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The Possibility of Using Characters of the Female Genital Armature for Species Diagnostics and Classification of the Genus *Mellicta* Billberg, 1820 (Lepidoptera, Nymphalidae): 1. *Mellicta athalia* (Rottemburg, 1775) Species Group

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Abstract—The morphology of female genital armature of seven species of the genus *Mellicta* belonging to the *M. athalia* species-group from different localities of their ranges is analyzed. The main distinctive features are described and their variability and use for species identification are assessed. It is shown that some characteristics of female genitalia can be used to clarify the systematic position of species within the genus. Keys to species of the *athalia* group based on female genitalia are given.

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First of all, we have to touch upon the status of the studied taxon, which remains an open question. Morphologists and taxonomists tend to consider *Mellicta* as a subgenus within the large genus *Melitaea* (Hesselbarth et al., 1995; Oorschot and Coutsis, 2014, etc.). In his fundamental work, Higgins (1955) regarded *Mellicta* as a separate genus, his opinion being mostly based on the differences between *Mellicta* and *Melitaea* in the male genital morphology as well as in geographic distribution. Many other researchers accepted his view and considered *Mellicta* a separate genus (Devyatkin, 2000; Korshunov, 2002, etc.). We also adhere to this opinion and proceed from the pragmatic definition of a genus given by Mayr (1971), who considered this taxonomic category as "a monophyletic group of species, which is separated from other taxa of the same rank (other genera) by a decided gap." Mayr (1971) clearly indicated that "other taxa of the same rank" may be groups of species that are now called paraphyletic, i.e., including not all the descendants of the common ancestor. The status of *Mellicta* as a separate genus is supported by its differences from *Melitaea* in the structure of male and female genitalia. The male genitalia of *Mellicta* are characterized by a well-developed tegumen that often bears a pair of sclerotized prongs of the subuncus. The size and shape of the subuncus are of great significance for identification of species of the genus *Mellicta*; by contrast, the subuncus is absent in representatives of the genus *Melitaea*. Besides, the aedeagus of nearly all the species of *Mellicta* has a well-developed distal ostium-keel, which is poorly developed or absent in males of *Melitaea*. The female genitalia in the genus *Melitaea* typically possess auriculae, or complex chitinized folds located at the junction of the antevaginal plate and the antrum. In females of *Mellicta* the auriculae are absent or considerably reduced. Molecular data (Leneveu et al., 2009) showed *Mellicta* to be a natural monophyletic group while *Melitaea* sensu stricto proved to be paraphyletic. However, the latter taxon can still be considered as a genus if we follow Mayr's definition cited above.

Fritillaries of the genus *Mellicta* Billberg, 1820 are among the most difficult groups of butterflies in terms of species diagnostics. Their identification is hindered, first of all, by high individual and intraspecific variation of their wing patterns. Reliable identification is based on characters of male genitalia, which were repeatedly described and illustrated in the literature (Hormuzaki, 1911; Sushkin, 1913; Reverdin, 1922; Verity, 1940; Higgins, 1955; Niculescu, 1964; Lukhtanov and Lukhtanov, 1994; Devyatkin, 2000; Korshunov, 2002; Dubatolov et al., 2005; Bush, 2011, etc.).

Almost no attention has been given to the possibility of using the characters of female genitalia for species identification. Higgins (1955) provided illustrations of the female genitalia of several, mostly European species of the genus *Mellicta* but did not comment on the variability or diagnostic value of their individual elements. Dubatolov and co-authors (2005) made a key to the five Far Eastern species based on the female genitalia but gave no illustrations. There are a few publications devoted to a detailed study of the female genitalia of some representatives of the genus *Mellicta* (Nekrutenko, 1985; Churkin and Devyatkin, 2005; Kolesnichenko and Bush, 2015).

The goal of this work was to study the morphology of the female genitalia of representatives of the genus *Mellicta* from different localities of their ranges and to determine the variability of individual structures and their usefulness for species diagnostics and classification.

MATERIALS AND METHODS

We have studied the material kept in the Zoological Museum of Moscow State University (ZMMU), Zoological Institute of Russian Academy of Sciences, St. Petersburg (ZIN), Department of Entomology of Lomonosov Moscow State University (DEMSU), and also our own collections and the material provided by private collectors.

Genital preparations were made using the following technique. The part of abdomen with the genitalia was dissected, placed in an Eppendorf tube filled with 10% NaOH solution, and macerated for 7 h at 55°C in an INB 400 precision incubator. Then the preparation was cleaned of muscles and fat tissue, rinsed in water, and photographed with a Canon PowerShot G9 camera and a Zeiss Stemi 2000-C stereomicroscope at 2.5× objective lens magnification and 10× eyepiece magnification. The examined preparation was put in a blister filled with glycerol and pinned under the corresponding collection specimen. Altogether, 107 female genital preparations of 7 species of *Mellicta* close to *M. athalia* were documented. The drawings and photos were processed in Adobe Photoshop. The genitalia are described using the terminology of Higgins (1941) and Nekrutenko (1985).

