Molecular Biology Research Communications 2026;15(2):117-130 DOI:10.22099/mbrc.2025.54085.2198

Original Article MBRC Open Access

Molecular and Morphological evidence support the delimitation of a new genus, *Hafezia gen. nov*. in Arabideae (Brassicaceae)

Ahmad Reza Khosravi[*,#], **Atena Eslami-Farouji**[*,#]

Department of Biology, College of Science, Shiraz University, Shiraz, Iran

ABSTRACT

Recent molecular phylogenetic analyses within the tribe Arabideae (Brassicaceae) have uncovered unresolved lineages that challenge current generic boundaries. In this study, we incorporate molecular data with morphological evidence to resolve a long-standing taxonomic ambiguity, resulting in the description of a new monophyletic genus, *Hafezia* gen. nov., together with two new combinations, *H. aucheri* (Boiss.) A.R. Khosravi & A. Eslami-Farouji and *H. parvula* (Dufour ex DC.) A.R. Khosravi & A. Eslami-Farouji. Integrative taxonomy and phylogenetic insights, such as indels and substitution nucleotide variants, confirm the distinct assignment of these taxa, previously misassigned to *Arabis* L. Morphological reassessment, including traits such as simple, long setaceous hairs, notched petals, winged stamens, not compressed, not subtorulose or torulose fruits, supports their separation. The new genus naturally grows in the Mediterranean and west of the Irano-Turanian floristic regions. Our findings highlight the significance of integration of taxonomic investigations with the molecular investigations in clarifying evolutionary relationships and provide a revised key for accurate identification within Arabideae.

Keywords: Arabideae; *Arabis*; *Hafezia*; Cruciferae; Iran

INTRODUCTION

The genus *Arabis* L. (Arabideae, Cruciferae) has long been the subject of extensive taxonomic and phylogenetic investigations [1-5]. This genus, comprising approximately 80-99 species, is widely distributed across temperate regions of the northern hemisphere, excluding Mexico [2, 6]. Historically, *Arabis* and its allies posed significant taxonomic challenges due to their heterogeneity, reflecting poly- or paraphyletic lineages that were artificially grouped [2, 3, 7-10]. Early classifications based on morphology [11] lacked evolutionary context, resulting in generic complexes that required re-evaluation. Subsequent phylogenetic investigations using molecular data have provided clearer evolutionary insights. These studies led to the separation of unrelated lineages previously classified within *Arabis*. These include genera such as *Arabidopsis* Heynhold (described in 1842), *Boechera* Á.Löve & D.Löve, *Catolobus* (C.A. Mey.) Al-Shehbaz, *Dendroarabis* (C.A. Mey.) D. German & Al-Shehbaz, *Fourraea* Greuter & Burdet (Greuter and Burdet 1983), and *Pennellia* Nieuwl., *Streptanthus* Nutt, *Turritis* Tourn. ex

---

#: Both authors contributed equally

*Corresponding Authors: Department of Biology, College of Science, Shiraz University, Shiraz, Iran; Tel/Fax: +98 71 36137394; Email: arkhosravi@shirazu.ac.ir AND atena.eslami@shirazu.ac.ir

pISSN 2322-181X eISSN 2345-2005

L., [see 8, 12-14]. These phylogenetic advancements have contributed significantly to understanding generic delimitation within *Arabis*. However, despite these efforts, certain aspects remain weakly defined, necessitating further consideration.

While recent phylogenetic studies, such as those by Karl and Koch [3] and Walden et al. [5], suggest that two species within *Arabis*—*A. aucheri* Boiss. and *A. parvula* Dufour ex DC.—diverge from other members of the genus. *Arabis aucheri* and *A. parvula* constructed a distinct clade within Arabideae, and phylogenetically nested as a sister group to the *Draba* clade and the *Aubrieta* clade [5]. Therefore, this study aims to focus on the distinguishing morphological features across these taxa and evaluate the taxonomic status of these species. It proposes the establishment of a new genus to accommodate them, presenting two new combinations in the light of morphological traits and insights derived from molecular phylogenetic analyses.

MATERIALS AND METHODS

Plant material: To achieve the aforementioned objectives, we conducted a meticulous examination of both fresh and dry plant materials from specimens of *Arabis*, *Draba* Dill. ex L., and *Aubrieta* Adans during field studies across Iran from 2021 to 2024. These specimens have been formally deposited in the Herbarium of Shiraz University (HSHU). Moreover, we critically analyzed online databases from various virtual herbaria (B, BGBM, G, GBIF, HBG, JE, K, P, RBGE, and W), along with multiple Floras, including those of Iran, Europe, Middle Europe, Iberica, Orientalis, Turkey, and the USSR [15-21]. A thorough morphological examination was performed on representative specimens of *Arabis*, *Aubrieta*, *Draba*, as well as two newly identified taxa, *Arabis parvula* and *Arabis aucheri*. To establish sufficient morphological distinctions between the new entities and other *Arabis* species, we systematically documented the presence or absence of morphological features for each taxon based on referenced floras.

The list of studied *A. aucheri* and *A. parvula* accessions is provided in the Table S1. As phylogenetic analyses have confirmed *Draba* and *Aubrieta* as monophyletic genera, we included *Draba rimarum* (Rech.f.) A.R. Khosravi & A. Eslami-Farouji (previously classified within *Arabis* and now recognized as *D. rimarum* [4] and *Aubrieta parviflora* as representative taxa. For further reference, voucher specimens of *D. rimarum* can be found in our recent publication [4], while the voucher details for *Au. parviflora are* provided in Table S1.

Regarding phylogenetic analyses, authorities have conducted several notable studies to date [e.g., 3, 5, 9, 22], and their efforts have sufficiently confirmed the recognition of the new entity. Accordingly, we constructed an IQ Tree [23] using the best-fit model identified by Bayesian Information Criterion (BIC) scores and weights: GTR+F+G4. This analysis was based on concatenated genetic markers—ITS, alcohol dehydrogenase, and chalcone synthase [3]—to reestablish the distinct phylogenetic placement of the new genus described herein. Representatives from the genera *Arabis*, *Aubrieta*, and *Draba* were included, with *Pseudoturritis turrita* (L.) Al-Shehbaz was designated as the outgroup. The voucher information for the dataset used in this study is provided in Table S2. All sequences were aligned, edited by Mega version 11.0.13 [28], and concatenated with SequenceMatrix 1.7.8 software [29]. The resulting phylogenetic tree was visualized using FigTree version 1.4.3. Subsequently, we conducted a detailed manual inspection of the ITS, *trn*L-F, alcohol dehydrogenase, and chalcone synthase sequence alignments to annotate informative indels (insertions and deletions) and identify single-nucleotide apomorphic sites relevant to molecular inference. Subsequently, a t×n binary matrix was generated, in which 0 and 1 were used to show the absence and presence of characters, respectively. The absence of a character corresponds to the lack of an indel or single-nucleotide substitution, while its presence refers to the occurrence of such a mutation. The resulting Excel file was then converted to the NEXUS format, and a new analysis was performed by PAUP (ver. 4.0b10) to construct the Maximum parsimony (MP) tree.

Regarding light and Scanning Electron Microscopy investigations, we followed the methodology of Khosravi and Eslami-Farouji [4] and the terminology of Vaughan et al. [24].

