men could come for a time to carry on their investigations, though how a professor could leave his college duties for a 'term of *two* years' is not evident to me.

But why give up the museum feature of the Smithsonian? Certainly the United States should not be without a national museum. And if the museum were given up, what would be done with the great collections already there, and with the magnificent building now under construction? Used simply as a research laboratory this building would accommodate all the investigators in the entire country. With such a start as has now been made it would seem a great pity to discontinue one of the most popular and instructive attractions of the national capital, and to distribute to other museums the exhibition and working collections there brought together.

In the first article noted it is stated that 'In our universities the pedagogic element is predominant to a degree quite unknown in the German universities, and the body of investigators in them in any one field is too small to create that which is the most stimulating thing in all research—an atmosphere of investigation.' It is certainly true that most of us who are in university work are heavily burdened with pedagogic duties; but President Gilman once said, 'Sterile intellects attribute their non-productiveness to overwork, when a more acute diagnosis detects a lack of will-power.' The statement in the above quotation in regard to the absence of the 'atmosphere of investigation' in American universities seems to me to be rather sweeping. Of course in a majority of our colleges the number of men in each department is so small that it is difficult to create an atmosphere of investigation, but that there is such an atmosphere in many of our best institutions is an undoubted fact.

In conclusion, I should say—let the Smithsonian *continue* to be the nucleus of a great national institute of research, and, without diminishing the importance of the museum feature, let sufficient funds be made available to carry on the additional work suggested in the two articles quoted. ALBERT M. REESE.

SYRACUSE UNIVERSITY.

SPECIAL ARTICLES.

YELLOW MICE AND GAMETIC PURITY.

THE attention of readers of SCIENCE has been directed by Professors Morgan (1905) and Wilson (1906) to the curious method of inheritance of yellow pigmentation among mice, according to observations made by Cuénot (1905). Cuénot found that yellow in mice behaves as an ordinary Mendelian character dominant over all other types of pigmentation, but peculiar in that it can never be obtained in a homozygous condition, yellow mice forming regularly two sorts of gametes, one sort being yellow, the other sort being in some cases gray, in other cases black, and in still others chocolate.

These surprising observations carry with them important theoretical conclusions. Already they have been interpreted in ways very different by Cuénot and by Morgan. A fuller knowledge of the facts may show which interpretation is correct, or whether possibly neither is adequate without some modification. It is important first fully to establish the facts. With this idea in mind (and, I confess, inclined to be sceptical because I had found yellow so different in behavior in guinea-pigs and rabbits from what Cuénot reports it to be in mice) I have recently made a reexamination of some breeding records of fancy mice, reared in 1900–1901, in connection with an investigation of sex-determining factors in mammals. The purely incidental records of color-inheritance have not previously been published, and I should hesitate to publish them now in their fragmentary condition, did they not serve to supplement and in the main to corroborate the more extensive observations of Cuénot.

My original stock of mice, obtained from a near-by breeder, consisted of the following sorts: (1) black-white spotted mice, some homozygous, some containing chocolate as a recessive character; (2) chocolate (or chocolate-white) mice, homozygous or else containing recessive total albinism; (3) yellow mice (three in number) all of a clear reddish yellow color above, but almost white below. Young were obtained from one only of the three yellow mice, a male (♂ C). A second male was not used in the breeding experiments. The third yellow animal, a female, was sterile by every sort of mating tried, a considerable number, which fact is of interest in connection with Cuénot's experience, to the effect that yellow mice are feeble in reproductive capacity, though vigorous and even savage. (4) The fourth category of mice consisted of a pair of *very large* albinos and their three young. Subsequent experiments showed that these albinos transmitted as latent characters in their gametes either yellow or chocolate, but in no case black pigmentation.

Other yellow mice were obtained (1) by mating the yellow male with chocolate females, (2) by mating the albinos mentioned to black animals, and (3) by mating a chocolate female with one of the albinos.

The experiments which will be described in detail relate to crosses of the yellow mice *inter se* or with mice of other colors.

