Phylogeny and a revised tribal classification of Menispermaceae (moonseed family) based on molecular and morphological data

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Abstract The Menispermaceae, a largely tropical family of dioecious and predominantly climbing plants, have been the subject of various molecular studies that confirmed its monophyly and the para- and polyphyly of most of the currently recognized tribes. The newly recognized assemblages have been variously named informally in different studies. Here we present a comprehensive phylogenetic hypothesis of the Menispermaceae based on the analyses of three molecular markers (*matK*, *trnL-F*, *ndhF*) and 41 morphological characters for the most extensive taxonomic and geographic sampling of the family as compared to earlier studies. Phylogenetic relationships were inferred using maximum parsimony, maximum likelihood, and Bayesian approaches. Our results of the combined molecular and total-evidence datasets corroborate earlier findings, with an improved support for major clade contents. A new tribal classification of the Menispermaceae is proposed, in which nine clades are grouped within the subfamilies Chasmantheroideae and Menispermoideae, forming themselves two well-supported clades. Within the Chasmantheroideae, the two clades recovered are here recognized as tribes Burasaieae and Coscinieae; within the Menispermoideae the seven identified clades are recognized as tribes Anomospermeae, Cissampelideae, Limacieae, Menispermeae, Pachygoneae, Spirospermeae, and Tiliacoreae. Of these, Spirospermeae is newly described, while the names, if not the circumscriptions, of the remaining tribes are adopted from earlier treatments. The subfamilies and most tribes here identified are further diagnosed by unique combinations of morphological characters. A few genera not sampled for the molecular analysis are provisionally assigned to the recognized tribes based on their floral, fruit, endocarp, and seed features.

Keywords classification; diagnostic characters; Menispermaceae; moonseed; morphology; phylogeny

Supplementary Material Electronic Supplement (Tables S1–S3; Figs. S1 & S2) and DNA sequence alignment are available in the Supplementary Data section of the online version of this article at http://www.ingentaconnect.com/content/iapt/tax

■ INTRODUCTION

Menispermaceae (Ranunculales), commonly known as the moonseed family, are a medium-sized clade of dioecious, mostly climbing plants, along with a few trees, shrubs, and herbs, that are primarily distributed in the tropical regions of the World. Although never dominant, the large Menispermaceae lianas are always represented in tropical floristic studies (Gentry, 1991), and constitute a characteristic element in the physiognomy of tropical rainforests (Gentry, 1991; Richards, 1996; Wang & al., 2012). Current estimates for the taxonomic diversity of the family are about 72 genera and 526 species (Ortiz, unpub.). Most Menispermaceae plants are rich in various types of alkaloids (Barbosa-Filho & al., 2000; Aniszewski, 2007), and the family is perhaps best known as a source of curare, the South American arrow poison (Krukoff & Smith, 1937; Krukoff & Moldenke, 1938), after which the genus *Curarea* Barneby & Krukoff was named (Barneby & Krukoff, 1971). The family also includes many species with diverse, documented ethnobotanical uses in different regions of the World (e.g., Phillips, 1991 and references therein; De Wet & Van Wyk, 2008).

The family has an abundant and diverse fossil record assigned to extinct and extant genera (Reid & Chandler, 1933; Manchester, 1994; Doria & al., 2008; reviewed in Jacques, 2009a). The earliest fossil assigned to the Menispermaceae is the endocarp of *Prototinomiscium* Knobloch & Mai from the Turonian (Upper Cretaceous, 91 Ma) of central Europe (Knobloch & Mai, 1984, 1986), although its affinities to the Menispermaceae have not yet been critically evaluated (Jacques, 2009a; Herrera & al., 2011; Wefferling & al., 2013).

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Miers (1851) established the first supra-generic classification of the family, an arrangement that was formalized by Hooker & Thomson (1855) in their *Flora Indica*, and later further extended to the whole family by Bentham & Hooker (1862). These main classifications for Menispermaceae were reviewed in Ortiz & al. (2007). The most recent comprehensive work in the family was the monograph of Diels (1910), who recognized eight tribes, with the tribe Menispermeae being further divided into three subtribes. Like earlier workers (Miers, 1851, 1871; Hooker & Thomson, 1855; Bentham & Hooker, 1862; Baillon, 1874; Prantl, 1888), Diels (1910) emphasized characters of the fruit (e.g., endocarps and seeds), in combination with floral and vegetative characters, acknowledging that reliance on only a few characters would result in the grouping of heterogeneous elements. Although all subsequent workers of the family have followed Diels's system or some modification of it, there has been a common agreement of the need for its re-assessment (Barneby, 1970, 1972; Thanikaimoni & al., 1984; Forman, 1968, 1985, 1986).

In 1993, Kessler modified Diels's classification system and recognized only five tribes, distinguished by the endosperm (presence vs. absence), its degree of rumination (strongly ruminate vs. weakly ruminate or continuous), and the type of cotyledons (non-foliaceous and adpressed vs. foliaceous and divaricate). In his new tribal arrangement, the genus *Pachygone* Miers was omitted, although he did recognize the tribe Pachygoneae; this oversight was later corrected by Kubitzki (2007).

Earlier phylogenetic studies based on DNA sequence data (Ortiz & al., 2007; Wang & al., 2007a; Hoot & al., 2009) have indicated that the aforementioned characters traditionally used in infrafamilial classifications in the Menispermaceae are highly homoplasious, and are therefore unreliable in establishing predictive classifications. Moreover, these earlier studies have also shown that most tribes recognized by Diels (1910) and Kessler (1993) are para- or polyphyletic, with the newly recovered assemblages being variously named informally (Ortiz & al., 2007; Wang & al., 2007a, 2012; Jacques & Bertolino, 2008; Hoot & al., 2009; Jacques & al., 2011).

Although these studies contributed significantly to the knowledge of evolutionary relationships within Menispermaceae, some questions remained unanswered while others arose as a result of newly accumulated data that uncovered novel and/or complex patterns of relationships. For instance, the study of Wang & al. (2012), which included improved taxonomic sampling over earlier studies and which focused on global diversification of the family, did not resolve uncertain phylogenetic relationships in large genera that had questionable monophyly (e.g., species in *Antizoma* Miers, *Cissampelos* L., and *Tinospora* Miers). Similarly, the most recent phylogenetic study of the family (Wefferling & al., 2013), which focused on fruit evolution, also failed to resolve these ambiguous relationships, instead, it confirmed some of the incongruent placements that were also found in Jacques & al. (2011), such as the affinities of *Diploclisia* Miers species and *Strychnopsis* Baill., respectively, and the uncertain placement of *Perichasma laetificata* Miers.

The contrasting patterns of relationships recovered by Wang & al. (2012) and Wefferling & al. (2013), especially with regard to the placements of *Diploclisia* and *Strychnopsis*, had direct bearing on the delimitations of two major clades that were otherwise monophyletic. It is likely that the insufficient taxon coverage among these earlier studies have contributed to the inconsistencies regarding the major clades recovered. As a result, a comprehensive view of the contemporary knowledge of the systematics of the family is still lacking. The present study aimed to correct these inconsistencies by increasing the taxon coverage, which would result in an improved phylogenetic framework over that of Wang & al. (2012), especially at lower taxonomic levels.

Here, through the addition of 41 taxa to the data from the study of Wang & al. (2012), we present the most extensively sampled phylogeny of the Menispermaceae, in terms of genera, and species that spans all its geographical distribution, and for the first time we include species of the African genera *Dialytheca* Exell & Mendonça, *Sarcolophium* Troupin, and *Syrrheonema* Miers. Moreover, we also sampled species that have a long history of uncertainty regarding their taxonomic placement and phylogenetic affiliations, i.e., *Cissampelos capensis* L.f., *Cissampelos madagascariensis* (Baill.) Diels, *Tinospora* aff. *uviforme* (Baill.) Troupin, and *Tinospora caffra* (Miers) Troupin. In particular, because *C. capensis* has at times been taxonomically associated with *Antizoma* (Diels, 1910), its affinities with the latter genus, which is represented by two of its three species in our study, are evaluated in detail here. Several genera in need of re-evaluation are identified, and in order to avoid confusion these genera are referred to by their current accepted names, as established in their latest taxonomic revisions, throughout this paper, pending new formal combinations.

We evaluate diagnostic morphological characters for the major clades recognized in our comprehensive species-level phylogeny derived from a combined analysis of three molecular markers (*matK*, *trnL-F*, *ndhF*), and propose a revised, tribal classification of the Menispermaceae. The increased taxonomic sampling in this study improves our understanding of the affinities within all major clades, and clarifies the taxonomic affiliations of genera with historically ambiguous placements. Hence, we synthesize all major modifications and novel re-alignments of taxa from previously published molecular phylogenies of the family Menispermaceae. The recognized tribes are also diagnosed by unique combinations of morphological characters, thus allowing the establishment of a robust, coherent working phylogenetic hypothesis on which to base future taxonomic and evolutionary studies in the Menispermaceae. Names of major clades used throughout the manuscript, other than subfamilies, are those of our proposed tribal classification.

■ MATERIALS AND METHODS

Taxon sampling. — Because an increased taxon sampling is an important determinant of phylogenetic resolution and accuracy (Heath & al., 2008), an effort was made to maximize taxonomic representation in this study, thus allowing an improved phylogenetic framework of the family. Included here are 130 taxa (63 genera, 128 species, 1 subspecies, 1 variety), for a total of 136 samples of the Menispermaceae. The Malagasy C*issampelos madagascariensis*, of uncertain taxonomic affinities, is represented by three individuals; we also included four individuals for the pantropical and morphologically variable *C. pareira* L. Three genera and 14 species (including 1 variety), were included for the first time in phylogenetic analyses of the family (Appendix 1).

Our extensive taxon sampling is representative of the narrowly circumscribed tribal system of Diels (1910). Kessler's tribal circumscriptions have all been shown to be para- or polyphyletic (Ortiz & al., 2007; Wang & al., 2007a; Hoot & al., 2009; Jacques & al., 2011). Our sampling also includes members of all major lineages recovered by previous molecular phylogenetic studies (Ortiz & al., 2007; Jacques & al., 2011; Wang & al., 2012; Wefferling & al., 2013) (Table 1), with increased representation for large as well as small but geographically widespread genera. With very few exceptions, all genera sampled are represented in the dataset by at least two species. Effort was made to sample taxa with a long history of ambiguous taxonomic placements, such as *Cissampelos capensis*, *C. madagascariensis*, *Tinospora* aff. *uviforme*, and *T. caffra*.

Geographic distribution of the species in the clades is mostly indicated by the geographic areas where they occur, and loosely corresponds to the floristic subkingdoms and floristic regions as defined by Takhtajan (1986), e.g., Indomalesia comprising Indian, Indochinese, and Malesian regions, Australian subkingdom comprising the Northeast and Southwest regions.

Morphological data. — Morphological characters were used here as an independent dataset as it has been shown that they increase node support when combined with molecular datasets (Wang & al., 2009). Characters representing vegetative and reproductive morphology were scored primarily from direct observation of herbarium specimens; these were supplemented and/or cross-referenced with information from the literature, such as Miers (1871), Diels (1910), Troupin (1962), Forman (1986, 1991, 2007), Harley & Ferguson (1982), and Ortiz & al. (2007). We increased the number of characters for the morphological matrix of Ortiz-Gentry (2010) from 11 to 41 characters (Appendix 2). Reinterpretation of some of the characters resulted in a modified coding. For example, here the "subapical-adaxial" labeling replaces the "lateral" in Ortiz-Gentry (2010) for remnants of styles that are located between the apex and the base of the fruit to avoid confusion with the lateral sides of the fruit as defined in Ortiz (2012), also see Wefferling & al. (2013). Similarly, we modified the character "cotyledon form" to include "embryo form" as the latter is made up of both, the cotyledon and the radicle. Variation in stamen arrangement, ornamentation of the endocarp surface, and seed forms referred to in the text is illustrated in Figs. 1–3. Moreover, as the fruits in Menispermaceae develop unequally, with the abaxial side developing more than the adaxial side, a schematic representation of the abaxial, adaxial, and lateral sides of the endocarps as used here are illustrated in Fig. 2A & B.

We followed the conventional coding as described by Hawkins & al. (1997), which codes absence of a structure as an independent state. While the absence/presence scoring method may introduce redundancy, it has been suggested that its use avoids questionable assumptions regarding ordered and unordered observations (Pleijel, 1995). Polymorphic characters—i.e., characters observed with more than one state in the same taxa, are scored as such (e.g., "1,2"), as it has been suggested that variable character states may provide phylogenetic signal (Wiens & Servedio, 1997).

Molecular data. — The climbing habit and the pantropical distribution of the Menispermaceae make it difficult to obtain

Table 1. Number of genera sampled and major clades recovered in Menispermaceae in this study and several previous studies.

This study *matK+trnL-F+ndhF+* morphology	Ortiz & al. (2007) *ndhF*	Jacques & al. (2011) *atpB+rbcL*	Wang & al. (2012) *atpB+rbcL+matK+* *ndhF+trnL-F*	Wefferling & al. (2013) *atpB+rbcL+matK*
63 genera sampled	48 genera sampled	57 genera sampled	59 genera sampled	53 genera sampled
Chasmantheroideae	**Clade I**	**Clade 1**	**Tinosporoideae**	**Tinosporoideae**
Burasaieae	Expanded Tinosporeae	Expanded Tinosporeae	Expanded Tinosporeae	Expanded Tinosporeae
Coscinieae	Coscinieae	Coscinieae	Coscinieae	Coscinieae
Menispermoideae	**Clade II**	**not resolved**	**Menispermoideae**	**Menispermoideae**
Menispermeae	Menispermeae	Clade 1	Menispermeae	Menispermeae
Anomospermeae (incl. *Diploclisia* Miers)	Clade A not sampled	Expanded Anomospermeae *Diploclisia*	Clade A	Expanded Anomospermeae *Diploclisia*
Limacieae	*Limacia* Lour.	*Limacia*	*Limacia*	*Limacia*
Tiliacoreae	Tiliacoreae	Expanded Tiliacoreae	Tiliacoreae	Expanded Tiliacoreae
Pachygoneae	Clade C		Clade C	
Spirospermeae	Clade B		Clade B2	
Cissampelideae			Clade B1	

fresh material. Even when fresh material is available, the DNA is readily degraded, likely due to the abundance of secondary compounds that characterizes the family. In this study, we often used herbarium specimens, from which extracting DNA to amplify and sequencing low-copy nuclear genes is rather challenging. Efforts were made to amplify and sequence the internal transcribed spacer region (ITS), which is easy enough to amplify and has been used in phylogenetic analyses of tribe Menispermeae (sensu Diels, 1910) by Hong & al. (2001) and Wang & al. (2007a). In this study, we carried out a preliminary evaluation of ITS sequences from 22 genera representing all major clades in the Menispermaceae, and found a high level of sequence divergence among taxa, which lead to alignment issues. These ITS sequences ranged from 535 to 585 bp in

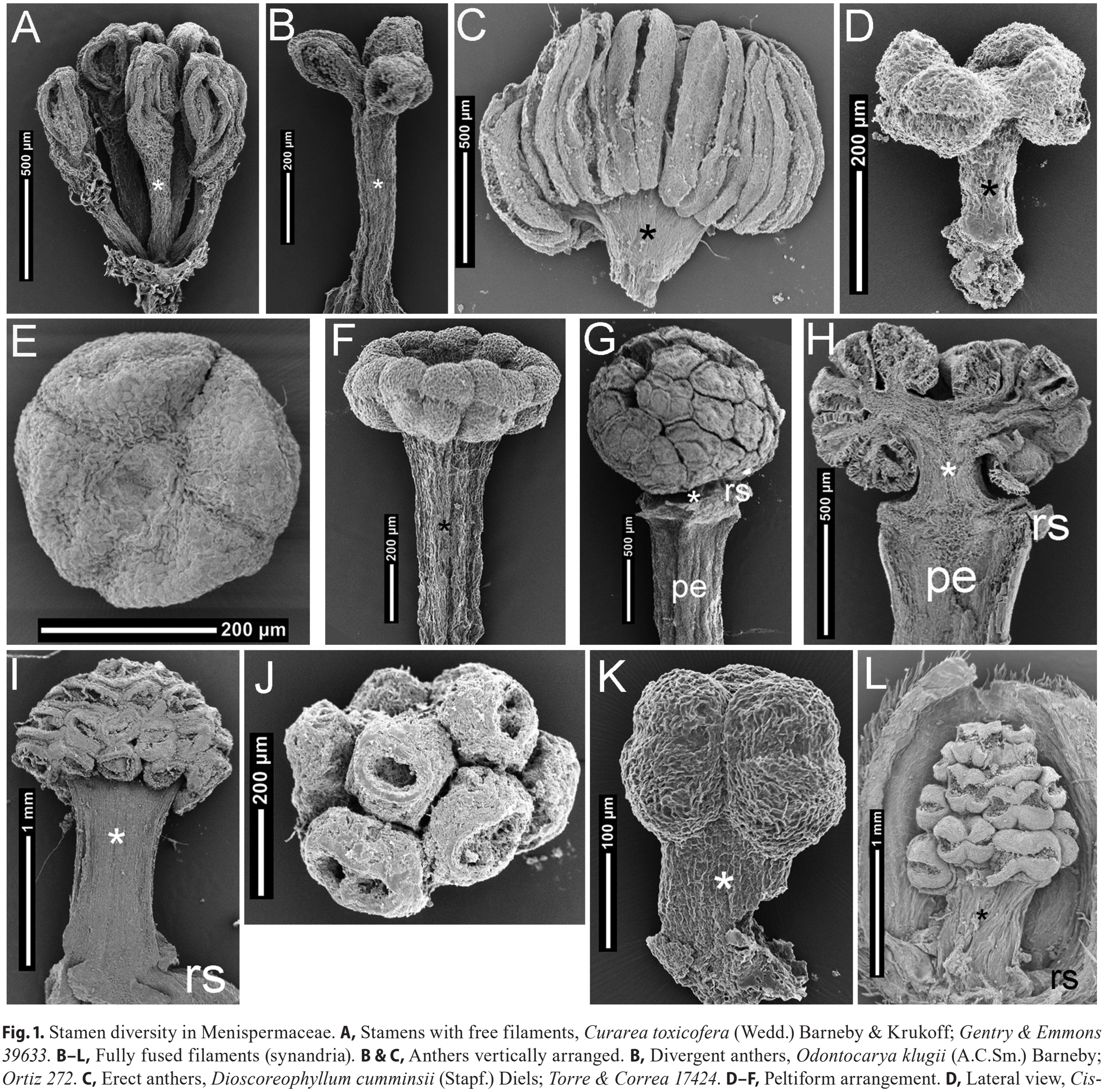


Fig. 1. Stamen diversity in Menispermaceae. **A,** Stamens with free filaments, *Curarea toxicofera* (Wedd.) Barneby & Krukoff; *Gentry & Emmons 39633*. **B–L,** Fully fused filaments (synandria). **B & C,** Anthers vertically arranged. **B,** Divergent anthers, *Odontocarya klugii* (A.C.Sm.) Barneby; *Ortiz 272*. **C,** Erect anthers, *Dioscoreophyllum cumminsii* (Stapf.) Diels; *Torre & Correa 17424*. **D–F,** Peltiform arrangement. **D,** Lateral view, *Cissampelos andromorpha* DC.; *Van der Werff & al. 21576*. **E,** View from above, *Cissampelos tropaeolifolia* DC.; *Ortiz 298*. **F,** Lateral view, *Aspidocarya uvifera* Hook.f. & Thomson, *Palee 992*. **G–L,** Subglobose/pyramidal arrangement. **G,** Anthers in a flower bud, *Anamirta cocculus* (L.) Wight & Arn.; *Wiraman 608*. **H,** Longitudinal section of a flower bud of *A. cocculus* showing connate filaments broadened distally; *Fosberg 53537*. **I,** Horizontal-subglobose arrangement of anthers in a flower after anthesis in *A. cocculus*; *Cramer 3595*. **J,** Horizontal-subglobose arrangement of anthers, *Arcangelisia flava* (L.) Merr.; *Witford 70*. **K,** Horizontal-suglobose arrangement of anthers, *Odontocarya tripetala* Diels; *Pipoly & al. 12280*. **L,** Horizontal-pyramidal arrangement of anthers, *Albertisia delagoensis* (N.E.Br.) Diels; *Marques 227*. — Asterisk (*) indicates filament; pe = pedicel; rs = remnant of sepal. All voucher specimens are at MO.

