

**COLIAS ELECTO ELECTO L. AB. CAPENSIS AB. NOV. (LEP.: PIERIDAE):
A NEW ABERRATION OF THE AFRICAN CLOUDED YELLOW FROM
THE CAPE, SOUTH AFRICA**

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Abstract

A new aberration *Capensis* of *Colias electo electo* L. (Lep.: Pieridae) is described and illustrated.

Introduction

Colias electo L. is one of the commonest and most widespread of African butterflies. It can usually be found throughout the year in most of its range and apparently lacks a diapause at any stage. Seven subspecies have been described: the nominate *electo* (Linnaeus 1763) from South Africa, Namibia, Botswana and Zimbabwe; *hecate* (Strecker 1900) from North Angola, West Africa and Congo; *pseudohecate* (Berger 1940) from East Africa, Sudan, Ruanda-Urundi, south and east Abyssinia and Somalia; *meneliki* (Berger 1940) from north and central Abyssinia and Erythrea; *mukana* (Berger 1981) from Zaire (and Malawi ?); *manengoubensis* (Darge 1968) from Cameroun; and *philbyi* (Berger 1953) from Saudi Arabia.

In the Western Cape Province of South Africa, which has winter rainfall with cool weather, the typical winter form of the adult is smaller (38 mm) than the summer form (45mm) and has a darker underside. Also, the wing bases are often darkened on their upper sides. In the Western Cape, the spring and early summer rainfall, together with artificial irrigation, provoke rapid growth of larval foodplants, cultivated lucerne and clovers, and there is a resultant massive population increase of *C. electo*. Elsewhere, in the Orange Free State, Natal and Transvaal, it is the summer rainfall which triggers this increase in population. Under these ideal conditions, the adults are larger and more brilliant, and lack the darker scales on their undersides. At certain times, millions of adults can be seen swarming in lucerne fields, particularly in areas of sheep and ostrich farming where lucerne and clovers are grown for fodder. When drought conditions occur in summer, the size of the adult butterfly is variable and depends upon the amount of food eaten as a final instar larva. Miniature adult specimens can often be found measuring only 32 mm.

C. electo exhibits pronounced sexual dimorphism. In ssp. *electo*, the ground colour is orange (yellow + red = orange), but in ssp. *hecate* and ssp. *mukana* the ground colour of the "coloured" female can be predominantly lemon yellow (i.e., lacking red pigment). The areas of lemon-yellow ground colour in the females of ssp. *hecate* can be variable in size, particularly in northern Angola, but in females of ssp. *mukana* these yellow areas are restricted to the hind wings. Both fore and hind wings have broad black marginal borders, which are unbroken in the male, but in the female they contain spots of lemon yellow.

Both sexes have a dark discocellular spot near the centre of the forewings. In the male this DFW discocellular spot is highly iridescent. If a light source is adjusted to the necessary angle, the black scales of the DFW discocellular spot change colour to a metallic navy blue. These iridescent "blue" scales are generally absent from the dark border, but occasionally one or two occur along the inner edge of the black border. Blue scales are never present on the ventral surface. Females appear either to completely lack these metallic blue scales or to have just one or two.

Males have a sex brand on the upperside hind wing, near the costa and near to the base in s7. This sex brand is covered with long and short oval, scent-bearing scales, which differ greatly from normal wing scales.

As with many members of the genus *Colias*, the female of *C. electo* is dimorphic, occurring in the typical orange form and in a white form. The latter, (f. *aurivilliusi* Keferstein) occurs in varying percentages throughout the year and is genetically controlled, behaving as a dominant to the common orange form in a balanced polymorphism.

Variation in the female mainly concerns the lemon-yellow spotting of the dark border, which may be reduced or absent, variation in size and colour of the VHW discocellular spot (this has a larger and an adjacent smaller pupil) and reduction in grey scales of both fore and hind wing. The ground colour can also vary from the normal orange through a range of intermediates to yellowish white. A large number of female forms have been described, as follows:

<i>C. electo electo</i> Linnaeus	f. <i>aurivilliusi</i> Keferstein 1882
	f. <i>overlaeti</i> Berger 1940
	f. <i>kostlani</i> Strand 1911
	f. <i>flavescens</i> Eisner 1963
<i>C. electo hecate</i> Strecker	f. <i>bunda</i> Berger 1940
	f. <i>elizabethae</i> Berger 1940
	f. <i>katangae</i> Berger 1940
<i>C. electo pseudohecate</i> Berger	f. <i>licina</i> Berger 1940
	f. <i>lecerfi</i> Berger 1940
	f. <i>splendens</i> Berger 1940
	f. <i>millari</i> Stoneham 1957
	f. <i>africana</i> Stoneham 1957
	f. <i>ambreana</i> Stoneham 1957
	f. <i>dormonti</i> Dufrane 1947
	f. <i>fontenai</i> Berger 1980
<i>C. electo meneliki</i> Berger	f. <i>bafanae</i> Berger 1940

Although slight variation of the ground colour does occur in males of *C. electo*, pronounced variation in the male is extremely rare. Named forms of the male are usually extreme melanics such as f. *eremna* Vari (1976) or the very beautiful violet

and fuscous brown f. *elysium* Kroon (1985) taken in the Orange Free State, South Africa. Another rather worn example of this very rare melanic can be seen in the British Museum Collection, cabinet 42, drawer 142. The specimen is also from South Africa and was collected by A. Duncan at Groote Schuur, Rondebosch, Cape Town, in August 1901. A buff-coloured male, f. *pauper* Berger, is described from Saudi Arabia (Berger 1953). An albinistic male was illustrated in Pennington (Dickson & Kroon, 1978) but this insect has hind wings which are partly orange and therefore it is not a typical "white male". White males have been recorded from several species of *Colias* but not yet from *C. electo* (Remington 1954). These white males may be genetically unrelated to the sex-limited white forms of *Colias* females.

