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Intrapopulation Variability of Wing Pattern in *Hyponephele maureri* (Staudinger, 1886) (Lepidoptera: Nymphalidae: Satyrinae) and Its Taxonomic Significance

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Abstract. The study of intrapopulation variability in wing pattern and morphometric parameters in several populations of *Hyponephele maureri* (Staudinger, 1886) (Lepidoptera: Nymphalidae: Satyrinae) revealed that the patterns of significant differences in wing shape and coloration among individuals are similar for all studied populations. The observed uniformity in variations indicates the absence of differences necessary for distinguishing subspecies. Therefore, based on the established intrapopulation variability and the absence of diagnostic differences, the previously described subspecies *H. maureri subnephele* (Stshetkin, 1963) should be considered a junior subjective synonym of the species in question, i.e., *H. maureri = H. maureri subnephele*. This taxonomic revision emphasizes the importance of considering intrapopulation phenotypic variability when distinguishing subspecific taxa in Lepidoptera.

Keywords: Lepidoptera, Nymphalidae, morphological features, systematic position, Tajikistan

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Внутрипопуляционная изменчивость рисунка крыльев у *Hyponephele maureri* (Staudinger, 1886) (Lepidoptera: Nymphalidae: Satyrinae) и её таксономическое значение

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Аннотация. В результате проведённого исследования внутрипопуляционной изменчивости рисунка крыльев и морфометрических параметров у нескольких популяций бабочек вида *Hyponephele maureri* (Staudinger, 1886) (Lepidoptera: Nymphalidae: Satyrinae) выявлено, что закономерности проявления значительных различий в форме крыльев и окраске у особей одинаковы для всех изученных популяций. Наблюдаемое единообразие в вариациях свидетельствует об отсутствии различий, необходимых для выделения подвидов. Следовательно, на основании установленной внутрипопуляционной изменчивости и отсутствия диагностических различий, ранее описанный подвид *H. maureri subnephele* (Stshetkin, 1963) должен рассматриваться как младший субъективный синоним, то есть *H. maureri = H. maureri subnephele*. Этот таксономический пересмотр подчеркивает важность учёта внутрипопуляционной фенотипической изменчивости при разграничении подвидовых таксонов чешуекрылых.

Ключевые слова: Lepidoptera, Nymphalidae, морфологические особенности, систематическое положение, Таджикистан

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Introduction

The genus *Hyponephele* Muschamp, 1915, includes about 40 species found exclusively in the Palearctic Region, from North Africa and Portugal to Far Eastern Russia and China, most found in Central Asia, which is the center of the species diversity, [Samodurov et al., 1995; Eckweiler, Bozano, 2011] or these species are endemic to this region's mountains [Dubatolov et al., 1994]. About 20 species of this genus are found in Tajikistan, of which five are endemic to Tajikistan [Korb, Bolshakov, 2016].

Representatives of the genus *Hyponephele* are characterized by pronounced morphological variability, which covers a wide range of features. This variability manifests both in the parameters and coloration of the wings, as well as in the details of the genital structure. It is important to note that most significant variations become apparent only when studying extensive series of materials collected from different populations. Research on the morphological variability of representatives of

this genus inhabiting the territory of Russia and a number of other states of the former USSR has been presented in a number of fundamental works [Samodurov et al., 1995, 1996, 1997, 1999, 2000, 2001]. In addition, there are molecular genetic studies [Lukhtanov, Pazhenkova, 2021]. These publications provide detailed information about these morphological fluctuations and have served as the basis for the description of several new taxa. These studies are of utmost importance for further in-depth research on the intrapopulation variability of *Hyponephele* butterflies, particularly for understanding the mechanisms of speciation and adaptation within this taxonomic group.

The taxon *Hyponephele maureri* (Staudinger, 1887) was described by Staudinger in 1887 as variations (*Epinephele haberhaueri* var. *maureri* Staudinger, 1887) from the Alai range of Kyrgyzstan, the type locality "Südliche Alaj" [Staudinger, 1887]. Seitz, 1909 places this species in the *Hyponephele kirghisa* group (*Epinephele kirghisa maureri*). Korshunov and Dubatolov [1987] were the first to designate this taxon as *H. maureri*.

In Tajikistan, this species was first mentioned in the works of Groum-Grzhimailo [1890] and is given as *E. haberhaueri* var. *maureri* from Karategin Region. Stshetkin [1963] erroneously indicates the taxon *Hyponephele* (*Epinephele*) *rueckbeli* (Staudinger, 1887) for Tajikistan, referring to materials collected on the Hazrati Shoh ridge in the Khoja-Mumin hill, where he also described a new subspecies of this species, *H. rueckbeli subnephele* (Stshetkin, 1963). Later, Y.L. Stshetkin and Y.Y. Stshetkin [1975] mentioned this subspecies for the Peter the Great Mountain ridge as well. However, it should be noted that *H. rueckbeli* is found exclusively on the territory of Kyrgyzstan, and the subspecies described by Stshetkin (ssp. *subnephele*) morphologically corresponds to *H. maureri*, not *H. rueckbeli*. Samodurov et al. [1995], as well as other authors [Tuzov et al., 1997; Tshikalovets, 2003; Korb, Bolshakov, 2016; Davlatov, 2024] consider ssp. *subnephele* as a subspecies of *H. maureri*.

