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Phylogeny of *Acanthophyllum* s.l. revisited: An update on generic concept and sectional classification

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Abstract The generic boundary of the broadly defined *Acanthophyllum* s.l., the third-largest genus of the tribe Caryophylleae (Caryophyllaceae), has been a subject of taxonomic confusion. *Acanthophyllum* s.l. now includes five minor genera previously recognized as independent. Among these small genera, the inclusion of *Allochrysa*, *Ochotonophila*, and *Scleranthopsis* within *Acanthophyllum* s.l. was confirmed by previous molecular studies, while the positions of *Diaphanoptera* and *Kuhitangia* remained uncertain. We have performed an updated molecular study of *Acanthophyllum* s.l. including an increased sampling of the genera and sections assigned to this group, using intron sequences of the chloroplast gene *rps16* and nuclear ribosomal internal transcribed spacer (ITS) sequences. *Cyathophylla*, *Heterochroa*, and *Saponaria* were chosen as outgroups for performing phylogenetic analyses using maximum likelihood and Bayesian methods. The present results suggest that, in addition to the genera mentioned above, both *Diaphanoptera* and *Kuhitangia* should also be synonymized within *Acanthophyllum*. Sections *Diaphanoptera*, *Kuhitangia* and *Pseudomacrostegia* are introduced as new infrageneric taxa within *Acanthophyllum*. Our results also indicate that some annual species of *Saponaria* are closely related to *Acanthophyllum*.

Keywords annual *Saponaria*; Caryophylleae; *Diaphanoptera*; Irano-Turanian; *Kuhitangia*; sect. *Macrostegia*

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INTRODUCTION

The genus *Acanthophyllum* C.A.Mey. s.l. (referred to hereafter as “*Acanthophyllum*”) is one of the larger genera of the Caryophyllaceae Juss., comprising 90–100 species distributed in the Irano-Turanian region. It belongs to the tribe Caryophylleae Lam. & DC. and represents the third-largest genus of the tribe, after *Dianthus* L. (about 300 species, see e.g., Valente & al., 2010; Hernández-Ledesma & al., 2015) and *Gypsophila* L. (about 150 species, see, e.g., Hernández-Ledesma & al., 2015; Madhani & al., 2018). *Acanthophyllum* species are perennial subshrubs, predominantly forming cushions with spiny leaves (see, e.g., Bittrich, 1993, and Pirani & al., 2014) (Fig. 1). In the broad sense, the genus would include the following five minor genera that were previously treated as separate: *Allochrusa* Bunge ex Boiss., *Diaphanoptera* Rech.f., *Kuhitangia* Ovcz., *Ochotonophila* Gilli, and *Scleranthopsis* Rech.f. (Pirani & al., 2014). The inclusion of *Allochrusa*, *Ochotonophila*, and *Scleranthopsis* within *Acanthophyllum* has been recently confirmed by Pirani & al. (2014), while the types of *Diaphanoptera* and *Kuhitangia* have not been investigated from the molecular point of view. A recent molecular study of the tribe Caryophylleae revealed that a few taxa from *Gypsophila* should also be included in *Acanthophyllum* (Madhani & al., 2018).

Kuhitangia is a small and barely known genus of perennial, cushion-forming subshrubs, which is distributed in Central Asia and includes two species, i.e., *K. popovii* (Preobr.) Ovcz. (the type of the genus according to Ovczinnikov, 1967) and *K. knorringiana* (Schischk.) Bondarenko. Before being transferred to *Kuhitangia*, both species were variously treated either as *Acanthophyllum* or as *Gypsophila* by different authors (Schischkin, 1936; Barkoudah, 1962; Ovczinnikov, 1967, 1968). When establishing the genus *Kuhitangia*, Ovczinnikov (1967) compared it with *Acanthophyllum*, *Gypsophila*, *Kohlrauschia* Kunth, and *Petrorhagia* (Ser.) Link. *Kuhitangia* was morphologically differentiated from *Acanthophyllum* mainly based on the long peduncles that much exceed the cushion, small petals that lack a claw, and many-seeded capsules opening by four teeth (Ovczinnikov 1967, 1968). Some authors (e.g., Bittrich, 1993, and Hernández-Ledesma & al., 2015) treated *Kuhitangia* as a synonym of *Acanthophyllum*, while others (e.g., Takhtajan, 2009) recognized the genus as independent.

Diaphanoptera was originally described from Iran with the single species *D. khorasanica* Rech.f. (Rechinger, 1940). It is a small Irano-Turanian genus of six species of multi-stemmed subshrubs distributed in Afghanistan, Iran, and Turkmenistan. It is morphologically similar to *Acanthophyllum*, from which it can be distinguished by diaphanous (translucent) wings on the calyx as well as non-spiny leaves (see Rechinger, 1940) (Fig. 1I–L). *Diaphanoptera* species are mainly local endemics or occur in restricted distribution areas (Schiman-Czeika, 1988; Kiani & al., 2013). Four of the six species have been sampled in recent phylogenetic studies of Caryophyllaceae. Pirani & al. (2014) revealed that *Diaphanoptera* in its traditional concept is not monophyletic and includes at least two phylogenetically distinct groups. However, *D. khorasanica*, the type of the genus, was not included in that study, rendering the phylogenetic position of the genus unresolved.

Allochrusa, in the traditional sense, is a small genus of ca. eight subshrubby perennial species distributed in NW Iran, Turkey and Transcaucasia (Mahmoodi & Nejad Falatoury, 2016). Possessing enclosed stamens and non-spiny leaves (Fig. 1F–H), *Allochrusa* was considered as distinct from *Acanthophyllum* (Bunge, 1867). However, some authors reduced *Allochrusa* to an infrageneric taxon within *Acanthophyllum* (e.g., Golenkin, 1893; Schischkin, 1936). Pirani & al. (2014) sampled three *Allochrusa* species (including the type, *Al. versicolor* (Fisch. & C.A.Mey.) Boiss.), and the inclusion of *Allochrusa* in *Acanthophyllum* was confirmed.

The results of the most comprehensive molecular study of the tribe Caryophylleae (Madhani & al., 2018) indicated that the traditional boundaries of *Saponaria* L. need to be reassessed, as the annual *S. viscosa* C.A.Mey. did not group with the monophyletic clade holding biennial and perennial species of the genus. Instead, *S. viscosa* together with *Cyathophylla chlorifolia* (Poir.) Bocquet & Strid, formed a clade closely related to *Acanthophyllum*, raising a question about the phylogenetic position of the annual species of *Saponaria*.

Regarding the infrageneric classification of *Acanthophyllum*, Pirani & al. (2014) showed that the 11 sections are generally monophyletic, or rendered as monophyletic after a few species are removed. Among the surveyed sections are sect. *Macrostegia* (Boiss.) Pax and sect. *Oligosperma* Schischk. ex Schiman-Czeika, two groups with considerable internal

morphological heterogeneity. Section *Macrostegia* includes taxa with both spiny (e.g., *A. bracteatum* Boiss.), and non-spiny (e.g., *A. korolkowii* Regel & Schmalh., *A. coloratum* Schischk.) leaves. Non-spiny members of the section have not been included in previous molecular investigations, and their phylogenetic relationship with the spiny ones has not been investigated. The other morphologically diverse group, sect. *Oligosperma*, is the largest (ca. 30 species) and most widespread section of the genus, whose members can be found from NW Iran to W China. Morphological characters used for separating species of sect. *Oligosperma* are confusing, and a few species of the section have overlapping features. This taxonomic complexity was reflected in the previous study of the group (Pirani & al., 2014), in which internal relationships within the section were not satisfactorily resolved using ITS and *rps16* data. The latter study concluded that a more extensive sampling of the section might help resolve the species.

Principal aims of the present study are: (1) to test the phylogenetic position of *Kuhitangia* using molecular data, (2) to further investigate the phylogenetic status of *Diaphanoptera* and *Allochrusa* using expanded taxon sampling, and (3) to reassess monophyly of *Acanthophyllum* sect. *Macrostegia* and sect. *Oligosperma* using more inclusive sets of taxa.

