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Unveiling a longstanding misinterpretation: revisiting phylogenetic and morphological evidence from *Arabis verna* (L.) W.T.Aiton, supports the description of a monospecific taxon, *Pseudoarabis* A.R. Khosravi & A. Eslami-Farouji *gen. nov.*

Ahmad Reza Khosravi[1,*,†], Özlem Çetin[2], Atena Eslami-Farouji[1,*,†]

1) Department of Biology, College of Science, Shiraz University, Shiraz, Iran
2) Department of Biotechnology, Faculty of Science, Selçuk University, Konya, Türkiye

ABSTRACT

The tribe Arabideae includes various species worldwide with ornamental features; however, it has undergone taxonomic revisions and has been reclassified into different genera. Despite the available literature, the taxonomic assignment of some taxa requires further consideration. This study therefore addresses the true taxonomic position of *Arabis verna* (L.) W.T.Aiton, which is not phylogenetically nested within other *Arabis* species but is instead closely related to *Aubrieta* Adans,. The species is naturally distributed in Southwest Asia, North Africa, and South Europe, and its taxonomic delimitation has remained unresolved. Phylogenetic evidence from previous authorities, together with our morphological observations, supports the distinct status of *A. verna* from the genus *Aubrieta*. Consequently, *A. verna* is excluded from *Aubrieta* and transferred to a newly established genus, *Pseudoarabis* A.R. Khosravi & A. Eslami-Farouji gen. nov., and the new combination, *P. verna* (L.) A.R. Khosravi & A. Eslami-Farouji comb. nov. is proposed.

Keywords: Arabideae; *Arabis*; *Aubrieta*; new genus; Cruciferae

INTRODUCTION

The genus *Arabis* L. is regarded as an ornamental plant with eye-catching flowers. One of its species, *Arabis verna* (L.) W.T.Aiton—locally known as spring rock-cress—found in rocky areas. This plant blooms with white, violet, and blue flowers between April and May, and is horticulturally important as an ornamental species in parks and gardens. Interestingly, it has a spreading feature; hence, this plant is critically used as a ground cover in rock gardens (https://www.nature-and-garden.com). According to resources such as http://plantiary.com, this annual herb prefers full sun to partial shade, with well-drained soil, and moderate moisture conditions.

In the case of taxonomic delimitation of taxa within Arabideae, the polyphyly or paraphyly of the genus *Arabis* (Arabideae, Brassicaceae) has been represented by various researchers [e.g., 1, 2]. Indeed, the taxonomic and phylogenetic studies have redrawn the generic and specific delimitations of various taxa [e.g., 3, and references therein]. Thus, taxonomic adjustments have

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†These authors have equally contributed to this work.
*Corresponding Authors: Department of Biology, School of Science, Shiraz University, Shiraz, Iran;
Tel: +98 71 3613 7394; Email: arkhosravi@shirazu.ac.ir AND atena.eslami@shirazu.ac.ir

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led to the segregation of taxa from *Arabis* (e.g., *A. verna* [4]), *Hafezia aucheri* (Boiss.) A.R. Khosravi & A. Eslami-Farouji, and *H. parvula* (Dufour ex DC.) A.R. Khosravi & A. Eslami-Farouji, as noted in Khosravi and Eslami-Farouji [5].

While working on the family Brassicaceae and gathering data on the specific delimitation of various specimens available at the Herbarium of Shiraz University (HSHU), doubts were raised about the taxonomic status of *Arabis verna*. This taxon was preliminarily published by Linnaeus in 1753 as *Hesperis verna* L., and later transferred to the genus *Arabis* by W.T. Aiton in 1812. Later, Titz [6] stated that this genus is easily distinguished from related taxa and has no taxonomic problems. In 1973, Titz asserted that the origin of *A. verna* remains a subject of debate. Indeed, authorities have dealt with this taxon; some reassigned this taxon within *Aubrieta* Adans. [4, 7], while others demonstrated its distinct identity [8]. However, none of the researchers assigned *A. verna* in its true classification.

Morphologically, the annual *A. verna* is not close to the perennial *Aubrieta*. Indeed, the *Aubrieta* sister (*A. verna*) is similar to the genus *Arabis*, and shares amplexicaul or auriculate stem leaves, silique fruits, and saccate sepals with this taxon. Moreover, A. *verna* is morphologically close to *A. nova* by having dentate leaves and zigzag fruiting. The only distinct difference of *A. verna* from the remaining annual *Arabis* specimens is petal color. *Arabis verna is* characterized by violet petals, whereas almost all others are white. *Aubrieta* and its segregate (*A. verna*) are readily distinguished by life form (perennial vs. annual), stem leaves (non-auriculate vs. auriculate), style and pedicel size (elongated vs. short), style and pedicel width (narrower than fruits vs. the same as the fruit width), filaments (toothed and dilated at base vs. toothless and dilated), fruit shape (broad vs. narrow), and seeds (biseriate vs. uniseriate) (these characters are within Koch et al. [8] research). According to Muhammed [4], although the genus *Aubrieta* is readily differentiated from its relatives by having linear teeth in its outer filaments, the specific delimitation of this taxon is a matter of controversy, but this is not the subject of this study.

