

ADDITIONAL FOSSIL SPECIMENS OF *EOPHYLICA* (RHAMNACEAE) IN MID-CRETACEOUS AMBER FROM THE HUKAWNG VALLEY, MYANMAR

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ABSTRACT

The recently described fossil angiosperm genus *Eophylica* (Rhamnaceae) was based on 18 amber-embedded specimens derived from two sites in northern Myanmar. A vegetatively similar fossil, which came from the same amber mines but which lacked flowers, had been previously described as a putative green alga and given the name *Electrophycus*. The dimensions and vegetative aspect of that taxon's holotype specimen are identical with those of the *Eophylica* fossils. Four additional specimens were acquired by the senior author after the publication of *Electrophycus*, all of which have a single terminal flower that is either immature or essentially fully formed. Using techniques of floral dissection, high magnification microscopy, and microphotography of the better-developed flowers, we present a more detailed picture of the floral organs, especially the stamens and style, of *Eophylica*. These flowers differ from the holotype specimen of *Eophylica* and 3 of its paratypes in that they possess involucre bracts of a so-called 'pseudanthial head,' a structure that the authors of *Eophylica* had only ascribed to certain other paratype specimens of the genus.

RESUMEN

El género de angiospermas fósiles recientemente descrito *Eophylica* (Rhamnaceae) se basó en 18 especímenes incrustados en ámbar derivados de dos sitios en el norte de Myanmar. Un fósil similar, desde el punto de vista vegetativo, que procedía de las mismas minas de ámbar pero que carecía de flores, había sido descrito previamente como una supuesta alga verde y recibió el nombre de *Electrophycus*. Las dimensiones y el aspecto vegetativo del espécimen holotipo de ese taxón son idénticos a los de los fósiles de *Eophylica*. El autor principal adquirió cuatro especímenes adicionales después de la publicación de *Electrophycus*, los cuales tienen una sola flor terminal que es inmadura o completamente formada. Usando técnicas de disección floral, microscopía de gran aumento y microfotografía de las flores mejor desarrolladas, presentamos una imagen más detallada de los órganos florales, especialmente los estambres y el estilode *Eophylica*. Estas flores difieren del espécimen holotipo de *Eophylica* y 3 de sus paratipos en que poseen brácteas involucrales de la llamada 'cabeza pseudantial', una estructura que los autores de *Eophylica* solo habían atribuido a otros especímenes paratipo del género.

INTRODUCTION

A recent paper by Shi et al. (2022) describes fossil flowers in mid-Cretaceous amber, collected at two sites in northern Myanmar, which are interpreted as important to understanding both the paleogeography of Rhamnaceae and the history of southern hemisphere fire-adapted plant communities, particularly in South Africa. The amber and its included fossils originated in Gondwana and reached southern Asia via plate tectonic displacement. In a detailed study, the fossils were identified by Shi et al. (loc. cit.) as two newly described species related to the extant South African and Indian Ocean genus *Phylica*. One of these was placed in *Phylica* itself, the other in a new genus named *Eophylica*. By coincidence, a sterile specimen that is vegetatively similar to this new genus had been described and published only three years previously by the senior author of the present paper. Like the holotype of *Eophylica*, its source was an amber mine in the Hukawng Valley, Myanmar. Due to its small size, tufted growth habit, and delicate linear appendages, the plant was judged to be a terrestrial alga. It was assigned to order Chaetophorales and described as the new genus *Electrophycus* (Poinar & Brown 2019). This publication was mentioned by Shi et al., but they did not use this name, citing the Poinar and Brown specimen as being "incomplete," i.e., lacking flowers. It is clear from examination of the figures in the two papers, however, that the linear, elongate, densely stellate-pubescent appendages, which were taken by the authors of *Electrophycus* to be the branches of a terrestrial alga, are essentially identical with the leaves of *Eophylica* as illustrated by Shi et al. (loc. cit.).

Putting aside any possible nomenclatural difficulties posed by the duplication of generic names, we report here on 4 additional specimens from the Poinar amber collection that were acquired by the senior author after the publication of *Electrophycus*. All of these have the long, linear, stellate-pubescent leaves of *Eophylica* and bear a single terminal flower (Figs. 1, 2). In two of these, the flower is too immature to show its internal structure, but the other two have nearly mature flowers with well-developed perianth, stamens, and pistil. In one of these, the ovary could not be exposed during specimen preparation without injuring the sepals and stamens, but in the other, a longitudinal section of the complete flower was obtained. Under microscopic examination it was seen to be similar, in its essential details, to the type specimen of *Eophylica priscastellata* Shi, Wang & Engel (Shi et al. 2022, figs. 2a, b). All 4 flowers are subtended by upright, acutely-tipped involucral bracts, resembling the involucre “pseudanthial heads” illustrated by Shi et al. (loc. cit.) in their figs. 1c, 1g, and Supplement figs. 7d, 11a, 15a, and 17a.

