SETITHECA LATIVALVA GEN. ET SP. NOV., A FOSSIL FLOWER OF LAURALES 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

ABSTRACT

A single staminate flower preserved in mid-Cretaceous Myanmar amber is described as **Setitheca lativalva** gen. et sp. nov. The fossil's affinities appear to be with Monimiaceae and allied families of order Laurales. The perianth is composed of ca. 12 spirally arranged tepals of varying size and shape. A single whorl of 10 stamens is attached to the margin of a flat central disc. There is no gynoecium. In some of the stamens, the bilocular anthers are held upright, but in the others, the filaments are arched abaxially and the anthers are reflexed. Dehiscence is extrorse via 2 lateral, dorsally-hinged valves, as also occurs in some members of Hernandiaceae. The spherical pollen appears to be inaperturate. Such features as the unisexual flowers, valvate anthers, and a perianth of numerous, spirally arranged tepals are consistent with assignment of the fossil to this order of angiosperms.

RESUMEN

Se describe una sola flor estaminada conservada en ámbar del cretácico medio de Birmania como **Setitheca lativalva** gen. et sp. nov. Las afinidades del fósil parecen ser con Monimiaceae y familias relacionadas del orden Laurales. El perianto está compuesto por ca. 12 tépalos dispuestos espiralmente de tamaño y forma variable. Un verticilo simple de 10 estambres está unido al margen de un disco central plano. No hay gineceo. En alguno de los estambres, las anteras biloculares son erectas, pero en los otros, los filamentos están arqueados abaxialmente y las anteras son reflejas. La dehiscencia es extrorsa por dos valvas laterales 2 lateral, giradas dorsalmente, como también ocurre en algunos miembros de Hernandiaceae. El polen esférico parece ser inaperturado. Tales características como flores unisexuales flores, anteras valvadas, y un perianto de numerosos tépalos, dispuestos espiralmente son consistentes con la asignación del fósil a este orden de angiospermas.

INTRODUCTION

In our previous studies of flowers from mid-Cretaceous Myanmar (Burmese) amber deposits, it has not always been possible to make a firm placement of the fossils in a modern angiosperm family. Some examples of families to which such amber flowers have been assigned, however, are Poaceae (Poinar 2004), Lauraceae (Poinar 2017), and Cunoniaceae (Chambers et al. 2010; Poinar & Chambers 2017). Only tentative assignments were offered for Monimiaceae (Poinar & Chambers 2005), Cornaceae (Poinar et al. 2007), and Dilleniaceae (Poinar & Chambers 2018), while no familial relationship was suggested for 3 fossils (Poinar et al. 2008; Poinar et al. 2013; Poinar et al. 2016).

In a discussion of the paleogeographic history of the amber deposits (Poinar 2018), it was hypothesized that the fossils originated in early-Cretaceous araucarian forests in the Southern Hemisphere continent of Gondwana. Their present location north of the equator is due to tectonic drift of the West Burma Block, perhaps as part of the Greater India Plate, northward from Gondwana to Asia during the Cretaceous and into the Eocene. This proposal may help to explain an apparent relationship of some of the fossil insects and angiosperms to higher taxa that presently are limited to the Southern Hemisphere (Poinar 2018). As discussed below, the flower described here may have its closest affinities with members of the Laurales, especially families traditionally allied with the Monimiaceae (Renner 1999).

The perianth of *Setitheca,* like that of various genera of Magnoliidae, is not differentiated into a calyx and corolla but rather is composed of numerous spirally arranged, irregularly shaped tepals (Figs. 1, 2). The receptacle is obconic (Figs. 2, 3). Centered on its truncate apex is a flat disc on whose margin are attached 10 stamens in a single whorl (Fig. 1). The filaments are short and taper upward from a thickened base, on the abaxial side of which is a pair of thin, elongated, perhaps glandular appendages (Fig. 4). Anther dehiscence is by 2 dorsally

