

Article



http://dx.doi.org/10.11646/phytotaxa.144.2.1

Sabinaria, a new genus of palms (Cryosophileae, Coryphoideae, Arecaceae) from the Colombia-Panama border

GLORIA GALEANO & RODRIGO BERNAL

Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apartado 7495, Bogotá, Colombia. gagaleanog@unal.edu.co, rgbernalg@gmail.com

Abstract

The new palm genus *Sabinaria* (Cryosophileae, Coryphoideae, Arecaceae) and the new species *Sabinaria magnifica* from the Colombia-Panama border are described and illustrated. *Sabinaria* differs from other genera in the tribe in the leaf blades with a single deep, medial, abaxial split, and short abaxial splits in each segment, mostly unisexual flowers with biseriate perianth, calyx connate with the corolla at a single place on its margin, large, tightly appressed, persistent rachis bracts that hide the pistillate flowers, and fruits tightly packed and hidden among leaf bases, often covered by litter.

Resumen

Se describen e ilustran el nuevo género de palmas *Sabinaria* (Cryosophileae, Coryphoideae, Arecaceae) y la nueva especie *Sabinaria magnifica*, de la frontera entre Colombia y Panamá. *Sabinaria* difiere de otros géneros en la tribu por la lámina foliar con una sola división abaxial central y cortas divisiones abaxiales en cada uno de los segmentos, flores principalmente unisexuales con perianto biseriado, cáliz connato con la corola en un solo punto en su margen, grandes brácteas del raquis fuertemente adpresas y persistentes, que ocultan las flores pistiladas, y frutos apiñados, ocultos entre las bases de las hojas y a menudo cubiertos por hojarasca.

Introduction

The Serranía del Darién, the mountain range that forms the border between Colombia and Panama, is one of the most poorly botanised areas in both countries, due to difficult access. Paradoxically, this area is of the utmost relevance, having been the bottleneck for the migration of the land biota between North America and South America after the final closure of the isthmus, now believed to have taken place in the Miocene, 15 Mya (Montes *et al.* 2012), rather than in the Pliocene, as formerly assumed (Taylor 1991). Recent exploration in the northern foothills of the Serranía (Hoyos-Gómez *et al.* 2013) has started to reveal a fascinating flora. Among palms, several interesting findings have been made, including a remarkable fan palm in the tribe Cryosophileae, which represents a hitherto undescribed genus.

Materials and methods

We first studied an incomplete herbarium specimen of the new species kept at JAUM and then collected specimens ourselves at the type locality, including flowers at anthesis and ripe fruits. We compared this material with available descriptions of all coryphoid genera (Dransfield *et al.* 2008) and with herbarium specimens and living plants of most genera in the tribe Cryosophileae.

Results

Sabinaria R. Bernal & Galeano gen. nov.

Diagnosis. Solitary, unarmed, monoecious palm with induplicately palmate leaves, the petiole basally split, the blade silvery whitish below, medially divided almost to the base by an abaxial split, the two halves lacking any further deep abaxial splits, but with a short abaxial split present at the apex of each leaf segment. Inflorescence interfoliar, branched to 1–2 orders, each branch subtended by a large, conspicuous bract, with mostly unisexual flowers, staminate ones exposed beyond the bracts, with 20–23 stamens connate by their broadened filament bases, the pistillate flowers restricted to the lower portion of the proximal rachillae and hidden by large persistent rachis bracts, with a single carpel and staminodes with no anthers, a few pistillate flowers sometimes bearing 1–2 anthers. Fruit uniseminate, with eccentric, inconspicuous, stigmatic remain. Endosperm homogeneous, embryo basal. Seedling with undivided eophyll. Differs from other Cryosophileae in the lack of deep abaxial splits besides the medial one, the unisexual flowers, the large, persistent rachis bracts that hide the pistillate flowers, and the tightly packed fruits hidden among the leaf bases. Most closely resembles *Itaya*, from which it differs in the unisexual flowers with the sepals connate with the petals at one single place, the large rachis bracts that hide the basal portion of the rachillae, and the tightly packed fruits.

