



Sinomenium macrocarpum sp. nov. (Menispermaceae) from the Miocene–Pliocene transition of Gray, northeast Tennessee, USA

Yu-Sheng (Christopher) Liu^{a,*}, Frédéric M.B. Jacques^b

^a Department of Biological Sciences, East Tennessee State University, Johnson City, Tennessee 37614-1730, USA

^b Department of Palaeobotany and Palynology, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

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ABSTRACT

The present study documents the first confirmed fossil record of *Sinomenium* in Menispermaceae, *Sinomenium macrocarpum* sp. nov., from the recently discovered Gray Fossil Site in Tennessee, southeastern USA. The fossil species is represented by more than 120 endocarps, all of which are characterized by their horseshoe-shaped form and occurrence of highly ornamented protuberances on both dorsal and lateral crests. A combination of their relatively large size and highly developed of protuberances on the surface of endocarp warrants the new species. The new species is justified through a detailed comparison with the related and published extant and fossil species. The discovery of the genus in North America appears to support that the Gray site in southern Appalachian region represented a forest refugium during the late Neogene when the global cooling was intensified and grasslands were globally expanded.

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1. Introduction

The monotypic genus *Sinomenium* Diels of Menispermaceae is endemic to eastern Asia. It is usually a large woody vine or climber up to 20 m and mostly confined to the lowland forests of tropical and subtropical central and southern China, Japan and the Garwhal Himalaya (Kessler, 1993; Luo et al., 2008). It grows predominantly in lower altitudes, but some are found up to 2100 m (Kessler, 1993). It is also widely used as a medicinal plant to treat arthritis and other inflammatory conditions because its root and stem contain the alkaloid sinomenine (Luo et al., 2008). Menispermaceae are part of the basal Eudicots (Hoot et al., 1999; APG II, 2003). The tribe Menispermeae to which *Sinomenium* belongs, is recently found to be polyphyletic (Ortiz et al., 2007; Wang et al., 2007; Hoot et al., 2009). *Sinomenium* is found as a sister-group of *Menispermum* (Wang et al., 2007; Hoot et al., 2009), forming either the first diverging clade of Menispermaceae (Hoot et al., 2009), or an early diverging clade (Wang et al., 2007).

The taxonomic diversity and geographical distribution of menispermaceous plants seem to be more complicated in the geological past than those of today. Menispermaceous fossils, particularly endocarps, are well documented in Europe, Asia, and North America (Scott, 1954; Chandler, 1964; Gregor, 1977; Collinson, 1986; Fairon-Demaret and Smith, 2002; Jacques and De Franceschi, 2005; Jacques

and Guo, 2007). Furthermore, leaf fossils with affinities of Menispermaceae have been reported from all over the world (Hill, 1989; Doria et al., 2008). The fossil records of this family are recently summarized in detail by Doria et al. (2008) and Jacques (2009a). Although only one fossil endocarp species has been reported within its modern range, i.e. Plio–Pleistocene of central Japan (Miki, 1941), the genus *Sinomenium* was well represented in central and southern Europe during the Neogene (e.g., Mai, 1997; Martinetto, 2001; Jacques, 2009a). Like many other eastern Asian endemic plants, the fossil record of *Sinomenium* has shown that its endemic distribution appears to be related to the distributional range contraction along with the fluctuations of climate and evolution of tectonics during the Cenozoic (Ferguson et al., 1997; Manchester, 1999; Manchester et al., 2009). However, it is unknown if *Sinomenium* had ever distributed in North America. Two *Sinomenium*-like leaf types, aff. *Sinomenium*, have been reported from the late Paleocene to early Eocene of southwestern Wyoming (Wilf, 2000). The fossils are characterized by the morphology and venation patterns similar to Menispermaceae. These characters include base deeply cordate/lobate, primaries 5 or more palinactinodromous, secondaries widely spaced, tertiary and higher veins random reticulate, and margin thickened with a fimbrial vein. Having compared with Wolfe's USGS Cleared Leaf Collection, Wilf considered that the fossils would resemble either the following modern taxa of Menispermaceae, e.g. *Sinomenium acutum*, *Tinospora caffra*, and *Odontocarya* sp. or the leaves of an extinct menispermaceous endocarp (cf. *Atriaecarpum*). However, no taxonomic treatment on the fossil leaves has been done (Wilf, 2007, personal communications). Leaves of *Sinomenium* are often so variable that the

* Corresponding author. Tel.: +1 423 439 6920; fax: +1 423 439 5958.
E-mail address: liuc@etsu.edu (Y.-S.(C.) Liu).

determination in fossil is almost impossible unless leaf cuticles are preserved. Fossil pollen of *Sinomenium* has been reported from the Pliocene of Italy (Pini et al., 2002). Pollen grains of *Sinomenium*, *Menispermum* and other genera in tribe Menispermaceae are reported indistinguishable (Harley and Ferguson, 1982); therefore, pollen data though maybe plentiful contribute little for the fossil history of this group. There is no doubt that endocarps have so far provided the best fossil data towards our understanding of the diversity of Menispermaceae in the geological past.

In this article, the fossil endocarps from the Gray site are morphologically compared with related extant and published fossil taxa of Menispermaceae. This leads to establish the first confirmed fossil *Sinomenium* record in North America. Paleoeological implications of this new find are also discussed.

2. Material and methods

Fossil endocarps were collected from the laminated clay excavated at the Gray Fossil Site (GFS) in Washington County of Tennessee (36.5°E, 82.5°W; Fig. 1). The site was found in May 2000 during a road construction project (Clark et al., 2005). A series of auger drillings suggest that the GFS deposits consist of about 40 m of a sequence of finely laminated clays, silts and fine sands intermixed with isolated gravel lenses and extend laterally about 30,000 m² (Shunk et al., 2006). The GFS is now interpreted as the fill of eleven separate sinkholes developed on a fold limb within Knox Group (Cambrian–Ordovician) dolostones (Shunk et al., 2006; Whitelaw et al., 2008). Shunk et al. (2006) recognized three facies at the site, i.e. graded, laminated, and subaerial, in ascending order (Fig. 2). Subsequent excavation and bulk sieving from the near-top laminated facies have yielded diverse groups of well preserved plant and animal fossils (Hulbert et al., 2009). The co-occurrence of a dwarf tapir (*Tapirus polkensis*) and short-faced bear (*Plionarctos* sp.) within the laminated facies constrains the layer to be a Late Hemphillian age (7 to 4.5 Ma), viz. latest Miocene to earliest Pliocene (Shunk et al., 2006).

A large quantity of fossil fruits and seeds have been uncovered from the laminated facies, out of which menispermaceous endocarps are likely sorted due to their characteristic horseshoe-shaped form. Totally 121 specimens were obtained and assigned to *Sinomenium*.

