First record of an 'Alba' male in the supposed female sex-limited 'Alba' polymorphism of *Colias croceus* (Geoffroy in Fourcroy, 1785) (Lepidoptera, Pieridae)

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With 2 figures

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ABSTRACT: Within the scope of a butterfly survey on Porto Santo (Madeira Archipelago, Portugal), an 'Alba' male of *Colias croceus* was detected and collected. Although older literature sources report occurrences of rare 'Alba' colour morphs in males of other *Colias* species, for example, in *C. philodice*, recent publications consider the colour polymorphism of *C. croceus* to be strictly limited to females. The detected 'Alba' male of *C. croceus* will be described. The assumption that the 'Alba' polymorphism is based on a simple Mendelian inheritance in which sex determination and colour polymorphism are in complete genetic linkage is doubtful.

Keywords: Lepidoptera, *Colias croceus*, *Colias philodice*, colour morphs in males, Porto Santo, Madeira Archipelago, sex determination.

RESUMO: No âmbito de uma pesquisa de borboletas no Porto Santo (Arquipélago da Madeira, Portugal), foi detetado e coletado um macho 'Alba' de *Colias croceus*. Embora fontes mais antigas da literatura relatem ocorrências de raras formas de coloração 'Alba' em machos de outras espécies de *Colias*, por exemplo, em *C. philodice*, publicações recentes consideram o polimorfismo de cores de *C. croceus* estritamente limitado às fêmeas. O macho 'Alba' de *C. croceus* detetado é descrito. A suposição de que o polimorfismo 'Alba' é baseado em uma simples herança mendeliana, na qual a determinação do sexo e o polimorfismo da cor estão em completa ligação genética, é duvidosa.

Palavras-chave: Lepidoptera, *Colias croceus*, *Colias philodice*, formas de coloração nos machos, Porto Santo, Arquipélago da Madeira, determinação do sexo.

INTRODUCTION

About one-third of the approximately 90 species within the genus *Colias* (Lepidoptera, Pieridae) show a distinct pigment polymorphism in the female butterflies (Remington, 1954; Limery & Morehouse, 2016). Apart from the typically yellow / orange-coloured females, whitish-coloured females occur. In *C. croceus*, this form had been described as f. *helice* Hübner, 1779. Such forms are generally called 'Alba' forms. According to Remington (1954), this 'Alba' polymorphism is based on a simple Mendelian inheritance controlled by a single locus with two alleles, transmitted autosomally by both sexes, and dominant in the female but never expressed at all by males. Females which carry the dominant allele '*A*' have white wings, and homozygous recessive '*aa*' females exhibit yellow / orange wings like conspecific males. The phenotypes of males should therefore not show this 'Alba' polymorphism. Gerould (1911), Goldschmidt (1912), Hovanitz (1950), and Remington (1954) emphasised that this phenotypic manifestation is strictly 'sex-controlled'.

Lorkovics & Herman (1961) pointed out that white males in *C. croceus* do not occur, neither in nature nor in butterfly breeding experiments. Also, in recent publications concerning *C. croceus* (*e.g.*, Woronik & Wheat, 2017; Woronik *et al.*, 2018a, 2018b, 2019), the occurrence of 'Alba' forms in males had not been mentioned. In all these investigations, it is assumed that two colour morphs in females and one colour morph in males occur and that 'Alba' forms do not exist in males. The maintenance of the two female morphs is based on a balanced polymorphism. Woronik & Wheat (2017) identified the locus that causes the colour polymorphism in *C. croceus*. Further aspects on physiology and life-history strategies as well as further investigations on the genetic basis of this polymorphism can be found in Woronik *et al.* (2018a, 2018b, 2019) and provide conclusive and remarkable results. In all these publications, however, the occurrence of male 'Alba' forms in *C. croceus* is not discussed.

The phenomenon of colour polymorphism in the *Colias* species with two different female colour morphs (orange / white) and one male colour morph (orange) was first detected by Gerauld (1911) for *C. philodice* (Godart, 1819). Later, this could also be demonstrated for other *Colias* species for North America (*C. eurytheme* (Boisduval, 1852); *C. interior* (Scudder, 1862); *C. christina* W. H. Edwards, 1863) and for Europe (*C. edusa* (Geoffroy in Fourcroy, 1785); *C. myrmidone* (Esper, 1780); *C. hyale* (Linnaeus, 1758)); see Gerould (1923) and Remington (1954).

