

FLOWERS FROM TZIMOL QUARRY, CHIAPAS: EVIDENCE OF LABILE MERISM DURING THE LATE CRETACEOUS

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Abstract

Background: The Cretaceous Terrestrial Revolution represents a key interval in the evolutionary history of major terrestrial groups, including angiosperms. In recent years, the worldwide record of Cretaceous flowers has increased substantially, providing valuable information on the evolution, as well as the ecological and phylogenetic relationships of the early flowering plants; however, reports from low latitudes of North America are still scarce.

Questions: Do the flowers from Tzimol, Chiapas, Mexico, support the idea of diversification and differentiation of the angiosperms during the Late Cretaceous?

Studied species: *Kanalflorus variabilis*.

Study site and dates: Tzimol Quarry (Fm. Angostura), Chiapas, Mexico 2023–2024.

Methods: Using light microscopy, we described and identified the fossil flowers by comparing them with extant angiosperms. Furthermore, to explore their potential phylogenetic relationships, we used a morphological matrix which was analyzed through parsimony optimization.

Results: *Kanalflorus variabilis* is proposed as a new extinct genus and species based on bisexual flowers, pedicelled, with an enlarged receptacle, and a reduced calyx, apopetalous corolla with 5–6 concave petals, alternipetalous stamens, basifixed anthers, a nectarial ring disk, and a half-inferior ovary. Its floral structure is similar to eudicots, especially with extant members of the Apiales order, due to the meristic variation of the perianth.

Conclusions: *Kanalflorus variabilis* exhibits a labile meristic pattern, providing evidence of the diversity and morphological complexity of angiosperms during the Late Cretaceous.

Keywords: Campanian, eudicots, fossil flowers, meristic pattern.

Resumen

Antecedentes: La Revolución Terrestre Cretácica representa un período clave en la historia evolutiva de los principales grupos terrestres, incluidas las angiospermas. En los últimos años, el registro mundial de angiospermas fósiles del Cretácico ha aumentado sustancialmente, aportando información valiosa sobre la evolución, así como de las relaciones ecológicas y filogenéticas de las primeras plantas con flor. Sin embargo, los registros provenientes de latitudes bajas de América del Norte siguen siendo escasos.

Preguntas: ¿Las flores cretácicas de Tzimol, Chiapas, México apoyan la idea de diversificación y diferenciación de las angiospermas durante el Cretácico Tardío?

Especies de estudio: *Kanalflorus variabilis*.

Sitio y años de estudio: Cantera Tzimol (Fm. Angostura), Chiapas, México 2023–2024.

Métodos: Usando microscopía óptica, describimos e identificamos las flores fósiles comparándolas con angiospermas actuales. Además, para explorar sus potenciales relaciones filogenéticas se empleó la matriz morfológica, la cual se analizó a través del criterio de optimización por parsimonia.

Resultados: *Kanalflorus variabilis* se propone como un nuevo género y especie extinta con base en flores bisexuales, pediceladas, con receptáculo extendido, y un cáliz reducido, corola apopétala con 5–6 pétalos cóncavos, estambres alternipétalos, anteras basifijas, y un ovario semiinfero. Su estructura floral es similar al de las eudicotiledóneas, y especialmente con miembros actuales del orden Apiales, debido a la variación merística del perianto.

Conclusiones: *Kanalflorus variabilis* presenta un patrón merístico lábil, proporcionando evidencia de la diversidad y complejidad morfológica de las angiospermas durante el Cretácico Superior.

Palabras clave: Campaniano, eudicotiledóneas, flores fósiles, patrón merístico.

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The Cretaceous Terrestrial Revolution (KTR) is recognized as a key interval for the diversification of major terrestrial lineages, including angiosperms or flowering plants (Lloyd *et al.* 2008, Benton *et al.* 2022). Thus, the study of its fossil record is crucial for a comprehensive understanding of its evolutionary history (Doyle & Endress 2010, Friis *et al.* 2011, Coiro *et al.* 2019, Schönenberger *et al.* 2020, Friis *et al.* 2025, which supports the early and greatest diversification of angiosperms with the differentiation of the main extant clades occurred from the Hauterivian-Aptian interval and extended until the Late Cretaceous (Friis *et al.* 2011, 2025, Coiro *et al.* 2019, Puebla & Prámparo 2025).

Specifically, the fossil flowers are an invaluable source of information for understanding their morphological diversification and the temporal emergence of novel structures across angiosperms (López-Martínez *et al.* 2023). Merism, or the number of organs in the floral whorls (whorled phyllotaxis) or series (spiral phyllotaxis), constitutes one of the determining factors in the establishment of the floral structure (Endress 2010). It is more or less stable in some groups, such as the case of the core eudicot clade, where the pentamerous condition is dominant (Ronse De Craene 2010); however, there are deviations in different groups, including the Apiales order (Plunkett *et al.* 2018).

Apiales includes seven families based on molecular systematics (Kårehed 2003, Chandler & Plunkett 2004, Plunkett *et al.* 2004a, b). Among these, Apiaceae and Araliaceae have a higher diversity (Kårehed 2003, Manchester *et al.* 2017). According to Nuraliev *et al.* (2019), hexamerous merism occurs frequently within the limits of the natural variation of many species with normally pentamerous whorls in the lineage (Plunkett *et al.* 2018). Such is the case of *Heptapleurum venulosum* (Wight & Arn.) Seem. (= *Schefflera venulosa* (Wight & Arn.) Harms), which frequently has pentamerous flowers and occasionally displays hexamerous flowers (Nuraliev *et al.* 2014).

