FOSSIL FLOWERS OF *LACHNOCIONA CAMPTOSTYLUS* SP. NOV., A SECOND RECORD FOR THE GENUS IN MID-CRETACEOUS MYANMAR AMBER

George O. Poinar, Jr.
Department of Integrative Biology
Oregon State University
Corvallis, Oregon 97331, U.S.A.
poinarg@science.oregonstate.edu

Kenton L. Chambers
Department of Botany and Plant Pathology
Oregon State University
Corvallis, Oregon 97331, U.S.A.
chamberk@science.oregonstate.edu

ABSTRACT

Two flowers embedded in a single block of amber from Myanmar are here proposed as a second species of the previously described fossil genus *Lachnociona*. The mid-Cretaceous age of the fossils was earlier established through paleontological and U-Pb isotope dating methods. Because they lie within millimeters of each other in the amber, the flowers are assumed to have come from the same parent plant. One flower is hermaphrodite while the other is functionally pistillate. They differ by the number of styles—4 in the perfect flower and 5 in the unisexual one—and most notably by the presence, in the perfect flower, of 10 conspicuous nectar glands forming a disc above the whorl of stamens. The pistillate flower has no such glands. In the new species, the arched styles are widely divergent and the ovary is fully inferior, while in the earlier-described *Lachnociona terriae*, the flower is functionally pistillate, with styles that are erect and connivent or connate. It could not be determined whether the ovary is superior or half-inferior. The best-preserved anther in the perfect flower of **L. camptostylus** resembles, in its dorsal filament attachment and hooked filament tip, a vestigial anther present in the flower of *L. terriae*. Pollen of the new species is tri- or tetracolpate. As proposed in the previous paper, the genus may have participated in the early diversification of the rosid clade of eudicots.

RESUMEN

Dos flores incluidas en una pieza de ámbar de Birmania se proponen como una segunda especie del género fósil *Lachnociona* descrito previamente. La edad de los fósiles en el Cretácico medio se estableció previamente mediante métodos de datación paleontológicos y los isótopos U-Pb. Debido a que están a milímetros una de otra en el ámbar, se asume que las flores proceden de la misma planta. Una flor es hermafrodita mientras que la otra es funcionalmente pistilada. Difieren en el número de estilos—4 en la flor perfecta y 5 en la unisexual—y lo más notable por la presencia, en la flor perfecta, de 10 glándulas de néctar conspicuas formando un disco encima del verticilo de estambres. La flor pistilada no tiene esas glándulas. En la nueva especie, los estilos arqueados son bastante divergentes y el ovario es totalmente ínfero, mientras en la previamente descrita *Lachnociona terriae,* la flor es funcionalmente pistilada, con estilos que son erectos y conniventes o connatos. No se puede determinar si el ovario es supero o semiínfero. La antera mejor conservada en la flor perfecta de **L. camptostylus** parece, por su unión dorsal al filamento y ápice del filamento ganchudo, una antera vestigial presente en la flor de *L. terriae*. El polen de la nueva especie es tri- o tetracolpado. Como se propone en el artículo anterior, el género puede haber participado en la diversificación temprana del clado de las rósidas de las eudicotiledóneas.

INTRODUCTION

This paper is a continuation of our studies of fossil flowers derived from amber that was secondarily deposited in mid-Cretaceous oceanic sediments now being mined in northern Myanmar (Burma). Details of the location of the amber are given in the following section. A recently obtained block of amber contains 2 similar and closely adjacent flowers (Fig. 1), which are here described as a new species of the previously recognized genus *Lachnociona* (Poinar et al. 2008). In that paper, the genus was compared with representatives of several families of rosids and Saxifragales, but no assignment to a particular modern family was suggested. Of the 9 other genera of fossil angiosperms that we have described from these amber deposits, only 3 have been explicitly ascribed to an extant family. These are Poaceae (Poinar 2004), Cunoniaceae (Chambers et al. 2010; Poinar & Chambers 2017), and Lauraceae (Poinar 2017). Tentative assignments were offered for Monimiaceae (Poinar & Chambers 2005), Cornaceae (Poinar et al. 2007a), and Dilleniaceae (Poinar & Chambers 2018a). For the remaining 3 genera, we made no suggestions regarding their relationship to a given modern family (Poinar et al. 2016; Poinar et al. 2013; Poinar & Chambers 2018b). The environment occupied by these mid-Cretaceous angiosperms is hypothesized to have been a tropical or subtropical forest, possibly located in the Southern Hemisphere continent of Gondwana (Poinar et al. 2005; Poinar 2018; Poinar & Chambers 2018a, b). The

J. Bot. Res. Inst. Texas 12(2): 655 – 666. 2018

Fig. 1. ***Lachnociona camptostylus*. The 2 flowers as originally positioned in a single block of amber. Note bracts on pedicel of lower, pistillate flower (arrows). Scale bar = 2.1 mm.**

amber has been shown to be derived from the resin of an araucarian tree, probably the genus *Agathis* (Poinar et al. 2007b).