Description. Medium-sized, solitary, unarmed, pleonanthic, monoecious arborescent palm. Stem erect, with inconspicuous leaf scars. Leaves numerous, induplicate, palmate; sheath medially split below the petiole, the margins without fibres; petiole slender, long, biconvex, with sharp margins; adaxial hastula well developed, truncate, abaxial hastula a low rim; blade medially divided almost to base by an abaxial split into two symmetrical or slightly asymmetrical halves, these divided to ca. 1/10 their length into single fold segments that are slightly bifid at apex; segments with inconspicuous cross-veins, the undersurface silvery-whitish. Inflorescence interfoliar, branched to one order, basal rachillae sometimes with a few second-order rachillae; prophyll bicarinate; peduncular bracts at least 5, large and inflated; rachis bracts similar to the peduncular bracts, persistent and tightly appressed to the proximal portion of the rachilla and hiding the pistillate flowers; rachillae straight, cylindrical. Flowers borne on a short pedicel and subtended by a small and narrow triangular bract, mostly unisexual, pistillate ones on the proximal portion of proximal rachillae, the remaining staminate, a few pistillate flowers sometimes bearing 1-2 anthers. Staminate flowers with three connate sepals, these fused with the corolla at a single place on the margin; petals three, connate into a tubular corolla, sometimes two of the petals completely free to base; stamens 20-23, exserted at anthesis, the filaments connate by their fleshy bases into several irregular groups of 1–6, these in turn connate further below with each other and basally adnate with the corolla, filiform at the apex; anthers oblong, dorsifixed, versatile, bifid at base and apex. Pistillate flowers similar to the staminate ones; staminodes similar to the stamens but lacking the anthers and the thin portion of the filament; gynoecium unicarpellate, eccentrically ovoid, narrowed to a slender curved style and an oblique papillose stigma. Fruit obovoid to turbinate or subglobose, uniseminate, with eccentric inconspicuous stigmatic remain; epicarp minutely tuberculate with sparse perforations, smooth with the naked eye; mesocarp thick, endocarp not differentiated. Seed ovoid to subglobose, with homogeneous endosperm; embryo basal. Seedling with lanceolate eophylls, whitish below.

Type species: Sabinaria magnifica Galeano & R. Bernal

Etymology:—Named after our daughter Sabina Bernal Galeano, with the suffix *-ria* arbitrarily chosen, in accordance with Art. 20 of the International Code of Nomenclature (McNeill et al. 2012).

Sabinaria magnifica Galeano & R. Bernal sp. nov.

Diagnosis. Stem solitary, 1–6 m tall, 9–12 cm diam.; leaves 20–35, induplicately palmate, with a long, basally cleft petiole; blade circular, sometimes inequilateral at base, 1.4–1.6 m diam., divided almost to the base into two large halves, these not divided again, each with 36–42 single-fold segments. Inflorescence interfoliar; peduncle at least 30 cm long; rachis 42–62 cm, with 32–40 rachillae up to 20 cm long, the basal portion of proximal rachillae bearing only pistillate flowers and deeply hidden by large rachis bracts, the distal portion and distal rachillae with staminate flowers. Staminate flowers 4–5 mm long, with 20–23 stamens. Pistillate flowers 7–11 mm long, with 14–19 staminodes that bear no anthers. Fruits closely packed, 3.6–4.4 cm long., 3–3.6 cm diam., with inconspicuous,

eccentrically apical stigmatic residue; seeds oblong-ovoid, 2.4–2.7 cm long, 2.2–2.3 cm wide, with ellipsoid hilum and subbasal ascending raphe branches; endosperm homogeneous; embryo basal (Figs. 1–14).