The descriptive terminology for both living and fossil menispermaceous endocarps are lack of consistency (Chandler, 1961; Dorofeev, 1963; Forman, 1974; Thanikaimoni, 1984, 1986; Manchester, 1994; Mai, 1997; Martinetto, 2001; Jacques, 2006, 2009a,b). A schematic illustration demonstrated by large endocarps of *Menispermum canadense* is made to unify the terms used in the present study (Fig. 3). Generally, endocarps of the tribe Menispermaceae have both the dorsal and lateral crests flanked on both sides by transverse

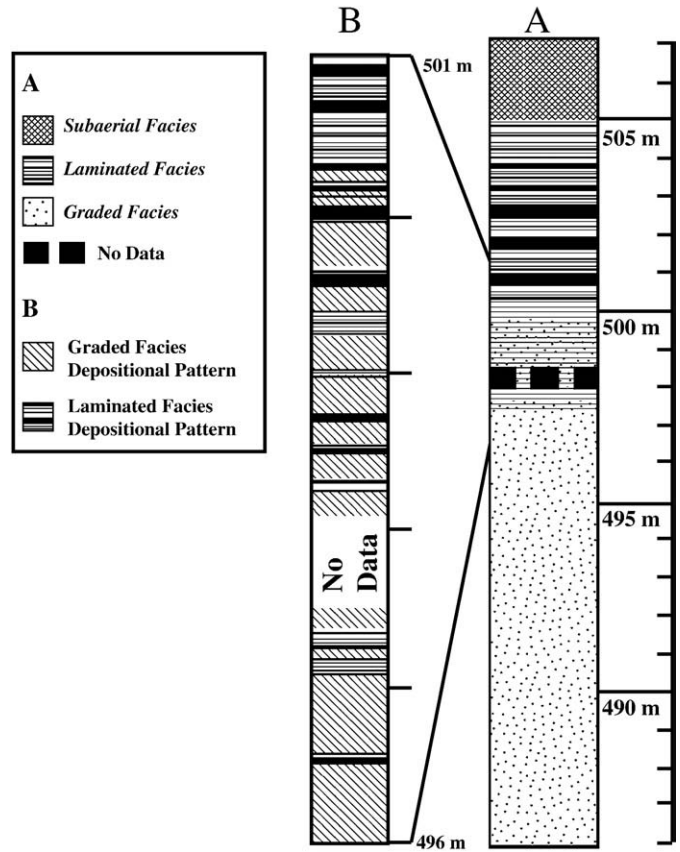


Fig. 2. Diagram showing stratigraphy of the Gray Fossil Site (redrawn from Shunk et al., 2006). (A) Stratigraphic column showing distributions of three distinct facies within upper 20 m of lacustrine GFS sediments. (B) Details of transition from graded facies to laminated facies occurring between 497 to 501 m elevations. Plant fossils were collected from laminated facies from 500 to 505 m elevations.

protuberances. The use of the term condyle has been confused (Dekker, 1983; Jacques, 2006). We follow the strict definition of Dekker (1983), meaning the intrusion of the endocarp as seen from inside the seed cavity. In other words, condyle denotes the depressed central part, which is delimited by lateral crest and ventral notch.

Fossil endocarps are determined through close comparisons with living materials, as reviewed in detail by Tiffney (1991). Forman (1974) pointed out that the distinct patterns of raised ornamentation on the surface of the endocarp in Menispermaceae are hidden within the fruit. To reveal the surface of endocarp from herbarium specimens, some simple preparation is necessary. The following method is after Forman (1974) and Tiffney (1991).

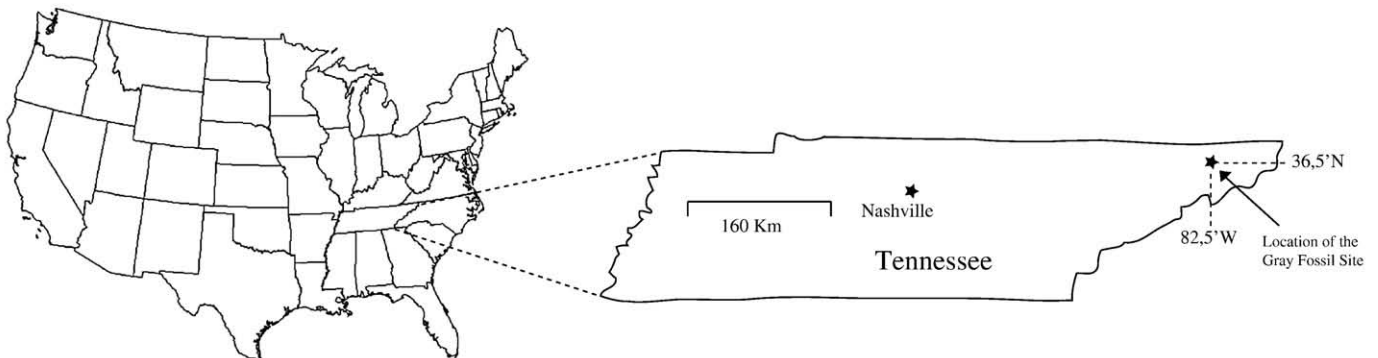


Fig. 1. Map showing the location of the Gray Fossil Site, northeast Tennessee (modified from Shunk et al., 2006).

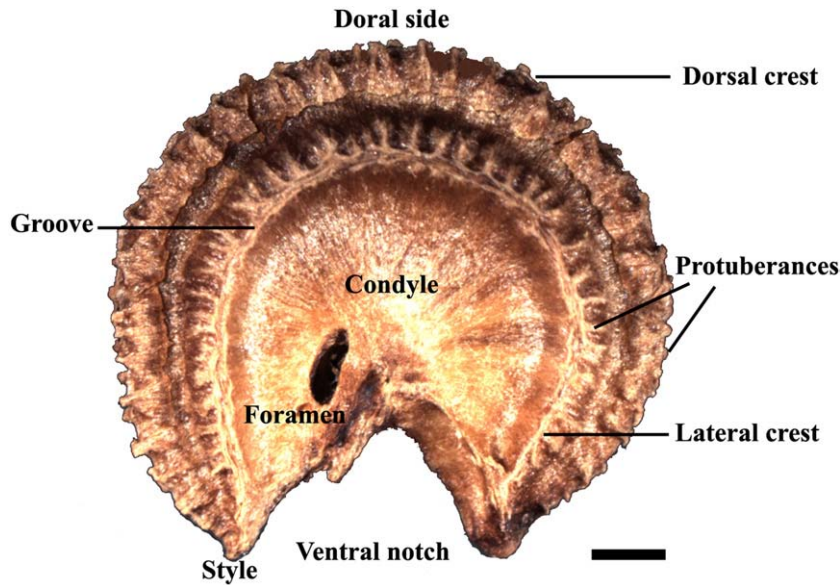


Fig. 3. Endocarp of extant *Menispermum canadense* L. (collected from Wisconsin) showing the terminology used in the present study (scale bar = 1 mm).

