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ORIGINAL ARTICLE

Systematics of the Iranian genera *Aphanopleura*, *Demavendia*, *Haussknechtia*, *Psammogeton*, and *Zeravschania* (Apiaceae tribe Pimpinelleae)

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Abstract

Previous molecular phylogenetic investigations of Apiaceae tribe Pimpinelleae have focused primarily on its largest genus *Pimpinella* and its closest allies. The monophyly and phylogenetic placements of five Iranian genera of the tribe have not been addressed sufficiently (*Aphanopleura*, *Demavendia*, *Haussknechtia*, *Psammogeton*, and *Zeravschania*). To examine relationships, a nrDNA ITS matrix including 169 accessions representing 49 genera of Apiaceae (including 10 Iranian taxa not analyzed previously) and a cpDNA *rps*16 matrix containing 37 accessions representing 24 genera of the family, representing the greatest sampling to date of the aforementioned genera, were subjected to phylogenetic analyses using Bayesian inference and maximum parsimony methods. The trees obtained showed a close affinity among the examined species of *Aphanopleura*, *Psammogeton* and several species of *Trachyspermum*. Neither *Aphanopleura* nor *Psammogeton* resolved as monophyletic, and *A. leptoclada* allied with *Pimpinella*. The genera *Demavendia*, *Haussknechtia* and *Zeravschania* also comprised a well-supported clade, with *Demavendia* and *Haussknechtia* (in the ITS trees) arising from within a paraphyletic *Zeravschania*. To recognize monophyletic genera, one new combination is proposed in *Pimpinella* and six new combinations are proposed in *Psammogeton*. A broader circumscription of *Zeravschania* to include *Demavendia* and *Haussknechtia* may also be warranted, but must await further study.

Keywords Apioideae · Systematics · *Trachyspermum* · Umbelliferae

Introduction

Tribe Pimpinelleae Spreng. includes the genera *Aphanopleura* Boiss., *Arafoe* Pimenov & Lavrova, *Bubon* L., *Demavendia* Pimenov, *Frommia* H.Wolff, *Haussknechtia* Boiss., *Nothosmyrnium* Miq., *Phellolophium* Baker, *Pimpinella* L., *Psammogeton* Edgew., and *Zeravschania* Korovin (Downie et al. 2010). It also includes segregates from other genera, such as *Cryptotaenia africana* Drude, *Physospermopsis cuneata* H.Wolff, and two species of *Trachyspermum* Link (*T. scaberulum* (Franch.) H.Wolff and *T. triradiatum* H.Wolff; Downie et al. 2010). Six genera of Pimpinelleae occur in Iran (*Aphanopleura*, *Demavendia*, *Haussknechtia*, *Pimpinella*, *Psammogeton,* and *Zeravschania*), of which only *Demavendia* and *Haussknechtia* are endemic (Hedge et al. 1987; Mozaffarian 2007; Mousavi et al. 2021). The members of Pimpinelleae in Iran are morphologically diverse and cannot be identified easily, although most species have small fruits (shorter than 5 mm) covered by glochidiate hairs (except in *Demavendia* and *Zeravschania* where the fruits are glabrous). Representatives of the tribe have been included in several molecular phylogenetic studies using nuclear ribosomal DNA internal transcribed spacer (nrDNA ITS) sequences (Downie et al. 2000a, b, 2001; Valiejo-Roman et al. 2006; Spalik and Downie 2007; Ajani

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et al. 2008; Zhou et al. 2008; Downie et al. 2010; Magee et al. 2010; Wang et al. 2014; Fernández Prieto et al. 2018; Mousavi et al. 2021). However, in all of these studies, several Iranian genera were incompletely sampled and the available results do not support the monophyly of four genera in their current circumscriptions: *Aphanopleura* (Fig. 1a–b), *Pimpinella*, *Psammogeton* (Fig. 1f–g), and *Zeravschania* (Fig. 1l–o).

Pimpinella is the largest genus of the tribe, includes about 150 species, and is taxonomically the most challenging. The genus is widely distributed in the Old World through Europe, Africa, and Asia, with the majority of species (ca. 125 spp.) occurring in Asia (Wolff 1921; Pimenov and Leonov 1993, 2004; Pu and Watson 2005). Members of the genus are characterized by cordate-ovoid or oblong-ovoid leaves and laterally compressed mericarps constricted at their commissures, each bearing five filiform ribs (Pu and Watson 2005). *Pimpinella* sensu lato (s.l.) is highly polyphyletic, with its members assigned to no less than seven tribes and other major clades within Apiaceae (Downie et al. 2010; Wang et al. 2014; Fernández Prieto et al. 2018). Nineteen species of *Pimpinella* occur in Iran, of which six (*P. tragioides* Boiss., *P. deverroides* Boiss., *P. pastinacifolia* H.Wolff, *P. khorasanica* Engstrand, *P. anisactis* Rech.f. and *P. khayyamii* Mozaff.) are endemic (Hedge et al. 1987; Mozaffarian 2007; Khajepiri