Males with the sex-limited colouration have always been of interest to geneticists. Cockayne (1932) suggested that such males could not be produced unless some abnormal occurrence takes place during cell division. He also proposed that the white colour was due to a defective development of the scales. This was, of course, incorrect. Although Cockayne stated that he had never examined any of these white males, he suggested that they probably have very thin scales, rolled up and devoid of pigment. This description does suggest that he had examined some insects exhibiting such deformities (perhaps similar to ab. *capensis*?).

The colour of orange *Colias* involves the largely independent synthesis and deposition of orange-producing pigments (red + yellow) within the coloured scales, which gives rise to the orange or yellow colours by the differential reflection/absorption of the various wavelengths of white light. In contrast, the UV iridescence (not reflectance) is the result of the structuring of a cuticular interference filter, of necessarily small dimensions, on the upper cuticular surface of the dorsal cells. The pinkish-violet or lilac flash which can be seen on the wings of fresh males arises from the fact that the long-wavelength tail of the UV spectral distribution of the flash extends into the violet end of the visible spectrum where our eyes can pick up the tail. *C. electo* males and females have both fore and hind wings strongly iridescent. Mate selection is up to the female, and males lacking a proper UV signal are usually rejected. White females of the genus *Colias* never show UV iridescence even in those species in which non-white females are as brilliantly iridescent as their males.

Discovery

In mid-November 1987, while harvesting barley on a farm near Riviersonderend, Cape Province, L. McLeod noted that a high percentage of the male *C. electo* which were entering the field from the foothills of the Riviersonderend Mountains, were of an unusual pale form. It was estimated that 10% of the population were of this unusual form, greatly lacking the normal orange ground colour. When in flight these unusual males somewhat resembled normal females because of the greenish-yellow colour of the underside hind wings, and this resulted in normal males giving chase. A closer inspection of some of the butterflies feeding on flowers of the thistle *Berkheya rigida* (Thunb.) indicated that the differences were substantial and

relatively constant. Consequently, during a brief lunch break, two of these pale-coloured males and a miniature example of an extremely unusual white form of the female were collected. Further examination of these specimens confirmed that they were indeed extremely unusual and that the population was worthy of further investigation.

Unfortunately the area was not visited in 1988, but in November 1989 L. McLeod again visited the locality, this time armed with a net. As previously, the unusual form was present, although in fewer numbers, and twenty specimens, both male and female, and some being of poor quality, were taken. Both the 1990 and 1991 seasons experienced severe drought and the lack of larval food plants caused a population crash resulting in only a few normal *C. electo* being seen. Throughout the Western Cape cultivated lucerne and clovers were harvested early because of lack of food for sheep.

In 1992, rains were frequent in spring and continued into summer. In mid-November a large population of *C. electo* was to be seen with approximately 1% f. *capensis*. A good series was taken and the consistent characters of the aberration were confirmed. During the period 1992 to 1999, the studies of this interesting aberration continued and several breeding programmes were undertaken without successfully reaching a conclusion concerning its genetics. Wild-caught female ab. *capensis* produced only typical forms and no aberrations appeared in the F1 and F2 generations.

The existence of this aberration was first mentioned in the 2nd Edition of Pennington's Butterflies of Southern Africa (Pringle, Henning & Ball 1994) page 281.

Colias electo electo ab. *capensis* ab.nov.

This is a very complex phenotype, all aspects of which are expressed as a malformation of scales, both in terms of pigment deposition and in proper cuticular structuring. The range of variability suggests that homozygotes and heterozygotes are present in some sort of semi-dominant mutation.

Holotype ♂: Riviersonderend, Cape, South Africa 08.X.93. (L. McLeod). In the British Museum (Natural History) collection.

Paratype ♂♂: a series from the same locality. One specimen in the British Museum (Natural History) collection and the remainder in the collection of L McLeod.

Scales of the DFW of all males lack the normal compliment of orange pigment, some retaining traces and others being completely transparent. In the latter examples, most of the normally orange scales are grossly deformed in shape, being rolled on their long axes. Scattered scales also show this deformation in those individuals with slightly reduced orange pigment.