Dry fruit specimens from herbarium sheets were first boiled in water for about ten minutes to soften the pericarp, which could then be removed with a fine toothbrush. As much as possible of the soft tissue adhering to the surface of the endocarp was brushed away and then cleaned with the toothbrush. The endocarps were left in petri dish to dry exposed to the air for at least one day. The endocarps were examined by Olympus SZX12 dissecting microscope and images were captured digitally by Microfire. Surface details of endocarps were studied by standard techniques of scanning electron microscopy (SEM), using the Zeiss DSM 940 SEM model.

Both the comparative living endocarps and fossil specimens were deposited in the fossil collection at the East Tennessee State University and General Shale Brick Natural History Museum at the Gray Fossil Site.

3. Systematic descriptions

Order Ranunculales Dumortier

Family Menispermaceae A.L. de Jussieu

Genus *Sinomenium* Diels

Species *Sinomenium macrocarpum* sp. nov. Liu et Jacques (Plate I, 1–6; Plate II, 1–9; Plate III, 1–12)

Specific diagnosis: Endocarp horseshoe-shaped in lateral view, ventral notch straight; relatively large, length 4.1–6.7 mm, width 3.3–5.7 mm, thickness 0.9–2.1 mm, length–width ratios 1.1–1.5; on lateral crest developed 22–25 ridges, while on dorsal crest 25–30 ridges well-developed; foramen oval and tiny with its diameter less than 0.3 mm.

Description: Endocarp bisymmetrical, laterally compressed, ovate to slightly oblique in later view, with a straight to concave ventral notch and a round dorsal margin (Plate I, 1; Plate II, 1, 4, 7; Plate III, 1, 3, 5, 7–12); endocarp length 4.1–6.7 mm (average = 5.4, standard deviation = 0.53, $n = 30$), width 3.3–5.7 mm (average = 4.4, standard deviation = 0.47, $n = 30$), thickness 0.9–2.1 mm (average = 1.5, standard deviation = 0.35, $n = 11$); dorsal margin of endocarp with a crest (i.e. dorsal keel) in the plane of symmetry (Plate I, 1; Plate II, 1, 4, 7; Plate III, 1, 3, 5, 7–12); both lateral faces with a broad, shallow, and smooth concavity (i.e. condyle) rimmed by a horseshoe-shaped ridge (lateral crest) dividing dorsal and ventral ornamentation (Plate I, 1; Plate II, 1, 4, 7; Plate III, 1, 3, 5, 8, 11, 12); endocarp wall on condyle covered by elongated sclerenchymous cells arranged in parallel groupings (Plate I, 4–6); both dorsal and lateral crests decorated by radially aligned ridges (Plate I, 2; Plate II, 2, 5, 8; Plate III, 2, 4, 6), dorsal

crest ornamented by 2-row 25–30 well-developed and alternately arranged ridges (Plate I, 2) while lateral crest with 2-row 22–25 protuberances which are well-developed on the side facing dorsal crest and weakly developed on the other side facing condyle (Plate I, 3; Plate II, 3, 6); a median groove present on both dorsal and lateral crests where 2-row radially aligned ridges meet each other (Plate I, 2, 3; Plate II, 3, 6); a tiny and oval foramen piercing the endocarp near the stylar limb (Plate I, 1; Plate II, 1, 4, 7; Plate III, 1, 3, 5, 7–12).

Etymology: The specific epithet *macrocarpum* is given for the larger endocarps than those of the extant species (*Sinomenium acutum*).

Holotype: ETMNH 3839, East Tennessee State University and General Shale Brick Natural History Museum Fossil Collections (ETMNH) (Plate I, 1–3).

Paratypes: ETMNH 3836 (Plate II, 1–3), ETMNH 3838 (Plate II, 4–6).

Material: Totally 121 endocarps, with 30 complete ones (ETMNH 3812–3835, 3837, 3840–3842).

Type locality: Gray Fossil Site, Washington County, northeastern Tennessee, USA (36.5°E, 82.5°W).

Stratigraphic position: near the top layer of the laminated black clay.

Age: Late Hemphillian (latest Miocene to earliest Pliocene).

4. Comparison and discussion

In surveying the endocarps of 116 living species of 55 genera, representing 75% of the taxa in Menispermaceae, Jacques (2006, 2009b) indicates that the family has drupaceous fruits with morphologically diverse endocarps. The morphology of endocarps of Menispermaceae includes two forms, i.e. the straight and horseshoe-shaped endocarps (Thanikaimoni, 1984; Jacques, 2006, 2009b). The majority are straight or curved (curvature of whole tissue, e.g. horseshoe-shaped or partly curvature), while only a few species have globose endocarps. Almost all of the endocarps furthermore show a peculiar structure, condyle. In other words, the condyle is a structure diagnostic in Menispermaceae, with an exception only in eight genera (*Arcangelisa*, *Aspidocarya*, *Disciphania*, *Orthomene*, *Penianthus*, *Pycnarrhena*, *Sphenocentrum* and *Tinomisium*) (Jacques, 2009b). Ornamentation of endocarps, however, is quite diverse, from being either smooth or rugose to bearing grooves and ridges. Numerous curved endocarps, especially when crustaceous, bear transverse ridges such as in *Stephania* and *Tiliacora*.

