Unexpected cryptic diversity revealed through integrative analysis within isolated populations of the Graylings (Lepidoptera: Nymphalidae: Satyrinae) in the Western Balkans

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Abstract. The Balkan Peninsula is a European biodiversity hotspot, home to unique endemic species like the Graylings (genus *Pseudochazara*) (Lepidoptera: Nymphalidae: Satyrinae). In July 2017, the first author discovered an unknown *Pseudochazara* population near Krastë, central Albania, over 130 km from known populations in south-eastern Albania and north-western Greece. Another population was found in July 2022 near Lurë in the same massif. Initially classified as *P. tisiphone* Brown, 1981 in the atlas "Fluturat e Shqipërisë," this study shows these populations evolved allopatrically due to geographical isolation. We present new findings based on unpublished data from multiple expeditions between 2015–2023, and through an extended comparison with related *Pseudochazara* populations. We conducted a comprehensive biometric analysis of morphologic traits in males and females (habitus, androconial scales, and genitalia) alongside a systematic differentiation based on the mt COI gene from specimens collected in Albania and Greece. Our results show that the central Albanian populations found in the eastern belt of the Mirdita zone in the vast inner Albanides Massif are distinct from known *P. tisiphone* populations in the western ophiolitic belt, and the surroundings of the Pindos Massif in Greece. Systematic positioning indicated these populations form a distinct monophyletic cluster, closely related to sister species *P. orestes* and *P. tisiphone*, but genetically closer to *P. orestes*. Morphologically, they exhibit intermediate traits and unique androconial scales, similar to *P. cingovskii* Gross, 1971 from North Macedonia. Based on current taxonomic insights, we describe the unique populations from central Albania as a new cryptic species within the '*P. hippolyte*' clade of the genus, *Pseudochazara misjai* Parmentier, **sp. nov**.

This paper further discusses our integrative analysis and emphasizes the importance of conservation efforts in Albania, hosting the exclusive habitats of this new species and being a stronghold for rare *Pseudochazara* species in Europe.

Samenvatting. Het Balkan schiereiland is een hotspot voor biodiversiteit in Europa, de thuisbasis van vele unieke endemische soorten, waaronder die van het geslacht *Pseudochazara* (Lepidoptera: Nymphalidae: Satyrinae). In juli 2017 ontdekte de eerste auteur een onbekende *Pseudochazara* populatie nabij Krastë in centraal Albanië, op meer dan 130 km afstand van gekende populaties in het zuidoosten van Albanië en het noordwesten van Griekenland. Een andere populatie werd in juli 2022 gevonden nabij Lurë, in hetzelfde massief. Aanvankelijk geclassificeerd als *P. tisiphone* Brown, 1981, zoals ook gedocumenteerd in de vlinderatlas "Fluturat e Shqipërisë", toont deze studie aan dat deze populaties allopatrisch evolueerden door geografische isolatie. We presenteren nieuwe bevindingen op basis van niet-gepubliceerde gegevens van meerdere expedities tussen 2015–2023, en via een uitgebreide analyse in vergelijking met aanverwante *Pseudochazara* populaties. Een uitgebreide biometrische analyse werd uitgevoerd op basis van morfologische kenmerken bij mannetjes en vrouwtjes (habitus, androconiale schubben en genitaliën) naast een systematische differentiatie op basis van het mt COI-gen van exemplaren verzameld in Albanië en Griekenland. Onze resultaten laten zien dat de centraal-Albanese populaties in de oostelijke gordel van de Mirdita zone binnen het langgerekte 'Inner Albanides' massief verschillen van de bekende *P. tisiphone* populaties in de westelijke ophiolytische gordel van dat massief en de omgeving van het Pindos massief in Griekenland. Systematische positionering toonde aan dat deze populaties een afzonderlijke monofyletische cluster vormen, nauw verwant aan de zustersoorten *P. orestes* en *P. tisiphone*, maar genetisch dichter bij *P. orestes*. Morfologisch vertonen ze tussenliggende kenmerken en unieke androconiale schubben, vergelijkbaar met die van *P. cingovskii*, Gross 1971 uit Noord-Macedonië. Gebaseerd op de huidige taxonomische inzichten beschrijven we de unieke populaties uit centraal Albanië als een nieuwe cryptische soort binnen de '*P. hippolyte*'-clade van het genus, *Pseudochazara misjai* Parmentier, **sp. nov**.

Dit artikel bespreekt verder de details van onze integratieve analyse en benadrukt het belang van inspanningen voor natuurbehoud in Albanië, dat de exclusieve habitats van deze nieuwe soort herbergt en een sterkhouder is voor zeldzame *Pseudochazara* soorten in Europa

Abstrakt. Gadishulli Ballkanik paraqet një zonë tipike të biodiversitetit evropian, ku takohen specie endemike të rralla si Graylings (gjinia Pseudochazara) (Lepidoptera: Nymphalidae: Satyrinae). Në korrik të vitit 2017, autori i parë i këtij punimi zbuloi një popullatë të panjohur më parë të Pseudochazara afër zonës së Krastës, në Shqipërinë qëndrore, mbi 130 km larg popullatave të tjera të njohura në Shqipërinë juglindore dhe në Greqinë veriperëndimore. Një tjetër popullatë e këtij lloji u identifikua në korrik të vitit 2022 pranë Lurës. Kjo popullatë u klasifikua taksonomikisht si P. tisiphone Brown, 1981 në Atllasin "Fluturat e Shqipërisë". Ky studim tregon se popullatat e këtij lloji kanë evoluar në mënyrë alopatrike për shkak të izolimit gjeografik. Në këtë botim, ne paraqesim gjetje të reja nga krahasimi midis popullatave të Pseudochazara, duke u bazuar në të dhëna të papublikuara më parë, nga ekspedita të shumta midis vitit 2015-2023. Nga ekzemplarët e mbledhur në Shqipëri dhe Greqi, zhvilluam një analizë të plotë biometrike të tipareve morfologjike tek meshkujt dhe femrat (pamja e jashtme, luspat androkoniale dhe organet gjenitale), të krahasuar me një analizë filogjenetike të gjenit mt COI. Rezultatet tona tregojnë se popullatat e takuar në Shqipërinë qëndrore, në anën lindore të zonës së Mirditës në masivin e brendshëm të gjerë të Albanideve, janë të dallueshme nga popullatat e njohura të P. tisiphone që takohen në brezin ofiolitik perëndimor dhe rrethinat e masivit të Pindit në Greqi. Përfundimet filogjenetike tregojnë se këto popullata formojnë një grup të veçantë monofiletik, të lidhur ngushtë me specie *P. orestes* dhe *P. tisiphone*, por gjenetikisht janë më afër me specien *P. orestes*. Morfologjikisht, ato shfaqin tipare të ndërmjetme dhe shkallë unike androkoniale, të ngjashme me *P. cingovskii* Gross, 197 të takuar në Maqedoninë e Veriut.Bazuar në njohuritë aktuale taksonomike, ne i përshkruajmë këto popullata unike të takuar në Shqipërinë e mesme si një specie të re, e fshehur brenda kladës '*P. hippolyte*' të gjinisë *Pseudochazara*, si specie e re *Pseudochazara misjai* Parmentier, **sp. nov**.

Ky punim thellon më tej analizën tonë të integruar dhe thekson rëndësinë e përpjekjeve të ruajtjes dhe kërkimin e habitatet optimale për këtë specie të re në Shqipëri, si një vend potencialisht të rëndësishëm për takimin e këtyre specieve të rralla të gjinisë *Pseudochazara* në Evropë.

Résumé. La péninsule balkanique est un hotspot européen de la biodiversité, abritant des espèces endémiques uniques comme dans le genre *Pseudochazara* (Lepidoptera : Nymphalidae : Satyrinae). En juillet 2017, le premier auteur a découvert une population inconnue de *Pseudochazara* près de Krastë, dans le centre de l'Albanie, à plus de 130 km des populations connues du sud-est de l'Albanie et du nord-ouest de la Grèce. Une autre population a été trouvée en juillet 2022 près de Lurë dans le même massif. Initialement tous classées comme *P. tisiphone* Brown, 1981 dans l'atlas « Fluturat e Shqipërisë », cette étude montre que ces populations ont évolué de manière allopatrique à cause d'un isolement géographique. Nous présentons de nouvelles découvertes basées sur des données non publiées provenant de plusieurs expéditions réalisées entre 2015 et 2023, et à travers une comparaison étendue avec des populations apparentées de *Pseudochazara*. Nous avons effectué une analyse biométrique extensive des traits morphométriques chez les mâles et les femelles (habitus, androconies et organes génitaux) ainsi qu'une différenciation systématique basée sur le gène mt COI à partir de spécimens collectés en Albanie et en Grèce. Nos résultats montrent que les populations albanaises centrales trouvées dans la chaîne orientale de la zone du Mirdita dans le vaste Massif 'Inner Albanides' sont distinctes des populations connues de *P. tisiphone* dans la chaîne occidentale ophiolite du Massif et dans les environs du Massif du Pinde en Grèce. Le positionnement systématique a indiqué que ces populations forment un groupe monophylétique distinct, lié aux espèces sœurs *P. orestes* et *P. tisiphone*, mais génétiquement plus proche de *P. orestes*. Morphologiquement, ils présentent des traits intermédiaires et des androconies uniques, similaires à *P. cingovskii* Gross, 1971 de Macédoine du Nord. En accord avec les connaissances taxonomiques actuelles, nous décrivons les populations uniques du centre de l'Albanie comme une nouvelle espèce cryptique dans le clade « *P. hippolyte* » du genre, *Pseudochazara misjai* Parmentier, **sp. nov**.

Cet article approfondit notre analyse intégrative et souligne l'importance des efforts de conservation en Albanie, qui héberge les habitats exclusifs de cette nouvelle espèce et constitue un bastion pour les espèces rares de *Pseudochazara* en Europe.

Key words: *Pseudochazara misjai* sp. nov. — *Pseudochazara orestes* — *Pseudochazara tisiphone* — *Pseudochazara cingovskii* — Morphometrics — Androconia — Phylogenetics — Endemics — Balkan Peninsula — Albania.

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Introduction

The Balkan Peninsula is one of the European hotspots for biodiversity, with unique habitats that shelter rare butterfly species, including endemics. Within the genus *Pseudochazara*, or Graylings (Lepidoptera: Nymphalidae: Satyrinae) different species have been identified and described in the last half-century, proving that the Balkans are a stronghold for the genus in Europe.

