

Only a single specimen was obtained by Mr. Robert. It agrees exactly with the figs. 14 and 15 above cited, the shell there depicted also having been collected at Corumba. On comparing this specimen with d'Orbigny's types, I have come to the conclusion, in agreement with Mr. Pilsbry, that the change of name proposed by M. Ancey for this shell was not necessary.

BULIMULUS CORUMBAENSIS Pilsbry.

Bulimulus corumbaensis Pilsbry, Man. Conch. ser. 2, vol. xi. p. 68, pl. xiv. figs. 3-8.

The colour, as described by Pilsbry, is fairly typical, but the ground-colour may vary from "opaque white" to a vinous tint, and "the dark brown or corneous longitudinal streaks" are sometimes replaced by pellucid stripes. The form also is variable, some specimens being broader and more robust than others. Mr. Pilsbry described this species from specimens collected at Corumba by Mr. Herbert H. Smith.

DRYMÆUS PÆCILUS d'Orbigny.

Drymæus pæcilus, Pilsbry, Man. Conch. ser. 2, vol. xi. p. 285, pl. xlix. figs. 49-57.

This species varies considerably in size, form, and colour. Six of the seven Matto Grosso specimens are whitish or yellowish, and most have upon the body-whorl seven more or less interrupted dark zones, the four uppermost being sufficiently disconnected to appear like rows of spots, whilst the three lower ones are but very slightly interrupted. Pilsbry's figure 50 represents this form, except that the spire is hardly acuminate enough. His fig. 53 is rather like the seventh specimen, which, however, is still more darkly coloured.

3. The Present State of Knowledge of Colour-heredity in Mice and Rats. By W. BATESON, M.A., F.R.S., F.Z.S., Fellow of St. John's College, Cambridge.

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With the revival of interest in the experimental study of variation and heredity which has followed the discovery of Mendel's work, Mice have naturally been chosen by several investigators as a subject for experiment. To the breeder mice offer attractions from their small size, cheapness, healthiness, and rapid rate of multiplication. They have further the great advantage that the same male can be simultaneously tested with several females. They are, however, short-lived, $1\frac{1}{2}$ years being a high limit of the breeding age. There are also more serious drawbacks. They are extremely addicted to eating their young. It is not easy to label a live mouse in a permanent fashion, and special

methods have to be adopted for tracing the identity of the individuals, which in such work is indispensable. Another difficulty arises from the fact that mice present few readily estimable features of structure. Also, though there are now many types of colour, few of them as yet exist as pure strains, and hence it is not easy to obtain reliable material with which to begin the experiments. Nevertheless, in spite of these drawbacks, the subject is a good one, and there can be no doubt that our knowledge of heredity can be rapidly extended by experiments on mice. As regards Rats the case is similar, save in one respect, in which there is a very remarkable difference, namely that the colour-types of fancy rats are as yet extremely few. For this reason, though the scope of experiment is reduced in the case of rats, some serious complications are eliminated, and certain fundamental questions, as, for example, the relation of pied to self-coloured varieties, could probably be studied more easily in rats than in mice.

As a great deal of work on these species is now being done, it has seemed to me useful to codify the chief information already at our disposal, and to state as carefully as is yet possible some of the more immediate problems presented by the existing facts.

It would greatly assist discussion of these problems if uniform names could be used for the colour-types. An attempt is therefore made to suggest such names, and to indicate how the types may be recognised. The specimens examined for this purpose have been obtained chiefly from Mr. J. Wilson Steer, of 45 Raleigh Road, Hornsey, N., and from Mr. Atlee, of Royston, Cambs., and I am greatly indebted to both of these well-known breeders of mice for information and assistance. The microscopical examination and discrimination of the types was carried out by Miss F. M. Durham. This work is only in a preliminary stage and, it is hoped, will form the subject of a separate communication.

Microscopical examination shows the hairs of mice to contain numerous minute medullary spaces separated from each other by bridges of keratin. These spaces are arranged in longitudinal rows, the number of which varies from one to four (perhaps five), thick hairs having usually more rows than thin hairs. The pigment is deposited in two ways:—(1) massed in the proximal walls of the medullary spaces, and (2) scattered in the external cortex. Since air bubbles out of the spaces when reagents are applied, the spaces probably open to the exterior.

The pigments in wild *M. musculus* or *sylvaticus* are readily seen to be of three kinds:—(1) Densely opaque *black*. (2) Less opaque *brown*. (3) Transparent *yellow*. The chemical nature of these pigments and their possible relations to each other seem to be quite obscure. If the hairs are cleared of air, the three kinds of pigment can be recognised. On treating with 40 per cent. aqueous solution of potash, the yellow dissolves at once. The brown disappears much more slowly, but is rather more soluble than the black, which can

withstand the treatment more than 24 hours, though ultimately it also (and the keratin) disappears.

The brown may be present in both medulla and cortex; the black is chiefly deposited in the medulla, but may be cortical also, while it is doubtful whether the yellow is ever present except in the medulla.

All these pigments may coexist in the same hair; but hairs are found with only black and brown, others containing only black and yellow. Other types possibly occur. The lighter colour is mostly peripheral (in hairs which contain other colours), but brown often is present in the cortex at levels where the medulla contains black.

In *M. sylvaticus* the condition is similar, but the amount of black is less.

The different colour-types of fancy mice are due to the presence or absence of one or more of these pigments in various amounts. Both the yellow and the brown may exist separately, without any other pigment being discoverable, but, so far, no mouse has been seen having *black* only, some brown being always associated with black.

Each chief type of coloration, black, brown, and yellow, exists in at least two forms—the one more *intense*, the other more *dilute*. The dilution, which affects both medulla and cortex, seems to be due to greater scarcity of the pigment-granules, not to diminution in their size.

The following list includes all the types examined, though some probably remain to be seen. Waltzing mice, so far, have not been examined. The fanciers' names are generally retained, as on the whole distinctive and practical. Owing, however, to the ambiguity in the use of the term "fawn" to denote both "yellow" and colorations containing other pigments, the term "yellow" is used for the type containing yellow pigment only.

1. *Ordinary Cinnamon* (or *Agouti*). The colour of *M. musculus*, having same *three* pigments. Exists in at least two strains, one rather darker than the other. This is doubtless the "grey" of most writers. Pied forms and strains common.

2. *Golden Agouti*. Like (1) but yellower. Contains *brown* and *yellow*, without black.

3. *Sable*. This rather striking type is like (1) on the back, but with yellow hairs interspersed at sides. Flanks almost wholly yellow. Pied with white this colour gives the so-called "tricolor."

4. *Blue-and-tan*. Not examined microscopically. [Probably sable in which black is diluted.]

5. *Chocolate = Plum*. Contains brown alone. May be pied.

6. *Silver-fawn*. A diluted form of (5). Many hairs have colourless tips.

7. *Yellow*. Contains yellow only. Often called "fawn," though this term is also applied sometimes to colour containing brown or black. When dark pigment is present in association with predominant yellow the colour is spoken of as "dingy" or "sooty fawn."

8. *Cream*. Diluted yellow.

9. *Black*. Both black and brown present, without yellow. The bases of the hairs are the darkest, and the black does not extend to the tips of the large contour hairs, which are brown. Hairs behind the ears or on belly are a still lighter brown. Complication arises from the fact that at least two kinds of black exist, known as "black" and "sable-bred black," viz. thrown by sables. These two kinds probably differ in their heredity-properties. Pied forms common.

10. *Blue*. Diluted form of (9); both black and brown pigments coexisting. Blues may be thrown by the "blacks" (not sable-bred) and then breed true. Pied forms exist.

11. *Albino*. No pigment in any part. As albinos, however produced, breed true to the albino character generally, if not universally, individuals of dissimilar origins are often mixed together. One strain at least, that of Mr. Atlee, is recognised in the fancy as having special features of size and shape, and has been kept distinct for many generations.

12. *Black-eyed white*. Strains of this type have been independently produced twice, perhaps oftener. The degree of pigmentation in the eye varies in at least one strain, some eyes being full black, others looking blackish red. Whether the type ever breeds quite true we cannot say. In our experience offspring with small black marks occur (compare phenomenon seen in albino Guinea-pig, p. 76).

13. *Variegated*. In these, irregular *small* spots of black or chocolate occur on a white ground. Such forms are quite distinct from the ordinary piebald and Dutch-marked (viz. like the Dutch rabbit) combinations of colour with white.

In comparing colours care must be taken that specimens are of similar age and in similar moult-stages. Differences of intensity of colour are of course characteristic of different strains, and probably intermediates can be found; but there is no doubt of the practical distinctness of each of the forms enumerated. "Brindling," viz. lighter or even white hairs distributed as ticking, occurs in some of the coloured varieties, as in rabbits, but we have not been able to examine specimens.

As to the age and mode of origin of the several forms little is known certainly. Several conditions are plainly due to resolution of compound characters, such as often follows crossing in animals and plants. The blue, the black-eyed white, and the variegated are certainly productions of the last few years; the rest (? sable) have existed for a long time.

