

# A NEW FOSSIL SPECIES OF *COLPOTHRINAX* (ARECACEAE) FROM MID-TERTIARY MEXICAN AMBER

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## ABSTRACT

A fossil palm flower in Late Oligocene to Early Miocene amber deposits of Chiapas, Mexico, is described as the new species *Colpotherinax chiapensis*. The flower is perfect and complete, with a calyx tube bearing 3 small, triangular lobes, and 3 ovate-lanceolate, spreading or recurved petals that are connate basally into a shallow tube. The 6 stamens are attached at the mouth of the corolla tube; their slender, subulate filaments are widened basally, slightly connate, and bear large, versatile, laterally dehiscent anthers. The ovary, loosely enclosed in the corolla tube, is composed of 3 closely adjacent, separate carpels. The united style is three-grooved, well-exserted, and slightly shorter than the filaments, with an acute tip and smooth, non-papillate stigma. The 3 modern species of *Colpotherinax* differ from the fossil in having the filaments shorter, more widely tapering, and united basally to form a better developed staminal tube.

## RESUMEN

Una flor fósil de palmera de depósitos de ámbar del Oligoceno tardío al Mioceno temprano de Chiapas, México, se describe como la nueva especie *Colpotherinax chiapensis*. La flor es perfecta y completa, con tubo del cáliz que lleva tres lóbulos triangulares pequeños y 3 pétalos ovado-lanceolados, extendidos o recurvados que están connados basalmente en un tubo poco profundo. Los 6 estambres están adheridos a la boca del tubo de la corola; sus filamentos delgados, subulados, están extendidos basalmente y ligeramente connados, y llevan unas anteras grandes, versátiles, dehiscentes lateralmente. El ovario, incluido en el tubo de la corola, está compuesto de 3 carpelos independientes muy próximos entre sí. El estilo unido con tres surcos está bien exerto y es ligeramente más corto que los filamentos, con un extremo agudo y estigma liso no papiloso. Las 3 especies modernas de *Colpotherinax* difieren de las fósiles por tener los filamentos más cortos, menos afilados, y unidos basalmente para formar un tubo estaminal mejor desarrollado.

## INTRODUCTION

A new fossil species of palms, described here as *Colpotherinax chiapensis*, is represented by 4 flowers embedded in Mid-Tertiary amber from a mine in the state of Chiapas, Mexico. The floral morphology of the species is similar in general features to the modern genus *Colpotherinax*, whose three species are found in Cuba and Central America, from Guatemala to Panama (Evans 2001). The pistil, in particular, is like that of this genus, with 3 separate but apposite carpels and an elongate style, which appears to be fused and grooved rather than composed of 3 separate units. The style tip is tapering and lacks an enlarged stigma. The basally connate petals, forming a short tube surrounding the ovary, and the almost completely united sepals with short, triangular lobes, provide further similarities. Principal differences are in the androecium of *C. chiapensis*, in which the longer, linear-subulate filaments are widened only near the base and slightly united into a staminal tube. The anthers are large, dorsifixed, and latrorse in dehiscence, as described for *Colpotherinax* (Dransfield et al. 2008). The probable age of the fossils, 22.5–26 Ma, is commensurate with an estimated mean stem age for the genus of 28.56 Ma (Bacon et al. 2012). The species' Mexican origin gives evidence for an evolutionary radiation of *Colpotherinax* in the Caribbean region, as suggested by Bacon et al. (op. cit.) for *Copernicia* and certain other genera of tribe Trachycarpeae.

## MATERIALS AND METHODS

The specimen originated from an amber mine in the northern mountain ranges (Chiapas Highlands) of the Simojovel area in Chiapas, Mexico. Maps of the area are given in Poinar (1992). Amber from Chiapas, which was produced by *Hymenaea mexicana* (Poinar & Brown 2002), occurs in lignitic beds among sequences of

primarily marine calcareous sandstones and silts. The particular amber under study is associated with the Balumtun Sandstone of Early Miocene and the La Quinta Formation of Late Oligocene, with radiometric ages from 22.5–26 Ma (Berggren & Van Couvering 1974). The amber is secondarily deposited in these marine formations and may be somewhat older than the above dates. The original vegetation was probably a wet to moist tropical to subtropical forest.

