

Fossil moonseeds from the Paleogene of West Gondwana (Patagonia, Argentina)

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PREMISE OF THE STUDY: The fossil record is critical for testing biogeographic hypotheses. Menispermaceae (moonseeds) are a widespread family with a rich fossil record and alternative hypotheses related to their origin and diversification. The family is well-represented in Cenozoic deposits of the northern hemisphere, but the record in the southern hemisphere is sparse. Filling in the southern record of moonseeds will improve our ability to evaluate alternative biogeographic hypotheses.

METHODS: Fossils were collected from the Salamanca (early Paleocene, Danian) and the Huitrera (early Eocene, Ypresian) formations in Chubut Province, Argentina. We photographed them using light microscopy, epifluorescence, and scanning electron microscopy and compared the fossils with similar extant and fossil Menispermaceae using herbarium specimens and published literature.

KEY RESULTS: We describe fossil leaves and endocarps attributed to Menispermaceae from Argentinean Patagonia. The leaves are identified to the family, and the endocarps are further identified to the tribe Cissampelideae. The Salamancan endocarp is assigned to the extant genus *Stephania*. These fossils significantly expand the known range of Menispermaceae in South America, and they include the oldest (ca. 64 Ma) unequivocal evidence of the family worldwide.

CONCLUSIONS: Our findings highlight the importance of West Gondwana in the evolution of Menispermaceae during the Paleogene. Currently, the fossil record does not discern between a Laurasian or Gondwanan origin; however, it does demonstrate that Menispermaceae grew well outside the tropics by the early Paleocene. The endocarps' affinity with Cissampelideae suggests that diversification of the family was well underway by the earliest Paleocene.

KEY WORDS Danian; early Eocene; endocarp; Huitrera Formation; leaf fossil; Menispermaceae; Paleocene; Salamanca Formation; South America.

Menispermaceae Juss., commonly known as the moonseed family, are climbing plants (rarely trees, herbs, or epiphytes) distributed throughout the tropics and into temperate regions of eastern North America, eastern Asia, and southeastern Australia (Miers, 1874; Forman, 1986; Kessler, 1993; Jacques et al., 2007). Despite recent advancements in our understanding of the relationships among the living species, the early evolutionary history of the family is still unclear (Jacques, 2009a; Herrera et al., 2011). Traditionally, a Laurasian origin hypothesis was favored (Raven and Axelrod, 1974; Kessler, 1993; Jacques, 2009a), but a tropical African/Gondwanan origin during the Cretaceous was also proposed (Thanikaimoni, 1986). Recently, molecular phylogenetic studies have converged on a revised model of menisperm relationships (Table 1), leading to the

hypothesis that the family originated in tropical Indomalasia during the mid-Cretaceous, followed by rapid diversification of the crown group throughout the tropics during the latest Cretaceous to early Paleogene (Wang et al., 2012; Ortiz et al., 2016).

The family is characterized by drupaceous fruits with distinctive reniform, horseshoe, or hairpin-shaped bony endocarps composed of sinuous sclereids. These endocarps are frequently preserved as fossils (Jacques, 2009a) and are known from Paleocene and younger deposits. They provide direct evidence of the distribution of the family in the past and are critical for interpreting its evolutionary and biogeographic history (Thanikaimoni, 1984, 1986; Tiffney and Manchester, 2001; Doria et al., 2008; Tiffney, 2008; Jacques, 2009a; Liu and Jacques, 2010; Herrera et al., 2011; Jacques et al., 2011; Wang

TABLE 1. Classification of Menispermaceae Juss. from Ortiz et al. (2016).

Subfamily	Tribe
Chasmantheroideae Luerss.	
	Burasaieae Endl.
	Coscinieae Hook.f. & Thomson
Menispermoideae Arn. in Wight & Arnott	
	Anomospermeae Miers
	Cissampelideae Hook.f. & Thomson
	Limacieae Prantl in Engler & Prantl
	Menispermeae DC.
	Pachygoneae Miers
	Spirospermeae R.Ortiz & Wei Wang
	Tiliacoreae Miers

et al., 2012; Han et al., 2017). There are many reports of fossil leaves assigned to *Menispermites* Lesq. dating back to the mid-Cretaceous (Lesquereux, 1874; Golovneva et al., 2015), but not all can be accepted as reliable occurrences of the family (Forman, 1986; Doria et al., 2008). A handful of species are known from fossil woods (Vozenin-Serra et al., 1989; Bonde, 1997; Poole and Wilkinson, 2000); however, the oldest of these, *Anamirta pfeifferi* Bonde from

the Paleocene of India, is in need of re-evaluation and may not be Menispermaceae (Bonde, 1997; Jacques and De Franceschi, 2007; Smith et al., 2013; Wheeler et al., 2017). Fossil endocarps from the Turonian (Upper Cretaceous) of Europe were thought to support a Laurasian origin for the family (Knobloch and Mai, 1986), but this identification is ambiguous (Jacques, 2009a; Herrera et al., 2011; Jacques et al., 2011; Wefferling et al., 2013). The flowers described as *Callicrypta chlamydea* Krassilov and Golovneva (2004) from the Cretaceous of Russia are similar to Menispermaceae, but they have incompletely sealed carpels that are dorsiventrally compressed, unlike extant Menispermaceae (K. Wefferling, University of Wisconsin, personal communication), and may be related to other Ranunculales (Krassilov and Golovneva, 2004). Currently, we consider leaves and endocarps from the Paleocene of North America, Europe, and northern South America to be the oldest reliable prior records of the family (Knobloch, 1971; Mai, 1987; Doria et al., 2008; Herrera et al., 2011).

Here, we report and describe fossilized endocarps of early Paleogene Menispermaceae from Patagonia for the first time. We also describe and evaluate previously mentioned menispermaceous leaves. The fossils were collected from the early Paleocene (early Danian) deposits of the Salamanca Formation and the early Eocene (Ypresian) deposits of the Huitrera Formation. Finally, we discuss the implications of these fossils for the biogeographic history of the family.

MATERIALS AND METHODS

A fossil endocarp was collected from the Palacio de los Loros-2 locality (PL-2 of Iglesias et al., 2007; Clyde et al. 2014; Comer et al., 2015) of the early Paleocene (early Danian) Salamanca Formation in southeastern Chubut Province, Argentina (Fig. 1). We also examined the single menisperm leaf fossil collected from the nearby Palacio de los Loros-1 locality (PL-1). This leaf specimen was first reported as morphotype SA060 with a thumbnail illustration and description and suggested affinity to Menispermaceae by Iglesias et al. (2007: fig. 2y; tables DR2, DR3). The age of the PL-1 & 2 localities has been constrained to the early Danian using the recently revised chronostratigraphic framework of the Salamanca Formation in the study area. This framework is based on age-diagnostic foraminifera, calcareous nannofossils, dinocysts, and paleomagnetic data from the unit, as well as radiometric dates from stratigraphically lower and higher units (Clyde et al., 2014; Comer et al., 2015). Locality PL-2 is in geomagnetic polarity Chron C28n (64.67–63.49 Ma on the 2012 Geomagnetic Polarity Timescale per Gradstein et al., 2012). Locality PL-1 is in geomagnetic polarity Chron C29n (65.69–64.96 Ma on the 2012 Geomagnetic Polarity Timescale per Gradstein et al., 2012). The

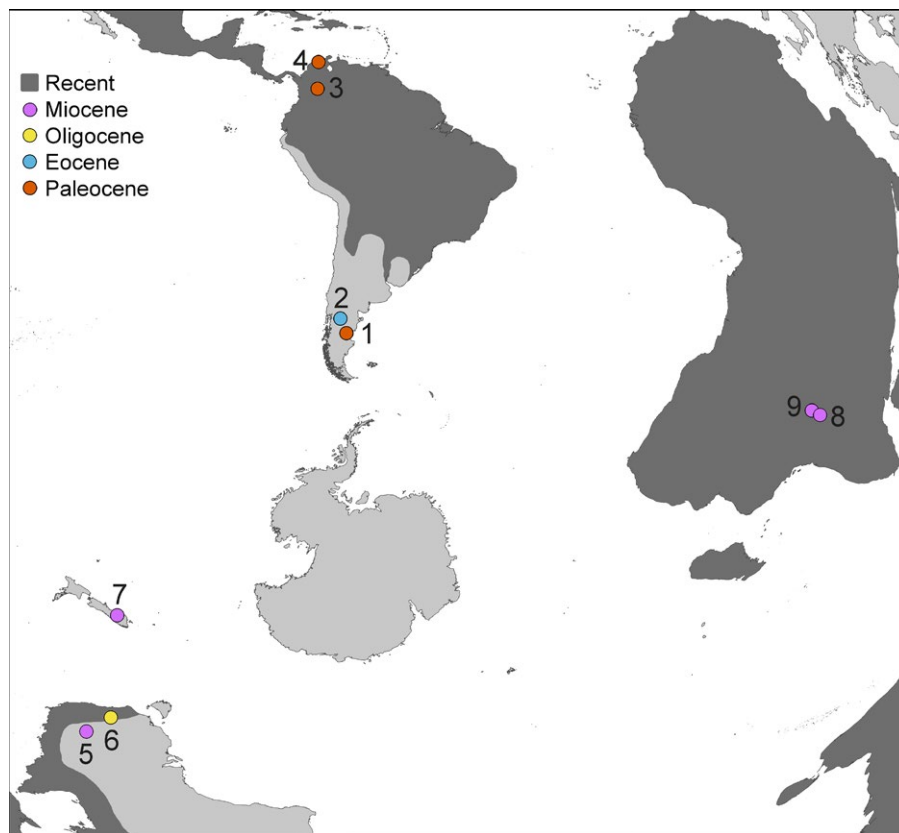


FIGURE 1. Map showing the Recent distribution of Menispermaceae (dark gray) and the locations where fossil endocarps of Menispermaceae have been collected on the southern land masses (Table 7). 1 = Palacio de los Loros, Early Danian, Salamanca Formation, Chubut, Argentina (this work), 2 = AL-1, Early Eocene, Huitrera Formation, Chubut, Argentina (this work), 3 = Paleocene Cerrejón Formation, Colombia (Herrera et al., 2011), 4 = Paleocene Bogotá Formation, Colombia (Herrera et al., 2011), 5 = unnamed Miocene deposits in Australia (Wellman and McDougall, 1974), 6 = unnamed Oligocene deposits in Australia (Rozeffelds, 1991), 7 = Miocene Foulden Maar locality, New Zealand (Conran et al., 2014), 8 = Miocene Ngorora Formation, Kenya, (Jacobs and Kabuye, 1987), 9 = Miocene Rusinga Beds, Democratic Republic of Congo (Chesters, 1957).

