

Virola dominicana sp. nov. (Myristicaceae) from Dominican amber

George Poinar, Jr. and Royce Steeves

Abstract: The Myristicaceae is a member of the early diverging angiosperm order Magnoliales; however, the family is poorly represented by fossil collections. We describe *Virola dominicana* sp. nov. (Myristicaceae), the first record of fossilized Myristicaceae flowers, from mid-Tertiary (45–15 million years ago) Dominican amber. The description is based on 24 male flowers in 17 pieces of amber, thus providing some indication of intraspecific variation, including a two-tepaled flower. Diagnostic characters of the new species are the long-simple or few-branched trichomes on the perianth margins, the small pollen grains, and a short staminal column. These fossils also show co-occurring insects, some of which could be *Virola* pollinators. It is speculated that *V. dominicana* disappeared from Hispaniola during the Pliocene–Pleistocene cooling events leaving no native members of the Myristicaceae in this region today. Additionally, these fossils demonstrate that Myristicaceae was present in the Western Hemisphere during the mid-Tertiary.

Key words: *Virola dominicana*, Myristicaceae, Dominican fossil amber, paleobotany.

Résumé : La famille des Myristicaceae regroupe des angiospermes à divergence ancienne de l'ordre des Magnoliales; cependant, la famille est peu représentée dans les collections de fossiles. Les auteurs décrivent le *Virola dominicana* sp. nov. (Myristicaceae), la première mention de fleurs de Myristicaceae, provenant d'ambre Dominicain, remontant au milieu du Tertiaire, il y a 45–15 millions d'années. Ils basent la description sur 24 fleurs mâles réparties dans 17 pièces d'ambre, fournissant ainsi des indications sur la variation intraspécifique, incluant deux fleurs à deux tépales. Les caractères diagnostiques de la nouvelle espèce comportent des trichomes longs et simples ou faiblement ramifiés, aux marges du périanthe, de petits grains de pollen et une courte colonne staminée. Ces fossiles montrent simultanément des insectes pouvant être des pollinisateurs du *Virola*. Les auteurs suggèrent que le *V. dominicana* aurait disparu de l'Hispaniola au cours des événements de refroidissement survenus pendant le Pliocène-Pleistocène, ne laissant aucun membre indigène des Myristicaceae dans cette région aujourd'hui. De plus, ces fossiles démontrent que la famille des Myristicaceae était présente dans l'hémisphère occidental au milieu du Tertiaire. [Traduit par la rédaction]

Mots-clés : *Virola dominica*, Myristicaceae, ambre fossile Dominicain, paléobotanique.

Introduction

Amber, the fossilized resin of woody plants, may contain a great wealth of ancient organisms and is one of the best media for preserving delicate structures like flowers. Not only is the perianth often preserved, but also details of trichomes and even complete pollen cells. Flowers up to 100 million years old have been preserved in amber, although these cannot be assigned to extant genera (Poinar and Chambers 2005; Chambers et al. 2010). Flowers found within Dominican amber have been used to identify members of the genera *Persea* (Lauraceae) (Chambers et al. 2011a), *Trichilia* (Meliaceae) (Chambers et al. 2011b), and *Trochanthera* (Balanophoraceae or Moraceae) (Poinar et al. 2008).

The Myristicaceae, or nutmeg family, comprises an assemblage of canopy to subcanopy trees of some 21 genera and about 500 species distributed in tropical and subtropical regions of Central and South America, Asia, Africa, and Madagascar (Doyle et al. 2004; Smith 1937). Despite the family's phylogenetic placement within the early diverging magnoliid grade of angiosperms (Soltis et al. 2011), the Myristicaceae are poorly represented by fossil collections. Fossilized wood (Boureau 1950), leaves (Wolfe 1977), pollen (Frederiksen 1973; Jan du Chene et al. 1978), and fruits and seeds (Berry 1929; Doyle et al. 2008) have been described as belonging to the Myristicaceae; however, few can be unambiguously assigned to the family.

