

## Genotypic variability in western European members of the *Erebia tyndarus* species group (Lepidoptera, Satyridae)

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### Summary

Relationships between West European species of the *Erebia tyndarus* group have been investigated by means of enzyme electrophoresis. Within *E. cassioides* s.l. two genetically distinct groups of populations exist, one occurring in the eastern Alps (*E. cassioides* s.str.) and another in the western Alps, the Italian Apennines and the Pyrenees (*E. (cassioides) carmentis* Fruhstorfer, 1909). In order to ensure nomenclatural stability, a neotype has been designated for *Papilio cassioides* Reiner & Hohenwarth, 1792.

### Zusammenfassung

Die Beziehungen zwischen West-europäischen Arten der *Erebia tyndarus* Gruppe wurden mit der Hilfe elektrophoretischer Methode untersucht. Bei der *E. cassioides* s.l. kann man zwei genetisch verschiedene Populationengruppen unterscheiden: eine in den Ost-Alpen (*E. cassioides* s.str.) und die andere in den West-Alpen, in den italienischen Apenninen und in den Pyrenäen (*E. (cassioides) carmentis* Fruhstorfer, 1909). Um eine nomenklatorische Stabilität zu erreichen, wurde für *Papilio cassioides* Reiner & Hohenwarth, 1792 ein Neotyp gewählt.

### Résumé

Les relations phylétiques entre les espèces ouest-européennes du groupe de *Erebia tyndarus* ont été étudiées au moyen de l'analyse électrophorétique des enzymes. Deux groupes de populations génétiquement distinctes ont été décelées au sein d'*E. cassioides* s.l., l'une vivant dans les Alpes orientales (*E. cassioides* s.str.) et l'autre comprenant les populations des Alpes occidentales, des Apennins italiens et des Pyrénées (*E. (cassioides) carmentis* Fruhstorfer, 1909). Dans l'intérêt de la stabilité de la nomenclature, un néotype de *Papilio cassioides* Reiner & Hohenwarth, 1792 a été désigné.

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## Introduction

WARREN (1936) originally classified the *Erebia tyndarus* species complex within a broader *E. pluto* group. It was considered to include *E. tyndarus* (Esper, 1781), *E. ottomana* Herrich-Schäffer, 1847 and *E. callias* Edwards, 1871, each subdivided into many subspecies. A number of later authors contributed to raising to species rank one or another of these subspecies, whereas meanwhile a few totally new species have been described. Currently, also *E. cassioides* (Reiner & Hohenwarth, 1792), *E. hispania* Butler, 1868, *E. iranica* Grun-Grshimailo, 1895, *E. dromulus* Staudinger, 1901, *E. calcarius* Lorković, 1953 and *E. nivalis* Lorković & de Lesse, 1954 are considered distinct species by most authors, so bringing the total of members of the *E. tyndarus* group to nine.

As male and female genitalia are very similar throughout the group (DE LESSE, 1960) and as a consequence of the fact that these species are rarely found in cohabitation, NICULESCU (1985) reverted to the original suggestion of Warren that they should all be considered separate subspecies within a polytypic complex. In at least one case, however, cohabitation does occur: *E. (iranica) transcaucasica* and *E. ottomana* are known to fly together in E. Turkey. Members of the *E. tyndarus* group are characterized by their small size, rounded wing shape, the presence of a normally reduced orange-brown stripe on the apical third of the wings, surrounding a pair of small black spots, pupillated white. The hind wings are normally ash-grey on the ventral surface, often with a yellowish tinge in the females. Males lack androconial scales. In the male genitalia, the valva shows a series of upwards and rearwards directed spines, the most proximal of which is normally the largest. The rear half of the valva itself recalls that of *E. pluto* (Warren, 1936), as it tapers caudad rather smoothly, without any real interruption between what this author called a 'shoulder', a 'neck' and a 'head'. Caterpillars appear finely pubescent due to the presence of many short setae. All taxa of this group are alpine or subalpine, perhaps with the exception of *E. ottomana*, which can often colonize the upper parts of the montane vegetational level. All are Palearctic, but the range of *E. callias* extends to the Nearctic.