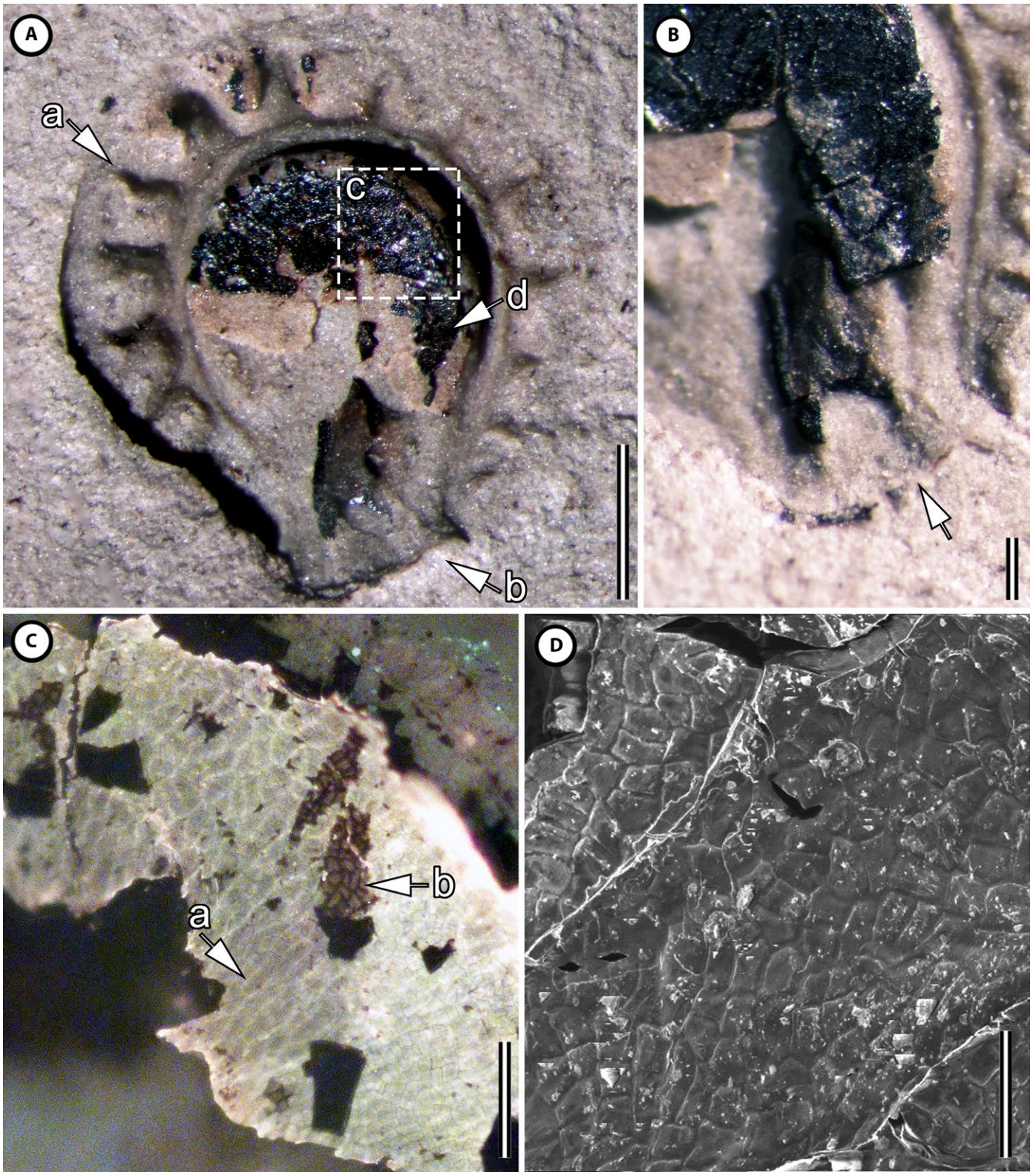


FIGURE 2. *Stephania psittaca* sp. nov. (MPEF-Pb 6801) from the PL-2 site, early Danian Salamanca Formation, Chubut, Argentina, holotype. (A) Lateral view of the endocarp showing 13 ribs (a) intruding the horseshoe-shaped (hippocrepiform) locule that wraps around the condyle, dashed box (c) indicates the area of image C, (b) indicates the area shown in image B, (d) points the location of image in D. (B) Close-up of the base of the endocarp; note the straight ventral foramen (at arrow). (C) Close-up of the endocarp wall; (a) points to an area where the preserved cellular details fluoresce, (b) points to area where preserved cellular details in brown (low intensity fluorescence). (D) SEM close-up of the cell outlines preserved on the endocarp wall. Scale bars, A: 0.5 mm; B: 0.2 mm; C: 0.1 mm; D: 50 μ m.

fossils at PL-1 are preserved in sandstones and siltstones of lateral accretion deposits, whereas the fossils at PL-2 are preserved in a poorly laminated mudstone that was deposited in tidally influenced fluvial swale-fill (Comer et al., 2015). The precise geographic location of the Palacio de los Loros localities was reported by Clyde et al. (2014).

Another endocarp was collected from an early Eocene locality in northwestern Chubut Province, Argentina, designated as AL-1 (for nearby Puesto Alvarez as discussed by Wilf et al. 2009). The AL-1 locality is 5 km south of the main fossiliferous section of the well-known Laguna del Hunco exposures (Berry, 1925; Wilf et al., 2003) and likewise belongs to the Tufolitas Laguna del Hunco of the Huitrera Formation in the Middle Río Chubut Volcanic-Pyroclastic Complex (Aragón and Mazzoni, 1997; Aragón et al., 2004). A combination of radioisotopic and paleomagnetic analyses indicates that the Laguna del Hunco flora was deposited during the early Eocene climatic optimum, approximately 52 Ma (Wilf et al., 2003). The AL-1 locality is stratigraphically lower than volcanic ash bed 2211A at Laguna del Hunco, which yielded a 52.22 (± 0.22) Ma date on sanidine (Wilf et al., 2003, 2005; Wilf, 2012) that provides a robust minimum age estimate for the fossil endocarp. A menispermaceous fossil leaf (Morphotype TY047 of Wilf et al., 2005) was also collected from the principal Laguna del Hunco exposures on a float slab (MPEF-Pb 6803; float is talus material lacking exact stratigraphic provenance data) and is also approximately 52 Myr old.

The fossil specimens are housed in the paleobotanical collection of the Museo Paleontológico Egidio Feruglio (MEF; repository acronym MPEF-Pb) in Trelew, Chubut Province, Argentina. Photographs were taken using a Canon EOS 7D DSLR Camera; microscopic details were photographed at MEF under low-angle lighting with a Nikon DS Fi1 camera mounted on a Nikon SMZ1000 stereoscope with a DS-L2 control unit and a DS-Fi3 camera mounted on an Eclipse 50i compound microscope with a DS-L4 control unit (Nikon, Melville, NY, USA). SEM images were obtained from the Servicio de Microscopía y Rayos X from the Centro Atómico Bariloche. The images were processed and sometimes laterally composited (stitched) using Adobe Photoshop CS2 and CC (Adobe, San Jose, CA, USA). We compared the fossils with specimens of extant species from the L. H. Bailey Hortorium Herbarium (BH), Plant Biology Section, School of Integrative Plant Science, Cornell University (Table 2) and from the National Cleared Leaf Collection (NCLC), Smithsonian National Museum of Natural History as well as with the images and descriptions provided by Jacques et al. (2009b), Doria et al. (2008), Herrera et al. (2011), and Wefferling et al. (2013). Terminology for the description of fruits follows Ortiz (2012) and Wefferling et al. (2013). Terminology for the description of leaves follows Ellis et al. (2009). Biogeographic hypotheses were evaluated by plotting fossil occurrence data against time, using the online ODSN Advanced Plate Tectonic Reconstruction Service (O.D.S. Network, 2004) to estimate paleolatitude.

SYSTEMATICS

Endocarps

Family—Menispermaceae Juss.

Subfamily—Menispermoidae Arn. in Wight & Arnot

TABLE 2. Comparative material of extant Menispermaceae. List of examined comparative material at the Bailey Hortorium (BH), and the National Cleared Leaf Collection (NCLC), National Museum of Natural History, Washington D.C.

Species	Specimen number	Provenance
<i>Anamirta cocculus</i> (L.) Wight & Arn.	BH 135493	Philippines
<i>Anamirta paniculata</i> Colebr.	BH 135492	Sri Lanka (cult.)
<i>Anomospermum chloranthum</i> Diels	BH 135477	Bolivia
<i>Antizoma calcarifera</i> Miers	BH 120559	Namibia
<i>Antizoma calcarifera</i> Miers	BH 120560	South Africa
<i>Antizoma calcarifera</i> Miers	BH 120561	South Africa
<i>Cissampelos ovatifolia</i> DC	BH 135472	Brasil
<i>Cissampelos ovatifolia</i> DC	BH 033650	Venezuela
<i>Cissampelos pareira</i> L.	BH 031895	Nicaragua
<i>Cissampelos fasciculata</i> Benth.	NCLC-H 1098	Peru
<i>Cocculus carolinus</i> (L.) DC	BH 135478	U.S.A.
<i>Cocculus carolinus</i> (L.) DC	BH 135482	U.S.A.
<i>Cocculus carolinus</i> (L.) DC	BH 114670	U.S.A.
<i>Cocculus carolinus</i> (L.) DC	BH 135489	U.S.A.
<i>Cocculus diversifolius</i> DC	NCLC-H 1089	U.S.A.
<i>Cocculus trilobus</i> Merrill	NCLC-H 1093	Japan
<i>Cyclea hypoglauca</i> Diels	BH 135494	Hainan
<i>Cyclea hypoglauca</i> Diels	BH 135495	China
<i>Cyclea polypetala</i> Dunn.	NCLC-H 1099	China
<i>Diploclisia glaucescens</i> (Blume) Diels	BH 135458	China
<i>Limacia oblonga</i> (Wall.) Miers	NCLC-H 1119	Sumatra
<i>Menispermum canadense</i>	BH 097283	U.S.A.
<i>Menispermum canadense</i>	BH 097284	U.S.A.
<i>Menispermum canadense</i>	BH 097285	U.S.A.
<i>Menispermum canadense</i>	BH 087739	U.S.A.
<i>Menispermum canadense</i>	BH 097287	U.S.A.
<i>Menispermum canadense</i>	BH 097288	U.S.A.
<i>Pericampylus glaucus</i> (Lour.) Merr.	BH 135439	China
<i>Pericampylus glaucus</i> (Lour.) Merr.	BH 135441	China
<i>Spirospermum pendulifolium</i> DC	BH 135457	U.S.A. (cult.)
<i>Stephania japonica</i> (Thunb.) Miers	BH 135449	Japan
<i>Stephania aculeata</i> F.M.Bail.	BH 135448	Australia
<i>Stephania hernandiifolia</i> Walp.	BH 135447	Australia

Tribe—Cissampelideae Hook.f. & Thomson

Genus—*Stephania* Lour.

