



Monograph

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Review of the fritillary species systematically close to *Melitaea lutko* Evans, 1932 (Lepidoptera: Nymphalidae) with analysis of their geographic distribution and interrelations with host plants

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Abstract. This review considers a fascinating, from a zoogeographical viewpoint, group of closely related species: *Melitaea lutko* Evans, 1932, *M. timandra* Coutsis & van Oorschot, 2014, *M. mimetica* Higgins, 1940 stat. rev. and *M. shahvarica* sp. nov. It is a taxonomical and geographical review of these species, and data on the biology of *M. shahvarica* sp. nov. and nominate subspecies of *M. timandra* are discussed. A new species, *M. shahvarica* sp. nov. from Shahvar Mt. (Iran), and a new subspecies, *M. timandra binaludica* subsp. nov. from Kuh-e-Binalud Mts (Iran), are described. The specific structure of the group given in previous publications is critically evaluated. Hypotheses about a possible phylogenesis of the study group are provided.

Keywords. Nymphalinae, taxonomy, phylogenesis, coevolution, adaptation.

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Introduction

The taxon *Melitaea robertsi lutko* from Chitral (Pakistan) was described by Evans (1932) as a subspecies of *Melitaea robertsi* Butler, 1880. Higgins (1940) considered *M. lutko* to be a well-differentiated species and described the subspecies *mimetica* from Balochistan (Pakistan). In addition to differences in external morphology, Higgins identified the main differences in the structure of the male genital armature. He noted that the caudal process of valva in *M. mimetica* is more slender and less curved inwards, and the long and thin harpe lacks teeth on the inner side, in contrast to *M. lutko*. Higgins also pointed out differences in the structure of the saccus in both taxa, noting, however, that the development of the saccus in different specimens varies (Higgins 1940, 1941).

The taxon *Melitaea delerei* Heydemann, 1954 from Afghanistan, which is systematically close to *M. lutko*, was described as a different species (Heydemann 1954). This report presents black-and-white

photographs of the male and female, as well as a drawing of the male genitalia. Based on external morphology and genitalia structure, the taxon *M. delerei* was considered as a synonym of *M. lutko mimetica* (Higgins & Wiltshire 1956), either as one of the subspecies of *M. lutko* (Sakai 1981) or as a synonym of the nominative subspecies (Balletto & Kudrna 1989).

Later, Higgins (1981) assigned the species status for the taxon *mimetica*, apparently on the basis of differences in male genitalia. However, Higgins did not specify the reasons for such taxonomic rearrangements. At first, this position was not understood by researchers who touch upon the systematics and distribution of *M. lutko* (Devyatkin & Tuzov 1988; Tuzov 1993), and the taxon *mimetica*, to which these authors attributed the Turkmenian population, was considered by them as a subspecies of *M. lutko*. Later, the species status of the taxon *mimetica* was restored (Tuzov & Churkin 2000) but without explaining the reasons for this rearrangement.

Van Oorschot & Coutsis (2014) published a fundamental work on the genus *Melitaea*, with a description of *M. timandra* Coutsis & van Oorschot, 2014 from the territory of Turkmenistan, systematically close to *M. lutko*. However, the justification and interpretation of the stated facts raise many questions and doubts. When studying *M. lutko* from different populations, van Oorschot & Coutsis stated the following: on the territory of Afghanistan (Koh-i-Baba Mts) and Pakistan (Balochistan), there are populations of butterflies in which male genitalia are generally characterized by a slender and long caudal process of valva and a long harpe without teeth on the inner side. This type of structure of the male genitalia was called type ‘A’. Other specimens of *M. lutko* from populations in Afghanistan (Koh-i-Baba Mts) as well as Turkmenistan, on the contrary, are usually characterized by a short and wide caudal process of valva and harpe armed with a large number of powerful teeth on the inner side (type ‘B’). Some male specimens from Afghanistan (Koh-i-Baba Mts, Firyuzkuh and Panjshir Valley) and from Pakistan (Balochistan) have genitalia intermediate in structure between types ‘A’ and ‘B’. Transitional specimens were not found among the populations of *M. lutko* from Turkmenistan. Based on these facts, Van Oorschot & Coutsis believe that male specimens with genitalia type ‘A’ should be considered *M. lutko* proper, and male specimens with genitalia type ‘B’ are described as a new species *M. timandra*. As an argument, van Oorschot & Coutsis refer to their personal experience studying male genitalia in the genus *Melitaea*. In their opinion, the revealed difference in the structure of genitalia of the two populations mentioned above is sufficient to distinguish one of them as a different species. In the opinion of van Oorschot & Coutsis, the transitional type of male genitalia indicates hybridization between *M. lutko* and *M. timandra*.

Van Oorschot & Coutsis (2014) studied 29 male genitalia preparations of a *lutko* species group mainly from Afghanistan and Turkmenistan. Of these, they attributed 10 preparations to *M. lutko*, and the other 10 preparations to *M. timandra* (of which only 7 originated from the territory of Turkmenistan). They attributed the remaining 9 preparations as belonging to males born as a result of hybridization between *M. lutko* and *M. timandra*.

It should be noted that the conclusions made by van Oorschot & Coutsis are based on several assumptions. Based on the concept of inconsistency in the description of the genitalia of *M. lutko* made by Evans (1932) and Higgins (1941), as well as on their own interpretation of the terminology used by Evans for the description of the male genitalia structure, they concluded that male genitalia of the nominative subspecies correspond to type ‘A’. Thus, in their opinion, the male genitalia of *M. lutko* from Chitral (Pakistan) should be characterized by a long, thin caudal process of valva and the absence of teeth on the inner surface of the harpe. And genitalia of the nominative subspecies, depicted by Higgins, are morphologically transitional between the types ‘A’ and ‘B’. These conclusions directly contradict those of Higgins (1941).

The morphological characterization of the male genitalia of *M. lutko mimetica* by Higgins (1940) also raised objections from van Oorschot & Coutsis (2014). First, they state that the genitalia appendages change their shape and degree of curvature when the preparation shrinks. In this respect, the degree of ‘curvature’ of the caudal process of valva and its width when viewed from above (in dorsal aspect) cannot, in their opinion, be a morphological feature. Secondly, the saccus varies within quite large limits, which does not allow using its shape for diagnosis. They also considered the taxon *delerei* as a transition between types ‘A’ and ‘B’ on the basis of the only paratype studied and the analysis of the *delerei* genitalia shown in the figure (Heydemann 1954). From all of the above, the further logic of the authors’ actions is quite predictable. They reduce the two taxa that are systematically close to *M. lutko* to a synonym of the nominative subspecies.

In our opinion, all these complex logical constructions with many assumptions were the result of a lack of collectible material. So, for example, as follows from the text of the examined publication, van Oorschot & Coutsis did not study male genitalia of the *M. lutko* population from Chitral, which belongs to the nominative subspecies.

However, in several subsequent papers on butterflies of Pakistan and Afghanistan (Tshikolovets & Pagès 2016; Tshikolovets *et al.* 2018), the taxa *mimetica* and *delerei* are listed as subspecies of *M. lutko*.

Our research shows that there are four types of male genitalia apparatuses in the studied species group. Two types (types ‘A’ and ‘B’ in the interpretation of van Oorschot & Coutsis) occur together in central Afghanistan, type ‘B’ is also found in Turkmenistan and Iran, and type ‘A’ is found in Pakistan (Balochistan). This is consistent with the opinion of other authors (van Oorschot & Coutsis 2014). Butterflies from Chitral (*M. lutko* proper) are characterized by a special type of genitalia apparatus and represent a separate species. We did not find specimens of males with transitional morphological features of genitalia from type ‘A’ to type ‘B’, or between these types and *M. lutko* from Chitral. Another type of genitalia occurs in specimens from Shahvar Mt. (Iran).

In this report, we propose four different but quite closely related species in the studied species group – *M. lutko*, *M. mimetica*, *M. shahvarica* sp. nov. and *M. timandra* with two subspecies, whose existence is largely due to the isolation of populations and environmental conditions. All four species are well distinguished from each other by the structure of both the male and female genitalia. We also give a detailed description of the preimaginal stages of the existing and newly described taxa, their biology, relationships with host plants, and possible phylogeny scenarios based on our own field and laboratory studies.

Material and methods

Collection material and genitalia preparation

We studied the material stored in the collection of the Entomology Department of the M.V. Lomonosov Moscow State University, that based on our own collections from Iran and Turkmenistan, and that of other collectors from Afghanistan, Pakistan, and Turkmenistan in the collection of the Zoological Museum of Moscow State University (Moscow), as well as material from private collections. In all, we studied 3 ♂♂ and 1 ♀ of *M. lutko*, 79 ♂♂ and 108 ♀♀ of *M. timandra timandra*, 136 ♂♂ and 32 ♀♀ of *M. timandra binaludica* subsp. nov., 53 ♂♂ and 16 ♀♀ of *M. mimetica*, 85 ♂♂ and 22 ♀♀ of *M. shahvarica* sp. nov., including the following type specimens: *M. robertsi lutko* Evans, 1932, holotype ♂, photo (British Museum Natural History, London); *M. lutko mimetica* Higgins, 1940, paratype ♀, photo (British Museum Natural History, London); *M. timandra timandra*, holotype ♂ and paratype ♂, photo (Naturalis Biodiversity Center, Leiden, Zoological Museum), paratypes ♂ and ♀ (Entomology Department of the M.V. Lomonosov Moscow State University); *M. timandra binaludica* subsp. nov., holotype ♂ (State Darwin Museum, Moscow) and paratypes ♂ and ♀ (Entomology Department of the M.V. Lomonosov

Moscow State University); *M. shahvarica* sp. nov., holotype ♂ (State Darwin Museum, Moscow) and paratypes ♂ and ♀ (Entomology Department of the M.V. Lomonosov Moscow State University).

Genitalia preparations were made for most of the male and female specimens. The copulatory organs were dissected according to the standard procedure: the part of the abdomen bearing the genital apparatus was separated from each specimen and placed for maceration for three days in a 10% KOH solution. Then the genitalia were extracted from the alkali, cleaned of muscle and fat tissue, washed sequentially in water and 75% ethyl alcohol, placed in a blister filled with glycerin, and pinned under the corresponding specimen.

Egg collection

The eggs of *M. shahvarica* sp. nov. and *M. timandra timandra* were collected in nature. The eggs of *M. mimetica* and *M. binaludica* subsp. nov. were extracted from the abdomens of collected specimens stored in the museum of Entomology Department of the M.V. Lomonosov Moscow State University. Eggs suitable for taxonomic study were obtained from dry female collection specimens by enzymatic digestion of the abdomen according to the method described by Junker *et al.* (2006). The extracted eggs were washed free from tissue fragments and fat in a detergent solution. The geometry of heavily crushed eggs extracted from old specimens was restored by osmotic shock: the eggs were placed for an hour in a saturated NaCl solution, then in distilled water.

Photography

Genitalia preparations and caterpillars were photographed using a Canon EOS 6D digital camera with a Canon MP-E 65 macro lens. Each object was documented as a series of consecutive shots with a gradually changing focus distance, these later being merged into one image on a personal computer using the Combine ZM focus stacking software.

Butterflies were photographed using a Canon EOS 6D digital camera. The images were processed using Adobe Photoshop.

Scanning Electron Microscopy (SEM)

Material for SEM fixed in a mixture of formaldehyde-ethyl alcohol-acetic acid, cleaned, dehydrated in a graded series of ethanol solutions and acetone, dried in a Hitachi NCP-1 critical point dryer, coated with gold in a Hitachi IB-3 ion spraying unit, and examined using a Jeol JSM-6380 scanning electron microscope.

Keeping of early stages in laboratory conditions

The eggs were kept in Petri dishes on a filter paper substrate until the caterpillars emerged. Caterpillars of younger instars in groups of 10–15 were kept in closed 480 cm³ plastic containers with perforated walls. Starting from the third instar, the caterpillars were transferred into 2000 cm³ plastic containers. The bottoms of the containers were lined with filter paper. The filter paper was changed daily. The caterpillars were kept at room temperature, under natural light and humidity, and with *ad libitum* nutrition. Diapausing caterpillars (20 individuals) were placed in 480 cm³ closed plastic containers with perforated walls. The containers were filled with fragments of sandstone shale, between which the caterpillars were placed. Four containers were placed in a 2000 cm³ open container, the bottom being lined with wet filter paper. To avoid mold formation, the filter paper was changed once each three days. Until the end of September, the diapausing caterpillars were kept darkened at room temperature. In October, the containers were placed for two weeks in a refrigerator at +10°C, then the containers were moved to a refrigerator at +4°C and were kept under these conditions until March–May. Some eggs and caterpillars of different instars were fixed in 75% ethyl alcohol for further photographing and microscopic examination.

Terminology

We use the terminology of Kuznetsov (1915), Hinton (1946), Gerasimov (1952), Niculescu (1965), and Beck (1960) to describe the morphology of caterpillars, and the terminology of Salkeld (1984) was used to describe the eggs. The terminology of the genital structures is given according to Higgins (1941) and of the wing pattern according to Nekrutenko (1985) and Kolesnichenko (1999). The spelling of geographical names, dates, and surnames of collectors on the labels is given unchanged. Data on the distribution of host plants are given in the publications *Flora of the USSR* (Shishkin *et al.* 1954), *Flora of Turkmenistan* (Nikitin *et al.* 1954), *Flora Iranica* (Hedge 1982), *Guide to Middle Asian plants* (Abdullayeva *et al.* 1987), and *Flora of Pakistan* (Hedge 1990).

Abbreviations

The following abbreviations are use in the text:

FW	=	fore wing
HW	=	hind wing
UNH	=	underside of the hind wings
UNS	=	underside of the wings
UPF	=	upper side of the fore wings
UPH	=	upper side of the hind wings
UPS	=	upper side of the wings
UNF	=	underside of the fore wings
t.	=	town
v.	=	village
vall.	=	valley
vic.	=	vicinities
velayat	=	territorial administrative unit in Turkmenistan equal to our district

Institutional acronyms

BMNH	=	British Museum Natural History, London, UK
EDMSU	=	Entomology Department of the M.V. Lomonosov Moscow State University, Russia
ICZN	=	International Code of Zoological Nomenclature
NBC	=	Naturalis Biodiversity Center, Zoological Museum, Leiden, the Netherlands
SDM	=	State Darwin Museum, Moscow, Russia
ZIN	=	Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia
ZMA	=	Zöologisch Museum, Amsterdam, the Netherlands
ZMMSU	=	Zoological Museum of the M.V. Lomonosov Moscow State University, Russia

Results

Class Insecta Linnaeus, 1758
 Order Lepidoptera Linnaeus, 1758
 Family Nymphalidae Swainson, 1827
 Subfamily Nymphalinae Swainson, 1827
 Tribe Melitaeini Newman, 1870

Genus *Melitaea* Fabricius, 1807

Fig. 1–30, Tables 1–6

Our study indicates the existence of four independent species within the complex under consideration: *M. lutko*, *M. mimetica*, *M. shahvarica* sp. nov., and *M. timandra*. The latter species is well differentiated into two subspecies that are isolated both geographically and ecologically.

Melitaea lutko Evans, 1932

Figs 1A–B, 2A, E, I, M, 3H–I, 4E, 5, 16I, 18D–E, 29F, 30

“*Melitaea robertsi lutko*, nov.” – Evans, 1932: 185. Type locality: “Chitral” [Pakistan, Chitral town vicinity, Lutko (= Lutkho) river valley]. The type locality in the work of Evans (1932) is indicated by Chitral without more precise details. The holotype, by the label data, comes from the valley of the Lutko River, along the riverbed where the road runs from the city of Chitral to the settlement of Garam Chashma.

Type material

Holotype (Fig. 1A–B)

We have photos of the holotype ♂ at our disposal with the following labels: “type, *lutko* / Evans” (handwritten label); “WHE – 1932 – 274” (printed label); “Chitral / Lutko v.[alley] / 9000/ 1.06.30” (handwritten label); BMHN.

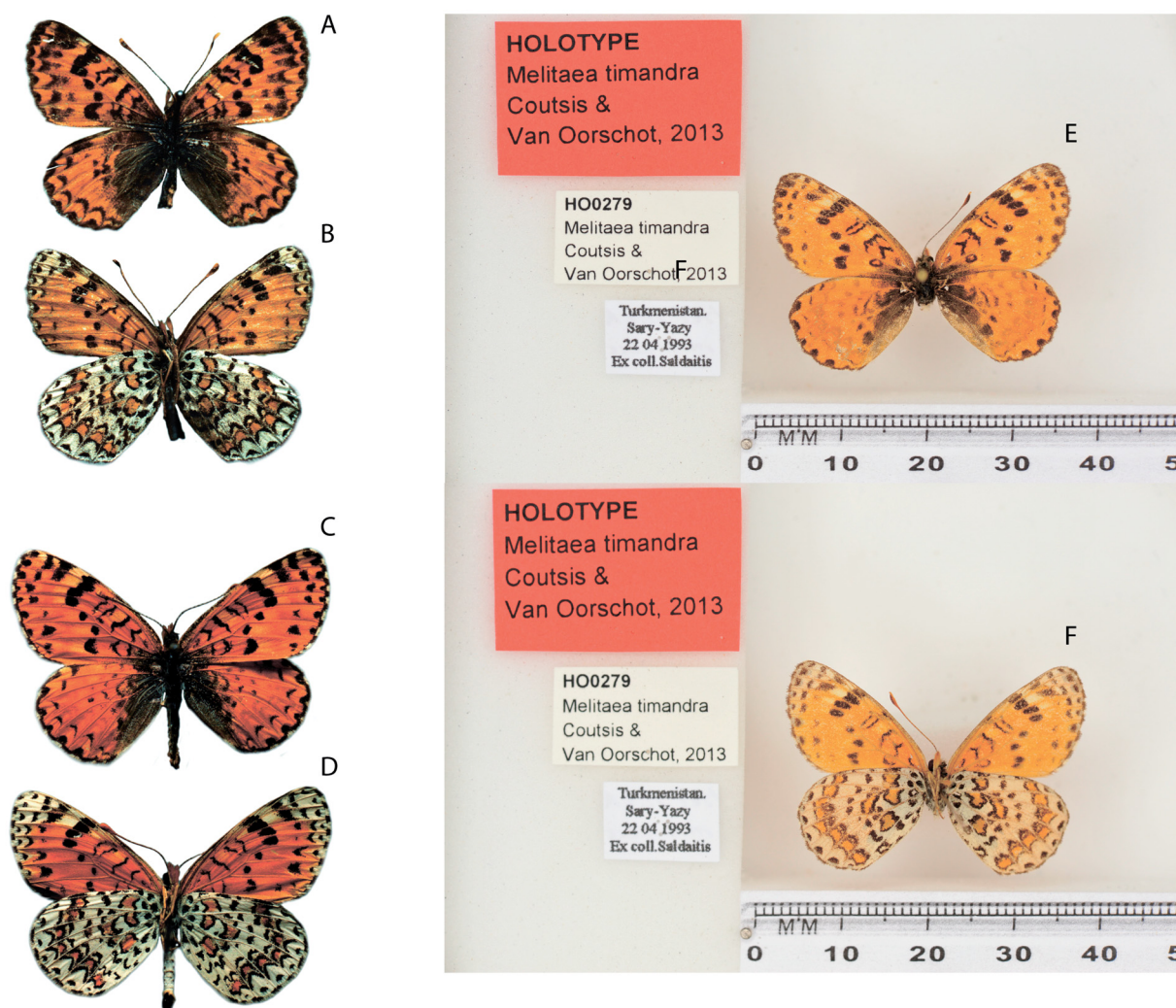


Fig. 1. Type specimens of *M. lutko* Evans, 1932, *M. mimetica* Higgins, 1940, and *M. timandra* Coutsis & van Oorschot, 2014. A, C, E. UPS. B, D, F. UNS. A–B. *M. lutko*, holotype, ♂ (BMNH). C–D. *M. mimetica*, paratype, ♀ (BMNH). E–F. *M. timandra*, holotype, ♂ (ZMA). A–D photos by A. Devyatkin; E–F, by Eulalia Gasso Miracle.

Material examined

PAKISTAN • 2 ♂♂ (all dissected), 1 ♀ (dissected); Chitral, Chaghbini CGNP [Chitral Gol National Park]; alt. 2700 m; 5 Jun.2012; EDMSU.

Redescription

Male (Fig. 2A, I)

WINGS. FW length is 16.5–18 mm, in holotype – 18 mm; UPS ground color is bright red-orange (the holotype, which has faded with time (Fig. 1A), has UPS ground color yellowish-orange); UPS black pattern strongly developed; UPS black marginal border is rather wide with large marginal spots along the outer edge of the wings; UPF submarginal row is well developed and formed by well-defined black strokes, UPH submarginal row represented by lunules often connected with each other (Fig. 1A); UPF

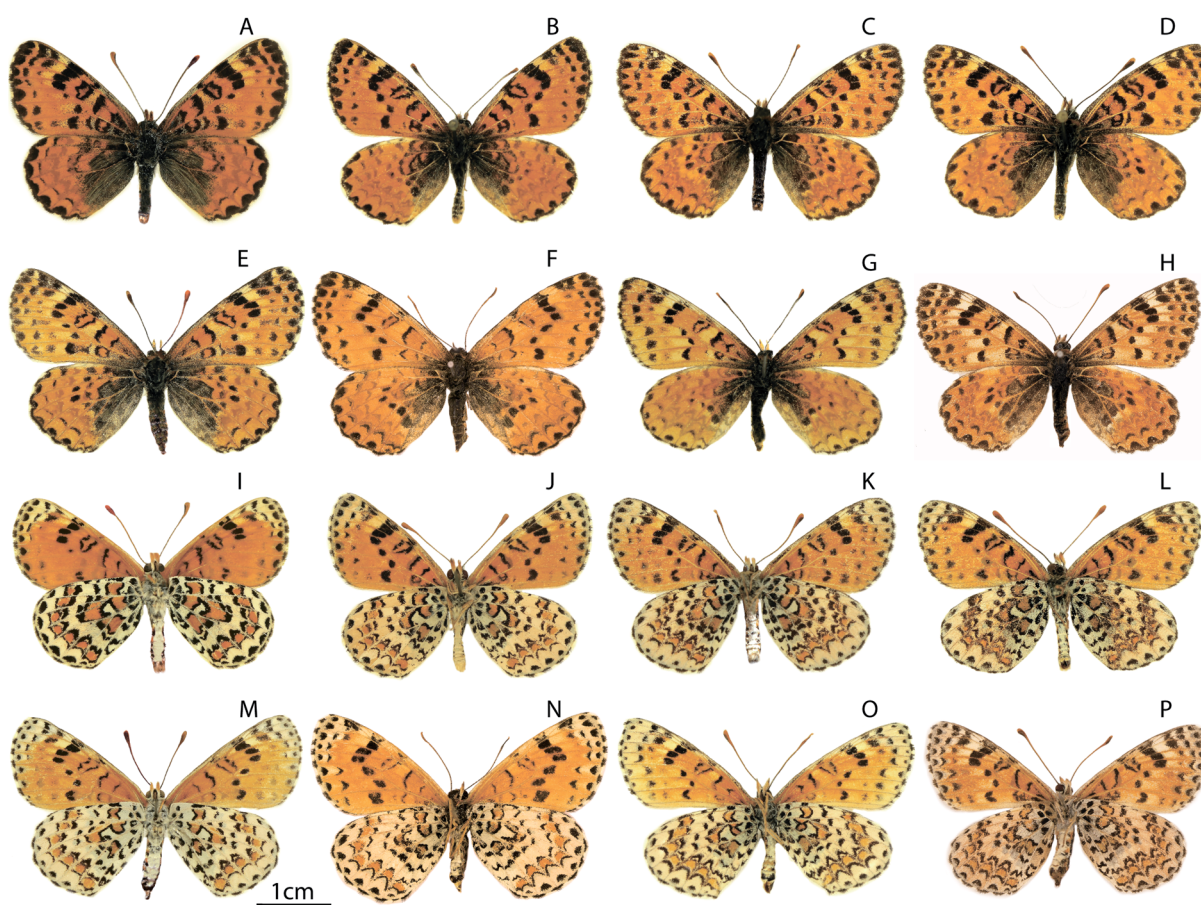


Fig. 2. Adults of *Melitaea lutko* Evans, 1932 and *M. timandra binaluduca* subsp. nov. **A–H.** UPS. **I–P.** UNS. **A, I.** *M. lutko*, ♂, Chitral Gol National Park, Chitral, Pakistan, alt. 2700 m. **B, J.** *M. timandra binaluduca* subsp. nov., ♂, Iran, S Khorasan Prov., 35 km N Birjant t. **C, K.** *M. timandra binaluduca* subsp. nov., ♂, Central Afghanistan, Bamian Prov., Band-e-Amir, Dzhudoi-Kvak Gorge, alt. 3200 m. **D, L.** *M. timandra binaluduca* subsp. nov., ♂, Afghanistan, Bamian Prov., Band-e-Amir, alt. 3200 m. **E, M.** *M. lutko*, ♀, Chitral Gol National Park, Chitral, Pakistan, alt. 2700 m. **F, N.** *M. timandra binaluduca* subsp. nov., ♂, Iran, Mazandaran Prov., S macroslopes of Albors Mts, 80 km SE of Sari, 5 km NE Foulad Mahhaleh v., E slopes of Sultan Kuh Mt., alt. 2000 m. **G, O.** *M. timandra binaluduca* subsp. nov., ♀, Afghanistan, Bamian Prov., Band-e-Amir, alt. 3200 m. **H, P.** *M. timandra binaluduca* subsp. nov., ♀, Central Afghanistan, Bamian Prov., Band-e-Amir, Dzhudoi-Kvak Gorge, alt. 3200 m.

discal spots enlarged and fused near the costa; UPF postdiscal pale-yellowish area, located behind the black discal spots, is weakly expressed or expressed only at the costal edge; UPH discal row is usually absent; UPH black basal suffusion covers more than $\frac{1}{3}$ of the wing surface. Higgins (1941: pl. 9 fig. 5) gives an image of a male specimen from Murree, in which the UPH basal suffusion covers at least half of the wing area. UNF is bright red-orange, with a well-defined pale area of the outer edge of the wing between the veins Sc and M2; UNH ground color is white with an admixture of dark scales. UNH lunules forming the proximal edge of submarginal orange fascia outwardly concave and sharply pointed between veins M3 and Cu2.

