On the Cross-breeding of Two Races of the Moth Acidalia virgularia.

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A. INTRODUCTION.

The general interest which has been aroused of recent years by the various researches which have been undertaken in investigation of the working of Mendel's Law of Heredity, and the adaptability of the Order Lepidoptera to such investigation, have led us not only to reconsider the results of some earlier and undirected experiments in moth-breeding, but also to seek out some peculiarly suitable species in order to take in hand a more exhaustive course of study along the lines most likely to yield further results in elucidation of Mendelism.

Résumé of some Previous Rearing Experiments.

Perhaps a brief reference should be made to our previously recorded attempts at pedigree-breeding.

Lasiocampa quercûs.—Crossings of the various local races were carried out extensively by A. Bacot and J. C. Warburg in 1896–1900, and the results of their work detailed in 'The Entomologist's Record,' vol. 13, pp. 114–116, 237–240, 256–259, 313–317, 338–342. The outstanding feature, as regards a possible bearing on Mendelism, is that two races from the same geographical region, when hybridised, produced progeny that segregated into the two parent forms, whereas when the southern French var. *meridionalis*, Tutt, was crossed with the Scottish var. *callunæ*, Palmer, no such segregation occurred, the larvæ being of an intermediate type.

Forres — Triphœna comes (Agrotis comes, Stgr. Cat.).—Some rather unsystematic breeding experiments with the interesting Forres forms of this species were made in 1902–1903 by ourselves and others, and are recorded in 'The Entomologist's Record,' vol. 15, pp. 217–221 ; vol. 16, pp. 1–5. The progeny from two wild melanic females segregated, that from ♀ A being divisible into 74 typical and 93 melanic, that from ♀ B into 39 typical and 22 melanic. From brood A offspring was obtained, namely, a batch from a single melanic pairing and a batch from melanic " stock " ; the former gave 25 typical and 52 melanic, the latter 20 typical* and 48 melanic;

* " Nine " in 'Ent. Rec.,' vol. 16, p. 3, line 19, is a *laps. cal.* or misprint for " seven."—L. B. P.

the total, therefore, 45 typical and 100 melanic. Thus the segregation was Mendelian in its completeness, but less so in its proportions.

Cluny.—A little later, A. Bacot followed up this experiment with another on the same species, this time with material from Cluny, Aberdeenshire. The results are recorded and discussed in the 'Proceedings of the Entomological Society of London' for 1905, pp. lxvii–lxxi,* and more briefly in 'The Entomologist's Record,' vol. 17, pp. 340–341. In the generation F^1 60 per cent. of non-melanic against 40 per cent. of melanic were reared from melanic ♂ × non-melanic ♀. In F^2 100 per cent. non-melanic appeared from non-melanic parents, the melanic ♂ grandparents showing no influence; on the other hand, from extracted *melanic* pairings of like parentage, F^2 consisted of : in two broods, 30 per cent. non-melanic to 70 per cent. melanic ; in another brood, 21 per cent. non-melanic to 79 per cent. melanic. In F^3, so far as tested, both forms bred true, *i.e.*, two pairings of non-melanic × non-melanic produced non-melanic offspring only (6 and 22 specimens respectively), and two pairings of melanic gave melanic only (24 and 12 specimens respectively). The strain was becoming weakly through inbreeding, and here died out. There is some suggestion here that non-melanic is recessive to melanic, though some of the proportions are rather inexact.

Xanthorhoë ferrugata (Coremia unidentaria).—A long series of experiments, extending from 1894 to 1898, was undertaken by L. B. Prout with a view to obtaining light on the curious colour-dimorphism of this species, and the results have been published in considerable detail in the 'Transactions of the City of London Entomological and Natural History Society' for 1897, pp. 26–34, and Tutt's 'British Lepidoptera,' vol. 5, pp. 61–64, and summarised in a later memoir, entitled " *Xanthorhoë ferrugata* and the Mendelian Hypothesis " ('Trans. Ent. Soc. Lond.,' 1906, pp. 525–531). These showed, as Mr. L. Doncaster pointed out in an interesting supplementary note ('Proc. Ent. Soc. Lond.,' 1907, pp. xx–xxii), *roughly* Mendelian proportions on the assumption that the black form was recessive to the purple. It seems to us curious, however, in spite of the large percentage of deaths which introduced a factor of indefiniteness, that one pairing of heterozygotes (No. 3 on p. 528 of the paper) should have yielded in F_1 11 specimens showing the recessive coloration as against only 6 showing the dominant—the "expectation" being 4 recessive against 13 dominant, or at best 5 against 12. At any rate, the species shows nearly complete segregation, and will be a valuable one for future Mendelian research.

