PHANTOPHLEBIA DICYCLA GEN. ET SP. NOV., A FIVE-MEROUS FOSSIL FLOWER IN 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

ABSTRACT

A fossil flower in mid-Cretaceous amber from Myanmar (Burma) is described as the new genus and species **Phantophlebia dicycla.** The perianth of the flower is composed of two 5-merous whorls of tepals, the outer tepals being smaller and more irregular in shape than the inner. All the tepals are distinctly vascularized, with few to many major veins that are connected above by an irregular network of veinlets. The flower's 5 stamens are opposite the inner tepals, with bilocular anthers that dehisce by latrorse, oblique slits. No gynoecium can be seen beneath the air bubble covering the center of the flower. The fossil shares some characteristics with myrsinoid members of family Primulaceae.

RESUMEN

Se describe una flor fósil del ámbar del Cretácico medio de Myanmar (Birmania) como el nuevo género y especie **Phantophlebia dicycla.** El perianto de la flor está compuesto de dos verticilos pentámeros de tépalos, los tépalos externos son más pequeños y de forma más irregular que los internos. Todos los tépalos están bien vascularizados, con pocas a muchas venas que están conectados por una red irregular de pequeñas venas. Los cinco estambres de la flor están opuestos a los tépalos internos, con anteras biloculares que se abren por hendiduras latrorsas, oblicuas. No se ha visto gineceo debajo de la burbuja de aire que cubre el centro de la flor. El fósil comparte algunas características con miembros mirsinoides de la familia Primulaceae.

INTRODUCTION

In spite of the present difficulty in obtaining fossiliferous amber from mines in northern Myanmar, due to civil unrest in the region (Sokol 2019), an increasing number of new angiosperm taxa have recently been described from these Cretaceous-age deposits (Crepet et al. 2016; Poinar 2018b; Liu et al. 2018; Poinar & Chambers 2018a, b; 2019a, b, c, d; Chambers & Poinar 2020; Poinar & Chambers 2020). In continuation of these studies, a recently obtained flower from Myanmar amber is here described as the new genus and species *Phantophlebia dicycla*. The most distinctive feature of the fossil is its perianth, which is composed of two 5-merous whorls of conspicuously veined tepals (Figs. 1–3). The flower's 5 stamens are positioned opposite the inner tepals. The gynoecium is probably absent. The similar texture and venation of the two whorls of perianth parts led to our describing them as tepals. However, in view of their differences in size and shape, an alternative terminology would be to refer to the outer parts as sepals and the inner as petals. In the discussion below, we found these terms to be helpful when comparing the fossil with some modern families having flowers with stamens opposite the petals.

The flower of *Phantophlebia* appears to be functionally staminate. It therefore joins a number of other Myanmar amber fossils in which the sampled flowers are unisexual. These include *Palaeoanthella* (Poinar & Chambers 2005), *Lachnociona* (Poinar et al. 2008; Poinar & Chambers 2018b), *Tropidogyne* (Chambers et al. 2010; Poinar & Chambers 2019c), *Setitheca* (Poinar & Chambers 2018a), and *Valviloculus* (Poinar et al. 2020). In their review of Early- to Mid-Cretaceous fossil flowers, especially of the Magnoliidae, Friis et al. (2011) mention principally bisexual genera, an exception being the Brazilian genus *Endressinia* (Magnoliales) of Late Aptian-Early Albian age, described from flowers with only carpels and staminodes (op. cit , p. 223). The cited studies of Myanmar fossils have thus revealed additional diversity of breeding systems in Mid-Cretaceous angiosperms.

