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Molecular phylogeny of *Hipparchia* Fabricius, 1807 (Lepidoptera: Nymphalidae: Satyrinae) with description of an overlooked species from the Zagros mountains, Iran

ALIREZA NADERI[1], WOLFGANG TEN HAGEN[2] & VAZRICK NAZARI[3*]
[1] *National Natural History Museum & Genetic Resources, Tehran, Iran;*
a2naderi@yahoo.com; *https://orcid.org/0009-0003-5878-6333*
[2] *Frühlingstrasse 1, 63853 Mömlingen, Germany;*
tenhagen@t-online.de; *https://orcid.org/0009-0006-8249-5562*
[3] *Department of Biology, University of Padova, Padova, Italy;*
https://orcid.org/0000-0001-9064-8959
* *Corresponding author,* *vazrick.nazari@unipd.it*

Abstract

Using sequence data from four nuclear genes alongside DNA barcodes, we reconstructed the evolutionary history of genus *Hipparchia* Fabricius, 1807. Our phylogeny supported the previously proposed subgeneric classification for the genus and revealed an overlooked taxon close to *H. fatua* (Freyer, 1845) from the Zagros mountain range in Western Iran, here described as a new species, *Hipparchia lunulata* **sp. nov.** We also confirm that the range of *H. fatua sichaea* (Lederer, 1857), originally described from Beirut, extends to the westernmost part of the Zagros mountains in Iran.

Key words: Brush-footed butterflies, Palearctic, subgeneric classification, new species

Introduction

For decades, the palearctic butterfly genus *Hipparchia* Fabricius, 1807 has been a continuous source of disagreement among lepidopterists for delimitation of its species (Kudrna 1977, García-Barros & Martín 1991, Smith & Shreeve 1993, Cesaroni *et al.* 1994, Wakeham-Dawson & Kudrna 2000, Wakeham-Dawson *et al.* 2003, 2004; Russell *et al.* 2007, Jutzeler *et al.* 2007, Descimon & Mallet 2010, Coutsis & Bozano 2018, Jutzeler 2021). Major reference checklists such as Fauna Europaea, Catalogue of Life, iNaturalist and GBIF vary in their adopted taxonomy for this genus. The latest treatment of *Hipparchia* by Sbordoni *et al.* (2018) has recognized 35 species grouped under five subgenera: *Hipparchia* Fabricius, 1807 (7 species), *Parahipparchia* Kudrna, 1977 (14 species), *Neohipparchia* de Lesse, 1951 (4 species), *Pseudotergumia* Agenjo, 1947 (8 species), and *Euhipparchia* Kudrna 1977 (2 species). Under subgenus *Neohipparchia,* the taxa *fatua, statilinus, hansii* and *powelii* are recognized as valid species (Sbordoni *et al.* 2018).

Hipparchia fatua Freyer, 1843, commonly known as Freyer's Grayling, has a relatively wide range from SE Europe though the Anatolian plateau and the Levant to western and northern Iran and Turkmenistan. It is morphologically very similar to, and sympatric across most of its range with, its sister species *H. statilinus* (Hufnagel, 1766). Both species show considerable geographic variation, however *H. statilinus* is distinguishable from *H. fatua* by a number of diagnostic characters, including smaller size and the obfuscation of the submarginal and discal lines on the underside of the hindwings.

Observed phenotypic differences primarily in the development of markings on the underside of the wings in various populations of *H. fatua* have led to recognition of several subspecies: The nominotypical ssp. *fatua* Freyer, 1843 (TL: Marmara region, Turkey, see Hesselbarth *et al.* 1995) flies from the Balkans and Greece to the Caucasus; ssp. *sichaea* Lederer, 1857 (TL: Beirut) in Lebanon, Jordan, Israel and Syria; and ssp. *persiscana* Verity, 1937 (TL: "above Keredj, in the Elburz Mts.") in N. and C. Iran to Turkmenistan (Kopet-Dagh). Taxa *klapperichi* Gross & Ebert, 1975 (TL: "Elburs S-Seite: Damavand")(Ebert *et al.* 1975) and *dagi* Korshunov & Krasilnikova, 1990 (TL:

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Turkmenia, Bakhardensky district, Ipay-Kala valley)(Korshunov 1990) have been previously synonymized with ssp. *persiscana* (Tshikolovets *et al.* 2014; Sbordoni *et al.* 2018). Clinal variations and transition zones seem to exist between some of these populations (Benyamini 2022), and thus delineation of the exact geographical boundaries between these subspecies has thus far remained elusive.

In recent years, molecular studies have increasingly been employed to resolve long-standing taxonomic issues in Satyrini (Nazari *et al.* 2009, Kleckova *et al.* 2015, Verovnik & Wiemers 2016, Pyrcz *et al.* 2017, Lukhtanov & Dubatolov 2020, Usami *et al.* 2021), however no comprehensive analysis of *Hipparchia* is so far published. Using DNA barcodes, we tested the genetic structure among various populations of *H. fatua* in order to understand how it corresponds to the subspecific scheme recognized based on morphological characteristics. To answer additional questions on classification in this group, we expanded our gene and taxon sampling to include four previously published nuclear genes (EF-1a, wg, GAPDH and RPS5) and representatives from nearly all known species of *Hipparchia* and its sister genera in Satyrini.