C. dominula.—We may further mention that Mr. L. W. Newman, of Bexley, a careful and successful breeder of Lepidoptera, has recently observed

* On p. 13, line 8, " 45 % " is a misprint for " 40 %."—L. B. P.

apparent Mendelian dominance in the typical form of *Callimorpha dominula* over its yellow-hindwinged aberration *rossica*, and of *Abraxas grossulariata* over the aberration *varleyata*. He has very obligingly furnished us with statistics, so far as the experiments have yet gone; and as they are hitherto unpublished, we take this opportunity of putting them on record. Of *C. dominula*, a type ♂ × *rossica* ♀ paired in 1906 produced in 1907 a brood consisting entirely of typical specimens; a pair of these gave in 1908 the following result: 34 typical, 10 ab. *rossica*—there was a great mortality among the larvæ before and during hibernation, fully 60 per cent. dying. Of *Abraxas grossulariata*, a type ♂ × *varleyata* ♀ paired in 1907, produced in June–July, 1908, a brood consisting entirely of typical specimens; pairings from these gave, as a partial second brood, October–November, 1908, 24 of the type (including one aberrant but *not* varleyata) and 7 ab. *varleyata*—the rest of the larvæ now hibernating.

After some consultation we decided upon the small geometrid moth known as *Acidalia* (or *Ptychopoda*) *virgularia*, Hüb., as meeting the essential conditions. There are, be it observed, practical difficulties to be encountered with many species, which have been overlooked by theorisers on the nature of the work that *ought* to be done by Lepidopterists. Thus many moths are exceedingly difficult to pair in confinement; many are extremely averse to inbreeding, so that an inbred strain cannot be continued beyond two or three generations; many are difficult to bring through the winter, or require food-plants which are not always obtainable.

Convenience in Rearing.—*Acidalia virgularia*, on the other hand, will feed, apparently, on almost anything belonging to the vegetable kingdom, leaves of all sorts—whether fresh or withered—sliced carrot, etc., proving equally acceptable to it; it pairs very readily, is continuously-brooded throughout the summer, feeds up rapidly and generally without need of hibernation, and does not deteriorate through continuous inbreeding; moreover, its small size is a practical convenience both for the accommodation of large numbers of larvæ in a small space and for bringing large numbers of the set moths under the eye at the same time. Few, if any, other British species would offer all these advantages to the same degree; and as *Acidalia virgularia* produces in the south of France a race so different-looking from the British that more than one British field naturalist on seeing it has failed to recognise even the species, it is not difficult to trace the influence of the respective parent strains in crossings.

Origin of Stock.—Ova and pupæ of the southern French form were kindly supplied by Mr. H. Powell, F.E.S., from Hyères; wild moths of the London

b 2

form by Mr. J. E. Gardner, of Clapton, N.E.   The former race is distinguished by its white or cream-coloured ground, almost devoid of grey dusting, and scarcely variable except in the intensity of the transverse black lines, which may be strong (the tendency in the particular strain with which we worked), or broken up into dots, or obsolescent; the latter is variable within limits, but always with the pale (not white) ground-colour profusely dusted with dark grey atoms, whether these be uniform throughout or more concentrated in certain areas.   The Hyères form is therefore described in our experiments as "light" (L), the London form as "dark" (D).   It is necessary to add that more or less intermediate phases of variation occur in some parts of Germany, Italy, etc., so that we have been dealing with *local races* rather than fixed recurrent "aberrations" or with incipient species.

The first cross-pairing was obtained on June 21, 1906, and filial generations I–X (F_1 to F_{10} on the well-known Bateson method) appeared from August, 1906, to November, 1908.   Altogether, 5531 specimens have been analysed in preparing these notes, so that they may be regarded as fairly comprehensive as an indication of the behaviour of this particular cross-pairing.

B. STATISTICAL RESULTS.

General Remarks.—Altogether our breeding of *Acidalia virgularia* has been carried out to the tenth filial generation, and 5531 specimens have been subjected to careful analysis, exclusive of a few which have been more indefinitely summarised but which are confirmatory of the general results. We feel that we may, therefore, speak authoritatively on the general course of inheritance in the cross-breeding of these races, and that the imperfection of our statistical analysis is not due to ignorance of the forms with which we are dealing, but to the fact that their hybridisation really gives *no segregation capable of analysis by the human eye.*   It is necessary to dwell somewhat on this point.   At first sight it might appear a confession of incompetence to have to state—as we do quite frankly—that our figures are only approximations, and that in many cases a re-count (either by another entomologist or even by ourselves) might easily result in a slight modification of them; but when it is understood that there is, in the cross-breeds, every conceivable intergrade, it must be manifest that the distinction between "dark" and "intermediate" on the one hand, and "light" and "intermediate" on the other, becomes purely one of degree, and it is absolutely impossible to draw a perfectly consistent line throughout.   Having made a special study of the family *Geometridæ* for nearly twenty years, one of us (L. B. P.) can at least claim to have acquired that eye for slight differences in them that will have

safeguarded him against any material error of judgment in the present investigations.

As regards the pure stock, or presumable homozygotes, inbreeding for ten generations, under more or less artificial conditions, has not had the very slightest influence on the pretty Hyères form nor, in the aggregate, on the London form.   Excepting a single dark specimen, which was obviously an accidental importation (perhaps on food-plant, as the moth is so common in Mr. Bacot's neighbourhood), upwards of 400 specimens show not the slightest deviation from the clean whitish ground-colour which characterises the Hyères race.   The dark form, which varies more in a wild state, naturally showed a greater range, and one or two broods, apparently by some accidental selective agency, became lighter than the normal ; but here, again, we can confidently affirm that, among some 400 specimens, none have occurred which could possibly be mistaken for the " light."*   It follows, therefore, that the bulk of those which we have classed as " intermediate " can be with certainty explained as blends originating from the hybridisation.