J. Bot. Res. Inst. Texas 14(1): 73 – 80. 2020
https://doi.org/10.17348/jbrit.v14.i1.898

MATERIALS AND METHODS

The history of discovery of Myanmar amber, including the geologic setting of the mines at Noije Bum 2001 Summit Site and lithology of the amber-containing marine sediments, is described by Cruickshank and Ko (2003). These authors place the age of the deposits as Late Albian, 97–110 Ma, based on palynological and marine paleontological (ammonite) analyses. A later study by Shi et al. (2012) utilized U-Pb dating of zircons to establish a maximum age of 98.79 ± 0.62 Ma for the volcanic clasts that had been deposited in the sediments contemporaneously with the amber. We use the term mid-Cretaceous for this time period, which is transitional between Late Albian and Early Cenomanian (Cohen et al. 2013; Manchester et al. 2018). The amber has been shown to be derived from the resin of members of the Araucariaceae, a family of conifers which includes the Australasian genus *Agathis* (Poinar et al. 2007).

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

DESCRIPTION

Phantophlebia Poinar & K.L. Chambers, **gen. nov.** Type Species: *Phantophlebia dicycla* Poinar & K.L. Chambers, sp. nov.

Flower probably staminate, perianth glabrous, tepals in two whorls of 5 each, those of the outer whorl small, quincuncial, unequal, narrowly to broadly elliptic, oblanceolate, or obovate, obtuse, with 3–7 main veins interconnected by a network of veinlets (Fig. 2), tepals of the inner whorl larger and up to 3 times longer than the outer tepals, explanate, ± equal, connate basally, broadly ovate, acute or acuminate, with ca. 7–9 main veins that branch above and are similarly interconnected (Figs. 1, 3), stamens 5, inserted opposite the inner tepals on their connate basal portion, filaments linear, longer than anthers, glabrous, anther attachment basal, anthers angular-oblong, bilocular, dehiscence latrorse by oblique slits, epidermis papillate, connective not prolonged (Figs. 4, 5), anthers absent from 3 filaments, perhaps due to insect predation (note insect trapped under the air bubble [Fig. 4]), gynoecium probably 0, pedicel 0 or detached below outer tepals (Fig. 2), pollen unknown.

Phantophlebia dicycla Poinar & K.L. Chambers, **sp. nov.** (**Figs. 1–5**). 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, *unknown amber miner s.n.* (holotype: Accession number B-An-16, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331 (U.S.A.).

Flower diameter 4.7 mm as measured between tips of longest inner tepals, outer tepals 0.6–0.8 mm long, 0.4–0.6 mm wide, inner tepals 1.6–1.9 mm long, 1.1–1.4 mm wide, filaments 0.3 mm long, anthers 0.3–0.4 mm long, 0.1–0.2 mm wide.

Etymology.—Genus name from the Greek "phanto," evident, visible, and "phlebos," vein, referring to the conspicuous venation of the tepals. Species epithet from the Greek "di," two, double, and "kyklos," circle, ring, referring to the biseriate perianth.

DISCUSSION

Due to the presence of an air bubble resting on the center of the flower, it is not possible to say with certainty that a gynoecium is lacking. However, careful study shows that the bubble rests directly on the fossil, leaving no space for a pistil below it. *Phantophlebia* can be uniquely characterized by its 5 antipetalous stamens and biseriate, pentamerous perianth of well differentiated and conspicuously veined tepals. Another unique feature may be the unusual form of oblique lateral dehiscence present on 3 anther locules (Figs. 4, 5). However, one locule appears to have been damaged by insect predation (Fig. 5). Certain other characteristics of *Phantophlebia* have been found previously in Myanmar amber flowers. For example, a basal fusion of perianth parts, as in the fossil's inner tepaloid whorl, was described earlier for the single whorl of tepals in *Tropidogyne* (Chambers et al. 2010) and *Dispariflora* (Poinar & Chambers 2019a). The papillate epidermis of the anthers is reminiscent of a

