

Article

Paired Flowers of Core Eudicots Discovered from Mid-Cretaceous Myanmar Amber[†]

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Abstract

A pair of connected flowers preserved in a mid-Cretaceous (early Cenomanian) Myanmar amber is described and named *Antiquigemina pilosa* Wang and Li gen. et sp. nov. *Antiquigemina pilosa* has bisexual flowers with a calyx of at least 3 sepals, a corolla of 5 petals, a whorl of at least 4 stamens and a tricarpellate pistil with a semi-inferior ovary. The differences in style divergence and calyx presence between paired flowers indicate different developmental stages. Considering that differentiated calyx and corolla and pentamery of corolla are features frequently observed in core eudicots, we propose treating *Antiquigemina pilosa*, which has a pentamerous perianth and differentiated sepals and petals, as an earlier representative of core eudicots. *Antiquigemina pilosa* provides first-hand evidence for the early diversification of core eudicots.

Keywords: angiosperm; fossil flower; core eudicots; Myanmar amber; paired flowers



Academic Editor: Mathias Harzhauser

Received: 21 September 2025

Revised: 25 November 2025

Accepted: 3 December 2025

Published: 9 December 2025

Citation: Li, F.; Huang, W.; Wang, X. Paired Flowers of Core Eudicots Discovered from Mid-Cretaceous Myanmar Amber. *Taxonomy* **2025**, *5*, 67. <https://doi.org/10.3390/taxonomy5040067>

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1. Introduction

Core eudicots, characterized by pentamerous whorled flower parts, distinct sepals and petals, and tricolpate pollens [1], constitute a major part of the diversity of extant angiosperms. The earliest fossil records of core eudicots are found near the boundary of the Early Cretaceous and Late Cretaceous, indicating the radiation of core eudicots during that time [2–9]. These findings correspond with recent molecular estimates that revealed that core eudicots originated during the Barremian to Aptian, with most subordinate orders originating from that time to the Late Cretaceous [10–12]. However, owing to the relatively limited fossil records of early core eudicots, the details of this radiation remain elusive [2–9]. Flowers preserved within Myanmar ambers from the latest Albian–earliest Cenomanian offer a great chance for understanding the radiation of core eudicots. More than 30 species of fossil flowers have been described within Myanmar ambers, several of which have been identified as core eudicots [2–7].

In this work, we report a pair of flowers directly linked through their pedicels and a short stalk, preserved within amber from the Mid-Cretaceous. These flowers provide direct evidence indicating the early diversification of core eudicots.

2. Materials and Methods

The samples were collected from the Noije Bum 2001 Summit Site, Hukawng Valley, Kachin, Myanmar (26°20' N, 96°36' E) (Figure 1). The age of the sample is the earliest

Cenomanian, late Cretaceous (98.79 ± 0.62 Ma) according to the U–Pb dating of zircons [13]. The sample was immersed in oil and then photographed via a ZEISS Axio Zoom V16 stereomicroscope (Zeiss, Germany). The samples were scanned via a Zeiss Xradia 520 versa X-ray microscope (Zeiss, Germany) for micro-CT. The 3D reconstruction and virtual sections were generated via VGStudio MAX 3.0. Floral diagrams were illustrated, and all the figures are organized for publication in Adobe Illustrator CC 2015.

