# *STROMBOTHELYA* GEN. NOV., A FOSSIL ANGIOSPERM WITH TWO SPECIES IN MID-CRETACEOUS MYANMAR AMBER

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ABSTRACT

**Strombothelya,** a new genus of fossil angiosperms from Myanmar amber deposits, is represented by 2 flowers that are here described as separate species. Flowers of *Strombothelya* have 5 spreading, more or less distinctly veined sepals. Petals are absent. There are 10 inwardly arching stamens and a half-inferior ovary, whose broadly conic superior portion terminates in 1 or 3 stout, columnar, apically truncate styles. The superior portion has a papillate surface that was probably nectariferous. The inferior portion of the ovary in both species is obconic and 5- or 10-ribbed. The fossils are comparable in certain respects to the genus *Tropidogyne,* described earlier from the same amber deposits. The 3 species of *Tropidogyne* have flowers with 5 or 10 stamens and 2 or 3 slender, curved, acutely-tipped styles. The inferior portion of the ovary is strongly 10-ribbed, while the superior portion is flat or cushion-shaped and bears a lobed nectar-disc. *Strombothelya* and *Tropidogyne* inhabited a Cretaceous araucarian rainforest, which may have been located in the Southern Hemisphere continent of Gondwana.

RESUMEN

**Strombothelya**, un nuevo género fósil de angiosperma de depósitos de ámbar de Myanmar, está representado por 2 flores que se describen como especies distintas. Las flores de *Strombothelya* tienen 5 sépalos extendidos, con venas más o menos distintas. Los pétalos están ausentes. Hay 10 estambres arqueados hacia adentro y un ovario semi-ínfero, con la parte superior anchamente cónica que termina en 1 o 3 estilos fuertes, columnares, truncados apicalmente. La parte superior tiene una superficie papilosa que probablemente era nectarífera. La parte inferior del ovario en ambas especies es obcónica y con 5 o 10 costillas. Los fósiles son comparables en ciertos aspectos con el género *Tropidogyne,* descrito previamente de los mismos depósitos de ámbar. Las 3 especies de *Tropidogyne* tienen flores con 5 o 10 estambres y 2 o 3 estilos delgados, curvados, con extremo agudo. La parte inferior del ovario tiene 10 costillas fuertes, mientras que la parte superior es plana o almohadillada y lleva un disco nectarífero lobulado. *Strombothelya* y *Tropidogyne* habitaron una pluvisilva de araucarias, que pudo estar localizada en el continente de Gondwana del hemisferio sur.

## INTRODUCTION

Previous studies of angiosperm flowers in mid-Cretaceous Myanmar amber have been reviewed by Poinar (2018b) and Liu et al. (2018). Thus far, 15 new fossil genera have been described from the Noije Bum 2001 Summit Site. In addition to *Lijinganthus* of Liu et al. (op. cit.), 10 genera are listed in Poinar and Chambers (2018b), 2 more in Poinar (2018b), and 1 each in Poinar and Chambers (2019a) and an accompanying paper (Poinar & Chambers 2019c). The amber deposits have been dated at ca. 100 Ma, to which we apply the general term "mid-Cretaceous, a transitional period comprising the latest Albian and earliest Cenomanian series (Cohen et al. 2013). Nine of the fossils were given tentative assignments to modern orders or families, while 6 remain unassigned. Most of the genera are represented by a single species. However, in *Lachnociona* (Poinar et al. 2008; Poinar & Chambers 2018b), there are 2 species, and in *Tropidogyne* (Chambers et al. 2010; Poinar & Chambers 2017, 2019b), 3 species have been described. *Strombothelya* bears comparison with the latter genus, in which the species are characterized by 5 stout, spreading, reticulately veined sepals and a conspicuously 10-ribbed inferior ovary. Although similar in overall construction to *Tropidogyne,* the flowers of *Strombothelya* differ in that their sepals are less strongly veined and the inferior portion of the ovary is either 5- or 10-ribbed (Figs. 1–3). The gynoecium of *Strombothelya* is broadly conic in its superior portion and bears either 1 or 3 erect, cylindrical, apically truncate styles (Figs. 2, 4). In *Tropidogyne,* on the other hand, the gynoecium has 2 or 3 styles, and the superior portion is flat or rounded, not conic. In *Tropidogyne pikei,* the 3 styles are short, curved, sharply acute, and arise from a flat-topped ovary (Chambers et al. 2010, fig. 2). In *Tropidogyne pentaptera,*

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the apex of the ovary is cushion-shaped, with 2 long, arching, taper-tipped styles (Poinar & Chambers 2017, fig. 6), while in *T. lobodisca,* the 2 styles are like those of *T. pentaptera* but arise from a 5-lobed disc (Poinar & Chambers 2019b, figs. 1, 3). Fruits of both genera were probably indehiscent, and in *Tropidogyne,* at least, the persistent sepals may have served as wings to aid in seed dispersal.

