JOURNAL OF
THE LEPIDOPTERISTS' SOCIETY

Volume 33 | 1979 | Number 2

Journal of the Lepidopterists' Society
33(2), 1979, 77–111

SUBSPECIFIC VARIATION IN BUTTERFLIES: ADAPTATION AND DISSECTED POLYMORPHISM IN *PIERIS* (*ARTOGEIA*) (PIERIDAE)

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ABSTRACT. Subspecific variation of butterflies has in the past been attributed (with doubtful justification) to local ecological factors. In part I of this paper, main types of variation in wing-color and marking in the *Artogeia napi-bryoniae-melete* group are described. Genetic control is relatively simple and known phenocopies result from environmental abnormalities unrelated to any actual local conditions.

In part II, selective agents are considered to exercise little or no control over subspecific pattern-differences. Physiological adaptation is certain, but visible characters appear not to be specially adapted to present local conditions.

In part III, the extreme selectionist position is rejected. Phenotypic differences have arisen historically, often in consequence of the dissection of polymorphisms, and are maintained by the succession of genetic path-choices in effectively isolated populations. Territorial changes have involved the retention of pattern-elements in biotopes far removed, geographically and ecologically, from the places of origin. Common possession of even superficial characters, when genetically identical, implies phylogenetic relationship.

Some consequences of range-changes of populations are discussed.

In this paper it will be maintained that wing-pattern (and other phenotypic) variation among subspecies of butterflies is generally controlled not by present ecology but by factors having an historical aspect. Arguments will be related particularly to the group *Artogeia napi* + *bryoniae* + *melete*. The genus *Artogeia* Verity was formerly included in *Pieris* Schrank; however, Kudrna (1974) and Higgins (1975) have correctly separated it.

For the past hundred years, collectors have amassed long series of butterflies and moths showing the variation of species among different localities, with the expectation that the significance of the diversity would reveal itself, thus exposing the processes of evolution. I think this expectation has generally been disappointed. But at the turn of the century it was believed quite generally that the visible differences between local races expressed their close adaptation to contemporary environmental conditions.

This thesis received considerable support from the experiments of Standfuss (1900) and others on the heat-and-cold treatment of lepidopterous pupae. These appeared to show (*inter alia*) that central European races were convertible into the semblance of Mediterranean races by moderate heat, or into phenocopies of Scandinavian races by moderate cold. It was supposed that environmental factors themselves had the power to produce phenotypes better adapted to cope with them, and that a process rather like that known later as genetic assimilation (Waddington, 1953) had produced the climatic races. The argument was in some degree circular, being based on an initial assumption that the supposed climatic forms were adaptive.

Some local departures from the idealized type were held to be directly environmental, as when marshy conditions were themselves supposed to shift the phenotype in a particular direction, such influence not being inherited. Other deviations were correctly recognized as selective and heritable: "chalk" forms of a butterfly or moth were whiter than heath forms (Poulton, 1890: 157; Ford, 1945: 124; Ford, 1955: 97). There was, therefore, ample excuse for naturalists who attached what might now be called ecological import to all local variations.

Their attitude persists among many lepidopterists. Thus Dennis (1973), in a study of the spotting on the wings of the satyrid butterfly *Coenonympha tullia* Müller in a Welsh colony, concluded that "certain broad spatial features emerge that may prove vital to an understanding of the ecological pressures on *C. tullia*," when his painstaking analysis had established that localized demes differ in spot arrangement. I do not question that local variation occurs, in genotypes as well as in phenotypes; but it is by no means certain that the groups delimited by marking owe their visible differences to their present ecologies. Another example is the strange data concerning spotting on the hindwing of *Maniola jurtina* L. in England, claimed as providing ideal material for investigating adaptation and the action of natural selection (Dowdeswell, 1956). No adaptation was detected, and the basis of natural selection remained quite uncertain, "presumably of a physiological nature."

The significance of wing-pattern is a matter of natural history, requiring in the first place no very specialized techniques for its appraisal.

Indeed, the replacement of the chase by genetic experiment, and even the application of statistical methods, have not in most cases explained geographic variation at specific or subspecific levels though we are able to talk more precisely about it. Nevertheless, I will attempt to reassess the position—the present position—in relation to one group of pierid butterflies. This is a very narrow foundation on which to erect any general principles, but it may be adequate to invalidate the extreme neo-Darwinian dogma.

PART I. MORPH SYSTEMS IN THE *ARTOGEIA NAPI* SPECIES-GROUP

In the species-cluster *Artogeia napi* L., *A.* (*n.*) *bryoniae* Ochsenheimer and *A. melete* Ménétriès, we are faced with groups of almost conspecific taxa, with wing ground-colors varying from nearly pure white to deep golden yellow and to a tawny ochre, carrying melanic markings varying from intense and extensive to evanescent. The ground-colors are due to related pterins, and the melanic pattern has a common basis in all the populations.

The wing-pattern variation of the *napi-bryoniae* group in Europe was meticulously described and figured by Müller & Kautz (1939). Their treatment of the Asiatic and American taxa was very incomplete and included few or no illustrations. Indeed, I know of no comprehensive study of the Nearctic members of this group, nor have I myself all the material necessary for such an undertaking. *Artogeia melete* and some associated Asiatic species were the subject of illustrated papers by Sheljuzhko (1960–69). The present work is not concerned with the characterization of taxonomic entities as such, nor will descriptions be in greater detail than is required by subsequent discussion. The accompanying figures (Figs. 1–40) are far from illustrating the total range of variation encountered in the superspecies: nor do they include any forms that can fairly be regarded as "aberrations."

It will be convenient to consider background colors (sections 1, 2), the markings of the hindwing underside (section 3), and upperside markings (sections 4, 5). Finally the reflection of ultraviolet light, invisible to vertebrates, will be dealt with in section 6.

These groupings of characters do not exhaust those which might be considered to have a fairly simple polymorphic basis. For example, in many *Artogeia* taxa there is normally a small orange-yellow lunule or streak near the base of the hindwings, below. Furthermore, in some Asiatic species, but not others, the forewing discal cell is invaded below by black scales (character "nigrosparsa"). These appearances will not be considered further here.

1. The sulphurea Schöyen polymorphisms[1]

European A. *napi* subspecies typically have a white upperside; the underside of the hindwings and of the forewing apices (i.e. those parts exposed when the insect is at rest) are yellow in ground-color. The remainder of the forewing underside is white. In the male the yellow is usually rather paler than in the female.

In the rare variant formerly bred by Head (1939; see also Bowden, 1954) the white pigment is replaced by lemon-yellow, which may be very brilliant if the adult develops at a high temperature. When this yellow is paler, it can be seen that the hindwing underside remains brighter than the upperside: that is, the typical pattern persists. This form occurs equally in both sexes, and is recessive to wild type.

Another sulphurea allele appears to be responsible for Thompson's pale yellow, a form which is fairly distinct in the female, but often almost indistinguishable from wild type in the male. It also is recessive, but is dominant to Head's form. It is uncertain how commonly the gene or gene-combination determining it occurs in England and in other parts of Europe. A genetic study was made by Bowden (1961), but further work on a wider basis is desirable.

Whereas Head's bright yellow does not occur regularly in any natural population, a form indistinguishable from Thompson's, and with the same dominance relationships, is typical of A. (*napi*) *marginalis* Scudder of Oregon. It may occur also in certain other American populations, but at present it is not known whether it is anywhere in polymorphic balance with the white form (Bowden, 1970).

In various *bryoniae* populations of the eastern Alps (and probably elsewhere) a dominant gene in some of the individuals prevents the development of the lemon-yellow (sepiapterin) color but does not affect the ochreous color which many females show (see section 2). The resulting male phenotype (f. subtalba Schima) is white above and below, but nearly all the corresponding females have hindwing undersides which remain ochreous, though their lemon tinge has been lost. The frequency of this gene (another allele of the sulphurea series: Bowden, 1963) is locally as high as 0.25 in the alpine region and the system is there truly polymorphic.

In those European *napi* populations in which the great majority of females are white above, the subtalba morph is virtually unknown. Nor does it appear in the arctic ssp. *adalwinda* Fruhstorfer. The extent and

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[1] Infra-subspecific names (such as sulphurea) are not italicized, but are given the author's name when first used. The names of characters, if new or not well known, are put in quotes when first used, but not afterwards.

mode of its known occurrence in mainland Asia (e.g. Amur) is unfortunately still obscure.

In the eastern Nearctic species *A. virginiensis* Edwards a subtalba gene (also dominant and an allele of sulphurea: Bowden, 1966) is fixed. Here males as well as females possess a little ochreous pigmentation, which prevents a conspicuous white underside in either sex. On the other hand the sympatric *P.* (*napi*) *oleracea* Harris has a light lemon-yellow underside in both male and female, and we have not yet encountered a subtalba form in it.

Artogeia melete melete (Japanese) appears to lack sepiapterin in both sexes, but here again males as well as females have considrable ochreous pigmentation (especially on the hindwing underside). This could be regarded as a subtalba form, but it differs genetically from Schima's original subtalba, being apparently recessive when hybridized with typical *napi* (Bowden, 1975).

