RESEARCH ARTICLE

Pitardia resurrected: A new member of subtribe Menthinae (Lamiaceae)

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Abstract Despite tremendous progress towards clarifying phylogenetic relationships within the mint family (Lamiaceae), uncertainty remains regarding relationships among some major clades as well as the proper placement of some genera. While researching the genus *Nepeta*, a species from northeastern Morocco, *N. nepetoides*, attracted our attention due to its distinct morphology relative to other species of *Nepeta*. To explore the systematic position of *N. nepetoides*, Bayesian and maximum likelihood analyses were conducted using chloroplast, nuclear ribosomal, and low-copy nuclear markers. For phylogenetic analyses, a total of 5 accessions and 49 samples were newly sequenced for this publication, with the remainder coming from previous studies. Results from all three gene regions suggest that *N. nepetoides* should not be treated within *Nepeta*, but instead recognized as a distinct genus, the resurrected *Pitardia*. In addition, *Pitardia* is not even in the same subtribe as *Nepeta* (Nepetinae), and instead should be considered as a member of the subtribe Menthinae, a group that includes most of the culinary spices (e.g., oregano, peppermint, thyme) from the mint family. Notably, all analyses point to *Pitardia* being sister to the rest of subtribe Menthinae. Furthermore, lectotypes are designated for *P. nepetoides* and *P. caerulescens*, the taxonomic status of *Pitardia* is reassessed, and an updated and extended morphological description of *Pitardia* is provided based on herbarium specimens and field observations.

Keywords Morocco; *Nepeta*; Nepetinae; North African flora; oregano; *Pitardia*; thyme

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

The mint family (Lamiaceae) is a cosmopolitan group that contains about 7000 species, and is of importance both economically and ecologically (Harley & al., 2004). During the past few decades, great progress has been achieved towards clarifying the boundaries of and phylogenetic relationships within Lamiaceae (Cantino, 1992a,b; Cantino & al., 1992; Wagstaff & al., 1998; Harley & al., 2004; F. Zhao & al., 2021). Despite this progress, uncertainties persist regarding relationships among some major lineages as well as the proper placement of some genera (MEGC, 2018; Serpooshan & al., 2018; F. Zhao & al., 2021; Antar & al., 2022; Chen & al., 2022; Rose & al., 2022; Y. Zhao & al., 2023).

The Lamiaceae contains 12 subfamilies and 22 tribes (F. Zhao & al., 2021). The largest of these subfamilies is the Nepetoideae, with about 3400 species that are divided into three tribes, Elsholtzieae, Mentheae, and Ocimeae (Harley & al., 2004; F. Zhao & al., 2021). The largest tribe within the Nepetoideae (and Lamiaceae) is the Mentheae, with about 60 genera and more than 2000 species treated within five subtribes (Harley & al., 2004, Moon & al., 2009; Drew & Sytsma, 2012). Recently, Rose & al. (2023) examined continental disjunctions and phylogenetic relationships within one of these five subtribes, the Nepetinae. This subtribe contains about 375 species including *Nepeta cataria* L., which is the type of the Nepetoideae.

Nepeta L. (sensu Harley & al., 2004) comprises about 260 species, is the largest genus within Nepetinae, and the second-largest genus within tribe Mentheae (Budantsev, 1993; Harley & al., 2004; Serpooshan & al., 2018; Dirmenci & al., 2023; Rose & al., 2023; WFO, 2023). The genus is native to the Mediterranean region and temperate Eurasia, generally occurring in xeric or steppe environments, and is most species-rich in montane Central and Southwest Asia, the western Mediterranean region, and the Yunnan region of China

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(Budantsev, 1993). *Nepeta cataria*, or catnip, is widely sold commercially and native to Eurasia, but has naturalized across temperate North America, southeast South America, southeast Australia, and New Zealand. Aside from catnip, other species of *Nepeta* are important economically for both horticulture (e.g., catmint [*N.* ×*faassenii* Bergmans ex Stearn, *N. racemosa* Lam.]) and medicinal purposes (Salehi & al., 2018; Süntar & al., 2018; Selvi & al., 2022). The genus is also ecologically valuable throughout its range for its pollinator services (Hassan, 2010; Barbir & al., 2016).

The generic delimitation of *Nepeta* has been muddled by the often-variable nature of morphological features used to delimit taxa within the genus (Budantsev, 1993; Jamzad & al., 2003; Serpooshan & al., 2018). While researching the genus *Nepeta*, a poorly known species, *N. nepetoides* (Batt. ex Pit.) Harley, attracted our attention. *Nepeta nepetoides* was effectively and validly published as *Pitardia nepetoides* "Battandier" (monotypic genus; Fig. 1A) by Joseph Pitard (1918), and then re-published as an isonym by Battandier (1919) (see Taxonomic treatment). The species is endemic to the eastern Middle Atlas and High Atlas Mountains in northeastern Morocco (Tafoughalt region) and is poorly understood due to a paucity of collections. Battandier considered it distinct from *Nepeta* based on having 2 stamens (vs. 4 in *Nepeta*) and a more slender inflorescence with condensed lower verticillasters. However, Battandier (1919) remarked that in some respects (e.g., 10-nerved calyx) it was similar to *N. apuleji* Ucria (but *N. apuleji* actually has a 14–15-nerved calyx; Fig. 1B), and that in general it was somewhat difficult to differentiate from *Nepeta* (Fig. 1). Later, *Pitardia caerulescens* Maire (1929) was described from the eastern High Atlas Mountains near Midelt and from the Middle Atlas Mountains in the eastern sector of Morocco. Subsequently, in 1941, *P. gracilis* Andr. was described from Zegzel in the Oriental region of Morocco by Andreánszky (1941), who emphasized that "*P. gracilis* is not similar to *Nepeta apuleji* due to different inflorescence structure and habit, but it is more similar to *Micromeria* Benth. and *Satureja* L., except it only has two stamens and is therefore a *Pitardia*." Later, Harley & al. (2003) transferred *Pitardia* to *Nepeta*, stating that apart from having two stamens, *Pitardia nepetoides* was indistinguishable from *Nepeta*. Harley & al. (2003) went on to point out that other "unrelated" species within *Nepeta* also expressed two stamens. In addition, Harley & al. (2003) stated that "*P. caerulescens* may well be conspecific with *P. nepetoides*, the type species, but so far there is no further information on

Fig. 1. Species of *Nepeta* and relatives from Morocco. **A**, *Pitardia nepetoides*; **B**, *Nepeta apuleji*; **C**, *N. atlantica*; **D**, *N. barbara*; **E**, *N. granatensis*; **F**, *N. multibracteata*; **G**, *N. nepetella* subsp. *amethystina*; **H**, *N. stachyoides*; **I**, *N. tuberosa* subsp. *reticulata*. — All photos taken by first author.

P. gracilis. These additional species do not affect the status of *Pitardia*."

For this study, we examined several populations of *Nepeta nepetoides* in the field, recent herbarium collections of *N. nepetoides*, and greenhouse specimens from the Zegzel region grown from seed. We used the specimens above to examine how the morphology of *N. nepetoides* compares to other species of *Nepeta*. To further discern how *N. nepetoides* is related to *Nepeta*, we analyzed sequence data from the chloroplast (cpDNA) consisting of *ycf1*, the *ycf1*-*rps15* spacer, and the *trnL*-*trnF* and *rpl32*-*trnL* spacer regions, nuclear ribosomal internal and external transcribed spacers (ITS, ETS) (nrDNA), and the low-copy nuclear gene *PPR-AT3G09060* (*PPR*). We used three separate datasets to evaluate whether *N. nepetoides* should indeed be included within *Nepeta*, and to estimate the phylogenetic placement of *N. nepetoides* within the Mentheae. In addition, we provide lectotypifications, an updated treatment of the species, as well as a detailed morphological description based on herbarium specimens, field observations, and collections.

■ MATERIALS AND METHODS

Taxonomy and sampling. — The nomenclature here broadly follows Harley & al. (2004). Specifically, *Hymenocrater* Fisch. & C.A.Mey, *Lophanthus* Adans. and *Marmoritis* Benth. are not treated in *Nepeta* s.l. following Serpooshan & al. (2018). Conversely, we follow Chen & al. (2022) in treating *Hyssopus* L. and *Lallemantia* Fisch. & C.A.Mey as part of *Dracocephalum* L. For *Pitardia* (*Nepeta nepetoides* and allies), type specimens and additional herbarium material were examined from CLF (image!), G (image!), MARS (image!), MPU (image!), P (image!) and RAB (Appendix 1). Voucher specimens were deposited in the RAB Herbarium. Lectotypifications follow the guidelines of the *International Code of Nomenclature for algae, fungi, and plants* (*ICN*, Turland & al., 2018). The lectotypes of *Pitardia nepetoides* and *P. caerulescens* are designated based on a thorough examination of available syntypes (see detailed discussion in the Results section). The selected lectotype and its associated isolectotypes were identified using morphological comparisons and annotations from historical records. Digital twins of the designated specimens were also reviewed where available. In addition, the first author conducted extensive field observations from the type localities and other populations of *Pitardia* (Appendix 1) in 2023 and 2024. Morphological observations and measurements of *Pitardia* populations were based on both fresh plants collected in the field and herbarium specimens. The conservation status of *Pitardia* was assessed according to IUCN guidelines (IUCN Standards and Petitions Committee, 2024). For phylogenetic analyses, a total of 5 accessions and 49 samples were newly sequenced for this publication.

DNA extraction and sequencing. — DNA was extracted from field collected silica-dried leaves and herbarium specimens (Appendix 2) with the DNeasy Plant Mini Kit (Qiagen, Valencia, California, U.S.A.). We performed polymerase chain reactions (PCRs) using thermal cycler conditions for the cpDNA, nrDNA, and *PPR* regions as described in Drew & al. (2014). For amplification during the PCR process, we used TaKaRa Ex Taq (Otsu, Shiga, Japan). We subsequently diluted PCR products in water (15×). PCR products were cycle sequenced and electrophoresed with an Applied Biosystems 3730XL DNA Analyzer at the University of Arizona Genetics Core.

