Taxonomy of the traditional medicinal plant genus *Ferula* (Apiaceae) is confounded by incongruence between nuclear rDNA and plastid DNA

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The aim of this study was to identify major clades in the economically important and taxonomically difficult genus *Ferula* (Apiaceae tribe Scandiceae subtribe Ferulinae) to provide a classification framework. Phylogenetic relationships among 126 of *Ferula* spp. and eight species of its sister genus *Leutea* were evaluated based on nuclear ribosomal (nr) DNA ITS and three plastid regions: the *rps16* intron, the *rpoC1* intron and the *rpoB-trnC* intergenic spacer. One hundred and fifty-three accessions were considered including type specimens of seven species. Congruence between nrDNA and plastid DNA data was assessed using a hierarchical likelihood ratio test. Phylogenetic trees were inferred using maximum likelihood and Bayesian methods. Terminals introducing topological conflict were ascertained using two approaches: identifying (1) these with significantly different positions between nrDNA and plastid DNA trees; and (2) a set of rogue taxa in combined trees that, when removed, increased tree resolution and bootstrap support. The results demonstrate significant incongruence between nrDNA and plastid DNA data that persisted after the removal of 41 terminals identified as having significantly different position in nrDNA and plastid DNA trees or after the removal of 13 terminals identified as rogue taxa. Comparison of nrDNA and plastid DNA trees suggest intensive reticulate evolution, particularly in the Irano–Turanian floristic region. Traditional classification systems of the genus are not supported by molecular data, whereas some lineages apparent in molecular trees, particularly Chinese and Mediterranean endemics, are congruent with morphological characters and/or biogeography. We select lectotypes for several infrageneric names and propose a new classification system of the genus with four subgenera and ten sections.

ADDITIONAL KEYWORDS: Ferulinae – infrageneric classification – *Leutea* – molecular phylogeny – reticulate evolution – typification.

INTRODUCTION

Among the genera of Apiaceae, *Ferula* L. is one of the largest, includes many species commonly used in traditional medicine and is a promising source of biologically active ingredients. However, the current classification system of the genus does not match the phylogenetic trees, providing little support for research and commercial use. With many species, a wide distribution and poorly understood morphology, the genus epitomizes all the nightmares of a taxonomist. The c. 170 species of this Eurasian...
genus are distributed from the Canary Islands in the west through the Mediterranean region, Middle East and Central Asia to western China in the east and northern India in the south (Korovin, 1947; Pimenov & Leonov, 1993). The genus has not been taxonomically revised since the monograph of Korovin (1947). Regional floristic treatments resolved some critical issues but also contributed to the taxonomic confusion because they were inconsistent with one another (Korovin, 1951, 1959; Pešmen, 1972; Safina & Pimenov, 1984; Chamberlain & Rechinger, 1987; Safina & Pimenov, 1990). Substantial morphological variation in the genus has resulted in the description of multiple nearly indistinguishable species, which are sometimes represented in herbarium collections by few, poorly preserved specimens. Fruits and basal leaves are essential for correct identification (Pešmen, 1972); the latter, however, are often absent at fruit maturity in monocarpic taxa. Because of the large size of these plants, herbarium specimens usually include only lateral branches and lateral divisions of basal leaves. An experienced taxonomist may identify most species from flowering material (Chamberlain & Rechinger, 1987), but, as underlined by Korovin (1947), the circumscription of species should be based on observations of living plants because it requires examination of complete specimens with roots, stem bases, basal leaves, inflorescence, flowers and ripe fruits. Given these constraints, a taxonomic revision of Ferula seems currently impossible for a single taxonomist. Therefore, it would be useful to subdivide the genus into smaller, monophyletic and workable units that could be subject to partial revisions.

In his monograph, Korovin (1947) established several subgenera and sections based mostly on habit and vegetative features. Safina & Pimenov (1983, 1984, 1990) contested these infrageneric divisions and proposed an alternative classification system inferred from fruit morphology and anatomy. However, subsequent molecular studies have not supported either of these treatments, indicating that the infrageneric classification system of Ferula has to be constructed anew (Kurzyna-Młynik et al., 2008; Panahi et al., 2015). Ferula was traditionally classified in tribe Peucedanaceae (Pimenov & Leonov, 1993). However, immunochemical studies demonstrated that the genus is not closely related to other genera in this tribe (Shneyer, Borschtschenko & Pimenov, 1995; Shneyer, Kutyavina & Pimenov, 2003). Phylogenetic studies using nuclear ribosomal internal transcribed spacer (nrDNA ITS) sequence variation revealed that Ferula is placed in tribe Scandiceae and forms a clade with Dorema D.Don and Leutea Pimenov (Kurzyna-Młynik et al., 2008). This clade was formally recognized as subtribe Ferulinae. However, the resolution of the ITS tree was low and the infrageneric subclades received moderate internal support. Subsequent analyses using ITS and three non-coding plastid DNA (plastid DNA) sequences showed that Leutea is sister to Ferula, whereas Dorema is nested in it; consequently, Dorema was subsumed under Ferula (Panahi et al., 2015). However, the phylogenetic signal differed significantly between nrDNA and plastid DNA markers resulting in a poor resolution of the tree at the infrageneric level. Moreover, this study included only 68 Ferula spp. of > 170 recognized in the genus.

Here, we further investigate the phylogenetic relationships in Ferulinae using a comprehensive sampling of species and analysing data from nuclear and plastid genomes. Our aim is the identification of major clades of Ferula that may be subject to partial taxonomic revisions and, therefore, provide a phylogenetically meaningful classification system of the genus.

MATERIAL AND METHODS

Taxon sampling

One hundred and fifty-three samples of Apiaceae were examined for nrDNA ITS and plastid DNA sequence variation (Table S1). The ingroup comprised eight Leutea spp. and 126 Ferula spp. We obtained sequences from 72 samples for this study, with the others having been previously published (Kurzyna-Młynik et al., 2008; Panahi et al., 2015). The former genus Dorema that is now subsumed in Ferula (Panahi et al., 2015) was represented by six species. The analysed samples included type material of seven species: F. gabrielii Rech.f., F. kashanica Rech.f., F. serpentinica Rech.f., F. sharifii Rech.f. & Esfand., F. stenocarpa Boiss. & Hausskn. ex Boiss., F. tabasensis Rech.f. and Leutea nematoloba (Rech.f.) Pimenov. Taxonomic treatment for the Middle Eastern and Central Asian members of Ferula generally follows the Flora Iranica account (Chamberlain & Rechinger, 1987) with some amendments (Czerepanov, 1995, She & Watson, 2005; Mozaffarian, 2007). The outgroups included two representatives of other major lineages of Scandiceae: Glauocosciadium cordifolium (Boiss.) B.L.Burtt & P.H.Davis and Thapsia thapsioides (Desf.) Simonsen, Ronsted, Weitzel & Spalink (Panahi et al., 2015). Species names with authorities, voucher information and GenBank accession numbers for the samples included in this study are listed in Table S1.