Before passing to a consideration of the crosses, I should mention that the yellow mice obtained in my experiments were of two distinct types in their *adult* pelage. In their first coat all alike were of a clear yellow color, like the three original yellow mice. This character was retained in a part only of the yellow mice produced in my experiments; the others developed in their adult (second ?) coat a certain amount of chocolate pigment found associated with the yellow pigment granules, especially toward the base of the hairs. Animals of this second sort I shall call *sooty yellow,* to distinguish them from the *clear yellow* type, in the hair of which only yellow pigment is found. Sooty yellow mice are undoubtedly included in Bateson's (1903) category of 'dingy or sooty fawn' formed 'when dark pigment is present in association with predominant yellow.' Cuénot evidently had under observation both clear yellow and sooty yellow animals. He states that the yellow race contains numerous unfixable variations, not hereditary, ranging from a clear orange yellow to a sooty or grayish yellow not very different from the color of gray mice. The statement that these variations are *not hereditary* seems to me unfortunate, as seeming to imply that characters are not inherited, unless in conformity with known laws of inheritance.

The following observations corroborate Cuénot's statement that yellow is a dominant character in mice. Two clear yellow mice (♀ 3.2^{a} and ♂ 3.1^{c}), own brother and sister, born of a chocolate female (♀ 3) mated with the original clear yellow male (♂ C), produced, in three successive litters, 8 yellow and 2 chocolate young. The same female bore, by another clear yellow male, 2 yellow and 1 chocolate young. Accordingly her total young by mates of her own color were 10 yellow and 3 chocolate, a close approximation to the 3:1 Mendelian ratio. It is clear that chocolate was present as a recessive character in the yellow parents. Black was as certainly *not* present as a recessive character, since it is known to dominate over chocolate, when present in the same zygote with it.

Not all of the yellow young produced by these matings had the same clear yellow color as their parents. Three of them proved to be sooty yellow, on attaining their adult coat; four remained clear yellow, like the parents; and the remaining three died before attaining the second coat, so that they can not be more accurately classified.

The recessive nature of chocolate in relation to yellow is further indicated by the following matings between a chocolate and a yellow individual, the young being in all cases either chocolate or yellow in color, never black.

Parents.				Young.			
Clear Yellow.		Chocolate.		Clear Yellow.	Sooty Yellow.	Yellow, Type not Determined.	Chocolate.
♂ C	×	♀ 3	=	2			4
♂ 3.1^{c}	×	♀ 3	=	1		2	2
♂ 3.1^{c}	×	♀ 3.1^{a}	=	1		3	4
♂ C	×	♀ 3.1^{a}	=			7	3
♂ C	×	♀ 3.2^{b}	=			1	2
♂ C	×	♀ 4	=		1	2	4
♀ 32	×	♂ 49	=			1	4
Totals,				4	1	16	23

The total number of yellows produced in these matings is 21, of chocolates 23. Unfortunately the type of the yellow young is left uncertain by my records in all except five cases. Four of the five were clear yellows and one a sooty yellow.

The three yellow animals employed in these matings, ♂ C, ♂ 3.1^c and ♀ 32, evidently bore chocolate as a recessive character, but not black. For if black had been present as a recessive character, it should have made its appearance as an active character in half of the young produced, but not one of the 44 young recorded in this table was black pigmented. It is perfectly clear, however, from Cuénot's statement that black *may* be present in a yellow mouse as a recessive character. That statement is supported by the following observation:

A yellow female, ♀ 35, own sister to yellow ♀ 32 previously mentioned, was mated with the same chocolate male, ♂ 49, with which ♀ 32 had been mated. She produced three young, two of which were yellow pigmented, and one *black*. The difference in the gametic condition of these two sisters is readily explained. Their mother was an albino which transmitted to each of them the dominant yellow which they manifested; their father was a black animal which bore recessive the chocolate character. Evidently he transmitted black to ♀ 35, but chocolate to ♀ 32. Accordingly the gametic formula of ♀ 35 was yellow (black recessive), but that of ♀ 32 was yellow (chocolate recessive).

The chocolate male (♂ 49), like chocolate mice in general (see Allen, 1904), transmitted no pigment character other than chocolate. Mated with three different chocolate females he produced 11 young, all chocolate pigmented. He was mated likewise with three black females, each of which bore chocolate as a recessive character. These matings produced 4 black and 2 chocolate young. In no other mating, except with yellow ♀ 35, did he produce black pigmented young.

