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New data on the biology of *Melitaea interrupta* Kolenati, 1846 fritillary (Lepidoptera: Nymphalidae) with an analysis of its preimaginal stages features diagnostic value

Новые данные по биологии шашечницы *Melitaea interrupta* Kolenati, 1846 (Lepidoptera: Nymphalidae) с анализом диагностического значения признаков преимагинальных стадий

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КЛЮЧЕВЫЕ СЛОВА: Nymphalinae, *Melitaea didyma*, *Melitaea persea*, *Melitaea latonigena*, морфология, жизненный цикл, яйцо, гусеница.

ABSTRACT. The life cycle at all stages from the egg to the imago of *Melitaea interrupta* Kolenati, 1846 fritillary has been studied in the laboratory conditions. Some of the *M. interrupta* caterpillars from one clutch complete their development during one season passing six instars, the other part goes on hibernation at fourth instar. We compared the preimaginal stages features of *Melitaea didyma* (Esper, [1778]), *M. interrupta*, *Melitaea persea* Koller, 1849, and *Melitaea latonigena* Eversmann, 1847, belonging to the *M. didyma* species group. The eggs size, shape and the number of lateral ribs on their surface are diagnostic features. For the first instar caterpillars the body size and head capsule chaetotaxy are of diagnostic importance. The last instars caterpillars of the species studied differ in body color.

РЕЗЮМЕ. Жизненный цикл шашечницы *Melitaea interrupta* Kolenati, 1986 изучен в лабораторных условиях на всех стадиях, от яйца до имаго. Часть гусениц из одной кладки *M. interrupta* закачивает свое развитие в течение одного сезона, проходя шесть возрастов, другая часть уходит на зимовку в четвертом возрасте. Мы сравнили признаки преимагинальных стадий шашечниц *Melitaea didyma* (Esper, [1778]), *M. interrupta, Melitaea persea* Kollar, 1849 и *Melitaea latonigena* Eversmann, 1847, входящих в видовую группу *M. didyma.* Размеры, форма яиц и количество латеральных ребер на их поверхности являются диагностическими признаками. Для гусениц первого возраста диагностическое значение имеет размер тела и хетотаксия головной капсулы. Гусеницы последнего возраста изученных видов отличаются окраской тела.

Introduction

Melitaea interrupta Kolenati, 1846 fritillary belongs to the species group systematically close to *Melitaea didyma* (Esper, [1778]). This species is widespread in the Caucasus and Transcaucasia, in Turkey, Iran, and Turkmenistan [Hesselbarth *et al*., 1995; Tuzov *et al*.,

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2000; Kemal, Koçak, 2011; Tshikolovets, Nekrutenko, 2012; Tikhonov *et al*., 2025]. Some brief data on the biology of *M. interrupta* are presented in the scientific literature [Hesselbarth *et al*., 1995; Tikhonov *et al*., 2025]. However, there is no complete description of all the development stages and the species life cycle as a whole. There are no data on the preimaginal stages comparative morphology for *M. interrupta* and related species.

The data accumulated in the course of the latest scientific research increasingly confirm that in different Lepidoptera systematic groups, early stages morphological features can have a much more noticeable diagnostic significance than the imago morphology or the genitalia structure [Rougerie, Estradel, 2008; Spitsyn, Spitsyna, 2025]. In *Melitaea* fritillaries these features are particularly pronounced in the egg chorion ultrastructure, head capsule chaetotaxy, and caterpillar coloration [Kolesnichenko, Kotlobay, 2023]. Morphology of the preimaginal stages combined with imago morphology and molecular genetic methods in the Lepidoptera taxonomy makes it possible to identify the material with a high degree of reliability and to make systematic constructions closer to natural ones than based only on classical approaches (wing pattern morphology and genitalia structure), or only on molecular genetic data.

In the first decade of May 2022, in Southern Dagestan, Russia, we collected a couple of *M. interrupta* in copula (Fig. 1a) and two fertilized females. We obtained fertile eggs, tracked the complete development cycle of this species in the laboratory, studied and described egg chorion ultrastructure and all the caterpillar instars, and pupa morphology. These findings on *M. interrupta* life cycle allowed us to provide a comparative analysis of the eggs and younger instars caterpillars morphological features with those of related species — *M. didyma*, *Melitaea persea* Kollar, 1849 and *Melitaea latonigena* (Eversmann, 1847), as well to compare the last-instar caterpillar and pupa of *M. interrupta* with those of *M. didyma*.

This research aims not only to describe *M. interrupta* life cycle in whole and its early development stages but to test the possibility to use the preimaginal stages morphological features for the taxonomy of closely related, often difficult to distinguish by genitalia and imago morphology, fritillary species from the *M. didyma* group.

Material and Methods

MATERIAL COLLECTION AND KEEPING OF IMAGOES AND EARLY STAGES IN THE LABORATORY CONDITIONS. *M. interrupta* imagoes were collected on 9 and 11 May 2022 in the vicinity of Maraga village, Tabasaran District, Republic of Dagestan, Russia, 41º57’ N, 48º07’ E (Fig. 1b), at 450–550 m a.s.l. Eggs for further study were selected from clutches laid in cages by fertilized females. The butterflies were kept in plastic ventilated containers with a volume of 1800 cm^3. To stimulate egg laying, a host plant (*Plantago* sp.) was placed in the container. While the butterflies were kept in the container, they were fed a sugar solution applied to a cotton swab. The caterpillars were kept at temperature from +25° to +27 °C in same containers (Fig. 1c). The containers were cleaned of excrement and plant debris daily and the host plant leaves (*Plantago* sp.) were replaced/added as needed. Pupation took place in the same containers (Fig. 1d). Some specimens of each *M. interrupta* development stage (egg, each age of caterpillar and pupa) were fixed in 70% ethanol for further study.

The eggs of *M. didyma*, *M. latonigena* and *M. persea* were collected in nature in Rostov Reg., Russia, Altai Mts., Russia and Shahvar Mt., Iran, respectively. Some of the eggs were fixed in 70% ethyl alcohol. The other part was kept in a cage until the first instar caterpillars were released. The eggs of *M. didyma* from W Kazakhstan and Saratov Reg., and *M. latonigena* from E Sayan were extracted from the abdomens of dry females by enzymatic digestion method described by Junker *et al*. [2006]. The last instar caterpillars of *M. didyma* were collected in nature on a host plant (*Plantago* sp.) in Rostov Reg. The studied imago specimens are stored in the museum of Entomology Department of the M.V. Lomonosov Moscow State University.

SCANNING ELECTRONIC MICROSCOPY (SEM). Material for SEM was fixed in 75% ethanol, cleaned, dehydrated in a graded series of ethanol solutions and acetone, dried in a Hitachi NCP-1 (Hitachi Corp., Japan) critical point dryer, coated with gold in a Hitachi IB-3 (Hitachi Corp., Japan) ion spraying unit, and examined using a JEOL JSM-6380 (JEOL Ltd., Japan) scanning electron microscope.

PHOTOGRAPHY. Larvae and pupa were photographed using a Canon EOS 6D (Canon Corp., Japan) digital camera with a Canon MP E 65 (Canon Corp., Japan) macro lens. Each object was documented as a series of consecutive shots with a gradually changing focus distance, which were later merged in one image on a personal computer using the Combine ZM (Freeware by Alan Hadley, UK) focus stacking software.

MEASUREMENTS AND TERMINOLOGY. Measurements of caterpillars and eggs were made using the ImageJ (National Institutes of Health, USA) software. 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.

ABBREVIATIONS AND INSTITUTIONAL ACRONYMS. The following abbreviations and institutional acronyms are used in the text: EDMSU — Entomology Department of the M.V. Lomonosov Moscow State University; SEM — Scanning Electronic Microscopy.

Results and discussion

Life cycle of *Melitaea interrupta* Kolenati, 1846 observations in laboratory

A pair of *M. interrupta*, caught in copula at noon on May 9, 2022, continued to mate throughout the day and separated on the morning of May 10. On May 12, female from this pair laid 185 eggs (clutch No. 1) and lived until May 21. Two other fertilized females, captured in nature on May 11, laid clutches of 39 (clutch No. 2) and 38 (clutch No. 3) eggs on May 13 and 14, respectively. According to literature data [Tikhonov *et al*., 2025], the clutch size of *M. interrupta* averages 30–50 eggs. Probably, female from pair in copula laid all the eggs at the same time due to stressful conditions. Clutches No. 2 and No. 3 were formed from the rest of the eggs while most of them were laid even before females capture.

