CHAINANDRA ZEUGOSTYLUS GEN. ET SP. NOV., A MID-CRETACEOUS AMBER FOSSIL WITH SAGITTATE ANTHERS OPENING WIDELY AT MATURITY

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ABSTRACT

A flower preserved in 100 Ma amber from Myanmar is described here as **Chainandra zeugostylus,** a new genus and species of fossil angiosperms. The anthers in *Chainandra* are sagittate at the base and have only a short connective. They dehisce by means of a circumferential stomium, the dorsal and ventral sides of each locule forming flaps that become widely separated. The style of *Chainandra* is columnar and two-branched above the middle, and the fully inferior ovary bears an epigynous nectar disc but lacks well-defined ribs or veins. In *Tropidogyne, Lacknociona,* and *Strombothelya*, similar genera described earlier from the same amber deposits, the styles are either unbranched or are 3–5-branched to near the base, and the ovary is half-inferior to inferior, its lower portion often being distinctly veined and ribbed. Morphology of the stamens and gynoecium of the three genera suggests that they are early members of the eudotyledons.

RESUMEN

Se describe una flor conservada en ámbar de 100 Ma de Myanmar, como **Chainandra zeugostylus,** un nuevo género y especie de angiospermas fósiles. Las anteras de *Chainandra* son sagitadas en la base y tienen solo un conectivo corto. Su dehiscencia es por medio de un estomio anular, los lados dorsal y ventral de cada lóculo forma alas que se separan ampliamente. El estilo de *Chainandra* es columnar y tiene dos ramas por encima de la mitad, y el ovario completamente ínfero lleva un disco nectarífero epigino pero carece de costillas o venas bien definidas. En *Tropidogyne, Lacknociona,* y *Strombothelya*, géneros similares descritos previamente de los mismos depósitos de ámbar, los estilos son tanto sin ramificar como 3–5 ramificados hasta cerca de la base, y el ovario es de semiínfero a ínfero, su parte inferior está a menudo venada y con costillas. La morfología de los estambres y gineceo de los tres géneros sugiere que son miembros tempranos de eucotiledóneas.

INTRODUCTION

Fossiliferous amber continues to be commercially available from mines in Kachin Province, Myanmar, despite governmental restrictions due to civil unrest in the region (Sokol 2019). Over 25 new genera of angiosperms have been described in recent years based on fossil flowers from this mid-Cretaceous amber (cited in Chambers & Poinar 2020; Poinar et al. 2020). An assignment to class Magnoliidae has been suggested for most of these fossils, especially because of the form and mode of dehiscence of their anthers, which show a resemblance to certain present-day members of families such as Lauraceae, Monimiaceae, Atherospermataceae, and Hernandiaceae (Perkins & Gilg 1901; Endress & Stumpf 1990; Rohwer 1993). However, *Lijinganthus* (Liu et al. 2018) is described as belonging to the core eudicots, and *Phantophlebia* (Poinar & Chambers 2020) shows some similarity to myrsinoid members of the Primulaceae. The flower described here as *Chainandra zeugostylus* may be another Myanmar fossil that is best assigned to the eudicots. It is compared below to the previously described genera *Tropidogyne* (Chambers et at. 2010; Poinar & Chambers 2017; 2019b), *Lachnociona* (Poinar et al. 2008; Poinar & Chambers 2018), and *Strombothelya* (Poinar & Chambers 2019a), but it differs from one or more of these in its mode of anther dehiscence, its pistil,[1] and the presence of an entire-margined nectar disc on the ovary. The fossil is partially damaged, having lost one sepal and the anthers of most of the stamens. Aside from this, it is structurally intact, and its stamens, in particular, add significantly to knowledge of anther morphology in mid-Cretaceous angiosperms. In all three genera, the perianth parts form a single whorl and are here termed sepals, whereas in *Lijinganthus* and *Phantophlebia*, mentioned above, there are two

[1]**The term *pistil* as used here refers to an angiospermous seed-bearing structure comprising a simple or compound ovary, whether superior or inferior, plus one or more styles and stigmas.**

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well-differentiated whorls of perianth parts. Despite their floral similarities, *Tropidogyne*, *Lachnociona*, *Strombothelya*, and *Chainandra* are well enough differentiated to be maintained as separate genera. Except for *Tropidogyne*, which has been tentatively assigned to the Cunoniaceae (Chambers et al. 2010; Poinar & Chambers 2019b), no relationship to a modern family is here proposed for this group of fossil genera.

