

# Fruits of *Sabia* (Sabiaceae) from the Miocene of western North America and their biogeographic significance

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**ABSTRACT.** Distinctive, reticulately sculptured ellipsoidal endocarp impressions have been discovered in Middle Miocene lake deposits of Idaho and eastern Oregon in the northwestern USA. We describe a new species based on these endocarp impressions and compare them morphologically with previously described extinct and extant species of *Sabia* (Sabiaceae) using light microscopy and micro-CT scanning. *Sabia megacarpa* sp. nov. endocarps are distinguished by their large size but resemble other species of *Sabia* in their asymmetric elliptical shape, reticulate surface ribs, unilocular morphology and gland-dotted endocarp surface. Although *Sabia* is now native to Southeast Asia and Malesia, the fossil record indicates this genus was formerly present in Europe and North America. The new species indicates that *Sabia* survived until at least 16 million years ago in western North America.

**KEYWORDS:** Fossil plants, Cenozoic, Tertiary, Idaho, Oregon

## INTRODUCTION

The Middle Miocene floras of Idaho and eastern Oregon document a diverse temperate flora that includes many plants which no longer live in the Pacific Northwest of North America but are now native in eastern North America and/or eastern Asia (Chaney and Axelrod, 1959; Smiley and Rember, 1985; Manchester and Chen, 2006). This biogeographic pattern of disjunction is applicable for many modern plants (Wen, 1999). Inferences of routes and timing of dispersal of different plant groups are informed by fossil occurrences as well as the distribution patterns of modern day flora (Huang et al., 2016; Areces-Berazain et al., 2021). During much of the Cenozoic, the Bering land bridge was a potential route for dispersal of plants and animals between Asia and North America,

particularly during climatically warm intervals of the Eocene and Early to Middle Miocene (Tiffney, 1985). Many genera that became widespread across the northern hemisphere by the Miocene have much reduced ranges today due to subsequent extirpation brought on by climatic cooling and drying (Axelrod and Schorn, 1994; Manchester, 1999; Manchester et al., 2009).

In this article, we consider a new species of fruit that has been recovered occasionally as impression fossils in Middle Miocene floras of Idaho and eastern Oregon, but not previously described or discussed. Based on their distinctive morphology we conclude that the fruit conforms to the Asian genus *Sabia* of the protealean family, Sabiaceae. This conclusion is supported by studies with reflected light microscopy and micro-CT scanning in comparison with extant species of this genus.

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Although *Sabia* is confined in its modern native distribution to East Asia, the genus has also been reported based on endocarps from the Late Cretaceous of Germany, Czech Republic (Knobloch and Mai, 1986), and Hungary (Bodor et al., 2012); the Miocene of Poland (Czeczott, 1959), and Germany (Gregor, 1978), and the Pliocene of France (Geissert and Gregor, 1981; Geissert et al., 1990) and Italy (Martinetto, 1998). *Sabia* has been recognized previously in the Eocene of western North America, notably Oregon and Montana, based on endocarps called *Sabia prefoetida* (Becker) Manchester (Becker, 1969; Manchester, 1994). The current report, indicating that the genus was still present in western North America as recently as 15 to 16 million years ago, along with unequivocal Eocene records, predate the estimate of 7.65 Mya for divergence of the extant species of the genus deduced from chloroplast sequence data (Chen et al., 2022).

## MATERIALS AND METHODS

The fruit impression specimens were collected from four Middle Miocene fossil floras in Idaho and Oregon, western USA (Fig. 1): the Succor Creek flora of Sucker Creek Formation, at the Idaho-Oregon border (Graham, 1963; Fields, 1996); the Ponderosa flora (Fields, 2017; Fields and Ertter, 2021) at Payette Lake in central Idaho, and from the Emerald Creek (P37 in Smiley and Rember, 1979) and Oviatt Creek (Boyd, 1991) sites of northern Idaho. The fruits were collected along with other megafossils by cleaving shale in the field. The fossil sites represent lake and pond deposits best known for their abundant leaf remains, but occasional cones, fruits and flowers are preserved as well. The specimens are preserved as impressions, molds and casts in shale and siltstone with little or no organic tissue remaining. The fossils are housed in the paleobotanical collections at the Florida Museum of Natural History, University of Florida, Gainesville (UF), the University of Idaho, Moscow, and the Orma J. Smith Museum of Natural History at the College of Idaho, Caldwell (CIDA) accompanied by specific location data for the sites UF 18240 (Molloy Ranch, Succor Creek, Oregon), UF 18849 (canal site, Succor Creek,



