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Tropidogyne pentaptera, sp. nov., a new mid-Cretaceous fossil angiosperm flower in Burmese amber

GEORGE O. POINAR, JR. & KENTON L. CHAMBERS

Abstract

The fossil flower *Tropidogyne pikei* CHAMBERS, POINAR & R. T. BUCKLEY, previously described from Burmese amber has five spreading, epigynous sepals with five major veins and branched, anastomosing veinlets. On top of the inferior ovary is a broad, flat nectar gland from which project three short, arched styles (CHAMBERS et al. 2010). The present paper describes the flowers of another species of this genus, *T. pentaptera* sp. nov., based on seven separate specimens from the same amber bed. The new species has spreading, veiny sepals, a nectar disc, and a ribbed inferior ovary like *T. pikei*, but differs in being bicarpellate, with two elongate, slender styles, and in the ribs of its inferior ovary lacking darkly pigmented terminal glands. A relationship of these fossils to the family Cunoniaceae is proposed, in particular to *Ceratopetalum* D. DON, an extant Southern Hemisphere genus known from fossils of the Tertiary Period.

Key words: Burmese amber, fossil flower, *Tropidogyne pentaptera* sp. nov., Cretaceous angiosperm.

1. Introduction

The amber-embedded flower *Tropidogyne pikei* was previously described from the mid-Cretaceous Noije Bum 2001 Summit Site in Myanmar and tentatively assigned to the family Cunoniaceae, a largely Southern Hemisphere family of 27 genera distributed from South America and islands of the Caribbean to southern Africa, Madagascar, Australia, New Guinea, the Malay Peninsula, and islands of the South Pacific (BRADFORD et al. 2004; CHAMBERS et al. 2010). *Tropidogyne pikei* has five spreading, epigynous sepals with five major veins and branched, anastomosing veinlets. Its inferior ovary has ten distinct ribs, each of which shows a darkly pigmented, possibly glandular area at the apex. On top of the inferior ovary is a flat, three-lobed nectar gland from which project three short, arched styles (CHAMBERS et al. 2010). The present paper describes another species of this genus, *T. pentaptera* sp. nov., based on seven newly discovered fossil flowers from the Noije Bum 2001 Summit Site. The new species has spreading, veiny sepals, a nectar disc, and a ribbed inferior ovary like the previous fossil, but it differs in having only two elongate, slender styles and in the ribs of its ovary lacking darkly pigmented terminal glands. A relationship of these two fossil species to the family Cunoniaceae is proposed, in particular to *Ceratopetalum* D. DON, an extant Southern Hemisphere genus known from fossils of the Tertiary Period (BARNES et al. 2001). An explanation is proposed for the fossils' disjunction from the Cretaceous continent of Gondwanaland.

Acknowledgements

The authors thank ALEX E. BROWN for assistance in obtaining the fossil flowers and Debora Carroll, OSU Valley Library, who helped with the reference literature. ROBERT HILL kindly gave permission for use of the image depicting the venation in a sepal of the extant *Ceratopetalum succirubrum* (Fig. 4, insert). We are grateful to PETER STEVENS and an anonymous reviewer for providing useful notes and suggestions.

2. Materials and methods

The specimen originated from the Noije Bum 2001 Summit Site amber mine excavated in the Hukawng Valley and located southwest of Maingkhwan in Kachin State (26°20'N, 96°36'E) in Myanmar. Based on paleontological evidence, this site was dated to the late Albian of the Early Cretaceous (CRUICKSHANK & KO 2003), placing the age at 97 to 110 Ma. A more recent study using U-Pb zircon dating 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 from the Noije Bum 2001 Summit Site indicate an araucarian tree source for the amber (POINAR et al. 2007a). Observations and photographs were made with a Nikon SMA-10R stereoscopic microscope at 80x 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.

