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Phylogeny of tribe Mentheae (Lamiaceae): The story of molecules and micromorphological characters

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Abstract Mentheae are the largest tribe in the family Lamiaceae and economically important, including herbs like mint, sage and thyme. The evolutionary history of this tribe was reconstructed based on ITS and *trnL-trnF* spacer sequence data of 71 species, representing 47 out of 65 genera. The resulting phylogeny was used to analyse the distribution of selected morphological characteristics such as sexine ornamentation of pollen, nutlet shape with existence of abscission scar and its form, and trichome types. Two monophyletic groups are recognized, which largely correspond to the current subtribal circumscription. Subtribe Salviinae is monophyletic, including the genus *Melissa* which was a genus of uncertain affinity in Mentheae. Subtribe Menthinae is not monophyletic since *Cleonia*, *Horminum*, *Hyssopus*, *Lycopus* and *Prunella* are more closely related with subtribe Nepetinae. Although we could not detect any morphological synapomorphies for each clade, morphological variation seems to be correlated with the molecular phylogeny. A circular abscission scar without distinct lateral areole occurred mainly in Salviinae, while the majority of the species of Mentheae and Nepetinae had a clear areole at the abscission scar. In addition, a reticulate sexine ornamentation is rather common in the Menthinae clade.

Keywords Lamiaceae; Mentheae; micromorphology; phylogeny

■ INTRODUCTION

The mint family (Lamiaceae or Labiatae) has a cosmopolitan distribution and includes over 236 genera and 7000 species (Stevens, 2001 onwards). The first classification of Lamiaceae was published by Bentham (1876) and is still significant today because of its comprehensiveness at the generic level. Briquet's (1895–1897) classification was heavily based on Bentham's classification with only minor modifications. Erdtman (1945) divided Lamiaceae into two subfamilies based on palynological features (Lamioideae: tricolpate and bi-nucleate pollen, Nepetoideae: hexacolpate and tri-nucleate pollen). Although he did not make any suggestions at lower taxonomic level, his system is largely congruent with Bentham's classification. On the basis of an extensive survey of pollen, ovule, embryo sac, and seed morphology, Wunderlich (1967) proposed a new classification of the family and recognized a subfamily published as Saturejoideae (but incorrect under the *ICBN*; Sanders & Cantino, 1984) that corresponds closely to Erdtman's Nepetoideae. Questions about the monophyly of Lamiaceae subfamilies arose together with the extended acquisition of pollen characters (Cantino & Sanders, 1986). Cantino & Sanders (1986) identified several putative synapomorphies for subfamily Nepetoideae but could not find any evidence for the monophyly of the subfamily Lamioideae sensu Erdtman (1945) which has many features in common with former family Verbenaceae. Cantino & al. (1992) rearranged Lamiaceae into eight subfamilies based on total evidence (mainly morphological data). Consequently, Erdtman's Lamioideae were split into six subfamilies including many genera previously placed in the family Verbenaceae (Harley & al., 2004). Nepetoideae are consistently recognized as a well supported monophyletic subfamily based on both molecular and morphological evidence (Erdtman, 1945; Cantino, 1992; Wagstaff & al., 1995; Harley & al., 2004).

The tribe Mentheae consists of nearly half of Nepetoideae species. This tribe, which includes many herbs that are used for medicines, cosmetics, and spices, has an undeniable economic importance. Not surprisingly the current circumscription of the tribe Mentheae based on molecular data strongly differs from traditional morphological classifications (Bentham, 1876; Briquet, 1895–97; Wunderlich, 1967). Since Cantino & al. (1992) proposed a new classification of Lamiaceae, the monophyly of Mentheae is mostly supported by both molecular and morphological approaches (Wagstaff & al., 1995; Prather & al., 2002; Jamzad, 2003; Harley & al., 2004; Trusty & al., 2004; Walker & al., 2004; Edwards & al., 2006; Walker & Sytsma, 2007). Within Mentheae only Harley & al. (2004) suggested a subtribal delimitation into three subtribes: Menthinae, Nepetinae, and Salviinae. However, the monophyly of those subtribes and the intergeneric relationships were never assessed, and the diagnostic morphological characteristics are obscure. Our previous work focused on the systematic relationships of Mentheae sensu Harley & al. (2004) based on morphology of leaves, fruits and pollen as potential diagnostic characteristics (Moon, 2008; Moon & al., 2008a–c, 2009a,b). The phylogenetic significance of these morphological characters could not be fully explored because a molecular phylogeny of the tribe was lacking. All molecular phylogenetic hypotheses available are restricted to certain groups and the proposed intergeneric relationships are only partly congruent with each other (Wagstaff & al., 1995; Prather & al., 2002; Jamzad, 2003; Harley & al., 2004; Trusty & al., 2004; Walker & al., 2004; Edwards & al., 2006; Walker & Sytsma, 2007).

The major aim of this study was to reconstruct a framework phylogeny of the entire Mentheae, using published molecular sequence data from GenBank. The resulting topologies are used to evaluate the phylogenetic signal of selected micromorphological characteristics from both vegetative (leaf) and reproductive organs (pollen and nutlet).

■ MATERIALS AND METHODS

We selected ITS and *trnL-trnF* spacer sequences of 71 taxa of tribe Mentheae from GenBank, covering 47 out of 65 genera (Harley & al., 2004). Based on the analysis of Wagstaff & al. (1995) *Lavandula multifida* L. was chosen as outgroup. This genus belongs to the tribe Ocimeae, which is closely related with tribe Mentheae within subfamily Nepetoideae. For the Bayesian analysis *Lavandula angustifolia* (ITS) and *L. rotundifolia* (*trnL-trnF* spacer) were added to the outgroup in order to calculate the support value of the ingroup. Alignment was done manually with MacClade v.4.04 (Maddison & Maddison, 2000). The list of all taxa with GenBank accession numbers is provided in the Appendix.

Both maximum parsimony (MP) and Bayesian (BI) analyses were performed with ITS and *trnL-trnF* spacer sequences separately and combined. MP analyses were done with PAUP* v.4.0b10 (Swofford, 2002) using a heuristic search with 1000 replicates, tree bisection reconnection branch swapping and holding 5 trees at each step. Clade support values were calculated using a bootstrap analysis with 1000 pseudo-replicates (Felsenstein, 1985). For each replicate a heuristic search was conducted with the same settings as described above.

Model selection for BI analyses was done using Modeltest v3.06 (Posada & Crandall, 1998). For all datasets Modeltest selected the GTR+I+G model. The combined analyses were performed with a partitioned model approach. BI analyses were performed with MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Each BI analysis consisted of two parallel Markov chain Monte Carlo (MCMC) runs of four chains performed with a length of one million generations and a sample frequency of one tree for every 1000 generations. The first 50% of the sampled trees were treated as burn-in and discarded. The remaining trees were used to calculate a majority-rule consensus tree. The sump command in MrBayes was used to check whether the two separate analyses converged on similar log-likelihoods. Additionally convergence of the chains was checked using Tracer v.1.4 (Rambaut & Drummond, 2007). For all analyses the effective sampling size of each parameter was found to exceed 100, suggesting acceptable mixing and sufficient sampling.