The relationship between *Strombothelya* and *Tropidogyne* may be rather distant, at best, and the new genus varies even further from the family Cunoniaceae, to which *Tropidogyne* has been tentatively assigned (Chambers et al. 2010; Poinar & Chambers 2017, 2019b). Therefore, we are making no suggestion as to the taxonomic position of *Strombothelya* in the present paper.

## MATERIALS AND METHODS

Our specimens of *Strombothelya* and *Tropidogyne* were obtained from amber mines at the Noije Bum 2001 Summit Site in the Hukawng Valley SW of Maingkhwan, Kachin Province. The sediments containing the amber were first dated by Cruickshank and Ko (2003), using marine paleontological (ammonite) and palynological evidence. Their assigned age was 97–110 Mya, in the Late Albian. Shi et al. (2012) used U-Pb radiometric dating of volcanic zircons in the sediments to give an age of 98.79 ± 0.62 Mya, near the Albian/Cenomanian boundary. The source of the amber has been determined to be resin from trees belonging to the Araucariaceae, perhaps the genus *Agathis* (Poinar et al. 2007).

Observations and photographs were made with 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

**Strombothelya** Poinar & K.L. Chambers, **gen. nov.** (**Figs. 1–9**). Type Species: *Strombothelya monostyla* Poinar & K.L. Chambers, sp. nov.

Flowers pedicellate, bisexual, actinomorphic, calyx epigynous, regular, ± rotate, sepals 5, equal, lanceolate, 3-veined from the base (Fig. 9) or venation indistinctly reticulate (Fig. 5), petals 0, androecium of 10 stamens opposite and alternate with the sepals, filaments linear, slightly or strongly arched adaxially (Figs. 2, 8), anthers oblong, dithecal, dehiscent by longitudinal slits, filament attachment sub-basal (Figs. 1, 2, 8), ovary half-inferior, the superior portion broadly conic (Figs. 2, 4, 7), surface evenly papillate or the papillae in numerous lengthwise rows (Figs. 4, 7), styles 1 or 3, erect, columnar, truncate, stigma short-pubescent, not enlarged (Figs. 1, 2, 4, 7), the inferior portion of ovary obconic, glabrous, with 5 or 10 ribs, ribs rounded (Fig. 3) or acutely ridged (Fig. 9), pedicel puberulent or glabrous (Figs. 2, 8), pollen spherical, exine alveolate, colpi 3?, indistinct (Fig. 6).

*Etymology.*—Genus name from the Greek "strombos," a top or cone, and "thelys," female, referring to the conic upper portion of the ovary.

**Strombothelya monostyla** Poinar & K.L. Chambers, **sp. nov.** (**Figs. 1–6**). Type: MYANMAR (BURMA). Kachin: amber mine in the Hukawng Valley SW of Maingkhwan, 26°20'N, 96°36'E, 2018, *unknown amber miner s.n.* (holotype: catalogue number B-An-10, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

Flower 2.3 mm long excluding pedicel, calyx 6.0 mm wide as measured between sepal tips, sepals 2.0–2.4 mm long, 1.5 mm wide, venation indistinctly reticulate, surface glabrous, margins ciliate (Figs. 1, 2, 5), stamen filaments ca. 1.5 mm long, strongly arched adaxially (Figs. 1, 2, 4), anthers 0.8–1.0 mm long, 0.5 mm wide, superior portion of ovary 1.5 mm wide at the base, 1.0 mm tall, surface evenly papillate (Fig. 4), inferior portion of ovary narrowly obconic, 1.0 mm long, 5-ribbed, the ribs low, rounded (Fig. 3), style 1, 2.0 mm long, 0.3 mm in diameter (Fig. 4), pedicel 3.2 mm long, puberulent (Fig. 2), pollen diameter 29 µm (Fig. 6).

*Etymology.*—Species name from the Greek "monos," one, and "stylos," pillar or column, referring to the single, erect style.

