DISPARIFLORA ROBERTAE GEN. ET SP. NOV., A MID-CRETACEOUS FLOWER OF POSSIBLE LAURALEAN AFFINITY FROM MYANMAR AMBER

George O. Poinar, Jr.

Department of Integrative Biology
Oregon State University
Corvallis, Oregon 97331, U.S.A.
poinarg@science.oregonstate.edu

Kenton L. Chambers

Department of Botany and Plant Pathology
Oregon State University
Corvallis, Oregon 97331, U.S.A.
chamberk@science.oregonstate.edu

ABSTRACT

Three flowers of a fossil angiosperm preserved in amber from Myanmar (Burma) are described as the new genus and species **Dispariflora robertae.** Although joined in a single cymose inflorescence, the flowers are variable in size and, in addition, they possess an unusual perianth in which 1 sepal is much enlarged and leaf-like, while the remaining 4 are smaller and unequal. The flowers each have 1 superior pistil with a peculiarly plumose and bristly ovary. The number of stamens is uncertain because most were lost before floral preservation, but scars on the receptacle suggest that at least 15 were present. The bithecal anthers open by longitudinal slits and basal glands may have been present on the filaments. Taken as a whole, the floral features that characterize *Dispariflora* suggest an affinity with members of Laurales, especially several Southern Hemisphere families allied with the Monimiaceae.

RESUMEN

Se describen tres flores de un fósil de angiosperma conservadas en ámbar de Myanmar (Birmania) como el nuevo género y especie **Dispariflora robertae.** Aunque están reunidas en una inflorescencia simple cimosa, las flores son variables en tamaño y, además, tienen un perianto inusual en el que un sépalo de aspecto de hoja está muy ensanchado, mientras que los otros cuatro son más pequeños y desiguales. Las flores tienen un pistilo súpero con un ovario peculiarmente plumoso y con cerdas. El número de estambres es incierto porque la mayoría se perdieron antes de la conservación de las flores, pero las cicatrices del receptáculo sugieren que había al menos 15. Las anteras con dos tecas se abren por hendiduras longitudinales y pudieran haber existido glándulas en los filamentos. Tomadas en conjunto, las características florales que caracterizan *Dispariflora* sugieren una afinidad miembros de Laurales, especialmente varias familias de hemisferio sur relacionadas con Monimiaceae.

INTRODUCTION

Amber from mines in northern Myanmar (Burma) continues to provide interesting angiosperm fossils of mid-Cretaceous age, ca. 100 Mya. Details of the location and age of the fossiliferous deposits are given in the following section. In a previous paper (Poinar & Chambers 2018b) 10 publications were listed in which we described novel genera and species of fossil flowers from Myanmar amber. Three of the fossils were placed in modern families (Cunoniaceae, Lauraceae, Poaceae), while the rest could only tentatively, if at all, be assigned to present-day groups. The fossil described here as *Dispariflora robertae* is believed to be allied with the order Laurales. Its most unusual characteristics are a markedly anisophyllous calyx and a dichasial partial inflorescence with flowers of different sizes (Fig. 1). One of the sepals is quite leaf-like and is much larger than the other 4 sepals. Among modern genera, *Glossocalyx* (Siparunaceae) shows a similar enlargement of 1 of its 5 sepals (Pax 1891, fig. 69; Renner & Hausner 2005, pp. 37–38, fig. 6A). In present day angiosperms having specialized inflorescences such as umbels, capitulae, or spadices, a mixture of different flower sizes or functions is common. Floral differences associated with adaptations for outcrossing vs. self-pollination (i.e., chasmogamy vs. cleistogamy—see Lord 1981; Ellstrand et al. 1984) also may be found in the same inflorescence. However, in *Dispariflora* the flowers are cymosely arranged, not cleistogamous, and are all bisexual as far as can be determined. We recently described another fossil from Myanmar amber (Poinar & Chambers 2018a) in which the 6 available flowers, all from a single inflorescence, differed in calyx size and pubescence as well as the degree to which the corolla was exserted from the sepals. In that case, no adaptive significance was attributed to such differences.

The floral morphology of *Dispariflora*, when compared with various present-day representatives of Monimiaceae and related families, suggests a combination of features that individually are more or less

J. Bot. Res. Inst. Texas 13(1): 173 – 183. 2019

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

scattered among modern genera of Laurales, an order of 7 families, 100 genera, and 2500 to 2800 extant species (Renner 1999).

MATERIALS AND METHODS

Fossiliferous Myanmar amber is derived from mines at the Noije Bum 2001 Summit Site in the Hukawng Valley, SW of Maingkhwan, Kachin Province. The amber was secondarily deposited in oceanic sediments by streams draining an adjacent forested landmass. Based on marine paleontological data (ammonites) and palynological evidence, the sediments were dated as late Albian by Cruickshank & Ko (2003), with an assigned age of 97–110 Ma. More recently, Shi et al. (2012), using U-Pb dating of volcanic zircons, placed the sediments at 98.79 ± 0.62 Ma, near the Albian/Cenomanian boundary. We refer to this date as mid-Cretaceous. Based on data from nuclear magnetic resonance (NMR) spectra, as well as the presence of araucarioid wood fibers in the amber, the original source of the amber is presumed to be resin from a tree of the Araucariaceae, perhaps the genus *Agathis* (Poinar et al. 2007). Having originated in an ancient coniferous forest, the amber may be considerably older than the oceanic sediments from which it is now being mined.