#### DESCRIPTION

***Colpothrinax chiapensis*** K.L. Chambers, Poinar, & A.E. Brown, sp. nov. (Figs. 1–4). TYPE: MEXICO. CHIAPAS: amber mine in Chiapas Highlands, Simojovel area, 2011, *unknown amber miner s.n.* (HOLOTYPE: see Fig. 1, catalogue number Sd-9-181A, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.; PARATYPES: see Fig. 2, catalogue number Sd-9-181B, Figs. 3–4, catalogue number Sd-9-181C, similarly deposited at Oregon State University).

Flowers hermaphrodite, ca. 6 mm in diameter when petals spread, calyx cupulate, glabrous, 0.4 mm (Fig. 4), sepals united, with 3 free, triangular, 0.4–1.1 mm lobes, petals 3, glabrous, ovate-lanceolate, ca. 3.3 mm, spreading or reflexed, with numerous parallel veins and no raised mid-nerve adaxially (Fig. 1), shallowly grooved abaxially (Fig. 2), tip boat-shaped (Fig. 1), stamens 6, exerted, glabrous, filaments subulate, 1.0–1.2 mm, widened at base, the connate portion short (Fig. 3), attached at the mouth of the corolla tube, anthers ca. 2.3 mm, dorsifixed, locules 4, dehiscence latrorse (Fig. 2), gynoecium glabrous, 3-carpellate, ovary loosely enclosed in corolla tube (Fig. 1), carpels free, apposite, style appearing united, ca. 1.2 mm, 3-grooved, tip acute, stigma not enlarged (Fig. 2).

*Etymology.*—from the fossils' origin in Chiapas, Mexico.

#### DISCUSSION

The fossils differ from other genera of Trachycarpeae in such features as the enlarged anthers, persistent petals (cf. *Pritchardia*), cupulate calyx (cf. *Brahea*, *Acoelorrhaphe*), long filaments (cf. *Copernicia*), and presence of a staminal tube (cf. *Serenoa*) (see Dransfield et al. 2008, pp. 272–285, for illustrations). The orientation of the flowers does not allow measurement of the depth of the corolla tube. In other respects, the fossils can be matched with excellent descriptions and floral illustrations of *Colpothrinax* in Uhl and Dransfield (1987), Dransfield and Uhl (1998), Dransfield et al. (2008), and Evans (2001). Whether the proposed new species falls within the full morphological variation of any of the extant taxa is uncertain, but we believe that the androecium, in particular, sets it apart from *Colpothrinax wrightii* (Bailey 1940) and *C. cookii* (Read 1969), and the large petals and long, subulate, scarcely united filaments are adequately distinct from *C. aphanopetala* (Evans 2001). The published treatments of the 3 modern species include much information about stem and leaf morphology, inflorescence, pollen (esp. Dransfield et al. 1990), habitats, and associated vegetation. Vegetative and inflorescence morphology is, of course, unknown for *C. chiapensis*, as is the pollen; however, the species' preservation in resin from *Hymenaea mexicana* is evidence of moist tropical or subtropical forest vegetation as the preferred habitat.

The phylogenetic relationships of the genera of tribe Trachycarpeae (Dransfield et al. 2008 [formerly Livistoneae, Dransfield et al. 2005]) have begun to be clarified by recent molecular studies utilizing nuclear and plastid DNA (Asmussen et al. 2006; Roncal et al. 2008; Baker et al. 2009; Bacon et al. 2012). In the first 3 papers cited, *Colpothrinax* is in a clade that includes several other genera with which it had previously been associated, including *Pritchardia*, *Washingtonia*, *Serenoa*, *Acoelorrhaphe*, *Brahea*, *Livistona*, and *Chamaerops*. However, in the report by Bacon et al. (2012), involving *matK*, *ndhF*, *trnD-trnT* and 3 nuclear loci, *Colpothrinax* is alone in a highly supported clade that is sister to 2 large clades containing, *inter alia*, *Brahea*, *Chamaerops*, *Serenoa*, *Acoelorrhaphe*, and *Livistona*, and is well separated from *Washingtonia* and *Pritchardia*. The subtribal classification of Trachycarpeae is presently in flux, it appears, as perhaps is true also in other large families now under intensive molecular phylogenetic study.

