ZYGADELPHUS AETHEUS GEN. ET SP. NOV., AN UNUSUAL FOSSIL FLOWER FROM MID-CRETACEOUS MYANMAR AMBER

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ABSTRACT

The flower described here as **Zygadelphus aetheus** gen. et sp. nov. was obtained from amber mines in Myanmar, preserved in marine sedimentary deposits dating to the mid-Cretaceous Period, ca. 99 My in age. The perianth consists of ca. 10 spirally arranged tepals that vary in size and shape. The stigmatic tips of two styles are visible, the remainder of the gynoecium being hidden from view by the crowding of stamens and perianth parts toward the center of the flower. There is a whorl of 4 stamens, the anthers of which have the feature, probably unique among angiosperms, of possessing a small but complete accessory stamen arising as an appendage on their dorsal surface. Anthers of both types of stamens are bilocular and dehisce by dorsally hinged valves. Presence of pollen in the accessory anthers indicates that they functioned in reproduction. Under the assumption that the fossil is not merely a teratological mutant in an otherwise normal-flowered species, it is here given taxonomic status as representing a peculiar type of floral development, now extinct, that existed during an earlier stage of angiosperm evolution.

RESUMEN

La flor que se describe aquí como **Zygadelphus aetheus** gen. et sp. nov. se obtuvo de las minas de ámbar de Myanmar, preservado en depósitos sedimentarios marinos que datan del Cretácico medio, hace ca. 99 millones de años. El perianto consiste en ca. 10 tépalos dispuestos espiralmente que varían en tamaño y forma. Son visibles los extremos estigmáticos de dos estilos, el resto del gineceo está escondido por la acumulación de estambres y partes del perianto hacia el centro de la flor. Hay un verticilo de 4 estambres, cuyas anteras tienen la característica, probablemente única entre las angiospermas, de poseer un pequeño pero completo estambre accesorio surgiendo como un apéndice en su superficie dorsal. Las anteras de ambos tipos de estambres son biloculares y dehiscentes por valvas giradas. La presencia de polen en las anteras accesorias indica que son funcionales en la reproducción. Bajo la asunción de que el fósil no es meramente un mutante teratológico de otra especie de flores normales, se le da aquí un estatus taxonómico como representante de un tipo peculiar de desarrollo floral, ahora extinto, que existió durante un estadio anterior de la evolución de las angiospermas.

INTRODUCTION

Among the 17 new genera of fossil flowers we have described from mid-Cretaceous Myanmar amber (listed in Poinar 2018b; Poinar & Chambers 2018c, 2019a, b, c), examples of unusual or abnormal morphological characteristics have sometimes been found. A case in point is *Endobeuthos paleosum* (Poinar & Chambers 2018a), in which the stamens have a thick anther connective and a single, lateral, bisporangiate theca. Another example is the presence of greatly enlarged, leaf-like sepals in *Dispariflora robertae* (Poinar & Chambers 2019a). In both taxa, several such flowers were present in the amber, and the traits were judged to be characteristic of the fossil species as a whole. In other cases, single flowers were found that possessed a peculiar structural trait which we assumed was not typical of the entire species. Examples of this are the two abnormally juxtaposed sepals and one aborted stamen in the hermaphrodite flower of *Lachnociona camptostylus* (Poinar & Chambers 2018b), the two sepal-like staminodes in the pistillate flower of *Tropidogyne lobodisca* (Poinar & Chambers 2019c), and the one flower out of 7 in *Tropidogyne pentaptera* (Poinar & Chambers 2017) that had 6 rather than 5 sepals.

In *Zygadelphus aetheus,* it is difficult to interpret the peculiar and seemingly abnormal development of what might be termed "piggyback" stamens on the anthers of the primary stamens. One possibility is that the flower resulted from a unique teratological mutation. However, because the accessory stamens are reproductively functional and are present on all the primary stamens, they are here taken to be a normal feature of the fossil taxon and worthy of being described taxonomically. How this type of androecium might have benefitted the reproductive adaptations of the species is difficult to imagine. The species seems to exemplify a unique but

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ultimately unsuccessful form of development, which arose at an early stage in angiosperm floral evolution.