**Figure 1.** Distribution of fossil sites from which *Sabia megacarpa* has been recovered. Satellite image courtesy US Geological Survey, accessed via Google Earth

Oregon), CIDA CI-178 (Above the fish site, Succor Creek, Idaho), UF 18596 (Emerald Creek, Idaho), UF 18343 (Oviatt Creek, Idaho), and CIDA CI-135 (Ponderosa, Idaho).

The sites at Emerald Creek and Oviatt Creek, near Clarkia, Idaho, are associated with the Priest Rapids Member of the Wanapum Basalt (Smiley and Rember, 1985), indicating an age in the range of 15.9 to 16.1 Ma based on U–Pb dating of zircon-bearing ash beds (Kasbohm and Schoene, 2018). Rhyolites of the Sucker Creek Formation dated at  $15.98 \pm 0.05$  to  $16.02 \pm 0.02$  Ma based on  $40\text{Ar}/39\text{Ar}$  analyses of sanidine crystals (Black, 2021) likely indicate a maximum age for the lacustrine beds from which the Succor Creek fossils have been recovered.

Visual observations were done with a Wild M5 dissecting microscope. Dimensions of fossilized specimens were taken with an electronic caliper. Macro-photography was performed with a Canon Rebel XSi DSLR camera at variable magnifications with a Canon EF-S 60 mm macro lens. Close-up photographs were taken with a WILD M400 microscope fitted with the Canon Rebel XSi camera. Intralux 250HL Volpi fiber optic lighting was adjusted for low-oblique illumination. Computed Tomography (Micro-CT scanning) was performed at the University of Florida Nanoscale Research Facility utilizing a GE Phoenix V|Tome|X M dual-tube nano-CT system. For scans of the fossils, we used settings of 129kv and 200  $\mu\text{A}$ , with 2100 images taken at 131 ms, yielding a voxel size resolution of 27.1  $\mu\text{m}$ . For scans of the extant fruits, we used the same apparatus with lower voltage and higher amperage: 60kv, 380  $\mu\text{A}$ , with 2000 images taken at 200 ms with a voxel size of 28.96  $\mu\text{m}$ . Photoshop CS6 was used for constructing comparative image plates.

Modern endocarps and seeds of Icacinaceae, Rosaceae and Sabiaceae, particularly those of *Iodes*, *Prunus*, *Rubus* and *Sabia*, were studied in initial morphological and anatomical comparisons. For *Sabia*, we made detailed analyses of *Sabia limoniacea*, *S. dielsii* and *S. discolor* from specimens at Missouri Botanical Garden Herbarium and the paleobotanical modern reference collection at the Florida Museum of Natural History. Eocene fossils for comparison were studied at the Peabody Museum, Yale University (YPM) and the Burke Museum of Natural History and Culture at University of Washington (UWBM).

## SYSTEMATICS

### Genus *Sabia* Colebr.

#### *Sabia megacarpa* Latchaw et Manchester **sp. nov.**

Figs 2, 3A, B

**Diagnosis.** Fruit unilocular, endocarp reniform, laterally flattened and bisymmetric with a plane of symmetry parallel to the plane of compression in the sediment, lensoidal in

transverse section. Length 15–22 mm, width 9–15 mm, thickness ~1.2 mm. Apex and dorsal margin rounded, ventral margin straight. Basal attachment scar prominent, transversely elongate and lip-like. Endocarp surface with a pattern of 4–6 elongate ridges which fan obliquely outward from the attachment scar and dichotomize and anastomose distally to form a reticulate pattern. Areoles of the reticulum proximally elongate, becoming smaller and more isodiametric toward the periphery.