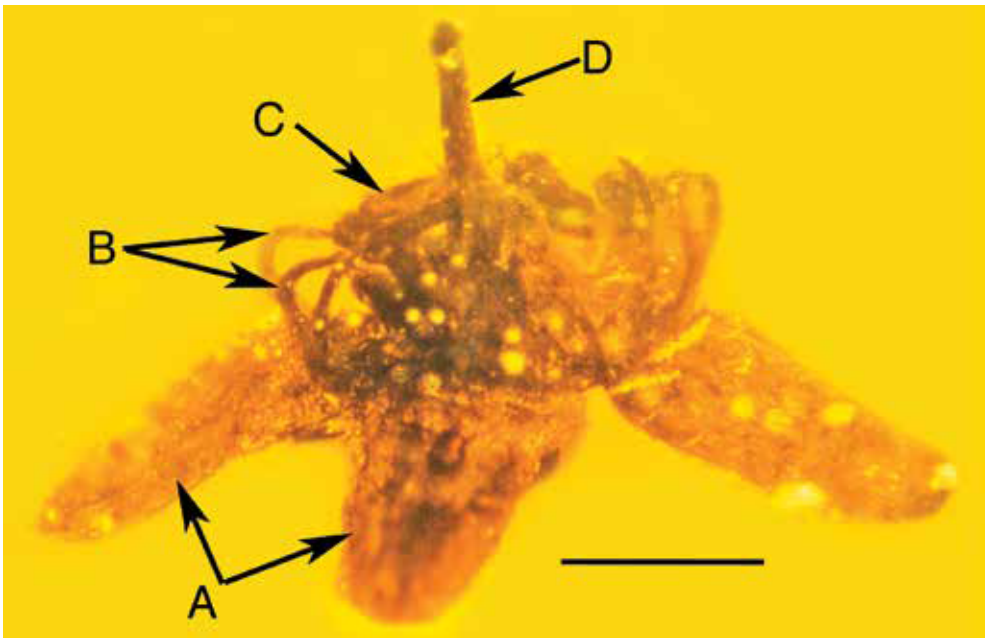


Fig. 1. *Strombothelya monostyla.* Flower in apical view. **A.** Sepals. **B.** Stamen filaments. **C.** Anther. **D.** Style. Scale bar = 1.3 mm.

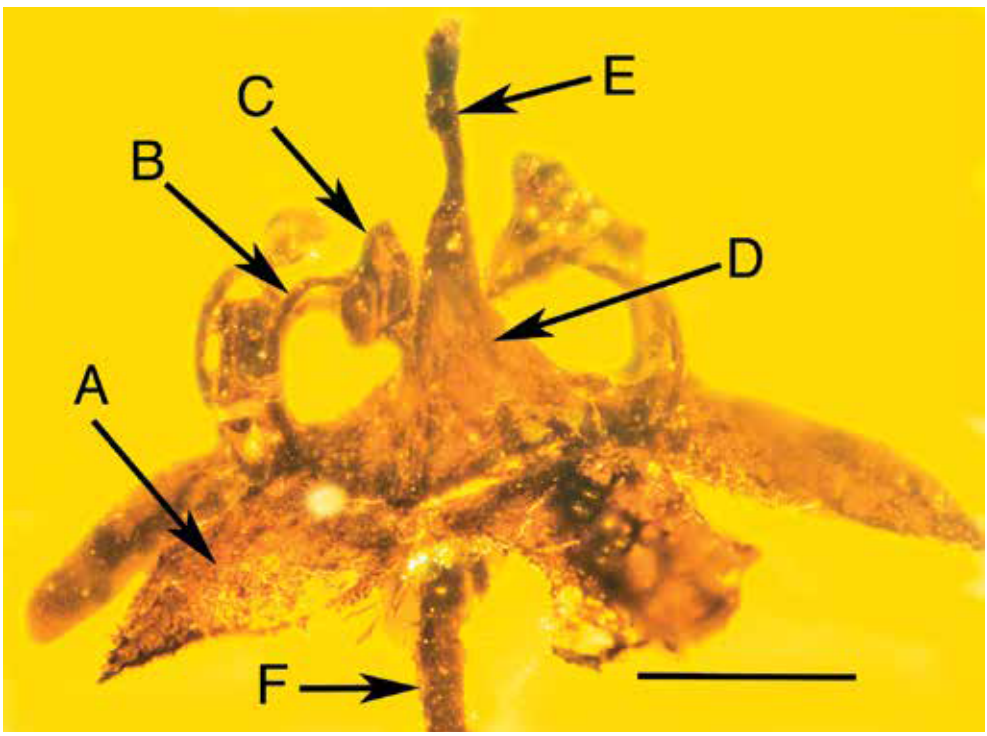


Fig. 2. *Strombothelya monostyla.* Flower in lateral view. **A.** Sepal. **B.** Stamen filament. **C.** Anther. **D.** Superior portion of ovary. **E.** Style. **F.** Pedicel. Note that 1 stamen has broken off on this side of the flower. Scale bar = 1.3 mm.

