ENDOBEUTHOS PALEOSUM GEN. ET SP. NOV., FOSSIL FLOWERS OF UNCERTAIN AFFINITY FROM MID-CRETACEOUS MYANMAR AMBER

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ABSTRACT

Endobeuthos paleosum gen. et sp. nov. is based on 6 flowers preserved together in a single block of mid-Cretaceous amber from Myanmar (Burma). The calyx is composed of ca. 50+ small, helically arranged sepals. The corolla consists of 5 imbricate petals forming a sheath-like structure that is usually concealed within the calyx. The petal tips are often spreading and exserted from the calyx. There are numerous stamens, each of which consists of a filament and an enlarged anther connective with a single lateral, bisporangiate theca. Dehiscence is extrorse. The tips of 3 or 4 styles are visible, indicating that the flowers are bisexual. The fossils possess unique features that prevent assignment to any modern family. However, the numerous sepals and stamens and a thickened anther connective may suggest an association of *E. paleosum* with the family Dilleniaceae.

RESUMEN

Endobeuthos paleosum gen. et sp. nov. está basado en 6 flores preservadas juntas en un bloque simple de ámbar del Cretáceo medio de Myanmar (Birmania). El cáliz está compuesto por c. 50+ sépalos pequeños, dispuestos helicoidalmente. La corola consiste en 5 petalos imbricados que forman una estructura en forma de vaina que normalmente está oculta dentro del cáliz. Los extremos de los petalos están esparcidos y exertos del cáliz. Hay numerosos estambres, que consisten en un filamento y un conectivo de la antera ensanchado con una teca lateral simple, bisporangiada. La dehiscencia es extrorsa. Son visibles los extremos de 3 o 4 estilos, que indican que las flores son bisexuales. Los fósiles tienen características únicas que impiden su asignación a cualquier familia moderna. Sin embargo, los sépalos numerosos y estambres con un conectivo engrosado en la antera pueden sugerir una asociación de *E. paleosum* con la familia Dilleniaceae.

INTRODUCTION

The flowers are unusual in having a calyx of numerous, helically arranged sepals (Figs. 1, 3). The 5 petals overlap marginally to form a sheath-like structure that is covered by the calyx in 5 of the 6 available flowers, with only the spreading petal tips visible (Fig. 2). In one flower, the upper half of the corolla is exserted from the calyx (Fig. 3). The calyx has a covering pubescence of stellate trichomes whose density varies from flower to flower, making it sometimes difficult to observe and count the sepals. Where the stamens are not obscured by inclusions in the amber they are seen to possess a slender filament and a thickened anther connective bearing a single abaxial, bisporangiate theca (Fig. 5A). Dehiscence of the sporangia releases a mass of pollen grains (Fig. 5B). After pollen dispersal, the withered connective forms a characteristic narrow strap (Fig. 5C). In one case, the face of the flower could be observed, with 3 or 4 styles projecting from the mass of stamens (Fig. 4). If this interpretation is correct, the flowers in our sample were structurally bisexual. Pollen grains are tricolpate (Fig. 6).

MATERIALS AND METHODS

The fossils originated in a deposit of amber in oceanic sediments at the Noije Bum 2001 Summit Site mine, excavated in the Hukawng Valley in Myanmar (Burma). Based on marine paleontological evidence, this site was dated to the late Albian of the Early Cretaceous (Cruickshank & Ko 2003), placing the age at 97–110 Ma. A more recent study, using U-Pb dating of zircons in volcanic clasts, determined the age to be 98.79 ± 0.62 Ma, at the Albian/Cenomanian boundary (Shi et al. 2012). Nuclear magnetic resonance (NMR) spectra and the presence of araucarioid wood fibers in amber samples at the site indicate an araucarian source for the amber (Poinar et al. 2007). Observations and photographs were made with a Nikon SMA-10R stereoscopic

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Fig. 1. *Endobeuthos paleosum*. Lateral view of 2 flowers. **A.** Calyx of helically arranged sepals. **B.** Stamen with anther withered after release of pollen. Scale bar = 1.1 mm.