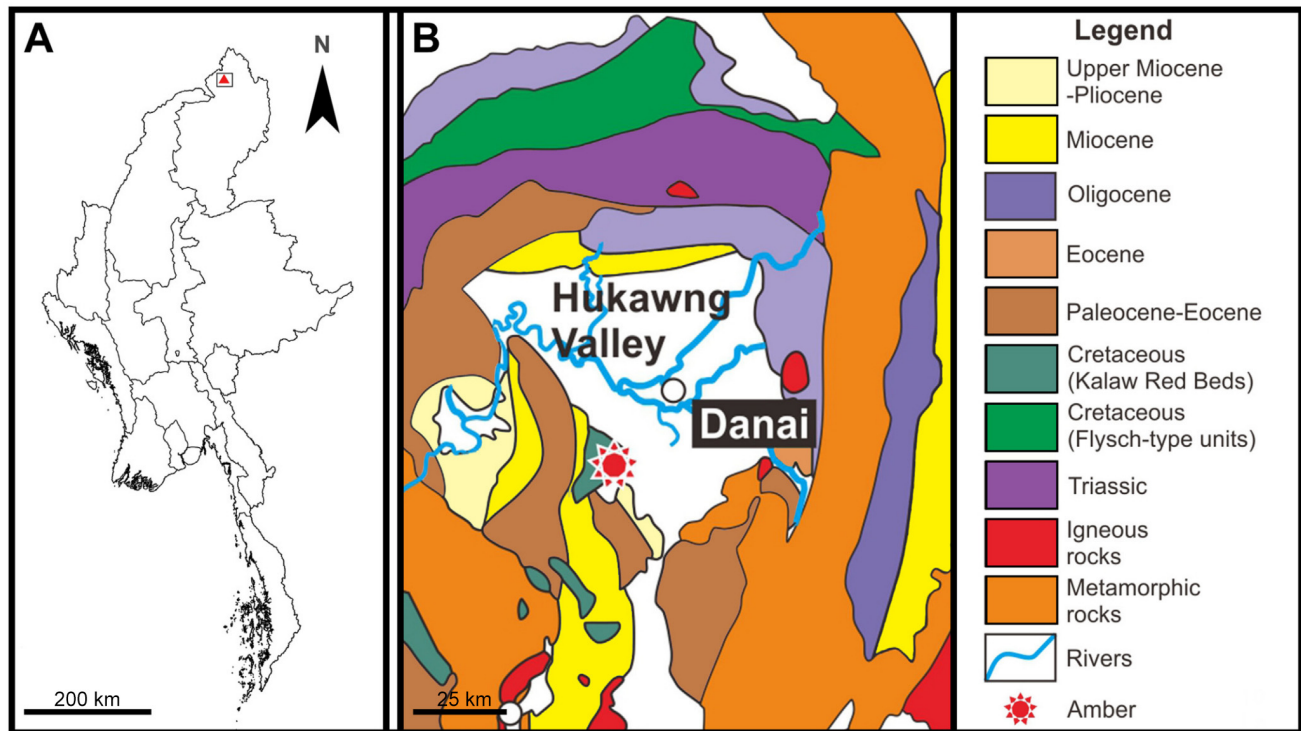


Figure 1. (A) Map of Myanmar; the red delta indicates the position of the Hukawng Valley in Myanmar. (B) Geographical map of the amber locality (circle) in the Hukawng Valley (modified from Cruickshank and Ko, 2003 [14]). Map from Google Earth Pro (2024), Maxar Technologies, used according to Google Earth Terms of Service.

3. Systematics

Angiospermae

Eudicots

Family *Incertae sedis*

***Antiquigemina* Wang and Li gen. nov.**

Generic diagnosis: Flowers in pairs, each subtended by a bract, bisexual. Floral cup bearing at least 3 sepals, 5 petals and at least 4 stamens. Stamens comprising a filament and a dorsifixed bilocular anther. Pistil solitary, tricarpeolate, with a bifurcated style. Ovary semi-inferior.

***Antiquigemina pilosa* Wang and Li gen. et sp. nov.**

Holotype: PB206703, housed in the collection department of Nanjing Institute of Geology and Palaeontology.

Specific diagnosis: In addition to that of the genus, pedicels and bracts covered by trichomes. Sepals and petals triangular, involute, and covered by unicellular, unbranched soft hairs. Sepals smaller than petals. Calyx caducous.

Etymology: *Antiqui-* from the Latin word *antiquus*, emphasizing the relatively early age. *Gemina* from the zodiac sign *Gemini*, standing for the paired flowers. *pilosa* for trichomes or hairs covering bracts, pedicels and petals.

Description

A pair of flowers was preserved within a piece of brownish amber (Figure 2A–J). Two flowers grew on two pedicels in the axil of a bract (Figure 2A–C). The glabrous stalk measures 1.2 mm in length and 0.5 mm in diameter (Figure 2K). The bracts were covered by trichomes ranging from 1.4 mm long and 0.6 mm wide to 2.7 mm long and 0.8 mm wide (Figure 2K). These flowers were designated Flower (A) and Flower (B) according to bract size: Flower (A) has a larger bract and Flower (B) has a smaller bract (Figure 2A–C).