Ventrally, the principal phenotypic difference is the "grey" submarginal apex and outer border of the FW. This is caused by the depigmentation of the scales of both the upper and lower layers and occurs in 8-15 scale rows back from the fringe. What

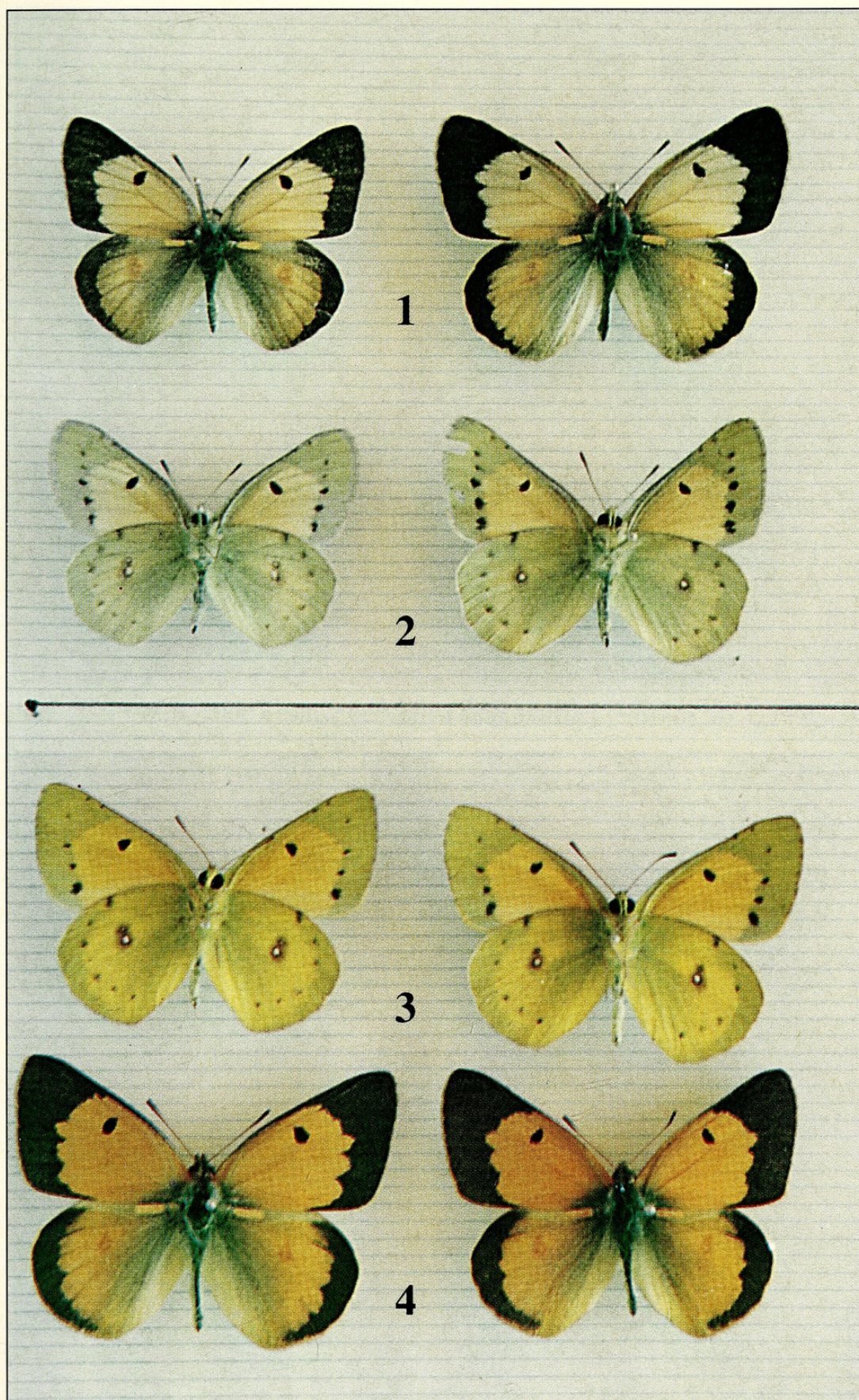


Plate N. *Colias electo electo* L. 1. ab. capensis ab. nov. upperside ♂; 2. ab. capensis ab. nov. underside ♂; 3. typical form underside ♂; 4. typical form upperside ♂.

