WINGED FRUITS OF *FRIISIFRUCTUS ALIGERI* GEN. ET SP. NOV. FROM THE LATE CRETACEOUS OF WESTERN NORTH AMERICA

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Premise of research. Fossil flowers and fruits with unresolved affinities among extant angiosperms may potentially represent extinct families or orders. The characterization and systematic assessments of such fossils will undoubtedly further our understanding of extinct angiosperm diversity, which is crucial for reconstructing the evolution of angiosperms in deep time. Here, we report two three-dimensionally preserved winged fruits from Campanian (~82–80 Ma) deposits on Sucia Island, Washington State, that represent a new genus. We explore potential phylogenetic relationships of this genus relative to higher taxa across the angiosperm phylogeny.

Methodology. The fossils were studied using microcomputed tomography (μCT) scanning and light microscopy. A three-dimensional reconstruction of one winged fruit was created from the μCT scans. The phyloscan method was used to assess the systematic positions of the winged fruits. Using the reconstruction, the fossil fruits were compared to extant angiosperms and extinct winged fruits to assess potential affinities.

Pivotal results. The μCT scans and reconstruction of the winged fruit reveal a pentamerous perianth, five pairs of fin-wings, two whorls of persistent stamens, five semicircular nectary pads, an inferior unilocular ovary, and a style with three stylar branches. Phyloscan analyses recover the winged fruits within the rosid clade, but they cannot be assigned to any extant family or order within the group because of differing floral and fruit morphologies.

Conclusions. The winged fruits are assigned to *Friisifructus aligeri* gen. et sp. nov. This new genus and species add to the diversity of winged fruits from the Cretaceous, which are relatively uncommon. Moreover, the unique morphology of *Friisifructus* indicates that this genus may belong to an extinct family of rosids.

Keywords: Campanian, microcomputed tomography, Nanaimo Group, rosids, fabids, Combretaceae, fin-winged fruit.

Online enhancements: appendix, videos.

Introduction

Exposed along the western coast of North America, Upper Cretaceous deposits of the Nanaimo Group preserve a diversity of Late Cretaceous angiosperms (Mindell et al. 2014; Atkinson 2016, 2020; Atkinson et al. 2016, 2017, 2018; Scharfstein et al. 2020; Tang et al. 2022). Campanian (84–72 Ma) exposures of this unit preserve the earliest-known occurrences of several important extant families such as Cornaceae, Meliaceae, and Cunoniaceae (Atkinson et al. 2016, 2017; Atkinson 2020; Tang et al. 2022), the latter two being important rainforest lineages. Moreover, Smith et al. (2013) reported a permineralized ranunculalean liana stem from the Hornby Island locality, which suggests that some of these Campanian assemblages may reflect early occurrences of structurally complex rainforest-like communities. Overall, there is a steady accumulation of paleobotanical data from the Nanaimo Group indicating that the western coast of North America is an important region for studying the Cretaceous diversification of angiosperms (see also Atkinson 2022). While much of this paleobotanical work has focused on living families and orders, there has been relatively less attention on Campanian angiosperms with unresolved affinities.

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Fossils with unresolved affinities to higher taxa (e.g., order and family levels) play a critical role in understanding the early evolution of angiosperms. Because of their unique floral morphologies, these fossils potentially represent previously unknown extinct lineages, as they cannot be confidently assigned to extant angiosperm orders or families (Sun et al. 2002; Coiro et al. 2020). Characterizing and assessing the systematic positions of enigmatic fossils within the angiosperm phylogeny can inform us about extinct diversity and trait evolution in deep time. Moreover, such fossils provide crucial data for inferring macroevolutionary patterns that molecular phylogenies cannot do with extant taxa alone (Doyle and Endress 2010, 2014; Quental and Marshall 2010; Sauquet and Magallón 2018). Therefore, reconstructing the early evolution of angiosperms will require an understanding of both extinct and extant angiosperm diversity.

Here, we describe a new genus and species *Friisifructus aligeri* Tang, S.Y. Smith & Atkinson based on two three-dimensionally preserved winged fruits from Campanian-aged Nanaimo Group deposits of Sucia Island, Washington State. Persistent floral structures on the winged fruits allow us to explore potential relationships of *Friisifructus* among extant angiosperms by using the phyloscan method. We then discuss potential affinities to higher taxa based on the phyloscan results. The new genus provides crucial data in understanding the early diversity of extinct angiosperms.

Material and Methods

The holotype (KUPB C2056A, C2056B) was identified within a calcium carbonate concretion from shallow marine deposits exposed at Fossil Bay on Sucia Island State Park, Washington State. The material was collected by Mr. David Starr and Mr. Jim Goedert, with the appropriate permits provided by the Washington State Parks and Recreation Commission. An additional specimen (KUPB C2100) was later recovered by Drs. Atkinson and Smith in a calcium carbonate concretion from Sucia Island (with permits). Exposures on Fossil Bay belong to the Cedar District Formation of the Nanaimo Group and, based on biostratigraphy and magnetostratigraphy, are early to mid-Campanian in age (~82–80 Ma; Ward et al. 2012). Fossil biota recovered from Sucia Island include ammonites, terrestrial gastropods, inoceramid bivalves, and a theropod femur (Ward 1978; Roth 2000; Ward et al. 2012; Peecook and Sidor 2015), as well as fossil plants such as *Ceratopetalum suciensis* Tang & Atkinson (Tang et al. 2022) and *Suciacarpa starrii* Atkinson (Atkinson 2016).

The two specimens were imaged using a Canon EOS 5DS camera with a macro lens (Canon, Tokyo). Additional detailed images of the holotype were taken using a Nikon SMZ25 stereomicroscope with a Nikon DS-Fi3 camera attachment (Nikon, Tokyo). Both counterparts of the holotype were glued back together for X-ray microcomputed tomography (μCT) scanning at the University of Michigan CTEES facility using a Nikon XT H 225ST industrial μCT system. A Perkin Elmer 1620 X-ray detector panel and a tungsten reflection target were used with scan conditions set at 128 kV and 133 μA, using a 1.1-mm copper filter, resulting in a 17.13-μm pixel size resolution. Scans were acquired using the program Inspect-X (Nikon) and segmented using the software Mimics 22.0 (Materialise, Leuven, Belgium) to reconstruct a three-dimensional image of the fruit. The software Avizo 9 Lite 3D (Thermo Fisher Scientific, Waltham, MA) was used to take measurements of the reconstruction. Data are archived on MorphoSource (Boyer et al. 2016) under project title "Fin-winged fruit of *Friisifructus*." The specimen is housed in the Division of Paleobotany Collections, Biodiversity Institute, University of Kansas (KUPB).