Here, we described and identified *Kanalflorus variabilis* Hernández-Damián, Quintanar-Castillo, Rubalcava-Knoth, & Cevallos-Ferriz, gen. & sp. nov, based on ten samples of fossil flowers, which represent a new extinct taxon from Tzimol Quarry, Chiapas, Mexico. This expands the fossil record of angiosperms in the low latitudes of North America and adds evidence of differentiation of the major clade of the flowering plants during the Late Cretaceous.

Materials and methods

Geological setting. Tzimol locality is a Lagerstätte found in the state of Chiapas, southeastern Mexico. It consists of numerous quarries opened on the southwestern side of the Ochuxhob town, which belongs to Tzimol Municipality, positioned between 16° 12' 57.52" and 16° 13' 49.22" N and 92° 15' 00" and 92° 16' 1" W, about 12 Km west of the Comitán de Domínguez city (Figure 1; Alvarado-Ortega *et al.* 2020, Díaz-Cruz *et al.* 2022). The Tzimol locality is part of the Angostura Formation, which is characterized as an 1,100 m thick sequence of limestones, marls, and fine sands exposed along the Central Depression and Upland region of Chiapas (Sánchez-Montes de Oca 1979, Ferrusquía-Villafranca 1996, Cros *et al.* 1998).

According to Alvarado-Ortega *et al.* (2020), the Tzimol site is characterized by a sequence of parallel laminate marls with fine textures, showing no evidence of bioturbation, sedimentary gradation, or turbidity structures. This sequence corresponds to the middle-upper section of the Angostura Formation, named by Sánchez-Montes de Oca (1979). The age is supported by the presence of *Radiolites acutocostata* (Adkins 1930), also reported in the uppermost part of the Sierra Madre Formation (Pons *et al.* 2016), which suggests a Campanian age (Alvarado-Ortega *et al.* 2020, Alvarado-Ortega 2024).

The fossil assemblage recovered from Tzimol is rich and diverse. It includes microfossils such as foraminifera and algae as well as macrofossils of plants, vertebrates (*e.g.*, Díaz-Cruz *et al.* 2022, Alvarado-Ortega 2024), and invertebrates as trigonid bivalve, spatangoid echinoids, gastropods, and scaphopods (Alvarado-Ortega 2024). Most of the fossils reported from this site are considered autochthonous elements, including the marine organisms, while the presence of plants suggests that the deposit basin was close to the continent (Alvarado-Ortega *et al.* 2020).

Fossil Description and Comparisons. Ten fossil flowers preserved as impressions/compressions, which were found as isolated flowers. The samples are deposited in the Colección Nacional de Paleontología, Museo María del Carmen Perilliat M., Instituto de Geología, Universidad Nacional Autónoma de México. The fossil material was observed

using a Zeiss Axio Zoom.V16 microscope with transmitted white light and photographed using a camera AxioCam 503 Color. A composite image was created using both image stacking and image stitching to visualize the entire specimens with Adobe Photoshop.

Phylogenetic position of fossil flowers. To explore the phylogenetic position of the fossil flowers, we included the fossil material in a matrix of floral morphological characters previously published by Martínez-Millán & Crepet (2014). The final morphological matrix was built up using the software WinClada-Asado v. 1.61 (Nixon 2004). The matrix includes 112 terminals, including the Tzimol fossil material. Characters were coded as binary discrete (12) and multistate (11) characters, of which 16 were codified for the fossil material ([Table S1](#)).

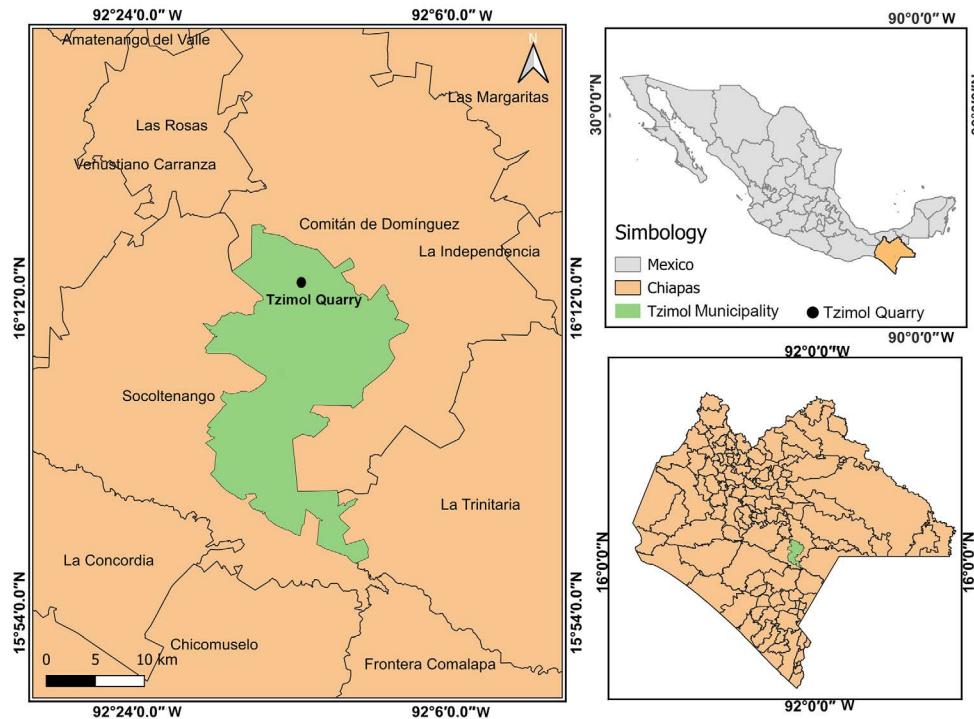


Figure 1. Schematic map showing the geographic position of Tzimol, Chiapas, Mexico (based on Alvarado-Ortega *et al.* 2020).

