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AMERICAN NATURALIST

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FACTORS AND UNIT CHARACTERS IN MENDELIAN HEREDITY

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Columbia University

The factorial hypothesis has played an important rôle in Mendelian heredity, and while students of Mendel's principles have had on the whole a pretty clear idea of the sense or senses in which they have made use of factors or symbols, yet those not engaged in the immediate work itself have, I believe, often been misled in regard to the meaning attached to the term factor, and by the assumed relation between a factor and a unit character. The confusion is due to a tendency, sometimes unintentional, to speak of a unit character as the product of a particular unit factor acting alone, but this identification has no real basis. It has, in fact, more than once been repudiated, yet the confusion has been so persistent that I venture to try to make clear my own position at least—it is one I think with which in the main many students of heredity will agree—in regard to the relation between unit-factors and unit-characters. I shall do this by means of several examples taken from my breeding experiments with the fly, *Drosophila ampelophila*.

The eye of this fly is red. A mutant arose with a vermilion eye. Crossed to the wild or red-eyed fly, the new color proved to be a Mendelian recessive.

According to the scheme that Mendel followed, red, *R*, and vermilion, *V*, are symbolized as complete and contrasting characters carried by the germ-plasm of the hybrid. They are assumed to separate in the germ-cells, and as a consequence two kinds of these cells are produced.

According to a more modern interpretation, known as the presence and absence theory, vermilion is supposed to arise through the loss of something from the germ-plasm of the wild fly. This something is not supposed to be the factor for vermilion, but another factor. On this scheme the red eye would be represented by the letters *RV*, and the vermilion eye by *rV;* as though the vermilion color arose through the loss of a red factor.

The relative advantages of these two modes of representation become apparent when two pairs of factors are involved. For instance, a new eye color—pink—appeared as a mutant. It, also, was recessive to red. Mendel's scheme would make the pink character the mate of the red character, just as vermilion had been before. But if pink and vermilion were mated to each other, it is not clear whether vermilion and pink should be treated as contrasted characters, or whether each should still be treated as allelomorphic to red. If either of these alternatives is adopted, the scheme fails to account for what actually happens. Mendel did not meet with such a situation, for none of his paired characters involved two changes in kind in the same organ, and consequently the problem did not exist for him.

Bateson did meet with just this situation in the case of the comb of fowls and the coat color of mice. His scheme, if applied to the present case of the eye colors in *Drosophila,* would be to represent red by *RV*, vermilion by *rV*, and pink by *Rv*. This scheme illustrates first why when vermilion is bred to pink a red-eyed fly, *rVRv,* should result; second, why in the second generation the proportion 9:3:3:1 should appear;[1] and third why in the eye

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[1] Except in so far as modified by sex-linkage.

color series a new color is expected in the F_2 generation, represented here by rv. This new color I called orange, and since rv only meant two absences, I followed the conventional method and added the symbol O to stand for orange. The completed formulæ were:

RVO	red
rVO	vermilion
RvO	pink
rvO	orange

This is identical with the scheme that Bateson adopted for the mouse color series, viz:

$GBCh$	gray
$gBCh$	black
$GbCh$	cinnamon
$gbCh$	chocolate

In a later paper (1912) I used the symbol P instead of R, so that the series stood:

PVO	red
pVO	vermilion
PvO	pink
pvO	orange

Let us now examine some of the possible interpretations of these symbols to see in what sense the letters were used for factors.

It is undoubtedly *implied, on the presence and absence scheme,* that something is *lost* from the original germplasm PVO when the vermilion pVO arises. The vermilion color is supposed to be the product of what is left when this something (called P) is lost. It is not supposed on this hypothesis that the vermilion factor alone is responsible for the vermilion color, for it is hypothetically only a part of what is left when something (P) is lost. Yet it is the identification of the vermilion factor with the vermilion eye-color that the opponents of Mendelism seem anxious to impute to the Mendelians.

Again, when the pink eye mutant appeared, it would have been assumed, on the presence and absence theory, that something was lost, so that the formula is *PvO*. Here again the pink color is the result of all that is left when something (*V*) is lost. Pink is not assumed to be produced by a factor *P*, but by what is left when a factor *V* is lost. An egg is supposed to have lost something and vermilion developed, another egg is assumed to have lost something else and pink developed. It was the loss of the vermilion factor that allowed pink color to develop, and the loss of the pink factor that allowed vermilion color to develop. When pink and vermilion are mated together, the original color—red—is restored, because on this scheme what each has lost is made good by what is found in the other.

To my series of eye color factors the letter *O* was added to indicate the nature of the color produced when two factors, *P* and *V*, were assumed to be absent. The symbol *O* at that time did not seem to stand in the formulæ on the same footing as *P* and *V*, because it stood for a color, and not for a factor that had been lost from the germ-cells of the wild fly. But since on the presence and absence scheme *O* stood for the residuum after *P* and *V* were lost it stood for the same sort of thing as did *P* and *V*, for *P* and *V* also stood for residua, *when they were not used as symbols for factors*. This will be made clearer later.

When the experiments had progressed to this stage, a new eye color appeared that was called eosin. Mated to orange it gave red; therefore, it seemed that this mutant must have contained *P* and *V*, and I inferred that it owed its color to the loss of an imaginary *O* factor. Eosin was represented, therefore, by *PVo*. But a moment's thought will show that on this scheme, *as long as P and V are present, any* loss from the germ-plasm (giving a new eye color) added to orange should give red, because orange would contain what the new mutant had lost.

The history of this case will show how, with the best of intentions, one may be led into a paradoxical position in regard to the use of factors. Even admiting that the representation is purely symbolic, the letters used may unintentionally come to stand for different things. Thus in the case first cited, the letter *P* in the formula *vP* stood for a *residuum* that gave pink, but in the formula *Vp,* the letter *p* stood for the loss of a *P-factor,* yet *p* is the allelomorph of *P*, which latter, as stated, meant the residuum when *V* was lost. In other words, a double meaning was attached to *P,* for it stood both for the *P*-factor, which was only a part of the residuum, and also for the residuum as a whole. It is this doubleness of meaning that gives the opponents of Mendelian inheritance an occasion to impose upon the factorial hypothesis a meaning that is really foreign to it. Admitting that the Mendelians themselves have not always taken the pains to state explicitly that the symbols represent both a factor and a residuum, there is still little or no justification in imputing to the presence and absence theory the view that a given character, pink color, for instance, is the product of a pink factor alone. The attempt to impute to the factorial hypothesis the same interpretation that Weismann made use of in his theory of determinants rests largely upon an erroneous understanding of the symbolism employed. Weismann identifies each character of the organism as the product of a special determinant. The factorial hypothesis assumes only that the cell in one case is different from the cell in the other, the difference relating, it is true, to some part, but the character produced may be the result of the whole or of much of the cell, and not of one part alone.

There is a further difference between these two points of view. A change in a factor may have far-reaching consequences. Every part of the organization capable of reacting to the new change is affected. Though we seize upon the most conspicuous difference between the old type and its mutant, and make use of this alone, every student of heredity is familiar with cases where more than the part taken as the index is affected. Weismann's theory, on the other hand, seems as a rule to identify each character with a special determinant for that character, and his meaning is clear when it is remembered that the process of development on Weismann's view is a process of sorting out of the determiners of the germ-plasm into different regions of the body. The factorial hypothesis makes no such assumption, but refers differentiation to the interaction of the parts on each other—every cell retaining the full complex of the original germ-plasm. Hence the possibility of the far-reaching effects of any change in the germ-plasm!

II

The presence and absence *system of nomenclature* (aside from its implications as to what is meant by presence and absence) has till the present time justified itself, when properly interpreted, by its usefulness. It seems to me that as a system of nomenclature it may be used, if one so desires, quite apart from the idea, that a loss in a character involves necessarily a loss in the germ-plasm. I can bring forward one clear case at least that seems to me difficult to explain if absence is taken literally to mean the loss of a factor from the germ complex. I refer to a mutation "backwards," which in the older terminology meant reversion, or atavism.[2] In my pure cultures (at rare intervals) individuals have appeared like the original progenitors of the stock. I have not scrupled to put aside this evidence, because contamination, even with extreme care, will occasionally occur; and even if a reversion had occurred there would be no way of proving that it was such and not contamination. In fact, eosin first appeared in white-eyed stock and seemed to arise through reversion, but at the same time it seemed so improbable that this could happen that I tried to account for its appearance in a roundabout way. Now I should say that the factor *w* reverted to *W*.

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[2] It is needless to add, perhaps, that atavism by recombination is not here for a moment brought into question.

But the clear case referred to above is the following: Quite recently there appeared in a culture bottle that had been producing for more than four months (probably for twelve generations) only wingless flies, an individual with one "wingless" wing and one normal wing on the other side. Here the evidence is conclusive that reversion had occurred. The wingless stock in which the asymmetrical form arose had purple eyes and the same eye color was present in the new type. As the eye color was relatively new at the time the chance that contamination had occurred was rendered very unlikely. Had contamination by a red-eyed fly occurred, making the new type a heterozygote, the eye color would have been the dominant red. When the asymmetrical fly (♂) was bred to wingless females only wingless flies appeared, for three or more generations. The reversion, therefore, was somatic and did not involve the germ-plasm, yet this fact does not invalidate the question here raised.

In the light of this evidence, as well as the evidence from ever-sporting varieties (that may also be considered, I think, as mutating and reverting as regular processes), I believe it unwise to commit ourselves any longer to a view that a recessive character is necessarily the result of a loss from the germ-cell. We need only assume that some readjustment occurs, and as the result a new factor is produced. A simile may make this clearer, if not taken too literally. If we suppose that a factor is a labile aggregate, and that a rearrangement in it occurs, then the new aggregate in connection with the other parts of the cell produces a character that differs from the old one. Here there need be no loss, but only a change in configuration with a corresponding change in the end product in which the changed part plays a rôle, along with the other parts of the cell. A factor, in this sense, may exist in two or more forms according to the state of equilibrium; one of its states is dominant-producing, and the other is recessive-producing. Such a view may make it easier for us to appreciate that a mutation need not be a loss, and that a recessive may revert in the sense that it may mutate. In chemical terms, the process is reversible.

III

As I have pointed out, the presence and absence nomenclature, if properly understood, offers no practical difficulties so long as only two changes in the same organ are involved, but in experiments with *Drosophila* we have passed beyond this stage and must have at command a system by means of which more than two factors may be easily and conveniently represented. How impossible it becomes to use the presence and absence nomenclature when new characters are appearing may be shown by the following illustrations.

As already stated, Mendel's method of representing the allelomorphic pairs sufficed so long as one new character is contrasted with the original one. In this sense the relation of a vermilion-eyed mutant to the red-eyed fly could be fully represented by treating red (R) and vermilion (V) as allelomorphs. But when another mutation in eye color appeared the scheme was no longer feasible. Now, in the same sense in which it became necessary to supplant Mendel's scheme by another one, it becomes necessary to change the presence and absence scheme when a third mutation appears in the same organ; for, the presence and absence scheme is not sufficiently elastic to allow the introduction of a new term in the series, unless a complete revision of the method is made each time that a new mutation in kind occurs.

For example, when it becomes desirable to compare the eosin eye with the vermilion-pink (or orange eye already known) it becomes puzzling to know what symbols to adopt. If, as I assumed, the symbol O in VPO is changed to small o, then the formula for eosin becomes VPo. But this is inconsistent with the scheme already adopted because the small letter o stands for a character called eosin. If to avoid this ambiguity a letter E (or e) is introduced for eosin the situation is even more puzzling.

The only logical method that could be followed, if an attempt is made to apply consistently the current scheme of presence and absence[3] would be the following:

When it becomes necessary to construct a series, let us say one involving three characters (*PVE*), the three double recessives (*Pve, pVe, pvE*) must be made up and suitable names given to them, the initial letters of these names then become the factors sought. Such a procedure not only involves holding in suspense the naming of the factors until all the double recessives have been obtained, but involves renaming all the factors, each time a new series is made up.[4] This method is not likely to recommend itself if a simpler one can be employed. The plan here advocated avoids such difficulties.

The first letter (or the first and second or some other significant letter) of the name of the new character stands, as heretofore, as its symbol; thus *P* stands for the pink factor and small *p* stands for the correlative factor of the pink-eyed fly. Whether small *p* represents the loss of the *P* factor, or a change in that factor when the pink eye appears, is immaterial. The large letter represents the dominant character in conformity with the current scheme.[5] The eye color series will then be:

Red	*PVE*
Vermilion	*PvE*
Pink	*pVE*
Vermilion-pink	*pvE*
Eosin	*PVe*
Eosin-vermilion	*Pve*
Eosin-pink	*pVe*
Eosin-pink-vermilion	*pve*

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[3] It is the nomenclature that is here brought into question and not, for the moment, the underlying conception of presence and absence, for even in my scheme this conception might still be held if it seemed desirable to do so.

[4] When, as in the case of the mouse colors, all the members of the series are known, there is no difficulty in finding suitable symbols, for the current names of the characters give the letters for the symbols.

[5] When a new *dominant* character appears it is represented by the capital letter and its allelomorph in the original form by a small letter.

The same scheme might be followed by using the small letters for the factors in the original red eye: thus red = *pve;* and the capital letter for the corresponding factor in the mutant; thus, vermilion = *pVe,* etc. A disadvantage of this scheme is that the large letter now stands for a recessive condition and the small letter (its allelomorph) for a dominant condition. Usage has, however, made us accustomed to interpreting a large letter as a dominant, its corresponding recessive (its allelomorph) by a small letter and therefore the plan first suggested seems more desirable. It is with much reluctance that I suggest this change in our present nomenclature. It has become necessary, however, in the case of the *Drosophila* to find some way to represent consistently those cases in which three or more factors are involved in the same organ. The change is not one of any theoretical importance, but a practical necessity for all cases of this kind. When one new character is contrasted with the original one, Mendel's way may still be the simplest and easiest way of formulating the results, and will, no doubt, be followed. When two new characters are involved the formula of presence and absence is a sufficient way of representing the symbols. But when new mutations are appearing some other plan must be adopted. The one here suggested has at least two merits: it is as easy to use as either of the foregoing for one and for two characters, and can also be utilized when any number of further mutations appear in the same organ.

The scheme applied to body colors is as follows: Two mutants arose, yellow and black, and by recombination, a "brown" or yellow-black fly was obtained. The symbols would be wild fly = *YYBB,* yellow = *yyBB,* black*YYbb,* and yellow-black *yybb.* Two other mutations in body color have appeared, both dark, one is called ebony, *eb* and the other sable, *s.* When brought in connection with the preceding mutation the gametic symbols would be:

Wild fly	YBE_bS
Yellow	yBE_bS

Black	YbE_bS
Yellow-black	ybE_bS
Ebony	YBe_bS
Sable	YBE_bS
Etc.	

Another combination is represented by certain wing mutations. A mutant called miniature appeared and may be represented by m; another mutant appeared, called rudimentary, and may be represented by r; and a third form, produced by recombination, was called miniature-rudimentary, mr. The symbols for this series would be:

Wild fly	MR
Miniature	mR
Rudimentary	Mr
Rud.-min.	mr

Later several other mutations in wings also appeared. Six of these may be selected for illustration, viz: Vestigial,[6] v_g; Bifid, b_i; Arc, a_r; Curved, c_v; Jaunty, j; Balloon, b_a. If these are brought into connection with the foregoing the symbols for the wild fly in terms of these factors would be:

$$\text{Wild Fly} = M, R, V_g, B_i, A_r, C, J, B_a.$$

In order to study the relation of these characters to each other it has become necessary to combine many of them and in order to represent the results some system of symbols must be adopted. Obviously, it would be highly undesirable to be obliged to revise the system each time that any of these new mutations are brought into relation with those that have already been compared.

It may be asked, why may not the current scheme be retained, since in most cases only two characters are likely to be involved and characters can always be contrasted in pairs on this scheme? The answer is that more

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[6] This is the wingless fly of former papers.

characters in the same organ have already been obtained, and it is at least as important to have a scheme by which they can be represented as it is to have a scheme where two characters only are studied. Moreover, the more characters that are obtained that show association in inheritance the further we may hope to go in our analysis of the consitution of the germ-plasm, which is admittedly the fundamental problem in the study of heredity. We must have some convenient way of representing the symbols in order to carry out this analysis, and on the grounds of convenience alone some scheme other than the current one must be found, at least for such a case as this of *Drosophila*. Another scheme has, in fact, been adopted by Baur and Hagedoorn. The letters that stand for the factors bear no relation to the name of the characters involved. This scheme allows the addition of any number of new factors to a series under consideration. In practise, however, this plan makes it extremely difficult to understand what any formula means without continual reference to the key of symbols used. We have found in practise that the scheme is so puzzling when several factors are under consideration that we have been led to follow the current method of representing each factor by the initial letter (or other suggestive letters) of the character that it stands for. Except in this regard the method of formulation here suggested is similar in principle to the A.B.C. scheme of Baur.

VERTICAL DISTRIBUTION OF THE CHÆTOGNATHA OF THE SAN DIEGO REGION IN RELATION TO THE QUESTION OF ISOLATION *VS.* COINCIDENCE

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Introduction

Ever since Jordan ('05) called attention to the almost universal neglect of Moritz Wagner's contention that geographical isolation is an important factor in the formation of species, "Jordan's Law" ('05, p. 547) that "given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort," has been subject to much controversy and diversity of opinion. The conclusions of those biologists dealing with land fauna have, as a rule, emphasized the fact of isolation, whereas those of the marine biologist have tended to emphasize the fact of coincidence, or at least to doubt the truth of isolation. It is therefore part of the business of the marine biologist, through whose investigations new and important data have been accumulated, to throw as much light as possible upon the problems of isolation and coincidence. This is particularly true with regard to data concerning the Chætognatha because, as pointed out by Kofoid ('07), the group is exclusively marine and pelagic, and so completely circumscribed as to make it probable that their entire evolution has taken place within the confines of the open sea.

At the outset, the fundamental differences in the problem with reference to land and marine fauna must be emphasized. Kofoid ('07, p. 241) has pointed out that "barriers are far less in evidence in the environment of the pelagic fauna than in that of the shore or of the land," and that, while there do exist "limited regions along the margins of great ocean currents" which might afford means of hydrographic isolation, changes in hydrographic conditions such as temperature, density, substances in solution, illumination, etc., are so gradual that stratified areas do not exist to any large extent. Furthermore, land faunas are segregated into neighboring or remote areas almost entirely with reference to latitude and longitude. With pelagic faunas this is not necessarily, perhaps not usually, the case, for a third dimension—*depth*—is involved. It therefore follows that closely related pelagic organisms may be *coincidently distributed as regards latitude and longitude, and still be completely isolated in their vertical distribution.*

This fact signifies that data respecting the isolation of a pelagic fauna will be wholly inadequate unless the vertical distribution of the particular species or group under consideration be capable of determination and analysis. In his discussion of "the coincident distribution of related species of pelagic organisms as illustrated by the Chætognatha" Kofoid ('07), while recognizing the force of this point, has utilized data pertaining almost exclusively to latitude and longitude. This was consequent upon no lack of appreciation on his part of the real problem involved, but solely to the fact that the necessary data were missing. Moreover, what little has been previously discovered relative to the vertical distribution of this group was based upon observations scattered over such large areas as to make any approach to critical analysis of the problem of isolation almost impossible. However, through the efforts of the San Diego Marine Biological Station, a mass of data has been collected which enables an entirely new light to be thrown upon this problem.

Since 1904 this station has centered its collecting upon an irregular area of about 30 square miles lying between 32° 20′ and 33° 30′ N., and between the coast and 119° W. From this small area 68,962 specimens comprising ten species of Chætognatha have been collected, and, as all depths between the surface and 350 fathoms have been examined with horizontal closing nets, the depth from which each specimen was obtained is known with the nearest approach to certainty permitted by any known method of collecting. As a critical analysis of this data has been published elsewhere [see Michael ('11)] reference must be made to that paper for the methods, problems and details involved in determining the vertical distribution of each species, so that, in the following pages, only the fruits of that research bearing directly upon the present subject-matter will be discussed. It will be shown (1) that of the most closely related "couplets" of species only one has been taken from the San Diego region, (2) that, of those species occurring in this region, each has its own definite and *specific* manner of vertical distribution, (3) that the most diverse species (morphologically) have the most coincident vertical distribution, and (4) that, while several species have sometimes been taken in the same haul, rarely more than one was represented by sexually mature individuals.

RELATIONSHIPS BETWEEN THE SPECIES OF CHÆTOGNATHA

Adopting Ritter-Záhony's ('11 *b*) careful revision of the Chætognatha as our starting point, the group becomes separable into six genera, *Sagitta, Pterosagitta, Spadella, Eukrohnia, Heterokrohnia* and *Krohnitta*. *Sagitta* is represented by eighteen valid and four rather doubtful species, *Pterosagitta* is represented by one, *Spadella* by one, *Eukrohnia* by two, *Heterokrohnia* by one and *Krohnitta* by two.

Now the eighteen valid species of *Sagitta* fall into two sharply contrasted groups by virtue of the presence or absence of a *collarette* which is a conspicuous thickening of the epidermis posterior to the head. Ten species are provided with this structure, while in eight it is entirely missing. The species comprising each group are listed below:

Species with Collarette

S. bipunctata
S. decipiens
S. neglecta
S. regularis
S. ferox
S. planktonis
S. hispida (*robusta* Doncaster)
S. tenuis
S. pulchra
S. sibogæ

Species without Collarette

S. enflata
S. hexaptera
S. lyra
S. gazellæ
S. serratodentata
S. bedoti
S. elegans
S. macrocephala

Those species having the *collarette* may be further separated into diverse groups by means of the following *main* characteristics: (1) Those in which the body is transparent as contrasted with those in which it is opaque, (2) those in which the collarette extends to the ventral ganglion as contrasted with those in which it never extends more than half way to the ganglion, (3) those in which the anterior fin extends to the ventral ganglion as contrasted to those in which it does not, (4) those having more than 50 per cent. of the posterior fin in front of the tail-septum as contrasted with those having more than 50 per cent. of the fin behind the tail-septum, and (5) those in which the anterior fin is shorter than the posterior fin as contrasted with those in which the posterior fin is the shorter. Let it not be thought that these are the only characteristics used to differentiate the various species of *Sagitta* provided with the *collarette*. Far from it! Many others of great specific importance are made use of, but, if classified according to those just enumerated, the most closely related "couplets" remain inseparable while those species not so closely related are readily separated from each other. This may be graphically represented by arranging these five pairs of contrasted characteristics into a series of "rows" and "columns" and then writing the names of the species, having those in question in each square made by the intersecting "arrays." Such an arrangement is given below:

TABLE I.

	More than 50 Per Cent. of Posterior Fin in Front of Tail-septum	Less than 50 Per Cent. of Posterior Fin in Front of Tail-septum	Anterior Fin Shorter than Posterior Fin	Anterior Fin Longer than Posterior Fin
Body transparent.	*S. bipunctata* *S. decipiens* *S. pulchra*	*S. tenuis*	*S. bipunctata* *S. decipiens* *S. tenuis*	*S. pulchra*
Body opaque.	*S. planktonis* *S. sibogæ*	*S. neglecta* *S. regularis* *S. ferox* *S. hispida*	*S. neglecta* *S. regularis* *S. hispida*	*S. planktonis* *S. ferox* *S. sibogæ*
Collarette extending to ventral ganglion	*S. planktonis*	*S. neglecta* *S. regularis* *S. ferox*	*S. neglecta* *S. regularis*	*S. ferox* *S. planktonis*
Collarette not extending over half way to ventral ganglion.	*S. bipunctata* *S. decipiens* *S. pulchra* *S. sibogæ*	*S. hispida* *S. tenuis*	*S. bipunctata* *S. decipiens* *S. hispida* *S. tenuis*	*S. pulchra* *S. sibogæ*
Anterior fin extending to ventral ganglion.	*S. planktonis* *S. pulchra* *S. sibogæ*	*S. neglecta* *S. regularis* *S. ferox* *S. tenuis*	*S. neglecta* *S. regularis* *S. tenuis*	*S. ferox* *S. planktonis* *S. sibogæ* *S. pulchræ*
Anterior fin not extending to ganglion.	*S. bipunctata* *S. decipiens*	*S. hispida*	*S. bipunctata* *S. decipiens* *S. hispida*	

An examination of this table shows that in every square where *S. bipunctata* occurs there also *S. decipiens* is found, and the same relation holds between *S. neglecta* and *S. regularis*. These four species, then, are to be regarded as constituting two very closely related "couplets." A third "couplet," whose constituent species are somewhat less closely related, is that of *S. ferox* and *S. planktonis*, which only differ in the proportional extent of the posterior fin in front of the tail-septum. The remaining species are clearly distinct.

Turning attention to those *Sagitta* devoid of the collarette, *S. enflata, S. hexaptera, S. lyra, S. gazellæ* and *S. bedoti* are exceedingly transparent, while *S. serrato-*

dentata, S. elegans and *S. macrocephala* are opaque. While the three opaque species are unmistakably distinct, we find that, in the transparent group, *S. enflata* and *S. hexaptera* form one closely related "couplet" while *S. lyra* and *S. gazellæ* make another. This is shown more clearly below:

TABLE II.

	Posterior Fin Extends Caudally to Seminal Vesicles	Posterior Fin Never Extends to Seminal Vesicles	Anterior Fin Confluent with Posterior Fin	Anterior and Posterior Fins Always Separated by an Interval
More than 50 per cent. of posterior fin in front of tail-septum.	*S. lyra* *S. gazellæ*	*S. enflata* *S. hexaptera*	*S. lyra* *S. gazellæ*	*S. enflata* *S. hexaptera*
Less than 50 per cent. of posterior fin in front of tail-septum.	*S. bedoti*			*S. bedoti*

All told, then, we have in the genus *Sagitta* five closely related "couplets" of species. It is not to be presumed that every "couplet" expresses the same degree of closeness between its two members, for such is not the case. Unquestionably the two species most closely related are *S. neglecta* and *S. regularis,* and the two least so—*S. ferox* and *S. planktonis*. Now if we list these "couplets" in one column and the species so far taken from the San Diego region in another, the interesting fact is evident that, except in one case, the San Diego *Sagitta* contain only one species of each "couplet." Such lists are given below.

San Diego Sagitta	*"Couplets"*
S. neglecta	*S. neglecta-S. regularis*
S. bipunctata	*S. bipunctata-S. decipiens*
S. lyra	*S. gazellæ-S. lyra*
S. enflata	*S. enflata-S. hexaptera*
S. hexaptera	
S. planktonis	*S. planktonis-S. ferox*
S. serratodentata	

Looking to the other genera we find *Eukrohnia* composed of two species (*E. hamata* and *E. fowleri*), *Krohnitta* of two (*K. subtilis* and *K. pacifica*), and *Heterokrohnia, Pterosagitta* and *Spadella* of one each. Now *E. hamata* and *E. fowleri* form an exceedingly closely related "couplet," but only the former is known to occur in the San Diego region. Again, *K. subtilis* and *K. pacifica* are so nearly alike that it is very difficult to describe their differences although they are probably valid species. Yet, only the first has been found in California waters. Of the three remaining genera *Heterokrohnia* and *Spadella* are not represented in our collections, and *Pterosagitta* by only one individual of its single species *P. draco*.

In so far, therefore, as the relationships among the Chætognatha have been correctly interpreted, it is evident that, except for the occurrence of both *S. enflata* and *S. hexaptera,* there is no instance of two of the most closely related species having been taken from the San Diego region.

GENERAL DISTRIBUTION OF THE "COUPLETS"

Having pointed out that only one of a "couplet" of the most closely related species occurs in the San Diego region, it will be interesting to ascertain to what extent the same relation holds in other parts of the world. Furthermore, wherever both members of a "couplet" are recorded from the same vicinity it will be to the point to determine, if possible, to what extent their distribution within the area is coincident or isolated.

S. NEGLECTA AND S. REGULARIS

The members of this "couplet" may be designated as warm water, epiplanktonic species whose northern and southern limits of distribution are 35° N. and 9° S. The highest surface temperature recorded in connection with their capture is 29° C. and the lowest 15°.5 C. They were both originally described by Aida ('97) from Misaki

Harbor, where, so far as known, they are coincidently distributed.

In the *Siboga* area Fowler ('06) records 45 surface hauls containing either one or the other species. Of these, 35 contained *S. neglecta* but not *S. regularis,* and 6 contained *S. regularis* but not *S. neglecta.* In only 4 hauls were both species obtained. When we remember the large area covered by this expedition these results point toward contiguous and slightly overlapping, rather than coincident distribution.

The two expeditions of the *Pola* to the Red Sea obtained both *S. neglecta* and *S. regularis.* The collections of the first expedition (1895/96) were made in an area limited by 21° 27′ and 29° 45′ N., and 32° 30′ and 38° 30′ E., while those of the second (1897/98) were made somewhat further south and east within the limits of 15° 1′ and 28° 42′ N., and 32° 56′ and 42° 31′ E. Ritter-Záhony ('09) records 32 surface hauls made during the first expedition that contained one or other of the two species. Of these, 25 contained only *S. regularis,* 6 only *S. neglecta,* while in but one haul were both species taken. During the second expedition 27 surface hauls were made of which 12 contained *S. neglecta* only, 10 *S. regularis* only, and 5 contained both. These data strongly suggest that the two species are distributed in contiguous regions which overlap considerably along the edges.

Of the other expeditions, the *Biscayan, Plankton* and *National* failed to catch either species. The *Gauss* obtained both in the region of Port Natal, but never in the same hauls. Doncaster ('02) records both under the names of *S. septata* and *S. bedfordii* from the Maldive and Laccadive Archipelagoes, but nothing is stated as to whether they were obtained in the same hauls or not. Ritter-Záhony ('10*a*) records *S. regularis* from Sharks Bay, Australia, but failed to find *S. neglecta.*

S. BIPUNCTATA AND S. DECIPIENS

S. bipunctata is a eurythermal, euryhyaline and cosmopolitan species recorded from the epiplankton of the arctic, sub-arctic, north temperate, tropical and south temperate Atlantic Ocean, the south temperate and tropical Indo-Australian Ocean, and the north temperate Pacific Ocean, as well as from the mesoplankton of the north temperate and tropical Atlantic. Its northern limit is 74° N. and its southern 28° S. The highest temperature recorded in connection with its capture is 33°.6 C., while the lowest is 0°.2 C. *S. decipiens,* on the other hand, is mesoplanktonic. Both were taken from the Bay of Biscay, *S. decipiens* from between 100 and 200 fathoms, and *S. bipunctata* only in open vertical hauls made between 50 and 200 fathoms to the surface, the total yield being only 7 specimens. Ritter-Záhony ('10 *b,* p. 4) records both from the Irish Sea, but, in regard to *S. decipiens,* says: "*S. decipiens* is purely mesoplanktonic and in the Irish area was only found at depths varying from 164 to 1,150 fathoms." Concerning *S. bipunctata* he says that it is "confined to the epiplankton. . . . The quantity of *S. bipunctata* in the upper epiplankton is larger than in the lower." Finally, both species have been taken in the Atlantic Ocean between 60° N. and 8° S. but, while *S. decipiens* occurred only in open nets from below 100 fathoms and in closing nets from between 100 and 600 fathoms, *S. bipunctata* occurred only in the epiplankton. From this evidence it seems that wherever the two species occur in the same region they are isolated by their manner of vertical distribution.

S. LYRA AND S. GAZELLÆ

S. lyra is a cold water, nearly eurythermal species ranging from 73° N. to 7° 33′ S., the highest temperature recorded in connection with its capture being 18°.6 C. and the lowest 1°.1 C. It has been found in the epiplankton of the arctic, sub-arctic and north temperate Atlantic, and sub-antarctic Pacific Oceans, as well as in the mesoplankton of the sub-arctic, north temperate and tropical Atlantic, the tropical Indo-Australian and the north temperate Pacific oceans. *S. gazellæ,* on the other hand, is a rare form. A few specimens were first taken during the *Gazelle* expedition from the Indian Ocean (43° S.) from a depth of 75 and 1,300 fathoms. It is also recorded from the Atlantic Ocean (35°.5 S.), where it was taken in a single haul from about 1,400 fathoms, and from the Antarctic Ocean between 60° and 66° S., where it was taken from 10, 25 and 50 fathoms. These data indicate that *S. gazellæ* is confined to the southern hemisphere and tends to be distributed circumpolarly. Records of the *Gauss* expedition show that out of 88 hauls containing either *S. lyra* or *S. gazellæ,* 39 contained only the former, 42 only the latter, and 7 both species.

S. ENFLATA AND S. HEXAPTERA

S. enflata is a warm water purely epiplanktonic species whose northern and southern limits of distribution are 40° 24′ N. and 34° 52′ S. The highest temperature recorded in connection with its capture is 32° C. and the lowest 15°.5 C. It has been taken from the north temperate, tropical and south temperate Atlantic, the south temperate and tropical Indo-Australian and the north temperate Pacific oceans. *S. hexaptera,* on the other hand, is a eurythermal, nearly cosmopolitan species found in the lower epiplankton or mesoplankton of the arctic, sub-arctic, north temperate, tropical and south temperate Atlantic, the south temperate and tropical Indo-Australian and the north temperate and sub-antarctic Pacific oceans. Its northern and southern limits of distribution are 74° N. and 28° S., while the extremes of temperature recorded in connection with its capture are 29° C. and 6° C.

Both species have been taken together from the same areas during a number of expeditions. In the *Siboga* area Fowler ('06) records 58 surface hauls containing one or other of the species, of which 31 contained both, while 26 contained *S. enflata* but not *S. hexaptera*, and only one contained *S. hexaptera* alone. During the first expedition of the *Pola* to the Red Sea 32 surface hauls were made which contained both species, 21 which contained *S. enflata* but not *S. hexaptera*, and only one which contained *S. hexaptera* alone. During the second expedition not a single *S. hexaptera* was taken in surface hauls that was not accompanied by *S. enflata*, there being 13 hauls containing both and 29 containing *S. enflata* alone. Finally, during several expeditions covering parts of the Adriatic, Ionian and Ægean seas, Ritter-Záhony ('08) records 45 surface hauls containing *S. enflata*, of which 6 also contained *S. hexaptera*, and only 4 hauls in which the latter species was taken without the former.

These data certainly indicate a high degree of coincidence. However, the fact that *S. enflata* is rarely reported other than from the upper epiplankton and that *S. hexaptera* is more typical of the lower epiplankton and mesoplankton, suggests isolation with respect to sexual maturity. Concerning this Ritter-Záhony ('10 *b*), who has been very careful to distinguish immature from mature specimens, says: "Like *S. serratodentata*, *S. hexaptera* is a species which can not endure low temperatures until it has reached the adult stage. . . . We do not, as a rule, find large specimens until we come to the lower epiplankton." Until more is known regarding the stages of growth of these specimens taken on the surface together with *S. enflata* we can not regard the cases of coincidence revealed above as anything more than negative evidence of isolation.

S. PLANKTONIS AND S. FEROX

S. planktonis is a eurythermal species recorded from both epi- and meso-plankton of the north temperate Atlantic and Pacific oceans. It has not been reported north of 32° 45′ N., nor south of 8° 30′ S., except for a few small specimens from the Antarctic between 65° and

66° S. Its temperature range is from 27° C. to 4°.7 C. *S. ferox,* on the other hand, is a warm-water species confined, so far as known, to the epiplankton of the tropical Indo-Australian region. Both species were taken during the *Siboga* expedition, but, while *S. ferox* was taken in abundance from the surface, *S. planktonis* was taken only from the mesoplankton. There is no record of both having been taken in the same hauls except in those made with open vertical nets.

E. HAMATA AND E. FOWLERI

It is still an open question in my mind whether *E. fowleri* is a valid species or merely a synonym for *E. hamata.* Ritter-Záhony ('11 *b*) describes certain differences, but the characters used appear indicative of variation within the species rather than of constant specific characters. If they should prove synonymous, then *Eukrohnia* would be represented by only one species. However, assuming their validity, then *E. hamata* would be distributed in the mesoplankton of the Indian, Altantic and Antarctic oceans, while *E. fowleri* is rarer and perhaps more cosmopolitan, occurring in the Irish sea between 200 and 1,100 fathoms, in the Bay of Biscay below 325 fathoms, in the Malay Archipelago below 460 fathoms, and rarely in the open Atlantic below 500 fathoms. It might be added that *E. hamata* also occurs in the epiplankton of the Arctic and Antarctic regions, while *E. fowleri* always remains confined to the mesoplankton. During the *Plankton* expedition the species were taken together in only one closing-net haul made between 500 and 600 fathoms, and only twice out of 18 open vertical hauls from a variety of depths.

K. SUBTILIS AND K. PACIFICA

K. subtilis is regarded as a eurythermal cosmopolitan species ranging from 60° 12′ N. to 29° 30′ S. The temperature corresponding to its capture varies from 30°.8

C. to 5°.3 C. It is reported from both epi- and mesoplankton of the north temperate and tropical Atlantic and tropical Indo-Australian oceans, as well as from the epiplankton of the south temperate Atlantic and south temperate Indo-Australian oceans and from the mesoplankton of the north temperate Pacific. *K. pacifica,* on the other hand, is a warm-water epiplanktonic species from the tropical Atlantic and Indo-Australian, and the north temperate Pacific oceans. Its northern limit is 35° N. and its southern 7° 30′ S. During the *Siboga* expedition both species were taken together in but one haul, and that one made by an open vertical net from 1,000 fathoms. This is the only instance, so far as I can ascertain, where both species have been obtained from the same area.

In summing up we find that the members of each "couplet" tend to be isolated in one way or another. *S. neglecta,* for instance, maintains a distribution which, while overlapping more or less, is contiguous rather than coincident with that of *S. regularis.* In the case of *S. bipunctata* and *S. decipiens* the data show that wherever both are taken within the same area the former is confined to the epiplankton, while the latter occurs only in the mesoplankton. With *S. lyra* and *S. gazellæ* the distribution is never coincident, but, in some instances, contiguous and overlapping. *S. enflata* and *S. hexaptera* present the most striking evidence in favor of coincidence but, even here, the chances are that only the immature of *S. hexaptera* occur in the upper epiplankton, so that an effective physiological isolation is probably maintained. *S. planktonis* and *S. ferox,* while they do occur together in the *Siboga* area, are isolated by their manner of vertical distribution, *S. ferox* being epiplanktonic and *S. planktonis* mesoplanktonic. The members of the doubtful "couplet" comprising *E. hamata* and *E. fowleri* are only rarely taken in the same net hauls, which indicates contiguous rather than coincident distribution, although this appearance may be due entirely to the fact that *E. fowleri* is not abundant anywhere. Finally, *K. subtilis* and *K.*

pacifica have never been taken from the same region, excepting in the case of the *Siboga* expedition when they were obtained together in only one haul from 1,000 fathoms to the surface.

VERTICAL DISTRIBUTION OF THE CHÆTOGNATHA OF THE SAN DIEGO REGION

The 68,962 specimens of Chætognatha obtained from the San Diego region were distributed among the various species as follows:

S. bipunctata	51,670
S. enflata	10,127
S. serratodentata	6,575
S. lyra	271
S. neglecta	127
E. hamata	72
K. subtilis	50
S. planktonis	41
S. hexaptera	28
P. draco	1

Turning attention first to those species that must be regarded as visitants rather than residents of this region we find that *S. enflata, S. neglecta,* and the single specimen of *P. draco* were all obtained from the upper epiplankton mainly during February, 1905, when the surface temperature was 15°.5 C. One surface haul made on the morning of February 25 obtained 3,500 *S. enflata,* many of which were sexually mature, 9 immature *S. neglecta,* and the single very immature specimen of *P. draco*. A second surface haul, made the same morning, contained 3,100 *S. enflata* (most of them sexually mature) and 75 immature *S. neglecta*. Six more *S. enflata* and 38 immature *S. neglecta* were obtained in a surface haul made on April 29, 1905, and a seventh *S. enflata* in a surface haul made on June 11, 1908. Of the remaining *S. enflata,* 3,507 were obtained in open vertical hauls (from ten fathoms or less) during the fall of 1904, 3,500 having been taken in one haul. The five remaining *S. neglecta* were also obtained in the same haul, and the 13 *S. enflata,* still unaccounted for, were all obtained in open vertical hauls from 45, 75, 110 and 290 fathoms.

These data indicate that these three species can not be regarded as typical of the San Diego region, and since they occur abundantly in the surface waters of more tropical seas where the temperature reaches 34° C., it seems likely that they have been carried here by currents from the warmer regions, although no such currents are known with certainty. The probability of this supposition is somewhat increased because of their reoccurrence here during the past winter after an absence of over two years.

Of the remaining species, *S. bipunctata*, *S. serratodentata*, and *S. lyra* are the most typical of the San Diego region. The number of each species obtained from the various depths with horizontal nets is shown in the following table:

TABLE III

TOTAL NUMBER OF SPECIMENS OBTAINED WITH THE HORIZONTAL NETS

Depth in Fathoms	*S. bipunctata*	*S. serratodentata*	*S. lyra*	Number of Hours of Hauling
0–25	30,733	93	5	108.1
25–75	275	106	20	11.0
75–150	10	106	20	6.5
150–250	0	174	17	3.1
250–350	0	43	54	5.4

This table reveals the fact that *S. bipunctata* was obtained in by far the greatest numbers between the surface and 25 fathoms, and that it was not taken at all below 150 fathoms. *S. serratodentata,* on the other hand, appeared in greatest abundance between 150 and 250 fathoms, and *S. lyra* between 250 and 350 fathoms. However, the mere tabulation of the number of specimens taken from the various depths does not reveal the true significance of the data, for it is obvious, from the last column, that the amount of hauling, and consequently the amount of water filtered, has varied with the depth so that the *relative* density or abundance in the various depths is not represented by the total number of specimens obtained. A more accurate and justifiable presentation is to express the total number of specimens obtained from each of the above depths in terms of the average number per unit of time consumed in hauling. The following table reveals this relative abundance of the three species as thus determined:

TABLE IV

RELATIVE ABUNDANCE OR AVERAGE NUMBER OF SPECIMENS OBTAINED PER 20 HOURS OF HAULING[1]

Depth in Fathoms	*S. bipunctata*	*S. serratodentata*	*S. lyra*
0–25	5,685	17	1
25–75	420	193	36
75–150	31	326	61
150–250	0	1,123	110
250–350	0	159	200

It is evident that this table brings into still more striking relief the fact that *S. bipunctata* is most abundant between the surface and 25 fathoms, from where it decreases in abundance as the depth increases, while *S. serratodentata* increases from a minimum between the surface and 25 fathoms to a maximum between 150 and 250 fathoms, and *S. lyra* increases from a minimum near the surface to a maximum in the deepest water (250 to 350 fathoms). While it is very improbable, owing to variations in many environmental conditions affecting the abundance of the three species in the various depths, that subsequent collecting would ever result in *exactly* the same averages as given above—it is just as improbable that, if the hauls were distributed in approximately the same manner, with regard to such environmental conditions, as those from which the above data were derived, we should find the relative abundance much altered. Consequently it is no exaggeration to say that *each of these three species has its own definite and specific manner of vertical distribution just as truly as each has its own*

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[1] As relative abundance is independent of the particular unit of time selected for standardizing the data, a unit of 20 hours has been used instead of the more obvious 1 hour in order to eliminate fractions in the case of *S. lyra*.

specific morphological characteristics, and it would be quite as easy to identify the species from an analysis of data regarding its vertical distribution within an area *analogous* to the San Diego region as it would from the usual taxonomic descriptions.

Detection of specific differences in the vertical distribution of the remaining species is rendered more uncertain because so few specimens have been obtained. However, by taking the species one at a time, it will be seen that tendencies, at least, toward specification are revealed.

Sagitta planktonis

Eliminating those catches made with open vertical nets as of little or no value in determining the depths from which specimens were obtained, we find that seven *S. planktonis* were taken between the surface and 150 fathoms, two between 150 and 200 fathoms, six between 200 and 250 fathoms, and eleven between 250 and 300 fathoms. If we separate those obtained with horizontal from those obtained with vertical closing nets the relative abundance of the species in these various depths may be expressed as in the following table:

TABLE V

Relative Abundance of *Sagitta planktonis*

Depth in Fathoms	Horizontal Closing-Net Catches Showing Number of Specimens per 20 Hours of Hauling	Vertical Closing-Net Catches Showing Number of Specimens per 500 Fathoms of Hauling
0–150	1	none
150–200	5	1
200–250	8	8
250–350	19	18

This table shows that this species increases in abundance as the depth increases and reaches its maximum in the neighborhood of 300 fathoms. When we realize that approximately the same relative abundance is obtained from independent considerations of data supplied by horizontal and vertical closing nets, this conclusion is placed upon solid ground, in spite of the few specimens dealt with.

SAGITTA HEXAPTERA

Some indication of the relative abundance of this remaining species of *Sagitta* may be gleaned from the following table:

TABLE VI

RELATIVE ABUNDANCE OF *Sagitta hexaptera*

Depth in Fathoms	Horizontal Closing-Net Catches Showing Number of Specimens per 100 Hours of Hauling	Vertical Closing-Net Catches Showing Number of Specimens per 1,000 Fathoms of Hauling
0–50	9	none
50–100	88	4
100–150	none	2
150–350	none	none

When to the evidence contained in this table we add that the species was not obtained in hauls made with open vertical nets from above 45 fathoms, the facts suggest that *S. hexaptera* maintains its maximum abundance between 50 and 100 fathoms. The number of specimens, however, is too small to afford basis for any more positive conclusion.

