# POLYMORPHISM AND TAXONOMY

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Received 15.x.54

This article is based upon an address delivered at Christchurch, New Zealand, on 17th May 1951, during the Seventh Science Congress of the Royal Society of New Zealand. It occupied pp. 245-253 of the published Report on that Congress,* which was published in January 1953. Apart from a few preliminary generalisations here omitted, it contains an account of some genetic work which had occupied a considerable amount of time for several years. The volume in which it appeared is by no means easily accessible outside the Dominion ; but it was thought that the offprints, which it was proposed to distribute rather widely among geneticists, would both provide easy access to the data here presented, and help to draw the attention of biologists to a Symposium which contains valuable contributions to many aspects of science. These offprints, however, were lost in transit from New Zealand to Britain. Accordingly, the Editors of *Heredity* were so good as to suggest that the article might be reprinted in this journal, if the necessary permission could be obtained. This was readily granted by the Royal Society of New Zealand, for which I am most grateful. I wish also to express my sincere thanks to the Editors of *Heredity* for insuring wider publicity to this work.

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POLYMORPHISM has been defined (Ford, 1937, 1945) as the occurrence together in the same habitat of two or more distinct forms of a species in such proportions that the rarest of them cannot be maintained merely by recurrent mutation. The essential features of this definition have often been discussed (see also Ford, 1952), so that it is only necessary to point out here that it excludes continuous variation (as exemplified by human height), geographical races, the segregation of rare recessives (such as the majority of albinos), and the appearance of heterozygous mutants subject to elimination by selection. However, the term necessarily includes two distinct situations. A permanent or *Balanced Polymorphism* is due to a balance of selective agencies in which diversity is favoured and uniformity opposed : as in sex, or in all those instances in which the heterozygote is at an advantage compared with either of its corresponding homozygotes. On the other hand, a *Transient Polymorphism* involves only the temporary diversity of a population, which takes place while a previously disadvantageous gene spreads and displaces its allelomorph. This will generally occur owing to change in the environment or when a species colonises a new habitat.

Now a balanced polymorphism provides certain outstanding advantages for the study of evolution by experimental means. On

* (1953) : Royal Society of New Zealand ; Report of the Seventh Congress, Christchurch, May 15-21, 1951. (Honorary Editor : M. A. Black.) Pp. 143-154. (Published by the Royal Society of New Zealand, incorporated.)

the one hand, since discontinuous variation is involved, some simple switch-mechanism must control the development of one or another of the polymorphic forms ; and this is usually (though not always) achieved by the segregation of a pair, or at the most very few pairs, of genes. Moreover, the population is, as it were, " sensitised " to the occurrence of both the allelomorphs at such loci, since even the rarer of them will be much commoner than those that are maintained only by mutation pressure. Thus, in a balanced polymorphism there is ground for supposing that the adjustments of the gene-complex to a particular gene may often take place rather quickly and thus respond to the diverse conditions of different environments. It will be realised that continuous variations, controlled wholly on a multifactorial basis, may be expected to react even more quickly to selection ; yet the segregation of a pair of allelomorphs provides certain advantages for genetic analysis absent from the multifactorial situation.

Bearing these facts in mind, it seemed worth while to use balanced polymorphism to obtain some information on the genetics of geographical races. Thus, among other aspects of this question, it is desirable sometimes to analyse what is meant by the statement, frequently found in the literature of systematics, that the same form of a species occurs in two different parts of its range. In such a context " the same " usually means little more than visible or measurable similarity and we rarely have any indication whether or not the apparent identity extends to the mechanism producing it.

In Britain the moth *Triphaena comes* Hb. (family Agrotidæ) provides suitable material for such an enquiry. This species varies in size from about 4 to 4·5 cm. across the expanded wings. It has an extremely wide distribution and is generally common. In England and southern Scotland it is, with rare exceptions, monomorphic. The fore-wings are of a pale ochreous-brown, the hind-wings yellow with a black sub-marginal band.

