THYMOLEPIS TOXANDRA GEN. ET SP. NOV., A MID-CRETACEOUS FOSSIL FLOWER WITH HORSESHOE-SHAPED ANTHERS

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ABSTRACT

The fossil flower described here as **Thymolepis toxandra** is from amber deposits in Myanmar which have been dated as ca. 100 Ma. The perianth consists of 12 tepals of varying size and shape, arranged in decussate pairs at the summit of an obconic floral cup. The epidermis of some of the tepals is densely papillate-secretory. The flower is bisexual, the androecium consisting of 2 stamens whose anthers are bisporangiate, hippocrepiform, and densely hirsute. The gynoecium is visible only as a bilobed stigma or as the tips of two postgenitally fused styles, the remainder of the pistil(s) being hidden by the perianth and floral cup. It is suggested that the fossil may be an early representative of family Monimiaceae.

RESUMEN

La flor fósil descrita aquí como **Thymolepis toxandra** procede de los depósitos de ámbar de Birmania que han sido datados de ca. 100 Ma. El perianto consiste en 12 tépalos de tamaño y forma variados, dispuestos en pares decusados en el extremo de una copa floral obcónica. La epidermis de algunos tépalos es densamente papilosa y secretora. Las flores son bisexuales, el androceo consiste en 2 estambres cuyas anteras son bisporangiadas, hipocrepiformes, y densamente hirsutas. El gineceo es visible solo como un estigma bilobulado o como los extremos de dos estilos con fusión postgénita, el resto del pistilo(s) está oculto por el perianto y la copa floral. Se sugiere que el fósil puede ser un representante temprano de la familia Monimiaceae.

INTRODUCTION

Amber deposits in the Hukawng Valley of northwestern Myanmar are a well-known source of mid-Cretaceous plant and animal fossils, although access to the mines has recently become difficult due to civil unrest in the region (Sokol 2019). As detailed below, the deposits have been dated by both paleontological and radiometric methods, falling in a time period between the Lower Cretaceous Albian and the Upper Cretaceous Cenomanian stages (Cohen et al. 2013). Continuing studies of fossil flowers in Myanmar amber have led to the description of at least 20 new genera (Crepet et al. 2016; Poinar 2018b; Liu et al. 2018; Poinar & Chambers 2018; 2019 a, b, c; 2020 a, b). The phylogenetic connection most frequently cited for these recently described genera is the magnoliid order Laurales, although many of the fossils cannot readily be placed in a modern family or order.

In the flower described here as *Thymolepis toxandra*, the perianth consists of 12 unequally sized tepals arranged in what appear to be 6 decussate pairs (Figs. 2–4). The inner tepals are erect or folded in such a way that the reproductive parts of the flower are almost completely hidden (Fig. 4). The two exposed stamens are unusual in having densely hirsute, hippocrepiform anthers (Figs. 4–8). The apex of the gynoecium is visible as a V-shaped, bilobed stigma or perhaps the tips of two postgenitally fused styles (Figs. 4, 5, 9). The upper epidermis of the larger tepals is densely glandular with secretory papillae (Figs. 4, 5). Preserved next to the flower is a wasp (Hymenoptera: Apocrita), which is the subject of a separate paper (Poinar 2019). As discussed below, features of the perianth and androecium of *Thymolepis* are suggestive of a possible relationship with Monimiaceae sens. strict., a Lauralean family that today is best developed in the Southern Hemisphere (Renner et al. 2010). It has been proposed that Myanmar amber had its source in Gondwana in the Early Cretaceous and was carried to Southeast Asia via plate tectonics in conjunction with India (Poinar 2018a). A connection between *Thymolepis* and Monimiaceae would therefore not be out of place phytogeographically, despite the amber's current location in the Northern Hemisphere.

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MATERIALS AND METHODS

The principal amber mines in Myanmar yielding plant and animal fossils are at the Noije Bum 2001 Summit Site, located in the Hukawng Valley in Kachin Province. The amber was derived from the resin of members of the conifer family Araucariaceae (Poinar et al. 2007) and was secondarily redeposited in marine sediments. These deposits were first dated by Cruickshank and Ko (2003), using paleontological (ammonite) and palynological evidence to provide an age estimate of 97–110 Ma. Later, Shi et al. (2012) applied radiometric U-Pb dating methods to volcanic zircons in the sedimentary matrix, assigning an age of 98.79 ± 0.62 Ma, at the Albian/Cenomanian boundary.