The classification of the genus *Mellicta* used herein is based on the work of Higgins (1955) and the recently published systems (Devyatkin, 2000; Korshunov, 2002; Oorschot and Coutsis, 2014).

The material examined (the geographic names, dates, and collectors' names are cited exactly as in the labels):

Mellicta athalia (Rottemburg, 1775). 1 ♀, "Great Britain, East Blean Wood, VC 15 TR 1864, 4/07/2008 VVP, V. Proklov leg." (coll. M.G. Bush); 2 ♀, "Ukraine, Kiev Reg., Brovarsky distr., Zavorichi v., 29.05.2014, I. Pljustsch" (DEMSU); 1 ♀, "Chernigov reg, Konotop t. vicinity, 10.07.92, R. Kabakova" (DEMSU); 3 ♀, Georgia, Likani Vill., Imereti Range, 2000 m, 5–9.VIII.1936, A. Tsvetaev (ZMMU); 1 ♀, 19.VII.1924, "Transcaucasia, Bakuriani, G. Pashin" (ZMMU); 2 ♀, Tver Prov., Zapadnodvinskii Distr., env. of Polyaki Vill., 20 and 28.VII.93, K. Kolesnichenko (DEMSU); 1 ♀, Chelyabinsk Prov., Ilmen Reserve, 22.VI (coll. M.G. Bush); 6 ♀, Altai, env. of Ust-Koksa Vill., 12–17.VI.2010, M.G. Bush leg. (coll. M.G. Bush); 2 ♀, "E. Kazakhstan, Sarym-Sakty Mts, 12 km SSW Soldatovo v., 1300 m, 11–13.06.12, N 49°07′, E 85°04′, R. Yakovlev" (DEMSU); 1 ♀, env. of Magadan, 1.VII.1964, A. Tsvetaev (ZMMU); 1 ♀, Magadan Prov., Tenkinskii Distr., 15 km of Kulu Vill., Kolyma water balance station, 3.VI.2006, A.G. Bush leg. (coll. M.G. Bush).

M. caucasogenita (Verity, 1930). 1 ♀, North Caucasus, Teberda, Mukhu River, 16.VII.1940, A. Tsvetaev (ZMMU); 1 ♀, North Caucasus, Teberda, Garaly-Kol River, 1.VII.1916, G. Pashin (ZMMU); 1 ♀, North Caucasus, Teberda, Malaya Khatipara Range, 21.VI.1916, G. Pashin (ZMMU); 1 ♀, North Caucasus, Teberda, Malaya Khatipara Range, 1900 m, 28.VII.1940, A. Tsvetaev (ZMMU); 2 ♀, "N. Osetia, S slopes of Skalysty Mts., Kavirhoh r., 4 km NEE Arhoh pass, 1930 m, 24.07.2009, N 42°50′15″, E 044°15′30″, V. Savitsky" (DEMSU); 1 ♀, Armenia, Goris Mt., 1700 m, 26.VI.1974, A. Tsvetaev (ZMMU); 1 ♀, 6.VII.1925, "Armenia Ross. Delizhan, V. Gamburtsev" (ZMMU); 1 ♀, "Georgia. Marneulsky Distr., Burma v. vicinity, 600 m. 23.06.1968, Selivanov" (DEMSU); 3 ♀, Georgia, Likani Vill., Imereti Range, 2000 m, 5–8.VIII.1936, A. Tsvetaev (ZMMU); 1 ♀, 5.VII.1924, "Transcaucasia, Bakuriani, G. Pashin" (ZMMU).

M. ambigua (Ménétriés, 1859). 1 ♀, lectotype, "*Athalia* var. *Ambigua* Mén. Amur sept., Schrenk, Amur sept, coll. Acad. Petrop." (ZIN); 2 ♀, "Nicolajefsk, coll. Dieckmann, Graeser legit." (ZIN); 2 ♀, Komsomolsk-on-Amur, 26.VI.2005, A. Kapkaev (coll. S. Churkin); 1 ♀, "Siberia orient.[alis], Maak" (ZIN); 1 ♀, Selemdzha Distr., Mariinsk, 23.VI.1971,

L. Nikolaevsky (DEMSU); 1 ♀, Sakhalin, Pilvo, 24.VI.1910, Derbok (ZIN); 4 ♀, Karym Distr., 10 km E of Urulga Vill., Ingoda River, 23–29.VI.1995, K. Kolesnichenko (DEMSU); 1 ♀, "Eastern Sibiria, Lake Baikal, Khamar-Daban Mts., h = 600 m, Slyudyanka river, taiga, June 21, 2002, Y. Shevnin" (DEMSU); 1 ♀, "pref. Nagano, Tobiro," 19–21.VII.67 (ZMMU); 1 ♀, "Japan, Nagano," 21.VII.54 (ZMMU); 12 ♀, "S. Primor'e reg., Pogranichny distr., Barabash-Levada v., 18–26.07.95, K. Kolesnichenko" (DEMSU); 4 ♀, "Vladivostok, Graeser leg." (ZIN); 3 ♀, Chuguev Distr., env. of Zametnoe, 6.VI.2006, K. Kolesnichenko (DEMSU); 1 ♀, env. of Obluchye, Berezovaya Pad, 1–6.VII.2002, K. Kolesnichenko (DEMSU); 6 ♀, env. of Svobodny, Kostyukovka, 5–9.VII.1995, K. Kolesnichenko (DEMSU); 1 ♀, Russia, Yakutia (Sakha) Republic, Eveno-Batyntai National Okrug, env. of Dzhergalakh Vill., right bank, 2–13.VII.2011, Kurmaev A.V. (DEMSU); 1 ♀, Yakutia, Batagai Vill. area, E terrace of Yana River, 29.VI.2010, Kurmaev A.V. (DEMSU); 1 ♀, Yana River, 50 km downstream of Verkhoyansk, 4.VII.27, Tkachenko (ZIN).