KROHNITTA SUBTILIS

Regarding this species, we find that the horizontal closing nets obtained four specimens from 200 fathoms, but none from above or below this depth. The vertical closing nets, on the other hand, obtained twelve from between 50 and 200 fathoms, 25 from between 200 and 250 fathoms, and five from between 250 and 300 fathoms. Only three were obtained by the open vertical nets and those in one haul made from 250 fathoms to the surface. The following table gives a more accurate idea of the relative abundance of this species:

TABLE VII

RELATIVE ABUNDANCE OF *Krohnitta subtilis* BASED ON VERTICAL CLOSING NET CATCHES

Depth in Fathoms	Average Number of Specimens per 1,000 Fathom Haul
0–50	none
50–200	18
200–250	63
250–300	20

The table indicates that *K. subtilis* maintains its maximum abundance between 200 and 250 fathoms, and all the data agree that it does not occur above 50 fathoms.

EUKROHNIA HAMATA

Two specimens of this species were taken with horizontal closing nets from 110 fathoms, two from 300 fathoms, and two from 350 fathoms. The vertical closing net obtained nine from between 25 and 50 fathoms, one from between 150 and 200 fathoms, six from between 200 and 250 fathoms, and one from between 250 and 300 fathoms. None were obtained in open vertical hauls made from above 250 fathoms. These data show that *E. hamata* is typical of the mesoplankton, and suggest that the region of maximum abundance is in the neighborhood of 250 fathoms.

The essential facts presented in this brief discussion of vertical distribution may best be summed up by classifying so far as possible the various species within the San Diego region on the basis of similarities and differences in their manner of distribution. When this attempt is made we find that a key somewhat as follows may be built up:

KEY TO THE SPECIES OF CHÆTOGNATHA OF THE SAN DIEGO REGION BASED ENTIRELY UPON FACTS OF DISTRIBUTION

A. Species conspicuously epiplanktonic, very rarely extending to a depth of 150 fathoms .... *B*.
AA. Species conspicuously mesoplanktonic, very rarely occurring above 100 fathoms .... *E*.
B. Species confined to the upper 10 fathoms .... *D*.
BB. Species whose depth of maximum abundance is below 10 fathoms .... *C*.
C. Species occurring in large numbers and distributed from the surface to 75 fathoms, but occurring in much the greatest abundance between the surface and 25 fathoms...*S. bipunctata*.
CC. Species not occurring in large numbers, the region of greatest abundance being at least below 40 fathoms.......*S. hexaptera*.
D. Species occurring rarely, but in large numbers (1,000 or more per haul not being unusual) ....*S. enflata*.
DD. Species occurring rarely and in very small numbers (more than 100 per haul being unusual) ....*S. neglecta*.

E. Species increasing in relative abundance as the depth increases, reaching a maximum at a depth of 250 fathoms or more.....*F*.
EE. Species increasing in relative abundance as the depth increases, but reaching a maximum between 150 and 250 fathoms......*G*.
F. Species of relatively common occurrence above 150 fathoms..*S. lyra*.
FF. Species whose occurrence above 150 fathoms is exceedingly rare ....*S. planktonis*.
G. Species never occurring above 50 fathoms...............*K. subtilis*.
GG. Species never occurring above 25 fathoms ....*E. hamata*.
GGG. Species occurring at irregular times above 25 fathoms, and sometimes even on the surface ....*S. serratodentata*.

It is unnecessary to state that this key is not published for the purpose of furnishing a ready means of identifying the various species of Chætognatha. Perhaps, when all the species from the four quarters of the globe have been studied as critically in regard to their behavior and ecological relations as they have in regard to their morphology, it will be possible to construct a ready means of identification on such a basis, but at present we can do no more than point out that the key does work for the San Diego region and ascertain what this fact signifies.

Its primary significance is that species are quite as distinguishable from their manner of distribution as from their morphological characteristics. In other words, each species has its own definite and distinctive mode of behavior and each adapts itself to the hydrographic and other elements of its environment in quite as definite a way as any of the other species.

This being true, the question at once arises: To what extent are morphological differences between the species proportional to, or correlatable with, their distributional differences. Ritter ('09) has pointed out that, if "change of environment and of environed organism are wholly and inseparably linked together," one ought to be able to measure and correlate the differentials between organisms with the differentials between their environments. However, in attempting to find such a "necessary correlation" in the case of *Halocynthia johnsoni,* native to the San Diego region, and *H. hauster,* native to the Washington coast, the results were negative. It is unnecessary to point out that this is an exceedingly important line of investigation, for, if change of environment and of environed organism are not *inseparably* linked together, the hypothesis of "natural selection," with its attendant hypotheses of "survival of the fittest," "struggle for existence," etc., *are at stake.* Ask yourself if it is not *a priori* impossible for any of these hypothetical factors to operate in the formation of species except on the basis of variations in structure which are *more* or *less* adapted to the conditions of existence in which an organism finds itself? Again, does not logic demand that, if isolation be a *necessary* cause of species formation, two *similar* species must occupy similar but not identical or vastly different environmental complexes, because both could not be *equally* adapted to the same conditions by virtue of their *organic difference* nor to radically different conditions by virtue of their *organic similarity?*

Such questions sufficiently indicate the importance of our inquiry regarding the relation between the morphological and distributional characteristics of species and in this connection the key reveals the fact that *those species having the most coincident vertical distribution are those having the greatest morphological difference.* In other words, when the Chætognatha of this region are classified in the usual taxonomic fashion, five groups can be distinguished, of which each group contains species having the same fundamental *morphological* characteristics; but, when classified according to similarities and differences in vertical distribution, the species constituting any one of the five groups are those differing from each other in fundamental *distributional* characteristics. We have, then, two methods of classification, one of which results in groups of similar morphological but dissimilar distributional species, while the other results in groups of similar distributional but dissimilar morphological species. To illustrate concretely, the groups resulting from each method of classification are tabulated below:

Groups of Similar Distributional Species		Groups of Similar Morphological Species	
Group 1	*S. enflata*	Group 1	*S. enflata*
	S. neglecta		*S. hexaptera*
Group 2	*S. bipunctata*		*S. lyra*
	S. hexaptera	Group 2	*S. bipunctata*
Group 3	*S. lyra*		*S. neglecta*
	S. planktonis		*S. planktonis*
Group 4	*S. serratodentata*	Group 3	*S. serratodentata*
	K. subtilis	Group 4	*K. subtilis*
	E. hamata	Group 5	*E. hamata*

By referring to the key (p. 35) it will be seen that *S. enflata* is separable from *S. neglecta* only by the fact that the former occurs in large numbers while the latter occurs in small numbers. These two species then constitute Group 1 of similar distributional species, but, while *S. enflata* falls in Group 1 of similar morphological species, *S. neglecta* is found in Group 2. It will therefore be worth while to see just how extensively the one species is morphologically differentiated from the other. To this end I have arranged, in the following table, some of the most striking differences between the two species.

TABLE VIII

STRUCTURAL DIFFERENCES BETWEEN *Sagitta enflata* AND *Sagitta neglecta*

Structures	*Sagitta enflata*	*Sagitta neglecta*
Collarette.	Entirely wanting.	Extending nearly to the ventral ganglion.
Anterior fin.	Separated from ventral ganglion by an interval of 17–26 per cent. of total length of animal.	Extends to the ventral ganglion.
Length of anterior fin.	7.4–15.9 per cent of total length of animal.	18–23 per cent. of total length of animal.
Length of posterior fin.	12–18 per cent. of total length of animal.	21–26 per cent. of total length of animal.
Extent of posterior fin.	Not more than half way from tail-septum to seminal vesicles.	To seminal vesicles.
Per cent. of posterior fin in front of tail-septum.	More than 50.	Less than 50.
Appearance of body.	Very transparent.	Opaque.
Width of body.	7–12 per cent. of total length of animal.	4.2–6.4 per cent. of total length of animal.

Muscles.	Weak and thin.	Strong and thick.
Lateral fields.	Very large.	Very small.
Length of tail.	16–24 per cent. of total length of animal.	26–30 per cent. of total length of animal.
External process of vestibular ridge.	At least 10 times longer than broad.	Not over 4 times longer than broad.

Doubtless the number of differences could be increased were we to search details, but the twelve set forth in the above table sufficiently emphasize the fact that the two species are fundamentally distinct from a morphological point of view. It would, in fact, be difficult to find any species within the genus more differentiated from *S. enflata* than is *S. neglecta.*

Looking to Group 2 of similar distributional species and referring to the key (p. 35) we find that *S. bipunctata* is separable from *S. hexaptera* only by virtue of occurring in large numbers and maintaining its maximum abundance above 25 fathoms, whereas *S. hexaptera* occurs in small numbers and maintains its maximum abundance below 40 fathoms. In contrast to this we find that, while *S. hexaptera* occurs in Group 1 of similar morphological species, *S. bipunctata* occurs in Group 2. The following table, therefore, reveals their most fundamental structural differences.

TABLE IX

STRUCTURAL DIFFERENCES BETWEEN *Sagitta bipunctata* AND *Sagitta hexaptera*

Structures	*Sagitta bipunctata*	*Sagitta hexaptera*
Collarette.	Conspicuous but not extensive.	Entirely wanting.
Length of body.	12–17 mm. when mature.	24–55 mm. when mature.
Width of body.	5–7 per cent. of length.	7.3–11 per cent. of length.
Length of anterior fin.	15.9–23.7 per cent. of total length of animal.	8.6–11.8 per cent. of total length of animal.
Interval between anterior fin and ventral ganglion.	5–9 rarely 10 per cent. of total length of animal.	11.5–18.5 per cent. of total length of animal.
Extent of posterior fin.	To seminal vesicles.	Never to seminal vesicles.
Vestibular ridge.	Provided with the usual skeletal parts.	Without the usual skeletal parts.
Anterior teeth.	5–7 in number.	2–3 in number.

Posterior teeth.	12–14 in number.	2–4 in number
Seizing jaws.	Without crest.	Provided with short massive crest.

This table shows similar and just as fundamental morphological distinctions as those found between *S. enflata* and *S. neglecta*.

Group 3 of similar distributional species is composed of *S. lyra* and *S. planktonis*, and on referring to the key (p. 36) we see that the two species are distinguishable only by the fact that *S. lyra* is of relatively common occurrence above 150 fathoms. However, we find that *S. lyra* is placed in Group 1 of similar morphological species, while *S. planktonis* is placed in Group 2. The following table reveals the main morphological differences between the two species.

TABLE X

STRUCTURAL DIFFERENCES BETWEEN *Sagitta lyra* AND *Sagitta planktonis*

Structures	*Sagitta lyra*	*Sagitta planktonis*
Collarette.	Entirely wanting.	Massive, extending to ventral ganglion and anterior fin.
Body.	Translucent, nearly transparent. Tumid, but not retaining its form well.	Exceptionally opaque. Firm and rigid, retaining its form almost perfectly.
Muscles.	Weak and thin.	Strong and thick.
Length of anterior fin.	31.4–44.5 per cent. of total length of animal.	18.8–27 per cent. of total length of animal.
Relation of anterior fin to posterior fin.	Confluent.	Separated by an interval of 8–11 per cent. of total length of animal.
Extent of posterior fin.	To seminal vesicles.	Never to seminal vesicles.
Length of tail.	15.6–24.8 per cent. of total length of animal.	24–38 per cent. of total length of animal.
Lateral fields.	Large.	Very small.
Vestibular ridge.	Skeletal parts missing.	Skeletal parts well developed.
Posterior teeth.	3–9, rarely 10 in number.	11–15 in number.

Here again we find that there is no question concerning the great morphological difference between these two similar distributional species.

Finally we find that Group 4 of similar distributional species consists of *S. serratodentata, K. subtilis,* and *E. hamata,* and by referring to the key (p. 36) we see that they are separable only by the fact that *S. serratodentata* occurs to some extent above 25 fathoms, while *E. hamata* never occurs above this depth, and *K. subtilis* never occurs above 50 fathoms. Yet, we have as members of this group three species *belonging to three genera,* so that there can be no question regarding their fundamental morphological difference.

In what way then do these facts answer our question: "To what extent are morphological differences between species proportional to, or correlatable with, their distributional differences?" It is obvious that the only reply permitted by our data is that there is a *very definite correlation,* but one that is the *exact reverse* of what would *a priori* be expected on the basis of the Darwinian theory of "natural selection"; namely, that the morphological difference between two species is *inversely* proportional to their distributional difference, or, to state it otherwise, the coefficient of correlation between morphological and distributional differences among species approximates closely to —1.

Relation between Species Obtained in the Same Hauls with Respect to Sexual Maturity

Under this head it is proposed to briefly consider the evidence of physiological isolation or coincidence between species relative to their maturity in those cases where two or more were obtained in a single haul. It is obvious that open vertical and vertical closing net hauls do not yield data relevant to this question, for the reason that the vertical distance covered is so great (25 fathoms or more) that it is impossible to tell whether the specimens of two or more species were taken from the same depth or not. Concerning the horizontal hauls, however, this objection can not be made, and when they are examined we find that only 14 out of 148 surface hauls and 23 out of 108 closing-net hauls obtained more than one species.

TABLE XI

SURFACE HAULS THAT OBTAINED MORE THAN ONE SPECIES

Haul No.	Species Obtained	No. of Specimens Obtained	Stage of Maturity
216	*S. bipunctata*	200	Over 50 fully mature
	S. hexaptera	2	Both small and very immature.
411	*S. enflata*	3,500	Over half fully mature.
	S. neglecta	9	One nearing, but none fully mature.
	S. bipunctata	75	All small and very immature.
	S. serratodentata	1	Very immature, ovary barely visible.
	P. draco	1	Very immature, ovary not visible.
412	*S. enflata*	3,100	Many fully mature.
	S. hexaptera	4	All small and very immature.
	S. serratodentata	1	Very immature, ovary barely visible.
	S. bipunctata	64	All small and immature.
	S. neglecta	75	None even approaching maturity.
473	*S. enflata*	6	One mature, the rest nearly so.
	S. neglecta	38	All immature.
	S. bipunctata	6	One nearly mature, the others clearly immature.
1,416	*S. enflata*	1	Nearly but not quite mature.
	S. bipunctata	1,620	All stages, many fully mature.
1,422	*S. bipunctata*	9	Several stages, one fully mature.
	S. planktonis	1	Very immature, ovaries invisible.
1,426	*S. serratodentata*	10	All small and immature.
	S. bipunctata	1,250	All stages, many fully mature.
1,582	*S. serratodentata*	7	All small and immature.
	S. bipunctata	600	All stages, 25 mature or nearly so.
1,591	*S. serratodentata*	5	All small and immature.
	S. bipunctata	200	All stages, but mostly immature.
1,605	*S. serratodentata*	1	Small and very immature.
	S. bipunctata	35	Mostly immature.
1,686	*S. hexaptera*	1	Small and very immature.
	S. bipunctata	1,600	All stages, over 200 fully mature.
1,716	*S. serratodentata*	1	Small and very immature.
	S. bipunctata	50	Mostly immature, one fully mature.
1,738	*S. serratodentata*	14	All small and immature.
	S. bipunctata	105	All stages, some fully mature.
1,772	*S. serratodentata*	1	Small and immature.
	S. bipunctata	9	All small, none fully mature.

Concerning the 14 surface hauls, the following table reveals the fact that in only one haul (1,416) were representatives of two species taken which were nearly mature, and in this case the one specimen of *S. enflata* did not appear to be fully mature. In every other haul only one species was represented by sexually mature individuals.

The following table, which contains data relative to hauls made with horizontal closing nets, shows no instance of two species having been taken in the same haul both of which were represented by sexually mature individuals.

The facts revealed in Tables XI and XII, when taken together with the foregoing discussion of vertical distribution, suggest that the various species reach maturity for the most part during different seasons, and that fertilization probably takes place in different strata of water according to the species. In the case of *S. enflata,* for instance, fertilization unquestionably takes place between the surface and ten fathoms and then only during the winter, if at all, in the San Diego region. With *S. bipunctata,* on the other hand, evidence is at hand [see Michael ('11)], which space forbids presenting here, showing that the species maintains a "center of migration" between 15 and 20 fathoms, from which center the species moves up and down in response to variations in light, temperature, salinity and other factors of its environment, which facts indicate that fertilization is mainly, if not exclusively, confined to this depth of 15 to 20 fathoms. In the case of *S. hexaptera* only the immature have been taken above 50 fathoms, which shows that fertilization must take place below this depth. Again, only the very immature of *S. serratodentata* have been taken above 100 fathoms, except at night when the larger specimens ascend to 50 fathoms. Similarly with *S. lyra,* the larger more nearly mature specimens do not occur above 200 fathoms to any extent, and so on with the other species.

It is quite true that much more knowledge is needed concerning the vertical distribution of most of the species before positive conclusions relative to the depth at which fertilization occurs can be advanced. Were the deeper water (below 350 fathoms) thoroughly investigated, dif-

TABLE XII

HORIZONTAL CLOSING NET HAULS THAT OBTAINED MORE THAN ONE SPECIES

Haul No.	Depth in Fathoms	Species Obtained	No. of Specimens Obtained	Stage of Maturity
1,873	5	*S. lyra*	1	Small and very immature.
		S. bipunctata	5	3 fully mature, 2 immature.
1,877	15	*S. serratodentata*	4	All small and immature.
		S. bipunctata	6	All small and immature.
1,748	25	*S. lyra*	5	All very small and immature.
		S. serratodentata	6	One nearly mature, the rest very immature.
		S. bipunctata	4	Small and remote from maturity.
1,761	25	*S. lyra*	1	Very small and immature.
		S. bipunctata	1	Nearly but not fully mature.
1,851	25	*S. serratodentata*	7	All small and immature.
		S. bipunctata	2	Nearly but not fully mature.
1,858	35	*S. serratodentata*	2	Small and immature.
		S. bipunctata	1	Nearly but not fully mature.
1,476	50	*S. hexaptera*	1	Remote from maturity.
		S. bipunctata	300	All stages, several mature.
		S. planktonis	1	Remote from maturity.
1,575	75	*S. serratodentata*	76	Mostly large and nearly mature.
		S. bipunctata	65	? ? ? ? ?
1,688	100	*S. lyra*	4	Very small and immature.
		S. serratodentata	4	One nearly mature, the rest remote from maturity.
1,714	100	*S. lyra*	1	Small and immature.
		S. serratodentata	9	One nearly mature, the rest small and immature.
1,757	100	*S. lyra*	1	Large and nearly mature.
		S. bipunctata	2	? ? ? ? ?
1,813	100	*S. lyra*	2	Large but not mature.
		S. serratodentata	12	All large but none fully mature.
1,979	100	*S. lyra*	1	Large but not mature.
		S. serratodentata	30	All stages, none fully mature.
1,927	125	*S. lyra*	11	All stages, two nearly mature.
		S. serratodentata	21	All large, none fully mature.
		S. planktonis	1	Small and very immature.
1,735	160	*S. lyra*	1	Small and very immature.
		S. serratodentata	16	All large and nearly mature.
1,926	200	*S. lyra*	13	All stages, none fully mature.
		S. serratodentata	46	All stages, some nearly mature.
		S. planktonis	1	Large but very immature.
		K. subtilis	3	Very immature.

Haul No.	Depth in Fathoms	Species Obtained	No. of Specimens Obtained	Stage of Maturity
1,948	200	*S. lyra*............	2	Large but not mature.
		S. serratodentata....	13	Large, some nearly mature.
1,978	200	*S. lyra*............	1	Large but not mature.
		S. serratodentata....	29	Large and nearly mature.
		K. subtilis.........	1	Very immature.
1,732	220	*S. lyra*............	1	Large but immature.
		S. serratodentata....	13	Large and nearly mature.
1,557	250	*S. lyra*............	50	All stages, several nearly if not fully mature.
		S. serratodentata....	24	Large but immature.
1,729	250	*S. lyra*............	2	Small and immature.
		S. serratodentata....	17	Large, some nearly mature.
1,550	350	*S. lyra*............	2	Large but not mature.
		S. planktonis.......	3	Large and nearly mature.
1,567	350	*S. serratodentata*....	2	Small and immature.
		E. hamata.........	2	Large and nearly mature.

ferentials would undoubtedly be established between *S. lyra* and *S. planktonis* with reference to their depths of maximum abundance. Again, more extensive data relative to all depths, by increasing the number of specimens and hauls with which to deal, would enable us to split the region of 250 to 350 fathoms, for instance, and thus distinguish strata and establish specific differences within much smaller limits. However, on the basis of data already accumulated, all the evidence points toward the probability that the fertilization of each species normally takes place within the limits of its depth of maximum abundance.

SUMMARY AND GENERAL SIGNIFICANCE OF THE DATA

In the foregoing pages the following facts relative to the question of isolation and coincidence have been revealed:

1. Of the most closely related "couplets" of species only one occurs in the San Diego region, except in the case of *S. enflata* and *S. hexaptera,* the former of which can not be regarded as resident in this vicinity.

2. The general distribution of each member of a "couplet" is never entirely coincident with that of the other, but varies from a contiguous and overlapping to a radically isolated distribution, according to the "couplet."

3. Each species occurring in the San Diego region has its own definite and specific manner of vertical distribution just as truly as it has its own specific morphological characteristics.

4. Those San Diego species having the most similar vertical distribution are those possessing the most distinctive morphological characteristics or, to state it otherwise, the morphological difference between species is inversely proportional to their distributional difference.

5. Whenever two or more species have been obtained in the same haul, never more than one was representd by sexually mature individuals.

6. With one or two *possible* exceptions, the mature specimens of each species occur in different strata of water.

On the basis of these facts we are forced to conclude (*a*) that the more closely related species of Chætognatha are isolated from each other either horizontally, vertically or by virtue of physiological differences causing fertilization to take place in different strata of water, and (*b*) that "Jordan's Law" is only partly true, when tested by vertical distribution, for, while the more closely related species do not inhabit the *same* environment, they do inhabit the most *remote* environments.

Aside from these obvious conclusions the primary significance of this paper is that of emphasizing the need of more *exhaustive* and *quantitative* data relative to organisms, on the one hand, and their environments, on the other, before any *solid* basis can be had upon which to build theories regarding the operation of isolation, adaptation, natural selection, mutation and other factors supposedly concerned in the evolution of species. The existence of this need relative to pelagic organisms and their conditions of vertical distribution is readily recognized and our first impression may be that the extent of this *particular* need is exceptional, but an acquaintance with the literature on evolution shows plainly that the need is very general. Indeed, this literature is fairly bulging with evidences of mimicry, protective coloration, natural selection, etc., based upon an abundance of data concerning many organisms as well as their environments, which data, while supporting the hypotheses, rarely include any facts relative to the *essentially quantitative* nature of either the organisms or the environments investigated. The mere fact that this sort of data supports a hypothesis and that the logic is sound is not *adequate scientific* proof that the hypothesis is true, for, as Pearl ('11) and others have demonstrated, *logic may carry conviction, be supported by numerous data, and still prove erroneous when the quantitative relations of the facts included in such data are considered.* Therein lies the mischief of much of our *a priori* reasoning relative to evolution, namely, that it causes us to depend so largely upon *logic* that we overlook or neglect as insignificant the quantitative nature of organisms and particularly of environments. Our most urgent present need, therefore, is not so much the accumulation of additional *qualitative* data as it is an *exhaustive* and *quantitative* treatment of those facts now at hand.

While the biometrician and, to some extent, other students of evolution are treating their data quantitatively, the ease with which large numbers of individuals of pelagic species may be obtained without apparently diminishing the supply, gives an unusual opportunity to the marine biologist for applying quantitative methods on an extensive scale to many of the important problems of evolution. If all the planktological expeditions would join hands by publishing *all the data* relative to *every* haul (those that did not as well as those that did contain the species or group under consideration) and by recording the approximate, if not the exact, number of specimens of each species obtained, instead of publishing only data relative to successful hauls and recording the species as abundant or rare, many problems now so largely discussed from hypothetical points of view could be analyzed entirely on a *factual* basis without involving committal to any hypothesis whatsoever. For instance, by such means it would be possible:

1. To measure the degree of variation in the *habits* of distribution of species.

2. To measure the extent of correlation between variation in the vertical distribution of species and variation in their horizontal distribution.

3. To measure the degree of correlation between morphological and ecological characteristics of species, and so arrive at an accurate analysis of the causes of adaptation.

4. To measure the *range* of adaptation accompanying the same structures.

5. To measure the *range* of variation in structure adapted to the same environmental conditions.

6. To analyze the *natural* behavior of a species without involving the necessity of first placing collected individuals under the artificial conditions of the laboratory and then reading the results, arrived at by experiment, back into their natural environment. I do not wish to minimize in the least the immense value of laboratory experiments on behavior, but, no matter how great the achievement, such experiments can not afford a reliable basis for interpreting the *natural* behavior of a species until it becomes possible to re-create nature in miniature.

While these are but a few of the problems that are urgently calling for solution, I can not help but feel that, in the foregoing pages, we have touched the fringe of a line of quantitative investigation destined to yield much of importance to the student of evolution.

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A FAMILY OF SPOTTED NEGROES

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IT is the purpose of this note to put on record an interesting variation in human skin color which made its appearance as a mutation or sport in a negro family of the southern United States some sixty years ago and has shown itself fully hereditary through two generations of offspring. The nature of the variation is shown in Figs. 1–4. It consists of a "piebald" condition of the skin, which is spotted with white in a fairly definite pattern, not[2] unlike that of certain domesticated animals. A more-or-less continuous white area begins on the top of the head, which has a crest of white hair, extends down over the face (where, however, it may be interrupted) and broadens out on the chest, which is either entirely white or finely mottled. In the whitest individuals the chest area extends around the sides of the body on to the back (see Fig. 4), but fails to reach the mid-dorsal line. It also extends on to the arms in like proportion to its extension elsewhere on the body, but the lower forearm and hands, like the feet, are in all observed cases dark. The ventral white area continues downward from the waist line, and in at least one case (Fig. 4) covers the legs, which are nearly free from black spots down to the knees. There larger and more numerous specks of black begin, which become continuous above the ankles.

If we should describe the pattern in terms of its black

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[1] The material on which this paper is based was collected by the senior author; the junior author has merely assisted in preparing the material for publication.

[2] A photograph in our possession of the same four individuals shown in Fig. 1 together with the father of the three children, taken when the children were small, but now too faded for successful reproduction, makes it clear that the pigmented areas have not changed in position during the intervening period. As in other piebald mammals the pigmented areas have definite boundaries fixed at birth and not subsequently changeable.

FIG. 1. Mrs. Eliza D., her sons Jim and Robert (the taller one) and daughter, Lillie. Photographed 1910.

areas, we should mention as its most prominent feature the *back-stripe* (Fig. 4) which begins on the head and extends the entire length of the trunk, narrowing below and ending on the buttocks. In the taller son, Robert,

FIG. 2. Back view of Mrs. Eliza D., seen in front view in Fig. 1.

Fig. 1, the back-stripe is so wide that it covers the sides of the body also.

The original mutant, founder of this line of spotted negroes, Mrs. S. A., is still living. She was born in 1853 in Louisiana, both her parents being normally colored negroes, the father "dark," according to the statement of her husband who grew up in the same neighborhood and states positively that there were no spotted negroes previously in that region. The colored skin of Mrs. S. A. is "medium dark" as is that of her husband, who is entirely normal in appearance, being free from spots.

The pair were married in 1868 and have had fifteen children, all of whom are living, a fact which indicates a healthy vigorous stock. Of the children eight are spotted like the mother, the remaining seven being normal, without spots, but varying in

FIG. 3. Lillie, daughter of Mrs. Eliza D. Compare Fig 1.

depth of pigmentation, as is usual in mulatto families. The pigmentation of spotted children and grandchildren likewise varies in intensity from light mulatto to coal black. The white spots are however in all cases entirely devoid of pigment.

FIG. 4. Back view of Jim, seen in front view, at the left of Fig. 1.

Six of the fifteen children of Mr. and Mrs. S. A., three normal and three spotted, married normal negro mates and have had from two to four children each. The normals have had only normal children, in all seven. The spotted ones have had nine spotted and two normal children.

The normal children of Mr. and Mrs. S. A. who married consisted of two daughters and one son; the spotted ones consisted of two sons and one daughter. There is evidently no sex-limitation in the transmission of the spotted pattern, which behaves consistently as a simple Mendelian dominant character, the only peculiarity of the case being the excess of spotted grandchildren over the expected one half. But this quite probably is a chance deviation due to the small numbers under consideration, or to failure to secure as complete a report of the unspotted as of the spotted grandchildren.

The descendants of Mr. and Mrs. S. A. are now widely scattered through the United States and Europe, certain of the spotted ones being connected with "museums." Their peculiarity is therefore an economic asset and not likely to interfere with their racial increase. The individuals thus far produced are clearly from their parentage all heterozygous for the spotted character, which they transmit in half only of their germ-cells. If in the course of time two spotted individuals of this race, not closely related, should marry each other, we might on Mendelian principles expect the production of a new type of individual, one homozygous in spotting, which would transmit the character in *all* its germ-cells. What the *somatic* character of such an individual would be we can at present only conjecture. Our experience with the domesticated animals leads us to think that it certainly would not be an albino with pink eyes and unpigmented or faintly pigmented skin, since true albinism is genetically entirely distinct from spotting with white and is recessive in heredity whereas this character is dominant. More likely it would resemble "black-eyed whites" such as occur among mice, rabbits, guinea-pigs, cats, dogs, cattle and horses. Our experience with these animals would lead us to expect that the homozygote in this strain of spotted negroes would be either wholly white, that is, with snow-white skin and hair but with colored eyes, or spotted but with pigmented areas still further reduced in extent than in the heterozygote. Some student of genetics generations hence may be able to answer the question. To this end we shall deposit with the Eugenics Record Office at Cold Spring Harbor, N. Y., our original data including the correct names and present whereabouts of these people.

Three of the spotted children of this family, of whom we have been unable to secure pictures, are undoubtedly identical with "The Three Striped Graces" figured (Plate VV) and described (p. 248) by Pearson, Nettleship and Usher in "A Monograph of Albinism in Man," London, 1911, after Hutchinson, *British Medical Journal*, June, 1910, p. 1480. The names given by Pearson, *et al.*, for the three individuals are "Mary, Rose and Fanny," which agree sufficiently well with individuals VII, VIII and X, of our table. Our own information obtained from members of the family indicates that *at present* VII is in America, while VIII, X and XIV together with the grandchild, Beatrice, are in Europe.

TABLE

DESCENDANTS OF MR. AND MRS. S. A., THE FORMER A NORMAL, THE LATTER A SPOTTED NEGRO

Children	*Grandchildren*
I. Mrs. Eliza D., spotted, Figs. 1 and 2; Mate, mulatto.	1. Spotted son (dead);
	2. Spotted, Jim (pigment dark), Figs. 1 and 4;
	3. Spotted, Robert (pigment light), taller son, Fig. 1;
	4. Spotted, Lillie (pigment medium dark), Figs. 1, right, and 3.
II. Mrs. Eugenia —, normal; Mate, colored.	Two normal.

III.	Mr. Horace A., spotted;	1. Normal, light brown;
	First mate, light mulatto;	2. Spotted, brown;
		3. Spotted, brown;
	Second mate, black.	1. Spotted, black.
IV.	Mr. Jake A., normal;	Three normal.
	Mate, colored.	
V.	Mr. John A., spotted;	1. Spotted, Beatrice;
	Mate, dark.	2. Normal;
		3. Spotted.
VI.	Mrs. Jane —, normal;	Two normal.
	Mate, colored.	
VII.	Marie, spotted.	
VIII.	Rosa, spotted.	
IX.	Dolphus, normal.	
X.	Fannie, spotted.	
XI.	Maggie, normal.	
XII.	Bennie, spotted.	
XIII.	Louis, normal.	
XIV.	Sadie, spotted.	
XV.	Hattie, normal.	

THE EFFECT OF FERTILIZERS ON VARIATION IN CORN AND BEANS

J. K. SHAW

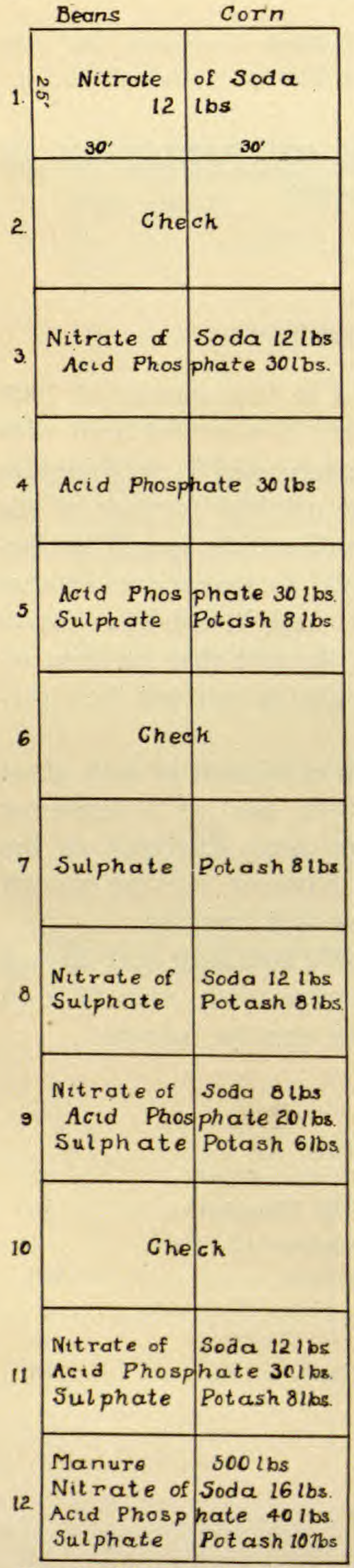
Massachusetts Experiment Station

The data here reported were secured in the summer of 1909 from a field of sweet corn and beans which were fertilized with nitrogen phosphorus and potash separately and in combination after the manner described later. The original purpose of the investigation was to determine if the differences caused by fertilization were in any degree transmitted to succeeding generations. Owing to development of other work it has been impossible to carry this on as planned. It is thought that the data secured may have sufficient interest and value to warrant their presentation.

The plot of land used appeared much exhausted of both plant food and humus. It had previously been used as a raspberry patch. It lay on a gentle southeastern slope sheltered on the opposite side by a belt of woods which, however, was far enough distant to prevent injury from shade or root trespass.

The field was rectangular in shape, 300 feet long and 60 feet wide. It was divided crosswise into twelve plots, each 25 × 60 feet. The fertilizers and their amounts were as follows:

Plot		Lbs.
1.	Nitrate of Soda	12
2.	Check	
3.	Nitrate of Soda	12
	Acid Phosphate	30
4.	Acid Phosphate	30
5.	Acid Phosphate	30
	Sulphate of Potash	8
6.	Check	
7.	Sulphate of Potash	8
8.	Nitrate of Soda	12
	Sulphate of Potash	8
9.	Nitrate of Soda	8
	Acid Phosphate	20
	Sulphate of Potash	6
10.	Check	
11.	Nitrate of Soda	12
	Acid Phosphate	30
	Sulphate of Potash	8
12.	Manure	500
	Sulphate of Potash	10
	Acid Phosphate	40
	Nitrate of Soda	16



	Beans	Corn
1.	25' Nitrate 12 30'	of Soda lbs 30'
2.	Che	ck
3.	Nitrate of Acid Phos	Soda 12 lbs phate 30 lbs.
4	Acid Phosp	hate 30 lbs
5	Acid Phos Sulphate	phate 30 lbs. Potash 8 lbs
6	Chec	k
7	Sulphate	Potash 8 lbs
8	Nitrate of Sulphate	Soda 12 lbs Potash 8 lbs
9	Nitrate of Acid Phos Sulphate	Soda 8 lbs phate 20 lbs. Potash 6 lbs
10	Che	ck
11	Nitrate of Acid Phosp Sulphate	Soda 12 lbs hate 30 lbs. Potash 8 lbs.
12	Manure Nitrate of Acid Phosp Sulphate	500 lbs Soda 16 lbs. hate 40 lbs Potash 10 lbs

Fig. 1. Plan of Experimental Area.

It is seen that plots 1, 3, 4, 5, 7, 8 and 11 received the several fertilizing materials singly and in combination in what may be called normal amounts of 12 pounds nitrate of soda, 30 pounds acid phosphate and 8 pounds sulphate of potash; plot 9 received all these in considerably smaller amounts; while in plot 12 an excess of the chemicals was applied together with a liberal quantity of ordinary barnyard manure, the idea being to supply here a maximum of the stimulus that ordinary fertilizing materials may be expected to afford. The lower half of the entire plot was planted to corn and the upper half to beans. These facts are graphically shown in Fig. 1. One half of the nitrate and the entire amounts of the other materials were applied broadcast on June 8 and harrowed in. The corn was of the Red Cory variety and was planted June 14, and the Davis white wax beans the next day in drills running lengthwise of the area. Both were thinned where necessary to give the corn space of four inches and the beans three inches. The remainder of the nitrate was applied about three weeks after planting, but the exact date can not be given. The plants were cared for in the usual way and the measurements taken from September 14 to 16, or possibly a few days later. With the corn a record was made of the following: distance from ground to uppermost ear, distance from ground to lowest branch of tassel, and the number of ears formed. Where ear-bearing suckers occurred, the same records were made in such a manner as to indicate their parent stalks. The plants on space of two feet on each end of the plots were omitted in the measurements.

TABLE I

EFFECT OF FERTILIZER ON YIELD OF CORN

Plot	Total Stalks	Barren Stalks, Per Cent.	2-Eared Stalks, Per Cent.	Per Cent. Ear-bearing Suckers
1. Nitrate of soda	241	2.90	1.66	3.32
2. Check	248	43.15	.40	.40
3. Nitrate of soda Acid phosphate	281	5.34	4.27	7.47
4. Acid phosphate	244	44.26	.60	.41
5. Acid phosphate Sulphate of potash	229	35.37	.00	.87
6. Check	251	29.87	.00	.40
7. Sulphate of potash	314	28.03	.00	.64
8. Nitrate of soda Sulphate of potash	269	4.83	3.35	7.06
9. Nitrate of soda Acid phosphate Sulphate of potash (⅔ normal)	255	9.80	1.57	5.88
10. Check	225	28.44	.44	.88
11. Nitrate of soda Acid phosphate Sulphate of potash (normal amounts)	241	7.05	3.73	10.37
12. Nitrate of soda Acid phosphate Sulphate of potash (in excess) Manure	248	4.43	10.09	39.92
Av. 3 Checks		33.82	.28	.56

Table I gives figures bearing on the productiveness of the corn, and indicates that the deficient element was nitrogen.[1] There is no indication that the addition of potash or phosphorus decreased the number of barren stalks at all, nor did either alone increase the number of two-eared stalks of ear-bearing suckers, though there appears to be considerable benefit from each when applied with nitrogen, and still more when all three are supplied. The addition of manure results beneficially in all ways, possibly on account of its physical action as well as by the direct addition of plant food.

---

[1] While the discussion following is in terms of the elements of fertility, it is of course possible that other carriers of the same elements might have given different results. It has seemed simpler to express the matter in terms of the elements and with a full reading of the text no misunderstanding on this point is possible.

TABLE II

Variation in Stature of Corn Plants

Plot	Ear Height			Stalk Height		
	Mean	Standard Deviation	Coefficient of Variability	Mean	Standard Deviation	Coefficient of Variability
1. Nitrate of soda	11.61 ±.19	4.20 ±.13	36.18 ±1.26	46.68 ±.25	5.80 ±.18	12.42 ±.40
2. Check	11.78 ±.19	3.36 ±.14	28.52 ±1.23	45.26 ±.29	6.72 ±.20	14.84 ±.46
3. Nitrate of soda Acid phosphate	13.18 ±.17	4.39 ±.14	33.37 ±1.07	50.42 ±.25	6.14 ±.18	12.18 ±.35
4. Acid phosphate	12.00 ±.20	3.39 ±.14	28.25 ±1.24	44.76 ±.29	7.07 ±.22	13.56 ±.48
5. Acid phosphate Sulphate of potash	11.69 ±.19	3.36 ±.13	28.75 ±1.21	43.07 ±.31	7.03 ±.22	16.33 ±.53
6. Check	11.64 ±.16	3.22 ±.12	27.66 ±1.07	45.71 ±.29	6.74 ±.20	14.72 ±.45
7. Sulphate of potash	12.61 ±.17	3.67 ±.12	29.02 ± .99	47.02 ±.27	7.16 ±.19	15.28
8. Nitrate of soda Sulphate of potash	13.53 ±.18	4.15 ±.12	30.45 ± .96	50.45 ±.28	6.84 ±.22	13.56 ±.40
9. Nitrate of soda Acid phosphate Sulphate of potash ($\frac{2}{3}$ normal)	13.02 ±.19	4.25 ±.13	32.64 ±1.13	49.49 ±.30	7.05 ±.21	14.25 ±.43
10. Check	10.33 ±.16	3.28 ±.12	31.75 ±1.31	42.12 ±.29	6.45 ±.21	15.31 ±.50
11. Nitrate of soda Acid phosphate Sulphate of potash (normal amounts)	13.37 ±.18	4.05 ±.13	30.29 ±1.05	51.38 ±.30	6.98 ±.22	13.59 ±.44
12. Nitrate of soda Acid phosphate Sulphate of potash (in excess) Manure	15.36 ±.22	4.97 ±.15	32.36 ±1.10	56.65 ±.31	7.25 ±.22	12.80 ±.38
Av. 3 Check	11.25	3.29	29.31	44.36	6.64	14.96

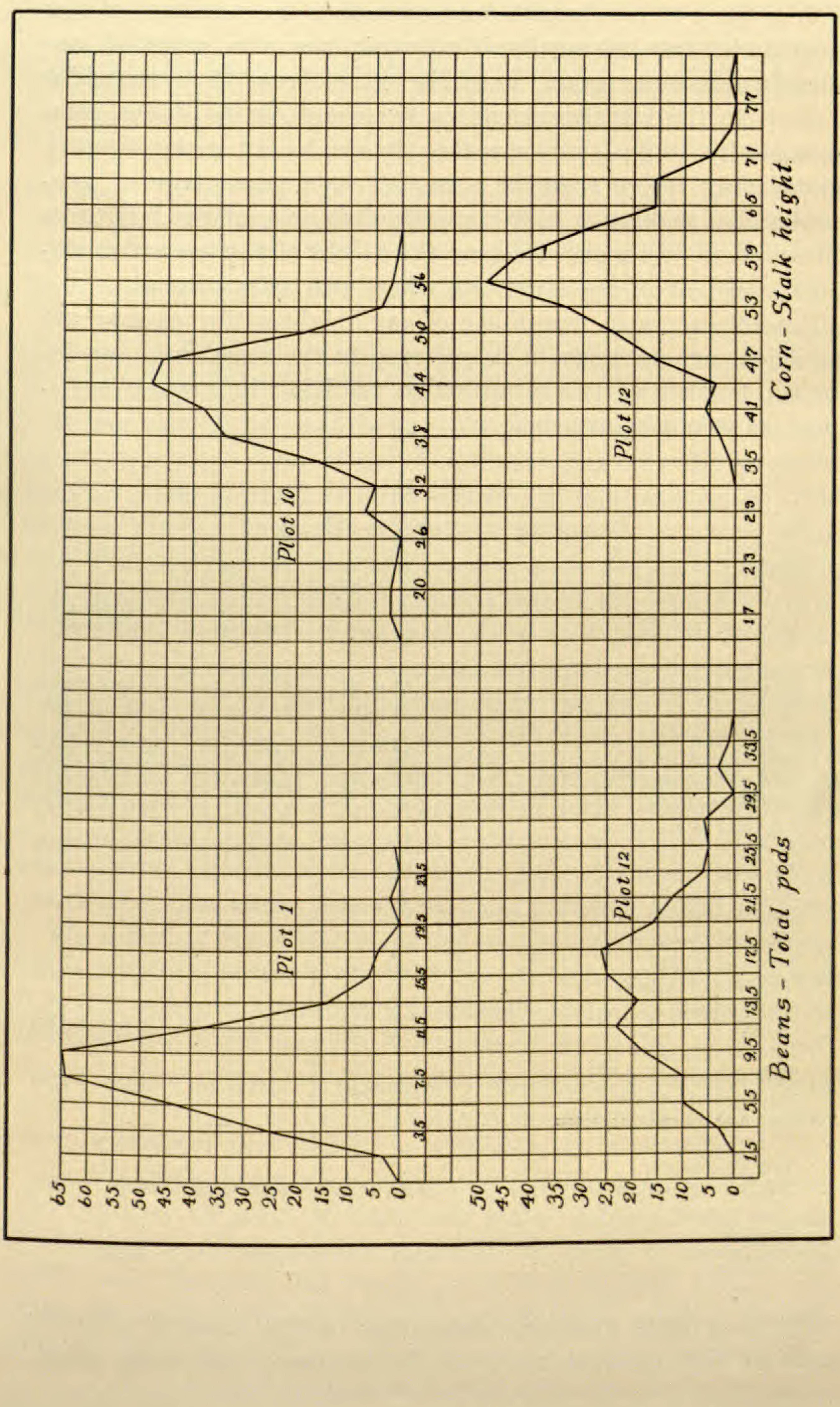


FIG. 2. Variation in Beans and Corn.