Observations and photographs were made with a Nikon SMZ-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

Thymolepis K.L. Chambers & Poinar, **gen. nov.** Type species: *Thymolepis toxandra* K.L. Chambers & Poinar, sp. nov.

Flower bisexual, pedicellate, perigynous, perianth of 12 tepals arranged in 6 decussate pairs, the lowest two pairs small, elliptic-lanceolate, the next two pairs larger, obovate or oblong (Figs. 2, 3), the inner two pairs smaller, oblong or linear-lanceolate (Fig. 4), upper epidermis of the larger tepals with glandular-secretory papillae (Figs. 4, 5), stamens two, bilocular, locules hippocrepiform, hirsute (Figs. 6–8), filament and connective hirsute or puberulent (Figs. 6, 7), dehiscence probably by one continuous marginal slit, apex of gynoecium V-shaped, with two papillate stigmatic lobes, the lobes perhaps formed by postgenital lateral fusion of two styles, remainder of pistil(s) not visible, pollen unknown.

Thymolepis toxandra K.L. Chambers & Poinar, **sp. nov.** (**Figs. 1–9**). Type: MYANMAR (BURMA), Kachin Province: amber mine in the Hukawng Valley SW of Maingkhwan (26°20'N, 96°36'E), *unknown amber miner s.n.* (holotype: Accession number B-An-18, deposited in the Poinar Amber Collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

Pedicel ca. 3.7 mm long, flower ca. 4.3 mm long, 6.4 mm wide measured between tips of the largest spreading tepals, tepals of lower two pairs 1.8 mm long, 1.0 mm wide (Figs. 2, 3), tepals of next two pairs 3.0 mm long, 2.1 mm wide, uppermost tepals 2.0 mm, 1.2 mm wide (Fig. 4), anthers 0.6 mm long, 0.3 mm wide (Figs. 6, 7), stigmatic lobes or style tips 0.4 mm long, 0.2 mm wide (Fig. 9).

Etymology.—Genus name from the Greek "thymos," wart, and "lepis," scale, referring to the glandular-papillate epidermis of the tepals. Species name from the Greek "toxon," bow, and "andros," man, referring to the hippocrepiform anthers.

DISCUSSION

No complete description of the perianth or reproductive organs is possible, due to the crowded and somewhat contorted nature of the tepals (Figs. 2–4). Our best interpretation of tepal arrangement is as a series of decussate pairs of differing sizes. The innermost pairs of tepals effectively conceal all but the tip of the gynoecium. There are only two stamens, which form a pair on one side of the flower. If more stamens were present originally, they may have been removed by insect predation, as has been observed in some other Myanmar amber fossils. However, because there is no obvious damage to other parts of the *Thymolepis* flower, it is possible that only two stamens were present from the beginning. The gynoecium of the flower, other than its two-lobed stigma, is hidden by the perianth and floral cup (Figs. 3, 4). Efforts to visualize the structure of the flower, using micro-CT scanning techniques, were unsuccessful due to the decayed condition of the inner tissues. Fortunately, the exposed anthers and stigma display some distinctive features that allow comparison of the fossil with certain modern angiosperms, especially the Lauralean family Monimiaceae.

Anthers with hippocrepiform (horseshoe-shaped) locules like those of the fossil (Figs. 6–8) are known in a wide variety of angiosperm families, being common, *inter alii,* in Balanophoraceae, Gesneriaceae, Malvaceae,

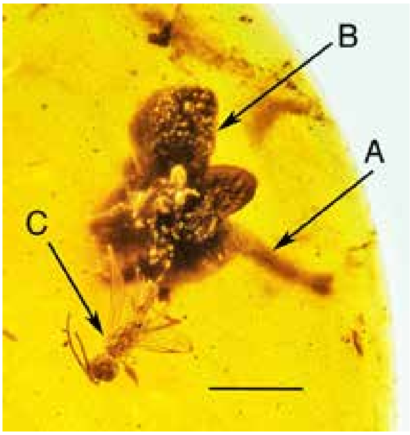

Fig. 1. ***Thymolepis toxandra*****. Original piece of amber containing the fossils. A. Pedicel. B. Flower. C. Wasp. Scale bar = 2.4 mm.**