Preparatory polishing of the amber followed by microscopic examination of the two most mature flowers provides a different view of floral morphology, particularly of the androecium, than was figured previously (Shi et al. loc. cit.). Descriptions, measurements, and figures are presented for these two additional specimens of *Eophylica*, which supplement previous knowledge of this significant fossil taxon.

MATERIALS AND METHODS

Mines in northern Burma, now Myanmar, have been known since antiquity as a source of amber that is both a valuable gemstone and a reservoir of abundant fossilized organisms (Poinar et al. 2006). Despite present day civil unrest and frequent military incursions in the area, amber continues to be mined and exported for sale in cities of adjacent China (Sokol 2019; Poinar & Ellenberger 2020). In recent years, over 25 new genera of fossil angiosperm flowers have been described in this amber (cited in Chambers & Poinar 2020; Poinar et al. 2020; Poinar & Chambers 2020). The geology of the Hukawng Valley mines was described by Cruickshank and Ko (2003), who used palynological evidence and ammonite fossils to date the amber deposits as Late Albian, 97–110 Ma. A more exact age of 98.79 ± 0.62 Ma was obtained by Shi et al. (2012), based on radiometric U–Pb dating of zircons in volcanic clasts contemporaneous with the amber. The latter date has been adopted by subsequent authors such as Crepet et al. (2016), Liu et al. (2018), and Shi et al. (2022). The source of the amber is reported to be members of the conifer family Araucariaceae, perhaps the genus *Agathis* (Poinar et al. 2007).

The specimens described in this study are from Kachin Province, Myanmar, and were derived from the Noije Bum 2001 Summit Site amber mines. These lie in the Hukawng Valley SW of Maingkhwan, $26^{\circ}20'N$, $96^{\circ}36'E$. The 4 specimens are assigned accession numbers B-An-23A, B-An-23B, B-An-23C, and B-An-23D, and are deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.

For the present study, observations were made using a Nikon SMA-10R stereoscopic microscope at 80x and a Nikon Optiphot microscope with magnifications up to 600x. 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

Photographs taken before final specimen preparation show the single terminal flower of our fossils (Figs. 1, 2). The sessile or short-pedicelled flower (confusingly called a “pseudanthium head” or “flower head” by Shi et al. 2022, figs. 1c, g, and Supplement) is closely surrounded by an involucre of erect, acuminate bracts. We note that in the holotype specimen of *Eophylica priscastellata*, as well as in 3 paratypes (Shi et al. loc. cit., figs. 1a, c, d, e, l), the involucral bracts are absent, perhaps because they were deciduous shortly before flower maturity. The absence of an involucre is also true of the flowering specimen of *Eophylica* that was illustrated as a so-called gymnosperm seed by Xia et al. (2015). The flower shown in Figs. 2 and 3 is too immature to merit further study. However, two other specimens, shown in Figs. 4–7, are better developed, and these were prepared