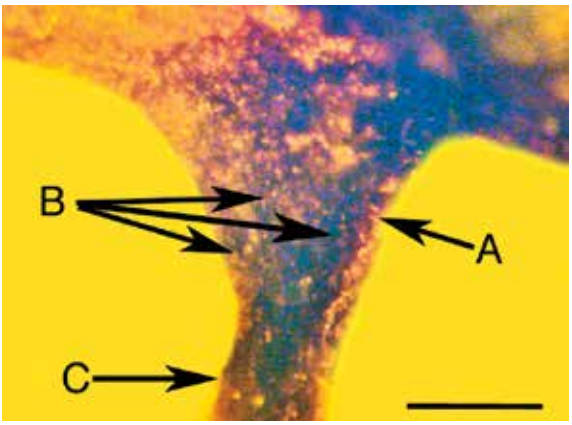


Fig. 3. *Strombothelya monostyla*. Base of flower. **A.** Inferior portion of ovary. **B.** Ribs. **C.** Pedicel. Scale bar = 0.7 mm.

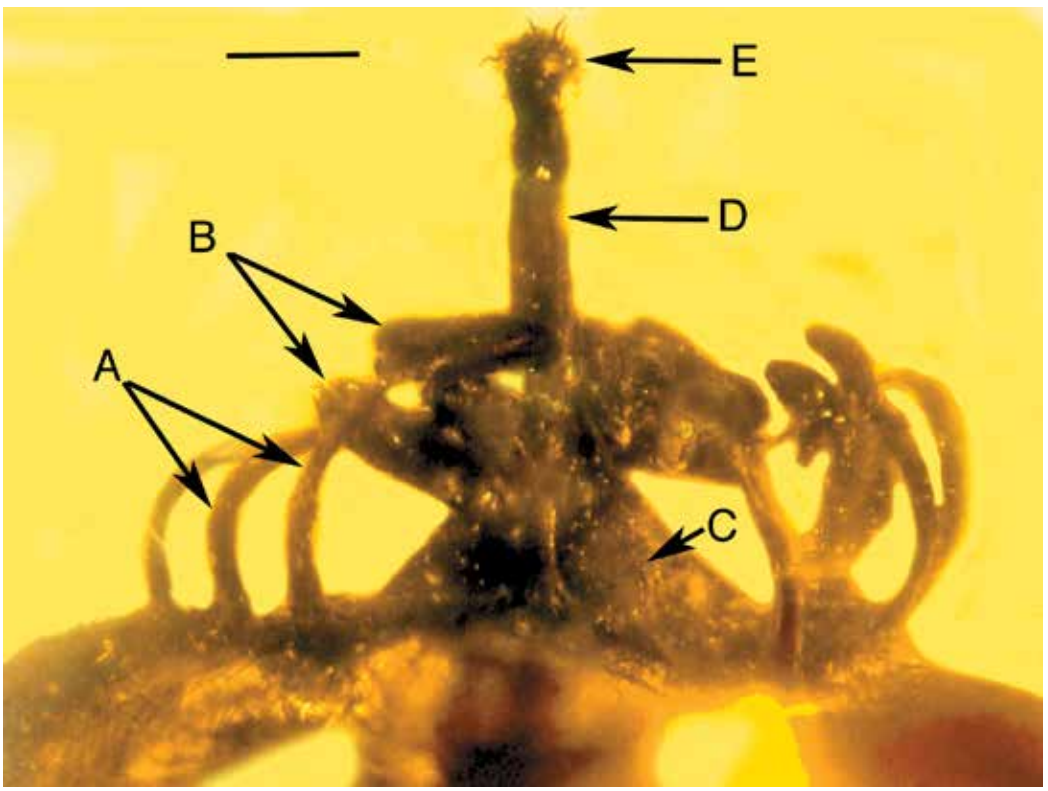


Fig. 4. *Strombothelya monostyla*. Reproductive parts. **A.** Stamen filaments. **B.** Anthers. **C.** Upper portion of ovary. **D.** Style. **E.** Stigma. Scale bar = 0.54 mm.