The phyloscan method (Schönenberger et al. 2020) was used to test the systematic positions of the winged fruits described in this work. This method uses a floral character matrix and angiosperm molecular backbone to assess the most parsimonious position(s) of fossil flowers. Persistent floral characters preserved on the holotype were scored to assess phylogenetic affinities among angiosperm orders and families. Results from the phyloscan analysis allowed us to easily exclude clades with different floral plans from taxonomic consideration. Phyloscan data files and all outputs can be accessed online via MorphoBank (project 4239; O'Leary and Kaufman 2011) in the document folders titled "Phyloscan analysis files" and "Phyloscan outputs." Scoring justifications are detailed in appendix A1.

Systematics and Results

Angiospermae

Core Eudicots (sensu APG IV 2016)

Rosids (sensu APG IV 2016)

Order—Incertae Sedis

*Genus—*Friisifructus *Tang, S.Y. Smith & Atkinson, gen. nov.*

Generic diagnosis. Fruit developing from epigynous flower, unilocular with up to 10 wings on hypanthium. Wings run longitudinally along long axis of fruit. Each wing margin continuous with a calyx lobe margin. Marginal vein absent from wings. Persistent pedicel, five free calyx lobes, two whorls of stamens, five nectary mounds, and a single style with three stylar branches persistent on fruit.

Etymology. *Friisifructus* is named in honor of paleobotanist Dr. Else Marie Friis for her extensive work and dedication toward characterizing extinct angiosperm diversity.

*Type Species—*Friisifructus aligeri *Tang,*
S.Y. Smith & Atkinson, sp. nov.

Specific diagnosis. As for genus. Five free calyx lobes triangular in shape with acute apex and anastomosing veins. Wings organized into five pairs, with each one appressed to adjacent ones near fruit apex, spreading apart from one another in the central area of fruit and converging and fusing at base. At least two vascular bundles enter base of the locule and diverge, lining margins of the locule. Nectary mounds opposite calyx lobes and surrounding androecium.

Holotype. KUPB C2056A, C2056B (figs. 1–4).

Paratype. KUPB C2100 (fig. A2).

Locality. Fossil Bay, Sucia Island, Washington State (lat. 48.749330°N, long. 122.900798°W).

Stratigraphic position and age. Cedar District Formation, Early to Middle Campanian (ca. ~82–80 Ma).

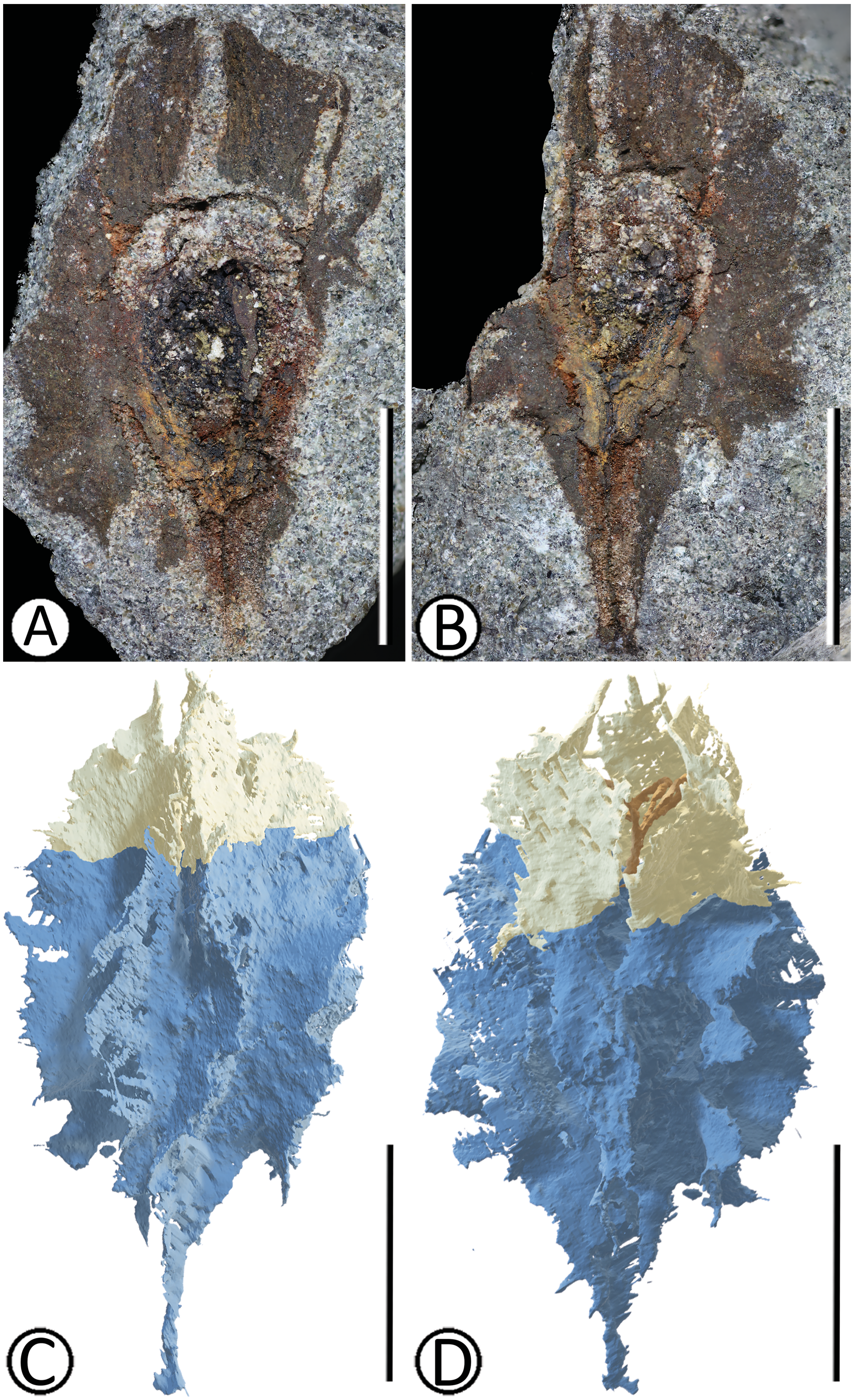

Fig. 1 General morphology of *Friisifructus aligeri* Tang, S.Y. Smith & Atkinson gen. et sp. nov., KUPB C2056A, C2056B. *A*, Exposed rock shows fossil counterpart A with fin-wings and unilocular ovary. Scale bar = 8 mm. *B*, Exposed rock shows fossil counterpart B with a pedicel, fin-wings, and unilocular ovary. Scale bar = 8 mm. *C*, 3D reconstruction of the fruit showing fin-wings extending from calyx margins. Scale bar = 7 mm. *D*, 3D reconstruction of the fruit in a different angle showing the persistent style and fin-wing morphology. Scale bar = 7 mm. Blue indicates the fruit body, cream indicates calyx lobes, and orange indicates the style.

