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Compared morphology and distribution of the taxa described of *Pseudochazara williamsi* (Romei, 1927) [= „*Pseudochazara hippolyte*“ Esper from Spain] Are they valid subspecies or only the result of phenotypic plasticity (ecological forms)?

(Lepidoptera, Nymphalidae, Satyrinae)

by

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Abstract: A study, illustration and a morphological comparisson of all current known populations (some for the first time) of *Pseudochazara williamsi* (Romei, 1927), as well a its distribution in Spain. Considering *Pseudochazara williamsi* (Romei) (= all the taxa described of *Pseudochazara* de Lesse, 1951, from Spain) as a different species of the Asian taxon *Pseudochazara hippolyte* (Esper, 1784). *Pseudochazara williamsi* (Romei) is an Iberian endemism, limited to southeastern areas of the Iberian Peninsula (Spain), known only from the Provinces of Granada, Almería and Murcia. As a result of this morphological study I conclude that the populations of *P. williamsi* (Romei), as well as the taxa described as subspecies, should be treated as ecotypes (ecological forms, local forms), result of an important phenotypic plasticity, due to its ability to change the phenotype in order to obtain a certain degree of mimetism required for camouflage (color and drawings of the underside hind wings) with the terrain of its environment. These ecological forms (four, with several local forms), are of no taxonomical and nomenclatural significance, since there is no solid foundation to justify their subspecific validity.

Resumen: Se estudia, ilustra y compara la morfología de todas las poblaciones conocidas (algunas por primera vez) de *Pseudochazara williamsi* (Romei, 1927), así como su distribución en España. Considerando a *Pseudochazara williamsi* (Romei) (= todos los taxones descritos de *Pseudochazara* de Lesse, 1951, de España) una especie diferente de la especie asiática *Pseudochazara hippolyte* (Esper, 1784). *Pseudochazara williamsi* (Romei) es un endemismo ibérico, limitado al sureste de la península Ibérica (Spain), conocido únicamente de las provincias de Granada, Almería y Murcia. Como resultado de este estudio morfológico, se concluye que las poblaciones de *P. williamsi* (Romei), así como los taxones descritos como subespecies, deberían considerarse como ecotipos (formas ecológicas, formas locales), resultado de una importante plasticidad fenotípica, debido a su capacidad de cambiar el fenotipo con el fin de obtener un cierto grado de mimetismo necesario para camuflarse (color y dibujos del reverso de las alas posteriores) con el terreno de sus biotopos. Estas formas ecológicas (cuatro, con varias formas locales), no tienen ningún significado taxonómico ni nomenclatural, ya que no existen fundamentos sólidos que justifiquen su validez subespecífica.

Introduction: *Pseudochazara hippolyte* (Esper, 1784) was described from specimens obtained from the Ural mountains (southern Russia), area separated by almost 5.000 km (!) in straight line from south-eastern Spain. Subsequently, Romei (1927: 138) described „*williamsi*“ as a subspecies of the previous, with specimens collected in the Sierra Nevada (Granada Province), despite the great distance between both populations and, strikingly, solely on basis of external morphological similitude of the imagos. Years after, new localities of *Pseudochazara* de Lesse, 1951 were described from southeast of the Iberian Peninsula, some of which are far away from the Sierra Nevada, reaching its known distribution to the southwest of Murcia Province. Some authors considered these new populations as belonging to the nominal type taxon („ssp. *williamsi*“), but others, on account of morphological differences (color, wing pattern, size) and geographical separation, described them as a new subspecies of „*Pseudochazara hippolyte*“ (Esper). More recently, some authors (I am of the same opinion) tend to separate the Asian taxon *P. hippolyte* (Esper) from the existing Iberian taxon (in Fauna Europaea, 2013), under the name of *Pseudochazara williamsi* (Romei), which include all the described taxa from southeastern Spain. In the current article the subspecific validity of these described taxa will be discussed.