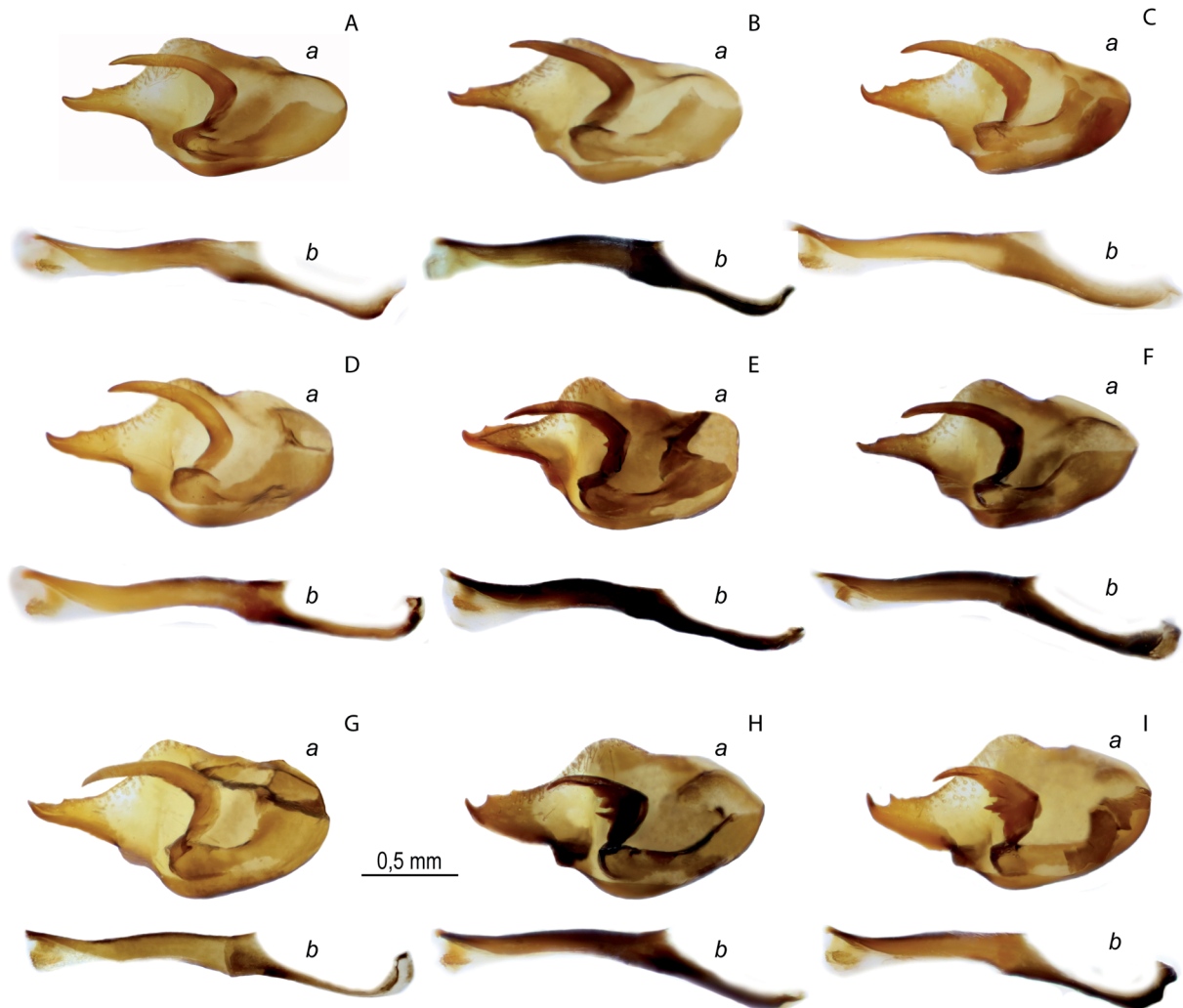


Fig. 3. Male genitalia (a = valva; b = aedeagus). **A–G.** *Melitaea mimetica* Higgins, 1940. **H–I.** *M. lutko* Evans, 1932. **A.** Pakistan, Balochistan, Quetta, Urak, alt. 2400–2700 m. **B.** Pakistan, Balochistan, Quetta, Urak, alt. 2400–2700 m. **C.** Central Afghanistan, Ghor Prov., 17 km E Changcharan, 15 km S of Bandi-Ali, Gazak Mts, alt. 2400 m. **D.** Central Afghanistan, Ghor Prov., 17 km E of Changcharan, 15 km S of Bandi-Ali, Gazak Mts, alt. 2400 m. **E.** Afghanistan, Bamian Prov., 10 km S of Bamian t., Hushkak v. vicinity, alt. 2700–2800 m. **F.** Afghanistan, Bamian Prov., Punjab Distr., 10 km NE of Varas v., alt. 2400 m. **G.** Central Afghanistan, Ghor Prov., 17 km E of Changcharan, 15 km S of Bandi-Ali, Gazak Mts, alt. 2400 m. **H.** Chitral Gol National Park, Chitral, Pakistan, alt. 2700 m. **I.** Chitral Gol National Park, Chitral, Pakistan, alt. 2700 m.

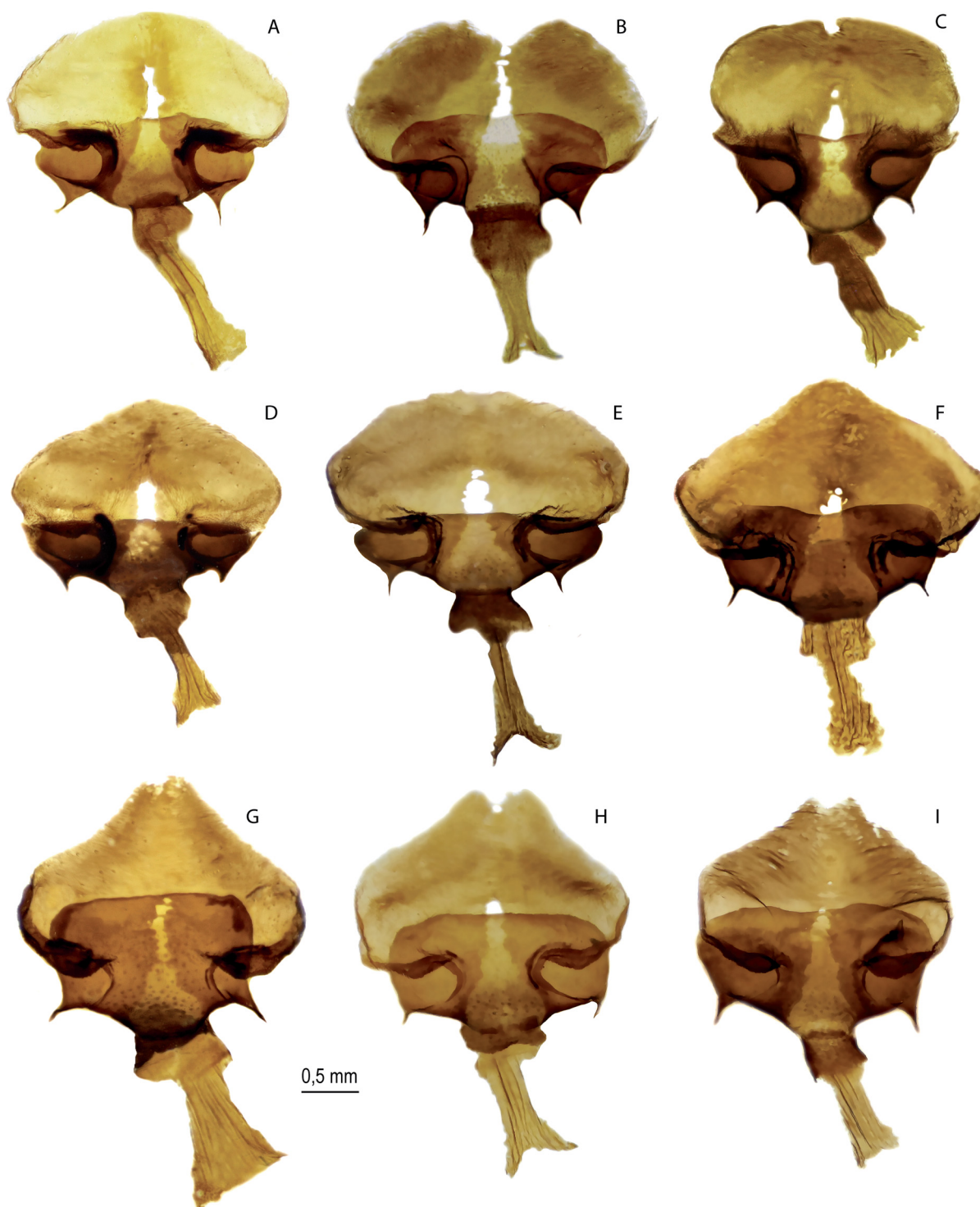


Fig. 4. Female genitalia (without the anal papillae, copulatory bursa, and anterior and posterior apophyses). **A–D.** *M. shahvarica* sp. nov., Iran, Semnan Prov., Shahrud area, S macroslope of Shahvar Mts, alt. 2200–2400 m. **E.** *M. lutko* Evans, 1932, Chitral Gol National Park, Chitral, Pakistan, alt. 2700 m. **F–I.** *M. mimetica* Higgins, 1940. **F.** Pakistan, Balochistan, Quetta, Urak, alt. 2400–2700 m. **G–H.** Afghanistan, Bamian Prov., Punjab Distr., 10 km NE of Varas v., alt. 2400 m. **I.** Central Afghanistan, Ghor Prov., 17 km E of Changcharan, 15 km S of Bandi-Ali, Gazak Mts, alt. 2400 m.

MALE GENITALIA (Figs 3H–I, 16I, 18D–E, 29F). Expanded and powerful caudal process of broad valva with 1–3 small spines on its dorsal surface and with a thin distal outgrowth curved inward. The relatively short harpe is noticeably expanded in the central part, on its inner surface there is a powerful median tooth and smaller teeth on both sides of it. The length of the harpe is about a third of the length of the valva. The aedeagus is distally straight, only slightly curved. The posterior part of the aedeagus is at an angle to the anterior part and is directed downward. There is a protrusion on the ventral side at the junction of both parts of the aedeagus. Saccus is thin, pointed at the top. Higgins (1941) pointed out that the size and shape of the saccus are not constant.

The genitalia of studied males of *M. lutko* generally coincide with the description of Higgins (1941). It should be noted that Higgins made a drawing of the genitalia, placing the valva at another angle (almost perpendicular to the microscope lens) compared to the photos in this review. Because of this, the caudal process of the valva in Higgins' drawings visually looks thinner than it actually is. The originality of Higgins' illustrations was pointed out by van Oorschot & Coutsis (2014).

Female (Fig. 2E, M)

WINGS. FW length is 20 mm. Higgins (1941) noted that the female is usually a little larger than the male. UPS ground color is orange-red. In general, the UPS black pattern is less developed than in males. Higgins (1941) observed slightly melanic female specimens; with UPF postdiscal yellowish-pale area expressed, there is also a yellowish spot in the discoidal cell. The UPF submarginal row has black spots, the UPH submarginal row has black lunules. The UPH black discal row is well developed. The UNS pattern of the female is similar to that of the male.

FEMALE GENITALIA (Fig. 4E). The postvaginal plate is oval. The antevaginal plate is narrow in dorsoventral direction, and its outer edge does not extend beyond the boundaries of the bend of the postvaginal plate (auricules). The bacillus is long and thin and is connected to the antrum by a thin lintel.

Distribution (Fig. 5)

Pakistan: Khyber Pakhtunkhwa Province, the vicinity of Birmoglasht, Chitral, Malakand. According to Higgins (1941) the species is distributed from Murree (Punjab) to Chitral. Gasse (2021) considers the reference to the habitation of *M. lutko* in Murree to be erroneous, but he does not give arguments for this.



Fig. 5. Distribution of *M. lutko* Evans, 1932. For a description of the dots with letters see Fig. 30.

***Melitaea mimetica* Higgins, 1940**

Figs 1C–D, 3A–G, 4F–I, 6–8, 16D–H, 18F–I, 29C, E, 30; Table 1

Melitaea lutko [sic] *mimetica* Higgins, 1940: 52. Type locality: “Balochistan, Khojak” [Pakistan, Balochistan, Khojak Pass].

“*Melitaea delerei* nov. spec.” Heydemann, 1954: 415, pl. 35 fig. 9 (holotype ♀), pl. 35 fig. 8 (allotype ♂), fig. 10 [genitalia]. Type locality: “Kabul Umgebung” [Afghanistan, Kabul vicinity].

Remarks

The taxon *delerei* was described from two specimens: 1 ♀ (holotype) and 1 ♂ (allotype). The butterflies were collected in the vicinity of Kabul on 23 May 1951 and 28 Apr. 1953, respectively. The text contains photos of the holotype ♀ and the allotype ♂ (Heydemann 1954). The author of the original description does not mention the existence or number of other type specimens. Van Oorschot & Coutsis (2014) provide other data on the type material of *delerei*, and these are quoted here without changes: “Type material: ♂ holotype, 4 ♂♂, 2 ♀♀ paratypes (coll. Görgner, including ♂ with yellow label stating “Kabul, ♂, 23.5.1951, leg Delere, Heydemann, Kiel”, ♂ with orange label stating “♂, *Mel. dodgsoni delerei*, Hdm.”, ♂ with red label stating “male, Holotypus *Mel. delerei* Hdm. 11.54.)”. The type material is stored in the Ernst Görgner collection (Cosswig Anhalt, Germany). We do not know the reason for such a serious discrepancy in the data on the type material of the taxon *delerei*.

Type material

The taxon *mimetica* is described based on the holotype, allotype, and 10 paratypes from Balochistan (Pakistan) from the following localities: Khojak, Ziarat Rd., Zaghun, Gawar, Sheik Wazil, Urak and Quetta (Higgins 1940). The number and the gender of specimens for each collection point are not specified. According to Smith (1988) the type material stored in the BMNH consists of 3 ♂♂, 1 ♀ with the labels “Pakistan, Zaghun, 6000 ft.” and 1 ♀ with the label “Gawar”. The storage location of the type specimens from Sheik Wazil, Urak and Quetta is unknown.

The type locality of the holotype is mentioned by Higgins as Khojak Pass, and the place of capture of the allotype is mentioned as “Ziarat Rd.” (Higgins 1940). However, in the work devoted to the bibliography and catalog of type specimens of taxa described by Higgins (Smith 1988), it is indicated that the specimen marked by Higgins as an allotype has the label “Khojak”, and the holotype, on the contrary, has the label “Ziarat Rd.” In accordance with recommendation 76A.1.3. (ICZN 2004), the holotype should be considered a specimen caught on the Khojak Pass.

Paratype (Fig. 1C–D)

We have photos of the paratype (allotype), ♀, with the following labels: “Holotype [!]” (printed label); “Ziarat Rd. / Balochistan, 6000 w. / 20.04.31” (handwritten label); “Roth. B.-1” (printed label); “*Melitaea lutko mimetica* / type ♂, L. G. Higgins” (handwritten label); “*Melitaea lutko / mimetica* Higgins / C. R. Smith det. 1986, Holotype (!)” (handwritten + printed label); BMNH.

Notes on diagnosis

The taxon *delerei* was considered as a synonym of the taxon *mimetica* based on external features and the structure of the genitalia (Higgins & Wiltshire 1956), or together with the taxon *mimetica* as a synonym of *M. lutko* (van Oorschot & Coutsis 2014). In the latter case, they were able to study the genital apparatus of the paratype of the taxon *delerei*, whose structure in their opinion is transitional between *M. lutko* and *M. timandra*. However, the description of *M. delerei* clearly states that one of the features of the male is a very long and thin harpe without teeth on the inner side, which is a characteristic feature of *M. mimetica*. In general, the genital apparatus of the male *delerei*, an image of which is given by Heydemann (1954), is characterized by a thin caudal process of the valva with 2–3 teeth located distally on the dorsal side

and a long braid-shaped harpe. Judging from the image, the male and female have a well-expressed postdiscal pale area on the UPF. In this case, we agree with Higgins' opinion and believe that the taxon *delerei* has all the distinctive features of *M. mimetica* and should be treated with the latter as a synonym. We do not exclude the subspecies status of the taxon *delerei*, but a final decision can be made only after the identification and study of the holotype and additional material from Afghanistan.

Material examined

PAKISTAN – **Balochistan** • 2 ♂♂ (all dissected), 2 ♀♀ (all dissected); Quetta, Urak; alt. 2400–2700 m; 10–14 May 1983; Eckweiler leg.; EDMSU • 1 ♂; Ziarat; alt. 2400–2700 m; 17–23 May 1983; Eckweiler leg.; EDMSU.

AFGHANISTAN – **Bamian Prov.** • 6 ♂♂ (5 dissected); 10 km S of Bamian t., Hushkak v. vicinity; alt. 2700–2800 m; 2 Jun. 2012; O. Pak leg.; EDMSU • 7 ♂♂ (5 dissected), 3 ♀♀ (all dissected); Punjab Distr., 10 km NE of Varas v.; alt. 2400 m; 20 May 2012; I. Pljushtch leg.; EDMSU • 1 ♀ (dissected); 8 km S of Bamian, Koh-e-Baba Mts, Dara-e-Khushkak; alt. 2930 m; 12 Jun. 2016; I. Pljushtch leg.; EDMSU • 7 ♂♂; Punjab Distr.; 10 km NE of Varas vil.; alt. 2400 m; 21 May 2012; I. Pljushtch leg.; coll. I. Pljushtch • 13 ♂♂, 5 ♀♀; Punjab Distr., Varas vil.; alt. 2400 m; 21 May 2012; I. Pljushtch leg.; coll. I. Pljushtch. – **Ghor Prov.** • 7 ♂♂ (5 dissected), 2 ♀♀ (1 dissected); 17 km E of Changcharan, 15 km S of Bandi-Ali, Gazak Mts; alt. 2400 m; 26 May 2012; O. Pak leg.; EDMSU • 3 ♂♂ (all dissected), 1 ♀ (dissected); 16 km E of Changcharan, Bandi-Ali v. vicinity; alt. 2400 m; 26 May 2012; I. Pljushtch leg.; EDMSU • 1 ♂ (dissected), 1 ♀ (dissected); Bayan Ridge, 15 km S of Changcharan, Kindival valley; alt. 2800 m; 27 May 2012; I. Pljushtch leg.; EDMSU • 1 ♂; Bayan Ridge, Changcharan circ., Kindival valley; alt. 2800 m; 27 May 2012; I. Pljushtch leg.; coll. I. Pljushtch • 4 ♂♂; 16 km E of Changcharan, Bandi-Ali vil.; alt. 2400 m; 26 May 2012; I. Pljushtch leg.; coll. I. Pljushtch. – **Kabul Prov.** • 1 ♀; Gargha; alt. 2000 m; 1 Jun. 2010; I. Pljushtch leg.; coll. I. Pljushtch.

Redescription

Male (Fig. 6A–D, I–L)

WINGS. FW length is 17.5–19 mm, the paratype is 18 mm. UPS ground color is yellow-orange or pale orange-red; UPS black marginal border is thin with well-defined marginal spots along the outer edge of the wings; UPS submarginal row represented by small pointed black lunules; UPF discal row is formed by expanded black spots fused with each other near the costa; UPF postdiscal pale-yellowish area, located behind the black discal spots, is well expressed along the entire length and contrasts with the general background. There is a pale-yellowish spot in the distal part of the discoidal cell; UPH discal row is usually reduced; UPH basal suffusion covers no more than $\frac{1}{3}$ of the surface of the wing. UNF ground color is pale orange-red, with a well-defined pale area of the outer edge of the wing between the veins Sc and Cu1 and in postdiscal area between veins Sc and M1. UNH ground color is white without the admixture of dark scales. UNH lunules forming the proximal edge of submarginal orange fascia outwardly concave and sharply pointed between veins M3 and Cu2.

MALE GENITALIA (Figs 3A–G, 16D–H, 18F–I, 29C, E). The valva is oval with a slender caudal process, usually with one small spine (or without it) on the dorsal surface in the distal part. The long harpe is narrow, without spines (or in rare cases with one or two weakly developed spines) on the inner side. The aedeagus is curved in the central part, distally with a rounded convex dorsal edge. The posterior part of the aedeagus is mostly located at an angle to the anterior part and is directed downward. There is often a well-marked protrusion on the ventral side at the junction of the two parts of the aedeagus. The wide saccus is rounded distally, its length being 1.5 times greater than the width.

Female (Fig. 6E–H, M–P)

WINGS. FW length is 20–21 mm. UPS ground color is pale orange-red. UPF postdiscal pale area is well expressed and represented by whitish-yellow spots fused to the costal edge and contrasting well with the

wing ground color. UPF well-marked pale macule is present in the discoidal cell. UPF submarginal row on the is represented by dark pointed spots, and on the UPH by thin black lunules. UPH black distal row is absent or weakly expressed. UNH pattern is similar to that of males.

FEMALE GENITALIA (Fig. 4F–I). The postvaginal plate is rounded-trapezoidal in shape. The antevaginal plate is expanded in the dorsoventral direction, its outer edge noticeably extends beyond the boundaries of the bend of the postvaginal plate (auricles).

Preimaginal stages: eggs (Fig. 7, Table 1)

Material examined: 10 eggs from 1 ♀; Afghanistan, Ghor Prov., 16 km E of Changcharan, Bandi-Ali v. vicinity, alt. 2400 m.

The egg is barrel-shaped. The height of the eggs is from 624.0 µm to 626.6 µm, the width is from 598.0 µm to 603.5 µm. The sculpture of the micropile region is formed from four to five rows of penta-hexagonal cells of various lengths and widths. The diameter of the micropile rosette in the widest part

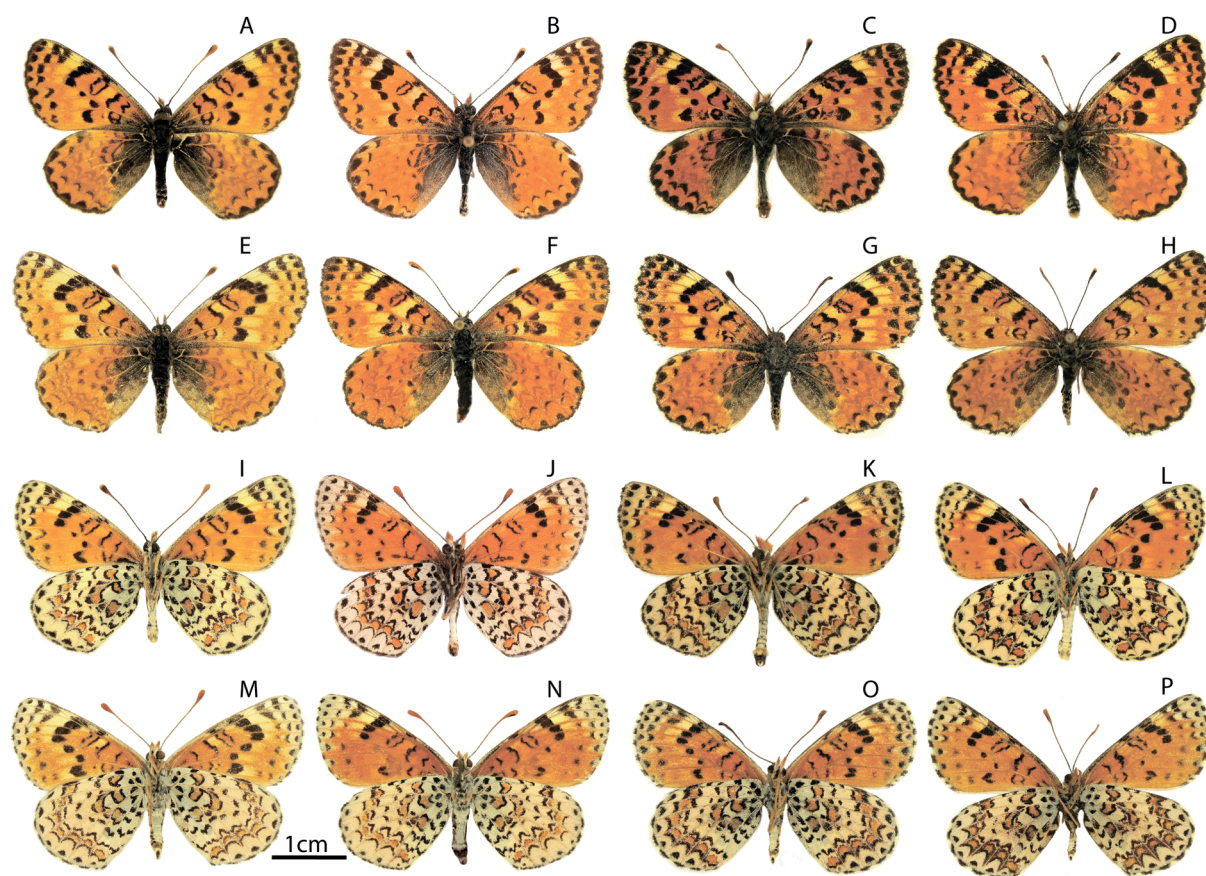


Fig. 6. Adults of *M. mimetica* Higgins, 1940. **A–H.** UPS. **I–P.** UNS. **A–B, I–J.** ♂, Pakistan, Balochistan, Quetta, Urak, alt. 2400–2700 m. **C, K.** ♂, Afghanistan, Ghowr Prov., Bayan Range, 15 km S of Chagcharan, Kindival vall. **D, L.** ♂, Afghanistan, Bamian Prov., Punjab Distr., 10 km NE of Varas v., alt. 2400 m. **E–F, M–N.** ♀, Pakistan, Balochistan, Quetta, Urak, alt. 2400–2700 m. **G, O.** ♀, Central Afghanistan, Bamian Prov., 8 km S of Bamian, Koh-e-Baba Mts, Dara-e-Khushkak, alt. 2930 m. **H, P.** ♀, Afghanistan, Bamian Prov., Punjab Distr., 10 km NE of Varas v., alt. 2400 m. **B, J** photos by Dr Eckweiler).

varies from 37 μm to 41 μm . The micropile rosette is formed by 8–9 primary quatro-pentahedral cells 5.0 μm to 16.0 μm wide and 9.0 μm to 23.0 μm long. The micropile is rounded in shape with an average diameter of 6.6 μm . There are 23–24 lateral longitudinal ribs that limit the micropile area and decrease to $\frac{1}{3}$ of the egg surface. The transverse ribs are weakly expressed. Below the lateral ribs the chorion is relatively smooth.

A distinctive feature of the morphology of eggs of *M. mimetica* is their well-defined barrel shape. In addition, *M. mimetica* has the smallest eggs among the representatives of the *lutko* group. Their maximum height is 626.6 μm . However, the egg of *M. timandra*, which is oval with a slight narrowing

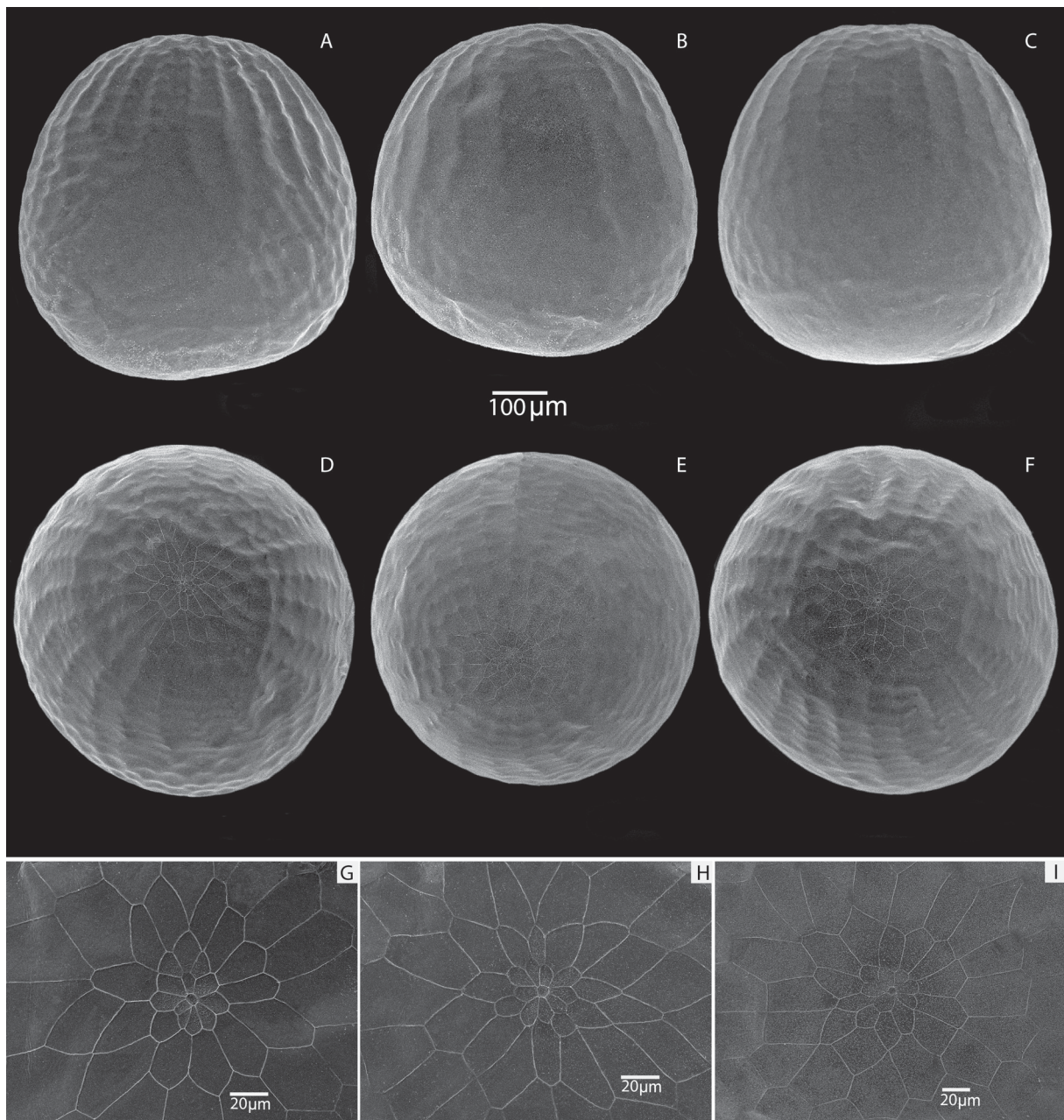
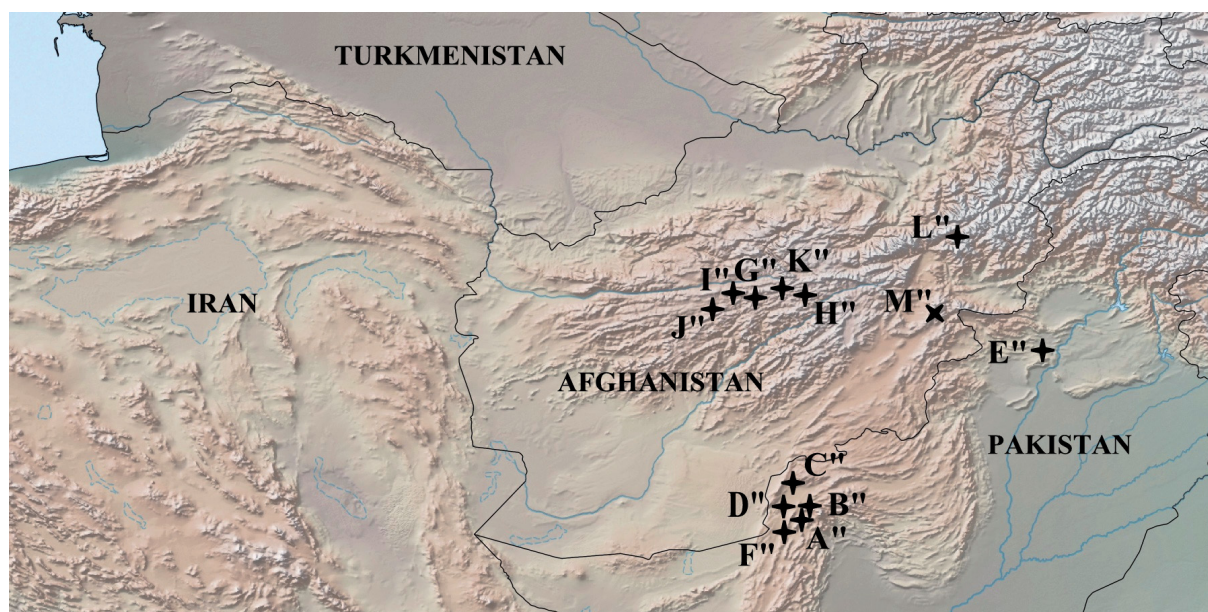


Fig. 7. Eggs of *Melitaea mimetica* Higgins, 1940, Afghanistan, Ghor Prov., 16 km E of Changcharan, Bandi-Ali v. vicinity, alt. 2400 m. **A–C.** Lateral view. **D–F.** View from above. **G–I.** Micropile area.