The karyological study of this group, carried out by LORKOVIĆ (1941) and DE LESSE (1960), demonstrated that haploid chromosome complements vary between species. *E. tyndarus* and *E. cassioides* have  $n = 10$ ; *E. calcarius*  $n = 8$ ; *E. nivalis*  $n = 11$ ; *E. callias*  $n = 15$ ; *E. hispania hispania*  $n = 25$ ; *E. hispania rondoui*  $n = 24$ ; *E. ottomana*  $n = 40$ ; *E. iranica iranica* and *E. iranica savalanica*  $n = 51$ ; *E. (iranica) transcaucasica*  $n = 52$ , *E. dromulus*  $n = 51$  or  $52$ .

WARREN (1955, 1981) taking again in consideration the taxonomy of this group, came to rather different conclusions. This author, in fact, doubted that *E. cassioides*, first described from the Großglockner (Austria), really inhabits this region. As a consequence of the fact that Reiner & Hohenwarth's figure, later designated as lectotype of *E. cassioides* (LORKOVIĆ & DE LESSE,

1955) cannot be identified with any known species, he considered *E. cassioides* a nomen nudum, perhaps to be identified with *E. nivalis*, a species also described from the Großglockner. He also split what was formerly known as *E. cassioides* into two species, namely *E. neleus* (Freyer, 1833) and *E. aquitania* Fruhstorfer, 1909, on the basis of some subtle morphological characters of the wing shape (more pointed in *E. neleus*). Among more recent authors, however, only von MENTZER (1960) followed this suggestion; most other authors (DE LESSE, 1956; HIGGINS, 1975, etc.) maintained *E. cassioides* as a valid and single species.

The present work deals with the West European members of the *Erebia tyndarus* species group and aims at the clarification of some of the taxonomic problems outlined above, by the study of electromorph variation. Only *E. cassioides arvernensis* Oberthür, 1908, from the Mont Dore (Auvergne, France) and *E. cassioides dolomitensis* Goltz, 1930 from the Italian Dolomites and Caravanche Alps remain, for the moment, unstudied.

## Materials and methods

### *Preparation of samples*

Twenty-four populations of the *E. tyndarus* species group were scored for electromorph variability, for a total 290 specimens. Collection data for each of these populations are listed in Tab. 1, where, as regards western populations of *E. cassioides*, WARREN'S (1955, 1981) suggestion that *E. neleus* and *E. aquitania* may represent separate species was followed, for the sake of clarity. One population of *E. gorge* from Colle del Dragone (Province of Potenza, S. Italy) was included as an outgroup.

The wings were immediately removed on collection with sharp scissors and the whole bodies were frozen in liquid nitrogen while still alive. The specimens were stored in the same medium. Samples were prepared for electrophoresis as follows. Individual butterfly bodies were thawed in 250 µl of an ice-cold homogenizing solution (NADP 0.125 mM, 2-mercaptoethanol 1.14 mM; pH range between 6-8) and macerated with an electric tissue grinder. Centrifugation at 13,000 x g for 15 minutes permitted the separation of a clear supernatant. Care was taken to avoid overheating during both homogenization and centrifugation. Homogenates were stored at -80°C in 5-15 µl aliquots in microtubes.

### *Electrophoresis*

Electrophoresis was carried out on Cellogel sheets at 4°C. Buffer systems and staining techniques were similar to those described by MEERA KHAN (1971) and RICHARDSON *et al.* (1986). Thirteen gene-enzyme systems were studied for a total of 17 loci. Genetically interpretable banding patterns could be obtained for: glycerol-3-phosphate dehydrogenase (E.C.1.1.1.8) (αGPD), malate dehydrogenases (E.C.1.1.1.37) (MDh-1, 2), isocitrate dehydrogenases (E.C.1.1.1.42) (IDh-1, 2), 6-phosphogluconate dehydrogenase (E.C.1.1.1.44) (6PGD), glucose-6-phosphate dehydrogenase (E.C.1.1.1.49) (G6PD), glutam-

Table 1  
Populations of the *Erebia tyndarus* group sampled. Western populations of *E. cassioides* are classified according to Warren