MATERIALS AND METHODS

Taxon sampling. — We have sampled all currently recognized taxa of *Acanthophyllum* s.l. represented in previous studies, as well as 38 DNA sequences that were generated in this study, including 19 nuclear ribosomal internal transcribed spacer (ITS) and 19 *rps16*. The new sequences correspond to three accessions assigned to *A.* sect. *Macrostegia*, five accessions assigned to *A.* sect. *Oligosperma*, three accessions assigned to *A.* sect. *Paniculata* Golenk., two accessions assigned to *Allochrusa*, three accessions assigned to *Kuhitangia*, two accessions assigned to *Diaphanoptera*, and one annual *Saponaria* species.

Heterochroa desertorum Bunge, *H. violacea* (Ledeb.) Walp., *Yazdana shirkuhensis* A.Pirani & Noroozi, and *Cyathophylla viscosa* (C.A.Mey.) Madhani & Rabeler served as outgroup taxa (Madhani & al., 2018; Noroozi & al., 2020). Voucher information and GenBank accession numbers for all included specimens are listed in Appendix 1.

Typification information. — Details about type specimens of the basionyms of the new combinations included here are based on examining protologues and searching major indices (Tropicos – <http://www.tropicos.org/>; JSTOR Global Plants – <https://plants.jstor.org/>; GBIF – <http://gbif.org/>), as well as websites of individual herbaria (BM, E, G, K, WU) for extant specimens. We have examined a digital image from at least one of these sources for any specimen with a cited barcode.

DNA extraction, amplification, and sequencing. — Total genomic DNA was extracted from herbarium materials, deposited at FUMH, H, LE, TARI, TASH, and TK, using the DNeasy Plant Mini kit (Qiagen; Germantown, Maryland, U.S.A.) according to the manufacturer's protocol, or the 2× cetyltrimethylammonium bromide (CTAB) extraction protocol (Doyle & Doyle, 1987). The nuclear ribosomal internal transcribed spacer (ITS) region and the complete intron of the plastid *rps16* gene were amplified using primers P17/26S-82R and *rpsF/rpsR2R*, respectively (Oxelman & al., 1997; Popp & Oxelman, 2001). Amplification products were purified using PEG (Joly & al., 2006), or the GenElute PCR Clean-Up kit for PCR product purification (Sigma Aldrich; Saint Louis, Missouri, U.S.A.) according to the manufacturer's instructions. Sequencing was performed by Macrogen (Seoul, South Korea and Amsterdam, The Netherlands) using PCR primers P16S/ITS4 (Eggens & al., 2007; Popp & Oxelman, 2007) and *rpsF2a/rpsR3R* (Popp & al., 2005) for ITS and *rps16*, respectively. Sequences were trimmed, assembled and aligned using Geneious v.6.1.2 (<https://www.geneious.com/>). The MUSCLE Plug-in was used with the default setting. The best substitution model for each alignment was selected using jModelTest v.2.1.4 (Darriba & al., 2012). The GTR+ Γ +I and GTR+ Γ models were determined as the best-fit models for nuclear and chloroplast markers, respectively. The alignments for both the ITS and the *rps16* datasets are available as supplementary Appendices S1 and S2, respectively.

Phylogenetic analyses. — Phylogenetic analyses were performed using maximum likelihood (ML) and Bayesian

inference (BI). The ML analysis was carried out using the IQ-TREE web server (<http://iqtree.cibiv.univie.ac.at/>) using 1000 bootstrap replicates, obtained by the ultrafast bootstrap approximation (UFBoot) (Minh & al., 2013). Bayesian inference (BI) of the individual gene analyses was performed using MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001) at the CIPRES portal (<http://www.phylo.org/index.php/portal/>) with default prior settings, for 20 million MCMC generations. The quality of the analysis was checked by comparing likelihood values and parameter estimates from different runs in Tracer v.1.6 (<http://tree.bio.ed.ac.uk/software/tracer/>), and 25% of the trees were discarded as burn-in. The remaining trees were summarized in a 50% majority-rule consensus tree.

Construction of the secondary structure of ITS1 sequence. — Although Pirani & al. (2014) showed that *Acanthophyllum* s.l. is a monophyletic clade, placement of *Diaphanoptera afghanica* (accession number KF924632) outside of this clade raised the question of the possible polyphyly of *Diaphanoptera*. The ITS sequence obtained from type material (*Podlech 21075* [MSB]) and a BLAST search did not show any fungal or algal contamination. Moreover, analysis of two ITS sequences of *Saponaria kermanensis* (accession numbers KX184037 and KX184038, obtained from GenBank), along with the sequences from the tribe Caryophylleae available in GenBank and the present study, showed a different position for these two accessions (data not shown). The mean divergence value between the KX184037 and the KX184038 sequences is 8%, and based on a phylogenetic analysis, the *S. kermanensis* under accession no. KX184037 fell within *Acanthophyllum* close to *S. makranica*, while the divergent ITS allele (KX184038) was placed outside of *Acanthophyllum*. Therefore, to be sure about orthology of these sequences, we reconstructed the secondary structure of ITS1 to find the highly conserved motif (Liu & Schardl, 1994; GGCRY-(4 to 7n)-GYGYCAAGGAA) in ITS1. The ITS1 of *D. afghanica* and both mentioned *S. kermanensis* taxa were folded using the Mfold program at 37°C (folding at 10°C and 20°C resulted in identical structures), hosted at the M. Zuker web server (<http://mfold.rna.albany.edu/?q=mfold>).

RESULTS

Phylogenetic analyses. — Trees yielded by ML and BI analyses of individual plastid and nuclear markers were mostly congruent within each marker. Therefore, only the results of BI analyses are presented and discussed here, and those of ML analyses are summarized in Fig. 2.

Members of both datasets resolved within two main well-supported clades, clades 1 and 2, in both the ITS and the *rps16* tree (Fig. 2). Phylogenetic positions of the taxa treated in the present survey are summarized below.

Diaphanoptera khorasanica and *D. transhyrcana* (Preobr.) Rech.f. & Schiman-Czeika comprise a monophyletic clade together with *D. lindbergii* Hedge & Wendelbo and *D. stenocalycina* Rech.f. & Schiman-Czeika, which is strongly supported on both the ITS (PP 0.99) and the *rps16* (PP 1) tree.

Kuhitangia popovii and the two individuals of *K. knorringiana* nest in a monophyletic clade with strong support (PP 0.97) in the ITS tree, while they appear within an unresolved polytomy in the *rps16* tree (Fig. 2).

Allochrysa lutea Falat. & Mahmoodi, *Al. persica* Boiss., *Al. versicolor*, and *Al. bungei* Boiss. form a monophyletic clade with strong support (PP 1) in the ITS tree (Fig. 2). Monophyly of these taxa is not obtained in the *rps16* tree, where *Al. lutea* and *Al. persica* fall out of the core group of *Acanthophyllum* sect. *Allochrysa* (Bunge ex Boiss.) A. Pirani & Rabeler (Fig. 2). *Allochrysa gypsophiloides* (Regel) Schischk. and *Al. paniculata* (Regel & Herder) Ovcz. & Czukav. resolve as a monophyletic clade in the ITS tree, while *Al. tadshikistanica* Schischk. does not group with any of the *Allochrysa* species (Fig. 2). On the *rps16* tree, *Al. gypsophiloides* and *Al. tadshikistanica* do not form a monophyletic clade and reside in different groups (Fig. 2).

Saponaria kermanensis and *S. makranica* Rech.f. form a monophyletic clade within *Acanthophyllum* in the ITS tree (Fig. 2). Although our survey lacks an *rps16* sequence for *S. kermanensis*, *S. makranica* nests within *Acanthophyllum* in the *rps16* tree (Fig. 2).

Our analyses showed that *Acanthophyllum coloratum*, *A. korolkowii*, and *A. sarawschanicum* Golenk. do not fall within the core group of sect. *Macrostegia*. In the ITS tree they resolve as a monophyletic clade (with low support; PP 0.7) together with *A. aphananthum* Rech.f. and *Allochrusa tadshikistanica* (Fig. 2). In the *rps16* tree, *A. coloratum* and *A. sarawschanicum* make a strongly supported clade (PP 0.97) together with *Al. tadshikistanica*, while *A. korolkowii* shows a remote relationship to this clade (Fig. 2).

