

GENETICAL STUDIES IN THE MOTHS OF THE
GEOMETRID GENUS *OPORABIA* (*OPORINIA*)
WITH A SPECIAL CONSIDERATION OF MELAN-
ISM IN THE LEPIDOPTERA.

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(With 18 Text-figures.)

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I. INTRODUCTORY.

THE genus *Oporabia* (now becoming known as *Oporinia*)¹ is a homogeneous genus of the Geometridae, occurring throughout the Holarctic region, but in spite of its enormous range possessing very few species, in which peculiarity it resembles its nearest allies the genera *Venusia* and *Cheimatobia*. From the former the original phase of both *Oporabia*

¹ And in America as *Epirrhita*!

and *Cheimatobia* has been derived; the latter appears to have diverged from their common ancestor at some fairly early stage in its existence. With *Venusia*, owing to the period of its active life cycle, we are not at present interested; in the case of *Cheimatobia* matters are somewhat different, for in opposition to the indications of its apterous and subapterous females, it approaches so closely to *Oporabia* in all its other essential characteristics as to render any investigation in that genus incomplete without their joint genetical possibilities being considered.

In view of this limitation in the number of species included one would have anticipated that the genus would prove, from the standpoint of specific differentiation, an easy subject for study; such has not, however, been the case, as only comparatively recently have the relationships between the forms it includes been understood with any degree of exactitude. As a result of recent researches it can now be confidently stated that the genus comprises two species and two subspecies, the species *Oporabia autumnata* with its subspecies *O. filigrammaria*, and the species *O. dilutata* with *O. christyi*. So chaotic did the variation of the species appear, and so prone were they to vary along parallel lines and to form local races resembling each other, that entomologists, even whilst keeping the subspecies *O. filigrammaria* distinct, consigned the remainder of the forms, comprising two species, one subspecies and countless local races, into one specific dustbin which they labelled *Oporabia dilutata*. Such a procedure would have been impossible had they had the slightest knowledge of the insects not as dried specimens but as living creatures, each with its special life history and specialised habitat. In this lumping they were excelled by Meyrick¹, who in this as in all similar cases cut the knot of his difficulties by lumping all, the very striking *O. filigrammaria* included, under the same specific title. Ignoring the practice of Meyrick as thoroughly unscientific, the action of entomologists in general ended in the severing of two of the most closely allied forms, and the uniting of two of the most physiologically diverse forms in the British Fauna. This was most vividly proved by the almost perfect homology of the chromosomes in the gametogenesis of hybrids between *O. autumnata* and *O. filigrammaria* and its absolute lack in the case of the *dilutata*—*autumnata* hybrids.

For the order which now obtains in the genus three workers are responsible, Prout, Allen and myself; Prout and Allen worked from the standpoint of the systematist and I from that of the geneticist, although necessarily my labours unearthed many facts of great value to systematics.

¹ Meyrick, *British Lepidoptera*, p. 224 (1896).

Thanks to these workers, then, the forms are easily separated on structural characters derived from both sexes but especially from the male. In fact, the forms are most readily differentiated by separating the males and then allowing the females to fall naturally into their own places. The primary division into the two species proper is best based on the genitalia, a prominent hook on the genital claspers marking *O. dilutata* (Fig. 1) and *O. christyi* (Fig. 2), and its absence *O. autumnata* (Fig. 3) and *O. filigrammaria* (Fig. 4). To distinguish *O. dilutata* and *O. christyi* one then examines the sternite of the eighth abdominal segment upon which in this genus there are two chitinous projections known as octavals. If these be approximated the insect is *O. christyi*, but if not it is *O. dilutata*. Similarly, by examining the same structures, *O. autumnata* and *O. filigrammaria* can be discriminated. If the excavation between the octavals be slight we are dealing with *O. autumnata*; if deep *O. filigrammaria*. In this case the smaller number of hairs on the cristae of *filigrammaria* will give abundant confirmatory evidence; in the former none is necessary. Further major and minor characters serving to distinguish all four forms in both sexes are indicated in Tables I and II below, and as far as the genitalia are concerned illustrated on Figs. 1, 2, 3, 4; for the sake of comparison and to emphasise the relationship between the two genera *Oporobia* and *Cheimatobia* the genitalia of *Cheimatobia brumata* and *C. boreata* are supplied on Figs. 5 and 6.

The life histories of all of these insects follow the same general course, all four forms of *Oporobia* and the two species of *Cheimatobia* hibernating as ova, which hatch as the trees leaf in spring. The larvae feed up exceedingly rapidly in May and early June. When they emerge from the egg they are rather slim in build and of a brown colour, very dark in *autumnata* and *filigrammaria* but lighter in *dilutata* and *christyi*. When adult they are stout and in colour green, of shades and markings varying with the species and subspecies; exact details of the specific and other differences both in ova and larvae are supplied in Tables I and II. As the larvae attain their full growth they bury themselves in the loose debris at the base of the trees and shrubs utilised as food plants and spin small compact oval cocoons constructed, in the more external layers, of fragments of earth, leaves, moss and so on cemented by silken threads, and on the inside of a waterproof coating of pure silk. In these they pupate and remain in this condition until the cooler days of the last weeks of August, or of September and October call the moths forth, the exact period of this event depending on the species, subspecies and local races.

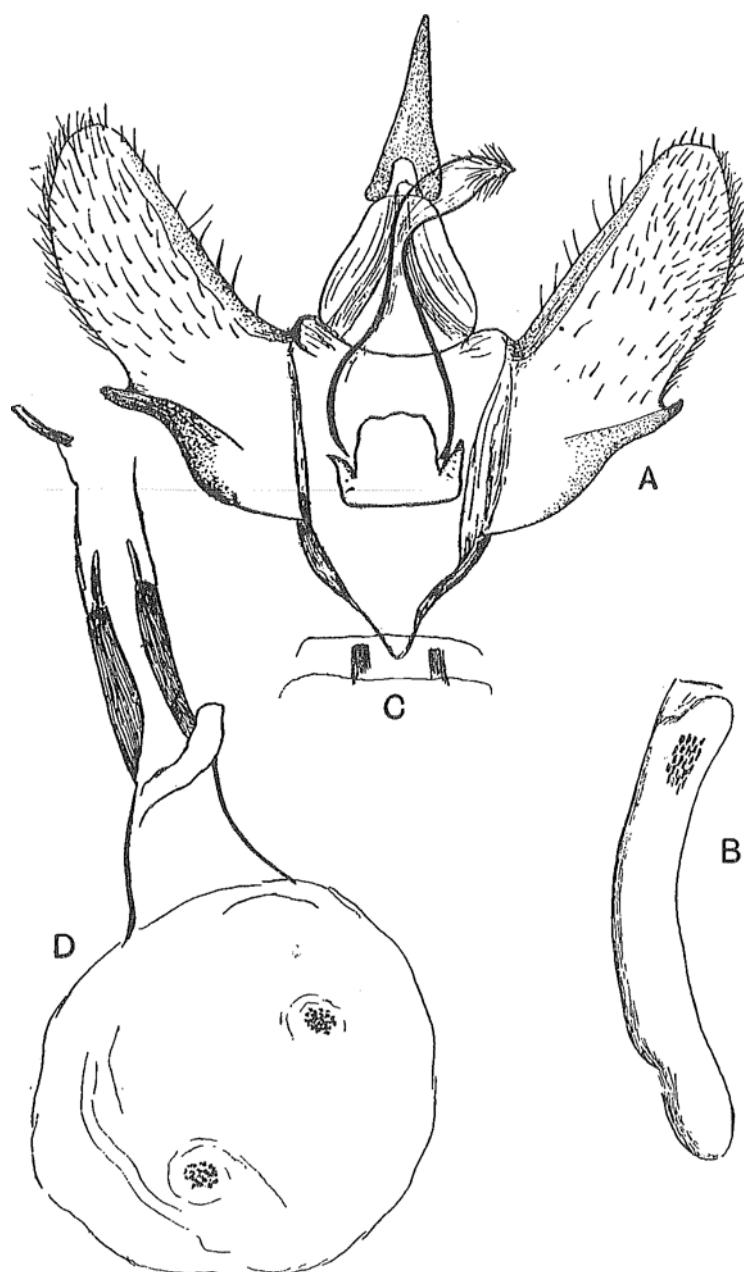


Fig. 1. The genitalia of both sexes of *O. dilutata*.

A = the male genitalia without aedeagus. B = Aedeagus. C = Octavals.
D = The female genitalia.

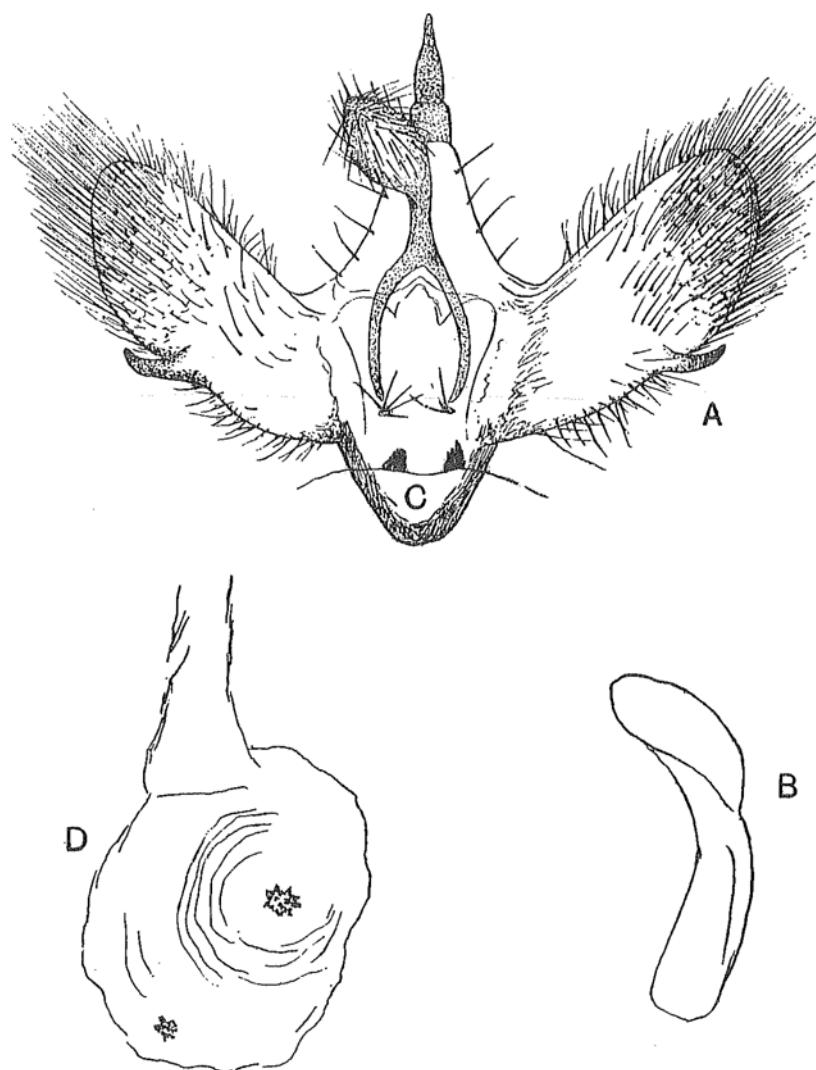


Fig. 2. The genitalia of *O. christyi*.

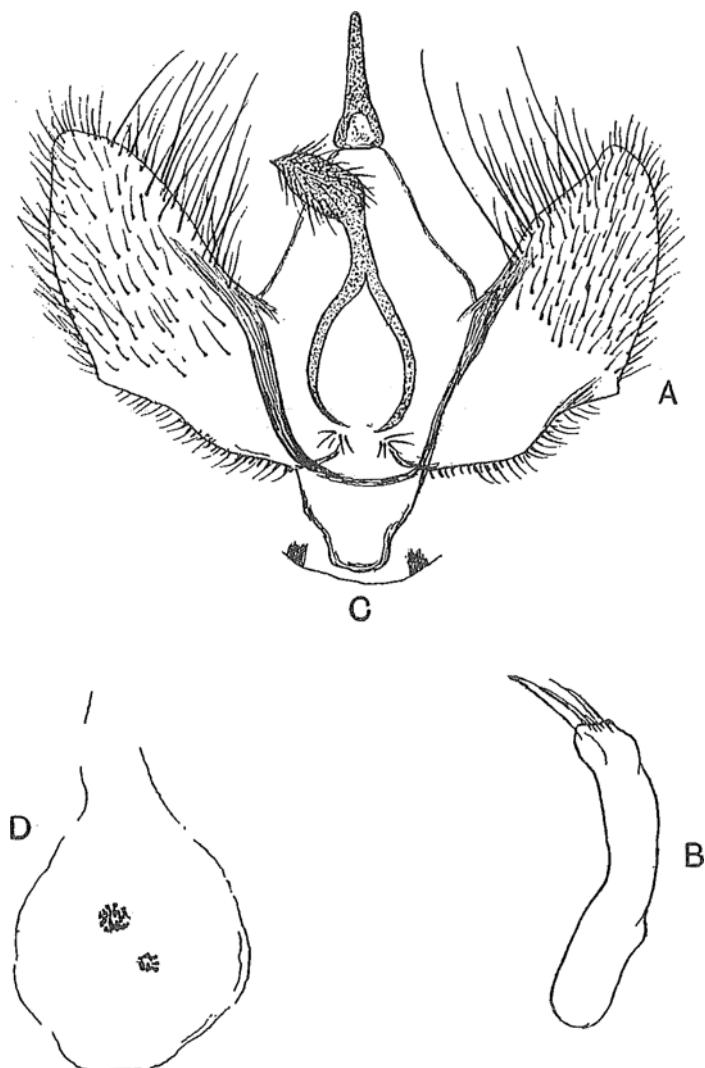


Fig. 3. The genitalia of *O. autumnata*.

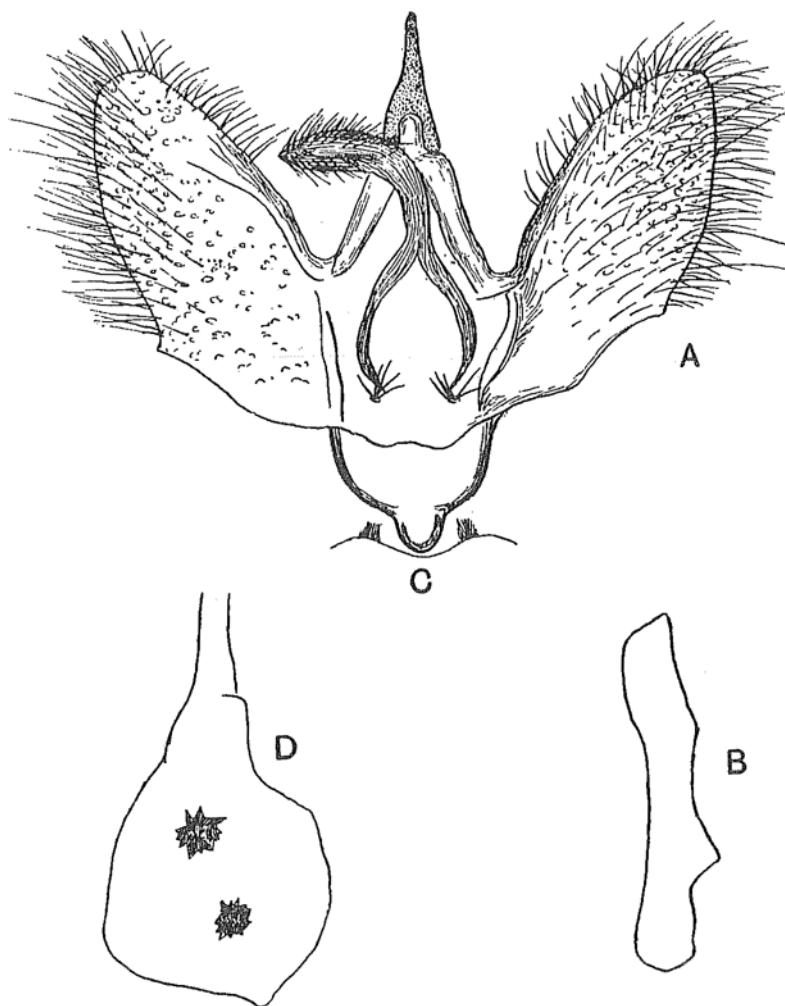


Fig. 4. The genitalia of *O. filigrammaria*.

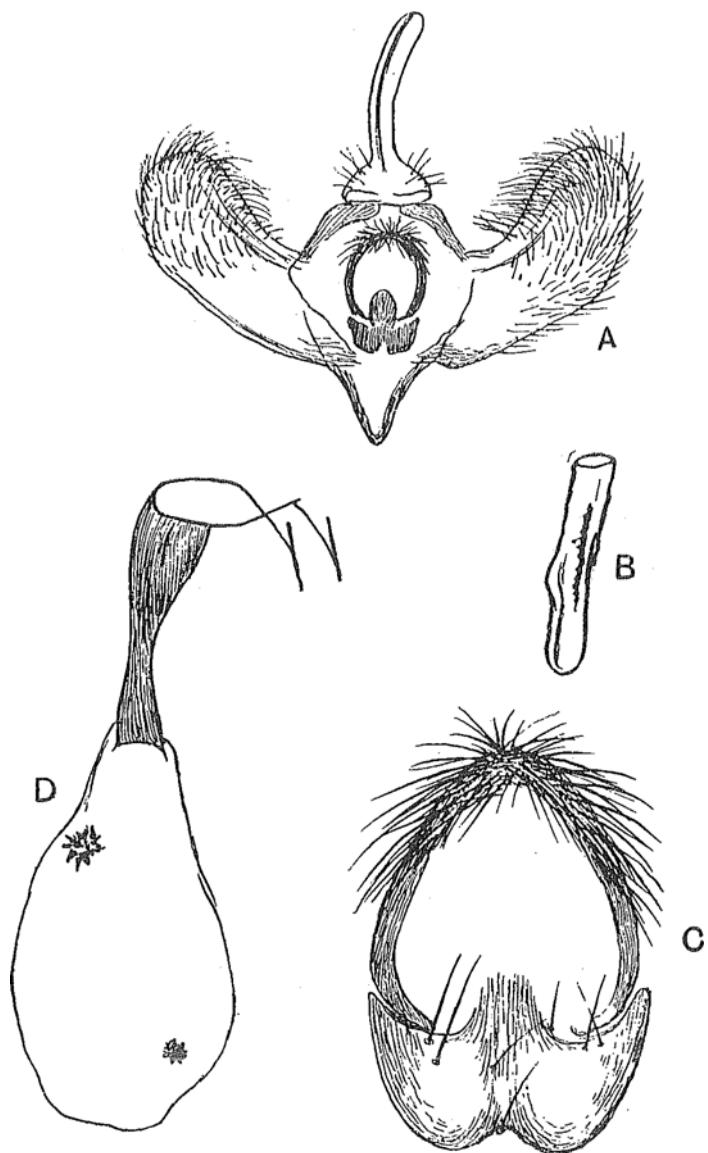


Fig. 5. The genitalia of *C. brumata*.

A = Male genitalia without aedeagus. B = Aedeagus. C = Labides. D = Female genitalia.

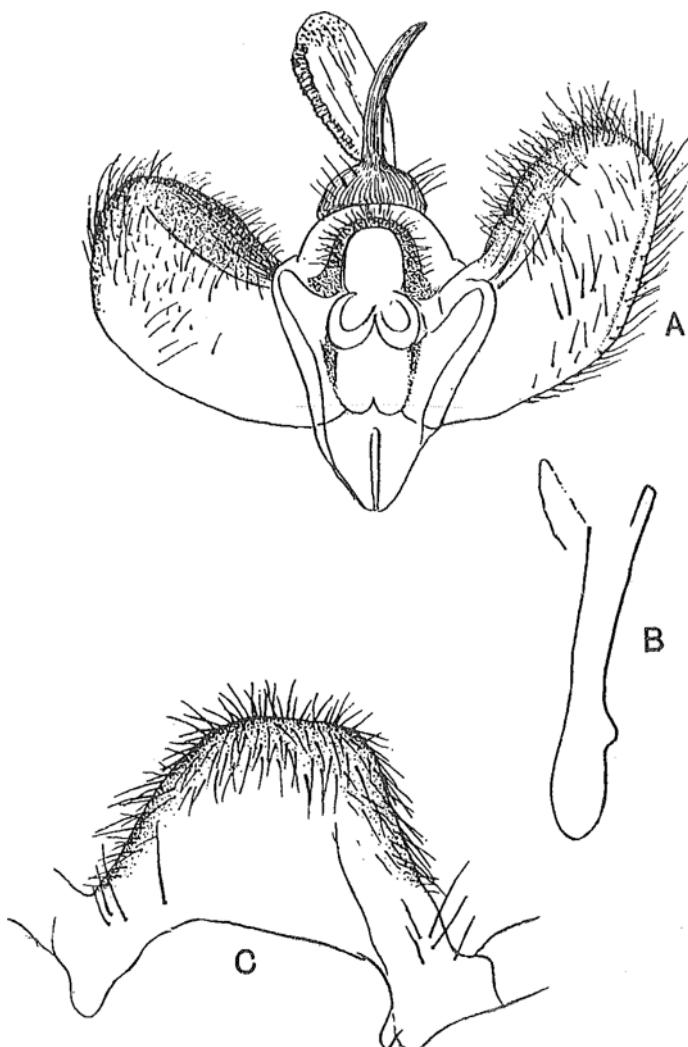


Fig. 6. The genitalia of *C. boreata*. Male only.

The imagines emerge in the afternoon and remain during the rest of their first day at the base of the tree boles and amongst the herbage. After the first evening's flight they rest higher up, often enough very conspicuously on tree trunks, but sometimes on smaller twigs and amongst leaves. Both sexes, the female in particular, delight to sit on the smaller twigs with their wings encircling them. *O. filigrammaria* in some of these respects necessarily differs; both sexes sit on heather twigs, but if rocks are available they may be seen dotted about them in considerable numbers. In all cases the insects are easily startled or dislodged, the males flying high and far and the females but a short distance; in fact, not uncommonly the female feigns death and drops amongst the herbage.

The eggs are laid at the base of buds either on the bud itself, between it and the stem, or under tiny curled pieces of bark where they remain sheltered from all the vicissitudes of winter.

It was my good fortune to discover all of the forms referred to above in my own immediate neighbourhood and therefore within easy reach for study. I at once commenced to experiment with them, and very early indeed I discovered their interspecific fertility and, in certain cases, that of the hybrids of the F_1 generation. These latter observations, coupled with the discovery of the constancy of the several local races evolved from *O. autumnata* and *O. dilutata*, formed a combination so attractive to a geneticist that I determined to avail myself of the opportunities thus offered and to submit the whole of the phenomena presented to more intense study. In doing so I propounded for solution the following problems:

(1) Seeing that *O. autumnata* and *O. filigrammaria* are perfectly fertile when crossed, and since the F_1 hybrid generation is likewise fertile when paired *inter se* or when back-crossed with either parent species, is the type of inheritance shown explicable on strictly Mendelian lines?

(2) What light do the hybrids between *O. autumnata* and *O. dilutata* throw on the same problem?

(3) Further, since *O. autumnata* and *O. filigrammaria* differ in mean size in both sexes, what information can be gleaned from their study as to the inheritance of size?

(4) How do these same two forms maintain their distinctness even when free to cross through their colonisation of the same or adjacent areas?

(5) Do the differences between the various local races, as well as

those between *O. autumnata* and *O. filigrammaria* and between *O. dilutata* and *O. christyi*, invariably reappear in the offspring?

(6) If so, is this actually due to heredity and therefore germinal, or is it ontogenetic, i.e. due to like environmental impulses acting anew on each individual of the successive generations to produce like effects?

(7) If actually germinal, how do the differences arise and how are they fixed; are we concerned with "germinal" mutation or with acquired characters depending on the prolonged action of environmental agencies and their final registration in the germ cells with subsequent inheritance?

(8) Are the current explanations of melanism in the Lepidoptera in harmony with the facts; and what evidence has the genus *Oporobia* to offer on the subject?