Material & Methods

Genitalia dissections were carried out by Wolfgang ten Hagen on eight males from Turkey and Iran using the methodology outlined by Higgins (1975) and photographed using standard equipment. Additional published genitalia dissections (e.g. Kudrna 1977, Korshunov 1990, Sbordoni *et al.* 2018) were also examined. COI barcode sequences for nearly all species of *Hipparchia*, already made available through previous studies, were retrieved from GenBank. New samples of *H. fatua* were selected primarily from the collections of AN and WtH. Among others, we could not sample *H. fatua dagi* Korshunov & Krasilnikova, 1990 from Kopet-Dagh mountains. Our sampling was also poor for Turkey where fresh material could not be found, and in addition, no suitable material was available for *H. powelli* (Oberthür, 1910) from Algeria. Leg tissue and standardized procedures were used to obtain the barcodes at the Center for Biodiversity Genomics in Guelph, Canada, and 29 new sequences were deposited on GenBank (Accessions PQ884485–PQ884514). Most samples yielded full-length COI barcode sequences and the total length of our dataset was 658 base pairs. Specimen data is publicly available in the BOLD dataset "DS- FATUA" (dx.doi.org/10.5883/DS-FATUA). Sixteen species of Satyrini were selected as outgroups. In addition to COI barcode sequences, where available, four nuclear gene sequences (EF-1a, wg, GAPDH and RPS5) were also retrieved from GenBank and added to the dataset (Table 1). Alignment of sequences was carried out using MUSCLE modules implemented in AliView 1.28 (Larsson, 2014) and double-checked visually. A maximum likelihood tree was obtained using IQTree web server (Nguyen *et al.*, 2015). Bayesian analysis was conducted in BEAST (Suchard *et al.*, 2018) for 20 million generations and the results were tested using TRACER 1.7.1 (Rambaut *et al.*, 2018). Several secondary calibration points were adopted from previous studies (Wiemers *et al.* 2020, Kawahara *et al.* 2023): The splits between *Brintesia* and *Kanetisa* (3.68 mya), *Neominois* and *Oeneis* (7.09 mya), *Hipparchia tilosi* and *H. bacchus* (3.18 mya), and *Melanargia* and Satyrini (28.67 to 32.12 mya). Uncorrected *p*-distances were calculated in MEGA 11.0.8 (Tamura *et al.* 2021).

Results

Molecular data. In our phylogenetic analyses, within a well-supported monophyletic genus *Hipparchia*, we recovered five strongly-supported clades corresponding to subgenera *Hipparchia, Parahipparchia, Euhipparchia, Pseudotergumia* and *Neohipparchia* (Fig. 1). Our DNA barcoding results placed our single specimen of *H. fatua* from Western Iran (Kordestan: Saghez–Marivan) together with samples of *H. fatua sichaea* from Israel and away from those in Northern Iran (ssp. *persiscana*). Our specimens from the Zagros mountains (Markazi, Esfahan and Fars provinces) displayed a remarkable genetic (barcode) distance (4.5±0.2%) from other *H. fatua* populations, signaling distinction at a species level. This distance is much higher than those between some of the other conventionally accepted species of *Hipparchia*, e.g. between *H. pisidice* and *H. tewfiki* (2.9%), or between *H. gomera* and *H. tilosi* (3.5%) (Table 2). In our phylogenetic reconstructions, these samples grouped together in a distinct clade separate from all other *H. fatua*, and our dated BEAST analysis also showed that the last common ancestor of this group with *H. fatua* split in late Miocene, around 9.79 mya (Fig. 1).

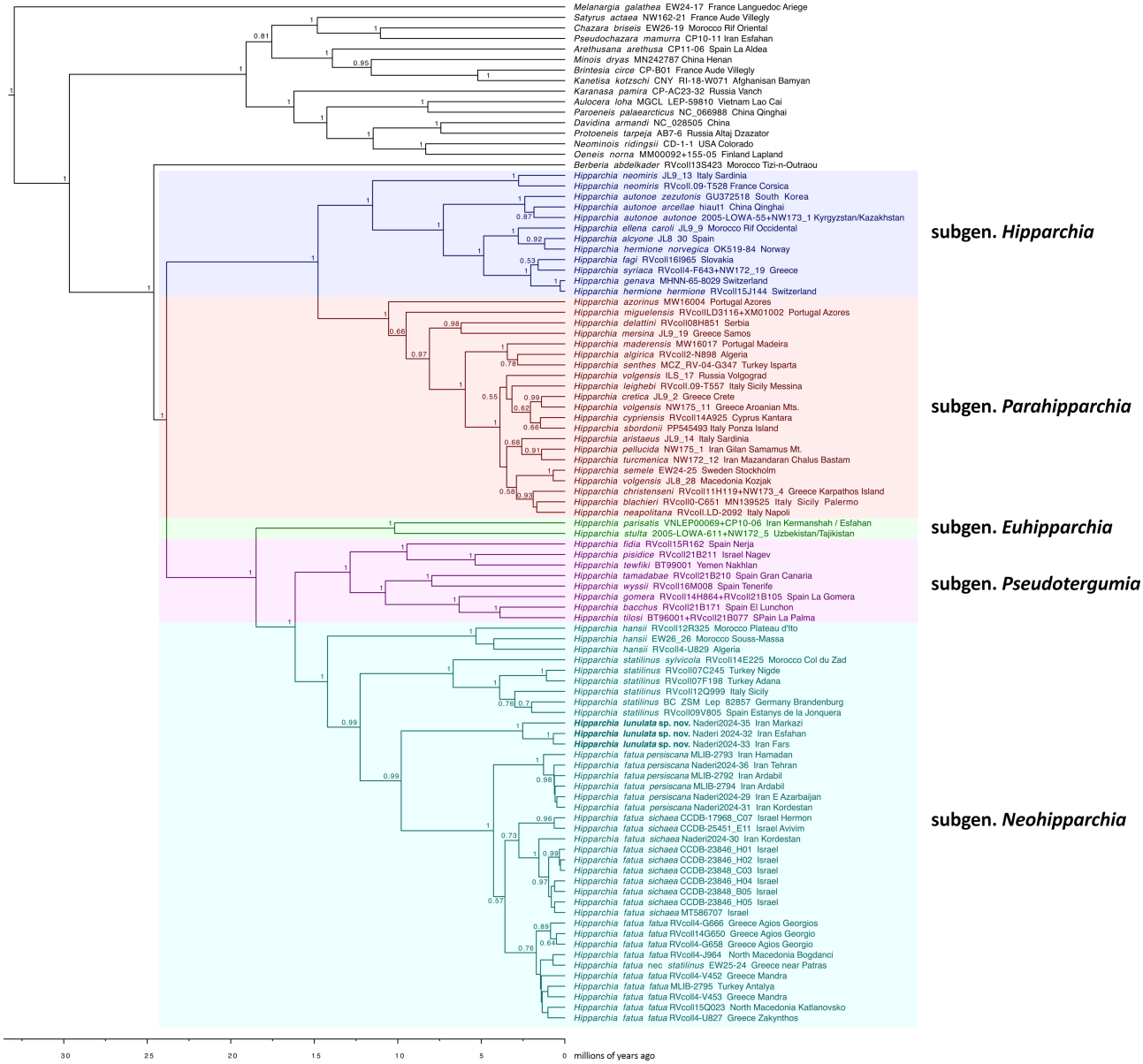

FIGURE 1. Multigene BEAST phylogeny of the genus *Hipparchia* showing Bayesian Posterior Probabilities for supported nodes.

