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Two in, one out: A comprehensive phylogeny of the tribe Elsholtzieae (Nepetoideae, Lamiaceae) sheds new light on its generic delimitation

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Abstract Elsholtzieae, the smallest tribe of the subfamily Nepetoideae (Lamiaceae), consists of approximately 70 species within eight genera. The tribe is primarily distributed across East and Southeast Asia, with China, Korea, and Japan representing the center of its diversity. Previous studies have indicated the polyphyly of *Keiskea* and *Elsholtzia*; however, due to the limited sampling and the use of only a few DNA markers, the relationships within and between the genera of Elsholtzieae remain unsatisfactorily understood. In this study, we present the most comprehensive phylogenetic analyses of Elsholtzieae to date, utilizing five chloroplast markers (*matK*, *ndhF*, *rbcL*, *trnL-F*, *ycf1*) and two nuclear regions (ITS, ETS). Our results confirm the monophyly of Elsholtzieae, which are resolved into five major clades, while at the same time confirming the non-monophyly of *Keiskea*, *Elsholtzia*, and possibly *Perilla*. Consequently, based on the molecular phylogenetic analyses combined with morphological and geographical evidence, we propose an expanded circumscription of the genus *Perilla* to include *Keiskea* and *Mosla*, and reinstate the genus *Paulseniella* to accommodate three species traditionally included in *Elsholtzia*. The newly recognized *Elsholtzia* s.str. is monophyletic with five well-supported lineages, while further work is needed to fully clarify its infrageneric classification. Furthermore, we provide an identification key for all the genera of Elsholtzieae reflecting these taxonomic changes, and checklists of *Paulseniella* and *Perilla*.

Keywords *Elsholtzia*; *Keiskea*; Lamiaceae; Nepetoideae; *Perilla*; taxonomy

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

INTRODUCTION

Elsholtzieae is the smallest tribe within the subfamily Nepetoideae of Lamiaceae, ranking after Mentheae and Ocimeae (Harley & al., 2004; Zhao & al., 2021). It is characterized by a weakly 2-lipped corolla, divergent stamens, and an asymmetric disk with an elongated anterior lobe (H.W. Li & Hedge, 1994; Harley & al., 2004; Chen & al., 2016). The tribal name Elsholtzieae was first proposed by Wunderlich (1967) and later validated by Sanders & Cantino (1984). Initially, Cantino & al. (1992) included six genera within Elsholtzieae based on morphological evidence: *Collinsonia* L., *Elsholtzia* Willd., *Keiskea* Miq., *Mosla* (Benth.) Buch.-Ham. ex Maxim., *Perilla* L., and *Perillula* Maxim. A molecular phylogenetic study by Chen & al. (2016) revealed that *Ombrocharis* Hand.-Mazz., a genus previously listed as *incertae sedis* by Harley & al. (2004), belongs to Elsholtzieae and is sister to *Perillula*. Chen & al. (2016) also uncovered that two species of *Elsholtzia* form a clade phylogenetically distant from the rest of the genus. Following this finding, Mayta-Anco & al. (2016) proposed a new genus for this clade, *Vuhuangia* Solomon Raju & al., increasing the number of genera within the tribe to eight. As currently circumscribed, Elsholtzieae comprises more than 70 species predominantly distributed across East Asia. Notably, *Collinsonia* is restricted to eastern North America, representing the sole genus of Elsholtzieae documented in the New World (Gleason & Cronquist, 1991; P. Li & al., 2017).

Among these genera, *Perilla* contains a single species, *P. frutescens* (L.) Britton, with 2–4 varieties distinguished by differences in leaf morphology, fruiting calyx, and nutlets (Liu & Zhang, 1998; Guo & Wang, 2000). Although native to East Asia, *P. frutescens* is cultivated worldwide for its culinary and medicinal uses. Initially, Bentham (1832–1836) assigned *Perilla* to the tribe Mentheae, while Briquet (1895–1897) later established subtribe Perillinae within the tribe Satureieae, placing *Perilla* alongside *Collinsonia*, *Mosla*, *Micheliella* Briq. (currently included in *Collinsonia*), and *Perillula*. Eventually, Cantino & al. (1992) transferred these genera to Elsholtzieae.

Mosla, comprising 15 species, is primarily distributed across China, Japan, and Korea, with *M. dianthera* (Buch.-Ham. ex Roxb.) Maxim. extending into eastern Russia, the western Himalayas, and Southeast Asia (S.L. Zhou & al., 1997). *Mosla* and *Perilla* exhibit high morphological similarity, sharing several key characteristics such as a raceme-like thyrse formed by 1-flowered cymes (i.e., with each verticillaster having two flowers), accrescent fruiting calyces, and nutlets with distinct supra-reticulate surfaces (H.W. Li & Hedge, 1994; S.L. Zhou & al., 1997; Harley & al., 2004; Jeon & al., 2020; Wang & al., 2024). *Mosla* is subdivided into two sections: *M.* sect. *Mosla* and sect. *Orthodon* C.Y.Wu & S.J.Hsuan., based on their differences in bracts, calyces, and nutlets (H.W. Li, 1977).

Keiskea consists of seven species distributed in China and Japan. It is characterized by raceme-like thyrses formed by

1-flowered cymes, campanulate and ± 2-lipped calyces, long-exserted stamen filaments that are bearded at base, and nutlets often reduced in number by abortion (Hsuan, 1977; H.W. Li & Hedge, 1994; Harley & al., 2003). Bentham (1876) initially placed *Keiskea* within Mentheae, while Briquet (1895–1897) later transferred it to Pogostemoneae. Cantino & al. (1992) assigned both *Keiskea* and *Collinsonia* to Elsholtzieae, suggesting a close relationship between the two genera. In line with their ideas, Harley & al. (2003) synonymized *Keiskea* with *Collinsonia* based on their similarities in inflorescence architecture, calyx and corolla shapes, and number of mature mericarps per fruit. However, subsequent studies have consistently rejected this synonymization, revealing that the two genera exhibit different pollen and pericarp micromorphology (S.L. Zhou & al., 1997; Hong, 2007; Jeon & al., 2020; Wang & al., 2024), and do not form a monophyletic group (Chen & al., 2016; P. Li & al., 2017; Wang & al., 2024; Jin & al., 2025).

The traditionally defined *Collinsonia* comprises four species and is endemic to eastern North America, with the southeastern United States being its center of diversity (Peirson & al., 2006). *Collinsonia* is characterized by a relatively lax, raceme-like thyrse formed by 1-flowered cymes, corolla with deeply fimbriate middle lobe of lower lip, and typically only one mature nutlet per fruit due to abortion (Shinners, 1962; Harley & al., 2003; Peirson & al., 2006). Flowers of *C. canadensis* L. and *C. punctata* Elliott bear only two fertile stamens (with the anterior pair being reduced), whereas those of *C. anisata* Sims and *C. verticillata* Baldwin ex Elliott possess four fertile stamens. Briquet (1895–1897) recognized the latter two species as a separate genus, *Micheliella.* He considered *Collinsonia* to contain two species, treating *C. punctata* as a synonym of *C. canadensis*, while accepting *C. scabriuscula* Ait. (currently included in *C. canadensis*) as a distinct species. Shinners (1962), however, did not adopt Briquet's segregation of *Micheliella*. Instead, he subdivided *Collinsonia* into *C.* subg. *Collinsonia* and *C.* subg. *Micheliella* (Briq.) Shinners, based primarily on the inflorescence morphology rather than stamen number. In his treatment, *C.* subg. *Collinsonia* included *C. canadensis* (with *C. punctata* as its synonym), *C. serotina* Walter (with *C. anisata* as its synonym), and *C. tuberosa* Michx. (now included in *C. canadensis*), whereas *C.* subg. *Micheliella* comprised only *C. verticillata*. Peirson & al. (2006) revised the species boundaries in *Collinsonia* based on phenetic analyses and recognized four species: *C. anisata*, *C. canadensis*, *C. punctata*, and *C. verticillata*. They rejected *C. serotina* as an ambiguous name. Phylogenetic analysis by P. Li & al. (2017), however, included three individuals of *C. canadensis*, which did not form a monophyletic group. One accession of *C. canadensis* (PNLI20120467) was recovered in a sister position to an accession identified by them as *C. serotina*. In our phylogenetic analyses, we included all the sequences generated by P. Li & al. (2017) under the name "*C. serotina*".

Ombrocharis, a monotypic genus endemic to China, was established by Handel-Mazzetti (1936) based on his own collection made in 1918. The genus is characterized by woody tubers, raceme-like thyrses formed by 3-flowered cymes, long internodes between cymes, distinctly pedunculate cymes, 11-veined calyces, and stamens that are included in the corolla (H.W. Li & Hedge, 1994; Chen & al., 2016; J.J. Zhou & al., 2016; Jin & al., 2025). On the basis of the external morphological characters given in the protologue, H.W. Li & Hedge (1994) assigned *Ombrocharis* to the subtribe Lamiinae within Lamioideae. However, Cantino & Sanders (1986) transferred it to Nepetoideae based on its hexacolpate, 3-celled pollen. Following its rediscovery at the type locality, a molecular phylogenetic study revealed its placement within Elsholtzieae, in which it is closely related to *Perillula* (Chen & al., 2016). *Perillula* is another monotypic genus endemic to Japan (Murata & Yamazaki, 1993), exhibiting several morphological similarities with *Ombrocharis*. The two genera differ primarily in stem and leaf morphology (Murata & Yamazaki, 1993; H.W. Li & Hedge, 1994; S.L. Zhou & al., 1997; Chen & al., 2016).

Vuhuangia, recently segregated from *Elsholtzia* by Mayta-Anco & al. (2016), comprises two species characterized by spike-like thyrses, stamen filaments adhering to the upper lip of the corolla, a disk with an elongated anterior lobe shorter than the ovary, and nutlets with sub-basal abscission scars (Wu & Huang, 1974; H.W. Li & Hedge, 1994; Pu, 2012; Jin & al., 2025). Briquet (1895–1897) placed *V. flava* (Benth.) Molinari & al. (as *E. flava* Benth.), together with about a dozen of the other species, within *E.* sect. *Aphanochilus* (Benth.) Benth. subsect. *Stenelasmeae* Briq., characterized by linear-subulate bracts and glossy nutlets. *Vuhuangia penduliflora* (W.W.Sm.) Mayta & al. was unknown at the time of Briquet's treatment. Wu & Huang (1974) followed Briquet's (1895–1897) morphological circumscription of the subsection and included both species therein. Later, Mayta-Anco & al. (2016) established *Vuhuangia* as a distinct genus based on the phylogenetic results of Chen & al. (2016) and cytological evidence of Funamoto & al. (2012).

Elsholtzia, the largest genus of the tribe, comprises 41 species widely distributed in eastern Asia, with its highest diversity in southwestern China (H.W. Li & Hedge, 1994; Harley & al., 2004; Bongcheewin & Chantaranothai, 2008; Jin & al., 2025). The genus is characterized by dense, cylindrical, sometimes secund thyrses, lanceolate, ovate or flabellate bracts,

exannulate calyces, and a disk with the elongated anterior lobe longer than the ovary (H.W. Li & Hedge, 1994; Harley & al., 2004; Jang & al., 2010; Jeon & al., 2020). Initially, Bentham (1832–1836) placed *Elsholtzia* in the tribe Mentheae, while Briquet (1895–1897) transferred it to Pogostemoneae. Sanders & Cantino (1984) eventually formally established the tribe Elsholtzieae. Infrageneric classification of *Elsholtzia* has long been contentious due to its contradictory morphological diversity, leading to several rearrangements at the sectional and intrasectional levels. Bentham (1832–1836) divided *Elsholtzia* into three sections based on inflorescence architecture and bract morphology: *E.* sect. *Aphanochilus*, sect. *Cyclostegia* Benth., and sect. *Elsholtzia*. Briquet (1895–1897) further divided *E.* sect. *Aphanochilus* into two subsections (unranked in the synopsis but explicitly termed as subsections on page 353 of his work): *E.* subsect. *Platyelasmeae* Briq. and subsect. *Stenelasmeae*. Wu & Huang (1974) later accepted these subsections and recognized eight series within *E.* sect. *Aphanochilus* subsect. *Stenelasmeae*. In a subsequent taxonomic revision, Press (1982) raised *E.* sect. *Aphanochilus* subsect. *Platyelasmeae* to the section level and synonymized *E.* sect. *Cyclostegia* with *E.* sect. *Elsholtzia*. Notably, none of the classifications cited above corresponds precisely to the phylogenetic relationships within *Elsholtzia*, highlighting the need for a comprehensive reassessment based on modern understanding (Wang & al., 2024).