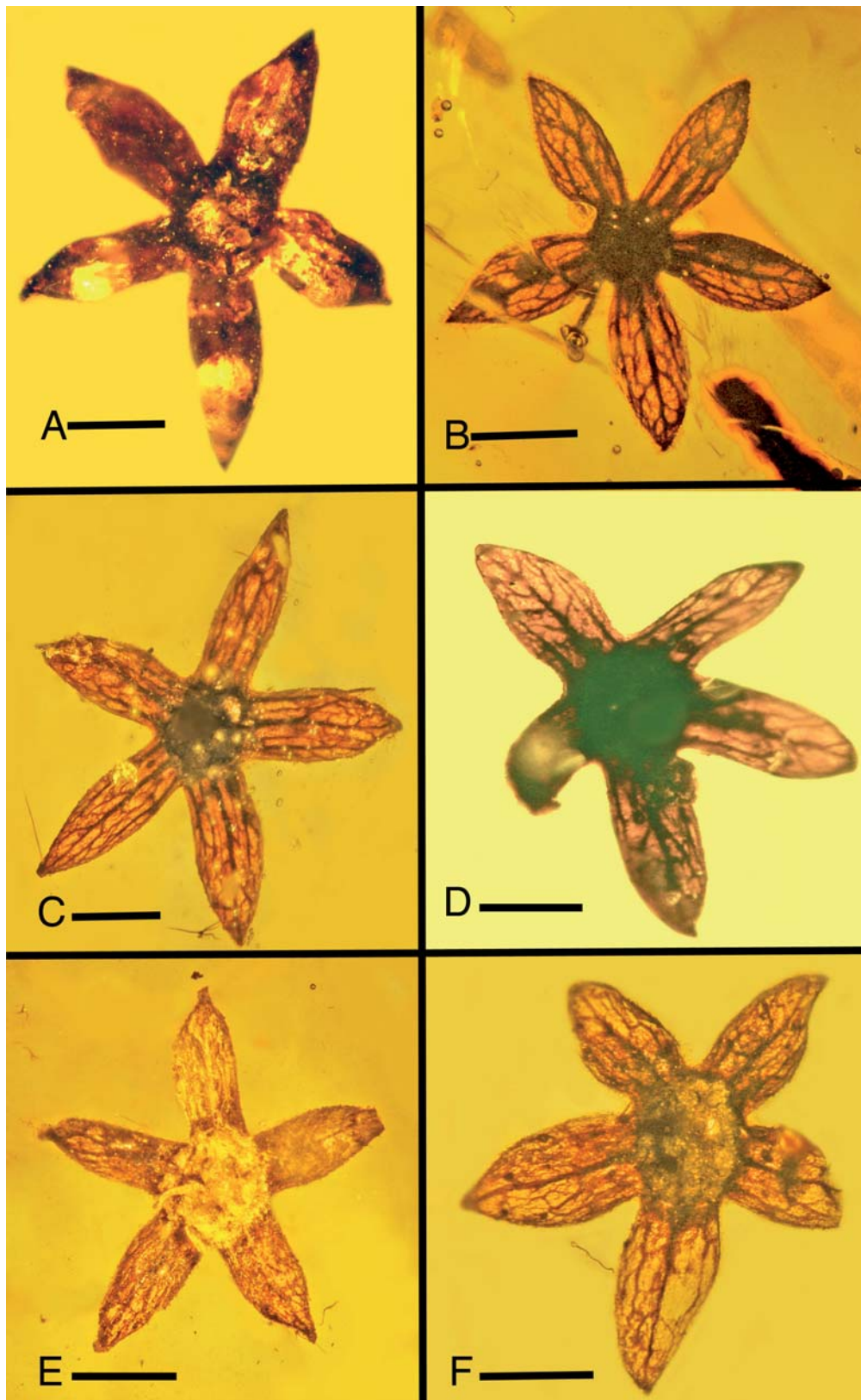


Fig. 1. Five-sepal specimens of *Tropidogyne pentaptera* sp. nov. examined in this study. A: Holotype. Bar = 1.0 mm. B: Paratype B. Bar = 1.2 mm. C: Paratype C. Bar = 1.0 mm. D: Paratype D. Bar = 0.9 mm. E: Paratype E. Bar = 0.9 mm. F: Paratype F. Bar = 1.0 mm.

3. Description

Order Oxalidales BRECHT. & J. PRESL

Family Cunoniaceae R. BR.

Genus *Tropidogyne* CHAMBERS,
POINAR & R. T. BUCKLEY, 2010

Tropidogyne pentaptera sp. nov.
Figs. 1–6

E t y m o l o g y : From the Greek “penta”, five, and “pteron”, wing, based on the 5 firm, spreading sepals.

T y p e s : Holotype: accession number B-An-5A. Paratypes: Accession numbers B-An-5B, B-An-5C, B-An-5D, B-An-5E, B-An-5F, B-An-5G. All specimens deposited in the POINAR amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.