(9) In all of the problems enunciated how far has "natural" selection played its part?

By a perusal of the above questions it will be seen that I undertook the work without allowing my natural bias against the Lamarckian position to prejudge the case; what answers I obtained to them will be discovered in the succeeding pages.

II. VARIATION—SUBSPECIES—LOCAL RACES—MELANISM.

(a) General.

In the introductory remarks I indicated that the genus *Oporobia* included two species and two subspecies, *O. autumnata* with its subspecies *O. filigrammaria*, and *O. dilutata* with *O. christyi*. It now behoves us therefore to consider the exact relationship, if such consideration is possible, between these pairs of forms, and incidentally to assure ourselves of the value to be attached to the term subspecies.

In my earlier work I was always sceptical of the existence of such things as subspecies and shrank from using the word. Prolonged study of the present genus has considerably altered my views in this respect, so that I have come to recognise the existence of such entities as exceedingly probable, and in any case the use of the word as justified. In *Oporobia* the two subspecies recognised, when assessed at their true value, do not depart very widely from the Jordanian concept of the "little species," or, as I have usually called it, the "microgene." Furthermore, the probable course of development of *Oporobia filigrammaria* gives us some hint that such subspecies or microgenes may have arisen by a long period of isolation not in itself of sufficient duration or of such a type as to allow of divergences of full, unchallengeable, specific value.

Any exact or even approximate definition of what constitutes a subspecies is, however, an enormously complicated matter, rendered the more so by the uncertainty as to what a species itself really is.

If we compare *O. autumnata* and *O. filigrammaria* we find that in important structural characters they differ not at all; moreover, they are perfectly fertile when mated together. Nevertheless, when one actually tabulates the differences (as I have done below, as well as those between *O. dilutata* and *O. christyi*) we find that the insects fail to agree in many minor points both in structure and in life history. In addition each has the power of setting up its own peculiar local races—races each one of which is characteristic of its own locality, but in *filigrammaria* never altering its fundamental details to show that its degree of differential evolution passes from that of its fellows elsewhere toward the *O. autumnata* with which it is phylogenetically connected: and the same remarks apply to *O. dilutata* and *O. christyi*. Probably the best view to assume concerning the subspecies is to regard the term as covering those cases in which we have groups sufficiently differentiated from those pronounced by systematists as good species for one to regard them as possible species, but upon which one is forced to suspend one's judgment, either because of a lack of clarity as to what a species is, or because one cannot gain sufficient of the essential details upon which to found a decision free from any tendency to waver. The very great difficulties in the way of gaining the necessary decisive facts are emphatically shown when the perfect fertility between *O. autumnata* and *O. filigrammaria* and between *O. dilutata* and *O. christyi* is contrasted with the puzzling behaviour in that respect of certain forms of the genus *Orgyia* which I can only regard as subspecies; the matured judgment of years of study will not permit me to treat them as being of specific rank. These are those subspecies of *Orgyia antiqua* known as *O. badia*, found in Pacific North America, and *O. nova* in North America east of the Rocky Mountains. In every character the two American forms are widest apart, *O. badia* being almost unrecognisable as the same species as *O. nova* when one examines larva, pupa and imago. *O. antiqua* from Europe on the contrary is excessively near to *O. nova* and thus differs greatly from *O. badia*.

Nevertheless, whilst the two American forms, when crossed together, are reciprocally fertile and continue so as long as one cares to pursue the experiment, when one crosses either of the American forms with the European the cross is only fertile when the European insect provides the female; but, as before, the brood so produced can be inbred in-

definitely. The case of *Lymantria dispar* and its subspecies *japonica* produces evidence of the same value.

Local races are in quite another category and no genus is more prone to their development than *Oporobia*, the insects in nearly every habitat displaying local facies. These races are clearly brought into being in response to environmental forces of varying incidence which are not powerful enough to push the insect on to an evolutionary plane palpably higher than that of its relatives in other stations. The differences exhibited may be in any feature—markings, habit, period, etc., each and all being involved,—but they never attain to differences in structure even of the low order existing between *O. autumnata* and *O. filigrammaria*; there is never any difficulty in assigning the insects to the species to which they belong. So near do some genuine local races approach what systematists pronounce the type that only very careful biometrical study can demonstrate that difference in modal condition indicative of the local race.

In general, however, if a sufficiently great number of individuals be assembled from any given area (restricted it may be in some cases but of considerable extent in others) and placed alongside a similar assemblage from another point it will instantly be impressed upon one that the two sets are not alike. Sometimes each individual in the one differs from each in the other by some more or less tangible characters or degree of development of those characters, and sometimes only the majority of individuals show this difference; nevertheless it exists, and such diverse sets can only be regarded as local races.

In *Oporobia*, whilst the differentiation of subspecies and local races is fairly easy, great difficulty lies in the way of assigning any given specimen in the absence of exact data to its correct group, so great is the degree of fluctuating variation exhibited in wing markings. No species or subspecies is free from it, although *O. christyi* is least affected, *O. filigrammaria* being next in order. But, let it be noted, even they can cover the whole range. In all the ground colour can vary from almost pure white to black; the markings in all may be absent, undecided, scattered, condensed into bands, heavy or light and so on with every possible combination of these and the ground colour; even the discoidal point achieves the apparently impossible by displaying great variability.

Haphazard as all this seems, it is in reality quite regular; indeed so regular is it that all four forms possess parallel variations. So obvious was this that when once I knew of the existence of the Carpet-

banded¹ aberration of *O. dilutata* I predicted the occurrence of similar *autumnata* and *filigrammaria* forms and these I have since discovered. A banded *O. christyi* has not yet appeared but it will turn up.

This ordered condition of the seemingly irregular, the appearance of so many wonderful aberrational forms and aberrations in parallel series throughout the species and subspecies of the group is so striking as to suggest that Eimer's theory of Orthogenesis² has some foundation in

TABLE I.

Summary of characters differentiating O. autumnata and O. filigrammaria.

			<i>Oporubia autumnata</i>	<i>O. filigrammaria</i>
Ova...	...	Description	Salmon pink; pitted, ridges marked but pits shallow	Much the same; perhaps slightly larger and colour duller
"	...	Hatch ...	Date varies with season ...	Always much earlier
Larvae	...	Description	Applegreen varying slightly in intensity in the local races	Blackish green, mottled appearance; head smoky, smaller
"	...	Food ...	Betula, Alnus, Larix, Pinus	Calluna, Erica, Vaccinium
"	...	Pupate ...	In typical form late, in larch feeding form earlier	Always preceding any true <i>autumnata</i> form
Imagines	...	Emerge ...	In typical form early October to November; in larchwood form September 16th to September 30th	August 20th—September 20th
"	...	Markings and size	Ground often white, varies to grey; may be melanic; markings generally distinct but feeble and suffused in larch form; female rather large	Colour similar; markings and bars heavier and clearer especially subterminal bar and on hind-wings; glossier; smaller; wings narrower; female smaller in proportion to male
Male genitalia	Octavals ³		Not large, widely apart; depression between shallow	Nearer; depression deeper
"	Cristae ⁴		About 19	About 7
"	Labides ⁵ ...		Head wide; vestiture thin	Head narrow
Female genitalia	Signa ⁶ of Bursa copulatrix		Small and scobinate ...	Larger
Chromosome Number	Haploid ...	38	37
	Diploid ...	76	74

¹ That is possessing a complete central band like *Melanithia (Larentia) ocellata*, *Melanippe (Larentia) rivata* and *M. (L.) sociata*.

² Eimer, *Orthogenesis d. Schmetterlinge*, Leipzig (1897).

³ Chitinous projections on 8th sternite.

⁴ Patch of stiff hairs on juxta.

⁵ Pair of rods rising from the chitinous bar extending from the costae of the valves; fused and ending in a hairy head in these species.

⁶ Chitinous armature of bursa copulatrix.

actual truth. Furthermore, these phenomena afford, with other similar cases in many genera like *Lycaena* and *Taueniocampa*, some degree of proof of the principle.

TABLE II.

Summary of characters differentiating Oporabia dilutata and O. christyi.

		Description	<i>Oporabia dilutata</i>	<i>O. christyi</i>
Ova		Glossy, ruby in colour, pitting feeble	A little smaller, glossier
Larvae ...	Hatch ...		Varies	The same
" ...	Description		Green, often purple marked	The same
" ...	Food ...		Quercus, Crataegus, Acer, etc.	Betula, etc.
Imagines ...	Emerge ...		October	The same
" ...	Markings, size, etc.		Ground very variable; discoidal point large; angle of elbowed line rounded; sweeps toward discoidal point	Ground whitish generally; discoidal point small; angle of elbowed line a right angle as in autumnata
Male genitalia	Octavals ...		Same size as autumnata	Insect a little smaller
"	Labides ...		Far apart	Very near
"	Valves ...		Head narrow	Head wide
Chromosome Number	Haploid ...	30	?
	Diploid ...	60	?

(b) *The Evolution of the Subspecies Oporabia filigrammaria.*

Evolved as we have seen from *Venusia cambrica*, whose life history was interwoven inextricably with that of the northern tree *Pyrus aucuparia*, *Oporabia autumnata* accepted birch as a food and was thus enabled to colonise much of the Boreal circumpolar continent of Mid Tertiary times, just as had many of its contemporaries like *Lycia hirtaria* and *Poecilopsis lapponaria*. So like that of *P. lapponaria*, *Nyssia zonaria*, *Anthrocera purpuralis*, *A. achilleae* and *Platyptilia tessuraductyla* are many points of its history that, in view of my detailed treatment of the Bistoninae elsewhere¹, no repetition is necessary here.

Only one fact must be singled out, and that is, that as with the last mentioned five insects, the climax of glacial conditions saw the insect in Europe split into two widely separated colonies, one located in South Eastern Europe and the other in stations far to the west of the British Islands of today.

With these preliminaries we have reached a stage at which the modern history of what now represents the original *O. autumnata* may be regarded as commencing.

¹ Harrison, "The Geographical Distribution of the Moths of the Geometrid Subfamily Bistoninae," *Naturalist*, pp. 164—166, 194—198, 273—278, 377—382 (1916).

One cannot too strongly insist on the enormous environmental differences between the two European sections. That to the east was confined to forests restricted by the barrier of the ice to a dry and rigorous continental climate, whilst the western division existed on low lying shores and islands exposed to a moist oceanic climate modified by the presence of the ice. For thousands of years they persisted thus. Save for oscillations in habitat depending primarily on temporary ameliorations in the climate, the continental colony had to suffer but little change in food. All known inter-glacial deposits yield birch in one form or other; nor is alder lacking. Consequently, for all this period the conditions under which it lived were not altered substantially, with the result that it underwent no significant change in form or habit. Far different, however, was it with that marooned, as it were, on the then far flung shores of Western Europe; to understand fully how different, let us pause to glance for a moment at the vicissitudes of the moorland vegetation in the British area in late pre-glacial and early glacial times.

Heather (*Calluna vulgaris*), a Pliocene product of Ericaceous type, very soon after its evolution on western lands long since submerged by the Atlantic rollers, had united with its more southern brethren of the genus *Erica*, its more robust northern relatives of the genus *Vaccinium* and many other ericetal plants of northern predilections like *Betula*, *Salix* and *Empetrum*, to form an association favouring certain soils. So successful were such communities that the oncome of the glacial period saw them in firm possession of all suitable habitats in the British Islands.

But as the ice sheets crept westward, exposure to steady Atlantic gales, coupled with chilly breezes from the ice-bound land for countless years, had its effect on these societies. Gradually the birch was eliminated, not only through the influence of the winds but also by the incessant fretting of the land by the ocean waves, producing low treeless coasts and islands not unlike what we observe in the Hebrides and Falkland Islands today. Upon such, typical low-growing ericetal vegetation alone flourished. By degrees, with the vanishing of the birch, *Oporabia autumnata* transferred its attentions to *Calluna*. Now, instead of feeding on a leafy deciduous tree in comparative shelter, it fed openly on a low-growing evergreen shrub subject to climatic conditions strange in ways other than those depending on the probably warm and short glacial summer.

Aestivating as it did in the pupal condition, and its emergence as imago in late summer being correlated with the development of the

pupae in response to an exposure to a period of diminishing daily temperatures, it is clear that individuals derived from early hatching ova and from more rapidly feeding up larvae would tend to be exposed earliest to this optimum state of falling temperature and thus would emerge earlier. On the contrary, individuals exhibiting retarded development would tend to emerge so late that the rapid appearance of early winters would destroy them before they could secure the perpetuation of their species. In this fashion, by natural selection, a race provided with early hatching ova and pupae would be built up; *Calluna*, not being a deciduous shrub, would by that very fact favour early emergence and assist this development.

Parallel with the acceptance of a *Calluna* diet another change, probably connected with the difference in nutritive value of *Calluna* and *Betula* to *Oporabia*, occurred, and that was size diminution—a phenomenon that always manifests itself when larvae feed on foliage less nourishing than their own special food and as happened with *O. autumnata* larvae experimentally transferred from birch to heather. But its germinal fixation as well as that of the diet habit itself as a hallmark of the race is another matter. Are we dealing with genuine Lamarckian effects or with a Weismannian case of parallel selection? Are insects whose germinal composition induces that small size which would of necessity demand a shorter larval period than the normal being selected with those undergoing selection because of their speedy feeding up on other grounds? Probably the bulk of present day opinion would favour the Weismannian view but personally I am far from ruling that of the Lamarckian out of court.

The repeated failures in experiments projected to test the validity of the inheritance of acquired characters savour too much of attempting to determine all that occurs in a long express train whilst one compartment flashes by. Besides, one must attach some value to evolutionary experiments in bacteriology even if Sumner's¹ results with mice and Kammerer's² with amphibia are to be neglected. It seems to me that the experience of a hundred thousand years may sooner or later be indelibly impressed on the germ plasm of the race.

¹ Sumner, "The Appearance in the Offspring of Artificially Produced Parental Modifications," *Am. Nat.* Vol. XLIV. (1910). Sumner, "Some Effects of Temperature upon Young Mice and the Persistence of Such Effects in a Subsequent Generation," *Am. Nat.* Vol. XLV. (1911).

² Kammerer, "Direkt induzierte Farbaufassungen und deren Vererbung," *Zeit. f. ind. Abst. u. Vererb.* Vol. IV. (1911). Also similar papers.

Another explanation of the earlier appearance is, however, possible. This *Calluna*-feeding *autumnata* which we will hereafter call *fili-grammaria* differs in several minor structural points—cristae, octavals, intensity of wing markings—as well as one major point, the loss of a single chromosome. Now this latter divergence must be mutational in origin; one cannot conceive such a fundamental difference arising by selection. It is therefore possible enough that the change in the life history is intimately bound up with these differences in size and other points, and that all arise from the mutation involving the loss of a chromosome, each tending to the conservation of the race and therefore in the end characteristic of it.

The same might be suggested as an explanation of the curiously significant colour scheme of the larva, both in respect to the actual colours and to its pattern. To this view, however, one great objection can be advanced; they approach too unmistakably to those obtaining in the larvae of other heather feeders like *Anarta myrtilli*, *Agrotis agathina*, *Eupithecia nanata*, and the case is too closely parallel to that of all *Pinus* feeders, whether lepidopterous or hymenopterous, for the matter to be one of a chance mutation. As is generally recognised, mutations take place in all directions from the modal condition and their precise course is a matter of chance; therefore to explain the convergence of the larval designs and colours in all the above ericetal lepidoptera, appertaining to widely separated groups, on such a basis seems too far fetched. We seem rather to be dealing with characters evolved in direct response to environmental forces, like those in Poulton's *Amphidasys betularia*, and fixed by their long continued incidence, aided perhaps by natural selection.

To sum up, attaching due weight to all of the observed facts, chromosome difference included, and considering their origin dispassionately¹, in my opinion the divergences from type *autumnata* are best explained as being brought about by stimuli of the environment, and thus more readily explicable on Lamarckian grounds.

Favourable inter-glacial interludes then saw the subspecies in its present-day guise ready to seize any opportunity of advance, and the waning of the ice, with the exposure of its huge deposits of glacial drift, gave it unique scope for doing so, so readily does *Calluna* invade such ground. But advance was bound to be northward; thus the incipient moorlands along the then common western shores of Scotland and Ireland would be first colonised, followed, as the ice yielded still further and con-

¹ I commenced these studies from a pronounced anti-Lamarckian standpoint.

ditions approached the normal, by gradual infiltration inland until all the heather clad hills of later glacial times were held. Then a slowing-up would intervene, for invading northern forms which had utilised the Scandinavian route as an inter-glacial means of escape from south-eastern Europe would act as a check until recurring glacial conditions restricted the movements of both groups.

Finally the ice vanished and ground capable of colonisation was once more open and to some extent regained, but once again slowly, for we must not forget that *Calluna* is a plant of south-western origin and was passing from more into less favourable areas, and this tardiness kept back the insect, with the result that before the continent was attained the British Islands had come into being.

Advance south-eastward, likewise, was slow; in that direction dense masses of migrating southern forms blocked the way until at length when equilibrium was set up Great Britain was separated from Ireland and the western islands from both; thus the insect was in possession of habitats closely approximating to those it holds today; if one thing is more certain than any other concerning British vegetation it is that the bulk of our heather clad moorlands with their peculiar plant formations are more primitive, i.e. are in a more natural state, than any others.

Accustomed as *O. filigrammaria* had become to a diet of ericaceous plants during the ice age, it had not lost the faculty of feeding up easily and satisfactorily on the *Betula*, *Alnus* and other plants of its earlier days. Yet despite this, even in the birch-heather associations of moorland slopes, the female instinctively lays its eggs on *Calluna* or *Erica*, the birch being entirely neglected. Year after year I have beaten birches in such associations—even seedling trees not so tall as the surrounding heather—on a moor where both type *O. autumnata* and the subspecies *O. filigrammaria* occur, and never has the birch produced *filigrammaria* nor the heather *autumnata*. And this is the more wonderful when one considers the ease with which the confined insect oviposits in chip boxes, on muslin threads, in cotton wool and the like, and on trees when in the semicaptivity of a roomy muslin cage. How has this instinctive choice of *Calluna* and *Erica* become engrained in the germ plasm? It seems very unlikely that it is mutational, and impossible that it should be selectional when due regard is paid to the facts outlined above; once again the evidence strongly urges one to the Lamarckian view that long years of compulsory oviposition on these plants, whether because they were ericaceous or simply because they were low-growing or because of

similar circumstances, have so affected the organism that the habit has been impressed germinally.

(c) *The Evolution of the Local Races.*

Our task now is to trace the sequence of more recent changes in the main species—changes much less profound than those just examined but still, from a genetical standpoint, equally important.

Prior to doing so we must outline the movements of the main body of the species penned up, in all probability, on birch clad plains of Eastern Europe. As I have pictured elsewhere¹, almost certainly all plants and animals of northern proclivities regained our islands from their glacial retreat *via* Scandinavia in warmer inter-glacial times. Amongst these were birches, the remains of which occur so freely in inter-glacial peat deposits both on the land of today and that submerged long ago beneath the Baltic and North Seas. Accompanying the birch would be its insect guests of boreal type, from which we see that *O. autumnata* very early reached our shores; so early indeed was it that like many forms it reached Ireland and the north and west of England ere separation took place.

Having thus very briefly reconstructed the course of *autumnata* to its present range we shall, henceforth, confine ourselves more or less to its movements in the Cleveland district of Yorkshire, the scene of our studies in the evolution of local races.

To equip ourselves for such an enquiry our first object must be the attainment of a broad view of the post-glacial changes in moorland life. The moorlands, here, are of pre-glacial origin and in places like Rosedale have never been over-ridden by ice, from which it appears not impossible that life persisted on the driftless area throughout glacial times. Still we must be careful to notice that, exactly as in Greenland today, whilst *Calluna* may have survived there one would hardly expect such trees as birch and alder to persist. Therefore, for all practical purposes, in considering the post-glacial history of *O. autumnata* we may commence our researches with the recolonisation of the whole country in the equable climate immediately succeeding the great ice age, when the Arctic Flora, in itself decidedly of ericetal tendencies and thus providing a splendid nucleus for moorland plant communities, gradually yielded under the influence of more genial and drier days. Of the condition of the moors then we have ample evidence in the peat beds. Favoured by the cli-

¹ Harrison, "The Geographical Distribution of *Dimorpha versicolora* and what it suggests," *Ent. Mo. Mag.* May, 1916.

mate, far and wide, on dale and hill alike, the moors supported huge birch forests relieved along the streams by alders and giving place to oak and mixed woods nearer sea level. Naturally, its fate being linked up with birch and alder, *O. autumnata* would be equally widespread.

But this dry, warm epoch did not last. A steadily increasing rainfall stimulated the ever greedy Sphagnum bogs, and working down from badly drained moors through slacks and gills the developing peat slowly engulfed the birches, as even a casual glance at the stacks of newly cut peat on the remoter moors will reveal, as well as chance exposures elsewhere. Finally all birches, except those growing in ravines supporting a briskly moving stream and those on well drained slopes lower down the dales, were exterminated. Much later even the latter woodlands were destroyed in satisfying the demands of the mediaeval (if not earlier) exploiter of the outcrops of ironstone.

Thus under diverse influences the area under birch was reduced to minute proportions, and on the whole of the northern slopes, including the Eston outlier, almost exterminated, as a glance at those portions of Jeffery's 1772 map of Yorkshire given on Figs. 7 and 8 will show. Neither on Eston Moor nor in Lonsdale is any considerable woodland depicted as existing. And the accuracy of the map cannot be impugned, so correctly are the old established oak-ash woods on the north-east slopes of Eston Moor, Airyholme Wood and Easby Wood indicated; these still flourish just where Jeffery places them.

Such a fate as befell the birches would inevitably have overtaken the insect had not the close botanical relationship of birch and alder always enabled it to use the latter tree as food. And these facts, fortunately enough, put us in the position of being able to assert that toward the close of the eighteenth century, when the period of afforestation set in, the northern colonies of *O. autumnata* were confined to alders lining the various beck sides and those surrounding certain moorland springs and pools, with the possible addition of stray birches. In particular those on the northern outlier known indifferently as Eston or Barnaby Moor were so limited.

A dozen years or so after the publication of Jeffery's map the first attempts at moorland reclamation were made in Kildale and Lonsdale and on Kempswthen by Sir Charles Turner. In Kildale much of the land so reclaimed was destined for agricultural purposes, but in Lonsdale the efforts were directed towards the establishment of plantations including both deciduous and coniferous trees, the upper slopes receiving Scotch fir and larch and the lower oak.

But the afforesting was carried out in a thoroughly unscientific manner, the fatuous planting of oaks, etc., directly on the heather ending in failure so disastrous that not a dozen have survived to the present day. The failure of the projected oakwood was recognised very early and pointed out by Tuke¹ in 1800.

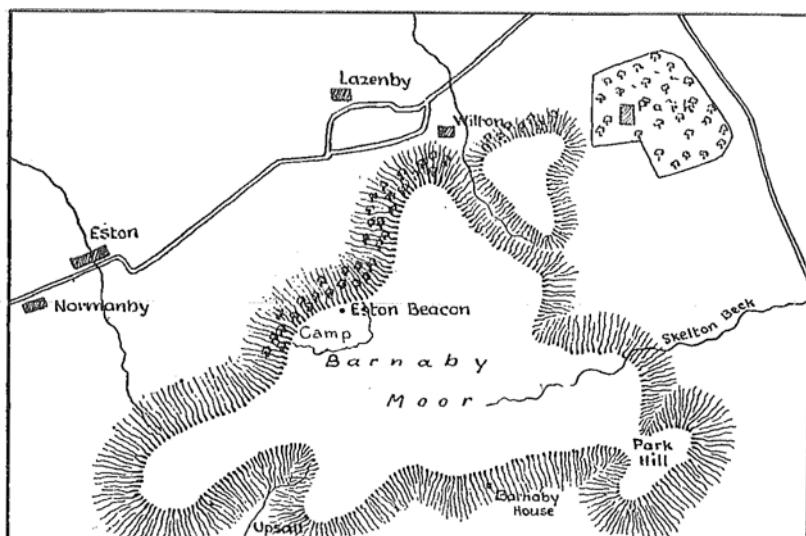


Fig. 7. Eston Moor from Jeffery's 1772 map of Yorkshire.