Observations and photographs were made with a Nikon SMA-10R stereoscopic microscope at 80× and a Nikon Optiphot microscope with magnifications up to 600×. Helicon Focus Pro X54 was used to stack photos for better clarity and depth of field. In some of the figures, background details were removed to improve the image.

DESCRIPTION

Dispariflora Poinar & K.L. Chambers, **gen. nov.** Type Species: *Dispariflora robertae* Poinar & K.L. Chambers, sp. nov.

Inflorescence a partial dichasial cyme, flowers variable in size, short-pedicellate, pedicels strigose, each flower subtended by a pair of small bracts (Figs. 1–3), receptacle obconic, externally strigose (Fig. 4), calyx irregular, sepals 5, distinct or slightly connate basally, largest sepal leaf-like, over 3× as long as next longest sepal, the remaining 3 sepals gradually shorter (Fig. 2), corolla lacking, stamens mostly disarticulated and dispersed, their number estimated as ca. 15 based on scars remaining on the receptacle (Fig. 5), filaments slender, thickened at the base, incurved, anther attachment basal, anthers ellipsoidal, bithecal, dehiscent by 2 longitudinal slits, apex truncate (Figs. 6, 7), pistil[1], simple (?), superior, ovary with numerous short, sharp bristles on one side and a plumose tuft of fine trichomes on the other, style columnar, short, rather thick, stigma capitate, truncate, smooth (Figs. 8, 9), pollen monocolpate or dicolpate (Fig. 10).

Etymology.—Genus name from the Latin "dispar," different, unequal, and "flos, floris," flower.

Dispariflora robertae Poinar & K.L. Chambers, **sp. nov.** (**Figs. 1–10**). Type: MYANMAR (BURMA). Kachin: Noije Bum 2001 Summit Site amber mine in the Hukawng Valley, SW of Maingkhwan, 26°20'N, 96°36'E, *unknown amber miner s.n.* (holotype: accession number B-An-8, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

Note.—Although described separately, below, the 3 flowers together comprise the type collection. The entire inflorescence, from the base of the lower pedicel to the tip of the sepal of flower F1, is 16.0 mm.

Flower No. 1 (Figs. 1, 3, 9): Receptacle partially obscured, ca. 1.8 mm long, 0.9 mm wide, largest sepal oblanceolate-elliptic, 9.0 mm long, 3.2 mm wide, venation reticulate with 3 principal veins from the base, next largest sepal lanceolate, 3.0 mm long, 1.0 mm wide, venation similar, third sepal sharply recurved, abaxially strigose, fourth sepal lanceolate, 2.3 mm long, 1.0 mm wide, fifth sepal broadly linear, 1.6 mm long, 0.5 mm wide, remaining stamen incurved, ca. 0.7 mm long, style 0.2 mm long (Figs. 3, 5).

Flower No. 2 (Figs. 1, 2, 4): Receptacle 1.3 mm long, 0.5 mm wide at apex (Fig. 4), largest sepal narrowly oblanceolate, 5.0 mm long, 0.6 mm wide, venation as in flower No. 1, next largest sepal elliptic, 1.8 mm long, 0.4 mm wide, third sepal broadly linear, 1.4 mm long, 0.2 mm wide, fourth sepal lanceolate, 1.3 mm long, 0.2 mm wide, fifth sepal sharply reflexed (Fig. 2), pedicel 3.2 mm long.

[1]Pistil is considered by some to be an ambiguous term. In the present context, it refers to a gynoecium composed of an ovary, a single style, and an undivided stigma.

