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 predominately in lower altitudes, but some are found up to 2100 m (Kessler, 1993). It is also widely use 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 the basal Eudicots (Hoot et al., 1999; APG II, 2003) belongs, is recently found to be polyphyletic (Ortiz et al., 2007; 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 palmatodromous, 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 Menispermeae, e.g. Sinomenium acutum, Tinospora caffra, and Odontocarya sp. or the leaves of an extinct menispermaceous endocarp (cf. Atraciaarpum). However, no taxonomic treatment on the fossil leaves has been done (Wilf, 2007, personal communications). Leaves of Sinomenium are often so variable that the
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*, *Menispernum* and other genera in tribe Menispermeae 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 Menispermeae 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 Menispermeae. This leads to establish the first confirmed fossil *Sinomenium* record in North America. Paleoenvironmental 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 mesispermaceous 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 mesispermaceous 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 *Menispernum canadense* is made to unify the terms used in the present study (Fig. 3). Generally, endocarps of the tribe Mesispermeae have both the dorsal and lateral crests flanked on both sides by transverse 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 Mesispermeae 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).
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, 2) while lateral face 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 styal 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, Orthomone, Penianthus, Pycnarrhena, Sphenocentrum and Tinomiscium) (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.
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 classification 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 1. Fossil and extant endocarps of Sinomenium. Scale bars: Figs. 1, 2 = 1 mm; Figs. 3 = 0.5 mm; Figs. 4, 7 = 20 μm; Figs. 5, 8 = 200 μm and Figs. 6, 9 = 100 μm.

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 parallel 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.
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 Tinosporaeae, 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 Menispermaeae (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 Menispermaeae, the horseshoe-shaped endocarps are in about 20 genera spreading in two tribes, Pachygoneae and Menispermeae (Jacques, 2009b). A comparison is made to distinguish the 20 genera from two 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, Pericaplymus, Sarcopetalum, and Stephania) have endocarps with two dorsal crests. Moreover, Stephanthus 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, Rhaptonema, 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 Limacina made of two large lateral cavities and that in Limacopsis 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 Menispernum and Sinomenium.

Recent molecular systematic study of Menispermaeae suggests a reduced Menispermeae from a traditional large tribe concept with 16 advanced genera to two basal genera, i.e. Menispernum 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 Menispernum can be separated from Sinomenum 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 Menispernum is made to help with determination of the fossil endocarps and separation between the endocarps of Sinomenium and Menispernum (Table 2).

It is evident that the fossil endocarps from the Gray site are different from the two species of Menispernum 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 1, 4–6 with Plate 1, 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 ridges 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 militizeri 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; Doroffeev, 1955; Kirchheimer, 1957; van der Burgh, 1987; Martinetto and Gregor, 1989; Martinetto, 1996; Mai, 1997; Cavallo and Martinetto, 2001) and Siberia (Doroffeev, 1963; Takhtajan, 1974).

Mai (1997) suggested that the two Eocene endocarps from England, Polorosinomenium Chandler and Wardenia Chandler (now Wardensheppy Eye) (Collinson, 1983), should be reconsidered as Sinomenium, due to their minor characteristic differences probably only at the specific rather than generically. Recently, a new extinct menispermaceous genus, Sinomeennes, 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 Sinomeennium-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 militizeri, S. macrocarpum has more ridges developed on dorsal crest. With a combination of characters, S. macrocarpum therefore represents a new species.

5. Paleoecology

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 taphirs 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.
Note:

- Hyperbaena has two endocarp types, i.e. hairpin-shaped and horseshoe-shaped.
- Pachygone has three types of endocarps, i.e. hairpin-, horseshoe-, and feniform shaped.
- Cissampelos has two endocarp types, i.e. hairpin-shaped and horseshoe-shaped.
- 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 paleoclimatic 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

Table 1
Comparison of horseshoe-shaped endocarps in Menispermaceae. Two genera, Caryomene and Echinostepha, are described as horseshoe-shaped endocarps, but no observations were performed by Jacques (2009b). Diplolysia, a genus of the tribe Menispermaceae, has their endocarp either hairpin-shaped or quite elongated; therefore, it is excluded from the comparison. Data modified from Jacques (2009b).