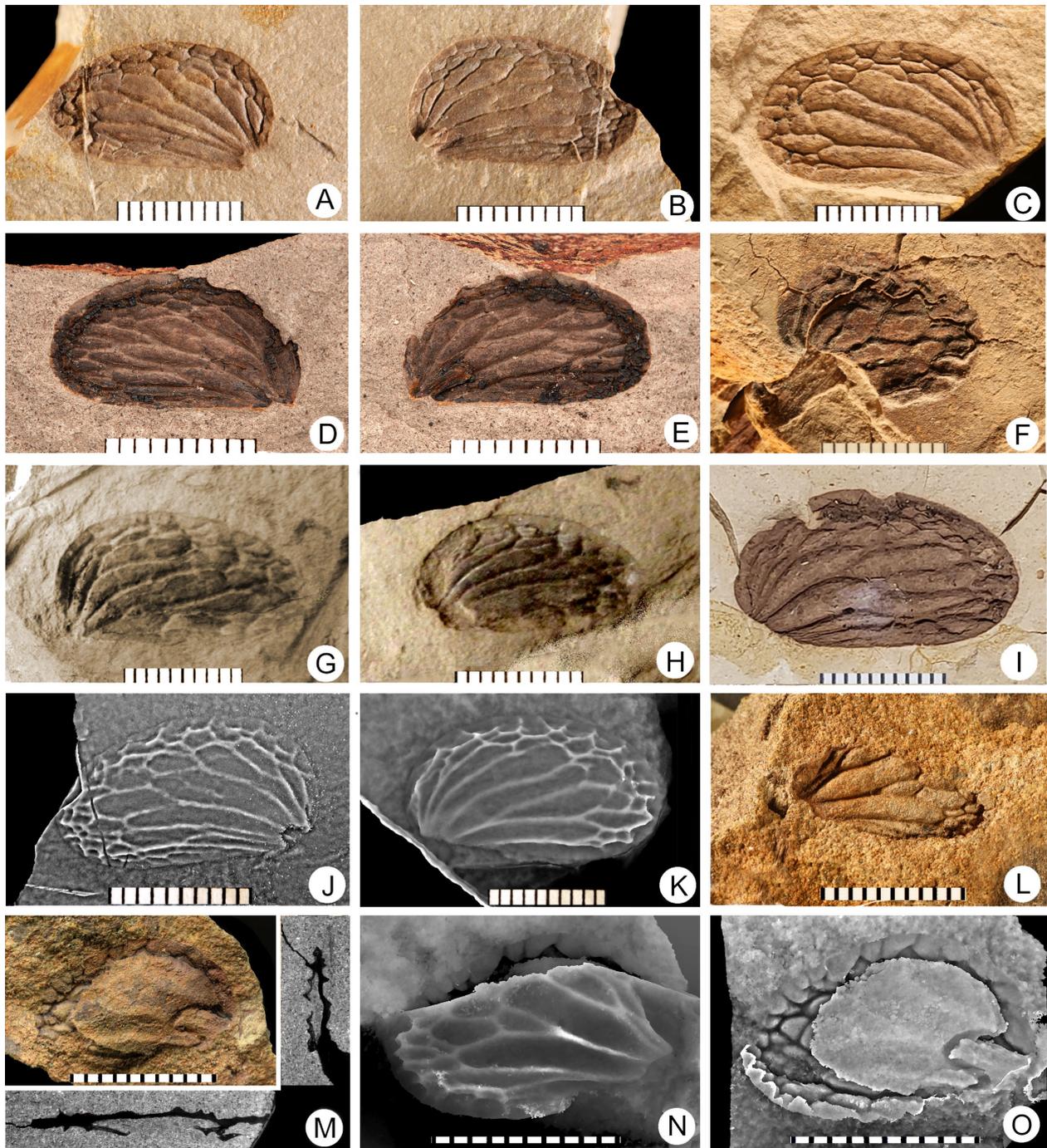
**Holotype**, designated here. UF18849-51723 [Succor Creek, Oregon, canal site].

**Paratypes.** CIDA 207035, UF18240-51867 [Succor Creek, Oregon], CIDA 205061 [Succor Creek, Idaho], UF18343-25459 [Oviatt Creek, Idaho], CIDA 202494, 202500 [Ponderosa flora, Idaho].

