PHYRTANDRUS PENTALEPIDUS GEN. ET SP. NOV., A UNIQUE FOSSIL FLOWER OF UNKNOWN AFFINITY FOUND IN MID-TERTIARY DOMINICAN AMBER

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ABSTRACT

Phyrtandrus pentalepidus gen. et sp. nov. was collected from Mid-Tertiary amber deposits in the Dominican Republic. Morphologically it displays a peculiar mixture of traits from both monocotyledons and dicotyledons, but its monosulcate pollen would remove it from membership in the eudicots. Beginning at the base, the 5 floral whorls consist of (1) 5 small subtending bracts, (2) 5 ± equal tepals opposite the bracts, (3) 5 fertile stamens alternating with the tepals, (4) 3 staminodes, 2 well-developed and 1 much reduced, each opposite a tepal, and (5) 2 fertile stamens and 1 rudimentary staminode, the 2 stamens each opposite a tepal and the staminode positioned above a stamen of the outer whorl. No pistil is present. The mixture of 5-parted and 3-parted floral whorls, combined with the monocot-like pollen, makes it difficult to assign the fossil to any modern angiosperm family.

RESUMEN

Phyrtandrus pentalepidus gen. et sp. nov. se colectó en los depósitos de ámbar el Terciario medio en la Republica Dominicana. Morfológicamente muestra una mezcla peculiar de trazos tanto de monocotiledóneas como dicotiledóneas, pero su polen lo sacaría de las eudicotiledóneas. Comenzando por la base, los 5 verticilos florales consisten de (1) 5 brácteas pequeñas que subtienden, (2) 5 ± tépalos iguales opuestos a las brácteas, (3) 5 estambres fértiles alternando con los tépalos, (4) 3 estaminodios, 2 bien desarrollados y 1 muy reducido, cada uno opuesto a un tépalo, y (5) 2 estambres fértiles y 1 estaminodio rudimentario, los 2 estambres cada uno opuesto a un tépalo y el estaminodio posicionado encima de un estambre del verticilo exterior. No hay pistilo presente. La mezcla de verticilos florales de 5-partes y de 3-partes, combinado con el polen semejante a monocotiledónea, hace difícil asignar el fósil a cualquier familia de angiosperma.

INTRODUCTION

As reviewed in the following section, amber deposits in the Dominican Republic have been various dated as 15–20 or 30–45 Ma. The tropical forest that contributed fossils to the amber was described by Poinar & Poinar (1999), who mentioned a number of invertebrates, especially insects, as well as some plant fossils which were then available. More recently, a series of papers, itemized by Chambers & Poinar (2015), have added the following 12 families to the flora: Fabaceae, Arecaceae, Burseraceae, Chrysobalanaceae, Commelinaceae, Lauraceae, Meliaceae, possibly Moraceae, Myristicaceae, Poaceae, Rhamnaceae, and Ticodendraceae. Among these are 10 previously undescribed genera. Two further families published recently are Celastraceae (Chambers & Poinar 2016) and Loganiaceae (Poinar & Strewe 2016). The fossil described here does not lend itself to easy placement in any extant family of paleo-herbs or monocotyledons, although the monosulcate pollen would suggest a relationship within this group. The principal difficulty is in the 3 outer floral whorls (counting bracts), each composed of 5 parts rather than 3 or 6. Yet the 2 inner whorls each clearly comprise just 3 stamens or staminodes. The lack of a gynoecium is also a drawback to familial assignment.