The relevant morphological characteristics from previously published data were mapped on the strict consensus tree from the MP analysis of the combined dataset using MacClade v.4.04 (Maddison & Maddison, 2000). Individual characteristics were traced on the tree to identify morphological synapomorphies.

■ RESULTS

The aligned data matrix of ITS sequences comprises 658 characters, including 255 variable characters, while the *trnL-trnF* spacer sequences contain 1041 characters with 135 variable characters. In what follows the results from the combined data (ITS + *trnL-trnF* spacer) are described.

Parsimony analyses. — Analysis of the combined dataset recovered 308 most parsimonious trees with a length of 2032 steps (consistency index, CI, = 0.45, retention index, RI, = 0.68, rescaled consistency index, RC, = 0.31; Fig. 1). In the strict consensus tree three main groups could be recognized: clade A is sister to a group with two subclades B and C that have a sister relationship. Although clade C does not appear as a monophyletic group in the separate analyses of ITS and *trnL-trnF* spacer sequences, we tentatively named each clade in order to help clear explanation. Group A is always recognized as a well supported monophyletic. In the combined analysis this clade received a high bootstrap value (BS = 97). However, group B was recovered in the separate analysis of *trnL-trnF* spacer sequences as a monophyletic group without support. In the combined analysis group B has a low bootstrap support (BS = 53) and this clade is compatible with subtribe Salviinae sensu Harley & al. (2004). Based on our combined analysis group C is monophyletic but without BS support. It is noteworthy that all members of the supported subclade (BS = 66) within group C correspond to subtribe Nepetinae sensu Harley & al. (2004). However, in the topology from *trnL-trnF* spacer sequences group C is well resolved and consists of basal four clades (Fig. 3A).

Bayesian analyses. — The Bayesian phylogeny reconstruction is shown in Fig. 2, indicating the differences between datasets. The monophyly of group A is always recovered with 100% Bayesian posterior probabilities (BPP). The phylogenies from *trnL-trnF* spacer sequences (BPP = 95) and combined data (BPP = 100) clearly show clade B as monophyletic. However, in the BI analysis with ITS sequence data only, the main branch for group B was not supported and remained two polyphyletic groups (Fig. 2). The combined BI analysis, however, resulted in a fully resolved phylogeny. Four basal subclades (named group C), which are comparable with the MP analysis of *trnL-trnF* spacer sequences (Fig. 3A). Interestingly the phylogeny suggested by BI of *trnL-trnF* spacer sequences is similar to the phylogeny generated by MP analysis based on our combined dataset (Fig. 3B).

When we consider all phylogenetic information available, groups A and B are monophyletic groups that correspond to the subtribes Menthinae and Salviinae respectively. Although our taxa sampling is deficient to prove the monophyletic origin at generic level, most genera come out as monophyletic except

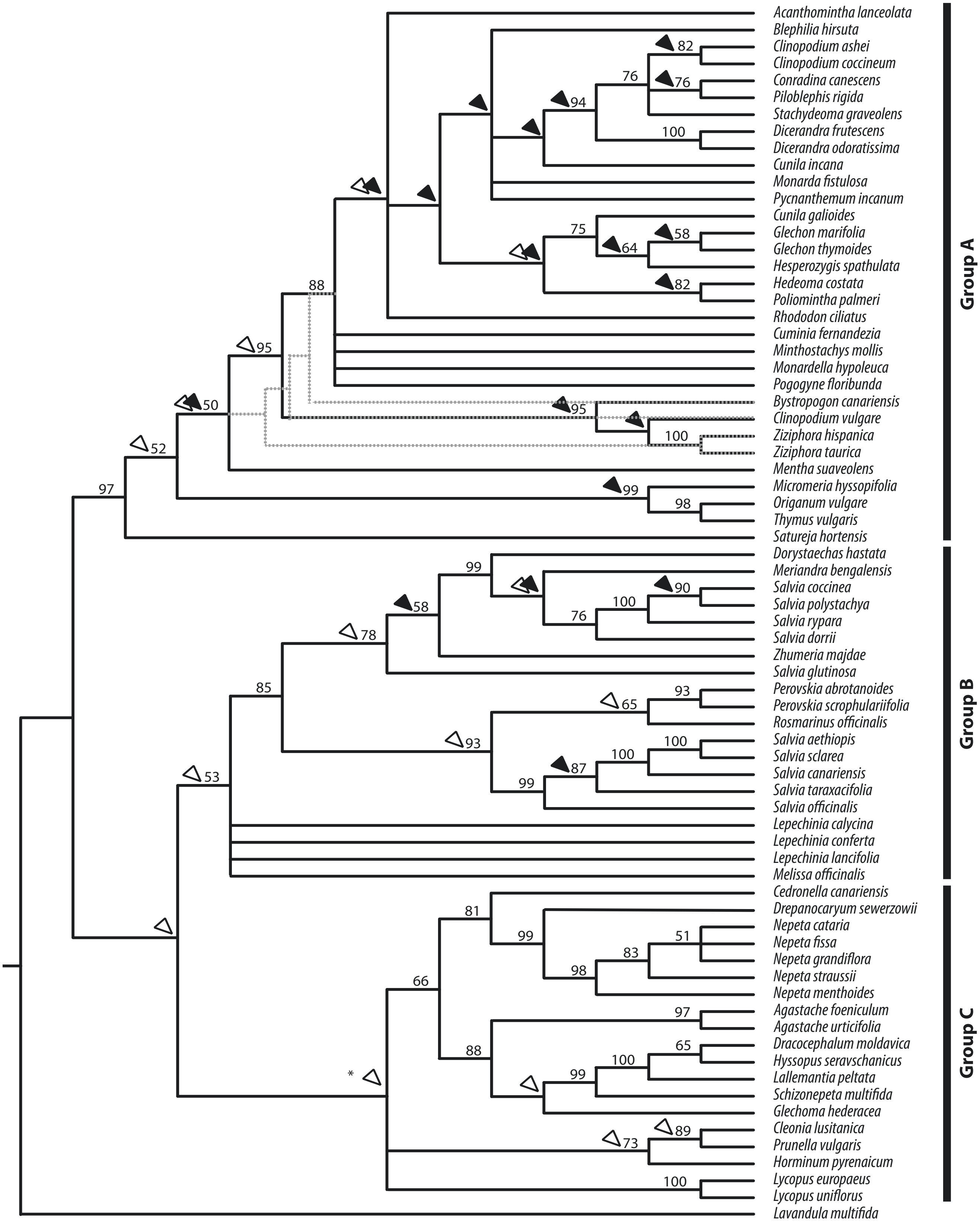

Fig. 1. Strict consensus tree from maximum parsimony analysis of the combined sequence dataset of ITS and *trnL-trnF* spacer. Bootstrap values (>50%) are indicated above the branches. Arrow heads indicate the collapsed branches in the strict consensus trees which generated from separate dataset (white: ITS; black: *trnL-trnF* spacer). The grey line indicates the topology based on *trnL-trnF* spacer data. Clades with asterisk differ in the *trnL-trnF* spacer analysis (of Fig. 3).

Fig. 2. Majority-rule consensus tree from Bayesian inference based on the combined sequence dataset of ITS and *trnL-trnF* spacer. Posterior probabilities are indicated above branches. For further explanation see Fig. 1.