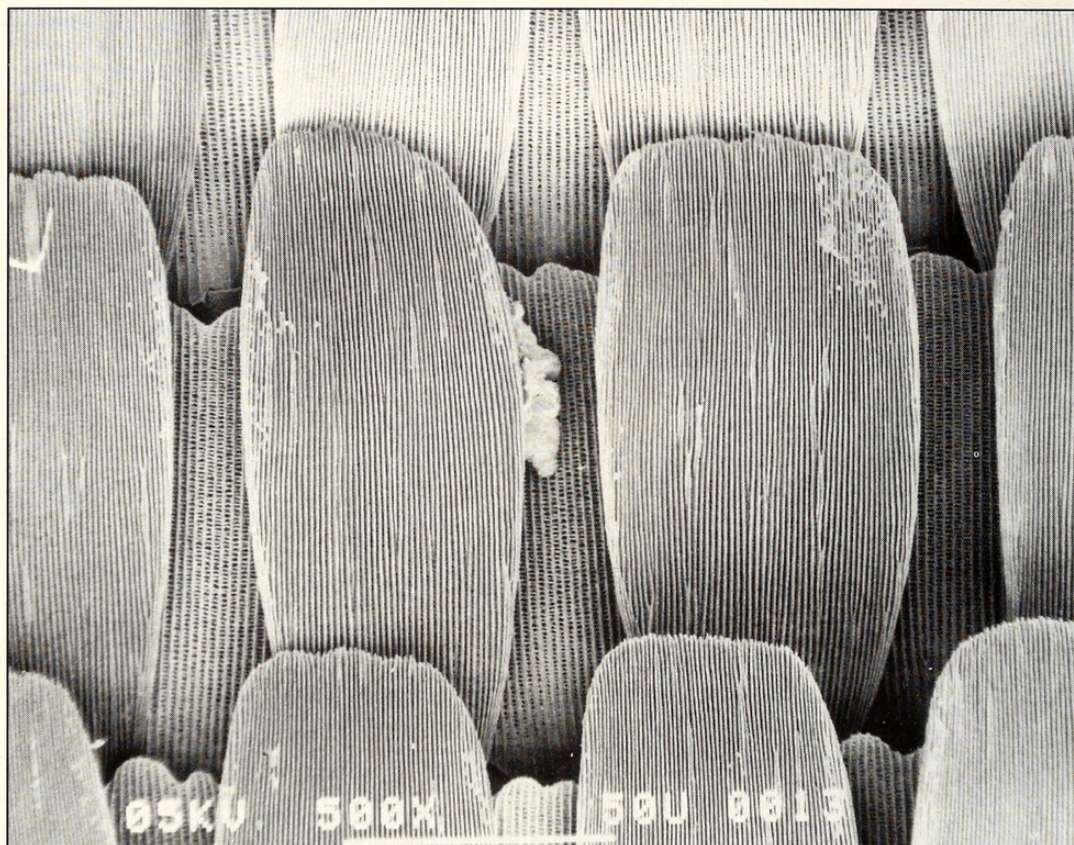


Plate O. *Colias electo electo* — normal male iridescent scales x 500 (SEM)

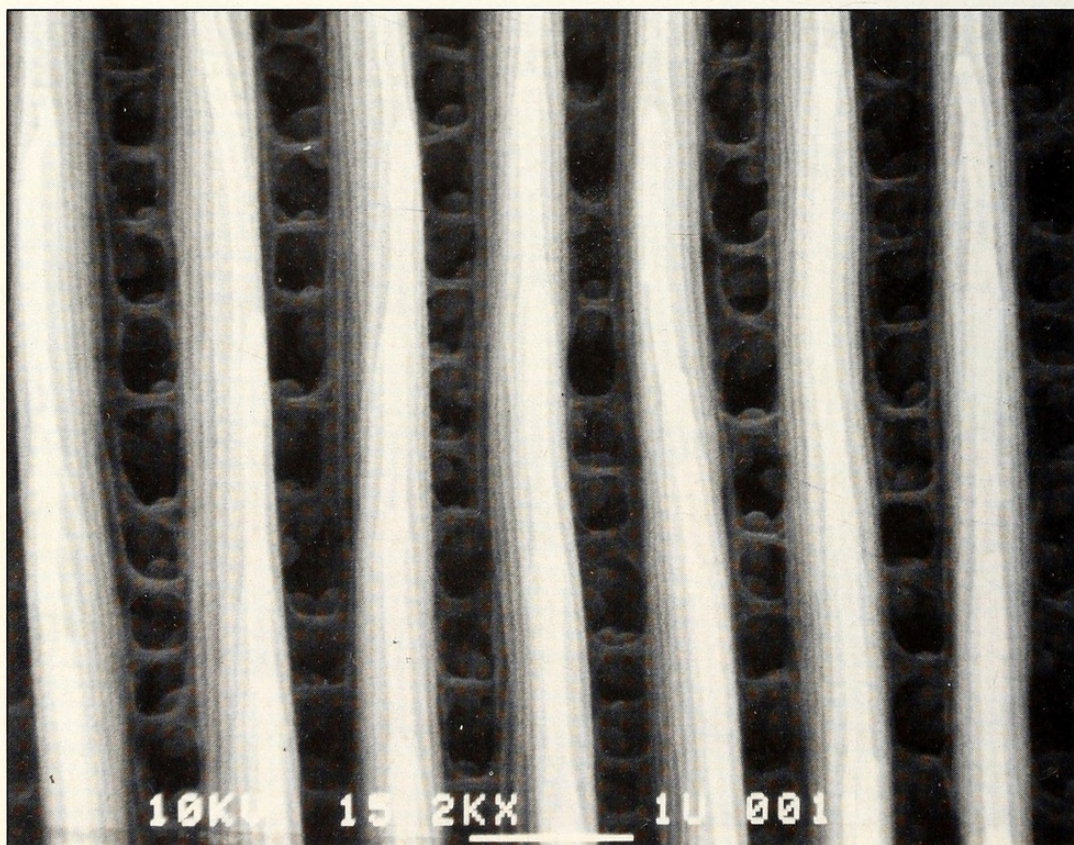


Plate P. *Colias electo electo* — normal male iridescent scales x 10,000 (SEM) Longitudinal ridges with interference mirrors.



Plate Q. *Colias electo electo* ab. *capensis* — male iridescent scales x 100 { SEM } Note the large proportion of deformed UV scales.



Plate R. *Colias electo electo* ab. *capensis* — male iridescent scales x 5010 (SEM) Note the malorientation of longitudinal ridges.