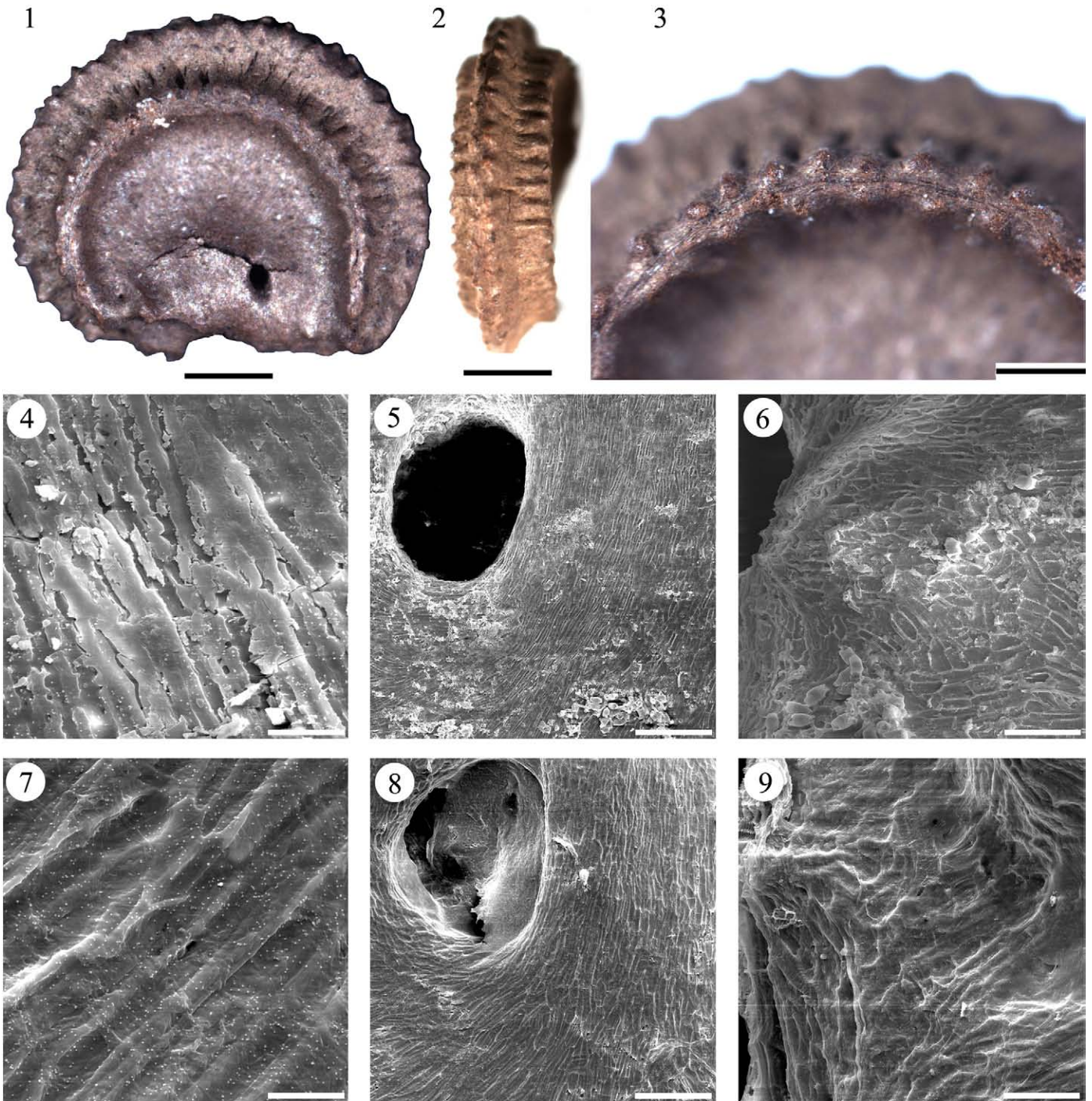


Plate I. Fossil and extant endocarps of *Sinomenium*. Scale bars: Figs. 1, 2 = 1 mm; Fig. 3 = 0.5 mm; Figs. 4, 7 = 20 μ m; Figs. 5, 8 = 200 μ m and Figs. 6, 9 = 100 μ m.

- 1–6. *Sinomenium macrocarpum* sp. nov. from the Gray Fossil Site, top layer of the laminated black clay, northeastern Tennessee, USA.
1. Holotype, ETMNH 3839. Lateral view showing the horseshoe-shaped endocarp with a C-shaped lateral crest and more or less straight ventral notch.
 2. Dorsal view of holotype showing highly ornamented protuberances on both dorsal and lateral sides.
 3. Close-up of holotype on lateral view showing lateral crest flanked with well-developed protuberances. Note the clear groove on the surface of lateral crest.
 4. SEM close-up of another endocarp, ETMNH 3842, showing the surface detail of condyle. Note the arrangement of paralleling elongate endocarp cells on the surface.
 5. Same endocarp as Fig. 4. SEM close-up of foramen and surrounding area showing the same pattern of endocarp cell arrangement.
 6. Same endocarp as Fig. 4. SEM close-up of dorsal crest. Note the endocarp cells are much shorter than those on condyle.
 - 7–9. *Sinomenium acutum* (Thunb.) Rehd. et Wils., extant endocarp for comparison (collected from Yunnan, southwestern China; C.Y. Yu 1960/8, KUN). Note the similar patterns of endocarp cell arrangement on areas of condyle, around foramen, and dorsal crest with those of fossil.
 7. SEM close-up of condyle.
 8. SEM close-up of foramen and surrounding area.
 9. SEM close-up of dorsal crest.

The classification of Menispermaceae is traditionally based on the fruit characters (Diels, 1910; Forman, 1974; Kessler, 1993), although these characters are found not to be sufficient to warrant the classi-

fication of the family (Jacques, 2009b). Thanikaimoni (1984) proposed an atlas of menispermaceous endocarps, but only with very short descriptions at the generic level with no reference to the