The ssp. *subnephele* was described based on specimens found in southern Tajikistan. Unfortunately, the storage location of the type species of this subspecies is unknown, and it is most likely lost. However, our long-term studies of *H. maureri* in the southwestern and central parts of Tajikistan have revealed specimens with similar morphological features. The morphological similarity between these specimens casts doubt on the reliability isolation of ssp. *subnephele* as a separate subspecies. To clarify the current situation, we conducted a study of the morphological features of the butterflies of *H. maureri* group inhabiting in Tajikistan.

Material and methods

To prepare this paper, we used the authors' materials collected in Southwestern and Central Tajikistan from 2019 to 2024 at the altitude of 1,500 to 1,800 m, in the following locations:

1. Hazrati Shoh ridge (1,500–1,800 m a.s.l., 38°21'47.20"N, 70°02'06.50"E), June–July, 2019–2023 – 44♂ and 10♀;
2. Hissar ridge (1,500 m a.s.l., 36°44'12.78"N, 68°37'59.86"E) July, 2023–2024 – 19♂ and 4♀;
3. Rashton ridge (1,500–1,800 m a.s.l., 38°35′19.02"N, 69°25′24.28"E), July, 2024 – 17♂ and 7♀;
4. Rangontau ridge (1,500 m a.s.l., 38°21′19.70"N, 68°44′27.61"E), June, 2023 – 21♂ and 4♀;
5. Sanglok ridge (1,600 m a.s.l., 38°19′27.08"N, 69°14′58.57"E), June, 2023 – 16♂;
6. Vakhsh ridge (1,600 m a.s.l., 38°32′10.47"N, 69°49′54.85"E), June, 2018 – 9♀;
7. Peter the Great ridge (1800 m a.s.l., 38°49′18.66"N, 70°19′23.33"E), June, 2022 – 15♂ and 4♀.

The butterfly's wingspan, wing coloration, wing patterns, the number and shape of the eyespot both upper and under sides of the wings, as well as the structure of the males' genitals were studied. The nomenclature of wing veins and cells is given according to B.N. Schwanwitsch [1924]. The wingspan of the butterflies was measured from the tip of one forewing to the tip of the corresponding other forewing when fully extended. We assessed the color and intensity of the wing background visually by comparing them with reference specimens from existing collections. The analysis of the variability of the number of eyespots on the wings of butterflies was carried out according to D. Turner's scheme [1963], which was developed to characterize the clinal variability of *Coenonympha tullia* (Müller, 1764). This scheme involves numerical coding starting

from the coastal edge of each wing. All observations were made using a stereoscopic microscope with a magnification of 1× or 20×. The collected data were recorded using a simple card system, where corresponding points were marked for each wing and each surface (upper/under), divided by population affiliation.

Standard descriptive statistics methods were applied to quantify the collected data. We calculated key indicators reflecting the variability of traits in the studied populations. In particular, the maximum (max) and minimum (min) values of each feature were determined, as well as the arithmetic means (x). To assess the degree of data dispersion and the reliability of the obtained mean values, the arithmetic error (m) and coefficient of variation (CV) were calculated. The reliability of the identified patterns and differences was confirmed using variance analysis with the Fisher (F) test. The statistical significance of the results was determined at the significance level of $P < 0.05$. In addition, a percentage ratio was used to clarify the proportional distribution of traits among individuals in populations.

The photographs of butterflies and their genitalia were taken with a NIKON D7000 digital camera connected to a NIKON SMZ 1500 stereomicroscope.

Morphology

The wing coloration of males of *H. maureri* is dark brown from upper side. On the subapical area of the forewings, there is one or sometimes two transverse eyespots ochreous on the edges. In the central part of the wing, the ochreous coloration is visible, with varying degrees of development, that is, sometimes covered with brown scales. Due to the degree of scale coverage, the ochreous coloration is in some cases barely visible. There is a brownish-black stripe in the disc area, stretching from bottom to top, that is, towards the costa, extending to the central cell without reaching the costa. The hindwings are without any patterns. On the upper side, starting from the base to the postdiscal area, the forewings have a pronounced reddish-ochreous coloration, while the tornal, costa and marginal area are brownish. The number of eyespots is two, and sometimes one. The upper one is slightly larger and has a white smear in the middle. The hindwings are brownish at the back, and the base has blurred brownish-green scales. The number of eyespots varies from four to five (see Fig. 1, a-b, d-e etc.).