MATERIALS AND METHODS

The amber mines currently most active in Myanmar are in the Hukawng Valley, Kachin Province, at the Noije Bum 2001 Summit Site. Cruickshank and Ko (2003) provided a thorough geological description of the site and discussed the origin of its fossiliferous deposits. Based on paleontological (ammonite) and palynological evidence, they dated the amber as Late Albian, 97–110 Ma. A later study by Shi et al. (2012), using U-Pb dating of volcanic zircons that were co-deposited with the amber, gives the more narrowly defined age of 98.79 ± 0.62 Ma, between the Late Albian and Early Cenomanian series (Cohen et al. 2013). The term mid-Cretaceous is often applied to this time span (Manchester et al. 2018). The source of the ambers has been shown to be resin from members of the Araucariaceae, perhaps the Southern Hemisphere genus *Agathis* (Poinar et al. 2007).

As in our previous studies, observations were made using a Nikon SMA-10R stereoscopic microscope at 80× and a Nikon Optiphot microscope with magnifications up to 600×. 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

Chainandra Poinar & K.L. Chambers, **gen. nov.** Type Species: *Chainandra zeugostylus* Poinar & K.L. Chambers, sp. nov.

Flower pedicellate, bisexual, perianth regular, calyx epigynous, sepals 5, equal, oblong-lanceolate, spreading, venation reticulate, usually with one main vein from the base (Fig. 1), petals 0, androecium diplostemonous, stamens 10, inserted at the margin of an epigynous disc (Fig. 1), filaments linear, glabrous, straight or arched (Figs. 1, 2), anthers deeply sagittate, bithecal, filament attachment dorsal, connective short, the thecae separate below the middle (Fig. 3), dehiscence extrorse by a an encircling stomium, with the dorsal wall of each theca reflexing distally to gape open the locule (Fig. 4), anther epidermis papillate (Fig. 3), ovary inferior, obconic, glabrous, not evidently veined or ribbed (Fig. 1), epigynous disc present, entire-margined (Fig. 1), style stout erect, glabrous, divided above the middle into two columnar branches (Fig. 2), stigmas terminal, pedicel glabrous, pollen unknown.

Chainandra zeugostylus Poinar & K.L. Chambers, **sp. nov.** (**Figs. 1–4**). Type: MYANMAR (BURMA). Kachin: Amber mine in the Hukawng Valley SW of Maingkhwan, 26°20′N, 96°36′E, 2019, *unknown amber miner s.n.* (holotype: Catalogue number B-An-20, deposited in the Poinar Amber Collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

Flower 4.0 mm wide as measured across opposing sepals, sepals 1.7 mm long, 0.7 mm wide, stamen filaments 1.3 mm long, anthers 0.5 mm long, 0.3 mm wide, epigynous disc 1.0 mm wide, inferior ovary 0.6 mm long, 1.0 mm wide at the summit, style 1.3 mm long, the branches 0.6 mm long

Etymology.—Genus name from the Greek "chaino," I gape, and "andros," male, referring to the widely spreading anther thecae. Species epithet from the Greek "zeugos," team, pair, and "stylos," column, referring to the two columnar style branches.

DISCUSSION

The most striking features of the flower of *Chainandra zeugostylus* are its anthers. They are deeply sagittate, with only a short connective, and dehiscence is by means of a circumferential stomium which allows the dorsal and ventral walls of each theca to spread widely apart at maturity (Fig. 4). In certain other characteristics, such as its calyx of 5 reticulately veined, spreading sepals, its diplostemonous androecium, its two-branched style, and its obconic, inferior ovary bearing an epigynous disc, *Chainandra* resembles some members of the previously described genera *Tropidogyne, Lachnociona,* and *Strombothelya*, as cited in the Introduction. In the three

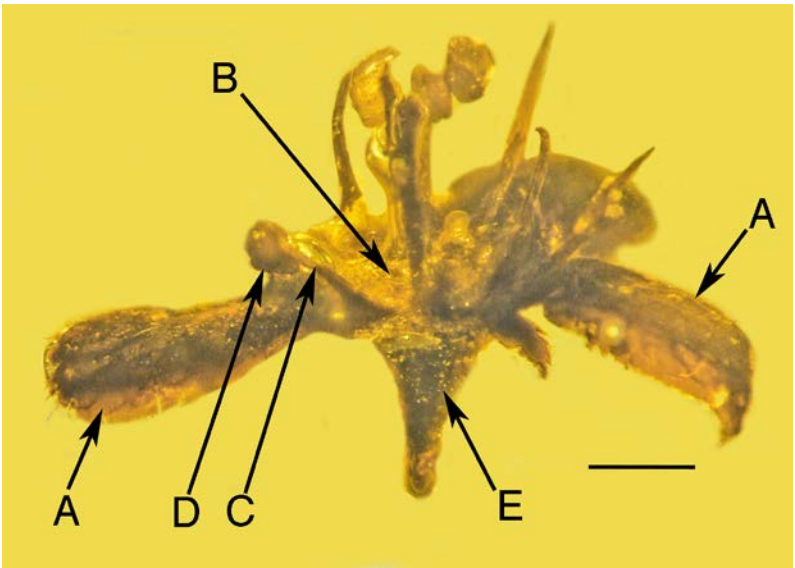

Fig. 1. *Chainandra zeugostylus*. Flower in lateral view. **A.** Sepals. **B.** Epigynous disc. **C.** Stamen filament. **D.** Anther. **E.** Ovary. Scale bar = 0.6 mm.

