

## BULLETIN OF THE IRAQ NATURAL HISTORY MUSEUM

Iraq Natural History Research Center & Museum, University of Baghdad

<https://jnhm.uobaghdad.edu.iq/index.php/BINHM/Home>

Copyright © Bulletin of the Iraq Natural History Museum Online ISSN: 2311-9799, Print ISSN: 1017-8678

*Bull. Iraq nat. Hist. Mus.*

(2024) 18 (1): 187-207.

<https://doi.org/10.26842/binhm.7.2024.18.1.0187>

### ORIGINAL ARTICLE

## RELICT SPECIES FROM AN AFRICAN ORIGIN IN SOUTHWEST ASIA: INSIGHTS INTO THEIR BIOGEOGRAPHY AND CONSERVATION

 Moslem Doostmohammadi\*,  Fatemeh Moein\*\* and  Firouzeh Bordbar\* ♦

\*Department of Biology, Faculty of Science, Shahid Bahonar University of Kerman, Kerman, Iran.

\*\*Plant and Animal Biology Department, Faculty of Science and Technology, University of Isfahan, Isfahan, Iran.

♦ Corresponding author: [bordbar@uk.ac.ir](mailto:bordbar@uk.ac.ir)

Received: 11 Sept. 2023, Revised: 9 March 2024, Accepted: 10 Mar. 2024, Published: 20 June 2024



This work is licensed under a [Creative Commons Attribution 4.0 International License](https://creativecommons.org/licenses/by/4.0/)

### ABSTRACT

The Zagros Mountain range in western Iran is an area of species endemism within the Irano-Anatolian biodiversity hotspot. A couple of relict and morphologically isolated species have been reported for the Zagros Mountains, yet their distribution patterns in relation to the geological and climatic history of the region are not fully understood. *Clinopodium kallaricum* (Jamzad) Bordbar, 2019 (Lamiaceae), *Hypericum dogonbadanicum* Assadi, 1984 (Hypericaceae), and *Iranoaster bachtiaricus* (Mozaff.) Kaz. Osaloo, Farhani & Mozaff. 2018 (Asteraceae) are local endemic species restricted to Zagros with no clear affinities to the Irano-Turanian or other Northern Hemisphere temperate species. Previous studies suggested some afromontane relations for these species, beyond the Saharo-Sindian lowlands. Here, we provide dated phylogenies for these three species, to assess the most probable drivers behind this pattern of distribution. Our results represent that the split between these taxa and their relatives is not contemporaneous, implying different biogeographical histories. *I. bachtiaricus* originated in the Middle Miocene, while *C. kallaricum* and *H. dogonbadanicum* are relatively younger (late Miocene early Pliocene). The divergence of these taxa coincided with the major geological and climatic events of the Miocene, mainly the collision of the Afro-Arabia and Eurasia plates in 18-16 Mya and the aridification of the Sahara (started in 11-7 Mya), followed by a shift in the vegetation of the Sahara from subtropical/steppe to arid desert. The possible relict nature of these species is discussed, and the role of the Saharo-Sindian Region as a vicariant agent is highlighted, which could have subdivided formerly uniform populations and subsequently accelerated the allopatric speciation.

Keywords: *Clinopodium*, Disjunctend distribution, *Hypericum*, *Iranoaster*, Relict species.

### INTRODUCTION

The Irano-Turanian phytogeographical region is a vast area covering many highlands in south western Asia (Zohary, 1973). It is characterized by a high degree of continentality and a

## Relict species from an African origin

low amount of precipitation during the growing season (Djamali *et al.*, 2011). This region harbors many species-rich plant lineages, such as *Astragalus* L., *Cousinia* Cass., *Acantholimon* Boiss., *Eremurus* M.Bieb., *Silene* L., and *Nepeta* L. Recent phylogeographical studies have confirmed that the Irano-Turanian Region was the center of origin and diversification of many plant lineages, which then radiated to other neighboring areas, including the Mediterranean region (some examples are: Font *et al.*, 2009; Manafzadeh *et al.*, 2014; Malik *et al.*, 2017; Panahi, 2019; Žerdoner Calasan *et al.*, 2021; Doostmohammadi *et al.*, 2022).

The Zagros Mountain range, which extends from the northeast of Iraq to the south of Iran, is situated in the central part of the Irano-Turanian Region. It is covered by the so-called “Kurdo-Zagrosian steppe-forest” composed of *Quercus brantii* Lindl. Woodlands mostly in the northern and western regions, *Artemisia* steppes in drier regions, and alpine vegetation in several high peaks (Zohary, 1973; Noroozi *et al.*, 2020). The Zagros mountain is regarded as a separate unit (either in the form of a district, a sub-province, or a province) of the Irano-Turanian region, exhibiting strong and striking distribution patterns (Zohary, 1973; Takhtajan, 1986; Akhani, 2004, 2007) and is identified as an “area of endemism” having a high number of endemic species along with several endemic genera [such as *Azilia* Hedge & Lamond (Apiaceae), *Ergocarpon* C. C. Towns (Apiaceae), *Hausknechtia* Boiss. (Apiaceae), and *Zeugandra* P.H.Davis (Campanulaceae) (Noroozi *et al.*, 2018, 2019)]. A high proportion of the Zagros plant species belong to the Irano-Turanian Region (Noroozi *et al.*, 2020), while there are surprisingly some isolated and morphologically distinct species such as *Hypericum dogonbadanicum* Assadi (Hypericaceae), *Clinopodium kallaricum* (Jamzad) Bordbar (Lamiaceae), and *Iranoaster bachtiaricus* (Mozaff.) Kaz. Osaloo, Farhani & Mozaff. (Asteraceae), which are of high phytogeographical interest. These species have striking morphological differences with other Irano-Turanian species, and previous studies have proposed some African relations for them (Robson, 1987; Farhani *et al.*, 2018; Bordbar and Mirtadzadini, 2019).

*Hypericum dogonbadanicum* Assadi, 1984 (Hypericaceae) is a sub-shrubby chasmophyte species, described about 40 years ago from southwestern Zagros (Assadi, 1984). This species is clearly distinct from any other *Hypericum* species known from Iran, and Assadi (1984) suggested a relationship between *H. dogonbadanicum* and *H. balearicum* L. (sect. *Psorophytom* (Spach) Nyman) from the Balearic Islands in Spain, based on its habit, leaf margins, and stamen structure. Later, Robson (1987), criticized this idea, and based on several diagnostic morphological characters, demonstrated that *H. dogonbadanicum* belongs to sect. *Campylosporus* (Spach) R. Keller, with surprising close affinities to the Socotran endemic *H. socotranum* R. D. Good. *Hypericum* sect. *Campylosporus* is a group of about 10 shrubs and trees distributed in sub-tropical and tropical mountains of SW Arabia and eastern Africa [south of the Saharo-Sindian lowlands (Robson, 1985)], and the only species of this section growing above the Saharo-Sindian Region is *H. dogonbadanicum*.

*Clinopodium kallaricum* (Jamzad) Bordbar 2019 (Lamiaceae) initially was introduced as a species of the genus *Satureja* L. (*S. kallarica* Jamzad, Jamzad, 1992), but was transferred to

Doostmohammadi *et al.*

*Clinopodium simense* group by Bordbar and Mirtadzadini (2019) based on morphological and molecular evidences. Members of *C. simense* group are morphologically very similar and apparently closely related to each other (Ryding, 2006). *Clinopodium kallaricum* is confined to the Zagros Mountains (north of the Saharo-Sindian region); while the other species of this group are distributed in the tropical high mountains of eastern Africa, south of the Saharo-Sindian regional zone. They are morphologically similar in a more or less creeping habit, with the sub-sessile glands only on the lower surface of the leaves and the diverging thecae (Bordbar and Mirtadzadini, 2019).