Flower (A) and Flower (B) are similar in size, measuring 2.2–2.7 mm in diameter. Both flowers are bisexual, each consisting of a slender pedicel, a floral cup, a calyx, a corolla, an androecium, and a pistil (Videos S1 and S2). The pedicels measure 4.9 mm in length and 220–300 µm in width and are covered by trichomes (Figure 2A,K). The petals and sepals are separated, triangular in shape, and reflexing outwards (Figure 2D,E,G,H). Unicellular, unbranched soft hairs are found on the petals under a stereomicroscope (Figure 3A,B). Flower (B) has both a calyx and a corolla (Figure 2H,I). The corolla comprises five petals measuring 1.0–1.2 mm in width at their widest point and 1.7–3.2 mm in length. The calyx comprises at least three sepals, which are smaller than the petals, measuring 0.7–1.0 mm in width at their widest point and 1.2–1.3 mm in length. Flower (A) has a corolla of only five petals (Figure 2E,F), each measuring 0.7–1.2 mm in width at the widest point and 1.2–2.0 mm in length. The calyx in Flower (A) is absent. Both Flower (A) and Flower (B) have a petal split into two lobes (Figure 2E,F,H–J).

The androecium comprises at least four stamens in a whorl, mostly alternating with the petals but one opposite in Flower (B) (Figures 2H and 3C–E; Videos S1 and S2). A stamen consists of a filament and anther. The filament exserts above the margin of the floral cup, tapering distally, and measuring 1.1–1.2 mm in length and 80–120 µm in diameter at the base (Figure 3C). The anther is dorsifixed and bilocular (Figure 3F–G). Each locule is ovoid in shape, measuring 1.3 mm in length, 430 µm in width and 310 µm in height, latrorse, and dehisces longitudinally (Figure 3F–G). The anther is absent in several stamens (Figure 3C). The pistil is located in the center of the flower and includes a stigma, style and ovary. The style of Flower (A) bifurcated at an angle of 30 degrees (Figure 3C,H), with two branches measuring 1.0–1.3 mm, whereas the pistil tip of Flower (B) barely bifurcated (Figure 3I,J). The stigma and style measure 1.9–2.1 mm in length and 310 µm in diameter at the style base. The floral cup encloses more than 80% of the length of the ovary, suggesting a semi-inferior ovary. The ovaries are tricarpellate (Figure 3K). The placenta and ovules are obscure.

Remarks

There are minor differences between the results of the stereomicroscopic observations and the micro-CT reconstructions (Figure 2A–C). Micro-CT failed to reveal all the anthers and some stamens because of their weak density contrast against the amber matrix. The pistil of Flower (B) can be observed via micro-CT reconstruction but cannot be observed directly under a stereomicroscope (Figure 2A,B and Figure 3C), probably because of differential preservation. The characteristics based on observations via both methods are more credible.

The sepals are similar to the petals in shape, the sizes of the sepals (0.7–1.0 mm in width and 1.2–1.3 mm in length) are distinct from those of the petals (1.0–1.2 mm at their widest point and 1.7–3.2 mm in length), suggesting that the perianth parts can be distinguished as calyx and corolla in *Antiquigemina pilosa*.