A. japonica, described by Shirôzu (1952) as a subspecies of *napi*, is specifically distinct from both *A.* (*n.*) *napi* and *A. melete* (Bowden, 1978a). In appearance it approaches very closely the artificial hybrid between these two species, but it is of subtalba form and again the subtalba is recessive to *napi* wild-type. In this species the underside of the male is white, *not* ochreous.

A. dulcinea Butler and some other far eastern taxa possess subtalba forms, but in all these cases it is still uncertain whether a balanced polymorphism exists.

2. The female form flava Kane

As mentioned above, in some (particularly alpine and arctic) populations the wings of the female (but not of the male) are tawny or ochreous yellow. The responsible pigment (erythropterin, possibly with other related compounds) is present not only on the upperside but also on the hindwing underside, though not normally on the underside forewing disc. Occasionally even this area is more or less ochreous: in ssp. *neobryoniae* Sheljuzhko such specimens are not rare; they occur also in the arctic ssp. *adalwinda*.

In ssp. *britannica* Verity of Ireland and Scotland the sex-limited ochreous variant has wrongly been regarded as an aberration, and named flava Kane. In fact it occurs regularly in both populations and its ground-coloration is apparently identical with that typical of *adalwinda* females. As it is unrecognizable in the male and even in the female has variable expression, its genetics have perhaps never been adequately investigated. The results published by Lorković (1962), however, allow the possibility that in *bryoniae* it is unifactorial and dominant, if incompletely so, the depth of color developed depending presumably upon modifying genes. The results (1956 and unpublished) from my own hybridizations between *bryoniae*-like subspecies and various white forms are in accordance with this finding.

The occurrence of ochreous pigmentation in both sexes of *A. virginiensis* and *A. melete* has been mentioned above. Since in these species the pigment switch is not completely sex-controlled, it must in some way differ genetically from that in *A. napi* and *bryoniae*.

The apparent association of flava color with ultraviolet reflectance will be discussed in section 6.

3. The underside "green veining"

The species-group is characterized by the borders of black or grey scales on either side of the veins on the hindwing underside. When the ground-color is yellow, the visual effect is greenish, though this effect is lost if the black is too dense or the ground-color is white.

For the purpose of comparisons we shall take as standard the black bordering as it appears in the spring emergence of English *A. napi* (Figs. 2, 7). In the non-diapause generations the density of the bordering is much reduced: an extreme reduction appears in *A. napi meridionalis* Heyne (Figs. 13, 17) of Mediterranean countries. Curiously, warming English *napi* pupae after completion of diapause leads to slightly *increased* melanic scaling on the underside (Bowden, 1978b). In any one population the width of the border does not usually vary very much, though very broad borders (obscuring most of the ground-color) frequently occur in *A. napi adalwinda* (Fig. 26) and *A. n. hulda* Edwards.

A rather broad, vaguely defined vein-bordering characterizes *A. virginiensis* (Fig. 29) and helps to separate it from the sympatric but ecologically distinct *A.* (*n.*) *oleracea*. In the Near East flies *A.* (*n.*) *dubiosa* Röber (=*pseudorapae* Verity); the better known non-diapause generations have vein-marking so nearly obliterated as to justify both its names, but in the diapause generation form suffusa Verity, which appears to belong to *dubiosa*, carries very broad vein-stripes.

A. (*n.*) *oleracea* (Figs. 32, 34), like *A. melete* (Fig. 21), has narrow and sharply defined vein-marking, which in the spring emergence can be extremely densely black or chocolate-black. In the non-diapause generation (Figs. 37, 39) the borders remain narrow, but are only slightly pigmented and often hardly visible. This "acuta" type of vein-bordering, found also in the Californian *A.* (*n.*) *venosa* Scudder, is dominant over both European wild type and the suffused bordering of *A. virginiensis*

(Bowden, 1972). It retains its general character in hybrids repeatedly back-crossed to European *napi*, but the "summer" veining is then more visible than in the pure *oleracea* gene-complex. The acuta veining of *A. melete* (Figs. 21, 23) also is dominant in hybrids (Bowden, 1975).

All these modifications of the underside veining are retained when the subspecies concerned are bred in England. It should be said that though the "seasonal" dimorphism is normally a simple consequence of the diapause/non-diapause alternative, some intermediate phenotypes (on both surfaces of the wings) can occur in special circumstances (Bowden, 1978b).

4. The upperside markings

Again it is convenient to regard the markings of spring *napi* of southern England (Figs. 1, 6) as normal, as well as most appropriate for the comparison of univoltine populations such as *A. n. adalwinda* and *A.* (*n.*) *bryoniae*.

In the male (Fig. 1) the forewing discal spot varies in size within the same subspecies and may be absent, though in this case one or two spots on the underside of the forewing (Fig. 2) normally remain. The female marking (Fig. 6) includes on the forewing two discal spots, with often a supra-discal spot more or less covered by the extension of the apical. The pre-apical costal mark prominent in *A. krueperi* Staudinger is sometimes faintly represented, and may be distinguishable from the supra-discal spot proper (when both are present) by a different degree of melanization. These additional spots are sometimes apparent in males also (especially in non-diapause emergences), but a dark streak along the hind margin is normally characteristic of the female sex. The dark basal suffusion is more extensive in the female, whose forewing veins are lined-in, especially towards the outer margin, where this black scaling commonly expands to form dark triangles.

On the fore-margin of the hindwing of both sexes there is usually a black spot, more or less in line with the forewing discal spots but homologous rather with the apical. Marking along the hindwing veins is variable, but generally light.

In *bryoniae*-like forms (Figs. 4, 9, 27) the female radial vein-marking is intensified and broadened, and an additional streak ("Saumstrich" or "bryo-streak") appears outside the middle of the lower (i.e. posterior) discal spot; basal and marginal dark suffusions may also become extensive. The combinations of these elements in various proportions are infinitely varied, so that no two females are entirely alike. Stipan et al. (1960) attempted the thankless task of completing Kautz's descriptive naming (Müller & Kautz, 1939) of the main possible forms. Development varies between and sometimes within populations from a mere bryo-streak to the extereme f. concolor Röber, approached by Fig. 9. The not uncommon f. "meta" is illustrated in Fig. 5. Clearly the *bryoniae* phenotypes cannot be due to a single dominant gene, as has sometimes been supposed. Apart from modifiers, there may be several linked major genes involved. Probably only the "radiata" element has been adequately studied genetically, and this is indeed a simple dominant (Lorković, 1962).

In non-diapause individuals (Figs. 3, 8) the spots become more prominent, the radial markings less so. Extreme forms, in this direction, are found in the summer broods of *A. n. meridionalis.* Females representative of this subspecies (Fig. 16) lack even the marginal black streak continuing the upper edge of the lower discal spot; this streak is always absent in *A. rapae* L. (Fig. 20).

Even in summer males, the discal spot can be completely absent (as it is in *Pieris brassicae* L.), but this is uncommon in Europe. The aspect of both sexes is changeable by a varied development of the supra-discal spot and its confusion with the apical (Fig. 12).

The upperside markings of *A. melete* (Figs. 22, 24) differ from those of *A. napi* by their greater intensity and breadth, which frequently leads to their confluence. In the male *melete* the second discal spot appears regularly.

5. Restricted upperside markings

When over-wintering pupae which have completed diapause are held at varying temperatures between 0°C and the temperature of normal development (ca. 6–8°C) some individuals are diverted to produce a "superspring" form (Figs. 14, 19). Though the forewing apical spot and the corresponding spot on the hindwing may persist, the discal spot markings disappear completely or almost so, even from the female and even on the underside, and the radial viens are more or less blackened throughout their length. In extreme examples the sexes become alike (Bowden, 1978b). This form, which can be obtained in several (perhaps all) European subspecies, including *adalwinda* and *bryoniae* (Fig. 18), may be called "restricta"—the name referring to a character and not to any taxonomic entity. Genetically, the treated insects showing it are quite normal (usually wild type) for their subspecies.

Some Nearctic *napi* subspecies present a similar or more extreme appearance even in their natural temperature regime. *P.* (*n.*) *oleracea* may be quoted: in both diapause and non-diapause generations (Figs. 31–34, 36–39) the *napi* spot-markings are faint or completely absent, the apical marking is weak and there are no spots even on the underside of the forewings; on the upperside even radial marking is slight or absent. In *oleracea-napi* hybrids this genetically determined restricta behaves as a simple recessive, linked with the dominant acuta (Bowden, 1972).

Ssp. *marginalis* (Figs. 35, 40) is slightly less restricta in phenotype than *oleracea*; females usually show the black streak on the forewing hind-margin, the adjacent discal spot (rather weakly) and sometimes a very weak anterior discal spot. Crosses with *oleracea* suggest, however, that the same restricta gene is present in both subspecies.

Ssp. *venosa* Scudder of California lacks the restricta character, though acuta is present; in this it resembles some taxa of eastern Asia.