Morphological data. A comparison of the wing pattern elements between the populations of *H. fatua* highlights the differences in overall appearance in males, but especially in females, across the range of the species (Fig. 2, 3). Individuals of ssp. *persiscana* from Northern Iran show a light grey ground color and poorly developed markings on the undersides of the hindwings, in contrast to specimens of ssp. *sichaea* or ssp. *fatua* from Europe and Turkey that show a much darker coloration on the underside of both wings. In addition, minor variation is evident in the male genitalia among dissected samples representing subspecies of *H. fatua*. Even though the male genitalia of individuals from the Zagros mountains appear similar to those of ssp. *fatua* and ssp. *persiscana*, they can all be reliably distinguished by subtle differences in the development of the dorsal sub-terminal triangular extension of valvae (Fig. 4). These unique synapomorphies in wing pattern and genitalia differentiate the Zagros populations from *H. fatua* (Table 3) and confirm the genetic hint provided by the DNA barcodes. Here we describe this population as a new species:

TABLE 1. Material examined and GenBank accessions.

	species	Locality	COI sampleID	COI	EF-1a	wg	GAPDH	RpS5
OUTGROUPS								
	Arethusana arethusa	Spain: La Aldea (Navarra)	CP11-06	DQ338863	DQ339018	DQ338728	GQ357500	GQ357626
	Aulocera loha	Vietnam: Lao Cai, Sa Pa	MGCL:LEP-59810	ON436381	OK736806	OK746908	OK720168	OK733592
	Berberia abdelkader	Morocco: Tizi-n-Oufraou, djebel Ayachi, W Midelt	RVcoll13S423	ON436896	OK737304	OK747322	OK720619	OK734073
	Brintesia circe	France: Aude, Villegly	CP-B01	DQ338865	DQ339020	DQ338729	EU141474	EU141370
	Chazara briseis	Morocco: Rif oriental	EW26-19	DQ338866	DQ339021	DQ338730	GQ357502	GQ357628
	Davidina armandi	China	not given	NC_028505	OK737403	OK747421	-	OK734171
	Kanetisa sp. 'kotschi'	Afghanistan: Bamyan, Kohi-Baba Mts.	CNY:RI-18-W071	ON436909	OK737314	OK747334	OK720629	OK734084
	Karanasa pamira	Russia: Vanch	CP-AC23-32	DQ338869	DQ339025	DQ338734	GQ357505	GQ357631
	Melanargia galathea	France: Languedoc, Ariege	EW24-17	DQ338843	OQ239287	GQ201380	EU528398	OQ240069
	Minois dryas	China: Henan, Jigongshan mountain range	not given	MN242787	JX185940	OK746705	-	-
	Neominois ridingsii	USA: Colorado, Montrose Co.	CD-1-1	DQ338870	DQ339026	DQ338735	OK719983	OK733404
	Oeneis norna	Finland: Lapland, Enontekioe/ Russia:Altai	094-15	HM396371+LC155512	OK736609	KP888806	KP888729	KP888761
	Paroeneis palaearcticus	China: Qinghai	papal1	NC_066988	KM200200	KM200296	KM200253	KP888732
	Protoeneis tarpeia	Russia: Altaj, Dzazator	AB7-6	KP888693	LC155694	KP888809	KP888730	KP888764
	Pseudochazara mamurra	Iran: Isfahan	CP10-11	DQ338598	DQ339028	DQ338737	GQ357507	GQ357633
	Satyrus actaea	France: Aude, Villegly	NW162-21	GQ864807	GQ864901	GQ864495	GQ865030	GQ865494
Subgenus Hipparchia								
	fagi	Slovakia: Banska Bystrica, Plesivec	RVcoll16I965	MW499890	-	-	-	-
	hermione	Switzerland	RVcoll15J144	MW500497	-	-	-	-
	hermione genava	Switzerland: Hohtenn VS	MHNN-65-8029	OZ182466				
	hermione norvegica	Norway	OK519-84	PQ884491	-	-	-	-
	"alcyone" (= hermione)	Spain	JL8_30	MW318466	-	MW318711	MW317725	-
	syriaca	Greece: Granitis / Greece: Corfu, Sgourades	RVcoll.14-F643+NW172_19	PQ884497+MN752724	-	MN752841	MN752790	-

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TABLE 1. (Continued)

	species	Locality	COI sampleID	COI	EF-1a	wg	GAPDH	RpS5
	ellena caroli	Morocco: Rif Occidental, Djebel Tisirene	JL9_9	MW318469	-	MW318713	MW317727	-
	neomiris	Italy: Sardinia	JL9_13	MN752721	-	-	MN752783	-
	neomiris	France: Corsica	RVcoll.09-T528	MH418890	-	-	-	-
	autonoe	Kyrgyzstan: Tienshan / Kazakhstan: S. Altai Mts	2005-LOWA-55 +NW173_1	FJ663599+MN752717	-	-	MN752791	-
	autonoe arcellae	China: Qinghai	hiaut1	KM111644	KJ805876	KM200294	KM200251	KM200277
	autonoe zezutonis	South Korea	not given	GU372518	GU372609	-	-	-
Subgenus Parahipparcia								
	semele	Sweden: Stockholm	EW24-25	DQ338868+OW121739	DQ339023	DQ338732	-	-
	semele neapolitana	Italy: Campania, Napoli, Isola Ischia, monte Epomeo	RVcoll.LD-2092	MN144726	-	-	-	-
	semele leighebi	Italy: Sicily, Messina, Stromboli Island	RVcoll.09-T557	MN139839	-	-	-	-
	sbordonii	Italy: Ponza Islad	not given	PP545493				
	cretica	Greece: Crete	JL9_2	MN752718	MW317900	MN752837	MN752786	-
	volgensis	Russia: Volgograd	ILS_17	KY000499	KY000503	-	-	-
	volgensis	Greece: Aroanian Mts.	NW175_11	MW318475	-	MW318825	MW317824	-
	volgensis	Macedonia: Kozjak	JL8_28	MN752725	-	MN752834	MN752782	-
	(volgensis) delattini	Serbia	RVcoll08H851	MW500978	-	-	-	-
	christenseni	Greece: Lefkos, Karpathos / Greece: Karpathos Is.	RVcoll11H119+NW173_4	MW318470	-	MW318823	MW317822	-
	pellucida (pellucida)	Iran: Gilan, Ramsar. Samamus Mts.,	NW175_1	MN752722	KY000501	MN752842	MN752792	-
	cypriensis	Cyprus: Kantara	RVcoll14A925	MW499240	-	-	-	-
	mersina	Greece: Samos	JL9_19	MN752720	MW317899	MN752836	MN752785	-
	turcmenica	Iran: Chalos, Bastam	NW172_12	MW318479	-	MW318820	MW317819	-
	aristaeus	Italy: Sardinia, Monte Tomesi	JL9_14	MN752716	-	MN752835	MN752784	-
	(aristaeus) algirica	Algeria	RVcoll.12-N898	PQ884510	-	MW318826	MW317825	-