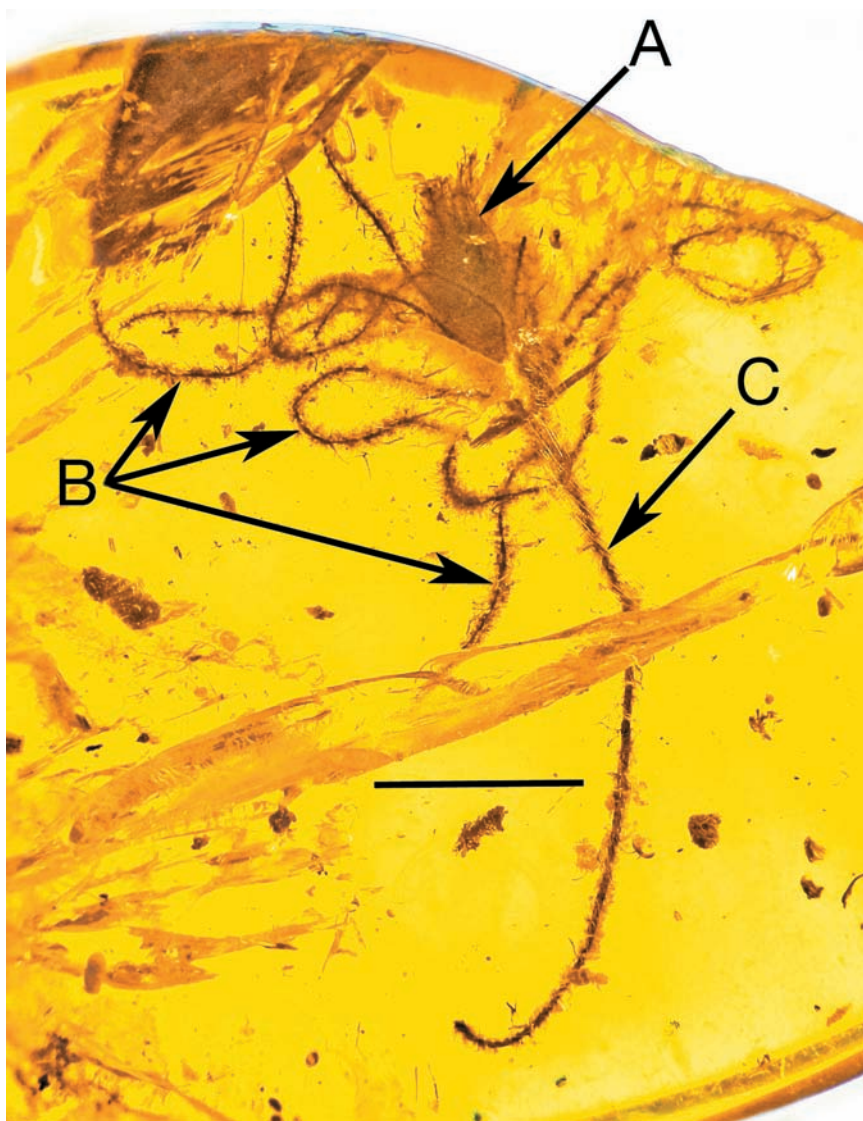


FIG. 1. *Eophylica priscastellata*, specimen B-An-23E. **A.** Terminal flower surrounded by a whorl of involucral bracts. **B.** Leaves, showing indumentum of stellate trichomes. **C.** Stem. Scale bar = 2.3 mm.

by polishing the amber to expose the flowers' internal structure. This processing removed most of the involucre and some of the sepals, revealing the reproductive organs.

In specimen B-An-23A (Figs. 4, 5), a sepal, 3 stamens, and the style were exposed, but further polishing to uncover the ovary would have been too damaging to these organs. Conspicuous in the specimen are much-elongated, probably multicellular, capillary trichomes, many of which bear a terminal cluster of fine, stellate segments. Such stellate clusters, both stalked and sessile, are abundant on the leaves, bracts, and sepals and are a diagnostic character of the genus. The three exposed stamens have elongate, linear-oblong, bilocular anthers, with a stout connective (Fig. 5A) that bears a small, acute terminal appendage. The anthers are 2.1

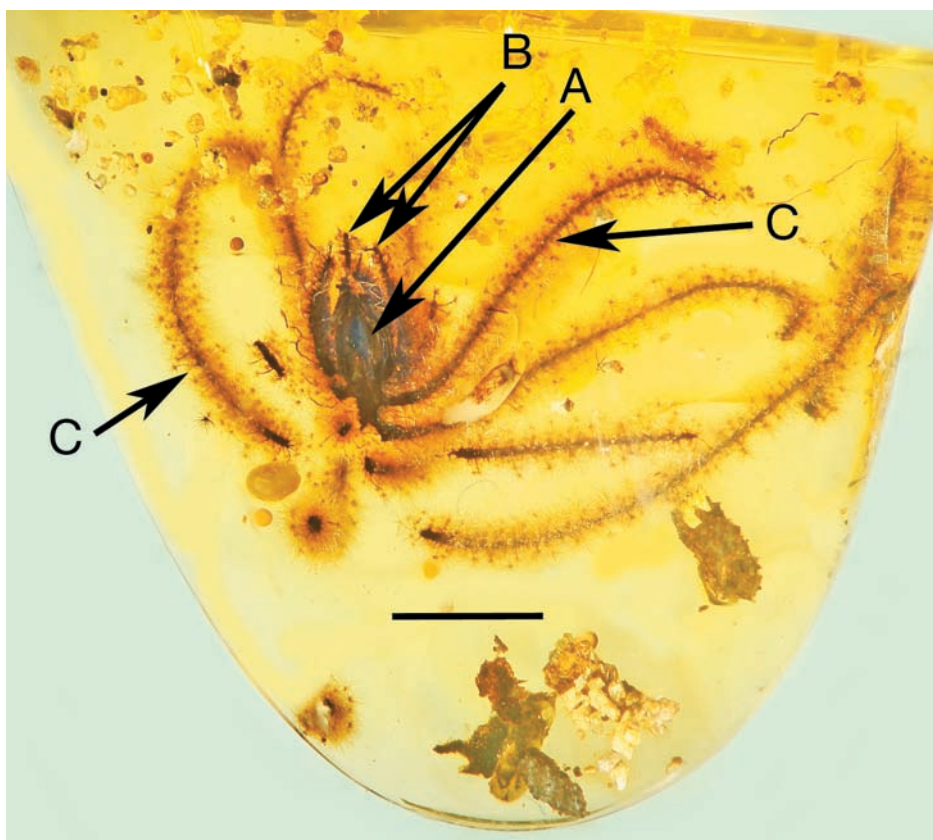


FIG. 2. *Eophylica priscastellata*, specimen B-An-23C. Inflorescence following partial removal of involucre. A. Immature terminal flower. B. Remaining involucral bracts. C. Leaves. Scale bar = 1.7 mm.

mm long, and the filaments, although partly polished away, are at least 1.0 mm long. The stamens of *Eophylica* are not mentioned in the genus or species descriptions by Shi et al. (loc. cit., Supplement), being illustrated only in small reproductions of micro-XCT scans and in drawings (their figs. 3c, d, and j). In Fig. 5, the style is stout, 0.6 mm wide, and at least 4.0 mm long. The stigma is hidden behind some extraneous stellate trichomes. Lying in front of the style is a small remnant of a sepal that was mostly removed during specimen preparation (Fig. 5F).