Caterpillars from clutches No. 1 and No. 2 began to emerge on May 20, and from clutch No. 3 on May 21.

On average, *M. interrupta* eggs take 7–8 days to develop. According to previously published data, the eggs obtained from a second-generation female of a similar *M. didyma* species needs 5–6 days for development [Tikhonov *et al*., 2025].

Further developmental observations were carried out preferably on caterpillars from clutch No. 1.

The first caterpillar instar lasted six days, the second — four days, the third — four days, the fourth — three days, the fifth — two days, the sixth — seven days. Some of the caterpillars (24 individuals) developed slowly and went on diapause on June 17, reaching the fourth instar. On June 15, non-diapausing caterpillars began to pupate. Thus, the development period for non-diapausing caterpillars from clutch No. 1 was 26 days. The caterpillar stage in clutches No. 2 and No. 3 lasted 31–32 days. Most of the caterpillars and pupae from these two clutches later died from infection. We assume that the longer period of development in these clutches is caused by infection. Most likely, the females were infected in nature and laid in the cage already infected eggs. According to data for *M. didyma*, the caterpillar stage in laboratory conditions lasts 32–36 days [Tikhonov *et al*., 2025]. The number of instars is 6 for non-diapausing caterpillars, and 7 for diapausing ones. Some *M. didyma* caterpillars of the first generation are also capable to diapause under unfavorable conditions [Tikhonov *et al*., 2025]. Similar data were obtained for *M. persea* [Hesselbarth *et al*., 1995]. From 10 to 20% of the first-generation caterpillars continued to develop and gave birth to the second generation, the rest went on diapause. Obviously, such a strategy is a protective mechanism against the mass death under possible adverse conditions and increases the population survival rate. For *M. persea*, from 5 to 7 larval instars are indicated and it is noted that development in nature can vary greatly even within the same biotope and depends on the mesoclimate, in particular on the development site illumination [Hesselbarth *et al*., 1995].

The pupal stage from clutch No. 1 lasted 8–9 days, the first butterflies appeared on June 23. The pupal stage from clutches No. 2 and No. 3 lasted 9–10 days, the first butterflies began to emerge on June 29. A similar duration of the pupal stage (8–9 days) was observed for the non-diapausing generation in *M. didyma* [Tikhonov *et al*., 2025].

The complete cycle from egg to adult in the non-diapausing generation of *M. inerrupta* ranges from 43 to 50 days (Table 1). In *M. didyma*, the life cycle in laboratory conditions is 45–51 days [Tikhonov *et al*., 2025].

***Melitaea interrupta* Kolenati, 1846 preimaginal stages morphology**

EGG EXTERNAL MORPHOLOGY (Table 2, Fig. 2a–c).

SEM material examined. 8 eggs from 2 clutches; 12–14 May 2022; 41º57’ N, 48º07’ E.

The egg has a well-defined oval shape. The height of the egg is from 729,41 to 762,28 μm, the width is from 615 to 700,92 μm. The height to width ratio is on average 1,12. The micropile rosette is formed by 9–11 primary quadra-pentahedral cells with width from 3,72 to 16,83 μm and length from 4,64 to 35,36 μm. The micropile is rounded in shape, with an average diameter of about 10,16 μm. There are 20–22 lateral longitudinal ribs in the micropile region which fall to ⅓ of the egg surface.

The freshly laid eggs are green.

CATERPILLAR EXTERNAL MORPHOLOGY.

First instar caterpillar (Figs 3a; 6a, b).

SEM material examined. 4 first instar caterpillars, ex ovo 20 May 2022. Female collected: 9 May 2022; 41º57’ N, 48º07’ E.

The body length of a caterpillar recently hatched from an egg is about 1,5 mm. A caterpillar hatched from an egg is light green with a black head, covered with long hairs.

The width of the head capsule is 413.78 ±3.19 μm, the height is 402.06 ±9.6 μm (Table 8, Fig. 4a, b). From the side, the head capsule is triangular, expanding to the area of the oral organs. The labrum with a width of 134.4±0.4 μm is divided into 2 blades. The distance between the bristles is shown in Table 7.

Second instar caterpillar (Fig. 6c, d).

Material examined. 2 second instar caterpillars, ex ovo 20 May 2022. Female collected: 9 May 2022; 41º57’ N, 48º07’ E.

The body length is about 3.5 mm. The head capsule is black, more or less rounded, approximately 504,5 μm wide and about 539,5 μm high (Table 8, Fig. 4c, d), covered by black hairs. The simple 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 main color is brown, the head is black and the scoli are brown. The main lines of the

Table 1. The duration of the life cycle stages in the non-wintering generation of *Melitaea interrupta*.
Таблица. 1. Продолжительность стадий жизненного цикла у незимующего поколения *Melitaea interrupta*.

Stage	Duration (days)
Egg	7–8
1th instar larva	6–7
2th instar larvae	4–5
3th instar larvae	4–5
4th instar larvae	3–4
5th instar larvae	2–3
6th instar larvae	7–8
Pupa	8–10

Table 2. Measurements of the egg of *Melitaea interrupta*.
Таблица 2. Размеры яиц *Melitaea interrupta*.

Paramener	Egg height (μm)	Egg width (μm)	Primary cell length (μm)	Primary cell width (μm)	Number of primary cell	Micropile diameter (μm)	Number of lateral ribs	Height to width ratio
Average value (μm)	750.91	668.82	19.01	9.64	10	10.16	20	1.12
Standard deviation	20.68	28.02	9.09	3.39	1.66	2.06	0.83	0.02

body are expressed due to a darker color. The head capsule of second-instar caterpillars changes proportions in addition to size. In first-instar caterpillars, the head capsule width is always greater than the height. In second-instar caterpillars, the head extends in the dorso-ventral direction, the height becomes greater than the width.

Third instar caterpillar (Fig. 6e, f).

Material examined. 2 third instar caterpillars, ex ovo 20 May 2022. Female collected: 9 May 2022; 41º57' N, 48º07' E.

The body length is about 5 mm. The main color is black with flesh-colored specks. The head is orange with the black area of simple eyes. The scoli of unpaired linea dorsalis and paired linea subdorsalis are orange, the scoli of linea epistigmalis and linea hypostigmalis are flesh-colored.

Fourth instar caterpillar (Fig. 6g, h).

Material examined. 2 fourth instar caterpillars, ex ovo 20 May 2022. Female collected: 9 May 2022; 41º57' N, 48º07' E.

The body length is about 8–10 mm. The head capsule is orange-red, rounded, 1.6 mm wide and about 1.6 mm high, covered by 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. Frons darkened at the edges, triangular epistomum whitish with darkened basis. Sutura metopica (the seam dividing vertex on two hemisphere) is black colored. The body pattern is formed by a black main background with light flesh-colored small specks. Linea dorsalis is marked by blackish scoli, linea subdorsalis are orange. The scoli of linea epistigmalis are blackish with flesh-colored apex. The scoli of linea hypostigmalis are flesh-colored.

The overwintering larvae (Fig. 6i, j).

Material examined. 2 fourth instar caterpillars, ex ovo 20 May 2022. Female collected: 9 May 2022; 41º57' N, 48º07' E.

The fourth instar caterpillar, going into hibernation, shrinks up. The body length is about 5–6 mm. The head capsule is reddish with the black area of simple eyes (Fig. 7c, d). The body pattern is black. The scoli of linea dorsalis are black. The scoli of linea subdorsalis and linea epistigmalis are orange. The scoli of linea hypostigmalis are flesh-colored.

Fifth instar caterpillar (Fig. 6k, l).

Material examined. 2 fifth instar caterpillars, ex ovo 20 May 2022. Female collected: 9 May 2022; 41º57' N, 48º07' E.

The body length is 14–16 mm. The head capsule is orange-red, rounded, approximately 2 mm wide and about 2 mm high, covered by black hairs (Fig. 7e, f). 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. Frons noticeably darkened at the

Fig. 1. *Melitaea interrupta* Kolenati, 1846 in natural and laboratory conditions: **a** — pair in copula; **b** — habitat, Maraga v., Tabasaran distr., Rep. Dagestan; **c** — caterpillars in the plastic cage; **d** — emergence of imago from pupa.

