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There are several reasons why the Lepidoptera provide material especially well suited to certain aspects of scientific research, in particular, perhaps, those within the field of ecological genetics. In the first place, one must mention the beautiful colour patterns of the imagines, which make it possible to analyse many components of their variation with especial ease and efficiency. Secondly, and no doubt originating from their striking aesthetic charm as well as their dramatic metamorphoses, butterflies have been one of the two animal groups most studied by generations of naturalists (birds being the other). Thus it comes about that we possess an immense fund of information on their ecology; these insects really have attracted more attention and for a longer period than any others, and the knowledge so obtained is of practical importance as a background for many types of biological research. It has indeed gradually accumulated until Lepidopterists have found the need to establish an International Society such as ours, in which the old natural history is transformed into an important branch of modern science. Yet let us not forget the entomologists of an earlier age. Some who were collecting butterflies and moths 120 years ago have been my personal friends and I know what fine field workers they were: their store of information, largely centred upon habit and behaviour, for the most part died with them, but it was great.

When we consider the impact of the Lepidoptera upon scientific research, one point strikes us at the outset or else is accepted as a basis inherent in the material we use: that is to say, their taxonomy. For if

we are to study any large assemblage, of whatever kind, it is necessary to classify it hierarchically. In doing so we must create some system giving us confidence in the names applied to the groups we use. It is perhaps invidious to single out any of those who have laboured to establish the nomenclature of the Lepidoptera. However, I would at least mention Mr. Francis Hemming, whose death some years ago was so serious a blow to this work, and Dr. C. F. dos Passos, of our own Society, to whose studies in this field at the present time taxonomy owes so much.

But what of the groups which the taxonomist names? We are all aware that though many possible classifications could be applied to them, that in general use is based upon relationship, so that it reflects one important aspect of reality; that is to say, evolution. It is our aim that the Lepidoptera placed in any one taxonomic division, whether it be small or great, species or family, should be more closely related to one another by actual descent than they are to any other organisms upon earth. Thus if the arrangement be represented diagrammatically, the result should produce a geneological tree.

We should certainly enquire whether that object, so basic to our endeavours, has been attained. Is the classification of butterflies and moths something more than a man-made convenience; does it indeed reflect affinity? We have a fair guarantee in that matter arising from the work of taxonomists themselves, who generally take into account the widest range of characters in making their decisions: morphological and physiological and in all the stages of the life history. But we can test its success when we extend to it a new criterion. We shall be on sure ground if independent evidence supports conclusions reached in ignorance of it.

Many years ago it seemed to me worthwhile to seek such confirmation. I obtained it by examining the chemistry of the wing pigments of butterflies and moths. These indeed proved to be strictly related to a classification which had taken no account of them. We have time to cite one instance only. Consider the flavones: these are non-nitrogenous pigments, ranging from deep yellow to ivory-white and derived ultimately from plants. Certain Lepidoptera make use of them to colour their scales, others do not. But those which employ them in that way are not scattered at random among the rest. Thus in the family Pieridae, flavones are never found except in the sub-family Dismorphiinae, and even there in but a proportion of the species (19 out of 58 tested: from a total nominally assessed as 108). Yet, with one exception independently admitted to be a taxonomic error, those in which they occur had been grouped together, although this particular quality which they share was unknown

to the entomologists who classified them (Ford, 1941); many other similar corroborations have subsequently been obtained.

Bearing these advantages in mind, the Lepidoptera have naturally been extensively used in scientific research, and a few examples of the problems they have helped to illuminate may briefly be considered here. We may first take the question of selection-pressure, and indicate two of the instances in which it has been evaluated.

The butterfly *Maniola jurtina* L., which is single brooded in Britain and most of Europe, has provided information on this subject. A criterion of that insect's adaptive adjustment is supplied by the spots on the underside of the hind wings. These may be absent or present in any number up to five, arranged as a curving submarginal row. They are controlled by polygenes which influence also other characteristics of greater importance to the organism and of these the spots may be taken as an outward and visible sign. Thus they affect the date of emergence, the more spotted specimens appear earlier, and also affect liability to destruction by certain parasites. These polygenes moreover, play an important part in adjusting the gene-complex to the needs of the population. When the butterflies are reared in a cool laboratory, with a temperature fluctuating in the region of 15° C, the heritability of spotting is 0.83 in the females and 0.14 in the males (McWhirter, 1969). At higher temperatures, the environmental component, so much greater in the males than in the females, is reduced; for at 22° C heritability actually approaches 1.0 in the females and it reaches 0.4 in the males. Thus selection has much genetic variability on which to operate.