J. Bot. Res. Inst. Texas 12(2): 643 – 653. 2018

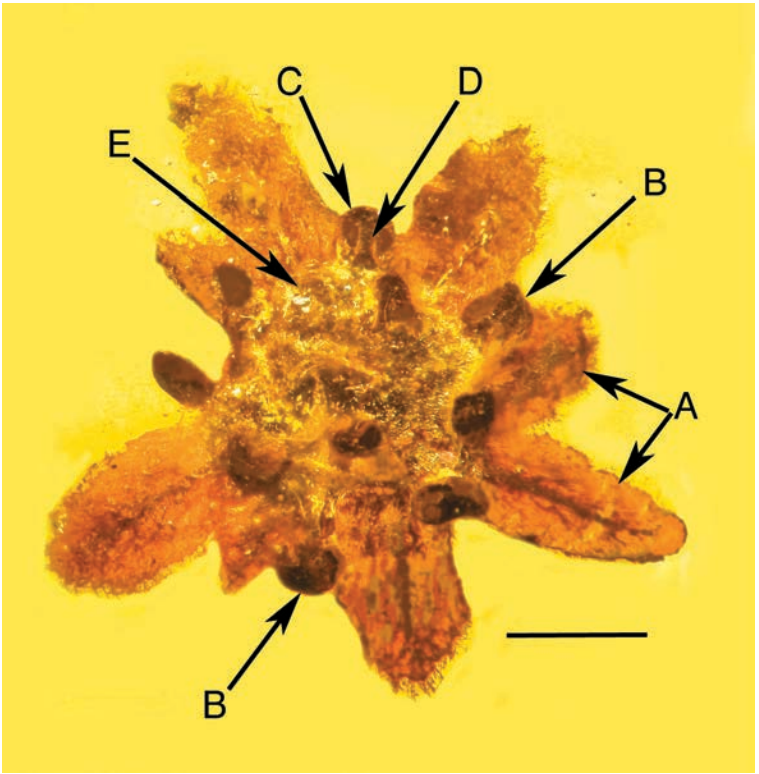

Fig. 1. *Setitheca lativalva*. Flower in apical view. **A.** Tepals. **B.** Stamens. **C.** Anther. **D.** Filament. **E.** Disc. Scale bar = 1.7 mm.

hinged lateral valves (Figs. 4, 5). The possible taxonomic significance of this rare type of valvate anthers is discussed below. Pollen grains, as well as can be determined, are more or less spherical and inaperturate (Figs. 6, 7).

The fossil record of angiosperms in the Cretaceous Period, including the various ways by which flowers and fruits have been preserved, has been described in detail by Friis et al. (2011). These authors questioned the proposed age of amber deposits in the Hukawng Valley of Myanmar (op. cit., p. 34) and suggested that the morphological organization displayed by the floral remains is too advanced to be of mid-Cretaceous age. They proposed a Late Cretaceous or even Early Cenozoic age for the amber. However, as reported below and in our earlier papers, both paleontological and radiometric data support an age for the amber at or close to the Upper Albian—Lower Cenomanian boundary. Flowers now known from Myanmar amber thus add to the variety of floral structures and adaptations in early angiosperms, as have already been described from the mesofossil compressions and charcoalifed flowers used in analyses by Friis et al. (2011). Our proposed placement of *Setitheca* in the Laurales is consistent with the reported Early Cretaceous age of angiosperm floral remains, including those from the Puddledock locality in Virginia, that were assigned to this order (Crane et al. 1994; von Balthazar et al. 2007, Friis et al. 2011, pp. 232, 484).

MATERIALS AND METHODS

The amber containing the fossil was obtained from mines at the Noije Bum 2001 Summit Site in the Hukawng Valley, located southwest of Maingkhwan in Kachin State, Myanmar (Poinar et al. 2005). Based on marine paleontological data (ammonites) and palynological (pollen) evidence, the amber-bearing strata were initially