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TABLE 1. (Continued)

	species	Locality	COI sampleID	COI	EF-1a	wg	GAPDH	RpS5
	(aristaeus) blachieri	Italy: Sicily, Palermo, Monte Busambra, Sicily Island	RVcoll.10-C651	MN139525	-	MW318822	MW317821	-
	senthes	Turkey: Isparta, Yenisarbademli	MCZ:RV-04-G347	ON437028	OK737448	OK747454	OK720753	OK734215
	maderensis	Portugal: Madeira, Fonte do Louro (1500 m)	MW16017	MN829486	-	-	-	-
	azorinus	Portugal: Azores, Algar do Carvao, Terceira (600 m)	MW16004	MN829483	MN829465	-	-	-
	azorinus miguelensis	Portugal: Azores, St. Miguel	RVcollLD3116+XM01002	PQ884500+MN829487	-	-	-	-
Subgenus Euhipparchia								
	parisatis	Iran: Kermanshah, Bisotun / Iran: Esfahan	VNLEP00069+CP10-06	PQ884503+DQ338867	DQ339022	-	MW317712	MW317443
	stulta	Tajikistan: Kulyab: Khodzamumin Mts	NW172_5	MW318478	-	MW318821	MW317820	-
Subgenus Pseudotergumia								
	fidia	Spain: Nerja	RVcoll15R162	PQ426988+PQ452847	-	PQ433486	PQ433440	-
	wyssii	Spain: Montana Ayosa, Tenerife	RVcoll16M008	PQ426996+PQ452872	-	PQ433511	PQ433465	-
	tamadabae	Spain: Parque Natural Tamadaba, Gran Canaria	RVcoll21B210+RVcoll21_210	PQ426994+PQ452863	-	PQ433502	PQ433456	-
	bacchus	Spain: El Lunchon, El Hierro	RVcoll21B171+RVcoll21B171	PQ884492+PQ452836	MN829466	PQ433475	PQ433429	-
	gomera	Spain: Barranco de Argaga, La Gomera	RVcoll14H864+RVcoll21B105	PQ884498+PQ452850	MN829468	PQ433489	PQ433443	-
	tilosi	Spain: Mirador de los Espejos, Los Tilos, La Palma	BT96001+RVcoll21B077	MN829489+PQ452869	-	PQ433508	PQ433462	-
	pisidice	Israel: Negev mountains	RVcoll21B211	PQ426989+PQ452855	-	PQ433494	PQ433448	-
	tewfiki	Yemen: Naklan, south of IBB, to Taez	BT99001	PQ426995+PQ452864	-	PQ433503	PQ433457	-
Subgebus Neohipparchia								
	statilinus	Germany: Brandenburg	BC ZSM Lep 82857	MH420075	-	-	-	-
	"	Morocco: Col du Zad	RVcoll14E225	MT260559+PQ452858	-	PQ433497	PQ433451	-

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TABLE 1. (Continued)

species	Locality	COI sampleID	COI	EF-1a	wg	GAPDH	RpS5
"	Italy: Monti Peloritani, Sicilia	RVcoll12Q999	MN139042+PQ452857	-	PQ433496	PQ433450	-
"	Spain: Estanys de la Jonquera	RVcoll09V805	GU676109+PQ452856	-	PQ433495	PQ433449	-
"	Turkey: Nigde	RVcoll07C245	PQ884501				
"	Turkey: Adana	RVcoll07F198	PQ884495				
hansii	Morocco: Souss-Massa, Adrar n' Aklim, E Igherm	EW26_26	-	MW317891	MW318702	MW317719	MW317451
"	Morocco: Plateau d'Ito	RVcoll.12-R325+RVcoll12R325	PQ884513+PQ452854	-	PQ433493	PQ433447	-
"	Algeria	RVcoll.14-U829	PQ884507	-	-	-	-
fatua fatua	North Macedonia: Bogdanci, Gjavato	RVcoll14J964	MW499734+PQ452839	-	PQ433478	PQ433432	-
"	North Macedonia: Katlanovsko	RVcoll15Q023	MW502094	-	-	-	-
"	Greece: near Patras	EW25-24	DQ338596	DQ339024	DQ338733	GQ357503	GQ357629
"	Greece: Mandra	RVcoll.14-V452	MW502345	-	-	-	-
"	Greece: Mandra	RVcoll.14-V453	MW501954	-	-	-	-
"	Greece: Zakynthos	RVcoll.14-U827	MW501332	-	-	-	-
"	Greece: Agios Georgios	RVcoll14G666	PQ452838	-	PQ433477	PQ433431	-
"	Greece: Agios Georgio	RVcoll14G650	MW501988	-	-	-	-
"	Greece: Agios Georgio	RVcoll.14-G658	MW501343	-	-	-	-
"	Turkey: Antalya	MLIB-2795	PQ884493	-	-	-	-
fatua persiscana	Iran: Ardabil	MLIB-2792	PQ884489	-	-	-	-
"	Iran: Hamadan	MLIB-2793	PQ884488	-	-	-	-
"	Iran: Ardabil	MLIB-2794	PQ884485	-	-	-	-
"	Iran: Tehran, Garmabdar, Routeh	Naderi2024-36	PQ884499	-	-	-	-
"	Iran: E Azarbaijan, NE Miyaneh, Yele Qarshow village	Naderi2024-29	PQ884514	-	-	-	-
"	Iran: Kordestan, 10 km to Sanandaj, Tunnel pass way	Naderi2024-31	PQ884504	-	-	-	-
fatua sichaea	Iran: Kordestan, 20 km to Marivan from Saghez	Naderi2024-30	PQ884490	-	-	-	-
"	Israel: Hermon	CCDB-17968 C07	PQ884512	-	-	-	-
"	Israel: Avivim	CCDB-25451 E11	PQ884486	-	-	-	-

