Nota lepid. 4 (4) : 155-158 ; 31. XII. 1981 ISSN 0342-7536

Character displacement in butterflies – a fiction (*) ?

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Character displacement is a much disputed phenomenon in evolutionary literature, or rather it is not a phenomenon itself, but an explanation for the phenomenon that if two species are only partly sympatric they may differ in another way in the area where they occur together than outside the area of overlap. Although known for more than a century, the phenomenon was termed "character displacement" only in 1956 by Brown & Wilson. The basic idea stressed by these authors is that the force which causes the change of a character is natural selection arising from the presence, in the same environment, of another and similar species. Thus it seems to be an extension of what is known as the Gause principle of competitive exclusion that says that no two species can coexist at the same locality if they have identical ecological requirements.

Character displacement implies a change of a character, i.e. it is not an original, but a derived condition, and as the change is due to sympatry with an ecologically similar species, it follows that the sympatry is a derived condition as well. Grant (1972), who gave an interesting review of the problems around the phenomenon, correctly remarked that the change can be away from or towards the other species, i.e. it can be either divergent or convergent. To make character displacement a plausible explanation the following questions must be answered :

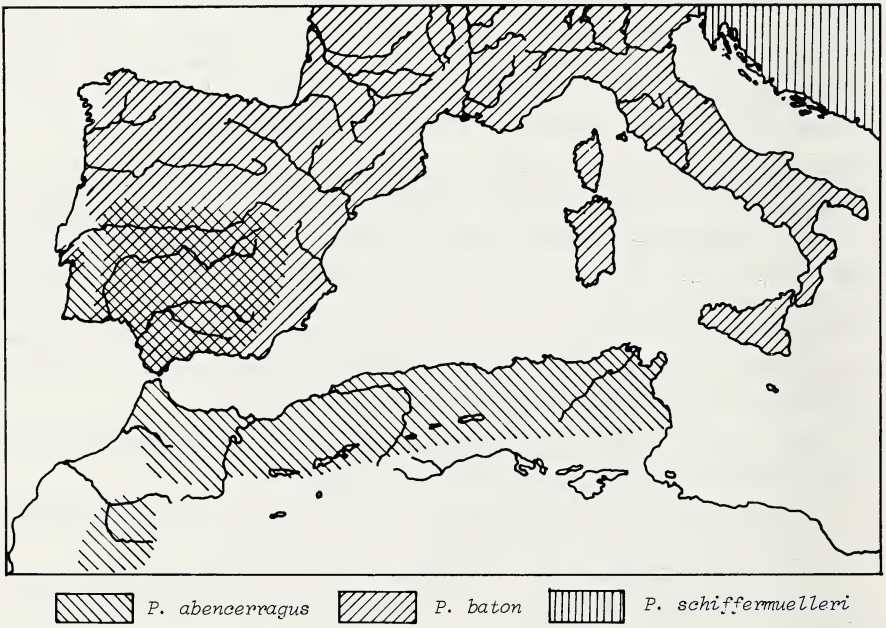
1. The species concerned must originally have had separate distributions. Thus the distribution history must be reconstructed.
2. The pre-contact character states must be identified to find the direction of the change. It implies knowledge of the phylogeny.
3. As character displacement is supposed to be correlated to the ecology (mainly feeding) of the species, the ecological requirements of the species concerned must be known.
4. As the change of a character state is supposed to be due to the presence of another species, a prediction must be made of the character state in the zone of sympatry in the absence of character displacement to judge if the

(*) Summary of a paper presented at the second European Congress of Lepidopterology, Karlsruhe, April 1980.

supposed displacement is not part of the general tendency in geographic variation.

A critical analysis of many supposed cases of character displacement in birds by Grant (1972) revealed that several cases can be as convincingly interpreted in other ways, that other cases illustrate the different principle of character release, and still others are too complex to be entirely explained by character displacement. This illustrates the difficulty in making character displacement a plausible explanation for a particular kind of variation.

As far as I know butterflies have never been studied as to the possible occurrence of character displacement. I will give here one possible example in European butterflies to illustrate how important the knowledge of the evolutionary and distributional history is for the explanation of the variation found.