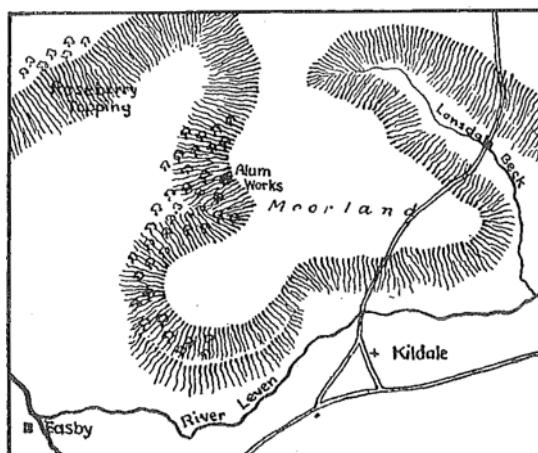


Fig. 8. Lonsdale and Kildale from Jeffery's 1772 map of Yorkshire.

¹ Tuke, *General View of the Agriculture of the North Riding of Yorkshire* (1800).

Subsequently the blanks have been filled, in part artificially with larch, spruce and alder, and in part naturally with mountain ash and alder so that the lower portion of the wood may be classed as mixed larch and alder with the latter predominating (amongst which occur old Scotch firs and poplars), whilst the upper produces spruce and Scotch firs with occasional birches in the open spaces near the hill crests. Mountain ashes occur sporadically everywhere. Also as shown on the map on Fig. 9, growing in a mass surrounded by these unusual associates, still exists a small patch of oaks.

That we are here dealing with the recolonisation of deforested areas is perhaps hinted at by the intrusion of scattered low-lying stretches of the common bluebell (*Scilla nutans*), apparently quite at home with such strange associates as *Trientalis europaea*.

Thus we see that early in the nineteenth century we had in Lonsdale an alderwood continuous with the alders, willows and aspens marshalled along Lonsdale Beck, succeeded as we ascend the dale by a few oaks which were isolated by great stretches of larch, pine and alder from all contact with similar trees—and this is the position as it appears on the 1860 Ordnance Survey.

But the alders edging the stream, as we have demonstrated, like those in Ingleby Parish, Farndale and elsewhere, supported an *autumnata* colony which, as soon as circumstances admitted of the passage, colonised the new wood; their fate we shall consider below.

We must now return to Eston Moor; shortly after the foundation of the plantations in Kildale and Lonsdale the enclosure of common lands began, and amongst the land so enclosed were the portions of Eston Moor marked Wilton Wood and Normanby Intake Plantation on Fig. 10. Almost immediately irregular parts of the former were planted with larch and Scotch fir; these parts included a narrow wedge just south of the Beacon, narrow irregular patches skirting the lower boundaries of the enclosure, and a narrow strip with parallel sides joining up the former and otherwise disjoined parts. The upper part surrounding the Beacon was left untouched as was the broad central area, and both, when the 1860 Ordnance Survey map was produced, were heather and *Nardus* moorland and are labelled "Lighthouse Fields" and "Wilton Moor" respectively. Both supported (and still support) a few alders and odd birches around the Carr pools. Subsequently, some score or so of years later, the whole of the open portion of the enclosed area was planted with larch and fir.

Half a mile away, matters at Normanby and Upsall Intakes pursued

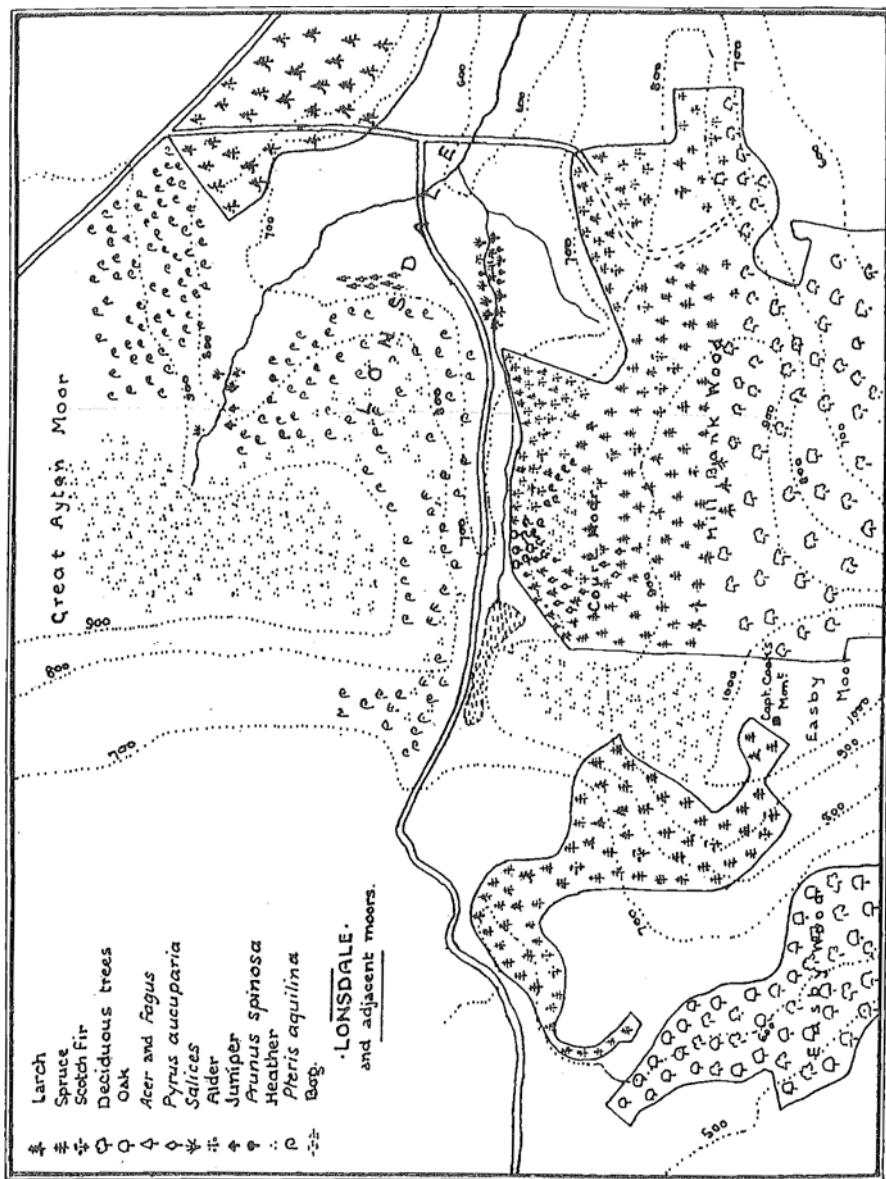


Fig. 9. Map of Lonsdale and adjoining moors showing the vegetation and altitudes.

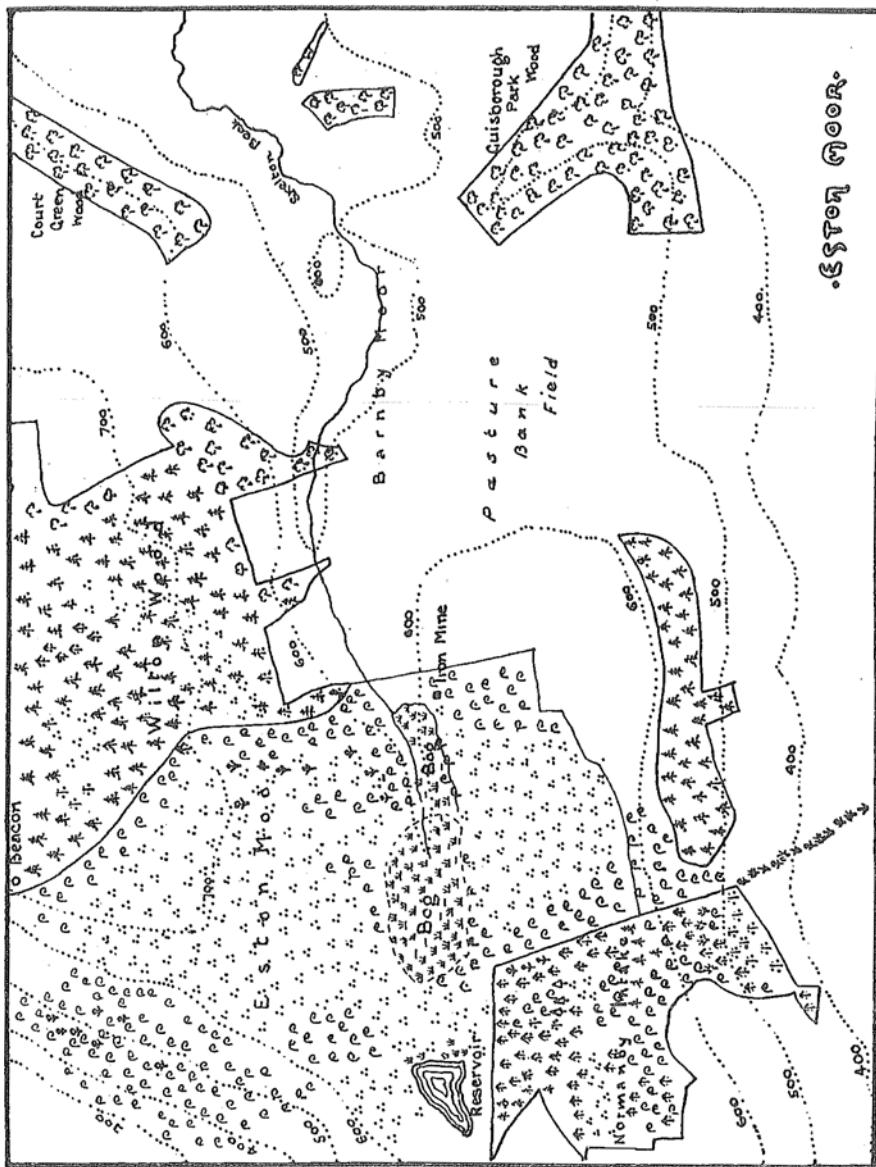


Fig. 10. Map of Eston Moor, Wilton pinewood and Normandy birchwood showing vegetation and contours.

a different course. Probably influenced by the fact that efforts had been made to bring the western end of the moor under cultivation in the middle ages renewed attempts were directed towards the same end. As advised in Marshall's *Rural Economy*¹, a row of birches was planted just within the northern boundary wall to act as a wind shield, and at the same time the land was broken into fields. Failure once more ensued as the soil composed of weathered Moor Grit is too light for successful agricultural operations, and the plan was abandoned. In order to avoid waste the "Intake" was then planted with larch and fir. Thus, in the early "eighteen hundreds," Wilton Wood and Normanby Intake Plantation were coniferous in character but included isolated clumps of birch and alder, and this was exactly the position when the 1860 Ordnance Survey was made. If any difference is perceptible between the two, it is that the latter wood is represented as being the more closely provided with coniferous trees.

By the very fact of the enclosures the alders along Skelton Beck and around the Moorland Carrs were left exposed and have been destroyed, only traces of their former presence being left. Thus early in the nineteenth century all communications between Wilton and Normanby Woods via the alders of the moor pools and streams were broken. Nevertheless, conditions within the woods still agreed; slope, elevation, exposure, vegetation quite coincided; the sole difference lay in the fact that Wilton Wood lay on the geologically younger sandstones of the Lower Estuarine series whereas Normanby Intake lay on the older Moor and Fossiliferous Grits.

Such agreement held until about the year 1885 when drastic changes took place in the Intake Plantation. A heavy north-east gale so damaged the trees that many broke off, and as the wood was ruined the remainder were felled. When I first visited the wood in 1906 the decayed stumps of those cut down still remained as did also the jagged trunks of those hurled down by the wind. Except at the extreme south-east (see Fig. 10) the only coniferous trees left were two seedling pines and one larch. In their stead were springing up in all directions crowds of birch saplings, obviously, from their north to south trend, proceeding from those originally acting as a wind shield; now (1919), almost the whole area once under pine and larch is occupied by birch. Fully one half of this ground has been gained since 1906. With this birch, around the old pools still survive the alders of times long gone by. In contrast

¹ Marshall, *Rural Economy of Yorkshire* (1796).

to this Wilton Wood, from a coniferous standpoint, is quite untouched, whilst birch and alder alike are vanishing.

From this we glean that the once continuous Eston colony of *Oporobia autumnata* was, about the year 1800, broken into two distinct portions separated by half a mile of heather and bracken; from that period until 1860 and onward until 1885 these two sections, although disjoined, continued to exist under identical environment. After 1885 the conditions fundamentally altered; one division had to live in a coniferous wood in which birch and alder were being suppressed, and the other in a birch-wood (with some alder) where conifers were disappearing.

With these changes corresponding changes of an evolutionary nature have occurred in the respective portions of the old *autumnata* colony which exhibit themselves especially in the following four features: (1) the mean sizes of the two races are different; (2) their food plants are distinct—birch in the one case and larch (rarely pine) in the other; (3) the Wilton Wood insect is a duller, feebly marked insect with its variation range swinging round this as a modal condition, whereas the birch insect presents us with diverse strains with an abundance of pale silvery and barred forms as well as of feebly marked forms including those just referred to; (4) the pinewood insect emerges in September and is quite over by the end of that month; on the contrary the birch insect rarely occurs in September, in which month I have seen but two wild specimens—a male in 1910 and a female in 1916; it only becomes abundant about October 10. So great was the divergence in this respect that for several years after my discovery of the insect amongst the larches, in spite of careful search conducted on the same days as I climbed the hill specially to secure material from the pinewood, I missed the birch colony and actually published a note to the effect that the insect did not occur there. Only a casual visit in mid October, 1909; in search of Arachnida, revealed its presence and demonstrated why it had escaped previous observation.

And the wonderful thing about these differences is that they must have arisen in the period between 1886 (when the environments ceased to be alike) and 1907, when my acquaintance with the insect commenced.

That they do not depend upon the ground vegetation seems obvious because amongst the larches, where alone the insect occurs in Wilton Wood, the plant associations differ in no important respect from those of the birch wood, as the following table, including for facility in reference the vegetation of the alderwood in Lonsdale, will show.

The ground vegetation thus not being the decisive factor, it seems

that for an explanation of the changes we must look to the passage to birch in the one case and to larch in the other.

Of this, in the case of size, we can adduce experimental proof very readily; a birch diet quickly restores the pinewood *autumnata* to its former greater mean size; nor need the question of changed food delay

TABLE III.

The vegetation of Wilton Pine Wood, Normanby Intake Birch Wood and Lonsdale Alder Wood.

Plant	Birch Wood (open)	Pine Wood (closed)	Alder Wood (has some open spaces)
<i>Pinus sylvestris</i>	...	R*	A
<i>Larix decidua</i>	...	R	A
<i>Betula alba</i> (agg.)	...	A	R
<i>Alnus rotundifolia</i>	...	O	R
<i>Satiz caprea</i>	...	VR	VR
<i>Populus nigra</i>	...	—	—
<i>Quercus robur</i> (agg.)	...	VR	One { Common in one restricted area
<i>Pyrus Aucuparia</i>	...	R	C
<i>Crataegus oxyacantha</i>	...	R	R
<i>Fagus sylvatica</i>	...	One	—
<i>Acer pseudoplatanus</i>	...	Odd examples	—
<i>Oxalis acetosella</i>	...	A	A
<i>Cardamine pratensis</i>	...	—	O
<i>Viola Riviniana</i>	...	C	—
<i>V. palustris</i>	...	—	C
<i>Stellaria holostea</i>	...	—	C
<i>Gaulium saxatile</i>	...	A	A
<i>Potentilla Tornentilla</i> (agg.)	...	A	R
<i>Calluna vulgaris</i>	...	C	LC
<i>Erica Tetralix</i>	...	C	LC
<i>E. cinerea</i>	...	C	LC
<i>Vaccinium Myrtillus</i>	...	C	LA
<i>V. vitis-idaea</i>	...	—	—
<i>Empetrum nigrum</i>	...	C	C
<i>Trientalis europaea</i>	...	—	—
<i>Rumex acetosella</i>	...	A	A
<i>R. acetosa</i>	...	—	C
<i>Deuchampsia flexuosa</i>	...	A	LA
<i>Molinia caerulea</i>	...	C	—
<i>Agrostis</i> spp.	...	C	Not C
<i>Festuca ovina</i>	...	C	Not C
<i>Nardus stricta</i>	...	LA	R
<i>Holcus mollis</i>	...	—	—
<i>Scilla non-scripta</i>	...	—	—
<i>Luzula multiflora</i>	...	C	O
<i>Juncus</i> spp.	...	LC	L
<i>Pteris aquilina</i>	...	LA	LC
<i>Blechnum Spicant</i>	...	R	R
<i>Lastrea</i> spp.	...	R	C
<i>Bryophytes</i>	...	A	C
<i>Fungi</i>	...	A	A
<i>Lichens</i>	...	R	C

* The frequency symbols are:—A, abundant; C, common; O, occasional; R, rare; VR, very rare; LC, LA, locally common, locally abundant.

us. With the inhibition of birch and alder by the larches and pines the insect, if it had to survive, had to accept substitutes either in one or both of these. This it found in larch, upon which it subsists exclusively in the western part of the wood. Its birch instinct has not, however, been lost; about half a mile within the wood where a little island of birches lies surrounded by pine and larch, larvae can be beaten from either birch or larch. Neither of the first two differences is germinal, the other two stand upon a vastly different plane. Both are germinally fixed and both remain unaffected by any amount of rearing under a changed environmental complex.

In investigating the change in the modal state of the wing pattern one must guard against the assumption that any extension of the range of normal variation has occurred; what has happened, in reality, is a very definite contraction of that range of such intensity as to throw the modal condition into a position giving the two races facies so diverse as to suggest an apparent discontinuity. This, examination proves not to occur, for the alteration in mean proceeds directly from a preferential preservation of the darker, suffused, feebly marked forms and an accompanying elimination of the paler and the banded genetical strains existing in birchwood *O. autumnata* not only on Eston Moor but on Waldrige Fell¹, Co. Durham; in Cos. Tyrone and Fermanagh, Ireland; and Cos. Perth and Kincardine, Scotland.

To emphasise the fact that we do not here encounter any development of new varietal forms or range, just prior to writing the previous sentence I deliberately and without bias took all of my long series of pinewood insects and likewise those from the birchwood, and having examined them individually, assigned each to what I should have considered its point of origin had they been placed before me for judgment as being certainly from either pine or birchwood but exactly which unknown. So treated I should have allocated eleven birchwood individuals (10 males and 1 female) out of 71 (15.5 %) to the pinewood and six pine specimens (5 males and 1 female) out of 144 (= 4.16 %) to the birch. In connection with this test, in the case of these last examples a remarkable fact was apparent when I placed them alongside similar individuals derived from the birchwood. I found that they resembled the darker examples of their class, and further it was forced upon me that considered simply as Cleveland insects, with particular history unknown, they would have been deemed representatives of the alderwood in Lonsdale—a totally unexpected result of a casual test. Whence it will

¹ For the vegetation on Waldrige Fell, see Fig. 12, p. 239.

be seen that the pinewood race or races are derived from those in the birchwood by a process of selection working against the pale silvery insects which one looks upon as type *O. autumnata*.

Let us proceed to investigate the mechanism of this limitation. In the birchwood the silvery insects do most certainly blend best with the trunks upon which they rest; so, too, do the darker insects of the other wood with the dull-toned larch bark. But as a protection in the daytime this would be valueless should they be molested by tits or other insectivorous birds and like enemies. All of the insects, pale, medium or dark, at once betray themselves by flying off the trunks, even when the disturbing agent is yards away. Selection thus would not be preferential. Except for a solitary pair of wood pigeons, and once a thrush, the birchwood has to me always seemed void of bird life; matters, however, are different in the pines. There birds are much more prevalent, bull-finches and other birds abound, but during all my years of observation I have never seen a single *Oporobia* of any species attacked by birds by day! At night time the position changes; amongst the birches few if any nocturnal birds occur, for the trees are not well enough grown to harbour them. In the pines hosts of owls and night-jars aided by bats wreak terrific havoc on the insect life of the wood, as the number of lepidopterous wings and coleopterous elytra lying about show.

Recognising this fact, I have from time to time critically examined all of the detached *O. autumnata* forewings I have seen in the wood. In all I have noted 17; two of these, both dark, were entangled in the floccose web of the very abundant spider *Amaurobius fenestralis*, and 15 lay on the grass—in some cases in pairs. Those taken by the spider are negligible; chance ensnarement explains them. The other 15, in a population where the dark individuals outnumber the pale by more than 25 to 1, actually included a majority of pale wings! This cannot be a mere matter of chance; selection must be at work—and natural selection carried out by bats, owls and night-jars. These in the uncertain twilight of the wood at the flight-time of the moth would more readily secure the more conspicuous paler strains, thus progressively eliminating them. The observation that the paler examples yet existing were more heavily barred than the bulk of the parallel birch forms suggests that even the barred birch form itself is not an elementary strain, but was capable of movement in the mode when submitted to selection, either natural or artificial.

In my opinion, therefore, it is to natural selection, carried on by nocturnal birds in company with bats, we have to look to explain the

rapid change in average condition the insect has displayed in the pinewood.

But the change in the period of emergence is a matter much less susceptible of explanation. It cannot be mutational for three reasons: (1) it is universal in a wood of tremendous extent in which free communication between the preferred larch zones is barred by belts of pure pines, and, in one case, by a stretch of *Nardus stricta* moor; (2) had it been mutational no selective factor acting in favour of the new character can be at work, for it presents no apparent advantage aiding selection; (3) it affects both of the germinal strains occurring in the wood.

The second objection amongst these three also indicates that pure selection, whether by the agency of birds, bats, arachnids or ichneumons, acting on the race as a whole cannot explain the anomaly, even had I not put the matter to test by trying by selection to set up an early emerging strain from birchwood parents. Having secured most exceptionally a September birch female I bred from her earliest progeny in the succeeding year and continued the procedure for three generations, with the result that the last brood reared emerged on the average a fortnight later than birch broods from wild parents reared alongside them. The experiment was therefore discontinued. Even had it been a success artificially, and it is conceivable that it would have been had I continued for a hundred (!) years, in a state of nature, unlike what occurred in the evolution of *O. filigrammaria*, no advantage accrues from early emerging, so nothing presses the balance down in that direction. On the contrary a positive disadvantage manifests itself, for early laid ova of *O. autumnata* have been known to hatch the same year; larvae from these must perish when the trees shed their leaves.

We are thus forced to cast about for explanation in other directions. That we must look to causes operating within the pinewood, and therefore environmental, seems certain, for parts of the wood are as far apart as they are from the birchwood, and yet throughout the early emergence obtains.

Neglecting genuine pine and larch feeding lepidoptera, the most prominent insects in the wood are *Phigalia pedaria*, *Tephrosia bistor-tata*, *Gonodontis bidentata*, *Hybernia marginaria*, *Cidaria suffumata*, *Melanippe sociata*, *Larentia multistrigaria*, *Orthosia helvola* and *Xanthia circellaris*. Classifying these on the basis of food plants we find that the first four are not genuine larch feeders but have adopted it as food; three feed on *Galium saxatile*, and two are listed as feeding on trees not found in the wood and are presumably in the position of the first four,

but of this I have no proof. If we classify them according to their period of emergence seven appear between March and June (both inclusive) and always distinctly later than the same species at sea level or further south, whilst *O. helvola* and *X. circellaris* emerge in autumn, slightly in advance of their relatives elsewhere; their displacement, although in the same direction, is not so pronounced as that of *O. autumnata*. Nevertheless we have gained some sort of clue to the solution of our problem; the anomaly is connected with species hibernating as ova, aestivating as pupae and with autumnal emergence.