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TABLE 1. (Continued)

species	Locality	COI sampleID	COI	EF-1a	wg	GAPDH	RpS5
"	Israel	CCDB-23846 H02	PQ884508	-	-	-	-
"	Israel	CCDB-23846 H01	PQ884509	-	-	-	-
"	Israel	CCDB-23848 C03	PQ884494	-	-	-	-
"	Israel	MT586707	MT586707	-	-	-	-
"	Israel	CCDB-23846 H05	PQ884505	-	-	-	-
"	Israel	CCDB-23846 H04	PQ884502	-	-	-	-
"	Israel	CCDB-23848 B05	PQ884496	-	-	-	-
lunulata sp. nov.	Iran: Esfahan, 2 km S. Daran, TV Tower Road	Naderi2024-32	PQ884511	-	-	-	-
"	Iran: Fars, Shiraz, Dashte Arjan	Naderi2024-33	PQ884487	-	-	-	-
"	Iran: Markazi, Tafresh, Naghusan	Naderi2024-35	PQ884506	-	-	-	-

TABLE 2. Average uncorrected *p*-distances between species of *Hipparchia* in subgenera *Euhipparchia, Pseudotergumia* and *Neohipparchia*.

	H. stulta	*H. parisatis*	*H. tewfiki*	*H. pisidice*	*H. tilosi*	*H. gomera*	*H. bacchus*	*H. tamadabae*	*H. wyssii*	*H. fidia*	*H. hansii*	*H. statilinus*	*H. fatua*	*H. lunulata*
H. stulta														
H. parisatis	5.2													
H. tewfiki	6.7	7.6												
H. pisidice	6.7	7.6	2.9											
H. tilosi	7.0	7.3	5.3	5.3										
H. gomera	7.4	7.6	4.6	5.6	3.5									
H. bacchus	7.6	7.0	5.6	5.6	2.9	3.3								
H. tamadabae	8.2	7.6	6.5	6.4	5.6	5.6	5.0							
H. wyssii	7.6	7.8	6.5	7.1	5.2	5.9	5.3	5.6						
H. fidia	7.6	7.1	4.6	5.5	5.2	4.9	5.0	6.1	7.0					
H. hansii	7.7	8.1	7.1	7.8	7.1	5.9	7.3	7.8	8.1	7.4				
H. statilinus	7.7	8.4	7.6	7.5	7.0	6.9	6.9	7.6	8.3	7.0	7.0			
H. fatua	6.7	7.1	6.1	6.3	6.0	6.1	5.9	7.1	7.8	6.2	7.1	6.0		
H. lunulata sp. nov.	6.7	7.1	6.2	6.5	6.3	5.7	5.3	7.6	8.1	5.3	6.6	5.9	4.5	

TABLE 3. Morphological diagnostic characters between *H. lunulata* **sp. nov.** and *H. fatua.*

Character	***H. lunulata* sp. nov.**	***H. fatua***
Ground color	Brownish	Brown to black
Hindwing Submarginal area	White lunulate pattern	Monotonous with the ground color
Androconial patch	Wide	Relatively narrow
Hind Wing shape	Less undulated	More strongly undulated
Hind Wing marginal black line	Present	Absent or very weak
dorsal sub-terminal triangular extension of valvae	Strongly developed	Weakly developed in ssp. *persiscana*, elongate in ssp. *fatua*, rounded in ssp. *sichaea*

***Hipparchia lunulata* Naderi & Nazari, sp. nov.**
(Figs. 2A–B, H–I; 3B, 4A–B)

Type materials. Holotype: ♂, **Iran, Esfahan,** 2 km S. Daran, TV Tower Road, 2500m, 28–29.VII.2015, leg. A.R. Naderi, coll. code 446b, SampleID Naderi2024–32 (barcoded). Deposited in the coll. National Natural History Museum and Genetic Resources (MMTT), Tehran, Iran.

FIGURE 2. adults of *Hipparchia*. A–G: males, H–N: females, upperside and underside of the wings. **Males: A.** *H. lunulata* **sp. nov.** Holotype (Esfahan); **B.** *H. lunulata* **sp. nov.** PT (Fars); **C.** *H. fatua persiscana* (Chalus rd, N Karaj); **D.** *H. fatua "dagi"* (Golestan Park); **E.** *H. fatua sichaea* (Syria: Tartus); **F.** *H. fatua fatua* (Turkey: Balikesir); **G.** *H. statilinus* male (Turkey: Gümüshane). **Females: H.** *H. lunulata* **sp. nov.** PT (Lorestan); **I.** *H. lunulata* **sp. nov.** PT (Lorestan); **J.** *H. fatua persiscana* (Dizin); **K.** *H. fatua sichaea* (Iran: Kordestan); **L.** *H. fatua sichaea* (Syria: Hama); **M.** *H. fatua fatua* (Turkey: Dikili); **N.** *H. statilinus* (Turkey: Izmir).

