceolate, concave, about 2 mm long and acute. The sepals are 3-3.5 mm long, united up to ¼ - ½ of their length. The petals are 3-4 mm long and 4-5 mm broad at the base (Fig. 4A). The stamens are 2-2.5 mm long; they remain inflexed until the beginning of the anthesis. The filaments are united up to approximately ¼ - ½ of their length. The anthers are basifixed, with a large connective (Fig. 4C-D). The carpels are 4-4.5 mm long, cylindrical, with the ovarian region slightly angular-ovoid (Fig. 4B, 4E). PTTT is superficially formed by 2-3 cell layers. In the ovule, the outer and the inner integuments are 6-7 and 4-5 cell layers thick, respectively, towards the micropyle; the observed nucellus was only three cell layers thick. The micropyle is directed to a lateral side of the carpel (Fig. 4B).

The floral base has between three and four vascular bundles in the central region. The periphery is served by a ring of 14-15 scattered vascular bundles that will serve the external region of the receptacle. Between eight and nine vascular bundles and nine to eleven intercalated procambial strands serve each sepal. Between 12-18 vascular bundles and 4-5 intercalated procambial strands serve each petal (Fig. 4B). The endothecial tissue is 12-15 cell layers thick (Fig. 4D). Each carpel is basally served by three vascular bundles. Towards mid-length the ovary has one ventral and one dorsal vascular bundle, together with 2-3 peripheral procambial strands (Fig. 4B). No vascular bundles are present in the ovule. In the style, only a dorsal vascular bundle is present, which extends up to the stigma. The scarce presence of raphides throughout the flower is compensated with a high density of tanniferous cells. Tannin idioblasts are abundant in most of the floral tissues. They are profusely present in the mesophyll of the perianth organs, between the vascular bundles and the abaxial epidermis (Fig. 4B), and the peripheral region of the receptacle. In the flower subtending bract, such cells are scattered in the mesophyll, which is 2-3 cells thick. Low amounts of tannins occur towards the distal portion of the filaments, the connective and the endothecium. Idioblasts were not observed neither in the basal ovary nor in the staminal tube.

Cryosophila warscewiczii (Wendl.) Bartlett

The flowers are 3.5-4 mm long and 2.5-2.8 mm wide, broadly ovoid, slightly 5-angled from above (Fig. 5A, 5C). They have a short pedicel of 0.2-0.4 mm, which leaves a shallow cup under the floral base after flower abscission. The floral base is approximately 1 mm long, well developed and with the shape of an inverted cup. The flower subtending bracts are about 1 mm long, lanceolate, concave, acute and curved upwards. The sepals are 2-2.6 mm long and 1.5-2 mm broad, lanceolate, slightly dentate at the apex and united for 0.6-1.2 mm (Fig. 5A). The petals are 2-2.5 mm long and 1.6-1.8 mm broad; somewhat serrate at apex, slightly adnate to the sepals at the base. The stamens are 3 mm long, with filaments about 2 mm long, forming a tube of 1 mm (Fig. 5B), which is basally adnate to the corolla. The connectives are fleshy and elongate. The anthers are basifixed, 1 mm long; the thecae have the same length, being shortly bifid at the base and the apex (Fig. 5A, 5C). Carpels are 1-1.5 mm long. The style is elongate, 1-1.2 mm long, arcuate, weakly compressed. Towards the micropyle, the inner integument is 2-3 cell layers thick, whereas the external one is 5-6 layers thick (Fig. 5F).

The floral base contains undifferentiated parenchyma, which has several vascular traces that serve the floral organs. Each sepal has five vascular bundles and 8-10 procambial strands. Approximately 12-16 vascular bundles, interspersed with 8-10 procambial strands, were observed in the corolla (Fig. 5B). The staminal tube is formed by elongated cells with thin walls (Fig. 5B, 5D). The dorsal side of each carpel is served by one vascular bundle extending up to the stigmatic