**Strombothelya grammogyna** Poinar & K.L. Chambers, **sp. nov.** (**Figs. 7–9**). Type: MYANMAR (BURMA). Kachin: amber mine in the Hukawng Valley SW of Maingkhwan, 26°20'N, 96°36'E. 2018, *unknown amber miner s.n.* (holotype: catalogue number B-An-12, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

Flower 4.2 mm long excluding pedicel, calyx 4.0 mm wide as measured between sepal tips, sepals 2.5 mm long, 1.0 mm wide, distinctly 3-veined from the base (Fig. 9), surface and margins glabrous (Figs. 7, 9), stamen

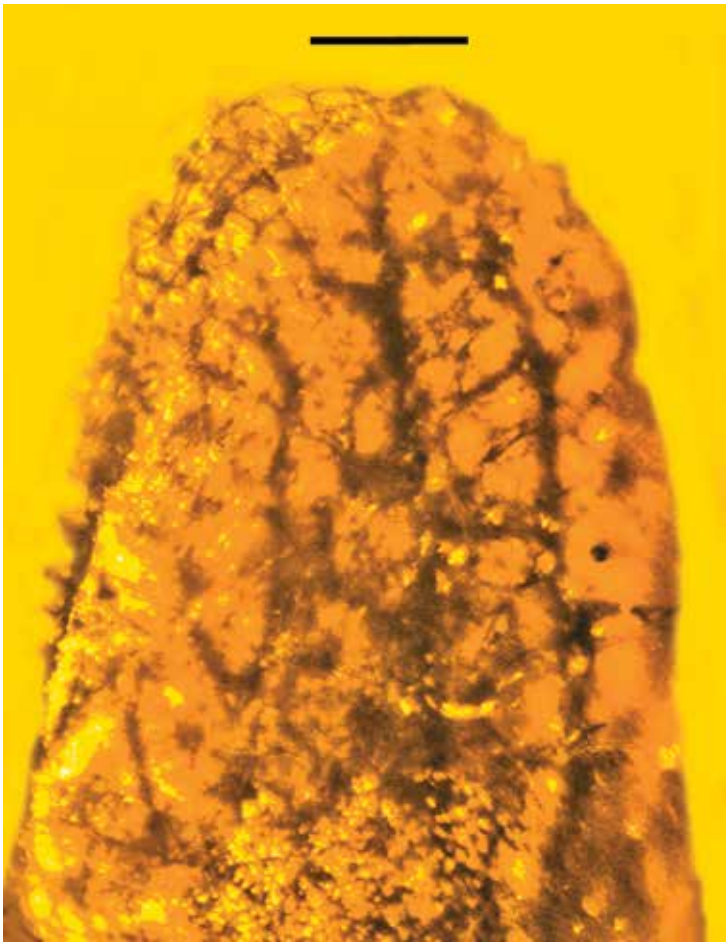

**Fig. 5. *Strombothelya monostyla*. Sepal showing reticulate venation. Scale bar = 0.4 mm.**

filaments ca. 1.0 mm long, slightly curved adaxially (Fig. 8), anthers 1.0 mm long, 0.5 mm wide, superior portion of ovary 1.0 mm wide at the base, 0.8 mm tall, surface papillate, the papillae arranged in numerous lengthwise rows (Fig. 7), inferior portion of ovary broadly obconic, 1.5 mm long, 10-ribbed, the ribs acutely ridged (Fig. 9), styles 3, 1.7 mm long, 0.2 mm in diameter (Figs. 7, 8), pedicel 7.5 mm long, glabrous.

*Etymology.*—Species name from the Greek "gramme," line, and "gyne," woman, from the multiple lines of papillae on the conical pistil.

## DISCUSSION

Although *Strombothelya* bears some resemblance to *Tropidogyne,* which we earlier described from Myanmar amber, it differs in certain features of the calyx and gynoecium which are taken to be of generic significance. We were able to characterize *Tropidogyne* from a total of 9 specimens, 1 of *T. pikei,* 7 of *T. pentaptera,* and 1 of *T. lobodisca* (Chambers et al. 2010; Poinar & Chambers 2017, 2019b). The stout, spreading, reticulately-veined sepals and prominently 10-ribbed inferior ovary are consistent features of the genus. Its 3 species differ mainly in the number and length of the styles and the form of the nectar disc surmounting the ovary. In *Strombothelya,* the 5 or 10 ribs of the inferior portion may either be broad and rather obscure or narrow and distinctly ridged

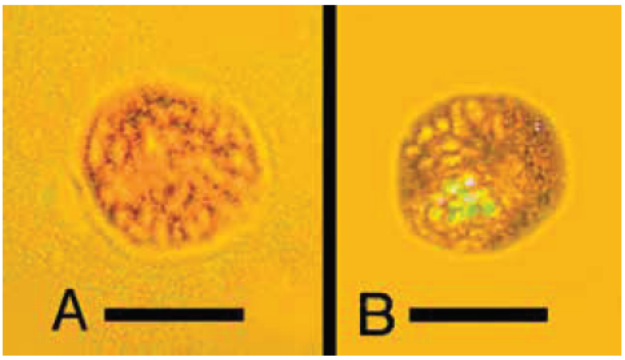


Fig. 6. Comparison of pollen grains. **A.** *Strombothelya monostyla*. Scale bar = 23 µm. **B.** *Tropidogyne pentaptera*. Scale bar = 24 µm.

