

CYATHITEPALA PAPILLOSA GEN. ET SP. NOV., A MID-CRETACEOUS
FOSSIL FLOWER FROM MYANMAR AMBER WITH VALVATE ANTHERS

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ABSTRACT

Although partially damaged prior to its preservation in coniferous resin, the flower of *Cyathitepala papillosa* retains enough morphological features to justify its description as a new genus and species of fossil angiosperms. The perianth is incomplete, but there are at least 6 large outer tepals and numerous smaller, spirally arranged inner ones. The limbs of some of the larger tepals are cup-shaped and face abaxially, while the smaller inner tepals are flat or have adaxially folded margins. There is an inner series of erect, apically truncate tepals surrounding the stamens. The surfaces and margins of the tepals are densely papillate. There is a whorl of ca. 12 stamens with anthers that dehisce by two dorsally hinged valves. Nothing remains of the receptacle or pedicel of the flower, but the superior portion of the pistil is conic and bears two columnar, erect styles. The fossil is compared with three previously described fossil genera, *Setitheca*, *Zygadelphus*, and *Strombothelya*, which were suggested as having a possible relationship with certain families of order Laurales.

RESUMEN

A pesar del daño parcial anterior a su conservación en resina de coníferas, la flor de *Cyathitepala papillosa* retiene suficientes características morfológicas para justificar su descripción como un nuevo género y especie fósil de angiospermas. El perianto es incompleto, pero hay al menos 6 tépalos externos grandes y numerosos internos más pequeños, ordenados espiralmente. Los limbos de algunos de los tépalos más grandes son en forma de copa y miran abaxialmente, mientras los tépalos internos más pequeños son planos o tienen los márgenes doblados adaxialmente. Hay una serie interna de tépalos erectos, truncados apicalmente rodeando a los estambres. Las superficies y márgenes de los tépalos son densamente papilosos. Hay un verticilo de ca. 12 estambres con anteras cuya dehiscencia es por dos valvas que se abren dorsalmente. No hay restos del receptáculo o pedicelo de la flor, pero la porción superior del pistilo es cónica y lleva dos estilos erectos columnares. El fósil se compara con tres géneros de fósiles descritos previamente, *Setitheca*, *Zygadelphus*, y *Strombothelya*, que sugieren tener posibles relaciones con ciertas familias del orden Laurales.

INTRODUCTION

The fossil flower described here as *Cyathitepala papillosa* is a further addition to the some 19 new genera of angiosperms previously described from Myanmar amber (details in Liu et al. 2018; Poinar 2018; Poinar & Chambers 2020b). The floral morphology of this selection of mid-Cretaceous fossil taxa is quite diverse, including both spiral and whorled perianths, petaliferous and apetalous forms, bisexual and unisexual flowers, few to many stamens, anthers with longitudinal, valvate, or hippocrepiform dehiscence, pistils with inferior, half-inferior, or superior ovaries, arcuate or erect styles, terminal or decurrent stigmas, and mono-, di-, or tricolpate (porate) pollen. The epidermis of the stamens and/or tepals in several fossils is densely papillate (*Setitheca*, Poinar & Chambers 2018; *Zygadelphus*, Poinar & Chambers 2019b; *Dasykothon*, Poinar & Chambers 2020a; *Phantophlebia*, Poinar & Chambers 2020b). In *Thymolepis* (Chambers & Poinar 2020), the tepal epidermis is papillate-glandular, with the remains of exudate droplets preserved in the amber from the time when the flower first fell into tree resin.