The monotypic genus *Iranoaster* (Mozaff.) Kaz.Osaloo, Farhani & Mozaff., 2018 (Asteraceae), was recently established based on the enigmatic *Aster bachtiaricus* Mozaff., 1996 from western/central Zagros (Farhani *et al.*, 2018). Farhani *et al.* (2018) argued that *A. bachtiaricus* is different from other Northern Hemisphere *Aster* species in “having thick woody rootstock, many heteromorphic leaves, solitary capitulum, 4-seriate phyllaries, reflexed ligulate flowers, and 1-seriate pappus” and their molecular phylogenetic analyses demonstrated that *A. bachtiaricus* is not closely related to the bulk of *Aster* and is placed between the basal lineages of the Southern Hemisphere and other Northern Hemisphere taxa of the tribe Astereae. Therefore, they treated this species as a separate, monospecific genus restricted to the Zagros Mountains.

The co-occurrence of these isolated taxa in the Zagros Mountains brings up the question of whether they share a common evolutionary history. This research aimed to answer this question based on a dating analysis with addressing their phytogeographical aspects. Biogeographical analysis was also carried out for *Clinopodium kallaricum* (Jamzad) Bordbar, 2019 (Lamiaceae) as an example, to examine the hypothesis of the center of origin. Besides, the conservation importance of the Zagros Mountain in relation to save these remarkable species is highlighted.

#### MATERIALS AND METHODS

The geographical location of The Zagros Mountains within the Irano-Turanian Region in SW Asia is shown in Map (1).

**Data matrix preparation and node calibration:** Three different sequence data sets were prepared for the three studied species and their allied species, which were then aligned and analyzed separately. All sequences were extracted from Genbank (Appendix). For combining different regions, they were concatenated together without partitioning.

***Hypericum dogonbadanicum*** Assadi, 1984 (Map 2): Sequences of ITS and *trnL-trnF* regions for 29 species of *Hypericum* and close genera were extracted from GenBank and concatenated. Our taxon sampling scheme covered all available sequences of members of *H.* sect. *Campyloporus* together with representatives from the major lineages of the genus *Hypericum* as recognized in recent molecular phylogenetic studies (Meseguer *et al.*, 2013; Nurk *et al.*, 2013). Two calibration points were used for *Hypericum dogonbadanicum*. A normal prior was assigned to the crown of Hypericaceae (the split between *Eliea* and the rest of the tree) with a

## Relict species from an African origin

mean of 65.2 Mya and a standard deviation of 11 obtained by Ruhfel (2011). To constrain the crown age of *Hypericum*, a lognormal prior was used with an offset of 33.9 Mya and a standard deviation of 0.7 based on Arbizova (2005) and Meseguer *et al.* (2013).

***Iranoaster bachtiaricus*** (Mozaff.) Kaz.Osaloo, Farhani & Mozaff., 2018: A subset of sampling from previous studies (Brouillet *et al.*, 2009; Farhani *et al.*, 2018), including 23 species were extracted from Genbank for ITS and ETS regions and then combined for alignment. Our sampling strategy for dating analysis from among the huge tribe Astereae was based on covering major clades of the tribe (from both northern and southern Hemisphere lineages), according to previous phylogenetic studies (Brouillet *et al.*, 2009; Farhani *et al.*, 2018). Nodes were calibrated assigning a normal distribution with the mean of 38.68 million years as the secondary calibration and a standard deviation of 2.1 for the split between the tribes Astereae and Anthemideae according to Panero and Crozier (2016).

***Clinopodium kallaricum*** (Jamzad) Bordbar, 2019 (Map 3): A total of 68 species from *Clinopodium* and related genera were sampled from Genbank for dating analysis. DNA sequences of the nuclear region (ITS) and two chloroplast regions (*matK* and *trnL-trnF*) were combined for alignment. *Clinopodium* is a non-monophyletic group (Bräuchler *et al.*, 2010; Bordbar and Mirtadzadini, 2019), and our sampling covered all main sub-clades and lineages of this genus together with other closely related genera. A node prior was calibrated for the most recent common ancestor (MRCA) of *Acinos* Mill. and *Ziziphora* L. (15.398 Mya with a SD of 2.8) (Rose *et al.*, 2022), with a normal distribution.

**Sequence alignments and divergence time estimates:** Each data set was aligned using MAFFT (Multiple Alignment using Fast Fourier Transform) v.6.0 (Katoh and Toh, 2008) with manual adjustment. The BEAST.XML input files were generated using BEAUTi v 1.10.4 and divergence times were estimated using BEAST v 1.10.4, (Suchard *et al.*, 2018). Rate evolution was modeled in an uncorrelated lognormal relaxed clock framework (Drummond *et al.*, 2006), and priors for the branch rate were assumed to be a Yule process under an HKY substitution model. The BEAST analyses were performed with two independent runs of Markov Chain Monte Carlo each for 10 million generations, sampling every 200 generations. The convergences of the chains and estimated sample sizes (ESSs) were confirmed to be sufficiently high (>200) in Tracer v 1.7.1 (Rambaut *et al.*, 2014). Tree Annotator v 1.10.4 was used to find the maximum clade credibility reporting median node ages after discarding the first 10% of the generations as burn-in.

**Ancestral area reconstruction:** The ancestral area of *Clinopodium kallaricum* was estimated based on the molecular dated tree generated in BEAST. The ancestral area of the tree species was estimated based on three models: the dispersal extinction-cladogenesis (DEC), the likelihood model (DIVA-LIKE) model, and the BAYAREA-LIKE model. For each model, we tested the additional parameter “j” as well (Matzke, 2014). The j parameter represents the relative pre\_event weight of the founder event. The best model was selected based on the AIC scores. Considering the patterns of distribution and endemism, we categorized the seven geographical regions. A (East Asia), B (Euro-Siberian Region), C (Mediterranean Region), D

Doostmohammadi *et al.*

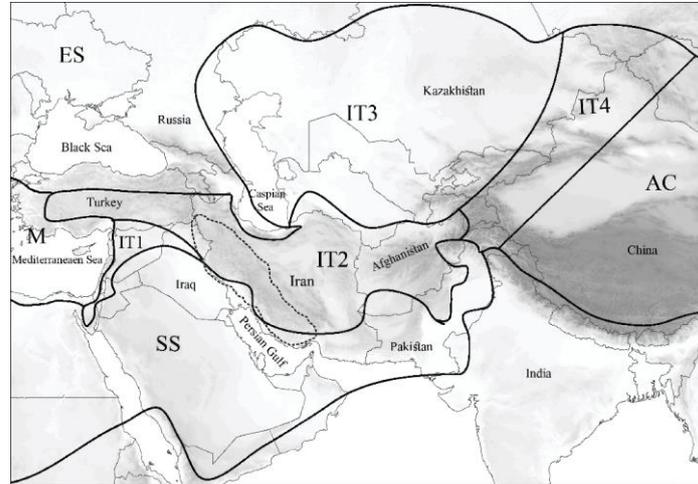
(South-west Asia), E (North Africa), F (Southern America), and G (East and Central Africa). The BioGeoBEARS package in R was used to conduct the analysis (Matzke, 2013).

