Revised taxonomy of selected fossil endocarp species in the Menispermaceae using a morphometric approach

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ABSTRACT

Several Cenozoic endocarp remains from the northern hemisphere have been described with strong affinities to either *Menispermum* L. or *Sinomenium* Diels, a monophyletic group of menispermous vines. It has been proposed that all of these fossil species are synonymous and should be included within *Sinomenium*. In order to evaluate this suggestion, we have studied the morphological variation ranges in the menispermous endocarps with geometric morphometrics, and then the ranges of the selected fossil endocarps is compared to the ranges of modern endocarps. The shape of each endocarp is described using eight landmarks and 17 semilandmarks, accounting for the outline and the positions of lateral

ridge and foramen on the endocarps. Endocarp ornamentation is studied by statistical comparisons of the number of transverse ridges. It is concluded that the ranges of variation within the fossil genera, all morphologically related to horseshoe-shaped endocarps in Menispermaceae, are found not to be greater than that in the only extant species of *Sinomenium*, *S. acutum* (Thunb.) Rehder & Wilson. *Sinomenium macrocarpum* Liu & Jacques, 2010 differs from the other fossil species of *Sinomenium* by its higher number of transverse ridges. All other fossil species of *Sinomenium*, except *S. macrocarpum*, and *Wardensheppeya* Eyde, 1970 are synonymous. *Menispermum*? *taylori* Chandler, 1964 is transferred to *Sinomenium*. The fossil genus *Palaeosinomenium* Chandler, 1961 is confirmed through the obliquity of its endocarp, but all species are found to be synonymous. *Menispermicarpum rariforme* Chandler, 1961 is also included in *Palaeosinomenium*.

RÉSUMÉ
Taxonomie révisée de certaines espèces d'endocarpes fossiles de Menispermaceae par une approche morphométrique.
Plusieurs restes d'endocarpes du Cénozoïque de l'hémisphère nord ont été décrits comme ayant de fortes affinités avec soit *Menispermum* L. soit *Sinomenium* Diels, un groupe monophylétique de lianes des Menispermaceae. La synonymie de toutes ces espèces et leur inclusion dans *Sinomenium* ont déjà été proposées. Pour évaluer cette proposition, nous avons étudié l'étendue des variations morphologiques des endocarpes de Menispermaceae par morphométrie géométrique, et ensuite l'étendue de cette variation pour les espèces fossiles sélectionnées est comparée à l'étendue de la variation pour les espèces actuelles. La forme de chaque endocarpe est décrite grâce à huit landmarks et 17 semilandmarks, représentant le contour et les positions de la crête latérale et du foramen pour chaque endocarpe. L'ornementation des endocarpes est étudiée par une comparaison statistique du nombre de côtes transversales. On peut conclure que l'étendue de la variation dans les genres fossiles, tous morphologiquement liés aux Menispermaceae à endocarpes hippocrépiformes, n'est pas plus importante que celle observée dans la seule espèce actuelle de *Sinomenium*, *S. acutum* (Thunb.) Rehder & Wilson. *Sinomenium macrocarpum* Liu & Jacques, 2010 diffère des autres espèces fossiles de *Sinomenium* par son plus grand nombre de côtes transversales. Toutes les espèces fossiles de *Sinomenium*, à l'exception de *S. macrocarpum*, et de *Wardensheppeya* Eyde, 1970 sont synonymes. *Menispermum*? *taylori* Chandler, 1964 est transféré dans *Sinomenium*. Le genre fossile *Palaeosinomenium* Chandler, 1961 est confirmé par l'obliquité de son endocarpe, mais toutes ses espèces sont synonymes. *Menispermicarpum rariforme* Chandler, 1961 est aussi inclus dans *Palaeosinomenium*.

INTRODUCTION

Numerous menispermaceous fossil endocarps have been found in the temperate regions of North America and Europe (e.g., Chandler 1961; Takhtajan 1974; Manchester 1994; Jacques & De Franceschi 2005). As the most temperate genera in Menispermaceae are *Menispermum* L. and *Sinomenium* Diels

(Diels 1910), it is not surprising that fossil endocarps showing the unique horseshoe-shaped outline have affinities with the *Menispermum-Sinomenium* complex. Molecular analyses also recognize this complex as monophyletic (Wang *et al.* 2007; Hoot *et al.* 2009; Jacques *et al.* 2011). A recent morphometric study on modern Menispermaceae endocarps (Jacques & Zhou 2010) demonstrated that the endocarps from the *Menispermum-Sinomenium* complex have a different shape from other horseshoe-shaped endocarps of the Menispermaceae. Fossils are placed in either *Menispermum*, *Sinomenium*, or in the extinct genera *Wardensheppeya* (Chandler) Eyde, 1970 and *Palaeosinomenium* Chandler, 1961. More than 15 fossil species have been described as part of this complex (Jacques 2009b), far more than the three to five species recognized in the modern flora. *Palaeosinomenium* (six species) and *Wardensheppeya* (three species) occur only in the Palaeogene, whereas the fossil species of *Sinomenium* (three fossil species) have been reported principally in the Neogene and sometimes in the Oligocene (Jacques 2009b). *Menispermum* (two fossil fruit species) occur in European Palaeogene and Neogene. Having considered that the range of shape variation of these fossil endocarps might fall within the range of the monotypic *Sinomenium*, Mai (1997) proposed a putative synonymy of *Wardensheppeya* and *Palaeosinomenium* with *Sinomenium*. However, the question has not yet been resolved. Furthermore, due to its key phylogenetic position in the basal eudicots (Savolainen *et al.* 2000; APGII 2003) and relatively rich fossil record (Doria *et al.* 2008; Jacques 2009b), Menispermaceae are critical and useful to provide evidence on the diversity of early eudicots.

Endocarps have a suite of systematically important characters. Both Diels (1910) and Kessler (1993) used seed and endocarp characters to discriminate between their tribes and genera. Furthermore, it is practical that the morphology of the menispermaceous endocarps is helpful in quick specimen identification (Jacques 2009a). Morphometry has been proven a powerful tool to characterize some of the modern endocarps (Jacques & Zhou 2010).

The fossil species of the *Menispermum-Sinomenium* complex are mainly morphospecies based on endocarp remains (Jacques 2009b). Attribution of the fossils to this complex is based on several diagnostic features (Jacques 2009a): horseshoe-shaped endocarps with excavated faces, bearing one lateral ridge on each face, and having a large central area largely ventrally opened, with a foramen near the stylar limb. Several fossil genera have been described in this complex based on several diagnostic features. Chandler (1961: 159) described *Palaeosinomenium* as having "a more oblique endocarp and elongate foramen" relative to *Menispermum* and *Sinomenium*. *Palaeosinomenium* species vary in the position of the foramen and the shape of the ventral margin (Chandler 1963). *Wardensheppeya* (under the name *Wardenia*) was characterized as having endocarps "with wide marginal flange" and "straight or concave ventral margin" by (Chandler 1961:158) and species vary in the position of the foramen and endocarp ornamentation (Chandler 1962, 1963). In contrast, for *Sinomenium*, the systematic treatment is quite different. Some species (*S. dielsii* Szafer, 1947, *S. militzeri* Kirchheimer, 1943) were already transferred to *S. cantalense* (E.M.Reid) Dorofeev, 1955, synonymy accepted there on (e.g., Mai 1997). The fossil record of the latter species has long been reported from different localities and different ages (Table 1). The concept of *S. cantalense* is therefore broader than the concepts of *Palaeosinomenium* and *Wardensheppeya* species. The intraspecific variability of extant species is key to choose between a broad or narrow concept for the fossil species, but has not been analysed yet. Therefore, there is no clear evidence to support synonymizing some fossil species or in the continued recognition of others.

As diagnostic features used to distinguish among taxa refer to the endocarp shape, morphometric methods provide a mathematically based, less biased method to study and characterize shapes among taxa (Jensen 2003). Traditional morphometric methods have proved to be useful in the revision of *Ampelocissus* fossil seeds (Chen & Manchester 2007).

When dealing with morphometrics, different methods are available (Jensen 2003; Adams *et al.* 2004). Traditional morphometrics deals with multivariate analysis of different measurements (Sokal & Sneath 1963; Sneath & Sokal 1973). Geometric morphometrics, first developed by Bookstein *et al.*

TABLE 1. — Endocarps studied in the morphometrics analysis. *, Inclusion in this genus is not certain according to the authority.