One of the 2 flowers described here is hermaphrodite (Figs. 1–6) while the other is functionally pistillate, having well-developed styles but stamens with the anthers lacking or abortive (Figs. 1, 7–9). In these respects, it is similar to the previously described species *Lachnociona terriae* (Poinar et al. 2008). It seems likely that both flowers came from the same parent plant, and the new species is therefore gynomonoecious. The perianth parts, identified here as sepals, are 5 in both flowers, but in the hermaphrodite flower, 2 are positioned unusually close together (Fig. 3), resulting in an irregular calyx. This may be a developmental anomaly, however, because the pistillate flower has a regular perianth (Fig. 9). Two stamens in the hermaphrodite flower are fully

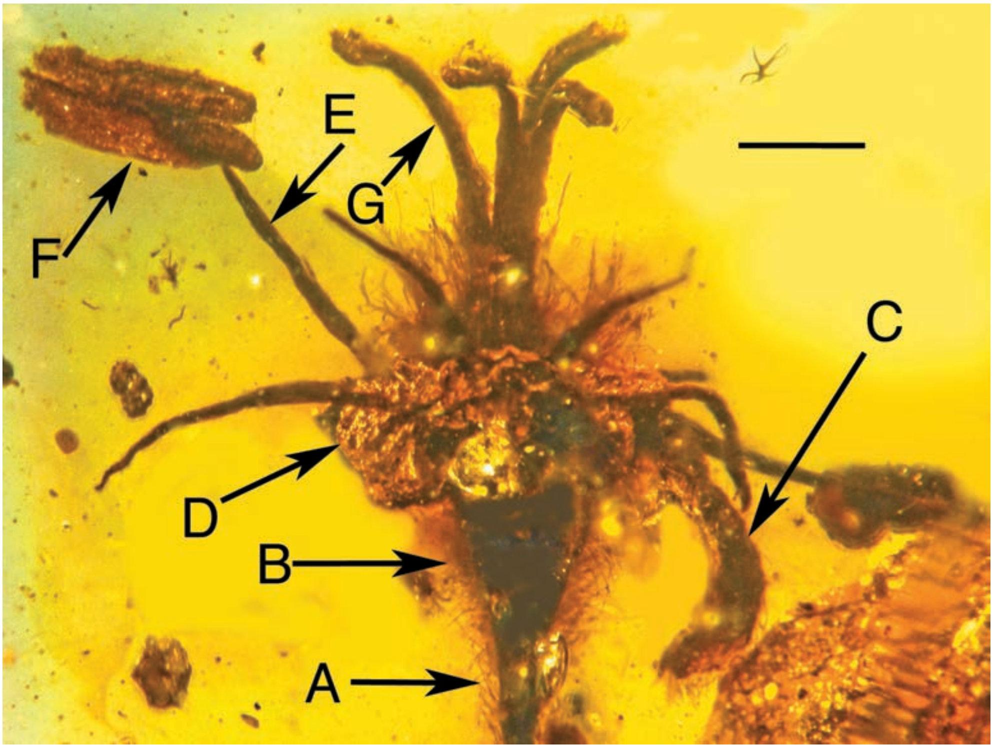

Fig. 2. ***Lachnociona camptostylus*. Hermaphrodite flower, lateral view. A. Pedicel. B. Ovary. C. Sepal. D. Nectar gland. E. Filament. F. Anther. G. Style. Scale bar = 0.5 mm.**

formed, but the other filaments have lost their anthers (Figs. 2, 3). The number of stamens is at least 8 and probably would have been 10, were it not for abnormal development of the calyx. Ten nonfunctional stamens were previously observed in the pistillate *L. terriae* flower. Of the 3 filaments visible in the pistillate flower of *L. camptostylus*, 1 has a tiny, abortive anther (Fig. 7). The hermaphrodite flower has 4 styles (Fig. 5) and the pistillate one has 5 (Fig. 8). The ovary, although mostly hidden by the reflexed sepals, is fully inferior in both flowers. The styles of both are divergent and arched abaxially, thus differing from the columnar arrangement of almost fully connivent or connate styles in *L. terriae*. The stigmas of *L. camptostylus* are decurrent ventrally from the stylar tips, like those of *L. terriae*.

