VALVILOCULUS PLERISTAMINIS GEN. ET SP. NOV., A LAURALEAN FOSSIL FLOWER WITH VALVATE ANTHERS FROM MID-CRETACEOUS 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

Urszula T. Iwaniec
Skeletal Biology Laboratory
College of Public Health and Human Sciences
Oregon State University
Corvallis, Oregon 97331, U.S.A.

Fernando E. Vega
Sustainable Perennial Crops Laboratory
U. S. Department of Agriculture
Agricultural Research Service
Beltsville, Maryland 20705, U.S.A.
Fernando.Vega@usda.gov

ABSTRACT

The flower described here as **Valviloculus pleristaminis,** a new genus and species of fossil angiosperms, was obtained from Myanmar amber deposits dating to the mid-Cretaceous period. The flower is staminate, with an ovoid, hollow floral cup. The perianth consists of 6 tepals, one of which was lost prior to preservation. Numerous helically arranged stamens are borne at the summit of the flower. The anthers are bilocular, with pollen sacs that dehisce by laterally hinged valves. The tip of the connective bears a cup-shaped appendage. The gynoecium is represented only by a cluster of vestigial styles centered among the stamens. The fossil is provisionally assigned to order Laurales, its closest affinities being with the families Monimiaceae and Atherospermataceae.

RESUMEN

La flor descrita aquí como **Valviloculus pleristaminis,** un nuevo género y especie de angiospermas fósiles, se obtuvo de depósitos de ámbar de Myanmar que datan del Cretácico medio. La flor es estaminada, con una copa floral ovoide, hueca. El perianto consiste en 6 tépalos, uno de los cuales se perdió antes de la conservación. Numerosos estambres dispuestos helicoidalmente nacen en el extremo de la flor. Las anteras son biloculares, con sacos polínicos dehiscentes por valvas unidas lateralmente. El extremo del conectivo lleva un apéndice acopado. El gineceo está representado solo por un grupo de estilos vestigiales centrados entre los estambres. El fósil se asigna provisionalmente al orden Laurales, sus afinidades más cercanas son con las familias Monimiaceae y Atherospermataceae.

INTRODUCTION

Valviloculus pleristaminis is a further addition to the some 20 new genera of flowering plants recently named from fossils in mid-Cretaceous Myanmar amber (Crepet et al. 2016; Poinar 2018b; Liu et al. 2018; Chambers & Poinar 2020; Poinar & Chambers 2020a, b). An evolutionary connection with the basal angiosperm order Laurales has been proposed for several of these genera. Distinctive features of these fossils that suggest such a relationship include an unusual form of monoporate pollen (Poinar & Chambers 2020a), horseshoe-shaped anthers (Chambers & Poinar 2020), and anthers with valvate dehiscence, the valves hinged either apically (Crepet et al. 2016; Poinar 2017) or laterally (Poinar & Chambers 2018; 2019; 2020c). The floral morphology of *Valviloculus,* as we interpret it, has some features found in the Hernandiaceae, Monimiaceae, and Atherospermataceae, although anthers with laterally hinged valves are rare or absent in the latter two families (Kubitzki 1993; Lorence 1985, figs. 13, 21; Renner 1999, tab. 4). The flower is unisexual, perigynous (see below), and its tepals apparently are arranged in two whorls of 3 or as 3 decussate pairs. The androecium of the fossil consists of 50 or more helically arranged stamens. The closed, hollow floral cup is a distinctive feature of *Valviloculus*, being unlike the staminate flowers in almost all genera of modern Laurealean families. Unfortunately, pistillate or perfect flowers of the genus, which might help to verify our interpretation of the fossil, have not yet been reported from Myanmar amber.