Etymology. The specific epithet *aligeri* refers to the wings present on the fruit.

Description. The three-dimensionally preserved fruits are epigynous and radially symmetrical with a unilocular ovary (fig. 1). The μCT scans (see videos 1, 2) and three-dimensional reconstruction (see video 3) of the holotype revealed five pairs of wings, persistent calyx lobes, stamens, nectary mounds, and a style with three stylar branches (figs. 1, 2*A*, 2*D*–2*F*, 3*D*, 3*E*, 4*A*–4*D*). Persistent floral characters are best preserved on the holotype, so much of the description is based on this specimen. The fruits are 17–20 mm long from the base of the pedicel to the tip of the calyx lobes and 6–8 mm wide, including the wings. Without the wings, the holotype measures 6 mm wide. Five free calyx lobes persist on the fruit that are triangular, with acute or abraded apices (figs. 1*C*, 1*D*, 2*A*, 2*B*) showing a valvate aestivation. The calyx lobes measure 2.9–3.3 mm wide at the base and 3.1–4.5 mm long. Near the base of the calyx lobes, the margins of each lobe are continuous, with a wing that extends longitudinally along the length of the hypanthium (figs. 1, 2*B*). Adjacent wings are appressed at the base of the calyx lobes, diverge or spread apart from one another along the central area of the fruit, and then fuse at the lower third of the fruit, forming pairs of wings (figs. 1*C*, 1*D*, 2*B*). Central separation of adjacent wings may be a rupturing of a single wing, but we interpret these structures as pairs of wings because of the consistent morphology and location seen among each pair (see videos 1–3).

Venation patterns can be observed on the fossil fruits as dark "coalified" tissue. These dark vascular bundles are present in the pedicel (figs. 3*A*, 3*B*, A2) and approach the base of the locule (fig. 3*A*). Additional vasculature can be seen longitudinally lining the locule (fig. 3*C*). When the holotype is submerged under ethanol, veins can be seen entering the calyx lobes, where they immediately anastomose and end blindly toward the margins of the lobes (fig. 3*D*, 3*E*).

Micro-CT scans revealed raised semicircular mounds of tissue that are present opposite each calyx lobe and surround the androecium (fig. 2*D*–2*F*). Based on the position and raised structure, the mounds of tissue are interpreted to be nectary lobes. Four abraded stamen filaments are observed as well as an unattached structure that we interpret as a fifth stamen (figs. 2*D*–2*F*, 4*A*, 4*B*). The abraded stamen filaments measure 0.3–1.6 mm long. Two abraded stamens appear to form an inner whorl of stamens opposite the calyx lobes (fig. 2*A*, 2*D*). The unattached stamen filament opposite a calyx lobe appears to be part of an outer whorl of stamens, but this unattached structure (fig. 4*A*, 4*B*) may have moved positions after abscission. The remaining two abraded stamens appear to form an outer whorl that alternates with the calyx lobes, suggesting that the androecium is obdiplostemonous (fig. 2*D*). Based on the arrangement of the stamen filaments, a total of 10 stamens arranged in two whorls are inferred. Four of the persistent stamens have a typical narrow filament shape, but one stamen has a laminar shape (figs. 2*D*, 4*A*). Laminar stamen filaments may indicate the presence of staminodes or a different morphology for one whorl of stamens, but without additional specimens it is unclear whether additional laminar stamens were present.

The gynoecium is inferior with a unilocular ovary (figs. 1*A*, 1*B*, 2*C*). The ovary measures 5 mm in diameter and 8 mm long. Micro-CT scans revealed a style with three curved branches that are 2.8 mm in height (fig. 4*C*; video 4). The style is fused at the base and separates into three style branches that are curved downward (fig. 4*C*, 4*D*; video 4). Seeds or ovules were not observed because the internal structure of the ovary was not preserved.

Phylogenetic Analyses

Thirteen most parsimonious positions were recovered for *F. aligeri*. These positions were recovered among crown group Myrtales, stem group Fagales, crown group Cucurbitales, crown group Malpighiales, and stem group rosids (fig. 5).

Discussion

Fossil fin-winged fruits are commonly recovered from Cenozoic deposits, but few have been reported from the Cretaceous (Collinson and van Bergen 2004; Manchester and O'Leary 2010). Fruits with a fin-winged morphology have two or more lateral wings that extend along the longitudinal axis of the fruit body (see Manchester and O'Leary 2010), such as *Friisifructus aligeri* gen. et sp. nov. from Campanian deposits of Sucia Island. The recovery and characterization of *F. aligeri* contributes novel data on the morphological diversity of Cretaceous fin-winged fruits. All 10 fin-wings on *F. aligeri* are continuous with the margins of persistent calyx lobes and continue along the hypanthium longitudinally. The wings are organized into pairs, and, basipetally, adjacent wings are appressed to one another, spread apart near the middle of the hypanthium, and then fuse near the basal third of the fruit. Since each wing is continuous with a calyx lobe margin, we infer them to be outgrowths of the respective sepals. The fin-wings are tattered as a result of the absence of a marginal vein. A persistent pentamerous perianth, two whorls of stamens, nectary mounds, and a fused style with three stylar branches are present on the fruit as well as a persistent pedicel. The absence of clear suture lines leads us to infer that the fin-winged fruits are not schizocarpic. Based on the unique fruit morphology of *Friisifructus*, the indehiscent fruit was shed as an individual unit and was likely wind dispersed, similar to fin-winged fruits of Combretaceae (Exell and Stace 1972; Stace 2007), or dispersal by water may be possible based on the fin-wing morphology of *F. aligeri*. For instance, the pairs of fin-wings may be able to trap air to allow the fruit to stay afloat in water.