In some parts of central and north Scotland and in the Scottish islands, however, this is a dimorphic insect, for a dark variety, *curtisii* Newmn., constitutes a considerable proportion of the population. Its frequency in different areas has not yet been established. It may, in some parts, reach 50 per cent. of the population, perhaps more ; though nowhere, to my knowledge, does it so far displace the normal *comes* that this is reduced to the status of a rare variety. *T. comes comes* is subject only to minor variation in colour, sometimes becoming rather greyish or reddish, but *T. c. curtisii* is extremely variable : the fore-wings range from a mahogany shade to intense black, while the yellow of the hind-wings is also clouded with black scales, slightly in the less dark forms but sometimes very heavily in those that are blackish. The correlation between the amount of melanin on the fore and hind wings is, however, far from complete, which much increases the difficulty of classifying the *curtisii* forms.

As long ago as 1905, it was shown by Bacot that *curtisii* is unifactorial

and nearly, but not quite, dominant. The heterozygotes are nearly always distinguishable from the recessives (the normal *comes*) without difficulty but heterozygous and homozygous *curtisii* overlap so that, when segregating, these two genotypes tend to fall in a bimodal distribution, or at least one in which the extreme dark forms are unduly common. Thus it seems that the darkest *curtisii* are nearly always homozygotes and the lightest heterozygotes, but those of intermediate shade cannot be assigned with confidence to one or the other class.

As is usual when all three genotypes are to any degree distinguishable, the heterozygotes are the most variable and the commoner homozygotes (*comes*) the least. These variations of *curtisii* are certainly largely genetic, for doubtless that form is sensitised to the effects of many other genes against which *comes* is buffered. It is unfortunate that the colour-phases occurring within the range of activity of the *curtisii* gene, both when heterozygous and homozygous, have received many distinct names (*rufo-nigrescens*, *nigrescens*, *nigra*, and others) which are often used in place of *curtisii* as if something distinct from it, so obscuring the genetic situation. In the present account these will be ignored, and *curtisii* extended to cover all the colour-phases controlled by the semi-dominant gene (*C*), responsible for the dark forms, compared with the pale recessive *comes* (*cc*).

It has long been known that *curtisii* occurs on the mainland of northern Scotland and that it is also found in the Hebrides on the west coast, and in Orkney at the eastern end of the north coast. The form is said to be similar in these two groups of islands and I could see no difference when specimens from them were compared. Yet Barra, in the Outer Hebrides, whence my western material was obtained, is in a direct line 100 miles from the nearest point on Orkney, though the Scottish mainland lies between them. However, Barra is separated by 25 miles of sea from the nearest point on the mainland, and by 15 miles from the island of Skye, which is so nearly a peninsula that it may be treated as a part of the Scottish coast. Between Orkney and the north coast of Scotland runs the Pentland Firth, six miles wide at the narrowest point, in which is the small wind-swept island of Stroma.

It is clear, therefore, that the population of *Triphaena comes* on Barra and Orkney are very isolated from one another. For this insect is not a regular migrant, a fact confirmed by the circumstances that specimens of the *curtisii* forms do not become scattered from northern and central Scotland, where they are common, to be caught as stragglers in the south of that country or in northern England. Similarly, a small and exceptional colony of dimorphic *T. comes* in which *curtisii* occupies a proportion of the population does, or did, exist on the sandhills of Lancashire. Yet *curtisii* was quite restricted to it.

I obtained specimens of *Triphaena comes* from Barra and Orkney in order to compare their genetics. The few females that reached

me (providing my first generation, B.I from Barra and O.I from Orkney) had all been fertilised in the open by unknown males. Four refused to lay, and I lost completely three broods of larvæ owing to disease. Unfortunately the species produces but one generation per year. However, the larvæ feed on many common low-growing plants and are easy to rear.

The insects obtained during the course of this work were classified into 5 colour-groups as shown, for each brood, in the table, in which