Clinopodium, *Cunila* and *Salvia*. Especially *Salvia* is clearly a poly/paraphyletic group, divided into at least two clades within group B (Figs. 1–2). The genera *Lepechinia* and *Melissa* are undoubtedly members of subtribe Salviinae even though their generic delimitation remains unclear. Menthinae genus *Hyssopus* is closely related to subtribe Nepetinae (group C). Other Menthinae genera such as *Cleonia*, *Horminum*, *Lycopus* and *Prunella* should be considered as potential members of subtribe Nepetinae according to our molecular phylogenies. However, in the BI topology of the combined dataset *Cleonia*, *Horminum*, *Lycopus* and *Prunella* come out as sister to group A and B with moderate posterior probabilities (BPP = 92).

Morphological characteristics. — The selected morphological characteristics are mapped onto the simplified MP consensus topology from the combined ITS and *trnL-trnF* spacer dataset (Figs. 4–5).

Pollen (Fig. 4A–E). – Within Mentheae three different types of sexine ornamentation could be defined such as perforate, reticulate, and bireticulate (Fig. 4C–E). According to our results, each sexine ornamentation type has evolved several times independently (Fig. 5). In fact, the pollen morphological variation is continuous and it seems too homoplastic to imply phylogenetic signal. Nevertheless the reticulate sexine type is rather common in group A while the bireticulate pattern occurs as diagnostic characteristic for small clades in groups B and C.

Fruits (Fig. 4F–L). – Regarding the nutlet features, the shape, position and presence of an areole at the abscission scar are informative characteristics (Fig. 4K). The presence of a minute abscission scar is an apomorphy of group B while the presence of a triangular abscission scar is a diagnostic feature for genera *Cleonia* and *Prunella* (Figs. 4J, 5). An areole at the abscission scar occurs commonly in groups A and C while a distinct areole is lacking in group B (Fig. 5).

Indumentum (Fig. 4M–R). – In Mentheae simple unicellular and uniseriate non-glandular trichomes, capitate and peltate glandular trichomes are distributed widely over the leaf surface (Fig. 4M–N, P, R). The occurrence of branched non-glandular trichomes (Fig. 4O) and pilate glandular trichomes (Fig. 4Q) is likely an apomorphic condition for certain taxa such as *Acanthomintha lanceolata*, *Dorystaechas hastata* and *Dracocephalum parviflorum* (Fig. 5).

■ DISCUSSION

Our phylogenetic hypothesis of Mentheae is based on the most extensive sampling of the tribe to date. The topologies of the ITS, *trnL-trnF* spacer, and combined trees are more or less similar. However, some conflicts were found between the ITS and *trnL-trnF* datasets.

In Mentheae two monophyletic groups are clearly defined. The largest clade, group A, includes 26 genera, which are all members of subtribe Menthinae. Group B consists of genera of subtribe Salviinae including *Lepechinia* and *Melissa*. The rest members of Mentheae show somewhat incongruent relationship depends on the dataset and methods of analysis. The strict consensus tree of MP analysis proposed another monophyletic group C while this group was segregated into four small clades as basal group in Bayesian tree (Figs. 1–3).

Traditional classifications of Mentheae. — The monophyletic nature of Mentheae was supported by molecular and morphological approaches (Cantino & al., 1992; Harley & al., 2004). Not surprisingly the current classification of Mentheae sensu Harley & al. (2004), which considered total evidence, strongly differs from older classifications that were purely based on morphological characters.

Our results reflect the tribal relationships as proposed by Wunderlich (1967), which are more or less similar to Briquet's (1895–97) circumscription except for the subfamilial affiliations. Briquet (1895–97) recognized the present tribe Mentheae as a member of subfamily Lamioideae (published as Stachydoideae; Sanders & Cantino, 1984) except for the genus

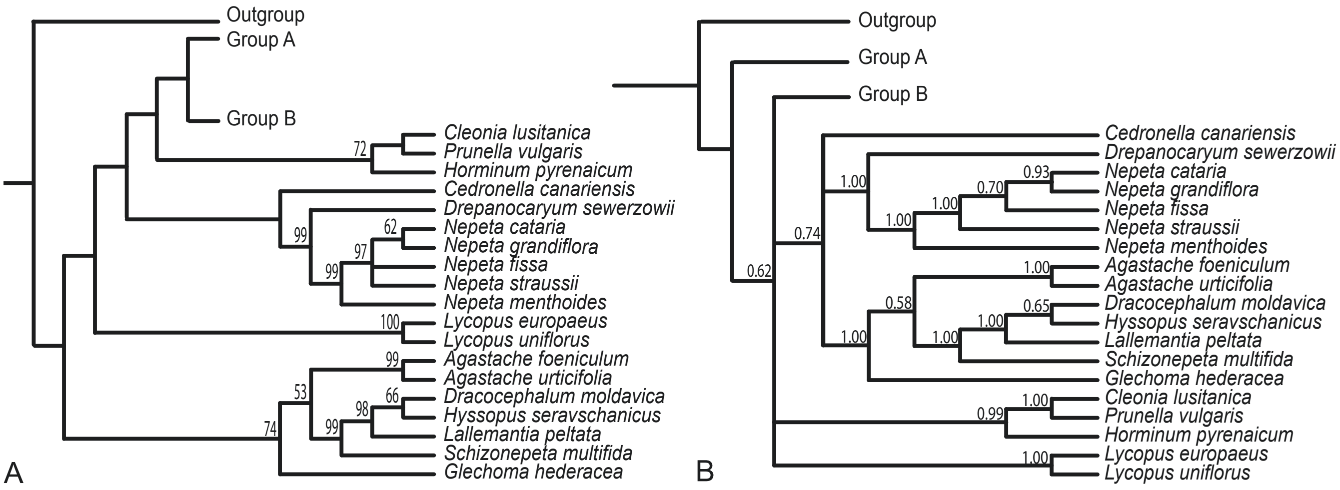

Fig. 3. Trees based on *trnL-trnF* spacer sequences of group C. **A,** Strict consensus tree from maximum parsimony analysis. **B,** Majority-rule consensus tree from Bayesian inference. Bootstrap values (>50%) and posterior probabilities are indicated above the branches.

Rosmarinus (in his subfamily Ajugoideae). However, Briquets' Lamioideae are a polyphyletic assemblage according to the molecular phylogenetic results (Cantino & al., 1992; Wagstaff & Olmstead, 1997; Wagstaff & al., 1998) and members of this subfamily are scattered over the two largest subfamilies, Lamioideae and Nepetoideae sensu Harley & al. (2004). On the other hand, all genera of the present tribe Mentheae belonged to subfamily Nepetoideae of Wunderlich (1967), which closely corresponds to Nepetoideae sensu Harley & al. (2004).

According to Wunderlich (1967), group A includes Glechoneae, Monardeae, Melissineae, Menthineae and Thymineae. Rosmarineae, Lepechinieae, Meriandreae, Salviineae and Melissineae are found in group B, and group C includes the tribes Hormeineae, Prunelleae, Hyssopinae, and Menthinae (see also Table 1). Representatives of two subtribes, Melissineae and Menthineae occur in more than one of our major groups. All members of Melissineae except *Melissa* (Wunderlich, 1967) belong to group A (i.e., genera *Clinopodium*, *Cunila*, *Dicerandra*, *Hedeoma*, *Poliomintha*, *Satureja*). Although genus *Melissa* has an unclear subtribal position in the most recent classification (Harley & al., 2004), molecular phylogenies suggest that *Melissa* is a member of Salviinae (group B). *Lycopus* was classified in subtribe Menthineae but *Lycopus* never belonged to group A even if each phylogeny suggests somewhat different affinities like a member of Nepetineae (Fig. 1) or sister of Menthinae and Salviinae (Fig. 2).