J. Bot. Res. Inst. Texas 14(2): 359 – 366. 2020
https://doi.org/10.17348/jbrit.v14.i2.1014

MATERIALS AND METHODS

Amber from Myanmar has been known commercially for centuries and has been the source for over 870 species of plant and animal fossils (Ross 2018; Poinar 2018a). Mines currently in operation are at the Noije Bum 2001 Summit Site, whose geology was described by Cruickshank and Ko (2003). These authors dated the amber deposits as Late Albian, 97–110 Ma, based on paleontological (ammonite) and palynological evidence. Subsequently, a more exact age of 98.79 ± 0.62 Ma was determined by Shi et al. (2012) using radiometric U–Pb dating of zircons in volcanic clasts contemporaneous with the amber. We apply the term mid-Cretaceous to this time period, which spans the latest Albian and earliest Cenomanian series (Cohen et al. 2013). Poinar et al. (2007) utilized nuclear magnetic resonance spectroscopy, augmented by an anatomical study of wood fragments, in assigning the amber to resin from members of family Araucariaceae, perhaps the Australasian genus *Agathis*.

As in our previous studies of fossils in amber, the observations were made using 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.

Micro-CT examination of the flower, performed with a Scanco µCT40 scanner (Scanco Medical AG, Bassserdorf, Switzerland) at a voxel size of 6×6×6 microns (55 kVp x-ray voltage, 145 µA intensity, and 200 ms integration time), provided a nondestructive 3-dimensional evaluation. The filtering parameters, sigma and support, were set to 0.8 and 1, respectively. Segmentation was conducted at an empirically determined threshold of 180 (scale 0–1000).

DESCRIPTION

Valviloculus Poinar, K.L. Chambers, & F.E. Vega, **gen. nov.** TYPE SPECIES: *Valviloculus pleristaminis* Poinar, K.L. Chambers, & F.E. Vega, sp. nov.

Flower pedicellate, staminate, the ovoid floral cup closed at the apex, hollow within, the interior cavity empty (Fig. 6), epidermis covered with multicellular papillae (Figs. 1, 2), tepals probably 6, one tepal having been lost from the fossil before preservation, remaining 5 tepals spreading, arched upward, blades triangular, acute, abaxial epidermis papillate (Figs. 1, 2), stamens ca. 50, helically arranged, ± sessile (Figs. 3, 4), anthers bilocular, pollen sacs introrsely dehiscent by laterally hinged valves (Figs. 3, 4), connective bearing a cup-shaped apical appendage (Fig. 4), vestigial styles 30+, tightly clustered in the center of the flower (Figs. 3, 5, 6), functional pistils 0, pollen spherical, inaperturate (Fig. 7).

Valviloculus pleristaminis Poinar, K.L. Chambers, & F.E. Vega, **sp. nov.** (**Figs. 1–7**). TYPE: MYANMAR (BURMA). KACHIN PROVINCE: Noije Bum 2001 Summit Site amber mine in the Hukawng Valley SW of Maingkhwan, 26°20'N, 96°36'E, 2019, *unknown amber miner, s.n.* (HOLOTYPE: Accession number B-An-8-19, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

Pedicel, as preserved, 1 mm long, flower 2.7 mm wide as measured across opposing tepals, floral cup 1.7 mm high, 1.2 mm wide at the apex (Fig. 6), tepals 1.0 mm wide at the base, 1.3 mm long, anthers 45 µm long, 2.7 µm wide (Figs. 1, 3), vestigial styles 40–50 µm long, pollen grains 15–16 µm in diameter (Fig. 7).

Etymology.—Genus name from the Latin "valva," leaf of a folding door, valve, and "loculus," compartment, referring to the mode of anther dehiscence. Species epithet from the Latin "plerus," very many, and "stamen," referring to the numerous stamens.

DISCUSSION

The unusual floral characteristic of laterally (i.e., dorsally) attached anther valves in *Valviloculus* is best known in the genera *Hernandia* and *Illigera* of family Hernandiaceae (Endress & Hufford 1989; Endress & Stumpf 1990). It is also found in *Monimia amplexicaulis*, family Monimiaceae (Lorence 1985, figs. 13, 21). Microphotographs and CT scans of the fossil (Figs. 4, 6), show the stamen filaments to be either very short or