Two matings were made between an albino (bearing latent the yellow and chocolate characters) and homozygous black individuals as follows:

Albino Parent.		Black Parent.		Yellow Young.	Black Young.
♂ 2.1^a	×	♀ 1	=	1	3
♂ 2.1^a	×	♀ 1.3^c	=	2	1
Totals,				3	4

The expectation is equal numbers of yellow and of black young, on the hypothesis that yellow dominates both black and chocolate and that black dominates chocolate.

Another albino, own sister to ♂ 2.1^a and like him bearing latent the yellow and the chocolate characters, was mated with black individuals of the same family as those used in the foregoing matings but bearing chocolate as a recessive character. The result was as follows:

Albino Parent.		Black Parent.		Yellow Young.	Black Young.	Chocolate Young.
♀ 2.1^b	×	♂ 1.1^b	=	2		1
♀ 2.1^b	×	♂ 1.2^b	=	2	2	1
Totals,				4	2	2

The expectation in this case is that young of three sorts will be produced in the proportions, 2 yellow, 1 black, 1 chocolate, which is exactly realized in the totals obtained.

A mating was likewise made between an albino, ♂ A (father of the albinos ♂ 2.1^a and ♀ 2.1^b used in the two experiments just described, and like them bearing latent the characters yellow and chocolate) and a chocolate female ♀ 3.2^b, used also in matings with yellow ♂ C. This mating produced one yellow and one chocolate young, three other young dying before their coat pigments were developed.

These various observations harmonize entirely with the statements of Cuénot, showing that in mice the order of dominance of the three pigments of the hair is *yellow, black, chocolate,* each dominating those which follow it in the series, but being recessive in relation to those which precede it. This order is the more surprising because in rabbits and guinea-pigs black is dominant over yellow. In guinea-pigs black is dominant also over chocolate, but in rabbits a pure chocolate is unknown.

The occurrence of two distinct types of yellows is a matter deserving further attention. The sooty yellow type may evidently be heterozygous, since it may be produced by a cross between yellow and chocolate (see mating ♂ C × ♀ 4), but clear yellow may likewise be produced in the same way and may be likewise heterozygous, as is shown further by the result of mating clear yellows *inter se.* Clear yellows so mated may produce, as we have seen, both chocolate animals and those of the sooty yellow type. Whether sooty yellows may in turn produce clear yellows, my experiments do not show, but this seems highly probable. Whether these two types differ in gametic formula is at present uncertain. The few yellow animals from which I secured young were evidently all heterozygous, like the 81 yellow mice of generation F_2 tested by Cuénot. They were also clear yellow, all except one. That one, a sooty yellow female, bore a litter of three young by a black mate; two of the young were yellow and one black.

In the hair of clear yellow animals, I have found only yellow pigment granules; but in the hair of a sooty yellow which I examined, chocolate granules occur sparingly, with the yellow ones.

Yellow heterozygotes may probably also develop *black* pigment in their adult coat, when black is the recessive character present. For Dr. G. M. Allen, when studying color-inheritance under the writer's direction, obtained a pair of yellow mice, about four weeks old, from a breeder in Washington, D. C., and within a short time these animals began to develop small spots of *black* upon the back. Unfortunately Dr. Allen was soon after forced by the assumption of other duties to discontinue his experiments with the yellow type, and since that time I have been unable to secure material for further study of the matter.

Cuénot finds in his experiments that *all* yellow mice tested by him are heterozygous, like blue Andalusian fowls (Bateson, Saunders and Punnett). He believes, what seems entirely reasonable, that this is due to infertility of gametic unions between yellow and yellow. It will be a matter of interest to see whether further investigations confirm this interpretation, or whether an explanation can be found on the ground of gametic contamination, as suggested by Morgan, or of multiplicity of factors giving rise to yellow, as to the pigmentation of stocks and sweet-peas according to recent investigations of Bateson, Saunders and Punnett (1906).