Crosses obtained.—Cross-pairings were obtained in each generation, usually in reciprocal crosses, and in not a few instances in duplicate.   In many cases the progeny of the crosses was also carried on down to the generation collateral with that of F_{10} from the original cross.   The complete scheme upon which we intended to work may be indicated as follows :—

Pure dark (D).—F_1 to F_{10}.
Pure light (L).—F_1 to F_{10}.
Dark by light (called cross-pairing A).—F_1 to F_{10}.
Light by dark (cross-pairing a).—F_1 to F_{10}.
Dark by light, ex F_1 (B).—F_2 to F_{10}.
Light by dark, ex F_1 (b).—F_2 to F_{10}.
Dark by light, ex F_2 (C).—F_3 to F_{10}.
Light by dark, ex F_2 (c).—F_3 to F_{10}.
Dark by light, ex F_3 (E).—F_4 to F_{10}.
Light by dark, ex F_3 (e).—F_4 to F_{10}.
Dark by light, ex F_4 (F).—F_5 to F_{10}.
Light by dark, ex F_4 (f).—F_5 to F_{10}.
Dark by light, ex F_5 (G).—F_6 to F_{10}.
Light by dark, ex F_5 (g).—F_6 to F_{10}.
Dark by light, ex F_6 (H).—F_7 to F_{10}.

* One curious strain is dealt with separately below, as its actual origin is altogether problematical.

Light by dark, ex F_6 (*h*).—F_7 to F_{10}.
Dark by light, ex F_7 (*I*).—F_8 to F_{10}.
Light by dark, ex F_7 (*i*).—F_8 to F_{10}.
Dark by light, ex F_8 (*J*).—F_9 to F_{10}.
Light by dark, ex F_8 (*j*).—F_9 to F_{10}.
Dark by light, ex F_9 (*K*).—F_{10}.
Light by dark, ex F_9 (*k*).—F_{10}.

Or in tabular form (see p. 139).

The actual hiatus in the carrying out of this scheme will be seen from the details which follow. The number of the dark × light crosses that faded out would suggest some inherent tendency to weakness in this rather than in the reciprocal cross; yet the oldest hybrid of all was a dark × light (*A*) and continued vigorous to the last. None of the hybrid strains was labelled "*D*," this letter being reserved for the pure dark strain.

In addition to these systematic crossings, a few quadroon broods and complex crossings of hybrids were obtained.

Most of the continuations of the broods were from single pairings, but occasionally—as when a number of specimens had emerged simultaneously and we could not be sure that they had not mated unobserved—we bred from stock. The question of the influence of individual parental characteristics as opposed to broader racial ones was not the least interesting in connection with our work.

It is to be remarked that the percentage of deaths in the early stages was generally quite insignificant, and that many of the broods reared to the imago state were so rich in individuals relatively to the fecundity of the species, that our statistics are incontrovertibly much more representative than those obtained from *Xanthorhoë ferrugata*, where the pupal deaths were often enormously numerous.

Since it is impossible to forecast what statistics may ultimately assume unexpected importance, the following record tends to err, perhaps, in the direction of over-completeness. Such deductions as we have been able to draw from the mass of figures will be reserved for the next section of this paper.

BROOD *A*.—This was started in duplicate, one of the strains being lost at F_5. The reciprocal cross (*a*) was not obtained, as we had no dark ♀ of assured virginity.

(1) In the generation F_1 there were 62 specimens, all true intermediates with variation inconsiderable. In F_2, 66 specimens, variation considerable, 5 quite dark (perhaps less *brownish* than the pure Clapton race), others

Gen.	D.	L.	D × L A.	L × D a.	D × L B.	L × D b.	D × L C.	L × D c.	D × L E.	L × D e.	D × L F.	L × D f.	D × L G.	L × D g.	D × L H.	L × D h.	D × L I.	L × D i.	D × L J.	L × D j.	D × L K.	L × D k.
1	×	×	×	×																		
2	×	×	×	×	×	×																
3	×	×	×	×	×	×	×	×														
4	×	×	×	×	×	×	×	×	×	×												
5	×	×	×	×	×	×	×	×	×	×	×	×										
6	×	×	×	×	×	×	×	×	×	×	×	×	×	×								
7	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×						
8	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×				
9	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×		
10	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×

approaching this or mottled or banded with dark; none approaching the pure light form. In F_3, 21 specimens, variation slight, follow their actual parents *very closely—i.e.* all were intermediates. In F_4, 54 specimens, variation rather considerable in ♀'s, less in ♂'s; 2 ♀ dark, much as in F_2; several quite as light as F_1, none pure light. In F_5, 47 specimens, variation rather considerable, none very light, 7 ($4\male$, 3 ♀) dark.