The female also has a monotonous brown or dark brown wing coloration, but the ochreous color on the forewings is more pronounced than in males. The hindwings have a small clearance of reddish-ochre coloration. Both wings on the underside have the same morphological features as in males. The fringes are whitish-grey and sometimes brownish-grey (see Fig. 1, c, f, i, etc.).

The main morphological differences of the ssp. *subnephele* according to Stshetkin [1963] include strong darkening of the ochreous coloration on the upper side of the forewings in males (and usually in females) with monochromatic brown hindwings and the absence of eyespots. Unlike on the under side of the wings, most of the eyespots on the upper side are without a white central dot, and their number on the hindwings is usually reduced to four though frequently to two (rarely three or one) in females, or even none at all (Fig. 1, r–s).

Results

Wing parameters of the studied specimens. The wingspan of butterflies varies depending on the population and sexes. This indicator ranges from 26 to 36 mm in males and from 32 to 39 mm in females.

The analysis of the wingspan of *H. maureri*, collected in various mountain ridges, demonstrates interesting sexual dimorphisms and regional features. In all the studied locations, with the exception of the Sanglok and Vakhsh ridges where female samples were absent or represented by a small number of individuals, there is a tendency for females to have a larger wingspan than males. The minimum wingspan values for both males and females range from 26 to 36 mm, while the maximum values reach 36–39 mm. The average wingspan values in females, as a rule, exceed the average values in males. For example, on the Hazrati Shoh ridge, the average wingspan of males is 29.18 ± 0.40 mm, and that of females is 36.50 ± 0.76 mm. Similar trends may be observed on other ridges where sufficient samples of both sexes were present.

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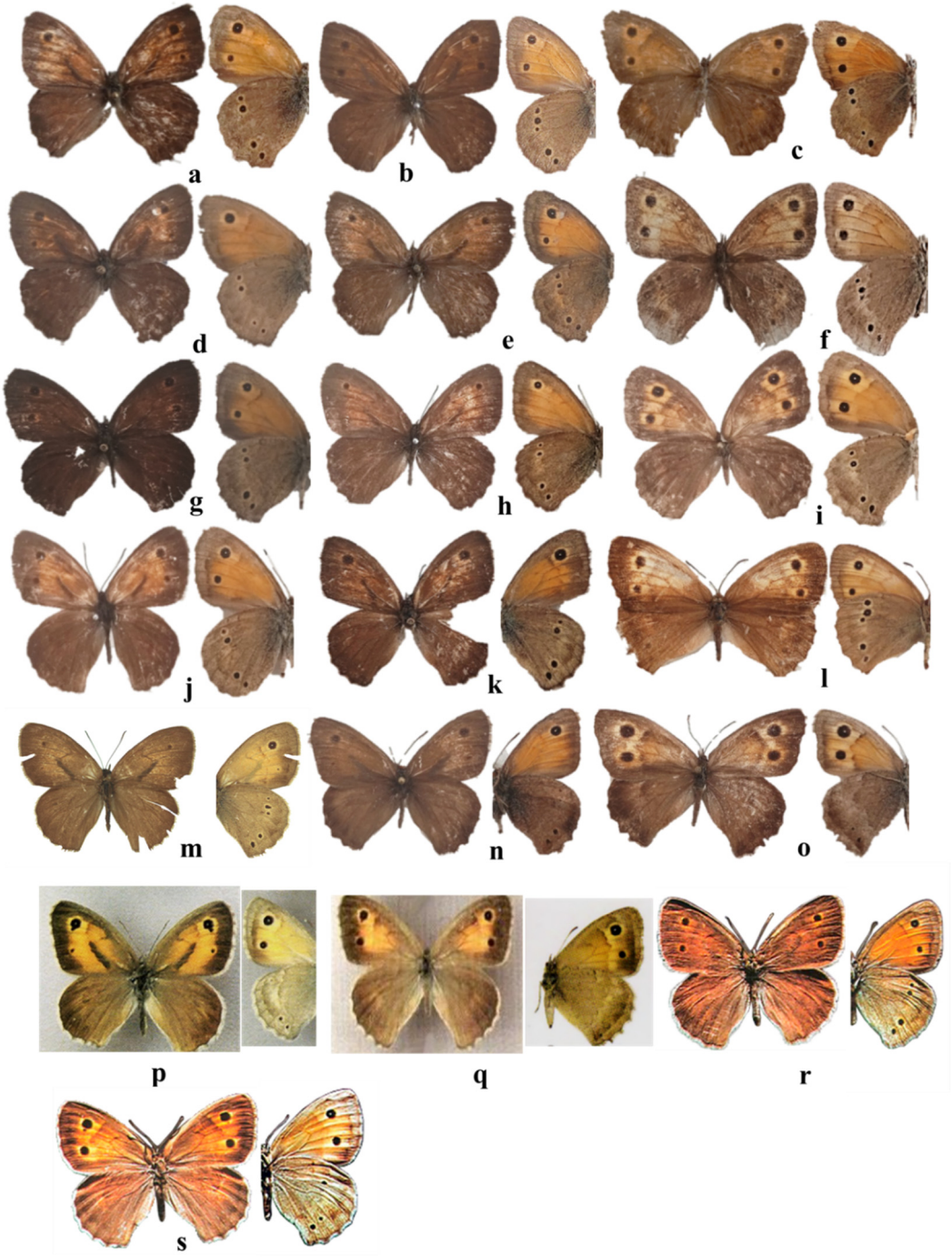