Species	Number of endocarps	Site	Age
Menispermicarpum Chesters, 1957			
M. rariforme Chandler, 1961	1	London Clay	Eocene
Menispermum Linnaeus, 1735			
M. canadense Linnaeus, 1753	21	?	Recent
"*M. crassicarpum*" cf. Reid & Reid, 1915	1	Tegelen	Late Pliocene
M. dauricum DC., 1818	25	?	Recent
M. reidii Geissert, Gregor & Mai, 1990	1	Sessenheim	Late Miocene-Early Pliocene
M. cf. *reidii* Geissert, Gregor & Mai, 1990	1	Castelletto Cervo II, Italy	?Late Pliocene
M. taylori Chandler, 1964*	1	London Clay	Eocene
M. sp.	1	John day, Oregon	Oligocene
Palaeosinomenium Chandler, 1961			
P. hantonense Chandler, 1963	1	London Clay	Eocene
P. obliquatum (Chandler) Chandler, 1961	1	London Clay	Eocene
P. pulchrum Chandler, 1961	2	London Clay	Eocene
P. ucrainicum Dorofeev, 1974	4	Ukraine	Eocene
P. venablesi Chandler, 1961	4	London Clay	Eocene
	2	Clarno Beds, Oregon	Eocene
Sinomenium Diels, 1910			
S. acutum (Thunb.) Rehder & Wilson	46		Recent
S. cantalense (E.M.Reid, 1920) Dorofeev, 1955	2	Pont-de-Gail, France	Late Miocene
	1	Ukraine	
	1	Abkhazia	Miocene
	3	Poland	Pliocene
	1	Poland	Miocene
	26	NW Italy	Pliocene
	20	Cava Toppetti II, central Italy	Late Pliocene
S. macrocarpum Liu & Jacques, 2010	24	Gray, Tennessee	Late Miocene-Early Pliocene
S. sibiricum Dorofeev, 1974	4		Oligocene
Wardensheppeya Eyde, 1970			
W. davisii (Chandler) Eyde, 1970	4	London Clay	Eocene
	2	Le Quesnoy, France	Eocene
W. marginata (Chandler) Eyde, 1970	1	London Clay	Eocene
W. poolensis (Chandler) Eyde, 1970	2	London Clay	Eocene

(1985), extracts size variation from the analysis and only deals with shape (Bookstein 1991). Geometric morphometric methods are very useful for the comparison of fossil and extant species, as some post-depositional processes could have modified the size of the fossil remains. In the landmark methods and Thin Plate Splines (TPS) analysis (Rohlf & Slice 1990), an object is described by homologous landmarks (Bookstein 1991; Jensen 2003). These landmarks positions vary depending on the size, shape and orientation of each specimen (Adams *et al.* 2004). The analysis of landmarks begins with a superimposition process in order to remove size and orientation from the analysis (Bookstein 1986; Rohlf & Slice 1990). The combination of landmark coordinates is then used as a descriptor of each object shape (Bookstein 1991; Adams *et al.* 2004). Landmark methods have been successfully used in some botanical studies (e.g., Jensen 1990; Shipunov & Bateman 2005). However, the availability of only few homologous points on the studied endocarps limits the application of this landmark approach in the present study (Adams *et al.* 2004). The other type of morphometrics study is the study

of outlines, using eigenshape analysis (Lohmann 1983) or elliptic Fourier functions (McLellan & Endler 1998; Olsson *et al.* 2000). Outline methods are not congruent with different methods giving different results (Rohlf 1986; Adams *et al.* 2004). For the *Menispermum-Sinomenium* complex, the variation in ornamentation ranges from almost lacking to highly developed transverse ridges. Those ridges modify the outline and may interfere with the description of the general shape of an endocarp using outline methods. The solution to this problem is the semilandmark approach (Bookstein 1997), which enables the description of an object's outline using landmarks (Bookstein 1997; Monteiro *et al.* 2005) bearing only one Cartesian coordinate, namely the normal direction to the outline (Bookstein 2002). During the Procrustes superimposition procedure, the semilandmarks are allowed to slide along the outline. As the semilandmarks are placed on a curve, the difference in curvature between two specimens could increase the bending energy abnormally if they were fixed; therefore, we used sliding semilandmarks (i.e. they are allowed to slide along the outline). The combination of landmarks and semilandmarks can be successfully used in shape analysis (Monteiro *et al.* 2005). This approach, then, is the best to use for the case of fossil menispermous endocarps, viz. few homologous points but several homologous lines, as it has already been done for modern endocarps of the family (Jacques & Zhou 2010). Geometric morphometrics has already been applied successfully in fossil studies, like on trilobites (Webster & Hughes 1999; Delabroye & Cronier 2008), ostracods (Aiello *et al.* 2007), sharks (e.g., Nyberg *et al.* 2006; Whitenack & Gottfried 2010), reptiles (e.g., Bonnan 2007; Bonnan *et al.* 2008), and humans (e.g., Harvati 2003; Holliday *et al.* 2010). But, to our knowledge, it is the first to be applied in palaeocarpology.

The present study aims first to estimate intraspecific shape variability in the modern species of *Menispermum* and *Sinomenium* and allied fossil species; secondly to describe shape differences between these species and genera; and finally to propose a revision of the considered fossil endocarps and a revised systematic of the group.

MATERIAL AND METHODS

SAMPLING AND DIGITIZATION

This study included 92 extant and 111 fossil endocarps, representing 18 species of *Sinomenium-Menispermum* complex (Table 1; Appendix 1). Modern endocarps were taken from herbarium sheets and photographed under a stereoscopic microscope (Nikon SMZ1500) coupled with a digital camera (Nikon digital sight DS-U). Pictures of fossil endocarps were scanned from publications or taken by the authors. Italian specimens pictured for the study are mainly from the following Pliocene localities: Ca' Viettone (Martinetto 1995), Castelletto Cervo I (Cavallo & Martinetto 2001), Cava Toppetti II (Martinetto 2001), Sento (Basilici *et al.* 1997), Ronco Biellese (Martinetto 1995), Villafranca d'Asti (Martinetto 1995). As neither pictures nor complete specimens are available, *Palaeosinomenium becvae* Knobloch, 1971 was not included in this study. Because *Althaea crassicarpa* Reid & Reid, 1915 was already compared with *Menispermum* by Reid (1920) and Geissert *et al.* (1990), we included it under the name "*Menispermum crassicarpum*". We included *Menispermicarpum rariforme* Chandler, 1961 in our study, despite of its unsolved affinities, but it could be allied with the *Menispermum–Sinomenium* group. Actual holotypes of all fossil species except *S. sibiricum* Dorofeev, 1974 have been observed by the authors.

DATA ACQUISITION

The same lateral face of each specimen was digitized using TPSdig (Rohlf 2006a). All these images were captured at a resolution of 640 × 480 pixels. When the specimens from the literature were not figured showing this same face, we horizontally flipped the picture (both faces are approximately symmetric) to provide a consistent face orientation for shape analysis. The outline was determined by hand using "curve drawing tools". The same technique was used to digitize the top of the lateral ridge. All lines start and finish on landmark points. The lines are re-sampled to equally distant points: nine for the dorsal margin (numbers 3 to 11), six for the ventral margin (numbers 20 to 25) and eight for the lateral ridge (numbers 12 to 19). Landmarks describing those lines, except their extremities, were
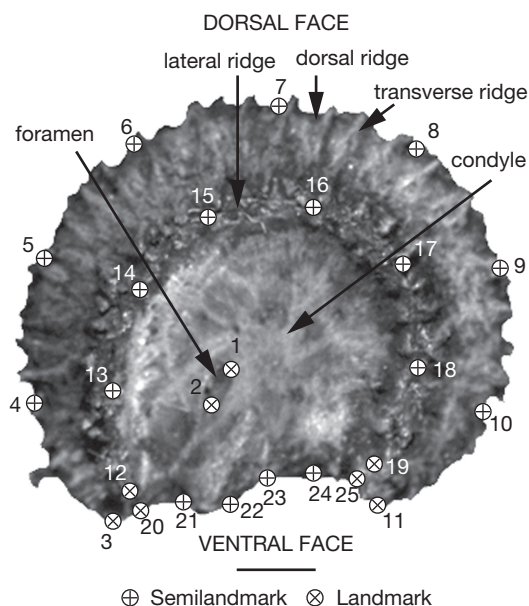
Fig. 1 — Position of landmarks and semilandmarks on a Menispermaceae endocarp. Scale bar: 1 mm.

