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Phylogenetics, biogeography, and staminal evolution in the tribe Mentheae (Lamiaceae)[1]

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- *Premise of the study:* The mint family (Lamiaceae) is the sixth largest family of flowering plants, with the tribe Mentheae containing about a third of the species. We present a detailed perspective on the evolution of the tribe Mentheae based on a phylogenetic analysis of cpDNA and nrDNA that is the most comprehensive to date, a biogeographic set of analyses using a fossil-calibrated chronogram, and an examination of staminal evolution.
- *Methods:* Data from four cpDNA and two nrDNA markers representing all extant genera within the tribe Mentheae were analyzed using the programs BEAST, Lagrange, S-DIVA, and BayesTraits. BEAST was used to simultaneously estimate phylogeny and divergence times, Lagrange and S-DIVA were used for biogeographical reconstruction, and BayesTraits was used to infer staminal evolution within the tribe.
- *Key results:* Currently accepted subtribal delimitations are shown to be invalid and are updated. The Mentheae and all five of its subtribes have a Mediterranean origin and have dispersed to the New World multiple times. The vast majority of New World species of subtribe Menthinae are the product of a single dispersal event in the mid-late Miocene. At least four transitions from four stamens to two stamens have occurred within Mentheae, once in the subtribe Salviinae, once in the subtribe Lycopinae, and at least twice in the subtribe Menthinae.
- *Conclusions:* Worldwide cooling trends probably played a large role in the diversification and present day distribution of the tribe Mentheae. Additional work is needed to ascertain relationships within some Mentheae genera, especially in the subtribe Menthinae.

Key words: BEAST; biogeography; DEC; Mentheae; staminal evolution; *ycf1*.

The field of molecular phylogenetics has progressed tremendously in the past 20 years, to the point where it is now possible to test complex hypotheses involving phylogenetic relationships, biogeographical models of dispersal, range expansion, vicariance, and evolutionary transitions in character states involving groups ranging from closely related species (e.g., Carlson and Holsinger, 2010; Valente et al., 2010) to major lineages of plants (e.g., Friedman and Barrett, 2008; Bell et al., 2010). Along with an ever-increasing amount of publicly available phylogenetic data, a concurrent increase in powerful data analysis programs has made these advances possible. Historical biogeography was once a highly speculative endeavor, often invoking questionable land bridges, subjective dispersal scenarios, and rigidly held vicariance assumptions (Croizat, 1962; Donoghue, 2011). The discipline has moved forward to the point where biogeographic and phylogenetic analyses can be performed separately and subsequently integrated, lending some independence to the process and removing much of the speculation (Drummond and Rambaut, 2007; Ree and Smith, 2008; Moore and Donoghue, 2009; Yu et al., 2010). Likewise, model-based approaches have expanded the repertoire of tools beyond simple parsimony in examining competing hypotheses of character evolution (Pagel and Meade, 2007; Maddison and Maddison, 2010). These innovations can aid in our understanding of how and when organisms evolved and offer unprecedented insights regarding organismal evolution in general (Hickerson et al., 2010; Goldberg et al., 2011).

The mint family (Lamiaceae) is the sixth largest family of flowering plants and one of the most economically important. Harley et al. (2004) defined seven subfamilies within Lamiaceae in a classification that was heavily influenced by morphological (Cantino and Sanders, 1986; Cantino et al., 1992) and more recent molecular (Wagstaff et al., 1995, 1998; Wagstaff and Olmstead, 1997) findings. Subfamily Nepetoideae is the largest of the seven subfamilies within Lamiaceae, containing almost one third of the genera (~105/236; Harley et al., 2004) and about half of the species (~3600/7200; Harley et al., 2004). It is also the best supported of the seven subfamilies within Lamiaceae (Wagstaff et al., 1995, 1998; Paton et al., 2004). Notable synapomorphies for Nepetoideae include hexacolpate pollen, presence of rosmarinic acid, an investing embryo, gynobasic style, and exalbuminous seeds (Cantino and Sanders, 1986; Harley et al., 2004). Nepetoideae contains numerous familiar plants, such as oregano (*Origanum*), thyme (*Thymus*), rosemary (*Rosmarinus*), sage (*Salvia*), spearmint and peppermint

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(*Mentha*), savory (*Satureja*), bee balm (*Monarda*), lemon balm (*Melissa*), catnip (*Nepeta*), basil (*Ocimum*), and lavender (*Lavandula*). Within Nepetoideae, three tribes are currently recognized (Elsholtzieae, Mentheae, and Ocimeae). Mentheae is by far the largest of these three, containing about 65 genera and 2300 species (Harley et al., 2004).

In addition to being the largest recognized tribe in Lamiaceae in terms of species and genera, tribe Mentheae is also remarkably diverse in terms of distribution, floral form, breeding system, and habit. Species from Mentheae naturally occur virtually worldwide and are present on six continents (Appendix S1; See Supplemental Data with the online version of this article). Flower size varies from a few millimeters (e.g., *Lepechinia dioica*) to several centimeters (e.g., *Salvia patens*), and a wide range of flower colors is present. Importantly, transition in stamen number between four and two occurs within Mentheae, although the number of such independent shifts is unknown. Stamen-number shift in Mentheae may be correlated with subsequent staminal evolution. For example, stamens have independently and convergently been modified into highly complex and diverse lever mechanisms in the paraphyletic, two-stamen genus *Salvia* (Walker and Sytsma, 2007), and these staminal features presumably enhance pollination success and are unique in flowering plants (Claßen-Bockhoff et al., 2004). Along with this remarkable variation in floral form and pollination biology, some unusual breeding systems that are not typically found in Lamiaceae occur within tribe Mentheae. These include dioecy (*Lepechinia* sect. *Parviflorae*), gynodioecy (*Mentha*, *Thymus*, and several other genera), and heterostyly (*Salvia brandegeei*; Barrett et al., 2000). In terms of habit diversity, species within Mentheae range from small annuals (e.g., *Pogogyne*) to low trees (e.g., *Lepechinia heteromorpha*), with the majority occurring as herbaceous perennials. Although members of Mentheae are typically found in open savanna habits with strong seasonal contrasts, they have diversified into other habitats. Finally, these radiations show strong biogeographic signal in Mediterranean Europe, eastern Asia, North America, South America, but little in most of Africa, Australia, and Southeast Asia. The astounding diversity within Mentheae begs several questions regarding the origin and patterns of diversity within the tribe.

A number of molecular studies have been conducted concerning Mentheae (Wagstaff et al., 1995; Prather et al., 2002; Trusty et al., 2004; Paton et al., 2004; Walker et al., 2004; Bräuchler et al., 2005, 2010; Edwards et al., 2006; Walker and Sytsma, 2007; Drew and Sytsma, 2011), and have consistently found Mentheae to be monophyletic. Since the work of Harley et al. (2004), several molecular (Trusty et al., 2004; Walker et al., 2004; Bräuchler et al., 2005, 2010; Edwards et al., 2006; Walker and Sytsma 2007; Drew and Sytsma, 2011) and morphological (Moon et al., 2008, 2009, 2010; Ryding, 2010a, b) studies have focused on Mentheae and groups within it. These studies have been generally consistent in showing that the three subtribes of Mentheae defined by Harley et al. (2004) are not all monophyletic, and a number of genera are not placed or appear misplaced (Ryding, 2010a; Drew and Sytsma, 2011). Moreover, many questions concerning the relationships among and within genera remain, especially in subtribe Menthinae (Bräuchler et al., 2010; Drew and Sytsma, 2011).

To date, no single molecular phylogenetic study has possessed either the taxon coverage or phylogenetic resolution to address these subtribal issues. We present here a detailed perspective on the evolution of a species-rich clade of mints (tribe Mentheae, Lamiaceae) based on a phylogenetic analysis of plastid DNA (cpDNA) and nuclear ribosomal DNA (nrDNA), a biogeographic set of analyses using a fossil-calibrated chronogram, and an examination of staminal evolution. This study represents the most comprehensive phylogenetic analysis within Mentheae in terms of genera (64 of the 65 genera recognized by Harley et al. (2004)) and molecular characters (~8000 cpDNA characters and ~1300 nrDNA characters). The large or widely distributed genera have multiple species sampled. We employed four cpDNA regions (*ycf1*, *ycf1-rps15* spacer, *trnL-F,* and *rpl32-trnL* [UAG]) and the internal and external transcribed spacer regions of nrDNA (ITS and ETS). Using this well-resolved phylogenetic framework, we incorporated fossil calibrations to answer important questions within tribe Mentheae involving phylogenetics, biogeography, and character evolution. What are the relationships between the three subtribes, and are the subtribes valid as currently proposed? What is the geographic origin of Mentheae? When did it diversify in the New World? How has tribe Mentheae radiated within the New World? Is there a pattern to staminal evolution within Mentheae?

MATERIALS AND METHODS

***Nomenclature*—**Generic circumscription used in this paper follows the treatment of Harley et al. (2004), with the following two exceptions: (1) *Acinos*, which was treated as part of *Clinopodium* by Harley et al. (2004) and (2) *Killickia* (Bräuchler et al., 2008), which was treated as part of *Micromeria* by Harley et al. (2004), are treated as distinct genera here. *Micromeria* section *Pseudomelissa*, transferred to *Clinopodium* by Bräuchler et al. (2006), is referred to as *Micromeria* (*Micromeria dalmatica* and *M. thymifolia*) in this paper.

***Sampling and outgroups*—**A total of 121 accessions were included in this study (Appendix 1). For analyses involving cpDNA, 115 accessions were included. Of these 115 accessions, 105 were sampled from within subfamily Nepetoideae. Within Nepetoideae, seven taxa were included from tribes Elsholtzieae (2) and Ocimeae (5), and 98 accessions were sampled from Mentheae. Within Mentheae, 58 of the 65 genera (Harley et al., 2004) were included, with complete generic sampling from subtribes Salviinae and Nepetinae. Genera of tribe Mentheae recognized by Harley et al. (2004) but not included in the cpDNA analyses were *Gontscharovia*, *Heterolamium*, *Pentapleura*, *Piloblephis*, *Saccocalyx*, *Stachydeoma*, and the potentially extinct (Harley et al., 2004) *Eriothymus* from subtribe Menthinae, and the monotypic genus *Heterolamium* from subtribe Nepetinae. All nine subtribes of Nepetoideae as recognized by Harley et al. (2004) were sampled. Seven genera representing five subfamilies of Lamiaceae outside of Nepetoideae were included. *Lindernia dubia* (Linderniaceae) and *Phryma leptostachya* (Phrymaceae) were used as outgroups. For the cpDNA data set, we were unable to obtain sequences from the *rpl*32-*trnL* (UAG) region for *Cleonia lusitanica* or *Meriandra bengalensis*.

The nrDNA data set included 108 accessions, all of which are within subfamily Nepetoideae; 106 accessions were sampled from within subtribe Mentheae, with 64 of the 65 genera recognized by Harley et al. (2004) represented. The only genus not sampled was the potentially extinct *Eriothymus*. Effort was made to include appropriate multiple accessions from genera that are large (e.g., *Salvia*, *Clinopodium*) and/or have broad geographic distributions (e.g., *Cunila*, *Agastache*, *Lycopus*). The genera *Collinsonia* and *Elsholtzia* from subtribe Elsholtzieae served as outgroups (monophyletic) based on the findings of Drew and Sytsma, 2011). For the nrDNA data set, ETS sequences were not obtained for *Gontscharovia*, *Killickia*, *Pentapleura*, *Piloblephis*, *Saccocalyx*, *Stachydeoma* (ITS sequences for these six taxa were downloaded from GenBank), or *Cleonia*.

***DNA extraction, amplification, and sequencing*—**DNA was extracted from silica-dried plant material and herbarium specimens (Appendix 1) using the DNeasy Plant Mini Kit (Qiagen, Valencia, California, USA) according to the manufacturer's specifications. The one modification to the protocol involved heating the extracts at 65°C for 30 min (instead of 10) to break down secondary compounds that might interfere with subsequent PCR amplifications. PCR procedures were similar to those described in Sytsma et al. (2002). PCR products,

obtained with TaKaRa Ex Taq (Otsu, Shiga, Japan), were diluted 30× in water prior to cycle sequencing. After cycle sequencing, the product was cleaned using Agencourt CleanSeq magnetic beads (Agencourt, Beverly, Massachusetts, USA). Cycle sequencing reactions used the ABI PRISM BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, Foster City, California). Samples were electrophoresed on an Applied Biosystems 3730xl automated DNA sequencing instrument, using 50 cm capillary arrays and POP-7 polymer. Data were analyzed using PE-Biosystems version 3.7 of Sequencing Analysis at the University Wisconsin-Madison Biotechnology Center. Because the first ~1000 base pairs of *ycf1* are in the inverted repeat in the mint family (Drew, 2011) and relatively uninformative (Perry and Wolfe, 2002), only about 100 bp of this region was amplified. The remaining ~4600 nucleotides of *ycf1* and 500 nucleotides of the *ycf1-rps15* spacer were amplified and sequenced using a series of 14 overlapping primers (Drew and Sytsma, 2011). The plastid region *trnL-F* was amplified primarily by using the 'C' and 'F' primers, but the internal 'D' and 'E' primers were necessary for some herbarium specimens (Taberlet et al., 1991). For most accessions, PCR amplifications and sequences for *rpl32-trnL* used the primers listed in Shaw et al. (2007). For some herbarium material, it was necessary to use Nepetoideae specific internal primers (bd259f: CCA ATT CCA TTT CCT RGT G; bd866r: GTT TTA TTG TGG ATT TTA GAC TCT TC) for amplification and sequencing. ITS was amplified using the primers Lue1 (Baldwin, 1992) and ITS4 (White et al., 1990) for most taxa. The internal primers ITS2 and ITS3 (White et al., 1990) were used to amplify material from herbarium specimens. Combinations of these primers were used for sequencing. ETS was amplified and sequenced as described in Drew and Sytsma (2011). One accession from the ITS data set, *Hyssopus officinalis*, displayed far more polymorphisms (~30) than other accessions sampled in the nrDNA data sets. To ensure we used only a single functional copy of ITS in our analyses, we cloned ITS in *Hyssopus*. For cloning, the initial PCR product was obtained as described above. The PCR product was then gel purified with QIAquick Gel Extraction Kit (Qiagen), ligated into a pGEM T-Vector (Promega, Madison, Wisconsin, USA), cloned in *E. coli* DHB-5α competent cells (Invitrogen, Carlsbad, California), reamplified, and sequenced.

***Sequence analyses and divergence time estimation*—**All sequences were edited in Sequencher 4.7 (Gene Codes, Ann Arbor, Michigan, USA) prior to being manually aligned in the program MacClade 4.08 (Maddison and Maddison 2005). Our alignment techniques followed the procedure elucidated by Wheeler (1996). Gaps were treated as missing data and indels were not coded. Alignments used in this study are available in the online database TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S12395). The cpDNA and nrDNA data sets were analyzed separately as described below. Congruence between the cpDNA and nrDNA data sets (with only taxa in common) was assessed using the incongruence length difference (ILD) test (Farris et al., 1994) as implemented in the program PAUP* v4.0b10 (Swofford, 2002). Incongruence, as indicated by the ILD test, was further explored in two ways. First, nodes in disagreement between data sets were examined for support values to check for strong discordance. Second, one or more taxa were removed in an iterative process prior to phylogenetic analysis and implementation of the ILD test to find any taxa contributing to the discordance. Bayesian analysis of the combined dataset was performed in the program MrBayes v.3.1.2 (Huelsenbeck and Ronquist, 2001) and implemented on the Cyberinfrastructure for Phylogenetic Research (CIPRES) cluster (http://www.phylo.org/). We used the default settings and ran our analysis for 3 million generations. The first 25% of trees were discarded as burn-in.