6. Ultraviolet patterns

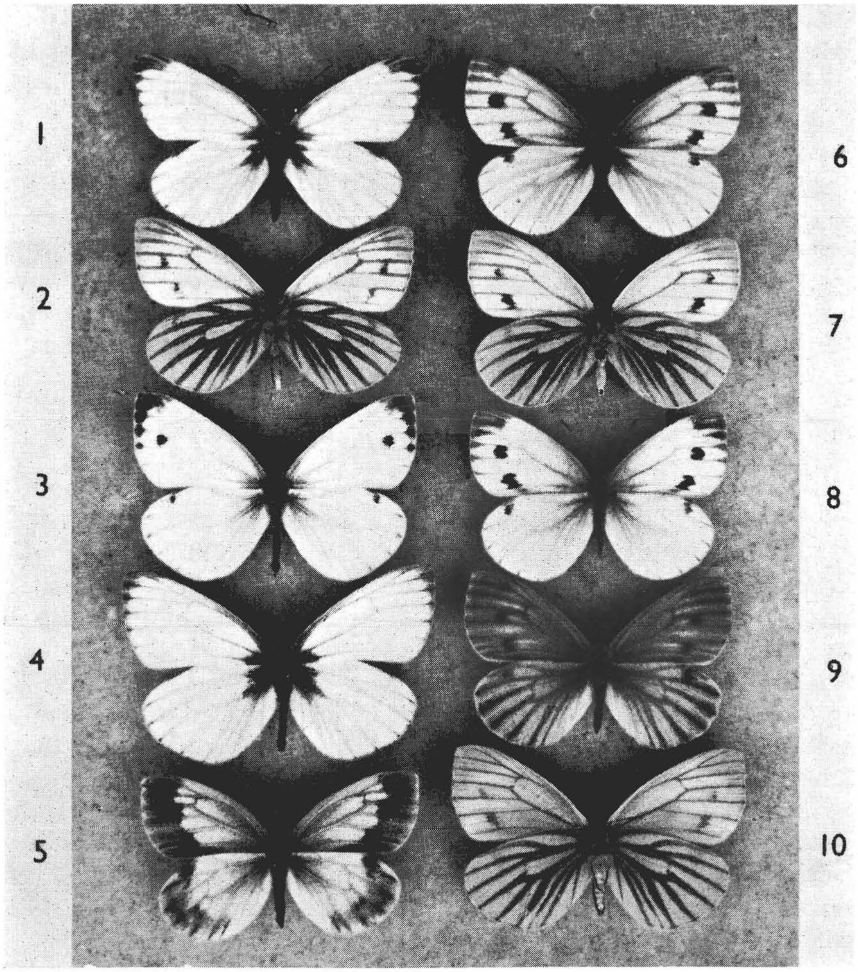
In recent years many workers have studied the reflection of ultraviolet light by butterflies. Among the Pieridae, the yellow butterflies such as *Gonepteryx* (Nekrutenko, 1964), *Colias* (Ferris, 1973) and *Eurema* (Ghiradella *et al.*, 1972) show ultraviolet-reflecting patches in the male only, and these are structural, a complex lamellar system on the ridges of the scales producing optical interference.

In *Artogeia*, on the contrary, the males usually remain dark (as do the females also in *A. napi napi*), but in many subspecies the female upperside reflects more or less strongly. This is so particularly in those European taxa in which the female ground-color is ochreous, but *A.* (*n.*) *macdunnoughii* Remington of Colorado and *A. melete* have nearly white females which are rather brightly reflective. Experiment shows that absorption by varying concentrations of leucopterin in the wing-scales and (in the females) structural reflection are responsible for the differences (Bowden, 1977).

PART II. ADAPTATION AND SELECTIVE NEUTRALITY

From the time of Darwin (1859) on, the basic idea connecting variation with evolution has been that of adaptation—often a vaguely formulated idea, leading to tautological arguments whose circular character easily escaped detection.

In some balanced systems, such as the melanisms (Kettlewell, 1973) and the mimetic complexes (Sheppard, 1961), there are indeed good reasons for supposing that primary selective advantages are involved and often the basis of selection can be proposed with confidence. The selection is intraspecific, acting on the individual, so that in particular circumstances one allele is favored up to an equilibrium level. Population



EXPLANATION OF FIGURES

FIG.	1	N	L.	ups.	♂	'65 *X*2
	2	N	L.	uns.	♂	'69w^i22
	3	N	S.	ups.	♂	'50 Herts.
	4	B	L.	ups.	♂	'73b^i10
	5	(BN)^2	S.	ups.	♀	'52*t*10
	6	N	L.	ups.	♀	'46 Cornwall
	7	N	L.	uns.	♀	'69w^i25
	8	N	S.	ups.	♀	'44 Essex
	9	B	L.	ups.	♀	'63*E*59
	10	B	U.	uns.	♀	'73*b*25

Abbreviations: A = ssp. *adalwinda* (Lappland), B = ssp. *bryoniae* (Swiss), (BN)^2 = F$_2$ hybrid ♀B × ♂N, D = ssp. *meridionalis* (Corsica), J = sp. & ssp. *melete* (Japan), K = ssp. *neobryoniae* (Kärnten), KA = F$_1$ hybrid ♀K × ♂A, M = ssp. *marginalis* (Oregon), N = ssp. *septentrionalis* (England), O = ssp. *oleracea* (New Hampshire, U.S.A.), Ra = sp. & ssp. *rapae* (England), V = sp. & ssp. *virginiensis* (Connecticut, U.S.A.). L. = from diapause pupa, S. = from non-diapause pupa, ups. = upperside, uns. = underside. Figures and italic letters following sex-signs are individual identifications.

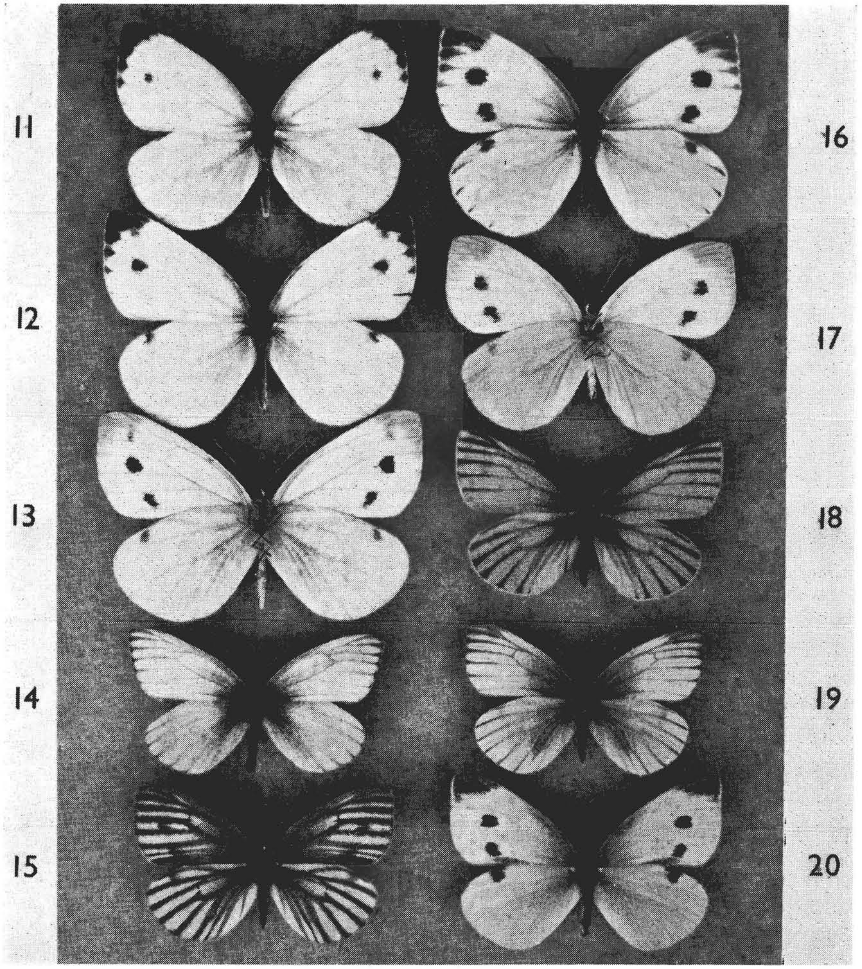


FIG. 11 D S. ups. ♂ $'64d^{vi}45$
12 D S. ups. ♂ $'64d^{ii}5$
13 D S. uns. ♂ $'64d^{ii}11$
14 N L. ups. ♂ $'70t^{i}8$
15 KA L. ups. ♀ '53*a*24
16 D S. ups. ♀ $'64d^{iii}25$
17 D S. uns. ♀ $'64d^{vi}74$
18 B L. ups. ♀ '72A24
19 N L. ups. ♀ $'70t^{i}6$
20 Ra S. ups. ♀ '64 Herts.

Editor's Note: Figures reduced to 0.88 of original size.

density is not usually determined by such selection: it can seldom happen that the population-level of an insect is fixed by the bird predation which is selecting the cryptic or mimetic adult.