Рис. 1. *Melitaea interrupta* Kolenati, 1846 в природных и лабораторных условиях: **a** — пара in copula в природе; **b** — место обитания, окр. с. Марага, Табасаранский район, Респ. Дагестан; **c** — гусеницы в пластиковом садке; **d** — выход бабочки из куколки.

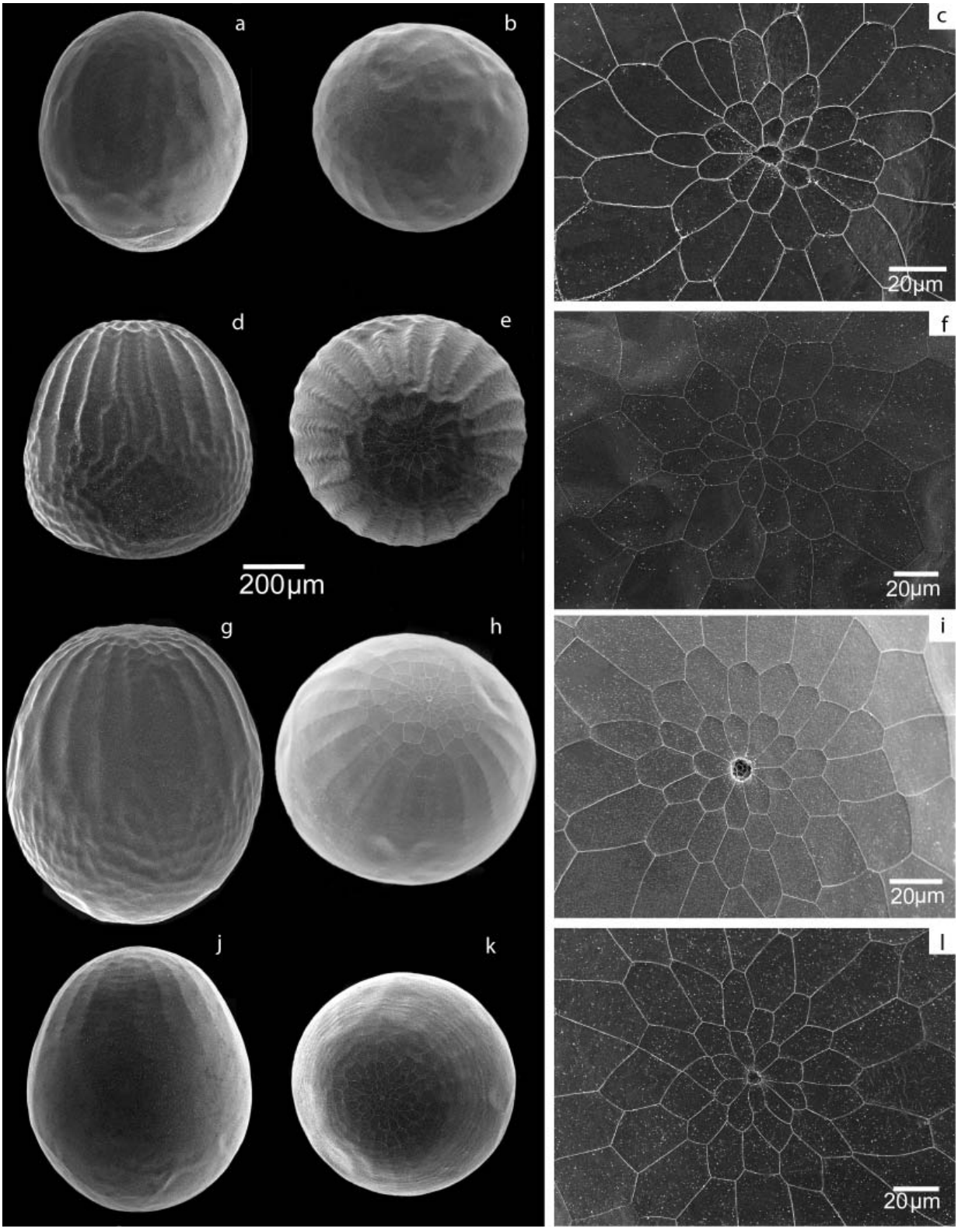

Fig. 2. The eggs of *Melitaea interrupta* Kolenati, 1846 in comparison with those of some representatives of *Melitaea didyma* (Esper, [1778]) species–group: **a–c** — *M. interrupta*; **d–f** — *M. didyma*, Rostov Reg.; **g–i** — *Melitaea latonigena* Eversmann, 1847*,* Orlik, E Sayan; **j–l** — *Melitaea persea* Koller, 1849, Shahvar Mt, Semnan Prov., Iran; **a, d, g, j** — lateral view; **b, e, h, k** — view from above; **c, f, i, l** — micropile area.
Рис. 2. Яйца *Melitaea interrupta* Kolenati, 1846 в сравнении с таковыми некоторых представителей видовой группы *Melitaea didyma* (Esper, [1778]): **a–c** — *M. interrupta*; **d–f** — *M. didyma*, Ростовская обл.; **g–i** — *Melitaea latonigena* Eversmann, 1847*,* Орлик, Восточный Саян; **j–l** — *Melitaea persea* Koller, 1849, гора Шахвар, пров. Семнан, Иран; **a, d, g, j** — вид сбоку; **b, e, h, k** — вид сверху; **c, f, i, l** — область микропиле.