We may concentrate here upon the female spot-frequencies since, being subject to greater major variability, they are more diagnostic than those of the males, which are nearly always unimodal at two spots. Not so the females, in which the spot-frequencies are diverse and characteristic.

The Isles of Scilly are an archipelago in the Atlantic 30 miles from the south-western extremity of England. We have studied *Maniola jurtina* upon a number of the Islands there, some large (682 acres or more), others small (40 acres or less). The difference in area between the two types is, therefore, at least 17 times. Female spotting differs greatly from one to another of the small Islands (it may be unimodal at 0 or at 2, or bimodal with the greater mode either at 0 or at 2), retaining its characteristic value on each, year after year. It is, however, similar on the major areas of all the large islands (with approximately equal values at 0, 1 and 2 spots), a frequency not found on the small ones. What, may be enquired, is the meaning of such distinctions. In interpreting them we have to

remember that the spotting is stabilised at characteristic values on each island. This in itself excludes an explanation based on random genetic drift, so does the size of the various populations involved, for they may comprise thousands of imagines, ascertained by the technique of marking, release and recapture. We have indeed strong reasons for thinking that the butterflies are adjusted to the distinct ecology of each small Island but to the average of the conditions on the much more diversified large ones, and such averages tend to resemble one another (Ford, 1965).

It has also been suggested that the Founder principle operates here. Yet changes in these highly constant spotting types have actually been witnessed as the result of rare cataclysms. They have produced new and stabilised spot-frequencies differing as much from the old as those on one small Island differ from another.

We may consider the situation on White Island, which is divided into two parts, each about a quarter mile long, by a low narrow neck of land. This was covered by sand and shingle during a great storm in the winter of 1957-58. As a result, the *Maniola jurtina* population was subdivided. That on the southern half of the Island, previously stabilised with a mode at no spots, changed at once to a condition unimodal at one spot and remained for eleven years at the new frequency; until in 1969 the recently created barrier ceased to be effective owing to the growth of plants upon it and the spotting returned to its pre-1958 values. A selection-pressure of 68 per cent with 5 per cent confidence limits at 31-81 per cent, in favour of one-spotted individuals was needed to produce that result in 1958 (Creed *et al.*, 1964).

Turning briefly to *Maniola jurtina* as found in south-west England, the females there are bimodal at 0 and 2 spots, though in the rest of the country and throughout Continental Europe, except in its more peripheral regions, they are unimodal at 0 (Dowdeswell & McWhirter, 1967). Though the boundary between the two frequencies has repeatedly altered its position by several miles in a single generation of the butterfly, one type changes into the other in a few yards; it does so along a line crossing the peninsula of Devon from north to south. No physical boundary is involved and imagines of the respective stabilisations are constantly intermingling where they meet (Creed *et al.*, 1959).

In 1957 the boundary between the bimodal and unimodal types moved three miles eastward. This involved selection of 65 per cent, with 5 per cent, confidence limits of 31 to 82 per cent, against two-spotted individuals in the population involved. Such high selection-pressures now prove to be usual in the micro-evolution of the Lepidoptera, as we find them to be in other organisms.

