

DASYKOTHON LEPTOMISCUS GEN. ET SP. NOV., A FOSSIL 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

A new fossil angiosperm, **Dasykothon leptomiscus**, is described from mid-Cretaceous amber deposits in the Hukawng Valley of north-western Myanmar (Burma). The flower is post-anthesis except for one stamen that retains its pollen. The perianth is slightly irregular and composed of 5 ovate or lance-linear, erect or incurved sepals. The ca. 12 stamens have slender, elongate filaments and dorsifixed, bithecal, longitudinally dehiscent anthers. The superior ovary bears 2 long, curved styles. Germinating pollen grains observed on the stigmas are monoporate and have the peculiar feature of a grooved ridge encircling the grain from pole to pole. This structure is hypothesized to be an evolutionary elaboration of the meridionally syncolpate sulcus found in some members of the Atherospermataceae. The generalized floral morphology of the fossil prevents ready taxonomic assignment to a modern family.

RESUMEN

Se describe un nuevo fósil de angiosperma, **Dasykothon leptomiscus**, de depósitos de ámbar del Cretácico medio en el valle de Hukawng del noroeste de Myanmar (Birmania). La flor está en post-anthesis excepto por un estambre que retiene su polen. El perianto es ligeramente irregular y está compuesto de 5 sépalos ovados o linear-lanceolados, erectos o incurvados. Los ca. 12 estambres tienen filamentos delgados y anteras dorsifijas, con dos tecas, dehiscentes longitudinalmente. El ovario súpero lleva 2 estilos largos y curvados. Los granos de polen germinados en los estigmas son monoporados y tienen la característica peculiar de una cresta surcada que circunda el grano de polo a polo. Se hipotetiza que esta estructura sea un cambio evolutivo del surco sincolpado meridionalmente que se encuentra en algunos miembros de las Atherospermataceae. La morfología floral generalizada del fósil impide una asignación a una familia moderna.

INTRODUCTION

Myanmar amber, dating from the mid-Cretaceous at ca. 99 Ma, is a continuing source of fossil flowers illustrative of the early morphological radiation of magnoliid and eudicot angiosperms (Crepet et al. 2016; Liu et al. 2018; Poinar 2018b; Poinar & Chambers 2018a, b, c; 2019a, b, c). Although difficult to obtain due to civil unrest in the country (Sokol 2019), samples of amber, sometimes in the form of smoothly ground pieces of jewelry (Poinar & Chambers 2019a; this report) periodically become available to paleontologists. Age of the amber deposits, as detailed in the following section, was determined by both marine paleontological methods and the use of radiometric techniques applied to the near-shore sediments containing the amber. Originally formed from the resin of trees belonging to the family Araucariaceae (Poinar et al. 2007), the amber may be considerably older than the sediments into which it was washed by stream erosion from adjacent forested habitats. The plant described here as *Dasykothon leptomiscus* is represented by a single bisexual, apetalous flower borne on a slender, elongate pedicel (Fig. 1). The perianth is composed of 5 erect or adaxially curved sepals, and petals are absent. The ca. 12 stamens have mostly lost their anthers or bear a fully dehiscent anther remnant (Figs. 2, 3). The 1 undehiscent anther is bithecal and has a dorsally inserted filament (Fig. 4). The ovary is superior with 2 elongate, spreading styles, one of which became bent backwards over the top of the flower at the time of preservation in the resin (Figs. 2, 4). Single-pored pollen grains, observed in the process of germinating on the stigmatic surface of the styles, have the unique feature of a grooved meridional ridge encircling the grain from pole to pole (Figs. 6–8). A hypothesis for the possible evolutionary origin of this feature is presented in the Discussion. The monoporate pollen morphology precludes placement of the fossil among the tricolpate eudicots (Judd et al. 2002), and a more likely relationship may be with families of order Laurales.