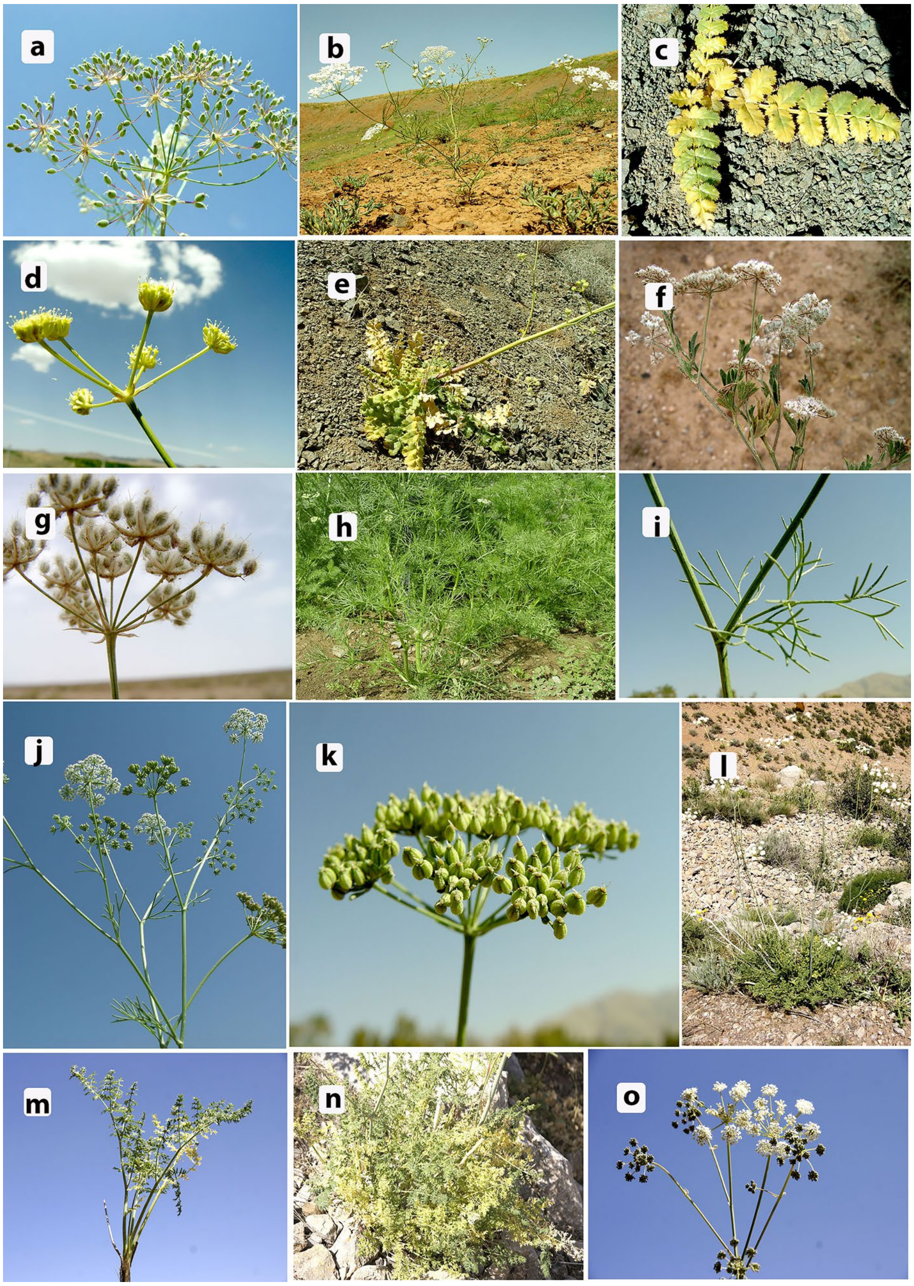

Fig. 1 Representative species of Iranian genera of tribe Pimpinelleae under study in their natural habitats. **a**, **b**, *Aphanopleura trachysperma*; **c**–**e**, *Demavendia pastinacifolia*; **f**, **g**, *Psammogeton canescens*; **h**–**k**, *Trachyspermum copticum*; and **l**–**o**, *Zeravschania aucheri*. All images by V.M.

et al. 2010). The relationships among many of these SW Asian *Pimpinella* species have been reported previously (Tabanca et al. 2005; Fereidounfar et al. 2016; Khajepiri et al. 2010). Fruit anatomical studies of Iranian *Pimpinella* confirmed differences between *P. anthriscoides* Boiss. and other species of *Pimpinella* and resulted in the placement of this species into the new genus *Pseudopimpinella* F.Ghahrem., Khajepiri & Mozaff. [*as Pseudopimpinella anthriscoides* (Boiss.) F.Ghahrem., Khajepiri & Mozaff.; Khajepiri et al. 2010]. *Pimpinella anthriscoides* has been transferred to the genus *Aegopodium* L. as *A. tribracteolatum* Schmalh. and *P. anthriscoides* var. *cruciata* (Bornm. & H.Wolff) V.A.Matthew has been transferred to *Tamamschjanella* Pimenov & Kljuykov as *T. cruciata* (Bornm. & H.Wolff) Pimenov & Zakharova (Zakharova et al. 2012). The monotypic Iranian genus *Opsicarpium* Mozaff. and the polytypic genus *Reutera* Boiss. have been merged recently with *Pimpinella* (Fereidounfar et al. 2016).

Aphanopleura and *Psammogeton* each include five species distributed mainly in the Iranian highlands (Hedge et al. 1987). They are morphologically similar, being small annual plants having white petals and laterally compressed mericarps covered by trichomes (Hedge et al. 1987). *Demavendia* is a monotypic genus [*D. pastinacifolia* (Boiss. & Hausskn.) Pimenov] endemic to Iran and Turkmenistan. *Zeravschania* includes nine species distributed in Iran, eastern Turkmenistan, Afghanistan, and Pakistan (Hedge et al. 1987; Mozaffarian 2007; Pimenov et al. 2007). *Demavendia* and *Zeravschania* possess similar membranous bracts and bracteoles and differ by their leaf shape (Hedge et al. 1987). *Haussknechtia* is a monotypic genus (*H. elymaitica* Boiss.) characterized by globose ultimate umbels (Hedge et al. 1987; Mozaffarian 2007). The Iranian genera *Aphanopleura*, *Demavendia* (Fig. 1c–e), *Haussknechtia*, *Psammogeton*, and *Zeravschania* have heretofore been poorly investigated phylogenetically. Previous phylogenetic studies suggested the non-monophyly of *Aphanopleura*, *Psammogeton*, and *Zeravschania*, and revealed the placement of these taxa along with *Demavendia* and *Haussknechtia* (and the Asian genus *Nothosmyrnium* Miq.) as basal branching lineages within the tribe (Spalik and Downie 2007; Wang et al. 2014; Fernández Prieto et al. 2018).

The main aim of this study is to investigate the monophyly and phylogenetic placements of the Iranian genera assigned to tribe Pimpinelleae, particularly those constituting the most basal branching lineages within the tribe that were underrepresented in previous molecular phylogenetic analyses (i.e., *Aphanopleura*, *Demavendia*, *Haussknechtia*, *Psammogeton*, and *Zeravschania*). We also highlight the morphological characters supporting each of the resolved clades containing these taxa.

Materials and methods

Sampling strategy and marker selection

We included all genera but one previously assigned to tribe Pimpinelleae and many species from throughout the entire range of each genus. The genus *Bubon*, reinstated with the single species *B. macedonicum* L. and separated from *Athamanta* L. in tribe Scandiceae by Spalik et al. (2001), could not be included because material was unavailable. We included representatives from most tribes and other major clades of Apiaceae subfamily Apioideae (Downie et al. 2010) and rooted all trees with *Sanicula epipactis* E.H.L. Krause (subfamily Saniculoideae). The nrDNA ITS region, comprising ITS1, 5.8S rDNA, and ITS2, and the plastid *rps*16 intron were selected as markers for phylogenetic analyses. These markers were suggested as effective and informative for tribal- and generic-level assignments in Apiaceae (Downie et al. 2010). We newly generated the sequences of 10 taxa for ITS and nine taxa for *rps*16 from the following Iranian species: *Aphanopleura breviseta* (Boiss.) Heywood & Jury, *A. leptoclada* Lipsky, *A. trachysperma* Boiss., *Demavendia pastinacifolia* (Boiss. & Hausskn.) Pimenov, *Opopanax armeniacus* Bordz., *Psammogeton stocksii* (Boiss.) Nasir, *Trachyspermum ammi* (L.) Sprague, *T. copticum* (L.) Link, *Zeravschania membranacea* (Boiss.) Pimenov, and *Z. pauciradiata* (Tamamsch.) Pimenov. We did not have access to material of *Aphanopleura zangelanica* Gogina & Matsenko because it is not distributed in Iran. We downloaded all available ITS and *rps*16 intron sequences of Pimpinelleae from GenBank and created a data matrix for each marker. The final nrDNA ITS data set included 169 accessions representing 49 genera (including the aforementioned 10 species not analyzed previously) and the cpDNA *rps*16 data set included 37 accessions representing 24 genera. The number of included taxa in the *rps*16 data set was considerably smaller than that of ITS due to failed PCR or sequencing efforts for the *rps*16 region and the preponderance of ITS sequences available in GenBank. The accessions included in this study, including voucher information for the newly generated sequences, are presented in Appendix. A list of all new combinations proposed in this study is presented in Table 2.

DNA extractions, PCR amplifications, and sequencing

Total genomic DNA was extracted from dried leaves removed from herbarium sheets held in the herbarium of the Research Institute of Forests and Rangelands, Tehran

(TARI) using a NucleoSpin Plant DNA Extraction kit (Macherey–Nagel, Düren, Germany) according to the manufacturer's protocol. For PCR-amplification of the nrDNA ITS region, we used primer pairs ITS4 and ITS5 (White et al. 1990). The cpDNA *rps*16 intron region was amplified using primer pairs rpsF and rpsR3R (Oxelman et al. 1997; Petri and Oxelman 2011; Kool et al. 2012). PCR amplifications were performed in T-Personal 48 (Biometra, Göttingen, Germany), Primus 96 plus (MWG: Biotech, Ebersberg, Germany), or 2720 (Applied Biosystems, Carlsbad, California, U.S.A.) thermocyclers. Cycle sequencing was performed using the BigDye Terminator v.3.1 Cycle Sequencing kit (Applied Biosystems). PCR products were sequenced bi-directionally using an ABI 3730 DNA Analyzer 48-well capillary sequencer (Applied Biosystems).