Species—*Stephania psittaca* Jud et Gandolfo sp. nov.

Holotype here designated—MPEF-Pb 6801 (Fig. 2A–D).

Age, source, and stratum—Early Danian (early Paleocene), Salamanca Formation, Chubut Province, Argentina. PL-2 locality, Chron C28n (64.67–63.49 Ma).

Diagnosis—Endocarp obovate in lateral view; dorsal crest broad-rounded, of uniform thickness, lacking spines; locule cast hippocrepiform (horseshoe-shaped), with unequal limbs and conspicuous radially aligned intrusive ribs; lateral face concave, imperforate; vascular trace ventral, nearly straight.

Etymology—The specific epithet is derived from *psittacus* (Latin, parrot), in reference to the type locality name “Palacio de los Loros,” which comes from the abundance of burrowing parrots (*Cyanoliseus patagonus*) living in the cliffs of a palace-like local butte.

Description—Specimen MPEF-Pb 6801 is an adpressed, obovate, bilaterally compressed, lamiform unilocular endocarp without a counterpart (Fig. 2A). The endocarp is obovate in lateral view with a smooth, broad-rounded abaxial (dorsal) crest and a straight ventral (adaxial) margin. It is 2.6 mm long by 2.3 mm wide. A hippocrepiform locule cast runs from the proximal end of the endocarp, along the abaxial wall, and around a condyle to the distal end of the endocarp. At least 13 radially aligned ribs are visible in the locule cast (Fig. 2A, at arrow a). The limbs of the curved locule cast are unequal, and the tips are 0.88 mm apart (measured from tip of the short limb to tip of the longer limb). The longer limb of the locule cast is at the distal stylar end of the fruit. The lateral face of the endocarp is obovate and imperforate, and the carbonized remains of the endocarp indicate that the lateral face of the endocarp is concave. This concave lateral face corresponds to the double external condyle sensu Jacques (2009b). A nearly straight ventral vascular strand ascends from the base of the condyle area and approaches the locule near the center of the endocarp (Fig. 2B, at arrow), as in extant *Stephania* Lour.

Several distinct layers are visible on the lateral face of the endocarp. The lowest layer is tan, followed by a layer with cellular details visible under epifluorescent light. These fluorescing cells tend to be elongate and oriented radially with respect to the endocarp (Fig. 2C, at arrow a). Above the fluorescing layer is another thin layer of polygonal cells that appears brown under fluorescence (Fig. 2C; at arrow b). Finally, there is a layer of coalified plant material. Impressions of the cells are visible on the coalified plant material under SEM (Fig. 2D).

Family—Menispermaceae Juss.

Subfamily—Menispermoidae Arn. in Wight & Arnot.

Tribe—Cissampelideae Hook.f. & Thomson
Menispermaceae sp. endocarp (Fig. 3A, B).

Exemplar—MPEF-Pb 6802 a, b. Puesto Alvarez 2010 collection.

Age, source, and stratum—Ypresian (Early Eocene), Tufolitas Laguna del Hunco, Huitrera Formation, Chubut Province, Argentina, AL-1 locality.

Description—Specimen MPEF-Pb 6802 comprises a part and counterpart of a compressed endocarp (Fig. 3A, B). The endocarp is bilaterally compressed and lamiform. It is nearly circular in lateral view, 8.4 mm long and 8.3 mm wide. The dorsal crest is smooth. A crescent-shaped locule (Fig. 3B, L) runs from the proximal end of the endocarp where the pedicel attached (Fig. 3B, P), along the abaxial wall of the endocarp to the distal end of the endocarp, around a ventral intrusion (condyle). We interpret the numerous trapezoidal locule intrusions (Fig. 3A at arrows a and b) as corresponding to two dorsal crests that are joined by transverse ridges. The limbs of the curved locule cast are approximately equal, and the tips are 4.8 mm apart, measured from the tip of each limb. The lateral face is imperforate.

Leaves

Family—Menispermaceae Juss.

Genus—*Wilkinsoniophyllum* Jud, Gandolfo, Iglesias, et Wilf gen. nov.

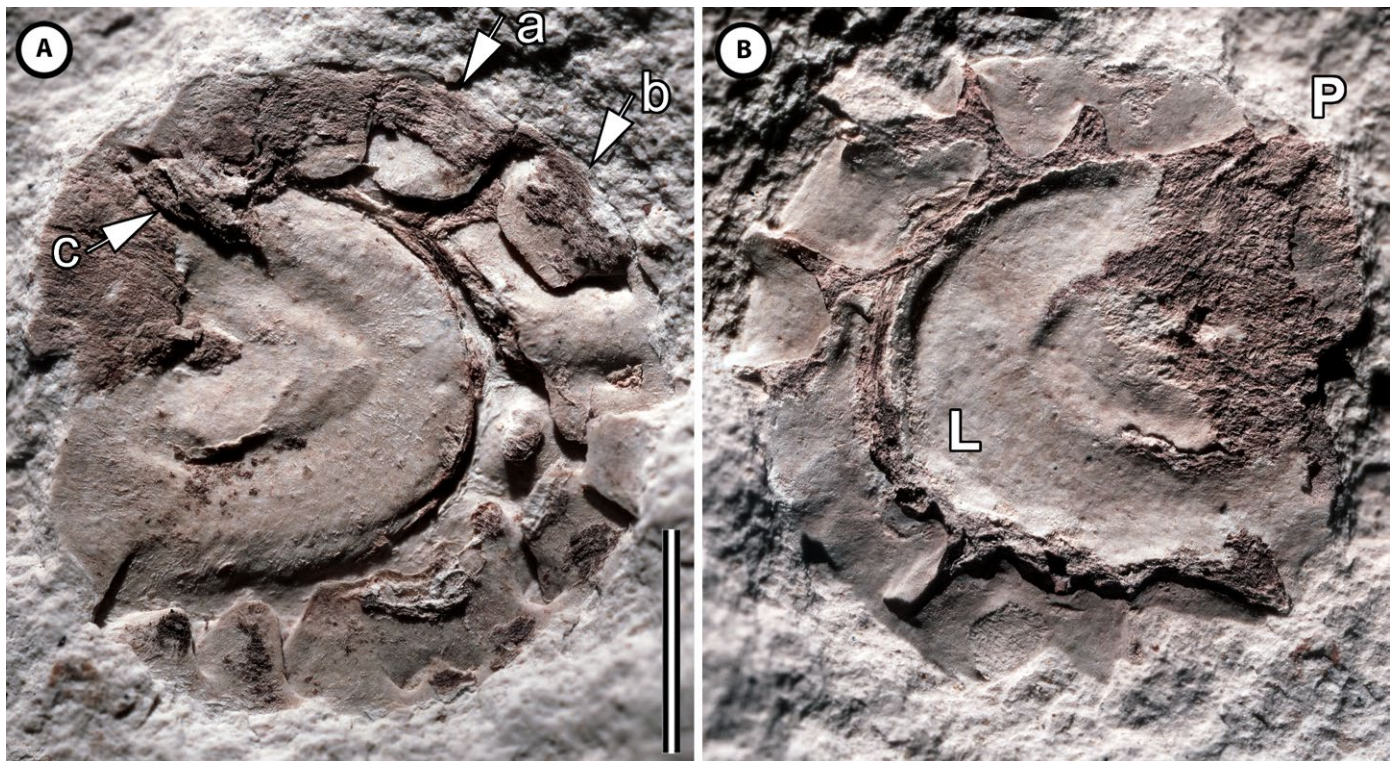


FIGURE 3. Menispermaceae sp. endocarp (MPEF-Pb 6802a, b from the AL-1 locality, Huitrera Formation, Chubut, Argentina, composite images. (A) Lateral view of the endocarp (MPEF-Pb 6802a) showing locule intrusions (a, b) and vascular trace (c). (B) Counterpart (MPEF-Pb 6802b). P = pedicel attachment, L = locule. Scale bar, 3 mm.

Diagnosis—Leaf simple, petiolate with an upper pulvinus; blade attachment marginal; blade simple, wide ovate; base concavo-convex, obtuse; apex rounded, obtuse, mucronate; margin entire. Primary venation suprabasal actinodromous; central primary slightly wider than lateral primaries; lateral primaries ascending about two-thirds the distance to apex into apical half of lamina; secondary vein framework brochidodromous, secondary veins excurrent, ascending from the central primary with the lowermost pair diverging near the middle of the blade, central secondary veins alternate, simple agrophic veins present; tertiary vein framework alternate percurrent; fourth to sixth order vein framework regular polygonal reticulate; areoles regular, polygonal, lacking freely ending veinlets; fimbrial vein present.

Etymology—Named for Dr. H. P. Wilkinson in honor of her contributions to our understanding of leaf morphology and anatomy in Menispermaceae (Wilkinson, 1978, 1986, 1989).

Species—*Wilkinsoniophyllum menispermoides* Jud, Gandolfo, Iglesias, et Wilf gen. et sp. nov.

Holotype here designated—MPEF-Pb 2052a, b (Fig. 4A–D). Informal previous reference: morphotype SA060 of Iglesias et al. (2007), considered to belong to Menispermaceae.

Age, source, and stratum—Early Danian (early Paleocene), Salamanca Formation, Chubut Province, Argentina. PL-1 locality, Chron C29n (65.69–64.96 Ma).

Diagnosis—As for the genus *Wilkinsoniophyllum*.

Etymology—The epithet “menispermoides” refers to the similarities between this fossil leaf and those extant in the family Menispermaceae.