In Takáts & Mølgaard (2015), the existence is demonstrated of a reduced genetic distance among the different species of *Pseudochazara* from the Balcan Peninsula: between 0,15% and 0,46% for the group of species „*amymone-graeca-mniszechii-orestes-cingovskii*“. Some species („*amymone-graeca*“) differ only in one nucleotid (genetic distance of only 0,15%). With such small genetic difference, these authors asked themselves where is the limit between species and subspecies within the studied *Pseudochazara*. In this same paper, also the mitochondrial COI sequencing of a “GenBank” specimen is included, access number KP871026, coming from the Sierra de Gádor, S. Almería Province, S. Spain [refered in that article as „*Pseudochazara hippolyte augustini*“ (sic); leg. F. Gil-T.), and is compared with material of the Asiatic *Pseudochazara hippolyte hippolyte* (Esper). Resulting in a difference of only three nucleotids for the same mitochondrial COI region. This is to say, the same genetic distance (0,46%) and the same nucleotid differential (three) that exist between the Balcan species „*mniszechii-cingovskii*“ and „*orestes-cingovskii*“.
However, regardless of what was previously commented, I consider, that a similar morphology (which also occur

among other *Pseudochazara* species) between the Asian taxon (*P. hippolyte* Esper) and the Iberian *P. williamsi* (Romei) could be explained as an evolutionary convergence, homoplasy. This is to say, a parallel evolution, under equivalent environmental pressures, which tend to develop similar characters (morphological, physiological, ethological, etc.) in different, although close, evolutionary lines (species).

Recently, in Gil-T (2016), the distribution of *P. williamsi* (Romei) in Spain was reviewed and updated. In this reference, the taxa described belonging to this species were not treated, as well as their taxonomy, which is dealt with in the current work.

Material and Method: I have examined a significantly large number of specimens of *P. williamsi* (Romei) from all the known existing localities in Spain (fig. 1). From some of these localities I examined and compared samples for the first time: Sierra de Baza and Sierra Seca, located in the central area and northeast of Granada Province, respectively; and Revolcadores, SW. Murcia Province. These specimens were examined both, in nature and from collections, some of which are illustrated in the figs. 2 & 3, representing the existing variability in each locality, as well as specimens showing the typical morphology from each locality.

Distribution of *Pseudochazara williamsi* (Romei, 1927) in the Iberian Peninsula: In Gil-T (2016), the distribution of this species in Spain (SE. Iberian Peninsula) was reviewed. As result, its known distribution was expanded with new populations (inside three new UTM 10x10 km grids). Also, four UTM 10x10 grids, mentioned in previous references of other authors, were considered erroneous. The populations of five UTM grids were considered as extinct or virtually extinct.

We may see in the fig. 1 two maps, the top one reflects the known distribution, the other indicates the name of the mountains or mountain ranges (= Sierras) were the colonies are located. The extinct populations shown in the map are (from north to south): one grid in the Sierra Espuña (Murcia Province) and three grids in the Sierra de Filabres (Almería Province). In other UTM grid (Guillimona, NE Granada Province) its population I consider very probably extinct. The causes of these extinctions are explained in Gil-T (2016).

Types of geological substrates in their localities, factor that defines the color soil: Of no doubt, the geological substrates of the different mountains where this species flies is an important characteristic to be taken into account, since the colouring of the wings (essentially the underside of the hind wings) is the result of its adaptation to the predominant color and characteristics of the soil of existing habitat. We may see the variability of the geological features found throughout the range of the distribution of this species:

- Sierra Nevada, Sierra de Baza and Sierra de Filabres: Sierra Nevada is a mountain range located mainly in the Province of Granada, and its most eastern part extends to the Province of Almería, in E. Andalusia Region, S. Spain. After the Alps, its the highest mountain range of western Europe. It has almost 80 km in length and its surface is of over 2.000 km². Geologically, we can differentiate the following zones [and where *P. williamsi* (Romei) colonies are found] within the Sierra Nevada:
  - Central zone, the highest altitudes: integrated mainly of graphitic mica-schist. In other words, dark rocks of slatey aspect, frequently quartzite veined (bright yellow or white color that stand out from the dark background), siderite and iron oxide. A great part of the nearby Sierra de Filabres and the highest eastern sector of the Sierra de Baza is composed of the same materials (silica substrate).
  - Western zone (west and southwest of Sierra Nevada): formed by dolomites and limestone materials, also dolomite marbles. In the Sierra de Baza, sector of calcareous summits where *P. williamsi* (Romei) was studied, the substrate type is also composed of limestones and dolomites.
  - Eastern zone of Sierra Nevada: outcrop of basic rocks, like the peridotites of Cerro del Almirez, of an intense brownish-red color.
- Sierra Seca, Sierra de la Sagra, Guillimona and Revolcadores: the soil substrate (high mountain terrain) essentially present calcareous reliefs. In the Sierra Guillimona (karstic reliefs) consisting in sandstones and marls; Sierra Seca, Sierra de la Sagra and Revolcadores: substrate formed by limestone and dolomites.
- Sierra de María and other mountains of its surroundings: substrates formed by carbonated materials, mainly composed by limestones and dolomites, which gives the terrain a clear-whitish ground color.
- Sierra de Gádor: substrate formed by limestones, with summits of a distinctive ochre-redish ground color.