## RESULTS

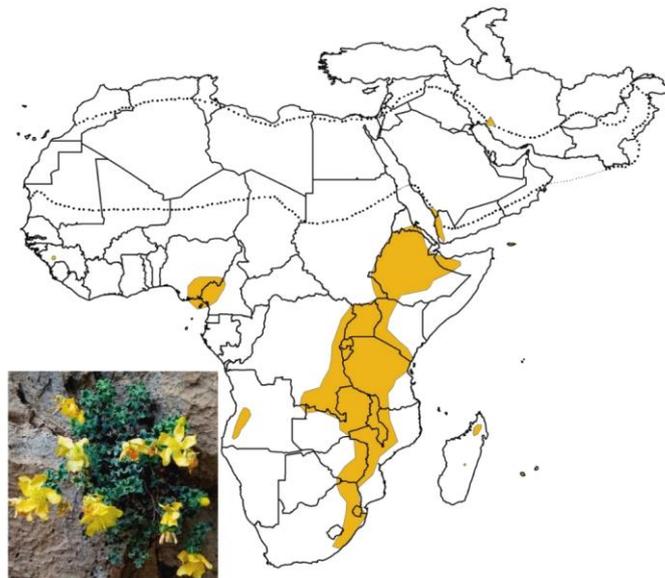
The phylogenetic reconstructions by Beast analysis and based on limited sampling in the present study, are to a large extent, congruent with previous comprehensive phylogenetic studies on *Hypericum* (Meseguer *et al.*, 2013; Nurk *et al.*, 2013), *Clinopodium* (Bräuchler *et al.*, 2010; Bordbar and Mirtadzadini, 2019), and the tribe Astereae (Brouillet *et al.*, 2009; Farhani *et al.*, 2018) and are therefore reliable. Molecular clock calculations indicated different divergence times for the three species. Based on the dating analysis, *Iranoaster bachtiaricus* diverged from its close species in about 17.1 Mya (95% HPD; 11.01–23.51) (Diag. 1). Our Beast analyses confirmed the previous studies, suggesting the intermediate position of *I. bachtiaricus* between Southern Hemisphere lineages and temperate Northern Hemisphere genera (Farhani *et al.*, 2018; Jafari *et al.*, 2015). *Clinopodium kallaricum* assembled in a monophyletic sub-clade together with other members of *C. simense* group, confirming previous studies (Bordbar and Mirtadzadini, 2019) (Diag. 2). The estimated divergence age of *C. kallaricum* is 4.9 Mya (95% HPD; 2.2–8.51). *Hypericum dogonbadanicum* represents a phylogenetic position between the African clade of *H. revolutum* Vahl and some northern Hemisphere (mostly East Asian) species, including *H. ascyron* L., *H. monogynum* L. and *H. elatoides* R.Keller (Diag. 3). It was diverged from the later three species in 8.03 Mya (95% HPD; 4.52–12.25), and the divergence age (stem age) of their clade (composed of *H. dogonbadanicum* and the three mentioned species) is about 10.48 Mya (95% HPD; 6.65–15.25).

Our result of biogeographical analysis for *Clinopodium kallaricum* and related species showed that DEC (dispersal extinction cladogenesis) is the best model for explaining of *Clinopodium* biogeographical history. Based on the biogeographical result (Diag. 4). *Clinopodium* clade and allied species have had widespread distribution following the vicariance of East Asia and the African clade about 8 Mya. Another vicariance event occurred about 5 Mya between Africa and Southwest Asian (*Clinopodium kallaricum*) species.

Relict species from an African origin

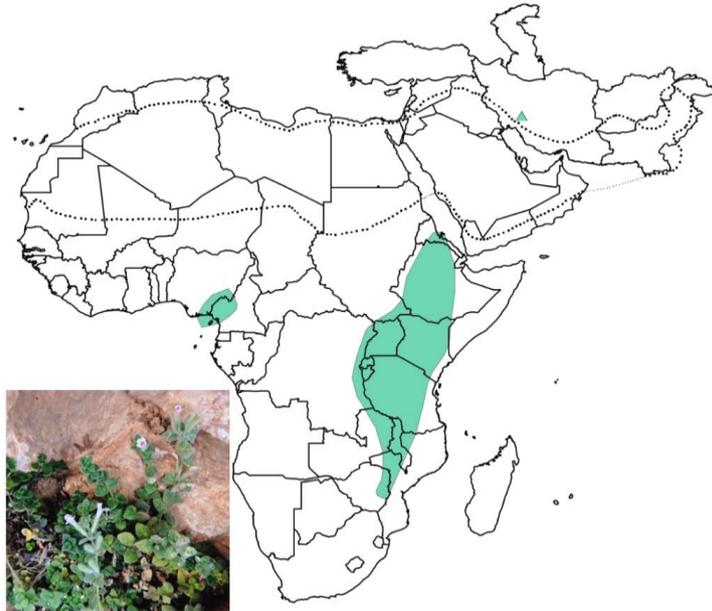


**Map (1):** Phytogeographical subdivisions of SW Asia, according to Leonard (1988-1989) IT: Irano-Turanian Region with its sub-regions designated by numbers 1 to 4, ES: Euro-Siberian, M: Mediterranean, SS: Saharo-Sindian, AC: Central Asiatic. The dashed line outlines the Zagros Mountain range in the west of Iran.

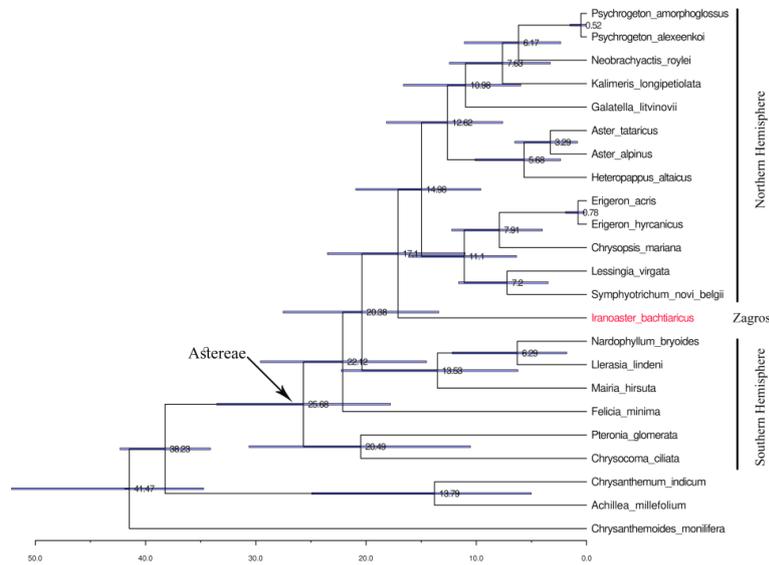


**Map (2):** General distribution of *Hypericum* sect. *Campylosporus* (based on Robson, 1985 and Assadi, 1984). Triangle and inset photo indicate *H. dogonbadanicum*. [Dashed line represents the Saharo-Sindian regional zone].

Doostmohammadi *et al.*



**Map (3):** General distribution of *Clinopodium simense* species group (based on Ryding (2006) and Bordbar and Mirtadzadini (2019)). Triangle and inset photo indicate *C. kallaricum*. Dashed line represents the Saharo-Sindian regional zone.



**Diagram (1):** Dated phylogenetic tree of tribe Astereae retrieved from BEAST. Estimated divergence age values are represented for each node.

Relict species from an African origin

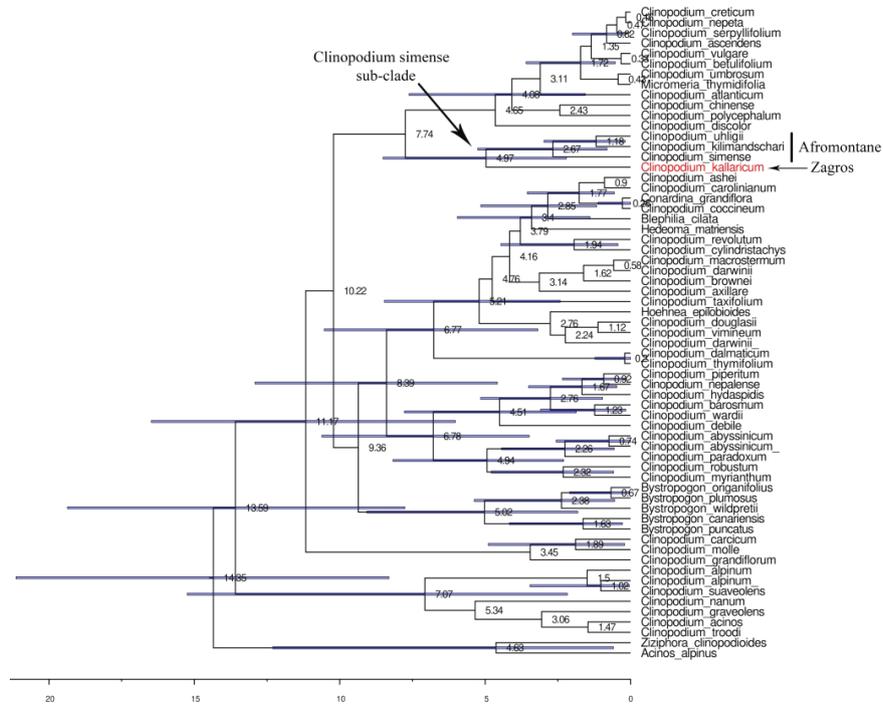


Diagram (2): Chronogram of *Clinopodium* and related genera inferred from BEAST. Dating values are represented above nodes.