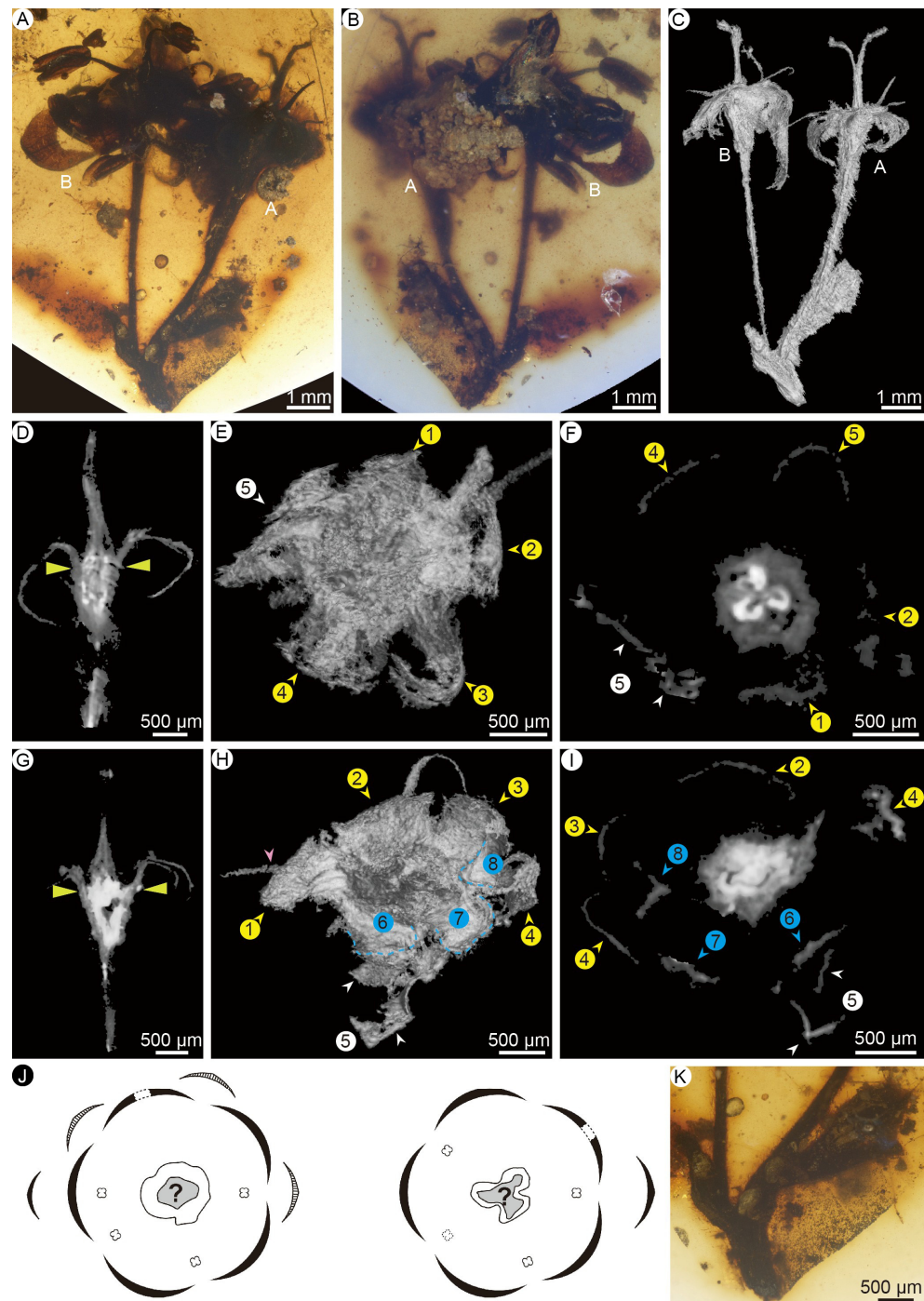


Figure 2. Paired flowers of *Antiquigemina pilosa* (PB206703): (A,B) General morphology of *A. pilosa* from both sides of the amber. (C) Micro-CT reconstruction of *A. pilosa*. (D) Longitudinal section of Flower (A). Note the attachment of the perianth on the same level of the ovary (triangles). (E) Bottom view of Flower (A). (F) Transverse section of Flower (A). (G) Longitudinal section of Flower (B). Note the attachment of the perianth on the same level of the ovary (triangles). (H) Bottom view of Flower (B). (I) Transverse section of Flower (B). For (E,F) and (H,I), we numbered sepals and petals. The yellow arrows indicate the petals. The blue arrows indicate the sepals. The white arrows indicate the lobed petal. The pink arrow indicates an antepetalous stamen. (J) Flower diagram of flowers B (left) and A (right). Stamens with solid lines are observed via at least one method (stereomicroscopy or micro-CT). Stamens with broken lines are preserved only as filament residues. The petals with dotted line intervals are the lobed petals. Question marks indicate the lack of detailed information of the gynoecium. (K) Enlargement of A, showing the paired bracts on the fragmented stalk.