Recent molecular phylogenetic studies on *Elsholtzia* and Elsholtzieae as a whole have greatly improved the understanding of generic boundaries within the tribe (Pu, 2012; Chen & al., 2016; P. Li & al., 2017; Sun & al., 2022; Wang & al., 2024; Jin & al., 2025). Although these studies generated different topologies depending on the employed markers, the overall phylogenetic framework of Elsholtzieae is consistent, containing five well-supported major clades (Fig. 1). The clades are listed as follows: Clade I: *Ombrocharis* + *Perillula*, Clade II: *Mosla* + *Keiskea* + *Perilla* + *Collinsonia* (referred to as the MKPC clade by Wang & al., 2024, due to its high support values and distinctive morphology), Clade III: *Vuhuangia*, Clade IV: an unnamed group including three species of *Elsholtzia* (*E. cephalantha* Hand.-Mazz., *E. densa* Benth., *E. eriostachya* Benth.), and Clade V: core *Elsholtzia* containing the remaining taxa of the genus. Clades III, IV, and V, which belong to the traditionally defined *Elsholtzia*, exhibit contradictory systematic positions among different studies. Therefore, the boundary and relationships of *Elsholtzia* need a thorough reassessment based on comprehensive investigations. Another issue concerns the monophyly of *Keiskea.* The genus is poorly investigated in previous studies, while the existing evidence—based either on individual cpDNA and/or nrDNA fragments (P. Li & al., 2017) or on numerous single-copy orthologous nuclear genes (Wang & al., 2024; Jin & al., 2025)—consistently indicates that *Keiskea* is not monophyletic. Consequently, studies with a broader taxon sampling are required to clarify the phylogenetic relationships within Elsholtzieae, along with the redefinition of its genera to achieve monophyly.

In this study, we utilize an extensive taxon sampling, using five plastid fragments (*matK*, *ndhF*, *rbcL*, *trnL-F*, *ycf1*) and two nuclear regions (ETS, ITS) to: (1) reassess the backbone phylogeny of the tribe Elsholtzieae, (2) clarify generic relationships within the tribe, and (3) update a phylogeny-based delimitation of genera with newly elucidated morphological synapomorphies.

MATERIALS AND METHODS

Taxon sampling and choice of markers. — A comprehensive global sampling was conducted to cover all the eight currently recognized genera of Elsholtzieae. In total, 93 samples were included representing 61 species and 8 additional infraspecific taxa. The sampling encompassed: (1) all the species of *Collinsonia*, *Ombrocharis*, *Perilla*, *Perillula*, and *Vuhuangia*; (2) 5 of the 7 species of *Keiskea* (71%); (3) 8 of the 15 species of *Mosla* (53%); and (4) 38 of the 41 species of *Elsholtzia* (93%) across their native ranges in China, Japan, Korea, Kyrgyzstan, Mongolia, Russia, and Thailand. The type species of all these genera were included. The unsampled species (primarily members of *Mosla*) were currently impossible to obtain from field or herbarium collections due to budget and time limitations. Nevertheless, integrating evidence from existing studies ensures that this sampling gap does not affect the overall validity of our conclusions. The following taxa are newly sampled and sequenced: (1) three species of *Mosla* (*M. dianthera*, *M. hangchouensis* Matsuda, *M. scabra* (Thunb.) C.Y.Wu & H.W.Li), (2) both species of *Vuhuangia* (*V. flava*, *V. penduliflora*), (3) one species each of *Keiskea* (*K. elsholtzioides* Merr.), *Collinsonia* (*C. canadensis* L.), *Perillula* (*P. reptans* Maxim.), and *Ombrocharis* (*O. dulcis* Hand.-Mazz.), and (4) XXX species of *Elsholtzia*.

To maximize the morphological and geographical coverage, additional sequences were obtained from GenBank (www.ncbi.nlm.nih.gov/genbank/). For example, sequences of all the five species of the North American genus *Collinsonia*

were retrieved (including "*C. serotina*"). Three species from the tribe Mentheae (*Salvia glutinosa* L., *S. miltiorrhiza* Bunge, *Mentha spicata* L.) and two from Ocimeae (*Coleus xanthanthus* C.Y.Wu & Y.C.Huang, *Isodon amethystoides* (Benth.) H.Hara) were selected as the outgroup based on previous phylogenetic studies (i.e., Chen & al., 2016; P. Li & al., 2017; Zhao & al., 2021); their sequences were also obtained from GenBank.

Five chloroplast markers (the genes *matK*, *ndhF*, *rbcL*, *ycf1*, and the intergenic spacer *trnL-F*) and two nuclear ribosomal DNA regions (internal transcribed spacer, ITS; external transcribed spacer, ETS) were selected for phylogenetic analyses, as these markers have been successfully used in previous phylogenetic studies of Elsholtzieae (Chen & al., 2016; P. Li & al., 2017; Sun & al., 2022). Voucher information and GenBank accession numbers are listed in Appendix 1.

DNA extraction, amplification and sequencing. — Total genomic DNA was extracted either from herbarium specimens following Zeng & al. (2018) or from silica gel-dried leaf material using the CTAB method (Doyle & Doyle, 1987). Primers, mixtures, and PCR procedures for *matK*, *ndhF*, *rbcL*, and *trnL-F* followed those of Chen & al. (2014), while for *ycf1*, ITS, and ETS followed those of Chen & al. (2016). Sequencing was conducted by the Invitrogen sequencing service (Invitrogen, commercial sequencing facility, Guangzhou, China) using the same primers as for PCR amplifications. All sequences were aligned using the MAFFT plug-in in Geneious v.11.0.3 (Kearse & al., 2012) and manually adjusted using PhyDe v.0.9971 (Müller & al., 2010). The sequence characterization statistics were calculated in PAUP v.4.0b10 (Swofford, 2002), and the relevant information was extracted from the generated log files.

Phylogenetic analyses. — Phylogenetic reconstructions for both combined cpDNA and nrDNA datasets were performed using maximum likelihood (ML) and Bayesian inference (BI) methods. ML analysis was conducted using MAxMLHPC2 v.8.2.12 (Stamatakis, 2014) and BI using MrBayes v.3.2.7a (Ronquist & al., 2012) through the Cyberinfrastructure for Phylogenetic Research Science (CIPRES) Gateway (Miller & al., 2010), following Xiang & al. (2020). The best substitution models for each dataset were estimated under the Akaike information criterion (AIC) score using jModelTest2 (Darriba & al., 2012). The phylogenetic trees were visualized and edited using the online website Interactive Tree Of Life (iTOL) v.7 (https://itol.embl.de/; Letunic & Bork, 2021).

Nomenclatural solutions. — The nomenclature has been verified and revised at all ranks according to the rules of botanical nomenclature (Turland & al., 2025), to ensure the correct interpretation of historical literature and stability of accepted names.

RESULTS

Sequence characterization. — In this study, a total of 378 sequences were newly generated. The combined and aligned cpDNA dataset had a length of 9220 bp, including 873 bp from *matK*, 2241 bp from *ndhF*, 501 bp from *rbcL*, 879 bp from *trnL-F*, and 4761 bp from *ycf1*. Among these positions, 2748 (29.80%) were variable and 2174 (23.58%) were parsimony-informative. The length of the aligned nrDNA dataset was 1171 bp (744 positions for ITS and 430 positions for ETS), of which 652 sites (55.68%) were variable and 579 sites (49.44%) were parsimony-informative. A summary of the characteristics for all datasets is presented in Table 1 and all datasets are provided Appendix 2.

Phylogenetic reconstruction based on the combined cpDNA dataset. — Phylogenetic analyses based on the combined cpDNA dataset using both ML and BI analyses produced highly consistent tree topologies (Fig. 2; suppl. Figs. S1, S2). The ML tree (Fig. 2) is therefore further discussed below with the support values of ML bootstrap (ML-BS) and Bayesian posterior probabilities (BI-PP) provided in brackets.

The tribe Elsholtzieae was strongly supported as monophyletic (Fig. 2; ML-BS = 100%, BI-PP = 1.00; all support values follow this order below) and consisted of five major clades (clade numbers correspond to Fig. 1). Clade I (100%, 1.00), containing *Ombrocharis* and *Perillula*, was resolved as sister to the clade comprising the rest of the tribe (100%, 1.00). Within the latter, Clade III (100%, 1.00), the *Vuhuangia* clade, was recovered as sister to a larger (although weakly supported) clade, which includes Clade II (100%, 1.00; the MKPC clade), Clade IV (100%, 1.00; the clade containing three *Elsholtzia* species designated here as "*Paulseniella*"), and Clade V (100%, 1.00; the core *Elsholtzia* clade). Clade II was recovered as sister to Clade IV + Clade V, although this relationship received low supports. Within Clade II, the monophyletic *Collinsonia* (100%, 1.00) is sister to the clade comprising *Keiskea*, *Mosla*, and *Perilla* (100%, 1.00). Notably, *Keiskea* was confirmed to be paraphyletic, with its seven accessions distributed across four distinct lineages, while *Mosla* and *Perilla* were embedded within it. In addition, the monophyly of *Perilla* is questioned, as two out of the three accessions

of *P. frutescens* var. *hirtella* (Nakai) Makino (KT220691, KT220692) formed a clade distantly placed from the rest of the genus. Clade IV was recovered as sister to Clade V, although this sister relationship was poorly supported. Within Clade V, five distinct lineages were identified, each receiving the maximum support value (100%, 1.00).

Phylogenetic reconstruction based on the combined nrDNA dataset. — Phylogenetic analyses of the nrDNA dataset using both ML and BI methods produced topologically congruent trees (Fig. 3, suppl. Figs. S3, S4) strongly supporting the monophyly of Elsholtzieae. Five major clades were recovered, with their composition aligning with those in the cpDNA trees (Fig. 3, suppl. Figs. S1, S2). However, placement of certain groups and relationships within clades exhibited slight differences (Fig. 3). Notably, for many nodes, the support values were generally lower in the nrDNA trees compared to the cpDNA trees, particularly for the positions that showed incongruence between the two topologies.

A significant topological discrepancy between the cpDNA and nrDNA trees was the placement of Clade III and Clade IV. In the nrDNA tree, Clade IV has a weakly supported sister position to the rest of the tribe except for Clade V (Fig. 3), rather than clustering with Clade V as resolved in the cpDNA tree (Fig. 2). In addition, Clade III was recovered as sister to Clade I (78%, 0.97), with Clade II being their sister group (85%, 1.00). Remarkably, Clade V remained monophyletic and well-supported (100%, 1.00). Within this clade, five lineages were further delineated, with their species composition identical to those in the cpDNA tree, although the position of the *E. bodinieri* + *E. heterophylla* clade was slightly different.

DISCUSSION

Backbone phylogeny of Elsholtzieae. — This study conducted the most comprehensive taxon sampling of Elsholtzieae to date, using five chloroplast markers and two nuclear regions. A total of 61 species were encompassed, representing 79% of all currently known species within the tribe. Twelve species are unsampled (3 spp. of *Elsholtzia*, 2 spp. of *Keiskea*, and 7 spp. of *Mosla*).