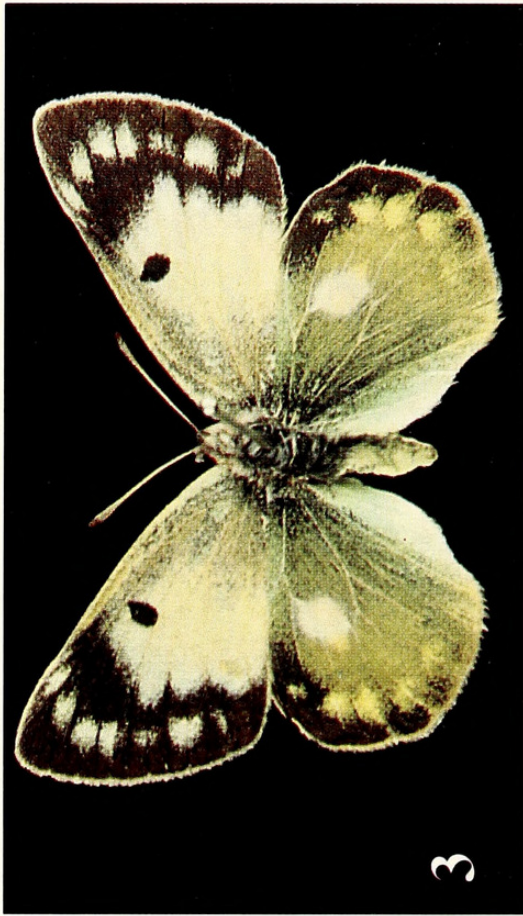


Plate S.

- 1. *Colias electo electo* f. *aurivilliusi* ab. *capensis* ♀ underside
- 2. *Colias electo electo* ab. *capensis* ♀ underside

- 3. *Colias electo electo* ab. *capensis* ♀ upperside
- 4. *Colias electo electo* ab. *capensis* ♀ underside

the eye sees as a grey border is the translucent wing membrane showing through. Some examples of ab. *capensis* lack this grey border and thus its presence and width do not correlate with the other distinguishing characters. The fringe itself is lacking the normal pink colouration, which is so obvious in normal specimens. This pink colouration can best be seen in the chrysalis stage just prior to eclosion. In ab. *capensis* the fringe is grey. The body hairs, the antennae, and the tibio-tarsal portions of the legs, which are pink in normal specimens, are cream in ab. *capensis*.

A further significant character is the colour of the ventral surfaces, which is greener than in males of typical *C. electo*. This may possibly be a result of the reduction in the red pigment, which is present ventrally along with the yellow and melanin (yellow + melanin = green). To the eye, the ventral surface appears to be a paler yellow than typical *C. electo*. The male sex brand of ab. *capensis* is of a bright cream colour.

In males of ab. *capensis*, iridescence appears to be correlated with the level of scale malformation, which affects the interference filters of the cuticle. Thus iridescence may be strong or weak in areas where scale malformation is scattered, and can also be limited in distribution to areas which do not exhibit malformation of scales, such as strips along the posterior margins of the forewings, or the area of the discocellular spot, which can be both brightly pigmented and intensely iridescent. The UV flash in ab. *capensis* appears to be lilac/violet when compared to the pink/red of typical *C. electo*, but because the flash is never strong in the former, this observation may be unreliable. The UV wing patterns as seen by the insects themselves must be extremely variable in ab. *capensis* and one can only guess at the effect of this on courtship and mating.

Allotype ♀: Riviersonderend, Cape, South Africa 08.X.93 (L. McLeod). In the British Museum (Natural History) collection.

Paratype ♀ ♀: A series taken from the same locality. In the collection of L. McLeod.

Females of ab. *capensis* exhibit similar scale deformities and reduction of pigmentation as described for males, but the range of variation is more extreme. In the majority of females, pigmentation is greatly reduced and the DFW and DHW are generally of a pale salmon-pink (somewhat dirty looking) and the dark borders are less pronounced. Other examples exhibit only a partial reduction of orange pigmentation accompanied by a yellow suffusion on the DHW. A few show hardly any reduction at all of orange pigmentation. The pink colour of the fringe, tibio-tarsal portions of the legs, and the body hairs, is lacking and the VFW grey borders can be pronounced or not, again not correlated with the scale depigmentation and deformation.

The VHW shows a much more extreme change of ground colour and is generally green. There is nevertheless a degree of variation in the ground colour, some specimens being a most extraordinary vivid turquoise and others a dark yellow. In female ab. *capensis* there is a tendency to be combined with ab. *radiata*, the latter sometimes being very pronounced. The discocellular spot of the female DHW also

exhibits some colour changes in *ab. capensis* and can range from the bright orange of the typical form, through salmon-pink, pale pink, cream and white. This variation may also accord with the idea of homo- and heterozygotes.

In the white female form of this aberration, *f. aurivilliusi ab. capensis*, the ground colour remains white, as in the typical *f. aurivilliusi*, thus the depigmentation does not appear to affect the presence of leucopterin. However, the grey borders of the VFW are present (in the only three specimens taken) and are very prominent at the apex, completely separating the lemon yellow patches from the fringe. In the typical form, the lemon yellow patches reach the bright pink fringe without being separated by a border.

The discocellular spots of the DHW of typical *f. aurivilliusi* are a greyish white, occasionally tinged with pale yellow, and surrounded by a pink suffusion. *f. aurivilliusi ab. capensis* also has greyish-white DHW discocellular spots, but the pink suffusion is absent.

The miniature "white" female taken in 1987 lacks any trace of coloured pigment in the non-melanin containing scales of the dorsal and ventral hind wings. Under low magnification, the DFW are furry looking, resulting from extreme rolled deformities of the scales. To the naked eye the ground colour of VHW and VFW is a silvery grey colour with a slight mother-of-pearl reflection (probably from the translucent wing membrane).