In the second nearly mature flower, B-An-23E (Figs. 6, 7), remaining pieces of the involucre are visible at the base of the inferior ovary, with the tip of one bract still in position in back of the flower (Fig. 6D). This flower also has many examples of the darkly-stained capillary trichomes and the dense covering of stellate trichomes seen in B-An-23A, above. The inferior ovary is globose—i.e. round in x-section—and 1.3 mm in diameter. Its internal structure is not well preserved in our specimen. There is an evident tissue layer on the top of the ovary that is probably equivalent to the epigynous disc described for *Eophylica priscastellata* (labeled “fd” in fig. 3d of Shi et al.). The 3 visible sepals are borne separately on the apex of the ovary and there is no calyx tube, despite the use of this term in the species diagnosis by Shi et al. (loc. cit., Supplement). The sepals, sectioned longitudinally (Fig. 7A), are stellate-pubescent dorsally, 3.4 mm long, and smoothly arched adaxially, much as in fig. 3j of Shi et al. (loc. cit.). The 3 visible stamens are smaller than those in flower B-An-23A, the anthers and filaments being approximately equal and 0.4–0.6 mm long. The form of the stamens in

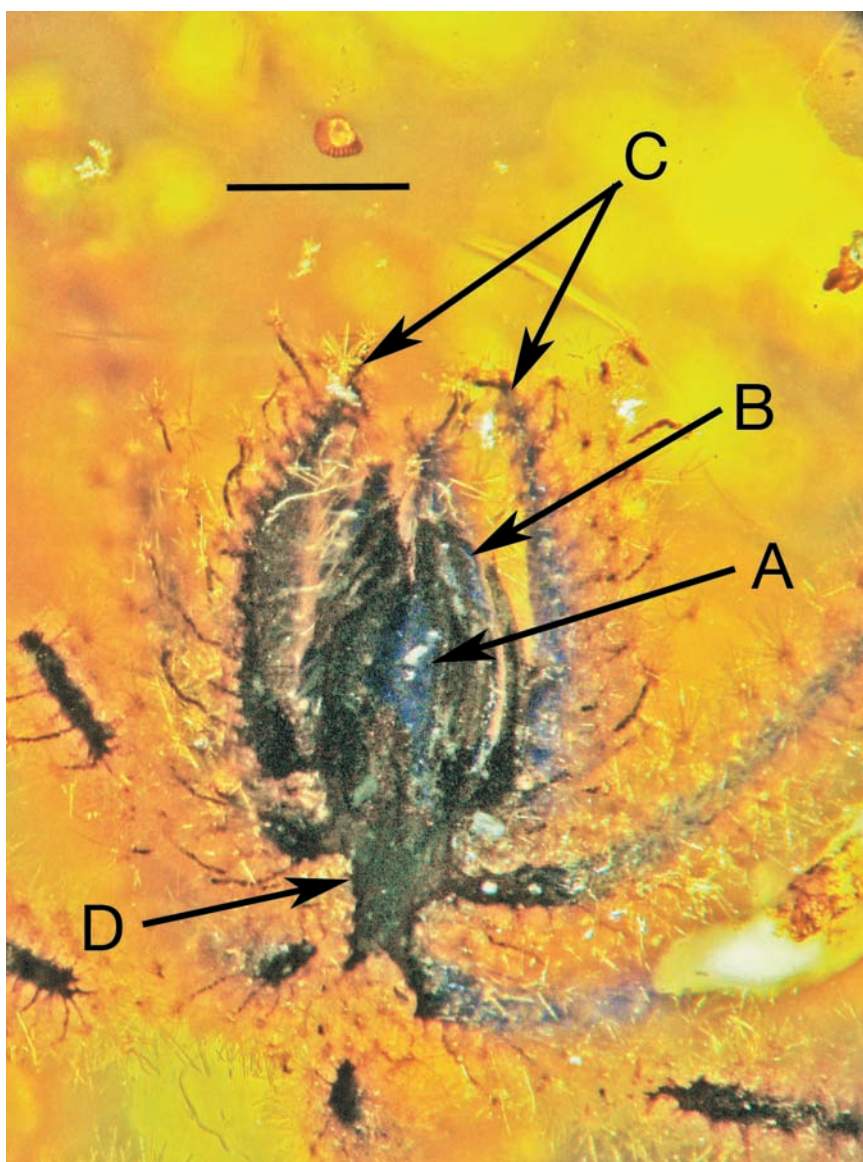


FIG. 3. *Eophylica priscastellata*, specimen B-An-23C. As in Fig. 2. A. Immature flower. B. Sepal. C. Remaining involucral bracts. D. Pedicel. Scale bar = 0.7 mm.