T y p e l o c a l i t y : Myanmar (Burma), amber mine at the Noije Bum Summit Site 2001, Hukawng Valley, southwest of Maingkhwan, state of Kachin (26°20'N, 96°36'E).

T y p e h o r i z o n : Albian/Cenomanian boundary (98.79 +/- 0.62 Ma) of the mid-Cretaceous.

D i a g n o s i s : Flowers bisexual, actinomorphic; sepals five, valvate, slightly connate at base; petals absent; androecium

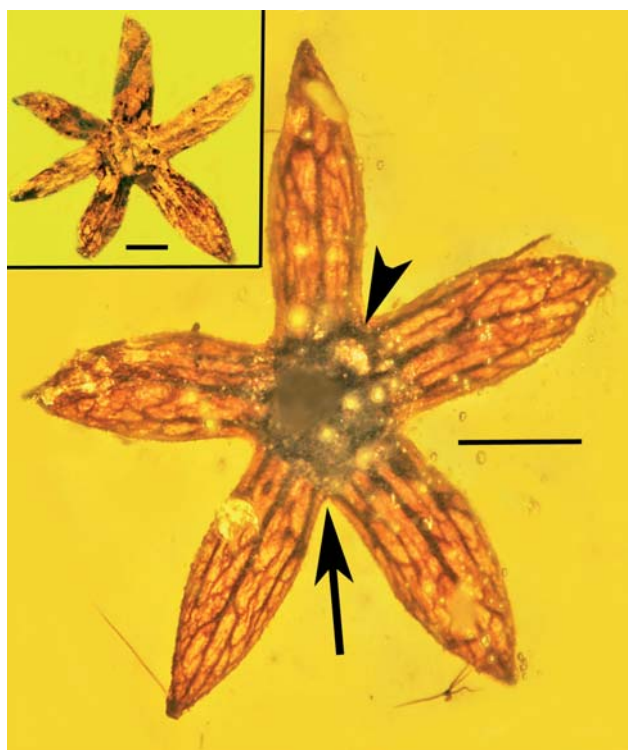


Fig. 2. Flower of *Tropidogyne pentaptera* sp. nov., paratype C, showing basal fusion of sepals (arrow) and connection between lateral veins (arrowhead). Bar = 0.9 mm. Insert shows six-sepaled flower (paratype G). Bar = 0.6 mm.

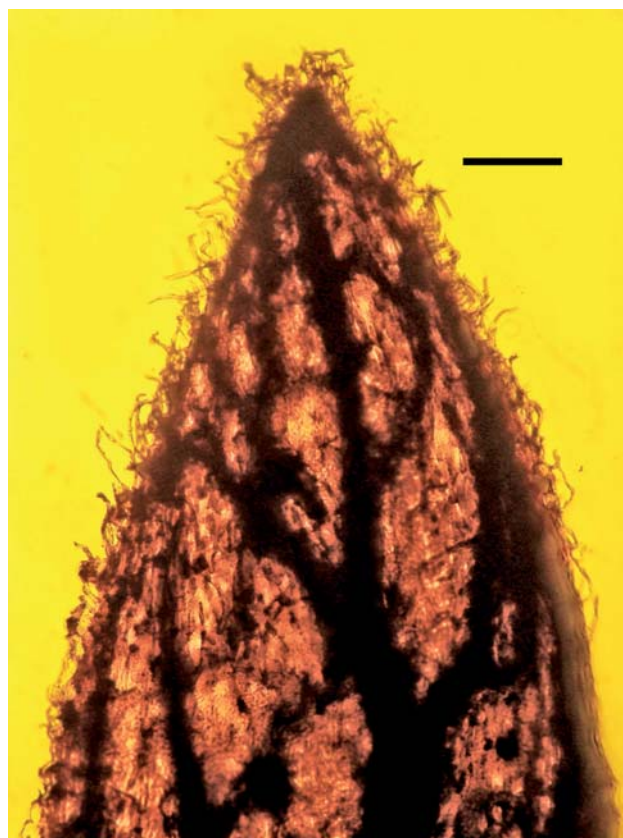


Fig. 3. Margin, venation and pubescence of a portion of a sepal of *Tropidogyne pentaptera* sp. nov. Paratype B. Bar = 0.1 mm.

of five stamens with free filaments inserted at margin of epigynous disc; disc adnate to apex of ovary; ovary inferior, comprising two fused carpels, becoming semi-inferior in fruit, styles two, distinct, diverging; stigmas terminal; pollen with external spotting of the exine.