Alignment and phylogenetic analyses

The sequences were aligned using default parameters in Mafft v.7 (Katoh and Standley 2013), and alignment errors were corrected using Mesquite 2.75 (Maddison and Maddison 2011). Bayesian inference (BI) and maximum parsimony (MP) analyses were done for each data set on the CIPRES server (Miller et al. 2010). Before running the BI analysis, the optimal substitution models were estimated using the Akaike information criterion (AIC) in jModelTest v.0.1.1 (Posada 2008). The general time reversible model of nucleotide substitution with gamma-shaped rate variation and a proportion of invariable sites (GTR + I + G) was the estimated best-fit model for ITS and GTR + G was the estimated best-fit model for *rps*16. For BI, we used MrBayes v.3.2.6 (Ronquist and Huelsenbeck 2003) with 20 million generations for each data set. Trees were sampled every 1000 generations with the default of three "heated" and one "cold" chain. According to the results obtained from Tracer v.1.7.1 (Rambaut et al. 2018), the burn-in values were 10% and 13% for ITS and *rps*16 datasets, respectively. The effective sample sizes (ESS) were 438.3 and 271.8 for ITS and *rps*16 datasets, respectively. The obtained trees from each data set were summarized using a 50% majority-rule consensus tree. Bayesian posterior probability (PP) values were presented on the trees. For MP, we used PAUP* v.4.0b10 (Swofford 2003). Characters were equally weighted, the heuristic search was set with random sequence addition, tree-bisection-reconnection branch swapping, 50 random addition sequence replicates, and the maxtree option set to 20,000. The obtained trees were summarized using a strict consensus tree. Bootstrap (BS) values were calculated using heuristic searches with the bootstrap nreps set at 5,000. Additional details describing the alignment and phylogenetic strategies and analyses used are presented in Mousavi et al. (2021).

Results

A summary of alignment characteristics and parsimony statistics for the ITS and *rps*16 data sets is presented in Table 1. The ITS matrix had over 2.5 times as many parsimony-informative characters as did the *rps*16 intron matrix. We present only the trees obtained from BI analyses of these data sets. Though the number of accessions differed considerably between these two data sets, their results were largely congruent in revealing the groupings of the Iranian genera under study, their non-monophyly, and the placement of *A. leptoclada* in a clade within *Pimpinella saxifraga* L., the nomenclatural type of *Pimpinella*. The ITS and *rps*16 alignments are available in the Online Resources 1, 2.

Although the tribe Pimpinelleae comprised a highly supported, monophyletic group in the ITS phylogeny (PP = 1, BS = 98, Clades A-F, Fig. 2), it was not resolved as monophyletic in the *rps*16 trees (Fig. 3). In both sets of trees, several clades can be recognized in Pimpinelleae. The Iranian species of *Pimpinella* fell within the *Pimpinella* core group (i.e., Clades E and F). In the ITS trees, Clade A had strong support (PP = 1, BS = 98) and included members of *Aphanopleura*, *Nothosmyrnium*, *Psammogeton*, and *Trachyspermum*. Neither *Aphanopleura, Psammogeton*, nor *Trachyspermum* resolved as monophyletic. Clade B contained representatives of the Iranian genera *Demavendia*, *Haussknechtia,* and *Zeravschania*. *Demavendia* and *Haussknechtia* comprised monophyletic sister groups, with this clade arising from within a paraphyletic *Zeravschania*. The single accession of *A. leptoclada* allied weakly with *Pimpinella procumbens* H.Wolff in Clade F. Clades C-F comprised *Pimpinella* species already attributable to tribe Pimpinelleae in previous studies, plus all examined accessions of *Physospermopsis* H.Wolff, the Afro-Malagasian members of the genera *Frommia, Phellolophium* and *Cryptotaenia* DC., and *Arafoe*. *Pimpinella saxifraga*, the type of the genus, occurred in Clade F. Twelve additional species of *Pimpinella* (14 accessions) fell outside of tribe Pimpinelleae, none of which occur in Iran.

Table 1 Alignment characteristics and parsimony statistics for the ITS and *rps*16 data sets used in this study

Markers	*rps*16	ITS
Number of terminals	37	169
Sequence length [bp]	709–876	216–610
Aligned length [bp]	1050	720
Constant characters [bp]	788	213
Parsimony-uninformative characters [bp]	113	117
Parsimony-informative characters [bp]	149	390
Parsimony-informative characters [%]	14.1	54.1

Fig. 2 Majority-rule consensus tree inferred from Bayesian Inference analysis of nrDNA ITS sequences. Numbers above the branches indicate posterior probability values; those below branches indicate MP bootstrap values for similar clades occurring in the MP strict consensus tree. The major clades recognized in tribe Pimpinelleae (Clades A-F) comprise a monophyletic group. The relationships of those accessions indicated in red are those highlighted in the present study