RESULTS

This study marks the first investigation into the enigmatic "ghost" lineage comprising *A. aucheri* and *A. parvula* as distinct entities. Our findings are derived directly from the examination of fresh plant materials, supplemented by herbarium specimens and virtual herbaria. We provide a detailed description and visual representation of the distinctive morphological traits that differentiate these taxa from the original *Arabis* (Figs. S1-S6, Table S2).

As demonstrated in previous analyses [e.g., 3, 5] and this study (Fig. 1), the distinct identities of *A. aucheri* and *A. parvula* are well-designated. The results closely aligned with those of Karl and Koch (2013) and outline the genetic differentiation of *Arabis* into distinct clades: the Arabis alpina clade, Arabis nordmanniana clade, Arabis auriculata clade, and the main Arabis clade. Additionally, other studied taxa, including *Draba*, *Aubrieta*, and *Arabis aucheri* were nested within distinct clades. Based on phylogenetic analyses performed by the researchers [e.g., 5], *Draba* and *Aubrieta* have emerged as the most closely related genera to *A. aucheri* and *A. parvula*.

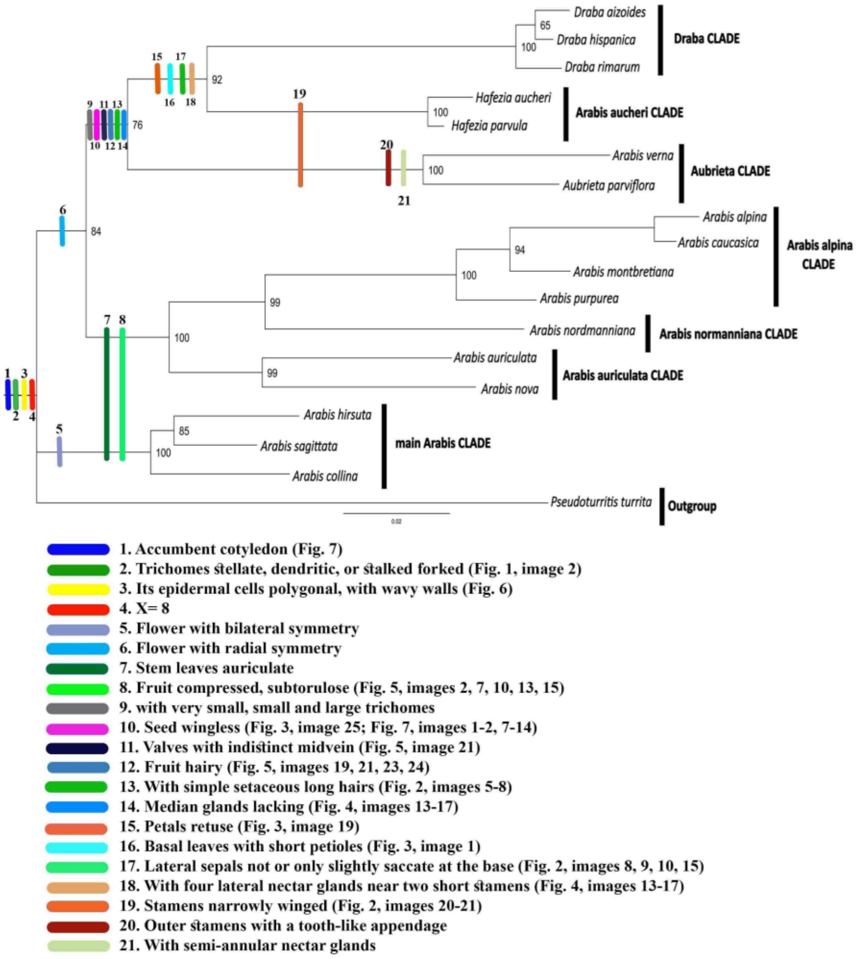

Figure 1: The common morphological characters identified in representatives of the genera *Arabis*, *Aubrieta*, *Hafezia*, and *Draba* are presented in this study. The phylogenetic tree has been constructed following the framework proposed by Karl and Koch (2013), using a combination of three genetic markers: ITS, Chalcone synthase, and alcohol dehydrogenase. Morphological characters that are infrequently observed in the studied genera have been excluded from analysis.

We manually examined indels (insertions and deletions) within the ITS, *trn*L-F, alcohol dehydrogenase, and chalcone synthase sequence datasets to identify phylogenetically informative variation across the clade Arabis aucheri and its related clades. A final sequence dataset for all investigated molecular markers demonstrated 13 indels (insertions or deletions) and 242 substitutions with unique synapomorphies and phylogenetic signals (Table 1).

Table 1: The list of synapomorphic indels and substitution nucleotides associated with the deeper phylogenetic divergence among the studied taxa in *Arabis aucheri* and related species is provided.

Deeply and recently diverged clades	Number of indels	Number of nucleotide substitutions
Arabis aucheri, Draba & Aubrieta Clades	Alcohol dehydrogenase: 1	Alcohol dehydrogenase: 4 Chalcone synthase: 1
Aubrieta & Arabis aucheri Clades	---	Alcohol dehydrogenase: 3 Chalcone synthase:5
Aubrieta & Draba Clades	---	Alcohol dehydrogenase: 1
Arabis aucheri & Draba Clades	---	Alcohol dehydrogenase: 2 Chalcone synthase: 5 ITS: 1 *Trn*L-F: 1
Draba clade	Alcohol dehydrogenase: 2 *Trn*L-F: 1	Alcohol dehydrogenase: 15 Chalcone synthase: 16 ITS: 4 *Trn*L-F: 12
Arabis aucheri clade	Alcohol dehydrogenase: 1 *Trn*L-F: 1	Alcohol dehydrogenase: 10 Chalcone synthase: 15 ITS: 2 *Trn*L-F: 11
Aubrieta clade	Alcohol dehydrogenase: 1 *Trn*L-F: 1	Alcohol dehydrogenase: 16 Chalcone synthase: 8 ITS: 15 *Trn*L-F: 3
Arabis nordmanniana, Arabis alpina, Arabis auriculata, Aubrieta Clades	---	Chalcone synthase: 1
Arabis alpina, Arabis nordmanniana & Arabis auriculata Clades	---	Alcohol dehydrogenase: 4 Chalcone synthase: 1
Arabis nordmanniana & Arabis auriculata Clades	---	Chalcone synthase: 1
Arabis alpina & Arabis nordmanniana Clades	---	Alcohol dehydrogenase: 3 Chalcone synthase: 1
Arabis nordmanniana, Arabis alpina, Arabis aucheri Clades	---	Alcohol dehydrogenase: 1
Arabis alpina Clade	---	Alcohol dehydrogenase: 5 Chalcone synthase: 10 ITS: 4
Arabis nordmanniana Clade	Chalcone synthase: 1	Alcohol dehydrogenase: 9 Chalcone synthase: 3 ITS: 5
Arabis auriculata Clade	Alcohol dehydrogenase: 1 Chalcone synthase: 1	Alcohol dehydrogenase: 1 Chalcone synthase: 2 ITS: 7
Main Arabis clade	ITS: 1 *Trn*L-F: 1	Alcohol dehydrogenase: 2 Chalcone synthase: 2 ITS: 7 *Trn*L-F: 3
Outgroup	---	Alcohol dehydrogenase: 6 Chalcone synthase: 14

Note: For more information, see Figure 1 and Supplementary Tables S3-S4. We used the non-italicized format for each clade name because each clade refers to more than one species.