Table 1. Measurements of the egg of *M. mimetica* Higgins, 1940.

	Egg height (μm)	Egg width (μm)	Micropile rosette diameter (μm)	Micropile diameter (μm)	Primary cell width (μm)	Primary cell length (μm)
Average value	625.6	600.9	39.1	6.6	9.1	14.2
Standard deviation	0.9	1.8	1.4	0.1	2.2	2.8


Fig. 8. Distribution of *Melitaea mimetica* Higgins, 1940. For a description of the symbols with letters, see Fig. 30. \times = *M. mimetica mimetica* Higgins, 1940; \times = *M. mimetica delerei* Heidemann, 1954.

in the apical region (Kolesnichenko & Kotlobay 2020), has a height of about 850 μm , whereas that of *M. shahvarica* sp. nov., whose eggs are pear-shaped, has an average height of about 700 μm . In addition, the *M. mimetica* micropile rosette is formed by 8–9 primary cells, while in the *M. timandra* egg the micropile rosette is formed by 9–10 cells, and in the *M. shahvarica* egg the micropile is surrounded by 7–8 primary cells.

Distribution (Fig. 8)

Pakistan: Balochistan, Punjab; Afghanistan: Panjshir Gorge, Koh-i-Baba Ridge, mountains in the vicinity of Punjab, Bandi-Bayan Ridge.

Melitaea timandra Coutsis & van Oorschot, 2014

This species is represented by two subspecies: nominate, inhabiting the plains of the eastern part of Turkmenistan, and *binaluduca* subsp. nov. found in the mountainous regions of eastern Iran and central Afghanistan.

Melitaea timandra timandra Coutsis & van Oorschot, 2014
Figs 1E–F, 9, 10A–F, 11A–C, 12–13, 17A–C, 19 A–C, 29G, 30; Table 2

“*Melitaea timandra* Coutsis & van Oorschot, sp. nov.” van Oorshot & Coutsis, 2014: 72, pl. 14 figs 23, 25, pl. 15 fig. 1, genitalia: pl. 44 fig. 16, pls 186–187. Type locality: “Turkmenistan, Sary-Yazy” [Turkmenistan, SE Kara-Kum, Mary velayat, vicinities of Sary-Yazy village].

Type material

Holotype (Fig. 1E–F)

TURKMENISTAN • “Turkmenistan, Sary-Yasy; 22.04.1993; ex coll. Soldatis”; NBC HO0279.

Paratypes

TURKMENISTAN • 1 ♂, 1 ♀; Badkhyz Reserve, Kepeli cordon; 20–23 Apr. 1986; A. Devyatkin leg.; EDMSU. Designated as paratypes by van Oorschot & Coutsis (2014).

Remarks

It is necessary to elucidate upon the issues of identification of the holotype, the type locality and the origin of the paratypes of *M. timandra*.

Unfortunately, van Oorschot & Coutsis (2014) made many inaccuracies when describing the taxon *timandra*. In the text of the description, “Turkmenistan, Kopet Dag, Sary-Yazy” is indicated as the type locality of the taxon *timandra*. This indication of the type locality leads to uncertainty, since the village of Sary-Yazy is located 200 km from the nearest spurs of the Kopet Dag Ridge. As a holotype, they indicate a specimen from the de Heer collection while not providing data on either the collector or the date of collection and without reference to the image of the type specimen. From the caption to the drawing of the genitalia of the holotype (van Oorschot & Coutsis 2014: 264, table 186), it already follows that it comes from the locality “Turkmenistan, Kopet Dag, Kara-Kala” and is in the ZMA collection. This information contradicts the original designation of the holotype and the type locality (the village of Kara-Kala is located at more than 600 km northwest of the village of Sary-Yazy). Some inaccuracies in the comments made by one of the authors (van Oorschot & Coutsis 2014) have been corrected by Coutsis (2016). In the table of preparations of the genitalia, the non-existent locality “Mary-Yazy” was corrected to “Sary-Yazy” and the confusion in the attribution of the depicted genitalia to one or another species was eliminated. It is obvious that there was confusion when labeling the specimens collected, and the two names were combined – the city of Mary, the center of the velayat of the same name, and the village of Sary-Yazy, located about 150 km south of it. The curator of the collection in Leiden, Ms Eulália Gassó Miracle, where the type specimens of *M. timandra* are currently stored, kindly provided us with photos of the holotype and its labels, from which it follows (Fig. 1E–F) that the type locality of the holotype is the village of Sary-Yazy.

In addition, all indications of the findings of *M. timandra* in the Western Kopet Dag, given by the authors of the description of the taxon *timandra*, as well as available in the scientific literature, raise doubts about the reliability and need additional verification and confirmation. It is highly likely that they are based on erroneous labeling of specimens. Tuzov & Churkin (2000) provide photos of *M. lutko*, corresponding in external morphology to the taxon *timandra*, allegedly caught by the second author from Kara-Kala.

A more complicated story takes place with a specimen from the vicinity of Kara-Kala, which appears as a paratype of the taxon *timandra* (van Oorschot & Coutsis 2014). The male from the Monjukly Ridge is mentioned on page 348 in the general list of specimens whose genitalia have been studied by these authors. The copy number and the number of the genital preparation are, respectively, NO 1102 and JC 5197. The information on the label is as follows: “Kopet Dag, SW of Monjukly Mt. range, Saf

Kara-Kala, 10. iv. 1992” without the name of the collector. There is a note to this specimen: “paratype, mtDNA sequencing by Wahlberg (NW 15–3 & 16–1)”. Images of the specimen itself and genitalia are not given, it is also completely unclear how many specimens with similar labels besides the one mentioned are included in the type series. In the text of the description of the subspecies *timandra* (van Oorschot & Coutsis 2014: 70) in the enumeration of paratypes there is the following entry: “2 ♂, 2 ♀, Kara-Kala (sic!), 20. iii. 1991; 1 ♂, same locality but 10. iv. 1992”. Since the date of the capture of the last male coincides with the above label, it can be assumed that the mentioned specimen from the Monjukly Ridge was meant. This specimen was used in the work on the assessment of molecular evolution of the genus *Melitaea* (Leneveu *et al.* 2009) as a voucher under the number NW15–3, but already with the label “West China” (sic!). A photo of a sequenced voucher specimen with a label is contained in the database of electronic resources (Anonymous 2016). A special investigation undertaken by the authors of the present publication showed that none of the collectors indicated on the labels caught *M. timandra* on the Monjukly Ridge or in the Kara-Kala area. It is likely that there was a substitution of labels as a result of negligence in the subsequent processing and transfer of the collected specimens to the collections. We believe that all references to *M. timandra* from the Kara-Kala area are the result of erroneous identification of the collection site, and all specimens with similar labels originate from the vicinity of the village of Sary-Yazy.

Material examined

TURKMENISTAN • 5 ♂♂ (2 dissected), 10 ♀♀ (3 dissected); Badkhyz Reserve, Kyzyl-Jar Gorge; 27 Apr. 1986; A. Devyatkin leg.; EDMSU • 2 ♂♂ (all dissected), 1 ♀ (dissected); same collection data as for paratypes; EDMSU • 5 ♂♂ (2 dissected), 2 ♀♀; Dushak; 30 Apr. 1987; A. Devyatkin leg.; EDMSU • 1 ♀ (dissected); Bakharden; 4 May 1987; A. Devyatkin leg.; EDMSU • 2 ♀♀ (all dissected); Chaacha; 1 May. 1987; A. Devyatkin leg.; EDMSU • 28 ♂♂ (10 dissected), 33 ♀♀ (5 dissected); Sary-Yazy; 25 Apr. 1992; I. Pljusch leg.; EDMSU • 18 ♂♂ (6 dissected), 21 ♀♀ (3 dissected); same collection data as for preceding; S. Churkin leg.; EDMSU • 1 ♂; Murgab river, Sary-Yazy; 23 Apr. 1992; S. Churkin leg.; EDMSU • 2 ♂♂, 1 ♀; 30 km E of Bairam-Ali, Zahmet station; 22 Apr. 1991; I. Pljusch leg.; EDMSU • 1 ♂ (dissected); Kara-Kum Des., 30 km of Mary-Tedjen, 30 km SW of Mary; 6 Apr. 1979; B. Sokolov leg.; EDMSU • 1 ♀; Kushka; 24 Apr. 1992; EDMSU • 1 ♀; Bairam-Ali vic.; Apr. 1977; V. Potopolskiy leg.; ZMMSU • 2 ♂♂; Repetek; ZIN • 11 ♂♂, 12 ♀♀; Sary-Yazy; 24–25 Apr. 1992; S. Churkin leg.; coll. S. Churkin • 2 ♂♂, 2 ♀♀; Sary-Yazy; 25 Apr. 1993; S. Churkin leg.; coll. S. Churkin • 1 ♂; same collection data as for preceding; 18 Apr. 1987; A. Kotlobay leg.; coll. A. Kotlobay • 2 ♂♂, 2 ♀♀, same collection data as for preceding; 18 Apr. 1993; A. Kotlobay leg.; coll. A. Kotlobay • 1 ♀; Mary Reg., v. Bairam-Ali vic.; 15 Apr. 1987; A. Kotlobay leg.; coll. A. Kotlobay.

Redescription

Male (Fig. 9A–D, I–L)

WINGS. FW length is 18–21.5 mm, in the holotype 19.5 mm, in the paratype 21 mm. UPS ground color is bright yellow-orange. UPS black pattern is partly reduced; thin UPS black marginal border with well-defined marginal spots along the outer edge of the wings; UPS submarginal row formed by fine black spots or strokes; UPF discal row represented by rather small black spots usually fused near the costa; UPF postdiscal pale area, located behind the black discal spots, represented by disconnected pale-yellowish macules located along the entire length. There is a weak pale-yellowish macule in the distal part of the discoidal cell; UPH discal row is absent; UPH basal suffusion is poorly developed and covers no more than ¼ of the wing surface. UNF is yellow-orange with a well-defined whitish postdiscal macules and pale area of the outer edge of the wing between the veins Sc and M2; and along the outer edge of the wing between the veins Sc and M2. UNH ground color is white, without admixture of dark scales. UNH lunules forming the proximal edge of submarginal orange fascia are usually not sharply pointed.

MALE GENITALIA (Figs 10A–F, 17A–C, 19A–C, 29G). Valva is elongated, its length is 2 times greater than the width with a relatively short and wide caudal process, with a spine on the dorsal side of its distal part. Harpe is thickened in the central part due to the presence of teeth on the inner surface. Aedeagus with a slightly convex dorsal edge, its posterior part is mostly located at an angle to the anterior part and is directed downward. When both parts of the aedeagus are joined, there is a well-marked protrusion on the ventral side. Thin saccus is pointed distally, its length is 2 times greater than the width. In some specimens saccus is deeply divided into relatively wide rounded lobes.

Female (Fig. 9E–H, M–P)

WINGS. FW length is 20–25 mm, the paratype is 22 mm. UPS ground color is pale orange-red. Externally the female is similar to the male, but UPF postdiscal pale-yellowish area is well expressed. There is a well-defined pale macule in the discoidal cell. UPF submarginal row is represented by thin black strokes. UPH black discal row is usually absent. UNS pattern is similar to that of males.

FEMALE GENITALIA (Fig. 11A–C). The postvaginal plate is rounded-triangular in shape. The antevaginal plate is narrow in the dorsoventral direction, its outer edge does not go beyond the boundaries of the bend of the postvaginal plate (auricles).

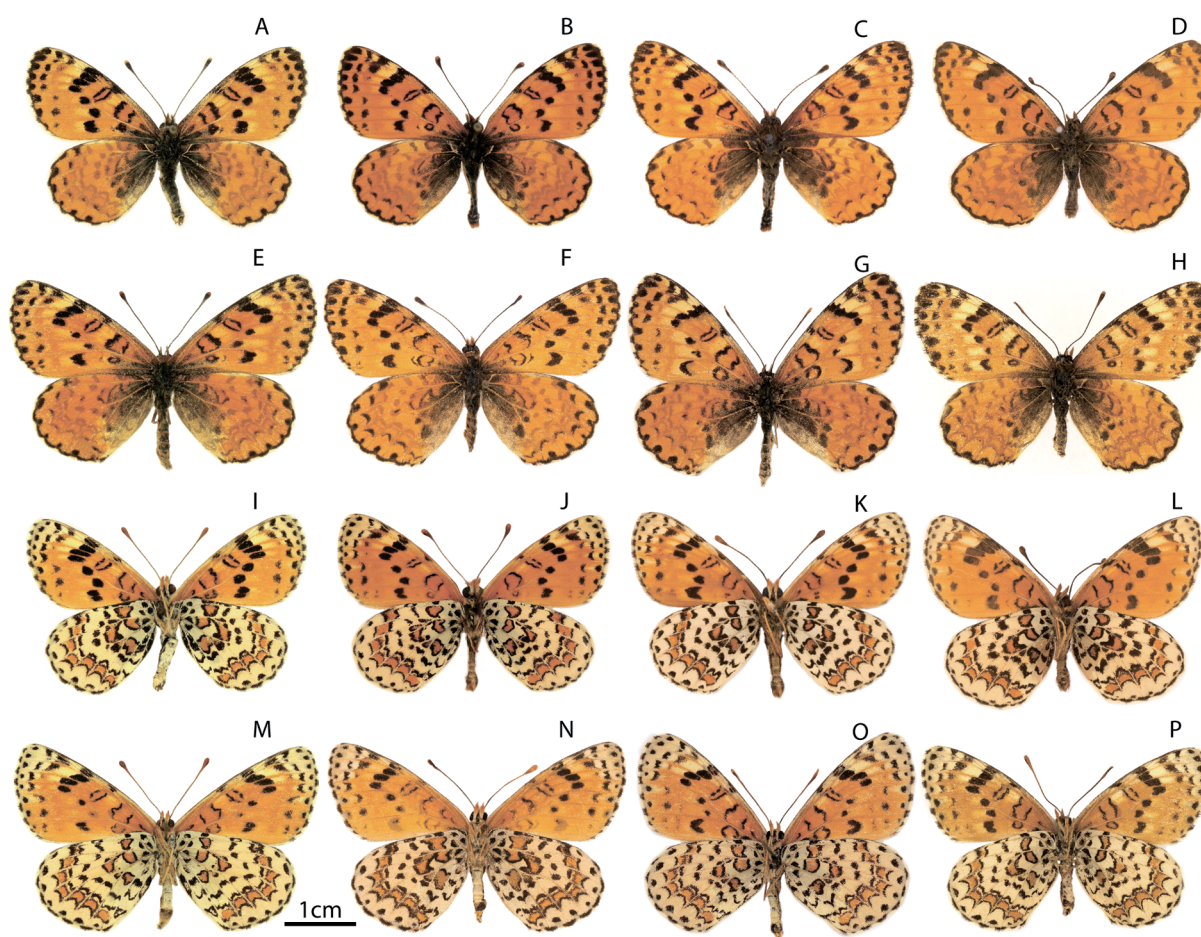


Fig. 9. Adults of *Melitaea timandra timandra* Coutsis & van Oorschot, 2014. A–H. UPS. I–P. UNS. A–D. ♂, Turkmenistan, Sary-Yazy, alt. 300 m. E–H. ♀, Turkmenistan, Sary-Yazy, alt. 300 m. I–L. ♂, Turkmenistan, Sary-Yazy, alt. 300 m. M–P. ♀, Turkmenistan, Sary-Yazy, alt. 300 m.



Fig. 10. Male genitalia (a = valva; b = aedeagus). **A–F.** *Melitaea timandra timandra* Coutsis & van Oorschot, 2014. **G–O.** *M. timandra binaludica* subsp. nov. **A–C.** S Turkmenistan, Sary-Yazy, alt. 300 m. **D.** Paratype, Turkmenistan, Badkhyz Reserve, Kepeli. **E–F.** S Turkmenistan, Sary-Yazy, alt. 300 m. **G–L.** Iran, Rezavi Khorassan Prov., Kuh-e-Binalud Mts, Dorrud v. vicinity, alt. 2430 m. **M.** Central Afghanistan, Bamian Prov., Band-e-Amir, Dzhudoi-Kvak Gorge, alt. 3200 m. **N.** Band-e-Amir, Hazarajat, Afghanistan. **O.** Afghanistan, Bamian Prov., Band-e-Amir, alt. 3200 m.

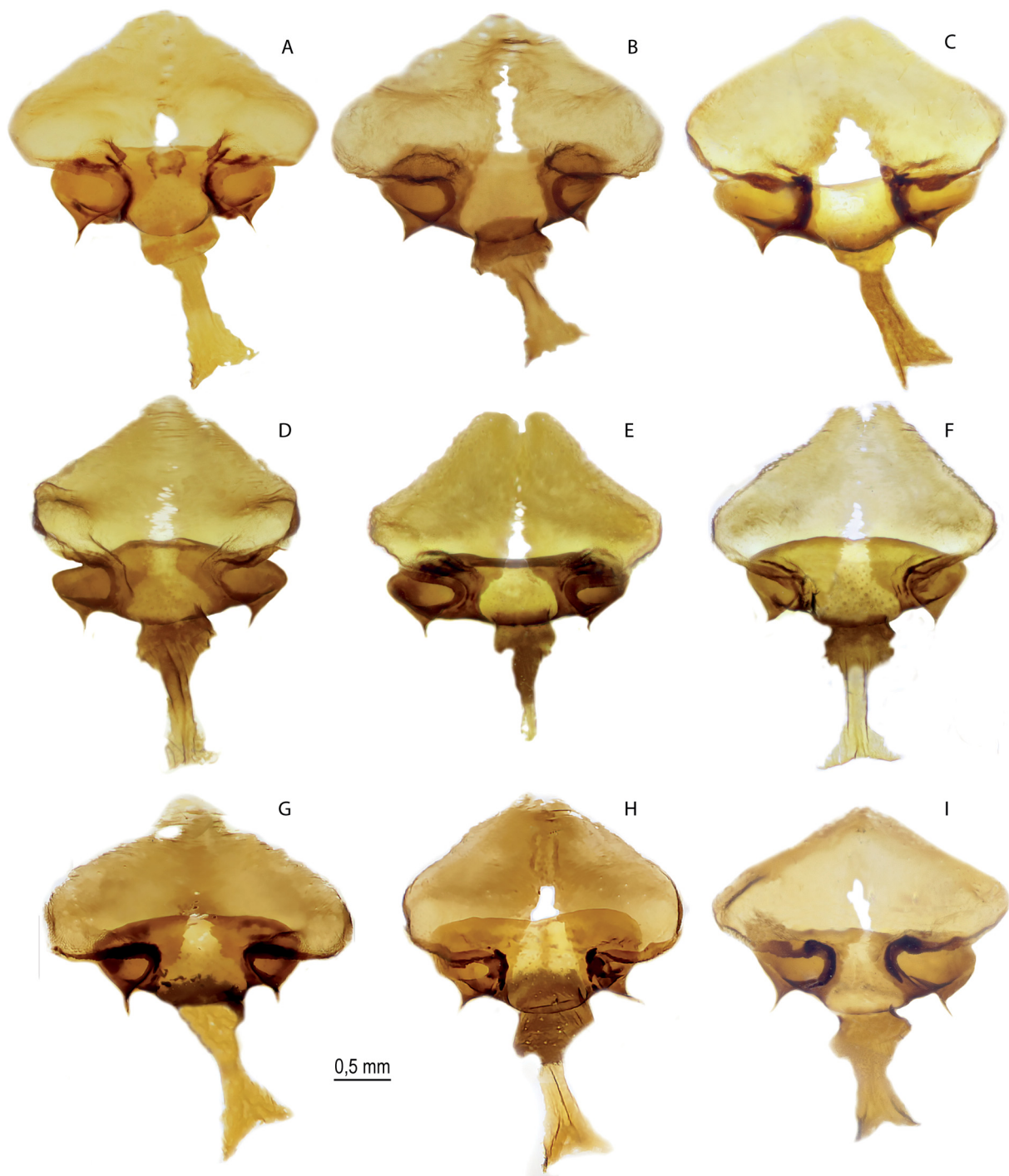


Fig. 11. Female genitalia (without the anal papillae, copulatory bursa, and anterior and posterior apophyses). **A–C.** *Melitaea timandra timandra* Coutsis & van Oorschot, 2014, S Turkmenistan, Sary-Yazy, alt. 300 m. **D–I.** *M. timandra binaludica* subsp. nov. **D–F.** Iran, Rezavi Khorassan Prov., Kuh-e-Binalud Mts, Dorrud v. vicinity, alt. 2430 m. **G–H.** Iran, Mazandaran Prov., S macroslopes of Albors Mts, 80 km SE of Sari, 5 km NE of Foulad Mahhaleh v., E slopes of Sultan Kuh Mt., alt. 2000 m. **I.** Afghanistan, Bamian Prov., Band-e-Amir, alt. 3200 m.

Preimaginal stages: egg (Fig. 12, Table 2)

Material studied: 1 ♀, 3 eggs, Turkmenistan, Badkhyz Res., Kyzyl-Dzhar. 2 ♀♀, 18 eggs, S Turkmenistan, Sary-Yazy.

The egg is oval. The height of the egg varies from 686.0 µm to 691.6 µm, the width is from 547.0 µm to 555.6 µm (Table 2). The sculpture of the micropilar area is formed from four to five rows of penta-hexagonal cells of various lengths and widths. The diameter of the micropile rosette in the widest part varies from 49.5 µm to 61.0 µm. The micropilar rosette is formed by 7–10 primary quatro-pentahedral

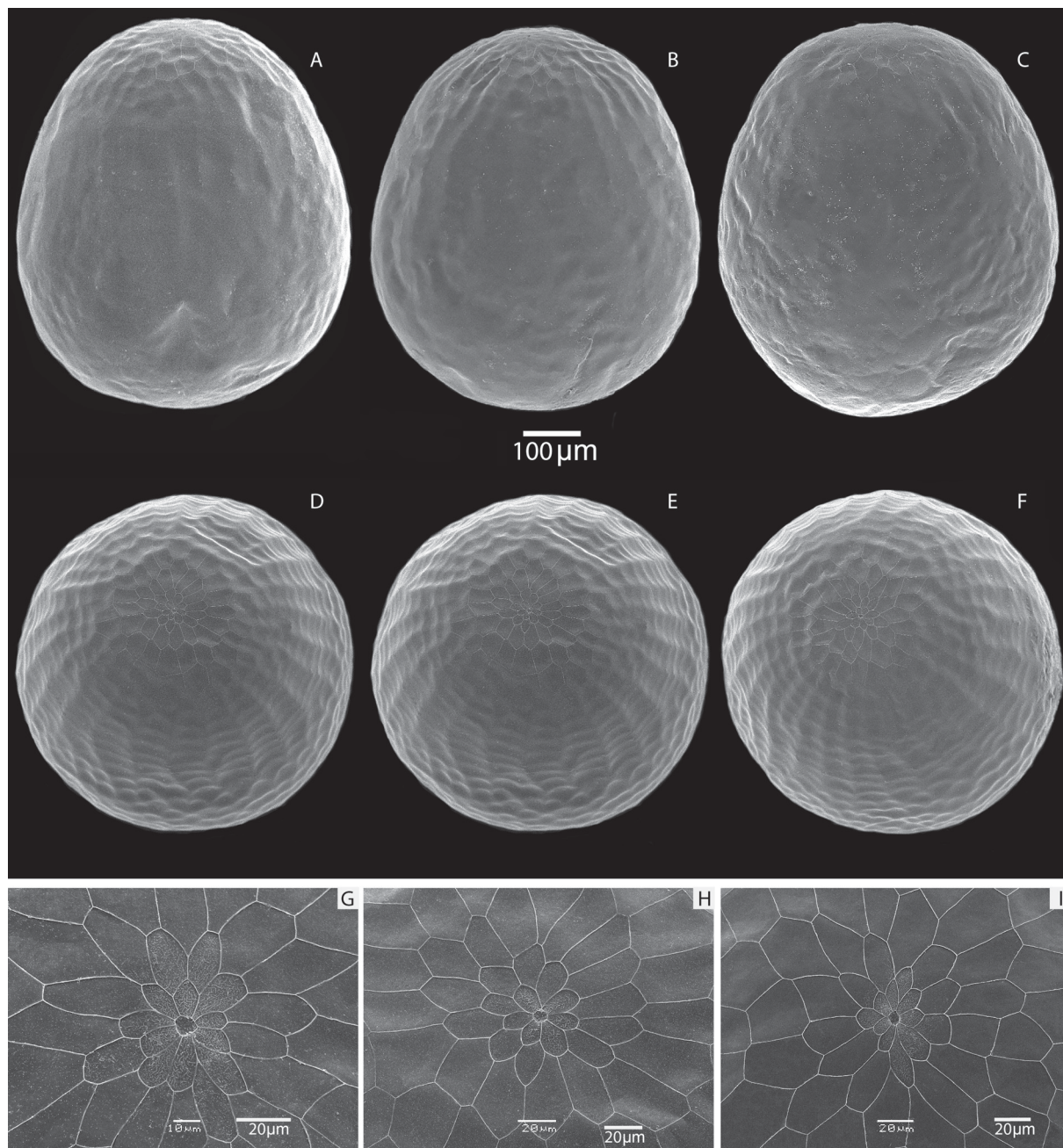


Fig. 12. Eggs of *Melitaea timandra timandra* Coutsis & van Oorschot, 2014, S. Turkmenistan, Sary-Yazy. A–C. Lateral view. D–F. View from above. G–I. Micropile area.

Table 2. Measurements of the egg of *M. timandra timandra* Coutsis & van Oorschot, 2014.

	Egg height (µm)	Egg width (µm)	Micropile rosette diameter (µm)	Micropile diameter (µm)	Primary cell width (µm)	Primary cell length (µm)
Average value	688.2	551.5	55.2	7.8	10.5	19.4
Standard deviation	2.7	1.9	5.2	1.2	2.6	5.5

cells with a width from 5.0 µm to 17.0 µm and a length from 9.0 µm to 37.0 µm. The micropile is rounded in shape, with an average diameter of about 8 µm. 26–28 lateral longitudinal ribs limit the micropilar area and drop to $\frac{1}{3}$ of the egg surface. The transverse ribs are pronounced in most of the eggs studied. Below the lateral ribs, the chorion is relatively smooth.

The eggs of the nominate subspecies are similar in shape to *M. timandra binaludica* subsp. nov. (Kolesnichenko & Kotlobay 2020). A distinctive feature of the morphology of the eggs of *M. timandra timandra* is their smaller size. In *M. timandra binaludica* the egg height is more than 750.0 µm, and the width is just over 600.0 µm. The micropilar rosette of *M. timandra timandra* is formed by 7–9 primary cells, while the micropile of the egg of *M. shahvarica* sp. nov. is surrounded by 7–8 primary cells.