Locality	Country, Region	No.	Symbol
Coll. de las Sabinas	Spain, Sierra Nevada, Granada	10	H1 ( <i>hispania hispania</i> )
P.to de San Glorio	Spain, Cantabrian M.tns, Cantabria	10	N1 ( <i>neleus</i> )
Emb. de Urdiceto	Spain, Pyrenees, Huesca	13	H2 ( <i>hispania rondoui</i> )
P.to de Envalira	Andorra, Pyrenees	14	N2 ( <i>neleus</i> )
Mont Camigou	France, Pyrenees, Pyr. Or.	16	H3 ( <i>hispania rondoui</i> f. <i>goya</i> )
Le Tanargue	France, M. Vivarais, Ardèche	9	O1 ( <i>ottomana tardenota</i> )
C.le dell'Agnello	Italy, Cottian Alps, Piedmont	14	A1 ( <i>aquitania</i> )
Val Veny	Italy, Graian Alps, Val d'Aosta	11	A2 ( <i>aquitania</i> )
P.so Gran S. Bernardo	Italy, Pennine Alps, Val d'Aosta	14	Ty ( <i>tyndarus</i> )
Alpe Pozze, m 1800	Italy, Alpi Retiche, Trentino	12	C1 ( <i>cassioides</i> )
Alpe Pozze, m 2000	Italy, Alpi Retiche, Trentino	14	C2 ( <i>cassioides</i> )
Alpe Pozze, m 2300	Italy, Alpi Retiche, Trentino	12	C3 ( <i>cassioides</i> )
Val Nambrone	Italy, Alpi Retiche, Trentino	10	C4 ( <i>cassioides</i> )
Zirknitztal	Austria, Hohe Tauern, Carintia	13	C5 ( <i>cassioides</i> )
Hochtor	Austria, Hohe Tauern, Carintia	6	Ni ( <i>nivalis</i> )
M. Altissimo di Nago	Italy, Baldo M.nt, Trentino	13	O2 ( <i>ottomana benacensis</i> )
M. Cavallo	Italy, Prealpi Carniche, Friuli	12	Ca ( <i>calcaris</i> )
P.so di Pradarena	Italy, Appennino Tosco-Emiliano, Emilia	8	A3 ( <i>aquitania</i> )
M. Cimone	Italy, Appennino Tosco-Emiliano, Emilia	14	A4 ( <i>aquitania</i> )
F.la del Fargno	Italy, Appennino Marchigiano, Marche	16	N3 ( <i>neleus</i> )
M. Cristo	Italy, Appennino Abruzzese, Abruzzi	13	N4 ( <i>neleus</i> )
Val. Capo la Serra	Italy, Appennino Abruzzese, Abruzzi	12	N5 ( <i>neleus</i> )
Majella	Italy, Appennino Abruzzese, Abruzzi	12	N6 ( <i>neleus</i> )
Colle del Dragone	Italy, Pollino, Lucania	12	N7 ( <i>neleus</i> )
Colle del Dragone	Italy, Pollino, Lucania	1	Go ( <i>gorge</i> )

ate-oxaloacetate transaminases (E.C.2.6.1.1) (GOT-1, 2), glutamate-pyruvate transaminase (E.C.2.6.1.2) (GPT), hexokinase (E.C.2.7.1.1) (HK), pyruvate kinases (E.C.2.7.1.40) (PK-1, 2), phosphoglucomutase (E.C.2.7.5.1) (PGM), mannosephosphate isomerase (E.C.5.3.1.8) (MPI), phosphoglucose isomerase (E.C.5.3.1.9) (PGI), esterase (E.C.3.1.1.1) (Es). Isozymes and alleles were designed numerically according to their decreasing mobility rate.

### Statistical analyses

Several genetic distance indexes were calculated (Cavalli-Sforza and Edward arc and chord distances, 1967; Rogers **D**, 1972; Wright's modification of Rogers **D**, 1978; Nei's **D**, 1972; Hillis modification of Nei's **D**, 1984). Dendrograms using UPGMA method of SOKAL & SNEATH (1963) and FITCH & MARGOLIASH method (1967) were constructed from these distances. A phylogenetic tree connecting all populations studied was obtained by the "Continuous Characters Maximum Likelihood Method" (CONTML; FELSENSTEIN, 1981, 1985). This program assumes that each locus evolves by genetic drift, so that gene frequencies may be considered to behave like particles undergoing pure Brownian-motion.