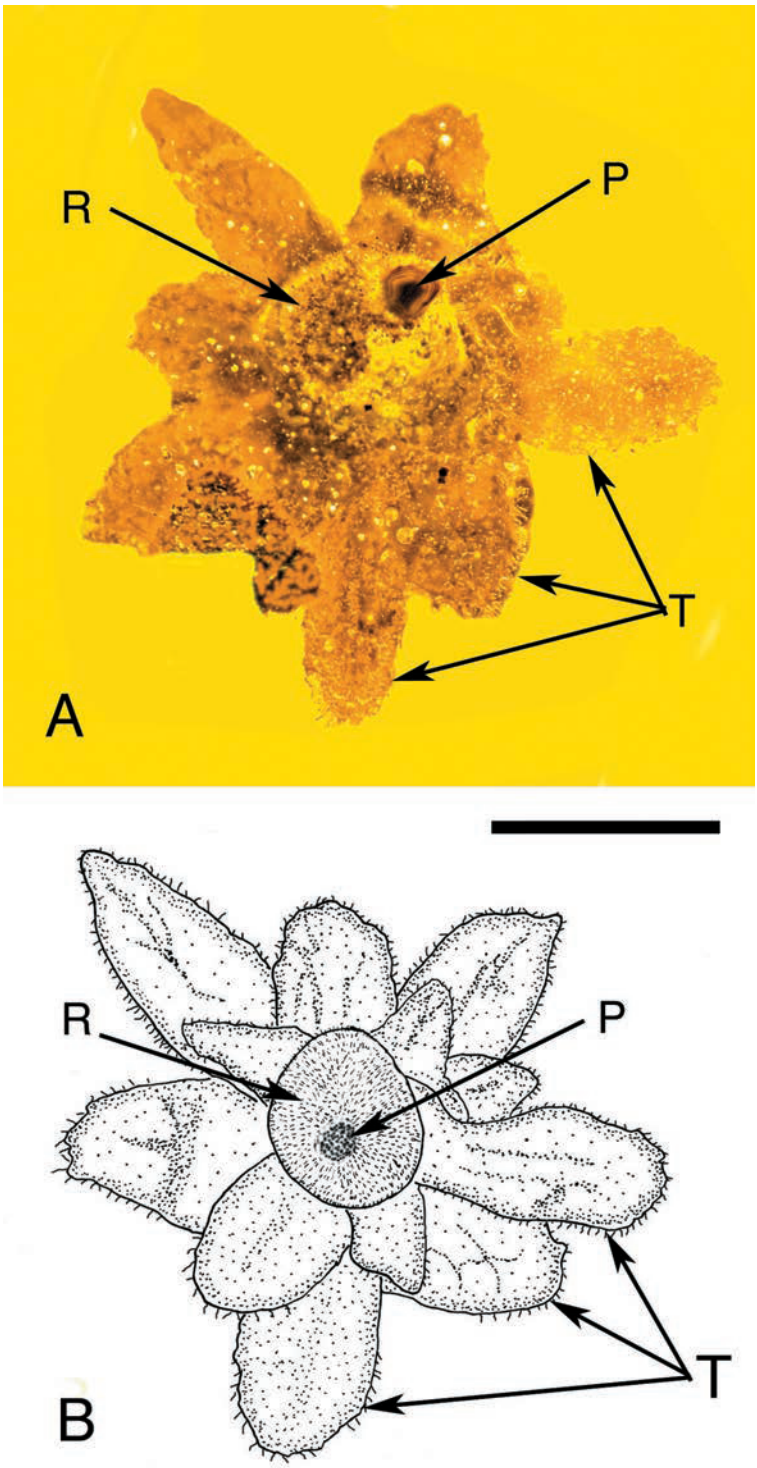

Fig. 2. *Setitheca lativalva.* **A.** Flower in basal view. **T.** Tepals. **R.** Receptacle. **P.** Broken stump of pedicel. **B.** Drawing of flower in basal view, with labels as in fig. 2A. Scale bar = 1.7 mm for both A and B.

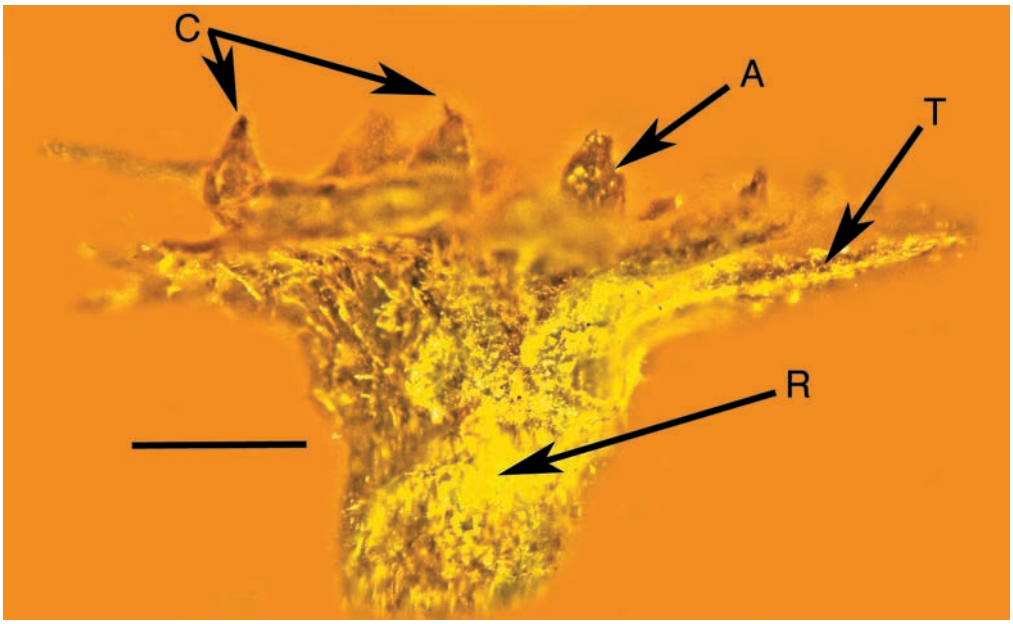

Fig. 3. *Setitheca lativalva*. Flower in lateral view. **A.** Anther. **C.** Apiculate tips of connectives. **T.** Tepal. **R.** Receptacle. Scale bar = 0.9 mm.

assigned to the Upper Albian (97–110 Ma) of the Early Cretaceous (Cruickshank & Ko 2003). A later study, using U-Pb dating of zircons, determined the age to be 98.79 ± 0.62 Ma (Shi et al. 2012). Because samples used in the latter study were taken from marine sediments in which the fossils had been redeposited from their terrestrial origin, the amber must be even older than this date. Nuclear magnetic resonance (NMR) spectra and the nature of wood fibers in specimens from the Noije Bum 2001 Summit Site indicate that the source for the amber was resin from a tree of the Araucariaceae (Poinar et al. 2007).

Observations and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot compound microscope with magnifications up to 800×. Helicon Focus Pro X64 was used to stack photos for better depth of field. Background details were removed to improve the image in the various figures.

DESCRIPTION

Setitheca Poinar & K.L. Chambers, **gen. nov.** Type Species: **Setitheca lativalva** Poinar & K.L. Chambers, sp. nov.