BEAST analysis for divergence times—Phylogenetic and divergence time analyses for both data sets were performed under Bayesian inference (BI) using BEAST v1.6.1 (Drummond and Rambaut, 2007), a program that estimates phylogenies and divergence times simultaneously. The cpDNA and nrDNA data sets were each partitioned in an attempt to accommodate sequence rate heterogeneity. The cpDNA data set had three partitions: (1) the first and second codon positions of *ycf*1*,* (2) the third codon position of *ycf1*, and (3) the noncoding spacer regions. The nrDNA data set had two partitions: (1) the ITS region and (2) the ETS region. The partitions were subsequently analyzed for rate constancy among lineages using the likelihood ratio test (Felsenstein, 1988) as implemented in PAUP*. Rate constancy was rejected for all partitions, so we used a relaxed clock model as implemented in BEAST. To optimize efficiency within BEAST, we undertook several trial runs of 10–20 million generations and analyzed the results using the program Tracer v1.5 (Rambaut and Drummond, 2007). For all runs, we estimated rate change using the uncorrelated lognormal model. These results were then used to determine the number of generations necessary to achieve an effective sample size (ESS) of at least 200 and to optimize the operator settings for our final analyses. Additionally, after the optimal operator settings were determined, we ran BEAST (15 million generations, sampling every 1000) using different combinations of fossil calibrations (cpDNA data set). We also ran BEAST using an empty data set (Drummond et al., 2006) to assess the influence of our priors on the posterior distribution.

For each of our three data partitions in the cpDNA data matrix, we used a model of evolution as determined by the Akaike information criterion (AIC; Akaike, 1974) as implemented in the program ModelTest v3.7 (Posada and Crandall, 1998). The GTR + G + I model was favored for both codon partitions of *ycf1*, while the TVM + G + I model was suggested for the noncoding spacer regions. These models were then used as molecular evolution models for each respective partition in BEAST by choosing the "unlink substitution model" option and adjusting the appropriate prior and operator settings (for the TVM model). Clock models were also unlinked, and we used a Yule tree prior. To appropriately root the analysis (Soltis et al., 2011; Lamiales phylogeny we produced using GenBank sequences), constraints were included to make *Phryma* + Lamiaceae monophyletic, and also to make Lamiaceae monophyletic (*Lindernia* then being the ultimate outgroup). We constrained two nodes within Nepetoideae with log-normal priors and constrained the root of the tree with a uniform prior distribution (see below). During trial runs, we observed that if we did not constrain the root of the tree, BEAST provided unreasonably ancient (>100 Myr) dates for the root (and also for *Phryma* + Lamiaceae). For the cpDNA BEAST analysis, we ran 15 million generations on four separate computers, each starting with a randomly generated tree. Samples were taken every 2000 generations, and the first three million generations of each run were discarded as burnin. The resulting 6000 trees from each run were combined with the program LogCombiner v1.6.1. The trees were then interpreted by the program TreeAnnotator v1.6.1 prior to visualization in the program FigTree v1.3.1.

For the nrDNA data set, two separate BEAST analyses were conducted. The first analysis included all 108 accessions and had two nodes constrained (see below). In this analysis, we constrained the crown of subtribe Menthinae using an age range based on the 95% confidence intervals (CIs) from our plastid analysis, and the *Lepechinia/Melissa* most recent common ancestor (MRCA) was constrained with a log-normal prior. The tribe Mentheae is a diverse clade of over 2300 species, and aligning ITS (especially) and ETS across this group was challenging. In an effort to reduce the effects of numerous small gaps and several difficult-to-align areas within Mentheae-wide nrDNA alignment, a second analysis of the nrDNA data set was conducted which only included subtribe Menthinae with *Agastache* and *Cedronella* of subtribe Nepetinae as an outgroup. This reduced alignment was much cleaner, and since most of the phylogenetic discordance between the nrDNA and cpDNA phylogenies was within subtribe Menthinae, we felt it was important to reduce alignment uncertainty as much as possible to achieve more accurate BEAST results. For the subtribe Menthinae-only data set, we constrained the crown of Menthinae with an age range based on the 95% CIs from our plastid analysis (uniform prior). Both of the nrDNA data sets were analyzed as two partitions—ITS and ETS. For each of the nrDNA partitions, we used a model of evolution as determined by the AIC in ModelTest (GTR + G + I). For both of the nrDNA analyses, we ran 10 million generations on two separate computers, each starting with a randomly generated tree. Samples were taken every 500 generations, and the first two million generations of each run was discarded as burnin. The resulting 16 000 trees from each run were combined with the program LogCombiner v1.6.1. The trees were then interpreted by TreeAnnotator v1.6.1 prior to visualization in FigTree v1.3.1.

Calibration points for cpDNA—The root of the cpDNA tree, corresponding to the split between Linderniaceae + Phrymaceae and Lamiaceae, was constrained with a uniform distribution ranging from 60 to 107 Myr. These ages are based on the findings of previous asterid-wide and larger angiosperm dating papers (Wikström et al., 2001; Bremer et al., 2004; Janssens et al., 2009; Magallón and Castillo, 2009; Bell et al., 2010). The minimum age of 60 Myr was based on the lower CI crown estimate for the Lamiales given by Wikström et al. (2001). The upper limit of 107 Myr was chosen based on the upper CI crown estimate for the Lamiales in Janssens et al. (2009). Since the CIs (upper and lower bounds) from other large dating papers involving the asterids (Bremer et al., 2004; Magallón and Castillo, 2009; Bell et al., 2010) all fall within the uniform prior that we imposed on the root, we consider these boundaries conservative (but see Ho and Phillips, 2009). Although Lamiaceae are not well represented in the fossil record (Harley et al., 2004), there are enough accepted fossils within the family to confidently use them as calibration points in this study. The Nepetoideae crown within the cpDNA was constrained with a log-normal prior having an offset of 49 Myr, a mean of 2.6, and a standard deviation

(SD) of 0.5. The 49-Myr offset is based on an Early Eocene hexacolpate fossil pollen sample identified by Kar (1996). Hexacolpate pollen is extremely rare within angiosperms and is a synapomorphy for subfamily Nepetoideae (Harley et al., 2004). Kar (1996) identified the fossil as *Ocimum*, which is within Nepetoideae, but based upon the comments of Harley et al. (2004), we felt it was conservative to place the fossil at the crown of Nepetoideae as opposed to elsewhere (crown of the *Ocimeae*). The assigned mean of 2.6 to the offset of 49 Myr allows for the possibility that the Coniacian hexacolpate fossil described by Boltenhagen (1976a, b) is truly Nepetoideae. This fossil was listed as "pending" by Muller (1981) due to its temporal distance from other Nepetoideae pollen fossils. For both the cpDNA and Mentheae-wide nrDNA phylogenies, we constrained the MRCA of *Melissa* and *Lepechinia* with a log-normal distribution with an offset of 28.4 Myr, a mean of 1.5, and a SD of 0.5. The offset was based on a fossil fruit of *Melissa* from the Early-Middle Oligocene (Reid and Chandler, 1926; Martínez-Millán, 2010).

Calibration points for nrDNA—Due to difficulties in aligning the nrDNA data across Lamiaceae, the nrDNA analysis relied on two accessions within tribe Elsholtzieae for outgroups. Since we did not have broad sampling outside tribe Mentheae, we did not use the Kar (1996) fossil for calibration in the nrDNA analysis. For the Mentheae-wide nrDNA analysis, we constrained the crown of tribe Mentheae with an age range of 40–52 Myr, and the crown of subtribe Menthinae with a range of 17–25.3 Myr (both dates based upon the 95% CIs from our cpDNA analysis; both nodes were constrained with uniform priors). Additionally, the MRCA of *Melissa* and *Lepechinia* was constrained as described for the cpDNA analysis. For the nrDNA BEAST analyses of only subtribe Menthinae, we constrained the crown of Menthinae with the 95% CI dates (17–25.3 Myr; uniform prior) from the cpDNA analysis.

***Reconstruction of ancestral areas*—**Ancestral area reconstruction (AAR) and estimating spatial patterns of geographic diversification within tribe Mentheae were done with two contrasting methods and accompanying assumptions implemented in the programs Lagrange (Ree and Smith, 2008) and Statistical Dispersal–Vicariance Analysis (S-DIVA; Ronquist, 1997; Yu et al., 2010). Biogeographic data for genera and species within tribe Mentheae were compiled from distributions in the literature (Harley et al., 2004). Mentheae are distributed broadly but, except for a few genera each, are largely absent from Australia and sub-Sahara Africa. Six areas for ancestral area reconstruction (AAR) were delimited by continental divisions based on present and past separations of continents. These areas are shown in Appendix S1 (see online Supplemental Data) and comprise (1) North and Central America (N), (2) South America (S), (3) Mediterranean region including Europe, northeastern Africa (mountains of Ethiopia), west and southwestern Asia, and most of India (M), (4) Asia including eastern and southeastern Asia (A), (5) sub-Saharan Africa (F), and (6) Australia including New Guinea, Papua New Guinea, New Caledonia, New Zealand, and the Pacific Islands (U). The geological time scale of the Geological Society of America (Walker and Geissman, 2009) was used to determine time splits between epochs within the Tertiary Period.

Dispersal–extinction–cladogenesis analyses—Lagrange incorporates an explicit likelihood model of dispersal routes available at historical intervals and estimates dispersal and extinction parameters, while allowing area persistence and/or vicariance, as part of the dispersal–extinction–cladogenesis (DEC) model (Ree and Smith, 2008). The model of dispersal route possibilities between pairs of areas was based in part on the model of Clayton et al. (2009), but augmented and enhanced with geological event dates (Tiffney, 1985; Scotese, 2001; Morley, 2003). In particular for Mentheae, we employed timing of geological events (formation or break-up) involving the Beringian land bridge between Asia and North America, the North Atlantic connection between North America and Europe, bridging of North America (including Mexico) to South America, southern Gondwanan temperate connections of South America to Australia via Antarctica, and the northward push of both Africa and the Australian region toward southwestern Asia and southeastern Asia, respectively (Table 1). Dispersal probabilities range from 0.1 for well-separated areas to 1.0 for contiguous areas and are provided for three time intervals spanning the estimated time frames for tribe Mentheae and subtribe Menthinae. All ancestral ranges of two combined areas were permitted based on extant and potentially plausible ranges. The BEAST generated Bayesian trees (see above) from the cpDNA analysis of Mentheae and the nrDNA analysis of Menthinae were entered into Lagrange. For a given node in each tree, the AAR was accepted if it was greater than two likelihood units relative to alternative AAR scenarios.

Statistical-DIVA analyses—S-DIVA minimizes some of the shortcomings inherent in DIVA (Ronquist, 1996, 1997; Nylander et al., 2008; Harris and Xiang, 2009; Kodandaramaiah, 2010). DIVA optimizes distributions for each node by allowing vicariance but minimizing assumptions of dispersal and extinction. S-DIVA extends DIVA by permitting assessment of phylogenetic uncertainty by examining multiple trees (in our case, a random subset of post burn-in Bayesian trees; Perl script from Cacho et al., 2010). Subsets of 1000 random Bayesian trees from each of the two analyses of Mentheae cpDNA and Menthinae nrDNA were used to estimate probabilities of ancestral areas at each node. We explored the impact of restricting the number of unit areas allowed in ancestral distributions by using the maxareas option (all possible, 4, and 2 areas). AAR for all nodes was visualized on each of the single Bayesian trees obtained in the Bayesian runs. For some groups, we did not have complete geographic sampling. In these instances, we coded appropriate taxa with multiple geographical ranges to reflect the geographic diversity present within the clades. The following species were given geographic ranges that reflected their respective clade and not the actual species distribution of the taxa: *Salvia sclarea* (native to the Mediterranean region, additionally coded for North America), *Salvia polystachia* (native to North America, additionally coded for South America), *Lycopus* (both accessions given additional Mediterranean code), *Dracocephalum bullatum* (native to Asia, additionally coded for the Mediterranean), *Origanum vulgare* (native to the Mediterranean region, additionally coded for Asia), *Mentha microphylla*, *Mentha spicata*, and *Mentha pulegium* (native to the Mediterranean region, additionally coded for Africa, Asia, and Australia), and *Hesperozygis rhododon* (native to South America, additionally coded for North America). It must be acknowledged, however, that *Hesperozygis* may not be monophyletic.

***Estimating transitions in staminal evolution*—**We explored the evolutionary transitions of stamen number (four or two) in Mentheae in terms of number of shifts, directionality of change, and timing using the phylogenetic framework provided with BEAST analysis of cpDNA and nrDNA. We implemented maximum likelihood (ML) and BI optimization of staminal evolution (Pagel, 1999) using both the ML and Markov chain Monte Carlo (MCMC)-based BayesMultiState options in the program BayesTraits v.1.0 (Pagel and Meade, 2007) and using a random set of 100 Bayesian posterior probability (PP) trees obtained from the 1000 trees used in S-DIVA (see above). We analyzed separately staminal evolution using trees uncovered in both the Mentheae-wide cpDNA and Menthinae-restricted nrDNA analyses. To reduce some of the uncertainty and arbitrariness of choosing priors under MCMC, we used the hyperprior approach (the rjhp command) as recommended (Pagel et al, 2004; Pagel and Meade, 2004, 2007, 2008). Combinations of hyperprior values (exponential or gamma, mean and variance) and rate parameter values were explored to find acceptance rates when running the Markov chains of between 20 and 40% (as recommended by Pagel and Meade, 2007). All subsequent analyses used the reversible-jump hyperprior command (rjhp gamma 0 10 0 10) that seeded the mean and variance of the gamma prior from uniform hyperpriors on the interval 0 to 10, and a rate parameter of 2 or 25 (for cpDNA and nrDNA, respectively).

RESULTS

***cpDNA analysis*—**The aligned cpDNA data matrix was 8772 nucleotides long (*ycf1*, 5841; *ycf1-rps15*-spacer, 902; *trnL-trnF*, 1207; *rpl32-trnL*, 1415). A total of 844 characters were excluded due to long uninformative insertions or ambiguous alignment. After these nucleotides were removed, the aligned matrix was 7928 bp (*ycf1*, 4977; *ycf1-rps15*-spacer, 697; *trnL-trnF*, 1142; *rpl32-trnL*, 1115) long. For the remainder of this paper, we use the following criteria for clade support values: well supported or strongly supported, 0.99–1.00 posterior probability (PP); moderately supported, 0.8–0.98 PP; and weakly supported, 0.70–0.79 PP. In the cpDNA phylogeny, a clade of *Callicarpa* together with the Australian genus *Prostanthera* is well supported as sister to the rest of the mint family (Fig. 1). The other five genera that were sampled from outside of Nepetoideae form a clade that is sister to a monophyletic subfamily Nepetoideae. Within Nepetoideae, the seven genera sampled from the tribes Elsholtzieae (*Elsholtzia* and *Collinsonia*) and

TABLE 1. Dispersal probabilities among areas implemented in Lagrange for tribe Mentheae. See Fig. 1 and text for delimitation of areas and bases of dates. Dispersal probabilities are given for 0–5 Ma, 5–30 Ma, and 30–47 Ma, respectively.