Comparative morphology and notes about taxa described of *Pseudochazara williamsi* (Romei, 1927): Four taxa of „*Pseudochazara hippolyte*“ (Esper) have been described from Spain, which I will consider as ecotypes (isolated populations adapted to a particular set of environmental conditions), specifically as ecological forms since it is the conclusion determined at the end of this article. As the ecotypes have no main taxonomic rank in modern biological classification, without nomenclatural significance, I will refer to these from now on and along the entire article as "ecotype" followed by the old subspecific name given (this latter in quotation marks, as they are considered without taxonomic value), without it to entail any taxonomical or nomenclatural significance nor its validity, with the purpose to relate them easily with their distribution in the maps.

These ecotypes (see fig. 2 -upperside-, and fig. 3 -underside-), ecological forms, and by chronological order of description are:

- Ecotype "*williamsi*": described in Romei (1927: 138) with specimens from Sierra Nevada (Granada). Romei recognised that “the underside of the hind wings, which is of an almost uniform tinge in Eastern forms [Russia], is instead nicely variegated in Andalusia. Every Andalusian specimen differs in a striking way both from Russian types and others Oriental forms [Asia]“.

  - Fore wing length (base-apex, in a straight line): a range between 19 mm (dwarf specimens) and 26 mm (n = 50).
  - Upperside (fig. 2: 1-7): variable ground color, some specimens, are similar to those of the second and fourth ecotypes mentioned hereafter.
  - Underside (fig. 3: 1-8): variable and concordant with the geological characters of the terrain, whose color and substrate varies in the whole range occupied by the summit areas of Sierra Nevada (of almost 80 km in length). It will be discussed in more detail in the following section.
  - Populations of this ecotype (ecological form) exist in theSierra Nevada (see fig. 1), the Sierra de Filabres (extinct), and in the Sierra de Baza (studied here for the first time). These two latter (Sierra de Filabres and Sierra de Baza), are very similar in morphology and within the same variational range as those existing in the Sierra Nevada (on limestone substrate): postdiscal zone of the underside hind wings of a more clear or whitish color.

- Ecotype „*aislada*“: described in Eitschberger & Steiniger (1973) with specimens from Sierra de María (NE. Almería Province). In basis of its paler color, mainly in the underside of the wings (see the color of its type of geological substrate) with respect to the ecotype “*williamsi*”.
  - Fore wing length (base-apex): ranging between 22 mm and 26 mm (n = 33). Average size similar to the ecotype “*williamsii*” as well as to the following ecotype.
  - Upperside: fig 1: 20-24: the color of the fresh specimens is similar to the ecotype “*williamsi*”. In specimens freshly emerged, the ground color of the upperside is similar to the populations of other ecotypes.
  - Underside: fig. 3: 13-16: lighter color. Note: the ground color of the specimens are influenced (as well as by soil color, see types of substrates) by their aging. In this way, the specimens with more days of life mostly show a paler tone. This also occurs in other butterflies, eg. *Aricia morronensis* (Ribbe, 1910), which was discussed in Gil-T (2009).
  - Populations adscribed to this ecotype (ecological form): some mountains belonging to the Natural Park of Sierra María-Los Vélez and east of Sierra de Orce (W. Sierra de María, NE. Almería Province).
- Ecotype „*augustini*“: described in Weiss (1980) with specimens from the Sierra de Gádor (S. Almería Province). In comparison to the ochre ground color of the upperside (fig. 2: 25-30) and underside (fig. 3: 17-22) of both wings - note the geological substrate color type. The upperside of a certain number of specimens are very much alike to the ecotype “*williamsi*” as well as to the next ecotype mentioned („*reverchoni*“).
  - Fore wing length (base-apex): a range between 23 mm and 26 mm (n = 29). Average size similar to those belonging to the previous two ecological forms (ecotypes).
  - Populations placed to this ecotype (ecological form): limited only to Sierra de Gádor (S. Almería Province), mountains nearby (south) of Sierra Nevada
- Ecotype „*reverchoni*“: was described (“preliminarily”, sic!) very briefly in Tarrier (1993: 35) with specimens taken from Guillimona (NE. Granada Province) alleging: “race constantly inferior in size to all the other ones” and as “moderately coloured, intermediate between *aislada* and *augustini*”. Neither the holotype nor any of the paratypes are illustrated. Not indicated the number of paratypes (cited as “numerous specimens”, sic!). The colour reffered to in Tarrier (1993) is quite arguable, this may be seen in fig. 2 (8-19) and fig. 3 (9-12): the upperside of some specimens are much alike to the ecological forms „*williamsi*“ and „*augustini*“. The underside colouring, however, resembles the ecotype „*aislada*“.
  - Fore wing length (base-apex): individuals range between 19 mm (dwarf specimens) and 23 mm (n = 31). Although an aproximate 40% of specimens are similar in size to other ecological forms, the average size is somewhat smaller (fig. 4: ♀♀ of the four ecotypes, to the same scale). In fig. 5 we may see (♂♂ to the same scale) the major and minor sizes that I have observed in both „*williamsi*“ and „*reverchoni*“ ecotypes. The dwarf specimens are more common in „*reverchoni*“ ecotype
  - Populations adscribed to this ecotype (ecological form): in NE. Granada Province (see fig. 1): a)- Guillimona, where very probably is now extinct: the reasons of its probable extinction are mentioned in Gil-T (2016); b)- Sierra Seca, locality given to know in Gil-T & Ibáñez (2009); c)- a record from Sierra de la Sagra need confirmation, but if it really exists, it would undoubtedly be the same ecotype; and d)- W. Murcia Province: Revolcadores.