Subdivision of Mentheae. — Within Mentheae sensu Harley & al. (2004) we describe three groups, which likely reflect the evolutionary relationships within Mentheae. Group A is the largest and best-supported clade in Mentheae which consists of members of subtribe Menthinae only (Figs. 1–2). This clade is characterized by reticulate pollen grains and the circular shape of the abscission scar with an expanded area on the nutlets (Figs. 4K, 5). All analyses in the present study recover a large subclade of 19 New World Menthinae genera (*Acantomintha* to *Pogogyne*) although the relationships between these genera remain unclear. The close relationships of the New World genera are consistent with the findings of earlier molecular studies (Prather, 2002; Trusty & al., 2004; Edwards & al., 2006). It is notable that perforate pollen occurs only in the New World clade (Fig. 4C). However, we could not discover any macromorphological synapomorphy for this clade. Although our sampling is insufficient to discuss infrageneric relationships, the genera *Clinopodium* and *Cunila* appear to be para- or polyphyletic. In particular, *Clinopodium* has species both in the New and Old World. While the North American species *Clinopodium ashei* and *Clinopodium coccineum* belong to the New World clade, the Mediterranean *Clinopodium vulgare* is closely related to the Old World genera *Bystropogon* and *Ziziphora*. Both *Clinopodium* and *Cunila* deserve special attention in subsequent studies.

Subtribe Salviinae is always established as a well supported monophyletic clade (group B, Figs. 1–2). According

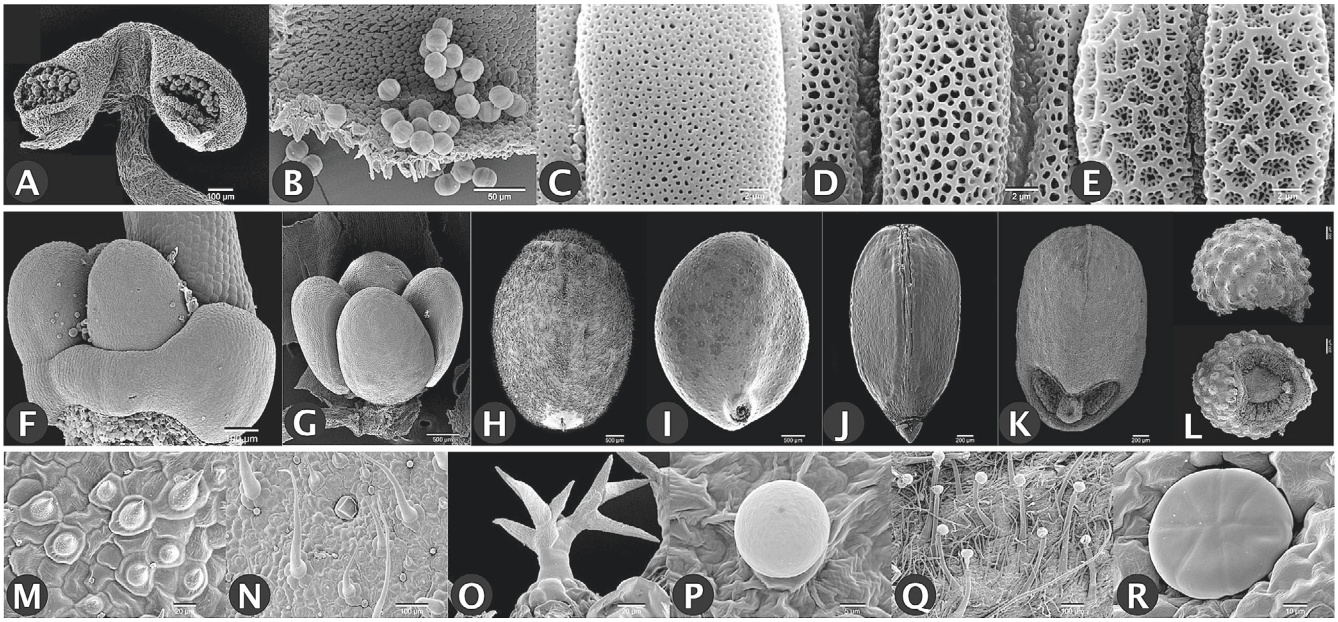

Fig. 4. Representative micromorphological features of Mentheae. **A,** Anther with pollen grains in *Dicerandra odoratissima*. **B,** Pollen grains on inner locule wall of anther in *Rhododon ciliatus*. **C,** Perforate sexine ornamentation in *Lepechinia calycina*. **D,** Reticulate sexine ornamentation in *Blephilia ciliata*. **E,** Bireticulate sexine ornamentation in *Salvia aethiopis*. **F,** Ovary with gynobasic style in *Glechoma hederacea*. **G,** Four nutlets of *Hoehnea minima*. **H,** Minute abscission scar in *Lepechinia calycina*. **I,** Round abscission scar in *Salvia dorrii*. **J,** Triangular abscission scar in *Prunella vulgaris*. **K,** Round abscission scar with lateral areola in *Blephilia ciliata*. **L,** Concave abscission scar in *Drepanocaryum sewerzowii*. **M,** Simple unicellular non-glandular trichome of *Clinopodium vulgare*. **N,** Uniseriate non-glandular trichomes of *Mentha pulegium*. **O,** Branched non-glandular trichome of *Perovskia abrotanoides*. **P,** Capitate glandular trichome of *Agastache urticifolia*. **Q,** Pilate glandular trichomes of *Acanthomintha lanceolata*. **R,** Peltate glandular trichome of *Blephilia ciliata*. H–L, adopted from Moon & al., 2009a; O and R adopted from Moon & al., 2009b.