(2) In generation F_1 all were true intermediates, though somewhat variable; a subordinate race-characteristic was perhaps adumbrated, which became more pronounced in a few specimens of each brood from A_2 to A_6, namely, a tendency to darkening in the *outer area* of the wings (a common characteristic of some species of *Acidalia*, such as *A. politata*, etc.). In F_2–F_6 the variability increased, but according to no fixed rule; in F_6 (20 specimens) the range was from almost pure light (very weakly marked) to almost pure dark, with intergrades. Two pairings were obtained in F_6, one of light × light, the other dark × light; the former yielded, as F_7, 47 specimens of remarkable constancy, most of which might be called pure light, three perhaps light-intermediate; the latter yielded, as F_7 (from fine dark ♂ × light ♀), some half-dozen specimens only. F_8, from the former of the two F_7 broods, consisted of 13 pure light and one (♂) intermediate; another F_8, from *stock* (of the latter of the two F_7 broods), also of 14 specimens, differed strikingly from its cousin brood in tone, all being intermediate, and somewhat variable. F_9 was again duplicated, one batch (labelled A ix ⊙), from light parents, consisted of 81, the majority light, but only about 30 per cent. pure light; the other batch (A ix ✳), also from light parents, gave 6 only, all pure light. F_{10} (ex. A ix ⊙), 21 specimens, ranged from light (1 or 2) to true intermediate (2 or 3), the majority light but *very slightly dusted*.

BROOD B.—Carried only to the fifth generation (strictly speaking, the *fourth* generation; but, as shown in our "scheme," it has been thought better throughout to give uniform numbering to collateral lines, *i.e.*, to regard as F_2 the grandchildren of the original stock even though with strain B the crossing of the two races only commenced a generation later, with strain C two generations later, and so on). In generation F_2 there were 14 specimens, variation inconsiderable, all intermediate, lines rather weak. In F_3, 34 specimens, variation not great, similar to parent brood, but 3 or 4 distinctly light—beginning to "throw back" towards ♀ grandparent. For F_4 a duplicate pairing was obtained; one brood, 31 specimens, averaged distinctly paler than F_3, several closely approaching the pure light; the other brood, 52 specimens, also varied little, but more closely resembled the parent brood, only 3 or 4 (♀'s) being whitish the rest intermediate. In F_5, from the

former of the two F_4 broods, 32 specimens varied little, though not absolutely inappreciably, all light, yet not quite so pure as the original Hyères strain.

BROOD *b.*—Obtained in duplicate, one strain carried on to generation F_5, the other to F_{10}.

(1) An interesting strain on account of an apparently hereditary predominance of the female sex, figures therefore given in full. In F_2 (28 ♂, 36 ♀) all were intermediates, though somewhat more variable than most first crosses. F_3 was duplicated; one brood (13 ♂, 17 ♀) showed considerable variation, ranging, in both sexes, from pure dark, through intermediates, to nearly, but not quite, pure light; the other brood (13 ♂, 24 ♀) also varied rather considerably : 3 almost pure dark, a few others approaching these, others intermediate or lightish, 7 with a characteristic facies, almost of the pale, well-lined Hyères form, yet less extreme and less white. F_4, from the former of the F_3 broods, consisted of 14 ♂, 25 ♀ : both sexes quite variable, several ♂'s dark, 1 or 2 ♀'s light (not strongly lined), the ♀'s thus averaging somewhat the lighter. In F_5 (17 ♂, 27 ♀) the range of variation was much as in F_4. Adding the above numbers together, we find that this strain yielded only 85 ♂ against 129 ♀, a proportion of 2 : 3.

(2) This proved on the whole a very stable strain, though generations F_4 to F_6 varied more. F_2 was very uniform, intermediate. F_3 (7 only) similar, may have been a shade darker and a few showed a dark *border*, which became a feature of the strain. F_4 distinctly variable, though not quite reaching either extreme; a dark *central* shade, quite a feature of some, lacking in others. F_5 (19 only) very similar to F_4, but smaller, and perhaps hardly so variable. F_6 (66) strongly variable, particularly in the expression or suppression of the two rows of transverse dots, there being a sudden outcrop of specimens in which they are very pronounced—none such being observable in F_2 to F_5. Where these dots are on a white ground (14 specimens), " pure light " is produced ; the rest are intermediate to dark, none very dark. F_7 consisted of 3 only, intermediate, weakly marked, but 2 with the borders darkened. F_8, 23 specimens, a singularly uniform brood, a phase of " intermediate " without strong dusting or lines of dots, the distal margin often darker. F_9 was duplicated, but both the broods (46 and 11 specimens respectively) closely followed F_8, though a few in the larger brood were a little more heavily dusted. F_{10} was almost a failure, only one (intermediate) specimen coming through.

BROOD *C.*—Continued to generation F_9. In F_3 there were only 3 poor specimens, apparently intermediate, but no exact analysis possible. F_4, a large batch, moderately variable, range from almost pure light to darkish

but hardly dark ; about half tend toward the light side. F_5 are similar to F_4, but perhaps less variable, very few pure light; might in the aggregate be termed light-intermediates. F_6, 36 specimens, are pretty variable, about 11 light (only with a stronger central shade than in the pure Hyères strain); 1 or 2 others nearly as light, weaker-marked; the rest intermediate to darkish, nothing extremely dark. The darkest pair available was used for parentage of F_8. F_8 (4 ♂, 16 ♀) are rather large, variable, the average dark, could perhaps be classified as 11 (3 ♂, 8 ♀) dark, 5 (♀) intermediate, 4 (1 ♂, 3 ♀) light, though not quite pure, but there are very gentle gradations ; duplicate pairings out of F_7 (labelled *C* viii (2) and *C* viii (3)) vary somewhat less, *C* viii (2) (33 specimens) being intermediates, slightly variable in detail, and *C* viii (3) all being possible London forms (*i.e.*, dark), variable only in detail. F_9 was obtained only from the second of the above (*C* viii (2)); the specimens numbered 35, still intermediates, not unlike the parent brood.