Table II shows the variation in stature of the corn plants. With respect to ear height it is seen that the addition of the mineral elements, especially if nitrogen was also supplied, apparently raised the mean. It will be remembered that ear height is taken to the uppermost ear in two-eared stalks, and a comparison with Table I indicates that the ear height is significantly greater only where there is a considerable percentage of two-eared stalks, making it very probable that none of the fertilizers influenced in any marked degree the height of the ear on single-eared stalks, or of the lower ear where two were present.

The differences in variability of ear height so far as they are significant are probably to be referred to the same cause, an increased number of two-eared stalks resulting in greater variability, as would be expected.

TABLE III

Variation in Yield of Beans

Plot	Pods per Vine		Coefficient of Variability
	Mean	Standard Deviation	
1. Nitrate of soda	8.63 ± .14	3.49 ± .10	40.441 ± 1.36
2. Check	4.81 ± .14	3.18 ± .10	66.11 ± 3.21
3. Nitrate of soda Acid phosphate	9.62 ± .23	5.25 ± .16	54.42 ± 2.43
4. Acid phosphate	7.61 ± .18	3.94 ± .13	51.77 ± 1.60
5. Acid phosphate Sulphate of potash	10.71 ± .25	5.05 ± .17	47.15 ± 1.93
6. Check	9.13 ± .22	4.34 ± .15	47.53 ± 2.02
7. Sulphate of potash	10.09 ± .18	3.76 ± .13	37.26 ± 1.41
8. Nitrate of soda Sulphate of potash	9.82 ± .16	3.59 ± .11	36.56 ± 1.30
9. Nitrate of soda Acid phosphate Sulphate of potash ($\frac{2}{3}$ normal)	12.26 ± .21	4.39 ± .15	35.79 ± 1.36
10. Check	6.75 ± .16	2.96 ± .11	43.85 ± 1.93
11. Nitrate of soda Acid phosphate Sulphate of potash (normal amounts)	13.20 ± .21	5.01 ± .15	37.95 ± 1.30
12. Nitrate of soda Acid phosphate Sulphate of potash (in excess) Manure	15.34 ± .30	6.09 ± .22	38.38 ± 1.54
Av. 3 Check	6.89	3.49	52.49

There is little evidence that either of the mineral elements alone or both together increased the stature of the whole plant, though nitrogen did have this effect. Nitrogen together with either phosphorus or potash had a more pronounced effect, and when all three were applied together in plot 11 the stature was still greater. Increasing the amounts of the commercial fertilizers and adding manure in plot 12 gave still taller corn.

The standard deviation is apparently increased by the mineral elements either alone or together, while nitrogen operates to lessen this measure of variability. When all are used together both influences seem to operate and the standard deviation is increased, but not so much as with the mineral elements alone. The increase of the standard deviation where considerable amounts of complete fertilizer is added is not in proportion to the increased mean, and the coefficient of variability is lessened.

It was not found possible to make any measurements bearing on the vegetative vigor of the bean plants; the only figures available are those of yield as measured by the total number of pods on each plant. Table III indicates that potash was most effective in increasing the mean number of pods per vine, though it will be remembered that this element was of the least avail with corn. Nitrogen seems next, and there is a possible beneficial effect from phosphorus. When all are applied the average is higher even on the plot receiving only two thirds the normal amount. Increasing the quantity of chemicals and adding manure increase still further the yield. The results are not as consistent as in the case of stalk height of corn. This variability in yield finds further expression in the larger variation within each plot as expressed by the coefficients of variability which are nearly three times as great as those for stalk height of corn.

The effect of the single elements on the standard deviation is not very clear, but it seems that two or more together increase it, but if nitrogen is present this increase is not in proportion to the increased mean and the coefficient of variability is lessened. There is some indication that potash has a similar effect. Owing to the uncertainty of pod setting a great many data are necessary in order to give definite information on these points.

In Fig. 2 is shown graphically the difference in the effect of the fertilizer on yield of beans and stalk height of corn. This shows that fertilizers greatly extended the range of variation of total pods per vine; the minimum is only slightly raised, but there are many more plants with a considerable number of pods and the maximum number of pods per vine too is markedly increased. There is a greater "scatter" to the distribution. With the stalk height of corn the "scatter" is not much increased, but the whole polygon is moved bodily to a higher position. The fertilizer had a direct effect on every stalk of corn, increasing its stature, but it had little effect on the productiveness of a few of the bean plants, though increasing that of most of them.

J. K. SHAW

MASSACHUSETTS EXPERIMENT STATION

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ADAPTATION THROUGH NATURAL SELECTION AND ORTHOGENESIS[1]

PROFESSOR MAYNARD M. METCALF

OBERLIN COLLEGE

Mr. President, Members of the Society, and Friends: When the president of our society, Professor Conklin, asked me to open this discussion, he suggested that I speak in advocacy of natural selection as the dominant factor in adaptation, saying that several speakers would follow who would attack this conception. As I understand it, a paper in advocacy of natural selection is desired not so much that it may be a target at which following speakers may direct their shafts, as that this conception may not stand without defenders.

It involves some temerity to speak to an audience of American naturalists upon natural selection, for the conception is more than a decade old. It dates even from the dark ages of the middle of the last century, and we naturalists, like the Athenians to whom Paul spoke, are continually seeking some new thing. I can not even, as DeVries and Bateson in the case of Mendel's principles, claim the honor of a re-discoverer, for through all the years since its first promulgation the conception of natural selection has been constantly to the fore and has been discussed and re-discussed until many, I fear, have wearied of it, and for this very reason may be ready to give too undiscriminating welcome to other conceptions that seek to supplant the old idea.

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[1] Read at the Symposium on Adaptation at the meeting of the American Society of Naturalists, Cleveland, January 2, 1913.

There are two sets of factors in producing and determining the direction of evolution, those within the organism, and those external to it. In earlier studies of evolution the external factors received by far the most attention, and only recently have the internal factors begun to receive the thought they deserve. Of the external factors, natural selection is the one for which the largest claims have been made and the one whose claims have been most cordially allowed. I think, however, there are few, if any, of us who do not feel that some of the advocates of natural selection have gone too far. Wallace, for example, would not allow that there are any characters of animals or plants which are not useful to their possessors and have not been perpetuated and emphasized because of this usefulness. Admitting, as we must, that we know but little of the intimate life of organisms, and that the use of many really most useful characters may fail to impress us only because of our ignorance of real conditions, still I think most of us feel not only that the claim that all structures and qualities of organisms are useful is an exaggerated claim, but that very many characteristics are either of indifferent quality, or are so slightly useful as not to be of selection value, or even are slightly disadvantageous. The more closely one studies any organism the more will he become impressed with the number of these non-useful or doubtfully useful qualities, and close and careful students are likely to find their vision of natural selection grow dim, like the pilgrim who, in the midst of the woods, could not see the forest for the trees.

But as we view organic nature in its wider aspects is there any other feature so prominent as the adaptation of organisms to their environment and to the lives they must live in the midst of this environment? However many details of structure or behavior may fail to show their utility, still it remains true that there is no phenomenon of organic nature more impressive than adaptation.

In our study of evolution we have, then, this thing to explain—namely, the universal prevalence of a high degree of adaptation of organisms in habit, function and structure, to their environment, and yet the presence of many qualities, for the most part minor qualities, which so far as we can judge, are non-adaptive. I would suggest for your consideration the propositions that the broader adaptive features are due to natural selection, and that the non-adaptive minor characters are the result partly of factors within the organism, and partly of external factors other than natural selection. This paper will not refer further to these other external factors, but will discuss one of the factors within the organism.

Evidence accumulated during the last decade seems to indicate that fluctuating variations are not significant, and that only mutations are stable and can serve as a foundation for evolution. Perhaps we have accepted this statement a little too hastily. The actual evidence in its favor is not all that could be desired, but it seems to be the general opinion to-day. If this opinion is well founded, it is through the study of the origin and nature of mutation that we may hope to gain most light upon the problem of the origin of adaptation.

When one comes to think of it, we really know very little of mutation. Few instances have been carefully observed and recorded. But in the midst of this scant knowledge of mutation one fact stands out clearly, that mutation apparently is not indeterminate, occurring in all directions equally, and changing from generation to generation, as would be the case were it purely fortuitous. Our best studied instances of mutation are still seen in *Œnothera lamarckiana,* and in all the observations upon the mutation of this species nothing is more patent than that there are certain definite tendencies for particular mutants of very complex and very clearly recognizable types to appear generation after generation, in numbers that are very much greater than could be accounted for by any chance aggregation of unit characters to make these few well-marked types.

In 1905 I wrote as follows:

> In the Amsterdam Garden the mutant *albida* appeared in four different generations from *lamarckiana* parents, previous to 1902, 15 *albida* appearing in one generation, 25 in another, 11 in another and 5 in another. *Nanella* appeared 5 times in one generation, and in other

generations, respectively, 3, 60, 49, 9, 11 and 21 times. *Lata, oblonga, rubrinervis* and *scintillans* appeared frequently.

In the fourth generation, along with 14,000 *lamarckiana* plants, there appeared 41 *gigas,* 15 *albida,* 176 *oblonga,* 8 *rubrinervis,* 60 *nanella,* 63 *lata* and 1 *scintillans,* all bred from *lamarckiana* seed. In the fifth generation, similarly bred from pure *lamarckiana* seed, among 8,000 *lamarckiana* plants were found 25 *albida,* 135 *oblonga,* 20 *rubrinervis,* 49 *nanella,* 142 *lata* and 6 *scintillans.* In the fourth generation one plant in 80 was *oblonga.* In the fifth generation one plant in 60 was *oblonga.* DeVriês himself says: "A species therefore, is not born only a single time, but repeatedly, in a large number of individuals and during a series of consecutive years.

Oblonga differs from the parent species *lamarckiana* not in a single feature, but in an elaborate complex of characters. The other mutants likewise are distinguished from *lamarckiana* by a complex of characters rather than by a single feature.

The mutation can hardly be entirely fortuitous if, for several generations, out of every thousand offspring of pure *lamarckiana* parents, there appear more than ten plants marked by the particular complex group of characters which designate *oblonga.* Were *oblonga* demarcated from *lamarckiana* by but a single character, it would be remarkable to find it appearing repeatedly and in such numbers. When we remember that it is defined by an extensive series of characters differentiating it from *lamarckiana* and from all other mutants observed, are we not led to the conclusion that mutation in *Œnothera lamarckiana* is not wholly fortuitous, but is to a degree predetermined; and that there is some tendency to the production of the *oblonga* and other types in numbers much greater than would be secured by purely fortuitous and indeterminate mutation?

Mutation in our most carefully observed instance, therefore, is clearly determinate. There is in *Œnothera lamarckiana* a tendency to mutate in certain definite directions generation after generation. This trend to mutation in certain particular directions is an example of a condition within the organism which might decidedly affect the course of the future evolution of this *Œnothera* and its descendants.

But we can safely go further. Not only have we evidence that there exist tendencies to produce certain mutants repeatedly, paleontological records show, I believe, that there have existed trends toward an increasing emphasis upon certain characters and that these trends, in some instances at least, lay along lines that produced no more perfect adaptation of their possessors to their environment.

Neumayr's well-remembered figures of fossil *Paludinas* from Slavonian lake deposits show an increasing rugosity of shell and irregularity of aperture, but the separate steps of this change could hardly have been of selection value and have occurred under the control of natural selection. One is irresistibly drawn to believe that there was in these *Paludinas* an internal tendency to mutate from generation to generation toward increasing rugosity of the shell and increasing irregularity of its aperture.

Similar trends in the development of limb and tooth structure of the horse were long ago emphasized by American paleontologists. There is no conceivable utility in the modified shell form of the *Paludina,* and, in the case of the horse, the wonder is that the race has not long ago been exterminated. Among the Cephalopods are some forms which show most complex patterns of the partitions. There are complete intergrading stages shown in the known species between simple suture lines and the most fantastically fimbriated. There seems here, again, to be evidence of a trend toward increasing convolution of the sutures, rather than evidence of the appearance of a useful character and its increase by successive steps each of selection value. In a somewhat similar way, over-ornamentation and bizarre character developed in the Trilobites by steps which can hardly be imagined useful. Many such examples might be cited.[2]

It may seem that I am arguing against the importance of natural selection, but I think I am not, and for this reason: the very trends, of whose existence I think we have good evidence, are themselves subject to natural selection, and if they are in hurtful directions, they will ultimately cause the extermination of the species exhibiting them. I very much doubt if such a monstrosity as the horse could long persist, except for man's aid, for it

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[2] On the afternoon of the day when this paper was read Professor B. M. Davis reported that among the offspring of his *Œnothera* hybrids were some mutants with flowers larger than either parent species, and that for two generations (as far as his experiments went) the flowers increased in size. This is apparently an example of just such a trend in mutation as I have indicated above.

is about the least adaptable beast we know. The Cephalopods with complex partitions have all perished. The bizarre Trilobites similarly persisted each for but a brief period.

I would not claim that the over-ornamentation in these cases was the cause of extermination. It seems more probable that it is merely one noticeable indication of a general unbalanced condition of the organism, a condition affecting probably function as well as structure. I suspect that more species have perished because of physiological maladjustment than from any disadvantageous structural qualities.

In quatenary times in numerous species, great emphasis seems to have been laid upon bulk and the very hugeness of some of these species probably aided in their extermination.

Non-adaptive qualities, when first appearing, may often be comparatively harmless, at least may not be sufficiently hurtful to lead to the extermination of the species in which they appear. But qualities comparatively innocent in their beginnings, when over-emphasized by such trends as we are discussing, may go beyond the limit that even long suffering nature will allow and extermination follow. The goblin of natural selection will get him in the end if he doesn't watch out. It is a case of giving the species rope enough and letting it hang itself. Instead, therefore, of supplanting natural selection, such orthogenesis as this really acts in the end to aid in eliminating many species whose characters in their beginnings were indifferent, natural selection finally dominating and compelling adaptation.

Since mutation-trends in helpful directions will be aided by selection, through the destruction of the rivals of their possessors, while hurtful trends will cause extermination, we see that natural selection has a determinative influence upon the direction of evolution, steering the species along safe paths of progress.

Further advance in the study of the method of evolution may be expected from the study of trends in mutation. Such study should be continued for many years, breeding in great numbers for many generations from some highly mutating stock. Such work can not well be undertaken by a single individual, for it should continue through several human generations. It should be undertaken by some institution which will ensure the endurance of the investigation beyond the present generation. Possibly the best object for such study would be the Syracuse Trilliums—*Trillium grandiflorum*—whose remarkable variation Britcher[3] has so well described. Variation in these Syracuse Trilliums is more universal and more extensive than in any other plants or animals I know. It is so great that it can hardly be of the fluctuating type. It is, in all probability, true mutation, and if so it offers the best opportunity I know for the study of the phenomena of mutation.

SUMMARY

Organisms show adaptation in their more important characters, while many of their minor characters fail to show their utility.

There are definite tendencies to mutation in particular directions, and there is abundant paleontological evidence of trends toward increasing modification in particular directions.

Qualities so appearing may be indifferent in their beginnings, but may through this orthogenesis become sufficiently useful or hurtful to affect selection. Such trends, when they affect physiological qualities, are likely to bring about an unbalanced, distorted physiological condition and be peculiarly hurtful. Probably this has been one of the chief causes of the disappearance of species.

Orthogenesis as thus interpreted is but the handmaiden of natural selection which, acting upon all qualities thus developed to major proportions, will cause them to disappear if ill-adapted. At the same time advantageous trends will be encouraged in the struggle for existence and the direction of evolution be turned toward further adaptation.

Adaptation is the most salient result of evolution and natural selection its great cause.

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[3] H. W. Britcher.

ADAPTATION IN THE LIVING AND NON-LIVING[1]

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THE fundamental differences in concept and mode of thought, which may be remarked between the sciences of the living and those of the non-living, are perhaps nowhere better exemplified than in the interpretations and in the degree of prominence which they respectively give to the idea of adaptation. A general survey of the natural sciences results in the somewhat startling discovery that biology is the only one of these which deals conspicuously with this idea. I have, therefore, been led to take, for my present paper, the somewhat bizarre title which has been announced, and I shall here attempt partially to set forth some characteristics and implications of the biological concept of adaptation, and, in certain respects, to compare these characteristics and implications with those of similar concepts which have the place of adaptation in the sciences of the non-living. The term adaptation is used in a passive and in an active sense. I shall consider the two sorts of adaptations in order.

Passive Adaptations.—Adaptations are characteristics, properties or qualities attributable to natural objects. They imply, however, not only mere qualities, but also the presence or absence, in the object considered, of *potentialities* or *capabilities* to be or to do certain things under certain conditions. The term always lays stress on potentialities but it does not imply at all that these are, or have been, realized. If they were actually realized, it would amount to a redundancy to note the existence of the adaptations at all; an adaptation "caught in the act," an already realized potentiality, is so self-evident that we do not need to mention it as such. In such a

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[1] Read at the Symposium on Adaptation at the meeting of the American Society of Naturalists, Cleveland, January 2, 1913.

case, the statement of the realization implies the potentiality, for an object is obviously adapted to doing and being what it does and is.

However, doing and being are only relative, for any object may change its state more or less effectively and may possess attributes in different degrees, and our interest in realized potentialities lies not in the *fact*, but in the *degree* of adaptation. Furthermore, the degree of adaptation depends clearly upon the extent to which the object considered possesses those properties or qualities about which our idea of adaptation centers, and so attention is at once turned to the properties or qualities as such.

I may draw an illustration of actually observed adaptations from the science of geology, which perhaps interests itself as much in the survival and distribution of rock masses as does biology in the survival and distribution of living things. My example has to do with the natural selection and distribution of certain boulders and pebbles in a deep Californian valley.

At the time of the filling of the Salton sink by the unruly Colorado River, the only loose stones of the inundated area that were able to keep themselves in contact with the air were fragments of pumice. These were adapted to float upon water, and they largely refused to be submerged. With the rising waters they also rose, and thus were able to take advantage of air movements to redistribute themselves. Had it not been for the floating adaptation, these pumice pebbles would have suffered temporary extinction in the form of submergence, and they would not have been able to survive and to gain dominance in the pebble population of certain Salton beaches which they forthwith proceeded to invade. We have reason to believe that this sort of spontaneous migration of pumice pebbles has taken place many times before in the Salton valley, at periods and seasons when edaphic and climatic conditions happened to favor such readjustments of the tension lines, and that the present distribution of these curiously endowed stones has been largely brought about through their possession of the floating adaptation.

Probably a geologist would not mention adaptation in this connection; he might succinctly state the apparent specific gravity of pumice, and might then proceed to present the case in terms of this internal character and in terms of more or less quantitatively known features of the surroundings; for the idea of adaptation here takes account of the low specific density of the rock and the ability to float upon water implied thereby, and to state that pumice is adapted to float is redundant, after we know its specific density. For aught I know also, there may be different species of pumice, some of which might be observed to float higher or a longer time upon water, and in such case, what we might term the varying degrees of adaptation in the different species should be quantitatively brought out—and then dismissed—by an adequate study of the internal qualities of the rocks.

But not nearly all of the potentialities discoverable in natural objects are of this realized, and consequently directly observable sort. The future is no doubt pregnant with hitherto untested adaptations and our imagination frequently suggests these as problems. Of course modern natural science responds to the proposal of this sort of adaptation, *try it and see if it is true,* and many of us are busy just now in doing this very thing.

If we find observational proof of the suggested property, interest in its adaptational aspect fades, for the case then passes over into my first category, of actually observed adaptations. Also, the experimental test of a proposed potentiality—as to whether it is attributable or not to the object considered—is but a case of observation, properly prepared for. Not readily finding the necessary conditions and the object together in nature, we find them separately (at different places or times) and proceed to bring them together. Thus my first experience of the Salton valley was had at a time when it contained little or no visible water. Let us suppose that interest was at that time aroused in the distribution of pumice pebbles upon certain areas of the dry valley floor, and let us suppose that a previous migration of these, similar to the one just described, was suggested as a possibility. At that time the direct test by observation was not possible, but the whole question—as far as the floating adaptation is concerned—could have been settled readily enough either by bringing water to the pebbles or by taking some of the pebbles to water. But of course we should have been dealing, in this instance again, with the determination of the presence or absence of a certain property in the pebbles, as related to a certain property of water.

In the vast majority of the cases of this sort that attract our attention at the present time, however, natural science is unable to obtain direct observational tests, even of the experimental sort, and some indirect method of comparison must be resorted to. Now, indirect methods for determining the degree of a proposed adaptational property consists in nothing more than the determination, by whatever means may be convenient, of the degree to which this property exists in the object considered. Thus, without ever bringing water and pumice together, it is perfectly possible to establish the ability of the latter to float, as by determining the comparative weights of equal volumes of the two substances.

From what has preceded it is suggested that every passive adaptation that we may consider resolves itself, upon adequate analysis, into a problem of the measurement and quantitative comparison of qualities or properties of objects. If neither the direct experimental test nor the requisite measurements can be carried out, then the suggestion of an adaptation is no different from the statement of any other problem for which no method of attack has yet been devised. But it must be recognized in this connection that the usual biological adaptation is not always appreciated as a problem in comparative measurement, and that its proposal, especially if made by one in an authoritative position, is far too apt to be received as a declaration rather than as a question. Thus, for example, our elementary texts may tell the innocent beginner that brightly colored flowers are better adapted to fertilization by insects than are their less gaudy neighbors, and without critical analysis, a very complex and exceedingly difficult problem is at once regarded as solved. As a matter of fact, this problem involves comparative measurements for which methods have not yet been devised, so that the cautious biologist must regard the question of this proposed adaptation as utterly beyond us for the present.

Apparently possible potentialities which have not been actually observed in nature, or which have not a basis in quantitative comparisons so as to be possible of definite establishment or refutation, have not played an important rôle in the modern development of the sciences of the non-living, and consequently the adaptational aspect of the qualities of natural objects is seldom mentioned in these sciences. The relative ease with which the qualities of the non-living may now be analyzed into fundamental concepts renders the use of any other terms than those of matter and energy quite out of place in their serious discussions. On the other hand, biological inquiry has still much to do with theoretical attributes which can not be put to any satisfactory test, and this condition may be in part responsible for the prevalence of the adaptational point of view in our science. It seems to be partly because biological problems are too complex for ready analysis at present, that the adaptational properties of living things are so often stated in terms other than those of the fundamental concepts of matter and energy.

In this connection it is, however, to be remembered that ease of analysis depends as much upon the state of the analyzing mind as upon the complexity of the analyzed object. A mind is conceivable, I think, that would consider the phenomenon of cell division as just as capable of analysis as is that of a chemical reaction like flame; and we are sure that there have been in the past (and are indeed at present) minds to which flame would appear quite as hopeless of analysis as does cell division to us. I have said that the qualities of living things are too complex for analysis at present, I might as well have said that we are at present too ignorant and too feeble to analyze such qualities. Our science is young yet, not in years, perhaps, nor yet in absolute achievement, but in the relation of its present phase of development to the task which is set before it. It appears to be this youthful quality in biology which may partially explain, as I have said, the somewhat startling generalization with which we began.

Active Adaptations.—Biological writing employs the term adaptation in an active sense as well as in the passive one heretofore considered in this paper, and it remains to give some attention to this usage, and to an apparent confusion of cause and effect which is connected therewith. To obtain a clearly legitimate case of active adaptation we shall have to turn to human affairs, for reasons which will soon be evident, and the familiar adaptation of the watch will serve our need as well as any other. The little machine is complex, too complex for most of us to understand, and it seems to be much better adapted than any living thing to long-continued, uniform motion of a certain specified kind. If I make inquiry regarding the causes, or antecedent conditions, to which this adaptation is due, I find that the various parts have been made and assembled with reference to the very adaptation which I am investigating. In my search after causal relations I have been entrapped in a mesh of uninvestigated psychological phenomena and have discovered the puzzling truth that the watch is what it is, simply because *it was to be what it is!* In other words, the cause of the effect which we are considering is regarded as some sort of disembodied spirit of the effect itself, and this effect, in order to be the cause of itself must have existed before it came into being.

Of course we realize that we have thus come into contact with the darkest problem with which biological science has to deal, namely, the problem of human purposeful action and of the human will. While I see no reason for doubting that this problem may eventually yield to analysis and comparative measurements, yet it must be admitted that progress in this direction has only just begun, so that anything but the most superficial considerations in this connection is at present but waste of time and trouble. We have here, for the present, to acknowledge our fundamental ignorance, and to hold our minds in that state of suspended judgment to which, in less complex affairs, students of all the natural sciences have become used.

Although we are as yet unable to analyze into simple terms of matter and energy the antecedents which conditioned the adaptation that is before us in the watch, yet it seems that our analysis of the universe about us has progressed far enough so that we may be justified in frankly maintaining that the problem of purposeful causation has no place in any of our considerations, excepting solely those wherein human consciousness has been involved among the causal conditions. To employ other terms, I think we are bound to regard the nature of the future outcome of all processes as totally non-existent, and consequently absolutely without influence in the present, excepting alone (and temporarily) those processes for which the human will is accounted a necessary antecedent.

We may now inquire as to the causes which have been in operation to bring about the peculiarly low specific gravity of the pumice pebbles in my case of the floating adaptation of these bodies. We are assuredly unable to state these causal conditions in anything approaching completeness, but we are nevertheless sure that human purposefulness has played absolutely no part in the matter, so that we put the floating adaptation of these pebbles entirely out of mind as soon as we begin our search for the causes thereof.

Geology, it seems, does not find purposeful action necessary in its explanations. Neither does any progress come from a consideration of purposeful changes in the readjustments of atoms with which chemistry deals, nor in the phenomena of heat migration which constitute a portion of the field of physics. Modern astronomy sees no purposeful activity in the motions of sidereal space, nor does meteorology seek in the effects of a storm any suggestion of the causes which brought it into being. Many branches of biological science, however, although confessedly not dealing with human purposeful activity, seem frequently to seek in the future the causes of the present. Thus our science teems with purposeful reactions, and this feature of the idea of adaptation adds its influence to the ones already mentioned, playing an important rôle in keeping the sciences of the non-living essentially and fundamentally separate from those of the living.

The history of the idea of causation in the natural sciences suggests much that may have a bearing on our judgment as to whether this present distinction between the two groups of sciences is necessary and permanent or merely temporary and passing. To primitive man all problems were too complex for adequate analysis, and purposeful activities of many kinds were devised to explain not only the doings of his fellow men but also the doings of all nature. The whole world was then a world of teleological causation. The heavenly bodies moved and the chemical elements combined or separated according to the capricious wills of innumerable deities and demons. Men then heard in the howling of the storm and in the rumble of the earthquake the terrible voices of the spirits of the air and earth. All living things were endowed with a man-like consciousness and power of willing to do, and everything struggled with everything else in a never-ending conflict of capricious wills.

In the development of our race, however, an increasing experience of deterministic causal relations has been accompanied by a progressive effort to expunge the idea of purposefulness from our thinking. The numerous mythological personages just called to mind have gradually suffered a curtailing of their powers for good and evil, and have, in general, by natural science at least, been totally discarded. Many relics of the past of course remain in all our mental life; many of our words and not a few of our instinctive modes of thought are survivals from the teleological period of our development. Jupiter and Venus still play their part in modern astronomy, and Vulcan's name is still heard among geologists. But obvious teleological expressions have been generally outgrown and discarded by all of the sciences that deal with the non-living. In biology alone they persist, mainly as personifications of plants and animals, making our modern writings a curious jumble of exactly stated observations and conclusions, together with many statements that might have been taken bodily from primitive fairy-tales. Foreseeing of the future and conscious purpose are apparently attributed to living things in which we have no evidence for the existence of consciousness. The eye develops in the animal *in order that* it may see, the leaves of the plant are *for the purpose* of obtaining carbon dioxid from the atmosphere. The list of such statements might be made very long, but you are quite familiar with their nature.

Not only are the organisms with which we deal frequently personified to the extent of attributing to them the foresight and will needed to carry out complicated plans, but they are also frequently supposed to be capable of making *a mistaken judgment.* I find in Gibson's translation of Jost's "Plant Physiology," 1907 (page 389), an excellent example of this assumption, where it appears that one lower organism may be clever enough to outwit another. The statement in question reads, "The gall, for example, is of service only to the insect, but is highly disadvantageous to the plant; we must assume, indeed, by way of explanation, that the insect succeeded in deluding the plant, so that instead of treating the insect as an enemy and an intruder it behaved towards it as if it were a bit of itself."

I think it is perfectly clear that the non-biological sciences have all passed through a much earlier stage in which purposeful adaptations were seriously considered, and it seems quite as clear that such concepts are not any longer accepted in the serious studies of these sciences. There seems also to be no doubt that the biological sciences, notably in their physiological aspects, are tending at the present time more and more to adopt a non-teleological point of view. From these points I again draw the conclusion that ours is a developmentally young science, that it still retains features of its early youth, and that the concept of purposeful adaptation is one of these features, sooner or later to be totally abandoned, even as the same concept has already been abandoned by the other natural sciences.

If my conclusion should be wrong, then one of two propositions must follow: either the sciences of the non-living have fallen into error, ought to have retained the concept of purpose in natural phenomena, and will sooner or later return to this concept; or else there is a great and fundamental difference between the living and the non-living, and teleology has a logical place in considerations of the former objects but not in those of the latter. Although it is to be realized that the possibility of one or the other of these propositions can not be rigidly denied at the present time, yet the probability of either one is definitely decreased by every analytical conquest of science. The controversy here suggested—which seems in our time as wastefully to absorb our energies as did the discussion of special creation in the time of Charles Darwin—is characterized by this peculiar feature, that, while all evidence presented *for* teleological causes is conspicuously based upon our ignorance and present inability to analyze our problems, the evidence offered in the opposite direction is just as conspicuously positive and consists of cases which have already been subjected to relatively complete analysis. As Cowles[1] has pointed out, there has never been any retrogression in these matters; *all* phenomena now explained non-teleolgically were once explained teleologically, but no non-teleological explanation once attained, has ever been replaced by one involving purpose. Under these circumstances, a pragmatic judgment must be rendered, at least tentatively, in favor of the position here taken, that teleological thinking should have, and will at length have, no place in our science at all.

Conclusion.—I think it is to be concluded from the considerations here set forth that there is nothing known of the nature of living things which should lead the biological sciences to base their inquiries on any other methods or modes of thought than those employed in the sciences of the non-living. In both its aspects, passive and active, the dominance of the concept of adaptation, which now distinguishes our science from the non-biological ones, is related to the comparatively youthful stage of development so far attained by biology, and not to any observed character of the living objects with which we deal. It seems obvious that biology is advancing slowly but steadily along the path already traversed by the other natural sciences, and I think our present operations may best be guided by the hypothesis that all these sciences will eventually come to deal with the same fundamental concepts and modes of thought. Should this condition of affairs ever come to actual attainment, then the discussions which now center about the idea of adaptation might be expected to give place to other discussions of causal relations between measured qualities and properties of the objects dealt with, such as are already beginning to be common in many lines of biological study.

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[1] Cowles, H. C., in Coulter, Barnes and Cowles, "Text-book of Botany," 2: 948. 1911.

ADAPTATION IN ANIMAL REACTIONS[1]

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IN recent times no feature of animal or plant life has been accorded greater emphasis than adaptation, and this property has been repeatedly declared to be one of the fundamental characteristics, if not the most fundamental, of living bodies. Nevertheless, the field of organic adaptation has been scarcely more than superficially surveyed. With the naïve instinct of the collector, the biologist has been content to roam over this vast territory and gather here and there what seemed to him to be striking examples of adaptation till our texts are rich storehouses of instances of nature's apparent ingenuity. How well founded even the more striking of these examples are, no one really knows, though the effect of the whole collection on the naturalist is to engender in him a feeling akin to awe for the adaptive capacity of living beings. May it not be, however, that we overestimate this aspect of organic nature and emphasize beyond reason its real value as a factor in the organic world? It is my opinion, at least, that many animal reactions which we have been accustomed to call adaptations should not be thus designated, and that the difficulties that we often meet in attempting to account for such reactions are due to our consideration of them from the standpoint of adaptations when in reality they are far from being such.

Adaptations are indissolubly connected with the activities of animals and plants. We are only just beginning to learn that an organism in its essentials is an active, working system, that the moment we think of it as

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[1] Read at the Symposium on Adaptation at the meeting of the American Society of Naturalists, Cleveland, January 2, 1913.

a machine standing still, we divest it of precisely that element which is most distinctive of it. The anatomical conception of an organism as a mechanism at rest, useful and important as it has been and is still, is thus fundamentally defective. The essential feature of every living thing is incessant activity, and adaptations are part and parcel of this activity. Even such apparently passive examples as the adaptation of a moth to the bark of the tree on which it rests depends for success as much on the position of the moth's body, the pose of its wings, etc., all features of muscular action, as upon the color pattern of the exposed parts. Thus adaptation, like other truly organic phenomena, exhibits a fundamental dependence on organic activity, a condition that favors the conception of the organism as put forward long ago by Lamarck.

But adaptation is not only essentially associated with the activities of organisms; it is also conditioned by the continuity of this activity. Every organic line of descent has had its past history and can look forward to a possible future. The continuity thus indicated is an essential part of organic nature. The inorganic may at any moment be completely resolved into its elements and recombined at the next moment into a new order without violating the law of its existence. But an organism can not undergo such a revolution without annihilation; an animal or plant subjected to such a process would cease to exist. Hence life is not only activity; it is activity so directed as to be continuous, to be self-perpetuating. Continuity of action is, therefore, an inherent part of the make-up of living things, and adaptation is conditioned by this continuity in that those reactions are adaptive which make for a continuance of life.

Strictly speaking, adaptations exist no more in nature than does a species; it is a word in the dictionary, a figment of the human brain. Just as the systematist finds the individual animal or plant the real object of his investigation, so the student of adaptation finds individual animal movements the material for his study. Broadly speaking, these movements range from the hidden internal processes in the animal economy to the more obvious external forms of behavior.

The very fact that adaptations have been classed under one head to the exclusion of other forms of animal reactions has given them a certain undue prominence, but this is not the only reason for their usurping more than a fair share of attention. Many animal reactions that are in no proper sense adaptations have been brought under this head, and in certain quarters this process of appropriation has gone to such an extent that every animal reaction has been supposed to have some adaptive significance. How far this is from the truth can be made clear by a homely example. When a person faints, his best position for recovery is a horizontal one, and into approximately this position he is very likely to fall. Furthermore, he falls with limp muscles, a method which under the circumstances is much safer than that of falling with a tense body such as usually occurs in consciousness. Thus the position into which a fainting person falls and the method of arriving at it, have all the appearances of adaptations. Yet, in my opinion, any one who would interpret these movements as adaptations would lay himself open to a charge of unreality. The new position, favorable as it is for recovery, is in fact the mere consequence of the faint, and as such it completely loses any claim as an adaptation. That it is advantageous is purely incidental; it might equally well have been disadvantageous. Thus responses, even when of a favorable nature, are not necessarily adaptations, though they may resemble them to a striking degree. An adaptation is not only a favorable response, it is a favorable response especially developed to meet a particular emergency.

If it is so easy to point out pseudo-adaptations among our own activities, it is highly probable that they also occur among the responses of the lower animals. And such seems to be the case. That an isolated blastomere representing a half or a quarter of the egg of *Amphioxus* should be able under favorable conditions to develop into a complete larva is at first sight a surprising fact and seems to give evidence of a remarkable power of adaptation. But such an interpretation is far from justifiable. The growth of the isolated blastomere seems to me much more like the falling of a fainting person than like a process devised to meet a special emergency, and, important and illuminating as this growth is from the standpoint of our understanding of the mechanism of the egg, it is, I believe, a good case of pseudo-adaptation rather than of true adaptiveness. All eggs certainly do not show this trait and to single out the egg of *Amphioxus* and extol this reaction as an adaptation is to give to it weight beyond its deserts. To call this an adaptation is to read adaptation into it as only an overzealous advocate could do. Dame Nature under the circumstances might well be likened to a certain English poet, who, on visiting incognito an exposition of his own verses, was amazed at the wonders they were said to contain.

The majority of animal reactions are, in all probability, neither conspicuously advantageous nor disadvantageous to the life of the individual. They are dependent chiefly on the material composition of the given organism, and, so long as they are relatively indifferent to the continuance of life, they pass without special consequence. Relatively speaking only now and then do we have conditions where a vitally important form of response, an adaptive response, appears. On the whole the flow of action in the daily life of many organisms requires little of such special activity and proceeds at the level of mild indifference. In other words, adaptive reactions as the controlling factors in animal life are, I believe, by no means so universal as some of their advocates would have us think.

The world at large affords an environment in which each animal has a wide range for possible reactions and of a number of responses that might be made to a given set of conditions, one may be quite as appropriate for the continuance of life as another. In other words versatility seems to be a more truthful description of the actual conditions in animal life than the rather rigid state implied in the application of the idea of adaptive responses. Animal reactions in most cases seem to be more of the nature of fluctuations than of mutations, to borrow a related phraseology; they are individual idiosyncracies that are insignificant so far as the race is concerned and are usually not interfered with because of the generous latitude permitted by the environment. From this standpoint animal reactions have a variety whose explanation is to be sought for, as adaptations, but as an expression of the momentary physical and chemical make-up of the individual, a condition which does not easily repeat itself and which therefore agrees with the diversity of reactions exhibited by the organism.

Yet it is not for a moment to be assumed that adaptations are not evident among animal reactions. When it is remembered what enormous numbers of young are lost in the process of producing one adult and that much of this loss is due to misdirected animal reactions, it is impossible to believe that adaptations, as roughed out by a crude selective process, should not have become ingrained in most animals. In fact any adequate survey of the general field of animal reactions shows at once that the main topographic features are adaptational and when one reflects that this has probably been brought about in large part by the elimination of myriads of individuals mainly on the basis of some false step in their reactions, one is compelled to admit that in our zeal for the study of animal behavior, we may have missed the importance of the lesson to be drawn from animal misbehavior. But however this may be, I am convinced that, though the main reaction systems of animals are essentially adaptive, the details of their ordinary flow of responses is mostly free from adaptive influence and proceeds on lines determined chiefly by the momentary state of the individual concerned.

That animal reactions of an adaptive kind may possess qualities that apparently exceed the possibility of origin through selective operations has often been pointed out. In fact it is from this standpoint that adaptation as a sort of transcendental property of the organism has gained its most ardent votaries. And it must be admitted that the illustrations given in support of this view are most baffling and perplexing to the opponents. That a dog which has had its diet changed from bread to meat, should quickly exhibit a change in its pancreatic juice from a type well adapted to bread and poorly adapted to meat to another in which the reverse is true, is a fact of adaptation the explanation of which seems beyond reach. Here we are face to face with what appears to be a quick adaptation of a thoroughly successful kind and without the intervention of nervous activity. No wonder that in face of facts, such as these, the more speculative members of the biological camp seize their entelechies as the only weapons with which they may hope to do battle. But after all is the entelechy a reliable weapon. In all reactions of the kind just mentioned, we are prone to say that though there is not the least reason to suppose that intelligence has really intervened, the whole affair passes off as though directed by some such agent; hence we assume some intelligence-like factor, some entelechy, to be active for the time. But when we look at the matter deliberately, we must admit that intelligence is only our own expression for that aggregate of nervous states and actions which is our chief means of adaptation. To say then that one category of adaptive acts, the adjustment of secretions to particular kinds of food, has a fundamental resemblance to another category of adaptive acts, our intelligent performances, is not to offer an explanation but to leave the matter where it was. When we know more of the real nature of intelligence, we shall be in a better position to attack the problem of adaptive reactions, and, conversely, when we know more about adaptive reactions, we shall be in a better position to attack the problem of intelligence. Meanwhile, do not let us deceive ourselves by confusing an argument in a circle with real progress. In attempting a solution of the problem of adaptive reactions, it is well to remember that entelechies and other like notions do not really bring us forward, for they are at most soporifics to the mind that would naturally be excited to research by precisely those questions that they tend to obscure.

In conclusion then I would maintain that the details of animal reactions are in the main free from adaptive restraint and that their diversity is dependent chiefly upon the fluctuating momentary condition of the animal body; further, that the main outlines of animal reactions are adaptive, but that when we attempt to explain this condition by assuming that it is dependent upon something like intelligence, we are arguing in a circle, for intelligence is merely our name for our own chief means of adaptation.

ADAPTATION FROM THE POINT OF VIEW OF THE PHYSIOLOGIST[1]

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I FEEL much ashamed in having to expose my intellectual nakedness before the members of this society. When I came to this meeting I supposed that adaptation, or the fitness of organisms to their environments, was a physiological truism; that fishes were fitted by their structures and functions to a life in the water; that frogs were so constituted that they could live either on land or in water; and I was even so ignorant as to believe that many structures of a bird's body adapted it to flight. But it appears from the paper of one of my colleagues that in all of these things I was most woefully mistaken.

I feel some hesitation, also, in appearing before a society composed largely of American students of genetics, for I have no new and confusing terminology to propose; and owing to my ignorance of the language they speak and of the short-hand symbols sometimes employed, I am, perforce, compelled to speak in ordinary English which may be understood by any one; all of which, I fear, must invest all I have to say with an air of superficiality, or even of simplicity. I am besides a confirmed conservative in the matter of evolution, holding fast to the explanation of adaptation given by Darwin of natural selection of small variations; having little or no confidence that genes, unit characters, mutations, saltations, allelomorphs, determiners, inhibitors, dominants and recessives, genotyes and phenotyes, are anything more than ghosts, without substance; and looking always for simple explanations of a physical and chemical kind, capable of

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[1] Read at the Symposium on Adaptation at the meeting of the American Society of Naturalists, Cleveland, January 2, 1913.

expression in ordinary language, of the apparent complexities of evolution. I avow myself as a physiologist to be a follower of Darwin, admiring his methods of careful experiment and observation, his long cogitations, and with confidence in the soundness of his judgment. There has been a tendency of recent years in certain quarters to belittle his work, to make fun of his conclusions, to deny that evolution has been a slow and steady continuous process, as the rocks show, and to assert that it has taken place by a hop, skip and a jump, and that it would have taken place anyway without natural selection. Physics and chemistry have attempted to express the physical world in terms of matter and energy, and many biologists are attempting to extend this method to the living world. While this is a necessary and admirable thing to do, it must not be forgotten that in doing so they are neglecting the main fact of life, consciousness, and that the phenomena of life can not be accounted for if this is neglected. It is obvious, too, that the physicist, with his present conception of matter and energy, is making as great a mistake in neglecting the psychical side of matter as the biologist would make if he neglected the physical side. For the psychical, like the physical, must be due to the properties of the atoms, or at least is associated always with them. For the atoms are the same in living and lifeless, their properties are inherent in them and can not be taken away and added to them as if they were wagons, which changed horses, as Du Bois Raymond has put it.

It is my opinion that physiology comes powerfully to the support of Darwin's conclusions; that it shows clearly that there are no such things as independently variable, unit characters; that a jump is a physiological impossibility; and that most so-called mutations are in reality reversions, as Darwin thought; and in this position physiology is, I believe, supported by paleontology.

But while accepting many of Darwin's conclusions, we must all admit that many phenomena are very hard to understand on the basis of Darwin's explanations. Among these difficulties, most of which were recognized by Darwin, there are the phenomena of parallel evolution among different species and genera, which, though diverse, appear all to be moving forward in the same direction; the phenomena of steady, limited progress in one direction which point toward orthogenetic variation; the phenomena of the appearance of rudiments and their development until useful. It is exactly these difficulties upon which physiology throws some light; and it is of them that I particularly wish to speak.

In the evolution of animals two movements may be perceived: a spreading out and a progress; a diversification and a movement forward. The first movement is illustrated by the formation of many different species in one genus; or of many genera of the same type of animal; the second by the movement forward in the line of evolution of all these species. These two movements were not sharply distinguished by Darwin, but they have been more or less clearly recognized by several philosophers. It is this double movement which has given the animal kingdom the form of a branching tree instead of a single trunk. Darwin dealt mainly with the first of these movements, which gives rise to genera, species and varieties; which is shown by the diversification of animals and plants in domestication by human selection; and he explained it by the progressively better adaptation of forms to particular environments. He believed the second movement, the movement upward, was due to the same cause.

It is the second movement which has been so hard to explain and which has particularly puzzled the paleontologist; the successive series of dominating types on the earth's surface culminating in man; the progress steadily toward the goal of consciousness and intelligence.

The question which I wish to raise is whether these two movements, which are at right angles to each other, may not be due to the natural selection of two different kinds of adaptations: first, adaptations of form and function to different kinds of environments; and second, the natural selection of the function of irritability, or, in other words, to the selection of adaptability, or the adaptation to changeableness of environment. Selection of the first kind of adaptations may have given rise to varieties, species, genera of the same type of animal, and have produced the spreading, or diversification; while selection of the second kind of adaptation may have produced the movement onward and upward of all animal forms.

These two kinds of adaptations do not always go together and selection of the one may outweigh the other. It is because selection to a specific environment sometimes is more important than selection of adaptations to changeableness, that not all organisms have progressed in the scale of evolution equally rapidly: but some have persisted in special environments with slight changes of structure for very long periods, or may even have retrogressed; while other forms, in which the second adaptation has been rigorously selected, have moved rapidly onward and upward, and show little adaptation to any special environment.

