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Microtopographic phenotypic variation in *Plebejus bellieri* (Oberthür, 1910) (Lepidoptera, Lycaenidae, Polyommatainae)

Abstract: The molecularly based study by Toro-Delgado *et al.* (2025) demonstrates an identical genomic structure in all Sardinian-Corsican-Elban populations of *Plebejus bellieri* (Oberthür, 1910). However, the notable number of microtopographic phenotypic variations in wing patterns in the various insular biotopes is surprising. Possible influences from environmental causes emerge and are described in detail. The complex history relating to the discovery and taxonomy of Sardinian taxa, sometimes thought in the past to be conspecific with *P. idas*, is reported. The results of a careful study of the androconial morphology and wing pattern of the various island phenotypes of *P. bellieri* are presented.

Riassunto: *Variazioni fenotipiche microtopografiche di Plebejus bellieri (Oberthür, 1910) (Lepidoptera, Lycaenidae, Polyommatainae)*
Gli studi condotti su base molecolare da Toro-Delgado *et al.* (2025) dimostrano identica struttura genomica di *Plebejus bellieri* (Oberthür, 1910) in tutte le popolazioni sardo-corso-elpiane. Sorprende, peraltro, il notevole numero di variazioni fenotipiche microtopografiche dei disegni alari nei diversi biotopi insulari. Emergono possibili influenze da parte di cause ambientali descritte dettagliatamente. Viene riportata la complessa storia relativa alla scoperta ed alla tassonomia dei taxa sardi, ritenuti talvolta in passato conspecifici con *P. idas*. Si espongono i risultati di uno studio accurato della morfologia androconiale e del pattern alare dei vari fenotipi insulari di *P. bellieri*.

Key words: *Plebejus idas* complex, *P. bellieri*, endemic Mediterranean polyommatainae, taxonomy.

INTRODUCTION

Our understanding of the phylogeny and taxonomy of Lycaenidae has greatly benefited from the advent of widely available molecular methods. Results of the work by Talavera *et al.* (2013), based on several nuclear and mitochondrial markers, have not only demonstrated the monophyly of the morphologically based *Polyommatus* group established in Eliot's (1973) seminal paper, but scaffolded its many genera into a wide-ranging phylogenetic system, thereby setting the basis for further taxonomic studies.

Improvements have not always been as clear-cut as regards species-level taxonomy. Just to make an example, the early cytological work of de Lesse (1969) could finally demonstrate the species-level separation of *Lysandra coridon* and *L. hispana*, but left many doubts on the relationships between the latter and *L. albicans* arising from discrepancies between karyology and morphology, which have not been dispelled by later morphological and molecular studies (Wiemers *et al.*, 2020). More in general, although sequencing of the COI-5P 'barcoding' fragment proved a very useful tool for sorting taxonomically unknown materials for various kinds of studies, the hopes initially raised by the supposed existence of a 'barcoding

gap' that would allow to disentangle species rank taxonomy from variation more strictly related to population genetics, have proved unfounded (Wiemers & Fiedler, 2007). The hybridization between widely recognized butterfly species at sites where they come into more or less marginal contact, already suggested by the above-mentioned morphological and karyological works, is demonstrated to be relatively widespread. As many as 7 hybrids between species of *Lysandra* and of other polyommataine genera, and another 11 at the intrageneric level have been (unnecessarily) named in the literature, while several more were left unnamed (see Schurian, 1989). Known cases of barcode-sharing, probably at least sometimes deriving from mitochondrial introgression, are multiplying (Wiemers & Fiedler 2007).

The *P. idas* complex includes several taxa, distributed over a wide Euro-Asian area, which, thanks also to their polyphagous larva, have adapted to strongly different habitats and to many thermal and altitudinal conditions. Many subspecies of *P. idas* have been described. Verity (1943) recognized 16 Italian 'races' while, more recently, Tshikolovets (2011) restricted them to 8 European subspecies (including *P. i. bellieri* s.l.).

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THE HISTORICAL BACKGROUND

The discovery of *Plebejus bellieri* in Sardinia has a long and troubled history, which brings to mind the tormented life of Idas, a strong and violent demigod from Greek mythology, who Zeus finally struck with a terrible lightning bolt.

The species currently known as *Plebejus bellieri* was first described as *Plebeius argyrognomon* var. *corsica* Tutt, 1909, and independently redescribed one year thereafter by Oberthür (1910) as *Lycaena argus bellieri*, on materials from Corsica: Bastelica (Locus Typicus). Oberthür was strangely unaware of Tutt's publication, while Tutt was himself unaware that his own specific epithet had already been used to identify *Lycaena aegon* var. *corsica* Bellier, 1862, a name currently deemed on taxonomic grounds to represent a subspecies of *Plebejus argus* Linné, 1758. As a consequence, in case both taxa are classified under *Plebejus*, as is the current use (Wiemers *et al.*, 2018), Tutt's name becomes a junior secondary homonym of Bellier's and is therefore invalid (ICZN, Art. 53.3, 47.3). All this was, anyway, unknown to Oberthür, who had not proposed '*bellieri*' as a substitution name, but simply to designate a separate subspecies of what is now *Plebejus idas*. The ♂ lectotype of *Lycaena argus bellieri* Oberthür, 1910, labelled: "Bastelica, 7.7.'05., H. Powell/ Ex Oberthür Coll., Brit. Mus. 1927-3. / NHMUK (E) X 265250", was designated by Bálint (1999) and is housed in the collections of the London Natural History Museum (NHMUK).