MATERIALS AND METHODS

Fossiliferous Myanmar amber from the Noije Bum 2001 Summit Site in the Hukawng Valley, Kachin Province, occurs in marine sediments that were initially dated as Late Albian, 97–110 Ma, using paleontological (ammonite) and palynological methods (Cruickshank & Ko 2003). A more narrowly defined estimate of 98.79 ± 0.62 Ma was obtained by Shi et al. (2012), based on radiometric U-Pb dating techniques applied to volcanic zircons extracted from the amber deposits. It is convenient to use the term mid-Cretaceous for this time period, which is transitional between the latest Albian and earliest Cenomanian series (Cohen et al. 2013). The amber may have originated in the Southern Hemisphere continent of Gondwana and been transported northward by plate tectonics, attaching to Southeast Asia in the Eocene epoch (Poinar 2018a).

Observations and photographs were made with a Nikon SMA-10R stereoscopic microscope at 80 \times and a Nikon Optiphot microscope with magnifications up to 600 \times . 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 image clarity.

DESCRIPTION

Dasykothon Poinar & K.L. Chambers, **gen. nov.** TYPE SPECIES: *Dasykothon leptomiscus* Poinar & K.L. Chambers, sp. nov.

Flower pedicellate, bisexual, hypogynous, calyx irregular, sepals 5, 2 of them linear-lanceolate, erect, straight, the other 3 ovate, erect, cupped inward, the epidermis densely hispid-strigose abaxially and papillate in lines (Figs. 2–5), petals 0, stamens ca. 12, mostly represented only by elongate, linear filaments, with 4 remaining anthers dehiscent and empty (Figs. 2, 3), the 1 undehiscent anther being linear-lanceolate, bithecal, and dorsifixed (Fig. 4), ovary(s) superior, mostly concealed by the perianth and stamen filaments, surface strigillose (Figs. 2, 3, 5), styles 2, elongate, divergent, the tip curved upward, 1 of them being bent over as an artifact of preservation (Figs. 2–4), stigmas small, terminal (Figs. 2, 4), pedicel slender, strigillose (Figs. 1, 2, 3, 5), pollen grains lenticular, ovoid-elliptic in outline, monoporate, with a single, meridional grooved ridge encircling the grain, germination pore polar, exine finely granular (Figs. 6–8).

Dasykothon leptomiscus Poinar & K.L. Chambers, **sp. nov.** (Figs. 1–8). TYPE: MYANMAR (BURMA). KACHIN PROVINCE: amber mine in the Hukawng Valley SW of Maingkhwan, 26°20'N, 96°36'E, 2018, *unknown amber miner s.n.* (HOLOTYPE: catalog number B-An-15, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

Floral pedicel 6.7 mm long, linear-lanceolate sepals 1.1 mm long, 0.3 mm wide, ovate, cupped sepals 0.9 mm long, 0.4 mm wide, stamen filaments 2.6–4.2 mm long, undehiscent anther 0.7 mm long, 0.3 mm wide, ovary 0.8 mm long (estimated), styles 3.0 mm long, pollen grains 18–21 μ m long, 11–13 μ m wide.

Etymology.—Genus name from the Greek “dasys,” hairy, shaggy, and “kothon,” cup, from the cup-shaped, pubescent perianth. Species name from the Greek “leptos,” thin, and “mischos,” stalk, stem, from the slender pedicel of the flower.

DISCUSSION

The erect sepals and numerous stamen filaments of *Dasykothon leptomiscus* allow too limited a view of the interior of the flower for an adequate description of the ovary. Fortunately, the elongated styles are well exposed, and their stigmas could be examined for the presence of germinating pollen grains (Figs. 7, 8). The calyx of *Dasykothon* is irregular, being composed of 2 differently shaped kinds of sepals, and in this respect it is not unique among genera recently described from Myanmar amber. For example, in *Dispariflora robertae* (Poinar & Chambers 2019a), the calyx is exaggeratedly heterosepalous and the 5 sepals are quite leaf-like in texture and venation. In *Endobenthos paleosum* (Poinar & Chambers 2018a), the calyx is composed of numerous helically arranged sepals of varying lengths. Spirally arranged sepals (tepals) of differing shapes are seen in *Setitheca lativalva* (Poinar & Chambers 2018b) and *Zygadelphus aetheus* (Poinar & Chambers 2019c). In the former, there are ca. 12 tepals of varying shapes, ranging in length from 0.7 to 2.0 mm. In the latter, the 10 sepals range from ovate to lanceolate, oblanceolate, or spatulate. A comparison was made between the perianth