length and yielded an aligned matrix of 800 bp that included multiple ambiguous regions (matrix available upon request from W. Wang). Issues of highly divergent ITS sequences in Menispermaceae were also encountered by Hong & al. (2001) who found genetic distances of 51% to 65% among the taxa they sampled resulting in removal of *Aspidocarya* Hook.f. & Thomson, *Tinomiscium* (Miers) ex Hook.f. & Thomson, and *Arcangelisia* Becc. from their analyses in order to obtain meaningful results for the Menispermeae sensu Diels (1910). The issues detailed above illustrate the difficulties in using ITS data for estimating relationships across the family. Therefore, the present study used the following plastid markers only: *matK* and *ndhF* genes, and *trnL-F* regions (*trnL* intron, *trnL* [UAA] 3′ exon-*trnF* [GAA] intergenic spacer). These molecular markers have provided the highest number of parsimony-informative sites, allowing the resolution of major clades in previous studies of the family (Ortiz & al., 2007; Wang & al., 2012). With the exception of *Cissampelos owariensis* P.Beauv. ex DC. and *Stephania rotunda* Lour., which are both missing *matK* and *trnL-F*, *Sarcolophium suberosum* (Diels) Troupin missing *matK*, *Syrrheonema hexastamineum* Keay and *Tinospora caffra* missing *ndhF*, all included taxa have been sampled for the three markers. DNA isolation, PCR amplification, sequencing, and sequence alignment followed procedures outlined in Ortiz

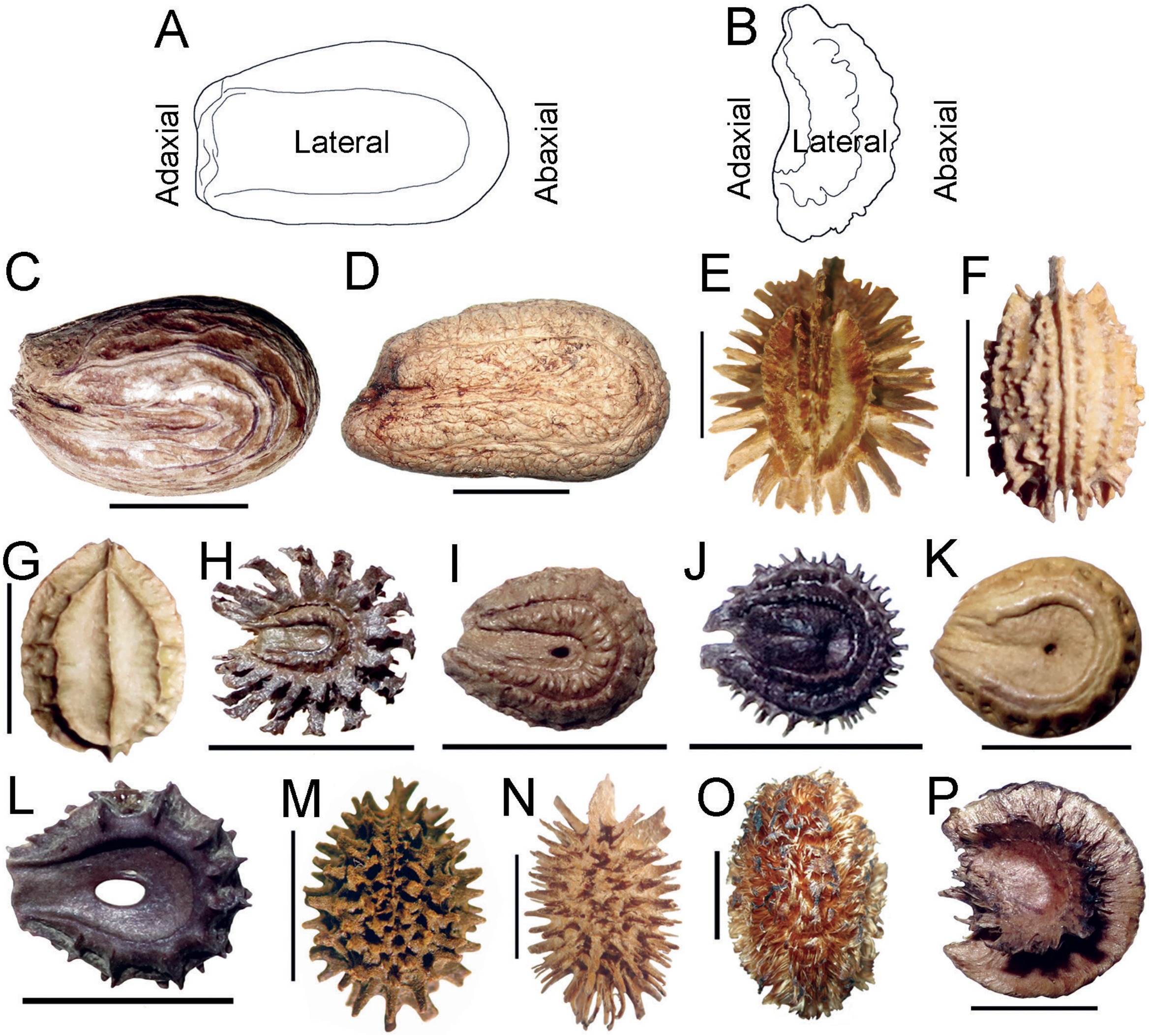


Fig. 2. Schematic representation of the two major types of endocarp shapes, their respective axis and endocarp surface ornamentation in Menispermaceae. **A,** Endocarp laterally compressed. **B,** Endocarp abaxially-adaxially compressed. **C,** Ribbed, *Chondrodendron tomentosum* Ruiz & Pav.; *Perea & Torres 2745.* **D,** Rugose, *Abuta rufescens* Aubl.; *Ortiz 344.* **E–G,** Longitudinally ridged. **E,** *Disciphania calocarpa* Standl.; *Sinaca 231.* **F,** *Odontocarya tripetala* Diels; *Ortiz 192.* **G,** *Disciphania mexicana* Bullock; *Lott 3688.* **H–L,** Longitudinally and transversally ridged. **H,** *Cissampelos tropaeolifolia* DC.; *Ortiz 247.* **I,** *Cissampelos ovalifolia* DC.; *Diaz 1026.* **J,** *Cyclea hypoglauca* (Schauer) Diels; *Yu & Butt 20939.* **K,** *Cissampelos arenicola* M.Nee & R.Ortiz; *Mereles 5075.* **L,** *Stephania* sp.; *Wang 0296.* **M & N,** Irregularly aculeate. **M,** *Dioscoreophyllum cumminsii* (Stapf) Diels; *Breteler 30-9-1987.* **N,** *Kolobopetalum* sp.; *Stone 5026.* **O,** Fibrous, *Burasaia madagascariensis* DC.; *Rabenantoandro 1262.* **P,** Winged, *Legnephora moorei* (F.Muell.) Miers; *Sharp AQ 767632* (BRI) — Scale bars: C, D, M & O = 1 cm; E–L, N & P = 0.5 cm. A–D, H–L & P, lateral view of endocarps; E–G & M–O, abaxial view of endocarps. All voucher specimens with the exception of *L. moorei*, are at MO.

& al. (2007) and Wang & al. (2012). Five difficult-to-align regions in *trnL-F*, representing 166 sites, were excluded from the analyses. Three species of Berberidaceae, two species of Ranunculaceae, and two species of Lardizabalaceae were included as outgroups. Voucher information and GenBank accession numbers are listed in Appendix 1.

Phylogenetic analysis. — Each individual marker and the combined three-marker datasets were analyzed by maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) methods in PAUP* v.4.0b10 (Swofford, 2003), RAxML v.7.0.4 (Stamatakis, 2006), and MrBayes v.3.5 (Ronquist & al., 2012), respectively. For MP analysis, heuristic searches were conducted with 1000 replicates of random addition, saving one tree per replicate during stepwise addition, using the tree-bisection-reconnection (TBR) branch swapping, MulTrees in effect, and steepest descent off. Clade support was measured by bootstrap analysis with 1000 replicates, 10 random taxon additions, and heuristic search options. RAxML was performed with the GTR+Γ substitution model for each region, and support for the clades was assessed using the fast bootstrap option, with 1000 replicates. Bootstrap values (BS) for clade support were indicated as follows: strong, 80%–100%; moderate, 60%–79%; weak, <60%.

For BI analysis, each DNA region was assigned its own best-fit model, as determined by the Akaike information criterion (AIC) via jModelTest v.2.1.4 (Posada, 2008). Two independent Markov Chain Monte Carlo (MCMC) runs were conducted simultaneously, each with three heated and one cold chains, for 10 million generations, sampling one tree every 1000 generations, and starting with a random tree. Stationarity of the runs was assessed using Tracer v.1.5 (Rambaut & Drummond, 2009). A majority-rule (>50%) consensus tree was constructed after removing the burn-in samples (the first 25% of sampled trees). Posterior probabilities (PP) for clade support were indicated as follows: strong, 0.95–1.0; moderate, 0.80–0.94; weak, <0.80.

The morphological data as well as the combined morphological and molecular dataset (hereafter referenced to as the total-evidence dataset), were analyzed using MP and BI approaches as described above for the combined molecular dataset. For BI analysis, the morphological data were run under the datatype = standard option, and only variable sites had the possibility of being sampled (coding = variable).

To infer morphological synapomorphies for the major clades recognized, selected characters were optimized onto the Bayesian tree recovered from the combined molecular dataset. Optimizations were performed in Mesquite v.3.04 (Maddison & Maddison, 2015) using maximum unordered parsimony.

The phylogenetic signal of morphological characters was explored using the TreeFarm Package implemented in Mesquite v.3.04 (Maddison & Maddison, 2015). We first obtained the number of parsimony steps for each character on the Bayesian tree recovered from the combined molecular dataset, which served as our reference tree. We then created a null model by generating 10,000 randomized trees by reshuffling the terminal taxa on our reference tree. The null model is a distribution of steps of the characters on all random trees, with a percentile boundary of 0.05 (Laurin, 2004). Individual characters were considered to have phylogenetic signal if the percentile value of the number of steps on the randomized trees fell outside the lower percentile boundary (Laurin, 2004).

Taxonomy and classification. — Formal taxonomic recognition of groups was based on monophyly (Forey & al., 1992; Backlund & Bremer, 1998) and morphology. Clades here recognized at the tribal level are supported with ≥80% (BS) and ≥95% (PP) in the analyses of the combined molecular

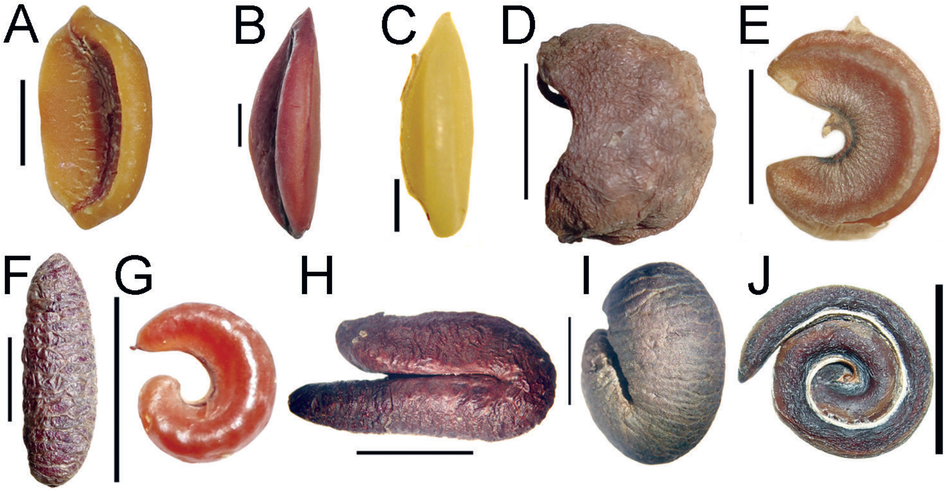


Fig. 3. Seed forms. **A–C,** Naviculiform. **A,** *Odontocarya truncata* Standl.; *McPherson 11762.* **B,** *Tinomiscium petiolare* Hook.f. & Thomson; *Averyanov & al. 4877.* **C,** *Disciphania domingensis* Urb.; *Garcia 582.* **D,** Subglobose, *Coscinium fenestratum* Colebr.; *DeWilde 15479.* **E,** Semiannular-crescentic, *Menispermum canadense* L.; *Ortiz & Pruski 488.* **F,** Ellipsoid, *Orthomene schomburgkii* (Miers) Barneby & Krukoff; *Ortiz 201.* **G,** Cochleate, *Cocculus carolinus* (L.) DC.; *Ortiz & Pruski 487.* **H,** Hippocrepiform, *Abuta rufescens* Aubl.; *Ortiz 344.* **I,** Unciform, *Anomospermum grandifolium* Eichler; *Vásquez 34439.* **J,** Spiral, *Spirospermum penduliflorum* DC.; *Rabevohitra 4912.* — Scale bars: A, B, E, G & J = 0.5 cm; C = 0.43 cm; D, F, H & I = 1 cm. All seeds are on lateral view. All voucher specimens are at MO.

and the total-evidence datasets, respectively. In addition, the named tribes are diagnosed either by unique morphological character or by a combination of homoplasious morphological character states.

Genera not sampled for the molecular phylogenetic analysis are provisionally assigned to a recognized tribe based on their morphology; these genera are listed in boldface in their respective tribes. This revised tribal classification was developed using the sequencing convention for naming (Wiley, 1981), and in selecting names we followed the rules of the *International Code of Nomenclature* (*ICN*, McNeill & al., 2012). Priority, authorships, and ranks of names were determined by examining the original publications and the Indices Nominum Supragenericorum Plantarum Vascularium (Reveal, 2011–). The use of generic names and authorities follows the Index Nominum Genericorum (Farr & Zijlstra, 1996–).

■ RESULTS

Morphological data. — The morphological data matrix had 8% missing data, of which 7% were for features of the female condition and 13 characters, which correspond to 32%, were polymorphic in the dataset (Electr. Suppl.: Tables S1 & S2). Missing data were particularly striking for *Limacia* Lour., which is poorly represented in herbarium collections. Summary of the characteristics of the dataset and tree statistics from the MP analyses are presented in Table 2. The MP and BI analyses of the morphological dataset retrieved similar topologies that show largely unresolved relationships, except for two of the major clades, Cissampelideae (PP = 0.77; MP-BS = 73%) and Coscinieae (PP = 0.99; MP-BS = 100%), that were also found in the combined molecular analyses. The 50% majority rule consensus tree of the parsimony analysis is presented in Fig. S1 (Electr. Suppl.).

Molecular data. — Summary of the characteristics of the molecular datasets and tree statistics from the MP analyses are presented in Table 2. The MP analyses of the individual molecular markers (trees not shown) recovered topologies that are highly congruent with each other and with those obtained via the MP, ML, and Bayesian analyses of the combined dataset. The few incongruences among the individual markers were weakly supported or were not resolved in their strict consensus trees (not shown). The combined molecular dataset comprised 4765 characters. All analyses of the combined dataset recovered similar topologies, two large sister clades, the Chasmantheroideae (PP = 1.0; ML-BS = 99%; MP-BS = 91%) and Menispermoideae (PP = 1.0; ML-BS = 100%; MP-BS = 98%), and nine other major clades that are all strongly supported. These are here recognized at the tribal level. The majority-rule (>50%) consensus tree recovered from the BI analysis of the combined molecular dataset is shown in Fig. 4 and is used to represent the estimated phylogeny of the Menispermaceae and unless otherwise indicated, it is the focus of our discussion.