All of the four newly examined species of sect. *Oligosperma* (*Acanthophyllum aculeatum* Schischk., *A. elatius* Bunge, *A. pulchrum* Schischk., *A. pungens* Boiss.) reside within the monophyletic clade including the rest of the section in the ITS tree (Fig. 2). However, *A. pulchrum* does not group within sect. *Oligosperma* in the *rps16* tree (Fig. 2).

Construction of the secondary structure of ITS1. — The highly conserved motif (Liu & Schardl, 1994) in ITS1 for *Diaphanoptera afghanica* (see Fig. 3) and *Saponaria kermanensis* (KX184038) does not form a hairpin structure (data not shown), which means these divergent ITS alleles are non-functional paralogues.

DISCUSSION

The generic boundaries of *Acanthophyllum* with its five small allied genera have been doubtful. Although inclusion of *Allochrusa*, *Ochotonophila*, and *Scleranthopsis* in *Acanthophyllum* was confirmed by previous molecular studies (Pirani & al., 2014; Madhani & al., 2018), the phylogenetic placement of the genera *Diaphanoptera* and *Kuhitangia* remained uncertain. The present study discusses the phylogenetic status of *Diaphanoptera* and *Kuhitangia* and further surveys the monophyly of traditional *Allochrusa* and its infrageneric taxa. Moreover, monophyly of the two heterogenic sections *Macrostegia* and *Oligosperma* is reassessed using additional Central Asiatic species. The sampled taxa were grouped within two well-supported clades in both the ITS and the *rps16* tree (Fig. 2). These clades firmly correspond to the clades I and II in Pirani & al. (2014). The obtained results are classified and interpreted below.

Phylogenetic position of *Kuhitangia*. — All three sampled specimens representing both recognized species of *Kuhitangia* nested within *Acanthophyllum* in both the ITS and the *rps16* tree (Fig. 2), which confirms the inclusion of *Kuhitangia* within *Acanthophyllum*. These taxa reside within a monophyletic clade in the ITS tree (PP 0.97), but their relationship is not resolved in the *rps16* tree (Fig. 2). Apart from the molecular data that confirm the inclusion of *Kuhitangia* within *Acanthophyllum*, morphological characters used by Ovczinnikov (1967) for describing *Kuhitangia* (long peduncles, petals lacking a claw, many-seeded capsules) are also found in *Acanthophyllum*. For example, long peduncles much exceeding the cushion are also seen in *Acanthophyllum* sect. *Scapiflora* Schiman-Czeika; non-clawed petals are seen in *A. sordidum* Bunge ex Boiss. and *A. aphananthum*; *A. glandulosum* Bunge ex Boiss. may contain many-seeded capsules (see Schiman-Czeika, 1988). Moreover, *Acanthophyllum* and *Kuhitangia* have also been separated based on their mode of capsule dehiscence, i.e., transverse rupture of capsule in *Acanthophyllum*, and capsule opening by four teeth in *Kuhitangia* (Bondarenko, 1971). However, capsule dehiscence into four valves has also been reported in *Acanthophyllum* (e.g., *A. adenophorum* Freyn, *A. longicalyx* Hedge & Wendelbo, and *A. laxiflorum* Boiss.) (Schiman-Czeika, 1987). Therefore, we suggest treating *Kuhitangia* as a section of *Acanthophyllum* (see below).

Phylogenetic status of *Diaphanoptera*. — The type of the genus, *Diaphanoptera khorasanica*, is included in a strongly supported monophyletic clade together with *D. lindbergii*, *D. stenocalycina*, and *D. transhyrcana* within *Acanthophyllum* in both the ITS and the *rps16* tree (Fig. 2). The generic positioning of *D. transhyrcana*, by traditional taxonomy, has been doubtful. It was first described as a species of *Acanthophyllum* (Preobraschensky, 1920). Schischkin (1936) also considered this taxon as a member of *Acanthophyllum* and placed it under subg. *Allochrusa* (Bunge) Schischk. Czerepanov (1981) transferred it to the genus *Allochrusa*, which he considered as distinct from *Acanthophyllum*. Ultimately this taxon was transferred to the genus *Diaphanoptera* by Rechinger & Schiman-Czeika (1988).

Diaphanoptera ekbergii and *D. afghanica* fall outside of the core clade of *Diaphanoptera*. The ITS sequences of the latter

reside outside of *Acanthophyllum* (see below under Non-functional paralogous sequence of *Diaphanoptera afghanica* and *Saponaria kermanensis*). *Diaphanoptera ekbergii* is the only member of this group with a prostrate habit and simple non-branched stems, while the other members of the genus are characterized by ascendant habit and branched stems.

We suggest reducing *Diaphanoptera* to a section of *Acanthophyllum* containing *D. khorasanica*, *D. lindbergii*, *D. stenocalycina*, and *D. transhyrcana*. The sectional position of *D. ekbergii* and *D. afghanica* cannot be resolved based on the available data and awaits more comprehensive studies.

Non-monophyly of *Allochrusa*. — After description of *Allochrusa* by Bunge (1867), the genus was included in *Acanthophyllum* by Golenkin (1893) and Schischkin (1936). Golenkin recognized *Allochrusa* at section rank, whereas Schischkin treated *Allochrusa* as a subgenus of *Acanthophyllum* and recognized two sections. One of these sections, i.e., sect. “*Versicoloria* Schischk.” (this section’s name was later validated as sect. *Allochrusa*; Pirani & Rabeler, 2017) occurs in the western part of the Caspian Sea, while the second group (sect. *Paniculata* Golenk.) occurs east of the Caspian Sea. Pirani & al. (2014) showed that the investigated members of sect. *Allochrusa* (*Al. bungei*, *Al. versicolor*) and sect. *Paniculata* (*Al. paniculata*) resolve into two separate groups. Here, we have sampled two additional species assigned to sect. *Allochrusa* (*Al. lutea*, *Al. persica*), and two additional members of sect. *Paniculata* (*Al. gypsophiloides*, *Al. tadshikistanica*) to reassess the phylogenetic relationships among the elements of traditional *Allochrusa*. The present results firmly confirm the remote phylogenetic relationship between sect. *Allochrusa* and sect. *Paniculata*. Besides, both the ITS and the *rps16* tree (Fig. 2) show that *Al. tadshikistanica* is not closely related to members of sect. *Paniculata*, rather it is allied to three members of sect. *Macrostegia* (e.g., *A. coloratum*, *A. korolkowii*, and *A. sarawschanicum*). *Allochrusa tadshikistanica* was first described as a species of *Allochrusa* (Schischkin, 1932). It was later transferred to *Acanthophyllum* subg. *Allochrusa* and classified within sect. *Paniculata* together with *A. paniculatum* Regel & Herder and *A. gypsophiloides* Regel (Schischkin, 1936). It differs from the latter two taxa in having shorter petals (ca. equal to sepals) and bracts with membranous margins (versus exerted petals and scarious bracts in sect. *Paniculata*). Membranous bracts and bracteoles are among the distinctive features of sect. *Macrostegia*. We suggest that *Al. tadshikistanica* should be placed into a new section under *Acanthophyllum* (see below).

Inclusion of annual *Saponaria* results in a new concept of *Acanthophyllum* s.l. — The molecular survey of the tribe Caryophylleae by Madhani & al. (2018) showed that the annual *Saponaria viscosa* had an odd phylogenetic position and resides as sister to *Cyathophylla chlorifolia*. As a result, they transferred *S. viscosa* to the genus *Cyathophylla*. This *Cyathophylla* clade (containing *C. chlorifolia* and *C. viscosa* (C.A.Mey.) Madhani & Rabeler) can be considered as an appropriate outgroup for *Acanthophyllum*. We here tested the phylogenetic position of two more Irano-Turanian annual *Saponaria* species, i.e., *S. kermanensis*, and *S. makranica*. Surprisingly, both taxa resolved within *Acanthophyllum* (Fig. 2). This also contradicts the alternative treatment of *S. kermanensis* in *Psammophiliella* Ikonn. by Ikonnikov (1976) and *S. makranica* in *Gypsophila* by Ghazanafar (1986). Our results necessitate a revision of the concept of habit in *Acanthophyllum* s.l. Subshrubby to somewhat woody habit was used as key character to distinguish *Acanthophyllum* in the tribe Caryophylleae (Pirani & al., 2014). The present results indicate that *Acanthophyllum* in a broad sense also contains annual non-woody elements. Furthermore, polyphyly of *Saponaria* is suggested as all of the examined annual species of the genus show a remote relationship with the biennial and perennial ones.