Laboratory procedures

Total genomic DNA was extracted from c. 10–20 mg of dried plant material using the DNeasy Plant Mini Kit (Qiagen, Valencia, CA, USA) following the
amplify the primers ‘s16inF’ and ‘s16inR’ (Panahi of the aforementioned external primers and internal (Panahi ‘3exonR’ (Calviño intron was amplified using primers ‘5exonC’ and (Panahi regions, we used external primers ‘C1exF’ and ‘C1exR’ (Panahi et al., 2015). For some samples, this region was divided into parts and amplified using a combination of the aforementioned external primers and internal primers ‘s16inF’ and ‘s16inR’ (Panahi et al., 2015). To amplify the rpoC1 intron and parts of the flanking exon regions, we used external primers ‘C1exF’ and ‘C1exR’ and internal primers ‘C1inF’ and ‘C1inR’ (Panahi et al., 2015). The rpoB-trnC intergenic spacer region was amplified with primers ‘rpoB’ and ‘trnC GCA R’ (Shaw et al., 2005). For some samples, the external forward primer ‘rpoB’ was unsuccessful and was replaced with ‘rpD’; additionally, internal primers ‘RP’, ‘TP’, ‘rpA’ and ‘1R’ were used to overcome amplification and sequencing problems. The sequences and position of these primers and the details of PCR amplification are provided elsewhere (Panahi et al., 2015).

PCR products were separated using 1% agarose gel with ethidium bromide or Midori Green DNA Stain (ABO) and purified using the QIAEX II Agarose Gel Extraction Kit (Qiagen). Sequencing from both strands was performed using Big Dye terminators (Applied Biosystems, Foster City, CA, USA). The chromatographs were assembled and edited using SeqMan Pro ver. 12 (Dnastar, Madison, WI, USA).

**SEQUENCE AND PHYLOGENETIC ANALYSES**

The sequences were initially aligned using the default pair-wise and multiple alignment parameters in CLUSTAL X (Larkin et al., 2007) and adjusted manually using Mesquite 3.2 (Maddison & Maddison, 2017). Gaps were positioned to minimize nucleotide mismatches and treated as missing data in phylogenetic analyses. Poorly aligned regions that may interfere with phylogenetic estimation were located using trimAl v.1.2 with the –automated1 option (Capella-Gutiérrez, Silla-Martínez & Gabaldón, 2009) and excluded from the analyses.

Congruence of the datasets was assessed using a hierarchical likelihood ratio test (hLTR) implemented in Concatепillar ver. 1.7.2 (Leigh et al., 2008). Phylogenetic trees were inferred using the maximum likelihood (ML) method implemented in RAxML ver. 8.2.4 (Stamatakis, 2014) and the Bayesian inference (BI) method implemented in MrBayes ver. 3.2.6 x64 MPI (Ronquist et al., 2012). Several groups of accessions had identical sequences for some markers analysed. Each of these groups was represented by a single terminal in phylogenetic analyses. In the resulting trees, these terminals were added forming a polytomy composed of zero-length branches.

ML analyses included 200 searches starting from distinct randomized maximum parsimony trees. Branch support (BS) was evaluated based on 1000 rapid bootstrap replicates. To assess whether the number of replicates was sufficient, a posteriori bootstopping analysis was carried out with the extended majority-rule consensus tree as a criterion of convergence. All analyses were performed with GTR + G substitution model, which was most efficiently implemented and optimized for RAxML and thus recommended by the author (Stamatakis, 2014). For plastid data and combined nuclear and plastid data, partition schemes were inferred using PartitionFinder ver. 2.1.1 (Lanfear et al., 2016) with branch lengths linked and BIC options.

Bayesian analyses comprised two independent runs, each with four Monte Carlo Markov chains that were run for 40 000 000 generations with a sampling frequency of 1000 generations and default priors for the parameters of nucleotide substitution model. The initial 25% of saved trees were discarded and the results were summarized on the 50% majority rule consensus tree. The effective sample size (ESS) for the estimated parameters and the convergence of the independent runs were checked using Tracer ver. 1.6.0 (Rambaut et al., 2014). The model of nucleotide substitution for independent analyses of nrDNA ITS data was selected with ModelGenerator ver. 0.85 (Keane et al., 2006). For the analyses of plastid data and combined nuclear and plastid data, partition schemes and substitution models were inferred using PartitionFinder comparing the models implemented in MrBayes.

Two methods were used to identify problematic terminals, i.e. those that introduce putative topological conflict or decrease branch support: (1) compat.py (Kauff & Lutzoni, 2002, 2003) and (2) the RogueNaRok algorithm (Aberer, Krompass & Stamatakis, 2013). The first compares support values for trees inferred from different partitions (e.g. nrDNA and plastid DNA) and identifies terminals that occur in different and well-supported clades. We therefore compared clades occurring in nrDNA and plastid DNA trees choosing the values of BS ≥ 75 and PP = 1 as thresholds for ML and Bayesian analyses, respectively. In contrast, the RogueNaRok algorithm identifies a set of rogue terminals that, if pruned from the bootstrap trees, results in a consensus tree with more resolved polytomies (i.e.}

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containing additional bipartitions) or with increased support values. We applied this algorithm to identify rogue taxa in ML analyses of combined data. The terminals identified by this algorithm were pruned from the ML bootstrap trees, which were then summarized on the best tree. Bootstrap support values for major clades were compared to those obtained from the analyses of unpruned trees.

To check whether the terminals identified with both methods introduced incongruence between nrDNA and plastid DNA, we excluded them from the matrices and repeated the hierarchical likelihood ratio tests (hLTR) with Concaterpillar. The data for this study have been deposited in TreeBASE, study number 21677 (http://purl.org/phylo/treebase/phylows/study/TB2:S21677).

RESULTS

SEQUENCE CHARACTERISTICS

Alignment of the sequences was relatively unambiguous. In the matrices trimmed with trimAl, the ITS region was more variable for the ingroup than the concatenated plastid DNA regions, with 25.5% variable positions as opposed to 10.0% in the latter (Table 1). Seventy-two ITS sequences were non-unique, distributed in 17 groups comprising two to 16 terminals each. In the concatenated plastid DNA data, 38 accessions were non-unique and distributed in 16 groups of two to four terminals each. However, in the matrix of combined nrDNA and plastid DNA data, only six pairs of accessions had all sequences identical. Each group of identical sequences was represented by a single terminal in subsequent phylogenetic analyses.