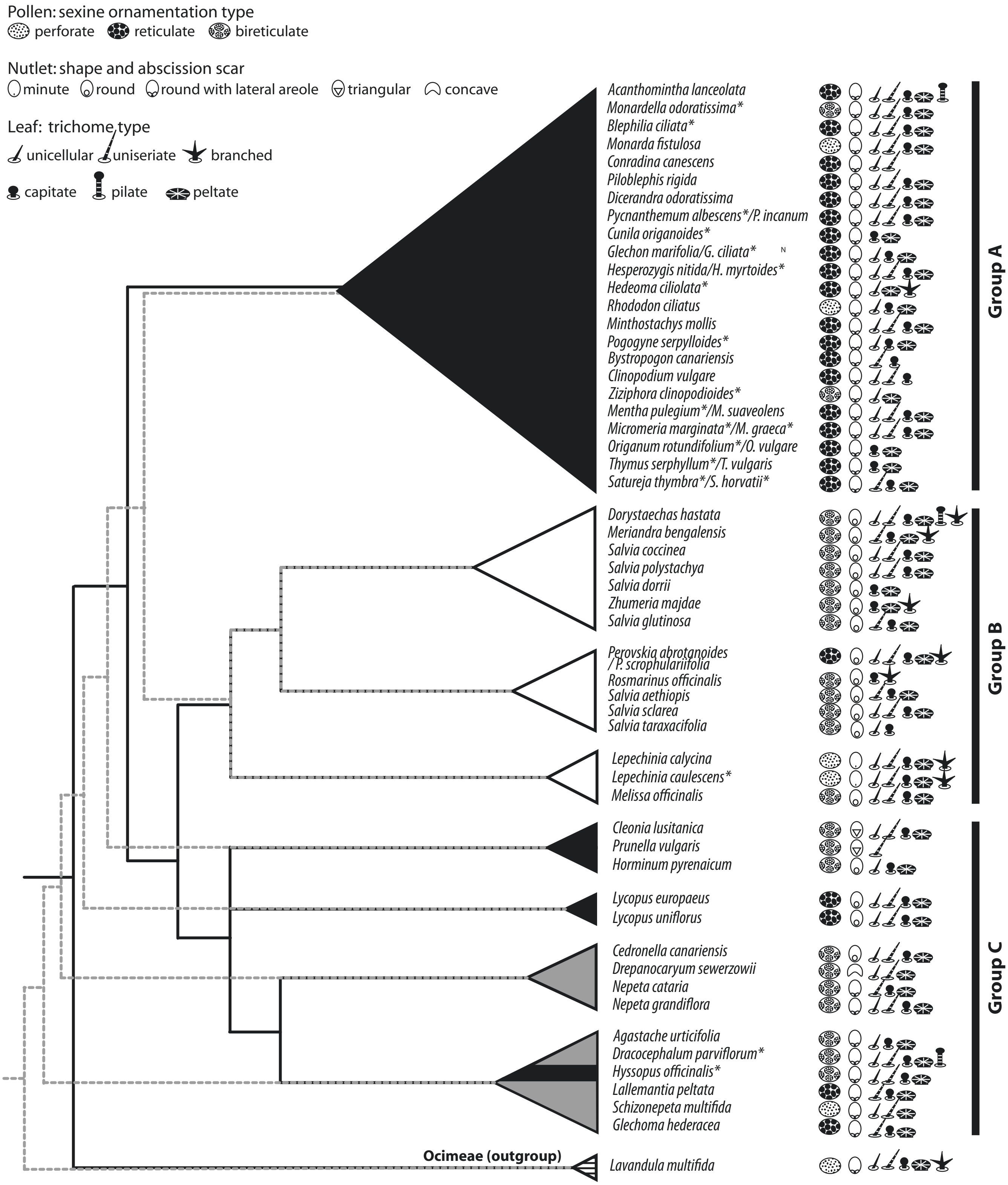

Fig. 5. Representative morphological features mapped onto the simplified consensus tree from the combined dataset. The solid line reflects the strict consensus tree from the maximum parsimony analysis and the grey line the majority-rule consensus tree obtained by Bayesian inference. For each taxon the subtribal position is shown within the clades; black = Menthinae, white = Salviinae, grey = Nepetinae. Taxa indicated by an asterisk were included in the present study but lacking in molecular dataset; their phylogenetic position is estimated by assuming that genera are monophyletic. The second-listed taxon following the dash represents nutlet features. Pollen data are from Moon & al. (2008a–c), nutlet data from Moon & al. (2009a), trichome data from Moon & al. (2009b) except for *Lavandula multifida* (trichome data: Cantino, 1990; pollen and nutlet data: Moon, H.-K., unpub. data), and sexine ornamentation of *Zhumeria majdae* from Cantino & Sanders (1986).

Table 1. Taxonomic history of the examined Mentheae genera with possible subgroup position based on Fig. 1. N.I.: not indicated.

Tribe Mentheae sensu Harley & al., 2004	Bentham, 1876	Briquet, 1895–97	Wunderlich, 1967	Subgroup
Subtribe Menthinae				
Acanthomintha (A. Gray) Benth. & Hook. f.	Tribe Satureineae, subtribe Melisseae	Tribe Glechoneae	Tribe Glechoneae	A
Blephilia Raf.	Tribe Monardeae	Tribe Monardeae	Tribe Monardeae	A
Bystropogon L'Hér.	Tribe Satureineae, subtribe Menthoideae	Tribe Satureieae, subtribe Thyminae	Tribe Saturejeae, subtribe Thyminae	A
Cleonia L.	Tribe Stachydeae	Tribe Stachydeae, subtribe Brunellinae	Tribe Stachydeae, subtribe Prunellinae	C
Clinopodium L.	Tribe Satureineae, subtribe Melisseae (as *Calamintha*)	Genus *Satureia* sect. *Clinopodium*	Genus *Satureja*	A
Conradina A. Gray	Tribe Satureineae, subtribe Melisseae	Tribe Satureieae, subtribe Melissinae	Tribe Saturejeae, subtribe Melissinae	A
Cuminia Colla	Tribe Satureineae, subtribe Menthoideae	Tribe Satureieae, subtribe Menthinae	Tribe Saturejeae, subtribe Menthinae	A
Cunila D. Royen ex L.	Tribe Satureineae, subtribe Menthoideae	Tribe Satureieae, subtribe Thyminae	Tribe Saturejeae, subtribe Thyminae	A
Dicerandra Benth.	Tribe Satureineae, subtribe Melisseae (as *Ceranthera*)	Tribe Satureieae, subtribe Melissinae (as *Ceranthera*)	Tribe Saturejeae, subtribe Melissinae (as *Ceranthera*)	A
Glechon Spreng.	Tribe Satureineae, subtribe Melisseae	Tribe Glechoneae	Tribe Glechoneae	A
Hedeoma Pers.	Tribe Satureineae, subtribe Melisseae	Tribe Satureieae, subtribe Melissinae	Tribe Saturejeae, subtribe Melissinae	A
Hesperozygis Epling	N.I.	N.I.	N.I.	A
Horminum L.	Tribe Satureineae, subtribe Lepechineae	Tribe Hormineae	Tribe Hormineae	C
Hyssopus L.	Tribe Satureineae, subtribe Menthoideae	Tribe Satureieae, subtribe Hyssopinae	Tribe Saturejeae, subtribe Hyssopinae	C
Lycopus L.	Tribe Satureineae, subtribe Menthoideae	Tribe Satureieae, subtribe Menthinae	Tribe Saturejeae, subtribe Menthinae	C
Mentha L.	Tribe Satureineae, subtribe Menthoideae	Tribe Satureieae, subtribe Menthinae	Tribe Saturejeae, subtribe Menthinae	A
Micromeria Benth.	Tribe Satureineae, subtribe Melisseae	Genus *Satureia*	Genus *Satureja*	A
Minthostachys (Benth.) Spach	Genus *Bystropogon*	Genus *Bystropogon*	N.I.	A
Monarda L.	Tribe Monardeae	Tribe Monardeae	Tribe Monardeae	A
Monardella Benth.	Tribe Satureineae, subtribe Menthoideae	Tribe Satureieae, subtribe Thyminae	Tribe Saturejeae, subtribe Thyminae	A
Origanum L.	Tribe Satureineae, subtribe Menthoideae	Tribe Satureieae, subtribe Thyminae	Tribe Saturejeae, subtribe Thyminae	A
Piloblephis Raf.	Genus *Satureja* (sect. *Pycnothymus*)	Genus *Satureja* (sect. *Pycnothymus*)	N.I.	A
Pogogyne Benth.	Tribe Satureineae, subtribe Melisseae	Tribe Satureieae, subtribe Melissinae	Tribe Saturejeae, subtribe Melissinae	A
Poliomintha A. Gray	Tribe Satureineae, subtribe Melisseae	Genus *Hedeoma*	N.I.	A

Table 1. Continued.