Monophyly of sect. *Macrostegia* and sect. *Oligosperma*. — *Acanthophyllum* sect. *Macrostegia* comprises 10 species in the *Flora Iranica* and the *Flora of the U.S.S.R.* areas (Schiman-Czeika, 1988; Schischkin, 1936). Almost half of the species of this section (*A. coloratum*, *A. elongatum* Preobr. ex Schischk., *A. korolkowii*, *A. sarawschanicum*) are endemic to Central Asia. Section *Macrostegia* appeared as monophyletic in the previous molecular study of the group, which mainly sampled SW Asiatic members of the section (Pirani & al., 2014). In the present study, three of the four Central Asiatic species of this section were sampled as well. Analyzing data of both the nuclear and plastid markers showed that *A. coloratum*, *A. korolkowii*, and *A. sarawschanicum*, three non-spiny taxa assigned to sect. *Macrostegia*, do not group with the spiny members of the section. These three species resolved into a strongly supported clade (PP 1.0) together with *Al. tadshikistanica* on the ITS tree (Fig. 2). However, *A. korolkowii* does not group with *A. coloratum*, *A. sarawschanicum*, and *Al.*

tadshikistanica in the *rps16* tree (Fig. 2). The common feature between the latter and the three Central Asiatic species of sect. *Macrostegia* is non-spiny leaves. Here we suggest that taxa with non-spiny leaves should be excluded from sect. *Macrostegia* and transferred to a new section (sect. *Pseudomacrostegia* sect. nov., see below).

As the largest and taxonomically the most complicated group within *Acanthophyllum*, sect. *Oligosperma* contains about 30 species according to Schischkin (1936), Schiman-Czeika (1988), and Pirani & al. (2013). Schischkin (1936) made a further division of this section and proposed five series (not validly published according to Art. 39.1 of the *Shenzhen Code*; Turland & al., 2018), whereas Schiman-Czeika (1988) did not recognize these series. Eighteen species assigned to this section have already been investigated in the previous study by Pirani & al. (2014) that showed the section is monophyletic, and that *A. caespitosum* should be excluded from the section. However, the relationships between species of the section remained largely unresolved. In the present study, five specimens representing four additional species of this section were studied. On the ITS tree, all sampled species of the section reside on a fully supported (PP 1.0) monophyletic group (Fig. 2). Except for *A. andarabicum* Podlech ex Schiman-Czeika and *A. pulchrum*, which fall out of the core clade of the section, the rest of the sampled species comprise a weakly supported (PP 0.87) monophyletic clade on the *rps16* tree (Fig. 2). This difference between the ITS tree and the *rps16* tree can be explained by different numbers of informative characters in nuclear and plastid datasets. Increased sampling in the present study was not of much help in resolving the relationships within the section. Furthermore, Schischkin's "series" did not resolve on the ITS and *rps16* trees.

According to the results obtained, although two main clades are recognized within *Acanthophyllum*, these clades do not match the two subgenera (*Acanthophyllum* [= "*Euacanthophyllum* (Boiss.) Schischk."], *Allochrusa* (Bunge) Schischk.) introduced by Schischkin (1936). As a consequence, the subgeneric classification of *Acanthophyllum* as suggested by Schischkin (1936) is not here confirmed. Moreover, based on our results, the number of sections within *Acanthophyllum* increases to at least 14. Since the ITS tree shows higher resolution, we have summarized the phylogenetic positions of these 14 sections on the ITS tree (Fig. 4). A list of species included in this study and their sectional placements based on the present results, as well as species with unresolved sectional positions, is presented in Table 1.

Non-functional paralogous sequence of *Diaphanoptera afghanica* and *Saponaria kermanensis*. —

Phylogeny relies on orthologous sequences, and using paralogous sequences and/or pseudogenes will result in an unreliable phylogenetic tree (Buckler & al., 1997; Moazzeni & al., 2014). Non-functional paralogues in ribosomal DNA (rDNA) or other genomes (e.g., mitochondrial genes) exist. Using the paralogues has already been reported for Caryophyllaceae (Popp & Oxelman, 2004) and other angiosperms (Buckler & al., 1997; Moazzeni & al., 2014).

The secondary structure of ITS1 for *Diaphanoptera afghanica* obtained from type material (*Podlech 21075* [MSB]) suggests that the divergent ITS allele is a non-functional paralogue. Thus, the placement of *D. afghanica* outside of the *Acanthophyllum* clade could possibly be explained by the inclusion of this paralogous copy in the phylogenetic analysis of Pirani & al. (2014). In the present study, we re-sequenced ITS and *rps16* markers from this specimen, but it failed for both markers. Regarding the morphological and geographical similarities of *D. afghanica* to the other species of the genus, it seems that a successful sequencing of orthologous alleles of this species would result in positioning of *D. afghanica* within the *Acanthophyllum* s.l. clade.

The highly conserved motif in ITS1 for KX184038 does not form a hairpin structure (data not shown), which means this divergent ITS allele is a non-functional paralogue. This might explain the remote positioning of the two *Saponaria kermanensis* samples both inside (KX184037) and outside (KX184038) of *Acanthophyllum*. Since the orthologue sequence (KX184037) resides within *Acanthophyllum*, it seems that *S. kermanensis* should be considered as a member of this clade.

Conclusions. — Recent molecular studies have notably improved our knowledge about generic delimitation and infrageneric classification of *Acanthophyllum*. However, sectional position of several species is still unclear. Moreover, species relationships within sect. *Acanthophyllum* and sect. *Oligosperma* have largely remained unresolved. Using additional molecular markers in future research on the genus would help to address these issues. A comprehensive molecular study on *Saponaria*, including all annual species, would also be another direction for future studies and help clarify generic boundaries

among *Saponaria* and allied genera, e.g., *Acanthophyllum* and *Gypsophila*.

New names and combinations. — In addition to the three new sections and combinations necessary for treating *Diaphanoptera* and *Kuhitangia* species as members of *Acanthophyllum*, combinations are made for two species of *Saponaria*, and one species each of *Ochotonophila* and *Allochrysa* that were described close to, or after, Pirani & al. (2014) was published.

Acanthophyllum sect. *Diaphanoptera* (Rech.f.) A.Pirani & Moazzeni, **comb. & stat. nov.** ≡ *Diaphanoptera* Rech.f. in Repert. Spec. Nov. Regni Veg. 48: 41. 1940 – Type: *Diaphanoptera khorasanica* Rech.f.

Diagnosis. – Perennial, low-growing plants, woody at base, multi-stemmed. Leaves non-spiny. Inflorescences with short peduncles, partial inflorescences lax dichasia, cymes or thyrses. Bracts and bracteoles leafy. Calyx with 5 ± prominent wings or nerves. Petals clawed. Ovary stipitate, ovules 6–19; capsules many-seeded, opening through four valves.

Acanthophyllum sect. *Kuhitangia* (Ovcz.) A.Pirani & Kovalchuk, **comb. & stat. nov.** ≡ *Kuhitangia* Ovcz. in Dokl. Akad. Nauk Tadzhiksk. S.S.R. 10: 50. 1967 – Type: *Acanthophyllum popovii* (Preobr.) Barkoudah.

Diagnosis. – Perennial subshrubs, woody at base, cushion-forming. Leaves spiny. Inflorescences with long leafless peduncles prominently exceeding the cushion, partial inflorescences ± dense cymes. Bracts and bracteoles acicular. Calyx lacks wings or prominent nerves. Petals lack a claw. Ovary with short stipe, many-ovuled; capsules many-seeded, opening through four valves.

Acanthophyllum sect. *Pseudomacrostegia* A.Pirani, Kovalchuk & A.Pavlenko, **sect. nov.** – Type: *Acanthophyllum sarawschanicum* Golenk.