The Myristicaceae is represented in the Neotropics by the following six endemic genera: *Bicuiba*, *Compsoeura*, *Iryanthera*, *Osteophloem*, *Otoba*, and *Virola*. The widespread and ecologically dominant genus *Virola* is represented by about 60 species restricted to lowland and cloud rainforests of Central and South America. *Virola* is differentiated from other Neotropical genera of Myristicaceae by possessing profuse red latex (rarely green-yellow) and irregularly branching (dendritic) or stalked-sessile stellate hairs on the surfaces of their leaves, flowers, and fruits. The flowers of these dioecious trees are very small (1–4 mm in diameter) and are composed of 3–4 tepals (undifferentiated petals) that are often covered in a dense dendritic or stellate pubescence. Extant species of *Virola* can be identified only by numerous vegetative and reproductive characters, as there exists a great deal of overlap among species for any one character (Smith 1937).

The objectives of this study are as follows: (i) describe the staminate flowers of *Virola dominicana* Poinar and Steeves, sp. nov., the only known fossil flowers of the family Myristicaceae, and (ii) quantify the floral variation that occurred within *Virola* in Hispaniola (modern-day Haiti and Dominican Republic) during the mid-Tertiary.

Materials and methods

The Dominican amber specimens were obtained from mines in the Cordillera Septentrional, between Puerto Plata and Santiago,

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of the Dominican Republic. Dating of Dominican amber is equivocal with the latest proposed age of 20–15 million years ago (mya) based on foraminifera (Iturralde-Vinent and MacPhee 1996) and the earliest as 45–30 mya based on coccoliths (Cêpek in Schlee 1990). In addition, Dominican amber is secondarily deposited in sedimentary rocks, which makes a definite age determination difficult (Poinar and Mastalerz 2000). Dominican amber was produced by the leguminous tree, *Hymenaea protera* Poinar (Poinar 1991), and a reconstruction of the Dominican amber forest based on amber fossils indicated that the environment was similar to that of a present-day tropical moist forest (Poinar and Poinar 1999).

Observations, drawings, and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and a Nikon Optiphot compound microscope with magnifications up to 600 \times . In some instances, Helicon Focus Pro X64 was used to stack photos for better clarity and depth of field.

Results

Seventeen pieces of Dominican amber, containing a total of 24 male and no female *Virola* flowers, were examined during the present study. Not all characters were evident on every flower because some had been partly polished away during preparation of the amber, partially eaten by herbivores, or slightly obstructed from view by other inclusions. The number of specimens examined for each numerical value is provided.

Description

Myristicaceae

Virola Aublet, 1775

Virola dominicana Poinar and Steeves, **sp. nov.** (Figs. 1–4)

SPECIFIC DESCRIPTION: Staminate flowers brown to orange-brown, length of the complete flower 3.4 (2.1–5.0) mm ($N = 16$), pedicel length 1.4 (0.7–2.0) mm ($N = 17$); perianth 3 (2)-lobed to middle or beyond, lobes thick, rounded to acute at apex, spreading at anthesis, length of perianth lobes 1.3 (0.7–3.3) mm ($N = 24$), greatest width of perianth lobes 0.9 (0.5–1.5) mm ($N = 23$), length of fused portion of perianth 0.9 (0.5–1.5) mm ($N = 19$), exterior surface of perianth covered with short, stubby, simple, or branched trichomes (see Supplementary Fig. S1¹), lobe margins with long, thick single to multiple-celled trichomes ranging from 0.1 to 0.3 mm in length; androecium 0.4–1.1 mm in length, stamens 3, apparently opposite of tepal lobes where visible in two specimens (see Supplementary Figs. S2 and S3¹), filaments fused in a column 0.2 (0.1–0.3) mm long ($N = 6$), anthers bithecate, extrose, dehiscent longitudinally, anther length 0.5 (0.3–0.8) mm ($N = 10$), anthers lacking a sterile apex; pollen apparently monosulcate, boat-shaped, ranging from 23–27 μm in length (Fig. 2F); pistillate flower unknown.

TYPE: Holotype deposited in the Poinar amber collection (accession # Sd-9-30A) and paratypes (Sd-9-30B through Sd-9-30R) maintained at Oregon State University, Corvallis, Oregon.