Taxonomic and nomenclatural problems concerning *P. bellieri* continued even after 1910. Verity (1943) mentioned *P. idas bellieri* as only occurring in Corsica and stated that he did not know of its presence in Sardinia. In fact, before 1958, various authors (Mola, 1916, 1919; Hartig & Amsel, 1951; Nabdil, 1957) did not recognize *P. bellieri* among specimens collected in this island, erroneously attributing them to *P. argus* or *P. argyrognomon*. Higgins & Riley (1983) mentioned this species from Sardinia only in the 5th edition of their well-known 'Guide' (but see Higgins 1975a), while Tolman & Lewington (1997) ignored Sardinian *P. bellieri* and cited it only in the edition of 2013. Many authors had evidently missed the publication by Galassi (1959) on the discovery of '*Lycaeides idas*' on the marine coast of Capo Caccia (northwest Sardinia). Biermann, who devoted himself particularly to this taxon, finally published his recordings obtained by Desulo in July 1974 and at Arcu Correboi, Dorgali, and Mt. Limbara in July

1979, all at relatively high elevations (Biermann & Hesch, 1982; Biermann, 2003).

In 1995, intrigued by the work of Galassi, who had prepared some specimens of '*P. idas*' collected on Capo Caccia for Prof. G. Fiori, then Head of the Institute of Agrarian Entomology of the University of Sassari, I went to the Museum of the said Institute to examine them. I was very surprised to observe that those 4 males and 2 females showed a completely different phenotype compared to that of the Gennargentu specimens in my collection. In 1996, on the occasion of my appointment as professor of Dermatology at the University of Sassari, I went to the peninsula of Capo Caccia to verify whether the colony of *P. bellieri* was still present. After several days of repeated and adventurous visits along the impervious coast of that promontory, I suddenly observed some small blues darting between bushes of giant euphorbia and spiny broom. I identified them as specimens of '*P. idas*'. Although dazed by that arid, wild, primitive, fascinating, unreal environment, scorched by a burning sun, while I was extricating myself from tangles of thorny shrubs of the garrigue and on the edge of cliffs overlooking the open sea, I had no doubt that the taxon of the Capo Caccia promontory was not the same as that of Gennargentu and that, alongside the mountain ones, there were colonies of maritime *P. bellieri* in Sardinia. At the end of the 1990s, together with D. Jutzeler, an expert in breeding lepidoptera for study purposes, we decided to undertake research on the preimaginal stages of populations of *P. bellieri* in the Sardinian-Corsican area and on the Isle of Elba, to verify any morphological differences between their eggs, larvae, and pupae. These investigations, although carefully conducted, did not provide clear evidence in this regard (Jutzeler & Leigheb, 2004). However, they confirmed the morphological differences of the imagines, as I maintained, between mountain populations (characterized by darker blue males, very wide black premarginal wing margins, and mostly brown females) and seaside populations (light blue, thinner black wing margins and blue-washed females).

In 1995, research by the La Sapienza University of Rome on the Lepidoptera of the islands of the Maddalena Archipelago (a Natural Park), in the North East of Sardinia, demonstrated the presence of *P. bellieri* in many of these islets: Isola Maddalena, Spargi, Santo Stefano, Budelli (Cobolli *et al.*, 2005); Jutzeler (2004) found it in Isola Santa Maria, and Balletto (2005) in

Caprera. In contrast, I neither found the taxon in the Asinara National Park, nor along the entire northern coast of Sardinia, from Argentiera to Stintino, and on the Isle of Tavolara, which I visited up to the summit accompanied by a military guard, in June 1995 (see also Leigheb *et al.*, 2005).