There has been a widespread opinion, following Fisher's (1930) argument, that genes having a neutral effect, that is on balance neither advantageous nor disadvantageous, are necessarily extremely rare. All

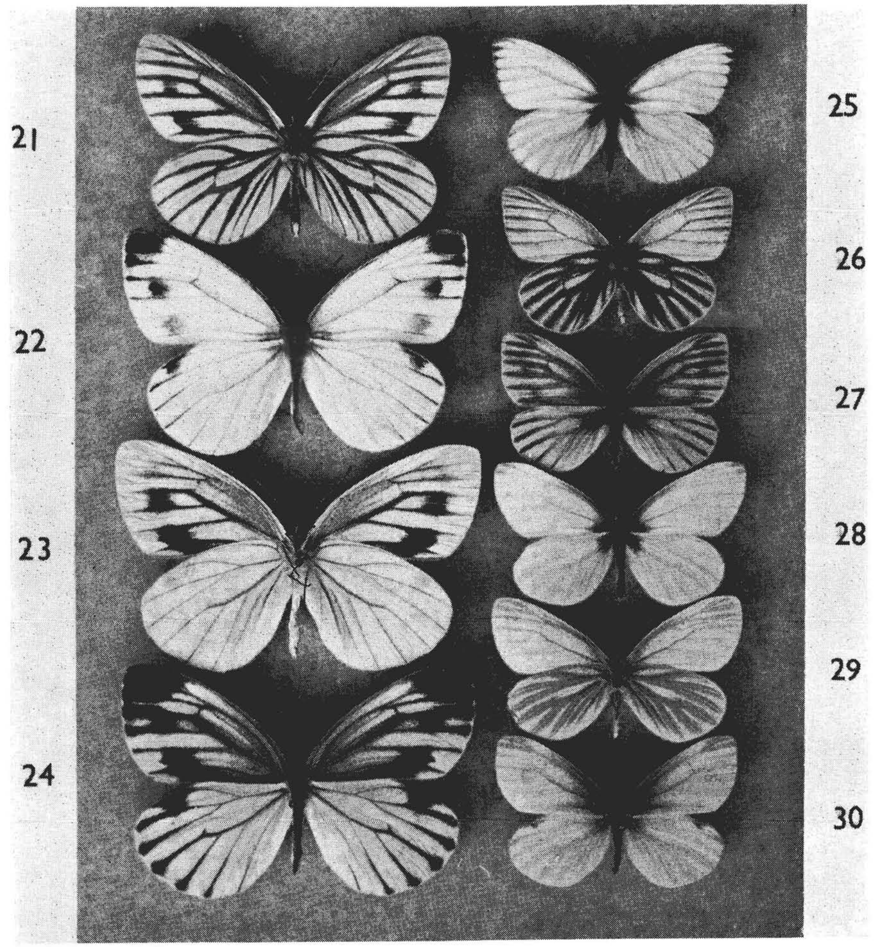


FIG. 21 J L. uns. ♂ '71*J*'11
22 J S. ups. ♂ '72*J*^{iii}16
23 J S. uns. ♂ '72*J*^{iii}10
24 J S. ups. ♀ '72*j*^{iii}7
25 A L. ups. ♂ '52*K*2
26 A L. uns. ♂ '54*d*33
27 A L. ups. ♀ '54*d*95
28 V L. ups. ♂ '72*v*6
29 V L. uns. ♂ '72*v*5
30 V L. ups. ♀ '66*y*^{ii}6

Abbreviations: A = ssp. *adalwinda* (Lappland), B = ssp. *bryoniae* (Swiss), $(BN)^2$ = F_2 hybrid ♀B × ♂N, D = ssp. *meridionalis* (Corsica), J = sp. & ssp. *melete* (Japan), K = ssp. *neobryoniae* (Kärnten), KA = F_1 hybrid ♀K × ♂A, M = ssp. *marginalis* (Oregon), N = ssp. *septentrionalis* (England), O = ssp. *oleracea* (New Hampshire, U.S.A.), Ra = sp. & ssp. *rapae* (England), V = sp. & ssp. *virginiensis* (Connecticut, U.S.A.). L. = from diapause pupa, S. = from non-diapause pupa, ups. = upperside, uns. = underside. Figures and italic letters following sex-signs are individual identifications.

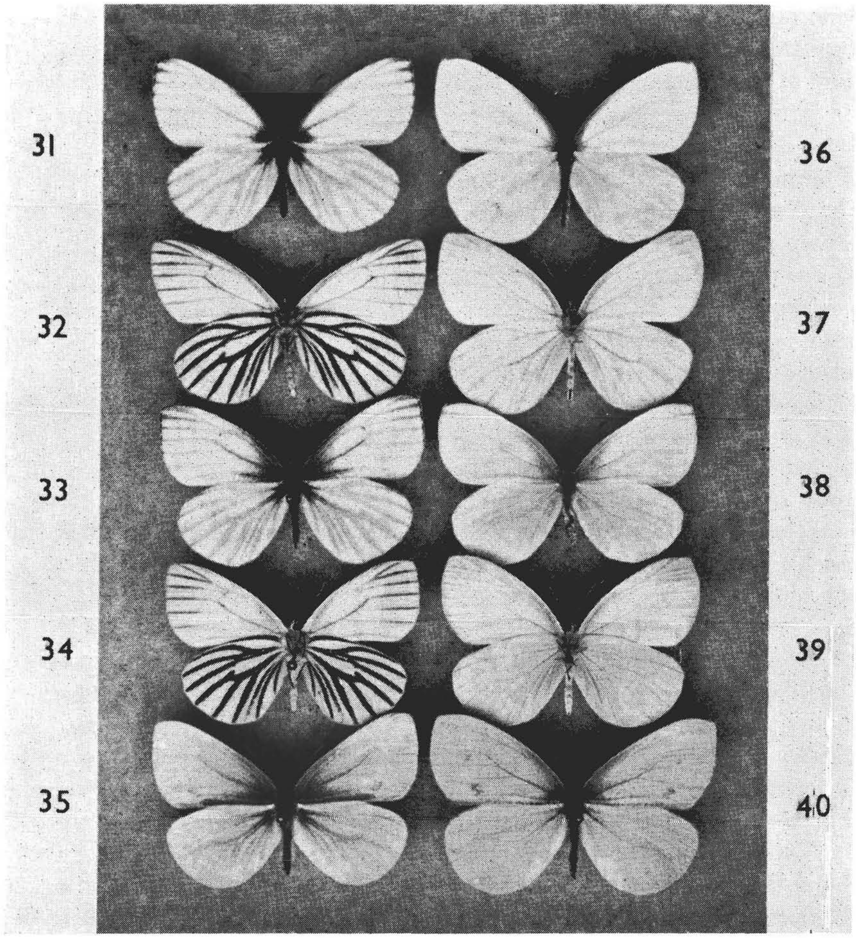


FIG. 31 O L. ups. ♂ '65o^{i}16
32 O L. uns. ♂ '65o^{i}13
33 O L. ups. ♀ '65o^{i}12
34 O L. uns. ♀ '65o^{i}39
35 M L. ups. ♀ '66M^{iii}10
36 O S. ups. ♂ '65O22
37 O S. uns. ♂ '65O27
38 O S. ups. ♀ '65O30
39 O S. uns. ♀ '65O32
40 M S. ups. ♀ '68o^{iii}9

Editor's Note: Figures reduced to 0.88 of original size.

present characters of subspecies must then be expected to have been positively selected, that is, to be "adaptive." When visible characters appear to have no conceivable selective value, appeals to the pleiotropy of genes are commonly made to escape the contradiction: a correlated physiological modification, perhaps affecting behavior or environmental response, is assumed. When the phenotype in question varies locally in frequency it is necessary to think of a covert character, controlled by the gene concerned, which would have different optimization in the various localities. Such characters are not entirely nonexistent, but how are they to be identified? And as Robson & Richards (1936: 274) remarked, "It is no use to smuggle these facts of specific differentiation into the proof of natural selection by an appeal to ignorance, or by an assumption of correlation." In fact an hypothesis supported by a supposition of pleiotropy has no standing until at least the close genetic linkage of a known associated effect has been independently established—calculation of a statistical correlation is seldom convincing by itself.

Moreover, as modifying genes were supposed ultimately to render unfavorable characters recessive (Fisher, 1929), so they should also reduce the penetrance or expressivity of such characters in pleiotropic systems. The appeal to pleiotropy itself admits that the positive selection of a gene need not imply positive selection for all the characters controlled by the gene; visible characters may then well be neutral. And if some of the characters controlled by a pleiotropic gene can be nonadaptive, these seems no reason why other phenotypic characters should not be so. Thus the argument from pleiotropy may be set aside as for our purpose irrelevant. Our concern here is with visible characters: have they been positively selected by external forces, or are they maintained as externally neutral factors in some well-balanced genetic complex? One should allow that even a character originally fixed by selection may thereafter become effectively neutral in a variable environment. For plants, Stebbins (1974) has pointed out that many complex adaptive structures have been retained long after the strong selective pressures that were required to establish them have ceased to exist (e.g. in self-fertilizing Leguminosae and apomictic Compositae). We shall suggest that whether or not genes can rarely be neutral, characters controlled by them quite commonly are. This can hardly be denied (Ford, 1945a: 78).