All analyses strongly support the monophyly of Elsholtzieae, resolving it into five major clades (Figs. 2, 3) that are consistent with the results of the previous studies (Pu, 2012; Chen & al., 2016; P. Li & al., 2017; Sun & al., 2022; Wang & al., 2024; Jin & al., 2025), although the relationships among these clades somewhat varied depending on the markers used. *Ombrocharis* and *Perillula* form a clade followed by the MKPC clade containing *Mosla*, *Keiskea*, *Perilla*, and *Collinsonia*; the remaining three clades pertain to traditionally defined *Elsholtzia*: *Vuhuangia*, the "*Paulseniella*" clade, and the core *Elsholtzia* clade.

Ombrocharis and *Perillula*, referred to as Clade I, branch from the basal node within Elsholtzieae in the cpDNA tree (Fig. 2), whereas the nrDNA tree group it with *Vuhuangia* (Fig. 3). Clade I is unique within the tribe in having raceme-like thyrses composed of 3-flowered pedunculate cymes. This inflorescence structure represents a distinct evolutionary trend, in contrast to the inflorescences of the later-diverging MKPC clade having 1-flowered, often sessile or shortly pendunclate cymes (Jin & al., 2025). Other common features of Clade I include tuber-like rhizomes, campanulate calyces and corollas, stamens that are included in the corolla, and anthers with small connectives (Maximowicz, 1875; Murata & Yamazaki, 1993; H.W. Li & Hedge, 1994; Harley & al., 2004; Chen & al., 2016). Our results together with those of the previous studies (Chen & al., 2016; P. Li & al., 2017; Jin & al., 2025) show that *Ombrocharis* and *Perillula* exhibit high morphological similarity and close phylogenetic relationship allowing their merging into a single genus, which has already been suggested by several studies (Chen & al., 2016; P. Li & al., 2017; Jin & al., 2025). We here prefer to keep them as distinct genera, unless future phylogenetic studies using extensive nuclear data yield consistent results.

Vuhuangia (Clade III) occupies the second earliest-diverging position (following Clade I) within Elsholtzieae according to the cpDNA tree (Fig. 2). The nrDNA tree, however, resolved *Vuhuangia* as sister to Clade I (Fig. 3). Furthermore, *Vuhuangia* has been resolved as sister to the "*Paulseniella*" clade based on numerous single-copy orthologous nuclear genes (Jin & al., 2025). This relationship is further supported by the finding that the inflorescence structure of both clades evolved from similar ancestral patterns, i.e., secund inflorescences with short pedicels (usually 1–2 mm), long internodes (>8 mm), and a high number of flowers per cyme (generally 3–6) (Jin & al., 2025). Regardless of its actual phylogenetic position (which remains unclear), *Vuhuangia* is a well-supported lineage which is at the same time unique morphologically within the tribe, e.g., having stamen filaments adhering to the upper lip of the corolla, disk with the elongated anterior lobe shorter than the ovary, and non-mucilaginous nutlets with sub-basal abscission scars (Huang, 1977; H.W. Li & Hedge, 1994; Pu, 2012; Mayta-Anco & al., 2016; Jeon & al., 2020). The chromosome number of *Vuhuangia* ($2n = 20$) is also rare within the

tribe (Funamoto & al., 2012).

The MKPC clade (Clade II) is one of the best-defined clades within the tribe (Chen & al., 2016; P. Li & al., 2017; Wang & al., 2024; Jin & al., 2025). In our cpDNA tree, it is weakly supported as sister to Clade IV + Clade V (Fig. 2), whereas the nrDNA tree group it with Clade I + Clade III (Fig. 3). The MKPC clade is characterized by 1-flowered cymes arranged in raceme-like thyrses, campanulate calyces with hairy throats, and (sub)spheroidal nutlets (H.W. Li & Hedge, 1994; S.L. Zhou & al., 1997; Harley & al., 2004; Peirson & al., 2006; Jeon & al., 2020; Wang & al., 2024; Jin & al., 2025). As it follows from the embedded phylogenetic position of the MKPC clade, its single arrangement of the flowers on a main inflorescence axis is a result of an evolutionary reduction of the number of flowers per cyme. This feature is unknown in any other clade of Elsholtzieae (Jin & al., 2025), which reinforces the distinctness of the MKPC clade.

The well-supported "*Paulseniella*" clade (Clade IV) comprises three species currently classified within *Elsholtzia*. In the cpDNA tree (Fig. 2), it occupies a sister position to the core *Elsholtzia* clade (Clade V), consistent with the previous findings (Chen & al., 2016; P. Li & al., 2017; Sun & al., 2022). The nrDNA tree, however, resolve "*Paulseniella*" as a basally branching lineage of the tribe (Fig. 3). Neither of the two positions is strongly supported. Using orthologous nuclear genes, Jin & al. (2025) resolved a third topology in which "*Paulseniella*" groups with *Vuhuangia*, a relationship supported by their common inflorescence traits (as discussed above). Clade IV and Clade V share several morphological traits, such as dense, cylindrical thyrses formed by several-flowered cymes. This similarity led to the traditional placement of members of these two clades in the genus *Elsholtzia.* However, species of "*Paulseniella*" can be differentiated from the core *Elsholtzia* by calyces with villous moniliform hairs outside, corollas short and subglobose above the base, and non-mucilaginous nutlets with papillate or depressed-punctate pericarp (see details below).

Reasons for the phylogenetic uncertainties and ways to overcome them. — The aforementioned nuclear-cytoplasmic discordance, particularly regarding the positions of *Vuhuangia* and "*Paulseniella*", the interspecific relationships within the core *Elsholtzia* and the MKPC clade, and the non-monophyly of certain species, were widely reported by the previous studies (Chen & al., 2016; P. Li & al., 2017; Wang & al., 2024; Jin & al., 2025). In particular, Wang & al. (2024) detected multiple gene tree discordances across several nodes and widespread cytonuclear conflicts, which introduced substantial phylogenetic noise and impeded the precise resolution of interspecific relationships. Both the evolutionary history of species and methodological differences in phylogenetic analyses contribute to the observed conflicts. Hybridization and incomplete lineage sorting (ILS) are suggested to be the primary factors causing this discordance (Wang & al., 2024; Jin & al., 2025). Hybridization, which is widespread within Elsholtzieae, could cause introgression and subsequent backcrossing, as well as chloroplast capture, leading to conflicts between the trees based on nuclear and chloroplast markers (Yang & al., 2021; Dunning & al., 2022; Wang & al., 2024). Furthermore, previous studies have detected several reticulation events across Elsholtzieae and introgression signals across its major lineages, especially during their early diversification, with dense network events detected in Clades I and IV, implying a complex evolutionary history (Wang & al., 2024; Jin & al., 2025). Moreover, the choice of molecular marker types, incomplete taxon sampling, and low nucleotide substitution rates could also cause different phylogenetic results (Jin & al., 2025).

The complex evolutionary history of Elsholtzieae requires more comprehensive and in-depth analyses. According to Wang & al. (2024), it is essential to apply diverse phylogenetic methods that explicitly handle heterogeneity of the data, and to improve models to better represent the underlying evolutionary process. Meanwhile, to confirm the hybridization events detected by the aforementioned studies, integration with other lines of evidence, such as geographical distribution and ecological niches, is needed (Jin & al., 2025). It is also important to integrate morphological features into the phylogenetic reconstruction and divergence time estimation, revealing the evolutionary pattern of Elsholtzieae through synthesized evidence. However, it must be noted that these aspects fall beyond the scope of this study, as our primary focus is resolving taxonomic issues—consolidating insights from prior evolutionary research to support the taxonomic treatments, rather than further exploring the underlying factors. Trait evolution, divergence time estimation, and evolutionary analyses represent promising directions for future in-depth research.

Expansion of *Perilla* to include *Keiskea* and *Mosla*. — The relationships among *Keiskea*, *Mosla*, and *Perilla* have long been contentious due to the limited taxon sampling in the previous molecular phylogenetic reconstructions (P. Li & al., 2017). In this study, the three genera formed a strongly supported clade sister to the New World genus *Collinsonia*. Whereas *Mosla* was recovered as monophyletic, both cpDNA and nrDNA trees support the polyphyly of *Keiskea* (Figs. 2, 3), which comprises four distinct lineages with *Mosla* and *Perilla* embedded within it. Furthermore, the cpDNA data indicate that *Perilla* is also non-monophyletic, with two out of the three accessions of *P. frutescens* var. *hirtella* grouping

with *K. elsholtzioides*.

These findings conflict with the earlier studies based on morphological similarities. S.L. Zhou & al. (1997) proposed that *Mosla* and *Perilla* are the closest relatives, based on their strongly supra-reticulate pericarps and discontinuous ridges on the pollen surface. Harley & al. (2003) found that *Keiskea* is similar to *Collinsonia* in inflorescence architecture, floral morphology, and fruit features (fruit often comprises only 1 or 2 mature nutlets), and nutlets are (sub)globose with small abscission scars). They considered the laciniate lower lobe of corolla to be the sole diagnostic feature of *Collinsonia*. Consequently, Harley & al. (2003) synonymized *Keiskea* with *Collinsonia*. However, they did not consider the supra-reticulate pericarp of *Keiskea*, which closely resembles that of *Perilla* (S.L. Zhou & al., 1997) but is readily distinguishable from the reticulate-cellular pericarp of *Collinsonia*. Then, Hong (2007) demonstrated that the pollen grains of *Keiskea* differ from those of *Collinsonia* in several aspects, providing further evidence against this synonymy. Further, the similarities highlighted by Harley & al. (2003) to merge *Keiskea* and *Collinsonia*, e.g., raceme-like inflorescence formed by 1-flowered cymes, campanulate 10-nerved calyx, subglobose nutlets, and disk with an elongated anterior lobe, are actually shared by the entire MKPC clade (Wang & al., 2024).

Through detailed morphological comparisons, we found that *Keiskea*, *Mosla*, and *Perilla* form a morphologically homogeneous group, exhibiting clear demarcation from *Collinsonia*. Previous studies have well-documented their differences in pericarp sculpture: *Keiskea*, *Mosla*, and *Perilla* exhibit a supra-reticulate pattern, whereas *Collinsonia* displays a reticulate-cellular pattern (S.L. Zhou & al., 1997; Jeon & al., 2020; Wang & al., 2024). Furthermore, the first three genera bear predominantly secund inflorescences that are unbranched and therefore cylindrical, whereas the inflorescences of *Collinsonia* are never secund and mostly exhibit a pyramidal outline due to the presence of lateral branches (H.W. Li & Hedge, 1994; Jin & al., 2025). Furthermore, *Keiskea*, *Mosla*, and *Perilla* can be easily distinguished by their floral features: pedicel shorter than calyx (to nearly absent); corolla tube shortly campanulate; middle lobe of lower corolla-lip slightly larger than the lateral lobes, entire or finely crenate (Hsuan, 1977; H.W. Li & Hedge, 1994). In contrast, *Collinsonia* is characterized by pedicel much longer than the calyx; corolla tube narrowly cylindrical; middle lobe of lower corolla-lip much larger than the lateral lobes, deeply fimbriate (Shinners, 1962; Peirson & al., 2006). The geographical distribution further supports their distinctness: *Keiskea*, *Mosla*, and *Perilla* are exclusively distributed in Asia, whereas *Collinsonia* is restricted to North America (Harley & al., 2003; Peirson & al., 2006; P. Li & al., 2017). In order to maintain the monophyly of *Keiskea* and possibly *Perilla*, taxonomic rearrangements that correspond to the phylogenetic results are needed. The first option is to split the MKPC clade into several genera, which is clearly untenable. Since the internal topologies of the MKPC clade exhibit conflicts between the cpDNA and nrDNA trees, *Keiskea* needs to be divided into four genera to achieve monophyly, three of which would be monotypic, and three new names would be required. This decision would undoubtedly contradict the principle of taxonomic parsimony. In addition, the splitting of *Keiskea* would cause problems in morphological characterization and distinction of the genera.