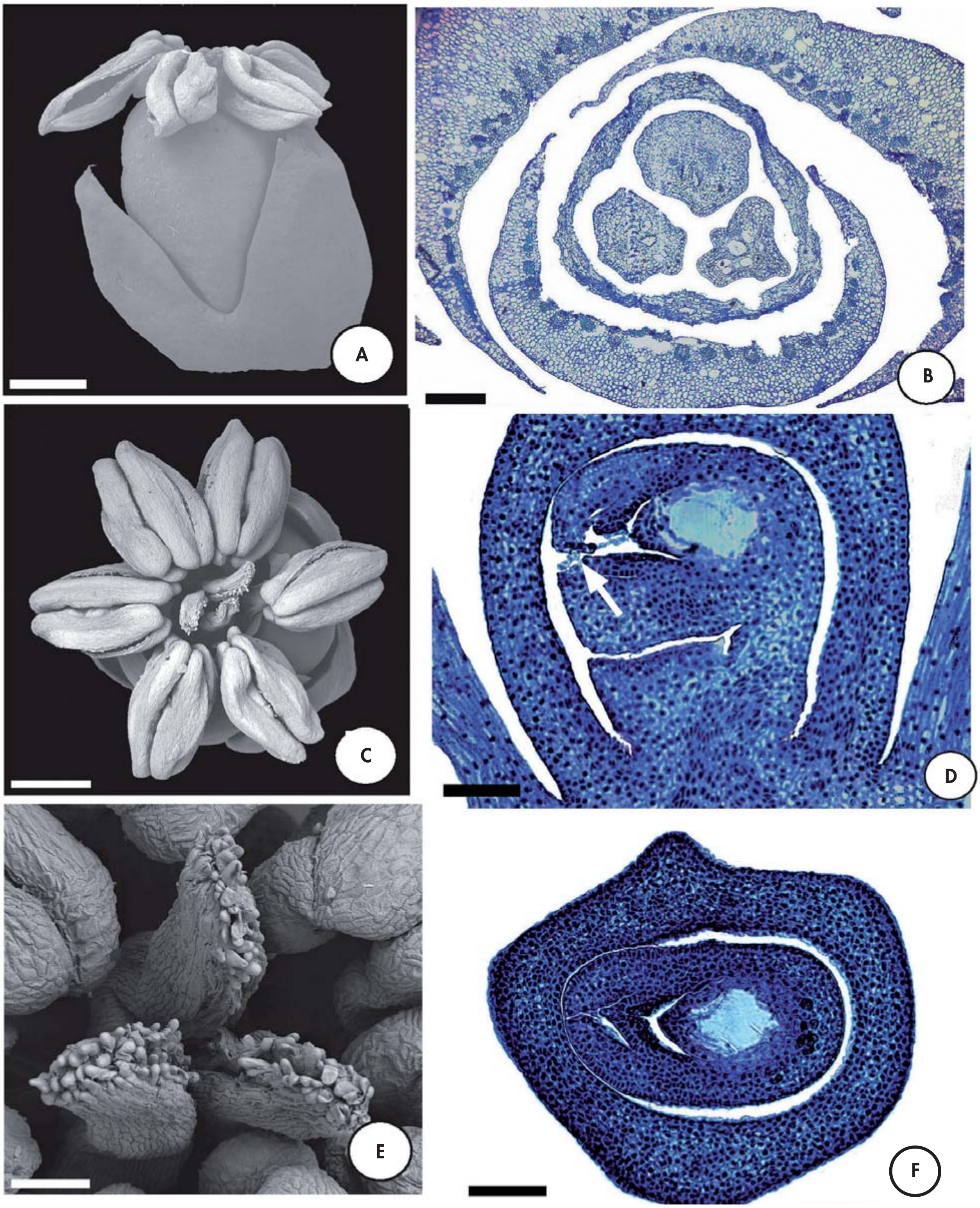

Fig. 5. – *Cryosophila warscewiczii* (Wendl.) Bartlett. **A.** Flower at anthesis (lateral view), scale bar = 600 µm; **B.** Transverse section of the flower (level of the styles), scale bar = 250 µm; **C.** Flower at anthesis showing radial arrangement of the anthers (upper view), scale bar = 600 µm; **D.** Longitudinal section of the ovary, arrow pointing to the micropyle, scale bar = 100 µm; **E.** Detail of the stigmas (upper view), scale bar = 100 µm; **F.** Transverse section of the ovary, scale bar = 100 µm.

base. At least one vascular bundle was observed in the funicle. Tanniferous cells are scarcely present in the sepals and staminal tube; raphides are widespread in the staminal tube and the style (Fig. 5B); however, they are scarce in the ovary walls. They are also present towards the ventral side of the thecae, especially in the endothecium.