The question how far *M. sylvaticus* has been used in the production of the varieties is a very important one. The experiment was suggested many years ago in 'Fancy Mice' and has probably been often tried. Mr. Atlee has given me a most circumstantial account of a cross with this species made by him nine years ago on black-and-white does, and I feel no reasonable doubt that it

was actually made. The first generation were "agoutis" of very large size. Later generations gave amongst others a strain of blue, and of black-eyed white. A strain of agouti has also been saved from it. He tells me that this formerly had the *white feet*, a character he carefully bred out. Such a cross may have affected the whole race of fancy mice at the present day. Our search for structural characters referable to *sylvaticus*, however, has failed to show any case of *one* pair of pectoral mammæ (as in *sylvaticus*) or any case of *long* hind foot. All specimens examined were pure *musculus* in these features. On the other hand, a feature sometimes seen in fancy mice, and greatly valued by exhibitors, is a *large eye*, much exceeding the size in an ordinary *musculus*. But this eye, though large, is still smaller than that of *sylvaticus*. Nevertheless the large eye is a modern feature in the fancy, and I think it not impossible it may have been derived from a *sylvaticus* ancestor. Further experiment alone can decide this question.

In order to appreciate what follows, the reader must have some acquaintance with at least the outline of the Mendelian principles of heredity. In their simplest expression these principles, as they are exhibited for instance in the experiments of Cuénot (12), are easily comprehended; but when we pass from these simplest phenomena to the more complex facts elsewhere witnessed, we soon reach difficulties which our experimental evidence is as yet only adequate to elucidate tentatively and in part.

Cuénot experimented by making reciprocal crosses between albino, pink-eyed, fancy mice, and wild grey mice (*M. musculus*). He was careful to use *wild* mice in order to be sure that his coloured form was pure. As a result he obtained always and without exception grey mice. In Mendelian terms, grey is therefore *dominant* over albinism, which is called by contrast *recessive*. The first filial generation thus produced, which we may conveniently call F_1 , when bred *inter se*, gave a total of 198 greys and 72 albinos, constituting the second filial generation, or F_2 . The ratio of dominants (D) to recessives (R) is here 2.75 to 1, a fairly near approach to the ratio 3:1, which on the simplest form of the Mendelian hypothesis is to be expected. In other words, the facts are, as Cuénot stated*, in agreement with the supposition that in the formation of the gametes of the hybrid F_1 , there is complete segregation of the grey colour from albinism, and that in both male and female hybrids there are on an average equal numbers of gametes produced bearing each of these two characters.

According to the same hypothesis, the grey mice in F_2 should consist of pure or *homozygous* greys (DD) and of *heterozygous* greys (DR) in the proportion of 1:2.

Cuénot tested this to some extent by breeding the F_2 dominants

* Cuénot's paper seems to be the earliest application of Mendelian principles to animals.

inter se, and found that some pairs gave the expected mixture, while others gave dominants only. Qualitatively therefore the result is the normal one. It is not stated that the "extracted" albinos were tested, but there is little doubt that, in accordance with *almost* universal experience, they would have produced nothing but albinos.

A leading fact illustrated by Cuénot's experiments, viz. the recessive nature of albinism, is borne out by the whole series of experiments under review. The fact is true of albinos in mice, rats, guinea-pigs* (Cumberland, 13; Castle, 7), and rabbits (Castle), so far as experiments have reached. Cases of the production of albinos by coloured rabbits (*e.g.* Polish by Dutch, albinos by silver-greys) are frequent in the fancier's literature. The contrary, the production of coloured animals by albinos, is not, so far as I know, illustrated by a single case, with the following exception. In the later editions of 'Fancy Mice' (Upcott Gill), Dr. Carter Blake, formerly secretary of the Anthropological Institute, commenting on the statement that albino mice of whatever parentage produce nothing but albinos, writes (p. 16) that a pair of albinos produced some brown-and-white, some plum, some grey, and some albinos. If this result occurred under all precautions, it stands alone.

Nevertheless we should be cautious in declaring the result impossible, for in Mendelian experiments the observer must be on the look out for the appearance of a character, elsewhere a definite dominant, *as the consequence of crossing two dissimilar recessives*. Not only may a dominant colour be produced by crossing two forms having a recessive colour,—*e.g.*, purple flowers by crossing the white *Datura laevis* with white *D. ferox*; purple flowers in Sweet-Pea by crossing white "Emily Henderson" round-pollened form with the long-pollened form of the very same white variety; purple flowers in the Stock by crossing two white varieties:—but also a dominant *structural* character, hoariness, may be produced by crossing glabrous (recessive) stocks of different colours, *e.g.*, red and cream, or red and white †. In each of these cases the appearance of an atavistic character occurs as a consequence of the union of gametes bearing dissimilar characters; but the character in which the reversion appears is of a class different from that in which the parental differentiation was seen.

The same may very possibly be true of animals also. But in each of the cases known, the two varieties united, though alike bearing the same recessive character, differ obviously in some other respect; and we know that the cross-bred raised by their union is a heterozygote, *i.e.* a zygote formed by the union of dissimilar gametes. It is, I think, scarcely likely that Carter Blake's case of the mice is really to be so regarded, and on the whole the hypothesis of error is more probable; but the possibility

* Small "smudges" are said to occur irregularly in albino cavies, however pure.

† This statement is based on results of experiments made by Miss E. R. Saunders, as yet unpublished.

that colour may be influenced by structure, and structure by colour, must be remembered.

Naturally we may inquire whether albinism in Man is not a similar recessive. Castle has given evidence pointing in this direction. The occurrence of albinism in the families of first cousins (see Day, Seligmann, &c.) is consistent with this view; but there are a few recorded cases of the occurrence of albinos in the offspring of albinos breeding with normal parents, where the hypothesis that the normal parent was DR is not at all easily admissible. No case of the union of two human albinos is known to me. The matter cannot here be further discussed, and the reader must refer to the literature, the most important paper being that of Cornaz*.

There are a few cases on record where the production of albino offspring by animals and plants must almost certainly be regarded as the occurrence of a new and original variation, though the cause of such sporting is entirely unknown.

We here encounter the first problem calling for experimental study. What is an albino? We know that it appears to form no pigment; but such a body has other characteristics also. While the blood of pigmented animals shows intravascular clotting on the injection of nucleo-proteids, that of the albino is declared to be unaffected. The mountain hare is said in this respect to behave as a normal in its summer coat, but as an albino after the winter change. How these differences are related to the want of pigment we do not know. Such an inquiry offers a wide field for experiment. In particular, we ought to know how the albino or the normal behaves towards the nucleo-proteids of an *albino*, and so forth. However this may be, there seems to be but little doubt that the albino-bearing gametes can generally segregate that character entire, as they divide from the colour-bearing gametes of the hybrid zygote of any colour; and if we knew more clearly what is the real physiological difference between colour-secreting and albino organisms, we might get a clearer conception of the nature of such segregation.

We may consider next the work of Crampe, which is on a large scale and relates entirely to Rats. His latest paper is dated 1885 (10), and consequently is pre-Mendelian in treatment. He bred nearly 14,000 rats, and made elaborate records and tables of conclusions. Many of these observations are readily available so far as they provide simply qualitative as opposed to quantitative evidence; but after many attempts I have not succeeded in unravelling the material enough to group the statistics in Mendelian form †. Though only a sketch can be here given, many of

* The student of albinism who refers to the paper of Legrain (Bull. Ac. Méd. Bruxelles, ix. 1866) should remember that it is the curious instance cited by Darwin (Life and Letters, i. p. 106) as a deliberate invention.

† The figures given (10) pp. 555 & 612 are the likeliest, but even these obviously contain certain heterogeneous elements now not distinguishable with confidence.

these qualitative observations are of great value and will provide a basis for future work.

In rats the Mendelian rules, in their simplest form, are plainly inadequate to express the facts, and we soon meet a number of deductions of specific application, each needing full investigation. Crampe's account is long and difficult to follow. At first sight also it seems not wholly consistent in certain particulars, but the conclusions here summarised seem well established.

Breeding albino rats with wild *M. decumanus*, Crampe found that F_1 might have *one of two forms*, being either a self-grey like the wild type, or grey with white marks. Unfortunately no precise description of this and of the other broken-coloured rats is given, and we do not know the precise extent and distribution of the white*. According as F_1 presented the first or second form, the subsequent offspring produced from F_1 bred *inter se*, differed. The whole series of colours presented by such offspring is arranged by Crampe in seven types, thus :—

1. Self-grey.
2. Grey with white marks.
3. White and grey.
4. White (albino).
5. Black-and-white.
6. Black with white marks.
7. Black without marks.

The self-coloured grey in F_1 gave in their posterity all the types *except 3 and 5*, but F_1 of type 2 gave all seven types.

The nature and cause of the heterogeneity in F_1 is as yet unexplained. Such an occurrence is, however, not rare. In my own poultry experiments for example, the dark feathers scattered in the white F_1 raised between a brown and a white breed may be either chequered or plain black. According as one or the other form appears in F_1 the posterity probably differ, though this point is not yet established in the case of poultry.

The existence of two classes in F_1 indicates in all probability the existence of two classes of gametes, either in the wild *decumanus* or in the albinos, but in which we cannot say. From the evidence, it seems that both forms of F_1 could be produced by the same pair of parents, but I cannot find the fact explicitly stated. Both forms occurred in F_1 not only when *decumanus* was crossed with albino, but also when it was crossed with type 3 and with type 5.

Only the albino could cause all seven types to appear in progeny (F_2 &c.) raised from a cross with the wild type.