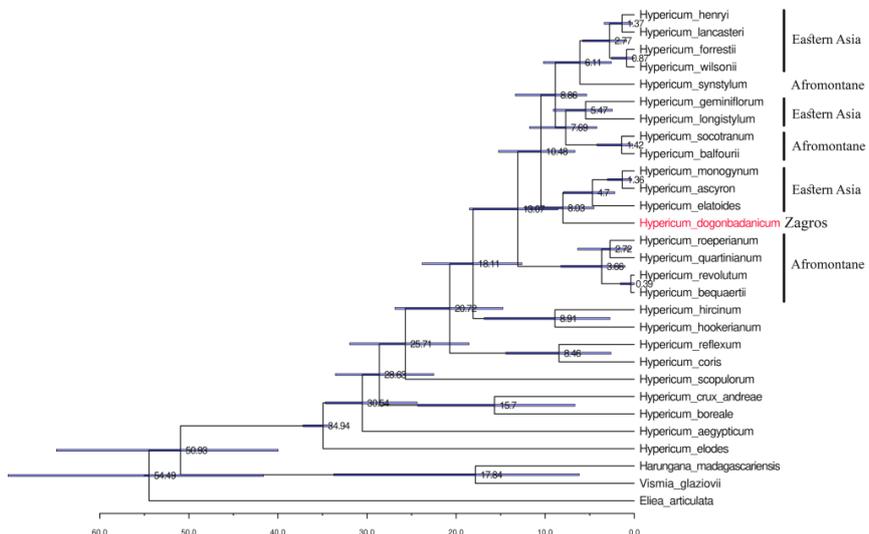
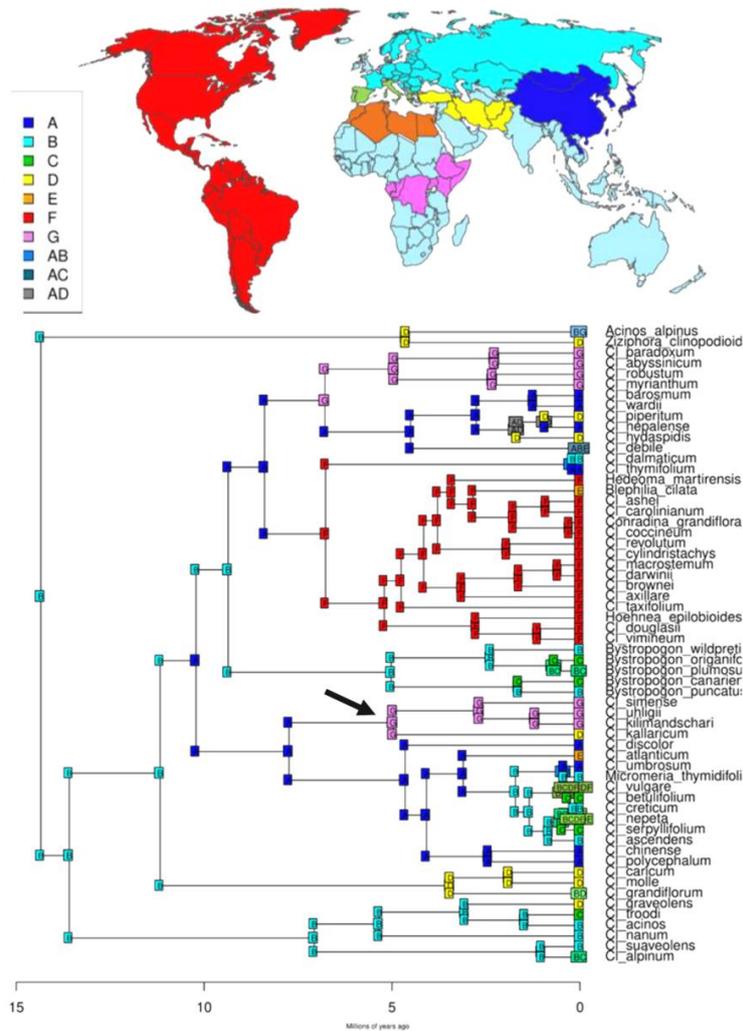


Diagram (3): Dated phylogenetic tree of *Hypericum* inferred from BEAST analysis. Divergence ages are represented for each node.

Doostmohammadi *et al.*



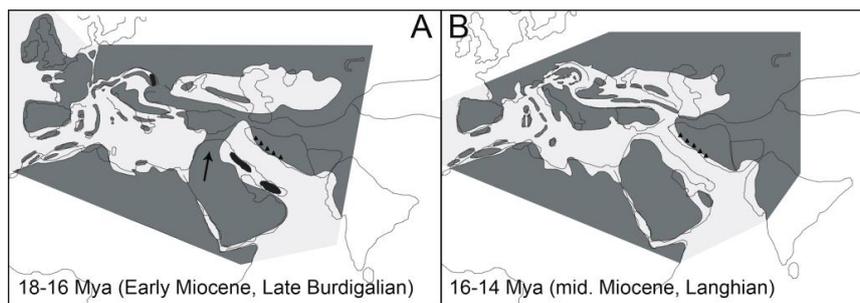
**Diagram (4):** Ancestral area estimation of the *Clinopodium kallaricum* and allied species based on the DEC model. Single capital letters indicate the different biogeographic units used in this study. Mixed letters represent combinations of units. The units next to species names represent the current geographic range of each species. The black arrow shows the split node of *Clinopodium kallaricum* from the African *Clinopodium* species.

## DISCUSSION

**Phylogeography:** Our dating results represent that the divergence times of these three taxa are not contemporaneous, suggesting that their distributions are ruled by at least two

## Relict species from an African origin

geological/climatic events. Tribe Astereae has been proposed to have originated in the southern hemisphere (most probably in South Africa), and then dispersed to other temperate areas of the northern hemisphere (Brouillet *et al.*, 2009; Mandel *et al.*, 2019). As mentioned before, *I. bachtiaricus* represents an intermediate position between the southern and northern Hemisphere genera (Diag. 1). The divergence time of *I. bachtiaricus* from its relatives in the early Miocene (about 17 Mya) coincides with the age of the Gomphotherium land bridge, which was created following the first collision of the Afro-Arabia and Eurasia plates (Map 4a). This land bridge disappeared in the middle Miocene (16-14 Mya) following the re-opening of the seaway between the Mediterranean and Indian Ocean (Map 4b; Rögl, 1999). It is therefore likely, that the ancestors of *I. bachtiaricus* could have migrated to western Iran through the first connection between Afro-Arabia and Eurasia and were subsequently left isolated in the Zagros Mountains after the re-opening of the sea between the Mediterranean and Indian Ocean. In addition, the major uplift of the Zagros Mountains took place in 15-12 Mya (Mouthereau *et al.*, 2012), which is another factor that could be responsible for the geographical isolation of this species.



**Map (4):** Tectonic movements in the Miocene. A: first collision of Afro-Arabia to Eurasia plates and formation of the Gomphotherium land bridge, represented by the arrow, B: re-opening of a seaway between the Mediterranean and Indian Oceans. Triangles represent the Zagros Mountains. (Based on Rögl, 1999).