BROOD *c*.—Continued to generation F_{10}. F_3 consists of 7 only, intermediates, apparently not variable. F_4 varies from almost extreme light to almost extreme dark, but with intermediates which preclude any possibility of splitting up into darks and lights. F_5 (16 only) is similar, but the preponderating tendency is on the dark side, only one being really light with strong lines of dots. F_6, 29 specimens, is perhaps even more variable, 4 or 5 at least being pure dark, 6 or 7 at least pure light, others nearing both extremes (especially the light side) and a few intermediate. F_7 (from light ♂ × dark ♀) showed quite moderate variation, most being rather uniform, lightish intermediate, 2 or 3 (♂) darker, without being strikingly dark. F_8, 52 specimens, are very variable : about 12 pure dark, about 12 pure light (only with well-expressed central shade), the rest grading through. F_9 was bred in triplicate ; brood *c* ix ⊙, 30 specimens, from intermediate parents, are very uniform, all being possible Clapton forms (dark), only 2 or 3 a little paler than would be normal for Clapton ; *c* ix ✳, 7 specimens, from lightish parents with distinct dot-lines, follow the parents closely ; the remaining brood (stock ?), 56 specimens, shows moderate variability, but mainly intermediate, the few darks and the few lights hardly quite pure. F_{10} was nearly a failure, but 5 specimens ex brood *c* ix ⊙ are all dark, 6 ex *c* ix ✳ all lightish, reproducing their parents' facies.

BROOD *E*.—Only continued for two generations. The original pairing, ex generation F_3, was obtained in duplicate.

(1) In generation F_4 55 specimens were reared, all intermediate, the variation not considerable. In F_5, 83 specimens, the variation is considerably greater, ranging from darkish (not extreme) to specimens closely approaching the pure light strain, though slightly less pure, with central shade better indicated.

(2) In generation F_4 58 were reared, all intermediate and remarkably constant. Excepting the slight sexual dimorphism, the variation might be said to be practically *nil*. Progeny not obtained.

BROOD *e.*—Continued to generation F_7. F_4 consisted of 77 specimens, all intermediate except, perhaps, one brownish ♀, which resembles some of the lightest London forms ; the other 76 exceedingly constant.   In F_5, 49 specimens, the variation is much greater, ranging from a few of each sex quite resembling the London forms to a few whitish, though certainly not pure. F_6, 78 specimens, extremely variable, though not definitely segregating ; a few very dark, several darkish, one darkened in outer area, numerous intermediate, numerous light or lightish, the black dot-lines then generally (not always) well expressed, some with, some without, the dark central shade, 2 or 3 agreeing fully with the pure light strain.   In F_7 only 6 moths were bred, from stock, variable from dark to light.

BROOD *F.*—Continued to generation F_8.   The original pairing was duplicated.

(1) F_5, 29 specimens, singularly enough, acted differently from *all* the other first crosses, being virtually a pure light brood, and we hoped that, for once, the light ♀ parent had acted as a dominant.   Fortunately a large offspring was obtained (from stock) consisting of 150 specimens.   These (F_6) are much more variable than F_5, but cannot be split up into light and dark definitely ; roughly classified, we made 45 light (perhaps a dozen *pure* light), 95 intermediate, 10 dark (none extremely), but the gradations are so extremely slight that a re-count would be almost sure to modify the figures somewhat.   Two pairings were obtained : one brood of F_7 (ex light ♂ × dark ♀) yielded 7 specimens, all more or less intermediate, 3 more dusted than the other 4 ; the other brood (ex light ⚥, with strong dot-lines), 6 specimens, all rather light, but only one with the lines sharp. F_8, from a pair of the lightest specimens in the former of the last-mentioned broods, again proved numerically inadequate, only 7 coming through ; these are rather variable, 6 being on the lighter side (2 or 3 pure, the others grading towards intermediate), the seventh strongly dusted (dark intermediate). Attempts to continue the strain proved unsuccessful.

(2) F_5 here consisted of 47 specimens, the variation not considerable, the general facies being very uniform, but the colour ranging from lightish (not pure) to a lightish intermediate.   Offspring was not obtained.

BROOD *f.*—Continued to generation F_{10}, though then on the verge of extinction. F_5, not variable, would certainly be classed as true intermediate, though rather on the light side. F_6, 64 specimens, is much more variable, two or three being pure light, several others closely approaching it, many

intermediate, and a few rather dark. F_7 (ex light ♂ × dark ♀) consists of 32 specimens, extremely uniform, all intermediates, with fairly distinct dot-lines. F_8, 44 specimens, again vary, yet with no absolutely pure white, and only 3 or 4 very *strongly* dark-dusted, nothing extraordinarily dark. Duplicate pairings were here obtained; from a rather dark ♂ × rather light ♀, sprang, as F_9 (labelled *f* ix ⊙), 28 specimens having a similar range to F_8; from an apparently intermediate pair, the ♀ darkened in outer margin, 33 specimens, rather constant, intermediate, nearly all well dusted on a whitish ground. F_{10}, 2 specimens only, agree with the F_9 brood last mentioned, from which they sprang.

