IRANIAN JOURNAL OF BOTANY 32(1), 2026
DOI: https://doi.org/10.22092/ijb.2026.371299.1554

A PHYLOGENETIC REVIEW OF TRIBE BUPLEUREAE, BUPLEURUM EXSCAPUM A NEW COMBINATION FOR HOHENACKERIA EXSCAPA

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Abstract
A phylogenetic study of the tribe Bupleureae (Apiaceae) was conducted using nrDNA ITS data. The results show that Bupleureae has a distinct position within the family, comprising two distinct clades. *Hohenackeria exscapa* is placed in a clade with other examined species of the genus *Bupleurum.* Traditionally, the genus *Hohenackeria*, was considered a close relative of *Bupleurum* but differs from it in having white flowers, sessile umbels, a conspicuous calyx, the absence of bracteoles and a carpophore. Phylogenetic results represented *Hohenackeria exscapa* within *Bupleurum* subgen. *Bupleurum*, close to *B. baldense*. Several morphological characters and phylogenetic signals support their relationships. Both species have slender tap roots, linear to oblong-lanceolate leaves that attenuate into a petiole with sessile cauline leaves. Flowers and fruits in *B. baldense* are generally enveloped by bracteoles, and pedicels are subequal and short, while in *H. exscapa* pedicels are shorter and umbels are hidden by radical leaves instead of bracteoles, so the concave bracteoles in *B. baldense* may play the hiding role for umbels. *Hohenackeria exscapa* was here subsumed within *Bupleurum* as a new combination.

Keywords: Apiaceae, *Bupleurum*, molecular phylogeny, new combination, nrDNA ITS, Iran.

Citation: Panahi, M. 2026: A phylogenetic review of Bupleureae, *Bupleurum exscapum*, a new combination for *Hohenackeria exscapa*. -Iran. J. Bot. 32(1): 32-45. https://doi.org/10.22092/ijb.2026.371299.1554

Article history
Received: 04 November 2025
Revised: 13 May 2026
Accepted: 28. May 2026
Published: 30 June 2026

مروری بر فیلوژنی Bupleureae، *Bupleurum exscapum* ترکیب جدیدی برای *Hohenackeria exscapa*

مهرنوش پناهی: استادیار پژوهش موسسه تحقیقات جنگل ها و مراتع کشور، سازمان تحقیقات، آموزش و ترویج کشاورزی، تهران، ایران

چکیده: مطالعه فیلوژنتیک طایفه Bupleureae (تیره چتریان) توسط داده‌های nrDNA ITS انجام گردید. نتایج نشان داد که Bupleureae یک موقعیت مجزا در تیره چتریان دارد. گونه *Hohenackeria exscapa* در یک شاخه همراه با سایر گونه‌های جنس *Bupleurum* قرار می‌گیرد. به‌طور مرسوم، جنس *Hohenackeria* در رابطه نزدیک با *Bupleurum* قرار داشت اما در صفاتی مانند گل‌های سفید، چترهای بدون دمگل، کاسبرگ‌های آشکار، و فقدان برگک و کارپوفور با آن متفاوت بود. نتایج فیلوژنتیک، *Hohenackeria exscapa* را در زیرجنس *Bupleurum*، نزدیک به گونه *Bupleurum baldense* قرار داد. چندین صفت ریخت‌شناسی به همراه سیگنال‌های فیلوژنتیکی رابطه خویشاوندی آنها را حمایت نمود. هر دو گونه دارای ریشه‌های راست کوتاه، برگ‌های خطی تا کشیده سرنیزه‌ای که در انتها

به صورت دمبرگ به ساقه چسبیده، با برگ‌های ساقه‌ای بدون دمبرگ می‌باشند. گل‌ها و میوه‌ها معمولا در *B. baldense* توسط برگک‌ها در برگرفته می‌شود و دمگل‌ها کوتاه و نابرابر هستند درحالیکه در *H. exscapa* دمگل‌ها کوتاه‌تر و چترهای گل توسط برگ‌های قاعده‌ای بجای برگک‌ها مخفی می‌شوند بنابراین، برگک‌های مقعر در *B. baldense* نقش مخفی نگهداشتن چترها را برعهده دارند. در این مطالعه، گونه *Hohenackeria exscapa* به جنس *Bupleurum* به‌عنوان یک ترکیب جدید انتقال می‌یابد.

INTRODUCTION

Bupleureae Spreng., as a monogeneric tribe of Apiaceae, is well delimited and has been the focus of recent molecular and evolutionary research. The genus *Bupleurum* L., one of the largest genera of Apiaceae with 185-195 species, is the only member of this tribe. This genus includes annual and perennial species, ranging from small herbs to shrubs, and growing from just a few centimeters up to 3 meters tall. It has a vast distribution occurring in Europe, North Africa, Macaronesia (Canary Islands and Madeira), Asia and North America to eastern China. Despite this broad distribution, most species are rather rare and restricted to small areas. *Bupleurum* spp. grow in a great variety of habitats; from sea level up to mountainous regions (the Himalayan Mt.); through saline, calcareous, to basaltic soils; in arid areas to dense forests (Tutin, 1968; Heywood, 1971; Rechinger & Snogerup, 1987; Plunkett & al., 2018). Several species such as *B. falcatum* L., *B. marginatum* Wall., *B. rotundifolium* L. and *B. fruticosum* L. are used traditionally in medicine and contain essential oils (Schischkin, 1951).

Bupleurum was traditionally recognized within the subfamily Apioideae, tribe Apieae as a natural group, mainly due to its unique feature of the leaves (simple and entire leaves) with two kinds of venation: pinnate-reticulate veins vs. mostly with parallel-veins (unusual character in the family); with conspicuous bracts and bracteoles (Drude, 1898; Heywood,1971; Wolff, 1910; Tutin, 1968). Recent molecular studies, have demonstrated that *Bupleurum* is an early branching genus in the subfamily Apioideae and tribe Bupleureae with distinct position in a basal clade (Plunkett & al., 1996; Katz-Downie & al., 1999; Plunkett & Downie, 1999). *Bupleurum* has been considered an ancestral group in Apiaceae, mainly because of having woody species and based on some of the earliest pollen fossil records known for the family (Gruas-Cavagnetto & Cerceau-Larrival, 1984). Most *Bupleurum* species from southwest China retain the primitive pollen type (from subrhomboid to subrotund or subellipsoid), appearing in the early Paleocene (Wang & al., 2008).

The current accepted classification of *Bupleurum* was adopted by Tutin in Flora Europaea (1968), basically following Wolf's work (1910). Recent phylogenetic studies have divided the genus *Bupleurum* into two subgenera: subg. *Penninervia* S.S.Neves & M.F.Watson and subg. *Bupleurum* (Neves & Watson, 2004). *Bupleurum* subg. *Penninervia* includes the Mediterranean woody and perennial species characterized by pinnate reticulate veins, while *Bupleurum* subg. *Bupleurum* comprises the majority of species spread to East Asia, distinguished by their parallel veins. Neves and Watson (2004) proposed that the genus likely originated near the western Mediterranean. Then the molecular studies confirmed that the two East Asian groups of the *Bupleurum* originated from species near the Mediterranean and spread eastward through the Middle East and the Caucasus to East Asia (Wang & al., 2008; Wang & al., 2011). Due to collision of the Indian Plate with the Eurasian continent (~ 50-25 Ma) and the rapid uplift of the Himalayas and the Tibetan Plateau, the divergence of the two subgenera of the *Bupleurum* has occurred (Song & al. 2024). Based on the last results, two hotspots of diversity have been recognized for *Bupleurum*: The Mediterranean Basin and the Himalaya-Hengduan Mountains region (Neves & Watson, 2004; Huang & al. 2021).

Traditionally, another genus *Hohenackeria* Fisch. & C.A.Mey., was introduced in close relationship with *Bupleurum* but differentiated by its white flowers, sessile umbels and conspicuous calyx, and the lack of bracteoles and of a carpophore (mericarps do not separate) (Tutin, 1968). Using molecular nrDNA ITS data, Downie & al. (2010) considered the placement of this genus within tribe Bupleureae.