As discussed previously (Poinar & Chambers 2018b), the fossil record of angiosperms in the Cretaceous Period has been well described by Friis et al. (2006, 2011). These authors questioned the proposed dating of Myanmar amber, however, suggesting that it may be of Late Cretaceous or even Early Cenozoic age. No evidence was given, except that a mid-Cretaceous age “appears much too old, judging from the organization of the flowers described so far” (Friis et al. 2011, p. 34). However, the age of the Myanmar amber deposits was dated at 97–110 Ma by paleontological (ammonite) procedures (Cruickshank & Ko 2003) and at ca. 98–99 Ma by U-Pb radiometric methods (Shi et al. 2012). The term “mid-Cretaceous” is used here in reference to these approximate dates, which lie near the Upper Albian-Lower Cenomanian boundary (Cohen et al. 2013). We consider the 10 genera of fossil flowers in Myanmar amber, cited above—some of which are vouchered from 2 or more specimens—as representing a significant addition to the fossil record of early angiosperms, which thus far has been principally elaborated by the work with mesofossil compressions and charcoalified flowers ably carried out by E.M. Friis and colleagues (Friis et al. 2011 and papers cited therein).

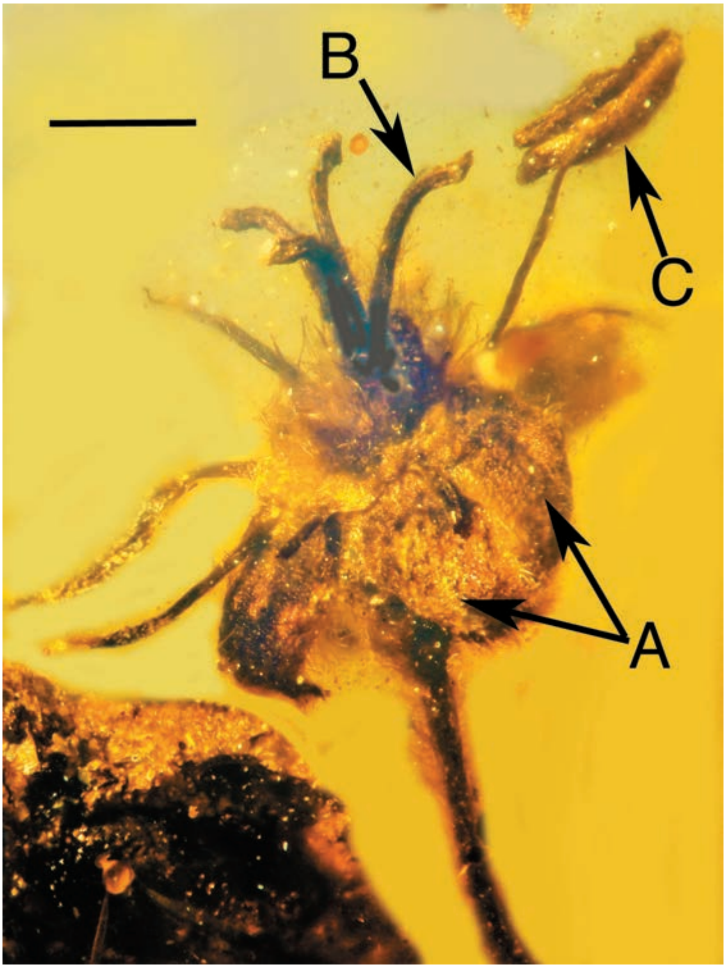

Fig. 3. ***Lachnociona camptostylus*****. Hermaphrodite flower, lateral view. A. Abnormally juxtaposed sepals. B. Style. C. Anther, showing longitudinal dehiscence. Note tufts of trichomes at base of styles. Scale bar = 0.7 mm.**

MATERIALS AND METHODS

The specimens were derived from amber mines at the Noije Bum 2001 Summit Site in the Hukawng Valley, located southwest of Maingkhwan in Kachin State, Myanmar (Poinar et al. 2005). The age of the amber deposits has been measured as ca. 97–100 Ma, as described in the previous paragraph. The fossils are found in strata of marine origin, the amber having been secondarily deposited from streams that drained an adjacent forested landmass. The amber itself, long known by the common name "burmite," must therefore be older than the sediments that are presently being mined.

Observations and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and a Nikon Optiphot compound microscope with magnification up to 800×. Helicon Focus Pro X64 was used to stack photographs for better depth of field. Background details were removed to improve the image in various figures.

DESCRIPTION

Lachnociona camptostylus Poinar & K.L. Chambers, **sp. nov.** (**Figs. 1–10**). Type: MYANMAR (BURMA). Kachin Province: Amber mine in the Hukawng Valley SW of Maingkhwan (26°20'N, 96°36'E), *unknown amber miner* (holotype: Accession number B-An-8A, deposited in the Poinar Amber Collection housed at Oregon State University, Corvallis, Oregon, U.S.A. Paratype: Accession number B-An-8B, similarly deposited. The original block of amber containing the flowers was cut into 2 blocks so as to separate the specimens for microscopic study and photography.