TABLE 2. — Description of landmarks. For definition of landmark types see Slice *et al.* (1996). Landmark numbers refer to Figure 1.

Landmark number	Description	Landmark type
1	Dorsal endpoint of the foramen	II
2	Ventral endpoint of the foramen	II
3	End of stylar limb	I
11	End of the other limb	I
12	Stylar end of lateral ridge	II
19	Other end of lateral ridge	II
20	Point on ventral margin corresponding to the base of lateral ridge, stylar side	III
25	Point on ventral margin corresponding to the base of lateral ridge, other side	III

changed to semilandmarks using TPSutil (Rohlf 2006b). The endocarp shape was then described using eight landmarks and 17 semilandmarks (Fig. 1; Table 2).

In addition, the number of transverse ridges was counted for each specimen.

DATA ANALYSIS

The shapes for each specimen were then aligned using General Procrustes Analysis with semilandmarks allowed to slide. The consensus shape was combined, and partial warps and relative warps (using $\alpha=0$) were calculated, using the software TPSrlw (Rohlf 2007). The relative warps analysis corresponds to the Principal Component Analysis (PCA) of all partial warps scores (Rohlf 1993; Rohlf *et al.* 1996). The PCA is preferred to Canonical Variance Analysis (CVA) because PCA does not require *a priori* grouping of the specimens whereas CVA does. CVA maximizes the difference between groups compared to differences within groups (Rohlf *et al.* 1996). As this study addresses the limits of the species, we prefer not to work with *a priori* groupings.

All partial warp scores were also used for a multivariate analysis. The similarity between seven groups (*Menispermum canadense* L., *Menispermum dauricum* DC., *Sinomenium acutum* (Thunb.) Rehder & Wilson, *Sinomenium macrocarpum* Liu & Jacques, other fossil *Sinomenium*, *Palaeosinomenium*, and *Wardensheppeya*) was tested using a non-parametric test, a one-way ANOSIM with Euclidean distance and 100 000 permutations (Clarke 1993). This choice was made because of the small sample size of some groups.

The number of transverse ridges was tested for equality between those seven groups. The hypothesis of normality was rejected for *Menispermum dauricum* (Shapiro-Wilk test: W=0.503, p=0.001782), so an ANOVA could not be used. Therefore, we used a non-parametric test, the Kruskal-Wallis test. In case of different means, post-hoc tests were performed based on Bonferroni-corrected pairwise Mann-Whitney test.

Due to the limitation of specimens, the following two fossil species, *Menispermum*? *taylori* Chandler, 1964 and *Menispermicarpum rariforme*, were not included in the statistic analyses. Some other species with only one specimen were grouped with other congeneric species for the statistical analysis, for example, *Palaeosinomenium obliquatum* (Chandler) Chandler, 1961 was grouped with all *Palaeosinomenium*.

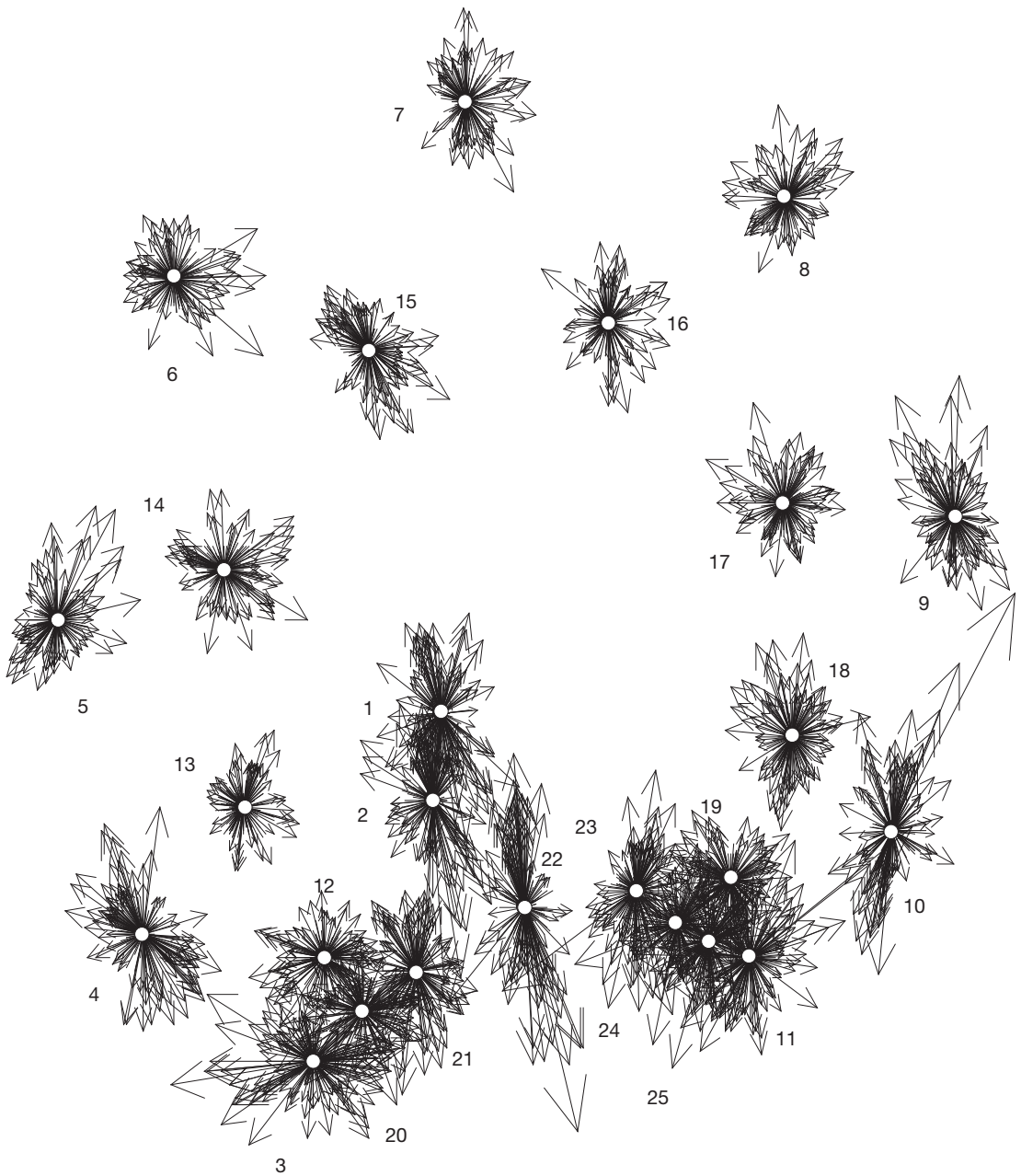All statistical analyses were performed with the software PAST version 1.75b (Hammer *et al.* 2001).

Fig. 2 — Consensus positions of all landmarks and semilandmarks for all studied specimens. The vectors indicate the position of landmarks and semilandmarks in our sampling.

LIMITS OF THE METHOD

The method can be used only with complete or almost complete endocarps. The only noticeable exception is when one half of an endocarp is complete. Indeed, the analysis cannot be made if one landmark is missing on one specimen. All speci-

mens must have the same number of landmarks (Adams *et al.* 2004).

The method studies the global shape of the object. If the shape of the object has been modified, the method analyses the deformed shape and not the original one of the object. If the deformation is exactly known, the actual shape can be reconstructed and analysed. Fossil endocarps might have undergone some deformation. However, we cannot reconstruct such deformation; therefore, we exclude from this analysis all clearly deformed endocarps.

Another problem might be differences in fossil preservation that can affect ornamentation. For ornamentation, we only use the number of transversal ridges and neither their size nor their shape (more or less thin or spiny) is considered; therefore we assume that, as long as transverse ridges are present, preservation process did not change their number. For the shape of endocarp, the method used in the present study, geometric morphometrics, excludes size from the analysis (Bookstein 1991), and therefore accounts for homothetic size differences due to preservation process. In case of non homothetic differences, this is a deformation and clearly deformed endocarps are excluded.

ABBREVIATIONS
ANOSIM   Analysis of similarity;
ANOVA   Analysis of variance.

RESULTS

CONSENSUS AND MEAN SHAPES
Figure 2 shows the consensus positions of landmarks and semilandmarks, as well as the vectors to all positions in the sampling, resulting from the General Procrustes Analysis. The most evident variation is observed in the ventral margin region.