Regarding *Hypericum dogonbadanicum*, our dated phylogenetic tree represents that it is assembled in a sub-clade with three Northern Hemisphere species. This sub-clade diverged from its African ancestor in about 10.4 Mya. Likewise, the split of *Clinopodium kallanicum* from its African relative dates back to about 4.9 Mya. It was inferred from the biogeographical analysis that the ancestor of *Clinopodium kallanicum* extended across eastern Africa to the late Miocene (Diag. 4). The divergence ages of both species in the late Miocene were probably governed by the same eco/geographical forces. It was formerly believed that the Sahara Desert is about 2-3 My old (Kroepelin, 2006). However, new findings suggest that the aridity of northern Africa and the creation of the Sahara Desert were triggered much earlier, in 11-7 Mya in the late Miocene, due to the shrinkage of Tethys Sea (Zhang *et al.*, 2014). At the end of the Messinian salinity crisis (5.33 Mya), the aridity of the Sahara and the Arabian Peninsula intensified (Colin *et al.*, 2008), which had a great impact on the diversification of plant species, acting as a vicariant agent that divided formerly widely

Doostmohammadi *et al.*

distributed populations north and south of this region (Zhang *et al.*, 2014; Chen *et al.*, 2014). Therefore, relict species of *C. kallaricum* and *H. dogonbadanicum* in the west of Iran are most probably the result of allopatric speciation in isolated populations above the Saharo-Sindian region. Another round of uplift of the Zagros Mountains has taken place about 5 Mya (Axen *et al.*, 2001; Mouthereau *et al.*, 2012), which could have intensified the isolation of these species. The role of the Saharo-Sindian region as a geographical barrier has been previously demonstrated in animals as well. It has been shown that the only species of elephant shrews north of the Sahara (*Elephantulus rozeti*) split from other species south of the Sahara due to the aridification and vegetation change in north Africa (Douady *et al.*, 2003). In addition to this species, there is another surprising biological link between Africa and SW Iran in the genus *Pteraulax* (Afrotropical diptera), with all species restricted to southern Africa while *P. oldroydi* resides in the western foothills of the Zagros Mountains (Abbassian-Lintzen, 1966).

On the opposite direction, the migration barrier of the Saharo-Sindian Region, also blocked plant species dispersal from the Irano-Turanian region into Africa. One example is the genus *Pterocephalus* (Caprifoliaceae), with a major distribution in the Mediterranean and Irano-Turanian regions, and one species, *P. frutescens* Hoscht, in the east African high mountains (Mayer and Ehrendorfer, 2000). In addition, expansion of the Saharo-Sindian lowlands pushed cold adapted Irano-Turanian species to higher elevations, which could lead to allopatric speciation in the sky islands of southern Iran (Doostmohammadi *et al.*, 2018). The evidence from this study points towards the idea that the Saharo-Sindian region has had a major role in diversifying of life in mountainous areas around this region, both on its northern and southern sides.

**Conservation aspects:** As an area of endemism within the Irano-Anatolian biodiversity hotspot, the Zagros mountain range harbors a rich diversity of plant species with a high rate of endemism (Noroozi *et al.*, 2018). This diversity mostly belongs to some super diverse Irano-Turanian genera such as *Astragalus*, *Acantholimon*, *Allium*, *Cousinia*, *Centaurea*, and *Dionysia*, which diversified not only in the Zagros but also throughout the highlands of the Iranian plateau, with a higher endemism in alpine elevations. The roles of the geological events of Zagros in the diversification of some of these genera are highlighted in recent studies (Bagheri *et al.*, 2017; Moharrek *et al.*, 2019; Doostmohammadi *et al.*, 2022). Along with this recently diversified species (neo-endemics), there are also some relict, paleo-endemic species in the Zagros Mountains. All three studied species are local endemics in western/central Zagros with small population sizes and limited areas of occupancies, which rank them as threatened species. *Clinopodium kallaricum* and *H. dogonbadanicum* are assessed as Critically Endangered (CR), according to criterion B of the IUCN red list categories, representing 8 and 11.703 km<sup>2</sup> of AOO's and 2.589 and 14.382 km<sup>2</sup> of EOO's, respectively. *Iranoaster bachtiaricus* is assessed as data deficient (DD), since it is known only based on the type collection. Moreover, the Zagros Mountain was a refugia for some Euro-Siberian species (e.g. *Pterocarya fraxinifolia* (Poir.) Spach, *Zelkova carpinifolia* (Pall.) K. Koch and *Quercus castaneifolia* Pant (Zohary, 1973; Akhiani and Salimian, 2003; Uzun and Khedir Galalae, 2022), which, together with several endemic genera, highlights the need for

## Relict species from an African origin

a proper conservation strategy throughout this unique mountain range, harboring the largest oak forests in the Middle East.

**Table (1):** Details of specimens of *Hypericum* and allies included in this study, including GenBank accession numbers.

Taxa	ITS	trnL-trnF
<i>Eliea articulata</i>	KC709409.1	KC709111.1
<i>Vismia glaziovii</i>	KC709410.1	KC709112.1
<i>Harungana madagascariensis</i>	KC709362.1	KC709062.1
<i>Hypericum elodes</i>	KC709393.1	KC709095.1
<i>Hypericum aegypticum</i>	KC709391.1	KC709091.1
<i>Hypericum scopulorum</i>	KC709395.1	KC709097.1
<i>Hypericum boreale</i>	KC709374.1	KC709074.1
<i>Hypericum crux-andreae</i>	KC709399.1	KC709101.1
<i>Hypericum hookerianum</i>	FJ694205.1	KC709148.1
<i>Hypericum hircinum</i>	KC709365.1	KC709065.1
<i>Hypericum coris</i>	KC709320.1	KC709011.1
<i>Hypericum reflexum</i>	KC709382.1	KC709081.1
<i>Hypericum quartinianum</i>	KC709428.1	KC709129.1
<i>Hypericum roeperianum</i>	KC709429.1	KC709131.1
<i>Hypericum revolutum</i>	KC709425.1	KC709046.1
<i>Hypericum bequaertii</i>	KC709426.1	KC709128.1
<i>Hypericum dogonbadanicum</i>	HE653454.1	KC709114.1
<i>Hypericum socotranum</i>	KC709394.1	KC709096.1
<i>Hypericum halfourii</i>	KC709397.1	KC709099.1
<i>Hypericum synstylum</i>	KC709304.1	KC708999.1
<i>Hypericum elatoides</i>	HE653456.1	KC709157.1
<i>Hypericum ascyron</i>	KC709330.1	KC709021.1
<i>Hypericum monogynum</i>	MH711394.1	KC709156.1
<i>Hypericum longistylum</i>	KC709445.1	KC709153.1
<i>Hypericum geminiflorum</i>	HM162838.1	KC709000.1
<i>Hypericum henryi</i>	KC709448.1	KC709159.1
<i>Hypericum forrestii</i>	FJ694202.1	KC709149.1
<i>Hypericum lancasteri</i>	KC709444.1	KC709161.1
<i>Hypericum wilsonii</i>	HE653658.1	-

**Table (2):** Details of specimens of tribe Astereae included in this study, including GenBank accession numbers.

Taxa	ITS	ETS
<i>Nardophyllum bryoides</i>	DQ479114.1	DQ479137.1
<i>Felicia minima</i>	FJ457935.1	-
<i>Chrysocoma ciliata</i>	FJ457941.1	-
<i>Psychrogeton alexeenkoi</i>	LC027403.1	LC387698.1
<i>Aster tataricus</i>	FJ539125.1	JN543749.1
<i>Psychrogeton amorphoglossus</i>	LC027404.1	LC387702.1
<i>Mairia hirsuta</i>	FJ457929.1	-
<i>Llerasia lindeni</i>	DQ479110.1	JQ042789.1
<i>Pteronia glomerata</i>	FJ457942.1	-
<i>Galatella litvinovii</i>	LC027393.1	LC387684.1

Doostmohammadi *et al.*

<i>Chrysopsis_mariana</i>	GQ892729.1	-
<i>Erigeron_acris</i>	ON527430.1	LC387676.1
<i>Erigeron_hyrcanicus</i>	LC027390.1	LC387681.1
<i>Neobrachyactis_roylei</i>	LC027400.1	LC387694.1
<i>Heteropappus_altaicus</i>	KJ711876.1	LC387690.1
<i>Aster_alpinus</i>	MH398798.1	LC387659.1
<i>Symphyotrichum_novi-belgii</i>	EU781308.1	JN315950.1
<i>Lessingia_virgata</i>	AF251624.1	AF251682.1
<i>Kalimeris_longipetiolata</i>	JN315936.1	JN315960.1
<i>Iranoaster_bachtiaricus</i>	LC027374.1	LC387661.1
<i>Chrysanthemum_indicum</i>	EF577298.1	JN315964.1
<i>Achillea_millefolium</i>	KR150185.1	-
<i>Chrysanthemoides_monilifera</i>	FJ861492.1	-

**Table (3):** Details of specimens of *Clinopodium* and allies included in this study, including GenBank accession numbers.