Menispermaceae, and monotropoid Ericaceae (Endress & Stumpf 1990). Of special interest to this study, however, is the frequent occurrence of hippocrepiform anthers in many genera of Monimiaceae subfamily Mollinedioideae (Endress & Stumpf op. cit., table 2; Perkins & Gilg 1901; Philipson 1993). With respect to the perianth of Monimiaceae, in such genera as *Peumus* and *Hortonia*, which represent early-diverging clades in the Monimiaceae (Renner 2005, fig. 5), the tepals are numerous and spirally arranged (Perkins & Gilg 2001, figs. 1, 2). In *Mollinedia*, a genus with hippocrepiform anthers, staminate flowers may have a flat or cup-shaped receptacle with two pairs of well developed, decussate tepals, while pistillate flowers have a globose receptacle with 4 tiny tepals (Perkins & Gilg 1901, figs. 6, 7). In the related genus *Macropeplus*, the receptacle is cup-shaped in both staminate and pistillate flowers, with two pairs of well-developed, spreading tepals (Perkins & Gilg op. cit., fig. 5). In *Wilkiea* and *Austromathaea*, also with hippocrepiform anthers and with cup-shaped or globose receptacles in both sexes, the perianth consists

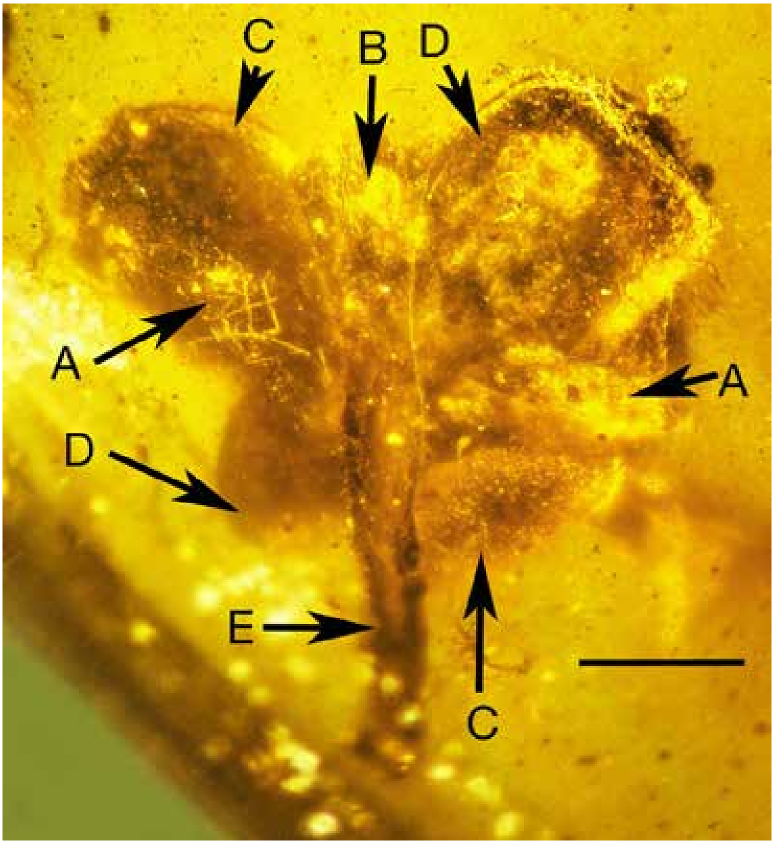

Fig. 2. ***Thymolepis toxandra*****. Flower in basal view. A. Members of the first pair of tepals. B. One member of the second pair of tepals, the other member being concealed by the pedicel. C. Members of the third pair of tepals. D. Members of the fourth pair of tepals. E. Pedicel. Scale bar = 2.0 mm.**