The new species differs from *T. pikei* in being bicarpellate, as in *Ceratopetalum*. Unlike the ten stamens of *T. pikei*, the new species appears to have only five stamens alternate with the sepals, with short, slender filaments inserted dorsally on the anthers (Fig. 5). The new species also differs in having two elongate, slender styles, instead of three short styles as in *T. pikei*, and in the ribs of the ovary lacking darkly pigmented terminal glands (Fig. 4). The growth habit of *T. pentaptera* was probably a rainforest tree, which is the most common growth form of members of the Cunoniaceae (BRADFORD 2004; KOOYMAN et al. 2014).

D e s c r i p t i o n : Pedicel 1.1–2.0 mm long, flower diameter across calyx 3.4–5.0 mm, sepals five (rarely six), epigynous, elliptic-lanceolate, 1.5–2.1 mm long, 0.8–0.9 mm wide, spreading, slightly connate basally (Figs. 1, 2), margins glabrous to minutely ciliate (Fig. 3), principal veins three–five, +/- parallel, with branching, reticulate veinlets especially in the distal 2/3, connecting vein (interwing vein sensu GANDOLFO & HERMSEN 2017) present between lateral veins of adjacent sepals (Fig. 2, arrowhead), diameter of disc 0.8–1.2 mm, petals 0 or deciduous, stamens deciduous, probably five in number, alternate with the sepals (Fig. 5), filaments slender, arched adaxially, 0.4 mm long, anther oval, dorsifixed, 0.7 mm long, 0.3 mm wide, with a

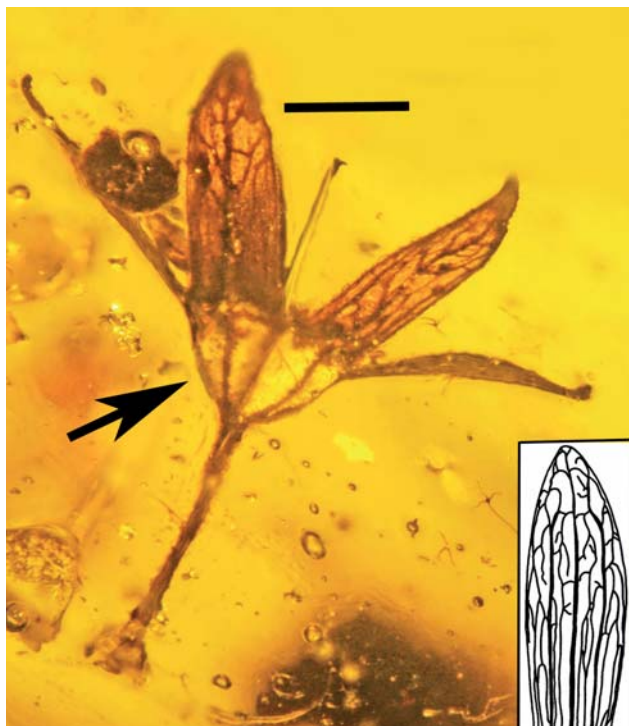


Fig. 4. Adnate hypanthium (arrow) showing 5 of the 10 longitudinal ribs of *Tropidogyne pentaptera* sp. nov., paratype F. Bar = 0.7 mm. Insert: Sepal of *Ceratopetalum succirubrum*, showing venation similar to the fossil.

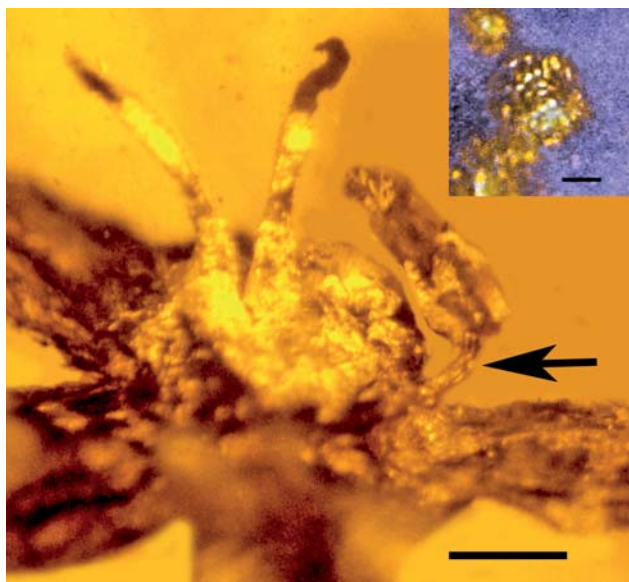


Fig. 5. Holotype (B-An-5A) of *Tropidogyne pentaptera* sp. nov. showing styles and stamen. Arrow points to filament. Anther shows distal connective protrusion. Bar = 0.5 mm. Insert shows pollen grain with verrucose exine. Bar = 8 μ m.