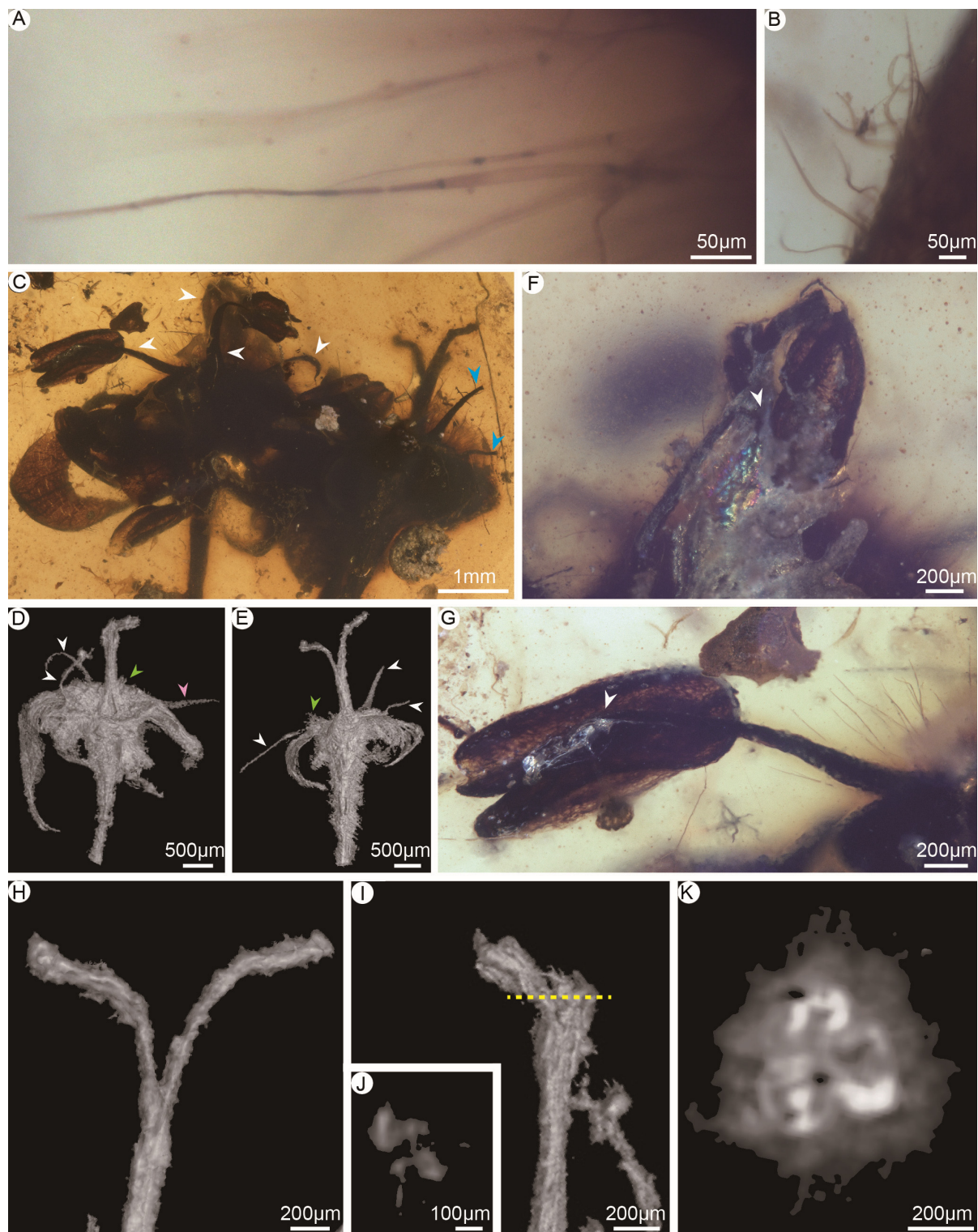


Figure 3. Hairs, stamens and pistils of *Antiquigemina pilosa*: (A,B) Unicellular unbranched hairs on petals. (C) Enlargement of Figure 1A showing stamens. The white arrows indicate the stamens in Flower (B), and the blue arrows indicate the stamens in Flower (A). (D,E) Side view of flowers A and B showing the positions of the stamens. The white arrows indicate stamen and alternate petals. The pink arrow indicates an antepetalous stamen. The green arrows indicate two prominent stamen bases. (F,G) Dorsifixed anthers. The white arrows indicate the position of the attachment of the anther. (H) Bifurcated style in Flower (A). (I) Slightly bifurcated style of Flower (B). (J) Transverse section from the yellow broken line in (I). (K) Transverse section of a tricarpellate ovary in Flower (A).

In *Antiquigemina pilosa*, the spacing between sepals or stamens is uneven. It is impossible to determine whether it is original or an artifact. Therefore, we use “at least” to describe this situation.