In addition to selection, one of the features operating in evolution is provided by isolation, as Darwin clearly points out. An aspect of this, a curious one seldom considered, has just been mentioned: that provided by selection so powerful that it can break up a population into two adjusted types, maintained without geographical discontinuities, a situation sometimes manifested by the formation of a reverse cline (Ford, 1965), as indeed in *Maniola jurtina*. That is to say, the distinguishing characteristics of two populations become accentuated towards the line where they meet; selection being powerful enough to eliminate the less well adjusted intermediate types at the interface between them. Since, as we have seen, one spot-adjustment can be converted into another, there is no question of a past gap in the distribution of this insect from which populations with distinct spotting-types have spread until they have come into contact. That, of course, can occur and it produces somewhat similar results to the one just mentioned, though not the conversion of a part of one race into the other. Thus the Scandinavian and European races of the Selidosemid moth *Bupalus piniarius* L. meet and interbreed across England at the level of Lancashire and Cheshire (Cockayne, 1912-13). The one must be an Ice Age relict which has retreated northwards, the other a Holocene colonist from Europe. Yet their approximation has not produced a cline. On the contrary, there is an area of high variability between these differing adjacent populations, within which the recombinants are constantly produced though they fail to spread in either direction so as to swamp the characteristics and balanced adaptations of the two forms.

We have not indeed extensive information on the genetics of speciation and racial differences in the Lepidoptera. The distinctions between the *Bupalus piniarius* races appear to be multifactorial. Those separating closely related species may be also, or they may include characters resulting from the action of major genes.

The Lycaenid genus *Aricia* contains two European species not separated until 1935. These are the bivoltine *A. agestis* Schiff., the northern limit of which is reached in southern England and northern Denmark, and the univoltine *A. artaxerxes* F. from northern Britain, Norway, Sweden and Finland (Frydenberg and Høegh-Guldberg, 1966). Each includes a number of more or less distinct races and their characteristics must not be confused with those of the species as a whole. For instance, the features distinguishing *artaxerxes artaxerxes* from *artaxerxes salmacis* consist of a white central spot on the upper side of the forewings and an absence of the central black dot within the white spots on the lower surface. That condition is due to a single gene recessive in effect.

However, a number of characters, none in itself entirely distinctive, separate *A. agestis* and *A. artaxerxes*. These are quantitative only, yet some are unifactorial: thus one is provided by the more heavily marked larva of the latter species, another by the larger submarginal orange lunules on the upper side of the imagines (Høegh-Guldberg, 1968; Høegh-Guldberg and Jarvis, 1969). No feature is said to be fully diagnostic of these two butterflies except the double and single brooded habit. This is by no means a specific trait in other Lepidoptera; it is not so, for instance, in the moth *Zygaena lonicerae* v. Schev. (Lane and Rothschild, 1961). In *Aricia* that quality seems to depend on combined environmental and genetic influences, the latter multifactorial. Here, however, it does seem to some extent to separate two groups specifically, for crosses between them are to some extent infertile.

A rather similar situation from the evolutionary point of view is provided by *Pieris napi* L. and *P. bryoniae* Ochs. It is now said that their chromosome numbers differ: $n = 25$ in *napi* and 26 in *bryoniae* (Bowden, 1966a). *P. napi* is Holarctic and occurs from sea-level up to high altitudes. *P. bryoniae* is alpine and boreal only, having a discontinuous distribution which includes parts of Scandinavia, the Alps, Central Asia and Canada. The two insects are separated by a number of features which tend to maintain their reproductive isolation: habitat, differences in time of flight, low viability of the hybrids and differential mating behaviour (Petersen, 1963). Their larval foods are not the same and though the males are very similar the females are highly distinct. *Bryoniae* differs from *napi* principally owing to the action of several major genes (Lorkovic, 1962): (1) *B*, which is autosomal and nearly dominant in effect spreading melanin along the veins, and (2) the gene *Y* which produces the ochreous-yellow ground-colour of *bryoniae*. It is incompletely dominant and is almost entirely sex-controlled to the females.

In addition, many populations of *bryoniae*, especially in the eastern Alps, are polymorphic for a gene *W* producing dominant white coloration on the underside of the hind wings and tips of the forewings (Bowden, 1963). This is allelic with that responsible for the two recessive yellow phases (*sulphurea*) found as rare recessive mutants in *P. napi*. It has been said that the polymorphism of this white-underside form (*subtalba*) is partly maintained by the lethality of the homozygotes. Bowden (1967) produced some evidence for this but certainly obtained homozygous whites. In this matter, a point of general importance must be recognised. That is to say, a selective disadvantage of 10 or 15 per cent may be effective in maintaining a polymorphism but very difficult to detect in experimental breeding.