The flower of *Cyathitepala* was damaged on one side before preservation, but the remaining tepals show that the perianth consists of numerous spirally arranged parts, gradually decreasing in size inwards from the base. Some of the basal ones are spreading and cupulate, the others are flat or with in-folded margins (Figs. 1, 2). The epidermis of all the tepals is densely papillate (Fig. 3). Tepals of the innermost series are erect, truncate, and have imbricate margins (Fig. 3). Although the androecium is partly obscured by air bubbles in the amber, there appear to be ca. 12 stamens in a central whorl (Fig. 5). Dehiscence of the anthers is by two dorsally hinged

valves, strongly resembling in this respect the anthers of *Setitheca* (Poinar & Chambers 2018) but with a papillate, rather than bristly, epidermis (Figs. 5, 6). Anthers with similar valvate dehiscence and papillate epidermis also characterize *Zygadelphus* (Poinar & Chambers 2019b), which otherwise is quite different from *Cyathitepala* in its perianth and stamens.

Due to damage at the base of the flower, the pistil of *Cyathitepala* cannot be fully characterized. The remaining superior portion of the ovary, visible through the damaged side of the perianth, is conic and bears two erect, columnar styles (Fig. 4). A similar pistil was observed in the two described species of *Strombothelya* (Poinar & Chambers 2019a), but those fossils had either one style or a columnar style with 3 branches, and their pistils included an inferior portion, which may have been present in *Cyathitepala* but is now missing. No close relationship is implied between this new fossil and *Strombothelya*, since the latter genus has only a single whorl of sepals along with non-valvate anthers.

Among known fossil flowers in Myanmar amber, *Cyathitepala* appears to be most similar to *Setitheca*, whose valvate anthers and numerous, spirally arranged tepals were taken as evidence of a possible relationship to families of the basal angiosperm order Laurales (Poinar & Chambers 2018). Because our morphological description of the present flower is necessarily incomplete, it is not possible to suggest an assignment of *Cyathitepala* to any extant family of angiosperms.

MATERIALS AND METHODS

Angiosperm fossils from Myanmar are derived from well known amber mines in the Hukawng Valley, located in the northwest part of the country. The geology of the area that is currently being mined, which is known as the Noije Bum 2001 Summit Site, was described by Cruickshank and Ko (2003). The source of the amber was resin from trees of family Araucariaceae, perhaps the genus *Agathis* (Poinar et al. 2007). The amber, with its included fossils, was transported into a nearshore marine environment, whose sediments were later uplifted by tectonic activity to form the continental deposits at Noije Bum. Cruickshank and Ko (op. cit.) dated the amber as Late Albian, 97–110 Ma, based on paleontological and palynological evidence. More recently, Shi et al. (2012) determined the age to be 98.79 ± 0.62 Ma, utilizing U–Pb dating of zircons in volcanic clasts contemporary with the amber. The term mid-Cretaceous can be applied to this time period, which is transitional between the latest Albian and earliest Cenomanian series (Cohen et al. 2013).

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. In some of the figures, background details were removed to improve the image.

DESCRIPTION

***Cyathitepala* Poinar & K.L. Chambers, gen. nov.** TYPE SPECIES: *Cyathitepala papillosa* Poinar & K.L. Chambers, sp. nov.

Flower bisexual, pedicel and receptacle unknown, perianth of numerous, spirally arranged tepals, outermost tepal enlarged, plane, broadly elliptic (Fig. 1), other basal tepals spatulate, the cupped limb directed abaxially (Fig. 4), inner tepals gradually reduced in size, the larger ones spatulate with adaxially folded margins (Figs. 1, 4), innermost tepals short, erect, apically truncate, with imbricate margins (Figs. 1, 2), stamens ca. 12, whorled (Fig. 5), filaments narrowly cylindrical, anthers oblong-ovoid, dehiscing by two dorsally hinged valves (Figs. 2, 6), inferior portion of the pistil, if any, missing from the fossil, superior portion conical, styles two, erect, columnar (Fig. 4), pollen unknown.

