

Original article

Fossil history of the Menispermaceae (Ranunculales)

Histoire fossile des Menispermaceae (Ranunculales)

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Abstract

The Menispermaceae family (Ranunculales) includes more than 500 extant species. Climbers represent the majority of this family, and these plants are now distributed in all of the tropical and subtropical regions of Americas, Asia and Africa. Their endocarps show a characteristic shape that is easily identified in the fossil floras. Numerous fossil leaves are also mentioned in the literature, but the methods for identifying these fossils are often outdated and need revision. Four tribes of Menispermaceae are present in the fossil record, including Fibraureae, Menispermeae, Pachygoneae and Tinosporeae. Only the Anomospermeae are potentially lacking. The Menispermaceae appear in the Palaeocene, and are common in the Eocene, of Europe and in North America as represented by endocarps and locule-casts. The species of this age show morphological diversification, corresponding with the current familial diversity. A few specimens from the Cretaceous period could be part of this Angiosperm family. Fossils after the Eocene are scarcer, despite several relatively rich outcrops. The maximal expansion of the Menispermaceae during the Palaeocene/Eocene limit correlates with the thermal optimum of the early Tertiary and also parallels the maximal expansion of tropical and subtropical floras. The relative richness of the Eocene era in Menispermaceae could be a consequence of more intense sampling in some regions. The bias in tribe representation can be explained by evolution, ecology or taphonomic hypotheses.

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Keywords: Menispermaceae; Fossil; Endocarp; Leaf; Wood

Résumé

La famille des Menispermaceae (Ranunculales) regroupe plus de 500 espèces actuelles. Cette famille, aujourd'hui présente dans toutes les régions tropicales et subtropicales d'Amérique, d'Asie et d'Afrique, est principalement représentée par des lianes. Ses endocarpes montrent une forme caractéristique facilement identifiable dans les flores fossiles. De nombreuses feuilles fossiles sont aussi mentionnées dans la littérature,

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mais ces identifications, souvent anciennes, nécessitent une révision. Quatre tribus sont présentes dans le registre fossile : les Fibraureae, les Menispermaceae, les Pachygoneae et les Tinosporeae ; seules les Anomospermeae en sont probablement absentes. Depuis le Paléocène, et particulièrement pendant l'Éocène, cette famille est présente en Europe et en Amérique du Nord soit comme endocarpes, soit comme moulages. Les espèces de cette époque montrent une diversification morphologique correspondant à la diversité actuelle de la famille. Quelques spécimens du Crétacé pourraient appartenir à cette famille angiospermienne. Après l'Éocène, les fossiles sont plus rares, malgré quelques gisements relativement riches. L'expansion maximale des Menispermaceae, durant la limite Paléocène/Éocène, correspond à l'optimum thermique et à l'expansion maximale des flores tropicales et subtropicales. La relative richesse de l'Éocène en Menispermaceae pourrait être une conséquence d'un échantillonnage plus important dans certaines régions. Le biais dans la représentation des tribus pourrait s'expliquer par des hypothèses évolutives, écologiques ou taxonomiques. © 2009 Elsevier Masson SAS. Tous droits réservés.

Mots clés : Menispermaceae ; Fossile ; Endocarpe ; Feuille ; Bois

1. Introduction

Menispermaceae are an extant family of basal Eudicots, in the order Ranunculales. They currently include 71 genera and about 512 species (Jacques et al., 2007). The family contains five tribes (Kessler, 1993):

- the Anomospermeae from South America (only the genus *Tiliacora* Colebr., dubiously included in this tribe is present in Africa and Asia);
- the Fibraureae found in Asia;
- the Menispermaceae from pantropical and temperate areas;
- the Pachygoneae from pantropical regions;
- the Tinosporeae found in pantropical areas.