It is especially to be noticed that both the genes *Y* and *W*, and probably *B*, occur as rare mutants in the normal population of *P. napi* (Bowden, 1963). We have here a clue to the extremely discontinuous distribution of *bryoniae*. That is to say, the genes capable of producing it are widely available when their action is appropriate to the ecology of this *Pieris* complex.

There are, of course, many instances in which a form controlled on a unifactorial basis appears to recur in isolation, though we do not know whether the same gene be responsible for it in the different habitats. Thus the Arctiid *Cynia mendica* Cl. is ordinarily a sexually dimorphic species with black males and white females bearing black dots. In the Irish race, *rustica*, the males are white like the females, due to the action of a gene sex-controlled in effect and giving intermediate heterozygotes (Onslow, 1912; Ford, 1967a, plate 10). Yet *rustica* recurs in a few populations in Europe, or else its phenotype does so.

The moth *Triphaena comes* Hb., Caradrinidae, provides one of the few instances in which a phenomenon of this kind has been analysed from a comparative point of view. The dark form, *curtisii*, occurs as a polymorphism in three isolated populations: the Outer Hebrides, the Highlands of Scotland and in Orkney. It is identical in appearance in all of them. It has been shown that the Hebridean and Orcadean populations are due to the action of one major gene and that it is the same in both places, but it is adjusted by different modifiers to give an apparently identical effect in each (Ford, 1955). Here we really do know what is meant when we say that the "same" form of the species occurs in two distinct areas.

From this point we are, by an easy transition, taken over to another system of variation, that of polymorphism, and to another aspect of evolution, that of *Industrial Melanism*.

The Lepidoptera are, of course, famous for providing that outstanding reaction to pollution. Though known in other groups, (*e.g.* *Adalia bipunctata* L. among the Coleoptera, Coccinellidae), it is in the moths that Industrial Melanism is most widespread and striking (Kettlewell, 1957, 1961). This is not the place in which to discuss that situation, for it merits long and detailed attention, but a few of the facts relating to it can briefly be summarised.

Many dozens of species have become black in the industrial areas of Britain (where approximately 100 are affected), Continental Europe, the U.S.A. and elsewhere. Nearly all are controlled by a single major gene, dominant in effect. They spread owing to the action of two agencies. One is bird predation of the less cryptically coloured forms: the melanic insects on light coloured bark and lichens; and the normal pale ones on

trees, fences and other sites which are blackened by pollution in manufacturing districts. The second agency responsible for the spread of industrial melanics is the evolution of heterozygous advantage, which is brought about in either of two ways or by a combination of them: 1) the accumulation of common lethal or semi-lethal mutants close to the locus controlling the polymorphism; 2) the evolution of dominance, operating in different directions upon the multiple effects of the switch-gene. This causes the disadvantageous qualities it determines to become recessive and the advantageous ones dominant, so ensuring the superiority of the heterozygotes over the other two genotypes.

The occurrence of Industrial Melanism provides an exceptionally sensitive test for the spread of pollution outwards, and down the prevailing wind, from industrial areas. Moreover, we have here excellent examples of evolution in progress, for the melanic forms of many moths even though unifactorially controlled have become progressively better adjusted to their environments, both in their physiology and in their colouring, by selection operating on their gene-complexes (Kettlewell, 1965).

Only very rarely is an industrial melanic recessive. The large Bombycid *Lasiocampa quercus* L. provides an instance of the kind on a moor in Yorkshire. The area is heavily polluted with soot and a blackish-brown form of the moth occurs there (Kettlewell, 1959). Probably it is preferentially selected by the large numbers of Gulls which prey upon the species in that locality. The blackish specimens at present amount to only about 5 per cent of the population; though of course the gene responsible for them must occupy approximately 35 per cent of available loci, more if the heterozygotes are at an advantage.

An identical melanic is also found occupying up to 70 per cent of the population on heather moors in northeastern Scotland. There the plants are stunted and widely spaced, exposing the black peaty soil and giving the whole area a dark appearance. Here we return to the aspect of isolation that has just been discussed, for this is another of the rare instances in which it has been studied experimentally. The result proved that the two apparently similar blackish forms, in Yorkshire and north-east Scotland respectively, are generically distinct, being produced by different major genes. That in the Scottish population, moreover, is not fully recessive in effect.