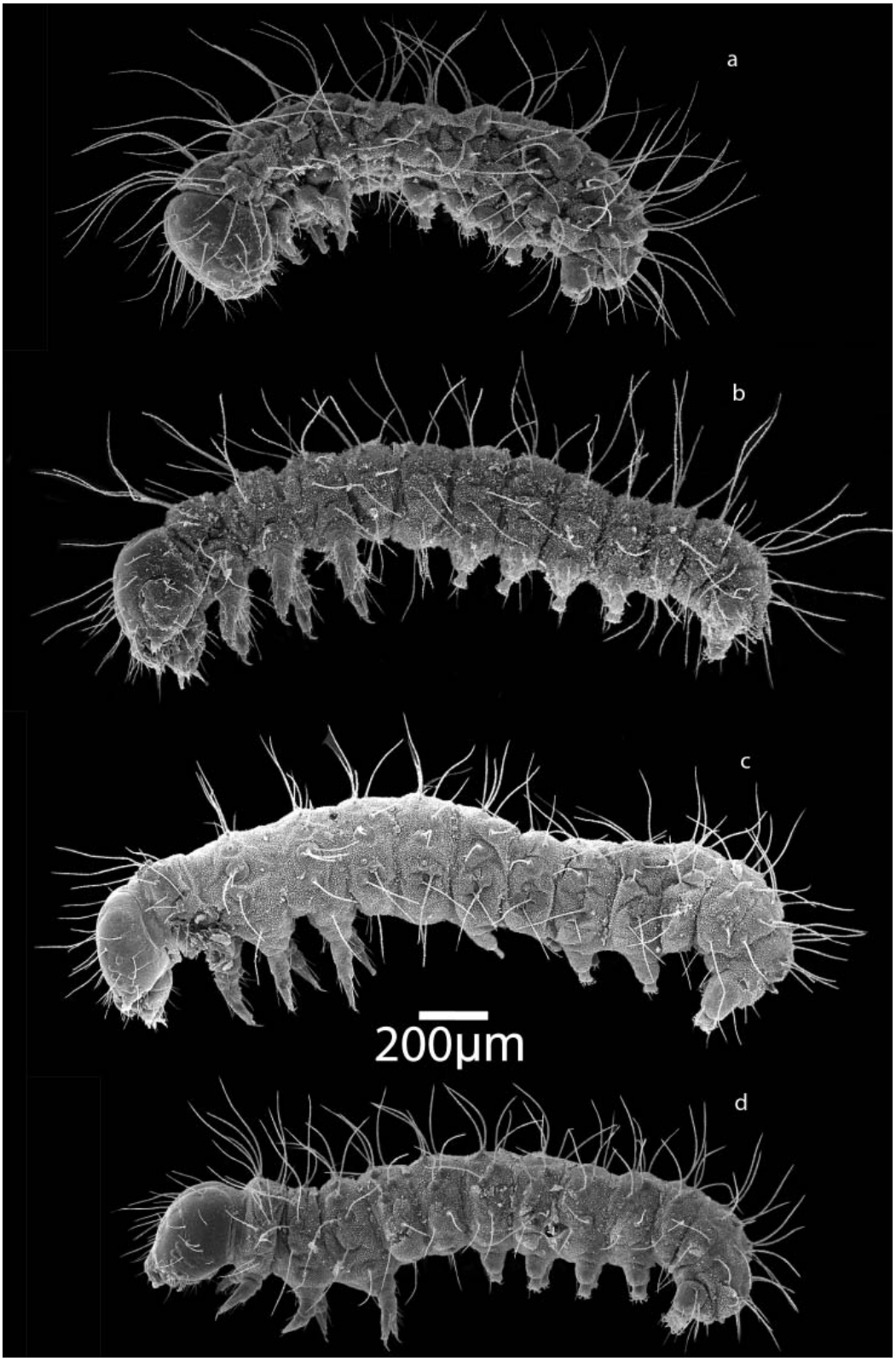

Fig. 3. First instar caterpillar, lateral view: **a** — *Melitaea interrupta* Kolenati, 1846; **b** — *Melitaea didyma pseudolatonigena* Yakovlev, 2002, Moren v., Rep. Tuva; **c** — *Melitaea latonigena* Eversmann, 1847, Tara Riv., Kosh-Agach Distr., Rep. Altai; **d** — *Melitaea persea* Koller, 1849, Shahvar Mt, Semnan Prov., Iran.
Рис. 3. Гусеницы первого возраста, вид сбоку: **a** — *Melitaea interrupta* Kolenati, 1846; **b** — *Melitaea didyma pseudolatonigena* Yakovlev, 2002, с. Морен, Респ. Тува; **c** — *Melitaea latonigena* Eversmann, 1847, р. Тара, Кош-Агач, Респ. Алтай; **d** — *Melitaea persea* Koller, 1849, гора Шахвар, пров. Семнан, Иран.

edges, triangular epistomum whitish. Labrum is black. The body pattern is formed due to bright yellow-orange scoli and the speckled darkened background color. The unpaired linea dorsalis bears pale-orange scoli. The paired linea subdorsalis is marked with bright orange-yellow scoli. The paired linea epistigmalis located above the spiracles has also orange-yellow scoli. The paired linea stigmata has a background color. The linea hypostigmalis is formed by pale 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 pale-yellow scoli placed near each other. The false legs and legs of the thoracic segments are pale.

Sixth instar caterpillar (Fig. 7a, b).

Material examined. 2 sixth instar caterpillars, ex ovo 20 May 2022. Female collected: 9 May 2022; 41º57' N, 48º07' E.

The body length is 23–25 mm. The head capsule is orange-red, more or less rounded, approximately 2.6 mm wide and about 2.6 mm high (Fig. 7g, h), covered by 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. Frons noticeably darkened at the edges, triangular epistomum whitish. Labrum is black.

The body pattern is formed due to bright yellow-orange scoli and the speckled darkened background color. The unpaired linea dorsalis bears pale scoli with black basis. The paired linea subdorsalis formed by orange-yellow scoli. The paired linea epistigmalis has pale flesh-colored scoli. The paired linea stigmata formed by black line with pale-colored spiracles. The linea hypostigmalis is formed by well developed flesh-colored line with pale orange scoli on each segment. 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 pale-yellow scoli placed near each other. The false legs and legs of the thoracic segments are pale.

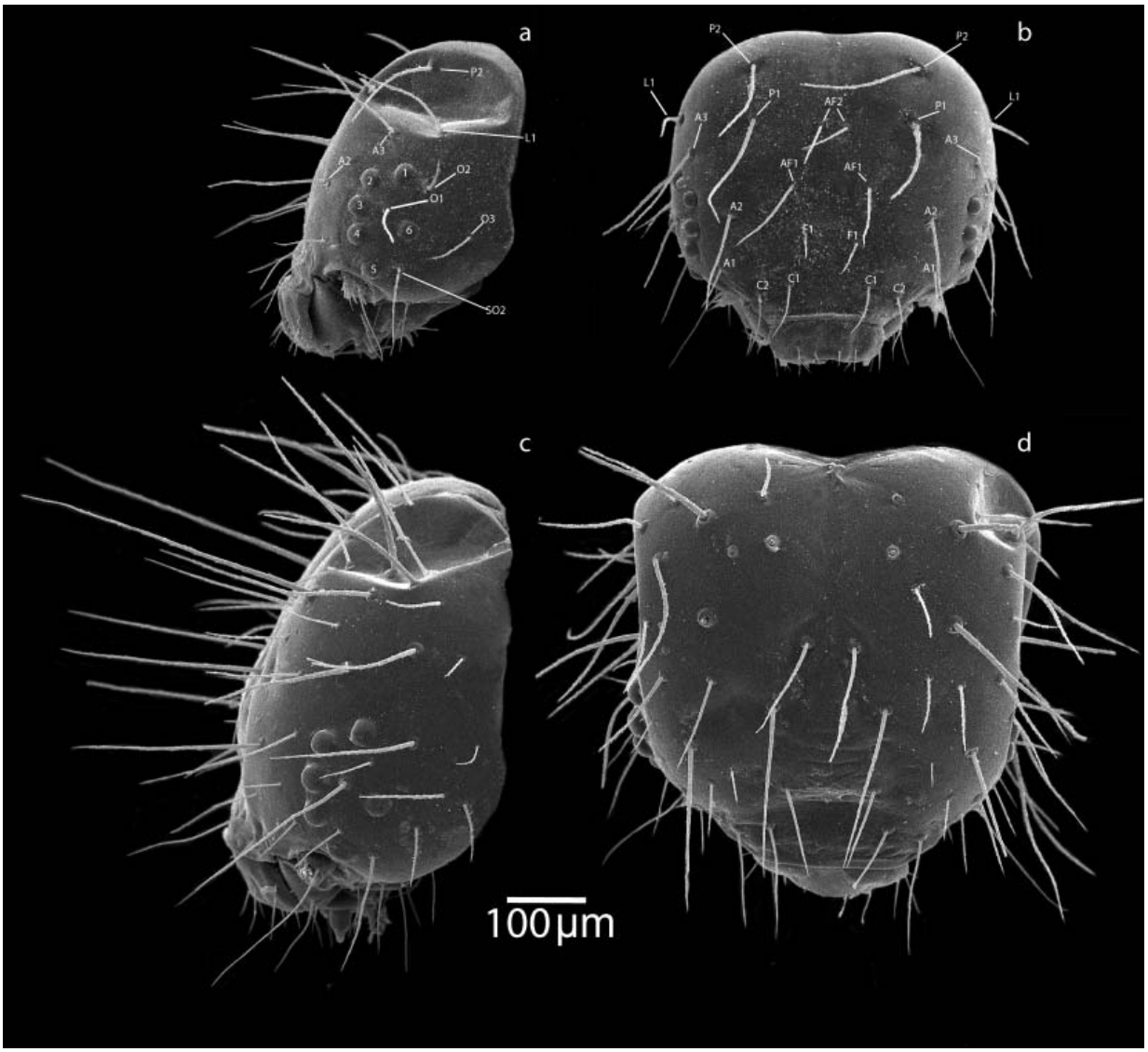

Fig. 4. Head capsule of the first and second instar caterpillars of *Melitaea interrupta* Kolenati, 1846: **a, b** — first instar caterpillar; **c, d** — second instar caterpillar; **a, c** — lateral view; **b, d** — front view.

Рис. 4. Головная капсула гусениц первого и второго возрастов *Melitaea interrupta* Kolenati, 1846: **a, b** — первый возраст; **c, d** — второй возраст; **a, c** — вид сбоку; **b, d** — вид спереди.