***Cyathitepala papillosa* Poinar & K.L. Chambers, sp. nov. (Figs. 1–6).** TYPE: MYANMAR (BURMA). Kachin Province: Noije Bum 2001 Summit Site amber mine in the Hukawng Valley SW of Maingkhwan, 26°20'N, 96°36'E, 2019, *unknown amber miner s.n.* (HOLOTYPE: Accession number B-An-17, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

Width of flower ca 2.75 mm, if largest outer tepal (Fig. 1) is equally matched on the damaged opposite side of the flower, largest remaining tepal 1.40 mm long, 1.30 mm wide, truncate tepals of inner whorl ca. 0.60 mm

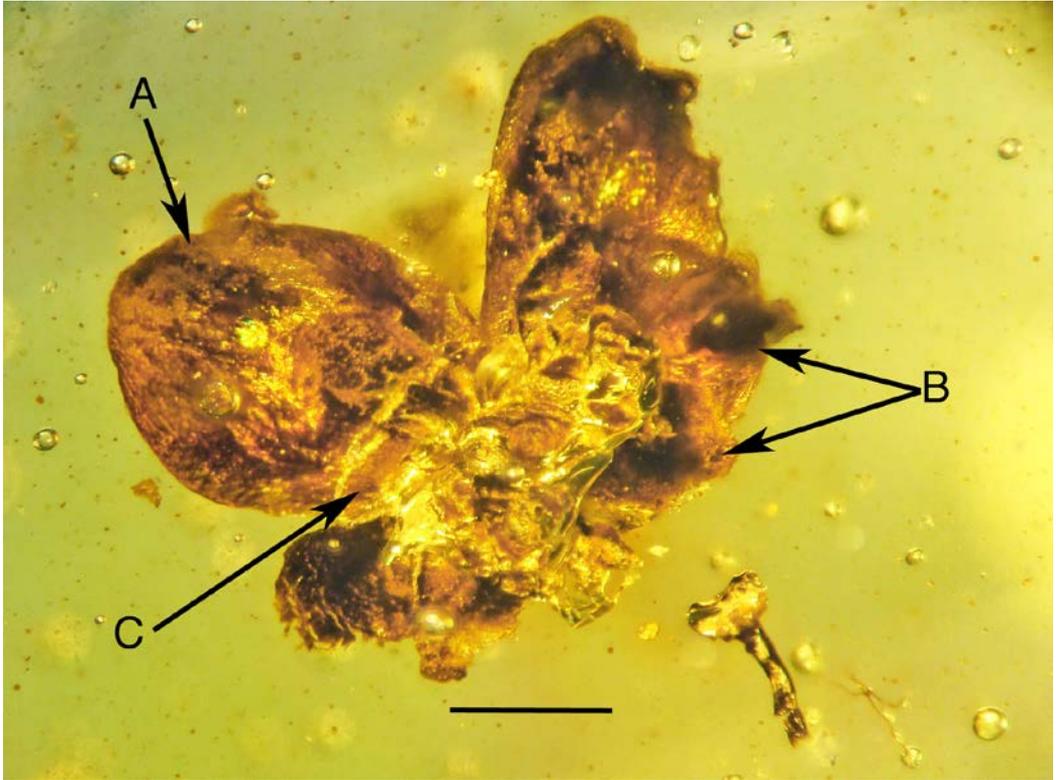


FIG. 1. *Cyathitepala papillosa*. Flower in apical view. A. Largest basal tepal. B. Tepals with inwardly folded margins. C. Erect, truncate inner tepal. Scale bar = 0.7 mm.

long, up to 0.40 mm wide (Fig. 2), stamen filaments ca. 0.18 mm long, anthers 0.20 long, 0.16 mm wide (Figs. 2, 6), superior portion of ovary 0.40 mm high, 0.60 mm wide, styles ca. 0.30 mm long (Fig. 4).

Etymology.—Genus name from the Latin “cyathus,” cup, ladle, and the botanical term “tepal,” referring to the shape of the outer tepals. Species epithet from the Latin “papilla,” bud, nipple, from the papillate epidermis of the tepals.