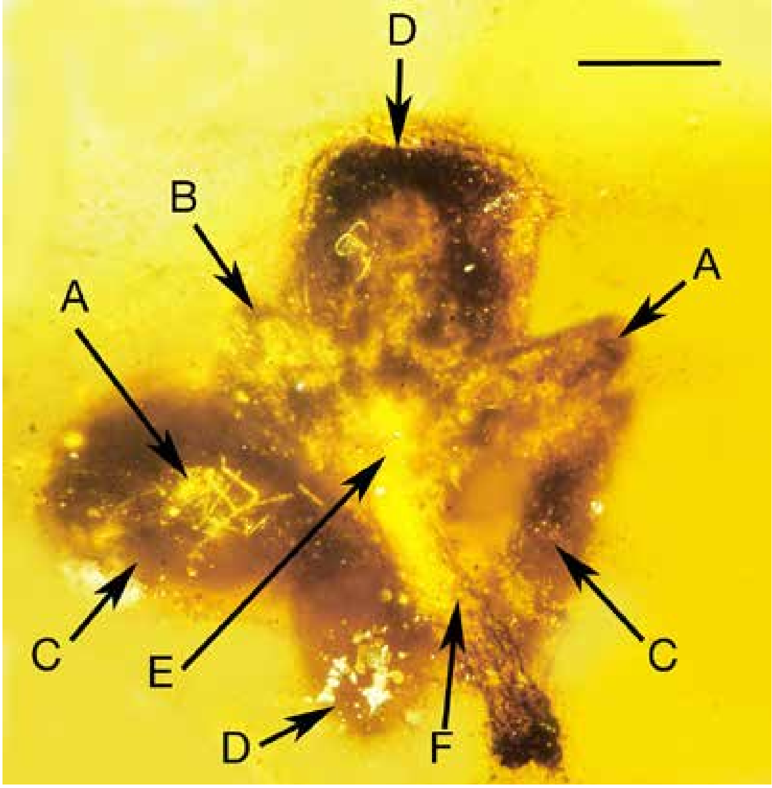

Fig. 3. ***Thymolepis toxandra*. Flower in basal view, at a lower focal level to emphasize the floral cup. A, B, C, D as in Fig. 2. E. Floral cup. F. Pedicel. Scale bar = 2.0 mm.**

of two pairs of tepals. Genera lacking hippocrepiform anthers but with a similar perianth of 4 small tepals include *Matthea*, *Steganthera*, and *Tetrasynandra*. From this brief review, *Thymolepis*, with its 6 pairs of perianth parts, appears to combine the larger number of tepals seen in *Peumus* and *Hortonia* with the paired, decussate condition of 4 tepals characterizing many genera of Mollinedioideae. The small number of stamens in *Thymolepis* would not be out of place in this subfamily, as there are only 4 stamens in the male flowers of *Anthobembix, Matthea, and Staganthera* (Perkins & Gilg 1901). Similarly, the low number of carpels in *Thymolepis* resembles the condition in *Hennecartia* and *Xymalos*, which have only one or two pistils in the female flowers (Perkins 1925).

The stigmatic lobes of the gynoecium in *Thymolepis* meet at an asymmetrical, V-shaped angle and are densely papillate (Figs. 4, 5, 9). Their form invites comparison with the pistillate flowers of *Mollinedia* and *Austromathaea* as discussed by Endress (1980, p. 87), where he describes the carpellary apices as “thick and contiguous, with the epidermal cells interlocking.” In his illustration of two adjacent styles joined laterally by interlocking epidermis (op. cit. fig. 50), he states that “carpellary apices (are) contiguous and secretory.” One might suggest, therefore, that the stigmatic lobes of *Thymolepis* are the contiguous tips of two laterally adherent styles and that their papillate surface has a secretory function as in *Austromathaea*. Endress and Igersheim (1997) provide a further discussion of stigmatic secretion in Monimiaceae, noting that when a hyperstigma is present in pistillate flowers (for example, in *Hennecartia*, *Kibara*, *Tambourissa*, and *Wilkiea*), there is a “plug of secretion through which pollen tubes grow down to the carpels, whose tips are also secretory. In other taxa only the carpels are connected by stigmatic secretion, or they may be postgenitally united in the receptive