Hierarchical clustering of the markers based on likelihood-ratio tests concatenated all three plastid DNA regions with \( P = 0.043 \) and corrected \( \alpha = 0.025 \); however, it failed to concatenate plastid DNA and ITS with \( P < 1 \times 10^{-6} \) and corrected \( \alpha = 0.017 \). For ITS data, ModelGenerator with the Bayesian information criterion (BIC) selected the SYM + G nucleotide substitution model. PartitionFinder partitioned the data into ITS and plastid DNA with the SYM + G and GTR + G + I substitution models, respectively.

PHYLGENETIC ANALYSES

Trees obtained from ML and Bayesian analyses were similar in topology; therefore, here we only show ML trees, whereas Bayesian trees are presented electronically in the Additional Supporting Information. We identify major clades with letters and their subclades with numbers; clades A–I refer to those recognized by Kurzyna-Młynik et al. (2008) and J–L are recognized here for the first time.

Separate analyses of nrDNA ITS and plastid DNA matrices of these data resulted in trees with notably different topologies. In the ITS trees, major clades of Ferulinae formed a basal polytomy (Figs 1 and S1), whereas in the plastid DNA trees relationships among those clades were better resolved, but also contained polytomies (Figs 2 and S2). However, several clades that were apparent in the ITS trees did not occur in the plastid DNA trees. Although some clades were present in the trees inferred from both datasets, numerous terminals were placed in different positions in these trees (Fig. S3).Compat.py identified 41 terminals that had significantly different positions in nrDNA and plastid DNA trees (Figs 1 and 2). Notably, the ITS tree was more congruent with the traditional taxonomic treatment of the genus than the plastid tree. For instance, all samples of \( F. \) gummosa Boiss. have identical ITS sequences and occurred in clade H, whereas each of them has a different plastid haplotype.

Table 1. Characteristics of the datasets used in phylogenetic analyses. Apart from sequence length variation, all numbers concern matrices without ambiguously aligned positions removed using trimAl program. Numbers in parentheses refer to the ingroup (Ferula).

| Datasets | ITS | rpoB-trnC spacer | rps16 intron | rpoC1 intron | plastid DNA | All combined |
|----------|-----|-----------------|-------------|-------------|-------------|-------------|
| Sequence length variation | 599–606 | 1191–1327 | 833–920 | 1045–1061 | — | — |
| Number of unambiguously aligned positions: | | | | | | |
| total | 604 | 1205 | 835 | 1048 | 3106 | 3710 |
| constant | 407 (450) | 1074 (1060) | 749 (767) | 963 (969) | 2755 (2796) | 3162 (3246) |
| autapomorphic | 98 (68) | 94 (79) | 61 (44) | 45 (40) | 200 (163) | 298 (231) |
| Parsimony informative | 99 (66) | 68 (66) | 43 (42) | 40 (39) | 151 (147) | 250 (233) |
| containing gaps | 17 (15) | 113 (79) | 43 (41) | 34 (25) | 190 (145) | 207 (160) |
| Percentage of gaps | 0.2 (0.19) | 0.13 (0.11) | 0.15 (0.15) | 0.09 (0.09) | 0.12 (0.11) | 0.14 (0.13) |
| Mean indel length [bp] | 1.16 (1.14) | 1.49 (1.33) | 1.26 (1.25) | 0.83 (0.78) | 2.70 (2.66) | 2.94 (2.96) |
| Maximum indel length [bp] | 4 (4) | 20 (20) | 21 (21) | 8 (8) | 21 (21) | 21 (21) |
Figure 1. Maximum likelihood tree inferred from analyses of nrDNA ITS sequence data for Ferulinae. Groups of accessions with identical sequences were represented in the analyses by single terminals and then resolved to polytomies with...
that was more closely related to representatives of other species than to conspecific individuals. Similar significant discrepancies occurred in *F. ovina* (Boiss.) Boiss. (clade A). Also noteworthy are the relationships among the four representatives of *F. asa-asoetida* L. (clade H), although they were not supported by high BS and PP values and, therefore, these samples were not identified as conflicting by compat.py. Based on ITS data, terminals 0433 and 2051 are identical and were grouped with 0148, whereas sample 0359 was placed on a different branch (Fig. 1). The latter, however, had the same plastid DNA haplotype as sample 0148, whereas accessions 0433 and 2051 were placed on distant branches (Fig. 2). This example suggests that the discordance between nrDNA and plastid DNA data does not concern exclusively the terminals identified by compat.py as conflicting. Indeed, despite removing these 41 samples from the nrDNA and plastid DNA matrices, these datasets remained incongruent in Concaterpillar analyses ($P < 1 \times 10^{-6}$, corrected $\alpha = 0.017$).

Major clades in the ML and Bayesian trees of combined data (Figs 3 and S4, respectively) were almost the same as those in the nrDNA trees, whereas the relationships among these clades were more similar to those in the plastid DNA trees. *Leutea* and *Ferula* were found to be sister taxa in Ferulinae; the monophyly of each genus was strongly supported both in ML and Bayesian analyses (BS $\geq 93\%$, PP = 1.0). In combined ML analyses of reduced data without conflicting terminals, major clades and their bootstrap support were similar to these in the tree obtained from full dataset (compare Figs 3 and S5).

In *Ferula*, there were 11 major clades in the combined ML tree (Fig. 3). All but clades H and L also occurred in nrDNA analyses (Fig. 1), whereas only four clades (B, D, L and J) were apparent in ML plastid trees (Fig. 2). In the Bayesian consensus tree from the combined data some clades collapsed into polytomies (Fig. S4).

The rogue taxa analysis using RogueNaRok identified 13 unstable terminals: six accessions belonging to clade A, one to clade E, one to clade G, four to clade H and *F. kuhistanica* Korovin, which does not have a definite placement (Fig. 3). The removal of these terminals from the dataset notably increased bootstrap support for clades E (from 69 to 87%) and H (from 12 to 49%); nevertheless, the bootstrap support for clade H remained low. The support for other clades changed only marginally (Fig. S5). Despite deleting these 13 taxa from the matrix, plastid DNA and nrDNA datasets remained incongruent in Concaterpillar analysis ($P < 1 \times 10^{-6}$, corrected $\alpha = 0.017$).