The albino was recessive to all the other six types, and albinos of whatever parentage gave nothing but albinos when bred

* First crosses shown me by Miss Douglas were grey except for an irregular but small amount of white on the chest and belly. I take this to be Crampe's type 2.

inter se. This point was elaborately tested. Crampe states that albinos true-bred for some generations behaved differently from extracted albinos, the former being, as he says, merely "absorbed," *i. e.* recessive, on crossing with colour; while extracted albinos gave, as I understand him, a mixture of ancestral forms when they were crossed with other types. This part of his paper (10. pp. 573-5) is difficult to follow; and I cannot find any example showing precisely the nature of the distinction he means to emphasise so far as *albinos* are concerned. We must here await fresh experiments. We readily see, however, that though in respect of its albinism we may regard the albino as always the same, it may obviously be retaining other characters derived from various progenitors. Accordingly we find, as will appear, albinos apparently of the same species manifesting different properties in crossing. I suspect, however, that Crampe is here extending to the albino a generalisation really based on a mistake arising from misconception respecting the phenomenon of dominance. [See note added p. 97.]

We may now, though the evidence is imperfect, consider the significance of the appearance of these many new forms in F_2 . This phenomenon is a most usual result of a cross between distinct varieties. It is the source of the majority of our new garden varieties, and of many at all events of the *colour*-varieties of domestic animals. In general terms we can declare that the result of the cross—the "asymmetrical fertilisation," to speak strictly—is the production of a diversity of gametes. Pending histological research, we cannot tell the origin of the characters borne by these gametes; but from many circumstances it seems inevitable that they must be regarded as created in such a case partly by *resolution* of the character brought in by the dominant—which we therefore call a *compound* character, and partly by the imperfect segregation of that compound or of its components from the recessive character (and its components if it be also resolvable). In most cases the process of resolution is not complete for *all* the gametes; and some of the gametes are bearers of the wholly or partly unresolved character, just as *all* the colour-bearing gametes were in Cuénot's simpler case. The Mendelian hypothesis leads us to believe that the actual numbers of each type of gamete will be on the average definite, and that the union of any two of them will give rise to a zygote of definite character.

The number of types of gametes and their several properties can only be determined on a minute analysis of each member of the series of zygotes by exhaustive breeding. No such evidence is yet complete in any one case, but we see already in certain cases that some of the F_2 are homo- and some hetero-zygous, and we are beginning to suspect the ratios of the gametic forms in a few simple cases.

Returning to Crampe's evidence, though the ratios are quite uncertain, we find that the several types had different properties.

On breeding specimens of each type *inter se* he found the following behaviour:—

Type 1	might give	Types	1	2	4	6	7
" 2	" "	"	1	2	3	4	5
" 3	" "	"			3	4	5
" 4	" "	"			4		
" 5	" "	"			4	5	
" 6	" "	"			4	5	6
" 7	" "	"			4		6

In other words, each type is dominant to albino and the wild type is dominant to all. The grey forms are dominant to the black. The black-and-white of type 5 is recessive to type 6, (black with white markings), but the self-coloured black does not contain type 5. These are some of the deductions from the table. The peculiarities of types 3 and 5 are especially noteworthy and call for fresh experimental study.

It appears that types 3 and 5 could be ultimately bred true. As to 6 and 7 the evidence is not very clear; but as I understand the account, neither was completely freed from throwing the other. The breeding in these types was the least successful and extensive. Possibly they are illustrations of the *Mittel-rassen* of de Vries. It is especially noteworthy that the grey-and-white type 3 and the black-and-white type 5 do not give rise to self-grey gametes or to self-black gametes, a fact found again in mice. We see therefore that there are gametes for black-and-white and for grey-and-white, each of which may behave as a single character and dominate over albino.

Similarly when pure black-and-white was crossed with the wild species, all the coloured types might appear in F_2 but no albinos (10. pp. 555-6). Therefore, in this very important case, when black-and-white of type 5 appeared in the posterity of such a cross, they were *all* homozygotes and produced only their own type (p. 555). This fact may furnish a useful basis for a new experiment. In strict accordance with our expectation, Crampe found that black-and-whites which gave albinos when bred *inter se*, gave albinos if crossed with albinos; but when they did not produce them themselves, they did not when bred with albinos.

The similar variety, grey-and-white (type 3), is always homozygous except when it appears as a dominant containing types 4 or 5. But if I rightly understand Crampe's use of the word "*constant*," type 5 is not produced by crossing type 3 with the wild form, unless it was already brought in as recessive to type 3. On the other hand, type 3 can be produced (in F_2) by crossing type 5 with the wild form. It is most desirable that the properties of these two types (3 and 5) should be fully explored. They give a chance of investigating the resolving powers of a recessive that is not albino, and free from several complications attending the use of the latter.

When we try to picture what is taking place in the resolution

effected by types 3 and 5, Crampe's figures, though too imperfect and irregular to justify a positive statement, show pretty clearly that these particular recessives do not appear nearly so often as 1 in 4; and consequently it is *prima facie* likely that some of the new types of gametes are formed by imperfect segregation, and are combinations containing elements of both the dominant and the recessive—a phenomenon indicated by experiments with other forms of animals and plants (*cf.* de Vries' resolutions of *Antirrhinum*).

These are some of the chief deductions apparent from Crampe's work. Many others will strike a careful reader and are indeed given by the author, but for these reference must be made to the original.

From the want of details the important question of the identity of the several types is not easy to settle, but I think that we may allot Crampe's varieties among the well-known types of rats, with fair confidence, as follows:—

1. The wild *decumanus*.

2. Like *decumanus*, but with a more or less sharply defined white area on the ventral surface (together perhaps with white on the feet).

3. Head and shoulders wild colour, forming the "hood" of the fanciers. This is continued in a broad *stripe* down the middle of the back to a *patch* on the rump. The rest of the body is white. The coloured area may be considerably extended on to the flanks, and more rarely* the dorsal stripe may be broken.

4. Albino.

5. Like 3, but black being substituted for wild colour.

6. Like 2, but black instead of wild colour. This type is known in the fancy as the "Irish" variety.

7. Self-coloured black.

With respect to the kinds of pigments in rats I have as yet no information. The distinction between black and the wild colour is apparently less sharp than in mice, and both black and black-and-white rats have a good deal of dark brown hair, especially in the edges of the black patches of the parti-coloured, and on the belly of the self-coloured black.

No doubt there is also some change with age, moulting, &c.†

Crampe (9. p. 393) mentions the black stripe in his black-and-whites, and there is practically no doubt that his var. 3 and var. 5 are correctly referred to the hooded and striped types. He remarks that by selecting those with stripes so wide that the rats were more black than white, he got no nearer to breeding blacks. Similarly whites could not be bred from the whitest grey-and-

* This is Miss Douglas' experience. In this respect strains doubtless differ, for Mr. F. Swann tells me he formerly kept a strain in which the stripe was generally broken.

† Crampe records (9. p. 395) changes with age in piebalds from "grey" to black and *vice versa*, both colours appearing together in the transition. The change in the direction of darkening seems to be normal as the adult fur grows. In the same place he mentions a rat as "*Gelb-grau*."

whites. The types are in fact definite, and cannot be built up by cumulative selection.

I am indebted to Miss Douglas for much information as to the varieties of rats and for the loan of specimens. She tells me that rats coloured otherwise than the varieties named are exceedingly rare. Irregularly piebald or spotted rats occasionally occur, but she has tried recently to obtain such rats from fanciers without success. In her experience the type 6 breeds true or nearly so. Of the blacks examined by me this type had less of the brown hair than type 7.

A striking feature appears from the rat-evidence, namely the absence of yellow, blue, chocolate, and indeed most of the varieties so familiar in fancy mice. On superficial examination, the colour of a wild rat is not very greatly different from that of a wild mouse. In rabbits also the yellow as well as the black forms are common. Yellows or yellow-and-whites are also familiar in guinea-pigs, fowls (buff, and "pile"), and pigeons. Miss Douglas has heard of a pair of cream-coloured rats, but otherwise I can find no records of any kind of yellow in the fancy. As blacks are so easily produced by resolution in the rat, the absence of the corresponding yellow and chocolate is remarkable. One is tempted to inquire whether the existence of black gametes does not suggest that yellow or at least chocolate gametes must also exist. The problem of their disappearance raises many important questions as to selective union between gametes, and others too elaborate to develop now. As there are no yellows, so also there are no chocolates.

Another noteworthy fact is the complete absence of blue rats. This particular stage in the diminution of the amount of dark pigment is well known in mice, rabbits, cats, and several birds, but it is unknown in rats. There is of course no question that such forms would have been preserved if they had been seen by fanciers. Either yellow or blue rats would be worth several pounds. We may take it therefore that these particular resolutions, or perhaps mutations, cannot be produced by any of the means by which they have been produced in other forms. Conceivably, if some distinct species were crossed with our fancy rats, some of these forms might be created. Similarly there are no "Himalayan" rats, *i. e.* pink-eyed with patches of colour (blackish or yellow), forms well known in rabbits, guinea-pigs, and in the "Japanese" waltzing mice.

To sum up the evidence as to rats, we have clear proof of the segregation of certain types of gamete—the albino, the black-and-white, and the grey-and-white, though the ratios in which they are produced by heterozygotes are not yet determined. Further, there is proof that certain of the colour-types exhibit definite valency (*Werthigkeit* of Tschernak) and dominate over each other according to a regular system. Of the other colour-types one, *viz.*, type 2, is almost certainly a definite heterozygote form, and is probably incapable of being made into a pure race.