Area	North/Central America	South America	Asia	Europe/North Africa	Africa-sub-Sahara	Australia
North/Central America	—	1.0/0.5/0.25	0.5/0.75/0.75	0.5/0.75/0.75	0.1/0.1/0.1	0.1/0.1/0.1
South America			0.1/0.1/0.1	0.1/0.1/0.1	0.1/0.1/0.1	0.1/0.1/0.5
Asia			—	1.0/1.0/1.0	0.25/0.1/0.1	0.75/0.5/0.25
Europe/North Africa				—	0.25/0.1/0.1	0.1/0.1/0.1
Africa-sub-Sahara					—	0.1/0.1/0.1
Australia						—

Ocimeae (*Hyptis*, *Isodon*, *Lavandula*, *Ocimum*, *Plectranthus*) form a weakly supported clade that is sister to the tribe Mentheae.

Within Mentheae, two strongly supported monophyletic large clades were recovered (Figs. 1–3): one consisting of subtribe Salviinae and the other including the previously recognized subtribes Nepetinae and Menthinae and two new subtribes Lycopinae and Prunellinae (see Discussion). Subtribe Salviinae contains two well-supported clades, a "*Salvia*" clade (sensu Walker and Sytsma, 2007) and a clade consisting of the genera *Chaunostoma*, *Lepechinia*, *Melissa*, and *Neoeplingia*. The clade containing the remaining four subtribes has two strongly supported clades (*Cleonia*, *Prunella*, *Horminum* representing subtribe Prunellinae; *Lycopus* representing subtribe Lycopinae) in a basal grade leading to a well-supported clade containing the other two subtribes Nepetinae and Menthinae. Within this latter clade, two well-supported clades emerge. One clade contains the genera of subtribe Nepetinae as defined by Harley et al. (2004) plus *Hyssopus*; the other clade contains most of the genera from subtribe Menthinae as delimited by Harley et al. (2004).

Within subtribe Nepetinae, *Cedronella canariensis* is sister to the rest of the subtribe, with two well-supported main clades being recovered among the remaining taxa. One clade (*Drepanocaryum*, *Nepeta*, *Hymenocrater*, *Lophanthus*, *Marmoritis*) appears to have originated in the Mediterranean/Central Asia region (Fig. 2) and spread to eastern Asia. The other clade (*Agastache*, *Dracocephalum*, *Glechoma*, *Hyssopus*, *Lallemantia*, *Meehania*, and *Schizonepeta*) has a much broader distribution (Fig. 2), with at least three separate lineages in North America. Subtribe Menthinae is broken into two major well-supported clades (Figs. 1, 3), one containing a group of Mediterranean genera (*Origanum*, *Micromeria* [sensu Bräuchler et al., 2006], *Thymbra*, *Thymus*, *Satureja*, and *Zataria*), and another clade containing the remaining taxa—some of which also have a Mediterranean distribution. Within the latter group, *Cyclotrichium* and *Mentha* form a well-supported clade that is sister to a clade containing *Ziziphora* + *Acinos*, the *Clinopodium* complex (Bräuchler et al., 2010), *Bystropogon*, and a large clade of New World taxa. *Bystropogon* is well supported as sister to the New World clade. Within the clade of New World taxa, four well-supported clades are recovered: (1) a clade containing two Central Mexican taxa (*Clinopodium taxifolium* and *Hedeoma piperitum*), (2) a group with the three CFP genera (*Acanthomintha*, *Monardella*, and *Pogogyne*), (3) a clade containing a South American accession of *Clinopodium* and both *Minthostachys* accessions, and (4) a clade containing 16 genera that range from central North America to southern South America. The latter clade is broken up into two groups, one that is North American in distribution and another with a mostly South American distribution.

***nrDNA analysis*—**The aligned nrDNA data matrix was 1280 nucleotides in length (ITS, 745; ETS, 535). After excluding 61 ambiguously aligned nucleotides our aligned matrix was 1219 base pairs (ITS, 700; ETS, 519). Ten ITS clones were examined for *Hyssopus officinalis*. All 10 clones formed a clade (with the sequence obtained from direct sequencing) when included in the Mentheae-wide data set (results not shown). Of the 10 clones, one clone was far more divergent than the other nine and was apparently responsible for the majority of the polymorphisms observed from direct sequencing. This divergent sequence was sister to the rest of the *Hyssopus* clones (and the directly sequenced product). Because of irregularities in the 5.8S region, we considered the divergent clone to be an ITS pseudogene, and for subsequent analyses we used one of the other nine clones randomly chosen (there was <1% variation between any of the other nine clones). The reduced Menthinae data matrix contained 1210 nucleotides (ITS, 701; ETS, 509). After excluding 41 ambiguously aligned nucleotides, the aligned nrDNA matrix was 1169 bp (ITS, q671; ETS, 498) long.

The overall topology of the nrDNA tree was similar to the cpDNA phylogeny, but in some areas the support was not as high. In particular, subtribe Salviinae was not strongly supported in the nrDNA analysis (Fig. 4). As in the cpDNA phylogeny, subtribes Menthinae and Nepetinae (together with subtribes Lycopinae and Prunellinae) formed a monophyletic group, but this clade was only moderately supported. Subtribes Lycopinae and Prunellinae formed a grade at the base of a monophyletic Nepetinae. Within Nepetinae, the major relationships largely mirrored the cpDNA tree. Subtribe Menthinae was strongly supported as monophyletic. As expected, the reduced Menthinae phylogeny (see Fig. 6) was similar in topology to the Mentheae-wide phylogeny (Fig. 4), but some nodes had higher support in the Menthinae-only phylogeny (support values not shown).

Relationships near the base of the subtribe Menthinae nrDNA tree were similar to that seen in the cpDNA tree, with the notable exception of *Mentha arvensis*. Three main clades were recovered within the subtribe Menthinae: (1) a clade containing *Acinos*, *Bystropogon*, *Clinopodium* (sensu Harley et al., 2004), and *Ziziphora*, (2) a clade consisting of *Micromeria* (*Clinopodium* sensu Bräuchler et al., 2006) and *Mentha arvensis* that is sister to (3) a clade containing taxa restricted to the New World. Within the New World clade, resolution was rather poor, but several moderate to strongly supported species grouping were recovered. The two accessions of *Acanthomintha* and *Pogogyne* form a moderately supported clade. Two species of *Cunila* sampled from Mexico form a well-supported clade with each other, but not with the other three *Cunila* accessions included in this study. As in the cpDNA phylogeny, the two accessions of *Minthostachys* and *Clinopodium taxifolium* form a clade, but in the nrDNA phylogeny these three accessions also form a clade

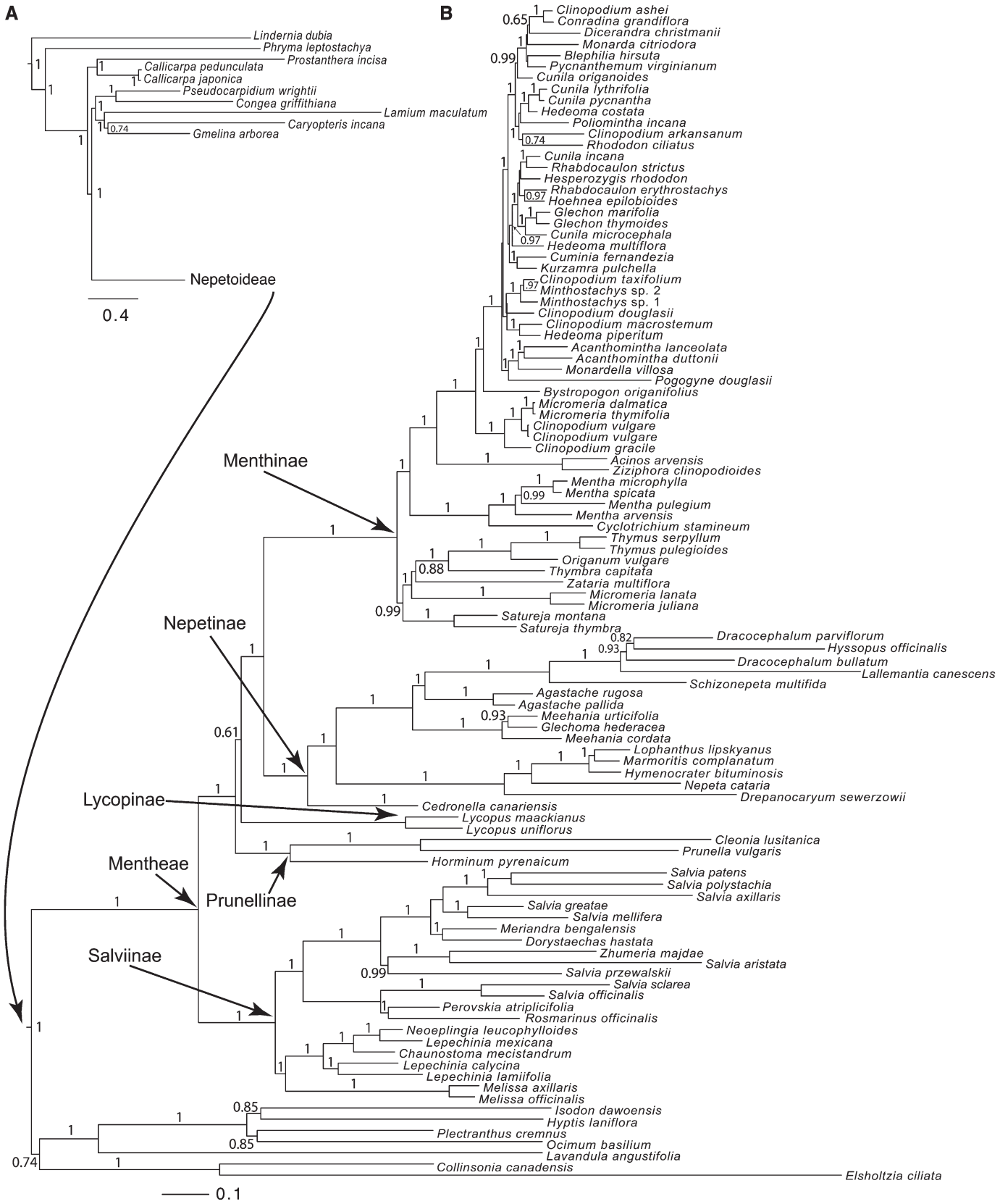

Fig. 1. Phylogram of the Lamiaceae as inferred from BEAST analysis of cpDNA data. *Lindernia* and *Phryma* were used as an outgroup. (A) Outgroup families and Lamiaceae outside of subfamily Nepetoideae. (B) Subfamily Nepetoideae and tribe Mentheae. Subtribes of Mentheae are shown as delimited in this study. Posterior probability support values are shown near corresponding nodes (branch lengths in units of substitution).

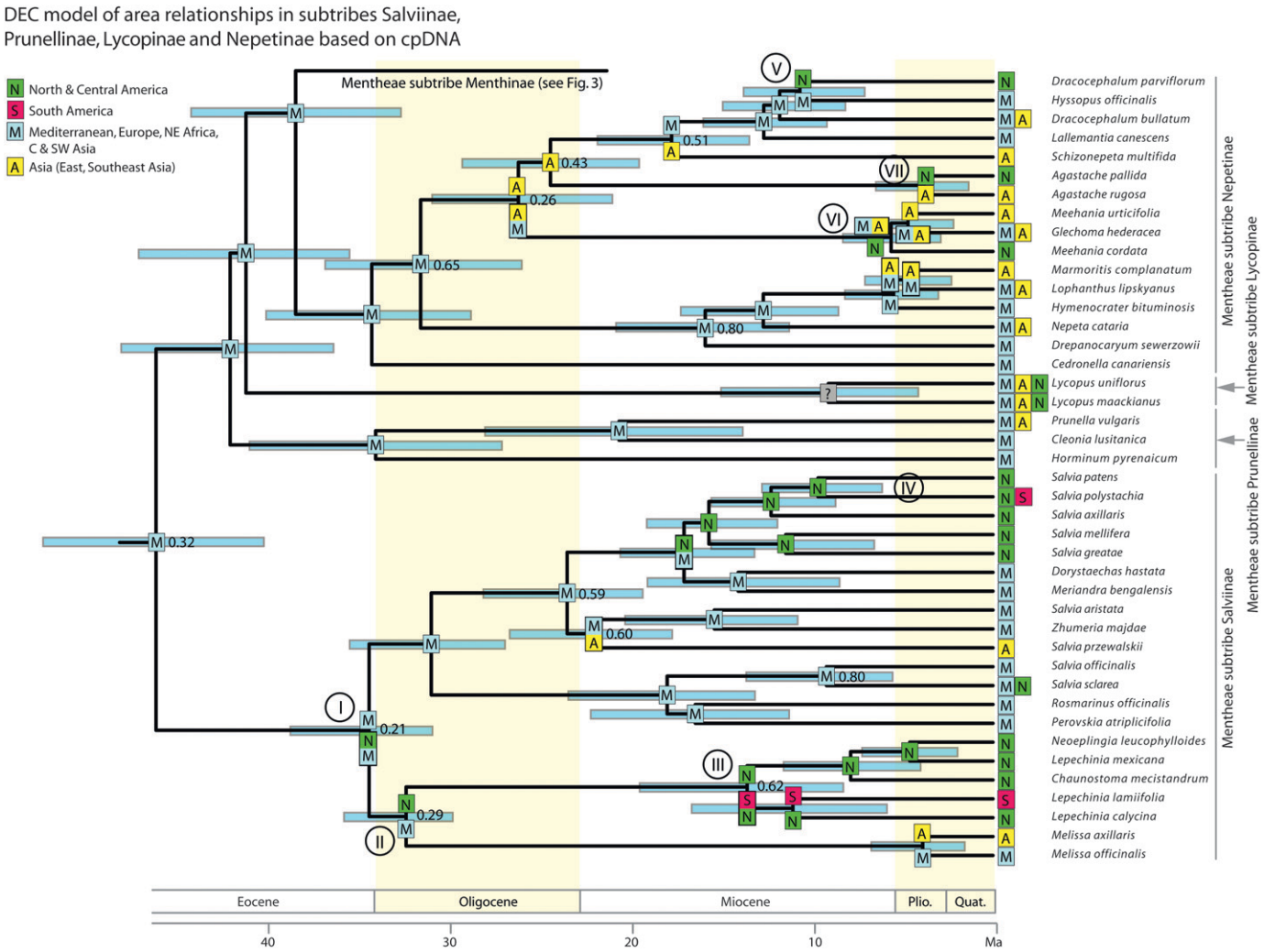

Fig. 2. Dispersal–extinction–cladogenesis (DEC) model of area relationships in Mentheae subtribes Salviinae, Prunellinae, Lycopinae, and Nepetinae based on the Bayesian inference cpDNA chronogram. Ancestral area reconstructions with highest likelihood are shown as colored boxes at each node. Single area boxes indicate an ancestor confined to a single geographic area; combined boxes indicate an ancestor with a distribution encompassing two or more areas; two boxes separated by a space indicate the ancestral ranges inherited by each of the daughter lineages arising from the node. For nodes with alternative reconstructions (within 2 log likelihood units of the maximum), the relative probability of the global likelihood for the optimal reconstruction is given. Scale bar indicates divergence times in my based on BEAST analysis. Blue bars represent 95% confidence intervals for the estimated mean dates. Yellow shaded regions represent the Oligocene and Pliocene/Quaternary. Numbered nodes represent biogeographic events discussed in the text.

with the Western North American species *Clinopodium douglasii*. *Cunila origanoides* forms a well-supported clade with sampled taxa of the "scrub mint clade" as defined by Edwards et al. (2006). The North American genera *Blephilia*, *Monarda*, and *Pycnanthemum* also form a well-supported monophyletic group. The three aforementioned genera form a moderately supported clade with a strongly supported group of southeastern South American genera. Within this clade, several fairly well-supported taxon groupings were recovered. Finally, a moderately supported clade containing 16 genera from the SE mint clade, the SE South American clade, and *Blephilia*, Monarda, and *Pycnanthemum* was recovered.