Diagnosis. – Perennial subshrubs, woody at base, non-cushion-forming. Leaves non-spiny. Inflorescences with ± long peduncles, partial inflorescences ± dense globose cymes or 3-flowered dichasia (in *A. tadshikistanica*). Bracts and bracteoles membranous or broadly hyaline margined, non-acicular. Calyx lacks wings or prominent nerves. Petals clawed. Ovary with short stipe, 4-ovuled; capsules one-seeded.

Acanthophyllum afghanicum (Podlech) A.Pirani & Zarre, **comb. nov.** ≡ *Diaphanoptera afghanica* Podlech in Mitt. Bot. Staatssamml. München 16: 542. 1980 – Holotype: Afghanistan. Prov. Baghlan: Andarab Tal, 5 km E Doshi, 920 m, 6 May 1971, Podlech 21075 (M n.v. [per Podlech, 1980]; isotypes: G barcode G00226761 [image online!], W No. 0048191 [isotype fragments, image online!]).

Acanthophyllum diaphanopterum A.Pirani & Moazzeni, **nom. nov.** ≡ *Diaphanoptera khorasanica* Rech.f. in Repert. Spec. Nov. Regni Veg. 48: 42. 1940, non *Acanthophyllum khorasanicum* Rech.f. in Repert. Spec. Nov. Regni Veg. 48: 43. 1940 – Holotype: Iran. Robot Safid inter Mashhad et Torbat-e Heydariyeh, 1700 m, 10 Jul 1937, Reching 1515 (W No. 1963-0003850 [image online!]; isotypes: BM barcode BM000522099 [image online!], K barcode K000742100 [image online!], NY barcode 00342485 [image online!], S No. S-G-8646 [image online!]).

Acanthophyllum ekbergii (Hedge & Wendelbo) A.Pirani & Rabeler, **comb. nov.** ≡ *Diaphanoptera ekbergii* Hedge & Wendelbo in Notes Roy. Bot. Gard. Edinburgh 31(2): 333. 1972 – Holotype: Afghanistan. Prov. Baghlan, N side of Salang Pass, 3200 m, 22 Jul 1969, Wendelbo & Ekberg W-9844 (E barcode E00301816 [image online!]; isotypes: G barcode G00226756 [image online!], GB barcode GB-0047146! [image online!], W No. 1972-0007315 [image online!]).

Acanthophyllum flavum (Dickoré & Freitag) A.Pirani & Rabeler, **comb. nov.** ≡ *Ochotonophila flava* Dickoré & Freitag in Edinburgh J. Bot. 70(3): 406. 2013 – Holotype: Afghanistan, Bamiyan Prov., 6.4 km SSE of Bamiyan [city], 2729 m,

34.7697°N, 67.8505°E, 03 Jun 2008, *Jacobs & Schloeder 1664* (M barcode M-0164353 [image online!]; isotype: E n.v. [fide Dickoré & Freitag, 2013]).

Acanthophyllum kermanense (Bornm.) A.Pirani & Rabeler, **comb. nov.** \equiv *Saponaria kermanensis* Bornm. in Repert. Spec. Nov. Regni Veg. 6: 302. 1909 \equiv *Psammophila kermanensis* (Bornm.) Ikonn. in Novosti Sist. Vyssh. Rast. 8: 273. 1971 \equiv *Psammophiliella kermanensis* (Bornm.) Ikonn. in Novosti Sist. Vyssh. Rast. 13: 117. 1976 – **Lectotype (designated here)**: Iran. Kuh i-Jupar, 2900–3800 m, 4 Jun 1892, *Bornmüller 2265, Iter Persico-Turcicum 1892-93* (JE barcode JE00016782 [image online!]; isotypes: K barcode K000725823 [image online!], P barcode P05017980 [image online!], WU No. 0107077 [image online!]).

Bornmüller did not indicate the location of the specimen cited in the protologue (Bornmüller, 1909). Bornmüller's original herbarium, including "zahlreichen darin enthaltenen Typen neuer Taxa" (numerous types of new taxa contained therein), was presented to B in 1938 (Wagenitz, 1960: 358). This suggests that it was his intent to have the type specimen of *S. kermanensis* at B. We are designating a lectotype for *Saponaria kermanensis* since the Caryophyllaceae (except for some Paronychioideae) was included in the list of 32 families that Wagenitz (1960) noted as "destroyed" during World War II. Of the four specimens of *Bornmüller 2265* that we located, the specimen at JE is chosen as the lectotype. Bornmüller was curator at JE (Herbarium Haussknecht) from 1904 to 1938 (Stafleu & Mennega, 1993) and, since some of the specimens of this collection may have been distributed in 1896 (see "Recd" on the K specimen and "Recu" on the P specimen), it seems likely that he would have had access to this specimen as well as that in his personal herbarium at the time of the publication of the protologue.

Acanthophyllum lindbergii (Hedge & Wendelbo) A.Pirani & Oxelman, **comb. nov.** \equiv *Diaphanoptera lindbergii* Hedge & Wendelbo in Arbok Univ. Bergen, Mat.-Naturvitensk. Ser., 18: 18. 1964 ("1963")– Holotype: Afghanistan. Inter Belchiragh et Darrah Abdullah, 1100 m, 28 May 1962, *Hedge & Wendelbo W-3692* (E barcode E00301815 [image online!]; isotypes: BG n.v., W No. 1972-0007395 [image online!]).

Acanthophyllum luteum (Falat. & Mahmoodi) A.Pirani & Kovalchuk, **comb. nov.** \equiv *Allochrusa lutea* Falat. & Mahmoodi in Phytotaxa 277(2): 193. 2016 – Holotype: Iran. Zanjan province, 20 km on the Zanjan–Tabriz road, beginning of Esfejin–Mirjan road, 1570 m, 36°44'22.38"N, 48°14'35.88"E, 5 Jun 2016, *Mahmoodi & Ashrafi 100472* (TARI!).

Acanthophyllum makranicum (Rech.f.) A.Pirani & Rabeler, **comb. nov.** \equiv *Saponaria makranica* Rech.f. in Pl. Syst. Evol. 141: 83. 1982 \equiv *Gypsophila makranica* (Rech.f.) Ghaz. in Nasir & Ali, Fl. Pakistan 175: 94. 1986 – Holotype: Pakistan. Makran: Nag inter Panjgur et Surab, Substr. Tonschiefer, 1300 m, 26°58'N, 64°06'E, 21 Apr 1965, *Rechinger 28265* (W No. 1994-0007441 [image online!]; isotypes: B barcode B 10 0366295 [image online!], G, barcode G00226955 [image online!], GZU [herb. Rechinger] barcode GZU000273158 [image online!], K, barcode K000725827 [image online!]).

Acanthophyllum stenocalycinum (Rech.f. & Schiman-Czeika) A.Pirani & Moazzeni, **comb. nov.** \equiv *Diaphanoptera stenocalycina* Rech.f. & Schiman-Czeika in Rechinger, Fl. Iranica 163: 334. 1988 – Holotype: Iran. [Golestan National Park] planitie "dasht" ad viam versus Almeh ducentem N Rebat-e Qareh Bil, 1200 m, 37°19'N, 56°26'E, 5 Jun 1975, *Rechinger 52881* (W No. 1988-0009800 [image online!]; isotypes: B barcode B 10 0365634! [image online!]; E barcode E00301814 [image online!], G barcode G00226755 [image online!], GZU barcode GZU000273151 [image online!], MA barcode MA 496942 [image online!], S No. S-G-8645 [image online!], WU No. 0035437! [image online!]).