Biology (Fig. 13)

Observations in nature on the behavior and biology of *M. timandra timandra* were carried out in 1991–1993 on the left bank of the Murgab River in the area of the Sary-Yazy reservoir in the vicinity of the village of Sary-Yazy in the Mary velayat of Turkmenistan. The flight of butterflies usually occurs in the first days of April and lasts for three to four weeks. The beginning and end of the flight period may shift by a week depending on weather conditions. The habitat of butterflies is typical of the southern zone of the Kara-Kum desert: ridge-bumpy and bumpy-cellular overgrown sands covered with psammophilic shrub and herbaceous vegetation (Fig. 13A). The absolute altitude of the area above sea level is 320–330 m. The relative height of the sand ridges and bumps is 10–15 m. The shrubs are represented by juzguns (*Calligonum* spp.) and sand acacia (*Ammodendron conollyi* Bunge ex Boiss.). The space between them is occupied by ephemeroïd-ephemeral grass communities, in which the background species are swollen sedge – ilak (*Carex physodes* M. Bieb.), celine (*Aristidia* spp.), eastern wheatgrass (*Eremopyrum orientale* Jaub. & Spach, bulbous bluegrass (*Poa bulbosa* L.), cheat grass (*Bromus tectorum* (L.) Kuntze). In spring, on the slopes of hills and ridges, small thickets of ferula (*Ferula* spp.) and single flowering plants of iris (*Iris* spp.) are occasionally found. Poppies (*Papaver pavoninum* Boiss. & Buhse) are common in inter-ridge depressions. Observations have established that the host plant of *M. timandra* in the studied region is *Phlomoides regeliana* (Aitch. & Hemsl.) Adylov, Kamelin & Makhm. (Fig. 13B), which forms sparse curtains with an area of up to several hundred square meters in the inter-ridge depressions. Together with *M. timandra* in this biotope fly blue *Neolycaena tengstroemi* (Erschoff, 1874), steppe clouded yellow (*Colias erate* (Esper, [1805]), painted lady (*Vanessa cardui* (Linnaeus, 1758)). *Melitaea timandra* butterflies are active in sunny weather in the first half of the day. Males are more active than females, moving throughout the territory occupied by the host plant. Females are restricted to short flights within a few, adjacent specimens of *Ph. regeliana*. For laying eggs, the female chooses a plant with a shaded basal leaf rosette. Laying is carried out directly on the soil near the leaf rosette (Fig. 13C). Before laying, the female samples the soil with the ovipositor for a few minutes, apparently choosing the optimal consistency, temperature, and humidity. Under one host plant, the female produces one fairly compact clutch (Fig. 13D). The number of eggs in the five studied clutches ranged from 28 to 152 (28, 67, 113, 150, 152 respectively). In two cases, it was possible to directly observe the process of egg laying in nature. Laying of 113 eggs lasted continuously for 45 minutes, 150 eggs – a little more

than an hour. Three females were placed in a cage, where after a fairly short time they also began to lay eggs on the bottom of the cage next to the host plant leaf placed there. The butterflies laid their eggs in three or four batches, several dozen in each clutch. The eggs are light, almost white, with a light yellowish-greenish color, with a diameter of about 0.5 mm. The further development of the eggs was monitored in the cage. The release of single caterpillars was noted on the third day, the mass emerging of caterpillars in the cage was observed 8–9 days after egg laying. The emerged caterpillars are slightly more than a millimeter long, they partially eat the chorion then switch to feeding on the host plant mining the leaf. The color of the body and the head capsule of newborn caterpillars of the first instar is a solid light green with a yellowish tinge. One of the caterpillars, which emerged from the egg three days after laying, went to molt in the second instar three days later. Unfortunately, for several reasons, further observations of the development of the caterpillars could not be carried out. The question at what stage happened the estivation and subsequent hibernation of *M. timandra* – the caterpillar of senior instars, or pupa – remains open.

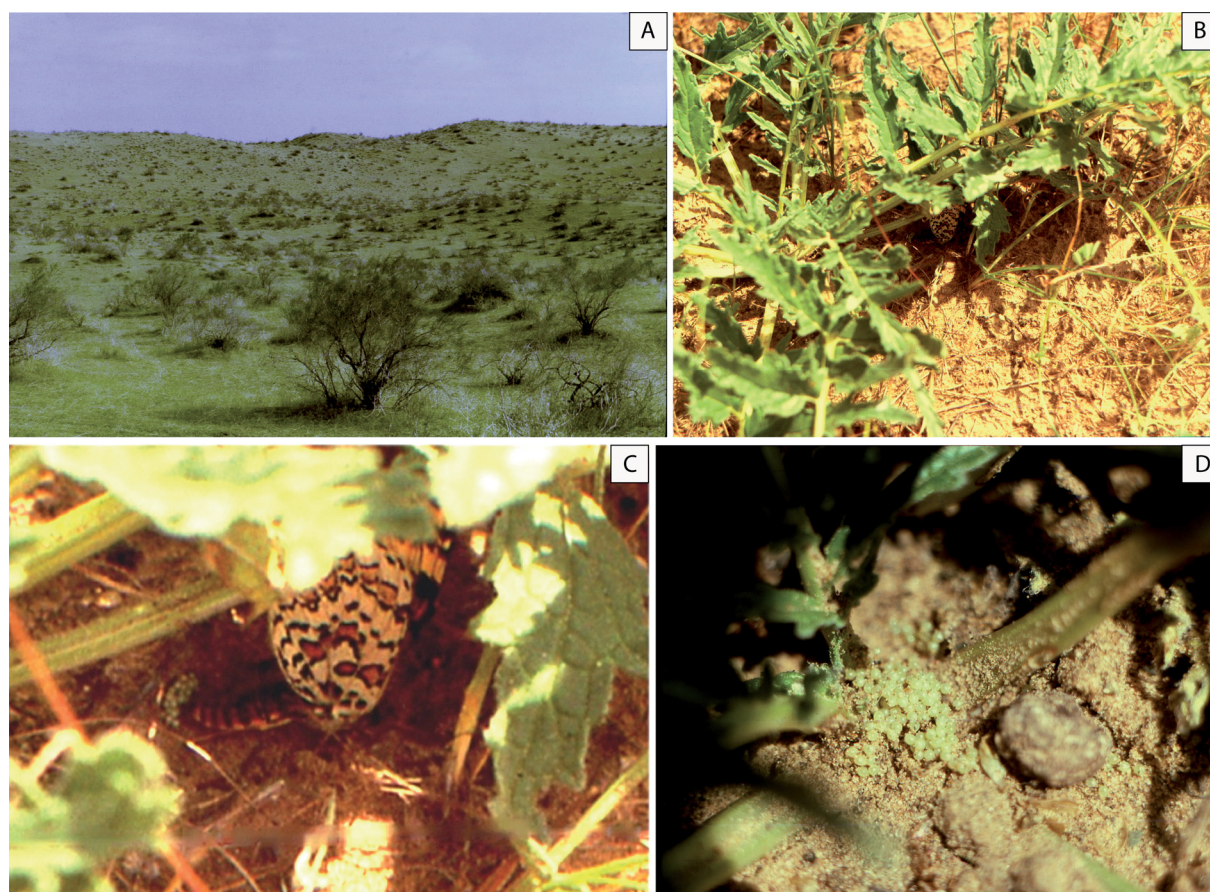


Fig. 13. Biotopes and biology of *Melitaea timandra timandra* Coutsis & van Oorschot, 2014. **A.** Bumpy-cellular overgrown sands on the left bank of the Murgab River, alt. 300 m, April 1993, the habitat of *M. timandra timandra*. **B.** *Phlomoides regeliana* (Aitch. & Hemsl.) Adylov, Kamelin & Makhm. – host plant for *M. timandra timandra*. The female laying eggs is visible under the leaves of the plant. **C.** The female of *M. timandra timandra* is ovipositing on the soil under the host plant leaf. **D.** Egg clutch of *M. timandra timandra* on the basal leaf rosette of *Ph. regeliana*.

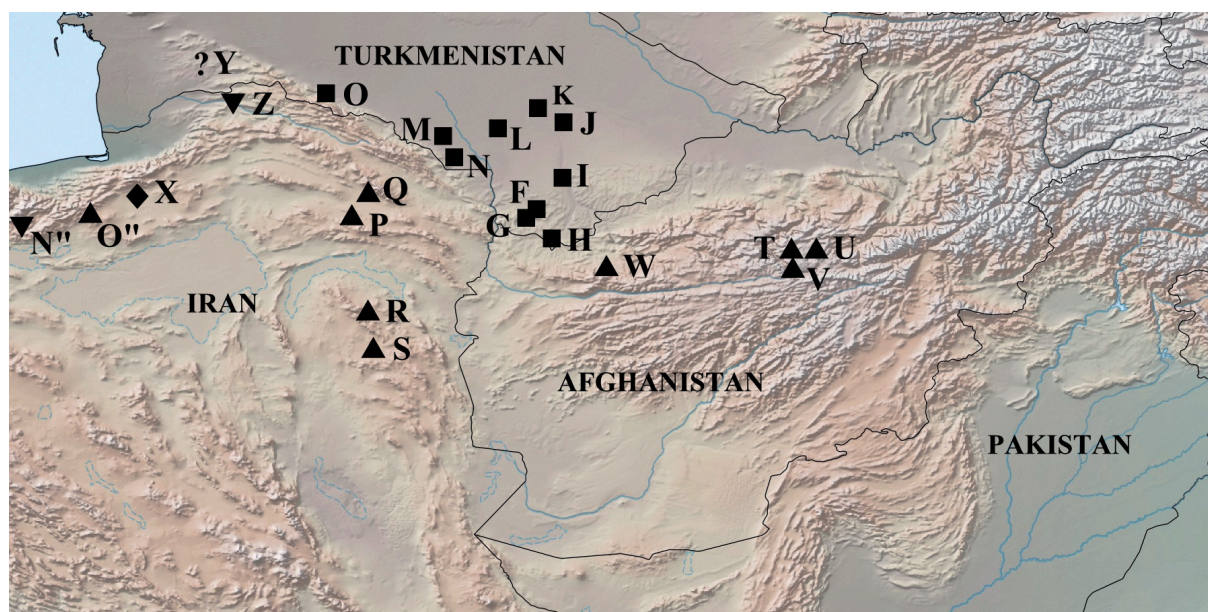


Fig. 14. Distribution of *Melitaea timandra timandra* Coutsis & van Oorschot, 2014, *M. timandra binaludica* subsp. nov. and *M. shahvarica* sp. nov. For a description of the points by letters, see Fig. 30. ■ = *Melitaea timandra timandra*; ▲ = *Melitaea timandra binaludica* subsp. nov.; ◆ = *Melitaea shahvarica* sp. nov.; ? = unconfirmed finds of *Melitaea timandra*; ▼ = *Melitaea timandra* with uncertain subspecies status.

Distribution (Fig. 14)

Turkmenistan: Badkhyz (Kyzyl-Jar Gorge, Kepeli), SE Kara Kum, Kopet Dag foothill plain (Bakharden). The main places of capture are located along the valley of the Murghab River (Sary-Yazy), up to the delta (Bairam Ali, Mary) and in the Tejen River basin (Dushak, Chaacha). To the north, it reaches Repetek. The village of Bakharden is the westernmost, and the vicinity of the village Repetek is the northernmost reliably known habitat of *M. timandra timandra*.

Melitaea timandra binaludica subsp. nov.

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Figs 2B–D, F–H, J–L, N–P, 10G–O, 11D–I, 14–15, 17D–I, 19D–I, 20, 29B, D, H, 30; Tables 3, 6

Differential diagnosis

Melitaea timandra binaludica subsp. nov. differs from the nominative subspecies in appearance by its smaller size, the absence or weakly expressed UPF postdiscal pale area in males, the presence of UPH discal row, the developed UPH basal suffusion and the presence of UNH dark scales both in males and females. In the structure of the male genitalia, the main distinguishing features should be considered a noticeably thinner caudal process of the valva (on average thinner than in the nominative subspecies) and a noticeably less wide central part of the harpe (1.5–2 times narrower than in the nominative subspecies). In addition, unlike the nominative subspecies, the harpe on its inner surface carries a smaller number of teeth.

Etymology

The name is toponymic and denotes the name of the mountain Ridge on which the type series was collected.

Type material

Holotype (Fig. 15A, I)

IRAN • ♂; Rezavi Khorassan Prov., Kuh-e Binalud Mts, Dorrud v. vicinity; alt. 2430 m; 12–13 May 2017; K. Kolesnichenko leg.; SDM.

Paratypes (Fig. 15B–H, J–P)

IRAN – **Rezavi Khorassan Prov.** • 82 ♂♂ (7 dissected), 18 ♀♀ (6 dissected); Kuh-e Binalud Mts, Dorrud v. vicinity; alt. 2430 m; 12–13 May 2017; K. Kolesnichenko leg.; EDMSU • 28 ♂♂ (20 dissected), 10 ♀♀ (7 dissected); Qadamgan area, Dorrud v. vicinity, Gerina v.; alt. 2000 m; 4 Jun. 2009; K. Kolesnichenko leg.; EDMSU • 2 ♂♂ (all dissected); Kuh-e-Binalud, 15 km SW of Zoshk; alt. 2300–2500 m; 7 Jun. 1999; Eckweiler leg.; EDMSU • 11 ♂♂; 6 km N of Gerine, Kuh-e-Binalud Ridge; 36°09'15.56" N, 59°10'54.01" E; alt. 2015 m; 9 May 2019; A.A. Kotlobay leg.; coll. A.A. Kotlobay. – **Mazandaran Prov.** • 1 ♀ (dissected); S macroslopes of Albors Mts, 80 km SE of Sari, 5 km NE of Foulad Mahhaleh v., E slopes of Sultan Kuh Mt.; alt. 2000 m; 2 May 2018; K. Kolesnichenko leg.; EDMSU • 1 ♀ (dissected); same locality as for preceding but 12 May 2019; A. Kotlobay leg.; EDMSU. – **Horossan Prov.** • 1 ♂ (dissected); 35 km N of Birjant t.; 28 Apr. 2006; K. Kolesnichenko leg.; EDMSU • 1 ♂ (dissected); 75 km N of Birjant t., Sedeh v. vicinity; alt. 1500 m; 27 Apr. 2005; R. Nazarov leg.; EDMSU.

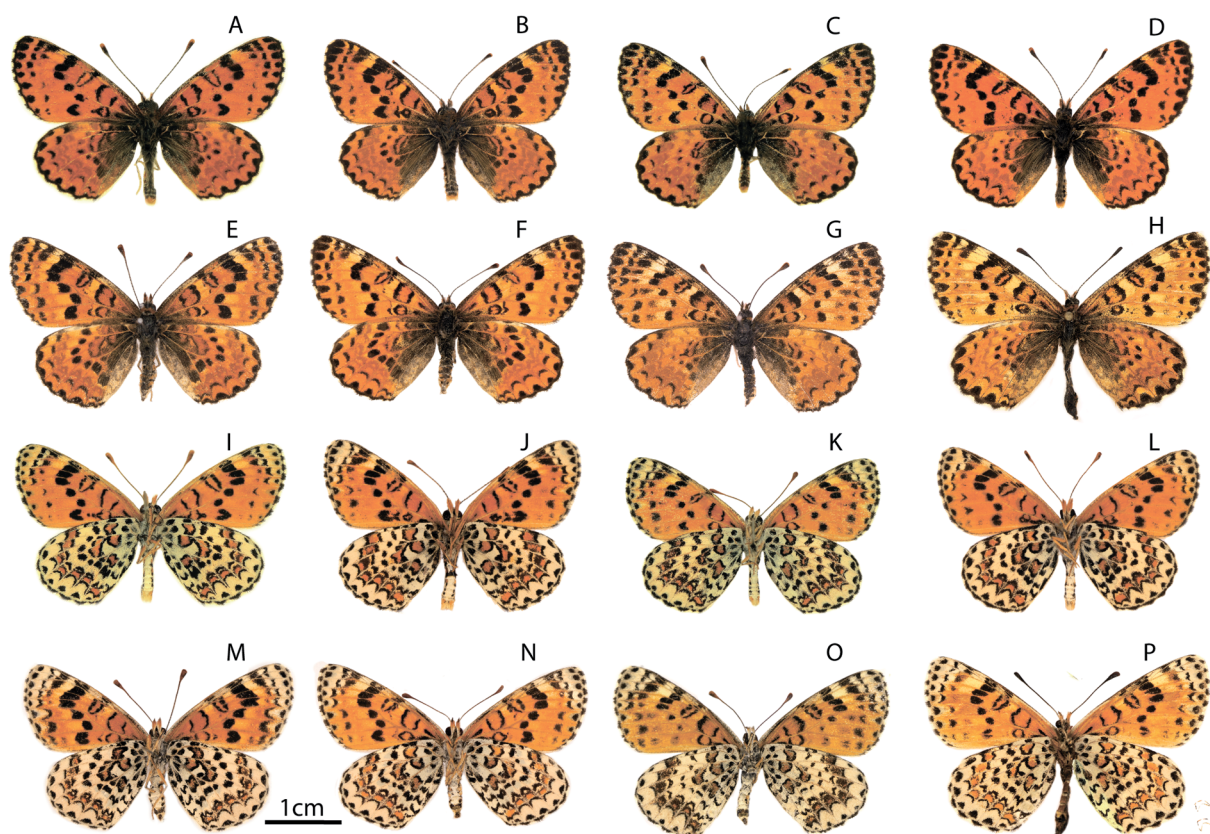


Fig. 15. Adults of *Melitaea timandra binaludica* subsp. nov. A–H. UPS. I–P. UNS. A, I. Holotype, ♂ (SDM). B–H, J–P. Paratypes (EDMSU). A–D, I–L. ♂, Iran, Rezavi Khorassan Prov., Kuh-e Binalud Mts, Dorrud v. vicinity, alt. 2430 m. E–H, M–P. ♀, same data as for preceding.

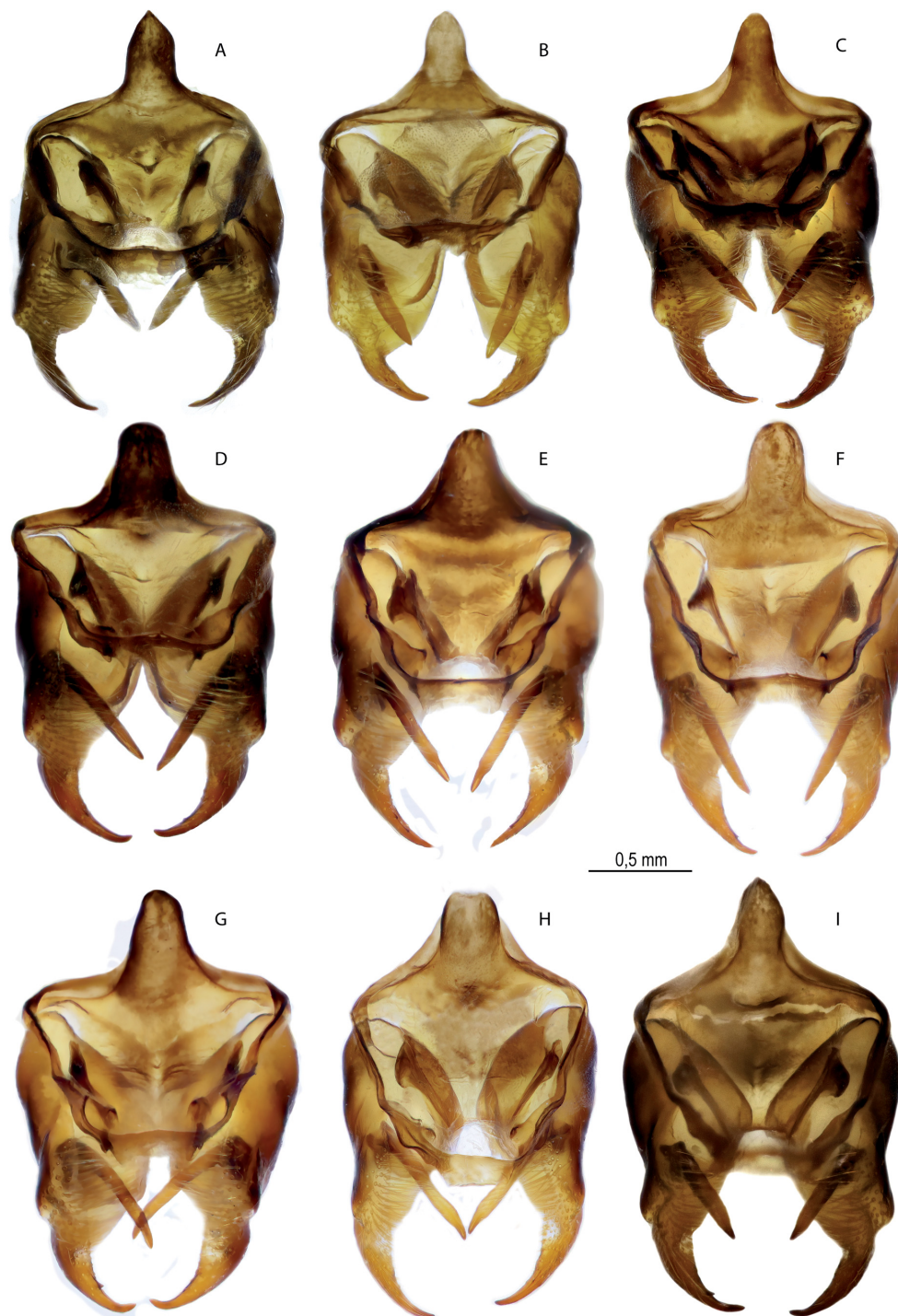


Fig. 16. Male genitalia (without aedeagus) in dorsal projection. **A–C.** *Melitaea shahvarica* sp. nov. **D–H.** *M. mimetica* Higgins, 1940. **I.** *M. lutko* Evans, 1932. **A–C.** Iran, Semnan Prov., Shahrud area, S macroslope of Shahvar Mts, alt. 2200–2400 m. **D.** Pakistan, Balochistan, Quetta, Urak, alt. 2400–2700 m. **E.** Afghanistan, Bamian Prov., 10 km S of Bamian t., Hushkak v. vicinity, alt. 2700–2800 m. **F.** Central Afghanistan, Ghor Prov., 17 km E of Changcharan, 15 km S of Bandi-Ali, Gazak Mts, alt. 2400 m. **G.** Afghanistan, Bamian Prov., Punjab Distr., 10 km NE of Varas v., alt. 2400 m. **H.** Afghanistan, Ghor Prov., 16 km E of Changcharan, Bandi-Ali v. vicinity, alt. 2400 m. **I.** Pakistan, Chitral, Chaghbini CGNP [Chitral Gol National Park], alt. 2700 m.

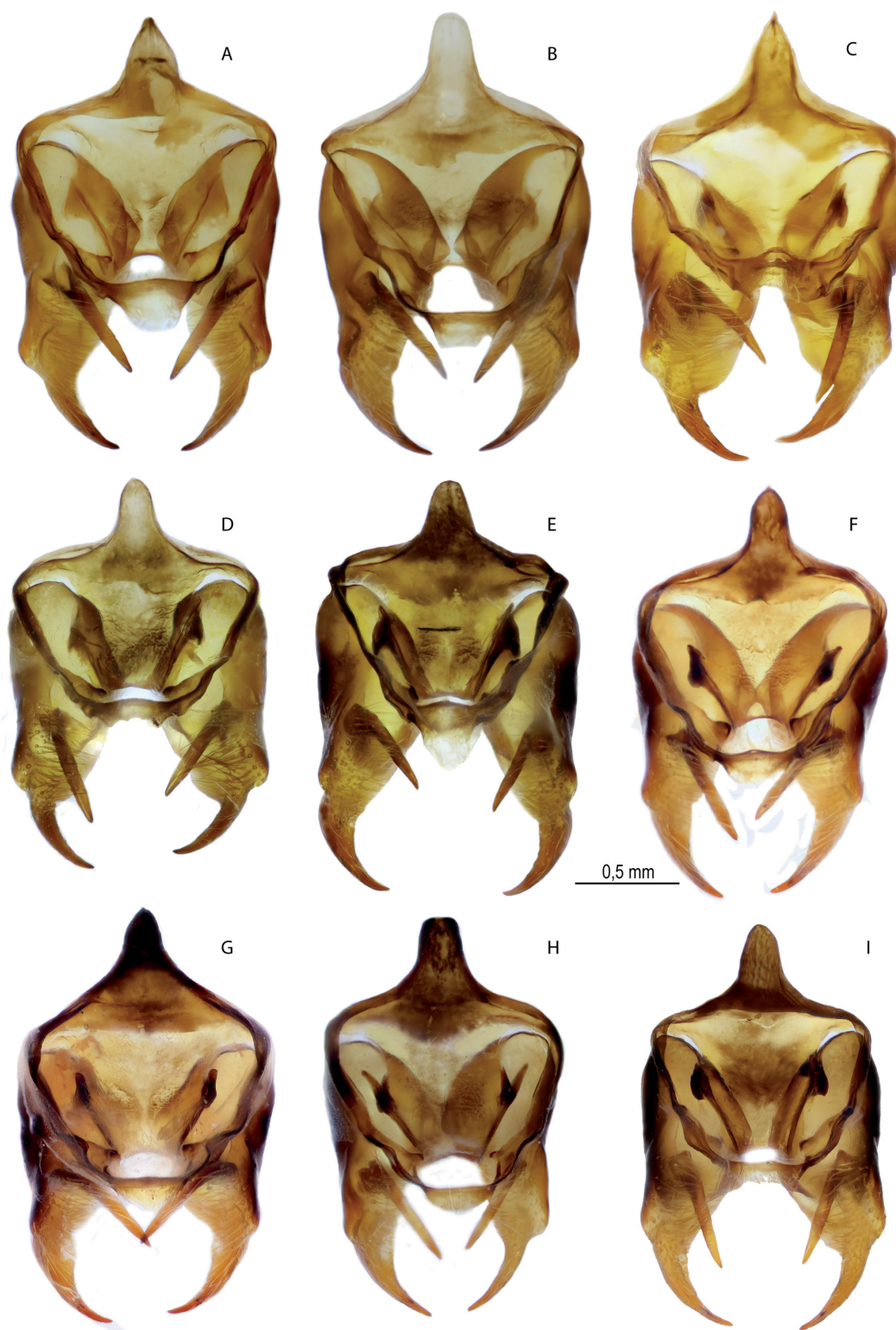


Fig. 17. Male genitalia (without aedeagus) in dorsal projection. **A–C.** *Melitaea timandra timandra* Coutsis & van Oorschot, 2014. **D–I.** *M. timandra binaludica* subsp. nov. **A–C.** S Turkmenistan, Sary-Yazy, alt. 300 m. **D–F.** Iran, Rezavi Khorassan Prov., Kuh-e-Binalud Mts, Dorrud v. vicinity, alt. 2430 m. **G.** Iran, Horossan Prov., 35 km N of Birjant t. **H.** Afghanistan, Bamian Prov., Band-e-Amir, alt. 3200 m. **I.** Central Afghanistan, Bamian Prov., Band-e-Amir, Dzhudoï-Kvak Gorge, alt. 3200 m.

AFGHANISTAN – **Bamian Prov.** • 4 ♂♂ (all dissected), 1 ♀ (dissected); Band-e-Amir, Dzhudoi-Kvak Gorge; alt. 3200 m; 1–2 Jul. 2009; O. Pak leg.; EDMSU • 1 ♂ (dissected); Hazarajat, Band-i-Amir; alt. 9400–11000 ft; 9–10 Jun. 1960; Colin Wyatt leg.; EDMSU • 5 ♂♂ (all dissected), 1 ♀ (dissected); Band-e-Amir; alt. 3200 m; 5 Jul. 2009; I. Pljushtch leg.; EDMSU.

Description

Male (Figs 2B–D, J–L, 15A–D, I–L)

WINGS. FW length is 16.5–18 mm, the holotype is 18 mm. UPS ground color is bright orange. UPS black pattern well developed; UPS thin black marginal border with well-defined proximal marginal spots along the outer edge of the wings; UPF submarginal row formed by black strokes, UPH – by thin



Fig. 18. Male genitalia and harpe. **A–C.** *Melitaea shahvarica* sp. nov. **D–E.** *M. lutko* Evans, 1932. **F–I.** *M. mimetica* Higgins, 1940. **A–C.** Iran, Semnan Prov., Shahrud area, S macroslope of Shahvar Mts, alt. 2200–2400 m. **D–E.** Pakistan, Chitral, Chaghbini, CGNP [Chitral Gol National Park], alt. 2700 m. **F–G.** Afghanistan, Bamian Prov., Punjab Distr., 10 km. NE Varas v., alt. 2400 m. **H–I.** Afghanistan, Bamian Prov., Panjub Distr., 10 km. NE Varas vil., alt. 2400 m.

lunules, usually not connected to the black marginal border; UPF discal row represented by well-defined black spots fused closer to the costa, UPH discal row is more or less developed and formed by small black spots reduced closer to the costa; UPF postdiscal pale-yellow area, located behind discal row, is weakly expressed or absent, usually there are 2–3 pale macules near the UPF costal edge; UPF pale-yellowish macule in the distal part of the discoidal cell is usually absent; UPH discal row is formed by fine black spots; UPH basal suffusion covers up to $\frac{1}{3}$ of the wing surface; UNF is bright orange with well-developed pale area along the outer edge of the wing between the veins Sc and M2, UNF pale macules in the postdiscal area is usually absent; UNH ground color is white, with an admixture of dark scales. UNH lunules forming the proximal edge of submarginal orange fascia outwardly concave and sharply pointed between veins M3 and Cu2.