Molecular markers. — We used two nrDNA markers (ITS, ETS), four cpDNA markers (*ycf1*, *ycf1*-*rps15* spacer, *trnL*-*trnF* spacer region, *rpl32*-*trnL* spacer region), and one low-copy nuclear gene (*PPR-AT3G09060*; *PPR*) for molecular phylogenetic analyses. The nrDNA, cpDNA, and *PPR* datasets were each analyzed separately. Our nrDNA and cpDNA datasets were based on data from Drew & Sytsma (2012). We removed some taxa (e.g., a few New World Menthinae; Drew & al., 2017a) from the datasets of Drew & Sytsma (2012) and added four accessions of *Nepeta nepetoides* and one accession of *N. apuleji* to the nrDNA, cpDNA datasets (three accessions of *N. nepetoides* for *PPR* dataset). The accession of *N. apuleji* was added because Battandier (1919) suggested this taxon was closely related to *N. nepetoides*. The nrDNA dataset had 93 accessions of Mentheae, representing and all five subtribes, as well as two outgroup taxa (95 total accessions; 5 accessions and 10 samples newly sequenced). The cpDNA dataset also included 93 accessions from within Mentheae, including representatives from all five subtribes, as well as 17 outgroup taxa (110 total accessions; 5 accessions and 15 samples newly sequenced). The *PPR* dataset contained 55 accessions (24 newly sequenced, the others from Drew & Sytsma, 2013; Drew & al., 2017b; Rose & al., 2023) from Mentheae, including all five subtribes, as well as two outgroup taxa for a total of 57 accessions. In total, 574 sequences were analyzed (*ycf1-rps15*, 110; *trnL-trnF*, 110; *rpl32-trnL*, 108; ITS, 95; ETS, 94; *PPR*, 57), of which 46 were newly generated (*ycf1-rps15*, 5; *trnL-trnF*, 5; *rpl32-trnL*, 5; ITS, 5; ETS, 5; *PPR*, 21) in this study and 528 were obtained from previous studies. Specimen voucher information and GenBank accession numbers are available in Appendix 2. Alignment files for the cpDNA, nrDNA, and PPR datasets are given in suppl. Appendices S1, S2, and S3, respectively.

For PCR amplification of the ITS region, the primers LEU1 (Andreasen & al., 1999) and ITS4 (White & al., 1990) were initially employed. Internal primers ITS2 and ITS3 (White & al., 1990) were subsequently used in conjunction with LEU1 and ITS4 for specimens that failed to amplify on the first attempt. For sequencing, various combinations of these primers were used. For ETS, *ycf1*, and *ycf1-rps15* spacer regions, primers from Drew & Sytsma (2011) were used. For newly sequenced accessions of *Nepeta nepetoides*, ~2250 nucleotides were amplified and sequenced from the 3′ end of *ycf1*, starting with primer 3738f (Drew & Sytsma, 2011). This dataset was incorporated into the *ycf1* alignment (including the *ycf1-rps15* spacer) from Drew & Sytsma (2012), which was approximately 5100 base pairs (unaligned characters) in length. For amplification of the *rpl32-trnL* region, primers from Shaw & al. (2007) were primarily used. However, for some specimens, the internal primer bd866r (Drew & Sytsma, 2012) was used in combination with *rpl32f* (Shaw & al., 2007). The cpDNA *trnL-trnF* markers were amplified and sequenced as in Drew & Sytsma (2013). Although low rates of nucleotide polymorphisms were observed (<1%) in *PPR* sequences, several accessions were cloned to evaluate allelic variation and copy number. The cloning procedure followed that of Drew & Sytsma (2013). Specifically, *Acinos arvensis* (Lam.) Dandy, *Hedeoma piperita* A.Gray, *Mentha pulegium* L., *Micromeria juliana* (L.) Benth. ex Rchb., *Origanum vulgare* L., and *Salvia patens* Cav. were cloned.

Phylogenetic analyses. — We used Geneious v.11.1.5 (Kearse & al., 2012) to contig and edit sequences, and subsequently aligned the sequences using Mesquite v.3.61 (Maddison & Maddison, 2019). The cpDNA, nrDNA, and low-copy nuclear regions were analyzed as separate datasets. We used RAxML v.8.2.12 as implemented on the CIPRES cluster (Miller & al., 2010) to perform maximum likelihood (ML) phylogenetic analyses for each dataset. Each of our three ML analyses used the GTR model as suggested by the RAxML developer (Stamatakis, 2014). Support values for clades were estimated by conducting 100 bootstrap (BS) repetitions using the rapid bootstrap option (-f a). MrBayes v.3.2.7 (Ronquist & al., 2012) as implemented on the CIPRES cluster was used to conduct Bayesian inference analyses (BI). The GTRGAMMA model was applied, and each analysis was run for 5,000,000 generations, with sampling every 1000 generations. The first 10% of samples were discarded as burn in. Convergence was assessed by ensuring that the average standard deviation of split frequencies fell below 0.01, which occurred within 500,000 generations for each dataset.

■ RESULTS

The goal of this study is to explore the phylogenetic position of *Nepeta nepetoides* in relation to *Nepeta* and the broader Mentheae. Thus, relationships outside of that focus are not discussed here. The Bayesian and ML trees were congruent in all analyses, and only Bayesian phylogenetic trees are shown in this paper (supplemental trees are Bayesian trees with condensed nodes expanded).

nrDNA analyses. — The aligned nrDNA dataset contained 1335 total characters. Prior to analysis, 100 ambiguously aligned sites were removed, resulting in a final dataset of 1235 base pairs (ITS, 699; ETS, 536). In both the ML and BI analyses, the four accessions of *Nepeta nepetoides* were recovered as a clade with ML BS = 100% and a Bayesian posterior probability (PP) value of 1.00 (Fig. 2A, suppl. Fig. S1). Within the *N. nepetoides* clade there was scant support for relationships between different accessions. Collectively, the clade of *N. nepetoides* was sister to the remaining members of subtribe Menthinae, with ML BS = 94% and a Bayesian PP value of 1.00 for the crown Menthinae (Fig. 2A, suppl. Fig. S1). In both analyses, the Menthinae + *Nepeta nepetoides* was sister to a clade that included the subtribes Lycopinae, Nepetinae, and Prunellinae (BS = 96%; PP = 1.00; Fig. 2A, suppl. Fig. S1). The sample of *N. apuleji* was recovered within the Nepetinae as sister to *N. cataria* (BS = 100%; PP = 1.00; Fig. 2A, suppl. Fig. S1).

cpDNA analyses. — The four gene cpDNA alignment contained 8657 characters. After removing ambiguously aligned sites, the dataset used for analyses contained 8158 nucleotide characters (*ycf1*, 5148; *ycf1-rpl15* spacer, 699; *trnLF*, 1117; *rpl32-trnL*, 1194). The four accessions of *Nepeta nepetoides* were recovered as a clade with ML BS = 100% and a BI PP value of 1.00 (Fig. 2B, suppl. Fig. S2). Within the *N. nepetoides* clade, the accessions from Sefrou and Skoura M'daz (BS = 100%; PP = 1.00) formed one subclade, while the wild and cultivated accessions from the Zegzel region formed another (BS = 88%; PP = 1.00). Consistent with the nrDNA analyses, both the ML and BI topologies recovered *N. nepetoides* as sister to all other Menthinae (BS = 65%; PP = 0.84; Fig. 2B, suppl. Fig. S2). In both analyses Menthinae was sister to the Nepetinae (BS = 100%; PP = 1.00; Fig. 2B, suppl. Fig. S2). Again, the sample of *N. apuleji* was recovered as sister to *Nepeta cataria* (BS = 100%; PP = 1.00; Fig. 2B, suppl. Fig. S2).

***PPR* analyses. —** The *PPR* dataset contained 1036 nucleotide characters. No characters were excluded from this dataset and the alignment did not contain any insertions or deletions. Previous studies have used *PPR-AT3G09060* in phylogenetic analyses within Mentheae and determined that the low-copy nuclear region is typically recovered as a single-copy gene within Mentheae, with the exclusion of the New World clade of Menthinae (Drew & Sytsma, 2013; Drew & al., 2017a; Chen & al., 2022; Rose & al., 2023). The three accessions of *Nepeta nepetoides* were recovered as a clade with ML BS = 100% and a BI PP value of 1.00, with scant support for relationships among accessions (suppl. Fig. S3). Again, the ML and BI analyses estimated *N. nepetoides* as sister to Menthinae (BS = 71%; PP = 0.99; suppl. Fig. S3). As in the nrDNA analyses, the Menthinae clade, including *N. nepetoides*, was sister (BS = 96%; PP = 1.00) to a clade composed of Lycopinae, Nepetinae, and Prunellinae (suppl. Fig. S3). The accession of *N. apuleji* was recovered within a clade with other *Nepeta* (BS = 100%; PP = 1.00; suppl. Fig. S3).

With the exception of *Hedeoma piperita*, the cloned samples showed no evidence of paralogy, and all cloned species were monophyletic when analyzed within the broader *PPR* dataset (results not shown). Some clones of *H. piperita* contained indels of 1–2 base pairs and these samples were interpreted as paralogs since the *PPR-AT3G09060* gene is coding and indels should occur in multiples of three. We chose one non-paralogous sequence of *H. piperita* at random to include in our *PPR* analyses. It should be noted that all clones of *H. piperita* (including paralogs) were recovered as monophyletic, as *H. piperita* was the only member of the New World Menthinae included in the *PPR* dataset. Previous work has indicated that the *PPR-AT3G09060* gene has undergone at least one duplication within the New World Menthinae but is generally present as a single copy in the Old World Menthinae as well as within most other Mentheae taxa (Drew & Sytsma 2013; Drew & al., 2017a; Drew & al., unpub. data). The *PPR-AT3G09060* gene has been employed in several studies within the Mentheae (Drew & Sytsma, 2013; Drew & al., 2014, 2017a,b; Chen & al. 2022; Rose & al., 2023).

