EOËPIGYNIA BURMENSIS GEN. AND SP. NOV., AN EARLY CRETACEOUS EUDICOT FLOWER (ANGIOSPERMAE) IN BURMESE AMBER

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ABSTRACT

Eoëpigynia burmensis gen. & sp. nov. is described from Early Cretaceous Burmese amber. The genus is characterized by small, perfect, actinomorphic flowers possessing a perianth with a single series of basally connate sepals, four distinct equal petals, four included stamens alternate with the petals, an inferior ovary, a single style with a bilobed stigma, and triaperturate pollen. Flowers with similar morphology occur in the family Cornaceae.

KEY WORDS: Burma, amber, eudicot flower, Early Cretaceous, Cornaceae

RESUMEN

Eoëpigynia burmensis gen. & sp. nov. se describe del ámbar birmano del Cretácico temprano. El género se caracteriza por tener flores pequeñas, perfectas, actinomórficas que tienen un perianto con una serie sencilla de sépalos connados en la base, cuatro pétalos independientes iguales, cuatro estambres inclusos alternando con los pétalos, un ovario ínfero, un estilo simple con estigma bilobulado, y polen triaperturado. Existen flores con una morfología semejante en la familia Cornaceae.

INTRODUCTION

Burmese amber has an interesting past dating back to AD 100 when an amber trade route was established with China. The first Europeans visited the mines in 1836 but it was not until 1896 that the amber was noted to contain insect remains. From AD 100 until 1936, the Burmese amber mines supplied amber to various parts of the world (Chhibber 1934). In 2001, a new amber mine was excavated in the Hukawng Valley, southwest of Maingkhwan in the state of Kachin (26°20'N, 96°36'E) (Poinar et al. 2005). This new amber site, known as the Noije Bum 2001 Summit Site, was dated to the Upper Albian (100 to 105 mybp) of the Early Cretaceous (Cruickshank & Ko 2003).

The Early Cretaceous age of amber from the Noije Bum 2001 Summit Site as determined by Cruickshank and Ko (2003) is supported by primitive insects from this deposit. For example, a bee was discovered still possessing characters of sphecid wasps, the group considered ancestral to bees (Poinar & Danforth 2006). An elcanid grasshopper was also found at this site, representing a group (Elcanoidea) that first appeared in the Early Permian and continued only to the mid-Cretaceous (Poinar et al. 2007). Thus, both paleontological data and inclusions in the amber support an Early Cretaceous age for deposits from the Noije Bum 2001 Summit Site.

Nuclear magnetic resonance (NMR) spectra of amber samples taken from that locality indicate an araucarian (possibly *Agathis*) source of the amber (Lambert & Wu, unpublished data 2002). While insects are dominant, the deposits have revealed some very interesting plant fossils, including a unisexual flower with affinities to the family Monimiaceae (Poinar & Chambers 2005) and two early bambusoid grasses (Poinar 2004). In the present paper, we describe a bisexual flower, provisionally assigned to the family Cornaceae, from the Noije Bum 2001 Summit Site.

MATERIALS AND METHODS

The flower is complete and well-preserved. One of the petals shows some evidence of insect damage, and fungal hyphae are associated with one of the anthers. The flower was in anthesis at entombment, and pollen grains occur on and adjacent to the anthers as well as on the stigma. The piece of amber containing the flower is square, measuring 5 mm in length by 5 mm in width by 1.5 mm deep. Examination and photographs were made with a Nikon stereoscopic microscope SMZ-10 R at 80 × and a Nikon Optiphot microscope at 800×.

DESCRIPTION

Eoëpigynia Poinar, Chambers & Buckley, gen. nov. Type species: *Eoëpigynia burmensis* Poinar, Chambers & Buckley, sp. nov.

Diagnosis.—Flowers small, bisexual, regular, epigynous; perianth tetramerous; calyx comprising a short crown (gamosepalous) at summit of ovary, sepal lobes incised, number uncertain; petals 4, separate, valvate, regular; stamens 4, free to base, in a single whorl, alternating with the petals, filaments linear, anthers introse, dorsifixed; pollen shed singly, pollen grains triaperturate (possibly tricolporate with thickened exine adjacent to colpi); gynoecium syncarpous, ovary inferior, style 1, stigma bilobed, pericarp wall thick-textured at anthesis, fruit type unknown; presence of floral disc not determinable.

Eoëpigynia burmensis Poinar, Chambers & Buckley, sp. nov. (**Figs. 1–2**). Type: MYANMAR (BURMA): Kachin: northern Myanmar, amber mine in the Hukawng Valley, SW of Maingkhwan, (26°20′N, 96°36′E), Aug 2005, *Buckley s.n.* (holotype: perfect flower (accession # ab 214) deposited in the collection of Ron Buckley, Florence, Kentucky 41042-8355, U.S.A.).