Geographically, *Hohenackeria* is distributed in the western Mediterranean, Turkey, the Caucasus, and south-west Asia (Iran) and contains two species: *H. exscapa* (Steven) Koso-Pol., which is a synonym of *H. bupleurifolia* Fisch. & C.A.Mey., and distributed from S. Spain, NW Africa, Turkey to Transcaucasus, and S. Iran. Another species is *H. polyodon* Coss. & Durieu distributed in C. Spain and Algeria (Dobignard & Chatelain, 2011). In Flora Iranica (Hedge & Lamond, 1987), the genus *Hohenackeria* was mentioned in the addendum with one species (*H. exscapa*) collected from southern Fars (Dasht-e Arzhan), Iran, and similarly noted in Flora of Iran (Mozzafarian, 2007). The type specimen was reported from Azerbaijan (USSR), Gandsham (Kruse, LE) (Hedge & Lamond, 1972). This is a small plant and less-known species that evolutionary would be important, representing a close affinity with *Bupleurum* species. However, during my work on Apiaceae tribes in the TARI herbarium and contributing to a research project on the subtribe Daucineae, I became intrigued by the distinctive life form of *H. exscapa*, which prompted a more detailed examination of this species. In this paper, I review tribe Bupleureae and its taxonomic classification, also determine the taxonomic position of *Hohenackeria exscapa* within it, and synonymize it under a new species of *Bupleurum*.

MATERIAL AND METHODS

Taxon and DNA sampling

To determine the relationship of *Hohenackeria exscapa* within the tribe Bupleureae, two herbarium samples were used to check morphological features, and one for molecular investigation. Another molecular sequence was retrieved from GenBank (it contains only ITS1 and ITS2 parts) and compared with the new Iranian sample. Based on previously available published ITS data on GenBank, a matrix (I=106 taxa) was organized with the sequences of various tribes of Apioideae. Then ITS sequences of various species of *Bupleurum* were collected from GenBank for preparing the second matrix (II=76 taxa). The voucher specimens and GenBank accession numbers of all species are given in Appendix 1 & Table 1, respectively. Multiple taxa were selected as outgroups, in accordance with previous phylogenetic results and pollen traits in early-diverging Apioideae, including three early branching Apioideae genera: *Sanicula epipactis* (Scop.) E.H.L.Krause, *Anginon difforme* (L.) B.L.Burtt, *A. paniculatum* (Thunb.) B.L.Burtt and 3 species of tribe Pleurospermeae (Plunkett & al., 1996; Neves & Watson, 2004; Baczynski & al. 2021).

The Genomic DNA of the selected specimen was obtained from c. 20 mg of dried leaves of the herbarium sample, and the PCR reactions and amplification of nrDNA ITS were performed, based on the protocol and details described previously (Panahi, 2023). The successful PCR products were selected, and the same primers were used for subsequent cycle sequencing. Cycle sequencing was performed by automated sequencing, using Big Dye terminators (Applied Biosystems, Foster City, CA, USA) in the laboratories of MomGene Knowledge-Enterprise in Tehran. The newly obtained sequence was deposited in GenBank (Table 1).

Alignment and phylogenetic analyses

DNA sequences were initially aligned in MAFFT (Katoh & al., 2019) and edited manually using Mesquite 3.8.1 (Maddison & Maddison, 2017) if necessary. In the phylogenetic analyses, all gaps were treated as missing data. All data matrices were trimmed in trimA1 using the PhyloSuite v 1.2.3 software (Xiang & al., 2023). The whole ITS datasets (I & II) were analyzed using the Maximum Likelihood (ML) and Bayesian inference (BI) methods separately using the PhyloSuite v 1.2.3 program. With BLAST searches of the NCBI database, almost all available accessions in Bupleureae were included in our analyses because of similarity in the sequences and the results of preliminary tests.

The maximum likelihood analyses of nrDNA ITS data were performed with GTR +G +I substitution models according to the corrected Akaike information criterion (AICc). All analyses were run with branch lengths Edge-Linked among partitions with 5000 Bootstrap numbers in Ultrafast, and branch support (BS) was evaluated based on 1000 rapid bootstrap replicates. Ultrafast bootstrap approximation results were presented in the consensus tree. Bayesian estimation of phylogeny was performed for each dataset (I & II) separately using MrBayes in PhyloSuite v 1.2.3, with 10 million generations and GTR+G model and a sampling frequency of 1000 generations with state frequency as fixed (empirical). The initial 25% of saved trees were discarded as burn-in, and the results were summarized on the 50% majority rule consensus tree. The convergence of the independent runs and effective sample size (ESS) for estimated parameters were checked using Tracer v.1.7.1 (Rambaut & al., 2018). The phylogenetic trees were visualized by FigTree v.1.4.4.

RESULTS

Phylogenetic analyses

The entire nrDNA ITS sequences across 106 species ranged from 584 to 613 bp in dataset I, which contains 192 constant sites and 346 parsimony-informative sites (approximately 32.8% constant and 59.2% parsimony-informative sites, respectively). In dataset II (Bupleureae + Outgroups), this region ranged from 571 to 632 bp across 76 species, and contained 226 constant sites and 217 parsimony-informative sites. In the first analyses of Apioideae tribes (dataset I), *Hohenackeria exscapa* was placed in tribe Bupleureae supportively (BS = 91, Fig. 1). The ITS sequences of *Bupleurum* species present in the matrix are highly divergent, and they differentiate from other members of the subfamily Apioideae as an independent tribe in the family Apiaceae. Also, the monophyly of *Bupleurum* in tribe Bupleureae was strongly supported, and *H. exscapa* is nested within it far from other tribes (Fig. 1).

Table 1. List of species in tribe Bupleureae with Outgroups (dataset II). Distribution of each species was taken from POWO 2025 (https://powo.science.kew.org/). GenBank accession numbers indicated in the ITS analyses. The new sequences of species are indicated by an asterisk.

Ingroup	Species	Distribution	ITS ID
Bupleureae			
Bupleurum L.	*B. acutifolium* Boiss.	SW. Portugal, S. Spain	AF467927
	B. album Maire	Morocco	AF467928
	B. aleppicum Boiss.	E. Türkiye to Syria and NW. Iran	PX230622
	B. angulosum L.	NE Spain	AF469008
	B. angustissimum (Franch.) Kitag.	Mongolia to N. China	OR502915
	B. balansae Boiss. & Reut.	Morocco	AF469681
	B. baldense Turra	W. & SW. Europe to Italy	AF469682
	B. barceloi Coss. ex Willk.	Baleares	AF477023
	B. benoistii Litard. & Maire	Morocco	AF477026
	B. bicaule Helm	Afghanistan to Siberia and Japan	OR502917
	B. boissieuanum H.Wolff	Central China	EU220931
	B. brevicaule Schltdl.	S. Türkiye to Jordan and Iraq	PX230624
	B. candollei Wall. ex DC.	N. Pakistan to China (W. Sichuan, NW. Yunnan)	GU269873
	B. canescens Schousb.	Morocco	AF477027
	B. chaishoui R.H. Shan & M.L. Sheh	China (NW. Sichuan)	OP433486
	B. chinense DC.	China to N. Korea	OR502921
	B. commelynoideum H. Boissieu	Tibet to China (W. Sichuan, NW. Yunnan)	GU269874
	B. densiflorum Rupr.	Central Asia to SW. Siberia & W. China	JN818033
	B. dumosum Coss. & Balansa	SE Morocco	AF477030
	B. dracaenoides Huan C. Wang, Z.R. He & H. Sun	China (Sichuan, Yunnan)	JQ365173
	B. exaltatum M.Bieb.	Europe to China	MT880980
	B. euphorbioides Nakai	S. Russian to Korea	JN818012
	B. falcatum L.	Europe to the Caucasus	AF479290
	B. fruticescens subsp. *fruticescens*	Spain	AF479292
	B. fruticescens subsp. *spinosum*	Spain	AF479296
	B. gerardii All.	S. Europe to W. Iran	AF479850
	B. gibraltaricum Lam.	S. Spain, NW. Africa	AF479852
	B. gracillimum Klotzsch	E. Afghanistan to the Himalaya	GU269886
	B. hamiltonii N.P.Balakr.	N. Pakistan to S. China & N. Indo-China	OR502930
	B. kurdicum Boiss.	E. Türkiye to NW. Iran	PX230623
	B. kweichowense R.H. Shan	China (NE. Guizhou)	OR502931
	B. lancifolium Hornem.	S. Spain to Iran	AF479853
	B. lateriflorum Coss.	Morocco	AF479855
	B. latissimum Nakai	Korea	AY551292
	B. leucocladum Boiss.	Syria to SW. Iran	PX230625
	B. longicaule Wall. ex DC.	SW. Siberia to N. Pakistan & S.C. China	GU269877
	B. longifolium L.	Central Europe to S. Russia	AF479856
	B. longeradiatum Turcz.	E. Siberia to Japan & S.C. China	OR502932
	B. malconense R.H. Shan & Y. Li	SE. Tibet to China (W. Sichuan, S. Gansu)	OP433483
	B. marginatum Wall. ex DC.	E. Afghanistan to C. China & N. Myanmar	OR502936
	B. microcephalum Diels	W. Himalaya, SE. Tibet to China	OP433476
	B. montanum Coss. & Durieu	Morocco (NW. Africa)	AF479859
	B. mundii Cham. & Schltdl.	S. Africa	AF479860
	B. odontites L.	Central & E. Medit.	AF479861
	B. oligactis Boiss.	Algeria & Tunesia	AF479864
	B. plantagineum Desf.	Algeria & Morocco?	AF479865
	B. praealtum L.	C. & S. Europe	AF481391
	B.pseudochaishoui Z. Chao	China (Sichuan)	OQ506349
	B. ranunculoides L.	Europe (in Mountains)	AF481395
	B. rigidum subsp. *paniculatum* (Brot.) H.Wolff	Spain & Morocco	AF481399
	B. rigidum subsp. *rigidum*	W. Medit.	AF481397
	B. rockii H.Wolff	China (Lijiang, Yunnan)	OR502938

