Melitaea nevadensis Oberthür, 1904, stat. rev.

(Adults: pl. 24, figs. 12–16; Genitalia: pl. 46, fig. 14, pls. 279–284)

Melitaea deione nevadensis Oberthür C. 1904, *Études de lépidoptérologie comparée* **1**: 11. Type locality: Spain, Sierra Nevada, Lanjarón. Type material: ♂ holotype, 1♂, 2♀ paratypes (BMNH), examined.

Synonymy

Melitaea athalia iberica Staudinger O. 1901, in Staudinger O. & Wocke M. 1871, *Catalog der Lepidopteren des europäischen Faunengebietes*: 32, Königliche Hofbuchhandlung H. Burdach, Dresden. Type locality: Spain, Sierra de Guadarrama, San Ildefonso. Type material: 2♂, 2♀ syntypes (ZMHU), examined. Junior primary homonym of *M. iberica* Oberthür, 1881. Synonymized with nominate *M. athalia* by Higgins L. G. 1955, *Transactions of the royal entomological Society of London* **106**(1): 45. **Syn. nov.**

Melitaea athalia nevadensis Oberthür C. 1909, *Études de lépidoptérologie comparée* **3**: 251. Synonymized with *M. athalia nevadensis* Oberthür, 1904 comb. nov., by Higgins L. G. 1955, *Transactions of the royal entomological Society of London* 106(1): 27.

Melitaea nevadensis Oberthür C. 1910, *Études de lépidoptérologie comparée* **4**: 672. Synonymized with *M. athalia nevadensis* Oberthür, 1904 comb. nov., by Higgins L. G. 1955, *Transactions of the royal entomological Society of London* **106**(1): 27.

Melitaea celadussa Fruhstorfer H. 1910, *Societas entomologica* **25**(13): 51. Type locality: France, Alpes Maritimes, Col de Tende. Type material: ♂ holotype, 5♂ paratypes (MNHN), examined by Bernardi G. & de Lesse H. 1951, *Bulletin de la Société entomologique de France* **56**: 142. Synonymized with nominate *M. athalia* by Higgins L. G. 1955, *Transactions of the royal entomological Society of London* **106**(1): 43. **Syn. nov.**

Melitaea athalia maxima Turati E. 1911, *Annuario Museo zoologico della r.Università di Napoli* 3: 19. Type locality: Italy, Calabria, Paola, Elba. Type material: not stated. Synonymized with nominate *M. athalia* by Higgins L. G. 1955, *Transactions of the royal entomological Society of London* **106**(1): 46. **Syn. nov.**

Melitaea athalia dejoneformis Verity R. 1914, *Bolletino della Società entomologica Italiana* **45**(1914): 208. Replacement name for *M. deione nevadensis* Oberthür, 1904, erroneously said [auct.] to be preoccupied by *M. parthenie nevadensis* Spuler, 1908. Synonymized with nominate *M. athalia* by Higgins L. G. 1955, *Transactions of the royal entomological Society of London* 106(1): 44. **Syn. nov.**

Melitaea athalia sicula Turati E. 1915, *Atti della Società Italiana di Scienze naturali e del Museo civico di Storia naturale di Milano* **53**: 600. Type locality: Italia, Sicily, Ficuzza. Type material: not stated. Synonymized with nominate *M. athalia* by Higgins L. G. 1955, *Transactions of the royal entomological Society of London* **106**(1): 49. **Syn. nov.**

Melitaea athalia tenuicula Verity, R. 1919, *Entomologist's Record and Journal of Variation* **31**: 193. Type locality: Italy, Bolognola, Monti Sibillini. Type material: holotype not stated, 1♂, 1♀ paratypes (BMNH), examined. Synonymized with nominate *M. athalia* by Higgins L. G. 1955, *Transactions of the royal entomological Society of London* **106**(1): 50. **Syn. nov.**

Melitaea athalia tenuis Verity R. 1919, *Entomologist's Record and Journal of Variation* **31**: 193. Type locality: Italy, Florence. Type material: 1♂, 1♀ syntypes (BMNH), examined. 48♂, 12♀ syntypes (depository unknown). Synonymized with nominate *M. athalia* by Higgins L. G. 1955, *Transactions of the royal entomological Society of London* **106**(1): 50. **Syn. nov.**

Melitaea athalides Verity R. 1919, *Entomologist's Record and Journal of Variation* **31**: 194. Type locality: Italy, Monti Sibillini. Type material: 1♂ syntype (depository unknown). Synonymized with nominate *M. athalia* by Higgins L. G. 1955, *Transactions of the royal entomological Society of London* **106**(1): 43. **Syn. nov.**

Melitaea athalia submaxima Verity R. 1924, *Entomologist's Record and Journal of Variation* **36**(suppl.): 40. Type locality: Italy, Toscana, Lucca. Type material: 11♂, 3♀ syntypes (depository unknown). Synonymized with nominate *M. athalia* by Higgins L. G. 1955, *Transactions of the royal entomological Society of London* **106**(1): 49. **Syn. nov.**

Melitaea athalia hispanica Wnukowsky W. 1929, *Zoologischer Anzeiger* **83**(9/10): 222. Replacement name for *M. athalia iberica* Staudinger, 1901, nec *M. aurinia iberica* Oberthür, 1881.