MATERIALS AND METHODS

In the Dominican Republic, mining for amber is carried out in the northern mountain ranges (Cordillera Septentrional), between Puerto Plato and Santiago. The amber was formed from resin of the leguminous tree *Hymenaea protera* (Poinar 1991). Assignment of an age to the amber involves studies of microfossils in the marine strata in which the amber was deposited after having been washed down by streams and rivers from the ancestral Mid-Tertiary forest. The youngest assigned age is 15–20 Ma, based on foraminifera (Iturralde-Vinent & MacPhee 1996), while an older date of 30–45 Ma was based on coccoliths (Cépek in Schlee 1990). The amber

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is found in sandstones of the Upper Eocene to Lower Miocene Mamey Group (Draper et al. 1994), and our terminology of "Mid-Tertiary" is an approximation of the range of published dates. According to Dilcher et al. (1992), "… the amber clasts, from all physical characteristics, were already matured amber at the time of redeposition into marine basins. Therefore the age of the amber is greater than Miocene and quite likely is as early as late Eocene." Additional Tertiary Caribbean amber deposits have been found in Puerto Rico and Jamaica (Iturralde-Vinent 2001), adding to the range in age of such deposits in the Greater Antilles.

Observations and photographs were made with a Nikon SMA-10 R stereoscopic microscope and Nikon Optiphot compound microscope with magnifications up to 600×. A Helicon Focus Pro X54 was used to stack photos for better clarity and depth of field.

DESCRIPTION

Phyrtandrus K.L. Chambers & Poinar, gen. nov. (**Figs. 1–3**). TYPE SPECIES: *Phyrtandrus pentalepidus* K.L. Chambers & Poinar, sp. nov.

Flower staminate, subtended by a whorl of 5 oblong-clavate bracts opposite the tepals (Fig. 2). Tepals 5 in a single whorl, ± alike, separate, sepaloid in texture, broadly oblong-ovate, strongly folded adaxially (Fig. 1). Outer whorl of stamens 5, fertile, laterally spreading, alternating with tepals, anthers basifixed, dithecal, with latrorse, longitudinal dehiscence (Fig. 1). Second anthoecial whorl of 2 well-developed staminodes and 1 oblong, rudimentary staminode, each opposite 1 of the tepals (Fig. 1), anther of 1 large staminode bearing a tangled mass of trichomes (Fig. 3), anther of other large staminode a spherical ball of grooved papillae (not illustrated), inner anthoecial whorl comprising 2 long-exserted fertile stamens opposite the remaining 2 tepals and 1 oblong, rudimentary staminode alternating with 2 tepals (Fig. 1). Gynoecium lacking. Pedicel slender, elongated (Fig. 2). Pollen monosulcate (Fig. 3).

Etymology.—From Greek "phyrtos," mixed, and "andros," man, male, based on the mixture of stamens and staminodes in 3 whorls of 3 or 5 parts.

Phyrtandrus pentalepidus K.L. Chambers & Poinar, sp. nov. (**Figs 1–3**). TYPE: HISPANIOLA. DOMINICAN REPUBLIC: amber mine in the northern mountain ranges (Cordillera Septentrional, between Puerto Plato and Santiago). 2012, *unknown amber miner, s.n.* (HOLOTYPE: Catalog number Sd-9-201, Deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.)

Width in apical view, including exserted stamens, 2.7 mm. Tepals 0.6 mm long, 0.5 mm wide, glabrous, apex rounded, margins entire (Fig. 1). Stamens of outer whorl 1.2–1.3 mm long, filaments 1.1–-1.2 mm long, columnar, glabrous. Well-developed staminodes of 2nd whorl 0.6–0.8 mm long, filaments 0.3 mm long, anthers 0.5–0.6 mm in diameter, rudimentary staminode ca. 0.2 mm long (partly obscured). Fertile stamens of innermost whorl 1.3–1.4 mm long, anthers 0.5–0.6 mm long, similar to those of outer whorl, filaments 1.2 mm long, thickened at base, rudimentary staminode ca. 0.4 mm long (partly obscured) (Fig. 1). Basal bracts 0.6 mm long, 0.5 mm wide near apex, 1 reduced supernumerary stamen present between 2 bracts (Fig. 2). Pedicel 2 mm long, glabrous. Pollen grains monosulcate, oblate to spherical in equatorial view, triangular in polar view, 24–29 µm in diameter

Etymology.—From Greek "penta," five, and "lepidos," scale, based on the 5-parted whorls of bracts and tepals.