*Table of broods*

| Brood | v. dark *curtisii* | dark *curtisii* | *curtisii* | *curtisii* to *comes* | *comes* | Total |
|---|---|---|---|---|---|---|
| B.I.3 | ... | ... | 1 | ... | ... | 1 |
| B.I.5 | ... | 1 | ... | ... | ... | 1 |
| O.I.1 | ... | 1 | ... | ... | ... | 1 |
| O.I.2 | ... | 1 | ... | ... | ... | 1 |
| O.I.7 | ... | 1 | ... | ... | ... | 1 |
| B.II.3 | 1 | 6 | 21 | ... | 15 | 43 |
| B.II.4 | 8 | 6 | 25 | 1 | 10 | 50 |
| O.II.1 | ... | 14 | 29 | ... | 36 | 79 |
| O.II.2 | ... | 3 | 3 | ... | ... | 6 |
| O.II.3 | ... | 1 | ... | ... | 1 | 2 |
| B.III.1 | ... | 10 | 31 | ... | ... | 41 |
| O.III.1 | ... | 9 | 18 | ... | 39 | 66 |
| O.III.2 | 1 | 25 | 41 | ... | 58 | 125 |
| B.IV.1 | 29 | 23 | 54 | 2 | 27 | 135 |
| B.IV.2 | 2 | ... | 4 | ... | 1 | 7 |
| B.IV.3 | 9 | 6 | 22 | 1 | 14 | 52 |
| B.IV.5 | ... | ... | ... | ... | 2 | 2 |
| O.IV.1 | 31 | 18 | 31 | 2 | 24 | 106 |
| O.IV.2 | 5 | 8 | 17 | ... | 5 | 35 |
| B.O.IV.2 | 10 | 14 | 24 | 11 | 15 | 74 |
| B.O.IV.4 | 3 | 4 | 7 | 4 | 5 | 23 |
| B.O.IV.5 | 11 | 10 | 16 | 7 | 19 | 63 |
| B.O.V.2 | 21 | 14 | ... | ... | ... | 35 |
| B.O.VI.1 | 13 | 1 | ... | ... | ... | 14 |
| B.O.VI.4 | 10 | 27 | ... | ... | ... | 37 |
| B.O.VI.5 | 68 | 9 | 1 | ... | ... | 78 |

the full data are recorded. The three darkest of these represent *curtisii* forms (very dark, dark, and normal *curtisii*). Then follows the one ("*curtisii* to *comes*") into which insects approximately intermediate between *curtisii* and *comes* were placed, while the lightest specimens represent *comes* itself. Owing to the lack of close correlation between the amount of darkening on the fore and hind wings and the mottled appearance of some of the specimens, it was often difficult to decide

where the more intermediate *curtisii* should be included ; consequently the " dark *curtisii* " group is rather arbitrary. The distinction between *curtisii* and *comes* was, however, nearly always clear, as was the correct classification of the darkest and lightest *curtisii*.

From the Barra insects I succeeded only in rearing two broods which constituted my second generation (the first reared in captivity). One of these, B.II.3, from the *curtisii* female B.I.3, proved rather anomalous, giving 28 *curtisii* forms (18 ♂, 10 ♀) and 15 *comes* (6 ♂, 9 ♀). It would indeed have been worth while to explore this situation, but the work would have required more time and space than I could afford.

My other brood from Barra, B.II.4, from the dark *curtisii* B.I.5, produced 39 *curtisii* forms (22 ♂, 17 ♀), 10 *comes* (7 ♂, 3 ♀) and a single male of intermediate shade. This is clearly an F.2 segregation, as indicated also by a group of extreme black insects certainly representing some of the homozygotes.

I raised three broods from wild Orkney females, which were all dark *curtisii* (O.I. 1, 2, 7), but two were of negligible size. They were as follows : O.II.1, 43 *curtisii* forms (17 ♂, 26 ♀) ; 36 *comes* (17 ♂, 19 ♀), evidently a 1 : 1 segregation ; O.II.2, 6 *curtisii* (4 ♂, 2 ♀) ; O.II.3, 1 *curtisii* and 1 *comes* (both ♂).

I feel some uncertainty as to whether brood B.II.3 represents a disturbed 3 : 1 or 1 : 1 ratio. B.II.4 is evidently segregating as a result of a mating between 2 heterozygotes, while O.II.1 is clearly a backcross family. O.II.2 and 3 are too small to distinguish between the two types of ratio.

It was now necessary to produce parallel generations (Gen. III) which would, with certainty, provide me with known heterozygotes. The insects emerged over a long period, making it difficult to obtain the requisite pairings. However, in the Barra line, using family B.II.4, I crossed two of the very black male *curtisii* with female *comes* but successfully reared only one brood (B.III.1) of 41 insects (16 ♂, 25 ♀), all *curtisii* and none of the darkest shade. These evidently were heterozygotes.