A consensus for each group was calculated (Fig. 3). The grid, representing the thin-plate transformation from the general consensus to the group consensus, allows characterization of the peculiar shape of each group possible relative to the overall consensus shape. *Menispermum canadense* (Fig. 3A) shows a strong concavity of the ventral margin

and a relatively larger condyle than the consensus shape. *Menispermum dauricum* (Fig. 3B) also shows a strong concavity of the ventral margin, but with a condyle only slightly relatively larger than that of *M. canadense*. *Sinomenium acutum* (Fig. 3C) is very similar in shape with the consensus shape. *Sinomenium macrocarpum* (Fig. 3D) has a consensus very similar to that of *S. acutum*. Other fossil *Sinomenium* (Fig. 3E) have a relatively higher dorso-ventral length and a relatively shorter limb-to-limb length than the consensus shape, and the extremities of the two limbs are relatively closer than the consensus shape. *Wardensheppeya* (Fig. 3F) has a relatively smaller condyle and relatively closer extremities of the two limbs than the consensus shape. *Palaeosinomenium* (Fig. 3G) has an almost flat ventral margin, a relatively small condyle and an obliquity of the whole endocarp.

RELATIVE WARPS ANALYSIS
The results of relative warps analysis are summarised by the representation of the first two main axes (Fig. 4; Table 3). The first relative warp axis discriminates most of the groups and corresponds to a modification of the concavity of the ventral margin, a contraction of the median length and a relative increase of dorsal flange size (or relative decrease of condyle size). The second relative warp axis discriminates between the recent and fossil *Sinomenium* and corresponds to an increase of the length relative to the height, a removal of the two limb extremities and a relative increase of dorsal flange size. Other relative warp axes do not discriminate between groups. There is some overlap between the groups. The shape of *Menispermum dauricum* is between those of *Sinomenium acutum* and *M. canadense*. *Wardensheppeya* is set between other fossil *Sinomenium* and *Palaeosinomenium*. *Sinomenium acutum* endocarps show a wide variability in shape.

The ANOSIM gives the following result, viz. mean rank within 6490, mean rank between 10710, R 0.4246, p(same)<1 × 10^{-5}. The hypothesis of similarity among the seven groups is rejected. Table 4 summarises the results of the post-hoc pairwise comparisons tests. The test is significant at 1% for all pairwise comparisons (hypothesis of similar-
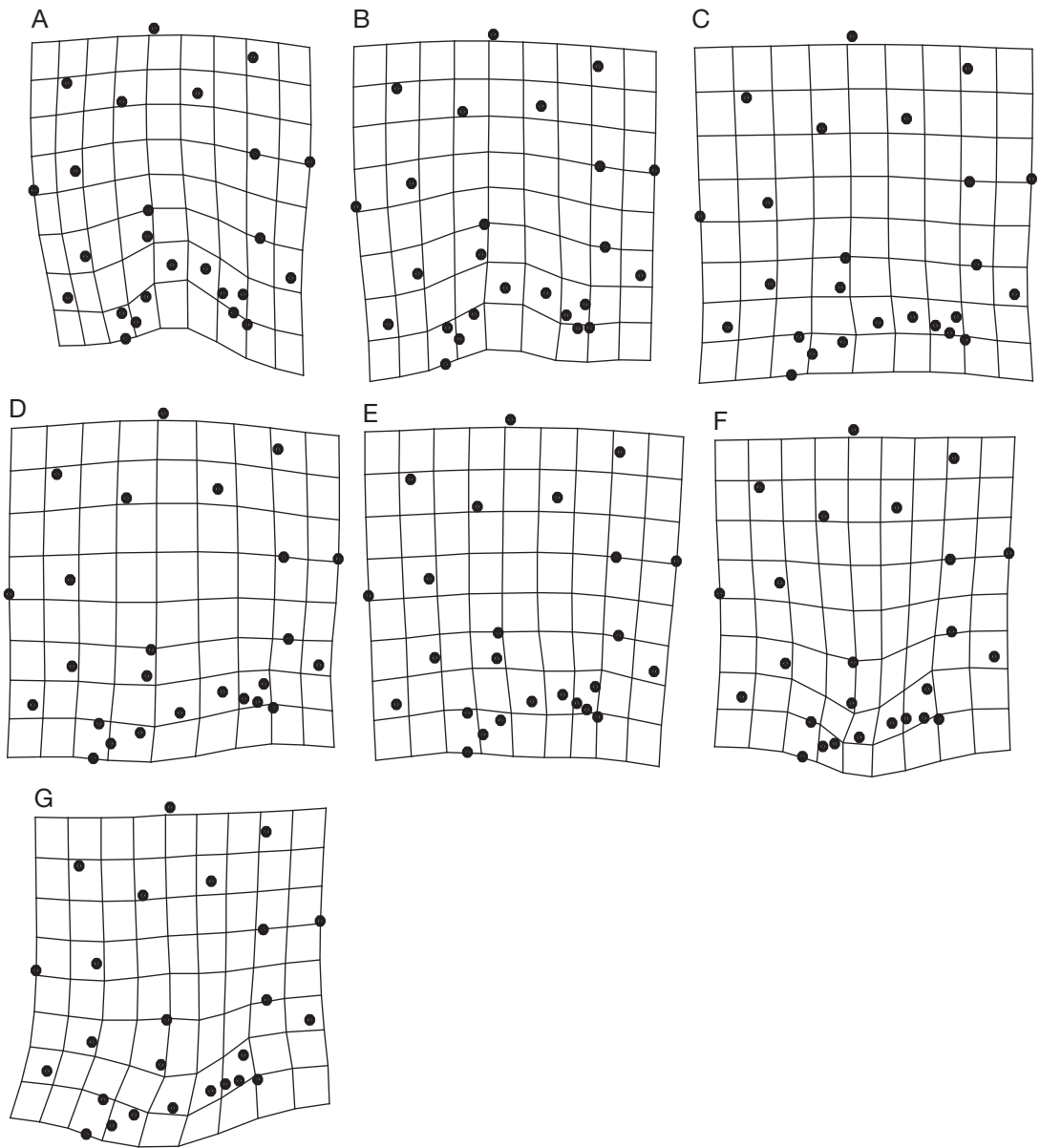
FIG. 3 — Consensus shape for each group of endocarp. The grid corresponds to the thin-plate transformation between the general consensus and the consensus of each group: **A**, *Menispermum canadense* L.; **B**, *Menispermum dauricum* DC.; **C**, *Sinomenium acutum* (Thunb.) Rehder & Wilson; **D**, *Sinomenium macrocarpum* Liu & Jacques, 2010; **E**, other fossil *Sinomenium* Diels; **F**, *Wardensheppeya* Eyde, 1970; **G**, *Palaeosinomenium* Chandler, 1961.

ity rejected) except for other fossil *Sinomenium* and *M. dauricum*; *S. acutum* and *S. macrocarpum*; *Palaeosinomenium* and *Wardensheppeya*. For *Pala-eosinomenium* and *Wardensheppeya*, and *M. dauricum* and other fossil *Sinomenium*, the test is significant at 5%.

Relative warps axis	Singular value	Percent explained	Cumulative percent explained
1	1.0316	35.52	35.52
2	0.7401	18.17	53.69
3	0.5899	11.56	65.25
4	0.4634	7.16	72.41
5	0.4045	5.46	77.87

ANALYSIS OF ORNAMENTATION

The number of transverse ridges for each group varies greatly, ranging from 11 to 44 (Fig. 5). *Menispermum canadense* has the highest number of transverse ridges, whereas *Sinomenium* (including both recent and fossil), *Palaeosinomenium* and *Wardensheppeya* have the lowest number of ridges. The number of ridges in *M. dauricum* is intermediate between those of *M. canadense* and *S. acutum*. The number of ridges in *S. macrocarpum* is intermediate between that of *M. dauricum* and other *Sinomenium* and *Wardensheppeya*.

The Kruskal-Wallis test gives p=2.267 × 10^{-22}, rejects the hypothesis of equality of means, and is followed by Mann-Whitney pairwise comparison post-hoc tests (Table 5). The p-values are significant for *M. canadense* and all other groups, and for *M. dauricum* and all other groups, except *S. macrocarpum*. The hypothesis of equality of ridge number cannot be rejected between *S. acutum*, fossil *Sinomenium* (except *S. macrocarpum*) *Palaeosinomenium* and *Wardensheppeya*. The test is significant at 5% between *S. macrocarpum* and *Wardensheppeya*.