Gerould (1911) pointed out for *C. philodice* that white males can occur in extremely rare cases. The author expected white males especially in areas with a particularly high number of white females (around 50%). One white male of *C. philodice* was observed in nature by W. L. W. Field (Gerould, 1911). Initially, 'Alba' forms in males were interpreted as recessive homozygotes, but they never appeared in breeding experiments ('among the 900 descendants of white females that I have raised, there has been not one white male'; Gerould, 1911). Gerould (1923) interpreted the white males as the result of a mutation in which the orange colouring is replaced by white pigments. According to Goldschmidt (1912), white males of *C. philodice* are only present after mutation, regardless of the genes that determine the colouration of the females. The possibility of a spontaneous loss of melanic colour (amelanism), yellow / orange colour (axanthism), or both (albinism) should be considered.

In the recent past, a white male of *C. philodice* was collected in West Lafayette, Tippecanoe County, Indiana, USA, by Alex Bic (16 September 2010), and a photo was published on the internet platform BugGuide on 4 April 2011 (http://bugguide.net/node/view/503074). However, no evidence of a male 'Alba' form in *C. croceus* was found in the literature.

MATERIAL AND METHODS

Porto Santo (42 km^2) is of volcanic origin, with an age of about 11.1 to 14.3 Ma, and is located about 40 km north-east of Madeira Island (Geldmacher *et al.*, 2000), separated by an ocean bed with more than 2,000 m depth. The highest peak is the Pico do Facho (517 m *a.s.l.*), geologically (as well as other summits of the island) mainly characterised by trachytic and basaltic structures. About one-third of the island is covered with quaternary sediments. According to Rivas-Martínez (2009), the bioclimate is classified as Mediterranean xeric-oceanic with significant summer aridity. Only the highest regions have a mesic xeric bioclimate.

The butterfly species (Papilionoidea) of Porto Santo (10 species, 204 individual observations) were mapped during visits in 2012 (16-20 March) and 2017 (19-31 March) by A. Kratochwil and A. Schwabe (Kratochwil *et al.*, 2018) on the basis of 1 km x 1 km grids. The 45 sites reflect the most important habitat types of the island (Kratochwil & Schwabe, 2018). Our observations demonstrated that *C. croceus* is

quite common throughout Porto Santo from sea level up to the highest mountains (38 sites; Figure 1 in Kratochwil *et al.*, 2018). *C. croceus* is euryanthic and could be detected on the flowers of 10 plant species belonging to 7 plant families (Kratochwil *et al.*, 2018).

RESULTS AND DISCUSSION

In the course of the butterfly monitoring, 77 detections of *C. croceus* were made. Among them, an 'Alba' female and an 'Alba' male were detected. Figure 1 shows the female orange form and the female white form of *C. croceus*. The hind wings of the 'Alba' female are dark coloured. Figure 2 shows an orange male and the detected 'Alba' male. The lower part of the forewing of the 'Alba' male and the basal part of the hind wing are characterised by a slightly orange tinge. The hind wings are dark coloured, similar to the 'Alba' form of the female. The sex can also be provided by the conspicuous scent scales (androconia) near the wing base in cell 7 of the hind wings, which are restricted to males (Fig. 2). In addition, aberrations of *C. croceus* females where the yellow spots are missing in the black outer band (ab. *pseudomas* Cockerell, 1889) as well as '*helice*' forms of ab. *pseudomas* (ab. *nigra* Aigner, 1906) were described; see Grieshuber & Lamas (2007).

Aguiar & Karsholt (2006) reported that *C. croceus* females var. *helice* (Hübner, 1879) were frequently seen on Porto Santo (5%-10% of all populations). In the Museu de História Natural do Funchal, three females of the form '*helice*' are deposited, collected in May 1942 (unknown collector, determined by J. T. Smit in 1998), as well as two females of the same form, collected on 30 March 1988 by F. Zino (determined by J. T. Smit in 1998).