Tribe Mentheae sensu Harley & al., 2004	Bentham, 1876	Briquet, 1895–97	Wunderlich, 1967	Sub-group
Prunella L.	Tribe Stachydeae (as *Brunella*)	Tribe Stachydeae, subtribe Brunellinae (as *Brunella*)	Tribe Stachydeae, subtribe Prunellinae	C
Pycnanthemum Michx.	Tribe Satureineae, subtribe Menthoideae	Tribe Satureieae, subtribe Thyminae (as *Koellia*)	Tribe Saturejeae, subtribe Thyminae	A
Rhododon Epling	N.I.	N.I.	N.I.	A
Satureja L.	Tribe Satureineae, subtribe Menthoideae	Tribe Satureieae, subtribe Melissinae	Tribe Saturejeae, subtribe Melissinae	A
Stachydeoma Small	Genus *Hedeoma*	Genus *Hedeoma*	N.I.	A
Thymus L.	Tribe Satureineae, subtribe Menthoideae	Tribe Satureieae, subtribe Thyminae	Tribe Saturejeae, subtribe Thyminae	A
Ziziphora L.	Tribe Monardeae	Tribe Satureieae, subtribe Melissinae	Tribe Saturejeae, subtribe Melissinae	A
Subtribe Salviinae				
Dorystaechas Boiss. & Heldr.	Tribe Monardeae	Tribe Meriandreae	Tribe Meriandreae	B
Lepechinia Willd.	Tribe Satureineae, subtribe Lepechineae	Tribe Lepechinieae	Tribe Lepechinieae	B
Meriandra Benth.	Tribe Monardeae	Tribe Meriandreae	Tribe Meriandreae	B
Perovskia Kar.	Tribe Monardeae	Tribe Meriandreae	Tribe Meriandreae	B
Rosmarinus L.	Tribe Monardeae	Tribe Rosmarineae	Tribe Rosmarineae	B
Salvia L.	Tribe Monardeae	Tribe Salvieae	Tribe Salvieae	B
Zhumeria Rech. f. & Wendelbo	N.I.	N.I.	N.I.	B
Subtribe Nepetinae				
Agastache J. Clayton ex Gronov.	N.I	Tribe Nepeteae	Tribe Nepeteae	C
Cedronella Moench	Tribe Nepeteae	Tribe Nepeteae	Tribe Nepeteae	C
Dracocephalum L.	Tribe Nepeteae	Tribe Nepeteae	Tribe Nepeteae	C
Drepanocaryum Pojark.	N.I	N.I	N.I	C
Glechoma L.	Genus *Nepeta*	Tribe Nepeteae	Tribe Nepeteae	C
Lallemantia Fisch. & C.A. Mey.	Tribe Nepeteae	Tribe Nepeteae	Tribe Nepeteae	C
Nepeta L.	Tribe Nepeteae	Tribe Nepeteae	Tribe Nepeteae	C
Schizonepeta (Benth.) Briq.	Genus *Nepeta*	Tribe Nepeteae	Tribe Nepeteae	C
Incertae Sedis				
Melissa L.	Tribe Satureineae, subtribe Melisseae	Tribe Satureieae, subtribe Melissinae	Tribe Saturejeae, subtribe Melissinae	B

to the first phylogenetic hypothesis based on cpDNA restriction site analysis, *Melissa* was sister to tribes Elsholtzieae and Mentheae (Wagstaff & al., 1995). However, the ITS analysis of Trusty & al. (2004) showed *Melissa* as a member of subtribe Salviinae but only low branch support was obtained for this relationship. Subsequent analyses confirmed this affinity with increased support (Paton & al., 2004; Walker & Sytsma, 2007). *Melissa* remains unassigned at subtribal level by Harley & al. (2004). *Lepechinia* is another troublesome genus with regards to the delimitation of Salviinae. This genus was suggested as a member of subtribe Salviinae for the first time in an initial molecular study by Wagstaff & al. (1995). Walker & al. (2004) showed the poly/paraphyletic nature of genera *Lepechinia* and *Salvia*, questioning the monophyly of Salviinae within Mentheae. In addition, they also included the problematic genus *Melissa* but were unable to suggest a clear taxonomic position for it. Walker & Sytsma (2007) clearly demonstrated the inclusion of *Melissa* and *Lepechinia* into subtribe Salviinae. Although the ITS analysis did not recover this group as a distinct clade, the *trnL-trnF* spacer and combined phylogenies suggested that Salviinae including *Lepechinia* and *Melissa* is monophyletic (Figs. 1–2).

Our study also provides further evidence on the polyphyletic nature of *Salvia*. Recent phylogenetic analyses show that the large genus *Salvia* is polyphyletic and consists of several separate New and Old World clades (Walker & al., 2004; Walker & Sytsma, 2007). Our phylogenies show a similar pattern: the New World taxa are found in a lineage together with the genera *Dorystaechas* and *Meriandra*, while the Old World taxa cluster with *Perovskia* and *Rosmarinus*. It is noteworthy that group B has generally bireticulate pollen grains and is characterized by a circular abscission scar on the nutlets. In addition, the presence of a minute abscission scar and branched nonglandular trichomes on the pericarp are putative apomorphies for Salviinae.

All members of subtribe Nepetinae belong to group C or basal clades together with genera *Cleonia*, *Horminum*, *Hyssopus*, *Lycopus*, and *Prunella* of subtribe Menthinae sensu Harley & al. (2004). While the genera *Cleonia*, *Horminum*, *Lycopus* and *Prunella* were found in a small clade within group C or remained unresolved (Fig. 1–3), *Hyssopus* has a close relationship with *Dracocephalum* as a putative member of subtribe Nepetinae instead of subtribe Menthinae (Figs. 1–3). However, morphological features do not support a position in Nepetinae for *Hyssopus*. *Hyssopus* has short posterior stamens whereas Nepetinae is characterized by having longer posterior stamens than the anterior ones.

The taxonomic position of *Prunella* and *Horminum* has been questioned in molecular approaches because of their close relationship with Nepetinae instead of Menthinae (Wagstaff & al., 1995). In the most recent phylogenetic hypothesis of Mentheae (Walker & Sytsma, 2007), the monophyly of Menthinae is still uncertain and the subtribal position of genus *Lycopus* remains undetermined. It is notable that the lineage with *Cleonia*, *Horminum*, *Lycopus* and *Prunella* is characterized by an abscission scar without an expanded area. In addition, *Cleonia*, *Horminum* and *Prunella* have bireticulate pollen grains. The genera *Cleonia* and *Prunella* were former members of the tribe Prunelleae that is characterized by similar morphological characters such as bireticulate pollen, triangular shape of the abscission scar without an expanded area (Figs. 4J, 5). In all molecular phylogenies available the taxonomic position of *Lycopus* remains controversial. Traditionally this genus is recognized as closely related with *Mentha*, the type of the tribal name Mentheae. However, several morphological characters of *Lycopus* such as the presence of two fertile stamens and nutlets with corky crests show that there are considerable differences between *Lycopus* and *Mentha* (Moon, 2003; Moon & Hong, 2006). Initially, Wagstaff & al. (1995) suggested *Lycopus* as a member of subtribe Menthinae but all subsequent hypotheses suggested *Lycopus* as closely related to Nepetinae (Trusty, 2004; Walker & Sytsma, 2007). Although *Cleonia*, *Horminum*, *Hyssopus*, *Lycopus* and *Prunella* appear to be closely related to subtribe Nepetinae, the phylogenetic signal is too weak to support this hypothesis (Figs. 1–3). Interestingly, the morphological distance of *Cleonia*, *Horminum*, *Hyssopus*, *Lycopus* and *Prunella* to other members of Menthinae suggests different affinities (Fig. 5).