**DISCUSSION**

**INCONGRUENCE BETWEEN nrDNA AND PLASTID DNA DATA**

Several factors may have contributed to the detected incongruence between nrDNA ITS and plastid DNA data. We cannot conclusively exclude accidental contamination or human error at various stages of laboratory procedures. Due to a limited availability of plant material, samples were mostly collected from old herbarium specimens, sometimes from crumbled leaves or flowers stored in envelopes. Such materials may be accidentally contaminated with tissues of other species, e.g. those stored in the same herbarium cabinets. Additionally, some PCR primers may be more specific to the contaminant than to the nominal species. As we explained in the Material and Methods section, for some difficult DNA samples, the selected markers were amplified and sequenced in parts using various combinations of external and internal primers. Partial sequences were then assembled based on overlapping regions. These regions were usually evolutionarily conserved, particularly in the plastid DNA markers, and did not vary much among species. Therefore, a chimaeric contig from sequences originating from different species might have passed unnoticed. For the same reasons, a human error would not have been easily detected. When rechecking the data from our previous paper on Ferulinae (Panahi et al., 2015), we found indeed that one sequence of the *rps16* intron (KJ660433) presumed to represent *Leutea glaucopruinosa* (Rech.f.) Akhani & Salimian was from a species of *Orlaya* Hoffm. (other plastid DNA markers from *L. glaucopruinosa* were correct and support the placement of this species in *Leutea*). Additionally, repeated sequencing for two species, *F. tadshikorum* Pimenov (*rps16* intron KJ660415) and *F. tuberifera* Korovin (*rpoB-trnC* spacer KJ660729), indicated that the DNA samples were probably contaminated with other species; therefore, these accessions were not used in the analyses presented here.

Despite the aforementioned problems, there are good reasons to conclude that the discrepancies between ITS and plastid DNA data are not artefacts but have resulted from biological processes. First, we repeated PCR and sequencing for some samples that exhibited zero-length branches. Bootstrap support and posterior probability for nodes that also occurred in Bayesian 50% majority-rule consensus tree (see Fig. S1) are given along the branches. Accessions identified by compat.py as conflicting are marked with different colour for each group. Major clades are bracketed; clades A–I follow Kurzyna-Mlynik et al. (2008). Outgroup taxa are omitted for simplicity.
Figure 2. Maximum likelihood tree inferred from analyses of combined plastid *rps16* intron, *rpoC1* intron and *rpoB-trnC* intergenic spacer sequence data for Ferulinae. See Figure 1 for details.
Figure 3. Maximum likelihood tree inferred from analyses of combined nrDNA ITS and plastid rps16 intron, rpoC1 intron and rpoB-trnC intergenic spacer sequence data for Ferulinae. Accessions identified as rogue with RogueNaRok algorithm are marked with a star sign. See Figure 1 for details.
striking incongruence and got the same results. Particularly, we confirmed that the three samples of *F. gummosa* with identical nrDNA ITS sequences have different plastid haplotypes that are more closely related to those occurring in other species than to each other. Second, the discordance between plastid DNA and nrDNA was observed for DNA samples processed in two laboratories: in Warsaw and in Tehran (the latter annotated ‘K’ in Table S1). Third, the discrepancies occurred more often in major clades than among them suggesting that they resulted from hybridisation or introgression between closely related species as exemplified by *F. gummosa* and its close relatives.

The evolutionary processes that may result in incongruence among molecular markers are hybridization, introgression, incomplete lineage sorting and homoplastic substitutions, particularly those that have a stabilizing effect on the stem-loop secondary structure in plastid DNA sequences. This incongruence may also result from sampling error of characters or/and taxa (Salichos, Stamatakis & Rokas, 2014). However, the recorded discrepancy is more likely biological than artefactual as exemplified by *F. gummosa*. Possible hybridization and introgression resulting in discrepancy between plastid DNA and nrDNA ITS data have also been reported in several other studies of Apiaceae (Lee & Downie, 2006; Spalik, Downie & Watson, 2009; Zhou et al., 2009; Bone et al., 2011; Yi, Jin & Wen, 2015; Banasiak et al., 2016).

Our results indicate that most intense reticulate evolution occurs among the species constituting clades A, E, G, H, I, K and L in ITS and combined data trees. These species along with members of clades B and C2 form a weakly supported superclade in plastid DNA trees (BS < 50%, PP = 0.99) comprising mostly Irano–Turanian species. Relationships in this superclade in the plastid DNA trees are fundamentally different from those occurring in the nrDNA trees. Conspecific samples more often group in the nrDNA trees than in the plastid DNA trees. The examples include *F. assa-foetida*, *F. szovitsiana* DC., *F. gummosa*, *F. samarkandica* Korovin, *F. hedgeana* Pimenov & Kljuykov etc. Moreover, the number of unique ITS sequences is rather low and several groups of species each have the same ribotype, particularly in clades A, G and H. This suggests that the exceptionally high number of species recognized in the genus is an artefact resulting from hybridization and taxonomic splitting rather than from diversification in the region. Intense reticulate evolution in *Ferula* explains why proposing an unambiguous hierarchical classification system of the genus is almost impossible. Hybridization and introgression blur boundaries among species and confound phylogenetic reconstructions, particularly when distant species exchange genetic material. Newly described species may represent local hybrid swarms, and inadequate sampling, particularly from Central and West Asia, does not allow for a precise delimitation of taxa.

**TOWARDS A NEW CLASSIFICATION SYSTEM**

There is no updated and comprehensive classification system of the genus. The most important regional and worldwide treatments of *Ferula* comprising infrageneric taxa include: (1) a revision for the Flora Orientalis (Boissier, 1872); (2) a synopsis of the genus in Engler and Prantl’s Die natürlichen Pflanzenfamilien (Drude, 1898); (3) the taxonomic monograph of the genus (Korovin, 1947); (4) a regional treatment for Kazakhstan (Safina & Pimenov, 1984). Korovin’s classification system of *Ferula* was adopted with some amendments in subsequent regional revisions for the former Soviet Union (Korovin, 1951), Turkey and the East Aegean islands (Peşmen, 1972) and the Flora Iranica region (Chamberlain & Rechinger, 1987). None of these treatments agrees with molecular phylogenetic trees (Kurzyna-Mlynik et al., 2008; Panahi et al., 2015; this study).

In accordance with our inference of a highly reticulated scenario of evolution in *Ferula*, when proposing a new classification system of the genus, a strict concept of monophyly, particularly in the Irano–Turanian superclade, would be misleading. This superclade is monophyletic in plastid DNA trees and collapses into a polytomy in the ITS and combined trees (Fig. 3). We recognize it as subgenus *Narhex* (Falc.) Drude with eight sections corresponding to clades A, B, E, G, H, I, K and L. In contrast, clades J, D and C1 are supported by both datasets and constitute early-diverging branches in plastid DNA trees. Accordingly, we recognize them as subgenera *Sinoferula*, *Safinia* and *Ferula*. In the latter, we also include clade C2, the affinity of which to C1 is supported by nrDNA and morphology. Below, we discuss these clades in the order from the bottom to the top of the combined tree (Fig. 3).