both flowers differs greatly from the androecium diagrammed for *Eophylica priscastellata* (Shi et al. loc. cit., fig. 3j), where the anthers are shown as small, globose or reniform structures on elongated capillary filaments. Parenthetically, in his monograph of *Phyllica*, Pillans (1942) describes the stamen filaments of the genus as “very short.” The style in flower B-An-23E is 1.3 mm long, and the stigma is divided into 3+ acute, triangular lobes (Fig. 7E). As expected, the corolla is absent in both of these almost-mature flowers.

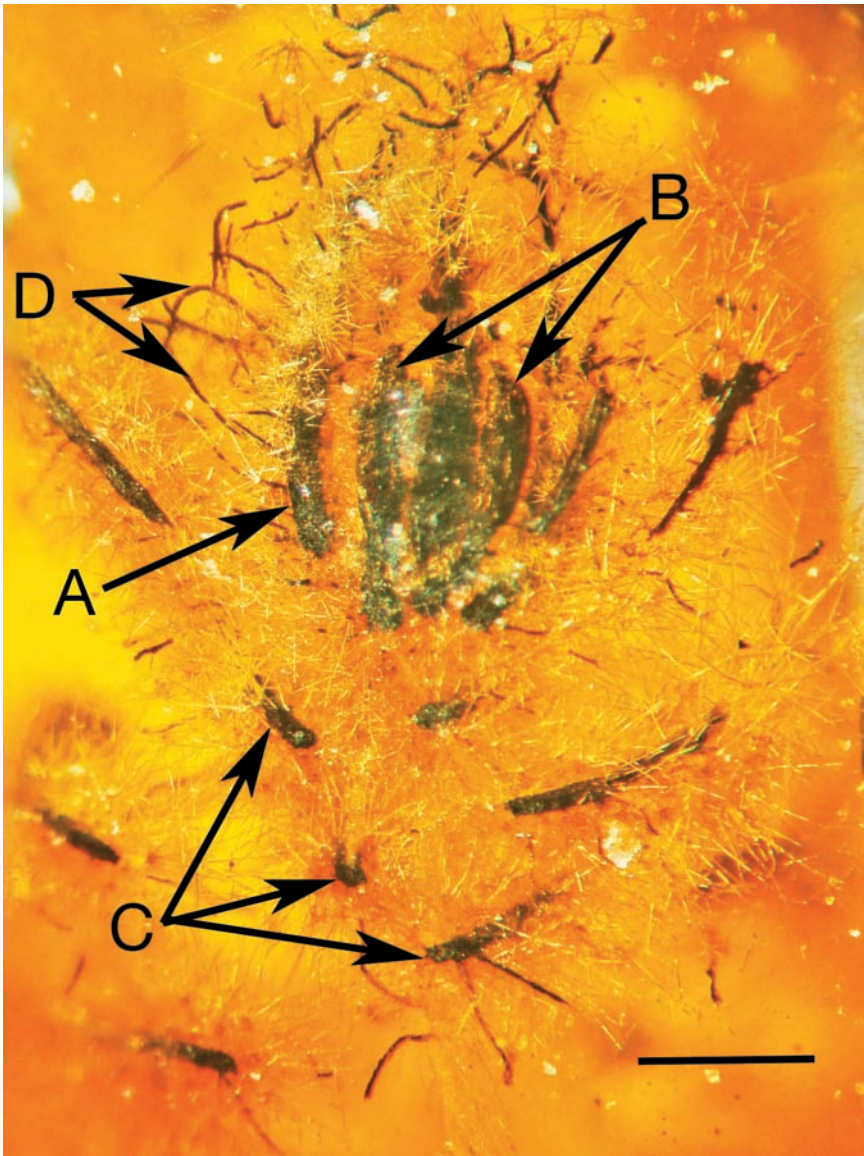


FIG. 4. *Eophylica priscastellata*, specimen B-An-23A. Terminal flower with ovary concealed by stellate trichomes. A. Sepal. B. Stamens. C. Vegetative leaves truncated by polishing of specimen. D. Capillary multicellular trichomes. Scale bar = 1.5 mm.