Phylogenetic study of *Cleonia*, *Horminum*, *Hyssopus*, *Lycopus*, *Prunella* and Nepetinae with other DNA markers and more extensive taxon sampling is necessary to obtain further information about the early evolution of Mentheae. In addition, careful macro/micromorphological study of these genera is essential to identify potential morphological synapomorphies.

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Appendix. GenBank accession numbers for taxa used in this study with indicating original references and voucher information for micromorphological characteristics of Mentheae. A dash indicates that the taxon was not sampled for this study. The material donated by seed banks is listed with the original accession number.

Taxon, GenBank accessions: ITS, *trnL-F*; voucher specimen for morphological study

Lavandula multifida L. (outgroup), AY506665[1], AY506630[1]; –. ***Lavandula angustifolia*** L. (second outgroup for MrBayes), EF437225*, –; *Moon 359* (LV)[P]. ***Lavandula rotundifolia*** Benth., –, AY505463[1]; –. ***Acanthomintha lanceolata*** Curran, DQ667333[2], DQ667522[2]; *Mason 12284* (BR)[L,P], *Hoover 2628* (K)[N]. ***Agastache foeniculum*** Kuntze, AY506660[1] AY506626[1] –. ***Agastache urticifolia*** (Benth.) Kuntze, DQ667247[2], AY570452[3]; *Bouharmont 26820* (BR)[L,P], *19811341* (BR)[N]. ***Blephilis ciliata*** (L.) Benth., –, –; *Radford 44758* (BR)[L,P], *Hleinain 1849* (K)[N]. ***Blephilis hirsuta*** (Pursh) Benth., AF369168[4], AY506605[1]; –. ***Bystropogon canariensis*** L., AY506634[1], AY506597[1]; *Bullemont 1855* (BR)[L,P], *Sespeang s.n.* (K)[N]. ***Cedronella canariensis*** (L.) Webb & Berthel, AY506656[1], AY506622[1]; *Linder 2670* (GH)[L,N], *Perrottet s.n.* (GH)[P]. ***Cleonia lusitanica*** L., DQ667309[2], DQ667495[2]; *Wall 45* (S)[L,P], *000194622* (BR)[N]. ***Clinopodium ashei*** (Weath.) Small, AY943483[7], DQ667437[2]; –. ***Clinopodium coccineum*** (Nutt. ex Hook.) Kuntze, AY943485[7], DQ667433[2]; –. ***Clinopodium vulgare*** L., AY506632[1], DQ667513[2]; *Cultivated 1994-2824* (K)[L,P], *19811341* (BR)[N]. ***Conradina canescens*** A. Gray, DQ667238[2], DQ667438[2]; *Godfrey 69283* (BR)[L,P], *Moldenke 1135* (K)[N]. ***Cuminia eriantha*** var. ***fernandezia*** (Colla) Harley, AY506636[1], AY506599[1]; –. ***Cunila galioides*** Benth., DQ667305[2], DQ667491[2]; –. ***Cunila incana*** Benth., DQ667316[2], DQ667504[2]; –. ***Cunila origanoides*** (L.) Britton., –, –; *Anonymus 323b* (BR)[L,P], *Palmer 33237* (K)[N]. ***Dicerandra frutescens*** Shinners AY506642[1] AY506606[1]; –. ***Dicerandra odoratissima*** Harper, DQ667234[2], DQ667434[2]; *Radford & Leonard 11479* (BR)[L,P], *Král 64645* (K)[N]. ***Dorystaechas hastata*** Boiss. & Heldr. ex

Appendix. Continued.