Description.—**Flower** bisexual, glabrous, length 1.5 mm; no free hypanthium evident; calyx lobes with incised margins, greatest length of calyx 0.34 mm; petals lanceolate-ovate, margins abaxially recurved, up to 0.95 mm long, 0.34 mm wide; stamens with ovoid anthers up to 0.15 mm long, filaments 0.54–0.61 mm long; stigma at level of anthers, estimated length of style 0.55 mm; length of ovary 0.54 mm; width of ovary 0.39 mm; diameter of pollen grains, 12–14 µm.

Etymology.—Genus name from the Greek "eos" dawn, "epi-" upon, and "gyne" female, from the age and the relation of the floral perianth to the ovary. Species named for the country of origin of the fossil.

DISCUSSION

Certain structures that would be helpful in the placement of *Eoëpigynia*, for example the presence of a floral disc, could not be observed due to the fossil's orientation in the amber. However, it was possible to view the flower from both sides to verify the characteristics described here. Based on its floral features, *Eoëpigynia* (Figs. 1, 2) represents a core eudicot that can provisionally be assigned to the family Cornaceae *sensu lato*, in the basal asterid order Cornales. The phylogenetic position of Cornales as sister to all the remaining asterids (perhaps excluding Ericales) is well confirmed by molecular studies (Stevens 2001 onwards; Hilu et al. 2003; Judd & Olmstead 2004; Bremer et al. 2004). The perfect flower, inferior ovary, compound style, 4-merous perianth and androecium, and possibly tricolporate pollen of our fossil are most similar to the modern genus *Cornus* (see illustrations in Wangerin 1910; Judd et al. 1999). The pollen of the fossil may be of particular importance in this placement. In an equatorial optical section (Fig. 1D) three distinct paired thickenings are seen in the exine marking what we assume are the three colpi (we could not focus our instrument clearly on a pore at this spot). This pattern is strongly reminiscent of SEM equatorial transections of *Cornus* pollen illustrated by Ferguson (1977), e.g. his figure 2c of thickened endexine in this area in *C. volkensii*, as well as his figures 4d of *C. disciflora* and 6c of *Curtisia dentata*. Because of the pollen orientation in the amber, we were unable to observe a pore face-on, where the characteristic H-shaped endoaperture thinning pattern of Cornaceae/Nyssaceae might be seen (Erdtman 1966; Ferguson 1977). The pollen grains of *Eoëpigynia* are smaller than in most of the types defined by Ferguson (1977) but are within the range of his *Curtisia*-type, described as 12–20 × 12–17 µm (p. 6). One might speculate that small pollen are related adaptively to the small size of pollinating insects of that period, for example the 2 mm-long bee recently described from Burmese amber by Poinar and Danforth (2006).