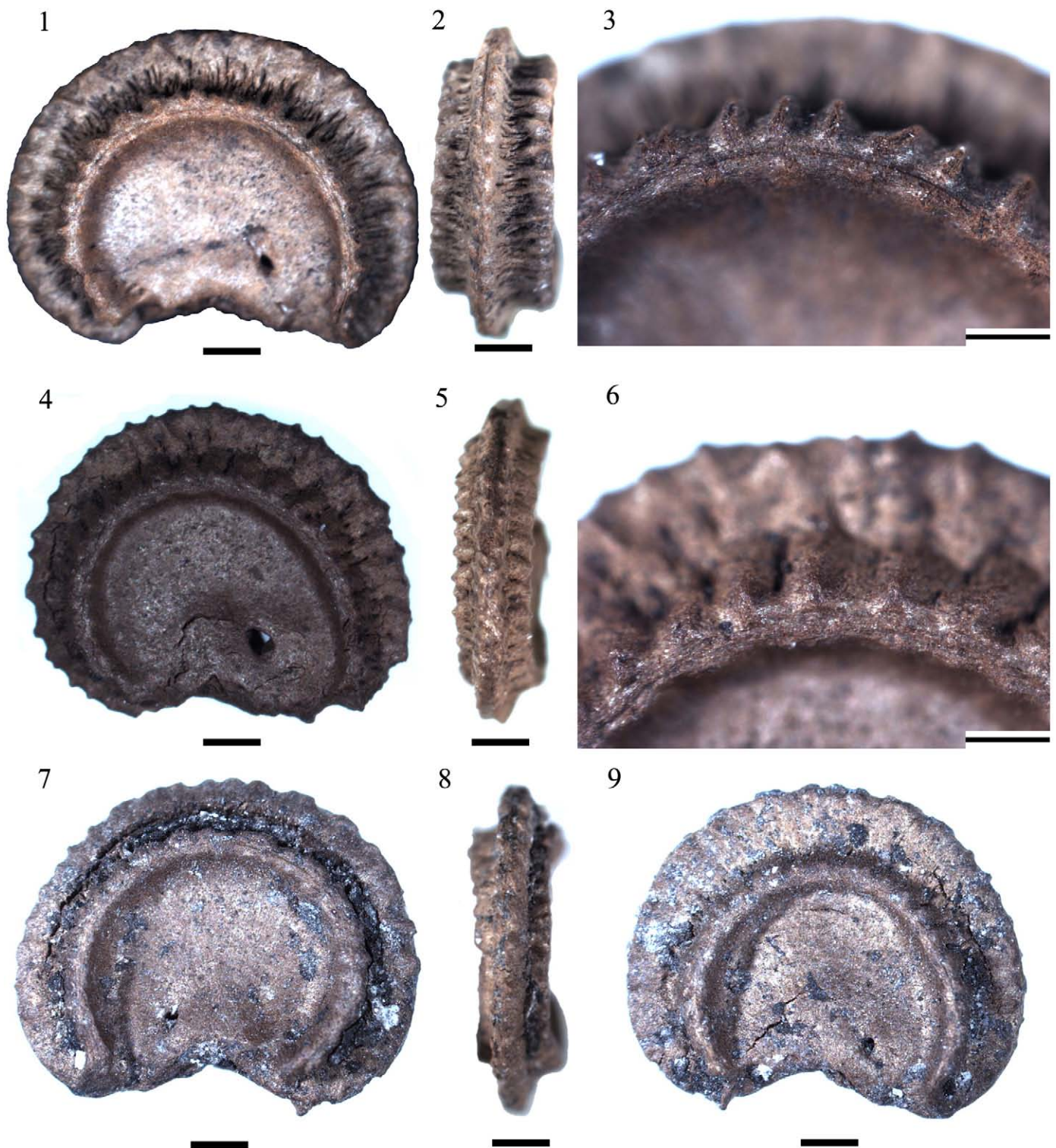


Plate II. Endocarps of *Sinomenium macrocarpum* sp. nov. from the Gray Fossil Site, northeastern Tennessee, USA. Scale bars: 1 mm in Figs. 1, 2, 4, 5, 7–9; 0.6 mm in Figs. 6, 9.

- 1–3. ETMNH 3836.
 1. Lateral view.
 2. Dorsal view showing the thickness of endocarp.
 3. Magnification from Fig. 1, showing the detail of lateral crest.
 4–6. ETMNH 3838.
 4. Lateral view.
 5. Dorsal view.
 6. Magnification from Fig. 4.
 7–9. ETMNH 3818.
 7. Lateral view showing the abraded protuberances.
 8. Dorsal view.
 9. Lateral view of another side of Fig. 7.

general shape of the endocarp. Forman (1956, 1974, 1997) only focused on Asian species for floristic revisions; the endocarp descriptions are included in general species description and are not always easily comparable between different groups.

The subdivision into tribes has always been based upon characters of the fruits and seeds. Only five tribes are accepted in Kessler's most recent treatment (Kessler, 1993). In tribe Menispermeae, the endocarps are almost all horseshoe-shaped and their dorsal crest bears much of the ornamentation. In some parts of the family, especially in the tribes Menispermeae and Tinosporeae, a remarkable variety of raised ornamentation on the surface of the endocarp is developed for different genera and species.

4.1. Placement into *Sinomenium*

The fossil endocarps from the Gray site are characterized by their horseshoe-shaped form and the presence of one dorsal crest and one lateral crest on each side, one foramen piercing on condyle, and smooth endocarp surface.

Horseshoe-shaped endocarps are quite common in Menispermaceae (Jacques, 2009b). Manchester (1994) mentioned that endocarps with the horseshoe-shaped locule and fluted dorsal surface are diagnostic of the tribe Menispermeae. Among more than 70 genera in Menispermaceae, the horseshoe-shaped endocarps are seen in about 20 genera spreading in two tribes, Pachygoneae and Menispermeae (Jacques, 2009b). A comparison is made to distinguish the 20 genera from both tribes in features such as endocarp surface, condyle, and size (Table 1). With either two or absence of lateral crests on each side, the endocarps from tribe Pachygoneae are different from the present fossils (Table 1). Within the tribe Menispermeae, five genera (*Cissampelos*, *Cyclea*, *Pericampylus*, *Sarcopetalum*, and *Stephania*) have endocarps with two dorsal crests. Moreover, *Stephania* has a central foramen and horseshoe-shaped thicker margin, which are different from *Sinomenium* (Miki, 1941). In the absence or weakly development of lateral crest, endocarps from five other genera (*Cocculus*, *Hypserpa*, *Rhaptonea*, *Sciadotenia*, and *Strychnopsis*) are distinct from the fossils in Gray. The occurrence of strip on both dorsal and lateral crests and small condyle can rule out *Legnephora*. The condyle in *Limacia* made of two large lateral cavities and that in *Limaciopsis* being completely closed are very distinct from the fossils. Finally, *Spirospermum* can be separated from the fossils due to its spiral cavity on condyle. Consequently, the present fossil endocarps show close resemblance with both *Menispermum* and *Sinomenium*.

Recent molecular systematic study of Menispermaceae suggests a reduced Menispermeae from a traditional large tribe concept with 16 advanced genera to two basal genera, i.e. *Menispermum* and *Sinomenium* (Hoot et al., 2009). These two genera are similar in endocarps in characters such as horseshoe-shaped form, depressed condyle, ridges on lateral crest, large ventrally opened central area, and a foramen near the stylar limb, which make the separation confused. Jacques (2006) proposed that *Menispermum* can be separated from *Sinomenium* by characters, such as the greater concavity of its ventral margin, higher number of transverse ridges, and bigger size. These criteria are useful, though sometimes they are a little confusing and vague when quantitative measurements are considered. According to our observations, a comparison between the fossil endocarps and species of living *Sinomenium* and *Menispermum* is made to help with determination of the fossil endocarps and separation between the endocarps of *Sinomenium* and *Menispermum* (Table 2).

It is evident that the fossil endocarps from the Gray site are different from the two species of *Menispermum* in that the former are smaller and have fewer ridges developed on both lateral and dorsal crests than the latter. The fossil endocarps resemble mostly those of *Sinomenium acutum* in both lateral and dorsal views (Table 2)

and surface details of condyle and dorsal crest under SEM (compare Plate I, 4–6 with Plate I, 7–9). It is concluded that the fossil endocarps from the Gray site can be classified as *Sinomenium*. However, it is necessary to mention that *Sinomenium macrocarpum* sp. nov. displays some minor differences from the living *Sinomenium acutum*, e.g. the fossils with more projected ridges on both lateral and dorsal crests and different angles formed between lateral crest and condyle (Table 2).

It is interesting to note that the number of transverse ridge appears to link to the size of the endocarp (Jacques, 2006; Table 2). The function of the transverse ridges is unknown, but probably in reinforcing the solidity of endocarp (Jacques and Bertolino, 2008), enforcing the seed cavity from being broken, or involving in the dissemination process/fruit dispersal.