BROOD *G*.—This cross was obtained, but not propagated beyond the single generation (F_6). The brood consisted of 69 specimens, slightly more variable than most first crosses, yet in no way startling. Most are quite normal intermediates, 2 or 3 might better be classed as dark, yet not extreme,

BROOD *g*.—Continued to generation F_{10}. In F_6, 35 specimens, the variation is inconsiderable, all being intermediate, though such variation as there is is towards the "light" side. F_7 was obtained from a lightish pair, and yielded 4 lightish specimens. F_8, 47 specimens, was again rather constant, a light-intermediate. F_9 was obtained in duplicate; one batch (labelled *g* ix ⊙, parents rather weakly marked) consisting of 18 specimens, intermediate, nearly all weakly marked, the colour ranging from darkish to lightish without extremes; the other batch (*g* ix ✳, from a better-marked pair) considerably variable, 49 specimens, mainly well-lined, about 12 almost the pure Hyères form, 3 or 4 approaching the London form, many intermediate. F_{10}, 47 specimens from the last-named brood, follows it well on the whole, nearly all being well-lined, though there is much variation in tone and many (especially of the darker ones) are rather strongly darkened towards the outer margin.

BROOD *H*.—Continued to the second generation of the cross, that is, to F_8. F_7, 56 specimens, is very constant, and very typical of the normal "first cross"—all intermediate. F_8, 49 specimens, is very variable; hardly any are quite pure light, only 1 or 2 pure dark (and not very intense); but there is almost every other variation, in size, strength of markings, general facies, and ground-colour.

BROOD *h*.—Continued to generation F_{10}. In F_7, 12 specimens, the variation is very slight, all being lightish intermediate. F_8, 36 specimens, is decidedly variable, the range being from pure light to darkish intermediate, with the usual intergrading. F_9 was duplicated; one batch (from light, well-lined parents) yielded 17 specimens, variable from pure light (though not intensely white) to intermediate, 11 or 12 having the lines rather strong; the other

batch yielded 16 specimens, hardly variable, intermediate to light-inter-mediate, weakly lined for the most part.   From the former of these batches sprang, as F_{10}, a brood of 17 specimens, rather constant, with a uniform facies which struck one as recognisable even when they were emerging ; all are intermediate in colour, the dusting weak, the lines rather strong.

BROOD *I*.—Obtained but not carried on.   The single family (F_8) consists of 46 specimens, intermediate, decidedly constant.

BROOD *i*.—Continued to generation F_{10}. F_8 consists of 22 specimens, rather constant, normal intermediates. F_9 was obtained in duplicate ; from one pair (labelled *i* ⊙) resulted a very variable brood of 32 specimens : 5 or 6 pure light, others near, 7 or 8 pure dark (some quite extreme), others near, and various intergrades; from the other pair (labelled *i* ◇) another variable brood, of 12 specimens only, mostly lightish-intermediate, 1 almost pure light, though slightly brown tinged, 1 pure dark, 2 darkish. F_{10} was reared from both these broods ; that from the former consisted of 44 specimens, intermediate to dark, presumably from some of the darker examples among the parent stock ; the latter of 25 specimens, varying in colour from white to intermediate, yet with a most conspicuously definite facies, all being well lined, with the central shade strong and clear cut in addition.

BROOD *J*.—F_9, 29 specimens, intermediate to lightish-intermediate, fairly constant. F_{10}, 5 only, certainly variable, though without extremes—altogether too few for generalisations.   The reciprocal cross (*j*) was not secured.

BROOD *K*.—Obtained in duplicate.   Both batches (56 and 38 specimens respectively) normal intermediates, the variation slight.   Some undersized specimens look a little pale, but this is because of their weak scaling.

BROOD *k*.—40 specimens, variation moderate, from light-intermediate to dark-intermediate.

The quadroons and other irregular crosses have next to be briefly dealt with.   In the first filial generation pure light ♂ was crossed with hybrid ♀ (out of the brood described as *A*, number (2) in this paper), and the strain carried on for four generations (F_2 to F_6).   It continued "intermediate," with the variation appreciable but not considerable, only in F_6 there were more of the whiter specimens.   In generation F_6 this quadroon race was crossed with the hybrid race called *f* in this paper ; the variation in the offspring (F_7) was only very moderate, ranging from light to lightish-intermediate.

Also in generation F_6, crosses of $b \times c$, $b \times f$, and $G \times C$ were obtained, but only $b \times f$ was followed up to subsequent generations.   All these three were

interesting, as in each case both the parents were more or less extreme, the ♂'s light and the ♀'s dark; the offspring of $b \times c$ (16 specimens) varied little, all being intermediate or lightish; that of $G \times C$ (4 specimens only) much more, the single ♂ bred being darkish, the 3 ♀'s light, weakly marked. In this generation (F_7) the specimens of $b \times f$ (34 in number) varied little, the range being from lightish-intermediate to lightish, almost reaching the pure Hyères form; the characteristic dark border of the parent strain b (2) entirely disappeared. In F_8, 47 specimens, the variation was considerably greater, ranging from pure light (about 8) to pure dark (2 or 3), the majority intermediate, and the extremes not very intense. F_9 was obtained in triplicate; from a light pair (especially the ♀) sprang a brood of 34 (labelled bf �«» ix), hardly variable, all light or lightish; from a somewhat intermediate pair a brood of 44 (labelled $bf \odot$ ix), variable, from lightish (not extreme) to dark—about 8 that might be likened to average London specimens; from stock a batch of 23 (labelled bf ⊗ ix), slightly variable, all light or lightish except 1, which is intermediate, brown. In generation F_{10} one brood was raised, simply labelled bf x, the note of its *exact* parentage having unfortunately been mislaid; it consists of 32 specimens, nearly pure light and not varying much, a few virtually of the Hyères form, but the larger number with a fairly distinct central shade.