We may next consider the further evidence regarding mice. By the great kindness of Mr. F. G. Parsons, I am permitted to include in this paper notes of 50 matings made by Mr. Parsons in conjunction with Dr. S. M. Copeman. These experiments were made with other objects in view and are still in progress, but as they stand they are a valuable contribution to the question of the inheritance of colour. The notes which Mr. Parsons has placed at my disposal are here given exactly as they were received. I have merely inserted the letters DR and DD according as the results show that the individual in question was a heterozygote containing albino, or that it was free from the albino character. Those not thus distinguished cannot be discriminated by the existing evidence.

The following abbreviations are used: *bl.*, black; *br.*, brown = chocolate; *blw.*, pied-black; *brw.*, pied-brown; *w.*, albino.

Experiments made by Mr. F. G. Parsons.

<i>Mating.</i>	<i>Offspring.</i>	
(1) w. ♀ A × blw. ♂ α (DR)	1 blw.	3 w.
(2) " × w. ♂ β.....	7 w.
(3) " × brw. ♂ (B×α) (DR)	1 brw.	3 w.
(4) w. ♀ B × blw. ♂ α (DR)	2 blw. 1 brw.	4 w.
(5) " × w. ♂ β.....	5 w.
(6) " × brw. ♂ γ (B×α) (DR)	5 w.
(7) " × " "	4 brw.	1 w.
(8) blw. ♀ C (? DD) × blw. ♂ α (DR)	3 blw. 1 brw.	(1 eaten ?).
(9) " × w. ♂ β.....	2 blw. 1 brw.	
(10) w. ♀ D..... × blw. ♂ α (DR)	2 bl. 1 br.	1 w.
(11) " × w. ♂ β.....	5 w. (1 eaten ?).
(12) " × brw. ♂ γ (B×α) (DR)	2 br.	6 w.
(13) " × " "	2 bl. 2 br.	4 w.
(14) " × blw. ♂ α (DR)	3 bl. 1 br.	2 w.
(15) w. ♀ E × blw. ♂ α (DR)	2 blw. 2 brw.	4 w.
(16) w. ♀ F × blw. ♂ α (DR)	1 blw. 1 brw.	2 w. (5 eaten ?).
(17) " × w. ♂ β.....	7 w.
(18) w. ♀ B ¹ (B×α) × blw. ♂ α (DR)	2 blw. ...	3 w. (2 eaten).
(19) w. ♀ B ² (B×α) × " "	2 blw. ...	1 w. (3 eaten).
(20) " × w. ♂ ε.....	8 w.
(21) w. ♀ B ³ (B×α) × blw. ♂ α (DR)	4 blw. ...	3 w. (1 eaten ?).
(22) " × w. ♂ ε.....	9 w.
(23) " × blw. C ²⁻¹ (C ² ×α) (DR)	5 blw. ...	2 w.
(24) blw. ♀ C ¹ (C×α) (? DD) × blw. ♂ α (DR)	7 blw.	
(25) " × w. ♂ ε.....	2 bl. 4 blw.	(1 eaten ?).
(26) brw. ♀ C ² (C×α) (DR) × blw. ♂ α (DR)	1 brw. 1 w.
(27) " × " "	2 blw. 2 brw.	2 w. (3 eaten).
(28) " × w. ♂ ε.....	1 blw. 4 brw.	1 w.
(29) " × brw. ♂ C ²⁻² (DD)	... 7 brw.	
(30) " × " "	... 6 brw.	
(31) " × " "	... 7 brw.	
(32) bl. ♀ D ¹ (D×α) (DR) × blw. ♂ α (DR)	5 bl.	2 w.
(33) " × blw. ♂ C ²⁻¹ (DR) (C ² ×α)	7 bl. 1 blw.	6*

<i>Mating.</i>	<i>Offspring.</i>
(34) bl. ♀ $D^2(D \times a)(DR)$ × blw. ♂ $a(DR)$	2 bl. 1 br. 2 blw.
(35) " " × w. ♂ ϵ	1 bl. 1 br. 3 blw. 2 w. (4 eaten).
(36) " " × brw. ♂ $C^{2-2}(DD)(C^2 \times a)$	3 bl. 2 br. 1 blw. (3 eaten).
(37) br. ♀ $D^3(D \times a)(DR)$ × blw. ♂ $a(DR)$	2 bl. 1 br. 3 w.
(38) " " × brw. ♂ $\gamma(DR)$	3 br. 2 brw. 3 w.
(39) " " × w. ♂ ϵ	1 bl. 1 blw. 1 brw. 2 w.
(40) w. ♀ $B^{2-1}(B^2 \times a)$ × blw. ♂ $a(DR)$... 2 blw. 3 w. (3 eaten).
(41) " " × " "	... 5 w.
(42) blw. ♀ $C^{1-2}(C^1 \times a)(DR)$ × blw. ♂ $a(DR)$... 7 blw.
(43) " " × " "	... 4 blw. 2 w.
(44) blw. ♀ $C^{1-3}(C^1 \times \epsilon)DR$ × brw. ♂ $\gamma(B \times a)(DR)$... 7 blw. 1 w.
(45) blw. ♀ $D^{2-3}(D^2 \times a)$ × blw. ♂ $a(DR)$... 5 blw.
(46) blw. ♀ $D^{3-3}(D^3 \times a)$ × brw. ♂ $C^{2-2}(C^2 \times a)(DD)$	1 bl. 1 br. 1 blw. (1 died).
(47) bl. ♀ $D^{1-1}(D^1 \times a)(DR)$ × w. ♂ ϵ	1 bl. 2 blw. 2 w.
(48) blw. ♀ $C^{1-2-1}(C^{1-2} \times a)$ × blw. ♂ $a(DR)$ 5 blw.
(49) blw. ♀ $C^{1-2-2}(C^{1-2} \times a)$ × blw. ♂ $a(DR)$ 7 blw.
(50) blw. ♀ $C^{1-2-2-1}(C^{1-2-2} \times a)$ × blw. ♂ $a(DR)$ 4 blw.

The mice originally introduced were 5 albino females, 2 albino males, 1 black-and-white male, and 1 black-and-white female, all of unknown extraction.

Several albinos were produced in the experiments. Mated with albinos they gave albinos only (41 in all). The original blw. ♂ a was heterozygous, containing albino, but the blw. ♀ C probably did not, though the figures are insufficient for proof. Both of the original blw. on mating with albino gave rise to some *brown* or brown^{*}-and-white offspring, and were probably giving off gametes of this nature. All such specimens were alike in tint except one which was distinctly lighter.

The families of the albino D (expts. 10-14) are especially interesting; for, as Mr. Parsons pointed out to me, all the 13 coloured offspring by two different *broken*-coloured males, one brw., the other blw., were *self*-coloured, brown, or black. This result resembles one obtained by Castle (5. p. 542), but the suggestion that such a pied individual is a mosaic which throws self-colour gametes is not readily applicable to this case. For here the peculiarity evidently lies in the gametes of the individual albino, since with other albinos the same males gave pied offspring. As Castle commonly obtained such self-coloured mice from albinos crossed with pied, it is likely that the peculiarity may belong to certain strains of albinos. The detailed account of his experiments, which is promised, may perhaps give an indication on this point.

Parsons' cases give besides some indications as to the ratios of the gametes. It will be seen that the relation of brown to black is not merely that of dominant and recessive, for either may give either. Nor can it be supposed that the brown is a mere heterozygous form. Each colour, whether self or pied, may be dominant over albino, and the figures show pretty clearly that in

* Microscopical examination of a specimen kindly sent by Mr. Parsons proved this colour to be "chocolate."

the blw. ♂ α the albino gametes equalled the browns and the blacks collectively, for with various albinos he gave 27 coloured (*q.v.*), 31 albinos, a near approach to equality. As regards the brw. ♂ γ , the evidence is that with 3 albinos he gave 11 coloured, 19 albinos. On the other hand, 4 heterozygous coloured females \times w. ♂ ϵ gave 16 coloured, 7 albinos. As the result of the reciprocity of these numbers, the total (adding expt. 23) of coloured to albinos, produced by all matings in the form DR \times R, is exactly 59 to 59. It is, however, difficult to believe that the departure from equality just named is simply fortuitous, for it is in each case steadily maintained through a series of families. If the figures are grouped according to mothers (instead of fathers, as here) these peculiarities are partly lost, but further experiment may possibly indicate that different kinds of heterozygotes are here to be distinguished.

Of matings in the form DR \times DR there are ten cases, expts. 26-7, 32-4, 37-8, 42-4 giving a total of 49 coloured, 14 albinos, the simple Mendelian expectation being 47.25 to 15.75.

In these experiments there is also good evidence of the appearance of dominants containing no albino, for example brw. ♂ (C^{2.2}), and probably blw.C¹.

Information given me by Mr. J. Wilson Steer and Mr. Atlee, and the experiments lately begun by Miss Durham and Mr. Staples Browne, enable me to add a few indications as to the probable specific behaviour of some of the colour-types in crossing, though these have at present only the value of hints for further experiment.

The agouti (*Mus musculus* colour) is of course dominant to albino, but so far has not been resolved in F₂, having apparently the same behaviour as the wild colour in Cuénot's experiments, but sometimes piebalds of agouti and white appear.

Yellow and black crossed have given sables or "dingy fawns."*

Chocolate \times albino may give, according to Mr. Steer, the wild *musculus* colour, doubtless by reappearance of the black pigment in association with brown of the chocolates. Probably the strains used had other differences also (*cf.* p. 97). Miss Durham has found chocolate a simple dominant over albino.