DISCUSSION

Although the flower of *Cyathitepala papillosa*, as preserved, is incomplete, the perianth is seen to consist of spirally arranged and variably shaped tepals, which decrease in size upward from the base (i.e., from the outer to the inner, in apical view). When dealing with fossil representatives of early-day angiosperms, it might be asked whether a spirally arranged perianth is more “primitive,” i.e., more like the ancestral type, than the whorled arrangement seen in most so-called “advanced” modern types. This question was specifically addressed by Endress and Doyle (2007) in a cladistic analysis of the perianth and androecium in 9 major groups of present-day basal angiosperms. These authors concluded that “(t)he most parsimonious ancestral state for floral phyllotaxis in angiosperms is equivocal, either spiral or whorled. ...” In our studies of flowers from mid-Cretaceous Myanmar amber, the perianth has usually consisted of one or two whorls of tepals (e.g., *Lachnociona*, Poinar & Chambers 2018c; *Strombothelya*, Poinar & Chambers 2019a; *Tropidogyne*, Poinar & Chambers 2019b; *Phantophlebia*, Poinar & Chambers 2020b). Previous examples of spiral arrangement have been *Endobeuthos*, with many \pm equal tepals (Poinar & Chambers 2018a), *Setitheca* (Poinar & Chambers 2018b), and *Zygadelphus* (Poinar & Chambers 2019c), the latter two having 10–12 tepals which increase in size

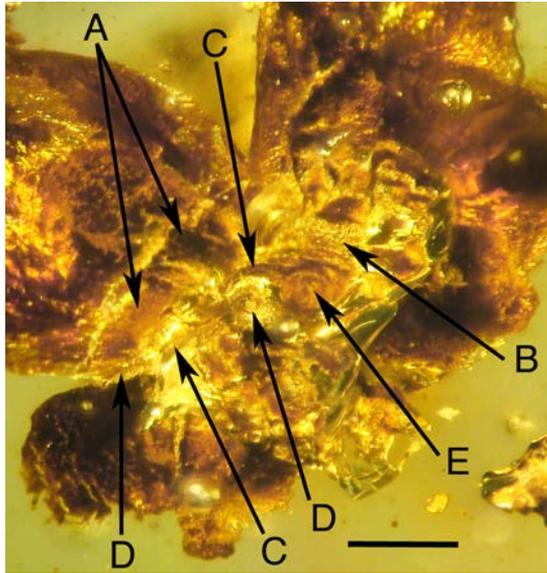


FIG. 2. *Cyathitepala papillosa*. Flower in apical view. A. Erect, truncate inner tepals. Note papillate apex. B. Bent-over inner tepal. Note papillate dorsal epidermis. C. Stamen filaments. D. Anthers with introrse dehiscence. E. Anther with extrorse dehiscence. Scale bar = 0.35 mm.