Phylogenetically, *Arabis verna* (*Aubrieta verna* (L.) Muhammed) was nested as the sister group to the *Aubrieta* clade in the studies by Karl and Koch [2] and Kiefer et al. [7]. Karl and Koch [2]. carefully studied the tribe Arabideae using ITS and *trn*L-F molecular markers, focusing on species delimitation within the tribe [2]. In this context, *A. verna* was integrated into the clade *Aubrieta* based on both genetic markers, with high posterior probabilities for ITS and low for *trn*L-F [2]. Kiefer et al. [7] used next generation sequencing (NGS) to investigate *Arabis* annuals.

Although *A. verna* and *Aubrieta* are grouped together, an investigation into their taxonomic delimitation is warranted. Thus, this study aims to revise the classification of *A. verna* (now treated as *Aubrieta verna*) through a straightforward examination of morphological features and phylogenetic findings over the past 25 years. Moreover, we strive to assign distinctive morphological characteristics that differ between *A. verna* and its sister, *Aubrietia*.

MATERIALS AND METHODS

Plant material: The distinctive morphological and micromorphological features of *A. verna* — including leaves, flowers, fruits, seeds, and trichomes—along with its sister group, *Aubrieta*, and their relatives within the tribe Arabideae (*Arabis*, *Hafezia* A.R. Khosravi & A. Eslami-Farouji, and *Draba* Dill. ex L.) were examined in Iran and Turkey (Table S1). The herbarium specimens studied are systematically archived in the Herbarium of Shiraz University (HSHU) and the Konya Herbarium (KNYA). Additionally, Floras from diverse regions of the world, as well as electronic databases from available virtual herbaria, were reviewed (for more information, see Khosravi and Eslami-Farouji [5]). To aggregate the most significant microstructural evidence, light microscopic photographs were captured following the approach of Khosravi and Eslami-Farouji [9]. Scanning Electron Microscopy (SEM) images were also recorded by the Central Laboratory of Shiraz University and were described using the terminology of Vaughan et al. [10].

Due to the extensive molecular investigations already conducted within the tribe Arabideae [e.g., 3, 7, and references therein], we refrained from replicating DNA extraction and Polymerase Chain Reaction (PCR) procedures. Instead, sequence datasets were directly extracted from NCBI (National Center for Biotechnology Information). The phylogenetic analyses—maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI)—were implemented using representative specimens of the tribe Arabideae (Table S2) together with *Pseudoturritis turrita* (L.) Al-Shehbaz as an outgroup. These analyses follow the same approach used by Khosravi and Eslami-Farouji [5], utilizing alcohol dehydrogenase, chalcone dehydrogenase, ITS, and *trn*L-F markers. The sequence information details used for the evolutionary analyses are listed in Table S2.

Besides morphological and micromorphological evidence, all four genetic markers were manually examined to identify exclusive and insightful indels (insertions and deletions) as well as single-nucleotide substitutions. Remarkably, both morphological and phylogenetic characteristics support the recognition of the new entity and its distinct taxonomic status within its close relatives, specifically *Aubrieta*. Eventually, a t×n binary matrix was constructed according to Khosravi and Eslami-Farouji [5], and a maximum parsimony tree was generated using PAUP (ver. 4.0b10). As *A. verna* is a more popular scientific name than *Au. verna*, we prefer to use the former within the draft until its true taxonomic position is clarified later in this study.

RESULTS

This research re-established a new monospecific genus through personal field observations (ARKH), herbarium materials from the Herbarium of Shiraz University (HSHU), the Konya Herbarium (KNYA), virtual herbaria, and a critical literature review. The distinctive morphological characters between the new entity and its related clades within Arabideae, especially the genus *Aubrieta*, were cautiously investigated. These traits are visualized and listed later in this study (Fig. 1).

The phylogenetic position of *Arabis verna* has been analyzed in various studies. In the most recent paper published by Kiefer et al. [7], *Arabis verna* is treated as *Aubrieta verna*, which confirms previous statements [4]. However, this study clearly evaluates the distinct taxonomic status of *A. verna* from phylogenetic and morphological perspectives.

Based on the previous authorities [e.g., 2], seven main clades identified from the available sequence dataset in NCBI, including the Main Arabis CLADE (*Arabis hirsuta* (L.) Scop., *A. pterosperma* Edgew., *A. modesta* Rollins, *A. serpyllifolia* Vill., *A. sagittata* (Bertol.) DC., *A. stelleri* DC., *A. collina* Ten., *A. procurrens* Waldst. & Kit., *A. bryoides* Boiss., and *A. carduchorum* Boiss.), Arabis auriculata CLADE (*A. auriculata* Lam. and *A. nova* Vill.), Arabis nordmanniana CLADE (*A. christianii* N.Busch, *A. graellsiiformis* Hedge, and *A. nordmanniana* (Rupr.) Rupr.), Arabis alpina CLADE (*A. alpina* L., *A. montbretiana* Boiss., *A. caucasica* Willd. and *A. purpurea* Sm.), Aubrieta CLADE (*Aubrieta canescens* (Boiss.) Bornm., *Au. libanotica* Boiss. & Hohen., *Au. pinardii* Boiss., *Au. columnae* Guss., *Au. olympica* Boiss., *Au. glabrescens* Turrill, *Au. gracilis* Spruner ex Boiss., *Au. scardica* (Wettst.) Gustavsson, *Au. deltoidei* (L.) DC., *Au. erubescens* Griseb., *Au. thessala* H.Boissieu, *Au. scyria* Halácsy and *Arabis verna*), Hafezia CLADE (*Hafezia aucheri* and *H. parvula*), and Draba CLADE (*Draba bruniifolia* Steven, *D. hispanica* Boiss., *D. aizoides* L., *D. pulchella* Willd. ex DC., *D. rimarum* (Rech.f.) A.R. Khosravi & A. Eslami-Farouji, *D. nemorosa* L., and *D. nuda* (Bél.) Al-Shehbaz & M.Koch). Aubrieta CLADE included two genera named under *Arabis* and *Aubrieta*. *Arabis verna*, within the Aubrieta CLADE, is critically different from the other *Arabis* species as well as from the *Aubrieta* specimens (Fig. 1). However, based on phylogenetic and morphological evidence, *Arabis verna* appears to be closely related to the *Aubrieta* species.