The question whether evolutionary progress is due to the selection of this second adaptation, that of adaptability, occurs very naturally to a physiologist, because, in the first place, the evolutionary development of consciousness and intelligence appears to him to be one of the most important, if not the most characteristic movement in evolution; and in the second place, his point of view in considering evolution and adaptation is somewhat different from that of the zoologist or the paleontologist. To him the organism does not appear constituted of bones, skin, horns, or other structures, but to be constituted essentially of a number of mechanisms in activity, each mechanism having a definite function to perform. Evolution, for the physiologist, is not evolution of structure primarily, but evolution of function; and he naturally expects to find that the adaptations of function have been of great importance in determining survival.

Of all the physiological properties of the original protoplasm upon which natural selection might be supposed to act, irritability, the most fundamental property of living matter, would seem the most probable point of attack; for irritability is that property of protoplasm in virtue of which it adjusts itself to its environment. It is the property of response; and since it is the environment which is acting as the judge of the excellence of the response and doing the selecting, it would seem that it must be upon this property that all organisms must be tested. It is, moreover, this property that Spencer has very acutely selected as the most fundamental characteristic of living organisms, namely, the power of continuous adjustment of internal to external conditions. It would seem probable that however well animals might be adapted to special environments by the action of natural selection, this particular property, or function, which has to do with the continuous adjustment of internal to external relations must have been throughout the whole course of evolution of predominant importance. And if there has been any unity in the progress; if the course of evolution has been at all in any single direction; and if the natural selection theory is true; it must be in the direction of the perfecting of this function.

I think this short statement will make it clear why the physiologist turns naturally to this fundamental quality, or property of living things, when he considers evolution and adaptation; for however organisms may vary in structure or other particulars, they all have irritability in common. Moreover, I think most physiologists will agree with me that this particular property has been too often neglected by most students of evolution, among whom physiologists have been unfortunately very rare.

Irritability shows itself in all cells by the power of internal change in response to an external change. In most cells of the body there is nothing especially adaptive in the nature of many of these responses; but it is quite otherwise, if we consider the organisms as wholes. It is clear that all organisms have not only the power of reacting to an external change, but many of their reactions are adaptive to a surprising degree. This is indeed the very crux of the difference between living organisms and lifeless things. A lifeless thing can not adjust its internal to its external relations so that it can continue to exist in a changed environment. A crystal in a solution of its kind must dissolve, if the concentration is kept ever so little below saturation; a whole universe must pass away, if anywhere within it there is a persistent uncompensated difference of potential. With living things it is quite otherwise. They have the power of interposing resistances to the potential difference. All living things without exception have adaptive responses so that they are able to continue in existence even though their surroundings change in many different ways. They possess adaptability. Their responses due to their irritability are adaptive responses. The irritability of the organism as a whole is, then, above everything else characterized by power of adaptive response.

It is not difficult to imagine how this specialization of the general property of irritability arose. Some of the indefinite responses of the original organisms to environmental change protected the organism against the change. Organisms with such responses survived and their descendants had the property of a limited adaptive response to this particular change. From this crude beginning further progress was easy. The changes in the environment, though many, are not indefinite in number, and adaptations in the nature of direct responses easily arose and were perfected.

Adaptability, then, appears to the physiologist as the master word of evolution. And many facts also may be urged as confirming this conclusion. For example, one and all of the great physiological mechanisms of the body have a single purpose: to secure adaptability. Not to adapt an organism to one environment, but to all environments, and thus to make it superior to all environments. Furthermore, the higher organisms are specially remarkable for the development of that master tissue of the body which is preeminently irritable and of which the main function is the adjustment of internal to external relations, the nervous system; and finally that the inference is sound may be concluded from the fact that it is by adaptability and by no other quality whatever that organisms may be arranged in the order of their evolutionary progress.

It is not at all surprising that adaptability should be the most important adaptation in nature, overpowering, except in special cases, and dominating all others. For there is but one certain thing in nature: namely uncertainty. The most constant feature of all environments, but particularly of land environments, has been their inconstancy. Changeableness is the chief characteristic of all environments, whatever their special characters may be. There are changes of light, temperature, climate, oxygen and carbon dioxide, moisture; changes due to the introduction of new species by migration upsetting nature's balance; changes in the food supply. Climates, flora and fauna change; change alone persists. Change is the essential thing. We may expect, therefore, if Darwin be correct in his conclusion that variation and natural selection account for evolution, that adaptation to changeableness must be the chief adaptation in nature, and more than all others, it must have determined the general course of evolution. This is found to be the case and the great physiological mechanisms of the body are designed, as already stated, to subserve this fundamental adaptation. Adaptability is that power which fits organisms to withstand the unexpected: the vicissitudes of life; special adaptations of form and color may contribute to the survival of animals; but the essential, or root, adaptation is to changeableness. By adaptation to all environments they become finally superior to all environments.

Superiority to environment, and not adaptation to it, is secured through the irritability of the organism considered as a whole.

The great mechanisms of the body which have this function are several. First, the heat-regulating mechanism, for by means of this organisms are rendered independent of the temperature of their environments. They can exist in the tropics or in the arctics and withstand the extremes of our own climate, while maintaining their activities. This is a complex mechanism consisting of insulating material in the skin; trophic nerves to the internal organs; a closed vascular system; a power of rapid oxidation; supra-renal capsules; pancreas; nervous coordination; sweat glands; evaporation of water in the lungs; temperature nerves. More than any other this mechanism enabled the mammals to conquer the reptiles and supplant them. The mammals became independent of the temperature of their environments. A mechanism not coming by jumps, but the rudiments found far down in the fishes and slowly evolved.

A second fundamental mechanism of great importance for the mammals in supplanting the reptiles and other animals probably was that concerned in immunity. Most of the toxins of poisonous reptiles are of a protein nature. The mammals have developed a mechanism, the details of which are still obscure, but which apparently consists in the conversion of these protein toxins into bodies which neutralize the toxins from which they are formed, that is, into antitoxins. We find, as a matter of fact, that at least many of the mammals are able apparently to make an anti-toxin out of any kind of a foreign protein. Besides this mechanism of defense, useful against bacteria, as well as against snakes, there is the primitive mode of phagocytosis and the chemical method of defense, which consists either in the prevention of absorption, or in the chemical neutralization of the poison by union with other substances. Thus the toxicity of phenols, benzoic acid and many alkaloids are neutralized. By this mechanism mammals are rendered superior to the attacks of many of their enemies and to this extent rendered superior to their environments.

Third, there is the mechanism for rendering mammals tolerably independent of the moisture content of their environment, a mechanism most highly developed in the reptiles. A mechanism formed by the replacing of the wet skin of the amphibian by a dry or scaly skin; the perfecting of the kidneys to maintain osmotic pressure of the blood; the control of the sweat glands and loss of water by the intestines; the development of membranes non-permeable to salts, so that animals may sit in fresh water and not lose their salts. One of the most interesting parts of this mechanism is shown in the reptiles and birds, in the substitution of uric acid for urea in their excretions. By this improvement reptiles have secured almost complete independence of the water content of their environments. They make enough water in their own bodies to supply their small losses. This again is a mechanism of which we can trace the steady growth without a break from the invertebrates to man.

A fourth great mechanism makes mammals independent of barometric fluctuations and less dependent on a fixed atmosphere. By means of their blood loaded with hemoglobin carried in corpuscles lacking all oxygen-consuming power, they are able to live on lofty plateaus, or in deep valleys; and in the presence of much or little carbon dioxide.

The mechanisms having to do with reproduction and the caring for the young afterward have this same advantage of rendering the mammals independent of environment.

A sixth mechanism is the alimentary mechanism, most highly perfected in man. This has rendered him independent of any particular kind of food. He can make his body of any kind of plant or animal. He can make carbohydrate out of protein and many other things. He can live in any climate largely because of this mechanism.

Again a complex mechanism, consisting of teeth, of digestive glands tearing proteins and carbohydrates to pieces, so that he can build up his own proteins from any other kind, useless amino acids being converted into sugar and urea.

The last and by far the most important of these great mechanisms of adaptability is that which provides for every contingency; for the unexpected. It seems that nature, after elaborating these other mechanisms to meet particular vicissitudes, has lumped all other vicissitudes into one and made a means of meeting them all. One can not but be pleased by the apparent ingenuity of this solution. I refer to the nervous mechanism. It is obvious how this mechanism, by substituting choice for blind instinct, consciousness for unconsciousness, developing memory, so that one can profit by experience, and intelligent adaptation of means to ends, has provided finally for all possible contingencies of the future. She has spoken her last word. Adaptability, or superiority to environment, was the end so blindly sought; memory, consciousness, choice were the means, shall I say the means as blindly adopted?

To the physiologist, then, adaptability appears to be the touchstone with which nature has tested each kind of organism evolved; it has been the yard stick, with which she has measured each animal type; it has been the counterweight against which she has balanced each of her productions. However well adapted to a specific environment a type might be, did it lack ever so little of its possibilities in this direction, it was sooner or later relegated to the scrap heap. Some forms, to be sure, persisted in special environments, where they were protected from competition, as in Australia; or where the environment was fairly constant, as in the sea; or in special environments for which they were highly suited; but the whole trend of evolution, with these exceptions, may be summed up by the statement: the general course of evolution has been always from the beginning to the end, in the direction of increasing adaptability or increasing perfection of irritability. This law may be put by the side of the law for the evolution of universes: all spontaneous change is in the direction of increasing entropy.

It is not by form, by color, by increasing complexity or simplicity, that animals may be classified in the order of their evolutionary appearance. It is by this property of adaptability and this alone. At the summit is man; now consciously attempting to carry on what nature has been unconsciously attempting these millions of years, and to secure mastery of his environment. Below him are the other placental mammals of lower intelligence; beneath them the marsupials, less adaptable than the mammals, because of lower brain power; then the reptiles independent of water, but not of temperature; the amphibia, only partially independent of water, but not of temperature; the teleosts able to live in salt and fresh water; the selachians, most without osmotic control and limited to the sea; the arthropods living on land and sea, but dependent on temperature, food and climate, cramped by an external skeleton, and with the fatal defect of running the alimentary canal through the nervous system, so that for higher brain power, either a new nervous system or a new alimentary canal would be needed; lower still the molluscs and annelids, closely limited to their environments; and last the echinoderms and protozoa. No adaptation or power of the body has been so consistently attacked by natural selection as this; and it is this property which seems to have been the determining factor in the general course of evolution and to have determined the steady development of the psychic powers.

I come now to the second part of my subject, namely, correlation. By the first part I have attempted to show that the selection of variations in adaptability is responsible for at least a part of the steady progress in one direction of many kinds of animals; and explains that unity of progress which has been one of the main causes for assuming orthogenesis. In this second part of the paper, I hope to show that the development of our knowledge of correlation removes some other difficulties which Darwin had to meet, and probably explains some other facts which have been urged as supporting orthogenesis.

Among the puzzles of evolution has been the steady growth of rudimentary structures which have apparently no function until they are considerably developed. I say *apparently* no function, for the physiologist has learned to be very cautious in saying that any part of the body is without function or use. A few years ago it was quite otherwise and it was supposed that various rudiments, like the appendix, the hypophysis, the pineal gland, the thymus and some other organs were without function; the surgeons were busy explaining how much better we were off without them; and the anti-Darwinian was fond of presenting these things as not consonant with the view of adaptation. At the present time the uselessness of these rudimentary structures is no longer affirmed. We must therefore be very cautious in supposing that any structure we see, no matter how insignificant it may appear, is without importance. Darwin himself felt the great fact of correlation, and his pangene theory was invented, in part, to account for these facts. He would be both astonished and delighted could he know how completely physiology has vindicated his appeal to correlation as the explanation of some difficulties.

Modern physiology has shown that the whole animal organism is correlated by means of internal secretions; that there is but one unit in the body, and that is the whole organism. By the work of Knowlton and Starling we now have the final proof of the correlation of the pancreas and muscles. The correlations between the hard and soft parts of the body are of still greater importance to the paleontologist, for it has been shown that the hard parts are not independently variable, but that they are dependent at every point upon the function of the soft, internal organs. Who would have dreamed that the character of the skin, the hair, the shape of the skull, the intelligence itself, the length of the limbs, or the speed of transformation of a tadpole into a frog would be dependent on the thyroid or thymus gland? That the minute parathyroids should be absolutely necessary to the life of an organism thousands of times their weight? Or that the development of the testes, the change of milk teeth to the permanent dentition, the growth of the bones of the extremities, should be dependent on the anterior lobe of that apparently useless rudiment, the hypophysis? Or that the secretion of milk and urine should depend on the posterior lobe of the same organ? Who had the temerity to suggest that the corpus luteum should be influencing the development of the mammary glands? Do we not see, indeed, that most of the characters of the body which have steadily developed from the fishes to man are secondary characters dependent on the anterior development of these ductless glands? Is this fact without significance to the paleontologist in helping him to understand the apparent steady progress in one direction, the appearance of orthogenesis? It will be asked, perhaps, what has caused the steady development of these glands. But the answer is not difficult. They are, in their turn, parts of the mechanism of adaptability which has been consistently selected in evolution. They are concerned not only in the growth of bone, but in the growth of the nervous system, the heat control of the body, the immunity mechanisms, the efficiency of muscles, and are in the chain of reproduction itself. These facts largely remove, in my opinion, the difficulties in understanding how rudimentary organs could be useful.

But not only do these facts remove these difficulties in the way of the selection theory, but they have a no less important bearing on the problem of heredity. They show that there can be no independently variable qualities in the animal body. The body is a unit, and I, at least, can imagine no part of it which can vary without influencing other parts. Correlations are everywhere. Pigment is often cited as a unit character, but how can it be so? Pigment is itself the result of a long and complex series of changes. If a given cell produces no pigment it is perfectly certain that its other chemical processes are to some degree modified also, so that these other things vary also. If this cell is changed so that it produces no pigment, then since it is the logical result of a long series of changes in the developing organism, those changes must have been different in animals producing pigment and no pigment. But this means, since each process in the early stage of development influences a multitude of processes in the final change, that there must be a host of differences correlated with the pigment change. As a matter of fact, Darwin long ago pointed out that pigment production was apparently correlated with other factors; particularly with vital resistance, a fact repeatedly mentioned to the writer, also by Whitman as a result of his experiments in pigeon breeding. Darwin cites the case of the Virginia pigs of which only the black ones could eat a poisonous root without losing their hoofs; and Whitman told me that always birds deficient in pigment were also somewhat deficient in other characters and were weaker.

The essential unity of the organism is not only fatal to the whole theory of unit characters, but it is an insuperable objection to the theory that evolution has been by jumps. The organism is a finely adjusted mechanism of a very complex kind; it seems impossible to a physiologist that one can cause a sudden large change in any part of it and have it continue to function; it is as incredible as if one should remove one of the wheels of a watch, replace it by a larger one, and expect the watch to continue to run. Such a simple matter as the replacement of urea by uric acid as an excretion, a change which the reptiles introduced in their differentiation from the amphibia, a change which might conceivably be brought about by the dropping out of a uricolytic enzyme, could not take place suddenly. The kidneys and all other organs of the body would need to be adjusted to this change.

Finally correlation has greatly enhanced the value of the old idea of checks in development and shows most clearly that no organ of the body ever reaches its full potentialities. What comes out of an egg is but one of the infinite potentialities contained in it. Velocity of development, like every other chemical reaction, is equal to the affinity divided by the resistance. If resistances are increased, or if vitality, in other words chemical affinity, be reduced, the development must stop sooner than normal; and we have the phenomena of reversion. If, on the other hand, the reverse takes place, if vitality is increased or resistance reduced, we have variation in the direction of evolution. The development of nonviable monsters is at one extreme of this process. Ontogeny is like a runner, taking the first hurdles easily, but always with increasing difficulty, sometimes trippling at one, sometimes at another, but never reaching the end of his race.

In conclusion then: to the physiologist it appears that the best explanation of adaptation is that given by Darwin of natural selection of small variations; that the essential unity of the progress in evolution toward consciousness and intelligence has been due to the natural selection of the fundamental property of irritability, for it is in virtue of this property that adaptability of organisms has been increased. The recognition of this fact removes one of the difficulties in the way of Darwin's theory. And, second, physiology by the establishment of the physiological correlation of all parts of the body, hard and soft, interposes a final objection, in my opinion, to the whole theory of unit characters, of independent variability of characters, and to the theory of evolution in any other way than by a slow and gradual process, which shall give time to the readjustments of every part of the body necessitated by a change, however slight, in any part of it.

THE FITNESS OF THE ENVIRONMENT, AN INQUIRY INTO THE BIOLOGICAL SIGNIFICANCE OF THE PROPERTIES OF MATTER[1]

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DARWINIAN fitness is compounded of a mutual relationship between the organism and the environment. Of this, fitness of environment is quite as essential a component as the fitness which arises in the process of organic evolution; and in fundamental characteristics the actual environment is the fittest possible abode of life. Such is the thesis which I seek to establish. This is not a novel hypothesis. In rudimentary form it has already a long history behind it, and it was familiar doctrine in the early nineteenth century. It presents itself anew as a result of the recent growth of the science of physical chemistry.

In the study of fitness it has been the habit of biologists since Darwin to consider only the adaptations of the living organism to the environment. For them in fact the environment, in its past, present, and future, has been an independent variable, and it has not entered into any of the modern speculations to consider if by chance the material universe also may be subjected to laws which are in the largest sense important in organic evolution. Yet fitness there must be, in environment as well as in the organism. How, for example, could man adapt his civilization to water power if no water power existed within his reach?

At first sight it may well seem that inquiry into such

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[1] Read at the Symposium on Adaptation at the meeting of the American Society of Naturalists, Cleveland, January 2, 1913.

[1] This paper consists chiefly of excerpts from a book of the same title soon to be published by the Macmillan Company.

a problem must end unsuccessfully in vague and unprofitable guesses. But the physico-chemical basis of life it at length firmly established. On the whole, the composition of living matter, its physical structure, the changes of matter and energy which constitute the metabolic process, together with the totality of such changes, which make up the fundamental economic process of that largest community which consists of all living beings, are all clearly defined.

THE CHARACTERISTICS OF LIFE

Under these circumstances it is certainly no rash enterprise to seek a definition of some of the essential characteristics of life.. Although it is probably far beyond our present power to make a complete study of the problem, I feel sure that a brief analysis will justify certain very definite conclusions. Life as we know it is a physico-chemical mechanism, and it is probably inconceivable that it should be otherwise. As such it possesses, and, we may well conclude, must ever possess, a high degree of complexity—physically, chemically and physiologically, that is to say, structurally and functionally. We can not imagine life which is no more complex than a sphere, or salt, or the fall of rain, and, as we know it, it is in fact a very great deal more complex than such simple things. Next, living things, still more the community of living things, are durable. But complexity and durability of mechanism are only possible if internal and external conditions are stable. Hence automatic regulations of the environment and the possibility of regulation of conditions within the organism are essential to life. It is not possible to specify a large number of conditions which must be regulated, but certain it is from our present experience that at least rough regulation of temperature, pressure, and chemical constitution of environment and organism are really essential to life, and that there is great advantage in many other regulations and in finer regulations. Finally a living being must be active, hence its metabolism must be fed with matter and energy, and accordingly there must always be exchange of matter and energy with the environment.

Obviously these few conclusions can make no claim to completeness. Fully to describe life, the discovery of many other fundamental characteristics is necessary, including such as are related to inheritance, variation, evolution, consciousness and a host of other things. But in the formation and logical development of such ideas there is danger of fallacy at every step, and, since the present list will suffice for the present purpose, further considerations of this sort are best dispensed with. This subject should not be put aside, however, without clear emphasis that the postulates which have been adopted above are extremely meager. The only motives for abandoning further search are the economy and the security which are thereby insured and the very great difficulty of extending the list.

The Environment

Even at the earliest period in the evolution of a typical star there appears to be a progressive variation in the chemical composition from center to periphery. Theoretically it seems inevitable that the heaviest elements should be concentrated in the interior and that those of lowest atomic weight should be present in the greatest amount near the surface. Actually, spectroscopic investigation fully confirms this view. Thus the spectra of typical hot stars show that hydrogen is an inevitable constituent of their superficial parts. Indeed the universal presence of hydrogen under such circumstances is undoubtedly one of the most clearly established facts of stellar astronomy. As stars cool and become red the spectral changes quite as unmistakably point to the presence of carbon. Accordingly we possess the best of evidence and the best of reasons for the belief that large quantities of hydrogen and carbon must exist at or near the surface when a crust forms upon a cooling star.

The nature of the chemical combinations into which these elements at first enter is perhaps open to some question. But as the temperature falls in the cooling of a sun or planet the affinities of carbon and hydrogen for oxygen increase so that carbonic acid and water must normally result. For oxygen is almost certainly present in the sun, it is found in meteorites, and the vast store of it in the earth's atmosphere and crust (roughly one half of their total mass) justify the belief that it is everywhere one of the commonest of elements. Hence an atmosphere containing water and carbonic acid appears to be a normal envelope of a new crust upon a cooling body. Even were not these substances at first present in such an atmosphere, volcanos must soon belch them forth in enormous quantities, to relieve the pressure which inevitable chemical processes set up.

In short just as living things permit themselves to be simplified into mechanisms which are complex, regulated, and provided with a metabolism the environment may be reduced to water and carbonic acid. These are simplifications counselled solely by expediency. Neither logical process is necessary, each involves a disregard for many circumstances which might be of weight in the present inquiry. But in the end there stands out a perfectly simple problem which is undoubtedly soluble. That problem may be stated as follows: In what degree are the physical, chemical, and general meteorological characteristics of water and carbon dioxide, *the primary constituents of the environment* and of the compounds of carbon, hydrogen and oxygen favorable to a mechanism which must be physically, chemically, and physiologically complex, which must be itself well regulated in a stable environment, and which must carry on an active exchange of matter and energy with that environment.

The first step in seeking a solution must be to review the data of physics and chemistry which describe the properties of water and carbonic acid, having due regard to their meteorological significance. Such data of the highest accuracy exist in great profusion, for almost every conceivable property of these substances has been studied with patient care. Next, the properties of the compounds of carbon, hydrogen, and oxygen must be considered, and some of the characteristics of the chemical reactions into which they enter must be discussed. For this examination the unparalleled development of the science of organic chemistry provides ample material. All of these things must be scrutinized quantitatively as well as qualitatively, and again there is no lack of necessary formation.

Immediately one advantage of the method here proposed becomes evident. We can deal with the familiar abstractions of physical science—specific heat, coefficient of expansion, solubility, heat of reaction, etc.—and thereby we shall gain all the advantages of the most exact sciences. No qualifications, no doubtful or contentious matter, no imperfect descriptions need enter.

In this manner it will be easy to estimate the absolute biological fitness in certain respects of water and carbonic acid, and at once a host of automatic results of their properties will become evident. Many of these results, such as the nearly constant temperature of the ocean, the ample rainfall, the freezing of water upon the surface, the great variety of carbon compounds, are familiar subjects of speculation, though since Darwin little interest has been manifested in them; others, only recently brought to light by the growth of physical science, are nearly or quite unknown in this connection. All deserve to receive more serious attention from biologists than is at present vouchsafed them, for they constitute a part of the very foundation of general biology, and they cause many of the phenomena with which man is concerned in his struggle for mastery of the environment.

Yet the mere exposition of such facts and relationships can not suffice in a discussion of the fitness of the environment. In the first place these are in the main familiar ideas, and if they were altogether conclusive to prove the existence of really significant fitness, if they could be regarded as alone adequate to establish the necessity of putting fitness by the side of adaptation as a coordinate factor in causing the marvels of life, it is hard to believe that they would have been so long neglected. In the second place there is nothing comparative about such information. Water is indeed a wonderful substance which fills its place in nature most satisfactorily, but would not another substance do as well? Is not ammonia, for example, a possible substitute? And are there not many other chemical bodies which might, in a very different world, serve equally useful purposes? Perhaps, too, the great variety of carbon compunds which are known to the chemist are known only because the vital processes furnish an abundance of material with which to experiment. Is it not possible, therefore, that another element, perhaps for instance silicon, may enter into even greater varieties of compounds? It is such questions, ever present in the minds of men of science yet never yet carefully scrutinized to see if an answer be possible, which, I suspect, have long deflected attention from this subject.

Clearly, therefore, it will be necessary to compare the properties of water and carbonic acid and of the carbon compounds with those of other substances. It will be necessary to find out whether these substances are not only fit but fittest—and this no doubt is a task of a very different sort. It may even seem, at first sight, an impossible one, but I hope to show that this is not the case, and that in spite of the incompleteness of our physical and chemical knowledge, it may be pressed to a satisfactory issue.

The very constant temperature of the ocean is a most important factor in the economy of nature. It constitutes, for example, a vital regulation of the environment of a large proportion of all the living organisms of the world, and it has many other important "functions." This constancy of temperature is in large part due to the magnitude of the specific heat of water. Other things being equal the greater the specific heat of water the more constant must be the temperature of the ocean. If then the specific heat of water, as is actually the case, be nearly or quite a maximum among all specific heats, it follows that the fitness of water in this respect is nearly maximal.

Again the ocean contains an astonishing variety of substances in solution, and they are present often in large quantities. In this manner a very great supply of food in very great variety is offered marine organisms. Of course such richness of the environment is an exceedingly favorable circumstance for the organism, and it is due principally to the ability of water to dissolve a multitude of things in large quantities. It is not to be supposed that the substances present in sea water are all of use to every organism. This need not be the case at all, but a variety of supplies which may be adapted to special requirements as they arise, here iodine, there copper, for instance, is a very genuine advantage. Further the vast utility of the solvent action of water in blood, lymph, and all the body fluids is too patent to call for comment. If, now, it can be shown that the solvent power of water is nearly or quite a maximum, as it really is, among all known solvents, then it must be evident that in another respect the fitness of water is nearly or quite maximal.

Again the amount of energy that is required to tear apart molecules of water and liberate hydrogen and oxygen is very great indeed, and when hydrogen and oxygen recombine to form water this energy must reappear,—under ordinary circumstances as heat. This fact too is very favorable for the organism, because almost all compounds which contain hydrogen yield a great deal of energy which can be tapped in the process of metabolism. If therefore the heat of combustion of hydrogen be nearly or quite a maximum, as it is, among all substances, it is clear that water is again, in another respect, most wonderfully fitted for life. Finally, if it be true, and such is the case, that very few of the substances which share the fitness of water in one of these characteristics, also share or approach its fitness in either of the others, and that none possesses all these qualifications in a degree that merits consideration, it must, I conceive, be admitted that so far as the investigation has proceeded, water is the only possible fit substance.

A criticism may here be made, are there not other substances which possess other groups of qualifications which water lacks? And that is a difficulty which is even harder to meet. But in the first place it is evident that there are not an infinity of important physical properties; in fact there are very few. And in the second place it is evident, both from centuries of experience in physical science and from the postulates above mentioned regarding life, which undoubtedly do in the main describe its physico-chemical characteristics, that very few properties indeed are of importance in the least comparable with those which I have mentioned. Finally it is in the highest degree probable that we are acquainted with most of the truly essential physical properties, and know them as biologically important, when they are so; and I believe it has been possible to consider them all, and thus make the argument complete.

Such is the nature of the argument; the facts, though no less important than those above indicated, are far too numerous to mention. They include the unique surface tension of water and its very great ionizing power, the absorption coefficient and ionization constant of carbonic acid, the extreme chemical activity of oxygen and hydrogen, the unique chemical combining power of carbon, the number, complexity, variety and chemical activity of the compounds and processes of organic chemistry, and the vast complexity of the chemical system which inevitably results from the reduction of a mixture of carbonic acid and water. These properties result directly in a bewildering variety of conditions which in the most varied ways promote complexity, durability and metabolism.

Analysis of all the facts justifies the following conclusions.

The physical and chemical properties which have been taken into consideration include nearly all those which are known to be of biological importance or which appear to be related to complexity, regulation and metabolism.

There are no other compounds which share more than a small part of the qualities of fitness of water and carbonic acid, no other elements which share those of carbon, hydrogen and oxygen.

None of the characteristics of these substances are known to be unfit, or seriously inferior to the same characteristics in any other substance.

Therefore the fitness of the environment is both real and unique.

In drawing this final conclusion I mean to assert the following propositions:

I. The fitness of the environment is one part of a reciprocal relationship of which the fitness of the organism is the other. This relationship is completely and perfectly reciprocal; the one fitness is not less important than the other, nor less invariably a constituent of a particular case of biological fitness; it is not less frequently evident in the characteristics of water, carbonic acid and the compounds of carbon, hydrogen and oxygen than is fitness from adaptation in the characteristics of the organism.

II. The fitness of the environment results from characteristics which constitute a series of maxima—unique or nearly unique properties of water, carbonic acid, the compounds of carbon, hydrogen and oxygen and the ocean—so numerous, so varied, so nearly complete among all things which are concerned in the problem that together they form certainly the greatest possible fitness. No other environment consisting of primary constituents made up of other known elements, or lacking water and carbonic acid, could possess a like number of fit characteristics or such highly fit characteristics, or in any manner such great fitness to promote complexity, durability and active metabolism in the organic mechanism which we call life.

It must not be forgotten that the possibility of such conclusions depends upon the universal character of physics and chemistry. Out of the properties of universal matter and the characteristics of universal energy has arisen mechanism as the expression of physico-chemical activity and the instrument of physico-chemical performance. Given matter, energy and the resulting necessity that life shall be a mechanism, then the conclusion follows that the atmosphere of solid astronomical bodies does actually provide the best of all possible environments for life.

VITALISM

Modern vitalism consists in asserting the existence of a directive tendency which manifests itself in or through the organism alone and is peculiar to life.

In such speculations the properties of matter and the processes of cosmic evolution have no place. Bergson indeed very definitely, and it would seem gratuitously, puts aside cosmic evolution, and also with slight reservations the properties of matter, as of no essential consequence in organic evolution.

Yet whoever is disposed to speculate about biological fitness, and not even the incomparable finesse of M. Bergson's dialectic can make fitness other than the most general result of the process of organic evolution, must now weigh well the cosmic processes. For, if allowance be made for the results of natural selection, fitness of environment has the greater claim to be considered.

The two fitnesses are complementary; are they then single or dual in origin? The simpler view would be to imagine one common impetus operating upon all matter, inorganic and organic, through all stages of its evolution, in all its states and forms and leading to worlds like our own through paths apparently purposeful. Such it seems to me is the natural hypothesis for the vitalist to adopt. But then vitalism vanishes, only teleology remains. Yet putting aside mechanistic differences is it not now lost in any case? Has not modern vitalism in accepting the limitation to entelechies or impetus destroyed itself?

The situation, briefly, seems to be as follows: Two evolutionary processes independently result in two complementary fitnesses, hence they are related. In the one process the origin of fitness is in part explained by a mechanistic hypothesis. Nevertheless many philosophers, as is their right, declare that in this process a further extra-physical influence is to be assumed. But any one who makes such an assumption for the one process must certainly make it for the other, thus he will be led to see impetus or entelechies everywhere. Under these circumstances it may be doubted if his acquaintance with the nature of his impetus or entelechies is so intimate that he will be able to distinguish the inorganic from the organic, for he has surrendered all positive physico-chemical differences between organic and inorganic bodies and processes to the mechanist. Hence, unless he is to make an arbitrary and unintelligible distinction, or to indulge in the spinning of cobwebs, his vitalism has ceased to be exclusively organic, in short, has ceased to be vitalism at all, and has become mere universal teleology.

The whole process of cosmic evolution from its earliest conceivable state to the present is, however, pure mechanism, as the most perfect induction of physical science, based upon each and all of its manifold successes in accounting for the phenomena of nature conclusively proves.

But if cosmic evolution be purely mechanistic and yet issue in fitness why not organic evolution as well? Thus once more we arrive, this time more completely, at the negation of vitalism. Mechanism is enough in physical science, which no less than biological science appears to manifest teleology; it must, therefore, suffice in biology. We possess two arguments; the argument that, except mechanistically, organic and inorganic phenomena are, in such aspects as concern physical science, alike, and, therefore, a specifically vital teleology is unnecessary, and the argument that inorganic science unquestionably has no need of non-mechanistic teleology. Hence we are obliged to conclude that metaphysical teleology is to be banished from the whole domain of natural science.

SHORTER ARTICLES AND DISCUSSION

MUTATIONS IN ŒNOTHERA BIENNIS L. ?

It is evident that the adherents of the mutation theory are sensitive to the doubts freely expressed concerning the status of *Œnothera Lamarckiana*, the behavior of which in throwing off marked variants is cited as the most important evidence for the origin of species by mutations. These doubts are in fact criticisms of the assumption that *Lamarckiana* is representative of a wild species and express the view that this plant is of hybrid origin and that its behavior is of the sort to be expected of a hybrid. Consequently, mutationists are likely to bring forward as rapidly as possible any evidence that may seem to indicate the appearance of clear inheritable variations of a marked character in forms of pure germinal constitution, *i. e.*, in homozygous material.

There are types of *Œnothera* that we have reason to believe are now very pure and have been so for a great many years. Such a form is the *biennis* of the sand dunes of Holland. This species has apparently been established in its habitats in Holland since pre-Linnean times. There has been little opportunity for chance hybridization and its habits of close or self pollination in the bud are greatly in favor of the continuation of its germ plasm in pure lines. Moreover, the type in experimental cultures of De Vries and others has proved to be constant. If then it could be shown that tested strains of this *biennis* are able to produce new forms of specific rank or even marked varieties the mutationists would have much stronger evidence in support of the mutation theory than that based on the behavior of *O. Lamarckiana*, a form unknown as the component of any native flora.

The title of a recent paper, "Mutation bei *Œnothera biennis* L.," by T. J. Stomps,[1] a former student of Professor De Vries, naturally then arouses interest especially since he is working with this same *biennis* of the sand dunes of Holland, a type well known to a number of botanists who are conducting experimental studies on œnotheras. A brief discussion of the claims indicated

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[1] Stomps, T. J., "Mutation bei *Oenothera biennis* L.," *Biologischen Centralblatt*, XXXII, p. 521, 1912.

by the title of this paper, an analysis of the evidence presented and its possible interpretation supplies the chief incentive for this review.

The greater part of this paper consists of a discussion of certain criticisms directed against the mutation theory by those who believe that *O. Lamarckiana* is of hybrid origin. Certain objections of Stomps appear to the writer well founded, but we shall not take the space to consider this portion of the paper since the greater interest attaches to the value of the direct evidence offered by him in support of the mutation theory.

When we come to the short account of the experimental work of Stomps we find that the so-called "mutants" were not derived from the pure Dutch *biennis* of the sand dunes but from a cross between this race and a type designated *O. biennis cruciata.* This fact seems to the writer of fundamental importance in judging the conclusions of Stomps. It should be made clear that the form "*O. biennis cruciata*" is recognized in the more recent taxonomic treatments as a true species sharply distinguished from types of *biennis* by its floral characters. Whatever may have been the origin of *O. cruciata* or its possible relationship to *O. biennis,* a cross between these types must certainly be regarded as a cross between two very distinct evolutionary lines and its product a hybrid in which marked modifications of germinal constitution are to be expected.

Œnothera cruciata differs from *O. biennis* most conspicuously in having very narrow linear petals, from 1–3 mm. wide, in sharp contrast to the broad heart-shaped petals characteristic of *biennis*. *O. cruciata* is found wild in certain regions of New England and New York and is consequently a native American species. Stomps assumes that the *cruciata* in Holland is a mutant from the Dutch *biennis,* but his belief rests upon no direct evidence. *Cruciata* has never appeared in the extensive cultures of the Dutch *biennis* grown by De Vries and Stomps. Neither have we any direct evidence that the American *cruciata* has come from any form of *biennis.* It is true that the species *cruciata* and *biennis* appear to be closely related, but it is equally clear that they constitute very distinct lines each with a long period of evolutionary independence. I can not see the justification for Stomps's attitude when he treats a cross between the *biennis* and *cruciata* of the sand dunes of Holland as though it were the combination of forms within the same species which have similar germinal constitutions.

Stomps lays emphasis on the purity of his material of *biennis* and *cruciata* which had been carried along for several years in pure lines from original wild plants of the sand dunes. He states that the crossing of these two forms is concerned alone with the floral peculiarities of *cruciata*, since in all other characters the two types are the same. It seems to the writer hardly possible that lines so well established as *biennis* and *cruciata* can be absolutely the same in all respects except that of flower form, although this is obviously the most important point of difference. The American forms of *cruciata* are exhibiting among themselves remarkable differences of germinal constitution.

The observations of Stomps are of interest. He obtained in the second generations from crosses between *biennis* and *cruciata* two marked variants. These are called *biennis nanella* and *biennis semi-gigas* because of the similarity to somewhat corresponding variants from *Lamarckiana*. We are not informed as to the proportions in which these new forms arose, a point of importance since we should like to know whether they are very rare, as say 1: 10,000, or more common.

The first variant, *biennis nanella*, appeared in the second generation of the cross *biennis* × *cruciata*. This cross gave an F_1 hybrid with heart-shaped petals as in the mother plant; no statements are made as to the size relations. In the F_2 generation there was a splitting into forms of *biennis* and *cruciata;* we are told nothing of the proportions of these individuals in the cultures or of their range of variation. One of the *biennis*-like forms presented a dwarf habit which distinguished it from the *biennis* parent in much the same way that *nanella* is distinguished from *Lamarckiana*. This plant, *biennis nanella*, differed from *Lamarckiana nanella* by the same characters that distinguish *biennis* from *Lamarckiana*. An important point of resemblance to *Lamarckiana nanella* lay in its sensitiveness to bacteria which Zeylstra discovered within the tissues of this type and showed to be responsible for certain abnormal characters. De Vries has shown that *Lamarckiana nanella* grown in a soil treated with calcium phosphate became healthy and Stomps found that his *biennis nanella* responded in a similar way to this treatment.

The second variant, *biennis semi-gigas*, appeared in a second generation from the reciprocal cross *cruciata* × *biennis*. This cross also gave an F_1 hybrid with flowers of the *biennis* type and in the F_2 generation there was likewise a splitting of the culture into forms of *biennis* and *cruciata*. One of the *biennis*-like forms presented a more vigorous habit and a larger size of buds, flowers and leaves, suggesting the differences between *Lamarckiana* and its derivative *gigas*. The style was longer than in *biennis* and self-pollination, characteristic of *biennis*, was impossible. This plant proved to be almost sterile.

A count of the chromosomes as shown by mitotic figures in meristematic tissue of young buds determined them to be 21 in number. This important fact placed the plant in that group intermediate between the usual types of *Œnothera* with 14 chromosomes and that very rare variant from *Lamarckiana*, called *gigas*, which has 28 chromosomes. It has recently been shown that certain plants that have been mistaken for *gigas* have 21 chromosomes and for these the name *semi-gigas* has been proposed. Consequently Stomps calls the plant from the cross *cruciata* × *biennis* with 21 chromosomes *biennis semi-gigas*.

The observation of this remarkable plant and the determination of its chromosome count is a matter of great interest. The fact that the number of the chromosomes (21) is not twice the number of the parent types (14) shows that the germinal variation did not take place after a normal fertilization, for a doubling of the number of chromosomes in the fertilized egg or embryo would give a plant with 28 chromosomes. It indicates that a gamete produced by one of the plants in the F_1 generation had 14 chromosomes and that this element combining with a normal gamete (7 chromosomes) produced this exceptional plant with 21 chromosomes.

I have suggested[2] a way in which gametes of an *Œnothera* might be formed with 14 chromosomes in place of the normal number. The presence of 28 chromosomes instead of the normal number 14, during a heterotypic mitosis in an *Œnothera* might come about from a somewhat earlier appearance of that premature division of the chromosomes which normally takes place as early as anaphase of this mitosis. Thus a pushing forward of this premature fission of the chromosomes from the anaphase to the metaphase of the heterotypic mitosis would result in the distribution of 14 chromosomes to each pole of the spindle. Another fission introduced before the metaphase of the homotypic mitosis would make possible a group of 4 nuclei at the end of the reduc-

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[2] *Annals of Botany*, Vol. XXV, p. 959, 1911.

tion divisions each with 14 chromosomes. From such nuclei gametes would be formed with 14 chromosomes.

The position of Stomps is clear. He believes that the Dutch *biennis* and *cruciata* have identical germinal constitutions except for the factors that determine floral structure and therefore with respect to other characters can be crossed as though they were homozygous. Since the cross gave two marked variants which differed from the parents in other respects than those of floral structure these two plants are mutants. These conclusions are then applied by Stomps to the problem of the status of *Lamarckiana* in the following line of reasoning. Since *biennis* mutates and since *biennis* is probably an older species than *Lamarckiana* it follows that mutations among the œnotheras are older than *Lamarckiana* and that consequently the mutations of this species can not be the result of hybridization.

The line of argument rests primarily on the assumption that *biennis* and *cruciata* have exactly the same germinal constitution except for floral characters. This I can not believe possible considering the long evolution back of the two lines. Why did Stomps find it necessary to cross *biennis* with *cruciata* to obtain his "mutants"? If homozygous in all respects except for flower structure why should not *biennis* alone or *cruciata* alone give the same mutants? From my point of view Stomps really made a cross between two rather closely related species and obtained *first* the segregation of flower types to be expected in the F_2 generation among which from my experience I should expect a wide range of variation, and *second* Stomps obtained two marked variants due to some germinal modification as the result of the cross.

This sort of phenomenon I am obtaining frequently in crosses of my races of American *biennis* and *grandiflora*. The *nanella* condition of dwarfed growth is very common in F_2 generations. And, last summer in an F_3 generation a large plant appeared with leaves so thick and stems, buds and flowers so stocky that I have hardly a doubt but that the cytological examination will show an increase in the number of chromosomes.

In so far as the observations of Stomps bear upon the problem of mutation my interpretation would be exactly the reverse of his. To me they further illustrate the same phenomenon that I am obtaining through my hybrids of *biennis* and *grandiflora*, namely, that behavior by which these hybrids in the F_2 generation throw off variants that in taxonomic practise would be considered new species readily distinguished from the parents of the cross and from the F_1 hybrid. I have this past summer found that F_2 hybrids similar in character to the F_1 will in the F_3 generation repeat the performance of the F_2 and throw off again some of the same marked variants.

It is a satisfaction to know that De Vries and Stomps stand firmly by the original definition of a mutation as a germinal variation (and this means inheritable) from a pure stock, *i. e.*, from homozygous material. This is a valuable concept whether or not mutation proves to be a rare phenomenon. Furthermore, one of the most important lines of experimental study is that which will endeavor to determine with precision the conditions under which true mutations may arise. There has been a loose usage of the term mutation which should it become prevalent will take from the word the significance described above, and reduce it to a meaning no more precise than that of a marked germinal variation from any source. If the word mutation is to be kept in the sense of De Vries it must be reserved for germinal variations from homozygous stock.

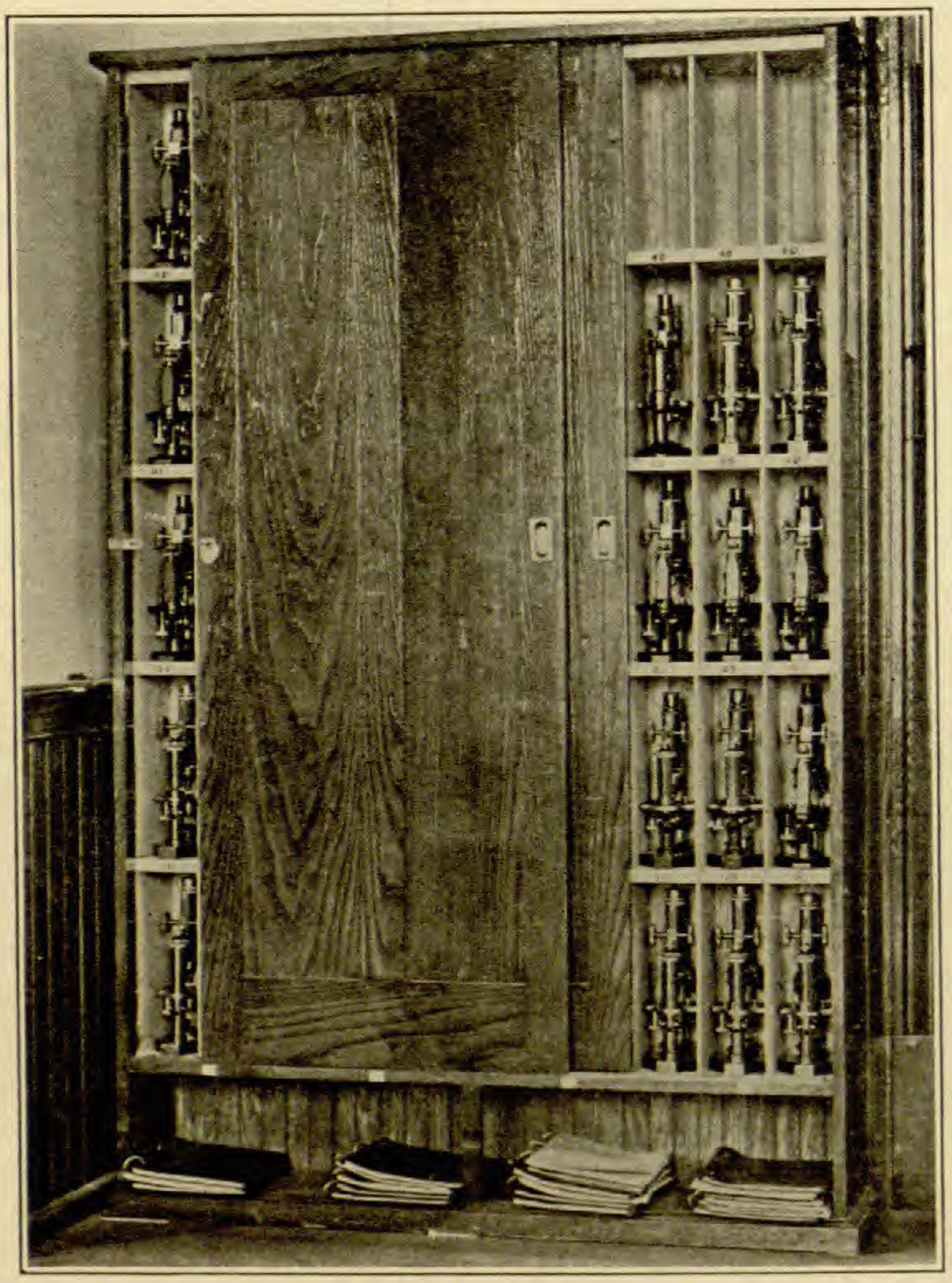
BRADLEY MOORE DAVIS

A CONVENIENT MICROSCOPE CASE

A VERY convenient case for holding microscopes, especially for large, beginning courses where two or more students in different sections use the same instrument, is shown in the accompanying photograph.