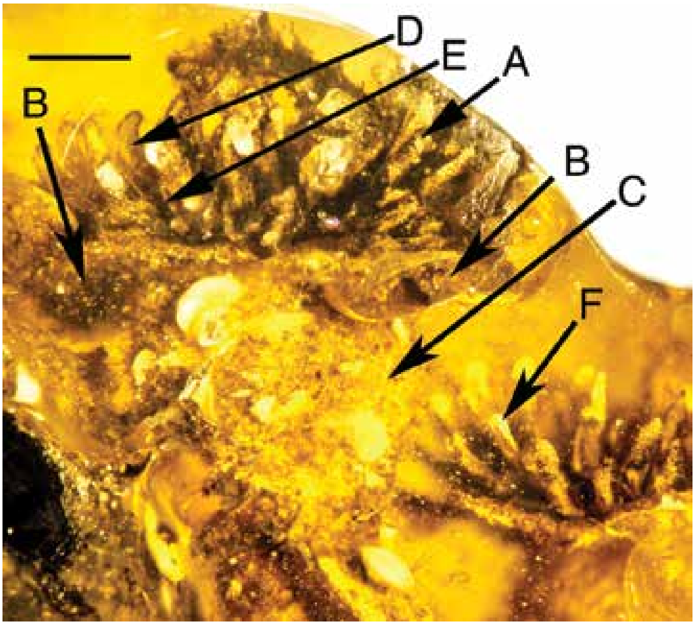

Fig. 2. *Endobeuthos paleosum*. Lateral view of one flower and stamens of a second. **A.** Dehisced anther with pollen. **B.** Lobes of corolla. **C.** Calyx. **D.** Enlarged anther connective. **E.** Stamen filament. **F.** Lateral theca on enlarged anther connective. Scale bar = 0.9 mm.

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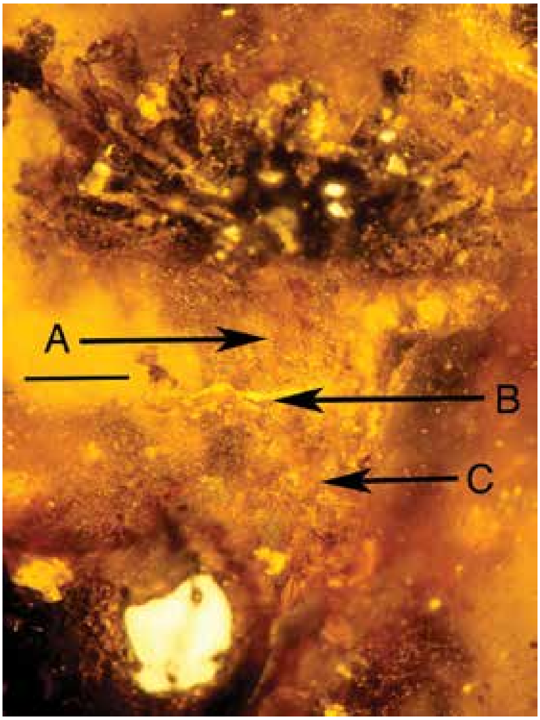

Fig. 3. *Endobeuthos paleosum*. Lateral view of flower with exposed corolla. **A.** Sheath formed by imbricate petals. **B.** Rim of calyx. **C.** Calyx. Scale bar = 1.0 mm.

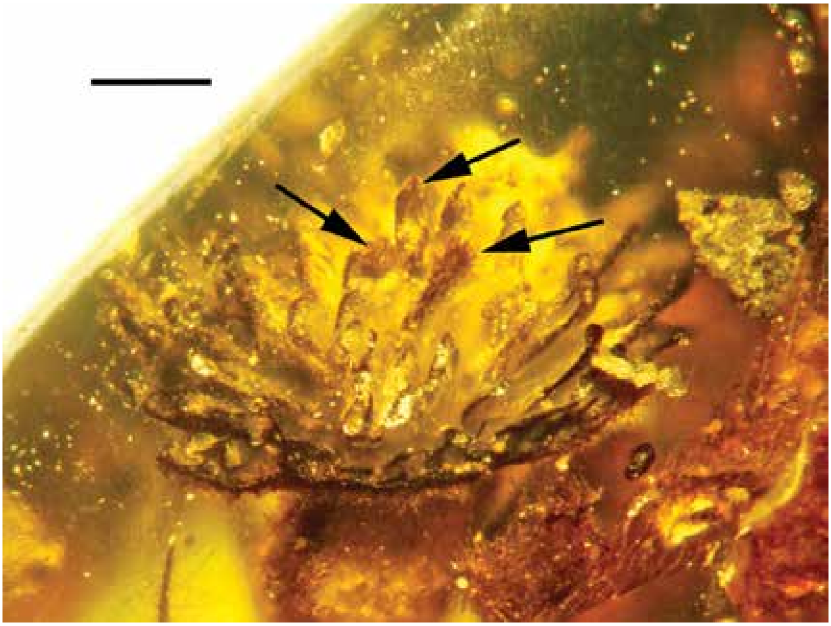

Fig. 4. *Endobeuthos paleosum*. Face of flower. Arrows show 3 styles partially exserted from among stamens. Note that in this flower, the corolla is not exposed. Scale bar = 0.9 mm.