In guinea-pigs, as I have elsewhere shown (1905), yellow is recessive in relation to black, yet exceptionally a yellow-coated animal may transmit black pigmentation in about half of its gametes. The black pigmentation so transmitted is always small in amount, being in reality the black constituent of a mosaic predominantly yellow in its composition. In the parent classed as yellow (but really mosaic in nature) the amount of black is extremely reduced, or black may be absent altogether from the hair, though present as peripheral skin pigment, as is frequently the case also in yellow animals when they breed entirely true. Now the small amount of black in individuals predominantly yellow may be considered an impurity, a contamination of the self-yellow character, with black. Such contamination can be brought about by crossbreeding and exists in various different degrees. For example, (1) yellow-pigmented guinea-pigs *always* possess black-pigmented eyes. (2) They may possess also black pigment in the skin of the extremities (soles of feet, ears) but not in the hair. *Cross-breeding with blacks will increase the amount of such black pigmentation in the extracted yellows.* Animals of these two types are *recessives* in relation to self black, or to a mosaic of black and yellow; they breed true among themselves.

Again, in rabbits, yellow is recessive in relation to black, but a yellow rabbit may bear black-tipped hairs on the ears and nose, indicating the presence of the black character in a greatly weakened condition. The black impurity, however, is not in a condition of recessiveness. Yellow rabbits never, in my experience, produce black ones. But two yellow rabbits may produce a brown one, that is a yellow rabbit with sooty 'peripheral' black pigmentation mixed with the yellow. These various facts are mentioned to show that yellow animals may contain traces at least of the black character, even when yellow is recessive to black.

The assumption which underlies the explanation of color inheritance given by Cuénot, and adopted by Bateson, is that recessives *lack altogether* a certain factor necessary for the production of the dominant pigment; that albinos, for example, have one factor necessary for the production of pigment, but lack a second factor *altogether*. Now granting that two such factors exist (they may or they may not), it is perfectly certain that many albinos possess *both* of them. For albino guinea-pigs and Himalayan albino rabbits actually do form hair pigments. There is nothing *altogether absent* from them which is a necessary factor in pigment production. In such cases, what distinguishes an albino mammal from any other sort, so far as our present knowledge goes, is a peculiarity in the distribution of the pigments over the body. Albino mammals lack pigment in the eye; what pigment they form is found at the extremities of the body.

Again, white-plumaged birds do not *lack altogether* some factor necessary for pigment formation. They invariably have pigmented eyes, but commonly lack pigment in their feathers. Nevertheless, the purest strains of white fowls are proverbially prone to form a 'black feather' occasionally. Can we say that the character, black plumage, is *altogether lacking* in white fowls? It is not present as a recessive character—I speak of established races, not cross-breds. Shall we say, with Cuénot, that an occasional black feather is a variation not heritable? By no means. In the white fowl with a black feather the black character is present, *every factor* of it! Those factors were likewise present in the white-plumaged parents of the bird in question, but they functioned less actively, so that no feather may have shown the black, though pigment was formed in the eye. The hypothesis of *absent factors* is inadequate to explain the observed facts, in at least a majority of known cases. By cross-breeding and selection we can alter the proportions of the different pigments in the coat *without eliminating* any. By repeated crossing of black with yellow, in guinea-pigs, we can weaken the activity of the black, so that while black pigment is still formed all over the body, it is formed in *less amount*. The black pigment is found in greatest amount at the extremities. If the process of weakening the black pigmentation is capable of being carried to its logical conclusion (a matter still under investigation), black pigment should finally disappear except at the extremities. Again, cross-breeding albino guinea-pigs with blacks increases the amount of black pigmentation formed at the extremities by the albinos, and induces a slight pigmentation of the coat generally, as I have elsewhere shown. How far the contamination of the albinos can be carried, I am unable as yet to say.