Fig. 1. Color variations of representatives of the genus *Hyponephele*:
H. maureri: a–b – male, c – female (Hazrati Shoh ridge); d–e – male, f – female (Hissar ridge);
g – male (Rashton ridge); h – male, i – female (Rahgontau ridge); j – male (Peter the Great ridge);
k – male (Sanglok ridge); l – female (Vakhsh ridge) (photo by A.M. Davlatov); m – male (Afghanistan)
[Tshikolovets, 2017]; *H. galtscha*: n – male, o – female (Hissar ridge)
(photo by A.M. Davlatov); *H. haberhaueri*: p – male, q – female [Tuzov et al., 1997];
ssp. *subnephele*: r – male, s – female [Samodurow et al., 1995]

Рис. 1. Варианты окраски представителей рода *Hyponephele*:
H. maureri: a–b – самец, c – самка (хр. Хазрати Шох); d–e – самец, f – самки (Гиссарский хр.);
g – самец (хр. Раштон); h – самец, i – самка (хр. Рангонтау); j – самец (хр. Петра Первого);
k – самец (хр. Санглок); l – самка (Вахшский хр.) (фото А.М. Давлатова);
m – самец (Афганистан) [Tshikolovets, 2017]; *H. galtscha*: n – самец, o – самка (Гиссарский хр.)
(фото А.М. Давлатова); *H. haberhaueri*: p – самец, q – самка [Tuzov et al., 1997];
ssp. *subnephele*: r – самец, s – самка [Samodurow et al., 1995]

The coefficient of variation (CV, %) indicates the relative variability of the trait within the sample. In males, CV ranges from 2.52 % (Peter the Great ridge) to 9.05 % (Hazrati Shoh ridge), which indicates a different degree of homogeneity of dimensional characteristics in the studied populations. In females, CV falls within the range of 3.20–6.57 %, which also indicates variability, but in general, females can be characterized as more uniform in size within individual samples.

Statistical analysis (F-test and P-value) shows that the sex differences in wingspan on the Hazrati Shoh, Hissar, Rashton and Rangontau ridges are not statistically significant ($P > 0.05$), with the exception of the Peter the Great ridge ($P < 0.05$). On the Peter the Great ridge, the value of $P < 0.05$ clearly indicates significant differences.

Thus, *H. maureri* demonstrates a pronounced sexual dimorphism in wingspan, with a predominance of larger individuals among the females. The variability of this trait is also noted both between individuals within populations and between different mountain ranges (Tab. 1).

Table 1
Таблица 1

Variability of wingspan in *Hyponephele maureri* individuals from surveyed localities of Southwestern and Central Tajikistan
Изменчивость размаха крыльев у особей *Hyponephele maureri* из обследованных локалитетов Юго-Западного и Центрального Таджикистана

Collection point / Место сбора	Number of individuals / Количество особей	min	max	x ± m	CV, %	F	P
Hazrati Shoh ridge	Male (n = 44)	26	36	29.18 ± 0.40	9.05	1.21	> 0.05
	Female (n = 10)	32	39	36.50 ± 0.76	6.57		
Hissar ridge	Male (n = 19)	28	32	30.11 ± 0.28	4.05	1.19	> 0.05
	Female (n = 5)	34	36	35.00 ± 0.50	3.20		
Rashton ridge	Male (n = 19)	30	34	32.21 ± 0.27	3.66	2.40	> 0.05
	Female (n = 7)	32	37	35.00 ± 0.69	5.22		
Rangontau ridge	Male (n = 21)	28	32	29.76 ± 0.27	4.20	3.03	> 0.05
	Female (n = 4)	31	36	33.25 ± 1.09	6.54		
Sanglok ridge	Male (n = 15)	28	32	30.13 ± 0.33	4.28	–	–
	Female (n = 0)	–	–	–	–		
Vakhsh ridge	Male (n = 0)	–	–	–	–	–	–
	Female (n = 9)	34	37	35.00 ± 0.37	3.20		
Peter the Great ridge	Male (n = 15)	29	31	29.73 ± 0.19	2.52	8.57	≤ 0.05
	Female (n = 5)	32	37	35.60 ± 0.98	6.15		

Note (here and below). Min and max – the minimum and maximum wingspan values in mm; x – the arithmetic mean; m – the standard error of the mean; CV – the coefficient of variation; F – Fisher's exact test; P – the statistical significance of the results.

Примечание (здесь и далее). Min и max – минимальное и максимальное значения размаха крыльев в мм; x – среднее арифметическое; m – стандартная ошибка среднего; CV – коэффициент вариации; F – критерий Фишера; P – статистическая значимость результатов.