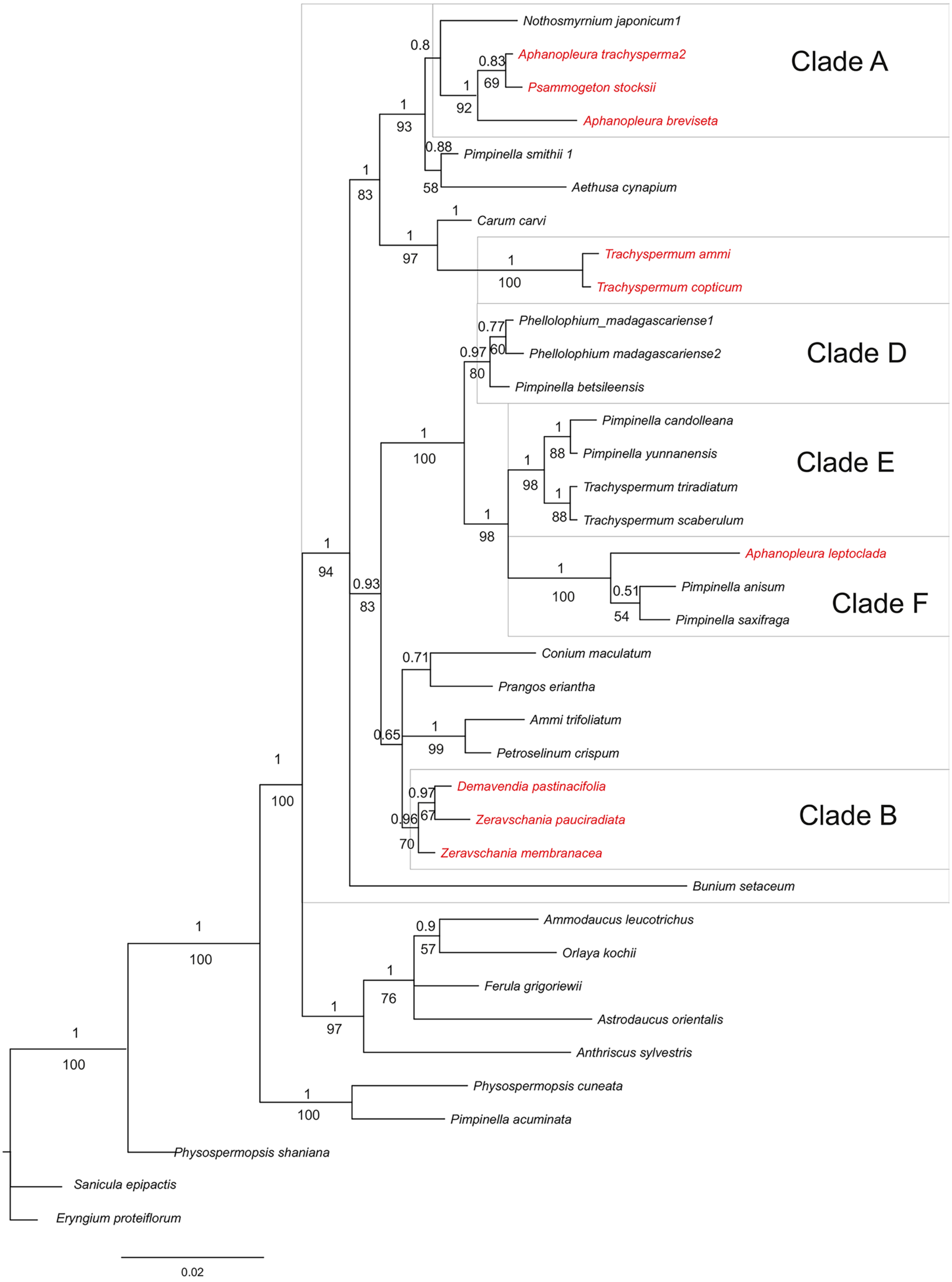

Fig. 3 Majority-rule consensus tree inferred from Bayesian Inference analysis of plastid *rps*16 sequences. Numbers above the branches indicate posterior probability values; those below branches indicate MP bootstrap values for similar clades occurring in the MP strict consensus tree. Tribe Pimpinelleae (Clades A-B and D-F; the same as those presented in Fig. 2) does not comprise a monophyletic group, as members of tribe Pyramidoptereae (incl. *Trachyspermum copticum*) and several other members of tribes Apieae, Careae, and Selineae and the *Cachrys* and *Conium* clades occur within

In the *rps*16 trees, the placements of the Iranian genera were similar, with *Psammogeton stocksii* arising from within a paraphyletic *Aphanopleura* and this clade sister group to *Nothosmyrnium* (Clade A) and *Demavendia* arising from within a paraphyletic *Zeravschania* (Clade B). *Aphanopleura leptoclada* was sister to the clade of *Pimpinella anisum* L. + *P. saxifraga*.

Discussion

Though *Pimpinella* is a polyphyletic genus, with its species occurring in at least seven different tribes and other major clades of subfamily Apioideae (Downie et al. 2010; Wang et al. 2014; Fernández Prieto et al. 2018), the Iranian species of *Pimpinella* examined herein all fall in the same well-supported group as *P. saxifraga*, the type of the genus. This group reflects the core *Pimpinella* group (Fernández Prieto et al. 2018) and is reflected in the current study by Clades E and F. The Iranian genera *Aphanopleura*, *Demavendia*, *Haussknechtia*, *Psammogeton*, and *Zeravschania*, along with *Nothosmyrnium* and several species of *Trachyspermum*, constitute basally branching lineages of tribe Pimpinelleae in the ITS trees (Clades A and B). Based on the phylogenetic results obtained herein, we recircumscribe *Psammogeton* to include six new combinations and transfer *Aphanopleura leptoclada* to *Pimpinella* (Table 2). We also highlight the morphological characters supporting each of the resolved clades containing these taxa.

Aphanopleura and *Psammogeton*

Aphanopleura is a genus of five species (*A. breviseta*, *A. capillifolia* Lipsky, *A. leptoclada* Lipsky, *A. trachysperma*, and *A. zangelanica*). *Aphanopleura zangelanica* was not included in our study. These species are distributed in Central and SW Asia, sometimes reaching China (2 spp.), but mostly they occur in Iran, Afghanistan, Turkmenistan, and Caucasus (Hedge et al. 1987). The plants are characterized by an annual life form, small and thin stems, ternate (3-segmented) leaves, the presence of bracts and bracteoles, a clearly dentate calyx, white to red petals, and mericarps ovate or almost circular, laterally compressed, and covered by papillate, clavate or capitellate trichomes. Previous molecular phylogenetic investigations of *Aphanopleura* only clarified its placement in Pimpinelleae, not its interspecific relationships (Spalik and Downie 2007; Zhou et al. 2008; Downie et al. 2010; Wang et al. 2014; Fernández Prieto et al. 2018). According to our results, *Aphanopleura* is a polyphyletic genus, with most of its species nested within Clade A. The type of genus, *A. trachysperma*, presents a sister group relationship with *Nothosmyrnium japonicum* Miq., while the other species of *Aphanopleura* within this clade assemble with *Trachyspermum* or *Psammogeton*. *Aphanopleura leptoclada* is nested within Clade F, supporting the hypothesis that its annual habit and other correlated morphological features have evolved independently in tribe Pimpinelleae. We transfer *A. leptoclada* into *Pimpinella* (see “Taxonomic Treatment” section), while acknowledging that the annual habit of this species is rare in *Pimpinella*.

Psammogeton includes five species distributed in Central and SW Asia, mainly in the Iranian Highlands (Hedge et al. 1987), and all species were included herein. Its members are characterized by an annual life form, bi-ternate leaves with lanceolate or cuneate ultimate segments, the presence of bracts and bracteoles, white to red petals, and oblong, slightly laterally compressed mericarps densely covered by a glochidiate indumentum. The geographical distribution and morphological features of *Aphanopleura* and *Psammogeton* are very similar, with only the mericarp indumentum used for their separation (Boissier 1872; Hedge et al. 1987). In this study, *Psammogeton* forms a robust clade in Clade A, along with *Aphanopleura breviseta* and *A. capillifolia*. These two *Aphanopleura* species show a closer relationship with *Psammogeton* than they do to the type species of *Aphanopleura* (*A. trachysperma*). For this reason, we transfer *A. capillifolia* into *Psammogeton* and resurrect *P. brevisetum* Boiss. *Aphanopleura breviseta* had been previously treated

Table 2 Names in *Pimpinella* and *Psammogeton* recognized as a result of this study

Currently used name	Newly recognized name
Aphanopleura breviseta (Boiss.) Heywood & Jury	*Psammogeton brevisetum* Boiss
Aphanopleura leptoclada Lipsky	*Pimpinella leptoclada* (Aitch. & Hemsl.) Mousavi, Mozaff. & Zarre
Trachyspermum anethifolium H.Wolff	*Psammogeton anethifolium* (D.Don) Mousavi, Mozaff. & Zarre
Aphanopleura capillifolia Lipsky	*Psammogeton capillifolium* (Regel & Schmalh.) Mousavi, Mozaff. & Zarre
Trachyspermum microcarpum Hedge, Lamond & Rech.f	*Psammogeton microcarpum* (Hedge, Lamond & Rech.f.) Mousavi, Mozaff. & Zarre
Trachyspermum paktianum Hedge, Lamond & Rech.f	*Psammogeton paktianum* (Hedge, Lamond & Rech.f.) Mousavi, Mozaff. & Zarre
Trachyspermum papillare (Boiss.) Hedge, Lamond & Rech.f	*Psammogeton papillare* (Boiss.) Mousavi, Mozaff. & Zarre
Trachyspermum roxburghianum H.Wolff	*Psammogeton involucratum* Mousavi, Mozaff. & Zarre

as a synonym of *P. brevisetum* Boiss. (Hedge et al. 1987; Mozaffarian 2007).