Comparisons with Fossil Fin-Winged Fruits

Among Cretaceous fin-winged fruits, *F. aligeri* most closely resembles *Dilcherocarpon combretoides* Manchester & O'Leary (Combretaceae) (Manchester and O'Leary 2010) in having an epigynous perianth and more than three fin-wings present (Manchester and O'Leary 2010; Reback and Manchester 2020). However, the fin-wings of *D. combretoides* are not continuous with the margins of persistent calyx lobes. Furthermore, only four fin-wings are present, and persistent floral characters were not preserved, which differentiates this taxon from *F. aligeri*. Additional fin-winged fruits described from Cretaceous deposits were not compared because those species have up to three fin-wings present (Manchester and O'Leary 2010). Overall, *Friisifructus aligeri* can be differentiated from previously described Cretaceous fin-winged fruits based on the number of wings present and its persistent floral characters.

Among Cenozoic fin-winged fruits, it is worth briefly comparing *F. aligeri* to *Carpolithus prangosoides* Berry (incertae sedis), recovered from Eocene deposits of southeastern North

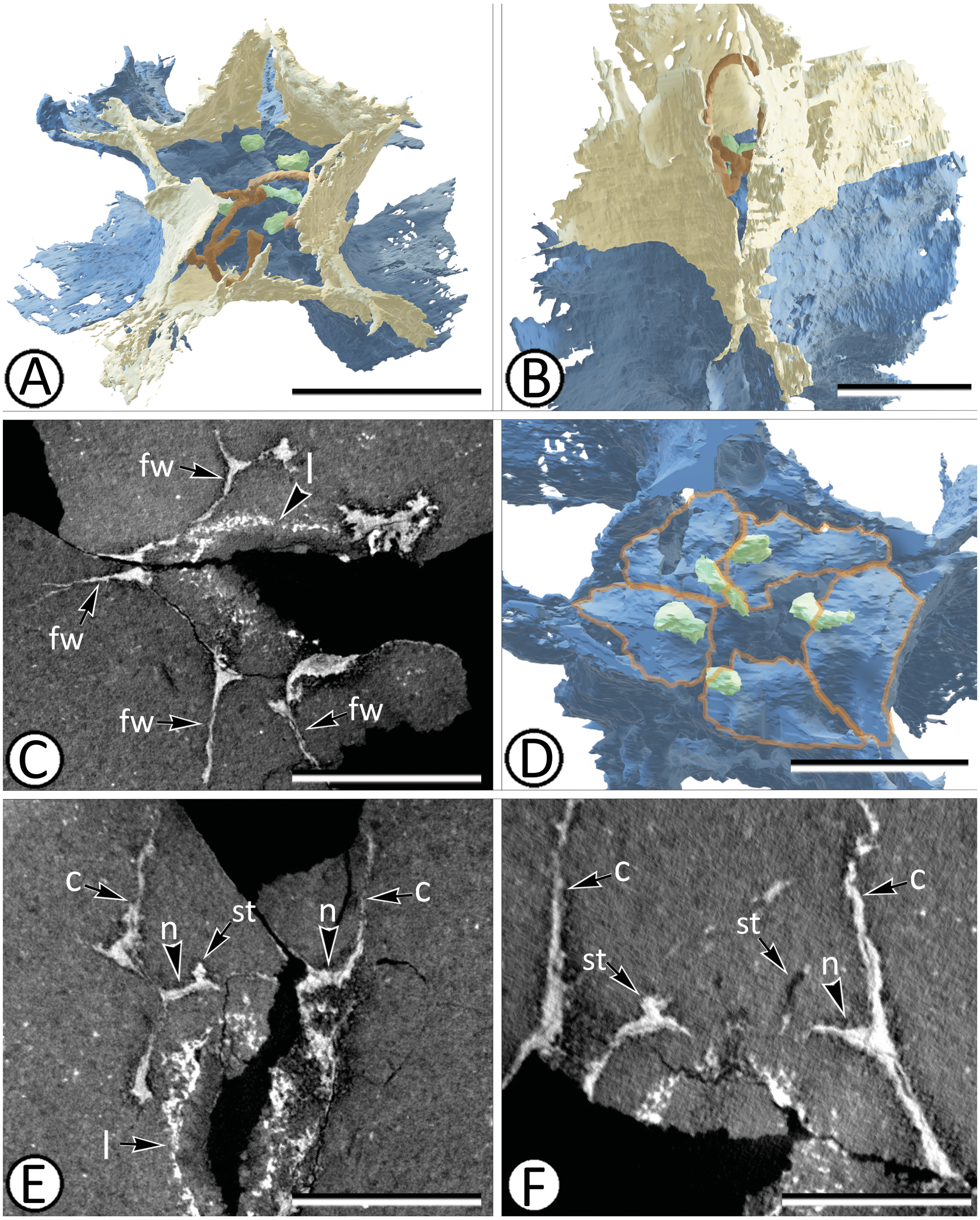

Fig. 2 Detailed view of persistent calyx lobes and androecium of *Friisifructus aligeri* Tang, S.Y. Smith & Atkinson gen. et sp. nov., KUPB C2056A, C2056B. *A*, Top-down view of the fin-winged fruit with a persistent style and stamen filaments apparent. Scale bar = 6 mm. *B*, Magnified view of calyx margins that form part of the fin-wings. Scale bar = 3 mm. *C*, Digital transverse section of the fin-winged fruit showing unilocular ovary (arrowhead) and surrounding fin-wings (arrows). Scale bar = 4 mm. *D*, Magnified top-down view of the fin-winged fruit with calyx lobes and style removed for a better view of the nectary mounds (traced in orange) and persistent stamen filaments. Scale bar = 3 mm. *E*, Digital longitudinal section (DLS) showing nectary mounds (arrowheads) located between the calyx lobes and stamens. Scale bar = 4 mm. *F*, DLS showing additional abraded stamen filaments and nectary mound. Scale bar = 2.5 mm. Blue indicates the fruit body, cream indicate calyx lobes, green indicates stamens, and orange indicates the style. c = calyx lobe; fw = fin-wing; l = locule; n = nectary mound; st = stamen.