The second option, which is to combine the lineages recovered within the MKPC clade into larger genera, has two reasonable solutions under the obtained phylogenetic results. One way is to merge the entire MKPC clade into a single genus under the name *Collinsonia*. However, the morphological distinctness and transcontinental geographical isolation of *Collinsonia* with respect to *Keiskea*, *Mosla*, and *Perilla* (outlined above) would render such a consolidated genus overly heterogeneous. Furthermore, this would require renaming *Perilla*, a widely recognized and economically important genus. *Perilla* (*P. frutescens*) has been a cherished medicinal and culinary herb since ancient times, widely cultivated and utilized globally (particularly in East Asia), thus exhibiting high practical and cultural importance. Transfer of *P. frutescens* to another genus will cause considerable confusion and inconvenience to medicinal, culinary, and horticultural industries. Such a change would directly contradict the principle of nomenclatural stability, as well as of prioritizing practical and applied utility. Another possible way is merging *Keiskea* and *Mosla* within *Perilla*, the latter name holding taxonomic priority as the earliest legitimate one. We consider this approach as the most suitable for several reasons, one of them being the retention of an intact *Collinsonia* s.str. The clade containing *Keiskea*, *Mosla*, and *Perilla* is highly supported and exhibits clear morphological and geographical distinctions from *Collinsonia*. Meanwhile, this approach allows to maintain the generic identity of *P. frutescens*. Adopting *Perilla* s.l. aligns with the consideration of Drew & al. (2017) in their proposal of *Salvia* s.l., which states that taxonomic revisions should meet the requirements of systematic research while serving broader societal applications.

Consequently, we choose to expand the circumscription of *Perilla* to include *Keiskea* and *Mosla*, proposing 21 new combinations (see Taxonomic treatment). It is worth noting that *P. frutescens* var. *hirtella* was partially nested within

Keiskea in the cpDNA tree (Fig. 2), and may warrant recognition as a distinct species. However, given the potential misidentification of its two accessions along with the poor support values, we argue that a more extensive sampling is necessary for making formal nomenclatural changes.

Reinstatement of *Paulseniella* from *Elsholtzia*. — Our cpDNA and nrDNA reconstructions, together with the earlier studies (Chen & al., 2016; P. Li & al., 2017; Sun & al., 2022; Wang & al., 2024; Jin & al., 2025), revealed that three species currently assigned to *Elsholtzia* (*E. cephalantha*, *E. densa*, *E. eriostachya*) form a distinct lineage referred here to as the "*Paulseniella*" clade (Figs. 2, 3).

The taxonomic history of these three species is rather complex. Bentham (1829) originally established the genus *Aphanochilus* Benth. without designating its type, which included *Elsholtzia eriostachya* (as *A. eriostachyus* Benth.) along with seven other species. Among these eight species names included by Bentham, *Aphanochilus incisus* Benth., which was based on *Mentha blanda* Lindl. nom. illeg. (= *Elsholtzia stachyodes* (Link) Raizada & H.O.Saxena), was the sole name validly published at that time. Consequently, *Aphanochilus incisus* automatically serves as the nomenclatural type of the genus name, invalidating the subsequent suggestion by Bongcheewin & al. (2015) to consider the first listed species, i.e., *Aphanochilus blandus* Benth. (≡ *Elsholtzia blanda* (Benth.) Benth.) as the type, as well as the latest designation of *Aphanochilus polystachyus* Benth. (≡ *Elsholtzia fruticosa* (D.Don) Rehder) as the type by Kumar (2023). Later, Bentham (1832–1836) reduced *Aphanochilus* under *Elsholtzia* as a section, i.e., *E.* sect. *Aphanochilus*. He also described the species *E. densa* without assigning it to any subgeneric group, but later he placed it in *E.* sect. *Aphanochilus* (Bentham, 1848). Briquet (1895–1897) subsequently classified *E. eriostachya* and *E. densa* in *E*. subsect. *Platyelasmeae* within *E.* sect. *Aphanochilus*. Shortly thereafter, Briquet (1907) proposed a new genus, *Paulseniella* Briq., with a single species, *P. pamirensis* Briq., which is now a synonym of *E. densa*.

In their updated subgeneric division of *Elsholtzia*, Wu & Huang (1974) placed *E. cephalantha*, *E. densa*, and *E. eriostachya* within *E.* sect. *Aphanochilus* (the genus *Paulseniella* was not mentioned in their treatment). *Elsholtzia cephalantha*, which is morphologically distinct, was assigned to its own series, *E*. sect. *Aphanochilus* subsect. *Stenelasmeae* ser. *Cephalanthae* C.Y.Wu & S.C.Huang. In contrast, *E. densa* and *E. eriostachya* were placed within *E*. sect. *Aphanochilus* subsect. *Platyelasmeae*, characterized by their broad-ovate bracts and black, unpolished nutlets (Wu & Huang, 1974).

Kitagawa (1935) established the genus *Platyelasma* Kitag., comprising four species: *P. calycocarpum* (Diels) Kitag., *P. densum* (Benth.) Kitag., *P. eriostachyum* (Benth.) Kitag., and *P. manshuricum* Kitag. However, this genus was later synonymized with *Elsholtzia*, with *P. calycocarpum*, *P. densum*, and *P. manshuricum* subsumed within *E. densa*, and *P. eriostachyum* regarded as *E. eriostachya*.

Species of the "*Paulseniella*" clade are small herbs with dense, non-secund thyrses. Despite being morphologically similar to the core *Elsholtzia*, "*Paulseniella*" possesses several clear diagnostic features. The most distinctive character is the presence of dense moniliform hairs outside the calyces and sometimes corollas (a type of indumentum never found in the core *Elsholtzia*) (Huang, 1977; H.W. Li & Hedge, 1994; Pu, 2012), as well as non-secund inflorescences with longer internodes within cymes (see below). Then, "*Paulseniella*" exhibits short, subglobose corollas widened at the midpoint and constricted at the throat, not or slightly exserted from the calyx (vs. mostly tubular-campanulate, dilated at the throat, and usually long-exserted), and fruiting calyx often with recurved teeth (vs. teeth not recurved). "*Paulseniella*" also possesses non-mucilaginous nutlets with unique surface sculpturing patterns, which are papillate in *E. densa* and *E. cephalantha* and depressed-punctate in *E. eriostachya* (vs. surface reticulate to irregularly verrucate, or with ridges, glandular scales, and striations) (Pu, 2012; Jeon & al., 2020; Wang & al., 2024). Finally, *E. densa* and *E. eriostachya* possess a hollow stem pith, which is solid in *E. cephalantha* and core *Elsholtzia*; the two former species also possess subsessile glandular trichomes, which are present on both leaf surfaces but sunken only on the adaxial surface (vs. either absent or sunken on the abaxial surface in *E. cephalantha* and core *Elsholtzia*) (Pu, 2012).

"*Paulseniella*" generally resembles the core *Elsholtzia* while exhibiting a distinct phylogenetic position, suggesting that it may have undergone a unique evolutionary trajectory and adaptation history. Jin & al. (2025) found that the inflorescence of "*Paulseniella*" (together with *Vuhuangia*) evolved from different ancestral states (non-secund, with internodes >8 mm long), compared to those of the core *Elsholtzia* (secund, internodes 4–8 mm long). Among the three species, both *E. densa* and *E. eriostachya* exhibit dense, cylindrical thyrses, while *E. cephalantha* has specialized corymb-like ones due to a gradual acropetal reduction in the length of internodes between cymes. Jin & al. (2025) supposed that the formation of compact inflorescence types is possibly influenced by altitudinal variations, explaining the uniqueness of *E. cephalantha*, which is exclusively distributed in high-altitude regions (H.W. Li & Hedge, 1994). Another remarkable feature of

"*Paulseniella*", the non-mucilaginous nutlets, is present in only two other groups within Elsholtzieae: *Vuhuangia* and *E. kachinensis* Prain. Pu (2012) noted that mucilage production is closely associated with ecological adaptation and seed dispersal strategies. In *Elsholtzia*, the rapid-maturing nutlets that disperse immediately afterward are non-mucilaginous, whereas the nutlets that persist after maturation produce the mucus (Pu, 2012). Consequently, this trait serves as a diagnostic feature and at the same time correlates with the fruit characters and habitat preferences.

Considering the molecular and morphological distinctions outlined above, as well as the insights into the evolution of inflorescence, we propose recognizing this clade as a distinct genus. Among the generic names applicable to the species group containing *E. cephalantha*, *E. densa*, and *E. eriostachya*, both *Paulseniella* and *Platyelasma* are available, of which the first one bears nomenclatural priority. Accordingly, we propose three new species-level combinations (see Taxonomic treatment).

Relationships within *Elsholtzia* s.str. — This study conducted the most comprehensive taxon sampling for *Elsholtzia* and includes all its sections and subsections adopted by Wu & Huang (1974) and Press (1982). Our sampling encompasses 38 of the 41 currently recognized species in the genus, with only *E. amurensis* Prob., *E. pubescens* Benth., and the recently described *E. zhongyangii* P.Li & X.J.Jin not included. By incorporating the taxa across the entire geographical distribution of *Elsholtzia* s.str., we obtained a highly supported phylogenetic reconstruction and resolved the earlier phylogenetic ambiguities (Pu, 2012; Chen & al., 2016; P. Li & al., 2017; Sun & al., 2022), providing a basis for a new, rational infrageneric classification.

Following the recognition of *Paulseniella* as a separate genus, core *Elsholtzia* (i.e., *Elsholtzia* s.str.) can be divided into five lineages (Figs. 2, 3), although relationships within the lineages remain unclear as they are different in the cpDNA and nrDNA trees. The backbone phylogenetic reconstruction of *Elsholtzia* obtained in our study is congruent with those in the previous studies (Sun & al., 2022; Wang & al., 2024), whereas the earlier studies failed to resolve the "*E. heterophylla* + *E. bodinieri*" lineage due to limited taxon sampling (P. Li & al., 2017; Jin & al., 2025). Although these five lineages are well-defined in our phylogenetic reconstructions, the complex taxonomic history and morphological heterogeneity of *Elsholtzia* make a comprehensive revision premature at this stage. Since no morphology-based classification has yet been proposed to correspond with the phylogenetic framework presented here, further studies are needed to identify morphological synapomorphies for each lineage and refine species-level relationships, ultimately leading to a coherent infrageneric classification system.

TAXONOMIC TREATMENT

As defined in this study, Elsholtzieae comprises seven genera: *Collinsonia* (4 species), *Elsholtzia* (38 species), *Ombrocharis* (1 species), *Paulseniella* (3 species), *Perilla* (22 species), *Perillula* (1 species), and *Vuhuangia* (2 species). In the light of the new assessment, we provide an updated identification key to all the genera of Elsholtzieae, aiming to clarify the generic boundaries within the tribe and facilitating practical taxonomic work. We also provide checklists of the reinstated *Paulseniella* and re-shaped *Perilla*.