**Etymology.** “Megacarpa” refers to the large size of the fruit relative to those of extant species.

**Description.** The endocarps are preserved as impressions or molds in siltstone and shale matrix, with grooves on the surface of the impression representing original ridges of the endocarp. The original surface relief of the endocarps is seen in the micro-CT scan imagery (Fig. 2J, K, N). The specimens from all five localities are similar in shape, size and surface ornamentation, leading us to treat them as a single species. At most localities, the fruits are preserved in fine grained shale or tuff and consequently are much flattened in the plane of symmetry and details of the seed and locule are not preserved. However, specimens in siltstone from the Ponderosa flora have retained their shape with minimal flattening and one of them preserves a locule cast within the mold of the endocarp (Fig. 2L–O), proving that the fruits were unilocular. From that specimen the original endocarp thickness, prior to sedimentation can be measured as the distance between the endocarp external surface and the locule infilling (Fig. 2M), ~0.8 mm.

The endocarps are reniform, 15–21 (avg. 15.5) mm long, 9–11 (avg. 10) mm wide with length/width ratio of 1.6–1.9, avg 1.8 ( $n = 7$ ), laterally compressed, and bisymmetric with a plane of symmetry parallel to the plane of compression in the sediment. The apical and dorsal margins are rounded whereas the ventral margin is straight. The basal attachment scar is



**Figure 2.** *Sabia megacarpa* sp. nov. from the Middle Miocene of Oregon and Idaho, USA. **A, B.** Part and counterpart impressions of an endocarp cleaved down the middle showing reniform outline with ridges radiating from the proximal scar and forming a distal reticulum. Canal site, Succor Creek, Oregon, UF18849-51723; **C.** Impression of a larger endocarp showing prominent ridges radiating from attachment scar at lower right transitioning to reticulum near distal margin. Molloy Ranch, Succor Creek, Oregon, UF18240-51867; **D, E.** Part and counterpart impressions of an endocarp from Succor Creek, Oregon [‘Watersnake locality’ CI-86], CIDA 207035A, B; **F.** Smaller specimen. Oviatt Creek, Idaho, UF18343-25459; **G, H.** Specimens from Emerald Creek, Idaho, UI 2022-1, 2; **I.** Succor Creek, Idaho CIDA 20506 [‘above fish locality’ CI-178]; **J.** Same specimen as B, depth map from CT scan, replicating the original surface of the endocarp, with reticulum of ribs (not grooves as they appear in the impression specimens). Note the attachment scar at lower right; **K.** Depth map from CT scan of specimen in C; **L–O.** One specimen from Ponderosa flora, CIDA202494a and counterpart CIDA202494b, **L.** Impression in siltstone by reflected light, **M.** Mold of endocarp and locule cast by reflected light (upper left) and virtual CT sections (lower and right), **N.** Reconstruction of complete fruit (both counterparts reassembled, and CT scanned), showing ribbed reticulate endocarp with a portion removed to show the locule cast inside, **O.** Same, with more of the endocarp digitally removed to show the smooth surface of locule and the stout attachment scar. Scale bars = 1 cm, calibrated in mm

prominent, transversely elongate, and lip-like (Fig. 2E, O). Four to six elongate ridges fan obliquely outward from the attachment scar and

dichotomize and anastomose distally to form a reticulate pattern (Fig. 2A–L). Areoles of the reticulum are elongated proximally, becoming