Description.—Holotype flower hermaphrodite, pedicellate, pedicel ebracteate, hirsute-villous (Figs. 1–3), sepals 5, spreading, strongly recurved (Figs. 2, 3), lance-ovate, upper surface hirsute-villous, calyx irregular due to the close juxtaposition of 2 sepals (Figs. 3, 4), petals 0, disc of ca. 10 nectar glands, glands lanceolate, spreading or recurved (Fig. 4), positioned above the sepals and forming a ring around the base of the styles (Figs. 2, 5), surface of glands pebbly (Fig. 4), stamens ca. 10, spreading, filaments linear, glabrous, tapered distally, 1 or more filaments weakly developed where 2 sepals are juxtaposed (Figs. 3, 4), anthers lost from all but 2 stamens, remaining anthers 4-loculed, linear, longitudinally dehiscent (Figs. 2, 6), connective not prolonged, filament inserted dorsally, the tip retrorsely hooked (Fig. 6), styles 4, arched and spreading abaxially (Figs. 2, 5), subglabrous, with tufts of hirsute trichomes at the base (Figs. 2, 3), tip blunt, stigmatic area ventrally decurrent, ovary inferior, hirsute-villous (Figs. 2, 3), pollen tri- or tetracolpate, exine rugose (Fig. 10).

Paratype flower functionally pistillate, pedicellate, pedicel bracteate (Fig. 1), subglabrous (Fig. 7), sepals 5, equally spaced, spreading, strongly recurved, subglabrous (Figs. 7–9), petals 0, stamens ca. 3, anthers 0 or vestigial (Fig. 7), nectar glands 0, styles 5, arched and spreading abaxially (Figs. 7, 8), subglabrous, with tufts of villous trichomes at the base, tip blunt, stigmatic area ventrally decurrent, ovary inferior, subglabrous (Fig. 7).

Dimensions of hermaphrodite flower (holotype): Pedicel 2.9 mm (Fig. 1), length of flower from base of ovary to top of arched styles 2.4 mm, width at apex of ovary 1.0 mm, length of sepals ca. 1.2 mm, basal width of sepals 0.8 mm, length of spreading nectar gland 0.2 mm (Fig. 4), maximum length of filaments 1.2 mm, length of anther 0.9 mm, width of anther 0.4 mm, length of ovary 1.0 mm, length of styles ca 1.2 mm, diameter of pollen grain 30 µm.

Dimensions of pistillate flower (paratype): Pedicel 2.5 mm (Fig. 1), length of bracts 1.5 mm and 2.0 mm, length of flower from base of ovary to top of arched styles 2.4 mm, width at apex of ovary 1.2 mm, length of sepals ca. 1.1 mm, basal width of sepals 0.7 mm (Fig. 9), length of ovary 0.8 mm, length of styles ca. 1.4 mm.

Etymology.—Species name from the Greek "kamptos," curved, and "stylos," column, referring to the curved styles. "Kion," the Greek stem of the genus name *Lachnociona,* is masculine in gender, hence the *-us* ending of the specific epithet.

DISCUSSION

Principal differences between the hermaphrodite and pistillate flowers, besides the presence or absence of fertile stamens, are 4 vs. 5 styles, a reduced pubescence of the pedicel and ovary of the pistillate flower, and most notably, the presence of distinctive nectar glands in the hermaphrodite flower, forming a ring-shaped disc just above the sepals (Fig. 5). It seems unusual that such glands should be present in only 1 of the 2 floral types, given their probable function as pollinator attractants. We interpret the irregular calyx of this flower, with 2 sepals placed unusually close together, to be a developmental anomaly (teratology). The pistillate flower of *Lachnociona camptostylus* is like that of *L. terriae* in having a perianth of 5 strongly recurved sepals, similar in shape and in their lightly pubescent upper surface. There are fewer sterile filaments remaining in *L. camptostylus*, but at least 1 retains an aborted anther as in the earlier-described species. The pedicel of *L. camptostylus* is lightly puberulent, and the inferior ovary is essentially glabrous (Fig. 7). This differs from the more obviously pubescent pedicel and ovary of *L. terriae.* Also, the pedicel of the latter species tapers into the gradually widening ovary, but in *L. camptostylus* the slender pedicel widens abruptly into an enlarged inferior ovary (compare Fig. 1 of Poinar et al. 2008 with Fig. 7 of the present paper). A ring of nectar glands is absent in the pistillate flowers of both species.

The most obvious difference between *Lachnociona camptostylus* and the previously described species is in