M. nevadensis (Obertür, 1904). 1 ♀, "Hispania; prov. Lerida, Vail d'Aran; Baqueira, 15–1600 m, 16–19.07.1975, Fam. Epstein leg." (ZMMU); 1 ♀, "Aspromonte, Calabria, dint. Gambarie, 1300 m, 25.06.71, col. F. Hartig" (DEMSU).

M. dejone (Geyer, 1832). 3 ♀, "Spain, Sierra Nevada, Capileira Vill., Rio Nante, N 36.991761, E –3.350043, 1550 m," 8–9.V.2014 (DEMSU); 2 ♀, "Algerie, Tlemcen," V.1972 (ZMMU); 1 ♀, "Algerie, Tlemcen," V.1973 (ZMMU).

M. britomartis (Assmann, 1847). 1 ♀, Vinnitsa Prov., Mogilev-Podolskii Distr., Lyadova Vill., 15.VI.2007, I. Plyushch (coll. M.G. Bush); 2 ♀, Vinnitsa Prov., Mogilev-Podolskii Distr., env. of Nemyya Vill., 14.VI.2007, I. Plyushch (coll. M.G. Bush); 1 ♀, Vinnitsa Prov., Mogilev-Podolskii Distr., env. of Nemyya Vill., 18.VII.2010, I. Plyushch (coll. M.G. Bush); 1 ♀, Tula Prov., Zaokskii Distr., right bank of Gorodenka River opposite Nizhnyaya Gorodnya Vill., 23.VI.2013, Bush leg. (coll. M.G. Bush); 1 ♀, Novosibirsk Prov., Iskitim Distr., right side of Shipunikha River valley between Evsino and Lozhok Vill., 2.VII.2013, M.G. Bush leg. (coll. M.G. Bush); 1 ♀, Novosibirsk Prov., Ordynskii Distr., Shenichnyi Log, 13.VII.2013, M.G. Bush leg. (coll. M.G. Bush); 1 ♀, Altai, Altai State Biosphere Reserve, Chiri outpost, steppified meadow, 10.VI.2012, T.V. Galinskaya leg. (coll. M.G. Bush); 1 ♀, Altai, env. of Ust-Koksa, 15.06.2010, M.G. Bush leg. (coll. M.G. Bush); 1 ♀, "E. Kazakhstan, Sarym-Sakty Mts, 12 km SSW Soldatovo v., 1300 m, 11–13.06.12, N 49°07′, E 85°04′, R. Yakovlev" (DEMSU); 1 ♀, "NE Kazakhstan, Saur Mts., B. Zhemenei riv., Zhanaturmyz v., 1600, 10–12.06.98, A. Klimenko" (DEMSU); 2 ♀, "Irkutsk prov., Ol'honsky distr., road Baiandai–Elantsy, Kosaia Step' v. vicinity, 10–11.07.03. K. Kolesnichenko" (DEMSU); 1 ♀, "S. Primor'e reg., Pogranichny distr., Barabash-Levada v., 18–26.07.95, K. Kolesnichenko" (DEMSU); 1 ♀, "W. Mongolia, Hovd aimak, Bulgan-gol Valley, Bayan-Gol basin, middle stream of Uljastajn-Sala river, Arshantyn-Nuruu Mts., 2100–2500 m, 20–23.06.2005, V. Doroshkin, R. Yakovlev & D. Ryzhkov" (coll. M.G. Bush).

M. plotina (Bremer, 1861). 1 ♀, "Irkutsk prov., 40 km NE from Irkutsk t., road to Ust'Ordynsk t., Kuda r., outlet of Kuiada r., Cheremushka v. vicinity, 8.07.03, K. Kolesnichenko" (DEMSU); 4 ♀, Amurskaya Prov., env. of Svobodny, Kostyukovka Vill., 5–9.VII.95, K. Kolesnichenko; 1 ♀, "Russia, Amur reg., Svobodny distr., Kostyukovka, 6–9.07.1995, leg. and coll. V. Tuzov" (DEMSU); 1 ♀, "S. Primor'e reg., Pogranichny distr., Barabash-Levada v., 18–26.07.95, K. Kolesnichenko" (DEMSU).