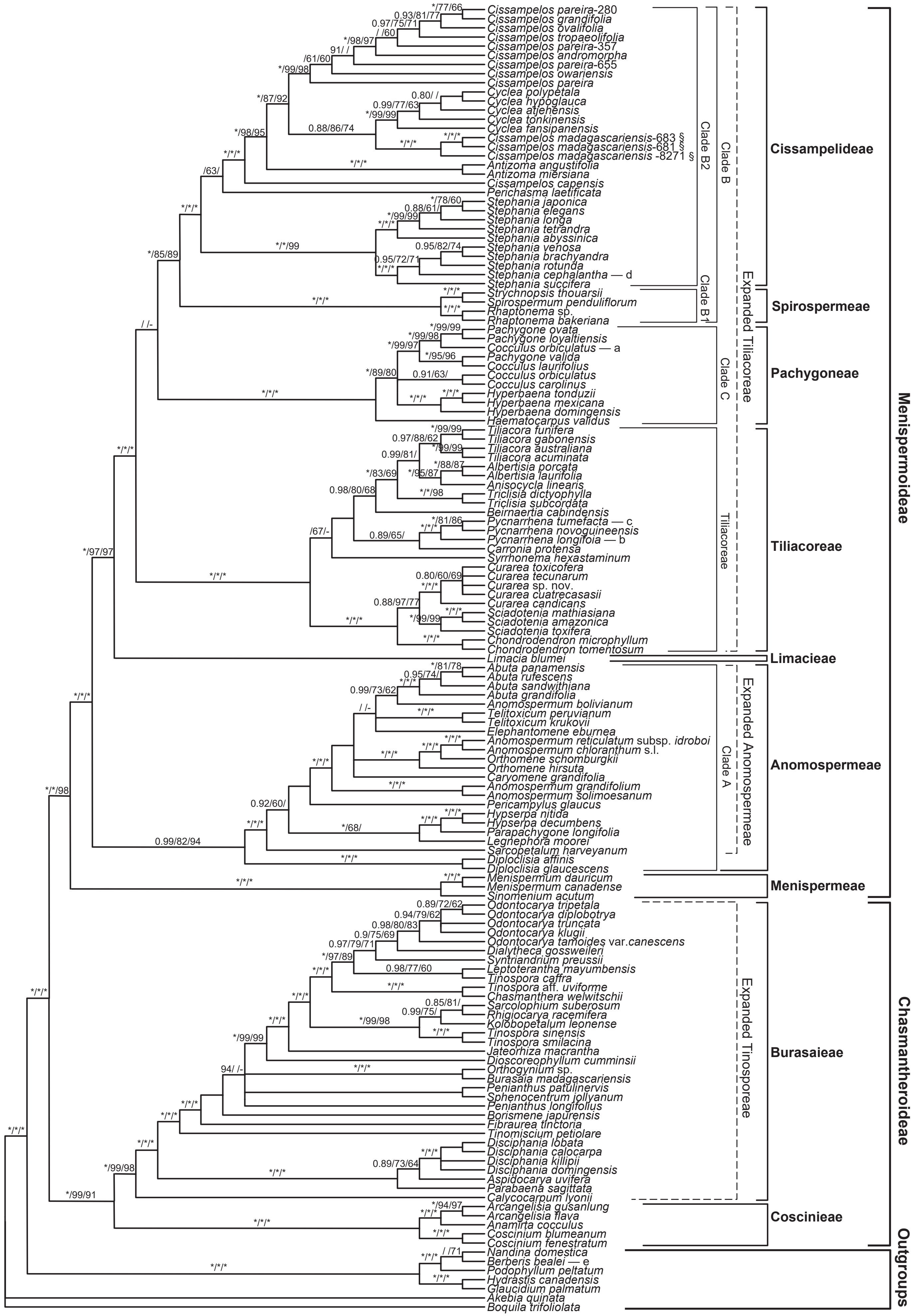
Total-evidence data. — Summary statistics from the MP analyses are shown in Table 2. Trees recovered from the MP and Bayesian analyses were mostly in agreement. The only discrepancy between the two topologies concerns the relationships of two major clades (Pachygoneae, Tiliacoreae), which is discussed below. All other relationships retrieved by both analyses (MP, BI), the two large sister clades, Chasmantheroideae (PP = 1.0; MP-BS = 95%), Menispermoideae (PP = 1.0; MP-BS = 99%), and all major nine clades are also found in the combined molecular dataset. Each of the nine major clades is strongly supported in both, the MP and BI analyses. The strict consensus tree from the parsimony analysis is presented in Fig. 5, and unless otherwise indicated, is also referred to in the discussion.

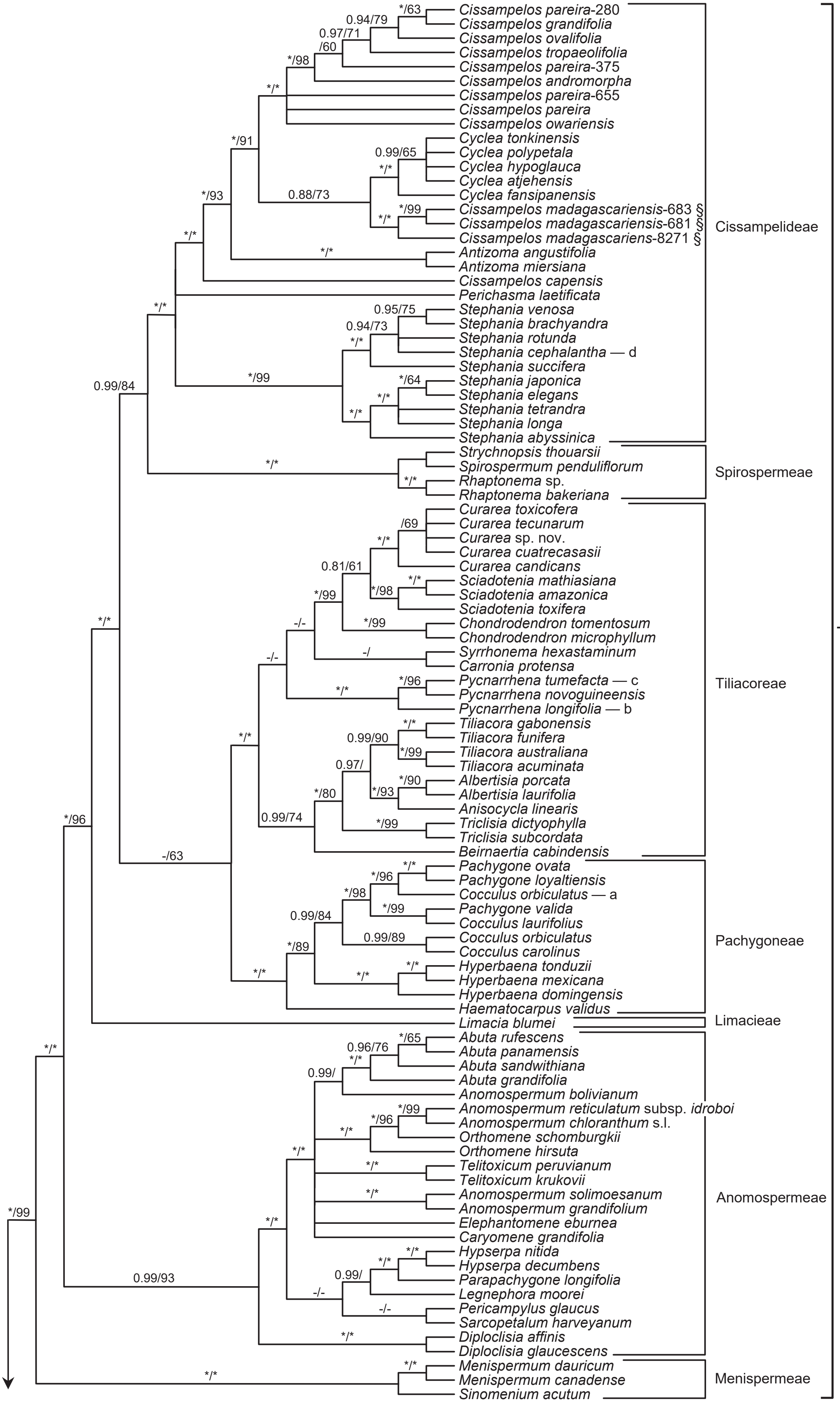
Morphological characterization. — Summary of consistency index (CI) and retention index (RI) values for each morphological character is presented in Table S2 (Electr. Suppl.). Diagnostic characters for the family Menispermaceae and for the major clades recognized in this study are shown in Fig. 6 and Table 3.

Table 2. Summary of characteristics and tree statistics from parsimony analyses of the various datasets.

Dataset	No. of total characters	No. of variable characters	No. of informative characters	No. of trees	Length of trees	Consistency index	Retention index	Rescaled consistency index
matK	1299	745	459	14,655	1587	0.57	0.86	0.49
trnL-F	1351	466	294	14,115	998	0.65	0.88	0.57
ndhF	2115	963	641	8,700	2538	0.55	0.86	0.47
Combined molecular dataset	4765	751	418	4	986	0.87	0.86	0.76
Morphology	41	41	40	330	248	0.33	0.85	0.28
Total evidence	4806	2127	1432	6,735	5496	0.55	0.85	0.47

Fig. 4. Bayesian tree based on the combined molecular dataset. Statistical support for clades is indicated by posterior probabilities, likelihood, and parsimony bootstrap, respectively. Support of PP ≥ 0.80 and BS ≥ 60 is shown. An asterisk (*) indicates BS = 100% or PP = 1.0, a dash (-) indicates branches not recovered in the corresponding analysis. Clades A–C, correspond to the labeling of Ortiz & al. (2007); expanded tribes as per Wefferling & al. (2013); B1 and B2 as per Wang & al. (2012); notations §, a–e, are indicated in notes in Appendix 1. ►


Cissampelos pareira-280
Cissampelos grandifolia
Cissampelos ovalifolia
Cissampelos tropaeolifolia
Cissampelos pareira-357
Cissampelos andromorpha
Cissampelos pareira-655
Cissampelos owariensis
Cissampelos pareira
Cyclea polypetala
Cyclea hypoglauca
Cyclea atjehensis
Cyclea tonkinensis
Cyclea fansipanensis
Cissampelos madagascariensis-683 §
Cissampelos madagascariensis-681 §
Cissampelos madagascariensis -8271 §
Antizoma angustifolia
Antizoma miersiana
Cissampelos capensis
Perichasma laetificata
Stephania japonica
Stephania elegans
Stephania longa
Stephania tetrandra
Stephania abyssinica
Stephania venosa
Stephania brachyandra
Stephania rotunda
Stephania cephalantha — d
Stephania succifera
Strychnopsis thouarsii
Spirospermum penduliflorum
Rhaptonema sp.
Rhaptonema bakeriana
Pachygone ovata
Pachygone loyaltiensis
Cocculus orbiculatus — a
Pachygone valida
Cocculus laurifolius
Cocculus orbiculatus
Cocculus carolinus
Hyperbaena tonduzii
Hyperbaena mexicana
Hyperbaena domingensis
Haematocarpus validus
Tiliacora funifera
Tiliacora gabonensis
Tiliacora australiana
Tiliacora acuminata
Albertisia porcata
Albertisia laurifolia
Anisocycla linearis
Triclisia dictyophylla
Triclisia subcordata
Beirnaertia cabindensis
Pycnarrhena tumefacta — c
Pycnarrhena novoguineensis
Pycnarrhena longifoia — b
Carronia protensa
Syrrhonema hexastaminum
Curarea toxicofera
Curarea tecunarum
Curarea sp. nov.
Curarea cuatrecasasii
Curarea candicans
Sciadotenia mathiasiana
Sciadotenia amazonica
Sciadotenia toxifera
Chondrodendron microphyllum
Chondrodendron tomentosum
Limacia blumei
Abuta panamensis
Abuta rufescens
Abuta sandwithiana
Abuta grandifolia
Anomospermum bolivianum
Telitoxicum peruvianum
Telitoxicum krukovii
Elephantomene eburnea
Anomospermum reticulatum subsp. idroboi
Anomospermum chloranthum s.l.
Orthomene schomburgkii
Orthomene hirsuta
Caryomene grandifolia
Anomospermum grandifolium
Anomospermum solimoesanum
Pericampylus glaucus
Hypserpa nitida
Hypserpa decumbens
Parapachygone longifolia
Legnephora moorei
Sarcopetalum harveyanum
Diploclisia affinis
Diploclisia glaucescens
Menispermum dauricum
Menispermum canadense
Sinomenium acutum
Odontocarya tripetala
Odontocarya diplobotrya
Odontocarya truncata
Odontocarya klugii
Odontocarya tamoides var.canescens
Dialytheca gossweileri
Syntriandrium preussii
Leptoterantha mayumbensis
Tinospora caffra
Tinospora aff. uviforme
Chasmanthera welwitschii
Sarcolophium suberosum
Rhigiocarya racemifera
Kolobopetalum leonense
Tinospora sinensis
Tinospora smilacina
Jateorhiza macrantha
Dioscoreophyllum cumminsii
Orthogynium sp.
Burasaia madagascariensis
Penianthus patulinervis
Sphenocentrum jollyanum
Penianthus longifolius
Borismene japurensis
Fibraurea tinctoria
Tinomiscium petiolare
Disciphania lobata
Disciphania calocarpa
Disciphania killipii
Disciphania domingensis
Aspidocarya uvifera
Parabaena sagittata
Calycocarpum lyonii
Arcangelisia gusanlung
Arcangelisia flava
Anamirta cocculus
Coscinium blumeanum
Coscinium fenestratum
Nandina domestica
Berberis bealei — e
Podophyllum peltatum
Hydrastis canadensis
Glaucidium palmatum
Akebia quinata
Boquila trifoliolata
Clade B2
Clade B
Clade B1
Clade C
Tiliacoreae
Expanded Tiliacoreae
Expanded Anomospermeae
Clade A
Expanded Tinosporeae
Cissampelideae
Spirospermeae
Pachygoneae
Tiliacoreae
Limacieae
Anomospermeae
Menispermeae
Burasaieae
Coscinieae
Menispermoideae
Chasmantheroideae
Outgroups


*/63
0.94/79
0.97/71
/60
*/98
/
Cissampelos pareira-280
Cissampelos grandifolia
Cissampelos ovalifolia
Cissampelos tropaeolifolia
Cissampelos pareira-375
Cissampelos andromorpha
Cissampelos pareira-655
Cissampelos pareira
Cissampelos owariensis
*/91
0.99/65
/
Cyclea tonkinensis
Cyclea polypetala
Cyclea hypoglauca
Cyclea atjehensis
Cyclea fansipanensis
*/93
0.88/73
*/99
/
Cissampelos madagascariensis-683 §
Cissampelos madagascariensis-681 §
Cissampelos madagascariens-8271 §
Cissampelideae
/
/
Antizoma angustifolia
Antizoma miersiana
Cissampelos capensis
Perichasma laetificata
/
0.95/75
0.94/73
/
Stephania venosa
Stephania brachyandra
Stephania rotunda
Stephania cephalantha — d
Stephania succifera
0.99/84
*/99
*/64
/
/
Stephania japonica
Stephania elegans
Stephania tetrandra
Stephania longa
Stephania abyssinica
/
/
Strychnopsis thouarsii
Spirospermum penduliflorum
Rhaptonema sp.
Rhaptonema bakeriana
Spirospermeae
/69
/
0.81/61
Curarea toxicofera
Curarea tecunarum
Curarea sp. nov.
Curarea cuatrecasasii
Curarea candicans
/
*/98
*/99
Sciadotenia mathiasiana
Sciadotenia amazonica
Sciadotenia toxifera
-/-
*/99
Chondrodendron tomentosum
Chondrodendron microphyllum
/
-/-
-/
Syrrhonema hexastaminum
Carronia protensa
*/96
/
Pycnarrhena tumefacta — c
Pycnarrhena novoguineensis
Pycnarrhena longifolia — b
Tiliacoreae
/
0.99/90
*/99
0.97/
Tiliacora gabonensis
Tiliacora funifera
Tiliacora australiana
Tiliacora acuminata
*/96
*/80
*/90
*/93
Albertisia porcata
Albertisia laurifolia
Anisocycla linearis
0.99/74
*/99
Triclisia dictyophylla
Triclisia subcordata
Beirnaertia cabindensis
-/63
/
*/96
*/98
Pachygone ovata
Pachygone loyaltiensis
Cocculus orbiculatus — a
0.99/84
*/99
Pachygone valida
Cocculus laurifolius
0.99/89
Cocculus orbiculatus
Cocculus carolinus
Pachygoneae
*/89
/
/
/
Hyperbaena tonduzii
Hyperbaena mexicana
Hyperbaena domingensis
Haematocarpus validus
Limacia blumei
Limacieae
Menispermoideae
/
0.96/76
*/65
/
0.99/
Abuta rufescens
Abuta panamensis
Abuta sandwithiana
Abuta grandifolia
Anomospermum bolivianum
*/99
*/96
/
Anomospermum reticulatum subsp. idroboi
Anomospermum chloranthum s.l.
Orthomene schomburgkii
Orthomene hirsuta
/
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Telitoxicum peruvianum
Telitoxicum krukovii
/
Anomospermum solimoesanum
Anomospermum grandifolium
Elephantomene eburnea
Caryomene grandifolia
Anomospermeae
*/99
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0.99/
Hypserpa nitida
Hypserpa decumbens
Parapachygone longifolia
Legnephora moorei
0.99/93
-/-
-/-
Pericampylus glaucus
Sarcopetalum harveyanum
/
Diploclisia affinis
Diploclisia glaucescens
/
/
Menispermum dauricum
Menispermum canadense
Sinomenium acutum
Menispermeae

■ DISCUSSION

The inferred phylogenies recovered here agree in part with those of earlier studies (Ortiz & al., 2007; Hoot & al., 2009 in part; Jacques & al., 2011 in part; Wang & al., 2012; Wefferling & al., 2013). Our results (Figs. 4, 5) are highly congruent with those of Wang & al., 2012 (cf. their figs. 1 and S2); however, our study, with an increased taxonomic sampling provides new insights into the relationships of several of the taxa in the family that have had a long history of taxonomic uncertainty. Hence, based on the phylogenetic hypothesis presented here we summarize previous findings where novel associations have been variously informally referred, into a formal tribal classification of the Menispermaceae.

Morphological characters and phylogenetic signal. — The MP and BI analyses of the morphological matrix yielded topologies that were largely similar. Support values for the recovered major clades were moderate, and relationships within major clades, with one exception, were for the most part unresolved (Electr. Suppl.: Fig. S1).

Low resolution and/or low support in morphological phylogenetic analyses have been partly attributed to character coding and/or homology assessments (Scotland & al., 2003), as well as to including more taxa (Ocampo & al., 2014; Sirichamorn & al., 2014). The low resolution and lack of support found here stems from homoplasy as indicated by the low CI values for many of the characters (Electr. Suppl.: Table S2). Similarly the issue of character coding may be obscuring our detection of potential synapomorphies. For example, all taxa with fully fused filaments were coded as having a synandrium, although we noted that they may have different ontogenies. Missing data may also be contributing to the lack of resolution as several taxa—notably *Limacia*—still remain unknown for many of the characters such as fruit and seeds (Electr. Suppl.: Table S1) that may have a potential for inferring relationships.