A notable indel was observed in the *trn*L-F region, comprising 367-bp to 373-bp insertion/deletion (GTAAAAT) that distinguishes the main Arabis clade from the remaining clades (Table S3). Another unique indel in the ITS molecular marker was identified in the main Arabis clade, spanning nucleotide positions 363 to 373 bp (GTAAAAT) (Fig. 2, Table S3).

Within Arabis auriculata Clade, two indels were identified: three 3-bp insertion (TTT) between positions 1233 and 1235 in the alcohol dehydrogenase gene, and a 4-bpindel (TATT) between nucleotide positions 460- 463 in the chalcone synthase molecular marker (Fig. 2, Table S3).

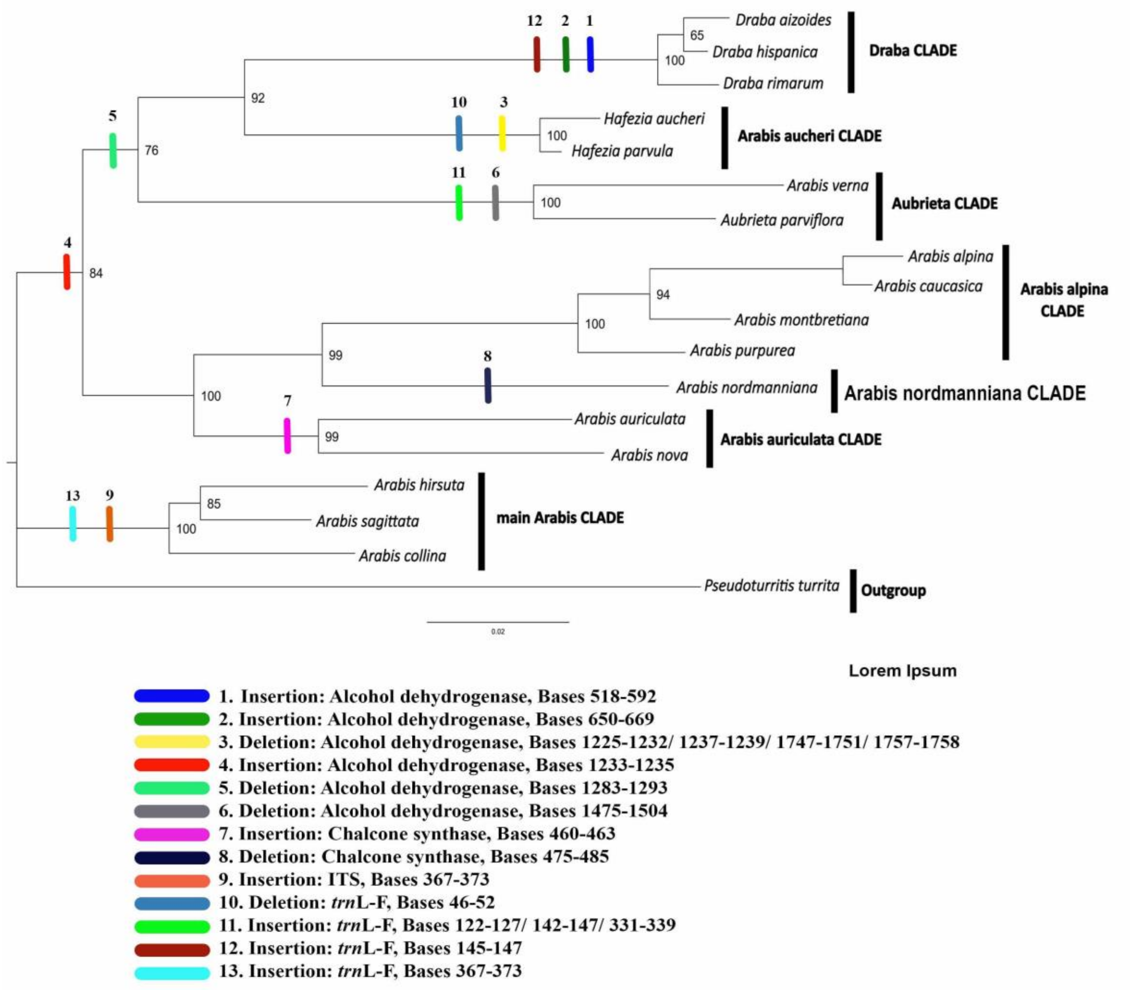

Figure 2: The list of synapomorphic indels (insertions and deletions) within the ITS, *trn*L-F, alcohol dehydrogenase, and chalcone synthase molecular markers across the Arabis aucheri clade and its relatives.

Arabis nordmanniana Clade is uniquely characterized by a 10-bp indel (AGTTAGTTTTT) spanning nucleotide positions 475-485 in the chalcone synthase molecular marker, absent in all other clades. No indels were detected in the Arabis alpina Clade across the examined markers (Fig. 2, Table S3).

A distinct 10-bp indel (TTGATATGTTG) between positions 1283-1293 in the alcohol dehydrogenase gene was found exclusively in Clades Arabis aucheri, Draba, and Aubrieta, suggesting a shared evolutionary signal among these clades. Additionally, two large indels were identified in the clade Draba: one spanning 518-592 bp and another from 650-669 bp in the alcohol dehydrogenase gene, with aligned sequences TGAGATTGAGATTGGTTCTTATGTA GGATTTTTGAAGAAAGGCTTAATCTTTCTTCATTTTTCAGTGTTTAAAGT and TTTAT TCATTTTTGGGTAGT, respectively (Fig. 2, Table S3).

In the *trn*L-F region, a 3-bp indel (AAG) was detected between positions 145-147. Several indels were also observed in Arabis aucheri Clade within the alcohol dehydrogenase gene:

1225-1232 bp (AGTCTTTT), 1237-1239 bp (GAC), 1747-1751 bp (CTAAT), and 1757-1758 bp (AA) (Table S3). Furthermore, a 7-bp indel (TTTTTTT) was found between positions 46-52 in the *trn*L-F molecular marker (Fig. 2, Table S3).

The Aubrieta clade is distinguished by a 30-bp indel (1475-1504 bp) in the alcohol dehydrogenase gene, and three additional indels in *trn*L-F molecular marker: 122-127 bp (TTATTA), 142-147 bp (TCTTGT), and 331-339 bp (TTAATTGAC), which collectively differentiate it from other clades (Fig. 2, Table S3).

Regarding the significance of single-nucleotide variants, unique single-nucleotide substitutions were also evaluated across all studied clades and are presented in Table S4. Indeed, distinctive nucleotide substitutions are useful in distinguishing clades at both deep and shallow levels of phylogenetic divergence. Here, we outline the synapomorphic indels and nucleotide substitutions across four molecular markers (alcohol dehydrogenase, chalcone synthase, ITS, *trn*L-F), observed in both deeply diverged main clades and more recently diverged (shallow) clades, as presented in Table 1. For example, one synapomorphic indel and five unique nucleotide substitutions differentiate the main clade, including Clades Draba, Arabis aucheri, & Aubrieta (Table 1). Additionally, five distinctive nucleotide substitutions were identified that separate another deeply diverged clade, comprising clades Arabis alpina, Arabis nordmanniana & Arabis auriculata (Table 1).