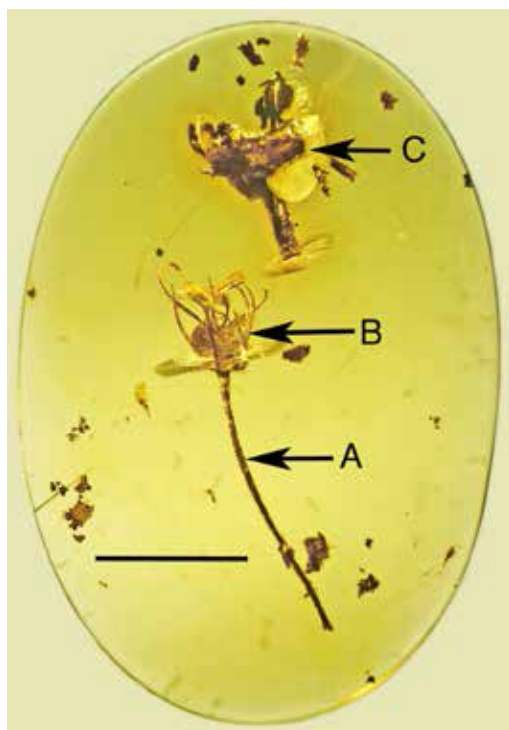


FIG. 1. *Dasykothon leptomiscus*. Original piece of amber containing the complete specimen. A. Floral pedicel. B. Flower. C. Unidentifiable plant inclusion. Scale bar = 3.7 mm.

of *Setitheca* and that described by Endress (1980) for *Hortonia angustifolia* (Monimiaceae), with 18 tepals of differing shapes, which are partly whorled and partly spirally arranged. The anthers of *Dasykothon* are bithecal with longitudinal dehiscence and hence do not have the specialized unithecal condition of *Endobenthos* anthers nor the valvate dehiscence of *Zygadelphus* and *Setitheca*. Excluding the present fossil, there have thus far been at least 15 new genera of angiosperms described from the Noije Bum 2001 Summit Site amber deposits (references cited in Poinar & Chambers 2019b), but considering the long period of time over which the Araucarian amber-producing forests probably existed, it cannot be assumed that all these newly described taxa were coexistent.

The lenticular pollen grains of *Dasykothon* are ovoid-elliptic in outline and have a single germination pore at one point in their circumference (Figs. 6–8). The most distinctive feature of the pollen is the grooved band or ridge completely encircling the grain from 1 side of the germination pore to the other. We were unable to find illustrations of pollen grains in modern magnoliid or non-monocot paleoherb angiosperms that match those of *Dasykothon* (Erdtman 1986). However, some members of the Laurales, as currently defined by the Angiosperm Phylogeny