RESULTS

As the result of this research, we have studied in detail the genitalia of females of seven morphologically close species of the *M. athalia* group from different localities, and determined their distinctive features, variation, and usefulness for species identification. The general scheme of female genitalia in the genus *Mellicta* is shown in Fig. 1; the anal papillae, copulatory bursa, and anterior and posterior apophyses are not depicted since, according to our results, they provide no diagnostic characters.

The copulatory opening (ostium bursae) leads into the dilated sclerotized funnel termed the antrum, which is located between the antevaginal plate (lamella antevaginalis) and the postvaginal plate (lamella postvaginalis). The antrum is connected to the ductus of the copulatory bursa (ductus bursae copulatrix), which often has a fork-shaped sclerotization termed the bacillus by Higgins (1941). The main characters that can be used to differentiate the closely related species of this group are the length ratio of the ante-

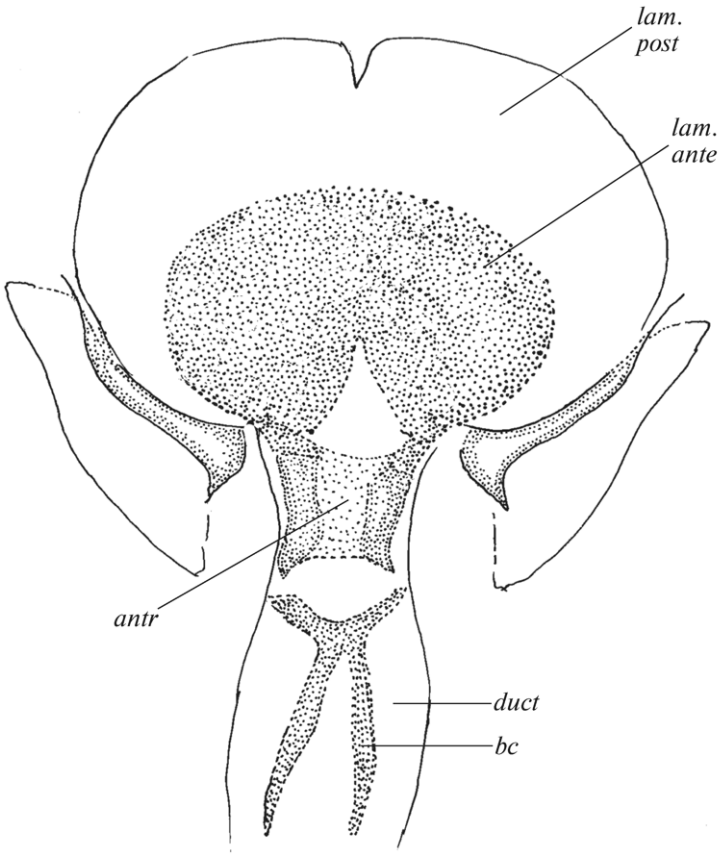

Fig. 1. Structure of the female genitalia in the genus *Mellicta* (without the anal papillae, copulatory bursa, and anterior and posterior apophyses): *duct*, ductus bursae copulatrix; *bc*, bacillus; *antr*, antrum; *lam. ante*, lamella antevaginalis (antevaginal plate); *lam. post*, lamella postvaginalis (postvaginal plate).

vaginal and the postvaginal plates, the morphology of the bacillus, and the morphology of the antrum.

Key to Species-Groups of the Genus Mellicta Based on Female Genitalia

1. Ductus with well-developed fork-shaped sclerotization (bacillus) of varying length (Fig. 1) ..... 2.

—Fork-shaped sclerotization (bacillus) absent or almost absent..... Species of *aurelia* group (partly).

2. Postvaginal plate does not protrude or slightly protrudes apically beyond antevaginal plate (Fig. 3, *1–4*); if postvaginal plate strongly protrudes, then antevaginal plate and antrum together form characteristic mushroom-shaped structure ..... 3.

—Postvaginal plate strongly protrudes apically beyond antevaginal plate. Protruding part at least one-third (often at least one-half) as long as antevaginal plate and antrum combined (Fig. 2; Fig. 3, *5–11*). Antevaginal plate and antrum together form rounded (sometimes somewhat elongated) or pyriform structure ..... Species of *athalia* group (partly).

3. Antrum narrowing. Antevaginal plate and antrum together form mushroom-shaped or pyriform structure. Postvaginal plate trapeziform with pointed angles protruding beyond antevaginal plate; sometimes rounded. Ductus apically (before divergence of strands of bacillus) without wide sclerotization ... . Species of *aurelia* group (partly).

—Antrum wide (Fig. 3, *1*, *2*); if antrum narrowing then ductus apically with wide sclerotization (Fig. 3, *3*, *4*). Postvaginal plate oval or oval-trapeziform, sometimes close to rectangular. Species occur in West Europe or North Africa .... Species of *athalia* group (partly).

Key to Species of the M. athalia Species-Group Based on Female Genitalia

1. Postvaginal plate only slightly protrudes apically beyond antevaginal plate (Fig. 3, 1–4). Species occur in West Europe or North Africa ..... 2.

