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A New Infrageneric Classification of *Meconopsis* (Papaveraceae) Based on a Well-supported Molecular Phylogeny

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Abstract—*Meconopsis* is an herbaceous genus native to the high altitude habitats across the Himalaya and adjacent plateau and mountain areas. Attractive *Meconopsis* flowers have spurred many European botanists to study the taxonomy of the genus resulting in numerous infrageneric classifications, dating from the first taxonomic revision in the late 19th century until the most recent monograph in 2014. All, however, were morphology-based treatments and largely inconsistent with one another. To investigate the incongruence among the previous taxonomic grouping strategies of the species in *Meconopsis* and settle the controversies, we employed a well-resolved molecular phylogeny built by analyzing four chloroplast markers (*trnL-trnF* intergenic spacer, *matK*, *ndhF*, and *rbcL*). We found that the evolutionary relationships revealed by our phylogeny disagreed to varying degrees with any infrageneric relationship suggested by previous authors. Therefore, we propose a revised classification based on our phylogenetic topology as well as the morphological and cytological patterns reflected by the phylogenetic structure. To achieve a practical and approachable system, we have tried to retain as much as possible of phylogenetically meaningful components from previous taxonomies for the genus. As a result, we used the four major clades of our *Meconopsis* phylogeny as the bases for infrageneric sections (*Meconopsis* sect. *Meconopsis, M.* sect. *Aculeatae, M.* sect. *Primulinae*, and *M.* sect. *Grandes*). A key to the sections is provided, followed by a description and composition of each.

Keywords—Blue poppy, Himalaya, phylogenetics.

Meconopsis Vig., also known as Himalayan poppy or blue poppy, is an Old World genus in the subfamily Papaveroideae of Papaveraceae. Viguier (1814) established *Meconopsis* based on a single Western European species, *Papaver cambricum* L., that served as the type until recently. However, all the species later added to *Meconopsis* were discovered in South and East Asia. Kadereit et al. (2011) proposed returning *Meconopsis cambrica* (L.) Vig. to *Papaver* because geographical and molecular evidence showed that *M. cambrica* is not related to the rest of the species subsequently placed in *Meconopsis*, but embedded in the phylogeny of *Papaver*. Grey-Wilson (2014) later placed *Meconopsis cambrica* in a newly circumscribed monotypic genus *Parameconopsis* Grey-Wilson, but molecular evidence (Yuan 2002; Kadereit et al. 2011; Xiao 2013; Liu et al. 2014) clearly supported that this species should be returned to *Papaver* rather than treated as segregate monotypic genus.

The exclusion of *M. cambrica* as well as two other species, *Meconopsis chelidonifolia* Bureau & Franch. and *Meconopsis oliveriana* Franch. ex Prain, is in agreement with molecular work (Yuan 2002; Kadereit et al. 2011; Xiao 2013; Liu et al. 2014). The relationships among *M. cambrica*, *Meconopsis*, *Cathcartia* Hook. f., and *Papaver* are illustrated in Fig. 1 (Xiao 2013). Grey-Wilson (2014) officially transferred *M. chelidonifolia* and *M. oliveriana* from *Meconopsis* to *Cathcartia*. However, *Cathcartia chelidonifolia* (Bureau & Franch.) Grey-Wilson was typified by syntypes, and the lectotype of *Cathcartia oliveriana* (Franch. ex Prain) Grey-Wilson was not clearly indicated. We designate a lectotype for each of these species at the end of the Taxonomic Treatment below.

As Grey-Wilson moved the original type *Meconopsis cambrica* out of *Meconopsis*, he (2012) proposed conservation of the generic name *Meconopsis* for the Asiatic species with a new type: *Meconopsis regia* G. Taylor. Because the Nomenclature Committee for Vascular Plants recommended Grey-Wilson's proposal (in *Taxon* 62(6): 1318. 2013), we use the generic name "*Meconopsis*" for the Asian species following Article 14.16 of the International Code of Nomenclature (McNeill et al. 2012).

Meconopsis has traditionally been considered to consist of ca. 50–80 species. This large range of species numbers was mostly due to different species concepts implemented in previous taxonomic works. The genus exhibits high morphological (examples shown in Fig. 2) and ecological diversity: species range from a few centimeters to more than 2 m in height, are distributed from 3,000 to 5,800 m in elevation, and grow in distinctive habitats such as mountain woodland, alpine meadow, or rocky slopes. Moreover, various polyploids have been reported in *Meconopsis* ($2n$ = 14, 22, 28, 56, 74, 76, 82, 84, and higher) (Ratter 1968; Ying et al. 2006; Kumar et al. 2013). However, there has not been any taxonomic scheme based on a comprehensive incorporation and evolutionary interpretation of the morphological, ecological, geographical, and cytological diversities in the genus. The lack of an integrated approach led to its ever-changing taxonomy over the last 200 yr. Previous taxonomic strategies for subdividing the genus (Prain 1895, 1906, 1915; Fedde 1909, 1936; Kingdon-Ward 1926, 1935; Taylor 1934; Wu and Chuang 1980; Chuang 1981; Grey-Wilson 2000, 2014) were based on different sets of morphological characters and growth habits that resulted in conflicting treatments. Here we discuss the two most influential and reasonably well-organized previous classifications of *Meconopsis* (Fedde 1909; Taylor 1934) as well as the most recently published monograph (Grey-Wilson 2014) to highlight the taxonomic inconsistency at the infrageneric level (Fig. 3B–D).

Fedde's (1909) classification was based on Prain's (1906) work, which divided *Meconopsis* into nine natural groups including Cambricae, Anomalae, Aculeatae, Primulinae, Bellae, Grandes, Torquatae, Robustae, and Chelidonifoliae. Prain (1906) also organized all his groups into two sections, *M.* sect. *Eumeconopsis* and *M.* sect. *Polychaetia,* based on leaf and stem trichome type. Fedde (1909) fully adopted Prain's (1906) system but assigned sectional rank to Prain's groups and elevated Prain's (1906) sections to subgenera (Fig. 3B).

Taylor (1934) also arranged the genus into two subgenera (Fig. 3C) which, however, were substantially different from those of Fedde's (1909). Taylor (1934) used the criterion of a stylar disc: the members of his *Meconopsis* subg. *Discogyne* were characterized by a style expanding into a flat disc surmounting the ovary; species of his *M.* subg. *Eumeconopsis*

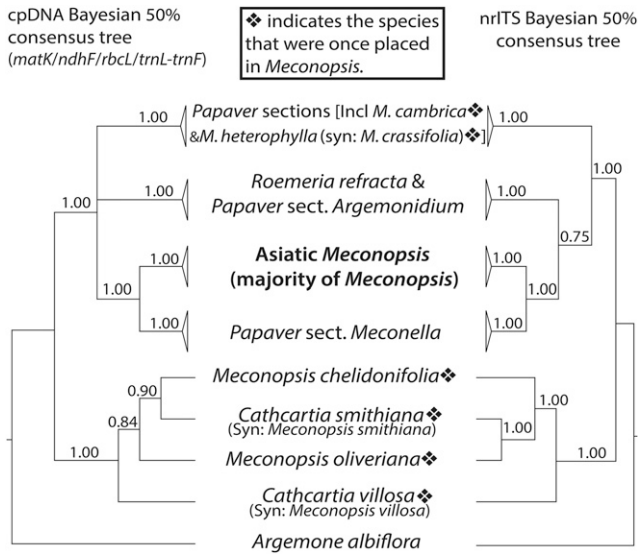

FIG. 1. cpDNA and nrITS phylogenies of *Meconopsis* and related genera inferred by Bayesian analysis, modified from Xiao (2013). Posterior probabilities presented above branches. Each triangle indicates a clade.

lacked this disc. His *M.* sect. *Polychaetia* (in *M.* subg. *Eumeconopsis*) that included the majority of the genus was divided into subsections and then series based on characters such as leaf persistence during winter, flower arrangement, and trichome type (Taylor 1934).