MORPHOLOGICAL INVESTIGATIONS

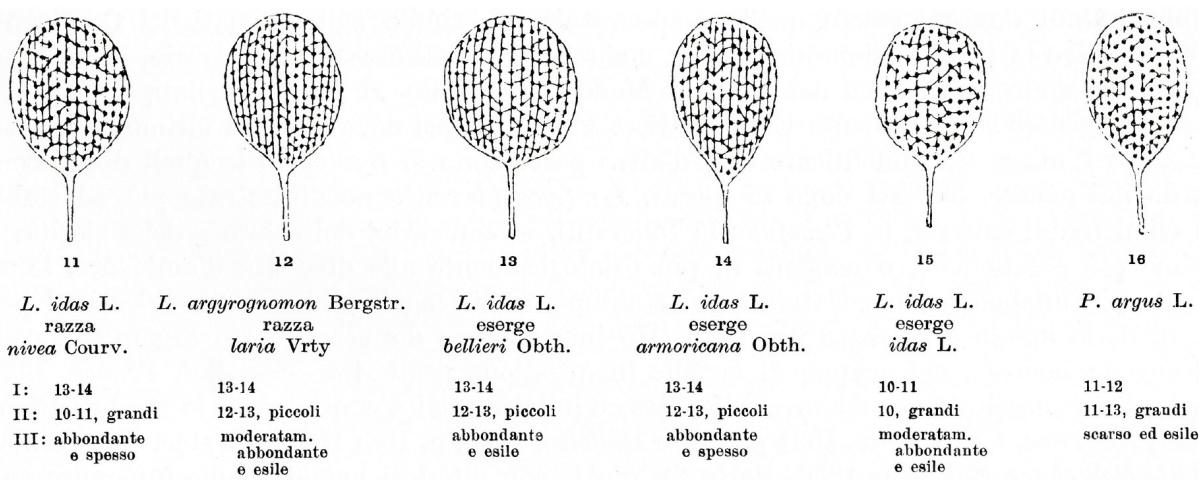
The study of male androconial scales, principally introduced by Müller (1877), became soon rather widespread among lepidopterists, and Eliot (1973) made extensive reference to androconial features. Courvoisier (1917, whose unnumbered plate was reproduced in Verity, 1943, p. 161) was the first to compare some continental 'races' of *P. idas* with *P. bellieri*, based on these features. Although the use of this character declined in more recent times, it was not completely abandoned, and a notable exception is represented by the paper by Ômura *et al.* (2017), for the case of *Celastrina*.

However, these studies were, in their vast majority, aimed at trying to resolve taxonomic problems by complementing results obtained from other morphological features, while very few of them were carried out at the intraspecific level or tried to relate variation in the shape of androconia with respect to the local ecological conditions.

As expected, the comparison between the shape of the androconia (s.a.) in my preparations and those presented by Courvoisier (Fig. 1) demonstrated a heterogeneity of appearance even within each single population. It follows that the phenotype of s.a. of each population must be attributed to the androconia that are percentage-wise more numerous when reading the entire slide. Such heterogeneity should not be surprising, bearing in mind that in some lycaenids, androconial morphology can also vary between annual generations (Ball, 1914). I did not consider the counting of the ribs and nodules of the s.a. very significant, having noted their difficulty in reading and their inconsistency in rereading, in addition to their non-specificity. Moreover, in Courvoisier's picture, we note an equal number of nodules (12/13) in *P. bellieri* and in *P. idas armoricana* and 13/14 ribs in both *P. idas nivea* and *P. argyrogynomon*.

The shape of the androconial scales of the studied colonies (Fig. 2) is described below.

- Italy, Valdieri Pian della Casa, 1700 m, Maritime Alps: *P. idas alpina*, Berge: small, oval, narrow at the peduncle, fig-shaped. Used as a control case for high elevation *P. idas*.
- Italy, Busseto, Emilia: *P. idas argellus*, Turati: ovoid, narrowed towards the peduncle. Used as a control case for low elevation *P. idas*.



Androconi di *Lycaeides* e di *Plebejus*, sec. Courvoisier.

I: Rilievi costoliformi; II: Noduli; III: Reticolo.

Fig. 1. Androconial scales of various 'races' of *P. idas* drawn by Courvoisier and reproduced by Roger Verity (1943, vol. 2, p. 162).

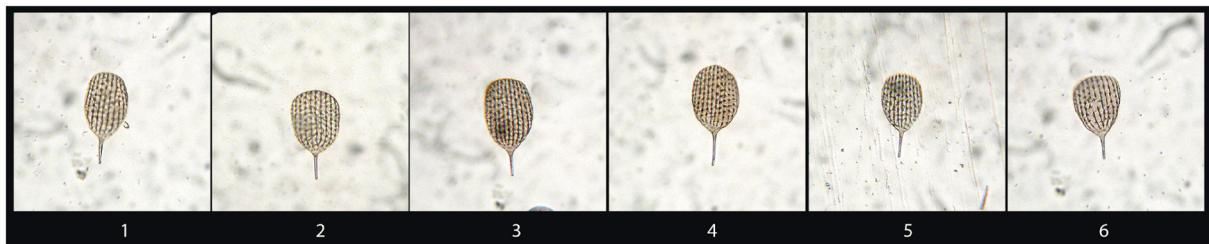


Fig. 2. Androconial scales of various populations of *P. bellieri* of the Sardinian-Corsican Complex investigated in this paper. 1) *P. bellieri* (Col D'Isa, Bastelica, Corsica); 2) *P. bellieri*, phenotype of Maddalena archipelago (Isle of Santo Stefano); 3) phenotype of Capo Caccia: (Capo Caccia, Alghero); 4) phenotype of Monte Limbara, Olbia; 5) mountain phenotype (Bruncu spina, Gennargentu); 6) mountain phenotype (Monte Iscudu, Gennargentu). Enl. 40×, G. Leigheb.