A classification of *C. croceus* into pure orange and pure white colour morphs in females is not always possible in this strict manner. Usually, the name 'Alba' or form '*helice*' in the broader sense includes all bright forms (white to yellowish wing colours). *C. croceus* shows specimens of different colour intensities and colour tones throughout its distribution area, which had been listed as forms, varieties, and aberrations. Grieshuber & Lamas (2007) mentioned 120 aberrations, 40 forms, and 7 varieties for *C. croceus*, which had been described and published by different authors. Although the International Code of Zoological Nomenclature does not consider names below the subspecies level, such forms, varieties, and aberrations are elements of the phenotypic variability of a taxon. Even if one has to assume that homonyms are among them, excluding homonyms should be possible

in many cases. Usually, in the case of *C. croceus*, these differences are shown in the colour of the wings. Such wing colour patterns, based on phenotypic plasticity, may be produced physiologically in response to environmental stress (*e.g.*, temperature, general stress response) and may also be genetically fixed in a population (Otaki *et al.*, 2010). This was shown particularly for the genus *Vanessa* (Hiyama *et al.*, 2012).

In the Madeira Archipelago, *C. croceus* females occur in numerous varieties (Salmon & Wakeham-Dawson, 1999), all of which are characterised by different colouration: for example, var. *cremonae* Verity, 1911; var. *dawsoni* Bollow, 1930; var. *geisleri* Bryk, 1923; var. *radiata* Nitsche, 1932; and var. *faillae* Stefanelli, 1900.

Limeri & Morehouse (2016) indicated that the ancestor of the Coliadinae was already polymorphic and that 'Alba' polymorphisms occurred. The Coliadinae include 203 taxa, and about half of the species are polymorphic in females (46%). In some cases, this polymorphism has repeatedly given rise to a monomorphism. The repeated loss of the polymorphism indicates that the 'Alba' polymorphism has a certain evolutionary instability (Limeri & Morehouse, 2016; Jamie & Meier, 2020).

Many studies have been carried out on the 'Alba' polymorphism in *Colias*. Descimon (1966) and Watt (1973) discovered the origin of the colour change by analysing the underlying differences in pteridine wing pigment synthesis. Graham *et al.* (1980) and Gilchrist & Rutowski (1986) found, for instance, different metabolism rates and fat body sizes as well as analysed the fecundity rates, the number of eggs per day, the survival probabilities of the eggs, and the lifespan lengths while comparing the two female colour morphs. They pointed out that concerning these parameters, the white colour morph in females is selectively advantageous compared with the orange morph. 'Alba' females may also benefit from their mimetic and cryptic colouration towards predators (Gilchrist & Rutowski, 1986). Nevertheless, white butterflies are not always advantageous in selection because certain biotic and abiotic factors have contrast-selective effects (Hovanitz, 1950; Nielsen & Watt, 2000). Thus, white females are less attractive to males (Graham *et al.*, 1980), and males show less courtship persistence with white females (Marshall, 1982). The transfer of nutrients by spermatophores is also much lower in 'Alba' females than in yellow / orange females, owing to the lower number of mating males (Boggs & Watt, 1981). In particular, if other white butterfly species are present, this would be unfavourable for partner interactions of these *Colias* species. In mark-release-

recapture experiments, GILCHRIST & RUTOWSKI (1986) showed in *C. eurytheme* that 'Alba' females have longer residence times than orange females who emigrate for reasons of male harassment.

The two female colour morphs show different temperature-dependent development rates (GRAHAM *et al.*, 1980; NIELSEN & WATT, 2000). Thus, 'Alba' forms in females of *C. croceus* have higher fitness under cold conditions, orange forms under warm conditions (WORONIK *et al.*, 2018a). 'Alba' phenotypes are more common in the distribution area of their species in the northern parts or at higher altitudes (GERAULD, 1923; HOVANITZ, 1944a, 1944b, 1950; REMINGTON, 1954) of the region. In contrast, 'Alba' females absorb less solar heat than orange females and avoid overheating (WATT, 1973; KINGSOLVER, 1983; KINGSOLVER & WATT, 1983).

There exists no doubt that in the case of *C. croceus*, 'Alba' forms can also exist in males. However, the interrelationships here seem to be much more complicated than previously assumed in the literature. The question arises of whether comparable examples exist in other animal groups and, if so, what solutions occur.