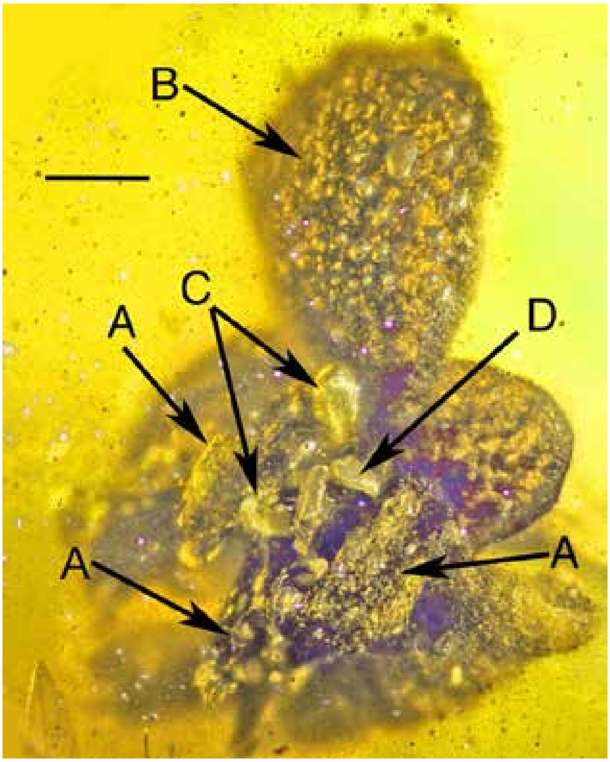

Fig. 4. *Thymolepis toxandra*. Flower in apical view. **A.** Three tepals of the 2 inner pairs. One tepal is reflexed and out of sight. **B.** Tepal with papillate epidermis. Note droplets showing the remains of glandular exudate. **C.** Stamens. **D.** Lobe of stigma. Scale bar = 1.2 mm.

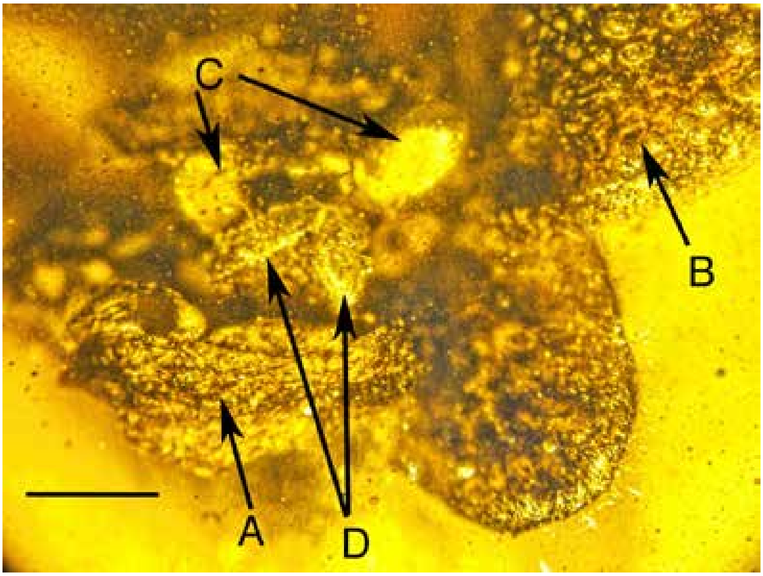

Fig. 5. *Thymolepis toxandra*. Close-up of floral apex. **A.** One of the two Innermost tepals. **B.** Tepal with secretory epidermal papillae. **C.** Stamens. **D.** Lobes of stigma. Scale bar = 0.7 mm.