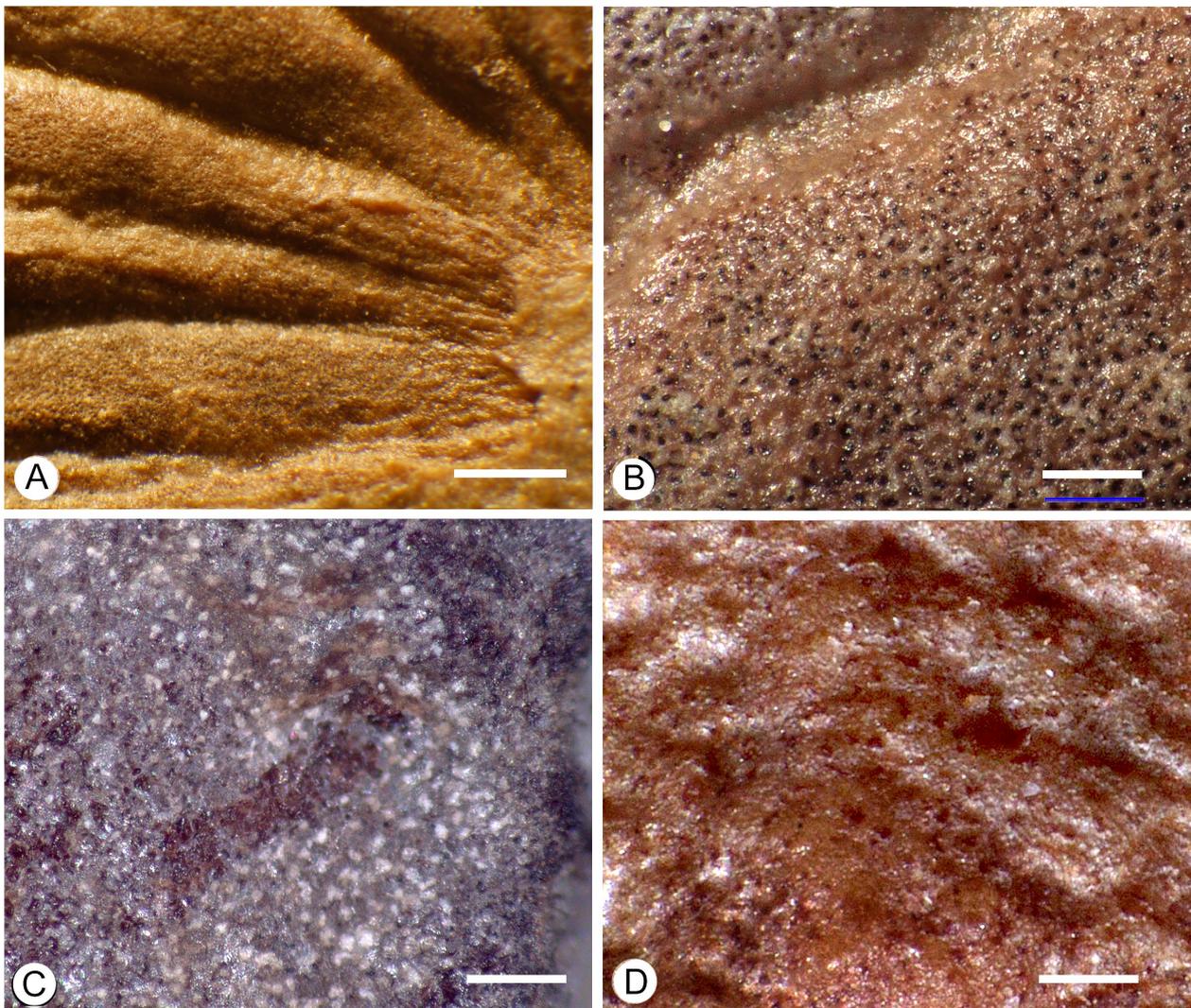
smaller and more isodiametric toward the periphery. Upon magnification, the fossils show the impression of isodiametric cells representing the outer surface of the endocarp (Fig. 3A, B). The surface is punctate with the indentation of individual isodiametric cells. In some specimens darkly pigmented nodules are distributed one-per-cell over the surface (Fig. 3B).

## DISCUSSION

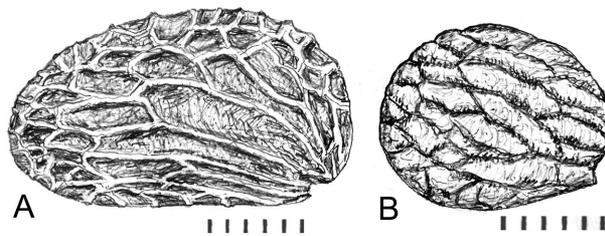
### TAXONOMIC PLACEMENT

We compared the fossils with endocarps of various families known to have unilocular reticulately ribbed endocarps. In the Icacinaceae, reticulate ribbing occurs in several genera of the tribe Iodeae, such as *Iodes* and *Natsiatum*.