***Combined data set analysis*—**Combining the cpDNA and nrDNA data sets estimated a phylogeny that had higher support in some areas (e.g., subtribe Menthinae) than either individual data set analysis (Appendix S2, see online Supplemental Data). In the combined data set analysis, relationships that conflicted between the two separate phylogenies were resolved in favor of that supported by cpDNA, likely due to the overwhelming number of cpDNA relative to nrDNA characters. The ILD test indicated significant ($P < 0.001$) incongruence between the two data sets. Iteratively removing potentially rogue taxa (e.g., *Mentha arvensis*, *Agastache* spp.) did not appreciably lower incongruence. After comparing the individual plastid and nuclear phylogenies to each other and to the combined data set phylogeny, it became obvious the nrDNA and cpDNA data sets have partially different histories. Thus, we only present uncombined results in this paper.

***Discrepancies between cpDNA and nrDNA phylogenies*—**The two major differences between the cpDNA (Figs. 1–3) and nrDNA (Fig. 4) phylogenies regard (1) the placement of several genera (*Lycopus*, *Cleonia*, *Horminum*, *Prunella*) with respect to

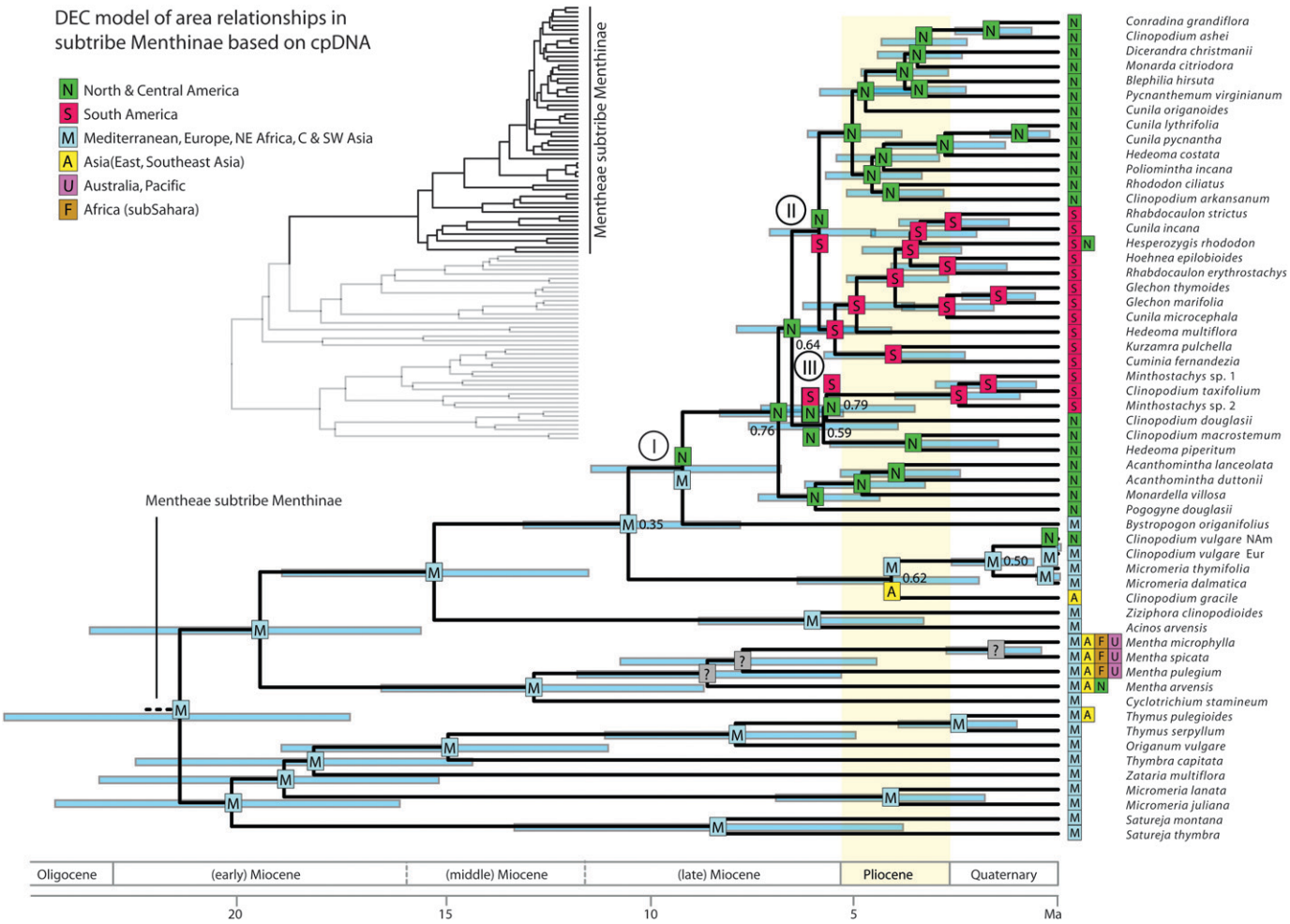

Fig. 3. Dispersal–extinction–cladogenesis (DEC) model of area relationships in Mentheae subtribe Menthinae based on the Bayesian inference cpDNA chronogram. Ancestral area reconstructions with highest likelihood are shown as colored boxes at each node. Single area boxes indicate an ancestor confined to a single geographic area; combined boxes indicate an ancestor with a distribution encompassing two or more areas; two boxes separated by a space indicate the ancestral ranges inherited by each of the daughter lineages arising from the node. For nodes with alternative reconstructions (within 2 log likelihood units of the maximum), the relative probability of the global likelihood for the optimal reconstruction is given. Scale bar indicates divergence times in my based on BEAST analysis. Blue bars represent 95% confidence intervals for the estimated mean dates. Yellow shaded region represents the Pliocene. Numbered nodes represent biogeographic events discussed in the text.

Nepetinae, and (2) the sister clade to the New World Menthinae. In the cpDNA phylogeny (Figs. 1, 2), a clade of *Horminum*, *Cleonia*, and *Prunella* and a clade of two *Lycopus* accessions (both of these clades are on long branches) form a grade at the base of a monophyletic Nepetinae + Menthinae. In the nrDNA phylogeny (Fig. 4), these two clades reverse order and form a grade at the base of the subtribe Nepetinae.

In the cpDNA data set, *Bystropogon* from the Canary Islands is strongly supported as sister to a clade containing all the New World Menthinae (except *Mentha arvensis*). In contrast, the nrDNA tree shows a well-supported clade containing *M. arvensis* and *Micromeria* (*Clinopodium* sensu Bräuchler et al., 2006) as sister to the rest of the New World Menthinae. In the nrDNA tree, *Bystropogon* sits in a well-supported clade with *Acinos*, *Clinopodium* (sensu Harley et al., 2004), and *Ziziphora*. Additionally, *Agastache* had a somewhat different placement in the two phylogenetic analyses. The cpDNA analysis (Figs. 1, 2) placed *Agastache* as sister to a clade consisting of *Dracocephalum*, *Hyssopus*, and *Lallemantia*, whereas the nrDNA analysis (Fig. 4) placed *Agastache* as sister to a clade of *Glechoma*, *Heterolamium*, and *Meehania*. Both of these relationships were at least moderately supported in their respective phylogenies, indicating a hard incongruence between the data sets. There were other differences between the two phylogenies, especially within the New World Menthinae, but most of the differences involved nodes that were not mutually well supported.

***Divergence time analyses with BEAST*—**The BEAST chronogram of the Mentheae-wide cpDNA is depicted in two parts for clarity: Fig. 2 (subtribes Salviinae, Prunellinae, Lycopinae, and Nepetinae) and Fig. 3 (subtribe Menthinae). This chronogram is based on two fossils constraining the Nepetoideae crown and the *Melissa* stem. When using only the *Melissa* fossil as a calibration point in the cpDNA data set, the results were highly congruent with our analysis that used two fossil calibration points. For example, with only one fossil calibration (*Melissa* fossil) the Nepetoideae crown node was found to have originated 52.3 million years ago (Ma) (95% CI = 42.3–62.2)

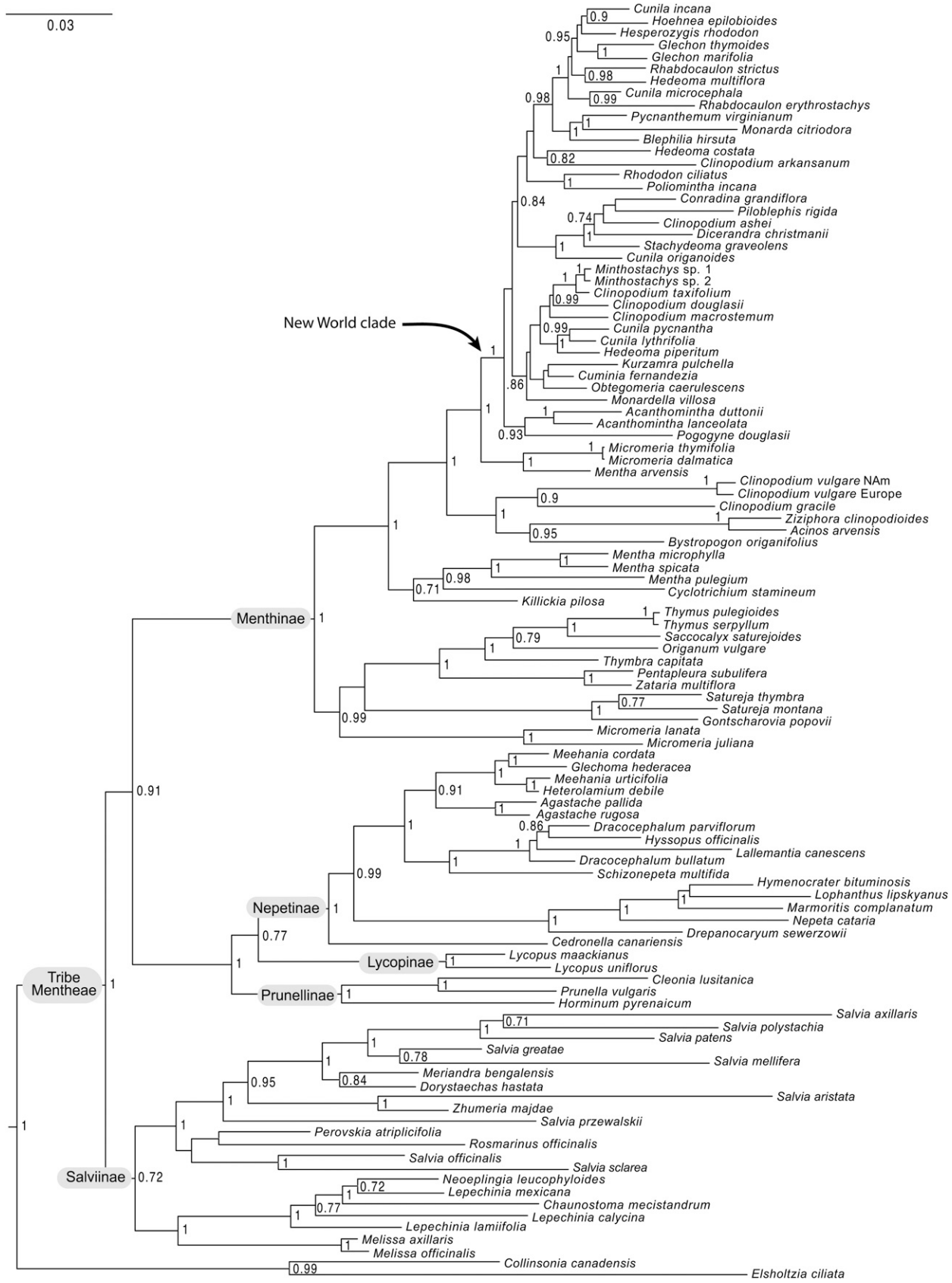

Fig. 4. Phylogram of tribe Mentheae as inferred from BEAST analysis of nrDNA data (branch lengths in units of substitution). *Collinsonia* and *Elsholtzia* from the tribe Elscholtzeae were used as an outgroup. Posterior probability support values are shown near corresponding nodes.

vs. 57.6 Ma (95% CI = 52.4–63.7) with the Nepetoideae crown additionally constrained. In general, using only the *Melissa* fossil as a calibration point gave younger results for nodes (results not shown). In general, the results (as discussed in this paper) from the *Melissa*-only calibration were within the 95% CIs of the analysis that used two fossil calibrations. Similarly, when using only the Nepetoideae fossil as a calibration point (results not shown), the ages of nodes were in general agreement with ages from the two fossil constraint analysis. However, two calibration points provided narrower confidence intervals than when using only one fossil. During BEAST trial runs (with this as well as other data sets), we observed that confidence intervals generally got smaller with more calibration points.

Our results suggest that subfamily Nepetoideae diversified around 57 Ma at the Paleocene-Eocene border (Fig. 5). The extant members of tribe Mentheae (crown node) arose 46 Ma in the mid-Eocene (Fig. 2). All the subtribes arose by the Eocene-Oligocene border (ca. 34 Ma; Fig. 2). Generic differentiation in all subtribes except Menthinae occurred by the late Miocene or early Pliocene (Fig. 2). Generic differentiation of Old World (primarily Mediterranean) Menthinae also occurred during the late Miocene, but differentiation within the North and South American subclade of Menthinae was far more recent in the Pliocene (Fig. 3).

The BEAST dating analysis results for the nrDNA BEAST analysis of tribe Mentheae were similar to those based on cpDNA, especially for the nrDNA chronogram for subtribes Salviinae, Prunellinae, Lycopinae, and Nepetinae (data not shown). The different placement of Lycopinae and Prunellinae in the nrDNA phylogeny (Fig. 4) relative to the cpDNA phylogeny (see Figs. 1, 2) caused those nodes to be younger in the nrDNA chronogram. The reduced Menthinae-only nrDNA chronogram is depicted in online Appendix S3. Despite the more substantial taxa sampling between cpDNA and nrDNA in subtribe Menthinae, the nodal dates in this nrDNA chronogram of Menthinae match fairly closely with those in the cpDNA chronogram (Fig. 3). The crown age of Menthinae is slightly younger with nrDNA. As seen in the cpDNA BEAST analysis, most of the New World generic differentiation is in the Pliocene.