This family is also well-known for its fossils (Reid and Chandler, 1933; Manchester, 1994), as they were proven to be important for understanding the evolution of the family (Scott, 1956; Thanikaimoni, 1984, 1986; Jacques and Guo, 2007). The modern affinities of the fossils from this family are still debated. Some authors propose that the fossils are closely associated with extant taxa of South-East Asia fossils (Reid and Chandler, 1933; Manchester, 1994; Jacques and De Franceschi, 2005), while others insist on a closer association with African taxa (Thanikaimoni, 1984). These suggestions make it quite difficult to draw conclusions on the origin of the family. A recent molecular study (Anderson et al., 2005) estimates an age of 105 to 116 million years for the family and between 70 and 80 million years for the crown group.

Our knowledge of the phylogeny and evolution of the Menispermaceae is still quite limited, even with recently improved molecular or morphological approaches (Jacques et al., 2007; Ortiz et al., 2007; Wang et al., 2007; Jacques and Bertolino, 2008). All of these studies show that the major tribe definitions (Diels, 1910; Kessler, 1993) are not satisfactory; the studies even show some inconsistencies with each other. However, as no consensus has yet emerged on the new delineations for tribes, I will use the tribes proposed by Kessler (1993), which focus on the diagnostic characteristics of each fossil.

Table 1

Features of Menispermaceae endocarps according to the tribal classification. Information from: Forman (1968, 1972, 1974, 1975, 1984, 1985); Dekker (1983); Thanikaimoni (1984); Jacques (in press¹).

Caractères des endocarpes de Menispermaceae selon la classification en tribu. Informations de : Forman (1968, 1972, 1974, 1975, 1984, 1985); Dekker (1983); Thanikaimoni (1984); Jacques (sous presse¹).

Tribe	Endocarp features
Anomospermeae	Endocarp partly curved with septiform, externally inconspicuous, condyle
Fibraureae	Straight endocarp with condyle absent, or represented by a ventral groove or two invaginated ventral concavities
Menispermeae	Whole endocarp curved with lamelliform condyle
Pachygoneae	Endocarp partly curved with septiform or reduced condyle, or endocarp straight with a condyle represented by a ventral groove
Tinosporeae	Straight endocarp with condyle as a spherical or elliptical ventral concavity

This paper will concentrate on reviewing all of the known Menispermaceae macrofossils in order to give a better understanding of their history and evolution. The pollen fossil record is not dealt in this paper as it is almost only based on Russian literature for Cretaceous and Palaeogene records (Doria et al., 2008). Moreover, Thanikaimoni (1984) explained that the identification of Menispermaceae pollen in fossil state was not easy, as the basic type of Menispermaceae pollen is common in dicots. The recent paper of Doria et al. (2008) gives a list of references for the pollen record.

2. Materials and methods

The literature on fossil floras was screened in a search for information related to Menispermaceae. For each period of time, we have an idea of the known Menispermaceae diversity on each continent. Each occurrence of Menispermaceae was classified according to its age and geography.

For each genus present in the fossil record, the organs represented in a fossil state were listed. Using information from the fossil description, parallels with modern groups can be proposed. It is often not possible to assign generic similarities, but the diagnostic characteristics, such as type of endocarp, are sufficient for proposing tribal affinities. As recent molecular phylogenies do not give detailed information of the delineation of monophyletic clades (Ortiz et al., 2007; Wang et al., 2007), I chose to use a morphological classification, the one of Kessler (1993). For fossil endocarps, when no likeness was proposed in a former publication, I undertook a comparison of the fossil description with the endocarps of recent taxa to generate a proposed affinity (Jacques, in press¹). This comparison focused on endocarp curvature, type of condyle and ornamentation. The tribal affinities of the endocarps were recognized through the characteristics listed in Table 1.

3. Results

3.1. Taxonomic views

Most of Menispermaceae genera found in the fossil record can be attributed to a tribe (Table 2). Among the five Menispermaceae tribes, only the Anomospermeae are not found

¹ Jacques, F.M.B., In press. Survey of the Menispermaceae endocarps. *Adansonia*.