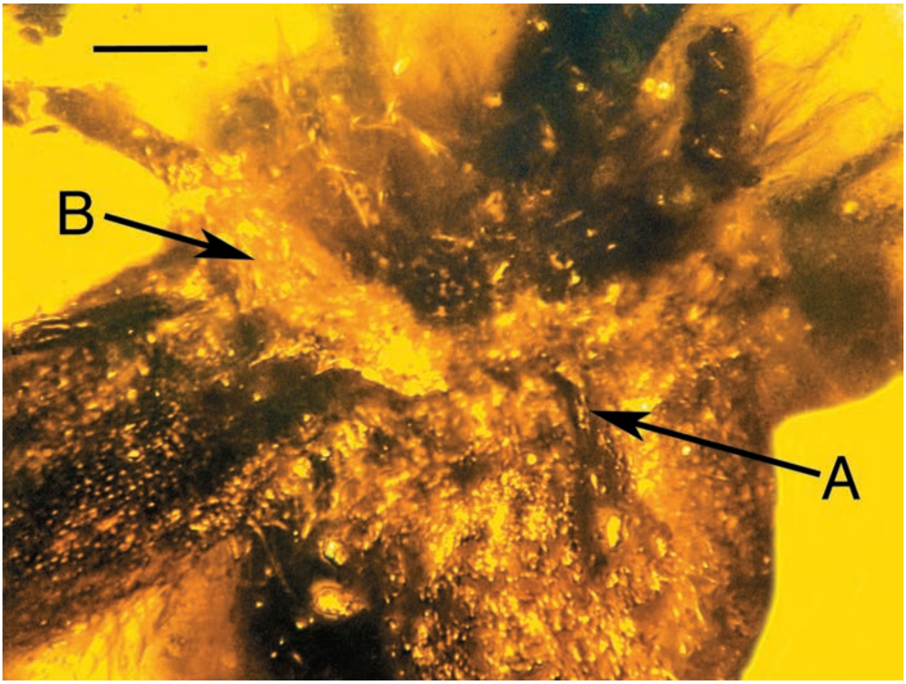

Fig. 4. *Lachnociona camptostylus*. Hermaphrodite flower, as in figure 3. **A.** Abortive stamen filament above abnormally placed sepal. **B.** Elongated, spreading nectar gland. Scale bar = 0.3 mm.

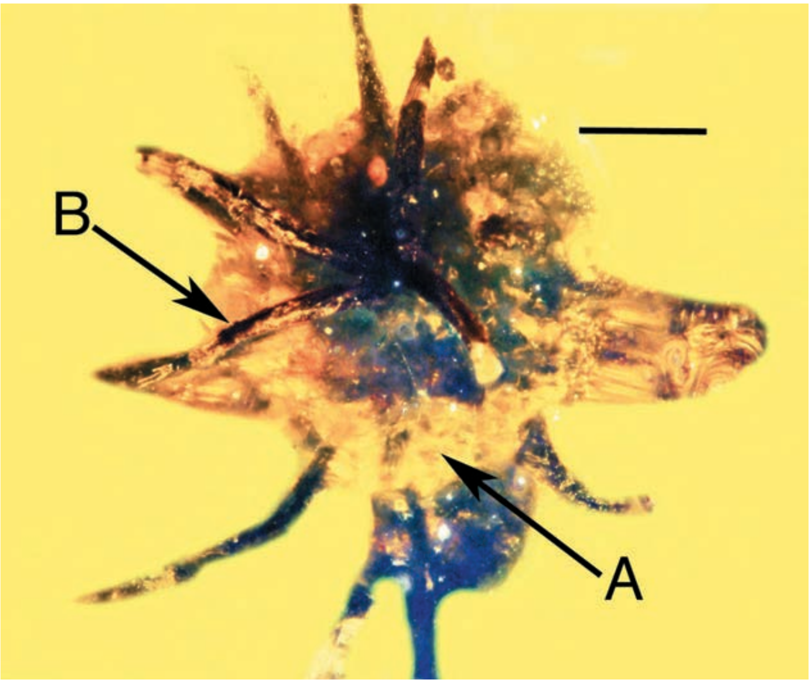

Fig. 5. *Lachnociona camptostylus*. Hermaphrodite flower, apical view. **A.** Ring of nectar glands. **B.** 1 of 4 styles. Scale bar = 0.6 mm.

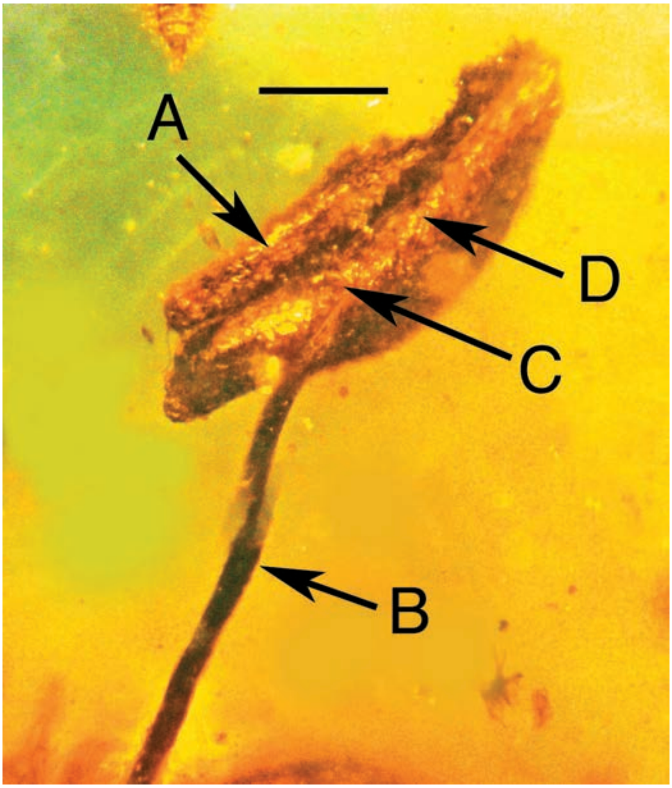

Fig. 6. ***Lachnociona camptostylus*. Stamen of hermaphrodite flower. A. Locule of anther. B. Filament. C. Hook on tip of filament, where dorsally attached to anther. D. Connective, not prolonged at apex. Scale bar = 0.3 mm.**