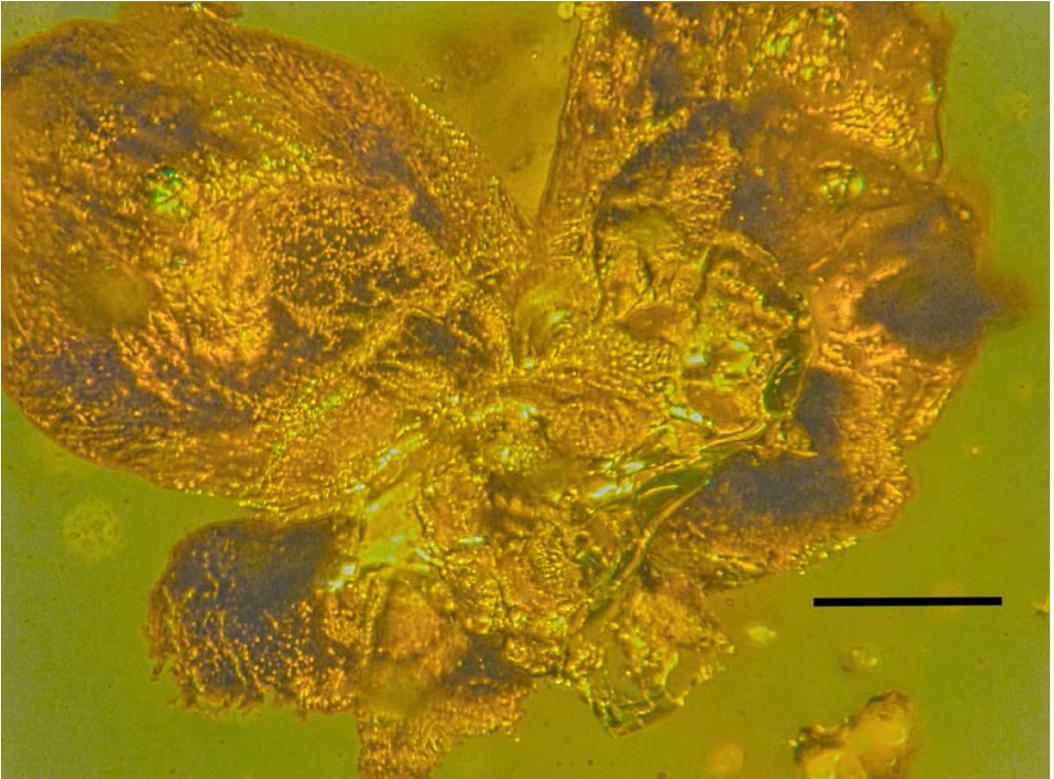


FIG. 3. *Cyathitepala papillosa*. Flower in apical view, with lighting modified to show papillate epidermis of tepals and anthers. Scale bar = 0.4 mm.

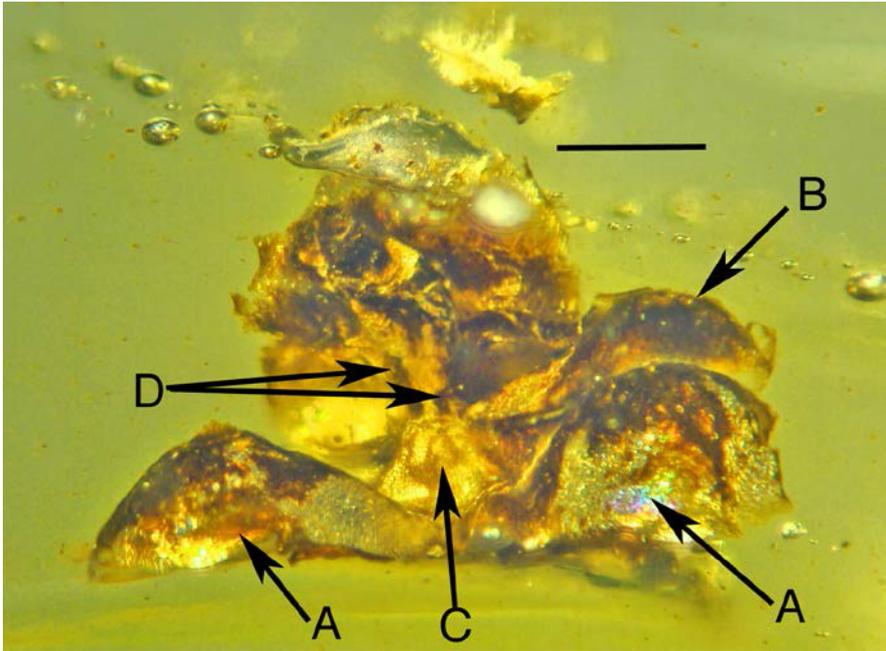


FIG. 4. *Cyathitepala papillosa*. Flower in lateral view. A. Abaxially cupped tepals. B. Tepal with adaxially folded margins. C. Conical upper portion of pistil. D. Styles. Scale bar = 0.4 mm.