Table 2 (Continued)

	Organs present in fossil record			Number of fossil species	Distribution	
	Fruit	Leaf	Wood		Fossil	Present
<i>Calycocarpum</i> Nutt. ex Torr. Gray, 1838	X	–	–	2	NA, Eu	NA
<i>Chandlera</i> Scott, 1954	X	–	–	1	NA	f
<i>Curvitinospora</i> Manchester, 1994	X	–	–	1	NA	f
<i>Frintonia</i> Chandler, 1961	X	–	–	1	Eu	f
<i>Jateorhiza</i> Miers, 1849	X	–	–	1	Eu	Af
<i>Odontocaryoidea</i> Scott, 1954	X	–	–	1	NA	f
<i>Palaeoskapha</i> Jacques and Guo, 2007	X	–	–	1	As	f
<i>Parabaena</i> Miers, 1851	X	–	–	2	Eu	As
<i>Syntrisepalum</i> Chesters, 1957	X	–	–	1	Af	f
<i>Tinospora</i> Miers, 1851	X	X	–	8	NA, Eu, As	As, Au, Af
Incertae sedis						
<i>Menispermaphyllum</i> Hill, 1989	–	X	–	1	Au	f
<i>Menispermicarpum</i> Chesters, 1957	X	–	–	2	Eu, Af	f
<i>Menispermities</i> Lesquereux, 1874	–	X	–	45	NA, SA, Eu, Ac, As	f
<i>Menispermophyllum</i> Velenovsky, 1900	–	X	–	1	Eu	f
<i>Menispermoxylon</i> Vozenin-Serra and Privé-Gill, 1989	–	–	X	2	Eu, As	f

in the fossil record. Forty-four genera occur in the fossil record, and 27 of these are known only from fossils. At the generic level, the Menispermaceae diversity is greater in fruit (mostly endocarp) specimens than in leaf or wood specimens (Table 3). However, at the specific level, we see that numerous leaf species were placed in the organ genus *Menispermities* Lesquereux, 1874. Half of the species diversity corresponds to previously described leaf specimens.

Table 3

Organ diversity in the Menispermaceae fossil record. Note. The sum of the genera percentages exceeds 100% because some genera are known from several organs.

Diversité des organes de Menispermaceae présents dans le registre fossile.

Organ	Number of genera showing this organ in the fossil record	Percentage of genera showing this organ in the fossil record (in %)	Number of species showing this organ in the fossil record	Percentage of species showing this organ in the fossil record (in %)
Fruit	34	77.2	56	41.5
Leaf	14	31.8	76	56.3
Wood	2	4.5	3	2.2

3.2. Putative Cretaceous records

In North America, Cretaceous specimens have been attributed to the family. *Menispermites* was described from Alaska (Hollick, 1930: 136), in Canada (Dawson, 1894; Bell, 1963) and in the United States (Knowlton, 1898, 1900, 1909; Ward, 1905; Berry, 1914, 1915, 1919, 1925; Dorf, 1942); and some *Cocculus* DC. 1817 were found in the United States (Berry, 1915, 1919).

Menispermaceae are represented in Central Europe during the Cretaceous by different genera: *Menispermophyllum* Velenovsky, 1900 (Fric and Bayer, 1900), *Cocculus* (Velenovsky, 1887; Bayer, 1896; Fric and Bayer, 1900; Němejc and Kvaček, 1975), known only from leaf fossils, and *Prototinomiscium* Knobloch and Mai, 1984 (Knobloch and Mai, 1986), which comprises the only fossil fruit specimens of Menispermaceae known for the Cretaceous. *Cocculus* was also found in Georgia (Kolakovsky, 1955), and *Menispermites* was found in Portugal (Teixeira, 1948).

Menispermaceae are known in Asia, both as *Menispermites* (Kryshtofovich, 1918, 1920; Oishi, 1940; Vakhrameev, 1952; Lebedev and Markova, 1962; Takhtajan, 1974; Herman, 1991; Kimura, 2000; Volynets, 2006) and *Cocculus* (Kryshtofovich, 1918). A fossil wood, *Anamirta pfeifferi* Bonde, 1997, was described from the Intertrappean of India (Bonde, 1997), and its age likely varies from the Upper Cretaceous to Palaeocene.

Some leaf specimens of *Menispermites* and *Cocculus* were also found in the Arctic (Heer, 1882; Seward, 1926).