Psammogeton, as circumscribed herein, includes species of *Trachyspermum* and *Aphanopleura*. This group is characterized by an annual or occasionally perennial habit, ultimate leaf segments mostly linear, bracts and bracteoles absent or small (shorter than 3 mm), and ovoid-globose mericarps covered by a diverse array of trichrome types (i.e., clavate, capitellate, tubular papillose, T-shaped, glochidiate, inflated vesicles, tubercles, or scales). *Aphanopleura trachysperma*, the type of the genus, is separate from the *Psammogeton* clade and is sister to *Nothosmyrnium*. It is distinct from members of the *Psammogeton* clade primarily by its much longer and conspicuous involucral bracts.

Trachyspermum

Trachyspermum includes some 12 to 15 species (Pimenov and Leonov 1993; Downie et al. 2000c; Wang et al. 2014). *Trachyspermum copticum* (L.) Link (a synonym of *T. ammi* (L.) Sprague) is the type of the genus (Fig. 1h–k). *Trachyspermum* is another taxonomically challenging genus (Pimenov and Leonov 1993). The genus was originally described based on a few general characters (Link 1821), such as pinnate involucral leaves, a striate, finely muricate mericarp having a short rough indumentum, a 5-merous and rudimentary calyx, a withering style, and a conical stylopodium, resulting in a vague circumscription. The genus is distributed worldwide, but predominantly occurs in Asia. The Iranian Highlands is a diversification center of the genus and harbors ten species including the newly described *T. reginei* Ajani & Mozzaff. (Hedge et al. 1987; Ajani and Mozafarian 2019). The description of the genus was revised in Flora Iranica (Hedge et al. 1987) to include plants having the following features: annual or perennial habit, 1 to 3-pinnate leaves with linear ultimate segments, distinct calyx teeth, white petals incurved at apex, ovate or elliptic mericarps with prominent obtuse ribs and narrow at apex, and densely covered by white vesicular, papillose, T-shape or setulose indumentum (each type of indumentum characterizes a separate species), and a depressed or conical stylopodium. The members of *Trachyspermum* are only obscurely distinguishable from *Aphanopleura*, *Pimpinella,* and *Psammogeton*, with the main differences among them associated with the mericarp indumentum. *Pimpinella* possesses pilose, papillose or tuberculate trichomes, *Aphanopleura* (in its traditional circumscription, sensu Hedge et al. 1987) has clavate trichomes, *Psammogeton* bears glochidiate or martelliform trichomes at its apex, and *Trachyspermum* has papillose mericarps (Hedge et al. 1987). In addition, the perennial species of *Trachyspermum* are morphologically similar to *Pimpinella,* differing only in their number of vallecular vittae (which are 2–4 in *Pimpinella* and one in *Trachyspermum*; Hedge et al. 1987).

Very few species of *Trachyspermum* were included in previous molecular phylogenetic studies, but not the type species *T. copticum* (Downie et al. 2000c, 2010; Zhou et al. 2008). These previous studies, though based on a limited sampling of species, rendered *Trachyspermum* as polyphyletic, with its members placed in three different tribes: *T. aethusifolium* Chiov. in Echinophoreae; *T. ammi* in Pyramidoptereae; and *T. scaberulum* and *T. triradiatum* H.Wolff in Pimpinelleae (Downie et al. 2010). The latter two species were recently united under *Pimpinella scaberula* (Franch.) H.Boissieu (Pimenov 2017) and in our study are placed in Clade E alongside members of *Pimpinella*. This placement is in accordance with previous studies (Magee et al. 2010; Wang et al. 2014; Pimenov 2017; Fernández Prieto et al. 2018).

Some species assigned previously to *Trachyspermum*, viz. *T. roxburghianum* (DC.) H.Wolff (= *T. involucratum* (Roxb.) H.Wolff), *T. anethifolium* H.Wolff, *T. microcarpum* Hedge, Lamond & Rech.f., *T. papillare* (Boiss.) Hedge, Lamond & Rech.f., and *T. paktianum* Hedge, Lamond & Rech.f., are nested within Clade A and show close affinity to *Psammogeton*. As a consequence, we transfer these species to *Psammogeton*. *Trachyspermum copticum*, a synonym of *T. ammi* (Menglan et al. 2005) and the type of the genus, is placed among the members of tribe Pyramidoptereae. Accordingly, the genus *Trachyspermum* is circumscribed narrowly.

Demavendia, Haussknechtia, and *Zeravschania*

Zeravschania, as circumscribed currently, includes nine species in SW Asia (Pimenov et al. 2007). It was originally described as a monotypic genus from the western Pamir-Alai mountains in Central Asia (Korovin 1948). The type of the genus, *Z. regeliana* Korovin, was not sufficiently described originally due to its lack of mature fruits. Subsequent morphological studies have shown that its mericarps are dorsally compressed and possess filiform dorsal ribs beside marginal ones that develop into wings (Hedge et al. 1987; Mozaffarian 2007). The most important characteristics of the genus are its white membranous and broadly ovate or lanceolate bracts and bracteoles. The phylogenies presented herein show *Zeravschania* as paraphyletic (Clade B), with all examined accessions of *Demavendia* and *Haussknechtia* nested within. To recognize a monophyletic *Zeravschania*, one treatment would be to include members of *Demavendia* and *Haussknechtia* in a broadly circumscribed *Zeravschania*. The monotypic genus *Demavendia* [*D. pastinacifolia* (Boiss. & Hausskn.) Pimenov] is endemic to Iran and also bears white, membranous bracts. The species currently placed in *Demavendia* and *Zeravschania* were previously treated as members of *Peucedanum* [unranked] *Membranacea* Boiss.

which was characterized by such membranous bracts and bracteoles (Boissier 1872). Leaf shape and margin provide important differences between these two genera. *Demavendia* possesses large oblong leaf segments with irregularly dentate margins, whereas *Zeravschania* has ovate, ovate-oblong or lanceolate leaf segments which are 2−4-ternate at its ultimate segments. Sister group to *Demavendia* and *Zeravchania* in the ITS trees is the monotypic genus *Haussknechtia* Boiss. (*H. elymaitica* Boiss.), a species characterized by tall plants up to 2 m or more, having sessile, very dense, and globose ultimate umbels (Hedge et al. 1987). We refrain herein from presenting a new formal taxonomic treatment of this group, in which *Zeravschania* is circumscribed much wider to include members of both *Haussknechtia* and *Demavendia*, due to the low resolution of relationships within the corresponding clade. *Demavendia* and *Zeravschania* are obviously closely related, especially upon considering their phylogenetic placement and morphological similarities. *Haussknechtia* also shows a close phylogenetic relationship to these genera, although its morphology is quite distinct. Further molecular phylogenetic investigations involving more informative markers should shed light on the relationships among *Demavendia*, *Haussknechtia*, and *Zeravschania*.

Taxonomic treatment

Psammogeton is circumscribed broadly to include species previously assigned to *Aphanopleura* and *Trachyspermum*. We increase the number of species under *Psammogeton* to 12 and reduce the number of species under *Aphanopleura* to two. In total, we recognize seven new combinations and resurrect one name.

New combinations

Pimpinella leptoclada (Aitch. & Hemsl.) Mousavi, Mozaff. & Zarre, **comb. nov.** ≡ *Carum leptocladum* Aitch. & Hemsl., Trans. Linn. Soc. Bot. Ser. 2, 3: 66. 1888–1889. ≡ *Aphanopleura leptoclada* (Aitch. & Hemsl.) Lipsky, Izv. Imp. Akad. Nauk V, 4: 377. 1898. ≡ *Carum aphanopleura* Koso-Pol., Not. Syst. Herb. Hort. Bot. Petrop. 3, 18: 70. 1922. —LECTOTYPE (**designated here**): Afghanistan, Herat Prov., Hari-rud valley, 5 Jun 1885, *J.E.T. Aitchison 603* (G barcode G00359737; isolectotypes: FI barcode FI014839, GH barcode GH00075662, W barcode W1963-0000628). —SYNTYPES: Afghanistan, 5 Jun 1885, *J.E.T. Aitchison 603* (P barcode P00834708); Afghanistan, Herat, Hari-rud valley, 1884, *J.E.T. Aitchison 603* (C barcode C10008329).