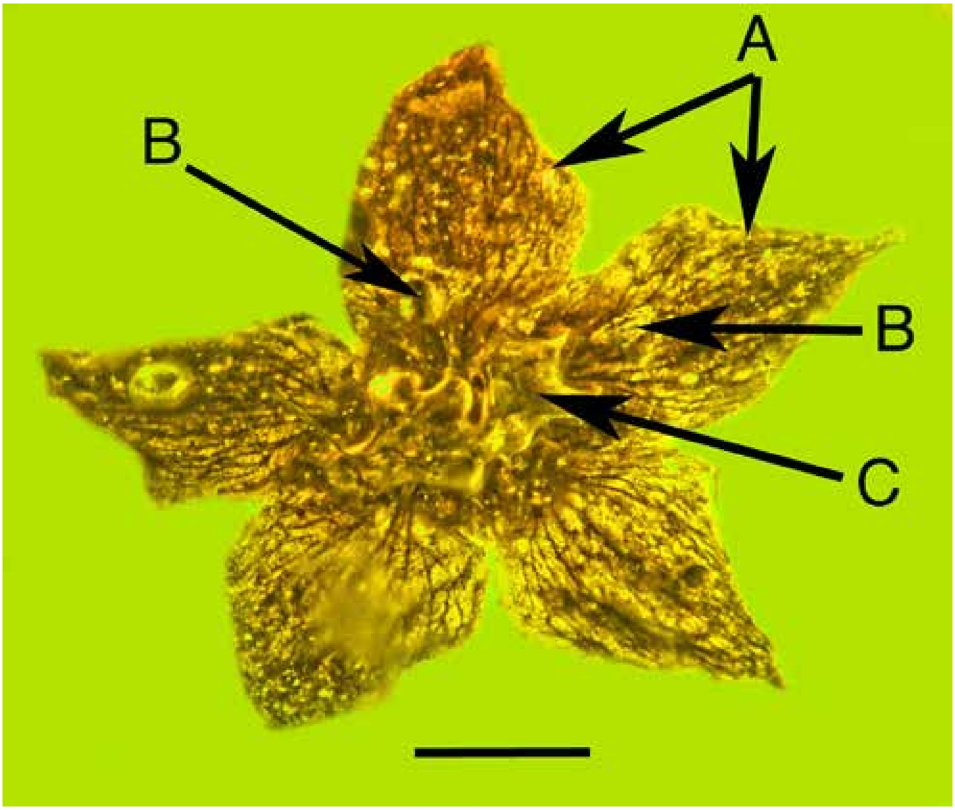

Fig. 1. ***Phantophlebia dicycla.*** **Flower in apical view. A. Tepals of the inner perianth whorl. B. Stamens. C. Air bubble covering center of flower. Scale bar = 1.0 mm.**

similar condition seen on the filaments and anthers of *Zygadelphus* (Poinar & Chambers 2019d). Insects are rarely found in close association with flowers in amber, but in the present case, there are the remains of a beetle that was trapped under the air bubble when the flower became mired in resin (Fig. 4).

There is considerable diversity in the form of the perianth in recently described mid-Cretaceous amber fossils. A biseriate perianth of 5 sepals and 5 petals was described by Liu et al. (2018) in the eudicot flower *Lijinganthus*. In the Lauralean fossil *Jamesrosea*, there is an imbricate series of ca. 12 ovate tepals borne on the rim of the floral cup (Crepet et al. 2016). *Cascilaurus* (Poinar 2017) has 6 tepals in two whorls of 3 each. In *Setitheca* and *Zygadelphus* (Poinar & Chambers 2018a; 2019d), the perianth is composed of numerous, spirally arranged and variously shaped tepals (ca. 12 spreading tepals in the former genus, 10 erect ones in the latter). In *Dispariflora* (Poinar & Chambers 2019a), there is a single whorl of 5 tepals, one of which is leaf-like and 3 to 4 times as long as the others. A single whorl of equal or unequal tepals characterizes the genera *Lachnociona, Strombothelia*, *Tropidogyne*, and *Dasykothon* (Poinar & Chambers 2018b; 2019b, c; 2020a). Conspicuous venation of the perianth, a defining feature of *Phantophlebia*, is characteristic also of *Tropidogyne* and *Dispariflora*, but these genera differ in other important respects from the present fossil.