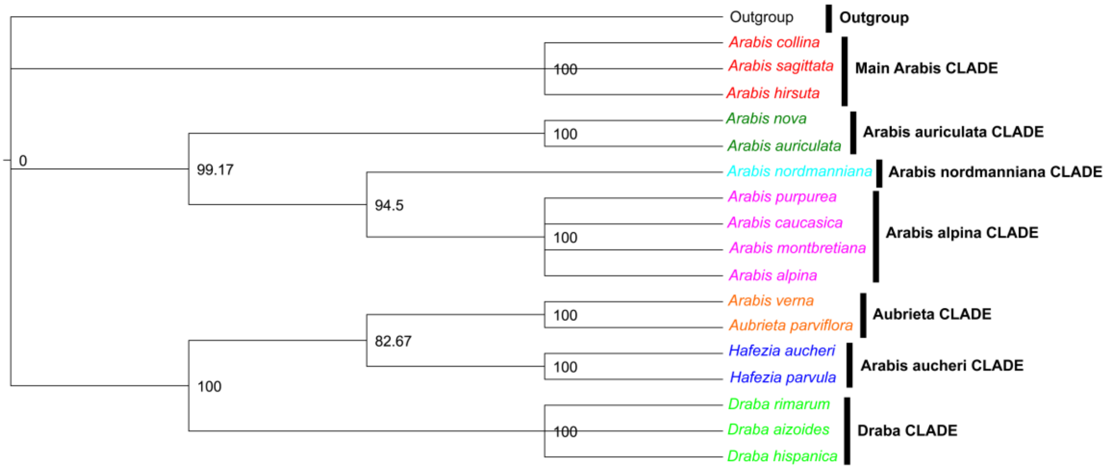

Figure 3: A Maximum parsimony (MP) tree generated from a t×n binary matrix, in which 0 and 1 were used to show the absence and presence of characters, respectively. These characters directly correspond to indels (insertions or deletions) and single-nucleotide substitutions in each clade. For more information, see Table 1.

In less deeply diverged clades (Fig. 1), such as the combination of Arabis aucheri and Draba clades (with nine substitutions), and the Arabis alpina & Arabis nordmanniana clades (with five substitutions), distinctive nucleotide substitutions were detected from their relatives.

In recently diverged clades, three synapomorphic indels and 47 nucleotide substitutions clearly distinguished the Draba clade from its closest relatives. The distinctive phylogenetic position of the Arabis aucheri clade is also well-supported by two indels and 38 nucleotide substitutions (Table 1). Additionally, the Aubrieta clade is differentiated by two indels and 42 substitutions. No indel is detected in the Arabis alpina clade, while Arabis nordmanniana and Arabis auriculata clades are characterized by one and two indels, respectively. However, all three clades are fully separated based on 19, 17, and 10 nucleotide substitutions, respectively. The main Arabis clade is further distinguished from the remaining recently diverged clades by two indels and 14 nucleotide substitutions.

All the aforementioned indels and nucleotide substitutions are considered synapomorphic characters that broadly distinguish the Arabis aucheri Clade, supporting its reassignment to a new genus. Interestingly, the t×n binary matrix, incorporating apomorphic characters such as indels (insertions or deletions) and single-nucleotide substitutions, clearly revealed the main clades within Arabideae, as well as the distinct identities of *A. aucheri* and *A. parvula* (Fig. 3).

Consequently, this study investigates the key morphological characteristics of these species alongside representatives of *Draba* and *Aubrieta*.

Duration: The genus *Arabis* comprises annual, biennial, or perennial plants, with subshrubs being a rarity. Among *Arabis* species, the majority are perennial, while some exhibit an annual or biennial life cycle. Notably, *A. aucheri* and *A. parvula* belong to this annual group. *Draba* species display both annual and perennial life cycles, while *Aubrieta* specimens are perennials (Table 2).

Trichome: Through our observations of light microscopy (LM) photographs, we concluded that trichomes play a critical role in the generic circumscription of the studied taxa. A detailed examination of trichomes revealed significant variations within the representative genera we studied. The trichomes vary in size, shape, and type, and are primarily classified as eglandular trichomes, which include simple and stalked branch *indumenta* (Table 2, Fig. S1).

Long and setaceous simple trichomes are observed in *A. aucheri*, *A. parvula*, *Aubrieta parviflora*, and *Draba rimarum*, whereas *A. caucasica* Willd and *A. nova* Vill are characterized by short and non-setaceous trichomes (Figs. S1, S2). This type of trichome is also found in *Au. parviflora* and *D. rimarum* (Figs. S1, S2). *Arabis sagittata* (Bertol.) DC. is distinguished by non-setaceous simple trichomes (≤0.5 mm, very rarely up to 1 mm) and branched bifid trichomes. Furthermore, stalked branched trichomes, subclassified into bifid, trifid, and tetrafid indumenta, are observed in nearly all studied taxa, including the original *Arabis*, *A. aucheri*, *A. parvula*, *Aubrieta*, and *Draba* (Fig. S1). In contrast, 8-armed and dendroid trichomes are rarely distinguished (e.g., *Draba*) (Fig. S1, 28-35). However, branched trichomes differ among the studied representatives regarding size and density (Table 2, Figs. S1, S2).

Table 2: Morphological characters of the new genus, *Hafezia*, and its relatives

Taxa/ traits	***Arabis caucasica***	***Arabis nova***	***Arabis sagittata***	***Hafezia aucheri***	***Hafezia parvula***	***Draba rimarum***	***Aubrieta parviflora***
Duration	Perennial	Annual	Biennial	Annual	Annual	Perennial	Perennial
Branched Trichomes	Very small & small	Very small & small	Large & small	Very Small, small	Branched Trichomes	Very small & small	Very small & small
Simple trichome	Absent	Absent	Long & not setaceous	Long & setaceous	Long & setaceous	Long & setaceous	Long & non-setaceous
Stem leaves at the base	Ariculate	Ariculate	Ariculate	Rounded	Rounded	Cuneate, very rarely auriculate	Attenuate
Lateral sepal base	Saccate	Saccate	Saccate	Not saccate	Not saccate	Not saccate	Not saccate
Petal apex	Rounded or truncated	Rounded or truncated	Rounded or truncated	Emarginate	Emarginate	Emarginate	Rounded
Median nectar glands	Present	Present	Present	Absent	Absent	Absent	Absent
Filament	Wingless	Wingless	Wingless	Winged	Winged	Usually wingless	Winged & toothed
Fruiting pedicel	Long & thin	Short & thick	Long & thin	Short & thick	Short & thick	Long & thin	Long & thin
Fruit	Compressed	Compressed	Compressed	Not Compressed	Not Compressed	Compressed	Not compressed
Fruit surface	Torulose or subtorulose	Torulose or subtorulose	Torulose or subtorulose	Not subtorulose or torulose	Not subtorulose or torulose	Not Torulose or subtorulose	Not subtorulose or torulose
Fruit valve	With a distinct midrib	With a distinct midrib	With a distinct midrib	With an indistinct midrib	With an indistinct midrib	With an indistinct midrib	With an indistinct midrib
Fruit cover	Glabrous	Glabrous	Glabrous	With hair	With hair	Glabrous or with hair	With hair
Seed	Winged	Wingless	Winged	Wingless	Wingless	Wingless	Wingless

According to trichome cell size, we follow the evaluations of our recent manuscript [4]. Thus, within *Draba,* trichomes are categorized into five size classes: very small (<100 µm), small (100-200 µm), medium (>200-500 µm), large (>500 µm), and very large (>800 µm) (Fig. S1, 37-44). As this has been previously published, we have not elaborated further. Curious readers can refer to our earlier work on the distinct entity of *D. rimarum*. Except for some representatives of *Arabis* (e.g., *A. nova* and *A. caucasica*), which have very small and small trichomes, the rest are characterized by four trichome size levels, similar to *Draba.* The trichome size in *A. sagittata* is medium, very rarely reaching up to 800 µm. (Fig. S1). The largest simple trichomes are observed in *A. aucheri*, *A. parvula*, *D. rimarum*, and *Au. parviflora*, respectively (Figs. S1, S2). Overall, based on Figure 1, very small, small, medium, and large trichomes are observed in the Draba clade, the Arabis aucheri clade, and the Aubrieta clade. Interestingly, near each large trichome, very small to small trichomes are observed in *A. aucheri*, *A. parvula*, *D. rimarum*, and *Au. parviflora*. This is regarded as a common morphological character for this group (Table 2, Fig. S1).