In the Yorkshire population, where recessiveness is complete, an additional feature of interest is to be noticed. That is to say, a recessive black form of the larva also exists, which is absent from the Scotch locality. It is due to a separate gene from that giving rise to the dark imagines, but

the two loci are closely linked: in fact they are probably being built into a super-gene.

This indeed is characteristic of co-adapted genes when polymorphic. Selection tends to produce close linkage between them so that the appropriate features can segregate together. For polymorphism involves discontinuous variation, as in the human blood groups, in which even the rarer form is maintained selectively. The phases are indeed balanced either ecologically, as to some extent in butterfly mimicry, or by a superiority of the heterozygotes (Ford, 1965). Thus the evolution of super-genes, as of heterozygous advantage, will generally take place in polymorphism which must in view of these attributes be a very common phenomenon. It is, moreover, one which must nearly always be controlled genetically, by the segregation of a major gene or a super-gene. Environmental differences are indeed able to affect profoundly entire broods and populations, as in seasonal variation (which we see, for instance, in the Nymphaline butterfly *Araschnia levana* L.) (Ford, 1967b). They are hardly capable, however, of evoking discontinuous variability throughout a considerable region. This indeed becomes an impossibility when, as in polymorphic situations, the frequencies of the forms must be appropriately adjusted to differing ecological situations.

Polymorphism is usual in the Batesian mimicry of butterflies, in which its properties are clearly seen. For as the relative numbers of mimics sheltering under their resemblance to a distasteful form rises, so the benefit they obtain from doing so declines until it is lost and converted into a disadvantage. Therefore selection will favour the tendency for a Batesian mimic to copy several models. This it must do by means of polymorphism: evoking a mechanism, that is to say, which avoids intermediates and and therefore the production of unprotected forms.

Yet the switch-gene necessary to achieve this must have arisen by mutation, and we cannot expect its original effects to have been accurately adjusted so as to resemble a particular model. That is achieved gradually by selection, acting upon the gene-complex, within the ambit of the controlling major gene. Thus it is repeatedly found that mimicry even when "unifactorial" becomes imperfect in crosses with a race in which the appropriate model is absent (Clarke and Sheppard, 1960a).

The two major consequences of polymorphism are also exemplified in mimicry. The phases of a Batesian mimic often include non-mimetic forms which, as in normal polymorphic situations (the white and yellow females of *Colias*, for instance: Remington, 1954), are maintained by heterozygous advantage. This, and the selective adjustment involved, is demonstrated by the fact that mimics can sometimes exist even at high

frequencies outside the range of their models (as in the *Polytrophus* race of *Papilio dardanus* Brown, in the mountains east of Lake Victoria). That they do so demonstrates their physiological advantage; it demonstrates also the importance of their deceptive colour-patterns, for the accurate resemblance of these is lost in such circumstances (Clarke and Sheppard, 1960*b*).

The adjustments of mimicry are usually multiple, requiring the combined action of co-adapted genes. These must be held together in appropriate combinations by close linkage; their inappropriate ones, also produced, are eliminated by selection in the same way as are ordinary disadvantageous mutants. Clarke and Sheppard (1960*c*) have illustrated very clearly the evolution of such super-genes in mimicry. In this connection, their work on the Asiatic *Papilio memnon* L. is impressive (Clarke *et al.*, 1968). This species has numerous polymorphic female forms, some non-mimetic and some mimetic. Of the latter, one (*achates*), copies a tailed model (*Atrophaneura coon* F.), though the others do not, and it is accordingly provided with a tail. The gene responsible for this is included within the super-gene for colour-pattern so that it may operate in the necessary genetic setting, but not otherwise. However, the race of *P. memnon* inhabiting the Island of Palawan is exceptional, being invariably tailed, a condition also due to the action of a single gene. But this is not included within the super-gene controlling colour-pattern, for in this instance wing-shape is unassociated with mimicry.