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

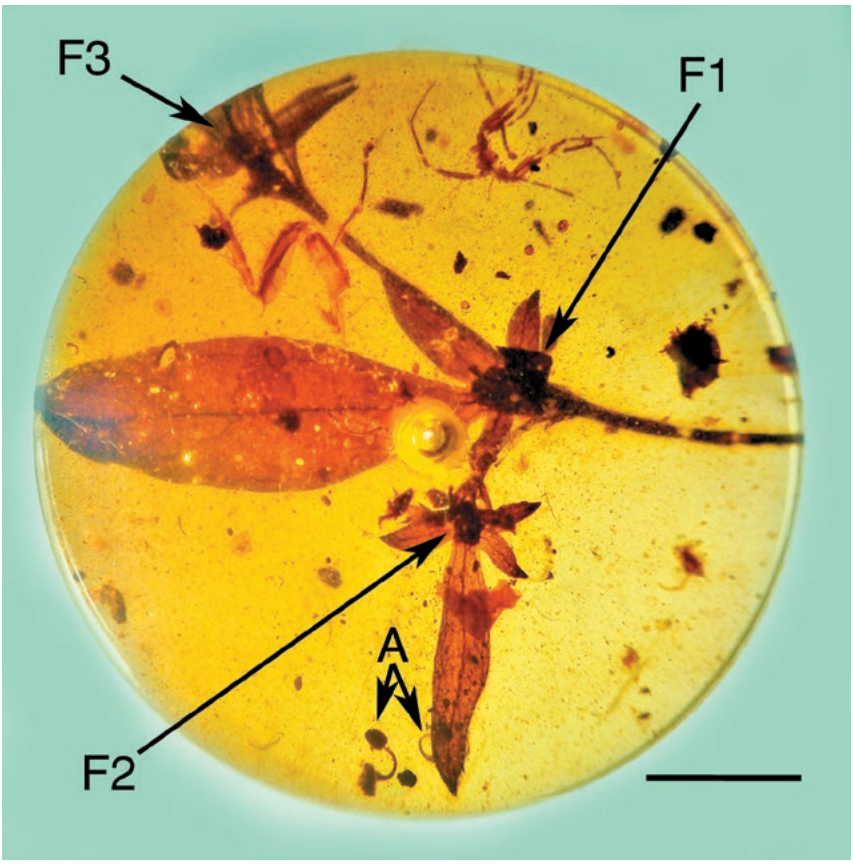

Fig. 1. ***Dispariflora robertae.*** **Bead-like piece of amber containing the partial inflorescence of 3 flowers, labeled F1, F2, F3 for reference. A. Disarticulated stamens from some other flower(s) in the inflorescence. Scale bar = 3.0 mm.**

Flower No. 3 (Figs. 5, 8): Receptacle 0.5 mm wide, bearing basal scars of disarticulated stamens, sepal 1, 2.2 mm, sepal 2, 2.1 mm, sepal 3, 1.3 mm, remaining stamen with filament 0.7 mm long, anther 0.6 mm long (Fig. 5), pistil 1.1 mm long, ovary 0.7 mm, echinate-bristly on one side, finely plumose on other side, style 0.4 mm, stigma capitate, 0.2 mm wide (Fig. 8).

Disarticulated stamen (Figs. 1, 7): Filament curved, glabrous, ca. 1.0 mm long, base 0.2 mm wide, possibly with remnant of a basal gland (Fig. 7), anther 0.4 mm long, 0.3 mm wide. Pollen spherical, monocolpate or dicolpate, 16-18 µm in diameter (Fig. 10).

Etymology.—Species name in honor of Roberta Poinar, who kindly donated the type specimen.

DISCUSSION

The specimens of *Dispariflora* described here demonstrate that flowers were continuously added to the inflorescence by the production of new lateral branches below existing flowers. Figure 4 shows a young flower arising from the axil of a bract below flower No. 2. Coincidentally, there is a second specimen of *Dispariflora* known from Myanmar amber, illustrated by Fangyuan et al. (2015) but not formally described, which provides further information about the variation in flower size that characterizes this genus. In the latter specimen, 4 flowers are present, but those with the largest leaf-like sepal are on lateral branches arising below terminal flowers with a smaller leaf-like sepal. In our specimen (Fig. 1), the largest sepal is on the terminal flower, not on

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

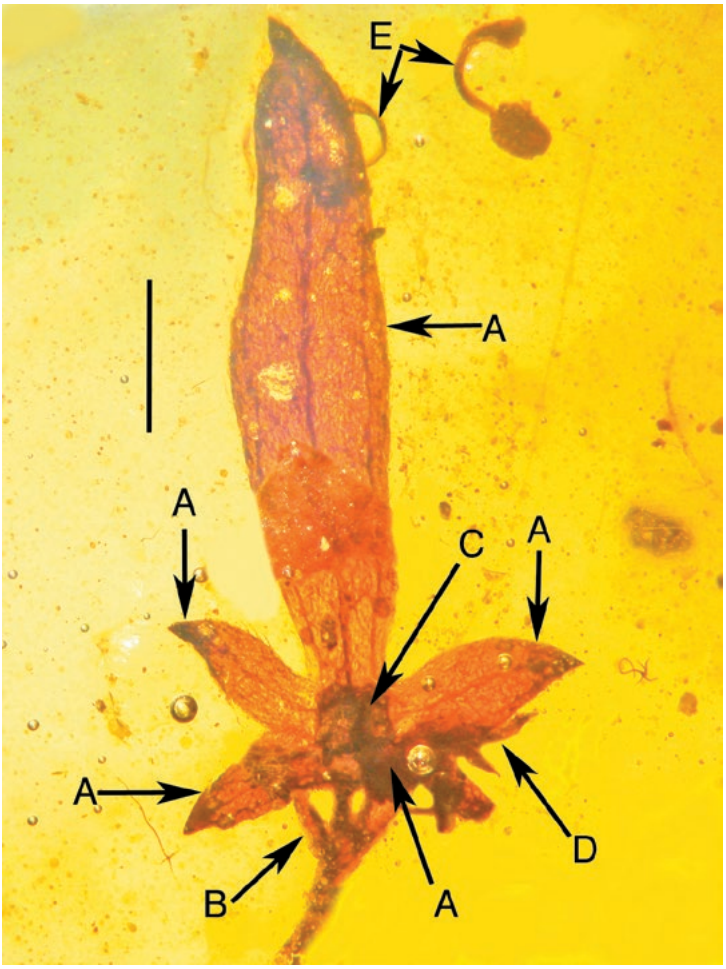

Fig. 2. *Dispariflora robertae*. Flower F2, apical view. **A.** Sepals. **B.** Bract. **C.** Receptacle. **D.** Immature lateral flower. **E.** Disarticulated stamens. Scale bar = 1.2 mm.

the lateral flowers below it. Apparently, there were differences in the size of floral meristems at the apex and branches of the cyme, which led to the observed larger and smaller flowers, but there is no consistent pattern in floral meristem size at one position or the other. Even larger flowers must have been present, because the 2 disarticulated stamens (Figs. 2, 7), presumed to belong to this inflorescence, are too large to have been associated with any of the 3 extant flowers in the amber. A similar disarticulated stamen was present in the fossil inflorescence photographed by Fangyuan et al. (2015).