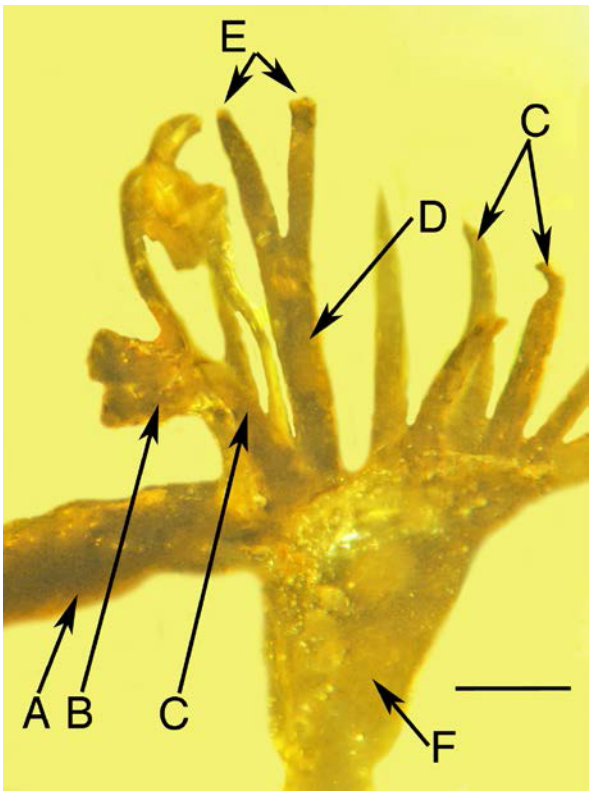

Fig. 2. *Chainandra zeugostylus*. Enlarged lateral view of flower. **A.** Sepal. **B.** Anther. **C.** Filaments. **D.** Style. **E.** Style branches. **F.** Ovary. Note that several filaments have lost their anthers. Scale bar = 0.5 mm.

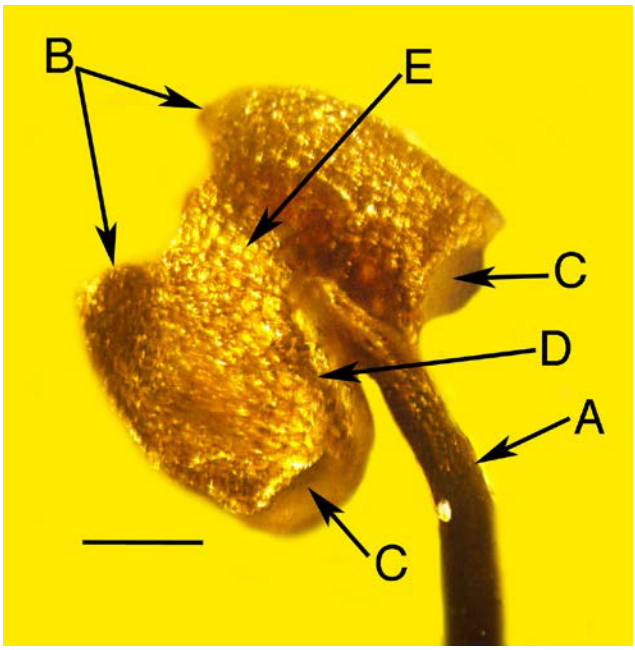

Fig. 3. *Chainandra zeugostylus*. Stamen with anther beginning to dehisce. **A.** Filament. **B.** Thecae of anther. **C.** Openings at base of thecae. **D.** Line of dehiscence. **E.** Connective. Note papillate epidermis. Scale bar = 180 µm.