DISCUSSION

THE SHAPE SIGNAL

The maximal shape variation is observed on the ventral margin (Fig. 2). The dorsal margin is represented by many semi-landmarks, whereas the ventral margin groups more landmarks (Fig. 1). Therefore, the concentration of the variation near the ventral margin could be an artefact. However, the variation observed at the ventral margin concerns changes in the concavity of the ventral margin

(Fig. 3), and then represents a real shape signal. On the contrary, there is no change in the convexity of the dorsal margin.

Transverse ridges may be a source of other homologous points, and hereby of other landmarks. However, the number of transverse ridges is not constant even in the same species (Fig. 5). Besides, all transverse ridges of one endocarp are of similar structure, as we cannot discriminate between them. Therefore, we cannot reconstruct homologies (if they do exist).

INFRAGENERIC RELATIONSHIPS

The relative warp analysis (Fig. 4) exhibits the shape differences between specimens. A detail of the results is given for the fossil specimens (Fig. 6). The positions of the different species of the same genus occupy the same morphospace. For example, the postion of several endocarps of *Wardensheppeya davisii* (Chandler) Eyde, 1970 in the graph appears to surround that of the only known specimen of *W. marginata* (Chandler) Eyde, 1970. *Palaeosinomenium obliquatum* is plotted at almost the same position as one (of six) specimen of *P. venablesi* Chandler, 1961. Each fossil genus, in morphospace, represents less variability than in extant *S. acutum*, as they occupy a smaller area of the plot. When describing the different species of *Wardensheppeya* (under the name *Wardenia*), Chandler (1961, 1962, 1963) discriminated between the species based on their shape and, and to a lesser degree, their ornamentation. Having used morphometrics, we noticed that the shape does not represent a diagnostic character useful for discriminating in species of *Wardensheppaya* and *Palaeosinomenium*. There are also variations in endocarp ornamentation within the modern species, e.g., *M. dauricum* varies from almost smooth to having pronounced transverse ridges. Similarly, although the species in *Palaeosinomenium* from the Eocene London Clay were defined primarily by their shapes (Chandler 1925, 1961, 1963), the present morphometric study clearly shows that this feature cannot be safely applied in fossil endocarp determination. Chandler (1961) stated that *P. pulchrum* Chandler, 1961 displays a greater obliquity than *P. venablesi*; however, our results (Fig. 6) show that the obliquity of *P. pulchrum* is not greater than
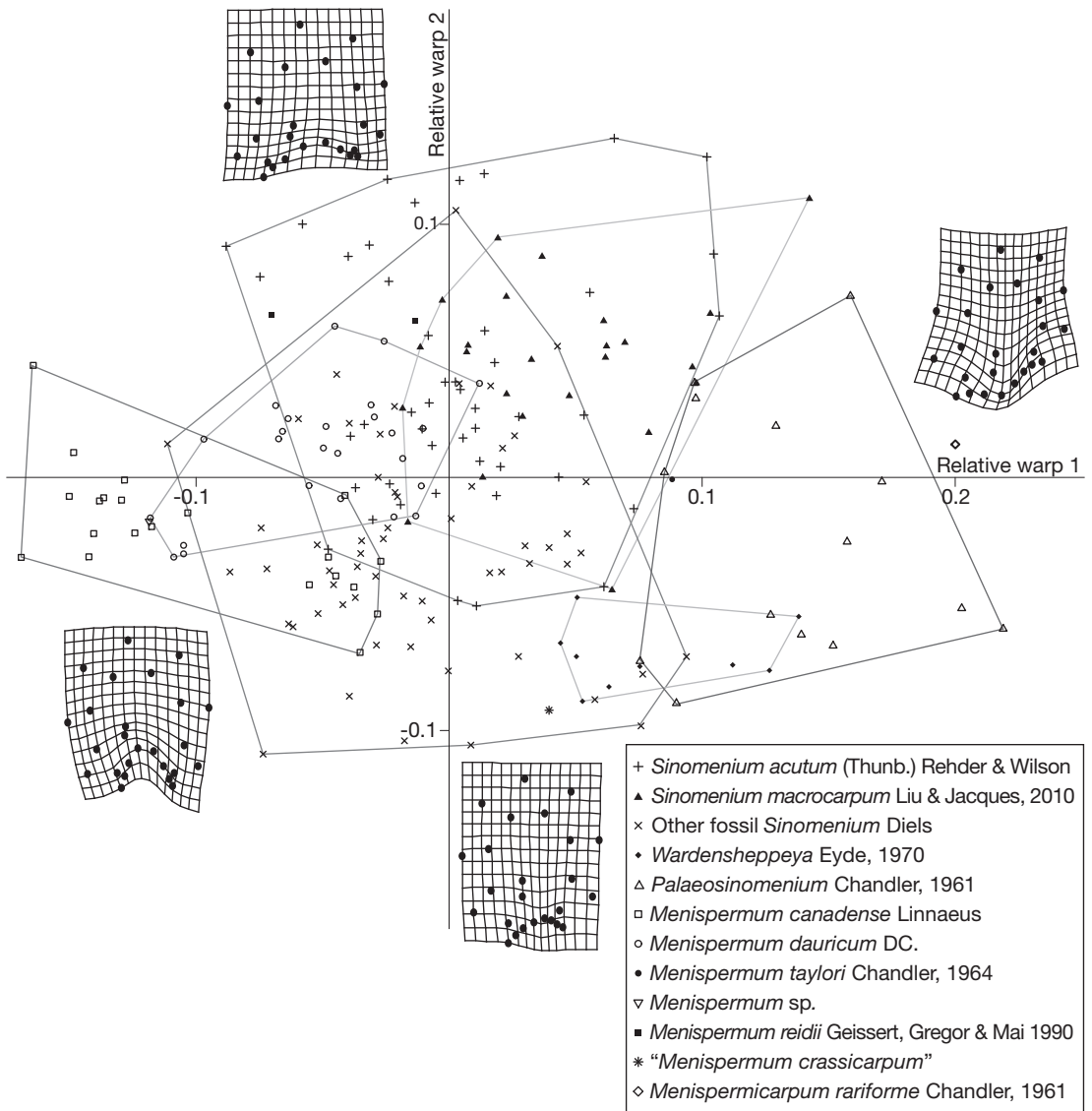
FIG. 4 — Relative warps analysis of shape of Menispermaceae endocarps, axes 1 and 2. The sketches along the axes correspond to the shape modification. Hulls surround each group.

that of *P. venablesi*. Furthermore, our morphometric analysis supports that all the fossil specimens of *Sinomenium* examined in the present study, except *S. macrocarpum*, can be grouped into one species. Despite the morphological similarity with *S. acutum* (Fig. 4; Table 4), *S. macrocarpum* differs from the former in its ornamentation (Fig. 5; Table 5).

As the difference between them is based only on ornamentation, their inclusion in the same genus seems correct. The fossil record of *S. cantalense* shows that this fossil species appears extremely diverse and exhibits a wide range of variations. To better examine the diversity of this fossil species, we separated the specimens according to their localities

TABLE 4. — ANOSIM post-hoc pairwise comparison of shape of Menispermaceae endocarps. Lower-half values are Bonferroni corrected p-values. Upper-half values are uncorrected p-values. Abbreviations: **, significant test at 1%; *, significant test at 5%; **0**, indicates a result lower than the lowest value that can be displayed by the software; ***M.***, *Menispermum*; ***S.***, *Sinomenium*.

	M. cana-dense	M. dauricum	S. acutum	S. macro-carpum	Other fossil Sinomenium	Palaeo-sinomenium	Warden-sheppeya
M. canadense		2.0×10^{-5}	0	0	0	0	0
M. dauricum	5.6×10^{-4}**		0	0	4.5×10^{-4}	0	0
S. acutum	0**	0**		0.01874	0	0	0
S. macrocarpum	0**	0**	0.5247		0	0	0
Other fossil Sinomenium	0**	0.0126*	0**	0**		0	1.0×10^{-5}
Palaeosinomenium	0**	0**	0**	0**	0**		3.8×10^{-4}
Wardensheppeya	0**	0**	0**	0**	2.8×10^{-4}**	0.0106*	

TABLE 5. — Mann-Whitney pairwise comparison post-hoc test for equality of means (number of transverse ridges on endocarps). Upper-half values, uncorrected p values. Lower-half values, Bonferroni corrected p-values. Abbreviations: **, significant test at 1%; *, significant test at 5%; **1**, indicates that the resolution of the software cannot distinguish the actual value from 1; ***M.***, *Menispermum*; ***S.***, *Sinomenium*.