The case here shown was built to stand in a shallow offset in the laboratory near a door, and fills a small space that would otherwise be wasted. As is seen from the numbers below the sections, it will hold fifty standard microscopes. Each instrument has a number on the base to correspond to the number on its respective section. Across the floor of each section, at the back, is nailed a 2 in. × 2 in. strip of wood to stop the base of the microscope and to serve as a shelf for the extra oculars. Holes of the proper diameter in the shelf would hold these oculars more safely. The doors slide easily on a metal track with ball-bearing wheels and have brass pushes set flush with the surface of the wood. They may be fastened with a catch or with a lock and key.

Below the case proper is a shelf to hold laboratory books. An improvement over the case here shown would be to have two shallow shelves, in place of one, divided into sections for the further alphabetical distribution of the books. The case here described is 84 inches high, 51 inches wide, and 13 inches deep, outside measurements.



There is wasted, of course, a vertical strip about four inches wide in the center of the case where the doors overlap, but it is always hidden, whether the doors be open or shut.

Such a case, if well made, is practically dust-proof, and is economical not only of space but of money as well, since the cost of the individual microscope boxes may be saved in buying new instruments. A case similar to this has been used by the writer for several years and has proved entirely satisfactory.

ALBERT M. REESE

A LITERARY NOTE ON THE LAW OF GERMINAL CONTINUITY

THE distinctive theory of germinal continuity or continuity of the germ-plasm is, historically speaking, of much more recent origin that the broader doctrine of genetic continuity from which it was derived and with which, in the usage of some writers, it is made synonymous. Genetic continuity in its widest sense embodies the proposition that "living matter always arises by the agency of preexisting living matter,"[1] and in a more restricted sense means that all living cells must be derived by continuous lineage from the cells of preexisting generations. The theory of germinal continuity, in its most highly developed form, conceives the germinal protoplasm as dividing into two portions, from one of which the somatic or body cells of the offspring are developed while the other portion is reserved unchanged for the formation of the reproductive material of the adult individual. The general doctrine of continuity is fundamentally essential to both these theories, but germinal continuity, at least in any Weismannian sense, always involves the further assumption of a transmission from generation to generation of an unmodified residue of the specially organized germinal substance, the germ-plasm, through a definite series of cells, but this concept does not imply that there is necessarily a direct connection between the germ-cells of consecutive generations.

To Richard Owen the credit is usually given of being the first to recognize the distinction between body-cells and germ-cells and thus to foreshadow the idea of germinal continuity. Writing in 1849, he said:

> Not all the progeny of the primary impregnated germ-cell are required for the formation of the body in all animals: certain of the derivative germ-cells may remain unchanged and become included in that body which has been composed of their metamorphosed and diversely combined or confluent brethren: so included, any derivative germ-cell or the nucleus of such may commence and repeat the same processes of growth by imbibition, and of propagation by spontaneous fission, as those to which itself owed its origin; followed by metamorphoses and combinations of the germ-masses so produced, which concur to the development of another individual; and this may be, or

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[1] Huxley, T. H., "Lay Sermons, Addresses and Reviews," New York, 1870, p. 350.

> may not be, like that individual in which the secondary germ-cell or germ-mass was included.
>
> When the primary division of the impregnated germ-cell takes place, it must divide its properties with its matter between the two cells resulting from the spontaneous fission of its nucleus: and this result must follow every subsequent division. It is scarcely figurative therefore to say that the primary or parent germ-cell has equally divided its spermatic virtue amongst its countless progeny.[2]

Owen's suggestions apparently received no consideration and were later disregarded by the author himself. Somewhat similar ideas were expressed by Haeckel[3] in some of his earlier speculations. Galton, says Weismann,[4] was the first to express ideas resembling the theory of germinal continuity, but these ideas were later considerably modified.[5]

A clear expression of the conception of germinal continuity is found in the writings of Jäger, but his ideas made little impression, and inaccurate citation of his work has sometimes caused his disparagement. In 1877, restating previously expressed propositions, he said:[6]

> The basis of heredity consists in this, that throughout whole series of generations the germ-protoplasm of animals retains unchanged its specific quality in spite of all external influences. In the actual ontogeny the available germ-protoplasm may divide into two groups, the *ontogenetic,* from which the existing individual is formed, and the *phylo-*

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[2] Owen, Richard, "On Parthenogenesis," London, 1849, pp. 5–6, 63–64.

[3] Haeckel, E., "Generelle Morphologie," 1866, pp. 287–289.

[4] Weismann, A., "The Germ-plasm, A Theory of Heredity," New York, 1902, p. 198.

[5] Galton's early ideas were expressed as follows:

"From the well-known circumstance that an individual may transmit to his descendants ancestral qualities which he does not himself possess, we are assured that they could not have been altogether destroyed in him, but must have maintained their existence in a latent form. Therefore each individual may properly be conceived as consisting of two parts, one of which is latent and only known to us by its effects on his posterity, while the other is patent, and constitutes the person manifest to our senses.

"The adjacent and, in a broad sense, separate lines of growth in which the patent and latent elements are situated, diverge from a common group and converge to a common contribution, because they were both evolved out of elements contained in a structureless ovum, and they, jointly, contribute the elements which form the structureless ova of their offspring."—Galton, F., "On Blood-relationship," *Proceedings of the Royal Society of London,* Vol. 20, 1872, p. 394.

[6] Jäger, G., "Physiologische Briefe," *Kosmos,* Jahrg. I, Bd. I, 1877, p. 17.

genetic, which is reserved until the time of puberty for the formation of the reproductive material. This reservation of the phylogenetic material I designated as the Continuity of the Germ-protoplasm.[7]

This clear expression of the doctrine of germinal continuity apparently does not appear in Jäger's later work,[8] to which reference is usually made.

Weismann in his essay on the "Continuity of the Germ-plasm,"[9] assumed that he was the first to give expression to this conception but in a later work[10] made acknowledgments to other authors who had anticipated his theory. With respect to Jäger, however, he said:[11]

> The praiseworthy attempt to do justice to my predecessors in this particular subject has perhaps been carried too far. In Geddes and Thompson's "Evolution of Sex" (p. 93), for instance, a quotation is given from Jäger which seems to prove that he anticipated me with regard to the theory under consideration. The quotation in which this idea is expressed is, however, not taken from the book published in 1878 but from an essay written ten years later, and it concludes with the following words: "This reservation of the phylogenetic material I described as *the continuity of the germ-plasm.*" But no mention is made by Jäger of the continuity of the germ-plasm in his book which ap-

---

[7] The original language of these statements is as follows: "In der 'Zeitschrift für wissenschaftliche Zoologie' Bd. XXVII habe ich unter den Titel 'Ueber die Bedeutung der Geschmak- und Geruchstoffe' ein Erörterung der chemischen Seite der Vererbungsfrage gegeben, nachdem ich schon vorher in meinen 'Zoologischen Briefen' der physikalischen Seite einige Betrachtungen gewidmet hatte. Ich will es um Folgenden versuchen, dieser Frage einige neue Anhaltspunkte abzugewinnen und das dort Gesagte zu ergänzen.

"Meine früheren Auseinandersetzungen gingen dahin: Das Fundament der Vererbung besteht darin, dass durch grosse Reihen von Generationen hindurch das Keim Protoplasma eines Thieres eine sich stets gleichbleibende spezifische Beschaffenheit allen Anfechtungen von aussen zum Trotz bewahre. Ich sagte: Bei der jedesmaligen Ontogenese scheide sich das verfügbare Keimprotoplasma in zwei Gruppen, die *ontogenetische,* aus welcher das jeweilige Individuum aufgebaut wird und die *phylogenetische* welche reservirt werde, um zur Zeit der Geschlechtsreife die Fortpflanzungstoffe zu bilden. Diese Reservirung des phylogenetischen Materials bezeichnete ich als Continuität des Keimprotoplasmas."

[8] Jäger, G., "Lehrbuch der allgemeinen Zoologie," Leipzig, 1878, II Abtheilung.

[9] "Der Continuität des Keimplasmas," Jena, 1885; Essay IV in authorized translation, 2d ed., 1891, p. 163.

[10] "The Germ-Plasm, A Theory of Heredity," New York, 1902, pp. 198–202.

[11] *L. c.*, p. 200, footnote.

peared in 1878, in which a connection between the germ-*cells* of different generations is supposed to exist:—and this is not the case. The entirely new statement of his ideas has been influenced by those contained in my essays which had appeared in the meanwhile.

As a matter of fact the quotation from Jäger which Weismann repudiates actually appeared more than eight years before the publication of Weismann's essays, as the quotation from *Kosmos,* given above, clearly shows. Although Jäger coined the expression "Continuity of the Germ-plasm," the idea involved seems to have attracted no attention until after the essays of Weismann had aroused general scientific interest.

Jäger also assumed a material connection between the germ-*cells* of different generations,[12] and, in what Weismann characterizes as "a few casual remarks," Rauber[13] expressed a conception which some authors interpret as the same idea.

In the account of his exhaustive researches on the differentiation of the reproductive cells Nussbaum gave clear expression to the doctrine of the continuity of the germ-*cells,* which in a strict sense means that germ-cells arise directly from one another. The views held by Nussbaum[14] were in part set forth in the following words:

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[12] See preceding quotations from Weismann.

[13] Rauber, A., "Formbildung und Formstörung in der Entwicklung von Wirbelthieren," *Morphologische Jahrbuch,* Vol. 6, 1880, p. 4. The "casual remarks" are as follows:

"Die beiden Theilstücke, deren Verbindung das neue Wesen bewirkt, sind bei den höheren Thierformen enthalten in besonderen Organen, den Keimdrüsen. Da aber die Keimdrüsen die folgende Generation beherbergen, so erscheint ein Individuum als der Träger zweier Generationen, seiner eigenen sowie der folgenden Generation. Insoweit er der Träger seiner selbst ist, stellt er eine Person im engeren Sinne dar; er ist der *Personaltheil* der dualistischen Anlage. Die Träger der Zukünftigen Generation, die Keimdrüsen, stellen dagegen den *Germinaltheil* der dualistischen Anlage dar.

"Personal- und Germinaltheil gehen aber von *einem* befruchteten Ei aus, *ein* solches Ei enthält den Stoff mit dem Kräfteplan zu der genannten dualistischen Anlage. Man kann darum auch von einem Personaltheil und Germinaltheil des befruchteten Eies reden."

[14] Nussbaum, M., "Zur Differenzierung des Geschlechts im Thierreich," *Archiv für mikroskopische Anatomie,* Bd. 18, 1880, p. 112. The text of the original is worded thus:

"Es theilt sich demgemäss das gefurchte Ei in das Zellenmaterial des Individuums und in die Zellen für die Erhaltung der Art. In beiden Theilen geht die Zellenvermehrung continuirlich weiter; nur tritt im Leibe des Individuums die Arbeitstheilung hinzu, während in seinen Geschlechtszellen sich eine einfache additionelle Theilung vollzieht. Die beiden Zellen-

> The segmented ovum divides into the cell-material of the individual and into the cells for the preservation of the species. In both divisions the cell-multiplication proceeds continuously, but in the body of the individual division of labor occurs, while in the reproductive cells simple division only takes place. Both groups of cells and their offspring are propagated quite independently of each other, so that the reproductive cells have no share in the development of the tissues of the individual, and no seminal or ovicular cell arises from the cell-material of the individual. After the segregation of the reproductive cells the history of the individual and that of the species are entirely distinct, and because of this relation the "constancy" of the species is more easily understood; that is, the sharp persistence of the phenomenon of atavism by means of which ancestral traits are transmitted. For sperm and ovum are not derived from the cell-material of the parent organism, but have a common origin with it. However, since they are preserved within it, they are subject to the conditions which modify the parent organism; therefore the transmission of "acquired" characteristics is not excluded.

Nussbaum is said by some to be the first to suggest the idea of the cellular continuity of successive generations, but this conception is clearly implied in Virchow's aphorism[15] ''omnis cellula a cellula,'' and was fully stated in 1858 in the Law of Genetic Cellular Continuity first clearly formulated by Virchow[16] as follows:

> Just as an animal can originate only from an animal and a plant only from a plant, so every cell must arise from a preexisting cell. Although there are individual cases in which strict proof is still wanting, yet the principle is firmly established that for all living beings, whether they be entire plants or animal organisms or integrant parts of the same, there exists an eternal law of *continuous development.*

---

gruppen und ihre Abkömmlinge vermehren sich aber durchaus unabhängig von einander, so dass die Geschlechtszellen an dem Aufbau der Gewebe des Individuums keinen Antheil haben, und aus dem Zellenmaterial des Individuums keine einzige Samen- oder Eizelle hervorgeht. Nach der Abspaltung der Geschlechtszellen sind die Conti des Individuums und der Art völlig getrennt, und wir glauben aus diesem Verhalten die 'Constanz' der Art, d.h. die in der Erscheinung des Atavismus gipfelnde Zähigkeit, mit der sich die Eigenthümlichkeiten der Vorfahren vererben, begreiflicher zu finden. Denn Samen und Ei stammen nicht von dem Zellenmaterial des elterlichen Organismus ab, sondern haben mit ihm gleichen Ursprung; da sie aber in ihm aufbewahrt werden, so sind sie auch den Bedingungen unterworfen, welche auf den elterlichen Organismus modificirend einwirken, weshalb die Vererbung der 'erworbenen' Eigenschaften nicht ausgeschlossen ist.''

[15] *Archiv für Pathologische Anatomie,* Bd. 8, 1855, p. 23.

[16] ''Die Cellularpathologie im ihrer Begründung auf physiologische und pathologische Gewebelehre,'' Berlin, 1858, p. 25.

On the other hand, to Nussbaum is sometimes credited the theory of germinal continuity, but in such cases authors apparently do not sharply distinguish continuity of the germ-*plasm* from continuity of the germ-*cells*. Thus Minot[17] says:

> We owe to Moritz Nussbaum the theory of germinal continuity—the only theory of heredity which seems tenable at the present time. According to this theory, the germ-cells are set aside during the segmentation of the ovum and preserve the essentially undifferentiated qualities of the protoplasm and nucleus of the ovum, from the division of which they arise.

However, irrespective of the conclusions that may be reached as to whom priority in the statement of the theory of germinal continuity belongs, it is to Weismann that credit must be given for the development of this doctrine into an important theory of heredity.

There would seem to be a gain in precision and clearness of expression in discussions involving the idea of continuity in development if a distinction were always made between (1) *genetic continuity, or biogenesis,* (2) *genetic cellular continuity,* (3) *continuity of the germ-cell* and (4) *germinal continuity.* Thus restricted the term germinal continuity expresses more closely the conception held by the greatest exponent of this theory. Since Jäger first used the phrase "Continuity of the Germ-plasm" I suggest that his name be linked with that of Weismann in referring to this principle, which may well be called the Jäger-Weismann Law of Germinal Continuity, the esential doctrine of which is thus expressed:[18]

> In each ontogeny, a part of the specific germ-plasm contained in the parent egg-cell is not used up in the construction of the body of the offspring, but is reserved unchanged for the formation of the germ-cells of the following generation.

However, the real significance of Weismann's theory of germinal continuity and its bearing on theories of heredity can not be fully appreciated without at least a general acquaintance with the somewhat voluminous literature of this subject.

W. W. STOCKBERGER

BUREAU OF PLANT INDUSTRY,
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[17] Minot, C. S., "Laboratory Text Book of Embryology," Philadelphia, 1910, p. 28.

[18] Weismann, A., "Essays upon Heredity and Kindred Biological Problems," authorized translation, 2d edition, Oxford, 1891, p. 170.

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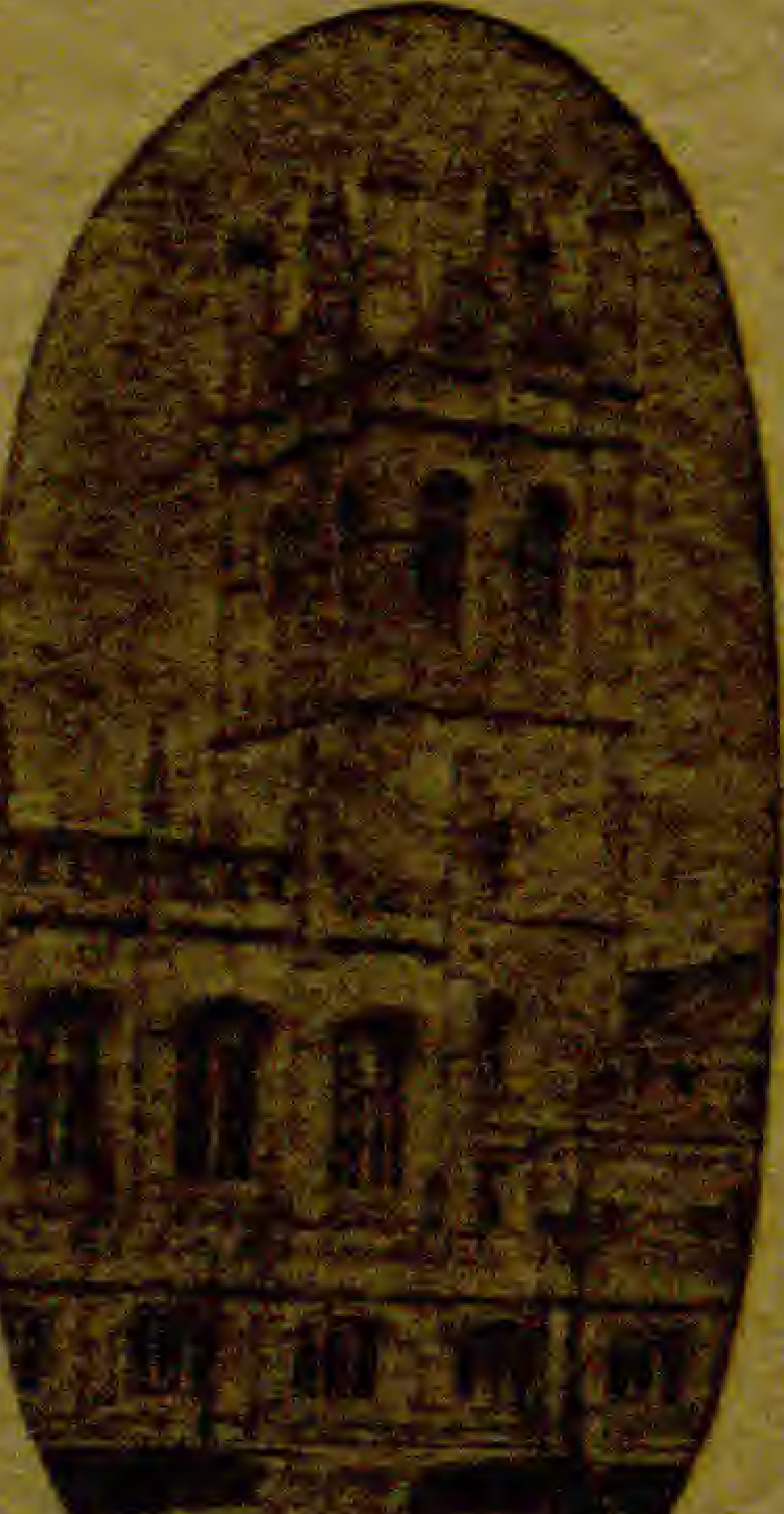

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DISTRIBUTION AND SPECIES-FORMING OF ECTO-PARASITES[1]

PROFESSOR VERNON LYMAN KELLOGG

STANFORD UNIVERSITY, CALIFORNIA

I

FOUR years ago I completed, and published in Wytsman's "Genera Insectorum," a catalogue of the Mallophaga (biting bird lice) of the world. This list gives the host distribution of each of the known species and the place or country of capture of the actual host individuals for all cases in which these localities had been recorded. It is, then, a classified list of the known Mallophagan species with their known geographic and host distribution.

I have now in hand, nearly completed, as complement to this already published catalogue, a classified list of all the hosts, bird and mammal, from which Mallophaga have been taken, together with the names of all the parasites recorded from each species, and not only again the actual geographical records of capture but also a statement of the general geographical distribution of each host species. I have determined, for the birds at least, which form the great bulk of the hosts, the synonymy of the various names used for them by the various collectors and reduced them all to the basis of the British Museum Catalogue of the Birds of the World.

By these two lists, namely, the catalogue of parasite

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[1] Parts of this paper were read before a general meeting at the Second International Congress of Entomology, Oxford, August, 1912.

species with hosts, and the catalogue of host species with parasites, this group of ectoparasitic insects should be accessible to a wider attention and a more thoroughgoing study from entomologists than it has hitherto had. Indeed the group is deserving of some special attention from general naturalists because of the interesting significance of the conditions of distribution and species forming which obtain in it. It is to the setting out of a few facts and some of the significance concerning distribution and species forming among these insects that the present paper is devoted.

II

The Mallophaga compose a small fairly homogeneous group of about fifteen hundred insect species (as so far known), which pass their whole lives on the bodies of birds and mammals. Those species found on birds are never found on mammals, and those on mammals never occur on birds. Indeed, with exceptions in only two genera, the Mallophaga of birds are of distinct families from those of mammals, the two groups being distinguished structurally by the loss in the mammal-infesting kinds of one of the two tarsal claws, an adaptation connected with the difference between the feathers and hair of the hosts as habitat. Of the 1,500 known Mallophagan species less than one hundred are mammal-infesting, the others all occurring exclusively on birds.

As to the relations of the Mallophaga to other insects I am convinced that they should be treated as a distinct order, finding their nearest affinities in the wingless Psocidæ, such as *Atropos*, the familiar book louse. This relationship is shown not only by similarities in external structure, some of which, however, are only examples of parallelism or adaptive convergence, but by certain more important common characters of internal anatomy, notably a curious pharyngeal sclerite (perhaps the greatly modified hypopharynx), found in both these groups and nowhere else among insects. The habitat and food habits, also, of the two groups add to the likelihood of the derivation of the Mallophaga if not directly from the Atropidæ, at least from an ancestor that might well have been the conmon progenitor of both types.

The Mallophaga are all of small size, ranging from 1.5 to 10 mm. in length, with the great majority of them not more than 4 or 5 mm. long and from 1 to 2 mm. in width. The body is much flattened dorso-ventrally, offering an interesting adaptive contrast, in this respect, to the laterally flattened fleas of similar habitat. The body is always wholly wingless, usually strongly chitinized and smooth. The mouth parts are of true biting type, the food being bits of hair or feather or dermal scales, and dried or fresh blood only incidentally and not by a direct breaking of the skin of the host. There are no compound eyes, but a single pair of ocelli placed on the lateral margins of the much flattened head, and the antennæ are from three- to five-segmented, and in about half the genera are capable of being concealed in a small protecting groove on the ventral face of the cheeks. The legs are of normal number, rather long and strong, flattened and fitted for running and clinging. The body is whitish, pale brownish or even dark-brown, often well patterned by blotches or bands of light to black-brown, on the paler ground. These markings almost always indicate specially heavily chitinized portions of the body wall.

The eggs are fastened to the hairs or feathers of the host, and the hatching young are much like their parents in appearance except for their smaller size and paler, unpatterned softer skin. They acquire maturity without any marked metamorphosis. They run freely about from birth, and feed on the hairs or feathers just as their parents do. Neither they nor the adults leave the body of the host except under unusual circumstances. In henhouses the parasites of the fowls have been occasionally found on the perches or in the nests, but I have often sought carefully, without finding a single parasite, on seaside rocks from which I had just frightened scores of closely massed resting cormorant, pelicans and gulls, all of them bird kinds whose individuals are practically always well parasitized. When a bird dies or is killed some of its Mallophagous parasites will sometimes wander off of the cold body, but usually they remain on the body and die there within a few days. Before dying they frequently grasp a feather barbule with their strong mandibles and are found there firmly fixed after death.

That they can not live, except unusually, for more than a few days off the body of the warm-blooded host I have proved by keeping them on feathers in ovens at the temperature of the bird body or on feathers in vials next my own body. They die in from two or three to six or seven days off the host body, or on it after death of the bird. It may be that the normal life of the adult Mallophagan is but a week long, but the fact that the young die off the host, or on it after its death, just as soon as the adults, indicates that the parasites are simply unable to live apart from their live hosts, for the only two apparent conditions peculiar to life on a bird's body, namely, a certain constant temperature and feathers for food, are certainly not difficult to reproduce off the body.

At times of actual contact of the bodies of their hosts they undoubtedly migrate from bird to bird. Thus they can move from male to female, or *vice versa* at mating, from mother and father to fledglings in the nest, and from individual to individual of the same species in the case of gregarious birds perching together.

The Mallophaga are, then, true, permanent ecto-parasites, of simple development, some degradation and adaptive modification of body, which occur in the number of one to several species on probably all kinds of birds and mammals, and on practically all bird and mammal individuals, but which, except in special and rather uncommon cases of unusual abundance, cause little serious injury to their hosts. The familiar constant searching of the plumage with the bill by birds is almost always due to the slightly irritating influence of these small parasitic insects, but only rarely can this annoyance reach such a pitch as to interfere much with the bird's feeding or resting or sleeping. And the loss of minute bits of feather can certainly be of no consequence at all. The Mallophaga then may be called benignant parasites, as contrasted with the malevolent, blood-sucking fleas and true lice affecting the same hosts.

III

With this fleeting acquaintanceship with the various principal structural and physiological characters of our group of insects, we may attend now to some of the special facts of their distribution and their inter-ordinal relationships, and to the problems which these facts pose to us.

First, with regard to the taxonomic conditions within the group. I have divided the order into two sub-orders, sharply distinguished by certain structural differences whose physiological or ethologic significance, however, is not at all plainly apparent. The most convenient recognition character for this sub-ordinal separation is the condition of the antennæ, short, broad, capitate, three-segmented and concealed in special antennary fossæ in one group; longer, slender, five-segmented, projecting and without receiving fossæ, in the other.

Each suborder contains two families, one of which, with two-clawed members, occurs exclusively (with the exception of one or two species in each of four genera in one case) on birds, and the other, with one-clawed members, exclusively on mammals. Both of the mammal-infesting families include but one genus each; while the two bird-infesting families include fifteen and ten genera, respectively.

The whole order then, with its one thousand five hundred species, comprises but twenty-seven genera, grouped into four families, arranged in two suborders. The disposition of the species among the genera has a rather extraordinary aspect. Nine, or one third, of all the genera, are represented by but one species each; seven are represented by from two to ten species; three are represented by from twenty to thirty species, three by from forty to sixty-five species, one by one hundred and fifty species, one by two hundred, and three by from two hundred and twenty-five to two hundred and fifty species. Thus while sixteen genera contain less than ten species each, four genera contain more than two hundred species each.

This extraordinary condition of the species in their relation to each other presents an attractive problem. What is its significance? What are indeed the special conditions influencing species-forming within the group?

From many years' work with these insects, including the description of several hundred new species, and the examination of long series of individuals of species in several different genera, I can say with confidence that the evolutionary factor of isolation plays a conspicuous part in Mallophagan species-forming. One soon comes to the acceptance of a very flexible species description for any given Mallophagan kind. While the score of individuals of one kind that one may collect from a single host individual will agree well with each other as to details of structure and pattern, the specimens of the same kind from another host individual of the same host species collected either in the same locality or a distant one, and the specimens from a third host individual and from a fourth and fifth, and so on, will all show many obvious, if mostly small, variations from the specimens taken from the first or any other host individual.

That is, each host individual is, in a way, a small island, biologically considered, with its inhabitants more or less nearly completely isolated from the inhabitants of other host islands. So that each species is made up of many dislocated small groups which may have, as when they are on birds of solitary habit, but little opportunity for mixing and cross-breeding with the members of the species-body as a whole. The group on one host bird may meet the group on the mate of this host, and these two mingling groups may send their representatives or their offspring to the young of the two mated hosts. But that is about the extent of their participation in the life and character of their species as a whole, and it is an extent which plainly must result in the establishment of an hereditary strain characterized by the special slight structural idiosyncrasies peculiar to the few ancestors from which the strain takes its origin. In the case of the parasites of more gregarious bird kinds, as the seabirds that mass for rest or brooding on ocean rocks or shore cliffs, or the swallows and swifts that live in colonies in caves and chimneys, or those gallinaceous birds like the partridges of California that gather in close bands of two or three score individuals, or others of any kind of similar habit which may give chance for repeated actual personal contact of body with body sufficient to permit of migration of the wingless but active parasites from bird to bird, this element of isolation is less accented. But it still plays an important figure. For both the winglessness and the manifest stay-at-home habits of the parasites make their movement from host to host at best a desultory and almost accidental one.

This combination of conditions, then, may serve to explain partly both why each species must be given a very flexible description and why one might describe and name, if he liked, many varieties of each species; and it explains, in some measure, why there are a good many species in the order, and why there are many in each of a few genera, although it does not explain, perhaps, why there are some genera with very few, and indeed even, so far as yet known, single species.

The explanation of the actually small number of genera and families depends, I think, upon one of the conditions in the life of the Mallophaga which is directly opposed, in its influence, in a way, to the isolation condition making for a variation that results in numerous varieties and species. It is this. Although the different host species may differ much among themselves as to habitat, habits, plumage markings, etc., yet as places of residence and providers of food for their external parasites they are all much alike. The temperature is the same, the feathers as food are about the same. Although the parasite's host may live in the water, the parasite itself, safely tucked away next the skin or among the feathers, lives on dry land in free air, for the water, even where it continually covers part of the plumage, as in swimmers, or occasionally all of the plumage, as in divers, only touches the plumage surface. Beneath this surface it is always dry and there is always free air.

Thus despite an isolated life for the inhabitants of each host island, and the great variety of these islands as regards name and relation to phyletic mainlands, the actual life conditions are monotonously alike on all these islands. So that there is, for the Mallophaga, no such variety of conditions of habitat and food and food-getting and mate-seeking and egg-concealing and young-rearing as would tend sharply to select and promote variations, with a result of genus and family making. There is no external influence at work promoting wide divergence. The generic and family distinctions tend to be few; the varietal and specific tend to be many.

IV

As a direct outcome of these conditions of life of the Mallophaga there arises an extremely interesting state of affairs concerned with their host and geographic distribution, a state of affairs which reveals, I think, a principle or fundamental consideration concerning the distribution of wingless ecto-parasites in general. This special subject may be introduced by a swift résumé of our present knowledge of the facts of the distribution of the Mallophaga. In this résumé I include some particular illustrations, by examples, of certain special distributional conditions.

As Mallophaga have been taken so far from but a hundred species of mammals, representing 48 genera, 24 families and 5 orders, any special scrutiny of the conditions of their distribution among mammalian hosts would hardly be worth while. But such scrutiny can certainly now be advisedly undertaken as regards the distribution among birds. For the Mallophagan host list includes already more than 1,100 bird species, representing 33 of the recognized 35 orders of living birds. The known living bird species number, according to the British Museum Catalogue, about 18,500. This catalogue, I should note, elevates to the position of species, or at least to the seeming of species, by cataloguing them binomially, the so-called varieties or trinomially dubbed subspecies of the continental and North American ornithologists; and I have followed this custom in my list—although against my belief in its taxonomic implication—for the sake of having a common and universally accessible basis for the host names.

Thus one out of every seventeen known living bird species is now included in the Mallophagan host list, as are 625 out of the 2,700 recognized living bird genera, and 120 out of the 160 living bird families. As comparatively few bird kinds are still unknown, and as on the other hand only a good beginning has been made in finding and describing the Mallophagan kinds, it is certain that the list of hosts of these parasites will increase rapidly in proportion to the total number of bird species. From the proportion of the number of different bird hosts parasitized by each Mallophagan species and the proportion of bird families and genera already in the host list, I estimate, roughly, the total number of living Mallophagan species to be about 5,000.

From the three Acarinate or Ratitian bird orders, namely, the Rheiformes, or South American rheas, the Casuariiformes or Australian cassowaries, and the Struthioniformes or African ostriches, only five species of Mallophaga have so far been recorded. On the rheas occur three species of *Lipeurus*, one being found on each of two host species and the other two on a third. On one species of Australian cassowary are found two Mallophagan kinds, one of which is the same species as that found on two of the South American rheas, while from the African ostrich, *Struthio camelus,* are recorded two parasite species, one of which is the same as that found on the third rhea. Here, at the very outset, is a remarkable case of distribution. Identical parasitic species on hosts as widely separated, geographically, as Australia and South America and Africa, but hosts all of a certain degree of genealogic affinity.

The order Tinamiformes, the tinamous of South America, curious birds, rather pheasant-like but presumably not really pheasants nor true Galliformes of any kind, is represented by eleven species in the Mallophagan host list. Most of these tinamous are well parasitized, a species of *Nothura* having four parasite species, one of *Crypturus* five, one of *Tinamus* six, one of *Rhynchotus* eight and another of *Tinamus* even nine parasite species representing five genera, of which two are peculiar to the group. Of the other Mallophagan genera found on the tinamous two that specially characterize the pheasants and other gallinaceous birds are, by odds, the most commonly represented. And this condition suggests another interesting problem. Is it going to be possible to get suggestions regarding the phyletic affinities of hosts from the character of their parasitic fauna? Take, for example, an order of birds troublesome to the ornithological taxonomists. Will the evidence of the presence on members of this order of certain parasitic genera characteristic of another order indicate their affinities to this second order? It does indeed seem, in the case of the Tinamiformes and Galliformes, as if the evidence from the Mallophagan distribution was in conformity with that suggested by certain structural similarities in the two groups.

The great order Galliformes, including the pheasants, partridges, quail, etc., is represented in the host list by seventy-eight species, from which are recorded about 150 Mallophagan species representing six genera, two of which, *Goniodes* and *Goniocotes,* are the most abundantly represented and occur much more commonly on birds of this order than those of any other unless it be the Tinamiformes, just spoken of. The other Mallophagan species recorded from the Galliformes belong to the large genera *Lipeurus, Colpocephalum* and *Menopon* which include species from most bird orders. The Mallophagan genus *Docophorus,* the second largest of all in the matter of number of species, and abundantly represented on almost all other bird groups, is totally unrepresented on the Galliformes. The Gallinaceous birds are, as a rule, strongly parasitized both as regards number of Mallophagan species and number of individuals. One of the brush-turkeys, *Megapodius,* has ten parasitic species, the painted Chinese pheasant has nine, and the Texan quail, eight. The domestic fowl has twelve Mallophagan species and its reputed ancestor, the wild Indian jungle fowl, *Gallus bankiva,* four, all of which occur on its domesticated descendant. The Mallophagan species *Lipeurus variabilis* is common to nine different hosts of the family Phasianidæ.

The small order of so-called pigeon grouse, the Pteroclidiformes, has two species in the host list, each parasitized by the single Mallophagan species, *Nirmus alchatæ,* not found on other birds. The two hosts species have overlapping geographic ranges.

The Columbiformes, or doves and pigeons, are represented in the host list by 40 species. The Mallophagan genera *Goniodes* and *Goniocotes,* so common also on the pheasants and tinamous, are very well represented among the pigeon parasites. The single Mallophagan species *Lipeurus baculus* is recorded from nineteen of the forty pigeon host species, whose geographic distribution includes Europe, Asia, Africa, North America, Malaysia, Australia, Madagascar and the Galapagos Islands. The European-Asiatic rock dove, *Columba* *livia,* immediate ancestor of the domestic pigeon, has two Mallophagan parasites of which one, the wide-spread *Lipeurus baculus,* is found on the domestic pigeon. The other species, *Goniocotes compar,* is common to several other wild doves, but, curiously enough, it has not been recorded from the domestic pigeon. The isolated Galapagos Island dove, *Nesopelia galapagoensis,* peculiar, both in genus and species, to these islands, is parasitized by *Lipeurus baculus,* and by four other Mallophagan species not found on any other pigeons.

From the hoazin, strange aberrant bird of the Amazon forests, and single representative of the order Opisthocomiformes, I have recorded three Mallophagan parasites, two of them new species, and one a member of the genus *Goniocotes,* a genus rather characteristic of the pheasants and pigeons. It is exactly to the pheasant-like birds that ornithologists seem at present inclined to associate this lonely South American bird.

The Ralliformes, or rails, gallinules and coots, are represented in the Mallophagan host list by twenty-three species. One small genus of parasites, *Oncophorus,* is almost limited to the order. The old world coot, or mudhen, *Fulica atra,* has seven Mallophagan species representing six genera. Its congeneric sister species of the new world, *Fulica americana,* has twelve Mallophagan species, of which five are identical with those found on the old world coot. The parasite species *Oncophorus bisetosus* occurs on six different rails, three of them North and Central American and three of them Malaysian and Australian.

The Podicipedidiformes, or grebes, are represented in the host list by six out of the 25 known species of the order, from which are recorded eight Mallophagan kinds. On five of the six grebe species occurs the Mallophagan species *Menopon tridens,* found elsewhere also on certain loons, auks and ducks. The six grebes are geographically distributed as follows: two new world, three old world, and one circumpolar.

Seven species of Mallophaga have been taken from four species out of the known five of the order Colymbiformes or loons, one of which is limited to the old world with three circumpolar in range. On three of these loons occurs the Mallophagan species *Docophorus colymbinus,* and *Nirmus frontalis* is common to two, and *Menopon tridens* to two. But the continuity of geographical range among the loons does not seem to have produced any special effect of commonness of parasites to different host species. In the preceding order, for example, that of the grebes, there is more commonness of Mallophagan species, although at the same time more isolation of the hosts geographically.

From two penguins representing the order Sphenisciformes, three Mallophagan species have been recorded. Two of these belong to the genus *Goniodes,* a genus best represented among the pheasants and pigeons. The third is type-species of a genus so far not elsewhere recorded.

The Procellariiformes, or petrels and albatrosses, of which about a hundred living species are known, are represented in the host list by thirty-two species, and give evidence of being a strongly parasitized group of birds. Ten Mallophagan kinds have been taken from one species of *Puffinus,* nine from another, eight from another and seven from a fourth. Besides these, four other species of *Puffinus* are in the host list. On the four *Puffinus* species most infested there is one parasite kind common to all, and four parasite species common to three of them. Six species of albatrosses, genus *Diomedea,* are included among the Procellariiform hosts. On five of them occurs the giant Mallophagan species *Lipeurus ferox,* 10 mm. long, and on five also the large, broad species *Eurymetopus taurus.* Nine species of Mallophaga have been recorded from the single albatross species *Diomedea albatrus,* of the North Pacific Ocean. Four Mallophagan genera, each of them containing but a single species, are peculiar to the order. The birds of this order range the great oceans in overlapping zones and reaches.

The order Alciformes, including 29 known living species of auks, murres and puffins, is represented in the host list by sixteen species which are parasitized by sixteen Mallophagan species belonging to but two genera, *Docophorus* and *Nirmus,* with the exception of one species of *Menopon.* These two genera are, however, not at all limited to the Alciformes, but are two of the largest and most widely distributed of the Mallophagan genera. *Nirmus citrinus* occurs on four Alciform hosts, and *Nirmus maritimus, Docophorus celedoxus* and *Docophorus montereyi* on three each. *Nirmus pacificus* and *Docophorus atricolor* occur on two each.

The homogeneous order Lariformes, or gulls and terns, including 122 known living species, is represented by fifty species in the host list, of which two dozen belong to the gull genus *Larus,* and one dozen to the tern genus *Sterna.* Gulls and terns are strongly parasitized. Thirteen species of Mallophaga, representing four genera, have been recorded from *Sterna fuliginosa,* and ten species from the tropical noddy, *Anous stolidus.* The gull and tern parasites are mostly of the genus *Docophorus* and *Nirmus* with some *Menopon* and *Colpocephalum* and a few *Lipeuri. Docophorus lari* occurs on nineteen species of *Larus,* and *Nirmus bilineolatus* on eleven. *Docophorus melanocephalus* occurs on four species of *Sterna.* Many of the members of this bird order range widely, but some are limited to new world or old world shores.

The large order of waders and shore-birds, the Charadriiformes, is represented in the host-list by sixty-three species. The Mallophagan genus *Nirmus* is especially commonly met with on these birds, and has many species characteristic of them. From the cosmopolitan sanderling, *Arenaria interpres,* with its individuals from old and new world meeting in high latitude breeding grounds, fourteen Mallophagan species have been recorded, of which six are *Nirmi.* Ten Mallophagan kinds occur on the European curlew, *Numenius arquata,* of which one occurs also on the new world curlew, *Numenius longirostris.* It is the only Mallophagan so far recorded from this host. *Hæmatopus galapagoensis,* limited to the Galapagos Islands, has three Mallophagan species, of which one is peculiar to it, one is a duck-infesting species, probably a normal straggler under conditions which I shall explain later, and one is a form found also on *Hæmatopus ostralegus,* the common oyster-catcher of Europe, Central Asia and Africa. The old world avocet, *Recurvirostra avocetta,* has six Mallophagan species, while the new world avocet, *Recurvirostra americana,* has four, of which two, *Nirmus pileus* and *Nirmus signatus,* are common to both hosts. The other two are new. Two species of the curious aberrant Charadriiform family Parridæ occur in the host-list, each having but a single Mallophagan species, and that the same for both hosts. One of the host species is limited to Australia, while the other ranges from India to the Malay Peninsula.

The Gruiformes, or cranes, thirty-four living species, are represented in the host-list by twelve species, parasitized by twenty Mallophagan kinds. The herons and egrets, order Ardeiformes, are represented by forty-five species. *Lipeurus leucopygus* occurs on both the old world bittern, *Botaurus stellaris,* and the new world one, *Botaurus lentiginosus.* It occurs also on two other herons, both old world species. From *Butorides sundevalli,* peculiar to the Galapagos Islands, I have had four species, all previously described by me from various maritime birds of the Pacific. This is a case of straggling, but as I shall point out later in connection with the conditions shown by certain other Galapagos Island hosts, a case of what may be called normal straggling, unusual on the whole, but possible and especially common in the case of Galapagos, and perhaps other, island hosts.

The Palamedeiformes, or South American screamers, are represented in the host-list by two species, parasitized by three Mallophagan kinds. One of these is common to both hosts. The flamingoes, constituting the order Phœnicopteriformes, are parasitized by four species of Mallophaga of four different genera.

The Anseriformes, swans, geese and ducks, are represented in the host-list by sixty-four species, seven being swans, nine geese and the rest ducks. The swans have a Mallophagan genus, *Ornithobius,* peculiar to them, which occurs on four out of the seven species. The species *bucephalus* of this genus occurs on two old world and one new world species. Six of the seven swan kinds belong to the genus *Cygnus.* Three of these are old world, two new world and one circum-polar in range. *Trinoton conspurcatum* has been recorded from the three old world and the single circumpolar species, and *Docophorus cygni* from two old world and one new world species. *Cygnus cygnus* of Europe has six Mallophagan species. The curious Australian swan *Chenopsis atrata* has two parasite species neither of which occurs on any other swan. Among the geese are three species of *Anser,* two of them old world and one new world, with the parasite *Lipeurus jejunus* common to them all, and four species of *Branta,* one of which also carries *Lipeurus jejunus.* This Mallophagan species also occurs on the domestic goose. The forty-four species of ducks of the list are parasitized by forty-two species of Mallophaga. Of these, *Docophorus icterodes* is recorded from eleven duck species, *Lipeurus squalidus* from fifteen and *Trinoton luridum* from nineteen, these duck kinds including African, Asiatic, European, North American, South American and cosmopolitan species. A duck kind from Australia and Malaysia has four parasitic species, all peculiar to it. Three species of ducks have the three most familiar duck-infesting Mallophaga, mentioned above, common to them all. *Anas boschas,* the ancestor of the domestic duck, has these three and just one more. But so far only one of the three has been recorded from the domestic duck. While many species of ducks, and most individuals of the species, are parasitisized, it is rare that more than two or three or four—the maximum is actually six—Mallophagan species are found on a single host species. The great bulk of the parasitization comes from comparatively few Mallophagan species, notably the three species already named.