**Clade J: subgenus Sinoferula**

The monophyly of this small group is supported in all analyses (BS = 100% and PP = 1.0 in combined trees), but it has not hitherto been recognized as a natural taxon. Its included *F. licentiana* Hand.-Mazz., *F. kingdon-wardii* H.Wolff and *F. olivacea* (Diels) H.Wolff ex Hand.-Mazz. that are endemic to China and have one distinctive common feature: they are glabrous throughout, in contrast to all other Chinese congeners that are hispid, pubescent or puberulent at least on the abaxial side of leaves (She & Watson, 2005). Numerous Irano–Turanian congeners also lack indumentum...
(Chamberlain & Rechinger, 1987) but the geographical ranges of these groups do not overlap. The fruits of *F. kingdon-wardii* and *F. olivacea* have prominent dorsal and lateral ribs and single vallecular and two commissural vittae, which are sepalate (Wang et al., 2016). Similar fruits occur in *F. bungeana* Rigat, which was not included in our molecular analyses due to incomplete availability of plastid markers. Based on the nrDNA ITS sequence, this species is allied with clade A. The plant is, however, densely pubescent. Septate vittae also occur in clade C, mostly comprising Mediterranean taxa (Safina & Pimenov, 1990).

**Clade D: subgenus Safinia**

Although three species of clade D were identified by compat.py as introducing topological conflict, these discrepancies concerned within-group relationships and the clade was strongly supported in trees inferred from combined data (BS = 93%, PP = 1.0). It encompasses Central Asian endemics with the notable exception of *F. hezarlalehzarica* Ajani from Iran. Clade D has never been recognized as a separate taxon; however, it is reasonably well corroborated by fruit anatomy. Fruits of *F. equisetacea* Koso-Pol., *F. koso-poljanskyi* Korovin, *F. grigorievii* B.Fedtsch. and *F. decurrens* Korovin are characterized by a subcircular disposition of vittae, a development of a subepidermal layer of the ducts (these may, however, be obsolescent in mature fruits of *F. grigorievii*), and the parenchymatic ribs, hypendocarp and funicle (Safina & Pimenov, 1990). However, this combination of characters is not unique in the genus as *F. lipskyi* Korovin is similar to these species (Safina & Pimenov, 1990; Safina, Ostroumova & Pimenov, 2014). *Ferula lipskyi* was placed in clade A based on ITS sequence only (Kurzyn-Mlynik et al., 2008). Additional sampling from this species is necessary to confirm its distant position from the species of clade D. The similarity of *F. hindukushensis* Kitam. to *F. koso-poljanskyi* was noticed by Chamberlain & Rechinger (1987). When describing *F. hezarlalehzarica* from the Hezar and Lalehzar mountains in Iran, Ajani & Ajani (2008) indicated the two former species as its closest relatives. The name of this subgenus honours botanist Lucia K. Safina for her contribution to the taxonomy of the genus.

**Clade C: subgenus Ferula**

This group includes two distinct subclades, C1 and C2, that have each strong support from posterior probability and bootstrap analyses, but their sister relationship is supported only in nrDNA analyses. Seven species that form clade C1 are mostly Mediterranean, including *F. communis* L., the type species of the genus. This group has long been regarded as natural, although some distantly related taxa were also usually included. *F. assa-foetida* is nevertheless synonymous with *F. narthex* Renet. The Irano–Turanian group includes the type species of several subgeneric names: *Narthex* (Falc.) Drude, *Soranthus* (Ledeb,) Drude, *Dorematoides* (Kauffm.) Drude, *Euryangium* (Koef.) Drude, *Scorodosma* (Koef.) Drude, *Merwia* (B.Fedtsch.) Korovin and *Dorematoides* Korovin. The first four names were published simultaneously by Drude (1898), so none has priority. We therefore select *Narthex* as its type, which is incorrect. Falconer (1847) described *Narthex* as a genus with a single species, *Narthex assa-foetida* (‘assafoetida’), including Linnaean *F. assa-foetida* in synonymy. The type specimen of *F. assa-foetida* is Kaempfer's specimen from Disguun (Chamberlain & Rechinger, 1987). Falconer claimed that his *Narthex assa-foetida* was the true *assafoetida* of Kaempfer. He was, however, mistaken and described a new species. Boissier (1872) renamed this species as *F. narthex* Boiss. suggesting its placement in section *Peucedanoides* Boiss. *Narthex assa-foetida* is nevertheless synonymous with *F. assa-foetida*, not *F. narthex*.
Clade L: section Glaucoselinum (Schischk.) Pimenov
The similarity between the two species in this clade was first noticed by Korovin (1962), who segregated them from Peucedanum L. into Talassia Korovin. Pimenov (1983) transferred them to Ferula and placed them in a separate section but without subgeneric assignment and repeated this treatment in the subsequent revision of the genus for Kazakhstan (Safina & Pimenov, 1984). Because the validity of Korovin’s Talassia was problematic, Pimenov (1983) used a sectional name Glaucoselinum that was first introduced in Peucedanum.

Clade E: section Macrorrhiza Korovin
This group includes five species occurring in the Irano–Turanian region; all species are glabrous (Chamberlain & Rechinger, 1987). Its support in the combined ML analyses was rather weak (BS = 69%), which is not surprising because two inclusive species were placed in significantly distant positions in plastid DNA trees. Three representatives of this clade (F. oopoda (Boiss. & Buhse) Boiss., F. clematidifolia Koso-Pol. and F. varia Trautv.) have been subject to carological studies and have similar mericarp anatomy identified as type VIII (Safina & Pimenov, 1984). However, superficially similar fruits occur in F. korshinskyi Korovin, a member of clade A.

Clade B: section Soranthus
Ferula karelinii Bunge and F. sibirica Willd. form a strongly supported clade in combined analyses (BS = 100%, PP = 1.0). These species were excluded from the genus by Korovin (1947) and recognized in monospecific genera Schumannia Kuntze and Soranthus Ledeb., particularly in the regional treatments for the former Soviet Union and Asia, even in some relatively recent accounts (Schischkin, 1951; Vinogradova, 2004; She et al., 2005). Their fruit morphology and anatomy lies, however, in the diversity range of Ferula (Pimenov & Kirillina, 1980). Both species have fruit type III based on the typology of Safina & Pimenov (1984); these authors placed F. karelinii in section Merwia (B. Fedtsch.) Koso-Pol., comprising species with fruit type II, while retaining F. sibirica in the monotypic section Soranthus.

Clade A: section Peucedanoides
This large clade encompasses species occurring in Central Asia and in the south-western part of the Irano–Turanian region. It includes all species of former Dorema examined for molecular markers (Panahi et al., 2015) and nearly all examined species of subgenera Peucedanoides and Dorematoides that are, however, intermingled. Its monophyly was reasonably well supported in combined analyses (BS = 88%, PP = 1.0), but most internal nodes received BS < 50%. Its two major subclades in the combined tree received no support in ITS and plastid DNA analyses.