The most recent treatment of *Meconopsis* was by Grey-Wilson (2014), who excluded a few species (*M. cambrica, M. chelidonifolia, M. oliveriana*, *Cathcartia villosa* Hook.f. (syn: *M. villosa*), and *Cathcartia smithiana* Hand.-Mazz. (syn: *M. smithiana*)), relative to Taylor's (1934) treatment (Fig. 3 legend). Examined by the evidence from recent molecular phylogenetic studies (Yuan 2002; Carolan et al. 2006; Xiao 2013; Liu et al. 2014), the genus *Meconopsis* proposed by Grey-Wilson is a monophyletic taxon. Grey-Wilson (2014) divided the genus into four subgeneric divisions: subgenera *Meconopsis*, *Grandes*, *Discogyne*, and *Cumminsia* (shown in Fig. 3D). His *M.* subg. *Meconopsis* is similar to Fedde's (1909) *M.* sect. *Robustae* or Taylor's (1934) *M.* subsect. *Eupolychaetia*; his *M.* subg. *Grandes* is based on Fedde's *M.* sect. *Grandes*; and his *M.* subg. *Discogyne* corresponds to Fedde's *M.* sect. *Torquatae* or Taylor's *M.* subg. *Discogyne*. However, Grey-Wilson's (2014) concept of *M.* subg. *Cumminsia* had never been proposed before. Grey-Wilson's (2014) taxonomy is also much more complex than Fedde's (1909) or Taylor's (1934) by adding more subdivision levels, especially in his *M.* subgen. *Cumminsia*. For example, the majority of species in Taylor's (1934) *M.* ser. *Aculeatae* was divided to four sections which were further broken down into series by Grey-Wilson (2014).

Despite the removal of the outgroup species, the infrageneric classification of *Meconopsis* remains equivocal (Fig. 3B–D). Classifications based on selected morphological similarities have not reached a well agreed upon and stable taxonomy over the last 200 yr. Recent molecular phylogenetic studies (Yuan 2002; Liu et al. 2014) both employed *trnL-trnF* and ITS sequences. These two markers generated phylogenetic incongruences, and neither was sufficient to resolve the relationships within the genus (resulted in large basal polytomies). A low copy nuclear marker was utilized to investigate hybridization and polyploidization pattern in the genus (Xiao and Simpson 2014). However, because the species of *Meconopsis* range from diploid to dodecaploid and higher, estimating phylogenetic relationship using nuclear genes is problematic due to the difficulty and uncertainty of eliminating the effect of paralogy/orthology conflation and recombination. Therefore, we relied on single-copy chloroplast markers in this study to build a well-resolved molecular phylogeny for *Meconopsis*. Our resulting cpDNA tree guided the determination of taxonomic groups: each new section was based on a clade that matches, or shares close similarity in contained species with, previously published infrageneric groups, and is defined by the shared morphological and cytological characteristics of its included species.

Materials and Methods

Taxon Sampling—We sampled 40 species of *Meconopsis* (accessions) for this study that represent every section and series of Fedde (1909), Taylor (1934), and Grey-Wilson (2014). The first author made the determinations of the specimens. Although species delimitations are not in the scope of this study, it is worth noting that certain species have been defined very differently by authors. For example, we previously tested the species delimitation using phylogenetic methods and we found that "species" in Grey-Wilson's *M.* ser. *Heterandrae* together with most of the "species" in his *M.* ser. *Racemosae* formed a species complex called *Meconopsis horridula* complex (Xiao and Simpson 2015). Because these lacked clear species delimitations, we do not agree on specific ranks for most of the "species" in Grey-Wilson's (2014) *M.* sect. *Racemosae.* Thus, we did not highlight any species in Grey-Wilson's *M.* ser. *Heterandrae* in Fig. 3D. Nine outgroup species (accessions) were selected and sampled based on previous phylogenetic studies of *Meconopsis* (Yuan 2002) and *Papaver* (Carolan et al. 2006). Samples were collected from the wild, from the living collection in the Royal Botanical Garden at Edinburgh, and (with permission) from specimens in various herbaria. Species names, authorities, collection information, and sequence information are listed in Appendix 1. In addition, we included four *Meconopsis* accessions from Yuan's (2002) study, and downloaded their *trnL-trnF* spacer sequences from GenBank. Their vouchers and sequence information are also listed in Appendix 1. Genetic markers for our accessions that could not be successfully amplified, or for Yuan's (2002) accessions that were not available in GenBank, were coded as missing data (Appendix 1).

DNA Extraction, PCR, and Sequencing—Genomic DNA was extracted from silica-dried leaf materials or herbarium specimens using the DNeasy Plant Minikit (Qiagen, Valencia, California, USA). We chose the cpDNA marker *trnL-trnF*, which was shown to be phylogenetically informative in previous studies of Papaveroideae (Yuan 2002; Carolan et al. 2006). We also selected the cpDNA marker *rbcL* because it is commonly used for molecular dating in basal eudicot families (Wikström et al. 2001; Anderson et al. 2005; Bell et al. 2010) and also showed sequence variations in the species of *Meconopsis* we tested. Additionally, the cpDNA markers *matK* and *ndhF* were tested and selected because they were easy to amplify and significantly contributed to the resolution of the relationships at sectional level in *Meconopsis*. PCR amplification was carried out in 12 μL reaction volumes with 1–20 ng DNA, 1.0 unit of *Taq* polymerase (labmade, The University of Texas at Austin), 0.5X Failsafe Buffer B (Epicentre Biotechnologies, Madison, WI, USA), and 2.0 μmol/L primers. Forty-five PCR cycles were performed at 95°C for 30 sec, 50°C for 45 sec, and 72°C for 45 sec for each cycle. Internal primers were designed for amplifying herbarium samples. Primer pairs used are listed in Appendix 2. All of the PCR products were visualized on agarose gel containing Syber Safe DNA gel stain (Invitrogen, Eugene, Oregon, USA). Successfully amplified products were cleaned using ExoSap (Exonuclease I: New England Biolabs Beverly, MA, USA; Shrimp Alkaline Phosphatase: Progema, Madison, WI, USA) following the manufacturers' protocols. Cleaned PCR products were sequenced using an ABI 3730 DNA Analyzer at the Institute for Cell and Molecular Biology Core Facility at The University of Texas at Austin. Amplifying primers were used for sequencing. In addition, internal primers were also used for sequencing if the amplicon was longer than 900 base pairs (i.e. *rbcL*, *matK*, and *ndhF*).