Although the exact number of stamens per flower in *Dispariflora* is not known, both intact and disarticulated stamens (Figs. 6, 7) provide evidence of the overall structure of these organs. We interpret the anthers to be bithecal, dehiscing by longitudinal slits, and lacking an apiculate tip on the connective. This is similar to anthers occurring in some genera of Monimiaceae, for example, but differs from the valvate anthers of Atherospermataceae, Hernandiaceae, Lauraceae, and Siparunaceae (Philipson 1993 [as Monimiaceae subfam. Atherospermatoideae]; Kubitzki 1993; Rohwer 1993; Renner & Hausner 2005). The number of pollen sacs could not be determined. The mature anther in Figure 6 superficially matches, in its mode of dehiscence, those of *Hortonia* (Monimiaceae; Endress 1980), which were shown by that author to be tetrasporangiate.

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

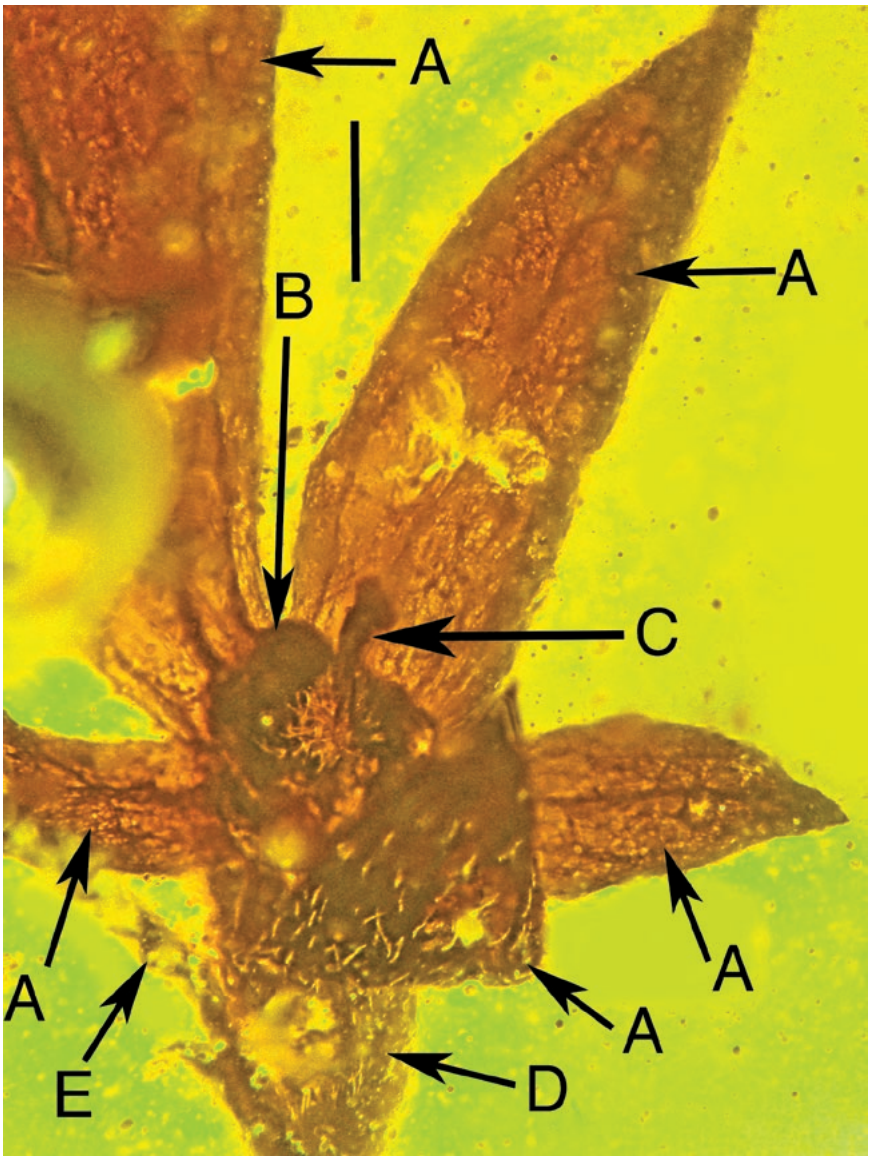

Fig. 3. *Dispariflora robertae.* Flower F1, apical view. **A.** Sepals. **B.** Stamen. **C.** Style. **D.** Bract. **E.** Pedicel of lateral flower. Scale bar = 0.6 mm.

It was mentioned previously that the fossils resemble the West African dioecious genus *Glossocalyx* in having one much-enlarged sepal. However, in that taxon the reproductive organs are covered by a floral roof (velum) with a central pore through which the styles or stamens emerge, as in *Siparuna* (Perkins & Gilg 1901, figs. 24, 28; Renner & Hausner 2005). We have no suggestions as to the function of the enlarged sepal of *Dispariflora*. It appears to be nothing more than a distant morphological parallelism with the otherwise unrelated *Glossocalyx*.