DISCUSSION

In the above description, the organs of the outer subtending whorl are referred to as bracts rather than sepals because they are opposite, not alternate with, the perianth parts (tepals). The 5 stamens of the outer androecial whorl are alike, fertile, and widely spreading on long filaments (Fig. 1). On the other hand, the 2 inner whorls are each made up of 2 large male organs (stamens or staminodes) and 1 small, rudimentary structure, and except for 1 rudiment, these organs are opposite the tepals, hence alternate with the stamens of the outer whorl. The rudimentary staminode of the innermost whorl does alternate with 2 of the tepals, however. The 1 supernumerary stamen between 2 bracts on the underside of the flower (Fig. 2) is taken to be a developmental abnor-

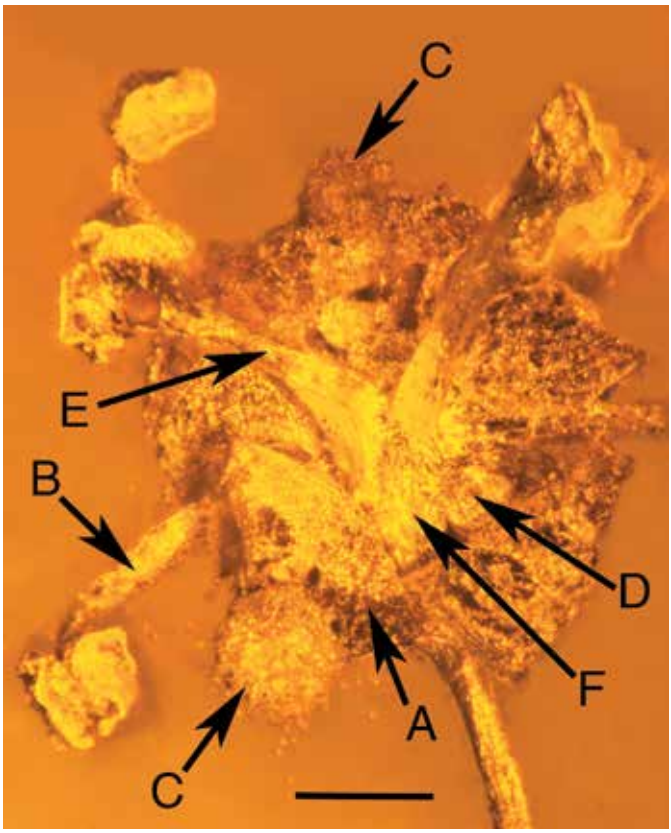

Fig. 1. ***Phyrtandrus pentalepidus*** **in Dominican amber. Apical view. A. Adaxially folded tepal. B. Fertile stamen of the outer whorl. C. Well-developed staminodes of the middle androecial whorl. D. Rudimentary staminode of the middle whorl. E. Fertile stamen of the inner androecial whorl. F. Rudimentary staminode of the inner whorl. Scale bar = 0.4 mm.**

mality. The 2 well-developed staminodes of the 2nd androecial whorl may have had a specialized function, which we hypothesize was related to pollination. With no obvious nectaries at the base of the inner stamens, the enlarged sterile anthers (Fig. 3) might have acted as odor- or nectar-producing organs to attract insect visitors. Upon landing on a staminate flower, the insects would become dusted with pollen from the adjacent fertile anthers, for transport to a pistil-bearing flower of the same species. Whether such flowers were bisexual or strictly pistillate is, of course, unknown at present, but in the future such a fossil might, with luck, be discovered in Dominican amber deposits, to complete the description of *Phyrtandrus* reproduction. Parenthetically, in the enlarged view of the anther of a well-developed staminode (Fig. 3), some of the pollen grains appear to have a strand-like attachment to a trichome, which may represent a sticky exudate related to the glandular nature of the anther.