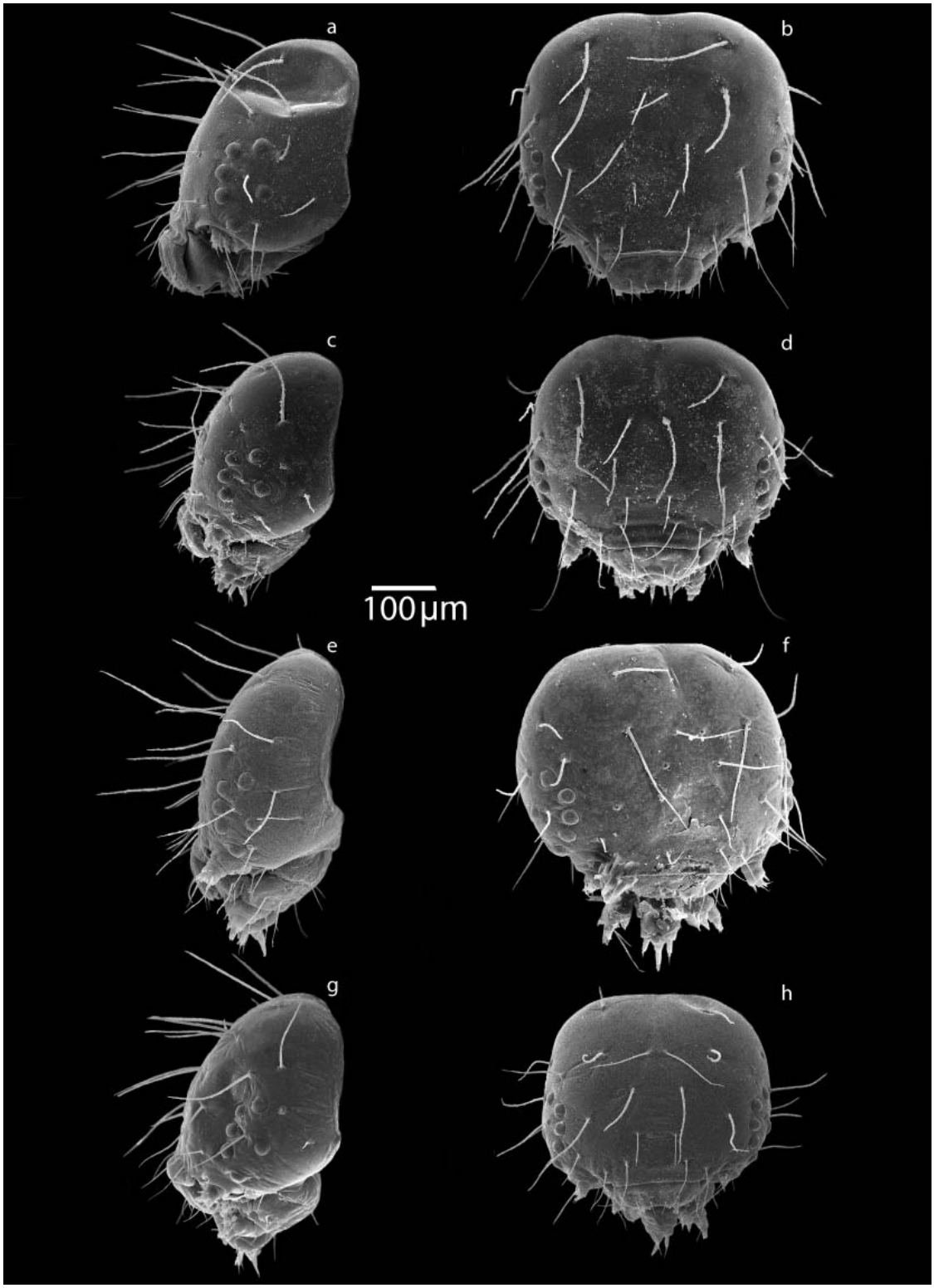

Fig. 5. Head capsule of the first instar caterpillar of *Melitaea interrupta* Kolenati, 1846 in comparison with those of some representatives of *M. didyma* species–group: **a, b** — *M. interrupta*; **c, d** — *M. didyma pseudolatonigena* Yakovlev, 2002, Moren, Tuva Rep.; **e, f** — *M. latonigena* Eversmann, 1847, Tara R. Kosh-Agach Distr., Altai Rep.; **g, h** — *M. persea* Koller, 1849, Shahvar Mt, Semnan Prov., Iran; **a, c, e, g** — lateral view; **b, d, f, h** — front view.

Рис. 5. Головная капсула гусениц первого возраста *Melitaea interrupta* Kolenati, 1846 в сравнении с другими представителями видовой группы *M. didyma*: **a, b** — *M. interrupta*; **c, d** — *M. didyma pseudolatonigena* Yakovlev, 2002, с. Морен, Респ. Тува; **e, f** — *M. latonigena* Eversmann, 1847, р. Тара, Кош-Агач, Респ. Алтай; **g, h** — *M. persea* Koller, 1849, гора Шахвар, пров. Семнан, Иран; **a, c, e, g** — вид сбоку; **b, d, f, h** — вид спереди.

Fig. 6. I–V instar caterpillars of *Melitaea interrupta* Kolenati, 1846: **a, b** — first instar caterpillar after hatching; **c, d** — second instar; **e, f** — third instar; **g, h** — fourth instar; **i, j** — wintering fourth instar caterpillar; **k, l** — fifth instar; **a, c, e, g, i, k** — lateral view; **b, d, f, h, j, l** — view from above.
Рис. 6. I–V возраста гусениц *Melitaea interrupta* Kolenati, 1846: **a, b** — первый возраст гусеницы после выхода из яйца; **c, d** — второй возраст; **e, f** — третий возраст; **g, h** — четвертый возраст; **i, j** — четвертый возраст зимующей гусеницы; **k, l** — пятый возраст; **a, c, e, g, i, k** — вид сбоку; **b, d, f, h, j, l** — вид сверху.

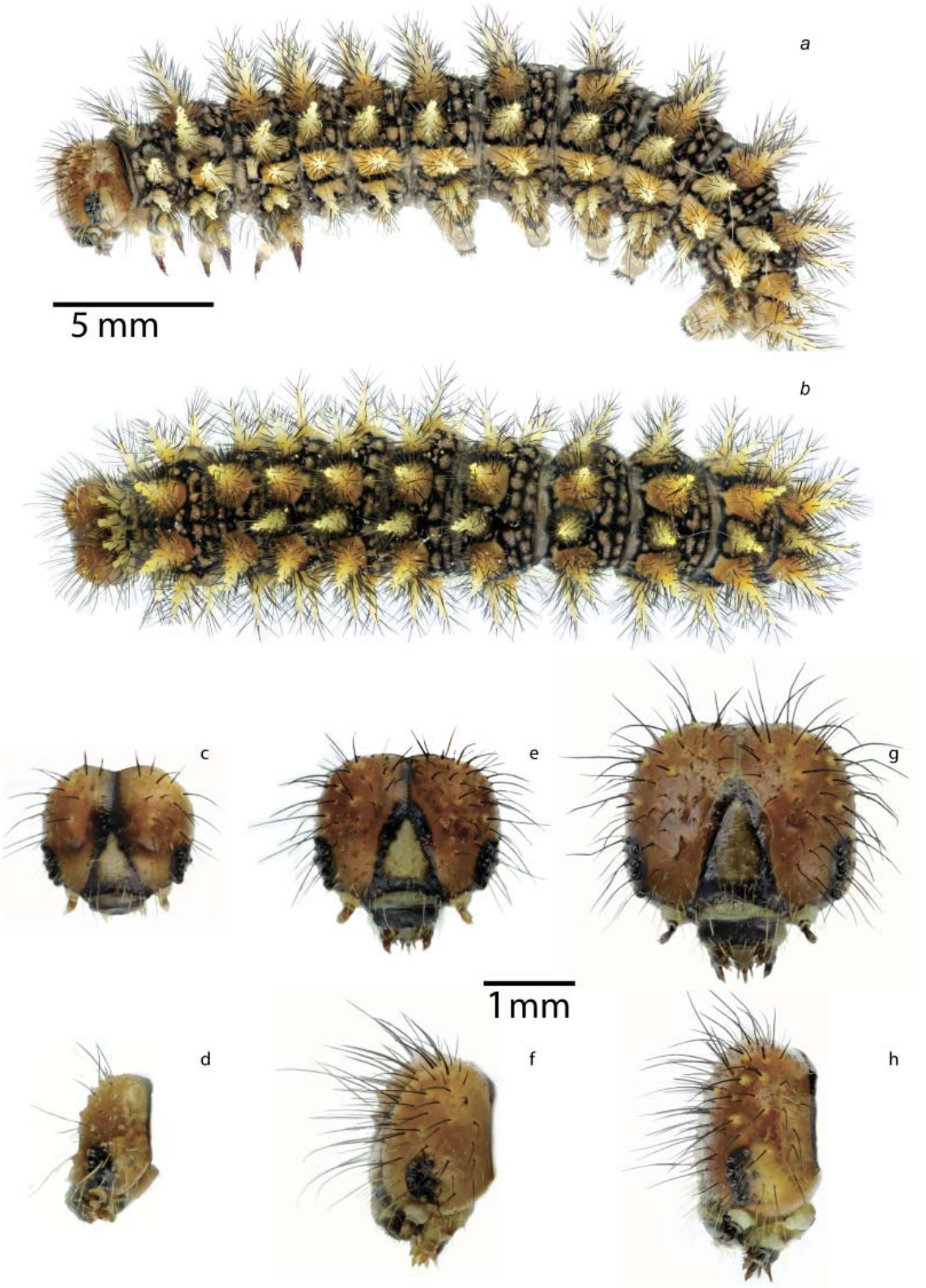

Fig. 7. VI instar caterpillar and head capsules of IV–VI instars caterpillar of *Melitaea interrupta* Kolenati, 1846: **a, b** — sixth instar caterpillar; **c, d** — fourth instar caterpillar, head capsule; **e, f** — fifth instar caterpillar, head capsule; **g, h** — sixth instar caterpillar, head capsule; **a, d, f, h** — lateral view; **b** — view from above; **c, e, g** — front view.