***Ancestral area reconstruction*—**Results from the DEC analysis in Lagrange (Figs. 2, 3; Appendix S3) and S-DIVA (online Appendices S4–S6) were largely congruent for ancestral area reconstruction (AAR). Under both models, AAR was similar when using either the cpDNA or nrDNA tree. Additionally, results using maxarea 4 or 2 were similar, although less complex, as compared to two areas (DEC results were more similar than were S-DIVA results when maxarea was adjusted). Generally, maxarea limited to 4 or 2 provided identical results except for nodes already with complex AAR (e.g., within subtribe Nepetinae; Fig. 2; Appendix S5). For clarity, only the maxarea limited to 2 AAR results are shown.

S-DIVA unambiguously identifies the Mediterranean/Europe area as ancestral for tribe Mentheae and for each of its five subtribes using either the cpDNA (Appendix S5) or nrDNA tree (data not shown). The diverse clade of New World taxa within subtribe Menthinae has an origin in North America based on both the nrDNA (Appendix S4) and cpDNA tree (Appendix S6). Node probabilities less than 95% are more common in this New World subclade of subtribe Menthinae, and thus more uncertainty exists concerning the number of dispersal events from North to South America. S-DIVA analysis using the cpDNA tree indicates only two such dispersals at the beginning of the Pliocene (Appendix S6), whereas the nrDNA tree (with more taxa of Menthinae and a different topology) suggests three dispersals in the Pliocene (Appendix S4).

Under the likelihood DEC model implemented in Lagrange, the AAR with the highest likelihood score for each node is depicted in the cpDNA (Figs. 2, 3) and nrDNA chronograms (Appendix S3). The relative probability of the most likely AAR is given for nodes where likelihood scores were not significantly different between multiple reconstructions within the confidence interval of 2 log likelihood units (Edwards, 1992; Ree and Smith, 2008). Globally across all nodes within Nepetoideae, the inferred dispersal rate is low (0.02), and the extinction rate is negligible (one event in Nepetoideae outside of tribe Mentheae). Two main types of range inheritance are seen. First, there are instances of dispersal resulting in range expansion. These are most common in the Miocene with dispersals to North America from the Mediterranean/Europe representing the largest number (9), followed by dispersal to Asia from the Mediterranean/Europe (6). Second, there is vicariance by cladogenesis, where the ancestral range encompassing two areas subdivides between daughter lineages. Examples of these two kinds of inferred events, dispersal and vicariance, are seen in the origin of the *Lepechinia* clade in subtribe Salviinae (Fig. 2). First, a migration event across the North Atlantic land bridge from Europe to North America occurred prior to the Oligocene (Fig. 2, event I). Second, the stem lineage of *Lepechinia* and *Melissa* underwent a vicariant split of the combined ancestral Mediterranean/Europe + North America area (Fig. 2, event II).

Mentheae and the five subtribes within it all appear to have a Mediterranean origin (Fig. 2). Except for the crown of subtribe Salviinae, North America only became an important area for radiation of the subtribes of Mentheae after the late Miocene (Figs. 2, 3; Appendix S3). The importance of South America as a dispersal point or as a combined area with North America was even more recent (e.g., for subtribe Menthinae; Fig. 3; Appendix S3). Australia/Pacific Islands and sub-Saharan Africa are minor areas for the tribe Mentheae and involve only long distance dispersal in a few widespread genera (e.g., *Mentha*). Widespread taxa such as *Lycopus* (Fig. 2) and *Mentha* (Fig. 3; Appendix S3) present problems in AAR using DEC.

***Staminal evolution analysis*—**BayesTraits analyses of stamen number transition using ML and BI gave very similar results. Generally, nodes were more resolved under the ML rather than BI framework using the same sets of 100 random PP trees. That is, BI often would detect at low probability a transition event deeper into the tree (toward the root) from the main transition node, whereas ML would not at these deeper nodes. Thus we present here only the more conservative perspective of staminal evolution based on BI. The transition from the plesiomorphic four stamens to two stamens occurred twice in tribe Mentheae outside subtribe Menthinae based on cpDNA (Fig. 5) and nrDNA (data not shown). The transition to two stamens is seen in the "*Salvia*" clade within subtribe Salviinae and in subtribe Lycopinae. These two transitions involve both Old World and New World clades. However, within subtribe Menthinae (Figs. 5, 6), the transition to two stamens has occurred only once (*Ziziphora*) outside of the New World based on cpDNA (Fig. 5) or nrDNA (Fig. 6). Despite the more recent diversification of the New World Menthinae (and thus less well supported branches), the shift from four to two stamens (and back) is more complicated. At least two separate origins of the two stamen feature followed by up to four reversals are evident in the cpDNA

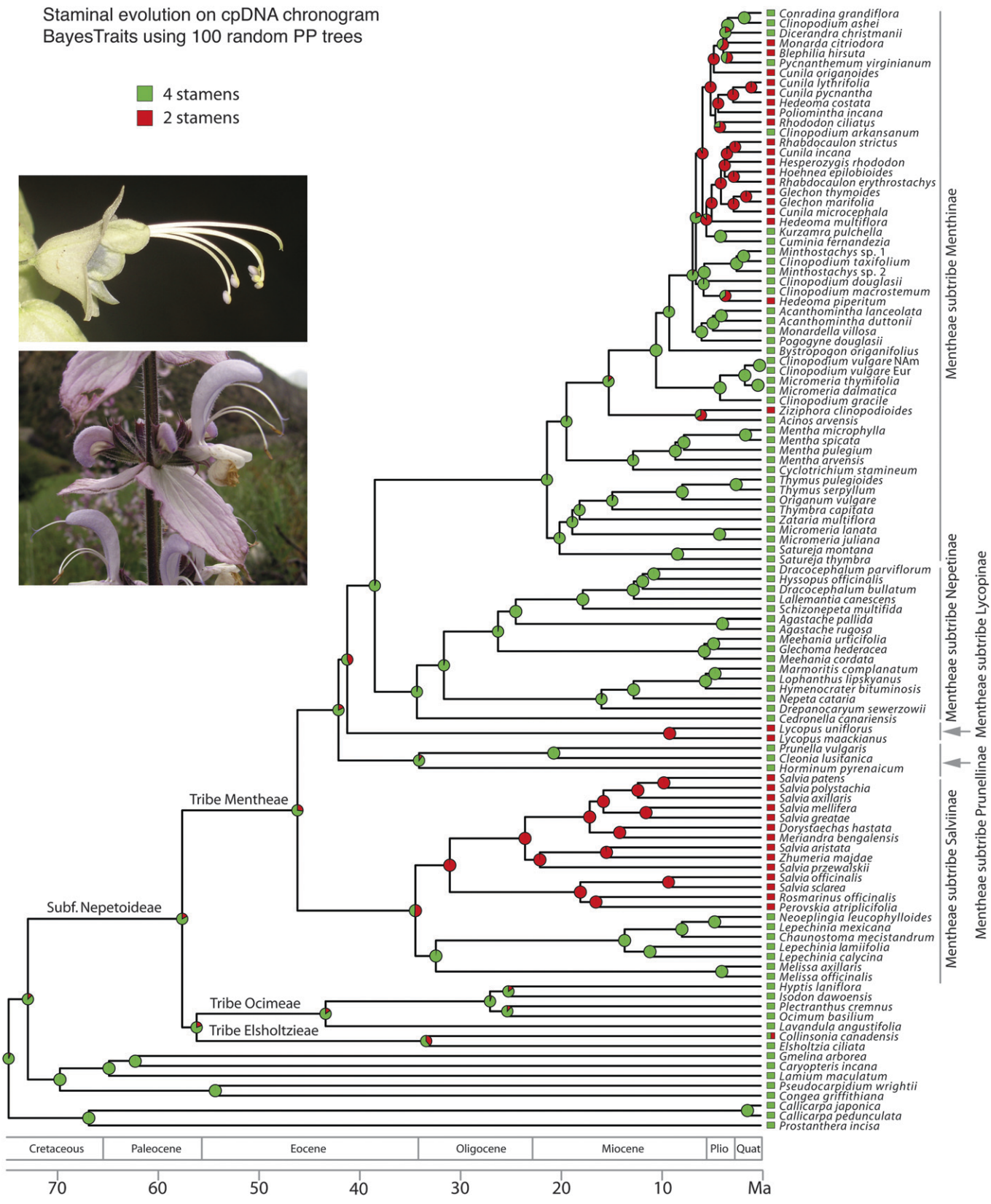

Fig. 5. Staminal evolution within the five subtribes of Mentheae as inferred under Bayesian framework in BayesTraits using 100 random posterior probability (PP) trees from the Bayesian analysis of cpDNA data. Nodal probabilities of 2 and 4 stamen states are depicted on the Bayesian tree of Fig. 1. Scale bar at bottom of figure indicates divergence times in my based on BEAST analysis. (Top photo: *Chaunostoma mecistandrum*, 4 stamens; bottom photo [*credit:* Alexey Yakovlev]: *Salvia sclarea*, 2 stamens).

tree (Fig. 5). The more heavily sampled nrDNA tree for Menthinae (Fig. 6) also indicates two likely transitions to two stamens followed by up to three reversals.

DISCUSSION

The results presented here are based on the most comprehensive phylogenetic analysis ever conducted of tribe Mentheae, an important set of genera worldwide that often represents a significant component of herbaceous or even woody elements in Mediterranean and similar vegetation types. For the first time, 64 of the 65 recognized genera in the tribe have been evaluated, placed within a fossil-calibrated timeframe, and examined for transitions in a staminal feature widely regarded as key to species diversification in some genera (e.g., *Salvia*; Walker and Sytsma, 2007). The tribe is shown to be monophyletic and comprised of five, not three, subtribes. Ancestral area reconstruction places the origin of Mentheae in the broad Mediterranean region around 47 Ma in the mid-Eocene, about 9 Myr after the crown diversification of subfamily Nepetoideae at the Paleocene-Eocene border. Using this well-resolved phylogenetic framework, we discuss systematic, biogeographic, and evolutionary issues within tribe Mentheae.

***Subtribal delimitations*—**Both the cpDNA and nrDNA phylogenetic results (Figs. 1, 4) conflict with the subtribal designations of Harley et al. (2004). For the remainder of this paragraph, the placement of each genus by Harley et al. (2004) is given in parentheses. *Melissa* (incertae sedis) and *Neoeplingia* (Menthinae) are in a clade with the genera of subtribe Salviinae. *Heterolamium* (incertae sedis) and *Hyssopus* (Menthinae) are in a well-supported clade (Figs. 1, 4) with all genera of subtribe Nepetinae. The genera *Cleonia*, *Horminum*, *Lycopus*, and *Prunella* (Menthinae) form a grade at the base of either Nepetinae + Menthinae (cpDNA; Fig. 1) or Nepetinae (nrDNA; Fig. 4).

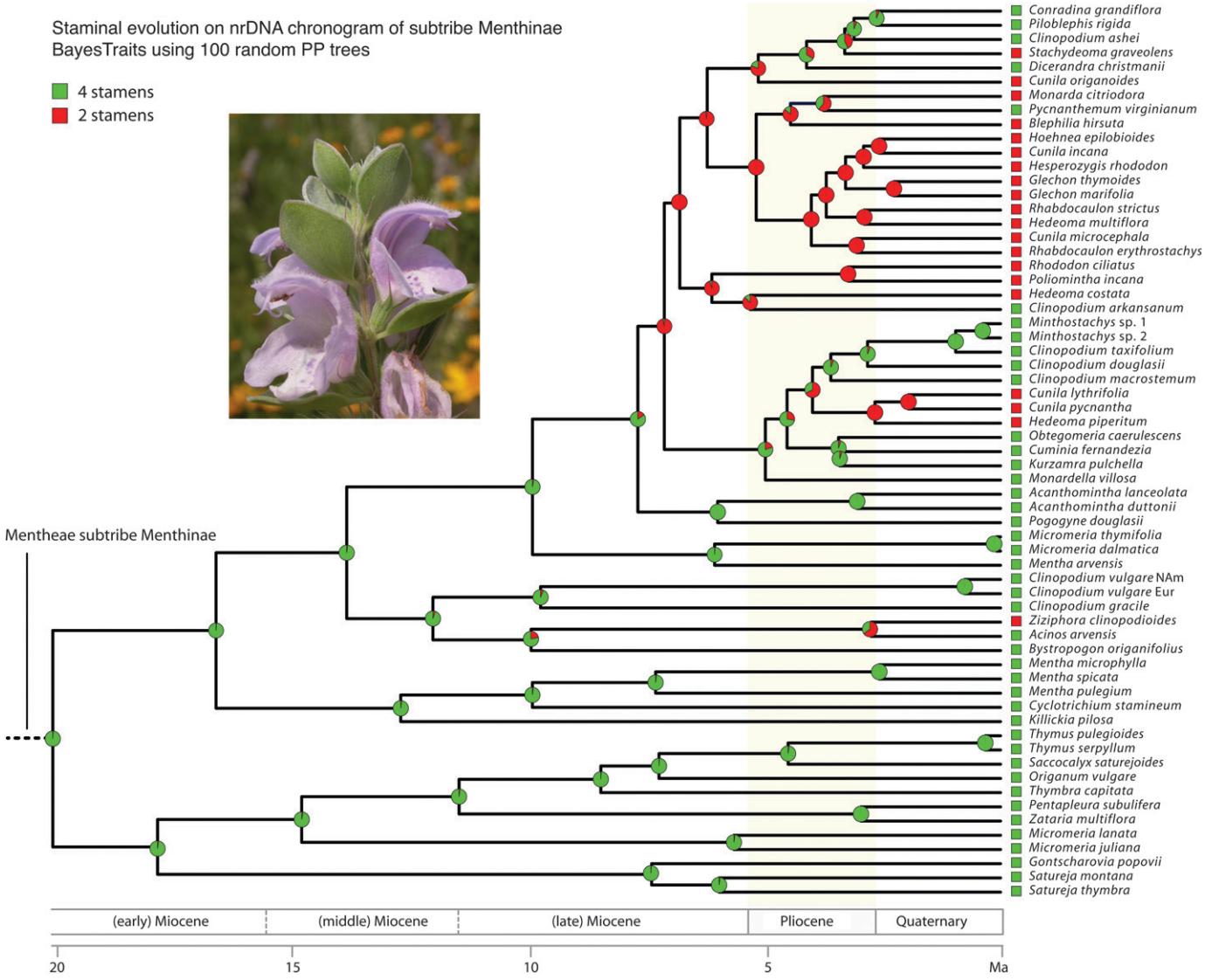

Fig. 6. Staminal evolution within only the subtribe Menthinae of tribe Mentheae as inferred under Bayesian framework in BayesTraits using 100 random posterior probability (PP) trees from the Bayesian analysis of nrDNA data. Nodal probabilities of 2 and 4 stamen states are depicted on the Bayesian tree of Fig. 5. Scale bar at bottom of figure indicates divergence times in my based on BEAST analysis. (Photo: *Glechon marifolia*).

Thus, we argue for the recognition of subtribes Prunellinae and Lycopinae. Subtribe Menthinae (except for *Neoeplingia*, *Hyssopus*, *Cleonia*, *Horminum*, *Lycopus*, and *Prunella*) as defined by Harley et al. (2004) was strongly supported as monophyletic (Figs. 1, 4). For the sake of simplicity, the subtribes within Mentheae will be discussed as delimited in Appendix 2 for the remainder of this paper.