Since the first description of *Pseudochazara sintenisi cingovskii* Gross, 1971 by Gross from the mountains near Prilep, currently, North Macedonia (NMK), the description of new taxa progressed quickly. In the same decade, many new species and subspecies were described, subspecies changed from status, changed again, and later brought to the species level based on new genetic analysis. Without aiming to present a complete overview of the taxonomical history, we highlight some of the taxonomic-nomenclatural acts that are important because of the present study. In 1976, Brown published an important review paper describing new insight based on extended explorations in the mountainous region of north-western Greece, to the frontier of Albania.

In his paper, he described *Pseudochazara amymone* Brown, 1976 and raised *Pseudochazara cingovskii* to the species level. However, the latter was based on populations in the Smolikas Massif, Western Greece, and later he realised the distinctiveness to *P. cingovskii* from NMK to describe the same population as a new subspecies of *P. cingovskii tisiphone* Brown, 1981 (Brown 1981), while the position of *P. cingovskii* as a bona species remained. Later, this taxon was attributed as a subspecies of *Pseudochazara mamurra* (Herrich-Schäffer, [1846]), a species distributed in Turkey, Asia Minor, and based on similarities in androconial scales, not having genomic analysis available at that time. Only more recently, and based on distinctive phylogenetics (deep divergent clades), it was split from *P. mamurra* and raised to species level as *P. tisiphone* Brown, 1981 (Takáts & Mølgaard 2016).

In the same year, *Pseudochazara orestes* De Prins and van der Poorten, 1981 was described from Drama, Mt. Falakron, north-eastern Greece, as a distinct species (De Prins & van der Poorten 1981). The description was based on an integrative biometric analysis, showing its distinctive character in androconia, male and female wing patterns compared to its closest sister species of *P. tisiphone* and *P. cingovskii*. Remarkably, in the original description, W. De Prins mentions that "it was first attributed as an unknown population of *P. c. tisiphone* … in north-eastern Greece", based on a resembling habitus, but further assessment of collected voucher specimens provided convincing support to describe it as a new bona species.

After a decade of descriptions of new taxa, other insights have drawn attention, such as the expanded distribution range of *P. cingovskii* in NMK. This species has been found in different new localities next to the Type locality, situated in the same mountain massif (Švara *et al.* 2016). More southwards, *Pseudochazara geyeri* (Herrich-Schäffer, [1846]) has been reported from the Galičica Park, near Lake Ohrid, bordering Greece. Other searches in the western part of the country, close to the border of Albania, did not reveal other *Pseudochazara* populations and the genus is not present in the mountains north of Bitola and north-west of Lake Ochrid (Švara *et al.* 2016).

Recent research dealt with the genetics of the genus and later some important new insights have been published. While the genus sometimes shows limited variability between species, a phylogenetic reconstruction through barcoding of the COI mtDNA gene confirmed the monophyly of the majority of populations that have been accepted as bona species presently. Importantly, in the study by Takáts and Mølgaard (2016), it was found that the genus consists of three, deeply diverged species-group clades, of which we present here only the Balkan ones: a) the '*P. mamurra*' species group (including *Pseudochazara graeca* (Staudinger, 1870) and *Pseudochazara amymone* Brown, 1976); b) the '*P. pelopea*' species group, and c) the *'P. hippolyte'* species group on which we will focus in this paper, with currently *P. tisiphone, P. cingovskii* and *P. orestes* as the three known species occurring in the western Balkans. With this information, different expeditions were organised to explore further this region, focusing on the many little-known biotopes in Albania.

During the first expedition in the country in 2015, the enigmatic *P. amymone* and *P. tisiphone* were observed in the Korçë region at multiple sites, near the villages of Bobosthicë, Drenovë, and Gjergjevicë. While *P. amymone* was regarded as very rare, we could confirm its very local presence; however, *P. amymone* is not uncommon in the species' typical habitat with very dark ophiolitic soil substrate. The sympatric-flying *P. tisiphone* was equally common in its habitat with a wider range of ophiolitic biotopes.

Triggered by the unresolved enigma of confirmation of *P. amymone* in northern Greece, the type locality of its initial description by Brown in 1976, the first author undertook a new expedition to further explore the Albanian-Greek border region with resembling soil substrates for *P. amymone* and *P. tisiphone* as observed in the Albanian Korçë region. However, while the latter species was observed in its typical habitat with ophiolitic soil substrate, e. g. near Distrato, *P. amymone* could not be confirmed in northern Greece, despite thorough search efforts in multiple targeted and promising ophiolitic habitat sites. Other entomologists also came to the same conclusion despite their efforts in the last decade (Eckweiler 2012). As far as the authors know, there is no other hard proof of the existence of *P. amymone* in Greece, except for a photo of a worn male specimen. Probably the population could have disappeared, as it has been observed that the specimens of *Pseudochazara* spp. (amongst other butterfly species) are by far less common in numbers in northern Greece than in Albanian biotopes, probably due to increased grazing pressure and other anthropogenic threats.

In July 2017, during an expedition further exploring unknown regions in the western Balkans and central Albania, the first author, together with D. Vincke, discovered an unknown population of *Pseudochazara* sp. in a mountainous area with ophiolitic and intermixed soil substrate near Krastë, the vicinity of the city of Bulquize, in several localities of at least 130 km distance from the known populations in the Korçë region, Albania. This observation was also confirmed independently at about the same time by J. Couckuyt and S. Cuvelier during their joint expedition, and, shortly after, these observations were merged in a new distribution atlas of Albanian Lepidoptera: "Fluturat e Shqipërisë". The observations of the unknown *Pseudochazara* specimens were identified as the northernmost population of *P. tisiphone* at its northern distribution limit in the Balkans. The identification was based on the external morphological characters of a few specimens and a single rough measurement of male androconial scales (Cuvelier *et al*. 2018).

During the next few years, the authors undertook new expeditions, further exploring the remote regions and investigating promising ophiolitic and intermixed habitats in the western Balkans, focusing on central to eastern Albania, and extending to the borders of NMK and Kosovo. On July 23rd–24th 2022, in a joint expedition, both authors, together with R. Fero, explored ophiolitic and intermixed habitats in the Lurë-Dejë National Park, Lurë region of central Albania, and discovered a new unknown population of *Pseudochazara* sp., but about 30 km further northwards. This discovery was quickly linked to the populations studied near Krastë, Bulqizë back in 2018, and, as such was included as the new northernmost population of *P. tisiphone* in the updated distribution atlas of Albanian Lepidoptera (Cuvelier *et al.* 2023).

In July 2023, the first author further explored the central Albanian region, situated between the areas of Lurë-Bulquize and southeastern Korçë, to untangle a possible shared connection between the *Pseudochazara* sp. populations in that region and those populations discovered in central Albania. Additionally, a series of extra voucher specimens from various central Albanian *Pseudochazara* spp. populations were collected for further study.

Altogether, these new observations lead to new insights, presented in this work. Whilst previous publications were based on incomplete distribution information or limited morphological and genetic analysis (Cuvelier 2023), in this study, we thoroughly analysed all the data on multiple *Pseudochazara* spp. voucher specimens of the '*P. hippolyte*' species group in an integrative way, combining genetics with biometric analysis. This work led to the delineation of a new taxon which is described in the present paper. We present our conclusions based on our current discoveries in morphometrics and genetics of the genus, focusing on the populations from the western Balkans.

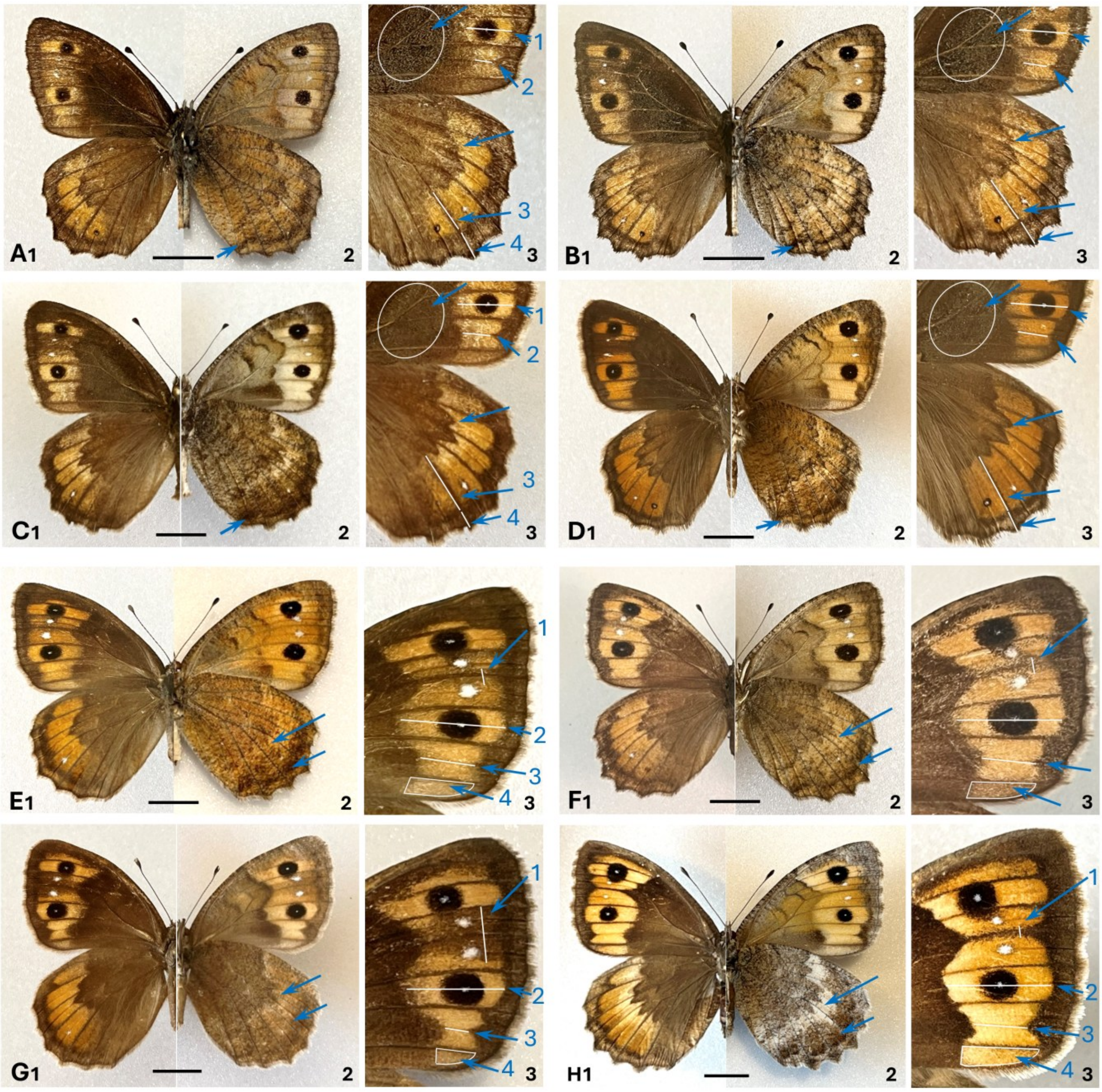

Fig. 1. Habitus and typical traits of males (A-D) and females (E-H) of *P. misjai* sp. n. (A-B, E-F) and closely related taxa *P. tisiphone* (C-D) and *P. orestes* (H). Figure small index numbers: 1, upper side, 2, underside, 3, detail of wings. Blue arrows indicate habitus traits; analyzed wing traits indicated with blue numbers (see method section for details). A, E. Albania, Dibër prov., env. Bulqizë, 18-19.vii.2017. B, F. Albania, Dibër prov., 19.vii.2017. C. Greece, Ioannina, env. Distrato, 18.vii.2016. D. Albania, Dibër prov., env. Bobosthicë, 19.vii.2018. G. Albania, Dibër prov., env. Gjergjevicë, 20.vii.2023. H. Greece, Thessaloniki, env. Granitis 14.vii.2016. All specimens: leg. & coll. and © L. Parmentier.