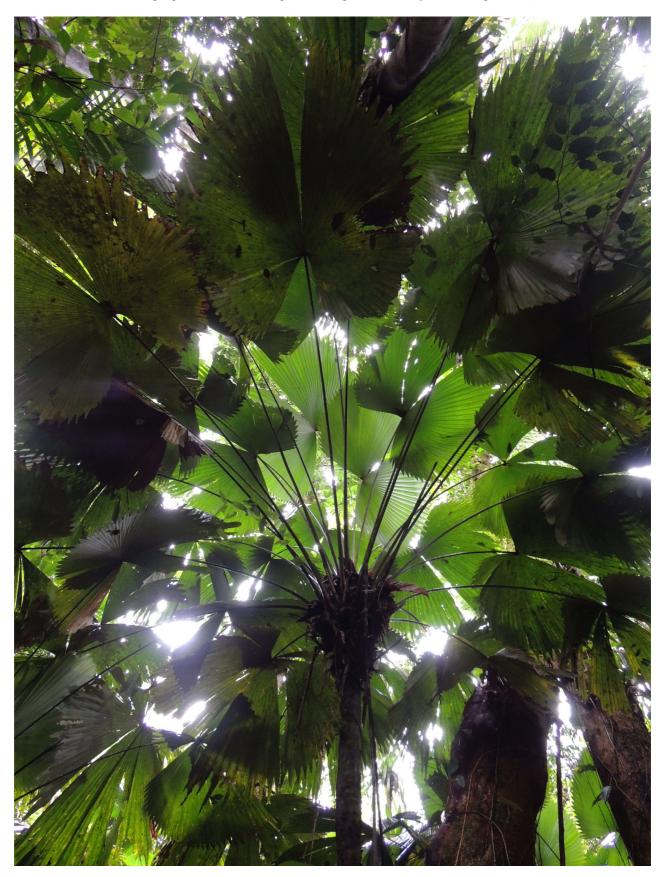


FIGURE 1. Habit of Sabinaria magnifica near Capurganá, Colombia.



FIGURE 2. Stem of Sabinaria magnifica.



FIGURE 3. Leaf base of *Sabinaria magnifica*.



FIGURE 4. A leaf of *Sabinaria magnifica* held by Angie Henao.



FIGURE 5. Leaf undersurface of Sabinaria magnifica.



FIGURE 6. Adaxial hastula of Sabinaria magnifica.

Solitary, unarmed palm. Stem 1–6 m tall, 9–12 cm diam., light brown, smooth, with inconspicuous leaf scars. Leaves 20–35, induplicately palmate; sheath + petiole ca. 319 cm long, sheath basally cleft for ca. 43 cm, brown-woolly internally; petiole biconvex, rhomboid in transverse section, the margins sharp toward base, green, covered below with a deciduous scaly and light brown tomentum, 2 cm wide at the middle; adaxial hastula tubular, truncate, ca. 1 cm long; abaxial hastula forming a low rim; blade flat, rigid, sometimes inequilateral at base, 1.4–1.6 m diam., divided almost to the base into two large halves, these divided to ca. 1/10 their length into single fold segments, each with 36–42 single-fold segments, these free at the apex for 5–9 cm; basal segments 34-50 cm long, 1.4-1.7 cm wide, bifid at the apex for ca. 5 mm; distal segments 104 cm long, 4.2 cm wide, the free portion with a shoulder on each side just above the adaxial split, bifid at the apex for ca. 5 mm, the two tips rounded and slightly unequal, glossy above, with numerous cross-veins of two sizes, silvery-whitish below. Inflorescences and infructescences interfoliar, basally erect, the distal half arching laterally, with branches of first order or sometimes the basal branches with a few rachillae; peduncle at least 30 cm long, 1.5 cm wide at apex, subcylindrical; prophyll deeply buried among the leaves, at least 31 cm long, 3.5 cm wide, slightly two-keeled, acute and abaxially split at the fibrous apex, yellowish when fresh, covered, especially toward base, with a light brown woolly tomentum; peduncular bracts at least five, ca. 26-27 cm long, 6 cm wide, chartaceous, persistent, acute at apex, covered with light brown, woolly, more or less persistent tomentum; rachis 46–62 cm long, subcylindrical; rachillae 32–40, each raquilla subtended by a large, persistent, chartaceous, cream-coloured bract with indumentum similar to that of the peduncular bracts, progressively smaller toward the apex, fraying into fibres in fruit; basal bracts 20–22 cm long, ca. 7 cm wide, middle bracts 13-16 cm long, 5-6 cm wide, apical bracts 4-6 cm long, 0.5-1.5 cm wide; rachillae of the proximal one half with both staminate and pistillate flowers, those of the distal half bearing only staminate



FIGURE 7. Apex of middle leaf segments of Sabinaria magnifica.