4.2. Comparison to fossil taxa

The fossil endocarps of *Sinomenium* were first recognized by Kirchheimer (1943), who reported *Sinomenium militzeri* from the lower Miocene of Wiesa and Kamez, Germany (Mai, 1997). Up till now, more than five species, including *Sinomenium acutum* (modern species) from the Pliocene to Pleistocene of Japan (Miki, 1941; Momohara et al., 1990; Momohara and Mizuno, 1999), have been reported mainly from the Neogene of central and southern Europe (e.g., Reid, 1920, 1923; Szafer, 1947, 1954, 1961; Dorofeev, 1955; Kirchheimer, 1957; van der Burgh, 1987; Martinetto and Gregor, 1989; Martinetto, 1996; Mai, 1997; Cavallo and Martinetto, 2001) and Siberia (Dorofeev, 1963; Takhtajan, 1974).

Mai (1997) suggested that the two Eocene endocarps from England, *Palaeosinomenium* Chandler and *Wardenia* Chandler (now *Wardensheppeya* Eyde) (Collinson, 1983), should be reconsidered as *Sinomenium*, due to their minor characteristic differences probably only at the specific rather than generic level. Recently, a new extinct menispermaceous genus, *Sinomenites*, was established by Nikitin (2006) on the basis of some Eocene endocarps from Siberia. The endocarps of *Sinomenites* are similar to those of *Sinomenium*, but they can be distinguished from those of *Sinomenium macrocarpum* in that the former are smaller in size and almost rounded in outline (Table 3; Nikitin, 2006). A detailed morphometric comparison on the published fossil *Sinomenium* (including *S. macrocarpum* sp. nov.) or *Sinomenium*-like endocarps will be published separately. A brief comparison in morphology of endocarps is thus provided below (Table 3). It is evident that the fossil endocarps of the Gray site are distinct from previously published species in their overall size, and higher numbers of ridges on both lateral and dorsal sides.

In conclusion, it is clearly shown that the endocarps of *Sinomenium macrocarpum* are obviously different from those of other published fossil species. *S. macrocarpum* has the largest endocarps. Furthermore, except *Sinomenium militzeri*, *S. macrocarpum* has more ridges developed on dorsal crest. With a combination of characters, *S. macrocarpum* therefore represents a new species.

5. Paleocology

Since the Gray site was found in 2000, a great diversity of fossils has been uncovered, enriching the ancient biota which is barely known in southeastern North America. Evidence from the fossil salamanders, turtles, and mammals at this site suggests a unique paleoecological environment developed in southern Appalachians during the late Neogene, when the vegetation transition from the C₃ dominated forest to C₄ grassland and the global climate deterioration began to emerge (Wallace and Wang, 2004; Schubert and Wallace, 2006). The rare occurrence of equids but prolific number of individual tapirs support the dominance of an arboreal setting, that is, a ponded environment surrounded by trees (Wallace and Wang, 2004). This reconstruction of North American late Neogene forest refugium is

further confirmed by studies of stable isotope analyses of bulk and serial samples of fossil tooth enamel from all ungulates present at the Gray site (DeSantis and Wallace, 2008). The abundant presence of

Sinomenium, along with dominant tree (*Quercus*, *Carya*), shrub (*Corylopsis*) and vines (*Vitis*, *Sargentodoxa*) taxa, provides further evidence of forested setting at the Gray site.

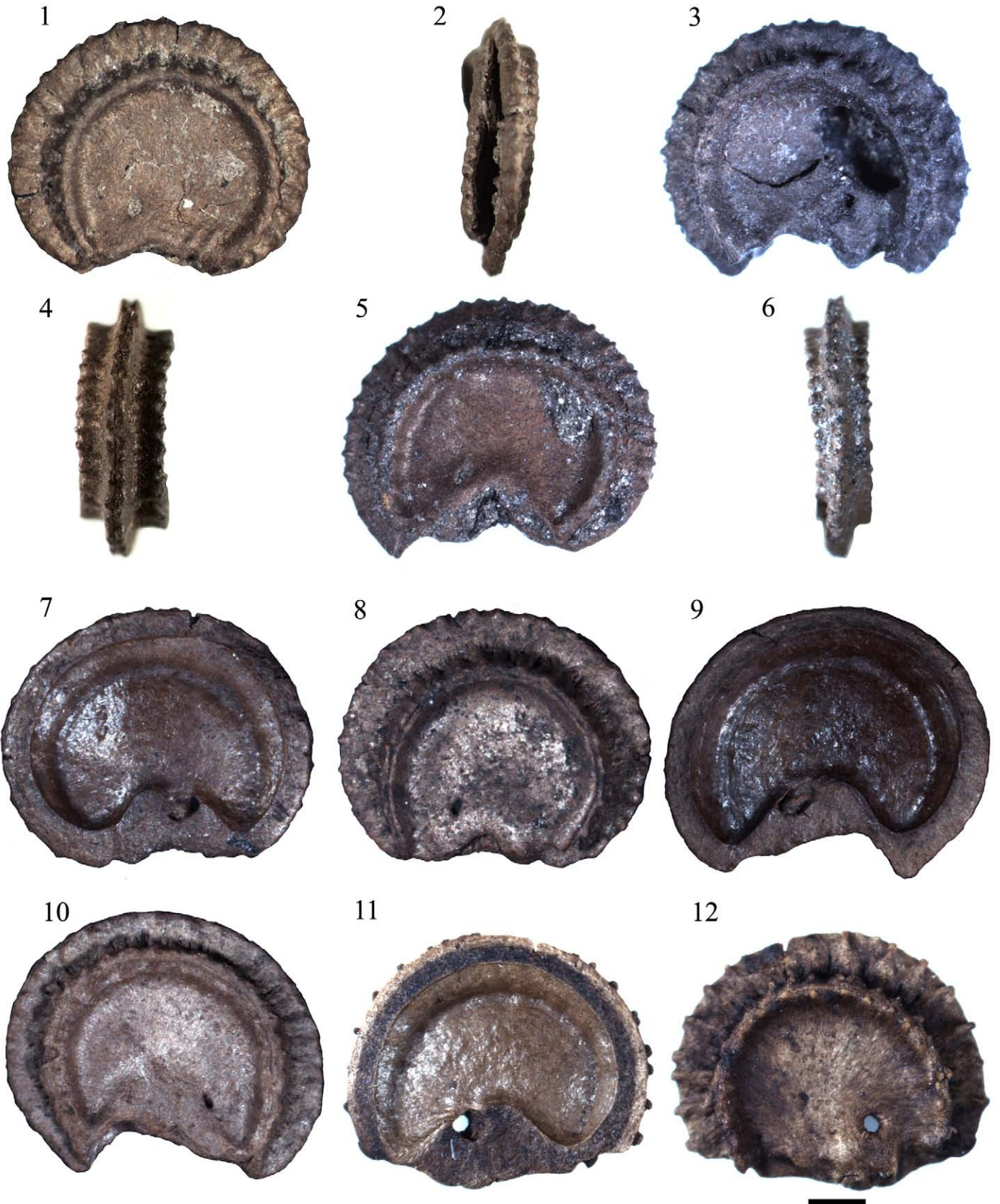


Table 1

Comparison of horseshoe-shaped endocarps in Menispermaceae. Two genera, *Caryomene* and *Echinostephia*, are described as horseshoe-shaped endocarps, but no observations were performed by Jacques (2009b). *Diploclesia*, a genus of the tribe Menispermeae, has their endocarp either hairpin-shaped or quite elongated; therefore, it is excluded from the comparison.