—Postvaginal plate noticeably protrudes apically beyond antevaginal plate (protruding part usually at

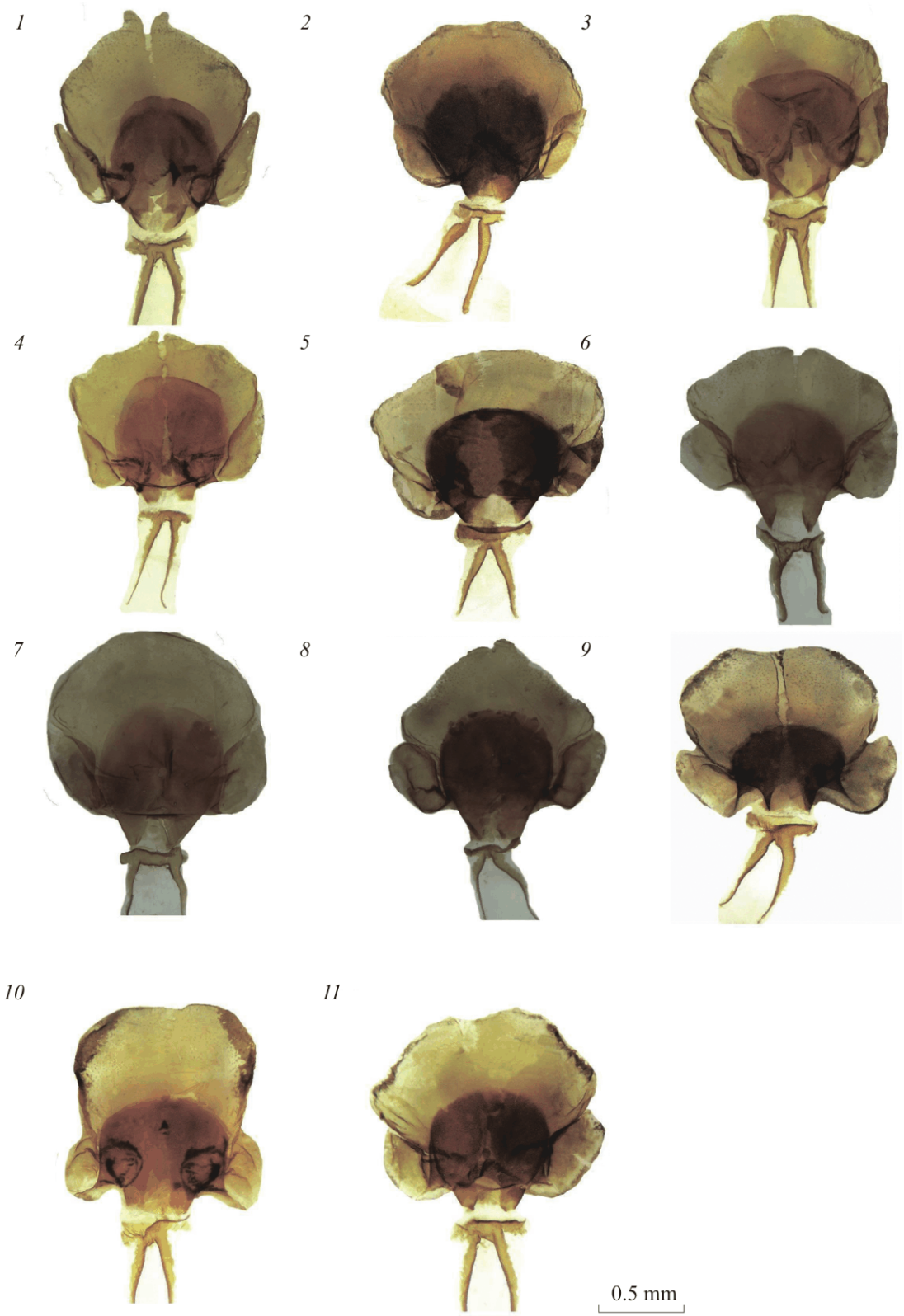

Fig. 2. Female genitalia (without the anal papillae, copulatory bursa, and anterior and posterior apophyses) of *Mellicta athalia* (*1–5*), *M. caucasogenita* (*6–8*), and *M. ambigua* (*9–11*) from different localities: (*1*) Altai, env. of Ust-Koksa; (*2*) Tver Prov., Zapadnodvinskii Distr.; (*3*) Chernigov Prov., env. of Konotop; (*4*) Magadan Prov., Tenkinskii Distr.; (*5*) Georgia, Imereti Range, Likani; (*6*) Armenia, Goris; (*7*) North Caucasus, Teberda; (*8*) Georgia, Imereti Range, Likani; (*9*) Khabarovsk Terr., Ulchskii Distr. (lectotype); (*10*) Primorskii Terr., Pogranichny Distr.; (*11*) Baikal, Khamar-Daban Range.