Fossils with 5-merous, dichlamydeous flowers in which the stamens are opposite the petals, as in *Phantophlebia* (its inner tepals being homologous to petals), may be uncommon in the Cretaceous. Friis et al. (2011, fig. 17.10) illustrate 3 such examples: the Rose Creek flower from the Dakota locality in Kansas and Nebraska, an unnamed asterid from Åsen, Sweden, and an unnamed primuloid flower from the Mira locality,

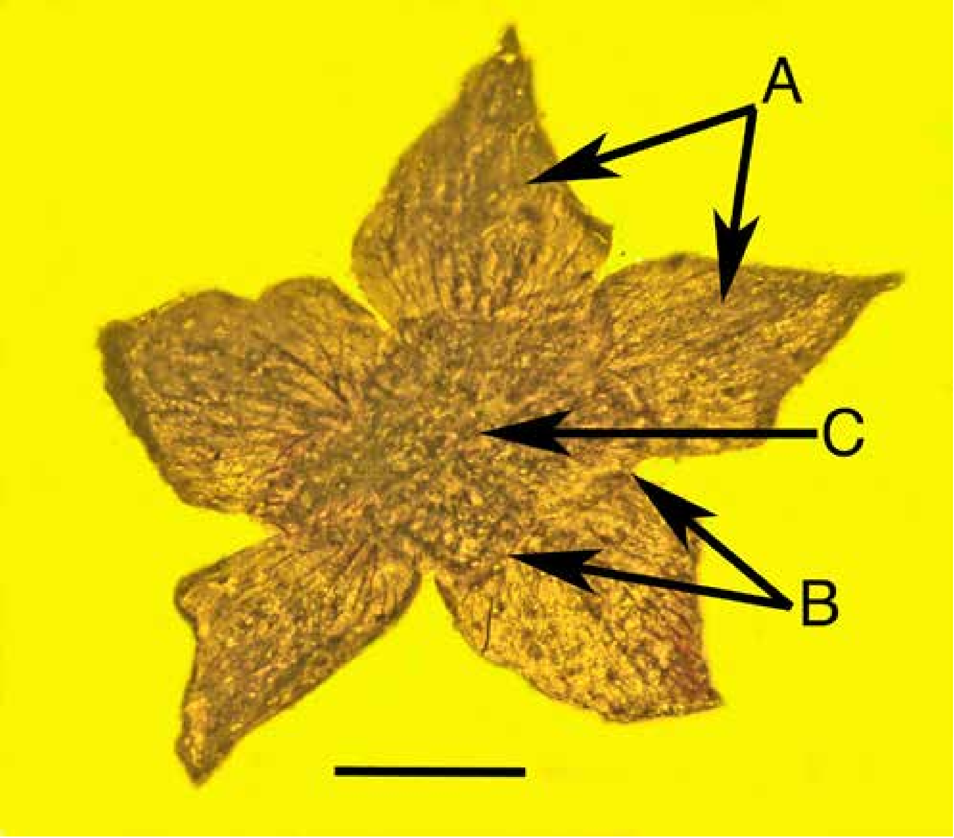

Fig. 2. *Phantophlebia dicycla.* Flower in basal view. **A.** Tepals of the inner perianth whorl. **B.** Tepals of the outer perianth whorl. **C.** Broken off tip of pedicel. Scale bar = 1.0 mm.

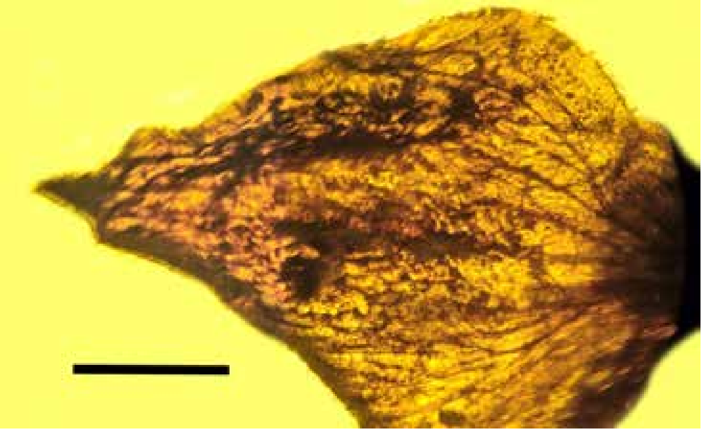

Fig. 3. *Phantophlebia dicycla.* Inner tepal, showing pattern of venation. Scale bar = 0.4 mm.