The external appearance of the specimens from Sierra Seca and Revolcadores (both are compared and studied in current paper for the first time) are morphologicaly identical to those of Guillimona.

The distribution and association to the four ecological forms previously referred to, may be seen in the fig. 6.

Are valid subspecies or only the expression of phenotypic plasticity? Discussion: Various authors have dealt with the possible reasons of the remarkable phenotypic variation shown in some species of *Pseudochazara*. Considering that this could be related with specific ecological requirements of these butterflies. Above all, in the wing color adaptation to prevailing substrate of the soil (geologic characteristics) of their habitats, thus obtaining an optimum mimetism with the terrain thanks to the wing patterns and their cryptic colouring. Mainly, since the underside of the wings are the most visible part of the body of the butterfly while at rest (Weiss, 1980; Tennent, 1993; Tolman & Lewington, 1997 and others).

Tennent (1993), with respect to the north African species *P. atlantis* (Austaut, 1905), affirms: „wether such differences warrant separation at ssp. level is a subjetive assessment but, since almost every population that the author has come across displays slightly different colouration, variants are probably most appropriately considered ecological forms rather than true subspecies".

Anastassiu et al. (2009) affirm respect to wing coloration of new discovered colonies of *P. graeca* (Staudinger, 1870): „intermediate between that of ssp. *graeca* and of ssp. *coutsisi*, clearly suggesting that a character cline is involved here, and that coutsisi cannot anymore be defined as a valid subspecies, but instead should be treated as an extreme form" and „that division of the taxon into two subspecies is inappropriate, and that the various wing colour schemes represent nothing else than forms".

Phenotypic plasticity is the ability of an organism to change its phenotype in response to changes in their environment. This is also defined as the capacity of a single genotype to exhibit a range of phenotypes in response to variation in the habitat. This capacity is supposed to be adaptive (Futuyma, 2013). We have seen the influence that the color and the geological structure of the soil produces on hind wing underside patterns. With respect to the size variation between several populations, we may say (generally speaking) that the ecological form „*reverchoni*" (population situated farther north) is slightly smaller. On the other hand, the populations situated southerly of the range of distribution of this species are larger in size. It is accepted that this variation in size is influenced by complex climatic factors, being the most important of all, the average starting date of the frost-free period and the average annual temperature in the region. Deriving in geographic forms that live under the specific micro-climatic conditions whithin their habitats. The butterflies living in southern habitats are usually larger than those living farther north because the favorable period for their development is relatively longer. The size variation is depends significantly on the average starting date of the frost-free period and annual average temperature in a given area.

Although the DNA barcoding may help to confirm the existence of certain subspecies, it seems that in the case of some species of *Pseudochazara* the genetic distance between the different species is neither relevant nor useful to clearly separate these and even less to clearly support the idea of different subspecies.