Parsimony analyses were performed with TNT v. 1.5 (Goloboff & Catalano 2016) using the traditional search option through the TRB algorithm with 10,000 repetitions in groups of 100. The analysis is based on Wagner tree sequences of random addition, from which we retained 50 trees following the standard strategy for less than 120 terminals (Nixon 2004). Since ambiguously supported branches on the most parsimonious trees (MPTs) collapsed, identical and suboptimal trees were removed to obtain the final consensus tree. To calculate the stability level or robustness of the clades (Holmes 2003), a bootstrap analysis was carried out (Felsenstein 1985) using 1,000 repetitions and obtaining a consensus tree.

The fossil flowers were compared with representative extant members of *Apiales* due to their consistent position recovered in the parsimony analysis using specialized bibliography (*e.g.*, Nuraliev *et al.* 2010, 2014).

Results

Subdivision. Angiospermae

Genus. Kanalflorus Hernández-Damián, Quintanar-Castillo, Rubalcava-Knoth, & Cevallos-Ferriz., gen. nov.

Etymology. K'anál means star in Tojolabal (a Mayan language) and *florus* Latin for *flowers*

Type species. **Kanalflorum variabilis** Hernández-Damián, Quintanar-Castillo, Rubalcava-Knoth, & Cevallos-Ferriz., sp. nov.

Species. **Kanalflorum variabilis** Hernández-Damián, Quintanar-Castillo, Rubalcava-Knoth, & Cevallos-Ferriz., sp. nov. ([Figure 2](#))

Etymology. From the word variable, due to the labile merism of perianth.

Holotype. IGM-PB 1615

Paratypes. IGM-PB 1616, IGM-PB 1617, IGM-PB 1618

Additional specimens examined. IGM-PB 1619, IGM-PB 1620, IGM-PB 1621, IGM-PB 1622, IGM-PB 1623, IGM-PB 1624

Generic and specific diagnosis. Bisexual, actinomorphic flowers about 20.0-30.0 mm in diameter; reduced calyx; sepals forming a truncate rim ([Figure 2A, B](#)); free corolla, five to six triangular petals, each spreading with acute apex, about 0.5–0.6 mm wide and 0.8–10.0 mm long ([Figure 2C-L](#)), margin of petals smooth and entire; nectary disk on top of ovary ([Figure 2C, D](#)); alternipetalous, basifixed anthers, longitudinal dehiscent, filaments 3.0-5.0 mm ([Figure 2C, D, I, J](#)); half-inferior ovary ([Figure 2A, B, K, L](#)).

Description. Bisexual actinomorphic flowers with perianth differentiated into calyx and corolla, on a large pedicel ([Figure 2A, B](#)). The calyx is reduced, with apparently the sepals forming a truncate or small truncate rim of ca. 0.2 mm in size ([Figure 2A, B](#)). The corolla is prominent, ca. 0.8-10.0 mm, and consists of 5-6 free, triangular petals with an acute apex and attenuate base petals; they apparently lack distinct venation ([Figure 2C-L](#)). Two stamens differentiated into filaments and anthers. The filaments 3.0-5.0 mm in length and 0.3-0.4 mm in thickness ([Figure 2C, D, I, J](#)). Anthers are oblong to ellipsoidal, measuring 2.0-2.5 long, 1.0 mm wide, basifixed with longitudinal dehiscence slits ([Figure 2C, D, I, J](#)). A nectary disk is present ([Figure 2C, D, G, H](#)). The gynoecium is half-inferior ([Figure 2A, B, G, H, K, L](#)). The Tzimol specimens exhibit varying degrees of deformation inherent to their preservation, most of the specimens are transversally flattened ([Figure 2C, E, G, I, K](#)), and only one specimen is longitudinally compressed ([Figure 2A](#)). The androecium is probably pentamerous to hexamerous; this interpretation is based on the merism of the perianth.

Age. Late Cretaceous (Campanian)

Locality. Tzimol

Phylogenetic analysis. Two separate analyses of the hexamerous and pentamerous flowers of Tzimol produced ten most parsimonious trees each. The strict consensus tree of the hexamerous flowers has a length of 186 steps (L = 186), a consistency index (CI) of 0.18, and a retention index (RI) of 0.67, whereas the strict consensus tree of the pentamerous flowers has a length of 186 steps (L = 186), a consistency index (CI) of 0.18, and a retention index (RI) of 0.66 Both separate analyses recovered a clade including *Eremosyne* Endl., ((*Aralia* L., *Phyllonoma* Willd.), Tzimol_hexamerous/pentamerous, (*Apium* L., *Melanophylla* Baker)) ([Figure 3A, B](#)).

The simultaneous parsimony analysis of the pentamerous and hexamerous flowers from Tzimol produced twenty most parsimonious trees. The strict consensus tree has a length of 190 steps (L = 190), a consistency index (CI) of