Sectional assignments in Mentheae—Harley et al. (2004) recognized three subtribes within Mentheae (Salviinae, Nepetinae, Menthinae; Appendix 2), largely based upon morphological (Cantino and Sanders, 1986; Cantino et al., 1992) and molecular (Wagstaff et al., 1995; Wagstaff and Olmstead, 1997; Cantino and Wagstaff, 1998; Wagstaff et al., 1998) evidence. Since the work of Harley et al. (2004), there have been several molecular (Trusty et al., 2004; Paton et al., 2004; Walker et al., 2004; Bräuchler et al., 2005, 2010; Edwards et al., 2006; Walker and Sytsma, 2007; Drew and Sytsma, 2011) and morphological (Moon et al., 2008, 2009, 2010; Ryding, 2010a, b) studies focused on and within Mentheae that have further clarified relationships within the tribe. Based upon the aforementioned studies and the phylogenetic results (Figs. 1, 4) presented in this paper we are proposing subtribal recircumscriptions of Menthinae, Nepetinae, and Salviinae as listed in Appendix 2.

In agreement with our phylogenetic results, morphological characters such as pericarp structure (Ryding, 2010a), absence or near absence of calyx crystals (Ryding, 2010b), and abscission scar characters (Moon et al., 2010) support placing *Cleonia*, *Horminum*, and *Prunella* into a distinct subtribe (Prunellinae). Wunderlich (1967) treated *Cleonia* and *Prunella* as a distinct tribe (Prunelleae), but treated *Horminum* separately (tribe Hormineae). Likewise, the presence of only two stamens, a unique pericarp structure (Ryding, 2010a), and a very long branch in both cpDNA (Fig. 1) and nrDNA (Fig. 4) analyses support subtribal status for *Lycopus* (Lycopinae). Aside from their morphological and genetic distinctiveness, placing the four genera into two distinct subtribes (as opposed to within Nepetinae) is prudent because the phylogenetic placement of the two groups in nrDNA and cpDNA analyses is discordant.

We are therefore formally proposing one new subtribe within tribe Mentheae and resurrecting another:

Lycopinae *B. T. Drew & Sytsma, subtribe nov. TYPE: Lycopus L.*Rhizomatous perennials, leaves toothed to lobed, two fertile exserted stamens (except *Lycopus virginicus*), staminodes minute or absent, style exserted, inflorescences axillary, calyx 4–5 lobed, corolla white, usually less than 5 mm long, fruits tuberculate with thickened pericarp, abscission scar without an expanded area.

Included genus: *Lycopus*

Prunellinae *(Dumortier) B. T. Drew & Sytsma, TYPE: Prunella L.*Annual or perennial herbs, leaves entire to pinnately lobed, stamens 4 with bireticulate pollen, inflorescences verticillate, calyx 10 or 13 nerved, nutlets ovoid to rounded, abscission scar triangular to circular, without an expanded area.

Included genera: *Cleonia*, *Horminum*, *Prunella*

Taxonomic considerations at the generic level—A striking feature from both the cpDNA and nrDNA analyses is the number of genera that are not monophyletic. Within subtribe Menthinae, *Cunila*, *Clinopodium*, *Hedeoma*, and *Rhabdocaulon* are clearly paraphyletic in both nrDNA and cpDNA analyses. *Micromeria* (sensu Harley et al., 2004) is also not monophyletic, as first shown by Bräuchler et al. (2005). In the nrDNA tree, *Mentha* is paraphyletic. In subtribe Nepetinae, as previously discussed, *Meehania* and *Dracocephalum* are paraphyletic in both data sets. Subtribe Salviinae also has nonmonophyletic genera (e.g., *Salvia*), but these results have been discussed elsewhere (Walker et al., 2004; Walker and Sytsma, 2007; Drew and Sytsma, 2011).

Cunila has not received much attention since the original circumscription by Epling (1937) and is clearly in need of taxonomic revision based on both the cpDNA and nrDNA phylogenies. Of the five *Cunila* accessions included in this study, only the two Mexican species (*Cunila lythrifolia* and *C. pycnantha*) form a clade. The other species sampled fall within a clade of southeastern South American genera (*Cunila incana* and *C. microcephala*) and a clade of southeastern North American taxa (*Cunila origanoides*). The species of *Cunila* sampled here fall in clades with strong geographic signal, and the phylogenetic results presented here could reflect in part past hybridization events with other genera. However, the fact that the genus is morphologically heterogeneous and has an extremely disjunct range lends credence to the argument that the genus should be reevaluated with more extensive sampling of species and geographic populations.

Clinopodium has received much attention in Bräuchler et al. (2010) and will not be discussed here other than to say that the treatment as put forth by Doroszenko (1986) should be revisited. *Hedeoma* also is clearly paraphyletic, with each of the three accessions sampled placed into different but well-supported clades more or less corresponding to geographical affinities. The two accessions of *Rhabdocaulon* included here were also not monophyletic.

In the cpDNA tree, two samples of *Micromeria* (sensu Harley et al., 2004) were part of a well-supported monophyletic clade that also included three accessions of *Clinopodium* (Fig. 1), a finding in agreement with Bräuchler et al. (2005). On the basis of their findings, Bräuchler et al. (2006) formally transferred *Micromeria* section *Pseudomelissa* to *Clinopodium*. In our nrDNA phylogeny (Fig. 4), however, the two *Micromeria* accessions are in a well-supported clade with *Mentha arvensis*, and the *Clinopodium* accessions (with which *Micromeria* share similar cpDNA) are in a different well-supported clade with *Acinos* (*Clinopodium* in Harley et al., 2004), *Bystropogon*, and *Ziziphora*. Our nrDNA results question the validity of the taxonomic transfer of Bräuchler et al. (2006), which were justified largely by their cpDNA phylogenetic analysis (Bräuchler et al., 2005). Low-copy nuclear results (B. T. Drew and K. J. Sytsma, unpublished data) corroborate the nrDNA results presented here. Our limited sampling within this group prevents clear recommendations about the taxonomic placement of *Micromeria* section *Pseudomelissa*, but clearly its placement within *Clinopodium* is dubious based on the nrDNA evidence presented here. This situation illustrates the danger and subsequent taxonomic confusion that can arise from making taxonomic changes based on only cpDNA data. Interestingly, though nearly every other genus within subtribe Menthinae was well discussed in Bräuchler et al. (2010), this problematic issue was not addressed.

In both the cpDNA and nrDNA phylogenies a well-supported clade of southeastern South American taxa emerged consisting of *Cunila*, *Glechon*, *Hedeoma multiflora*, *Hesperozygis*, *Hoehnea*, and *Rhabdocaulon*. As discussed above, several of these genera are not monophyletic. Although certainly not comprehensive, this study represents the most detailed molecular phylogenetic study

to date on this little studied South American clade and illustrates the need to investigate this group more thoroughly. We are currently developing low copy nuclear markers to aid in the phylogenetic reconstruction of this group.

***Biogeography and dating*—**Members of Mentheae, like others of subfamily Nepetoideae, possess mericarps as the functional dispersal unit. The dispersal of these nutlets (reviewed by Boumann and Meeuse, 1992; Harley et al., 2004) is limited. Myxospermy is common in Mentheae and presumably aids in fixing the mericarps to the soil in the immediate vicinity of the parent. Special adaptations to aid in more long-distance dispersal are seen in Mentheae, but these appear to be of recent origin and advantageous in habitats outside the primary one seen in Mentheae—open savannas subject to seasonal climate. These include wings, apical hairs, or scales on the nutlets and inflated calyces for wind dispersal, flotation "sacs" for water dispersal, myxospermy variants and calyx spines for epizoochory, and even tumbleweed habit for wind dispersal of the entire plant (Harley et al., 2004). In general, the biogeographic spread of Mentheae must be interpreted as migration across existing land bridges and the rarer, long-distance dispersal events across land or water barriers. Although there are conspicuous examples of widespread genera (e.g., *Lycopus*, *Mentha*, *Salvia*) and even species (*Prunella vulgaris*) in Mentheae, the tribe has rarely dispersed to and colonized Australia, Southeast Asia, or sub-Saharan Africa. As our biogeographic analyses indicate, few shifts are invoked to North America and especially South America despite the considerable diversity seen today in these regions.

The biogeographic and temporal radiation of Mentheae presented here is based on calibrations of two fossils: the earliest known hexacoplate pollen that defines Nepetoideae and a more recent *Melissa* fruit fossil. We did not use the reported nutlet fruit fossil from Europe attributed to *Lycopus* of subtribe Lycopinae (Mai, 1985) because of the long branch leading to the genus (Fig. 2). However, its Oligocene date is consistent with the long stem of *Lycopus* (Fig. 2). Similarly, we did not use the *Salvia* pollen from late Miocene deposits in Alaska (Emboden, 1964) because of both uncertainties with its placement in the "Salvia" lineage and our lack of sampling within this lineage. However, its age is also consistent with the ages of several branches of New World *Salvia* (Fig. 2). Thus, despite the lack of a strong fossil record for the family, the subfamily, and tribe Mentheae, a consistent and clearer biogeographic scenario is emerging for this remarkable radiation.

Our analyses (DEC: Figs. 2, 3, Appendix S3; S-DIVA: Appendices S4–S6) strongly support the idea that tribe Mentheae had a southern European/southwestern Asian origin and subsequently radiated toward a nearly cosmopolitan distribution. The crown radiation of subfamily Nepetoideae occurred at the Paleocene/Eocene boundary (57–52 Ma), Mentheae arose in the mid-Eocene (46 Ma), and all five subtribes (Salviinae, Prunellinae, Lycopinae, Nepetinae, and Menthinae) were extant by the close of the Eocene and the beginning of the Oligocene (Fig. 2). All five subtribes (Fig. 2) appear to have Mediterranean origins, and all five subtribes still have a major presence in the Mediterranean region and biome. The crown radiation of Mentheae occurred after the Early Eocene Climatic Optimum (52 Ma) with global temperature decreasing and seasonality increasing (Thompson, 2005; Graham, 2011). Early versions of shrubland/savanna vegetation with its characteristic ligneous sclerophyll features are known from northern regions of the Mediterranean already by the Late Eocene based on fossil macrofloras (Palamarev, 1989; Thompson, 2005). Intensification of both aridity and temporal rhythm of seasonal rainfall occurred in the Mediterranean through the late Tertiary and culminated in the Pliocene (3 Ma) events that largely generated the present-day Mediterranean biome (Suc, 1984). A similar history is seen within North America in the initial rise of the Madrean-Tethyan sclerophyll vegetation (Axelrod, 1975, 1988; Raven, 1973; Raven and Axelrod, 1978). Much of the radiation of the Old World lineages of Mentheae corresponds to timing of these global climatic shifts, as has been demonstrated for other Mediterranean lineages (Mansion et al., 2008; Salvo et al., 2010).

The DEC analysis suggests that the crown of subtribe Salviinae (Fig. 2, event I) had a combined area (in part) comprising the Mediterranean/North America at the Eocene/Oligocene boundary (33 Ma), implying range extension to North America sometime after the rise of Mentheae in the middle Eocene (46 Ma). Soon afterward in the Oligocene (Fig. 2, event II), a vicariant split gave rise to the sister lineages of Old World *Melissa* and New World *Lepechinia*. The timing of this trans-Atlantic migration event (Eocene/Oligocene boundary) is supported to some extent by Axelrod's (1975) postulation of the existence of a continuous, trans-Atlantic, evergreen, sclerophyllous vegetation forming first in the early Eocene and continuing onto the end of the Oligocene. More recent paleobotanical and geological evidence indicates, however, that a continuous, trans-Atlantic land bridge was interrupted after the early Eocene (Graham, 1993; Hohmann et al., 2006) making direct overland migration for Mentheae not possible at that time. However, Tiffney (1985, 2000) and Tiffney and Manchester (2001) argue, using fossil evidence and dated phylogenies, that a physically *dis*continuous, trans-Atlantic migration route between western Eurasia and North America for plant taxa tolerant of higher-latitude climate may have existed until the Oligocene or probably even the Miocene (Tiffney and Manchester, 2001). Two such discontinuous routes that might have played a role in this early movement to North America are the Thulean (45°–50°N) and DeGeer (10°15° farther north) as described by Graham (1993).

Within subtribe Salviinae, extensive radiations began in the middle Miocene and involved at least two other separate dispersals to the New World in the "Salvia" lineage (Fig. 2). Our sampling within subtribe Salviinae is rather limited, but at least two dispersals from North America (*Lepechinia* and *Salvia*) to South America are shown to have occurred (Fig. 2, events III and IV). The former dispersal occurred sometime prior to the middle Miocene (14–10 Ma) and before the closure of the Panama Isthmus. The latter dispersal is much more recent and gave rise to the extremely species-rich South American clade of *Salvia* sect. *Calosphace* (represented here by *Salvia polystachia* native to North America (Mexico) but sister to the large South American lineage; Walker 2006).

Several genera (*Dracocephalum*, *Meehania*, *Agastache*) within subtribe Nepetinae exhibit geographical disjunctions between North America and Eastern Asia/Eurasia. Our results (Fig. 2, events V–VII) show that these disjunctions occurred at different times. *Dracocephalum* is a fairly large genus of ~70 species, with 69 species native to Eurasia (one in N. Africa) and one species native to Northern North America. The Eurasian/North American disjunction is shown to be at 10 Ma in the late Miocene (Fig. 2, event V). *Dracocephalum*, however, is not monophyletic in either the cpDNA (Figs. 1, 2) or nuclear (Fig. 4) data sets, with at least *Hyssopus* (Figs. 1, 2, 4) and possibly *Lallemantia* (Fig. 4) embedded within it. *Meehania* is comprised of

six species from East Asia (5) and eastern North America (1). The geographical separation of this genus occurred at Ma, at the beginning of the Pliocene (Fig. 2, event VI). Like *Dracocephalum*, *Meehania* is also not monophyletic in our analyses (Figs. 1, 2, 4). In the cpDNA phylogeny (Figs. 1, 2), *Glechoma* is embedded within *Meehania*, and in the nrDNA phylogeny (Fig. 4) *Glechoma* and *Heterolamium* are each embedded within *Meehania*. In both the cpDNA and nrDNA analyses, these four accessions form well-supported clades. Although *Heterolamium* was not included in the cpDNA analysis here, Drew and Sytsma, (2011) demonstrated that *Heterolamium* was sister to *Meehania urticifolia*, and *Glechoma hederacea* was sister to these two taxa. *Agastache*, with one species native to East Asia and ~21 species native to North America, shows a geographical split at 4 Ma in the Pliocene (Fig. 2, event VII). Further sampling of North American *Agastache* will be necessary to unambiguously demonstrate the monophyly of the North American taxa and the directionality of dispersal between East Asia and North America.

Subtribe Menthinae (at least as indicated by the extant taxa we sampled) shows a fairly slow rate of diversification beginning in the early Miocene and then subsequent rapid diversification toward the late Miocene, especially in the New World (Fig. 3, Appendix S3). In both the cpDNA and nrDNA trees, dispersal to the New World is shown to have taken place around 8–9 Ma in the late Miocene. Perhaps as a response to worldwide cooling and aridification since the mid-Miocene (Woodruff et al., 1981; Zachos et al., 2001; Graham, 2011), subtribe Menthinae shows a major diversification within the New World beginning near the Miocene/Pliocene boundary. This major diversification involves two separate dispersal/migration events to South America at 4–5 Ma (Fig. 3, events II, III). This scenario of two migrations from North America to South America in subtribe Menthinae is consistent with the nrDNA chronogram with different taxa sampling and relationships (Appendix S3) and with S-DIVA analysis of both cpDNA and nrDNA (Appendices S4, S6). The timing of these two events and subsequent diversification in both North and South America strongly suggests migration over an almost completely formed Panama Isthmus (Keigwin, 1978).