distal connective protrusion (Fig. 5), ovary inferior, becoming semi-inferior in fruit (Fig. 6), bowl-shaped, 0.7–0.9 mm long, 1.2–1.3 mm wide at apex, hypanthium adnate, with 10 prominent veins forming longitudinal ribs (Fig. 4), additional veinlets obscure, apex of ribs lacking enlarged, pigmented glands, styles two, curved outward, 0.7–1.2 mm long (Figs. 5, 6), stigmatic tip acute, pollen diameter 17–23 μ m, exine finely verrucose externally (Fig. 5 insert).

Remarks: Finding a specimen with six sepals (B-An-5G, Fig. 2 insert) is interesting. We assume that the extra sepal represents a developmental anomaly in which one primordium divided at an early stage, producing two similar organs. We did not find any isolated pollen grains that might have shown the number of colpi. The speckling of the pollen exine (Fig. 5, insert) is similar to that illustrated for Cunoniaceae by ERDTMAN (1966).

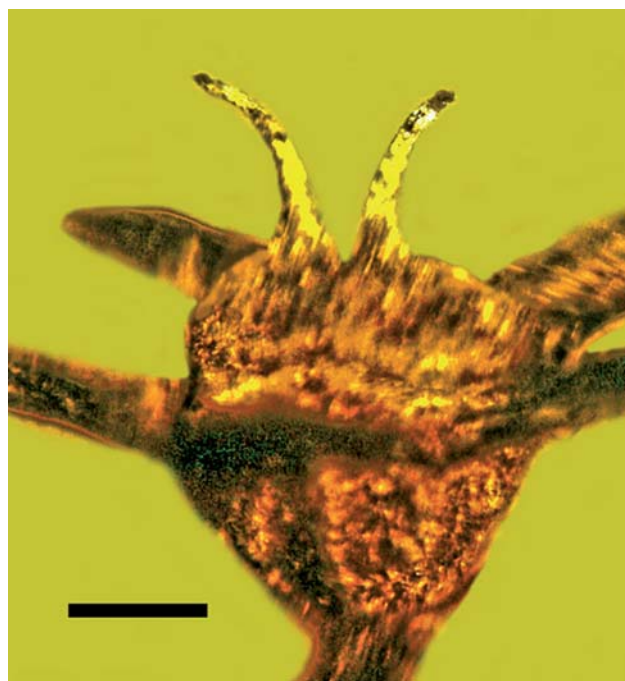


Fig. 6. Fruit of *Tropidogyne pentaptera* sp. nov. showing rounded upper portion of semi-inferior ovary. Paratype E. Bar = 1.0 mm.

4. Discussion

In the publication of *Tropidogyne pikei* by CHAMBERS et al. (2010), there is a detailed discussion of the similarities of this flower to those of present-day *Ceratopetalum* of the Cunoniaceae. The comparison works equally well for *T. pentaptera*, with the added features of a pair of elongated styles and a semi-inferior fruiting ovary by which these fossils resemble *Ceratopetalum* but differ from *T. pikei*. Only in its five rather than ten stamens and the slight basal connation of the sepals does *T. pentaptera* differ from the modern genus. Although the comparison is entirely floral, since no vegetative parts are preserved in the amber, we

are emphasizing the morphological relationship to *Ceratopetalum* more positively here than in the earlier paper, in particular because we have evidence from another Burmese amber fossil, discussed below, that Mid-Cretaceous fossils from this amber may bear a surprising and unsuspected similarity to modern angiosperm groups that were thought to be tens of millions of years younger. Another point to be noted is that fruits of *Ceratopetalum* are already well known in the Cenozoic fossil record, as discussed by GANDOLFO & HERMSEN (2017), who found fossils referable to this genus in the Early Eocene of Patagonia and who cite previous reports of Eocene to Miocene fossils of *Ceratopetalum* from Australia (BARNES & HILL 1999).