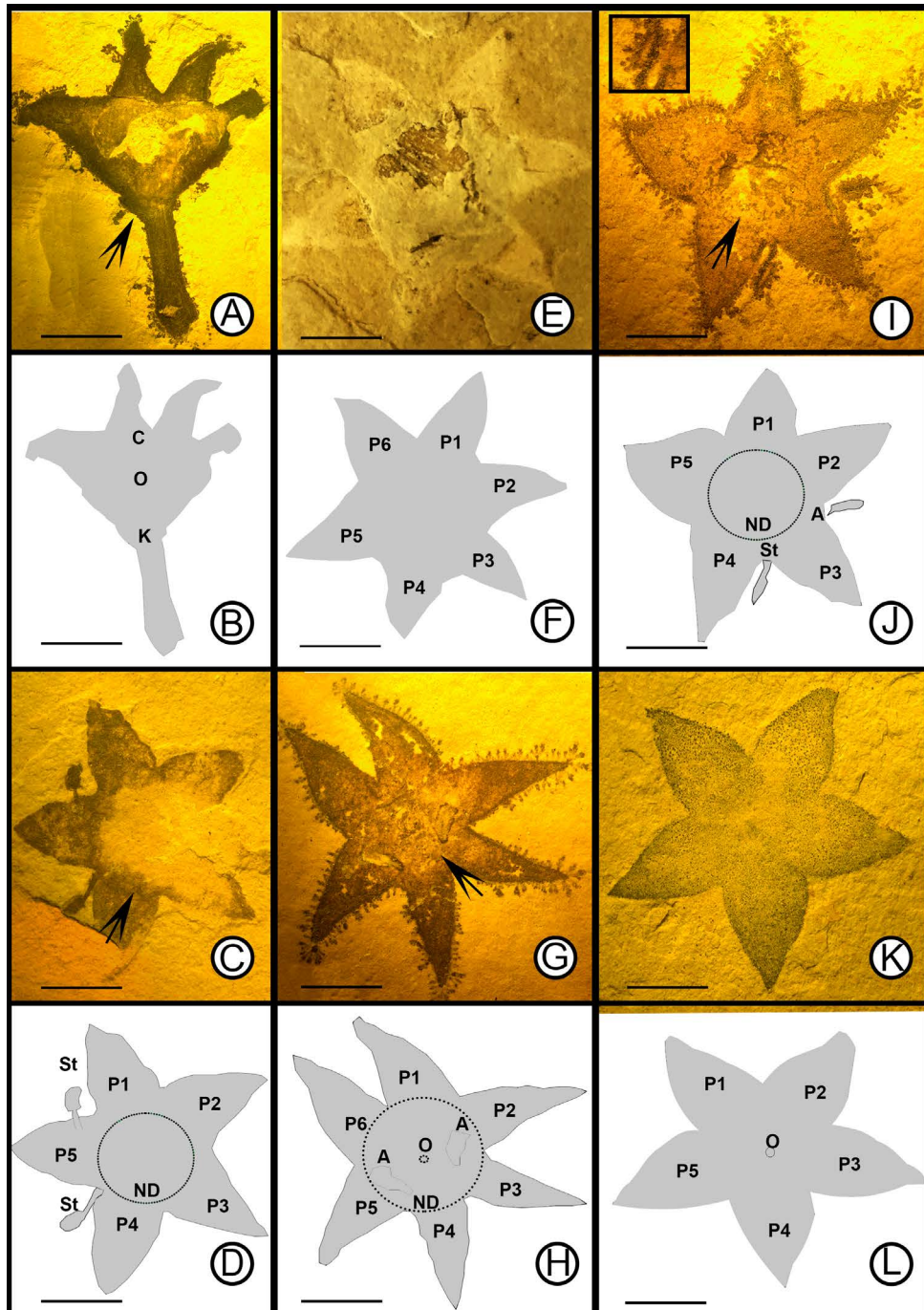


Figure 2. Flowers of *Kanalflorem variabilis* gen. et sp. nov. from Tzimol, Chiapas, Mexico. (A) Laterally compressed specimen showing pedicel and differentiated perianth, including reduced calyx and free petals (IGM-PB 1615) (B) Drawing of sample 3995-1 with reduced calyx, corolla, and half-inferior. (C) Transversally compressed specimen 3995-2, five petals, alternipetalous stamens, and five stamens inferred from symmetry, and nectarial disk. (D) Drawing of sample 3995-2 with five petals, two stamens, and a nectarial disk. (E) Transversally compressed specimen 3995-3 with six petals. (F) Drawing of sample 3995-3 with hexamerous corolla. (G) Transversally compressed specimen 3995-4 with six petals, nectarial disk, anthers, and ovary. (H) Drawing of sample 3995-4 hexamerous corolla, stamens bent into the floral center, nectarial disk, and ovary. (I) Transversally compressed specimen 3995-5 with pentamerous corolla, alternipetalous stamens, and basifixed anthers. (J) Drawing sample 3995-5 with five petals, an alternipetalous stamens, and anther. (K) Transversally compressed specimen 3995-6, pentamerous corolla, nectarial disk, and ovary. (L) Transversally compressed specimen, nectarial disk, and ovary. Symbols: K = calyx, C = corolla, S = sepal, P = petal, ND = nectarial disk, St = stamen, O = ovary. scale = 10.0 mm.