However, in this family primary longitudinal ridges of the reticulum run parallel to the long axis of the fruit (Stull et al., 2012), whereas in these fossils the ridges run oblique to the long axis (Fig. 4A). The drupes of some Rosaceae have endocarps with similarities to our fossils (Mai, 1984). For example, some species of *Prunus* subgenus *Amygdalus* have an endocarp with a similarly reticulate pattern (e.g. *Prunus lycioides* (Spach) C.K.Schneid.; Yazbek, 2010), however, the surface pattern is formed by grooves, rather than ridges. The related roseaceous genus, *Prinsepia*, has endocarps that can be similar in shape to those of our fossil (Pl. 41, figs 1–5 in Mai, 1984); however, again, the ornamentation pattern is dominated by grooves rather than ridges (Fig. 4B). In addition, the endocarps of *Prunus* and *Prinsepia* endocarps are more inflated than those of our fossils.



**Figure 3.** Endocarp surface of fossil and extant *Sabia* species. **A.** UF18849-51723' *Sabia megacarpa* sp. nov. impression of endocarp ridges; **B.** Same as A, higher magnification showing cellular pattern with regularly spaced dark dots; **C.** Extant *Sabia dielsii* endocarp surface, UF2491; **D.** *Sabia limoniacea* endocarp surface, UF2486. Scale bars = 1 mm in A, 200  $\mu$ m in B–D. Scale = 5 mm