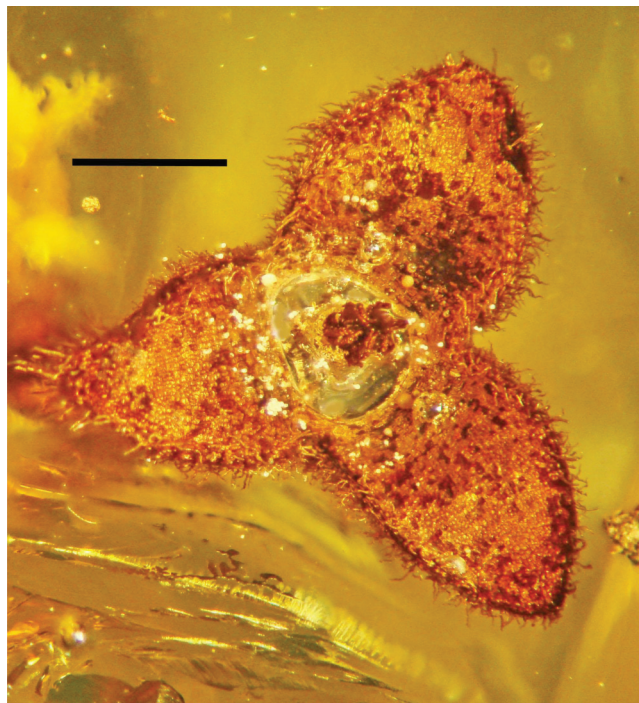
TYPE LOCALITY: Amber mine in the northern mountain ranges (Cordillera Septentrional) of the Dominican Republic (DD latitude and longitude: 19.4, –70.4).

ETYMOLOGY: The specific name is based on the country of origin of the fossil.

Discussion

Despite their early origination in angiosperm evolution and their current pantropical distribution, the fossil record of the Myristicaceae is rather meager and no fossil flowers have been described prior to this study. Eocene fossil seeds and fruit casts

Fig. 1. Holotype of *Virola dominicana* sp. nov. showing stubby trichomes on the lobe blades and long trichomes on the lobe margins. Note also white pollen grains within the flower diameter. Scale bar = 800 μm .



from Texas were described as *Myristica catahouleensis* Berry (Berry 1929; Chesters et al. 1967); however, Doyle et al. (2008) postulate that these represent molds of an endocarp of Mastixiaceae (Cornales). Leaf fragments from the Eocene of Borneo described as *Myristicophyllum minus* Geyler (Andrews 1970) and wood described as *Myristicoxylon princeps* E. Boureau (Boureau 1950; Collinson et al. 1993) from Oligocene–Miocene deposits in the Sahara have both been attributed to the Myristicaceae. In addition, Miocene (~23–5 mya) and Eocene (~56–34 mya) fruits from Germany and England were assigned to the Myristicaceae and described as *Myristicacarpum miocaenicum* Gregor and *Myristicacarpum chandlerae* Doyle, Manchester and Sauquet, respectively (Collinson et al. 1993; Doyle et al. 2008). Myristicaceous pollen from the Eocene of Nigeria was described as *Echimonocolpites major* du Chêne (Collinson et al. 1993).

A seed described as *Virola tertiaria* Berry from the Oligocene of Peru is the only previous putative fossil of the genus *Virola* (Berry 1929); however, a transversely broken specimen does not possess tegminal ruminations, which would be indicative of *Virola* (Doyle et al. 2008). A flower of *Virola* in Dominican amber was previously depicted, but not described (Poinar and Poinar 1999).

Several floral apomorphies set Myristicaceae apart from other members of Magnoliales, such as small unisexual flowers (<1 cm diameter) with a perianth constructed of three tepals, connate anthers, and stamen filaments fused to form a central column (Sauquet et al. 2003). The male flowers described in this study exhibit these diagnostic characters, making them the first confirmed fossil flowers of the family Myristicaceae, and are among the few fossil collections distinctly of Myristicaceae origin. *Virola dominicana* is known only from these 24 flowers entrapped in 17 pieces of mid-Tertiary Dominican amber. The spreading tepal lobes of *V. dominicana* resemble modern-day *Virola* species. However, extant species have branched or mostly stellate trichomes

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjb-2013-0019>.