The key that can explain and support what is indicated about the appearance of these phenotypes, as well as to confirm that we are dealing with ecological forms can be found in the Sierra Nevada (mountains range of almost 80 km in length), where the genetic exchange between the populations *P. williamsi* (Romei) is not interrupted. In the Sierra Nevada different local forms appear, undoubtedly related to the different color and structure of the geological substrate. The underside of the hind wings, belonging to some of these forms, can be seen in fig. 7. Color and drawings that camouflage the butterflies with their environment. The wings (fig. 7: a-d) belong to populations located in calcareous summits, limestone and dolomite substrate compounds, the post discal area of the wings are paler, whitish; the wings (fig.7: e-f) belong to other distant population from the previous, found also on limestone substrate; and the wing (fig. 7: g) of a specimen belonging to the central zone of the Sierra Nevada, on dark slate-type rocky soils (siliceous substrate), with the background of the post-discal, discal and basal areas of the wing much darker.

Conclusion: For the reasons previously exposed, I consider that all *Pseudochazara williamsi* (Romei) populations should be considered (unless new molecular studies, DNA barcode, prove otherwise) as ecotypes, result of an important phenotypic plasticity in this taxon, better and specifically defined as local forms or ecological forms. Which adopt the degree of mimicry more adequate to camouflage with the terrain of their biotopes. These ecological forms are of no taxonomical significance, since there is no solid foundation justifying its subspecific validity.

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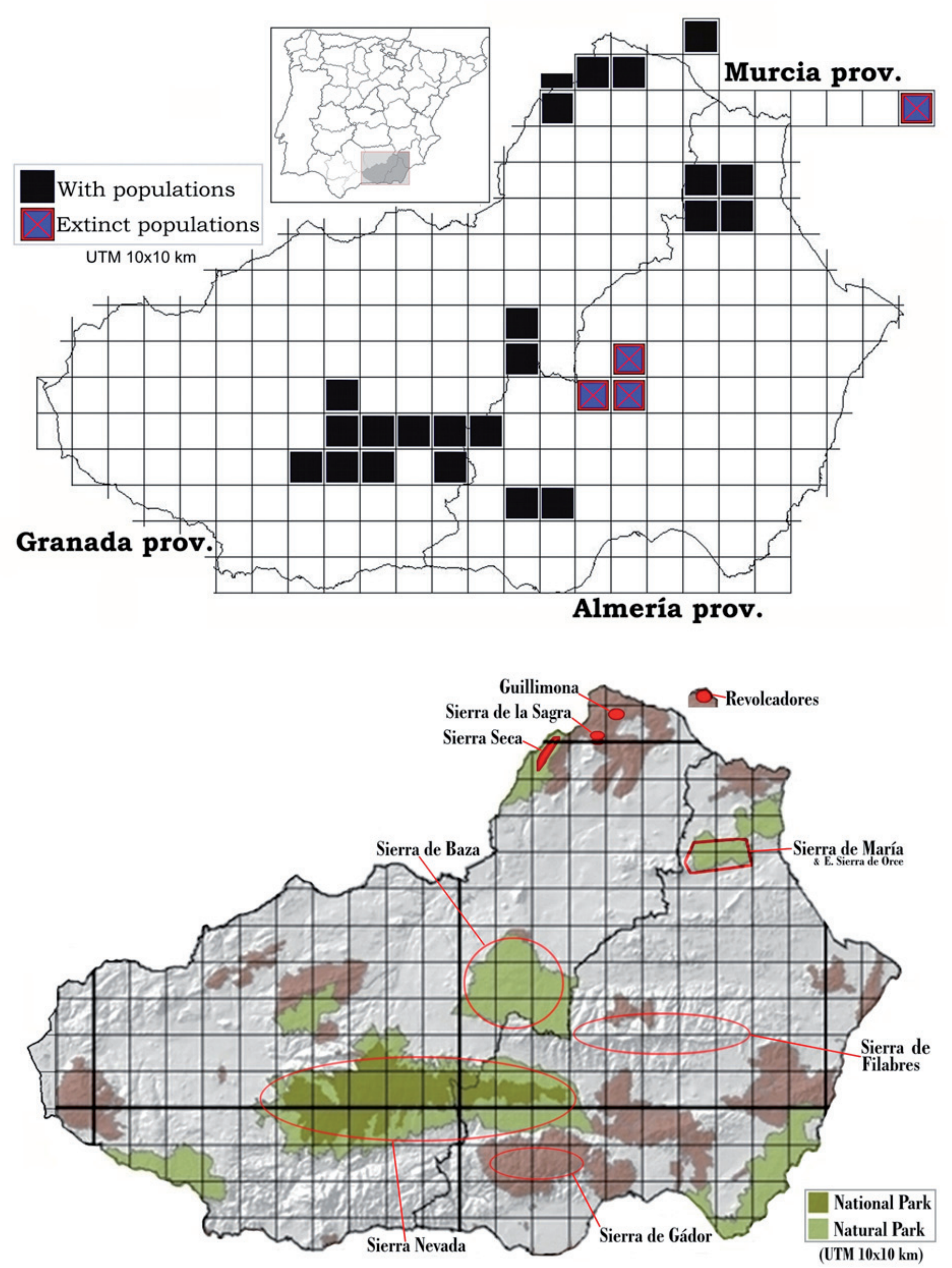

Fig. 1: Distribution of *Pseudochazara williamsi* (Romei, 1927) in Spain (SE. Iberian Peninsula).