Sable \times black-and-white, according to the same authority, has given sables, though in this case the result will probably be found to differ according as the black-and-white is homo- or heterozygous.

Sables bred together have given sable, black, and dingy fawn in the same litter.

Blue \times albino has given a full black, sometimes with white patches on tail.

Two yellows (from an inbred strain 4 years old) gave 1 yellow and 2 chocolates (*Steer*). This last occurrence is unexpected and needs careful verification.

* More recently Miss Durham has thus bred some full blacks. Reliable and extensive information as to the result of mating yellows with blacks is greatly needed.

Variiegated black-and-white \times chocolate-and-white gave on one occasion (*Steer*) 5 black-eyed whites and 1 chocolate-and-white.

As mentioned above, blue may be recessive to black and breed true from its first appearance, and will doubtless prove to be a homozygous colour.

We may now pass to a consideration of the crosses made with "Japanese" waltzing mice. The exact physiological nature of the waltzing habit seems to be still uncertain. Reference to the work especially of Cyon, Rawitz, and Zoth shows that, though malformation of the labyrinth is not infrequently associated with this condition, at least the degree of the structural malformation varies considerably.

The origin of the variation is still more obscure. Mouse-fanciers have assured me that something like it may appear in strains inbred from the normal type, though I cannot find an indubitable case. Such an occurrence may also be nothing but the appearance of a rare recessive form. Certainly it is not a *necessary* consequence of in-breeding, witness von Guaita's long series of inbred albinos. From analogy with other cases, we should be prepared to find that the existence of such a structural feature in one of the gametes had an effect on the colour of the heterozygote; but the evidence, as we shall see, is on the whole unfavourable to this view.

As to crossing of waltzers and albinos, the earliest evidence is that of Haacke, whose records are qualitative only. Crossing waltzers, blue-grey with white marks, and albinos, he obtained mice generally self-grey (? agouti), more rarely self-black. Their offspring occasionally had a small white mark on the ventral surface.

The next large body of evidence is that of von Guaita (19), who used black-and-white waltzers with dark eyes (von Guaita *in litt.*) and an inbred strain of ordinary albinos. From this cross, F_1 was always (from 4 pairs) a self-coloured house-mouse, and was also like that wild type in size (being larger than the waltzer and smaller than the albino) and in wild disposition. F_2 , raised from F_1 bred *inter se*, consisted of albinos and 4 coloured types—black, grey, black-and-white, grey-and-white. The totals were 30 coloured, 14 albinos. On the expectation of 3:1 there should have been 33 and 11, so that the excess of albinos is distinct, though the numbers are small; but when all *certain* cases of $DR \times DR$ (taking albino as R) are included, the numbers are 117 coloured and 43 albinos, coming very near indeed to the expectation 120 to 40. There can therefore be no doubt that the heterozygotes produced on an average equal numbers of albino gametes, and of gametes bearing the various colour-types.

There are only two matings certainly in the form $DR \times R$. These gave 23+1 coloured, 20+1 albinos, closely approaching the expected equality.

In (20) Table I., from 1st and 5th pairs, we have families of 17 coloured and 13 coloured respectively, showing pretty clearly that

some of the coloured individuals contained no albino. As far as the few observations went, the extracted albinos gave only albinos. So far therefore the Mendelian hypothesis harmonises well with the phenomena.

When, however, we begin to consider the relations of the several colour-types to each other, we meet some important problems. The original waltzers are described as black-and-white. Of what pigments the black was made up we do not know. Probably it contained both the black and the brown elements. However this may have been, the reversionary heterozygote clearly did, though whether it also contained the *yellow* pigment is not so clear.

On examining the details as to the offspring of the several pairs, it appears that though the self-greys may, as the first cross proves, contain all the other 3 coloured types and the albino, the grey-and-white contain the albino only. Similarly the black-and-white can only contain the albino, so far as the evidence goes. But black seems to be dominant over black-and-white.

The facts are not sufficient to make these deductions quite certain; and, in particular, since the evidence in rats shows that grey-and-white may dominate over black-and-white, it may be merely from accident in the choice of individuals that no black-and-white was produced by any of the grey-and-white mice.

The families from the 4th pair on Table I., and from the 3rd pair on Table II., are especially interesting as giving indications as to the gametic ratios in a complex case, though the evidence is insufficient to determine these ratios. In the first case black-and-white \times black gave 10 black, 15 black-and-white, 7 albino. Both parents were heterozygotes containing albino, being each raised from self-greys \times white. From the facts it is clear that one parent at least was giving off gametes black, black-and-white, and white; and from the indication that black is dominant to black-and-white, it is probable that this parent was the black. The simplest supposition is, then, that the black-and-white gave off blw. and w., and that the black gave off bl. and blw. in equal numbers, and whites equal to their sum. This distribution would give the ratio

$$1 \text{ bl.} : 2 \text{ blw.} : 1 \text{ w.},$$

and where experiment gave

$$10 \text{ bl.} : 15 \text{ blw.} : 7 \text{ w.}$$

we should expect

$$8 \text{ bl.} : 16 \text{ blw.} : 8 \text{ w.},$$

which fits well. But in the 3rd pair on Table II. we have a blk. \times albino giving

$$7 \text{ bl.} : 16 \text{ blw.} : 20 \text{ w.},$$

where, on the hypothesis suggested, we should expect *equality* between bl. and blw., and the discrepancy is considerable and emphatic.

Pending further experiment, the relations of bl. to blw. and to white cannot be stated with any confidence. Another point

calling for elucidation is the distinction between the black-and-white of the original waltzers and the black-and-white of subsequent generations. F_1 from albino and the waltzers was the atavistic grey, but there is no indication that the subsequent heterozygotes between blw. and albino were grey; or more strictly there is a great deal of evidence that they were usually blw. The suggestion also that the atavistic colour was due to the union of the waltzing and non-waltzing character seems to be plainly excluded, because even normal albinos in later generations proved to be heterozygotes of waltzing and non-waltzing gametes. At present, therefore, we cannot declare what was *the* difference between the original pure gametes which caused the reversion when they were united.

Lastly, there is a difficulty, perhaps the most serious of all, in the result of the union of albino \times self-grey (19. p. 328, 2nd pair; both parents being in F_2) which gave 13 grey, 3 grey-and-white. I see at present no suggestion as to the gametic production of the grey parent in this case which can be made with any probability, consistently with the other facts. Possibly the diversity of gametes lay with the albino.

I now pass to an examination of the evidence of Darbishire, who crossed ordinary albino mice with waltzers. The waltzers used were "pale fawn"-and-white with *pink* eyes, thus outwardly corresponding somewhat with one of the breeds of rabbits called "Himalayan." The nature of the pigmentation described as "fawn" is not specified; but from the results, and especially from the distinction drawn by the author between "fawn," "fawn-yellow," and "yellow," there can be little doubt that the fawn was composed of both yellow pigment and a dark pigment, probably black. Twenty-nine pairs were used in the production of F_1 . The offspring of 23 of these pairs, 120 individuals, had grey colour. All except one had more or less white or whitish, differing in extent. Some had more white than the waltzers, while in others the whitish colour only appeared on the belly. The pure albinos gave on the whole more fully coloured, the extracted albinos less fully coloured heterozygotes. The tint of the grey is further classified into "pale wild colour" and "dark wild colour," both being stated to be such as occur in *musculus*. Full details as to distribution are given (*q. v.*).

Of the remaining six pairs, four gave one or more mice with the colour-patches *black* (with grey brethren in three families) as follows:—

Pair.	Patches.	
	Grey.	Black.
XXVII.	1
LXXVII.	1	3
LXXVIII.	4	3
LXXXV.	6	2
	11	9

Lastly two pairs gave both greys and yellows, thus:—

<i>Pair.</i>	<i>Patches.</i>	
	<i>Grey.</i>	<i>Yellow.</i>
XII.	2	3
LXXXIV.	5	4
	<hr style="width: 100%;"/>	<hr style="width: 100%;"/>
	7	7

In the original account and in the discussion of the facts by Professor Weldon in 'Nature,' the offspring of the 29 families are referred to as having consisted of a mixture of greys, yellows, and blacks; and the fact that only certain families gave blacks and certain families yellows, and that no family gave both blacks and yellows, is not emphasised. We can conceive that both yellows and blacks *might* be associated with greys when "fawns" are crossed with albinos, but till the phenomenon occurs it need not be considered in this connection*.

To proceed with the fundamentally important question of the purity of the coloured race, we are informed that the original waltzers were bred together for some months and gave only offspring like themselves. The number of individuals thus tested and the number of offspring raised from them are not given, but we may conclude that they were considerable. When, however, we regard this evidence of purity in the light of the facts provided by the six families which gave either yellows or blacks, we perceive that if "fawn" is dominant to yellow and to black, the occurrence of yellows and blacks in the crosses with albino is readily explained. We have in fact only to suppose that in family 27 the coloured mother, and in families 77, 78, 85 the coloured fathers, contained *black*; and that in families 12 and 84 the coloured fathers contained *yellow*; and the results are fairly clear. The chance of seeing the impurity by merely crossing fawns together would not be very great. Most of them evidently were pure, and since black \times yellow certainly *may* give a dingy fawn heterozygote, the impurity would probably not be demonstrated unless fawns containing black bred together, or fawns containing yellow bred together. By breeding the mother of family 27 with the father of 77, 78, or 85, some test of this suggestion might have been made. Of course we have as yet no direct experimental proof that fawn is dominant to black and to yellow; but since sables can throw blacks, and since in rats grey-and-white is dominant to black-and-white, it seems very possible that these "fawns" may also have been thus dominant.