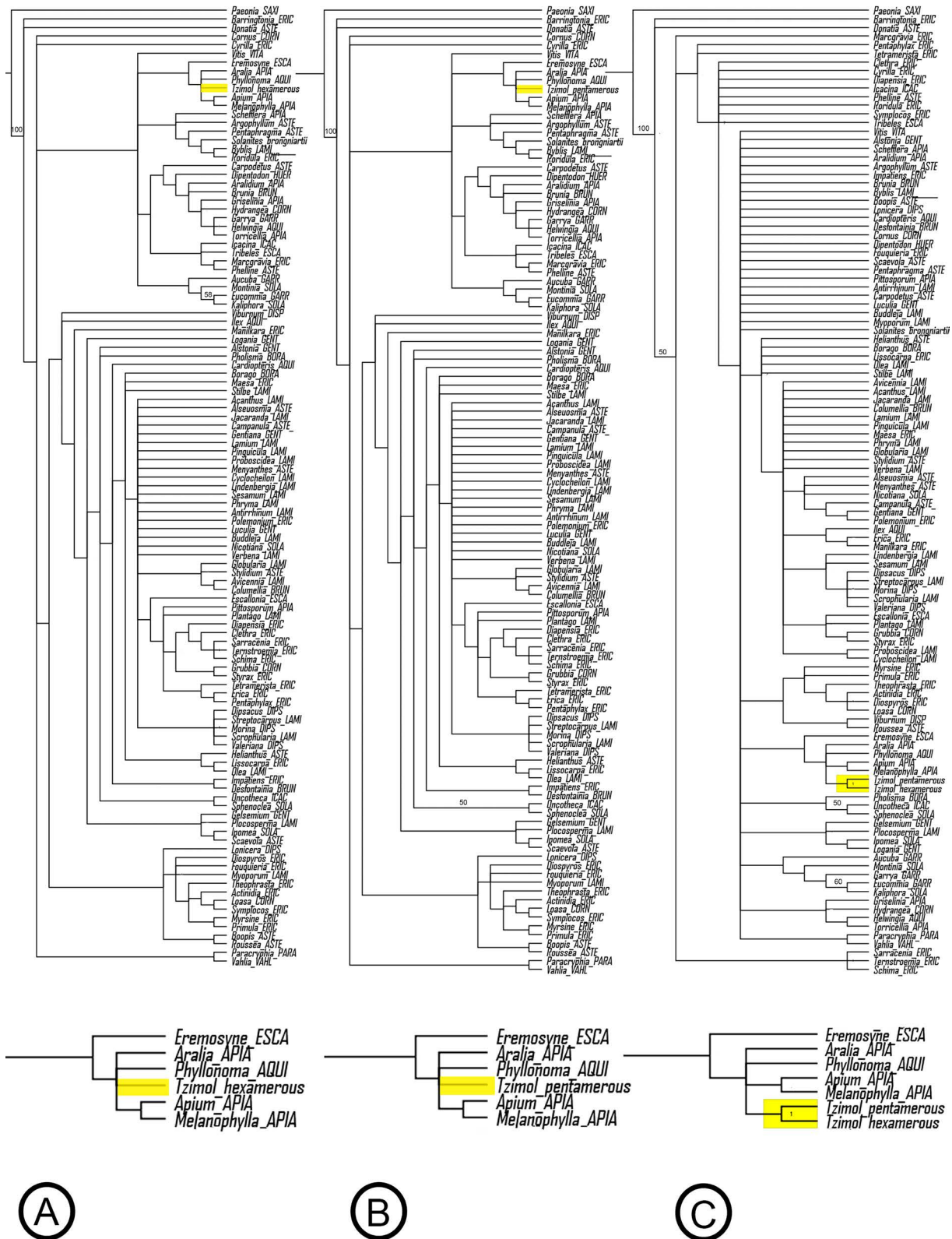


Figure 3. Phylogenetic positions of *Kanalforum variabilis*. Strict consensus trees obtained under the parsimony criterion; only bootstrap values above 50 % are shown. (A) Hexamerous flowers from Tzimol. (B) Pentamerous flowers from Tzimol. (C) Combined dataset including hexamerous and pentamerous flowers.

0.15, and a retention index (RI) of 0.60. This analysis recovered a clade that includes *Eremosyne*, (*Aralia*, *Phyllonoma*, (*Apium*, *Melanophylla*), and the two morphotypes of fossil flowers (Tzimol_pentamerous, Tzimol_hexamerous)) (Figure 3C). However, the relationship between fossil flowers and extant taxa is unresolved.

Discussion

Phylogenetic analysis. The consensus trees exhibit a topology that is partially comparable to the one reported for Asteroideae and Campanulids. It includes ((Metteniusales + Oncothecales) (Bruniales (Asterales (Apiales, Desfontainiales, Dipsacales, Escalloniales, Paracryphiales)))) (e.g., Bremer *et al.* 2002, Stevens 2001 onwards). Differences between the topologies can be explained by the different sources of information used for phylogenetic inferences, as well as the inclusion of fossil flowers (e.g., Bateman & Hilton 2009, Coiro 2024).

The three strict consensus trees obtained from the parsimony analysis recovered a clade forming a polytomy that includes the fossil material along representative members of the order Apiales, including Araliaceae (*Aralia*), Apiaceae (*Apium* L.), and Torricelliaceae (*Melanophylla*), as well as *Phyllonoma* (Phyllonomaceae, Aquifoliales) (Figure 3). The phylogenetic analysis was conducted to establish the position of the fossil flowers from Tzimol with their potential nearest extant relatives. Since the characters coded for the fossil were restricted to floral morphology (16 characters).

The fossil material has a support value that is low in all topologies, this is an indirect measure of the limited characters that support the topology (Holmes 2003). Consequently, fossil taxa are frequently associated with lower bootstrap values compared to extant taxa (e.g., Martínez-Millán & Crepet 2014).

The position of the fossil flowers within the phylogenetic framework represents a hypothesis of their relationships, one that will require additional evidence to be fully supported. Nevertheless, the analyses consistently recover the fossil flowers as more closely related to extant members of Apiales and Aquifoliales.

Comparison with extant taxa. Floral structures from Tzimol, Chiapas have characteristics with several families of eudicots based on the nectary position. In the core eudicots, the nectary position appears to be associated with any floral organ. In many rosids, the nectaries commonly form on the receptacle at the base of the floral organs, whereas

Table 1. Comparison of Cretaceous flowers from Tzimol with Araliaceae, Celastraceae, Rhamnaceae, Solanaceae, and Vitaceae. Uncommon character for the group is indicated within parentheses (based on Gerrath *et al.* 2015, Simpson 2019, Patel *et al.* 2024).