Taxonomic treatment. — Based on the molecular and morphological evidence presented here, we formally resurrect the genus *Pitardia* and the species *P. nepetoides*. The other two species previously treated within *Pitardia*, *P. caerulescens* and *P. gracilis*, are treated as synonyms of *P. nepetoides*. Furthermore, a more comprehensive species description for *P. nepetoides* is provided, and lectotypes are designated for both *P. nepetoides* and *P. caerulescens*.

Pitardia nepetoides Batt. ex Pit., Contr. Fl. Maroc: 31. 1918 ≡ *Nepeta nepetoides* (Batt. ex Pit.) Harley in Kew Bull.

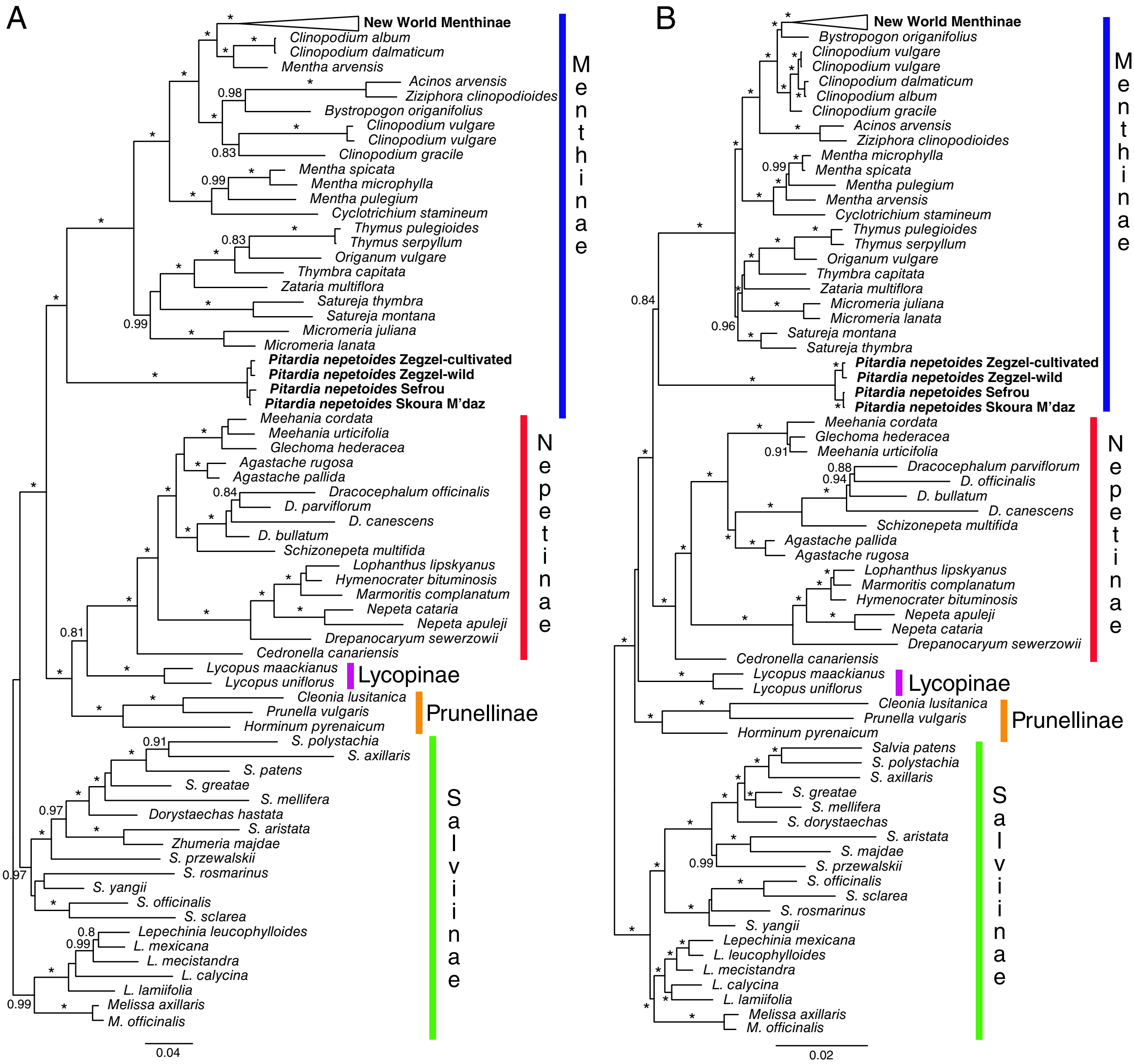

Fig. 2. Phylogenetic results based on Bayesian inference, with outgroup taxa removed. **A**, Nuclear ribosomal DNA (ITS, ETS) phylogeny; **B**, Chloroplast DNA (*ycf1*, *ycf1-rpl15*, *trnL-F*, *rpl32-trnL*) phylogeny. — Posterior probability (PP) values are shown near nodes. Asterisks indicate 1.00 PP support. Only nodes with PP > 0.80 are labeled. Subtribe delimitations are shown at right.

58(2): 488. 2003 – **Lectotype (designated here):** Morocco. Sefrou, in collibus, Oct 1912, *Pitard 2335* (P barcode P04366851!; isolectotypes: G barcode G00435182!, P barcode P04366850!).

= *Pitardia caerulescens* Maire in Bull. Soc. Hist. Nat. Afrique N. 20: 34. 1929 – **Lectotype (designated here):** Morocco. In Atlantis Medii montibus in rupestribus calcareis clivi occidentalis montis, Ichouhadda, 1700 m, 24 Jun 1927, *Maire s.n.* (P barcode P04366841!; isolectotype: MPU barcode MPU002054!).

= *Pitardia gracilis* Andr. in Index Horti Bot. Univ. Budapest. 5: 20. 1941 – Type: Morocco. In rupibus calcareis vallis Zegzel in montibus Béni-Snassen in Maroccano boreali-orientali (not found).

Suffrutescent multi-stemmed perennials, aromatic; stems 20–50 (–60) cm tall, ascending to erect, slender, quadrangular, sometimes striate, glabrescent to slightly scabrous with few sessile glands and numerous glandular papillae. Leaves opposite, 4–12 mm wide and 6–14 mm long, green, short petiolate to subsessile, broadly ovate to ovate-lanceolate, cordate at base, rounded to acute at apex, coarsely crenate to serrate at margins, (0–) 2–6 (–7) teeth on each side, rigid, eucamptodrome venation, numerous glandular papillae on both sides, few eglandular hairs on central nerves and sparse punctate glands on the abaxial side; petioles 1–6 mm long, becoming shorter in upper leaves. Inflorescence 3–15 (–20) cm long; verticillasters 2–12 (–14)-flowered, usually remote, sometimes condensed into false spikes in the upper part; cymes subsessile to pedunculate, peduncles 0.5–10 mm long. Floral leaves/bracts 3–6 (–7) mm in the axils of each verticillaster. Bracteoles numerous, elliptic to lanceolate-subulate, 2–4 mm long, entire, densely glandular papillate, ± scabrous to ciliate at margins, upper and internal bracteoles less than one-third of calyx tube, lower and outer bracteoles sub-equal to half the length of calyx tube. Calyx 5.5–8 mm long, 1–2 mm wide, tubular, curved, mouth oblique, covered with sparse to dense eglandular hairs, especially on the margins and veins, interspersed with densely glandular papillae, glabrous inside, usually purple, especially in the upper half and teeth, 10-veined, veins clearly visible, tube 3–5 mm; teeth 5, 2–3.8 mm long, unequal, shorter than the tube, oblong-lanceolate, lanceolate to acuminate, scabrous at margins; upper middle tooth longer and wider than the others, and usually oblong-lanceolate. 5-lobed corolla 13–16 mm long, generally pale pink (to pale blue), spotted with white dots, or pale purple at lips, tube clearly exserted from calyx, pubescent outside, glabrous inside; upper lip 2-lobed, hood-shaped, straight curved compressed; lower lip trifid, ± convex, middle lobe slightly longer than lateral lobes, entire, lateral lobes generally wider than the oblong-ovate middle lobe. Stamens 2, anterior pair absent; the filaments inserted in the middle of the corolla tube; anthers with 2 fertile thecae, divided, purple, usually included in upper lip or subexserted. Style exserted, glabrous, bifid. Nutlets brown, oblong, 1–1.2 mm long, smooth, minutely tuberculate.

Ecology and distribution. – All populations of *Pitardia nepetoides* are found growing on or beside rocky calcareous schist escarpments, steep valleys, and gorges, in ± shaded habitats, only rarely escaping into forests. This species has a wide altitudinal range, ranging from 250 m (a.s.l.) in the Béni-Snassen region of Berkane Province (MPU090263) to 2300 m (a.s.l.) at Jbel Ighez-Diz in the Oriental High Atlas (Maire, 1929). However, its presence is limited to small populations in specific ecological niches, indicating that the species requires specific ecological conditions such as certain types of bedrock. This species is also characterized by a long flowering season that begins in April and lasts until the end of October. At the end of its cycle, it becomes leafless. In early spring, the developing plants have relatively crowded verticillasters. The internodes lengthen during the spring, forming ± dense bushy tufts that are typically pendulous on escarpments or erect in rock crevices or among large rocks. During this time, the flowering stems become longer with widely spaced verticillasters, with the upper ones usually much depleted. Towards the end of summer, the verticillasters become largely flowerless. The plants begin a new cycle in September, but the development of the inflorescences is weak compared to the spring period.