DISCUSSION

The figures provided here add important details to the description of *Eophylica*, especially as regards the stamens and style. Using traditional methods of specimen preparation and microscopy, close-up images of pubescence traits as well as the form and structure of the reproductive organs were obtained, and more exact measurements of the androecium and style were possible. The single species described for *Eophylica*, named *E. priscastellata*, is based on 18 specimens, collected from two different mining areas which vary in age from

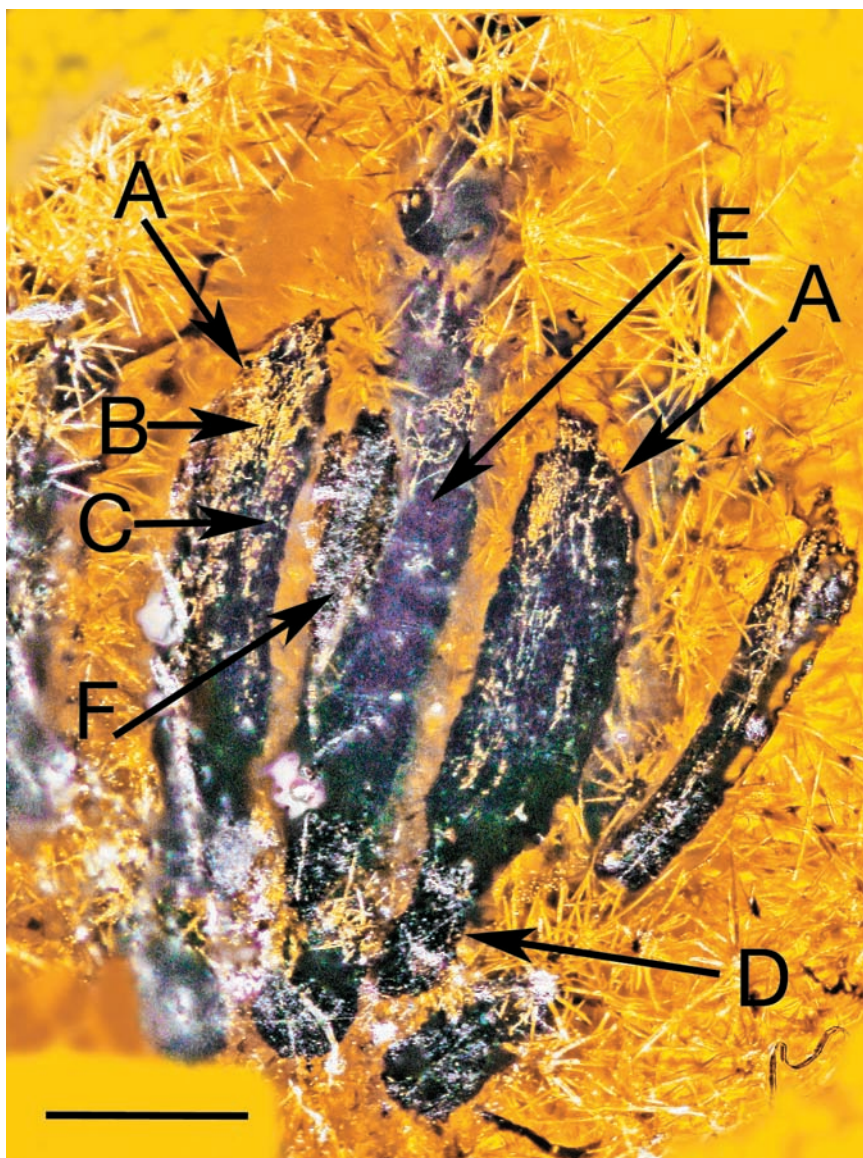


FIG. 5. *Eophylica priscastellata*, specimen B-An-23A. Enlargement of flower. **A.** Stamens. **B.** Anther connective. **C.** Anther locule. **D.** Stamen filament. **E.** Style. **F.** Remnant of sepal. Scale bar = 0.6 mm.

ca. 110 Ma to ca. 99 Ma (Xing & Qiu 2020; Shi et al. 2022). This name therefore can serve as a convenient appellation for Myanmar *Eophylica* fossils from this time period, including a certain amount of specimen-to-specimen floral variability, as shown by our fossils and those of Shi et al. (loc. cit.).

In a number of our previous publications describing new genera of Myanmar amber fossils, we have discussed the phytogeographic affinities of this flora, its origin being in the Early Cretaceous continent of Gondwana (Poinar 2018; Chambers & Poinar, 2020; Poinar et al. 2020). Shi et al. (loc. cit.) describe the trans-Tethyan migration of the India Plate from Gondwana to SE Asia, which carried the amber fossils from their