As discussed below, the phylogenetic connections of the genus may be with lauralean members of Class Magnoliidae. Anthers opening by two valves are characteristic of various genera in families such as Atherospermataceae, Hernandiaceae, and Gomortegaceae (Renner 1999). We have previously described *Setitheca,* a Myanmar amber fossil with unequal, spirally arranged tepals and anthers with two dorsally-hinged valves (Poinar & Chambers 2018b), which we assigned to Order Laurales. Although at least two styles appear to be present in *Zygadelphus,* nothing is known about other characteristics of the gynoecium which might help to align the fossil with a modern family.

MATERIALS AND METHODS

This fossil, like the others that have been described from Myanmar amber (see above), comes from mines at the Noije Bum 2001 Summit Site in the Hukawng Valley, Kachin Province. The amber originated as the resin of araucarian trees, perhaps of the genus *Agathis* (Poinar et al. 2007). By stream erosion from its source in terrestrial forests, it was secondarily deposited in off-shore sediments. Later tectonic elevation of the deposits made them available for modern-day mining activities. Based on marine paleontological (ammonite) and palynological evidence, Cruickshank & Ko (2003) dated the site to the late Albian Period, placing the age at 97–110 Ma. A more recent study (Shi et al. 2012) utilized U–Pb dating of zircons in volcanic clasts to determine a more exact age of 98.79 ± 0.62 Ma, at the Albian/Cenomanian boundary. As a result of its marine redeposition, the amber may be considerably older than the dated sediments in which it is found today.

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 photos for better clarity and depth of field. In some of the figures, background details were removed to improve the image.

DESCRIPTION

Zygadelphus Poinar & K.L. Chambers, **gen. nov.** Type Species: *Zygadelphus aetheus* Poinar & K.L. Chambers, sp. nov.

Flower apparently bisexual, pedicellate, pedicel bearing a small bract below the flower (Fig. 1), receptacle shallowly cup-shaped, perianth of ca. 10 unequal, spirally arranged tepals, tepals mostly ascending or erect, varying from ovate to lanceolate, oblanceolate, or, if spatulate, having a round or oval, thin-textured limb and a linear, thickened claw, the tepal margins entire or irregularly lacerate (Figs. 1, 2, 3), primary stamens 4, filaments linear (Fig. 4), possibly with a pair of pebbly-surfaced basal appendages (not illustrated), anthers bilocular with valvate dehiscence, valves dorsally hinged, surface pebbly (Figs. 3, 6), terminal appendage 0, accessory stamens with a short filament and ovoid, bilocular anther, the filament and dorsally hinged anther valves having a pebbly surface (Figs. 3, 5, 6), pollen grains present in open locules (Fig. 6), gynoecium visible only as the stigmatic tips of two styles (Fig. 6).

Zygadelphus aetheus Poinar & K.L. Chambers, **sp. nov.** (**Figs. 1–6**). Type: MYANMAR (BURMA). Kachin: amber mine in the Hukawng Valley SW of Maingkhwan, 26°20'N, 96°36'E. 2018, *unknown amber miner s.n.* (holotype: Catalogue number B-An-14, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

Pedicel ca. 1.75 mm long, glabrous below, lightly strigose distally (Fig. 1), receptacle 0.8 mm wide, tepals varying from 0.75–2 mm long, spatulate tepals with limb 1.2–1.5 mm wide, claw 0.5 mm long (Figs. 1, 2), primary stamens with filaments 0.45–0.56 mm long (Fig. 4), primary anther 0.3 mm long, 0.16 mm wide, accessory stamens with filaments 0.32 mm long, anthers 0.28 mm long, 0.17 mm wide (Fig. 3), epidermis of anthers and filaments pebbly (Figs. 3, 6).

Etymology.—Genus name from the Greek "zygos," yoke, and "adelphos," twin, brother, referring to the attachment of one stamen to the anther of another. Species name from the Greek "aethes," unusual, strange, referring to the unusual form of androecium.