The characters evaluated here are labile, hence, with very few exceptions, no unique morphological features that diagnose each one of the major clades can be identified, but characters in unique combinations do diagnose most of the major clades recognized in this study (Table 3). Despite the labile nature of the studied characters, the phylogenetic signal analysis indicated that most of these characters are not randomly distributed, but instead show strong phylogenetic signal (Electr. Suppl.: Table S3), although the presence of phylogenetic signal in homoplasious characters remains insufficiently understood. This lack of understanding may stem from the limitations of current

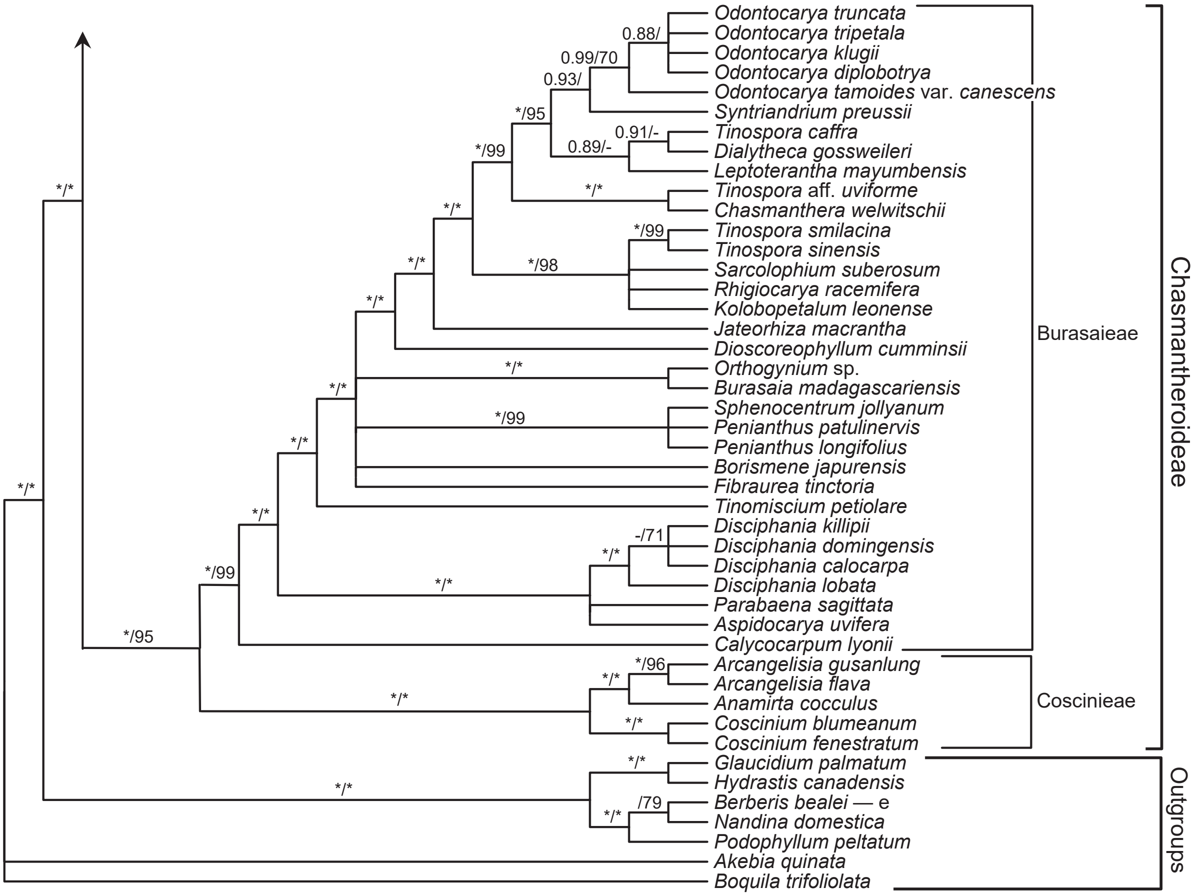
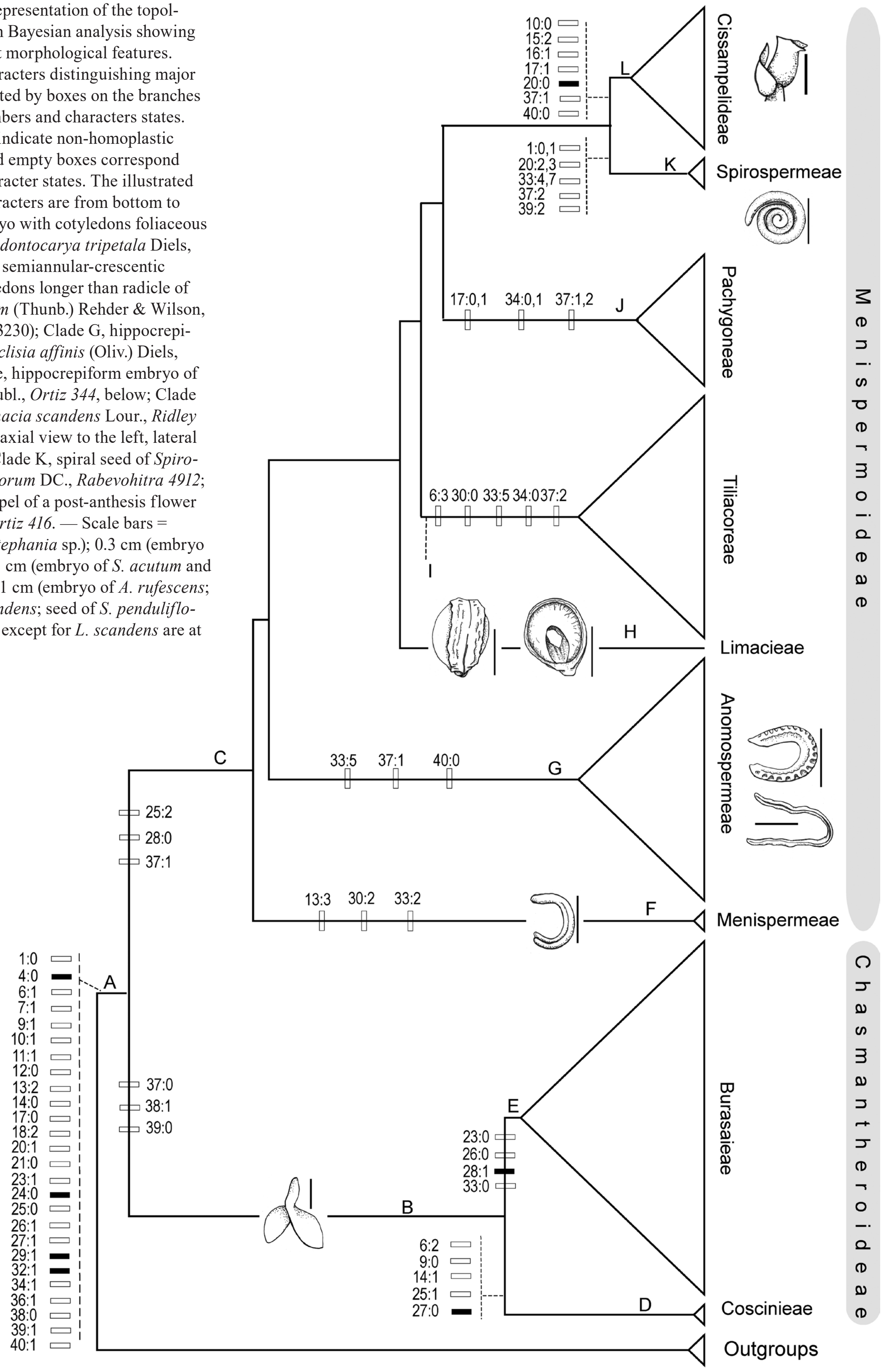


Fig. 5. Strict consensus tree of the parsimony analysis of the total-evidence dataset. Numbers above the branches indicate posterior probabilities (PP ≥ 0.80) and parsimony bootstrap values (BS ≥ 60). An asterisk (*) indicates PP = 1.0 or BS = 100% ; a dash (-) indicates branches not recovered in the corresponding analysis; notations §, a–e, are indicated in notes in Appendix 1.

Fig. 6. Schematic representation of the topology recovered from Bayesian analysis showing clades with distinct morphological features. Morphological characters distinguishing major clades are represented by boxes on the branches with character numbers and characters states. Black filled boxes indicate non-homoplastic character states and empty boxes correspond to homoplastic character states. The illustrated morphological characters are from bottom to top: Clade B, embryo with cotyledons foliaceous and divaricate of *Odontocarya tripetala* Diels, *Ortiz 293*; Clade F, semiannular-crescentic embryo with cotyledons longer than radicle of *Sinomenium acutum* (Thunb.) Rehder & Wilson, *T0330* (MO-045273230); Clade G, hippocrepiform seed of *Diploclisia affinis* (Oliv.) Diels, *Yasdong s.n.*, above, hippocrepiform embryo of *Abuta rufescens* Aubl., *Ortiz 344*, below; Clade H, endocarp of *Limacia scandens* Lour., *Ridley 1895* (BOGOR), abaxial view to the left, lateral view to the right; Clade K, spiral seed of *Spirospermum penduliflorum* DC., *Rabevohitra 4912*; Clade L, single carpel of a post-anthesis flower of *Stephania* sp., *Ortiz 416*. — Scale bars = 0.1 cm (carpel of *Stephania* sp.); 0.3 cm (embryo of *O. tripetala*); 0.5 cm (embryo of *S. acutum* and seed of *D. affinis*); 1 cm (embryo of *A. rufescens*; endocarp of *L. scandens*; seed of *S. penduliflorum*). All vouchers except for *L. scandens* are at MO.



methods of estimation, inaccuracy in tree topology, and errors in the data themselves, among others (Ocampo & al., 2014).

Two major clades within Menispermaceae. — The split of the Menispermaceae into two large clades has been identified before (Ortiz & al., 2007; Wang & al., 2009, 2012; Wefferling & al., 2013), these were formally recognized as the Tinosporoideae (as Chasmantheroideae here, see the Taxonomy section), and the Menispermoideae (Wang & al., 2009). These two sister clades were also recovered in this study, with strong support in all analyses, Chasmantheroideae (PP = 1.0; ML-BS = 99%; MP-BS = 91%) and Menispermoideae (PP = 1.0; ML BS = 100%; MP-BS = 98%, Fig. 4).

Both sister clades are well-characterized morphologically; the Chasmantheroideae have spathuliform embryos (ch. 37:0), foliaceous (ch. 38:1), and more or less divaricate cotyledons (ch. 39:0) (Fig. 6, clade B; Table 3; Wang & al., 2009; Ortiz-Gentry, 2010). *Penianthus* Miers and *Sphenocentrum* Pierre, derived within this clade, share seeds without endosperm and fleshy adpressed cotyledons. Of these features, however, spathuliform embryos and foliaceous cotyledons are linked as they appear to vary together in our reconstruction (not shown). Divaricate cotyledons are used here as an independent state, however, they are also to be included in the fundamental division of incumbent (i.e., our dorsiventrally adpressed), and accumbent (laterally adpressed) cotyledons. Preliminary evaluations of the character states suggest the incumbent character state as the ancestral condition in the family (not shown). The Menispermoideae are morphologically diagnosed by drupelets with subbasal or basal stylar scar (ch. 25:2), laterally compressed endocarps (ch. 28:0), strap-like embryos (ch. 37:1) (Fig. 6, clade C; Table 3; Wang & al., 2009; Ortiz-Gentry, 2010). Other features such as hemianatropous ovules, curved endocarps (also seeds and embryos), and adpressed cotyledons (i.e., not divaricate) inferred as the ancestral character states in the family (not shown) are predominantly retained in most members of the Menispermoideae. Additionally, the bilaterally compressed, laminiform or septiform condyle, referred to as *Menispermum*-type condyle, is characteristic of the Menispermoideae (Ortiz, 2012). Most members of the Menispermoideae share drupelets with subbasal or basal remnant of the style/stigma, but

Table 3. Diagnostic characters for the family Menispermaceae and the recognized major clades shown in Fig. 6.

Node	Diagnostic characters
A	**Dioecy (ch. 4:0);** male—and female—sepals arranged in two whorls (ch. 6:1)*; three sepals per whorl (ch. 7:1, ch. 18:2)*; petals in male—and female—flowers present (ch. 9:1)*; petals arranged in two whorls (ch. 10:1)*; male—and female—flowers with three petals per whorl (ch. 11:1)*; petals free (ch. 12:0); male flowers with six stamens (ch. 13:2)*; filaments free (ch. 14:0)*; anthers with vertical dehiscence (ch. 17:0); female flowers with three carpels (ch. 20:1)*; two ovules (ch. 21:0)*; hemianatropous ovules (ch. 23:1)*; **fruits drupelets/monocarps (ch. 24:0);** apical stylar scar (ch. 25:0)*; curved endocarp (ch. 26:1)*; compressed endocarp (ch. 27:1), with an **ornamented surface (ch. 29:1); presence of condyle (ch. 32:1);** presence of endosperm (ch. 34:1)*; large embryos (ch. 36:1)*; fleshy cotyledons (ch. 38:0), adpressed cotyledons (ch. 39:1,2); cotyledons longer than radicle (ch. 40:1)*. The family is also distinguishing by its free carpels, this feature was not coded in the morphological matrix.
B	Embryos spathuliform (ch. 37:0)*; cotyledons foliaceous (leaf-like) (ch. 38:1)*; and cotyledons more or less divaricate (ch. 39:0)*.
C	Druplets with remnant of style/stigma subbasal to basal (ch. 25:2)*; laterally compressed endocarps (ch. 28:0)*; strap-like embryos (ch. 37:1)*. Hemianatropous ovules, curved endocarps (seeds and embryos), and adpressed cotyledons (i.e., not divaricate), are ancestral character states in the family and are predominantly retained in this clade (not shown).
D	Flowers with three whorls of sepals (ch. 6:2)*; flowers lacking petals (ch. 9:0)*; all filaments (at least partially) fused (ch. 14:1)*; druplets with remnant of style/stigma subapical-adaxial (ch. 25:1)*; **endocarps and seeds subglobose—i.e., not compressed—ch. 27:0).**
E	Anatropous ovules (ch. 23:0); endocarps and seeds straight (ch. 26:0)*; **endocarps (and seeds) abaxially-adaxially (i.e., dorsiventrally) flattened (ch. 28:1);** naviculiform seeds (ch. 33:0)*. Druplets with remnant of style/stigma apical is the plesiomorphic condition in the family and is predominantly retained in this clade (not shown).
F	Stamens more than six (ch. 13:3); endocarps longitudinally and transversally ridged (ch. 30:2)*; seeds semiannular-crescentic (ch. 33:2)*.
G	Hippocrepiform seeds (and embryos) (ch. 33:5)*; strap-like embryos (ch. 37:1)*; cotyledons shorter than radicle (ch. 40:0)*.
H	**Endocarps with a raised abaxial longitudinal band** and the lateral sides weakly convex with large external apertures. These features were observed only in the Limacieae and hence not included in the morphological matrix.
I	Male flowers with four or more whorls of sepals (ch. 6:3)*; endocarps longitudinally grooved, ribbed or rugose abaxially (e.g., dorsally) (ch. 30:0)*; seeds hippocrepiform (ch. 33:5)*; seeds without endosperm (ch. 34:0)*; embryos subcylindric (ch. 37:2)*.
J	Anthers with longitudinal or transverse dehiscence (ch. 17:0,1)*; seeds without endosperm (present in *Cocculus* DC.) (ch. 34:0,1)*; embryos subcylindric (strap-like in *Cocculus*) (37:1,2)*.
K	Climbers or trees (ch. 1:0,1)*; six or more carpels (ch. 20:2,3)*; seeds cochleate or spiral (ch. 33:4,7)*; embryos subcylindric (ch. 37:2)*; cotyledons laterally adpressed (ch. 39:2)*.
L	Male flowers with one whorl of petals (ch. 10:0)*; presence of synandria (ch. 15:2)*, anthers arranged horizontally on a peltiform connective (ch. 16:1)*; anthers transversally dehiscing (ch. 17:1)*; **Female flowers with a single carpel (ch. 20:0);** embryo strap-like (ch. 37:1)*; cotyledons shorter than radicle (ch. 40:0)*.

Character states in bold are likely synapomorphies; asterisks (*) denote diagnostic character states that are subsequently reversed and/or evolved in parallel in taxa which are not closely related.

Orthomene Barneby & Krukoff and *Pycnarrhena* Miers ex Hook.f. & Thomson, have drupelets with apical and subapical-adaxial stylar scars; both are derived within the Menispermoideae (Fig. 4).

In our study, with a significantly increased taxonomic sampling, our results corroborate the finding of Wang & al. (2012) and to some extent the findings of Wefferling & al. (2013) but differ from those of Hoot & al. (2009) and Jacques & al. (2011). In particular, we recovered nine major clades of which two are in the Chasmantheroideae and seven are in the Menispermoideae.

Major clades in Chasmantheroideae. — The two clades recovered in this study confirm earlier findings (Ortiz & al., 2007; Hoot & al., 2009; Jacques & al., 2011; Wang & al., 2012; Wefferling & al., 2013). Support for the Coscinieae is strong in the combined molecular (PP = 1.0; ML-BS = 100%; MP-BS = 100%; Fig. 4), and in the total-evidence analyses (PP = 1.0; MP-BS = 100%; Fig. 5). Clade content of the Coscinieae recovered here is in agreement with that of Jacques & al. (2011) and Wang & al. (2012), and is the same as Diels's Coscinieae (as Anamirteae in Diels, 1910), namely *Anamirta* Colebr., *Arcangelisia* Becc., and *Coscinium* Colebr. Taxa in the Coscinieae share flowers with three whorls of sepals (ch. 6:2), flowers that lack petals (ch. 9:0), stamens with all filaments (at least partially) connate (ch. 14:1), drupelets with subapical-adaxial stylar scar (sublateral, lateral, ventral, sensu Forman, 1986; ch. 25:1), and subglobose endocarps (i.e., endocarps not compressed; ch. 27:0) (Fig. 6, clade D; Table 3). Flowers lacking petals are however, also found in other, not closely related taxa such as *Abuta* Aubl. of the Anomospermeae and a few others in the Burasaieae. *Coscinium* and *Arcangelisia* are each strongly supported as monophyletic. The monotypic *Anamirta* is sister to *Arcangelisia* with strong support in all analyses, both genera share a number of characters (not shown), such as male flowers with numerous stamens (ch. 13:3), fully fused filaments (i.e., they have a synandrium, ch. 15:1) with anthers that are horizontally arranged and together form a subglobose head (Fig. 1G–J), and anthers with transverse dehiscence (ch. 17:1). *Anamirta* and *Arcangelisia* also share tricolporate pollen, where the "ectoapertures are sunken colpi covered with a granular membrane" (Ferguson, 1978). Subhemispherical or subglobose seeds (Forman, 1986) (Fig. 3D) are shared by *Coscinium* and *Anamirta*; mature seeds were not observed in *Arcangelisia*. The subglobose endocarp and subglobose seeds, although coded here as independent characters, show the same distribution, hence they are linked. The three genera in this clade have embryos with thin, foliaceous, and divaricate cotyledons. The cotyledons are irregularly folded in *Arcangelisia* as originally reported by Beccari (1877), but those of *Coscinium* do not conform to earlier reports of being "sinuate-laciniate" (e.g., Miers, 1864; Forman, 1986), but are instead ovate-elliptic and divaricate.

A strongly supported Burasaieae is recovered here (Figs. 4, 5). Our results agree with previous studies (Ortiz & al., 2007; Hoot & al., 2009; Jacques & al., 2011; Wang & al., 2012; Wefferling & al., 2013) by extending the former Tinosporeae to include *Fibraurea* Lour., *Burasaia* Thouars, and *Tinomiscium* of Fibraureae (sensu Diels, 1910), and *Penianthus* and *Sphenocentrum* of Penianthеae (sensu Diels, 1910). By including 12 additional species belonging in this clade, including several species of *Tinospora* that span its broad geographic distribution, we confirmed in this study the polyphyly of this genus (Figs. 4, 5). The Australian *Tinospora smilacina* Benth., and the Asian *T. sinensis* (Lour.) Merr. are sister taxa, while the African *T. caffra* is found as sister to *Leptoterantha* Louis ex Troupin, and the Malagasy *T.* aff. *uviforme* is recovered as sister to the African *Chasmanthera* Hochst. (Fig. 4).