3.3. Palaeogene records

Numerous Menispermaceae leaves were found in the North American Palaeogene of Alaska (Hollick, 1936; Wolfe, 1966, 1977), Canada (McIver and Basinger, 1999) and the United States (Glenn, 1906; Potbury, 1935; MacGinitie, 1941, 1969; LaMotte, 1952; Hickey, 1977; Crane et al., 1990). The greatest diversity of Menispermaceous genera occurs in the Clarno formation, which provides numerous fruits (Manchester, 1994). Other sites in the United States, including Alaska (Hollick, 1936), contain different Menispermaceae endocarps (Tiffney, 1999; Pigg and Wehr, 2002).

During the Palaeogene, the Menispermaceae were very diverse in Europe. Numerous fossil endocarps were found in the London Clay (Reid and Chandler, 1933; Chandler, 1961a, 1961b, 1962, 1963, 1964, 1978; Eyde, 1970), in Belgium (Fairon-Demaret and Smith, 2002), in western Germany (Collinson, 1988; Wilde and Frankenhäuser, 1998; Wilde, 2004), in France (Jacques and De Franceschi, 2005) and in Central Europe (Knobloch, 1971; Mai, 1987). Some leaves have been found in France (Laurent, 1899, 1912), Belgium (Saporta and Marion, 1878) and Eastern Europe (Takhtajan, 1974). A fossil wood was also found in the London Clay (Poole and Wilkinson, 2000).

In Asia, some Menispermaceae leaves were discovered from Palaeogene outcrops in Japan (Tanai, 1972), China (Guo et al., 1984) and Borneo (Geyler, 1878). However, in Borneo, the genus *Entoneuron* Geyler, 1978 is based on only one specimen that is badly preserved. Fruits of *Palaeoskapha* Jacques and Guo, 2007, *Palaeosinomenium* Chandler, 1961 and *Diploclisia* Miers, 1851 (Manchester et al., 2005) occur in Chinese Eocene formations. Some *Sinomenium* Diels, 1910 endocarps were found in Siberia (Dorofeev, 1963).

In South America, some *Menispermites* leaves were recently described in the Palaeocene of Colombia (Doria et al., 2008).

During the Eocene, Menispermaceae also occurred in Australia, and various organs are represented, including the leaves of *Menispermaphyllum* Hill, 1989 in New South Wales (Hill, 1989)

and the fruits of *Rhytidocaryon* von Mueller, 1876 in both New South Wales (von Mueller, 1883) and Tasmania (Selling, 1950).

3.4. Neogene records

A few *Cocculus* leaves were found in the United States during the Neogene (LaMotte, 1952; MacGinitie, 1962).

The fruit *Sinomenium* is the most common fossil in the Neogene of Europe. However, some other fossil endocarps were found, including *Brueckelholzia* Gregor, 1977, *Cyclea* Arn. and Wight, 1840, *Menispermum* L., 1735 and *Parabaena* Miers, 1851, in Germany (Kirchheimer, 1957; Czecczot and Skirgiello, 1967; Geissert, 1972; Gregor, 1978; Van der Burgh, 1987), France (Reid, 1920; Huard and Klingebiel, 1965; Geissert, 1967; Geissert et al., 1990), Italy (Bertoldi and Martinetto, 1995; Cavallo and Martinetto, 1996, 2001; Martinetto, 1996, 2001a, 2001b; Basilici et al., 1997; Martinetto and Ravazzi, 1997; Fischer and Butzmann, 2000) and Central Europe (Szafer, 1947, 1961; Lancucka-Srodoniowa, 1966; Knobloch, 1981; Meller et al., 1999; Meller and Hofmann, 2004). Some *Cocculus* and *Menispermum* leaves were found in France (Saporta and Marion, 1876; Boulay, 1892), Hungary (Andreánszky, 1959) and Georgia (Kolakovsky, 1955).

Different Menispermaceae leaves were found in the Neogene of Japan (Tanai and Suzuki, 1963; Ozaki, 1991; Tanai, 1972) and in Central Asia and Siberia (Takhtajan, 1974). A fossil wood, *Menispermoxylum* Vozenin-Serra and Privé-Gill, 1989, dating from the Miocene, was described in Thailand (Vozenin-Serra et al., 1989).