Material and Methods

Sample collection and storage

All butterflies were collected by Laurian Parmentier at the different biotopes investigated in Greece, in the provinces Ioannina, and Drama; in Albania, in the provinces of Korçë and Dibër. Samples from the Lurë study site (Dibër prov.) were collected by Xhuliana Qirinxhi and Laurian Parmentier. Collected samples were put in glassine envelopes in the field, and a unique code was assigned to each sample. The samples were subsequently stored in cooled plastic boxes. Taking into consideration the possibility of unstudied variation between different populations (Dapporto *et al.* 2022), multiple voucher specimens of males and females were collected in each study site. All collected samples were set, to be later used for the morphometric analysis of habitus', and sexual trait analysis (in males: for studying androconial scales and genitalia structures), and genetic analysis based on mt COI gene. All vouchers were stored in L. Parmentier's collection (LPAcoll, Zulte, Belgium). Pictures of biotopes were taken with an iPhone 6 or 13, and butterflies in their biotope with a Canon 70D and a 100 mm macro lens.

Biometric analysis

External wing traits

An extended study on the different traits of wing vouchers, assessing the sympatric and externally resembling taxa *P. tisiphone* and *P. amymone*, was consulted (Cuvelier & Mølgaard 2015). Based on the conclusions of the previous investigators, wing traits that could be significant for external identification and our comparative analysis were reviewed. We made a selection, while merging the existing information and our own additional observations, to select a series of morphologic traits for comparative morphometrics differentiating the *Pseudochazara* spp. populations of the '*P. hippolyte*' species group in Albania and *P. orestes* belonging to the same species group but originating from western Greece. For wing morphometrics of males and females (indicated with blue numbers), the set of traits was selected as shown in Fig. 1. The forewing (FW) length served as a basis to calculate the relative proportion of wing size and the degree of individual intra-specific variation.

Males

Trait 0 (basis). FW length from thorax to wing apex (mm);

Trait 1. FW width at the submarginal band across the centre of the ocellus in cell S2 (mm);

Trait 2. FW width at the narrowest position of the submarginal band in the centre of cell S1b (mm);

Trait 3. Hindwing (HW) width at the submarginal band at the position of vein M_3;

Trait 4. HW thickness at the marginal grey/brown band.

Females

Trait 0 (basis). FW length from thorax to wing apex (mm);

Trait 1. FW breadth of the (darkened) veins in the postdiscal band, next to the position of the small white ocelli (situated between the eyespots);

Trait 2. FW width of the submarginal band across the centre of the ocellus in cell S2 (mm);

Trait 3. FW width of the narrowest position of the submarginal band in the centre of cell S1b (mm);

Trait 4. FW surface of the orange zone at the end of the post-discal band in cell S1a (generally surrounded by darkened brown colouration between vein v1B-wing edge and postmedian-marginal zone).

Androconial scales

In *Pseudochazara* species, the morphological characters of androconial scales can be used in morphometrics for the determination of the systematic position of a taxon (Brown 1976; Gross 1978). Androconia appear to be relatively consistent in overall size and shape within and between species (Wakeham-Dawson & Kudrna 2000; Wakeham-Dawson *et al*. 2007), and thus, we included this trait for a morphometric assessment of voucher specimens obtained from different *Pseudochazara* spp. populations in the western Balkans. Androconia were studied following the method described in Wakeham-Dawson & Kudrna (2000), with slight adaptations. The subsequent steps were followed: the androconial scales were removed from the forewing sex brands of male specimens by gently sliding, with very light pressure, a calibrated microscope cover-slip over the sex brands. The slips were then placed on microscope slides and fixed only on the four slip corners. The shape of androconial scale morphology was documented by measuring its length and breadth following Gross (1978). Here, the androconial scale length (AL) from basal stem to terminal points, the androconial scale breadth (AB) across the widest point of the lamina (mm), and the ratio A (AL/AB; no units) that represents the overall shape of androconia scales are used. Measurements of AL and AB were performed with a Dino-Lite® Edge Microscope, model AM7915MZT, that had been calibrated according to the manufacturer's instructions (on three calibration points: 25×, 100× and 200×), to obtain accurate measurements of 1 µm. A double-check of each sample preparation was performed by measuring the distance of the calibrated cover glass slide (1 mm) for each sample; five and ten androconial scales per specimen were measured (where possible).

DNA extraction and sequencing

To construct a genetic relationship tree of the genus *Pseudochazara* and sampled populations in Albania and Greece, the analysis was based on a selection of samples (males and females) taken from the different populations. DNA extraction was done following the protocol described in Parmentier *et al*. (2022), using the primers LepF1 (ATTCAACCAATCATAAAGATATTGG) and LepR1 (TAAACTTCTGGATGTCCAAAAAATCA) for the COI amplification, to obtain a full DNA barcode fragment of 658 base pairs (bp). PCR reactions and settings were identical. Barcoding was done by LGC Genomics, Berlin, Germany. A quality check was performed before sequences were further used in the genetic analysis. All new COI sequences are deposited in GenBank with the following accession numbers:

SUB14839155 LPcoll24_Ps1M	PQ612759
SUB14839155 LPcoll24_Ps2M	PQ612760
SUB14839155 LPcoll24_Ps3M	PQ612761
SUB14839155 LPcoll24_Ps4M_**HT**	PQ612762
SUB14839155 LPcoll24_Ps5F	PQ612763
SUB14839155 LPcoll24_Ps6M	PQ612764
SUB14839155 LPcoll24_Ps7M	PQ612765
SUB14839155 LPcoll24_Ps8M	PQ612766
SUB14839155 LPcoll24_Ps9M	PQ612767

Alignment and phylogenetic reconstruction

The COI analysis involved 73 sequences (62 sequences mined from GenBank and 9 from our material). For the COI-based phylogeny, sequences of different lengths (from 618 to 658 bp) were included in the final dataset alignment. The alignment and the phylogenetic

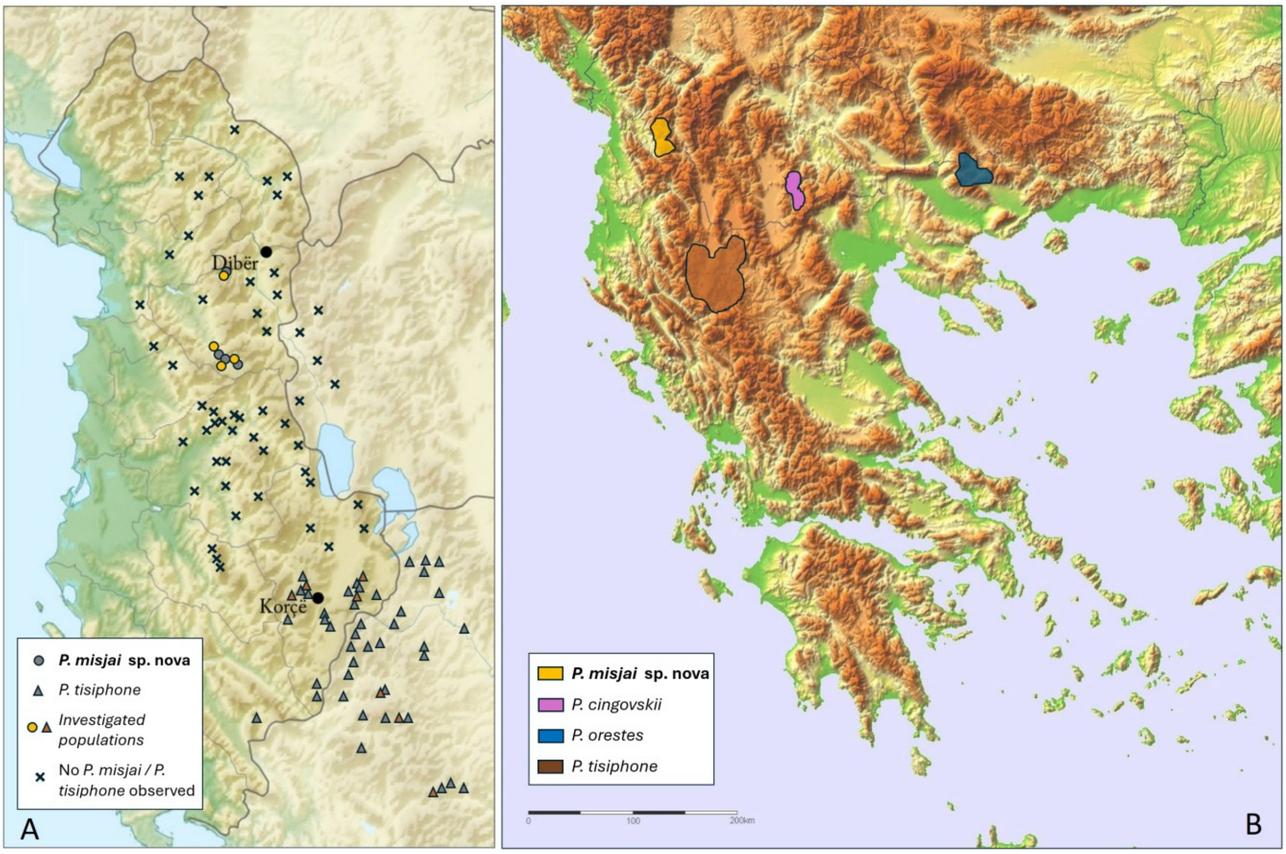

Fig. 2. A. Map with *Pseudochazara* observations in the western Balkans: Albania and bordering countries of Greece and North Macedonia. Localities of *P. tisiphone* and *P. misjai* sp. nov. are indicated, as well as localities with zero-observations, based on literature records and new unpublished observations during the 2015–2023 expeditions. Voucher specimens of investigated populations in this study are indicated with coloured symbols.