Curiously, no one seems to maintain that characters which have become specific ones are fixed by environmental agencies. *Clossiana selene* Schiffermüller and *C. euphrosyne* L. are now sympatric and the differences in their patterns owe nothing to present local conditions. How are the wing-markings of *Nymphalis antiopa* L. determined? Normalizing selection is working on ancestral genotypes, probably with no visible response to ecological conditions. If we consider two *Artogeia* species which have become sympatric, say *A. napi* and *A. rapae*, it is clear that at some unknown time these had a common stock, which has since been subject to repeated splitting. It would be difficult to believe that present ecology determines their pattern-differences; why then should we believe that it does so for allopatric ssp. *napi* and ssp. *oleracea*?

In the last few years Fisher's "dogma," which led to various paradoxical results in the hands of other mathematicians, has indeed appeared less cogent. "Mutations" rather suddenly came to include not only conspicuous alterations of the phenotype but also changes in proteins, detectable by electrophoresis, and even replacement of one genetic codon by a synonymous one. Changes in proteins in the course of evolution were investigated by their analysis in nearly and distantly related taxa (Goodman et al., 1971). King & Jukes (1969) concluded, rightly or wrongly, that at the molecular level most evolutionary change might be due to selectively neutral mutations and genetic drift. Kimura & Ohta (1971) also maintained that the protein polymorphisms known from electrophoretic data were transient phases in the random-walk fixation of neutral mutations. Theoretical difficulties were exploited, or explained away, by the mathematical population-geneticists (e.g. Karlin & Nevo, 1976) though, as M. Nei said in discussion, "We cannot make a general inference about nature from a study of a specific mathematical model." But evidently a belief that neutral mutations may have a part to play, at the allozyme or even at the morphological level, no longer involves the scientific ostracism of its holder.

ADAPTATION IN *ARTOGEIA*

In what sense are the characters which visibly differentiate related populations of *Artogeia* adaptive? What common agencies could be expected to exert selective pressure, on the basis of visible characters?

Firstly, the physical environment itself might be directly operative, or might interact with physiological processes.

Secondly, predation by birds, lizards and various arthropods might be influenced by the procryptic or apostatic patterns of individuals.

Thirdly, such predation might be reduced, in unpalatable groups, by warning coloration.

Fourthly, intraspecific pairing might be facilitated, and interspecific pairing discouraged, by the butterflies' recognition only of the appropriate patterns.

These, the more obvious possibilities, will now be considered.

1. Physical environment

It must first be remarked that the genus *Artogeia*, as well as many Satyridae, has been particularly influenced by the climatic changes of the last few hundred thousand years, and it may well be that some distribution-changes are too recent for close approach to genetic equilibrium. As will be seen, this may affect the validity of some arguments.

Subspecies in this group differ in mean size, but so do the two or three generations annually within a subspecies. Particularly common is a slight dwarfing in later summer emergences, attributable to the effect of drought on food-plants. In general, however, *napi* populations from the Mediterranean region tend to produce large adults. Levins (1968) has remarked that contra-gradient variation is common among invertebrates—those in hotter, drier regions may be "genetically" larger to attain the same actual size in their own environment. One effect of the conflicting factors has been to produce some extreme individuals in these climates (cf. Holl, 1914; Warren, 1970). Inter-subspecific dimensional comparisons are therefore best made between insects reared together in captivity; otherwise it is easy to draw incorrect conclusions.

The physical environment certainly exercises control over other physiological adjustments, and also modifies the expression of subspecific wing-characters in each individual; but convincing evidence for its selective influence on these last has been almost entirely lacking.

The absorption of solar radiation and its conversion into heat assists poikilothermic animals to become active. Watt (1968) has studied the thermoregulation of six species and subspecies of *Colias* and shown experimentally that the greater melanization of the underside in the higher altitude populations helps them to approach their optimum temperature by appropriate orientation behavior.

Two circumstances may be thought to favor the suggestion of a similar role for the melanic marking of *A. napi*, as has indeed been postulated by Shapiro (1977) in the case of *A. n. venosa.* Firstly, the underside veining of the summer broods is always lighter than that of the spring emergence of the same subspecies. Secondly, the summer broods of the Mediterranean populations are less extensively melanized below than those of central and northern Europe. However, the interrelation between the directly environmental (diapause/non-diapause) and the inherited factors in these differences makes it difficult to estimate the likelihood of their adaptive origin.

Nor is climatic basis of the melanic cline very certainly established. Descimon & Renon (1975), working with the satyrid butterfly *Melanargia galathea* L. in France, found a melanization gradient exactly contrary to that presented by *A. napi* populations; nevertheless they did not fail to find an eco-climatic rationale.

Again, the explanation usually given for the ochreous color and melanization of ssp. *bryoniae* and *adalwinda* females is that the pigmentation serves to increase absorption of radiation and so enables these females to reach a relatively high body-temperature at high altitudes and latitudes. However, the males too need to attain a certain temperature for successful fertilization; also *Pontia callidice* Hübner at even higher altitudes lacks ochre pigment and is not particularly heavily marked.

In the *Colias* polymorphism involving the form alba (or helice Hübner) the frequency of the paler pterin pigmentation actually increases towards the far north (Hovanitz, 1944), although Watt (1974) showed that in *C. eurytheme* Boisduval orange females heat up more rapidly in sunlight than alba females, as would be expected from their greater absorption of blue light. But Lorković & Herman (1963) confirmed the unequal viabilities of the *C. croceus* Fourcroy genotypes at different temperatures in experimental conditions which presumably eliminated any color effect. Descimon's (1976) conclusion would make the color-difference an incidental consequence of the diversion of nitrogenous compounds from pigment formation to egg-nutrition in the helice form.

Petersen (1952, 1955) has shown a correlation of ochreous pigmentation with relatively heavy melanic marking in *Artogeia* populations of mixed phenotype (ssp. *neobryoniae*). Since both characters are more or less completely dominant, this correlation might be, at least in part, a consequence of hybridization of a genotype producing both with a genotype producing neither. There is no evidence of linkage (Lorković, 1962; Bowden, 1956 and unpublished): the expected recombinations take place in the experimental F_2 and the corresponding phenotypes are to be found also in the wild. In the Fennoscandian territories occupied by ssp. *adalwinda*, *bicolorata* Petersen and *napi*, Petersen (1949) found that the clines for female ochreous ground-color and for heavy melanic marking did not altogether coincide.

Lorković (1962) concluded that "we can say very little about possible pleiotropy of the color genes" and that if there were no correlation with physiological and ecological characteristics there must be a directly genetic selective advantage. Local variation of the frequency of morphs was earlier considered to be a reliable indication of the action of selection. Perhaps this begged the question a little.

How the subtalba balance is maintained, ecologically or genetically (by heterozygous advantage), is not yet known. Bowden (1967) disproved the suggestion of lethality of the homozygote, but could not exclude, in the varying genotypes of the eastern Alps, the possible association of subtalba with linked genes which reduced the number of homozygous females in some broods.

Ford (1964: 291) says, "The *bryoniae* complex of genes and characters evidently fits the butterfly for life at high altitudes and latitudes. . . ." but "It seems unlikely that the same genes are responsible for *bryoniae* throughout the whole of its discontinuous distribution." Since the different elements of the *bryoniae* phenotype (see above, under "Upperside markings") are unequally developed in different localities less than 500 km apart, this is certainly true to some extent, but his further discussion would suggest that *bryoniae* is not a monophyletic group, similar characters having instead been selected, by similar environmental conditions, in local stocks. This is difficult to believe: Petersen (1958) was so convinced of the common origin of the female patterns in ssp. *bryoniae* and ssp. *adalwinda* that he was prepared to allot the latter subspecies to the "species" *bryoniae*, although it belonged reproductively to *napi*.

Robinson (1971) offered the following on f. subtalba: "In either *napi* or *bryoniae* the subtalba form occurs as part of a polymorphism, but in *Pieris virginiensis* the form is actually the wild type. In the Nearctic habitat of *virginiensis* the conditions so favour subtalba that the wild type found in either *napi* or *bryoniae* is completely lacking." Such an ecological "explanation" explains nothing; besides, it is partly contradicted by the *napi*-wild-type coloration of the sympatric *A.* (*n.*) *oleracea*.

A further objection to facile ecological derivations is that in this group of butterflies each population has some freedom to select its own habitat in a locally varying environment. The phenotype, in fact, comes to choose the kind of selection to which it will be exposed (Waddington, 1967). It is even reasonable to suppose that if the American and European *napi* populations were wholly interchanged they would survive by this means, each with its own markings, though the *oleracea* colonies in Europe would not necessarily persist in the precise localities now occupied by *A. napi*.

2. Cryptic patterns

It seems obvious enough that the veined pattern of the underside contributes much to crypsis at rest, as do the mottled patterns of some other pierids (*Pontia*, *Euchloe*). The usually yellow ground-color, whether lemon or ochre in tint, adds to the success of this effect. It is notable that in most of those morphs or subspecies which lack the lemon-yellow sepiapterin, the females or even both sexes have available another pigment (essentially erythropterin) which produces a pale orange (ochreous) effect (Bowden, 1966). The basic pattern of the underside can thus well be called adaptive.