In the Orkney line I had to make backcrosses using individuals of family O.II.1. These provided me with two families in the succeeding generation (that parallel to B.III.1). They consisted of O.III.1, 27 *curtisii* forms (14 ♂, 13 ♀) ; 39 *comes* (24 ♂, 15 ♀) ; and O.III.2, 67 *curtisii* (26 ♂, 41 ♀), and 58 *comes* (32 ♂, 26 ♀). Here evidently, as expected from the parents, the total of 94 *curtisii* were also all heterozygotes. The extreme black forms were absent from them, as in B.III.1, except for a single specimen in O.III.2 which can hardly be other than an abnormally dark heterozygote.

We now reach the critical generation of the experiment. In the Barra line a number of pairings were obtained between males and females of heterozygous *curtisii* in brood B.III.1, and two large broods, each segregating in a 3 : 1 ratio resulted from them. They were

B.IV.1, 106 *curtisii* (46 ♂, 60 ♀), 27 *comes* (10 ♂, 17 ♀) and 2 intermediate specimens (1 ♂, 1 ♀). Also B.IV.3, 37 *curtisii* forms (15 ♂, 22 ♀), 14 *comes* (5 ♂, 9♀) and 1 intermediate male. There were also two families which were nearly lost through disease : B.IV.2, 6 *curtisii* (all male) and 1 *comes* (female) ; also B.IV.5, 2 *comes* (1 ♂, 1 ♀).

In the Orkney line, 2 heterozygous *curtisii* in O.III.1 were mated to give two broods : O.IV.1, 80 *curtisii* (49 ♂, 31 ♀) and 24 *comes* (15 ♂, 9 ♀), with two doubtful specimens both male. Also brood O.IV.2 of 30 *curtisii* (11 ♂, 19 ♀) and 5 *comes* (all male).

While the brood III insects were emerging, it became clear that the time had arrived to allow the *curtisii* gene to segregate as an F.2 ratio in a mixed Barra and Orkney genetic background. For it was by then fairly evident that the *comes* form is almost fully recessive. Indeed, when the whole of the third generation broods could be examined, it was seen that among a total of 412 segregating specimens (252 *curtisii* ; 159 *comes*) in the second and third generations, only one was doubtful. The B.I and O.I insects are here excluded as they might have been selected. These numbers were later raised with the addition of the B.IV and O.IV broods, to 6 unclassifiable specimens (those listed in the table as " *curtisii* to *comes* ") out of 749 (comprising 511 *curtisii* forms and 232 *comes*).

Accordingly a (heterozygous) male from B.III.1 was crossed with a heterozygous Orkney female from O.III.1 to give the brood B.O.IV.2 of 74 insects (43 ♂, 31 ♀), and brood B.O.IV.4 of 23 insects (9 ♂, 14 ♀), resulting from a similar pairing. Also, making the reverse cross, a heterozygous female from B.III.1 was mated with a heterozygous male from O.III.2, producing B.O.IV.5 of 63 insects (38 ♂, 25 ♀). Several more of these crosses were tried but were failures.

In broods B.O.IV.2, 4 and 5, segregation in the ratio 1 *CC* : 2 *Cc* : 1 *cc* was, of course, taking place, but it did not produce a clear discontinuity between *curtisii* and *comes* as heretofore. On the contrary, a failure of dominance occurred, and the insects consisted of an almost unclassifiable series from normal *comes* to the darkest *curtisii*. It is especially to be noticed that this was confirmed in all three broods in which the genetic background of the Barra and Orkney insects had been mixed.

One point which gave rise to a good deal of trouble remains to be considered. It might be suggested that *curtisii* in Barra and Orkney is produced by different genes having similar effects (like the three genes for Rex coat in the rabbit, or four of the genes producing *retinitis pigmentosa* in Man). The interaction which might then occur on crossing could result in a seriation which it would be difficult to unravel, and similar in general appearance to that encountered.