Key to the genera of Elsholtzieae

1. Plants with tuber-like rhizomes; cymes distinctly pedunculate, 3-flowered 2
1. Plants without tuber-like rhizomes; cymes sessile or with very short peduncle (up to 6 mm), never 3-flowered (with 1 flower or more than 3 flowers) 3
2. Stems erect; leaf blade oblong-ovate, 4–12 cm long ..... ***Ombrocharis***
2. Stems decumbent at base and ascendent to erect distally; leaf blade broadly ovate, 1.5–4 cm long ..... ***Perillula***
3. Stamen filaments adhering to the upper lip of corolla; anterior lobe of disk shorter than ovary; abscission scar of nutlet sub-basal ..... ***Vuhuangia***
3. Stamen filaments not adhering to corolla surface; anterior lobe of disk longer than ovary; abscission scar of nutlet basal 4
4. Thyrse cylindrical, spike-like or corymb-like; cymes several-flowered; calyx exannulate inside 5
4. Thyrse raceme-like; cymes 1-flowered; calyx annulate inside 6
5. Calyx with dense moniliform hairs outside; corolla subglobose; pericarp papillate or depressed-punctate, non-mucilaginous ..... ***Paulseniella***

5. Calyx glabrous, sparsely hairy or rarely densely hairy, without moniliform hairs outside; corolla tubular or campanulate; pericarp reticulate to tuberculate, mucilaginous (rarely non-mucilaginous and then glandular-scaly at surface) ***Elsholtzia***
6. Middle lobe of lower corolla lip entire or finely crenate; pericarp supra-reticulate. Asia (especially East Asia) .....***Perilla***
6. Middle lobe of lower corolla lip deeply fimbriate; pericarp reticulate-cellular. Eastern North America.....***Collinsonia***

Paulseniella Briq. in Bot. Tidsskr. 28: 246. 1907 – Type: *Paulseniella pamirensis* Briq. (= ***Paulseniella densa*** (Benth.) Bo Li & C.L.Xiang).

= *Elsholtzia* subsect. *Platyelasmeae* Briq. in Engler & Prantl, Nat. Pflanzenfam. IV(3a, 146–147): 327. 1897 ≡ *Platyelasma* Kitag. in Nakai, Rep. Exped. Manchoukuo Sect. IV 2: 24. 1935 ≡ *Elsholtzia* sect. *Platyelasmeae* (Briq.) Press in Bull. Brit. Mus. (Nat. Hist.), Bot. 10(1): 70. 1982 – Type (designated by Kitagawa in Nakai, Rep. Exped. Manchoukuo Sect. IV 2: 25. 1935): *Elsholtzia eriostachya* Benth. (≡ ***Paulseniella eriostachya*** (Benth.) C.L.Xiang & Bo Li).

= *Elsholtzia* ser. *Cephalanthae* C.Y.Wu & S.C.Huang in Acta Phytotax. Sin. 12(3): 340. 1974 – Type: *Elsholtzia cephalantha* Hand.-Mazz. (≡ ***Paulseniella cephalantha*** (Hand.-Mazz.) Bo Li & C.L.Xiang).

Description. – Annual herbs, erect to diffuse; stems ascending, pubescent to ± glabrous. Leaves simple, petiolate, oblong to lanceolate or broadly ovate-triangular, margin serrate to crenate, villous. Thyrses terminal and axillary, dense, cylindrical or corymb-like, non-secund; cymes several-flowered, sessile; flowers pedicellate; bracts broadly ovate or linear to spathulate, villous. Calyx campanulate or cup-shaped, usually 8-veined, with dense long white or yellowish moniliform hairs outside, conspicuously accrescent in fruit (becoming broad-cylindrical or infundibular, often with enlarged and upcurved teeth); teeth 5, ± equal, shorter or longer than calyx tube, triangular or linear-lanceolate, ciliate. Corolla small, white, yellow or purplish, included in calyx or slightly exserted from it, with yellow non-moniliform hairs or white to purple moniliform hairs outside; tube included in calyx or slightly exerted from it, subglobose above base, gradually dilated upward; limb zygomorphic, 2-lipped and 4-lobed (1/3), upper lip emarginate, lower lip 3-lobed with middle lobe larger than lateral ones; or limb ± actinomorphic, 5-lobed with lobes equal, broadly ovate or ± triangular. Stamens 4, ± equal or anterior pair slightly longer, included in corolla or slightly exserted. Style included in corolla, subequally 2-lobed at apex; disk 4-lobed, anterior lobe elongated and digitately enlarged. Nutlets globose or ellipsoid, surface papillate or ± smooth and depressed-punctate, non-mucilaginous; abscission scar basal.

Distribution. – This genus is mainly distributed in northern and central China, extending into Central Asia and the Himalayan region.

Checklist of the species of *Paulseniella*

1. ***Paulseniella cephalantha*** (Hand.-Mazz.) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Elsholtzia cephalantha* Hand.-Mazz. in Acta Horti Gothob. 9(5): 90. 1934.

2. ***Paulseniella densa*** (Benth.) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Elsholtzia densa* Benth., Labiat. Gen. Spec. 714. 1835 ≡ *Platyelasma densum* (Benth.) Kitag. in Nakai, Rep. Exped. Manchoukuo Sect. IV 2: 25. 1935.

= *Dysophylla ianthina* Maxim. ex Kanitz, Növényt. Gyüjtések Gróf Széchenyi: 46. 1891 ≡ *Elsholtzia ianthina* (Maxim. ex Kanitz) Dunn in Notes Roy. Bot. Gard. Edinburgh 6(28): 152. 1915 ≡ *Elsholtzia densa* var. *ianthina* (Maxim. ex Kanitz) C.Y.Wu & S.C.Huang in Acta Phytotax. Sin. 12(3): 344. 1974.

= *Elsholtzia calycocarpa* Diels in Bot. Jahrb. Syst. 29(3–4): 560. 1900 ≡ *Platyelasma calycocarpum* (Diels) Kitag. in Nakai, Rep. Exped. Manchoukuo Sect. IV 2: 25. 1935 ≡ *Elsholtzia densa* var. *calycocarpa* (Diels) C.Y.Wu & S.C.Huang in Acta Phytotax. Sin. 12(3): 344. 1974.

= *Paulseniella pamirensis* Briq. in Bot. Tidsskr. 28: 246. 1907.

= *Platyelasma manshuricum* Kitag. in Nakai, Rep. Exped. Manchoukuo Sect. IV 2: 26. 1935 ≡ *Elsholtzia manshurica* (Kitag.) Kitag. in Rep. Inst. Sci. Res. Manchoukuo 3(App. 1): 379. 1939.

3. ***Paulseniella eriostachya*** (Benth.) C.L.Xiang & Bo Li, **comb. nov.** ≡ *Aphanochilus eriostachyus* Benth. in Wallich, Pl. Asiat. Rar. 1: 29. 1830 ≡ *Elsholtzia eriostachya* (Benth.) Benth., Labiat. Gen. Spec.: 163. 1833 ≡ *Platyelasma eriostachyum* (Benth.) Kitag. in Nakai, Rep. Exped. Manchoukuo Sect. IV 2: 25. 1935.

= *Elsholtzia pusilla* Benth., Labiat. Gen. Spec.: 714. 1835 ≡ *Elsholtzia eriostachya* var. *pusilla* (Benth.) Hook.f. in Hooker,

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Fl. Brit. India 4: 645. 1885 ≡ *Platyelasma eriostachyum* var. *pusillum* (Benth.) Kitag. in Nakai, Rep. Exped. Manchoukuo Sect. IV 2: 25. 1935.

Perilla L., Gen. Pl., ed. 6: 578. 1764 – Type: *Perilla frutescens* (L.) Britton.
= *Dentidia* Lour., Fl. Cochinch.: 869. 1790 – Type: *Dentidia nankinensis* Lour. (= ***Perilla frutescens*** (L.) Britton).
= *Hedeoma* sect. *Mosla* Benth., Labiat. Gen. Spec.: 366. 1834 ≡ *Mosla* (Benth.) Buch.-Ham. ex Maxim. in Bull. Acad. Imp. Sci. Saint-Pétersbourg, sér. 3, 20: 456. 1875 – Type (designated by Babu & Nayar in Taxon 18: 596. 1969): *Lycopus diantherus* Buch.-Ham. ex Roxb. (≡ ***Perilla dianthera*** (Buch.-Ham. ex Roxb.) Bo Li & C.L.Xiang), **syn. nov.**
= *Keiskea* Miq. in Ann. Mus. Bot. Lugduno-Batavi 2: 105. 1865 – Type: *Keiskea japonica* Miq. (≡ ***Perilla japonica*** (Miq.) Bo Li & C.L.Xiang), **syn. nov.**
= *Orthodon* Benth. in J. Linn. Soc., Bot. 9: 167. 1865, nom. illeg., non R.Br. in Trans. Linn. Soc. London 12: 578. 1819 – Type: *Orthodon japonicus* Benth. (= ***Perilla perforata*** (Miq.) Bo Li & C.L.Xiang).

Description. – Annual to perennial herbs, erect, usually branched, usually strongly aromatic. Leaves simple, petiolate, margin dentate. Thyrses terminal and axillary, raceme-like, spike-like or capitate, mostly secund; cymes 1-flowered; flowers pedicellate; bracts usually small, bracteoles absent. Calyx campanulate, 10-veined, accrescent in fruit, usually gibbous at base, 5-toothed, with teeth subequal or unequal (then calyx 2-lipped, with 3-toothed upper lip and 2-toothed lower lip), hairy outside, annulate inside at throat or between teeth. Corolla white, yellow, pink to purple; tube long-exserted from calyx or included, campanulate, narrow at base and gradually dilated toward throat, glabrous or annulate inside; limb ± 2-lipped; upper lip emarginate or 2-lobed; lower lip 3-lobed, with middle lobe larger and usually finely crenate (sometimes entire), with lateral lobes equal, rounded, entire at margin. Stamens 4 (subequal or anterior pair slightly longer) or 2 (with anterior pair reduced), exserted from corolla or rarely included; filaments straight, divergent; thecae 2, divaricate or parallel and becoming slightly divergent; connective distinct; disk 4-lobed, anterior lobe elongated and digitately enlarged. Style included in corolla or long-exserted, 2-lobed at apex, lobes subequal or unequal. Nutlets ± globose, surface supra-reticulate, mucilaginous; abscission scar basal, dot-like.

Distribution. – This genus is primarily distributed in East Asia, with its type species (*P. frutescens*) also cultivated in eastern North America and Europe.

Checklist of the species of *Perilla*

1. ***Perilla australis*** (C.Y.Wu & H.W.Li) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Keiskea australis* C.Y.Wu & H.W.Li in C.Y.Wu & H.W.Li, Fl. Reipubl. Popularis Sin. 66: 585. 1977 ≡ *Collinsonia australis* (C.Y.Wu & H.W.Li) Harley in Kew Bull. 58(2): 486. 2003.

2. ***Perilla bracteata*** (Doan ex Suddee & A.J.Paton) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Mosla bracteata* Doan ex Suddee & A.J.Paton in Kew Bull. 61(4): 620. 2007.

3. ***Perilla cavaleriei*** (H.Lév.) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Mosla cavaleriei* H.Lév. in Repert. Spec. Nov. Regni Veg. 9(211–213): 247. 1911 ≡ *Orthodon cavaleriei* (H.Lév.) Kudô in Mem. Fac. Sci. Taihoku Imp. Univ. 2: 81. 1929.

4. ***Perilla dadoensis*** (K.K.Jeong, M.J.Nam & H.J.Choi) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Mosla dadoensis* K.K.Jeong, M.J.Nam & H.J.Choi in PhytoKeys 208: 188. 2022.