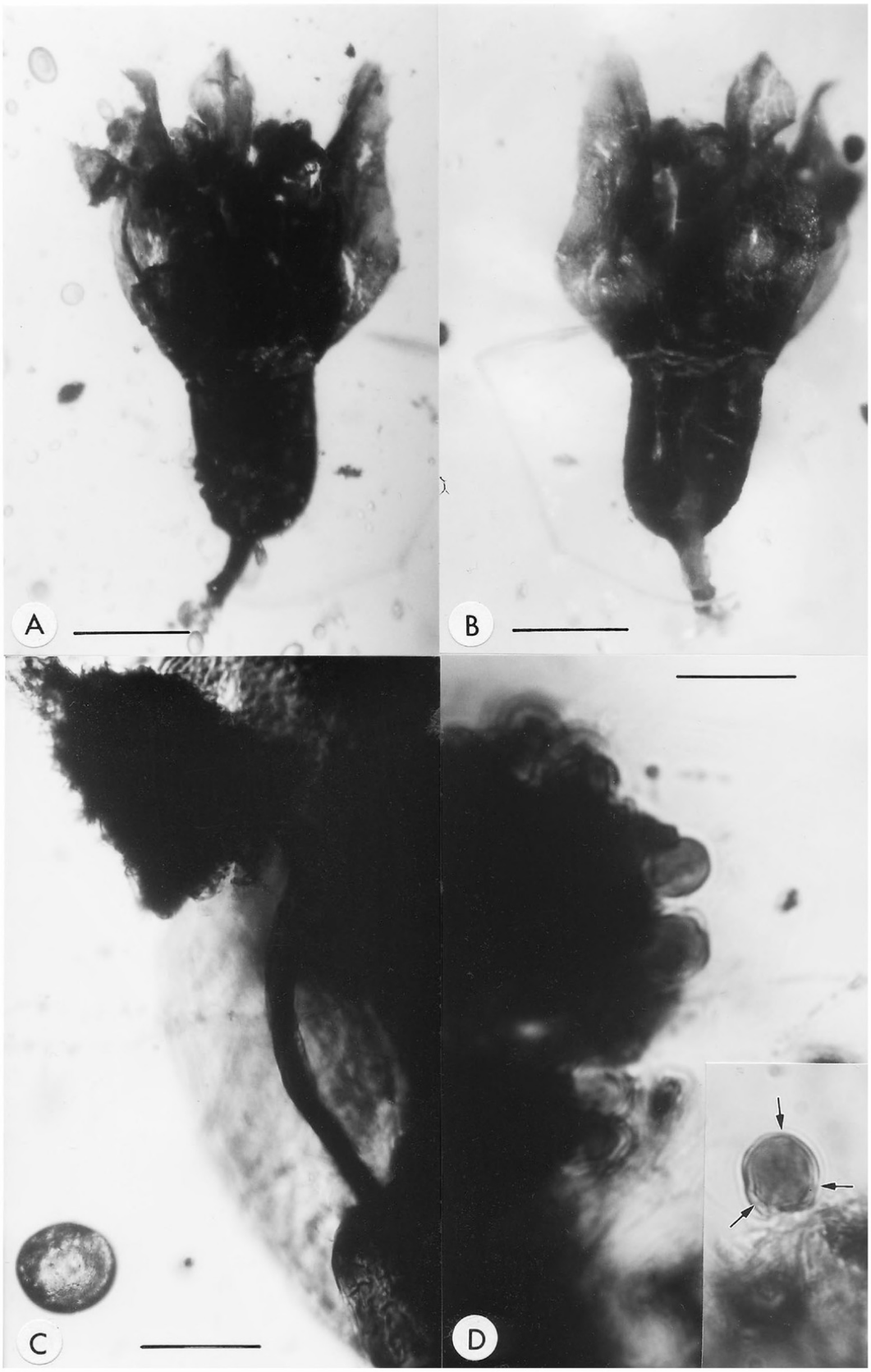

Fig. 1. *Eoëpigynia burmensis* in Burmese amber. A. One side of flower. Scale bar = 0.34 mm. B. Opposite side of flower. Scale bar = 0.34 mm. C. Stamen: anther covered with triangular pollen mass held together by fungal hyphae. Scale bar = 0.17 mm. D. Pollen grains on anther. Insert shows individual pollen grain (arrows indicate aperture areas surrounded by thickened exine. Scale bar = 18 µm.