Both *Tinospora caffra* and *T. uviforme* have had a long history of taxonomic instability (Troupin, 1962). The two were originally described in different genera, *T. caffra* in *Desmonema* Miers (non Raf.) (Miers, 1867) and *T. uviforme* in *Chasmanthera* (Baillon, 1885). They were placed by Troupin (1949) in his *Hyalosepalum* Troupin, which he later reduced to synonymy under *Tinospora* (Troupin, 1962). Our results thus represent the first insight into the relationships of this large and broadly distributed genus, hence provide a strong background for studies to further address the relationships and the taxonomy of *Tinospora* and allied genera (Wang & al., unpub.).

Most other species-rich genera in the Burasaieae, with two or more species included in our study, are monophyletic (Figs. 4, 5). For example, species of *Odontocarya* Miers, the largest and most widespread neotropical genus, are resolved in a well-supported clade. Our results differ from those of Ortiz & al. (2007) who questioned the monophyly of the genus, because they found *Borismene* Barneby nested within it. This position of *Borismene* was likely due to mixed samples, as analyses using different samples did not recover this placement of *Borismene* (Ortiz-Gentry, 2010). *Disciphania* Eichler, the other strictly neotropical, large genus in the Burasaieae is strongly supported as monophyletic (Figs. 4, 5). The status and affinities of *Penianthus* are still unclear, as the species sampled here (e.g., *P. longifolius* Miers and *P. patulinervis* Hutch. & Dalz.) are not recovered as sister taxa, although support for an alternate relationship is low (Fig. 4).

Burasaieae are morphologically characterized by the anatropous ovules (ch. 23:0), straight endocarps (and seeds) (ch. 26:0) that are adaxially-abaxially flattened (i.e., concave-convex or boat-shaped) (ch. 28:1), and naviculiform seeds (ch. 33:0) (Fig. 3A–C; Fig. 6, clade E; Table 3). Of these features, the endocarp compression (ch. 28:1) and naviculiform seeds (ch. 33:0) show similar distributions when reconstructed (not shown) and therefore may not be independent, whereas drupelets with the apical remnant of the style/stigma, is a plesiomorphic condition for the family, and is retained in the Burasaieae. Other features, although not diagnostic, are relatively common in some members of the Burasaieae, such as the absence of petals (ch. 9:0) and fully fused filaments (ch. 15:2). The only other taxon with a fruit having an apical stylar scar is *Orthomene* of the Anomospermeae (see also Diels, 1910), but it has a cylindrical seed with an entirely ruminate endosperm. Other morphological features of Burasaieae include an inner ovary wall that differentiates into convex, *Calycocarpum*-type condyles (Ortiz, 2012). Those latter features may also be found in members of Coscinieae, at least in *Coscinium* and *Anamirta*, but we have not been able to study the development of the ovaries of those taxa.

Major clades in Menispermoideae. — Seven clades are recovered in the Menispermoideae, each with strong support in all analyses (Figs. 4, 5). Our results are in agreement with those found by Wang & al. (2012), but differ in clade content and clade support from those of Hoot & al. (2009), Jacques & al. (2011), and Wefferling & al. (2013).

The Menispermeae as sister to all other Menispermoideae have strong support in all analyses (Figs. 4, 5), and includes *Menispermum* L. and *Sinomenium* Diels. This placement agrees with previous studies (Ortiz & al., 2007; Ortiz-Gentry, 2010; Wang & al., 2012; Wefferling & al., 2013); but differs from those of Hoot & al. (2009) and Jacques & al. (2011), where Menispermeae were found as sister to all other Menispermaceae. Morphologically, Menispermeae are diagnosed by a combination of features such as male flowers with many stamens (ch. 13:3), endocarps longitudinally and transversally ridged abaxially (ch. 30:2), and the characteristic crescentic moon-shaped seeds (ch. 33:2) (Fig. 3E; Fig. 6, clade F; Table 3). Crescentic moon-shaped seeds are also present in *Sarcopetalum* F.Muell., *Pericampylus* Miers, *Legnephora* Miers, of the Anomospermeae (Figs. 4, 5) and is scattered in a few representatives of the Cissampelideae clade. However, in embryos of these other genera the cotyledons are shorter than the radicle. An additional morphological feature of the Menispermeae is the characteristic unequal development of the middle zone of the adaxial (ventral) ovary wall (Ortiz, 2012), and as a result the endocarp is somewhat angled adaxially (Jacques, 2009b; Jacques & Zhou, 2010; Ortiz, 2012). The latter feature is also observed in *Pericampylus glaucus* (Lam.) Merr. and to some extent in *Sarcopetalum harveyanum* F.Muell., both in the Anomospermeae.

The Anomospermeae are recovered with strong support (Figs. 4, 5). Our results agree with those found by Wang & al. (2012), and confirm the placement of species of *Diploclisia* as sister to the remaining Anomospermeae, with strong support in all analyses (Figs. 4, 5). When *Diploclisia glaucescens* (Blume) Diels was the only species sampled in the genus, it was recovered as sister to the remaining Menispermoideae (Hoot & al., 2009; Jacques & al., 2011; Wefferling & al., 2013), rather than sister to the rest of Anomospermeae.

The Anomospermeae comprise all genera included by Diels (1910) in his Anomospermeae as well as some of the taxa formerly included in his Menispermeae such as *Legnephora*, *Hypserpa* Miers, *Sarcopertalum*, *Pericampylus*, *Diploclisia*, and *Parapachygone* Forman (Figs. 4, 5). *Parapachygone* is a recently described, monospecific genus that was segregated from *Pachygone*, and has lanceolate to oblong, penninerved leaves, staminate flowers with about 20 stamens, and female flowers lacking staminodes; *Pachygone* s.str., here included in Pachygoneae, has ovate, palmatinerved leaves, staminate flowers with six stamens, and female flowers with six staminodes (Forman, 2007).

Within Anomospermeae, the monophyly of *Diploclisia*, *Hypserpa*, *Telitoxicum* Moldenke, and *Abuta* is well-supported (Figs. 4, 5). Of the neotropical Anomospermeae, neither *Anomospermum* Miers nor *Orthomene* as currently circumscribed are monophyletic, confirming earlier findings (Ortiz & al., 2007; Ortiz-Gentry, 2010; Jacques & al., 2011; Wang & al., 2012). Species of *Anomospermum* sect. *Elissarrhena* (Miers) Barneby & Krukoff (e.g., *A. bolivianum* Krukoff & Moldenke, *A. grandifolium* Eichler, and *A. solimoesanum* (Moldenke) Krukoff & Barneby) are scattered across the Anomospermeae clade, whereas species of *Anomospermum* sect. *Anomospermum* (e.g., *A. reticulatum* subsp. *idroboi* Krukoff & Barneby and *A. chloranthum* Diels, s.l.) are placed in a clade that also includes species of *Orthomene*, a segregate from *Anomospermum* (Barneby & Krukoff, 1971), with strong support (Figs. 4, 5). Species in this latter clade share strongly fleshy petals and a "bony" endocarp texture. The other well-supported group includes two of the three species from sect. *Elissarrhena*, *A. grandifolium* and *A. solimoesanum*. *Anomospermum bolivianum*, the only other member of sect. *Elissarrhena*, is recovered as sister to the *Abuta* clade, with strong support in all analyses (Figs. 4, 5). A comprehensive taxon sampling of both *Anomospermum* and *Orthomene*, is needed to address the taxonomy of these large, canopy lianas.

With the inclusion of some members of former Menispermeae, the newly circumscribed Anomospermeae are rather morphologically heterogeneous, and difficult to diagnose. However, hippocrepiform seeds (and embryos) (ch. 33:5) in combination with strap-like embryos (ch. 37:1) may distinguish the clade. Cotyledons shorter than the radicle (ch. 40:0) are found in the early branching members (though we did not observe seeds of *Parapachygone*); such shorter cotyledons are also present in the Cissampelideae, though in different combinations. The neotropical members, which are derived within the Anomospermeae, all share seeds with entirely ruminate endosperm, and embryos with cotyledons longer than the radicle (Fig. 6, clade G; Table 3).

The Limacieae lineage, represented here by *Limacia*, an Indomalesian genus, is recovered as sister to a large clade that contains remaining Menispermoideae (our Tiliacoreae, Pachygoneae, Spirospermeae, and Cissampelideae) (Figs. 4, 5), and agrees with earlier molecular studies (Ortiz & al., 2007; Hoot & al., 2009; Jacques & al., 2011; Wang & al., 2012; Wefferling & al., 2013). Morphological features for Limacieae include endocarp with a raised longitudinal band along the abaxial side (dorsal, sensu Forman, 1986), and lateral sides that are weakly convex and have large external apertures (Ortiz-Gentry, 2010) (Fig. 6, clade H). This character was only observed in the Limacieae and we have not included it in the morphological matrix. No fertile material for the Limacieae was available in this study, hence floral and fruit characters were not evaluated.

Tiliacoreae, with a significantly increased taxon sampling, are recovered in this study, with strong support in all analyses (Fig. 4), and corroborate previous findings (Ortiz & al., 2007; Wang & al., 2012). The Tiliacoreae were also recovered in the studies of Hoot & al. (2009), Jacques & al. (2011) and of Wefferling & al. (2013), but had weak support and a reduced taxon sampling. Relationships of Tiliacoreae with remaining Menispermoideae are still uncertain, it is here recovered either as sister to (Pachygoneae+(Spirospermeae+Cissampelideae)) in the combined molecular (Fig. 4), or as sister to the Pachygoneae in the total-evidence dataset (Fig. 5), both placements are weakly supported. However the Tiliacoreae recovered here are more densely sampled than in previous studies and are well-supported, hence we recognize a more inclusive Tiliacoreae than that included in the "Expanded Tiliacoreae" of Hoot & al. (2009), Jacques & al. (2011), and Wefferling & al. (2013). After the exclusion of *Haematocarpus* Miers (here placed in the Pachygoneae), the Tiliacoreae recovered in this study essentially consist of Diels's (1910) Tiliacoreae. Within Tiliacoreae, the neotropical taxa, namely *Chondrodendron* Ruiz & Pav., *Curarea*, and *Sciadotenia* Miers, form a well-supported clade (Figs. 4, 5), whereas the clade consisting of Australian, Asian, African, and Malagasy taxa has low support (Fig. 4). There is no support for this latter clade in the total-evidence analysis (Fig. 5). All genera represented by more than one species in this clade (i.e., *Albertisia* Becc., *Chondrodendron*, *Curarea*, *Pycnarrhena*, *Sciadotenia*, *Tiliacora* Colebr., *Triclisia* Benth.), are recovered as monophyletic (Fig. 4). Our study also recovered the monotypic *Beirnaertia* Louis ex Troupin as sister to (*Triclisia*+(*Tiliacora*+(*Anisocycla*+*Albertisia*))) clade. This placement of *Beirnaertia* has moderate to strong support and agrees with the results of Wang & al. (2012). In the study of Jacques & al. (2011), *Beirnaertia* is found unresolved within their Tiliacoreae, whereas in Wefferling & al. (2013) it is recovered as sister to *Albertisia*. Morphologically, *Beirnaertia* is set apart from remaining Old World Tiliacoreae in having male flowers with three free stamens and broad and fleshy filaments (Troupin, 1962), and a large, laterally flattened endocarp that is conspicuously ribbed (Troupin, 1962; Thanikaimoni & al., 1984).

Tiliacoreae are distinguished by a combination of features such as the male flowers with four or more whorls of sepals (ch. 6:3), endocarps longitudinally grooved, ribbed or rugose abaxially (ch. 30:0; Fig. 2C, D), seeds hippocrepiform (reniform in *Pycnarrhena*) (ch. 33:5), seeds lacking endosperm (ch. 34:0), and embryos subcylindric (ch. 37:2) (Fig. 6, clade I; Table 3). Most members of the Tiliacoreae lack endosperm, but it is present in *Tiliacora* where it is secondarily derived. Noticeable fleshy cotyledons are found in all members of Tiliacoreae, as expected in seeds lacking endosperm where the cotyledons serve as the sole food storage organ. Other features that are common in the clade, although not diagnostic, include anthers with transverse dehiscence (ch. 17:1) and cotyledons laterally adpressed (ch. 39:2). Moreover, carpel number shows a complex pattern of variation in the tribe, ranging from three to six or more than six (ch. 20:1,2,3) in *Tiliacora* (not shown). Our study also recovers a well-supported Pachygoneae (Figs. 4, 5). Included in the Pachygoneae are *Haematocarpus*, *Hyperbaena* Miers ex Benth., *Pachygone*, and *Cocculus* DC., in agreement with the results of Wang & al. (2012) and Wefferling & al. (2013). In the study of Jacques & al. (2011), Pachygoneae (their Clade C) were weakly supported and differed in clade content (e.g., *Rhaptonema*+*Strychnopsis*, of our Spirospermeae are found unresolved within their Clade C). Among Pachygoneae genera with more than one species sampled in our study, *Cocculus* is not monophyletic (Figs. 4, 5), as found in earlier studies (Ortiz & al., 2007; Wang & al., 2012). *Cocculus carolinus* (L.) DC. and *C. orbiculatus* (L.) DC. are recovered as sister taxa, with low support in the combined molecular analysis (Fig. 4), but strongly supported in the total-evidence analysis (Fig. 5); they both share female flowers with six carpels. A second accession of presumably conspecific *Cocculus orbiculatus*, also with six carpels, and *C. laurifolius* DC., which has three carpels, are found associated with species of *Pachygone* (Figs. 4, 5). The two accessions of *C. orbiculatus* are not recovered as sister taxa (Figs. 4, 5), suggesting that they are not conspecific, and therefore the name *C. trilobus* may need to be reinstated. Our results therefore highlight the need for detailed studies to clarify the taxonomy of *Cocculus* species, and also show that *Cocculus* and *Pachygone* are similar in their floral structures as well as in their endocarp and condyles, as noted by Miers (1871). Thus, future studies addressing relationships between those two genera should consider a greater taxonomic and character sampling. Although Pachygoneae and Tiliacoreae are recovered as independent clades, each with strong support, relationships between them and the remaining Menispermoideae remain uncertain (see discussion above). With the exception of *Cocculus*, which has continuous endosperm, Pachygoneae members are morphologically similar to Tiliacoreae in that they lack endosperm (ch. 34:0), and most members have subcylindric embryos (ch. 37:2), but these are strap-like in *Cocculus* (37:1) (Fig. 6, clade J; Table 3). Anthers with transverse dehiscence (ch. 17:1) are shared by *Cocculus* and *Pachygone*, anthers with vertical dehiscence are found in early-diverging *Hamaetocarpus* and in *Hyperbaena* (ch. 17:0). Moreover, although carpel numbers are variable, three carpels are common in the Pachygoneae.

Spirospermeae are strongly supported in all analyses (Figs. 4, 5), and include the Malagasy *Rhaptonema* Miers, *Strychnopsis* Baill., and *Spirospermum* Thouars, in agreement with the results of Wang & al. (2012). Their placement as sister to the Cissampelideae is also well-supported (Figs. 4, 5). In the study of Jacques & al. (2011), the *Strychnopsis*+*Rhaptonema* clade was found nested within an unresolved Tiliacoreae. Whereas Wefferling & al. (2013) found *Strychnopsis*—the only species of our Spirospermeae sampled in their study—as sister to eight taxa here included in our Tiliacoreae (Figs. 4, 5). Morphologically, Spirospermeae are rather variable for the characters evaluated, hence difficult to diagnose. Nevertheless the combination of the tree habit (ch. 1:1), six or more carpels (ch. 20:2,3), cochleate or spiral seeds (ch. 33:4,7) together with subcylindric embryos (ch. 37:2), and cotyledons laterally adpressed (ch. 39:2) (Fig. 6, clade K; Table 3) are found only in the Spirospermeae. Within the tribe, *Spirospermum* and *Strychnopsis* share the tree habit and also spiral seeds, whereas the climbing habit (ch. 1:0), the ancestral condition for the family, as inferred by our character state reconstruction (not shown), is retained in *Rhaptonema*, which also has cochleate seeds. The latter feature is also found in *Sciadotenia toxifera* Krukoff & A.C.Sm., *Perichasma* Miers, and some species of *Cocculus*, none immediately related to Spirospermeae, and also in the monospecific *Limaciopsis* Engl., an unplaced African taxon not yet sampled in any molecular study. Seeds of *Rhaptonema* have scanty endosperm, which is completely absent in S*ciadotenia toxifera*, scarce in *Limaciopsis* and abundant in *Perichasma*, and *Cocculus*. Other features that may distinguish the Spirospermeae, but not included in the morphological matrix, are male inflorescences arranged in cymules and stipitate drupelets.

With an increased sampling, Cissampelideae, including *Antizoma*, *Cissampelos*, *Cyclea* Arn. ex Wight, *Perichasma*, and *Stephania* Lour., are recovered in this study with strong support (Figs. 4, 5). Our results agree, in part, with those found in earlier studies (Ortiz & al., 2007; Hoot & al., 2009; Jacques & al., 2011; Wang & al., 2012; Wefferling & al., 2013). Within the Cissampelideae, *Stephania* is recovered as monophyletic and splits into two clades, confirming results from earlier studies (Hong & al., 2001; Wang & al., 2012). Morphologically, *Stephania* is characterized by its male flowers with two whorls and free perianth parts (Meng & al., 2012). The affinities of *Perichasma* are still uncertain, it is recovered as sister to remaining Cissampelideae (*Cissampelos capensis*+(*Antizoma*+(*Cissampelos*+*Cyclea*))). But, in the study of Wang & al. (2012), *Perichasma* is recovered as sister to *Stephania*, with low to moderate support. *Perichasma* was described by Miers (1866, 1871), who distinguished it from *Stephania* by its compound, racemose male inflorescence (vs. a compound umbel), and by its anthers lacking connectives and dehiscing with an apical operculum. Later authors included it in *Stephania* (Bentham & Hooker, 1867; Diels, 1910; Troupin, 1962). At present, however, *Perichasma* is recognized as distinct from *Stephania* (Kundu & Guha, 1977), mainly on the basis of the absence of a connective and the opercular dehiscence of the anthers (vs. transversal in *Stephania*). Although relationships of *Perichasma* in our study are still unresolved, it is likely that its affinities are with *Stephania*, with which it also shares triporate pollen (vs. tricolporate in *Cissampelos* and *Cyclea*; Harley & Ferguson, 1982).