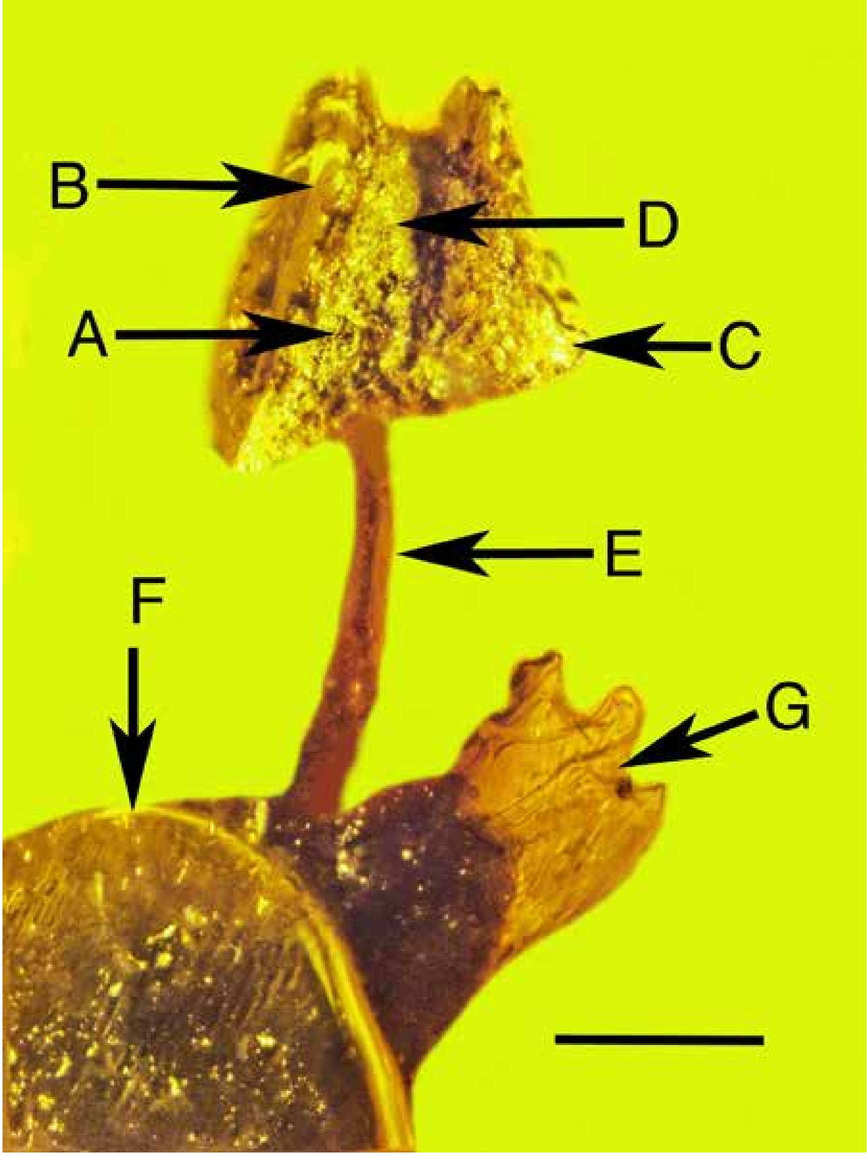

Fig. 4. ***Phantophlebia dicycla*****. Stamen. A. Anther locule showing latrorse dehiscence. Note papillate epidermis. B. Interior of locule. C. Second locule. Note oblique angle of dehiscence. D. Connective. E. Filament. F. Air bubble. G. Wings of beetle trapped under air bubble. Scale bar = 200 µm.**