Fig. 2. Male flowers, indument, and pollen of *Virola dominicana*. (A) Lateral view of paratype of *V. dominicana* in Dominican amber. Scale bar = 850 μm . (B) Frontal view of two-lobed flower of *V. dominicana* in Dominican amber. Scale bar = 480 μm . (C) Long, straight trichomes on the margin of a perianth lobe of the holotype of *V. dominicana* in Dominican amber. Scale bar = 105 μm . (D) Pollen grains of *V. dominicana* in Dominican amber. Note upper boat-shaped grain. Scale bar = 23 μm . (E) Lateral view of two-lobed flower of *V. dominicana* in Dominican amber. Scale bar = 820 μm . (F) Detail of pollen grains of the holotype of *V. dominicana* in Dominican amber. Scale bar = 22 μm .

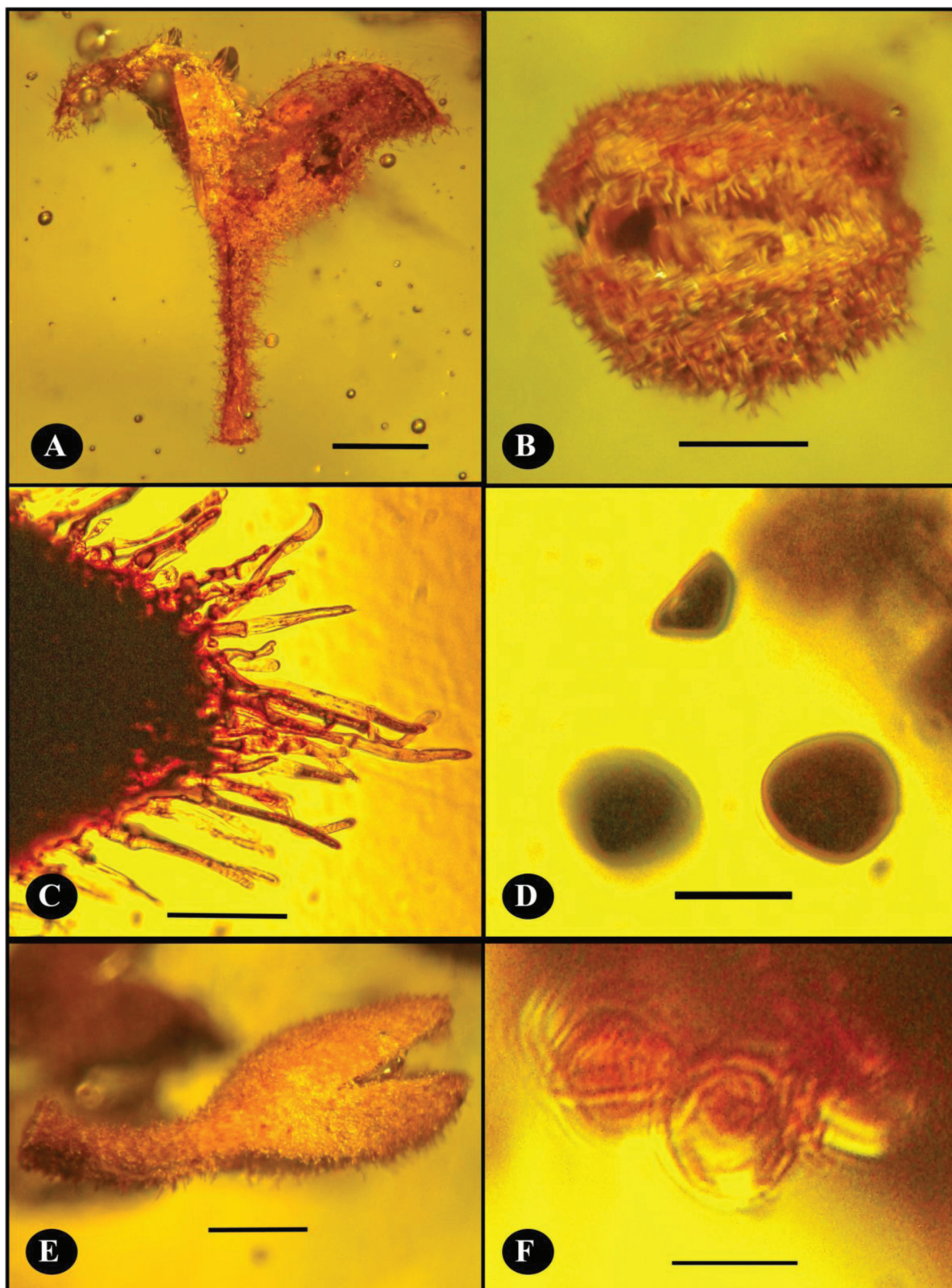
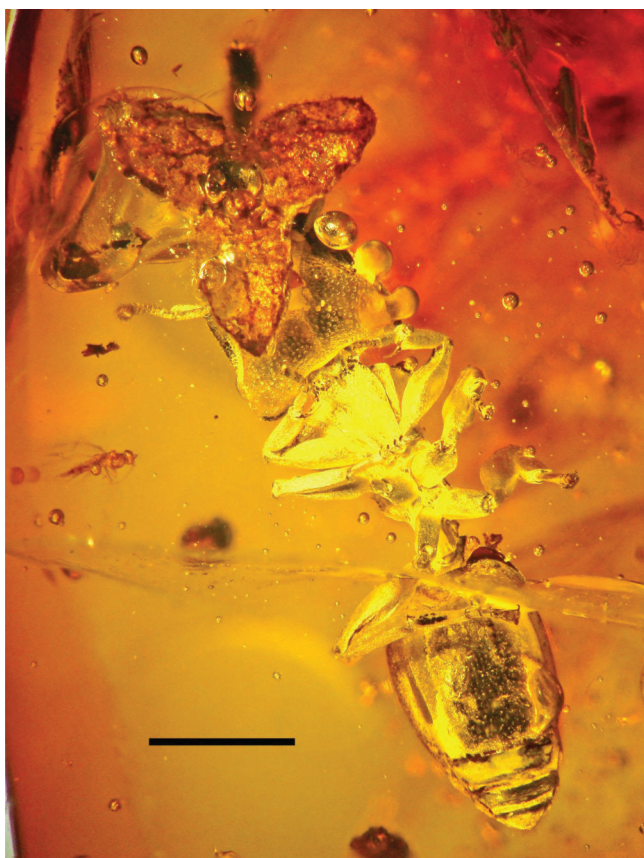