Flower staminate, receptacle obconic, perianth of ca. 12 spirally arranged tepals, tepals free, imbricate, spreading, variable in size and shape (Figs. 1, 2), petals 0, stamens 10, attached to the irregular margin of a flat disc in the center of the flower, filaments short, thickened at the base, anthers erect or sharply recurved abaxially (Figs. 1, 4), bilocular with protruding thecae, thecae bearing variously sized setae, dehiscing by 2 dorsally hinged lateral valves (Figs. 4, 5, 7), connective apiculate (Figs. 3, 5), base of filament with 2 thin, elongate, perhaps glandular appendages (Fig. 4), pollen spherical, inaperturate (Figs. 6, 7), pistil 0, pistillate flowers unknown.

Setitheca lativalva Poinar & K.L. Chambers, **sp. nov.** (**Figs. 1–8**). Type: MYANMAR (BURMA). KACHIN: northern Myanmar. Amber mine in the Hukawng Valley SW of Maingkhwan (26°20'N, 96°36'E), *unknown amber miner* (holotype: accession number Burmese-1032, deposited in the amber collection of Grand Huang, 564 Darwin Blvd, Edison, New Jersey 08820, U.S.A.).

Flower of maximum width 4.9 mm as measured between tips of longest tepals, receptacle puberulent, 1.7 mm long, 1.8 mm wide at the apex (Fig. 3), perianth irregular, tepals triangular to lanceolate, elliptic, or broadly

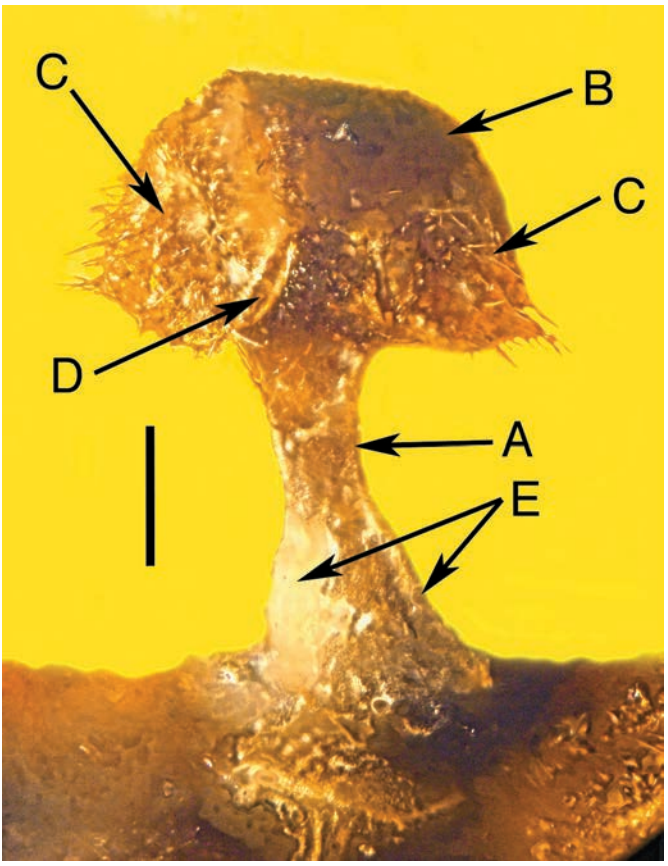

Fig. 4. *Setitheca lativalva*. **Stamen with reflexed anther in apical view. A. Filament. B. Anther. C. Valves covering pollen locules. D. Partially opened valve showing interior of locule. E. Basal appendages. Scale bar = 0.1 mm.**

linear (Figs. 1, 2), length 0.7–2.0 mm, width 0.6–1.0 mm, apices acute or obtuse, margins irregular, ciliate (Fig. 8), venation mostly obscure, disc ± 2.0 mm in diameter (Fig. 1), stamen filaments ca. 0.3 mm long, narrow, tapering distally from a thickened base, basal appendages (glands) 0.2 mm long, thin, narrowly triangular (Fig. 4), anthers basifixed, 0.2 mm long, sparingly strigose (Figs. 4, 7), valves 0.1 mm wide, 0.17 mm long at the base, with a rounded margin, pollen diameter 40 µm.

Etymology.—Genus name from the Latin "seta," bristle, and "theca," container, referring to the setae present on the anther locules. Species name from the Latin "latus," side, and "valva," leaf of a folding door, referring to the lateral valves of the anther.