<table>
<thead>
<tr>
<th>Tribe Pachygoneae</th>
<th>Endocarp surface</th>
<th>Condyle Size (L×W×T mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hyperbaena⁵</td>
<td>One slight dorsal crest, two lateral crests on each side; surface with reticulated ridges</td>
<td>Double intrusive condyle coma-shaped</td>
</tr>
<tr>
<td>Pachygone⁵</td>
<td>One slight dorsal crest, no lateral crest; surface reticulate; no ridges</td>
<td>Double external condyle not perforated; a strip partly hiding it ventrally</td>
</tr>
<tr>
<td>Syrythorna</td>
<td>One dorsal crest, dorsal face with two lateral concavities, lateral concavities, lateral crest absent; surface reticulate</td>
<td>Central area totally perforated</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Tribe Menispermaceae</th>
<th>Endocarp surface</th>
<th>Condyle Size (L×W×T mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cissampelos⁵</td>
<td>Two dorsal crests, two lateral crests on each side; all crests bearing spines; surface smooth</td>
<td>Double external condyle, not perforated; sometime inconspicuous</td>
</tr>
<tr>
<td>Cocculus</td>
<td>One dorsal groove/crest, lateral crest absent; one lateral groove on each side, with numerous transverse ridges</td>
<td>Double external condyle, perforated or not perforated</td>
</tr>
<tr>
<td>Cylea</td>
<td>Two dorsal crests with 16 small spines, two lateral crests on each side; surface smooth</td>
<td>Inconspicuous</td>
</tr>
<tr>
<td>Hyperbaena</td>
<td>One slight dorsal crest, lateral crest absent; surface reticulate</td>
<td>Double external condyle partly filled</td>
</tr>
<tr>
<td>Legnephora</td>
<td>One small/high strip on dorsal crest, one high strip on lateral crest; surface smooth</td>
<td>Double external condyle, not perforated; central area either small or large</td>
</tr>
<tr>
<td>Limacia</td>
<td>One large dorsal band with rugose surface overlapping partly the lateral faces; surface smooth</td>
<td>Condyle made of 2 large lateral cavities</td>
</tr>
<tr>
<td>Limacopsis</td>
<td>One dorsal crest, one lateral crest on each side; with small transverse ridges; surface smooth</td>
<td>Double external condyle, not perforated; central area either small or large</td>
</tr>
<tr>
<td>Menispernum</td>
<td>One dorsal crest, one lateral crest on each side, connected by short transverse ridges; surface smooth</td>
<td>Double external condyle, not perforated; central area either small or large</td>
</tr>
<tr>
<td>Pericampylus</td>
<td>Two dorsal crests, two lateral crests on each side; all crests bearing spines; surface smooth</td>
<td>Double external condyle, not perforated</td>
</tr>
<tr>
<td>Rhamnophora</td>
<td>One dorsal crest, lateral crest absent; surface rugose, slightly ornamented</td>
<td>Seed cavity filled, condyle very limited</td>
</tr>
<tr>
<td>Sarcepetalia</td>
<td>Two dorsal crests, two lateral crests on each side; all crests bearing spines; surface smooth</td>
<td>Double external condyle, not perforated; central area large</td>
</tr>
<tr>
<td>Sciadotenia⁵</td>
<td>One dorsal crest, lateral crest absent; surface irregular and reticulate</td>
<td>Double external condyle, not perforated</td>
</tr>
<tr>
<td>Sinomenium</td>
<td>One dorsal crest, one lateral crest on each side, connected by short transverse ridges; surface smooth</td>
<td>Double external condyle, not perforated; central area either small or large</td>
</tr>
<tr>
<td>Spirospermum</td>
<td>One dorsal crest, one lateral groove on each side, connected by numerous transverse ridges; dorsal face with two lateral concavities</td>
<td>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</td>
</tr>
<tr>
<td>Stephania</td>
<td>One or two dorsal crests, one lateral crest on each side; connected by few to many transverse ridges or spines</td>
<td>Double external condyle, not perforated</td>
</tr>
<tr>
<td>Strychnopsis</td>
<td>Endocarp without excavated faces; one dorsal crest, one slight dorsal crest on each side; surface slightly reticulate</td>
<td>Central area filled, limiting the condyle to a sharp line surrounding it</td>
</tr>
</tbody>
</table>

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. Lateral view. 2. Dorsal view. 3. Lateral view showing a broken condyle. 4. Dorsal view showing the well-developed protuberances, particularly on the lateral crests. 5, 6. ETMNH 3814. 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. ETMNH 3825. 10. Lateral view of inner endocarp. 11. Lateral view of outer endocarp. 12. Lateral view of outer endocarp.
distribution of this genus requires a CMMT of $-7.3$ to $-21$ °C (Luo et al., 2008).

The mechanisms of fruit dispersal in Menispermaceae are generally not well understood. There is no report about how Sinomium fruits disperse. The endocarps of Elephantomene eburnea, 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 Sinomium disperse in the Neogene, although many tapirs are found at the Gray site (Hulbert et al., 2009). Taphonomically, the fossil endocarps of Sinomium were found associated with the tapir and rhino skeletons and a red panda jaw.

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References


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

Note:
- (Reid 1920) reported this site as the Early Pliocene. It is now accepted as the Late Miocene (Mai and Martinetto, 2006).
- 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).