An interesting discovery has lately been made which, in a sense, bridges the gap between the Batesian and Müllerian situations. In the latter, a number of inedible and warningly coloured butterflies, or other insects, shelter under a common colour-pattern, so that the lesson of distastefulness learned by a predator attacking one of them may apply to all. Brower, Brower & Corvino (1967), working on *Danaus plexippus* L., find that in this instance the objectionable substances present in the imago are derived from the larval food. When, however, as occasionally happens, such larvae eat non-poisonous plants, the resulting butterflies lack their normal protection and so shelter under the reputation of inedibility gained by the majority of the species, a situation which Brower *et al.* name *automimicry*. It may well involve many species in addition to *D. plexippus*.

Variation may be cryptic and, since as a gene spreads it will tend to generate heterozygous advantage and therefore become polymorphic, cryptic polymorphism must be widespread and important. Its existence is now being detected by means of electrophoresis, by which at least a

proportion of the protein-variability present in organisms can be recognised. Appropriate staining techniques can sometimes demonstrate all three genotypes controlling alternative esterases, and it has repeatedly been found that the heterozygotes are in excess of expectation, so establishing their superiority. Lewontin and Hubby (1966) who were pioneers in this work have indeed attempted to show that such protein diversity cannot be due to heterozygous advantage. They were lead to that view by the intrusion into their argument of two errors, well exposed by Milkman (1967). First, that the genes controlling distinct polymorphisms act independently. Yet as Milkman remarks, "artificial selection has taught us nothing if not the cumulative effect of genes at many loci." Secondly, Lewontin and Hubby hold that the unit of selection is the gene, whereas it is the individual. On the latter, and correct, basis Milkman develops a simple calculation which demonstrates the power of heterozygous advantage to maintain protein polymorphism.

Johnson and Burns (1966) using starch-gel electrophoresis found that the butterfly *Colias eurytheme* Bd. is subject to great protein (esterase) polymorphism, which differed both quantitatively and qualitatively in two populations from localities in Texas approximately 100 miles apart. Indeed, this technique has opened up a number of new possibilities in the analysis of adaptation and micro-evolution in general.

When in the 1920's I was envisaging the experimental study of evolution in wild populations, it seemed necessary to concentrate upon situations which promote rapid adaptation. Three of these proved highly satisfactory for that purpose but a fourth, the spread of species into new territories, was disappointing. I deduced that in the instances which happened to be available for study at the time, the adjustments which must surely be taking place were largely physiological. The technique of electrophoresis now provides an opportunity for testing that view. Numerous instances of species colonising new lands spring to mind. One may mention the Palearctic *Pieris rapae* L., which has become one of the commonest butterflies in the U.S.A. since it was introduced there in the middle of the last century. Has it adjusted its protein variation to live in the New World? Electrophoresis will probably provide an answer to that question.

A somewhat exceptional type of polymorphism occurs in a single population of the moth *Panaxia dominula* L., Hypsidae (Ford & Sheppard, 1969). Its study has produced results which call for some comment. The species has one generation in the year and is widespread in Continental Europe and southern England; occurring in marshes and along river banks, where

the larvae feed chiefly upon *Symphytum*. The polymorphism occurs naturally in a single locality only, one of 17 acres in Berkshire. This has certain peculiar features of soil and ecology which may account for the exceptional characteristics of the moth there.

Its polymorphism is controlled by a pair of alleles in which all three genotypes are distinct. It is therefore possible to calculate gene-frequency by inspection, which has so far been done yearly from 1939 to 1970. Moreover, the numbers in the colony have been assessed by the technique of marking, release and recapture from 1941 onwards. It is possible to determine how fast a gene can spread if both its frequency and the size of the population in which it occurs be known. In this instance, for the first time, both these requirements were met. The annual fluctuation in the ratio of the alleles proved to be too great to be the result of random processes, such as genetic drift, and must be due to selection changing sometimes in frequency and direction.

In this instance, the polymorphism is not controlled by heterozygous advantage; indeed there is a clear indication that there has not yet been time for this to evolve in the community. The diversity is, in fact, maintained by assortative mating, for the females favour pairing with males of either of the two phases to which they do not belong.

The heterozygotes are somewhat variable. Indeed it proved possible by only four generations of selection in the laboratory on the one hand significantly to increase and on the other to diminish their expression, in the sense of departure from the normal homozygous type: that is to say, changing the terminology, to make them respectively more dominant or more recessive.