It is difficult to get around the fact that the outer, 5-merous parts of the flower of *Phyrtandrus*—bracts, tepals, and outer stamen whorl—are eudicot in makeup, while the inner two whorls of stamens and staminodes, plus the monosulcate pollen, are monocot-like. If the flower had evolved from a monocot ancestor, by loss of 1 stamen and 1 tepal from the outer whorls, then the 5 outer stamens should be opposite the remaining tepals—as is the usual position in families of monocots (Cronquist 1981; Kubitzki et al. 1998; Stevens 2001 onwards; Reveal & Pires 2002). Note that 5 of the 6 inner stamens and staminodes (including 2 rudimentary staminodes) are opposite the 5 tepals, with only one rudimentary organ alternating with 2 tepals—as if a tepal

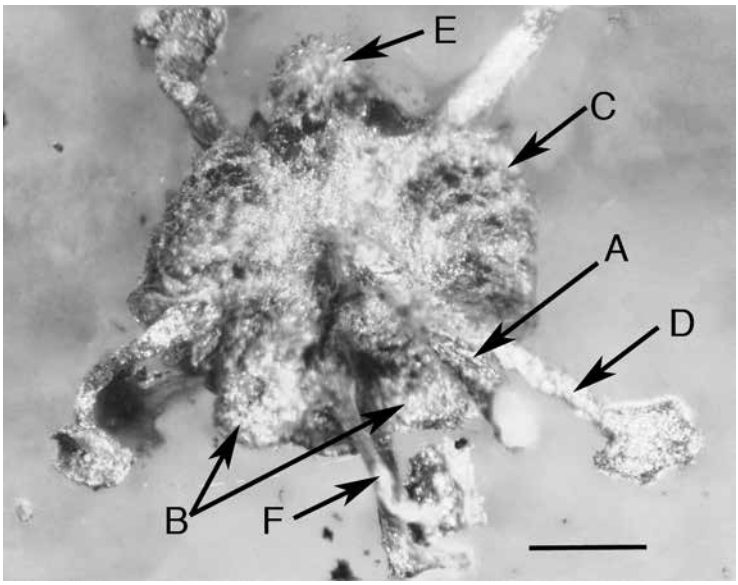

Fig. 2. *Phyrtandrus pentalepidus* in Dominican amber. Basal view. **A.** Pedicel. **B.** Bracts of the outer subtending whorl. **C.** Tepal. **D.** Fertile stamen of the outer androecial whorl. **E.** Anther of well-developed staminode. **F.** Supernumerary fertile stamen. Scale bar = 0.4 mm.

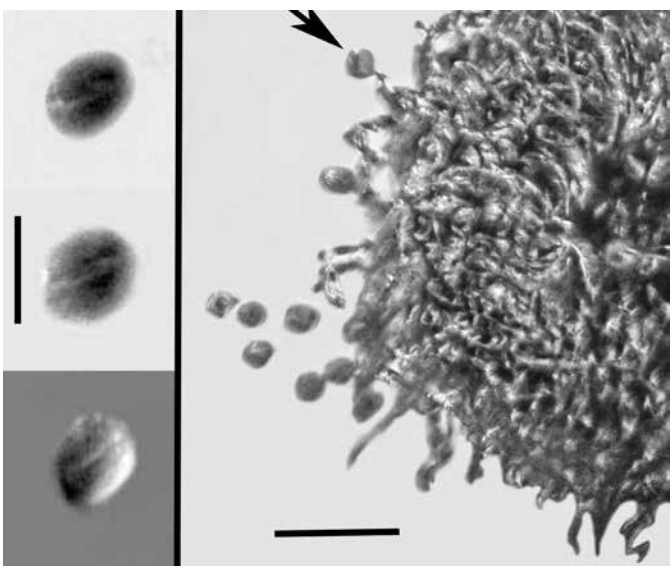

Fig. 3. *Phyrtandrus pentalepidus* in Dominican amber. Portion of the anther of 1 well-developed staminode. Note tangle of trichomes and pollen from adjacent fertile anthers. Arrow shows monosulcate nature of pollen. Scale bar = 0.108 mm. Insert: Three pollen grains. Scale bar = 30 μm.