Diagnosis: Annual plants, stem puberulent or glabrous, 10–40 cm tall; leaves ternate with linear or oblong-linear ultimate segments; ultimate umbels long pedunculated; bracts 2−5, linear-lanceolate, membranous, scabrous at margins; bracteoles present; umbellules numerous with filiform rays; petals white or red, dorsally pilose; mericarps ovoid-globose or ovoid, covered by dense claviform or capitate indumentum.

Distribution: Iran (mostly in the northeast), Afghanistan, Tajikistan, Turkmenistan, and Uzbekistan.

Psammogeton anethifolium (D.Don) Mousavi, Mozaff. & Zarre, **comb. nov.** ≡ *Pimpinella anethifolia* D.Don, Prodr. Fl. Nepal. 184. 1825. ≡ *Athamanta anethifolia* (D.Don) Wall., Numer. List no. 569. 1829. ≡ *Ptychotis anethifolia* (D.Don) DC., Prodr. 4: 108. 1830. ≡ *Carum anethifolium* (D.Don) C.B.Clarke in Benth. & Hook.f., Fl. Brit. India, 2(6): 683. 1879. ≡ *Trachyspermum anethifolium* (D.Don) H.Wolff, Pflanzenr. IV, 228(90): 90. 1927. —LECTOTYPE (**designated here**): Nepalia, 1821, *N. Wallich 569* (K barcode K000685646; isolectotypes: G barcode G00367346, M barcode M0172780).

Diagnosis: Annual plants, pubescent, up to 40–50 cm tall; leaves small, 1–4 cm long, ternate with linear ultimate segments; ultimate umbels small, with unequal, and filiform rays; bracts and bracteoles numerous, linear, ± as long as the peduncles; petals white; mericarps rounded-elliptic, pubescent.

Distribution: Nepal (endemic).

Psammogeton capillifolium (Regel & Schmalh.) Mousavi, Mozaff. & Zarre, **comb. nov.** ≡ *Pimpinella capillifolia* Regel & Schmalh., Izv. Imp. Obshch. Lyubit. Estestv. Moskovsk. Univ. 34(2): 29. 1881. ≡ *Aphanopleura capillifolia* (Regel & Schmalh.) Lipsky, Izv. Imp. Akad. Nauk. 4: 379. 1896. = *Carum capillifolium* (Regel & Schmalh.) Koso-Pol., Bull. Soc. Imp. Naturalistes Moscou n.s., 29: 199. 1915 (publ. 1916). —TYPE: Kazakhstan, Karatan of fluv. Tschygan [Tschilak, am Nordabhang der Berge Karatan], 1880, *A. Regel s.n.* SYNTYPEYNTYPE; Kazakhstan, Turkestan: Suleimanfels bei Osch., 25 May 1880, *A. Regel s.n.* (P barcode P03214061; isosyntype: MPU barcode MPU019088).

Diagnosis: Annual plants; glabrous, sometimes purplish-red in lower parts of stem; leaves petiolate, 2-pinnate or 2-ternate, ultimate segments filiform or linear; umbels long, usually with more than 2 flowers and unequal rays; bracts absent or one; bracteoles lanceolate or linear; mericarps broadly ovate.

Distribution: Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, Uzbekistan, and China.

Psammogeton microcarpum (Hedge, Lamond & Rech.f.) Mousavi, Mozaff. & Zarre, **comb. nov.** ≡ *Trachyspermum microcarpum* Hedge, Lamond & Rech.f., Fl. Iran. 162: 342. 1987. —TYPE: Afghanistan, Kabul, in valle Logar 12 km S Kabul prope "Stupa Guldara", 1970 ma. s. l., in rupibus verticalibus, 24 Sep 1967, *H. Freitag 1991* (holotype M Hb.Freitag; isotypes: E, W barcode W0054255).
Diagnosis: Perennial plants, stem up to 40 cm; leaves trisected or pinnate with cuneate ultimate segments; umbels with 2–5 unequal rays; bracts and bracteoles linear or setaceous; mericarps ovate-elliptic, covered with T-shaped trichomes; stylopodium conical.

Distribution: Afghanistan (endemic).

Psammogeton paktianum (Hedge, Lamond & Rech.f.) Mousavi, Mozaff. & Zarre, **comb. nov.** ≡ *Trachyspermum paktianum* Hedge, Lamond & Rech.f., Fl. Iran. 162: 343. 1987. —TYPE: Afghanistan, Jaji, slopes 1 km below Alikhe, 20 Aug 1907, *H.Freitag 1829* (holotype M Hb. Freitag; isotypes: E barcode E00000356, MSB barcode MSB003195, MSB barcode MSB003196).

Diagnosis: Perennial plants; leaves long petiolate, subtripinnate with cuneate-trisected or acute ultimate segment; umbels long, thin, pedunculated with 4–6 rays; bracts subulate; bracteoles lanceolate; petals white and short papillous; mericarps ovoid or subpyriform, covered with short trichomes.

Distribution: Afghanistan (endemic).

Psammogeton papillare (Boiss.) Mousavi, Mozaff. & Zarre, **comb. nov.** ≡ *Reutera papillaris* Boiss., Diagn. Pl. Orient. Ser. 2, 2: 76. 1856. ≡ *Pimpinella papillaris* (Boiss.) Benth. & Hook.f. ex Drude, in Engler & Prantl, Natürl. Pflanzenfam. III, 8: 196. 1898. ≡ *Carum papillare* (Boiss.) Koso-Pol., Bull. Soc. Imp. Naturalistes Moscou n.s., 29: 198. 1915 (publ. 1916). ≡ *Trachyspermum papillare* (Boiss.) Hedge, Lamond & Rech.f., Fl. Iran. 162: 342. 1987. —LECTOTYPE (**designated here**): Afghanistan, Jumra and Karabagh, *W.Griffith s.n.* (K, barcode K000685651; isolectotype: E, barcode E00000357).

Diagnosis: Perennial plants; leaves pinnate with linear, acuminate ultimate segments, cauline leaves linear-filiform, apiculate; umbels with few, unequal, thin rays; bracts and bracteoles lanceolate, acute, unequal, densely hirsute, hyaline at margin; petals white, short hirsute; mericarps ovoid, covered with dense T-shape trichomes; stylopodium depressed or conical.

Distribution: Afghanistan (endemic).