Increased temperature acting on the pupae may at once be ruled out; forcing in the genus acts as a retarding influence. But is the position the same if the ova hatch earlier than the normal? Is this early hatching accompanied by accelerated emergence? These points are readily put to the test. I took *autumnata* ova, forced them out in February and had them in pupae by March 28, exactly eleven weeks before their brethren in nature. And these pupae, kept under as natural conditions as possible, yielded their imagines simultaneously with their wild relatives! Still, precocious hatching ova may play their part as we shall discover later.

What then determines the development of *Oporobia* imagines if not increased temperatures? They emerge in response to exposure to a stimulus of a progressive fall in mean daily temperature, as I proved by submitting half of a brood of pupae to a gradual fall in low temperatures and the other half to a similar fall in higher ones. The former delivered their imagines first.

Here, apparently, we have got at the root of the matter, for owing to the dense masses of moss, pine needles and decaying *Lastrea* fronds retaining their moisture, and aided by the closer canopy overhead, the pinewood attains a lower maximum summer temperature and a higher winter one than the open, less moss-grown birchwood—and the difference is perceptible at once as one enters them. In consequence, the optimum period of exposure to low temperatures capable of stimulating pupal development is experienced sooner in the pinewood, and the insect emerges earlier. This dragging backward of the period of aestivation is bound to be aided by early hatching ova. Furthermore, such early ova would be more advantageously placed in the larchwood than amongst the birches, for the latter leafs later in the Clevelands as the following dates for two successive years will show: larch April 15, birch April 23; larch April 24, birch May 5. Thus any precocious individuals would die on the one and succeed on the other.

This early leafing in itself may be an active agent in causing ova to hatch early, for eggs laid on larch buds would be exposed to the elevated temperature due to the rapid metabolism of the expanding buds much sooner than those on birch and would therefore hatch earlier. In addition, the superior transpiration of *Larix* over *Betula* during winter and spring when both are denuded of leaves may, indirectly, serve to secure the same end.

This explanation would meet the facts of the case admirably, but the following fact must be emphasised; to grant its germinal fixation is to adopt the Lamarckian view. In my opinion this is the correct explanation, its fixation being brought about by its score or more years of incidence. Taken to a height of 1000 feet in Northumberland, at sea level in Yorkshire, at 300 feet in Durham, in Kent, London and Ireland, with wonderful uniformity the pinewood ova hatch the earlier, and their imagines develop the sooner—facts that render the evidence of my breeding experiments as to its germinal nature the more emphatic.

Whether it fits in with one's bias or not, with persistent unanimity every little point connected with the divergence in habit and instinct in these researches points to such features being genuine Lamarckian effects.

Before leaving the subject of the pinewood insect I must mention that in 1908 I beat several aberrational larvae from *Pinus sylvestris* which were ornamented with rusty patches approximating the larvae in appearance to the condition of such pine feeding larvae as *Elloptia prosapiaria*; these have never occurred again, thus any study as to their genetic behaviour is rendered impossible.

The case of the Lonsdale alderwood race need not detain us long. There the conditions are not fundamentally different from the mean of those of the Eston birch and pine woods. We have the more open nature of the one and its less accumulations of moss and needles, coupled with the presence of owls and night-jars to act as selective agents, in conjunction with the abundant patches of larch and pine tending to preserve by selection the darker individuals, but much less rigorously than in Wilton Wood. Inevitably a progression of the modal condition towards darkness has been displayed, resulting in the production of a race including strains intermediate in many respects to the other two. But, nevertheless, the period of emergence is not significantly moved; the very rapid rise in temperature in the wood during June, July and August owing to its patchy, open nature, aided by the very late leafing (often late May) of the alder, definitely ensures this.

Only one further fact remains to be brought forward, and we are finished with the local races; in spite of the presence of many larches never once have I beaten a larva from that tree in the alderwood, yet every single individual of the few birches, whether in the open spaces or amongst the alders, has yielded the larva, which conclusively proves that the larch diet in the pinewood was only assumed as a last resort.

(d) *The case of Oporabia dilutata and its subspecies O. christyi.*

To describe in detail the pre-glacial migrations of these two forms here would be unprofitable; firstly those of *O. dilutata* agree too closely with those of *Apocheima hispidaria*, which I have worked out previously¹, and secondly the recognition of *christyi* as a subspecies has been too recent to admit of its present distribution being worked out, and thence its movements in the past deduced. We shall therefore confine ourselves to a brief study of the Cleveland local races of *O. dilutata*.

Laying aside the case of *O. christyi* as being impossible of study for reasons similar to those just adduced, its local habitats not being fully ascertained, we are left with two recognisable races. One of these is the ordinary suffused melanic form with a considerable range of fluctuating variation and the other a brilliant silvery form attached to the little island of oaks within the coniferous and alderwood in Lonsdale. Although separated by a ridge 1000 feet high, the nearest colony of *O. dilutata* to the latter is barely three-quarters of a mile away in Easby oakwood, where the species exhibits melanism of a most pronounced type.

As regards the oak island two views are possible: first that it represents the remains of Sir Charles Turner's unfortunate experiments in 1782; and second that, if the presence of *Scilla nutans* and *Holcus mollis* can be used as corroborative evidence, it represents the surviving portions of primaeval oakwoods, long since demolished otherwise by human interference, which have been subsequently isolated by the planting of alder, larch and fir.

In any case it must have been cut off for over a hundred years from the oaks in Easby and Airyholme Woods, with which of old it may have been continuous around the spur of the hill between Lonsdale and Kildale. Segregated from influences of the nature of directly induced and of infiltrated melanism so disturbing in these other colonies

¹ Harrison, "The Geographical Distribution of the Moths of the Geometrid Subfamily Bistoninae," *Naturalist*, pp. 317—320 (1917).

of *O. dilutata*, the insect here clings to the pale ground of the original exponents of the species which the others have abandoned.

We thus see brought into action on a minor scale that geographical isolation, which in parallel ways throughout the world and in a specially striking way in the volcanic valleys of the Sandwich Islands, has been so prolific in the production of new species.

(e) *The question of Melanism.*

We now turn our attention to the vexed question of melanism in the lepidoptera—a most striking genetical phenomenon and one that has progressed and is progressing under our very eyes. Of this phase of variation the genus *Oporobia* in all its species, but more especially in *O. dilutata*, affords excellent examples.

In our investigation, although primarily concerned with *Oporobia*, we shall not restrict ourselves solely to that genus but shall treat the matter from a broad standpoint, adducing instances from any genus or species capable of illustrating any given point; to do otherwise would be an ill-judged procedure, so productive are other genera in melanic species.

As to the inciting cause many theories have been devised; cold humidity, soil, light deficiency, food and smoke each having had its advocate in the past either in the crude form of direct cause or as indirect units in a more complex system. But the most plausible theory yet advanced was that urged by Tutt¹ in his paper on "Melanism and Melanochroism," and based in the interaction of moisture, smoke and natural selection. Despite the plausibility of this combination the operation of some of the other possible agencies is not to be dismissed lightly. Cold, for instance, so offhandedly cast to one side by Tutt, is the direct agent in producing the melanism in two cases to be referred to shortly. We may not agree with Walsingham that the necessity of blackish tones because they are absorptive of heat has, helped by natural selection, ended in their acquirement and fixation; too many instances of pale Arctic and Alpine lepidoptera can be cited to disprove its universal occurrence. Nevertheless, the "cold" theory is the only one explanatory of such cases as *Dicranura vinula* var. *phantoma* and *Poecilopsis isabellae*. Both of these insects are derived from forms with whitish ground colour, the former from the type *D. vinula* and the latter

¹ Tutt, "Melanism and Melanochroism in British Lepidoptera," *Entomologists' Record*, Vols. I. and II. (1890, 1891).

from *Poecilopsis pomonaria*. Both, likewise, when scale development is taking place are exposed to low temperatures, the former to the frosts of a Murmansk and North Finland spring, and the latter to autumnal frosts at an elevation of 800—1000 metres in the Alps of the Tyrol.

Now laboratory experiments on lines imitating these climatic conditions have been undertaken by Standfuss, Pictet, Federley, Merrifield, Fischer and others. Pupae just at the critical point in scale development were exposed to various low temperatures and as a result insects, sometimes, but not always, melanic, were produced. Most of these authors contented themselves merely with securing the aberrative forms, but Federley¹ tried to correlate the melanism with scale condition. He discovered that the temperature employed had not only lessened the actual number of scales, but, in addition, it had diminished the volume of the individual scales, and this is precisely the condition seen in *D. vinula* var. *phantoma* and *Poecilopsis isabellae*. Let us consider the effects of this; during histolysis and histogenesis in the pupae notable changes are taking place; tissues are breaking down and reforming themselves with a necessary elaboration of waste products which must be eliminated. One of the media of this removal is the vestiture of scales and hairs on the insect's body. Consequently, when the secretion of the haemolymph, which is the mechanism of the passage, flows or is injected into the newly formed scales, instead of supplying a large number of scales with a normal capacity it supplies few scales with small capacity. Therefore, if the secretion responds as usual to enzyme action, each scale present will receive a greater quantity of the pigment so generated than usual, which means that the insect would appear melanic. Melanism is not a case of the genesis of new colours but is quantitative. For example, it is quite well known that straw-coloured—nay almost white—*Melitaea athalia*, *M. parthenia* and *Brenthis euphrosyne*, as well as those almost black, can be captured; yet these almost diametrically opposed colours are precisely the same, only in the latter case the great quantity of the brown pigment produces an outward semblance to black.

This then serves to explain not only the natural forms of *D. vinula* var. *phantoma* and *P. isabellae* but also some of the artificial results of temperature experiments on *Lymantria dispar* and other species.

From this line of argument it would seem likely that, unless registered in the germ plasm, the melanism of the two natural instances would yield to simple experiment in the laboratory as does that in the

¹ Federley, "Lepidopterologische Temperatur. Experimente mit besonderer Berücksichtigung der Flügelschuppen," *Festschrift f. Palmen*, Helsingfors (1905).

artificial aberrations of *L. dispar*. If it does not, then we are dealing with a further Lamarckian effect.

Similarly one cannot deny that under artificial conditions moisture induces parallel phenomena, and by the same mechanism of scale reduction, but unfortunately such variation, unlike what occurs naturally, is equally liable to be accompanied by albinistic forms. Furthermore, the artificial state is pathological and not hereditary, being coexistent with damaged scales; in natural melanism such as the moisture-smoke theory seeks to explain the scales are as perfect as in the ordinary form. For the same and other reasons we must not delay to examine the other alleged stimuli.

Tutt's theory of the united effect of smoke and moisture stands on much firmer ground. Briefly, as summarised¹ by its author, it is: Humidity *produces*² melanism; the environment of the particular species determines how far and in what direction melanism may or may not be developed; *natural selection* may counteract, modify or *intensify* the tendency to melanism.

As a sort of corollary to this, to explain melanism in districts like the west of Ireland and Scotland far removed from smoky manufacturing towns, he suggested that there the necessary blackening of the resting places of the insects, which enabled natural selection to work, was obtained by the direct darkening of rock surfaces from exposure to heavy rainfall.

Later, however, Tutt appeared to shift his position; in place of the statement that moisture definitely produces melanism we find him stating³ instead that "Moisture plays an important if indirect part"—a vastly different position from the first one of direct cause and effect.

To include all of the cases of melanism occurring in the British Islands we may summarise Tutt's later views as follows:

- (1) By its indirect action on rocks, etc. moisture blackens their surfaces in districts remote from urban areas.
- (2) In urban areas such influence is augmented by the deposition of soot and its fixation by moisture.
- (3) Natural selection acting progressively in favour of melanochroic forms resting in positions so darkened urges the species towards its culmination in total melanism.

¹ *Entomologists' Record*, Vol. 1, p. 96.

² The italics are mine.

³ *British Lepidoptera*, Vol. 1, p. 65, 1899.

And this, except for those who like Doncaster¹ have assumed a non-committal attitude, has come to be the opinion of every lepidopterist who has ventured to make a reasoned enquiry into the matter. For my part I can only say that I disagree completely, because I believe the theory to be erected on erroneous assumptions due to the acceptance of generalisation in place of particularisation as to our climatic conditions, added to a complete misconception of the actual condition of tree trunks and rock surfaces, both in the smoke zones and in other affected regions. In particular Tutt's crucial instance of smoke-blackened greenhouses is an extremely unfortunate choice. The blackening of white paints cannot be compared with the supposed darkening of tree trunks, for the former is strictly chemical and proceeds directly from the action between the sulphuretted hydrogen of coal smoke and the basic lead carbonate in the paint producing black lead sulphide according to the following equation :—



No one will venture to assert that light coloured tree barks contain lead salts !

Laying aside this particular statement as merely due to oversight or lack of exact chemical knowledge I adduce as the basis of my disagreement the appended facts which I shall discuss seriatim.

(1) Independent of such local melanism as that discovered by my friend Goodwin in Kent affecting *Boarmia consonaria* and *B. consortaria*, certain affected districts like that surrounding Middlesbrough (rainfall 24·9 inches), that near Newcastle (rainfall 28 inches) and the Moray Firth (rainfall 26 inches) are situated in the driest portions of our country. Alone this fact need not have excited wonder, but when one mentions that in each of the cases the type of melanism exhibited is peculiar to the neighbourhood the matter becomes of extreme importance.

For instance, near Newcastle and Middlesbrough *Boarmia repandata* and *Oporobia dilutata* are both melanic, yet no one could mistake say Middlesbrough *repandata* for examples from Birtley or Gateshead near Newcastle, so marked is the facies of the insect proper to each district. As one passes from the towns in both cases the melanism disappears and the insect becomes typical. In other words the melanism is strictly localised, and has arisen independently in its own special region irrespec-

¹ Doncaster, L., "A Collective Inquiry as to Progressive Melanism in Lepidoptera," *Entomologists' Record*, Vol. xviii. Nos. 7—10 (1906).

tive of what has happened elsewhere. Much the same holds true of Moray Firth *Triphaena comes*¹.

(2) Both in winter and summer I have made prolonged critical examinations concerning the colouration of the bark of the trees in Middlesbrough Park, in which vicinity more soot is produced and carried down to vegetation than in any other locality I have worked. I confidently assert that, except when jutting branches deliberately shut off the action of the rain, the trunks are not significantly different in tone from those in the rural districts of Durham and Yorkshire far removed from urban influence. The Scotch firs remained reddish grey, the white poplars greenish grey, the birches silvery, the ashes ashen and so on. The same is correct too of trees growing in the Team valley, North Durham, within the smoke zone not only of the local works of Birtley but of Newcastle and Gateshead, and in the Team valley melanism of a most aggressive type affecting hosts of species is rampant. To gain some kind of appreciation of the condition of tree trunks in the latter neighbourhood at night time, on March 9th, 1919, a starlight night with moon somewhat obscured, I walked down the valley from Birtley towards Gateshead and studied the trees. Their paleness was so much exaggerated that I found myself classifying pale sycamore trunks as silver birches until nearer approach revealed the specialised buds and twigs of the sycamore.

(3) In damp districts I deny that the effect of heavy rainfall is to blacken either rock faces or tree trunks. In my experience, gained in the west of Durham and Northumberland (rainfall 44 inches), in Ireland and in Scotland the moisture favours the development of algae, lichens and bryophytes which are far from being black in hue; in many cases the rocks become bright in colour owing to the presence of such highly coloured lichens as the very common bright orange *Physcia parietina*.

(4) Another fatal objection seems to lie in the fact that only insects resting in such blackened positions should be capable of assuming a melanic guise under the action of natural selection. This is not the case, and examples illustrative of the point are easy to obtain. For instance, *Larentia multistrigaria* (except very rarely) rests by day on the sheltered side of tufts of *Nardus stricta* amongst which its food-

¹ Tutt says that this has arisen by natural selection working on an insect resting on peat; my only objection is that it can't! Probably no worker save myself has ever had a dozen examples of the Moray Firth insect captured at rest by day; without exception these were taken from grass tufts and not from bare soil of any kind—peat or otherwise.

plant, *Galium scabratum*, creeps; in two localities, one in each of the areas I have studied, in Normanby Intake Plantation near Middlesbrough and on Birtley Fell near Newcastle, the melanic race *nubilata* is rapidly developing. The case is particularly impressive in the first named instance for, if by any chance the insect rested on bare ground—and I have never seen it do so although I have observed thousands of wild specimens—it would have to sit on a light coloured soil composed of weathered Moor Grit. And the same applies to the case (amongst others) of *Dasytoma salicella*, the males of which at Birtley exhibit progressive melanism in spite of their sitting in March on the light yellow grass culms of the previous year; this, too, holds with *Xylophasia monoglypha*, which almost uniformly hides itself at the base of *Nardus*, *Poa*, *Brachypodium* and similar plants, from which I have often dislodged it when in search of Arachnids.

(5) Furthermore, the same argument demands that melanic forms should not be generated when the insects concerned, whilst yet tree-frequenting, do not rest on dark surfaces; again the facts directly oppose the theory.

On Waldridge Fell, in the industrial district of North Durham, there is a colony of *Asphalia flavicornis* isolated far from any other colony of the same insect. This moth in its typical form has silvery grey wings and sits on birch trunks and twigs. Now the birches it haunts possess the usual silvery bark and purplish twigs, yet the insect there assumes an intensely melanic guise such as I personally have never seen elsewhere; nor have I seen it referred to in literature. On Eston Moor, where again the birches do not differ perceptibly from those seen by me in secluded Highland glens in Scotland, the insect likewise shows signs, not so emphatic as the fully developed melanism of Waldridge, but still quite unmistakable, of strong melanochroic tendencies.

To produce another instance is not difficult, although in this case the insect rests on alder leaves. Both in Lonsdale in Cleveland and in Chopwell Wood in Durham the moth *Melanthis bicolorata* is plentiful, and shows a great range of melanic and melanochroic aberrations, and in neither case can smoke blackening explain their dominance. The undersides of the alder leaves are no darker than those in Upper Allendale where the rainfall is 44 inches per annum, and the insects the whitest I know.

(6) Of the same nature but of different weight is the evidence yielded by woodland insects in the west of Scotland and Ireland. To

choose our own *Oporabia dilutata* as an example; it produces its silveriest forms in those very districts. Whatever melanism exists there does not affect woodland moths; it manifests itself in insects found on spray-drenched and open spaces, whether rocky or sandy in nature.

(7) Lastly, to demonstrate that the effect of natural selection is quite negligible as a factor in progressive melanism, I carefully studied the case of *Polia chi*, which in the Team Valley produces about 50 % each of typical and of the melanic forms grouped under the name *olivacea*, and near Middlesbrough about 10 % of dark and 90 % pale forms. For several years and on every day during their season—rain or fine—either my wife or my brother carefully noted the positions of the insects resting on three walls: (1) old and dark in parts, proceeding from Birtley to Newcastle; (2) old light yellow sandstone, proceeding to Burnmoor; (3) mixed new greyer sandstone and old reddish ones leading to Chester-le-Street. On these three walls I have seen up to three hundred examples daily, so that the present test is not confined to few insects; in the evening full particulars would be given to me, and sometimes alone and sometimes accompanied by my brother I would go over the ground to investigate the fate of the insects observed earlier in the day. Never was there any diminution of numbers in which more *olivacea* vanished than type *chi*; as a matter of fact we used to consider it a marvellous thing if even a single one had disappeared.

Now to proceed. The melanism both of the continuous type shown by *Larentia multistrigaria*, *O. dilutata* and *O. autumnata* as well as the discontinuous form encountered in *Amphidasya betularia* var. *double-dayaria* and *Boarmia consonaria* is germinally fixed, so that any possibility of its being ontogenetic is excluded; besides, except in the very unlikely case of its being possible to affect mature ova and spermatozoa by the same agency and in the same direction as the somata are affected, the impossibility of its being other than germinal is capable of absolute proof in many insects like *Spilosoma lubricipeda*, *Orgyia antiqua* and *Lycia hirtaria*. In all of these cases gametogenesis is completed long before scale and pigment formation, so that unless the germ plasm were in itself capable of giving rise to melanic forms the phenomenon would not be observed in succeeding generations. And if it did occur merely as a somatic aberration, then, not being germinal, selection either artificial or natural would not be capable of fixing melanism of the degree already attained, much less of urging it on to its climax in such totally melanic forms as *Oporabia dilutata* var. *melana* or *Gonodontis bidentata* var.

nigra. Owing to the evidence of *S. lubricipedu* and the other insects named above, we are thus forced to accept the position that the exact cause inducing the melanism acts or becomes potent for future action during the larval life of the insect, and with certain insects very early in that life. This incidentally explains why the so-called temperature aberrations cannot reproduce their kind.

The phenomenon being one initiated in larval life, it seems physically impossible for environmental moisture to act through the soma so as to affect at one and the same time the cells of the soma and those germinal in character. We are therefore driven to search for other causes.

I am quite aware that mechanical and physical disturbances, such as centrifugal force and X-rays, have been shown capable of producing somatic melanism, but each of these agencies acts at the so-called critical point of early pupal life, and by crippling special cells at the one time, and the whole organism at others. For these reasons it would be profitless to discuss them at length here.

Such being the case what have I to offer in their place? Let us consider what other drastic changes have been noted in the affected areas under consideration simultaneously with the appearance of melanism. The most striking is the decadence of cryptogams, more particularly of the mosses, liverworts and lichens, and to a less degree the ferns. This most certainly originates from smoke contamination. No one who has studied the cryptogamic botany of North Durham and North Yorks would fail to contrast the rich moss and lichen floras recorded for Long Acre Wood (1)¹ in the Team Valley by Winch ninety years ago with their paucity now. Of the lichens only the ubiquitous and apparently iron-constitutioned *Cladonia pyxidata* persists, and of the mosses only the accommodating *Fissidentes*, *Mnium hornum*, *Hypna* and a few others remain. The same holds good but to a less extent in Cleveland; there one would look in vain in the northern portions for the hosts of lichens listed by Mudd half a century ago.

But in the two cases differences are easily recognised; in the Durham locality, whilst matters with the mosses slightly ameliorate as we leave the soot zone, the apparent extermination of the lichens has been more complete. Besides *Cladonia pyxidata* I am only acquainted with two patches of well-grown lichens in the Team Valley, and both of these are *Parmelia saxatilis*. In the Clevelands as one leaves Middlesbrough the lichens reappear, *puri passu*, so that in the remoter dales the whole flora comprises the same species and in the same abundance as fifty years ago.

¹ The figures refer to those on the map shown on Fig. 11.