5. ***Perilla dianthera*** (Buch.-Ham. ex Roxb.) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Lycopus diantherus* Buch.-Ham. ex Roxb., Fl. Ind. 1: 145. 1820 (‘*dianthera*’) ≡ *Mosla dianthera* (Buch.-Ham. ex Roxb.) Maxim. in Bull. Acad. Imp. Sci. Saint-Pétersbourg 20: 457. 1875 ≡ *Orthodon diantherus* (Buch.-Ham. ex Roxb.) Hand.-Mazz., Symb. Sin. 7(4): 933. 1936.
= *Ocimum polycladum* Link, Enum. Hort. Berol. Alt. 2: 119. 1822.
= *Mosla formosana* Maxim. in Bull. Acad. Imp. Sci. Saint-Pétersbourg, sér. 3, 20(3): 459. 1875.
= *Mosla grosseserrata* Maxim. in Bull. Acad. Imp. Sci. Saint-Pétersbourg, sér. 3, 20(3): 458. 1875 ≡ *Orthodon grosseserratus* (Maxim.) Kudô in Mem. Fac. Sci. Taihoku Imp. Univ. 2: 79. 1929.
= *Mosla lysimachiiflora* Hayata, Icon. Pl. Formos. 8: 104. 1919 ≡ *Orthodon lysimachiiflorus* (Hayata) Masam. in Trans.

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= *Mosla remotiflora* Y.Z.Sun in Contr. Biol. Lab. Sci. Soc. China, Bot. Ser. 7: 55. 1932.
= *Orthodon punctatus* var. *tetrantherus* Hand.-Mazz. in Acta Horti Gothob. 9(5): 89. 1934.
= *Orthodon hirtus* H.Hara in J. Jap. Bot. 12(1): 44. 1936 ≡ *Mosla hirta* (H.Hara) H.Hara in J. Jap. Bot. 30(1): 25. 1955.
= *Orthodon tenuicaulis* Koidz. in Acta Phytotax. Geobot. 5(1): 47. 1936.
= *Orthodon grosseserratus* var. *nanus* H.Hara in J. Jap. Bot. 14(1): 75. 1938 ≡ *Orthodon hirtus* f. *nanus* (H.Hara) H.Hara in J. Jap. Bot. 17(7): 396. 1941 ≡ *Mosla dianthera* var. *nana* (H.Hara) Ohwi ex Huang & Cheng in H.L.Li, T.S.Liu, T.C.Huang, T. Koyama & C.E. DeVol, Fl. Taiwan 4: 489. 1978.
= *Orthodon mayebaranus* Honda in Bot. Mag. (Tokyo) 53: 50. 1939.

6. ***Perilla elsholtzioides*** (Merr.) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Keiskea elsholtzioides* Merr. in Sunyatsenia 3: 258. 1937 ≡ *Collinsonia elsholtzioides* (Merr.) Harley in Kew Bull. 58(2): 486. 2003.
= *Keiskea elsholtzioides* f. *purpurea* X.H.Guo in Bull. Bot. Res., Harbin 7(2): 137. 1987.

7. ***Perilla exfoliata*** (C.Y.Wu) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Orthodon exfoliatus* C.Y.Wu in Acta Phytotax. Sin. 10(3): 232. 1965 ≡ *Mosla exfoliata* (C.Y.Wu) C.Y.Wu & H.W.Li in Acta Phytotax. Sin. 12(2): 231. 1974.

8. ***Perilla fordii*** (Maxim.) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Mosla fordii* Maxim. in Bull. Acad. Imp. Sci. Saint-Pétersbourg, sér. 3, 31: 89. 1886 ≡ *Orthodon fordii* (Maxim.) Hand.-Mazz. in Acta Horti Gothob. 9(5): 89. 1934.
= *Mosla chinensis* Maxim. in Bull. Acad. Imp. Sci. Saint-Pétersbourg, sér. 3, 29: 177. 1883 ≡ *Orthodon chinensis* (Maxim.) Kudô in Mem. Fac. Sci. Taihoku Imp. Univ. 2: 75. 1929, non *Keiskea sinensis* Diels in Notizbl. Bot. Gart. Berlin-Dahlem 9: 199. 1924.
= *Calamintha clipeata* Vaniot in Bull. Acad. Int. Géogr. Bot., sér. 3, 14(183): 184. 1904.
= *Mosla japonica* var. *angustifolia* Makino in Bot. Mag. (Tokyo) 21: 157. 1907 ≡ *Mosla angustifolia* (Makino) Makino in J. Jap. Bot. 2: 24. 1922 ≡ *Orthodon angustifolius* (Makino) Masam. in Mem. Fac. Sci. Taihoku Imp. Univ. 11(4): 391. 1934.
= *Mosla coreana* H.Lév. in Repert. Spec. Nov. Regni Veg. 9: 248. 1911 ≡ *Orthodon coreanus* (H.Lév.) Honda, Nom. Pl. Jap.: 297. 1939.
= *Mosla chinensis* var. *kiangsiensis* G.P.Zhu & J.L.Shi in Acta Phytotax. Sin. 33(3): 305. 1995.

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= *Melissa maxima* Ard., Animadv. Bot. Spec. Alt.: 28. 1764.
= *Ocimum acutum* Thunb. in Murray, Syst. Nat., ed. 14: 546. 1784 ≡ *Perilla acuta* (Thunb.) Nakai in Bot. Mag. (Tokyo) 42: 474. 1928.
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= *Dentidia purpurascens* Pers., Syn. Pl. 2: 135. 1806.
= *Dentidia purpurea* Poir. in Lamarck, Encycl., Suppl. 2: 466. 1812.
= *Ocimum salvioides* B.Heyne ex Roth, Nov. Pl. Sp.: 272. 1821 ≡ *Lumnitzera salvioides* (B.Heyne ex Roth) Spreng., Syst. Veg. 2: 687. 1825 ≡ *Plectranthus salvioides* (B.Heyne ex Roth) Benth., Labiat. Gen. Spec.: 45. 1832.
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= *Perilla ocimoides* f. *citriodora* Makino in Bot. Mag. (Tokyo) 28: 180. 1914 ≡ *Perilla citriodora* (Makino) Nakai in Bot. Mag. (Tokyo) 31: 285. 1917.
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10. ***Perilla glandulosa*** (C.Y.Wu) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Keiskea glandulosa* C.Y.Wu in Acta Phytotax. Sin. 10(3): 236. 1965 ≡ *Collinsonia glandulosa* (C.Y.Wu) Harley in Kew Bull. 58(2): 486. 2003.

11. ***Perilla hangchouensis*** (Matsuda) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Mosla hangchouensis* Matsuda in Bot. Mag. (Tokyo) 26: 314. 1912 ≡ *Orthodon hangchouensis* (Matsuda) C.Y.Wu in Acta Phytotax. Sin. 10(3): 230. 1965.
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12. ***Perilla japonica*** (Miq.) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Keiskea japonica* Miq. in Ann. Mus. Bot. Lugduno-Batavi 2: 105. 1865 ≡ *Collinsonia japonica* (Miq.) Harley in Kew Bull. 58(2): 486. 2003.
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= *Orthodon japonicus* Benth. in J. Linn. Soc., Bot. 9: 167. 1865 ≡ *Mosla japonica* (Benth.) Maxim. in Bull. Acad. Imp. Sci. Saint-Pétersbourg, sér. 3, 20: 461. 1875, non *Keiskea japonica* Miq. in Ann. Mus. Bot. Lugduno-Batavi 2: 105. 1865.
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15. ***Perilla longispica*** (C.Y.Wu) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Orthodon longispicus* C.Y.Wu in Acta Phytotax. Sin. 10(3): 231. 1965 ≡ *Mosla longispica* (C.Y.Wu) C.Y.Wu & H.W.Li in Acta Phytotax. Sin. 12(2): 230. 1974.

16. ***Perilla macrobracteata*** (Masam.) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Keiskea macrobracteata* Masam. in Trans. Nat. Hist. Soc. Taiwan 30: 341. 1940 ≡ *Collinsonia macrobracteata* (Masam.) Harley in Kew Bull. 58(2): 486. 2003.

17. ***Perilla pauciflora*** (C.Y.Wu) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Orthodon pauciflorus* C.Y.Wu in Acta Phytotax. Sin. 10(3): 231. 1965 ≡ *Mosla pauciflora* (C.Y.Wu) C.Y.Wu & H.W.Li in Acta Phytotax. Sin. 12(2): 230. 1974.

18. ***Perilla scabra*** (Thunb.) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Ocimum scabrum* Thunb. in Trans. Linn. Soc. London 2: 338. 1794 ≡ *Orthodon scaber* (Thunb.) Hand.-Mazz., Symb. Sin. 7(4): 933. 1936 ≡ *Mosla scabra* (Thunb.) C.Y.Wu & H.W.Li in Acta Phytotax. Sin. 12(2): 230. 1974.
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= *Mosla leucantha* Hayata, Icon. Pl. Formos. 8: 104. 1919.

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19. ***Perilla sinensis*** (Diels) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Keiskea sinensis* Diels in Notizbl. Bot. Gart. Berlin-Dahlem 9(83): 199. 1924 ≡ *Collinsonia sinensis* (Diels) Harley in Kew Bull. 58(2): 486. 2003.

20. ***Perilla soochouensis*** (Matsuda) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Mosla soochouensis* Matsuda in Bot. Mag. (Tokyo) 26: 134. 1912 ≡ *Orthodon soochouensis* (Matsuda) C.Y.Wu in Acta Phytotax. Sin. 10(3): 230. 1965.

21. ***Perilla szechuanensis*** (C.Y.Wu) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Keiskea szechuanensis* C.Y.Wu in Acta Phytotax. Sin. 10: 236. 1965 ≡ *Collinsonia szechuanensis* (C.Y.Wu) Harley in Kew Bull. 58(2): 486. 2003.

22. ***Perilla tamdaoensis*** (Phuong) Bo Li & C.L.Xiang, **comb. nov.** ≡ *Mosla tamdaoensis* Phuong in Bot. Zhurn. (Moscow & Leningrad) 67(8): 1135. 1982.

AUTHOR CONTRIBUTIONS

BL and CLX conceived this research. BL, ZPS, JFX, BB, SK, APS, TF, FC, YPC, and CLX collected materials. ZPC performed the experiments. BL, DZM, YPC, and CLX analyzed the data. 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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Table 1. Characteristics of datasets constructed in the present study.

Dataset	Number of taxa	Length (bp)	Variable sites	Parsimo-ny-informative sites	Proportion of parsimo-ny-informative sites
matK	92	873	226	172	20%
ndhF	71	2241	538	380	17%
rbcL	96	501	41	32	6%
trnL-F	98	879	211	159	18%
ycf1	98	4761	1738	1415	30%
combined cpDNA	98	9220	2748	2174	23.58%
ITS	96	744	319	279	38%
ETS	89	430	334	300	70%
combined nrDNA	98	1171	652	579	49.44%

FIGURE LEGENDS

Fig. 1. Comparison of the molecular phylogenies of Elsholtzieae from previous studies.

Fig. 2. Phylogenetic tree of Elsholtzieae based on the combined cpDNA (*matK*, *ndhF*, *rbcL*, *trnL-F*, *ycf1*) dataset using maximum likelihood (ML) method with the bootstrap values (ML-BS) and Bayesian posterior probability values (BI-PP) indicated at nodes as ML-BS/BI-PP. An asterisk (*) denotes full support (ML-BS = 100%, BI-PP = 1.00), while a dash (–) indicates ML-BS < 50% or BI-PP < 0.90. Clade numbers correspond to Fig. 1. Genera of Elsholtzieae are color-coded. *Paulseniella* and *Perilla* s.l., which are taxonomically revised in the present study, are highlighted in red bold. Multiple accessions of the same species are numbered according to Appendix 1.

Fig. 3. Phylogenetic tree of Elsholtzieae based on the combined nrDNA (ITS, ETS) dataset using maximum likelihood (ML) method with the bootstrap values (ML-BS) and Bayesian posterior probability values (BI-PP) indicated at nodes as ML-BS/BI-PP. An asterisk (*) denotes full support (ML-BS = 100%, BI-PP = 1.00), while a dash (–) indicates ML-BS < 50% or BI-PP < 0.90. Clade numbers correspond to Fig. 1. Genera of Elsholtzieae are color-coded. *Paulseniella* and *Perilla* s.l., are taxonomically revised in the present study, are highlighted in red bold. Multiple accessions of the same species are numbered according to Supplementary Appendix 1.