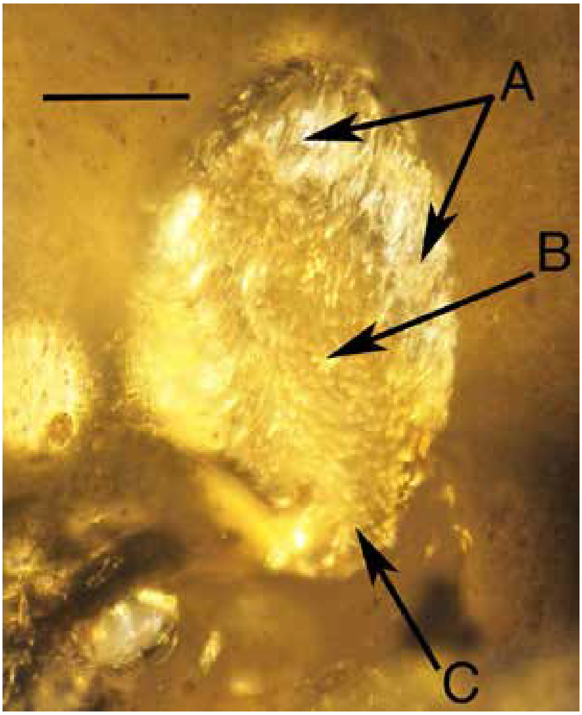

Fig. 6. *Thymolepis toxandra*. First stamen. **A.** Hippocrepiform locules of anther. **B.** Anther connective. **C.** Filament. Locule on the left is partly hidden by an inclusion in the amber. Scale bar = 0.2 mm.

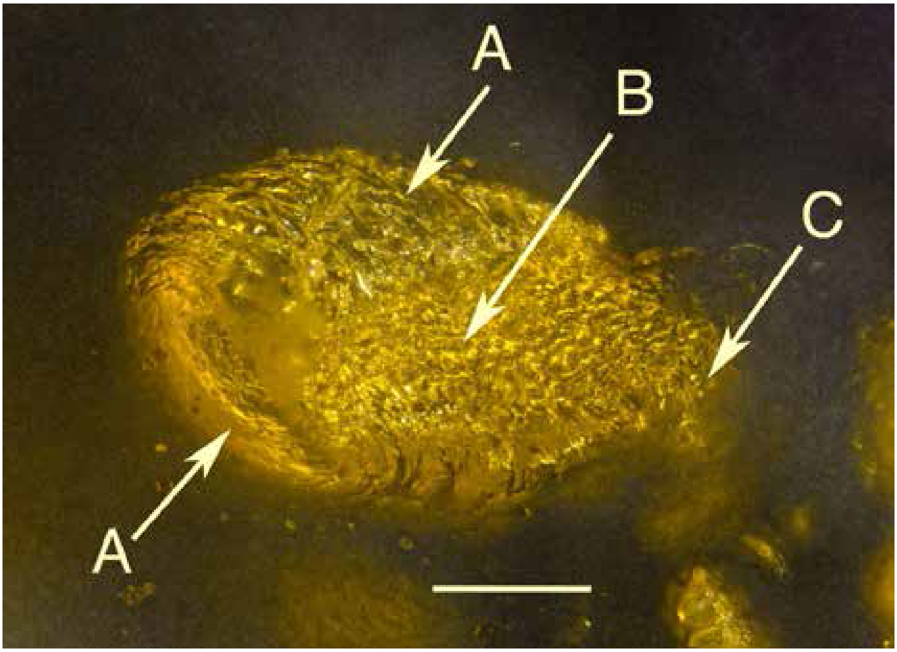

Fig. 7. *Thymolepis toxandra*. Second stamen. **A.** Anther locules. **B.** Anther connective. **C.** Filament. Scale bar = 0.2 mm.

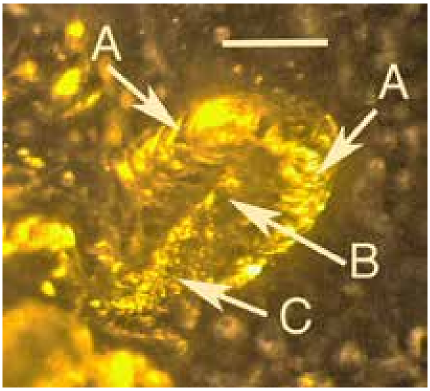

Fig. 8. *Thymolepis toxandra*. Second stamen, brightly illuminated to show hippocrepiform anther locules. **A.** Locules. **B.** Connective. **C.** Filament. Scale bar = 0.2 mm.