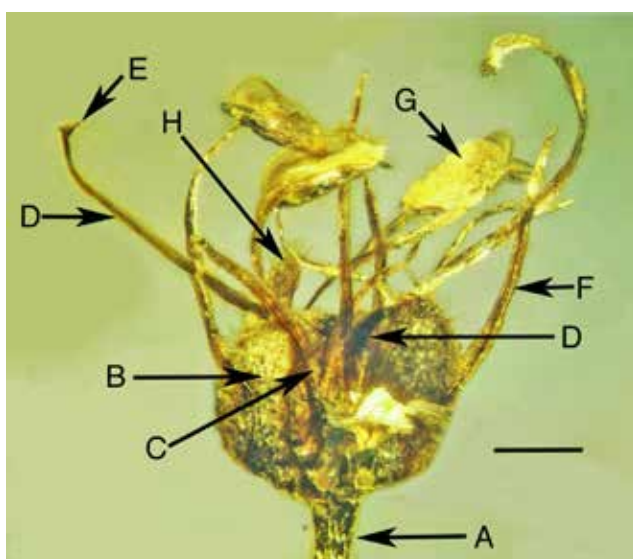


FIG. 2. *Dasykothon leptomiscus*. Flower in lateral view. A. Pedicel. B. Ovate, cupped sepal. C. Ovary. D. Styles. E. Stigma. F. Filament, G. Dehiscent anther. H. Tip of erect, linear-lanceolate sepal. Scale bar = 0.5 mm.

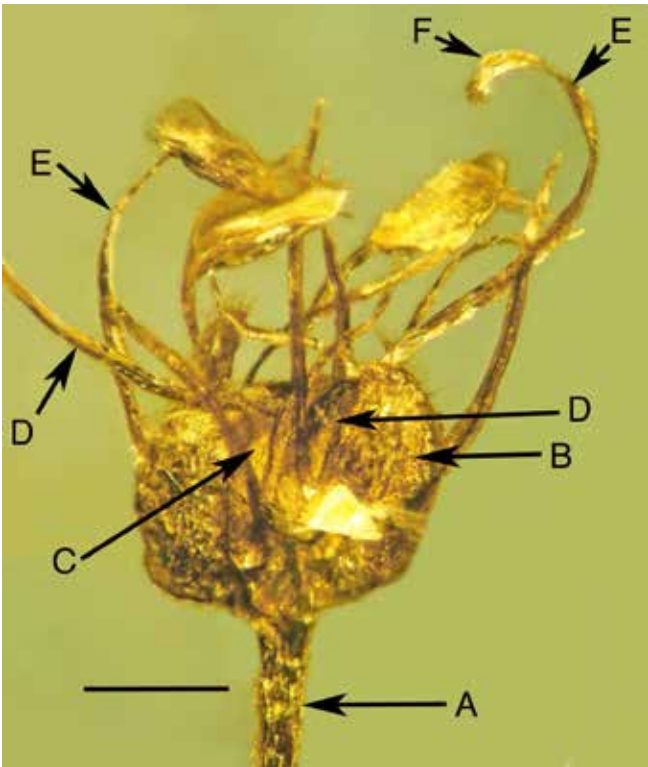


FIG. 3. *Dasykothon leptomiscus*. Flower as in Fig. 2, at a different focal level. A. Pedicel. B. Ovate sepal. Notes lines of papillae. C. Ovary, D. Styles. E. Filaments. F. Vestigial anther. Scale bar = 0.7 mm.

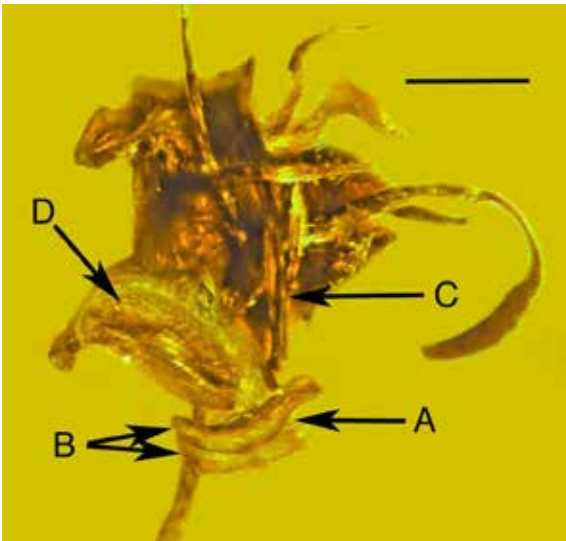


FIG. 4. *Dasykothon leptomiscus*. Flower in apical/lateral view. A. Undehiscent anther. B. Thecae of anther. C. Style, arched over from other side of flower. D. Erect, linear-lanceolate sepal. Scale bar = 0.7 mm.