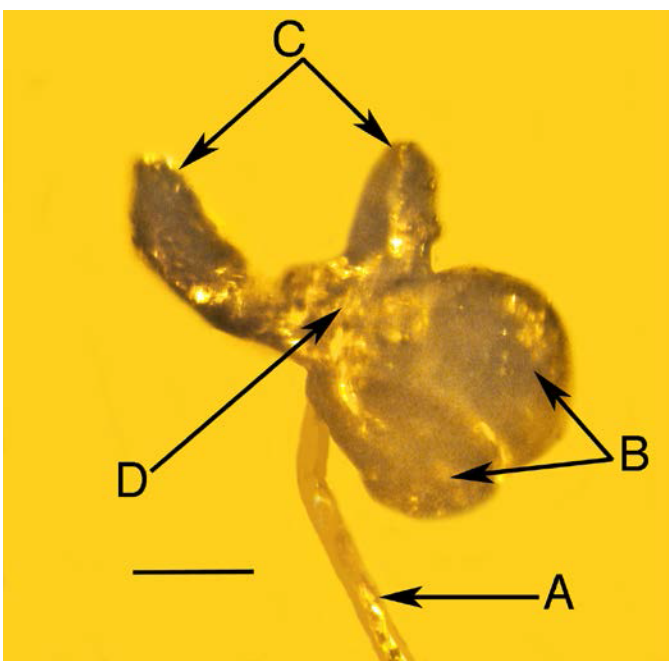

Fig. 4. *Chainandra zeugostylus*. Stamen after dehiscence of anther. **A.** Filament. **B.** Reflexed dorsal walls of thecae. **C.** Spreading ventral walls of thecae. **D.** Connective. Scale bar = 225 µm.

described species of *Tropidogyne*, the ovary is inferior, is conspicuously 5- or 10-ribbed, and is topped by a 3–5-lobed, flat, often glandular-pitted nectar disc (Chambers et al. 2010; Poinar & Chambers 2017; Poinar & Chambers 2019b). Flowers obtained thus far are principally pistillate. A single well-developed stamen was observed in *T. pentaptera* (Poinar & Chambers 2017), whose anther has a lengthy connective and appears to dehisce by two lengthwise stomia. In this species and in *T. lobodisca*, there are two separate, slender, abaxially curved styles which are stigmatic all along their inner surface, thus differing from the single erect, columnar style of *Chainandra*.

The genus *Lachnociona* comprises two species, *L. terriae* (Poinar et al. 2008), known from a single pistillate flower, and *L. camptostylus* (Poinar & Chambers 2018), based on one pistillate and one bisexual flower. In both species, the ovary is fully inferior but is so darkly pigmented that no veins or ribs are visible. The 5 styles of *L. terriae* are erect and appear to be columnar and closely connivent to near the tip, but in *L. camptostylus*, there are either 4 or 5 separate styles which are arched and widely spreading. Nectaries are not visible in the flower of *L. terriae*, but in the perfect flower of *L. camptostylus*, there are 10 enlarged, glandular nectaries forming a ring around the base of the styles. The one remaining anther of this flower is sagittate and dorsifixed but has an elongated connective and thecae that open by longitudinal slits. The sepals in both species are strongly recurved but are too darkly pigmented to show their venation. The genus is thus well differentiated from *Chainandra* in the morphology of its anthers and styles, its recurved sepals, and its lack of an epigynous nectar disc.

The two species described in *Strombothelya* (Poinar & Chambers 2019a) are alike in having a half-inferior ovary in which the conical superior portion is covered with vertical lines of glandular, probably nectar-secreting papillae (op. cit., fig. 7). There are 5 or 10 distinct ribs on the inferior part of the ovary. In *S. monostyla*, there is a single erect, columnar style, and in *S. grammogyna*, the stout, erect style is 3-branched from below the middle (Parenthetically, we originally described this as comprising three separate styles, but upon reexamination, the three branches are seen to be united below into a single column). The sepals of both species are 3-veined from the base, with inter-vein reticulations, rather than being single-veined as in *Chainandra*. However, the venation may be variable from one sepal to another in both genera. The anthers of *Strombothelya* are dorsifixed and slightly sagittate, but they have a long connective and appear to dehisce by a lengthwise slit in each theca. *Strombothelya* differs from *Chainandra*, therefore, in its unbranched or 3-branched style, its ribbed half-inferior ovary, its mode of anther dehiscence, and its cone-shaped rather than disc-shaped nectary.

No pollen was recovered from the flower of *Chainandra zeugostylus* and the available specimens of *Tropidogyne* have been principally pistillate, but in *Lachnociona camptostylus*, the pollen was clearly of a tricolpate or tetracolpate eudicot type (Poinar & Chambers 2018, fig. 10). In *Strombothelya monostyla*, pollen was difficult to photograph due to opacity of the amber, and it was not clear whether the few grains observed were tricolpate or acolpate (Poinar & Chambers 2019a, fig. 6).

The morphological differences among these fossil flowers support their classification as separate genera. *Chainandra* differs from the others in its anther morphology and mode of dehiscence, and its gynoecium, which combines a fully inferior, non-ribbed ovary, an entire-margined nectar disc, and an erect, two-branched style. Features shared by the four genera, such as the compound, inferior ovary and anthers that are sagittate, dorsifixed, and dehiscent by longitudinal or peripheral stomia rather than by valves (Endress & Stumpf 1991), suggest they are members of the mid-Cretaceous "core eudicot boom," as defined by Liu et al. (2018).

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