Cissampelos on the other hand, is paraphyletic, with *Antizoma* and *Cyclea* nested in it (Figs. 4, 5). We confirm the placement of *Cissampelos capensis* as sister to (*Antizoma*+(*Cissampelos*+*Cyclea*)), as found in the study of Jacques & al. (2011). The taxonomic affinities of *C. capensis* have been historically uncertain; at present it is included in *Cissampelos* (Botha, 1980), but was placed in *Antizoma* (Diels, 1910), based on its two sepals and two petals in the female flowers, as compared with only one (rarely two) in *Cissampelos*. Perianth number is variable in *C. capensis*, especially in female plants where we find 2–4 petals in different degrees of fusion, and most commonly these are located lateral, rather than opposite to the adaxial suture of the carpel as in *Cissampelos* sensu str., as noted by Ortiz & Nee (2014). *Cyclea* is recovered as monophyletic in this study with strong support (Figs. 4, 5). Our results also indicate that *Cissampelos madagascariensis* does not group with the remainder of *Cissampelos* (Figs. 4, 5), which is a novel finding in this study. The three accessions of the little-known *C. madagascariensis* form a clade that is recovered as sister to *Cyclea*, with moderate support (Figs. 4, 5). The species was originally described in *Cyclea* by Baillon (1885), and was placed in *Cissampelos* by Diels (1910), likely on the basis of its large inflorescence bracts and its free sepals as compared with the usually inconspicuous inflorescence bracts and the fused sepals observed in *Cyclea*. The exclusion of both *Cissampelos capensis* and *C. madagascariensis* would render *Cissampelos* monophyletic. Likewise, *Antizoma* is monophyletic if *C. capensis* is not included in it, as indicated in previous studies (Jacques & al., 2011). The two *Antizoma* species sampled here form a strongly supported clade that is sister to the *Cissampelos*+*Cyclea* clade (Figs. 4, 5).

Hence, the most satisfactory taxonomic solutions are: to recognize *Cissampelos capensis* as a new genus, different from *Cissampelos* and from *Antizoma*; and to exclude *C. madagascariensis* from *Cissampelos* and to include it in *Cyclea* (Ortiz & al., in prep.). Morphologically, *C. madagascariensis* resembles *Cyclea* by the female flowers with two sepals and two petals that are located on each side of the adaxial suture of the carpel, rather than opposite to it, and by the male flowers with the synandrium conspicuously exerted.

Additionally, within *Cissampelos*, the several accessions from different geographical regions of *C. pareira* do not group together. They are found associated with other *Cissampelos* species within the clade (Figs. 4, 5). Earlier molecular studies suggested the lack of monophyly in *Cissampelos pareira*, although support was lacking (Hoot & al., 2009), and a similar conclusion was reached from a specimen-based floristic study of Mesoamerican Menispermaceae (Ortiz, unpub.). As the species has a pantropical distribution, an extensive sampling across its geographic range is needed to address the taxonomy of this medicinally important species.

Morphologically, the Cissampelideae are distinguished by the male flowers with a single whorl of petals (ch. 10:0), stamens with fully fused filaments (synandrium) (ch. 15:2), anthers arranged horizontally on a peltiform connective (ch. 16:1; Fig. 1D), anthers dehiscing transversally (ch. 17:1), single carpel in the female flower (ch. 20:0), embryo strap-like (ch. 37:1), and cotyledons shorter than radicle (ch. 40:0) (Fig. 6, clade L; Table 3).

Within Cissampelideae, many taxa, i.e., the clade made up by *Antizoma*, *Cissampelos*, and *Cyclea*, share male flowers with a single whorl of sepals (ch. 6:0), with four sepals per whorl (ch. 7:2), one petal (ch. 11:0), four stamens (ch. 13:1), and female flowers with one or two sepals (ch. 18:0,1). Most of these characters (not included in Fig. 6) show a similar distribution in our optimization suggesting that these changes may be linked.

Taxonomy and classification. — Based on the results of our combined molecular and total-evidence analyses, as well as building on results of previous studies, a revised infrafamilial classification for the family Menispermaceae is proposed. Our study includes the most extensive taxon sampling so far and the data used are from fast-evolving plastid regions that have been demonstrated to be useful in elucidating relationships at higher taxonomic levels (Löhne & al., 2007; Harbaugh & al., 2010; Morrone & al., 2012). Thus, we predict that the topology presented here, hence the boundaries of the tribes recognized, will not be drastically altered in future studies.

We formally recognize two subfamilies and nine tribes; these are diagnosed by unique combinations of mostly homoplastic morphological characters (Table 3). There is some degree of congruence between the lineages identified by the molecular analyses and the tribal delimitations of earlier authors, particularly those of Diels (1910). For instance, the Coscinieae, first established by Diels (1910), is monophyletic and is here accepted as originally circumscribed. Other tribes such as his Anomospermeae and Hyperbaeneae are in need of re-circumscriptions. His Hyperbaeneae are expanded to include *Cocculus*, *Pachygone*, and *Haematocarpus*, the latter having been removed from Tiliacoreae. The inclusion of *Pachygone* in Hyperbaeneae results in the tribal name being changed to Pachygoneae following the principles of nomenclature. Also noteworthy is the incorporation of *Legnephora*, *Hypserpa*, *Sarcopetalum*, *Parapachygone*, *Pericampylus*, and *Diploclisia*, formerly in Menispermeae, into our newly circumscribed Anomospermeae. We merge Fibraureae, Penianthеae, and Tinosporeae into Burasaieae. This tribal name was first used by Endlicher (1850) and comprised only *Burasaia*, which was then placed in Lardizabalaceae.

In Kessler's (1993) classification Penianthеae were included in his Pachygoneae, a placement not supported in this study. The inclusion of Fibraureae in Tinosporeae (i.e., Burasaieae in this study) has been suggested by earlier workers (e.g., Barneby, 1972; Forman, 1986); other rearrangements, such as the inclusion of Penianthеae in Tinosporeae (Burasaieae), have only recently been suggested (Ortiz & al., 2007). Similarly, our results also confirmed a close relationships of *Rhaptonema*, *Spirospermum*, and *Strychnopsis*, as found by Wang & al. (2012). Due to lack of resolution (e.g., Jacques & al., 2011) or insufficient sampling (e.g., Wefferling & al., 2013) this clade was not recovered in previous studies. These genera were all formerly placed in Menispermeae (Diels, 1910; Kessler, 1993) and are here recognized in Spirospermeae. In sum, three tribal names previously proposed by earlier workers in the family are here newly circumscribed and resurrected: Pachygoneae, which replaces the later name Hyperbaeneae, Cissampelideae was used by Hooker & Thomson (1855), and Limacieae was used by Prantl (1888). The name Spirospermeae is here proposed as new.

We were unable to obtain samples of nine monospecific genera. Based on the evaluation of the morphology of representatives of those genera, they were assigned to tribes here recognized. *Eleutharrhena* Forman, *Macrococculus* Becc., *Pleogyne* Miers, and *Synclisia* Benth., are assigned to Tiliacoreae based on their lack of endosperm and thick and hippocrepiform seeds. The fruit and seed of monotypic *Ungulipetalum* Moldenke are at present unknown but the genus is here considered to belong to Tiliacoreae on the basis of its 4-whorled perianth in staminate flowers, the inner whorl being valvate. Barneby & Krukoff (1971) noted that *Ungulipetalum* resembles *Sciadotenia* (Tiliacoreae), and suggested that these two might even be congeneric. *Chlaenandra* Miq. and *Platytinospora* (Engl.) Diels, with one species each, are placed in the Burasaieae, they both share fruits that have an apical stylar remnant, foliaceous and divaricate cotyledons, and an adaxially ruminate endosperm. *Echinostephia* (Diels) Domin is here placed in Anomospermeae, as it shares the semiannular-crescentic endocarp (and seed) with *Sarcopetalum* and *Legnephora* and three stamens with *Sarcopetalum* (Wang & al., 2012). In addition, a BLAST search against NCBI, indicates that the two DNA barcoding sequences of *Echinostephia*, *rbcL* (GenBank accession No. KM895873) and *trnH-psbA* (GenBank accession No. KM895232), are very similar to those of *Sarcopetalum*. *Limaciopsis* is characterized by having seeds with scanty endosperm and a cochleate embryo/seed with subcylindric cotyledons (Troupin, 1962; Ortiz-Gentry, 2010). The cochleate embryo/seed and the scanty and continuous endosperm are similar to known Spirospermeae. Although the endosperm of *Limaciopsis* and that of *Spirospermum* were described as being ruminate (Troupin, 1962; Kessler, 1993), our observations indicate that the endosperm of both taxa is both scanty and not ruminate. We therefore suggest that the affinities of *Limaciopsis* might be with the Spirospermeae, as did Wang & al. (2012) on the basis of its large drupelets and its spiral seeds. Of the remaining genera listed in Kessler (1993), the type of *Synandropus* A.C.Sm. was found to be a mixed collection that includes euphorbiaceous leaves and a staminate inflorescence of *Odontocarya*, and was therefore reduced it to synonymy of *Odontocarya* sect. *Somphoxylon* (Ortiz, 2011). *Cionomene* Krukoff is a synonym of *Elephantoneme* Barneby & Krukoff (Barneby, 1993), *Leichardtia* F.Muell. is placed in Euphorbiaceae (Diels, 1931), whereas *Juppia* Merr. is in the Cucurbitaceae (Lu & al., 2011).

A revised tribal classification of Menispermaceae. — The two major clades correspond to the two subfamilies: Chasmantheroideae and Menispermoideae. Within each, there are two and seven clades, respectively, corresponding to the nine recognized tribes. Whereas subtribe Cocculinae of Diels's (1910) Menispermeae is polyphyletic, the affinities of subtribes Cissampelinae and Stephaniinae are still uncertain, and thus, rendering their formal classification as subtribes premature at this stage.

Menispermaceae Juss., Gen. Pl.: 284. 1789, nom. cons. – Type: *Menispermum* L.

Distinguishing morphological features for the family include: dioecy; male—and female—flowers with sepals arranged in two whorls, three sepals per whorl; petals in male—and female—flowers present, arranged in two whorls, both with three free petals per whorl, male flowers with six, free stamens, anthers with vertical dehiscence, female flowers with three, free carpels, two ovules per carpel, the ovules hemianatropous; drupelets with apical stylar scar; endocarps—seeds and embryos—curved, endocarps compressed, surface ornamented, presence of a condyle, presence of endosperm, large embryos, fleshy and adpressed cotyledons, and cotyledons longer than radicle (Fig. 6, clade A; Table 3). Although initially two ovules are present in the carpel, only one reaches maturity. The family is distributed mostly in the tropics of the world. Of the nine tribes recognized here, members of the Coscinieae are all found in the Indomalesian region, and confirmed members of Spirospermeae are all found in Madagascar (Electr. Suppl.: Fig S2). All other tribes include species from different floristic regions of the world. Within these tribes, the neotropical members are all found embedded within eastern Asian, Indomalesian, and African and Malagasy assemblages (Electr. Suppl.: Fig. S2).

Subfam. **Chasmantheroideae** Luerss., Handb. Syst. Bot. 2: 574. 1880 (“Chasmanthereae”) – Type: *Chasmanthera* Hochst.
= Tinosporoideae Wei Wang & Z.D.Chen in Perspect. Pl. Ecol. Evol. Syst. 11: 100. 2009 – Type: *Tinospora* Miers.

Distinctive features of this subfamily include spathuliform embryos with foliaceous, more or less divaricate cotyledons (Fig. 6, clade B; Table 3).

I. Tr. **Coscinieae** Hook.f. & Thomson, Fl. Ind.: 177. 1855 – Type: *Coscinium* Colebr.
= Anamirteae Diels in Engler, Pflanzenr. IV.94 (Heft 46): 103. 1910 – Type: *Anamirta* Colebr.

Distinctive features of Coscinieae are flowers with three whorls of sepals, petals absent, stamens with all the filaments (at least partially) fused, drupelets with the remnant of the style/stigma subapical-adaxial, and endocarps and seeds subglobose (i.e., not compressed) (Fig. 6, clade D; Table 3). Other common features in the tribe include male flowers with many stamens, anthers horizontally arranged together forming a subglobose head, and the anthers with transverse dehiscence.

Genera (3). – *Anamirta* Colebr. (1 sp.), *Arcangelisia* Becc. (3 spp.), and *Coscinium* Colebr. (2 spp.). Coscinieae comprise six species that are predominantly distributed in the Indomalesian region (Electr. Suppl.: Fig. S2).

II. Tr. **Burasaieae** Endl., Gen. Pl. Suppl. 5: 25. 1850 – Type: *Burasaia* Thouars.
= Tinosporeae Hook.f. & Thomson, Fl. Ind.: 179. 1855 – Type: *Tinospora* Miers.
= Chasmanthereae Baill., Hist. Pl. 3: 23, 38. 1871 – Type: *Chasmanthera* Hochst.
= Fibraureae Diels in Engler, Pflanzenr. IV.94 (Heft 46): 115. 1910 – Type: *Fibraurea* Lour.
= Penianthеae Diels in Engler, Pflanzenr. IV.94 (Heft 46): 184. 1910 – Type: *Penianthus* Miers.

Distinctive features of this tribe include anatropous ovules, endocarps (and seeds) straight, abaxially-adaxially-compressed (i.e., dorsiventrally flattened), and naviculiform seeds (Fig. 6, clade E; Table 3). Another feature predominantly found in this tribe includes drupelets with the remnant of the style/stigma apical.

Genera (24). – *Aspidocarya* Hook.f. & Thomson (1 sp.), *Borismene* Barneby (1 sp.), *Burasaia* Thouars (4 spp.), *Calycocarpum* (Nutt. ex Torr. & A.Gray) Spach (1 sp.), *Chasmanthera* Hochst. (2 spp.), ***Chlaenandra*** Miq. (1 sp.), *Dialytheca* Exell & Mendonça (1 sp.), *Dioscoreophyllum* Engl. (3 spp.), *Disciphania* Eichler (25 spp.), *Fibraurea* Lour. (2 spp.), *Jateorhiza* Miers (2 spp.), *Kolobopetalum* Engl. (4 spp.), *Leptoterantha* Louis ex Troupin (1 sp.), *Odontocarya* Miers (incl. *Synandropus* A.C.Sm.) (36 spp.), *Orthogynium* Baill. (1 sp.), *Parabaena* Miers (7 spp.), *Penianthus* Miers (4 spp.), ***Platytinospora*** (Engl.) Diels (1 sp.), *Rhigiocarya* Miers (2 spp.), *Sarcolophium* Troupin (1 sp.), *Sphenocentrum* Pierre (1 sp.), *Syntriandrium* Engl. (1 sp.), *Tinomiscium* Miers ex Hook.f. & Thomson (1 sp.), and *Tinospora* Miers (36 spp.).

Genera in bold face were not sampled in the molecular study. Burasaieae comprise 139 species that are widespread in their distribution. They are found in South and Central America, Indomalesia, Africa, Madagascar, and eastern Asia (Electr. Suppl.: Fig. S2).

Subfam. **Menispermoideae** Arn. in Wight & Arnott, Prodr. Fl. Ind. Orient.: 4. 1834 (“Menispermeae”) – Type: *Menispermum* L.
= Cocculoideae Kostel., Allg. Med.-Pharm. Fl.: 495. 1833 (“Cocculineae”) – Type: *Cocculus* DC.
= Cissampelidoideae Luerss., Handb. Syst. Bot. 2: 576. 1880 (“Cissampelideae”) – Type: *Cissampelos* L.
= Pachygonoideae Luerss., Handb. Syst. Bot. 2: 573. 1880 (“Pachygoneae”) – Type: *Pachygone* Miers.

A later isonym which has no nomenclatural standing (*ICN*, Art. 6) was proposed by Wang & Chen (Wang & al., 2009). The name Menispermoideae has priority at the subfamily rank and is here being used instead of the older Cocculoideae in accordance with article 19.4 of the *ICN*.

Distinctive features of this subfamily include drupelets with the remnant of the style/stigma subbasal to basal, laterally compressed endocarps, and strap-like embryos (Fig. 6, clade C; Table 3). Other features predominantly found in this tribe are hemianatropous ovules, endocarps (and seeds and embryos) curved (straight in *Orthomene*), and adpressed cotyledons (i.e., not divaricate).

III. Tr. **Menispermeae** DC., Syst. Nat. 1: 510–511. 1817 (“Menispermeae verae”) – Type: *Menispermum* L.

Distinctive features of this tribe include numerous free stamens, endocarps longitudinally and transversally ridged, semiannular-crescentic seeds (Fig. 6, clade F; Table 3), and cotyledons longer than the radicle.

Genera (2). – *Menispermum* L. (2 spp.) and *Sinomenium* Diels (1 sp.). The Menispermeae comprise three species that are distributed in North America, eastern Asia, and Indomalesia (Electr. Suppl.: Fig. S2).

IV. Tr. **Anomospermeae** Miers in Ann. Mag. Nat. Hist., ser. 2, 7: 36. 1851 – Type: *Anomospermum* Miers.
= Hypserpeae Miers in Ann. Mag. Nat. Hist., ser. 3, 13: 12. 1864 – Type: *Hypserpa* Miers.

Distinctive morphological features for this tribe are difficult to find, due to the inclusion of diverse taxa that were formerly in Menispermeae. However the hippocrepiform seeds (and embryos), in combination with strap-like embryos, and cotyledons shorter than the radicle (Fig. 6, clade G; Table 3), may distinguish the tribe. Within Anomospermeae, the neotropical members form a clade and are distinguished by a seed with endosperm that is entirely ruminate and embryos with cotyledons longer than the radicle; the paleotropical genera have continuous endosperm.

Genera (13). – *Abuta* Aubl. (31 spp.), *Anomospermum* Miers (8 spp.), *Caryomene* Barneby & Krukoff (5 spp.), *Diploclisia* Miers (2 spp.), ***Echinostephia*** (Diels) Domin (1 sp.), *Elephantomene* Barneby & Krukoff (1 sp.), *Hypserpa* Miers (10 spp.), *Legnephora* Miers (5 spp.), *Orthomene* Barneby & Krukoff (4 spp.), *Parapachygone* Forman (1 sp.), *Pericampylus*

Miers (3 spp.), *Sarcopetalum* F.Muell. (1 sp.), and *Telitoxicum* Moldenke (8 spp.).

The Anomospermeae comprise 80 species that are found in South and Central America, Indomalesia, New Caledonia, Australia, and in eastern Asia (Electr. Suppl.: Fig. S2).

V. Tr. **Limacieae** Prantl in Engler & Prantl, Nat. Pflanzenfam. 3(2): 88. 1888 – Type: *Limacia* Lour.

Distinctive features of this tribe include endocarp with a raised longitudinal band along the long axis, the lateral sides of the endocarp weakly convex and with large external apertures. These features are found only in the Limacieae and hence were not scored in the morphological matrix. Additionally, it should be noted that although the condyle was described as two-chambered and laterally perforated (Forman, 1986), it conforms to the bilaterally compressed general type of Ortiz (2012) (Fig. 6, clade H; Table 3).

Genus (1). – *Limacia* Lour. (3 spp.).

The Limacieae comprise three species that are distributed in Indomalesia (Electr. Suppl.: Fig. S2).