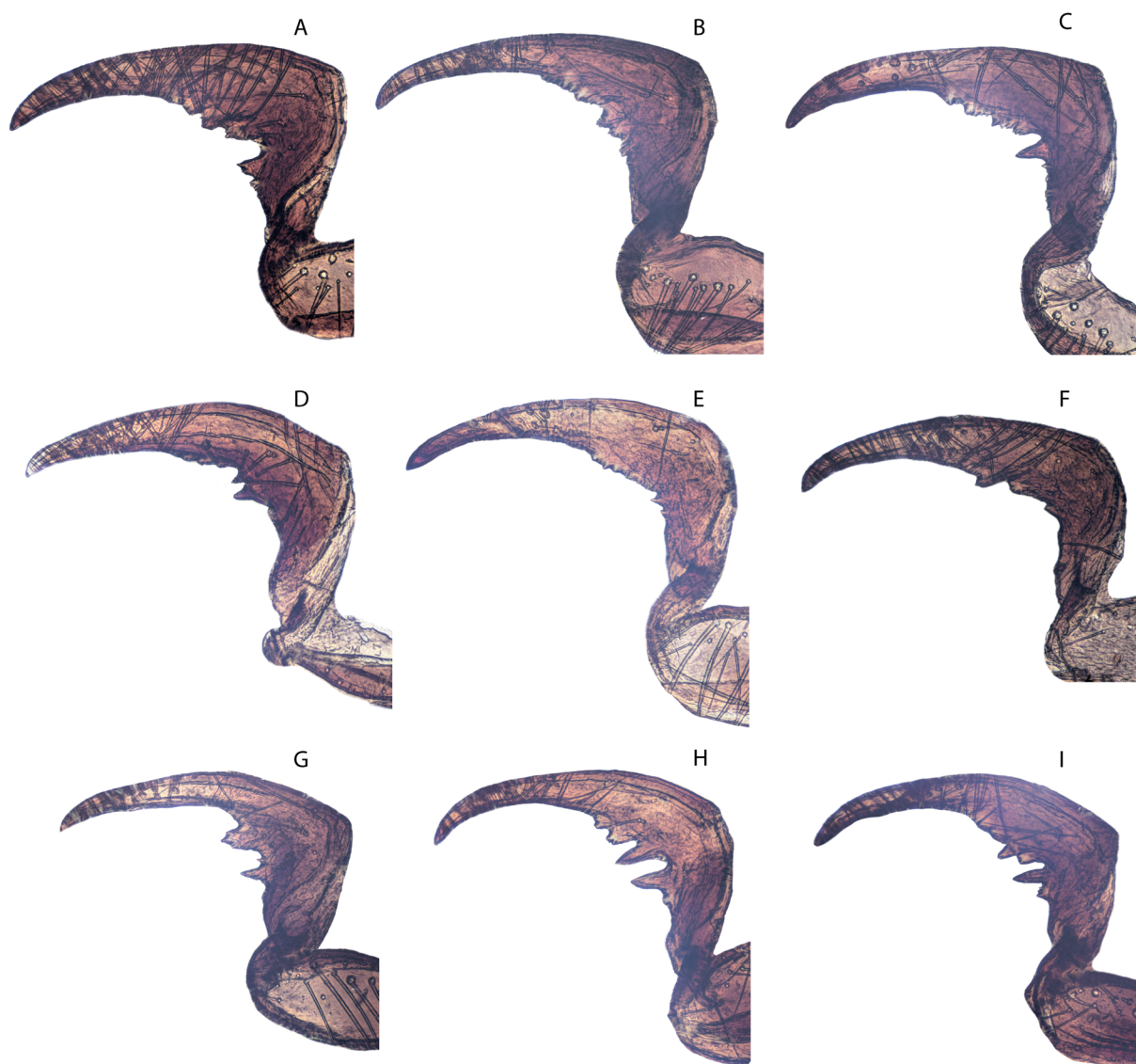


Fig. 19. Male genitalia and harpe. **A–C.** *Melitaea timandra timandra* Coutsis & van Oorschot, 2014. **D–I.** *M. timandra binaludica* subsp. nov. **A–C.** Turkmenistan, Sary-Yazy, alt. 300 m. **D–F.** Iran, Rezavi Khorassan Prov., Kuh-e-Binalud Mts, Dorrud v. vicinity, alt. 2430 m. **G.** Afghanistan, Bamian Prov., Band-e-Amir, alt. 3200 m. **H.** Afghanistan, Bamian Prov., Band-e-Amir, Dzhudoi-Kvak Gorge, alt. 3200 m. **I.** Afghanistan, Band-e-Amir, Hazarajat.

Table 3. Measurements of the egg of *M. timandra binaludica* subsp. nov.

	Egg height (μm)	Egg width (μm)	Micropile rosette diameter (μm)	Micropile diameter (μm)	Primary cell width (μm)	Primary cell length (μm)
Average value	792.6	666.0	78.2	7.8	10.5	19.4
Standard deviation	33.8	18.7	6.3	1.2	2.6	5.5

MALE GENITALIA (Figs 10G–O, 17D–I, 19D–I, 29B, D, H). In general, the size of the genitalia is smaller than that of the nominative subspecies. Valva with a relatively narrow (on average narrower than that of the nominative subspecies) caudal process, usually with several small spines on the dorsal surface. The relatively short harpe is somewhat expanded in the central part and bears a small number of noticeable teeth on the inner surface. The expanded part of the harpe is 1.5–2 times narrower than that of the nominative subspecies. Aedeagus with a rounded convex dorsal edge, its posterior part is mostly located at an angle to the anterior part and is directed downward. When both parts of the aedeagus are joined, there is a well-defined protrusion on the ventral side. Narrow saccus is distally pointed, its width is 2–3 times less than the length.

Female (Figs 2F–H, N–P; Fig. 15E–H, M–P)

WINGS. FW length is 17.5–20 mm. Externally the female is similar to the male, but the pattern is more contrasting. UPF postdiscal pale area is more developed than in the male. There is a well-developed pale macule in the discoal cell between the first and second discal spots. UPH submarginal row is usually reduced. UNS pattern is similar to that of males.

FEMALE GENITALIA (Fig. 11D–I). In general, the genitalia are similar to those of the nominative subspecies. The postvaginal plate is roundly triangular in shape. The antevaginal plate is narrow in the dorsoventral direction, its outer edge does not extend beyond the boundaries of the bend of the postvaginal plate (auricules).

Preimaginal stages: egg (Fig. 20, Table 3)

Material examined: 4 specimens, 27 eggs, Iran, Rezavi Khorassan Prov., Qadamgan area, Dorrud v. vicinity, Gerina v., alt. 2000 m.

The description of the egg of *M. timandra binaludica* subsp. nov. was given earlier based on 5 eggs examined using a scanning electron microscope (Kolesnichenko & Kotlobay 2020). Additional material made it possible to more accurately identify real diagnostic features.

The egg is the largest among the representatives of the *lutko* group. It is oval and noticeably elongated in the dorso-ventral direction (Kolesnichenko & Kotlobay 2020). The height of the egg varies greatly from 761.0 μm to 855.0 μm , the width is from 627.5 μm to 703.0 μm (Table 3). The sculpture of the micropilar area is formed from four to five rows of penta-hexagonal cells of various lengths and widths. The diameter of the micropilar rosette in the widest part varies from 78.0 μm to 90.0 μm . The micropilar rosette is formed by 7–9 (in rare cases 10) primary quadro-pentahedral cells with a width from 6.0 μm to 15.0 μm and a length from 9.0 μm to 27.5 μm . The micropile is rounded in shape, with an average diameter of about 8.0 μm . Lateral longitudinal ribs from 26 to 30 limit the micropile area and fall to $\frac{1}{3}$ of the egg surface. The transverse ribs are expressed in the first third of the egg surface. Below the lateral ribs, the chorion is relatively smooth.

In general, the eggs of *M. timandra binaludica* subsp. nov. are similar to those of the nominate subspecies. A distinctive feature of the morphology of the eggs of the new subspecies is their well-pronounced elongated-oval shape. In the nominate subspecies, the egg shape is also oval, but not so elongated dorsoventrally. In addition, the eggs of *M. timandra binaludica* subsp. nov. are the largest, their maximum height is 850.0 μm , while the height of those of the nominate subspecies is about 700.0 μm .

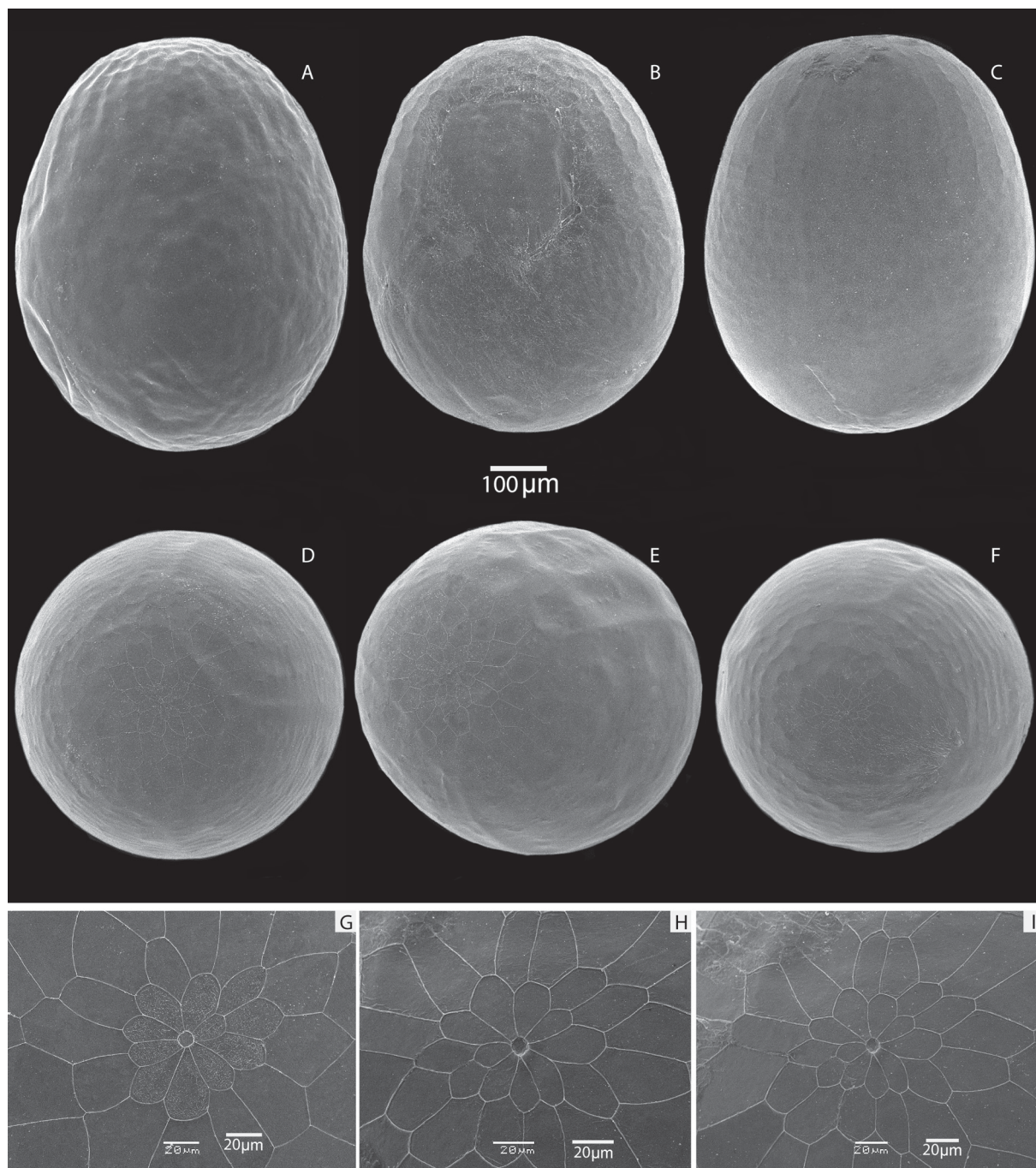


Fig. 20. Eggs of *Melitaea timandra binaludica* subsp. nov., Iran, Kuh-e-Binalud Mts. **A–C.** Lateral view. **D–F.** View from above. **G–I.** Micropile area.

Biology

The biology of the new subspecies in the Kuh-e-Binalud mountains and the early stages were described in detail by the authors earlier (Kolesnichenko & Kotlobay 2020).

Distribution (Fig. 14)

Iran: Turkmen-Khorassan Mts, Kuh-e-Binalud Ridge, Kayen Mts; Afghanistan: Band-e-Amir.

The described subspecies *M. timandra binaludica* subsp. nov. undoubtedly should also include specimens of *M. timandra* (*M. lutko mimetica* from the authors), caught by V. Eckweiler in Iran on Kuh-e-Binalud Ridge in the vicinity of Zoshk and Firizi (Tshikolovets *et al.* 2014). The butterflies on the published photos (Tshikolovets *et al.* 2014: tables Ixi, 1–2) have an external similarity with the specimens of *M. timandra binaludica* available to us from the same place, caught at the same time by the same collector. The butterflies from the Bandi Amir Valley, identified by the authors (Tshikolovets *et al.* 2018) as *M. mimetica*, should also be attributed to the described subspecies *M. timandra binaludica*.

Melitaea shahvarica sp. nov.

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Figs 4A–D, 14, 16A–C, 18A–C, 21–28, 29A, 30; Tables 4–5

Differential diagnosis

Melitaea shahvarica sp. nov. differs well from the close species *M. timandra* in its smaller size (small specimens of *M. timandra binaludica* subsp. nov. have a wingspan of more than 16.5 mm, while the wingspan of *M. shahvarica* is on average 16.5 mm), a noticeable reduction in the black pattern of the UPS (absence of submarginal lunules, weak development of black basal darkening and complete or partial absence UPH discal spots), absence of developed deposition of UNH dark scales, presence of UPF fused costal black dots of the submarginal and postdiscal rows centered by pale-orange spot. For the male genitalia, a characteristic feature is the presence of a noticeable protrusion of the ventral side, due to which the valva is visually noticeably expanded in the central part, so the length of the valva is only 1.5 times as great as the width. In *M. timandra*, the ventral protrusion of the valva is smoothed and the length of the valva is at least 2 times as great as the width (Fig. 29). The aedeagus is characterized by the absence of a noticeable protrusion on the ventral side at the junction of the anterior and posterior parts so both parts of the aedeagus are approximately on the same straight line. The female genitalia are characterized by an oval postvaginal plate.

Etymology

The name is toponymic and denotes the name of the mountain on the slopes of which the type series was collected.

Type material

Holotype (Fig. 21A, I)

IRAN • ♂; Semnan Prov., Shahrud area, S macroslope of Shahvar Mt.; alt. 2200–2400 m; 5–6 May 2018; K. Kolesnichenko leg.; SDM.

Paratypes (Fig. 21B–H, J–P)

IRAN – **Semnan Prov.** • 34 ♂♂ (10 dissected), 8 ♀♀ (4 dissected); same collection data as for holotype; EDMSU • 2 ♂♂ (all dissected); same collection data as for holotype but 18–19 May 2017; EDMSU • 16 ♂♂ (10 dissected), 5 ♀♀ (all dissected); Shahrud area, S macroslope of Shahvar Mts, Tohar v. vicinity; 7–8 May 2009; K. Kolesnichenko leg.; EDMSU • 32 ♂♂ (3 dissected), 9 ♀♀ (2 dissected), Gerdab.

Elburs Ridge, Shahvar Mt.; alt. 2200 m; 6–7 May 2018; A.A. Kotlobay leg.; coll. A.A. Kotlobay • 9 ♂♂; same collection data as for preceding but 9 May 2019; coll. A.A. Kotlobay.

Description

Male (Fig. 21A–D, I–L)

WINGS. FW length is 16–17 mm, the holotype is 17 mm. UPS ground color is bright orange-red. UPS black pattern reduced; UPS thin black marginal border with well-defined small marginal spots along the outer edge of the wings; UPF submarginal row usually represented by black dots or strokes. UPH submarginal row is absent or reduced. A characteristic feature for most specimens of the new species is the UPF black macule located between veins Sc and R5 and formed by the fused submarginal and postdiscal costal dots centered with orange or pale spot; UPF discal row represented by small black spots not fused with each other, UPH discal row absent or formed by small black spots reduced closer to the costa; UPF postdiscal pale-yellowish area, located behind the black discal spots, is weakly expressed or

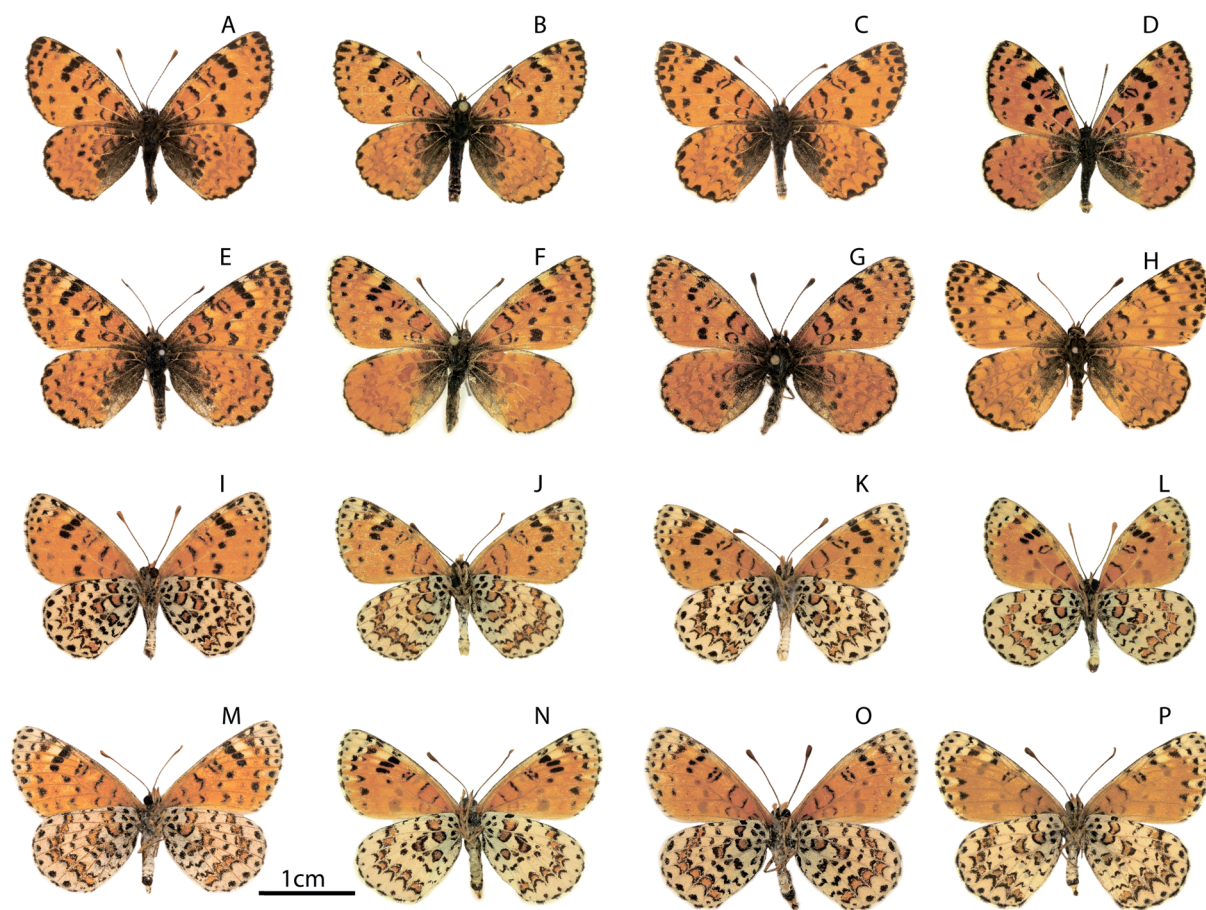


Fig. 21. Adults of *Melitaea shahvarica* sp. nov. A–H. UPS. I–P. UNS. A, I. Holotype, ♂ (SDM). B–H, J–P. Paratypes (EDMSU). A–C. ♂. Iran, Semnan Prov., Shahrud area, S macroslope of Shahvar Mt., alt. 2200–2400 m. D. ♂. Iran, Semnan Prov., Shahrud area, S macroslope of Shahvar Mt., Tohar v. vicinity, alt. 2200 m. E–H. ♀. Iran, Semnan Prov., Shahrud area, S macroslope of Shahvar Mt., alt. 2200–2400 m. I–K. ♂. Iran, Semnan Prov., Shahrud area, S macroslope of Shahvar Mt., 2200–2400 m. L. ♂. Iran, Semnan Prov., Shahrud area, S macroslope of Shahvar Mts, Tohar v. vicinity, alt. 2200 m. M–P. ♀. Iran, Semnan Prov., Shahrud area, S macroslope of Shahvar Mt., alt. 2200–2400 m.

expressed only at the costal edge: usually, only 2–3 yellowish macules situated near the costa; UPF pale-yellowish macule in the distal part of the discoidal cell weakly expressed; UPH basal black suffusion covers less than $\frac{1}{4}$ of the wing surface; UNF pale area along the outer edge of the wing between the veins Sc and M2 is well developed; UPH discal macules are either absent or expressed only as a row of dots between the veins A2–M3, in rare cases UPH discal row developed and formed by small and delicate macules (Fig. 21A); UNF pale macules in the postdiscal area are not pronounced; white UNH ground color with a slight admixture of dark scales; UNH lunules forming the proximal edge of submarginal orange fascia outwardly concave and sharply pointed between veins M3 and Cu2.

MALE GENITALIA (Figs 16A–C, 18A–C, 22, 29A). A broad valva with a wide and elongated distal caudal process with 2–3 small spines on the dorsal surface. The relatively short harpe is expanded in the central part with a small number of separately spaced or fused teeth on the inner surface. Curved aedeagus with a rounded convex dorsal edge. There is a smooth bend on the ventral surface of the aedeagus at the junction of the anterior and posterior parts, as a result of which the aedeagus looks S-shaped. Saccus is thin, its length is 2 times as great as its width. In some specimens the saccus is deeply divided into relatively wide rounded lobes.

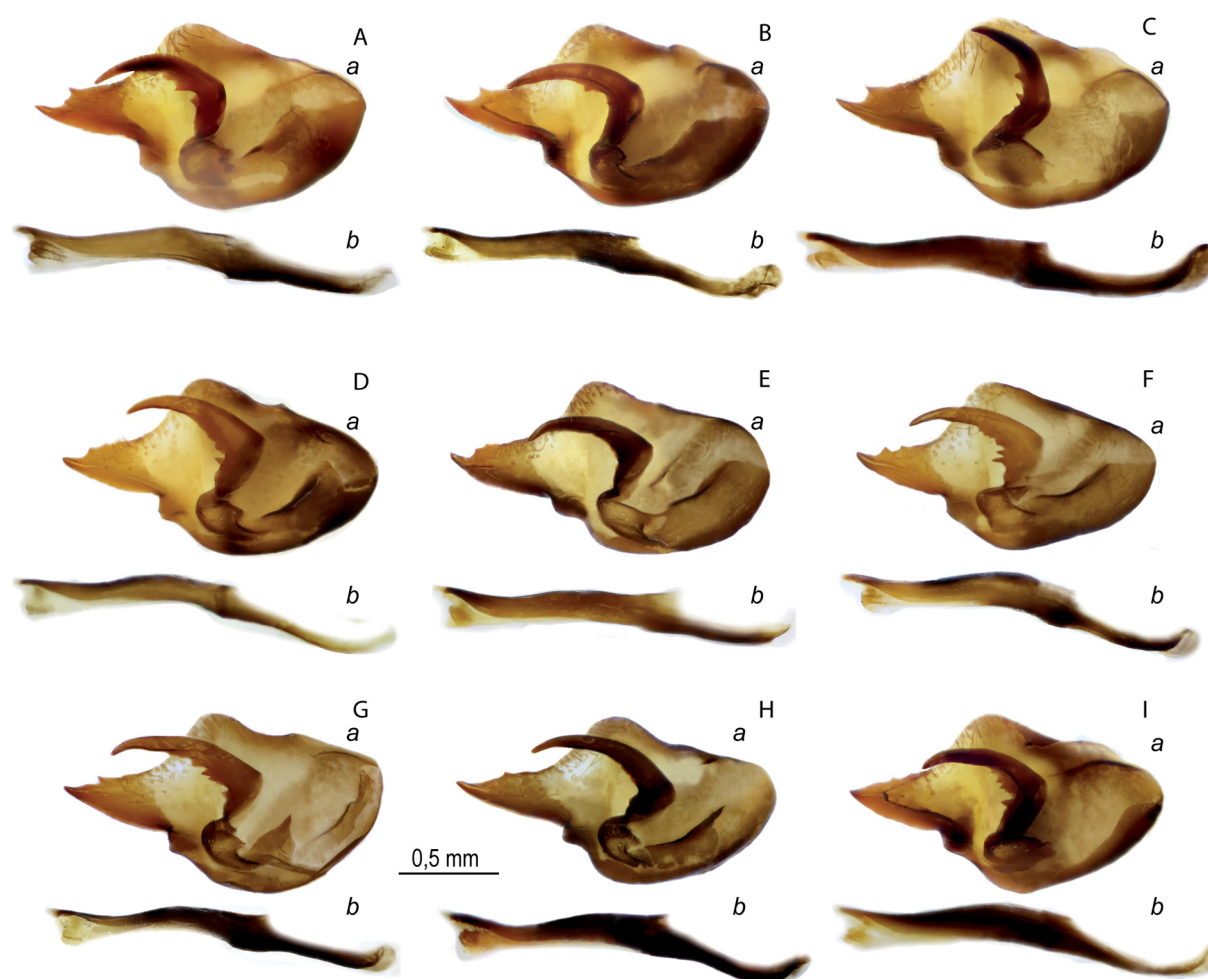


Fig. 22. Male genitalia of *Melitaea shahvarica* sp. nov. (a = valva; b = aedeagus). Iran, Semnan Prov., Shahrud area, S macroslope of Shahvar Mts, alt. 2200–2400 m.

Female (Fig. 21E–H, M–P)

WINGS. FW length is 19–20 mm. UPS ground color is bright orange; UPF postdiscal pale area is more pronounced than in the male; there is a distinct pale macule in the distal part of discoidal cell; UPH submarginal and discal rows are usually reduced, but in some specimens well developed (Fig. 21E); UNH discal row usually represented by 2–4 black spots near the costa; UNS pattern is generally similar to that of the males, but the main color is bright white.

FEMALE GENITALIA (Fig. 4A–D). The postvaginal plate is oval or wide-oval, in rare cases-oval-triangular. The antevaginal plate is narrow in the dorsoventral direction, its outer edge does not extend beyond the boundaries of the bend of the postvaginal plate (auricles).

Preimaginal stages (Figs 23–26, Tables 4–5)

Egg (Fig. 23, Table 4)

Material examined: 26 eggs from three clutches: Iran, Semnan Prov., Shahrud area, S macroslope of Shahvar Mts, alt. 2200–2400 m.

The egg has a well-defined pear shape. The height of the egg is from 699.4 μm to 700.6 μm , the width is from 606.5 μm to 610.0 μm (Table 4). The sculpture of the micropile region is formed from four to five rows of penta-hexahedral cells of various lengths and widths. The diameter of the micropile rosette in the widest part varies from 41.0 μm to 54.4 μm . The micropile rosette is formed by 7–8 primary quadra-pentahedral cells with width from 7.0 μm to 17.6 μm and length from 10.0 μm to 25.0 μm . The micropile is rounded in shape, with an average diameter of 5.1 μm . There are 24–26 lateral longitudinal ribs in the micropilar region which fall to $\frac{1}{3}$ of the egg surface. The transverse ribs are often not or weakly expressed. Below the lateral ribs, the chorion has a cellular structure. The freshly laid eggs are yellow.

In contrast to *M. timandra binaludica* subsp. nov., whose eggs are oval with a slight narrowing in the apical region (Kolesnichenko & Kotlobay 2020), the eggs of *M. shahvarica* sp. nov. are characterized by a pear shape. In addition, the eggs of *M. timandra binaludica* are on average larger, their maximum height is about 850.0 μm , in *M. shahvarica* the egg height is on average about 700.0 μm . In *M. timandra*, the micropile rosette is formed by 9–10 primary cells, and in *M. shahvarica*, the micropile is surrounded by 7–8 primary cells.