	M. cana-dense	M. dauri-cum	S. acutum	S. macro-carpum	Other fossil Sinomenium	Palaeo-sinomenium	Warden-sheppeya
M. canadense		0.0003845	6.963×10^{-11}	2.658×10^{-8}	2.22×10^{-11}	1.438×10^{-6}	2.099×10^{-5}
M. dauricum	0.008075**		4.489×10^{-10}	0.01552	8.188×10^{-12}	4.895×10^{-6}	6.302×10^{-5}
S. acutum	1.462×10^{-9}**	9.428×10^{-9}**		3.592×10^{-6}	0.1928	0.2646	0.4737
S. macro-carpum	5.583×10^{-7}**	0.3259	7.543×10^{-5}**		5.115×10^{-8}	0.001406	0.0001854
Other fossil Sinomenium	4.662×10^{-10}**	1.719×10^{-10}**	1	1.074×10^{-6}**		0.6232	0.9461
Palaeo-sinomenium	3.02×10^{-5}**	0.0001028**	1	0.02953*	1		0.9202
Warden-sheppeya	0.0004408**	0.001324**	1	0.003893**	1	1	

or taxonomic synonym, i.e. France (Pont-de-Gail), northwestern italy, central Italy, eastern Europe, and "*S. militzeri*", a fossil species already included in *S. cantalense*. It should be noted that a slight shape difference among specimens from northwestern and central Italy exist, i.e. specimens from central Italy are the most recent (Late Pliocene) and are the most similar to modern ones, whereas specimens from north-western Italy are slightly older in age (Pliocene) and are more similar to *Wardensheppeya*. This suggests that the evolution from the oldest form (represented by *Wardensheppeya*) to the modern ones might have been gradual.

GENERIC RELATIONSHIPS

It is clear that the first relative warp axis permits separations of most genera (Fig. 4), namely *Menispermum*, *Sinomenium* and *Palaeosinomenium*. However, this axis does not allow us to distinguish between *Wardensheppeya* and *Sinomenium*. On a morphometric basis, we follow the proposition of Mai (1997) for a synonymy between *Wardensheppeya* and *Sinomenium*. However, we reject the proposed synonymy of *Palaeosinomenium* and *Sinomenium*.

Menispermum dauricum and *S. cantalense* are significantly different at 5% in the shape analysis (Table 4) and are significantly different at 1% for the number of transverse ridges (Table 5). Therefore, we consider them as two different species.

The difference between *Palaeosinomenium* and *Wardensheppeya* is significant at 5% but not at 1% (Table 4). Those two groups have comparatively few specimens, so the test is not as robust as it might be with more specimens. There is a difference between
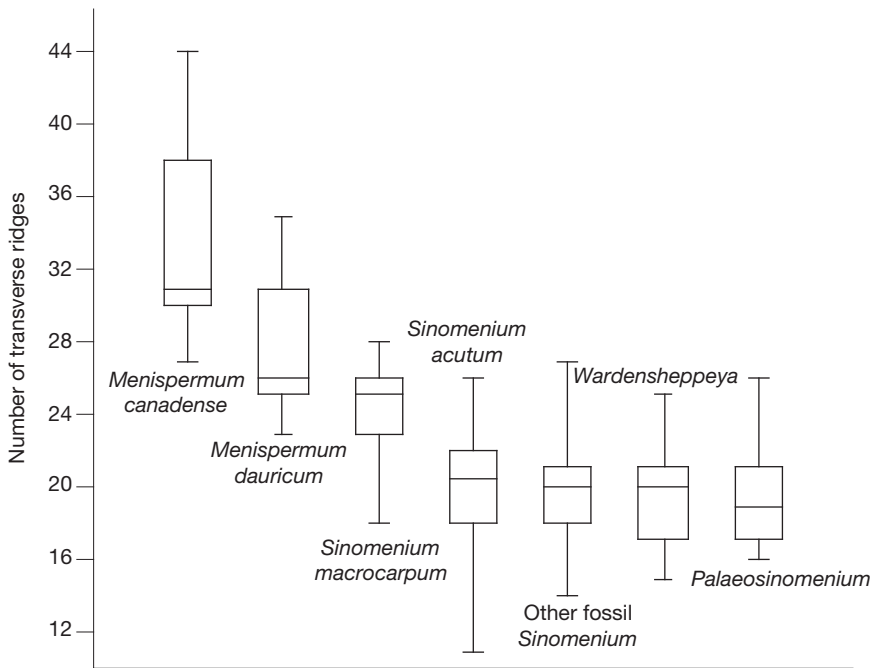
FIG. 5 — Comparisons of number of transverse ridges between groups. Mean, confidence intervals, and lower and upper limits are indicated for each group.

the two genera according to the first relative warp axis (Fig. 4). Therefore, we consider them different; morphometrics suggests some specimens (Fig. 4) might be transferred from one genus to the other.

Menispermicarpum rariforme seems to be linked with *Palaeosinomenium* through its obliquity (Fig. 4). Chandler (1961) stated that the ornamentation linked it with *Cissampelos*, even if they are very different in shape. As *Cissampelos* endocarps bear two lateral flanges on each side (Jacques 2009a) and *M. rariforme* only one, the statement of Chandler appears erroneous. She described the presence of the three rows of transverse ridges, but the inner one corresponds to the condyle side of the lateral flange. This feature is also sometimes seen on *P. pulchrum*. Therefore we believe that *M. rariforme*, a species based on only one specimen, should be included in *Palaeosinomenium*.

When describing *Menispermum? taylori*, Chandler (1964) stated that the inclusion of the species to the genus *Menispermum* is "tentative". The specimen is much abraded so the ornamentation is not observable. Chandler (1964) interpreted *M.? taylori* as having a straighter ventral margin than the other *Menispermum* species, being smaller in size than living species, and that the central area of *M.? taylori* is relatively larger than that of *Wardensheppeya*. Consequently, Chandler (1964) concluded that *M.? taylori* most closely resembles *Menispermum*. However, some fossil and recent *Sinomenium* have a relatively larger condyle than the known *Wardensheppeya* (Fig. 4). Furthermore, the features listed by Chandler (1964) appear to correspond more to *Sinomenium* than to *Menispermum*. Therefore, we suggest that *M.? taylori* should be included in *Sinomenium*.

Meyer & Manchester (1997) described a fossil *Menispermum* from the Oligocene of the John Day Formation in North America, but no specific assignment was discussed. In our analysis (Fig. 4), this fossil is found to locate at the border in the plotting graph between *M. dauricum* and *M. canadense*. However, its high number of transverse ridges (37) makes it closer to *M. canadense* (Fig. 5).

Menispermum reidii Geissert, Gregor & Mai, 1990 is represented by a single specimen from the Mio-Pliocene of eastern France (Geissert *et al.* 1990), while a putative second specimen was identified from the Pliocene of north western Italy as *Menispermum* cf. *reidii* (Cavallo & Martinetto 2001). In our analysis (Fig. 4), they are both found close to *M. dauricum*, and the number of transverse ridges (31 and 33, respectively) is also similar to that of *M. dauricum* (Fig. 5). Therefore, we confirm the generic identification of this species and consider its nearest living relative as *M. dauricum*.

It has been proposed that *Althaea crassicarpa* resembles *Menispermum* (Reid 1920; Geissert *et al.* 1990). In our analysis (Figs 4; 6), this fossil "*Menispermum crassicarpum*" shows a close similarity to the extinct *Sinomenium cantalense*. This resemblance is also confirmed by both having the same number of transverse ridges (Fig. 5). However, the specimen is badly preserved, so the taxonomic status cannot be solved until more specimens become available.

DIAGNOSTIC FEATURES

The genus *Palaeosinomenium* differs from both *Menispermum* and *Sinomenium* by a more oblique and elongate endocarp (Chandler 1961). Our results (Figs 3F; 4) confirm the obliquity of the *Palaeosinomenium* endocarp. However, our study does not show any peculiar differences concern-ing the shape and relative size of foramen, even if this structure is highly variable (Fig. 2). Chandler (1961) described the ventral margin of *Palaeosinomenium* as concave to convex, the consensus shape of *Palaeosinomenium* (Fig. 3G) shows a flat ventral margin, confirming this interpretation. The difference in ornamentation between *P. hantonense* Chandler, 1963 and other species of the genus, namely that the former has more conspicuous ridges than the latter (Chandler 1963), is not diagnostic enough, as the ornamentation is quite variable in modern species of *Menispermum* and *Sinomenium*.