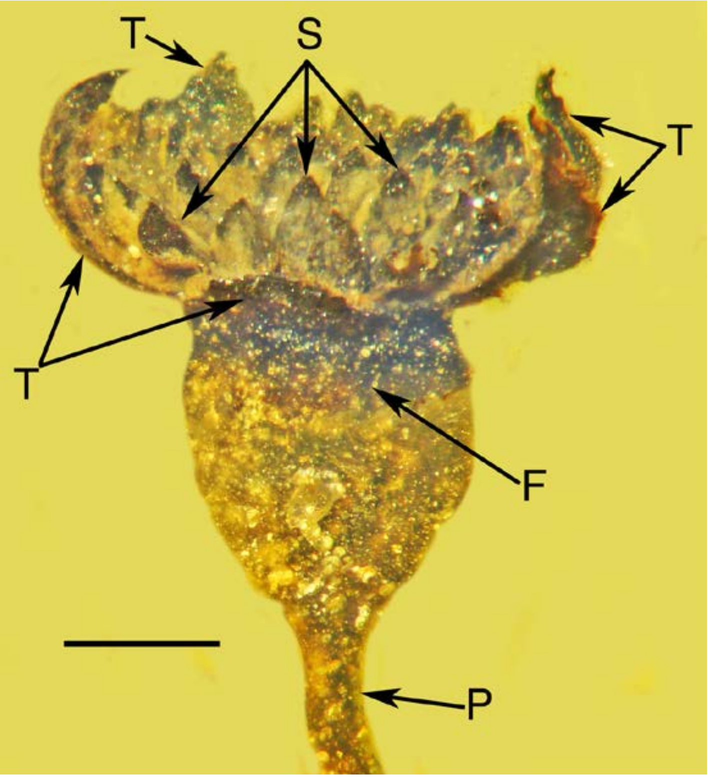

Fig. 1. *Valviloculus pleristaminis.* Flower in lateral view. **F.** Floral cup. Note papillate surface. **P.** Pedicel. **S.** Stamens. **T.** Tepals. Between the furthest 2 tepals is the space occupied by a missing tepal. Scale bar = 0.8 mm.

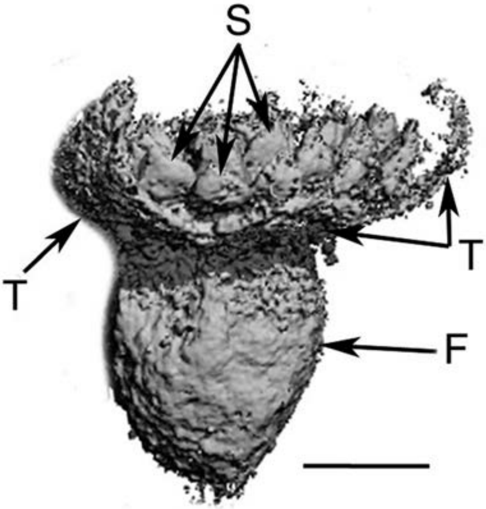

Fig. 2. *Valviloculus pleristaminis*. 3-D reconstruction of the flower produced by Micro-CT scanning. **F.** Floral cup. **S.** Stamens. **T.** Tepals. Compare with Fig. 1 taken from a similar position. Scale bar = 0.9 mm.

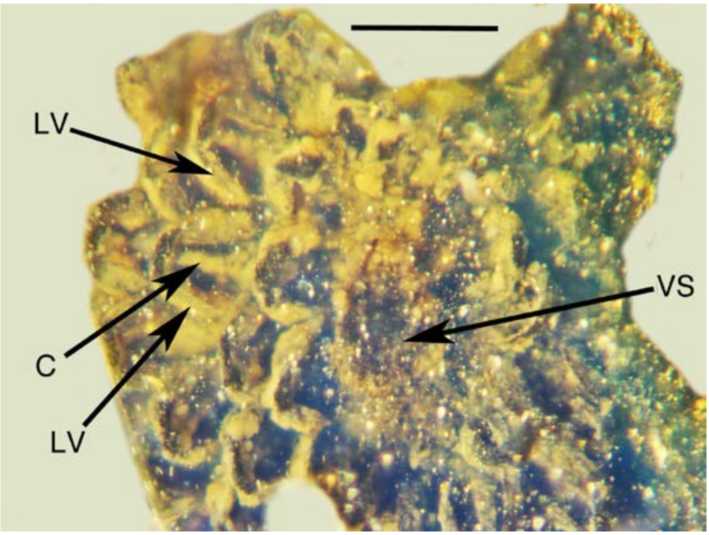

Fig. 3. ***Valviloculus pleristaminis*****. Center of flower in apical view. C. Anther connective. LV. Lateral valves of dehisced anthers, VS. Central cluster of vestigial styles. Scale bar = 78 µm.**