Plate tectonic models and paleobotanical stratigraphic evidence for the Panama Isthmus region place the emergence of continuous land surfaces at 3.5 Ma (Coates et al., 1992; Graham, 1992, 1999, 2010), with perhaps more temperate habitats not available until 2.5 Ma (Jackson et al., 1996; Graham, 2010). Although mammal and even bird interchange between North and South America is timed to this closure (Marshall and Cifelli, 1990; Webb, 1991; Weir et al., 2009; Cody et al., 2010; Smith and Klicka, 2010), this is not true for plants that are more capable of overseas dispersal. Most plant lineages migrating from the north and dated with molecular clocks are inferred to have crossed the Panama Isthmus prior to its final closure (Cody et al., 2010; Hoorn et al., 2010). Of the six (of 25 total) plant lineages identified as crossing a closed Panama Isthmus (Cody et al., 2010), all but the legume *Platymiscium* (Saslis-Lagoudakis et al., 2008) appear to be very recent in age and not examples of North to South American plant migrations held in check until the closure of the isthmus. Mentheae subtribe Menthinae may thus be an exception, as well as exhibiting two separate migrations from North America to South America across a more or less continuous Panama Isthmus, both of which radiated extensively after making the crossing.

Staminal evolution—The transition from four stamens to two stamens is a notable feature within Lamiaceae and most importantly within tribe Mentheae. The shift to two stamens is clearly the first step necessary (preadaptation) for the evolution of the staminal lever mechanism in *Salvia* (Walker and Sytsma, 2007) and is important in pollination and species proliferation (Claßen-Bockhoff et al., 2004). The secondary transition to staminal lever device has arisen at least three times in a broadly paraphyletic *Salvia* (Walker et al., 2004; Walker and Sytsma, 2007). In the broader context of Mentheae, it was previously unclear how often the first transition to two stamens occurred and how often reversals occurred back to four stamens. These cpDNA and nrDNA analyses provide the first Mentheae-wide phylogenetic framework to address these questions.

The four-stamen flower is shown to be the ancestral condition within tribe Mentheae (Fig. 5). The transition to two-stamen flowers has independently occurred multiple times (Figs. 5, 6). Within subtribe Salviinae, there is only one transition from four to two stamens, occurring as a synapomorphy for the large "*Salvia*" clade (Fig. 5). The only other shift to two stamens occurring outside of subtribe Menthinae is found in *Lycopus* and could be considered a synapomorphy for subtribe Lycopinae. Within subtribe Menthinae, there have been multiple reductions from four to two stamens (Figs. 5, 6), but only one outside of the New World (*Ziziphora*). Due to the apparently rapid diversification of South America Menthinae and our incomplete sampling within larger genera, it is also unclear whether reversions back to four stamens have occurred (Figs. 5, 6).

It might be tempting to correlate shifts in stamen number and thus causation to increased diversification of lineages. However, this is premature in tribe Mentheae for several reasons. First, our sampling of subtribe Menthinae, although complete at the generic level, did not sample comprehensively within some of the larger genera. Also, many of these genera are shown here (and previously) to be paraphyletic or even polyphyletic (e.g., *Clinopodium*, *Cunila*, *Hedeoma*, *Rhabdocaulon*). Thus, we do not yet have the ability to assign species numbers to terminal lineages in Menthinae, a necessity to perform diversification analyses. Second, although the shift to two stamens within subtribe Salviinae is striking, leading to ~1200 species in the "*Salvia*" clade vs. ~50 species in its sister clade (including *Melissa*, *Lepechinia*), it may not be causative but rather a preadaptation for the stamina lever. These shifts to staminal lever mechanisms several times within "*Salvia*" are more strongly correlated with species numbers (Walker and Sytsma, 2007). Thus, future morphological and analytical studies should address in more detail these transitions from four to two stamens within the tribe Mentheae. Have the transitions occurred in the same way? What effect has the transition had on subsequent floral/pollinations diversification? Are these separate transitions correlated with increased species diversification (speciation minus extinction) relative to sister groups with four stamens? Why have stamen number shifts occurred more frequently in South American lineages of subtribe Menthinae than elsewhere?

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APPENDIX 1. Voucher information and GenBank accessions for the present study. RBG-Edinburgh = Royal Botanic Garden-Edinburgh, RSABG = Rancho Santa Ana Botanical Garden, UCBG = UC-Berkeley Botanical Garden. DBG = Denver Botanical Garden, NTBG = National Tropical Botanical Garden.

Taxon, Country of origin, *Voucher*; GenBank: *ycf1-rps15*, *trnL-trnF, rpl32-trnL,* ITS, ETS.

Acanthomintha duttonii (Abrams) Jokerst, cultivated-UCBG *H. Forbes s.n.* (UC); JQ669219, JQ669020, JQ669271, JQ669072, JQ669141; ***Acanthomintha lanceolata*** Curran, USA, *Crosby & Morin 14383* (MO); JF289000, DQ667522; JQ669272, JQ669073, JQ669142; ***Acinos arvensis*** Dandy, USA, *Judziewicz 14160* (WIS); JQ669220, JQ669021, JQ669273, JQ669074, JQ669143; ***Agastache pallida*** (Lindl.) Cory, Mexico, *B. Drew 118* (WIS); JF289001, JF301357, JQ669274, JQ669075, JQ669144; ***Agastache rugosa*** (Fisch. & C.A. Mey.) Kuntze, Japan, *H. Kanai, K Hasagawa, K. Ohkubo 8916* (WIS); JQ669221, JQ669022, JQ669275, JQ669076, JQ669145; ***Blephilia hirsuta*** (Pursh) Benth., USA, *T. Cochrane 13609* (WIS); JF289002, JF301358, JQ669276, JQ669077, JQ669146; ***Bystropogon origanifolius*** L'Hér., cultivated-USA, *B. Drew s.n.* (WIS); JQ669222, JQ669023, JQ669277, JQ669078, JQ669147; ***Callicarpa japonica*** Thunb., cultivated-UCBG 68.0362, *H. Forbes s.n.* (UC); JQ669223, JQ669024, JQ669278; ***Callicarpa pedunculata*** R. Br., cultivated-UCBG 2003.0363, *H. Forbes s.n.* (UC); JQ669224, JQ669025, JQ669279; ***Caryopteris incana*** (Thunb. ex Houtt.) Miq., cultivated-UCBG 1989.0459, *Erskine et al., SICH395* (UC); JF289003, JF301359, JQ669280; ***Cedronella canariensis*** (L.) Webb & Berthel., Canary Islands, cultivated-UCBG, 2004.0788, *Royl 6859* (UC); JF289004, JF301360, JQ669281, JQ669079, JQ669148; ***Chaunostoma mecistandrum*** Donn. Sm., El Salvador, *J.A. Monterrosa & R. A. Carballo 213* (MO); JF289005, JF301361, JQ669282, JF301342, JF301311; ***Cleonia lusitanica*** L., Spain, *D. Sanches & R. Garilan s.n.* (F); JF289006, DQ667495, DQ667309; ***Clinopodium arkansanum*** (Nutt.) House, USA, *B. Drew 80* (WIS); JF289007, JF301362, JQ669283, JQ669080, JQ669149; ***Clinopodium ashei*** (Weath.) Small, USA, *J. Walker 742* (WIS); JF289008, DQ667437, JQ669284, DQ667237, JQ669150; ***Clinopodium douglasii*** (Benth.) Kuntze, USA, *B. Drew 206* (WIS); JQ669225, JQ669026, JQ669285, JQ669081, JQ669151; ***Clinopodium gracile*** (Benth.) Kuntze, China, *Yau 8715* (WIS); JQ669226, JQ669027, JQ669286, JQ669082, JQ669152; ***Clinopodium macrostemum*** (Moc. & Sessé ex Benth.) Kuntze, Mexico, *B. Drew 147* (WIS); JQ669227, JQ669028, JQ669287, JQ669083, JQ669153; ***Clinopodium taxifolium*** (Kunth) Govaerts, Ecuador, *B. Drew 228* (WIS); JQ669228, JQ669029, JQ669288, JQ669084, JQ669154; ***Clinopodium vulgare*** L., USA, *B. Drew 81* (WIS); JF289009, JF301363, JQ669289, JQ669085, JQ669155; ***Clinopodium vulgare*** L., Portugal, *Riina 1579* (WIS); JQ669229, JQ669030, JQ669290, JQ669086, JQ669156; ***Collinsonia canadensis*** L., USA, cultivated-UCBG 1984.0696, *Raiche s.n.* (UC); JF289010, JF301364, JQ669291, JQ669087, JQ669157; ***Congea griffithiana*** Munir, cultivated-Hawaii, *Lorence 9944* (PTBG); JQ669230, JQ669031, JQ669292; ***Conradina grandiflora*** Small, USA, cultivated-Bok Tower Gardens 38717, *B. Drew s.n.* (WIS); JF289011, JF301365, JQ669293, JQ669088, JQ669158; ***Cuminia fernandezia*** Colla, Chile, *Stuessy et al., 11580* (OS); JQ669231, JQ669032, JQ669294, JQ669089, JQ669159; ***Cunila incana*** Benth., Uruguay, *K. Sytsma 7224* (WIS); JF289012, DQ667504, JQ669295, DQ667316, JQ669160; ***Cunila lythrifolia*** Benth., Mexico, *Rzedowski 251* (WIS); JQ669232, JQ669033, JQ669296, JQ669090, JQ669161; ***Cunilla microcephala*** Benth., Uruguay, *K. Sytsma 7247* (WIS); JF289013, DQ667491, JQ669297, JQ669091, JQ669162; ***Cunila origanoides*** (L.) Britton, U.S.A, *Stoots s.n.* (WIS); JQ669233, JQ669034, JQ669298, JQ669092, JQ669163; ***Cunila pycnantha*** B.L. Rob. & Greenm., Mexico, *Ruiz 3150* (WIS); JQ669234, JQ669035, JQ669299, JQ669093, JQ669164; ***Cyclotrichium stamineum*** (Boiss. & Hohen.) Manden. & Scheng., Iraq, *Gillett 9444* (US); JQ669235, JQ669036, JQ669300, JQ669094, JQ669165; ***Dicerandra christmanii*** Huck & Judd, USA, cultivated-Bok Tower Gardens, *B. Drew s.n.* (WIS); JQ669236, JQ669037, JQ669301, JQ669095, JQ669166; ***Dorystaechas hastata*** Boiss. & Heldr. ex Benth., cultivated RBG-Edinburgh 1972–0177D, *J. Walker s.n.* (WIS); JF289014, AY570454, JQ669302, DQ667252, JF301312; ***Dracocephalum bullatum*** Forrest ex Diels, China, *Boufford et al., 31785* (GH); JF289015, JF301366, JQ669303, JQ669096, JQ669167; ***Dracocephalum parviflorum*** Nutt., USA, *Thomas s.n.* (WIS); JQ669237, JQ669038, JQ669304, JQ669097, JQ669168; ***Drepanocaryum sewerzowii*** (Regel) Pojark., Tajikistan, *Rinziraeva 7540* (MO); JF289016, DQ667517, JQ669305, JQ669169; ***Elsholtzia ciliata*** (Thunb.) Hyl., USA, *B. Drew 210* (WIS); JF289017, JF301367, JQ669306, JQ669098, JQ669170; ***Glechoma hederacea*** L., USA, *B. Drew 69* (WIS); JF289018, JF301368, JQ669307, JQ669099, JQ669171; ***Glechon marifolia*** Benth., Uruguay, *K. Sytsma 7214* (WIS); JF289019, DQ667489, JQ669308, DQ667303, JQ669172; ***Glechon thymoides*** Spreng. Brazil, *C. Mondin 1421* (F); JQ669238, JQ669039, JQ669309, JQ669100, JQ669173; ***Gontscharovia popovii*** (B. Fedtsch. & Gontsch.) Boriss., Tadzhikistan, *Vvedensky s.n.* (M); GU381438; ***Gmelina arborea*** Roxb. ex Sm., cultivated-NTBG 750691.001, *T. Flynn 3103* (PTBG); JQ669239, JQ669040, JQ669310; ***Hedeoma costata*** A. Gray, Mexico, *J. Walker 2143* (WIS); JQ669240, JQ669041, JQ669311, DQ667236, JQ669174; ***Hedeoma multiflora*** Benth., Uruguay, *K. Sytsma 7243* (WIS); JQ669241, JQ669042, JQ669312, JQ669101, JQ669175; ***Hedeoma piperitum*** Benth., Mexico, *B. Drew 92* (WIS); JF289020, JF301369, JQ669313, JF301343, JF301313; ***Hesperozygis rhododon*** Epling, Brazil, *G. Hatschbach 44939* (WIS); JQ669242, JQ669043, JQ669102, JQ669176; ***Heterolamium debile*** (Hemsl.) C.Y. Wu, China, *Zhiduan 960093* (MO); JQ669103, JQ669177; *Hoehnea epilobioides* (Epling) Epling, Brazil, *G. Hatschbach 8-13-1984* (F); JQ669243, JQ669044, JQ669314, JQ669104, JQ669178; ***Horminum pyrenaicum*** L., cultivated-RBG-Edinburgh 1997-2109a, *J. Walker s.n.* (WIS); JF289022, AY570456, JQ669315,DQ667257, JF301314; ***Hymenocrater bituminosis*** Fisch. & C.A. Mey., Armenia, *K. Tamanyan & George Fayvush 4-2004* (NY); JQ669244, JQ669045, JQ669316, JQ669105, JQ669179; ***Hyptis laniflora*** Benth., Mexico, *B. Drew 41* (WIS); JF289024, JF301370, JQ669317; ***Hyssopus officinalis*** L., cultivated-DBG 003224/2, *M. Kintgen s.n.* (KHD); JF289023, JF301371, JQ669318, JQ669106, JQ669180; ***Isodon dawoensis*** (Hand.-Mazz.) H. Hara, cultivated-UCBG 90.066, *Erskine et al., 392* (UC); JF289025, JF301372, JQ669319; ***Killickia pilosa*** (Benth.) Bräuchler, Heubl & Doroszenko, South Africa, *C. Bräuchler 3810* (M); GU381382; ***Kurzamra pulchella*** Kuntze, Chile, *Werdermann 957* (MO); JQ669245, JQ669046, JQ669320, JQ669107, JQ669181; ***Lallemantia canescens*** Fisch. & C.A. Mey., cultivated-DBG 940037, *M. Kintgen s.n.* (KHD); JF289026, JF301373, JQ669321, JQ669108, JQ669182; ***Lamium maculatum*** L., cultivated, *B. Drew 75* (WIS); JF289027, JF301374, JQ669322; ***Lavandula angustifolia*** Mill., cultivated, *J. Walker 2565* (WIS); JF289028, AY570457, JQ669323; ***Lepechinia calycina*** (Benth.) Epling ex Munz, USA, *B. Drew 197* (WIS); JF289029, JF301375, JQ669324, JF301344, JF301315; ***Lepechinia lamiifolia*** (Benth.) Epling, Peru, *B. Drew 178* (WIS); JF289034, JF301379, JQ669325, JF301348, JF301320; ***Lepechinia mexicana*** (S. Schauer) Epling, Mexico, *B. Drew 164* (WIS); JF289035, JF301380, JQ669326, JF301349, JF301321; ***Lindernia dubia*** (L.) Pennell, U.S.A, *B. Drew 79* (WIS); JQ669246, JQ669047, JQ669327; ***Lophanthus lipskyanus*** Ik.-Gal. & Nevski, Uzbekistan, *Vassiljeva* (WIS); JF289039, JF301384, JQ669328, JQ669109, JQ669183; ***Lycopus maackianus*** Makino, Japan, *Julita 661* (WIS); JQ669247, JQ669048, JQ669329, JQ669110, JQ669184; ***Lycopus uniflorus*** Michx., USA, *J. Walker 2586* (WIS); JF289040, DQ667488, JQ669330, DQ667302, JQ669185; ***Marmoritis complanatum*** (Dunn) A.L. Budantzev, China, *D.E. Boufford et al., 32012* (GH); JQ669248, JQ669049, JQ669331, JQ669111, JQ669186; ***Meehania cordata*** Britton, China, *A. E. Radford 45379* (WIS); JQ669249, JQ669050, JQ669332, JQ669112, JQ669187; ***Meehania urticifolia*** (Miq.) Makino, China, *Lai Shushen & Shan Hanrong s.n.* (MO); JF289041, JF301385, JQ669333, JQ669113, JQ669188; ***Melissa axillaris*** (Benth.) Bakh. f., China, *D.E. Boufford et al., 24526* (HUH); JQ669250, JQ669051, JQ669334, JQ669114, JQ669189; ***Melissa officinalis*** L., cultivated-UW-Madison, *B. Drew 70* (WIS); JF289042, JF301386, JF301353, JF301325, JQ669335; ***Mentha arvensis*** L., USA, *B. Drew 82* (WIS); JF289043, JF301387, JQ669336, JQ669115, JQ669190; ***Mentha microphylla*** K. Koch, Portugal, *Riina 1575* (WIS); JQ669251, JQ669052, JQ669337, JQ669116, JQ669191; ***Mentha pulegium*** L., Portugal, *Riina 1574* (WIS); JQ669252, JQ669053, JQ669338, JQ669117, JQ669192; ***Mentha spicata*** L., USA, *J. Walker 2566* (WIS); JQ669253, JQ669054, JQ669339, DQ667244, JQ669193; ***Meriandra bengalensis*** (Konig ex Roxb.) Benth., Yemen, ***Lavranus & Newton 15796*** (MO); JF289044, DQ667518, DQ667329, JF301326; ***Micromeria dalmatica*** Benth., cultivated-DBG 811288, *M. Kintgen s.n.* (KHD); JQ669254, JQ669055, JQ669340, JQ669118, JQ669194; ***Micromeria juliana*** (L.) Bentham ex Reichb., cultivated-UCBG 91.0995,