The specimen of *Pitardia nepetoides* numbered *Pitard 2335* (P04366851) bears the most complete and detailed label information. While “2335” is a later addition and not originally designated by Pitard, this specimen is chosen for its morphological clarity and historical significance.

Among the syntypes of *Pitardia caerulescens* examined, the specimen P04366841 was selected as the lectotype due to its well-preserved condition and completeness of label data. The isolectotype MPU002054 corroborates the morphological and geographical details provided in the protologue.

Lectotypification. – *Pitardia* was described as *Pitardia nepetoides* Battandier (the type of the genus), gen. et sp. nov. based on Battandier’s description in *Contribution à l’etude de la flore du Maroc* published by Pitard in 1918. The type locality was stated as “Maroc central: Sefrou. […]. Coteaux rocheux”, but no collector number or specific location details were provided in the protologue. Pitard’s introduction states that he conducted botanical collections during a mission commissioned by the Société de Géographie de Paris from 1911 to 1913, covering northern, western, southeastern desert, occidental, and central Morocco, including Sefrou. Given that he collected specimens during this expedition and later published the results, it is reasonable to consider all specimens attributed to him from Sefrou as syntypes. In *Contributions à la flore atlantique*, Battandier (1919) listed “Sefrou, Maroc occidental (Pitard)” (p. 66) as the type locality. However, in *Bulletin de la Station de Recherches Forestière du Nord de l’Afrique*, Battandier (1921) revised the type locality to “Maroc central: Sefrou” and included a drawing of the general habit, leaves, and flower parts (t. 21). All three publications affirmed *Pitardia* as a new genus. Battandier (1921) further noted that Professor Pitard had provided him with many Moroccan plant specimens in 1913. Among these, he identified specimens resembling *Nepeta* but differing by having only two stamens and a calyx with 10 veins. Based on these distinctions, he proposed *Pitardia* as a new genus. The authorship "Batt. ex Pit." is justified because Pitard (1918) was the first to publish *Pitardia nepetoides* "Battandier" as "gen. et sp. nov.", thereby simultaneously describing both the genus *Pitardia* and the species *P. nepetoides*. In doing so, he explicitly attributed the species name to Battandier, making Battandier the original proposer of the name. Battandier (1919) subsequently published a description of *Pitardia* as a "novum genus" and again included the species *P. nepetoides* (as "spec. nova"), consequently, both names are isonyms in the second publication and have no nomenclatural status. According to the *ICN*, Pitard's 1918 description constitutes the valid publication of both the genus and the species. Therefore, the correct authorship of the species is *Pitardia nepetoides* Batt. ex Pit. In our efforts to identify the correct type specimen and locality, two specimens with different label information were obtained. These specimens were collected by Pitard in Sefrou: "Morocco. Sefrou, *Pitard s.n.* (MPU006506) and Sefrou, in collibus, October 1912, *Pitard 2335* (P04366850, P04366851, G00435182)".

Since no repository was specified in the protologue, all material collected by Pitard from this locality must be considered syntypes. As explained above, the only confirmed type locality information is that Pitard collected the specimens in Sefrou. Since no additional specimens from the mentioned collection are available, we consider these specimens as part of the original material used in the genus and species description (Pitard, 1918). Upon comparing the general morphological characteristics of these specimens, we concluded that they were collected close to each other and possibly on the same date. Furthermore, Pitard's original handwritten label on the lectotype includes the habitat description "Coteaux rocheux" (rocky slopes), which does not appear in later publications (Battandier, 1919, 1921) and was not transcribed onto the printed label. Consequently, we designate *Pitard 2335* with barcode P04366851 (P!) (suppl. Fig. S4) as the lectotype, while the specimens with barcodes P04366850 (P!) and G00435182 (G!) are recognized as isolectotypes.

Pitardia caerulescens was described by Maire (1929) based on multiple specimens, including six syntype specimens from Morocco: Prope Midelt in monte Ighez-Diz, 1922, *Delon 11* (MPU002056); In Atlantis Medii montibus in rupestribus calcareis clivi occidentalis montis, Ichouhadda, 1700 m, 24 Jun 1927, *Maire s.n.* (P04366841, MPU002054); Haute Moulouya: Midelt, gorges de l'Oued Bou-Adil, 1300 m, May 1925, *Jahandiez 128* (MPU002055); In Atlantis Medii montibus in dumotis et paucis supra Tamkrarant solo margaceo, 1500–1800 m, 23 Jun 1927, *Maire s.n.* (MPU002057, P04366842).

Among these syntypes the specimens *Maire s.n.* (P04366841, MPU002054) are the most complete, well-preserved, and representative of the taxon. Therefore, the specimen with barcode P04366841 (P!) (suppl. Fig. S5) is designated as the lectotype (suppl. Fig. S5), while MPU002054 (MPU!) is an isolectotype.

According to our surveys and herbarium specimens, the plant is found in four main regions in Morocco. The first region is the central Middle Atlas Mountains, in the Sefrou region where the type was originally collected and described. This region extends to Tazekka National Park and includes Bad Boudir and Bab Azhar. The second region is the eastern Middle Atlas Mountains, comprising several sites including the cascades and escarpments of Skoura M'daz, Jbel Ouarirt, the valleys of Maghraoua, Tamtroucht, Jbel Ichouhadda near Berkine, Guelb Rahal and Bou Naceur Mountains (MPU090259). The third region is the Oriental region, especially the Beni-Snassen Mountains, Zegzel Gorge, Jbel Tamedjout above Zegzel, the hills of Argan Tree, the Tafoughalt region and other mountains in Berkane Province. The fourth region is the High Moulouya in the Oriental High Atlas, including the Jbel Ighez-Diz and Bou Adil gorges.

IUCN Red List. – As noted above, *Pitardia* is a monotypic genus. However, *P. nepetoides* has two synonyms: *P. caerulescens* and *P. gracilis* (see below). While assessing the Red List status of the species, we considered the geographic and ecological range of the genus as well as threats on all named taxa. Our results indicate that although the species is distributed across four main regions (details given above), its populations are very small and confined to very specific habitats. Based on the first author's observations, the accessible plants are threatened in the Oriental Middle Atlas and High Atlas by overgrazing. However, plants growing in escarpments within these regions are generally inaccessible, allowing them to flower and disperse seeds and thus maintain populations in these areas. Previously, *P. nepetoides* (as *Nepeta nepetoides*) was classified as Vulnerable (VU) by Fennane (2021) according to the B2ab(ii,iii) criteria. Based on exhaustive literature reviews, field surveys, and herbarium studies, we conclude that the species should remain classified in the VU category as indicated by Fennane (2021) because its area of occupancy is estimated to be less than 2000 km^2 and its populations are severely fragmented (IUCN Standards and Petitions Committee, 2024).

■ DISCUSSION

***Pitardia* should be recognized as a distinct genus within subtribe Menthinae. —** The nrDNA, cpDNA, and *PPR* analyses all indicate that *Nepeta nepetoides* is sister to the subtribe Menthinae and should no longer be treated within the genus *Nepeta*. This relationship is consistently supported across all analyses. Additionally, *Pitardia* should be classified as a member of subtribe Menthinae rather than Nepetinae based on our molecular data. This discovery also aligns with the morphological differences between the two groups.

Morphologically, *Pitardia nepetoides* is more compatible with Menthinae than Nepetinae. For example, *P. nepetoides* has only two expressed stamens, while nearly all taxa within subtribe Nepetinae have four stamens (at least in male flowers of gynodioecious taxa). Although some species of *Nepeta* have underdeveloped (or barely developed) anterior stamens, all species still possess at least staminodes (Budantsev, 1993). Within the Menthinae, however, species in several genera have only two expressed stamens (e.g., *Glechon* Spreng., *Hesperozygis* Epling, *Rhododon* Epling, *Satureja*), and several other genera contain species with only two fertile stamens with two staminodes (Harley & al., 2004; Drew & Sytsma, 2012; Duman & al., 2023). While most *Satureja* species possess four stamens, *S. hasturkii* (a recently described species) was found to have only two stamens (Duman & al., 2023). In addition, the aroma from crushed leaves of *P. nepetoides* suggests a kinship with the Menthinae. While some species of *Nepeta* from Central and East Asia have glandular-punctate leaves, this feature is not typical of Nepetinae. In contrast, several genera of Menthinae (e.g., *Hedeoma* Pers., *Killickia* Bräuchler & al., *Monardella* L., *Origanum* L., *Satureja*) share this trait with *Pitardia*.

The circumscription of Menthinae by Harley & al. (2004) is the basis for our current understanding of the group. However, there is no single morphological nor chemical feature given from Harley & al. (2004) that unites Menthinae. This is perhaps one reason that the group has only recently been recognized in its present form, and why new additions (i.e., *Pitardia*) and subtractions (i.e., *Cleonia* L., *Horminum* L., *Hyssopus*, *Lycopus* L., *Neoeplingia* Ramamoorthy & al. and *Prunella* L.) have continued since (Drew & Sytsma, 2012; Drew & al., 2014). Although we know of no morphological characters that unequivocally unite *Pitardia* with subtribe Menthinae, the placement of *Pitardia* within Menthinae is certainly compatible with the morphology of both taxa as well as molecular evidence. Another option would be to recognize *Pitardia* in a novel subtribe, but this seems unwarranted and unnecessary.

Several closely related genera within the Menthinae, such as *Origanum*, *Satureja*, and *Thymus* L., have economic value as spices and medicinal herbs (Selvi & al., 2022; Duman & al., 2023). The discovery of a new closely related taxon to these ethnobotanically important taxa is noteworthy and potentially economically valuable. Further research is needed to explore possible applications of *Pitardia* for human use.