Although *Cryosophila kalbreyeri* (Burret) Dahlgr. and *C. stauracantha* (Heynh.) R. Evans were also studied, their descriptions are not included in the results. They differ mainly in the size of the flowers, the degree of fusion of floral organs and the distribution of the idioblasts throughout the floral tissues.

Diagnostic characters for the species of Itaya

Itaya amicorum H. E. Moore

The flowers are 4-5 mm long and 3-4 mm wide, ovoid (Fig. 6A-B). The flower has a conspicuous pedicel about 1 mm long, covered with 1-3-cellular hairs (Fig. 6A). The subtending bract of the flower is ca. 1 mm long, lanceolate-acute, with crenate apex (Fig. 6A). Sepals three, 1.5-2 mm long and 1-1.1 mm broad at the base, lanceolate with the apex acute and crenate; united from the base up to $^1/_2$-$^2/_3$ of their length. Petals are basally adnate to the sepals. Petals three, 1.5-2 mm long and 3.5-4 mm broad at the base, slightly connate basally; broadly triangular in outline, irregularly dentate apically and congenitally adnate to the androecium for about 1 mm at basal level (Fig. 6A, 6H). The perianth is on both sides covered with very short papillae. The androecium consists of 15-17 stamens. The filaments are 2-2.5 mm long, congenitally united, forming a tube up to mid-length. The filament tips are free (Fig. 6A-B). The connective region is more or less thick but very short and twisted. The anthers are versatile, dorsifixed, slightly bifid and mammillate at the base and the apex (Fig. 6B). The anther walls are very thin, almost restricted to the endothecium. Each theca is 1-1.5 mm long. The position of the stamens with respect to the perianth organs is irregular due to the filaments being disposed in a continuous ring. The gynoecium is 4-4.5 mm long, unicarpellate (Fig. 6C). The carpel is densely covered with papillae, which are particularly well differentiated and become longer on the style (Fig. 6C-E). In addition, the carpel is surrounded by the staminal tube more or less up to the base of the style. The ovary is circular-elliptic in cross section, 1-1.2 mm wide. The style is elongate and somewhat recurved. The stigma is ca. 1 mm long, recurved, flattened and secretory (Fig. 6D, 6F). There is no constant pattern in the position of the carpel relative to the perianth organs. The ovule is anatropous; it does not fill all the locule. The outer and inner integuments are 8-9 and 2-3 cell layers thick, respectively. Apparently, only the outer integument forms a straight narrow conduct at the micropylar region (Fig. 6I).

No vascular supply was observed in the floral subtending bracts. Between 20 and 25 vascular bundles that derive from the pedicel serve the floral base; they form two rings. The inner ring consists of approximately 5-8 vascular bundles and the outer ring 15-17. The floral base is formed mainly by parenchyma, which remains uniform up to the base of the carpel (Fig. 6G); then, the staminal tube and the perianth organs separate. The vasculature in the sepals is reduced; normally one vascular bundle is present, composed by a few cells and serving only the basal portion. The mesophyll is only 2-4 cell layers thick. Between five and six vascular bundles serve each petal. They are located mostly towards the abaxial side (Fig. 6H). The vascular tissue that serves the androecium corresponds to the outer ring mentioned above. Towards mid-length of the flower, where the staminal tube becomes independent from the corolla, this ring remains constant. There is one vascular bundle serving each stamen up to the filament tip. Between one and two central vascular bundles, surrounded by an outer ring of 6-8 procambial strands, serve the base of the carpel. Up to the mid-length of the locule, there are one dorsal and two ventral vascular bundles together with 7-8 procambial strands at the periphery (Fig. 6I). Close to the style base there is one dorsal and two ventral vascular bundles together with 4-5 lateral procambial strands. They are also present upwards in the basal region of the stigma, although the ventral bundles could not be observed and only one lateral procambial strand serves each side of the ventral slit (Fig. 6J). At least one dorsal and two lateral vascular bundles extend up to the stigma. The ovule is served by one vascular bundle, which reaches the base of the funicle. Raphide idioblasts are spread in most floral organs, whereas tannins appear unevenly. The former are frequently present throughout the carpel, surrounding the vascular bundles in the floral base and scattered in the ovary. Upwards, near the style basal region, they become particularly large and abundant, grouped in a ring that surrounds the ventral slit; then, their size and frequency decrease, being almost absent in the basal region of the stigma (Fig. 6H-I). Raphide idioblasts are also present in the petals, between the vascular bundles at the basal level, and in the staminal tube, mainly towards mid-length. Additionally, few raphides may be present at the base of the funicle and the mesophyll of the sepals. They are completely absent in the flower subtending bract and the stigma. Tanniferous cells form a continuous layer in the inner integument and are also scattered between the funicle and the integuments (Fig. 6I), in the floral base, the connective region and the stigma.