AUTHOR CONTRIBUTIONS

AP: Supervising the study, specimen study, plant collection, laboratory procedures, molecular analyses, manuscript preparation. HM: Plant collection, laboratory procedures, molecular analyses, manuscript revision. SZ: Providing some sequences, manuscript revision. RKR: Nomenclatural editing, manuscript revision, providing some references, some taxonomic novelties in the study group. BO: Providing some sequences, manuscript revision. AVP: Specimen study, plant collection. AK: Specimen study, plant collection, laboratory procedures, manuscript revision. — AP, <https://orcid.org/0000-0003-4937-5711>, apirani@um.ac.ir; HM, <http://orcid.org/0000-0002-2406-2666>, hmoazzeni@um.ac.ir; SZ, <https://orcid.org/0000-0001-9159-1800>, zarre@khayam.ut.ac.ir; RKR, <https://orcid.org/0000-0002-6765-0353>, rabeler@umich.edu; BO, <https://orcid.org/0000-0002-6104-4264>, bengt.oxelman@bioenv.gu.se; AVP, <https://orcid.org/0000-0003-2494-02>, alexpavlenko1974@gmail.com; AK, <https://orcid.org/0000-0001-8704-4644>, andriy.kovalchuk@helsinki.fi.

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Appendix 1. Voucher information.

Species name, geographic origin, collector(s), voucher, (herbarium), GenBank accession numbers for ITS and *rps16*, respectively (* indicates sequences generated in this study; – indicates missing data).

Acanthophyllum acerosum Sosn., Iran, W Azarbaijan, Zarre & al. 41900 (TUH), KF924680, KF924732; *Acanthophyllum aculeatum* Schischk., Uzbekistan, Nuratau mountains, Qo'ytosh range, Botschantzev & Kamelin 01042334 (LE), *MN310905, *MN310752; *Acanthophyllum adenophorum* Freyn, Iran, Khorassan, Pirani & Moazzeni 1947 (TMRC), KF924679, KF924731; *Acanthophyllum allochrusoides* (Gilli) A.Pirani, Afghanistan, Bamian, Wendelbo & Ekberg W9801 (GB), KF924627, KF924682; *Acanthophyllum andarabicum* Podlech ex Schiman-Czeika, Afghanistan, Baghlan, Podlech 10985 (MSB), KF924678, KF924730; *Acanthophyllum andersenii* Rech.f. & Schiman-Czeika, Iran, Khorassan, Anders & Peterson 320 (GB), KF924677, KF924729; *Acanthophyllum anisocladum* Schiman-Czeika, Afghanistan, Lugar, Ekberg W9180 (GB), KF924676, KF924728; *Acanthophyllum aphananthum* Rech.f., Afghanistan, Kabul, Rechinger 31265 (M), KF924626, KF924681; *Acanthophyllum borsczowii* Litv., Iran, Khorassan, Zarre & al. 41034 (TUH), KF924675, KF924727; *Acanthophyllum bracteatum* Boiss., Iran, Kohghiluyeh & Boyerahmad, Pirani & Moazzeni 2104 (TMRC), KF924674, KF924726; *Acanthophyllum caespitosum* Boiss., Iran, Hamadan, Zarre & al. 41903 (TUH), KF924673, KF924725; *Acanthophyllum cerastioides* (D.Don) Madhani & Zarre, NW Pakistan, Swat, in valle Jabba E Kolalai, substr. Granit, 1600–2200 m, 4 Jun 1965, Rechinger 30724 (M), MF401122, MF401168; *Acanthophyllum coloratum* Schischk., Kyrgyzstan, jugum Ferganense, declive generale boreali-orientale, systema fl. Alabuga, 2400 m, 6 Aug 1995, Lazkov & Milko 01042337 (LE), *MN310906, *MN310753; *Acanthophyllum crassifolium* Boiss., Iran, Mazandaran, Pirani & Moazzeni 41702 (TUH), KF924672, KF924724; *Acanthophyllum crassinodum* Yukhan. & J.R.Edm., Iran, Kerman, Pirani & Moazzeni 2923 (TMRC), KF924671, KF924723; *Acanthophyllum diezianum* Hand.-Mazz., Iran, Khorassan, Zarre & al. 41040 (TUH), KF924670, KF924722; *Acanthophyllum ejtehadii* Mahmoudi & Vaezi, Iran, Khorassan, Pirani & Moazzeni 2181 (TMRC), KF924669, KF924721; *Acanthophyllum elatius* Bunge 1, Turkmenistan, Karakum desert, sands near lake Ýasga, Rodin & al. 01042340 (LE), *MN310907, *MN310754; *Acanthophyllum elatius* 2, Tajikistan, Amu Darya basin, sand ripple on the second terrace, Nikitin 01042342 (LE), *MN310908, *MN310755; *Acanthophyllum glandulosum* Bunge ex Boiss., Iran, Khorassan, Zarre & al. 41037 (TUH), KF924668, KF924720; *Acanthophyllum gracile* Bunge ex Boiss., Iran, Semnan, Pirani & Moazzeni 2989 (TMRC), KF924667, KF924719; *Acanthophyllum grandiflorum* Stocks, Afghanistan, Bamian, Podlech 1340 (MSB), KF924666, KF924718; *Acanthophyllum gypsophiloides* Regel 1, Kazakhstan, Karatau mountains, Boralday range, Koshkarata river valley, Ebel 004118 (TK), *MN310913, *MN310760; *Acanthophyllum gypsophiloides* 2, Uzbekistan, Tashkent region, clayey-stony slope above Chatkal river, 9 Jun 2015, Gaziev iso– H 1773967 (TASH), *MN310914, *MN310761; *Acanthophyllum heratense* Schiman-Czeika, Iran, Isfahan, Pirani & Moazzeni 2152 (TMRC), KF924665, KF924717; *Acanthophyllum herniarioides* (Boiss.) Madhani & Zarre, Tajikistan, N von Dushanbe Anzob-Pass im Gissar-Massiv, ca. 3400 m, 14 Jul 1975, Mueller-Doblies 75083 (B), MF401123, –; *Acanthophyllum heterophyllum* Rech.f., Iran, Kerman, Pirani & Moazzeni 2921 (TMRC), KF924664, KF924716; *Acanthophyllum honigbergeri* (Fenzl) Barkoudah, E Afghanistan, Gardes, in altoplanitie lapidosa vallis Logar 50 km N Gardez, 33°37'N 69°09'E, 2000 m, Rechinger 35371 (B), MF401125, MF401176; *Acanthophyllum kabulicum* Schiman-Czeika, Afghanistan, Ghazni, Frey s.n. (GB), KF924663, KF924715; *Acanthophyllum kandaharicum* Gilli, Iran, Khorassan, Joharchi & Zangouei 36245 (FUMH), KF924662, KF924714; *Acanthophyllum korolkowii* Regel & Schmalh., Turkmenistan, SW part of Uchtagan