The density of very small and small trichomes is also maximum in *A. aucheri*, *A. parvula*, *D. rimarum*, and *Au. parviflora* (Fig. S1). Except for the taxa exhibiting the highest density of large trichomes (Fig. S1, 27-35), representatives of *Arabis* are predominantly covered by very small to small branched trichomes (2- to 4-armed), accompanied by dendroid indumenta (Table 2; Fig. S1, 1-17).

Regarding stalk and ray size, the greatest sizes are observed in *A. aucheri* (2525 µm), *A. parvula* (2500 µm), *D. rimarum* (simple trichomes up to 1800 µm), *A. sagittata* (1000 µm), and *Au. parviflora* (474 µm). The highest stalk-to-ray proportions are estimated in *Au. parviflora,* and *D. rimarum,* and *A. aucheri* (46-76), whereas the lowest ratios are exhibited by *Arabis* representatives (41-43).

Leaf: The basal leaves of *A. aucheri*, *A. parvula,* and *Draba* species exhibit short petioles (Fig. S3). However, most *Arabis* species have long petioles. Among the defining features of the genus *Arabis*, the presence of auriculate or amplexicaul stem leaves stands out in most species (Fig. S3, 3-6). However, exceptions exist; species such as *A. aucheri* and *A. parvula* exhibit rounded stem leaf bases (Fig. S3). Moreover, stem leaves are cuneate and attenuate at the base in *D. rimarum* and *Au. parviflora*, respectively.

Sepal: In most *Arabis* species, the base of the lateral sepals takes on a saccate form; however, a few species deviate slightly, exhibiting either partially saccate or entirely non-saccate forms. Notably, *A. aucheri* and *A. parvula* belong to the non-saccate categories. *Draba rimarum* shares a similar sepal shape at the base to that of *A. aucheri* and *A. parvula,* whereas the sepals in the genus *Aubrieta* are saccate or non-saccate (Fig. S3).

Petal: Within *Arabis* species, the petal apex is typically rounded or truncate. However, *A. aucheri* and *A. parvula,* as well as *D. rimarum,* have an emarginate tip, setting them apart from other *Arabis* species (Fig. S3). In some *Draba* species, the petal apex is rounded (Table 2).

Stamen: In both *Arabis* and most *Draba* species, filaments lack wings or teeth. However, in the case of *A. aucheri* and *A. parvula,* similar to the genus *Aubrieta*, their filaments are winged (Table 2; Fig. 1, Fig. S3, 20-21).

Nectar glands: In the case of nectar glands, both *Draba* and *A. aucheri* and *A. parvula* are similar. They possess four lateral nectar glands near two short stamens (Fig. S4, 13-17). Additionally, we observed that representatives of the genus *Aubrieta* lack median glands, similar to *Draba* and *A.aucheri* and *A. parvula* (Clades Draba, Arabis aucheri and Aubrieta) (Fig. S4, 9-17). The nectar glands in *Aubrieta* are semi-annular in shape, open from the inside, and elongate downward toward two horns (Fig. S4, 9-12). *Arabis caucasica, A. nova,* and *A. sagittata exhibit* both median and lateral glands (Fig. S4, 1-8). However, the number of nectar glands varies within the genus *Arabis* [see 25]. For example, *A. nova* has four lateral and two median glands (or none) positioned near short stamens (Fig. S4, 1-4), while *A. Caucasica* and *A. sagittata are* characterized by two lateral and two median glands (Fig. S4, 5-8). In *A. caucasica*, the lateral nectaries are semi-annular and open inside, while the median ones are erect (Fig. S4, 5-8). Moreover, the lateral glands toward the gibbous parts of the lateral sepals elongate downward (Table 2; Fig. S4, 5-8).

Fruit pedicel: In both *A. aucheri* and *A. parvula*, the fruit pedicel is notably short and thick. Interestingly, its thickness aligns with that of the fruit—a unique characteristic that is very rarely observed in other *Arabis* species. Similar to the genus *Arabis*, long and thin fruiting pedicels are also detected in *Draba* and *Aubrieta* species (Figs. S3, S5).

Fruit: Across most *Arabis* species, the fruit typically exhibits a compressed form and may appear torulose or subtorulose (Fig. S5, 1-17). However, *A. aucheri* and *A. parvula* fruits are not compressed; instead, they are subtetragonous (Fig. S5, 18-22). Furthermore, these two species lack the torulose or subtorulose condition (Fig. S5, 18-22). Additionally, while most *Arabis* species are characterized by fruit valves with a prominent midrib (Fig. S5, 1-17), *A. aucheri* and *A. parvula* display an indistinct midrib (Fig. S5, 18-22). Considerably, the fruits of these two species, along with *Aubrieta* species (Fig. S5, 23-25), are densely covered in indumentum, a feature rarely observed in other species. The fruit is compressed in most *Draba* species (Fig. S5, 26-29), while it is compressed to non-compressed in *Aubrieta* (Fig. S5, 23-25). Fruit surface and valves are not subtorulose or torulose and without a distinct midrib in both mentioned species (Table 2, Fig. S5). The presence of hairy fruits is a common morphological characteristic of the clades Draba, Arabis aucheri, and Aubrieta (Fig. 1).

Septum: Across all studied taxa, the epidermal cells are arranged in parallel and wavy patterns along the axis of the fruit, and the configuration of all epidermal septum cells is irregularly polygonal, sinuate, or non-sinuate in shape (Fig. S6). *Aubrieta parviflora* septum cells are primarily characterized by polygonal shapes and lack elongated cells (Fig. S6, e-f), while *Arabis* (Fig. S6, a-d), *A. aucheri* (Fig. S6, g-h), and *Draba* (Fig. S6, i) contain these elongated cells. Notably, the highest number of elongated cells is observed in *A. aucheri* and *Draba* (Fig. S5, g-i).

The septum cell size differs between *Arabis* species (*A. caucasica* and *A. nova*) (Fig. S6, a-d) and *Au. parviflora* (Fig. S6, e-f), *A. aucheri,* and *D. rimarum* representatives (Fig. S5, g-i). *Arabis* specimens exhibit the same cell size (Fig. S6, a-d), while *D. rimarum* and *A. aucheri* have similar cell sizes (Fig. S6, g-i). Interestingly, *Arabis* species display the maximum septum cell size (Fig. S6, a-d), while the smallest is found in *Aubrieta parviflora* (Fig. S6, e-f). The septum cell sizes of *A. aucheri* and *D. rimarum* fall between these two extremes (Fig. S6, g-i). The cell wall thickness is dissimilar among the studied taxa; for example, the septum cell wall thickness is highest in *Arabis* specimens, whereas the lowest cell wall thickness is detected in *Draba rimarum* (Fig. S6, i). In the fruit septum, cell outlines are arranged into two distinct types: sinuate and slightly undulated. The former is readily detected in the studied species of *Arabis* (*A. caucasica* and *A. nova*) (Fig. S6, a-d), while the latter is displayed in the other studied species (*Au. parviflora*, *A. aucheri*, and *D. rimarum*) (Fig. S6, e–i).