DISCUSSION

When describing an amber-embedded angiosperm fossil, it is unusual to have more than one flower accessible for examination. In our past work on Myanmar amber, multiple specimens of the species being analyzed were available in only 3 cases (*Micropetasos,* Poinar et al. 2013; *Tropidogyne,* Poinar & Chambers 2017; *Endobeuthos,* Poinar & Chambers 2018). In the case of *Setitheca*, with only a single staminate flower at hand, we are missing information about the gynoecium that might help to verify its proposed assignment to Order Laurales. For example, the obconic base of the flower, described here as a receptacle (Figs. 2–4), may, in pistillate flowers of

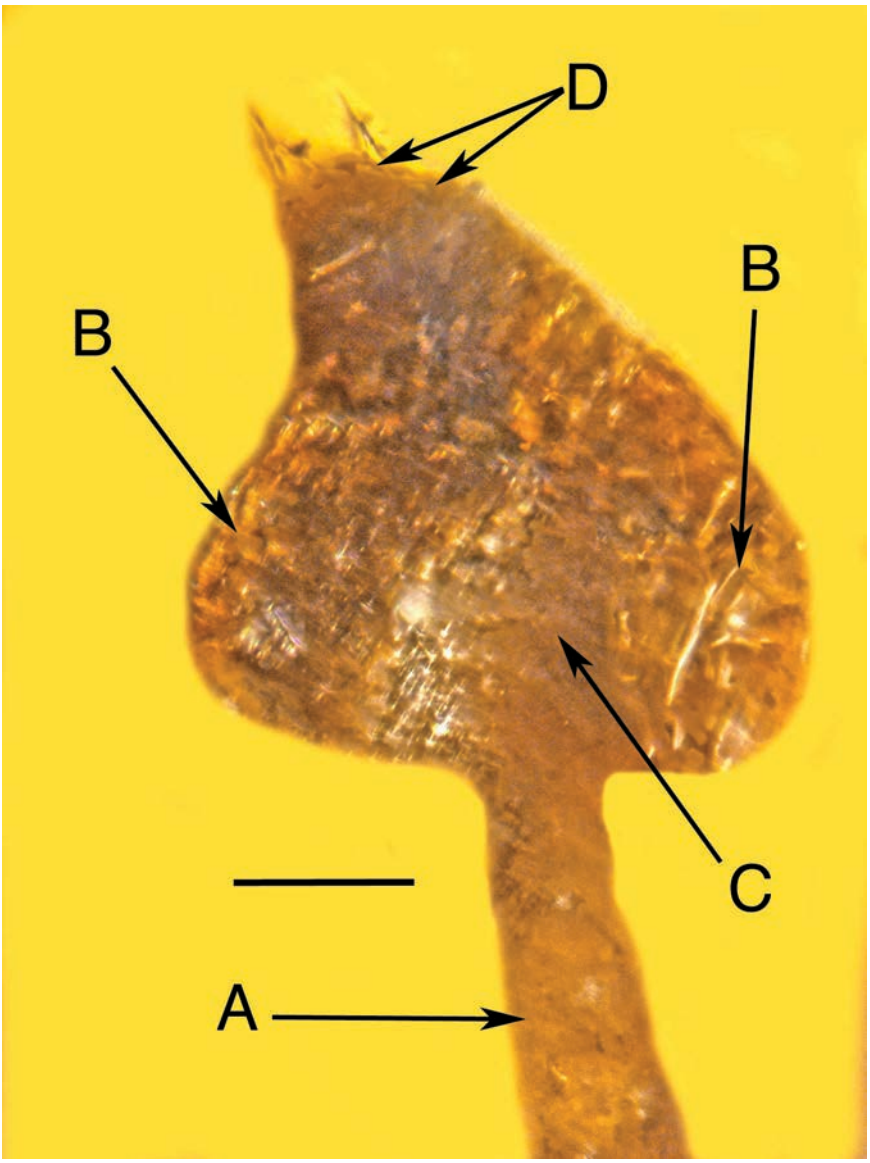

Fig. 5. *Setitheca lativalva*. Anther in oblique dorsal view. **A.** Filament. **B.** Pollen locules. **C.** Connective. **D.** Apiculate tip. Scale bar = 0.05 mm.

the species, be equivalent to the hypanthium that in many lauralian taxa surrounds or is fused with the gynoecium (e.g. Philipson 1993, fig. 97 E, N; Renner 2004, fig. 128 G).

Other distinguishing features of the fossil, especially the androecium, support the proposed placement of *Setitheca* in order Laurales. The whorl of 10 stamens around a central disc approaches the arrangement seen in Monimiaceae (e.g. *Peumus,* Pax 1891, fig. 65 C, E; Philipson 1993, fig. 94 B) and Atherospermataceae (*Atherosperma* Pax 1891, fig. 68 E; *Laurelia* Perkins & Gilg 1901, fig. 24 C, M). Valvate anthers characterize most families of Laurales (e.g. Atherospermataceae, Gomortegaceae, Hernandiaceae, Lauraceae, Siparunaceae), but not Calycanthaceae and Monimiaceae. Lateral anther valves that open along a dorsal hinge, as in *Setitheca*