Psammogeton involucratum Mousavi, Mozaff. & Zarre, **comb. nov.** ≡ *Apium involucratum* Roxb. in Fleming, Asiat. Res. 11: 157. 1810. ≡ *Athamanta roxburghiana* Wall., Cat. no. 571. 1829, nom. superfl. ≡ *Ptychotis roxburghiana* DC., Prodr. [A.P. de Candolle] 4: 109. 1830, nom. superfl. ≡ *Pimpinella involucrata* (Roxb.) Wight & Arn., Prodr. Fl. Ind. Orient. 1: 369. 1834. ≡ *Carum roxburghianum* (DC.) Benth. & Hook.f., Gen. Pl. 1: 891. 1867, nom. superfl. ≡ *Carum involucratum* (Roxb.) Baill., Hist. Pl. 7: 179. 1879. ≡ *Carum involucratum* (Roxb.) Kuntze, Rev. Gen. 265. 1891, nom. illeg., non Baill. ≡ *Trachyspermum roxburghianum* Craib, Fl. Siam. Enum. 1: 788. 1931. ≡ *Trachyspermum matthewii* M.R.Almeida, Fl. Maharashtra 2: 363. 1998, nom. superfl. —LECTOTYPE (selected by I.M.Turner, 2014 in Kew Bulletin 69: 9489): Roxburgh drawing no. 1388 Icones Roxburghianae no. 1388 (K!, available online at http://apps.kew.org/floraindica/home.do).
= *Trachyspermum stictocarpum* (C.B.Clarke) H.Wolff, Pflanzenr. (Engler) Umbellif.-Apioid.-Ammin. 89. 1927. ≡ *Carum stictocarpum* C.B.Clarke, Fl. Brit. India 2: 681. 1879. —LECTOTYPE (**designated here**): India, Maharashtra, Concan, *J.E. Stocks and J.S. Law s.n.* (K barcode K000685630; isolectotypes: K barcode. K000685631, K000685629). —SYNTYPE: *J.S. Law s.n.* (K barcode K000685632).
= *Carum stictocarpum* var. *hebecarpum* C.B.Clarke, Fl. Brit. India 2: 682. 1879. —LECTOTYPE (**designated here**): India, Maharashtra, Concan, *J.E. Stocks s.n.* (K barcode K000685626; isolectotype: K barcode K000685627). —SYNTYPE: India, Maharashtra, Concan, *J.S. Law s.n.* (K barcode K000685628).

Diagnosis: Annual plants; stem 20–100 cm; leaves petiolate, blade ovate, 2-pinnate or ternate-pinnate with narrowly oblong ultimate segments; umbels 2–4, pedunculated, with 4–12 filiform rays; bracts and bracteoles few, linear-subulate or ciliate; mericarps ovoid, densely hirsutulous or glabrescent.

Distribution: Java, India, Malaysia, Borneo, Philippines, Vietnam, Laos, New Guinea, Thailand, Andaman Islands, Myanmar, China, and Bangladesh.

Resurrected name

Psammogeton brevisetum Boiss., Fl. Or. 2: 1079. 1872. ≡ *Cuminum brevisetum* (Boiss.) Kos-Pol., Bull. Soc. Imp. Nat. Mosc. Ser. Nov. 29: 209. 1916. ≡ *Aphanopleura breviseta* (Boiss.) Heywood & Jury, Ombell. Contrib. Pluridisc. Syst. 2: 733. 1977 (publ. 1978). —LECTOTYPE (designated here): Iran, Inter Kerman et Jesd, May.1859, *A. von Bunge* (P barcode P00834707).
= *Athamantha grisea* Stapf & Wettst., Denkschr. Akad. Wiss. Wien. Math. Nat. Kl. 51, 2: 319. 1886. —Lectotype (designated here): Iran, Kuschkek inter Hamadan & Teheran, 19 Jul 1882, *T.Pichler s.n.* (JE barcode JE00003614).

= *Psammogeton flabellatus* Bornm. & Gauba, Repert. Spec. Nov. Regni Veg. 36: 341. 1934. —TYPE: Iran, Keredj: Salzberge bei Mardabad (SW Keredj in der Salzsteppe), 1934, *D.E. Gauba s.n.* (Holotype: B barcode B100366020).

Diagnosis: Annual plants; stem 3–30 cm; leaves ternate or bi-ternate, petiolate, densely covered by short indumentum; umbels pedunculate with 5–10 rays; bracts 5, short, membranous at margin, subulate; bracteoles 5–7, lanceolate; petals white, curved at apex; mericarps oblong-ovoid covered by clavate, or vesiculate trichomes.
Distribution: Central Iran (endemic).

Appendix

Accessions of Pimpinelleae and other taxa of Apiaceae subfamilies Apioideae and Saniculoideae included in the study. Previously published nrDNA ITS and *rps*16 sequences are represented herein by GenBank accession numbers only. The first GenBank number following a species name refers to ITS and the second for *rps*16, except for those instances where there are three numbers and these refer to separate ITS1, ITS2, and *rps*16 sequences. A single GenBank number often refers to ITS but in a few instances it refers to *rps*16. The number “1” or “2” added to the species name coincides with their placement in Figs. 2 and 3. For those species with newly generated ITS and *rps*16 sequences, voucher information including species name, geographical origin, *collector(s)*, *vouchers* (herbarium: TARI, Tehran Ariamehr Research Institute) is provided. Species names in brackets follow the taxonomic treatment proposed in the present study.