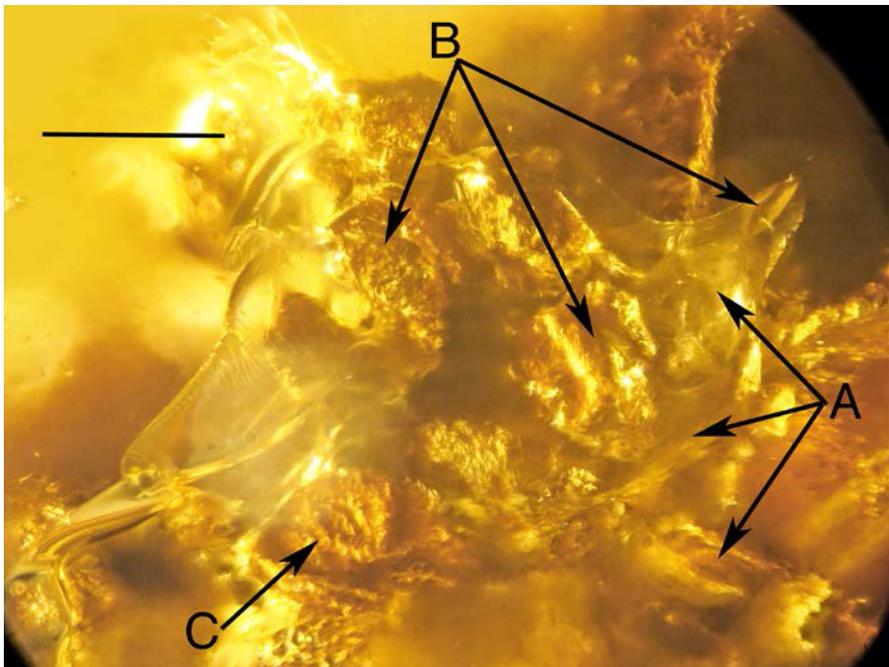


FIG. 5. *Cyathitepala papillosa*. Apical view of stamens. A. Filament. B. Adaxially dehiscent anthers. C. Valve of abaxially dehiscent anther (see also Fig. 6). Scale bar = 0.2 mm.