Ingroup	**Species**	**Distribution**	**ITS ID**
	B. rotundifolium L.	Medit. to Asia	AF481400
	B. salicifolium R.Br.	Canary Islands	AF481928
	B. scorzonerifolium Willd.	Siberia to Korea and N. & E. China, Central & S. Japan	OR502939
	B. semicompositum L.	Canary Islands to Turkmenistan	AF481929
	B. shanianum X.G.Ma & X.J.He	Tibet to China (Yunnan)	OR502940
	B. sibiricum Vest ex Spreng.	S. & E. Siberia to N. China (Chifeng, Neimeng)	OR502941
	B. sikangense X.J. He & C.B. Wang	Tibet	OR502943
	B. smithii H. Wolff	N. & E. Central China	OR502947
	B. stellatum L.	Alp Europe	AF481930
	B. subspinosum Maire & Weiller	Morocco	AF481931
	B. tenuissimum L.	Europe to the Caucasus	AF481932
	B. triradiatum Adams ex Hoffm.	Siberia to N. Japan (Xinjiang)	OR502948
	B. thianschanicum Freyn	Central Asia to W. Xinjiang	GU570608
	B. wenchuanense R.H. Shan & Y. Li	China (NW. Sichuan)	MF428549
	B. yinchowense R.H. Shan & Y. Li	N. China	OR502951
	B. yunnanense Franch.	SE. Tibet to China (Sichuan, Yunnan)	GU269883
Hohenackeria Fisch. & C.A.Mey.	*H. exscapa* (Steven) Koso Pol.	Iran, Fars: Shiraz to Dashte Arzhan, 1700 m, *Mozaffarian 83581* TARI	PZ476668*
		S. Spain, NW. Africa, Türkiye to Transcaucasus, W. & S. Iran	AF337178
Outgroups			
	Anginon difforme (L.) B.L.Burtt		AF459742
	Anginon paniculatum (Thunb.) B.L.Burtt		AF467922
	Sanicula epipactis (Scop.) E.H.L.Krause		EU070740
Pleurospermeae	*Eremodaucus lehmanii* Bunge		EU169268
	Korshinskia olgae (Regel & Schmalh.) Lipsky		GQ379341
	Physospermum cornubiense DC.		AF077904

Trees obtained from ML and Bayesian analyses of dataset II were similar in topology, except for the position of the fourth subclade in subgenus *Bupleurum* (sister with subclades A & C in ML analysis and sister with all clades in BI analysis supportively), so the consensus tree inferred from BI analysis is shown here. The phylogenetic results of dataset II confirmed the two main subgenera in the genus, *B.* subgenus *Penninervia* and *B.* subgenus *Bupleurum*, in concordance with the earlier research (Fig. 2). 68 species of *Bupleurum* were included in our analyses, and most of them were located within subgenus *Bupleurum* in four subclades that are geographically separated. Subclade **A** contains most Chinese and Siberian species, introduced as the East Asia II group by Song & al. (2024). Some species with vast distribution from Europe, Central Asia to China, such as *B. exaltatum* M.Bieb., *B. ranunculoides* L., *B. longifolium* L., *B. bicaule* Helm, and *B. thianschanicum* Freyn have occurred in this group as well as some species with narrow distribution, such as B. *latissimum* Nakai (from Southern Korea) and *B. euphorbioides* Nakai (in S. Russia to Korea).

The subclade **B** includes the Mediterranean and NW African species (European elements), which contain Iberian, Macaronesian elements, and several species of SW Asia were positioned supportively there with a long branch, likely reflecting less sampling from this region. Subclade **C** comprises East Asia I group (as discussed by Song & al., 2024), which contains the Qinghai-Tibet Plateau and Hengduan Mountain elements in one group, and the other sister group comprises the elements distributed from Europe to Caucasus (Iran) except *B. mundii* Cham. & Schltdl., which is endemic to S. Africa. The fourth small clade represented two annual species, *H. exscapa* and *B. baldense*, in a separate position, sister to subclade C (I refrain from grouping it separately because of the lack of sampling from E. Mediterranean and SW Asia) (Fig. 2). The sequences of *B. baldense* have a long indel (24 bp) that differentiates it from other *Bupleurum* species. The *H. exscapa* 83581 specimen has similar sequences with its' GenBank accession (AF337178) but differs in a few nucleotide substitutions, which may be referred to different geographic sampling (the former from Fars, Iran and the latter from Spain).