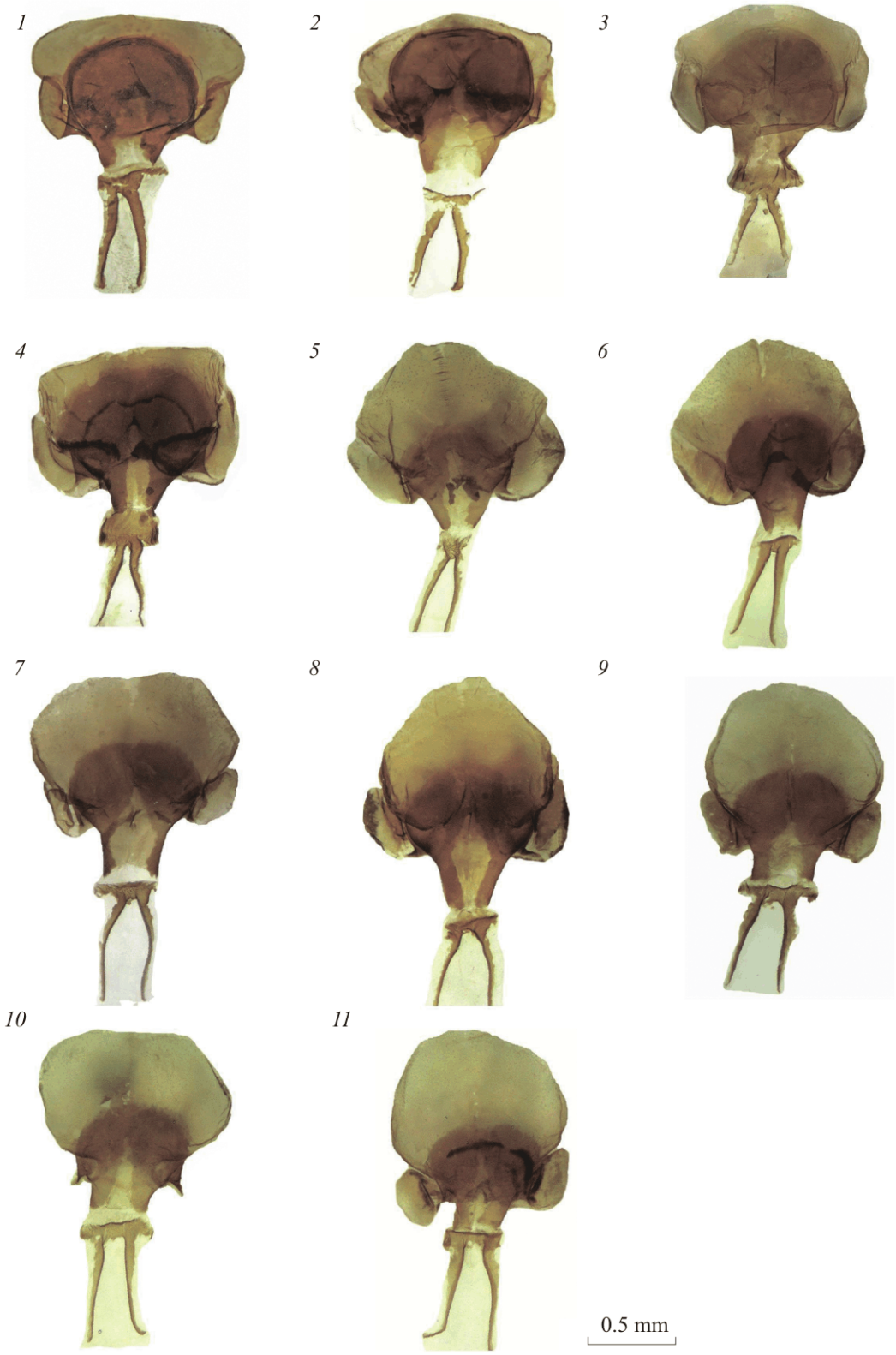

Fig. 3. Female genitalia (without the anal papillae, copulatory bursa, and anterior and posterior apophyses) of *Mellicta nevadensis* (*1*, *2*), *M. dejone* (*3*, *4*), *M. britomartis* (*5–8*), and *M. plotina* (*9–11*) from different localities: (*1*) Spain, Lerida Prov.; (*2*) South Italy, Calabria; (*3*) Algeria, Tlemcen; (*4*) Spain, Sierra Nevada; (*5*) Irkutsk Prov., Olkhonskii Distr.; (*6*) South of Primorskii Terr., Pogranichny Distr.; (*7*) Novosibirsk Prov., Iskitim Distr.; (*8*) Tula Prov., Zaokskii Distr.; (*9*) Amurskaya Prov., Svobodny; (*10*) Irkutsk Prov., Oktyabrskii Distr., env. of Cheremushki; (*11*) Primorskii Terr., Pogranichny Distr.

least one-third as long as antevaginal plate and antrum combined) ..... 3.

2. Ductus apically (before divergence of strands of bacillus) with wide sclerotization (Fig. 3, *3*, *4*) .... *M. dejone*.

—Ductus apically (before divergence of strands of bacillus) without wide sclerotization (Fig. 3, *1*, *2*) .. .. *M. nevadensis.*

3. Antrum short. Antevaginal plate and antrum together form rounded (sometimes somewhat elongated) structure (Fig. 2) ..... 4.