The indels, insertions and deletions, as well as single nucleotide substitutions, were manually evaluated within the studied genetic markers (alcohol dehydrogenase, chalcone synthase, ITS, and *trn*L-F). This enabled the assessment of the well-documented common characters among the existing ancient and recent evolutionary splits (Tables S3-S4). Overall, four genetic markers indicate a total of 22 insertions or deletions (indels) and 277 unique substitutions, which emerged as synapomorphic characteristics and evolutionary signals. Here, we first describe indels; single-nucleotide substitutions will be discussed thereafter.

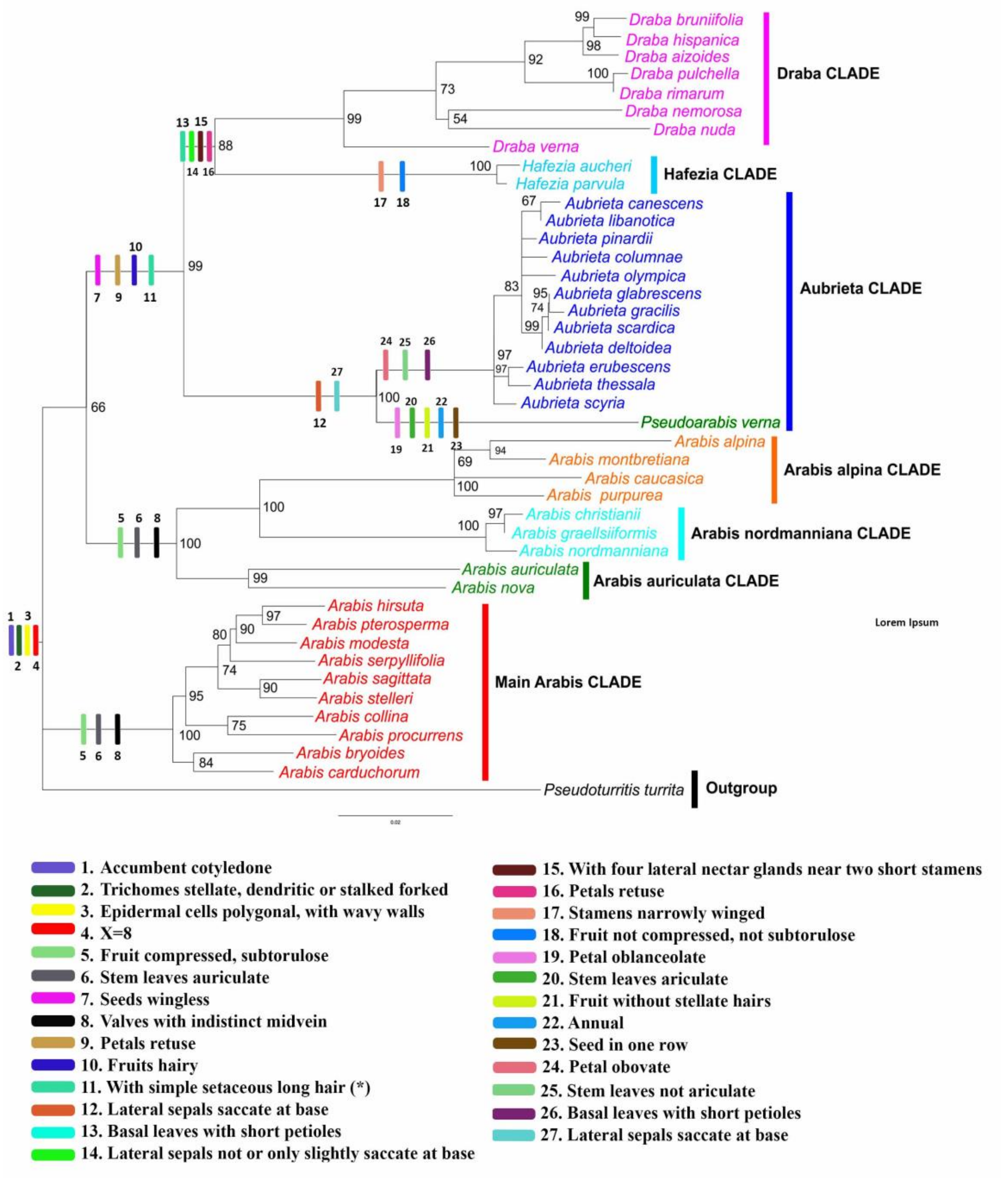

Figure 1: The consensus phylogenetic tree was reconstructed based on the research of Karl and Koch [2], which employed four genetic markers: alcohol dehydrogenase, chalcone synthase, ITS, and *trn*L-F. Distinctive morphological traits (12 to 27) observed in representatives of the clade Aubrieta, including *Aubrieta* itself and the novelty *Pseudoarabis verna*, are represented here. Asterisk (*) within the Figure directly corresponds to the lack of trichome (glabrous) in some accessions of *Pseudoarabis verna*. To clarify other common traits within the tribe Arabideae, we incorporated characters from the recent work of Khosravi and Eslami-Farouji [5]. Clade names are not italicized in this draft.