flowers; basal rachillae 18–20 cm long, the proximal 1/3 thick, 5–7 mm wide, adaxially flattened and without flowers, abaxially with pistillate flowers separated from each other 1–2 mm, mostly with no anthers and only a few of them with 1-2 anthers, the distal 2/3 of proximal rachillae almost cylindrical, ca. 3 mm diam., with staminate flowers spirally arranged all around the rachilla, separated from each other 1-3 mm; middle rachillae 12–14 cm long, the proximal 2 cm similar to the corresponding area of the basal rachillae, otherwise as described for the staminate portion; apical rachillae 3-4 cm long, bearing only staminate flowers and appearing like the staminate portion of basal rachillae. Flowers whitish when fresh, borne on a short pedicel and subtended by a small, narrow triangular bract. Staminate flowers 4-5 mm long, 3-3.5 mm wide, oblong; sepals three, 1.3–2 mm long, connate into a 0.8–1 mm long cupule with three ovate long-acuminate lobes ca. 1 mm wide, fused with the corolla at a single place on the margin; corolla tubular, oblong, 2.5–3.2 mm long, the petals connate for ca. 34 their length, with three rounded to triangular lobes ca. 1 mm wide, sometimes two of the petals completely free to base; stamens 20–23, exserted ca. 1 mm beyond the corolla; filaments connate by their fleshy bases into several irregular groups of 1-6, these in turn connate farther below with each other and basally adnate with the corolla, filiform at the apex, the free portion ca. 1 mm long, tapering to a filamentous apex ca. 0.5 mm long; anthers ca. 1 mm long, 0.2 mm wide, oblong, basally bifid, shortly bifid to rounded apically; pistillode absent. Pistillate flowers 7-11 mm long, ca. 2.5 mm wide, mostly similar to the staminate ones; sepals three, 1.3–2 mm long, connate in a 0.8–1 mm cupule with three ovate long acuminate lobes, fused with the corolla at a single place on the margin; corolla tubular, oblong, 2.5–3.5 mm long, the petals connate for ca. 3/4 their length, with three rounded to triangular lobes, sometimes two of the petals completely free to base; staminodes 14-19, only slightly exserted from the corolla, filaments basally connate into a fleshy tube adnate to the corolla base, the free portion fleshy and subulate, ca. 1.5 mm long, sometimes with an apical 0.5 mm filamentous apex; anthers oblong, ca. 1 mm long, similar to those of the staminate flowers; gynoecium unicarpellate, 4–5 mm long, ovoid at the base, tapering to a slender, flattened, curved style and a papillose stigma ca. 2 mm long; ovule hemianatropous, laterally attached, bearing a large oblique

aril. *Fruits* closely packed along the basal portion of the proximal, thickened rachilla stumps, these up to 7 cm long, 7–8 mm thick, individual fruits obovoid to turbinate or subglobose, green when immature, yellowish green when nearly mature, finally turning black, 3.6–4.4 cm long., 3–3.6 cm diam., with inconspicuous, eccentrically apical stigmatic residue; epicarp minutely tuberculate with sparse perforations, smooth with the naked eye; seeds oblong-ovoid, 2.4–2.7 cm long, 2.2–2.3 cm wide, with ellipsoid hilum and subbasal ascending raphe branches; endosperm homogeneous; embryo basal. *Seedling* with lanceolate eophyll, whitish below, ca. 30 cm long, 4–5 cm wide.



FIGURE 8. Inflorescence of Sabinaria magnifica.



FIGURE 9. Detail of staminate flowers of *Sabinaria magnifica*. Photo by Saúl Hoyos.

FIGURE 10. Proximal rachilla of *Sabinaria magnifica* showing staminate flowers (above) and pistillate flowers (below).

Type:—COLOMBIA. Chocó: Municipio de Acandí, Quebrada El Brillante, 8 km southwest of Capurganá, 130 m elev., 8°34'59.4" N, 77°23'09.9" W, 29 August 2013, *G. Galeano, R. Bernal, S. Hoyos & N. Echavarría* 9062 (holotype: COL; isotypes: CHOCO, FMB, JAUM, K).

Etymology:—The Latin epithet *magnifica* refers to the strikingly beautiful aspect of the palm.