The **differences** among the subspecies probably cannot: all variants evidently work sufficiently well. If one compares *oleracea* with *napi*, it is difficult to suppose that the former benefits from its more conspicuous veining in spring, since this veining practically disappears in non-diapause emergences. Can its American niche demand veining more definite than the European in spring, less definite in summer? Have these butterflies, in all localities, less need for crypsis in summer than in spring? It is difficult to answer these questions in the affirmative. The differences are surely not cryptically adaptive.

The subtalba polymorphism (where it exists as such) could be maintained by selection of apostatic forms (Clarke, 1969), in this case by preferential predation of the locally commoner form of male. In the female, with its greater reliance upon crypsis, the morphs are not very unlike (relative to the variation within each morph) and even the most discriminating predators would hardly distinguish between them. But this possible mechanism may in any case be precluded by aposematism.

3. Warning coloration

Poulton (1890: 185) remarked, "The colours which produce . . . the greatest effect, upon the eye of an insect-eating vertebrate, are black and white. . . ."

It has been stated that *Pieris* and *Artogeia* (especially perhaps *P. brassicae*) are distasteful to birds, and that the white color is aposematic. I have indeed observed that sparrows (*Passer domesticus* L.) are not always effectively deterred from taking *P. brassicae*, and a captive European gecko captured and ate the same insect. Collenette (1935) quotes numerous anecdotal reports of attack by birds on *P. brassicae* and *A. rapae* (and on an occasional *A. napi*); in very few was the insect rejected after being secured. However, there were some observations of definite avoidance. Probably attacks are far fewer than a palatable insect would suffer.

Indeed, Rothschild *et al.* have recently established (Marsh & Rothschild, 1974) that all three British whites feeding on crucifers contain toxic substances which would render them relatively noxious to birds, though only *P. brassicae* is sufficiently so to have evolved aposematic rather than cryptic coloring in the larval stage. The mimicry is Mullerian rather than Batesian, since not only is the supposed model, *brassicae*, usually less numerous than *rapae* and *napi*, but these mimics are themselves toxic.

Certain further facts do support the synaposematic hypothesis:

(i) The close pattern-resemblance of *Artogeia rapae* to *Pieris brassicae*, an insect otherwise so different as to merit its full generic separation (cf. Warren, 1961, Kudrna, 1974).

(ii) The full development of the same pattern in *A. napi* only in the Palaearctic region, where *A. rapae* flies naturally.

(iii) The formation of a similar Mullerian (?) group in eastern Asia, by *A. melete*, *A. japonica* and *A. napi*, again with *A. rapae*. Here the superficial resemblance of *japonica* to *melete* is very close indeed (*A. melete* is toxic—Rothschild, Marsh & Bowden, unpublished).

However, one would say that, to predators, differences in the black upperside patterns exhibited by *A. napi* subspecies in most different localities would probably be irrelevant, neither adding to nor detracting from any deterrent effect. And *napi* does vary independently of its "models" within the European and east Asiatic regions. *A. ergane* Geyer, which belongs to the wider *napi* grouping, is a much closer mimic of *A. rapae.*

If, as seems likely, the white butterflies evolved originally from yellow or orange ones not unlike *Colias*, the aposematic effect of white may have contributed to its success in replacing orange. But orange-and-black, too, is a warning coloration, and Collenette (*loc. cit.*) quotes a case of house sparrows taking white butterflies but neglecting *Colias.*

The pale lemon yellows found in rare variants in Europe would be aposematically inferior to both orange and white, but if so the fixation of "pale yellow" in the ssp. *marginalis* of Oregon requires a special explanation which is lacking at present.

White is conspicuous in nearly all *Pieris* and *Artogeia*, cxcept that in the *bryoniae*-like subspecies the females are dark and show little white. Since the females' individual protection is the more important to the species, there is an implication here that the males' gain from their whiteness is by no means indispensable.

4. Pair-formation

The experiments of Eltringham (1933), well summarized by Ford (1945b), showed that male butterflies recognize their females at a distance by their color. One can observe that male whites will approach any white butterflies, including other males, though at close quarters scent cues and behavior patterns become more important.

On the other hand Petersen and collaborators found that searching male *bryoniae* are attracted (from a distance) to white *napi* females, even in marked preference to their own dark females (Petersen, 1963).

Petersen's experiment needs repeating and extending, but his reported result could be expected from the apparently dull female coloration, if *bryoniae* react equally to ochreous and white stimuli. But there is a complicating factor: these tawny females reflect ultraviolet light, whereas most white and lemon-yellow males and females do not. As has long been known (Lubbock, 1899) insects not only distinguish colors but also see the near ultraviolet so that these "dark" females might appear brightly ultraviolet. Such reflection is not in fact confined to ochreous individuals but is just as strong in certain "white" females, for example those of *A.* (*n.*) *macdunnoughii.*

The absorption of ultraviolet light by the males' wings renders them "colored" to the females and may help to release pairing behavior, though in conditions of proximity scent is almost certainly predominant. Obara (1970) claims to show that ultraviolet reflection is the only signal exciting sexual behavior in the *A. rapae* male, and that markings, size and shape of the wings (and even scent) are all irrelevant. This conclusion cannot, of course, be extended to *A. napi,* many of whose females do not reflect ultraviolet.

Adaptation for sexual selectivity between species is given by the existence of any specific difference readily perceptible by the insects concerned; neither form is "superior" to the other, advantage for both being obtained merely by magnifying the difference.

What, then, should be our assessment of the influence of local selective pressures on the visible characters which distinguish related *Artogeia* populations? Wide variability of essentially the same designs would itself suggest either that the variants are approximately neutral in effect, or else that a number of separate optima exist, each related to the local environment. The latter alternative does not accord with observed similarity of phenotype over geographic areas comprising a range of biotopes. For example, the extensive biotopes of *napi* and *oleracea* in Europe and America vary greatly, as from moorland to deciduous forest, and the heterogeneity is relatively small-scale, with Nearctic and Palaearctic habitats overlapping in character. Clearly the sharply veined phenotype is not being selected by positive environmental pressures peculiar to the New World.

Many subspecies of *A. napi* can be regarded as exerges in the sense of Verity (1925, 1953). In his quoted case of *Mellicta athalia athalia* Rottemberg and *M. a. celadussa* Fruhstorfer, the chief observable distinction is in the male genitalia, but fully fertile interbreeding nevertheless occurs along the subspecific frontier, introgression producing a hybrid zone varying between 50 and 160 km in traceable width (Higgins & Riley, 1970; Higgins, 1975; Guillaumin & Descimon, 1976). Should one suppose that one form of genitalia is adaptive in the conditions of northern and central Europe, the other in Spain and Italy?

Similarly, within the *A. napi* group androconial scale shapes vary; we can see no advantage in this, though as Lorković (1970) has pointed out, variation (if it occurred) in the male scent disseminated might contribute to sexual discrimination; at the specific level the lemon-verbena scent of *A. napi* is quite distinct from the faint sweetbriar of *A. rapae*

(Ford, 1945b). The seasonal androconial differences described by Warren (1961–1967) also must surely be nonadaptive.

We have shown above (see also Bowden, 1978b) that both upper- and underside markings in the *A. napi* group are subject to direct environmental modification; differences between post-diapause and non-diapause adults often exceed those between distinct species. Nor is there sufficient reason to suppose that these phenotypic departures are primarily adapted to special seasonal requirements, though advantage may be taken of them when they favor physiological adjustments. The restricta marking of *oleracea* is nearly phenocopied by European subspecies subjected to an unnatural temperature regime. It is not impossible that the facies characteristic of the various populations are determined by rate-genes which produce differential realization of the elements of the basic pattern, and the seasonal differences are brought about quasi-automatically. Current utility of a character need not imply adaptive origin; the well documented cases of pre-adaptation (cf. Huxley, 1942) are sufficient evidence of this.

There is no need to doubt that these *Artogeia* are well attuned to their rather wide niches, and that this adaptation was achieved through natural selection. Local adaptation, however, seems to be physiological—in respect of such matters as voltinism, temperature-tolerance, etc. This will prevail, whether or not every element of pattern is optimal for the necessary processes.

In the subspecies of *A. napi*, it appears that ecological conditions may now exert little beyond normalizing selection on the genes controlling some visible characters. Elements of the wing-pattern, if they are thus unresponsive to the particular milieu, can be given the greater weight in taxonomy at the species-level and below. The general principle is exemplified even by genitalia and androconia (cf. Robson & Richards, 1936: 299; Ford, 1945a: 79).

Limits of Selection Theory

As Lewontin (1974) remarks, we cannot know the overall importance of balancing selection by demonstrating that it exists—of course it exists. The problem is, what proportion of observed genic variation is maintained by selection? The school of ecological genetics would attempt to solve the problem by establishing and quantifying the selective forces involved in as many cases as possible. But it is doubtful whether anyone has succeeded in measuring the net fitnesses of genotypes for any locus in any species in any natural environment (Lewontin, 1974: 236). Indeed, even attempts to assess reliably the mean relative advantages of alleles in experimental conditions are defeated by the difficulty of securing a representative set of individuals for the trial (e.g. Bowden, 1967). And necessarily, where selection is frequency-dependent, the establishment of equilibrium proportions implies that the genotypes present are equally fit at that equilibrium. It is to equilibria that published mathematical treatments generally refer—and they are almost powerless to involve real time. Fitness may depend not only on the character of the remainder of the genome, but also on the gene's own frequency in the population (Dobzhansky, 1970). Hartl & Cook (1976) claimed to show that purely random selection could maintain genetic polymorphisms even when the expected fitness of each genotype was the same.