Portugal. The Rose Creek flower, of mid-Cretaceous age, was later described as *Dakotanthus* (Manchester et al. 2018) and was found to have 10 rather than 5 stamens. The asterid from Sweden, Late Santonian-Early Campanian in age (Friis et al. 2011, p. 380) is bisexual, distinctly petaliferous, and has large nectaries alternating with the stamens. The unnamed flower from Mira, Portugal, is of Campanian-Maastrichtian age (Friis et al. 2010, p. 343). It also is bisexual, petaliferous, and has a ring-shaped nectary surrounding the pistil.

There are several modern angiosperm families in which the stamens are equal to and opposite the petals. Some well-known examples are Vitaceae, Rhamnaceae, and Primulaceae,. The flowers of Vitaceae are usually

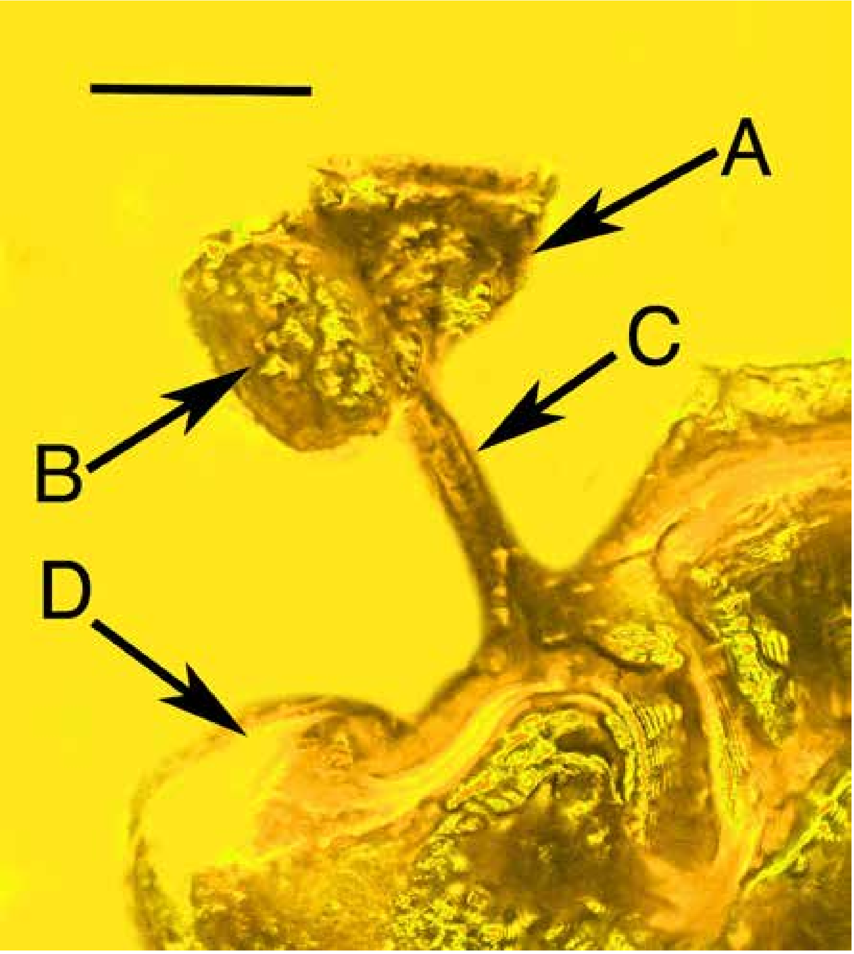

Fig. 5. ***Phantophlebia dicycla*. Second complete stamen. A. Anther locule, showing oblique dehiscence. B. Second locule, truncated on the outer side by possible insect damage. C. Filament. D. Air bubble. Scale bar = 300 µm.**

bisexual. They differ from *Phantophlebia* in having a small, cupulate or ring-shaped calyx with much reduced teeth or lobes (Wen 2007). According to Sussenguth (1953, p. 214), the petals are never basally united. Dehiscence of the anthers is introrse rather than latrorse as in *Phantophlebia*. The oldest known fossils of Vitaceae are from the Deccan Traps in India, of Late Cretaceous-Early Paleocene age (Manchester et al. 2013).