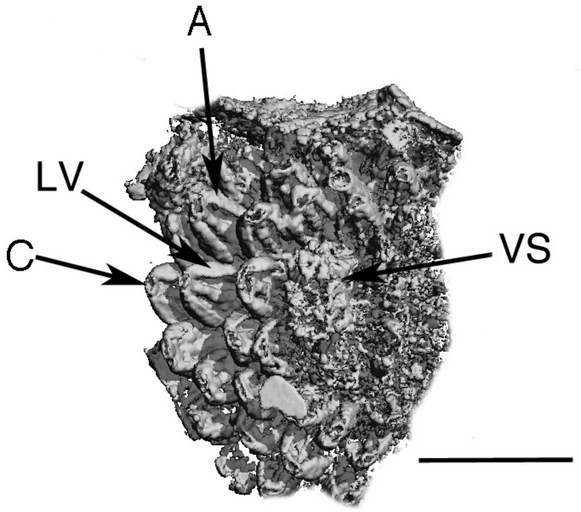

Fig. 4. ***Valviloculus pleristaminis*****. 3-D reconstruction of flower in apical view. A. Anther. C. Cup-shaped terminal appendage of anther connective. LV. Lateral valve of dehisced anther. VS. Central cluster of vestigial styles. Compare with Fig. 3 taken from a similar position. Scale bar = 83 µm.**

absent, much like the stamens illustrated for *Hernandia nymphaeifolia* by Endress & Lorence (2004, fig. 3). The stamens of the fossil are too crowded to show whether paired glands are present at the filament base (Fig. 4). A unique characteristic of *Valviloculus* may be the minute, cup-shaped terminal appendage on the anther connective, perhaps representing a secretory gland (Fig. 4). Anthers with a terminal sterile extension of the connective were already present in some fossil flowers of the Early Cretaceous (Friis et al. 2013, pp. 401–402), but no appendages are described as cup-shaped. In the Myanmar amber fossil *Jamesrosea* (Crepet et al. 2016) and

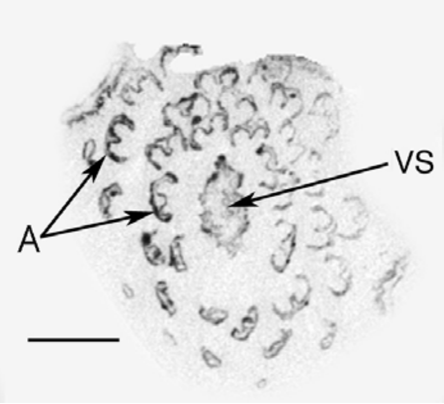

Fig. 5. ***Valviloculus pleristaminis*. Micro-CT scan of stamens in apical view. A. Cross-sections of dehisced anthers showing open valves. VS. Central cluster of vestigial styles. Compare with Figs. 3 and 4. Scale bar = 50 µm.**