Examination under stereoscan and transmission electron microscopy

When examined under stereoscan (SEM) and transmission (TEM) electron microscopy (Plates O to W), the iridescence scales of the dorsal surface are seen to exhibit an almost total collapse of the scale's air space which normally intervenes between the upper and lower surfaces, a space which in normal scales is supported by a series of thin cuticular struts or trabeculae. In *ab. capensis*, what remains of this space is filled with debris, with no trace of the trabeculae or of the large granules of pteridine pigment (pterinosomes) which are present in the air space of normal scales. The "creaminess" or pale-colour of *ab. capensis* males, and probably the pale females as well, certainly arises from this failure of the pigment to be correctly deposited.

As a result of the collapse of the scale's air space the UV interference mirrors of these iridescence scales are also badly disorientated. This makes the iridescence omni-directional, thus dissipating the reflected energy, and is probably the reason why the UV iridescence of *ab. capensis* is relatively weak and non-directional.

None of the coloured scales anywhere else on *ab. capensis* contain pterinosomes. For example, the ventral scales of males are empty of these pigment bodies. Since these scales are coloured (albeit with a shade different from that of a normal male) and are not collapsed, one must conclude that the mutation is affecting the formation of pterinosomes, but not the synthesis of pigment or the cuticular structures supporting the dorsal surface of the scale. From this information it can be concluded that the principal effect of the mutant is to prevent the formation of the large granules of pteridine pigments and that the collapse of the dorsal UV iridescent scales, which eliminates the air space of these scales, is a secondary result.

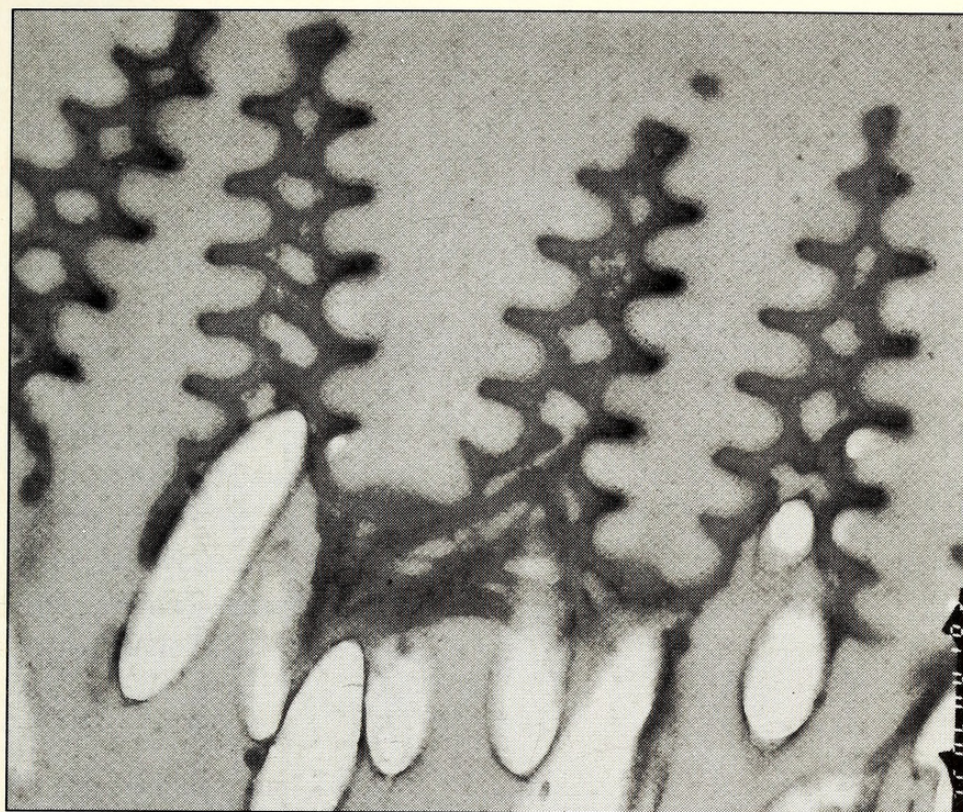


Plate U. *Colias electo electo* — normal male iridescent scales x 35,000 (TEM)