Phylogenetic Analyses—Sequences were assembled in Geneious 5.5 (http://www.geneious.com, Kearse et al. 2012), and aligned using Geneious Alignment (implemented in Geneious) with the default setting and 5 refinement iterations. Alignments were then reviewed and refined

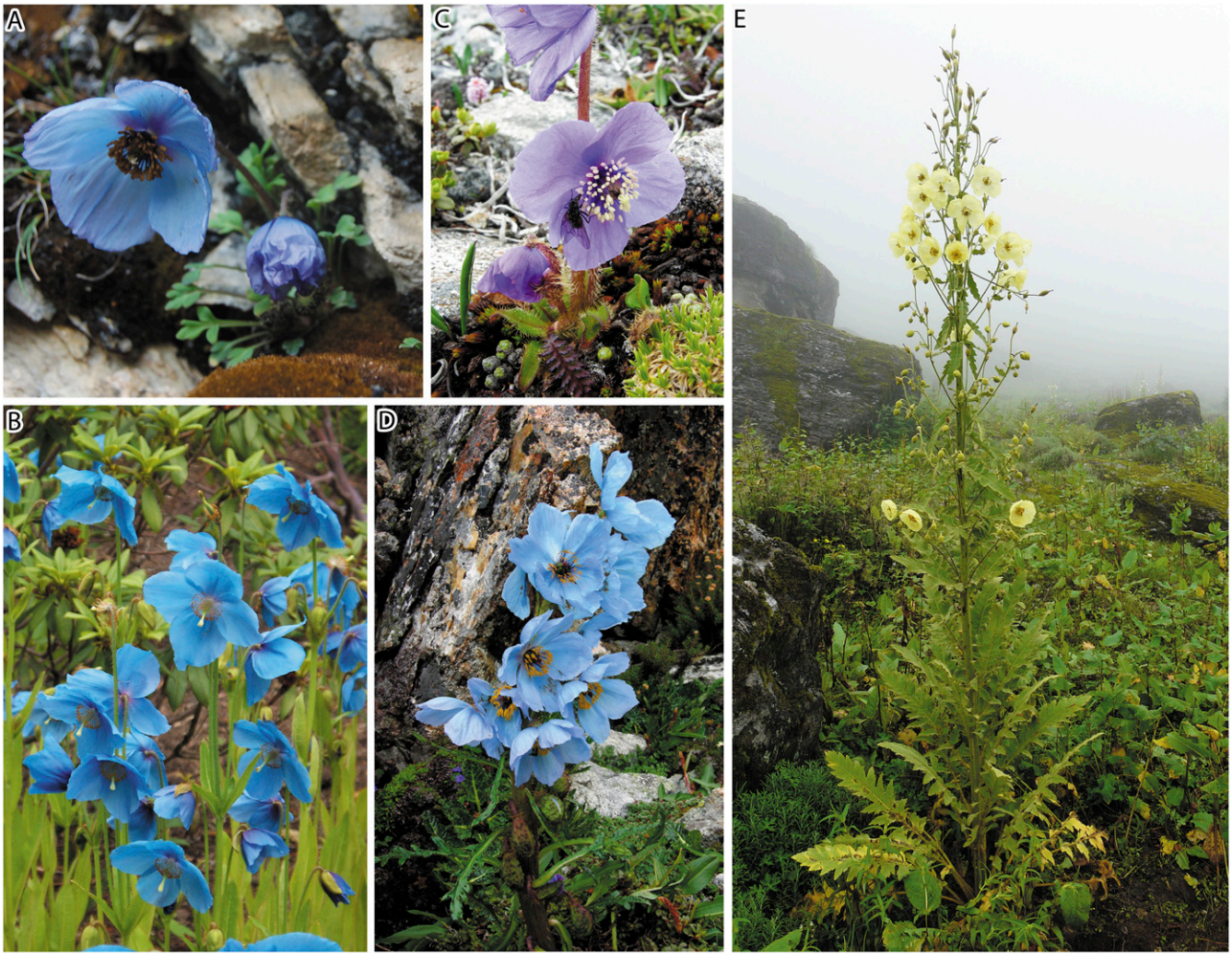

Fig. 2. Morphological overview of a species in each of the proposed *Meconopsis* sections. A. *M. bella* (in *M.* sect. *Primulinae*). B. *M. grandis* cultivar (in *M.* sect. *Grandes*). C. *M.* sp. (in *M.* sect. *Aculeatae*) (possibly a hybrid between named species). D. *M. speciosa* (in *M.* sect. *Aculeatae*). E. *M. paniculata* (in *M.* sect. *Meconopsis*).

manually. Concatenated cpDNA data was analyzed using MrBayes v3.1.2 (Huelsenbeck and Ronquist 2005). Partition analysis was conducted for the combined cpDNA dataset with each cpDNA marker treated as a separate partition. The evolutionary models of nucleotide substitution were first selected by jModelTest (Posada 2008) under the Akaike information criterion (AIC), and we used the models most similar to the best fit models estimated by jModelTest and that were also available in MrBayes v3.1.2 for each gene partition: GTR+G for *rbcL*, GTR+I+G for *ndhF*, GTR+G for *matK*, and GTR+G for *trnL-trnF* dataset. Prior probability distributions on all parameters were set to the defaults. Twenty million generations were run using a Markov chain Monte Carlo method with four chains. Trees were collected every 100th generation. With 25% burn-in, a 50% majority-rule consensus tree was calculated to generate a posterior probability (PP) for each node.

Results and Discussion

We obtained and analyzed 1756 nucleotide positions (with 358 variable sites) of *matK*, 1648 positions (with 231 variable sites) of *ndhF*, 1085 positions (with 588 variable sites) of *trnL-trnF*, and 1395 positions (with 55 variable sites) of *rbcL* sequences. The data are available from the Dryad Digital Repository: DOI:10.5061/dryad.1cr40 (Xiao and Simpson 2017). The recovered phylogenetic relationships within *Meconopsis* are illustrated in Fig. 3A, in which we show only the most closely related outgroup species, *Papaver alpinum*. The posterior probabilities were labeled above the branches on the resulting Bayesian consensus cpDNA tree. This phylogeny provided for the first time well resolved relationships among different subgroups of *Meconopsis*. Based on the resulting tree, we divided the genus into four monophyletic sections (Fig. 3A): *Meconopsis* sect. *Meconopsis* (PP = 1.00), *M.* sect. *Aculeatae* (PP = 0.95), *M.* sect. *Primulinae* (PP = 0.97), and *M.* sect. *Grandes* (PP = 0.82). Our new sections are color coded for easy examination of inconsistencies in earlier treatments (Fig. 3). Within each of our sections, we have not extensively studied species delimitations and reticulation patterns at the molecular level and are therefore reluctant to subdivide further each section before additional studies are conducted.