Melitaea helvetica aranensis de Sagarra I. 1930 (1931), *Butlleti de la Institucio Catalana d'historia natural* 7: 115. Type locality: Spain, Val d'Aran, Banhs de Tredòs, Salardú. Type material: ♂ holotype (MCNB). Synonymized with nominate *M. athalia* by Higgins L. G. 1955, *Transactions of the royal entomological Society of London* **106**(1): 42. **Syn. nov.**

Melitaea helvetica pusilla Rocci U. 1932, *Memorie della Società entomologica Italiana* **10**: 209. Type locality: Italy, Liguria, Valle Bisogno, Valle Scrivia. Type material: not stated. Synonymized with nominate *M. athalia* by Higgins L. G. 1955, *Transactions of the royal entomological Society of London* **106**(1): 48. **Syn. nov.**

Melitaea athalia biedermanni Querci O. 1932, *Treballs del Museu de Ciensis Naturals de Barcelona* **14**: 128. Type locality: Portugal, Serra da Estrela, Covilhã. Type material: ♂ holotype (MCNB). Synonymized with nominate *M. athalia* by Higgins L. G. 1955, *Transactions of the royal entomòlogical Society of London* **106**(1): 43. **Syn. nov.**

Nomenclature

In Rezbanyai-Reser (1987: 51) the following nomenclatural combination is proposed for *M. nevadensis*:

Mellicta athalia (*nevadensis*) *celadussa* Fruhstorfer, 1910.

The above nomenclatural arrangement is not supported by the ICZN, and furthermore ssp. *celadussa*, as already stated, is a junior synonym of *M. nevadensis*.

Material

Specimens seen: about 600 (BMNH, RMNH, SMNK, SMNS, ZFMK, ZMA, ZMHU, ZSM, coll. Coene, de Heer, Eckweiler, Görgner, Schurian, ten Hagen).

Genitalia studied: 15.

Mounted genitalia seen: 124.

Selected illustrations in literature

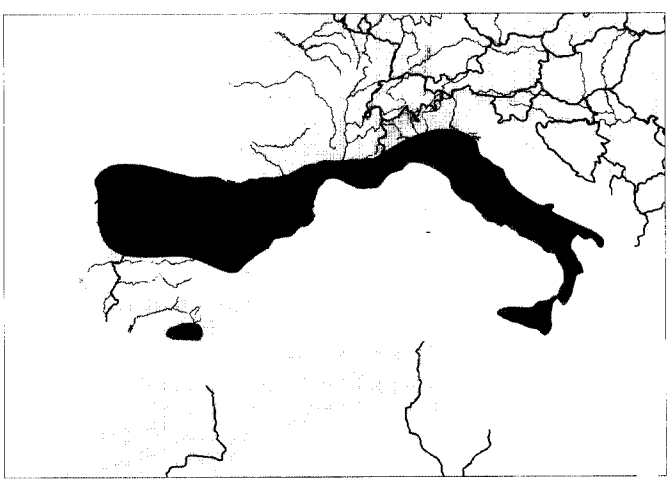
Adults: Manley & Allcard (1970: pl. 10, figs. 13–17, as *Mellicta athalia*); Tolman (1997: pl. 52, as *Mellicta athalia*); Olivares *et al.* (2011: pp. 242, 243; cuaderno de campo, bloque IV, p. 20, both as *Melitaea athalia*).

Genitalia: Reverdin (1921: p. 320, fig. 2, as *Melitaea pseudathalia*); Verity (1950: vol. IV, pl. XVI, fig. 6, as *Melitaea athalia*).); Fernández-Rubio *et al.* (1974: p. 147, figs. 2, 6, 10, as *Mellicta athalia*); Fernández-Rubio (1977: part II, pl. 38, as *Mellicta athalia*); Alexis (1987: p. 47, figs. 13, 14 as *Mellicta athalia*).