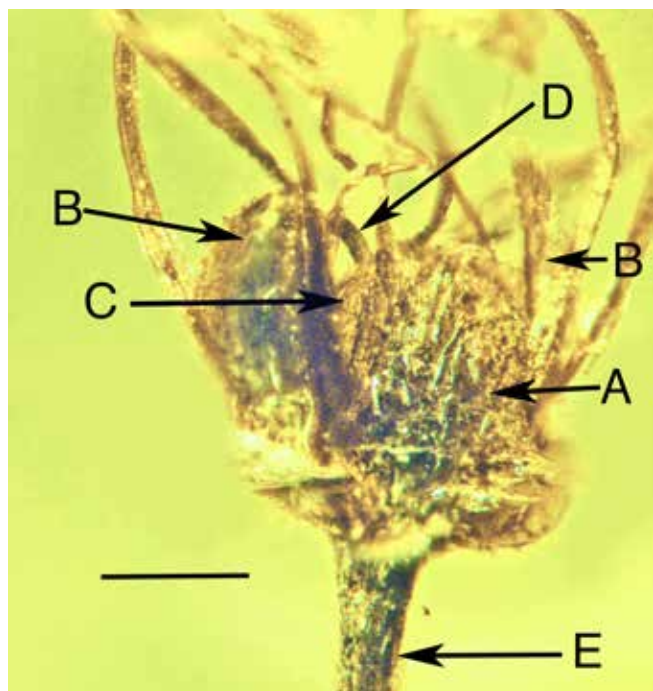


FIG. 5. *Dasykothon leptomiscus*. Reverse lateral view. A. Ovale, cupped sepal. B. Erect, linear-lanceolate sepals. C. Ovary. D. Style. E. Pedicel. Scale bar = 0.7 mm.

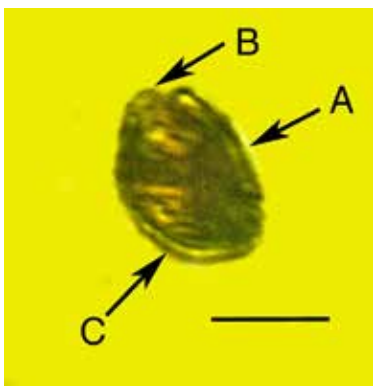


FIG. 6. *Dasykothon leptomiscus*. Isolated pollen grain. A. Pollen grain. B. Germination pore. C. Meridional encircling ridge. Scale bar = 13 μ m.

Group (Renner 1999; Stevens 2001 onwards), show pollen grains with a meridionally encircling sulcus. The sulcus may either be uniform throughout or \pm constricted in the equatorial region of the cell and expanded at the poles (Sampson 1996; parenthetically, Money et al. [1950] define the constricted portions as polar and the 2 expanded regions as lateral). In the examples of *Laurelia* and *Laureliopsis* (Atherospermataceae), the sulcus is narrowed at the equator and expanded at the poles (Sampson 1975, figs. 5, 6; Sampson 1996, figs. 1, 2). Similar grains are illustrated for *Atherosperma moschatum* (Sampson & Foreman 1988, figs. 1–3). However, in *Daphnandra micrantha* (Atherospermataceae), the encircling sulcus is continuous and scarcely narrowed at the equator (Sampson & Foreman 1988, figs. 5, 6), although the degree of narrowing may vary among different samples in this and the other genera (Money et al. 1950, p. 392). The different types of apertures and sulci in genera of Atherospermataceae are summarized in Table 1 of Sampson (1996).