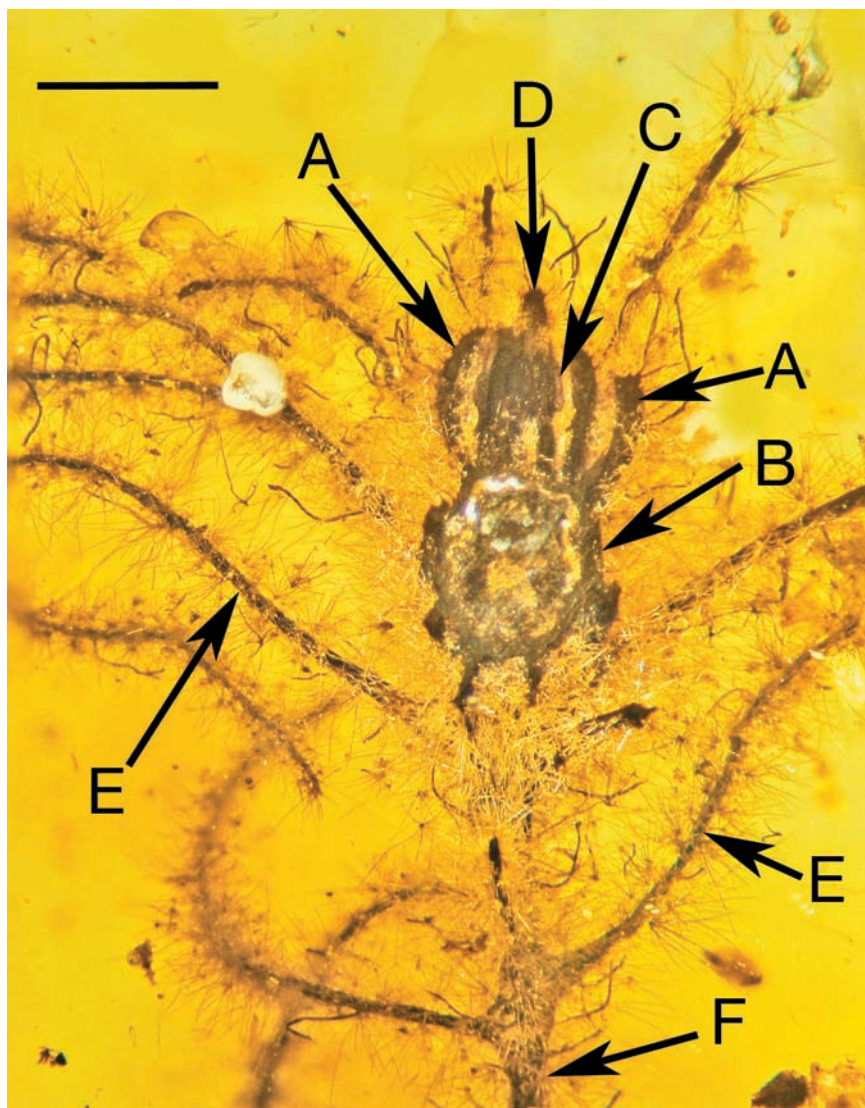


FIG. 6. *Eophylica priscastellata*, specimen B-An-23E. Terminal portion of plant with flower cut in vertical section. A. Sepals. B. Inferior ovary. C. Stamen. D. Tip of remaining involucre bract. E. Leaves showing pubescence of stellate trichomes. F. Stem. Scale bar = 2.7 mm.

Southern Hemisphere origin to their present position. There is ample geologic evidence for this particular reconstruction as it concerns the history of the amber fossils (Metcalf 2013; Westerweel et al. 2019). It is not our purpose here to add further to discussions of the phylogeny of *Eophylica* or of this fossil's possible significance when reevaluating the history of fire-adapted angiosperms in Cretaceous Gondwana (Shi et al. 2022). The results of these authors' study should be of considerable interest to fire ecologists and plant systematists in the present-day continents derived from the breakup of that ancient land mass.