PART III. DISSECTED POLYMORPHISM IN SUBSPECIATION

Dissection of Polymorphisms

Many distinctive characters, as we have indicated, are controlled by single genes, and if the differing patterns coexisted in one population—as they sometimes do—would constitute a classical genetic polymorphism (Ford, 1940, 1961).

Lewontin (1974) has said, on the basis of observations on *Drosophila*, that "the overwhelming preponderance of genetic differences between closely related species is latent in the polymorphisms existing within species." This must be even truer of those between subspecies, but we frequently find that within *Artogeia* populations there is in fact little heterozygosity in respect of the distinctive characters that we recognize—hence indeed their taxonomic value.

I shall not attempt to discuss here the general question of the maintenance of heterozygosity in *Artogeia* populations. In very few insect species are sufficient data available—certainly not yet in *A. napi*. Studies of enzyme polymorphisms, how they are balanced and how dissected within and between its populations, may soon provide such data and at the same time suggest phylogenetic relationships. Gene-frequencies close to fixation are very insensitive to selection and have hardly any implications about the recent past; on the other hand a gene-frequency close to 0.5 offers chiefly information about the recent past and essentially none about the remote past (Lewontin in Moorhead & Kaplan, 1967).

Consider a former polymorphic species extending its range and in the course of ages being divided by geographic catastrophe or otherwise into isolated subspecies. In subspecies *b* one morph may become fixed, in ssp. *c* the other, while ssp. *a* retains the original polymorphism. Even if *a* later becomes extinct, the dissected polymorphism (Bowden, 1970) is still traceable in *b* and *c*. This must have been a common sequence for the differentiation of characters of slight as well as of marked adaptive significance. Ford (1945a: 83) quotes the striking case of the arctic fox, *Alopex lagopus* L.

In the sulphurea polymorphisms of *A. napi*, the alleles (four if one includes the near-extinct bright yellow) probably became established by three successive dimorphisms of this kind, though one cannot yet determine their order.

There is of course a general if not universal condition for the maintenance of polymorphism (while it lasts), that the population over a period should be at least as viable with two morphs as it would be with either alone. When the morphs have become fixed in allopatric populations or even distinct species, it seems that at some time and place this condition has ceased to be satisfied.

But this overlooks some consequences of the variation within the precursor population. Since its genotype is not uniform, the samples taken from it to produce *b* and *c* will have differed, and if these founder populations have been small, either originally or in subsequent fluctuations, some genes included in *a* may not be represented at all in *b* (or *c*). Moreover, as May (1976) reminds us, replicate lines from the same initial population, kept in identical conditions, can reach very different limit-compositions, as a result of statistical accidents early in the breeding program.

The so-called fixation of one morph theoretically does not involve the permanent elimination of the other, even in a single population. Recurrent mutation may be expected to cause its persistence as the heterozygote at a very low fluctuating level, even if with intermissions. It might seem that this could permit the reconstitution of the polymorphism if selection-pressures came to favor it, or even the evolution of a new genotype around the temporarily rare allele. But the chance of this must steadily decline and finally vanish.

The irreversibility of evolutionary changes was postulated by Meyrick (1884), though apparently only for changes of generic or higher rank. Muller (1939) already concluded, "The determination of the exact mutational path of evolution involves a large element of accident and . . . this path can never really be retraced, nor paralleled, in a second evolutionary sequence, nor can the same complex genic system be twice arrived at." At any level, the principle follows from the mutual dependence of genes in their operation. As a mutant at one locus proceeds towards fixation, other parts of the genotype undergo changes, so that a simple reverse mutation no longer restores the original condition. For true restoration a series of reverse changes must take place in the correct order—with probability approaching zero. An evolutionary event is reversible: an evolutionary history is not (Dobzhansky, 1970). Thus I believe that lost characters are rarely restored, and perhaps never with quite the original genetic mechanism.

While our precursor species remains intact, we have a number of individuals, occupying the same niche, in competition. But if *b* and *c* are separated geographically, interbreeding ceases and so does reproductive competition. The two daughter gene-pools evolve along separate historical successions, genotypes in *b* now competing only with other *b* genotypes; whether *c* has evolved "superior" genotypes is irrelevant. Thus it is not certain that *b* and *c* are both better adapted in their own locations: it is possible that they would do equally well if interchanged.

Species appear to have been free to make a wide range of replies to the same ecological demands. It is remarkable how different organisms in the same habitat, and even in practically the same niche, utilize such diverse means of "adaptation" to it (thus of course modifying the niche). The strength of their defense against the selective tyranny will be appreciated more readily by the botanist (Willis, 1940; Gavaudan, 1967; Stebbins, 1974) than by the zoologist, who is tempted to endow his mobile subjects with niches of any complexity that his theories demand. "Within any gene-pool there exist several . . . alternative gene combinations that might adapt the organism to any new environment. The particular adaptive combination that will become established will depend largely upon the nature of the gene-pool already present" (Stebbins, 1974). If a population could be divided *equally* between two separate identical biotopes, it is probable that even then two identical subspecies would not be formed.

Only in its marginal habitats is the adaptation of a species critical for its survival. Butterflies are able to accomodate variation in the reproductive success of the "same" population by factors of ten or twenty to one (much larger fluctuations have been quoted for other organisms); beside such ratios selective advantages of even five or ten percent related to a particular imaginal character (even fertility) are quite insignificant **if they apply between separated populations**. This does not mean that, within each, selection does not still act on the character—merely that the apparent alternatives are not in competition, if the taxa concerned are no longer interbreeding. Allopatric differences cannot be maintained by selection between them.

The relative stability of a subspecific genotype results from its achievement of an adaptive peak, almost any small departure from which will involve disadvantage. In a widespread species there are many such peaks, and although some are "higher" than others, a particular population will normally be unable to pass from one to another. Only where a cline exists peaks are not separate but form, as it were, an elevated ridge, allowing free variation in the clinal character.

In any one environment, at any time, there may be several adaptive peaks accessible to a population. Once it is on a slope, selection will drive it upwards, but it cannot climb two separate peaks at once unless it is no longer panmictic. The initial difference which determines the peak to be climbed is at that stage probably nearly neutral.

Nor does the peak genotype's integration imply that any one character has optimum individual adjustment. This is clear enough where distinct "island" subspecies occur in the same climatic region; examples are well known in *Erebia* (Satyridae). In that genus the different wing-patterns may tell us something about past relationships, but very little about present ecology.

"Les corps inanimés ne dependent pas du temps. Les corps vivants lui sont indissolublement liés. Chez eux, aucune structure ne peut être détachée de l'histoire" (Jacob, 1970). Whatever is, is good—but it may not be the best.

Origins, Range-changes and Hybridization

In recent years systematists (e.g. Brundin, 1972; Darlington, 1970; Croizat *et al.*, 1974) have been debating newly formulated ideas on biogeography. The accepted view, deriving originally from Darwin, had been that a species arose at a particular place and if successful spread therefrom. Adams (1902) provided criteria for the determination of centers of origin, the most important being the "location of the greatest differentiation of a type." Matthew (1915) deduced that the most advanced species would be found at the center of origin and the most primitive or conservative in peripheral areas. However, Hennig's (1966) "phylogenetic systematics," sometimes identified with cladism, implies that speciation is always by division of a pre-existing species-stock (e.g. by geographic catastrophe) to produce vicariant populations which then evolve separately in their own areas: these are recognizable as belonging to one monophyletic group by their common possession of derived ("apomorphous") characters. One of Hennig's rules states that species with the most primitive characters are found in the area earliest occupied by the group—thus contradicting the formerly accepted view.

Some of the contestants approached bigotry in their philosophical discussions, and the subject can now be advanced only by consideration of particular examples.

Too little is yet known about *Artogeia.* Using Adams' criterion, the genus was given an origin in central Asia, and writers such as Müller & Kautz (1939) supposed that species and subspecies spread therefrom to the north, west and east, reaching North America via the Bering area. These taxa, then, differed even at the start of their journeys and retained their characters long after arrival. On the other hand, Hennig-Brundin principles would suggest that, while any secondary characters held in common are evidence of common descent, the characters distinguishing the subspecies arose only in the various localities after contacts were interrupted, and represented the results of local adaptation.

Both alternatives are too simple. The evolution of *Artogeia*, in Pliocene and Pleistocene times, has been complicated by relatively rapid alterations of climate and by fluctuating sea levels affecting the extent of exposed ice-free land. Time-scales are such that, in many if not all cases, territories must have changed since the differentiation of the taxa—a process almost indistinguishable in its results from conventional dispersal. One has to suppose that major continental drift in the Atlantic area occurred too early to affect *Artogeia*, but some seas, and some mountain ranges, are younger.