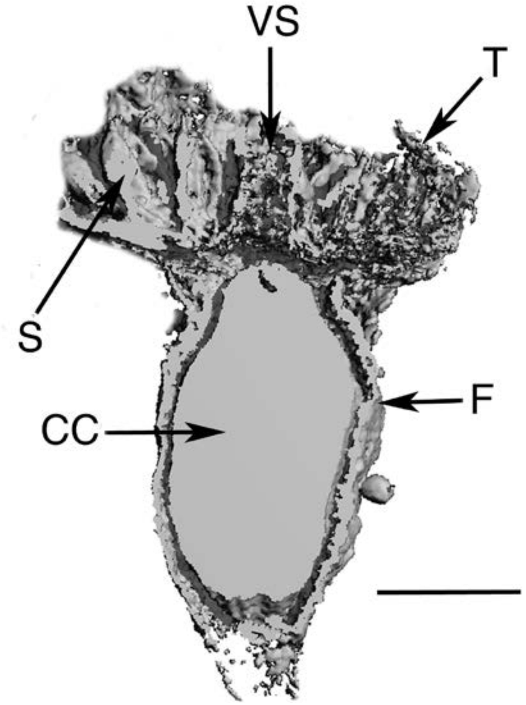

Fig. 6. ***Valviloculus pleristaminis*. Vertical section of flower by Micro-CT scan. CC. Empty central cavity of floral cup. F. Floral cup. Note closed apex. T. Tepal. VS. Column of connivent vestigial styles. S. Stamen. Scale bar = 0.7 mm.**

in modern monimioid genera such as *Peumus* (Endress & Hufford 1989, fig. 81), *Mollinedia* (Perkins & Gilg 1901, fig. 6), and *Tambourissa* (Lorence 1985, p. 89), anthers may have an acute appendage at the tip.

Among the fossil angiosperms thus far known from Myanmar amber, *Valviloculus* is most similar to *Setitheca* (Poinar & Chambers 2018), which was described from a staminate flower with an enlarged receptacle and anthers having laterally hinged valves. However, *Setitheca* has only 10 stamens, which are positioned in a whorl at the edge of a flat central disc, and its perianth consists of 12 spirally arranged tepals of varying size and shape (Poinar & Chambers 2018, figs 1, 2). Its receptacle and tepals are densely hispidulous externally, rather than glandular-papillate as in *Valviloculus*. A taxonomic assignment to order Laurales was proposed for *Setitheca*, based on the similarity of its anthers to those of *Hernandia* and its perianth to that of *Hortonia,* which has 18, mostly spirally arranged, tepals (Endress 1980b). However, it is unknown whether the female flowers of the genus were perigynous, i.e., with pistils surrounded by a floral cup, or had a fully inferior ovary. Our use of the term floral cup for the enlarged lower portion of the *Valviloculus* flower is based on a comparison with certain members of the Atherospermataceae, as described below. In top view (Fig. 3) and vertical cross-section (Fig. 6), the flower of *Valviloculus* shows a central cluster of 30+ short, linear structures that arise at the apex of the empty cavity occupying the lower part of the flower. These organs do not resemble staminodes, as for example, in *Daphnandra* (Endress 1992, fig. 2; Foreman & Whiffin 2007, fig. 22F, G) or *Jamesrosea* (Crepet et al. 2017, fig. 2D), and they differ so much from the adjacent functional stamens that, by their position and structure, they are here interpreted as persistent vestigial styles.

The large, hollow cavity within the body of the flower, as revealed by CT-scanning (Fig. 6), is a surprising feature of the fossil and leads to an interpretation that may link the genus to families in the order Laurales. Phylogenetic relationships among the group of families formerly included in Monimiaceae (Perkins & Gilg 1901; Philipson 1993) were clarified by Renner (1998; 1999; 2004) based on cpDNA gene and spacer sequences. In the currently recognized families Monimiaceae, Atherospermataceae, Siparunaceae, and Gomortegaceae, variously shaped floral cups are almost always present (Renner 1999, tab. 4). The floral cup, especially in

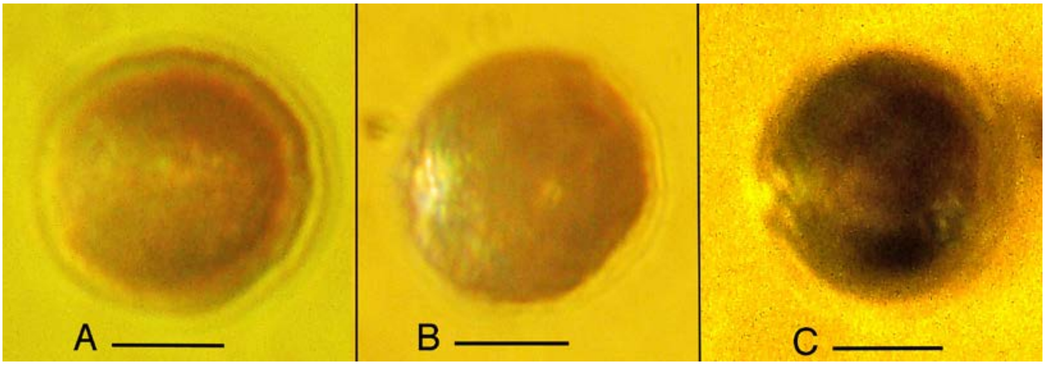

Fig. 7. ***Valviloculus pleristaminis.*** **Pollen grains. A. Scale bar = 6.0 µm. B. Scale bar = 7.0 µm. C. Scale bar = 7.0 µm.**