Pubescence of the pistil of *Dispariflora* is unusual, consisting of 2 different types of trichomes on opposite sides of the ovary (Figs. 8, 9). We have not found anything exactly like this in the literature on Monimiaceae

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

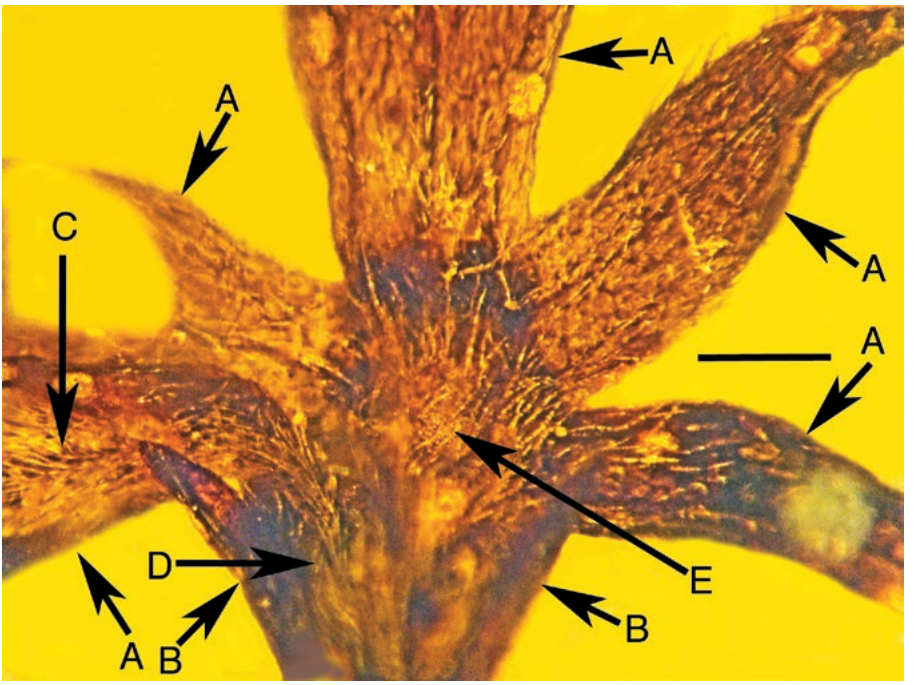

Fig. 4. *Dispariflora robertae.* Flower F2, basal view. **A.** Sepals. **B.** Bracts. **C.** Developing lateral flower. **D.** Pedicel of lateral flower. **E.** Receptacle. Scale bar = 0.5 mm.

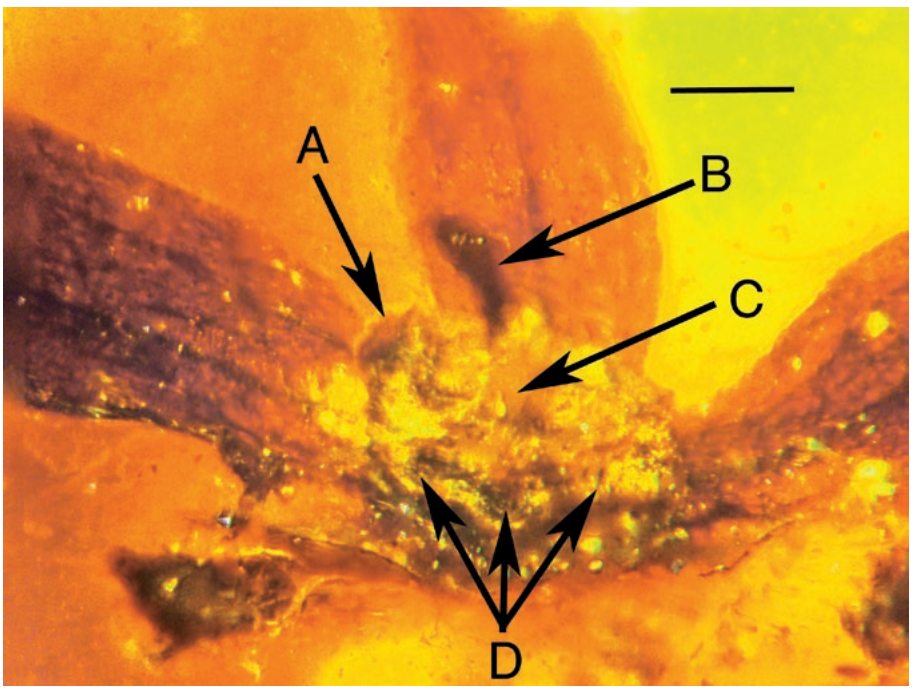

Fig. 5. *Dispariflora robertae.* Flower F3, lateral view of receptacle. **A.** Stamen. **B.** Style. **C.** Pistil. **D.** Scars left by disarticulated stamens. Scale bar = 0.2 mm.