Facts such as these are difficult to explain on the hypothesis of two or more factors separately heritable, unless we suppose further that those factors are inherited in varying degrees or amounts. Explanation is rendered still more difficult when we come to consider characters other than pigments, such, for example, as polydactylism. For this reason I have carefully avoided incorporating the terminology of the 'factor' hypothesis into my published papers on heredity, and have referred to characters as more or less completely *active*, or in some cases as *latent*, a usage in harmony with that of Tschermak (1906). Bateson, Saunders and Punnett (1906) have recently criticized this usage, but I believe time will justify present caution in the adoption of the factor hypothesis. Morgan (1905) has attempted to combine the latency idea with the factor idea, but with results not very satisfactory from either point of view.

It seems to me, rather, that we must recognize, along with the fundamental principle of unit characters in heredity, the fact that characters may exist *in varying states of activity*.

The presence of one character often *inhibits* the activity of another. When in guinea-pigs the characters black and yellow are present together, yellow is largely inhibited. If yellow is made more active by repeated crossing with homozygous yellow, black is partially inhibited. In mice the relation of these pigment characters is apparently reversed. If in mice black and yellow are present together, the activity of *black* is largely inhibited; *wholly* so in the first coat and sometimes in the second, though not in the eyes; *partially* so in the adult pelage of sooty yellows. We can not suppose that some *factor* of black, wholly absent in the young, has been supplied in the adult. If so, whence has it come? Nor can we suppose that any *factor* of black is absent in either of two yellow mice, which produce black offspring. Black was not *absent,* but *inhibited!* Removal of the inhibiting character, yellow, allows black to resume activity in the young. And yet we can not suppose that yellow is in mice invariably inhibiting in its action on black. For yellow pigment, as well as black, is formed in the coat of wild gray mice. And Cuénot recognizes that yellow may 'vary' to such an extent as to be very similar to the gray of wild mice. Black is inhibited (dominated) only by yellow in that peculiar state of activity which it has in self-yellow mice, or, as I have elsewhere (1905) expressed the matter, in that condition of *'relative potency'* which it has in yellow mice. It is not impossible that a black race of mice could be found (or created) in which black had sufficient potency to dominate ordinary yellow, as it does in guinea-pigs and rabbits. Or, what would amount to the same thing, a yellow strain might be formed so lacking in relative potency (inhibiting effect) that in crosses with it, black would remain fully active. I have pointed out (1905) one similar case (of partially reversed dominance) in which certain smooth guinea-pigs form gametes of such potency as to partially inhibit in their cross-bred young the usually dominant 'rough' character of the coat. That the action in question was a temporary one, one of *inhibition,* was shown by the fact that the rough character could be recovered in full intensity in generation F_2.

Bateson, Saunders and Punnett have also shown recently (1906) that white plumage in poultry, ordinarily a dominant character, may in certain strains function as a recessive. The different behavior of yellow, in relation to other pigment types, in mice and in guinea-pigs, becomes less surprising when we learn that within the same species the relative potency of a character may vary to such an extent that it functions sometimes as a dominant, sometimes as a recessive character, in crosses with the same alternative type.

In several recent papers I have pointed out the fact that the theoretical 'purity of gametes' of Mendelian inheritance does not exist. No more does the *purity of factors* exist. We can not avoid the idea of impurity of the gametes, by introducing the conception of 'factors,' for the factors are as certainly impure as the gametes.

To sum the matter up, it is certain that unit characters exist, but it is equally certain that the units are capable of modification; gametic segregation certainly occurs in some cases (Mendelian inheritance), it does not occur in others (blending inheritance); *factors* of characters certainly exist, when characters are demonstrably complex and result from the coexistence of two or more simpler ones, as, for example, a purple pigmentation due to coexistence of red and of blue chloroplastids in plants. But let us in no case introduce more factors into our hypotheses than can be shown actually to exist.

BIBLIOGRAPHY.

ALLEN, G. M.

1904. The heredity of coat-color in mice. Proc. Am. Acad. Arts and Sci., vol. 40, pp. 61-163.

BATESON, W.

1903. The present state of knowledge of colour-heredity in mice and rats. Proc. Zool. Soc., London, 1903, 2, pp. 71-99.

BATESON, W., SAUNDERS, E. R., AND PUNNETT, R. C.

1906. Experimental studies in the physiology of heredity. Reports to the Evolution Committee of the Royal Society, III., 53 pp., 4 figs.

CASTLE, W. E.