Taxa	ITS	trnI-trnF	matK
<i>Acinos alpinus</i>	AY227141	AY506594	
<i>Blephila cilata</i>	MK585131	GU381580	GU381743
<i>Bystropogon canariensis</i>	AY506634	-	GU381726
<i>Bystropogon origanifolius</i>	GU381409	GU381565	GU381727
<i>Bystropogon plumosus</i>	AY704586	-	-
<i>Bystropogon wildpretii</i>	AY704584	-	-
<i>Bystropogon punctatus</i>	AY704582	--	-
<i>Clinopodium aascendens</i>	-	-	AY840152
<i>Clinopodium abyssinicum</i>	GU381403	GU381548	GU381710
<i>Clinopodium alpinum</i>	-	AY840180	AY840145
<i>Clinopodium ashei</i>	DQ667237	-	-
<i>Clinopodium atlanticum</i>	-	GU381531	GU381697
<i>Clinopodium axillare</i>	DQ017565	-	-
<i>Clinopodium barosmum</i>	GU381393	-	GU381683
<i>Clinopodium betulifolium</i>	-	GU381532	GU381698
<i>Clinopodium brownei</i>	GU381426	GU381593	GU381593
<i>Clinopodium caricum</i>	-	KX38187	-
<i>Clinopodium caroliaunum</i>	-	-	GU381748
<i>Clinopodium chinense</i>	-	-	KX526668
<i>Clinopodium coccineum</i>	F369164	GU381585	AY840150
<i>Clinopodium creticum</i>	-	GU381533.	AY840175
<i>Clinopodium cylindristachys</i>	DQ0171562	-	-
<i>Clinopodium dalmaticum</i>	JQ669340	-	-
<i>Clinopodium darwini</i>	-	GU381601	-
<i>Clinopodium debile</i>	-	GU381530	GU381696.
<i>Clinopodium discolor</i>	-	GU381539.	-
<i>Clinopodium douglasii</i>	JQ669081	JQ669026	-
<i>Clinopodium grandiflorum</i>	GU012002	-	KX526666
<i>Clinopodium graveolens</i>	-	-	GU381667
<i>Clinopodium hydaspidis</i>	GU381391	GU381515	GU381681

## Relict species from an African origin

<i>Clinopodium kallaricum</i>	GU381539.	MK680006	-
<i>Clinopodium klimandschari</i>	-	GU381558	GU381721
<i>Clinopodium macrostemum</i>	JQ669083	385720694	-
<i>Clinopodium molle</i>	-	KX381819	-
<i>Clinopodium myrianthum</i>	GU381405	-	-
<i>Clinopodium nanum</i>	GU381385	-	GU381666
<i>Clinopodium nepalense</i>	-	-	GU381680
<i>Clinopodium nepeta</i>	-	GU381534	AY840151
<i>Clinopodium paradoxum</i>	GU381402	GU381543	GU381706
<i>Clinopodium piperitum</i>	GU381388	GU381511	GU381677
<i>Clinopodium polycephalum</i>	-	-	GU381701
<i>Clinopodium revolutum</i>	GU381436	GU381609	AY840170
<i>Clinopodium robustum</i>	GU381404	GU381553	GU381716
<i>Clinopodium simense</i>	GU381407	GU381559	GU381722
<i>Clinopodium suavelens</i>	-	-	GU381665.
<i>Clinopodium taxifolium</i>	JQ669084	385720695	-
<i>Clinopodium thymifolium</i>	JQ669121	62002162	AY840162
<i>Clinopodium troodi</i>	-	-	GU381671
<i>Clinopodium umbrosum</i>	-	GU381537	GU381700
<i>Clinopodium vimineum</i>	-	-	GU381760
<i>Clinopodium vulgare</i>	JQ669085		MG225194
<i>Clinopodium wardii</i>	GU381392	GU381516	-
<i>Clinopodium uhligi</i>	GU381406	GU381561	GU381724
<i>Conradina grandiflora</i>	-	AY943442	AY943512
<i>Hedeoma martirensis</i>	GU381428	GU381596	
<i>Hoehnea epilobioides</i>	-	-	GU381731
<i>Ziziphora clinopodioides</i>	GU381386	GU381508	GU381756

## CONCLUSIONS

The Saharo-Sindian region, as a major geographical feature of North Africa and the Arabia, and its ecological changes during that time, have had a considerable impact on plant diversification in the surrounding mountainous areas, both on its northern and southern sides. As shown here, the Saharo-Sindian region acted as a vicariant agent, which resulted in the allopatric speciation of several isolated species in the Zagros Mountains in the west of Iran. These relict and locally endemic species require urgent conservation action.

## AKNOWLEDGMENTS

The authors wish to thank Dr. Mansour Mirtadzadini for his helpful comments on the initial version of the manuscript. No funding was received for conducting this study.

## CONFLICT OF INTEREST STATMENT

"The authors have no conflicts of interest to declare".

## LITERATURE CITED

Abbassian-Lintzen, R. 1966. Bombyliidae (Diptera) of Iran. II. *Pteraulax oldroydi* new species. *Annals and Magazine of Natural History*, 9(103): 321-324. [\[CrossRef\]](#)

Doostmohammadi *et al.*

- Akhani, H. and Salimian, M. 2003. An extant disjunct stand of *Pterocarya fraxinifolia* (Juglandaceae) in the central Zagros Mountains, W Iran. *Willdenowia*, 33(1): 113-120. [[CrossRef](#)]
- Akhani, H. 2004. A new spiny, cushion-like *Euphorbia* (Euphorbiaceae) from south-west Iran with special reference to the phytogeographic importance of local endemic species. *Botanical Journal of the Linnean Society*, 146(1): 107-121. [[CrossRef](#)]
- Akhani, H. 2007. Diversity, biogeography, and photosynthetic pathways of *Argusia* and *Heliotropium* (Boraginaceae) in South-West Asia with an analysis of phytogeographical units. *Botanical Journal of the Linnean Society*, 155(3): 401-425. [[CrossRef](#)]
- Arbuzova, O. 2005. *Hypericum* L. In: Budantsev, L. (ed), Iskopaemye tsvetkovye rastenija Rossii I sopredel'nyh gosudarstv [Fossil Flowering Plants of Russia and Adjacent Countries], Vol. 4 Nyctaginaceae-Salicaceae. Izdatelstvo Nauka Leningradskoe otdnie, Leningrad, 48pp.
- Assadi, M. 1984. New species and new plant records from Iran. *Iranian Journal of Botany*, 2 (2): 83-94. [[Click here](#)]
- Axen, G. J., Lam, P. S., Grove, M., Stockli, D. F. and Hassanzadeh, J. 2001. Exhumation of the west-central Alborz Mountains, Iran, Caspian subsidence, and collision-related tectonics. *Geology*, 29(6): 559-562. [[CrossRef](#)]
- Bagheri, A., Maassoumi, A. A., Rahiminejad, M. R., Brassac, J. and Blattner, F. R. 2017. Molecular phylogeny and divergence times of *Astragalus* section *Hymenostegis*: An analysis of a rapidly diversifying species group in Fabaceae. *Scientific Reports*, 7: 14033. [[CrossRef](#)]
- Bordbar, F. and Mirtadzadini, M. 2019. *Clinopodium kallaricum*—an unexpected new member of the tropical African *C. simense* group from flora of Iran. *Phytotaxa*, 411(1):49-56. [[CrossRef](#)]
- Bräuchler, C., Meimberg, H. and Heubl, G. 2010. Molecular phylogeny of Menthinae (Lamiaceae, Nepetoideae, Mentheae)—Taxonomy, biogeography and conflicts. *Molecular Phylogenetics and Evolution*, 55(2): 501-523. [[CrossRef](#)]
- Brouillet, L., Lowrey, T. K., Urbatsch, L., Karaman, V., Sancho, G., Wagstaff, S. and Semple, J. C. 2009. Phylogeny and evolution of the Astereae (Asteraceae). p. 449-490. In: Funk, V. A., Susanna, A., Stuessy, T. and Bayer, R. (eds), Systematics, Evolution and Biogeography of the Compositae, IAPT, Vienna, Austria