Lobed petals in both Flower (A) and Flower (B) may lead to two different interpretations of flower merosity (Figure 2E,F,H,I). If each lobe is considered a single petal, then the number of petals might be interpreted as six rather than five. It is notable that the sum of the widths of two adjacent lobes equals that of a normal petal, suggesting that their forms are more likely a consequence of the splitting of an original petal, thus making alternative interpretations less likely. The presence of lobed petals in *Antiquigemina pilosa*, on one hand, may indicate that its corolla has a high developmental plasticity, as ancestral petals may sometimes possess the plasticity of lobation before canalization. Notably, lobed petals are frequently seen in *Lithophragma* (Saxifragaceae). On the other hand, lobed petals may result from accidental external damage. The arrangement of stamens and petals in *A. pilosa* may appear deviated from the “standardized”, “typical”, “canalized” flower of core eudicots. Such deviations are conceivable and are a factual status of angiosperm flowers before their canalization, which occurred later in the geological history, especially when the Mid-Cretaceous age of *A. pilosa* is taken into consideration.

Several stamens comprise only a filament, without an anther, suggesting that they might be staminodes. However, the alternative possibility that the anthers abscised naturally or broke off due to taphonomic reasons cannot be excluded. Thus, in this work, we collectively refer to all filaments with or without an anther as stamens.

4. Discussion

4.1. Development of the Paired Flowers

The differences between the Flower (A) and Flower (B) include the presence of the calyx and the bifurcation of the style. Considering that these two flowers are physically connected, there are three possible explanations for this phenomenon: (1) functional specialization between the two flowers; (2) preservation bias between the two flowers; and (3) different developmental stages of the flowers. However, the flower pair of *Antiquigemina pilosa* is unlikely to have functional specialization given that both are bisexual and of similar size. The absence of sepals in Flower (A) should result from a secondary cause, as explained in the second and third possibilities. Thus, in the original state, the two flowers should have identical floral organization.

Bifurcation of the style may be a sign of gynoecium maturation. For example, the degree between style lobes of *Litchi chinensis* gradually increases during gynoecium development [15]. Similarly, the obvious bifurcated style in Flower (A) may indicate that the flower is more mature than that in Flower (B), whose stigma only shows a slight bifurcation, suggesting that these flowers are in different (rather than the same) developmental stages. The developmental stage of Flower (B) later than that of Flower (A) can also account for the absence of sepals in Flower (A). Three sepals take up half a whorl in Flower (B), but they are absent in Flower (A), probably due to *Antiquigemina pilosa*'s caducous calyx. Sepals in a caducous calyx fall off before other flower parts do. When fossilized, the sepals in Flower (A) may have fallen completely, whereas Flower (B) still has three persistent sepals. The less severe calyx abscission in Flower (B) than in Flower (A) also aligns with the developmental order of Flower (B) after Flower (A).

The paired flowers at different developmental stages provide clues for categorizing the inflorescence of *Antiquigemina pilosa*. The paired flowers of *A. pilosa* may be the distal part of a botryoid inflorescence or a cyme [16]. Consecutive development is common within the distal flower pairs of these inflorescences [16]. The alternative hypothesis is that paired flowers in *A. pilosa* are equal to paired flowers in Caprifoliaceae *s.l.* [17] or part

of the paired-flower cyme, as in Lamiales [18]. This hypothesis, which is consistent with asynchronously developed paired flowers, can further explain why there are two bracts associated with *A. pilosa*. However, considering that the formation of such inflorescences involves complex specializations [18–22], more evidence is needed to determine whether these specializations emerged during the early diversification of core eudicots that occurred 99 million years ago [13].

4.2. Comparison with Extant Angiosperms

The solitary tricarpellate pistil of *Antiquigemina pilosa* is distinct from extant basal angiosperms, including the ANA clade [23] and magnoliids [24]. Five distinct petals in a whorl of *A. pilosa* distinguish it from monocots, which are characterized by trimerous flowers [1]. An alternative interpretation of petal number, treating each lobe of the lobed petal in pentamerous interpretation as a distinct petal (Figure 2F,I), is still at odds with monocots. Two whorls of similar trimerous perianths whose bases fit tightly, forming a perianth plane in some monocots (e.g., *Xerophyta humilis* (Baker) Durand & Schinz), may be similar to the corolla of *A. pilosa* under micro-CT. However, the three sepals in Flower (B) of *A. pilosa* defy this interpretation, as the gap in this whorl suggests that their calyx is composed of more than three members.