Fig. 3. A planthopper (Hemiptera: Fulgoroidea) adjacent to a paratype flower of *V. dominicana* in Dominican amber. Scale bar = 490 μm .



Fig. 4. A worker *Cephalotes squamosus* (Hymenoptera: Formicidae) with its head in an open paratype flower of *V. dominicana* in Dominican amber. Scale bar = 1.4 mm.



on the lobes (Smith 1937; Croat 1978; Sabatier 1997), whereas the lobes of *V. dominicana* appear to possess mostly simple or few-branched trichomes. The most diagnostic character affiliating these fossils with members of *Virola* is the high density of the pubescence on the tepals, which sets these flowers apart from the essentially glabrous *Iryanthera*, *Otoba*, and *Osteophloem* (whose species possess 3, 3, and 12–20 anthers, respectively; Sauquet 2003). Although *Bicuiba oleifera* and some *Compso-neura* species possess t-shaped or stellate hairs, they are short and sparsely distributed

(puberulent to subglabrous) in comparison with the relatively long and dense hairs of many *Virola* taxa. Additionally, *Compso-neura* spp. possess 4–12 anthers, whereas all the fossils examined possessed only three anthers. The anther length of *V. dominicana* (0.3–0.8 mm) is considerably shorter than most extant *Virola* species (0.6–1.9 mm) as measured in eight extant *Virola* species; Smith 1937; Steeves 2011). The shape and size range of the pollen of *V. dominicana* (23–27 μm) falls within the range of members of the genus (22–35 μm) (Walker and Walker 1979). The two-lobed flower (Figs. 2A and 2B) may represent a developmental anomaly, as flowers consisting of two petal lobes are rarely observed in extant *Virola* (R. Steeves, personal observations). Staminate flowers of extant *Virola* spp. are easily deciduous, likely due to their thinner and longer pedicels, compared with thick and stout pistillate flowers, which rarely fall to the ground (R. Steeves, personal observation). Exclusively male fossil flowers may have been found if *V. dominicana* exhibited similar pedicel traits as extant species.