Seed: Among most *Arabis* species, approximately 69% of seeds possess wings, while a smaller proportion (21%) lack them (Fig. S7, 1-6). Notably, *A. aucheri*, *A. nova*, and *A. parvula* fall into the category of wingless seeds, characterized by their absence of a keeled margin. The genera *Draba* and *Aubrieta* are similar to the new entity and lack wings in their seeds (Table 2, Fig. S7, 7-9;13-15).

Except for *D. rimarum* (Fig. S7, 13-15), which has an oval seed shape, the seeds of the remaining taxa are oblong to elliptic (Fig. S7). *Draba rimarum* also differs in its spapillate–tuberculate ornamentation (Fig. S7, 13-15), while the other genera studied are characterized by reticulate ornamentation (Fig. S7, 1-12). However, the size and number of rings, as well as the size of craters (ocellate secondary structure) within each ring, vary. *Arabis aucheri* has the highest density and the lowest ring size (Fig. S7, 10-12), while *Au. parviflora* has the largest ring size with lower density (Fig. S7, 7-9).

Based on light microscopy images, mucilage production occurred whenever seeds were immersed (placed) in water, but the level varied among the specimens studied, and mucilaginous cells exhibit a distinct shape. *Arabis aucheri* exhibited the highest level of thickening on the outer tangential wall (Fig. S7, 10-12), while only slight amounts were present in the remaining taxa (Fig. S7).

Based on the studied representatives of the tribe Arabideae, the diameter of mucilage is maximum in the *Au. parviflora* (35.41 µm), while the smallest amount is found in *A. aucheri* (9.61 µm). The diameters of the studied *Draba* and *Arabis* species fall between these two extremes (Fig. S7). The number of mucilage cells was also estimated in a constant area of 40 $µm^2$. The highest density was observed in *A. aucheri* (38/40 $µm^2$), whereas the lowest density was detected in *Aubrieta* (2/40 $µm^2$). The number of mucilage cells is 18, 30, and 38 in *A. caucasica* (18), *A. nova* (30), and *D. rimarum* (38) in 40 $µm^2$, respectively (Fig. S7).

Phylogenetically, we identify some distinctive morphological characteristics considered either ancestral or derived (Fig. 1), which will be discussed later.

DISCUSSION

The generic placement of taxa within the tribe Arabideae has been addressed by various authorities [e.g., 3, 5, 9, 26]. Nevertheless, our current understanding of the generic morphological delimitation within the clade *Arabis* remains incomplete, and additional investigations will likely reveal further novelties.

Phylogenetically, we extensively examined several phylogenetic data regarding the tribe Arabideae from various scientists (e.g., Walden et al. [5], and references therein), and tried to explain common morphological characters for each distinct clade. Consequently, we are defining these characters herein:

Certain morphological characters, such as the presence of accumbent cotyledons, stellate, dendritic, or stalked forked trichomes, polygonal epidermal cells with wavy walls, and a base chromosome number of X=8, distinguish tribe Arabideae from other clades within the family Brassicaceae (Fig. 1). The genus *Arabis* is distinctive from the remaining clades (Draba, Arabis aucheri, and Aubrieta). Indeed, compressed and subtorulose fruits, along with auriculate stem leaves, are identified as common characteristics for the traditional *Arabis*, which includes the Arabis alpina clade, Arabis nordmanniana clade, Arabis auriculara clade, and the main clade Arabis (Figs. S3, S5, 1-17). Interestingly, the main *Arabis* clade is distinguished from the aforementioned clades by its bilaterally symmetrical flowers (Fig. 1), whereas the other clades are characterized by radially symmetrical flowers. Notably, Aubrieta, Arabis aucheri, and Draba Clades can be differentiated from the traditional *Arabis* based on six common characters (Fig. 1). The morphological features comprise simple setaceous long hairs, non-auriculate stem leaves, wingless seeds, valves with an indistinct midvein, and the presence of indumentum on the fruits (Fig. 1, Figs. S1-S3, S7). However, *Draba* species with auriculate stem leaves and winged seeds are very rare.

The clade *Aubrieta* is readily distinguished from the remaining clades by having a tooth-like appendage at the outer stamens (Fig. 1). However, the clade *Aubrieta* is similar to the clade *A. aucheri* in having narrowly winged stamens and fruits that are neither compressed nor subtorulose (Fig. 1).

The *A. aucheri* and *Draba* clades differ from the remaining clades by three common characters: basal leaves with short petioles, lateral sepals that are either not saccate at the base, and the presence of four lateral nectar glands near two short stamens without median glands (Fig. 1).

Based on indels outlined in Table S3, the distinctiveness of each clade (Fig. 1) is well-supported, and this finding corresponds with the results reported by Zhu [30]. Redelings and his colleagues [31] stated that indels, including insertions and deletions, are one of the most important causes of genetic variations. They also noted that the absence of standardized methodologies for evaluating this variation led to the exclusion of this information from analysis [31]. Indeed, most researchers tend to focus on point mutations—particularly nucleotide substitutions (Table S4)—rather than indels [31]. Earlier, Britten et al. [32] identified indels as the second significant form of genomic variation after point mutations. This observation was later corroborated by Birth and his research team [33]. The gaps resulting from indels are not only informative for resolving deeper evolutionary divergences [34], but also help to distinguish related species [35]. Additionally, it has been suggested that the phylogenetic character weight of an indel exceeds that of a nucleotide substitution [36]. Recent research published in 2024 highlights that indels are irreversible events and that insertion/deletion regions play a critical role in revealing phylogenetic signals [37].

In the course of field observations, taxonomic revisions of *Arabis* specimens within the Herbarium of Shiraz University (HSHU), along with a critical literature review [e.g., 2, 3, 5], we encountered a distinct taxonomic and phylogenetic position for *A. aucheri* and *A. parvula*. *Arabis aucheri* belongs to the eastern Mediterranean and west Irano-Turanian floristic regions and is closely related to *A. parvula,* which belongs to the west Mediterranean floristic region. We assume that both species are vicariant. Walden et al. [5] showed that *A. parvula* and *A. aucheri* do not belong to the genus *Arabis,* and they are phylogenetically sister to *Draba* and *Aubrietia*. There are common morphological traits between these two species, as well as the *Draba* and *Aubrietia* genera (Fig. 1, Table 2).

Notably, the use of homoplastic characters or characters (e.g., accumbent cotyledons, branched indumentum, latiseptate fruits) that evolved multiple times within the family Brassicaceae is not useful in generic circumscription [8] and leads to the wrong assignment or generic circumscription of taxa. Additionally, hybridization, reticulation, incomplete lineage sorting, and polyploidization lead to problematic gene trees within the tribe Arabideae, hindering the discovery of the true evolutionary history of taxa [2, 5, 22].