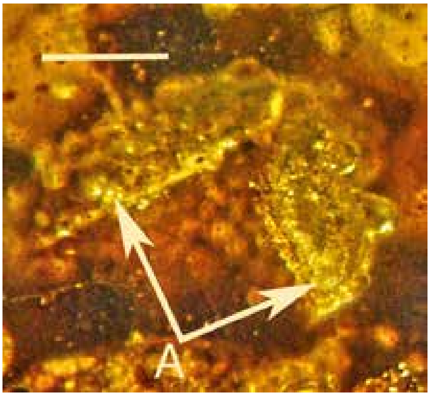

Fig. 9. *Thymolepis toxandra*. Apex of gynoecium at high magnification. **A.** Stigmatic lobes. Note single-celled secretory papillae along margins. Scale bar = 0.2 mm.

part. . . .” (op. cit., p. 133). As previously noted, the upper tepals in *Thymolepis* surround the pistil, leaving only the stigmatic lobes exposed. It may be that mucilaginous secretions from the stigma aided pollination of the otherwise concealed gynoecium (Fig. 9).

The papillae on the upper surface of the tepals were secretory, as is evident in figures 4 and 5 showing where droplets of exudate were preserved when the flower was first engulfed by resin 100 million years ago. The hirsute pubescence of the anthers in *Thymolepis* may be unique to the genus. The nearest approach to this condition that we have found in the literature on Monimiaceae are the hispidulous anthers of some species of *Steganthera* illustrated by Perkins (1925, figs. 23, 25), although the locules are transversely dehiscent rather than hippocrepiform in the taxa as pictured.

According to molecular phylogenetic studies (Renner 2004; Renner et al. 2010), *Peumus, Monimia, Palmeria,* and *Hortonia* belong to the 4 earliest-diverging clades in the Monimiaceae. Of these, only *Hortonia* has bisexual flowers, and none have hippocrepiform anthers. If the hypothesis is correct that *Thymolepis* is an early member of the Mollinedioideae clade, its age of 100 Ma is close to the time at which this line is proposed to have diverged from the *Hortonia* clade (100.1 Ma, Renner 2004; 82.95 Ma, Renner et al. 2010). Its bisexual flowers and hypanthium of more numerous and morphologically variable tepals differentiate *Thymolepis* from modern genera of the subfamily, which have evolved unisexual flowers and a small number of often much reduced tepals.

As noted by Friis et al. (2011, p. 244), flowers or other reproductive parts of Monimiaceae are unknown in the fossil record. The oldest fossils of the family used In the molecular clock studies of Renner et al. (2010) were woods from the Eastern Cape Province (87–83 Ma) and Cape Ross Island, Antarctica (83–71 Ma). Younger fossils included leaves from the Paleocene/Eocene boundary (ca. 57 Ma), from the Antarctic Peninsula, and Early Oligocene woods from Oman (34–28 Ma). If the morphological features of *Thymolepis* described above are true indicators of the proposed relationship, the fossil provides a glimpse into an early stage of floral evolution in mollinedioid Monimiaceae.

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REFERENCES

Cohen, K.M., S. Finney, & P.L. Gibbard. 2013. International Chronostratigraphic Chart. International Commission on Stratigraphy. www.stratigraphy.org

Crepet, W.L., K.C. Nixon, D. Grimaldi, & M. Riccio. 2016. A mosaic Lauralean flower from the Early Cretaceous of Myanmar. Amer. J. Bot. 103:290–297.

Cruickshank, R.D. & K. Ko. 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. J. Asian Earth Sci. 21:441–455.

Endress, P.K. 1980. Ontogeny, function and evolution of extreme floral construction in Monimiaceae. Pl. Syst. Evol. 134:79–120.

Endress, P.K. & A. Ingersheim. 1997. Gynoecium diversity and systematics of Laurales. Bot. J. Linn. Soc. 125:93–168.

Endress, P.K. & S. Stumpf. 1990. Non-tetrasporangiate stamens in the angiosperms: Structure, systematic distribution, and evolutionary aspects. Bot. Jahrb. Syst. 112:193–240.