Our proposed *Meconopsis* sect. *Meconopsis* (e.g. *M. paniculata*, Fig. 2E) is significantly different from any previous treatment. Species in this section (highlighted in blue in Fig. 3B–D) were traditionally divided into two separate groups (i.e. Fedde's *M.* sect. *Robustae* and *M.* sect. *Torquatae*; Taylor's *M.* subsect. *Eupolychaetia* and *M.* subg. *Discogyne*; Grey-Wilson's *M.* subg. *Meconopsis* and *M.* subg. *Discogyne*). However, such treatments made Fedde's *M.* sect. *Robustae,* Taylor's *M.* subsect. *Eupolychaetia,* and Grey-Wilson's *M.* subg. *Meconopsis* all

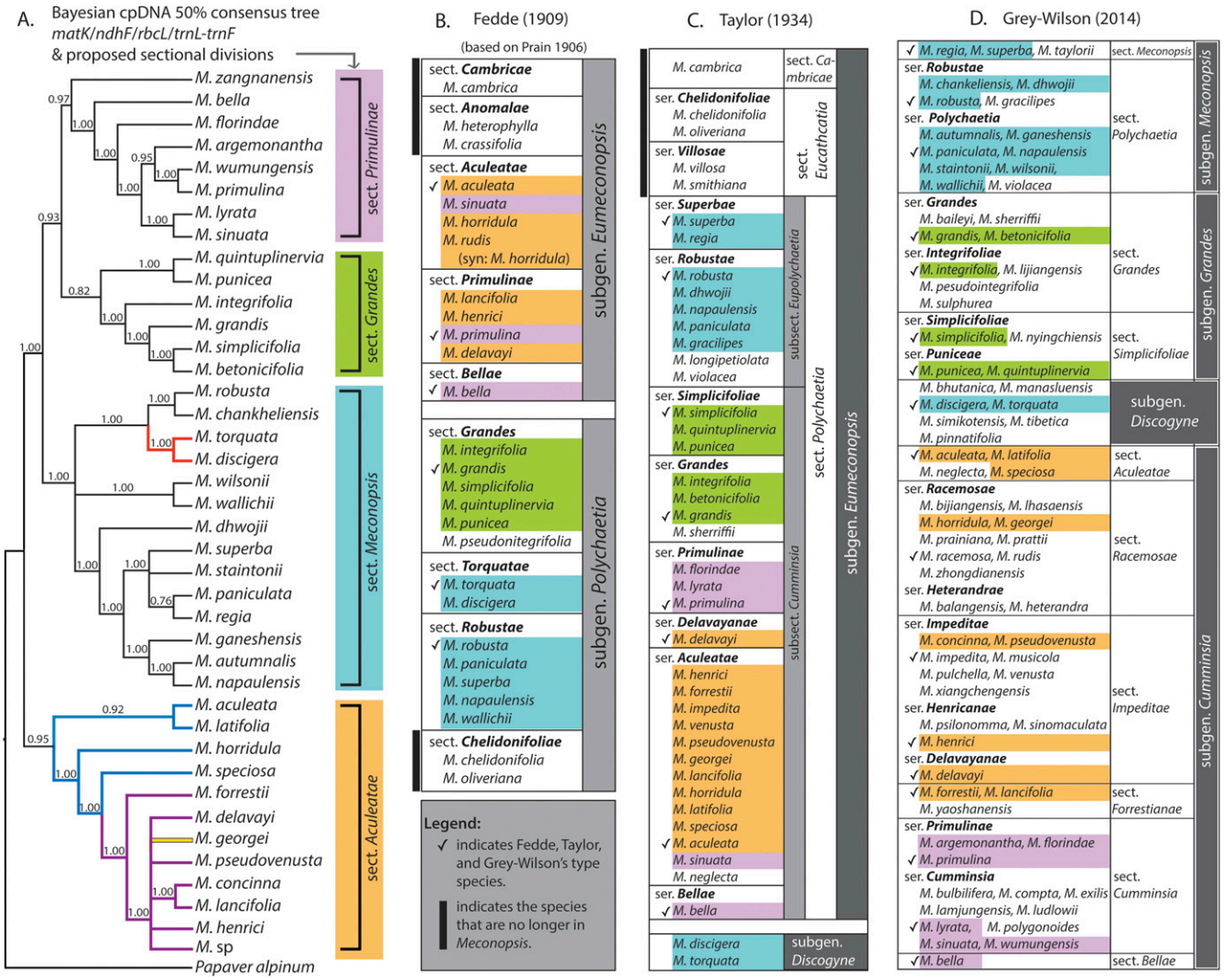

FIG. 3. Proposal of new sectional classification of *Meconopsis* based on cpDNA phylogeny and previous classifications by Fedde (1909), Taylor (1934), and Grey-Wilson (2014). A. Posterior probabilities are labeled above branches. The blue, purple and yellow branches on the phylogeny indicate its terminal taxon's petal color; and the red branches highlight morphologically distinct species in *Meconopsis* sect. *Meconopsis*. Species in the same new section are marked by a color-coded bracket. B–D. The same color codes are used to indicate the placements of taxa we studied under the taxonomic schemes of (B) Fedde (1909), (C) Taylor (1934), and (D) Grey-Wilson (2014). Taxa not tested in our phylogenetic study due to lack of experimental materials are non-shaded in B, C, and D.

paraphyletic. Furthermore, none of the subdivisions in Taylor's (1934) *M.* subsect. *Eupolychaetia* or those in Grey-Wilson's (2014) *M.* subg. *Meconopsis* is monophyletic according to the phylogenetic result (Fig. 3A).

The grouping strategy of our *Meconopsis* sect. *Aculeatae* (e.g. *M.* sp and *M. speciosa*, Fig. 2C, D) is most similar to that of Taylor's (1934) *M.* ser. *Aculeatae*. Taylor's *M.* ser. *Aculeatae* is not monophyletic because it included *M. sinuata* and did not include *M. delavayi* (Fig. 3A, C), but most of its species share a common ancestor and the same chromosome number ($2n$ = 56). Thus with a minor modification guided by the phylogenetic tree, we transformed Taylor's *M.* ser. *Aculeatae* to our monophyletic *M.* sect. *Aculeatae.*

The *Meconopsis* sect. *Primulinae* (e.g. *M. bella*, Fig. 2A) we proposed is somewhat similar to Grey-Wilson's *M.* sect. *Cumminsia*. Our *M.* sect. *Primulinae* includes both Grey-Wilson's *M.* sect. *Cumminsia* and *M.* sect. *Bellae* because of their phylogenetic relatedness as well as morphological consistency. It is notable that species in our *M.* sect. *Primulinae* (highlighted by pink in Fig. 3B–D) and *M.* sect. *Aculeatae* (highlighted by orange in Fig. 3B–D) were never clearly separated from each other in any previous classification. For example, in Fedde's (1909) *M.* sect. *Primulinae*, the type species *M. primulina* is not related to the rest of the section which actually belong to our *M.* sect. *Aculeatae*. Taylor's (1934) *M.* ser. *Aculeatae* is polyphyletic due to the inclusion of *Meconopsis sinuata*, a species in our *M.* sect. *Primulinae.* Grey-Wilson's (2014) *M.* subg. *Cumminsia*, a polyphyletic group, combined both taxa, our *M.* sects. *Aculeatae* and *Primulinae.* However, our reconstructed phylogeny indicated that each of these two taxa has its own distinct evolutionary history, which was only reflected by our proposed classification. We will further discuss their morphological similarities and differentiation in the Taxonomic Treatment below.

Our *Meconopsis* sect. *Grandes* (e.g. *M. grandis*, Fig. 2B) closely corresponds to Feddes's *M.* sect. *Grandes* or Grey-Wilson's (2014) *M.* subg. *Grandes*. Grey-Wilson (2014) further divided this group into *M.* sects. *Grandes* and *Simplicifoliae*, a method similar to that of Taylor's (1934). However, the position of

M. simplicifolia on our cpDNA phylogeny does not support their treatments.

In summary, each of the new sections we proposed is a monophyletic group based on the reconstructed cpDNA phylogeny. Traditional *Meconopsis* classifications employed selected morphological similarities and were found largely inconsistent with the monophyly of the grouping in light of our resulting tree. Monophyly, an objective standard in our method, can minimize artificial preference and can be used to fairly evaluate the incongruence among traditional taxonomies. The value of the previous treatments was also incorporated into our system by retaining the previous taxonomic units that are supported by the phylogenetic result. We defined each section by the shared morphological characteristics and cytological patterns of its contained species, which will be described and discussed below along with the key to each section. As mentioned earlier, species delimitations have not been systematically investigated. We have applied phylogenetic species concept consistently throughout our study and provided an "Included Species" list for each section based on our observation, analyses, and best estimation. However, these tentative lists should be updated when future investigations are available.