Description—The leaf is simple and petiolate. The preserved petiole is 4.3 mm long and 1.7 mm wide at the point of attachment to blade, which we interpret as the upper pulvinus (Fig. 4A, D at arrow a). The petiole attachment is marginal (Fig. 4A, D). Slightly more than half of the blade is preserved, but one lateral half is nearly complete. The original shape is wide ovate (assuming medial symmetry). The blade is 6 cm long and 3.2 cm from medial primary to right margin (estimated L:W 0.9). The base is concavo-convex and the apex is obtuse, rounded (Fig. 4A, B), and has a mucronate tip that is 0.4 mm long (Fig. 4B at arrow b). The primary vein framework is suprabasal actinodromous with three primary veins and two basal secondary veins (Fig. 4A, D). The midvein is slightly wider than lateral primaries, reaching the leaf apex and extending into the mucronate tip. Lateral primary veins diverge from the medial primary at 33° and 43°; they extend about five-sixths the distance to apex into the distal half of the lamina. The secondary vein framework is brochidodromous, and the secondary veins are alternate and diverge from the medial primary vein at 50–65°. The secondary veins are curved toward the apex and join the supradjacent veins by serial loops at wide angles; the secondary angles are uniform, with spacing increasing toward base. The agrophic veins are simple with looping minor secondary veins. An incompletely preserved fimbrial vein tapers from the base (Fig. 4D, at arrows b and c) toward the apex (Fig. 4C at arrow; 4B at arrow a). The tertiary venation is mixed opposite/alternate percurrent, and the tertiary vein course is

generally straight with the angles increasing exmedially. The fourth order veins are regular polygonal reticulate and forming areoles that are 0.3–1.0 mm wide. The fifth order veins are regular polygonal reticulate, while the sixth order of veins is regular polygonal reticulate. Areolation is well developed; the areoles are 4- to 5-sided and of uniform size (Fig. 4B).

Family—Menispermaceae Juss.

Genus—*Menispermites* Lesq.

Species—*Menispermites calderensis* Jud, Gandolfo, Iglesias et Wilf. (Fig. 5A–C).

Previous informal reference: morphotype TY047 of Wilf et al. (2005, table A2).

Holotype here designated—MPEF-Pb 6803.

Age, source, and stratum—Ypresian (Early Eocene), Tufolitas Laguna del Hunco, Huitrera Formation, Middle Rio Chubut Volcanic-Pyroclastic Complex, Chubut Province, Argentina, LHF 0038 float sample.

Diagnosis—Leaf simple, petiolate; blade attachment subpeltate; blade ovate, nearly symmetrical; base broadly rounded, cordate, base angle reflexed; apex acute, retuse; margin entire. Primary venation suprabasal actinodromous, basal veins departing from the petiole insertion point; central primary slightly wider than lateral primaries; first pair of lateral primaries arching laterally and about one-quarter the distance to apex, second pair extending about two-thirds the distance to apex into apical half of lamina; secondary vein framework brochidodromous, secondary veins excurrent, ascending from the central primary with the lowermost pair diverging near the middle of the blade, central secondary veins alternate or subopposite, simple to compound agrophic veins; tertiary vein framework mixed alternate/opposite percurrent; fourth and fifth vein order framework regular polygonal reticulate; areoles regular, polygonal; fimbrial vein conspicuous.

Etymology—The specific epithet “calderensis” means “of the caldera,” referring to the caldera-lake depositional setting of the Tufolitas Laguna del Hunco (Aragón and Mazzoni, 1997).

Description—The leaf is simple and notophyllous, and ovate with a nearly symmetrical lamina, 7.8 cm long by 6.6 cm wide (Fig. 5A). The petiole attachment is subpeltate, and the petiole insertion to the blade is not straight (i.e., it is perpendicular or oblique) (Fig. 5C, at arrow). The base is broadly rounded, reflexed, and cordate (Fig. 5C), and the apex is retuse with an acute angle (86°) (Fig. 5A, B). The margin is unlobed and entire. The primary vein framework is suprabasal actinodromous (Fig. 5A), with five basal veins departing from the petiole insertion, and the central primary slightly wider than the lateral primaries (0.55 mm vs. 0.30–0.50 mm). The outermost pair of veins are basal secondary veins that run along the margin and join the agrophic complex associated with the lateral primary veins. The lateral primary veins extend about two-thirds the distance to apex and contribute to simple agrophic veins with looping minor secondary veins (Fig. 5A). The secondary vein framework is brochidodromous; 2–4 pairs of alternate or subopposite, excurrent secondary veins depart from the central primary toward the apex

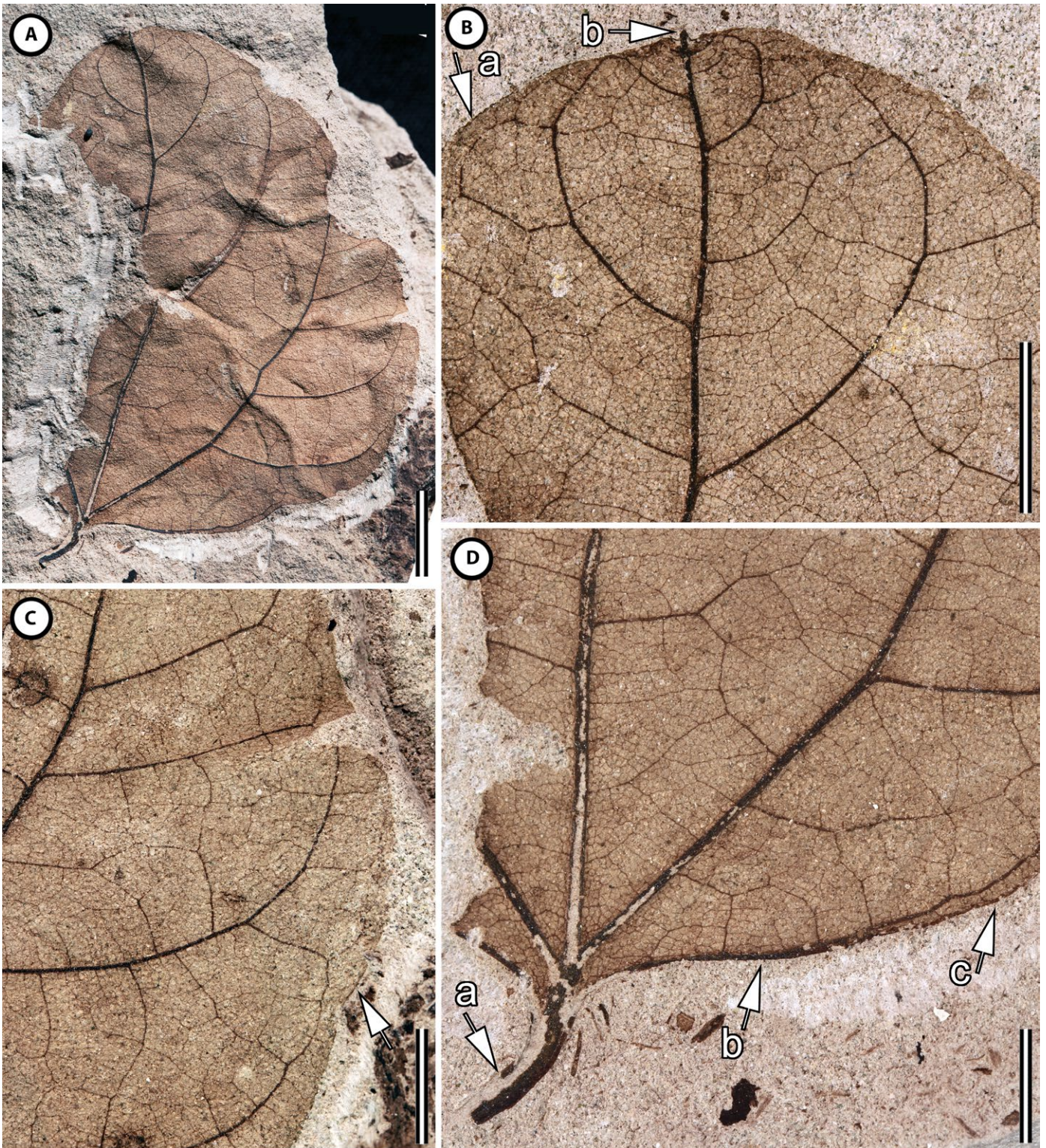


FIGURE 4. *Wilkinsoniophyllum menispermoides* MPEF-Pb 2052a (holotype) from the early Danian PL-2 locality in the Salamanca Formation. (A) General aspect; note the marginal petiole insertion, the broad concavo-convex base, and the mucronate apex. (B) Close-up of the apex; note regular areoles without freely ending veinlets, the thin fimbrial vein (a) and the mucro (b). (C) Close-up of the right margin; note the incompletely preserved fimbrial vein (at arrow). (D) Close-up of the base; note the wide, curved petiole remnant interpreted as the upper pulvinus (a), and the tapering fimbrial vein (b, c). Scale bars, A: 1 cm, B–D: 5 mm.