Species formerly classified in Dorema have simple umbels that are arranged laterally on a flowering stem, whereas most umbellifers have compound umbels that terminate the growth of the stem. The umbels of species classified by Korovin (1947) in Dorematoides are proliferating: a new umbel grows in place of the central umbellule forming a pseudoverticillate inflorescence and restoring its monopodial growth. This type of inflorescence can be seen as transitory between terminal compound umbels characteristic for most Ferula spp. and lateral simple umbels occurring in former Dorema. Korovin (1939) attributed the name Dorematoides to Regel and Schmalhausen. In fact, this name was introduced by Regel (1878) as group ‘E. Doremoides’ in a key to some Ferula spp. (with letters identifying successive groups) and repeated in a similar context in a subsequent paper (Regel & Schmalhausen, 1878). ‘Doremoides’ included only F. schtschurowskiana Regel & Schmalh. ex Regel (‘F. tschzurosksiana’). The name was unranked and without any authorship in contrast to some formal names listed in these papers. Moreover, in Regel (1878), a parallel group in ‘Sectio II. Asa foetida’ was named ‘D. Juga vittata’, subsequently changed to ‘D. Jugivittatae’ in Regel & Schmalhausen (1878), suggesting that these groups were intended as informal and hence not validly published. Korovin (1947) corrected the name to Dorematoides taking into account the declension of Greek noun dorema, dorematos (‘gift’) and provided a Latin diagnosis. Therefore, he should be regarded as the sole author of the name at the subgeneric rank. Such an interpretation solves the problem of its typification. Vinogradova (2004) lectotypified ‘section Dorematoides Regel & Schmalh.’ with F. caspica M.Bieb. However, neither Regel (1878) nor Regel & Schmalhausen (1878) included F. caspica in group ‘Doremoides’, but indicated F. schtschurovsksiana as its sole element. Korovin (1947) placed six species in subgenus Dorematoides indicating the proliferating umbels as their major feature, which makes these species somewhat similar to Dorema. In molecular analyses, F. schtschurovsksiana was placed in clade G, whereas F. caspica with two other members of subgenus Dorematoides [F. feruloides (Sted.) Korovin and F. dubjanskyi Korovin] were assigned to clade A that also includes former Dorema spp. The choice of F. caspica over F. schtschurovsksiana better preserves the original meaning of Dorematoides sensu Korovin. Since Dorematoides was described by Korovin as a subgenus, the author of the combination at sectional rank is Vinogradova (2004), who published it inadvertently when citing Korovin’s original name with full reference.
Clade K: section Pachycarpa
The core of clade K, _F. gigantea_ B.Fedtsch. and _F. trachyphylla_ Rech.f. & Riedl, was supported in all analyses. In ITS and combined ML analyses, _F. diversivittata_ Regel & Schmalh. joined this group. _Ferula gigantea_ and _F. diversivittata_ were placed by Korovin (1947) in an unranked group (grex) _Pachycarpa_. _Ferula trachyphylla_ was described from Afghanistan and regarded as closely allied to _F. gigantea_ (Chamberlain & Rechinger, 1987), and this is confirmed by molecular data. We designate _F. gigantea_ as the lectotype of _Pachycarpa_ and use this name as the basionym for the sectional combination.

Clade I: section Euryangium (Kauffm.) Pimenov
The support for the monophyly of this group comes exclusively from nrDNA ITS data. Having been transferred to _Ferula_ from _Euryangium_ Kauffm., _F. sumbul_ (Kauffm.) Hook.f. has usually been recognized in a separate subgenus (Drude, 1898), section (Pimenov, 1979) or informal grex (Korovin, 1947) with one or two presumed close relatives, the affinity of which has not been confirmed by molecular data. The fruit anatomy of _F. sumbul_ is distinct (Safina & Pimenov, 1983); however, the other species from this clade have not yet been examined for fruit anatomical characters.

Clade G: section Scorodosma (Bunge) Boiss
Molecular data place 18 Central Asian and Iranian species in this clade. Although its monophyly is strongly supported in ITS and combined analyses (BS = 91%, PP = 1.0), the relationships among included species are poorly resolved. Many terminals were identified by compat.py as introducing topological conflict, and in the plastid DNA trees, they were intermingled with some members of clade H. Conspecific samples of _F. hedgeana_ and _F. samarkandica_ grouped only in ITS analyses, whereas they were intermingled with other species in plastid and combined analyses. This clade includes _F. foetida_ (Bunge) Regel, which had been regarded by Korovin (1947) and Chamberlain & Rechinger (1987) as having an isolated position in the genus and constituting a monospecific subgenus _Scorodosma_ (Bunge) Drude. However, Safina & Pimenov (1984) suggested that its relatives include _F. iliensis_ Krasn. ex Korovin and _F. tetricrma_ Kar. & Kir., the affinity of which is confirmed by our analyses.

Clade H: section Merwia
Species placed in clade H occur in the south-western part of the Irano–Turanian floristic region. Our results suggest that this group is subject to intense reticulate evolution blurring the boundaries among species. This is particularly troublesome because this group comprises several economically important species including _F. assa-foetida_ and _F. gummosa_.

The identity of _F. assa-foetida_ is contentious. A possible source of confusion is that the exudate asafetida is harvested from several _Ferula_ spp., not only representatives of clade H, e.g. _F. alliacea_ Boiss., _F. persica_ Willd. and _F. narthex_, but also distant relatives including _F. foetida_ (Drude, 1898; Korovin, 1959). Linnaean _F. assa-foetida_ was based on material collected by Kaempfer. Chamberlain & Rechinger (1987) compared the plate in Kaempfer (1712) and the type specimen in the Sloane herbarium at BM with the available herbarium material and identified only two gatherings that are conspecific with the type. One of these is Davis & Bokhari D.56275; this specimen was also used in our molecular studies (Number 0359). In nrDNA trees, it was placed close to _F. pseudalliacea_ Rech.f., in agreement with Chamberlain & Rechinger (1987), who regarded _F. assa-foetida_ and _F. pseudalliacea_ as closely allied and possibly conspecific. Three other samples of _F. assa-foetida_ grouped with _F. alliacea_, _F. gabrielii_ and other species harvested for asafetida (Chamberlain & Rechinger, 1987).