Diagnosis

Wings

Male: FW length 18–20 mm; both wing surfaces much as in *M. athalia*, sharing with it the latter's pronounced variability, but lacking HW upper side intense



and expanded black suffusion met with in *M. athalia* often in Balkans and rarely so elsewhere in its range.

Female: as in male, but FW often slightly longer, usually with more rounded outer margin, ground-colour upper side occasionally lighter and rarely intermixed with yellowish spotting.

Genitalia

As in *M. athalia*, but valval main element of distal process usually longer and always devoid of ventral extensions; dorsum of extended, rod-like part of main element at right angle with remainder of valval dorsum; tegumen in dorsal aspect either simple, or with small, usually rounded, at times triangular knobs in place of sub-unci, and exhibiting lateral bulge just basad of location where knobs may be found, this being usually more pronounced than in *M. athalia*.

Immature stages

All immature stages described and compared to those of *M. athalia* by Beuret (1933), who found in all of them the following significant differences between the two taxa: The egg of *M. nevadensis* is constantly larger than that of *M. athalia*, and its longitudinal ribs bear traces of fine cross-lines between them, which are absent in *M. athalia*. The full grown larva of *M. athalia* is overall black with rather large white spots, thick ivory white spines, and a clearly visible black line running down its dorsum, flanked by a multitude of white spots. In *M. nevadensis* the white spots are very small, the spines slenderer, orange or dark grey, and the dorsal black line scarcely visible. The pupa of *M. athalia* is always decidedly bigger than that of *M. nevadensis*, and its black maculation less extensive.

Similar reports on the pupae of the two species received from Coene (pers. com. 2009), who bred *M. nevadensis* from Sicily, and compared its pupae with those of *M. athalia*.

Distribution

Andorra, SE France, Italy (Sicily and continental Italy, excluding Alps and area NE of Venice), Portugal, Spain, Switzerland (Tessin).

Bionomics

Life history: As for *M. athalia* (Tolman 1997: 176).

Flight period: June–July.

Flight altitude: 100–2600 m.

Habitat: dry or damp grassy, flowery places, often among bushes, or in woodland clearings (Schwarzwalder *et al.* 1997: 157-165; Tolman 1997: 176).

Larval host-plants: as for *M. athalia* (Tolman 1997: 176), and in addition: Scrophulariaceae: *Digitalis ambigua*; Plantaginaceae: *Plantago subulata*, *P. albicans*; Asteraceae: *Centaurea jacea*, *C. calcitrapa*, *C. cyanus* (Gómez-Bustillo & Fernándes-Rubio 1974: vol. II, 191).

Intermediates by genitalia between *M. athalia* and *M. nevadensis*

(Genitalia: pls. 285–288)

Contact zone of *M. athalia* and *M. nevadensis*

In the contact zone of *M. athalia* and *M. nevadensis*, there exist populations with intermediate genitalic characters, undoubtedly attributable to hybridization between these two taxa. Occasionally such intermediates may be syntopic with either of the parent species, more rarely with both. These populations inhabit a rather narrow geographical area, roughly in the form of an arch (See map p. 123), that starts in France, on the north side of the Pyrenees, and extends NNE in a narrow zone varying from about 113–170 km in width, which at its start is roughly parallel to the coast of the Golfe du Lion, its inner boundary missing it by about 30–50 km, and then continues on to the west of the Rhône River, at first with its inner boundary at a distance from it of about 80 km, and eventually with its crossing the river near Dhombes, where it abruptly swerves ESE towards Switzerland. At the swerving point the zone reaches its maximum width of about 285 km, as well as its most northerly expansion, its outer boundary almost reaching the latitude of Paris. In Switzerland it extends in a WNW to ESE direction, being nowhere wider than about 75 km, and starts along the country's western and NW borders with France from a point just north of Lake Geneva, all the way to about 25 km ENE of Basle, with its inner boundary extending in a gentle arch from Lake Geneva, through Bern, to an area about 15 km south of Lucerne, and eventually to the country's SE borders, located at about 10–15 km ESE of Pontresina, and its outer boundary extending in an almost straight line from a short distance ENE of Basle, to just north of Zürich, and then continuing on to the vicinity of St. Gallen, and futher ESE along the common borders with Lichtenstein, Austria and Italy. From Switzerland it barely intrudes into Liechtenstein along the latter's southern borders, and also penetrates into southern Austria (Tyrol) at a maximum depth of about 20 km from the latter's southern borders with Switzerland and Italy. In Italy it is restricted to the NNE of the country, forming a wedge about 50 km wide and about 110 km long in the regions of Trentino-Alto Adige, S Tyrol, and extending to the east to the Dolomite Alps.