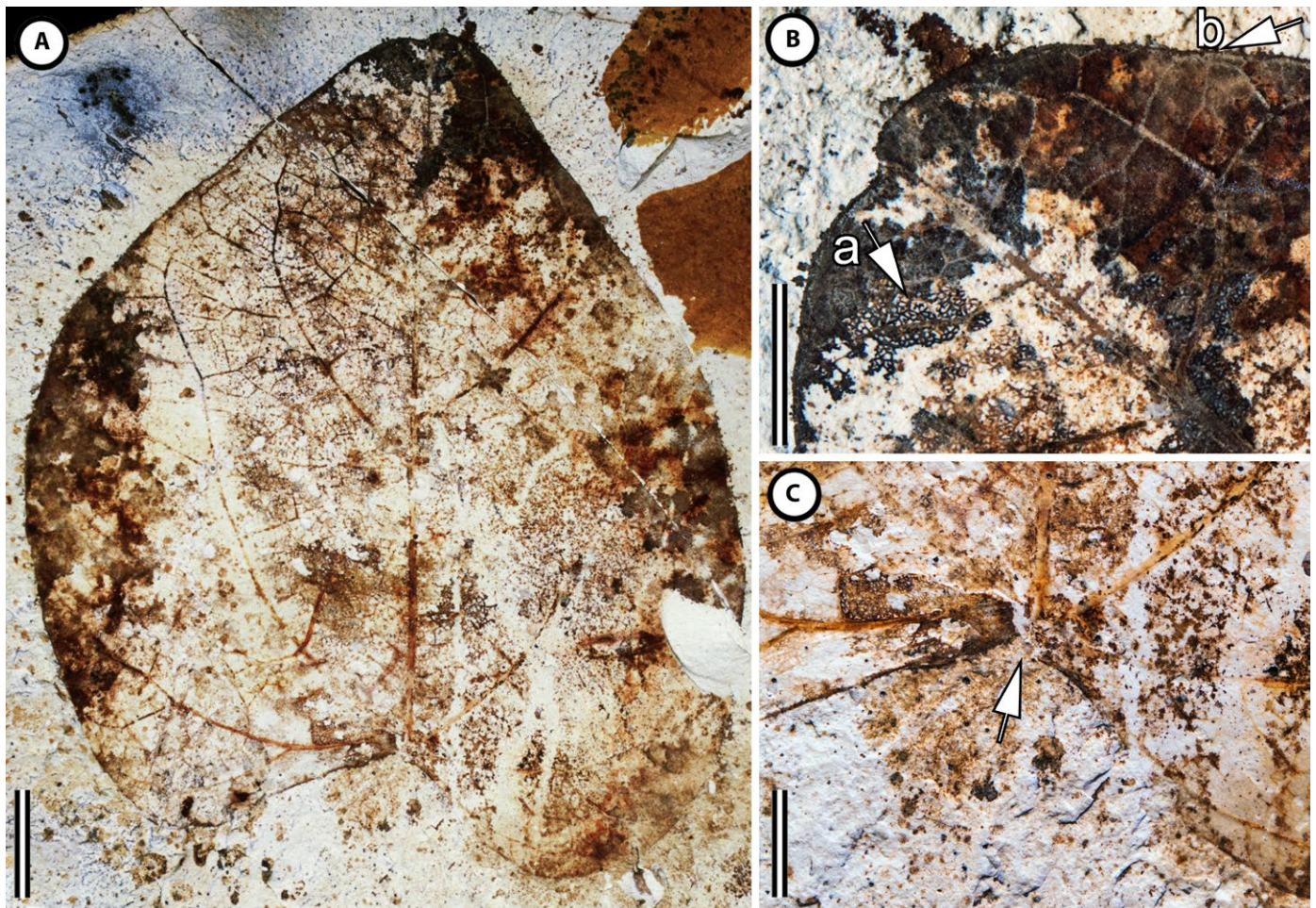


FIGURE 5. *Menispermites calderensis* sp. nov. MPEF-Pb 6803 (holotype) from the early Eocene Tufolitas Laguna del Hunco. (A) General aspect, showing shape and major venation patterns. (B) Close-up of leaf tip, showing retuse apex, regular polygonal areolation (a), and fimbrial vein (b). (C) Close-up of the leaf base showing sub-peltate petiole attachment (at arrow), and rounded cordate shape. Scale bars: A, C: 10 mm, B: 5 mm.

in the distal half of the blade. Intersecondary veins are present but weakly developed. The tertiary vein framework is mixed alternate/opposite percurrent. The fourth and fifth veins form a regular reticulum with well-developed 4–5-sided polygonal areoles (Fig. 5B at arrow a). There is a conspicuous fimbrial vein along the length of the margin (Fig. 5B at arrow b).

DISCUSSION

Endocarps: comparison with extant and fossil plants

Endocarps with a single curved locule and a lignified, adaxial intrusion of the placental region into the locule (a condyle) are only found in the Menispermaceae (Miers, 1851; Ortiz, 2012). There are two general types of condyles in the family, and they are synapomorphies of the two subfamilies (Table 1). The *Calyccarpum*-type characterizes the Chasmantheroideae, whereas the *Menispermum*-type characterizes the Menispermoideae. The *Calyccarpum*-type condyle intrudes the endocarp, resulting in a boat-shaped locule, whereas the *Menispermum*-type is characterized by differential growth of the lateral sides of the ovary wall, resulting in a bilaterally

compressed, crescent- to horseshoe-shaped endocarp (Ortiz, 2012). The fossil endocarps described here have *Menispermum*-type condyles, indicating that they were produced by plants of the subfamily Menispermoideae (Rao, 1981; Jacques et al., 2007; Jacques, 2009b; Herrera et al., 2011; Wefferling et al., 2013; Ortiz et al., 2016). Endocarps with *Menispermum*-type condyles are complex and morphologically diverse structures. Based on endocarp characters, Jacques (2009b) and Wefferling et al. (2013) provided keys to the extant Menispermaceae. Based on the key of Wefferling et al. (2013), both Patagonian endocarps conform to the clade now recognized as Cissampelideae (Ortiz et al., 2016).

The Patagonian endocarps are characterized by horseshoe to crescent-shaped locules, the dorsal ridge(s) of uniform thickness along both limbs, smooth and concave lateral faces, and in the case of *S. psittaca*, the transverse orientation of the conspicuous locule ribs and the nearly straight ventral foramen (Fig. 2B at arrow). This combination of characters is only found in the tribe Cissampelideae (Jacques, 2009b; Herrera et al., 2011; Wefferling et al., 2013; Ortiz et al., 2016). Similar laterally compressed endocarps with a single crescent or hippocrepiform locule are also found in the Anomospermeae, Menispermeae, and Pachygoneae (all Menispermoideae), but these three tribes are also characterized by

sublateral vascular traces, a character not present in *S. psittaca*. The one exception is *Pericampylus* Miers (Anomospermeae), which has a ventral vascular trace like *S. psittaca*, but which also has convex sculpturing on the lateral faces and a broader dorsal ridge on the distal limb than on the proximal limb (Wefferling et al., 2013), two features that are not present in the Patagonian fossils.

Cissampelideae comprise five extant genera, *Stephania* Lour., *Perichasma* Miers, *Antizoma* Miers, *Cissampelos* L., and *Cyclea* Arn. ex Wight. *Perichasma* may be a junior synonym of *Stephania*. Whereas some molecular studies suggest that *Stephania* and *Perichasma* are successive sister clades to the remaining Cissampelideae (Ortiz et al., 2016), others indicate that *Perichasma* is nested within *Stephania* (De Wet et al., 2014; Xie et al., 2015). Here we will refer to *Stephania*+*Perichasma* as *Stephania* s.l.

Most Cissampelideae are vines or lianas, but some are shrubs (*Antizoma*), epiphytes (*Stephania cyanantha* Welw. ex Hiern), or herbs (*Stephania herbacea* Gagnep.) (Rhodes, 1975; Kessler, 1993). The tribe presents several synapomorphies that are not preserved in association with the endocarps, such as monocarpellate flowers, flowers with a single whorl of petals, and stamens fused into a syndrium with a peltiform connective (Ortiz et al., 2016). In terms of endocarp morphology, there is a significant amount of variation among the members of the tribe. Variable characters include endocarp size, type of ornamentation (ribs and spines), the presence/absence of a condyle perforation, overall shape (obovate to subcircular), and the number of dorsal crests (one or two) (Jacques et al., 2007; Jacques, 2009b; Herrera et al., 2011; Wefferling et al., 2013; Ortiz and Nee, 2014).

Among Cissampelideae, the extant genera *Antizoma*, *Cyclea*, and *Cissampelos* are characterized by bilaterally and dorsiventrally compressed endocarps with lateral chambers and two lateral ridges on either side of the endocarp (Wefferling et al., 2013). They form a clade that is sister to *Stephania* s.l. (Ortiz and Nee, 2014; Ortiz et al., 2016). By contrast, *Stephania* s.l., and the likely related fossil genera *Menispina* Herrera, Manchester, Hoot, Wefferling, Carvalho & Jaramillo and *Palaoluna* Herrera Manchester, Hoot, Wefferling, Carvalho & Jaramillo from the Paleocene of Colombia (Herrera et al., 2011), lack lateral chambers and share one lateral ridge on either side of the endocarp, conspicuous radial ribs, the absence of other protrusions into the locule, and smooth concave lateral faces with or without a perforation (Jacques, 2009b).

The Patagonian endocarps have smooth lateral faces and lack lateral chambers, distinguishing them from *Antizoma*, *Cyclea*, and *Cissampelos*. The absence of spines along the dorsal crest(s) serves to distinguish them from the fossil genera *Menispina* and *Palaoluna*. The Paleocene endocarp conforms to the extant genus

Stephania s.l. (Table 3), in having smooth, concave lateral faces without perforation, a smooth dorsal crest, and conspicuous radial ribs in the locule (Fig. 6). In our survey of endocarps of extant Menispermaceae, the most similar are typically small (less than 10 mm long), have a smooth dorsal crest, and the lateral face is either imperforate or has only a small perforation (Jacques, 2009b; Smith et al., 2009; Herrera et al., 2011; Wefferling et al., 2013; De Wet et al., 2014). The affinity of the Eocene endocarp is not clear at this point. It differs from *Stephania* in having short, approximately equal locule limbs (crescent locule shape), but the shapes of the locule intrusions are difficult to assess. Thus, we have elected not to assign the Eocene specimen to a genus until additional material can be found and examined.

Several species of *Stephania* are known from fossil endocarps (Chesters, 1957; Kolesnikova, 1961; Dorofeev, 1974; Bhandari et al., 2009; Collinson et al., 2009, 2012; Herrera et al., 2011; Han et al., 2017), but they all differ from *S. psittaca* (Table 4, Appendix S3). The combination of an imperforate lateral face, small size (<5 mm long), and the relative length of the locule limbs serve to distinguish *S. psittaca* from previously described fossil species.

Leaves: comparison with extant and fossil plants

The occurrence of Menispermaceae among the fossil leaves from the Salamanca Formation (Fig. 4) was initially reported by Iglesias et al. (2007) as an informal menispermaceous morphotype (SA060) and cited later by several authors (Wang et al., 2007; Doria et al., 2008; Herrera et al., 2011). The features that indicate affinity with Menispermaceae are the mucronate tip, entire margin, actinodromous primary venation, fimbrial vein, and regular polygonal areolation; this combination of characters is diagnostic of Menispermaceae (Ortiz et al., 2007; Doria et al., 2008) and typical of the Cissampelideae (Table 5). The presence of the attached upper pulvinus is also useful for confirming affinity with Menispermaceae. The upper pulvinus is typical for the family, although it may be more or less developed in different species. In general, upper pulvini in Menispermaceae are characteristically swollen, curved, and often lack the longitudinal ribs and grooves that characterize the main petiole axis (easily visible in dried specimens); the upper pulvinus may be irregularly wrinkled, and lenticels may be present (Wilkinson, 1986, 1989). Upper pulvini are associated with orienting the leaves for optimal light interception, especially in climbing plants (Burkill, 1944; Wolfe, 1978).