The examined molecular markers provide conflicting results concerning the affinities of _F. gummosa_, a source of valuable galbanum. This oleo-gum-resin is subject to adulteration as the demand is higher than its production in Iran (Betti et al., 2010). Presumed adulterants include _F. assa-foetida_ and _F. ammoniacum_ (D.Don) Spalik et al. (Thomsen et al., 2004). Therefore, a clear circumscription of _F. gummosa_ is also of considerable economic importance. In our analyses, all samples of _F. gummosa_ have the same ITS sequence, which is also identical to those of _F. badrakema_ Kosopol., _F. linczevskii_ Korovin, _F. undulata_ Pimenov & J.V.Baranova, and _F. myrioloba_ Rech.f. In the plastid DNA tree, however, the representatives of _F. gummosa_ were placed in three distant clades, sometimes with their companions from the ITS tree. These results suggest that interspecific boundaries in this group are unclear; therefore, presumed adulterants as assessed through phytochemical studies may reflect a hybrid origin of harvested populations. Chamberlain & Rechinger (1987) suggested a close proximity of _F. gummosa_, _F. myrioloba_ and _F. badrakema_, which is confirmed by molecular trees. Pimenov & Kljuykov (1996) synonymized _F. badrakema_ under _F. gummosa_ and also reinstated _F. galbaniflua_ Boiss. & Buhse in this group. Chamberlain & Rechinger (1987) regarded _F. latisepta_ Rech.f. & Aellen and _F. undulata_ as closely related if not conspecific, also in agreement with molecular data. However, they placed _F. latisepta_ and _F. gummosa_ in separate infrageneric divisions.
CONCLUSIONS

The main aim of our study, to divide Ferula into smaller, monophyletic and workable units that may be subject to partial revisions, has only partly been accomplished. Although subgenera Sinoferula, Safinia and Ferula seem to be natural units, the most species-rich subgenus Narthex is difficult to resolve, possibly due to reticulate evolution blurring boundaries among species and sections. Our study suggests that multigene approach will be necessary to elucidate hybridization patterns and circumscribe species in this economically important genus.

TAXONOMIC TREATMENT

Ferula L., Sp. Pl. 1: 246. 1753.

Lectotype: Ferula communis L. (Hitchcock & Green, 1929: 140).

Subgenus Sinoferula Spalik, Puchałka & M. Panahi, subgen. nov.

Diagnosis: Plants entirely glabrous, endemic to China.

Etymology: from sino-, ‘Chinese’, and Ferula.

Type: Ferula kingdon-wardii H.Wolff.

Species included: F. kingdon-wardii H.Wolff, F. licentiana Hand.-Mazz., F. olivacea (Diels) H.Wolff ex Hand.-Mazz.

Subgenus Safinia Spalik, M. Panahi & Puchałka, subgen. nov.

Diagnosis: Subepidermal layer of secretory ducts well developed in mericarp including marginal ribs (wings); ribs, hypendocarp and funicle parenchymatic.

Etymology: dedicated to Lucia K. Safina to acknowledge her contribution to the taxonomy of Ferula.

Type: Ferula equisetacea Koso-Pol.

Species included: F. decurrens Korovin, F. equisetacea Koso-Pol., F. grigorievii B. Fedtsch., F. hezarlalhezarica Ajani, F. hindukshensis Kitam., F. koso-poljanskyi Korovin.

Subgenus Ferula

Section Ferula

= section Anatriches Korovin, Ill. Monogr. Ferula 9. 1947; lectotype (designated here): Ferula communis L.

Species included: F. communis L., F. glauca L., F. linkii Webb, F. loscosii (Lange) Willk., F. marmarica Asch. & Taub. ex Asch. & Schweif., F. sinaica Boiss., F. tingitana L.

Section Stenocarpa Puchałka & Spalik, sect. nov.

Diagnosis: Fruit c. 4–9 mm long (as opposed to 8–18 mm in section Ferula). Irano–Turanian.

Etymology: from the specific epithet of its type.

Type: Ferula stenocarpa Boiss. & Hausskn. ex Boiss.

Species included: F. coskunii H.Duman & Sağiroğlu, F. mervynii Sağiroğlu & H.Duman, F. stenocarpa Boiss. & Hausskn. ex Boiss.

Subgenus Narthex (Falc.) Drude in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 229. 1898.

Type: Narthex assa-foetida (L.) Falc. (= F. assa-foetida L.).
= subgenus Merwia (B. Fedtsch.) Korovin, Ill. Monogr. Ferula 8. 1947. Type: Merwia androssowii B. Fedtsch. (= F. litvinoviana Koso-Pol.).
= subgenus Scorodosma (Bunge) Drude in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 230. 1898. Type: Scorodosma foetidum Bunge (= F. foetida (Bunge) Regel).
= subgenus Soranthus (Lede.) Drude in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 230. 1898. Type: Soranthus meyeri Lede. (= F. sibirica Willd.).
= subgenus Peucedanoides (Boiss.) Korovin, Ill. Monogr. Ferula 9. 1947. Lectotype: Ferula orientalis L. (Vinogradova, 2004).
= subgenus Dorematoïdes Korovin Ill. Monogr. Ferula 10. 1947. Lectotype: Ferula caspica M.Bieb. (Vinogradova, 2004).
= subgenus Euryangium (Kauffm.) Drude in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 230. 1898. Type: Euryangium sambul Kauffm. (= F. sambul (Kauffm.) Hook.f.).

Section Glaucoselinum (Schischk.) Pimenov, Biol. Nauki 12: 77. 1983.

Type: Peucedanum transiliense Herder (= F. transiliensis (Herder) Pimenov).

Species included: F. renardii (Regel & Schmalh.) Pimenov, F. transiliensis (Herder) Pimenov.

Section Macorrhiza Korovin, Ill. Monogr. Ferula 10. 1947.

Lectotype (designated here): Ferula oopoda (Boiss. & Buhse) Boiss.
Species included: F. clematidifolia Koso-Pol., F. glabra Rech.f. & Riedl, F. oopoda (Boiss. & Buhse) Boiss., F. tabasensis Rech.f., F. varia Trautv.

Section Soranthus (Ledeb.) Pimenov in Safina & Pimenov, Feruly Kazakhstana 37. 1984.

Type: Soranthus meyeri Ledeb. (= F. sibirica Willd.).

Species included: F. karataviensis Bunge, F. sibirica Willd.

Section Peucedanoides Boiss., Fl. Or. 2: 983. 1872.

Lectotype: Ferula orientalis L. (Vinogradova, 2004)
≡ section Xeronarthex Korovin, Ill. Monogr. Ferula 9. 1947. Lectotype (designated here): Ferula orientalis L.
≡ section Dorematoideae (Korovin) V.M.Vinogr. in Travelev, Fl. Vostochnoĭ Evropy 11: 389. 2004. Lectotype: Ferula caspica M.Bieb. (Vinogradova, 2004).