VI. Tr. **Tiliacoreae** Miers in Ann. Mag. Nat. Hist., ser. 2, 7: 36. 1851 – Type: *Tiliacora* Colebr.

= Triclisieae Diels in Engler, Pflanzenr. IV.94 (Heft 46): 47. 1910 – Type: *Triclisia* Benth.

Distinctive features of this tribe include male flowers often with a four or more whorled calyx, endocarps with longitudinal grooves, ribs or rugose ornamentation abaxially, seeds hippocrepiform, endosperm absent (present in some species of *Tiliacora*), embryos subcylindric (Fig. 6, clade I; Table 3). Additional observed characters that were not scored in the matrix include the cotyledons frequently unequal and broader than the small radicle.

Genera (16). – *Albertisia* Becc. (19 spp.), *Anisocycla* Baill. (6 spp.), *Beirnaertia* Louis ex Troupin (1 sp.), *Carronia* F.Muell. (4 spp.), *Chondrodendron* Ruiz & Pav. (3 spp.), *Curarea* Barneby & Krukoff (5 spp.), ***Eleutharrhena*** Forman (1 sp.), ***Macrococculus*** Becc. (1 sp.), ***Pleogyne*** Miers (1 sp.), *Pycnarrhena* Miers ex Hook.f. & Thomson (9 spp.), *Sciadotenia* Miers (19 spp.), ***Synclisia*** Benth. (1 sp.), *Syrrheonema* Miers (3 spp.), *Tiliacora* Colebr. (22 spp.), *Triclisia* Benth. (15 spp.), and ***Ungulipetalum*** Moldenke (1 sp.).

Tiliacoreae comprise 111 species that are distributed in South and Central America, Indomalesia, Africa, and Madagascar (Electr. Suppl.: Fig. S2).

VII. Tr. **Pachygoneae** Miers in Ann. Mag. Nat. Hist., ser. 2, 7: 37. 1851 – Type: *Pachygone* Miers.

= Cocculeae Hook.f. & Thomson, Fl. Ind.: 176, 186. 1855 – Type: *Cocculus* DC.

= Hyperbaeneae Diels in Engler, Pflanzenr. IV.94 (Heft 46): 197. 1910 – Type: *Hyperbaena* Miers.

Distinctive features: Similar to Tiliacoreae, seeds without endosperm (species of the polyphyletic *Cocculus* have seeds with endosperm), embryos subcylindric (strap-like in *Cocculus*), and transverse dehiscence (vertical in *Hamaetocarpus* and *Hyperbaena*) (Fig. 6, clade J; Table 3).

Genera (4). – *Cocculus* DC. (9 spp.), *Haematocarpus* Miers (2 spp.), *Hyperbaena* Miers ex Benth. (22 spp.), and *Pachygone* Miers (12 spp.).

Tribe Pachygoneae comprise 45 species in South and Central America, North America, eastern Asia, Indomalesia, Australia, and New Caledonia (Electr. Suppl.: Fig. S2).

VIII. Tr. **Spirospermeae** R.Ortiz & Wei Wang, **tr. nov.** – Type: *Spirospermum* Thouars.

Description. – Climbers or erect shrubs or trees. Leaves simple, spiral, pinnatinerved to palmatinerved, chartaceous to subcoriaceous, glabrous on both sides or densely pubescent adaxially. Male inflorescences supra-axillary or on old wood; thyrsoid to narrowly paniculiform (*Spirospermum*), glabrous to densely pubescent; flowers short-pedicellate, in cymules, sepals 4–9, free, in two whorls, elliptic to obovate, petals 4–6(7), obovate, lateral margins inflexed, stamens 3–6, filaments variously fused, anthers dehiscing longitudinally, pollen tricolpate, fossaperturate. Female inflorescences thyrsoid or fasciculate cymes (*Rhaptonema*, *Strychnopsis*), glabrous or pubescent; flowers with 6–9 sepals, ovate, petals (5)6–9, obovate to spathuliform, lateral margins inflexed, staminodes absent, carpels (5)6–9(–11), glabrous or densely pubescent. Drupelets suborbicular, stipitate to sessile, glabrous or densely pubescent, remnant of style subbasal to basal, laterally compressed, endocarps curved, suborbicular or cochleate in outline, chartaceous, longitudinally and transversally ridged or longitudinally ridged and reticulate condyle septiform, seed with scanty, continuous endosperm, cochleate to spiral; embryo subcylindric (broader and thicker in *Rhaptonema*), cotyledons fleshy, shorter or longer than radicle, laterally adpressed, (Fig. 6, clade K; Table 3).

Distinctive features. – Tree habit (climbers in *Rhaptonema*), three stamens, six or more carpels, seeds cochleate or spiral, and subcylindric embryos with the cotyledons laterally adpressed (Fig. 6, clade K; Table 3). Other features of the Spirospermeae, not coded in the morphological matrix include the male flowers arranged in cymules, and stipitate drupelets.

Genera (4). – ***Limaciopsis*** Engl. (1 sp.), *Spirospermum* Thouars (1 sp.), *Strychnopsis* Baill. (1 sp.), and *Rhaptonema* Miers (7 spp.).

The Spirospermeae comprise approximately 10 species. The three unambiguously placed genera in this tribe are endemic to Madagascar (Electr. Suppl.: Fig. S2); however, if *Limaciopsis*, which was not sampled, is confirmed to belong here, the geographic distribution of the tribe would then extend to west-central tropical Africa.

IX. Tr. **Cissampelideae** Hook.f. & Thomson, Fl. Ind.: 194. 1855 – Type: *Cissampelos* L.

Diagnostic features of this tribe include male flowers with a single whorl of petals, the presence of synandria, the anthers horizontally arranged on a peltiform connective, anthers dehiscing transversally, female flowers with a single carpel, embryos strap-like, and cotyledons shorter than the radicle (Fig. 6, clade L; Table 3). Other common features in several members of this tribe are male flowers with a single whorl of sepals, these with four sepals per whorl, a single petal per whorl, four stamens, and female flowers with one or two sepals.

Genera (5). – *Antizoma* Miers (3 spp.), *Cissampelos* L. (23 spp.), *Cyclea* Arn. ex Wight (32 spp.), *Perichasma* Miers (2 spp.), and *Stephania* Lour. (68 spp.).

Cissampelideae comprise 128 species that are distributed in South and Central America, North America (not shown), Indomalesia, eastern Asia, Africa, and Madagascar (Electr. Suppl.: Fig. S2).

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Appendix 1. Taxa used in this study.

Taxon, country, voucher, and herbarium code for the new sequences only. Accession numbers: *matK*, *trnL-F*, and *ndhF*, respectively. An asterisk (*) indicates newly generated sequences in this study, a dash (–) denotes missing data.

Abuta grandifolia (Mart.) Sandwith, Peru, *Ortiz & al. 221* (AMAZ, MO), KX384044*, KX384107*, EF624258[1]. ***Abuta panamensis*** (Standl.) Krukoff & Barneby, Costa Rica, *Kriebel 3496* (MO), KX384045*, KX384108*, KX384084*. ***Abuta rufescens*** Aubl., JN051804[3], JN051738[3], EF624259[1]. ***Abuta sandwithiana*** Krukoff & Barneby, Peru, *Ortiz & al. 305* (AMAZ, MO), KX384046*, KX384109*, EF624260[1]. ***Albertisia laurifolia*** Yamam., EF143849[2], EF143880[2], JN051700[3]. ***Albertisia porcata*** Breteler, Gabon, *McPherson 16678* (MO), KX384047*, KX384110*, EF624261[1]. ***Anamirta cocculus*** (L.) Wight & Arn., EF143856[2], EF143887[2], EF624262[1]. ***Anisocycla linearis*** Pierre ex Diels, JN051805[3], JN051739[3], EF624263[1]. ***Anomospermum bolivianum*** Krukoff & Moldenke, Peru, *Ortiz & al. 294* (MO), KX384048*, KX384111*, EF624264[1]. ***Anomospermum chloranthum*** Diels s.l., JN051806[3], JN051740[3], EF624265[1]. ***Anomospermum grandifolium*** Eichler, JN051807[3], JN051741[3], EF624266[1]. ***Anomospermum reticulatum*** subsp. ***idroboi*** Krukoff & Barneby, JN051808[3], JN051742[3], EF624267[1]. ***Anomospermum solimoesanum*** (Moldenke) Krukoff & Barneby, JN051809[3], JN051743[3], EF624268[1]. ***Antizoma angustifolia*** (Burch.) Miers ex Harv., South Africa, *Burgoyne & N. Snow 4711* (MO), KX384049*, KX384112*, KX384085*. ***Antizoma miersiana*** Harv., South Africa, *Venter 9618* (MO), KX384050*, KX384113*, KX384086*. ***Arcangelisia flava*** (L.) Merr., JN051810[3], JN051744[3], EF624269[1]. ***Arcangelisia gusanlung*** H.S.Lo, China, Hainan, *Hong YP 99406* (PE), EF143852[2], EF143883[2], KX384087*. ***Aspidocarya uvifera*** Hook.f. & Thomson, EF143853[2], EF143884[2], JN051701[3]. ***Beirnaertia cabindensis*** (Exell & Mendonça) Troupin, JN051811[3], JN051745[3], EF624270[1]. ***Borismene japurensis*** (Mart.) Barneby, JN051812[3], JN051746[3], JN051702[3]. ***Burasaia madagascariensis*** DC., JN051813[3], JN051747[3], EF624272[1]. ***Calycocarpum lyonii*** (Pursh) A.Gray, JN051814[3], JN051748[3], EF624273[1]. ***Carronia protensa*** (F.Muell.) Diels, JN051815[3], JN051749[3], EF624274[1]. ***Caryomene grandifolia*** Barneby & Krukoff, JN051816[3], JN051750[3], EF624275[1]. ***Chasmanthera welwitschii*** Troupin, JN051817[3], JN051751[3], EF624277[1]. ***Chondrodendron microphyllum*** (Eichler) Moldenke, Brazil, *Thomas & al. 11802* (MO), KX384051*, KX384114*, KX384088*. ***Chondrodendron tomentosum*** Ruiz & Pav., JN051818[3], JN051752[3], EF624278[1]. ***Cissampelos andromorpha*** DC., JN051819[3], JN051753[3], EF624279[1]. ***Cissampelos capensis*** L.f., South Africa, *R.T. Schuh & al. PBI-SA07-L03-H013* (MO), KX384055*, KX384115*, KX384089*. ***Cissampelos grandifolia*** Triana & Planch., JN051820[3], JN051754[3], EF624280[1]. [§]***Cissampelos madagascariensis*** (Baill.) Diels, Madagascar, *P. Antilahimena & V. Razafindrahaja 8271* (MO), KX384052*, KX384116*, KX384090*. [§]***Cissampelos madagascariensis*** (Baill.) Diels, Madagascar, *Hong-Wa & Ortiz 681* (MO), KX384053*, KX384117*, KX384091*. [§]***Cissampelos madagascariensis*** (Baill.) Diels, Madagascar, *Hong-Wa & Ortiz 683* (MO), KX384054*, KX384118*, KX384092*. ***Cissampelos ovalifolia*** DC., Paraguay, *Zardini & Chaparro 60300* (MO), KX384056*, KX384119*, EF624281[1]. ***Cissampelos owariensis*** Beauv. ex DC., –, –, EF624282[1]. ***Cissampelos pareira*** L., EF143858[2], EF143889[2], JN051703[3]. ***Cissampelos pareira*** L., Madagascar, *Hong-Wa & Ortiz 655* (MO), KX384057*, KX384120*, KX384093*. ***Cissampelos pareira*** L., Dominican Republic, *Ortiz 357* (MO), KX384058*, KX384121*, KX384094*. ***Cissampelos pareira*** L., Peru, *Ortiz 280* (MO), KX384059*, KX384122*, KX384095*. ***Cissampelos tropaeolifolia*** DC., Peru, *Ortiz & al. 229* (MO), KX384060*, KX384123*, EF624283[1]. ***Cocculus carolinus*** (L.) DC., JN051821[3], JN051755[3], EF624284[1]. ***Cocculus laurifolius*** DC., EF143859[2], EF143890[2], EF624286[1]. ***Cocculus orbiculatus*** (L.) DC., EF143860[2], EF143891[2], EF624287[1]. [a]***Cocculus orbiculatus*** (L.) DC. (= ***Cocculus trilobus*** (Thunb.) DC.), DQ478611[5], EF143892[2], JN051704[3]. ***Coscinium blumeanum*** Miers ex Hook.f & Thomson, JN051822[3], JN051756[3], JN051705[3]. ***Coscinium fenestratum*** (Gaertn.) Colebr., JN051823[3], JN051757[3], JN051706[3]. ***Curarea candicans*** (Rich. ex DC.) Barneby & Krukoff, JN051824[3], JN051758[3], EF624288[1]. ***Curarea cuatrecasasii*** Barneby & Krukoff, Costa Rica, *Ortiz & Aguilar 324* (INB, MO), KX384061*, KX384124*, EF624289[1]. ***Curarea tecunarum*** Barneby & Krukoff, Peru, *Ortiz & Vásquez 214* (AMAZ, MO), KX384062*, KX384125*, EF624290[1]. ***Curarea toxicofera*** (Wedd.) Barneby & Krukoff, Peru, *Ortiz 184* (AMAZ, MO), KX384063*, KX384126*, EF624291[1]. ***Curarea* sp. nov. 1,** Ecuador, *Ortiz & Vargas 194* (MO, QCNE), KX384064*, KX384127*, EF624292[1]. ***Cyclea atjehensis*** Forman, Vietnam, *Ortiz & Huy 409* (HN, MO), KX384065*, KX384128*, KX384096*. ***Cyclea fansipanensis*** Gagnep., Vietnam, *Van der Werff & al. 17424* (MO), KX384066*, KX384129*, EF624293[1]. ***Cyclea hypoglauca*** (Schauer) Diels, EF143862[2], EF143894[2], JN051707[3]. ***Cyclea polypetala*** Dunn, EF143863[2], EF143895[2], JN051708[3]. ***Cyclea tonkinensis*** Gagnep., China, Yunnan, *Hong YP 99242* (PE), EF143864[2], EF143896[2], KX384097*. ***Dialytheca gossweileri*** Exell & Mendonça, Gabon, *Breteler 371* (MO), KX384067*, KX384130*, KX384098*. ***Dioscoreophyllum cumminsii*** (Stapf) Diels, JN051825[3], JN051759[3], EF624294[1]. ***Diploclisia affinis*** (Oliv.) Diels, EF143866[2], EF143898[2], JN051709[3]. ***Diploclisia glaucescens*** (Blume) Diels, EF143867[2], EF143899[2], JN051710[3]. ***Disciphania calocarpa*** Standl., Mexico, *Ortiz & al. 374* (MO), KX384068*, KX384131*, KX384099*. ***Disciphania domingensis*** Urb., Dominican Republic, *Ortiz & Pruski 354* (JBSD, MO), KX384069*, KX384132*, KX384100*. ***Disciphania killipii*** Diels, JN051826[3], JN051760[3], EF624295[1]. ***Disciphania lobata*** Eichler, Peru, *Ortiz 266* (AMAZ, MO), KX384070*, KX384133*, EF624296[1]. ***Elephantomene eburnea*** Barneby & Krukoff, JN051827[3], JN051761[3], EF624297[1]. ***Fibraurea tinctoria*** Lour., JN051828[3], JN051762[3], EF624298[1]. ***Haematocarpus validus*** (Miers) Bakh.f. ex Forman, JN051829[3], JN051763[3], JN051711[3]. ***Hyperbaena domingensis*** (DC.) Benth., JN051830[3], JN051764[3], EF624299[1]. ***Hyperbaena mexicana*** Miers, Mexico, *Ortiz & al. 371* (MO), KX384071*, KX384134*, KX384101*. ***Hyperbaena tonduzii*** Diels, Costa Rica, *Ortiz & al. 326* (MO), KX384072*, KX384135*, EF624303[1]. ***Hypserpa decumbens*** (Benth.) Diels, JN051831[3], JN051765[3], EF624304[1]. ***Hypserpa nitida*** Miers, EF143868[2], EF143900[2], JN051712[3]. ***Jateorhiza macrantha*** (Hook.f.) Exell & Mendonça, JN051832[3], JN051766[3], EF624305[1]. ***Kolobopetalum leonense*** Hutch. & Dalziel, JN051833[3], JN051767[3], EF624306[1]. ***Legnephora moorei*** (F.Muell.) Miers, JN051834[3], JN051768[3], EF624307[1]. ***Leptoterantha mayumbensis*** (Exell) Troupin, JN051835[3], JN051769[3], EF624308[1]. ***Limacia blumei*** (Boerl.) Diels, JN051836[3], JN051770[3], EF624309[1]. ***Menispermum canadense*** L., GU266604[6], JNO51771[3], EF624311[1]. ***Menispermum dauricum*** DC., DQ478613[5], AF335293[7], EF624312[1]. ***Odontocarya diplobotrya*** Diels, Peru, *Ortiz & Vilchez 269* (AMAZ, MO), KX384073*, KX384136*, EF624314[1]. ***Odontocarya klugii*** (A.C.Sm.) Barneby, Peru, *Ortiz & Cahuamari 272* (AMAZ, MO), KX384074*, KX384137*, EF624315[1]. ***Odontocarya tamoides*** var. ***canescens*** (Miers) Barneby, Paraguay, *Zardini 58979* (MO), KX384075*, KX384138*, KX384102*. ***Odontocarya tripetala*** Diels, JN051837[3], JN051772[3], EF624316[1]. ***Odontocarya truncata*** Standl., JN051838[3], JN051773[3], EF624317[1]. ***Orthogynium* sp.,** Madagascar, JN051839[3], JN051774[3], EF624318[1]. ***Orthomene hirsuta*** (Krukoff & Moldenke) Barneby & Krukoff, JN051840[3], JN051775[3], EF624319[1]. ***Orthomene schomburgkii*** (Miers) Barneby & Krukoff, Ecuador, *Ortiz & Vargas 201* (MO, QCNE), KX618680*, KX618679*, EF624320[1]. ***Pachygone loyaltiensis*** Diels, JN051841[3], JN051776[3], EF624321[1]. ***Pachygone ovata*** (Poir.) Miers ex Hook.f. & Thomson, JN051842[3], JN051777[3], EF624322[1]. ***Pachygone valida*** Diels, EF143850[2], EF143881[2], JN051713[3]. ***Parabaena sagittata*** Miers ex Hook.f. & Thomson, EF143854[2], EF143885[2], JN051714[3]. ***Parapachygone longifolia*** (F.M.Bailey) Forman, JN051843, JN051778, JN051715. ***Penianthus longifolius*** Miers, JN051844[3], JN051779[3], EF624323[1]. ***Penianthus patulinervis*** Hutch. & Dalziel, Ivory Coast, *M.T. Thijssen 378* (MO), KX384076*, KX384139*, –. ***Pericampylus glaucus*** (Lam.) Merr., EF143869[2], EF143901[2], EF624324[1]. ***Perichasma laetificata*** Miers, JN051856[3], JN051791[3], JN051724[3]. [b]***Pycnarrhena longifolia*** (Decne. ex Miq.) Becc., JN051845[3], JN051780[3], JN051716[3]. [c]***Pycnarrhena tumefacta*** Miers, JN051846[3], JN051781[3], JN051717[3]. ***Pycnarrhena novoguineensis*** Miq., JN051847[3], JN051782[3], EF624326[1]. ***Rhaptonema* sp.,** JN051848[3], JN051783[3], EF624327[1]. ***Rhaptonema bakeriana*** Diels, Madagascar, *McPherson 17143* (MO), KX384077*, KX384140*, KX384103*. ***Rhigiocarya racemifera*** Miers, JN051849[3], JN051784[3], EF624328[1]. ***Sarcolophium suberosum*** (Diels) Troupin, Gabon, *Breteler 12819* (MO), –, KX384141*, KX384104*. ***Sarcopetalum harveyanum*** F.Muell., JN051850[3], JN051785[3], EF624329[1]. ***Sciadotenia amazonica*** Eichler, JN051851[3], JN051786[3], EF624330[1]. ***Sciadotenia mathiasiana*** Krukoff & Barneby, Peru, *Ortiz & al. 259* (AMAZ, MO), KX384078*, KX384142*, EF624332[1]. ***Sciadotenia toxifera*** Krukoff & A.C.Sm., Peru, *Ortiz & al. 231* (AMAZ, MO), KX384079*, KX384143*, EF624333[1]. ***Sinomenium acutum*** (Thunb.) Rehder & E.H.Wilson, EF143870[2], EF143902[3], JN051718[3]. ***Sphenocentrum jollyanum*** Pierre, JN051852[3], JN051787[3], EF624334[1]. ***Spirospermum penduliflorum*** DC., JN051853[3], JN051788[3], JN051719[3]. ***Stephania abyssinica*** (Quart.-Dill. & A.Rich.) Walp. JN051854[3], JN051789[3], JN051720[3]. ***Stephania brachyandra*** Diels, EF143871[2], EF143903[2], JN051721[3]. [d]***Stephania cephalantha*** Hayata, EF143872[2], EF143904[2], JN051722[3]. ***Stephania elegans*** Hook.f. & Thomson, EF143874[2], EF143906[2], JN051723[3]. ***Stephania japonica*** (Thunb.) Miers, JN051855[3], JN051790[3], EF624335[1]. ***Stephania longa*** Lour., EF143875[2], EF143907[2], JN051725[3]. ***Stephania rotunda*** Lour., –, –, EF624336[1]. ***Stephania succifera*** H.S.Lo & Y.Tsoong, EF143876[2], EF143908[2], JN051726[3]. ***Stephania tetrandra*** S.Moore, EF143877[2], EF143909[2], JN051727[3]. ***Stephania venosa*** (Blume) Spreng., JN051857[3], JN051792[3], JN051728[3]. ***Strychnopsis thouarsii*** Baill., JN051858[3], JN051793[3], EF624337[1]. ***Syntriandrium preussii*** Engl., JN051859[3], JN051794[3], JN051729[3]. ***Syrrheonema hexastamineum*** Keay, Ivory Coast, *Jongkind 4906* (MO), KX384080*, KX384144*, –. ***Telitoxicum krukovii*** Moldenke, Peru, *Ortiz & al. 261* (AMAZ, MO), KX384081*, KX384145*, EF624338[1].