Habitat:—Known only from a small area at the base of the Serranía del Darién (Fig. 15), in the Department of Chocó, northwestern Colombia, between 100 and 250 m elevation. The area lay less than one kilometre away from the Colombia-Panama border, and the species most probably occurs also in that country. The area is covered by premontane moist forest-warm transition (BMh-PM) in Holdridge's life zone system (IGAC 1977), with an average annual rainfall of ca. 3000 mm.



FIGURE 11. Details of flowers and fruits of *Sabinaria magnifica*. A, portion of a basal rachilla at the transition between pistillate and staminate flowers (bar = 7 mm); B, staminate flower (bar = 2 mm); C, staminate flower seen from above (bar = 2 mm); D, detail of filaments and anther of staminate flower (bar = 1 mm); E, detail of sepals fusing with petals (bar = 2 mm); F, detail of two free petals in a staminate flower (bar = 2 mm); G, pistillate flower with two anthers (bar = 2 mm); H, pistillate flower (bar = 2 mm); I, detail of staminodial tube (bar = 1 mm); J, gynoecium (bar = 1 mm); K, fruit (bar = 20 mm); L, M, seed (bar = 10 mm); N, seed in vertical section (bar = 10 mm). Drawn by Marcela Morales Sánchez.



FIGURE 12. Infructescences of Sabinaria magnifica hidden among leaf bases. Photo by Saúl Hoyos.



FIGURE 13. Fruits of Sabinaria magnifica.



FIGURE 14. Seedlings and a juvenile of *Sabinaria magnifica*. Photo by Saúl Hoyos.



FIGURE 15. Google Earth image showing the type locality of *Sabinaria magnifica* (placemark).

Common name: *girasol* (Spanish, =sunflower)

Uses: The leaves are used casually as umbrellas.

Additional specimens:—COLOMBIA. Chocó: Municipio Acandí, corregimiento de Capurganá, vereda El Brillante, one hour walk from Río Muerto to Capurganá, 100 m elev., 8°34'59.4" N, 77°23'09.9" W, 26 March 2013, *S. Hoyos, N. López, P. Trujillo & N. Echavarría 2197* (JAUM)

Conservation status:—There is too little information available on the distribution of Sabinaria magnifica, and a assessment of its conservation status according to IUCN parameters is therefore not possible at the present time. The area where the palm grows has extensive forests for many kilometres on both sides of the Colombia-Panama border, and the palm was locally abundant, with hundreds of adults and plants in all size categories. No major imminent threats appear to be operating in the area, although selective logging does take place, and the zone is dangerously close to the Urabá region, one of the most severely deforested areas of Colombia. Because of this, the protection of this area should be given a high priority, considering its pivotal biogeographic relevance. The establishment of public and private protected areas in this zone should be strongly encouraged.

Key to the genera of Cryosophileae

3. Flowers unisexual; pistillate flowers restricted to the lower portion of the proximal rachillae, tightly hidden by the large rachis bracts; calyx connate with the corolla at one place on its margin; two of the petals sometimes completely free; fruits closely packed and hidden among the leaf bases; leaves with a deep, medial abaxial split and no further 3. Flowers hermaphroditic throughout the inflorescence or at least along the proximal portion of most rachillae, and then the distal flowers staminate; flowers not hidden by rachis bracts; calyx and corolla free from each other; petals always connate; fruits neither closely packed nor hidden among the leaf bases; leaves with many deep splits in addi-4. Flowers with a long, stalk-like base; proximal flowers on each rachilla hermaphroditic, distal flowers staminate; sta-4. Flowers lacking a stalk-like base, all hermaphroditic; stamens 18–24; leaf divided almost to base into 10–16 similar Stems with distinctive root spines, these often branched; stamens 6, the filaments connate in a ring; leaf sheath

Discussion

There is no doubt that the new species belongs to the tribe Cryosophileae, on account of its leaves with a central abaxial split, and flowers with a single carpel. The latter character, as well as the numerous stamens, are reminiscent of the Amazonian *Itaya* H.E.Moore (1972: 85), from which it differs in the unisexual flowers, the pistillate ones restricted to the base of the proximal rachillae, and tightly hidden by the large persistent rachis bracts, whereas in *Itaya* the rachis bracts are deciduous, and all flowers, which are hermaphroditic, are exposed. This is reflected in the infructescence, which in *Itaya* has fruits throughout most of the rachillae (see Galeano & Bernal 2010: fig. p. 113), whereas in *Sabinaria* fruits are restricted to the base of the lowermost rachillae, and are thus hidden among the litter-trapping leaf bases (Fig. 12). In fact, seedlings are common on the crown of most individuals.