- Corsica, Bastelica, Col d'Isa, 800-1200 m *P. bellieri*, Oberthür: elliptical, ovoid, oar-shaped (N. 1)
- Sardinia, Capo Caccia: monomorphic, large, ellipsoidal, or ellipsoidal slightly flattened at the top (N. 3)
- Sardinia, Islet of Santo Stefano, Maddalena archipelago: similar to the previous ones but a little shorter and wider (N. 2)
- Sardinia, Monte Limbara, 1050 m: small, elliptical, oar-shaped (N. 4).
- Sardinia, Genna Silana, 1017 m: small, oar-like, fig-shaped.
- Sardinia, Gennargentu, Bruncu Spina, 1570 m: very small, elliptical, oar-shaped (N. 5)
- Sardinia, Gennargentu, Monte Iscudu, 1200 m: small, fig-shaped, distally broader (N. 6)
- Sardinia, Gennargentu, Monte Spada, 1360 m: small, very narrow, ovoid, narrowly oar-shaped.

My control samples from the northern Italian plains (Busseto) and mountains (Maritime Alps) may therefore be compared with those of European *P. idas* and *P. bellieri* from Corsica, as Courvoisier did in his time. Apart from highlighting a certain level of polymorphism in the various shapes of the androconia of *P. idas* and *P. bellieri*, no other significant differences have been noted. The smaller dimensions in the continental Alpine colonies of *P. idas* are probably a consequence of the influence of altitude-related (over 1700 m) factors and do not seem to reflect any species-level differentiation.

In the two Sardinian colonies located in different seaside habitats, a slight hypertrophy of the s.a. is noted in the specimens from Capo Caccia (large, ellipsoidal, distally flattened) and, on the contrary, a modest reduction in size in those of the islets of the Maddalena Ar-

chipelago. In the mountain populations of 'mainland' Sardinia, the androconia are consistently smaller, oar- and/or fig-shaped and narrower, clearly differentiating themselves from those of seaside origins. Probably the morphology of androconia is less selective than their functional electivity for the production of species-specific pheromones.

Based on wing and androconial phenotypic diversity, as well as for different biotopes of insular *P. bellieri*, the following mycrothopographic populations are described.

DESCRIPTION OF PHENOTYPES OF *PLEBEJUS BELLIERI* POPULATIONS

Mountain phenotype of Sardinia (Fig. 3; column 1, first at left-hand)

Monte Gennargentu, Bruncu spina, Sardinia, 1500 m, 5-VII-1995 and 16-VII-1994, legit G. Leigheb, in the Collection of the Regional Museum of Natural History of Turin (MRSN).

2 ♂♂ and 2 ♀♀: same data, 9-VII-94 leg. et coll. G. Leigheb (Novara).

10 ♂♂ and 4 ♀♀ Monte Iscudu (Gennargentu), 1200 m, 3-VII-2011 leg. G. Leigheb.

9 ♂♂ and 4 ♀♀ Genna Silana (Desulo), m 1000, 3-VII-1990, leg. G. Leigheb.

14 ♂♂ and 6 ♀♀ Monte Limbara (Olbia), m 1000, 3-VII-1982; 10-VII-1988, leg. G. Leigheb.

Male. Wingspan from 21 to 25 mm. Size varies depending on sites, but is generally larger when compared to all other Sardinian-Corsican taxa. Smaller sizes prevail above 500 m.

Upper wing surface (Ups): background colour dull blue with a hint of violet component. *P. bellieri* (Fig. 3, Col-

umn 2, second from right hand) are bright blue. Wing ciliae white.

Premarginal black band very wide (from 2 to 3 mm) on all wings, with shaded medial margin. Forewings sprayed whitish scales on the medial third of costa. Lower wing surface (Uns). Ciliae white. Forewing: background colour gray with yellowish-brown hues.

Discal and postdiscal spots larger than in continental *P. idas*, all ringed greyish brown scales (white in *P. bellieri* of Capo Caccia phenotype).

Hindwing: background colour as in forewing. All black spots very well marked, ringed as on the forewing. All submarginal markings of considerable thickness; pre-marginal orange lunules large and well-visible.