The Pelecaniformes, 75 living species, including the pelicans, cormorants, boobies, man-o'-war and tropic birds, are represented in the host list by thirty-three species. Thirteen of these are cormorants of the genus *Phalacrocorax,* and nine are boobies of the genus *Sula. Lipeurus setosus* occurs on two African and two Australian and Malaysian species of *Phalacrocorax. Lipeurus toxoceros* occurs on one cosmopolitan cormorant and on two others, one of South and Central America and one of North America. *Lipeurus faralloni* is recorded from three North American west coast species. Five species of *Pelecanus,* three new world and two old world, are included in the list. *Menopon titan* occurs on two of the new world and one of the old world species, *Lipeurus bifasciatus* on one new world and both of the old world forms, and *Lipeurus forficulatus* on two new world and one old world species. Eleven species of Mallophaga are recorded from the cosmopolitan man-o'-war bird, *Fregata aquila,* and eight from the beautiful white tropic bird, *Phaeton æthereus.*

The Cathartidiformes, or new world vultures, are represented in the host list by four species. There are but nine species in the order. The four species in my list are the great condor of the Andes, ranging from Patagonia to Ecuador; the great king vulture of the northern Andes, Central America and Mexico; the rare Californian condor of northern Mexico, Baja California, and California north to its middle region; and finally, the ubiquitous turkey vulture, smaller and far more abundant than any of the others, that ranges over all of North America and, in winter, gets into northern South America. Thus the ranges of the four species combined extend the whole length of the western coast of the new world. And although each bird has its own stretch of coast mountains, the range of each overlaps that of some other. The individuals of all these bird species, except the last named, are few and solitary in habit, resting and nesting in inaccessible mountain places, but meeting a few of their kind occasionally at common table around some dead or dying animal. Turning now to the parasites of these lonely birds, we find one species, the well-marked, rather large *Lipeurus assessor* common to all four vulture species. But *assessor* has been taken from the wide-spread turkey vulture only in Panama, *i. e.,* within the range of the king vulture. *Læmobothrium delogramma* is also found on both the king and the turkey vultures, but has been taken from the latter host again only from Panama specimens. The king vulture and Californian condor, whose ranges overlap in Mexico, have one parasite species, *Menopon fasciatum,* common to both. These are the only cases of commonness of Mallophagan species to two or more of these great vulture kinds. And all are pretty well parasitized, seven Mallophagan species being recorded from the king vulture, five from the South American condor, five from the North American turkey vulture, and two from the Californian condor. It is well to keep in mind, in noting this rather abundant parasitization, that the feeding habits of the birds give some opportunity for the straggling of parasites from other bird or mammal kinds, serving, in the persons of moribund or just dead individuals, as prey. It is therefore indeed important to note that no mammal-infesting Mallophaga have been taken from any vulture, despite the excellent chances for such straggling. Perhaps the difference between a mammal and a bird host is too great to permit a parasite adaptively specialized for life on one to persist successfully on the other. Or perhaps there is a physiological antipathy, a negative chemotropism, too strong to permit the straggling. Yet I recall that in my days as a bird-collector and maker of skins, I repeatedly had the annoyance of discovering that I was a temporary host for individuals of parasites more normal to a duck or a barn owl than to man! But these wanderers seemed as anxious to leave their chance-found new host as was the host to be relieved of them; a few moments was the usual extent of their stay.

This point of the reluctance of Mallophaga to migrate, even with good opportunity, from normal or characteristic host, to another, is emphasized when we come to examine the parasitic conditions of the next bird order, the Accipitriformes, or falcons, hawks and eagles, almost all species of which capture living mammals of one kind or another. In the parasitic records of the seventy species of this order included in my host list, there is not a single record of a Mallophagan species of either of the strictly mammal-infesting genera, and there are but three or four records of bird-infesting species that are plainly stragglers from prey, as is, for example, a typical duck parasite recorded from an American hawk, and a pigeon parasite from a European falcon. In fact, the Mallophagan species taken from the birds of prey are about as characteristic of their host-group as are those of any other group, although there are, indeed, no parasitic genera wholly peculiar to the birds of prey. The Mallophagan species *Colpocephalum flavescens* is found on twenty-one Accipitrine species and *Nirmus fuscus* on eighteen, the hosts representing species from all parts of the world, including, for *Nirmus fuscus*, at least, Australia. They represent, too, most of the principal families and subfamilies of the order. *Colpocephalum flavescens* is found on *Thrysaëtos*, a new world eagle genus, on *Gypaëtus*, an old world eagle, and on one cosmopolitan species of *Aquila* and one old world *Aquila*. The eagles, like the great vultures, are characteristically solitary birds, only the members of each household, that is, male, female and young, coming into contact with each other. They are typical host islands. Some of the birds of prey are strongly parasitized, as the golden eagle, *Aquila chrysaëtus*, with nine Mallophagan species, and the South American caracara, *Polyborus tharos,* with eight.

In the Strigiformes, or owls, represented in our host list by nineteen host species, we have added confirmation of the Mallophagan hesitancy to straggle even with good opportunity. There is no record of a mammal parasite on any owl, nor but two or three of Mallophagan species characteristic of birds of other orders. Of the characteristic owl parasites, *Docophorus cursor* occurs on all three species of *Asio* included in the host list. One of these Asios is restricted to the Galapagos Islands, one ranges Mexico and temperate North America, and one occurs in both old and new worlds. The genus *Strix,* barn owls, is represented by two species, one the old world barn owl and the other the barn owl of temperate North America. The Mallophagan species *Docophorus rostratus* occurs on both of them. *Asio accipitrinus,* the cosmopolitan hawk owl, carries seven Mallophagan species.

The Psittaciformes, parrots and cockatoos, are represented in the host list by twenty-eight species, infested usually by only one to two or three parasite kinds, although five have been recorded from a Senegambian *Psittacus.* It is pleasant to note that the cruel New Zealand Keas, which have adopted the extraordinary habit of alighting on the backs of living sheep and tearing their flesh, even through to the vitals, have at least three Mallophagan parasite species to make life a little uncomfortable for them. One of these species, *Lipeurus circumfasciatus,* is recorded from three other parrots of Australia and Malaysia.

The catch-all order Coraciiformes, including the rollers, kingfishers, hoopoes, mot-mots, poor-wills, swifts and humming-birds, is represented in the list by forty-five species, of which six are kingfishers, six are hummers and five are swifts. Of the five swifts three are of the new world and two of the old. The Mallophagan genus *Nitzschia* is peculiar to the swifts and is found, represented by four species, on all five in my list. *Nitzschia pulicaris* is found on one old world and two new world species. The humming-birds are not badly parasitized, although three Mallophagan species have been recorded from a single one of these tiny host kinds. They are especially infested by the Mallophagan genus *Physostomum,* although species of this genus occur on several other passerine bird hosts.

The trogons, order Trogones, are represented in the host list by two species, infected by two Mallophagan species, both of the genus *Nirmus.* The Coccyzes, or cuckoos, represented by twenty-three species, have usually but one, although sometimes two or three Mallophagan kinds to a host species. And this condition of slight parasitization is also true of the five species of toucans and barbets, order Scansores, included in the list. *Docophorus latifrons* is recorded both from the common European cuckoo and, in varietal form, from the common American cuckoo.

The order Piciformes, the woodpeckers, is represented in the list by twenty-six species, each carrying but one to two or three Mallophagan kinds to its discredit. The woodpecker genus *Dendrocopus* is represented by six species of which five belong to the new world and one to the old world. *Docophorus superciliosus,* described from the old world species of *Dendrocopus,* occurs also on one of the new world species and also on another old world woodpecker of different genus. One of my Western American Mallophaga species occurs on three woodpecker kinds in California, one in Baja California and three in Costa Rica. It seems to be a pervasive parasite of American West Coast woodpeckers. Of the seven host species from which it is recorded three belong to the one genus *Melanerpes.*

The order Eurylæmiformes, or Malayan broadbills, is represented in the host list by one species parasitized by two species of Mallophaga, while the order Menuriformes, the beautiful lyre-birds of Australia, three living species, is also represented by one species, parasitized, however, by six Mallophagan species all peculiar to it.

This brings us to the last bird order of our list, the great group of Passeriformes, the perching and singing birds, with its various familiar families of flycatchers, swallows, wrens, thrushes, titmice, warblers, larks, finches and sparrows, tanagers, blackbirds, crows and jays, *et al.* It contains 5,000 known kinds, but is represented in our host list by but three hundred and eight species, divided among more than a score of families. Practically no Mallophagan species found on members of this order occur on birds of any other order. Two Mallophagan kinds have a wide host distribution within the order. *Docophorus communis* has a host list of one hundred and thirty Passeriform species, of which thirty-eight are members of the family Fringillidæ, this being more than half of all the Fringilline birds from which Mallophaga have so far been recorded. These one hundred and thirty hosts of *Docophorus communis* represent most of the families of the Passeriformes and, in their geographic distribution, all of the principal regions of the world. A score of varieties have been named within the species, and a score more might be. But this would be to say no more than that there is a wide variation among the members of the species, and to attempt to make categories of this variation is really labor lost. This large variability of *Docophorus communis* is simply the most conspicuous example within the order of that condition of persistent variation, due chiefly to isolation, that I spoke of at the beginning of this paper as a condition occurring in almost all the Mallophagan species; a variation fostered by isolation, unrestrained by cross-breeding, but not specially emphasized by adaptive modification, nor sharply selected for life and death value.

Another Mallophagan species widely spread among Passeriform hosts is *Nirmus vulgatus,* a species described by me several years ago and which I have so far taken from forty new world host kinds, including several genera and species peculiar to the Galapagos Islands. All the specimens from Galapagos Island hosts show a number of small but obvious distinguishing characters, and I have given them the varietal name *galapagoensis*. This constant distinction would indicate that the Galapagos individuals, though now infesting several different host kinds, are all descended from a single original introduction of the species; or that there is some external modifying condition of life on Galapagos Island birds that would produce a convergence among the descendants of ancestors representing several introductions, a supposition hardly tenable, especially in the light of the peculiar life conditions of the Mallophaga.

The Passeriform family Tyrannidæ, the new world flycatchers, is represented in the list by eighteen species parasitized by two Mallophagan species, of which but two, one being *Docophorus communis,* are recorded from old world Passeriform hosts. Although this family has a continuous geographical distribution over North, Central and South America, there is no unusual commonness of parasitic distribution in it. No one Mallophagan kind occurs on more than two flycatcher species, except in the Galapagos islands, where *Nirmus vulgatus* var. *galapagoensis* is found on all three of the flycatcher kinds occurring there. All the other Mallophagan species on these Galapagos flycatchers are forms restricted to the islands, although not to the flycatchers.

The swallows, Hirundinidæ, are represented by ten species of which two are old world, five new world, two both old and new world, and one from the Galapagos Islands. From them are recorded twenty Mallophagan species, of which *Menopon rusticum* is found on one old world, one new world, one old and new world, and one Galapagos Island host. *Docophorus excisus* is found on one old world and two new world hosts, and *Nirmus longus* on two new world and the two old and new world hosts. Seven Mallophagan species have been taken from the Galapagos Island swallow, of which one is found on two new world swallows and one is the *Menopon rusticum* already mentioned as common to one old world, one new world and one old and new world host.

Mallophaga have been taken from three species of wrens, Troglodytidæ, of three different genera. Two species of parasites have been taken from each host species, and no one of these Mallophagan species occurs on more than one host kind.

The Cinclidæ, or dippers, are represented in the list, by two species of *Cinclus,* one from the old world and one belonging to the new. One Mallophagan species, a *Menopon,* is common to both hosts, and each host species has, in addition, another Mallophagan species, a *Docophorus* in one case and a *Nirmus* in the other.

The Mimidæ, or mocking-birds, are represented by seven species, of which five belong to the genus *Nesomimus* peculiar to the Galapagos islands. The other two are North American. There is one Mallophagan species on each of the American mockers, and from one to as many as eight on the various Galapagos Island hosts. But the Mallophaga of the Galapagos Island mockers are mostly species common to numerous other birds of the islands, some of these birds being widely separated phyletically from the Mimidæ. For example, the characteristic *Lipeurus baculus* of the pigeons has been taken from one of the mockers. This apparently abnormal condition has a normal explanation that we shall take up in connection with certain still more conspicuous examples of the anomalies among the Galapagos records.

The Turdidæ, or thrushes, are represented in the list by twenty-three species. *Docophorus communis* occurs on nine of them. *Menopon thoracicum* is recorded from the old world *Turdus viscivorus* and from *Merula grayi* and *Catharus gracilirostris* from Costa Rica. The Sylviidæ, or old world warblers, are represented by five species, on four of which *Docophorus communis* is the only parasite. The Ampelidæ, or waxwings, are represented by four species, two of which are North American, one Central American, and one common to both old and new worlds. *Docophorous communis* and *Nirmus brachythorax* occur on three of the four species.

Mallophaga have been recorded from eight species of Laniidæ, or shrikes, of which three are old world species, three new world and two are Australian. *Docophorus communis* occurs on five of the old and new world species, but not on either of the Australian hosts. Four of the eight species belong to the genus *Lanius,* three being new world and the other an old world species. *Docophorus communis* occurs on them all.

The Paridæ, or titmice and chickadees, are represented in the host list by eleven species, four old world and seven new world. *Docophorus pari* is recorded from three old world species of three different genera. *Docophorus rutteri* occurs on two new world species of the same genus and the same geographical region. Mallophaga have been taken from three kinglets, family Regulidæ, two of them old world species and one new world. *Physostomum frenatum* is recorded from one old world and one new world host species.

The rather large family of Mniotiltidæ, or wood-warblers, is represented by twelve species, three of them from the Galapagos Islands, and the others from North, Central and South America. *Docophorus communis* is the only old world Mallophagan species occurring in the group, being found on three of the American host species.

The Drepanidæ, or honey creepers of the Hawaiian Islands, are represented in the list by three species of three different genera. Seven Mallophagan species, all except one peculiar to the host group, have been taken from these three hosts. One of the Mallophagan species is common to all three.

Mallophaga have been taken from five species of Alaudidæ, or larks, three of them old world, one new world, and one inhabiting both old and new worlds. *Docophorus communis* occurs on four of the lark species.

Only three other Mallophagan kinds have been recorded from the family.

The great family of sparrows and finches, the Fringillidæ, including nearly 1,200 bird kinds, is represented in the host-list by seventy-six species. The Mallophagan species *Docophorus communis* has been recorded from thirty-eight of these from the old and new worlds, and *Nirmus vulgatus* from eighteen, all from the new world. There have been almost no Mallophagan records made from old world hosts since I described *vulgatus,* which is possibly the explanation of the lack of any old world records for it, although it may really be that the species does not occur in[2] Europe. Among the Fringilline hosts of the Mallophaga there are nine species representing two genera, *Camarhynchus* and *Geospiza,* peculiar to the Galapagos Islands. Most of these nine host species are pretty strongly parasitized, one of them, indeed, *Geopiza fuliginosus,* having had nineteen Mallophagan species taken from it, the record as regards number of parasite species from a single host form. Of these nineteen Mallophagan species, four belong to the genus *Docophorus,* five to *Nirmus,* five to *Lipeurus,* two to *Colpocephalum,* two to *Menopon,* and one to *Goniocotes.* Among them are included all of the seven species that have been recorded from *Camarhynchus pallidus,* the most parasitized species of this sister sparrow genus peculiar to the islands. But also there are included several Mallophagan species found on various other host birds widely separated phyletically from *Geopiza* and *Camarhynchus.*

In fact, in studying the parasitization of the Galapagos Island birds—and I have had in hand two very full collections from them—one is struck by the breakdown of the general rule that the Mallophaga of one host group, as a genus or family or order, shall be more or less nearly exclusively confined to members of the group, and hence to be characteristic of it. For example, one does not expect to find the abundant duck parasite, *Trinoton luri-*

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[2] I have recently recorded *Nirmus vulgatus* from a starling from Egyptian Sudan.

dum on pigeons, nor the familiar pigeon parasite, *Lipeurus baculus* on ducks, and one does not so find them. Nor to find on sparrows or hawks Mallophaga of the genera *Ancistrona, Eurymetopus* and *Philoceanus,* characteristic of maritime birds; nor on owls or cuckoos to find certain maritime bird-infesting species of *Lipeurus* and *Docophorus,* genera in themselves represented by species on hosts of many orders. But in the two carefully made collections of Mallophaga from the Galapagos Islands, representing in their host lists practically all the bird species known to inhabit the islands, I have noted the exception to be the rule. And from interviews with the collectors—one of them was one of my own assistants—I have determined the probable reason for this unusual state of affairs. It is this. The birds of the land, the birds of the shore, and the birds of the sea meet and rest side by side on the shore rocks and sands. The land birds live chiefly not in the dense, almost impenetrable jungle of the interior of the islands, but in the outer or shore fringe of it. Here they meet and mingle with the hosts of sea birds that find resting and nesting ground on these few small bits of solid earth set in the midst of all the leagues of inhospitable moving waters that constitute their range. This brings about the opportunity and the reality of an abnormal but natural straggling, which results in an extraordinary and probably unique host distribution of the parasites. And thus it is that the little Galapagos Island sparrow, *Geospiza fuliginosa,* comes to be the bearer of more Mallophagan species than any other bird in the host list and has included among its guests many that more rightfully belong to birds of ocean and shore sands.

The Tanagridæ, or tanagers, are represented in the host list by ten species. *Menopon thoracicum* is common to four of them, all of Central American range. The Icteridæ, including the blackbirds, grackles, meadowlarks, and American orioles, are represented by twenty-two host species, and the Sturnidæ, or starlings, by seven.

The Paradiseidæ, the radiant birds of paradise, are represented in the list by eight species.

Finally, the Corvidæ, or crows and jays, are represented at present by thirty-two species, about one out of ten of the known kinds, of which thirteen belong to the genus *Corvus*. Both these numbers will be increased when I am able to incorporate in the list the records, already worked but not yet published, of a considerable collection of Mallophaga from the crows and jays of India, sent to me by Superintendant Annandale of the Indian Museum at Calcutta. The Corvidæ are provided with a number of parasite species characteristic of the family, such as *Docophorus atratus, Colpocephalum subæquale, Menopon mesoleucum, et al.* This latter parasite occurs on four species of *Corvus,* two of old world and two of new world range. *Colpocephalum subæquale* occurs on two North American and one European species of *Corvus.*

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From these examples of Mallophagan distribution illustrating various special conditions of host relations a number of rather important points of significance appear. Of two only, however, which indeed at bottom are really one, shall I speak. First, there is apparent in Mallophagan distribution a general faithfulness of parasite to host kind or group of related host-kinds, and this without much reference to geographical conditions. And second, there appears a plain tendency for a single parasite species to be common to two or more related host species, even though these hosts be so widely separated geographically and so restricted to their separate geographic ranges that all possible chance of contact between individuals of the different host species seems positively precluded. The American and the European avocets do not meet; nor do the American and European coots. Yet the two coots have five Mallophagan species in common, and the two avocets two. The American and European bitterns are both infested by a common parasite species.

The American and old world dippers or water ouzels are in the same case. The same Mallophagan species occurs on both an old world and a new world kinglet. One parasite species is common to two old world and two new world crows. Practically all of those isolated bird species found only on the Galapagos Islands are infested by Mallophaga that occur on related new world or even old world hosts.

Now, removing all cases of even an imaginable rare possible contact of bodies between these related but specifically distinct hosts, such as might occur in birds of circum-polar range, or in gregarious maritime kinds meeting on common mid-ocean islands, or in kinds occasionally exported by man from their normal range, etc., and there are still left many cases of this commonness of a parasite species to two or more usually rather closely related host species of quite distinct geographic range. How can this actual condition be explained?

I can see but one answer. That is, that the parasite species has been handed down practically unchanged to the present specifically and even generically distinct several bird species from their common ancestor of earlier days. The parasite species dates from the days of this ancestor. With the splitting up of the ancient host species due to geographic wandering and isolation of groups of its individuals, and their gradual divergence in plumage, color and pattern, shape of bill or toes or wings, caused partly by adaptation and partly by the simple persistence of chance variations fostered by the isolation and inbreeding, there has been no equivalent evolutionary divergence of the isolated groups of individuals of the parasite species. No adaptive changes have been necessary for it. It has indeed been broken into isolated groups of individuals, but no more than is normal to its life under conditions less novel. I have already pointed out the large variability that occurs within every Mallophagan species caused by the separation, more or less complete and persisting, of its individuals into little groups and family strains each isolated on its host island or succession of self-reproducing islands.

But the change of plumage markings, or of bill shape or even of food and flight habit, of the separating host kinds splitting off from a common ancestor need mean nothing much for the parasite. So although in time we come to have, derived from a common ancestor, an American avocet and a European one, an American coot and a European one, we do *not* have an American avocet- or coot-parasite and a European avocet- or coot-parasite. But the parasite of the common avocet or coot ancestor of the two present bird species remains unchanged and is thus a single species common to the two geographically separated, specifically distinct, never-meeting, host species.

If this is a true explanation for the commonness of a parasite of two separated host species, it is likely also the explanation of the larger phenomenon of the general faithfulness of certain parasite species or genera to certain bird groups—families, or even orders. I do indeed believe that it is a commonness of the genealogy rather than a commonness of adaptation that is the chief explanation of this restriction of certain parasite groups to certain host groups. It is in my eyes an unusually clear example of the potency of heredity. There is more nature than nurture in the upbringing of the Mallophaga.

Isolation and inheritance, then, are the two evolution factors especially concerned in the species-forming and the distribution of the Mallophaga. Adaptation seems to play a very subordinate part. And this is a rather unusual condition in insect biology. The plasticity of insect nature combined with the stresses of insect life and the necessary shifts for a living, have resulted in producing among the insects some of the most striking examples of adaptive evolution to be found in the kingdom of life. In the face of this fact, this little group of parasites may have by the very exceptionality of its evolutionary behavior, an enhanced interest for us!

CASTRATION IN RELATION TO THE SECONDARY SEXUAL CHARACTERS OF BROWN LEGHORNS[1]

H. D. GOODALE

STATION FOR EXPERIMENTAL EVOLUTION

Introduction.—It has often been observed, in many sexually dimorphic species of birds, that a female occasionally occurs which exhibits many of the characters of her mate. Frequently associated with this condition are alterations, more or less pathological, in the ovary. It has been said also that the male sometimes, and in particular the unsexed male of the domestic fowl, presents characters resembling those of the female. However, it has been pointed out that the supposed resemblance to the female can also be interpreted as due to the failure of the development of the normal adult male characters. In other words, these modified males may be referred to either a juvenile or to a female condition.

These considerations led, then, to the following questions. Will removal of the ovary from the young female fowl cause her to assume the characters of the male? Will removal of the testes from the young male cause him to assume any female characters or will it cause him to retain his own juvenile characters or will it be without effect? For answers the Brown Leghorns seemed to furnish particularly favorable material, because: first, the adult plumage, which is strongly sexually dimorphic, is practically identical with that of the Jungle fowl; second, the comb of the female, while proportionally smaller than that of the male, is larger than that of the male of many other varieties; third, there are at least

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[1] This paper with some changes was read before the American Society of Naturalists at Princeton, N. J., December 28, 1911. Since then the experimental results have been fully verified. Male characters have developed on 25 females, following ovariotomy. A complete account of the newer experiments will be published later.

three distinct stages in the development of the young bird's plumage before the adult color is reached. The first two stages do not exhibit sexual dimorphism, nor are they identical with that of the adult female. Sexual dimorphism appears first in the third juvenile plumage. At this stage, while the young female rather closely resembles the adult female, the young males in their *tout ensemble* are distinct from either the adult male or female, though sometimes feathers like those of the female may be found. A study of the characters of the Brown Leghorn capon or poullard, therefore, should show whether their characters are juvenile, male or female. For most characters, the results obtained from a preliminary set of experiments are clear cut.

Description of the Secondary Sexual Characters.—In Table I is given a comparative statement of the more pronounced secondary sexual characters common to nearly all races of domestic chickens. There are other differences between the sexes, which are more subtle and therefore not considered here. In Table II are given other secondary sexual characters found in the Brown Leghorns but not in all other races of chickens.

Comment on Tables.—Such exceptions to the general statements given in Table I as occur, are mainly negative, that is, they are characters which for one reason or another do not become patent, as for example, the failure of the whole or a part of the color pattern to become visible, particularly in the case of uniformly colored birds.

In considering plumage characters aside from shape of feather there are three features to be taken into account. First, the localization of color in certain definite regions of the body, thus forming the body pattern; second, the localization of color on definite regions of the feather, forming the feather pattern; third, the pigments themselves, which are associated with each pattern in various ways.

It is rather striking, that in spite of the numerous

TABLE I[2]

A COMPARATIVE STATEMENT OF THE CHIEF SECONDARY SEXUAL CHARACTERS OF DOMESTIC CHICKENS, COMMON TO NEARLY ALL VARIETIES

	Adult		Young of Both Sexes
	Male	Female	
Size, including comb	Relatively large.	Relatively small.	
Spurs......	Well developed.	Absent.	
Plumage form....	Hackle and saddle feathers long, narrow, pointed at tip.	Hackle feathers similar to those of male but relatively shorter and more rounded at tip; saddle feathers broad, relatively short and broadly rounded at tip.	Similar to female.
	Barbules absent on distal half of barbs of hackle, back, saddle, and wing bow feathers. Cf. Fig. 3, *A*.	Barbules absent from distal third of hackle feathers only; present elsewhere. Cf. Fig. 3, *D*.	Barbules present.
	Tail coverts, including sickles, long, curved and pointed.	Tail coverts, relatively short, broad and rounded at tips.	Similar to female.
Body color pattern..	Numerous distinct color areas; viz., hackle, cape, back, saddle, wing front, wing bow, wing bay, wing bar, primaries, tail, breast and ventral surface.	Relatively few areas; viz., hackle, tail, primaries, (wing bay?), breast, ventral surface, and remainder of body.	Varies with different breeds.
Feather pattern..	Usually uniform[3] or with central stripe.	Stippled or penciled when not like that of the male.	Varies with different breeds.
Behavior...	Relatively erect carriage, pugnacious, frequently crows, rarely "sings," appears to lack brooding instinct.	Relatively horizontal carriage, not pugnacious, does not crow, but "sings" a great deal when in laying condition, has brooding instinct.	Peeps for a time, then follows a period when voice is rarely used until approaching maturity.

varieties of domestic chickens, there is, with one exception, only one basic *body* pattern, that of the Jungle fowl. (See table.) All other patterns, with the exception of the white crest of certain Polish, must be considered as modi-

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[2] These tables make no pretense of giving all the characters which differ in the two sexes. I have also ignored minor details in some characterizations.

[3] Uniform, except as the under color can be distinguished from the surface color. See also text.

fications of the Jungle, usually by the loss or non-development of a part. I know of no other distinctive pattern in chickens, such as, for example, that exhibited by the Mallard in ducks.

TABLE II[2]

A COMPARATIVE STATEMENT OF THE CHIEF SECONDARY SEXUAL CHARACTERS OF BROWN LEGHORNS, OTHER THAN THOSE GIVEN IN TABLE I

	Adult		Juvenile (Third Stage)	
	Male	Female	Male	Female
Comb.....	Erect. Blade proportionately large.	Lops. Blade proportionately small.	Erect. Relatively large and of quick growth.	Erect. Relatively small and of slower growth.
Spurs.....	Present.	Usually absent, but frequently present in various conditions of development.		
Plumage color....	Hackle, reddish orange, with black central stripe; back and wing bow, dark crimson; saddle, reddish orange, often with black central stripe; wing bay, red; dorsal white area at base of tail; rest of body black.	Hackle, yellow, with dark-brown central stripe; breast, salmon; tail, primaries and concealed portions of secondaries, black; rest of body, dark and light brown, intermingled in pepper and salt fashion.	Mostly black, each feather being splashed with various amounts of red. Feathers of back often like those of young female. Body pattern of adult more or less clearly indicated.	Similar to adult but markings coarser.

The feather patterns fall into two groups, viz., those associated with sexual dimorphism and those not so associated. In the male there is no pattern of the first group. But penciling of the type found in the Dark Brahma female appears never to occur in the male and therefore belongs in the second class. Stippling is also usually distinctive of the adult female, but it occurs in the young male and under certain conditions (heterozygosis) in the adult male. In the Jungle female the stippling often approaches very closely the form of narrow concentric lines or vermiculations. Possibly the stippling of the Brown Leghorn female is due to the breaking up of such vermiculations and so is not strictly comparable with that due to heterozygosis. However this may be, stippling is normally a female or a juvenile male character. The males corresponding to these two types of females usually have uniformly colored feathers ventrally. The dorsal regions are less constant in type, being usually uniformly colored or else striped. In other breeds the feather pattern may be alike in the two sexes.

The question of behavior depends upon so many conditions, that only a few of the numerous reactions have been mentioned in the table.

The following comments are intended to apply only to Brown Leghorns.

While the comb of the female usually lops to one side or the other, it does not always do so. There are indications, moreover, that by proper matings this character could be transferred to the male.

Spurs are usually absent from the female, yet they are occasionally well developed. Their presence can not be taken as a certain indication of the assumption of a male character by the female, for there was an old Scottish race in which both sexes were spurred. Nor need they indicate the presence of an abnormal ovary, for in one case in which they had become well developed at 9 months of age, the hen proved to be a splendid layer. These spurred hens are probably due to the presence or absence in the germ plasm of some definite determiner, as certain of my breeding experiments indicate.

The plumage color within certain limits is variable, so that it is a little difficult to describe briefly. American fanciers recognize only one type of plumage color for each sex, that described in the "American Standard of Perfection," but beside the "Standard" female there is one in which the salmon breast is replaced by one of nearly the same color as the back. Beside the "Standard" male is one in which the striping of the hackle and saddle feathers is lost, and third, one in which there is some red in the under parts. It is evident, moreover, from experiments in cross breeding, that the body pattern of the Brown Leghorn is not a unit, but is composed of several parts.

These departures from the ideal and the probable variability in the gametic constitution of supposedly purebred stock may be expected to influence the behavior of the birds under castration. They indicate also that a character which at one time may behave as a secondary sexual character, at others forms a normal character of both races.

Experimental.—Without taking time to describe the details of the experiments, except to note that the gonads were removed from the chicks when they were 21–28 days old, that is, they were much younger than is the case in commercial caponization, we may proceed directly to a consideration of the results, taking up first the effects of castration on the male.

Seven of the castrated males reached four months of age, then three were accidentally killed. The autopsies on these three showed an entire absence of testicular material in two cases. The third had a tiny nodule, possibly testicular, on the mesentary near the former site of the testis.[4] All four survivors were kept until they were 16 months of age. Two were then killed for study. They developed the normal plumage of the male and were it not for the small comb and wattles they would have had nearly the same appearance as a normal cock (Fig. 1). They are, however, somewhat fuller plumaged and rather heavier looking birds than a normal cock. The spurs are well developed but on the other hand these capons are less active in their movements, are non-combatants and show no sexual instincts. They have never been heard crowing, though they may be made to squawk or even cluck like a *cock*.

One of these capons was somewhat anomalous in that he had much the same appearance as a normal cock. He had a large comb but did not crow. At one time he

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[4] Unfortunately this material was not sectioned.

showed some inclination to pay attention to the hens, but as far as I was able to observe, it never went as far as an attempt at copulation. At the autopsy it was found that there had been an autoplastic transplantation of a bit of the testis.

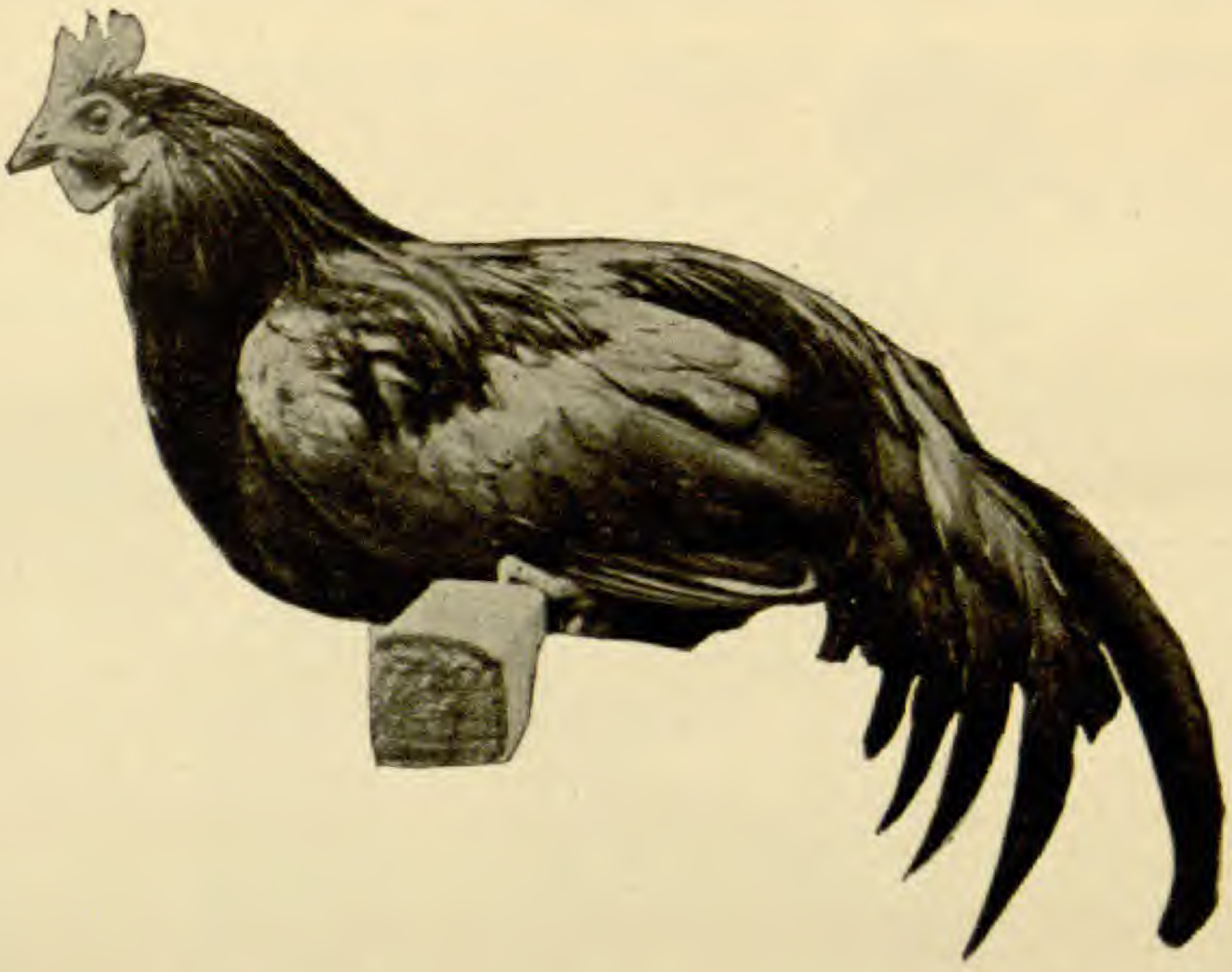

FIG. 1. Brown Leghorn Capon. The colors are exactly those of the male as given in Table II.

It will have been observed from the foregoing description, that the small comb of these capons is the only character which might be considered female. In all other points the characters of the capon are the characters of the cock, sometimes exaggerated (feather length), sometimes infantile (crowing instinct). None are positively female, except perhaps the comb, which is much too large to be purely infantile, and too small and of the wrong proportions to be that of a normal adult female. On the whole it most closely resembles that of the *mature young female* before she has actually commenced to lay, or of the adult female when out of laying condition. Comb size is affected by so many conditions that the question as to whether or not the capon has a female type of comb is not easily answered, and therefore must await further studies.

We may turn now to the effects of castration on the female. Unfortunately, only one of the females from which the ovary (naturally only the left, since it was assumed that the right had completely degenerated) was removed, reached maturity. There is no doubt as to the effect of ovariotomy on this individual (Fig. 2), which

FIG. 2. Female Brown Leghorn from which the ovary was removed. The colors, with the exception of some feathers as noted in the text, are those of the *male* as given in Table II. The long saddle feathers are hidden by the wing, but see Fig. 3, *C*.

commonly passed as a cock, with those unacquainted with the bird's history. Nevertheless, the assumption of male characters has not been quite complete, as is shown by a consideration of the following features. First, the presence of feathers on the back which are very much henlike (Fig. 3, *B*). Second, the wing bow is poorly developed. Third, the shank is too short for that of a cock. In some points of behavior, such as lack of the crowing instinct, non-combativeness, cackle and general indifference to the hens, she is hen-like. On the other hand, her carriage is cock-like and by suitable means she has been made to cluck like a cock and even to pay a little attention to the hens, though this last reaction was produced only once or twice. The peculiar shape and carriage of the tail probably has nothing to do with the effects of castration, since this bird had only half a rump. Moreover, a rumpless cock occurred in this same strain.

Some additional light on the question is afforded by the effect produced by castration on a second female, which died at the age of four months. When the first feathers of the third stage began to appear, they were like those of the young male. The later feathers, however, were those of the normal female. The explanation of this anomalous behavior was found at the autopsy, for it showed the presence of an ovary about one half the size of that of a normal chick of the same age. As long as the ovary or its normal secretion was practically absent, the development of this female was along lines similar to that of the male, but with the regeneration of the ovary development returned to its usual course.

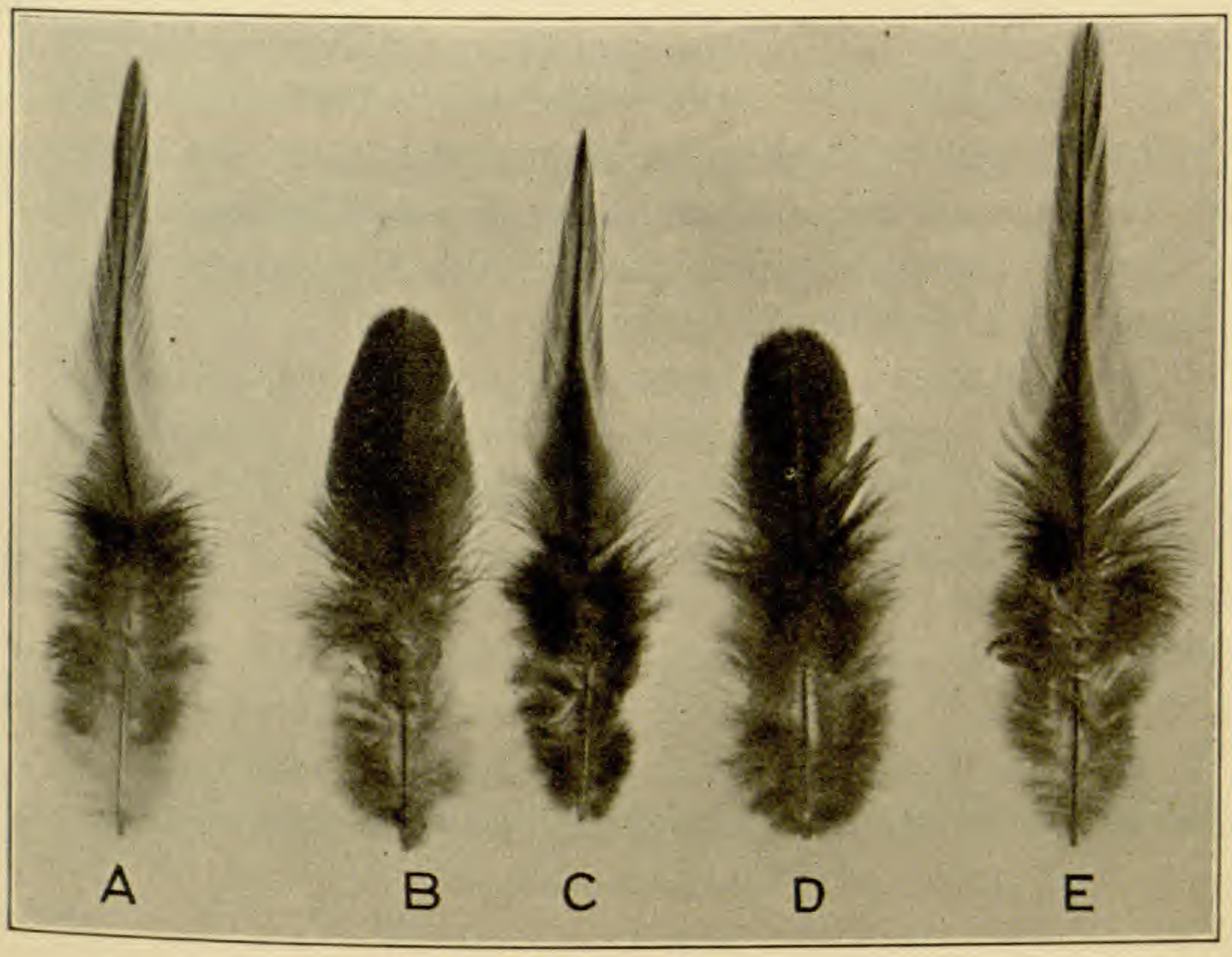

FIG. 3. Feathers from the saddle region of the various types of birds described. *A*, normal male; *B* and *C*, two sorts of feathers from the bird shown in Fig. 2; *D*, normal female; *E*, capon.

These experiments, then, indicate clearly that while the female may assume male characters following the removal of the ovary, the male assumes no positive female characters after removal of the testes.

Theoretical.—Certain of my breeding experiments have seemed to show that the Brown Leghorn plumage colors and pattern followed a sex-limited mode of descent. Certain difficulties, however, have arisen. As stated above, it has become evident that the coloration and pattern of the Brown Leghorns is not due to a single inheritable unit, but to a complex. This means that its more or less independent parts must be discovered and the mode of inheritance as well as the conditions under which each part becomes visible in the soma, worked out. Until this is done it will be impossible to say what part sex-limited inheritance plays in determining sexual differences. The following representation, then, is merely an attempt to formulate a working hypothesis.

The male may be considered to be duplex for an internal secretion S, produced by the testes, which is necessary for the full development of the comb and less clearly for the crowing instinct and sexual behavior, but not for plumage and spurs. In the female this secretion is replaced by one S' produced by the ovary. (S' may, perhaps, stand in some simple chemical relation to S.) To its effect is to be referred the female's form and color. When the ovary is removed or becomes pathological so that its normal secretion is no longer produced, then the male characters develop to an extent which is determined by factors at present unknown to us. Nor are we concerned here as to what part of the ovary or testis produces this secretion (or secretions, for S and S', respectively may well represent a number of secretions which behave in the same general way). In any case the internal secretion may be conceived to be associated with sex in the same manner as any other sex-limited character. The formula for the male would then be S♂ S♂, that for the female S♂S'♀. S' is of course to be considered dominant to S. If this scheme represents the actual condition of affairs it may not be necessary to suppose that the female Brown Leghorn is simplex for L where L represents the whole or a part of the male Leghorn pattern complex, for S' might be able to transform two doses of L into the condition observed in the female as well as one dose. This is, however, a matter to be tested by experiment.

In insects, Meisenheimer and others have shown that castration is without effect on the secondary sexual characters of either sex. This lack of association between the secondary sexual characters and the gonads may find its explanation in the absence of a modifying secretion from these forms, the secondary sexual characters being determined solely by differences in the gametic constitution of the sexes, for example of the form AA in one sex and AB in the other, B being dominant over A and linked with the sex determiner, in the usual fashion for a sex-limited factor.[5] Secondary sexual characters of insects would then belong to a different category from those of the birds. There is some evidence, however, that certain characters of the female fowl are not under the control of the secretion of the ovary, for they do not become male-like after the removal of the ovary and therefore are like the insects in this respect. This point requires further study.

There is one more point to be considered. I have shown that in the Brown Leghorns as well as in Rouen ducks that the male does not assume female characters as a result of castration. Does the adult male of other sorts of birds ever exhibit female characters? An affirmative answer is possible only in those cases in which the juvenile plumage of the male is like that of the female. But if we consider only those cases in which the juvenile male plumage is unlike that of the female, we shall find that conclusive evidence on this point is wanting, at least I have thus far been unable to secure such evidence.

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[5] There are, of course, other ways of representing this association.

SIMPLIFICATION OF MENDELIAN FORMULÆ

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PROFESSOR BESSEY in his recent presidential address[1] expresses the opinion that Mendelian terminology is needlessly complicated. This opinion most biologists will heartily endorse, and not a few Mendelians will be among their number. For those who work most extensively with Mendelian formulæ feel most keenly the need of simplification in these the tools of their investigations.

Professor Morgan, in the January NATURALIST,[2] makes a commendable effort to introduce reforms. I desire heartily to endorse his effort, but would suggest certain modifications in method.

The Mendelian may say in justification of existing usage that it has arisen naturally step by step as knowledge of Mendelian phenomena has advanced, but this is of course no justification of its continued use, if it has become a hindrance rather than a help in the further advance of knowledge.

Morgan clearly points out the two historical steps by which present usage was reached. The first of these was Mendel's original recognition of segregating dominant and recessive characters existing in contrasted pairs, and his convenient designation of the former by capitals and of the latter by small letters. This usage answered perfectly so long as only a single modification of any character came under consideration, and indeed Mendel's observations did not go beyond this. But this system broke down when characters more complex in nature came under observation, as for example when Cuénot showed that more than a single differential factor exists between gray mice and albino mice. (2) The ingenious and useful

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[1] *Science*, January 3, 1913.

[2] Vol. 47, pp. 5–16.

"presence and absence" hypothesis of Bateson was the second step which led to our present usage. On this hypotheses gray in mice is not the allelomorph of white, but of *no-gray;* while the allelomorph of white is color, or more properly speaking white is equivalent to *no-color* and *this* is the allelomorph of color.

Both of these steps have been amply justified by their utility in making possible the prediction of the previously unpredictable consequences of particular crosses.