Taxonomic remarks. — Morphologically, *Pitardia* can be distinguished from *Nepeta* by several characters (Table 1). First, *Pitardia* has only two stamens, with no discernible vestigial staminodes. While a few species of *Nepeta* have lower stamens that are greatly reduced or even staminodal, there are always four staminal structures present (in male flowers). Additionally, the calyx tube of *Pitardia* is 10-veined, while *Nepeta* typically possesses 15 (13–17) longitudinal veins. At anthesis, the upper corolla lip of *Pitardia* is folded and ± conceals the reproductive parts, in contrast to the open upper lip of *Nepeta*. The corolla shape of *Pitardia* is clearly distinct from *Nepeta*. Specifically, the median lobe of the lower lip of the corolla is convex and entire in *Pitardia* but generally crenulate in *Nepeta* (Figs. 1, 3, Table 1).

Maire (1929) distinguished *Pitardia caerulescens* from *P. nepetoides* based on morphological characters such as the number of teeth on each side of the leaves, shape of the base and tip of leaf blades, number of flowers per verticillaster, bract length, and the color of the calyx. However, all of these characters are variable. In the MPU Herbarium, *P. caerulescens* is represented by abundant material from the Middle Atlas Mountains in the eastern sector (Berkine, J. Ichouhadda, Tamtroucht, Guelb er-Rahal) and from the High Moulouya in the eastern High Atlas Mountains (J. Ighez-Diz, Bou Adil). Although two species of *Pitardia* (*P. nepetoides*, *P. caerulescens*) are recognized in the Flora of Morocco (Fennane & al., 2007), Dobignard (2009) states that *P. caerulescens* does not warrant taxonomic rank and should be treated as a synonym of *P. nepetoides*. In fact, it is difficult to differentiate Maire's specimens from that of Pitard, as only a few, often-variable morphological characters are used to separate the two taxa. Comparative morphological characters are summarized in Table 2 and Fig. 3, using populations from the Zegzel

Table 1. Morphological characters differentiating *Pitardia* from *Nepeta.*

Characters	*Pitardia*	*Nepeta*
Plant	Suffruticose	Generally herbaceous
Leaves	Punctate glands present	Punctate glands generally absent
Stamens	Two fertile stamens, anterior pair absent	Four stamens, generally all fertile, posterior pair longer than anterior pair
Calyx tube nerves	10-veined	(13–) 15 (–17)-veined
Corolla upper lip	Bilobed, lips folded at anthesis, generally ± hood-shaped, shallowly notched at the tip	Bilobed, lips open at anthesis, generally clearly bifid
Corolla lower lip	Trilobed, all three lobes ± located at the same level horizontally, lateral lobes of equal size and usually wider than the oblong-ovate middle lobe, middle lobe entire, not crenulated, always slightly longer than lateral ones	Trilobed, lobes horizontally not located at the same level, two small, patent or reflex lateral lobes placed above, central lobe placed below and much larger, concave, obovate, inversely cordate or reniform, sometime 2-lobulate or emarginate, with or without crenulated or undulated margins usually unequally dentate (Fig. 3)

and Sefrou regions that represent the characters of the type specimens of *P. nepetoides* and a population from Maghraoua that represents characters of *P. caerulescens*. However, in a population of *Pitardia* from Skoura M'daz (not included in Table 2) we found that the specimens have intermediate characters between the two species but were more similar to *P. caerulescens*. Therefore, we consider *P. caerulescens* to be a synonym of *P. nepetoides*.

Gábor Andreánszky (1941) published *Pitardia gracilis* as a new species based on morphological differences from Battandier's (1919) description, which reported that the inflorescence of *P. nepetoides* closely resembled *Nepeta apuleji*, with condensed lower verticillasters. Therefore, Andreánszky proposed *P. gracilis* as a distinct species due to its widely spaced inflorescences and lack of similarity to *N. apuleji*. However, Andreánszky indicated that he had not examined any specimens of *P. nepetoides*. We are confident that if Andreánszky had examined specimens of *P. nepetoides*, he would not have described *P. gracilis*, as the spacing of verticillasters is influenced by phenology and/or time of year. Since *P. nepetoides* is characterized by an extended flowering period, from April to late October, the inflorescence structure changes throughout the season. For example, specimen MPU071198, collected in Sefrou in April, shows relatively congested lower verticillasters, whereas specimen MARS46692, collected from the same region in late May, exhibits distant lower verticillasters. At the time of describing *P. gracilis* from Zegzel Gorge in 1941, many specimens in the Zegzel region had already been documented under the name *P. nepetoides*, including one examined by Maire (MPU090261). It is clear that populations from eastern Morocco (Tafoughalt, Zegzel, Berkane) do not warrant any taxonomic distinction and should be treated within *P. nepetoides*.

Fig. 3. Photographs comparing *Pitardia nepetoides* from populations in Maghraoua (M) and Zegzel (Z) in Morocco. **M1/Z1**, Habit; **M2/Z2**, Stem; **M3/Z3**, Leaf shape; **M4/Z4**, Punctate glands on abaxial side of leaves; **M5/Z5**, Verticillasters and shape of flowers; **M6**; Stamens and style; **M7**; Nutlets. — All photos taken by first author.

Table 2. Comparison of *Pitardia nepetoides* between the Sefrou and Zegzel regions and Maghraoua region.

Characters	*P. nepetoides* from Sefrou and Zegzel	*P. nepetoides* from Maghraoua (syn. *P. caerulescens*)
Stem	Glabrescent with sparse sessile glandular trichomes, usually striate, not scabrous	Glabrescent with sessile glandular trichomes, sometimes striate, slightly scabrous
Leaves	3–6 (–7) teeth on each side	0–4 (–5) teeth on each side
Whorls peduncle	Pedunculate (1–10 mm)	Subsessile (0.5–1.5 mm)
Verticillasters	2–8 (–10) flowers	2–12 (–14) flowers
Flower	Slightly curved	Clearly curved

AUTHOR CONTRIBUTIONS

BTD: Designed the study, conducted investigations, performed laboratory analyses (molecular analyses), and drafted the original manuscript; AHB: Conducted field surveys, collected data, performed laboratory analyses (morphological), species descriptions, and contributed to writing the manuscript; TD: Carried out lectotypification, differentiating morphological traits between tribes and genus, species descriptions and contributed to writing the manuscript; FC: Focused on ecology and conservation aspects and contributed to writing and improving the manuscript. All co-authors contributed to the manuscript and revised it critically. All authors have read and approved the final version of the manuscript and agreed to be accountable for all aspects of the work.

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LITERATURE CITED

Andreánszky, G. 1941. *Pitardia gracilis*. *Index Horti Bot. Univ. Budapest.* 5: 20–21.

Andreasen, K., Baldwin, B.G. & Bremer, B. 1999. Phylogenetic utility of the nuclear rDNA ITS region in subfamily Ixoroideae (Rubiaceae): Comparisons with cpDNA *rbcL* sequence data. *Pl. Syst. Evol.* 217: 119–135. https://doi.org/10.1007/BF00984925

Antar, G.M., Hays, M., Harley, R.M. & Drew, B.T. 2022. Phylogenetic placement and taxonomic revision of the genus *Monochilus* (Lamiaceae), a rare Brazilian endemic. *Syst. Bot.* 47: 1112–1121. https://doi.org/10.1600/036364422X16674054154188

Barbir, J., Azpiazu, C., Badenes-Pérez, F.R., Fernández-Quintanilla, C. & Dorado, J. 2016. Functionality of selected aromatic Lamiaceae in attracting pollinators in central Spain. *J. Econ. Entomol.* 109: 529–536. https://doi.org/10.1093/jee/tow004

Battandier, J.A. 1919. *Contributions à la flore atlantique*. Paris: Klincksieck. https://bibdigital.rjb.csic.es/idurl/1/13178

Battandier, J.A. 1921. Labiées ligneuses du Maroc constituant un nouveau type générique. *Bull. Sta. Rech. Forest. N. Afrique* 1: 200–201.

Budantsev, A.L. 1993. A synopsis of the genus *Nepeta* (Lamiaceae). *Bot. Zhurn. (Moscow & Leningrad)* 78: 93–107.

Cantino, P.D. 1992a. Evidence for a polyphyletic origin of the Labiatae. *Ann. Missouri Bot. Gard.* 79: 361–379. https://doi.org/10.2307/2399774

Cantino, P.D. 1992b. Toward a phylogenetic classification of the Labiatae. Pp. 27–37 in: Harley, R.M. & Reynolds, T. (eds.), *Advances in Labiatae Science*. London: Royal Botanic Gardens, Kew.

Cantino, P., Harley, R.M. & Wagstaff, S.J. 1992. Genera of Labiatae: Status and classification. Pp. 511–522 in: Harley, R.M. & Reynolds, T. (eds.), *Advances in Labiatae Science*. London: Royal Botanic Gardens, Kew.