Fig. 3. Sardo-corsican *P. bellieri* populations. Left to right and top to bottom. Column 1: mountain phenotype from Bruncu Spina, Gennargentu (♂ Ups); (♂ Uns); (Ups brown ♀); (Ups blue-washed ♀); (Uns brown ♀). Column 2: *P. bellieri* from Col d'Isa, Bastelica, Corsica (♂ Ups); (♂ Uns); (Ups blue-washed ♀); (♀ Uns). Column 3: phenotype from Capo Caccia, Alghero (♂ Ups); (♂ Uns); (Ups blue-washed ♀); (Uns ♀). Column 4: Maddalena archipelago phenotype from the Isle of Santo Stefano, Sardinia. (♂ Ups); (♂ Uns); (Ups blue-washed ♀); (Uns blue-washed ♀); (Ups brown ♀); (Uns brown ♀).

Female. Wingspan 23 to 26 mm.

Ups: dark brown with marginal black shading on the four wings. Females washed blue scales are less common than in the other phenotypes. More in detail: at Bruncu Spina (Gennargentu), 1500 m, out of 25 specimens in total, the females are 15, of which 12 are brown and 3 blue-washed. At Mt. Iscudu (Gennargentu), 1200 m, out of 14 specimens, 2 females are brown and 2 are blue. At Dorgali 1000 m, out of 27 specimens, the brown females are 7 and only 1 is blue. On Mt. Limbara, 1000 m, out of 32 specimens, the brown females are 6 and the blue ones 2 (even the dark ♀♀ have variable degrees of a slight blue suffusion on the wing bases).

Hind wings with orange lunules in numbers of two or three, centered by marginal black dots. 33% of the dark ♀♀ do not have orange lunules. Ciliae are variable, either white or brown, in darker individuals. Specimens with black borders may have white ciliae only at the apex of the forewings and/or also on the hindwings.

Uns: grey background colour with brown tones. All black spots are strongly marked on the four wings. Post-discal black spots very large (double the size of Corsican *P. bellieri* [c.b.], especially on the forewings) and with enormous development of the ovalised fifth spot. The pale rings around the black spots are obscured by dark scales (white in Capo Caccia taxa and c.b.).

Hindwings. Similar to males, with marked development of the pre- and sub-marginal pattern of orange lunulae; marginal ocelli pupillated blue scales, surmounted by a series of large black triangles and a band of white arrowhead-shaped lines (different from the dull marginal patterns of c.b.).

This phenotype, typical of the interior of Sardinia, is restricted to hilly and mountain habitats between 500 and 1600 m. Like those of all Sardinian-Corsican-Elban taxa, the adults come in a single generation. They are on the wing in the first three weeks of July, while those of the populations of the marine coast emerge in June. It occurs with small, wide-spaced colonies found in the clearings within the wooded areas sparsely overgrown with shrubs of *Genista corsica* (possible host plant), *Cistus*, *Rubus* sp., and *Helichrysum* (nectar sources); butterflies are generally abundant (Fig. 4) (Leigheb *et al.*, 2005). It was originally found only in the Gennargentu area and on Mount Limbara. The sites where its presence was confirmed during the present investigation are: Mt. Ispada, 1360 m, Mt. Iscudu, 1200 m, Bruncu spina, 1400-1570 m, on the Gennargentu mas-

sif; Seui, Barbagia Seulo, 800-900 m; Dorgali, Genna Silana, 1000 m; Mt. Limbara (Tempio Pausania), 800 m (Fig. 5, Bruncu Spina and Fig. 6, Mt. Limbara).

Sea-side phenotype of Capo Caccia promontory (Fig. 3; right-hand column)

Promontory of Capo Caccia (Natural Park), Alghero, Nurra Region, NW Sardinia, 5-VII-1995 legit Giorgio Leigheb, in coll. of the Regional Museum of Natural History, Turin (MRSN). ♀. Promontory of Capo Caccia, 9-VII-1994, legit Giorgio Leigheb. MRSN:10♂ and 10♀, idem: 9-VII-1994; 3-VII-1996; 9-VI-1998, in Coll. G. Leigheb.

Male. Wingspan 22 to 24 mm.