First instar caterpillar (Figs 24, 25A–B, Table 5)

The body length of a caterpillar recently hatched from an egg is about 2 mm ($1976.4 \pm 2.2 \mu\text{m}$) (Figs 24E–F, 25A). The body length of a caterpillar of the first instar before molting is about 3 mm (Fig. 25B). A caterpillar hatched from an egg is light green with a black head, covered with long hairs. The width of the head capsule is $412.5 \pm 0.2 \mu\text{m}$, the height is $322.5 \pm 0.7 \mu\text{m}$ (Fig. 24A). From the side, the head capsule is triangular, expanding to the area of the oral organs (Fig. 24C–D). The distance in the widest part of this triangle between the labrum and the base of the head is $240.0 \pm 1.4 \mu\text{m}$. The eyes are approximately the same size, their location is similar to that of *M. timandra binaludica* subsp. nov. (Kolesnichenko & Kotlobay 2020). The labrum with a width of $134.4 \pm 0.4 \mu\text{m}$ is divided into 2 blades. The arrangement of the bristles on the head capsule is conservative. The distance between the bristles is shown in Table 5.

We compared the distances between the bristles located on the lateral part of the head capsule of the first-instar caterpillars *M. shahvarica* sp. nov. (Table 5) and *M. timandra binaludica* subsp. nov. (Table 6). The location of the bristles and the distance between them on the head capsule are relatively stable for each species. Differences in the distance between the bristles in *M. timandra binaludica* and *M. shahvarica* are observed between L1–O1 (about 111.0 μm for *M. shahvarica* and about 113.0 μm for *M. timandra binaludica*) and L1–O3 (about 122.0 μm for *M. shahvarica* and about 127.0 μm for *M. timandra binaludica*).

Table 4. Measurements of the egg of *M. shahvarica* sp. nov.

	Egg height (μm)	Egg width (μm)	Micropile rosette diameter (μm)	Micropile diameter (μm)	Primary cell width (μm)	Primary cell length (μm)
Average value	700.1	608.0	46.5	5.1	12.5	21.2
Standard deviation	0.4	1.1	4.6	0.2	2.9	7.6

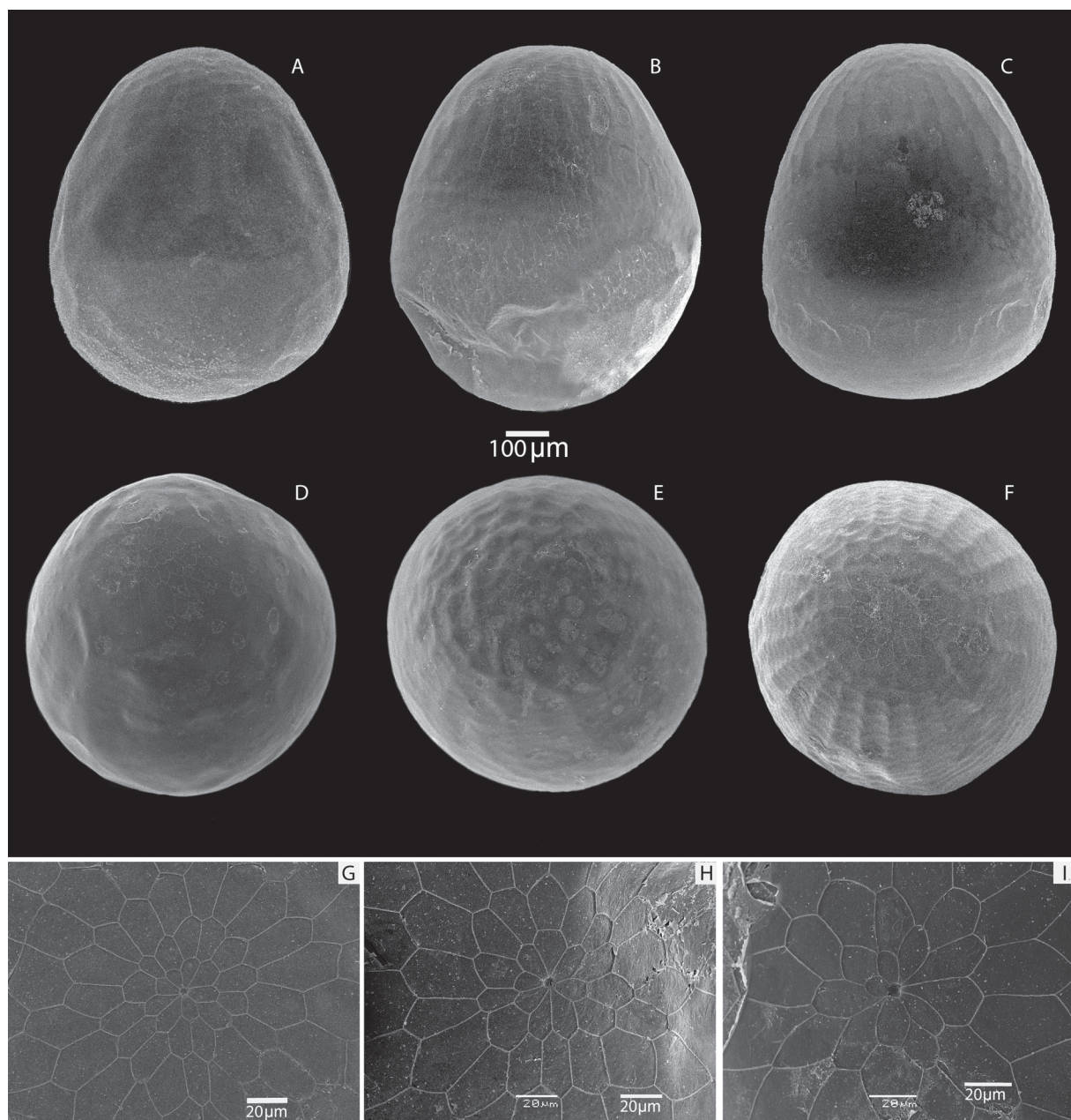


Fig. 23. Eggs of *Melitaea shahvarica* sp. nov., Iran, Semnan Prov., Shahrud area, S macroslope of Shahvar Mts, alt. 2200–2400 m. **A–C.** Lateral view. **D–F.** View from above. **G–I.** Micropile area.

Table 5. Distance between the bristles on the head capsule of *M. shahvarica* sp. nov.

Bristles	Average distance (μm)	Standard deviation
P1–P1	198.4	0.2
P2–P2	202.0	0.5
AF1–AF1	87.7	1.7
AF2–AF2	34.8	0.1
AF2–AF2	34.8	0.1
A1–A1	267.8	1.9
A2–A2	242.3	0.1
A3–A3	360.5	0.1
F1–F1	70.0	0.1
C1–C1	89.1	0.3
C2–C2	166.8	0.2
L1–O1	111.0	1.7
L1–O2	56.2	0.2
L1–O3	121.8	1.7
O1–O2	64.3	2.5
O2–O3	64.7	0.3
O1–O3	90.3	0.1
O3–SO2	79.8	0.3
O1–SO2	65.6	0.3

Second instar caterpillar (Fig. 25C)

The body length is about 3.5 mm. The main color is brown, the head and the scoli are black, the bases of the scoli are flesh-colored. The main lines of the body are expressed due to a darker color.

Third instar caterpillar (Fig. 25D)

The body length is about 4.5–5 mm. The main color is brown with flesh-colored specks. The head, the scoli and the tops of the legs are black. The black outgrowths of the linea dorsalis are located on a brown background and are present only on the abdominal segments. The bases of the scoli of the subdorsal stripe are bright yellow. The bases of the scoli of the dorsal and other stripes are flesh-colored.

Forth instar caterpillar (Fig. 25E)

The body length is about 9–12 mm. The head capsule is black. The body pattern is formed by a black main background with light orange or flesh-colored small specks. The scoli are light orange or flesh-colored. The segments of the thoracic part are characterized by the absence of yellow or flesh-colored scoli on the unpaired linea dorsalis. The paired linea subdorsalis is marked with flesh-colored scoli at their base. The linea epistigmalis paired stripe above the spiracles is black. Bright yellow scoli are located on each segment. The stigma pair (linea stigmata) is of the base color as well. The linea hypostigmalis is black

with flesh-colored scoli located on each segment. Linea basalis and linea subbasalis are black with a flesh-colored scoli on each segment.

Fifth instar caterpillar (Fig. 26A)

The body length is 15–17 mm. The head capsule is black. The body pattern is formed by bright yellow or flesh-colored scoli and a background color that varies from dark brown to black with pronounced flesh-

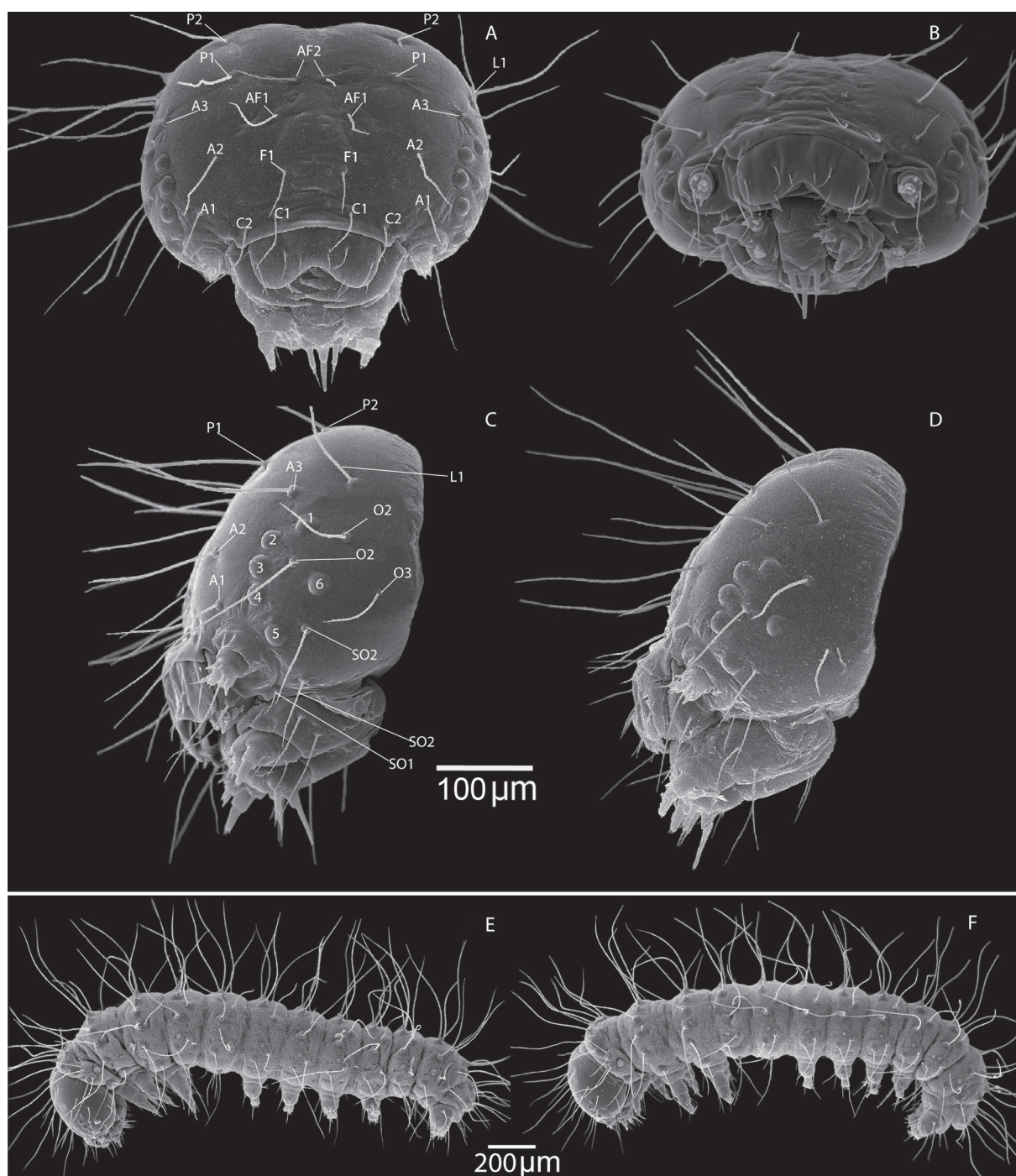


Fig. 24. First instar caterpillar of *Melitaea shahvarica* sp. nov. **A.** Head, bottom view. **B.** Head, front view. **C–D.** Head, lateral view. **E–F.** Caterpillar, lateral view.

colored specks. Unpaired linea dorsalis is marked with several bright yellow scoli with a dark (black or dark brown) base. However, there are no such outgrowths on the thoracic segments. The subdorsal (linea subdorsalis) and suprastigmal (linea epistigmalis) paired stripes located on the dorsal side and above the spiracles have a complete set of bright yellow scoli located on each segment of the body, with the exception of XII. Moreover, the scoli marking linea subdorsalis have a bright yellow base. The paired stigmata stripe (linea stigmata) has a background color. On each segment of the body (with the exception

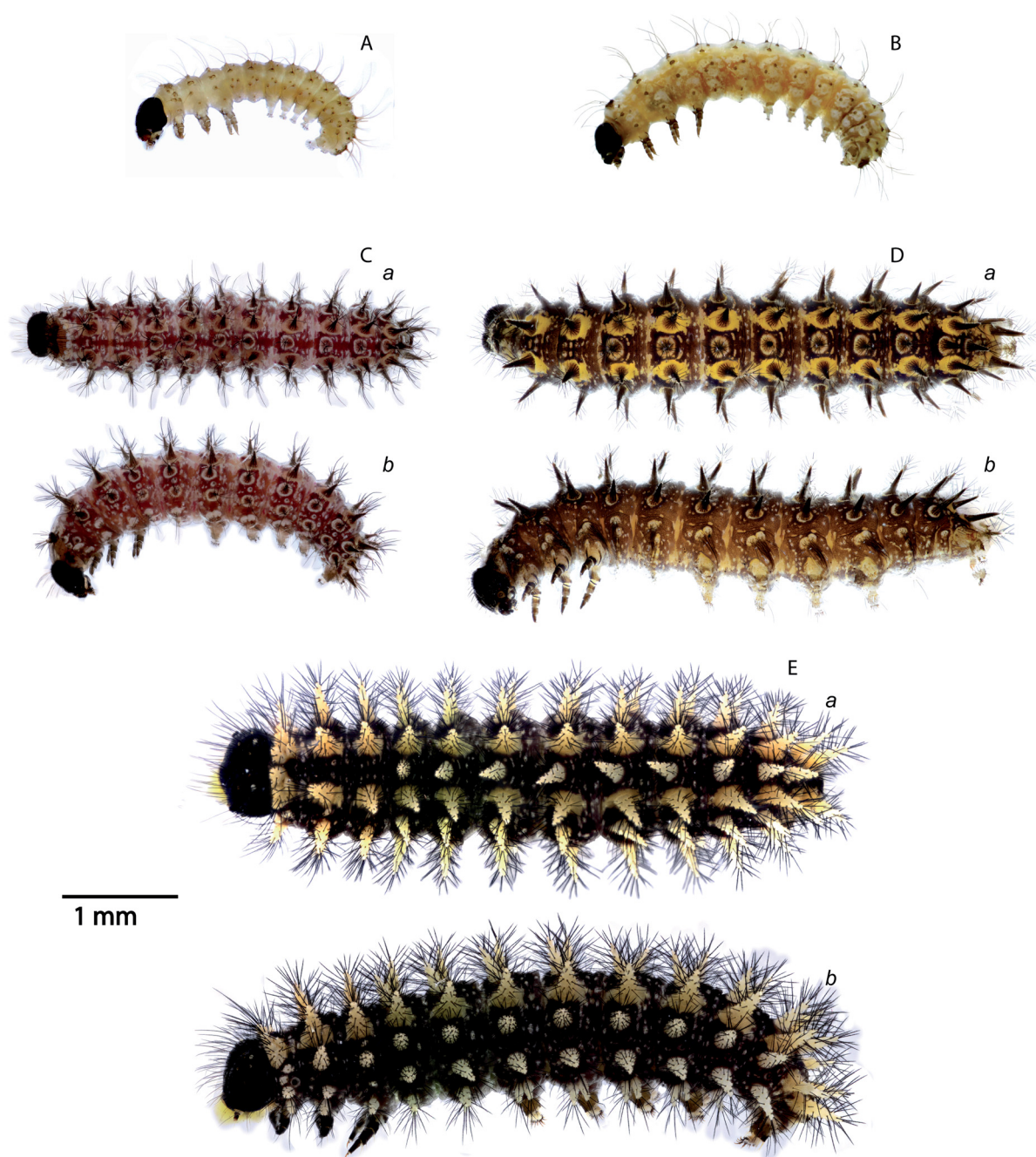


Fig. 25. I–IV instar caterpillars of *Melitaea shahvarica* sp. nov. (a = view from above; b = lateral view). **A.** First instar caterpillar after hatching. **B.** First instar caterpillar before molting. **C.** Second instar caterpillar. **D.** Third instar caterpillar. **E.** Fourth instar caterpillar.

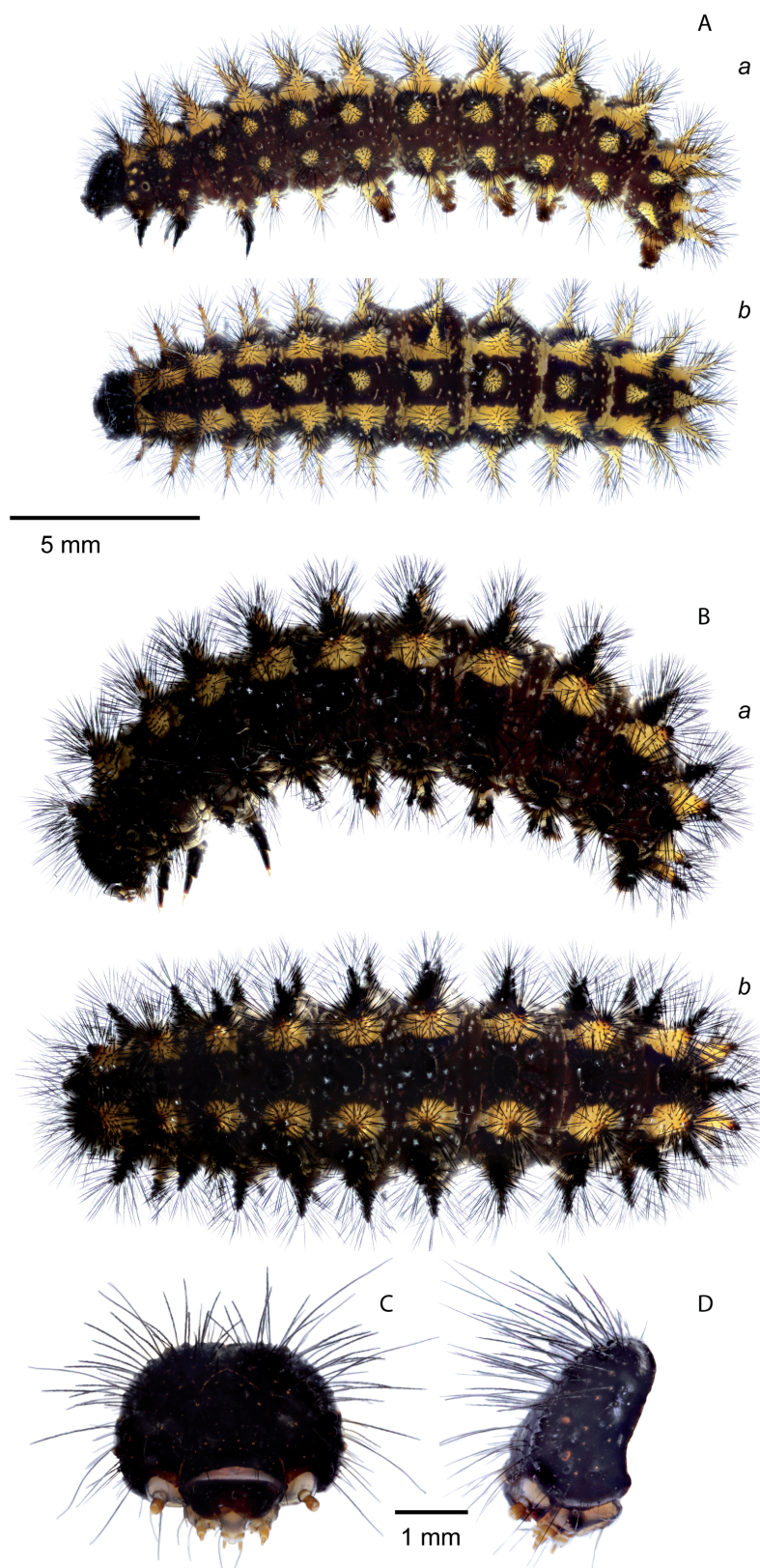


Fig. 26. V–VI instar caterpillars of *Melitaea shahvarica* sp. nov. (a = view from above; b = lateral view). **A.** Fifth instar caterpillar. **B.** Sixth instar caterpillar. **C.** Sixth instar caterpillar, head capsule, front view. **D.** Sixth instar caterpillar, head capsule, lateral view.

Table 6. Distance between the bristles on the head capsule of *M. timandra binaludica* subsp. nov.

Bristles	Average distance (µm)	Standard deviation
L1–O1	112.8	0.3
L1–O2	63.0	1.0
L1–O3	126.8	0.5
O1–O2	72.4	0.3
O2–O3	62.6	0.2
O1–O3	96.7	0.2
O3–SO2	88.1	0.0
O1–SO2	65.4	0.2

of the middle-thoracic, posterior-thoracic and last segments of the abdomen) in the middle of this stripe, under the base of the outgrowths, there are black spiracles bordered with yellow. The poststigmal line (linea hypostigmalis) is marked with a bright yellow scoli. Linea basalis and linea subbasalis (at the very bases of the legs) are located close to each other so that they practically form a single stripe with bright yellow scoli placed near each other. Poststigmal as well as basal and subbasal outgrowths are absent on the last segment of the body. The legs of the thoracic segments are black, the false legs are brown, with a flesh-colored border at the base.

It should be noted that the color described above is characteristic of some of the caterpillars that have passed into the fifth instar. For some of the caterpillars of the fifth instar, the black color of the main background and the presence of black scoli are characteristic, with the exception of the paired linea subdorsalis, whose scoli are painted in bright yellow.

Sixth instar caterpillar (Fig. 26B–C)

The body length is 19–21 mm. The head capsule is black, 2.8 mm wide and 2–2.3 mm high (Fig. 26C), covered with black hairs. The area of simple eyes is black. The eyes are approximately the same size, four of them are located closer to the epicranial suture, and two are closer to the occipital region. The forehead, the platypus, the frontal sclerites of the frontal sutures and the area of the epicranial suture are painted black. The body pattern (the 2nd and 3rd thoracic and all abdominal segments) is formed due to bright yellow scoli and the background black color. The unpaired linea dorsalis bears black scoli, there are no such outgrowths on the thoracic segments. The paired linea subdorsalis is marked with bright yellow scoli with a bright yellow base. The paired linea epistigmalis located above the spiracles has a complete set of black scoli located on each segment of the body, with the exception of XII. On the last segment, only the black dorsal and bright yellow subdorsal outgrowths are well developed. The paired linea stigmata has a background color. On each segment of the body (except for the middle-thoracic, posterior-thoracic and last segments of the abdomen), black spiracles are located in the middle of this stripe under the base of the outgrowths. The linea hypostigmalis is formed by black scoli. The linea basalis and subbasalis (at the very bases of the legs) are located close to each other so that they practically form a single stripe with black scoli placed near each other. Poststigmal, as well as basal and subbasal outgrowths are absent on the last segment of the body. The false legs and legs of the thoracic segments are black.

The described pattern refers to the caterpillars of the sixth instar, passing into the estivation mode.

Biology (Figs 27–28)

Observations in nature on the behavior and biology of *M. shahvarica* sp. nov. were carried out in May 2018 and 2019 and in the first half of July 2019 in the vicinity of the village of Gerdab on the southern macroslope of the Shahvar Mountain on the Elburs Ridge (36°31' N, 54°43' E). Observations on the development of eggs and caterpillars of *M. shahvarica* sp. nov. were performed from May to September 2018 and from May 2019 to April 2020 under laboratory conditions in Moscow.

Within the surveyed territory (Fig. 27A), *M. shahvarica* sp. nov. forms small but very dense local populations, strictly tied to the places of growth of the host plant. We found two populations at an altitude of 2150–2200 m and one at an altitude of 2500 m above sea level, separated by 2–3 km from each other. The flight of *M. shahvarica* imago at an altitude of 2150–2200 m begins, depending on weather conditions, at the beginning of the first or second decade of May and continues throughout the month. *Melitaea shahvarica* is the earliest species of fritillaries and one of the earliest, in terms of departure, species of butterflies on Shahvar Mt. At an altitude of 2500 m the flight starts 2 weeks later than at an altitude 2150–2200 m. The males fly out first, 5–7 days earlier than the females. Butterflies fly in the morning in sunny weather. Males patrol the bottoms of inter-ridge valleys in search of females. The butterfly rises to the top of the valley, passes over the ridge and descends across the neighboring valley, repeating the cycles of ascents and descents many times. At the most intensive flight period, up to 30 males flying in one direction are recorded in one place per hour. Fresh-born unfertilized females stay in the bottoms of valleys, sit on plants or make short flights. Fertilized females climb the slopes of the ridges to the places where the host plants grow.

The host plant of *M. shahvarica* sp. nov. is *Phlomoides molucelloides* (Bunge) Salmaki (Fig. 27C). *Phlomoides molucelloides* is occasionally found in dense beds consisting of several plants on crushed stone dumps along the banks of dry riverbeds at an altitude of 2000 m above sea level in a wide intermountain valley at the foot of the Shahvar mountain. But neither the imago nor the caterpillars of *M. shahvarica* was found at this station. At an altitude of 2150–2500 m above sea level, *Ph. molucelloides* occurs outlying spurs of the southern macroslope of Mount Shahvar on the upper third of the slopes of the western, northwestern and northern exposure, as well as on the tops of the ridges. It should be noted that the form of *Ph. molucelloides* growing in the described conditions is characterized by its miniature size. The height of the peduncle is usually only 5–10 cm, and even in the largest specimens does not exceed 20 cm. The growth station of *Ph. molucelloides* at an altitude of 2150–2500 m above sea level consists of steep rubble-clay scree and clay-rubble areas occupied by sparse friganoid communities of acantholimon (*Acantholimon* spp.), esparcetes (*Onobrychis* spp.), astragalus (*Astragalus* spp.) and cushion-shaped sagebrush (*Artemisia* spp.) with the latter dominating (Fig. 27B). *Phlomoides molucelloides* occurs in single plants or in small groups of 2–3 specimens almost across the specified territory, but sometimes forms very sparse (the distance between individual plants is from several to one and a half dozen meters) associations consisting of dozens to hundreds of plants and occupying a significant area. It is in such places that *M. shahvarica* lays eggs and caterpillars develop.