Friis, E.M., P.R. Crane, & K.R. Pedersen. 2011. Early flowers and angiosperm evolution. Cambridge University Press, Cambridge, UK. 585 pp.

Liu, Z-J., D. Huang, C. Cai, & Z. Wang. 2018. The core eudicot boom registered in Myanmar amber. Scientific Reports 8:16765. www.nature.com/scientificreports

Perkins, J. 1925. Übersicht über die Gattungen der Monimiaceae. Wilhelm Engelmann, Leipzig, Germany. 55 pp.

Perkins, J. & E. Gilg. 1901. Monimiaceae. In: A. Engler, ed. Das Pflanzenreich. Wilhelm Engelmann, Leipzig, Germany. IV. 101:1–122.

Philipson, W.R. 1993. Monimiaceae. In: K. Kubitzki, J.G. Rohwer, & V. Bittrich, eds. The families and genera of vascular plants. Springer-Verlag, Berlin, Germany. 2:426–437.

Poinar, G.O., Jr. 2018a. Burmese amber: Evidence of Gondwanan origin and Cretaceous dispersion. Hist. Biol. 2018:1–6.

Poinar, G.O., Jr. 2018b. Mid-Cretaceous angiosperm flowers in Myanmar amber. In: B. Welch & M. Wilkerson, eds. Recent advances in plant research, Nova Science Publishers, New York. Pp. 187–218.

Poinar, G.O., Jr. 2019. A new genus and species of wasp (Hymenoptera: Evanioidea: Praeaulacidae) associated with an angiosperm flower in Burmese amber. Palaeoentomol. 2:474–481.

Poinar, G.O., Jr. & K.L. Chambers. 2018. *Setitheca lativalva* gen. et sp. nov., a fossil flower of Laurales from mid-Cretaceous Myanmar amber. J. Bot. Res. Inst. Texas 12:643–653.

Poinar, G.O. Jr. & K.L. Chambers. 2019a. *Dispariflora robertae* gen. et sp. nov., a mid-Cretaceous flower of possible Lauralean affinity from Myanmar amber. J. Bot. Res. Inst. Texas 13:173–183.

Poinar, G.O., Jr. & K.L. Chambers. 2019b. *Strombothelya* gen. et sp. nov., a fossil angiosperm with two species in mid-Cretaceous Myanmar amber. J. Bot. Res. Inst. Texas 13:451–460.

Poinar, G.O., Jr. & K. L. Chambers. 2019c. *Zygadelphus aetheus* gen. et sp. nov., an unusual fossil flower from Mid-Cretaceous Myanmar amber. J. Bot. Res. Inst. Texas 13:467–473.

Poinar, G.O., Jr. & K.L. Chambers. 2020a. *Phantophlebia dicycle* gen. et sp. nov., a five-merous fossil flower in mid-Cretaceous Myanmar amber. J. Bot. Res. Inst. Texas 14:73–80.

Poinar, G.O., Jr. & K.L. Chambers. 2020b. *Dasykothon leptomiscus* gen. et sp. nov., a fossil flower of possible Lauralean affinity from Myanmar amber. J. Bot. Res. Inst. Texas 14:65–71.

Poinar, G.O., Jr., G.J.B. Lambert, & Y. Wu. 2007. Araucarian source of fossiliferous Burmese amber: Spectroscopic and anatomical evidence. J. Bot. Res. Inst. Texas 1:449–455.

Renner, S.S. 1999. Circumscription and phylogeny of the Laurales: Evidence from molecular and morphological data. Amer. J. Bot. 86:1301–1315.

Renner, S.S. 2004. Variation in diversity among Laurales, Early Cretaceous to Present. Biol. Skr. 55:441– 458.

Renner, S.S., J.S. Strijk, D. Strasberg, & C. Thébaud. 2010. Biogeography of the Monimiaceae (Laurales): A role for East Gondwana and long-distance dispersal, but not West Gondwana. J. Biogeog. 37:1227–1238.

Shi, G., D.A. Grimaldi, G.E. Harlow, J. Wang, M. Yang, W. Lei, Q. Li, & X. Li. 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Res. 37:155–163.

Sokol, J. 2019. Troubled treasure. Science 364:722–729.