Data modified from Jacques (2009b).

	Endocarp surface	Condyle	Size ($L \times W \times T$ mm)
<i>Tribe Pachygoneae</i>			
<i>Hyperbaena</i> ^a	One slight dorsal crest, two lateral crests on each side; surface with reticulated ridges	Double intrusive condyle coma-shaped	12 × 11 × 8.2
<i>Pachygone</i> ^b	One slight dorsal crest, no lateral crest; surface reticulate; no ridges	Double external condyle not perforated; a strip partly hiding it ventrally	9.1–9.6 × 8.2–9.4 × 4.5–4.8
<i>Syrhionema</i>	One dorsal crest, dorsal face with two lateral concavities, lateral concavities, lateral crest absent; surface reticulate	Central area totally perforated	13 × 12 × 8.7
<i>Tribe Menispermeae</i>			
<i>Cissampelos</i> ^c	Two dorsal crests, two lateral crests on each side; all crests bearing spines; surface smooth	Double external condyle, not perforated; sometime inconspicuous	4.4–6.8 × 3.9–5.8 × 1.8–2.7
<i>Cocculus</i>	One dorsal groove/crest, lateral crest absent; one lateral groove on each side, with numerous transverse ridges	Double external condyle, perforated or not perforated	5 × 4 × 2.1
<i>Cyclea</i>	Two dorsal crests with 16 small spines, two lateral crests on each side; surface smooth	Inconspicuous	4.8 × 4 × 2.7
<i>Hypserpa</i>	One slight dorsal crest, lateral crest absent; surface reticulate	Double external condyle partly filled	6.5 × 6.5 × 4.1
<i>Legnephora</i>	One small/high strip on dorsal crest, one high strip on lateral crest; surface smooth	Double external condyle, not perforated; central area either small or large	4.9 × 4.3 × 6
<i>Limacia</i>	One large dorsal band with rugose surface overlapping partly the lateral faces; surface smooth	Condyle made of 2 large lateral cavities	20.4 × 15.5 × 12.33
<i>Limaciopsis</i>	One dorsal crest, one lateral crest on each side; with small transverse ridges; surface smooth	Double external condyle, not perforated; central area either small or large	14.2–15.9 × 11.5–11.8 × 5.2–6.2
<i>Menispermum</i>	One dorsal crest, one lateral crest on each side, connected by short transverse ridges; surface smooth	Double external condyle, not perforated; central area either small or large	6–7.5 × 5–6.7 × 1.9–2.1
<i>Pericampylus</i>	Two dorsal crests, two lateral crests on each side; all crests bearing spines; surface smooth	Double external condyle, not perforated	5.7 × 5.5 × 2.4
<i>Rhaptonema</i>	One dorsal crest, lateral crest absent; surface rugose, slightly ornamented	Seed cavity filled, condyle very limited	19.9 × 16.4 × 11.3
<i>Sarcopetalum</i>	Two dorsal crests, two lateral crests on each side; all crests bearing spines; surface smooth	Double external condyle, not perforated central area large	5.9 × 4.6 × 2.9
<i>Sciadotenia</i> ^d	One dorsal crest, lateral crest absent; surface irregular and reticulate	Double external condyle, not perforated	12.7 × 10.5 × 7.1
<i>Sinomenium</i>	One dorsal crest, one lateral crest on each side, connected by short transverse ridges; surface smooth	Double external condyle, not perforated; central area either small or large	4.9–5.7 × 3–3.7 × 1.4–1.5
<i>Spirospermum</i>	One dorsal crest, one lateral groove on each side, connected by numerous transverse ridges; dorsal face with two lateral concavities	Spiral seed cavity making condyle a sharp line central area filled, limiting the double external condyle to a line between central and horseshoe-shaped areas	10.7 × 10.5 × 5.1
<i>Stephania</i>	One or two dorsal crests, one lateral crest on each side; connected by few to many transverse ridges or spines	Double external condyle, not perforated	7.1 × 5.4 × 2.2
<i>Strychnopsis</i>	Endocarp without excavated faces; one dorsal crest, one slight lateral crest on each side; surface slightly reticulate	Central area filled, limiting the condyle to a sharp line surrounding it	10.5 × 10.2 × 5.6

Note:

^a *Hyperbaena* has two endocarp types, i.e. hairpin-shaped and horseshoe-shaped.

^b *Pachygone* has three types of endocarps, i.e. hairpin-, horseshoe-, and reniform shaped.

^c *Cissampelos* has two endocarp types, i.e. hairpin-shaped and horseshoe-shaped.

^d *Sciadotenia* has two endocarp types, i.e. horseshoe-shaped and reniform.

The occurrence of multiple fossil crocodilians (*Alligator* sp.) at the Gray site constrains the paleoclimate condition with a Coldest Month Mean Temperature (CMMT) of more than 5.5 °C,

because temperature is the principal influence on the global distribution of crocodilians (Shunk et al., 2006). This is consistent with the discovery of *Sinomenium*. The current geographic

Plate III. Endocarps of *Sinomenium macrocarpum* sp. nov. from the Gray Fossil Site, northeastern Tennessee, USA. Scale bar for all the images = 1 mm.

- 1, 2. ETMNH 3812.
1. Lateral view.
2. Dorsal view. Note the slightly split of endocarp valves.
- 3, 4. ETMNH 3813.
3. Lateral view showing a broken condyle.
4. Dorsal view showing the well-developed protuberances, particularly on the lateral crests.
- 5, 6. ETMNH 3814.
5. Lateral view.
6. Dorsal view.
- 7, 8. ETMNH 3817.
7. Lateral view of inner endocarp showing the horseshoe-shaped smooth locule, which is bisymmetrical.
8. Lateral view of the outer endocarp valve same as Fig. 7.
- 9, 10. ETMNH 3825.
9. Lateral view of inner endocarp.
10. Later view of outer endocarp.
- 11, 12. ETMNH 3826.
11. Lateral view of inner endocarp.
12. Lateral view of outer endocarp.