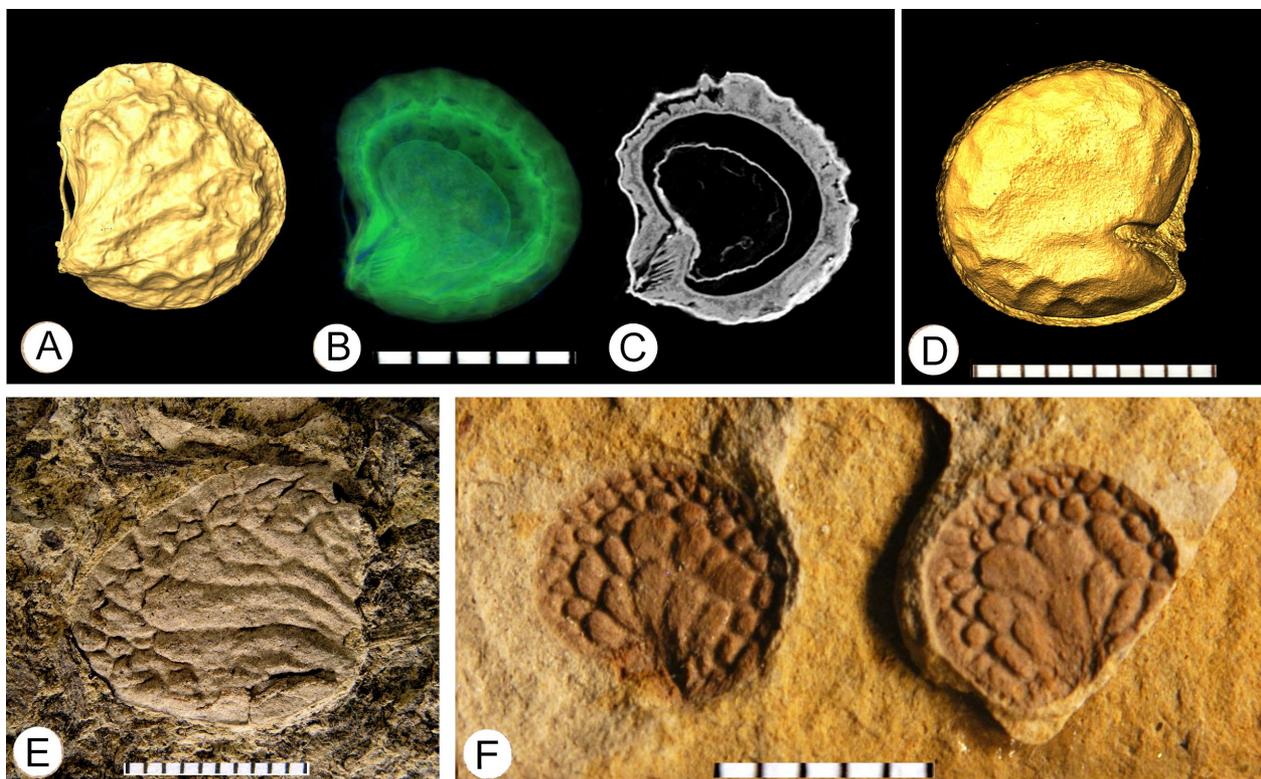


**Figure 4.** Diagrammatic illustrations emphasizing differences of endocarp ornamentation. **A.** *Sabia megacarpa* sp. nov., based on specimen in Fig. 2B, J, with reticulum of sharp ridges. Areoles of the reticulum are recessed (darkened); ridge crests illuminated; **B.** *Prinsepia uniflora* Batal. var *serrata* Rehd. (Rosaceae) endocarp with reticulum of grooves, indicated by dark shading, delimiting raised areoles. Based on photographic image of Mai (1984: pl. 41, fig. 2). Scale = 5 mm

The fossils conform in many features of morphology to the endocarps of extant *Sabia* (e.g. Fig. 5), including the lateral compression in plane of bisymmetry, unilocular condition, a prominent proximal scar, a relatively straight margin on one edge, and prominent ribs radiating from the attachment scar and dichotomizing and anastomosing to form a reticulate pattern. The fossil species has larger endocarps, however, ranging between 15 and 21 mm long, whereas drupelets of extant species range from

6.5 to 11.1 mm in length (Van de Water, 1980). In extant species of *Sabia*, the endocarps vary in shape from nearly as wide as long, to about 1.8 times longer than wide (Fig. 6 in Van de Water, 1980).

*Sabia megacarpa* endocarps are reniform in lateral view, typically almost twice as long as wide (length/width ratio of 1.6 to 1.9, avg. 1.8) with a rounded apical and dorsal margin, but with a relatively straight ventral margin (Figs 2A–E, G, H, 4A). We infer that the straight margin is due to proximity of an adjoining endocarp. In extant *Sabia*, “regularly two drupelets per flower are produced, which are, however, at the base connected with each other (‘paired’).” (Van de Water, 1980: 12). Consequently, the endocarps within the drupelets each have a straight ventral margin and a convex dorsal margin (Fig. 5). The style of the flower extends apically between the two drupelets or, when only one of the drupelets develops, runs along one side. In extant *Sabia* species the endocarp is usually characterized by a reticulate pattern formed by more or less prominent ribs. According to Van de Water



**Figure 5.** Micro-CT scan imagery of extant *Sabia* and reflected light imagery of fossil endocarps. **A–C.** *S. discolor*, Guangdong, China, MO3369392, micro-CT scan imagery, **A.** Surface rendering of fruit with style adjacent to flattened margin, **B.** Volume rendering with translucency to show seed within the locule, **C.** Sagittal section showing thin, light colored exocarp plus mesocarp, and thicker endocarp wall with single-seeded locule; **D.** *S. limoniacia*, Xishuangbanna Botanical Garden, Yunnan. CT scan surface rendering of locule surface; **E.** Endocarp cast of an undescribed species from the early Middle Eocene of Republic, Washington, UWBM 94577 locality b4131; **F.** Part and counterpart impressions of the holotype of *Sabia prefoetida* (Becker) Manchester, Beaverhead Basins flora, Montana, YPM PB 000894. Scale = 5 mm in A–C, F, 10 mm in D, E

(1980: 12), “The reticulation of the endocarp, which is usually distinctly visible on the outside of a dried drupelet, is often limited to the margin of the fruit. In some species the reticulation of the endocarp is faint or even absent. The shape and size of the drupelets as well as the reticulation of the endocarp together with the length of the persistent style provide important characters for identification of the species.”