sands, semi-fixed sands, *Pavlenko 1773968* (H), *MN310909, *MN310756; *Acanthophyllum korshinskyi* Schischk., Iran, Khorassan, *Pirani & Moazzeni 2123* (TMRC), KF924661, KF924713; *Acanthophyllum kurdicum* Boiss. & Hausskn. ex Boiss., Iran, Ilam, *Hamzehee & Lashkarbolooki 1756* (TARI), KF924660, KF924712; *Acanthophyllum laxiflorum* Boiss., Afghanistan, Lugar, *Ekberg W9184* (GB), KF924659, KF924711; *Acanthophyllum laxiusculum* Schiman-Czeika, Iran, Qom, *Pirani & Moazzeni 1941* (TMRC), KF924658, KF924710; *Acanthophyllum leucostegium* Schiman-Czeika, Iran, Bandar Abbas, *Ghahreman & Mozaffarian 5656* (TUH), KF924657, KF924709; *Acanthophyllum lilacinum* Schischk., Afghanistan, Badghis, *Podlech & Jarmal 29855* (MSB), KF924656, –; *Acanthophyllum longicalyx* Hedge & Wendelbo, Afghanistan, Jawzjan, *Freitag 6580* (MSB), KF924655, KF924708; *Acanthophyllum macrodon* Edgew., Afghanistan, Kandahar, *Hedge & al. W7641* (GB), KF924654, KF924707; *Acanthophyllum microcephalum* Boiss., Iran, Tehran, *Rajamand & Bazargan 32055* (TARI), KF924653, KF924706; *Acanthophyllum mucronatum* C.A.Mey., Iran, W Azarbaijan, *Assadi & Olfat 68668* (TARI), KF924652, KF924705; *Acanthophyllum myrianthum* (Rech.f.) Madhani & A.Pirani, C Afghanistan, Deh Kundi: in saxosis 10 km w Shahrestan, 33°40'N 66°35'E, versus Deh Kundi, 34°10'N 66°07'E, 2200 m, 1967, *Rechinger 36812* (B), MF401124, –; *Acanthophyllum oppositiflorum* Aytac, Turkey, Sivas, *Aytac 7476* (GAZI), KF924651, KF924704; *Acanthophyllum pachycephalum* Schiman-Czeika, Iran, Tehran, *Ganjalizadeh 6106* (TUH), KF924650, KF924703; *Acanthophyllum pachystegium* Rech.f., Afghanistan, Badakhshan, *Hedge & Wendelbo W9282* (GB), KF924649, KF924702; *Acanthophyllum paniculatum* Regel & Herder, [no detailed data available], JN589016, –; *Acanthophyllum pleiostegium* Schiman-Czeika, Afghanistan, Kataghan, *Grey-Wilson & Hower 1320* (GB), KF924648, KF924701; *Acanthophyllum pulchrum* Schischk., Tajikistan, stony slopes at Panj river, *Botschantzev & Egorova 01042349* (LE), *MN310910, *MN310757; *Acanthophyllum pungens* (Bunge) Boiss., Kazakhstan, NW ridges of Dzungarian Alatau, hamada, *Goloskokov 01042352* (LE), *MN310911, *MN310758; *Acanthophyllum raphiophyllum* (Rech.f.) Barkoudah, Afghanistan, Kapisa, *Podlech 12548* (MSB), KF924647, KF924700; *Acanthophyllum sarawschanicum* Golenkin, Uzbekistan, Kyr-Tau mountains, *Kamelin & al. 01042363* (LE), *MN310912, *MN310759; *Acanthophyllum scapiflorum* (Akhtar) Schiman-Czeika, Afghanistan, Kabul, *Podlech 31232* (MSB), KF924646, KF924699; *Acanthophyllum schugnanicum* Schischk., Afghanistan, Bamian, *Wendelbo & Ekberg W9796* (GB), KF924645, KF924698; *Acanthophyllum sordidum* Bunge ex Boiss., Iran, Isfahan, *Pirani & Moazzeni 2147* (TMRC), KF924644, KF924697; *Acanthophyllum speciosum* Rech.f. & Schiman-Czeika, Iran, Khorassan, *Pirani & Moazzeni 2186* (TMRC), KF924643, KF924733; *Acanthophyllum spinosum* C.A.Mey., Iran, Isfahan, *Pirani & Moazzeni 2150* (TMRC), KF924642, KF924696; *Acanthophyllum squarrosum* Boiss., Iran, Semnan, *Pirani & Moazzeni 2974* (TMRC), KF924641, KF924695; *Acanthophyllum stewartii* (Thoms. ex Edgew. & Hook.f.) Barkoudah, Afghanistan, Khost, *Anders 8994* (MSB), KF924640, KF924694; *Acanthophyllum stocksianum* Boiss., Afghanistan, Kandahar, *Toncev s.n.* (MSB), KF924639, KF924693; *Acanthophyllum subglabrum* Schischk., Afghanistan, Nangarhar, *Hedge & al. W7483* (GB), KF924638, KF924692; *Acanthophyllum tadshikistanicum* (Schischk.) Schischk., Tajikistan, Kara-Tau mountains, W of bridge over Kyzyl-Su river, crevices of limestone rocks, *Botschantzev & Egorova 01020716* (LE), *MN310917, *MN310764; *Acanthophyllum verticillatum* Hand.-Mazz., Iran, Markazi, *Mozaffarian & Sardabi 42175* (TARI), KF924637, KF924691; *Acanthophyllum xanthoporphyranthum* Hedge & Wendelbo, Afghanistan, Herat, *Hedge & al. W8003* (GB), KF924636, KF924690; *Acanthophyllum yasamin-nassehiae* Joharchi & Pirani, Iran, Khorassan, *Memariani & Zangouei 41448* (FUMH), KF924635, KF924689; *Allochrysa bungei* Boiss., Iran, E Azarbaijan, *Rechinger 43834* (M), KF924634, KF924688; *Allochrysa lutea* Falat. & Mahmoodi, Iran, Zanjan, *Mahmoodi & Ashrafi 100481* (TARI), *MN310915, *MN310762; *Allochrysa persica* Boiss., Iran, East Azarbayegan, *Assadi & Mozaffarian 30542* (TARI), *MN310916, *MN310763; *Allochrysa versicolor* (Fisch. & C.A.Mey.) Boiss., Turkey, Kars, *Nydegger 43597b* (MSB), KF924633, KF924687; *Cyathophylla viscosa* (C.A.Mey.) Madhani & Rabeler, Armenia, Vayotsdzor Prov., Vajk Distr, road Vajk–Kochbek, ca. 8 km ENE Vajk, gorge of Darab river, sandy area, 1380 m, 26 Jun 2002, *Optima Iter XI/1846* (M), MF401117, MF401165; *Diaphanoptera afghanica* Podlech, Afghanistan, Baghlan, *Podlech 21075* (MSB), KF924632, –; *Diaphanoptera ekbergii* Hedge & Wendelbo, Afghanistan, Takhar, *Podlech 11848* (MSB) & *11760* (MSB), KF924631, KF924686; *Diaphanoptera*

khorsanica Rech.f., Iran, Khorassan, SW Kalat-e Naderi, *Joharchi & Memariani 4545* (FUMH), *MN310918, *MN310765; *Diaphanoptera lindbergii* Hedge & Wendelbo, Afghanistan, Fariab, *Hedge & al. W8336* (GB), KF924630, KF924685; *Diaphanoptera stenocalycina* Rech.f. & Schiman-Czeika, Iran, Golestan, *Attar & Mehdigholi 24422* (TUH), KF924629, KF924684; *Diaphanoptera transhyrcana* (Preobr.) Rech.f. & Schiman-Czeika, Turkmenistan, Great Balkan (Uly Balkan) range, *Pavlenko 1773969* (H), *MN310919, *MN310766; *Heterochroa desertorum* Bunge, Russia, Tuviskaja ACCP, Tuva Distr., Ovjur, prope pagum Ak-Czyra Cleistogeneto-Nanphyteta Stepposa, 3 Aug 1973, *Timokhina & Daniljuk 6371* (M), MF401118, MF401171; *Heterochroa violacea* Fenzl, [no detail data available], JN589068, –; *Kuhitangia knorringiana* (Schischk.) Bondarenko **1**, Uzbekistan, Nuratau mountains, Ak-Tau range, *Neustrueva & Tzyetkova 01020721* (LE), *MN310920, *MN310767; *Kuhitangia knorringiana* **2**, Uzbekistan, northern slopes of Ak-Tau range, 22 km E of Nurata, *Botschantzev & Kamelin 01020720* (LE), *MN310921, *MN310768; *Kuhitangia popovii* (Preobr.) Ovcz., Turkmenistan, Köýtendag (Kugitangtau) range, *Ovczinnikov & Astanova 01020725* (LE), *MN310922, *MN310769; *Saponaria kermanensis* Bornm., [no detailed data available], (B: B100591988), KX184037, –; *Saponaria kermanensis*, [no detailed data available], (B: B100591987), KX184038, –; *Saponaria makranica* Rech.f., W Pakistan, Baluchistan, Makran: Nag, inter Panjgur, 26°58'N, 64°06'E, et Surab, 28°29'N, 66°19'E, 1300 m, *Rechinger 28265* (W), *MN310923, *MN310770; *Yazdana shirkuhensis* A.Pirani & Noroozi, Iran, Yazd, Shirkuh mts, *Noroozi 2827* (WU), MK637517, MK651077.

Appendix S1. The alignment file for the ITS dataset in Fasta format.

Appendix S2. The alignment file for the *rps16* dataset in Fasta format.

Figure captions

[Figures prepared to final size: Fig. 1-3: 2 columns wide, captions below; Fig. 4: 15 cm wide, caption below.]