Ups: light, bright blue (lighter than in mountain taxa

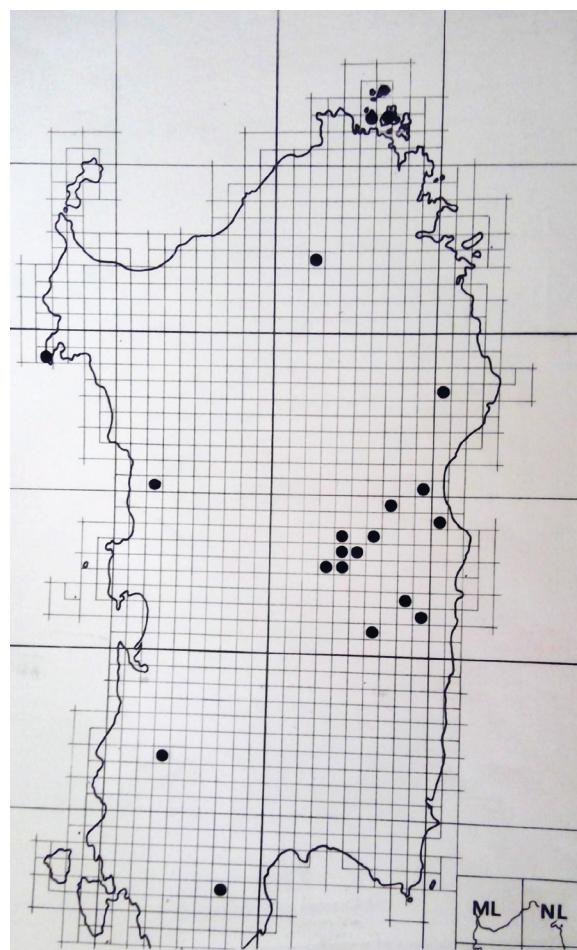


Fig. 4. Map of Sardinia showing sites where the presence of *P. bellieri* is known. Reproduced from: Leigheb *et al.* 2005.

and *P. bellieri*); premarginal black band thin (thinner than in mountain colonies and *belleri* from Corsica), with bluish-white shading on the wing base and the medial part of the costa (as in other populations). Ciliae white. Forewing veins obviously lined with black scales (as in c.b.) Hindwing: marginal black band wavy on medial edge due to the presence of submarginal black spots slightly projecting towards the discal area (less evident in *belleri* from Corsica).

Uns: background colour light gray (as in *belleri*). With white shading in basal areas. Postdiscal black spots large, the fifth one oval and medially expanded. Submarginal and marginal patterns of orange lunulae and pupillated ocelli well marked on both wings (pale or vestigial in c.b.). Ciliae white.

Female. On average, smaller than males. Most of the ♀♀ have more or less extensively blue-whashed wings, on Ups. Of 66 specimens observed from 1994 to 1998,

the males were 42, the brown females 10 (40% of the ♀♀), and the blue ones 14 (58%) (G. Leighb).

Ups: the blue scales extend to the medial third of the forewings, the medial half of the costa, and the lower two-thirds of the hindwings. The remaining wing portions are intensely blackish-brown with jagged medial limits. Wing veins are lined with black scales.

Uns: ground color a little darker than in males. A series of black spots larger than in c.b., especially the oval and medially shifted spot. Orange premarginal lunules well-marked and evident. Distal margin of hind wings blackish-brown with a series of internervular black dots on the medial edge. The brown ♀♀ are devoid of orange premarginal lunules (present in various numbers in mountain colonies).

The adults of the Natural Park of Capo Caccia are on the wing in June, and are restricted to the north-facing xerothermic Mediterranean sites of the maritime



Fig. 5. Mountain biotope towards Bruncu Spina, 1570 m, not far from Punta La Marmora, 1834 m (G. Leighb).

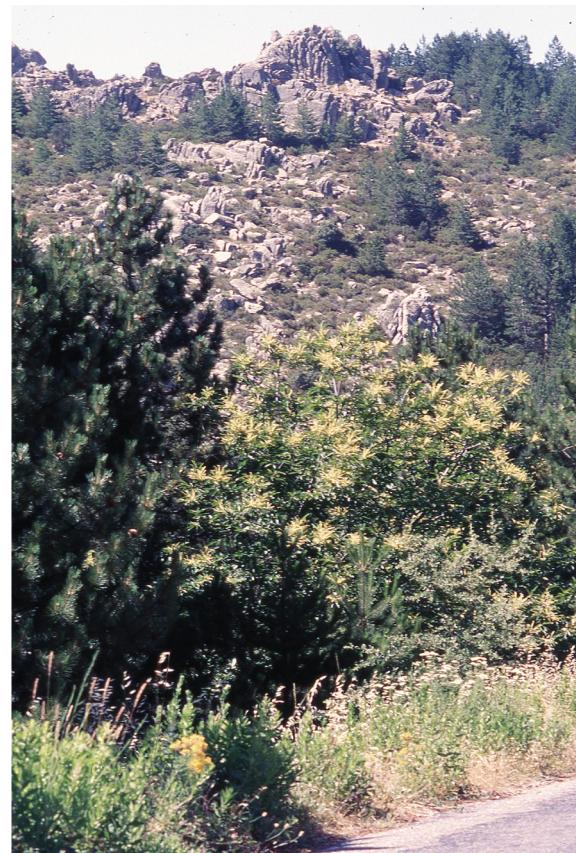


Fig. 6. Mountain biotope towards Monte Limbara, 1359 m, wooded or bushy areas with clearings (G. Leighb).

coast, subject to enormous temperature variations and lashed by impetuous winds and saltiness. Only two modest colonies, less than 1 km apart from each other, are known. The exposed geological substrate is of karstic limestone rocks showing frequent outcrops, grooves, and cavities covered by red earth, on which rare plant species grow, such as the endemic *Centauropa horrida*. *Stachys glutinosa*, *Cistus salvifolius*, and *Euphorbia dendroides* are also present, together with shrubs of *Genista sardoa* and *G. corsica* (Valsecchi, 1989), both potential food plants for the caterpillars of this butterfly (Figs. 7 and 8). In its southern strip, the complex nature of the promontory is characterized by *Juniperus phoenicea*, *Chamerops humilis nana*, and *Phyllirea*.