	Tzimol flowers	Rhamnaceae	Vitaceae	Solanaceae	Celastraceae	Araliaceae
Size flower	Medium	Small	Small	Small	Small	Small (medium)
Sex of flower	Bisexual	Unisexual bisexual	Unisexual bisexual	Bisexual	Bisexual (unisexual)	Bisexual (unisexual)
Reduced sepals	Present	Absent	Present	Absent	Absent	Present
Number of petals	5-6	4-5	4-5 (3-7)	5(4-6)	(3-)4-5(-6)	5 (3-12)
Nectarial ring disk	Present	Present	Absent (present)	Present	Present	Present
Number of stamens	?	4-5	4-5 (3-7)	5 (4 or 2 + 2)	(2-)3-5(-6)	5-10 (rarely 3-∞)
Position of stamens	Alternipetalous	Antipetalous	Antipetalous	Alternipetalous	Alternipetalous	Alternipetalous
Position of ovary	Half-inferior	Inferior (half-inferior)	Superior (half-inferior)	Superior	Superior	Inferior (half-inferior or superior)

in many asterids they form a disk around the ovary (Liao *et al.* 2025). This characteristic is comparable between the fossil material and several families including, Araliaceae, Celastraceae, Rhamnaceae, Solanaceae, and Vitaceae (Table 1). However, notable differences set them apart, Rhamnaceae and Vitaceae typically possess small flowers with antipetalous stamens (Gerrath *et al.* 2015, Patel *et al.* 2024), while the fossil flowers are medium sized with alternipetalous stamens (Figure 2C, D, I, J). Additionally, while Solanaceae, and Celastraceae, usually have flowers with alternipetalous stamens they often have well-differentiated sepals and superior ovary, in contrast, the fossil material has a reduced calyx and half-inferior ovary (Figure 2A, B). Finally, the fossil flowers display similarities to Araliaceae as both have reduced sepals as a rim, alternipetalous stamens, and a nectarial disk on top of a half-inferior ovary (Bernardello 2007, Plunkett *et al.* 2018).

Araliaceae includes about 50 genera and 1300 species distributed in tropical and subtropical regions of both hemispheres (Shang & Lowry 2007). The family is currently divided into two subfamilies: the species-rich Aralioideae and Hydrocotyloideae with only two genera, *Hydrocotyle* L. and *Trachymene* Rudge (Kang *et al.* 2023). Typically, Araliaceae exhibits a floral structure characterized by tetracyclic pentamerous flowers, where the calyx is smaller than the corolla, and the petals are free (Sokoloff *et al.* 2018). However, this floral pattern is highly variable, with many species showing significant differences in the number of organs within whorls or variations in merism (Philipson 1970, Eyde & Tseng 1971, Nuraliev *et al.* 2010).

Table 2. Comparison of Cretaceous flowers from Tzimol with polymeric flowers of Araliaceae. Uncommon character for the group is indicated within parentheses (based on Nuraliev *et al.* 2010, 2014, Sokoloff *et al.* 2018).

	Tzimol flowers	<i>Schefflera</i>	<i>Polyscias</i>	<i>Tetrapanax</i>
Calyx as rim	Present	Present	Present	Absent
Number of petals	5-6	(4-)5(-7+)	4-12(-20)	4(5)
Apopetalous corolla	Present	Present (absent)	Present (absent)	Present
Number of stamens	5	(2-)5-20(-100+)	4-12(-93)	4(5)
Ovary position	Half-inferior	Inferior half-inferior	Inferior (half-inferior or superior)	Inferior (half-inferior or superior)

Isomerous flowers, characterized by an equal number of sepals, petals, stamens, and carpels are common in Araliaceae; however, this floral pattern also displays modifications (Nuraliev *et al.* 2010). This variability can lead to the presence of polymeric flowers within the lineage, characterized by an increased number of floral parts (Sokoloff *et al.* 2007). In Araliaceae, polymeric flowers have been reported in *Schefflera* J.R.Forst. & G.Forst., *Polyscias* J.R.Forst. & G.Forst., and *Tetrapanax* (K.Koch) K.Koch (Nuraliev *et al.* 2010). The fossil flowers were compared with these, but they have differences (Table 2). For example, *Tetrapanax* has flowers with a copular corolla and pentamerous perianth (Nuraliev *et al.* 2014), while the fossil material has a pentamerous-hexamerous perianth with a rimmed corolla; these traits are comparable with the *Polyscias* and *Schefflera* genera (Table 2).

Schefflera s.l. has historically been considered the largest and most complex genus within Araliaceae, comprising around 600 species described and distributed across a wide geographic range. Due to its polyphyly, informal names are often used to refer to various groups within the genus, reflecting their geographic distribution: Afro-Malagasy, Asian, Melanesian, and Neotropical clades, alongside a small group generally referred to as *Schefflera* s.str. (Plunkett *et al.* 2018). The Asian *Schefflera* clade is particularly notable for its polymeric flowers (Figure 4). While many members of this group have tetracyclic, pentamerous flowers with free petals (Nuraliev *et al.* 2010, 2014). However, when analyzed in a phylogenetic framework, the fossil material was not recovered within the same clade as this genus (Figure 3). Additionally, *Polyscias* with ca. 210 species and a paleotropical to subtropical distribution, have bisexual flowers with a rimmed calyx similar to that of the fossil material. Notably, a hexamerous perianth is