B. Overview map of the central-western Balkans with an indication of the distribution of the new taxon and the closely related taxa *P. cingovskii*, *P. orestes* and *P. tisiphone* within the species complex. © L. Parmentier.

reconstruction was performed following the procedure described in Parmentier *et al*. (2022). We used Geneious Prime 2019.0.3 (https://www.geneious.com) software to align the sequences and then edited them manually. The final COI alignment included 658 sites, with 144 variable sites and 117 parsimony-informative sites. The NJ analysis was performed using the program MEGA X v. 11 and Tamura3-parameter+G as the optimal model (also estimated by MEGA) following the Aikaike Information Criterion (Tamura *et al*. 2021). Also, second-best models were run to check the consistency of the phylogenetic signal. To root the tree of the genus *Pseudochazara*, we used the results of the phylogenetic analysis given by Verovnik & Wiemers (2016) and Peña *et al*. (2011). As outgroups, we included several sequences of the closely related Satyrinae species, belonging to the genera *Chazara* and *Satyrus.* These sequences were mined from GenBank. The standard nonparametric bootstrap (Felsenstein 1985) (100 replicates) was used to evaluate the statistical nodal support of the tree, also calculated in MEGA X v. 11.

Statistics

To test differences between individual biometric traits of males and females (4 traits for males and females the dataset distributions of the individual traits datasets were checked, using the '*fitdistrplus*' package in R. Homoscedasticy and QQ plots. Datasets of biometric measurements for female habitus traits, male habitus traits and male androconial scale traits were analysed separately. Univariate statistics using the appropriate family (Gaussian or Student's t) were then applied for each measured trait and between pairs of species (i.e. between *P. misjai* sp. nov. – *P. tisiphone* – *P. orestes*, according to the available dataset for males and females) and to generate P-values at significance level of alpha=0.05. Besides univariate statistics, NMDS plots were generated for male and female morphometrics separately, comparing all measured habitus' traits in a visually comprehensive way. NMDS plots for male and female wing traits were calculated, based on 19 and 23 voucher specimens, respectively, using the Adonis script (Vegan package) in R (Oksanen *et al.* 2016). Ellipses indicating 95% confidence intervals represent species identifications based on COI results, obtaining three categories for females (*P. misjai* sp. nov. *, P. tisiphone* and *P. orestes*) and two for males (*P. misjai* sp. nov*., P. tisiphone*). In the NMDS analysis, the spatial distribution of the samples taken from their population in the western Balkans (central Albania: Dibër, north-western Albania: Korçë, north-western Greece: Ioannina, northeastern Greece: Drama), was also integrated as a factor obtaining categories 'Al_Dib, 'Al_Kor', 'Gr_Ioa', and 'Gr_Thes'. Posterior statistics was performed running a permutational, multivariate analysis of variance, using distance matrices with the Adonis call ('Vegan' package) in R (Oksanen *et al.* 2016).

Fig. 3. Habitats and specimens from *Pseudochazara* populations within the 'hippolyte' clade found in the eastern belt (A–D) an western belt (E–F) of the ophiolitic Mirdita zone in the Inner Albanides, Albania. **A.** Biotope near Bulqizë, Dibër prov.; note heavy mining works still active in these biotopes; **B.** ♀ nectaring in its biotope, Krastë, 19.vii.2017; **C.** Biotope near Krastë, Dibër prov.; **D.** ♂, Krastë, 18.vii.2017; **E.** ♀ *P. tisiphone* in its biotope near Gjergjevicë, Korçë prov., 17.vii.2022 ; **F.** Typical biotope near Gjergjevicë. © L. Parmentier.

Results

Distribution of *Pseudochazara* spp. populations in the western Balkans

In this study, focussing on the '*P. hippolyte*' clade situated in the western Balkans, 75 different locations dispersed over Albania, north-western Greece and western North Macedonia were visited (Fig. 2A), which were identified as potential sites for *Pseudochazara* spp. populations. Of them, only known populations of *P. tisiphone* in western Greece (Ioannina dist.) and southeastern Albania (Korçë dist.), and *Pseudochazara* sp. populations in the surroundings of Krastë-Bulqizë and Lurë region were observed, of which the latter are the main focus of this study. A special search effort was addressed to the mountainous regions flanking the Lumi Skumbin River and running across from Elbasan in the central-eastern part to Lake Ohrid in the western part of Albania, with negative results. In the Shebenik National Park, unpublished sites for *Pseudochazara amalthea* (Frivaldsky, 1845), were found near Skënderbej and Qarrishtë, but also in that region, no single observation

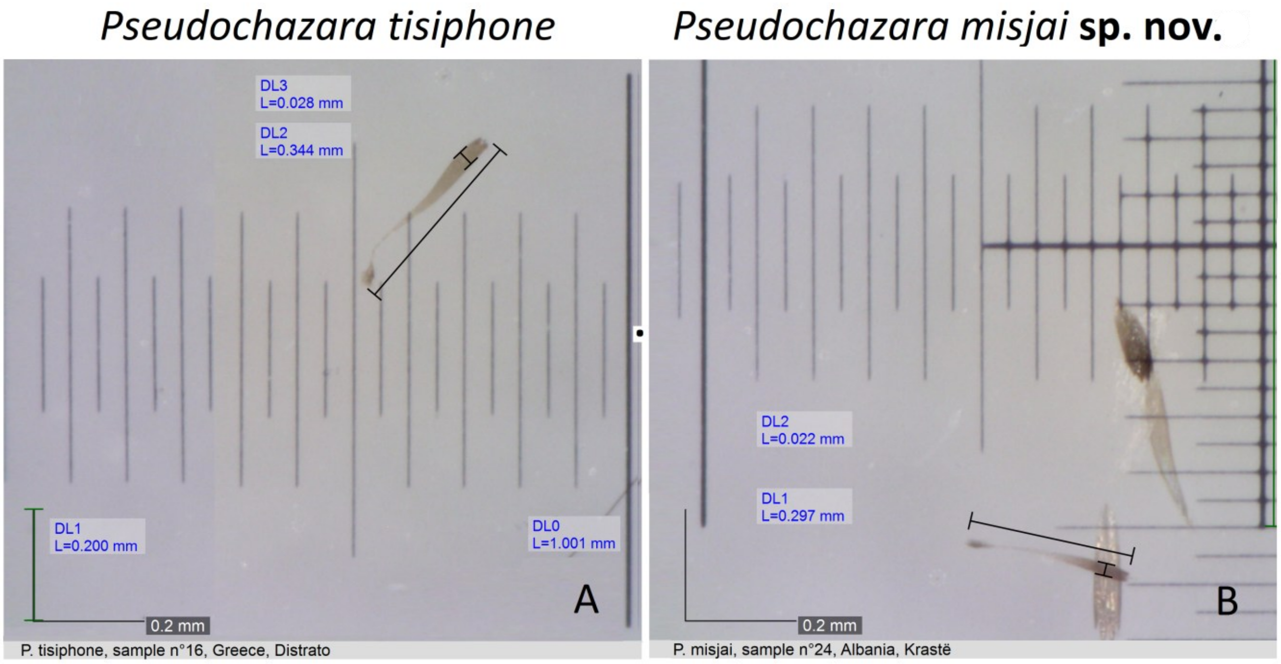

Fig 4. Androconial scale measurements of male *P. tisiphone* (A) and *P. misjai* sp. nov. (B) voucher specimen. Andoconial length (AL) and androconial scale breadth (AB) are given, as explained in the methods section; background lines from gridded cover slip (spacing = 50 µm); microscope calibration length: 0.200 and 1.001 mm. Microscope bar = 0.2 mm. © L. Parmentier.

was made for *P. tisiphone* or other *Pseudochazara* species within the same clade. In comparison, *P. amalthea* was found sympatrically with *P. tisiphone* (and also *P. amymone*) in the Korçë region (e.g. biotopes near Drenovë, Bobosthicë), while the latter was then found clearly outnumbering *P. amalthea*. Despite search efforts over multiple years, no intermediate *P. tisiphone* populations were found between Krastë-Bulqizë and the known distribution in the Korçë district. A summary of currently known populations of taxa within the '*P. hippolyte*' clade is shown in Fig. 2B.

Pictures of biotopes of *Pseudochazara* species found in Albania show that specimens are highly camouflaged when sitting with their wings closed, disappearing into the environment. Specimens of populations found in central Albania (sites Krastë-Bulqizë, Lurë) generally have a slightly more dirty-yellowish ground tone of their hindwing underside, mimicking the yellow-brownish colour of the stony habitats, while the ground tone of specimens found in the Korçë region is generally more darkened grayish-red brown (Fig. 3).

Pseudochazara misjai Parmentier sp. nov.

LSID: urn:lsid:zoobank.org:act:DEAE68B2-B9A7-405F-966D-C6F58A52F9BB

(Figs 1–7)

Diagnosis

Biometrics of androconial scales

A biometric analysis of androconial scales was performed on samples taken from different populations of the '*P. hippolyte*' clade in Albania and north-western Greece. The length (AL) and breadth (AB) of androconial scale were measured (Fig. 4) and the ratio was calculated (Table 1). The average AL was 0.30 mm and AB 0.022 mm, and the ratio (AL/AB) 13,82.

Results of statistical analysis (Table 1A) comparing repeated measurements (total N= 66±2) on voucher specimens (N=10±1) taken from the central Albanian populations (*P. misjai* sp. nov.) versus known *P. tisiphone* populations show that the AL is not different (3%), while both the AB and androconial ratio AL/AB is significantly different ($P<0.001$). Here, the average androconial breadth and androconial ratio in *P. misjai* sp. nov. versus *P. tisiphone* are found to be 14% and 11% lower, respectively.