In principle, *P. bellieri* is here protected by the Natural Park of Capo Caccia, but requires utmost care, being a rare relic in a rare biotope. Unfortunately, the area is already suffering significant tourist impact. This set of colonies, initially identified as *P. idas bellieri* by Galassi

(1959), was rediscovered by G. Leigheb in 1994 and has not yet been studied by molecular techniques.

Phenotypes of Maddalena archipelago (Fig. 3; column 4, last to the right)

Isola Santo Stefano, Archipelago of La Maddalena, N.E. Sardinia, 17-VI-1989, leg. M. Cobolli, M. Lucarelli and V. Sbordoni (in Coll. Sbordoni).

3 ♂♂, and 1 ♀, as above; in Coll. G. Leigheb (Novara). **Male.** Wingspan 20-23 mm. This is the smallest-sized *P. bellieri* of Sardinia.

Ups: forewings more slender than in the Capo Caccia colonies and c.b., with very convex outer margin. Ground colour indigo blue, intermediate between the Capo Caccia phenotype and Corsican *bellieri*; dusted light blue in basal areas. Black marginal band thin (thinner than in c.b.), with a series of internervular black dots along its medial edge (as at Capo Caccia). Ciliae are white.

Uns: grey, with a slight brown tone (darker than in c.b.).



Fig. 7. Capo Caccia promontory, Natural Park, with a view of the cliffs overlooking the sea and the karst plateau above (G. Leigheb).

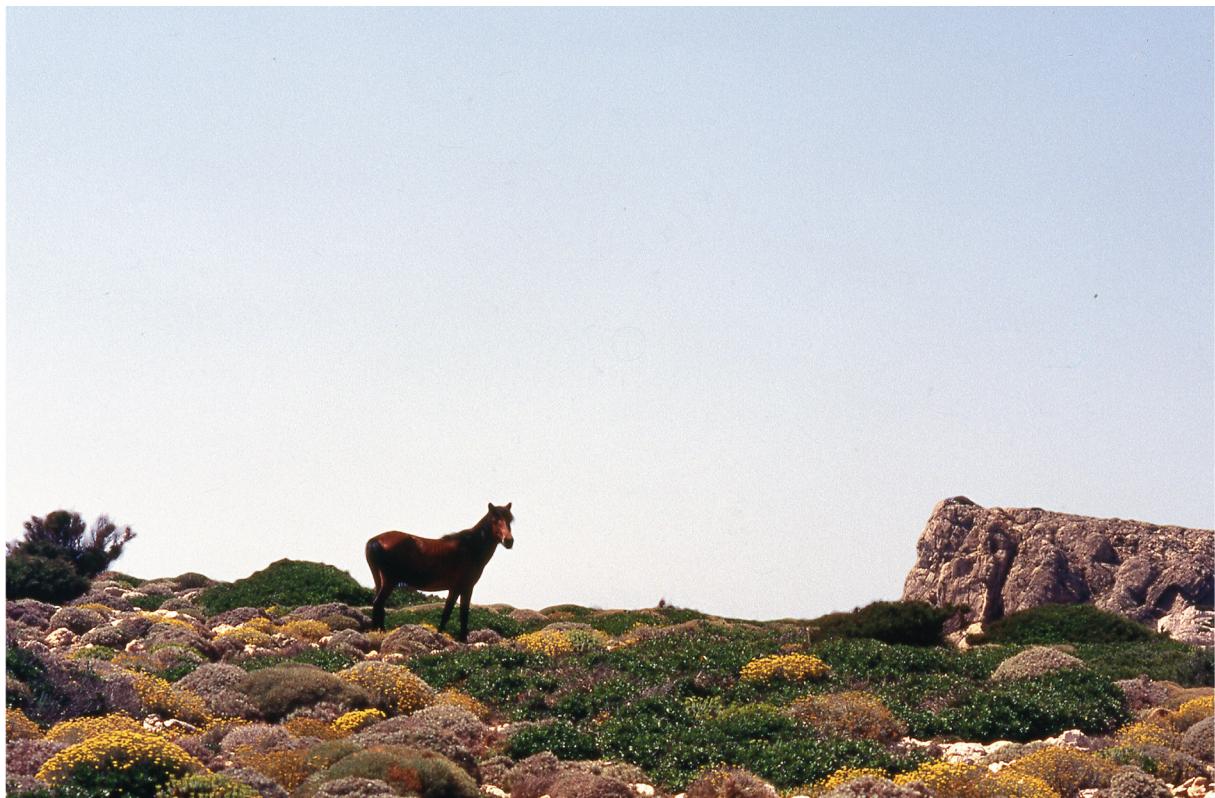


Fig. 8. Garigue on Capo Caccia, showing the poor herbaceous and bushy vegetation (G. Leigheb).