Similarities of *Tropidogyne* to *Ceratopetalum* are in the regular calyx of five valvate sepals that are lanceolate, firm, and spreading, the pattern of anastomosing sepal venation (Figs. 1–4, 4 insert), the connection between lateral veins of adjacent sepals (Fig. 2, arrowhead), the lack of petals (only *C. gummiferum* has petals), the diplostemonous androecium (in *T. pikei*), the short stamens with dorsally inserted filaments (ROZEFELDS & BARNES 2002, fig. 5), the anthers with a conspicuous connective protrusion (ROZEFELDS & BARNES 2002: 656, fig. 6), the well-developed epigynous nectar disc, resembling *C. gummiferum* in its lack of the puberulent zone described for all other species of *Ceratopetalum* (ROZEFELDS & BARNES 2002: 656, fig. 5), the bicarpellate pistil with elongate, recurved styles (in *T. pentaptera*), and the inferior ovary with ten-ribbed adnate hypanthium, becoming semi-inferior in fruit (Figs. 4, 6).

The oldest fossil flower assigned to Cunoniaceae is *Platydiscus peltatus* from the Santonian/Campanian boundary, 83.5+/-0.7 Ma, in Sweden (SCHÖNENBERGER et al. 2001). However, figures of this fossil in FRIIS et al. (2001: 331, 438) show five superior, separate carpels, quite unlike Australian *Ceratopetalum*. GANDOLFO & HERMSEN (2017) were reluctant to attribute a relationship of *Tropidogyne pikei* to *Ceratopetalum* because of the fossil's age and its occurrence in Burma, far from Australia. However, a recently submitted paper (POINAR & CHAMBERS, submitted 2017) sheds important new light on the Burmese amber fossils. In it, six capitula of Asteraceae, assigned by the authors to subfamily Barnadesioideae, the basal clade of the family, were found in amber from the Noije Bum Summit Site locality. This subfamily occurs only in the Southern Hemisphere and is recognized as the sister group to all other Asteraceae (FUNK et al. 2009, fig. 44.3). The earliest record of the subfamily was reported by BARREDA et al. (2015), based on pollen from a site in Antarctica dated to ca. 76–66 Ma. This record is itself much older than the previously estimated basal date for Asteraceae of 41–50 Ma (FUNK et al. 2009, fig. 44.8), and the date of 98.79 +/- 0.62 Ma for Barnadesioideae in Burmese amber is much greater yet.

The geological history of the Malaysian region provides a possible explanation of how the unexpectedly old Burmese amber flowers of Barnadesioideae and *Tropidogyne* became separated from related Asteraceae and Cunoniaceae of the Southern Hemisphere. Malaysia, including Burma, was formed during the Paleozoic and Mesozoic Eras by subduction of terranes that successively separated from Gondwanaland and were transported by continental drift northward across the Tethys Sea (HALL 2012; METCALFE 2013). The last of these parts of Gondwanaland to move northward was the India block, including Greater India Parts 1 and 2, which had been adjacent to western Australia (HALL 2012, fig. 26; METCALFE 2013, fig. 17). When this terrane reached Asia in the Middle Eocene, the northeastern part was adjacent to Burma (METCALFE 2013, fig. 28). We suggest that if the Noije Bum Summit Site amber deposit was part of Greater India when it sutured to Burma, both *Tropidogyne* and the Barnadesioid fossils would have originated in the late Early Cretaceous, when this fragment of Gondwanaland was adjacent to Australia. This proposal of a Southern Hemisphere origin explains the morphological similarity and, we believe, the taxonomic relationship of *Tropidogyne* to *Ceratopetalum*, leading to the conclusion that *Ceratopetalum*-like species of Cunoniaceae were present in Gondwanaland in the late Early Cretaceous. Our proposal is similar to one by PRASAD et al. (2005) for the grass family Poaceae. Based on a diversity of grass phytoliths in Late Cretaceous strata in India, these authors suggest that “crown-group Poaceae had diversified and spread before India became geographically isolated,” that is, when it was part of Gondwanaland.

Despite the previous lack of fossil evidence, an early occurrence of major groups such as Asteraceae and Cunoniaceae must now be accepted because of the well-preserved specimens discovered in Myanmar amber. Other examples may include previously described fossils with affinities to the families Monimiaceae (POINAR & CHAMBERS 2005), Cornaceae (POINAR et al. 2007b) and Lauraceae (POINAR 2017).

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