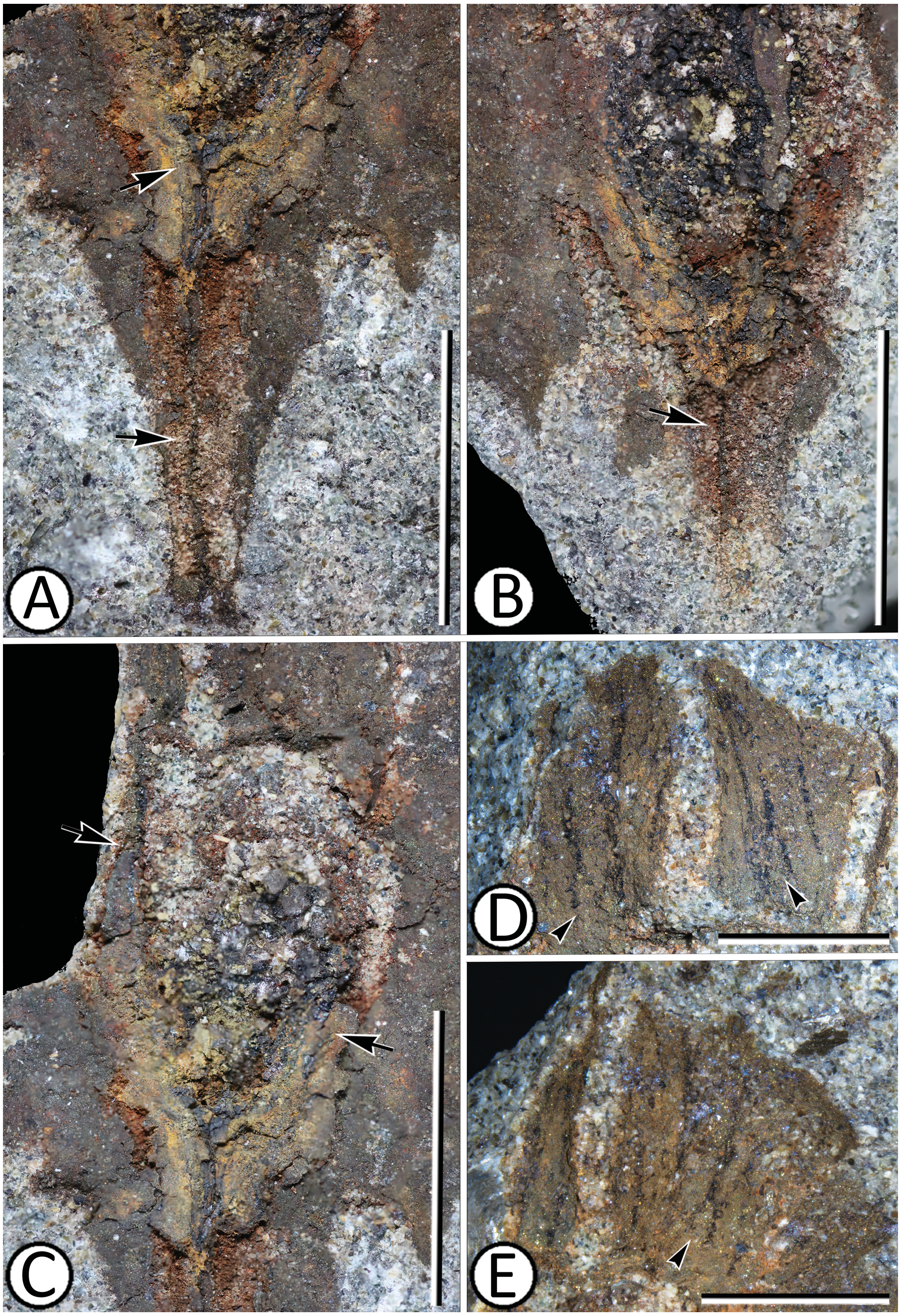

Fig. 3 Detailed view of *Friisifructus aligeri* Tang, S.Y. Smith & Atkinson gen. et sp. nov., KUPB C2056A, C2056B. *A*, Detailed view of the fruit base in fossil counterpart B showing dark vascular bundles (arrows) in the pedicel and approaching base of locule before curving upward. Scale bar = 5 mm. *B*, Detailed view of fossil counterpart A showing vascular bundles (arrow) approaching base of the locule. Scale bar = 5 mm. *C*, Unilocular ovary in fossil counterpart B showing vascular bundles lining the locule longitudinally (arrows). Scale bar = 6 mm. *D*, Calyx lobes of fossil counterpart A in magnified view showing anastomosing veins (arrows). Scale bar = 5 mm. *E*, Calyx lobes of fossil counterpart B in magnified view showing anastomosing veins (arrow). Scale bar = 4 mm.