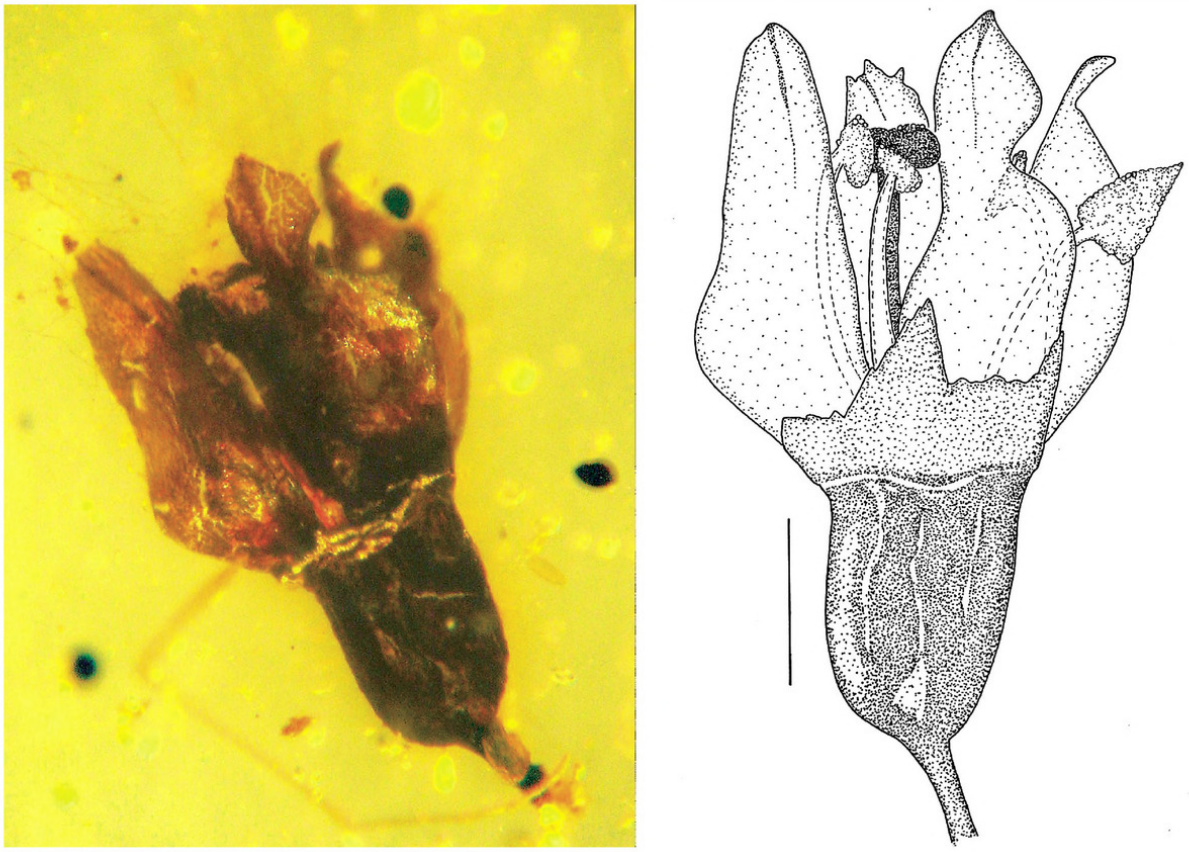

Fig. 2. Flower of *Eoëpigynia burmensis* in Burmese amber. Anther on right as described in Fig. 1C. Scale bar = 0.34 mm.

The generic makeup of Cornales, as well as family Cornaceae, has been reexamined in recent molecular phylogenetic studies (Xiang et al. 1998; Fan & Xiang 2003; Hilu et al. 2003; Judd & Olmstead 2004). It is proposed that Cornaceae be limited to two genera, *Cornus* and *Alangium*, and that other genera formerly assigned here be segregated to families Nyssaceae, Mastixiaceae, and Grubbiaceae. At the ordinal level, the once widely separated families Loasaceae and Hydrangeaceae are to be included in Cornales. If *Eoëpigynia* is placed in the larger context of this basal asterid clade, it shows that a simplified epigynous flower, with a single style, 4-merous perianth parts, and four stamens, arose early in the differentiation of this evolutionary line.

As pointed out by Gustafsson and Albert (1999), epigyny is not a recent phenomenon. Examples were found by Friis et al. (1994) in Early Cretaceous sediments in Portugal, originally dated as Valanginian or Hauterivian but now reassigned to the early Albian (Heimhofer et al. 2005). A probable relationship to Chloranthaceae has been established (Eklund et al. 2004). Phylogenetic studies have also shown that the evolution of ovary position has been dynamic, with at least 64 changes from hypogyny to epigyny but only 24 changes in the opposite direction (Gustafsson & Albert 1999; Soltis et al. 2003). In neither of these papers are Cornales specifically discussed, however. Modern Cornales are well represented in the Southeast Asian flora, with *Cornus* itself having a circumpolar Northern Hemisphere distribution (Wangerin 1910; Xiang et al. 2005). Reference fossils (fruit stones) attributed to the Cornelian-Cherry line of *Cornus* in the latter paper are taken from the careful review by Eyde (1988) and are Eocene or younger in age.

In studies using molecular phylogenetic dating methods with known fossil reference points (Bremer et al. 2004; Anderson et al. 2005), the Early Coniacian (88 mybp) cornalean genus *Hironoia* (Takahashi et al. 2002) has been used. Based on these papers, the age of the stem group asterids may be ca. 128 mybp, the Cornales and Ericales diverging soon afterwards (Stevens 2001 onwards). Anderson et al. (2005) place the separation of Cornales from remaining asterids at ca. 109 mybp. The reference fossil *Hironoia* consists of

three-dimensionally preserved drupes, with characters of the endocarp wall and dehiscence valves synapomorphic with the genera *Nyssa* and *Mastixia*. However, it could not be placed with certainty in one or the other genus. Another known cornalean fossil is *Tylerianthus* from the Upper Cretaceous Turonian Period, ca. 90 mybp (Gandolfo et al. 1998; Crepet et al. 2004), with affinities to the Hydrangeaceae. The putative cornacean fossil *Eoëpigynia* would extend the age of the clade, if used in similar dating studies. It would be well to note, however, that its generalized floral morphology would allow possible placement of this fossil in other epigynous clades of core eudicots as well, including Saxifragales, Myrtales and Asterales. Its similarity to Cornaceae, although highly suggestive, is not fully diagnostic of the proposed relationship. We know of no other fossil flower from the Cretaceous with the floral syndrome of this specimen.

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