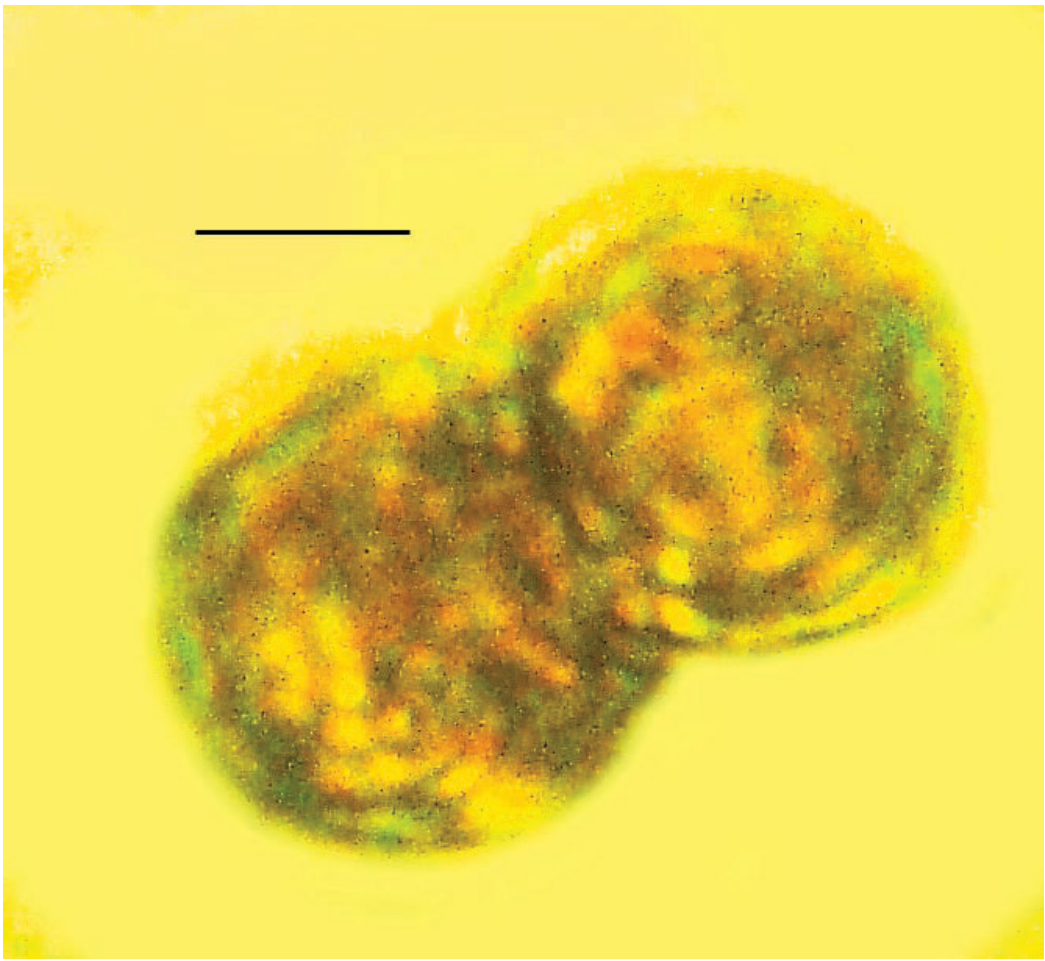

Fig. 6. *Setitheca lativalva*. Pollen grains. Scale bar = 18 µm.

(Figs. 5, 6), are rare, however, and thus far are known only in the genus *Hernandia* (Renner 1999, p. 1308). This unusual type of dehiscence is illustrated by Endress and Hufford (1989, figs. 128, 129) for the anthers of *Hernandia peltata*.

Anthers of *Setitheca* also are characterized by an apiculate extension of the connective (Figs. 3, 5). A discussion of the androecium of Early Cretaceous angiosperms by Friis et al. (2011, p. 401) cites Aptian-Middle Albian floras from Portugal as including many mesofossils that show an apical extension of the anther connective. A sterile apical appendage is also common in anthers of mid-Cretaceous flowers (op. cit., p. 402). In *Setitheca,* the appendages are obviously not long enough to have had a specialized function, such as floral protection or pollinator attraction, as in the modern genera *Asimina* or *Nelumbo* (Friis et al. 2011, p. 403; Endress & Hufford 1989, fig. 132). Illustrations of some genera of Monimiaceae, e.g. *Palmeria* and *Tambourissa* (Perkins & Gilg 1901, fig. 18), show apiculate anthers with a slightly extended connective much as in *Setitheca*. An isolated fossil stamen obtained at the Early-Middle Albian Puddledock locality, illustrated by Friis et al. (2011, fig. 16.10 C) is bilocular, with valvate dehiscence and an apiculate anther connective much like the anthers of *Setitheca*.

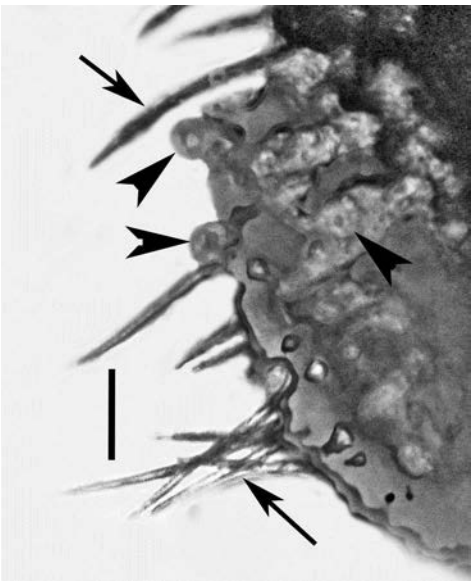

Fig. 7. *Setitheca lativalva*. Portion of the margin of anther valve, with pollen grains (arrowheads) and setae (arrows). Scale bar = 86 µm.