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

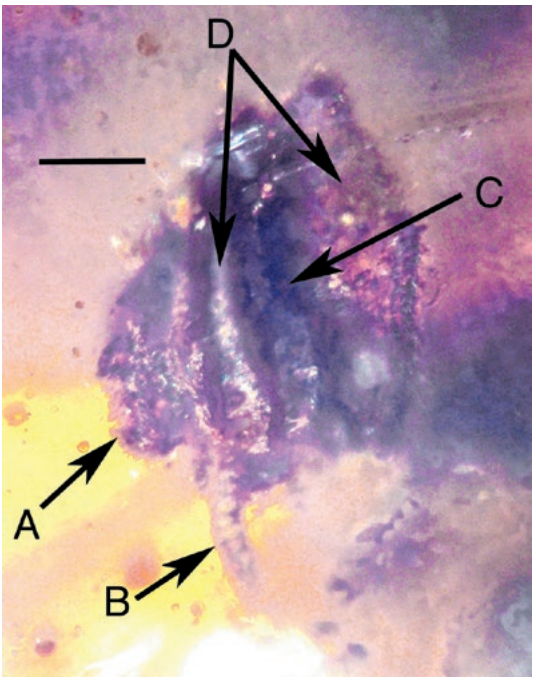

Fig. 6. *Dispariflora robertae.* Flower F2, persistent stamen after release of pollen. **A.** Anther. **B.** Filament. **C.** Cavity of theca. **D.** Separated walls of theca. Scale bar = 88 µm.

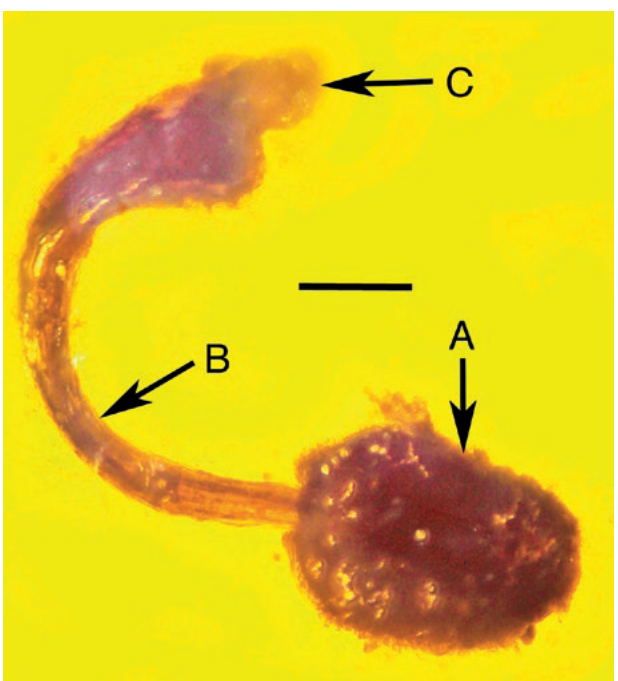

Fig. 7. *Dispariflora robertae.* Disarticulated stamen. **A.** Anther. **B.** Filament. **C.** Possible basal appendage. Scale bar = 156 µm.

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

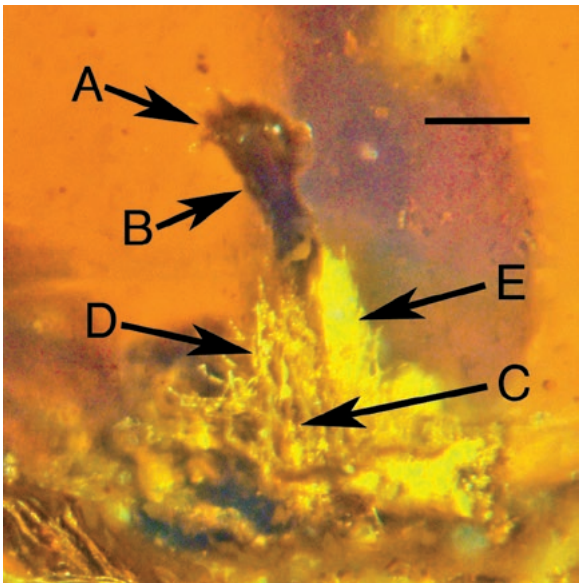

Fig. 8. *Dispariflora robertae.* Flower F3, pistil. **A.** Stigma. **B.** Style. **C.** Ovary. **D.** Echinate bristles. **E.** Plume of fine trichomes. Scale bar = 0.3 mm.

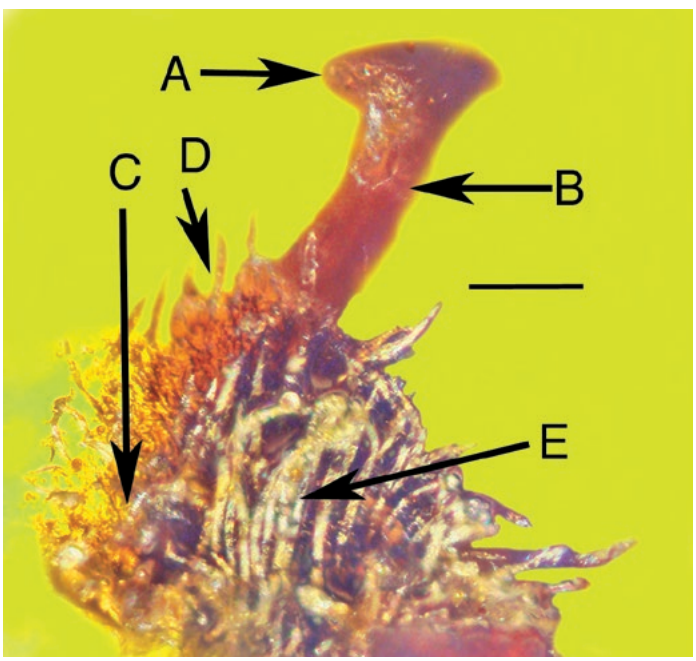

Fig. 9. *Dispariflora robertae.* Flower F1, pistil. **A.** Stigma. **B.** Style. **C.** Ovary. **D.** Echinate bristles. **E.** Fine trichomes. Scale bar = 90 µm.