Nevertheless it must not be forgotten that a score of miles out the lichens are materially influenced. How has this been brought about? The difference in the two cases, coupled with the progressive reappearance as the towns are left behind, shows us that the deleterious agent at work is the smoke, and that the apparent exaggeration of its effects

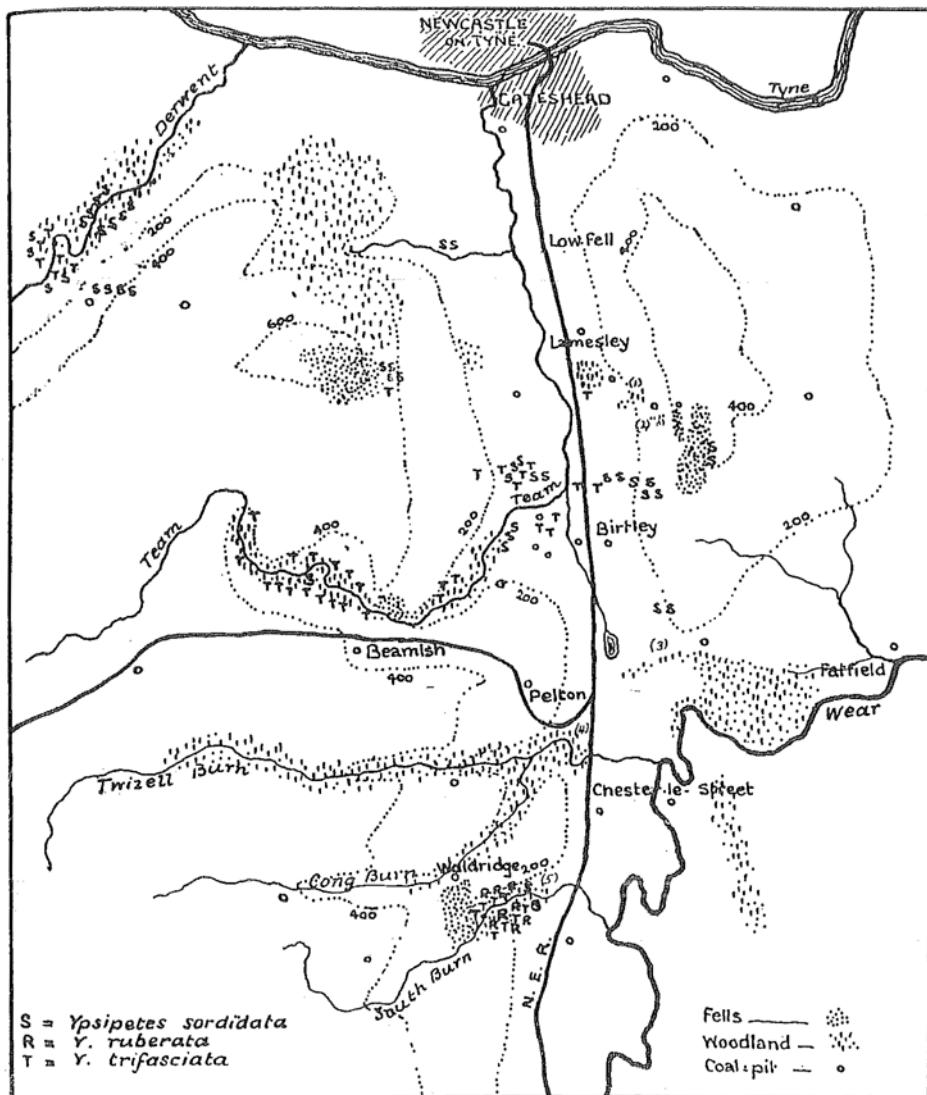


Fig. 11. General map of the Team Valley.

in Durham when compared with the conditions in Cleveland is due to the prolonged industrialisation of the more northern district and the comparatively recent development of Teeside Blast Furnaces and Chemical Works.

We must guard against assuming that the lichens are entirely gone, this is far from true, as careful search will indicate that many exist on walls and trees in the immature granulose condition. Their passage to the perfect condition has been prevented by the surrounding smoke and more particularly by the hydrocarbons of the ethylene series—not necessarily gaseous—it contains. Should anyone doubt the efficacy of this effect a simple test will demonstrate its truth. Plant a few sweet peas in a flower pot in the dark; let them grow until the etiolated epicotyl has attained some length. Then expose to town smoke. The epicotyl is at once flattened and very serious disturbances in growth ensue.

I have not elaborated this point simply to show that smoke affects vegetation but to show that such interference, whilst progressively diminishing as one leaves urban conditions, still possesses enormous powers at great distances from the source of the contamination. Now if the smoke, in addition to destroying vegetation, likewise conduces to melanism, then when continuous melanism develops it should likewise diminish as one leaves the town. Of the truth of this I have ample evidence drawn from both districts and seen in *Oporobia dilutata*, one of the very species we are studying. In Long Acre Dene Wood (1), probably the first due south of Gateshead and Newcastle to yield the insect in quantity, a good proportion are perfectly black, whilst those in Leyburn Hold Dene (2) are greenish black suffused forms, displaying the usual transverse bands; passing south of this to Lambton Woods (3) we find paler although still melanochroic forms; then finally we reach the Hermitage Wood (4) where, in addition to the Lambton forms, we capture ordinary pale typical insects.

In the same valley *Ypsipetes trifasciata*¹ shows the same progression in its melanism as we approach Gateshead from Waldrige Fell (5). In the latter locality the pale central band of the type still retains relics of its former silveriness, whilst just beyond Lamesley in the habitat nearest Gateshead all of the insects appertain to the completely black form known as *nigerrima*. The case of *Y. trifasciata* is worthy of special

¹ The "T" on the general maps of the Team Valley and of the Northern Cleveland shows the distribution of *Ypsipetes trifasciata*; the "R" and "S" give similar facts for *Y. ruberata* and *Y. sordidata*, respectively.

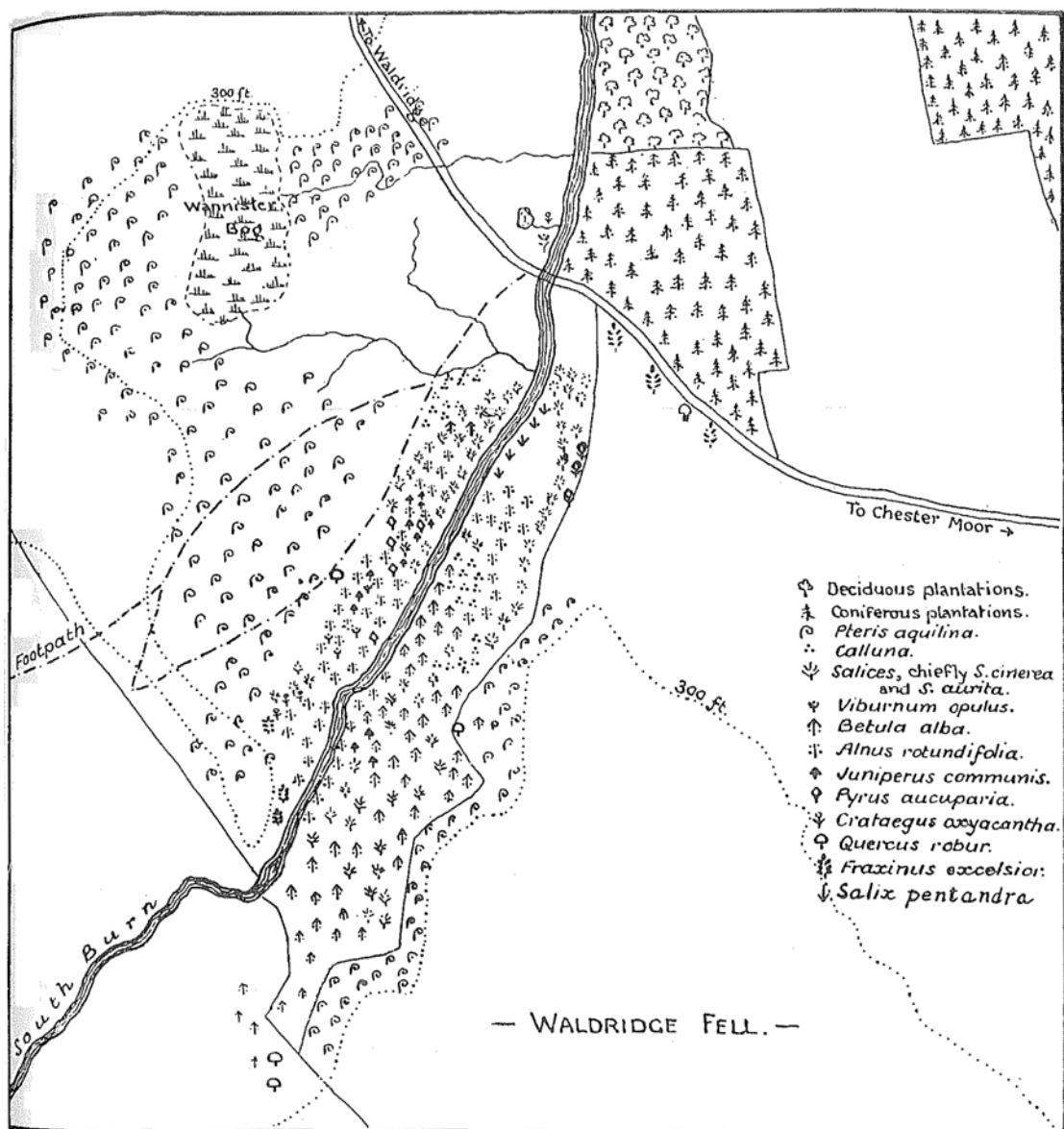


Fig. 12. Map of Waldridge Fell showing vegetation and altitudes.

attention because twenty-six years ago the insect was quite typical locally.

Near Middlesbrough *O. dilutata* is melanic right up to the base of the hills seven miles away; over the first ridge and not a mile away from the limit of melanism the moth is as pale as if taken in Ireland. In this district *Ypsipetes trifasciata* is more local; still there are two stations for it, one on the south face of Eston Moor and the other in Lonsdale, farther south. The insects from Eston are melanochroic whilst the others are quite ordinary.

But other species show the gradual decrease in melanism much more vividly as we recede from town conditions in Northern Cleveland. *Boarmia repandata* near the town is quite black; just three miles out it is grey, whilst specimens from Stokesley (see Fig. 13) are perfectly typical. So, too, near Middlesbrough and North Ormesby *Hybernia marginaria* exhibits total melanism; beyond a belt of three miles such a form is unknown.

Of the two areas the Middlesbrough one is the more striking; as we leave the borough the annual rainfall increases rapidly from 24·9 inches to 36 inches—reaching its maximum where the melanism is least. Instead of a direct relationship between rainfall and melanism an inverse one is manifested.

As a deduction from the facts laid down above I have satisfied myself on two points: (1) as far as urban areas are concerned moisture plays, if any, a very minor part; (2) the only agents correlated with the melanism in its incidence are the smoke and impurities thrown into the atmosphere through the springing up of great manufacturing towns. How the latter factor may conceivably act detailed consideration will determine; melanism in other than urban districts we shall reserve for treatment later.

Let us pause here to examine the chemical status of the black pigments found in the animal world generally, in order to equip ourselves for our proposed investigation as to their origin in the lepidoptera. These pigments known as melanins are not necessarily black; indeed, some are brown. They occur in skin, hair, wool, feathers, scales, muscles and various other parts of the bodies of animals of diverse affinities. In composition they are substances closely allied to proteins. In fact, as far as it is humanly possible to decide they are chemically the same as the humins, a series of bodies derived artificially from many albuminous substances by the action of enzymes or ferments.

Of the albumin-derived proteins tyrosin (parahydroxyphenylamino-

propionic acid) seems to be that utilised by enzymes to generate the pigment so universal in its occurrence in the animal kingdom. This, experimentally, not only by simple hydrolysis with acids, but also by the action of ferments like tyrosinase, develops coloured compounds of the humin type, and this is the kind of reaction we are to look for to account for pigment occurrence in lepidopterous scales and hairs. That means

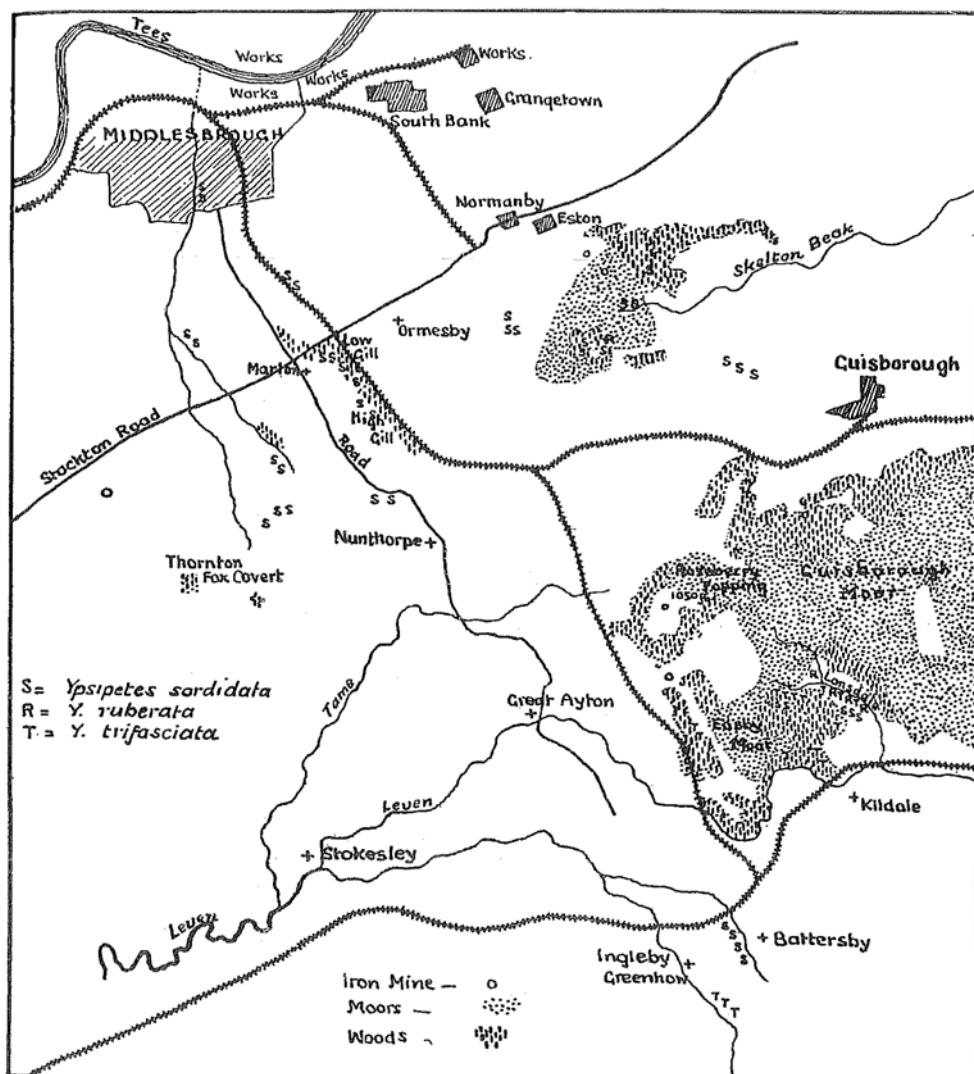


Fig. 13. General map of Middlesbrough District.

we have to demonstrate the existence in insects of such enzymes as tyrosinase and of protein-like bodies capable of yielding humins or melanins when hydrolysed, oxidised or submitted to enzyme action.

Proof of the latter point is easy; take a pupa of *Oporabia dilutata* and puncture the wing cases carefully. The light coloured haemolymph (yellowish in the males and greenish in the females) exudes; this on simple exposure to air shows the phenomenon of melanosis, that is to say it blackens. The haemolymph of insects is therefore endowed with compounds able under enzyme oxidation to yield black pigments.

It is equally easy to show that tyrosinase occurs in the haemolymph, but in this case, to secure adequate quantities for experiment, it is best to use large Sphingid or Saturniad pupae. Take say pupae of *Platysamia cecropia*. Pierce their wing cases; as before the pale haemolymph flows but naturally in much greater quantities. To this add ammonium sulphate and a precipitate is obtained. Dissolve this precipitate in a '05 % solution of sodium hydroxide; now add this tyrosinase solution to one of tyrosin. Soon a violet colouration appears which gradually darkens and finally a black flocculent precipitate is thrown down, to be recognised as one of the humins.

This insect-derived tyrosinase reacts similarly to yield pigmentary compounds with many other benzene derivatives containing the hydroxyl radicle. In the haemolymph the tyrosin does not exist as such but in its place is a chromogen closely related chemically and conforming to the latter condition; it, likewise, when acted on by the enzyme tyrosinase yields coloured compounds.

Now to return to our melanism; it is perfectly clear that when we consider the great difference between a typical *Boarmia consonaria* and its melanic form var. *nigra* we are dealing with a profound derangement of the ordinary metabolic scheme; nor can it be denied that this disturbance is inherited, and not ontogenetic. These melanic forms, whether reared in the centre of affected areas or in some remote corner where such are never heard of, always breed true. Whence it follows that the original insect showing the new character, in this species, showed it by a sudden change in germinal constitution—or had its somatoplasm and germ plasm equally affected by some environmental impulse. The former possibility in its simplest form may be dismissed when due allowance is made for the fact that there is no reason whatever why melanism so produced should be localised; it should, on the contrary, be universal. But if the altered metabolism gives its possessor great advantages in dealing with unusual food the position would be greatly altered. And

the food is unusual in districts wrapped in a constant mantle of chemical smoke. Despite the truth of my observations that tree trunks are not significantly darkened every leaf (I speak from my knowledge of the Middlesbrough district) bears a film of smoke-derived impurities composed of organic compounds, both aliphatic and aromatic, and various salts of potassium, manganese, iron, sodium and other metals. If this altered metabolism is as I postulated fitted to deal with quantities of these ingested with the food, then without doubt it will endow its possessor with a considerable start in the race of life. That foliage thus contaminated is injurious to lepidopterous larvae may be readily demonstrated. If larvae of such a species as *Asphalia flavigornis*, originating in some remote Scotch wood, are reared on birch grown in Middlesbrough they die one by one until all are gone. But it is quite probable that such a radically changed metabolism as that laid down in our theory above would render insects endowed with it more capable of dealing with smoke-borne impurities; so that those not possessing it would commence life under a severe handicap when submitted to urban conditions, and thus their ultimate supplanting by their affected relatives secured. Under this hypothesis the smoke itself would not directly induce the melanism but would in the end secure its being supreme.

There remains still another possibility; just as in Firth's¹ and MacDougal's² experiments the injection of various salts into the ovaries of such plants as *Epilobium roseum* and *Oenothera odorata* is stated to have produced noteworthy aberrational forms, so the smoke-derived chemical compounds, organic and inorganic alike, may have affected the germ cells of the insect. This action, whilst presumably most potent in early larval life when relations between somatic and germ cells are most intimate, could work at any larval stage; by its action the chromosomes, whether by detachment, replacement or removal of the side chains of their essential nitrogenous compounds, could be so altered in powers as to cause the setting up of a type of metabolism quite foreign to the insect; this could be the type just discussed. Such a course need not be that pursued by all of the insects under town influence any more than all of Firth's and MacDougal's plants bore seeds yielding mutations; such insects as did follow it, whether selection worked on colour, on constitutional hardiness, or on better equipment for dealing with foreign

¹ Firth, "An elementary Inquiry as to the Origin of Species," *Journal Army Med Corps*, Vol. xvi. pp. 497—504 (1912).

² MacDougal, "Alterations in Heredity induced by Ovarial Treatments," *Bot. Gazette*, Vol. li. pp. 241—257 (1911).

elements in the normal food, would in time be destined to replace the type since we have demanded that the germ cells are altered in potentiality and since we know that the germ plasm is continuous.

Now have we any proof of the possible existence of such a scheme of changed metabolism and of its not being disadvantageous to the organism involved? Not in the Insecta save by inference; we have its occurrence definitely¹ in the case of human beings.

In man occurs such a disturbance known as alcaptonuria. In this condition the urine becomes very abnormal; such bodies as tyrosin and its allies instead of having their benzene nuclei completely disintegrated by the slow combustion of vital processes, break down and yield intermediate products like uroleucic and homogentisic acids which when laid aside and submitted to hydrolysis or oxidation yield dark coloured pigments. These bodies, respectively dihydroxyphenyl lactic acid and dihydroxyphenyl acetic acid, are benzene derivatives possessing the necessary hydroxyl groups qualifying them for being acted upon by tyrosinase.

A person with metabolism of this curious type cannot be regarded as diseased; he lives and enjoys life quite unhandicapped. Any natural selection would fail to act against him; nay, should ever food be presented to him better dealt with by his than by the normal method then he would be the one with a start in life's race. A very important feature about this affection is that the available evidence² directly states that the condition is inherited.

There is thus a very suggestive parallelism between this disturbance and that formulated as the possible cause of melanism.

Grant then that, in the haemolymph and in the excretory products it contains after the reconstruction of the pupae succeeding histolysis, we have greater supplies than the normal of compounds for the insect tyrosinase to work on, then another fact favours the deposition of a melanin in quantity. Experiment has shown that ferments such as maltase have their action greatly accelerated by the presence of small quantities of such salts as potassium and sodium chlorides, manganese sulphate and so on. Have we not such present? They, especially the alkaline salts, must be taken in quantity on town grown foliage and cannot be excreted normally. They can thus during pigment formation affect the quantity produced and thus darken the insect.

We shall now return to such cases as the melanism of *Boarmia*

¹ And locally in the melanosarcoma of horses, particularly of grey ones.

² Kirk, *Brit. Med. Journ.* 2, 1017 (1886); *Journ. Anat. and Phys.* 23, 69 (1889).

consonaria and *B. consortaria* in Kent. It is quite possible that there London smoke deposits its last impurities, but not likely in spite of the fact that the Lancashire smoke affects Lake District lichens seventy miles away. So small is the area affected that I think we are dealing with the effect of some trivial, local cause¹ of an obscure nature leading to the necessary metabolic upset. Here perhaps it is best to remark that the very great similarity of the melanistic forms of the closely related species *Tephrosia bistortata*, *T. crepuscularia*, *Boarmia consonaria*, *B. consortaria*, *B. repandata* and *B. gemmaria* suggests that we are dealing with an atavistic character, and that the chemical change in the nucleus necessary for the reappearance of the old common form may not be a very profound one—a view that receives some little confirmation from the fact that the *cognataria* form of *Amphidasys betularia* found in all three of the known relict stations of Miocene forms, China, Eastern North America and Turkestan, shows much more pigment than type *betularia* and thus shows some approach to the melanistic *double dayaria*.

Lastly we have to deal with the melanism and melanochroism of such species as *Campptogramma bilineata*, *Dianthoecia conspersa*, *Triphaena comes*², *Melanippe fluctuata*, *Emmelesia albulata* and others in habitats along the west and north-west coasts and islands of Ireland and Scotland in particular, and to a less marked extent along coasts elsewhere. All the species feed on low-growing plants, and all show their melanism chiefly in coastal habitats; none are woodland species. Not even our very impressionable *O. dilutata* is included; had the melanism been of the usual type it was bound to join in, yet in these very areas wherever woodlands approach the sea the perverse insect, as if to defy the moisture theory, will persist in giving us the silveriest of silvery forms.

What have they in common? All live on spray-washed food and all therefore receive great quantities of the salts found in sea water of the type of sodium and magnesium chlorides, bromides, iodides, sulphates and similar salts so that conditions approaching those in urban areas are set up, possibly with the same effects. This, too, may be the cause of the melanochroism exhibited by other coast Noctuidae, its possible accentuation in the more insular Scotch and Irish stations being brought about by their more exposed and isolated positions giving greater scope for its advent and its subsequent predominance by inbreeding.

¹ It cannot be chance, for two species are affected.

² I know that *T. comes* is melanistic at certain inland stations, but these forms only exist where infiltration from the coast is possible; the metropolis, so to speak, of the melanism of that species lies on the Scotch coast between Burghead and the Orkney Islands.

III. BREEDING EXPERIMENTS.

(a) *Inheritance of Subspecific Characters and of those characterising the Local Races.*

In any enquiry directed towards elucidating the evolution of subspecies and local races nothing is more important than to determine whether such differences as they present are ontogenetic in character, i.e. developed anew in each generation in response to their own peculiar environmental influences or not.

The first experiment I initiated along these lines was conducted with the subspecies *Oporubia filigrammaria*. I obtained ova of this form from wild parents captured at an elevation of 1500 feet on one of the Lancashire moors not far from Burnley. These ova were wintered almost at sea level at Middlesbrough, North Yorkshire. As they hatched the resulting larvae were placed on birch, alder and other foods proper to *O. autumnata*. Without exception they accepted these, to them, unusual foods and fed up speedily and healthily, the pupae emerging toward the end of August and the beginning of September just when their relatives would be coming out amongst their native heather. Not a single sign of departure from their own racial characters in the direction of those of *O. autumnata* was manifested either in larval colouration, imaginal size, wing markings or in other features. The race was inbred and kept going under similar conditions for five successive seasons and the insects bred each year carefully scrutinised for any possible development of *autumnata* characters; never at any time was any hint of deviation from their own normal state given. The experiment was repeated, only in this case the larvae from wild moorland females were reared at an elevation of three hundred feet in North Durham, in a district not only producing *autumnata* but also a race of *filigrammaria* of characteristic type; again no *autumnata* characters appeared nor were there signs of passage to the local *filigrammaria* form. Obviously from these experiments only one conclusion can be drawn and that is that the subspecific and racial characters in *O. filigrammaria* are germinally fixed.

Here it is well to remark that never at any point in the half dozen years of inbreeding that this experiment involved were any traces of diminution in vigour displayed; inbreeding with this species¹, unlike

¹ And the same held true of birchwood *O. autumnata* when inbred for a similar period.

what is experienced in *Zenosoma orbicularia*, seems most emphatically not to injure the race.