1905. Heredity of coat-characters in guinea-pigs and rabbits. Carnegie Institution Publications, No. 23, 78 pp., 6 pl.

CUÉNOT, L.

1905. Les races pures et leurs combinaisons chez les souris. Arch. de Zool. Exp. (4), tom.

3, notes et revue, pp. cxxiii–cxxxii.

MORGAN, T. H.

1905. The assumed purity of the germ-cells in Mendelian results. Science, n. s., vol. 22, pp. 877–879.

TSCHERMAK, E.

1906. Ueber Bildung neuer Formen durch Kreuzung. Resultats sci. du Congrès internat. de Botanique, Wien, 1905, pp. 323–330. Fischer, Jena.

WILSON, E. B.

1906. Mendelian inheritance and the purity of the gametes. Science, n. s., vol. 23, pp. 112–113.

W. E. CASTLE.

ZOOLOGICAL LABORATORY, HARVARD UNIVERSITY, July 23, 1906.

PRELIMINARY DESCRIPTION OF TWO NEW SPECIES OF THE GENUS DICERATHERIUM MARSH, FROM THE AGATE SPRING FOSSIL QUARRY.

AMONG the commoner forms obtained by field parties of the Carnegie Museum in this rich deposit of bones, which has previously been described,[1] are two new species, provisionally referred to the genus *Diceratherium.* The fact that *Diceratherium* is found in this horizon, which has been regarded as late Tertiary (by Marsh as Pliocene) is highly interesting, and it was thought by the present writer (*l. c.,* p. 491) that it might possibly belong in the lower Miocene. The study of the new material reveals the fact that the animals here represented are apparently somewhat more modified than the Diceratheria from the John Day beds.

The geological horizon in which this quarry is situated is at the top of the Harrison beds (Dæmonelix beds of Barbour, or the upper Arikaree of Darton). This entire section, the Gering, the Monroe Creek, the Harrison and the Nebraska beds, which overlie the Oligocene, should, I think, be regarded as lower Miocene, though the Nebraska beds may possibly represent the middle Miocene.

Diceratherium niobrarensis, n. sp.

The type, No. 1,271, of this species is a well-preserved skull, with the nasals disarticulated at the fronto-nasal suture. The nasals were found in the talus below the point where the skull was obtained, and presumably belonged to it. The premaxillaries are wanting, as is also the posterior portion of the left zygomatic arch. Except P^1 and the incisors the dentition on both sides is beautifully preserved. The principal characters of the type are as follows: Skull mesaticephalic.

$$I\frac{1}{2?},\quad C\frac{0?}{0?},\quad P\frac{4}{3?},\quad M\frac{3}{3?}.$$

The brain-case is large, the occiput high, and there is a well-formed sagittal crest with a narrow and rather shallow groove in the median line. The frontals are quite broad and convex laterally. When the nasals, which undoubtedly belong to the same specimen, are placed in position, they, with the frontals and parietals, unite in displaying an antero-posterior saddle-shaped concavity on the top of the skull. Near the anterior extremity the nasals are provided with a pair of well developed horn-cores, about 24 mm. long, rugose and subtriangular in section. Anterior to the base of the horn-cores the nasals are rapidly abbreviated, terminating in a blunt point projecting forward and downward. The narial openings, the foramen magnum, and the orbits are large. The infraorbital foramen is situated above the anterior part of P^3. The zygomatic arch is rather slender. There is no large tubercle on the supra-occipital as in *Diceratherium armatum,* but there is a prominent median ridge, which continues from near the superior margin of the foramen magnum to the top of the inion. The foramen magnum is subtriangular in outline. The occipital condyles are large and well separated by a broad median notch inferiorly. The paroccipital and postglenoid processes are very prominent, and their bases almost touch one another. The posterior nares extend forward to the anterior part of M^2. As has been stated, the first premolar is unfortunately not present in the type, but another individual of the same species (No. 1,273) shows this tooth much more reduced than in *Diceratherium armatum.* All the teeth have internal and external cingula, and are otherwise quite similar to those found in the species from the John Day.

---

[1] *Annals of the Carnegie Museum,* Vol. III., pp. 487–494, 1906.