* When a compound character is crossed with a recessive, it sometimes happens that *components* of the compound appear already resolved in members of F_1 . For example, I have seen the "walnut" comb of the pure Malay fowl (which can be produced by synthesis of rose-comb and pea-comb in a more or less stable union) crossed with single comb give some rose, some pea, some walnut, as well as some single. Such a phenomenon will probably be demonstrated to be a *partial* monolepsis ("false hybridism"), and zygotes exhibiting the several components will probably not reproduce the excluded elements in their posterity.

The most striking fact about the F_1 heterozygotes (not mentioned in Darbishire's first paper) is that they all had *dark* eyes, though both parents had pink eyes. The albino showed itself a recessive as usual. Moreover, just as in von Guaita's case, the colour of the waltzers did not behave as a simple dominant, but formed a specific and reversionary heterozygote. It is especially interesting that this heterozygote should have been so nearly the same*, though Darbishire's original coloured form was "fawn"-and-white, while von Guaita's was black-and-white. This certainly suggests that the *completeness* of the reversion may have been due to the meeting of some other dissimilarities than those indicated simply by colour and albinism (*cf.* Steer's case of chocolates, p. 85). Other facts point in the same direction.

Moreover, if the "fawn-yellow" of Darbishire's class *b* is the same colour† as the pale fawn of the original waltzers, it is curious to find that in F_2 there were black-eyed (therefore presumably heterozygous) "fawn-yellows," when the colour *grey* would have been the natural expectation. This phenomenon may be compared with that seen in von Guaita's work, where original black-and-white \times albino gave greys; but in F_2 black-and-white may be a simple dominant over albino. (Compare also Parsons' evidence as to chocolate (= brown) with Steer's experience.)

The result of mating the wild-coloured F_1 together, as far as the detailed tabulation extended, was:

Albino	9	all pink-eyed.
Yellow	4	3 pink-eyed.
Fawn-yellow	6	3 pink-eyed.
Pale grey	9		
Dark grey	1		
Black	5		
"Lilac" ‡	3	1 pink-eyed
	<u>37</u>		

In all, therefore, 16 were pink-eyed and 21 dark-eyed, when equality is expected.

A postscript gives the number raised in F_2 (presumably from *wild* coloured F_1) as increased to 66, and though the individuals are not classified according to colours, the information is given that there were—

	Albinos pk-eyed.	Coloured pk-eyed.	Coloured (?all) dk-eyed.
	13	17	36
the expecta- tion being }	16.5	16.5	33

* Darbishire's being, however, mostly pied, while von Guaita's were selfs.

† Until qualitative details of these colorations are published, their exact nature can only be surmised.

‡ [From a specimen exhibited by Mr. Darbishire, I think this colour is probably one of the dilutions of *brown* pigment. It appeared to be a paler shade of the "silver" of fanciers.]

Before attempting further to analyse these facts, the results of wild-coloured $F_1 \times$ albino must be given. In the body of the paper 88 young so produced are recorded, viz., 39 albino, 31 wild-coloured (18 darker, 13 lighter), 15 black, 3 yellow. The total increased subsequently to 205, of which 111 were albinos and 94 had some colour in their coats, the specific colours not being as yet given. All the coloured individuals from this mating were dark-eyed, as would be expected. In accordance with the other results we should expect—

	105.5 albinos and 105.5 coloured with dark eyes,	
where experi- ment gave	} 111	" 94 " "

It is therefore clear that if we regard the gametes of F_1 as consisting of two kinds, colour-bearing and albino, in equal numbers on an average, this simple form of the Mendelian hypothesis fits the facts very closely, and the distribution of albinism and eye-colour is approximately what that hypothesis leads us to anticipate. When, however, we try to assign the ratios of the several colour-gametes to each other, and to determine the specific results of their unions, we encounter certain difficulties, though in all probability further experiment will enable us to make this analysis complete.

So far we have no knowledge of the specific composition of the several types seen in F_2 , and until they are bred separately *inter se* we can only predict the offspring with reserve. Any such prediction can only be made on the hypothesis that the regularity of the behaviour has been maintained, and that no original variation or mutation arises (as may happen for instance in peas and perhaps sweet-peas). We must also expect some irregularities from the fact already mentioned, that the several families in F_1 were not all comparable, and in subsequent generations it will be necessary to distinguish members of black-giving, or of yellow-giving families from the rest. Subject to these provisos, we expect the pink-eyed coloured types to give only pink-eyed when bred *inter se* and no albinos*, but that the dark-eyed will give both pink-eyed and dark-eyed; and that some of the offspring of dark-eyed mated *inter se* (or with albinos) will be albinos. The pink-eyed coloured forms mated with pure albinos will presumably give all dark-eyed offspring again †.

Similarly taking the types of F_2 singly, it is likely that dark-eyed yellows will give only yellows, perhaps creams, and albinos,

* Unless the phenomenon seen in the albino guinea-pig occurs.

† In Mr. Darbishire's third report (28) just published it is recorded that a pink-eyed yellow-and-white in F_2 bred with albinos gave 8 albinos, 11 grey-and-white, 1 yellow-and-white. The occurrence of albinos from this mating is of course a proof that the constitution of the pink-eyed yellow was in this case not that suggested in the present text. Experiments with other coloured members of F_2 are not yet given. The relation of the yellows to the rest must be regarded for the present as quite unknown. It may be remarked that yellow-and-white varieties both of rabbits, fowls, and pigeons are often peculiar in their inheritance, and rarely breed true for many generations.—July, 1903.]

while the dark-eyed blacks should give only blacks, perhaps blues, and albinos. The dark-eyed greys will probably give both blacks and yellows, though in view of von Guaita's evidence that grey may exist as a new homozygote, this is perhaps doubtful. As far as the published evidence goes, the most probable constitution of the several forms in F_2 is as follows:—

<i>Albinos</i>	albino × albino.
Pink-eyed yellows	yellow × yellow.
Dark-eyed	yellow × albinos.
Pink-eyed fawn-yellows ...	fawn-yellow × fawn-yellow.
Dark-eyed blacks	black × albino (?)
Dark-eyed greys	fawn × albinos (and perhaps some other combinations).
Pink-eyed lilacs.....	lilac × lilac.

The absence of blacks with pink eyes is noticeable, and raises the question whether there is not a permanent synthesis in these blacks.

Finally, we have two important problems, the nature of the *dark-eyed* fawn-yellows and of the *dark-eyed* "lilacs." As they are dark-eyed they presumably both contain albino. But as regards the first, it is difficult to see what the other gamete can be in that case. For from F_1 we learn that fawn × albino give *grey*, not fawn-yellow. On the other hand, as there are black and yellow gametes, we ought to find their heterozygote, which will presumably be *fawn*. But if this combination follows the rules of the others, the heterozygote should be pink-eyed, not dark-eyed. The number of dark-eyed fawn-yellows, three, is too few to make it likely that these are the black × yellows, which we expect to appear as a fairly frequent combination; and the general indications are quite unfavourable to the view that any considerable number of heterozygotes can be dark-eyed without the presence of the albino, though it is not impossible that such real synthesis may take place.

Next the "lilacs" raise certain questions. We must suppose that the dark-eyed "lilacs" contain albino; but in the offspring of F_1 × albino there are no "lilacs." As F_1 is giving off gametes capable of forming "lilacs," we see that the lilac × pure albino gives some other colour. Next, which of the groups can be supposed to represent the lilac-bearing gametes in their other combinations? This also is a question we cannot answer.

A similar difficulty is created by the scarcity of yellows in the offspring of F_1 × albino. There were only 3 in 88. We might have expected the numbers of yellows and blacks to be equal, but there were 15 blacks. Moreover, all the yellows were in *one* family. So far this is quite inexplicable. It probably indicates that some of the albinos possessed powers of resolution different from those of others, or conversely that some of the original "fawns" were more easily resolvable than others. [*cf.* Cuénot's new results (27), where blacks were resolved out, but apparently *no* yellows.]

A line of inquiry is suggested by the miscellaneous constitution of F_1 . We have seen that all members of F_1 are not alike, and it is not impossible that the greys from families which give no blacks or yellows may be different in constitution from greys in families which gave one or the other. If the individuality of the several parents of F_2 were given, this possibility could be examined. The fact that an original waltzer was giving off yellow or black gametes might be an indication that resolution of characters had already begun; and perhaps therefore the F_1 from different families, though alike grey, may be in some measure heterogeneous. In these cases it is most important that each individual parent and its offspring should be separately traceable.

It is not impossible that some light on these questions could be obtained by noting the sexes in which the several forms appear.

In view of the facts I do not understand the meaning of Darbishire's statement that "the inheritance of eye-colour is not in accordance with Mendel's results."* So far as the experiments are yet recorded, the behaviour of the eye-colour is typically Mendelian, and follows Mendelian expectation in its simplest form. The occurrence of albinos is similarly Mendelian, one albino in four being plainly indicated as the average from $F_1 \times F_1$ †.

* For further criticism of this statement see Castle and Allen (7).