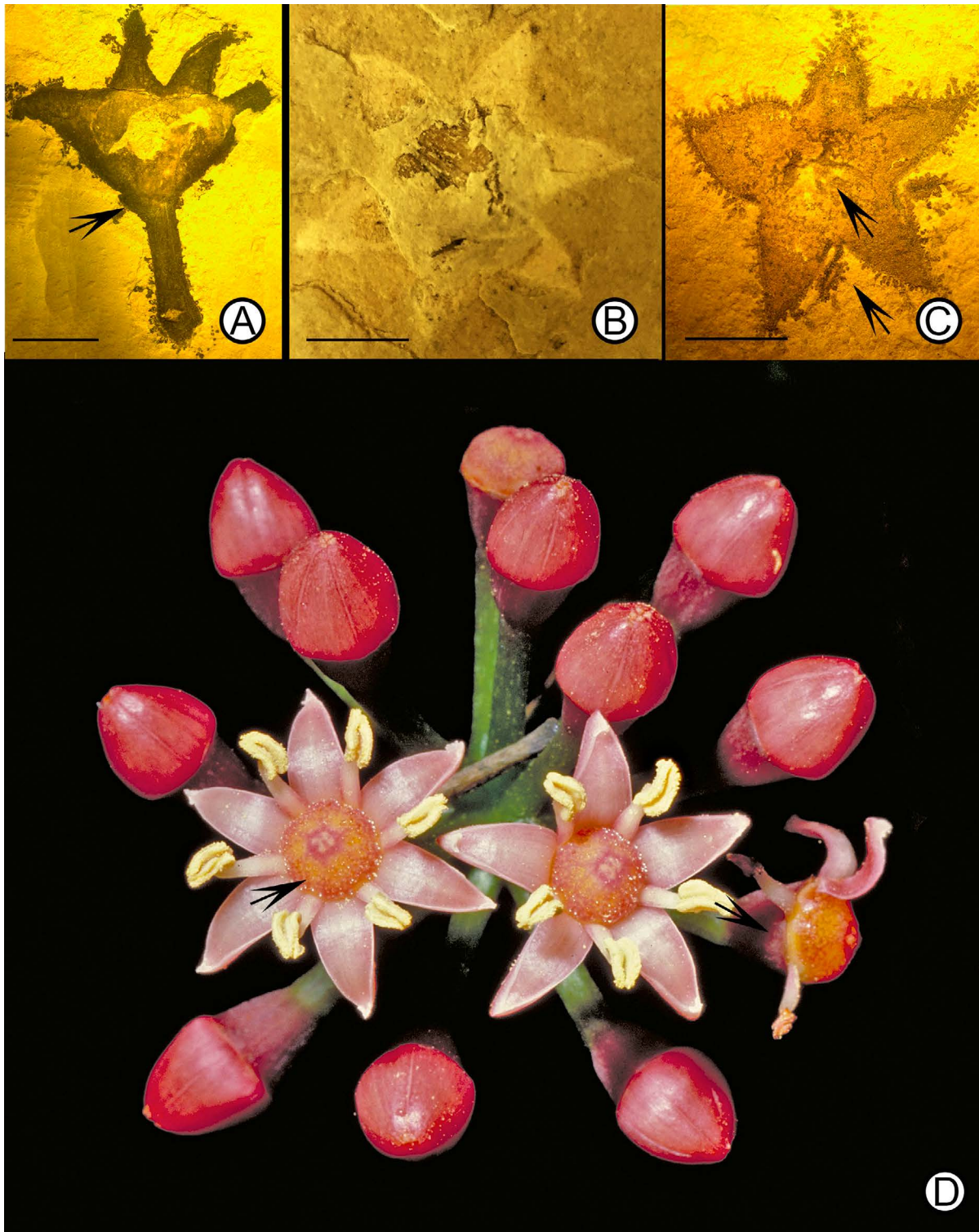


Figure 4. Comparison between the flowers of *Kanalflorem variabilis* gen. et sp. nov. from Tzimol, Chiapas, Mexico, and an extant *Polyscias* (Araliaceae). (A) Laterally compressed fossil specimen showing pedicel and differentiated perianth; arrow indicates the reduced calyx. (B) Hexamerous fossil flower. (C) Pentamerous fossil flower, left arrow indicates the nectarial disk, right arrow indicates a stamen. scale = 10.0 mm. (D) Hexamerous and pentamerous flowers of extant *Polyscias* (Araliaceae), left arrow indicates the nectarial disk, and right arrow indicates the reduced calyx. Photograph by Dr. Gerald D. Carr, Courtesy Professor, Department of Botany and Plant Pathology, Oregon State University.

reported within the genus, although half-inferior ovaries are rarely observed (Plunkett *et al.* 2018), as in the fossil material (Figure 4).

Within Apiales, the family Apiaceae comprises approximately 434 genera and 3,780 species (Stevens 2001). Flowers in this family are typically polysymmetric, tetracyclic, pentamerous, and possess a bicarpellate inferior ovary (Ajani *et al.* 2016). However, in the fossil material, the number of carpels could not be determined. Finally, the family Torricelliaceae comprises three genera *Torricellia* DC (Eastern Asia), *Melanophylla* (Madagascar), and *Aralidium* Miq. (Malesia) (Manchester *et al.* 2020). These genera have traditionally been classified within Cornales or Rosales (Plunkett *et al.* 2018) and have also been related to Araliaceae because of their similar floral structure (*e.g.*, Shaw 1972). However, they have differences including the type of inflorescence and lack of secretory canals (Shaw 1972).

Molecular analysis of Apiales have placed Torricelliaceae as a sister group of the Griselinaceae and Pittosporaceae grades, Apiaceae and Araliaceae clades (Kårehed 2003, Chandler & Plunkett 2004, Plunkett *et al.* 2004a). Torricelliaceae has morphological characteristics that distinguish them from other members of the Apiales order, such as Araliaceae. Among these characteristics are the flowers not arranged in umbels, and gynoecia are tricarpetate with only one fertile carpel.