H. Forbes s.n. (UC); JQ669255, JQ669056, JQ669341, JQ669119, JQ669195; ***Micromeria lanata*** (C. Sm. ex Link) Benth., cultivated-Wisconsin, *B. Drew s.n.* (WIS); JQ669256, JQ669057, JQ669342, JQ669120, JQ669196; ***Micromeria thymifolia*** Fritsch, cultivated-DBG 820510, *M. Kintgen s.n.* (KHD); JQ669257, JQ669058, JQ669343, JQ669121, JQ669197; ***Minthostachys mollis*** (Kunth) Griseb., Peru, *B. Drew 345* (WIS); JQ669258, JQ669059, JQ669344, JQ669122, JQ669198; ***Minthostachys mollis*** (Kunth) Griseb., Peru, *B. Drew 349* (WIS); JQ669259, JQ669060, JQ669345, JQ669123, JQ669199; ***Monarda citriodora*** Cerv. ex Lag., Mexico, *B. Drew 114* (WIS); JF289045, JF301388, JQ669346, JQ669124, JQ669200; ***Monardella villosa*** Benth., USA, *B. Drew 66* (WIS); JF289046, JF301389, JQ669347, JQ669125, JQ669201; ***Neoeplingia leucophylloides*** Ramamoorthy, Hiriart & Medrano, Mexico, *B. Drew 129* (WIS); JF289047, JF301390, JQ669348, JF301354, JF301327; ***Nepeta cataria*** L., USA, *B. Drew 72* (WIS); JF289048, JF301391, JQ669349, JQ669126, JQ669202; ***Obtegomeria caerulescens*** (Benth.), Colombia, *J.R.I. Wood 4974*, (K); GU381430; ***Ocimum basilicum*** L., cultivated, *J. Walker 2557* (WIS); JF289049, AY570462, JQ669350; ***Origanum vulgare*** L., USA, *B. Drew 77* (WIS); JF289050, JF301392, JQ669351, JQ669127, JQ669203; ***Pentapleura subulifera*** Hand.-Mazz., Iraq, *K. H. Rechinger 12085* (W); GU381449; ***Perovskia atriplicifolia*** Benth., cultivated, *J. Walker 2524* (WIS); JF289051, AY570464, JQ669352, DQ667223, JF301328; ***Piloblephis rigida*** (Bartram ex Benth.) Raf., USA, *Edwards 149* (FLAS); AY506644.1; ***Phryma leptostachya*** L., USA, *B. Drew 73* (WIS); JQ669260, JQ669061, JQ669353; ***Plectranthus cremnus*** B.J. Conn, USA, cultivated-UCBG 3.0347, *H. Forbes s.n.* (UC); JF289052, JF301393, JQ669354; ***Pogogyne douglasii*** Benth., USA, cultivated-UCBG 91.1071, *H. Forbes s.n.* (JEPS); JF289053, JF301394, JQ669355, JQ669128, JQ669204; ***Poliomintha incana*** (Torr.) A. Gray, USA, *Pideon s.n.* (WIS); JF289054, JF301395, JQ669356, JQ669129, JQ669205; ***Prostanthera incisa*** R. Br., cultivated-UCBG 87.1485, *H. Forbes s.n.* (UC); JQ669261, JQ669062, JQ669357; ***Prunella vulgaris*** L., USA, *J. Walker 3225* (WIS); JF289055, DQ667508, JQ669358, JQ669130, JQ669206; ***Pseudocarpidium wrightii*** Millsp., cultivated-Fairchild Botanical Garden, *Drew s.n.* (WIS); JQ669262, JQ669063, JQ669359; ***Pycnanthemum virginianum*** (L.) Durand & Jackson, USA, *B. Drew 85* (WIS); JQ669263, JQ669064, JQ669360, JQ669131, JQ669207; ***Rhabdocaulon erythrostachys*** Epling, Brazil, *Sergio A. L. Bordignon 851* (F); JQ669264, JQ669065, JQ669361, JQ669132, JQ669208; ***Rhabdocaulon strictus*** (Benth.) Epling, Uruguay, *Sytsma 7218* (WIS); JF289056, JF301396, JQ669362, JQ669133, JQ669209; ***Rhododon ciliatus*** (Benth.) Epling, USA, *Singhurst s.n* (TEX); JF289057, JF301397, JQ669363, JQ669134, JQ669210; ***Rosmarinus officinalis*** L., cultivated, *J. Walker 2558* (WIS); JF289058, AY570465, JQ669364, DQ667241, JF301329; ***Saccocalyx saturejoides*** Coss. and Dur., Algeria, *L. Faurel 5650* (MSB); GU381462; ***Salvia aristata*** Aucher ex Benth, Iran, *Wedelbo & Assadi s.n.* (E); JF289059, DQ667465, JQ669365, DQ667280, JF301336; ***Salvia axillaris*** Moc. & Sessé, Mexico, *J. Walker 3038* (WIS); JF289060, DQ667480, JQ669366, DQ667294, JF301330; ***Salvia greatae*** Brandegee, USA, *J. Walker 2511* (WIS); JF289062, AY570481, JQ669367, DQ667215, JF301331; ***Salvia mellifera*** Greene, USA, *J. Walker 2550* (WIS); JF289064, DQ667427, JQ669368, DQ667220, JF301338; ***Salvia officinalis*** L., cultivated-UCBG 7.0083, *M. Palma s.n.* (UC); JF289065, JF301398, JQ669369, JF301355, JF301332; ***Salvia patens*** Cav., cultivated-RBG-Edinburgh 1973-9197, *J. Walker s.n.* (WIS); JF289066, DQ667442, JQ669370; DQ667253, JF301333; ***Salvia polystachia*** Cav., cultivated-UCBG 92.052, *Breedlove & Mahoney 72286* (UC); JF289067, JF301399, JQ669371, JF30135, JF301334; ***Salvia przewalskii*** Maxim., cultivated-RBG-Edinburgh 1993-2067A, *J. Walker s.n.* (WIS); JF289068, DQ667443, JQ669372, DQ667254, JF301339; ***Salvia sclarea*** L., cultivated, *J. Walker 2527* (WIS); JQ669265, JQ669066, JQ669373, 667222, JF301335; ***Satureja montana*** L., cultivated-UCBG 2002.0593, *H. Forbes s.n.* (UC); JQ669266, JQ669067, JQ669374, JQ669135, JQ669211; ***Satureja thymbra*** L., cultivated-UCBG 2002.0540, *H. Forbes s.n.* (UC); JQ669267, JQ669068, JQ669375, JQ669136, JQ669212; ***Schizonepeta multifida*** Briq., Siberia, *Boyd 4805* (WIS); JF289070, JF301400, JQ669376, DQ667313, JQ669213; ***Stachydeoma graveolens*** (Chapm. ex A. Gray) Small, USA, *Edwards and Ionta 162* (FLAS); AY943492; ***Thymbra capitata*** Cav., cultivated-UCBG 96.0817, *H. Forbes s.n.* (UC); JF289071, JF301401, JQ669377, JQ669137, JQ669214; ***Thymus pulegioides*** L., Portugal, *Riina 1577* (WIS); JQ669268, JQ669069, JQ669378, JQ669138, JQ669215; ***Thymus serpyllum*** L., cultivated-USA, *J. Walker 2564* (WIS); JQ669269, JQ669070, JQ669379, DQ667242, JQ669216; ***Zataria multiflora*** Boiss., Iran, K. H. *Rechinger 51885* (MO); JQ669270, JQ669071, JQ669380, JQ669139, JQ669217; ***Zhumeria majdae*** Rech. f. & Wendelbo, *Terme 14573* (E); JF289072, DQ667524, JQ669381, DQ667335, JF301341; ***Ziziphora clinopodioides*** Lam., cultivated-DBG 980177, *M. Kintgen s.n.* (KHD); JF289073, JF301402, JQ669382, JQ669140, JQ669218;

APPENDIX 2. Sectional delimitations according to Harley et al. (2004) and the present study. Taxa in brackets indicate genera not recognized in Harley et al. (2004).

Harley et al. (2004)	Present study
Subtribe Menthinae	Subtribe Menthinae
[*Acinos* Mill.]	[*Acinos* Mill.]
Acanthomintha (A. Gray) Benth. & Hook. f.	*Acanthomintha* (A. Gray) Benth. & Hook. f.
Blephilia Raf.	*Blephilia* Raf.
Bystropogon L'Hér.	*Bystropogon* L'Hér.
Cleonia L.	*Clinopodium* L.
Clinopodium L.	*Conradina* A. Gray
Conradina A. Gray	*Cuminia* Colla
Cuminia Colla	*Cunila* D. Royen ex L.
Cunila D. Royen ex L.	*Cyclotrichium* Mandenova & Schengelia
Cyclotrichium Mandenova & Schengelia	*Dicerandra* Benth.
Dicerandra Benth.	*Eriothymus* Rchb.
Eriothymus Rchb.	*Glechon* Spreng.
Glechon Spreng.	*Gontscharovia* Boriss.
Gontscharovia Boriss.	*Hedeoma* Pers.
Hedeoma Pers.	*Hesperozygis* Epling
Hesperozygis Epling	*Hoehnea* Epling
Hoehnea Epling	[*Killickia* Bräuchler, Heubl & Doroszenko]
[*Killickia* Bräuchler, Heubl & Doroszenko]	*Kurzamra* Kuntze
Kurzamra Kuntze	*Mentha* L.
Mentha L.	*Micromeria* Benth.
Micromeria Benth.	*Minthostachys* (Benth.) Spach
Minthostachys (Benth.) Spach	*Monarda* L.
Monarda L.	*Monardella* Benth.
Monardella Benth.	*Obtegomeria* Doroszenko & P. D. Cantino
Obtegomeria Doroszenko & P. D. Cantino	*Origanum* L.
Origanum L.	*Pentapleura* Handel-Mazzetti
Neoeplingia Ramamoorthy, Hiriart & Medrano	*Piloblephis* Raf.
Pentapleura Handel-Mazzetti	*Pogogyne* Benth.
Piloblephis Raf.	*Poliomintha* A. Gray
Pogogyne Benth.	*Pycnanthemum* Michx.
Poliomintha A. Gray	*Rhabdocaulon* Epling
Pycnanthemum Michx.	*Rhododon* Epling
Rhabdocaulon Epling	*Saccocalyx* Coss. & Durieu
Rhododon Epling	*Satureja* L.
Saccocalyx Coss. & Durieu	*Stachydeoma* Small
Satureja L.	*Thymbra* L.
Stachydeoma Small	*Thymus* L.
Thymbra L.	*Zataria* Boiss.
Thymus L.	*Ziziphora* L.
Zataria Boiss.	Subtribe Prunellinae
Ziziphora L.	*Horminum* L.
Horminum L.	*Cleonia* L.
Hyssopus L.	*Prunella* L.
Prunella L.	Subtribe Lycopinae
Lycopus L.	*Lycopus* L.
Subtribe Salviinae	Subtribe Salviinae
Chaunostoma Donn. Sm.	*Chaunostoma* Donn. Sm.
Dorystaechas Boiss. & Heldreich ex Benth.	*Dorystaechas* Boiss. & Heldreich ex Benth.
Lepechinia Willd.	*Lepechinia* Willd.
Meriandra Benth.	*Meriandra* Benth.
Perovskia Kar.	*Melissa* L.
Rosmarinus L.	*Neoeplingia* Ramamoorthy, Hiriart & Medrano
Salvia L.	*Perovskia* Kar.
Zhumeria Rech. f. & Wendelbo	*Rosmarinus* L.
Subtribe Nepetinae	*Salvia* L.
Agastache J. Clayton ex Gronov.	*Zhumeria* Rech. f. & Wendelbo
Cedronella Moench	Subtribe Nepetinae
Dracocephalum L.	*Agastache* J. Clayton ex Gronov.
Drepanocaryum Pojark.	*Cedronella* Moench
Glechoma L.	*Dracocephalum* L.
Hymenocrater Fisch. & C. A. Mey.	*Drepanocaryum* Pojark.
Lallemantia Fisch. & C. A. Mey.	*Glechoma* L.
Lophanthus Adans.	*Heterolamium* C. Y. Wu
Marmoritis Benth.	*Hymenocrater* Fisch. & C. A. Mey.
Meehania Britton	*Hyssopus* L.
Nepeta L.	*Lallemantia* Fisch. & C. A. Mey.
Schizonepeta (Benth.) Briq.	*Lophanthus* Adans.
Incertae sedis	*Marmoritis* Benth.
Heterolamium C. Y. Wu	*Meehania* Britton
Melissa L.	*Nepeta* L.
	Schizonepeta (Benth.) Briq.