Hybridization

The question of hybridization between *M. athalia* and *M. nevadensis* is discussed in Reverdin (1921[1920]: 319–321; 1922: 24–46); Beuret (1931: 78–94; 1933: 424–455; 1954: 37–40); Giese (1933: 177–180); Bourgogne (1943: 174; 1948: 35–37; 1953: 131–176); Rezbanyai-Reser (1987: 56, 57).

Nomenclature

The following invalid subspecific names applied to specimens whose provenance is from areas where intermediates predominate, or whose genitalia clearly place them as such, are being listed hereunder:

Melitaea athalia helvetica Rühl 1888: 137. Type locality: Switzerland, Rhaetian Alps, Stella and Bergün. Type material: not stated. In Higgins (1955: 111) reference is made to "the intermediary character of the genitalia".

Melitaea athalia delminia Fruhstorfer, 1910: 51.Type locality: Italy, Südtirol, Klausen, Meran, Cogne. Type material: holotype not stated, 28♂, 15♀ paratypes (MNHN), all from Meran, examined by Bernardi & de Lesse (1951: 142). In Higgins (1955: 44) it is stated that "Rocci (1932), states that this = *pseudathalia*".

Melitaea athalia athalioides Turati & Verity, 1911: 208. Type locality: Italy, Valdieri, Piemonte. Type material: not stated. In Higgins (1955: 43) it is stated that it is "Said to form a "passage" between the two species [i.e. *M. athalia* and *M. nevadensis*]").

Melitaea athalia luciflua Fruhstorfer 1917: 5. Type locality: France, Haute-Savoie. Type material: ♂ holotype, 23♂, 9♀ paratypes (MNHN), examined by Bernardi & de Lesse (1951: 142).

Melitaea athalia melida Fruhstorfer 1919b: 182. Type locality: Switzerland, Lugano, Monte Generoso. Type material: ♂ holotype, 16 ♂ 6♀ paratypes (MNHN), examined by Bernardi & de Lesse (1951: 142).

Melitaea pseudathalia Reverdin, 1921: 320. Type locality: Switzerland, Versoix, Genève. Type material: ♂ lectotype designated by Beuret (1954a: 38, prep. no. 6267) (MHNG). Genitalia drawings in Reverdin (1921: 320), show them to be intermediate between those of *M. athalia* and those of *M. nevadensis*.

Melitaea synexergica Verity, 1930: 133. Type locality: Switzerland, Solothurn. In Higgins (1955: 500) it is stated that "the male genitalia intermediate between *athalia* and *celadussa* [=

nevadensis]".

Melitaea helvetica divergens Rocci, 1930: 184. Type locality: Italy, Lombardia. Type material: not stated.

Melitaea athalia hastensis Rocci, 1932: 208. Type locality: Italy, Asti, Piemonte. Type material: not stated.

Melitaea athalia melanagraphata Beuret, 1933: 451. Type locality: Switzerland, Tessin, Val Canaria. Type material: ♂ holotype, 15 (mixed) paratypes (NHMB). Named after bred specimens of *M. athalia* × *M. helvetica*.

Melitaea athalia mixtaceladussa Verity, 1940: 625. Type locality: France, Gèdre Pyrénées. Type material: 4♂, 1♀ syntypes (depository unknown). In Higgins (1955: 46) it is stated that "This form is said to differ from *celadussa* in showing a small sub-uncus in the male").

Material

Specimens seen: by genitalia, 117; without reference to genitalia, but on the basis of locality data and provenance, about 300 (ZMA).

Genitalia studied: 10.

Mounted genitalia seen: 107.

Selected illustrations in literature

Genitalia: Verity (1951: vol. IV, pl. 16, figs. 7, 8); Higgins (1955: 26, figs. 18, 19); van Oorschot (1963: 98).

Distribution map: Bourgogne (1953: 131 *et seq.*); Higgins, after Bourgogne (1955: 11, map 4).

Diagnosis

Wings

As in *M. athalia* and *M. nevadensis*.

Genitalia

These combine characters derived from both parent species, such as, for instance, near *nevadensis*-type valvae with *athalia*-type subunci (pls. 287, 288), or possess pure *nevadensis*-type valvae, combined with subunci that are of varying length, but always decidedly shorter than the long subunci of *M. athalia*, and decidedly longer than the extremely short, pointed stubbs often present in *M. nevadensis* (pls. 285, 286). Surely, however, these few examples do not represent the whole range of genitalic variation in the intermediates between *M. athalia* and *M. nevadensis*. It must also be added that the genitalia of the intermediates, even within a single area, show a high degree of character instability.