Male genitalia characters

As it has been reported in the literature that male genitalia within the *Pseudochazara* genus are variable and do not show a great discriminative character difference between species (see e.g., De Prins & van der Poorten 1981; Tolman & Lewington 1997), we still examined the male genitalia and compared specimens of *P. misjai* sp. nov. versus *P. tisiphone* collected from Greek and Albanian populations (Fig. 5). We confirm that male genitalia are quite variable, and so could not serve for differential detailed morphometrics in this study. However, some traits were found to be more pronounced and suitable for diagnosis comparing the two taxa, i.e., the tip of the valva is more sharpened in *P. tisiphone*, and the ventral structure of the uncus is more curved and its end more rounded compared to *P. misjai* sp. nov. (see indications with arrows in Fig. 5). On the costa of the valva, there is a hairy knob that is also well observable and comparable to that of *P. tisiphone*.

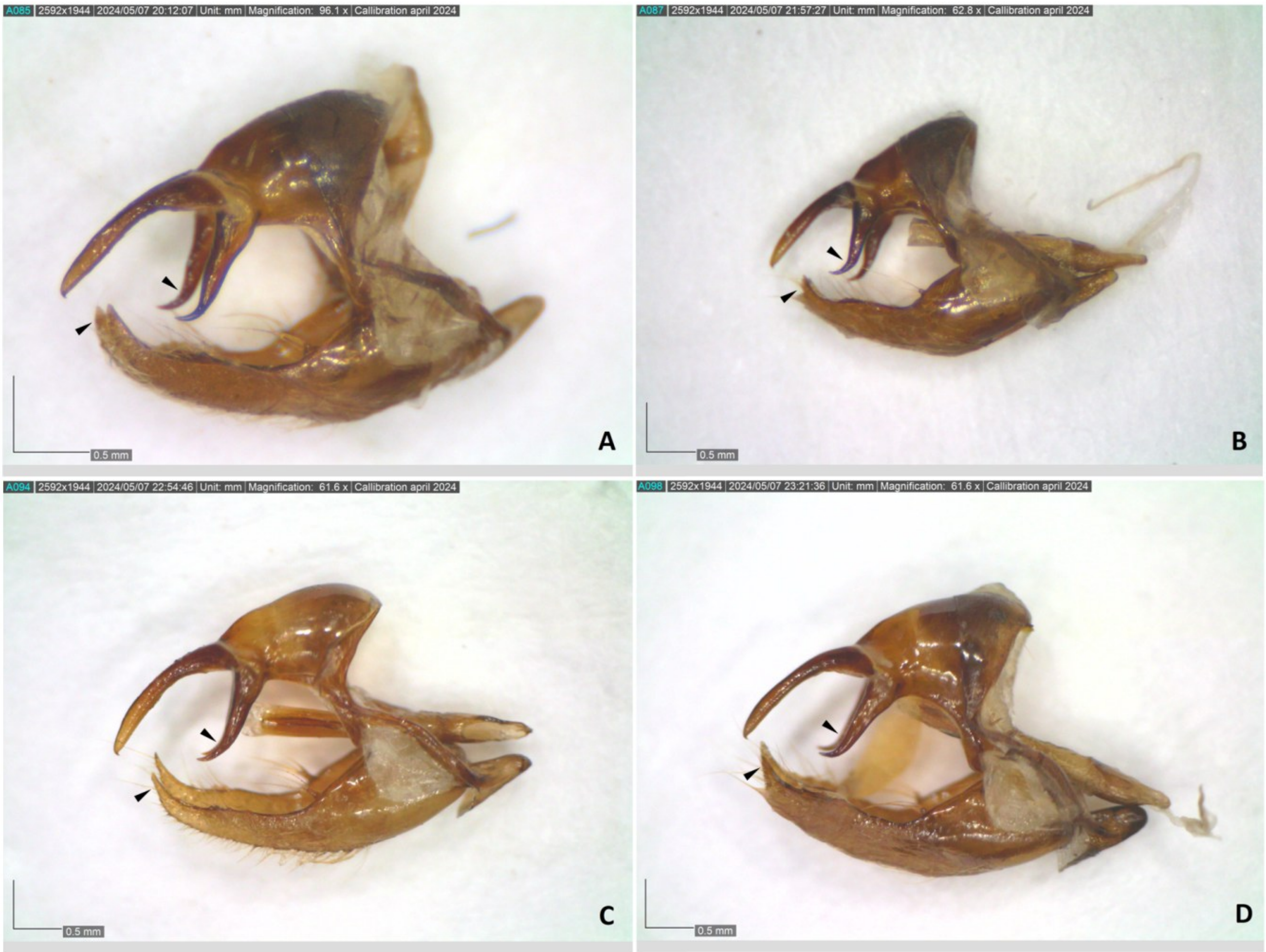

Fig. 5. Male genitalia of *P. misjai* **sp. nov.** (A–B) and *P. tisiphone* (C–D). **A.** Holotype; **B.** Paratype; **C.** *P. tisiphone* sample from population near Distrato, Greece; **D**. *P. tisiphone* sample from population near Gjergjevicë, Albania. Arrows indicate the tip of the valve and the ventral structure of the uncus (see main text for details). © L. Parmentier.

Morphometrics of wing habitus

All habitus' traits on the uppersides of *P. misjai* sp. nov.*,* *P. tisiphone* males and females (N=10 ±1) were measured, i.e. four traits and the total length of the forewing ('Trait 0') to calculate the ratios of the 1–4 traits used for univariate statistics. For females, extra voucher specimens of *P. orestes* were also included in the analysis (Table 1B, C).

Comparative statistics on individual male wing traits and ratios (Table 1B) showed that all traits, and all ratios, except that of Trait 1, i.e. "Width of the submarginal band across the centre of the ocellus in cell S2" were significantly different with strong P values. These traits can thus be used to discriminate between the two sister taxa.

Statistics on individual female wing traits (Table 1C) to make binary comparisons between *P. misjai* sp. nov. – *P. orestes* – *P. tisiphone* show that all measured traits and ratios are significantly different, except for trait 2 (width of the submarginal band across the centre of the ocellus in cell S2) which is different from P. *orestes* – P. *misjai* sp. nov./*P. tisiphone*, but, this trait seems not to be discriminatory when taking into account the ratios, as *P. orestes* females were shown to be generally bigger in size than *P. misjai* sp. nov. and *P. tisiphone* (see significant differences of Trait 0). Of them, it is also remarkable that the ratio of Trait 3, i.e. "The forewing width of the narrowest position of the submarginal band in the centre of cell S1b" could even be considered visually as a diagnostic trait for females between *P. misja* and *P. tisiphone*, but it is not a diagnostic trait between *P. misja* and *P. orestes,* showcasing that *P. misja* sp. nov. has at least an intermediate habitus between these two species for some characters.

Besides individual comparison of different wing traits and statistics thereof, we also performed an NMDS analysis, taking into account all measured traits per voucher specimen. As selected wing traits between males and females were different, we also ran the NMDS analysis separately for males and females. The result of the NMDS analysis makes it possible to visually interpret possible differences/similarities between test groups, as was made here between different allopatric populations (*P. misjai* sp. nov. – *P. tisiphone* – *P. orestes*) taken from different regions (Albania: 2 regions; Greece: 2 regions). It is clearly noticeable from the NMDS graphs that all populations are significantly separated from each other, as indicated by their almost non-overlapping confidence intervals (Fig. 6), generally confirming the results of individual analysis, which was also confirmed with multivariate statistics (all P values between test groups <0.002). Interestingly, voucher samples of *P. tisiphone*

Table 1. Results of morphometric analysis on androconia (A), male (B) and female (C) traits (see main text for details) of voucher specimens. N = number of investigated specimens; av = average value. P values (α =0.05) of comparative statistics of traits that are significantly different between species are in bold.

A. Morphometric analyis of androconial scales

Taxon	**Samples (N)**	**repeats (N)**	**AL (av. mm)**	**AB (av. mm)**	**ratio (AL/AB)**	**stdv (AL)**	**stdv (AB)**	**stdv (ratio)**
P. misjai sp. n. (av)	9	65	0.3	**0.022**	**13.82**	0.008	0.001	0.572
P. tisiphone (av)	10	68	0.309	**0.025**	**12.26**	0.013	0.002	0.653
Univariate, P value			0.084	**< 0.001**	**< 0.001**			
Δ difference (%)			3%	**14%**	**11%**			

B. Morphometric analyis of male wing traits

	Samples (N)	**Trait 0**	**Trait 1**	**Trait 2**	**Trait 3**	**Trait 4**	**ratio Tr.1**	**ratio Tr.2**	**ratio Tr.3**	**ratio Tr.4**
P. misjai (av)	9	28.665	5.222	2.013	5.666	3.087	0,182	0.071	0.198	0.108
P. tisiphone (av)	10	30.128	7.158	3.334	7.829	2.185	0,238	0.111	0.26	0.073
stdev (*misjai*)		1.544	0.393	0.418	0.327	0.24	0,013	0.018	0.018	0.007
stdev (*tisiphone*)		1.142	0.517	0.491	0.513	0.262	0,015	0.018	0.013	0.008
t. test, P value *misjai-this.*		**0.041**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**0.0002**	**< 0.001**	**< 0.001**

C. Morphometric analyis of female wing traits

	Samples (N)	**Trait 0**	**Trait 1**	**Trait 2**	**Trait 3**	**Trait 4**	**ratio Tr.1**	**ratio Tr.2**	**ratio Tr.3**	**ratio Tr.4**
P. misjai (av)	9	30.45	1.337	9.29	4.56	6.358	0.044	0.305	0.15	0.209
P. tisiphone (av)	10	30.56	3.74	9.238	3.041	3.205	0.122	0.302	0.1	0.105
P. orestes (av)	4	32.42	0.712	9.772	5.046	9.223	0.022	0.302	0.156	0.284
stdev (*misjai*)		1.135	0.147	0.398	0.399	0.77	0.006	0.011	0.011	0.022
stdev (*tisiphone*)		0.86	0.924	0.68	0.794	1.265	0.029	0.02	0.026	0.042
stdev (*orestes*)		0.649	0.265	0.249	0.116	0.842	0.008	0.01	0.002	0.024
t. test, P value *misjai-this.*		0.821	**< 0.001**	0.834	**< 0.001**	**< 0.001**	**< 0.001**	0.678	**< 0.001**	**< 0.001**
t. test, P value *misjai-orest.*		**0.004**	**0.012**	**0.03**	**0.011**	**0.002**	**0.005**	0.576	0.193	**0.002**
t. test, P value *this.-orest.*		**0.003**	**< 0.001**	**0.038**	**< 0.001**	**< 0.001**	**< 0.001**	0.925	**< 0.001**	**< 0.001**

taken from populations in Greece and Albania show intermixed habitus' traits, but are all different compared to those of voucher samples taken from central Albania, here being described as *P. misjai* sp. nov.