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

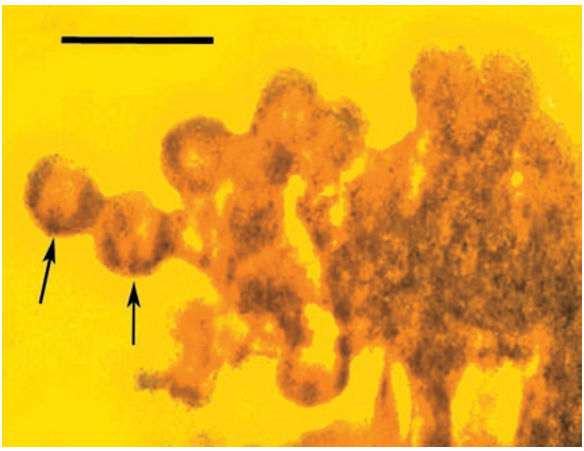

Fig. 10. Enlarged view of pollen grains showing colpi (arrows). Scale bar = 35 µm.

and related families. The description of pistils in *Dryadodaphne* (Atherospermataceae), a small genus ranging from New Guinea to Queensland, as "ellipsoid, silky on one side" (Philipson 1993, pp. 431–432) is suggestive. However, the floral morphology of this genus is otherwise unlike *Dispariflora* (e.g., its flowers are unisexual, the perianth of staminate flowers being tubular-turbinate and composed of 8 segments in 2 unequal series [Moore 1923]). In addition, the anthers open by pores, not slits (Philipson 1993, p. 431, key to genera). Pistils of *Atherosperma* (Australia and Tasmania) and *Laurelia* (with species in New Zealand and Chile), are plumose on both the ovary and style, but lack sharp bristles (Perkins & Gilg 1901, pp. 76–79; Philipson 1993, fig. 94K). *Matthaea*, in Monimiaceae, and *Daphnandra*, in Atherospermataceae, have pilose ovaries (Perkins & Gilg 1901, pp. 51–52, 74–75), but these genera differ from *Dispariflora* in their polyphyllous perianths and valvate anthers, as well as other floral traits.

Another unanswered question is whether there were basal glands on the stamen filaments of *Dispariflora*. Such glands are a common feature in modern families of Laurales (see Renner 1999, table 4, for a list of character states for many genera of this order). One disarticulated stamen of *Dispariflora* has a distinct enlargement at the base (Fig. 7), but whether or not this represents a glandular appendage is uncertain.

At the time the inflorescence became preserved in tree resin, a small cluster of pollen grains was extruded from one of the disarticulated stamens (Fig. 7). Close examination of these grains (Fig. 10) shows that at least 2 of them are positioned so that an elongate colpus is visible on one side, which we refer to as monocolpate. It is possible that the colpus wraps around the grain, as in the "meridionosulcate" grains described from several genera of Atherospermataceae (Sampson 1975, 1996; Sampson & Foreman 1988). The SEM photographs of pollen in *Atherosperma moschatum* (Sampson & Foreman 1988, figs. 1–3) illustrate grains of this type. Pollen of *Doryphora sassafras* (op. cit., figs. 9–11) is better described as dicolpate. The similarity of pollen in *Dispariflora* with certain genera of Atherospermataceae is interesting in view of our reference, above, to the pistils in *Dryadodaphne,* which are "silky on one side" like the pistil of *Dispariflora*. Nonetheless, the flowers in this family differ in many respects from the amber fossils. For example, the anthers have valvate dehiscence, the perianth is composed of numerous tepals in 2 or more whorls and is not enlarged or leaf-like, the pistils are numerous, the stigmas are not capitate, and the flowers are often monoecious or dioecious (Perkins & Gilg 1901, figs. 21–22).

As discussed elsewhere (Poinar 2018; Poinar & Chambers 2017, 2018b), plant and animal fossils in Myanmar amber dating to the mid-Cretaceous may have lived in the Southern Hemisphere continent of Gondwana, a part of which separated and drifted northward in the Triassic and Early Cretaceous (Hall 2012; Metcalfe 2013), finally connecting with the southern border of Asia in the Late Cretaceous and Eocene periods.

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

Monimiaceae, Siparunaceae, and Atherospermataceae, to which we have compared *Dispariflora,* are today distributed mainly in the Southern Hemisphere, consistent with a Gondwana origin for Myanmar amber. (Note, however, that these families do not form a monophyletic clade). The proposed assignment of *Dispariflora* to the Laurales is in agreement with the Early Cretaceous age of angiosperm fossils that have previously been assigned to this order (e.g., Crane et al. 1994; Friis et al. 2011, pp. 232, 484; Stevens 2001 and onwards).