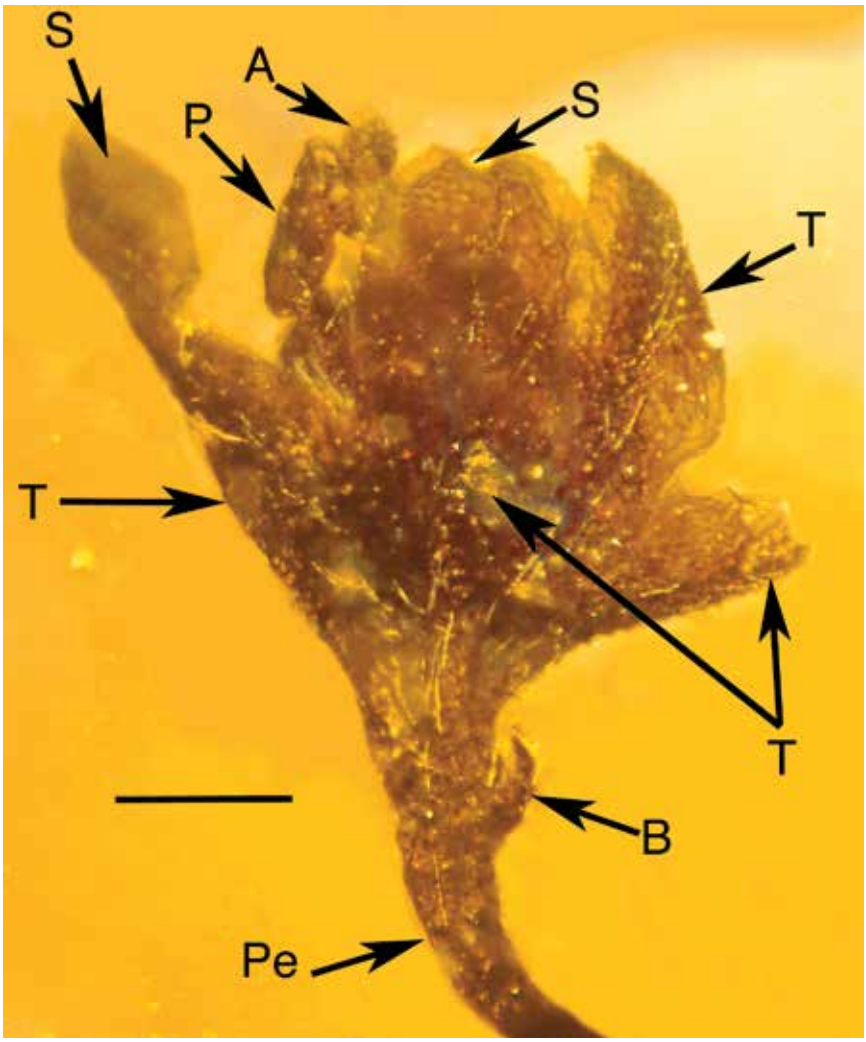

Fig. 1. ***Zygadelphus aetheus.*** **Flower in lateral view. A. Anther of accessory stamen. B. Bract. P. Anther of primary stamen (see also Fig. 4). Pe. Petiole. S. Spatulate tepals. T. Variously shaped tepals. Scale bar = 270 μm.**

DISCUSSION

The unique androecium of *Zygadelphus aetheus,* with a small accessory stamen present as a dorsal appendage on each of the primary anthers, is unknown among modern angiosperm as far as we can determine. In some other respects, the fossil shows similarities to *Setitheca lativalva,* a previously described flower from the same amber deposits (Poinar & Chambers 2018). Both taxa have a perianth of unequal, spirally arranged tepals, as well as stamens whose bilocular anthers dehisce by means of dorsally attached valves. In *Setitheca,* the one flower available for study was staminate, its central disc area showing no vestige of a pistil. Its large, conic, pubescent receptacle differs from the glabrous, shallowly cup-shaped one of *Zygadelphus,* and its perianth of 12 variably shaped, widely spreading tepals includes no spatulate types like those seen in the latter genus. Whether the flower of *Zygadelphus* is staminate or bisexual depends on the tentative identification of two style tips, barely showing among the incurved accessory stamens (Fig. 6). The 10 stamens of *Setitheca* have an