In Africa, the Rusinga flora from the Miocene yielded numerous Menispermaceae endocarps (Chesters, 1957a, 1957b); some new species are not even described yet (Collinson, personal communication).

Some *Menispermites* leaves were also found in Argentina (Frenguelli, 1953), and the leaf morphospecies *Chondrodendron brasiliense* Dolianti, 1949 is described from the Pliocene of Brazil (Dolianti, 1949).

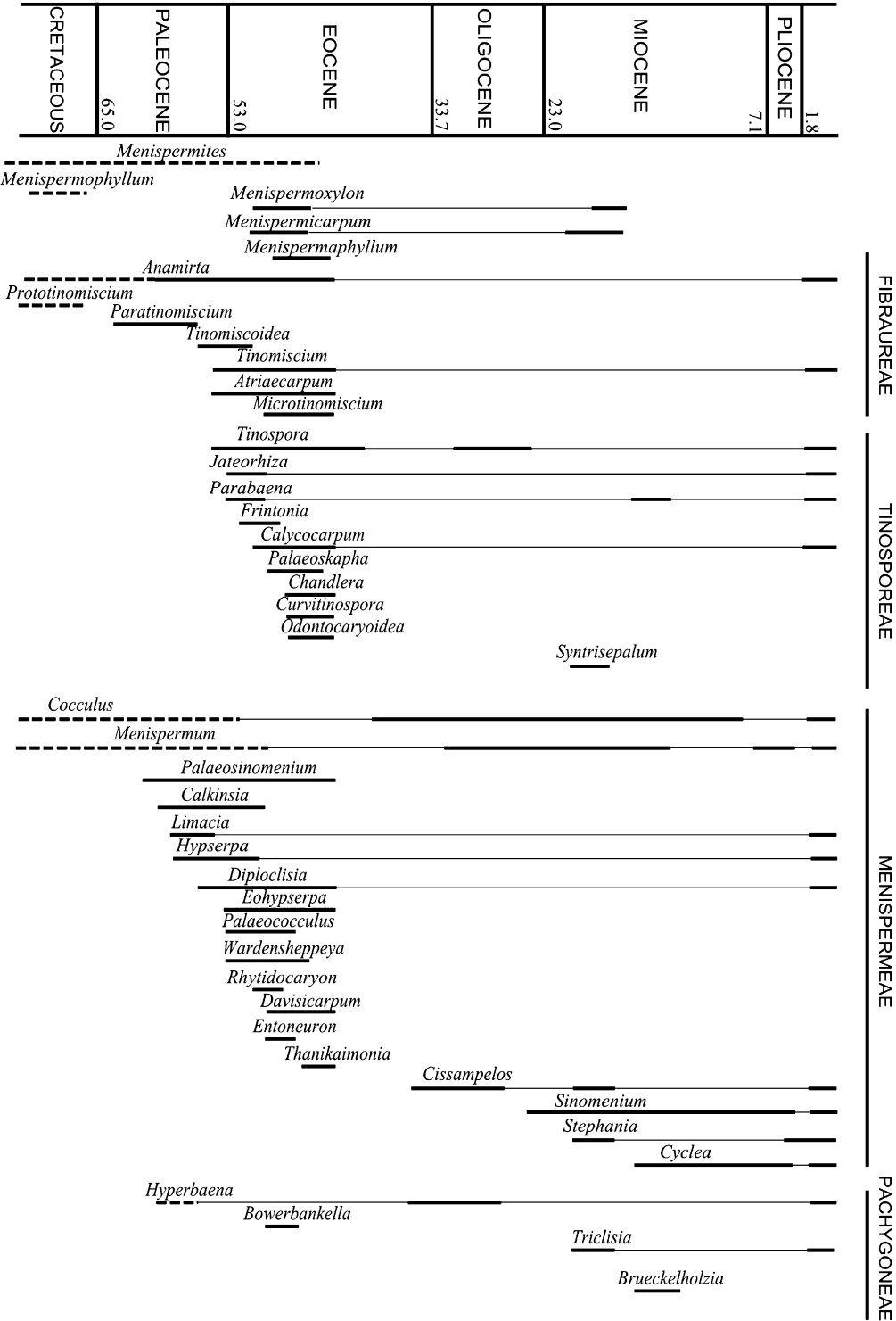
All of the information concerning occurrences of Menispermaceae genera during the Late Cretaceous and Cenozoic time periods are summarized on Fig. 1.