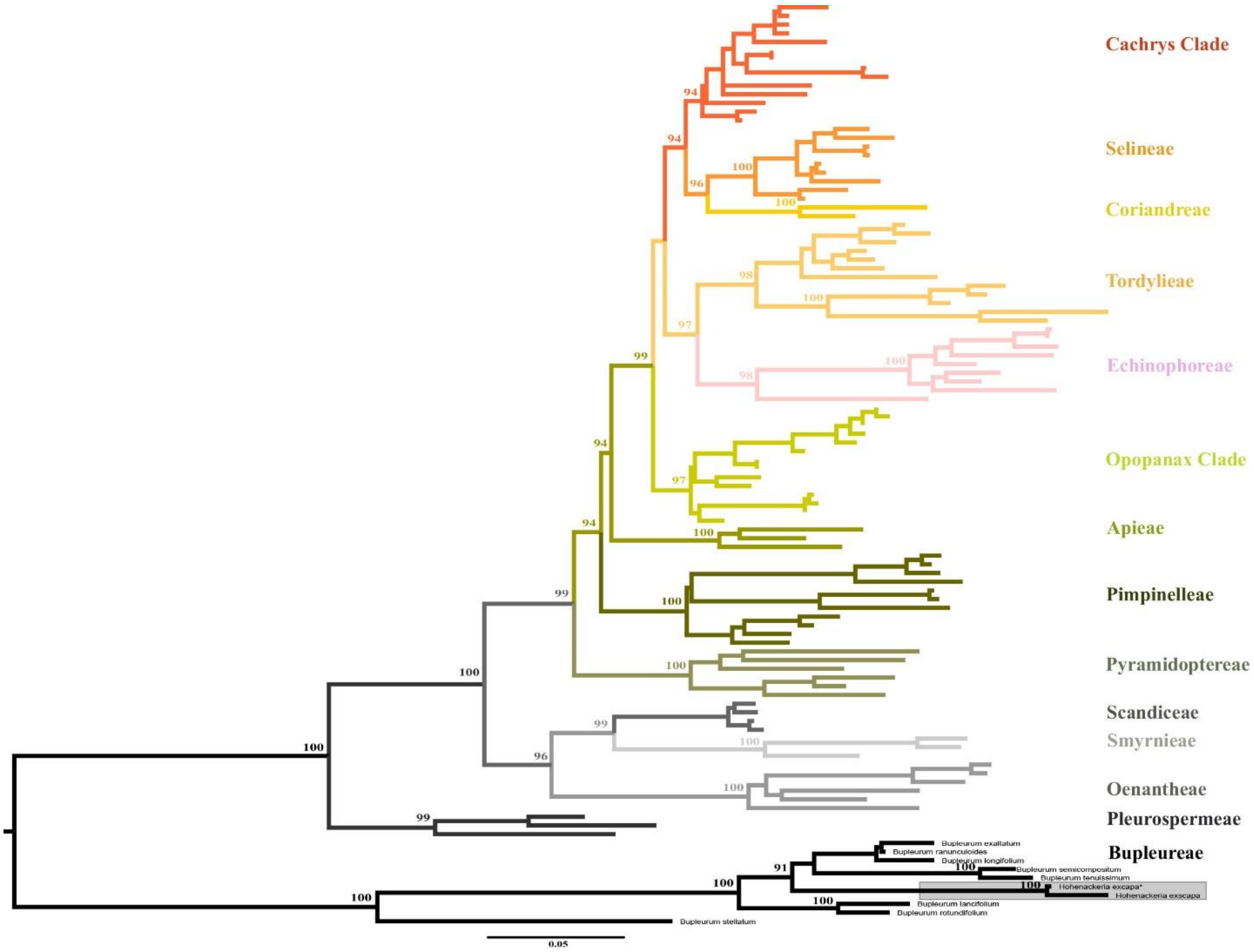

Fig. 1. The consensus tree inferred from ML analysis of 106 representatives of Apioideae tribes (clades) using nrITS sequence (dataset I). Bootstrap support of the consensus tree is given along branches. The position of *Hohenackeria exscapa* in Bupleureae is in the gray box. The outgroups were excluded from the tree.

Morphological analysis

The morphological characters of *Hohenackeria exscapa*, the genus *Bupleurum*, and *B. baldense* were compared based on the literature, and the main features of the studied taxa are shown in Table 2. Flora Iranica (Rechinger & Snogerup, 1987), Flora of Turkey and the East Aegean Islands (Hedge & Lamond, 1972; Snogerup, 1972), Flora of Iran (Mozaffarian, 2007), and Flora Europaea (Tutin, 1968) were used for these comparisons.

The genus *Bupleurum* occurs as glabrous, herbaceous annuals to perennial shrubs in nature, with taproots or branched rootstocks. The annual plant *Hohenackeria exscapa* shows morphological and phylogenetic affinity with the annual species *Bupleurum baldense* in certain characters, such as dwarf habit, slender tap roots, glabrous stems (Table 2., Figs. 3 & 4). Leaves in *B. baldense* are linear to oblong-lanceolate with scabrid margins and visible nerves, whereas in *H. exscapa*, these characters are similar, but rosulate leaves are sessile and do not have visible nerves.

Bracts and bracteoles in *Bupleurum baldense* have developed in lanceolate to ovate while bracts and bracteoles in *H. exscapa* are absent or only yellowish bracts that are seen with leaf-like structure. Stems in *H. exscapa* are absent or very short-stemmed (0.5-2 cm long), whereas this feature developed in *B. baldense* (2-30 cm long) as dichotomous. *Hohenackeria exscapa* has simple umbel and sessile flowers; developed rigid calyx lobes longer than petals; long erect styles and inconspicuous stylopodium, and to some extent conical vs. *B. baldense* has terminal and lateral simple umbels, but the other features were not checked due to unavailability of the specimen.

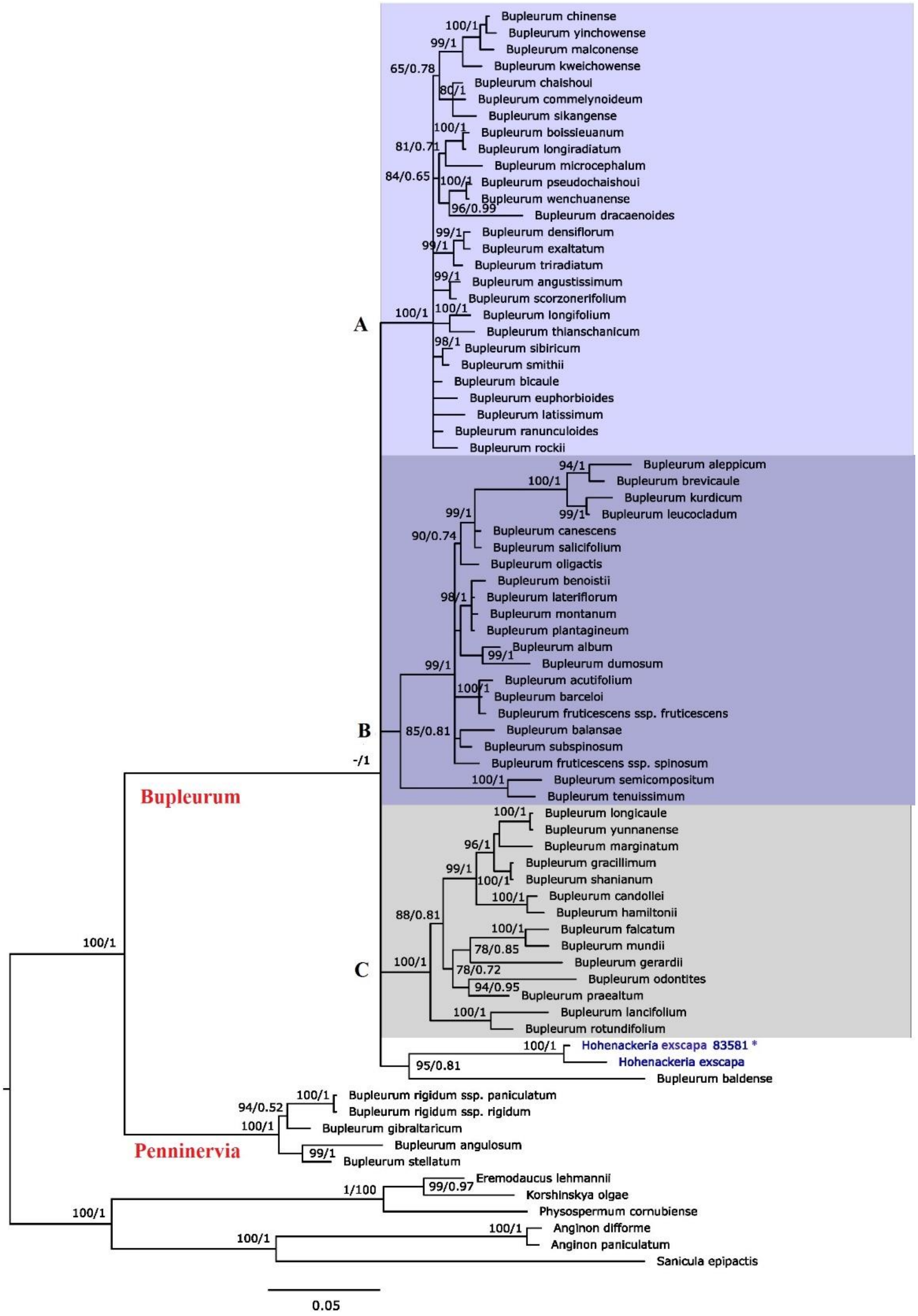

Fig. 2. The consensus tree inferred from BI analysis of 68 representatives of the Bupleureae tribe using ITS sequence (dataset II). Bootstrap support (left) and posterior probability (right) of the Bayesian 50% majority-rule consensus tree are given along branches. The position of *Hohenackeria exscapa* is in the subgen. *Bupleurum* in blue color.