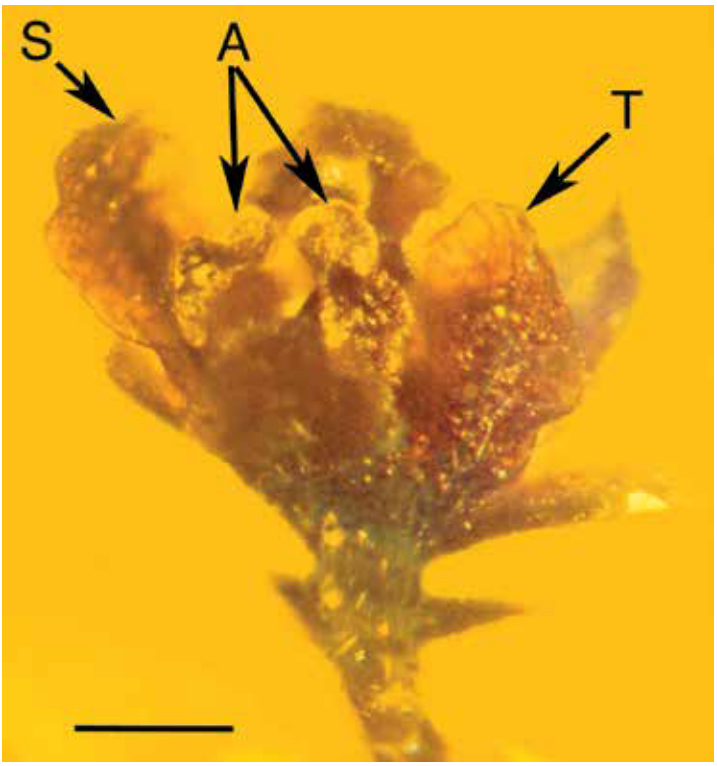

Fig. 2. *Zygadelphus aetheus.* Flower in lateral view. **A.** Anthers of accessory stamens. **S.** Spatulate tepal with thickened claw. **T.** Oblanceolate tepal. Scale bar = 550 μm.

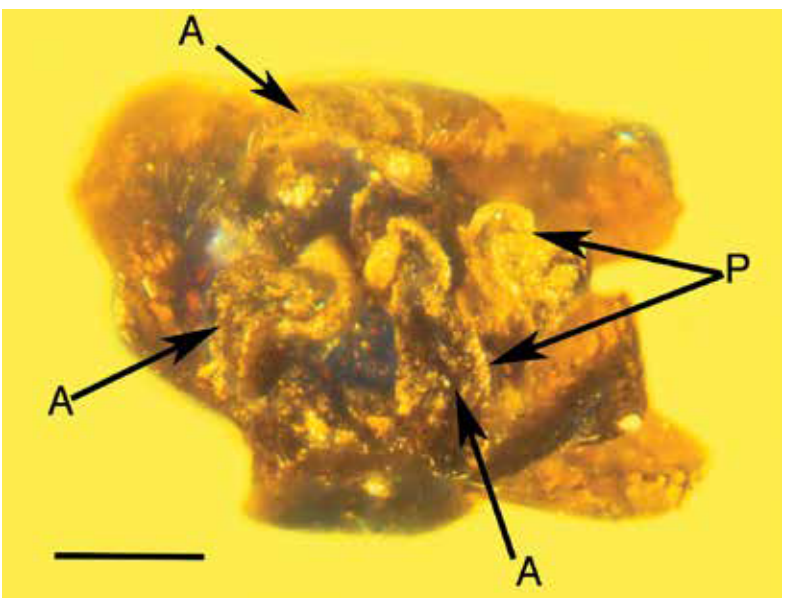

Fig. 3. *Zygadelphus aetheus.* Flower in top view. **A.** Anthers of primary stamens. **P.** Pebbly epidermis of primary and accessory anthers. Scale bar = 188 μm.