Even in a region as small and well-known as the British Isles, there is still some uncertainty about the relationships of the populations of *A. napi*. Its position is simpler than that of *Aricia agestis* Denis & Schiffermuller/*artaxerxes* Fabricius (Høegh-Guldberg & Jarvis, 1969), in that it is unnecessary to propose any specific separations, but there are parallelisms. Verity (1911, 1916) placed the dark-female butterflies of Ireland and Scotland in his ssp. *britannica*, while naming those of England as ssp. *septentrionalis*. Warren (1968) took the Scottish populations (but not the Irish) as belonging to the "species" *adalwinda*, and named them ssp. *thomsoni*; his view was based on a strange argument concerning their androconial scales. In 1970 Lees recorded the existence of a univoltine race in Yorkshire at about 300 m elevation. Thomson (1970) found that androconial *thomsoni* extended as far south as Yorkshire, but was everywhere at least partly bivoltine.

An adequate discussion would be out of place here. There seems little doubt that the Irish and Scottish populations, which regularly include ochreous females and darkly marked ones, derive partly from *adalwinda*-like insects which occupied the Channel area during the last stages of the Würm (Wisconsin) glaciation. In the short post-glacial period *A. napi napi* has invaded Britain from the South and its introgression has progressed so far that in southern England the modern ssp. *septentrionalis* hardly differs from the nominotypical subspecies. Even in Scotland there are probably now no pure relict "*adalwinda*." Indifferently as to whether they carry subarctic genes or not, all members of the Scottish demes are adjusted physiologically to their present biotopes. Where and how the original separation of *napi adalwinda* and *n. napi* took place is quite unknown.

In North America, mountains made conditions complex during the retreat of the ice, and true relict populations may exist—ssp. *marginalis* and perhaps *macdunnoughii*?

Even in the last ten thousand years or so insects whose predecessors were separated at much more remote periods have come into renewed contact while still interfertile. The resulting zone of secondary intergradation (Mayr, 1942) is commonly marked by a proliferation of forms in unstable polymorphisms. The instability is long-period and so cannot be established with certainty. Probable examples are to be found in the *Artogeia* "subspecies" *flavescens* Wagner and *neobryoniae*; the zones of introgression are quite deep, suggesting that the gene-complexes of the original constituent races were basically similar. Indeed without such similarity the gene-expression might be disturbed (Kettlewell, 1965, 1973). Variation in chromosome number within a population, as in *A.* (*n.*) *neobryoniae* (Lorković, 1970) may or may not lend support to the hypothesis of hybrid origin, but the significance of B-chromosomes in the *A. napi* group is still uncertain.

Warren (1966–69) has derived many apparently normal *Artogeia* species or subspecies from processes of hybridization (necessarily in secondary contacts). As he writes, we have for example *oleracea* and other Nearctic subspecies taking their origin from *A. narina* Verity × *A. dulcinea* Butler (Warren, 1968). These supposed parent species must be understood as ur-*narina* and ur-*dulcinea*, because they may since have undergone as much change as the "hybrids" evidently have. If we reject Warren's unsatisfactory androconial criterion of hybridism (Bowden, 1971) there is no obvious reason to exclude the possibility of an ur-*oleracea* contemporary with the precursors of *narina* and *dulcinea*. Hennig (1966) seems to take the view that when a new species has split off from an existing stem-species, the stem-species also must be taken as changed. I am not sure that this will always be so, when new species are formed from peripheral subspecies. Nor is the possibility of reticulate evolution (i.e. close hybridization) to be altogether excluded: there may sometimes have been more than contact-line introgression. We should try to infer phylogenies for our species from the evidence that we can collect, but a large element of conjecture will have to be tolerated.

The Alaskan *A.* (*n.*) *passosi* Warren may well be the *oleracea* × *hulda* hybrid that Warren (1968) supposes, though not reproductively isolated from either *oleracea* or *hulda*. In the secondary contacts of the *napi* populations of Scandinavia, the British Isles and southern Europe the distribution of characters in the conjoined populations has perhaps become clinal, with no definite limits to the mutual introgressions. If the characters are adaptive or have become linked to adaptive ones, local optimization may control the proportions of the morphs in a frequency-cline, but otherwise recognizable distinguishing characters reflect origins rather than adjustments to the varying environment. Stepped clines may be better considered as arrays of micro-subspecies, unless appropriate partial barriers can be found located at the steps. See, however, Endler (1977).

Ford (1949) treats British *Coenonympha tullia* populations as a presently interrupted cline, and postulates some flow of genes between many of them even today, but in fact his Merioneth × N. Scotland crosses showed disturbances almost too great for a mere cline of 700 km. Even a continuous cline, with its assumed equilibrium conditions, may not always be distinguishable from an historical pattern originating from range-change by differing routes.

Clarke (1970), commenting on the Cornish boundary phenomenon in *Maniola jurtina* (Creed *et al.*, 1959), suggested that two races of the species might have been involved, though Ford (1975) rejected this view with extreme scorn. Nevertheless, an "area effect" (Cain & Currey, 1963), of adaptation to inherited genotype rather than to external ecology, may indeed be operative.

CONCLUSIONS

Special

1. There is no evidence that the difference in *Artogeia napi* between narrow American underside veining and broader European veining is adaptive. Both crypsis and optimum radiation-absorption can be secured with either arrangement of black scales.
2. In the "summer" emergence of various subspecies there may be adaptive adjustment of the degree of underside blackening for the most favorable balance between cryptic and thermoregulatory functions.
3. The subtalba polymorphism, controlling production of sepiapterin or failure to produce it, is dissected in the *Artogeia napi* species-group. In certain populations, particularly in the alpine regions of the Old World, the polymorphism is a balanced one, at least on a medium time-scale. Though proportions of the morphs vary locally, no ecological basis is yet known and explanations may be historical.
4. Form subtalba may have reached the *bryoniae* butterflies from an ur-*melete* or related Asiatic taxon, but if so changes have since occurred in its genetic control.

5. Other alleles at the sulphurea locus will repay further study in a wider range of populations in the three continents concerned. The pale yellow forms are stabilized in at least one (probably relict) subspecies.

6. The significance of the *bryoniae* female marking remains uncertain. The taxa carrying it were in the past conspecific with other branches of the *napi* stem. Müller & Kautz (1939) considered it beyond question that these taxa represented the conservative (even archaic) descendants of the Pliocene, probably subtropical, insect. This is no more than conjecture, but not unreasonable; if it is correct, what we have to account for are not the dark females but the white males of *bryoniae* and both sexes of *napi*.

7. *Artogeia* adults are cryptic at rest, probably aposematic in flight. Local differences in pattern may be irrelevant in both respects.

General

8. Overt differences between allopatric populations of the same species or species-group need not be supposed in every case to have any present adaptive significance. Some varying characters shown in the course of a life cycle may be well adapted to the habitat, but many are approximately neutral. Competition between their holders can only be internal to a population. The central weakness of the extreme selectionist position may lie in its assumption that a determinable fitness is associated with any particular gene.

9. The permanence of subspecific characters (and still more of specific) depends on their tendency, once fixed in the genetic sense, to become irreversible in practice.

10. Characters that are now nonadaptive may have been evolved at a remote period in a locality far removed from the present habitat. Biogeography is not merely a branch of ecology. Ecological fallacy results from treating populations as stationary objects of local selective pressure; instead, they should be allowed a more active role, with every evolutionary quasi-random "choice" determined in some degree by the influence upon the genome of previous choices. The saying "Evolution always occurs somewhere else" is nearly true.

11. When the "same" character arises independently in two stocks by parallel evolution, parallelism will probably be incomplete and a genetic difference can sometimes be found, to alert the investigator.

12. Otherwise, the common possession of the same "nonadaptive" characters permits tentative conclusions on phylogenetic relationships. The barrier to the reversal of a genetic change is an increasing one,

allowing the established form to be taken as indicator (though not as final proof) of the affinity of subspecies which possess it.

13. Discontinuities of pattern-distribution can often be used to delimit demes whose past histories have not coincided.

14. Genetic histories do not repeat themselves, whatever the ecological pressures.

Murray (1972), discussing the work of Kimura & Crow and others on electrophoretic alleles in *Drosophila*, etc., says: "There are loci which are monomorphic in all populations, there are loci with rare variants, and there are loci which so variable that no 'wild type' can be identified. However, there is a kind of differentiation that is conspicuously absent, i.e. a pattern of variation with the fixation of different alleles in different localities. This last pattern is the expected outcome of allelic neutrality."

Publications on the allozymes of *Artogeia* are awaited. But is this missing pattern not to be found in the visible characters of this group?

In one sense, all important characters of the *napi* group are adaptive, and are maintained by soft selection (Wallace, 1968). But the visible differences between the various taxa, with which this paper has been concerned, are not primarily adaptations to the present environments but derive from historical "accidents" affecting neutral or nearly neutral polymorphisms in the distant past. As far as can be seen, there has always been more than one way forward for a subspecies. Even under strong selective pressures there are alternatives, and each option taken modifies the choices which will be presented in the future.

ACKNOWLEDGMENTS

I am indebted to an anonymous referee and to Dr. Bryan Clarke for valuable criticism of earlier versions of this paper.

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