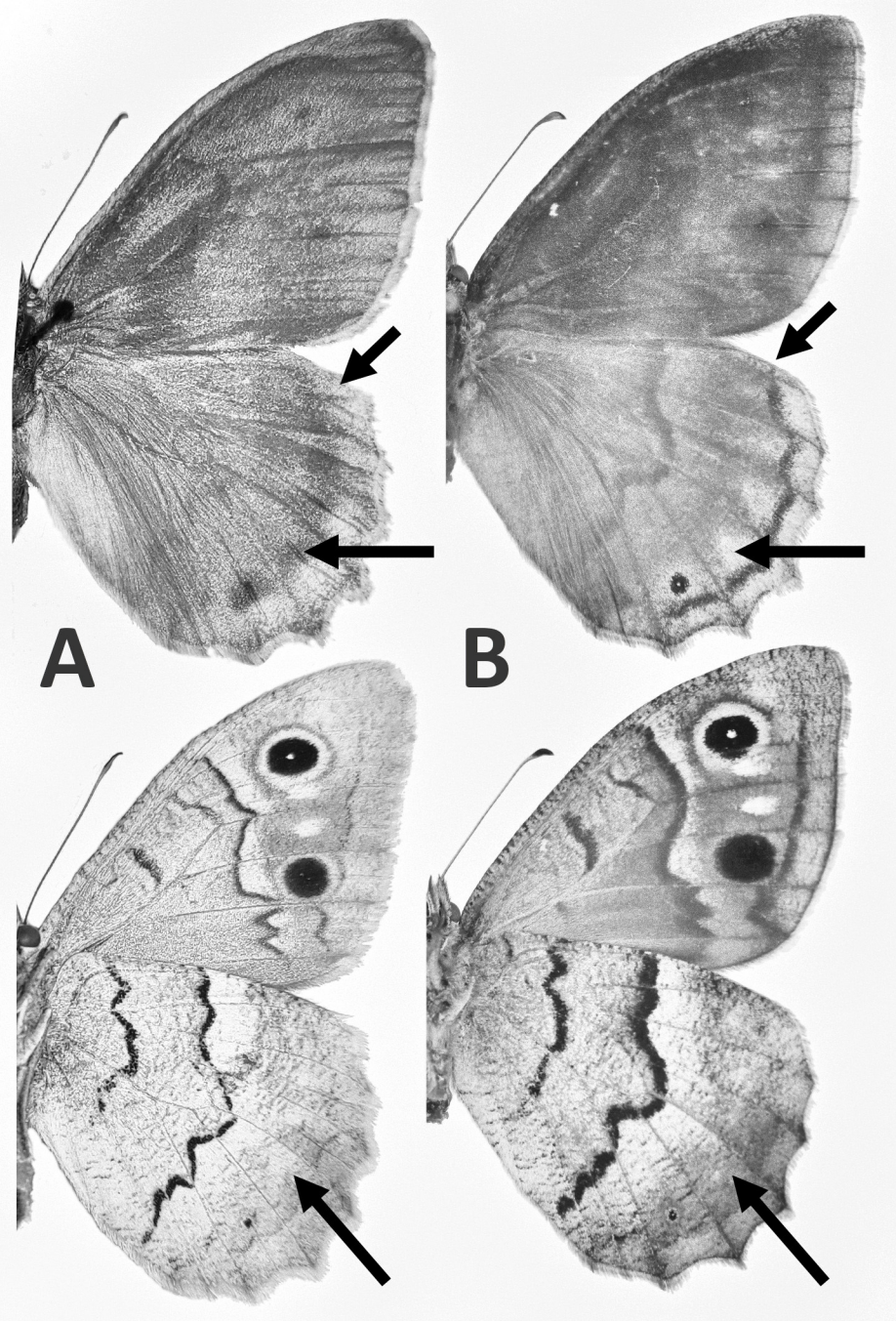

FIGURE 3. differential diagnosis between males of *H. fatua* (A) and *H. lunulata* **sp. nov.** (B). **A:** Iran, Chalus road, 15 km E Karaj, 1600 m, 7.VIII.1994, leg. et coll. Naderi; **B:** Iran, Fars, 15–20 m E. Neyriz, 2000–2100 m, 5.VII.1997, leg. et coll. W. ten Hagen.

Paratypes: Iran: Esfahan: 1♂3♀ Khansar, Sarcheshmeh, 2400m, 23.VIII.2005, leg. A. Harandi (coll. Harandi); 1♂1♀ *Ibid*, leg: M. Raddanipour (coll. Harandi); 4♂ Fereydounshahr, Alimakan, 2600m, 4.VIII.2008, leg. A. Harandi (coll. Harandi); 2♂ *Ibid*, eg: M. Raddanipour (coll. Harandi); 1♂ Natanz, Oureh, 2100m, 17.VIII.2023, leg. A. Harandi (coll. Harandi); 2♂1♀ Kashan, Niasar-Sericheh, 1650m, 29–31.VII.1983, leg. Pazuki/Hashemi (coll. Hayk Mirzayans Insect Museum [HMIM], Tehran). **Markazi**: 2♂ Tafresh, Naghusan, 2300m, 18.VII.2002, leg. A. R. Naderi (coll. Naderi); 1♀ Mahallat, 11. August. 1995, leg. A. Karbalai (coll. Zehzad); 2♂ Pass E Tafresh, 2400 m, 2–3.VIII.1998, leg. W. ten Hagen (coll. ten Hagen); 2♂ Kuh-e Goran (S side), 2450 m, 20–21.VII.1998, leg. W. ten Hagen (coll. ten Hagen). **Hamadan:** 2♂1♀ Avaj, 5.VIII.1996, leg. A. Karbalai (coll. Zehzad). **Lorestan:** 3♂2♀ Dorud, Saravand, 1900–2100 m, 4.VIII.1998, leg. W. ten Hagen (coll. ten Hagen); 3♂ 15 km E Dorud, Saravand, Darastaneh, 2000m, 6.VIII.1975, leg. Pazuki (coll. HMIM); 4♀ 30 Km W Dorud (Pass), 2100 m, 3–4.VIII.1998,

leg. W. ten Hagen (coll. ten Hagen); 4♂1♀ 55 Km E Khorram-Abad, 2000 m, 17.VII.1996, leg. W. ten Hagen (coll. ten Hagen); 1♂ Kuh-e Garrin, Pass Nurabad - Nahavand (E side of pass), 1900–2400 m, 8–9.VII.2000, leg. W. ten Hagen (coll. ten Hagen). **Chaharmahal-o Bakhtyari**: 1♂ Rokh pass, 2200m, 11.VIII.2023, leg. A. Harandi (coll. Harandi). **Kohkiluye va Boyerahmad:** 1♂ Kuh-e Dinar, Pass W Meimand, 2400–2700 m, 15. VII. 2000, leg. W. ten Hagen. **Fars**: 1♂ Dashte Arjan, 1900m, 20.X.2010, leg. A. Hofmann & J. Meineke (coll. Naderi); 1♂ 15–20 km E Neyriz, 2000–2100m, 5.VII.1997, leg. ten Hagen, dissection GP 19 1999 (coll. ten Hagen); 1♂ Kuh-e Hatun, NE Qaderabad, 2400–2600m, 17.VII.1999, leg. W. ten Hagen (coll. ten Hagen).