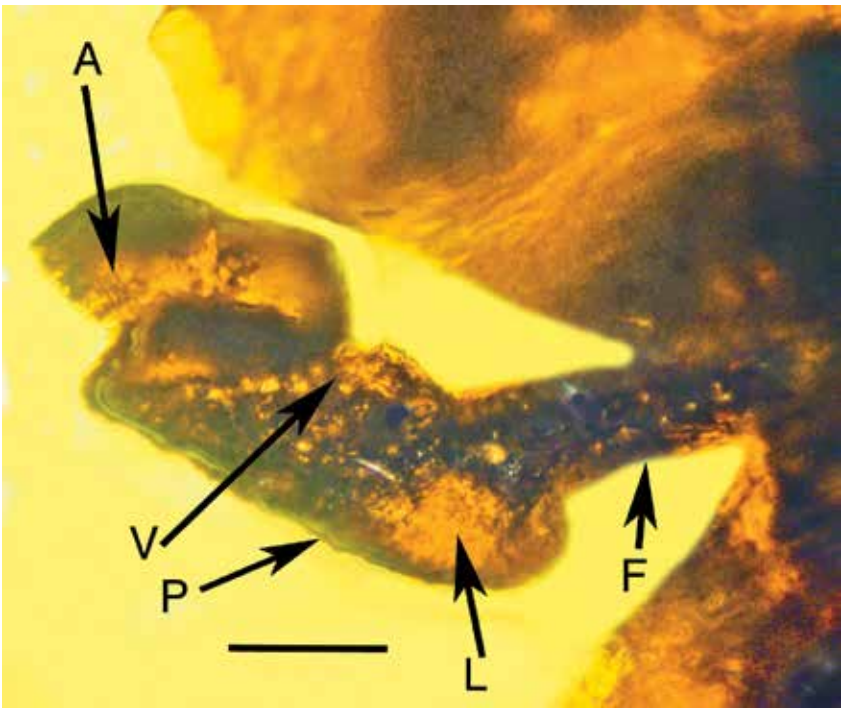

Fig. 4. *Zygadelphus aetheus.* Primary and accessory stamens. **A.** Anther of accessory stamen. **F.** Filament of primary stamen. **L.** Locule. **P.** Anther of primary stamen. **V.** Valve. Scale bar = 96 μm.

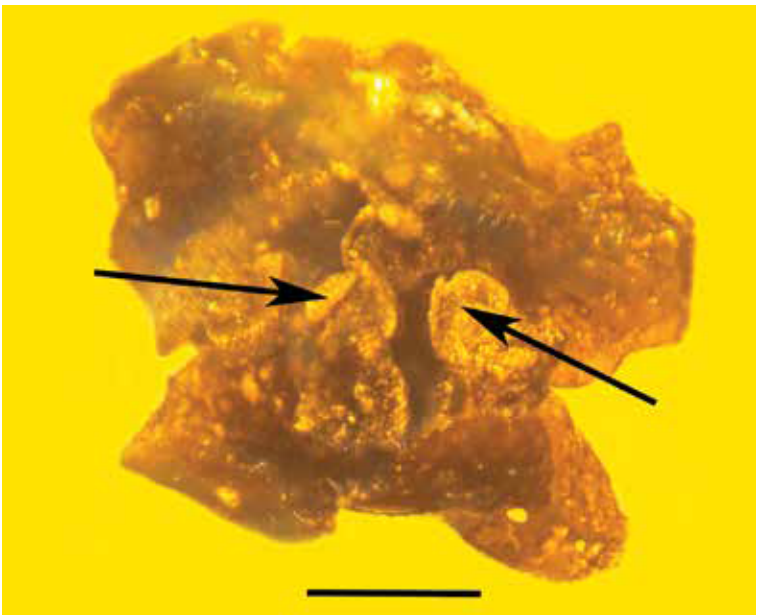

Fig. 5. *Zygadelphus aetheus.* Flower in top view. Arrows show 2 secondary anthers with open and closed valves. Note arrangement of tepals. Scale bar = 400 μm.