The fertilized female, sitting on the edge of the leaf of the host plant, feels the soil under the leaf rosette with the ovipositor for several minutes, choosing the optimal characteristics of the substrate for laying (Fig. 27D). Fourteen fresh clutches of *M. shahvarica* sp. nov. were found during the observation of egg-laying females and the examination of 38 plants of *Ph. molucelloides*. The size of clutches ranged from 24 to 146 eggs. The clutches were placed directly on the ground or rubble under the leaves of the basal rosette (Fig. 28A–B). All the clutches were found under host plants that had not yet begun to develop a peduncle. A total of 79 eggs were collected in nature in order

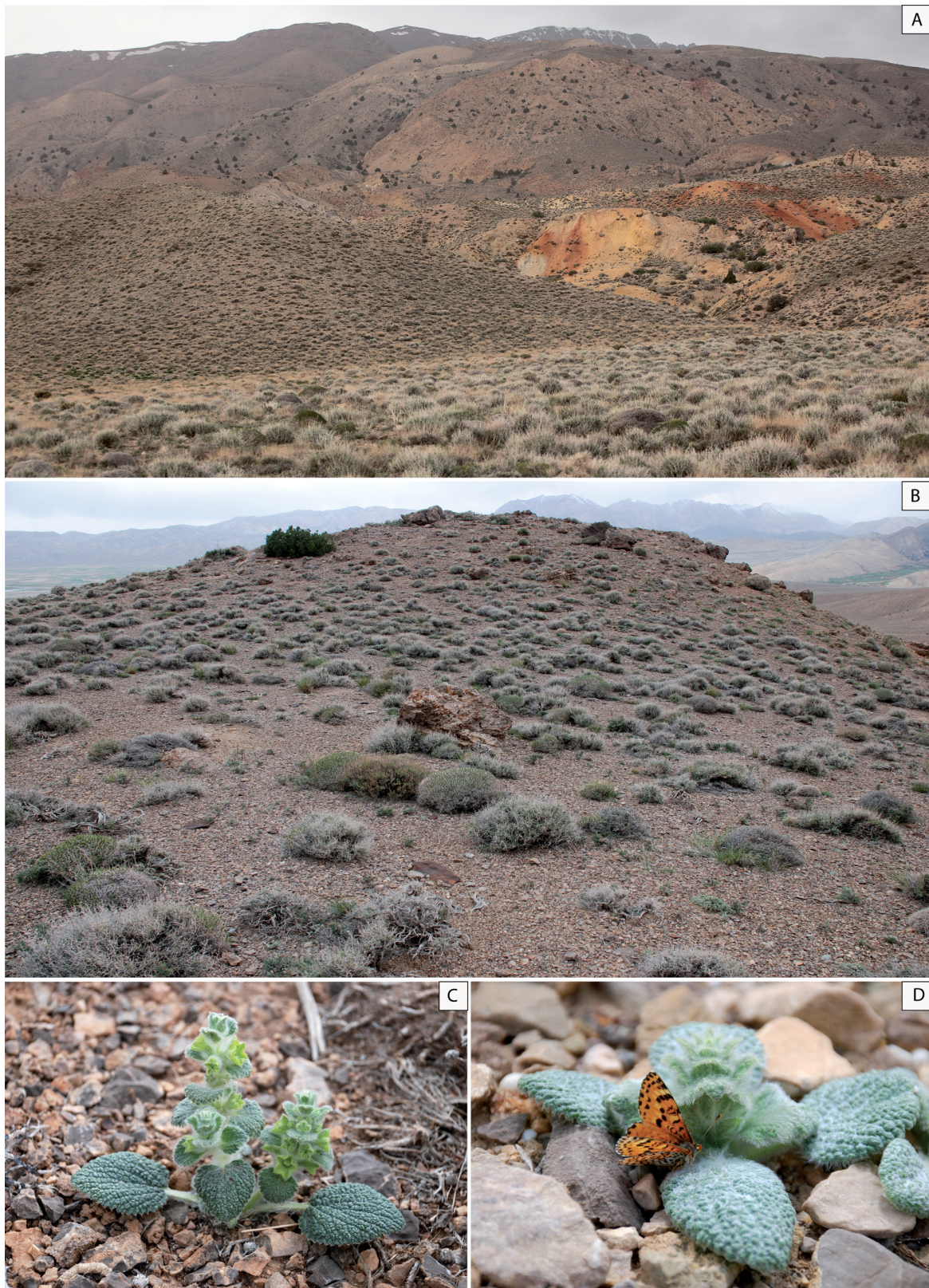


Fig. 27. Biotope, host plant, and adult of *Melitaea shahvarica* sp. nov. in nature. **A.** Shahvar Mt., E Elburs Ridge. **B.** Biotope with *Phlomoides molucelloides* (Bunge) Salmaki. **C.** Host plant *Ph. molucelloides*. **D.** Female on *Ph. molucelloides*.

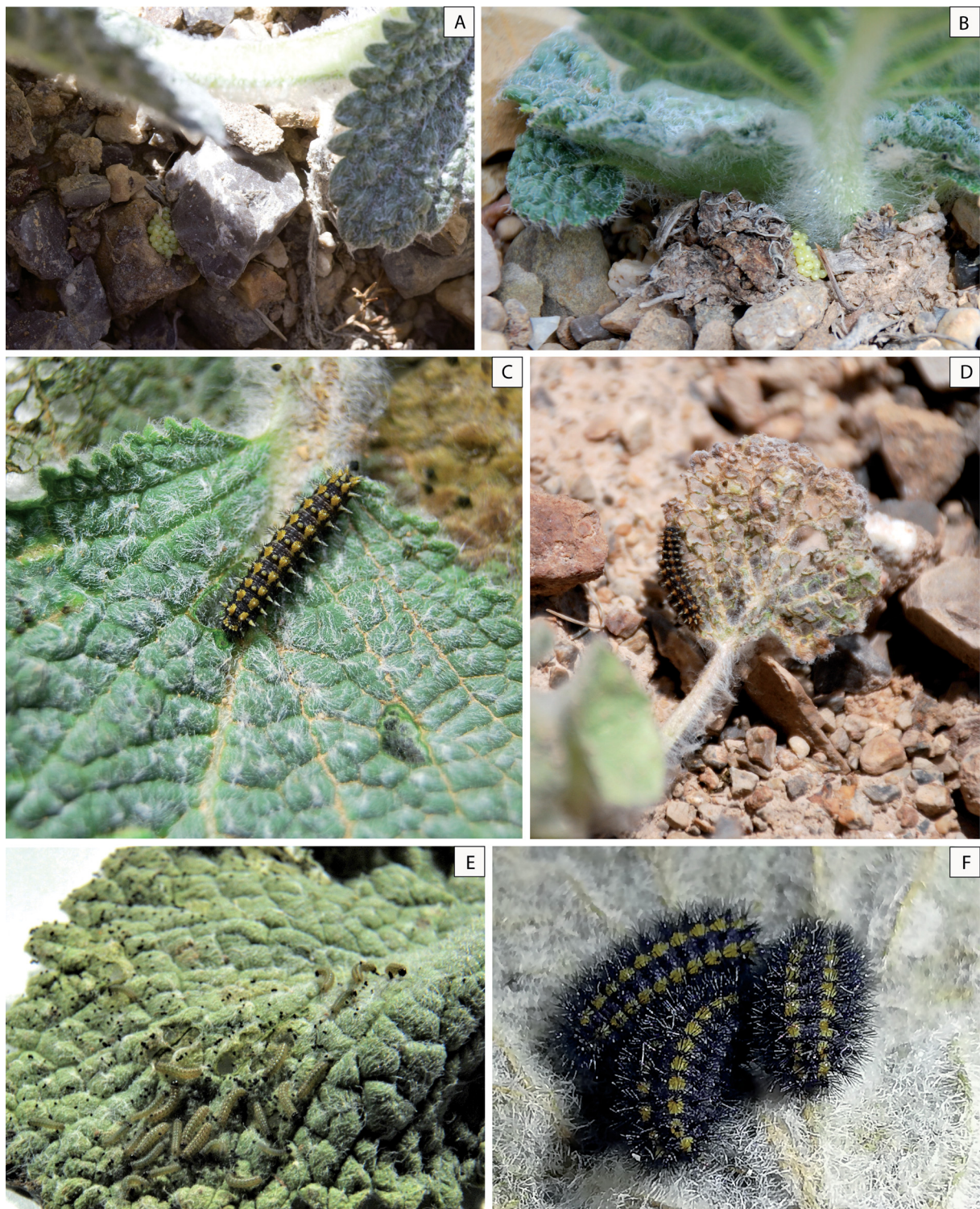


Fig. 28. Eggs and caterpillars of *Melitaea shahvarica* sp. nov. in nature and in the laboratory. **A–B.** Freshly laid eggs under a leaf of a host plant, May 2018, Iran, Shahvar Mt., alt. 2200 m. **C–D.** IV–V instar caterpillars on the leaves of the host plant *Phlomoides molucelloides* (Bunge) Salmaki, July 2019, Iran, Shahvar Mt., alt. 2500 m. **E.** I instar caterpillars in the laboratory, Moscow, May 2018. **F.** VI instar caterpillars during diapause, Moscow, October 2018.

to further monitor the development of the preimaginal stages of *M. shahvarica* under laboratory conditions. The female, placed in a small plastic cage with a host plant, laid 162 eggs in three batches, with an interval of 1–2 days. Freshly laid eggs are light yellow greenish in color, less than 1 mm in diameter. The hatching of the first caterpillars from the eggs begins after 3 days, and the mass release occurs on 7–9 days after egg laying. Of the 241 eggs (79 collected in nature and 162 obtained from the female in the laboratory) available to us, 233 caterpillars were born (96.7% yield). The day before the release, the part of the egg, where the head capsule of the caterpillar is located, darkens. Fresh-born caterpillars are about 1 mm long, light yellow-greenish in color, covered with long light hairs. The head capsule is dark brown. Immediately after emerging, the caterpillars partially eat the chorion and fall into a stupor for several hours. After coming out of the stupor, they gather in groups on the upper side of the leaf of the host plant (Fig. 28E). First, they scrape the surface, then gnaw through the leaf, leaving the veins intact. After 2–4 days after leaving the eggs, the caterpillars molt and pass into the second instar. Immediately after molting, the head capsule is pale green, after a few hours it turns black. The surface of the body of caterpillars of the second instar darkens, but instead of hairs, outgrowths of a light green color appear with a bunch of spines on top. The caterpillars actively feed and keep together in communities. In the second instar, the caterpillars spend 3–4 days and molt into the third instar. Caterpillars of the third instar are about 1 cm long, black, the head capsule is black. Dorsal and lateral outgrowths on the body are light yellow with a bunch of black spines on the top (Fig. 28C). The III instar lasts 5–7 days. The caterpillars of the IV instar do not differ in color from the caterpillars of the III instar. After passing into the IV instar, the caterpillars leave the groups and move on to an individual lifestyle. After another 5–7 days, the caterpillars pass into the V instar. In the vast majority of V instar caterpillars, the color of the lateral outgrowths changes from yellow to black, they stop feeding, seek shelter and fall into a stupor (Fig. 28F). A total of 17 V instar caterpillars did not change color and continued to feed. The cessation of feeding and the change in color occurred in these caterpillars a week after the transition to the VI instar. Changes in the behavior and appearance of the caterpillars clearly indicate a state of diapause. The transition to the diapause of caterpillars of III–V instars for many species of *Melitaea* is an obligate stage of the development cycle (Walberg *et al.* 2001). Of the 233 caterpillars, 210 (90.1%) survived to the diapause stage. The larvae died mainly from the last batch of eggs laid by the female in the cage. The caterpillars from this group were smaller in size and somewhat slower in development. The main cause of death was a violation of the molting process, caused, apparently, by birth defects of development. The caterpillars collected in nature at the beginning of July and fed further in the laboratory also passed to diapause at V instar. Of the 23 caterpillars of instars III–IV collected in nature, 21 (91.3%) survived to diapause. Thus, the development of *M. shahvarica* from the moment of egg laying to the departure of the caterpillars into diapause lasts, on average, about a month. In nature, in the conditions of the Shahvar Mountain, the vegetation of *Ph. molucelloides* at an altitude of 2150–2200 m ends in mid-June. The vegetative and generative parts of the plant completely dry out and the caterpillars of *M. shahvarica* are not observed on them. At an altitude of 2500 m, the vegetation of *Ph. molucelloides* continues until the first decade of July, and at this time, we still found caterpillars of III–IV instars of *M. shahvarica* on the host plants. According to observations in nature, the caterpillars of *M. shahvarica* actively feed in the morning and before sunset, the rest of the day they are sedentary, sitting on the underside of the leaf or on the soil under the leaves of the host plant. It should be noted that almost all *Ph. molucelloides* plants have completely sclerotized leaves by the end of the growing season. This indicates a mass feeding of caterpillars and a high density of local populations of *M. shahvarica*. The caterpillars of *M. shahvarica* are strict oligophages. Under laboratory conditions, we used *Phlomis tuberosa* Moench as a host plant, which is systematically close to *Ph. molucelloides* and grows wild in central Russia. The caterpillars of *M. shahvarica* rejected the proposed fresh leaves of other plants known as host for the genus *Melitaea* (Kolesnichenko 2006), such as plantain (*Plantago* spp.),

veronica (*Veronica officinalis* L.), wormwood (*Artemisia* spp.), and other species of Lamiaceae (*Lamium* spp., *Mentha* spp.).

We assumed that the caterpillar of *M. shahvarica* sp. nov., like that of most other members of the genus *Melitaea*, goes through seven instars in its development and must continue feeding after diapause and go through 1–2 more instars before pupation. Given the weather conditions on the Shahvar mountain, the output of the caterpillars of *M. shahvarica* from diapause should occur no earlier than the end of April. Unfortunately, we were not able to determine the factor that interrupts the diapause of the caterpillars and complete the development cycle of *M. shahvarica* in the laboratory. The caterpillars taken out of the refrigerator in March, April, and May did not respond to changes in light conditions, temperature, and humidity, to mechanical stimulation, or to the fresh host plant leaves. They did not show motor activity and soon died. Certain questions are also raised by the contradiction between observations of the development cycle of *M. shahvarica* in nature and in the laboratory. In nature, the emergence of the imago occurs in early May almost simultaneously with the beginning of the vegetation of the host plant. Obviously, in this case, the butterflies are born from overwintered pupae. Otherwise, the need for further nutrition for the caterpillar that has emerged from the diapause, two more instars and pupation would have shifted the appearance of the imago 2–3 weeks later, to the second half of May. In addition, we did not find in the first half of May any overwintered caterpillars or signs of their vital activity (leaf gnawing, droppings) despite a thorough examination of many host plants. The final answer to the question about the duration and stage of diapause in the development cycle of *M. shahvarica* should be given by further observations of the development of preimaginal stages both in nature and in the laboratory.

Distribution (Fig. 14)

Iran, Elburs Ridge, Shahvar Mt.

Of undoubted interest are the data (Tshikolovets *et al.* 2014; van Oorschot & Coutsis 2014) on the findings of butterflies from the *lutko* group (*M. lutko mimetica* in the authors' understanding) to the west and north of the habitat of *M. shahvarica* sp. nov. – on the Elburs Ridge in the vicinity of Demavend Mt. (label: Tehran, Elburz, Demavend, Ask, Lucien leg.) and on the Palyzan Ridge in the northwestern tip of the Turkmen-Khorosan Mountains (label: Golestan, E Maraveh Tappeh, N Ghazan Ghayeh, Palizan Mts). In the first case, it is about a single male, caught on 28 Jun. 1967, which, according to van Oorschot & Coutsis (2014), is characterized by a “transitional” type of the genitalia. However, the same authors expressed doubts about the correct labeling of this specimen on the grounds that for almost 50 years of active collecting of butterflies in the vicinity of Demavend Mt. there are no finds confirming the presence of representatives of the *M. lutko* group in this area. The presence of *M. timandra* on the Palyzan Ridge, in our opinion, is more realistic, despite the cardinal differences in the natural and climatic conditions of this area. It is not possible to say anything with certainty about the systematic status of these specimens since the authors of both these publications do not provide images of imago or genitalia. However, based on the characteristics of the habitat and the set of species of potential host plants (*Ph. labiosiformis* (Popov) Adylov, Kamelin & Makhm., *Ph. boissieriana* (Regel) Adylov, Kamelin & Makhm.), we believe that systematically the butterflies from Meraveh Tappeh should most likely be closer to *M. timandra binaludica* subsp. nov. despite the apparent proximity of the Palyzan Ridge to the type locality of *M. shahvarica* sp. nov. Our assumption is supported by the absence of significant barriers for the spread of *M. timandra binaludica* to the west, while *M. shahvarica*, which lives on the slopes of Shahvar Mt, is separated from the northwestern part of the Turkmen-Khorosan Mountains by a high ridge, the northern slopes of which are covered with very moist dense forests.

Key for determining the representatives of the *lutko* species group by males

1. Thin harpe is (similar in shape to a scythe) without teeth on its inner surface (Fig. 18F–I), in rare cases teeth are weakly expressed (Fig. 18F); when looking at the genitalia from above (Fig. 16D–H), the length of harpe is half of the length of valva; the slender caudal process of valva with one small spine in the distal part on the dorsal surface; the length of the caudal process is usually 3 times its width (Fig. 29C, E). Saccus is wide (Fig. 16E–I), distally rounded, its length is 1.5 times as great as width. UPS pattern is contrasting, with a well-developed UPF pale-yellow postdiscal area (Fig. 6A–D). Afghanistan, Pakistan: Balochistan *M. mimetica* Higgins, 1940
 - Harpe is noticeably thickened in the central part (it resembles a sickle in shape), there are always clearly visible teeth on its inner surface (Figs 18A–E, 19); when looking at the genitalia from above, the length of harpe is about a third of the length of valva (in the case of *M. shahvarica* sp. nov., it can be a half of the length) (Fig. 16A–C); the caudal process of valva is usually wide, with several spines in the distal part on the dorsal surface, the length of the caudal process is 1.5 times its width. Saccus is thin, distally pointed, its length is 2 times as great as width (Figs 16A–C, 17). UPS pattern of the is monophonic with a weakly developed UPF postdiscal pale-yellow area 2
2. Harpe is short, strongly expanded in the central part, its length is 2 times as long as width (Fig. 18D–E). On the inner surface of harpe there is a well-defined row of teeth with a powerful tooth in the central part and small teeth on both sides of it. The broad caudal process of valva is elongated and distally strongly inwardly concave with a pointed apex (Figs 3H–I, 29F). UPH black basal suffusion is well developed and covers more than a third of the wing surface, UPH submarginal row is formed by interconnected black lunules (Fig. 2A). Pakistan: Chitral, Birmoglasht, Malakand, Murree *M. lutko* Evans, 1932
 - The length of harpe is 3–4 times as great as width, there are small and rare teeth on the inner surface of harpe (Figs 18A–C, 19). The caudal process is distally not strongly inwardly concave with a pointed apex (Figs 10, 22, 29A–B, D, G–H). UPH black basal suffusion covers less than a third of the wing surface (Figs 2B–D, 9A–D, 15A–D, 21A–D) 3
3. Valva is sharply expanded in the central part, due to a well-marked protrusion of the ventral side, the length of valva is 1.5 times as great as width (Figs 22, 29A). The thin distal part of harpe is curved downwards, there are few teeth on its inner surface (Fig. 18A–C). The anterior and posterior parts of aedeagus are approximately on the same straight line, there is no protrusion at the junction of both parts of aedeagus on the ventral side (Fig. 29A). UPH submarginal row is often reduced. There is UPF black macule located between veins Sc and R5 and formed by the fused submarginal and postdiscal costal dots centered with orange or pale spot. UPH discal macules are either absent or expressed only as a row of dots between the veins A2–M3 (Fig. 21A–D). Iran: East Elburz *M. shahvarica* sp. nov.
 - Valva is elongated, its length is 2 times as great as width, the ventral protrusion of the valva is smoothed (Fig. 10). Harpe is noticeably thickened in the central part due to the presence of teeth on the inner surface (Fig. 19). The posterior part of aedeagus is mostly located at an angle to the anterior one and is directed downward, at the junction of both parts of aedeagus on the ventral side there is a well-marked protrusion (Figs 10, 29B). UPH submarginal row is well defined (with rare exceptions) (Fig. 15A–D). UPF black macule located between veins Sc and R5 and formed by the fused submarginal and postdiscal costal dots is absent. UPH discal row is well defined (ssp. *binaludica* subsp. nov.) or absent (ssp. *timandra*). Iran, Turkmenistan, Afghanistan *M. timandra* Coutsis & van Oorschot, 2014

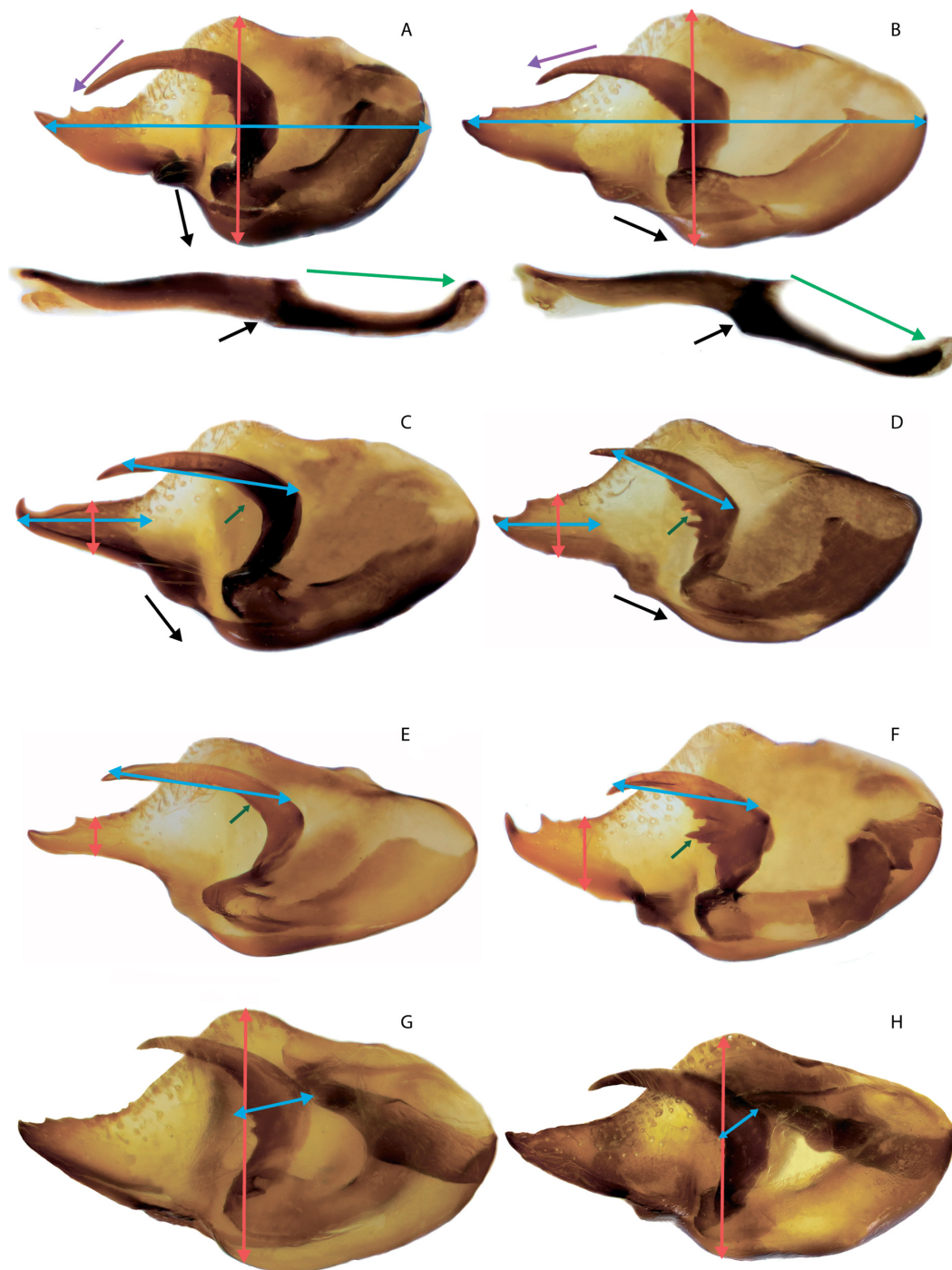


Fig. 29. Differences in the structure of valva and aedeagus of the *lutko* species group. **A.** *Melitaea shahvarica* sp. nov. **B, D, H.** *M. timandra binaludica* subsp. nov. **C–E.** *M. mimetica* Higgins, 1940. **F.** *M. lutko* Evans, 1932. **G.** *M. timandra timandra* Coutsis & van Oorschot, 2014. **A.** Iran, Semnan Prov., Shahrud area, S macroslope of Shahvar Mts, alt. 2200–2400 m. **B.** Iran, Rezavi Khorassan Prov., Kuh-e-Binalud Mts, Dorrud v. vicinity, alt. 2430 m. **C.** Afghanistan, Bamian Prov., Punjab Distr., 10 km NE of Varas v., alt. 2400 m. **D.** Afghanistan, Band-i-Amir, Hazarajat. **E.** Pakistan, Balochistan, Quetta, Urak, alt. 2400–2700 m. **F.** Pakistan, Chitral, Gol National Park, alt. 2700 m. **G.** Turkmenistan, Sary-Yazy, alt. 700 m. **H.** Iran, Rezavi Khorassan Prov., Kuh-e-Binalud Mts, Dorrud v. vicinity, alt. 2430 m.

Key for determining the representatives of the *lutko* species group by females

1. Postvaginal plate is triangular-shaped with wide lateral edges and narrowed distally (Figs 4F–I, 11) 3
 - Postvaginal plate is oval or broadly oval (Fig. 4A–E) 2
2. UPS black pattern is expanded and well developed: UPH basal suffusion covers at least a third of the wing surface, UPF postdiscal row, as well as UPH discal and submarginal rows are well developed along the entire length of the wings (Fig. 2E). Pakistan: Chitral, Birmoglasht, Malakand, Murree *M. lutko* Evans, 1932
 - UPS black pattern is reduced: UPH basal suffusion covers noticeably less than a quarter of the wing surface, UPF postdiscal row is represented by 1–2 dots at the costal edge, UPH discal and submarginal row are reduced or partly reduced (Fig. 21E–H). Iran: East Elburz *M. shahvarica* sp. nov.
3. The antevaginal plate is expanded in the dorsoventral direction, its outer edge extends beyond the boundaries of the bend of the postvaginal plate (auricles) (Fig. 4F–I); UPF with a well-defined pale-yellowish postdiscal area and pale-yellowish macule in the distal part of discoidal cell (Fig. 6E–H). Afghanistan, Pakistan: Balochistan *M. mimetica* Higgins, 1940
 - The antevaginal plate is narrow in the dorsoventral direction, its outer edge does not extend out or barely extends beyond the boundaries of the bend of the postvaginal plate (auricles) (Fig. 11); UPF with a weakly defined pale-yellowish postdiscal area (Figs 9E–H, 15E–H). Iran, Turkmenistan, Afghanistan *M. timandra* Coutsis & van Oorschoot, 2014

Discussion

Our research, including the study of extensive collection material, analysis of literature data as well as field studies of biology and distribution, allowed us to understand better the systematic status of different populations of *M. lutko*, *M. timandra*, *M. shahvarica* sp. nov. and *M. mimetica*, to clarify the boundaries of their natural habitats and to set up a hypothesis about the phylogenesis of the group and the reasons that led to the formation of four morphologically similar species.

Distribution and systematics

Melitaea lutko is distributed in northern Pakistan on the eastern spurs of the Hindu Kush (near Chitral and Malakand in Khyber Pakhtunkhwa Province and Merri in Punjab Province) at an altitude of 2700–3000 m.

Melitaea timandra occupies a wide range within Central Asia, covering several large areas of the Iranian Highlands from the Khorasan Mountains in Iran across the foothills of the Kopet Dag Ridge and the southeastern Kara-Kum Desert to the western spurs of the Hindu Kush in the Band-e-Amir Lakes region and the northern slopes of the Koh-i-Baba Ridge (Bamyan Province, Afghanistan). Within this range, *M. timandra* is represented by two subspecies: the nominate and the newly described in this publication. The nominate subspecies is distributed in the sands of the south-eastern part of the Kara-Kum (Murgab and Tejen valleys, Turkmenistan) and in the foothill region of Paropamiz (Badkhis, Turkmenistan), not rising above 700 m. On the western border of the range, the nominate subspecies reaches the desert sub-mountain plains in the area of the city of Baharden in Turkmenistan. *Melitaea timandra binaludica* subsp. nov. occupies the extreme north-eastern regions of the Khorasan Mountains (Kuh-e-Binalud, which is an orographically isolated ridge in the Razavi Khorasan Province), and in the south its range covers the Kayen mountain system in Southern Khorasan, which already belongs to the Eastern Iranian Mountain Region (Petrov 1955). To the West this subspecies is distributed to the eastern Elburz. To the East, the area of this subspecies covers the western Hindu Kush in Afghanistan. Ecologically, *M. timandra binaludica* is associated with gravelly slopes at altitudes from 1500–2500 m in the western part of the range and up to 3200 m in the eastern part.

The westernmost species *M. shahvarica* sp. nov. lives on the slopes of Shahvar Mt. (Semnan Province, Iran), which is a part of the Elburz Mountain system (Petrov 1955). The habitat of the species is confined to the tops of clay-crushed spurs covered with friganoid vegetation at an altitude of 2150–2500 m.

Melitaea mimetica is distributed to the South and not as widely as *M. timandra*. The extreme eastern habitat is in the vicinity of Gawar, Punjab Province, Pakistan. The absolute altitude there is no more than 500–600 m. In Afghanistan, the species is found in the vicinity of Kabul and in the Pansher Gorge at an altitude of 2200–2800 m. Further West, its range covers the Koh-i-Baba Ridge and the mountains in the vicinity of Punjab, Bamyān Province, where the species rises to an altitude of 4000 m, as well as the Band-i-Bayan Ridge in Gor Province at an altitude of 2400–2700 m. To the South, at a considerable distance from the habitats described above, *M. mimetica* is distributed in the northern part of Balochistan (Pakistan) in the arid mountains of the Quetta mountains junction at an altitude of 1600–2500 m.