### Results

Allele frequencies are shown in Table 2. The overall number of alleles detected at 17 loci of all *Erebia tyndarus* species group studied amounts to 64 (mean per locus 3.76, range 2-8). No locus proved monomorphic across the whole sample. An additional private allele (HK 110) was identified in *E. gorge*.

The allele GOT-1 90 was found in the three populations of *E. hispania* only; the allele GOT-1 110 is diagnostic for *E. nivalis*, PK-1 115 for *E. ottomana*. Studied populations of *E. tyndarus*, *E. neleus* (7), *E. aquitania* (4), *E. cassioides* (5), and *E. calcarius* (1) did not show any private allele.

All dendrograms obtained by the various distance and clustering methods outlined above concur to a single picture :

1. *E. gorge* (outgroup), as expected, proved to be the most genetically different taxon (**D** = 0.719). The *E. tyndarus* group, accordingly, may represent a monophyletic unit. Its first split occurs at Nei's **D** = 0.407.
2. Populations of *E. cassioides* (*E. neleus* + *E. aquitania*) from the Italian Apennines, the western Alps, the Pyrenees, the Cantabrian Mountains (western populations of *E. cassioides*, 11 populations) cluster together at much lower values (Nei's **D** = 0.015).
3. Populations of *E. cassioides* from the central-eastern Alps (eastern *E. cassioides*, 5 populations studied) also cluster together at low distance (Nei's **D** = 0.016).
4. Eastern and western *E. cassioides*, in contrast, cluster with each other at a considerably higher level of distance (Nei's **D** = 0.071).





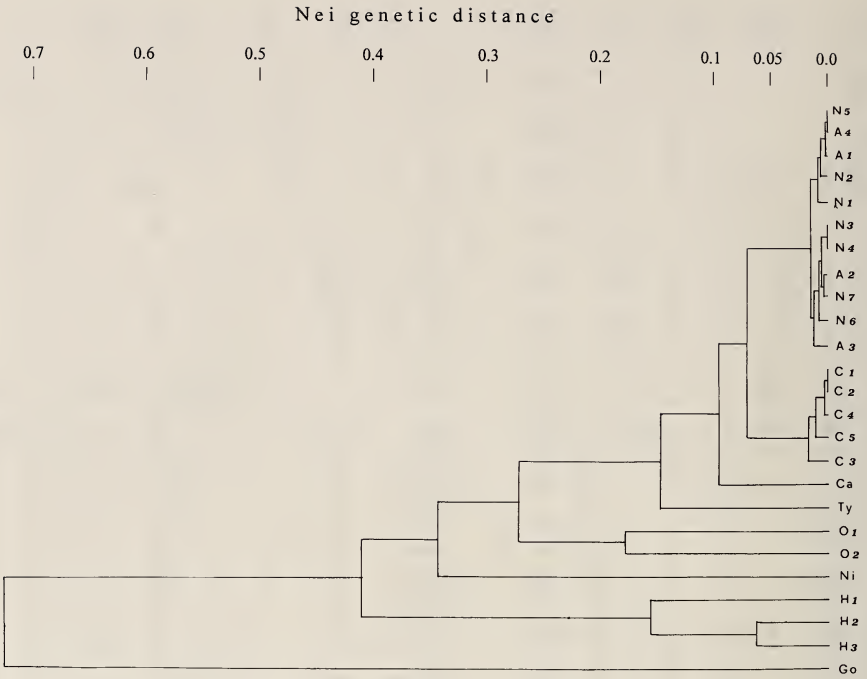


Figure 1. Dendrogram based on Nei's Distances.