Cichlid fishes form a model system in which colour polymorphism has been studied in detail for vertebrate taxa. For example, a cryptic morph can be commonly observed in female cichlid fishes (ROBERTS *et al.*, 2009). In rare cases, such polymorphisms are also found in male fishes, where they, however, disrupt the nuptial colouration. This scenario creates a sexual conflict as the polymorphism constitutes a selective advantage for females (camouflage) and a disadvantage for males (nuptial signal). According to ROBERTS *et al.* (2009), this sexual conflict is resolved by a strong linkage between the colour polymorphism locus and a novel sex-determining locus.

If these findings are compared with those of *C. croceus*, similar relationships might be found. The polymorphism will usually be accompanied by considerable advantages for the females. In *Colias*, for instance, adaptations to different climatic conditions and metabolic performance are influenced by these conditions. In the males, however, polymorphism makes little sense because only the orange phenotype seems essential for mating behaviour. Male UV colouration in *C. eurytheme* and other sulphurs, for example, *C. croceus*, is important for species recognition and sexual identification (SILBERGLIED & TAYLOR, 1978; RUTOWSKI, 1985). The wings of the males and females of *C. eurytheme* contain the pteridine pigments described by WATT (1964, 1967): xanthopterin (yellow), leucopterin (colourless), sepiapterin (yellow / orange), and erythropterin (red). Compared with the yellow / orange

female in 'Alba' forms, xanthopterin, sepiapterin, and erythropterin are reduced, but the colourless leucopterin is increased. The concentration of sepiapterin is determined by a single gene locus and a multiple-allele system (WATT & BOWDEN, 1966).

Because of their role in colour signal production in the male of *C. eurytheme* and other sulphurs, pteridines, in combination with multilayer thin-film nanostructures and broadband scattering features, may themselves provide important information for females in the mating process (RUTOWSKI *et al.*, 2005). It is supposed that in contrast to orange males, white 'Alba' males should always present a selective disadvantage, especially in the choice of a partner. The maintenance of the 'Alba' type over evolutionary time scales could be explained by the selection for tight linkage between the 'Alba' locus and the sex determiner locus. Unfortunately, 'Alba' males in *C. croceus* occur only in extremely rare cases, so clarifying the genetic basis would be difficult.

In addition to the importance of wing colouration for mating behaviour, the wing pigments, the morphological wing structures, and the position of the wings to sunlight are of great importance for thermoregulation. KINGSOLVER (1987) investigated the role of pteridine pigments and melanin patterns for thermoregulation in pierids. In the subfamily Coliadinae, the ventral melanin patterns of the hind wing bases are decisive for thermoregulation; in Pierinae, it is the entire dorsal wing surface. The whitish colouration of the Pierinae caused by leucopterin and isoxanthopterin is also found in the 'Alba' forms of *Colias*. For thermoregulation, the Coliadinae close all their wings ('lateral basking position'), whereas the Pierinae leave their wings open with different opening angles to regulate the intensity of reflection ('reflectance basking position'; KINGSOLVER, 1985). This phenomenon in Pierinae is phylogenetically derived (KINGSOLVER, 1987). However, the reflectance basking position only makes sense with pigments of bright wings. Nonetheless, the 'Alba' forms in *Colias* seem just as effective in thermoregulation as the orange forms via the method of 'lateral basking' (WATT, 1973).

It is inspiring to find such an extremely rare butterfly individual in one of the smaller islands of the Atlantic Ocean with mostly semi-arid conditions.

Fig. 1 – Orange female (left) and 'Alba' female (right) of *Colias croceus*, collected on Porto Santo Island (Madeira Archipelago), east of Capela de São Pedro, 31 m, N 33° 02' 49.5" W 16° 21' 32.5", 21 March 2017.

Fig. 2 – Orange male (left) and 'Alba' male (right) of *Colias croceus*, collected on Porto Santo Island (Madeira Archipelago), east of Capela de São Pedro, 31 m, N 33° 02' 49.5" W 16° 21' 32.5", 21 March 2017, and north Serra de Dentro, 70 m, 33° 05' 14.6" – 16° 18' 33.5", 21 March 2017.

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