In 1954 the polymorphism was started artificially by P. M. Sheppard in another isolated colony a mile away. It is now found that changes similar in type to those produced in the laboratory, but taking place much more slowly, are occurring in these two wild communities. The expression of the gene is becoming more dominant in the marsh where it occurred naturally and more recessive in the one where it was introduced. This is perhaps the first time that it has been possible to forestall experimentally an evolutionary change that has occurred subsequently in nature.

The most important outcome of using the Lepidoptera in scientific research, as indeed in applying the techniques of ecological genetics to organisms in general, is surely the discovery that natural selection is much more powerful than had previously been realised. We had been accustomed to think of a selection-pressure of 1 per cent in favour of advantageous qualities in nature as high. Today we realise that it frequently reaches 40 or 60 per cent. Here we must notice that these values

are often balanced in equilibrium, so that the overall selective advantage or disadvantage may indeed be small. Yet the powerful components involved facilitate rapid adjustments to changing conditions, a situation which alters fundamentally our concepts of micro-evolution.

Literature Cited

- BOWDEN, S. R. 1963. Polymorphism in *Pieris*: forms *subtalba* and *sulphurea* (Lep., Pieridae). Entomologist 96: 77-82.
- BOWDEN, S. R. 1966a. *Pieris napi* in Corsica (Lep., Pieridae). Entomologist 99: 56-68.
- BOWDEN, S. R. 1966b. Polymorphism in *Pieris*: "*subtalba* in *P. virginensis* (Lep., Pieridae). Entomologist 99: 174-82.
- BROWER, L. P., J. VAN Z. BROWER, AND J. M. CORVINO. 1967. Plant poisons in a terrestrial food chain. Proc. Nat. Acad. Sci. 57: 893-8.
- CLARKE, C. A. AND P. M. SHEPPARD. 1960a. The Genetics of *Papilio dardanus* Brown. II. Races Dardanus, Polytroplus, Meseres and Tibullus. Genetics 45: 439-57.
- CLARKE, C. A. AND P. M. SHEPPARD. 1960b. The evolution of dominance under disruptive selection. Heredity 14: 73-87.
- CLARKE, C. A. AND P. M. SHEPPARD. 1960c. The evolution of mimicry in the butterfly *Papilio dardanus*. Heredity 14: 163-73.
- CLARKE, C. A., P. M. SHEPPARD, AND I. W. B. THORNTON. 1968. The Genetics of the Mimetic butterfly *Papilio memnon*. Phil. Trans. roy. Soc. (B) 254: 37-89.
- COCKAYNE, E. A. 1912-13. Notes on *Bupalus piniarius* Linn., Trans. S. Lond. ent. nat. Hist. Soc. parts 22 & 23: 56-9.
- CREED, E. R., W. H. DOWDESWELL, E. B. FORD, AND K. G. MCWHIRTER. 1959. Evolutionary Studies on *Maniola jurtina*: the English mainland, 1956-7. Heredity 13: 363-91.
- CREED, E. R., E. B. FORD, AND K. G. MCWHIRTER. 1964. Evolutionary studies on *Maniola jurtina* (Lep., Satyridae): the "Boundary Phenomenon" in southern England 1961-1968. Heredity 19: 471-88.
- DOWDESWELL, W. H. AND K. G. MCWHIRTER. 1967. Stability of spot-distribution in *Maniola jurtina* throughout its range. Heredity 22: 187-210.
- FORD, E. B. 1941. Studies on the chemistry of pigments in the Lepidoptera with reference to their bearing on systematics. 1. The Anthoxanthins. Proc. roy. Ent. Soc. Lond. 16: 65-90.
- FORD, E. B. 1955. Polymorphism and Taxonomy. Heredity 9: 255-64.
- FORD, E. B. 1965 2nd edn. Ecological Genetics. Methuen & Co., London.
- FORD, E. B. 1967a 2nd edn. Moths. The New Naturalist Series, Collins, London.
- FORD, E. B. 1967b 3rd edn. Butterflies. The New Naturalist Series, Collins, London.
- FORD, E. B. AND P. M. SHEPPARD. 1969. The medionigra polymorphism of *Panaxia dominula*. Heredity 24: 561-9.
- FRYDENBERG, O. AND O. HÖECH-GULDBERG. 1966. The genetic difference between southern English *Aricia agestis* and Scottish *A. artaxerxes*. Hereditas 56: 145-58.
- HÖECH-GULDBERG, O. 1968. Evolutionary trends in the genus *Aricia* (Lep.). Natura Jutl. 14: 3-76.
- HÖECH-GULDBERG, O. AND F. V. L. JARVIS. 1969. Central and North European *Ariciae* (Lep.). Natura Jutl. 15: 1-119.
- JOHNSON, F. M. AND J. M. BURNS. 1966. Electrophoretic variation in esterases of *Colias eurytheme* (Pieridae). J. Lepid. Soc. 20: 207-11.