The reciprocal experiment of attempting to feed larvae obtained from birch-fed *autumnata* females on heather was carried out in the North Durham area with negative results as far as it went. The larvae attained the fifth instar and in that, as well as in the preceding four, they could not be distinguished from *autumnata* treated in the usual fashion. Owing probably to the difficulty of keeping *Calluna* fresh, and the consequent necessity of supplying them occasionally with stale food, they dwindled and died; not a single pupa was obtained.

Similar transplantation experiments were made in the case of the feebly marked pinewood race of *O. autumnata*. Ova from a mixed selection of wild females from Wilton Wood were brought down to Middlesbrough, where instead of 800 feet, the elevation above sea level is only 30 feet. When they hatched the young caterpillars were offered birch instead of their own larch or pine; without any hesitation they took it and were successfully reared. As a result imagines were obtained which in every characteristic marking of the race were indistinguishable from those captured in the pinewood; and this resemblance extended to the period of emergence of the imago which, against all probability, happened towards the end of September, just as did that of its wild relatives. But one difference was recognised; the imagines averaged a millimetre and a half larger than the wild specimens and now possess a mean size equal to that of the birch-frequenting race. The experiment was continued for three more years but no further change was perceptible. Except in size—a character in which they always agreed with the birchwood broods reared alongside of them—the evidence they have to offer is precisely that of *O. filigrumaria*, i.e. that the racial characters are germinally fixed; the size is ontogenetic in this instance.

Portions of four broods taken wild in the same pinewood were removed to the Team Valley, North Durham, where they were submitted to a hawthorn diet and were kept going for two years; the results were of the same order as those obtained in the last experiment. An increase of size but a retention of other characters, including those of habit, was exhibited. Clearly the increase in size depends on a removal from the less nutritious pine and larch to the more favourable birch or hawthorn.

In a further experiment ova from the Lonsdale alderwood (elevation 850 feet) were allowed to winter naturally in Middlesbrough and then reared (for three generations) under the same conditions as those used in the case of the pinewood race; again the racial characters were

absolutely immovable. In this instance I mixed the last domesticated brood with a random lot from the birchwood, and having shown him a wild and similarly chance lot of alderwood insects I submitted the mixture to a competent lepidopterist for separation. This he did most efficiently, not a single error being made despite the great natural convergence in facies of some individuals in the two races.

It is worthy of note now, that all friends to whom I have sent ova from various *autumnata* stations known to me always give it as their weighed opinion that any of the darker races prove the easier to rear; the birch feeding insect proving especially tricky in its behaviour. This coincides exactly with my own experience with the same insects and with my difficulties with larvae from pale Irish and Scotch birch females. In fact, although it is morally certain that I have bred more of these insects than any other worker, out of batches of ova from at least two dozen Irish females I have never reared a single imago.

To turn now to experiments with *O. dilutata*; ova from the very white strain attached to the Lonsdale oak island, from Easby Wood melanic females, from pale Irish females and from strigated females taken to the west of Middlesbrough were brought into Middlesbrough. The ova hatched in due course, and the larvae were reared there on food obtained just outside the borough boundary. This was continued for three seasons. In each and every case the insects bred true to their own type and showed the same range of fluctuating variation as it did.

Finally I obtained ova of *O. christyi*, the smaller subspecies of *O. dilutata*, from Ireland and reared them at Middlesbrough with *dilutata* and our own form of *christyi*, which is grey and less silvery in tone. Two years' rearing under the same conditions induced not the faintest trace of convergence; nor was one expected, for Nature conducts parallel experiments in the two localities known to me which produce both *dilutata* and *christyi*, one near Seamer in Cleveland and the other in Durham; in the former *christyi* is light grey and *dilutata* melanic, in the latter *christyi* is of the very pale type and *dilutata* of the medium grey tone, and they have always continued so as long as I have known them.

These observations demonstrate conclusively (1) that the differences between *christyi* and *dilutata* are germinal; (2) that their physiological reactions toward the agent inducing melanism, whatever it may be, are quite different.

(b) *Inheritance within the Limits of the Local Races.*

When I first conceived the notion that the *autumnata* races attached to the Wilton pinewood and the Lonsdale alderwood had been derived from that found in open birchwoods or alders in Cleveland and elsewhere, it became of paramount importance to determine whether the main birch types linked up by the apparently continuous fluctuating variation were inherited or not; whether any given female either gave or tended to give the whole range of variation; or, to state the problem once more, whether there were genetically diverse strains existing within the birchwood population. To answer my own question I captured three wild females, one a beautiful, clearly lined specimen with a pure white central area, a second of the strikingly barred *sandbergi* form and the third a dull expressionless grey with obliterated markings, and reared their progeny. In all cases the offspring leaned most unmistakably to their mother although some little approach toward other forms existed—a transition slightly more noticeable in the brood from the barred female. From pairs selected to be as nearly like their parents as possible further broods were obtained with a repetition of the previous year's results save that fluctuating variation seemed more steadied. After a further generation producing evidence of the same value the experiments were discontinued save in one instance. Reciprocal crosses between the insect with the white ground and melanochroic forms of the species *O. dilutata* were made; in both crosses the hereditary nature of the parental condition was perfectly obvious, the peculiar *autumnata* character proving almost dominant. Further evidence to the same effect was obtained in the experiment in sex-linked inheritance described below, where the male employed was of the weaker *sandbergi* form; that its characteristics are germinally impressed the condition of the F_2 generation emphatically proves.

Thus we have abundant proof that the population of the birchwood is mixed, being composed of strains genetically diverse and therefore capable of isolation when submitted either to artificial or to natural selection.

(c) *The Inheritance of Melanism.*

My experiments in this direction were very uninspiring as regards their indications. I paired a melanic Middlesbrough male with a white Irish female and reared the result of the cross to the F_3 generation.

My experience repeated that of Prout and Bacot¹ in their *Acidalia virgularia* work; to the very end a blend was obtained. So emphatic was this persistency in blending and the absence of any hint of segregation that the only explanation possible is that based on permanent gametic blending. This therefore agrees perfectly with what one sees whenever the inheritance of melanism of a perfectly continuous type is investigated, and contrasts violently with the uniform evidence of segregation seen in cases of discontinuous melanism like that of *Boarmia consonaria*.

(d) *Sex-linked Inheritance.*

Although I quite recognise the assumptions underlying the use of the word "sex-linked" as applied to the particular type of inheritance I am about to consider, in my opinion the use of Morgan's² word is preferable to that of "sex-limited" which covers, as Darwin intended, phenomena quite different from these.

That sex-linked inheritance of certain elements in wing-banding was exhibited by the moth genus *Oporabia* was first indicated in 1914 when I reared reciprocal crosses between *Oporabia dilutata* and *O. autumnata*; it was then perceived that whereas the males partook of the wing-markings of both species, the females, on the contrary, resembled the female of the species supplying the male participating in the original cross. In the case of the hybrid between *dilutata* female and *autumnata* male this resemblance was perfect but unfortunately only one F_1 female was bred and the matter was not proceeded with. Still worse was the predicament in the reverse cross where the influence of the male was not so perfect; here the F_1 females were devoid of ovaries. Furthermore, the back crosses involving both F_1 males proved almost completely unproductive. Very powerful barriers were therefore set to investigations employing these interspecific crosses. Knowing that such anomalies in sex condition did not exist in crosses between *O. autumnata* and *O. filigrammaria* exhaustive experiments were undertaken with these two forms, but they proved utterly fruitless.

Light, however, was thrown upon the subject in a very unlooked for fashion by breeding results involving the Carpet-banded mutation of *O. autumnata* which I shall call *latifasciata*. In this mutation the whole of the central area between and including the two median bands

¹ Prout and Bacot, "On the Crossbreeding of Two Races of the Moth *Acidalia virgularia*," *Proc. Roy. Soc. London*, Vol. LXXXI. Series B (1909).

² Morgan, "Sex-limited and Sex-linked Inheritance," *Amer. Nat.* Vol. XLVIII. (1914).

becomes blackish in extreme cases and suffused in those less so. Naturally the acquisition of a wild female¹ of this form, the first I had ever taken in the birchwood, caused me to speculate as to its genetic potentialities, so I paired it with a medium example of the barred form reared indoors. Anticipating with some confidence its dominant nature, I looked forward to an F_1 brood entirely of *latifasciata* form and including the first males of the type ever known. My expectations were utterly falsified for in 1917 in a brood comprising 47 individuals I obtained 22 perfectly typical females without the faintest sign of a complete bar and 25 males, all of which displayed the bar in the diluted form, showing incomplete dominancy. This, *prima facie*, was evidence of that type of sex-linked inheritance known as "criss-cross." Consequently, in addition to pairing the F_1 insects *inter se*, all of the crosses including this F_1 brood, the insect in its typical guise, and the allied species *O. dilutata* were made. All of the intraspecific crosses yielded fertile ova as also did two of the matings of the F_1 ♂ and *O. dilutata* ♀; on the contrary, after a disheartening waste of material, none of the ova laid in the cages containing F_1 ♀♀ and *dilutata* ♂♂ changed colour, and were therefore infertile.

My 1918 cultures therefore were the results of the following pairings :

- (1) F_1 ♀ × F_1 ♂.
- (2) F_1 ♀ × *O. autumnata* ♂.
- (3) *O. autumnata* ♀ × F_1 ♂.
- (4) *O. dilutata* ♀ × F_1 ♂.

The first two of these were exceptionally successful and yielded important results harmonising exactly with what was anticipated should the inheritance be of the sex-linked type ; nor was there any discrepancy between the results of the last two and one's expectations, only the number of imagines bred in these two cases was very meagre—just

TABLE IV.

Brood		Number of <i>latifasciata</i> females	Number of type females	Number of <i>latifasciata</i> males	Number of type males
F_1 generation ex <i>latifasciata</i> ♀ × type ♂	...	—	22	25	—
F_2 generation. (Same cross)	18	21	19	18
F_1 ♀ × type ♂	...	—	43	—	36
Type ♀ × F_1 ♂	...	2	1	1	3
<i>Dilutata</i> ♀ × F_1 ♂	...	—	—	2	—

¹ I have taken three *latifasciata* forms in Yorkshire and have heard of one taken in Fermanagh, Ireland, and all were females ; the similarity of this with the case of *Abraxas grossulariata* studied so exhaustively by Doncaster seems noteworthy.

what was expected from the last but certainly not in the third case. The exact composition of the broods, with that of the F_1 generation to complete the series, is appended in tabular form.

To anyone acquainted with the work of Morgan¹, Doncaster² and others and the ratios obtained in their sex-linkage work, this table adequately demonstrates that here we are dealing with a case where the male is sexually a homozygote and the female a heterozygote, and that the gene for *latifasciata*-ness is coupled with, or follows the distribution of, the male sex gene, or is located in the X chromosome, to give all of the various expressions used by different workers according to the views they accept.

In the conventional fashion, by the use of symbols, we can render this clearer by allowing L to stand for the *latifasciata* factor and A for its absence, or rather for the ordinary *autumnata*-ness. Then, since the original wild female was not pure for the character concerned, for its ova gave rise to both *autumnata* and *latifasciata*, we shall have to indicate its genotypic composition as $AL\delta\varphi$ producing the two kinds of gamete $A\varphi$ and $L\delta$ in equal numbers, and that of *autumnata* male as $AA\delta\delta$ yielding gametes all $A\delta$. This would ensure that on the fusion of the gametes producing the F_1 generation equal numbers of two zygotic types $AL\delta\delta$ and $AA\delta\varphi$ would appear. The latter appeared as typical females and the former as the heterozygous *latifasciata* males. At gametogenesis the $F_1\delta\delta$ produce two kinds of gamete, $A\delta$ and $L\delta$, and the females likewise two, $A\delta$ and $A\varphi$. Now how does this constitution of the F_1 gametes square with the results in the F_2 generation and in crosses 2, 3 and 4? In cross 2 we mate a pure *autumnata* male, therefore yielding gametes all of composition $A\delta$ with an $F_1\varphi$; these meet in fertilisation on our hypothesis with gametes constituted $A\delta$ and $A\varphi$ and thus develop zygotes of the forms $AA\delta\delta$ and $AA\delta\varphi$ which are ordinary *autumnata*—and precisely what the experiment yielded. Again in cross 3 a heterozygous *latifasciata* male was paired with an *autumnata* female. In this instance the male gives gametes of the two types $A\delta$ and $L\delta$ as does the *autumnata* female, but in this case they are of composition $A\delta$ and $A\varphi$; all four gametes are generated in equal quantities. Theoretically from this mating zygotes of four kinds, $AA\delta\delta$ (*autumnata* males), $AL\delta\delta$ (heterozygous *latifasciata* males), $AA\delta\varphi$ (*autumnata* females) and $AL\delta\varphi$ (heterozygous *latifasciata* females) should appear in equal proportions. As we

¹ Morgan. *Heredity and Sex*. Columbia Univ. Press, New York (1913).

² Doncaster. *The Determination of Sex*. Univ. Press, Cambridge (1914).

see, four types are obtained ; but whilst quite in accord with the prediction of equality when their paucity is considered this approximation cannot be deemed, in view of the small numbers, as very weighty evidence in favour of that equality.

Genetical analysis of the interspecific cross between *dilutata* female and *F₁ latifasciata* male need not delay us because the insects are too few to base any argument on.

There only remains then the *F₂* generation to discuss ; to bring it into being an *F₁* male, producing gametes *L♂* and *A♂*, was mated with a female of similar origin postulated in our scheme to yield equal numbers of gametes *A♂* and *A♀*. This, as one readily perceives, agrees exactly with the conditions in cross 3 ; naturally therefore the breeding results should be similar, i.e. four zygotic forms, heterozygous *latifasciata* males, *autumnata* males, heterozygous *latifasciata* females and *autumnata* females, should be obtained in equal numbers, as was indeed the case, the exact figures being 19 *latifasciata* males, 18 *autumnata* males, 18 *latifasciata* females, and 21 *autumnata* females. And the numbers dealt with are great enough to exclude any action due to mere coincidence.

It will be noted that two possible pairings are not included ; these are between heterozygous and homozygous *latifasciata* males on the one side and *latifasciata* females on the other ; the reason is obvious ; until *latifasciata* males had been secured simultaneously with similar females neither pairing was possible, the first becoming so in 1918 and the latter in 1919.

The complete agreement between predicted and actual results of the experiment thus serves to confirm the view that the gene determining progeny of the *latifasciata* type shares the distribution of the male sex factor, and furthermore that the original female was heterozygous for both, thereby confirming Doncaster's *grossulariata*—*lacticolor* results. Incidentally the fact emerges that a female homozygous for *latifasciata*-ness can never exist unless some further mutation determining a change in location of the gene for that character takes place.

We shall now take up the same question in connection with interspecific crosses between *O. dilutata* and *O. autumnata*. As was indicated above, reciprocal crosses between *autumnata* and *dilutata* exhibited inheritance on a sex-linked basis, apparently involving every gene determining wing markings in the cross between *autumnata* males and *dilutata* females, and only some in the reverse cross. But, unfortunately for the genetical analysis of these cases, in the latter all of the females

emerge months before their brothers, whilst in the former only one female was bred and was killed for dissection before its unique nature had been observed. Nor was the position of the males much better; their fertility was not greatly inferior to that of the pure species, but, on the contrary, the viability of any zygotes in the production of which their gametes took part was so slight that of the four possible back crosses only two gave larvae proceeding beyond the first instar. Moreover, of these two sets, members of only one managed to pupate, and it gave only five male pupae which died shortly after their maturation divisions commenced. Progress with these back crosses seemed impossible; nevertheless, in the hope that success might crown further efforts, they were repeated in 1915, when the families repeated the conditions of the previous season in every respect, one isolated female, wholly of *autumnata* facies, appearing in the *autumnata* ♂ × *dilutata* ♀ brood. This was paired immediately with an ordinary *autumnata* male and in due course 120 fertile ova agreeing exactly in size, colouration and sculpturing with genuine *autumnata* ova were deposited. They hatched in 1916 and gave rise to a brood of 87 imagines (50 males and 37 females); these proved in all respects and at all stages indistinguishable from pure *autumnata*. Crossed back with *autumnata* of pure wild blood and paired *inter se* they produced the same insect in 1917. This type of behaviour is susceptible of analysis and explanation as employed in the symbolical consideration of cross 2 above. It is probably a genuine case of sex-linked inheritance; still, a warning in this case is obligatory. The case is complicated by the absolute failure of reduction division in the gametogenesis of F_1 *autumnata* × *dilutata* hybrids, reinforced by the fact itself that only one female appeared in each of two broods.

Anomalies in chromosome behaviour other than the typical mechanism of sex-linkage may be at work. Furthermore, in 1917, when once more a single female was reared from several broods of the same hybrid, the female was half-sized and on pairing yielded no ova; subsequent dissection proved it to lack any trace of ovaries.

(e) *Hybridisation Experiments.*

(1) *Hybrids between O. autumnata and O. filigrammaria.*

The F₁ generation.

As we have insisted at several points above, *filigrammaria* begins to emerge from the pupae toward the end of August and continues to do so in diminishing numbers until mid September. Add to this the

noteworthy fact that forcing operations in the genus *Oporobia* are futile, and the possibility of crossing the two forms becomes very remote, but still not absolutely excluded. Precocious individuals of *O. autumnata* and belated representatives of *O. filigrammaria* occasionally overlap and therefore, if of opposite sexes, can be mated. Now this acts rather curiously in the matter of reciprocal crosses. In all of the species in the genus the males precede the females, with the necessary result that such overlapping specimens usually include female *filigrammaria* and male *autumnata*, and that combination is the one usually secured. However, in excessively rare instances, one can cage up *filigrammaria* males and phenomenally early *autumnata* females as I did, for the second time in my long continued work on the genus, in September 1918.

When the opposite sexes of the two forms are caged together so close are their pairing and physiological affinities that no matter how small the cage they pair the same evening; the pairing, as is usual in the genus, lasts for a few minutes. Eggs are deposited the following night and three days later betray their fertility by changing from green to pink. The percentage of fertile eggs does not deviate from that of the pure species, and the same holds true of their successful hibernation and subsequent hatching in spring.

The latter operation commences between the periods of the early hatching *filigrammaria* and the later *autumnata* but always inclining distinctly towards the latter. This curious fact is important inasmuch as it is apparent that the male parent is exhibiting the greater influence, not, as Toyama¹ found in the silk moth, *Bombyx mori*, the female. Opposed as this observation is to Toyama's results, nevertheless it agrees completely with those in my reciprocal crosses between univoltine and bivoltine races of *Selenia bilunaria*, in which the male habit determined the fate of the ova. Precise dates of emergence are of little value, so greatly do they oscillate from year to year according to the forwardness of the season; in 1918, for example, *O. filigrammaria* hatched on February 28th, *autumnata* on March 18th and the hybrid ova on March 14th; in contrast with this today, March 15th, 1919, not a single ovum of any of the species or hybrids evinces the slightest sign of movement.

As they hatched the larvae were supplied with hawthorn (*Crataegus oxyacantha*); this they accepted and fed on with such avidity that they were in the ground early in April, that is, earlier than *autumnata* and

¹ Toyama, "On the Hybridology of the Silk-worm," *Rept. Seric. Ass. Japan* (1906). Toyama, "On Certain Characters of the Silk-worm which are apparently non-Mendelian," *Biol. Centrbl.* Vol. xxxii. (1912).

later than *filigrammaria*. After allowing a reasonable time to elapse I removed the pupae from the cages and deposited them for aestivation in as natural a place as possible out of doors. They passed the summer without loss and appeared in due course, their first representative emerging seven days later than the earliest *filigrammaria* and ten days earlier than the first *autumnata*; in general it may be said that their whole period of emergence formed a perfect transition between those of the parental subspecies.

Description of Larvae.

As in *filigrammaria* the head was a dull smoky green. The ground colour was an olive green just intermediate to the blackish green of *filigrammaria* and the bright apple green of *autumnata*. The usual three white and yellow longitudinal stripes were present but their strengths varied, and agreed with those of neither parent. In *filigrammaria* the order of the strengths of the stripes is (1) Subdorsal, (2) Spiracular, (3) Supraspiracular; in *autumnata* this is (1) Spiracular, (2) Subdorsal and Supraspiracular equal; in the F_1 larvae the order was (1) Spiracular, (2) Subdorsal, (3) Supraspiracular—an evident compromise.

Ventrally, except that its ground is green, the markings strongly suggest *filigrammaria*.

On the whole the larva is clearly an intermediate to the dusky green *filigrammaria* with its violent contrasts and the more subdued lighter green *autumnata* with its less distinct stripes.

Pupae.

shown

No obvious differences exist between those of *autumnata* and *filigram-maria*; naturally therefore none exist between either and the F_1 lot. Only one point needs to be emphasised and that is that there is no lack of pupal viability shown, such as occurs in the F_1 generation of the *O. autumnata* ♂ \times *O. dilutata* ♀ cross.

Imagines.

In making the original pairing a *fliggrammaria* female with the two central bars as well as that preceding the subterminal pale line well developed was chosen, and paired with the usual pale grey pinewood *autumnata* male with much weakened central bands and almost obsolete basal lines, clouds and presubterminal band. From these parents I reared what at first sight seems a nondescript brood quite incapable of classification. Putting it alongside its cousins of both parent species broad differences are obvious. The general impression gained from the massed broods is that the F_1 insect as a whole is (1) less silky than

filigrammaria and (2) is of an ochreous grey tone entirely different from the monotonous quaker grey of *autumnata* or the violently chequered mass of *filigrammaria* where the powerful banding (of the deepest chocolate or carob brown obtainable) almost overpowers the dark fuscous shading of the ground and its pure white wedge-like interruptions. The significance of this will be grasped at once when attention is drawn to the fact that colour differences in these insects are not qualitative but are correlated with the quantity of pigment present. In *filigrammaria* the brown pigment is in excess; therefore it appears a photographic black; in *autumnata* it is slight and mixed with silvery white and hence looks grey; whilst in the hybrid it is medium so we get the impression of ochreous.

But, as with their cousins, a considerable range of fluctuating variation is observable in the vigour of the banding. Some, in the two central bands, are quite as clearly marked as *filigrammaria*, but this is counteracted by a lack of vigour in the presubterminal bar which combines the obsolescence of the corresponding *autumnata* band and the strength of that of *filigrammaria*. This, in combination with the lack of silkiness in tone, will always prevent one's confusing these insects with pure *filigrammaria*, in spite of their possessing the white wedges regularly outlining the cell in *filigrammaria* and occasionally perceptible on the nervures. Corroborative evidence too can be gleaned from the hindwings; on these *filigrammaria* possesses a well marked presubterminal band; *autumnata* displays a feeble one with a stronger terminal suffusion; the hybrid compromises.

From these heavily banded types we pass by degrees to insects exhibiting the whole range of variation in *autumnata* grey ground, in union with every degree of depth in the *filigrammaria* type of banding, so that in the end we reach, especially in the male, insects appearing at first sight indistinguishable from pure *autumnata* except in size. For the most part these betray their mixed blood not only in size but, on careful examination, in the exaggerated strength of the presubterminal band when compared with *autumnata*; if they do not, and the cases are few, the clear white wedges of *filigrammaria* serve to indicate their hybrid origin. But, whilst in all cases at least one of these points serves to direct one's judgment, in many of the most *autumnata*-like individuals both features appear to help one.

In connection with the relative size of the sexes the F_1 insect likewise seems intermediate. In *filigrammaria* the female size is 88.7 % of that of the male, in *autumnata* it is 90.7 %, and in the F_1 insects 89.8 %.

To sum up, as in size so in ground colour, markings, etc. both sexes, when due cognisance is taken of their fluctuating variation, and that of the parental forms, are clearly intermediate. But in spite of this I have not the slightest doubt that if captured wild about 80 % would be regarded as *autumnata* and 20 % as *filigrammaria* simply because, on the one hand, *autumnata* in its local races presents great variability in its banding, whilst on the other, *filigrammaria* nearly always appears in a heavily marked banded guise.

Genitalia.