ACKNOWLEDGMENTS

Valuable review comments and corrections were received from Susanne Renner and Peter Endress. We thank Deborah Carroll, OSU Valley Library, for assistance with reference materials.

REFERENCES

Crane, P.R., E.M. Friis, & K.R. Pedersen. 1994. Paleobotanical evidence on the early radiation of magnoliid angiosperms. Pl. Syst. Evol. (Suppl.) 8:51–72.

Cruickshank, R.D. & K. Ko. 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. J. Asian Earth Sci. 21:441–455.

Ellstrand, N.C., E.M. Lord, & K.J. Eckard. 1984. The inflorescence as a metapopulation of flowers: position-dependent differences in function and form in the cleistogamous species *Collomia grandiflora* Dougl. ex Lindl. (Polemoniaceae). Bot. Gaz. 145:329–333.

Endress, P.K. 1980. Floral structure and relationships of *Hortonia* (Monimiaceae). Pl. Syst. Evol. 133:199–221.

Fangyuan, X., Y. Gongda, Z. Qingqing, S. Gongle, & W. Bo. 2015. Amber—the elf through time and space. Science Press, Beijing. (In Chinese).

Friis, E.M., P.R. Crane, & K.R. Pedersen. 2011. Early flowers and angiosperm evolution. Cambridge University Press, Cambridge, UK.

Hall, R. 2012. Late Jurassic-Cenozoic reconstructions of the Indonesian region and the Indian Ocean. Tectonophysics 570–571:1–41.

Kubitzki, K. 1993. Hernandiaceae. In: K. Kubitzki, J.G. Rohwer, & V. Bittrich, eds. The families and genera of vascular plants. 2:334–338.

Lord, E.M. 1981. Cleistogamy: a tool for the study of floral morphogenesis, function, and evolution. Bot. Rev. 47:421–449.

Metcalfe, I. 2013. Gondwana dispersion and Asian accretion: tectonic and palaeogeographic evolution of eastern Tethys. J. Asian Earth Sci. 66:1–33.

Moore, S.M. 1923. A new genus of Lauraceae from New Guinea. J. Bot. 61:109.

Pax, F. 1891. Monimiaceae. In: A. Engler & K. Prantl, eds. Die natürlichen Pflanzenfamilien. 3(2):94–105.

Perkins, J. & E. Gilg. 1901. Monimiaceae. In: A. Engler, ed. Das Pflanzenreich. 4(101):1–122.

Philipson, W.R. 1993. Monimiaceae. In: K. Kubitzki, J.G. Rohwer, & V. Bittrich, eds. The families and genera of vascular plants. 2:426–437.

Poinar, G.O., Jr. 2018. Burmese amber: evidence of Gondwanan origin and Cretaceous dispersion. Hist. Biol. 2018:1–6.

Poinar, G.O., Jr. & K.L. Chambers. 2017. *Tropidogyne pentaptera* sp. nov., a new mid-Cretaceous fossil angiosperm flower in Burmese amber. Palaeodiversity 10:135–140.

Poinar, G.O., Jr. & K.L. Chambers. 2018a. *Endobeuthos paleosum* gen. et sp. nov., fossil flowers of uncertain affinity from mid-Cretaceous Myanmar amber. J. Bot. Res. Inst. Texas 12:133–139.

Poinar, GO., Jr. & K.L. Chambers. 2018b. *Setitheca lativalva* gen. et sp. nov., a fossil flower of Laurales from mid-Cretaceous Myanmar amber. J. Bot. Res. Inst. Texas 12:643-653.

Poinar, G.O., Jr., G.J.B. Lambert, & Y. Wu. 2007. Araucarian source of fossiliferous Burmese amber: spectroscopic and anatomical evidence. J. Bot. Res. Inst. Texas 1:449–455.

Renner, S.S. 1999. Circumscription and phylogeny of the Laurales: Evidence from molecular and morphological data. Amer. J. Bot. 86:1301–1315.

Renner, S.S. & G. Hausner. 2005. Siparunaceae. Fl. Neotropica Monogr. 95:1–256.

Rohwer, J.G. 1993. Lauraceae. In: K. Kubitzki, J.G. Rohwer, & V. Bittrich, eds. The families and genera of vascular plants. 2:366–391.

Sampson, F.B. 1975. Aperture orientation in *Laurelia* pollen (Atherospermataceae, syn. subfamily Atherospermoideae of Monimiaceae). Grana 15:153–157.

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.

Sampson, F.B. 1996. Pollen morphology and ultrastructure of *Laurelia, Laureliopsis* and *Dryadodaphne* (Atherospermataceae [Monimiaceae]). Grana 35:257–265.

Sampson, F.B. & D.B. Foreman. 1988. Pollen morphology of *Atherosperma, Daphnandra* and *Doryphora* (Atherospermataceae [Monimiaceae]). Grana 27:17–25.

Shi, G., D.A. Grimaldi, G.E. Harlow, J. Wang, M. Yang, W. Lei, Q. Li, & X. Li. 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Res. 37:155–163.

Stevens, P.F. 2001 onwards. Angiosperm phylogeny website. Version 14, July 2017 (and updated since).

This document is intended for digital-device reading only.
Inquiries regarding distributable and open access versions may be directed to jbrit@brit.org.