Рис. 7. Гусеница шестого возраста и головные капсулы гусениц IV–VI возрастов *Melitaea interrupta* Kolenati, 1846: **a, b** — гусеница шестого возраста; **c, d** — головная капсула гусеницы четвертого возраста; **e, f** — головная капсула гусеницы пятого возраста; **g, h** — головная капсула гусеницы шестого возраста; **a, d, f, h** — вид сбоку; **b** — вид сверху; **c, e, g** — вид спереди.

Fig. 8. Pupa of *Melitaea interrupta* Kolenati, 1846: **a, b, c** — "pale" form; **d, e** — "darkened" form; **f, g** — cremaster; **a, d, f** — lateral view; **b, e** — front view; **c** — back view; **g** — view from above.
Рис. 8. Куколка *Melitaea interrupta* Kolenati, 1846: **a, b, c** — "светлая" форма; **d, e** — "темная" форма; **f, g** — кремастер; **a, d, f** — вид сбоку; **b, e** — вид спереди; **c** — вид сзади; **g** — вид сверху.

External Morphology of the Pupa (Fig. 8).

Material examined. 2 pupae, ex ovo, pupation 15 June 2022. Female collected: 9 May 2022; 41º57'15'' N, 48º07'48'' E.

The height of pupa is about 15–16 mm, the width is about 5 mm. The ground color is white. Proboscis is black, face is white, eyes are bordered by brown from above. The forewing is white, with longitudinal black stripes and there are several small spots along the edges. There are two types of pupae: the first type formed by enlarged black pattern (Fig. 8d, e), the second one with reduced black pattern (Fig. 8a–c) White abdominal segments are covered by spines with colored by different combination of white and orange. Anal and genital area are orange between two elongated black macules. Rounded cremaster is reddish with its diameter about 1 mm. It is covered with numerous setae. The base of the cremaster is reddish (Fig. 8f, g).

Melitaea didyma (Esper, [1778]) species group, preimaginal stages morphological features: comparative analysis

To compare the similarity and differences in preimaginal morphological features of other species group representatives with *M. interrupta*, we studied the eggs and first instar caterpillars of *M. didyma*, *M. latonigena* and *M. persea*, as well as the last instar caterpillars and the pupa of *M. didyma*.

COMPARATIVE MORPHOLOGY OF EGGS.

***Melitaea didyma* (Esper, [1778]) (**Table 3, Fig. 2d–f).

SEM material examined. 5 eggs extracted from dried female; Karabau sands, Atyrau Reg., Republic of Kazakhstan; 0 m a.s.l.; 9 May 2013; 48º30' N, 52º52' E; EDMSU; 4 eggs extracted from dried female; Dyakovka v., Krasnokutsky Distr., Saratov Reg., Russia;10 July 2003; 50º43' N, 46º48' E; EDMSU; 4 eggs collected in nature; Kazanskaya v., Verhnedonskoi Distr., Rostov reg., Russia; 21 May 2012; 49º48' N, 41º08' E; EDMSU.

The egg of *M. didyma* is rounded. The height of the eggs varies from 725.84 to 812.78 µm. The width of the eggs varies from 670.62 to 778.24 µm. The average height-to-width ratio is 1.06. The micropile area includes from 8 to 11 primary cells. The length of the primary cells varies from 10.54 to 52.2 µm, the width from 6.22 to 22.28 µm. The average diameter of the micropile is 8.07 µm. There are from 20 to 22 lateral ribs.

***Melitaea latonigena* (Eversmann, 1847)** (Table 4, Fig. 2g–i).

SEM material examined. 5 eggs collected in nature; Tara riv. valley, Altay Republic, Russia; 2150 m a.s.l.; 18–19 July 2021; 49º46' N, 87º25' E; 5 eggs extracted from dried female; West Sayan Mts, vicinities of Mondy, Buryat Republic, Russia; 1500 m a.s.l.; 29 June 2023; 51º41' N, 100º58' E; EDMSU.

The eggs are oval in shape and large. The eggs height varies from 932.18 to 975.70 µm. The width ranges from 809.99 to 831.56 µm. The average height-to-width ratio is 1.15. The micropile area includes from 10 to 12 primary cells. The length of the primary cells varies from 12.12 to 42.55 µm, the width ranges from 6.36 to 20.07 µm. The average diameter of the micropile is 9.61 µm. Lateral ribs in the number of 18.

***Melitaea persea* Kollar, 1849** (Table 5, Fig. 2j–l).

SEM material examined. 14 eggs collected in nature; Shahvar Mt, Semnan Prov., Iran; 2200 m a.s.l.; 18 May 2017; 36º31' N, 54º43' E.

The eggs are oval-pear-shaped. The eggs height varies from 785.63 to 931.87 µm. The width ranges from 679.46 to 753.71 µm. The average height-to-width ratio is 1.18. The mi-

Table 3. Measurements of the egg of *Melitaea didyma*.
Таблица 3. Размеры яиц *Melitaea didyma*.

	Egg height (µm)	Egg width (µm)	Primary cell length (µm)	Primary cell width (µm)	Number of primary cells	Micropile diameter (µm)	Number of lateral ribs	Height to width ratio
General values for the species								
Average value (µm)	770.24	733.82	24.9	12.57	9	8.07	21	1.06
Standard deviation	34.47	34.42	7.84	3.94	1.14	1.20	0.75	0.03
Values for the population from W Kazakhstan								
Average value (µm)	812.78	763.51	32.18	16.41	9	7.2	21	1.04
Standard deviation	Parameter available for one egg only	10.71	7.25	3.38	0.57	1.31	0.7	Parameter available for one egg only
Values for the population from Saratov Region								
Average value (µm)	740.44	688.81	No angle to evaluate this parameter	No angle to evaluate this parameter	No angle to evaluate this parameter	No angle to evaluate this parameter	21	1.08
Standard deviation	13.15	13.79	No angle to evaluate this parameter	No angle to evaluate this parameter	No angle to evaluate this parameter	No angle to evaluate this parameter	0.7	0.03
Values for the population from Rostov Region								
Average value (µm)	793.67	746.08	20.96	10.49	10	8.59	21	1.04
Standard deviation	4.94	13.59	4.74	2.35	1.14	0.88	0.81	0.01