Van Oorschot & Coutsis (2014) provide data on the existence of specimens on the contact line of the ranges of *M. timandra* and *M. mimetica* (*M. lutko* in their understanding) in the Koch-i-Baba mountains, occupying an intermediate position between these two species in terms of the structure of the male genitalia. According to their data, the ‘intermediate’ specimens are hybrids between *M. lutko* and *M. mimetica*. Van Oorschot & Coutsis (2014) also include the taxon *delerei*, described from the vicinity of Kabul to the same ‘intermediate’ type. The main feature of the ‘intermediate’ type of genitalia is a shorter and wider caudal process of the valva. From our point of view, it is more plausible to assume that in the highlands of the Koh-i-Baba Ridge and in the vicinity of Kabul, where most of the ‘intermediate’ specimens come from, not hybrids of the two species fly, but *M. mimetica* itself. In our opinion, the genitalia of the two ‘intermediate’ specimens depicted in the publication of van Oorschot & Coutsis (2014: 265) undoubtedly belong to *M. mimetica*, although they bear the features indicated above. The assignment of specimens from the Koh-i-Baba Ridge and the vicinity of Kabul to *M. mimetica* is primarily evidenced by the characteristic structure of a thin elongated harpe without teeth on the inner side, or with minimally developed teeth. The shape of the caudal process of the valva, in our opinion, is quite variable (as can be seen even in Fig. 3A–G) and, considering only one feature (the shape of the caudal process), an erroneous conclusion can be made that such specimens belong to the close species *M. timandra*. We do not exclude that the nature and degree of morphological variability will allow us to consider these specimens as a subspecies of *M. mimetica* in the future, especially since the ecological habitat conditions of *M. mimetica* on the Koh-i-Baba Ridge differ significantly from those at the type locality of the nominative subspecies. Perhaps this is the already described taxon *delerei*. To confirm the hypothesis of the existence of a subspecies of *M. mimetica* in the Koh-i-Baba mountains, additional research is necessary, since the currently available collection material and literary data do not allow us to unequivocally confirm the assumptions made. Our opinion is supported by the fact that we did not find ‘intermediate’ specimens when studying the collection material available to us, including from the habitats mentioned above. All the preparations of the genitalia studied by us, with undoubtedly existing variability in the structure of the harpe and the caudal process of the valva, could be unambiguously attributed either to *M. timandra* or to *M. mimetica*. The results of our research do not allow us to say with complete confidence about the syntopia of these two species either, which is indicated by van Oorschot & Coutsis (2014). We have not found in the collections and in the literature irrefutable data on the simultaneous habitation of two species within the same location. We can only assume, with a serious degree of doubt, that the studied species are sympatric on the contact line. Mapping the localities of finds (as far as possible with an abundance of uncertainties in the labels) makes it very likely that the Koh-i-Baba Ridge is the boundary separating the ranges of the two species. *Melitaea timandra* is distributed along the northern slopes of the ridge and further north into the Band-e-Amir region. *Melitaea mimenica* inhabits the southern slopes and then spreads in the south-west and south-east directions.

Associations with host plants

The above description of the habitats shows how diverse the habitat stations of *M. lutko*, *M. timandra*, *M. shahvarica* sp. nov. and *M. mimetica* are: from flat sandy deserts to crushed-rocky mountain slopes up to altitudes of 4000 m. The plasticity in relation to the types of habitats in butterflies can be explained only by the similar ecological plasticity of host plants, the presence and availability of which is the main limiting factor determining the possibility for a species to inhabit a particular territory. In the case studied such a wide adaptability to various living conditions can be realized on the basis of two strategies of feeding behavior: either polyphagy or oligophagy associated with an ecologically plastic host plant. The monophagy and oligophagy of desert species and their close association with the host plant, as an adaptation to arid biotopes, were noted by Shchetkin (1965). Comparison of distribution of the nominative subspecies *M. timandra* and its host plant *Ph. regeliana* in Turkmenistan (Fig. 30) showed an absolute coincidence of specific habitats of butterflies and known places of growth of *Ph. regeliana* (Nikitin *et al.* 1954; Shishkin *et al.* 1954; Abdullayeva *et al.* 1987). In addition to the southern Kara-Kum and Badkhyz, *Ph. regeliana* is also common in the Bactrian lowlands, in the Gerirud Valley, and in the low mountains of the extreme north-east of Iran, in most cases at altitudes of 300–600 m, except for one point on the southern slopes of the Safed-Koch Ridge in the Paropamiz Mountains, where it rises above 1000 m (Shishkin *et al.* 1954; Hedge 1982). These data indicate that the main factor limiting the habitat of *M. timandra timandra* in the foothills and lowland semi-deserts is a strict dependence on a host plant with a similar geographical and altitudinal distribution. What then allows subspecies and populations of *M. lutko*, *M. timandra*, *M. shahvarica* and *M. mimetica*, with such a narrow food specialization, to climb mountains to a height of more than 4000 m and exist in completely different conditions for almost 2000 km in longitude and 1000 km in latitude? In our opinion, this is possible only if the species of the studied group, while conserving trophic relations, are in the process of cospecification with the host plant, or are capable of a food shift, that is, they switch to feeding on other species of the genus *Phlomoides*, growing in other altitude zones and in other climatic conditions. We believe that the reason for the expansion of the range of the ancestral form of the *lutko* group is the expansion of the range of the host plant and its moving to other high-altitude zones. The division of the studied group of fritillaries into four independent species and the formation of subspecies is closely related to the morphogenesis of a specific group of plants from the genus *Phlomoides*, formerly referred to the genus *Eremostachys* Bunge, and is the result of the process of coevolution of the host plant and the symbiont.

To check our assumptions about the food associations and the reasons for diversification, we compared the available data on the distribution of *M. lutko*, *M. timandra*, *M. shahvarica* sp. nov. and *M. mimetica* with data on the distribution of species of the former genus *Eremostachys* obtained from our own field observations and taken from literary sources (Nikitin *et al.* 1954; Shishkin *et al.* 1954; Hedge 1982; Abdullayeva *et al.* 1987; Hedge 1990; Salmaki *et al.* 2012a, 2012b). Modern taxonomy of plants under consideration, based on molecular genetic studies, suggests including all representatives of the former genus *Eremostachys* in the genus *Phlomoides* (Abdullayeva *et al.* 1987; Salmaki *et al.* 2012a). Nevertheless, even within the genus *Phlomoides*, they remain a separate monophyletic group. For the convenience of further discussion, we adhere to the system of sections of the genera of *Eremostachys* given in the fundamental work *Flora Iranica* (Hedge 1982). Plants of the former genus *Eremostachys* are widespread from the Balkans to Mongolia, including the entire territory of the Iranian Highlands, many species, often very close in systematic terms, ranging from deserts to highlands and from temperate to tropical climates. This group of plants is quite young in evolutionary terms. The process of rapid speciation in this group began in the Neogene (most likely in the late Miocene) as a product of xerophilization of ancient mesophilic mint family plants in the expanses of Central Asian deserts and semi-deserts formed as a result of the desiccation of the Tethys Sea and the subsequent aridization of the climate (Popov 1940; Hedge 1982). It is known that in mountainous areas with pronounced aridity, the penetration of lowland representatives of desert vegetation to significant heights is observed (Agakhanyants 1981). The greatest expert on the genus *Eremostachys*, Popov (1940), believed that the

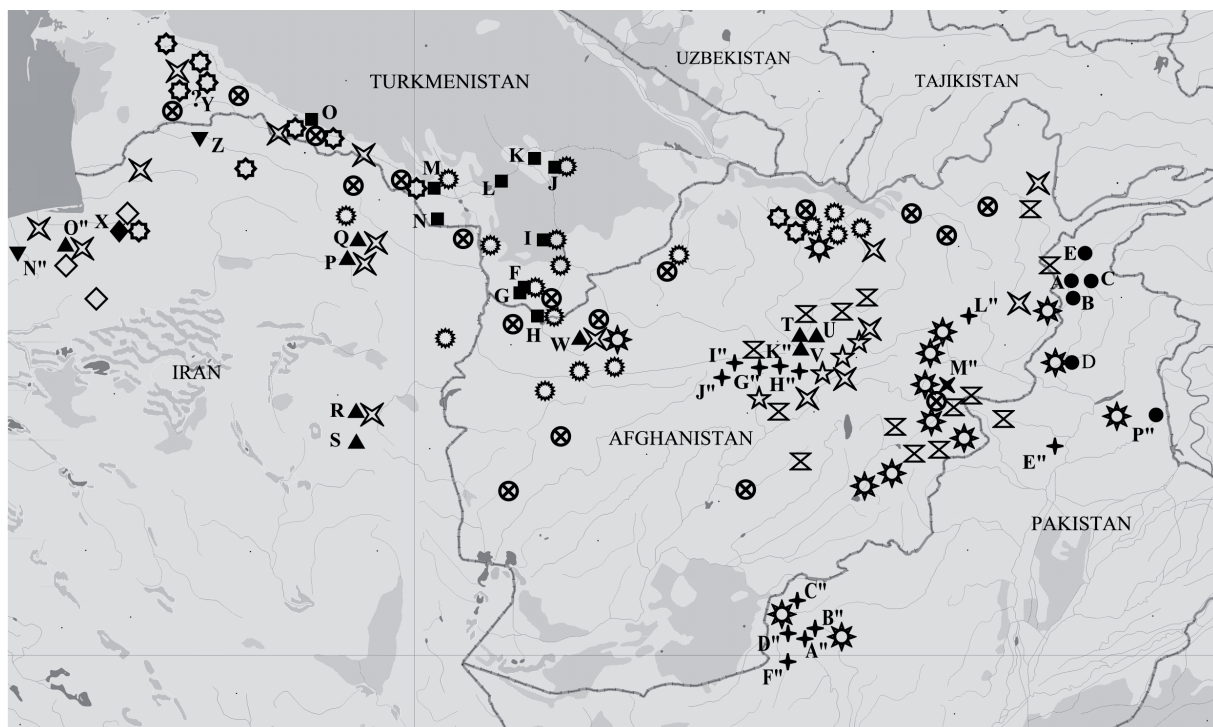


Fig. 30 (continued on next page). Distribution of the *lutko* species group fritillaries in combination with the distribution of known and suspected species of host plants from the genus *Phlomoides* Blume. ● = *Melitaea lutko* Evans, 1932; ■ = *M. timandra timandra* Coutsis & Oorschot, 2014; ▲ = *M. timandra binaludica* subsp. nov.; ◆ = *M. shahvarica* sp. nov.; ★ = *M. mimetica mimetica* Higgins, 1940; ✕ = *M. mimetica delerei* Heidemann, 1954; ? = unconfirmed findings of *M. timandra*; ▼ = *M. timandra* with an unclear subspecies status; ☼ = *Phlomoides regeliana* (Aitch. & Hemsl.) Adylov, Kamelin & Makhm.; ☼ = *Phlomoides boissieriana* (Regel) Adylov, Kamelin & Makhm.; ☆ = *Phlomoides laciniata* (L.) Kamelin & Makhm.; ✕ = *Phlomoides labiosiformis* (Popov) Adylov, Kamelin & Makhm.; ⚙ = *Phlomoides loasifolia* (Benth.) Kamelin & Makhm.; ◇ = *Phlomoides molucelloides* (Bunge) Salmaki; ✕ = *Phlomoides acaulis* (Beck ex Rech.f.) Salmaki; ⊗ = *Phlomoides labiosa* (Bunge) Adylov, Kamelin & Makhm. A. Pakistan, Chitral, Chaghbini CGNP, alt. 2700–3000 m. B. Pakistan, Khyber Pakhtunkhwa, Drosh. C. Pakistan, Khyber Pakhtunkhwa, Keon Nullah. D. Pakistan, Khyber Pakhtunkhwa, Malakand. E. Pakistan, Khyber Pakhtunkhwa, Birmoglasht. F. Turkmenistan, Badkhyz, Kepeli, alt. 700 m. G. Turkmenistan, Badkhyz, Kyzyl-Jar, alt. 700 m. H. Turkmenistan, Kushka, alt. 700 m. I. Turkmenistan, Murgab river, Sary-Yazy, alt. 300 m. J. Turkmenistan, 30 km E of Bairam-Ali, Zahmet, alt. 240 m. K. Turkmenistan, Bairam-Ali, alt. 230 m. L. Turkmenistan, Kara-Kum desert, 30 km W of Mary, alt. 200 m. M. Turkmenistan, Dushak, alt. 250 m. N. Turkmenistan, Chaacha, alt. 400 m. O. Turkmenistan, Bakharden, alt. 200 m. P. Iran, Khorossan Razavi, Kuh-e-Binalud Mts, Qadamgah area, Gerina, alt. 2000 m. Q. Iran, Khorasan Razavi, Kuh-e-Binalud Mts, 15 km SW of Zoshk, alt. 2300–2500 m. R. Iran, S Khorosan, 75 km N of Birjant, Sede, alt. 1500 m. S. Iran, S Khorosan, 35 km N of Birjant, alt. 1500 m. T. Afghanistan, Bamian, Band-e-Amir, Dzhudoi-Kvak Gorge, alt. 3200 m. U. Afghanistan, Bamian, Band-e-Amir, Hazarajat, alt. 3000–3200 m. V. Afghanistan, Bamian, Koh-i-Baba Mts, Joshanak, alt. 2800 m. W. Afghanistan, Heart, Qala-i-Naw, Kashka pass. X. Iran, Semnan, Shahvar Mt., alt. 2200–2500 m. Y. Turkmenistan, Kara-Kala, Monjukly Ridge, 300–700 m. Z. Iran, Golestan, E Maraveh Tappeh, N Ghazan Ghayeh, Palizan Mts. A''. Pakistan, Balochistan, Quetta, Urak, alt. 2500 m. B''. Pakistan, Balochistan, Ziarat, alt. 2500 m. C''. Pakistan, Balochistan, Khojak, alt. 1700 m. D''. Pakistan, Balochistan, Zaghum, alt. 1600 m; E''. Pakistan, Punjab, Gawar, alt. 500 m. F''. Pakistan, Balochistan, Sheik Wazil, alt. 1600 m. G''. Afghanistan, Bamian, Hushkak, alt. 2700–

most ancient representatives of the genus are distributed in the arid plains of the Central Asian steppes and deserts, and their advance from the foothills to the arid regions of the middle and high mountains is accompanied by active speciation. This statement is confirmed both by the morphology of plants (lowland species contain the most ancient details of the structure of the flower) and by the features of the habitats: lowland species are few and occupy vast territories, and dozens of species are known within the mountain regions and most of them are local endemics (Popov 1940; Hedge 1982; Salmaki *et al.* 2012a).

In total, more than 60 species of the former genus *Eremostachys* are known in the Iranian Highlands and adjacent territories (Hedge 1982). We did not consider endemic species with a very local distribution and species whose range is obviously outside the ranges of *M. lutko*, *M. timandra*, *M. shahvarica* sp. nov. and *M. mimetica*. However, we considered the maximum elevation of plant distribution, noting only those species that occur in the same altitude zone as the studied species of fritillaries. The comparison showed that the habitat area of almost every subspecies, either a separate population of *M. lutko*, *M. timandra*, *M. shahvarica* and *M. mimetica* coincides with the territory of growth of a certain species, or a small group of 2–3 systematically close species of *Phlomoides* (former *Eremostachys*) (Fig. 30).

The coincidence of the habitats of *M. timandra timandra* and the growth of *Ph. regeliana* has already been noted above. The host plant of *M. timandra binaludica* subsp. nov. on the Kuh-e-Binalud Ridge is *Phlomoides labiosiformis* (Kolesnichenko & Kotlobay 2020), which is systematically very close to *Ph. regeliana*. In the Afghan territory, in the western Hindu Kush, in the Band-e-Amir region, the subspecies *M. timandra binaludica* is apparently related to *Phlomoides acaulis* (Beck ex Rech.f.) Salmaki. For the population of *M. lutko* in Chitral, it is more difficult to assume host plants since the data available to us on the distribution of species of *Phlomoides* in Pakistan are of a general nature and are given without specifying the exact places of finds. Nevertheless, considering the available data on Chitral and relying on data for similar areas of the Hindu Kush in the neighboring Afghan Province of Nuristan, we believe that here, *M. lutko* is trophically related, most likely, to *Ph. acaulis* or to *Ph. labiosiformis*. Further south, in Malakand, the distribution of *M. lutko* coincides with the distribution of *Phlomoides loasifolia* (Benth.) Kamelin & Makhm. For *M. mimetica* on the Koh-i-Baba and Bandi-Bayan Ridges, the most likely candidates for host plants are *Phlomoides laciniata* (L.) Kamelin & Makhm. and *Ph. labiosiformis*. In the vicinity of Kabul and in Balochistan, *M. mimetica* is most likely related to *Ph. loasifolia*, *M. timandra*, *M. lutko* and, most likely, *M. mimetica* are trophically related to systematically close species of dissected-leaved *Phlomoides* from the *Phlomoides* section of the *laciniata* group, and *M. shahvarica* sp. nov. is related to the whole-leaved species *Ph. molucelloides* from the *molucelloides* section of the *molucelloides* group, which is separate systematically.

The data of the analysis on the distribution and relationships with possible host plants allows us to make the following assumptions, and if confirmed, it will be possible to further clarify and adjust the systematic status and ranges of various populations of species of the *lutko* group:

- the presence of host plants and suitable biotopes (arid gorges) makes the habitation of *M. timandra* in the Western and Central Kopet-Dag quite likely, despite the absence of indisputably confirmed finds at the moment;

2800 m. **H''**. Afghanistan, Bamian, Punjab Distr., 10 km NE of Varas, alt. 2400 m. **I''**. Afghanistan, Ghor, 17 km E of Changcharan, 15 km S of Bandi-Ali, Gazak Mts, alt. 2400 m. **J''**. Afghanistan, Ghor, Bayan Range, 15 km S of Changcharan, Kindival valley, alt. 2700 m. **K''**. Afghanistan, Bamiyan, Koh-i-Baba Mts, Panjao, alt. 3000 m. Afghanistan, Bamiyan, Koh-i-Baba Mts, Shah-tu-Kotal, alt. 4000 m. **L''**. Afghanistan, Kapisa, Pandshir valley, alt. 2200–2800 m. **M''**. Afghanistan, Kabul. **N''**. Iran, Tehran, Elburz Ridge, Demavend Mt., Ask, alt. 1800 m. **O''**. Iran, Semnan, Foulad Mohaleh, alt. 2200 m. **P''**. Pakistan, Punjab, Murree.

- the butterflies indicated by van Oorschot & Coutsis (2014) for Kala-i-Nao in Afghanistan (Safed-Koch Ridge, Western Paropamiz), given the natural conditions and a set of host plants, most likely belong to *M. timandra binaludica* subsp. nov., and not to *M. timandra timandra*;
- the natural conditions and the presence of *Ph. regeliana* make it very likely that *M. timandra timandra* inhabits the north of Afghanistan in the Bactrian Lowland, especially in the vicinity of Mazar-i-Sharif (Balkh Province), as well as in the vicinity of Herat in the Gerirud Valley (Herat Province).

The results of the study also confirm our assumption that *M. lutko*, *M. timandra*, *M. shahvarica* sp. nov. and *M. mimetica* are oligophagous at the species level and are trophically related to only six or seven systematically close species of the genus *Phlomoides* from the former genus *Eremostachys*, despite the huge species diversity and wide distribution of these plants in the territory under consideration. At the level of subspecies and individual populations, *M. lutko*, *M. timandra*, *M. shahvarica* and *M. mimetica* are monophagous, feeding on a local territory with only one species of *Phlomoides*, which is confirmed by our data from field studies of the biology of *M. timandra timandra* in Kara-Kum, *M. timandra binaludica* subsp. nov. on the Kuh-e-Binalud Ridge and *M. shahvarica* on Shahvar Mt.

Thus, the relationship between the *lutko* group fritillaries and their host plants can be a vivid example of how the trophic connection with an ecologically plastic host provides the symbiont with additional opportunities to expand living territories in a wide range of climatic and other physical conditions of the habitat in the process of coevolution.

Phylogenesis and adaptation

The above data on trophic relationships, geographical distribution of *M. lutko*, *M. timandra*, *M. shahvarica* sp. nov., *M. mimetica*, and their host plants, as well as literature data on the evolution of plants from the genus *Phlomoides* and fritillaries from the genus *Melitaea*, give us a reason to set up some hypothesis about the phylogenesis and adaptation of the *lutko* group.

We believe that the phylogenesis of species of the *lutko* group occurred in full accordance with the Eichler rules (Eichler 1942), according to which the evolution of taxa of symbionts of their hosts proceeds in parallel, and in phylogenetically more primitive hosts, symbionts are also primitive, and evolutionarily more advanced hosts carry more advanced symbionts. We suppose that the ancestral form for the entire *lutko* group, close to the *M. timandra timandra*, existed in the northern lowland foothills of Paropamiz, from where it moved into the mountains following the host plant. Apparently, the center of diversification of the *lutko* group was the mountains of the western Hindu Kush, which are at the same time one of the main centers of speciation for the *Phlomoides* plants of the former genus *Eremostachys* (Hedge 1982). According to molecular genetic studies, the origin of the genus *Melitaea* occurred about 20 Ma ago in the Early Miocene (Wahlberg 2006; Leneveu *et al.* 2009). The separation of the ancestral form of the *lutko* group, close to *M. timandra*, from the main evolutionary lineage of the genus *Melitaea* occurred in the Middle Miocene (Langhian Age) about 15 Ma ago during the climatic optimum in Central Asia (Leneveu *et al.* 2009). It is quite possible that this was due to the transition to host plants, which are the ancestors of the genus *Phlomoides*. In terms of the evolution of the genus *Melitaea*, the *lutko* group is an independent, separate phylogenetic lineage based both on morphological characters (Higgins, 1941) and on the data of molecular genetic analysis (Leneveu *et al.* 2009). The reason for the intensification of the speciation for many groups of organisms during the Quaternary period are climatic fluctuations, which, in turn, are the result of geological processes, such as the transgression of seas and glaciers and mountain uplifts (Albre *et al.* 2008). We believe that diversification in the *lutko* group began, as in the host plants under consideration, in the late Miocene (late Tortonian or Messinian Age) after climate cooling and aridification in Central Asia caused by the onset of glaciers from the north, the

final regression of the Tethys Sea and the uplift of Tibet and the Himalayas. The period of 5–7 Ma for the diversification of the *lutko* group seems to us very likely. Insect symbionts can maintain specialization in terms of the use of host plants for many millions of years (Stone *et al.* 2009). The question arises, according to what scenario did the coevolution of the considered group of symbionts and their host plants occur? Van Velzen (2013), who studied the relationship of African *Cymothoe* Hübner, [1819] butterflies and their host plants of the genus *Rinorea* Aubl. in the process of coevolution, found that the modern food associations of species of *Cymothoe* and *Rinorea* arose as a result of a process of sequential evolution. Moreover, the time gap between the beginning of the specialization of *Rinorea* host plants and *Cymothoe* butterflies is about 20 million years. The diversification of *Rinorea* began about 30 Ma ago, in the late Eocene, and the *Cymothoe* feeding on them arose in the late Miocene about 7.5 Ma ago (Van Velzen 2013). In the case of the evolution of the food associations of *Phlomoides* and the *lutko* group of fritillaries, it is quite possible that we are dealing with a process close to cospeciation, since the diversification of both began almost simultaneously in the late Miocene. Although, as field observations show, the process of coevolution of host plants and fritillaries of the *lutko* group is not limited to one scenario. If in the case of *M. timandra timandra* as well as *M. timandra binaludica* subsp. nov. and highly likely also *M. lutko* and *M. mimetica*, developing on systematically very close species of dissected-leaved *Phlomoides*, the classical Fahrenholz cospeciation (Fahrenholz 1913) can have played with a high degree of probability, then in the case of *M. shahvarica* sp. nov. and *Ph. molucelloides*, we see a clear food shift. The speciation of *M. shahvarica* apparently occurred relatively recently in the evolutionary history after the transition of nutrition of one of the forms close to *M. timandra* from *Phlomoides* of the *laciniata* group to *Ph. molucelloides*. If so, the case of *M. shahvarica* is an example of sequential coevolution after a food shift. The *molucelloides* group is younger in evolutionary terms than the *laciniata* group (Salmaki *et al.* 2012b). For this reason, we consider *M. shahvarica* evolutionarily the youngest species in the *lutko* group.

The diversification in the *lutko* group was accompanied by well-defined changes in morphological features, most noticeable in the structure of the genitalia. When moving from the foothills of Paropamiz in a south-westerly direction to eastern Iran (Kuh-e-Binalud Ridge), or in a south-easterly direction, up to the western Hindu Kush (northern slopes of Koh-i-Baba Ridge), we observe morphological changes in *M. timandra* only at the subspecific level, then, when moving to the borders of the general range of the *lutko* group further to the east (Chitral), to the south (from the southern slopes of the Koh-i-Baba Ridge to Balochistan) and to the west (Shahvar Mt.), changes in the details of the structure of the genitalia reach the species rank. Moreover, the most visible morphological changes in *M. lutko* (eastern species) and *M. mimetica* (southern species), compared with *M. timandra* (northern species), occur in opposite directions. In the first, the middle part of the harpe thickens, the armament of its inner part increases, the caudal process of the valva expands. In the second, by contrast, the harpe lengthens and becomes thinner, the teeth on the inner surface practically disappear, the caudal process of the valva narrows and lengthens. In the western species *M. shahvarica* sp. nov., the most noticeable differences are observed in the structure of the female genitalia.

Changes in the shape of the copulatory organs are an external manifestation of genetically linked biochemical and physiological changes that have an important adaptive function. Persisting and intensifying in the selection process, these morphological changes led to the reproductive isolation of individual populations and, as a result, the separation of *M. lutko*, *M. shahvarica* sp. nov. and *M. mimetica* from *M. timandra*.

After the geographical separation of populations, the subsequent genetic and morphological differentiation of lineages occurs as a result of adaptation to local factors (Hewitt 2004). Adaptation of *M. timandra binaludica* subsp. nov. and *M. shahvarika* sp. nov. in mountain conditions, living 2000 m higher than the nominative subspecies of *M. timandra*, as well as *M. lutko* and *M. mimetica*, rising above 4000 m, should

undoubtedly be accompanied by changes in biochemical functions at all stages of the life cycle. To the greatest extent, adaptive changes should affect the larval stage, which has the longest active period of life and is influenced by all possible significant factors, both abiotic (changes in the extreme side of the temperature regime, insolation, etc.) and biotic (changes in the physiological and biochemical features of host plants). Moreover, the latter factor is of decisive importance (Nation 2008). The content of nutrients in tissues, the production of phytohormones, the intensity of redox reactions changes when plants move from lowlands to mountains (Gorynshina 1979). Humidity and temperature conditions, the intensity of insolation and ultraviolet radiation have a significant impact on the nature of these changes. But if the adaptation of plants to stress factors in the conditions of the middle mountains is mainly associated with codification variability, then the mechanisms of genotypic variability are switched on in the conditions of the highlands (Shomansurov 1994). An obvious parallelism in the degree of adaptive variability, following the host plants, is also observed in the studied fritillaries of the *lutko* group: differences at the subspecific level arise when climbing from the desert plains of the Kara-Kum and the foothills of the Paropamiz to the middle mountains of eastern Iran and western Hindu Kush, and in the highlands of the Hindu Kush and Chitral, populations are divided at the species level. In the middle mountains, differences in the species rank arise as a result of a food shift, as in the case of *M. shahvarika* sp. nov.

There are other factors that, if other conditions are present, become decisive in terms of influencing the adaptive variability of host plants. Such factors are soil geochemistry and geochemical barriers (Gorynshina 1979). When comparing the distribution of various species of *Phlomoides* with the location of geological provinces on the territory of the Iranian Highlands and the Kara-Kum desert, a certain correlation is observed, which can also be traced in relation to the species of fritillaries of the *lutko* group associated with *Phlomoides*. More detailed study of these relationships should undoubtedly clarify the influence of geochemical factors on the genotypic variability of host plants, which could cause genotypic changes in the *lutko* group fritillaries, that, as a result, could have led to the splitting of the ancestral form into four different species.

We are aware that many of the assumptions made need to be verified and confirmed by field observations and experimental data. The next stage of studying the associations of the *lutko* group fritillaries and their host plants should be studies on dating phylogenetic events by the molecular clock method and determining phylogenetic congruence, which will allow answering the question about the timing and scenarios of the process of coevolution of the considered groups of organisms. The certain correlations found by us between the data on the systematics and zoogeography of the *lutko* group fritillaries, the distribution of their host plants and the geology of their habitat territories allow us to create the basis for the most interesting studies of evolutionary processes and biogeocenotic relationships of various levels on the example of such a seemingly inconspicuous and small group of living organisms as several close species of butterflies of the genus *Melitaea*.

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