Table 2Comparison of the fossil endocarps with extant species in *Sinomenium* and *Menispermum*. Data also compiled from published work (e.g. Nakayama et al. 2000).

Character	<i>Sinomenium macrocarpum</i>	<i>Sinomenium acutum</i>	<i>Menispermum canadense</i>	<i>M. dauricum</i>
Size ($W \times H \times T$ mm)	4.1–6.7 × 3.3–5.7 × 0.9–2.1	4–5.2 × 5–6.3 × 1.5–2.2	7 × 8 × 2	7 × 9 × 3
Lateral view	Slightly oblique or semicircular	Semicircular	Almost rounded	Same as <i>M. canadense</i>
Ventral notch	Same as <i>S. acutum</i>	Straight/slightly concave	V-shaped	Same as <i>M. canadense</i>
Protuberances on lateral crest	Developed on side facing dorsal crest, but weakly developed on side facing condyle	Well-developed on both sides	Weakly developed on side facing dorsal crest, absent on other side	Same as <i>M. canadense</i>
Number of protuberances	22–25	18–21	27–30	32–39
Foramen	Oval, very small (0.2–0.3 mm)	Circular, small (0.5 mm)	Elliptical, big	Same as <i>M. canadense</i> Same as <i>M. canadense</i>
Dorsal view				
Protuberances on dorsal crest	Same as <i>S. acutum</i>	Well-developed on both sides of crest and arranged alternately and oppositely	Well-developed on both sides of crest and arranged alternatively and oppositely	Same as <i>M. canadense</i>
Number of protuberances	25–30	20–21	35–38	32–40
Joint where dorsal and lateral crests meet	Same as <i>S. acutum</i>	Rough; ridges from dorsal Crest extend into lateral crest	Smooth; ridges from dorsal crest Not extend into lateral crest	Same as <i>M. canadense</i>
Angles between lateral and dorsal crests	Obtuse	Obtuse	Right	Same as <i>M. canadense</i>
Angles between lateral crest and condyle	Right	Obtuse	Obtuse	Same as <i>M. canadense</i>

distribution of this genus requires a CMMT of -7.3 – 21 °C (Luo et al., 2008).

The mechanisms of fruit dispersal in Menispermaceae are generally not well understood. There is no report about how *Sinomenium* fruits disperse. The endocarps of *Elephantomene eburnean*, an endemic menispermaceous species to northeastern South America, have been found in the stomach of a tapir (Henry et al., 2000), suggesting mammals are involved in the process. It is not known if this animal would have helped *Sinomenium* disperse in the Neogene, although many tapirs are found at the Gray site (Hulbert et al., 2009). Taphonomically, the fossil endocarps of *Sinomenium* were found associated with the tapir and rhino skeletons and a red panda jaw.

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Table 3Comparison of the fossil *Sinomenium* and *Sinomenium*-like endocarps.

Data from Reid (1920); Kirchheimer (1943); Szafer (1947); Chandler (1961); Dorofeev (1955, 1963); Edey (1970); Takhtajan (1974); Nikitin (2006).

Character	<i>S. macrocarpum</i> sp. nov.	<i>S. cantalense</i> (Reid) Dorofeev	<i>S. dielsii</i> Szafer	<i>S. militzeri</i> Kirchheimer	<i>S. sibiricum</i> Dorofeev	<i>Sinomenites baluevae</i> Nikitin ^b	<i>Palaeosinomenium</i> Chandler	<i>Wardensheppeya</i> (Chandler) Edey
1. Reference	This paper	Reid (1920); Dorofeev (1955)	Szafer (1947)	Kirchheimer (1943)	Dorofeev (1963); Takhtajan (1974)	Nikitin (2006)	Chandler (1961)	Chandler (1961); Edey (1970)
2. Age	Late Miocene–Early Pliocene	Late Miocene ^a	Miocene	Miocene–Pliocene	Oligocene	Late Eocene (Priabonian)	Eocene–Paleocene	Paleocene
3. Size (<i>W</i> × <i>H</i> × <i>T</i> mm)	4.1–6.7×3.3–5.7×0.9–2.1	4–5.8×3.3–4.1	3–5.6×3.2–5.6	3.9–6.4×3.2– 5.1×2.3	3.3–5×4.4–5.6	2.8×3.1	3.1–4×3.7–4.75×1.5– 1.6	3.5–5×3– 4×1.25
4. Lateral view	Slightly oblique or semicircular	Semicircular	Semicircular, almost rounded	Semicircular	Semicircular to reniform	Semicircular, almost rounded	Obliquely ovate	Reniform
4.1. Ventral notch	Straight/slightly concave	Nearly straight or weakly concave	Concave	Unknown	Straight or bent	Nearly straight or weakly concave	Somewhat concave	Short, slightly concave
4.2. Protuberances on lateral crest	Developed on side facing dorsal crest, weakly developed on side facing condyle	Same as <i>S. macrocarpum</i>	Same as <i>S. macrocarpum</i>	Higher ridges well on crest	Well-developed on side facing dorsal crest, weakly developed on side facing condyle	Well-developed on side and crest	Unknown	Unknown
4.3. Number of protuberances	22–25	20	<20	30	20–25	27–29	18–21	20
4.4. Foramen	Oval, very small (0.2–0.3 mm)	Oval	Unknown	Unknown	Small rounded or slightly elongated	Oval, small	Elongate, oblique and big (~1 mm)	Elongate and big (0.45–0.75 mm)
5. Dorsal view								
5.1. Protuberances on dorsal crest	Well-developed on both sides and alternately arranged	High ridges well- developed	Weakly developed	Well-developed	Weakly developed	Well-developed on both sides and alternately arranged	Unknown	Unknown
5.2. Number of protuberances	25–30	20	<20	30	20–25	27–29	Unknown	Unknown
5.3. Joint where dorsal and lateral crests meet	Not smooth; protuberances from dorsal reach lateral crest	Unknown	Unknown	Smooth	Not smooth	Not smooth, protuberances from dorsal reach lateral crest	Unknown	Unknown
5.4. Angle between lateral and dorsal crests	Obtuse	Unknown	Unknown	Unknown	Obtuse	Obtuse	Unknown	Right
5.5. Angle between lateral crest and condyle	Right	Unknown	Unknown	Unknown	Right	Right	Unknown	Right

Note:

^a Reid (1920) reported this site as the Early Pliocene. It is now accepted as the Late Miocene (Mai and Martinetto, 2006).^b When establishing a new extinct genus in Menispermaceae, Nikitin (2006) reported one species (type, *Sinomenites baluevae* Nikitin) along with three other undetermined taxa (*S. sp.1–3*). However, both *Sinomenites sp.2* and *S. sp.3* may not represent real affinities with *Sinomenites*, though *S. sp.1* is still considered as a correct determination (Nikitin 2009, personal communications).

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