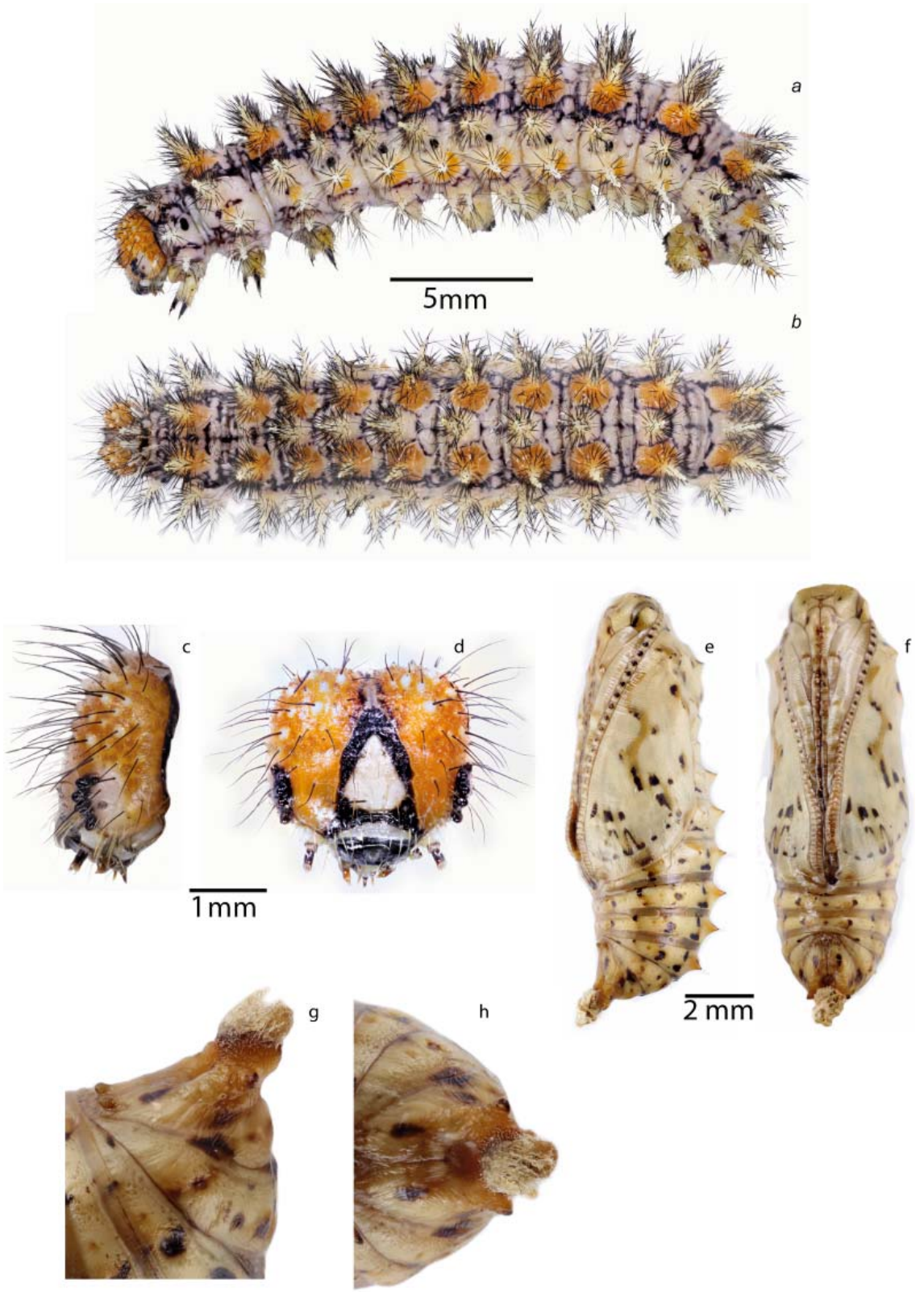

Fig. 9. Senior instar caterpillar and pupa of *Melitaea didyma* (Esper, [1778]): **a, b** — senior instar caterpillar; **c, d** — head capsule; **e, f** — pupa; **g, h** — cremaster; **a, c, e, g** — lateral view; **b, h** —view from above; **d, f** — front view; caterpillar — Rostov Reg., pupa — Karabau sands, W Kazakhstan.
Рис. 9. Гусеница последнего возраста и куколка *Melitaea didyma* (Esper, [1778]): **a, b** — гусеница последнего возраста; **c, d** — головная капсула; **e, f** — куколка; **g, h** — кремастер; **a, c, e, g** — вид сбоку; **b, h** —вид сверху; **d, f** — вид спереди; гусеница — Ростовская обл., куколка — пески Карабау, Западный Казахстан.

Table 4. Measurements of the eggs of *Melitaea latonigena*.
Таблица 4. Размеры яиц *Melitaea latonigena*.

	Egg height (μm)	Egg width (μm)	Primary cell length (μm)	Primary cell width (μm)	Number of primary cells	Micropile diameter (μm)	Number of lateral ribs	Height to width ratio
General values for the species								
Average value (μm)	949.38	820.68	25.37	12.79	11	9.61	18	1.15
Standard deviation	19.69	7.84	7.34	3.31	1.15	0.93	Parameter available for one egg only	0.01
Values for the population from Altai								
Average value (μm)	945.05	817.57	27	13.83	10	8.97	No angle to evaluate this parameter	1.15
Standard deviation	17.68	6.94	7.48	2.49	Parameter available for one egg only	Parameter available for one egg only		0.01
Values for the population from E Sayan								
Average value (μm)	955.88	825.33	24.62	12.31	11	9.93	18	1.16
Standard deviation	28.03	8.80	7.33	3.57	1.41	1.06	Parameter available for one egg only	0.02

Table 5. Measurements of the egg of *Melitaea persea*.
Таблица 5. Размеры яиц *Melitaea persea*.

	Egg height (μm)	Egg width (μm)	Primary cell length (μm)	Primary cell width (μm)	Number of primary cells	Micropile diameter (μm)	Number of lateral ribs	Height to width ratio
Average value (μm)	853.38	718.68	21.73	11.76	10	8.4	25	1.18
Standard deviation	51.44	26.04	4.73	2.26	1.66	1.23	2.41	0.03

cropile area includes from 8 to 13 primary cells. The length of the primary cells varies from 9.22 to 35.85 μm, the width ranges from 5.78 to 16.14 μm. The micropile diameter is on average 8.4 μm. Lateral ribs number ranges from 21 to 29.

Eggs of closely related species in *M. didyma* group differ morphologically, primarily in size and shape. The eggs of all the studied species are generally more or less oval, with the exception of *M. didyma*, whose eggs are rather barrel-shaped (the ratio of height to base width is 1.04–1.08). Eggs in *M. peresea* are closer to pear-shaped, with a wide base and narrow tip and a length-to-width ratio of 1.18. *M. latonigena* and *M. interrupta* have typically oval eggs. However, for the first species, eggs are large, and their height is about 950 μm, while for *M. interrupta* eggs are the smallest of all the studied species and their height is about 750 μm.

The primary cells number in the studied species ranges from 9–10 (*M. didyma*) to 10–11 (*M. latonigena*) and, apparently, has no diagnostic significance. The length and width of the primary cell varies greatly even within the same species. However, the smallest primary cells are characteristic of *M. interrupta* (their length is about 19 μm versus 21 μm in *M. persea*, 24–25 μm in *M. latonigena*, and 21–32 μm in *M. didyma*). The micropile diameter also varies even within the same species and ranges from just over 7 μm in *M. didyma* to almost 10 μm in *M. latonigena*. The largest micropile diameter in *M. latonigena* correlates with the large size of the egg itself.

The lateral ribs number on the egg chorion is a relatively stable species feature. The largest number of ribs is typical for *M. persea* egg (up to 25), *M. interrupta* egg has about 20 ribs, *M. latonigena* egg has no more than 18 ribs, and *M. didyma* egg typically has 21 lateral ribs.

The data the egg shape in the *M. didyma* species group has systematic features is quite consistent with the data we obtained earlier for other *Melitaea* representatives [Kolesnichenko, Kotlobay, 2022; Kolesnichenko, Kotlobay, 2023].

Comparative morphological characteristics of the first instar caterpillars in the *Melitaea didyma* (Esper, [1778]) species group

SEM material examined. 4 *M. interrupta* first instar caterpillars ex ovo 20 May 2022; Vicinity of Maraga village, Tabasaran District, Republic of Dagestan, Russia; 450–550 m a.s.l.; 41º57’ N, 48º07’ E; 4 *M. didyma* first instar caterpillars ex ovo; 27 June 20.2022; Vicinity of Moren village, Republic of Tuva, Russia; 1200 m a.s.l.; 50°18′ N 95°22′ E; 4 *M. latonigena* first instar caterpillars ex ovo; 28 July 2021; Tara riv. valley, Altay Republic, Russia; 2150 m a.s.l.; 49º46’ N, 87º25’ E; 3 *M. persea* first instar caterpillars ex ovo; 28 May 2017; Shahvar Mt, Semnan Prov., Iran; 2200 m a.s.l.; 36º31’ N, 54º43’ E.

Table 6. First instar caterpillar body length of species from *Melitaea didyma* group.
Таблица 6. Длина тела гусениц первого возраста видов группы *Melitaea didyma*.