4. Discussion

4.1. Systematic considerations

Leaf fossils provide most of the morphospecies diversity in Menispermaceae, whereas fruit diversity is responsible for most of the morphogeneric diversity (Table 3). Classification of Menispermaceae is mainly based on seed and fruit characteristics (Diels, 1910; Kessler, 1993). The endocarps show a wide range of shapes, easily recognizable at the generic level (Jacques, in press¹). In contrast, the leaf architecture of Menispermaceae is not very well-known. Most of the leaf species were described during the 19th century or the first half of 20th century, and they were almost completely included in the *Menispermites* genus, with only a few later revisions. The numerous morphospecies described in *Menispermites* could be due to the presence of several unrecognized genera in the fossil state. A detailed study of leaf architecture could lead to the identification of Menispermaceae leaves at the genus or species level (Wolfe, 1968).

Some of the Menispermaceae fossil identifications have to be regarded as uncertain. A few of the *Cocculus* fossil species described from leaves were demonstrated to be Trochodendraceae, not Menispermaceae; specifically, they were belonging to the genus *Zizyphoides* Seward and Conway,



1935 (Manchester et al., 1991). Dilcher (2008) stated that 70% of the leaf fossil species identified by Berry are wrong identification. Many *Menispermities* species were described by Berry, or by earlier worker in North America. They may have no affinity with Menispermaceae (Arnold, 1947). Therefore, all occurrences of *Menispermities* should be hesitantly classified as a Menispermaceae occurrence until a revision of these fossils is undertaken. Thanikaimoni (1984) recognized several types of venation in Menispermaceae leaf architecture, including compound, simple lobed and simple entire leaves. The most common types of venation are pinnate brochidromous and actinodromous brochidromous. However, venation can be also acrodromous or craspedromous. Several types can be found in one species. Only a detailed study of leaf architecture in modern species can lead to a complete revision of these *Menispermities* and *Cocculus* fossil species. Further information on epidermal cells and stomata (Ferguson, 1974; Cutler, 1975; Wilkinson, 1978, 1986; Hong et al., 2001) will be useful in resolving assignments, but only when these characteristics are studied in fossil leaves. However the picture is not so pessimistic: some studies are based on detailed analysis of venation and ultimate venation (Wolfe, 1966, 1968, 1977; Hill, 1989; Doria et al., 2008), and the assignment to Menispermaceae is based on better evidence. For the Russian record (Takhtajan, 1974), due to language difficulties, it is uneasy for the author to judge the quality of the assignment of the fossil leaves to Menispermaceae. The fossil morphogenus *Credneria* Zenker, 1833 brings quite more difficulties. Rüffle (1968) assigned some *Credneria* species to the Menispermaceae based on detailed leaf architecture study. Krassilov and Golovneva (2004) also linked *Credneria* with Menispermaceae. For other authors *Credneria* has affinities with Platanaceae (Richter, 1905; Knobloch, 1997; Narita et al., 2008; Tschan et al., 2008). Kvaček and Váňková (2006: 77), dealing with Platanaceae, expressed the idea that “*Credneria* represents a morphogenus that covers more than one natural genus, and it cannot be ruled out that it may even represent foliage of another family.” Therefore *Credneria* was not considered in the present review of Menispermaceae macrofossils.