Chen, Y.P., Turdimatovich, T.O., Nuraliev, M.S., Lazarević, P., Drew, B.T. & Xiang, C.L. 2022. Phylogeny and biogeography of the northern temperate genus *Dracocephalum* s.l. (Lamiaceae). *Cladistics* 38: 429–451. https://doi.org/10.1111/cla.12502

Dirmenci, T., Haloob, A., Celep, F. & Ghazanfar, S.A. 2023. Revision of the genus *Nepeta* L. (Lamiaceae) in Iraq. *Turk. J. Bot.* 47: 169–189. https://doi.org/10.55730/1300-008X.2754

Dobignard, A. 2009. Contributions à la connaissance de la flore du Maroc et de l'Afrique du Nord. Nouvelle série. 2. La flore du Nord-Maroc. *J. Bot. Soc. Bot. France* 46–47: 3–136. https://doi.org/10.3406/jobot.2009.1065

Drew, B.T. & Sytsma, K.J. 2011. Testing the monophyly and placement of *Lepechinia* in the tribe Mentheae (Lamiaceae). *Syst. Bot.* 36: 1038–1049. https://doi.org/10.1600/036364411X605047

Drew, B.T. & Sytsma, K.J. 2012. Phylogenetics, biogeography, and staminal evolution in the tribe Mentheae (Lamiaceae). *Amer. J. Bot.* 99: 933–953. https://doi.org/10.3732/ajb.1100549

Drew, B.T. & Sytsma, K.J. 2013. The South American radiation of *Lepechinia* (Lamiaceae): Phylogeny, divergence times, and evolution of dioecy. *Biol. J. Linn. Soc.* 171: 171–190. https://doi.org/10.3732/ajb.1100549

Drew, B.T., Cacho, N.I. & Sytsma, K.J. 2014. The transfer of two rare monotypic genera, *Neoeplingia* and *Chaunostoma*, to *Lepechinia* (Lamiaceae), and notes on their conservation. *Taxon* 63: 831–842. https://doi.org/10.12705/634.6

Drew, B.T., Liu, S., Bonifacino, J.B. & Sytsma, K.J. 2017a. Amphitropical disjunctions in New World Menthinae: Three Pliocene dispersals to South America following late Miocene dispersal to North America from the Old World. *Amer. J. Bot.* 104: 1695–1107. https://doi.org/10.3732/ajb.1700225

Drew, B.T., González-Gallegos, J.G., Xiang, C.L., Kriebel, R., Drummond, C.P., Walker, J.B. & Sytsma, K.J. 2017b. *Salvia* united: The greatest good for the greatest number. *Taxon* 66: 133–145. https://doi.org/10.12705/661.7

Duman, H., Dirmenci, T. & Özcan, T. 2023. A new annual *Satureja* (Lamiaceae) species from Turkey with molecular evidence, and lectotypification of two species. *Turk. J. Bot.* 47: 61–72. https://doi.org/10.55730/1300-008X.2744

Fennane, M. 2021. *Livre rouge de la flore vasculaire du Maroc*. Travaux de l'Institut Scientifique, Série Botanique, no. spécial: Premier centenaire de l'Institut Scientifique. Rabat: Institut Scientifique, Université Mohammed V.

Fennane, M., Ibn Tattou, M., Ouyahya, A. & El Oualidi, J. (eds.) 2007. *Flore pratique du Maroc*, vol. 2. Travaux de l'Institut Scientifique, Série Botanique, no. 38. Rabat: Institut Scientifique, Université Mohammed V.

Harley, R.M., Paton, A.J. & Ryding, O. 2003. New synonymy and taxonomic changes in the Labiatae. *Kew Bull.* 58: 485–489. https://doi.org/10.2307/4120633

Harley, R.M., Atkins, S., Budantsev, A.L., Cantino, P.D., Conn, B.J., Grayer, R., Harley, M.M., De Kok, R.P.J., Krestovskaya, T.V., Morales, R., Paton, A.J., Ryding, O. & Upson, T. 2004. Labiatae. Pp. 167–275 in: Kadereit, J.W. (ed.), *The families and genera of vascular plants*, vol. 7. Berlin: Springer. https://doi.org/10.1007/978-3-642-18617-2_11

Hassan, T. 2010. *Systematic studies on genus Nepeta L. Lamiaceae in Kashmir Himalaya*. Dissertation. University of Kashmir, Srinagar, India.

IUCN Standards and Petitions Committee 2024. *Guidelines for using the IUCN Red List categories and criteria*. Version 16. Prepared by the Standards and Petitions Committee. https://nc.iucnredlist.org/redlist/content/attachment_files/RedListGuidelines.pdf (accessed 28 Jan 2025)

Jamzad, Z., Chase, M.W., Ingrouille, M., Simmonds, M.S. & Jalili, A. 2003. Phylogenetic relationships in *Nepeta* L. (Lamiaceae) and related genera based on ITS sequence data. *Taxon* 52: 21–32. https://doi.org/10.2307/3647435

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C. & Thierer, T. 2012. Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28: 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Maddison, W.P. & Maddison, D.R. 2019. Mesquite: A modular system for evolutionary analysis. Version 3.61. http://www.mesquiteproject.org/

Maire, R. 1929. Contribution à l'étude de la flore de l'Afrique du Nord (Fasc. 14). *Bull. Soc. Hist. Nat. Afrique N.* 20: 12–42.

MEGC [Mint Evolutionary Genomics Consortium] 2018. Phylogenomic mining of the mints reveals multiple mechanisms contributing to the evolution of chemical diversity in Lamiaceae. *Molec. Pl.* 11: 1084–1096. https://doi.org/10.1016/j.molp.2018.06.002

Miller, M.A., Pfeiffer, W. & Schwartz, T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pp. 45–52 in: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, New Orleans, Louisiana, 14 Nov 2010. Piscataway: IEEE. https://doi.org/10.1109/GCE.2010.5676129

Moon, H.K., Hong, S.P., Smets, E. & Huysmans, S. 2009. Micromorphology and character evolution of nutlets in tribe Mentheae (Nepetoideae, Lamiaceae). *Syst. Bot.* 34: 760–776. https://doi.org/10.1600/036364409790139592

Pitard, M.J.-C. [1918]. *Contribution à l'étude de la flore du Maroc*. Printed work deposited by dépôt légal, Indre-et-Loire, 1918. http://ark.bnf.fr/ark:/12148/cb311181154

Ronquist, F., Teslenko, M., Van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Rose, J.P., Xiang, C.L., Sytsma, K.J. & Drew, B.T. 2022. A timeframe for mint evolution: Towards a better understanding of trait evolution and historical biogeography in Lamiaceae. *Bot. J. Linn. Soc.* 200: 15–38. https://doi.org/10.1093/botlinnean/boab104

Rose, J.P., Wiese, J., Pauley, N., Dirmenci, T., Celep, F., Xiang, C.L. & Drew, B.T. 2023. East Asian-North American disjunctions and phylogenetic relationships within subtribe Nepetinae (Lamiaceae). *Molec. Phylogen. Evol.* 187: 107873. https://doi.org/10.1016/j.ympev.2023.107873

Salehi, B., Valussi, M., Jugran, A.K., Martorell, M., Ramírez-Alarcón, K., Stojanović-Radić, Z.Z., Antolak, H., Kręgiel, D., Mileski, K.S., Sharifi-Rad, M., Setzer, W.N., Cádiz-Gurrea, M.L., Segura-Carretero, A., Şener, B. & Sharifi-Rad, J. 2018. *Nepeta* species: From farm to food applications and phytotherapy. *Trends Food Sci. Technol.* 80: 104–122. https://doi.org/10.1016/j.tifs.2018.07.030

Selvi, S., Polat, R., Çakılcıoglu, U., Celep, F., Dirmenci, T. & Ertuğ, Z.F. 2022. An ethnobotanical review on medicinal plants of the Lamiaceae family in Turkey. *Turk. J. Bot.* 46: 283–332. https://doi.org/10.55730/1300-008X.2712

Serpooshan, F., Jamzad, Z., Nejadsattari, T. & Mehregan, I. 2018. Molecular phylogenetics of *Hymenocrater* and allies (Lamiaceae): New insights from nrITS, plastid *trnL* intron and *trnL-F* intergenic spacer DNA sequences. *Nordic J. Bot.* 36(1–2): njb-01600. https://doi.org/10.1111/njb.01600

Shaw, J., Lickey, E.B., Schilling, E.E. & Small, R.L. 2007. Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: The tortoise and the hare III. *Amer. J. Bot.* 94: 275–288. https://doi.org/10.3732/ajb.94.3.275

Stamatakis, A. 2014. RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313 https://doi.org/10.1093/bioinformatics/btu033

Süntar, I., Nabavi, S.M., Barreca, D., Fischer, N. & Efferth, T. 2018. Pharmacological and chemical features of *Nepeta* L. genus: Its importance as a therapeutic agent. *Phytotherapy Res.* 32: 185–198. https://doi.org/10.1002/ptr.5946

Turland, N.J., Wiersema, J.H., Barrie, F.R., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T.W., McNeill, J., Monro, A.M., Prado, J., Price, M.J. & Smith, G.F. (eds.) 2018. *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress, Shenzhen, China, July 2017*. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books. https://doi.org/10.12705/Code.2018

Wagstaff, S.J., Hickerson, L., Spangler, R., Reeves, P.A. & Olmstead, R.G. 1998. Phylogeny in Labiatae s.l., inferred from cpDNA sequences. *Pl. Syst. Evol.* 209: 265–274. https://doi.org/10.1007/BF00985232

WFO Plant List 2023. *Nepeta*. In: World Flora Online Plant List. June 2023. https://wfoplantlist.org/plant-list/taxon/wfo-4000025901-2023-06?page=1

White, T.J., Bruns, T., Lee, S. & Taylor, J.W. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in: Innis, M.A., Sninsky, J.J. & White, T.J. (eds.), *PCR protocols: A guide to methods and applications*. New York: Academic Press. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Zhao, F., Chen, Y.P., Salmaki, Y., Drew, B.T., Wilson, T.C., Scheen, A.C., Celep, F., Bräuchler, C., Bendiksby, M., Wang, Q., Min, D.Z., Peng, H., Olmstead, R.G., Li, B. & Xiang, C.L. 2021. An updated tribal classification of Lamiaceae based on plastome phylogenomics. *B. M. C. Biol.* 19: 2. https://doi.org/10.1186/s12915-020-00931-z

Zhao, Y., Zhao, F., Salmaki, Y., Paton, A., Cai, J., Drew, B.T., Mahmoudi, C., Efimov, P., Turginov, O.T., Liang, C.Z., Chen, Y.P. & Xiang, C.L. 2023. Home at last: Molecular phylogenetic analyses support subsuming *Metastachydium* within *Phlomoides* (Lamiaceae). *Taxon* 72: 590–606. https://doi.org/10.1002/tax.12935

Appendix 1. Locations where population observations were made within the scope of this study and herbarium specimens studied.