Species	Body length µm	Average µm	Standard deviation
M. interrupta			
Caterpillar 1	1602.45	1577.285	35.59
Caterpillar 2	1552.12		
M. persea			
Caterpillar 1	1390.07	1347.98	42.09
Caterpillar 2	1305.89		
M. latonigena			
Caterpillar 1	2557.69	No angle to evaluate this parameter	Parameter available for one caterpillar only
M. didyma			
Caterpillar 1	1728.13	1910.02	257.23
Caterpillar 2	2091,91		

The average length of the first instar caterpillar in *M. latonigena* is 2557.7 µm, which is almost 1000 µm longer than in *M. interrupta* (Table 6). Such a significant size of the caterpillar fully corresponds to the large size of the *M. latonigena* eggs. In other cases, the correlation between egg and caterpillar size is not pronounced. The size of the *M. persea* egg is visually larger than that of *M. didyma* and *M. interrupta*, but the *M. persea* caterpillar is significantly smaller (1550.5 µm) than that of *M. latonigena* and *M. didyma*, which is quite comparable to the first instar caterpillar size in *M. interrupta*, egg of which has the smallest size among species examined. At *M. latonigena* and *M. didyma* first instar caterpillars are the largest, with lengths of 2557.7 and 1910.0 µm, respectively.

In the first instar caterpillars of all the species studied, the head capsule size does not differ significantly (Table 8). The largest size is in *M. latonigena* (width 432.66 µm), which is fully explained by the large size of the first instar caterpillars. Head capsule chaetotaxy is similar in all species. Nevertheless, there are differences between the species in the distances between the bristles, which are stable statistically (Table 7). The greatest distance between the O3-SO2 bristles is typical for *M. persea* (more than 95 µm), the smallest for *M. latonigena* (slightly more than 68 µm). *M. didyma* and *M. interrupta* occupy an intermediate position with a distance of 78 and 86 µm, respectively. *M. latonigena* is characterized by the largest distance between the O1-SO2 bristles (almost 87 µm versus 65–67 µm in *M. persea*, *M. interrupta*, and *M. didyma*). The distance between the parietal bristles of P2 is the largest in *M. didyma* and is almost 225 µm, the smallest in *M. latonigena* (slightly more than 188 µm), *M. persea* (more than 190 µm) and *M. interrupta* (206 µm). The greatest distance between

Table 7. Distance between the bristles on the first instar caterpillar head capsule of species from *Melitaea didyma* group.
Таблица 7. Расстояния между щетинками головной капсулы гусениц первого возраста видов группы *Melitaea didyma*.

	M. interrupta		***M. persea***		***M. didyma***		***M. latonigena***
Bristles	**Average distance µm**	**Standard deviation**	**Average distance µm**	**Standard deviation**	**Average distance µm**	**Standard deviation**	**Distance (data for one caterpillar only) µm**
L1-O1	**116.45**	4.93	**120.52**	8.96	**114.13**	1.02	**118.05**
L1-O2	**72.35**	7.36	**66.87**	2.99	**74.65**	0.86	**74.43**
L1-O3	**128.86**	1.91	**119.83**	2.79	**128.83**	5.84	**125.27**
O1-O2	**58.11**	5.50	**69.21**	1.83	**64.59**	0.05	**65.75**
O2-O3	**67.81**	8.77	**64.49**	4.32	**62.28**	1.53	**57.70**
O1-O3	**92.21**	8.18	**93.59**	6.72	**96.68**	4.67	**104.00**
O3-SO2	**86.18**	5.33	**95.22**	1.26	**78.32**	1.77	**68.18**
O1-SO2	**65.64**	4.96	**64.84**	3.31	**66.82**	0.45	**86.95**
P1-P1	**202.52**	8.67	**196.18**	5.72	**220.49**	the measurement was only on one larvae	**193.95**
P2-P2	**206.19**	7.96	**190.47**	12.61	**225.73**	the measurement was only on one larvae	**188.38**
AF1-AF1	**92.38**	7.44	**89.26**	4.67	**90.63**	the measurement was only on one larvae	**84.37**
AF2-AF2	**32.25**	4.55	**31.57**	3.30	**54.37**	the measurement was only on one larvae	**41.66**
A1-A1	**264.72**	14.25	**267.17**	2.74	**254.37**	the measurement was only on one larvae	**262.29**
A2-A2	**246.26**	13.66	**233.19**	13.53	**232.69**	the measurement was only on one larvae	**235.91**
A3-A3	**365.77**	1.64	**343.05**	9.44	**347.33**	the measurement was only on one larvae	**347.48**
F1-F1	**67.89**	3.88	**69.81**	3.26	**66.67**	the measurement was only on one larvae	**74.75**
C1-C1	**105.20**	5.06	**96.50**	12.62	**87.82**	the measurement was only on one larvae	**85.94**
C2-C2	**170.42**	8.45	**169.22**	3.90	**157.51**	the measurement was only on one larvae	**160.00**

Table 8. Caterpillar head capsule measurements of species from *Melitaea didyma* group.
Таблица 8. Размеры головной капсулы гусениц видов группы *Melitaea didyma*.

Species/ instar	*M. interrupta* first instar		*M. interrupta* second instar		*M. persea* first instar		*M. latonigena* first instar	*M. didyma* first instar
Parameter	Average µm	Standard deviation	Average µm	Standard deviation	Average µm	Standard deviation	µm	µm
Width	**413.78**	3.19	**504.51**	13.73	**398.64**	8.12	**432.66**	**395.32**
Height	**402.06**	9.58	**539.53**	18.13	**337.96**	33.14	**424.76**	**360.23**

the frontal bristles of AF2 is in *M. didyma* (more than 54 μm), for *M. latonigena* this distance is slightly smaller and is more than 41.5 μm. The smallest distance between these bristles is in *M. interrupta* and *M. persea* (32 and 31.5 μm, respectively). Slight differences between the species are observed in the distances between the paired C1 and C2 clypeus bristles.

Comparative morphological characteristics of *Melitaea interrupta* Kolenati, 1846 and *Melitaea didyma* (Esper, [1778]) last-instar caterpillars and pupae

M. didyma is the closest species to *M. interrupta*. Both species are found in the Caucasus, but their geographical ranges do not overlap [Tikhonov *et al*., 2025].

For late-instar caterpillars, body color is very important for identification. The head color of *M. didyma* and *M. interrupta* caterpillars is similar in general (Figs 7, 9). The head capsule of both species is orange-red with black macule situated in the of simple eyes. Frons noticeably darkened at the edges with whitish triangular epistomum and black labrum. The main differences are in the body color.

The basic color of *M. didyma* caterpillar is less darkened than that of *M. interrupta*. If we can say about the main *M. interrupta* background that there are white dots on a black background, then in the case of M. didyma we can say that there are black strokes on a white background. The paired linea subdorsalis in *M. didyma* is formed by red-orange scoli, which in sharply contrast with the general background, while in *M. interrupta* scoli of linea subdorsalis are pale-orange. However, the most striking distinguishing *M. didyma* caterpillar feature is the presence of a wide white stripe, which is formed by the fusion of linea epistigmalis, linea stigmata, linea hypostigmalis, linea basalis, and linea subbasalis.

The *M. didyma* pupa obtained in the laboratory has a reduced black pattern (Fig. 9e, f) and resembles the "light" type of *M. interrupta* pupae (Fig. 8a–c). However, it should be noted that the color variability of Lepidoptera pupae in nature largely depends on climatic conditions and age. In *M. didyma*, the paired outgrowths at the base of the cremaster are light with a black tip (Fig. 9g, h). In *M. interrupta*, these paired outgrowths are completely darkened (Fig. 8f, g).

Conclusion

M. interrupta goes through the life cycle from egg to imago release in a time starting from 43 days. Some of the caterpillars enter diapause at fourth instar, while the rest continue their development and pupate at sixth instar. This development strategy increases the survival rate of the population under possible adverse conditions. The diagnostic value of eggs in the *M. didyma* species–group is expressed primarily in size and shape. The number of lateral ribs can be considered a relatively stable feature. The first instar caterpillars within the group vary in size and this feature is consistent with the eggs size. The head capsule chaetotaxy is also of diagnostic importance. The last instar caterpillars differ well in body color. Despite all the coloration variability, which, like imago's, may depend on climate, its main trends persist regardless of weather conditions. A characteristic feature of the *M. didyma* caterpillar coloration is the fusion of several paired lateral lines into a wide white stripe located under the linea stigmata. In *M. interrupta*, only linea hypostigmalis is colored with a light or flesh color. Pupae of similar species differ in the coloration intensity and, apparently, in the cremaster color.

The fritillaries of *M. didyma* species group are very similar in appearance and often difficult to distinguish in genitalia and imago morphology. The possibility to compare the preimaginal stages in this closely related group allows us to find additional significant diagnostic features and carry out identification with greater reliability.

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