staminate flowers, may be cupulate and fully open at the apex (Perkins & Gilg 1901, figs. 3, 6), but in both staminate and pistillate flowers, it is more often ovoid or globose and nearly completely closed at the apex (Perkins & Gilg op. cit., figs. 7, 14; Endress 1980a). Dehiscence of the cup is circumcissle or by vertical slits, and in the latter case the stamens or fruits are exposed on reflexed segments of the cup (Lorence 1985, fig. 21C; Philipson 1993, fig. 95D, Q). Stamen numbers vary greatly between and within genera. For example, Lorence (1985) cites in *Tambourissa* (Monimiaceae) the species *T. purpurea* with 20–32 stamens per flower and *T. ficus* with up to 1800 stamens.

In the group of families mentioned above, bisexual flowers are known today only in *Hortonia* (Endress 1980b), in *Daphnandra*, *Doryphora*, and *Nemuaron* of the Atherospermataceae (Perkins & Gilg 1901, pp. 73–80), and in the Hernandiaceae (Kubitzki 1993; Duyfjes 1996). On the hypothesis that the predominantly unisexual flowers of Monimiaceae and their relatives arose from bisexual ancestors, a likely interpretation of *Valviloculus* is that the main body of the flower is a closed floral cup, with connivent vestigial styles of an ancestral bisexual flower fused to and filling the apical pore (Fig. 6). The numerous stamens of *Valviloculus* are attached at the apex of this perigynous cup, and in this interpretation, closure of the cup occurred below the level of the stamens, allowing them to be exposed in the male flower. In the bisexual ancestral form, the pistils would have occupied the interior of the floral cup, with their styles exserted through the apical opening.

Just such an arrangement of reproductive organs is present in the modern genus *Daphnandra* (Perkins & Gilg 1901, p. 75; Endress 1980a, figs. 73, 88; Endress 1992, fig. 3). In *Daphnandra repandula*, the pistils are attached basally inside an ovoid floral cup, and "at anthesis the styles elongate and their apices grow through the narrow upper end of the cup" (Endress 1980a, p. 90). The genus differs from *Valviloculus* in that its perianth parts are of two kinds, the outer two series being sepaloid and whorled or decussate, and the inner two series being larger and petaloid, with a total of up to 10 parts (Foreman & Whiffin 2007). There are 4–7 functional stamens, whose filaments bear a pair of basal glands, plus usually 2–3 inner whorls of staminodes. A further difference is that the anthers of *Daphnandra* dehisce extrorsely by two apically hinged valves and have no terminal appendage (Perkins & Gilg 1901, fig. 20E).

A fossil with some of the attributes of *Daphnandra* and of the hypothesized ancestor of *Valviloculus* is *Jamesrosea*, another mid-Cretaceous flower from Myanmar amber (Crepet et al. 2016). Although the authors do not specifically mention *Daphnandra*, their CT-scan of a vertical cross-section of *Jamesrosea* (op. cit., fig. 2H) much resembles the illustration of *Daphnandra tenuipes* by Perkins and Gilg (1901, fig. 20D), even down to the presence of staminodes between the pistils and the fertile stamens. The stamen filaments of *Jamesrosea* have a pair of basal glands, and the anthers are bilocular, opening by apically hinged valves like those of *Daphnandra*. They differ, however, by their introrse dehiscence and the possession of an attenuate terminal appendage (Crepet et al. 2016, fig. 1G). *Jamesrosea* has 4 simple pistils, while in *Daphnandra*, carpel numbers vary from 4 to 12 (Foreman & Whiffin 2007). The position of *Jamesrosea* as a member of the Laurales was confirmed by a cladistic morphological analysis, which placed the genus as sister to a clade of Atherospermataceae + Gomortegaceae (Crepet et al. 2016, fig. 3). Perhaps future studies of Myanmar amber will reveal examples of the pistillate or perfect flower of *Valviloculus* that accompanied the staminate one described here, leading to a better understanding of the position of the genus within order Laurales.