In generation F_8 a pairing was obtained between a ♂ out of brood H (intermediate or darkish, weakly-marked) and a ♀ out of brood c (intermediate or rather light, the central shade distinct). In generation F_9 a brood of 33 appeared, rather variable, from light-intermediate to dark (not intense), mostly weakly lined, a few strongly freckled. Their progeny (F_{10}, 19 specimens) are also variable, from light (3) to dark (5); 4 are intermediate, fairly well scaled, the rest more or less poorly scaled, weakly-marked.

It remains to notice a strain which must be treated as of uncertain ancestry, and which originated in F_6 and has been carried on to F_{10}. It was believed to have sprung from pure dark ancestry, a number of hibernating larvæ of F_3 in that strain having fed so slowly as to be still in the larval state when their nephew-brood of larvæ (*i.e.* pure dark F_4) arrived, and having been mingled therewith; but in F_6 the behaviour of the strain was so unprecedented that we feel forced to imagine there must have been some accidental importation of hybrid or light material, inexplicable though it is, considering the care that was taken. Of course, it is open to those who so desire to assume that there was here a true mutation, but as the white form has never been known in Britain, and inbreeding has not changed the rest of our pure dark stock, we ourselves cannot regard such a view as even worthy to be provisionally entertained, unless confirmation be forthcoming.

Brood D ✳.—This aberrant stock in F_6, which we called D ✳ vi, consisted of 41 specimens, 18 of them pure light, 2 nearly pure but browner in ground-colour, a few normal intermediates, and about 12 typical dark. By analogy with the rest of our material this would suggest being a second generation from a hybrid. On account of the riddle of its origin, 5 pairings from this brood were obtained, 2 others attempted proving infertile.

(1) From a light pair sprang, in F_7, a brood of 16 (labelled D ✳ vii (2)) all light, about half being quite extreme, the rest slightly more dusted.

(2) From another light pair, F_7 consisted of 47 (labelled D ✳ vii (3)), rather variable from pure Hyères form (4 or 5) to intermediates. Their progeny in F_8 (64 in all, from different pairings) varied conspicuously, the *majority* light to intermediate, perhaps only one really *dark*, and that not very extreme. In F_9 (two broods, 67 specimens) the variation was less, only ranging from light to intermediate; all the four actual parents were more or less light. In F_{10} (three broods, 96 specimens) the variation again increased somewhat, but with the lighter forms still in the ascendant and thoroughly dark ones only occurring, and sparingly, in *one* of the three broods—labelled D x (1) ⊙, and noteworthy for its darker average tone than its parent brood.

(3) From yet another light pair, F_7 (26 specimens, labelled D ✳ vii (4)) bred absolutely true to the extreme parent form (= wild Hyères type). One pairing produced, in F_8, a further brood of 24, all equally pure, unfortunately lost here. Another pairing produced, in F_8, a very *variable* brood of 45—15 pure light, about 15 others lightish to light-intermediate, the rest darker, 1 or 2 practically "dark." From a pairing of rather light, well-marked specimens in the latter of these (the variable) was obtained, in F_9, a brood of 38 varying much less than the parental one, indeed pretty constant light-intermediate, rather well-lined. Their offspring (F_{10}, 42 specimens) would nearly all be classed as "light-intermediate" in some sense, yet wonderfully variable within this limit; whitish weak-marked, similar examples but greyer behind the outer line, moderately light strong-marked, intermediate (2 or 3 strongly-marked, 2 or 3 weaker-marked) are all represented.

(4) From a dark pair, only three specimens were reared in F_7 (labelled D ✳ vii (6)). These were darkish intermediate. Fortunately a ♂ and a ♀ emerged together and copulated. The resultant F_8 (49 specimens) varied a good deal, one only being pure light, the rest about half intermediate (a few light-intermediate) and half darkish to dark, but with intergradations. F_9 (78 specimens, 3 broods) was moderately variable, but all should be classed as broadly "intermediates." F_{10} (49 specimens) was variable, ranging from intermediate to *dark*, the average darker than in F_9; perhaps about

20 would be called dark, but there is no clear line of demarcation. The return to a darker type might be called atavistic, but more probably the actual parents—which are not known—happened to be among the darkest ones of F_9.

(5) From a dark ♂ × light ♀, F_7 consisted of 21 specimens (labelled D ✳ vii (7)), all normal intermediates, with no appreciable variation. The strain was unfortunately lost.

C. General Conclusions.

From the foregoing mass of detail a few facts emerge with conspicuous clearness, and certain other points are sufficiently suggested to be worth putting forward, at least tentatively.