Benth., DQ667252[2], AY570454[3]; *Verlooue 3102* (BR)[L,P], *22338* (K)[N]. ***Dracocephalum moldavica*** L., AY506659[1], AY506625[1]; –. ***Dracocephalum parviflorum*** Nutt., –, –; *Collet 111* (BR)[L,P], *Bouharmont 32331* (BR)[N]. ***Drepanocaryum sewerzowii*** (Regel) Pojark., DQ667328[2], DQ667517[2]; *Vašák & Ziatník s.n.* (BR)[L,N,P]. ***Glechoma hederacea*** L., DQ667245[2], AY570455[3]; *Moon 300* (LV)[L,P], *Witte 15820* (BR)[N]. ***Glechon ciliata*** Benth., –, –; *Hochne s.n.* (K)[N]. ***Glechon marifolia*** Benth., DQ667303[2], DQ667489[2]; *Pedersen 3627* (BR)[L,P]. ***Glechon thymoides*** Spreng., DQ667310[2], DQ667496[2]; –. ***Hedeoma costata*** Hemsl., DQ667236[2], DQ667436[2]; –. ***Hedeoma ciliolata*** (Epl. & W.S. Stewart) R.S. Irving, –, –; *Rzedowski 5003* (GH)[L,N,P]. ***Hesperozygis myrtoides*** (A. St.-Hil ex Benth.) Epl., –, –; *Harley 20334* (K)[N]. ***Hesperozygis nitida*** (Benth.) Epl., –, –; *Dimbroswski 6442* (K)[L,P]. ***Hesperozygis spathulata*** Epl., AF369166[4], AY506602[1]; –. ***Horminum pyrenaicum*** L., DQ667257[2], AY506620[1]; *Cnops 21169* (BR)[L,P], *19782012* (BR)[N]. ***Hyssopus officinalis*** L., –, –; *Bondía & al. 1242GF* (BR)[L,P], *21456* (K)[N]. ***Hyssopus seravschanicus*** (Dub.) Pazij, AY506657[1], AY506623[1]; –. ***Lallemantia peltata*** (L.) Fisch. & C.A. Mey., AY506658[1], AY506624[1]; *Dagh s.n.* (BR)[L,P], *Vašák s.n.* (BR)[N]. ***Lepechinia calycina*** (Benth.) Epl. ex Munz, DQ667308[2], AY570458[3]; *Dechamps 4201* (BR)[L,N], *Sharsmith 4220* (BR)[P]. ***Lepechinia caulescens*** (Ortega) Epl., –, –; *Pringle 3264* (BR)[L,N,P]. ***Lepechinia lancifolia*** (Rusby) Epl., DQ667306[2], DQ667492[2]; –. ***Lycopus europaeus*** L., AY506652[1], AY506618[1]; *Hong 0008090* (KHUS)[L,P], *65115* (K)[N]. ***Lycopus uniflorus*** Michx., DQ667302[2], DQ667488[2]; *Moon0271801* (KHUS)[L,P], *Hong 010818* (KHUS)[N]. ***Melissa officinalis*** L., DQ189090[2], DQ667477[2]; *Sotiaux s.n.* (BR)[L,P], *Lammers 8460* (K)[N]. ***Mentha pulegium*** L., AY506645[1], AY506610[1]; *cultivated 1997-1897* (K)[L,P]. ***Mentha suaveolens*** Ehrh., AY506645[1], AY506610[1]; *69652* (K)[N]. ***Meriandra bengalensis*** (Roxb.) Benth., DQ667329[2], DQ667518[2]; *Lavranos & Newton 15796* (MO)[L,P], *Pappi 1528* (MO)[N]. ***Micromeria gracea*** (L.) Benth., –, –; *119960* (K)[N]. ***Micromeria marginata*** (Sm.) Chater, –, –; *cultivated 1995-1960* (K)[L,P]. ***Micromeria hyssopifolia*** Webb & Berthel, AY227142[1] AY840204[6]; –. ***Minthostachys mollis*** (Kunth.) Griseb., AY506638[1], AY506601[1]; *Asplund s.n.* (BR)[L,P], *Ellenberg 8740* (K)[N]. ***Monarda fistulosa*** L., DQ667318[2], AY506603[1]; *Bouharmont 8498* (BR)[L,P], *19901339* (BR)[N]. ***Monardella odoratissima*** Benth., –, –; *Howell 46064* (BR)[L,P], *Leiberg 885* (BR)[N]. ***Monardella hypoleuca*** A.Gray, AY506637[1], AY506600[1]; –, ***Nepeta cataria*** L., AJ515313[5], DQ667487[2]; *Kapps s.n.* (BR)[L,P], *1982178* (BR)[N]. ***Nepeta fissa*** C.A. Mey AJ421035[8] AJ505430[5]; –. ***Nepeta grandiflora*** M. Bieb., AY506655[1], AY506621[1]; *Moon s.n.* (LV)[L,P], *19580626* (BR)[N], *Sennen s.n.* (LV)[P]. ***Nepeta menthoides*** Boiss. & Buhse, AJ421002[8], AJ505431[5]; –. ***Nepeta straussii*** Hausskn. & Bornm., AJ421040[8], AJ505433[5]; –. ***Origanum rotundifolium*** Boiss., –, –; *cultivated 1968-19106* (K)[L,P], *19840672* (BR)[N]. ***Origanum vulgare*** L., DQ667243[2], AY506614[1]; *19840672* (BR)[N]. ***Perovskia abrotanoides*** Kar., AY506648[1], AY506615[1]; *Billiet & Leonard 6805* (BR)[L,P]. ***Perovskia schrophulariifolia*** Bunge, DQ667330[2], DQ667519[2]; *Kmoppun s.n.* (BR)[N]. ***Piloblephis rigida*** (Bartram ex Benth.) Raf., AY506644[1], AY506608[1]; *Holst & al. 4543* (MO)[L,P], *000194627* (K)[N]. ***Pogogyne floribunda*** Jokerst, DQ667331[2], DQ667520[2]; –. ***Pogogyne serpylloides*** (Torr.) Gray, –, –; *Rose 64044* (BR)[L,N,P]. ***Poliomintha palmeri*** Hemsl., DQ667311[2], DQ667498[2]; –. ***Prunella vulgaris*** L., AY506653[1], AY506619[1]; *Moon 360* (LV)[L,P], *182876* (K)[N]. ***Pycnanthemum albescens*** Torr. & A.Gray., –, –; *Kessler & al., 2648* (BR)[L,P]. ***Pycnanthemum incanum*** (L.) Michx., AY506640[1], AY506604[1]; *Wibbe s.n.* (BR)[N]. ***Rhododon ciliatus*** (Benth.) Epl., DQ667312[2], DQ667499[2]; *Correll 37399* (GH)[L,P], *000194665* (K)[N]. ***Rosmarinus officinalis*** L., DQ667241[2], AY570465[3]; *Cnops 83.56* (BR)[L,P], *Rechamps & Doutrelepont 2157* (BR)[N]. ***Salvia aethiopis*** L., DQ667272[2], AY570466[3]; *Rechter s.n.* (BR)[L], *Vašák s.n.* (BR)[N], *Sotiaux s.n.* (BR)[P]. ***Salvia canariensis*** L., DQ667256[2], AY570469[3]; –. ***Salvia coccinea*** Buc'hoz ex Etl., AY506651[1], AY506617[1]; *Lewalle 7322* (BR)[L], *Algerie s.n.* (BR)[N], *Wibbe 1879* (BR)[P]. ***Salvia dorrii*** (Kellogg) Abrams., DQ667229[2], DQ667430[2]; *Cronquist 10171* (BR)[L,P], *Coll 1909* (BR)[N]. ***Salvia glutinosa*** L., DQ667250[2], AY570480[3]; *Dechamps 2810* (BR)[L,N], *Sennen 1799* (LV)[P]. ***Salvia officinalis*** L., DQ667225[2], AY570488[3]; –. ***Salvia polystachya*** Orteg., DQ667292[2], DQ667478[2]; *Rodriguez 5019*[L,P], *Türckheim 1532* (BR)[N]. ***Salvia rypara*** Briq., DQ667266[2], DQ667452[2]; –. ***Salvia sclarea*** L., DQ667222[2], AY570492[3]; *Andre 11* (BR)[L,P], *64819* (K)[N]. ***Salvia taraxacifolia*** Coss. & Bal., DQ667209[2], AY570497[3]; *Lewalle 11087* (BR)[L,P], *Lewalle 10543* (BR)[N]. ***Satureja hortensis*** L., AY227143[1], AY506611[1]; –. ***Satureja horvatii*** Šilic, –, –; *Todorovic s.n.* (K)[N]. ***Satureja thymbra*** L., –, –; *cultivated 2001-823* (K)[L,P]. ***Schizonepeta multifida*** (L.) Briq., DQ667313[2], DQ667506[2]; *Amebyehko & Chnpnllehko s.n.* (MO)[L,P], *Maximoma 1234ab* (MO)[N]. ***Stachydeoma graveolens*** (Chapm. ex A. Gary) Small, AY943492[7], AY943457[7]; –. ***Thymus serpyllum*** L., –, –; *cultivated 1973-21043* (K)[L,P]. ***Thymus vulgaris*** L., AY506646[1], AY506613[1]; *28949* (K)[N]. ***Ziziphora clinopodioides*** Lam., –, –; *Vašák s.n.* (BR)[L,N,P]. ***Ziziphora hispanica*** L., AF369162[4], AY506595[1]; –. ***Ziziphora taurica*** M. Bieb., DQ667314[2], DQ667501[2]; –. ***Zhumeria majdae*** Rech. f. & Wendelbo, DQ667336[2], DQ667524[2]; *Wendelbo & Foroughi 15731* (K)[L], *Wendelbo 15731* (K)[N].

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[1] Trusty & al., 2004; [2] Walker & Sytsma, 2007; [3] Walker & al., 2004; [4] Prather & al., 2002; [5] Paton & al., 2004; [6] Bräuchler & al., 2005; [7] Edwards & al., 2006; [8] Jamzad & al., 2003; *unpublished data. [L] leaf, [N] nutlet, [P] pollen observations. For references see overleaf.