TROPIDOGYNE LOBODISCA SP. NOV., A THIRD SPECIES OF THE GENUS FROM MID-CRETACEOUS MYANMAR AMBER

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ABSTRACT
The fossil flower described here is the third species of Tropidogyne to have been collected from mid-Cretaceous amber deposits in the Hukawng Valley of northwestern Myanmar. The flower of Tropidogyne lobodisca differs from the 2 previously described species, T. pikei and T. pentaptera, in lacking stamens and having a 5-lobed nectar disc covering the apex of the ovary. Its 2 slender, curved, attenuate styles are like those of T. pentaptera in being stigmatic along the adaxial surface. The new species has 5 spreading, reticulately-veined sepals, a generic character of Tropidogyne. An unusual, probably teratological, feature is the presence of 2 sepal-like staminodes on one side of the flower, inserted at the base of the nectar disc where stamens would otherwise be found. The inferior portion of the pistil is obconic, with 5 distinct veins that connect to the mid-veins of the sepals.

RESUMEN
La flor fósil que se describe aquí es la tercera especie de Tropidogyne colectada en depósitos de ámbar del cretáceo medio en el valle de Hukawng del noroeste de Myanmar. La flor de Tropidogyne lobodisca difiere de las dos especies descritas previamente, T. pikei y T. pentaptera, en la falta de estambres y tener un disco nectarífero 5-lobulado cubriendo el ápice del ovario. Sus 2 estilos delgados, curvados, atenuados con como los de T. pentaptera por ser estigmaticos a lo largo de la superficie adaxial. La nueva especie tiene 5 sépalos esparcidos, con venación reticulada, un carácter genérico de Tropidogyne. Una característica inusual, probablemente teratológica, es la presencia de 2 estaminodios semejantes a sépalos en un lado de la flor, insertados en la base del disco nectarífero donde de lo contrario se encontrarían los estambres. La parte inferior del pistilo es obconica, con 5 venas distintas que conectan con el nervio medio de los sepalos.

INTRODUCTION
Tropidogyne lobodisca, described here, is the third known species of this genus of fossil angiosperms in Myanmar amber. Fifteen angiosperm genera, comprising 21 species, have thus far been described from these mid-Cretaceous deposits (Poinar 2018b; Poinar & Chambers 2018b, 2019a, b, c). The location of the collecting site and the age of the oceanic sediments in which the amber is found are described in the following section. The source of the amber, as determined from chemical and anatomical evidence, was resin from trees of the coniferous family Araucariaceae (Poinar et al. 2007), which were probably members of the paleo-Antarctic rain-forests discussed by Kooyman et al. (2014). The apex of the inferior, or perhaps half-inferior, ovary in Tropidogyne is topped by a convex nectar disc, which takes a different shape in each of the 3 species. As discussed below, the disc may be divided into 2 or 3 segments or, as in the present species, have a 5-lobed margin. The surface of the disc in all 3 species is rather deeply pitted, the pits probably containing glands for nectar secretion. The type flower of T. lobodisca is functionally pistillate, lacking stamens and instead having what we interpret as 2 anomalous sepaloid staminodes. Whether the species was monoecious or dioecious is unknown. The sepals of T. lobodisca are like those of the other 2 species in having 1 or 3 main veins and a reticulum of smaller veinlets.

In previous papers (Chambers et al. 2010; Poinar & Chambers 2017) we remarked on similarities between Tropidogyne and the extant genus Ceratopetalum, family Cunoniaceae. As discussed below, most Cunoniaceae have bisexual flowers, the exceptions being the dioecious genera Spiraeanthemum, Hooglandia, Pullea, and Vesselowskya (Bradford et al. 2004). Tropidogyne flowers are like Ceratopetalum taxa in their stout, strongly veined sepals, an inferior or half-inferior ovary, and 2 slender, curved styles, as in T. pentaptera and T. lobodisca (Fig. 1). The genera differ markedly, however, in the nature of the nectar disc, which in Ceratopetalum...
is smooth, doughnut-shaped, and separated from the styles by a ring of hispid trichomes (Rozefelds & Barnes 2002, fig. 5). In species of Tropidogyne, the styles arise directly from a broad, glabrous, pitted disc.

MATERIALS AND METHODS

Fossiliferous Myanmar amber is well known and much sought after by paleontologists, especially in China (Sokol 2019). The amber mines from which fossil flowers have been obtained are at the Noije Bum 2001 Summit Site, located in the Hukawng Valley in Kachin Province. First dated by Cruickshank and Ko (2003), the oceanic sediments containing the amber were given an age of 97–110 Ma, derived from paleontological (ammonite) and palynological evidence. Later, Shi et al. (2012) applied radiometric U-Pb dating techniques to volcanic zircons in the matrix of the deposits and assigned a more narrowly defined age of 98.79 ± 0.62 Ma, near the boundary between the Albian and Cenomanian series (Cohen et al. 2013). Poinar et al. (2007) determined that the amber was derived from the resin of trees belonging to the Araucariaceae, a family of conifers that includes the Southern Hemisphere genus Agathis. Originating in coastal forests, the amber was eventually redeposited in off-shore marine sediments, and its included fossils may therefore be considerably older than the assigned dates, above.

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 photographs for better clarity and depth of field. Background details were removed to improve the image of some of the figures.