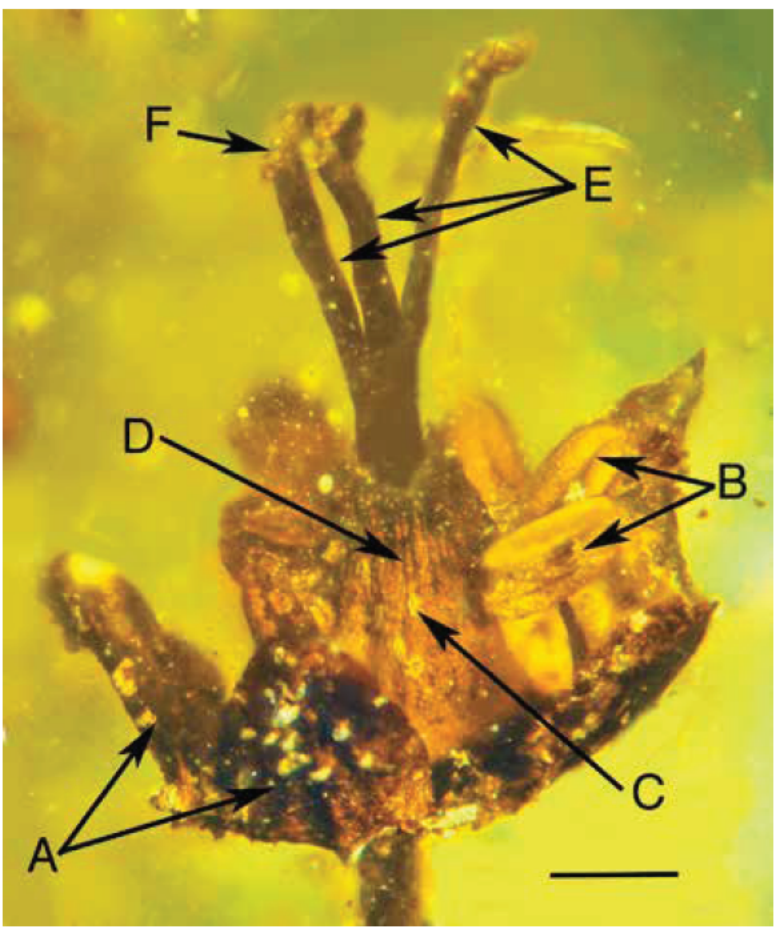


Fig. 7. *Strombothelya grammogyna*. Flower in lateral view. **A.** Sepals. **B.** Anthers. The lower anther and its filament are partly hidden by inclusions in the amber. **C.** Conic upper portion of ovary. **D.** Lengthwise lines of papillae. **E.** Styles. **F.** Stigma. Note extraneous bits of material adhering to this and the other 2 stigmas, perhaps due to sticky secretions in life. Scale bar = 0.9 mm.