were missing in that position. However, a simple evolutionary loss of 1 tepal from the perianth does not seem to answer the dicot/monocot character mixture, especially in view of the alternation of outer stamens with tepals. Another interesting feature of the genus is the presence of a subtending whorl of bracts opposite the tepals. Still another is the presence of a supernumerary stamen between two of the bracts, which we attribute to

a developmental abnormality. This stamen would be very difficult to explain as a normal feature of the flower, which otherwise has such a clear-cut androecium of 3 whorls.

Having been unsuccessful in searching the cited references for a close relative of *Phyrtandrus*, we suggest that the taxonomic assignment of this unusual flower preferably be left as an unanswered question. Description of a new higher taxon based on the fossil would require the fortuitous discovery of an accompanying pistillate flower.

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REFERENCES

Chambers, K.L. & G.O. Poinar, Jr. 2015. *Comopellis presbya* gen. et sp. nov. (Rhamnaceae) in Mid-Tertiary amber from the Dominican Republic. J. Bot. Res. Inst. Texas 9:361–367.

Chambers, K.L. & G.O. Poinar, Jr. 2016. *Lobocyclas anomala,* a new genus and species of Celastraceae subfamily Hippocrateoideae in dominican amber. J. Bot. Res. Inst. Texas 10:137–140.

Cronquist, A. 1981. An integrated system of classification of flowering plants. Columbia University Press, New York, U.S.A.

Dilcher, D.L., P.S. Herendeen, & F. Huber. 1992. Fossil *Acacia* flowers with attached anther glands from Dominican amber. In: P.S. Herendeen & D.L. Dilcher, eds. Advances in legume systematics. Part 4. The fossil record. Royal Botanic Gardens, Kew, U.K.

Draper, G., P. Mann, & J.F. Lewis. 1994. Hispaniola. In: S. Donovan & T.A. Jackson, eds. Caribbean geology: An introduction. The University of the West Indies Publishers' Association, Kingston, Jamaica. Pp. 129–150.

Iturralde-Vinent, M.A. 2001. Geology of the amber-bearing deposits of the Greater Antilles. Caribbean J. Sci. 37:141–167.

Iturralde-Vinent, M.A. & R.D.E. MacPhee. 1966. Age and paleographic origin of Dominican amber. Science 273:1850–1852.

Kubitzki, K., P.J. Ruddall, & M.C. Chase. 1998. Systematics and evolution. In: K. Kubitzki et al., eds. The families and genera of vascular plants. III. Flowering plants. Monocotyledons. Springer Verlag, Berlin, Germany. Pp. 23–33.

Poinar, G.L., Jr. 1991. *Hymenaea protera* sp. n. (Leguminosae: Caesalpinioideae) from Dominican amber has African affinities. Experientia 47:1075–1082.

Poinar, G.O., Jr. & R. Poinar. 1999. The amber forest. Princeton University Press, Princeton, New Jersey, U.S.A.

Poinar, G.O., Jr. & L. Struwe. 2016. An asterid flower from neotropical Mid-Tertiary amber. Nature Plants 16005:1–3.

Reveal, J.L. & J.C. Pires. 2002. Phylogeny and classification of the monocotyledons: An update. In: Flora of North America Editorial Committee, eds. Flora of North America north of Mexico. Vol. 26. Oxford University Press, Oxford, U.K. 26:3–36.

Schlee, D. 1999. Das Bernstein-Kabinett. Stuttgarter Beitr. Naturk. Ser. C, 28.

Stevens, P.F. 2001 onwards. Angiosperm Phylogeny Website, Version 12, July 2012 (updated since). Consulted July 2016. www.mobot.ore/MOBOT/research/APweb