The present taxonomic work represents the distinct taxonomic status of the new entity within the tribe Arabideae. The studied specimens of *A. aucheri* and *A. parvula* differ from the rest of the genera, especially *Arabis*, by some morphological traits such as having and none-saccate sepals (vs. saccate sepals), winged filaments (vs. non-winged filaments), thickened fruit pedicels (vs. none-thickened fruit pedicels), dense trichomes present on the fruit valve (vs. trichomes absent or sparse on fruit valve), with long setaceous simple trichomes (vs. without long setaceous simple trichomes), Not subtorulose or torulosefruit (vs. subtorulose or torulose fruit), base of cauline leaves rounded (vs. base of cauline leaves ariculate or amplexicaul). These diverse morphological characters raise questions about the true identity of *A. aucheri* and *A. parvula*. Regarding the phylogenetic position of *Arabis* species, all phylogenetic analyses performed from previous decades up to now [e.g., 5] have confirmed the separate status of our novelty. Karl and his colleagues [9] used a specimen of *A. aucheri* from Syria, which nested near *A. parvula* in phylogenetic analyses. They concluded that annual species of *Arabis* (the *Arabis* annuals) (e.g., *A. aucheri* and *A. parvula*) construct (form) a distinct clade [9]. However, the inclusion of *A. aucheri* and *A. parvula* in various molecular studies [e.g., 3, 5, 9] has not resolved their precise phylogenetic positions within the genus. *Arabis aucheri* and *A. parvula* have striking morphological resemblance, but they are taxonomically differentiated by fruit shape, ploidy level, and geographical distribution. Geographically, the former species is widely distributed, while the latter has a more restricted distribution. In 1999, Koch and his co-workers [12] stated that morphological variations are insufficient in investigations, and molecular markers are necessary to delimit taxonomic boundaries. Today, by using large-scale genomic datasets (e.g., >900 genes in Walden et al. [5]) have demonstrated the potential to improve the resolution in phylogenetic investigations. In contrast, it is clear that earlier phylogenetic studies relying on a few genetic markers sometimes led to ambiguity in taxonomic circumscription. Nonetheless, morphological data still provide valuable complementary insights, particularly in cases where molecular approaches yield inconclusive results. For instance, both of ITS and *trn*L-F markers represent the inclusion of *A. aucheri* among *Arabis* species, probably due to the presence of polyploidy among the studied specimens. *Arabis aucheri* is sister to *A. parvula* based on the ITS and *trn*L-F markers with high clade support, but they nested within other *Arabis* species with low clade credibility [3]. Additionally, Walden and her co-authors found that *A. aucheri* and *A. parvula* failed to cluster together when they built the tree using consensus sequences acquired from HybPhaser (see Fig. S1 in Walden et al. [5] study). They also mentioned that the clades *Aubrieta* and *Draba muralis* L. are relatives of *A. aucheri* and *A. parvula*, respectively [5]. They hypothesize that this replacement is probably due to their identical ploidy levels [5]. Subsequently, they used sequences from HybPiper and ASTRAL-pro (all assembled paralogs) to construct a tree [5]. In this case, *A. aucheri* and *A. parvula* were closely related to the Clades *Tomostima* Raf. and *Draba*, respectively, with high posterior probabilities. However, as demonstrated in Walden et al. [5], paralogue placement approaches—though powerful—can be confounded by polyploidy and ancient hybridization events, limiting their ability to completely resolve lineage boundaries (see Fig. S13 in Walden et al. [5]). It is striking interesting that 994 genes constructed a tree only with diploid specimens, unraveling the true identity of this plant, as it nested near the *Draba* and *Aubrieta* clades. Obviously, *A. aucheri* is a diploid plant (2n), while *A. parvula* underwent an autopolyploidization event and was determined to be a ghost lineage (Fig. S25, cluster 25 in Walden et al., [5] research). Thus, all data supported the removal of *A. aucheri* and *A. parvula* to their own true genus.

Our results represent that the *A. aucheri* and *A. parvula* merge (transferred) from *Arabis* to the new genus *Hafezia*. *Hafezia* was initially described by Boissier [27] as *Arabis aucheri* and remained for many years. ARKH, who examined several materials of the taxon, found the true taxonomic position and proposed the distinct identity of *A. aucheri* from that of *Arabis*.

Taxonomic treatment: ***Hafezia*** A.R. Khosravi & A. Eslami-Farouji, ***gen. nov.*** **Type:** *Hafezia aucheri* (Boiss.) A.R. Khosravi & A. Eslami-Farouji

Description: Herbs are annual. Trichomes are formed by simple hairs, 1-2.5 mm, and branched hairs with 2-4 arms, shorter than the simple ones. Stems erect, simple, or branched from the base. Basal leaves, few, small, roseate, short petiolate, marcescent during flowering. Cauline leaves sessile and rounded at the base, entire or dentate. Racemes ebracteate, rigid, elongated in fruit, and slightly flexuous. Fruiting pedicels ascending, divaricate, as thick as the fruit. Sepals ovate or oblong, the base of the lateral pair subsaccate or not, margin membranous. Petals white; blade spatulate, apex emarginate; claw shorter than sepals. Stamens 6, tetradynamous; filaments winged; anthers ovate or oblong, obtuse at apex. One nectar gland on each side of the two transversal stamens; nectar glands in the median position lacking. Fruit dehiscent siliques, linear, latiseptate; valves thickened, reticulate, with an obscure midvein, smooth; replum rounded; septum complete, membranous, translucent, veinless; style short or obsolete; stigma capitate, entire. Seeds uniseriate, wingless, without keeled margin, ovoid, reddish-brown; seed coat smooth or minutely reticulate, slightly mucilaginous when wetted; cotyledons accumbent (Fig. S1-S6).

Etymology:—*Hafezia* is named in honor of the great Persian poet of Iran, “Hafez”. His tomb is already situated in Shiraz, south of Iran, near Haft Tanan Mountain. Indeed, we collected *Hafezia aucheri* from this region.

Key to the species of *Hafezia*

1a. Fruit linear, 30-50 x 1-2 mm ……………………………………….………*H. aucheri*

1b. Fruit ensiform,13-30 x 1.2-2 mm ……………………………….….……*H. parvula*

Hafezia aucheri (Boiss.) A.R. Khosravi & A. Eslami-Farouji, ***comb. nov.***

Basionym: *Arabis aucheri* Boiss., Ann. Sci. Nat., Bot., sér. 2, 17: 52 (1842). ≡ *Erysimum aucheri* (Boiss.) Kuntze in Revis. Gen. Pl. 2: 933(1891), nom. illeg.TYPE: Syria, “Alep”, s. d., Aucher-Eloy 97 (holotype G-BOIS barcode G00332065!, isotypes: BM barcodes BM000583662! &BM000583663!, P barcodes P00747456!, P00747457! & P00747458!).

Hafezia parvula (Dufour ex DC.) A.R. Khosravi & A. Eslami-Farouji ***comb. nov.***

Basionym: *Arabis parvula* Dufour ex DC., Syst. Nat. 2: 228 (1821). ≡ *Erysimum parvulum* (Dufour) Kuntze in Revis. Gen. Pl. 2: 933 (1891). TYPE: Spain, Navarra, Anon., #S.N. Syst. Nat. 2: 228 (1821) (syntypes: Andrzejowski s.n. (G00204737) and Dufour s.n. (G00204736), here designated lectotype: Dufour s.n., G barcode G00204736).

Acknowledgments: The authors would like to thank Shiraz University for their financial support.

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

Authors' Contribution: Both authors (ARKH and AEF) contributed equally to the writing, editing, and analysis process of this manuscript.