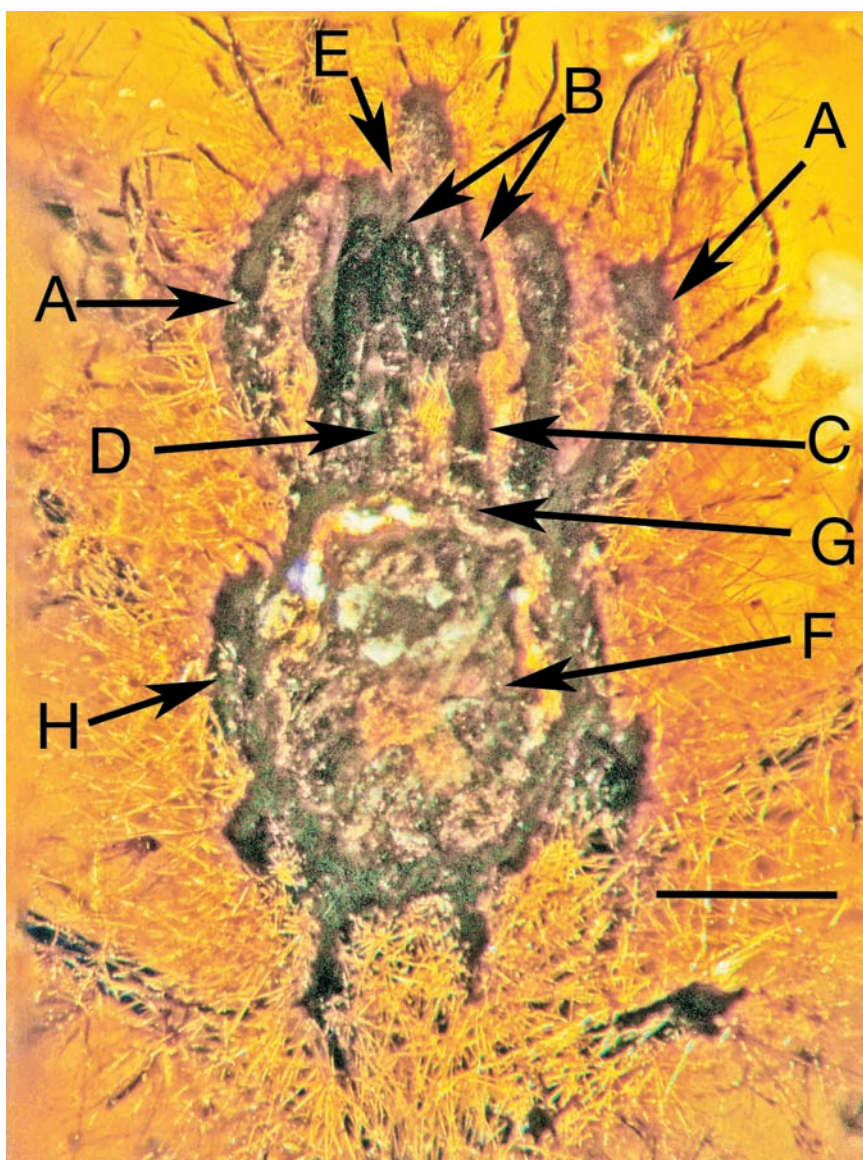


FIG. 7. *Eophylica priscastellata*, specimen B-An-23E. Enlargement of flower. A. Seps. B. Anthers. C. Stamen filament. D. Style. E. Stigma. F. Cavity of inferior ovary. G. Epigynous disc. H. Involucral bract truncated by polishing of specimen. Scale bar = 0.6 mm.

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VALIDATION OF THE PREVIOUSLY PUBLISHED NAME *ENDOBEUTHOS* *PALEOSUM*, A FOSSIL FLOWER IN MID-CRETACEOUS MYANMAR AMBER

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ABSTRACT

The name *Endobenthos paleosum*, previously published in this journal, was invalid due to the lack of a designation of one of the illustrations as the holotype specimen and the others as paratypes. This oversight is here corrected and the taxon name properly validated.

RESUMEN

El nombre *Endobenthos paleosum*, publicado anteriormente en esta revista, no era válido debido a la falta de la designación del espécimen de una de las ilustraciones como holotipo y las otras como paratipos. Este descuido se corrige aquí y el nombre del taxón se valida correctamente.

INTRODUCTION

In our publication of *Endobenthos paleosum*, a new genus and species of fossil angiosperms preserved in mid-Cretaceous Myanmar amber, 6 separate flowers are illustrated along with magnified views of the stamens and pollen present in the fossils. Because all the flowers are contained in a single block of amber, our assumption was that they had come from the same inflorescence, despite some differences in their calyx lengths and pubescence. It is possible, however, that the specimens may have come from different parental plants and coincidentally have been preserved together, a point that was not made clear in the paper. It has been called to our attention (A. Pavlova, pers. comm.) that for the taxon to be validly published, there should have been an explicit designation of one of the validating illustrations as the holotype and the remaining as paratypes. This is specified in Art. 43.3 of the International Code of Nomenclature for Algae, Fungi, and Plants (ICNAPF 2018) dealing with the names of new fossil species or infraspecific taxa published on or after 1 January 2001. The purpose of this note is to correctly validate the publication of this taxon by specifying which figure represents the holotype flower and which the paratypes.

CORRECTED TYPE DESIGNATIONS

Endobenthos Poinar & K.L. Chambers, **gen. nov.**, ex J. Bot. Res. Inst. Texas 12:136. 2018. TYPE SPECIES: *Endobenthos paleosum* Poinar & K.L. Chambers, sp. nov., op. cit. 134–137, here validated. Genus description is on page 136 of the above publication.

Endobenthos paleosum Poinar & K.L. Chambers, **sp. nov.**, ex J. Bot. Res. Inst. Texas 12:134–137. 2018. HOLOTYPE: catalogue number B-An-7A, **Fig. 3**, page 135; first paratype, catalogue number B-An-7B, **Fig. 1**, page 134, left hand flower; second paratype, catalog number B-An-7C, **Fig. 1**, page 134, right hand flower; third paratype, catalog number B-An-7D, **Fig. 2**, page 134, left hand flower; fourth paratype, catalog number B-An-7E, **Fig. 2**, page 134, right hand flower; fifth paratype, catalog number B-An-7F, **Fig. 7**, page 137. Specimens are deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon, 97331, U.S.A. Numbers refer to the 6 flowers embedded together in one block of amber. Species description is on pages 136–137 of the above publication.

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