The crown group of the Myristicaceae was estimated to have a Miocene origin based on molecular clock analyses of Doyle et al. (2004), which is not incongruous with the estimated age of the present fossils. However, this age estimate is surprisingly recent, given the pantropical distribution of the Myristicaceae, their poor potential for oceanic dispersal, and the considerably earlier estimates of crown group divergence (~89 mya) of closely related families such as the Annonaceae (Doyle et al. 2004; Pirie and Doyle 2012). This relatively young age estimate for the Myristicaceae could be an artifact of their poor fossil representation and (or) a result of a slower rate of molecular evolution compared with closely related families, leading to a miscalibration in the molecular clock estimate. Both the former and latter explanations are plausible, given the paucity of fossil evidence of the family and the fact that molecular investigations employing some of the most variable nuclear and chloroplast DNA markers have found low levels of molecular divergence among genera and species of Myristicaceae (Sauquet et al. 2003; Doyle et al. 2004; Steeves 2011). The fossil flowers described in this study place Myristicaceae in the neotropical region sometime between 45 and 15 mya, based on age estimates for Dominican amber (Iturralde-Vinent and MacPhee 1996; Schlee 1990).

Extant members of *Virola* are of significant ecological and ethnobotanical importance in the neotropics. *Virola* spp. are considered one of the 5–10 most abundant fruit-producing tree genera in South American (Pitman et al. 2001, 2002). The bright orange-red, fat-rich aril fruits are highly nutritious and are highly sought after by birds and spider monkeys (*Ateles paniscus* (Linnaeus, 1758)). Pollinators of *Virola* have been little studied. Beetles and thrips have been observed visiting flowers (Steeves 2011); however, no representatives of these groups occurred among the various insects found together with *Virola* flowers in the examined Dominican amber samples. Planthoppers occurred with *Virola* flowers in several amber pieces (Fig. 3) and may have been feeding on the plant's sap. Both worker and alate ants were associated with several *Virola* flowers in the amber samples. One of the identifiable ant species present in the amber along with *V. dominicana* is a worker *Cephalotes squamosus* (Hymenoptera: Formicidae) (Fig. 4). Extant *Cephalotes* spp. are polyphagous but do include pollen in their diet and take pollen back to the nest for larvae and nestmates. Since *Cephalotes* ants are known to visit flowers with extrafloral nectaries (de Andrade and Baroni Urbani 1999), they could potentially have acted as pollinators of *V. dominicana*. Although ants are not believed to be significant agents of pollination in extant *Virola* spp., ants have been observed on the male flowers of extant *Virola calophylla* (Steeves 2011) and could transfer the pollen to nearby female trees. The small and rather inconspicuous flowers of *Virola* spp. are unlikely to be predominantly visually attractive to pollinators. The flowers do, however, emit pungent odours (similar in smell to lilacs) that appear to attract insects even after male flowers have fallen to the ground (R. Steeves, personal observation). It is possible that the insects observed in the inclusions inspected

for this study represent individuals who were haphazardly trapped in the resin, but their close proximity to the flowers (particularly *Cephalotes squamosus*, Fig. 4) may indicate that the attraction of the fallen *V. dominicana* flowers is what led to their entrapment.

The Dominican amber forest was categorized as a tropical moist forest unlike any other found in the world today. During the Pliocene–Pleistocene global cooling period, many of the stentopic biota of the forest, such as stingless and orchid bees, *Mastotermes* termites, and various plants, including *Hymenaea protera* that produced the amber, were trapped by the island's isolation. Refugia were apparently rare or inadequate for many life forms (Poinar and Poinar 1999). It is likely that *V. dominicana* disappeared from Hispaniola during this cooling period. Although there are no native members of Myristicaceae in Hispaniola today (Liogier 1983), *Virola surinamensis* is native to nearby Guadeloupe Island, southward to Grenada in the Lesser Antilles (Smith 1937). The mainland distribution of contemporary *Virola* taxa encompasses lowland and montane rain forest habitats (1500 m elevation) from Guatemala to the southern and eastern extent of the Amazon Basin and the western coast of Ecuador (Smith 1937).