There are several similar characters between *Bupleurum* and *H. exscapa,* such as: life form, glabrous stem, entire linear to broadly elliptic leaves, glabrous petals with inflexed apical lobes, mericarps with 5 inconspicuous equal ribs, and the arrangement of vallecular vittae (1-5), 2-10 commissural vittae that are sometimes inconspicuous at maturity. The only morphological characters that differentiate *H. exscapa* from *Bupleurum* are: absent sepals; developed bracts and bracteoles, developed umbels and mericarps (present carpophore) in *Bupleurum*, and the form of styles.

Ecologically, *H. exscapa* grows in stony slopes and sandy-stony semi-deserts, also *Bupleurum* is scattered exclusively in the sub-tropic and temperate zones of the Old World (species growing from forest to desert conditions) except in a few species in North America and South Africa (Schischkin, 1951).

Fig. 3. a, *Hohenackeria exscapa* in habitat (Almeria, Spain); b & c, *Bupleurum baldense* in habitat (France) and flowers (photos were taken from GBIF available at https://www.gbif.org/)

DISCUSSION

The tribe *Bupleureae* is an important lineage within Apioideae due to its medicinal significance and its recently recognized evolutionary distinctiveness. Evolutionarily, leaf venation appears to be an important feature in the classification of flowering plants, and pinnately veined vs. parallel veined have been considered for the infrageneric classification of the genus *Bupleurum* (Schischkin, 1951; Neves & Watson, 2004). Boissier (1872) described the *Bupleurum* species with more characters other than leaf venation, such as habit, width, and texture of bracteoles, while Linnaeus (1753) divided it based on herbaceous and woody status. However, the woody character in *Bupleurum* exhibits some ancestral characteristics as a primitive state in the family that some species represented as shrubs and subshrubs. The annual habit has evolved at least twice within *Bupleurum.* This is evident from clades that consist predominantly of annual species such as *B. semicompositum* L. and *B. tenuissimum* L., which are annuals in the basal position of clade B (Fig. 2), as well in one subclade of clade C, which contains the annuals except the only two perennial herbs, such as *B. falcatum* and *B. mundii*. In contrast, in clade A, which contain mostly perennial herbs such as *B. rockii* H.Wolff, found on mountain slopes at elevations of 1900-4200 m, is grouped with *B. dracaenoides* Huan C. Wang, Z.R. He & H. Sun, with a shrubby state (Fig. 2). It is evident that the shorter life cycle increases the chances of evolutionary changes that led to increased diversity in annual plants. This could phylogenetically explain why clades composed exclusively of herbs and annuals exhibit longer branches than those consisting solely of perennials.

Our ITS results confirmed the position of two subgenera of *Bupleurum*: *Penninervia* and *Bupleurum*. The first subgenus includes *B. rigidum* L. (with two subspecies), *B. angulosum* L., *B. gibraltarium* Lam., and *B. stellatum* L. (*B. fruticosum* L., another member of this subgenus, was not examined here). These are shrubs and perennial herbs, all native to the Mediterranean region, while no other comparable morphological characters have yet been identified to differentiate among the elements of the subgenus. This feature is common to all the species of this subgenus, while the molecular signal from ITS is strong (by nucleotide substitution pattern and the presence of three indels), which separates these members of the subgenus *Penninervia* from the subgenus *Bupleurum*.

Table 2. Comparison of morphological characters of *Hohenackeria exscapa*, *Bupleurum baldense*, and the genus *Bupleurum* (original description by Boissier with further rectification from Flora Iranica, Flora of Turkey, and Flora Europaea)

	Hohenackeria exscapa **(Steven) Koso-Pol.**	***Bupleurum baldense*** **Turra**	***Bupleurum*** **L.**
Life form	Annual	Annual	Annual to perennial
Root	Slender tap root	Slender tap root	With taproots or branched rootstocks
Stem length (cm)	Without stem or very short stemmed, 0.5-2 cm long	Much-branched stem, 2-30 cm (dichotomous)	With a conspicuous stem, from 2 cm up to 300 cm
Stem pubescence	Glabrous	Glabrous	Glabrous
Leaves	Entire, sessile, oblanceolate blade, attenuate into petiole then broadened and winged, 3-6 × 0.2-0.5 cm, 3-nerved	Basal leaves attenuate to petiolate, cauline leaves sessile, linear to oblong-lanceolate, 1-8 × 0.2-0.5 (-1) cm, 3-5 nerved (visible)	Entire, linear to broadly elliptic, or perfoliate
Margin of leaves	Dentate scabrid	Narrowly scarious	Finely serrulate
Bracts	Absent or leaf-like	Lanceolate, long-acuminate or aristate, margin narrowly scarious	Linear-lanceolate to ovate or absent in some broad-leaved annuals
Bracteoles	Absent	Lanceolate to ovate, slightly concave, margin narrowly scarious	Linear to roundish
Umbel	Sessile, simple, nearly completely hidden by radical leaves	Terminal & lateral	Compound, usually well developed
Umbellets	6-16 flowered	5-10 flowers, unequal rays	(1-6) up to 25 flowers
Petals	Whitish, minute, 0.5mm long	Yellow, inflexed apical lobes are entire	Petals usually glabrous, yellow, white, or dorsally purplish
Fruits	Glabrous, 5-6 × 2-3 mm	Ovate-oblong, 2-2.5 × 0.5-1 mm, ridges filiform	Glabrous, slightly compressed laterally, ridges 5, linear to winged or rarely inconspicuous
Mericarps	undivided (carpophore absent), thickened below with distinct cylindrical beak	Oblong-elliptic, ridges filiform & smooth	carpophore free, bifurcated
Ribs	Corky, sub-inconspicuous, with 5 equal protruding thickened ribs	Not seen	ribs inconspicuous to (5) equal, narrow, acute, strongly protruding, winged
Vittae arrangement	Vallecular vittae 1, commissural 2–4, inconspicuous at maturity	Vallecular vittae 3-5	Vallecular vittae 1-5, commissural 2-10, rarely inconspicuous at maturity
Style	Long, erect, dichotomous	Not seen	Short
Stylopodium	Short-conical, distinctly stalked	Not seen	Flat to low-conical

In this group *B. angulosum* (endemic to the Pyrenees) and *B. stellatum* (endemic to the Alps and Corsica) are both herbaceous perennial species that show morphological affinity while *B. rigidum* (distributed in Iberica and NW Africa) has a unique venation type, with leaf variation, branching pattern, and length of flowering stem (Neves & Watson, 2004; Tutin, 1968).

Most *Bupleurum* species are placed in subgenus *Bupleurum*, which typically have 6 parallel-veined leaves (Neves & Watson, 2004). The plants of this subgenus are shrubs, subshrubs, perennial or annual herbs, geographically separated in our analysis, and no morphological signal is supported. The ITS molecular signal has differentiated the subclades by nucleotide substitutions in each group. It seems that the chloroplast genomes could be helpful; recent phylogenomic studies of the chloroplast genomes in *Bupleurum* revealed that this genome size is larger than that of the other genera in the Apiaceae, while the chloroplast genomes of the *Bupleurum* species showed only minor differences in sizes and length of several genes (Huang & al. 2021). Evidence from previous studies suggested that the genus *Bupleurum* originated somewhere in the western Mediterranean. The first branching clade in *Bupleurum* (subgen. *Penninervia*) occurs only in the western Mediterranean, and the eastern Mediterranean has high species diversity in annuals (Snogerup, 1972). ITS analysis indicates that the annual habit is a derived state (possibly having evolved more than once in the genus) (Neves & Watson, 2004).