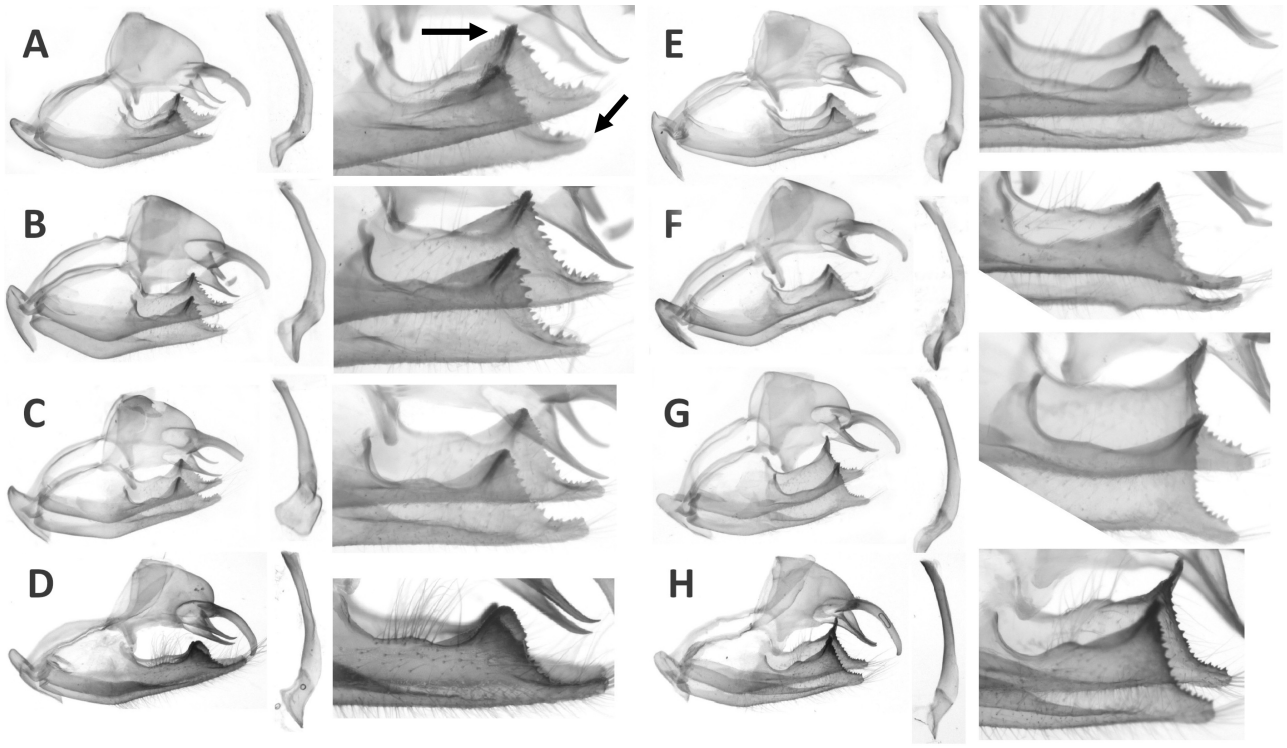

FIGURE 4. Male genitalia of *Hipparchia.* from left to right: Genitalia, phallus, and close-up of the dorsal sub-terminal triangular extension of valva. Arrows point to variable characters on the valva. **A.** *H. lunulata* **sp. nov.** GP19-1999 Fars: E. Neyriz; **B.** *H. lunulata* **sp. nov.** GP16-1999 Lorestan: E. Khorramabad; **C.** *H. fatua persiscana* GP17-1999 Kordestan: N. Divandarreh; **D.** *H. fatua sichaea* GP 44-2024 Syria: Tartus; **E.** *H. fatua fatua* GP18-1999 N.E. Turkey: Artvin; **F.** *H. fatua fatua* GP15-1999 NW Turkey: Canakkale; **G.** *H. statilinus* GP14-1999 W Turkey: Agais, Kaz Dagi, **H.** *H. statilinus* Turkey: Izmir. All dissections and photos by WtH.

Description. ***Male:*** Forewing Length (FWL) 30 mm; Upperside: Both wings ground color dark brown to blackish; forewing with an obscure but broad androconial patch; hindwing edge tends to be less undulated and more roundish; pale whitish margins especially on the hindwings very distinct, sometimes even extending into inner submarginal area as white lunules; a black line separates white margin from darker submarginal area; fringes white. Underside: close to *H. fatua persiscana* with a pale gray background; hindwing with a wide dark brown patch that extends from S2 to S5 in the marginal area. ***Female*****:** FWL 28 mm; Upperside: Both wings ground color dark brown but lighter than the male; forewing with two black eyespots in S2 and S5 and two white pupils in-between; the wing margins are paler than the ground-color of the wings; hindwings with broad white margins and distinctive submarginal lunules in S1 to S7. **Diagnosis** (Fig. 3)**.** The new species is easily distinguishable from *H. fatua* by the presence of a white margin on the upperside of the hindwings in males and the added white submarginal lunules in females. In *H. fatua* the upperside of the hindwings are almost uniformly deep brown to black with no white marginal lunules. In *H. lunulata* **sp. nov.**, the hind wings are more rounded and much less undulated than in *H. fatua*. The underside pattern of *H. lunulata* **sp. nov.** is similar to *H. fatua* but with a distinctive wide brown submarginal patch between S2 and S5 area on the hindwing. This patch is very faint or absent in *H. fatua*.

Male genitalia (Fig. 4). The dorsal sub-terminal triangular extension of valva well-developed, more robust than those in *H. fatua persiscana* (Fig. 4C), not as rounded as in *H. fatua sichaea* (Fig. 4D), and not as elongated as in *H. fatua fatua* (Fig. 4G) and *H. statilinus* (Fig. 4H) from Western Turkey.

Etymology. The name *lunulata* refers to the white submarginal lunules on the upperside of the hindwings.

Distribution and Ecology. The range of the new species is restricted to the central and southern parts of the Zagros mountains in Iran (Fig. 5). Adults fly very late in the season, usually in xerophytic habitats with thorny *Astragalus* and *Acantholimon,* and nectar on flowers of *Acantholimon* and *Acanthophyllum*. They are petrophilous and generally prefer to stay near the ground and rocks where the patterns on the underside of their hindwings provide an adaptive camouflage against predators. They can also be seen resting on the tree trunks in cool shady spots.