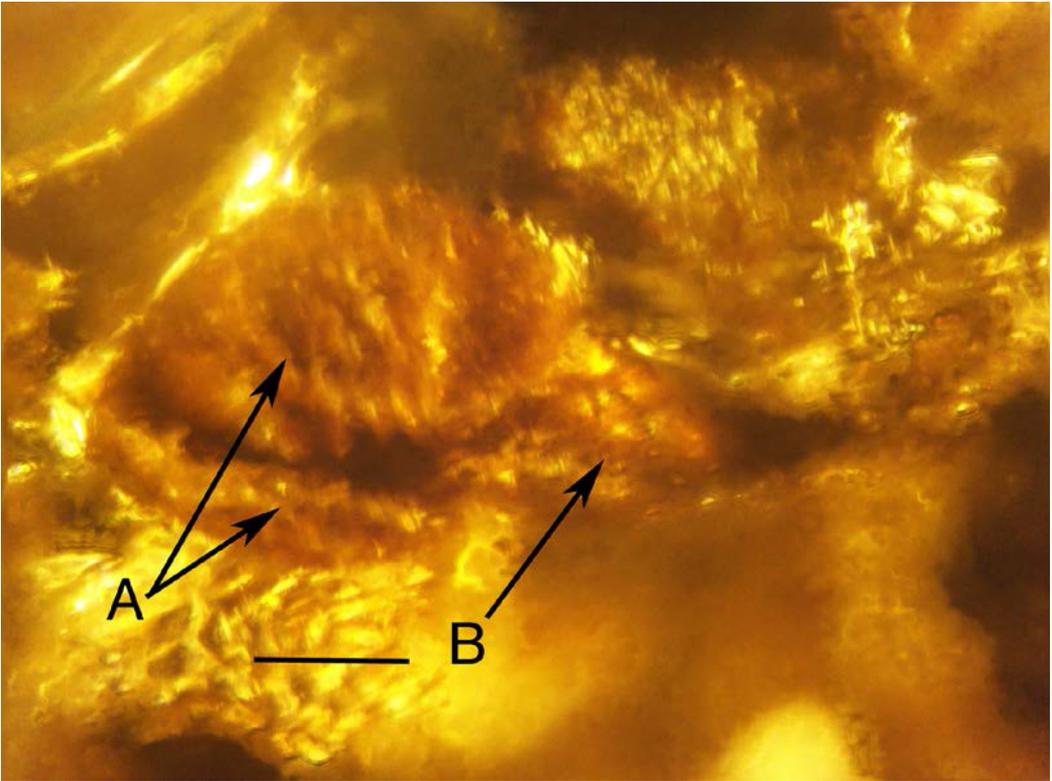


FIG. 6. *Cyathitepala papillosa*. Enlarged view of stamen with abaxially dehiscent anther. **A.** Anther valves. Note papillate epidermis. **B.** Filament. Scale bar = 80 μm .

inwardly from the base. The spiral arrangement in *Cyathitepala* thus differs from previously known examples in that the outer or basal tepals are the largest ones.

In discussing the possible phylogenetic relationships of *Setitheca* (Poinar & Chambers 2018b), the dorsally hinged anthers of the genus, which are like those of *Cyathitepala*, were compared with various members of the basal angiosperm order Laurales. This order is an attractive choice for such a comparison, because fossils from both the Early and Late Cretaceous have been attributed to it (Friis et al. 2011, pp. 484–485). Anthers that dehisce by valves are common in the Laurales (Perkins & Gilg 1901; Philipson 1993; Renner 2004). Anthers of the family Lauraceae are characterized by two or four apically hinged valves (Rohwer 1993), while in Atherospermataceae, Gormortegaceae, Siparunaceae, and two genera of Hernandiaceae there are just two apically hinged valves (Renner 2004). Only in *Monimia amplexicaulis* of the Monimiaceae (Lorence 1985, figs. 13, 21) and *Hernandia* and *Illigera* of the Hernandiaceae (Kubitzki 1993; Endress & Hufford 1989, figs. 128, 129) are the anther valves dorsally hinged as they are in *Setitheca* and *Cyathitepala*. With respect to the perianth, members of Laurales most often have one or two whorls of tepals or the tepals occur as decussate pairs (Perkins & Gilg 1901; Philipson 1993; Chambers & Poinar 2020), but in *Hortonia*, which represents an early-diverging clade of family Monimiaceae (Renner 2004; Renner et al. 2010), there are up to 18 tepals. The basal four tepals form two small, decussate pairs and the remaining 14 are larger and spirally arranged (Endress 1980, fig. 1). The anthers of *Hortonia* are 4-loculed and dehisce by longitudinal slits (Endress op. cit.), and they therefore are not comparable with *Cyathitepala* or *Setitheca*.

In *Setitheca*, a close examination of the stamens (as illustrated in fig. 1 of Poinar & Chambers 2018b)

shows that the direction of anther dehiscence is introrse, a fact not noted in the genus description (other than to say that the anther valves are dorsally hinged). In *Cyathitepala*, on the other hand, anther dehiscence appears to be both introrse and extrorse (Figs. 2, 5, and 6), assuming that the stamens were not twisted or displaced during the process of floral preservation. This is a parallel, of sorts, to modern genera of Lauraceae, in which anther dehiscence is typically introrse in the outer whorl of stamens and extrorse in the two inner whorls (Rohwer 1993).

Without more complete information on the gynoecium and perianth of *Cyathitepala*, it is not possible to go further in suggesting a relationship of the genus to any modern group of angiosperms.

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