The new intrafamilial relationships of palms revealed by molecular research have been used to investigate additional questions beyond taxonomy alone. These include the origin and global diversification of tropical rain forests (Couvreur et al. 2011) and the effects of Miocene dispersal on island radiations in tribe Trachycar-

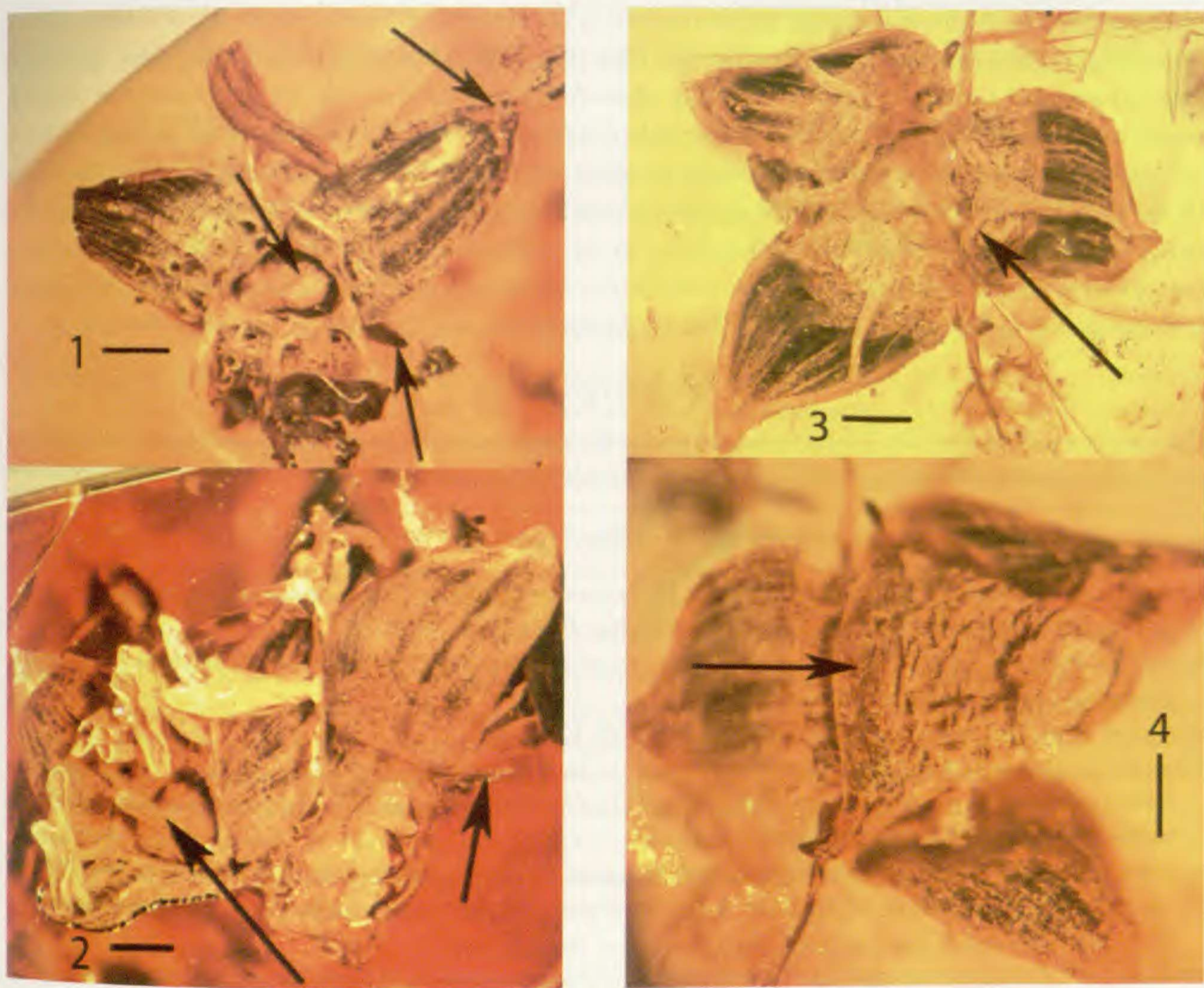


FIG. 1. *Colpothrinax chiapensis*, holotype. Apical view, with single remaining anther not yet dehiscent. Note parallel-veined petal with boat-shaped tip (upper arrow), gap between carpels (middle arrow), and sepal lobe (lower arrow). A bit of debris in the amber partially obscures the lower petal. Bar = 1.0 mm.

FIG. 2. *Colpothrinax chiapensis*, first paratype. Note laterally dehiscent anthers, grooved style (long arrow), and lobe of united calyx (short arrow). Flower at right has petal cupped upward and anther not yet dehiscent. Extraneous egg-like mass rests on floral pedicel. Bar = 1.0 mm.

FIG. 3. *Colpothrinax chiapensis*, second paratype. Apical view, showing slight basal fusion between adjacent filaments (arrow). Bar = 0.9 mm.

FIG. 4. *Colpothrinax chiapensis*, second paratype. Lateral view, showing lobed calyx cup (arrow) and stout pedicel. Bar = 0.47 mm.

peae (Bacon et al. 2012). In the first paper, a complete phylogenetic analysis of genera in family Arecaceae derived by Baker et al. (2009) is the basis for a plot of the number of palm lineages, from 120 Ma (Lower Cretaceous) to 26 Ma (Late Oligocene), showing a linear increase with time. Throughout this period and up to the present, tropical rain forests have been the predominant habitat for palms, but exceptions exist for certain “not tropical rain forest” groups (*Washingtonia* and *Serenoa* are examples) and others, like *Colpothrinax*, which the authors designate as “ambiguous.” As suggested