Aciphylla glacialis, KF160671; *Aegopodium tribracteolatum*, AY581783; *Aethusa cynapium*, AF110539; *Aletes macdougalii*, KF619604; *Ammi trifoliatum*, KJ473904; *Ammodaucus leucotrichus*, KT347642, KT347831; *Annesorhiza macrocarpa*, DQ368835; *Anthriscus sylvestris*, KT347715, KT347879; *Aphanopleura capillifolia* [*Psammogeton capillifolium*], DQ516368; *Aphanopleura breviseta* [*Psammogeton brevisetum*], Iran, Prov. Azarbaijan, ca 2 km from Tabriz to Bababaghi,1400 m a. s. l., *Mozaffarian 71,290* (TARI), MZ687311, MZ706974; *Aphanopleura leptoclada* [*Pimpinella leptoclada*], Iran, Prov. Yazd, Mehriz to Tezerjan, Sand dunes around the roads, 1500 m a. s. l., *Mozaffarian 77,439* (TARI), MZ687308, MZ706975; *Aphanopleura trachysperma*1, AF008629; *Aphanopleura trachysperma*2, Iran, Prov. West Azarbaijan, Maku, Shut, SE of Sufi village, 1070 m a. s. l., *Mozaffarian 94,396* (TARI), MZ687310, MZ706976; *Apium graveolens*, AH003471; *Arafoe aromatica*1, AF077874; *Arafoe aromatica*2, U78383, U78443; *Astrodaucus orientalis*, MG098986, AF123748; *Bunium allioides*, JX312805; *Bunium setaceum*, EF544477; *Bupleurum microcephalum*, GU269882; *Carum carvi*, KF454471, FJ385182; *Chamaesium paradoxum*, EU236161; *Choritaenia capensis*, DQ368842; *Conium maculatum*, AF110546; *Coriandrum sativum*, HQ377205; *Cryptotaenia africana1*, DQ516371; *Cryptotaenia africana*2, DQ516370; *Cymbocarpum wiedemannii*, GU291352; *Demavendia pastinacifolia*, AY911857, AY911863; *Demavendia pastinacifolia*, Iran, Prov. Tehran, W Tehran, Suleghun valley, 1500–2000 m a. s. l., *Assadi* & *Mozaffarian 32,621* (TARI), MZ687312, MZ706977; *Ducrosia flabellifolia*, DQ427051; *Echinophora chrysantha*, AF077883; *Erigenia bulbosa*, MG218514; *Eryngium proteiflorum*, EU070531; *Ferula grigoriewii*, KJ660784, KJ698392; *Frommia ceratophylloides*, DQ647630; *Galagania neglecta*, HM229391; *Haussknechtia elymaitica*1, EU169273; *Haussknechtia elymaitica*2, AY911859, AY911865; *Heteromorpha involucrata*, DQ368853; *Komarovia anisosperma*, AF077897; *Lecokia cretica*, EU169294; *Lichtensteinia trifida*, EU434683; *Muretia lutea*, DQ516359; *Nothosmyrnium japonicum*1, DQ516367, FJ385211; *Nothosmyrnium japonicum*2, EU236179; *Oedibasis tamerlanii*, HM229403; *Opopanax armeniacus*, Iran, Prov. East Azarbayejan: Mianeh, Bozgoush Mount. Neshagh village, 1880 m a. s. l., 2007, *Mozaffarian 93,480* (TARI), MZ687309; *Orlaya kochii*, AH003483, AF123733; *Ormopterum turcomanicum*, GQ379313; *Petroselinum crispum*, GQ148800, AF110544; *Phellolophium madagascariense*1, DQ647627, KJ173509; *Phellolophium madagascariense*2, KJ173483, KJ173508; *Physospermopsis cuneata*, FJ385055, FJ385221; *Physospermopsis shaniana*, EU236192, FJ385225; *Pimpinella acuminata*, EU236193, FJ385226; *Pimpinella affinis*, AY581780; *Pimpinella alismatifolia*, FM986448; *Pimpinella anisum*1, KR150177, KJ173510; *Pimpinella anisum*2, KR150177; *Pimpinella armena*, KX982510; *Pimpinella arguta*, JF831512; *Pimpinella aromatica*, AY581784; *Pimpinella aurea*, AY581785; *Pimpinella austriaca*, KX982512; *Pimpinella betsileensis*1, DQ647626, KJ173511; *Pimpinella betsileensis*2, KJ173488; *Pimpinella brachycarpa*, AY548230; *Pimpinella brachystyla*, GQ379270; *Pimpinella buchananii*, FM986455; *Pimpinella caffra*, FM986447; *Pimpinella candolleana*1, MH117649, FJ385227; *Pimpinella candolleana*2, MH117649; *Pimpinella cappadocica*, AY581786; *Pimpinella caudata*, JF831514; *Pimpinella chungdienensis*, JF831515; *Pimpinella confuse*, KX982508; *Pimpinella coriacea*, JF831516; *Pimpinella corymbosa*, AY581787; *Pimpinella cretica*, AY581788; *Pimpinella diversifolia*1, JF831517; *Pimpinella diversifolia*2, KF806585; *Pimpinella eriocarpa*, AY581790; *Pimpinella espanensis*, MH377861; *Pimpinella fargesii*, JF831518; *Pimpinella favifolia*1, FM986458; *Pimpinella favifolia*2, FM986453; *Pimpinella flabellifolia*, AY581791; *Pimpinella flaccida*, JF831519; *Pimpinella henryi*, EU236195; *Pimpinella heyneana*, GQ379276; *Pimpinella huillensis*1, FM986454; *Pimpinella huillensis*2, FM986443; *Pimpinella insignis*, AY941280, AY941308; *Pimpinella isaurica*, AY581792; *Pimpinella khayyamii*, KX982523; *Pimpinella kingdon-wardii*, JF831520; *Pimpinella kotschyana*, DQ516373; *Pimpinella krookii*, FM986445; *Pimpinella kyimbilaensis*, FM986452; *Pimpinella ledermannii*, FM986457; *Pimpinella lutea*, DQ516374; *Pimpinella major*1, MH377862; *Pimpinella major*2, KX982513; *Pimpinella nigra*, KX982509; *Pimpinella niitakayamensis*, DQ516375; *Pimpinella nudicaulis*, AY581794; *Pimpinella olivieri*1, KX982506; *Pimpinella olivieri*2, KX922690; *Pimpinella oliverioides*, AY581795; *Pimpinella oreophila*, FM986450; *Pimpinella peregrina*1, AY581797; *Pimpinella peregrina*2, AY581797; *Pimpinella peucedanifolia*1, AY581798; *Pimpinella peucedanifolia*2, KX982524; *Pimpinella procumbens*, MH377863; *Pimpinella puberula*, AY581799; *Pimpinella purpurea*1, JF831521; *Pimpinella purpurea*2, EU236197; *Pimpinella rhodantha*1, KX982511; *Pimpinella rhodantha*2, KX982511; *Pimpinella rhomboidea*, JF831522; *Pimpinella rigidistyla*, FM986459; *Pimpinella rockii*1, JF831523; *Pimpinella rockii*2, FJ385057; *Pimpinella rubescens*, JF831524; *Pimpinella saxifraga*1, MH377864, DQ133876; *Pimpinella saxifraga*2, AY581801; *Pimpinella serbica*, KX982507; *Pimpinella siifolia*1, MH377868; *Pimpinella siifolia*2, MH377867; *Pimpinella sintenisii*, AY581802; *Pimpinella smithii*1, GQ379272, FJ385230; *Pimpinella smithii*2, JF831526; *Pimpinella thellungiana*, JF831527; *Pimpinella tibetanica*, JF831528; *Pimpinella tragium*1, MH377869; *Pimpinella tragium*2, MH377869; *Pimpinella transvaalensis*, FM986449; *Pimpinella trifurcata*, FM986446; *Pimpinella valleculosa*, JF831529; *Pimpinella villosa*, MH377871; *Pimpinella yunnanensis*1, JF831530, FJ385231; *Pimpinella yunnanensis*2, JF831530; *Pleurospermum rivulorum*, HQ824798; *Postiella capillifolia*, DQ422829, DQ422848; *Prangos eriantha*, MT250532; *Prangos ferulacea*, KX982519; *Prangos lophoptera*, KU168369; *Psammogeton biternatum*, AF164839, AF164864; *Psammogeton canescens*, MG827069; *Psammogeton lamondiae*, MG827073; *Psammogeton ranunculifolius*, MG920277; *Psammogeton sp*., MG827076; *Psammogeton stocksii*, Iran, Prov. Baluhestan, Between Iranshahr and Bam, Bazman, 1200 m a. s. l., *Assadi 23,009* (TARI), MZ687313, MZ706978; *Pyramidoptera cabulica*, AF008631; *Sanicula epipactis*, EU169013, EU168959; *Selinum broteri*, AY179029; *Smyrnium olusatrum*, MK050086; *Trachydium simplicifolium*, FJ385067; *Trachyspermum ammi*, Iran, Prov. Baluchistan: Iranshahr to Chahbahar, Pole Jaligur over the Sarbay river, 300 m a. s. l., *Mozaffarian 74,383* (TARI), MZ687314, MZ706979; *Trachyspermum anethifolium* [*Psammogeton anethifolium*], MG827079; *Trachyspermum copticum*, Iran, Prov. Baluchistan: Khash to Iranshahr, Dashte Abkhan, 1400 m a. s. l., *Mozaffarian 72,711* (TARI), MZ687315, MZ706980; *Trachyspermum microcarpum* [*Psammogeton microcarpum*], MG920276; *Trachyspermum paktianum* [*Psammogeton paktianum*], MG827078; *Trachyspermum papillare* [*Psammogeton papillare*], MG920275; *Trachyspermum roxburghianum* [*Psammogeton involucratum*], MG827080; *Trachyspermum scaberulum*1, JF831531, FJ385258; *Trachyspermum scaberulum*2, EU236215; *Trachyspermum triradiatum*, EU236216, FJ385259; *Zeravschania aucheri*, AY911860, AY911866; *Zeravschania membranacea*1, AY911862, AY911868; *Zeravschania membranacea*2, Iran, Prov. Khorassan: Mashhad, Karde. All village, 1460 m a. s. l., *Mozaffarian 87,007* (TARI), MZ687317, MZ706982; *Zeravschania pauciradiata*, Iran, Prov. East Azarbaijan, Siahrud to Kakaleh, near to Kalaleh, 390 m a. s. l., *Ajani 1584* (TARI), MZ687316, MZ706981; *Zeravschania regeliana*, AY911861, AY911867.

Information on Electronic Supplementary Material

Online Resource 1. The alignment of nrDNA ITS sequences which has been used to reconstruct the ITS trees obtained in this study.

Online Resource 2. The alignment of plastid *rps*16 intron sequences which has been used to reconstruct the *rps*16 trees obtained in this study.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00606-021-01792-x.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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