Species included: F. akhtschakensis B.Fedtsch. ex Koso-Pol., F. ammoniacum (D.Don) Spalik & al., F. angreni Korovin, F. aucteri (Boiss.) Piwczynski & al., F. canescens (Ledeb.) Ledeb., F. caspica M.Bieb., F. ceratophylla Regel & Schmalh., F. czatkalensis Pimenov, F. dissecta (Ledeb.) Ledeb., F. downieorum Spalik & al., F. dshizakensis Korovin, F. dubhanskyi Korovin, F. fedoroviorum Pimenov, F. ferganensis Lipsky ex Korovin, F. feruloides (Steud.) Ledeb., F. glabriofila M.Panahi & al., F. gracilis (Ledeb.) Ledeb., F. gypsacea Korovin, F. haussknechtii H.Wolff ex Rech.f., F. hyrcana (Koso-Pol.) Puchalka & al., F. karatavica Regel & Schmalh., F. karatavisci (Regel & Schmalh.) Korovin ex Pavlov, F. karateginia Lipsky ex Korovin, F. kashanica Rech.f., F. kirialovii Pimenov, F. kopetdaghensis Korovin, F. korshinskyi Korovin, F. kryzyumka Korovin, F. lapidosus Korovin, F. leucogrova Korovin, F. macrocolea Boiss., F. michaelii M.Panahi & al., F. microcolea (Boiss.) Boiss., F. nuda Spreng., F. olgae Regel & Schmalh., F. orientalis L., F. ovina (Boiss.) Boiss., F. pallida Korovin, F. penninervis Regel & Schmalh., F. potanini Korovin ex Pavlov, F. rigida Fisch. ex DC., F. rubroarenosa Korovin, F. serovschanica Pimenov & J.V.Baranova, F. serovicosa Rech.f., F. songarica Pall. ex Schult., F. syreitschikowii Koso-Pol., F. tatarica Fisch. ex Spreng., F. tschimganica Lipsky ex Korovin, F. ugamica Korovin ex Baranov, F. xylorhachis Rech.f.

Section Pachycarpa (Korovin) Banasiak, M.Panahi & Spalik, comb. & stat. nov.
Basionym: Ferula grex Pachycarpa Korovin, Ill. Monogr. Ferula 8. 1947.

Lectotype (designated here): Ferula gigantea B.Fedtsch.

Species included: F. diversivittata Regel & Schmalh., F. gigantea B.Fedtsch., F. trachyphylla Rech.f. & Riedl.

Section Euryangium (Kaufm.) Pimenov, Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol 84: 107. 1979.

Type: Euryangium sumbul Kaufm. (= F. sumbul (Kaufm.) Hook.f.).

Species included: F. fedtschenkoana Koso-Pol., F. nuratavica Pimenov, F. sumbul (Kaufm.) Hook.f.

Section Scorodomas (Bunge) Boiss., Fl. Or. 2: 983. 1872.

Type: Scorodomas foetidum Bunge (= F. foetida (Bunge) Regel).
≡ section Palaeoarcthe x Korovin, Ill. Monogr. Ferula 9. 1947. Lectotype: Ferula foetidissima Regel & Schmalh. (Pimenov & Baranova, 1979).
≡ section Phyllites Korovin, Ill. Monogr. Ferula 9. 1947. Lectotype (designated here): Ferula kokanica Regel & Schmalh.
≡ section Saprosmia Korovin, Ill. Monogr. Ferula 8. 1947. Lectotype (designated here): Ferula kelifi Korovin.

Species included: F. botschantzevii Korovin, F. costata Korovin ex Nasir, F. eugeniai Kamelin, F. foetida (Bunge) Regel, F. foetidissima Regel & Schmalh., F. hedgeana Pimenov & Klukov, F. ileniss Krasn. ex Korovin, F. inciso-serrata Pimenov & J.V.Baranova, F. kelifi Korovin, F. kelleri Koso-Pol., F. kokanica Regel & Schmalh., F. mogoltavica Lipsky ex Korovin, F. nevskii Korovin, F. samarhakiana Korovin, F. schtschurovskiana Regel & Schmalh. ex Regel, F. tetterrima Kar. & Kir., F. violacea Korovin.

Section Merwia (B. Fedtsch.) Koso-Pol., Byull. Obshch. Estetovisp. Voronezhsk. Gosud. Univ. 1: 38. 1925.

Type: Merwia androssowii B. Fedtsch. (= F. litwinowiana Koso-Pol.).
≡ section Discicarpa Korovin, Ill. Monogr. Ferula 8. 1947. Lectotype (designated here): Ferula litwinowiana Koso-Pol.
≡ section Neonarthex Korovin, Ill. Monogr. Ferula 9. 1947. Lectotype (designated here): Ferula galbaniflua Boiss. & Buhse (= F. gummosa Boiss.)
≡ section Phacocarpa Korovin, Ill. Monogr. Ferula 8. 1947. Lectotype (designated here): Ferula lehmannii Boiss.

Species included: F. alliacea Boiss., F. assa-foetida L., F. badrakama Koso-Pol., F. behboudiana (Rech.f. & Esfand.) D.F.Chamb., F. blanchei Boiss., F. flabelliloba Rech.f. & Aellen, F. gabrielii Rech.f., F. gummosa Boiss., F. hirtella Boiss., F. karakalensis Korovin, F. latisecta
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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

Figure S1. Bayesian majority-rule consensus tree inferred from analyses of nrDNA ITS sequence data of Ferulinae. Groups of accessions with identical sequences were represented in the analyses by single terminals and then resolved to polytomies with zero-length branches. Posterior probabilities are given along the branches. Accessions identified by compat.py as conflicting are marked with a different colour for each group. Major clades are bracketed; clades A–I follow Kurzyna-Młynik et al. (2008). Outgroup taxa are omitted for simplicity.

Figure S2. Bayesian majority-rule consensus tree inferred from analyses of combined plastid rps16 intron, rpoC1 intron and rpoB-trnC intergenic spacer sequence data of Ferulinae. See Figure S1 for details.

Figure S3. Comparison of topologies of maximum likelihood trees inferred from nrDNA ITS data (left) and concatenated plastid DNA data (right). See Figures 1 and 2 for details.

Figure S4. Bayesian majority-rule consensus tree inferred from analyses of combined nrDNA ITS and plastid rps16 intron, rpoC1 intron and rpoB-trnC intergenic spacer sequence data for Ferulinae. See Figure S1 for details.

Figure S5. Maximum likelihood tree inferred from analyses of combined nrDNA ITS and plastid rps16 intron, rpoC1 intron and rpoB-trnC intergenic spacer sequence data for Ferulinae with the exclusion of 41 accessions indicated by compat.py as introducing topological conflict. Groups of accessions with identical sequences were represented in the analyses by single terminals and then resolved to polytomy with zero-length branches. Bootstrap support and posterior probability for nodes that also occurred in Bayesian majority-rule consensus tree are given along the branches.

Table S1. Representatives of Scandiceae subtribe Ferulinae and outgroups examined in this study with respective GenBank reference numbers. Collector’s data in bold face indicate the type specimens of respective species. Newly obtained sequences are identified with an asterisk behind the reference number.