Based on the phylogenetic analysis, the fossil material is also comparable to Phyllonomaceae, a Neotropical family with a single genus (*Phyllonoma*) of four species (Bittrich 2016). Fossil flowers are comparable to *Phyllonoma* because they are bisexual flowers with alternipetalous stamens shorter than the petals; however, they have differences, including the size (medium vs small), sepal (fusionate vs free) (Bittrich 2016), and the number of carpels, which remains unknown in the fossil material.

Although the position of the fossil material is consistent with extant members of Apiales, its phylogenetic relationship remains unresolved due to that the available morphological information is limited. Therefore, we propose the establishment of a new extinct genus and species, *Kanalflorus variabilis* Hernández-Damián, Quintanar-Castillo, Rubalcava-Knoth & Cevallos-Ferriz gen. et sp. nov., likely related to Apiales.

Merism in Apiales. The general floral structure of asterid lineage includes pentamerous, actinomorphic flowers with petals fused into a corolla tube, and five stamens alternating with the corolla lobes and inserted in the corolla tube (Endress 2010, Martínez-Millán 2010, Manchester *et al.* 2015). However, this pattern is modified in different grades. In Apiales, for example, flowers usually have free petal lobes and display a wide range of variation in whorl organ number and merism (Nuraliev *et al.* 2010, 2014, 2019, Sokoloff *et al.* 2018).

Apiales includes seven families based on molecular systematics (Kårehed 2003, Chandler & Plunkett 2004, Plunkett *et al.* 2004b). Among them, Araliaceae is one of the most diverse and exhibits substantial variation in perianth merism (Sokoloff *et al.* 2018). According to Nuraliev *et al.* (2019), a flower or floral whorl is considered polymorous when its merism exceeds six, given that five organs per whorl represents the “basic” condition in core eudicots (Ronse De Craene 2010, Jabbour *et al.* 2008). Meristic change in Araliaceae may be linked to the development of a calyptrate calyx or corolla, due to reduced pressure on the inner organs by the perianth, which increases the flexibility in organ initiation (Ronse De Craene 2016).

Parsimonious mapping of flower merism onto molecular phylogenetic trees suggests that polymery is a derived condition within the order (Sokoloff *et al.* 2007). However, the specific pathways leading to the acquisition of this floral pattern remain uncertain due to limited information on the floral structures involved (Nuraliev *et al.* 2010, 2014).

Cretaceous flowers display unique morphology, suggesting that they are probably represent extinct lineages, making their affinities to extant taxa level frequently debated (*e.g.*, Friis *et al.* 2017, Poinar & Chambers 2020, Friis *et al.* 2023, Puebla & Prámparo 2025). Here, *Kanalflorus variabilis* displays pentamerous and hexamerous flowers, a pattern comparable to that of several extant members of Apiales. Although a more specific taxonomic determination requires additional morphological evidence, this new fossil record provides valuable insight into the early evolutionary lability of floral merism in angiosperms. Its combination of characters suggests that it probably is part of the stem group of Apiales, potentially representing an early lineage that expanded into low-latitude regions of North America during the Late Cretaceous.

Records of fossil flowers in the Late Cretaceous. Late Cretaceous flowers often display unique morphologies and probably represent extinct lineages, making their affinities to extant taxa frequently uncertain (e.g., Friis *et al.* 2017, Poinar & Chambers 2020, Friis *et al.* 2023, Puebla & Prámparo 2025, Nunes *et al.* 2026). According to Friis *et al.* (2025), angiosperms are abundantly represented during the Late Cretaceous, a time that shows an increase in phylogenetic diversity linked to the radiation of core eudicots, particularly those characterized by pentamerous flowers, as reported for *Parasaurauia allonensis* J.A.Keller, P.S. Herendeen & P.R. Crane (Keller *et al.* 1996) and *Caliciflora mauldinensis* E.M.Friis, K.R.Pedersen & P.R.Crane (Friis *et al.* 2016). However, *Kanalflorus variabilis* exhibits hexamerous flowers, a condition uncommon in the Cretaceous record. Flowers with semi-inferior ovaries, as observed in *K. variabilis*, have also been documented in *Miranthus elegans* E.M.Friis, P.R.Crane & K.R.Pedersen, 2021 and *M. kvacekii* E.M.Friis, P.R.Crane & K.R.Pedersen, 2021 (Friis *et al.* 2021), although these exhibit five antepetalous stamens and five staminodes alternating with the petals. Furthermore, the alternipetalous stamens and the presence of a nectarial disk in *K. variabilis* are comparable to *Coahuilanthus belindae* L.Calvillo-Canadell & S.R.S.Cevallos-Ferriz (Calvillo-Canadell & Cevallos-Ferriz 2007), but the medium-sized flowers of *K. variabilis* contrast with the small flowers of *C. belindae*.

Late Cretaceous floras typically include angiosperm flowers that are relatively uniform in size and organization; most of them are very small, exquisitely preserved and sometimes abundant (Friis *et al.* 2011, 2025). Thus, *Kanalflorus variabilis* exhibits a unique combination of characters that expands the known morphological diversity of Late Cretaceous flowers, particularly regarding floral size and merism.

In conclusion *Kanalflorus variabilis* gen. & sp. nov. has a floral structure that closely resembles specially with members of the Apiales order, exhibiting characteristics such as pedicelled bisexual flowers, an enlarged receptacle, a reduced calyx, an apopetalous corolla with 5-6 concave petals, alternipetalous stamens, basifixed anthers, nectarial disk, and half-inferior ovary. Even if its relationship to living taxa is unresolved, this new record is evidence of the floral diversity during the Cretaceous and highlights the importance of fossils from Mexico as a source of information to complement the understanding of the early angiosperms.

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Supplementary material

Supplemental material for this article can be accessed here: <https://doi.org/10.17129/botsci.3751>

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