- KETTLEWELL, H. B. D. 1957. The contribution of industrial melanism in the Lepidoptera to our knowledge of evolution. *Advmt. Sci., Lond.* 52: 245-52.
- KETTLEWELL, H. B. D. 1959. New aspects of the genetic control of industrial melanism in the Lepidoptera. *Nature* 183: 918-21.
- KETTLEWELL, H. B. D. 1961. The phenomenon of industrial melanism in the Lepidoptera. *A. Rev. Ent.* 6: 245-62.
- KETTLEWELL, H. B. D. 1965. Insect survival and selection for pattern. *Science* 148: 1290-6.
- LANE, C. AND THE HON. M. ROTHSCHILD. 1961. Observations on Colonies of the Narrow-bordered Five-spot Burnet (*Zygaena lonicerae* von Schev.) near Bicester. *Entomologist* 94: 79-81.
- LEWONTIN, R. C. AND J. L. HUBBY. 1966. The amount of variation and degree of heterozygosity in natural populations of *Drosophila pseudoobscura*. *Genetics* 54: 595-609.
- LORKOVIC, Z. 1962. The genetics and reproductive isolating mechanisms of the *Pieris napi-bryoniae* Group. *J. Lepid. Soc.* 16: 5-19, 105-127.
- McWHIRTER, K. G. 1969. Heritability of spot-number in Scillonian strains of the Meadow Brown Butterfly (*Maniola jurtina*). *Heredity* 24: 314-18.
- MILKMAN, R. D. 1967. Heterosis as a major cause of heterozygosity in nature. *Genetics* 55: 493-5.
- ONSLow, THE HON. H. 1921. Inheritance of wing-colour in Lepidoptera. *J. Genet.* 11: 277-92.
- PETERSEN, B. 1963. Breakdown of differentiation between *Pieris napi* and *Pieris bryoniae* and its causes. *Zool. bidr. Upps.* 35: 205-62.
- REMINGTON, C. L. 1954. The genetics of *Colias* (Lepidoptera). *Adv. Genet.* 6: 403-50.

FERGUSON COLLECTION TO SMITHSONIAN INSTITUTION

Dr. Douglas C. Ferguson, formerly of the Nova Scotia Museum and Yale University, recently assumed a position as specialist on Geometroidea and Pyraloidea with the United States Department of Agriculture at the National Museum of Natural History. Shortly after joining the staff, Dr. Ferguson presented to the Smithsonian Institution his excellent collection of Lepidoptera. Over 51,000 insects are contained in this collection, of which nearly 48,000 specimens are Lepidoptera. Dr. Ferguson's donation represents over 23 years of concentrated collecting, conducted for the most part in the Atlantic Provinces of Canada. Nearly all major families of Lepidoptera are represented, and the total coverage of 3,000 species from an area previously not well documented in the collections of the National Museum is particularly noteworthy. The collection is extremely rich in Noctuoidea and Geometroidea, containing approximately 38,000 beautifully prepared specimens of those groups. Over 150 species of identified lepidopterous larvae, associated with reared adults, are also included. Although no holotypes are present in the collection, about 300 paratypes of 50 species are, as well as many undescribed species.

The addition of this generous gift has significantly improved the overall representation of North American Lepidoptera at the Smithsonian Institution.

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