The degree of wing coloration development. The wing coloration of the upperside of males and females is the same in all samples studied: solid dark brown color. The degree of yellow-ochre coloration on the upper side of the forewing varies in males, but it occurs in all samples in the same way. In some specimens, it is pronounced vividly, in others, it is barely noticeable, and sometimes it is absent altogether. The development of yellow-ochre coloration depends on the density of the coating with dark scales: with a weak coating, the color is visible, while in the case with a dense one, it is not. In females, this coloration almost does not vary. The color of the underside of the hindwings in both sexes is monotonous brown.

Considering the variability of coloration, three variants of forewing coloration can be distinguished for males of *H. maureri*:

– individuals with a well-developed yellow-ochre coloration,

– individuals with a poorly developed yellow-ochre coloration,

– individuals without a yellow-ochre coloration (a dark brown wing coloration).

Most often, especially among males, there are individuals with a weakly pronounced yellow-ochre coloration on the forewings. This form can be considered typical for the Tajik population of *H. maureri*. The coloration of the hind wings does not change in both sexes, remaining dark brown. It should be noted that there are no significant variations in the coloration of the wings in female *H. maureri*, which would allow them to be distinguished into separate variations (Fig. 1, a–n).

Analysis of data on the degree of development of the yellow-ochre coloration on the male forewings at various collection points reveals a number of important patterns, rather than simply stating the presence of morphological variability (Tab. 2). On the Hazrati Shoh ridge, there is a predominance of males with a poorly developed yellow-ochre coloration (70.45 %), which indicates a dominant tendency towards minimal expression of this trait. At the same time, the presence of 11.36 % of individuals with missing coloration and 18.18 % with well-developed coloration demonstrates some variability within the population. The population on the Hissar ridge has a relatively low percentage of males with not developed coloration (15.79 %) and, most importantly, the highest percentage of individuals with well-developed coloration (26.32 %).

Table 2
Таблица 2

Variability in the development of yellow-ochre coloration of the forewings in males of *Hyponephele maureri* from surveyed localities of Southwestern and Central Tajikistan
Изменчивость развития желто-охристой окраски передних крыльев у самцов *Hyponephele maureri* из обследованных локалитетов Юго-Западного и Центрального Таджикистана

Collection point / Место сбора	Number of individuals / Количество особей	Degree of yellow-ochre coloration development, % / Степень развития желто-охристой окраски, %		
		Well-developed / Хорошо развита	Poorly developed / Слабо развита	Absent / Отсутствует
Hazrati Shoh ridge	44	18.18	70.45	11.36
Hissar ridge	19	26.32	57.89	15.79
Rashton ridge	17	17.65	76.47	5.88
Rangontau ridge	21	33.33	52.38	14.29
Sanglok ridge	16	31.25	50.00	18.75
Vakhsh ridge	0	–	–	–
Peter the Great ridge	15	6.67	73.33	20.00

The Rashton ridge has the lowest proportion of males with missing coloration (5.88 %), which indicates the rarity of the complete absence of this trait. Combined with a significant proportion of poorly developed coloration (76.47 %), this highlights a strong tendency towards a minimal or weak yellow-ochre pigmentation. The Rangontau ridge has the maximum proportion of males with a well-developed coloration (33.33 %). In combination with the lowest proportion of poorly developed coloration (52.38 %), this is a clear indicator that the yellow-ochre coloration is the most intense among all the studied populations on this ridge.

On the Sanglok ridge, the proportion of well-developed coloration (31.25 %) is close to the maximum, however, a relatively high proportion of missing coloration (18.75 %) indicates a more balanced distribution of the trait, with the presence of both brightly colored and completely colorless individuals. The Peter the Great ridge is distinguished by the highest proportion of males with missing coloration (20.00 %), which indicates a pronounced tendency towards a reduction or complete absence of this trait. The low proportion of well-developed coloration (6.67 %) further confirms this trend.

The presented data clearly demonstrate that the degree of development of the yellow-ochre coloration of males' forewings is not uniform and there is a clear morphological variability between populations located on different ridges. The range of development of the trait varies from complete absence (up to 20 % in some populations) to prominent coloration (up to 33.33 % on the Rangontau ridge). Thus, although the difference in the degree of development of the yellow-ochre coloration of the male forewings between populations exists and is quite evident, it reflects intraspecific variability, and are not sufficient grounds for distinguishing subspecies.

The number of eyespots on the upper and under sides of the wings. The eyespots are located in the cells between the R_5–M_1 and Cu_1–Cu_2 veins (Fig. 2, a) on the upperside of the forewings in both males and females, though their number varies: males have two eyespots (more than 90 % in all studied populations); some individuals have small eyespots that merge with the main eyespot, or an underdeveloped second eyespot in the form of a small dot. It is noted that the number of eyespots on the upper and under sides of the forewing may vary (for example, one on the top and two on the bottom, or vice versa). The number of eyespots on the forewings of females varies from one to two (Tab. 3). Some specimens have a white dot in the center of the first eyespot.