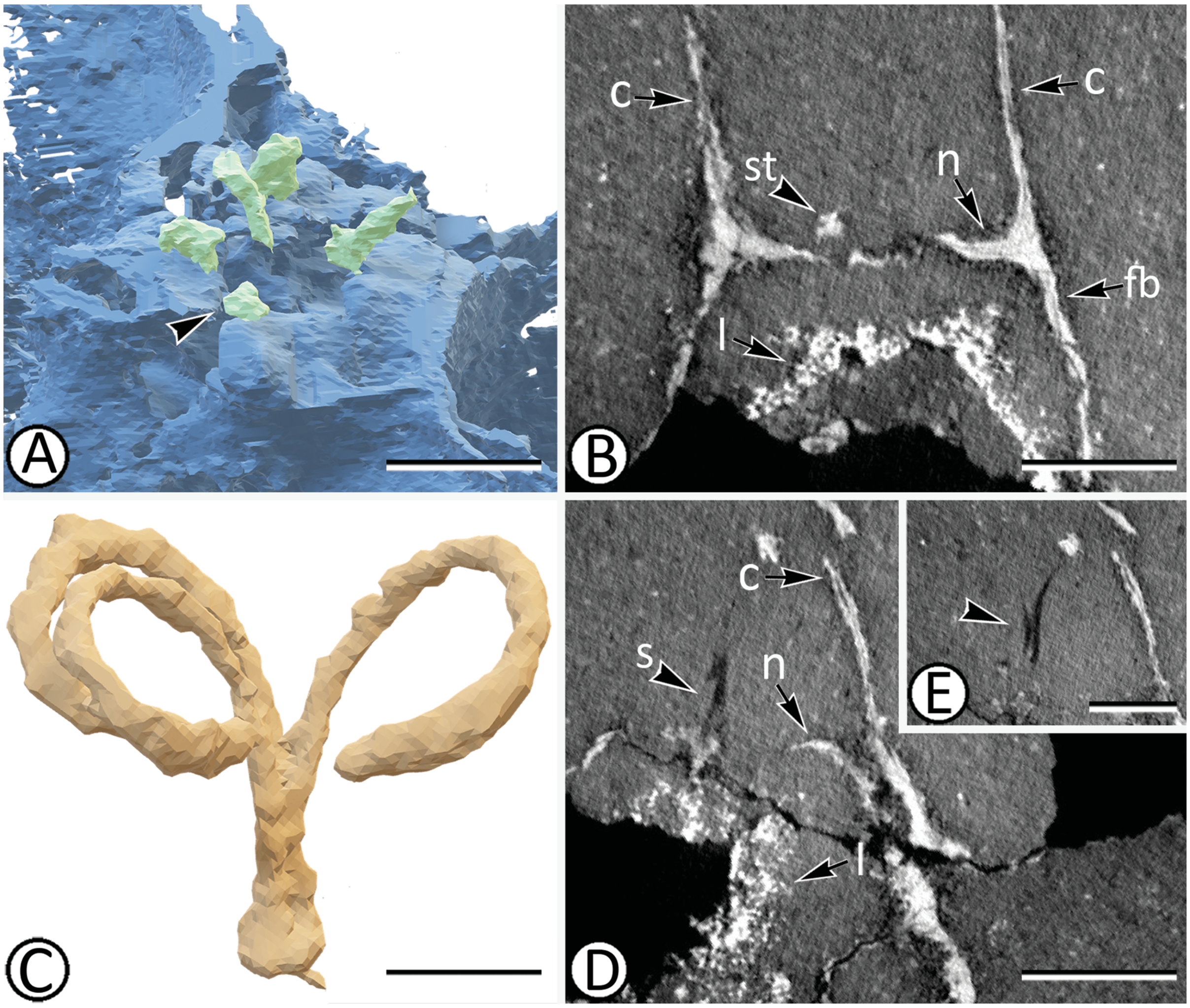

Fig. 4 Detailed view of the abraded stamens and persistent style of *Friisifructus aligeri* Tang, S.Y. Smith & Atkinson gen. et sp. nov., KUPB C2056A, C2056B. *A*, Magnified view of the androecium with calyxes and style removed showing four stamen filaments and the unattached fifth stamen (arrowhead). Scale bar = 3 mm. *B*, Digital longitudinal section (DLS) showing the unattached fifth stamen filament (arrowhead). Scale bar = 2 mm. *C*, Magnified view of the extracted style and three stylar branches of the fin-winged fruit. Scale bar = 1.5 mm. *D*, DLS showing the fused base of the style (arrowhead). Scale bar = 2 mm. *E*, DLS showing the separation of the stylar branches (arrowhead) as they begin to curve downward. Scale bar = 1.75 mm. Blue indicates the fruit body, green indicates stamens, and orange indicates the style. c = calyx lobe; fb = fruit body; l = locule; n = nectary mound; s = style; st = stamen.

America (Reback and Manchester 2020). Both species have an epigynous perianth and five fin-wings that radiate out and alternate with persistent calyx lobes (Reback and Manchester 2020). However, the fin-wings of *C. prangosoides* do not appear to expand from the margins of persistent calyx lobes and are elliptic in shape with a rounded base that differs from the wing morphology of *F. aligeri*. Furthermore, a pedicel and persistent styles are not present.

Potential Phylogenetic Positions of Friisifructus

The phyloscan analysis recovered 13 most parsimonious positions among the rosid clade for *F. aligeri*. The various positions recovered are most likely due to missing data and the limited number of sampled characters in the phyloscan data set. Each most parsimonious position recovered from the phyloscan analysis was assessed via comparative morphology.

Myrtales. Among crown group Myrtales, Vochysiaceae and Myrtaceae were recovered as most parsimonious positions for *F. aligeri*. Multiple most parsimonious positions among crown group Myrtales were recovered likely due to shared characters such as the presence of a whorled phyllotaxy and fused ovaries. However, incomplete character scoring for representatives of Myrtaceae may have affected the phyloscan results, because as many as 22 characters are scored as missing for each sampled species. Nonetheless, comparisons detailed below exclude Myrtaceae and Vochysiaceae from taxonomic consideration.

Differences in floral and fruit morphology easily differentiate Myrtaceae and Vochysiaceae from *Friisifructus*. For example, Myrtaceae typically has more than 10 stamens that are