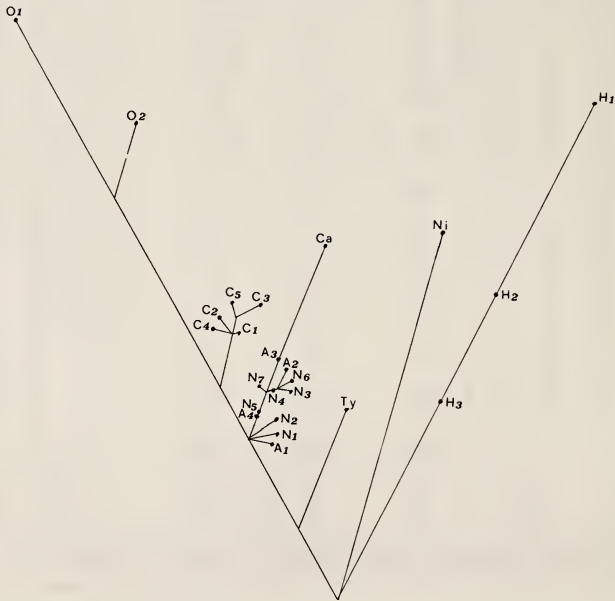


Figure 2. Dendrogram obtained by the Continuous Characters Maximum Likelihood method.



5. *E. cassioides* (*E. neleus* + *E. aquitania*), *E. tyndarus* and *E. calcarius* also cluster at similar levels (Nei's  $D$  [*E. cassioides* - *E. calcarius*] = 0.096 ; [(*E. cassioides* + *E. calcarius*) - *E. tyndarus*] = 0.147).
6. *E. nivalis* is the most genetically distant species of the *E. tyndarus*-*E. cassioides*-*E. calcarius* lineage (Nei's  $D \approx 0.3$ ).
7. The two populations of *E. ottomana* are genetically rather distant (Nei's  $D = 0.177$ ).
8. Among populations of *E. hispania* the closest are 'ssp. *rondoui*' and 'ssp. *goya*' (Nei's  $D = 0.063$ ), whereas the nominotypical form is genetically quite distinct (Nei's  $D = 0.155$ ).

The UPGMA cluster of Nei's genetic distances is shown in Fig. 1.

The 'phylogenetic' tree obtained by the Continuous Characters Maximum Likelihood Method, is shown in Fig. 2 and concurs with the tree shown in Fig. 1 in all its most important aspects.

## Discussion

All our results suggest that the distinction of *E. neleus* and *E. aquitania* is untenable and that this complex is well distinct from *E. nivalis*. The two populations collected at different altitudes on Großglockner, which we identified as *E. cassioides* (low altitude) and *E. nivalis* (high altitude) on characters of wing morphology, show a genetic distance of  $D = 0.358$ . Accordingly, and apart from other nomenclatural problems (see below) they can be identified as topotypic samples of their respective species.

It remains to be stressed that *E. cassioides* sensu lato is a complex of two genetically different groups of populations. One, including the type locality of *E. cassioides*, occurring at least in the Rhetian Alps and the Tauern. The other includes all populations from the Italian Apennines, the central and western Alps, the Pyrenees and the Cantabrian Mountains. The names by which these groups of populations can be identified will be dealt with further on.

The relatively small genetic distance between these two taxa (Nei's  $D = 0.071$ ) is probably a consequence of them having become separated in recent times. On the basis on Nei's calibration of the molecular clock these two taxa would have started to evolve independently about 0.35 Myr ago. Since this date gene flow was presumably interrupted by the intervening populations of *E. tyndarus*, a species already genetically distinct from the rest, having the fixed allele MPI 70 (absent from all populations of *E. cassioides* s.l. and otherwise only found in *E. hispania*) and lacking the allele PGI 100 (very common in *E. cassioides* s.l.). The interruption of gene flow between eastern and western populations of *E. cassioides* s.l. is demonstrated by the absence of allele 6PGD 100 from populations of the former. Subsequently, the rising temperature may have progressively confined western populations of *E. cassioides* to the mountain peaks of the Alps, Apennines, Pyrenees and Cantabrian Mountains. Nei's distances between these populations generally vary between 0.01 and 0.02,

which would place such events in the interval of 50,000 - 100,000 years bp. These distances, however, are too small to be reliable and should be confirmed by independent studies on mitochondrial DNA.

On purely morphological grounds populations of the 'western group' are not easily identified from nominotypical *Erebia cassioides*. The latter generally have slightly smaller size, more rounded wings at apex and are darker grey on ventral surface of the hindwings, with a normally less neatly black edged discal stripe. In females the hindwing colouration is silvery grey on ventral surface, with almost no hint of a yellowish or creamy wash. The opposite applies to populations of the 'western group'.