The other genus in the Cryosophileae with biseriate perianth and unicarpellate gynoecium is the Mesoamerican *Schippia* Burret (1933: 867), from Guatemala and Belize, which has hermaphroditic proximal flowers and staminate distal ones, and six stamens. The only species in this genus, *Schippia concolor* Burret (1933: 868), has small rachis bracts that do not hide the rachillae, flowers with a long stalk-like base, and leaves deeply split into numerous, narrow, single-fold segments. As in *Itaya*, infructescences of *Schippia* have fruits in most of their rachillae (see Dransfield *et al.* 2008, fig. p. 221), and the fruits are clearly exposed.

Leaf structure of *Sabinaria* is also unique among the Cryosophileae, as they have only one deep medial abaxial split (Figs. 4–5), and lack any of the deep secondary splits that are common to the tribe. Although some splits are often found in older leaves, these are irregularly located in either of the leaf halves, and are obviously caused by falling branches or other external factors rather than by leaf ontogeny. Instead of deep splits, each segment has a short, abaxial split ca. 5 mm long (Fig. 7).

Two unusual characters are found in the perianth of *Sabinaria*. First, the calyx is fused to the corolla at one place on its margin (Fig. 11, E), so that calyx and corolla appear like a single tissue arranged in two cycles. This character has not been recorded in the related *Chelyocarpus*, *Cryosophila* or *Itaya* (Castaño et al. 2011), nor in any other genus in the family (Dransfield et al. 2008). The ontogeny of this adnation deserves a detailed study, particularly because, unlike *Itaya*, sepals and petals in *Sabinaria* are similarly thick. The second unusual character of *Sabinaria* is the occasional lack of fusion between two of the petals, which results in an open tube (Fig. 11, F). The combination of these two unusual characters results in a perianth that is topologically uniseriate, although architecturally biseriate. This unusual perianth is particularly remarkable, as the Cryosophileae include some genera with distinctively deviating perianth, like *Chelyocarpus*, which has sepals and petals similar to each other, or *Zombia*, *Coccothrinax*, *Hemithrinax*, *Leucothrinax*, and *Thrinax*, which have perianth in a single, six-toothed whorl (Dransfield et al. 2008). The perianth of *Sabinaria* might represent an intermediate condition between the uniseriate and the biseriate perianth types found within the tribe.

The pistillate flowers of *Sabinaria*, deeply hidden among the tight rachis bracts, restrict access to large visitors like bees or large beetles. In the only inflorescence that we found in anthesis, there were trigonine bees visiting the exposed staminate flowers, whereas only small mystropine beetles were found among the pistillate flowers upon removing the bract.

The finding of *Sabinaria* in the contact zone between Mesoamerica and South America is particularly interesting, as this area is completely isolated from the ranges of both *Itaya* and *Schippia*, the two other Cryosophileae with unicarpellate gynoecium and biseriate perianth. *Itaya*, resolved as sister to all other members of the tribe (Baker *et al.* 2009) or sister to all other members except for *Chelyocarpus* (Roncal *et al.*

2008), is found on the other side of the Andes, 1300 km away in northwestern Amazonia. *Shippia*, on the other hand, is weakly supported either as sister to *Cryosophila* (Roncal *et al.* 2008), or to a clade comprising *Zombia*, *Coccothrinax*, *Hemithrinax*, *Leucothrinax* and *Thrinax* (Baker *et al.* 2009). The nearest population of *Schippia* is located ca. 1500 km northwest of *Sabinaria*. As it has been hypothesised that the unicarpellate condition evolved independently in *Itaya* and *Schippia* (Rudall et al. 2011), the discovery of a third unicarpellate member in the group, located in an area intermediate between them, may help clarify relationships in the tribe, particularly the uncertain position of *Schippia*.

Conclusions

The finding of this new genus adds one more element to the intriguingly disjunct distribution of most genera of the Cryosophileae and to their particular flower structure. Molecular, anatomical, and developmental studies of *Sabinaria*, as well as comparative studies of reproductive biology among members of the tribe may throw light on the evolution and dispersal of New World members of the Coryphoideae.