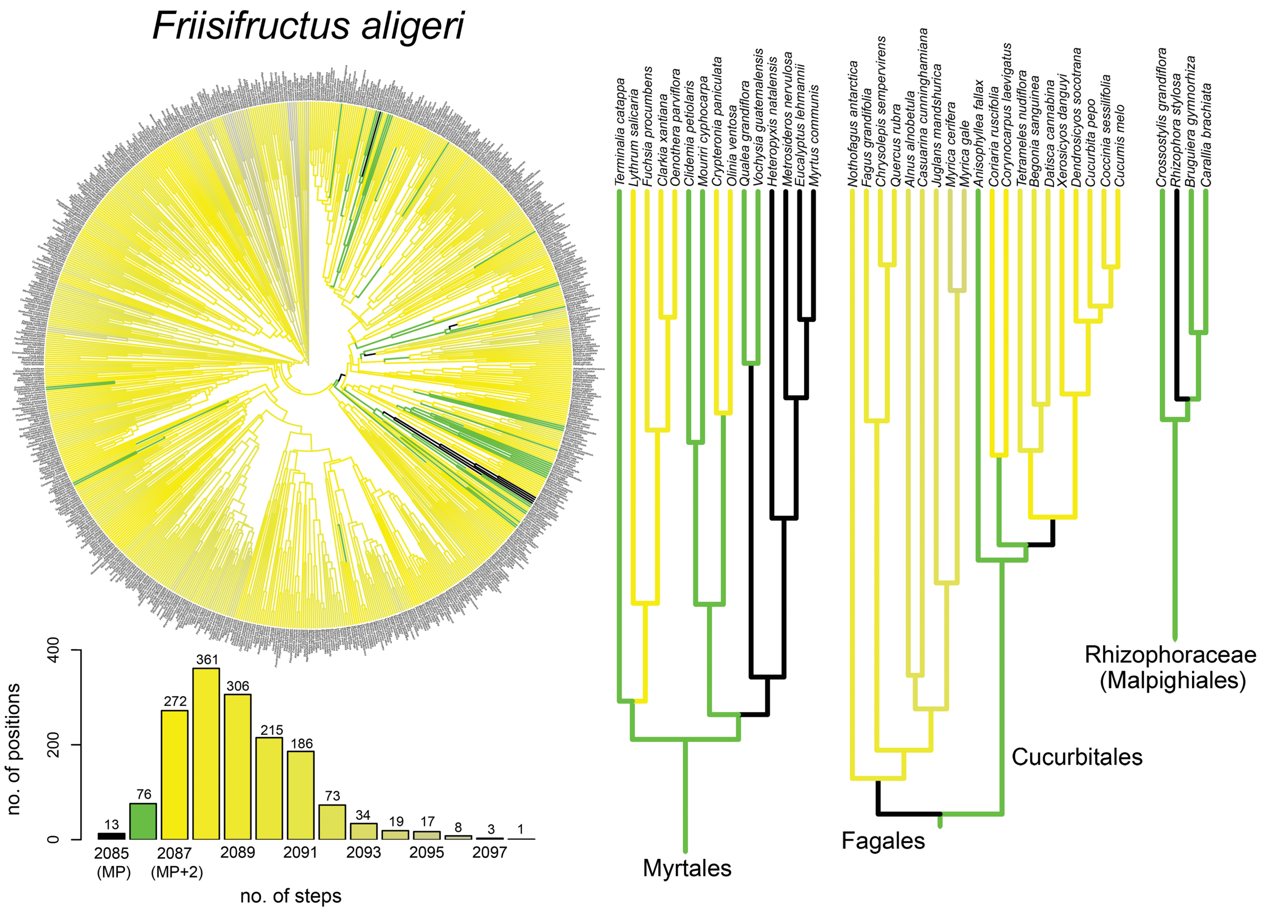

Fig. 5 Phyloscan results of *Friisifructus aligeri* Tang, S.Y. Smith & Atkinson gen. et sp. nov. A fan-shaped phyloscan tree shows most parsimonious positions indicated by the black branches on the tree. Most parsimonious positions +1 additional step are indicated by the green branches, while a gradient from yellow to gray shows subsequent parsimonious positions.

sometimes fused at the base of filaments to form fascicles (Wilson 2010). Vohysiaceae differs in having zygomorphic flowers with a single fertile stamen (Kawasaki 2007). Both families have a single style present with a terminal or capitate stigma (Kawasaki 2007; Wilson 2010) compared to the three stylar branches present in *Friisifructus*. Moreover, fin-winged fruits are not observed in the families Myrtaceae or Vochysiaceae (Kawasaki 2007; Manchester and O'Leary 2010; Wilson 2010). These differences preclude an assignment of *Friisifructus* to crown group Myrtales.

Fagales. The phyloscan method likely recovered stem group Fagales as a most parsimonious position because some characters (e.g., presence of inferior ovaries, whorled flowers, and three fused carpels) are shared with the sampled species and *Friisifructus*. While the unisexual flowers and fruits of extant Fagales clearly differ from those of *Friisifructus*, it is worth considering that Cretaceous bisexual fossil flowers, assigned to Fagales, indicate that unisexual flowers within the order evolved relatively recently (Schönenberger et al. 2001; Friis et al. 2006; Taylor et al. 2012). Based on the floral morphology of extant and extinct fagalean taxa, it is not unreasonable to consider a potential relationship with stem group Fagales for *Friisifructus*. However, differences in fruit morphology outlined below hinder a confident assignment to this group.

Fruits of fagalean taxa are typically nuts or samaras (Kubitzki et al. 1993; Larson-Johnson 2016), with the exception of fin-winged nut(lets) that are present in a few genera (Langdon 1947; Collinson and van Bergen 2004; Manchester and O'Leary 2010). Most fagalean fin-winged fruits, however, have a bilateral symmetry, with wings developing from bracts or the ovary wall (Kubitzki et al. 1993; Manchester and O'Leary 2010), which differs from the fin-winged fruit of *Friisifructus*. While fruits in Nothofagaceae can have fin-wings that diverge from hypanthium tissues, there are only two or three wings per nutlet, and they lack veins (Langdon 1947; Manchester and O'Leary 2010). These differences preclude the assignment of *F. aligeri* to this order.

Cucurbitales. Among crown group Cucurbitales, the branch leading to core Cucurbitales (Tetramelaceae, Datiscaceae, Begoniaceae, and Cucurbitaceae) was recovered as a most parsimonious position. Extant taxa of core Cucurbitales are characterized by the presence of trimerous unisexual flowers that are often apetalous and wind pollinated (Matthews and Endress 2004; Endress and Matthews 2006; Endress 2010), which greatly differs from *Friisifructus*. However, the core Cucurbitales sampled in the phyloscan and *Friisifructus* both share the presence of inferior ovaries and three fused carpels. Furthermore, other cucurbitalean families outside of core Cucurbitales sampled in the phyloscan matrix were scored to have pentamerous bisexual flowers with more than three carpels present. The families outside of core Cucurbitales are excluded from taxonomic consideration because of the presence of more than three carpels and superior ovaries in their flowers. Moreover, the fruit morphology of *F. aligeri* differs from that of core Cucurbitales and Cucurbitales as a whole.

Within Cucurbitales, fruits are mostly berries or capsules, and only a few genera within the families Begoniaceae and Cucurbitaceae have fin-winged fruits present (Manchester and O'Leary 2010). Fin-winged fruits of Begoniaceae are similar to *F. aligeri* in having fin-wings and a persistent pedicel present on the fruit. However, fin-winged fruits of Begoniaceae are dehiscent and have only up to three fin-wings that are often asymmetrical (Manchester and O'Leary 2010). Among extant members of Cucurbitaceae, a few genera have indehiscent fin-winged fruits that disperse with the pedicel attached, much like the fin-winged fruit of *F. aligeri*. Despite these similarities, fin-winged fruits of Cucurbitaceae differ in having up to four fin-wings present, and persistent floral parts are typically absent. Additionally, a marginal vein is present in the fin-wings of Begoniaceae and Cucurbitaceae (Manchester and O'Leary 2010), which is absent in *F. aligeri*. Fin-winged fruits of core Cucurbitales can be differentiated from *F. aligeri* based on the number of wings present, wing venation, and absence of persistent floral structures.

Malpighiales. One of the most parsimonious positions recovered in the phyloscan analyses was in crown group Malpighiales, specifically *Rhizophora stylosa* Griff. (Rhizophoraceae) for *F. aligeri*. *Rhizophora* L. was likely recovered as a most parsimonious position for *Friisifructus* because the genus was scored to have a whorled phyllotaxy, an inferior ovary, and fused styles present. In actuality, semi-inferior ovaries are present in *Rhizophora* (Schwarzbach 2014), but the phyloscan treats semi-inferior ovaries as inferior. This treatment of ovary position may have impacted results.