Taxonomic Treatment

MECONOPSIS Vig., Hist. Nat. Pavots: 48. Jan 1814 (*Papaver*), nom. cons. prop. (Grey-Wilson 2012).—TYPE: *Meconopsis regia* G. Taylor, typ. cons. prop. (Grey-Wilson 2012).

Herbs, monocarpic or polycarpic, with yellow or white latex; roots taproots or fibrous, or both. Leaves cauline and in basal rosettes or only in basal rosettes with the rosette leaves evergreen or senescing in winter, petiolated or sessile; lamina ovate, obovate, elliptic, oblong, oblanceolate, nearly linear, pinnatifid, pinnatisect, rarely bipinnatifid or bipinnate; margin entire, serrate, sinuate, lobed, or deeply divided. Flowers solitary, borne on basal scapes, or flowers arranged in raceme-like or panicle-like cymes; bracts leafy or reduced. Calyx caducous; sepals normally 2, occasionally 3 or 4 (particularly in terminal flowers). Corolla large and showy, often saucer- to bowl-shaped; petals commonly 4–8, rarely more than 12. Stamens numerous; filaments filiform, occasionally dilated; anthers commonly yellow to orange, but changing colors with age. Ovary superior, subspherical, ovate, or obovate to narrowly subcylindric; locule normally 1 with 3–6 fused carpels, ovules numerous; style often distinct but short, usually less than 1/2 of the ovary length, occasionally inconspicuous, sometimes basally expanding into a disk covering the top of ovary; stigma usually capitate or clavate, occasionally star-shaped with 3–9 stigmatic rays variously decurrent on style. Fruit a subspherical, ovate, obovate, or elliptic to subcylindrical capsule, dehiscing septicidally by 3–9 valves from apex to base usually for a short distance or occasionally to near the base. Seeds many, reniform, falcate-oblong, or elliptic-oblong; testa most commonly reticulated or corrugated, sometimes papillose. Chromosome number: $2n = 14, 22, 28, 56, 74, 76, 82, 84, 118, 120, 164$; $x = 7$.

Key to Sections

1. Monocarpic perennials. Basal rosette persistent through winter ..... 1. *M.* sect. *Meconopsis*
1. Polycarpic perennials, or monocarpic biennials or perennials. Leaves deciduous during the winter 2
   2. Plants usually densely hirsute with barbellate trichomes, often bearing a dense tuft of persistent leaf bases interspersed with dense barbellate bristles. Root-system fibrous or with slender taproot, or with a combination of the two ..... 4. *M.* sect. *Grandes*
   2. Plants glabrous to densely bristly with non-barbellate trichomes, often with simple sharp bristles, lacking persistent leaf bases or, if leaf-bases present, plants never densely bristly at the base. Root consisting of a taproot only 3
      3. Plants armed with dense to sparse sharp bristles, or rarely subglabrous. Taproot usually stout and elongated (exceeding 7 cm in length). Upper cauline leaves noticeably reduced in size relative to lower cauline leaves and basal leaves. Petals normally blue or purple-violet, rarely red, white, or yellow; when blue, usually more than 6 flowers per plant. 4
         4. Basal leaves usually lanceolate to elliptic-oblanceolate or oblanceolate; entire, pinnatilobate, or rarely pinnatisect or pinnaticompound at the margin; basally attenuating into petiole ..... 2. *M.* sect. *Aculeatae*
         4. Basal leaves narrowly oblong to narrowly lanceolate; more or less sinuate at the margin; tapering at the base into a long flattened petiole. ..... 3. *Meconopsis sinuata* (M. sect. *Primulinae*)
      3. Plants usually sparsely vestitured with weak trichomes or subglabrous. Taproot usually slender (less than 7 cm in length). Upper cauline leaves usually similar in size to the lower leaves. Petals usually pale blue to pale purple-blue, sometimes yellow or white; but never bright purple-violet; when blue, usually fewer than 5 flowers per plant ..... 3. *M.* sect. *Primulinae*

1. MECONOPSIS SECT. MECONOPSIS. *Meconopsis* subg. *Meconopsis*, Gen. *Meconopsis*: 43. 2014.—TYPE: *M. regia* G. Taylor, J. Bot. 67: 259. 1929.

Meconopsis sect. *Robustae* Fedde, Pflanzenr. (Engler) 40 (IV.104): 267. 1909.—TYPE: *M. robusta* Hook. f. & Thomson.

Meconopsis sect. *Torquatae* Fedde, Pflanzenr. (Engler) 40 (IV.104): 265. 1909. *Meconopsis* subg. *Discogyne* G. Taylor, Account Gen. *Meconopsis*: 107. 1934.—TYPE: *M. torquata* Prain.

Meconopsis subsect. *Eupolychaetia* G. Taylor, Account Gen. *Meconopsis*: 30. 1934.—TYPE: *M. paniculata* Prain.

Meconopsis subg. *Discogyne* (G. Taylor) Grey-Wilson, Gen. *Meconopsis*: 44. 2014.—TYPE: *M. discigera* Prain.

Monocarpic perennials with taproots; 0.3–2.5 m tall at anthesis, frequently more than 1 m tall. Stems and leaves hirsute or pubescent, commonly with barbellate or branched trichomes. Leaves retained in an evergreen dense basal rosette for a few years before flowering. Leaf blades oblanceolate or elliptic to oblong, pinnatifid or pinnatisect, with serrate, lobed or divided margins, up to 60 cm long. Inflorescence a raceme-like or panicle-like cyme most commonly with 1–5 (up to 15) flowered cymules; bracts leafy or reduced. Petals usually 4; commonly yellow, red, blue to violet. Ovary ellipsoid to oblong, usually setose, rarely glabrous; style distinct and short, occasionally expanding at the base into a disk surmounting the ovary; stigma normally capitate. Capsules oblong to ellipsoid, or ovoid to ellipsoid. Chromosome number $2n = 56$, rarely $2n = 28$.

Included Species—*Meconopsis autumnalis* P. A. Egan; *M. chankheliensis* Grey-Wilson; *M. dhwojii* G. Taylor; *M. discigera* Prain; *M. ganeshensis* Grey-Wilson; *M. gracilipes* G. Taylor; *M. manasluensis* P. A. Egan; *M. napaulensis* DC.; *M. paniculata* Prain; *M. pinnatifolia* C. Y. Wu & H. Chuang ex L. H. Zhou; *M. regia* G. Taylor; *M. robusta* Hook. f. & Thomson; *M. simikotensis*

Grey-Wilson; *M. staintonii* Grey-Wilson; *M. superba* King ex Prain; *M. taylorii* L. H. J. Williams; *M. tibetica* Grey-Wilson; *M. torquata* Prain; *M. violacea* Kingdon-Ward; *M. wallichii* Hook.; *M. wilsonii* Grey-Wilson.