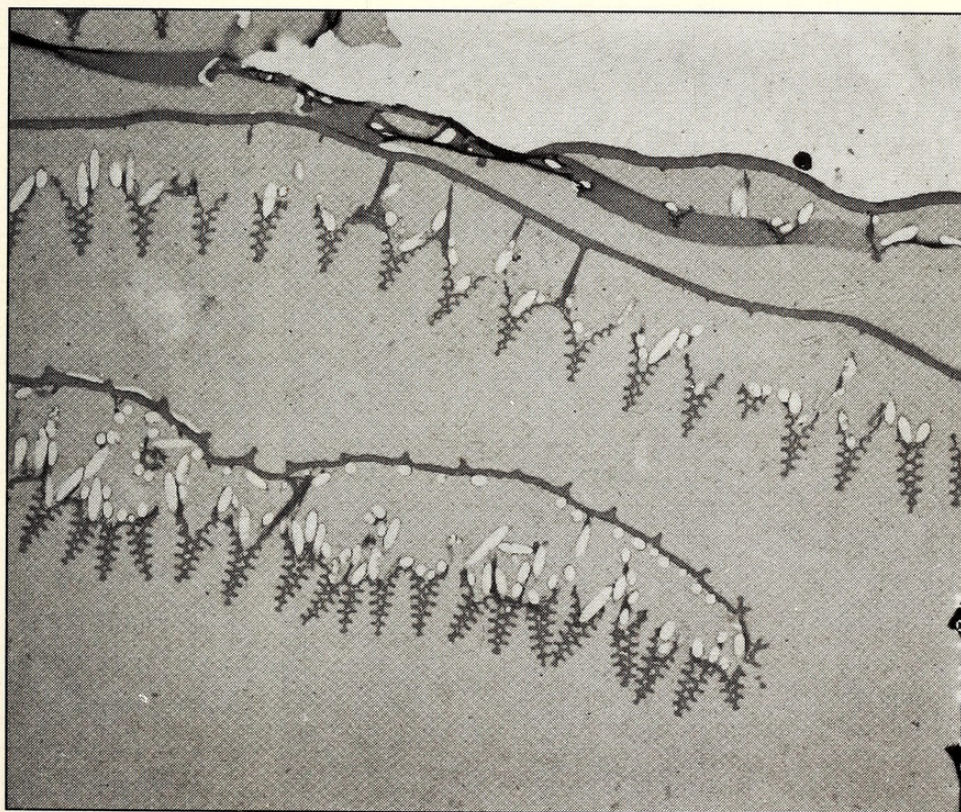


Plate T. *Colias electo electo* — normal male iridescent scales x 5000 (2 scales) (TEM)

Note the dorsal longitudinal ridges, air spaces and pigment granules

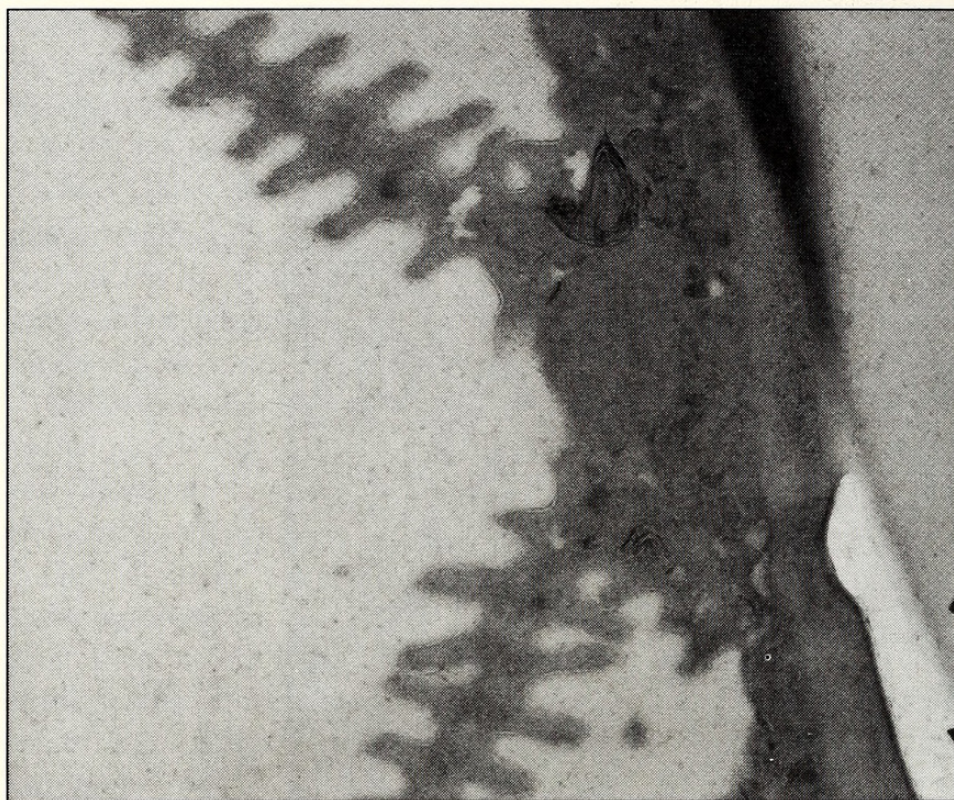


Plate W. *Colias electo electo ab. capensis* — male iridescent scales x 35,000 (TEM)