Careful comparisons of floral and fruit morphologies reveal that *Rhizophora* can be excluded from taxonomic consideration. For example, the genus *Rhizophora* is characterized by the presence of tetramerous flowers, a semi-inferior ovary with two locules, and a fused style with a lobed stigma (Schwarzbach 2014). *Friisifructus* differs from *Rhizophora* in having pentamerous flowers, a unilocular inferior ovary, and a fused style with three stylar branches present. Moreover, the fruits of *Rhizophora* are not winged.

Within crown group Malpighiales, fin-winged fruits are found only in the family Malpighiaceae (Manchester and O'Leary 2010). Winged fruits within the family can be samaras or schizocarpic (Davis et al. 2001; Davis and Anderson 2010). However, only a few genera with schizocarpic fruits exhibit a fin-winged fruit morphology in which two or more lateral wings extend longitudinally from the body (Manchester and O'Leary 2010). The fin-wings on the schizocarpic fruits of Malpighiaceae extend from mericarps that are dispersed separately. Two wings are typically present that extend unilaterally on the mericarps, and a marginal vein is present. Schizocarpic fin-winged fruits of Malpighiaceae clearly differ from the fin-winged fruits of *F. aligeri*, which is inferred to have dispersed as an entire unit.

Combretaceae. Morphological comparisons between Combretaceae and *F. aligeri* were originally assessed to compare fin-winged fruit morphology. Interestingly, the family was recovered as a most parsimonious position with one additional step. Combretaceae is characterized by the presence of small bisexual flowers, distinct stiff and glandular trichomes, a pentamerous perianth, two whorls of stamens, and an inferior unilocular ovary (Exell and Stace 1965; Stace 2007). Fin-winged fruits of the family have two to five wings that develop from the hypanthium and are often tattered once fruits are dispersed, as a result of the lack of a marginal vein (Stace 2007; Manchester and O'Leary 2010). However, differences described below preclude an assignment to Combretaceae.

While Combretaceae was recovered as a most parsimonious position with an additional step for *F. aligeri*, fin-wings extending from the margin of the calyx lobes and persistent floral parts differentiate the fin-winged fruit of *F. aligeri* from all Combretaceae. Fin-wings of combretaceous taxa only develop from the hypanthium, and persistent floral appendages typically are not present (Stace 2007; Manchester and O'Leary 2010). Moreover, *Friisifructus* differs from Combretaceae in having a fused style with three stylar branches present. A simple style with a punctiform stigma is present among extant Combretaceae (Stace 2007).

Friis et al. (1992) cautiously suggested that the extinct genus *Esgueiria* E.M.Friis, K.R.Pedersen & P.R.Crane may be a stem member of Combretaceae. *Esgueiria* is characterized by flowers with a pentamerous differentiated perianth, two whorls of stamens, an inferior unilocular ovary, and three styles (Friis et al. 1992; Takahashi et al. 1999). Styles may be free (*E. adenocarpa* and *E. miraensis*) or partially fused (*E. futabensis*), and receptacular mounds, which may potentially be nectaries, can be present outside the androecium (Takahashi et al. 1999). In addition, simple stiff hairs and peltate glandular trichomes are scattered on the fossil flowers. *Friisifructus* shares several characters with *Esgueiria*, such as the presence of an epigynous perianth, five persistent calyx lobes, two whorls of stamens, nectary mounds, and a tricarpellate, unilocular ovary. However, (preserved) trichomes are absent on the fin-winged fruits of *Friisifructus*. The calyx of *Friisifructus* differs in having a valvate aestivation, while the calyx of *Esgueiria* has an imbricate aestivation (Friis et al. 1992). Additionally, the fin-winged fruits are significantly larger in size compared to the flowers and immature fruits of *Esgueiria* (Friis et al. 1992; Takahashi et al. 1999). There are longitudinal ridges present on fruits of *Esgueiria*, which are absent in *Friisifructus* (Friis et al. 1992). Moreover, incomplete preservation of the androecium and gynoecium of the fin-winged fruits makes a comparison with *Esgueiria* difficult. Within *Friisifructus*, the morphology of the stamens and anthers and the number of ovules present in the gynoecium are unknown. Therefore, the family Combretaceae and the extinct genus *Esgueiria* are excluded from taxonomic consideration for *Friisifructus*.

Enigmatic Affinities among the Rosids

Recovered most parsimonious positions for *F. aligeri* were among Myrtales, Fagales, Cucurbitales, and Malpighiales, all of which are members of the rosid clade (APG IV 2016). At this time, *Friisifructus* cannot be confidently assigned to an extant angiosperm order or family, but we hypothesize that this genus potentially represents an extinct rosid lineage, specifically among the fabids. With the exception of Myrtales, all of the above orders are within the fabid clade (APG 2016). The fabids are composed of two major groups: the nitrogen-fixing clade and the COM (Celastrales, Oxalidales, Malpighiales) clade. However, unifying characters among the fabids that are shared with *Friisifructus* are difficult to identify (discussed in Endress and Matthews 2006, 2012; Endress 2010). In order to test this hypothesis, a phylogenetic matrix with more extensive character sampling for the rosids is needed, which is beyond the scope of the current study.

Conclusion

The fin-winged fruits of the new genus and species *Friisifructus aligeri* from Campanian deposits of western North America provide novel data on the extinct diversity of Cretaceous fin-winged fruits. Because of its unique fruit morphology, *F. aligeri* cannot be assigned within a living family (or order) of angiosperms. However, recent studies have highlighted that additional fossils in phylogenetic analyses can increase the accuracy of relationships for fossil (and living) taxa (Mongiardino Koch and Parry 2020; Mongiardino Koch et al. 2021). Therefore, we are hopeful that the inclusion of more extinct rosids exhibiting unique morphologies within phylogenetic analyses will help further elucidate evolutionary relationships for *Friisifructus* and other extinct higher taxa within this large clade of angiosperms. This will undoubtedly provide a better understanding of early angiosperm diversity and evolution in deep time.

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Data Availability

The fossil fruit of *Friisifructus aligeri* is curated at the University of Kansas Paleobotanical Collections (Biodiversity Institute) in agreement with Washington State Parks and Recreation Commission. Processed microcomputed tomography data are available online via MorphoSource under the project title “Fin-winged fruit of *Friisifructus*.” All data files associated with phylogenetic analyses and phyloscan results can be accessed online via MorphoBank (project 4239).

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