† As regards the waltzing character von Guaita's experiments agree with Darbishire's in showing that it was always recessive to the normal. No individual in F_1 , or in families produced by crossing F_1 with the pure normal, waltzed. In Darbishire's experiments $F_1 \times F_1$ gave 8 waltzers in 87 offspring, indicating 1 in 4 as the probable average. $DR \times R$ is not recorded. From von Guaita's matings in the form $DR \times DR$ the totals of families were 117 normal and 21 waltzers made up as follows:—

<i>Normal.</i>	<i>Waltzers.</i>
36	8
14	2
25	7
41	2
1	2
<hr/>	<hr/>
117	21

There is therefore a large excess of normals over the expected 3 to 1. This is possibly due to the delicacy of the waltzers, which are certainly much more difficult to rear than normals are. The small numbers in von Guaita's litters make it very likely that many were lost before such a character as this could be determined. On the other hand, we have to bear in mind that as the presence of waltzers is here the only proof that the matings were in the form $DR \times DR$, it is possible that the total of normals should really include some families which gave normals only.

$DR \times R$ gave 18 normal and 10 waltzers distributed in families thus:—

<i>Normal.</i>	<i>Waltzers.</i>
3	4
3	2
10	3
2	1
<hr/>	<hr/>
18	10

Here the same paucity of recessives is noticeable.

Von Guaita did not succeed in raising any offspring from extracted waltzers bred *inter se*.

All that can be positively asserted is that the qualitative result is in full agreement with the Mendelian expectation based on the absence of waltzers in F_1 , and that it is not impossible that there may be the expected equality in number between D and R gametes produced by F_1 .

As we have also seen, the colours taken collectively follow simple expectation; $F_1 \times F_1$ giving approximately 3 coloured to 1 albino, and $F_1 \times$ albino giving approximately equal numbers of each.

As to the frequencies and valencies of the particular colours nothing can be said with much confidence as yet, beyond the statement that F_1 gives off albino gametes about equal in number to the various coloured gametes collectively. In a discussion of this subject, Professor Weldon (25) has suggested that an average of *one albino in nine* might have been expected. I can see no reason why this proportion should be impossible in nature, from $F_1 \times F_1$. Its occurrence would, however, be remarkable and raise some important problems in gameto-genesis. So far, however, it has not been recorded. Professor Weldon is in error in stating (25. p. 34) that I have already dealt (4. p. 52) with such a case of 1 albino in 9. The case in question was that of *Antirrhinum*, where de Vries obtained from $F_1 \times F_1$ four forms in the proportion 9:3:3:1, the *one* being the white, which therefore occurred in the proportion of 1 in 16. This is the proportion Mendel himself conjectured might be found in a case of resolution, but I do not gather that he had actually observed such a case.

No case of resolution has yet been sufficiently studied for us to speak with any confidence as to the ratios of the gametes or the nature of the process of resolution. Tschermak has had cases of 1 recessive in 4, after resolution. In poultry I have had cases somewhat similar, to be described hereafter.

In apparently all recorded cases of resolution some gametes of F_1 carry the compound character unresolved. It is not at all easy to suggest a scheme which shall fit both the observed facts of resolution and those of cell-division. For example, suppose the gametes of F_1 to be 50 per cent. albino, 50 per cent. variously coloured, if segregation were complete. Let us consider the coloured gametes separately, and for simplicity assume there are only three kinds of them, viz. the unresolved grey, black, and yellow, the two latter being hypallelomorphs of grey. It is then clear that in whatever numbers the three types are each represented, so long as their sum equals the total of albino gametes, there must be more black character in any black gamete, and more yellow in the yellow gamete, than in any grey gamete; *or* there must somewhere be a cell-division in which a part of the yellow and a part of the black have been lost. If, for instance, the hybrid bore gametes in the proportions

2 grey (=black + yellow), 1 black, 1 yellow, 4 albino,

we recognise that unless the blacks and yellows carry double portions of their respective colours, part of the colour originally introduced into F_1 has been lost. Such doubling is not altogether inconceivable, though until histological methods are made applicable to these questions of gameto-genesis the possibility can hardly be tested. We note as a fact favourable to such a view, that the visible amount of pigment in a black or a yellow zygote is far

greater than the amount of the same pigment in the original compound colour. But this consideration cannot be allowed much weight, seeing that there may be an excess of pigment in *heterozygotes* produced even from two gametes apparently bearing no pigment elements at all (*cf.* p. 76). In the chemistry of pigmentation there may perhaps be interactions and cancellings so complex as to make this particular problem as yet quite insoluble.

Fuller analysis is especially needed also to determine the place of the pied and diluted colour-bearing gametes in the series, but it is fairly certain that they must be regarded as due to disintegration and imperfection of resolution of the colour from the albino character.

Future experiment must decide the conditions determining resolution. Cuénot, as I understand his paper, got none in the main experiment with wild mice; but he states that he obtained yellows, blacks, and piers "*accessoirement*" (perhaps by introducing some coloured fancy strain?).

From this survey of evidence mostly already published, it is clear that Mendelian analysis provides a means of elucidating a large part of the phenomena. The majority of the observations are in accord with the Mendelian hypothesis in a simple form. The true solution of several subordinate problems still remains obscure. The value of the Mendelian analysis will be the more appreciated when it is remembered that previously the whole body of facts must have been regarded as a hopeless entanglement of contradictions, as reference to any non-Mendelian discussion even of these very phenomena will show.

As I have elsewhere pointed out, the central phenomenon in Mendelian heredity is segregation. The characters in simplest cases are treated as units in gameto-genesis. In more complex cases there is resolution, sometimes also disintegration and imperfect segregation, leading to the formation of fresh units. The gametes bearing these units are produced in numerical proportions which on an average are also definite, but as yet these proportions have only been determined in the simple cases. There is no doubt that further experiment will determine them in complex cases also.

It is the object of Mendelian analysis to determine

- (1) the constitution of the several types of gamete produced by each type of zygote;
- (2) the numerical proportions in which each type of gamete is produced;
- (3) the specific result of the union of any two of the types of gamete in fertilisation.

Though for convenience we may still speak of inheritance as being "Mendelian" or "non-Mendelian," we are rapidly passing out of the initial phase of the inquiry in which such expressions are demanded. In our further investigations we are concerned not so much with the question of the applicability of the simplest

Mendelian hypothesis to special cases, as with the formulation of the specific laws followed by the several characters of various animals and plants in gameto-genesis and in union by fertilisation. As in chemistry, these laws must be worked out separately case by case, and each as it is determined has the value rather of fact than of hypothesis.

In dealing with this class of fact, special precautions are necessary in order to establish the identity and purity of any variety chosen for experiment. From the description of the varieties of mice given at p. 73 it will be seen that some colours may be easily confounded in description, though the pigments on which they depend have a different chemical behaviour. This is especially the case with regard to "fawn," "fawn-yellow," and "yellow." In such cases it is absolutely necessary that the presence or absence of *dark* pigment should be noted, and that some attempt should be made to distinguish the two dark pigments from each other.

In all attempts to trace laws of colour-heredity, colours of the various parts will usually have to be reckoned with. In horses, for example, the general body-colour, without that of the mane, tail, and fetlocks is likely to be an insufficient guide to the heredity. In man the heredity of eye-colour cannot be sufficiently investigated if it be separated from the colour of the hair, and so forth. For the present, therefore, Professor Pearson's conclusion that the Mendelian system does not apply to coat-colour of horses or to eye-colour in man should not be received without reserve. By neglect of the precautions named above many results may be described as conflicting with each other, which further analysis would show to be harmonious.

[*Note added July, 1903.*

When this communication was read I had not seen the important paper of Cuénot (27) dated March 1903. He states that grey mice of his F_2 when crossed with albino gave several *blacks*. These, when bred with certain albinos produced black heterozygotes, which bred *inter se* gave the Mendelian 3 black to 1 albino. Some of these latter blacks were then homozygous, and from them a pure strain of blacks was raised. This strain crossed with wild *musculus* behaved as a simple recessive, giving grey F_1 , with Mendelian ratios 3 grey to 1 black, or 1 grey to 1 black in F_2 , according as F_1 was mated with F_1 , or with black.

The fact that the original black did not appear in F_2 or in F_3 calls for elucidation. It suggests a possible difference between the albinos used either in producing F_1 or later, some individuals having the power of resolving the grey, while others had not that power.

Cuénot next records the new and important fact that the colour of the F_1 produced from his black strain \times albino differed according to the class of albino used. (1) Albinos extracted from

the cross with wild grey gave *grey* F_1 . (2) Albinos extracted from the cross with black gave *black* F_1 . (3) Albinos extracted from a cross with yellows (of complex origin) gave a mixture in F_1 , either of *yellows and greys*, or of *yellows and blacks*. There is therefore a proof that individual albinos, though outwardly alike, may belong to several distinct classes, exhibiting different properties in their heterozygous unions (*cf.* Parsons' case, p. 84). The resemblance of the heterozygote to the coloured type from which the albino was extracted is a new fact, the significance of which we cannot yet fully appreciate*. Cuénot tentatively makes the attractive suggestion that the particular colour of the heterozygote may depend on the association in the same zygote of various colour-constituents; and that though the albino is white in itself, it may carry on such constituents from a previous coloured parent. Then, according as one or other of these complementary constituents is brought in by the albino, the heterozygote will show the corresponding colour. The chief obstacle to this view is the fact that when a heterozygote shows reversion (as opposed to simple dominance) the reversion frequently includes *various* qualities, such as size, temperament, habit of growth, &c., as well as colour.