In the Rhamnaceae, flowers are most often bisexual and possess a dish-shaped to cup-shaped or cylindrical hypanthium (Medan & Shirarend 2004). Unlike *Phantophlebia,* the calyx lobes are usually larger and more firm in texture than the petals and have valvate, rather than imbricate or quincuncial aestivation. Petals are mostly small, distinct, and often cup-shaped or hooded distally. Anther dehiscence is introrse. Reports of fossil Rhamnaceae from the Cretaceous include *Coahuilanthus* (Calvillo-Canadell & Cevallos-Ferriz 2007), from Late Campanian in Mexico, and *Archipaliurus* (Correa et al. 2010), from Upper Maastrichtian in Colombia.

Primulaceae subgenus Myrsinoideae (formerly family Myrsinaceae) may offer the best examples of flowers with particular features that are comparable to *Phantophlebia*. The flowers of the subfamily are described as bisexual or often unisexual (Mez 1911; Ståhl & Anderberg 2004). The sepals are shorter than the petals, free, and often imbricate; the corolla lobes are usually rotate and often connate near the base, as in *Phantophlebia*.

The stamens are often sessile or have short filaments, but in some genera the filaments are longer than the anthers (Ståhl & Anderberg 2004, fig. 91). Anther dehiscence is introrse by longitudinal slits, but in the genus *Monoporus* of Madagascar, the locules are oblique, connivent at the tip, and open at the apex by one or 2 slit-like pores (Mez 1911, fig. 27F; Ståhl & Anderberg 2004, p. 280). In the anthers of *Phantophlebia* (Figs. 4, 5), the oblique slits approach each other at the tip but are not connivent. Anthers in Myrsinoideae are most often sagittate and dorsifixed but are rarely ovate or elliptic and basifixed (Mez 1911, p. 1) as in *Phantophlebia*.

Molecular clock dating of order Ericales, to which Primulaceae belongs, gives a constrained crown group age of 99.04 Ma (Magallón & Castillo 2009). Fossil flowers of Campanian-Maastrichtian age from Portugal were assigned to the primuloid clade by Friis et al. (2011, pp. 376–377) based on features of the calyx and gynoecium. In addition, fossil wood of *Ardisioxylon*, attributed to Myrsinaceae, has been reported from the end-Cretaceous Deccan Intertrappan Flora of India (Srivastava 2011).

Although the staminate floral morphology of *Phantophlebia* shows some similarities to members of the primuloid clade, nothing is known of the fossil's gynoecium or pollen. Until such information is available, the possible phylogenetic relationships of the genus must remain unresolved.

ACKNOWLEDGMENTS

We thank Steven Manchester for his helpful review comments. Debora Carroll, OSU Valley Library, provided valuable assistance with the literature.

REFERENCES

Calvillo-Canadell, L. & S.R.S. Cevallos-Ferriz. 2007. Reproductive structures of Rhamnaceae from the Cerro del Pueblo (Late Cretaceous, Coahuila) and Coatzingo (Oligocene, Puebla) formations, Mexico. Amer. J. Bot. 94:1658–1669.

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.

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

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

Correa, E., C. Jaramillo, S. Manchester, & M. Gutierrez. 2010. A fruit and leaves of Rhamnaceous affinities from the Late Cretaceous (Maastrichtian) of Colombia. Amer. J. Bot. 97:71–79.

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. 21:441–455.

Friis, E.M., K. Raunsgaard-Pedersen, & P.R. Crane. 2010. Cretaceous diversification of angiosperms in the western of the Iberian Peninsula. Rev. Palaeobot. Palynol. 162:341–361.

Friis, E.M., P.R. Crane, & K.R. Pedersen. 2011. Early flowers and angiosperm evolution. Cambridge University Press, Cambridge, UK. 585 pp.