Species in this section share characters of a perennial monocarpic habit and retention of a dense evergreen rosette of leaves for a few years before flowering, and the latter is absent in other sections in the genus. Most species in this section are tall plants (usually more than 50 cm and up to 2.5 m tall when mature). However, a subgroup (highlighted by red branch in Fig. 3A) in the section contains species usually less than 50 cm tall and characterized by the style expanding into a flat disc at the base. This unique disc structure was emphasized by all of the previous classifications and species with the disc structure had always been grouped into a distinct unit (i.e. Fedde's *M.* sect. *Torquatae*, Taylor's *M.* subg. *Discogyne*, or Grey-Wilson's *M.* subg. *Discogyne*). Our *M.* sect. *Meconopsis* for the first time recognized and put emphasis on the phylogenetic relatedness instead of relying on one morphological character to perform infrageneric division.

2. Meconopsis sect. Aculeatae Fedde, Pflanzenr. (Engler) 40 (IV.104): 255. 1909. *Meconopsis* ser. *Aculeatae* (Fedde) G. Taylor, Account Gen. *Meconopsis*: 78. 1934.—TYPE: *M. aculeata* Royle, Ill. Bot. Himal. Mts. [Royle] 1: 67. 1839.

Meconopsis ser. *Delavayanae* G. Taylor, Account Gen. *Meconopsis*: 76. 1934.—TYPE: *M. delavayi* Franch.

Meconopsis sect. *Racemosae* C. Y. Wu & H. Chuang, Acta Bot. Yunnan. 2(4): 374. 1980.—TYPE: *M. racemosa* Maxim.

Meconopsis sect. *Forrestii* C. Y. Wu & H. Chuang, Acta Bot. Yunnan. 2(4): 376. 1980. *Meconopsis* sect. *Forrestianae* Grey-Wilson, Gen. *Meconopsis*: 46. 2014.—TYPE: *M. forrestii* Prain.

Meconopsis sect. *Impediatae* Grey-Wilson, Gen. *Meconopsis*: 46. 2014.—TYPE: *M. impedita* Prain.

Monocarpic biennials, or perennials with taproots; up to 1 m tall at anthesis. Stems and leaves aculeate with simple non-barbellate trichomes, or occasionally subglabrous. Leaves senescing and deciduous during the winter. Leaf lamina ovate, oblanceolate to oblong, elliptic to oblong, pinnatifid, or pinnatisect with margins normally entire, lobed or divided, up to 25 cm long. Flowers borne on basal scapes, or in bracteate or ebracteate raceme-like cymes, or both. Petals 4–12, commonly blue or violet, rarely white, yellow, red or dark red. Ovary subspherical, or ellipsoidal to narrowly subcylindric, densely covered by sharp bristles to glabrous; style distinct; stigma capitate or clavate. Capsules oblong, ovoid, obvoid to narrowly subcylindrical. Chromosome number $2n = 56$, rarely $2n = 14$.

Included Species—*Meconopsis aculeata* Royle; *M. bikramii* Aswal (a rare species collected from Himalaya Pradesh in India, placed in this section because the original author suggested it is allied to *M. aculeate*; no material was available for examination and its palmately lobed lower cauline leaves cast doubt on its affinity); *M. concinna* Prain; *M. delavayi* Franch. Ex Prain; *M. forrestii* Prain; *M. georgei* G. Taylor; *M. henrici* Bureau & Franch.; *M. horridula* Hook. f. & Thomson; *M. impedita* Prain; *M. lancifolia* Franch.; *M. latifolia* Prain; *M. muscicola* Tosh. Yoshida, H. Sun & Boufford; *M. neglecta* G. Taylor; *M. pseudovenusta* G. Taylor; *M. pulchela* Tosh. Yoshida, H. Sun & Bouford; *M. venusta* Prain; *M. yaoshanensis* Tosh. Yoshida, H. Sun & Boufford.

As indicated by its name, *Meconopsis* sect. *Aculeatae* is characterized by sharp-pointed bristles on leaf and stem surface. Species in this section most commonly bear blue flowers (e.g. Fig. 2D) or purple-violet flowers (e.g. Fig. 2C). The flower colors of this section are indicated by branch color in Fig. 3A. The blue-flowered species, form a basal grade to the species with purple-violet flower which suggests that purple-violet is a derived characteristic in this section (Fig. 3A). Species with purple-violet flowers tend to be less robust with shorter stature and less dense bristles than the blue-flowered species, and were once believed to resemble the also short-statured species *Meconopsis primulina* (the type species of our *M.* sect. *Primulinae*). There is overlap at the characters of indumentum, stature, and leaf shape between the species with purple-violet flowers in our *M.* sect. *Aculeatae* and those in our *M.* sect. *Primulinae*, but the two sections can be easily separated by the petal color (Fig. 2A, C). Species in our *M.* sect. *Primulinae* do not have the deep purple-violet color of those in *M.* sect. *Aculeatae.* Additionally, our *M.* sect. *Primulinae* species are distributed mainly in the east Himalaya while the purple-violet flowered species in *M.* sect. *Aculeatae* are distributed mainly in the Hengduan Mountains. The phylogenetic evidence also strongly supports the separation of two genetically distant clades of *M.* sects. *Aculeatae* and *Primulinae*.

3. Meconopsis sect. Primulinae Fedde, Pflanzenr. (Engler) 40 (IV.104): 259. 1909. *Meconopsis* ser. *Primulinae* (Fedde) G. Taylor, Account Gen. *Meconopsis*: 71. 1934. *Meconopsis* sect. *Cumminsia* (Prain) Grey-Wilson, Gen. *Meconopsis*: 45. 2014.—TYPE: *M. primulina* Prain, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 64: 319. 1895.

Meconopsis sect. *Bellae* Fedde, Pflanzenr. (Engler) 40 (IV.104): 261. 1909. *Meconopsis* ser. *Bellae* (Fedde) G. Taylor, Account Gen. *Meconopsis*: 103. 1934.—TYPE: *M. bella* Prain.

Monocarpic or polycarpic perennials with taproots; frequently less than 25 cm tall, rarely exceeding 50 cm at anthesis (except in *Meconopsis sinuata* that ranges from 30–65 cm in height). Leaves and stems most frequently sparsely vestitured with weak non-barbellate trichomes or subglabrous, rarely aculeate with sharp bristles. Leaves senescing during the winter; lamina variable in shape and margin type, frequently less than 7 cm long (rarely exceeding 15 cm). Flowers born on basal scapes or arranged in simple cyme with 2–8 flowers in axils of upper cauline leaves. Petals 4–8, commonly pale blue to pale purple-blue, sometimes pink or yellow. Ovary usually ellipsoid to oblong, or narrowly ellipsoidal to narrowly subsylindric sometimes subspherical, usually subglabrous or with sparse bristles; style distinct, usually short, but sometimes longer than the ovary; stigma capitate. Capsules obovoid or narrowly obovoid to narrowly subcylindrical. The only known chromosome number (*M. bella*) is $2n = 22$.

Included Species—*Meconopsis argemonantha* Prain; *M. bella* Prain; *M. florindae* Kingdon-Ward; *M. lyrata* (H. A. Cummins & Prain) Fedde; *M. primulina* Prain; *M. sinuata* Prain; *M. wumungensis* K. M. Feng; *M. zangnanensis* L. H. Zhou.