Location of field studies conducted for this study (all population observations by the first author):

Morocco, Fès-Meknès, Taza Province, Maghraoua valley, 900–950 m, 33°54′53.190000″N, 04°02′53.352000″W, 17 May 2023, RAB114653. Morocco, Fès-Meknès, Sefrou Province, above waterfall near the city of Sefrou, 830–950 m, 33°49′44.226000″N, 04°51′05.316000″W, 4 Sep 2023, RAB114651. Morocco, Fès-Meknès, Boulemane Province, Skoura M'daz, 1150–1300 m, 33°30′57.912000″N, 04°51′05.316000″W, 26 Jul 2023, RAB114652. Morocco, Oriental: Berkane Province, Beni-Snassen, Zegzel gorge, 1490–1600 m, 34°50′13.314000″N, 02°21′27.276000″W, 23 May 2023, RAB114650.

Appendix 1. Continued.

Studied herbarium specimens:

Pitardia nepetoides Batt. ex Pit.
Sefrou region: G00435182, MARS46692, MPU006506, MPU071197, MPU071198, MPU090260, MPU090264, MPU1017734, P04366840, P04366843, P04527463, P04366851, P04366845, P04366850, P04366847, P04366848, P04366844, RAB99538.
Béni-Snassen region: CLF171236, CLF171237, MPU090261, MPU090262, MPU090263, MPU090265, MPU090266, MPU090267, MPU090268, MPU090269, MPU341388, MPU341389, MPU1017733, MPU1066065, P04366846, P04527465, P04366849, RAB61180, RAB99532, RAB99533, RAB99534, RAB99535, RAB99536.
Pitardia caerulescens Maire
Oriental Middle-Atlas region: MPU002054, MPU002057, MPU090258, MPU090259, MPU1017731, MPU1017732, MPU286075, MPU1296541, MPU1296542, P04366842, P04527464, P04366841, RAB99537.
Oriental High-Atlas region: MPU002055, MPU002056, MPU002056, MPU1017735.
Note: There is a specimen from Tizen Test in the Central High-Atlas collected by Jean Paul Peltier in 1985 (RAB46948), the specimen has no flower as it was still in the bud stage, so we are not sure of the identification of this specimen.

Appendix 2. Voucher information and GenBank accession numbers.

Taxon, Country of origin, *Voucher*; GenBank numbers: *ycf1-rps15*, *trnL-trnF*, *rpl32-trnL*, ITS, ETS, *PPR-AT3G09060* (– indicates missing squence; * indicates new sequence). DBG = Denver Botanical Garden, NTBG = National Tropical Botanical Garden, RBG-Edinburgh = Royal Botanic Garden Edinburgh, RSABG = Rancho Santa Ana Botanical Garden, UCBG = UC-Berkeley Botanical Garden.

Acanthomintha duttonii (Abrams) Jokerst, cultivated-UCBG, *H. Forbes s.n.* (UC), JQ669219, JQ669020, JQ669271, JQ669072, JQ669141, –; ***Acinos arvensis*** Dandy, U.S.A., *Judziewicz 14160* (WIS), JQ669220, JQ669021, JQ669273, JQ669074, JQ669143, OR199267; ***Agastache pallida*** (Lindl.) Cory, Mexico, *B. Drew 118* (WIS), JF289001, JF301357, JQ669274, JQ669075, JQ669144, KF307410; ***Agastache rugosa*** (Fisch. & C.A.Mey.) Kuntze, Japan, *H. Kanai, K. Hasagawa, K. Ohkubo 8916* (WIS), JQ669221, JQ669022, JQ669275, JQ669076, JQ669145, PV844732*; ***Blephilia hirsuta*** (Pursh) Benth., U.S.A., *T. Cochrane 13609* (WIS), JF289002, JF301358, JQ669276, JQ669077, JQ669146, –; ***Bystropogon origanifolius*** L'Hér., cultivated-U.S.A., *B. Drew s.n.* (WIS), JQ669222, JQ669023, JQ669277, JQ669078, JQ669147, PV844733*; ***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 & 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, OR199281; ***Cleonia lusitanica*** L., Spain, *D. Sanches & R. Garilan s.n.* (F), JF289006, DQ667495, –, DQ667309, –, –; ***Clinopodium ashei*** (Weath.) Small, U.S.A., *J. Walker 742* (WIS), JF289008, DQ667437, JQ669284, DQ667237, JQ669150, –; ***Clinopodium dalmaticum*** (Benth.) Bräuchler & Heubl. cultivated-DBG 811288, *M. Kintgen s.n.* (KHD), JQ669254, JQ669055, JQ669340, JQ669118, JQ669194, PV844746*; ***Clinopodium douglasii*** (Benth.) Kuntze, U.S.A., *B. Drew 206* (WIS), JQ669225, JQ669026, JQ669285, JQ669081, JQ669151, –; ***Clinopodium gracile*** (Benth.) Kuntze, China, *Yau 8715* (WIS), JQ669226, JQ669027, JQ669286, JQ669082, JQ669152, PV844735*; ***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 thymifolium*** Kuntze, cultivated-DBG 820510, *M. Kintgen s.n.* (KHD), JQ669257, JQ669058, JQ669343, JQ669121, JQ669197, PV844747*; ***Clinopodium vulgare*** L., U.S.A., *B. Drew 81* (WIS), JF289009, JF301363, JQ669289, JQ669085, JQ669155, PV844734*; ***Clinopodium vulgare*** L., Portugal, *Riina 1579* (WIS), JQ669229, JQ669030, JQ669290, JQ669086, JQ669156, PV844736*; ***Collinsonia canadensis*** L., U.S.A., cultivated-UCBG 1984.0696, *Raiche s.n.* (UC), JF289010, JF301364, JQ669291, JQ669087, JQ669157, OR199282; ***Congea griffithiana*** Munir, cultivated-Hawaii, *Lorence 9944* (PTBG), JQ669230, JQ669031, JQ669292, –, –, –; ***Conradina grandiflora*** Small, U.S.A., cultivated-Bok Tower Gardens 38717, *B. Drew s.n.* (WIS), JF289011, JF301365, JQ669293, JQ669088, JQ669158, –; ***Cuminia fernandezia*** Colla, Chile, *Stuessy & al. 11580* (OS), JQ669231, JQ669032, JQ669294, JQ669089, JQ669159, –; ***Cunila incana*** Benth., Uruguay, *K. Sytsma 7224* (WIS), JF289012, DQ667504, JQ669295, DQ667316, JQ669160, –; ***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, PV844737*; ***Dracocephalum bullatum*** Forrest ex Diels, China, *Boufford & al. 31785* (GH), JF289015, JF301366, JQ669303, JQ669096, JQ669167, PV844738*; ***Dracocephalum canescens*** L., cultivated-DBG 940037, *M. Kintgen s.n.* (KHD), JF289026, JF301373, JQ669321, JQ669108, JQ669182, OR199304; ***Dracocephalum ibericum*** M.Bieb., Turkey, *B. Drew 810* (ANK), –, –, –, –, –, OL807924; ***Dracocephalum officinale*** [***Hyssopus officinalis*** L.] (L.) Y.P.Chen & B.T.Drew, cultivated-DBG 003224/2, *M. Kintgen s.n.* (KHD), JF289023, JF301371, JQ669318, JQ669106, JQ669180, OL807919; ***Dracocephalum parviflorum*** Nutt., U.S.A., *Thomas s.n.* (WIS), JQ669237, JQ669038, JQ669304, JQ669097, JQ669168, OL807865; ***Drepanocaryum sewerzowii*** (Regel) Pojark., Tajikistan, *Rinziraeva 7540* (MO), JF289016, DQ667517, JQ669305, DQ667328, JQ669169, –; ***Drepanocaryum sewerzowii*** (Regel) Pojark., Tajikistan, *Potleen 30303* (LE), –, –, –, –, –, OR199296; ***Elsholtzia ciliata*** (Thunb.) Hyl., U.S.A., *B. Drew 210* (WIS), JF289017, JF301367, JQ669306, JQ669098, JQ669170, –; ***Glechoma hederacea*** L., U.S.A., *B. Drew 69* (WIS), JF289018, JF301368, JQ669307, JQ669099, JQ669171, OR199297; ***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, –; ***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, KF307409; ***Hesperozygis rhododon*** Epling, Brazil, *G. Hatschbach 44939* (WIS), JQ669242, JQ669043, –, JQ669102, JQ669176, –; ***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, PV844740*; ***Hymenocrater bituminosis*** Fisch. & C.A. Mey., Armenia, *K. Tamanyan & George Fayvush 4-2004* (NY), JQ669244, JQ669045, JQ669316, JQ669105, JQ669179, PV844741*; ***Hyptis laniflora*** Benth., Mexico, *B. Drew 41* (WIS), JF289024, JF301370, JQ669317, –, –, –; ***Isodon dawoensis*** (Hand.-Mazz.) H.Hara, cultivated-UCBG 90.066, *Erskine & al. 392* (UC), JF289025, JF301372, JQ669319, –, –, OR199303; ***Kurzamra pulchella*** Kuntze, Chile, *Werdermann 957* (MO), JQ669245, JQ669046, JQ669320, JQ669107, JQ669181, –; ***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, U.S.A., *B. Drew 197* (WIS), JF289029, JF301375, JQ669324, JF301344, JF301315, –; ***Lepechinia lamiifolia*** (Benth.) Epling, Peru, *B. Drew 178* (WIS), JF289034, JF301379, JQ669325, JF301348, JF301320, –; ***Lepechinia leucophylloides*** (Ramamoorthy, Hiriart & Medrano) B.T.Drew, Cacho & Sytsma, Mexico, *B. Drew 129* (WIS), JF289047, JF301390, JQ669348, JF301354, JF301327, –; ***Lepechinia mecistandra*** (Donn.Sm.) Moon, El Salvador, *J.A. Monterrosa & R.A. Carballo 213* (MO), JF289005, JF301361, JQ669282, JF301342, JF301311, KF307357; ***Lepechinia mexicana*** (S.Schauer) Epling, Mexico, *B. Drew 164* (WIS), JF289035, JF301380, JQ669326, JF301349, JF301321, –; ***Lepechinia salviae*** (Lindl.) Epling, Colombia, *Jabaily s.n.* (WIS), –, –, –, –, –, KF307382; ***Lindernia dubia*** (L.) Pennell, U.S.A, *B. Drew 79*

Appendix 2. Continued.