Among eudicots, a nearly inferior tricarpellate ovary, as observed in *Antiquigemina pilosa*, is relatively rare and might be informative of the affinities of *A. pilosa*. Although flowers with pentamerous perianths and a tricarpellate ovary in some basal eudicots have been explained as a transitional form toward the typical pentamerous flower in core eudicots according to flower development [1,25]. The pentamerous perianths, tricarpellate ovary and position of stamens in *A. pilosa* indicate that *A. pilosa* probably has not yet evolved into a typical pentamerous flower. However, the perianths of *A. pilosa* are clearly differentiated into sepals and petals, suggesting that *A. pilosa* is closer to core eudicots than to basal eudicots, whose calyx and corolla are usually poorly differentiated [1]. Therefore, the occurrence of *A. pilosa* indicates that core eudicots debuted on Earth 99 Ma ago.

Pentamerous flowers with a tricarpellate gynoecium are rarely seen in extant basal eudicots, although they have been seen in some Asterids (for example, Polemoniaceae) and Rosids (for example, Saxifragaceae, Cucurbitaceae, Passifloraceae). However, this rule does not appear applicable to early fossil angiosperms. For example, *Actinocalyx bohrii* and *Paradinandra suecica* are two fossil flowers with pentamerous perianths and tricarpellate gynoecia from the Late Cretaceous of Sweden [26] (Table 1). Another example is *Discoclethra valvata* from the Cretaceous of Central Europe, which has five sepals and three fruit valves [27] (Table 1). *Antiquigemina pilosa* is distinct from these three genera in its single split style (Table 1). The occurrence of *Antiquigemina pilosa* in the Mid-Cretaceous of Myanmar appended one more taxon to this exception list. The tricarpellate ovary has also evolved independently within several orders of core eudicots [28]. The relatively limited space for gynoecium development compared with the outer whorls probably leads to a reduction in carpel numbers [29]. Derivation through the specialization of pentamerous flowers may serve as an alternative hypothesis for the tricarpellate ovary of *A. pilosa*.

Table 1. Comparison among early fossil angiosperms with pentamerous flowers with three carpels, *Antiquigemina pilosa*, and the some core eudicot families with bisexual pentamerous or hexamerous tricarpetate flowers.

	Sepal Number	Petal Number	Stamen Number	Stamen Opposite to Petals?	Anther Attachment	Existence of Disk	Style	Ovary Position	Carpel Number	Placentation
<i>A. pilosa</i>	at least 3	5, free	at least 4	yes or no	dorsifixed	no	2-lobed	semi-inferior	3	unknown
Saxifragaceae	(3–) 5 (–10)	(4) 5 (6)	5/5 + 5	no	basifixed	no	2–3 divided	superior to inferior	2–3	axile or parietal
Rhamnaceae	(3) 4–5 (6)	(3) 4–5 (6)	4–5	yes	anther minute	yes	2–4-lobed	superior to inferior	2–4	basal
Myrtaceae	4–5	4–5	numerous	/	dorsifixed	yes	solitary	half inferior to inferior	1–5	parietal, axile or basal
Ancistrocladaceae	5	5	10 (5, 15)	/	basifixed	no	3 (4)-lobed	half-inferior	3 (4)	pendulous
Hydrangeaceae	4–12	4–12, connate	4—numerous	/	basifixed	no	1–12 divided	half inferior to inferior	2–12	axile at the base and parietal above
Loasaceae	(4–) 5 (–8), connate	(4–) 5 (–8), connate	numerous	/	basifixed	no	solitary	half inferior to inferior	3–5	parietal
Alseuosmiaceae	4–5 (6), connate	4–5 (6), connate	4–5 (6), connate	no	dorsifixed	yes	solitary	half inferior to inferior	2–3	axile
Argophyllaceae	5, connate	5, connate	5	no	basifixed	yes or no	solitary	half inferior to inferior	1–3	axile
Campanulaceae	(3–) 5 (–10), connate	(3–) 5 (–10), connate	(3–) 5 (–10)	yes	basifixed	yes	2–3-lobed	inferior, rarely half inferior or superior	2–5 (–10)	axile
Araliaceae	(3–) 5 (–12), connate	(3–) 5 (–12)	3—numerous	/	dorsifixed	yes	1—numerous	inferior, rarely half inferior or superior	2–5 (–numerous)	apical
Toricelliaceae	(3–) 5, connate	5	5	no	basi or dorsifixed	yes or no	3 divided	inferior	3	apical or axile
Caprifoliaceae s.l.	4–5 (6), connate	4–5 (6), connate	4–5	no	dorsifixed	yes or no	solitary or 2–3-lobed	inferior	3 (2–5)	axile or pendulous
Viburnaceae	2–5, connate	3–5 (6), connate	3–5 (6)	no	basi or dorsifixed	yes or no	solitary or 2–5-lobed	half inferior to inferior	2–5	axile or parietal
<i>Actinocalyx bohrii</i> (Ericaceae)	5, free	5, connate	5	no	basifixed	no	solitary	superior	3	central
<i>Paradinandra suecica</i> (Ericaceae)	5, free	5, connate	10 + 5	no	basifixed	no	3	superior	3	parietal
<i>Discoclethra valvata</i> (Clet-hraceae)	5, free/connate	?	?	?	?	yes	3	superior	3	axile