Indels Alcohol dehydrogenase: The outgroup is characterized by three insertions at nucleotide positions 24-34, 52-60, and 464-466. These inserted sequences are GTCAACGTGG, TTCTGCTT, and AAA, respectively. TAC is a unique insertion found exclusively in the Draba Clade at positions 1744-1746. Both the Hafezia and the Main Arabis Clades exhibit one deletion each. The deletion at positions 1749 to 1757 (ATGAGAAAAA) belongs to the Hafezia Clade, while the deletion from 705 to 706 (TG) is associated with the second Clade. The Alpina and the Arabis nordmanniana Clades share one insertion and one deletion as phylogenetic signals. These indels correspond to base positions 1467-1470 (ATCT) and 1534-1558 (TGTGGATCTT—TGAACCTAATAC), respectively. Two indels (an insertion and a deletion) were found in the Alpina Clade, which phylogenetically differentiate it from other clades. The insertion occurs at bases 1481-1494 (TTCGACATTTCTTG), whereas the deletion is observed at positions 382-389 (C--TTTTC). The Aubrieta Clade is distinguished by a unique synapomorphy involving two insertions at bases 86-88 (GTT) and 1525-1527 (GTT, CTG or CTA) (Table S3).

Chalcone synthase: No indels were detected in the Chalcone synthase genetic marker.

ITS: Four distinct deletions are detected in clades Aubrieta (at base positions 115-123 and 128-141) and Hafezia (bases 116-136), along with two species of *Arabis* (*Arabis stelleri* & *A. sagittata*), at positions 126-133 (Table S3).

***trn*L-F:** Six indels are distinguished as unique synapomorphic characters within the chloroplastic marker. Within the Hafezia clade, one indel was identified: a deletion spanning positions 37-45. Additionally, two indels were detected in the Aubrieta clade, including insertions at positions 156-158 (TCT/TGT) and 377-385 (TTAATTGAC). Other unique indels were related to the Draba clade. The first is a deletion spanning positions 156 to 158 bp (TCT/TGT), while the second is an insertion located at positions 159-160 (AA) (Table S3). The Main Arabis clade is markedly distinguished by an insertion (GTAAAAT/TTAAAAT) spanning nucleotide positions 413-419 (Table S3).

Single-nucleotide substitutions: Based on Table S4, a total of 277 single-nucleotide substitutions were detected among all studied long-standing and recently diverged clades.

Alcohol dehydrogenase: Among the 277 single-nucleotide substitutions, 137 are associated with the alcohol dehydrogenase gene. The outgroup (27), the Aubrieta clade (19), *Arabis verna* (18), and the clades Arabis nordmanniana (14) and Arabis alpina (12) exhibit the highest numbers of distinctive substitutions. The corresponding counts are indicated within the parentheses (Table S4).

Chalcone synthase: A total of 31 single-nucleotide substitutions are detected in the chalcone synthase marker. Within this genetic marker, the Hafezia clade with 11 single-nucleotide substitutions, and the Draba clade, with 7, indicate the highest levels of synapomorphic traits. The new entity (*Arabis verna*) is differentiated from the genus *Aubrieta* by a single-nucleotide substitution at position 692 (Table S4).

ITS: In general, 65 synapomorphic substitutions were distinguished in the nrDNA marker. The Aubrieta clade experienced the greatest number of substitutions (16), followed by the Arabis alpina clade, the Arabis nordmanniana clade, and the outgroup, each with nine, eight, and eight nucleotide substitutions, respectively. Interestingly, *Arabis verna* is characterized by three single-nucleotide substitutions, which confirms its distinctiveness from the genus *Aubrieta* (Table S4).

trn**L-F:** In total, 44 derived characters were found in the chloroplastic marker. The Hafezia clade is distinguished from the remaining clades by 10 substitutions. Additionally, *A. verna* is separated from the genus *Aubrieta* by a single substitution at position 258 (Table S4).

As mentioned above, *Arabis verna* was found to be a distinctive entity due to unique apomorphic single-nucleotide substitutions. Thus, the recognition of this taxon as a new entity and its placement within a new genus has been thoroughly confirmed here.

As elaborated in our recent work [5], all indels (insertions or deletions) as well as single nucleotide substitutions were used to generate a t×n binary matrix, from which a maximum parsimony tree was constructed (Fig. 2). In this tree, the close relationship between *A. verna* and *Aubrieta* is clearly demonstrated, but it provides no information regarding their distinct identity (Fig. 2). Besides phylogenetic signals, morphological evidence also underscores the distinct identity of *A. verna*, which is described herein:

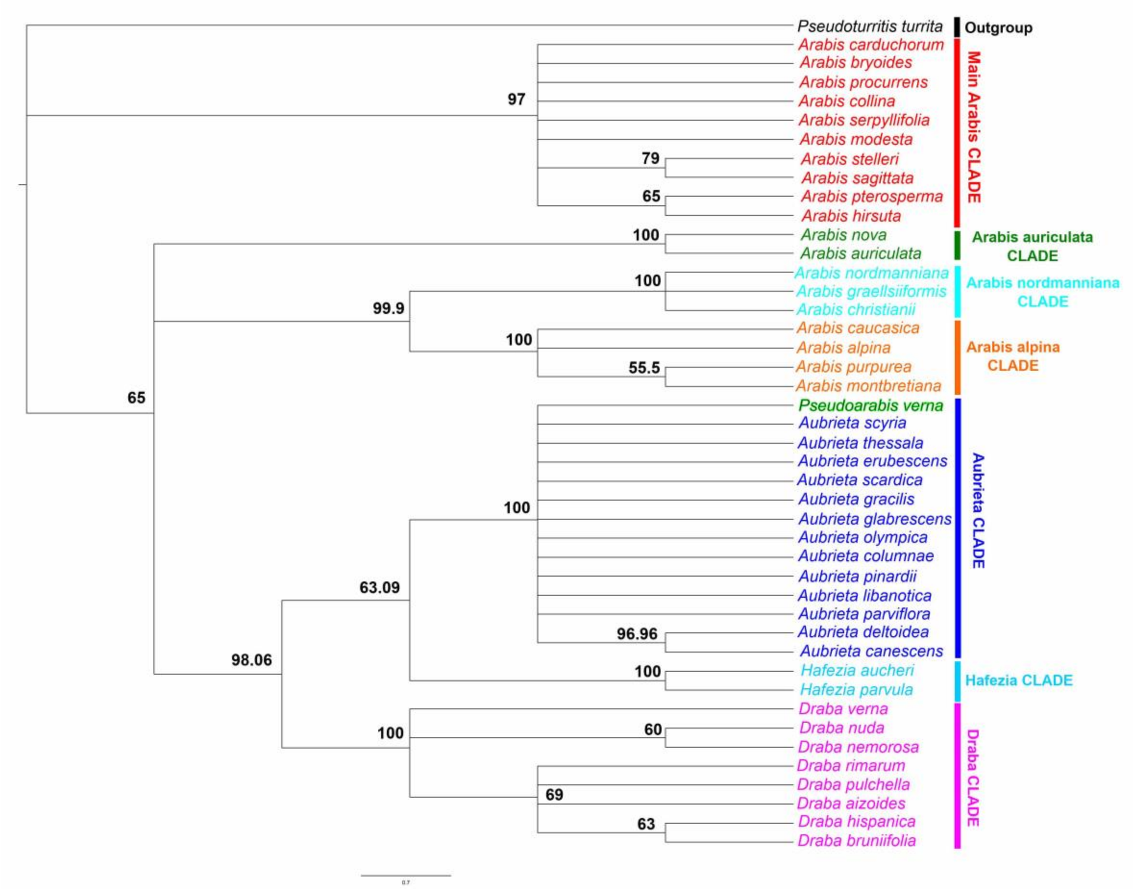

Figure 2: A Maximum parsimony (MP) tree was constructed from scores representing the presence (1) or absence (0) of indels and single nucleotide substitutions in a t×n binary matrix.

Besides phylogenetic signals, morphological evidence also underscores the distinct identity of *A. verna*, which is described herein:

Duration: *Arabis verna* represents an ephemeral, lightweight annual adapted to early-season growth in open and disturbed habitats, with erect, sparsely branched stems and minimal vegetative spread. *Aubrieta*, by contrast, is a perennial, robust, cushion-forming species with prostrate or ascending stems, dense leaf cushions, and persistent vegetative mats, reflecting adaptation to stable, xeric, and rocky habitats (Table 1).

Trichome: According to our observations through the light microscope (LM), trichome density is higher in *Aubrieta* than in *A. verna* (Fig. S1). In terms of trichome size, *A. verna* is characterized by larger trichomes (Fig. S1). Technically, both taxa exhibit various trichome types, which clarify their distinct taxonomic positions. For example, the frequency of tetrafid (four-armed) trichomes in *A. verna* is higher than in *Aubrieta* (Fig. S1). However, simple and branched trichomes, including bifid, trifid, tetrafid, and dendritic forms, are present on the surface of *Aubrieta* organs (Fig. S1). In some *Aubrieta* species and in *A. verna*, as noted in our previously published paper [5], simple trichomes are long and setaceous (Table 1).

Table 1: Morphological characters of the new genus, *Pseudoarabis*, and its closely related genus, *Aubrieta*.

Taxa/ Morphological characteristics	*Pseudoarabis*	*Aubrieta*
Duration	Annual	perennial
Trichome density	Lower	Higher
Trichome size	Larger	Smaller
Trichome type	Almost tetrafid & dendritic	simple & bifid, trifid, tetrafid
Leaf	Auriculate or amplexicaul	Not amplexicaule or auriculate
Petal shape	Oblanceolate or narrow obovate	Obovate or broadly obovate
Style length	Shorter	Longer
Filament	Without outer stamens with a linear tooth below the anther	With outer stamens with a linear tooth below the anther
Nectar Glands	Less developed	Conspicuously developed
Fruit pedicel	Short & thick	Long & thin
Fruit length	Longer	Shorter
Fruit trichome	Without stellate trichome	With stellate trichome
Septum cell type	Elongated, oblong cells with blunt or slightly tapering ends and thick, sinuous (wavy) anticlinal walls	Irregularly polygonal septum cells with slightly undulate, thick anticlinal walls
Septum cell size	Larger	Smaller
Seed size	Almost larger	Almost smaller
Seed mucilage orientation	Erect	Oblique
Seed mucilage ring size	Larger	Smaller

Leaf: The primary morphological feature that leads to the confusion and misinterpretation of *A. verna* as being within the genus *Arabis* is the presence of auriculate or amplexicaul stem leaves. In the case of *Aubrieta*, leaves are not amplexicaule or auriculate (Table 1).