Fig. 2. The variability of eyespots on the upper and under sides of the wings in the butterfly *Hyponephele maureri*:
a – upper side of the wing; b – under side of the wing (photo by A.M. Davlatov)
Рис. 2. Изменчивость глазчатых пятен на верхней и нижней сторонах крыльев *Hyponephele maureri*:
а – верхняя сторона крыла; б – нижняя сторона крыла (фото А.М. Давлатова)

The number of eyespots on the underside of the forewings in males varies from one to two (only permanent eyespots), located in the same cells as on the upper side (R_5–M_1 and Cu_1–Cu_2); up to 95 % of individuals in all studied populations have two eyespots on their forewings. Some specimens have white dots in the center of both eyespots, while others have only one white dot; specimens with only one eyespot may also have a white dot in the center. The number of eyespots on the underside of the hindwings ranges from four to five: three above and two below, located in the cells between the veins Rs–M_1 or Rs-M_1–M_2, Cu_2–A_2 and 2A–3A (see Fig. 2, b). The third upper eyespot is usually poorly developed, significantly smaller than the other ones, and is rare; up to 97 % of individuals in all populations have four eyespots, and there are also specimens with undeveloped eyespots. The white dots in the center of the eyespot can be expressed in various ways: only in the second upper eyespot, in the second upper and the first lower ones, or in both upper eyespots if absent in the lower ones; in some specimens, a white dot may be present on the underside of the right wing and absent on the left, sometimes the white dots are very small and difficult to distinguish. Females have similar morphological features to males, but they often have two eyespots on the underside of their forewings.

As for the number and location of the eyespots on the fore and hindwings of *H. maureri*, the following variations can be distinguished. Among males, the most common specimens are those with

two permanent eyespots located on the forewings between the veins R_5–M_1 and Cu_1–Cu_2. This form is considered typical. Also, among males, there is a variation with one eyespot (between veins R_5–M_1), while the second eyespot (between veins Cu_1–Cu_2) is absent. In females, it is impractical to distinguish variants based on the number of eyespots on the forewings, since females are dominated by individuals with two permanent eyespots. As for the hindwing, both males and females can be distinguished by two variants of the arrangement of the eyespots on the underside of the wing: in individuals with four eyespots and in those with five eyespots. In the studied population, individuals with four eyespots predominate over individuals with five eyespots.

Based on the analysis of the data presented in Table 3, which relate to the variability of the number of eyespots on the wings of *H. maureri* in various mountain ranges of Tajikistan, the following conclusions can be drawn.

The trait demonstrates a low quantitative variability. In all the studied individuals, the number of eyespots varies in a very narrow range: from one to two on the forewing and from three to four on the hindwing. The average values of the trait are consistently high and close to the maximum (1.90–1.95 for the forewings of males, 3.90–3.95 for the hindwings), which indicates the predominance of the maximum number of eyespots in most butterflies (two and four, respectively).

There was no pronounced clinal variability in the average number of eyespots. The averages for the different ridges are very similar. However, the level of variability (CV) in females varies more strongly between populations, possibly due to the small sample sizes (n = 1–10). The lowest variability in males was observed in the population of the Hasrati Shoh ridge (CV = 1.53 % for the hindwings), and the highest in females of the Hissar, Rangontau and Peter the Great ridges (CV = 14.29 % for the forewings).

Thus, the “number of eyespots” trait in *H. maureri* is highly conservative and stable, especially in males. Its variability is mainly qualitative (discrete) in nature (the presence of one or two, three or four eyespots) with extremely low quantitative variability. The main source of variability in populations is related to the sex of the individual, rather than to the regional location. The low CV values obtained (often < 5 %) are characteristic of stable, little-changing morphological features.

Table 3
Таблица 3

Variability parameters of the number of eyespots on the wings of *Hyponephele maureri* from surveyed localities of Southwestern and Central Tajikistan
Изменчивость числа глазков на крыльях *Hyponephele maureri* из обследованных локалитетов Юго-Западного и Центрального Таджикистана

Collection point / Место сбора	Number of individuals / Количество особей	Number of eyespots / Число глазков			
		min	max	x ± m	CV, %
Male (forewing) / Самцы (переднее крыло)					
Hazrati Shoh ridge	n = 44	1	2	1.95 ± 0.07	3.57
Hissar ridge	n = 19	1	2	1.95 ± 0.11	5.64
Rashton ridge	n = 17	1	2	1.94 ± 0.12	6.18
Rangontau ridge	n = 21	1	2	1.95 ± 0.09	4.61
Sanglok ridge	n = 16	1	2	1.94 ± 0.13	6.70
Vakhsh ridge	n = 0	–	–	–	–
Peter the Great ridge	n = 15	1	2	1.93 ± 0.14	7.25
Male (hindwing) / Самцы (заднее крыло)					
Hazrati Shoh ridge	n = 44	3	4	3.91 ± 0.06	1.53
Hissar ridge	n = 19	3	4	3.95 ± 0.12	3.04
Rashton ridge	n = 17	3	4	3.94 ± 0.13	3.30
Rangontau ridge	n = 21	3	4	3.90 ± 0.09	2.31
Sanglok ridge	n = 16	3	4	3.94 ± 0.13	3.30
Vakhsh ridge	n = 0	–	–	–	–
Peter the Great ridge	n = 15	3	4	3.93 ± 0.14	3.56