Bisexual, pentamerous or hexamerous flowers with inferior or half inferior tricarpetate ovaries can be found only in the following extant angiosperm families: Saxifragaceae (Saxifragales) [30]; Rhamnaceae (Rosales) [31] (pp. 320–338); Myrtaceae (Myrtales) [32]; Ancistrocladaceae (Caryophyllales) [33]; Hydrangeaceae [31] (pp. 202–215); Loasaceae (Cornales) [31] (pp. 239–254); Alseuosmiaceae, Argophyllaceae, Campanulaceae (Asterales) [34]; Araliaceae, Torricelliaceae (Apiales) [35]; and Viburnaceae, Caprifoliaceae s.l. (Dipsacales) [36]. Some Ericaceae taxa, including *Actinocalyx* and *Paradinandra*, might appear similar to *Antiquigemina pilosa* in certain aspects (e.g., basifixed anther, pentamery). However, they can be easily distinguished from *A. pilosa* by their connate petals and hy-

pogenous flowers (Table 1). A detailed comparison between *Antiquigemina pilosa* and these families can be found in Table 1. Among these families, those in Cornales, Asterales and Dipsacales can be distinguished from *A. pilosa* by their connate petals. Sepals in *A. pilosa* are distinct, lamellate, and thus differ from the tube-formed calyx with minute lobes in Araliaceae and Torricelliaceae. The disk that exists in Myrtaceae, Rhamnaceae and Loasaceae is absent in *A. pilosa*. Ancistrocladaceae usually have more whorls of stamens than *A. pilosa* does, and their anther attachment also differs. The lobed ovary in Saxifragaceae and the papillate stigma in Hydrangeaceae do not exist in *A. pilosa*.

Overall, the characteristic assemblage of *Antiquigemina pilosa* is not completely comparable to that of any extant angiosperm family. This reduces the possibility of *Antiquigemina pilosa* being a specialized form that evolves into an extant core eudicot family. Considering the relatively early age of *A. pilosa*, *A. pilosa* is more likely to be a unique extinct core eudicot that gives rise to no extant angiosperms. Thus, we put *A. pilosa* into *incertae sedis* at the family level.

5. Conclusions

The description of *Antiquigemina pilosa* enhances our knowledge of the diversity of the mid-Cretaceous Myanmar Amber Biota. This plant displays the morphological characteristics of core eudicots, but the systematic relationships of *A. pilosa* with other angiosperms remain elusive. The atypical character combination, on one hand, reveals a unique transitional, unstable, and uncanalized status of eudicot flowers in their early evolution; on the other hand, it underscores the existence of core eudicots in the mid-Cretaceous. Nonetheless, it is necessary to emphasize that the diversification of core eudicots already occurred about 100 Ma ago. As more investigations are carried out, more aspects of the early evolution of eudicots are expected to be unveiled.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/taxonomy5040067/s1>, Video S1: 3D reconstruction of Flower (A). Video S2: 3D reconstruction of Flower (B).

Author Contributions: Resources, W.H.; conceptualization, W.H. and X.W.; methodology, F.L. and X.W.; investigation, F.L.; writing—original draft preparation, F.L.; writing—review and editing, X.W. All authors have read and agreed to the published version of the manuscript.

Funding: This research was supported by the National Key Research and Development Program of China (2024YFF0807601) and the National Natural Science Foundation of China (42288201).

Data Availability Statement: The Micro-CT data is available at <https://www.scidb.cn/anonymous/eWl1MmF1> (accessed on 9 October 2025).

Acknowledgments: We appreciate Suping Wu for her help in micro-CT reconstruction and Yehao Wang for his help in amber grinding and polishing.

Conflicts of Interest: The authors declare that they have no conflicts of interest.

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