The parent forms are too nearly alike (more particularly in the females) in this respect for great differences to be seen in the F_1 insects. Perhaps in the males the octavals are nearer than in *autumnata* and without doubt there are more bristles on the crista*e*.

Fertility of the Imagines.

In accordance with one's expectation in dealing with hybrids between parents so closely allied physiologically both sexes of the F_1 insects were fully fertile either when paired *inter se* or crossed back on *O. autumnata* or *O. filigrammaria*. All of the possible matings were made, and all of the ova deposited were fertile to the extent of 100 %. From these the F_2 , $F_1 \delta \times filigrammaria \text{ } \varphi$, $filigrammaria \delta \times F_1 \varphi$, *autumnata* $\delta \times F_1 \varphi$ lots were reared, those of the $F_1 \delta \times autumnata \varphi$ being discarded owing to lack of cage room.

Like their parents the larvae of all these crosses were offered hawthorn, and like their parents they accepted it and fed up with trifling loss.

The F_2 generation.

The ova from the pairing $F_1 \delta$ and $F_1 \varphi$ hibernated as such and commenced to hatch just prior to *autumnata* (March 10, 1918). As in the F_1 generation, the imagines obtained appeared so as to overlap the periods of *autumnata* and *filigrammaria* and thus accompanied their relatives in a new F_1 lot reared alongside them.

Of this generation very little can be said except that in every characteristic, size, relative sizes of male and female (φ size = 89.8 % δ), wing markings, and so on they were like the F_1 brood from which they were bred; they were intermediate to the two pure species. In no way was segregation in F_1 gametogenesis, and subsequent recombination in the F_2 zygotes indicated by the reappearance of grandparental characters. In size this feature was displayed to a marked degree as we shall see

later. Although the variation in wing pattern cannot be studied statistically and therefore so accurately as size, the degree of variation was obviously less than in the F_1 lot, for the extreme banded forms of that generation showing some approach to *filigrammaria* were non-existent.

Now it has become the fashion to explain the absence of any appearance of segregation of the grandparental form in cases like this on the ground that in place of few clear cut unit characters depending on similarly definite genes we are dealing with hosts of factors segregating and recombining independently, some with and some without dominancy. Under these circumstances, it is urged, it would be futile except in thousands, perhaps millions, of cases to expect a perfect grandparental segregate; what we are to look for, we are told, is a smooth variational curve of more extended spread than in the F_1 brood. But we have pointed out that the variation exhibited is most markedly less than that shown by the F_1 insects, which cannot be explained on other grounds than the ordinary fluctuating and continuous variation due to the play of the more or less plastic germinal material of the pure species. Why then should we invoke multiple factors to explain F_2 variation and not that in F_1 ? To drag in two distinct explanations for one and the same phenomenon seems absurd.

The balance of probability lies in favour of the view that we are rather concerned with contamination of the gametes, or with permanent gametic blending; this I strongly suspect is the rule in interracial and interspecific crosses, if any weight at all attaches to their generally uniform evidence.

Again the insects proved completely fertile in both sexes and a number were confined for ova; these were successfully obtained and hatched in due season in the following year.

The F_3 generation.

As ova (hatched March 8, 1918) and pupae this generation offered no obvious peculiarities, but the case was different with the larvae, which in about one half of the instances tended to exhibit a massing of the darker dorsal suffusions on each side of the paler lines edging the dorsal vessel, particularly just before the anterior trapezoidal tubercles, in this fashion developing a pattern involving a series of dorsal lozenges. This was unusual enough for me to select a single larva for description but still not extraordinary enough to be considered beyond the possible range of variation. Nevertheless, in the light of subsequent knowledge, it was

evidently correlated with the advent of a previously unknown imaginal form which we shall discuss below.

The larvae fed up normally and the pupae passed the summer safely to yield a total of 86 imagines in autumn. These divided themselves sharply into two sections, one composed of 27 males and 8 females being precisely like their parents and therefore intermediate between true *autumnata* and *filigrammaria*. This intermediate portion needs no description and would not be further mentioned except to indicate that it included one teratological female in which the left antenna was duplicated. The other division composed of 24 males and 27 females was wholly dissimilar; *the individuals in it resembled neither their parents nor, save in a manner common to the genus, did they approach the pure species from which they had been derived*. Moreover, although fluctuating variation was present, still the impression one gained from the series was one of complete uniformity. In view of their peculiarities therefore they are worthy of a detailed description.

The ground colour is of an almost pure white interspersed with a few grey scales; in two cases, one male strongly and one female weakly, this is suffused with a smoky tinge. Across this ground passes a band differing widely in its build from that seen either in *autumnata* or *filigrammaria*—or even in *dilutata*. In ordinary pure species we have two central bands, each of which is composed of two lines more or less parallel, connected up by a suffusion varying in depth with the species and with the genetical type of the race within the species. In the *filigrammaria* female employed to produce the F_1 generation, the shading was so deep as to differ in no wise in intensity from that of the bounding lines; on the other hand, in the *autumnata* parent this was very much less concentrated. As we have seen the F_1 , F_2 , and a portion of the F_3 lots were intermediate in this respect. The band in the central area of the aberrant section is wholly distinct in design from any of these. Almost in every case the bounding lines of the bars in which they occur are distinct enough, although they give one a sense of being out of focus, but, what is more important, the outer member of the inner band is obsolete in all cases; in others (all males) the same fate has befallen the inner one of the outer band. In the latter event, the two existing lines tend to be united by a brownish suffusion and in all the examples the two normal outer ones show the same trend. Occasionally (to be exact in half a dozen examples), the line proper to the outer band moves toward the base of the wing and becomes central; here, likewise, a brownish suffusion tends to occupy the whole of the central wing area. Another curious

feature lies in the fact that the outermost line of all, where it intersects the sixth nervure, projects along it and causes the whole band to jut out at that point. Outward from the central band is a broadish white bar traversed by a wavy line; this, again, is much clearer than in any form previously considered. It is succeeded by an almost solid blackish suffusion in which the pale subterminal line is wholly or partially buried. Within the limits of this suffusion the nervures are heavily outlined in a perfect manner quite foreign to *filigrammaria* or *autumnata* or their other hybrids. A similar encroachment of the black scales outlining the nervures of the cell and those issuing from it is made along other nerves, so that in extreme cases the whole nervure system is lined in in black. At the same time a change in the relative position of the discoidal point is seen. Normally it lies in the angle of the elbowed line of the outer band. Here, in most examples, it lies on that line and even on others beyond it, a displacement never encountered in *autumnata* and *filigrammaria*. The total effect of this change in "band formula" is to throw the band into a condition recalling the narrowed complete carpet band observable in so many genera of the Larentiad group—even those removed fairly widely from *Oporabia*—and possibly, therefore, indicating that the completion of the band is reversal.

On the hindwings the terminal bands and suffusions are obsolescent but the increased strength of the black scaling outlining the nervures is very marked: in particular, the black V at the base of veins 3 and 4 in the forewings, just at their origin in the cell, is reproduced as one never sees it elsewhere.

What is the cause of this postponed or pseudo-segregation? Had it occurred in such forms as *Oenothera Lamarckiana* it would have been heralded as a genuine example of mutation. This explanation, however, is here excluded because the combinations which were used to synthesise the form are known. Although two generations removed, the original parents were hybrid in origin and the phenomenon, whatever it is, is one of hybridity, and its explanation must lie in some germinal disturbance brought about by that—and germinal irregularities were met with early. As will appear in my subsequent paper on the gametogenesis of these hybrids the chromosome complement of *filigrammaria* is 37 and that of *autumnata* 38—these being the haploid numbers. So nearly homologous are they that, in the gametogenesis of the F_1 hybrids, in many cases all of the *filigrammaria* chromosomes find mates; in other cases up to four do not, with the consequence that certain oocytes and spermatocytes are endowed with 38, 39, 40, 41, 42 or 43 chromo-

somes respectively, so that in forming the F_2 generation a combination of any two of these takes place. Thus the F_2 zygotes commence life with a mechanism intended to deal with 76 chromosomes at the most, in place of which 86 may occur in each nucleus. Consequently, in their gametogenesis, in addition to failures in homology, merely mechanical complications ensue ending not only in chromosome disturbance but in their actual loss and degeneration in the cytoplasm. In this case, if the chromosomes be in very truth the heredity bearers, then there cannot but be a manifestation of new characters or combinations in the imagines. The great uniformity of the F_2 pseudo-mutants, however, suggests that if this explanation is, as is almost certainly the case, true, then there must be some preferential setting up of some individual type of chromosome combination. Still it is quite possible that the other types may not render the zygotes possessing them in any way worthy of special note.

To my mind the importance of this result is very great; the parallel nature of the occurrence with those secured by De Vries and others in *Oenothera* suggests just as forcibly to me, as did other considerations to Bateson, that *Oenothera Lamarckiana* was and is not a pure type, and not being pure is no fit subject for ordinary genetical experiment, especially when no one has the faintest knowledge of its actual genotypic composition. Much less then can it be held a fit subject upon which to base such a fundamental doctrine as mutation. In thus pointing out the views I have been led to adopt concerning *Oenothera* I do not wish to deny that mutation occurs: that it does we have ample evidence in our own genus in the *latifasciata* aberrations of both *autumnata*, *filigrammaria* and *dilutata*, not to mention other well-known cases both in domesticated and wild animals and plants.

The Back Cross between the F_1 ♀ and O. autumnata ♂.

This was reared from a pairing of an *autumnata* male of the feebly marked, suffused pinewood form and a medium female from the F_1 lot. Ova were successfully obtained and wintered safely to emerge just prior to *autumnata* in the succeeding spring. The larvae revelled in the hawthorn they were offered and fed up rapidly without loss.

Of the larvae and pupae little can be said save that almost no signs of *filigrammaria* influence were discernible unless they lay in the slightest possible strengthening of the longitudinal stripes, the darker ground of head and body in *filigrammaria* failing to show any effect.

In the imagines (save in size) one looks likewise in vain for any

indication of *filigrammaria* blood ; their markings are absolutely those of typical *autumnata*. But they possess this very important feature ; their range of fluctuating variability is down to a minimum, for I have never possessed such a uniform brood from any female in the genus. They give one the impression of a deadly uninteresting monotony not even relieved by the usual sexual dimorphism of the group.

In variation exhibited they are far inferior to either pure *autumnata* or to *filigrammaria*, whereas if the multiple factor theory be the genuine explanation of the continuance of the F_1 blend here as well as in the F_2 lot, the range ought to have been much greater rather than much less. The independent segregation of all of many unit factors in the oogenesis of the F_1 female should have resulted in an immense field of variation when in zygotic combination with the gametes of the *autumnata* male. Again the evidence of the cross distinctly opposes the multiple factor scheme and its gametic purity ; it is all in favour of lasting gametic contamination or blending.

It will thus be seen that a single back cross has sufficed, to all intents and purposes, to cause the hybrid to revert to one of the parent species.

As in other cases the hybrid insects were fertile in all directions but only larvae from one mating in which they took part were reared to maturity ; these were the result of pairing the insects *inter se*. So alike were the insects involved that no selection of genotypes was possible. To ensure as variable a progeny as possible ten females, chosen at random, were caged up with a similar lot of males, and about a tenth of the mixed ova retained for breeding. In spite of these precautions, the insects bred showed no signs of segregation and in fact were indistinguishable in size or design from their parents and, furthermore, displayed the same limited extent of variation.

The Back Cross between autumnata ♀ and the F_1 ♂.

Owing to a shortage of cage room this cross was not proceeded with in 1918. During that season, however, a further F_1 brood derived from the same stocks as those employed in the 1917 experiments was reared. From this brood an average male was taken and paired with a female *autumnata* from the same strain as utilised before. Fertile ova were duly obtained, and the larvae issuing from them reared during the present season.

Up to the present (October 23rd, 1919) two-thirds of the pupae have yielded their imagines. These are of the same expressionless type

as those of the preceding cross and therefore display a very contracted range of variation. Once again a single back cross has apparently sufficed to restore the *autumnata* facies, and once again the evidence gained points to permanent gametic contamination.

The Back Cross between the F_1 ♀ and filigrammaria ♂.

Here a barred *filigrammaria* male such as was employed originally was paired with an F_1 female. The early stages need no special treatment but one must not omit to state that the larva leaned very distinctly toward *filigrammaria* in the strength of its stripes.

The imagines obtained, if they had been captured in nature, would undoubtedly have been regarded as *filigrammaria*, but nevertheless direct comparison with both *autumnata* and *filigrammaria* shows that they present clearly enough points of divergence which we shall proceed to point out.

Before doing so, it must be noted that their range of variation is, unlike that of the last cross, of the same extent as in the parents but emphatically not greater.

The first great difference between it and *filigrammaria* is the superior size, the mean being in both sexes slightly higher than that of the F_1 insect instead of less, a circumstance brought about by the undue weight of one of the superior size classes which two facts prove to be of no definite import: (1) in the female one of the lower classes is similarly overweighted but not enough to counterbalance the former; (2) the reciprocal cross shows no such features. The only other sign of the influence of *autumnata* worthy of special note is that, whilst every phase of variation of pure *filigrammaria* is encountered it is always toned down, no matter how small the degree, by the indecision introduced from *autumnata*.

To sum up, the insect comes very near to *filigrammaria* but shows very obviously its *autumnata* blood and is thus a good intermediate to the F_1 lot and *filigrammaria*. Thus we perceive that one back cross in this direction does not suffice to cause a reversion to the parent type. This being so, and the insect being perfectly fertile, it was once more crossed back on *filigrammaria*, females of this stock being paired with males of *filigrammaria*.

The Back Cross between the preceding and filigrammaria ♂.

The larvae of this cross were exactly the same as their cousins of pure *filigrammaria* blood which were reared in the adjoining cage. And the same remark is applicable to the imagines; of all the large number

reared only four would be regarded as other than pure *filigrammaria*, not even a specialist being able to detect the faintest indications of *autumnata*. In the case of *filigrammaria* it has required two back crosses to secure the passage back to that species.

As for the four aberrant individuals they show very considerable approach to the pseudo-mutants of the F_3 generation; in fact, one of them is precisely the same as those, and the other three only differ in being decidedly darker. The same consideration of mitotic dislocation is, in all probability, responsible for their appearance, because again in the gametogenesis of the back cross between F_1 ♀ and *filigrammaria* ♂ we are dealing with a second hybrid generation; the same interference as we considered possible in the case of the F_2 generation may be at work here. If this be the case a preferential setting up of a definite type of gamete, when such are aberrant, may conceivably result in similar phenotypic if not genotypic manifestations.

The Back Cross between F_1 ♂ and filigrammaria ♀.

This generation, except that we have the expected drop in mean size toward *filigrammaria*, agrees with that obtained in the reciprocal combination and cannot by any test save this one of size, which is certainly a matter of chance, be separated from them. Once more a single back cross has failed to restore the *filigrammaria* condition. The very

TABLE V.

Summary of sex ratios in the Oporabia autumnata-filigrammaria experiments.

Culture	Males	Females
<i>Oporabia autumnata</i> from Pinewood 81 63		
<i>Oporabia autumnata</i> from Birchwood 48 30		
<i>Oporabia filigrammaria</i> 90 106		
F_1 <i>Oporabia autumnata</i> ♂ (from pine) \times <i>O. filigrammaria</i> ♀ ... 19 60		
F_1 <i>Oporabia autumnata</i> ♂ (from birch) \times <i>O. filigrammaria</i> ♀ ... 33 30		
F_2 <i>Oporabia autumnata</i> ♂ (from pine) \times <i>O. filigrammaria</i> ♀ ... 51 31		
F_3 <i>Oporabia autumnata</i> ♂ (from pine) \times <i>O. filigrammaria</i> ♀ ... 51 35		
Back cross 1 = <i>Oporabia autumnata</i> (pine) ♂ \times F_1 ♀ (pine) ... 51 51		
Back cross 2 = <i>Oporabia filigrammaria</i> ♂ \times F_1 ♀ (pine) ... 30 31		
Back cross 3 = F_1 ♂ (pine) \times <i>Oporabia filigrammaria</i> ♀ ... 17 15		
Back cross 4 = <i>Oporabia filigrammaria</i> ♂ \times Back cross 2 ♀ ... 41 49		

obviously superior power of *autumnata* in this respect is very curious. One would have thought that the heavier barring in a palpable case of blending inheritance would have had a greater effect than the feebler state of *autumnata* in this respect, and that therefore there should have been a speedier reversion to *filigrammaria*. But one must not forget that *autumnata* is the phylogenetically older form and that *filigram-*

maria is derived from it, the anomaly may therefore be ancestral in cause.

The F₁ generation of the cross between autumnata ♂ and filigram-maria ♀, the autumnata being of the pale birch type.

This calls for no special remark; except in the absence of suffusion, the brood recalls in every way that of similar origin when the birch male was replaced by a pinewood male.

(2) *Hybrids between Oporobia autumnata and O. dilutata.*

Immediately after my discovery of *Oporobia autumnata* in Wilton pinewood I made preparations for securing the two possible crosses between it and *O. dilutata* and to that end reared a large number of pupae of both species which emerged in due time. Unfortunately I had not then realised the highly specialised nature of the pinewood race of *O. autumnata* in respect to its time of emergence, for I had conceived the idea that in dealing with great numbers some few at least would appear simultaneously with *O. dilutata* in October. Such an event, however, did not happen; without a single exception the *autumnata*

TABLE VI.

Summary of sex ratios in the Oporobia autumnata-dilutata experiments.

Culture	Males	Females
<i>Oporobia dilutata</i> . Totals of wild stocks from which parents of hybrids were chosen	77	72
<i>Oporobia autumnata</i> (birch). Totals of three broods from which parents of hybrids were chosen	85	69
<i>F₁</i> <i>Oporobia dilutata</i> ♀ × <i>O. autumnata</i> ♀ (3 broods)	... 52	47 (no ovaries)
<i>F₁</i> <i>Oporobia autumnata</i> ♂ × <i>O. dilutata</i> ♀ (6 broods)	... 6	0 ¹

nata had long since ceased to emerge when my first *dilutata* came out. The experiment was therefore a failure. Profiting in the succeeding season from this experience I beat a considerable quantity of wild *autumnata* larvae in addition to hosts of *dilutata* from diverse sources and once again provided myself with an abundance of pupae of both species. These preparations ended in complete success for when the first *dilutata* appeared in October I had both sexes of *autumnata* caged up. Placing a melanic *dilutata* female in a cage with *autumnata* males and *vice versa*, I confidently awaited results. Almost at once I had the pleasure of seeing ova deposited, and these in every case changed

¹ This result was obtained from over 400 pupae—all males—but which nearly all died as is one's usual experience in this cross. I have reared single females from this crossing in three different broods (otherwise male) in different years; they were indistinguishable from pure *O. autumnata* females.

colour, those from *dilutata* female to a dull ruby and those from *autumnata* females to salmon pink. It will thus be evident that cross fertilisation in no wise altered the colour of the fertile ovum of any given female from what it would have assumed on ordinary fertilisation. No acceleration in emergence due to hybridity was manifested, and in both instances the ova hatched in the April of the following year, when practically every ovum yielded a larva.

The larvae were offered hawthorn (*Crataegus oxyacantha*) and displayed no hesitation in accepting it. In habits both sets resembled *autumnata*, for they fed ravenously and showed neither wandering tendencies nor slowness in feeding up. No tangible differences¹ existed between the two hybrid larvae and both are lovely creatures, only one larva in the group, that of the hybrid between *dilutata* female and the F_2 *filigrammaria* ♀ × *autumnata* ♂, surpassing them in beauty of design. They possessed the pleasing soft apple green ground colour of *autumnata* with its more or less conspicuous yellow longitudinal stripes, and upon it were superimposed the reddish dorsal blotches of *dilutata*, toned down here to a delicate ferruginous red. They pupated, one and all, in early June. Since events in the two reciprocal crosses pursue different courses after pupation it is best to consider the two life histories subsequent to that event separately.

The F₁ generation of the cross between O. autumnata ♀ and O. dilutata ♂.

Before passing on, however, attention must be drawn to extraordinary abnormalities in the behaviour of certain hybrid larvae, resulting from the cross between *Oporinia autumnata* ♀ and *O. dilutata* ♂, in their penultimate instar. About fourteen of these, instead of moulting normally, spun a silken pad and thus attached themselves at the end of March to twigs of the food plant where they remained for over a fortnight without making the slightest endeavour to cast their skins—an event usually occurring two or three days after cessation from feeding. Without considering further possibilities I at once conceived the notion that they were attempting to resume some long abandoned habit of larval hibernation, and therefore removed most of them with the full grown larvae to the cages used for pupation; here, owing to their being overwhelmed by the random silken threads spun by larvae seeking

¹ Save in size in the first instar; as the cubical contents of an ovum of *dilutata* are less than two-thirds of those of an *autumnata* ovum any larva, hybrid or otherwise, produced from the latter is bound to be larger than one issuing from the former.

to enter the soil, they died. Luckily, I had taken the precaution of isolating one specimen to determine exactly what course it would pursue. For five weeks it remained motionless, and then it assumed a very unhealthy colour suggesting that it was moribund. Clearly, however, this colour change was only preparatory to exuviation, for when I looked at it later I discovered that it had moulted and had yielded, not a fifth stage larva, but a strange monstrosity, larval in colouration and semi-imaginal in structure. At first sight its anomalies seemed to exist chiefly in the pairs of unusual appendages borne by the meso- and metathorax, these evidently being external wing buds exactly comparable with those seen in heterometabolous forms like the Orthoptera. More minute inspection showed many further approximations to imaginal conditions which were more particularly visible on the structures appertaining to the head.

In size the head was much inferior to that of the last stage larva, and in this and in shape it agreed more nearly with the imago. Nor was the resemblance confined to size and shape, for the antennae were much longer than the ordinary larval type and possessed numerous joints, it being impossible to determine the exact number owing to their being fused; in shape they closely resembled an inverted Indian club. The eyes, moreover, partook of the characteristics of both larva and imago, for the imaginal compound eye was represented by rounded projections of normal size, more or less regularly reticulated but not developing regular facets; on the right member of these eye masses appeared two ocelli with rudiments of others and on the other one ocellus with rudiments.

The larval jaws were present and, as a matter of fact, apparently duplicated, but this I suspect to be due to imperfect moulting of the earlier pair.

The external wing rudiments were not all of equal length, that on the right of the mesothorax being 3 mm. long and the other three roughly 1.75 mm.; all possessed vestiges of the usual imaginal neuration.

The legs, whilst in the main larval, are difficult to describe owing to the presence of obvious traces of imaginal structures. Although perhaps a little flattened, the prolegs do not call for special treatment.

The advent of external wing buds in a holometabolous insect is capable of two explanations; either we are dealing with atavism, in which case we are receiving glimpses of the course matters took long ago in the evolution of winged imagines from original larval forms, or we are concerned with, on a large scale, the phenomenon of anticipation

noted in minor characters by Denso¹ and myself² in larvae of Sphingid and Bistonine hybrids. In my opinion the latter, from the evidence presented, is the correct view, i.e. that we have a precocious development of imaginal organs induced by the disturbing influence of hybridity.

Rare as this occurrence is, it is not unknown even in pure species, although as far as the Lepidoptera are concerned only one previous case is on record, that of larvae of *Bombyx mori* reared by Cesare Majoli in 1813; these were in every way similar to my *Oporobia*. In the Coleoptera—still holometabolous but not so complex in the mode of origin of its wings—other cases are known; in this group it is not so wonderful, for the invagination of the hypodermal cells destined to give rise to the wing buds is of a much simpler type, and very little displacement would cause their appearance externally. To the best of my knowledge the recorded instances in the beetles relate to the common *Tenebrio molitor*, and to *Anthrenus varius* and *Dendroides canadensis*. Our knowledge of the first case is the most extensive, for Prof. Heymons³, after his discovery of the first larva, was able to find others and give them detailed study. Busck⁴ added *Anthrenus varius* and Riley⁵ *Dendroides canadensis* to the meagre list of species displaying this abnormality. Making due allowance for the difference in order, these coleopterous freaks do not differ widely either from the conditions of Majoli's silkworms or of my *Oporobia* and are therefore directly comparable with them.