End of Table 3
Окончание таблицы 3

Female (forewing) / Самки (переднее крыло)					
Hazrati Shoh ridge	n = 10	1	2	1.90 ± 0.14	7.37
Hissar ridge	n = 4	1	2	1.75 ± 0.25	14.29
Rashton ridge	n = 7	1	2	1.71 ± 0.22	12.87
Rangontau ridge	n = 4	1	2	1.75 ± 0.25	14.29
Sanglok ridge	n = 0	–	–	–	–
Vakhsh ridge	n = 9	2	2	1.89 ± 0.21	11.11
Peter the Great ridge	n = 4	1	2	1.75 ± 0.25	14.29
Female (hindwing) / Самки (заднее крыло)					
Hazrati Shoh ridge	n = 10	3	4	3.90 ± 0.14	3.59
Hissar ridge	n = 4	3	4	3.75 ± 0.25	6.67
Rashton ridge	n = 7	3	4	3.86 ± 0.21	5.44
Rangontau ridge	n = 4	3	4	3.75 ± 0.25	6.67
Sanglok ridge	n = 0	–	–	–	–
Vakhsh ridge	n = 9	3	4	3.89 ± 0.21	5.39
Peter the Great ridge	n = 4	3	4	3.75 ± 0.25	6.67

The structure of the genitals. As shown in Figure 3, there were no significant differences in the structure of male genitalia between different samples of specimens. This allows us to conclude about the relatively low variability of the genital apparatus in this species.

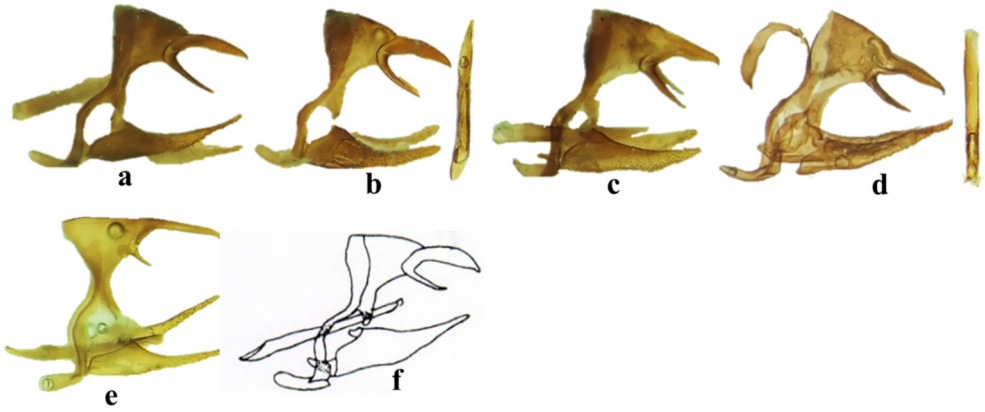

Fig. 3. Male genitalia of representatives of the genus *Hyponephele*:
H. maureri: a – Hazrati Shoh ridge; b – Rashton ridge; c – Hissar ridge; d – Sanglok ridge; *H. galtscha*: e – Hissar ridge (photo by A.M. Davlatov); *H. haberhaueri*: f – Zeravshan, Farob [Samodurov et al., 1995]
Рис. 3. Гениталии самцов представителей рода *Hyponephele*:
H. maureri: a – хр. Хазрати Шох; b – хр. Раштон; c – Гиссарский хр.; d – хр. Санглок; *H. galtscha*: e – Гиссарский хребет (фото А.М. Давлатова); *H. haberhaueri*: f – Зеравшан, Фароб [Samodurov et al., 1995]

Similar species. Morphologically, the butterfly *H. maureri* is similar to *H. galtscha* (Grum-Grshimailo, 1893) and *H. haberhaueri* (Staudinger, 1886). However, *H. galtscha* differs from them in the following: In males, the black stripe on the upper side of the forewing, extending from the base to the discal area, is somewhat thicker. There is always only one spot on the underside of the forewing. The eye-spot on the underside of the hindwing is smaller than in *H. maureri*. The general tone of the underside of the wings is dark brown. The females of *H. galtscha* differ from the female of *H. maureri* primarily in the more saturated dark brown color of the underside of the wings. In addition, an important distinguishing feature is the number and shape of the eyespots on the underside of the hindwings: in females, number of eyespots are usually fewer (one or two), and they are insignificant in size (see Fig. 1, n–o). The genitals of males of *H. galtscha* and *H. maureri* also have differences, especially in the shape of tegumen, uncus, and gnathos branches. In *H. galtscha*, the tegumen and valva are less wide, the gnathos branches are shorter, and the uncus, on the contrary, is longer than in *H. maureri* (see Fig. 3, e).