Species in this section tend to have a dwarf and slender aspect with short root and weak stem as well as a brittle and sparse indumentum. Although blue flowers are common in this section, most species tend to be more pale or faded than the bright blue color present in other sections. *Meconopsis sinuata* in this section is morphologically distinct being taller than other species and armed with dense spines. Unsurprisingly, *M. sinuata* used to be grouped with species in our *M.* sect. *Aculeatae* (e.g. in *M.* sect. *Aculeatae* in Fedde 1909, or *M.* ser. *Aculeatae* in Taylor 1934). However, it is easy to distinguish living plants of *M. sinuata* from species of *M.* sect. *Aculeatae* by the shape of ovary and style and especially by the leaf morphology (see the Key to Sections).

Meconopsis bella, another species in our *M.* sect. *Primulinae*, was traditionally placed in its own section (i.e. *M.* sect. *Bellae* in Fedde 1909 and Grey-Wilson 2014) or series (i.e. *M.* ser. *Bellae* in Taylor 1934), all based on its unique characteristic of a bell-shaped ovary. However, the general morphology (e.g. height, leaf shape, flower arrangement, petal color) of *M. bella* matches that of our *M.* sect. *Primulinae* and phylogenetic result supports the inclusion of *M. bella* in *M.* sect. *Primulinae,* which indicate that the unique feature of having a bell-shaped ovary does not warrant special status.

4. Meconopsis sect. Grandes Fedde, Pflanzenr. (Engler) 40 (IV.104): 262.1909. *Meconopsis* ser. *Grandes* (Fedde) G. Taylor, Account Gen. *Meconopsis*: 56. 1934. *Meconopsis* subg. *Grandes* (Fedde) Grey-Wilson, Gen. *Meconopsis*: 44. 2014.—TYPE: *M. grandis* Prain, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 64: 320. 1895.

Meconopsis ser. *Simplicifoliae* G. Taylor, Account Gen. *Meconopsis*: 49. 1934. *Meconopsis* sect. *Simplicifoliae* (G. Taylor) C. Y. Wu & H. Chuang, Acta Bot. Yunnan. 2(4): 375. 1980.—TYPE: *M. simplicifolia* (D. Don) Walp.

Monocarpic or polycarpic perennials with taproots or a fibrous root system or the combination; up to 1.5 m tall at anthesis. Leaves and stems hirsute with barbellate trichomes. Leaves senescing and deciduous during the winter; lamina frequently ellipic to narrowly oblanceolate, narrowly elliptic or narrowly lanceolate, longitudinally nerved and entire at the margin, sometimes oblanceolate to lanceolate- or elliptic-oblong with entire, serrate or lobed margins and pinnate venation; up to 30 cm long; uppermost cauline leaves sometimes aggregated in a false whorl and bearing flowers in their axils. Flowers normally fewer than 8, solitary on basal scapes, or in the axil of cauline leaves. Petals most commonly 4, or up to 10; blue, violet, yellow or red. Ovary usually ellipsoid to oblong, pubescent to hispid; styles commonly distinct, sometimes inconspicuous; stigma capitate or subclavate or star-shaped with 3–9 stigmatic rays variously decurrent relative to the style (in this condition, the style more or less resembling a star-shaped column). Capsules oblong to ellipsoid. Chromosome numbers from $2n = 74$ to 164, most frequently 84.

Included Species—*Meconopsis betonicifolia* Franch.; *M. biloba* L. Z. An, Shu Y. Chen & Y. S. Lian; *M. grandis* Prain; *M. integrifolia* (Maxim.) Franch.; *M. punicea* Maxim.; *M. quintuplinervia* Regel; *M. simplicifolia* (D. Don) Walp.; *M. sherriffii* G. Taylor.

The members of this section are easy to identify by their long and dense barbellate trichomes and the presence of a fibrous root system. Species in this section are more popular than those of other sections in Scottish gardens, not only for the brilliant colors of their large and showy flowers (Fig. 2B), but also for their easy cultivation and (frequent) polycarpic habit. This section also has the highest chromosome numbers among the genus with $2n = 74$, 76, 82, 84, 118, 120, 164.

Typified Species—

Cathcartia chelidonifolia (Bureau & Franch.) Grey-Wilson, Gen. *Meconopsis*: 374. 2014.—LECTOTYPE (designated here): CHINA. Sichuan: Ta-Tsien-Lou [Kangding], *P. G. E. Bonvalot & Prince Henri d'Orléans s. n.* (P, barcode 00739028; isolectotype: P, barcode 00739029).

Cathcartia oliveriana (Franch. ex Prain) Grey-Wilson, Gen. *Meconopsis*: 376. 2014.—LECTOTYPE (designated here): CHINA. Hubei, *Henry* 6863 (K, barcode K000653215; isolectotypes: BM, K).

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Appendix 1. Voucher and sequence information (Accession number; species name; (Collecting) country: Subdivision; voucher (herbarium); GenBank ID for *matK*, *ndhF*, *trnL-trnF*, *rbcL*. Accessions beginning with "X" were analyzed and sequenced in this study, and accessions beginning with "Y" were published by Yuan (2002). "-", denotes a missing sequence).