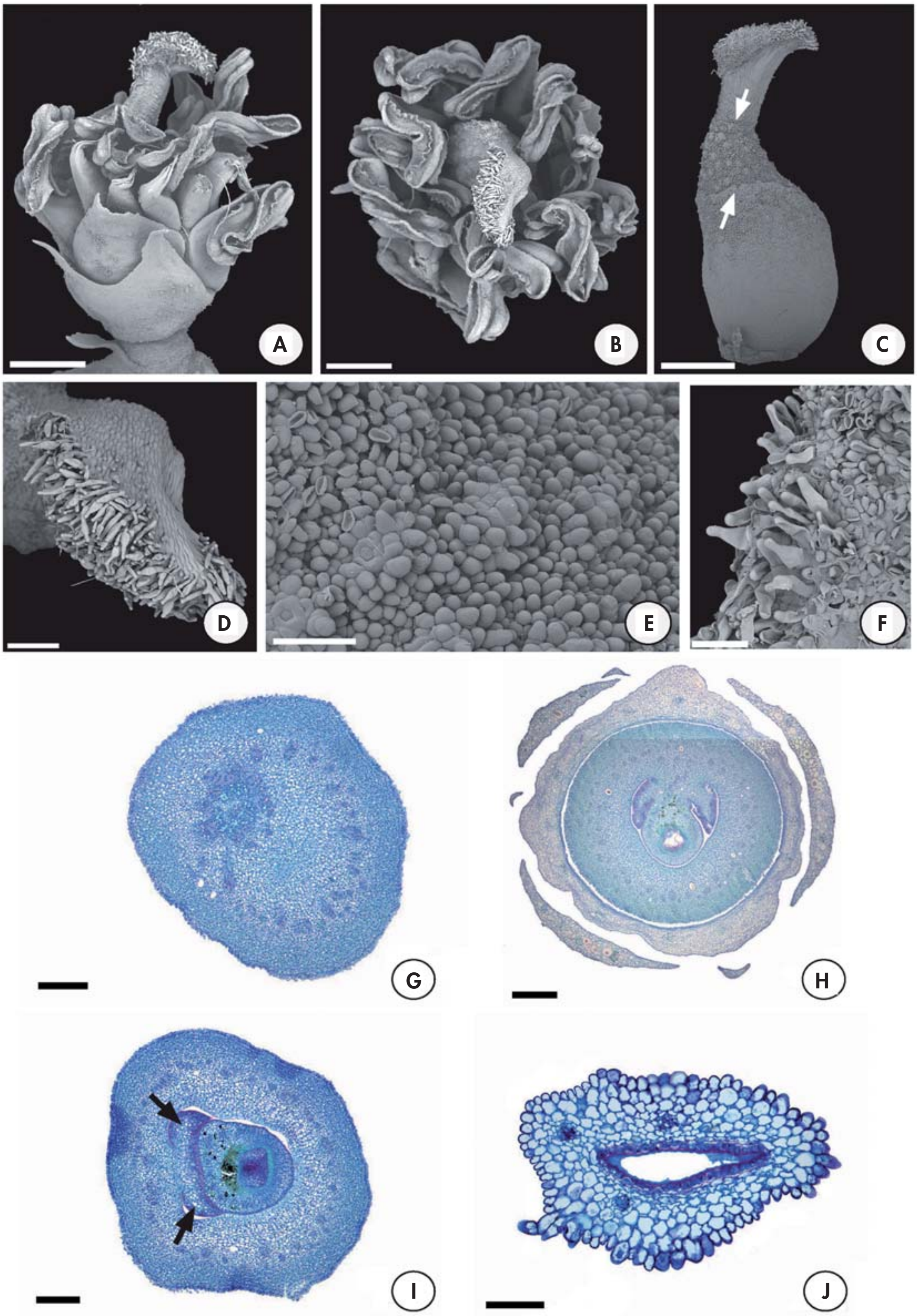

Fig. 6. – *Itaya amicorum* H. E. Moore. **A.** Flower at anthesis (lateral view), scale bar = 850 μm; **B.** Flower at anthesis (upper view), scale bar = 650 μm; **C.** Carpel (lateral view), arrows pointing to an extremely papillate zone of the style, scale bar = 800 μm; **D.** Stigma (upper view), scale bar = 200 μm; **E.** Detail of the epidermis of the style, scale bar = 100 μm; **F.** Detail of the stigmatic papillae, scale bar = 100 μm; **G.** Transverse section of the floral base, scale bar = 200 μm; **H.** Transverse section of the flower, scale bar = 400 μm; **I.** Transverse section of the ovary, arrows pointing to the funicular aril, scale bar = 200 μm; **J.** Transverse section of the style showing papillae, scale bar = 100 μm.

Discussion

Morphology and anatomy

This study shows that *Chelyocarpus*, *Cryosophila* and *Itaya,* and their species are strongly defined according to their floral morphology. UHL (1972a) studied the floral anatomy of three of the four species currently recognized for the genus *Chelyocarpus.* In our study we analyzed material of *C. dianeurus, C. repens* and *C. ulei.* Differences observed in the present study concerning *C. dianeurus* have strong implications for our current knowledge of palm floral structure and evolution. This species was described by UHL (1972a) as the only palm with tetramerous calyx and corolla, which led MOORE (1972) to infer a primitive position of *Chelyocarpus* (together with *Trithrinax* Mart.) within the palm family. Tetramery has been afterwards identified in staminate flowers of *Phytelepheae* (MOORE & UHL, 1982; UHL & DRANSFIELD, 1984). According to our results, the perianth of *C. dianeurus* is mainly trimerous in both the calyx and the corolla; however, in isolated cases we could also observe tetramery, with the fourth perianth organ always slightly reduced. Concerning this species we have identified also other divergences with respect to previous studies; our study shows that flowers in *C. dianeurus* have normally five stamens and unicarpellate gynoecia whereas MOORE (1972) and UHL (1972a), reported 8-9 stamens and 1-3 carpels. In addition, we found campylotropous and not hemianatropous ovules. Flowers of the type material of *C. dianeurus (Archer 2199)* were used by BURRET (1932) to describe the floral organs in the species, and according to UHL (1972a) only few flowers were available for her anatomical study. Based on the study of abundant material from four different collectors, we believe that present study better explains the floral morphology and anatomy of this taxon.