Fig. 2: Upperside of the ecotypes (ecological forms) of *Pseudochazara williamsi* (Romei, 1927) : „*williamsi*“ (1-7); „*reverchoni*“ (8-19); „*aislada*“ (20-24); and „*augustini*“ (25-30).

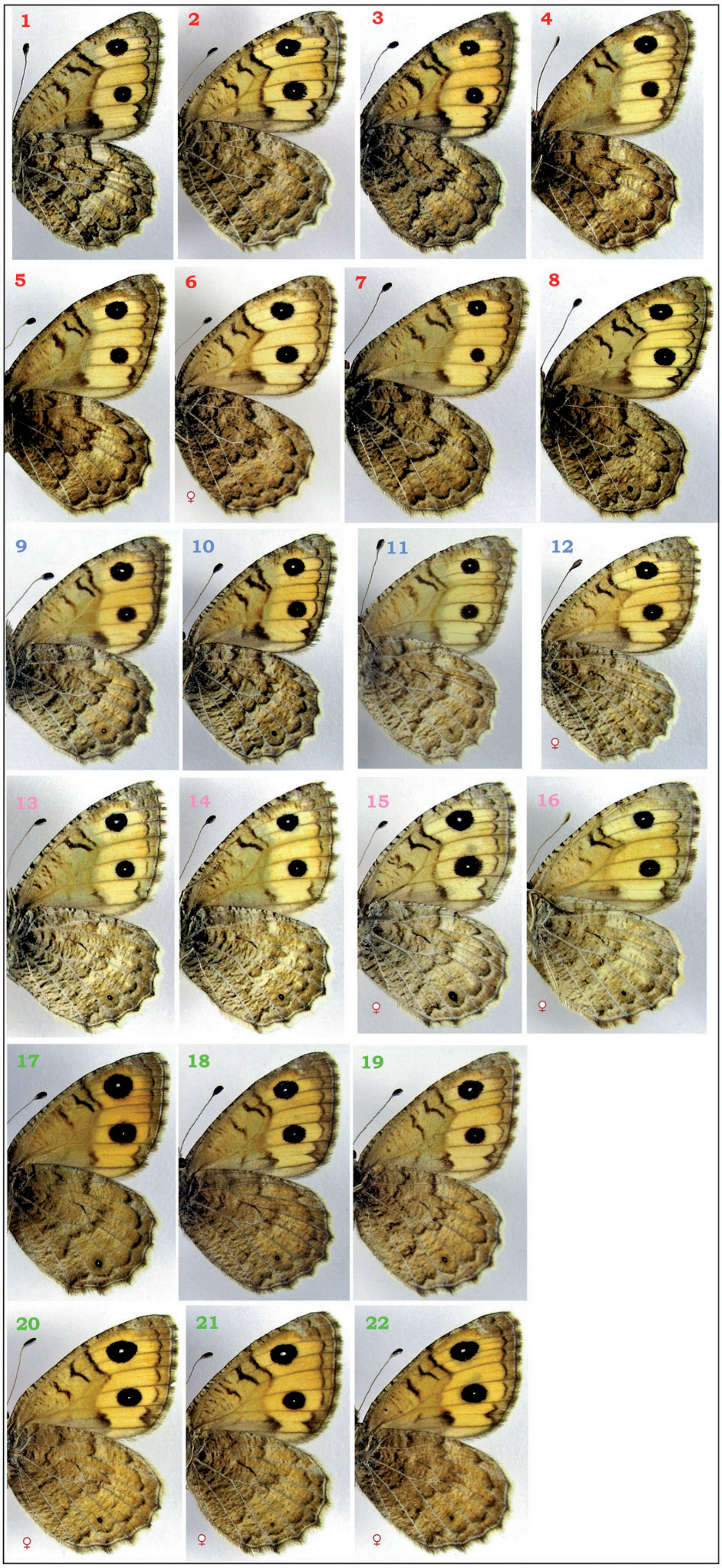

Fig. 3: Underside of the ecotypes (ecological forms) of *Pseudochazara williamsi* (Romei, 1927): „*williamsi*“ (1-8); „*reverchoni*“ (9-12); „*aislada*“ (13-16); and „*augustini*“ (17-22).