## Relict species from an African origin

- Chen, C., Qi, Z. C., Xu, X. H., Comes, H. P., Koch, M. A., Jin, X. J., Fu, C. X. and Qiu, Y. X. 2014. Understanding the formation of Mediterranean–African–Asian disjunctions: evidence for Miocene climate-driven vicariance and recent long-distance dispersal in the Tertiary relict *Smilax aspera* (Smilacaceae). *New Phytologist*, 204(1): 243-255. [[CrossRef](#)]
- Colin, C., Siani, G., Seguenia, F., Blamart, D., Giunta, S., Suc, J. P., Liu, Z., Frank, N. and Briquet, L. 2008. Reconstruction of Northern African monsoon between 6.2 and 4.9 Ma and possible relationships with Late Miocene events. *Comptes Rendus Géoscience*, 340(11): 749-760. [[CrossRef](#)]
- Djamali, M., Akhiani, H., Khoshravesh, R., Andrieu-Ponel, V., Ponel, P. and Brewer, S. 2011. Application of the global bioclimatic classification to Iran: implications for understanding the modern vegetation and biogeography. *Ecologia Mediterranea*, 37(1): 91-114. [[CrossRef](#)]
- Doostmohammadi, M., Samadi, N. and Ghorbanalizadeh, A. 2018. Phytogeography of Genu and Homag, two mountains with an Irano–Turanian flora in the Saharo–Sindian regional zone, South Iran. *Nordic Journal of Botany*, 36: e01808. [[CrossRef](#)]
- Doostmohammadi, M., Bordbar, F., Albach, D. C. and Mirtadzadini, M. 2022. Phylogeny and historical biogeography of *Veronica* subgenus *Pentasepalae* (Plantaginaceae): evidence for its origin and subsequent dispersal. *Biology*, 11: 639. [[CrossRef](#)]
- Douady, C. J., Catzeflis, F., Raman, J., Springer, M. S. and Stanhope, M. J. 2003. The Sahara as a vicariant agent, and the role of Miocene climatic events, in the diversification of the mammalian order Macroscelidea (elephant shrews). *Proceedings of the National Academy of Sciences*, 100(14): 8325-8330. [[CrossRef](#)]
- Drummond, A. J., Ho, S. Y. W., Phillips, M. J. and Rambaut, A. 2006. Relaxed phylogenetics and dating with confidence. *Plos Biology*, 4:e88. [[CrossRef](#)]
- Farhani, T., Kazempour-Osaloo, S., Zare-Maivan, H. and Mozaffarian, V. 2018. Evolutionary history of the tribe Astereae in the Flora Iranica area: systematic implications. *Phytotaxa*, 379(1): 95-117. [[CrossRef](#)]
- Font, M., Garcia-Jacas, N., Vilatersana, R., Roquet, C. and Susanna, A. 2009. Evolution and biogeography of *Centaurea* section *Acrocentron* inferred from nuclear and plastid DNA sequence analyses. *Annales of Botany*, 103(6): 985-997. [[CrossRef](#)]
- Jafari, F., Kazempour-Osaloo, S. and Mozffarian, V. 2015. Molecular phylogeny of the tribe Astereae (Asteraceae) in SW Asia based on nrDNA ITS and cpDNA psbA-trnH sequences. *Willdenowia*, 45(1): 77-92. [[CrossRef](#)]

Doostmohammadi *et al.*

- Jamzad, Z. 1992. Two new species from Labiatae in Iran. *Iranian Journal of Botany*, 5(2): 69-74. [[CrossRef](#)]
- Katoh, K. and Toh, H. 2008. Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics*, 9(4): 286-298. [[CrossRef](#)]
- Kroepelin, S. 2006. Revisiting the age of the Sahara Desert. *Science*, 312(5777): 1138-1139. [[CrossRef](#)]
- Leonard, J. 1988-1989. Contribution à l'étude de la Flore et de la Végétation des Déserts d'Iran, Fascicule. 8 (Étude des Aires de Distribution les Phytochories, les Chorotypes) and Fascicule. 9 (Considerapays Phytogéographiques Sur les Phytochories Irano-Touranienne, Saharo-Sindienne et de la Somalie-paysMasai); Jardin Botanique National de Belgique: Meise, Belgium.
- Malik, S., Vitales, D., Hayat, M. Q., Korobkov, A. A., Garnatje, T. and Vallès, J. 2017. Phylogeny and biogeography of *Artemisia* subgenus *Seriphidium* (Asteraceae: Anthemideae). *Taxon*, 66(4): 934-952. [[CrossRef](#)]
- Manafzadeh, S., Salvo, G. and Conti, E. A. 2014. A tale of migrations from east to west: The Irano-Turanian floristic region as a source of Mediterranean xerophytes. *Journal of Biogeography*, 41(2): 366-379. [[CrossRef](#)]
- Mandel, J. R., Dikow, R. B., Siniscalchi, C. M., Thapa, R., Watson, L. E. and Funk, V. A. 2019. A fully resolved backbone phylogeny reveals numerous dispersals and explosive diversifications throughout the history of Asteraceae. *Proceedings of the National Academy of Sciences*, 116(28): 14083-14088. [[CrossRef](#)]
- Matzke, N. J. 2013. Probabilistic historical biogeography: New models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. *Frontiers of Biogeography*, 5(4): 242-248. [[CrossRef](#)]
- Matzke, N. J. 2014. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in Island clades. *Systematic Biology*, 63(3): 951-970. [[CrossRef](#)]
- Mayer, V. and Ehrendorfer, F. 2000. Fruit differentiation, palynology, and systematics in *Pterocephalus* Adanson and *Pterocephalodes*, gen. nov. (Dipsacaceae). *Botanical Journal of the Linnean Society*, 132(1): 47-78. [[CrossRef](#)]
- Meseguer, A., Aldasoro, J. and Sanmartin, I. 2013. Bayesian inference of phylogeny, morphology and range evolution reveals a complex evolutionary history in St. John's wort (*Hypericum*). *Molecular Phylogenetics and Evolution*, 67(2): 379-403. [[CrossRef](#)]