Sepal: The Aubrieta clade (*A. verna* and *Aubrieta*) is characterized by saccate sepals. Rarely, a few species of *Aubrieta*, such as *Au. parviflora* Boiss., have non-saccate sepals. The presence of saccate sepals is a common feature in most species within the *Arabis* clade. This characteristic is another homoplastic trait that led to the misclassification of *A. verna* within *Arabis* (Fig. S2, 1-2, 12-15).

Petal: The petal color of the clade *Aubrieta* (purple), which includes *A. verna* and *Aubrieta*, is clearly distinguishable from the petal color of most *Arabis* specimens (white). The petal size of the species in the clade *Aubrieta* (*A. verna* and *Aubrieta*) is similar to and larger than that of *Arabis* specimens. *Aubrieta* and *A. verna* have both rounded, retuse or emarginate petal apices. The petals in *A. verna* are oblanceolate or narrow obovate, while in *Aubrieta*, petals are obovate or broadly obovate (Fig. S2, 3, 16; Table 1).

Gynoecium: The size of the style is as long as the fruit in *Aubrieta*. The ovary is characterized by biseriate ovules and a cylindrical style. Style length is longer in most of the *Aubrieta* species than that of *A. verna*. (Fig. S2, 6, 19; Table 1).

Stamen: *Aubrieta* is characterized by slightly winged filaments, and long outer stamens have appendages. The stamens are dilated in *A. verna* (Fig. S2, 4-5, 17-18; Table 1).

Nectar Glands: In *Arabis verna*, the floral nectaries consist of two semi-annular glands located in an extrastaminal position at the base of each transversal stamen. Median nectar glands are absent. The glands are relatively simple in form, indicating only slight enlargement of the abaxial portion. In *Aubrieta* (e.g., *Aubrieta parviflora*), the nectaries are likewise two in number and semi-annular in shape. They are positioned extrastaminally at the base of the transversal stamens. However, they are more elaborate than those of *Arabis verna*. The lateral glands exhibit distinct extensions toward the median region of the flower, and the abaxial portions are conspicuously developed (Table 1).

Fruit pedicel: The fruiting pedicel is short and thick in *A. verna*, whereas it is long and thin in *Aubrieta* (Fig. S2, 7-11, 20-22; Table 1).

Fruit: Fruits are varied in size and shape in *Aubrieta*. Some of them are compressed, while others are inflated. Furthermore, both silique and silicule fruits are observed in *Aubrieta*. In contrast to fruit width, fruit length is longer in *A. verna* than in *Aubrieta*. While fruits are inflated or terete in *Au. canescens*, the remaining are characterized by strongly compressed fruits (*A. verna*, *Au. pinardii*, and *Au intermedia*). Except for *A. verna*, stellate trichomes are observed in all *Aubrieta* species. Simple and 2-4 furcate trichomes are available in the fruits of *A verna*, whereas simple trichomes are rarely found in *Aubrieta* species, and the presence of 2-4 furcate trichomes is reported in some of the *Aubrieta* species [4] (Fig. S2, 7-11, 20-22; Table 1).

Septum: Based on micromorphological observations, the septum surface arrangement of *Arabis verna* is clearly distinct from that of *Aubrieta* and other genera within the tribe Arabideae (Fig. S3). Examination of the epidermal cell morphology in the septa reveals two distinct types. The first type, observed in *A. verna*, consists of elongated, oblong cells with blunt or slightly tapering ends and thick, sinuous (wavy) anticlinal walls. These cells are oriented parallel to the fruit's longitudinal axis (Fig. S3). In contrast, the second type, characteristic of *Aubrieta* and related Arabideae genera (*Arabis*, *Draba* and *Hafezia*) comprises irregularly polygonal septum cells with slightly undulate, thick anticlinal walls (Fig. S3). Furthermore, the septum cells of *A. verna* are noticeably larger than those of *Aubrieta* (Fig. S3; Table 1).

Seed: Based on our observations regarding seed features, all studied taxa, *Aubrieta* (*Au. parviflora*), *A. verna*, *Arabis* (*A. caucasica* and *A. nova*), *Draba* (*D. rimarum*), and *Hafezia* (*H. aucheri*) were significantly characterized by different seed size, mucilage length and diameter, shape, and density. In our recent paper [5], we assessed mucilage production by immersing seeds in water for 24 hours. The density and diameter of each mucilage layer were critically evaluated across the studied taxa (Figs. S4-S5; Table 1).

The mean seed length and width of *Arabis verna* (1352.13 µm, 794.62 µm) exceed those of *Aubrieta parviflora* (1081.96 µm, 657.10 µm). Additionally, the seed sizes of *A. caucasica* (1363.60 µm, 947.37 µm) and *Hafezia* (1276.70 µm, 758.96 µm) are similar to those of *A. verna*. *Aubrieta parviflora* and *A. verna* share oblong to elliptic seed shapes and reticulate ornamentation but differ in mucilage shape, seed length, width, and size. *Hafezia* mucilage shape is cylindrical, while the remaining taxa exhibited conical shape. *Aubriata* and *A. verna* differ critically in the mucilage orientation; the first is oblique, while the second is erect (Figs. S4-S5). According to our recent work [5], mucilage density was measured in an area of 40 μm^2. The clade *Aubrieta,* including *Au. parviflora* and *A. verna*, exhibited the largest mean mucilage diameter (35.41 µm and 44.55 µm) and the lowest mucilage density (2/40 μm^2). In contrast, the highest mucilage densities were observed in *Hafezia* (38/40 μm^2) and *Draba* (38/40 μm^2) [5]. Indeed, the largest ring and crater were observed in *A. verna* and *Au. parviflora*, respectively. The ring size is larger in *A. verna* than that of *Au. parviflora* (Figs. S4-S5).