Systematic position

A phylogenetic analysis based on mtDNA barcoding of the COI gene of different *Pseudochazara* taxa occurring in the Balkan peninsula is given in Fig. 7. The systematic reconstruction revealed three, deeply diverged clusters, i.e. the '*P. pelopea*' and '*P. hippolyte*' species group, and *P. amalthea* in an intermediate position between the two groups. This is fully in agreement with the results obtained by Verovnik & Wiemers (2016). Also, in agreement (related to their position, and similar levels of posterior probability scores), when focusing on the *P. hippolyte* species group, our phylogenetic reconstruction showed monophyly of three known lineages, attributed to *P. cingovskii*, *P. tisiphone* and *P. orestes*, with the former at the basic position. However, a fourth monophyletic lineage was found to split *P. orestes* into a second well-diverged lineage, grouping all samples from the central Albanian populations together. This distinct monophyletic lineage is separated from *P. tisiphone* at its basis and from *P. orestes*, with strong posterior probability scores. The position of the distinct new lineage can be situated in between *P. tisiphone* and *P. orestes* based on its mitochondrial DNA, and therefore shows a consensus with the morphometrics of males and females. It is also worth mentioning that, while a deep divergence split between the species groups is present, within these groups a lower genetic interspecific distance is observed; also within the '*P. pelopea*' species group, which shows the lowest genetic divergence of all between *P. graeca coutsisi* Brown, 1977 and *P. amymone* (Brown, 1976). Based on the aforementioned results, we describe here a new taxon *Pseudochazara misjai* Parmentier sp. nov.

Description

Male

Upperside. Forewing length 26–29 mm, comparable to *P. cingovskii*. Markings similar to those of *P. cingovskii*, with a narrower postdiscal band and zig-zag pattern at the median position more rounded compared to *P. tisiphone* and *P. orestes*. Forewing with prominent white ocelli in S3–S4, and two white-pupilled ocelli in S2–S3 and often S4. Brown marginal borders 3–4 mm wide on hindwings, generally thicker than *tisiphone*. The ground colour is brownish-grey with an orange haze, and the sex brand is distinctive with a reflecting greenish-grey tone (especially when put in an oblique position and in full sunlight). Well-defined fulvous orange postdiscal band variably dusted with brown and broken along veins by ground colour, especially along v4 of the forewing. Fringes grey, tipped white.

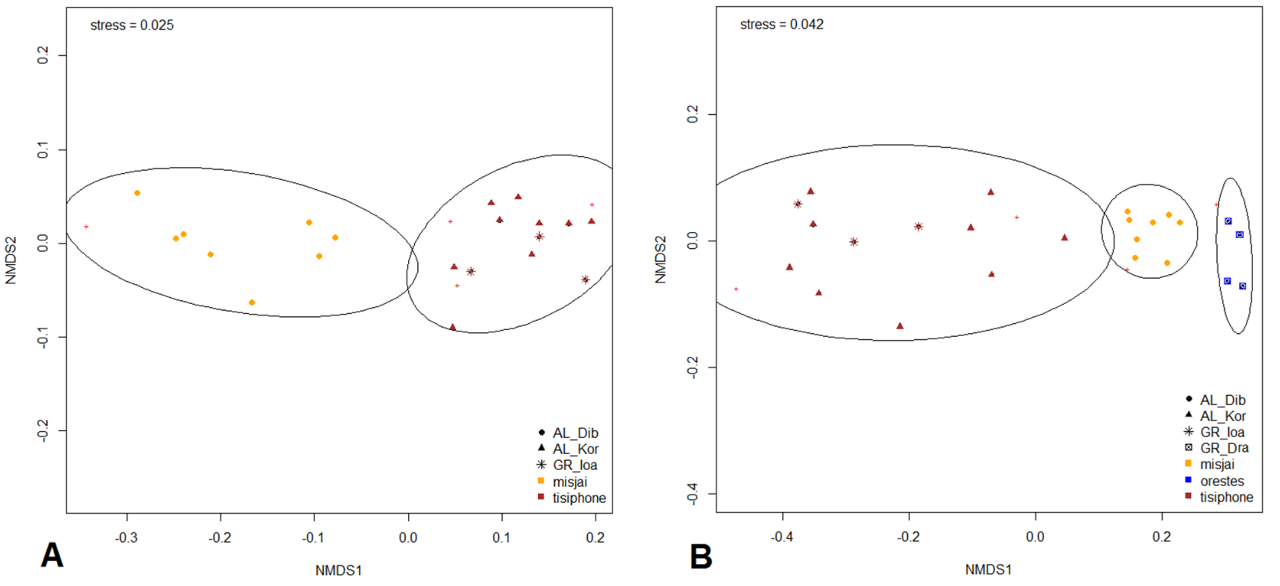

Fig 6. NMDS plots based on morphometrics of all wing traits (see text for details), visualized per sexe. A, males, B, females; Colours represent different species; symbols represent different regions where the samples were taken: AL_Dib = Albania, Dibër prov.; AL_Kor = Albania, Korçë prov.; GR_Ioa = Greece, Ioannina distr.; GR_Dra = Greece, Drama distr.

Underside. Ground colour dusky yellow-brown to dirty yellow. Underside markings of forewing similar to that of *P. tisiphone*. The discal line on the forewing is less marked compared to *P. cingovskii* and *P. orestes*. The base of the forewing is uniform yellowish-grey. Often a small ocellus in S3 and a smaller white ocellus in S4. Hindwing irrorate with fine darker markings and a prominent darkened line at the marginal position, more pronounced compared to *P. tisiphone*. Traces of a pale yellow postdiscal band occur after the vestigial grey discal and postdiscal lines.

Female

Similar but larger, forewing length 29–32 mm. Upperside markings of females resemble *P. orestes* more, with a reduced brown zone at vein M_4 between the small ocelli in cells 2 and 5 and positioned within the orange postdiscal band of the forewing, intermediate between *P. orestes* and *P. tisiphone* (see Fig. 2).

Characters of anroconial scales

The average androconial scale length (AL) and breadth (AB) for *P. misjai* sp. nov. was determined at 0.30 mm and AB 0.022 mm, respectively, and the ratio (AL/AB) was 13,82 (Fig. 5, and Table 1A). The shaft is narrow, gradually getting narrower towards the end. The AL is similar, but the AB and ratio is different from *P. tisiphone*. Classified according to the list of Gross (1978), the ratio can be attributed to class 1–2.

Holotype

♂ 18.vii.2017, Krastë near Bulqizë, Dibër prov, eastern belt of the Mirdita zone in the Inner Albanides Massif, Albania, 1000 m alt., Laurian Parmentier, leg. & coll. The holotype will be deposited in the collection of the Royal Belgian Institute of Natural Sciences (RBINS) in Brussels, Belgium.

Allotype (no name-bearing function see ICZN Recommendation 72A)

♀ 19.vii.2017, Bulqizë, Dibër prov, eastern belt of the Mirdita zone in the Inner Albanides Massif, Albania, 950 m alt., Laurian Parmentier Leg. & coll.

Paratypes

5 ♂, same locality as HT, but collecting dates 18-19.vii.2017, L. Parmentier, leg. & coll.;

3 ♀, same locality as HT, but collecting dates 18-19.vii.2017, L. Parmentier, leg. & coll.;

15 ♂, same locality as HT, but collecting dates 17-20.vii.2023, L. Parmentier, leg. & coll.

11 ♀, same locality as HT, but collecting dates 17-20.vii.2023, L. Parmentier, leg. & coll.;

2 ♂, Lurë Nnational Ppark, near Fushë-Lurë, 21.vii.2022, X. Qirinxhi, leg. & coll.;

1 ♂, Lurë N national Ppark, near Fushë-Lurë, 24.vii.2023, L. Parmentier, leg. & coll.;

2 ♀, Lurë N national Ppark, near Fushë-Lurë, 21.vii.2022, X. Qirinxhi, leg. & coll.;

3 ♂, 13.vii.2017, Bulqizë, Dibër prov., Albania, samples in RVcoll, with coll nrs 14U545, 14U546, 14U547 and barcodes available in Genbank, with accession numbers MW499272.1, MW500121.1 and MW502978.1.