## Relict species from an African origin

- Moharrek, F., Sanmartin, I., Kazempour-Osaloo, S. and Nieto Feliner, G. 2019. Morphological innovations and vast extensions of mountain habitats triggered rapid diversification within the species-rich Irano-Turanian genus *Acantholimon* (Plumbaginaceae). *Frontiers in Genetics*, 9: 698. [[CrossRef](#)]
- Mouthereau, F., Lacombe, O. and Vergés, J. 2012. Building the Zagros collisional orogen: Timing, strain distribution and the dynamics of Arabia/Eurasia plate convergence. *Tectonophysics*, 532: 27-60. [[CrossRef](#)]
- Noroozi, J., Talebi, A., Doostmohammadi, M., Rumpf, S. B., Linder, H. P. and Schneeweiss, G. M. 2018. Hotspots within a global biodiversity hotspot - areas of endemism are associated with high mountain ranges. *Scientific Reports*, 8: 10345. [[CrossRef](#)]
- Noroozi, J., Talebi, A., Doostmohammadi, M., Manafzadeh, S., Asgarpour, Z. and Schneeweiss, G. 2019. Endemic diversity and distribution of the Iranian vascular flora across phytogeographical regions, biodiversity hotspots and areas of endemism. *Scientific Reports*, 9: 12991. [[CrossRef](#)]
- Noroozi, J., Talebi, A., Doostmohammadi, M. and Bagheri, A. 2020. The Zagros mountain range. p. 185-214. In: Noroozi, J. (ed), Plant biogeography and vegetation of high mountains of central and south-west Asia. Plant and Vegetation, vol 17. Springer, Cham. [[CrossRef](#)]
- Nurk, N. M., Madrinan, S., Carine, M. A., Chase, M. W. and Blattner, F. R. 2013. Molecular phylogenetics and morphological evolution of St. John's wort (*Hypericum*; Hypericaceae). *Molecular Phylogenetics and Evolution*, 66(1): 1-16. [[CrossRef](#)]
- Panahi, M. 2019. Biogeographic reconstruction of the genus *Ferula* inferred from analyses of nrDNA and cpDNA sequences. *Iranian Journal of Botany*, 25(2): 79-94. [[CrossRef](#)]
- Panero, J. L. and Crozier, B. S. 2016. Macroevolutionary dynamics in the early diversification of Asteraceae. *Molecular Phylogenetics and Evolution*, 99: 116-132. [[CrossRef](#)]
- Rambaut, A., Suchard, M. A., Xie, D. and Drummond, A. J. 2014. Tracer v1.7. [[Click here](#)]
- Robson, N. K. B. 1985. Studies in the genus *Hypericum* L. (Guttiferae). 3. Sections 1. *Campyloporus* to 6 a. *Umbraculoides*. *Bulletin of the British Museum (Natural History). Botany*, 12(4): 163-325.
- Robson, N. K. B. 1987. An Iranian floristic link with Socotra in *Hypericum* (Hypericaceae). *Plant Systematics and Evolution*, 155: 89-92. [[CrossRef](#)]
- Rose, J. P., Xiang, C. L., Sytsma, K. J. and Drew, B. T. 2022. A timeframe for mint evolution: towards a better understanding of trait evolution and historical

Doostmohammadi *et al.*

biogeography in Lamiaceae. *Botanical Journal of the Linnean Society*, 200(1): 15-38. [[CrossRef](#)]

Rögl, F. 1999. Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). *Geologica Carpathica*, 50(4): 339-349.

Ruhfel, B. R. 2011. Systematics and biogeography of the clusioid clade (Malpighiales). Ph. D. Dissertation, The Department of Organismic and Evolutionary Biology Harvard University, Cambridge, Massachusetts, 224pp.

Ryding, O. 2006. Revision of the *Clinopodium simense* group (Labiatae). *Kew Bulletin*, 61(3): 419-432. [[Click here](#)]

Suchard, M. A., Lemey, P., Baele, G., Ayres, D. L., Drummond, A. J. and Rambaut, A. 2018. Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus Evolution* 4.

Takhtajan, A. 1986. Floristic regions of the world. University of California Press, Berkeley.

Uzun, A. and Khedir Galaley, A. M. 2022. *Zelkova carpinifolia* (Ulmaceae), a relict tree, first recorded in Iraq. *Folia Geobotanica*, 57(4): 303-317. [[CrossRef](#)]

Žerdoner Calasan, A., German, D. A., Hurka, H. and Neuffer, B. 2021. A story from the Miocene: Clock-dated phylogeny of *Sisymbrium* L. (Sisymbrieae, Brassicaceae). *Ecology and Evolution*, 11(6): 2573-2595. [[CrossRef](#)]

Zhang, Z., Ramstein, G., Schuster, M., Li, C. Contoux, C. and Yan, Q. 2014. Aridification of the Sahara desert caused by Tethys Sea shrinkage during the Late Miocene. *Nature*, 513: 401-404. [[CrossRef](#)]

Zohary, M. 1973. Geobotanical foundations of the Middle East. Gustav Fischer Verlag, Stuttgart, 765 pp.

## Relict species from an African origin

Bull. Iraq nat. Hist. Mus.  
(2024) 18 (1): 187-207.

## الأنواع الاثرية من أصل أفريقي في جنوب غرب آسيا: رؤى حول جغرافيتها الاحيائية والحفاظ عليها

\*مسلم دوست محمدي\*، فاطمة معين\*\* و فيروزة بردبار\*  
\*قسم علوم الحياة، كلية العلوم، جامعة الشهيد باهنر كرمان، كرمان، إيران.  
\*\*قسم بيولوجيا النبات والحيوان، كلية العلوم والتكنولوجيا، جامعة أصفهان، أصفهان، إيران.

الاستلام: 2023/9/11، المراجعة: 2024/3/9، القبول: 2024/3/10، النشر: 2024/6/20

### الخلاصة

تعد سلسلة جبال زاغروس في غرب إيران منطقة توطن الأنواع ضمن نقطة التنوع البيولوجي الإيرانية-الأناضولية. تم الإبلاغ عن اثنين من الأنواع الأثرية والمعزولة مظهرًا في جبال زاغروس، إلا أن أنماط توزيعها فيما يتعلق بالتاريخ الجيولوجي والمناخي للمنطقة ليست مفهومة بالكامل. و الأنواع التالية:

*Clinopodium kallaricum* (Jamzad) Bordbar, 2019 (Lamiaceae)

*Hypericum dogonbadanicum* Assadi, 1984 (Hypericaceae)

*Iranoaster bachtiaricus* (Mozaff.) Kaz. Osaloo, Farhani & Mozaff, 2018 (Asteraceae)

هي انواع مستوطنة محليًا مقتصرة على وسط غرب زاغروس ولا تظهر ارتباطات واضحة مع الأنواع الإيرانية-الطورانية أو الأنواع المعتدلة في نصف الكرة الشمالي. وقد أشارت الدراسات المظهرية والجزئية السابقة إلى وجود بعض العلاقات الأفريقية الجبلية لهذه الأنواع، بعيدًا عن الأراضي المنخفضة الصحراوية السندية. في هذه الدراسة، تم تقديم سلالات مؤرخة لهذه الأنواع الثلاثة، لتقييم الدوافع الأكثر احتمالًا وراء هذا النمط من التوزيع. وتمثل النتائج التي توصلت إليها هذه الدراسة إلى أن الانقسام بين هذه الاصنوفات وقربياتها ليس معاصرًا، مما يشير إلى أن التاريخ الاحيائي والجغرافي مختلف

لكل منها. اذ نشأ *Iranoaster bachtiaricus* في العصر الميوسيني الأوسط، في حين أن *C. kallaricum* و *H. dogonbadanicum* أصغر نسبياً (أواخر العصر الميوسيني و أوائل العصر البليوسيني). و قد تزامنت انقسامات هذه الأجناس مع الأحداث الجيولوجية والمناخية الرئيسية في الميوسين، مثل تصادم صفيحتي أفرو-عربية مع أوراسيا قبل 18-16 مليون سنة و قحل الصحراء الكبرى بسبب انكماش بحر تيثس (بدأ قبل 11-7 مليون سنة) تلاه تحول في الغطاء النباتي للصحراء الكبرى من شبه الاستوائي/السيبي إلى الصحراء الجافة. تمت مناقشة الطبيعة الأثرية المحتملة لهذه الأنواع، وتم تسليط الضوء على دور منطقة الصحراء السنديّة كعامل بديل، والذي كان من الممكن أن يقسم مجموعات سكانية موحدة سابقاً وبالتالي تسريع عملية الانتواع المتباين.