Acknowledgements

We are deeply grateful to Saúl Hoyos and Norman Echavarría, who first brought this species to our attention and accompanied us into the field, and to Álvaro Cogollo (JAUM), who sent us the original specimen on loan. Further field assistance was provided by Orlando Martínez, Angie Henao, Germán Henao, and Cristina Lopera. Marcela Morales Sánchez prepared the line drawing and Saúl Hoyos took some of the photographs. Fred W. Stauffer, William Baker, and two anonymous reviewers made valuable comments on the text.

References

- Baker, W.J., Savolainen, V., Asmussen-Lange, C.B., Chase, M.W., Dransfield, J., Forest, F., Harley, M.M., Uhl, N.W. & Wilkinson, M. (2009) Complete generic-level phylogenetic analyses of palms (Arecaceae) with comparisons of supertree and supermatrix approaches. *Systematic Biology* 58: 240–256. http://dx.doi.org/10.1093/sysbio/syp021
- Burret, M. (1933) *Schippia*, eine neue Palmengattung aus Brit. Honduras. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem* 11: 867–869. http://dx.doi.org/10.2307/3994638
- Castaño, F., Crèvecoeur, M., Pintaud, J.C. & Stauffer, F.W. (2011) Floral structure in the neotropical palms *Chelyocarpus* Dammer, *Cryosophila* Blume and *Itaya* H. E. Moore (Arecaceae). *Candollea* 66: 65–79.
- Dransfield, J., Uhl, N.W., Asmussen, C.B., Baker, W.J., Harley, M.M. & Lewis, C.E. (2008) *Genera Palmarum. The Evolution and Classification of Palms*. Kew Publishing, Royal Botanic Gardens, Kew in association with the International Palm Society and the L.H. Bailey Hortorium, Cornell University, 732 pp.
- Galeano, G. & Bernal, R. (2010) *Palmas de Colombia. Guía de Campo*. Editorial Universidad Nacional de Colombia, Bogotá, 688 pp.
- Hoyos-Gómez, S.E., Idárraga, A., Betancur, J. & Upegui, A. (2013) *Costa y Bosque-Plantas del Chocó Darién-Caribe*. Corporación Fragmento, Medellín, 187 pp.
- IGAC (1977) Zonas de vida o formaciones vegetales de Colombia. Instituto Geográfico Agustín Codazzi, Bogotá, 238 pp.
- Mcneill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K. Prado, J., Prud'homme Van Reine, W.F. Smith, G.F., Wiersema, J.H. & Turland, N.J. (2012) International Code of Nomenclature for algae, fungi, and plants (Melbourne Code) adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. Regnum Vegetabile 154. Koeltz Scientific Books, Koenigstein, Germany.
- Montes, C., Cardona, A., McFadden, R., Morón, S.E., Silva, C.A., Restrepo-Moreno, S., Ramírez, D.A., Hoyos, N., Farris, D., Bayona, G.A., Jaramillo, C.A., Valencia, V., Bryan, J. & Flores, J.A. (2012) Evidence for middle Eocene

and younger land emergence in Central Panama: implications for Isthmus closure. *Geological Society of America Bulletin* 124(5-6): 780.

http://dx.doi.org/10.1130/B30528.1

- Moore, H.E. (1972) Chelyocarpus and its allies Crysophila and Itaya (Palmae). Principes 16: 67-88.
- Roncal, J., Zona, S. & Lewis, C.E. (2008) Molecular phylogenetic studies of Caribbean palms (Arecaceae) and their relationships to biogeography and conservation. *Botanical Review* 74: 78–102. http://dx.doi.org/10.1007/s12229-008-9005-9
- Rudall, P., Ryder, R.A. & Baker, W.J. (2011) Comparative gynoecium structure and multiple origins of apocarpy in Coryphoid palms (Arecaceae). *International Journal of Plant Science* 172: 674–690. http://dx.doi.org/10.1086/659459
- Taylor, D.W. (1991) Paleobiogeographic relationships of Andean angiosperms of Cretaceous to Pliocene age. *Palaeogeography, Palaeoclimatology, Palaeoecology* 88: 69–84. http://dx.doi.org/10.1016/0031-0182(91)90015-J