A potentially interesting field for future research would be to investigate genetic distances between other 'subspecies' having similar distributions, such as those found within *E. pronoe*, *E. meolans*, etc. It may be worth noting that the presence of another species occurring between populations of an eastern and a western group may have contributed to an earlier interruption of the gene flow, as well as to keep the interruption in place by mutual exclusion, when more favourable environmental conditions took over. Where such a situation is lacking, e.g. for *E. euryale*, *E. pluto*, *E. gorge*, etc., there is enough morphological evidence to suggest that hybrid populations exist in between, where they probably represent the outcome of secondary hybridization events.

Another lineage is that of *E. hispania*, where even though no cohabitation can obviously occur between populations of the Pyrenees (N Spain) and Sierra Nevada (S Spain), genetic distances suggest that two different species are involved: *E. hispania* (Sierra Nevada) and *E. rondoui* (Pyrenees). Such a distinction is supported also by their different haploid chromosome complements ( $n = 25$  and  $n = 24$ , respectively) and external morphology.

It is finally worth mentioning that the only two western European populations of *E. ottomana*, the so called 'ssp. *tardenota*' and 'ssp. *benacensis*', sharply differ from each other on a genetic, as well as on a morphological basis. A final word on this subject, however, cannot be spoken until populations from the Balkan peninsula and Turkey have been analyzed.

## Nomenclature

### 1. The application of the name *Papilio cassioides* Reiner & Hohenwarth, 1792.

The reasons why WARREN (1981) considered Reiner & Hohenwarths' name a nomen nudum (i.e. a name that fails to conform to Articles 11-13 of the International Code of Zoological Nomenclature, ICZN) have been dealt with already. Such a contention, however, finds little support in the current edition of the ICZN, since the publication of this name not only was accompanied by a description, but a specimen (presumably the holotype), now lost, was also figured. Neither can this name be considered a nomen oblitum (i.e. a forgotten name, a term that has been omitted from recent editions of the ICZN), because it remains by far the most commonly employed name in current

literature. On the other hand, however, it is true that although both the description and the accompanying figure are taxonomically obscure, the description may subjectively be presumed to represent the taxon currently referred to as *E. nivalis* Lorković & de Lesse, 1954.

To preserve nomenclatural stability, therefore, we think that the most straightforward nomenclatural option is at this point to select a neotype, in accordance to provisions of Art.75 of the ICZN. Accordingly, we herewith designate the male specimen labeled : Zirknitztal : Großglockner : Austria, 30.07.1991, leg. L. Cassulo, deposited in the collection of the Museo Civico Giacomo Doria (Genoa, Italy) as neotype of *Papilio cassioides* Reiner & Hohenwarth, 1792.

## 2. Western and southern populations of the *Erebia cassioides* complex.

The discovery that two genetically different groups of populations can be identified within the *E. cassioides* complex resurrects WARREN'S (1955, 1981) suggestion, albeit on different grounds, that two different species may have been confused under this name. The name *Erebia neleus* (Freyer, 1833), however, probably cannot be employed for either of these, as it was proposed to designate some electrophoretically still unstudied populations from the Alps of Transsylvania (Retezat Mts) which may prove conspecific with *E. cassioides*.

Should populations of the 'western group' be found to be distinct at species or subspecies level, they should be designated by the name *Erebia (cassioides) carmenta* (*Erebia tyndarus carmenta* Fruhstorfer, 1909 — Soc. ent., 24 : 223 — type locality : N.Italy : Province of Aosta : Alpi Graie : Courmayeur), rather than *Erebia (cassioides) aquitania* (*Erebia tyndarus aquitania* Fruhstorfer, 1909 — Soc. ent., 24 : 125 — type locality : Maritime Alps). Although both names bear the same author and date, selecting *carmenta* will have the advantage of avoiding confusion with other treatments of the group. It is rather unfortunate, in this connection, that Reverdin's name '*murina*' cannot be employed, as infrasubspecific, and as such invalid on a nomenclatural basis (*E. tyndarus* var. *cassioides* forma *murina* Reverdin, 1909 — Bull. Soc. lépid. Genève, 1 : 292 — type locality : Le Moléson, Prealps of Freiburg's Gruyère, Switzerland).

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