Distribution

France (narrow zone extending from Pyrenees in a NNE direction, and swerving ESE to borders with Switzerland); Switzerland (narrow zone, starting from WNW borders with France and extending ESE through north central part of the country all the way to its SE extremity); Liechtenstein (southern borders with Switzerland); Austria (Tyrol, along southern borders with Switzerland and Italy); Italy (Trentino-Alto Adige, S Tyrol).

For more detailed information see Higgins (1955: 25).

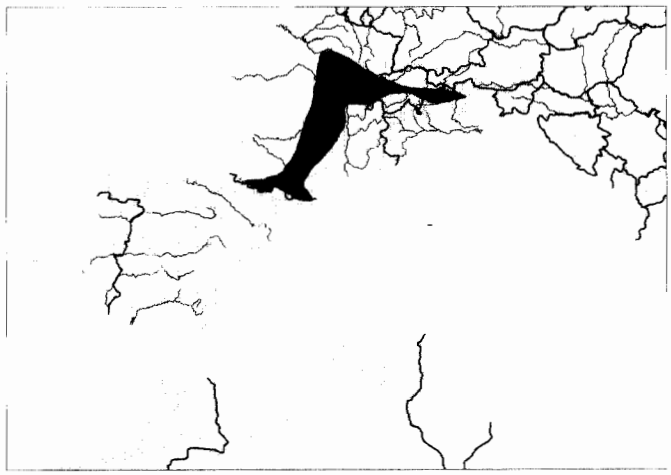
Bionomics

Life history, flight period, flight altitude, habitat and larval host-plants as for *M. athalia* and *M. nevadensis*.

Taxonomy

The question of whether or not *M. athalia* and *M. nevadensis* are two separate species, or subspecies of a single species still remains unanswered. Taxonomic positions on the issue vary, and as these are, without exception, subjective, they can only be regarded as tentative, pending further investigation into the problem.

In Higgins (1955: 26, 27) it is said that "It appears to me that the two forms *athalia* and *celadussa* [= *nevadensis*] represent true geographical races or sub-species. They occupy contiguous distribution areas and are vicarious, one replacing the other without invading its territory. Along the territorial boundary (...) the two forms fuse and produce intermediates (...). The butterfly provides perhaps the best documented and most perfect example of subspecific differentiation that occurs in the Palearctic Lepidoptera".



On the other hand Leneveu *et al.* (2009: 351) state that "A noteworthy result in the *athalia* group is that *Melitaea celadussa* [= *nevadensis*], which is usually considered a subspecies of *Melitaea athalia* (Higgins, 1941, 1955; Lafranchis, 2000), is not directly related to *M. athalia*. Our analyses show that *M. athalia* is more closely related to *Melitaea caucasogenita* and *Melitaea ambigua*, this species group being sister to the *Melitaea deione*/*Melitaea britomartis* branch, and finally *M. celadussa* [= *nevadensis*] being sister to that clade". In same work, p. 356, it is also stated that "Several patterns of phylogenetic relationships were rather surprising. First, the position of *M. celadussa* [= *nevadensis*] as sister to the *M. athalia* and *M. deione* clades clearly indicates that it is a separate species and not a subspecies of *M. athalia*, as has always been assumed. *Melitaea celadussa* [= *nevadensis*] and *M. athalia* are known to have a narrow hybrid zone where their ranges meet (Higgins, 1955); thus, the two species have not attained complete reproductive isolation, despite diverging from each other possibly 7 Mya. A more detailed study of the species pair would be necessary to discover whether there is gene flow between the species, but unpublished COI sequences of 14 *M. celadussa* [= *nevadensis*] and 12 *M. athalia* specimens from throughout their ranges suggest that mitochondrial DNA does not introgress (N. Wahlberg, unpubl. data)."

One item of special interest is that the zone of the intermediates appears to be geographically contained, not giving any hint of expansion. A hypothesis to this phenomenon would be that perhaps back-crosses between the intermediates and both their parent species might conceivably produce low viability offsprings, not permitting penetration of the intermediates into the parent species' territory and vice versa. In such a hypothetical instance the geographical area inhabited by intermediates would then act as a buffer zone between the ranges of *M. athalia* and *M. nevadensis*, thus prohibiting regular penetration of one parent species into the territory of the other. These hypotheses and questions, of course, may only be answered through future breeding experiments.

As *M. athalia* and *M. nevadensis* differ from each other by genitalia, by their immature stages and by mtDNA sequencing, and given the fact that their interbreeding dynamics have not as yet been fully studied and understood, we are inclined to consider them as separate species, albeit on a tentative basis, pending further investigation and information.