The pollen of *Valviloculus* is difficult to interpret due to the problem of photographing cells that are deeply embedded in the amber. The grains appear to have no well-defined pore or colpus, although a thin area may be present at one spot in the exine (Fig. 7). Inaperturate pollen is characteristic of the Monimiaceae (Foreman & Sampson 1987; Sampson 2000), whereas in the well-studied family Atherospermataceae, the grains are dicolpate or have a encircling meridional sulcus, as in *Daphnandra* (Sampson 1996; Sampson & Forman 1988).

The likelihood that certain angiosperm families first evolved on the Early Cretaceous continent of Gondwana is discussed by Poinar (2018a), with special reference to the fossil flowers preserved in Myanmar amber. Cited in particular are Cunoniaceae, Dilleniaceae, and Monimiaceae, the latter family now distributed in the southern continents of Australia, Malaysia, Africa, the Mascarene Islands, and South America (Renner et al. 2010, fig. 1). The conifer family Araucariaceae, which is implicated as the botanical source of the amber, has a similar distribution, excluding Africa (Mabberly 2008). Recent discussions of the geological origin of Southeast Asia (Hall 2012; Metcalfe 1990; Rangin 2017) propose that the West Burma Block, which includes the amber mines, broke away from Australia and rafted northward to its present location, either as a distinct entity or attached to the eastern portion of the Greater India Plate. The dating of its tectonic migration from Gondwana is not yet firmly established, but the 100 Ma age of the amber, with its included Southern Hemisphere-related plant and animal fossils, may factor into an eventual solution to this problem.

ACKNOWLEDGMENTS

We thank Dawn A. Olson for technical assistance. Deborah Carroll, OSU Valley Library, provided valuable assistance with the literature. Useful comments and suggestions by an anonymous reviewer are gratefully acknowledged.

REFERENCES

Chambers, K.L. & G.O. Poinar, Jr. 2020. *Thymolepis toxandra* gen. et sp. nov., a mid-Cretaceous fossil flower with horseshoe-shaped anthers. J. Bot. Res. Inst. Texas 14:57–64.

Cohen, K.M., S. Finney, & P.L. Gibbard. 2013. International Chronostratigraphic Chart. International Commission on Stratigraphy. www.stratigraphy.org

Crepet, W.L., K.C. Nixon, D. Grimaldi, & M. Riccio. 2016. A mosaic Lauralean flower from the Early Cretaceous of Myanmar. Amer. J. Bot. 103:290–297.

Cruickshank, R.D. & K. Ko. 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. J. Asian Earth Sci. 23:441–455.

Duyfjes, B.E.E. 1996. Hernandiaceae. In: Flora Malesiana, Ser. 1, 12:737–761.

Endress, P.K. 1980a. Ontogeny, function and evolution of extreme floral construction in Monimiaceae. Pl. Syst. Evol. 134:79–120.

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

Endress, P.K. 1992. Protogynous flowers in Monimiaceae. Pl. Syst. Evol. 181:227–232.

Endress, P.K. & L.D. Hufford. 1989. The diversity of stamen structures and dehiscence patterns among Magnoliidae. Bot. J. Linn. Soc. 100:45–85.

Endress, P.K. & S. Stumpf. 1990. Non-tetrasporangiate stamens in the angiosperms: Structure, systematic distribution and evolutionary aspects. Bot. Jahrb. Syst. 112:193–240.

Endress, P.K. & D.H. Lorence. 2004. Heterodichogamy of a novel type in *Hernandia* (Hernandiaceae) and its structural basis. Int. J. Pl. Sci. 165:753–763.