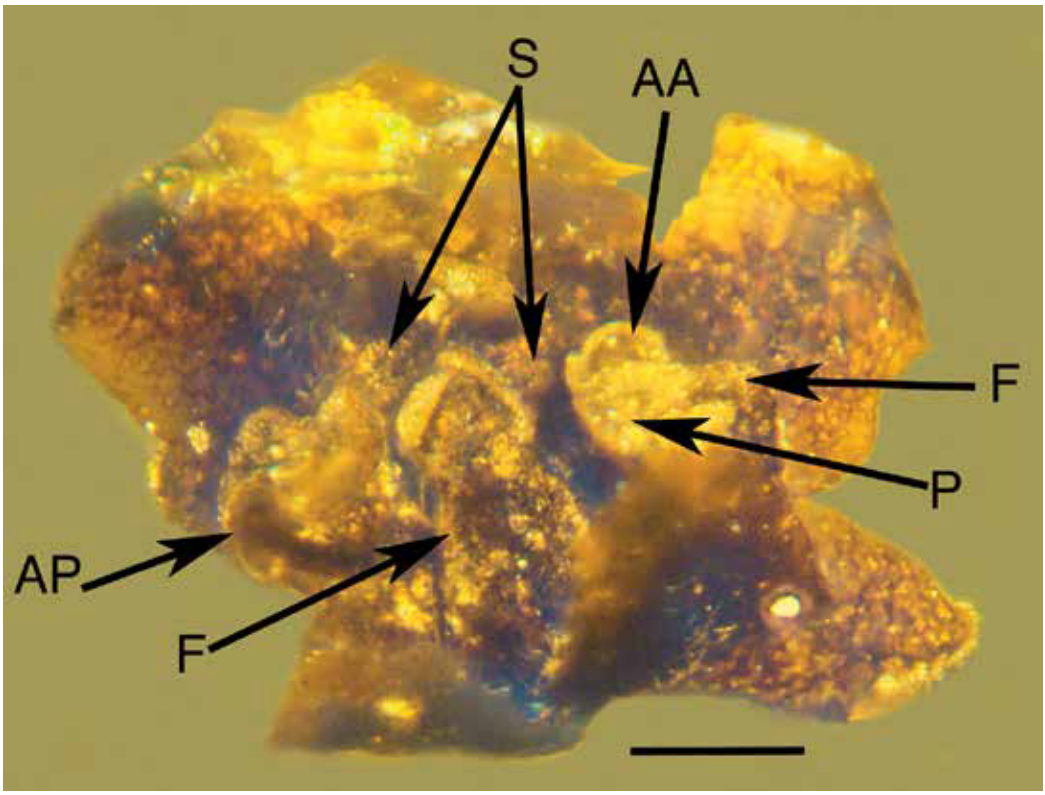

Fig. 6. *Zygadelphus aetheus.* Flower in top view. **AA.** Anther valve of accessory stamen. **AP.** Anther valve of primary stamen. **F.** Filaments of accessory stamens. **P.** Pollen. **S.** Tips of styles. Scale bar = 300 μm.

apiculate tip on the anther connective and lack the dorsally appended accessory stamens of the genus described here, but they resemble *Zygadelphus* in their mode of anther dehiscence (compare fig. 4 of Poinar & Chambers 2018, with figs. 4, 6). The two erect, thin-textured basal appendages on the filaments of *Setitheca* are unlike the tentatively-identified small, pebbly-surfaced appendages (not illustrated) in *Zygadelphus*.

Based on the totality of its floral characteristics, *Setitheca* was assigned a position in the magnoliid order Laurales, with affinities to such families as Atherospermataceae, Gomortegaceae, Hernandiaceae, and Monimiaceae (Perkins & Gilg 1901; Philipson 1993; Renner 1999; Renner & Chanderbali 2000). Like *Zygadelphus,* its polymerous perianth of spirally arranged, variously shaped tepals resembles that of *Hortonia angustifolia* (Monimiaceae) as illustrated by Endress (1980). The number of perianth parts is 18 in *Hortonia,* 12 in *Setitheca,* and ca. 10 in *Zygadelphus*. *Gomortega nitida* (Gomortegaceae), whose anthers bear two apically-hinged valves, also has a tepaloid perianth with an indefinite number of variably-shaped parts (Kubitzki 1993). Spatulate tepals with a narrow claw, like those in *Zygadelphus,* are not present in *Hortonia, Setitheca,* or *Gomortega*. Bilocular anthers with valvate dehiscence are common in Atherospermataceae, Gomortegaceae, and Hernandiaceae but rare in Lauraceae (Endress & Hufford 1989; Renner 1999). In most cases, the valves are hinged distally and open upward. However, two genera of Hernandiaceae, *Hernandia* and *Illigera,* have anthers like those of *Zygadelphus* (Figs. 3, 4, 6) and *Setitheca,* with dorsally attached valves which open laterally (Endress & Hufford 1989, figs. 128, 129; Renner 1999).

Features of the gynoecium of *Zygadelphus*, other than the papillate tips of two styles (Fig. 6), are unfortunately hidden by the upright perianth and inwardly curved accessory stamens. The stigmas, if correctly

interpreted, are in a position where they would have been thoroughly dusted by pollen from the accessory anthers. However, with only a single flower available for study, any speculation on the nature of the pistil(s) or of the species' reproductive system—whether by selfing or outcrossing, for example—is not warranted. The presence of an accessory set of stamens attached dorsally on the primary stamens is so unique, we believe, as to preclude the assignment of *Zygadelphus* to any modern family of angiosperms.

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