the conformation and pubescence of the stylar portion of the gynoecium. As has been noted, the styles in both floral types of *L. camptostylus* are separate, arched away from the center of the flower, and blunt at the apex. They are lightly pubescent at best. In *L. terriae*, the 5 styles form an erect, densely hirsute column, in which it cannot be determined whether the individual styles are connate or merely connivent. The acute stylar tips are separate and divergent. The stigmatic areas are similar in the two species in being ventrally decurrent from the stylar apex.

Only in the present species is a hermaphrodite flower of *Lachnociona* available for study. Its stamens reveal the unusual feature of a recurved hook at the tip of the filament, where it attaches to the anther (Fig. 6). This trait was described and illustrated for *L. terriae*, but in that case it was observed on the best-preserved sterile anther. The ring of nectar glands present in the hermaphrodite flower of *L. camptostylus* may have been a feature, also, of bisexual flowers in *L. terriae*, but there is no way of knowing whether this is truly a generic characteristic or merely a feature peculiar to the present species. A similar-looking glandular ring or disc was described and illustrated for the Upper Cretaceous (± 83 Ma) fossil genus *Scandianthus*, from Åsen, Sweden (Friis & Skarby 1982; Friis et al. 2011, fig. 17.10 C). Lobed nectaries are also illustrated for other Cretaceous fossils such as the “Rose Creek flower” and *Platydiscus peltatus* and for the modern rosid genera *Anisophyllea* and *Ceratopetalum* (Friis et al. 2011, pp. 328, 331, 438). In all these cited examples, the nectary-bearing flowers are hermaphrodite.

An inferior position of the ovary is now established for *Lachnociona*, although this was equivocal in *L. terriae* when first published. Two previously described genera from Myanmar amber that have an inferior

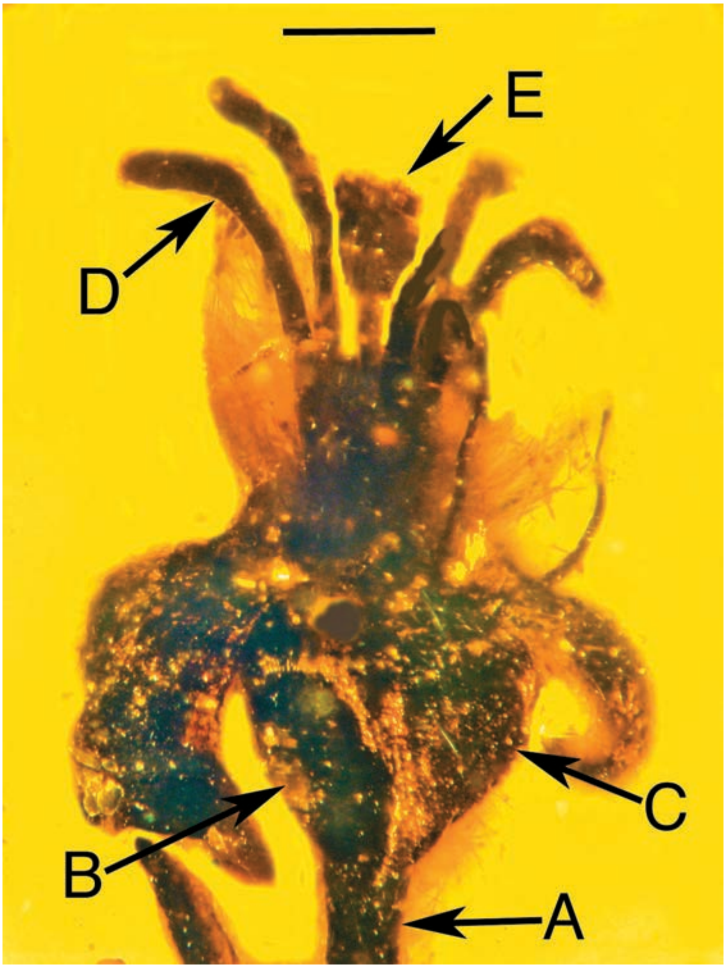

Fig. 7. ***Lachnociona camptostylus.*** **Pistillate flower, lateral view. A. Pedicel. B. Ovary. C. Sepal. D. Style. E. Aborted anther on 1 filament. Note tufts of trichomes and lack of nectar glands at base of styles. Scale bar = 0.6 mm.**