DESCRIPTION

Tropidogyne lobodisca 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. 2018, unknown amber miners s.n. (Holotype: catalogue number B-An-13, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

Flower pistillate, calyx epigynous, 3.4 mm wide as measured between sepal tips, sepals 5, spreading, 1.6 mm long, 0.6–0.8 mm wide, lanceolate, 1- or 3-veined from the base with reticulate veins, surface and margins glabrous, apex acute (Figs. 2, 3), petals 0, stamens 0, staminodes 2, sepaloid, paired on one side of the flower, 1.2 mm long, 0.5 mm wide, lanceolate, venation as in the sepals (Figs. 1, 2), ovary inferior or half-inferior, the apical nectar disc 0.6 mm in diameter, convex, 5-lobed, disc margins deeply indented, surface rugosely pitted (Figs. 1, 4), styles 2, 0.5 mm long, slender, curved abaxially, decurrently stigmatic on the adaxial surface (Fig. 1), inferior portion of ovary obconic, 0.7 mm wide at the apex, glabrous, 5-veined, the veins connecting to sepal mid-nerves, pedicel strongly bent, ca. 0.5 mm long, glabrous (Figs. 2, 3).

Etymology.—Species epithet from the Greek “lobos,” protuberance, lobe, and “diskos,” flat plate, disc, from the lobed nectar disc.

DISCUSSION

Our original search for similarities between the flowers of Tropidogyne and those of some modern angiosperm families led to a comparison with Ceratopetalum, an Australasian genus of Cunoniaceae (Chambers et al. 2010; Poinar & Chambers 2017; Poinar 2018a). Fossil fruits of Ceratopetalum, with 4 or 5 stout, reticulately-veined sepals, have been recovered from Cenozoic deposits of Eocene age in both Australia and South America (Barnes & Hill 1999; Barnes et al. 2001; Gandolfo & Hermsen 2017). As described and illustrated by Rozefelds and Barnes (2002, figs. 5, 6), flowers of Ceratopetalum are 4- or 5-merous, consistently epigynous (although the ovary is termed half-inferior by Bradford et al. 2004), and bicarpellate, with 2 arched, tapering, acutely-tipped styles. Anthers are dithecal, longitudinally dehiscent, and often bear a terminal appendage. A ring-shaped nectar disc is present between the stamens and styles. Tropidogyne shows a resemblance to Ceratopetalum in its 5 firm, spreading sepals with distinct venation (Poinar & Chambers 2017, figs. 1, 3, 4). The bicarpellate gynoea of T. pentaptera and T. lobodisca, with their 2 slender, arching styles, are like those of Ceratopetalum. However, the floral nectary is quite dissimilar in the 2 genera (Rozefelds & Barnes 2002, fig. 5; Poinar & Chambers...
2019b, fig. 1). Also, the styles of these Tropidogyne species have a decurrent stigma, which differs from the terminal stigma in Ceratopetalum but is similar to styles of the related genus Vesselowskya (Dickison 1989, fig. 4.3E). Given the differences in nectar discs and stigmas between the 2 genera, as well as the 40 Ma disparity in age between Tropidogyne and the oldest presumed fossils of Ceratopetalum, any suggestion of relationship must remain hypothetical at best.

_Tropidogyne lobodisca_ compares well with the 2 earlier-described species except in the distinctively 5-lobed form of its nectar disc and the fact that the inferior ovary has 5 main veins rather than the 10 veins of

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Fig. 1. _Tropidogyne lobodisca_. Flower in subapical view. A. Sepals. B. Sepaloid staminode. C. Nectar disc. D. Styles, showing decurrent stigma. Scale bar = 0.8 mm.
Fig. 2. *Tropidogyne lobodisca*. Flower in subapical view. A. Sepals. B. Tips of staminodes. C. Nectar disc. D. Pedicel. Scale bar = 1.0 mm.

Fig. 3. *Tropidogyne lobodisca*. Flower in basal view. A. Sepals. B. Mid-vein. C. Ovary. D. Pedicel. Scale bar = 0.8 mm.
T. pikei and T. pentaperta. The flower being structurally pistillate, nothing can be said about the androecium of the species, but its 2 slender, spreading styles much resemble those of T. pentaperta (Poinar & Chambers 2017, fig. 6). The long, decurrent stigmas of the 2 taxa are an important indicator of relationship. Parenthetically, in the first-described species of Tropidogyne, T. pikei, the flower has short, sharply-pointed, almost triangular styles with no obvious stigmatic surface (Chambers et al. 2010, fig. 2). With the new information that slender, elongated styles and decurrent stigmas characterize T. pentaperta and T. lobodisca, we might wish to propose that the styles of T. pikei are in fact stylodia, and that the flower is functionally staminate (op. cit., fig. 2, the anthers having been lost from all but 1 filament). Unisexual flowers might thus have been present in 2 of the 3 known Tropidogyne species. The sepal-like structures designated as staminodes in T. lobodisca (Figs. 1, 2) are positioned where a whorl of stamens would occur in a bisexual or male flower. Because they are only 2 in number and are not at all stamen-like in appearance, we believe them to be a developmental anomaly, in which the genes that determine sepal development functioned on the meristem in a region where stamens would normally be formed.

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REFERENCES