In general terms flowers of *Chelyocarpus* are relatively variable with respect to the number of organs in the floral whorls; which is congruent with the description of most species in the genus (MOORE, 1972; UHL & DRANSFIELD, 1987; KAHN & MEJIA, 1988; HENDERSON, 1995; HENDERSON & al., 1995). Thus, the differences in *C. dianeurus* between the study of UHL (1972a) and our study could be also attributed to the remarkable plasticity of the reproductive morphology of the species. Floral anatomy of *C. ulei,* as described by UHL (1972a), is supported by our results. However, *C. repens* does not clearly display the diagnostic characters that define *Chelyocarpus,* as described by UHL & DRANSFIELD (1987) and DRANSFIELD & al. (2008).

Cryosophila was studied by EVANS (1995), who found that characteristics of the inflorescence are critical for differentiating species within the genus. This is supported by the present study, which is based on almost half of currently recognized species. Hence, the species here analyzed can be well differentiated on the basis of their floral structure. UHL (1972a) studied the floral anatomy of *Cryosophila argentea* Bartlett (currently recognized as *C. stauracantha), C. warscewiczii* and two additional undetermined species in the genus. She did not observe significant differences in the four species and described only the anatomy of *C. argentea*. MORROW (1965) studied exactly the same material as UHL (1972a) for *C. stauracantha (Read 2330B)* and *C. warscewiczii (Bailey 558),* but he made a single description because he considered both species almost identical. In the present analysis, we found several features that permit to clearly differentiate the four species studied. The flowers are almost sessile in *C. guagara*, but they have a short pedicel in the rest of the species. The petals are adnate to the androecium in *C. stauracantha;* whereas they are adnate to the calyx in *C. kalbreyeri* and *C. warscewiczii.* The number of stamens ranges from five to seven in *C. kalbreyeri,* but is constantly six in the rest of the species. The style is longer in *C. guagara* than in the other species. The vascularization is more or less similar in the four species, but there are marked differences in the distribution of both tannin and raphide idioblasts throughout the floral organs.