Appendix 1. Voucher information and GenBank accession numbers for the combined cpDNA and nrDNA dataset. The order of data is as follows: Taxon, COUNTRY. State, voucher, GenBank accessions: *matK*, *ndhF*, *rbcL*, *trnL-F*, *ycf1*, ETS, ITS. Newly generated sequences are indicated in bold. Missing data are indicated with a dash (–); NA = not applicable/available.

Ingroup. ***Collinsonia anisata*** Sims, U.S.A. *16469*: –, –, KY624915, KY624984, KY625114, KY552552, KY552484. ***Collinsonia canadensis*** L., U.S.A. *2722*: KY624850, –, KY624916, KY624985, KY625115, KY552553, KY552485. ***Collinsonia punctata*** Elliott, U.S.A. Florida, *C.L. Xiang 1187*: –, KT210252, KT210257, KT210325, KT210349, KT210214, KT210241. ***Collinsonia serotina*** Walter, U.S.A. *14105*: KY624853, –, KY624920, KY624988, KY625119, KY552557, KY552489. ***Collinsonia verticillata*** Baldwin ex Elliott, U.S.A. *18484*: KY624854, –, KY624921, KY624989, KY625120, KY552558, KY552490. ***Elsholtzia angustifolia*** (Loes.) Kitag., SOUTH KOREA. Chungbuk, *Kim & al. KJS15005*: **PV137805**, **PV137859**, **PV112813**, **PV112759**, **PV112705**, **PV112867**, **PV138611**. ***Elsholtzia argyi*** H.Lév., CHINA. Hunan, Yizhang, *Y.P. Chen & al. EM1367*: **PV137806**, **PV137860, PV112814**, **PV112760**, **PV112706**, **PV112868**, **PV138612**. ***Elsholtzia beddomei*** C.B.Clarke ex Hook.f., Tak, THAILAND. *Chamchumroon & al. 4927*: **PV137807**, **PV137861**, **PV112815**, **PV112761**, **PV112707**, **PV112869**, **PV112869**. ***Elsholtzia blanda*** (Benth.) Benth., CHINA. Yunnan, *B.Y. Zhang 7A*: **PV137808**, **PV137862**, **PV112816**, **PV112762**, **PV112708**, **PV112870, PV138614.** ***Elsholtzia bodinieri*** Vaniot 1, CHINA. Yunnan, *C.L. Xiang & al. XCL508*: **PV137809**, **PV137863**, **PV112817**, **PV112763**, **PV112709**, **PV112871**, **PV138615**. ***Elsholtzia bodinieri*** Vaniot 2, CHINA. Yunnan, *Z.P. Sun & B.Y. Zhang SZP0007*: **PV137810, PV137864**, **PV112818**, **PV112764**, **PV112710**, **PV112872, PV138616**. ***Elsholtzia capituligera*** C.Y.Wu, CHINA. Yunnan, *Y.P. Chen & L. Jiang EM255*: **PV137811**, **PV137865**, **PV112819**, **PV112765**, **PV112711**, **PV112873**, **PV138617**. ***Elsholtzia cephalantha*** Hand.-Mazz., CHINA. Sichuan, *Z.P. Sun & Y.W. Wu SZP0026*: **PV137813**, **PV137867**, **PV112821**, **PV112767**, **PV112713**, **PV112875**, **PV138619**. ***Elsholtzia ciliata*** (Thunb.) Hyl. 1, RUSSIA. Moscow, *Bexob & al. 0498237*: **PV137814**, **PV137868**, **PV112822**, **PV112768**, **PV112714**, **PV112876**, **PV138620**. ***Elsholtzia ciliata*** (Thunb.) Hyl. 2, SOUTH KOREA. Gyeongnam, *Ryu & al. NABI-JS2254*: **PV137815**, **PV137869**, **PV112823**, **PV112769**, **PV112715**, **PV112877**, **PV138621**. ***Elsholtzia communis*** (Collett & Hemsl.) Dunn, CHINA. Yunnan, *Z.P. Sun SZP0071*: **PV137816**, **PV137870**, **PV112824**, **PV112770**, **PV112716**, **PV112878**, **PV138622**. ***Elsholtzia cyprianii*** (Pavol.) C.Y.Wu & S.Chow, CHINA. Guizhou, *C.L. Xiang & al. XCL1703*: **PV137817**, **PV137871**, **PV112825**, **PV112771**, **PV112717**, **PV112879**, **PV138623.** ***Elsholtzia cyprianii*** var. ***angustifolia*** C.Y.Wu & S.C.Huang, CHINA. *PNLI20120303-1*: KY624863, –, KY624930, KY624998, KY625129, KY552567, KY552499. ***Elsholtzia densa*** var. ***ianthina*** (Maxim. ex Kanitz) C.Y.Wu & S.C.Huang, CHINA. *LP150583-1*: KY624866, –, KY624933, KY625001, KY625132, KY552570, KY552502. ***Elsholtzia densa*** Benth. 1, CHINA. Yunnan, *C.L. Xiang & al. XCL1972* (KUN): **PV137819**, **PV137873**, **PV112827**, **PV112773**, **PV112719**, **PV112881**, **PV138625**. ***Elsholtzia densa*** Benth. 2, MONGOLIA. *Gubanov IA 0189411*: **PV137820**, **PV137874**, **PV112828, PV112774**, **PV112720**, **PV112882**, **PV138626**. ***Elsholtzia densa*** Benth. 3, Kyrgyzstan. *Seregin & al. 0874416*: **PV137818**, **PV137872**, **PV112826**, **PV112772**, **PV112718**, **PV112880**, **PV138624**. ***Elsholtzia***

eriocalyx C.Y.Wu & S.C.Huang, CHINA. Yunnan, *H.J. Dong & al.*: **PV137821**, **PV137875**, **PV112829**, **PV112775**, **PV112721**, **PV112883**, **PV138627**. ***Elsholtzia eriostachya*** (Benth.) Benth. 1, CHINA. *Pan. Li PNLI20120227-1*: KY624869, –, KY624936, KY625004, KY625135, KY552573, KY552505. ***Elsholtzia eriostachya*** (Benth.) Benth. 2, CHINA. Xizang, *E.D. Liu & al. 3291*: **PV137822**, **PV137876**, **PV112830**, **PV112776**, **PV112722**, **PV112884**, **PV138628**. ***Elsholtzia feddei*** H.Lév., CHINA. Sichuan, *C.L. Xiang & al. XCL1259*: **PV137823**, **PV137877**, **PV112831**, **PV112777**, **PV112723**, **PV112885**, **PV138629**. ***Elsholtzia fruticosa*** (D.Don) Rehder, CHINA. Yunnan, *Z.P. Sun & B.Y. Zhang SZP0001*: **PV137824**, **PV137878**, **PV112832**, **PV112778**, **PV112724**, **PV112886**, **PV138630**. ***Elsholtzia glabra*** C.Y.Wu & S.C.Huang, CHINA. Yunnan, *C.L. Xiang & al. XCL2021*: **PV137825**, **PV137879**, **PV112833**, **PV112779**, **PV112725**, **PV112887**, **PV138631**. ***Elsholtzia griffithii*** Hook.f., CHINA. Guangxi, *Z.P. Sun & J.F. Xiao DC02*: **PV137826**, **PV137880**, **PV112834**, **PV112780**, **PV112726**, **PV112888**, **PV138632**. ***Elsholtzia hallasanensis*** Y.N.Lee, SOUTH KOREA. *PNLI20120474*: KY624877, –, KY624944, KY625012, KY625143, KY552581, KY552513. ***Elsholtzia heterophylla*** Diels, CHINA. Sichuan, *Y.P. Chen & L.Q. Jiang EM635*: **PV137827**, **PV137881**, **PV112835**, **PV112781**, **PV112727**, **PV112889**, **PV138633**. ***Elsholtzia kachinensis*** Prain, CHINA. Guangxi, *Y.P. Chen & L. Jiang EM280*: **PV137828**, **PV137882**, **PV112836**, **PV112782**, **PV112728**, **PV112890**, **PV138634**. ***Elsholtzia lamprophylla*** C.L.Xiang & E.D.Liu, CHINA. Sichuan, *Y.P. Chen & al. EM1688*: **PV137829**, **PV137883**, **PV112837**, **PV112783**, **PV112729**, **PV112891**, **PV138635**. ***Elsholtzia litangensis*** C.X.Pu & W.Y.Chen, CHINA. Sichuan, *C.L. Xiang & F. Zhao XCL1933*: **PV137830**, **PV137884**, **PV112838**, **PV112784**, **PV112730**, **PV112892**, **PV138636**. ***Elsholtzia luteola*** Diels 1, CHINA. Sichuan, *Y.P. Chen & al. EM661*: **PV137831**, **PV137885**, **PV112839**, **PV112785**, **PV112731**, **PV112893**, **PV138637**. ***Elsholtzia luteola*** Diels 2, CHINA. Yunnan, *Y.P. Chen & al. EM1288*: **PV137832**, **PV137886**, **PV112840**, **PV112786**, **PV112732**, **PV112894**, **PV138638**. ***Elsholtzia minima*** Nakai, SOUTH KOREA. Cheju, *Chun & al. Se60730*: **PV137833**, **PV137887**, **PV112841**, **PV112787**, **PV112733**, **PV112895**, **PV138639**. ***Elsholtzia myosurus*** Dunn, CHINA. Yunnan, *Z.P. Sun & J.F. Xiao SZP82*: **PV137834**, **PV137888**, **PV112842**, **PV112788**, **PV112734**, **PV112896**, **PV138640**. ***Elsholtzia nipponica*** Ohwi, JAPAN. Tokushima, *T. Funamoto*: **PV137835**, **PV137889**, **PV112843**, **PV112789**, **PV112735**, **PV112897**, **PV138641**. ***Elsholtzia ochroleuca*** Dunn, CHINA. Sichuan, *Z.P. Sun & Y.W. Wu SZP0018*: **PV137836**, **PV137890**, **PV112844**, **PV112790**, **PV112736**, **PV112898**, **PV138642**. ***Elsholtzia ochroleuca*** var. ***parvifolia*** C.Y.Wu & S.C.Huang, CHINA. *PNLI20120153*: KY624884, –, KY624951, KY625019, KY625150, KY552587, KY552520. ***Elsholtzia pilosa*** (Benth.) Benth. 1, CHINA. Yunnan, *C.L. Xiang & al. XCL1381*: **PV137837**, **PV137891**, **PV112845**, **PV112791**, **PV112737**, **PV112899**, **PV138643**. ***Elsholtzia pilosa*** (Benth.) Benth. 2, CHINA. Xizang, *Y.P. Chen & al. EM1208*: **PV137838**, **PV137892**, **PV112846**, **PV112792**, **PV112738**, **PV112900**, **PV138644**. ***Elsholtzia pygmaea*** W.W.Sm., CHINA. Yunnan, *Z.P. Sun & B.Y. Zhang SZP0039*: **PV137839**, **PV137893**, **PV112847**, **PV112793**, **PV112739**, **PV112901**, **PV138645**. ***Elsholtzia rugulosa*** Hemsl., CHINA. Yunnan, *Z.P. Sun & B.Y. Zhang SZP0004*: **PV137840**, **PV137894**, **PV112848**, **PV112794**, **PV112740**, **PV112902**, **PV138646**. ***Elsholtzia saxatilis*** (Kom.) Nakai ex Kitag., CHINA. Jilin, *H.C. An AnHc0397*: **PV137841**, **PV137895**, **PV112849**, **PV112795**, **PV112741**, **PV112903**, **PV138647**. ***Elsholtzia serotina*** Kom., SOUTH KOREA. Inchon, *Kim J. H. KJH19623*: **PV137842**, **PV137896**, **PV112850**, **PV112796**, **PV112742**, **PV112904**, **PV138648**. ***Elsholtzia souliei*** H.Lév., CHINA. Xizang, *Y.P. Chen & al. EM1036*: **PV137843**, **PV137897**, **PV112851**, **PV112797**, **PV112743**, **PV112905**, **PV138649**. ***Elsholtzia splendens*** Nakai ex F.Maek., SOUTH KOREA. Inchon, *Sung C K HUN-20161960*: **PV137844**, **PV137898**, **PV112852**, **PV112798**, **PV112744**, **PV112906**, **PV138650**. ***Elsholtzia stachyodes*** (Link) Raizada & H.O.Saxena 1, CHINA. Sichuan, *Y.P. Chen & al. EM639*: **PV137845**, **PV137899**, **PV112853**, **PV112799**, **PV112745**, **PV112907**, **PV138651**. ***Elsholtzia stachyodes*** (Link) Raizada & H.O.Saxena 2, THAILAND. Chiengmai, *Suddee & al. 2123*: **PV137846**, **PV137900**, **PV112854**, **PV112800**, **PV112746**, **PV112908**, **PV138652**. ***Elsholtzia stauntonii*** Benth., CHINA. Hebei, *J.F. Xiao & al. HBWLS001*: **PV137847**, **PV137901**, **PV112855**, **PV112801**, **PV112747**, **PV112909**, **PV138653**. ***Elsholtzia strobilifera*** (Benth.) Benth. 1, CHINA. Sichuan, *C.L. Xiang & al. XCL1624*: **PV137848**, **PV137902**, **PV112856**, **PV112802**, **PV112748**, **PV112910**, **PV138654**. ***Elsholtzia strobilifera*** (Benth.) Benth. 2, CHINA. Xizang, *Y.P. Chen & al. EM1127*: **PV137849**, **PV137903**, **PV112857**, **PV112803**, **PV112749**, **PV112911**, **PV138655**. ***Elsholtzia winitiana*** Craib, CHINA. Yunnan, *X.X. Zhu & al. ZXX191643*: **PV137850**, **PV137904**, **PV112858**, **PV112804**, **PV112750**, **PV112912**, **PV138656**. ***Keiskea australis*** C.Y.Wu & H.W.Li, CHINA. *PNLI20130625*: KY624897, –, KY624965, KY625033, KY625164, KY552601, KY552534. ***Keiskea elsholtzioides*** Merr. 1, CHINA. *PNLI20120430-1*: KY624898, –, KY624966, KY625034, KY625165, KY552602, KY552535. ***Keiskea elsholtzioides*** Merr. 2, CHINA. Hunan, *Y.P. Chen & al. EM1379*: **PV137851**, **PV137905**, **PV112859**, **PV112805**, **PV112751**, **PV112913**, **PV138657**. ***Keiskea glandulosa*** C.Y.Wu, CHINA. *801502*: KY624900, –, KY624968, KY625036,