The question of the oldest Menispermaceae fossil has to be discussed, because it is useful for molecular dating (Anderson et al., 2005). The only available molecular dating using Menispermaceae (Anderson et al., 2005) involves *Prototinomiscium vangerowii*, which is known from the Upper Cretaceous of Central Europe (Knobloch and Mai, 1986). The few Menispermaceae fruits known from the Upper Cretaceous belong to this genus. This, it seems, is the best choice that can be made, considering that the identification of Menispermaceae fossil leaves has little reliability. However, *Prototinomiscium* is known from a few samples from only two outcrops. Its affinities are with the extant genus *Tinomiscium*, which has the least characteristic endocarp in Menispermaceae, due to its lack of condyle (Diels, 1910; Jacques and De Franceschi, 2005). The ventral concavity with a longitudinal ridge and apical placenta helps support this resemblance but does not confirm it. *Prototinomiscium* is smaller than other endocarps that show affinities with *Tinomiscium* (Knobloch and Mai, 1986). However, Palaeogene fossils showing affinities with *Tinomiscium* are smaller than the extant *Tinomiscium* (Chandler, 1961b; Jacques and De Franceschi, 2005); size is certainly not a good criterion for this group.

Fig. 1. Stratigraphy of fossil Menispermaceae genera. Dotted lines correspond to uncertain identifications. Numbers on the chart correspond to an estimated age of epoch limits in million years.

Stratigraphie des genres de Menispermaceae présents à l'état fossile. Les lignes discontinues correspondent à des identifications incertaines. Les nombres sur l'échelle stratigraphique correspondent à un âge estimé en millions d'années des limites d'époque.

Mai (1997) wondered if the fossil genera *Palaeosinomenium* and *Wardensheppeya* could be included in the modern genus *Sinomenium*. Preliminary results based on morphometrics analyses (Jacques and Zhou, 2008) show that the differences recognized as specific differences in fossil species description corresponds to an intraspecific range of differences in modern species, therefore the present number of fossil species in those three genera is certainly overestimated.

Palaeogene Menispermaceae floras from North America and Europe show strong affinities (Manchester, 1994). During the Palaeogene, floral exchanges may have been possible through the North Atlantic, via Greenland (Tiffney, 1985; Parrish, 1987). This link was clearly demonstrated for mammals (McKenna, 1975), and there is little doubt that the affinities between North American and European Menispermaceae fossil floras could be a result of these processes.

4.2. Ecology and distribution of the Menispermaceae

A broader Menispermaceae distribution, compared to present day, and diversity, compared to other Cenozoic epoch, was found during the Eocene (Fig. 1). The thermal optimum of the Cenozoic was reached during the Lower Eocene, with the presence of tropical to paratropical climates lacking seasonality in the mid-latitudes of the Northern Hemisphere (Upchurch and Wolfe, 1987). During the Lower Eocene, Australia also experienced a thermal optimum (Burbidge, 1960; Truswell, 1993). After that time, a process of cooling started with only a few warmer periods (Upchurch and Wolfe, 1987; Mai, 1995). European vegetation changed from evergreen to deciduous (Mai, 1989). The Menispermaceae and Tinosporeae that are the most diverse in the North American and European fossil records are also the least constrained to tropical climates, and living representatives are often found in North America (Ernst, 1964) and China today (Lo, 1996). These tribes could have been better adapted to the Eocene mid-latitude climates than the other tribes.

Modern species of Menispermaceae are most frequently present in tropical America, Africa and Asia. The similarities of mid-latitude Eocene floras in Europe and North America with present-day floras from South-East Asia have often been noted (Reid and Chandler, 1933; Manchester, 1994; Jacques and De Franceschi, 2005). The idea that is most often suggested is that Menispermaceae could be a family of Laurasian origin that later reached Gondwana. However, Thanikaimoni (1984) supported the idea that Menispermaceae could have emerged from Africa before the split of America and Africa and would have reached Laurasian territories subsequently. The occurrence of Menispermaceae in South Australia during the Eocene (Mueller, 1883; Selling, 1950; Hill, 1989) and in the Intertrappean beds in India (Bonde, 1997) supports the idea of a Gondwanan origin. The Menispermaceae were present at higher latitudes during the Eocene than they are today in both the Northern and Southern Hemispheres. The present-day distribution could then be considered a relict of an ancient distribution. For several taxonomic groups, Eastern Asia can be seen as a relict zone when compared to previously wide distributions (Tiffney and Manchester, 2001). Long distance dispersal could also explain some of the distribution patterns observed between modern Asian and North American genera, namely *Menispermum*, for which low genetic divergence has been found between disjuncts (Xiang et al., 2000).