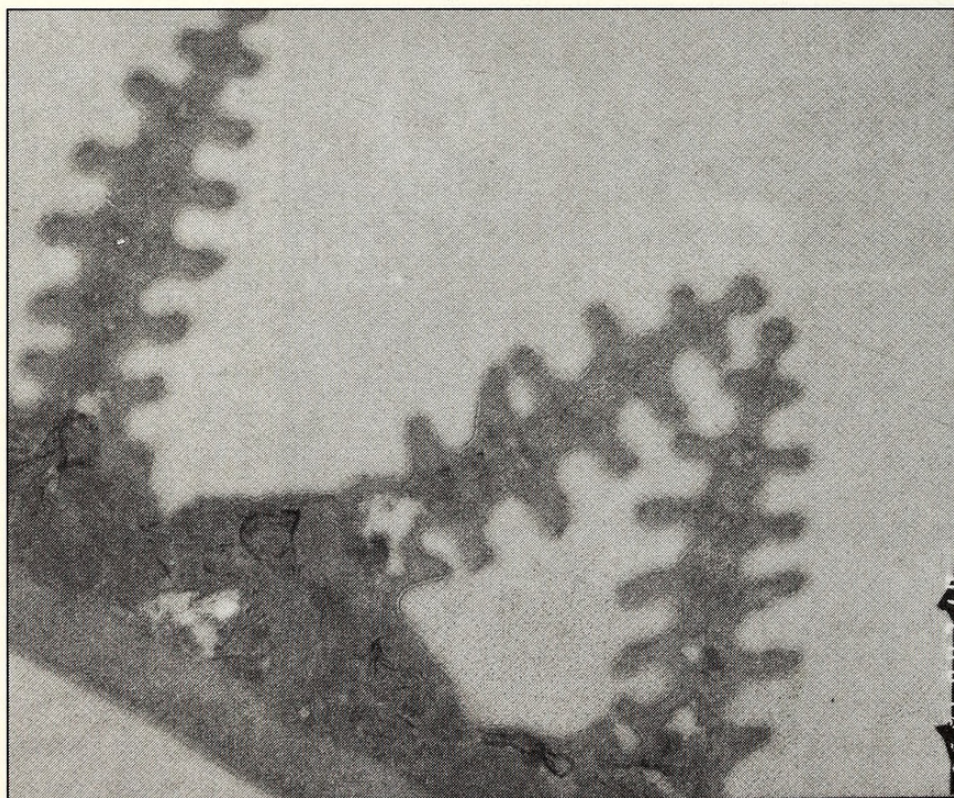


Plate V. *Colias electo electo ab. capensis* — male iridescent scales x 35,000 (TEM) Note the absence of air spaces, pigment granules and the malorientation of interference mirrors.

Habitat

The habitat in which *f. capensis* occurs is Grassy Fynbos on the lower slopes of foothills of the Riviersonderend Mountains. Also grassland, previously cultivated and fallow farmland with the thistle *Berkheya rigida* (Thunb.) and *Athanasia trifurcata* L. often dominant, with occasional plants of Lucerne, *Medicago sativa*, and Subterranean Clover *Trifolium subterraneum*. Of particular importance are the legumes *Trifolium angustifolium* L. which occurs in large clumps, and the low-growing *Lotus subbiflorus* Lag. The adult butterflies feed at the flowers of *Berkheya rigida*, *Medicago sativa* and *Limonium* spp. (Blue Statice). In winter months when flowers are sparse, *Oxalis purpurea* (Sorrel), *Rapistrum rugosum* (Wild Mustard) and *Raphanus raphanistrum* (Wild Radish) are important sources of nectar.

In the Western Cape *C. electo electo* lays eggs on *Robinia pseudoacacia* (Locust tree), *Medicago sativa* (Lucerne), *Trifolium africanum* (African Clover) and *Vicia sativa* (Vetch) (Claasens & Dickson, 1980).

Predation and parasitism

In the southern and south-western Cape, and possibly elsewhere in South Africa, a major predator of *C. electo* is the Bat-eared Fox *Otocyon megalotis* Desmarest. Adult foxes will concentrate their efforts to lucerne and clover fields when larvae are numerous and of a suitable size, particularly final instar larvae. A single fox can eat 1000-2000 larvae in a night. There is also a high level of predation from birds. The total predation results in a strong density-dependant mortality.

Conclusions and discussion

The very dramatic phenotype *Colias electo* ab. *capensis* results from an abnormal development of the orange scales of the upper wing surfaces and to a much lesser extent, of some of the yellow scales of the lower forewing surface. This abnormal development affects the pigment content of the scales as well as the scale shape, and it is the distorted shape of these scales, extensively so in some individuals, which indicates that the phenotype is an aberration. These malformations may independently involve scales of the orange upper surfaces of both wings, or only those of the forewings, as well as the apical and distal margins (not the fringe) of the VFW. It seems likely that much or all of this has a genetic basis.

From the field evidence, the question arises as to why this aberration has survived and achieved a high level of success (up to 10% of the population in some years). It has already been noted by other authors that the contemporary ecological conditions in the Western Cape are conducive to the evolution of endemics. What we are seeing here may be yet another example of just such an evolutionary progression – the success of a genetic aberration.

Under conditions of very large numbers, it has been noted that males of ab. *capensis* fly low to the ground because of being chased and mobbed by normal males. It would appear that normal males mistake them for females, perhaps because

of their reduced UV iridescence. It is considered unlikely that this change of flying habit is enough to ensure the survival of this aberration. Theoretically, in the wild it is most unlikely that male ab. *capensis* will be accepted by females because their UV iridescence is weak or abnormal. Male ab. *capensis* have never been seen *in copula* by the authors. One must therefore assume that it is the heterozygote female ab. *capensis* which readily accept normal males and thus continue the aberration in the population. In this way only heterozygotes are seen in wild populations.

Acknowledgements

Until his death in 1997 Ellis MacLeod was Assistant Professor in the Department of Entomology at the University of Illinois, at Urbana-Champaign. One of his interests was the genus *Colias* and it was for this reason I contacted him in 1989. During our several years of correspondence concerning ab. *capensis*, we decided to collaborate together on a paper describing the various facets of this intriguing aberration, but unfortunately he did not manage to submit any text before his untimely death. Ellis did however, organise and send some scanning electron micrographs, which had been taken by his colleague Jim Nardi. I would like to acknowledge the encouragement Ellis gave me in trying to unravel this complicated aberration. His collection of *Colias* is now housed at the Illinois Natural History Survey in Champagne, Illinois, 61820-6970, USA. My thanks also to Jim Nardi of the University of Illinois at Urbana-Champaign for his permission to reproduce the scanning electron micrographs and to Phillip Ackery of the British Museum (Natural History) for permission to examine the National collections.

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