REFERENCES

1. Al-Shehbaz IA. The genera of Arabideae (Cruciferae; Brassicaceae) in the southeastern United States. J Arnold Arbor 1988;69:85-166.
2. Koch MA, Karl R, German DA, Al-Shehbaz IA. Systematics, taxonomy and biogeography of three new Asian genera of Brassicaceae tribe Arabideae: An ancient distribution circle around the Asian high mountains. Taxon 2012;61:955-69.
3. Karl R, Koch MA. A world-wide perspective on crucifer speciation and evolution: phylogenetics, biogeography and trait evolution in tribe Arabideae. Ann Bot 2013;112:983-1001.
4. Khosravi AR, Eslami-Farouji A. Gain a better understanding of the true entity of *Arabis rimarum* Rech. f., a misapplied plant under the name *Draba aucheri* Boiss. (Brassicaceae). Feddes Repert 2023;134:157-174.
5. Walden N, Kiefer C, Koch MA. Unravelling complex hybrid and polyploid evolutionary relationships using phylogenetic placement of paralogs from target enrichment data. Bio Rxiv 2024;2024-06.
6. Kiefer M, Schmickl R, German DA, Mandáková T, Lysak MA, Al-Shehbaz IA, Franzke A, Mummenhoff K, Stamatakis A, Koch MA. BrassiBase: introduction to a novel knowledge database on Brassicaceae evolution. Plant Cell Physiol 2014;55:e3.
7. Koch MA, Haubold B, Mitchell-Olds T. Comparative evolutionary analysis of chalcone synthase and alcohol dehydrogenase loci in *Arabidopsis*, *Arabis*, and related genera (Brassicaceae). Mol Biol Evol 2000;17:1483-1498.
8. German DA, Al-Shehbaz IA. Five additional tribes (Aphragmeae, Biscutelleae, Calepineae, Conringieae, and Erysimeae) in the Brassicaceae (Cruciferae). Harvard Pap Bot 2008;13: 165-170.
9. Karl R, Kiefer C, Ansell SW, Koch MA. Systematics and evolution of arctic-alpine *Arabis alpina* (Brassicaceae) and its closest relatives in the eastern Mediterranean. Am J Bot 2012; 99:778-794.
10. Karl R, Koch MA. Phylogenetic signatures of adaptation: The *Arabis hirsuta* species aggregate (Brassicaceae) revisited. Perspect Plant Ecol Evol Syst 2014;16:247-264.
11. Schulz OE. Cruciferae. In: Engler A, Prand K, editors. Die natürlkhen Pflanzenfamilien, Cruciferae, 17B. Engelmann, Leipzig. 1936;227–658.
12. Koch M, Bishop J, Mitchell-Olds T, Koch M. Molecular systematics and evolution of *Arabidopsis* and *Arabis*. Plant Biol 1999;1:529-537.
13. Heenan PB, Mitchell AD, Koch M. Molecular systematics of the New Zealand *Pachycladon* (Brassicaceae) complex: generic circumscription and relationships to *Arabidopsis* sens. lat. and *Arabis* sens. lat. New Zeal J Bot 2002;40:543-562.
14. Al-Shehbaz IA. Transfer of most North American species of *Arabis* to *Boechera* (Brassicaceae). Novon 2003;381-391.
15. Busch N. Cruciferae. *Arabis* L.In: Komarov VL, Shishkin BK, editors. Flora USSR. BotanicheskiiInstitutAkademiiNauk SSSR. Vol. 21. Moscow and Leningrad. 1939;452-454.
16. Rechinger KH. Phytogeographia Aegaea. In: Rechinger-Moser F, editor. Denkschr Akad Wiss Wien, Math-Naturwiss Kl., Wien. 1951;1-208.

17. Hegi G. *Arabis* L. In: Lehmanns JF, editor. Illustrierte Flora von Mittel-Europa. Verlag, München, Band IV. 1960;240-264.
18. Jones BMG. *Arabis* L. In: Tutin TG et al. editors. Flora Europaea, Cambridge University Press, Cambridge. 1964.
19. Cullen J. Cruciferae. *Arabis* L. In: Davis PH, editor. Flora of Turkey and the East Aegean Islands. Vol. 1. Edinburgh University Press, Edinburgh. 1965;422-429.
20. Talavera S. *Arabis* L. In: Castroviejo S, Aedo C, Gómez Campo C, Laínz M, Montserrat P, Morales R, Muñoz Garmendia F, Nieto Feliner G, Rico E, Talavera S, Villar L, editors. Flora iberica, Vol. 4. Real Jardín Botánico, CSIC, Madrid. 1993;135–163
21. Boissier E. Flora orientalis. In: George H, editor. Basel, Geneve. 1867;XXXIV + 1017.
22. Koch MA, Karl R, Kiefer C, Al-Shehbaz IA. Colonizing the American continent: systematics of the genus *Arabis* in North America (Brassicaceae). Am J Bot 2010;97:1040-1057.
23. Trifinopoulos J, Nguyen LT, von Haeseler A, Minh BQ. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. Nucl Acids Res 2016;44:W232-W235.
24. Vaughan JG, Judith FLS, Whitehouse JM. Seed structure and the taxonomy of the Cruciferae. Bot J Linn Soc 1971;64:383-409
25. Erbar C. Nectary diversity in Brassicaceae in the context of phylogenetic considerations. Plant Divers Evol 2024;151-229.
26. Friesen N, Calasan AZ, Neuffer B, German DA, Markov M, Hurka H. Evolutionary history of the Eurasian steppe plant *Schivereckia podolica* (Brassicaceae) and its close relatives. Flora 2020;268:151602.
27. Boissier E. Plantae Aucherianae orientales enumeratae, cum novarum specierum descriptione. Ann Sci Nat 1842;2:45-91.
28. Tamura K, Stecher G, Kumar S. MEGA11: molecular evolutionary genetics analysis version 11. Mol Biol Evol 2021;38:3022-3027.
29. Vaidya G, Lohman DJ, Meier R. SequenceMatrix: Concatenation software for the fast assembly of multi-gene datasets with character set and codon information. Cladistics 2016:1096-0031.
30. Zhu T, Shi L, Doyle JJ, Keim P. A single nuclear locus phylogeny of soybean based on DNA sequence. Theor Appl Genet 1995;90:991-999.
31. Redelings BD, Holmes I, Lunter G, Pupko T, Anisimova M. Insertions and deletions: computational methods, evolutionary dynamics, and biological applications. Mol Biol Evol 2024;41:msae177.
32. Britten RJ, Rowen L, Williams J, Cameron RA. Majority of divergence between closely related DNA samples is due to indels. Proc Natl Acad Sci USA 2003;100:4661-4665.
33. Birth N, Dencker T, Morgenstern B. Insertions and deletions as phylogenetic signal in an alignment-free context. PLoS Comput Biol 2022:18:e1010303.
34. Belinky F, Cohen O, Huchon D. Large-scale parsimony analysis of metazoan indels in protein-coding genes. Mol Biol Evol 2010;27:441-445.
35. Gaya E, Redelings BD, Navarro-Rosinés P, Llimona X, De Cáceres M, Lutzoni F. Align or not to align? Resolving species complexes within the Caloplacasaxicola group as a case study. Mycologia 2011;103:361-378.
36. Paśko Ł, Ericson PG, Elzanowski A. Phylogenetic utility and evolution of indels: A study in neognathous birds. Mol Phylogenet Evol 2011;61:760-771.
37. Kurihara H, Shirai SM, Fujiwara K, Ikeda M. Indel variation in the mitochondrial ND5 region supports monophyly of the tribe Hippoglossoidini (sensuVinnikov et al. 2018) within the family Pleuronectidae. Ichthyological Res 2025;72:259-264.