Postdiscal and discal spots strongly marked, all circled light gray scales (as in the mountain phenotype). Orange submarginal lunules very evident (pale in c.b.). The reduction in width of the white premarginal band located distally to the series of black postdiscal spots is conditioned by the hypertrophy of the black spots (wider in c.b.). Marginal ocelli as in the Capo Caccia phenotype.

Female. Wingspan 20-22 mm.

Ups: normally washed bluish scales on a restricted part of wing surface, especially on hindwings, compared to c.b. and to the Capo Caccia phenotype. Veins lined black scales. Remaining wing parts intensely black-brown. The few brown females lack orange lunulae on hindwings. Submarginal black spots included in the marginal blackish band.

Uns: background colour gray, with a slight brown shade, darker than in Capo Caccia and c.b. colonies. All black spots strongly developed, circled in grayish white (as in the ♀♀ of all Sardinian-Corsican populations ex-

cept Capo Caccia). Orange lunulae, black arrowhead triangles, and marginal ocelli well developed, with well-marked blue pupils (paler in c.b.).

The adults of the Maddalena archipelago are on the wing in June. Small colonies inhabit the arid garrigues lashed by strong winds and showing important variation in temperature. The colonised sites are overgrown by poor, predominantly bushy vegetation and sparse shrubs of *Genista corsica*, a possible host plant. This subspecies has colonized almost all the islands of the Maddalena Archipelago, including Santa Maria, Budelli, and Santo Stefano, which are the smallest.

DISCUSSION

The above-reported observations, all based on features of the external morphology, have allowed us to make a global comparison between the various populations of *P. bellieri*. Karyotypic studies are unlikely to be useful at the taxonomic level, because although

unknown in this particular case, an identical chromosome number of 24 is shared across the entire *P. idas* complex. The examination of male genitalia, performed by Reverdin and Chapman (Verity, 1943, Vol. II, p. 168), demonstrated no difference between *P. idas* and *P. bellieri*. Genitalia sketchily illustrated by Higgins (1975b) and more recently studied by Volpe (in Jutzeler *et al.*, 2003) were unable to highlight any significant differences between the various taxa, although a careful re-examination of the latter slides showed that those of Mountain phenotype are more voluminous than in Corsican *P. bellieri* and the valvae are covered with more evident and thicker setae.

The morphological study of androconial scales has shown that:

- those of *P. bellieri* from Corsica (elliptical), similar to those of Mt. Limbara (smaller) and different from those, larger and “oar-shaped” of Capo Caccia, and completely different from mountain populations;
- those of mountain phenotype, although polymorphic between sites, are always small and show an “inverted fig” shape (Bruncu Spina, Monte Iscudu, Genna Silana), or a shortened or narrowed “oar blade” shape (Monte Spada);
- those from the Maddalena archipelago have stocky “shortened oar blade” shape and resemble those of Mt. Spada, but are smaller.

As regards the wing morphology of the four populations considered, reference has been made in the previous paragraphs. Seaside phenotypes of the Maddalena archipelago are the smallest in size, and their underside design is a miniature. Coastal and insular biotopes are exposed to extremely stressful climatic conditions in the channel between Corsica and Sardinia called “Bocche di Bonifacio”. In Corsica, in addition to *P. bellieri* of the internal mountainous areas, Manil & Diringer (2003) have reported the occurrence of a colony located at 300-500 m, close to the south-western marine coast (Porto), and perhaps similar to the phenotype of Capo Caccia. Males from this colony, described as ‘forma piana’ (a name unfortunately unavailable: ICZN, Art. 15.2), are in fact characterized by a thin terminal black band, while females are blue-washed. Finally, the Elban *P. villai*

(Jutzeler *et al.*, 2003) conclude the list of the *P. bellieri* morphae.

Another phenotypic characteristic, typical of the Sardinian-Corsican *P.b.*, concerns the size of the discal and postdiscal black spots on the ventral surface of wings. A striking example of variation in this feature is found in *P. idas nevadensis* and in the *P. idas* colonies from the Simplon Pass and Slovakia.

Objectively, the width of the marginal black band brings *P. bellieri* closer to the Capo Caccia phenotype and, to some extent, also to the taxon of the small Sardinian islands, while it clearly differs from mountain phenotypes. The latter undoubtedly represents the most well-defined phenotype, the one that most differs from Corsican *P.bellieri* and whose particular distinctive characteristics have been presented: specific wing and genital morphology, specific androconial scales, specific habitats. I have long been tempted to classify it as a separate species. I refrained from so doing because the sequences of its COI-5P ‘barcoding’ gene did not support such a separation (Dapporto *et al.*, 2022).

The polymorphic features of Sardinian populations are probably the result of an interbreeding mosaic among insular colonies of *P. bellieri*.

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