ovary are *Eoëpigynia* (Poinar et al. 2007) and *Tropidogyne* (Chambers et al. 2010; Poinar & Chambers 2017). Epigynous flowers are known from the Early Cretaceous (Friis et al. 2011, pp. 395–397), but they do not become common in the fossil record until Late Cretaceous (op. cit., pp. 395–399). Examples from the latter period with which *Lachnociona* might be compared are *Scandianthus* (Friis & Scarby 1982; Friis et al. 2011, fig. 17.10 C) and *Divisestylus* (Hermsen et al. 2003). These are similar to *Lachnociona* in having a well-developed disc around the base of the styles, but in both, the ovary is bicarpellate and strongly ribbed, not 4–5-carpellate and smooth-surfaced as in the present genus. A relationship to Saxifragaceae, in the traditional sense (Melchior 1964, pp. 201–206), was proposed for both Upper Cretaceous genera.

Pollen of the new species is described as tri- or tetracolpate. Of the 2 grains in figure 10, "A" shows 3 colpi in polar view, while "B" has 2 colpi clearly visible on one side, which are close enough together to allow for a total of 4 colpi. Such variation in number of colpi is not unusual for fossil or modern taxa. For example, pollen of the Upper Cretaceous fossil *Silvianthemum* (Friis 1990) was described as tricolpate, but tetracolpate grains were noted and illustrated (op. cit., pp. 9, 27). Tricolpate pollen firmly establishes *Lachnociona* as a eudicot, the

Fig. 8. ***Lachnociona camptostylus.*** **Pistillate flower, apical view. A. 1 of 5 styles. B. Sepal. Scale bar = 0.7 mm.**

informal category for all angiosperm families above the eumagnoliid clade of lower dicots (Friis et al. 2011, pp. 164–165).

Lachnociona terriae was previously compared with the fossil *Platydiscus* and 7 modern genera representing Saxifragales (Aphanopetalaceae), Cucurbitales (Anisophyllaeaceae), Sapindales (Simaroubaceae), and Oxalidales (Brunelliaceae, Cunoniaceae), with respect to 15 morphological characteristics (Poinar et al. 2006, Table 1). With the additional information now available for *Lachnociona*, we can add 4 new traits to be used in the above comparisons—the presence of spreading styles, a sometimes 4 carpellate gynoecium, a lobed nectar disc in the perfect flower, and bisexual flowers. When factored into the previous analysis, these changes increase the similarity of *Lachnociona* to members of Brunelliaceae and Cunoniaceae. There are 13 out of 16 character similarities with *Brunellia*, although this genus differs in its superior, apocarpous gynoecium and its sometimes tetramerous calyx and upright sepals (Orozco 2002). *Pullea* is also like the fossil genus in 13 characteristics, differing in the number of stamens and carpels, a half-inferior gynoecium, and a 5-lobed nectar disc (Bradford et al. 2004). *Vesselowskya* shows 12 matching traits with *Lachnociona*, differing in its bicarpellate, superior ovary, 3-merous perianth, and petals present in the staminate flower (Rozefelds et al. 2001). The