DISCUSSION

This study thoroughly evaluates the new entity of *A. verna* within the tribe Arabideae using morphological and phylogenetic evidence. Earlier investigations by Koch et al. [13] confirmed the close relationship between circum-Mediterranean (Middle East, North Africa, South Europe) *A. verna* and *Aubrieta*, based on nuclear, chloroplastic, and chalcone synthase datasets. Karl et al. [14], Yüzbaşıoğlu et al. [15], Kiefer et al. [16], and Hendriks et al. [17] also identified the close relationship between *Aubrieta* and *A. verna*. As previously demonstrated by Jordon-Thaden et al. [18] and Koch et al. [19], the credibility of the *Aubrieta* clade was well documented [14].

The clade *Aubrieta*, comprising *Aubrieta* and *A. verna* originated around 2.74 million years ago in the Mediterranean and Anatolian floristic regions within the Pleistocene [2]. The phylogenetic trees reconstructed using different markers resulted in the same topologies [14]. *Arabis verna* was found to be closely related to *Aubrieta* based on the ITS and *trn*LF markers [14]. Researchers also noted distinct morphological characteristics between *Aubrieta* and *A. verna* [20]. Koch et al. [20] constructed a haplotype network that corresponds to Karl and Koch [2], and *Aubrieta* and *A. verna* phylogenetically represent their affinity.

In 2017, Koch and his colleagues were the only scientists to adequately describe the differences between *A. verna* and *Aubrieta* as distinct taxa; however, this did not result in the definition of a new taxon [20]. Furthermore, Illinska and her colleagues suggested the distinct entity of *A. verna* [21]. Illinska et al. [21] proposed that *A. verna* and *Aubrieta* are the same entities, and could be combined, suggesting the name *Aubrieta* after the combination. Supporting Illinska’s idea, Muhammed [4], three years earlier, transferred *A. verna* to the genus *Aubrieta*, resulting in *Aubrieta verna*. He mentioned that *A. verna* is a young taxon due to its recent divergence from the genus *Aubrieta* in 1.4 Mya [4]. However, *Aubrieta* has been found to be a problematic taxon since it has been revised by different researchers [e.g., 4, 22].

According to Muhammed's research using chloroplast sequence data (*matK*, *trnD-trnT*, and *ycf6-psbM*), *A. verna* is phylogenetically closely related to *Au. canescens* and *A. pinardii* [4]. Moreover, based on his statements, a concatenated chloroplast dataset was constructed into a tree, which clades correspond to their geographical area distribution [4]. Geographically, *Arabis verna* belongs to the Pan-Mediterranean floristic region, while the other two taxa are dispersed in Anatolia [4]. In contrast, *trnH-psbA* and rps11-rp136 markers failed to show the phylogenetic status of *A. verna* [4]. However, the combined chloroplast data confirmed the close affinity of *A. verna* to *Au. canescens* and *A. pinardii* [4]. The BEAST analyses of the combined chloroplast genes also confirmed the idea of the close affinity of *A. verna* with *Au. canescens* and *Au. pinardii* [4]. However, it has been estimated that *A. verna* origin was earlier than the two species belonging to *Aubrieta* [4].

Nuclear genes showed different levels of resolution; for example, *duo1* lacks sufficient clade support, while *rpb2* was trustworthy enough [4]. The first marker does not show any genetically closed taxon to *A. verna*, while the second one shows its relation with *Au. intermedia* (PP 0.91). However, it must be noted that *Au. intermedia* was nested within different clades within this study. Muhammed [4] suggested the hybrid origin for this taxon. This result is incongruent with that of the chloroplast dataset [4]. The combination of both markers also represented the close affinity of *A. verna* and *Au. intermedia* (PP 0.82). Muhammed [4] stated that the results represented double peaks, which is a sign of gene duplication, instead of heterozygosity. Nevertheless, if double peaks belong to intron regions and the third position of codons, then it is most probably heterozygosity and not a duplication.

According to Muhammed [4], nuclear genome results reflect the same topology as the chloroplast genes, but with lower support. The presence of hybridization was approved in Muhammed's thesis in 2017, due to the topology dissimilarity between trees in nuclear and chloroplastic markers. Nevertheless, it was discussed that the level of hybridization is rare in the genus *Aubrieta* [4].

Subsequently, Walden et al. [3] generated a dendrogram of hierarchical clustering and outlined the distinct position of *A. verna*. Furthermore, *A. verna* is also considered the sister group to *Aubrieta* specimens in another phylogenetic tree constructed by Walden and her colleagues for paralog placement of clusters. According to Walden et al. [3], the pairwise synonymous substitution rates (Ks) of *A. verna* and *Aubrieta* (*Au. macrostyla* and *Au.*

canescens) are closely related; however, autopolyploidization leads to reproductive isolation and divergence of the two taxa due to differing polyploidy.