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

Magallon, S. & A. Castillo. 2009. Angiosperm diversification through time. Amer. J. Bot. 96(1):349–365.

Manchester, S.R., D.L. Dilcher, W.B. Judd, B. Corder, & J.F. Basinger. 2018. Early Eudicot flower and fruit: *Dakotanthus* gen. nov. from the Cretaceous Dakota Formation of Kansas and Nebraska, U.S.A. Acta Palaeobot. 58:27–40.

Manchester, S.R., D.K. Kapgate, & J. Wen. 2013. Oldest fruits of the grape family (Vitaceae) from the Late Cretaceous Deccan Cherts of India. Amer. J. Bot. 100:1849–1859.

Medan, D. & C. Schirarend. 2004. Rhamnaceae. In: K. Kubitzki, ed. The families and genera of vascular plants. Springer-Verlag, Berlin, Germany. 6:320–338.

Mez, C. 1902. Myrsinaceae. In: A. Engler, ed. Das Pflanzenreich. Wilhelm Engelmann Verlag, Leipzig, Germany. IV. 236. Pp. 1–437.

Poinar, G.O., Jr. 2017. A mid-Cretaceous Lauraceae flower, *Cascolaurus burmitis* gen. et sp. nov., in Myanmar amber. Cretaceous Research 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. Pp. 187–218.

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

Poinar, G.O., Jr. & K.L. Chambers. 2018a. *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.0., Jr. & K.L. Chambers. 2018b. Fossil flowers of *Lachnociona camptostylus* sp. nov., a second record for the genus in mid-Cretaceous Myanmar amber. J. Bot. Res. Inst. Texas 12:655–666.

Poinar, G.O., Jr. & K.L. Chambers. 2019a. *Dispariflora robertae* gen. et sp. nov., a mid-Cretaceous flower of possible Lauralean affinity from Myanmar amber. J. Bot. Res. Inst. Texas 13:173–183.

Poinar, G.O., Jr. & K.L. Chambers. 2019b. *Strombothelya* gen. nov., a fossil angiosperm with two species in mid-Cretaceous Myanmar amber. J. Bot. Res. Inst. Texas 13:451–460.

Poinar, G.O., Jr. & K.L. Chambers. 2019c. *Tropidogyne lobodisca* sp. nov., a third species of the genus from mid-Cretaceous Myanmar amber. J. Bot. Res. Inst. Texas 13:461–466.

Poinar, G.O., Jr. & K.L. Chambers. 2019d. *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. 2020. *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, & R. Buckley. 2008. An Early Cretaceous angiosperm fossil of possible significance in rosid floral diversification. J. Bot. Res. Inst. Texas 2:1183–1192.

Poinar, G.O., Jr., K.L. Chambers, U.T. Iwaniec, & F.E. Vega. 2020. *Valviloculus pleristaminis* gen. et sp. nov., a fossil Lauralean flower with valvate anthers from mid-Cretaceous Myanmar amber. J. Bot. Res. Inst. Texas 14: *submitted*.

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.

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.

Sokol, J. 2019. Troubled treasure. Science 364:722–729.

Srivastava, R. 2011. Indian Upper Cretaceous–Tertiary flora before collision of Indian Plate: A reappraisal of Central and Western Indian flora. Mem. Geol. Soc. India 77:281–292.

Ståhl, B. & A.A. Anderberg. 2004. Myrsinaceae. In: K. Kubitzki, ed. The families and genera of vascular plants. Springer-Verlag, Berlin, Germany. 6:266–281.

Sussenguth, K. 1953. Vitaceae. In: H. Melchior and E. Werdermann, eds. Die natürlichen Pflanzenfamilien. Duncker & Humblot, Berlin, Germany. Ed. 2. 20d:174–371.

Wen, J. 2007. Vitaceae. In: K. Kubitzki, ed. The families and genera of vascular plants. Springer-Verlag, Berlin, Germany. 9:467–479.