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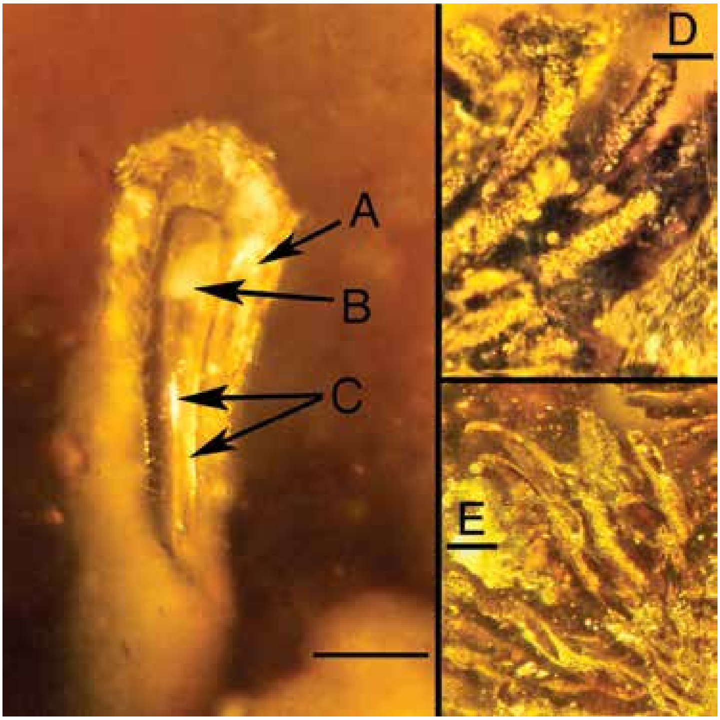

Fig 5. ***Endobeuthos paleosum*****. Stamens. A. Enlarged anther connective. B. Lateral bisporangiate theca. C. Sporangia. Scale bar = 0.05 mm. D. Dehisced anthers with pollen. Scale bar = 0.2 mm. E. Withered anthers after pollen dispersal. Scale bar = 0.2 mm.**

microscope at 80xx 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.

DESCRIPTION

Endobeuthos Poinar & K.L. Chambers, gen. nov. (**Figs. 1–7**). Type Species: *Endobeuthos paleosum* Poinar & K.L. Chambers, sp. nov.

Flowers bisexual, pedicellate, calyx accrescent, composed of numerous (50+) helically arranged sepals (Fig. 1), calyx surface lightly or densely stellate pubescent (e.g., Fig. 1), corolla sheath-like, enclosed within the calyx on most flowers, petals 5, erect, margins imbricate (Fig. 3), tips spreading (Fig. 2), stamens ca. 60 or more, filaments linear, terminating in a thickened anther connective (Fig. 2), which bears a single abaxial, bisporangiate theca (Figs. 2, 5A) dehiscing extrorsely to expose pollen (Fig. 5B); connective withering after pollen dispersal (Figs. 1, 5C), styles 3 or 4, partially concealed among the stamens (Fig. 4), pedicels elongate, puberulent (Fig. 7), pollen tricolpate, exine microechinate (Fig. 6).

Etymology.—From the Greek "endo," within, inner, and "beuthos," a woman's dress, based on the skirt-like corolla.

Endobeuthos paleosum Poinar & K.L. Chambers, sp. nov. Type: MYANMAR (BURMA). Kachin: amber mine in the Hukawng Valley SW of Maingkhwan, 26°20'N, 96°36'E, 2016, *unknown amber miner s.n.* (holotype: catalogue number B-An-7A, paratypes: catalogue numbers B-An-7B, B-An-7C, B-An-7D, B-An-7E, B-An-7F, 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.

Flowers 3.0–4.2 mm long, 3.2–4.6 mm wide, calyx 1.8–3.2 mm high, 1.5–2.0 mm wide, broadly campanulate

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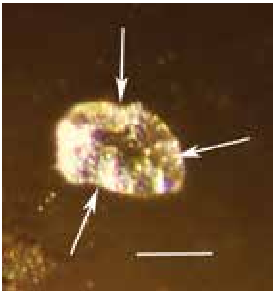

Fig. 6. ***Endobeuthos paleosum*. Tricolpate pollen grain. Arrows show colpi. Scale bar = 18 µm.**

Fig. 7. ***Endobeuthos paleosum*. Flower with immature Orthoptera. The insect is facing downward. Note puberulence of the floral pedicel. Scale bar = 1.8 mm.**

or urceolate (Figs. 1, 3, 7), sepals obovate or elliptic, acute or obtuse, 0.4–0.5 mm long, 0.4–0.5 mm wide (Fig. 1), exposed corolla sheath-like, 2.2 mm wide (Fig. 3), petal tips 1.0 mm wide, often exserted 0.6–1.0 mm from the calyx (Fig. 2), anther connective 0.8–1.1 mm long, 0.08–0.09 mm wide (Fig. 5A), theca linear, 0.5 mm long (Fig. 5B), remaining portion of floral pedicels 4–8 mm long (Fig. 7), pollen grains 32–36 µm in diameter (Fig. 6).