Appendix 1. Continued.

Telitoxicum peruvianum Moldenke, JN051860[3], JN051795[3], EF624339[1]. ***Tiliacora australiana*** Forman, JN051862[3], JN051797[3], JN051731[3]. ***Tiliacora funifera*** (Miers) Oliv., JN051863, JN051798, EF624340[1]. ***Tiliacora gabonensis*** Troupin, JN051864[3], JN051799[3], EF624341[1]. ***Tiliacora acuminata*** (Lam.) Miers, JN051861[3], JN051796[3], JN051730[3]. ***Tinomiscium petiolare*** Hook.f. & Thomson, EF143857[2], EF143888[2], JN051732[3]. ***Tinospora caffra*** (Miers) Troupin, Tanzania, *Sitoni & al. 1257* (MO), KX384082*, KC494032[4], –. ***Tinospora*** aff. ***uviforme*** (Baill.) Troupin, Madagascar, *P. Antilahimena 7571* (MO), KX384083*, KX384146*, KX384106*. ***Tinospora sinensis*** (Lour.) Merr., Thailand, *Wang H.C. 109* (HIB), EF143855[2], EF143886[2], KX384105*. ***Tinospora smilacina*** Benth., JN051865[3], JN051800[3], EF624343[1]. ***Triclisia dictyophylla*** Diels, JN051866[3], JN051801[3], EF624344[1]. ***Triclisia subcordata*** Oliv., JN051867[3], JN051802[3], EF624345[1]. **OUTGROUP:** ***Glaucidium palmatum*** Siebold & Zucc., AB069850[8], EF437113[9], AY145145[10]. ***Hydrastis canadensis*** L., AB069849[8], EF437112[9], AY145146[10]. [e]***Berberis bealei*** Fortune, DQ478617[5], FJ626558[11], JN051733[3]. ***Nandina domestica*** Thunb., AB069830[8], AF325912[12], AY145148[10]. ***Podophyllum peltatum*** L., AB069843[8], AF325904[12], AY145155[10]. ***Akebia quinata*** (Houtt.) Decne., AF542587[13], AM397152[14], AY145143[10]. ***Boquila trifoliolata*** (DC.) Decne., FJ626511[11], AF335291[7], EF624347[1].

1 – Ortiz & al. (2007); 2 – Wang & al. (2007a); 3 – Wang & al. (2012); 4 – Wefferling & al. (2013); 5 – Wang & al. (2007b); 6 – Hilu & al. (2008); 7 – Wang & al. (GenBank unpub.); 8 – Adachi & al. (GenBank unpub.); 9 – Wang & Chen (2007); 10 – Kim & al (2004); 11 – Wang & al. (2009); 12 – Liu & al. (GenBank unpub.); 13 – Hilu & al. (2003); 14 – Worberg & al. (2007).

Notes: Accepted names: a – *Cocculus orbiculatus* (L.) DC. var. *orbiculatus* is the accepted name for *C. trilobus* (Thunb.) DC., as per Luo & al. (2008), but the accession associated with *Cocculus trilobus* in our study, does not group with the accession of *Cocculus orbiculatus* (L.) DC., hence, *C. trilobus* should not be taxonomically subordinated to *C. orbiculatus* var. *orbiculatus*, and pending further phylogenetic and taxonomic studies in the genus, we do not use infraspecific categories for the name here; b – *Pycnarrhena longifolia* (Miers) Diels (= *Pycnarrhena cauliflora* (Miers) Diels); c – *Pycnarrhena tumefacta* Miers (= *Pycnarrhena celebica* (Boerl.) Diels) as per Forman (1986); d – *Stephania cephalanta* Hayata (= *Stephania cepharanta*); e – *Berberis bealei* Fortune (= *Mahonia bealei* (Fortune) Carrière), accepted name treated here as per Whetstone & al. (1997). § – Illegitimate combination.

Appendix 2. Morphological characters and the conventional coding of character states.

1. **Habit:** (0) Climber; (1) Shrub-tree; (2) Herb.
   Climber is used here to include lianas which are woody and usually canopy climbers and vines which are subwoody and frequently understory climbers. We combine shrub or tree into a single state; they are both erect and woody. *Cissampelos ovalifolia* DC. is frequently described as a herb or shrub; it is woody and reaches about 1 m tall, it is here coded as shrub-tree. *Antizoma angustifolia* (Burch.) Miers ex Harv., *A. miersiana* Harv., and *Cissampelos capensis* L.f. are all scrambling shrubs and are coded here as shrub-tree.
2. **Leaf type:** (0) Simple; (1) Compound.
   Disciphania cubijensis (R.Knuth) Sandwith and *Syntriandrium preussii* Engl. have heteromorphic leaves, some are 3–5-foliolate, while others are deeply digitate, the divisions of the blade being contracted into a naked costa and appearing petiolulate (Troupin, 1962; Barneby, 1970). This condition is more noticeable in *S. preussii*. We have not included *D. cubijensis* in this study, and *S. preussii* is coded as having simple and compound leaves.
3. **Venation type:** (0) Pinnatinerved; (1) Palmatinerved.
   Palmatinerved leaves as coded here include leaves where the main veins radiate from the base and arch towards the apex, independently of the secondary veins being distally pinnate.
4. **Breeding system:** (0) Dioecious; (1) Monoecious; (2) Hermaphroditic.

Staminate flowers. Menispermaceae are mostly a dioecious family and we coded sepals and petals as independent characters in both staminate and pistillate flowers, although it is likely that perianth characters of staminate and pistillate flowers of one species are linked. Some of the outgroup taxa have perfect flowers and here characters of sepals and petals were arbitrarily included in the staminate section, while in the pistillate section these characters were coded as inapplicable (–). Delimitation of floral parts in some Menispermaceae—and in some other Ranunculales—becomes blurred at times, as does the terminology for these floral parts. In the Menispermaceae with only a single perianth whorl, usually greenish in color, they have been called either tepals in *Penianthus* Miers and *Sphenocentrum* Pierre (Dekker, 1983), or sepals in *Abuta* Aubl. (Barneby & Krukoff, 1971) and *Legnephora* Miers (Forman, 2007). In this study, when only a single whorl of floral parts is present, they are coded as sepals, as is the single, colored perianth whorl of *Glaucidium palmatum* Siebold & Zucc.

5. **Sepal arrangement in male flowers:** (0) Spiral; (1) Whorled; (2) Decussate.
6. **Number of sepal whorls in male flowers:** (0) One whorl; (1) Two whorls; (2) Three whorls; (3) Four or more whorls.
7. **Number of sepals per whorl in male flowers:** (0) Two; (1) Three; (2) Four.
8. **Sepal fusion in male flowers:** (0) Absent; (1) Present.
9. **Petals in male flowers:** (0) Absent; (1) Present.
10. **Number of petal whorls in male flowers, when petals are present:** (0) One whorl; (1) Two whorls; (2) Three or more whorls.
11. **Number of petals per whorl in male flowers:** (0) One petal; (1) Three petals; (2) Four petals.
12. **Petal fusion in male flowers:** (0) Absent; (1) Present.
13. **Stamen number:** (0) Three; (1) Four; (2) Six; (3) More than six.
    In Menispermaceae with the filaments free or fused into a single column the number of anthers is taken to represent the number of stamens.
14. **Filament fused:** (0) Absent; (1) Present.
15. **Degree of fusion of filament:** (0) All filaments partially fused; (1) Only inner whorl of filaments fused; (2) All filaments fully fused, individual filaments discernible or not (synandrium).
    The term synandrium is frequently used in the Menispermaceae to describe filaments that are fused into a single column. However, our review of the literature and our study of herbarium specimens indicate that the term is interpreted differently by different workers and thus is inconsistently used. Here, we use the term "synandrium" when all filaments were fully fused (e.g., Fig. 1B–L). However we note that the synandrium in *Antizoma*, *Cissampelos* L., *Cyclea* Arn. ex Wight and *Stephania* Lour. is a smooth column, whereas in all the other taxa here coded as having synandria, the individual filaments are clearly visible.
16. **Anther arrangement with respect to the synandrium, when synandrium is present:** (0) Anthers vertical, basifixed. In a few species, e.g., *Jateorhiza macrantha* (Hook.f.) Exell & Mendonça, *Odontocarya klugii* (A.C.Sm.) Barneby, and *Odontocarya tamoides* var. *canescens* (Miers) Barneby, the anthers bend outwards and may appear horizontal (Fig. 1B); (1) Horizontal-peltiform anthers. The anthers are in a single series and radiate from the margin of a central, peltiform connective (cf. Miers, 1871) (Fig. 1D, F). The connective in *Dialytheca gossweileri* Exell & Mendonça is even broader appearing triangular and is coded as horizontal peltiform; (2) Horizontal-subglobose or pyramidal anthers that are aggregated in one or several series and variously shaped (Fig. 1G–L).
17. **Anther dehiscence:** (0) Vertical; (1) Transverse.

Appendix 2. Continued.

Pistillate flowers.

18. **Number of sepals per whorl in female flowers:** (0) One sepal; (1) Two sepals; (2) Three sepals.
19. **Number of petals per whorl in female flowers:** (0) One petal; (1) Two petals; (2) Three petals.
With very few exceptions, petal condition in female and male flowers is similar, thus we did not score presence/absence of petals in female flowers.
20. **Carpel number:** (0) One; (1) Three; (2) Six; (3) More than six.
21. **Number of ovules per carpel:** (0) Two; (1) More than two.
22. **Placentation:** (0) Marginal–sub-marginal; (1) Laminar; (2) Basal; (3) Parietal.
23. **Ovule orientation:** (0) Anatropous; (1) Hemianatropous.
We used the position of the attachment of the seed to the endocarp as a proxy for the type of ovule, i.e., distal attachment = anatropous ovule; central attachment = hemianatropous ovule.

Fruit and seed.

24. **Fruit type:** (0) Drupelet-monocarp; (1) Berry; (2) Follicle.
25. **Position of the remnant of the style/stigma on the fruit:** (0) Apical; (1) Subapical-adaxial; (2) Subbasal-basal.
This character is associated with endocarp-seed curvature and thus variation in its position parallels the variation in endocarp curvature. To capture the variation of this character we divided it rather arbitrarily in three states as follows: Apical-subapical codes for the remnant found either at the distalmost part of the fruit or near to it, opposite to the pedicel. This is equivalent to "terminal" as used by Forman (1986) for Malesian taxa. Subapical-adaxial indicates that the remnant is found distal to the pedicel but towards the adaxial side of the fruit, equivalent to "sublateral" of Ortiz & al. (2007), "lateral" of Ortiz-Gentry (2010), and "sublateral, "lateral, "ventral" of Forman (1986). Subbasal-basal is when the remnant is towards or near the pedicel of the fruit. The term "lateral" was used by Forman (1986) and by Wang & al. (2009), but this may be misleading given that it is also used to designate the two mirror sides of the fruit (see also Ortiz, 2012; Wefferling & al., 2013).
26. **Endocarp type:** (0) Straight; (1) Curved.
The endocarp molds the seed, and to avoid redundancy with character 37 (seed form), we code this character in a broad sense. Outgroup taxa lack endocarp; these are scored as non-applicable (–) for all endocarp related characters (ch. 26–32).
27. **Endocarp compression with respect to the longitudinal axis:** (0) Absent; (1) Present.
28. **Nature of endocarp compression with respect to the longitudinal axis of the fruit, when compression is present:** (0) Lateral; (1) Abaxial-adaxial (dorsiventral).
29. **Endocarp surface ornamentation condition:** (0) Absent; (1) Present.
30. **Type of endocarp ornamentation on abaxial surface:** (0) Longitudinally grooved, ribbed or rugose (Fig. 2C, D); (1) Longitudinally ridged and variously ornamented (Fig. 2E–G); (2) Longitudinal and transversally ridged (Fig. 2H–L); (3) Aculeate or tuberculate (Fig. 2M, N); (4) Surface hairs (Fig. 2O); (5) Winged (Fig. 2P).
This character attempts to code general patterns of ornamentation on the surface of the endocarp. Moreover, because in Menispermaceae, asymmetric development of the ovary results in laterally and abaxially-adaxially compressed endocarps, we focus on the ornamentation of the abaxial (i.e., dorsal) side only, in order to describe the ornamentation in equivalent parts of the endocarps, in all species. We followed the terminology of Stern (1992) to describe the shapes of the projections observed on the surface, and also referred to the terms used specifically for Menispermaceae especially in the works of Diels (1910), Barneby (1970), Barneby & Krukoff (1971), and Forman (1986).
31. **Endocarp texture:** (0) Papyraceous; (1) Chartaceous-crustaceous; (2) Woody; (3) Bony.
The terms used in the coding of states in this character are those of Stern (1992).
32. **Condyle condition:** (0) Absent; (1) Present.
There is great variation in condyle shape in the Menispermaceae, however, information for this character is missing for most taxa here and so we do not use this feature.
33. **Seed form:** (0) Naviculiform; (1) Subglobose; (2) Semiannular-crescentic; (3) Ellipsoid; (4) Cochleate; (5) Hippocrepiform; (6) Unciform; (7) Spiral; (8) Irregular; (9) Reniform.
There is extensive variation in seed shapes (Fig. 3A–J), and this is likely linked with character 32. In state (0), naviculiform seeds (Fig. 3A–C), are for the most part longer than wide and are deeply or shallowly excavated adaxially. State (1), subglobose seeds (Fig. 3D), represented by *Coscinium fenestratum* Colebr., are deeply excavated adaxially. State (2), semiannular-crescentic (Fig. 3E), is the characteristic moonseed shape. State (3), ellipsoid (Fig. 3F), here represented by *Orthomene schomburgkii* (Miers) Barneby & Krukoff, the seed is longer than wide, but only with a shallow groove adaxially. States (4) to (7) illustrate the main variations in curvature of the seed; cochleate (Fig. 3G); hippocrepiform (Fig. 3H); unciform (Fig. 3I); spiral (Fig. 3J). States (8 & 9), irregular and reniform, are not shown.
34. **Endosperm condition:** (0) Absent; (1) Present.
35. **Endosperm type:** (0) Continuous; (1) Adaxially (ventrally) ruminate; (2) Entirely ruminate.
36. **Embryo size:** (0) Small; (1) Large.
This character has an arbitrarily cut off at 0.6 mm, where ≤0.6 mm = small; >0.6 mm long, as in Ortiz & al. (2007).
37. **Embryo form:** (0) Spathuliform; (1) Terete, strap-like; (2) Subcylindric.
Some observations are taken from Miers (1871), complemented by our own. Spathuliform embryos have the cotyledons conspicuously broader than the radicle. Strap-like cotyledons are as broad as the radicle or only slightly broader. Subcylindric cotyledons are broad and thick; this state is usually associated with the lack of endosperm. Note that Ortiz-Gentry (2010) combined our states 1 and 2 into her subcylindric cotyledons.
38. **Cotyledon texture:** (0) Fleshy; (1) Foliaceous (leaf-like). Spathuliform embryos have the cotyledons foliaceous.
39. **Cotyledon orientation with respect to longitudinal axis of the fruit:** (0) Divaricate; (1) Dorsiventrally adpressed (incumbent), (2) Laterally adpressed (accumbent).
Although we code this character similar to Wefferling & al. (2013), we note that the fundamental division may be incumbent (dorsiventrally adpressed) and accumbent (laterally adpressed).
40. **Cotyledon length with respect to the radicle:** (0) Shorter than radicle; (1) Longer than radicle; (2) As long as radicle.
The divisions are more or less arbitrary.
41. **Pollen type.** (0) Tricolpate; (1) Tricolporate; (2) Triporate; (3) Irregular-inaperturate; (4) 6-cryptoporate.