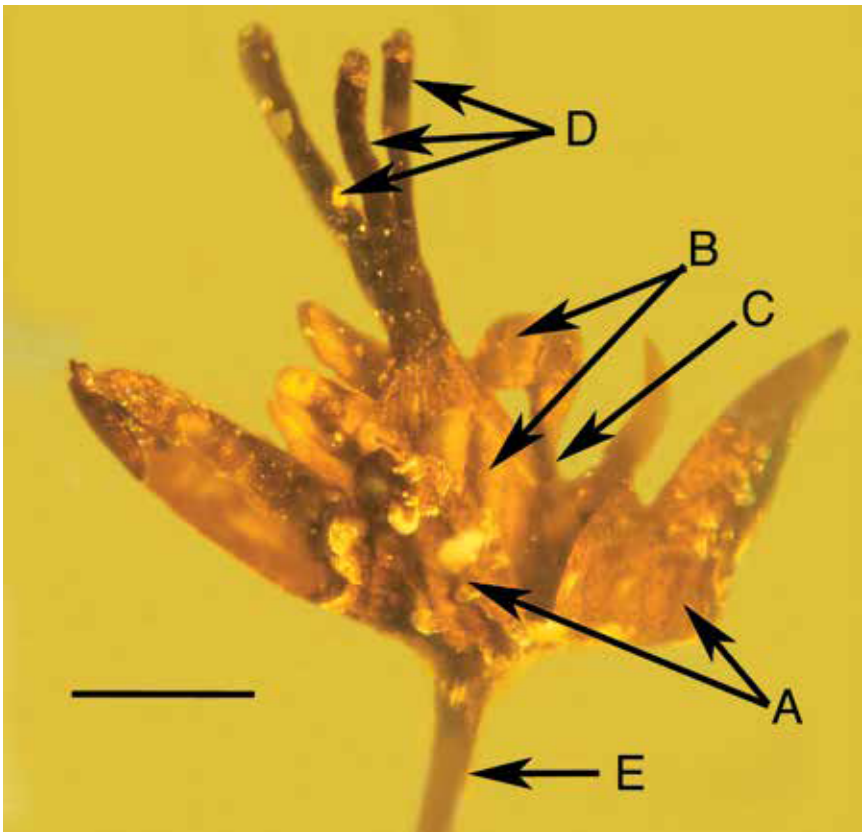


Fig. 8. *Strombothelya grammogyna.* **Lateral view from opposite side of flower. A. Sepals. B. Anthers. C. Filament. D. Styles. E. Pedicel. Some floral structures are partially obscured by inclusions in the amber. Scale bar = 0.8 mm.**

(Figs. 3, 9). The sepals possess either 3 distinct veins from the base (Fig. 9) or a reticulum of veinlets (Fig. 5). The gynoecium of *Strombothelya* differs significantly from *Tropidogyne* in that the superior region of the ovary is conic and has a papillate, probably nectar-secreting, surface. In species of *Tropidogyne,* the apex of the ovary is ± truncate and covered by a 2-, 3-, or 5-lobed, deeply pitted nectar-disc. The styles of *Strombothelya* are erect, columnar, and bluntly stigmatic at the tip, whereas in the 2 *Tropidogyne* species with elongate styles, these are slender, curved, and have a ventrally decurrent stigma.

Of the 2 species of *Strombothelya, S. grammogyna* most resembles *Tropidogyne* in the 10 acutely ridged veins of its inferior ovary, its 3-veined sepals (sepals in *Tropidogyne* are 3-veined from the base with a reticulum of interconnecting veinlets [Poinar & Chambers 2017, figs. 1, 2]), and the presence of 3 styles, as in *T. pikei*. *Strombothelya monostyla* is more distinctive, possessing only a single style and weakly-developed sepal venation. In studies of fossil angiosperms based only on individual flowers, with nothing known about the vegetative parts of the plants, it becomes a subjective choice by the investigators as to which characteristics to emphasize when making generic distinctions. As already indicated, our decision to describe a new genus in this case rests mainly on the stout, erect, columnar styles, the enlarged superior portion of the gynoecium, and the ovary's distinctive papillate surface, as displayed by *S. monostyla* and *S. grammogyna* (Figs. 4, 7). Although the 2 genera may have been relatively close evolutionarily, it is impossible to determine whether they were ever contemporaneous or sympatric in the Cretaceous amber forests of Myanmar.