Many species of Menispermaceae known from fossil leaves are assigned to the fossil genus *Menispermites* (Doria et al., 2008); however, the leaf from the Salamanca Formation (Fig. 4) does

TABLE 3. Comparison of the Patagonian (*) endocarp morphology with that of extant Cissampelideae (Menispermaceae).

Genus	Locule shape	Spiny dorsal crest	Lateral spines associated ribs	Perforated condyle	Lateral chambers	Basal sculpturing	One limb longer
AL-1. sp.*†	Cresc.	0	?	0	0	?	0
<i>S. psittaca</i> *†	Hipp.	0	1	0	0	?	0
<i>Antizoma</i>	Hipp.	0	0	0	1	1	1
<i>Cissampelos</i>	Hipp.	0	1	0/1	1	1	1
<i>Cyclea</i>	Hipp.	0	1	0/1	1	1	1
<i>Menispina</i> †	Hipp.	0	1	1	0	0	0
<i>Palaoluna</i> †	Hipp.	0	1	1	0	1	1
<i>Perichasma</i>	Hipp.	1	1	0/1	0	1	1
<i>Stephania</i>	Hipp.	0/1	0/1	0/1	0	1	0/1

Notes: Hipp.: hippocrepiform locule, Cresc.= crescent-shaped locule. (1) present, (0) absent, (†) extinct.

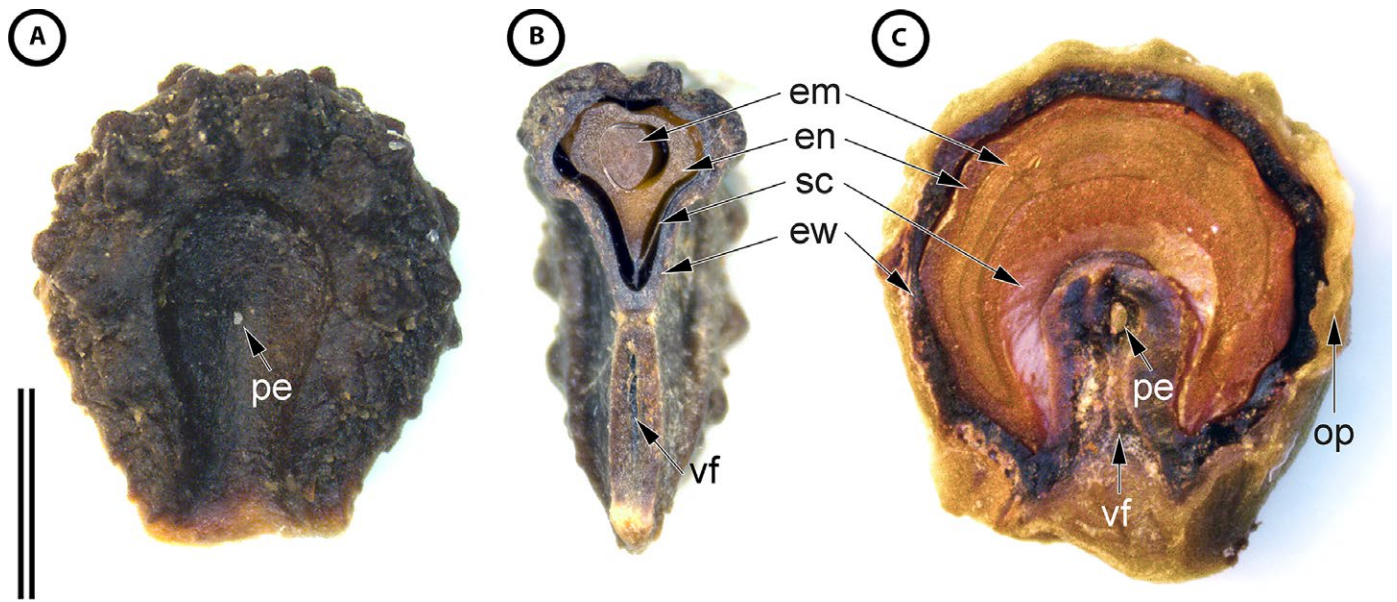


FIGURE 6. Endocarps of *Stephania japonica* (Thunb.) Miers (BH 135447). (A) Lateral view of the endocarp showing the concave lateral face with a minute perforation near the center (pe) and the horseshoe-shaped locule with ornamentation. (B) Near-coronal section of the endocarp, showing the embryo (em) embedded in the smooth endosperm (en), the surrounding seed coat (sc), and the endocarp wall (ew). Also note the glancing section of the ventral foramen (vf). (C) Sagittal section of the fruit, lightly stained with safranin, showing the embryo (em) embedded in the smooth endosperm (en), the surrounding seed coat (sc), the endocarp wall (ew), and the outer pericarp (op). Also note the small perforation of the condyle (pe) above the ventral foramen (vf).

TABLE 4. Comparison of the new species of *Stephania* (*) with other fossil species using characters defined in Appendix S3.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Reference
<i>Stephania psittaca</i> *	0	0	1	0	1	1	1	1	0	3	0	0	0	1	–	1	This study
<i>S. miocenica</i> Chesters	0	0	1	0	1	1	0	1	0	3	0	0	0	1	–	1	Chesters, 1957
<i>S. hootae</i> Collinson et al.	0	1	0	0	1	1	0	0	0	3	0	0	0	0	0	1	Collinson et al., 2012
<i>S. palaeosudamericana</i> Herrera et al.	0	0/1	1	0	1	1	0	1	0	3	0	0	0	0	0	1	Herrera et al., 2011
<i>Stephania</i> sp. (Tomsk)	0	0	?	0	1	1	1	1	0	3	1	0	0	0	0	1	Kolesnikova, 1961; Dorofeev, 1974
<i>Stephania</i> sp. (Nepal)	0	1	?	0	1	1	1	0	0	3	1	0	0	0	0	1	Bhandari et al., 2009
<i>S. wilfi</i> Han & Manchester	0	0/1	1	0	1	1	0	1	0	3	1	0	0	0	0	1	Han et al., 2017
<i>S. jacquesii</i> Han & Manchester	0	1	0	0	1	1	0	1	0	3	1	0	0	0	0	1	Han et al., 2017
<i>S. auriformis</i> (Hollick) Han & Manchester	0/1	1	0	0	1	1	1	1	0	3	0	0	1	0	0	1	Han et al., 2017

not conform to this genus because *Menispermites* leaves have cordate to truncate bases and basal actinodromous primary venation (Table 6). It also differs from the fossil genus *Menispermaphyllum* Hill because leaves of that genus also have basal actinodromous primary venation and preserved trichomes (Hill, 1989). Doria et al. (2008) noted a combination of leaf architectural characters useful for confirming affinity with Menispermaceae but not used in the circumscription of *Menispermites*. These features are the presence of a distinct fimbrial or marginal vein, peltate or subpeltate petiole attachment, and the regular polygonal 4th to 6th order vein framework. In *Wilkinsoniphyllum menispermoides*, a tapering fimbrial vein is present and the 4th to 6th order vein framework is regular polygonal, but the petiole attachment is marginal. Based on our observations of extant plants including those listed in Table 3, *W.*

menispermoides is most similar to some extant Menispermaceae such as *Cocculus carolinus* (L.) DC., and *Pachygone ovata* Miers ex Hook.f. & Thomson. These share marginal petiole attachment, an upper pulvinus, an obtuse concavo-convex base, three suprably actinodromous primary veins, two basal secondary veins, and a mucronate tip. If *W. menispermoides* and the co-occurring endocarp *Stephania psittaca* are in fact different organs of the same plant species, then that plant does not conform to *Stephania* because to our knowledge all *Stephania* have peltate leaves. Additional material showing attachment or a significant co-occurrence pattern is necessary to test this hypothesis.

By contrast, the leaf from the Huitera Formation does conform to *Menispermites*. The diversity of fossil species assigned to *Menispermites* includes leaves with ovate to wide-ovate blades,

TABLE 5. Comparison of the Patagonian leaf fossils* with leaves of selected extant Menispermaceae, with emphasis on Cissampelideae. Data obtained from the Bailey Hortorium and the National Cleared Leaf Collection (Table 2).