A hypothesis for the origin of the grooved ridge encircling the monoporate pollen grains of *Dasykothon* relates it to the meridional sulcus of grains in the genera described above. It was not possible to determine the polarity of the isolated pollen grains (Figs. 6–8). Nonetheless, we surmise that the single aperture is polar in the cell (Erdtman 1986, fig. 1), and that this condition is derived evolutionarily from a dicolpate ancestor by loss of the aperture from the other pole. The encircling ridge of the

Dasykothon pollen can then be ascribed to an extreme narrowing and thickening of a meridional sulcus of the type seen, for example, in the genus *Daphnandra*. By this hypothesis, the germination pore in *Dasykothon* is derived from one of the 2 polar sulci present in an ancestral *Daphnandra*-type pollen, changing from a colpate to a porate condition.

This theory of pollen evolution involving some early member of the Laurales does not find support in the overall floral morphology of *Dasykothon*, particularly its bisexual flowers, non-valvate anther dehiscence, and lack of a floral cup or paired basal glands on the filaments. No such combination of characteristics is found among modern genera of Monimiaceae sensu lato (Philipson 1993, including Atherospermataceae and Siparunaceae), which often have few to many separate carpels, a cup-shaped or globular receptacle, filaments with paired basal glands, or unisexual flowers. *Hortonia* (Monimiaceae) which resembles *Dasykothon* in its bisexual flowers and anthers that dehisce by longitudinal slits, differs in having 6–4 carpels, a perianth of numerous, spirally arranged tepals, and stamens with short filaments and enlarged basal nectar glands (Endress 1980; Money et al. 1950, fig. 20). Given the conflicting information from floral and pollen morphology, therefore, it seems best that *Dasykothon* be left without taxonomic assignment at this time.

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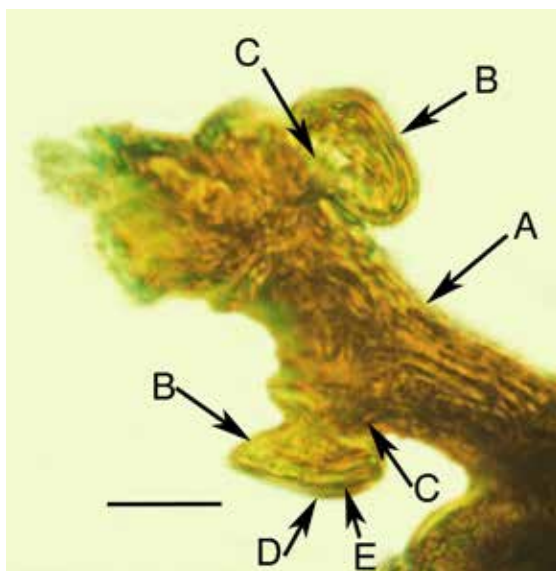


FIG. 7. *Dasykothon leptomiscus*. Stigma with attached pollen grains. A. Lobe of stigma. B. Germinating pollen grains. C. Emerging pollen tubes. D. Meridional ridge. E. Groove in ridge. Scale bar = 15 μ m.

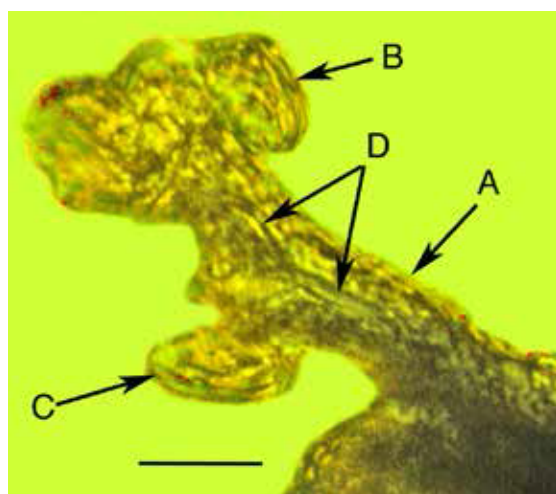


FIG. 8. *Dasykothon leptomiscus*. Stigma as in Fig. 6, at a different focal level. A. Lobe of stigma. B. Pollen grain (note grooved ridge). C. Pollen grain with emerging pollen tube. D. Pollen tubes in tissue of stigma. Scale bar = 19 μ m.

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