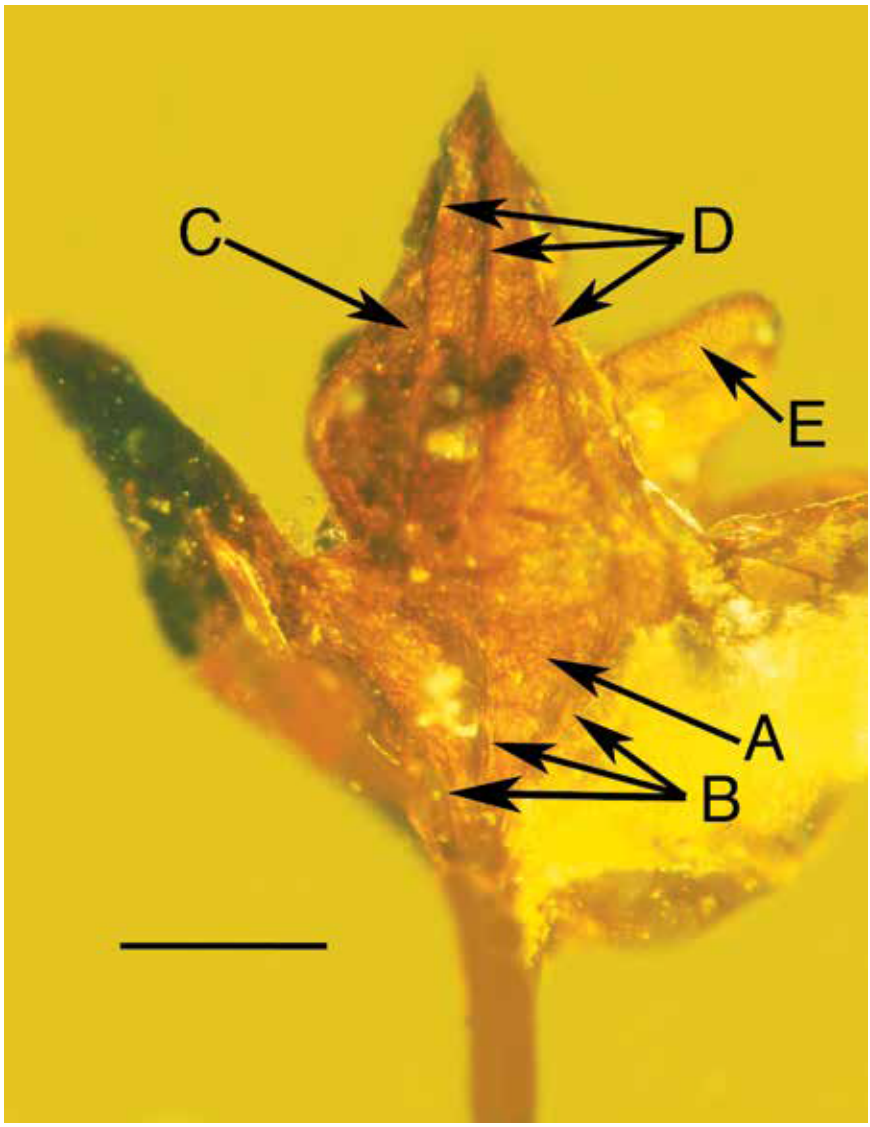


**Fig. 9.** ***Strombothelya grammogyna.*** **Basal view of flower. A. Inferior portion of ovary. B. Ribs. C. Sepal. D. Longitudinal veins. E. Anther. Scale bar = 1.0 mm.**

In an accompanying article (Poinar & Chambers 2019b), we discuss a possible relationship between *Tropidogyne* and *Ceratopetalum,* an extant Australasian genus of Cunoniaceae. Fossil fruits of *Ceratopetalum* have been described from Eocene localities in Australia and Argentina (Barnes & Hill 1999; Barnes et al. 2001; Gandolfo & Hermsen 2017), and illustrations of such fossils and of living species of *Ceratopetalum* (Rozefelds & Barnes 2002, fig. 5, 6) show a marked resemblance to *Tropidogyne.* Both genera have a partly or wholly inferior ovary and a calyx of 5 stout, spreading, reticulately veined sepals (Chambers et al. 2010; Poinar & Chambers 2017). Except for 1 species of *Ceratopetalum,* petals are absent in the 2 genera. *Ceratopetalum* has 2 arcuate, acutely tipped styles like those of *T. pentaptera* and *T. lobodisca,* but the stigma is terminal in *Ceratopetalum* and decurrent in the 2 *Tropidogyne* species. The nectary in *Tropidogyne* is discoid and variously

lobed, often with a roughly pitted surface (Poinar & Chambers 2017, 2019b), not like the smooth, ring-shaped nectary of *Ceratopetalum* (Rozefelds & Barnes 2002).

Although *Strombothelya* shares many floral characteristics with *Tropidogyne* and *Ceratopetalum*, the gynoecium, with its stout, erect style(s) arising from a conical ovary and tipped with a truncate, puberulent stigma, would be out of place among modern genera of Cunoniaceae (Engler 1930; Dickison 1989; Bradford et al. 2004). We therefore prefer that *Strombothelya* not be assigned to this or any other particular family of angiosperms.

In earlier publications (Poinar & Chambers 2017; Poinar 2018a), it was hypothesized that Myanmar amber deposits may have originated in Gondwana during the Early Cretaceous. Geological evidence (Hall 2012; Metcalfe 2013) suggests that Southeast Asia, including Myanmar, was assembled during the Paleozoic and Mesozoic eras by subduction of continental terranes, which had successively separated from Gondwana and been transported northward by plate tectonics. The Greater India Block, originally adjacent to Australia, reached Asia by the Middle Eocene, and its northeastern part perhaps formed what is now the northwestern section of Myanmar. The process of continental accretion has yet to be worked out in detail by geologists. Nonetheless, many of the plant and insect fossils thus far described from Myanmar amber (Poinar 2018a, b) provide biological evidence, we believe, for an origin in the Southern Hemisphere.

## ACKNOWLEDGMENTS

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