Species	Shape	Margin	Att.	Base	Apex	1°v.f	#1°	2°v.f	#2°	3°v.f.	aer.	m.u.v.	Tribe
<i>Menispermites calderensis</i> *	ovate	entire	subp.	b.r.-cord.	str., retuse	b.a.	5	br.	3–4	m.p.	poly.	fim.	
<i>Wilkinsoniophyllum menispermoides</i> *	ovate	entire	marg.	c-c	rnd., mucr.	s.b.a.	3	br.	2–3	a.p.	poly.	?	
<i>Anamirta cocculus</i> (L.) Wight & Arn.	ovate	entire	marg.	asym.	att.	pin.	1	euc.	8–9	a.p.	poly.	fim.	Cosc.
<i>Anamirta paniculata</i> Colebr.	ovate	entire	subp.	b.r.	rnd, mucr.	b.a.	5	br.	5–6	m.p.	poly.	fim.	Cosc.
<i>Anomospermum chloranthum</i> Diels	elliptic	entire	marg.	acute	str.-atten., mucr.	b.a.	5	br.-f.br.	2–4	a.p.	poly.	fim.	Anom.
<i>Antizoma calcarifera</i> Miers	oblong	entire	marg.	rnd.	rnd, mucr.	pin.	1–3	br.	3–7	ret.	?	?	Ciss.
<i>Cissampelos ovatifolia</i> DC	ovate	entire	pelt.-marg.	b.r.	rnd, mucr.	b.a.	5	br	1–2	m.p.	poly.	?	Ciss.
<i>Cissampelos pareira</i> L.	ovate	entire	pelt.	cord.-c-c	str.-rnd, mucr.	b.a.	3–7	br.	2–4	m.p.	poly.	fim.	Ciss.
<i>Cissampelos fasciculata</i> Benth.	ovate	entire	pelt.	cord.	att., mucr.	b.a.	5	br.-euc.	2–3	a.p.	poly.	fim.	Ciss.
<i>Cocculus carolinus</i> (L.) DC	ovate	entire-lobed	marg.	b.r.-cord.	rnd., mucr.	s.b.a.-b.a.	3–5	br.	2	m.p.	poly.	fim.	Pach.
<i>Cocculus diversifolius</i> DC	ovate	entire-lobed	marg.	cord.	str., mucr.	b.a.	7	br.	2–3	ret.	poly.	fim.	Pach.
<i>Cocculus trilobus</i> Merrill	ovate	entire-lobed	marg.	b.r.-cord.	rnd., mucr.	b.a.	5	br.	3	m.p.	poly.	fim.	Pach.
<i>Cyclea hypoglauca</i> Diels	ovate	entire	subp.-pelt.	cord.-b.r.	str.-rnd., mucr.	b.a.	5–11	br.	1–4	m.p.	poly.	fim.	Ciss.
<i>Cyclea polypetala</i> Dunn.	ovate	entire	marg.	cord.	att., mucr.	s.b.a.-b.a.	7	br.	4–6	m.p.	poly.	fim.	Ciss.
<i>Diploclisia glaucescens</i> (Blume) Diels	ovate	entire	marg.-subp.	b.r.-c-c	rnd., mucr.	b.a.	6–7	br.	1–2	m.p.	poly.	fim.	Bura.
<i>Limacia oblonga</i> (Wall.) Miers	elliptic	entire	marg.	trunc.-acute	acute	pin.	1	br.	6–8	m.p.	poly.	fim.	Lima.
<i>Menispermum canadense</i> L.	ovate	entire-lobed	subp.-pelt.	cord.	str.-rnd, mucr.	b.a.	5–12	br.	2–4	m.p.	poly.	fim.	Meni.
<i>Pericampylus glaucus</i> (Lour.) Merr.	ovate	entire	marg.-subp.	cord.-c-c	str., mucr.	b.a.	5–7	br.	2–3	m.p.	poly.	fim.	Anom.
<i>Stephania japonica</i> (Thunb.) Miers	ovate	entire	pelt.	NA	str., mucr.	b.a.	8–12	br.	1–5	m.p.	poly.	fim.	Ciss.
<i>Stephania aculeata</i> F.M.Bail.	ovate	entire	pelt.	NA	str., mucr.	b.a.	8–10	br.	3–5	m.p.	poly.	fim.	Ciss.
<i>Stephania hernandiaefolia</i> Walp.	ovate	entire	pelt.	NA	rnd., mucr.	b.a.	9–11	br.	2	m.p.	poly.	fim.	Ciss.
<i>Spirospermum pendulifolium</i> DC	ovate	entire	marg.	rnd.	str.	b.acr.	3–5	br.	2–3	ret.	poly.	fim.	Spir.

Notes: Att. = attachment; 1°v.f = primary vein framework; #1° = number of primary veins; 2°v.f = secondary vein framework; #2° = number of medial secondary veins; 3°v.f. = tertiary vein framework; aer. = aeration; m.u.v. = marginal ultimate venation; subp. = subpeltate attachment; marg. = marginal attachment; rnd. = rounded; cord. = cordate; c-c = concavo-convex; asym. = asymmetric; trunc. = truncate; b.r. = broad-rounded; pelt. = peltate attachment; b.r. = broad-rounded; cord. = cordate; c-c = concavo-convex; asym. = asymmetric; trunc. = truncate; rnd. = rounded; str. = straight; mucr. = mucronate; att. = attenuate; b.a. = basal actinodromous; b.acr. = basal acrodromous; pin. = pinnate; s.b.a. = suprabasal actinodromous; b.acr. = basal acrodromous; br. = brochidodromous; f.br. = festooned brochidodromous; euc. = eucamptodromous; m.p. = mixed percurrent; a.p. = alternate percurrent; ret. = reticulate; poly. = regular polygonal; fim. = fimbrial vein; Cosc. = Coscineae; Anom. = Anomospermeae; Ciss. = Cissampelideae; Pach. = Pachygoneae; Bura. = Buraiaieae; Lima. = Limacidae; Menispermieae; Spir. = Spirospermeae.

TABLE 6. Comparison of the Patagonian leaf fossils* with selected similar fossil leaves of Menispermaceae.

Species	Shape	Margin	Att.	Base	Apex	1°v.f	#1°	2°v.f	#2°	3°v.f.	aer.	m.u.v.	Age
<i>Menispermites calderensis</i> *	ovate	entire	subp.	broad-rnd., cord.	rnd., retuse	b.a.	5	br.	3–4	m.p.	poly.	fim.	Eo.
<i>Wilkinsoniophyllum menispermoides</i> *	wide ovate	entire	marg.	c-c	rnd., mucronate	s.b.a.	3	br.	2–3	a.p.	poly.	?	Pa.
<i>Chondrodendron brasiliense</i> Dolianiti	ovate	entire	subp.	rnd., slightly cord.	rnd., retuse	b.a.	7	br.	~2	?	?	?	Pli.
<i>Cissampelos rotundifolia</i> Potbury	wide ovate	entire	marg.	deeply cord.	rnd., retuse	b.a.	3	br.	4?	?	?	?	Eo.
<i>Menispermaphyllum tomentosum</i> Hill	wide ovate	entire	marg.	shallowly cord. to obtuse	attenuate to obtuse	b.a.	5	br.	2–3	m.p.	poly.	fim.	Ol.
<i>Menispermites hardemanensis</i> Berry	ovate	entire	marg.	truncate or slightly cordate	?	b.a.	3–5	ca. (br.)?	2–3	?	?	?	Eo.
<i>Menispermites acerifolia</i> Lesq.	ovate	lobed	marg.	nearly truncate to cuneate	lobed, acute	b.a.	3–5	?	1–2	?	?	?	K.
<i>Menispermites americanus</i> Berry	ovate	entire	marg.	broadly truncate or slightly cord.	bluntly pointed	pin.	1	ca. (br.)	4–5	?	?	?	Eo.
<i>Menispermites cerrejonensis</i> Doria et al.	ovate	entire	marg. - subp.	broad-rnd.	acute	b.a.	5–9	br.	2+	a.p.	poly.	fim.	Pa.

Notes: Att. = attachment; 1°v.f = primary vein framework; #1° = number of primary veins; 2°v.f = secondary vein framework; #2° = number of medial secondary veins; 3°v.f. = tertiary vein framework; aer. = aeration; m.u.v. = marginal ultimate venation; subp. = subpeltate attachment; marg. = marginal attachment; rnd. = rounded; cord. = cordate; c-c = concavo-convex; b.a. = basal actinodromous; pin. = pinnate; s.b.a. = suprabasal actinodromous; br. = brochidodromous; ca. = campylodromous; m.p. = mixed percurrent; a.p. = alternate percurrent; poly. = regular polygonal; fim. = fimbrial vein; Pli. = Pliocene; Eo = Eocene; Ol. = Oligocene; Pa. = Paleocene.

marginal to eccentrically peltate insertion of the petiole, and either an entire margin or an untoothed margin with 3–5 lobes (Doria et al., 2008). The primary vein framework of *Menispermites* leaves is actinodromous or acrodromous, and the secondary vein framework is brochidodromous to camptodromous. The tertiary vein framework may be alternate-percurrent, opposite percurrent, or mixed percurrent, but the higher order veins form a regular polygonal network with well-developed areolation. A marginal vein is usually present (Lesquereux, 1874; Wolfe, 1968, 1977; Doria et al., 2008). The Eocene leaf is most similar to *M. hardemanensis* Berry (1930), *M. americanus* Berry (1930), and *M. cerrejonensis* Doria et al. (2008); however it also shares features with *Cissampelos rotundifolia* Potbury (1935) from the Oligocene of California and *Chondrodendron brasiliense* Dolianiti (1949) from the Pliocene of Brazil, which are not assigned to *Menispermites* but perhaps should be. Nonetheless, *M. calderensis* differs from each of these in some features (Table 6), justifying the recognition of a new species.

Paleoenvironment

The affinity of the endocarps with Cissampelideae and the morphology of the leaves (an upper pulvinus in *W. menispermoides*, and a subpeltate leaf with a cordate base in *M. calderensis*) support the interpretation that these were climbing plants (vines or lianas), as are most extant Menispermaceae. Nearly all extant *Stephania* are climbing plants. These are the first reports of eudicotyledonous climbers from the Salamanca and Laguna del Hunco, adding to the known functional diversity of both paleofloras. Previously, Iglesias et al. (2007) reported the climbing fern *Lygodium* from the Salamanca Fm., and Carpenter et al. (2014) described the climbing monocot *Ripogonum* from Laguna del Hunco. Climbing plants, and climbing Menispermaceae in particular, are found in a wide range of habitats from tropical ever-wet (pluvial) forests to temperate deciduous forests; their diversity and abundance peaks in seasonal

tropical forests where they can exploit seasonal changes in water and light availability but are not subject to freezing (Schnitzer and Bongers, 2002; DeWalt et al., 2015). Such a climate is consistent with prior interpretations of data from the Salamanca Fm. and Laguna del Hunco, which indicate warm, frost free climates with minimal seasonality based on leaf physiognomy (Wilf et al., 2005; Iglesias et al., 2007; Hinojosa et al., 2011; Peppe et al., 2011), growth ring analysis of fossil woods (Brea et al. 2005), and the presence of indicator taxa such as alligatorids (Bona, 2005), Arecaceae (Romero, 1968; Archangelsky, 1973; Futey et al., 2012) in the Salamanca Fm. and *Papuacedrus* (Wilf et al., 2009) and diverse Podocapaceae (Wilf et al., 2017) at Laguna del Hunco.

Biogeography

The new fossil occurrences of Menispermaceae reported here are well outside the family's modern range in South America, and they significantly expand the geographic distribution of fossil Menispermaceae in the southern hemisphere (Fig. 1). This result demonstrates that the distribution of Menispermaceae in the southern hemisphere has contracted since the Paleogene. A similar pattern is also present in the northern hemisphere where Menispermaceae have disappeared from Europe and Alaska, areas where their fossils are well known (Hollick, 1936; Collinson et al., 2012). There are only a handful of reliable fossil occurrences of Menispermaceae from the southern continents (Table 7, Fig. 7). The ratio of northern to southern hemisphere fossil endocarp occurrences (where an occurrence is defined as one species at one site), is >7:1 ($n = 127$), but this disparity is likely driven primarily by sampling bias. The fossils described here emphasize the potential of increased sampling effort in southern hemisphere assemblages and permit the re-evaluation of alternative biogeographic hypotheses for Menispermaceae.

Historically, there were two main areas hypothesized as the place of origin of Menispermaceae: Laurasia (Raven and Axelrod,

TABLE 7. Fossil occurrences attributed to Menispermaceae from the southern landmasses.