COI sequence of the holotype

AACTTTATATTTTATCTTTGGAATTTGAGCAGGTATAGTA
GGTACATCTCTTAGTTTAATTATTCGAACAGAATTAGGTAAC
CCAGGGTTTTTGATTGGAGATGATCAAATTTATAATACTATC
GTTACAGCTCATGCTTTTATTATAATTTTTTTCATAGTGATAC
CTATCATAATTGGAGGATTTGGAAATTGACTTGTTCCTCTTAT
ACTAGGAGCTCCTGATATAGCTTTCCCCCGAATAAATAATAT
AAGATTTTGACTCTTACCCCCTTCTTTAATATTATTAATTTCAA
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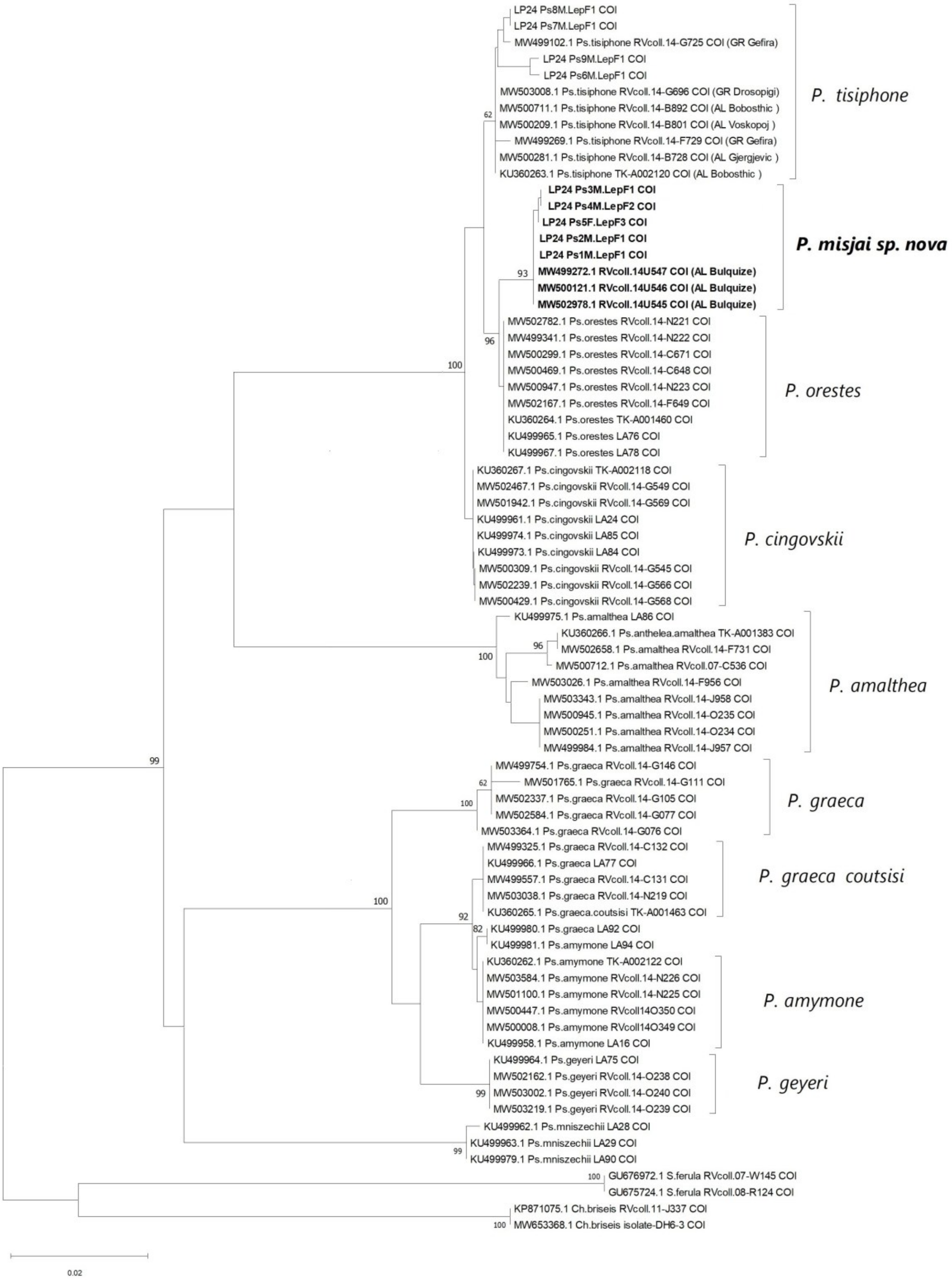

Fig. 7. Genetic analysis based on mtDNA barcoding of the COI gene of *Pseudochazara* taxa occurring in the Balkan peninsula, with the position of the monophyletic clade representing the new taxon *P. misjai* sp. nov. indicated in bold. Posterior probability scores > 60 are given next to each clade.

GTAGATTTAGCTATTTTTTCTCTCCATTTAGCTGGAATTTCCTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAACATACGAGTTAATAGTATAACTTATGATCAAATACCCTTATTTGTATGAGCTGTAGGAATTACAGCCTTATTATTATTACTTTCTCTTCCAGTATTAGCAGGAGCTATTACTATACTTTTAACAGATCGAAATTTAAATACCTCCTTTTTTGATCCTGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT

Etymology

The species is named after the late Prof. Kastriot Misja, 1933–2022, who was born in Elbasan, Albania and dedicated his whole life to studying Albanian butterflies in their natural habitats. Prof. Misja launched the first distribution atlas for Albania in 2005. The first author initially met him in 2017, when visiting the Faculty of

Natural Sciences at Tirana University, together with Prof. Anila Paparisto, and remembers his passionate stories, but also the difficulties when trying to publish a free work such as a natural history atlas of Lepidoptera back under the strict communist regime. A few days later, the new taxon was discovered near Krastë in central Albania.

Discussion

Habitus compared to sister taxa

Our analysis of habitus' traits of (barcoded) voucher specimens revealed that *P. misjai* sp. nov. exhibits both discriminative and intermediate traits between *P. orestes* and *P. tisiphone*. Morphometric results for males and females generally support this placement. While the overall habitus of the new taxon is closer to *P. tisiphone*, some traits show relatedness with *P. orestes*, in particularly Trait 3 in females ("The forewing width at the narrowest position of the submarginal band"). It is worth mentioning that one trait (Trait 1) did not discriminate at all between the three investigated taxa, i.e. "Forewing width of the submarginal band across the centre of the ocellus in cell S2", while this trait was included based on earlier research that proved to be a good diagnostic element between *P. tisiphone* and *P. amymone* males and females (Cuvelier & Mølgaard 2015). This reconfirms the observation made by De Prins & van der Poorten (1981) that there probably exists no specific trait that is as discriminative enough for the whole *Pseudochazara* species group, and that the selection of habitus' discriminative traits is probably only valid for a specific subcluster of species. Besides, for males, we showed that the androconial scale breadth (AB) and ratio (AL/AB) are unique and different from *P. misjai* sp. nov. and *P. tisiphone,* based on a good number of measurements of voucher specimens from scattered populations that represent the full known distributional range of the two taxa. When the androconial scales of *P. misjai* sp. nov. are classified according to the list of Gross (1978), the ratio can be attributed to class 1-2. Considering the androconial ratio of other closely related taxa, this is again an important difference between *P. tisiphone* and *P. orestes* as their androconial scale ratio was attributed to class 5 according to the same list. In contrast, the AL/AB ratio of *P. misjai* sp. nov. more resembles that of *P. cingovskii*, also attributed to the class 1-2 (Gross 1978; De Prins & van der Poorten 1981). This is remarkable as, based on habitus' traits, the new taxon generally more resembles *P. tisiphone*. We, therefore, stress that *P. misjai* sp. nov. is a cryptic taxon, sister to species *P. tisiphone*, *P. orestes* and *P. cingovskii* with similar but not identical morphologic traits.

In this study, our biometric analysis was based on classical microscopic measurements of habitus and male sexual traits. Our obtained results made it possible to compare the biometrics of related taxa described in the literature. Yet, recently, new insights have been published based on TEM microscopic measurements of butterfly scales, including the fine ultrastructure of androconia and surrounding wing scales that provide a basis for the delimitation of genera and species (Pan *et al*. 2022). Besides, in butterfly behavioural experiments, different studies have shown that the pheromone(s) released from the scent organs (androconia) plays a decisive role in the identification of related species (Andersson *et al.* 2007; Ômura *et al.* 2015; Darragh *et al.* 2017, 2019)also between sympatric cryptic taxa, as has been shown for the two cryptic Graylings species *Hipparchia fagi* Scopoli, 1763 and *Hipparchia hermione* Linnaeus, 1764 (Pinzari *et al.* 2018). Here, we did not investigate voucher specimens at this ultramicroscopic level, but this could also be an interesting element of study for biometric delimitation of closely related taxa such as those classified under the *Pseudochazara* genus.

Taxonomic position compared to sister species

The recent mitochondrial atlas of genetic diversity maximises the coverage of specimens and their mitochondrial genetic diversity per species throughout Europe. Here, it was already indicated that the *Pseudochazara* populations from central Albania represented a distinctive and unique haplotype compared to those populations situated in the Korçë region, known as *P. tisiphone*, as also a few samples from Bulqizë, Dibër prov. were included (taken from the 2018 expeditions) (Dapporto *et al.* 2022). In Cuvelier (2023) the genetic diversity map for *P. tisiphone* is reproduced, but no additional morphometric nor genetic analysis was added in this article, and so the same conclusion as in the updated edition of the atlas for Albanian Lepidoptera ("Fluturat e Shqipërisë") is repeated (Cuvelier *et al.* 2023), while it was also noted that the central Albanian population near Bulqizë, harbours a unique evolutionary unit (ESU) that needs further study.

Based on many voucher samples taken from different populations across the western Balkans, we demonstrated a clear phylogenetic split in the lineages formerly put together as *P. tisiphone*. Specifically, a distinct lineage encompasses all specimens from populations in the central-eastern part of the Albanides Massif, which is closely related to *P. orestes* and *P. tisiphone*, and with a strong supporting resolution (high posterior probability scores). However, with only about a 1% difference, the genetic distance between these sister taxa remains low regarding the average genetic distance between species within the *Pseudochazara* genus (see Takáts & Mølgaard (2016) for systematic delimitation of the complete genus). In this regard, one could argue that the new taxon should be treated as a subspecies. Following this rationale, based on its systematic position, it could best be positioned as a subspecies of *P. orestes*. Alternatively, *P. misjai* sp. nov. also could be treated as a subspecies of *P. tisiphone*, the other closest sister species. However, both these two alternative taxonomic positions would generate additional consequences. Firstly, if it were to be treated as a subspecies of *P. tisiphone*, then paraphyly of the taxon to sister species *P. orestes* is created, which is not the best option from a taxonomic point of view. Secondly, when treated as a subspecies of *P. orestes*, a strange distributional range would be created artificially as these two populations are the farthest separated (about 500 km distance). A third alternative solution would be to interpret the subcomplex as four intraspecific taxa if the polytypic species complex concept is applied (Lukhtanov *et al.* 2015). In this case these taxa would all be subspecies under the *P. cingovskii* species complex in the western Balkans. However, this would suggest putting at least *P. orestes* and *P. tisiphone* in a former taxonomic position that has been argued by multiple entomologists to be incorrect, especially when also considering their morphometric differences (Brown 1976; De Prins & van der Poorten 1981; Takáts & Mølgaard 2016; Verovnik & Wiemers 2016).

Here, and based on specific morphometric differences between *P. misjai* sp. nov., *P. orestes* and *P. tisiphone*, its isolated distribution, together with its distinct monophyletic taxonomic position, *P. misjai* sp. nov. is best to be treated as a new bona species, also following the current accepted taxonomical insights in the genus. In the context of the low genetic distance between these four sister taxa, it is valuable to also consider the position of some other taxa, in the '*P. mamurra*' species group (see COI relationship tree, Fig. 7), i.e. that of *P. amymone* with *P. graeca coutsisi,* and *P. mamurra* in Turkey: these sister taxa show even overlap in haplotypes, with a very low genetic interspecific difference but are still regarded as bona species based on their biomorphometric differences (Verovnik & Wiemers 2016). In general, it is clear that the majority of the *Pseudochazara* taxa occurring in the Balkans have evolved only recently. Further genetic studies based on full genome sequencing data would be interesting to have a better view of their evolutional relationship and to confirm the taxonomic positions of the different species that are currently based on their biometric differences and spatial distribution patterns.