Etymology.—From the Greek “palaios,” ancient.

DISCUSSION

The unusual features of *Endobeuthos* that make taxonomic assignment difficult are the numerous, helically arranged sepals, the sheath-like corolla commonly concealed in the calyx, and the numerous stamens, whose slender filaments support a thickened anther connective with a single bisporangiate, abaxial theca. Genera whose anthers have a single bisporangiate theca, as in Moringaceae (Dutt 1978) and in Olacaceae and

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Acanthaceae, as listed by Endress and Stumpf (1990, t. 2), differ from the fossils in their calyx, number of stamens, and other features. No anthers similar to the fossils were reported in the review of "Lower" Rosidae by Endress and Stumpf (1991).

In a further search for similarities to modern families, we eventually paid particular attention to the Dilleniaceae, based on information in Gilg (1895), Kubitzki (1970), Dickison (1970), and Horn (2007, 2009). A large number of sepals (7–18) had been reported for the genera *Tetracera* and *Dillenia* (Aymard 2003, p. 1; Horn 2007, p. 137). Polymerous androecia are common in the family as well (e.g., Endress 1997), with the 3 species of *Neodillenia* and some taxa if *Davilla* and *Tetracera* having up to 500 stamens (Aymard 1997, p. 121; Dickison 1970, p. 403; Fraga 2008, p. 358; Horn 2007, p. 137). In *Tetratracera*, it is common for the thecae to be partially separated by a thick connective (Gilg 1895, pp. 104; 110; Dickison 1970, pl. 1; Kubitzki 1970, fig. 1; Horn 2007, p. 145). One anther illustrated by Kubitzki (loc. cit.) shows a broad, "emarginate" connective with the thecae well separated. In *Tetracera scaberrimum* Miq. some anther connectives bear 2 separated thecae and others just 1 theca (pers. observ). The single theca on a thickened connective in *Endobeuthos* therefore bears some similarity to certain members of subfamily Doliocarpoideae and the genus *Tetracera* (Horn 2009, p. 809). However, the age of the fossils is so great that an ancestral connection with this family can only be hypothesized (see below).

In an earlier publication (Poinar & Chambers 2017) dealing with *Tropidogyne* from Myanmar amber, a discussion of the age and origin of the mid-Cretaceous fossils at this Malaysian locality included the citation of an unpublished earlier draft of this paper, later withdrawn from publication, in which *Endobeuthos* was mistakenly ascribed to the family Asteraceae. The Mesozoic geological history of India and the Malaysian region led us to consider the possibility that fossils in Myanmar amber might have had their origin on the continent of Gondwana, for example in Australia or in India before it detached, drifted northward across the Tethys Sea during the Cretaceous, and joined Asia in the Eocene (see Hall 2012; Metcalfe 2013). In discussing *Tropidogyne*, we emphasized its many similarities to the modern genus *Ceratopetalum*, family Cunoniaceae, which today is endemic to Australia and New Guinea. This taxonomic relationship is only hypothetical, and no fossils of *Ceratopetalum* are known from before the Eocene Period.

A similar relationship may be suggested between *Endobeuthos* and family Dilleniaceae, as discussed above. The modern distribution of Dilleniaceae includes Indomalaysia as well as southern Mexico, Mesoamerica, the Antilles, northern South America, central Africa, India, Australia, and New Guinea (Horn 2009, fig. 1). No close relationship can be ascribed for *Endobeuthos* and any extant genus of Dilleniaceae. Only in its numerous sepals and stamens, and in its thickened anther connective bearing, in this case, 1 rather than 2 bisporangiate thecae, might there be a similarity to *Tetracera* and some members of the subfamily Doliocarpoideae. The present evidence supporting a Southern Hemisphere origin for *Endobeuthos* is its presence in a Myanmar amber deposit, on a terrane that geological evidence suggests may have been part of Gondwana early in the Cretaceous Period.

An insect is embedded in the amber adjacent to one of the flowers (Fig 7). Cephalic and leg morphology of this immature insect place it within the Orthoptera, a group with well-known herbivores.

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