In the first place, there is most certainly no Mendelian dominance in coloration in the cross of the dark (London) race of *Acidalia virgularia* with the light (Hyères) race. With remarkable persistence, a first cross of the pure races produced a form *intermediate in coloration*. The sole exception, out of two dozen such crossings, is the brood noticed above as F, No. (1).

But, in the second place, it is perfectly well known that colour-dominance is not the essential feature of Mendelism. As Mr. Bateson says,[*] "The essential fact which Mendel discovered is the segregation of characters in gametogenesis." Now, as the intermediate form, which was so nearly universal in the first crosses, did not appear in either of the "pure" strains, it may well be taken as the normal manifestation of hybridity in this blend, corresponding to the "blue" Andalusian fowl and other well-known cases ; and it is certainly noteworthy that a rough resolution into a wider range of forms proved quite general in the F_2 generation. That proportions did not agree with expectation might be due to defective analysis. For example, the said "hybrid" or "intermediate" might have a wider range of variation than had been discovered by the investigators, who might thus have referred some hybrids to one of the "pure" forms. But a glance at our actual results convinces us that it is not generally too *few* intermediates that we obtained in F_2 but too *many*; and fortunately we know very accurately the limits of the variation of at least one of the pure races (L), so that there seems no chance, on the assumption of gametic purity, of our having classified pure "lights" as "intermediate." It is, however, further noteworthy that some, at least, of the extracted strains (light × light, ex hybrid, viz., A (2) in generation F_7,[†] ? B in generation F_5 (1), $b × f$ ◻ in generations F_9 and ? F_{10},

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[*] 'Progressus Rei Botanicæ,' 1906, p. 368.

[†] But if this was really "pure" whence came the single "intermediate" ♂ in its offspring ?

? D ✳ (1) in generation F_7, ? D ✳ (3) in generations F_7 and one section of F_8 ;* dark × dark, ex hybrid, viz., C (3) in generation F_8, c ⊙ in generations F_9 and F_{10}) attained a considerable standard of purity; and also that a few of the extremest (light × dark) pairings among hybrids (such as $b × c$, $b × f$, D ✳ (5), and ? A (2) in generation F_7) were the most reliable in producing again genuine intermediates. ($G × C$ was possibly an exception, but the parents here were not so extreme in colour as to render hybridity unthinkable.)

Another fact that can be stated with certainty is that our experiments have revealed no other decisive " reversion to type " than the kind which Mendelism would demand; the intermediates have been quite as stable as Mendelism would expect in hybrid pairings. Whatever be the explanation, it would appear that the hybrid form cannot be " bred out "; except in cases where a selective mating has been employed and the rest of the brood allowed to die out, intermediates have continued to appear through all the generations.

Without desiring to dogmatise, we feel it is necessary to remark that neither of the points last considered—the obtaining of a comparatively uniform type by selective mating and the persistence of intermediates under other circumstances—belongs exclusively to any one theory of heredity, while such occurrences as those noticed in the footnotes on broods A_2 and D ✳ (3) are harder to reconcile with Mendelism than with, for example, the Galtonian view. On the whole, the apparently large responsibility of direct parenthood suggests to us the idea of some such principle as is involved in the well-known formula of one-half the characters from the parents, one-fourth from the grandparents, etc.

Over and over again some trifling race-characteristic has interested us in a particular strain, including—besides the tendency for some broods to favour the slightly darker variations and others the lighter—obvious differences in the expression or suppression of the transverse " dot-lines," tendency to develop a dark central shade or a dark marginal area (for instance, brood b (2)), and so forth. Any of these would have been well worthy of minute study, either from a Mendelian or a non-Mendelian point of view, had time and opportunity allowed. We suspect, however, that in large measure they also would be found traceable to direct parentage, for it is certain that in some cases cousin-broods differ quite materially in some of these characteristics, and that a reference to their parents shows how closely these are followed; see, for instance, some of the references under the statistics of broods c, g, h, etc. The sex-predominance in brood b (1) was another peculiarity which deserved more attention than it received.

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* But how would Mendelism account for the (very variable) *other* section of F_s

We noticed also that the larvæ were very variable, and it is not impossible that an analysis of their variation might yield some results of value.

As a final impression, we would suggest that our failure to find Mendelian inheritance at work was due mainly to our bringing together two comparatively remote geographical races (as with Messrs. Warburg and Bacot's *Lasiocampa meridionalis* × *callunæ*) and that we, personally, now only expect to find segregation in the case of crosses of two forms occurring together (like the two forms of *Triphæna comes* or those of *Xanthorhoë ferrugata*), where a long course of natural selection has presumably eliminated the intermediates. We pointed out in the introduction that just such intermediates of *Acidalia virgularia* as were produced artificially by crossing our specimens from London and Hyères (localities where they are apparently quite unknown in a wild state) do occur in a state of nature in other parts of its geographical range.

A few pairings which occurred in generation F_{10} produced ova which have been handed to Mr. W. Bateson in the hope that he may be able to follow up our researches in the species. Unfortunately both the pure strains have been lost, but possibly Mr. Bateson will be able to extract them, by selective pairing, from the new hybrids, which we labelled M xi and m xi.