Sinomenium macrocarpum differs from other *Sinomenium* through its ornamentation; the number of ridges is higher than in *S. acutum*, confirming the results of Liu & Jacques (2010).

Menispermum differs from other genera in the greater concavity of its ventral margin (Figs 3; 4) and in the higher number of transverse ridges. *Menispermum* endocarps are usually bigger than those of *Sinomenium*, so it seems that the number of transverse ridges is linked to the size of the endocarp. The function of the transverse ridges is not known, although their structural role in reinforcing the solidity of endocarp has previously been hypothesized with no further evidence (Jacques & Bertolino 2008).

The differences mentioned above allow us to propose the following key and Table 6 for the determination of fossil species.

Key to the fossil endocarps of the *Sinomenium-Menispermum* complex

1. Endocarp oblique .... *Palaeosinomenium obliquatum*
— Endocarp straight 2

2. Ventral margin concave .... *Menispermum reidii*
— Ventral margin more or less straight 3

3. Number of transverse ridges generally less than 22 .... *Sinomenium cantalense*
— Number of transverse ridges generally more than 23 .... *Sinomenium macrocarpum*

In our study, modifications in the foramen are linked with shape modifications of the whole endocarp as shown by the first relative warp axis (Fig. 4). This can be linked to a structural constraint such that the foramen has to be on the endocarp. When the ventral margin concavity increases, the foramen hence cannot occupy a more "basal" position. Our measurement of the foramen (only two landmarks) can only describe its relative size and orientation; the shape
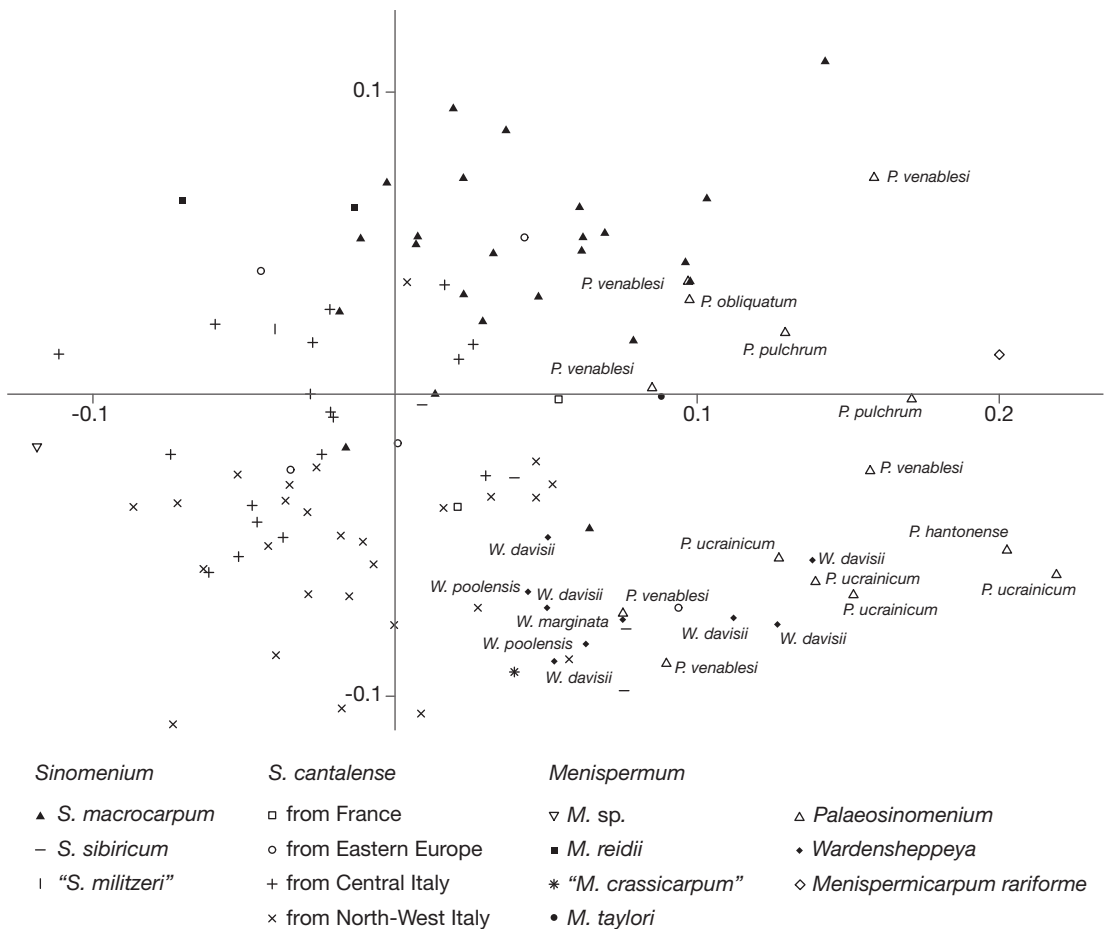
Fig. 6 — Detail of Figure 4 showing the placement of each fossil specimen of Menisermaceae endocarps in the relative warp analysis. "*Sinomenium militzeri*" is already recognized as a synonym of *S. cantalense*. The fossils of *S. cantalense* from different regions have been differentiated.

(circular vs. elongate) of the foramen cannot be described. The function of the foramen is still unknown. In the Menispermaceae, this feature is only present in the *Menispermum-Sinomenium* complex and *Sarcopetalum* (Jacques 2009a). The condyle is the result of the ossification of the placenta (Miers 1871; Dekker 1983). The foramen could be a means to continue to provide nutrition to the seed after ossification of the placenta; this personal hypothesis has to be verified with living material.

The modern species in the *Menispermum-Sino-menium* complex are also very variable in other morphological features. *Sinomenium acutum* has entire to lobed, glabrous to puberulous leaves; six sepals; six petals; nine or 12 stamens; nine staminodes; three carpels; and glabrous or pubescent fruits. In contrast, *M. dauricum* has glabrous to pubescent leaves: four to eight sepals; six to 12 petals; 12 or more stamens; six to 12 staminodes; two to four carpels; and glabrous fruit (Luo *et al.* 2008). The variations observed in the endocarps are not bigger than those observed in other organs. Therefore, we think that the fossil intraspecific variability should not be smaller than variability in modern specimens.

TABLE 6. — Table summarizing endocarp characters of the *Menispermum-Sinomenium* complex.

	Endocarp obliquity	Ventral margin concavity	Number of transverse ridges
Palaeo-sinomenium obliquatum	Oblique	Straight	≤ 22
Menispermum reidii	Straight	Concave	≥ 30
Sinomenium cantalense	Straight	Straight	≤ 22
Sinomenium macrocarpum	Straight	Straight	≥ 23

FOSSIL HISTORY

In molecular analyses, *Menispermum* and *Sinomenium* form a monophyletic group (Wang *et al.* 2007; Hoot *et al.* 2009) that is one of the early-diverging clades amongst Menispermaceae (Ortiz *et al.* 2007; Wang *et al.* 2007; Hoot *et al.* 2009). For the characters of shape (Fig. 4) and ornamentation (Fig. 5), *M. dauricum* seems to be intermediate between *Sinomenium acutum* and *M. canadense*. It seems that the evolution is opposite of the first relative warp axis, i.e. towards a greater concavity of the ventral margin and a relatively thinner dorsal flange. The fossil *S. macrocarpum* represents another evolutionary trend to a greater size (Liu & Jacques 2010), but without noticeable modification of shape.

The inclusion of *Wardensheppeya* in *Sinomenium* clearly expands the age of first appearance of this genus, i.e. early Palaeogene, when several other extant menispermaceous genera, e.g., *Tinospora* Miers were present as well (Chandler 1961; Jacques & De Franceschi 2005).

Sinomenium, including *Wardensheppeya*, was common in the northern hemisphere in the Cenozoic (Manchester *et al.* 2009). The fossil genus *Palaeosinomenium* is found only in the Palaeogene of Europe (Chanlder 1961; Knobloch 1971; Tahktajan 1974; Jacques & De Franceschi 2005) and North America (Manchester 1994). Fossil leaves assigned to *Menispermum* have been reported in the Palaeogene (references in Jacques [2009b]); however, some of the records are old and might not belong to *Menispermum* at all because the extant species for comparisons used by earlier workers in the fossil determinations have already been transferred to other menispermous genera (Jacques 2009b).