above, *C. chiapensis* was associated with the arborescent legume *Hymenaea*, marking its habitat as tropical or subtropical rain forest. One of the modern species, *C. wrightii*, has diverged ecologically and is distributed in semidry savannas and grasslands (Bailey 1940), while *C. cookii* and *C. aphanopetala* are in premontane and lower montane rain forests on upper slopes and ridges up to 1600 m elevation (with some exceptions at lower elevations in the latter taxon [Evans 2001]). The earlier-described amber fossil *Socratea brownii* (Poinar 2002) was another palm species associated with *Hymenaea mexicana* in the same Mid-Tertiary tropical forests as was *Colpothrinax chiapensis*.

The question of island dispersal and radiation, specifically in genera of tribe Trachycarpeae, is given de-

tailed attention by Bacon et al. (2012). Of interest here is the authors' estimation of the age of crown and stem nodes for the clades that they resolve within this tribe. The clade comprising *Colpothrinax* alone, mentioned above, is assigned a mean stem age of 28.56 Ma (dates for upper and lower age estimates were not well supported in posterior probabilities analysis). The mean crown age for the genus is 7.87 Ma, with upper and lower estimates of 14.44 and 2.74 Ma. The age range assigned to the Mexican amber (Berggren & Van Couvering 1974) of 26–22.5 Ma is therefore in good agreement with a stem position for *C. chiapensis*. It is reasonable that crown species radiation would have occurred later, in the Central American and Caribbean area. This is one of the regions of interest to Bacon et al. (op. cit.), which they specifically mention as characteristic of the evolution of this genus, as well as of *Rhapidophyllum*, *Brahea*, *Washingtonia*, and Caribbean *Copernicia* (their Fig. 5).

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