Chinese and Siberian species of *Bupleurum* mostly placed in subclade A that distributed widely from central and eastern of Asia and Europe (suggested as East Asia Group II by Song & al. (2024)) except several species that have not represented any relationships (making a single branch) such as *B. rockii* (a perennial endemic of Sichuan, NW. Yunnan), *B. ranunculoides* (a perennial herb in mountains of Europe), *B. latissimum* (endemic of Korea), *B. euphorbioides* (an annual endemic from S. Russian Far East to Korea, Table 1.). However, no more morphological signal supported subclade A, but ITS signals (nucleotide substitutions) and bootstrap support strongly this group (BS=100, PP=1, Fig. 2).

Fig. 4. Herbarium material, (left) *Hohenackeria exscapa* (83581, TARI); (right) *Bupleurum baldense* (KEW barcode KOO1733093).

Subclade B included the European, NW African, and SW Asian elements that are separated geographically as before suggested as the `Macaronesian' group, the `Iberian and Balearic' group, and the 'Eurasian heterogeneous group' (Neves & Watson, 2004). In the current study, four species from SW Asia were inserted in the data matrices (*B. aleppicum* Boiss., *B. brevicaule* Schltdl., *B. kurdicum* Boiss. and *B. leucocladum* Boiss.). These species are located close to the Macaronesian elements (*B. canescens* Schousb., *B. salicifolium* R.Br., and *B. oligactis* Boiss.) in a sister position (Fig. 2). By adding more species from this region, the real position would be determined, and the effect of long branched would be decreased.

Subclade C (including East Asia Group I elements suggested by Song & al. (2024)) represents species that are exclusively found in the Qinghai-Tibetan Plateau and the Hengduan Mountains (upper subclade, Fig. 2), and in the lower subclade, several elements with distribution from the European region to SW Asia (as Eurasian heterogeneous group) were placed. The only exception is *B. mundii*, as the southern African endemic, close to *B. falcatum*. *Bupleurum falcatum* is widely distributed from Europe to Eurasia, and new forms in *B. falcatum* have spread across Eurasia. Wang & al. (2008) suggested that the *B. falcatum* populations from different regions should be separated as different species, and I confirm that it needs to be studied more (choosing more taxa of this species in our preliminary analyses, they were situated separately, as non-monophyletic species within group C, then most were excluded from the matrix except one) through expending more sampling and using cpDNA molecular markers.

The Hengduan Mountains (Western Sichuan area) is one of the centers of diversity for *Bupleurum* species, and more than half of the species in China can be found in this region. The complex terrain and landforms, and diverse climate of ancient and modern times in the region, have created opportunities for natural interspecific hybridization, and the results of phylogenetic trees suggest the possibility of ancient chloroplast capture events (Chao & al., 2023). Due to the opinion that the radiation of euapioids occurred in Eurasia, with Bupleureae originating in Europe during the early Tertiary (Banasiak & al., 2013), the phylogenetic results of Calvino & al. (2016) showed the earliest diverging lineages of Apioideae and Saniculoideae originating in Africa and diversifying in situ since the Palaeocene, with no input from newcomers until the Miocene. After widespread distribution within Africa, many of the southern African-Eurasian disjunctions observed today are the result of extinctions driven by the increasing aridification of Africa from the Miocene onwards, so it seems that *B. mundii* is one of the relict species of Bupleureae in South Africa.

The Taxonomic position of *Hohenackeria exscapa*

Similar Morphological features among most species of *Bupleurum*, such as simple and entire leaves with parallel-veined, show the affinity of *Hohenackeria exscapa* to the genus *Bupleurum*. Moreover, habit and bract characters (leaf-like structures) will be important as used before in the classification of the genus (Wolff, 1910). Those morphological characters that differentiate *H. exscapa* vs. *Bupleurum* are very short-stemmed; simple umbel and sessile flowers; developed rigid calyx lobes longer than petals; long erect styles; undivided mericarps (carpophore absent) vs. *Bupleurum* that is stemmed (herbaceous annuals to perennial shrubs); developed umbel; absent calyx; short styles; flat to low-conical stylopodium. The number of vallecular vittae in *Bupleurum* is defined as important through anatomical work that separated the species into two groups (first group with solitary vallecular vittae and the second group with 2-5 vallecular vittae in several SW Asian species) (Ghahremaninejad & al., 2014). However, this character may include *H. exscapa* within the first group introduced by Ghahremaninejad & al. (2014). In phylogenetic results, *H. exscapa* was placed close to an annual species of *Bupleurum*, *B. baldense*, that both have slender tap roots; linear to oblong-lanceolate leaves that attenuate into a petiole with sessile cauline leaves (Figs. 3 & 4).

Bupleurum baldense has a native range distribution in the western Mediterranean from Spain to Italy, with the northernmost localities in Southern England. Seregin & al. (2015) reported the new record of *B. baldense* for Eastern Europe from the Crimea (as an alien along a railway to a busy cargo port). In Flora Orientalis (Boissier, 1987), the habitat of the species is described from Monte Greece, Macedonia, to Turkey, Armenia, and Iran (Mont. Nakhichevan) as a Caucasus element. These regions could cover the distribution of *H. exscapa* as well. Based on phylogenetic results, *B. baldense* is sister to *H. exscapa*, and morphologically has differentiated with the presence of bracteoles, terminal & lateral Umbels. Flowers and fruits in *B. baldense* are generally enveloped by bracteoles, and pedicels are subequal and short (1-3.5 mm), while in *H. exscapa* umbels are hidden by radical leaves, so it seems the concave bracteoles play this role in *B. baldense*.

Various degrees of ploidy (2n = 8, 12, 14, 16, 20, 22, 24, 26, 28, 29, 30, 32, 36, 42, 60, 64) have been reported for *Bupleurum* species, followed by aneuploidy and dysploidy that have occurred. The basic number is x=8 & 7 (Neves & Watson, 2004), while in

Hohenackeria exscapa 2n=32 and in *B. baldense* 2n=16 has been reported (Plunkett & al., 2018). However, these ploidy levels could occur during evolutionary changes in *Bupleurum* species. The similar habit in *H. exscapa* and *B. baldense* affected their growth in arid slopes and dry open habitats, which caused several morphological similarities, such as small herb, form of leaves, and number of nerves etc. Neves & Watson (2004), in their preliminary results, indicated that *H. exscapa* was included within *Bupleurum* subgenus *Bupleurum*, and this inclusion does not affect the main clades of *Bupleurum*. They confirmed that the annual herb *B. baldense* appeared in conflicting positions in their various analyses, and *B. baldense* with a long branch was placed in the basal position of subgenus *Bupleurum* (with low support). Therefore, they recommended adding more taxa, from eastern Mediterranean closely related annual species, which may resolve their reliable phylogenetic position. Neves & Watson (2004) suggested this species may be related to other annuals such as *B. rotundifolium*, *B. gerardii*, *B. praealtum* and especially *B. odontites*. I also suggest their opinion by adding more related taxa; the fourth subclade could get more support with short branches.

Taxonomic treatment

Bupleurum exscapum (Steven) M.Panahi, **comb**. **nov**.

Syn.: *Valerianella exscapa* Steven, In: Mém. Soc. Imp. Naturalistes Moscou 3: 251 (1812); *Hohenackeria exscapa* (Steven) Koso-Pol. In: Trudy Bot. Sada Jur’ev. 15(2-3): 120 (1914); *Hohenackeria exscapa* (Steven) Grande, Bull. Orto Bot. Regia Univ. Napoli 8: 73 (1926); nom. superfl. (POWO, 2026)

Type: Azerbaijan (USSR), Gandsham (Kruse, LE)

Other specimens seen: Iran, Fars, Shiraz to Dasht-e Arzhan, ca. 3 km to Dasht-e Arzhan, 2003, 1700 m, Mozaffarian 83581 (TARI); Ardabil, between Germi and Pars-Abad, 14/05/2016, 700 m, S. Ghaffari 106259 (TARI).

References

Baczynski, J., Milobedzka, A. & Banasiak, L. 2021: Morphology of pollen in Apiales (Asterids, Eudicots). -Phytotaxa, 478(1): 1-32. https://doi.org/10.11646/phytotaxa.478.1.1

Banasiak, L., Piwczynski, M., Ulinski, T., Downie, S.R., Watson, M.F., Shakya, B. & Spalik, K. 2013: Dispersal patterns in space and time: a case study of Apiaceae subfamily Apioideae. -J. Biogeogr. 40(7): 1324-1335.