From the life form point of view, *Arabis* perennials have larger flowers compared to annuals (e.g., *A. verna*). Unlike perennial outbreeders, the small flower size in *Arabis* annuals directly points out their autogamous breeding system [6, 23]. They also noted that, except for *A. verna*, perennials are characterized by pink to purple flower colors [23]. However, *Arabis* specimens that deviate from the main *Arabis* clade exhibit various flower colors [23]. Earlier, in 2004, Mutlu distinguished *A. verna* from other *Arabis* annuals by its violet petals (as opposed to white) and short filaments with an appendage (as opposed to without an appendage) [24]. Petals are almost purple to violet, and white petals are rarely distinguished in *Aubrieta*. According to Bornmüller [25], petals vary in petal size and color even in a species of *Aubrieta*. *Arabis verna* is characterized by white to violet petal color, while *Au. canescens* and *Au. pinardii* are distinguished by violet and purple petal colors, respectively [4]. The petals of *Aubrieta intermedia* that were nested near *A. verna* based on nuclear genes, determined by purple color [4]. The size of petals is smaller in *A. verna* compared to those of *Aubrieta* species [4].

Morphologically, winged stamens are a distinct characteristic of the genus *Aubrieta*, as proven many years ago by Boissier [11]. In this study, the lack of toothed stamens is clarified in *A. verna* as a distinct identity. Muhammed [4], who worked on *Aubrieta* and *A. verna*, stated that there is no informative character to show the distinct position of lineages in his study.

Based on Muhammed [4], in contrast to fruit size with a considerable variation, fruit characteristics such as trichome type are found to be trustworthy in taxonomy. Long and narrow fruits like those present in *A. verna* and *Aubrieta* are found to be ancestral based on phylogenetic studies within the tribe Arabideae [4].

Fruit size (length and width) varies among accessions due to phenotypic plasticity relating to a single taxon [4, 25]. In contrast to fruit width, fruit length is longer in *A. verna* than in *Aubrieta* (Fig. S2). While fruits are inflated or terete in *Au. canescens*, the remaining are characterized by strongly compressed fruits (*A. verna*, *Au. pinardii*, and *Au intermedia*) [4]. Except for *A. verna*, stellate trichomes are observed in all *Aubrieta* species [4]. Simple and 2-4 furcate trichomes are available in the fruits of *A verna*, whereas simple trichomes are rarely found in *Aubrieta* species, and the presence of 2-4 furcate trichomes is reported in some of the *Aubrieta* specimens [4] (Fig. S2). Furthermore, the septum cells of *A. verna* and *Aubrieta* are completely different from each other, which confirms the distinct entity of *A. verna* (Fig. S3).

Conclusion: Eventually, *A. verna* transferred to a new monospecific genus named under *Pseudoarabis* A.R. Khosravi & A. Eslami-Farouji gen. nov., thus, a new combination *Pseudoarabis verna* (L.) A.R. Khosravi & A. Eslami-Farouji comb. nov. is also designated herein.

Taxonomic treatment: ***Pseudoarabis*** A.R. Khosravi & A. Eslami-Farouji ***gen. nov.*** **Type**: *Pseudoarabis verna* (L.) A.R. Khosravi & A. Eslami-Farouji.

Description: Herbaceous annual, pubescent with both simple and branched hairs. Leaves with serrate to serrate-crenate margins; basal leaves oblanceolate, the blade gradually attenuate into a broad petiole; cauline leaves few (1-2), smaller, decreasing in size toward the apex of the stem, ovate, cordate, or slightly auriculate. Inflorescence lax, flexuous. Sepals erect, the lateral pair saccate at the base. Petals oblanceolate, with a rounded or slightly emarginate apex, white, pink, or violet-blue. Stamens with filaments flat and linear; anthers ovoid to subcylindrical. Nectaries are two semi-annular extrastaminal glands at base of transversal stamen; median glands absent. Ovary sessile, containing many ovules per locule. Style short; stigma capitate or cylindrical, ± bilobed. pedilcels thick; stigma Sessile. Fruit a linear silique, glabrous or pubescent, with numerous seeds; valves flat or flat-convex, each with a strongly marked median nerve; style < 1 mm, generally bilobed. Seeds arranged in a single row per locule, elliptical, blackish, wingless, usually slightly mucilage; cotyledons accumbent. Basic chromosome number: x = 8. Etymology: Owing to the similarity of this genus to *Arabis*, the genus was named *Pseudoarabis*. The genus *Pseudoarabis* includes a monospecific taxon as follows: *Pseudoarabis verna* (L.) A.R. Khosravi & A. Eslami-Farouji, *comb. nov*. Basionym: *Hesperis verna* L., *Sp. Pl.*: 664 (1753). ≡ *Turritis purpurea* Lam., *Fl. Franç.* 2: 491 (1779), nom. illeg. superfl. ≡ *Arabis violacea* Moench, *Methodus*: 259 (1794), nom. illeg. superfl. ≡ *Arabis verna* (L.) W.T. Aiton, *Hortus Kew*., ed. 2. 4: 105 (1812). ≡ *Erysimum vernum* (L.) Kuntze, *Revis. Gen. Pl.* 2: 934 (1891), nom. illeg. ≡ *Turrita vernalis* Bubani, *Fl. Pyren.* 3: 153 (1901), nom. illeg. superfl. ≡ *Aubrieta verna* (L.) Muhammed, *Ukrain. J. Ecol.* 9(1): 90 (2019).

Type: Lectotype: Herb. Burser IV: 47 (Lectotype designated by Ferrer-Gallego 2014).

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