There is no way of knowing if the pair of thin, elongate appendages at the base of the stamen filaments in *Setitheca* (Fig. 4) had a glandular function. Their form is much like the glands on the stamens of *Atherosperma moschatum* (Philipson 1993, fig. 94 H). Basal glands of various types are well known in many present-day genera of Laurales and often function as nectar-producing organs. Sometimes the glands are fused to form a cushion or collar (e g. *Laurelia sempervirens,* Perkins & Gilg 1901, fig. 21 D; *Hernandia peltata,* Endress & Hufford 1989, fig. 129). Another similarity of the androecium of *Setitheca* to some extant Laurales is the presence of bithecal anthers with 1 pollen sac per theca. Among Monimiaceae, the stamens may possess either 1 or 2 pollen sacs per theca (Endress & Hufford 1989, p. 60). In Hernandiaceae and Siparunaceae there is 1 pollen sac per theca (op. cit., p. 64, 65; Renner & Hausner 2005, fig. 11 F). In Lauraceae, anthers may be either 2- or 4-locular (Rohwer 1993). The sharp bristles decorating the pollen sacs of most stamens in *Setitheca* (Figs. 5, 8) may have been an adaptation to protect against herbivorous insects.

The perianth of *Setitheca* has proved to be something of a puzzle because of its irregularity, expressed in the varying sizes and shapes of the numerous tepals (Figs. 1, 2). Although spirally arranged, the tepals do not show a gradual progression of small outer ones to larger inner ones. A similarly polymerous perianth was illustrated by Endress (1980) for the genus *Hortonia* (Monimiaceae), in which the outer 2 pairs of small tepals are decussate and the remaining 16 parts are gradually larger and spirally arranged (op. cit. figs. 1, 2). As in *Setitheca, Hortonia* shows no differentiation of the perianth into sharply defined sepals and petals. *Hortonia* otherwise differs from *Setitheca* in that its flowers are bisexual, its anthers dehisce by slits, not valves, and the pair of nectary glands by each filament are enlarged and flaring. According to Philipson (1993, p. 426), the perianth parts in Monimiaceae sensu lato (including Atherospermataceae and Siparunaceae) may be spiral, whorled, or decussate.

Extant families of Laurales with relatively numerous perianth parts also include Hernandiaceae, in which the tepals may occur in 2 whorls of 3–6 each or in 1 whorl of 4–8 (Kubitzki 1993b, p. 334). An example is *Hazomalania* (op. cit., fig. 76), with 10 perianth parts of ± equal size arranged in 2 whorls of 5. In Atherospermataceae, *Laurelia sempervirens* from Chile is described as having the pistillate flowers with a perianth of 6–12 unequal tepals, those of the outer series being much smaller than the inner (Perkins & Gilg 1901,