Foreman, D.B. & F.B. Sampson. 1987. Pollen morphology of *Palmeria scandens* and *Wilkiea huegellana* (Monimiaceae). Grana 26:127–133.

Foreman, D.B. & T. Whiffin. 2007. *Daphnandra*. In: A.J.G. Wilson, ed. Flora of Australia. CSIRO Publishing, Collingwood, Australia. 2:95–100.

Friis, E.M., P.R. Crane, & K.R. Pedersen. 2013. 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, and V. Bittrich, eds. The families and genera of vascular plants. Springer Verlag, Berlin, Germany 2:334–338.

Liu, Z-J., D. Huang, C. Cai, & X. Wang. 2018. The core eudicot boom registered in Myanmar amber. Sci. Rep. 8:16765.

Lorence, D.H. 1985. A monograph of the Monimiaceae (Laurales) in the Malagasy region (Southwest Indian Ocean). Ann. Missouri Bot. Gard. 72:1–165.

Mabberly, D.J. 2008. Mabberley's plant book. Ed. 3. Cambridge University Press, Cambridge, UK.

Metcalfe, I. 1990. Allochthonous terrane processes in Southeast Asia. Phil. Trans. Roy. Soc. London A133:625–640.

Perkins, J. & E. Gilg. 1901. Monimiaceae. In: A. Engler, ed. Das Pflanzenreich. Verlag Wilhelm Engelmann, Leipzig, Germany. IV. 101:1–122.

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

Poinar, G.O., Jr. 2017. A mid-Cretaceous Lauraceae flower, *Cascolaurus burmitis* gen. et sp. nov., in Myanmar amber. Cretaceous Res. 71:96–101.

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

Poinar, G.O., Jr. 2018b. Mid-Cretaceous angiosperm flowers in Myanmar amber. In: B. Welch & M. Wilkerson, eds. Recent advances in plant research. Nova Science Publishers, New York, U.S.A. Pp. 187–218.

Poinar, G.O., Jr. & K.L. Chambers. 2018. *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. & K.L. Chambers. 2019. *Zygadelphus aetheus* gen. et sp. nov., an unusual fossil flower from mid-Cretaceous Myanmar amber. J. Bot. Res. Inst. Texas 13:467–473.

Poinar, G.O., Jr. & K.L. Chambers. 2020a. *Dasykothon leptomiscus* gen. et sp. nov., a fossil flower of possible Lauralean affinity from Myanmar amber. J. Bot. Res. Inst. Texas 14:65–71.

Poinar, G.O., Jr. & K.L. Chambers. 2020b. *Phantophlebia dicycle* gen. et sp. nov., a five-merous fossil flower in mid-Cretaceous Myanmar amber. J. Bot. Res. Inst. Texas 14:73–80.

Poinar, G.O., Jr. & K.L. Chambers. 2020c. *Cyathitepala papillosa* gen. et sp. nov., a mid-Cretaceous fossil flower from Myanmar amber with valvate anthers. J. Bot. Res. Inst. Texas 14:351–358.

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.

Rangin, C. 2017. Active and recent tectonics of the Burma Platelet in Myanmar. In: A.J. Barber, K. Zaw, and M.J. Crow, eds. Myanmar: Geology, resources and tectonics. Mem. Geol. Soc. London 48:53–64.

Renner, S.S. 1998. Phylogenetic affinities of Monimiaceae based on cpDNA gene and spacer sequences. Perspect. Pl. Ecol. Evol. Syst. 1:61–77.

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. 2004. Variation in diversity among Laurales, Early Cretaceous to present. Biol. Skr. 55: 441–458.

Renner, S.S., J.S. Struk, D. Strasberg, & C. Thébaud. 2010. Biogeography of the Monimiaceae (Laurales): A role for East Gondwana and long-distance dispersal, but not West Gondwana. J. Biogeog. 37:1227–1238.

Ross, A.J. 2018. Burmese (Myanmar) amber taxa, on-line checklist v. 2018.2. www.nms.ac.uk/explore/stories/natural-world/burmese-amber/

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

Sampson, F.B. 2000. Pollen diversity in some modern Magnoliids. Int. J. Pl. Sci. 161(6 Suppl.):S193–S210.

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.