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KY625167, KY552604, –. ***Keiskea japonica*** Miq. 1, JAPAN. *PNLI20120049-1*: KY624901, –, KY624969, KY625037, KY625168, KY552605, KY552537. ***Keiskea japonica*** Miq. 2, JAPAN. *PNLI20120049-2*: KY624902, –, KY624970, KY625038, KY625169, KY552606, KY552538. ***Keiskea macrobracteata*** Masam., CHINA. *3244*: –, –, KY624971, KY625039, KY625170, KY552607, KY552539. ***Mosla cavaleriei*** H.Lév., CHINA. *PNLI20120445*: KY624903, –, KY624972, KY625040, KY625171, KY552608, KY552540. ***Mosla chinensis*** Maxim., CHINA. *PNLI20120245*: KY624904, –, KY624973, KY625041, KY625172, KY552609, KY552541. ***Mosla dianthera*** (Buch.-Ham. ex Roxb.) Maxim., CHINA. Guangxi, *G.X. Hu & al. Hu0271*: **PV137852**, **PV137906**, **PV112860**, **PV112806**, **PV112752**, **PV112914**, **PV138658**. ***Mosla hangchouensis*** Matsuda, CHINA. Zhejiang, *H. Peng & al. DH17033*: **PV137853**, **PV137907**, **PV112861**, **PV112807**, **PV112753**, **PV112915**, **PV138659**. ***Mosla japonica*** (Benth. ex Oliv.) Maxim., JAPAN. *PNLI20120416*: KY624907, –, KY624976, KY625044, KY625175, KY552612, KY552544. ***Mosla scabra*** (Thunb.) C.Y.Wu & H.W.Li, CHINA. Guizhou, *C.L. Xiang & al. XCL1702*: **PV137854**, **PV137908**, **PV112862**, **PV112808**, **PV112754**, **PV112916**, **PV138660**. ***Mosla soochouensis*** Matsuda, CHINA. *PNLI20120414*: KY624909, –, KY624978, KY625046, KY625177, KY552614, KY552546. ***Mosla tamdaoensis*** VIETNAM. Phuong, *C-K-393*: KY624910, –, KY624979, KY625047, KY625178, KY552615, KY552547. ***Ombrocharis dulcis*** Hand.-Mazz. 1, CHINA. Hunan, *C.L. Xiang & al. 961*: –, KT210255, KT210258, KT210334, KT210358, KT210223, KT210250. ***Ombrocharis dulcis*** Hand.-Mazz. 2, CHINA. Hunan, *C.L. Xiang & al. XCL857*: **PV137855**, **PV137909**, **PV112863**, **PV112809**, **PV112755**, **PV112917**, **PV138661**. ***Perilla frutescens* f. *crispidiscolor*** Makino, NA, *P181*: KT220686, KT220686, KT220686, KT220686, KT220686, –, KT220695. ***Perilla frutescens*** var. ***acuta*** (Thunb.) Kudô, NA, *P177*: KT220685, KT220685, KT220685, KT220685, KT220685, –, KT220694. ***Perilla frutescens*** var. ***auriculatodentata*** C.Y.Wu & S.J.Hsuan ex H.W.Li, CHINA. *PNLI20130589*: KY624912, –, KY624981, KY625049, KY625180, KY552617, KY552549. ***Perilla frutescens*** var. ***crispa*** (Thunb.) H.Deane 1, NA, *P205*: KT220687, KT220687, KT220687, KT220687, KT220687, –, KT220696. ***Perilla frutescens*** var. ***crispa*** (Thunb.) H.Deane 2, NA, *P207*: KT220688, KT220688, KT220688, KT220688, KT220688, –, KT220697. ***Perilla frutescens*** var. ***hirtella*** (Nakai) Makino 1, NA, NA: KT220692, KT220692, KT220692, KT220692, KT220692, –, KT220701. ***Perilla frutescens*** var. ***hirtella*** (Nakai) Makino 2, NA, *B17*: KT220690, KT220690, KT220690, KT220690, KT220690, –, KT220699. ***Perilla frutescens*** var. ***hirtella*** (Nakai) Makino 3, NA, NA: KT220691, KT220691, KT220691, KT220691, KT220691, –, KT220700. ***Perilla frutescens*** (L.) Britton 1, NA, *P285*: KT220689, KT220689, KT220689, KT220689, KT220689, –, KT220698. ***Perilla frutescens*** (L.) Britton 2, CHINA. *PNLI20120096*: KY624911, –, KY624980, KY625048, KY625179, KY552616, –. ***Perilla frutescens*** (L.) Britton 3, CHINA. Jiangxi, *G.X. Hu & F. Zhao 135*: –, –, –, KT210330, KT210354, KT210219, KT210246. ***Perilla frutescens*** (L.) Britton 4, CHINA. Hunan, *G.X. Hu & F. Zhao 187*: –, –, –, KT210331, KT210355, KT210220, KT210247. ***Perilla frutescens*** (L.) Britton 5, NA, *P170*: KT220684, KT220684, KT220684, KT220684, KT220684, –, KT220693. ***Perillula reptans*** Maxim. 1, JAPAN. *PNLI20120417-2*: KY624914, –, KY624983, KY625051, KY625182, KY552619, KY552551. ***Perillula reptans*** Maxim. 2, JAPAN. *PNLI20120417-1*: KY624913, –, KY624982, KY625050, KY625181, KY552618, KY552550. ***Perillula reptans*** Maxim. 3, JAPAN. Tokushima, *T. Funamoto*: **PV137856**, **PV137910**, **PV112864**, **PV112810**, **PV112756**, **PV112918**, **PV138662**. ***Vuhuangia flava*** (Benth.) Molinari, Solomon Raju & Mayta 1, CHINA. Yunnan, *Z.P. Sun & al. SZP0072*: **PV137857**, **PV137911**, **PV112865**, **PV112811**, **PV112757**, **PV112919**, **PV138663**. ***Vuhuangia flava*** (Benth.) Molinari, Solomon Raju & Mayta 2, CHINA. *PNLI20120353*: KY624873, –, KY624940, KY625008, KY625139, KY552577, KY552509. ***Vuhuangia penduliflora*** (W. W. Sm.) Mayta, Solomon Raju & Molinari 1, CHINA. Yunnan, *Z.P. Sun & al. SZP0073*: **PV137858**, **PV137912**, **PV112866**, **PV112812**, **PV112758**, **PV112920**, **PV138664**. ***Vuhuangia penduliflora*** (W. W. Sm.) Mayta, Solomon Raju & Molinari 2, CHINA. *PNLI20120037*: KY624886, –, KY624953, KY625021, KY625152, KY552589, KY552522.

Outgroup. ***Coleus xanthanthus*** C.Y.Wu & Y.C.Huang, NA, NA: MT473748, MT473748, MT473748, MT473748, MT473748, –, –. ***Coleus xanthanthus*** C.Y.Wu & Y.C.Huang, CHINA. *L.J. Jiang s.n.*: –, –, –, –, –, MN116786, MN116780. ***Isodon amethystoides*** (Benth.) H.Hara, NA, NA: MT473767, MT473767, MT473767, MT473767, MT473767, MT473767, –, –. ***Isodon amethystoides*** (Benth.) H.Hara, CHINA. *Y.P. Chen & al. EM283*: –, –, –, –, –, MG232669, MG232762. ***Salvia glutinosa*** L., U.K. England, *2019-11*: MW752204, MW752204, MW752204, MW752204, MW752204, –, –. ***Salvia glutinosa*** L., IRAN. *21565*: –, –, –, –, –, MK204873, MK213203. ***Salvia miltiorrhiza*** Bunge, NA, NA: HF586694, HF586694, HF586694, HF586694, HF586694, –, –. ***Salvia miltiorrhiza*** Bunge, Hu & Shangguan, CHINA. Anhui, *Hu0099*: –, –, –, –, –, MG824361, MG824231. ***Mentha spicata*** L., NA, NA: MG256495, MG256495, MG256495, MG256495, MG256495, –, –. ***Mentha spicata*** L., NA, *J. Walker 2566*: –, –, –, –, –, JQ669193, DQ667244.

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SUPPLEMENTARY INFORMATION

Fig. S1. Maximum-likelihood tree of Elsholtzieae inferred from the combined cpDNA (*matK*, *ndhF*, *rbcL*, *trnL-F*, *ycf1*) dataset.

Fig. S2. Bayesian 50% majority-rule consensus tree of Elsholtzieae inferred from the cpDNA (*matK*, *ndhF*, *rbcL*, *trnL-F*, *ycf1*) dataset.

Fig. S3. Maximum-likelihood tree of Elsholtzieae inferred from the combined nrDNA (ITS, ETS) dataset.

Fig. S4. Bayesian 50% majority-rule consensus tree of Elsholtzieae inferred from the combined nrDNA (ITS, ETS) dataset.