Boissier, P.E. 1872: Umbelliferae, In: Flora Orientalis. vol. 2: 819–1090. Geneva, Basel.

Calvino, C.I., Teruel, F.E. & Downie, S.R. 2016: The role of the Sothern Hemisphere in the evolutionary history of Apiaceae, a mostly north temperate plant family. -Journal of Biogeography 43: 398-409. https://doi.org/10.1111/jbi.12651

Chao, Z., Hong, X., Xie, X., Huang, R. & Tian, E. 2023: Phylogenomic analysis of *Bupleurum* in Western Sichuan, China, including an overlooked new species. -Front. Plant Sci., 14: 1294670. https://doi.org/10.3389/fpls.2023.1294670

Dobignard, A. & Chatelain, C. 2011: Index synonymique Flore d’Afrique du Nord. Vol. 2. -Ville de Genève éditions des Conservatoires et Jardins Botaniques. Geneve.

Downie, S.R., Spalik, K., Katz-Downie, D.S. & Reduron, J.-P. 2010: Major clades within Apiaceae subfamily Apioideae as inferred by phylogenetic analysis of nrDNA ITS sequences. -Plant Div. Evol. 128(1–2): 111–136. https://doi.org/10.1127/1869-6155/2010/0128-0005

Drude, O. 1898: Umbelliferae. In: Engler, A., Prantl, K. (eds.). Die natürlichen Pflanzenfamilien. Vol. 3, Part 8: 63-250. -Leipzig: Wilhelm Engelman.

Ghahremaninejad, F., Hoseini, E. & Mozaffarian, V. 2014: Fruit anatomy of the genus *Bupleurum* L. (Apiaceae) in Iran. -Iran. J. Bot. 20(1): 51-70.

Gruas-Cavagnetto, C. & Cerceau-L′Arrival, M.-T. 1984: Apport des pollens fossiles d’ ombellifères à la connaissance paléoécologique et paléoclimatique de l'Éocène français. -Review of Palaeobotany and Palynology 40: 317-345.

Hedge, I.C. & Lamond, J.M. 1972: *Hohenackeria*. In: Umbelliferae, Davis, P.H. (ed.). Flora of Turkey and the East Aegean Islands 4: 393. -Edinburgh University Press, Edinburgh.

Hedge, I.C. & Lamond, J.M. 1987: *Hohenackeria*. In: Umbelliferae, K. H.Rechinger (ed.) Flora Irania 162: 526. -Graz, Austria: Akademische Druck- u. Verlagsanstalt.

Heywood, V.H. 1971: Systematic survey of Old World Umbelliferae. In: Heywood, V.H. (ed.). The biology and chemistry of the Umbelliferae. -London: Academic Press, pp: 31-41.

Huang, R., Xie, X., Chen, A., Li, F., Tian, E., & Chao, Z. 2021: The chloroplast genomes of four *Bupleurum* (Apiaceae) species endemic to Southwestern China, a diversity center of the genus, as well as their evolutionary implications and phylogenetic inferences. -BMC Genomics 22: 714. https://doi.org/10.1186/s12864-021-08008-z

Katoh, K., Rozewicki, J. & Yamada, K.D. 2019: MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. -Briefings in Bioinformatics 20 (4): 1160-1166.

Katz-Downie, D.S., Valiejo-Roman, C.M., Terentieva, E.I., Troitsky, A.V., Pimenov, M.G., Lee, B., &

Downie, S.R. 1999: Towards a molecular phylogeny of Apiaceae subfamily Apioideae: additional information from nuclear ribosomal DNA ITS sequences. -Plant Systematics and Evolution 216: 167-195.

Linnaeus, C. 1735: Systema Naturae. -Lugduni Batavorum, Leiden, Netherlands.

Maddison, W.P., & Maddison, D.R. 2017: Mesquite: a modular system for evolutionary analysis. Version 3.2. Available at: http://mesquiteproject.org

Mozaffarian, V. 2007: Umbelliferae, In: Assadi, M., Maassoumi, A.A.R. & Khatamsaz, M. (eds.). Flora of Iran, no. 54. -Research Institute of Forests and Rangelands, Tehran.

Neves, S.S., & Watson, M.F. 2004: Phylogenetic relationships in *Bupleurum* (Apiaceae) based on nuclear ribosomal DNA ITS sequence data. -Annals of Botany 93(4): 379-398. https://doi.org/10.1093/aob/mch052

Panahi, M. 2023: Phylogenetic relationships within *Ferula* sect. *Merwia* (Apiaceae, Ferulinae) inferred from nrDNA and cpDNA markers. -Iran. J. Bot. 29(2): 89-105. https://doi.org/10.22092/IJB.2023.363199

Plunkett, G.M., & Downie, S.R. 1999: Major lineages within Apiaceae subfamily Apioideae: a comparison of chloroplast restriction site and DNA sequence data. -American Journal of Botany 86: 1014-1026.

Plunkett, G.M., Soltis, D.E., & Soltis, P.S. 1996: Higher level relationships of Apiales (Apiaceae and Araliaceae) based on phylogenetic analysis of rbcL sequences. -American Journal of Botany 83: 499-515.

Plunkett, G.M., Pimenov, M.G., Reduron, J.-P., Kljuykov, E.V., Van Wyk, B.-E., Ostroumova, T.A., Henwood, M.J., Tilney, P.M., Spalik, K., Watson, M.F., Lee, B.-Y., Pu, F.-D., Webb, C.J., Hart, J.M., Mitchell, A.D., & Muckensturm, B. 2018: Appiaceae. In: Kadereit, J.W. & Bittrich, V. (eds.). Flowering Plants. Eudicots, The Families and Genera of Vascular Plants 15. -Springer International Publishing AG, part of Springer Nature. pp: 9-556. https://doi.org/10.1007/978-3-319-93605-5_2

Rambaut, A., Drummond, A., Xie, D., Baele, G. & Suchard, M. 2018: Posterior summarization in Bayesian phylogenetics using Tracer 1.7. -Systematic Biology 67: 901–904.

Rechinger, K.H. & Snogerup, S. 1987: *Bupleurum*. In: Rechinger, K.H., (ed.). Umbelliferae, Flora Iranica, no. 162: 269-297. -Graz, Austria: Akademische Druck- u. Verlagsanstalt.

Schischkin, B.K. 1951. Umbelliferae, In: Schischkin, B.K., (ed.). Flora of the U.S.S.R., 17: 195-251. -Izdatelstvo Akademii Nauk SSSR, Moskva-Leningrad.

Seregin, A.P., Yevseyenkov, P.E., Svirin, S.A. & Fateryga, A.V. 2015: Second contribution to the vascular flora of the Sevastopol area (the Crimea). -Wulfenia 22: 33-82.

Snogerup, S. 1972: *Bupleurum*. In: Umbelliferae, Davis, P.H. (ed.). Flora of Turkey and the East Aegean Islands 4: 393-418. -Edinburgh University Press, Edinburgh.

Song, Y.-x., Yang, C.-Y., Zhou, Y.-Y., & Yu, Y. 2024: Speciation and diversification of the *Bupleurum* (Apiaceae) in East Asia. -PhytoKeys 248: 41-57. https://doi.org/10.3897/phytokeys.248.132707

Tutin, T.G. 1968: *Bupleurum*. In: Tutin, T.G., Heywood, V.G., Burges, N.A., Moore, D.M., Valentine, D.H., Walter, S.M., & Webb, D.A. (eds.). Flora Europaea, Vol. 2: 345-350. -Cambridge University Press, Cambridge.