The dark pigmented nodules, distributed one-per-cell over the endocarp surface (Fig. 3B), conform to what we observed in fruits of extant *Sabia* (Fig. 3C, D). According to Van de Water (1980: 12), granules and dark dots [cells or groups of cells with dark deposits (probably tannin)] “can occur in many different parts of the plant, e.g. leaves, all floral parts, and drupelets... In all extant species the seeds are characterized by a conspicuously dark-dotted testa, but the presence and number of these cell-deposits in other parts of the plant such as the mesocarp vary considerably between the different species.” The dark dots seem to be a unique feature shared by the fossil and extant *Sabia* seeds. Upon magnified inspection of the endocarps of other extant genera with reticulately sculptured endocarps, such as *Iodes*, *Rubus* and *Prunus*, this feature was found to be lacking. Hence this trait provides additional supporting evidence for the identification of the fossils to *Sabia*. Therefore, we examined *Sabia* seeds of different extant species for comparison. Not every *Sabia* specimen showed the dots, but most of them did. In *Sabia dielsii*, the dots are whitish rather than dark (Fig. 3C); in *S. limoniacea* the dots appear reddish (Fig. 3D).

#### BIOGEOGRAPHIC CONSIDERATIONS

Today, *Sabia* is native to the Old World extending from India through eastern Asia, Malesia to New Guinea and the Solomon Islands with nineteen species (Van de Water, 1980), but the fossil record confirms former occurrences in Europe and North America. The genus was present in Asia by the Miocene as indicated by a fossil fruit from Yunnan, China (Zhao et al., 2004). The geographic source of the taxa that radiated into southeast Asia is uncertain, whether from Europe, where fruits are known as late as the Pliocene (Geisert and Gregor, 1981) or from North America

where they are now known to have been present as late as the mid-Miocene. The fruit of an undescribed species from the early Middle Eocene of Republic, Washington resembles *Sabia megacarpa* in its large size and prominent ribbing (Fig. 4E). The previously recognized Eocene endocarp species, *Sabia prefoetida* (Becker) Manchester from Montana and Oregon (Fig. 4F; Becker, 1969; Manchester, 1994) has smaller endocarps that are more similar to the extant Asian species.

Northwestern North America lies between two regions known for disjunct biological distributions: eastern Asia and eastern North America (Graham, 1972; Wen, 1999). Routes of migration of plants among continents of the Northern Hemisphere included two land bridges: the Bering land bridge linking western North America and Asia and the North Atlantic land bridge linking eastern North America and Europe via Greenland (Tiffney, 1985). The North American Land Bridge may have linked *Sabia* populations of Europe with those of North America during the Paleogene. The Bering land bridge is believed to have been accessible during much of the Cenozoic, but because of its high paleolatitude, the plants that traversed this land bridge were mainly temperate, rather than tropical, whereas the North Atlantic Land bridge was as at a lower latitude more suitable for thermophilic plants to traverse during the Paleogene (Tiffney and Manchester, 2001). During the Miocene, *Sabia* may have successfully migrated via the Bering bridge, so it is possible that the Asian diversification followed an introduction from North America via Beringia. However, another possibility is that *Sabia* arrived to southeast Asia from Europe as the barrier of the Turgai seaway receded in the late Cenozoic (Budantsev, 1992).

*Sabia* species today include woody climbers and more or less scandent shrubs (rarely recorded as small trees; Van de Water, 1980). Fruits of the genus have a fleshy mesocarp and red to purple exocarp and thus are attractive to birds that eat and disperse them. Long-distance dispersal is a likely explanation for the intercontinental expansion of *Sabia* during the late Cretaceous and Cenozoic. However, the large size of *S. megacarpa* fruits might argue against usual bird dispersal and favor mammals. One of the extant species with relatively large fruits, *S. limoniacea*, has been observed to be dispersed by civets (Kitamura

et al., 2002). Late Cenozoic regional extinction in North America and Europe due to climatic cooling and aridification explains the range reduction culminating in the current confinement to Southeast Asia and Malesia.

Recognition of *Sabia* adds to the diversity of Asian elements already recognized from the mixed mesophytic Miocene flora of Idaho and Oregon, including *Metasequoia*, *Glyptostrobus*, *Amentotaxus* (Kvaček and Rember, 2000), *Cercidiphyllum* (Smiley and Rember, 1985), *Tetracentron* (Manchester and Chen, 2006), *Trochodendron* (Manchester et al., 2018), and the extinct Japanese-American genus *Ozakia* (Manchester and Uemura, 2013).

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#### ADDITIONAL INFORMATION

**CONFLICT OF INTEREST.** The authors have declared that no competing interests exist.

**ETHICAL STATEMENT.** No ethical statement was reported.

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