X001; ***Argemone albiflora*** Hornem.; U. S. A.: Texas; *W. Xiao 090515* (TEX); JX087885, JX087848, -, JX087687. X002; ***Chelidonium majus*** L.; CHINA: Shaanxi; *W. Xiao 090814* (TEX); JX087914, JX087828, -, JX087694. X003; ***Meconopsis dhwojii*** G. Taylor; U. K. (cultivated); *W. Xiao RICB9* (E); JX087915, JX087815, JX087755, JX087699. X004; ***Meconopsis wallichii*** Hook.; U. K. (cultivated); *W. Xiao RICB10* (E); JX087895, JX087821, -, JX087711. X005; ***Meconopsis paniculata*** Prain; U. K. (cultivated); *W. Xiao RICB5* (E); JX087868, JX087830, JX087743, JX087720. X006; ***Meconopsis superba*** King ex Prain; U. K. (cultivated); *W. Xiao RICB7* (E); JX087858, JX087851, JX087735, JX087683. X007; ***Meconopsis simplicifolia*** (D. Don) Walp.; NEPAL: Bagmati; *Egan 4* (private collection); JX087891, JX087803, JX087751, JX087700. X008; ***Meconopsis grandis*** Prain; U. K. (cultivated); *W. Xiao RICB6* (E); JX087873, JX087832, -, JX087695. X009; ***Meconopsis betonicifolia*** Franch.; U. K. (cultivated); *W. Xiao RICB2* (E); JX087871, JX087806, -, JX087716. X010; ***Meconopsis integrifolia*** (Maxim.) Franch.; CHINA: Yunnan; *W. Xiao 080620* (TEX); JX087901, JX087804, -, JX087701. X011; ***Meconopsis horridula*** Hook. f. & Thomson; CHINA: Sichuan; *Boufford 33724* (A); JX087905, JX087812, JX087770, JX087712. X014; ***Papaver cambricum*** L.; U. K. (cultivated); *W. Xiao RICB1* (E); JX087883, JX087835, -, JX087689. X015; ***Meconopsis punicea*** Maxim.; CHINA: Sichuan; *Boufford 33684* (A); JX087862, JX087849, -, JX087718. X016; ***Meconopsis quintuplinervia*** Regel; CHINA: Sichuan; *W. Xiao RICB8* (E); JX087865, JX087831, -, JX087706. X017; ***Meconopsis henrici*** Bureau & Franch.; CHINA: Sichuan; *W. Xiao 090726-3* (TEX); JX087916, JX087809, JX087763, JX087728. X018; ***Meconopsis lancifolia*** Franch. ex Prain; CHINA: Yunnan; *W. Xiao 080621-1* (TEX); JX087857, JX087818, JX087750, JX087731. X020; ***Meconopsis speciosa*** Prain; CHINA: Yunnan; *W. Xiao 090703-2* (TEX); JX087920, JX087829, JX087781, JX087682. X022; ***Meconopsis delavayi*** Franch. ex Prain; U. K. (cultivated); *W. Xiao 090526* (TEX); JX087866, JX087816, JX087736, JX087688. X024; ***Cathcartia oliveriana*** (Franch. ex Prain) W. Xiao; CHINA: Shaanxi; *J. Z. Xiao 1* (TEX); JX087907, JX087791, JX087765, -. X026; ***Meconopsis aculeata*** Royle; U. K. (cultivated); *C5255* (E); JX087912, JX087820, -, JX087709. X027; ***Meconopsis bella*** Prain; NEPAL: Kone Khola; *McBeath 1496* (E); JX087919, JX087823, -, JX087723. X028; ***Meconopsis torquata*** Prain; CHINA: Xizang; *Ludlow 9904* (E); JX087875, -, JX087737, JX087696. X029; ***Meconopsis forrestii*** Prain; CHINA: Yunnan; *Fang1154* (Xiang Ge Li La Alpine Garden); JX087853, JX087807, JX087734, -. X031; ***Meconopsis zangnanensis*** L. H. Zhou; CHINA: Xizang; *Chen 25-960* (KUN); JX087884, JX087799, -, JX087705. X034; ***Cathcartia chelidonifolia*** (Bureau & Franch.) W. Xiao; U. K. (cultivated); *W. Xiao RICB4* (E); JX087897, JX087840, -, JX087690. X035; ***Meconopsis argemonantha*** Prain; CHINA: Xizang; *Bowes Lyon 11101* (E); -, JX087814, JX087778, -. X036; ***Meconopsis discigera*** Prain; BHUTAN: Upper Mo Chu District; *Bowes Lyon 15045* (E); JX087918, JX087824, JX087774, JX087686. X037; ***Meconopsis georgei*** G. Taylor; CHINA: Yunnan; *Forrest 30595* (E); JX087856, JX087792, JX087768, JX087693. X042; ***Meconopsis sinuata*** Prain; INDIA: Sikkim; *ESK 683* (E); JX087890, JX087785, -, JX087725. X045; ***Meconopsis wumungensis*** K. M. Feng; CHINA: Yunnan; *Liu 1990 July* (KUN); JX087922, -, -, JX087707. X046; ***Meconopsis wilsonii*** Grey-Wilson; CHINA: Sichuan; *Boufford 32733* (A); JX087924, JX087838, JX087740, JX087691. X047; ***Meconopsis primulina*** Prain; BHUTAN: Upper Mo Chu District; *Sargent 170* (E); JX087887, JX087843, -, JX087685. X052; ***Meconopsis concinna*** Prain; CHINA: Yunnan; *Boufford 35133* (A); JX087889, JX087841, JX087759, JX087721. X055; ***Cathcartia villosa*** Hook. f.; INDIA: Sikkim; *ESK 205* (E); -, JX087847, -, JX087708. X059; ***Papaver alpinum*** L.; U. K. (cultivated); *W. Xiao 090527-2* (TEX); JX087879, JX087836, JX087766, JX087719. X060; ***Papaver lateritium*** K. Koch; U. K. (cultivated); *W. Xiao 090527-3* (TEX); JX087900, JX087813, JX087776, JX087697. X063; ***Meconopsis staintonii*** Grey-Wilson; NEPAL: Larjung; *Stainton 747* (E); JX087893, -, -, -. X064; ***Meconopsis florindae*** Kingdon-Ward; CHINA: Xizang; *Kingdon-Ward 6206* (E); JX087870, JX087839, -, -. X065; ***Meconopsis chankheliensis*** Grey-Wilson; NEPAL: Chanke-Lekh; *Bailey 1936 June* (E); JX087904, JX087787, JX087753, JX087702. X069; ***Meconopsis autumnalis*** P. A. Egan; NEPAL: Bagmati; *Egan 17* (private collection); JX087872, JX087822, JX087748, JX087714. X078; ***Meconopsis napaulensis*** DC.; NEPAL: Bagmati; *Egan 29* (private collection); JX087906, JX087798, JX087760, JX087698. X081; ***Meconopsis* sp**; CHINA: Yunnan; *W. Xiao 090707-2* (TEX); JX079033, JX087888, JX087805, JX087744, -. X083; ***Meconopsis pseudovenusta*** G. Taylor; CHINA: Yunnan; *W. Xiao 090705-2* (TEX); JX087894, JX087796, JX087741, -. X095; ***Meconopsis ganeshensis*** Grey-Wilson; NEPAL: Bagmati; *Miyamoto 9400059* (E); JX087899, -, JX087772, -. X100; ***Meconopsis robusta*** Hook.f. & Thomson; NEPAL: Bajhang; *Nepal Bajhang 2009 Expedition 20913119* (E); KF777124, KF777123, KF777120, KF777121. Y1; ***Meconopsis lyrata*** (H. A. Cummins & Prain) Fedde; NEPAL: Bagmati; *Miyamoto 9484087* (E); -, -, AY328215.1, -. Y2; ***Meconopsis regia*** G. Taylor; NEPAL: above Doadi Khola; *Stainton 4627* (E); -, -, AY328224.1, -. Y3; ***Meconopsis latifolia*** Prain; INDIA: Kashimir; *Stewart 22563a* (unknown); -, -, AY328226.1, -. Y19; ***Cathcartia smithiana*** Hand.-Mazz.; CHINA: Yunnan; *GSE97 9592* (E); -, -, AY328247.1, -.

Appendix 2. Primer list: Primer name, primer sequences (source or reference). * indicates primers designed for this study.

trnL-trnF forward primer sequence, 5′-CGAAATCGGTAGACGCTACG-3′ (Taberlet et al. 1991); *trnL-trnF* reverse primer sequence, 5′-ATTTGAACTGGTGACACGAG-3′ (Taberlet et al.1991); *matK* forward primer sequence, 5′-ACTGTATCGCACTATGTATCA-3′ (Sang et al.1997); *matK* reverse primer sequence, 5′-GAACTAGTCGGATGGAGTAG-3′ (Sang & al.1997); *matK* internal forward primer sequence*, 5′-GGAGCATCCTTTAGTAGTGTTTAG-3′; *matK* internal reverse primer sequence*, 5′-ATTTATTCATMAAAAGAGGACTTCC-3′; *ndhF* forward primer sequence, 5′-CTGTCTATTCAGCAAATAAAT-3′ (shared by R.K. Jansen); *ndhF* reverse primer sequence, 5′-CGATTATAGGACCAATCATATA-3′ (shared by R.K. Jansen); *ndhF* internal forward primer sequence*, 5′-ATGGGATCATATCGAGCTG-3′; *ndhF* internal reverse primer sequence*, 5′-CCCATAAGAGCCATATTCTGG-3′; *rbcL* forward primer sequence, 5′-ATGTCACCACAAACAGARACTAAAGC-3′ (designed by R. Beaman); *rbcL* reverse primer sequence, 5′-CTTTTAGTAAAAGATTGGGCCGAG-3′ (designed by R. Beaman); *rbcL* internal forward primer sequence*, 5′-CCCTTTATGCGTTGGAGAGA-3′; *rbcL* internal reverse primer sequence*, 5′-CTCTGGCAAATACAGCCCTT-3′.