—Antrum elongated. Antevaginal plate and antrum together form pyriform structure (Fig. 3, *5–11*) ... 6.

4. Protruding part of postvaginal plate about as long as antevaginal plate and antrum combined (Fig. 2, 9–11) ..... *M. ambigua.*

—Protruding part of postvaginal plate noticeably shorter than antevaginal plate and antrum combined (Fig. 2, *2–8*) ..... 5.

5. Bridge present between strands of bacillus at their divergence (Fig. 2, *6–8*). Caucasus and Transcaucasia ..... *M. caucasogenita*.

—Strands of bacillus usually diverge from single point (Fig. 2, *1–5*) ..... *M. athalia*.

6. Antrum elongated (Fig. 3, *5–8*). Postvaginal plate rounded-trapeziform. Strands of bacillus usually diverge from single point, sometimes with inconspicuous bridge between them ..... *M. britomartis.*

—Antrum shorter and wider (Fig. 3, *9–11*). Postvaginal plate rounded. Distinct bridge usually present between strands of bacillus at their divergence .... *M. plotina.*

Descriptions of Female Genitalia of Species of the Mellicta athalia Group

Mellicta athalia (Rottemburg, 1775)
(Fig. 2, *1–5*)

Antevaginal plate indistinctly separated from antrum; this plate and antrum together form rounded structure, often with narrowing base. Postvaginal plate usually trapeziform (rarely rounded), considerably protruding beyond antevaginal plate. Its protruding part about half as long as antevaginal plate and antrum combined (Fig. 2, *2*, *3*, *5*). In some cases, postvaginal plate may be less (Fig. 2, *4*) or more (Fig. 2, *1*) than half as long as antevaginal plate. Ductus has well-developed fork-shaped sclerotization with 2 diverging strands (bacillus). Strands of bacillus usually diverge from one point (Fig. 2, *5*), but small bridge may occur between them in some cases (Fig. 2, *2*). This diagnostic character (divergence of strands of bacillus from one point) well expressed in cases of sympatry with closely related *M. caucasogenita*.

Mellicta caucasogenita (Verity, 1930)
(Fig. 2, *6–8*)

Structure of female genitalia of *M. caucasogenita* similar to that of *M. athalia*, differing largely in shape of bacillus: in *M. athalia* strands of bacillus diverge from one point in most cases, while in *M. caucasogenita* well-developed bridge usually occurs between strands of bacillus (Fig. 3, *7*); this bridge may be short in rare cases (Fig. 2, *8*). Diagnostic characters more distinct in cases of sympatry with *M. athalia*. Structure formed by antevaginal plate and antrum generally more elongated than in *M. athalia*.

Mellicta ambigua (Ménétriés, 1859)
(Fig. 2, *9–11*)

Antevaginal plate indistinctly separated from antrum; this plate and antrum together form rounded structure. Postvaginal plate trapeziform or rounded (Kolesnichenko and Bush, 2015). Protruding part of postvaginal plate about as long as antevaginal plate and antrum combined. Ductus with well-developed bacillus.

Mellicta nevadensis (Obertür, 1904)
(Fig. 3, *1*, *2*)

Postvaginal plate typically short, ellipsoid or trapeziform with lateral lobes, apically only slightly protruding beyond antevaginal plate. Ductus with wide and long bacillus. Antrum with well-developed sclerotization.

The species was previously known as *M. celadussa* (Fruhstorfer, 1910), but in one of the latest taxonomic publications (Oorschot and Coutsis, 2014) *celadussa* was shown to be a junior synonym of *nevadensis*.

Mellicta dejone (Geyer, 1832)
(Fig. 3, *3*, *4*)

Antevaginal plate rounded, weakly separated from antrum. Postvaginal plate with protruding lateral angles, apically only slightly protruding beyond ante-

vaginal plate. Ductus with long and thin (rarely rudimentary) strands of bacillus. Characteristic feature of female genitalia of *M. dejone*: wide apical sclerotization of ductus before divergence of strands of bacillus.

Mellicta britomartis (Assmann, 1847)
(Fig. 3, *5–8*)

Antrum elongated, basally narrowing, forming pyriform structure with antevaginal plate. Postvaginal plate trapeziform or rounded, considerably protruding beyond antevaginal plate. Protruding part of postvaginal plate varies from half as long to about as long as both antevaginal plate and antrum combined. Ductus with distinct fork-shaped sclerotization. Strands of bacillus thin, usually diverging from one point.

The recently described species *M. elenae* (Yakovlev, 2007) was synonymized with *M. britomartis* based on the male genital morphology (Oorschot and Coutsis, 2014). The genitalia of the paratypes of *M. elenae* (1 male and 1 female) examined by us corresponded to those of *M. britomartis*. The status of the taxon *elenae* needs to be clarified by additional research.

Mellicta plotina (Bremer, 1861)
(Fig. 3, *9–11*)

Female genitalia resemble those of *M. britomartis* but have some specific features: antrum shorter (rectangular); postvaginal plate rounded; distance between strands of bacillus at their divergence 1.5–2 times as great as that in *M. britomartis*. Strands of bacillus thin, with well-developed bridge between them.