A *Menispermum* endocarp occurs in the Oligocene of North America (Meyer & Manchester 1997) and resembles *M. canadense*, an endemic extant species in North America (Fig. 4). Interestingly, another endocarp species of *Menispermum*, *M. reidii*, is known from the Neogene of Europe (Geissert *et al.* 1990) and shows similarities with *M. dauricum*, an East Asian species (Fig. 4). The distribution of *M. canadense* and *M. dauricum* represents a classical eastern North America-East Asia disjunction, which has been suggested by molecular analysis to have formed as late as 0.28 million years (Xiang *et al.* 2000). The most recent molecular results indicate an older diversification of *Menispermum*: 8.2 million years (Jacques *et al.* 2011). Considering the geological history of these fossils, the present disjunct distribution of *Menispermum* may be relictual, which resulted from a contraction of a formerly wide distribution in the northern hemisphere to a restricted region. This pattern is shared with many other temperate seed plants (Manchester 1999; Manchester *et al.* 2009).

TAXONOMIC CONCLUSIONS

Based on the morphometric study, the following synonymy for *Sinomenium* and *Palaeosinoemium* is proposed.

Genus *Sinomenium* Diels *in* Engl.

Pflanzenreich 46, Menispermac: 254 (1910).

Wardenia Chandler non King, *The Lower Tertiary Floras of Southern England* I *Paleocene floras. London Clay flora (supplement)*: 158; pl. 16, fig. 8 (1961).

Wardensheppeya Eyde, *Taxon* 19: 650 (1970).

Sinomenium cantalense
(E.M. Reid) Dorofeev

Trudy Botanicheskogo Instituta Akademii Nauk SSSR. Ser. 1. Flora i Sistematika Vyssikh Rastenii. Acta Instituti Botanici Academiae Scientiarum URPSS 11: 129 (1955).

Menispermum cantalense E.M. Reid, *Bulletin de la Société Géologique de France*, sér. IV, 20: 66; pl. 3, figs 24, 25 (1920).

Sinomenium militzeri Kirchheimer, *Botanisches Archiv* 44: 384 (1943).

Sinomenium dielsii Szafer, *Rozprawy Wydzial Matamatyczno-Przyroniczy PAU, Dzial B: Nauki Biologiczne*, 72: 96; pl. 8, figs 15, 16, 21 (1947).

Menispermum taylori Chandler, *The Lower Tertiary Floras of Southern England* IV *A summary and survey of findings in the light of recent botanical observations*: 111; pl. 2, fig. 16 (1964).

Wardenia davisi Chandler, *The Lower Tertiary Floras of Southern England* I *Palaeocene floras. London Clay flora (supplement)*: 158; pl. 16, fig. 8 (1961). — *Wardensheppeya davisii* (Chandler) Eyde, *Taxon* 19: 650 (1970).

Wardenia poolensis Chandler, *The Lower Tertiary Floras of Southern England* II *Flora of the Pipe-clay Series of Dorset (Lower Bagshot)*: 62; pl. 7, figs 21, 22 (1962). — *Wardensheppya poolensis* (Chandler) Eyde, *Taxon* 19: 650 (1970).

Wardenia marginata Chandler, *The Lower Tertiary Floras of Southern England* III *Flora of the Bournemouth Beds; the Boscombe, and the Highcliff Sands*: 84; pl. 12, figs 17-22 (1963). — *Wardensheppeya marginata* (Chandler) Eyde, *Taxon* 19: 650 (1970).

Sinomenium sibiricum Dorofeev, *in* Takhtajan, *Magnolophyta Fossilia URSS* I: 96; pl. 117, figs 3-5, 7 (1974).

Genus *Palaeosinomenium* Chandler

The Lower Tertiary Floras of Southern England I *Palaeocene floras. London Clay flora (supplement)*: 159 (1961).

Palaeosinomenium obliquatum
(Chandler) Chandler

Bulletin of the British Museum (Natural History) Geology 5 (5): 118; pl. 25, figs 47-50 (1961).

Menispermum obliquatum Chandler, *Upper Eocene Flora of Hurndle Hants* I: 24; pl. 3, fig. 9 (1925).

Palaeosinomenium venablesi Chandler, *The Lower Tertiary Floras of Southern England* I *Palaeocene floras. London Clay flora (supplement)*: 159; pl. 16, figs 9-13 (1961).

Palaeosinomenium pulchrum Chandler, *The Lower Tertiary Floras of Southern England* I *Palaeocene floras. London Clay flora (supplement)*: 329; pl. 33, figs 5-7 (1961).

Menispermicarpum rariforme Chandler, *The Lower Tertiary Floras of Southern England* I *Palaeocene floras. London Clay flora (supplement)*: 331; pl. 33, figs 11, 12 (1961).

Palaeosinomenium hantonense Chandler, *The Lower Tertiary Floras of Southern England* III *Flora of the Bournemouth Beds; the Boscombe, and the Highcliff Sands*: 82; pl. 12, figs 10-12 (1963).

Palaeosinomenium ucrainicum Dorofeev, *in* Takhtajan, *Magnolophyta Fossilia URSS* I: 96; pl. 117, figs 11-14 (1974).

Acknowkedgements

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APPENDIX 1

List of studied specimens. Abbreviations: **ETMNH**, East Tennessee Museum of Natural History; **NHM**, Natural History Museum of London; **Tor**, Dipartimento di Scienze della Terra, University of Torino.

MODERN SPECIMENS

Menispermum canadense Linnaeus: KUN 0165280; J. Miller *et al.* 5500 (MO); S. D. Swanson 2328 (MO);

Menispermum dauricum DC.: KUN 0165236; KUN 0165256; PE 01071064; PE 01604656; PE 01071135; PE 0107010; PE 010711343;

Sinomenium acutum (Thunb.) Rehder & Wilson: KUN 0165595; KUN 0165572; KUN 0165585; KUN 0166855; KUN 0165604; KUN 0165594; KUN 0165565; KUN 0165610; KUN 0166336; KUN 0165600; KUN 0575891; KUN 0166848; KUN 0165631; KUN 0165642; KUN 0165650; KUN 0165624; Takhtajan 1974 (2 specimens).

FOSSIL SPECIMENS

Menispermicarpum rariforme Chandler, 1961: V.34573 (NHM);

Menispermum reidii Geissert, Gregor & Mai, 1990: P1336-440;

Menispermum cf. *reidii* Geissert, Gregor & Mai, 1990: GA5 A4L (Tor);

Menispermum taylori Chandler, 1964: V.45223 (NHM);

Palaeosinomenium hantonense Chandler, 1963: V.43306 (NHM);

Palaeosinomenium obliquatum (Chandler) Chandler, 1961: V.20049 (NHM);

Palaeosinomenium pulchrum Chandler, 1961: V.34585 (NHM); V.34586 (NHM);

Palaeosinomenium ucrainicum Dorofeev, 1974: K430 (1, 2, 3); K431;

Palaeosinomenium venablesi Chandler, 1961: V.29839 (NHM); V.29840 (NHM); V.30578a (NHM); V.30579 (NHM); UF 4595; USNM 354561;

Sinomenium cantalense (E.M.Reid) Dorofeev, 1955: K432-2 (Ukraine); K531 (Abkhazia); V.25625 (NHM); V.25684 (NHM) (France); BG2 A4V (Tor), BO1 A2V (2 specimens, Tor), CO1 A6T (Tor), CV5 A0E (Tor), CV106 A2G (7 specimens, Tor), CV106 A6H (6 specimens, Tor), GA1 A2T (4 speci- mens, Tor), GA3 B1Q (Tor), RB1 A2R (Tor), RB1 A6G (Tor), RDB1 A1M (Tor) (NW Italy); NJ0 B5B (4 specimens, Tor), NJ1 B7F (Tor), NJ4 B5D (Tor), NJ5 B5C (13 specimens, Tor), PU105395 (central Italy); 4 specimens published in Szafer (1961) without collection number (Poland);

Sinomenium macrocarpum Liu & Jacques, 2010: ETMNH 3812- 3827; 3832-3839;

Sinomenium sibiricum Dorofeev, 1974: K518 (3, 4, 5 ,6);

Wardensheppeya davisii (Chandler) Eyde, 1970: V. 29838 (NHM); V.51640 (NHM); without number (NHM); 40036 (P); 40037 (P);

Wardensheppeya marginata (Chandler) Eyde, 1970: V.43309 (NHM);

Wardensheppeya poolensis (Chandler) Eyde, 1970: V.40457 (NHM); V.40487 (NHM).