This study describes the first fossil flowers of the Myristicaceae, *V. dominicana*, preserved in mid-Tertiary Dominican amber. These fossils place the Myristicaceae in the Neotropical region during the mid-Tertiary and are likely fossils of an extinct *Virola* species. It is also possible that the species within these fossils diverged before the origin of the *Virola* genus, placing them within the *Virola* stem group (or possibly the stem group of another genus). However, because these fossils lack morphological characters that clearly distinguish them from extant *Virola*, we feel that it is most parsimonious to classify this extinct species within *Virola*. The uncertainty in this classification in conjunction with the largely unknown phylogenetic relationships among even extant genera should be kept in mind when using these fossils to calibrate divergence times in Myristicaceae. These specimens will, however, undoubtedly help future studies of the biogeography and evolutionary biology of these ecological and ethnobotanically significant trees.

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References

Andrews, H.N. Jr. 1970. Index of Generic names of fossil plants, 1820–1965. Geological Survey Bulletin 1300, Washington, D.C.

Berry, E.W. 1929. Early Tertiary fruits and seeds from Belen, Peru. Johns Hopkins Univ. Stud. Geol. 10: 137–180.

Boureau, E. 1950. Étude paléoxylologique du Sahara (IX). Sur un *Myristicoxylon princeps* n. gen., n. sp., du Danien d'Asselar (Sahara soudanais). Bull. Mus. Natl. Hist. Nat. 2: 523–528.

Chambers, K.L., Poinar, G.O., Jr., and Buckley, R. 2010. *Tropidogyne*, a new genus of Early Cretaceous Eudicots (Angiospermae) from Burmese amber. *Novon*, 20: 23–29. doi:10.3417/2008039.

Chambers, K.L., Poinar, G.O., Jr., and Brown, A.E. 2011a. A fossil flower of *Persea* (Lauraceae) in Tertiary Dominican amber. *J. Bot. Res. Inst. Texas*, 5: 457–462.

Chambers, K.L., Poinar, G.O., Jr., and Brown, A.E. 2011b. Two fossil flowers of *Trichilia* (Meliaceae) in Dominican amber. *J. Bot. Res. Inst. Texas*, 5: 463–468.

Chesters, K.I.M., Gnauck, F.R., and Hughes, N.F. 1967. Angiospermae. In *The fossil record*. Edited by W.B. Harland, C.H. Holland, M.R. House, N.F. Hughes,

A.B. Reynolds, M.J.S. Rudwick, G.E. Satterthwaite, L.B.H. Tarlo, and E.C. Wiley. Geological Society of London, Burlington House, London. pp. 269–288.

Collinson, M.E., Boulter, M.C., and Holmes, P.L. 1993. Magnoliophyta ('Angiospermae'). In *The fossil record 2*. Edited by M.J. Benton. Chapman & Hall, London. pp. 809–841.

Croat, T.B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford.

de Andrade, M.L., and Baroni Urbani, C. 1999. Diversity and adaptation in the ant genus *Cephalotes* past and present. *Stutt. Beitr. Naturkd. B*, 271: 1–889.

Doyle, J.A., Sauquet, H., Scharaschkin, T., and Le Thomas, A. 2004. Phylogeny, molecular and fossil dating, and biogeographic history of Annonaceae and Myristicaceae (Magnoliales). *Int. J. Plant Sci.* 165(Suppl. 4): S55–S67. doi:10.1086/421068.

Doyle, J.A., Manchester, S.R., and Sauquet, H. 2008. A seed related to Myristicaceae in the Early Eocene of Southern England. *Syst. Botany*, 33(4): 636–646. doi:10.1600/036364408786500217.

Frederiksen, N. 1973. New mid-Tertiary spores and pollen grains from Mississippi and Alabama. *Tulane Stud. Geol. Paleontol.* 10: 65–86.

Iturralde-Vinent, M.A., and MacPhee, R.D.E. 1996. Age and paleogeographical origin of Dominican amber. *Science*, 273: 1850–1852. doi:10.1126/science.273.5283.1850.

Jan du Chene, R., Onyike, M., and Sowunmi, M. 1978. Some new Eocene pollen of the Ogwashi-Asabe formation, South-Eastern Nigeria. *Rev. Esp. Micropaleontol.* 10: 285–322.