Fig. 1. Selected members of *Acanthophyllum* s.l. in natural habitats. **A–C**, *Acanthophyllum coloratum* (by Georgy Lazkov); **D & E**, *A. korolkowii* (by Alexander Pavlenko); **F–H**, *Allochrysa lutea* (by Mohammad Mahmoodi); **I & J** *Diaphanoptera khorsanica* (by Hamid Moazzeni & Farshid Memariani); **K**, *Diaphanoptera stenocalycina* (by Farshid Memariani); **L**, *Diaphanoptera transhyrcana* (by Alexander Pavlenko).

Fig. 2. Majority-rule consensus tree inferred from Bayesian analysis of ITS data (left side) and *rps16* data (right side). Posterior probability values are indicated above branches, ML bootstrap values below. Values below 0.5 or 50% are not shown. Colored boxes indicate taxa discussed in the present study.

Fig. 3. Putative secondary structures of the ITS1 RNA transcripts of *Diaphanoptera afghanica* (the ITS sequence obtained from Pirani & al., 2014). The conserved motif of Liu & Schardl (1994) [GGCRY-(4 to 7n)-GYGYCAAGGAA] is included in boxes.

Fig. 4. The phylogenetic positions of the 14 *Acanthophyllum* sections. Posterior probability values are indicated above branches, ML bootstrap values below. Values below 0.5 or 50% are not shown. The sections discussed in the present study are highlighted in bold, colored boxes. Sectional placement of species not included in boxes requires additional study.

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Table 1. A list of the recognized sections of *Acanthophyllum*, sectional position of species included in the present study, species excluded from their original sections and not repositioned in a new section.*

Recognized sections	Sect. <i>Acanthophyllum</i>	Sect. <i>Allochrusa</i>	Sect. <i>Aphanantha</i>	Sect. <i>Diaphanoptera</i>	Sect. <i>Kuhitangia</i>	Sect. <i>Macrodongta</i>	Sect. <i>Macrostegia</i>
Included species	<i>A. acerosum</i> <i>A. caespitosum</i> <i>A. crassifolium</i> <i>A. kurdicum</i> <i>A. microcephalum</i> <i>A. mucronatum</i> <i>A. oppositiflorum</i> <i>A. verticillatum</i>	<i>A. bungei</i> <i>A. lutea</i> <i>A. persica</i> <i>A. versicolor</i>	<i>A. aphananthum</i>	<i>A. diaphanopterum</i> <i>A. lindbergii</i> <i>A. stenocalycinum</i> <i>A. transhyrcanum</i>	<i>A. knorringianum</i> <i>A. popovii</i>	<i>A. macrodon</i> <i>A. grandiflorum</i> <i>A. xanthoporphyranthum</i>	<i>A. bracteatum</i> <i>A. gracile</i> <i>A. kandaharicum</i> <i>A. leucostegium</i> <i>A. pachystegium</i>
Excluded species	<i>A. pleiostegium</i>			<i>A. ekbergii</i>		<i>A. longicalyx</i>	
Recognized sections	Sect. <i>Ochotonophila</i>	Sect. <i>Oligosperma</i>	Sect. <i>Paniculata</i>	Sect. <i>Pleiosperma</i>	Sect. <i>Pseudacanthophyllum</i>	Sect. <i>Pseudomacrostegia</i>	Sect. <i>Scapiflora</i>
Included species	<i>A. allochrusoides</i>	<i>A. aculeatum</i> <i>A. adenophorum</i> <i>A. andarabicum</i> <i>A. andersenii</i> <i>A. borsczowii</i> <i>A. diezianum</i> <i>A. ejtheadii</i> <i>A. elatius</i> <i>A. heratense</i> <i>A. heterophyllum</i> <i>A. kabulicum</i> <i>A. korshinskyi</i> <i>A. laxiusculum</i> <i>A. lilacinum</i> <i>A. pachystegium</i> <i>A. pulchrum</i> <i>A. pungens</i>	<i>A. gypsophiloides</i> <i>A. paniculatum</i>	<i>A. crassinodum</i> <i>A. glandulosum</i> <i>A. schugnanicum</i> <i>A. spinosum</i>	<i>A. laxiflorum</i> <i>A. raphiophyllum</i> <i>A. stewartii</i>	<i>A. coloratum</i> <i>A. korolkowii</i> <i>A. sarawschanicum</i> <i>A. tadshikistanicum</i>	<i>A. anisocladum</i> <i>A. scapiflorum</i>

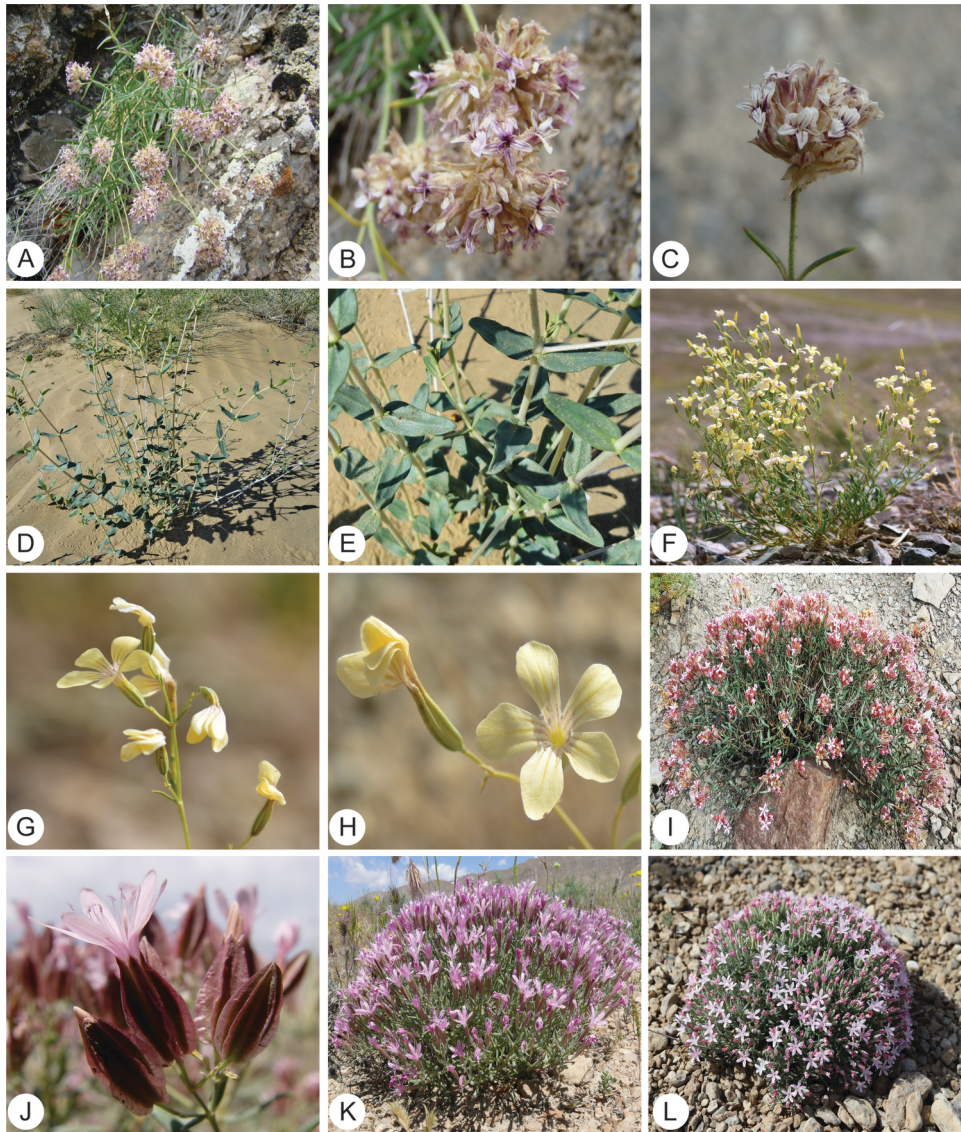
A. speciosum
A. squarrosum
A. stocksianum
A. subglabrum
A. yasamin-nassehiae

Excluded species

A. caespitosum

A. sordidum

* *Acanthophyllum cerastioides*, *A. hernarioides*, *A. honigbergeri*, *A. kermanense*, *A. makranicum*, and *A. myrianthum* have been transferred to *Acanthophyllum* which their sectional position is not resolved.



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