Fig. 4: ♀♀ (to same scale) of *Pseudochazara williamsi* (Romei, 1927), ecotypes (ecological forms): „*reverchoni*“ (A); „*aislada*“ (B); „*williamsi*“ (C); and „*augustini*“ (D).

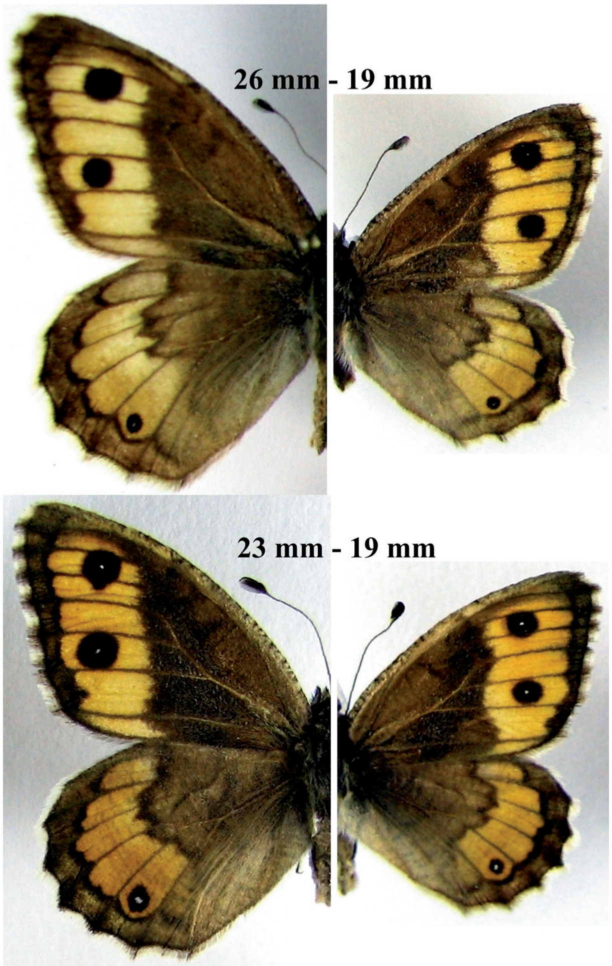

Fig. 5: Observed fore wing length (major and minor, in the same scale) in ♂♂, of the ecotypes (ecological forms) „*williamsi*“ (above) and „*reverchoni*“ (below).