It was natural that in applying the presence and absence hypothesis the usage of Mendel should have been retained, in accordance with which capital letters were used as the symbols of dominant characters and small letters as the symbols of recessive characters. But this retention has involved most unfortunate consequences and is, I believe, the real seat of our present difficulty.

Mendel's small letters stood for realities as truly as did the capitals. His A was a round form of pea, his a was a wrinkled form of pea; his B was a yellow-seeded, his b a green-seeded pea. But the significance of these terms has been changed under the presence and absence hypothesis. A still means a round pea, but a is simply a *not-round* pea; it may or may not be wrinkled. Likewise B is still a yellow-seeded pea, but b is nothing but a *not-yellow* pea; it may or may not be green under the presence and absence hypothesis. For all that b signifies now, the pea may be blue, violet, indigo or carmine.

It is most unfortunate, therefore, that the small letters, having lost their original significance, were not discarded altogether, for under the presence and absence hypothesis they have done nothing but cause mischief.

The investigator who employs them starts out well intentioned with a clear notion that the small letters stand for negation only, that they are merely signboards to show what characters he is talking about, but presently, unless he is unusually careful, we find him talking about them as if they stood for *something,* instead of nothing; he speaks of repulsions and couplings or associations between *a* and *B*, or even between *a* and *b*. Think of it! How can *something* be coupled with *nothing?* How can *nothing* be inseparably bound up with *nothing?* It seems to me the consequent effect on inheritance is *absolutely "nothing"!*

Not only do the small letters thus lead to confusion of thought, they also tend to make formulæ needlessly cumbersome, for they call for the use of *two* symbols for every character difference dealt with. These two symbols also are so much alike that both printer and reader are in momentary danger of confusing them, with the consequence that what is *is not,* and what is not *is!*

The small letters are not indispensable to accurate and exhaustive analysis of Mendelian phenomena, or to lucid exposition of them. See, for example, the fundamental researches of Cuénot into the color inheritance of mice, and his classic "notes" describing them. Like Cuénot, I have not found the use of the small letters necessary; but among nearly all other Mendelians the double terminology has become so nearly universal that a different usage seems almost to demand an apology. Indeed Lang[3] has suggested that such offenders against uniformity as Cuénot and I should be haled before an International Congress and be *directed* to conform; since which time I had almost abandoned hope of ever seeing improvement in the current confusing system, but Morgan's protest and proposal gives me new courage.

What we need first of all to symplify our present usage is to *abandon the dual terminology.* Where we are dealing with a *single* set of variations, let a *single* set of symbols suffice. Let us give up either the small letters or the large ones, it matters not which. If we retain *A*, then we have no need of *a,* for it is not, as Morgan at one time seems to assert and at another to deny, the "residuum" when *A* is lost; it means on the presence and absence hypothesis nothing but this, that *A* is not present. The rest of the organism is the "residuum." Morgan points

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[3] *Zeitsch. f. ind. Abstammungs- und Vererbungslehre,* 4, p. 40, 1910.

out and his paper illustrates amply how under the dual system "the letters used may unintentionally come to stand for different things." The obvious thing to do, if we attempt reform, is to omit the superfluous symbol, either the small letter or the large one.

Morgan, however, clings to the dual nomenclature, but suggests a reversal of the usual significance. Thus the factor for pink-eye, he assumes, is present only in animals which are *not* pink-eyed, and the factor for black body color, he suggests, is present in all sorts of flies *except* those which are black bodied. This is confusion worse confounded.

But, seriously, I do not see that it is possible to improve the existing terminology, so long as we use two terms of opposite significance with reference to a single germinal variation. Certainly merely reversing the significance of existing terms will not do it. What we need first of all is *one set of symbols,* used in a single significance.

If this reduction is allowed, then I think that another aspect of Morgan's proposition might be extremely useful, viz., *that a mutation which behaves as a recessive in crosses be designated by a small letter.* This proposition was put into effect more than three years ago in a paper dealing with color inheritance in mice, though Morgan does not seem to have observed it. See Castle and Little (1909).[4] In the paper cited, three recessive color factors of mice were designated by small letters, viz., "*d,* the dilution factor"; "*s,* the factor which causes *spotting* with white;" and "*p,* the pink-eye (or paucity) factor."

In that same paper all *dominant* color factors of mice were designated by capitals. This seems to me a very necessary complement to the use of small letters to express recessive variations, and is in entire harmony with Mendel's original usage. But neither of these proposals can help matters much, *unless we discard the duplicate set of symbols, which is the chief cause of present confusion.* Thus if we use *s* for spotting, then we have no

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[4] *Science,* N. S., Vol. 30, pp. 312–314.

occasion to use *S* for no-spotting. We simply leave out all reference to spotting, and we shall understand that there is none, but that the normal condition prevails.

To be very explicit, my proposals for simplification of Mendelian terminology are three:

1. To abolish the current dual terminology and use only *one symbol,* where a single variation from the normal is involved.

2. To use a *small letter* to designate the factor responsible for a variation which is *recessive* in crosses with the normal.

3. To use a *capital letter* to designate the factor responsible for a variation which is *dominant* in crosses with the normal.

These proposals were made in substance in publications of the year 1909 and are here renewed under encouragement of Morgan's suggestive paper. Let us see how they would work if applied to the cases enumerated by Morgan. The eye color series described by Morgan, *l. c.,* page 13, involving three recessive mutations, is as follows:

	Revised Terminology	Morgan's Terminology
Red	*normal*	*PVE*
Vermilion	*v*	*PvE*
Pink	*p*	*pVE*
Pink-vermilion	*pv*	*pvE*
Eosin	*e*	*PVe*
Vermilion-eosin	*ve*	*Pve*
Pink-eosin	*pe*	*pVe*
Pink-vermilion-eosin	*pve*	*pve*

The revised terminology is obviously shorter and simpler. It is obtained by merely omitting the capital letters from Morgan's terminology, letters which stand only for negations. The symbols used are suggestive of the names employed for the various color categories of eyes, whereas in Morgan's terminology the most conspicuous symbols are suggestive only of other categories than the true one.

The revised terminology is more convenient than

Morgan's in calculating the expected result of any mating, and it is equally reliable. The result of every possible mating within the series can be readily computed without the confusing presence of the large letters.

To those who have grown accustomed to the presence and absence terminology the objection will suggest itself that in naming the recessive character and ignoring its allelomorph, we are naming an absence or negative and disregarding what is present and positive. But this does not follow. Because a character is recessive it does not follow that it is negative. I quite agree with Morgan that the physiological condition which produces an eosin eye is as real as that which produces a vermilion, a pink or a red eye, and no mere negation; it is simply different. It is quite impossible to decide, from its behavior as a dominant or recessive in crosses, whether a character is positive or negative. This I have pointed out elsewhere (1911) and the same view has been repeatedly expressed by Shull. We have on record many instances in which one and the same character may behave at one time as a dominant, at another time as a recessive.

Our terminology may well recognize the dominant or recessive behavior of a variation, without implying anything as to its positive or negative nature, which must in many cases be conjectural or possibly non-existent. Different gradations of color, such as we have in the eye-series of Drosophila described by Morgan, may result merely from quantitative variations in cell constituents and consequent activities, nothing being lost. This idea concerning the possible nature of Mendelian factors in general I have developed elsewhere, concluding that "it is the substantial integrity of a quantitative variation from cell-generation to cell-generation that constitutes the basis of Mendelism. All else is imaginary."[5]

Morgan applies his altered system of nomenclature also to the body-color series and wing mutation series which he has discovered. This nomenclature we may simplify,

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[5] AMERICAN NATURALIST, Vol. 46, p. 358, June, 1912.

as we did in the case of the eye-color series, without impairing its utility.

BODY-COLOR SERIES

	Revised Terminology	Morgan's Terminology
Wild fly	*normal*	*YBES*[6]
Yellow	*y*	*yBES*
Yellow-black	*yb*	*ybES*
Ebony	*e*	*YBeS*
Sable	*s*	*YBEs*[7]

WING-MUTATION SERIES

	Revised Terminology	Morgan's Terminology
Wild fly	*normal*	*MR*
Miniature	*m*	*mR*
Rudimentary	*r*	*Mr*
Rudimentary-miniature	*mr*	*mr*

The taste of the reader will govern his choice between these two systems. Doubtless either can be used successfully, though the revised terminology seems to me preferable on the ground of simplicity and suggestiveness.

In the series with which Morgan has dealt, all the mutations under consideration are *recessive* in character, so that one can read the names of the varieties directly from his formulæ, if one disregards altogether his large letters and pays attention only to the small ones. To insure this I have suggested omitting the large ones.

But if one were to extend Morgan's terminology to a series in which *dominant* mutations as well as recessive ones occur, hopeless confusion would result. For here some of the large letters would stand for mutations, while others would stand for the negation of mutations, so that without a key constantly at hand the formulæ would be unusable.

If, however, we use the *single* system of symbols as I have suggested, a series which includes both dominant and recessive mutations may be handled without confusion. In this case every symbol is significant, and its

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[6] For simplicity I here use *E* instead of Morgan's *Eb*.

[7] Morgan's list here contains *S*, but this I suspect is a misprint for *s*; if so, it is a living witness to the dangers of the dual system.

dominant or recessive character is indicated by the symbol, whether large or small. For example, consider the mouse-color series as described by Castle and Little (1909). In the paper cited, nine color factors were described, three of which clearly recessive have already been mentioned, viz., *d, p* and *s*. The remaining six were considered dominant factors. Mr. Little has since suggested, and I think with good reason, that one of them had better be omitted, since its existence has not been demonstrated beyond question. The six as given were *C*, the color factor; *Y*, the yellow factor; *Br*, the brown factor; *B*, the black factor; *R*, the restriction factor (producing a yellow coat); and *A*, the agouti or gray factor.

Mr. Little would omit either *C* or *Y*, since it has not been shown beyond question that the effects which had previously been ascribed to these two are not due to one and the same agency.

With the eight symbols which would remain, three being small letters, the others being or beginning with capitals, it is possible to write, without duplication of terms, formulæ descriptive of the entire color series. But in so doing it would be necessary to designate the original or wild form in terms of factors supposed to be lost in its derivatives, and which have only come to light through such loss. This, as Morgan points out, involves redescribing the wild form every time a mutation arises and should be avoided if possible. I therefore favor Morgan's suggestion that each mutation as it arises be given some suitable descriptive name, the initial or other significant letter of which shall be its symbol. If, as is commonly true, the mutation is recessive in crosses with the wild or original type, its symbol will be a small letter. But if the mutation is dominant,[8] its symbol should be a large letter.

The original or wild type *need not be described in terms of its mutations*, as every duplicate system of terminology, even Morgan's, requires. The system would ac-

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[8] I have met two dominant mutations in guinea-pigs, one in rabbits, and one in mice, so that they can scarcely be called rare.

cordingly be capable of indefinite expansion without constant remodeling.

I favor Morgan's further suggestion that as new forms arise through recombination of simple "mutations" these be described, so far as possible, in terms of the simple mutations composing them. This principle is clearly illustrated in the names chosen by Morgan for the eye color series of Drosophila. It is surprising how little change this system necessitates in the common names with which we are already familiar, for example, in the mouse-color series.

The color mutations[9] of mice with which I am personally familiar number seven. If all of these are independent, *i. e.*, not "coupled" or "associated," there should be theoretically possible 127 different combinations involving one or more of them. A considerable proportion of these combinations has been produced in my laboratory in the course of the last twelve years, the earlier and simpler ones by Dr. G. M. Allen or myself, the later and more complex ones by Mr. Little, who has in press an extensive paper dealing with his investigations. I shall deal with the series as known up to 1909. The historical order of appearance of the mutations is now unknown; I shall place them in the alphabetical order of the symbols used. It is also unknown whether each of them arose directly from the wild type. More probably they did not, but experiment shows that they might have done so, since each behaves in crosses as if it had a distinct and independent basis in the germ-plasm.

WILD TYPE AND ITS SEVEN MUTATIONS

1. *Wild* = gray.
2. a = albino (transmitting gray in crosses).
3. b = black.
4. c = cinnamon.
5. d = dilute.

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[9] I use the term mutation in the sense of unit-factor variation, not in that of DeVries.

6. p = pink-eyed.
7. s = spotted.
8. Y = yellow.

The a mutation, however combined, if present in a homozygous condition, prevents the development of pigment in the skin, hair or eyes. The d mutation, under like circumstances, makes the pigmentation of the coat dilute, or pale; the p mutation reduces even more strongly the pigmentation of coat and eyes alike, but does it in a different way; the s mutation causes pigment to be altogether wanting in certain areas of the coat more or less definite in position and extent, which areas accordingly appear as white spots.

Combinations of these four mutations present no difficulties of description or recognition, though breeding tests alone suffice to differentiate the several sorts of albinos, since all look alike. The nomenclature also is perfectly simple. Thus,

ap = albino transmitting the pink-eye mutation in crosses.

adp = albino transmitting both dilution and pink-eye in crosses, etc.

Combinations of b, c, and Y, one with another, form the fundamental and best known color varieties, which will now be considered.

In the b mutation, the fur is black; in the c mutation, it is brownish gray, called cinnamon. In the Y mutation, the coat is yellow. Of the several mutations mentioned, Y alone is dominant over the wild gray, but it occurs only in a heterozygous state, and hence never breeds true.

The complete color series involving these three mutations, but excluding all others, is as follows:

Wild = gray.
b = black.
c = cinnamon.
bc = black-cinnamon (chocolate).
Y = yellow (giving also gray offspring).
bY = black-yellow (giving also black offspring).

cY = cinnamon-yellow (giving also cinnamon offspring).
bcy = black-cinnamon-yellow (giving also black-cinnamon offspring).

To express the modification which this series undergoes if the *d* mutation is added to it, we need only prefix the symbol *d* to each of the formulæ given and omit the term *wild* as no longer applicable. The series then becomes

d = dilute gray.
db = dilute black.
dc = dilute cinnamon.
etc.

Similarly an added *p* factor gives us the series

p = pink-eyed gray.
pb = pink-eyed black.
pc = pink-eyed cinnamon.
etc.

Also an added *s* gives us the series

s = spotted gray.
sb = spotted black.
sc = spotted cinnamon.
etc.

Adding both *d* and *p* gives us the series

dp = dilute pink-eyed gray.
dpb = dilute pink-eyed black.
dpc = dilute pink-eyed cinnamon.
etc.

Adding *d* and *s* gives us the series

ds = dilute spotted gray.
dsb = dilute spotted black.
dsc = dilute spotted cinnamon.
etc.

Adding *p* and *s* gives us the series

ps = pink-eyed spotted gray.
psb = pink-eyed spotted black.
psc = pink-eyed spotted cinnamon.
etc.

Adding simultaneously *d*, *p* and *s*, gives us the series

dps = dilute pink-eyed spotted gray.
dpsb = dilute pink-eyed spotted black.
dpsc = dilute pink-eyed spotted cinnamon.
etc.

We thus secure eight different variations of the fundamental color series, or a total of sixty-four colored varieties. By prefixing *a* to the formula for each of these varieties, we obtain formulæ for sixty-four different types of albinos, which though all looking alike (being snow white), yet would transmit in crosses the characteristics each of a different one of the sixty-four colored varieties.

We have thus accounted for the entire one hundred and twenty-eight variations which theoretically should result from recombining seven distinct mutations with the original form from which they sprang, and this has been done in relatively simple terms. Only one formula in the whole 128 contains as many as seven letters. *This is adpsbcY,* and would be read "an albino transmitting dilute pink-eyed spotted chocolate and dilute pink-eyed spotted yellow." All the other formulæ would contain from one to six letters. The current presence and absence system would require *sixteen letters* in every one of the 128 formulæ to express the same facts, and the same letter would in some of the formulæ be a capital and in others a small letter, so that the constant close attention of the reader would be required to decide in each case whether a particular mutation was or was not present. Morgan's system would be only slightly less cumbersome for it would require in each formula fourteen instead of sixteen letters, and the same confusion would result from the presence of duplicate large and small letters. The mere statement of these facts is sufficient to show that Mendelians can easily simplify their formulæ and make themselves more readily intelligible to each other and to their fellow biologists, if they are only willing to do so.

There is another reason why I favor Morgan's terminology (as here simplified); it commits us to no physiological theory, but simply states facts. We are not required to suppose that the wild form contains a number of factors which by mutation have been lost. We may still do so, but we are not *forced* to do so. We are free to suppose with Morgan that merely a "readjustment" has taken place, and to make no assumption as to its nature, unless we choose to do so. This course does not prejudice the investigator of the physiology of color production but leaves him free to frame such hypotheses as will from his point of view best meet the situation. He is not bound down, for example, to a hypothesis of chromogen and ferments and so tempted with Riddle to throw over all Mendelism simply because Mendelians have in his opinion misinterpreted chemical facts.

That terminology evidently is most desirable which states demonstrated facts most clearly and simply, and makes fewest assumptions as to their explanation. Otherwise the investigator may be led to conclusions based on his terminology rather than his facts, and this can lead only to disaster.

NOTES AND LITERATURE

SOME RECENT ADVANCES IN VERTEBRATE PALEONTOLOGY

THE study of the extinct life of the globe must ever be the central and basal point for an understanding of the manner in which evolution has taken place. The ultimate appeal in the theory of descent must necessarily rest with the facts in the history of animal and plant life as it is read from the records in the rocks. Organic evolution is now so firmly established in the minds of present-day scientists that a statement of its truth is no longer needed. But it is well for us to be cautious in our statements about evolution, in not expressing more than we can prove. It is quite possible that the vertebrates come from the arachnoids as Patten contends, but the evidence on this point is wholly lacking. It is also possible, nay even probable, that the crossopterygian ganoids gave rise to the land vertebrates and even a single species of this group *may* have been such an ancestor, but no one knows whether they did or not and to state, as many of our recent zoological text-books have done, that such *was* the origin of land vertebrates, is to state what is not known. It is true that the Stegocephali may have given rise to the reptiles, indeed there is very little difference between some of the reptiles and some of the Stegocephali but the proof of the descent of all reptiles from any one or all of the groups of the Amphibia is more than any one has yet given. The birds may and possibly did arise from the reptiles but the early stages are still unknown. It is the firm belief of many that paleontological proof will be forthcoming for sustaining the ideas expressed by the theory of organic evolution but the facts as they are brought to light by the study of paleontologists do not serve to show that this is true. Smith Woodward says that connecting links or even approximate links between nearly all of the great vertebrate groups are still wanting from our large collections. It may safely be said that 99 per cent. of all the collections of fossil vertebrates in the world serve to show diversifications of various groups of animals and *not* to connect them in any satisfactory way. There are, to be sure, connections and definite ones between the smaller groups of many vertebrates but not between the larger ones. Many writers, especially writers of text-books, assume much more than they can prove, and the great majority of the modern zoological text-books are sadly behind the times in matters of paleontological knowledge and works that serve as standards and bases for the construction of more elementary texts make the most bald misstatement of facts.

The general trend of paleontological research is to round out our knowledge of the diversity and structure of many groups; the establishment of a few new groups especially of lower rank; no one save Jaekel having had the temerity to propose new groups higher than sub-classes.

Not all of the recent work in vertebrate paleontology is reviewed here. Many excellent works have been sufficiently noted elsewhere but sufficient is here given to show the tendency of thought and work among the vertebrate paleontologists; that of attention to matters of structure, occurrence, association, interpretation of matters of organization and relationship, all of which are fundamental to safe conclusions regarding the larger problems of phylogeny. It is perhaps too early to arrive at such conclusions in regard to phylogeny as we should wish to have—but paleontology is 100 years old and more!

One of the more recent publications from the press of Gustav Fischer is a volume entitled "Die Abstammungslehre," a collection of twelve essays on the descent theory in the light of recent researches. The ninth essay is one by Dr. O. Abel, in which he discusses "Die Bedeutung der fossilen Wirbelthiere für die Abstammungslehre." Dr. Abel says there were two ways in which he might discuss his subject, either by giving a short résumé of the investigations of paleontologists or by discussing the methods of paleontological investigation and the bearing of the results of these methods on the descent theory. He has chosen the latter and has discussed his subject in a masterly manner. He has divided his paper into three parts with various sub-headings and discusses a phase of paleontological methods in each division. He discusses the alleged lack of material among paleontological specimens and shows that, in a few instances at least, there is more material available for study of the forms than there is for many of the recent species. The discussion of the value of reconstructions in paleontology is illustrated by various reconstructions of the pterodactyls from Wagler's restoration of *Pterodactylus* in 1830 to Eaton's restoration of *Pteranodon* in 1910. Dr. Abel contends that the reconstruction of a fossil species is valuable, since it gives graphically all that is known of that form at the time the restoration is given. The fact that it may be wrong is no reason why restorations should be abandoned, since they record the progress of our knowledge of animal forms.

Dr. Abel uses as an illustration of the genetic line of descent that of the Cetacea, in which group he is an acknowledged authority. His discussion is illustrated from previous papers. The descent of the whales has been brought about in the reduction of certain structures, such as the teeth and the limbs. As an illustration of a line of descent which has operated in the way of complication of structures he cites the elephant series which has been made well known through the researches of Andrews and Osborn. The reader notes with a sigh of relief that but little attention is given to the line of descent of the horse ("das Paradepferd der Paleontologie").

Dr. Abel's selection of the sea turtles as an example of Dollo's law that "A structure once lost or reduced in development of a race is never regained" is timely and refreshing since it has been but little used. He gives Wieland's restorations of *Archelon* and bases his conclusions on Dollo's researches on the phylogeny of *Dermochelys coriacea.* He discusses, in the two last sections of the chapter, "Stufenreihen" and illustrates his discussion by Dollo's work on the dipnoan fishes, illustrating forms from the lower Devonian to recent and, in the last section, "Ahnenreihen" he discusses the derivation of the *Sirenia* and illustrates by the pelvic girdles of the sea cows from the middle Eocene to recent.

The concluding remarks show a strong desire to further the relation between paleontology and zoology "damit wir mit vereinten Kräften unserem gemeinsamen Ziele, der Aufhellung der Stammesgeschichte, entgegenschreiten." In view of the fact that paleontology has been largely in the hands of the geologists this is a relation much to be wished.

Charles W. Gilmore[1] has described an interesting new form of Alligatoridæ from the "Hell Creek Beds" (Upper Cretaceous) of Montana. Only a portion of the skull was preserved for description. This has been restored into the shape of the

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[1] *Proc. U. S. Natl. Museum,* 41, 297–302, 2 pls.

modern *Alligator* skull. After comparison with *Diplocynodon, Alligator* and *Bottosaurus,* all members of the Alligatoridae, Gilmore has described the new alligator as *Brachychampsa montana,* new genus and species. He gives as the fundamental generic character of the form

> In the absence of a roof-like covering formed by the premaxillaries over the anterior part of the external nares, *Brachychampsa* differs from all known alligators, both recent and extinct.

Some of us may be inclined to question the validity of this character for a genus but further study will doubtless establish the form on a safe basis.

Dr. W. D. Matthew has reviewed briefly[2] the ideas relative to the posture and habits of life of the great ground sloth, *Megatherium,* and its allies from the Pleistocene of North and South America. Under Dr. Matthew's direction there has been prepared a small group of four of these large brutes in the attitudes which have been suggested as possible by the study of their skeletal anatomy. Two genera are represented—*Lestodon* and *Mylodon.* The *Lestodon* skeleton is mounted in the familiar pose of the *Megatherium* reared against a tree trunk and one *Mylodon* is digging at the roots of the same tree. The writer says:

> These poses illustrate the theory of the habits of the ground sloth deduced by Owen from the study of the skeleton—a model of scientific reasoning whose accuracy has never been impugned.

The same writer in a short article[3] describes a recently mounted skeleton of *Agriochœrus* as "a tree-climbing ruminant." The history of this genus is interesting in that

> its various parts have been referred to no less than three mammalian orders, the head to the artiodactyls, the fore foot to the creodonts and the hind foot to the Ancylopoda.

Dr. Matthew opens his paper with the remark that

> It seems somewhat paradoxical to imagine a ruminant climbing trees.

He says further:

> The *Agriochœrus,* however, while a member of the Oreodont family, and like them provided with ruminating teeth, had the limbs and feet modified in such a way as to enable it to climb trees as readily as a jaguar or other large cat.

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[2] *American Museum Journal,* XI, No. 4, p. 113.

[3] *American Museum Journal,* XI, No. 5, pp. 162–163.

No one is more entitled to a view on this subject than Dr. Matthew and even if we find it hard to accept his view of such a paradox yet it behooves us not to be too skeptical.

Dr. Bashford Dean[4] has described a new "fossil aquarium" recently installed in the American Museum of Natural History. Under his direction has been executed a group of Devonian fishes,

> all from a single locality (Cromarty) and a single rock layer in the Old Red Sandstone of Scotland, with the best evidences therefore, that the creatures shown really existed side by side.

The fishes shown seem to be swimming through the water as if alive. It must be a very attractive group to museum visitors.

A very interesting and extremely useful work on ichthyosaurs and plesiosaurs has been issued (1910) from the British Museum (Natural History) as "A Descriptive Catalogue of the Marine Reptiles of the Oxford Clay," Part I, compiled by Dr. Charles W. Andrews. The catalogue is largely based on the Leeds Collection which the British Museum has been acquiring for the past twenty years. The volume is issued in the usual excellent form of all the previous British Museum catalogues, the illustrative work being photogravure, zinc line and lithograph, all executed with great care and attention to details.

The frontispiece is a photogravure of a nearly complete, mounted skeleton of a plesiosaur (*Cryptocleidus oxoniensis*), a dorsal view of which species has been used by Abel for the frontispiece to his "Paleobiologie." The introduction discusses the taxonomic characters of the ichthyosaurs and plesiosaurs, the fauna of the Oxford clay and the distribution of the vertebrates. A single species of *Opthalmosaurus* is discussed, and the details of its anatomy are contained in the first 76 pages of the work, illustrated by 42 text figures (including a restoration of the skeleton) and two lithographic plates. Aside from a discussion of the possible identity of *Opthalmosaurus* and *Baptanodon* of America, the writer has confined his remarks to the osteologic details.

The plesiosaurs are more abundantly represented in species than are the ichthyosaurs. There are four genera discussed in the last 120 pages of the volume, illustrated by 52 text-figures, 8 lithographic and one photogravure plate (containing three restorations of the various forms). As in the previous portion

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[4] *Amer. Mus. Journal*, XI, No. 5, p. 161.

the writer has confined himself to the discussion of the details of osteology and this will make the work doubly useful to students who will find here an unbiased statement of the facts of structure of these two interesting groups of vertebrates. The work will thus be regarded as a standard book of reference on the forms there discussed. It may be regretted by some that the author has neglected the excellent opportunity to discuss such interesting factors as hyperphalangy, hyperdactyly, phylogeny, reduction of structures due to aquatic life, but perhaps this would be out of place in a museum catalogue and we may hope to have the views of Dr. Andrews on these subjects at some other time. The second volume of the series proposes to deal with the crocodiles and pliosaurs of the Oxford clay. The work will be looked for with much interest.

In a recent paper on *Edestus*[5] Dr. O. P. Hay discusses a recently acquired specimen of this interesting Carboniferous shark from the Des Moines Stage of Iowa, discovered in a coal mine near Lehigh some 18 years ago by a miner. The specimen shows the interesting relation of the so-called *spines* which have been assigned various places by various writers. The specimen seems to leave no doubt that the objects regarded hitherto as *spines* are in reality the mandibular and maxillary cartilages of a peculiar shark. Portions of the nasal and post-nasal cartilages are preserved and Dr. Hay indicates a depression as the olfactory pit. The cartilages are so crushed that the nature of the orbital cavities can not be determined. The maxillary cartilage is somewhat larger than the mandibular, as in the modern sharks. The paper is a very interesting contribution to the subject of Paleozoic sharks. He suggests that the forms *Toxoprion, Helicoprion* and *Lissoprion,* at present known only from detached pieces, may in time prove to have the relations exhibited by the present new species of *Edestus;* a relation which Dr. Eastman has claimed for some time obtained in the forms.

A new mosasaur is indicated by Charles W. Gilmore[6] based on imperfect remains from the Cretaceous of Alabama. Mr. Gilmore is inclined to establish a new genus on the characteristic form of the teeth of the new form. He calls the new genus *Globidens,* deriving his name from the Latin *globus* and *dens,* contrary to the usual custom of employing Greek roots for generic

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[5] *Proc. U. S. Natl. Museum,* 42, 31–38, pls. 1–2, April 25, 1912.

[6] *Proc. U. S. National Museum,* 41, 479–484, pls. 39–40, January 31, 1912.

terms. The species is without doubt valid and is a very interesting one in showing a new type of tooth for the mosasaurs, wherein the tooth is a rounded ball instead of being sharp as in the majority of known mosasaurs. From its rarity one may be inclined to question the normal condition of the teeth, but all the teeth display the same characters, so Mr. Gilmore is justified in his assumptions of the distinction of the form so far as the evidence goes. The species is said to be related to *Platecarpus* which is the common mosasaur of Kansas; but we may question whether it is a true mosasauroid.

Mr. Maurice G. Mehl[7] has described and illustrated an incomplete skull of the interesting and little known cotylosaur, *Pantylus cordatus* Cope, from the Permian Red Beds of Texas. The species has been given the rank of a suborder, the Pantylosauria, by Case in his monograph of the Cotylosauria. The form is, however, known only from the skull and such reference may be subject to revision. Mr. Mehl was able, from the recently acquired material, to more fully describe the dentition of this mollusc-feeding animal. He illustrates his discussion by several line figures.

The history of the dinosaurs will always be an interesting topic for paleontologists. The recent contribution by Mr. Charles W. Gilmore[8] is an attempt toward the completion of the history of this group of animals, wherein he describes "The Mounted Skeletons of *Camptosaurus* in the United States National Museum." His discussion is illustrated by drawings and photographs with a map of one of the Como, Wyoming, quarries showing the positions of the *Camptosaurus* bones in the quarry. The skeletons of the two species are mounted in the attitudes of walking on all fours and the erect attitude, which was possibly characteristic of many of the Theropoda. The animals are represented as being semiplantigrade in the hind foot and semidigitigrade in the fore.

Walter Granger[9] has given a few notes on the locality and manner of collection of "a new specimen of the four-toed horse" discovered "in the extreme northwestern corner of Wyoming, in the Wahsatch formation of the Big Horn Basin." Since the form had previously been known only from fragments of jaws containing teeth, the recent find is a remarkably large addition

[7] *Journal of Geology*, XX, No. 1, 21, 1912.

[8] *Proc. U. S. Natl. Museum*, 41, 687–696, pls. 55–61, February 8, 1912.

[9] *American Museum Journal*, XI, No. 3, pp. 85–88.

to the already rich collections of the American Museum. It is to be hoped that the skeleton will be shortly described.

"A Revision of the Amphibia and Pisces of the Permian of North America with a Description of Permian Insects" is the work of E. C. Case, Louis Hussakof and E. H. Sellards, issued as Publication No. 146 of the Carnegie Institution of Washington, on December 20, 1911. The larger part of the work, 148 pages, 51 text-figures and 25 plates, is given to the discussion of the Amphibia which constitutes Dr. Case's contribution to the volume. Ten families of Amphibia are discussed in an historical, systematic and morphological manner, the last two being given approximately equal space. The "historical" portion of the discussion consists of the history of discovery and the taxonomy of the Permian forms as viewed by various writers from Cope (1875) to Broom (1910). The chief taxonomic schemes are given, with lists of species.

The systematic section opens with a table of "Classification" which adopts the opinions of Zittel published many years ago and which, in the main, seems to represent the facts as we now know them. Dissent has already been made as to the inclusion of the Diplocaulidæ in the order Microsauria to which group of vertebrates they have not the slightest relationship. The anatomy and relationships of the group have been discussed elsewhere[10] and it will only be necessary to state here that the structure, as we now know it, seems to point to a relationship of the Diplocaulidæ with the true Amphibia, *i. e.*, the Branchiosauria and the Caudata. A new order, Diplocaulia, has been erected for the reception of the species of the family. It is only proper to say that Dr. Case includes the Diplocaulidæ with the Microsauria provisionally. In the morphological section Dr. Case says (p. 90):

> Jaekel's suggestion of the derivation of *Diplocaulus* from forms like *Ceraterpeton* and *Diceratosaurus* is very probably correct.

He gives not the slightest reason for the assumption of the correctness of this view, which, in the light of the facts, can not be regarded as other than preposterous. The derivation of *Diplocaulus* from such differently organized animals as *Ceraterpeton* and *Diceratosaurus* is fully as fanciful as Jaekel's suggestion to Dr. Traquair of the probable descent of *Hunsrückia* "jene ältesten Fische von terrestrischen Tetrapoden abstammen."

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[10] *Journal of Morphology*, XXIII, No. 1, March, 1912.

The section on the temnospondylous Amphibia is taken up with descriptions of the osteologic characters of the various species with little or no attempt at phylogenetic conclusions. This will make the present monograph the central point, a base of supply, from which future discussions must radiate. Dr. Case's work is reviewed more in detail by Mr. Mehl in *Science*, September 27, 1912, p. 408.

The second volume of Dr. Case's series of monographic studies on the American Permian vertebrates was issued October 25, 1911, as Publication No. 145 of the Carnegie Institution of Washington. In this volume Dr. Case has brought together all of the important facts concerning the "Cotylosauria of North America" with many notes on foreign genera. The volume has 121 pages, 14 plates, 52 text-figures and 71 bibliographic references. As in his previous volume on the "Pelycosauria" the author has divided this volume into the following sections: "Historical Review," "Classification," "Systematic Revision," "Morphological Revision" and "Conclusion."

The reptilian order Cotylosauria of Cope at present has assigned to it by paleontologists thirty genera, distributed in ten families and placed by Dr. Case in five suborders. Each species has the original description and a "revised description" so that later workers on these Permian reptiles will have at hand ready information concerning all the Cotylosauria known up to the end of the year 1911.

The members of the group are known mostly from fragmentary remains. Only in one case, that of *Diadectes phaseolinus* Cope, was the author able to restore the approximate skeleton of the species. Other forms have, however, been restored, notably, *Sclerosaurus* from Europe by von Huene, *Telerpeton* from Scotland by Boulenger, *Captorhinus* and *Seymouria* from Texas by Williston and *Labidosaurus* from Texas by Broili and Williston. Much still remains to be determined as to the structure of nearly all the species.

The facts of most general interest are the structure of the skull of these reptiles and the description of a brain cast of *Diadectes*, figured on Plate 7, Figs. 2 and 3. The structure of the skull allies the group with the stegocephalous Amphibia. The former notions of the Cotylosauria allied the group with the Stegocephala. Further study, however, has convinced Dr. Case that the group is "very far from occupying the primitive position assigned to it by Cope.'' Possibly new discoveries of the appendicular skeleton will widen this gap and give us more definite ideas of the organization of what are possibly the most primitive of the known Reptilia. Similar ideas were formerly held as to the position of the mammalian order Condylarthra, but further knowledge of the anatomy of the skeleton of the body has convinced Dr. Matthew that the group has many characters which are not at all primitive and which would seem to remove the group from an ancestral position.

The Cotylosauria originated probably as early as the middle Pennsylvanic, although the evidence for this is uncertain. Two genera of reptile-like forms known from the Carboniferous of Ohio and France, *Eosauravus* Williston and *Sauravus* Thevenin, are doubtfully assigned to the order. If these are not Cotylosauria then the order is Permian. The Cotylosaurian reptiles have been found in America, Europe and Africa. There is little relationship existing between the faunas of the various continents and the place of origin of the order is uncertain, since representatives are found on both sides of the water at practically the same time geologically. This same thing is true among other fossil vertebrates, notably *Eohippus*, the Branchiosauria, the Microsauria, the Embolomeri, etc. The significant conclusion is reached that:

> There is no single one of the Cotylosauria that can be considered as an ancestral form of the other reptiles. . . . It is impossible to derive the Diapsidan and Synapsidan types from the known Cotylosaurs.

The make-up of the work is excellent. The figures are many of them new and all are well executed. The author has drawn on published matter to the Cotylosauria and has inserted figures from Cope, Broili, Williston, Boulenger, Moodie, Thevenin, von Huene and others, for all of which proper credit is given. The photographic plates are an especial desideratum, for while it leaves the exact description of the elements somewhat uncertain to the reader, yet one feels more at ease on seeing a photograph of the material. Most of the specimens described are in Walker Museum at the University of Chicago and the American Museum of Natural History in New York City.

ROY L. MOODIE.

UNIVERSITY OF KANSAS

(*To be continued*)

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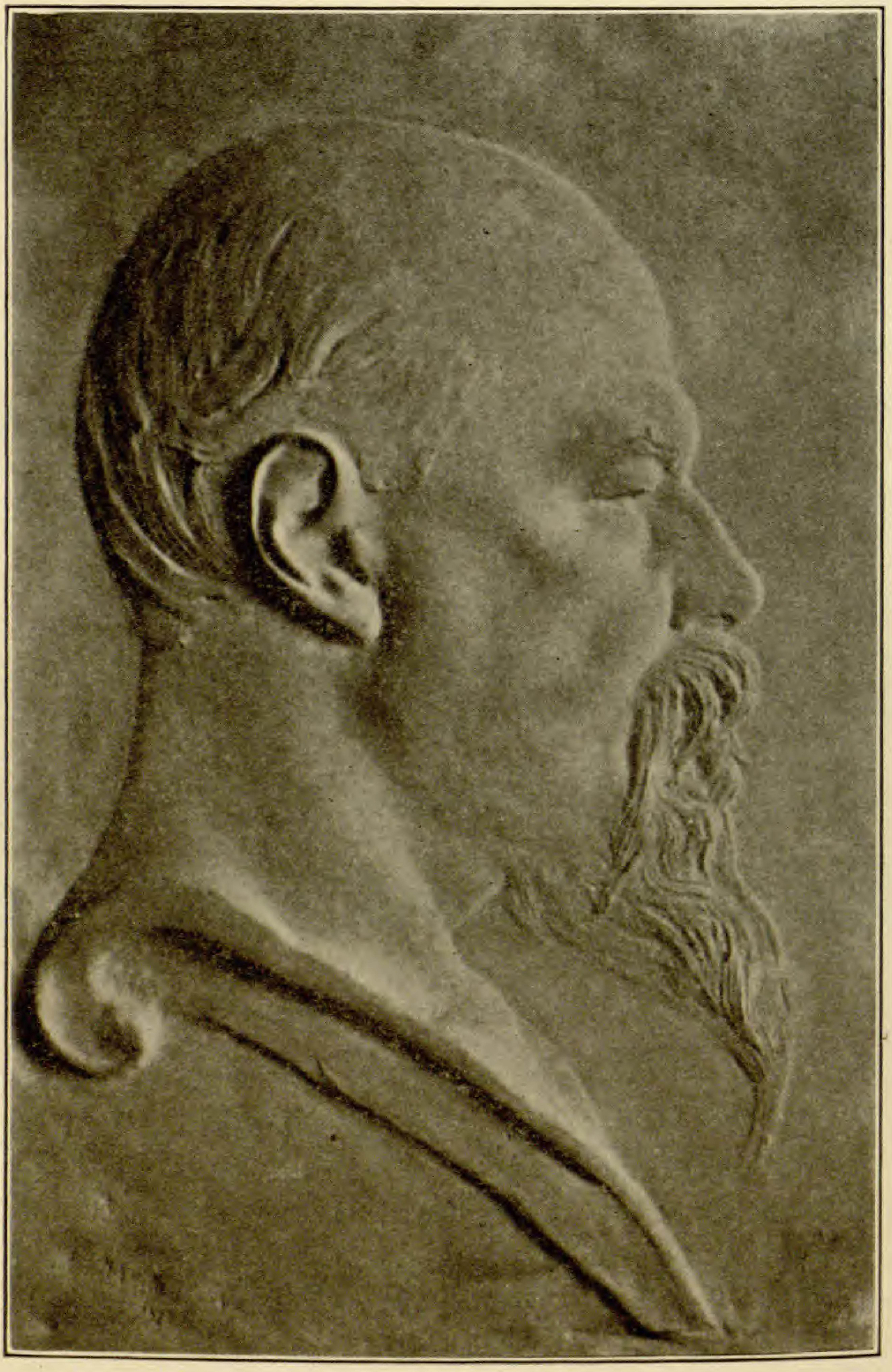

PROFESSOR ALPHEUS HYATT.

THE

AMERICAN NATURALIST

VOL. XLVII April, 1913 No. 556

ALPHEUS HYATT AND HIS PRINCIPLES OF RESEARCH[1]

DR. ROBERT TRACY JACKSON
BOSTON

PROFESSOR HYATT devoted his life to pure science in the best sense of the word. While known primarily for his work on fossil cephalopods, in his researches he covered a wide range of groups, doing critical work on sponges, bryozoans, pelecypods, gastropods, cephalopods and insects. He also published a number of purely philosophical papers on his subject. He taught zoology and palæontology, was a museum administrator, an organizer of societies, and maintained a seaside laboratory at Annisquam, Mass. He was fond of social life and was a most genial and charming host. With strong personal feelings and convictions, he was remarkably tolerant of differences of opinion. One of the most approachable of men, he was very kind and considerate to young men. The accompanying portrait is from a bas-relief made by Professor Hyatt's daughter, now the wife of Dr. Alfred G. Mayer.

Professor Hyatt was essentially philosophical in all his work, and his researches were largely devoted to evolutionary problems. His publications contain most important conclusions and generalizations. He discovered new principles and greatly expanded the principles of others, so that he was justly considered the founder of

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[1] A paper given before the Palæontological Society of America, at the New Haven meeting, December, 1912.

a school of evolutionary research. A leader in this school was the late Charles Emerson Beecher, an eminent professor in Yale University. I wish to point out briefly what these principles are, and their application, but without going into the question of who first enunciated the principles, which is often difficult to ascertain. For the present purpose it is sufficient to consider them as the principles that Hyatt made use of and welded into a component whole for phylogenetic investigation.

It was my privilege to be intimately associated with Professor Hyatt as a student and assistant from 1886, until his death, in 1902, and I can not too strongly express the help and pleasure derived from his boundless enthusiasm, ever ready sympathy and wise counsel. He was laborious and painstaking in his work, constantly urged the importance of large series of individuals for study, and the importance of the bearing of abnormal or pathological specimens. The value of a specimen to him was for what it showed, by itself, and in its relation to associated forms. He urged the comparative study of young and adult, living and fossil forms in a united study. To a zoologist the only difference that should be recognized between living and fossil animals is the condition of preservation and the time element. A study of the recent throws light upon the fossil, and conversely a study of the fossil throws light upon the recent. A united study of both recent and fossil gives a grasp upon a group that can not be attained from either alone.

Stages in development were constantly uppermost in Professor Hyatt's mind, not stages in the embryo only, which are the main conception of stages to most zoologists, but stages throughout the life of the individual, from the egg to the adult and old age. It was the later, or postembryonic, stages that he especially urged the importance of to the phylogenist, and he demonstrated that these later stages possess characters which are directly comparable to the adult condition of related forms. In other words, that the ontogeny of the individual gives in abbreviated form a recapitulation of the phylogeny of the group. This is the law of morphogenesis of Hyatt[2] by which he endeavored to demonstrate that a natural classification may be made by a system of analysis in which the individual is the unit of comparison, because its life in all its phases, morphological and physiological, healthy or pathological, embryo, larva, adolescent, adult and old (ontogeny), correlates with the morphological and physiological history of the group to which it belongs (phylogeny).

To the student of invertebrate fossils these animals present certain advantages, not only on account of their relative abundance, but also because, in many forms at least, from the study of a single specimen, one can gather in a more or less complete degree the stages through which it has passed in development. As Hyatt[3] says:

> How unreasonable it would seem to a student of fossil Mammalia, if he were requested to do what it would be appropriate to require from a student of fossil Cephalopoda, viz., to describe from the investigation of a single perfect fossil skeleton of an adult, not only the characteristics of the skeleton at the stage of growth at which the animal died, but the developmental stages of this same skeleton, and in case it were the remains of an old, outgrown animal, also, the retrograde metamorphoses through which it had passed during its last stages of decline. It might require a lifetime to make out the stages of a single species of mammal satisfactorily from the isolated specimens which would be found and the attempt would be hopeless for all the youngest stages of growth, while the bones were still cartilaginous. This kind of evidence, however, is readily obtainable among fossil Cephalopods . . . and it can be obtained in good collections everywhere.

While this is especially true of the tetrabranchiate cephalopods, it is also true in a more or less complete degree of some other groups of molluscs, as well as many brachiopods, echinoderms and corals.

As examples of types showing stages in development, the following may be cited. The living *Nautilus* has a close-coiled shell, but in its development passes through

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[2] A. Hyatt, "Genesis of the Arietidæ," Smithsonian Contributions to Knowledge, Washington, 1889.