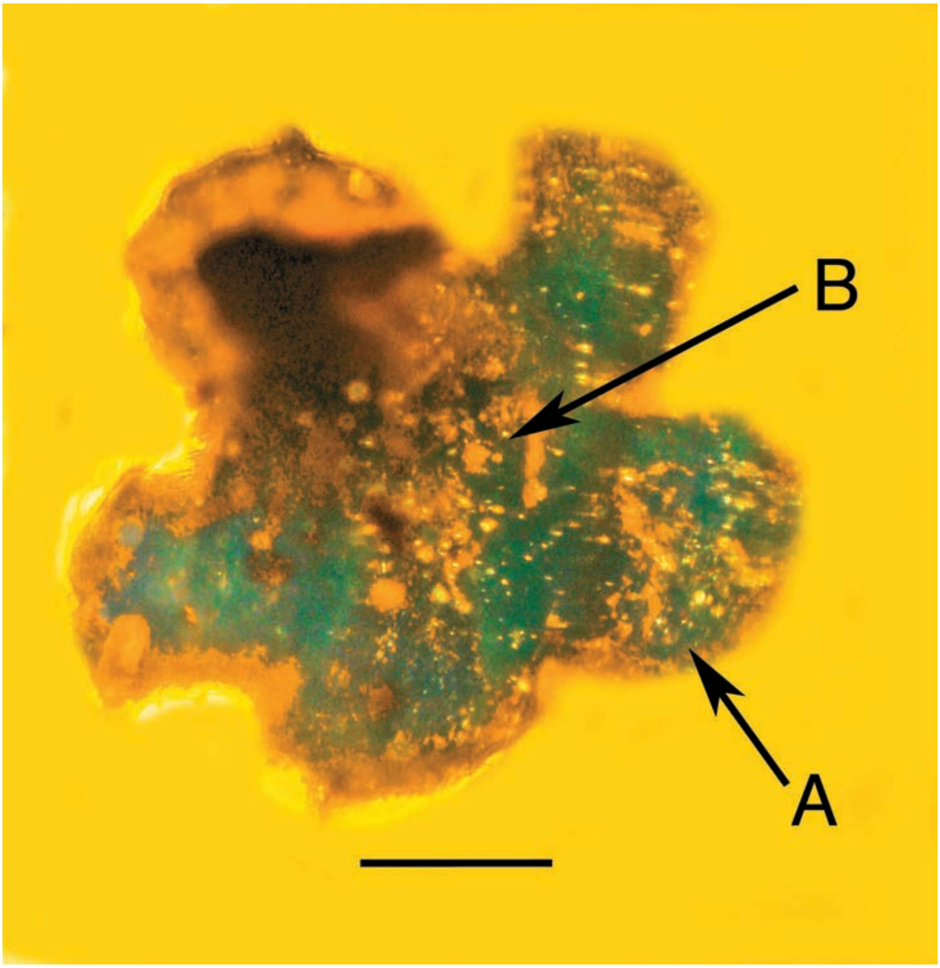

Fig. 9. ***Lachnociona camptostylus*. Pistillate flower, basal view. A. Sepal. B. Ovary. Note that 1 sepal is hidden behind pedicel. Scale bar = 0.6 mm.**

Upper Cretaceous fossil *Platydiscus peltatus* was suggested by its authors (Schönenberger et al. 2001; Schönenberger & von Balthazar 2006) as having floral similarities to Cunoniaceae. It also shows 12 characteristics in common with *Lachnociona* but differs in its 4-merous flowers, presence of petals, and largely superior ovaries. The remaining genera that were compared morphologically with *Lachnociona*, including *Anisophyllea* and *Aphanopetalum*, differ in 5 or more floral characteristics.

The fossil history of the rosid order Oxalidales, containing the modern families Cunoniaceae and Brunelliaceae, was treated by Friis et al. (2011) with emphasis on the well-studied genus *Platydiscus*. The order today includes approximately 2000 species distributed predominantly in the Southern Hemisphere. The fossil record for Cunoniaceae begins in the Maastrichtian of Australia and New Zealand and continues from the Late Eocene to the Middle Miocene (op. cit., p. 330). The genus *Tropidogyne*, described from mid-Cretaceous Myanmar amber (Chambers et al. 2010; Poinar & Chambers 2017), shows many similarities to the modern genus *Ceratopetalum*, suggesting an even earlier fossil record for the Cunoniaceae. Placing the newly described fossil species in *Lachnociona*, therefore, has added to the evidence for a suggested taxonomic alignment with the eudicot subclass Rosidae, especially with families Cunoniaceae and Brunelliaceae.

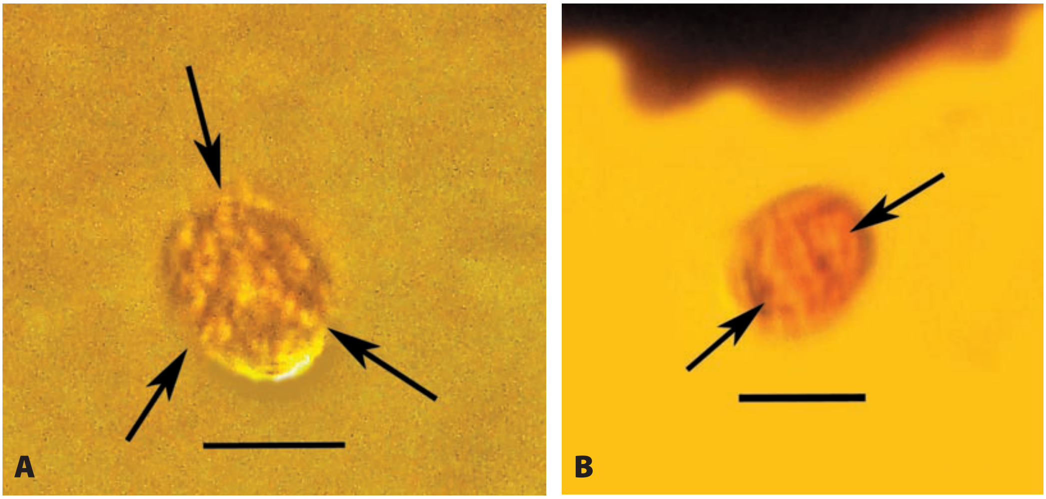

Fig. 10. *Lachnociona camptostylus*. Pollen grains. **A.** Polar view, showing 3 colpi (arrows). Scale bar = 27 µm. **B.** Lateral view, showing 2 closely spaced colpi (arrows) out of a probable total of 4 colpi. Scale bar = 25 µm.

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