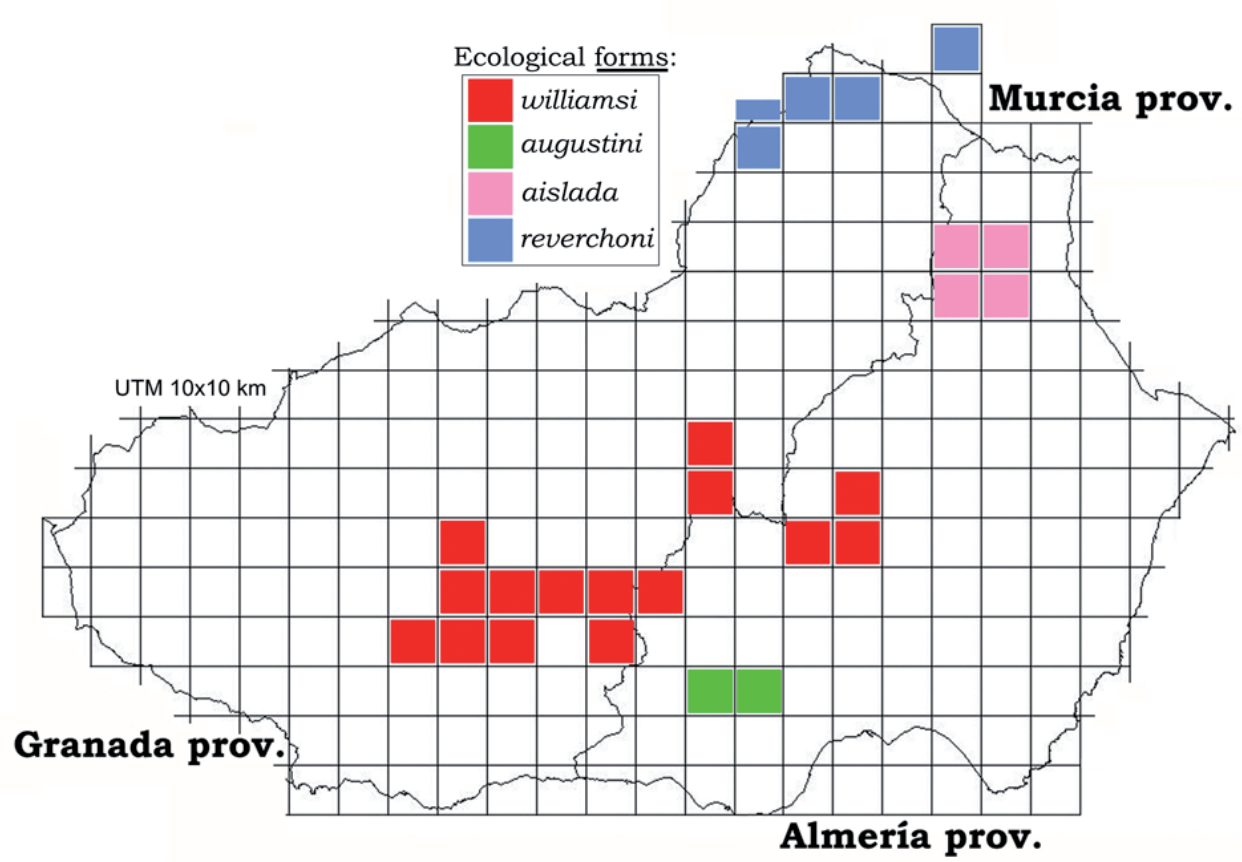

Fig. 6: Distribution and ascription of populations to the ecological forms of *Pseudochazara williamsi* (Romei, 1927).

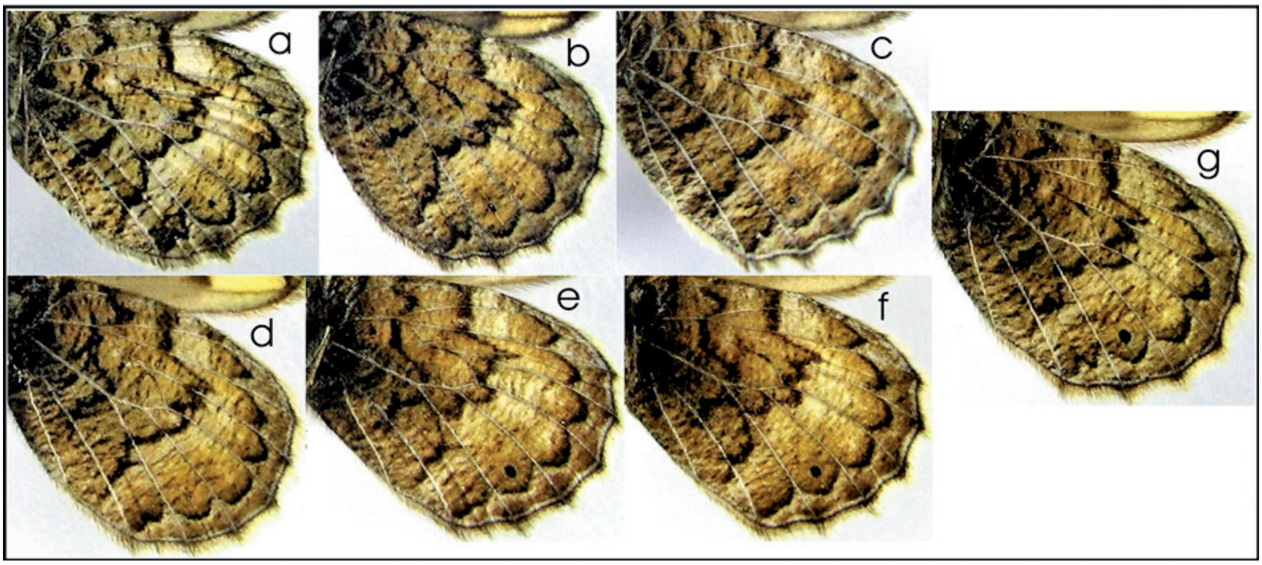

Fig. 7: Variation in the underside of the hind wings (color, drawings and background color) as an adaptation to the nature of the geological substrate: forms within of the ecotype „*williamsi*" (Sierra Nevada).

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