It is easy to test the identity of two mutant genes when recessive in effect, but more difficult to do so when they are semi-dominants. In this instance a mating was obtained between a pair of the blackest available specimens respectively of Barra (the male) from B.IV.1

and of Orkney origin (the female) from O.IV.1. A family of 35 specimens (22 ♂, 13 ♀), constituting B.O.V.2 resulted from this and all of them were of the darker *curtisii* forms. Three successful broods were produced by inter-breeding insects of this family : B.O.VI.1 of 14 (10 ♂, 4 ♀), B.O.VI.4, of 37 (14 ♂, 23 ♀) and B.O.VI.5, of 78 (46 ♂, 32 ♀). The whole of these 129 insects comprising the B.O.VI broods were *curtisii* and all but one were of the darker forms.

This evidence requires a brief examination. Suppose that two genes are in fact involved : true *curtisii* (*C*) and a visibly similar but genetically distinct one for dark colouration (*D*). By crossing homozygous dark insects from the two lines respectively (B.IV.1 and O.IV.1), each would then bring in the normal allelomorph of the other, and the brood B.O.V.2 would have the genetic constitution *CcDd*. If the two genes were additive in effect, the same result as that produced by *CC* would be obtained. If they were not additive, either the paler shade of the heterozygotes or some new colouring would be produced. These latter alternatives are excluded by the results.

However, on inter-breeding insects of B.O.V.2 if of the constitution *CcDd*, segregation should occur in a ratio 9 : 3 : 3 : 1 and one insect in 16 would be normal *curtisii*. The 129 specimens, all dark, that were obtained are sufficient to exclude this.

It may be objected, however, that in choosing the specimens from broods B.IV.1 and O.IV.1 homozygotes were not correctly identified and selected for breeding, and that one of these parents (clearly not both) was heterozygous. This would produce in B.O.V.2 a segregating brood of the hypothetical constitution 1 *CcDd* : 1 *Ccdd* (or the reverse). Such a misclassification, therefore, could only produce some light specimens, and in addition, raise the chances of obtaining normal *comes* in the succeeding (B.O.VI) generation. Thus it appears that the *curtisii* form in Barra and Orkney is due to the same gene (or to an allelomorph of it).

## I. DISCUSSION

The *curtisii* and *comes* forms prove to be clearly distinguishable, save on rare occasions, in the bred lines derived from Barra (Outer Hebrides) and Orkney females. Thus, among the 749 insects obtained in segregating families, I was only in serious doubt about the classification of about six specimens. However, there was a break-down in dominance when the two gene-complexes were mixed by inter-breeding, for the two classes were then no longer distinct (broods B.O.IV.2, 4 and 5). That is to say, since the *curtisii* gene was proved identical in these populations, dominance must have been achieved in them by the selection of a different set of " modifiers ".

The experimental design necessary to establish these results differs somewhat from that employed in other studies on dominance-modification. Thus, in his celebrated work on poultry, Fisher (1935, 1938) was concerned to put certain genes characteristic of some domestic

breeds back into the genetic setting of the wild jungle-fowl in which they must normally have the status of rare mutants. For that purpose it was necessary to make repeated back-crossings to the wild birds until the gene to be studied was immersed in a gene-complex which was predominantly that of the jungle-fowl type. Yet such repeated back-crossings would presumably have tended to restore dominance after inter-crossing the Barra and Orkney lines of *Triphaena comes*: for here, unlike the poultry instance, we are dealing with two races in both of which the same gene is common. By taking *curtisii* genes of Orkney origin and placing them in the genetic environment of the Barra insects, it may be presumed that *curtisii* would merely re-acquire semi-dominance in a somewhat different way, that appropriate to Barra. And, of course, a comparable result would be produced by the reverse procedure.

In these instances, the maximum lack of balance was obtained from the cross between Barra and Orkney material, without subsequent back-crossing. It was not deemed necessary to explore this situation by inter-breeding these families of mixed origin (B.O.IV.2, 4 and 5). Not because this would have been unrewarding, but because a breakdown sufficient to illuminate the taxonomic situation had been obtained without doing so, presumably because many of the genes by which the gene-complex is adjusted to give dominance were themselves operating on an additive and multifactorial basis. Moreover, such work requires so much time and space that nothing more could be undertaken than was requisite for the enquiry on hand.