A distinctive feature of males of *H. haberhaueri* is a wider black stripe on the upper side of the forewing, which surpasses even *H. galtscha* in width. In addition, the yellow-ochreous coloration of the upper side of the forewing is much more pronounced in both males and females of *H. haberhaueri* than in *H. maureri* and *H. galtscha* (see Fig. 1, p-q). The genitals of males of *H. haberhaueri* and *H. maureri* also have differences. In *H. haberhaueri*, the tugemen is narrower, and the uncus and branches of the gnathos are not as long as in *H. maureri*. In addition, the uncus of *H. haberhaueri* is slightly curved. The valva is also curved and directed upwards (see F. 3, f).

Ecology. The *H. maureri* species is distributed in Kyrgyzstan, Tajikistan, Uzbekistan and Afghanistan. In Tajikistan, it occurs at altitudes of 1,500–2,400 m above sea level. Depending on the location, the butterfly's flight starts from June to early August. It prefers steppes and mixed grass meadows (Figures 4, 5). The species is univoltine.

Fig. 4. Habitat of *Hyponephele maureri* in the Rashton ridge (Tajikistan)
(photo by A.M. Davlatov)
Рис. 4. Местообитание *Hyponephele maureri* на хребте Раштон (Таджикистан)
(фото А.М. Давлатова)

Discussion

The study has revealed a set of key morphological characteristics of *H. maureri* that are significant for the taxonomy of the species. The analysis of wing parameters, including their span, demonstrates the pronounced morphological plasticity of this species. There is a clear variability of these features, consistently observed in all the studied samples.

Specifically, a significant sexual dimorphism in wingspan has been identified. Across most studied locations, females consistently exhibited a larger wingspan than males, with average values on the Hazrati Shoh ridge reaching 36.50 ± 0.76 mm for females compared to 29.18 ± 0.40 mm for males. The differences in wingspan between the sexes were statistically significant only in the Peter the Great ridge ($P < 0.05$). For the rest of the studied populations, the values were $P > 0.05$, indicating the absence of statistical significance of the differences identified. Consequently, the general trend of a larger wingspan in females observed in the sample has not been confirmed as statistically significant

for most of the studied ridges, with the exception of Peter the Great ridge. The coefficient of variation (CV) for wingspan further highlighted differences between sexes, with males showing a broader range of variability (2.52 % to 9.05 %) compared to females (3.20 % to 6.57 %), suggesting that females are generally more uniform in size within individual samples. This variability in wingspan, while evident between individuals and populations, reflects intraspecific differences rather than grounds for subspecies differentiation.

Fig. 5. Habitat of *Hyponephele maureri* in the Hissar ridge (Tajikistan) (photo by A.M. Davlatov)
Рис. 5. Местообитание *Hyponephele maureri* на Гиссарском хребте (Таджикистан)
(фото А.М. Давлатова)

The yellow-ochre coloration on the male forewings presents another significant aspect of morphological variation. Regional differences in the development of this trait were pronounced, ranging from complete absence (up to 20 % in some populations on the Peter the Great ridge) to prominent coloration (up to 33.33 % on the Rangontau ridge). For instance, populations on the Hazrati Shoh ridge predominantly featured males with poorly developed coloration (70.45 %), while the Rangontau ridge showed the most intense yellow-ochre coloration (33.33 % of cases with a well-developed coloration). These extensive variations, particularly the range from minimal to maximal expression of coloration, underscore the intraspecific variability within *H. maureri* and are not sufficient for subspecies delimitation.

A contrasting pattern of stability has been revealed in the number of eyespots on the wings. This trait exhibits low quantitative variability, consistently falling within a narrow range (one to two on forewings, three to four on hindwings) across all individuals and populations. The average values are consistently high, suggesting a conservative and stable characteristic, particularly in males, with minimal quantitative variation (CV often < 5 %). While some variability in the CV for females was noted between populations, possibly linked to sample size, the overall conservative nature of the eyespots count suggests it is a highly stable morphological feature. The primary source of variation in eyespots number appears to be sex-related rather than geographical.

Taking into account the morphological data – including pronounced variability in wing parameters, marked sexual dimorphism in wingspan, high conservatism of genital structures and eyespot number, variability in coloration phenotypes across populations, and ecological homogeneity of habitats – we conclude that the previously described subspecies ssp. *subnephele* lacks sufficient morphological or ecological differentiation to warrant recognition as an independent taxonomic unit. The observed differences, particularly in wing metrics and dimorphic wingspan, represent intraspecific plasticity rather than discrete subspecific boundaries.

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