(WIS), JQ669246, JQ669047, JQ669327, –, –, –; ***Lophanthus lipskyanus*** Ikonn.-Gal. & Nevski, Uzbekistan, *Vassiljeva s.n.* (WIS), JF289039, JF301384, JQ669328, JQ669109, JQ669183, –; ***Lophanthus turcicus*** Dirmenci, Yıldız & Hedge, Turkey, *Dirmenci 3707* (ANK), –, –, –, –, –, OR199307; ***Lycopus maackianus*** Makino, Japan, *Julita 661* (WIS), JQ669247, JQ669048, JQ669329, JQ669110, JQ669184, –; ***Lycopus uniflorus*** Michx., U.S.A., *J. Walker 2586* (WIS), JF289040, DQ667488, JQ669330, DQ667302, JQ669185, OR199308; ***Marmoritis complanatum*** (Dunn) A.L.Budantzev, China, *D.E. Boufford & al. 32012* (GH), JQ669248, JQ669049, JQ669331, JQ669111, JQ669186, OR199309; ***Meehania cordata*** Britton, China, *A.E. Radford 45379* (WIS), JQ669249, JQ669050, JQ669332, JQ669112, JQ669187, –; ***Meehania fargesii*** (H.Lév.) C.Y.Wu, China, *Xiang 342* (KUN), –, –, –, –, –, OR199310; ***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 & al. 24526* (HUH), JQ669250, JQ669051, JQ669334, JQ669114, JQ669189, –; ***Melissa officinalis*** L., cultivated-UW-Madison, *B. Drew 70* (WIS), JF289042, JF301386, JF301353, JF301325, JQ669335, KF307390; ***Mentha arvensis*** L., U.S.A., *B. Drew 82* (WIS), JF289043, JF301387, JQ669336, JQ669115, JQ669190, –; ***Mentha microphylla*** K.Koch, Portugal, *Riina 1575* (WIS), JQ669251, JQ669052, JQ669337, JQ669116, JQ669191, PV844743*; ***Mentha pulegium*** L., Portugal, *Riina 1574* (WIS), JQ669252, JQ669053, JQ669338, JQ669117, JQ669192, PV844744*; ***Mentha spicata*** L., U.S.A., *J. Walker 2566* (WIS), JQ669253, JQ669054, JQ669339, DQ667244, JQ669193, PV844745*; ***Micromeria juliana*** (L.) Bentham ex Rchb., cultivated-UCBG 91.0995, *H. Forbes s.n.* (UC), JQ669255, JQ669056, JQ669341, JQ669119, JQ669195, OR199311; ***Micromeria lanata*** Benth., cultivated, *B. Drew s.n.* (WIS), JQ669256, JQ669057, JQ669342, JQ669120, JQ669196, –; ***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., U.S.A., *B. Drew 66* (WIS), JF289046, JF301389, JQ669347, JQ669125, JQ669201, –; ***Nepeta apuleji*** Ucria, Morocco, *Bakali s.n.* (RAB), PV844843*, PV844838*, PV844833*, PV821508*, PV844848*, PV844751*; ***Nepeta cataria*** L., U.S.A., *B. Drew 72* (WIS), JF289048, JF301391, JQ669349, JQ669126, JQ669202, OR199314; ***Nepeta nuda*** L., Turkey, *B. Drew 796* (ANK), –, –, –, –, –, OR199323; ***Nepeta podostachys*** Benth., Kyrgyzstan, *A. Naumenko s.n.* (NEBK), –, –, –, –, –, OR199327; ***Nepeta transcaucasica*** Grossh., Turkey, *B. Drew 1075* (ANK), –, –, –, –, –, OR199333; ***Nepeta ucranica*** L., Kyrgyzstan, *A. Naumenko s.n.* (NEBK), –, –, –, –, –, OR199335; ***Ocimum basilicum*** L., cultivated, *J. Walker 2557* (WIS), JF289049, AY570462, JQ669350, –, –, –; ***Origanum vulgare*** L., U.S.A., *B. Drew 77* (WIS), JF289050, JF301392, JQ669351, JQ669127, JQ669203, PV844752*; ***Pitardia nepetoides*** Batt. ex Pit., Morocco, Zegzel-cultivated, *Bakali s.n.* (RAB), PV844839*, PV844834*, PV844829*, PV844844*, PV821504*, PV844748*; ***Pitardia nepetoides*** Batt. ex Pit., Morocco, Sefrou, *Bakali s.n.* (RAB), PV844840*, PV844835*, PV844830*, PV844845*, PV821505*, PV844749*; ***Pitardia nepetoides*** Batt. ex Pit., Morocco, Skoura M'daz, *Bakali s.n.* (RAB), PV844841*, PV844836*, PV844831*, PV844846*, PV821506*, PV844750*; ***Pitardia nepetoides*** Batt. ex Pit., Morocco, Zegzel-wild, *Bakali s.n.* (RAB) PV844842*, PV844837*, PV844832*, PV844847*, PV821507*, –; ***Phryma leptostachya*** L., U.S.A., *B. Drew 73* (WIS), JQ669260, JQ669061, JQ669353, –, –, –; ***Plectranthus cremnus*** B.J.Conn, U.S.A., cultivated-UCBG 3.0347, *H. Forbes s.n.* (UC), JF289052, JF301393, JQ669354, –, –, –; ***Pogogyne douglasii*** Benth., U.S.A., cultivated-UCBG 91.1071, *H. Forbes s.n.* (JEPS), JF289053, JF301394, JQ669355, JQ669128, JQ669204, –; ***Poliomintha incana*** (Torr.) A.Gray, U.S.A., *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., U.S.A., *J. Walker 3225* (WIS), JF289055, DQ667508, JQ669358, JQ669130, JQ669206, OR199336; ***Pseudocarpidium wrightii*** Millsp., cultivated-Fairchild Botanical Garden, *Drew s.n.* (WIS), JQ669262, JQ669063, JQ669359, –, –, –; ***Pycnanthemum virginianum*** (L.) Durand & Jackson, U.S.A., *B. Drew 85* (WIS), JQ669263, JQ669064, JQ669360, JQ669131, JQ669207, –; ***Rhabdocaulon erythrostachys*** Epling, Brazil, *Sergio A.L. Bordignon 851* (F), JQ669264, JQ669065, JQ669361, JQ669132, JQ669208, –; ***Rhododon ciliatus*** (Benth.) Epling, U.S.A., *Singhurst s.n* (TEX), JF289057, JF301397, JQ669363, JQ669134, JQ669210, –; ***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 californica*** Brandegee, Mexico, *J. Walker 2541* (WIS), –, –, –, –, –, KY067376; ***Salvia dorrii*** (Kellogg) Abrams, U.S.A., *J. Walker 2541* (WIS), –, –, –, –, –, KY067380; ***Salvia dorystaechas*** B.T.Drew, cultivated-RBG-Edinburgh 1972-0177D, *J. Walker s.n.* (WIS), JF289014, AY570454, JQ669302, DQ667252, JF301312, –; ***Salvia greatae*** Brandegee, U.S.A., *J. Walker 2511* (WIS), JF289062, AY570481, JQ669367, DQ667215, JF301331, –; ***Salvia mellifera*** Greene, U.S.A., *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, KF307404; ***Salvia patens*** Cav., cultivated-RBG-Edinburgh 1973-9197, *J. Walker s.n.* (WIS), JF289066, DQ667442, JQ669370, DQ667253, JF301333, KF307405; ***Salvia polystachia*** Cav., cultivated-UCBG 92.052, *Breedlove & Mahoney 72286* (UC), JF289067, JF301399, JQ669371, JF301356, JF301334, –; ***Salvia przewalskii*** Maxim., cultivated-RBG-Edinburgh 1993-2067A, *J. Walker s.n.* (WIS), JF289068, DQ667443, JQ669372, DQ667254, JF301339, KF307406; ***Salvia roemeriana*** Scheele, U.S.A., *J. Walker 2515* (WIS), –, –, –, –, –, KF307407; ***Salvia rosmarinus*** Spenn., cultivated, *J. Walker 2558* (WIS), JF289058, AY570465, JQ669364, DQ667241, JF301329, KF307401; ***Salvia sclarea*** L., cultivated, *J. Walker 2527* (WIS), JQ669265, JQ669066, JQ669373, DQ667222, JF301335, –; ***Salvia yangii*** B.T.Drew, cultivated, *J. Walker 2524* (WIS), JF289051, AY570464, JQ669352, DQ667223, JF301328, KF307400; ***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 annua*** (Pall.) Schischk., Mongolia, *Neuffer 10224* (OSBU) –, –, –, –, –, OR199337; ***Schizonepeta multifida*** Briq., Siberia, *Boyd 4805* (WIS), JF289070, JF301400, JQ669376, DQ667313, JQ669213, –; ***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, PV844753*; ***Thymus serpyllum*** L., cultivated-U.S.A., *J. Walker 2564* (WIS), JQ669269, JQ669070, JQ669379, DQ667242, JQ669216, PV844754*; ***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, PV844755*.