We shall now return to the fate of the larvae pupating normally. Anticipating as usual an aestivation of some four months I allowed the pupae to harden for a fortnight or so and then proceeded to dig them up in order to store them under natural conditions. When I examined the cage for this purpose sixteen days after pupation, I was greatly astonished to find that a female had already emerged, and this observation caused me to scrutinise the pupae daily. And this proved a very fortunate thing, for during the next few days approximately one half of my stock emerged and every individual doing so proved to be a female.

¹ Denso, "Die Erscheinung der Anticipation in der ontogenetischen Entwicklung hybrider Schmetterlingsraupen," *Zeit. für Insektenbiol.* iv. (xiii.) pp. 128—135, 170—176, 201—208 (1908).

² Harrison, "Studies in the Hybrid Bistoninae," *Journal of Genetics*, Vol. vi. No. 2, p. 102 (1916).

³ Heymons, "Flügelbildung bei der Larve von *Tenebrio molitor*," *Sitz. Ber. Ges. Nat. Freunde*, pp. 142—144 (1896).

⁴ Busck, "Larvae of *Anthrenus varius* showing wing pads," *Proc. Ent. Soc. Wash.* Vol. iv. p. 123 (1897).

⁵ Riley, "The abnormal appearance of external wingbuds in larvae of holometabolous insects," *Ent. News*, Vol. xix. No. 9, pp. 136—137 (1908).

After waiting in vain six weeks for further emergences I unearthed the remainder of the pupae expecting them to be dead, but was astounded to discover that practically every pupa was alive and healthy, and that every one was a male. These were packed as usual in moss and cocoanut fibre in air-tight tin boxes and laid aside to be carefully inspected at intervals. No further moths put in their appearance until October, when the rest came out in company with the parent species.

Description and discussion of the resulting insects are greatly complicated by my unfortunate but unavoidable choice of melanistic *dilutata*, which at the time was the sole form of the insect accessible to me. Owing to the blurring effect of the melanism other details are rendered obscure. Very obviously, however, the males are strict intermediates when correct value is attached to every point, whilst just as certainly one would assign the females to pure *dilutata*. Here then was the first hint of that sex-linkage in inheritance in the genus which I have pursued at some length above. Subsequently, in order to clear away the indecision induced by the melanism I have employed ordinary birchwood *autumnata* and non-melanistic Irish *dilutata* in my later experiments, so that more exact comparison of the hybrid insects with their parents becomes possible.

In the light of these new broods I find but little to alter in my views; the male remains intermediate no matter what strain of *autumnata* is involved (and I have now succeeded in introducing all of the races known to me from birch, alder and pine); still I must confess that the closeness of the females to pure *dilutata* is not so decided, for on the clearer non-melanistic ground colours *autumnata* shows some, if varying, influence.

Full description of all of the imagines reared in the later trials would be impossible, such a wide range of variation is introduced by the continuous or fluctuating variation so prominent in both parent species. Due to this fluctuating variation in the males, one can almost say that a perfect transition exists from pure *autumnata* to pure *dilutata* in outward appearance. In spite of this their hybrid nature is at once betrayed to the expert by the peculiar texture of the wing scaling, which in every case compromises between the coarse whitish-yellow tone of *dilutata* and the fine silkiness of *autumnata*, and gives us a silvery grey ground quite unlike what one encounters elsewhere in the genus, but still recalling that exhibited by several other Larentiad species. One very important point must be singled out for special mention and that is that if the clear, sharply marked birchwood *autumnata* with the

silvery white central area provides the male, then that pattern is dominant, and the insect obtained differs in no respect from *autumnata* save in its cool grey ground. Similarly certain of the other *autumnata* patterns, for instance that of the distinctly barred *sandbergi*, show like tendencies but their dominance is never complete.

In the female the fluctuating variation is likewise great, although, as I have indicated previously, but rarely would this sex be deemed other than pure *dilutata* whether they were melanic or non-melanic—a fact that would not prevent the eye of the trained observer from detecting differences in many cases.

The indications of other structural characters are quite in harmony with those of the wing markings. The male antennae are absolutely intermediate between the finely jointed antennae of *autumnata* and the much coarser ones of *dilutata*, and the genitalia simply continue the tale. The hook on the valve is developed but remains quite small, and the head of the labides is intermediate in size. So, too, in the female the signa of the bursa copulatrix (Figs. 1, 2, 3, 4) on the whole favour *dilutata*, but some hint of *autumnata* may be gleaned from the sculpturing of the upper one.

In making the necessary dissections for the study of the female genitalia a very important feature was revealed; that the ovaries of the insect were lacking. And herein lies the explanation of the precocious appearance of the females, the two factors of emergence and completed gametogenesis being so correlated that the female leaves the pupa soon after the operation of oogenesis is finished. No oogenesis being possible with this hybrid, the insect develops and emerges at once. That delayed gametogenesis accompanies delayed emergence I can readily prove. In 1917 I had two lots of *dilutata* pupae, one of which had contracted a bacterial disease during the last larval skin which in many cases did not prove fatal; the other lot was not infected. Both lots were freely drawn on for material for cytological work, on the assumption that larvae which had successfully pupated could not be diseased. When microscopical preparations of the gonads were made it was found that in the healthy lot the maturation divisions were completed by the first week in September, whilst in the other the process had barely commenced at the end of the month. Then every germ cell, from oogonium to ovum, from spermatogonium to spermatozoon, was crowded with bacteria.

During that season the first wild imago of *dilutata* was seen in the woods on September 24th, and for practical purposes the species was over by October 13th, when on my searching for wild females for stock only

worn examples of that sex were captured. Roughly, the same period covered the emergence of my sound domesticated brood; on the contrary, the bacteria infected insects failed to show themselves until October 15th and straggled on, most unusually, until the middle of November. This *dilutata* brood was not alone in thus exhibiting the phenomena of infection and retardation, for both of the *dilutata-autumnata* crosses of that year likewise contracted the disease, and they too were late in emerging. Despite the infection, as is customary, the females of the *autumnata* ♀ × *dilutata* ♂ lot were obtained in June and July, proving thereby that the presence of bacteria did not inhibit somatic development; on the other hand the males of both broods, as well as the odd female of the reciprocal cross, instead of accompanying the alderwood insects only started to emerge on October 13th, subsequent to which date they yielded small numbers over a protracted period.

From what has been related it is manifest that further work with the hybrid females was hopelessly excluded, but matters with the males were different. Genitalia, primary and secondary, external and internal were alike perfect, the testes containing an abundance of well developed spermatozoa. Arrangements were therefore made to confine the males in cages with *autumnata* and *dilutata* females to secure the apparently certain back crosses. But matters did not proceed smoothly; ova were not forthcoming immediately, and it was only after a fairly long interval had elapsed that eggs were obtained. In the two crosses no marked differences in the fertility of the ova were noticed, some 30% in both cases being fertile. Spring, however, told a different tale, for every ovum from the pairing between *autumnata* ♀ and the F_1 ♂ collapsed after development had been initiated, whilst every fertile egg in the cross between *dilutata* ♀ and F_1 ♂ delivered a sturdy little larva which fed up speedily and, until the last moult, well. These larvae, in direct opposition to their ostensible three-quarters *dilutata* blood, could neither in design nor habits be distinguished from those of the F_1 generation of the *autumnata-dilutata* crosses. There was not the slightest sign of passage toward *dilutata*—a totally different phenomenon from the almost instant return, on back crossing, of the F_1 *autumnata* × *filigrammaria* insects to their parent forms. This undoubtedly depends directly on the different courses pursued in the gametogenesis of the two F_1 broods. In the *filigrammaria* ♀ × *autumnata* ♂ cross nearly all (sometimes actually all) of the chromosomes find mates previous to the first maturation division, so that a reduction division does occur accompanied, in my opinion, with an "averaging up" of the values attachable to the various

genes. On the contrary, in the *autumnata* ♀ × *dilutata* ♂ F_1 lot no pairing of chromosomes takes place at all, and in consequence all of the maturation divisions are equational. Every gamete then derived from the *autumnata* ♀ × *dilutata* ♂ males is endowed with the sum of the haploid chromosome numbers of *autumnata* and *dilutata*, i.e. it has $30 + 38 (= 68)$. In other words it has a full complement of those from each parent. When such gametes encounter in fertilisation those of *dilutata* a zygote is generated the cells of which contain a chromosome number of $30 + 30 + 38 (= 98)$ —a double set of *dilutata* and a single set of *autumnata* chromosomes. Now if the chromosomes are the heredity bearers and the various unit factors are located in them then the genes from *dilutata* are duplicated. But Nilsson-Ehle¹ and Shull² have shown in their experiments on chaff colour in grain and capsule shape in *Capsella* that duplicate genes are not necessarily cumulative in effect; whence it follows that in back crosses such as these, where no genuine reduction division takes place in the F_1 insects, the phenotype of the back cross may not vary perceptibly from that of the F_1 insect. Furthermore, since in the gametogenesis of the back cross pairing of homologous chromosomes will take place, its gametes will be identically the same as those of the F_1 insect so that reversal to parental type can never be brought about in the case of hybrids with such a form of gametogenesis. No matter through how many generations we pursue the experiments the constitution of the genotype produced can never differ from that obtained in the first back cross; thus a constant intermediate form will be maintained.

Of the larvae only five pupated, bacterial disease carrying off the rest. All of these were males and this is precisely the condition of the *dilutata* ♀ × *autumnata* ♂ broods in general; still, in view of the small numbers involved no definite importance can be attached to the fact. Before emergence three died simply through lack of viability, and two began to develop but were sacrificed for cytological purposes. However, this back cross has once more been obtained and I hope to pursue my investigation with it during the present season.

¹ Nilsson-Ehle, "Einige Ergebnisse von Kreuzungen bei Hafer und Weizen," *Bot. Notiser* (1908). Nilsson-Ehle, "Kreuzungsuntersuchungen an Hafer und Weizen," *Lunds Univ. Årsskr. N. S.* Vol. v. pp. 1—122 (1908).

² Shull, "Duplicate Genes for Capsule Form in *Capsella bursa-pastoris*," *Zeitsch. für Abst. und Vererb.* Vol. xii. pp. 97—149 (1914).

The F₁ Generation of the Cross between dilutata ♀ and autumnata ♂.

Of this cross little can be said save that one must refer to its lack of pupal viability. If 2% of all of the pupae laid aside in July are bred then a remarkable feat has been performed—and in the genus one usually rears 75% as a minimum. In all of the almost countless numbers of larvae of this particular parentage I have reared, only once have I exceeded this figure of 2%, and that was in 1915 when I raised over 12%. The mortality always becomes evident just when the maturation divisions are proceeding and may be due to some reaction between somatic and germ cells but how brought about one can only guess. Obscure hints, nevertheless, may be gleaned that such is the case from the fact that often enough the act of pairing and deposition of hybrid spermatozoa in the bursae copulatrices in certain Bistonine females is instantaneously fatal.

The insects bred in the present cross are nearly always males, and in that sex they cannot be separated when in representative series from those secured in the reverse cross. But curiously enough, beginning with my first experiment when I reared one female and seven males, I have on three separate occasions bred single females. It must not be assumed that this is due to differential viability of the sexes, for it is not so. Examination of brood after brood of dead pupae will show that they consist wholly of males. The case therefore becomes parallel to those of the crosses between *Tephrosia bistortata* ♀ and *T. crepuscularia* ♂, *Nyssia zonaria* ♀ and *Lycia hirtaria* ♂, *Nyssia graecaria* ♀ and *Lycia hirtaria* ♂ which I have discussed in a recent paper (now in the press) entitled "Studies in the hybrid Bistoninae; iv. Concerning the Sex and Related Problems." In brief my explanation is that the failure of the females is brought about by a difference in potential in the male sex genes in the species involved in the crosses.

The genetical behaviour of the odd females has already been described in the paragraphs on sex-linked inheritance and thus needs no further treatment here. That of the male does not differ greatly from that of the same sex of the reciprocal hybrid. I have never dared to risk one of the very rare females in pairing this *F*₁ generation *inter se*, but I have made the two possible back crosses with *O. autumnata* and *O. dilutata* females. With *autumnata* females about 25% of the ova deposited were fertile and with *dilutata* about one half that. All wintered satisfactorily enough, but none of the latter hatched and only two-thirds of the former. Although those hatching seemed healthy enough, they

died one by one before revealing characters sufficiently striking to admit of study.

Whether by mere coincidence or founded on some genuine physiological basis, it is observable that in all four back crosses, when the female in the back cross is the same as that entering into the original cross, then no ova hatch; and, on the contrary, if the female of the back cross is of the same species as that providing the male in the first cross, then the eggs hatch and the larvae progress more or less favourably. That the matter is more than mere coincidence the separate and confirmatory evidence of several broods seems to show.

(3) *Miscellaneous Pairings.*

For an exceedingly long time I have striven to obtain the necessary pairings for introducing *O. dilutata* into the *autumnata-filigrammaria* series of hybrids, but only to be thwarted year after year by the exasperating way in which almost invariably *O. filigrammaria* and any hybrid in which it took part were over before *dilutata* appeared: the latter species is immovable in its preference for the last days of September and for October as the period of its imaginal activities. However, 1917 put me in possession of a brood of *O. dilutata* which produced a small proportion of its members in September and these most luckily coincided in their emergence with stragglers of several of my *autumnata-filigrammaria* broods as well as with belated examples of *filigrammaria* itself. I was therefore able to enclose *dilutata* females with F_1 (*filigrammaria* ♀ × *autumnata* ♂) males, F_1 (*filigrammaria* ♀ × *autumnata* ♂) females with *dilutata* males, *dilutata* females with F_2 males of the same cross as well as to attempt reciprocal crosses between *dilutata* and *filigrammaria*; what these matings produced will be discovered below.

The Pairing of dilutata ♀ and the F_1 (filigrammaria ♀ × autumnata ♂) Male.

In this cross over a hundred ova were laid, and although I did not observe the pairing such had evidently taken place, for out of 114 ova seventeen changed colour from green to pink four days after deposition. This proved their fertility but, nevertheless, when spring made its influence felt, instead of turning to the dark steel blue of ova developing normally they collapsed and assumed a rusty hue and produced no larvae.

The Reciprocal Pairing to this.

Pairs caged up simultaneously with the last lot yielded ova, none of which changed colour. They were thus infertile—a fact that might

have been brought about either by a lack of physiological affinity between the possible parents or by a failure to copulate, the former being the more likely explanation, so readily do the *Oporobia* species cross pair.

The Cross between dilutata ♀ and the F₂ Male.

This mating proved, for this set of experiments, a very conspicuous success, for no fewer than 73 fertile ova were laid in the interstices of the muslin cage and hatched in March 1918. I offered them the usual pabulum employed by me, i.e. *Crataegus oxyacantha*, and this, as with all other *Oporobia*, hybrid or pure, was instantly accepted. All of the little larvae reached the second instar, when I began to lose a few. Still, in the end, 46 pupated.

These larvae were gorgeous creatures and far surpassed the magnificent caterpillars of the two *dilutata-autumnata* crosses. They possessed the beautiful green ground with the yellow bands and dorsal red blotches of those forms combined with a darker, olive green shading derived from *filigrammaria*—the whole scheme of colouration contrasting so as to yield a very striking effect. In the possession of this rich garb the larvae showed the presence of the three contributing forms *autumnata*, *filigrammaria* and *dilutata*.

They went to earth and spun cocoons in no wise unlike those of their congeners, and every single larva produced a fine healthy pupa which remained alive until late in August when the maturation divisions ought to have been proceeding. Then the fatal want of viability so often the bane of hybrid pupae in the production of which *dilutata* females have taken part exerted its influence, and every pupa died, just as is one's experience, with but rare exceptions, in the crosses referred to. Fortunately enough, to a careful observer the determination of the sex of pupae, even of small Geometrid pupae like these, presents no great difficulty, and it was readily ascertained that all of the 46 pupae were males—a result entirely in agreement with the composition of ordinary broods reared as the outcome of a pairing between *dilutata* ♀ and *autumnata* ♂. This observation determines that, in the power of the male sex gene, there is no significant difference between any derived from the *F₂* ♂♂ and those of pure *autumnata*.

The Pairing of filigrammaria ♀ and dilutata ♂.

Ova of this parentage were obtained with equal facility, but the number of salmon pink ones noted when the cage was opened only amounted to 19 out of 97. Clearly the pairing had been a success, but

from its meagre results in fertile eggs the physiological affinity between *dilutata* and *filigrammaria* must be exceedingly slight. Contrasting this with what is seen in the parallel *autumnata-dilutata* cross, where we obtain 100 %, fertile ova, and with care an equal number of imagines, we see that the relationship between *filigrammaria* and *dilutata* is of a different order from that between *autumnata* and *dilutata*. From this it follows immediately that there is a definite physiological difference between *autumnata* and *filigrammaria* lifting the latter to a higher evolutionary level than the former—a fact which the perfect fertility of the two forms and their various crosses and back crosses could not have revealed save in the minor disturbance in the F_1 hybrid gametogenesis.

From the 19 fertile eggs five larvae hatched, and of these four died without feeding; the fifth struggled into its second instar and then followed the majority, their weakness thus confirming the greater divergence between *dilutata* and *filigrammaria* as compared with that between *dilutata* and *autumnata*.

The Pairing between dilutata ♀ and filigrammaria ♂.

This cross pairing gave absolutely no fertile ova in 1917; a repetition, however, in 1918 has provided me with a brood of which at least 20 %, have changed colour and may possibly hatch during the present spring. As far as I have gone, the evidence of the present cross simply reinforces that of the last.

20 %.

The Crossing of Cheimatobia boreata ♀ and O. autumnata ♂.

Owing to the obvious parallelism between the relationship of the genera *Cheimatobia* and *Oporabia* and that between *Nyssia* and *Lycia*, it occurred to me that hybridity between the first named generic pair might be feasible. Moreover, I considered that if this were so, further information might be gained as to the inheritance of apterousness in a group far removed from the well worked Bistoninae. In pursuit of these possible crosses I caged reciprocal pairs of *Cheimatobia boreata* and *Oporabia autumnata* together and awaited events.

In the cage containing *boreata* males and *autumnata* females not a single egg was laid; nor was the matter greatly improved in the other cage. Instead of tucking neat little cakes of ova in the folds of the muslin the *boreata* females scattered their eggs irregularly over the cage. This occurrence is generally to be regarded as a certain indication of failure in fertilisation, produced either by oviposition without copulation or by some mechanical hindrance to the passage of spermatozoa from the bursa copulatrix through the ductus bursae. In this

case the latter is the correct explanation for seven ova passed from green to pink only to fail to develop in spring.

Similar attempts to pair *O. autumnata* and *Cheimatobia brumata* proved utterly futile, no ova appearing at all.

IV. SUMMARY.

(1) The genus *Oporobia* is of Boreal origin and distribution; it comprises within its limits in its British range two species, *Oporobia autumnata* and *O. dilutata*, each possessing a well defined subspecies and numerous local races.

(2) All of these forms, no matter what their value, display enormous variability, and their variations occur in parallel series.

(3) All develop melanic and melanochroic races and aberrations.

(4) It is suggested that the subspecies *Oporobia filigrammaria* was evolved from *O. autumnata* on non-glaciated areas to the west of the British Islands of today; this event was caused during the Glacial period by the action, direct and indirect, of changed climatic conditions.

(5) The genesis of local races, it is further pointed out, is brought about by natural selection limiting the range of variation by the elimination of genetical strains less protected in any given habitat.

(6) Almost certainly, many of the changes exhibited, both those of racial and those of subspecific value, are true Lamarckian effects. In particular, food instincts in *O. filigrammaria*, period of emergence in the pinewood race of *O. autumnata*, are only explicable on such a basis.

(7) The differences in size between the various local races of *O. autumnata* are shown to be ontogenetic and to depend on the food plant.

(8) Such characters as mark both subspecies and local races, save that of size, are proved experimentally to be germinally fixed.

(9) Genetically distinct strains exist within the local races as was demonstrated by experiment.

(10) It is urged that the currently accepted explanations of melanism, in which the inducing cause is stated to be moisture followed by natural selection directed by the darkened resting places in manufacturing and rainswept areas, do not adequately account for the phenomenon, the premises for such an argument not having been correctly determined.

(11) To replace this theory it is suggested that changed metabolism favouring resistance to, or actually induced by, the use of food contaminated with metallic salts and other compounds affords a more comprehensive explanation.

(12) The influence of natural selection in establishing melanism, when once developed, is not excluded, although the results from prolonged and exhaustive work on *Polia chi* showed that no selection, favourable either to dark or to light forms, took place in the day time from 5.30 A.M. to 7.30 P.M.

(13) The inheritance of melanism in the genus *Oporobia* is not on Mendelian lines.

(14) The inheritance of the carpet band in the *latifasciata* form of *O. autumnata* is on a sex-linked basis exactly the same as that of the *lacticolor* aberration of *Abraxas grossulariata*.

(15) In all probability the inheritance observed in the crosses between *O. autumnata* and *O. dilutata* is likewise of the sex-linked type; it may, nevertheless, be influenced by mitotic anomalies.

(16) To the *F₂* generation and in the back crosses the hybrids between *O. autumnata* and *O. filigrammaria* showed a perfect blend, no traces of Mendelian segregation being determinable.

(17) The evidence of the *autumnata-filigrammaria* crosses afforded no support to the multiple factor theory of size inheritance.

(18) In the *F₃* generation a delayed or pseudo-segregation is manifested in which a portion of the brood still remain intermediate whilst the remainder appeared in a uniform pseudo-mutational guise. This strongly recalls the behaviour of *Oenothera Lamarckiana* and suggests that the phenomena displayed by that plant are those of hybridity and not of mutation.

(19) A female from the intermediate portion of the *F₃* lot possessed three antennae.

(20) In the back crosses of the *F₁ filigrammaria × autumnata* lots one back cross with *autumnata* sufficed to restore the *autumnata* condition; on the contrary, it required the operation to be repeated twice to bring the insect back to the *filigrammaria* facies.

(21) In the *autumnata-dilutata* crosses very great disturbances were observed: (1) the females in the cross between *O. autumnata* ♀ and *O. dilutata* ♂ emerged three months before the males and possessed no ovaries; (2) the reverse cross rarely produces females, never more

than one per brood; (3) when such are encountered they are indistinguishable from pure *O. autumnata*, are fertile, never (no matter how paired up) behave otherwise than as pure *autumnata*; (4) the *dilutata* ♀ × *autumnata* ♂ lot display a great lack of viability in the pupal condition.

(22) Both sets of males are fertile but no imago has ever been reared from back crosses in which they took part.

(23) A larva endowed with wings appeared in one of the *autumnata* ♀ × *dilutata* ♂ broods.

(24) Certain crosses including all three forms *autumnata*, *filigrammaria* and *dilutata* were obtained; owing to the influence of the *dilutata* female used in their production, the same failure in viability as marked the F_1 lot from *dilutata* ♀ and *autumnata* ♂ was manifested.

(25) The crosses between *O. dilutata* and *O. filigrammaria* failed, apparently through lack of physiological affinity.

(26) The haploid chromosome numbers of *dilutata*, *autumnata* and *filigrammaria* are 30, 38, 37 respectively.

(27) An almost perfect reduction division takes place in the gametogenesis of F_1 *filigrammaria* ♀ × *autumnata* ♂ hybrids, only one or two chromosomes failing to find mates.

(28) No pairing of homologous chromosomes takes place in preparation for the maturation divisions of either of the F_1 *dilutata* × *autumnata* hybrids; no reduction division, therefore, occurs.

(29) Bacterial disease in which even the germ cells were affected attacked the larvae in many cultures; in such broods gametogenesis was postponed, thereby necessitating delayed emergence. Though infected, females of the cross *autumnata* ♀ × *dilutata* ♂ appeared at their accustomed time.

(30) Fertile ova were obtained in the intergeneric cross between *Cheimatobia boreata* ♀ and *O. autumnata* ♂; all, however, failed to hatch.

(31) No ova were obtained from the reciprocal cross to this or from either of those possible between *Cheimatobia brumata* and *O. autumnata*.