A cognate problem was alluded to (p. 88) in the discussion of von Guaita's facts. His original black-and-white \times albino gave a reversionary heterozygote; yet in F_2 both the black-and-white and the grey-and-white DRs present those colours as simple dominants over albino, as their offspring proved. Since in this case no new strain was introduced, the reference to pedigree is not sufficient to elucidate the whole difficulty.

The relation of the several classes of albinos to each other seems to be the next point for investigation, and a useful experiment might be made by breeding albinos extracted from one colour, with albinos extracted from another colour, the offspring to be then tested with a single pure coloured race. It is not impossible that the various types of albino will then themselves exhibit phenomena of segregation.

The new report of Mr. Darbishire (28) and Professor Weldon's comment (29) have appeared too late for adequate discussion here. It may, however, be remarked that both authors scarcely appreciate the Mendelian view when they state that according to it all albinos (or other recessives) may be treated as "in every respect similar." No one, I imagine, would suppose that the similarity need extend to characters other than the albinism. We are familiar with cases in which recessives, though alike in the recessive character, are dissimilar in other respects; and (as stated *supra* p. 76) may, when crossed together, even produce heterozygotes exhibiting a character known to be dominant over the particular recessive concerned. We should no more suppose all albino mice to be identical because they were albino, than all white sweet-peas

* Possibly it is to this phenomenon that Crampe refers in the statement discussed on p. 79 of this paper. I cannot, however, find a case of Crampe's exhibiting Cuénot's phenomenon.

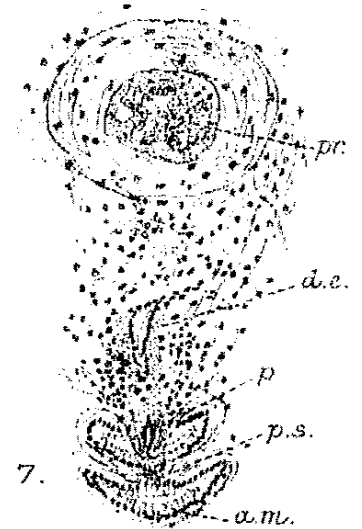
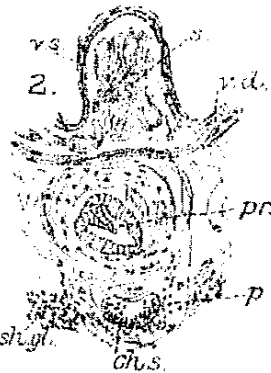
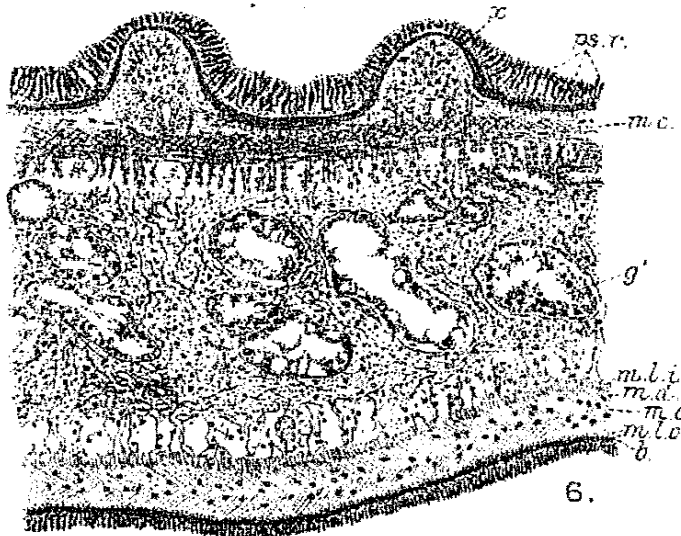
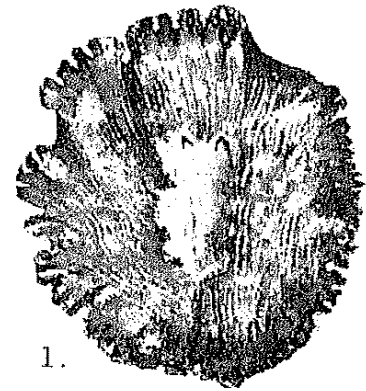
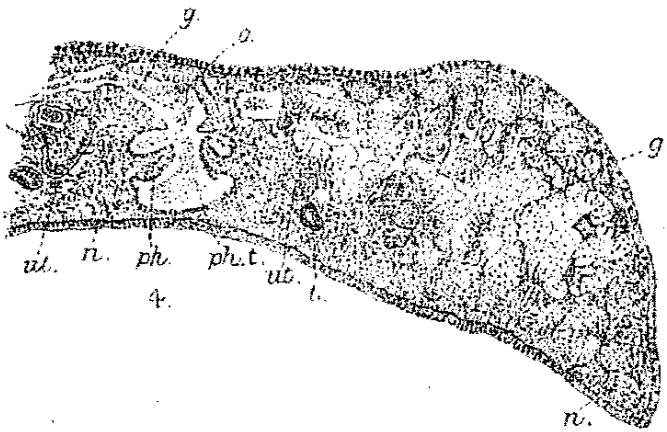
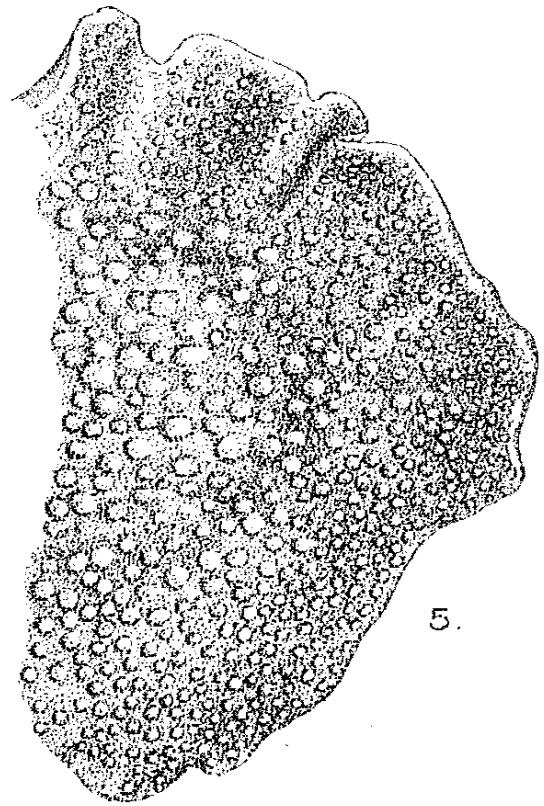
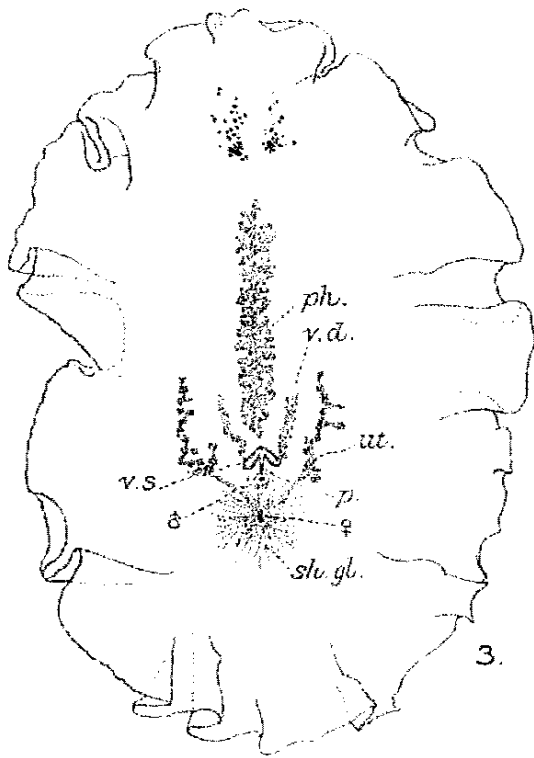
because they were white, or all glabrous stocks because they were glabrous.

Professor Weldon's appeal for the precise gametic formula of F_1 must at present go unanswered. Pending analysis of the various coloured types in F_2 , no one could give the statistical composition of the gametes of F_1 so far as coat-colour is concerned; and though the general composition of F_2 agrees closely with simple Mendelian expectation, the particular composition of the various types is a question that further experiment must decide. To take only one possibility, imperfect segregation is often seen in such cases of complex resolution. No criterion save the actual production of F_3 from F_2 can show whether any of the types of F_2 illustrate this phenomenon. When such evidence is forthcoming there is every likelihood that both the qualitative and quantitative composition of the gametes of F_1 will be determinable with approximate accuracy.]

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Figs 3-6. A.D. Darbishire. del. ad nat.

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PLANARIANS FROM ZANZIBAR.

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4. On the Marine Fauna of Zanzibar and British East Africa, from Collections made by Cyril Crossland in the Years 1901 and 1902.—Turbellaria Polycladida. Part I. *The Acotylea*. By F. F. LAIDLAW, B.A. Cantab., Assistant Demonstrator and Lecturer in Biology in the Owens College*.

[Received May 25, 1903.]

(Plate IX.† & Text-figures 3-7.)

Mr. Crossland's collection contains, so far as the *Acotylea* are concerned, specimens of four new genera and eight new species out of a total of nine species in all. This high percentage of novelties is not surprising when one remembers that but little is known of

* Communicated by the SECRETARY.

† For explanation of the Plate, see p. 113.