Distribution pattern of ophiolitic habitats in the western Balkans

Since the publication by Eckweiler in 2012, the distribution range of *P. tisiphone* was also broadened from north-eastern Greece to the south-western ophiolitic Mirdita zone of the Albanides Massif in Albania (Eckweiler 2012), and in subsequent years confirmed by us and various other entomologists in other places, but all in the same area. Cuvelier *et al*. (2018, 2023) reported a very remarkable extension to this known distribution range in the new distribution atlases of Albania. However, we have shown here that these little-known central Albanian populations actually represent a new cryptic species with its own distribution range and separated from that of *P. tisiphone* by at least 130 km. Currently, there have been no intermediate populations found, despite targeted searching efforts by us and other entomologists (pers. comm.). Consequently, the distribution range of *P. tisiphone* should be reduced again to its former known range. While we cannot guarantee that new population(s) of both taxa could be found in the future, based on our observations it is highly uncertain that a direct contact zone between the two species will be found, concluding an allopatric evolution as being the most likely. Mapping the four Balkan species within the '*P. hippolyte*' group, based on all available observations to date, reveals that three species — *P. orestes*, *P. cingovskii*, and *P. misjai* sp. nov. — have very restricted and similarly-sized distribution ranges. Additionally, the distribution range of *P. tisiphone* is also quite limited given the vast mountain massifs of the Balkans. Moreover, it is remarkable that three species can be situated in a zone with a radius of less than 100 km, i.e., *P. misjai* sp. nov. in central Albania, *P. cingovskii* in southern NMK, and *P. tisiphone* south of Lake Ohrid. This observation was also noticed by Brown (1981) when he described *P. tisiphone* as a separate taxon (Brown 1981), with the consequence that "a distance of only about 80 miles separates the Jugoslavian [currently: NMK] population of *P. cingovskii*", and that "it is interesting to speculate on the relationship of both taxa". In his paper, he stressed that the Smolikas Mountains are significantly isolated from the mountains of the NMK Massif where *P. cingovskii* is present, because of geographical elements, and that "such a separation seems to be reflected in a considerable endemic element in the area", triggering the evolution towards endemic species. Knowing the generally accepted status of both taxa as bona species (Takáts & Mølgaard 2016; Verovnik & Wiemers 2016). The explanation made by Brown (1981) is interesting, as it could also explain which factors may have played the biggest role in determining the distribution pattern of *P. tisiphone* and *P misjai* sp. nov., found in the vast inner Albanides Massif.

The ophiolitic formation of the Albanides, named as Mirdita zone, is generally characterised by 'ophiolites', which are in fact a merging of a bunch of soil types. Indeed, recent research showed that the zone can be separated into two types of ophiolitic belts which can be distinguished based on petrographic, geochemical and metalogenical features: the western and eastern belt of the Mirdita zone (see Suppl. Fig. 2) (Çina 2016). These belts also have another history, geologically. Additionally, the two belts are physically roughly divided in the middle by a long steep valley, formed by the Lumi Skumbin River and running from Elbasan town in the central-eastern part to Lake Ohrid in the western part. During the Jurassic period, the most important geological event of Albania was ocean spreading in the Mirdita zone, and the western belt is thought to have been composed of an ocean ridge, while the eastern belt by the development of an immature island arc (Beccaluva *et al.* 1994). Recent investigations have also evidenced that the different massifs of the western ophiolitic formation, i.e. where the habitats of *P. tisiphone* are situated, represent an evident variation of their composition from harzburgite to lherzolitic-types, and with periodite (Al_2O_3) as the main component. On the contrary, the Albanian eastern belt, to which the Bulqizë and Lurë Massifs belong, with habitats for *P. misjai* sp. nov., was formed by a more homogeneous harzburgite mantle, and with Jurassic sediments of karst (lime) layers. Here, chemical analysis also showed elevated levels of magnesium in the soil. The sedimentation (and mixture) of paler lime may also explain why the habitats of Lurë and Bulqizë-Krastë are slightly more yellowish brown compared to those found in, for example, Bobosthicë and Gjergjevicë, which are generally more dark-red brown. Additionally, in the geological study of Çina (2016), an interesting link is made with the composition of Greek mountain massifs, and of the eastern belt, a comparison was made with the Voúrnios Massif (northern Greece), while the western belt composition was closely related to the Greek Pindos Massif (western Greece). Important to mention here, is, that in the latter Greek Massifs, *P. tisiphone* populations are also present, but not in the former. While we do not have information on the exact impact of (chemical) soil type composition on grass species growth and their composition, as being the major food plants for the developing *Pseudochazara* larvae, it is still a valuable observation that could also explain a possible different co-evolution between the two species and their typical habitat with unique soil characteristics.

Generally, it seems that many of these isolated taxa are relict populations that evolved independently and dependent on their environment (Brown 1976). Indeed, the habitus of different isolated *Pseudochazara* species shows an important co-evolution with their rocky habitat, more specifically the colour of their hindwings reflects the colour of the stones and soil substrate to make them better camouflaged (De Prins & van der Poorten 1981). Related to *P. misjai* sp. nov., we compared the underside of a series of specimens with *P. tisiphone*, and noticed that the ground colour is more yellowish, compared to the generally darker-grey ground tone of *P. tisiphone* (Fig. 3), a habitus element that was also nicely illustrated by pictures for the other aforementioned species when sitting with closed wings in their specific rocky habitat (Takáts & Mølgaard 2016). Since for *P. misjai* sp. nov. these differences are subtle, and we did not perform exact colour measurements on hindwings (as other wing traits were more pronounced and found significantly different), it is still an observation in agreement with the rationale of an isolated population that co-evolved within its unique habitat. Further research on the impact of soil substrate, feeding plant composition and active genes in developing larvae within the genus of *Pseudochazara* could be interesting to untangle this unique relationship and possible co-evolution.

Conservation of Albanian biotopes

It is clear that the different *Pseudochazara* species in the western Balkans have specific requirements and are only present in a restricted area with suitable biotopes. Here, Albania plays a key role in conservation as the eastern belt of the Mirdita zone in the Inner Albanides Massif in central Albania is most likely the only area where suitable biotopes for *P. misjai* sp. nov. can be found. Together with Greece and NMK, each harbouring at least one endemic *Pseudochazara* species that only occurs on their territory, these countries play a key role in the conservation of these unique habitats, also being the stronghold for the genus in the Balkans. In contrast to Greece, part of the EU nature conservation scheme (Maes *et al.* 2019), and NMK, where *P. cingovskii* also gains a specific conservation status (Verovnik *et al.* 2013), to date, no specific nature conservation plans have been set up in Albania.

Since this small country harbours a unique and very high degree of biodiversity (e.g. more than 40% of European butterfly species are present, with a country surface of less than 0.5% of Europe), Albanian biotopes are certainly vulnerable to anthropogenic influence. Heavy mining and road widening activities are present in the immediate vicinity of *P. misja* sp. nov. biotopes situated in the Krastë-Bulqizë area, as illustrated in Fig. 3A. These industrial and transport activities certainly have a big impact on the population of the new species described in the present article. Besides, for the Lurë region, another human impact can be seen from the grazing intensity of sheep and goats. Grazing and farming can have a negative impact on the population survival; it has been reported for another endemic species found in the same region (Parmentier *et al*. 2022). Despite being situated in a National Park (Parku Kombëtar Lurë-Mali i Dejës) since 1966 to protect its ecosystems and biodiversity, local farmers still use many parts of it for grazing their livestock, without control or schemes, leading to overgrazing of the biotopes. While traditional grazing by small livestock can be beneficial, uncontrolled and overgrazing can have a devastating impact on butterflies, and other important insects such as bees; this fact has been increasingly reported in different parts of Europe (Kruess & Tscharntke 2002; Potts *et al.* 2009; Verbrugge *et al.* 2022). Indeed, even for countries which are part of the stricter EU nature protection program, such as Greece, overgrazing causes a serious threat; it seems that overgrazing becomes worse with climate change and drought more prominently affecting biotopes (own observations). Together with the further development of economic activities, such an evolution in Albania would be dramatic for its unique, biodiverse ecosystems refuging rare endemic species amongst an extended list of other species that can still be found in good numbers. We, therefore, argue that at least the Albanian endemics should be added to the national and European Red List of Butterflies to fully protect them (Van Swaay *et al.* 2010; Maes *et al.* 2019). As Albania's horizon is to become a member of the European Union, installing adequate nature legislation is strongly encouraged and it will be needed (e.g. EU Council Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora) to safeguard the rich biodiversity heritage of Albania for future generations.

Conclusion

In this paper, we present new insights for:

1) distribution data of *Pseudochazara* populations extracted from literature and obtained from our own expeditions in Albania and bordering regions in Greece and NMK;

2) a phylogenetic study based on COI barcoding integrating all Balkan *Pseudochazara* species and samples from different populations;

3) a comprehensive morphometric analysis of voucher specimens covering different populations in the western Balkans.

Our integrative approach showed significant differences between the central Albanian populations as compared to those situated in south-eastern Albania and north-western Greece, i.e. topotypical *P. tisiphone,* and closely related taxa *P. orestes*, situated in western Greece, and *P. cingovskii* in North Macedonia near Prilep. Based on this integrative analysis, and following the current taxonomic insights into the genus (Verovnik & Wiemers 2016), we concluded that the isolated *Pseudochazara* populations, situated in the eastern belt of the Mirdites in the Inner Albanides Massif in central Albania, should be regarded as a new, cryptic species, which we named after the late professor Misja Kastriot, *Pseudochazara misjai* Parmentier sp. nov.

Due to the taxonomic challenges in the genus posed by closely related sister taxa within the '*P. mamurra*' species group, as discussed in this paper, as well as the '*P. hippolyte*' species group, which exhibits sometimes low interspecific genetic variability and overlapping habitus traits, taxonomists may arrive at different interpretations, even if current nomenclature represents allopatrically evolved populations. Therefore, we encourage further study of the genus in the Balkans, integrating new analytical techniques, such as whole-genome sequencing for multi-locus comparisons, to confirm and refine current taxonomic insights.

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Supplementary material

S1. Extended images with details of androconial scale measurements of different populations investigated in this study; of each population at least one sample is shown.
Zie — http://www.phegea.org/Phegea/Appendices/Phegea53-1_S1.pdf **216 KB**

S2. Albanian ophiolitic formation with the indication of the eastern belt of the Mitdita zone.
Zie — http://www.phegea.org/Phegea/Appendices/Phegea53-1_S2.pdf **418 KB**

S3. Measurements of habitus traits of males and females, used in this study and calculated by the NMDS analysis as given in the main text.
Zie — http://www.phegea.org/Phegea/Appendices/Phegea53-1_S3.pdf **155 KB**