4.3. Sampling and taphonomic bias

Most Menispermaceae fossils come from the currently temperate regions of the Northern Hemisphere, although the family is now found mostly in intertropical regions. This phenomenon could reflect a bias towards examining floras from Europe and North America rather than those

from other regions. Therefore, new fossil outcrops from tropical regions could potentially reveal novel Menispermaceae fossils. The Lower Miocene (Chesters, 1957a, 1957b) floras at Rusinga, Africa also present a high diversity of Menispermaceae. The discovery of a new outcrop with a Menispermaceae fossil often leads to the description of new species, or even genera, of this family. Thus, our knowledge of the history of Menispermaceae is widely biased by the discovery of these outcrops. The fossil biodiversity of Menispermaceae is certainly underestimated.

Taphonomy could also explain the differences in the various tribes' occurrences. Modern Menispermeae and Tinosporeae are often less woody than Anomospermeae, Fibraureae and Pachygoneae. The former are more frequently found near streams whereas the latter are more likely to be found in the under storey (personal observation on collection notes). As fossilization is often favoured by water, a taphonomic bias could appear in favour of Menispermeae and Tinosporeae tribes.

A higher number of fossil leaves were found in North America compared to Europe. However, a higher number of fossil endocarps were found in Europe than in North America. This may be the consequence of the history of science. Tiffney (1990) explained that the study of fossil leaves was favoured in North America, whereas the study of fossil fruits was favoured in Europe.

The potential lack of tribe Anomospermeae in the fossil record can be linked to its evolution. This entire tribe, except the genus *Tiliacora* Colebr. 1822, is solely present in the South and Central Americas. These regions have only yielded a few Menispermaceae fossils, namely some *Menispermities* leaves (Doria et al., 2008). However, some newly described *Menispermities* species, *M. cordatus* Doria et al., 2008 and *M. guajiraensis* Doria et al., 2008, may have affinities with the tribe Anomospermeae (Doria et al., 2008). Under the hypothesis of South American evolution of Anomospermeae, it is not surprising that they are not found as fossils in other regions.

4.4. Ancient morphological diversity of the Menispermaceae

At the Palaeocene–Eocene limit, four of the five Menispermaceae tribes are present: Pachygoneae, Tinosporeae, Fibraureae and Menispermeae. Anomospermeae is the only tribe not represented during this period. The tribal diversity of Menispermaceae is therefore ancient, dating from at least the Upper Palaeocene. These findings are congruent with the molecular dating of this family, which proposed an age of 70 to 80 million years for the Menispermaceae crown group (Anderson et al., 2005).

The size of Menispermaceae endocarps varies across the fossil record. During the Eocene, fossil endocarps from Paris Basin are slightly smaller than those from London Clay (Jacques and De Franceschi, 2005). During the Miocene, fossil endocarps from Rusinga are bigger than modern endocarps and those of the Eocene in Europe (Chesters, 1957a). Tiffney (1984) indicates that seedling size depends on the plant's habit, habitat and on the seed's dispersion mode. These factors could have varied during Menispermaceae evolution. As the modern dispersion mode of Menispermaceae endocarps is not well known, it is almost impossible to draw conclusions on this point. However, one cannot exclude the possibility of taphonomic sorting or variable fossilization processes.

5. Conclusion

The Menispermaceae are well-represented in the fossil record. However, there is a great disparity in our understanding of the family's past biodiversity based on the systematic diversity

of either fruits or leaves. Fossil species based on leaf samples wait for a revision, which can be achieved only with a thorough knowledge of present-day Menispermaceae leaf architecture.

Taphonomic and sampling bias can explain differences in occurrences of the different tribes, as can climatic conditions and evolutionary history; however, it is often difficult to choose between these different explanations.

The questions regarding Menispermaceae palaeogeography seem fairly easy to answer due to the family's many occurrences in North America and Europe. However, the occurrence of fossils in the Southern Hemisphere indicates that the past history of Menispermaceae is more complicated. The distribution of the tribes in the past times is linked to their ecological requirements and their evolution. A well-sampled Menispermaceae phylogeny, including fossils, is a necessary tool for fully addressing this question.

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