It is worth adding that a study of specimens in collections leads me to suspect that while *curtisii* and *comes* in general remain quite distinct on the Scottish mainland, they may there be more often connected by intermediates which it is hard to classify than in the material from Barra and Orkney. It is, indeed, not unexpected that the greater isolation of an island may promote a better adjustment to the *curtisii* gene. It is possible, therefore, that when *curtisii* is bred from mainland localities, especially from the southern part of its range, the segregation, though still clear, may be less sharp than I myself found.

We cannot, of course, suppose that semi-dominance has been attained independently from the intermediate heterozygote in Barra and Orkney. For on the few occasions on which *curtisii* has already been bred, it proved to be semi-dominant also on the Scottish mainland, which intervenes between those islands (though it is hard to determine what the exact frequency of the intermediates may have been in such results). We may reasonably assume that the number of genes influencing dominance is very large, and that they will have other effects also. Where isolation permits it, selection will therefore act upon these to adjust them as may be required by the environment, while at the same time maintaining the balance necessary to ensure the semi-dominance of *curtisii*. Indeed, though an actual break in

distribution provides the most complete form of isolation, it does not provide the only geographical one. Mere distance can impede the free flow of genes and so build up a different adjustment, which may amount to sub-speciation, even at the opposite ends of a continuous cline (Ford, 1949).

It is now possible, therefore, in this instance, to extend the systematist's statement that the *curtisii* form of *T. comes* occurs both in the Outer Hebrides (Barra) and in Orkney, and to attach a genetic meaning to it. In both places *curtisii* is unifactorial, nearly dominant, and due to the same gene. But the similar adjustments of these two populations to that gene, giving it semi-dominance, have been achieved by different means : the " dominance modifiers " employed in Barra and Orkney are not the same.

In every fauna and flora, but particularly such as that of New Zealand, there are likely to be instances in which " the same " form occurs in distinct areas, and indeed, this situation will increase as the wild countryside becomes more subdivided by cultivation or the planting of imported timber. It would be a matter of much interest to determine the genetic basis of these, and other taxonomic situations, along the lines illustrated by the present work, in which advantage has been taken of the special properties of polymorphic material.

## 2. SUMMARY

1. The moth *Triphaena comes* (Agrotidæ) is monomorphic in England but dimorphic in central and northern Scotland and the Scottish Islands where, in addition to the normal *comes*, a dark form *curtisii* occupies a considerable proportion of the population. Its frequency in these localities has not yet been determined, but it is known to be high enough to indicate a balanced polymorphism.

2. The *curtisii* form occurs both in Barra (and elsewhere) in the Outer Hebrides and in the Orkney Islands, and these two populations are very isolated from one another.

3. *Curtisii* is unifactorial and nearly, but not quite, dominant to *comes*.

4. It has been shown that the same gene, or allelomorphs of it, control the *curtisii* forms in Barra and Orkney.

5. Though *curtisii* is apparently identical both in appearance and in genetic behaviour in these two places, it achieves that identity by different means, for the sets of " modifiers " which adjust its dominance are significantly different in these two islands.

6. Owing to the use of polymorphic material it has, therefore, been possible in this instance to analyse in some detail what is meant by the statement that " the same " form of a species occurs in two isolated localities.

## 3. REFERENCES

BACOT, A. 1905. *Proc. Ent. Soc. Lond.*, pp. lxvii-lxxi.
CAIN, A. J., AND SHEPPARD, P. M. 1950. *Heredity*, *4*, 275-294.
FISHER, R. A. 1935. *Philos. Trans. Roy. Soc.*, B*225*, 197-226.
FISHER, R. A. 1938. *Proc. Roy. Soc.*, B*125*, 25-48.
FISHER, R. A., AND FORD, E. B. 1947. *Heredity*, *1*, 143-174.
FORD, E. B. 1937. *Biol. Rev.*, *12*, 461-503.
FORD, E. B. 1945. *Ibid.*, *20*, 73-88.
FORD, E. B. 1949. *Genetics, Paleontology, and Evolution.* Princeton Univ. Press. Pp. 309-314.
FORD, E. B. 1953. The experimental study of evolution. *Brisbane Symposium Volume of A.N.Z.A.A.S.*, *28*, 143-154.
SHEPPARD, P. M. 1951*a*. *Heredity*, *5*, 125-134.
SHEPPARD, P. M. 1951*b*. *Ibid.*, *5*, 349-378.