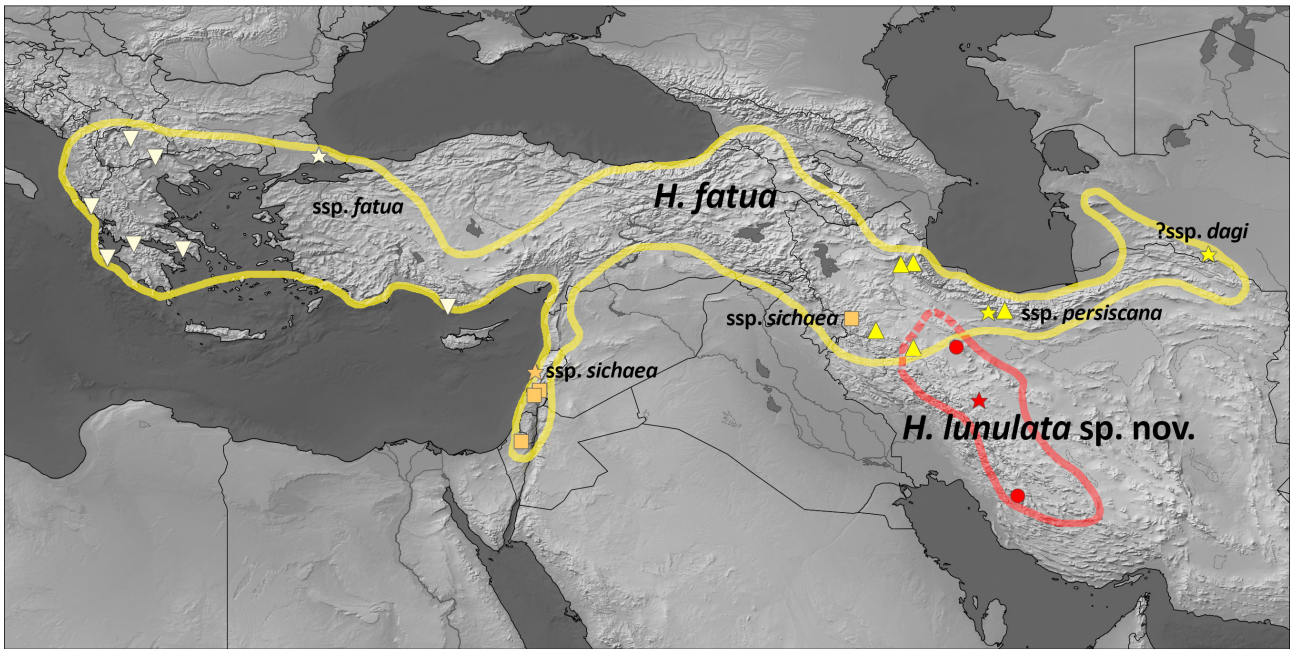

FIGURE 5. Sequenced specimens of *Hipparchia lunulata* **sp. nov.** (red) and *H. fatua* (yellow), and their approximate ranges (after Hesselbarth *et al.* 1995; Tshikolovets 1998, Tshikolovets & Nekrutenko 2012, Tshikolovets *et al.* 2014, Tshikolovets & Ben Yahuda 2020, Sbordoni *et al.* 2018). The type locality for each taxon is shown with a star. Map created using simplemappr.net (Shorthouse 2010).

Discussion

At the end of the glacial periods in the northern hemisphere, the Zagros Mountain range served as an unglaciated reservoir hosting many species which, after warming, gradually recolonized other areas. Today, the western parts of the Zagros mountains are humid and covered with dense oak forests, whereas the eastern and central parts are much drier and have a colder climate.

The range of *Hipparchia fatua* extends from the Balkans to Turkmenistan, however the exact boundaries between its recognized subspecies remain undefined. The paucity of material from Turkey in our study did not help in clarifying these boundaries. Historically, populations of *H. fatua* in north- and western Iran have been considered to belong to ssp. *persiscana*. We found that the populations in central Alborz mountains in north Iran share the same haplotype as those in west and northwest Iran (Ardabil, Azarbaijan Province), even though the latter possess a somewhat darker complexion. The status of populations in Kopet-Dagh mountains (ssp. *dagi* Korshunov & Kralinikova, 1990), previously synonymized with *ssp. persiscana* (Nazari 2003, Tshikolovets *et al.* 2014), remains unconfirmed by molecular means. Westwards, the range of ssp. *persiscana* extends to the eastern parts of Iranian Kordestan province (Fig. 5); however, our DNA analyses confirmed that samples of *H. fatua* from the western parts of this province close to the border with Iraq are genetically identical to those in the Levant, i.e. *H. fatua sichaea*, whose presence in Iran was recently questioned (Rajaei *et al.* 2023). This finding significantly expands the range of this subspecies from the Mediterranean coasts to the westernmost edges of the Zagros mountains, however, the exact distribution of this subspecies in southern Turkey and northern Iraq remains unclear. Unlike ssp. *persiscana* that prefers drier habitats, ssp. *sichaea* flies in river valleys in dense humid oak forests in the Iranian Kordestan, similar to its preferred habitats around Beirut. In addition, it is also possible that the range of the nominotypical ssp. *fatua* extends to the northwesternmost corner of Iran, however this remains to be confirmed by molecular means.

Our DNA analysis and examination of morphological characteristics revealed that populations from central and eastern Zagros were distinct from *H. fatua* at species level, described here as *H. lunulata* **sp. nov.** It seems clear that the range of the new species partially overlaps (at least) with that of *H. fatua persiscana* in western Iran (provinces of Lorestan and Hamadan), and it is likely that in places where they co-occur, they could also hybridize. Focused sampling in these areas followed by DNA analysis of the samples are required to confirm the existence and/or extent of the hybridization between the two species and clarify the boundaries between these taxa as well as those in Turkey, Iraq and Syria.

Our results also fully confirm the subgeneric scheme for the genus *Hipparchia* adopted by Sbordoni *et al.* (2018). A discussion on the taxonomy of the many species in *Hipparchia* however is beyond the scope of this study and should be investigated separately on a case-by-case basis.

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