Liogier, A.H. 1983. La flora de la Española II. Universidad Central Del Este, Santo Domingo.

Pirie, M.D., and Doyle, J.A. 2012. Dating clades with fossils and molecules: the case of Annonaceae. *Bot. J. Linn. Soc.* 169: 84–116. doi:10.1111/j.1095-8339.2012.01234.x.

Pitman, N.C., Terborgh, J.W., Silman, M.R., Núñez, V.P., Neill, D.A., Cerón, C.E., Palacios, W.A., and Aulestia, M. 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology*, 82: 2101–2117. doi:10.1890/0012-9658(2001)082[2101:DADOTS]2.0.CO;2.

Pitman, N.C., Terborgh, J.W., Silman, M.R., Núñez, V.P., Neill, D.A., Cerón, C.E., Palacios, W.A., and Aulestia, M. 2002. A comparison of tree species diversity in two upper Amazonian forests. *Ecology*, 83: 3210–3224. doi:10.1890/0012-9658(2002)083[3210:ACOTSD]2.0.CO;2.

Poinar, G.O., Jr. 1991. *Hymenaea protera* sp.n. (Leguminosae: Caesalpinioideae) from Dominican amber has African affinities. *Experientia* 47(10): 1075–1082. doi:10.1007/BF01923347.

Poinar, G.O., Jr., and Chambers, K.L. 2005. *Palaeoanthella huangii* gen. and sp. nov., an early Cretaceous flower (Angiospermae) in Burmese amber. *Sida*, 21(4): 2087–2092.

Poinar, G.O., Jr., and Mastalerz, M. 2000. Taphonomy of fossilized resins: determining the biostratigraphy of amber. *Acta Geol. Hisp.* 35: 171–182.

Poinar, G.O., Jr., and Poinar, R. 1999. *The amber forest: a reconstruction of a vanished world*. Princeton University Press, Princeton, N.J.

Poinar, G.O., Jr., Chambers, K.L., and Brown, A.E. 2008. *Trochanthera lepidota* Gen. and sp. nov., a fossil angiosperm inflorescence in Dominican amber. *J. Bot. Res. Inst. Texas*, 2: 1167–1173.

Sabatier, D. 1997. Description et biologie d'une nouvelle espèce de *Virola* (Myristicaceae) de Guyane. *Adansonia*, 19: 273–278.

Sauquet, H. 2003. Androecium diversity and evolution in Myristicaceae (Magnoliales), with a description of a new Malagasy genus, *Doyleanthus* gen. nov. *Am. J. Bot.* 90: 1293–1305. doi:10.3732/ajb.90.9.1293.

Sauquet, H., Doyle, J.A., Scharaschkin, T., Borsch, T., Hilu, K.W., Chatrou, L.W., and Le Thomas, A. 2003. Phylogenetic analysis of Magnoliales and Myristicaceae based on multiple data sets: implications for character evolution. *Bot. J. Linn. Soc.* 142: 125–186. doi:10.1046/j.1095-8339.2003.00171.x.

Schlee, D. 1990. Das Bernstein-Kabinett. *Stuttg Beitr Naturkunde*, 28(C): 1–100.

Smith, A.C. 1937. The American species of Myristicaceae. *Brittonia*, 2: 393–510.

Soltis, D.E., Smith, S.A., Cellinese, N., Wurdack, K.J., Tank, D.C., Brockington, S.F., et al. 2011. Angiosperm phylogeny: 17 genes, 640 taxa. *Am. J. Bot.* 98: 704–730. doi:10.3732/ajb.1000404. PMID:21613169.

Steeves, R.A.D. 2011. An intrageneric and intraspecific study of morphological and genetic variation in the Neotropical *Compsoeura* and *Virola* (Myristicaceae). Ph.D. dissertation, The University of Guelph, Guelph.

Walker, J.W., and Walker, A.G. 1979. Comparative pollen morphology of the American Myristicaceae genera *Compsoeura* and *Virola*. *Ann. Missouri Bot. Gard.* 66: 731–755. doi:10.2307/2398916.

Wolfe, J. 1977. Paleogene floras from the Gulf of Alaska region. *U.S. Geol. Surv. Prof. Pap.* 997: 1–108.