Wang, C.B., Ma, X.G., & He, X.J. 2011: A taxonomic re-assessment in the Chinese *Bupleurum* (Apiaceae): Insights from morphology, nuclear ribosomal internal transcribed spacer, and chloroplast (trnH-psbA, matK) sequences. -J. Systematics Evol. 49(6): 558-589. https://doi.org/10.1111/j.1759-6831.2011.00157.x

Wang, Q.-Z., Zhou, S.-D., Liu, T.-Y., Pang, Y.-L., Wu, Y.-K. & He, X.-J. 2008: Phylogeny and classification of Chinese *Bupleurum* based on nuclear ribosomal DNA internal transcribed spacer and rps16. -Acta Biologica Cracoviensia Series Botanica 50(2): 105-116.

Wolff, H. 1910: *Bupleurum*. In: Engler, A. (ed.). Das Pflanzenreich Regnis Vegetabilis Conspectus, IV.228: 36-173. -Leipzig, Germany: Verlag von Wilhelm Engelmann.

Xiang, C.U., Gao, F., Jakovlic, I., Lei, H.P., Hu, Y., Zhang, H., Zou, H., Wang, G.T., & Zhang, D. 2023: Using PhyloSuite for molecular phylogeny and tree-based analyses. -iMeta 2, e87

Appendix 1. List of tribes and species of subfamily Apioideae with GenBank accession numbers indicated in the ITS analyses (dataset I). The new sequences of species are indicated with an asterisk.

Apieae*: Apium graveolens* L. ON197183; *Ammi majus* L. MT513148; *Anethum graveolens* L. MN257763. ***Cachrys Clade***: *Azilia eryngioides* (Pau) Hedge & Lamond MT254197; *Bilacunaria microcarpa* (M. Bieb.) Pimenov & V.N. Tikhom. KJ700298; *Bilacunaria caspica* (DC.) Pimenov & V.N. Tikhom. KX452213; *Cachrys pungens* Jan ex Guss. KX452219; *Cachrys libanotis* Salzm. ex Ball KJ395460; *Diplotaenia damavandica* Mozaff. EU169259; *Diplotaenia cachrydifolia* Boiss. EU169258; *Ferulago macrocarpa* (Fenzl) Boiss. MK961982; *Ferulago galbanifera* (Mill.) W.D.J. Koch AF077889; *Prangos calligonoides* Rech.f. KU987656; *Prangos gaubae* (Bornm.) Herrnst. & Heyn MZ326711; *Prangos haussknechtii* Boiss. KJ395465; *Prangos persica* (Boiss.) M.G. Pimenov MT254217; *Prangos pabularia* Lindl. KJ395450. ***Coriandreae***: *Bifora radians* M. Bieb. KF843812; *Coriandrum sativum* L. HQ377204. ***Scandiceae***: *Ferula gummosa* Boiss. OR773129*; *Ferula szowitsiana* DC. OR773161*; *Leutea cupularis* (Boiss.) Pimenov OR773167*; *Leutea petiularis* (DC.) Pimenov KJ660836. ***Pyramidoptereae*****:** *Bunium elegans* (Fenzl) Freyn KF974538; *Froriepia subpinnata* (Ledeb.) Baill. MT254218; *Elwendia intermedia* (Korovin) Pimenov & Kljuykov MZ408935; *Oliveria decumbens* Vent. MT254209; *Thecocarpus meifolius* Boiss. MT254224; *Trachyspermum copticum* (L.) Link MZ687315. ***Echinophoreae***: *Anisosciadium orientale* DC. EU169245; *Dicyclophora persica* Boiss. AF073539; *Echinophora chrysantha* Freyn & Sint. AF077883; *Echinophora orientalis* Hedge & Lamond EU169267; *Ergocarpon cryptanthum* (Rech.f.) C.C. Towns. MT254200; *Mediasia macrophylla* (Regel & Schmalh.) Pimenov GQ379275; *Pycnocycla aucheriana* Decne. ex Boiss. AF073533; *Pycnocycla caespitosa* Boiss. & Hausskn. MW166363; *Pycnocycla nodiflora* Decne. ex Boiss. MW166362; ***Tordylieae***: *Heracleum antasiaticum* Manden. DQ427045; *Heracleum pastinacifolium* K. Koch EF043022; *Heracleum rechingeri* Manden. DQ427042; *Semenovia dichotoma* (Boiss.) Manden. FJ812151; *Semenovia eriocarpa* (Bornm. & Gauba) Lyskov & Kljuykov MN872505; *Tordylium maximum* L. MW166360; *Zosima absinthifolia* (Vent.) Link MN995902; *Cymbocarpum anethoides* DC. ex C.A. Mey. EU169253; *Cymbocarpum erythraeum* (DC.) Boiss. EU169254; *Ducrosia assadii* Alava DQ427043; *Ducrosia flabellifolia* Boiss. DQ427051; *Kalakia marginata* (Boiss.) Alava EU169293. ***Smyrnieae***: *Lecokia cretica* DC. EU169294; *Smyrnium cordifolium* Boiss. EU169320; *Smyrnium olusatrum* L. MT707556. ***Pleurospermeae***: *Eremodaucus lehmanii* Bunge EU169268; *Korshinskya olgae* (Regel & Schmalh.) Lipsky GQ379341; *Physospermum cornubiense* (L.) DC. AF077904. ***Pimpinelleae***: *Aphanopleura breviseta* (Boiss.) Heywood & Jury MZ687311; Demavendia pastinacifolia (Boiss. & Hausskn.) Pimenov MZ687312; *Haussknechtia elymaitica* Boiss. EU169273; *Pimpinella pastinacifolia* (Boiss.) H.Wolff PQ453064; *Pimpinella kotschyana* Boiss. DQ516373; *Pimpinella puberula* (DC.) Boiss. AY581799; *Pimpinella eriocarpa* Banks & Sol. AY581790; *Psammogeton canescens* (DC. ex Boiss.) Vatke MG827069; *Psammogeton stocksii* (Boiss.) Nasir MZ687313; Zeravschania membranacea (Boiss.) Pimenov MZ687317; *Zeravschania aucheri* (Boiss.) Pimenov MK328058. ***Opopanax Clade***: *Opopanax armeniacus* Bordz. MT254210; *Opopanax hispidus* (Friv.) Griseb. MT254212, KF843808; *Opopanax persicus* Boiss. & Heldr. MT254211, EU169300; *Smyrniopsis aucheri* Boiss. EU169318, EU169317; *Magydaris pastinacea* (Lam.) Paol. GQ379278; *Magydaris panacifolia* (Vahl) Lange EU169295; *Heptaptera anisopetala* (DC.) Tutin MT254206; *Petroedmondia syriaca* (Boiss.) Tamamsch. EU169309, EU169308; *Crenosciadium siifolium* Boiss. & Heldr. EU169252. ***Oenantheae***: *Berula erecta* (Huds.) Coville DQ005655; *Oenanthe aquatica* (L.) Poir. EF177732; *Oenanthe fistulosa* L. DQ005664; *Oenanthe silaifolia* M. Bieb. EU233943; *Sium sisaroideum* DC. DQ005688; *Helosciadium repens* (Jacq.) W.D.J. Koch AY360241. ***Selineae***: *Cervaria cervariifolia* (C.A. Mey.) Pimenov EU169250; *Dichoropetalum golestanicum* (Rech.f.) Pimenov & Kljuykov EU169289; *Dichoropetalum seseloides* (C. A. Mey.) Pimenov & Kljuykov EU169291; *Seseli arenarium* M. Bieb. MG697154; *Seseli libanotis* (L.) W.D.J. Koch MW691160; *Seseli tortuosum* L. MG697155; *Seseli transcaucasicum* (Schischk.) Pimenov & Sdobnina MG697134; *Xanthogalum purpurascens* Avé-Lall. MT707547; *Xanthogalum tatianae* (Bordz.) Schischk. MT707548; ***Bupleureae***: *Bupleurum lancifolium* Hornem. AF479853; *Bupleurum rotundifolium* L. AF481400; *Bupleurum exaltatum* M.Bieb. MT880980; *Bupleurum ranunculoides* L. AF481395; *Bupleurum longifolium* L. AF479856; *Bupleurum tenuissimum* L. AF481932; *Bupleurum stellatum* L. AF481930; *Hohenackeria exscapa* (Steven) Koso-Pol. 83581*, AF337178.