DISCUSSION

Representatives of the genus *Mellicta* are subdivided into two groups based on the structure of the male genitalia. The first group unites the species closely related to *M. athalia*, the second, those closely related to *M. aurelia* (Higgins, 1955; Devyatkin, 2000). The system used in the recent work by Oorschot and Coutsis (2014) generally agreed with the traditional scheme; however, the cited authors considered the genitalia of *M. britomartis* to be similar to those of *M. menetriesi* and, accordingly, placed *M. britomartis* in the group of species close to *M. aurelia*. In this communication we follow the classical system in which *M. britomartis* belongs to the *athalia* species group. According to the molecular data, in particular analysis of the nucleotide sequences of three genes: COI, EF-1α, and Wgl (Leneveu et al., 2009), species of the genus *Mellicta* form two distinct clades corresponding to the traditional groups. A similar result was obtained in our study of the female genital morphology.

The *athalia* species group includes *M. athalia*, *M. caucasogenita*, *M. ambigua*, *M. nevadensis*, *M. dejone*, *M. britomartis*, and *M. plotina*. The main character of the male genitalia uniting these species is the relatively narrow caudal process of the valva bending upwards or slightly downwards (or not bending at all), as compared with the robust and wide caudal process in *M. aurelia* and close species, which bends sharply downwards. Besides, all the members of the *athalia* group possess a well-developed ostium-keel of the aedeagus, while this keel is absent in a number of species close to *M. aurelia*.

The main distinctive feature of the female genitalia of the species close to *M. athalia* is well-developed fork-shaped sclerotization of the ductus, which is absent or partly reduced in most of the species close to *M. aurelia*. In addition, members of the *athalia* group are characterized by a narrower antevaginal plate and, with some exceptions (*M. nevadensis* and *M. dejone*), a long postvaginal plate strongly protruding beyond the antevaginal one; by contrast, the postvaginal plate is short in the majority of the species close to *M. aurelia*.

The following morphological subgroups can be distinguished within the group of species close to *M. athalia*. The first subgroup includes *M. athalia*, *M. caucasogenita*, and *M. ambigua*, i.e., the species placed most closely together by the male and female genital structure as well as by the molecular data. Males of these species have a fairly long caudal process of the valva and a well-developed subuncus. The females are characterized by a long postvaginal plate clearly protruding beyond the antevaginal one; the latter is rounded and indistinctly separated from the relatively short antrum.

The next subgroup comprises the West European species *M. nevadensis* and the West European–North African species *M. dejone*. These species differ from the rest mostly in the reduced prongs of the subuncus, the peculiar long and thin caudal process of the valva in males, and also in the short postvaginal plate, barely protruding beyond the antevaginal one, in females.

A slight discrepancy between the molecular and morphological data should be noted: according to the molecular data, *M. dejone* forms a clade with *M. brito-*

martis while *M. nevadensis* occupies a separate position. By contrast, morphological data indicate a somewhat separate position of *M. britomartis*, which is characterized by a shorter caudal process of the valva in males, directed slightly downwards and often bearing numerous secondary spines, and also by an elongated antrum and a long postvaginal plate clearly protruding beyond the antevaginal one, in females.

An even more distinct position is occupied by *M. plotina*, according to both morphological and molecular data. Morphologically, *M. plotina* most closely resembles *M. britomartis*, especially in the female genitalia: both species have an elongated antrum and a long postvaginal plate clearly protruding beyond the antevaginal plate.

Worth noting is a fairly clear correlation between the length of the postvaginal plate in females and the degree of development of the prongs of the subuncus in males: in species with a long subuncus the postvaginal plate strongly protrudes beyond the antevaginal one, while in species with a short or reduced subuncus the postvaginal plate barely protrudes or does not protrude at all beyond the antevaginal one. This correlation is observed both in the group of species close to *M. athalia* and in the group close to *M. aurelia*.

Geographic variation in the studied species overlaps with individual one, so that no distinct characters typical of particular geographic regions were found. Geographic variation may be revealed by analysis of more extensive material from different localities, which requires further research. It should be noted that in case of co-occurrence of close species their distinctive characters become more pronounced; this was demonstrated by the example of *M. athalia* and *M. caucasogenita*. The "marker" character in the female genitalia of these closely related species is the structure of the fork-shaped sclerotization of the ductus: in *M. athalia* the strands of the bacillus usually diverge from a single point while in *M. caucasogenita* there is a bridge between the strands. This character is distinct in *M. athalia* populations sympatric with *M. caucasogenita*; however, in localities where *M. caucasogenita* is absent individuals of *M. athalia* may have a bridge between the strands of the bacillus, as in *M. caucasogenita*. The phenomenon of certain characters (often marker ones) being more pronounced in sympatric populations of closely related species as compared with allopatric ones was termed "character displacement" (Brown and Wilson, 1956) and demonstrated in different groups of insects. In particular, we observed this trend in males of *M. athalia* (Bush, 2011) and Central Asian species of the genus *Melitaea* (Kolesnichenko et al., 2011).

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