Although in previous studies (MORROW, 1965; UHL, 1972a) the presence of a flower subtending bract has been reported for *C. stauracantha,* it could not been observed in the present study. UHL (1972a) suggested that the petals were basally adnate to the sepals in *C. stauracantha;* however, the present study, which is congruent with the results by MORROW (1965), shows that the petals are adnate to the androecium at a basal level. The stigma is morphologically well differentiated in the genus, formed by one central grove and two lateral ridges covered with numerous multicellular papillae. Nevertheless, UHL (1972a) could not detect a proper stigma and considered this region as the distal aperture of the carpel, with upper ventral margins bearing short unicellular trichomes. Regarding the ovule, a campylotropous (UHL, 1972a) vs. anatropous (MORROW, 1965) curvature has been suggested for the genus, though it was observed as hemianatropous in all the species of *Cryosophila* of our study.

Cryosophila kalbreyeri was split by EVANS (1995) into two subspecies: *C. kalbreyeri* subsp. *kalbreyeri* and *C. kalbreyeri* subsp. *cogolloi,* mainly based on their disjunct geographical distribution. Additionally, *C. kalbreyeri* subsp. *kalbreyeri* was distinguished from subsp. *cogolloi* by having inflorescences with shorter rachillae and smaller flowers (EVANS, 1995). Based on a preliminary morphological analysis of flowers of *C. kalbreyeri* subsp. *cogolloi,* studied in the Botanical Garden of Medellin (Colombia), and also in a complete morphological and anatomical study of *C. kalbreyeri* subsp. *kalbreyeri,* we could not find significant differences between the two taxa and propose to recognize only one taxon. Moreover, the differences between the two subspecies are restricted to a minor variation in the size of the flowers, which has been found also within the flowers of other species analyzed. This variation can be attributed to the morphological plasticity of the genus, which had already been pointed out by EVANS (1995).

Itaya was also included by Uhl (1972a) in her study of the floral anatomy of the *"Chelyocarpus alliance"*. In a comparison with her results, we found that in the present study the measurements of the flowers of *Itaya amicorum* are always smaller by a few millimetres. Uhl (1972a) found an androecium formed by 19-24 stamens, branched trichomes covering the stigmas and an hemianatropous ovule with an aril partially adnate to the carpel wall. In comparison, 15-17 stamens, simple papillae covering the stigma and an anatropous ovule were found in the present study.

Relationships between Chelyocarpus, Cryosophila *and* Itaya

Chelyocarpus, Cryosophila and *Itaya* share several morphological and anatomical reproductive characters: interfoliar inflorescences; hermaphrodite and solitary flowers; congenitally united sepals; carpels completely ascidiate (but plicate towards the stigmatic region), stigma profusely papillate; funicular aril and raphide idioblasts scattered in the floral base. However, most of these character states are not only relatively common in other members of the tribe *Cryosophileae* but also displayed in other *Coryphoideae* (Uhl & Dransfield, 1987; Dransfield & Uhl, 1998; Dransfield & al., 2008). In this sense, the *"Chelyocarpus alliance",* as defined by Moore (1972) and Uhl (1972a), is not supported by the present study on the floral structure. So far, molecular phylogenetic analyses including some (i.e. Baker & al., 1999; Asmussen & al., 2000; Asmussen & Chase, 2001; Hahn, 2002; Asmussen & al., 2006) or all genera of the tribe (Baker & al., 2009) have not been able to resolve relationships among the genera therein included.

Floral structure diversity in *Chelyocarpus* is rather unexpected for such a small genus and further studies are required to better define the evolutionary meaning of such plasticity. None of the molecular phylogenies so far proposed for the tribe has suggested a polyphyletic origin for the group and its remarkable floral diversity, especially unique in *C. repens,* deserves to be studied in detail in order to explore its evolutionary meaning. Tetramerous calyx and corolla are extremely rare in the palm family and the isolated cases that we observed in *C. dianeurus* may support a basal position of the genus within the tribe. This is also interesting in light of the analysis of Baker & al. (2009) in which a moderately supported sister relationship between *Chelyocarpus* with the Southern Cone genus *Trithrinax* was suggested. Ongoing efforts have been addressed in order to study in detail the floral structure in *Trithrinax* as well as to determine its phylogenetic position within *Cryosophileae*.

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