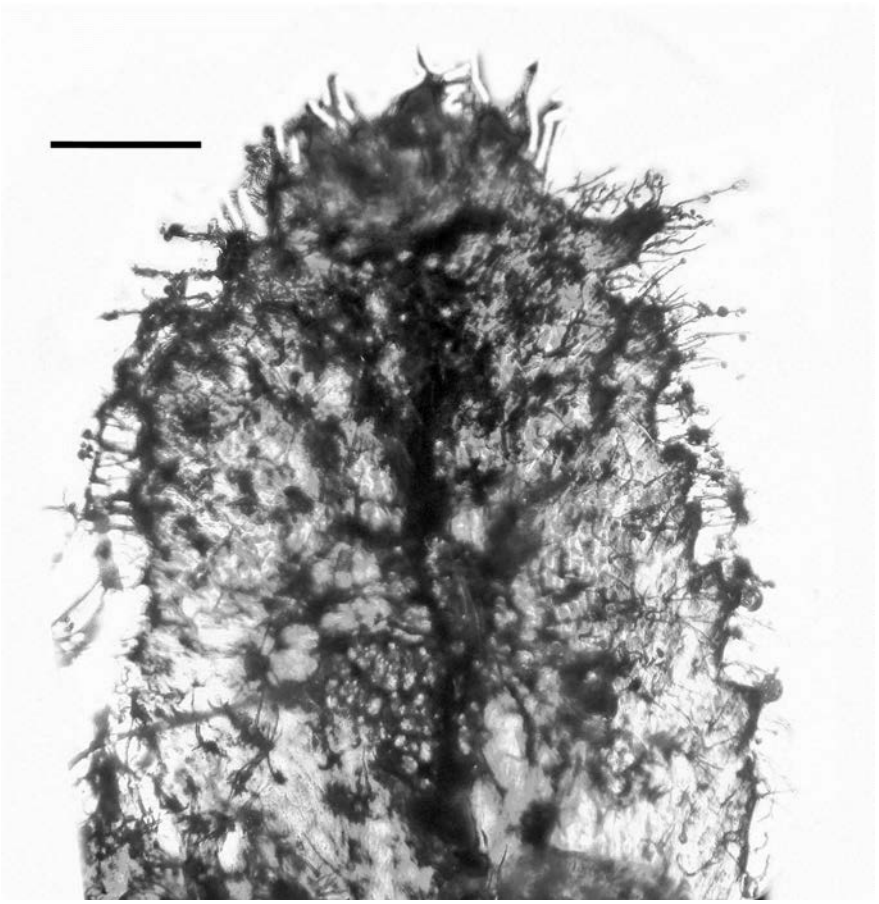

Fig. 8. *Setitheca lativalva*. Tip of a tepal. Note irregular ciliate margin. Scale bar = 0.2 mm.

pp. 76–77). The monotypic Chilean family Gomortegaceae has a tepaloid perianth that is "indistinctly trimerously whorled, with ca. 7–10, ovate to oblong lobes" (Kubitzki 1993a). The anthers of the 7–13 bilocular stamens differ from *Setitheca* in that they dehisce by 2 apically hinged valves, and the filament appendages are globular and glandular.

The above families and genera of Laurales, selected for comparison with *Setitheca*, are those whose relationships were examined in a combined morphological and molecular phylogenetic study by Renner (1999). Her sample of genera, representing the traditional families Lauraceae, Monimiaceae, Gomortegaceae, and Hernandiaceae (Pax 1891; Perkins & Gilg 1901; Kubitzki 1993a, b; Philipson 1993), fell into 2 principal groups or clades. Various morphological similarities and differences between *Setitheca* and some present-day members of Laurales are discussed above. However, having available only the single, staminate flower described here, we do not propose even a tentative assignment of the fossil to a particular extant family. We may hope that more can be learned about this extinct taxon if future studies of Myanmar amber provide us with additional examples of its floral variability.

ACKNOWLEDGMENTS

We thank Grand Huang for making the specimen available for study. Valuable comments and corrections were received from Susanne Renner and an anonymous reviewer. Loans of herbarium specimens from the U.S. National Museum and the New York Botanical Garden are also gratefully acknowledged.

REFERENCES

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.

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.

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

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

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

Kubitzki, K. 1993a. Gomortegaceae. In: K. Kubitzki, J.G. Rohwer, and V. Bittrich, eds. The families and genera of vascular plants. 2:318–320.

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

Pax, F. 1891. Monimiaceae and Hernandiaceae. In: A. Engler & K. Prantl, eds. Die natürlichen Pflanzenfamilien. III Teil, Abteil. 2:94–105, 126–129.

Perkins, J. & E. Gilg. 1901. Monimiaceae. In: A. Engler, ed. Das Pflanzenreich. Heft 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. 2:426–437.

Poinar, G.O., Jr. 2004. *Programinis burmitis* gen. et sp. nov., and *P. laminatus* sp. nov., early Cretaceous grass-like monocots in Burmese amber. Austral. Syst. Bot. 17:497–504.

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. 2018. Burmese amber: Evidence of Gondwanan origin and Cretaceous dispersion. Hist. Biol. 2018:1–6.

Poinar, G.O., Jr., R. Buckley, & A. Brown. 2005. The secrets of Burmese amber. Mid Amer. Paleontol. Soc. 29:20–29.

Poinar, G.O., Jr., R. Buckley, & H. Chen. 2016. A primitive mid-Cretaceous angiosperm flower, *Antiquifloris latifibris* gen. & sp. nov., in Myanmar amber. J. Bot. Res. Inst. Texas 10:55–62.

Poinar, G.O., Jr., K.L. Chambers, & R. Buckley. 2007. *Eoëpigynia burmensis* gen. et sp. nov., an early Cretaceous eudicot flower (Angiospermae) in Burmese amber. J. Bot. Res. Inst. Texas 1:91–96.

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

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

Poinar, G.O., Jr. & K.L. Chambers. 2018. *Endobeuthos paleosum* gen. et sp. nov., fossil flowers of uncertain affinity from mid-Cretaceous Myanmar amber. J. Bot. Res. Inst. Texas 12(1):133–139.

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, & J. Wunderlich. 2013. *Micropetasos*, a new genus of angiosperms from mid-Cretaceous Burmese amber. J. Bot. Res. Inst. Texas 7:745–750.

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. Monimiaceae. In: N. Smith, S.A. Mori, A. Henderson, D.W. Stevenson, and S.V. Heald, eds. Flowering plants of the Neotropics. Princeton Univ. Press, Princeton, NJ, U.S.A. Pp. 252–253.

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

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

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.

von Balthazar, M., K.R. pedersen, P.R. Crane, & E.M. Friis. 2007. *Potomacanthus lobatus* gen. et sp. nov., a new flower of probable Lauraceae from the Early Cretaceous (Early to Middle Albian) of eastern North America. Amer. J. Bot. 94:2041–2053.