The lycaenid *Pseudophilotes baton* is distributed over a large part of central, western and southern Europe (see fig.) (the semi- or full species *P. schiffermuelleri* Hemming is left out of consideration here). In central Europe (*P. baton baton*) the insects are relatively large, length forewing

10.5-13.5 mm, males rather light blue on upperside, underside light greyish with prominent dark spots and with conspicuous orange submarginal lunules on the hindwing. In the southern half of Spain (*P. baton panoptes*), the species is much smaller, length forewing 9-10.8 mm, the blue of the male is a little darker, the underside is darker grey with the dark spots clearly white-ringed and orange submarginal lunules vestigial or absent. The undoubtedly closely related *Pseudophilotes abencerragus* overlaps *P. baton* in the southern half of Spain ; further it occurs in N. Africa and Israel. It is a small insect, as large as *P. baton panoptes* which it also resembles in colour (generally a little darker above and below) and in the white-ringed spots on the underside of the hindwing.

Thus the two species, abundantly different where they do not occur together, are very similar where they do fly together. This seems to be a case of convergent character displacement, but let us consider the evidence. Although no phylogenetic studies have been carried out on these species, they are undoubtedly closely related and may be considered sister species. Supposing that *P. baton* arose in the northern and *P. abencerragus* in the southern Mediterranean, the sympatry in southern Spain is secondary. In view of the usual size of related species the small size of *P. abencerragus* and *P. baton panoptes* can be considered a derived state. Thus *P. baton* has changed in the direction of *P. abencerragus*. There is no reason to suppose that *P. baton* would be small in Spain in the absence of *P. abencerragus*. As the two species really fly together and even use the same food plants, at least partly (*Thymus ; P. abencerragus* also *Erica arborea* and *E. scoparia* ; Gómez Bustillo & Fernández-Rubio, 1974) there seems to be advantage in being small, as the caterpillar needs less of the common food. So far the evidence in favour of character displacement is not bad, although the advantage of having similar undersides is obscure. However, the whole explanation depends on the correct interpretation of the distributional and phylogenetic history. If, for instance, *P. abencerragus* is the African off-shoot of a small Spanish form of *P. baton*, which later re-invaded Spain, the variation observed has nothing to do with character displacement.

There are three more cases among European butterflies of apparently closely related species which are more similar where they fly together than in the areas where only one of the species is represented. The high mountain fritillaries *Boloria napaea* and *B. pales* are usually very similar, at least in the male sex. *B. napaea* is often larger and the markings are more linear. In part of the area of sympatry, in the southern and western Alps, the ssp. *palustris* of *B. pales* resembles *B. napaea* in the linear markings. It is difficult to see any ecological advantage in this similarity.

In the other two cases the similarity is apparently due to the same selective force working on the populations of the two species. In the widespread *Coenonympha arcania* the population living over 1600 m in the Alps have smaller eye-spots on the underside of the hindwing (ssp. *darwiniana*, often considered a separate species, but that is not important in this context) and thus resembles the closely related *C. gardetta*, which is restricted to the higher altitudes in the Alps. It is remarkable that in the higher parts of the Pyrenees, where *C. gardetta* does not occur, *C. arcania* is hardly different from lowland populations.

In skippers of the genus *Pyrgus* there is a general tendency of spot reduction on the upperside and a reduction in size, with increasing elevation. Thus, it is no surprise to find that the widespread *P. alveus* at higher altitudes in the Alps becomes similar to the closely related *P. warrenensis* which is restricted to higher altitudes. In the absence of *P. warrenensis, P. alveus* can still be supposed to be small and with reduced spots at higher altitudes.

Summing up, the evidence for character displacement in European butterflies is little convincing. Up to now I have found only a single example outside Europe that possibly indicates a complex case of partly convergent, partly divergent character displacement, viz. in the C. Asian *Pyrgus alpinus* group. The three constituting species vary geographically in size and/or markings. Where two species occur together, one is large and the other small, while in other areas the situation may be reversed. For details, see De Jong (1979). Other such cases will undoubtedly turn up, but generally speaking the interpretation of the variation in terms of character displacement will be very difficult, if only because we know so little about ecology. Nevertheless it seems worthwile to study geographic variation not for finding new subspecies, but for a better understanding of the processes governing evolution.

Literature

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