Name	Country	Age	Organ(s)	Reference	Affinity
<i>Stephania psittaca</i>	Argentina	Early Pa.	Endocarp	This study	Accepted
<i>Wilkinsoniophyllum menispermoides</i>	Argentina	Early Pa.	Leaf	This study	Accepted
<i>Menispermites calderensis</i>	Argentina	Early Eo.	Leaf	This study	Accepted
Menispermaceae sp.	Argentina	Early Eo.	Endocarp	This study	Accepted
<i>Anamirta pfeifferi</i>	India	Early Pa.	Wood	Bonde, 1997	Uncertain
<i>Chondrodendron brasiliense</i>	Brazil	Pli.	Leaf	Dolianiti, 1949; de Lima and Salard-Cheboldaeff, 1981; Mello et al., 2000; Doria et al., 2008	Accepted
<i>Cissampelos rusingensis</i>	Kenya	Mid Mi.	Endocarp	Chesters, 1957	
<i>Cissampelos</i> sp.	Kenya	Mid Mi.		Jacobs and Kabuye, 1987	Accepted
<i>Entoneuron melastomaceum</i>	Australia		Leaf	Geyler, 1878	Rejected
<i>Menispina evidens</i>	Colombia	Late Pa.	Endocarp	Herrera et al., 2011	Accepted
Menispermaceae undet.	New Zealand	Early Mi.	Endocarp	Conran et al., 2014	Accepted
<i>Menispermaphyllum tomentosum</i>	Australia	Mid Eo.	Leaf	Hill, 1989	Accepted
<i>Menispermites cerrejonensis</i>	Colombia	Late Pa.	Leaf	Doria et al., 2008	Accepted
<i>Menispermites cordatus</i>	Colombia	Late Pa.	Leaf	Doria et al., 2008	Accepted
<i>Menispermites guajiraensis</i>	Colombia	Late Pa.	Leaf	Doria et al., 2008	Accepted
<i>Menispermites horizontalis</i>	Colombia	Late Pa.	Leaf	Doria et al., 2008	Accepted
<i>Palaeoluna bogotensis</i>	Colombia	Late Pa.	Endocarp	Herrera et al., 2011	Accepted
<i>Rhytidocaryon wilkinsonii</i>	Australia	Mid Mi.	Endocarp	von Mueller, 1876	Accepted
<i>Sarcopetalum jackieae</i>	Australia	Ol.	Endocarp	Rozefelds, 1991	Accepted
<i>Stephania miocenica</i>	Kenya	Mid Mi.	Endocarp	Chesters, 1957	Accepted
<i>Stephania palaeosudamericana</i>	Colombia	Late Pa.	Endocarp	Herrera et al., 2011	Accepted
<i>Triclisia inflata</i>	Kenya	Mid Mi.	Endocarp	Chesters, 1957	Accepted

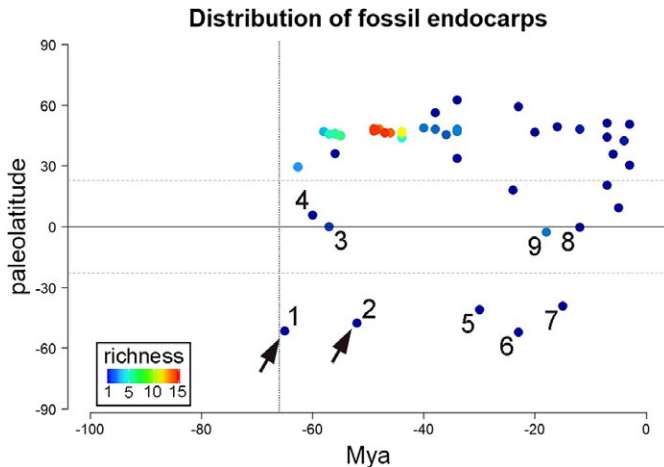


FIGURE 7. Age–paleolatitude plot showing the distribution of fossil Menispermaceae endocarps of Menispermaceae through time (Appendix S1; numbered points correspond to Fig. 1). Each point is a locality, and the color of the point indicates the number of fossil species known from endocarps at that locality (citations listed in Appendix S2). Arrows indicate the two endocarps described here. Note the absence of Cretaceous endocarps and richness and abundance of Laurasian Paleogene endocarps.

1974; Kessler, 1993; Jacques, 2009a) and Africa/Gondwana (Thanikaimoni, 1986; Hill, 1989; Rozefelds, 1991). Raven and Axelrod (1974) based the Laurasian origin hypothesis on the abundance of fossils from Eurasia, the mostly Laurasian distribution of closely related families, and on the contention that *Pycnarrhena* Miers, a primarily Asian genus, is basal in the family. *Pycnarrhena* is now considered derived within the tribe Tiliaceae (Ortiz et al., 2007) and therefore is not a good indicator of the ancestral distribution of the family. The Gondwanan/African hypothesis was based on the high diversity of presumed ancestral genera in tropical Africa (Thanikaimoni, 1986); however, many of these are now considered derived as well (Ortiz et al., 2016).

Molecular phylogenetic studies have led to two additional hypotheses of biogeographic origin based on the distribution of extant species and the topology of molecular trees (Hoot et al., 1999; Jacques et al., 2007; Ortiz et al., 2007, 2016; Wang et al., 2007, 2009, 2012, 2017; Wefferling et al., 2013). Previous estimates using fossil-calibrated molecular clocks suggested that Menispermaceae diverged from other Ranunculales sometime during the Early to mid-Cretaceous and that crown-group Menispermaceae began to diversify during the mid- to Late Cretaceous (Jacques et al., 2011; Wang et al., 2012; Magallón et al., 2015). Wang et al. (2012) reconstructed ancestral distributions throughout the phylogeny of Menispermaceae using statistical dispersal–vicariance analysis. They concluded that the common ancestor of extant Menispermaceae, as well as the common ancestors of each of the two subfamilies: Menispermoideae and Chasmantheroideae (Table 1), was present in the Indomalayan realm by the mid-Cretaceous. Wang et al. (2012) further concluded that crown-group Menispermaceae diversified during the latest Cretaceous to early Paleogene throughout the three major tropical land areas.

The biogeographic conclusions of Wang et al. (2012) and Ortiz et al. (2016) can be evaluated against the fossil record, especially given the wealth of relatively recent paleontological discoveries

(Appendices S1, S2). First, it is not clear whether Wang et al. (2012) and Ortiz et al. (2016) considered the conventionally understood arrangement of the continents during the Late Cretaceous and early Paleogene when hypothesizing an Indomalayan origin for Menispermaceae. At that time, there were four major tropical land areas: northern South America, Central Africa, Southeast Asia, and the island continent of India (Scotese, 2001). What is now the Indomalayan region was not a continuous floristic realm during the Late Cretaceous–early Paleogene. Second, warm wet climates suitable for tropical plants were also present at middle latitudes (Morley, 2011), and therefore, the area of suitable climate for the family was much larger. The distribution of fossil Menispermaceae (Fig. 7) demonstrates that during the Paleogene, Menispermaceae were diverse and widespread in the northern hemisphere. The discoveries reported here suggest the same was true of the southern hemisphere. Remarkably, there are no reliable fossil occurrences of menisperm fruits from the Cretaceous, but by the end of the Paleocene fossil fruits indicate that the family was globally distributed. Based on our investigation of the rich fossil record of endocarps (Fig. 7), we conclude that the modern distribution of the family does not provide a reliable indication of its geographic area of origin because it is obscured by a long history of climate change, dispersal, and local or regional extinction (extirpation). Fossils are critical to investigations of historical biogeography. In the case of Menispermaceae, the fossil record does not support an Indomalayan origin because such a region did not exist during the Cretaceous, but it does demonstrate that the family grew in mid-latitude forests by the early Paleocene (Fig. 7).

Molecular phylogenetic studies provide testable predictions about the age and origin of Menispermaceae and the various tribes. For example, Wang et al. (2012) hypothesized that crown group Cissampelideae began to diversify during the late Paleogene in Indomalaysia and/or the Afrotropics. It is possible that the fossil species *S. psittaca* and *W. menispermoides* are dispersed remains of the same biological species (despite separation by 0.29–2.20 Ma). Under this arguably tenuous hypothesis, this plant concept would not conform to *Stephania* because *Stephania* has peltate leaves. The more conservative approach would be to use 63.49 Ma (upper boundary of Chron 28n, containing PL-2 and the endocarp holotype) as a minimum age for the split between Cissampelideae and its sister, rather than the split between *Stephania* and its sister.

Remarkably, *Stephania* endocarps have been identified from the Eocene of Alaska (Hollick, 1936; Han et al., 2017), the Paleocene and Eocene of the western United States (Herrera et al., 2011; Han et al., 2017), the Paleocene of northern Colombia (Herrera et al., 2011), and the Paleocene of southern Argentina (this study). This broad New World distribution for the earliest *Stephania* fits the inferred locations of warm-wet (megathermal) paleoclimates in the New World during the early Paleogene (Morley, 2011), but it could not have been foreseen by the analysis of Wang et al. (2012) because only extant species were considered in their analysis; extant *Stephania* are exclusively Old World and diverged from other Cissampelideae by the late Paleogene. This highlights the importance of fossil evidence and relevant tectonic and climatic shifts for phylogeographic studies. Given the already widespread distribution of Menispermaceae and Cissampelideae by the Paleocene, we suggest that new collections from undersampled Upper Cretaceous deposits in the Tropics and in regions of the southern hemisphere that hosted warm and wet climates (Morley, 2011) could be productive sources of new menisperm fossils that would further improve our understanding of the evolution and biogeographic history of the family.

CONCLUSIONS

The fossils described here comprise the first known occurrences of living or fossil Menispermaceae in Patagonia and the southernmost occurrences of the family worldwide. Furthermore, the fossils from the Salamanca Formation are the oldest unequivocal evidence of the family worldwide, but their affinity with Cissampelideae implies that substantial diversification of the family had already taken place by the early Paleocene. The documentation of Menispermaceae in the Paleocene Salamanca Formation and Eocene Huitrera Formation increases the known taxonomic and functional diversity of both floras. Our evaluation of the global fossil record of endocarps does not discern between a Laurasian or Gondwanan origin during the Cretaceous. We hypothesize a tropical origin of the family sometime during the Cretaceous, and our findings demonstrate that the family was growing in warm mid-latitude forests of West Gondwana by the earliest Paleocene and into the Eocene.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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