[3] A. Hyatt, "Phylogeny of an Acquired Characteristic," *Proc. Amer. Phil. Soc.*, Vol. 32, 1894.

arcuate, loose-coiled, then close-coiled stages directly comparable to the adults of Paleozoic cyrtoceran, gyroceran and nautiloid representatives of its own group. As shown by J. Perrin Smith,[4] the highly evolved Cretaceous *Placenticeras pacificum* which in the adult has complex sutures, in the development of these parts passes through simpler stages which are comparable to the adult structures of nautiloid, goniatitic and glyphioceran forms, followed by stages in which the septa are comparable to those of early *Ammonites,* before it assumes its adult generic features. The recent *Pecten* has strongly marked ears, but the young shell is strikingly different, first having a rounded nuculoid form, followed successively by *Rhombopteria, Pterinopecten* and *Aviculopecten* stages before its adult character is attained. In Echini the recent *Goniocidaris* and other genera, both recent and fossil, have two or more columns of plates in each interambulacral area, but in the young they pass through a stage in which there is a single plate at the ventral border of the interambulacra, which is comparable as a stage in development to the adult of the Ordovician *Bothriocidaris* which retains a single column of plates in each interambulacral area in the adult. The Lower Carboniferous echinoid *Oligoporus* which in each ambulacrum has four columns of plates with, in addition, scattered isolated plates, passes through stages with primary plates only, as in *Palæechinus,* then primary and occluded plates as in *Maccoya,* followed by four columns, without isolated plates, as in *Lovenechinus,* before attaining its generic character. In Brachiopoda, as shown abundantly by Beecher and others, stages in development are shown in the exterior and interior of the shell and the brachial supports which can be closely correlated with adult characters of more primitive representatives in the group.

While stages in development from the young to the adult are typically all progressive, in senescence, the

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[4] J. P. Smith, "The Development and Phylogeny of Placenticeras," *Proc. California Acad. Sci.*, Ser. 3, Geology, Vol. 1, No. 7, 1900.

stages that appear are in the main regressive. Nautiloids and ammonoids, which are characterized by close-coiled shells, build loose-coiled or even uncoiled additions; specialized *Ammonites* with complex septa, in senescence build simpler septa. Palæozoic Echini, which are characterized by many columns of plates in an interambulacral area, lose some of these columns in old age growth, all in these features taking on simpler characters comparable to those seen in their own youth, and also comparable to the characters of adults in regressive series in their own groups.

As an aid in describing stages, Professor Hyatt[5] devised a classification of stages in development and decline which is a great convenience in exact description. In this classification the ontogeny is primarily divided into embryonic and postembryonic periods, the latter being for the most part the more important in phylogenetic work. Of embryonic stages the *protembryo* is represented by the egg and segmentation stages of the same, comparable to the simple and colonial Protozoa as adult forms. The *mesembryo* is the blastula stage, with a single layer of cells on the periphery of a hollow sphere, comparable to *Volvox* and *Eudorina,* the Mesozoa of Hyatt. The *metembryo* is the gastrula stage, comparable to the simplest of the sponges. The *neoembryo* is a later stage represented by the early ciliated cephalula stage of a brachiopod and the trochosphere of a mollusc, comparable to the embryo of chætopod worms and other Cœlomata. The *typembryo* is that stage in development when the features of the great group to which the animal belongs appear. In Mollusca the shell gland and plate-like beginnings of the shell appear at this stage. In brachiopods, two folds of the second segment of the embryo turn forward and the corneous shell begins to appear. The *phylembryo* is the completed embryonic stage and is the first ontogenetic stage that is applicable

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[5] A. Hyatt, "Values in Classification of the Stages of Growth and Decline with Propositions for a New Nomenclature." [Somewhat altered in later publications. R. T. J.] *Proc. Boston Soc. Nat. Hist.*, Vol 23, 1888.

in palæontological study. It is the stage in which the characters of the class to which the animal belongs are established. This period is represented by the protechinus of Echini, the protegulum of Brachiopoda, the prodissoconch of Pelecypoda, the protœcium of Bryozoa, the protoconch of Cephalous Mollusca and the protaspis of the Tritobita. This stage in development is represented in fossil as well as living forms in many types, and the primitive radicle that it represents as a phylogenetic stage has been pointed out as *Paterina* for the Brachiopoda by Beecher, as a nuculoid type for certain Pelecypoda, and as *Bothriocidaris* for the whole class of Echini by Jackson.

Of postembryonic stages the first are the *nepionic* or babyhood stages, abundantly recognizable in fossil as well as recent types. Succeeding these are the *neanic,* or youthful stages. The *ephebic* is the adult, or that stage in which the full species characters are evinced. Senescence or old age is expressed in *gerontic* stages, in which appear the loss of characteristic species features, and by such loss an approach is commonly made to the youthful character before such features are attained. Gerontic stages while in a measure repeating youthful characters, do so in the inverse order to that in which they are acquired in ontogeny. As shown abundantly by Hyatt, senescent features are prophetic of the adult characters in regressive series of the group.

In studies of ontogeny it often occurs that stages need to be further subdivided. For this purpose Professor Hyatt introduced the prefixes *ana, meta* and *para,* so that one can speak of the *ananepionic, metanepionic* or *paranepionic* stage of *Nautilus,* etc. By means of this simple nomenclature the life stages of any organism are divisible into ten main or thirty minor periods, which are thus readily and clearly expressed.

In ontogeny, as shown by overwhelming evidence, the organism passes through stages which repeat the characters of adults of more primitive types in serial order, and it is believed that this serial order may be safely accepted as a recapitulation of the phylogeny of the group in hand. Stages are not equally clear in all types, for stages may be skipped, or may be telescoped in specialized forms, but in primitive forms (*Nautilus, Lingula, Pecten, Cidaris*) they are astonishingly clear and complete. By some investigators stages have been denied and the recapitulation theory considered a myth. I can not enter into discussion here, but can simply say that it is felt that opponents have not considered the evidence. Cumings[6] has recently put the matter well in a defence of the Recapitulation Theory.

The principle of acceleration of development, originated by Professor Hyatt,[7] is at once an explanation of the existence of stages in development, and the loss, or skipping of stages as well. This principle maintains that features appearing at or near the adult period of development are inherited at earlier and earlier stages in successive generations until they exist only in the extreme young or are skipped as stages in development.

As examples of accelerations: In certain Palæozoic Echini the full number of columns of ambulacral and interambulacral plates are attained only in the adult. In more specialized species the similar columns are taken on much earlier in both areas than they appear in lower species (*Melonechinus*). The pelecypod *Hinnites* is attached by the fixation of one valve to foreign objects when about one fourth grown, and then loses its young pecteniform character. The allied *Spondylus* is attached when very much younger and thus earlier loses the similar stage. *Plicatula* is attached at the close of the prodissoconch stage and has lost the pecteniform stage altogether. In primitive tritobites (*Solenopleura, Sao*) the protaspis is rounded with neither dorsal eyes nor

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[6] E. R. Cumings, "Palæontology and the Recapitulation Theory," *Proc. Indiana Acad. Sci.*, twenty-fifth anniversary meeting, 1909.

[7] A. Hyatt, "On Parallelism between the Different Stages of Life in the Individual and Those in the Entire Group of the Molluscous Order Tetrabranchiata," *Mem. Boston Soc. Nat. Hist.*, Vol. 1, 1866, p. 203. See also [minutes of meeting of February 21, 1866] *Proc. Boston Soc. Nat. Hist.*, Vol. 10, pp. 302–303.

ornamentation. In the specialized genera *Acidaspis* and *Arges*, as shown by Beecher, both dorsal eyes and denticulate ornamentations occur in the protaspis.

In acceleration of development, when skipping of stages occurs, it is not the earliest or embryonic stages that are skipped, but later or postembryonic. Embryonic stages are clung to with striking pertinacity. Stages are often run together or telescoped as expressed by Grabau,[8] when in a specialized type more than one phase may be represented at a single stage, although such stages are clearly distinct in more primitive types.

As an outgrowth of Professor Hyatt's studies of stages in development, the principle of colonial development has been enunciated independently by Ruedemann[9] in Graptolites, by Cumings[10] in Bryozoa and by Lang[11] also in Bryozoa. These investigators show that in the growth of the colony there are distinct stages in development which can be correlated with the adult characters of more primitive colonial forms. In this respect the colony behaves as an individual. Cumings introduces the terms nepiastic, neanastic, ephebastic, gerontastic as descriptive adjectives of these colonial stages. It is felt that this special nomenclature for colonial stages is unnecessary and therefore undesirable, because the simpler the terminology can be kept in such work, the more likely it is to be widely accepted and made use of.

Another phase of stages is localized stages in development in which I[12] showed that throughout the life of the individual stages may be found in localized parts which

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[8] A. W. Grabau, "Studies of Gastropoda. III. On Orthogenetic Variation," AMER. NATURALIST, Vol. 41, 1907.

[9] R. Ruedemann, "Growth and Development of *Goniograptus thureaui* M'Coy," *Bull. N. Y. State Mus.*, No. 52, 1902.

R. Ruedemann, "Graptolites of New York." Pt. 1, *Mem. N. Y. State Mus.*, No. 7, 1904. Pt. 2, *idem*, No. 11, 1904.

[10] E. R. Cumings, "Development of Some Palæozoic Bryozoa," *Amer. Journ. Sci.* (4), Vol. 17, 1904.

[11] W. D. Lang, "The Jurassic Form of the 'Genera' *Stomatopora* and *Proboscina*," *Geol. Mag.*, dec. 5, Vol. 1, 1904.

[12] R. T. Jackson, "Localized Stages in Development in Plants and Animals," *Mem. Boston Soc. Nat. Hist.*, Vol. 5, 1899.

repeat the characters seen in youth and in the adults of more primitive types. Such localized stages are shown by many trees and other plants. In the oak, ash and hickory, suckers from the base of the tree have simple forms of leaves, comparable to those seen in young seedlings. Beneath the flower (rose, peony), at the tips of branches (hickory, sassafras) and in diseased or feeble growths (tulip-tree, red cedar) leaves often occur which in simplicity of character are comparable to those of seedlings or more primitive species in the group. Localized stages occur also in herbaceous plants as shown by Cushman.[13]

Amongst animals localized stages are shown where during growth there is an addition of similar parts as the plates in echinoderms, septa in cephalopods and in the developing zooids of colonies of corals and, according to Ruedemann, in Graptolites. In these types the parts as added present stages which are comparable to stages seen in the ontogenesis of the individual as a whole. In Echini new plates are added to the corona immediately below the oculars, and at this region throughout life the ambulacral plates are of a simple character, whereas the older earlier formed plates during their individual development may have taken on complex characters, for example, in *Centrechinus* (*Diadema*) ambulacral plates are compound, but close to the oculars are simple. In the Palæozoic family of the Palæechinidæ, the ambulacrum at the equator, or midzone, has from two to twelve columns of plates in each area, but in those genera with many columns there are only two columns dorsally in the area where new plates are added. In crinoids, in which the arms have the plates arranged in a biserial manner (*Encrinus, Platycrinus*) as shown by Grabau,[14] a uniserial arrangement exists at the tips

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[13] J. A. Cushman, "Studies of Localized Stages of Growth in Some Common New England Plants," AMER. NATURALIST, 1902; *idem*, "Studies of Localized Stages in Some Plants of the Botanic Gardens of Harvard University," AMER. NATURALIST, 1903.

[14] A. W. Grabau, "Notes on the Development of the Biserial Arms in Certain Crinoids," *Amer. Journ. Sci.* (4), Vol. 16, 1903.

where the young plates are added. In *Ammonites,* as *Placenticeras,* in which the sutures of the septa are complex, often in a very high degree, we find that at the inner, or umbilical, portion of each individual septum a simpler condition exists, and greater complexity is attained in passing from the ventral portion of the septum outward, or dorsally. This simpler ventral portion in an adult can be compared with the simpler condition in a whole septum of the young, or with the septum of the adult in a more primitive and geologically older representative of the group.

Parallelism is a most important principle and was constantly used by Professor Hyatt in his studies. Parallelism is the taking on of a similar form in independent lines of descent. It may help one in explaining the origin of structures, but is sometimes confusing as indicating a basis of relationship which is misleading. In Crustacea the recent isopod *Serolis* closely resembles a trilobite. The uncoiled gastropod shell *Vermetus* closely resembles the worm *Serpula. Spondylus, Chama* and *Mülleria* amongst Pelecypoda, and *Davidsonella* and *Derbya* among Brachiopoda are all attached by the calcareous fixation of one valve and closely resemble *Ostrea,* which has a similar habit of life. The complex septa of the Tertiary nautiloid *Aturia* closely resemble those of the Devonian ammonoid *Goniatites.* Echini with imbricating coronal plates were considered as related on account of this character, but this structure appears in several independent lines in the group. The recent deep-sea Echinothuriidæ have many rows of ambulacral plates only in the peristome. By this character they have been associated with the Palæozoic Lepidocentridæ which have the same feature. I believe however that it is purely a parallelism and not a basis for genetic connection.

Larval adaptation is the term applied to special features built up as youthful adaptations and which are not, therefore, of phylogenetic significance. Such adaptations are a marked feature of certain groups as the ventral spurs developed in the embryonic glochidial stage of the Unionidæ. Larval adaptations are most marked in the youthful stages of some insects, as in caterpillars. In most invertebrates, however, at least in postembryonic stages, larval adaptations are uncommon and can usually be eliminated as a factor in studying ontogenetic stages.

The Hyatt principles have been used as a working basis in the phylogenetic classification of three entire classes of animals, the Brachiopoda and Trilobita by Beecher[15] and the Echini by myself.[16] They have also been used as a basis of partial classifications of Cephalopoda by Hyatt himself, of Protozoa by Cushman,[17] of Pelecypoda by Jackson,[18] of Gastropoda by Grabau,[19] and also to a certain extent in suggesting genetic relationships in a number of other groups of animals and in plants by various investigators.

If I may be permitted to speak of my own studies. I have recently completed a phylogenetic study of the Echini, and throughout the work made use of the Hyatt principles. In this use there was no occasion to qualify a single one. To work out principles largely on one group (the Cephalopoda) as did Hyatt, and then to have his followers apply these principles successfully to many widely separate groups, and even to seek and ascertain facts on the basis of the implied principles, is strong evidence that he got at fundamental truths.

At present the phylogeny of invertebrates is little studied, palæontologists are largely occupied with questions of stratigraphy, and zoologists occupy themselves with other lines of work. In future, as phylogenetic work is prosecuted, I believe that Hyatt will be looked on as the master mind who pointed out the methods by which to ascertain the true phylogenetic relations of invertebrate organic forms.

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[15] C. E. Beecher, "Studies in Evolution," New York, 1901.

[16] R. T. Jackson, "Phylogeny of the Echini," *Mem. Boston Soc. Nat. Hist.*, Vol. 7, 1912.

[17] J. A. Cushman, "Developmental Stages in the Lagenidæ," AMER. NATURALIST, Vol 39, 1905.

[18] R. T. Jackson, "Phylogeny of the Pelecypoda," *Mem. Boston Soc. Nat. Hist.*, Vol. 4, 1890.

[19] A. W. Grabau, "Phylogeny of *Fusus* and Its Allies," Smithsonian Misc. Coll., Vol. 44, 1904.

THE BEARING OF TERATOLOGICAL DEVELOPMENT IN NICOTIANA ON THEORIES OF HEREDITY[1]

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IT is desirable, though difficult, to atack genetic problems by both pedigree-culture and cytological methods. It is desirable because the problems are viewed from different standpoints; it is difficult because few forms are especially favorable for either kind of work. The present paper is a preliminary report upon certain characters in a species fairly desirable from each point of attack.

Among plants teratological phenomena are common, especially those known as fasciations, Masters[2] citing, in 1869, 120 genera in which they were not infrequent.

The term fasciation is a broad one and includes, from a genetic standpoint, some very different phenomena. At least two distinct kinds of variation are now emphasized in genetic work, somatic and germinal, although often it is impossible to distinguish between them except by experimental cultures. Fasciation is a phenomenon of variation in which both types occur, though the evidence on this point is not all that could be desired. All observers agree that the fasciated character is constant and heritable in such races as *Celosia cristata*[3] (cockscomb), *Pisum sativum umbellatum*,[4] *Sedum reflexum cristata*,[5] some races of *Zea mays* and *Nicotiana*

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[1] Contribution from the Laboratory of Genetics, Bussey Institution of Harvard University.

[2] Masters, M. T., "Vegetable Teratology," pp. 9–21, London, 1869.

[3] De Vries, H., "The Mutation Theory," **2**: 68, 516–519, 1910; also Lynch, Irwin, "Evolution of Plants," *Journ. Roy. Hort. Soc.*, **25**: 17–31, 1900.

[4] De Vries, H., *ibid.*, p. 513, 1910. See also Lynch, I., *ibid.*

[5] Masters, M. T., *ibid.*, pp. 18–19, 1869.

[6] East, E. M., and H. K. Hayes, "Inheritance in Maize," *Conn. Agr.*

tabacum fasciata. On the other hand, many examples of fasciation are slight or severe somatic modifications, no more permanent than a swollen limb due to a bruise in our own bodies, or a bone spavin in a horse's foot, though the tissue proliferation may remain as a lasting scar. Examples of this form may be found in *Œnothera,*[7] *Nasturtium,*[8] *Picris hieracioides* and *Raphanus raphanistrum.*[9] Such modifications are imperfectly understood, but may be brought about directly or indirectly by external agencies such as bruises, culture methods and insect injuries to the initial meristem.

Aside from the work of Mendel[10] and De Vries,[11] the phenomena of fasciation have not been dealt with in the light of modern genetics. Mendel's investigations were made on a fasciated strain of pea (*Pisum sativum umbellatum*). When crossed with a non-fasciated strain the teratological character was recessive and segregated in F_2 in a simple 3:1 ratio. This result was essentially confirmed by Lock and Bateson, although environmental conditions were found by them to affect the character more than is usual in such phenomena.

De Vries failed to distinguish between fasciations strictly heritable and those non-heritable. The only con-

Exp. Sta. Bull., No. 167, and Contrib. from Lab. of Genetics, Bussey Inst. of Harvard Univ., No. 9, p. 133, Pl. XXII (*a*) and (*b*), 1911; also Emerson, R. A., personal communication, 1911.

[7] Knox, A. A., "Induction, Development and Heritability of Fasciations," Carnegie Inst. of Wash. Pub. **98**: 1–21, Pls. I–V, 1908.

[8] Knox, A. A., *ibid.*, p. 14.

[9] Molliard, M., "Cas de virescence et de fasciation d'origine parasitaire," *Rev. Gén. de Botanique,* **12**: 323–327, 1900; also Godron, A., "Mélanges de teratologie végétale," *Mem. Soc. d. Sc. Nat. d. Cherbourg,* **16**: 81–127, pp. 96–97, 1871–1872.

[10] Mendel, G. J., "Versuche über Pflanzen-Hybriden," *Verh. Naturf. Ver. in Brünn,* **10** Abh., p. I. See Bateson, W., "Mendel's Principles of Heredity," pp. 322, 328, 330, Cambridge Univ. Press, 1909.

[11] De Vries H., *ibid.*, III, "The Inconstancy of Fasciated Races," pp. 488–526, 1910; "Monstruosités héréditaires offertes en échange aux Jardins Botaniques," *Bot. Jaarboek,* **9**: 62–93, 1897; "Over de erfelykheid der fasciatiën. Avec un résumé en langue française," *Bot. Jaarboek Dodonaea,* **6**: 72, 1894; "Sur la culture des monstruosités," *Comptes Rendus,* **128**: 125, 1899; "Sur la culture des fasciations des espèces annuelles et biannuelles," *Rev. Gén. de Bot.,* **2**: 136, 1899.

stant fasciated race[12] with which he worked is the cockscomb and his experimental researches on this plant led him to conclude that "complete atavists," or normal plants carrying the fasciated character in a latent state, are very rare, and even under repeated selection are to be obtained in very small numbers. Further, the normal plants thus obtained do not breed true, but revert very soon to the abnormal condition. While investigations have not been made showing definitely that many of De Vries's fasciations were not heritable, but were simply somatic modifications, enough evidence is at hand from numerous sources to justify at least the expression of a strong doubt of their heritable character. According to the observations of Knox, fasciated stems in Œnotheras are not germinal in origin, but traceable directly, in most cases, to insect injuries. Observations by Molliard on *Raphanus* and *Picris* support this conclusion, while Godron was unable to secure fasciated individuals from the seeds of a *Picris* plant thus affected. The fact that fasciation appears in every generation of *Œnothera* plants in varying percentages, in certain cultures, especially those of a biennial nature, is best explainable on a re-infection basis. Spiral torsion races such as *Dipsacus sylvestris torsus* in De Vries's cultures behaved, from a genetic standpoint, in the same manner as his fasciated races. Races of *Dipsacus* species are rich in torsions in Holland and Denmark, but, according to Johannsen,[13] the seeds of torsus strains when grown in England produced normal progeny. This would indicate an environmental rather than a germinal basis as a causal factor.

In all of De Vries's experimental cultures of fasciated races (with the exception of *Celosia*) only a certain per cent. (averaging in most races 50 per cent. or less) of the individuals in each generation possessed the abnormality, and he was never able to breed a constant and

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[12] Possibly *Geranium molle fasciatum* may be an exception in which more than one unit factor is responsible for the anomaly. Otherwise it should have bred true at least by the sixth generation if the seed sown each year was from carefully guarded plants.

[13] Johannsen, W., public lecture IV, Boston, 1911.

genetically pure race. Even though he had been able to do this, doubt could still be cast upon the belief that he was dealing with a strictly heritable character, because the only method that seems to preclude doubt is crossing with the normal and securing the F_2 ratio. This method would eliminate the suspicion that minute bacterial or even ultra-microscopic organisms were acting as causal agents.

Emerson and East in their maize studies have obtained races breeding constant for fasciated ears. I have myself examined such a race in Emerson's cultures. Hus, on the other hand, with the same sort of an abnormality in the same plant species, *Zea mays,* secured results similar to those of De Vries.[14] Is the difference in results due to methods or to the nature of the plant abnormality itself? I shall consider the results of De Vries and others holding similar opinions in greater detail in a later paper, as such results entail an extended review.

THE PROBLEM AND THE MATERIAL

The problem to be discussed briefly in this paper is the relation of the cytological phenomena in the reduction divisions to certain segregating Mendelian characters, and the nature of these characters in development and inheritance.

The material upon which the study is largely based is a fasciated variety of *Nicotiana tabacum.* Although fasciations are very common in many genera and not infrequent in others, they have never been recorded (so far as I can determine) in *Nicotiana.* The present race was obtained from the selfed seed of a mutant found growing in a field of Cuban tobacco in the district of Partidos, near the town of Alquiza, Cuba, in 1907. I am indebted to Dr. E. M. East and to Mr. J. S. Dewey[15] for

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[14] Hus, H., and Murdock, A. W., "Inheritance of Fasciation in *Zea mays,*" *Plant World,* **14**: 88–96, 1911.

[15] Mr. J. S. Dewey is superintendent of the United States tobacco plantation belonging to the same company that controls the Cuban plantation near Alquiza.

data on this race, prior to the summer of 1910. The sport is characterized by a flattened, fasciated condition of the stem and floral structures, and a consequent increase in the number of leaves. The original mutant is described by Dewey as possessing 152 leaves on the main stalk, flowers abnormal, stem fasciated. When the abnormal plants were studied in more detail, many smaller teratological features were found, and these were especially plentiful in connection with the floral structures. The pistil frequently was incapable of functioning, because of various forms of tissue proliferation in the region of the stigma. The style was often shortened, coiled or fused near its base with an anther (staminody of the pistil). The ovary locules were very much increased in number, ranging from two (extremely rare) to as high

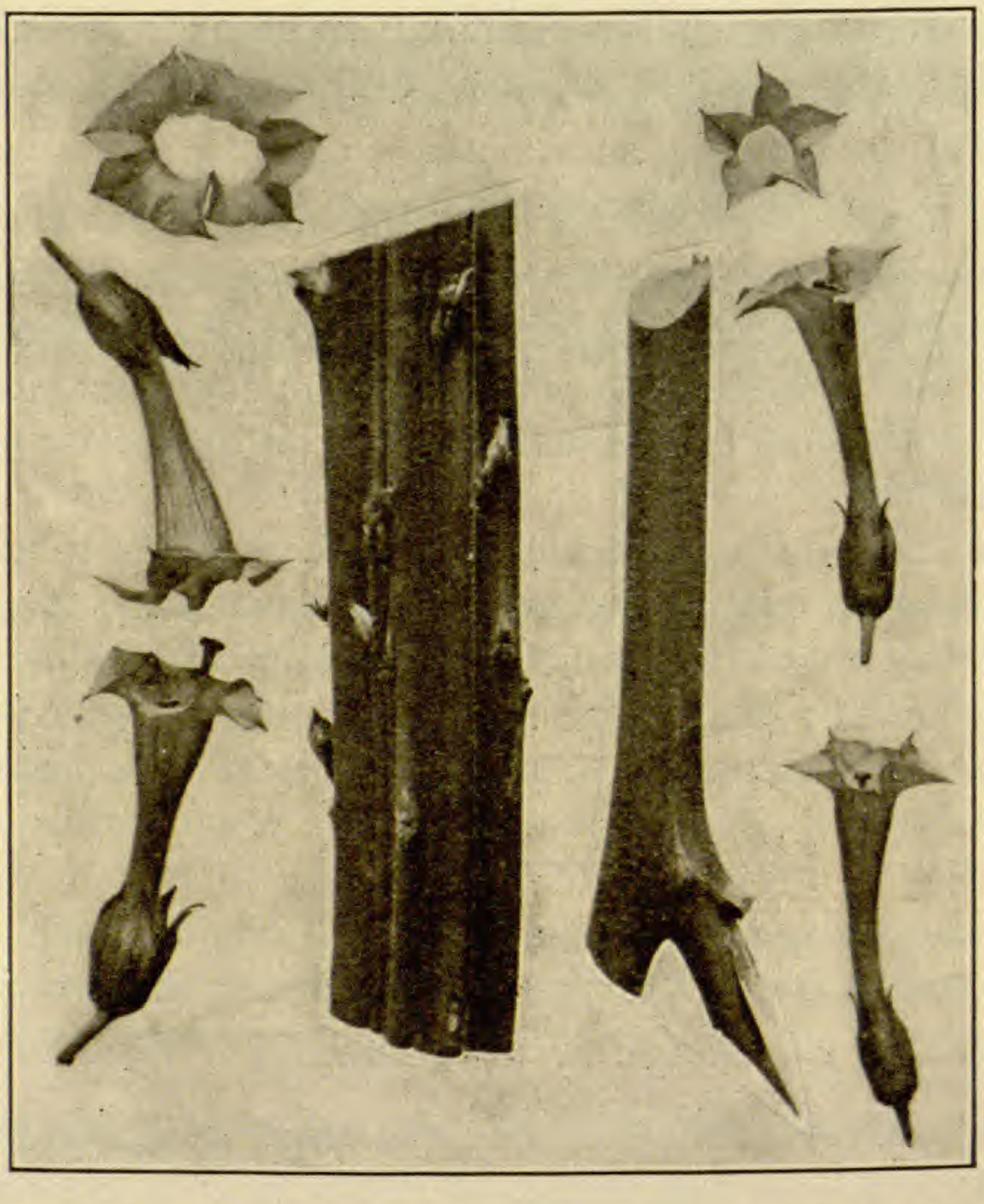

FIG. 1. Stems and flowers from the abnormal and normal strains of N. tabacum.

as twenty. Very often two or even three distinct pistils were formed in the same flower, all of which in some cases could function. The stamens were affected in both filament and anther. The filaments were often coiled, twisted, shortened or fused to the corolla. In rare cases, they were petaliferous. The anther deformities consisted of split anthers, anthers with small pistils growing from them—two or three to an anther being present in one case (pistillody of the anthers). The number of pollen sacs varied from the normal four to six.

The corolla and calyx were often split, and the lobes of the calyx and not uncommonly of the corolla, were irregular in size and shape. Occasionally the calyx and corolla merged into each other by a spiral twist. Two flowers sometimes were enclosed by the same calyx. Once or twice flowers have been found consisting of only a corolla and a few stamens, growing on the side of the normal corolla and partly fused with it. The corollas never show a doubling phenomenon to accommodate the increase in petal number but the circumference of the flower is extended, and very often these flowers are as regular and symmetrical as those of the normal. Two cases of leaves fused at the base have been found and the phyllotaxy is altered and irregular. The fasciated plants when young are practically indistinguishable from the normal. The anatomical features have not been investigated sufficiently for a report upon them at this time, and it is possible that differences between the normal and abnormal seedlings will be found when this part of the study is completed.

Five generations of the abnormal strain have been grown, amounting in all to over a thousand plants, and each individual plant has possessed the unmistakable characters of the original mutant. The monstrous character is, however, a variable one, since the stems may be extremely flattened throughout the greater part of their length or only flattened and fasciated toward their apical ends. Other characters, as already implied, fluctuate between extremes, depending in part on environment

A Comparison of Certain Characters of the F_1 and F_2 Generation of

303–1–12 is a type of extreme abnormalness. 301–1–2 represents the extreme *tabacum*. (304 × 402)–1–10 = normal F_2 segregate. (304 × 402)–1–12 = abnormal heterozygous F_2 segregate similar to the F_1 (304 × 402)–30.

		Stem	No. of Leaves	Height, In.	Flower	1	2	3	4	5	6	7	8
♀ P	303–1–12	V. abn.	69	76	Sepals . .	7	6	6	7	6	8	9	7
					Petals . .	12	9	6	10	11	12	11	13
					Stamens	12	12	7	12	8	13	11	12
					Ovary locules.	3–3–3	3–3	4	3–3–2	4–3	4–4	3–3	6–3
	301–1–2	N.(?)	33	68	Sepals . .	6	6	7	6	7	6	6	6
					Petals . .	7	6	7	7	8	8	7	7
					Stamens	7	6	6	7	7	7	7	7
					Ovary locules.	3	3	3	3	3	3	3	4
♂ P	402	N.	24	72	Normal as in (304 × 402)–1–10								
F_1	(304 × 402) –30	N.(?)	26	87	Sepals . .	6	6	7	6	6	6	5	6
					Petals . .	7	6	7	6	5	6	5	7
					Stamens	7	6	7	6	6	6	5	7
					Ovary locules.	3	3	3	2	2	3	2	2
F_2	(304 × 402) –1–10	N.	24	75	Sepals . .	5	5	5	5	5	5	5	5
					Petals . .	5	5	5	5	5	5	5	5
					Stamens	5	5	5	5	5	5	5	5
					Ovary locules.	2	2	2	2	2	2	2	2
	(304 × 402) –1–12	V. abn.	80	75	Sepals . .	10	12	6	8	10	7	8	9
					Petals . .	12	20	8	12	15	8	21	12
					Stamens	16	15	7	8	12	7	18	12
					Ovary locules.	6–10	6–3–4	5	3–3	3–4	4	6–4–2–2	4–3
	(304 × 402) –1–34	S. abn.	63	75	Sepals . .	8	7	7	7	7	6	6	6
					Petals . .	8	8	7	7	7	7	7	8
					Stamens	7	8	7	7	8	7	7	8
					Ovary locules.	3	3	3	3	4	3	3	3
	(304 × 402) –1–6	N.(?)	32	75	Sepals . .	5	6	6	6	7	5	6	6
					Petals . .	5	6	6	6	7	5	7	6
					Stamens	5	6	6	6	7	5	7	6
					Ovary locules.	2	3	2	3	3	3	3	3

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[16] Double flower.

ABNORMAL × NORMAL *Nicotiana* (304×402) WITH THOSE OF THE PARENT STRAINS

variation of the abnormal characters toward the normal. 402 is the normal *N.* F$_2$ segregate. (304 × 402)–1–34 = heterozygous F$_2$ segregate. (304 × 402)–1–6 =

9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
8	7	7	6	7	7	6	6	6	8	8	7	6	6	7	7	7	
11	12	11	10	8	8	7	9	9	16	8	10	7	7	11	7	11	
11	14	11	12	9	8	7	11	8	17	9	12	7	6	11	7	11	
3–3	4–6–4	5–3	3–4	3–3	5	4	3–2	4–4	8–5	5	2–4	3	3	3–1	3	3–3	
8	7	6	7	8	7	6	6	6	6	6	7	7	6	6	6	6	8[16]
8	7	8	7	8	8	9	8	7	7	7	7	8	7	8	8	5	7
10	7	6	7	7	7	8	9	7	6	6	7	7	6	8	7	5	7
4–2	4	3	3	4	3	3	2–3	4	4	3	3	3	3	4	3	3	3
Normal as in (304×402)–1–10																	
5	7	7	6	6	6	6	6	6	7	6	5	5	5	5	7	5	
5	7	6	6	7	6	6	7	6	7	6	6	6	5	6	7	7	
5	7	6	6	6	6	6	7	6	7	6	6	6	5	5	7	7	
3	2	3	2	3	3	3	3	3	3	3	3	3	2	3	3	2	
5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	
5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	
5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	
2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
7	8	8	12	7	10	6	7	8	8	7	7	7	7	8	7	8	
10	9	18	24	12	15	8	8	10	15	12	15	8	8	9	12	8	
7	9	16	24	8	18	7	7	6	15	8	10	7	8	8	10	8	
3	4–3	4–4–4–3	7–6–4–4	4	4–4–2	3	4	3	5–3	3–2	4–3	4	5	4	3–4	3–2	
8	7	8	9	8	7	8	7	8	7	12	9	8	8	8	12	11	
8	7	7	11	8	7	8	7	9	7	16	12	11	14	8	12	18	
7	7	8	10	7	7	7	7	9	7	16	12	11	14	7	12	15	
4	3	4	4–4	3	3	3	3	4	4	4–6–4	4–3	4–4	4–4	2	2–2	4–5–4	
5	5	5	5	6	6	6	6	6	5	5	5	5	6	6	5	6	
6	6	5	6	7	7	6	6	6	6	7	6	7	7	7	5	7	
6	6	5	6	6	7	6	6	6	6	6	5	7	6	6	5	7	
2	3	2	3	3	3	4	3	3	3	3	3	3	3	3	3	3	

and in part on the *innate* nature of the character itself. One may confuse this fluctuation to the arc made by a swinging pendulum. The arc through which the pendulum can swing is limited, but within those limits the arc may be medium, large or small, depending on the agencies that set the pendulum in motion. Agencies very different in nature may produce the same result. The pendulum is the material body which makes the arc recognizable as an entity, and in this simile may be compared to the gene for fasciation. When the pendulum is motionless, there is no arc, and there would be no fasciation if the gene remained potential.

A more definite idea of the characters of the plant and their variability may be secured by consulting the table on page 212. It should be stated that plants have been grown under many environments and with many variations in culture. But so far as our present interest goes, no very great changes have resulted. The race has always been clearly distinguishable in the adult state from the normal, whether grown under cramped greenhouse conditions, or out-of-doors; whether surrounded by a Cuban or a New England environment. No especial care, such as De Vries prescribes, regarding culture and transplantation has been given, and yet the anomaly has always bred absolutely true and no "atavists" have appeared.

The normal Cuban variety from which the fasciated strain arose is characterized by a normal round stem, regular phyllotaxy, flowers with five petals, sepals, stamens and a two-loculed ovary. The number of commercial leaves varies between 20 and 25, all leaf counts in the present investigation, being made by the commercial method.[17] Fertility is practically 100 per cent. Occasionally among hundreds of flowers examined a flower is found with an extra sepal or petal, otherwise abnormalities are unknown in our cultures of the normal variety.

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[17] All leaves were recorded up to the first leafless branch ("bald sucker"), exclusive of the first three basal leaves.

In the cultures at the Bussey Institution of Harvard University the normal Cuban is known as 402: the fasciated strain as 300–309, the range in numbers representing an attempt at selection.

METHODS

Data were collected on each plant and tabulated separately. The characters noted were, extent of fasciation in the stem; number of leaves, petals, sepals, stamens and ovary locules. Twenty-five flowers were taken from each plant and the parts of each flower recorded separately. In all crosses made the flowers were castrated in the bud and bagged. Pollen was taken only from anthers still in the closed bud and 95 per cent. alcohol was liberally used after each operation on hands and instruments. The Webber system of recording the plants by number was used. All seed was sown in sterilized soil and all possible care taken to avoid mixtures.

EXPERIMENTAL WORK

Numerous crosses were made between distinct species and the abnormal race, but all of the progeny were sterile, though the abnormal character was visible in their flowers and in the increased number of leaves which they bore.

Four crosses were made between normal *N. tabacum* varieties and the abnormal, all of which produced fertile F_1 plants. The most interesting of these is a cross of the abnormal with the normal Cuban variety from which it mutated. Three generations of this cross (304 × 402) have been grown. The F_1 generation consisted of 39 plants, the F_2 of 97 and the F_3 of 647, totaling 783 individuals. The F_1 was intermediate in character between the two parents, as the table will show. The F_2 gave the three expected types in the ratio of 1:2:1, the actual numbers being:

	Normal	Heterozygote	Abnormal
Actual	28	52	17
Expected	24	48	24

The F_2 selections gave the results expected in F_3. Counting the total progeny (248) from F_1 and F_2 heterozygotes, the figures are:

	Normal	Heterozygote	Abnormal
Actual	68	124	56
Expected	62	124	62

The F_2 heterozygotes were in appearance duplicates of the F_1 individuals and after a little experience could be easily distinguished from the abnormal homozygotes. Clean segregates were obtained from the heterozygous

FIG. 2. F_2 segregates from the abnormal × normal (304 × 402) Nicotiana. Abnormal homozygote, heterozygote and normal homozygote. The grandparents in appearance are duplicates of the two homozygotes

plants in both F_2 and F_3 and the homozygous normals and abnormals obtained in this manner bred true in F_3 and F_4. Not being satisfied that only one factor represented the difference between the normal and the abnormal, I thought that it might be possible, through selection, to secure a normal strain from the abnormal, or at least to modify the unit character, as Castle and his students appear to have done with the hooded pattern in rats.

Selection work was started by selecting from the cultures the most abnormal and the least abnormal plants as seed producers. The work was carried through two generations with no prospect of success and there it remains at present. Progeny of the least abnormal plants were as much fasciated and otherwise abnormal as the original parent strain growing beside it. And one could not distinguish the least abnormal from the most abnormal strain except by the label. So far as the work has progressed, this fasciated strain seems no more amenable to selection than the cockscomb with which De Vries worked, and of which he said "at present at least there seems not to be any prospect of obtaining a pure atavistic strain."[18]

From a comparison between the drawing in Gerarde's Herball of 1597[19] and certain woodcuts from old horticultural magazines with the plants as they are to-day, it does not appear that much change has taken place in the cockscomb fasciation since its introduction into Europe in 1570.

The changes in the expression of the comb that gardeners and florists will maintain have taken place as a result of selection can all be accounted for by the influence of the environmental factor.

Lock planted seeds of very slightly fasciated individuals of the F_2 generation of normal × fasciated stem in *Pisum*. The F_3 plants were almost, if not as much fasciated, as the original grandparent strain.[20]

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[18] De Vries, H., "The Mutation Theory," 2: 519, 1910.

[19] Gerarde, John, "Herball or Generall Historie of Plantes," 1st ed., pp. 323–325, Fig. on p. 323, 1597.

[20] Lock, R. H., *loc. cit.*, p. 106.

This fasciated strain of pea (Mummy Pea or *Pisum sativum umbellatum*) would appear to have been a very constant race, at least since 1597, when it was figured in Gerarde's "Herball."[21]

From the results of hybridization and selection, one may draw the conclusion that the fasciated mutant differed from the normal parent strain by only one factor and that it represents a mutation upon the variability of which selection has no modifying effect. The character itself appears to be due to one underlying cause and its variableness is only the external manifestation of the capricious working of that cause.

After completing a satisfactory study of the gross aspects of this character, a cytological investigation was made, with the hope that here might be found a clue to the cause or causes underlying the appearance of the anomaly.

CYTOLOGY

Much trouble in fixing material was caused through the presence of resinous substances in the tissues. Flemming's medium and strong solutions were finally found to be the most successful, although prolonged bleaching of the sections with H_2O_2 was necessary to eliminate the blackening. Care had to be exercised to secure quick penetration, as poor fixation and shrinkage were likely to result after a bath of over 24 hours. The preparations were stained in Heidenhain's iron hæmatoxylin and counterstained with clove oil saturated with erythrosin. This combination usually gave the best results —a deep black chromatin stain against a brilliant red background. Preparations were also stained with the safranin-gentianviolet-orange G combination of Flemming and restained with iron hæmatoxylin. This method gave very sharp outlines, not easily obtainable in some phases, when the ordinary hæmatoxylin method was used. Another combination which was found valuable in cases where the chromosomes were closely crowded

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[21] Compare with photograph in Darbishire, A. D., "Breeding and Mendelian Discovery," p. 22, Fig. 8, 1911.

together, as in certain metaphases, is safranin, magdala red and azure II. Large quantities of the fresh material of the anthers in various stages of maturity were stained with methyl green and microscopically examined. In most cases one anther of a bud to be fixed was inspected in this manner. This precaution was necessary as a check on the occurrence of artifacts from fixation.

Briefly, conditions in the normal Cuban variety (402) are as follows. The ordinary maturation processes are those cytologists have so often described for plants, and need no recapitulation here. The spireme in prophase is single and, just preceding diakinesis, breaks up into segments which take the form of twisted and horseshoe-shaped loops. The latter resemble Davis's figures for *O. grandiflora*.[22] Each loop consists of two spireme segments joined at one end, which in the later heterotypic phases separate and go to opposite poles. Each segment is interpreted as a somatic chromosome, and the members of a pair are homologues. The other phases present nothing peculiar. The homotypic chromosomes appear as entities first in very late anaphase of the first division. The reduced chromosome number, as determined by very numerous counts of heterotypic metaphases and anaphases, and homotypic telophases is 24, the $2n$ being 48. The somatic number ($2n$) was determined by adding together the homotypic telophase chromosomes of a tetrad and dividing the entire number by two. Polar views of the metaphase of the first division in sections of 10μ have repeatedly shown the 24 gemini, each geminal chromosome consisting of a diakinetic pair. Variation of chromosome number in these normal (402) anthers is very rarely, if ever, to be found. None was found in the present investigation. Irregular divisions are not common, although occasionally one sees lagging chromosomes. Usually the phases of a single pollen sac

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[22] Davis, B. M., "Cytological Studies on *Œnothera*. I. Pollen Development of *Œnothera grandiflora*," *Ann. Bot.*, **23**: 551–571, Pl. XLI, Figs. 31, 34, 36, 1909.

are more advanced at one end than at the other and the maturation processes are at a similar stage in the different sacs of the same anther. Cursory examination of reduction phenomena in the ovule confirmed these observations.

Many anthers of the abnormal (300–309) when examined cytologically, were entirely normal in all their phases of maturation. Others showed evidences of almost total sterility through premature breaking down of the archesporial tissue, while still others were only partially sterile. Anthers of this strain were mentioned earlier as sometimes having more than four pollen sacs. In such cases the maturation phases were in very different stages in the different sacs. In one sac the archesporium might be in early prophase, while in other compartments there would be almost mature pollen. This extreme variation in maturation was not confined to anthers with an abnormal sac number, but was often true of those normal in this respect. Conditions in the anthers of the abnormal strain are similar as regards the normal cytological phenomena, but various abnormalities are not uncommon. These manifest themselves in such a manner that one can not avoid believing that some subtle agent is at work here, too, distorting the internal as well as the larger so-called external characters. In both reduction divisions in all the strains examined, various abnormal phenomena are to be found which are not due to fixation or other technical operations. Contrasted with the normal (402) the maturation phases in different sacs of the same anther may be far apart. Nearly mature pollen is present in some sacs, while others in the same anther may not have progressed farther than diakinesis. Pollen tetrads are often rare in nearly mature anthers. This is true of at least five per cent. of those examined. Mother-cells may break down during early prophase, diakinesis or any of the later phases. In early prophase, the nuclear membrane may disappear and the whole archesporium disintegrate.

Again, I have found that in some sacs most of the archesporium has broken down, but some few cells seem to have escaped destruction and matured. The metaphase, so far as I have observed, is not so likely to be disturbed. An occasional premature splitting of the chromosomes takes place, increasing the number to be seen in the polar view of the nuclear plate. These are rare, but they have been observed in both the abnormal strain and the abnormal segregates. This feature has been referred to as a premature splitting,[23] but it may be interpreted as an actual increase in number such as Wilson found in *Metapodius*,[24] Stevens in *Diabrotica*[25] and Strasburger in *Wikstroemia*.[26]

In one pollen mother-cell, 51 chromosomes were clearly distinguishable, but disintegration had already commenced. In another case 30 were counted, the mother-cell appearing perfectly normal, although in the anther containing it irregular divisions were taking place. The nuclear metaphases in which such an increase in number can be seen are rare, but so far as I have observed, and I have counted many nuclear plates ideal for such work, they only occur in the abnormal or in the abnormal segregates. The heterotypic anaphases of the abnormal often show the chromosomes lagging or distributed promiscuously over the spindle. In only one case so far have I found irregular conditions in the telophase and this only in the case of one mother-cell. Counting is unsatisfactory in the anaphase of the first division, as the nucleus is small and the chromosomes are many.

Irregular divisions are present in the homotypic, but most of the abnormalities occur during the heterotypic mitosis.

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[23] Preparatory for the homotypic division.

[24] Wilson, E. B., "Studies on Chromosomes. V. The Chromosomes of *Metapodius*, a Contribution to the Hypothesis of the Genetic Continuity of Chromosomes," *Journ. of Exp. Zool.*, **6**: 147–205, 1909, 1 plate and 13 text figures.

[25] Stevens, N. M., "Further Observations on Supernumerary Chromosomes, and Sex Ratios in *Diabrotica soror*," *Biol. Bull.*, **22**: 231–238, figs. 1–13, 1912.

[26] Strasburger, E., "Chromomenzahl," *Flora*, **100**: 1910.

It is impossible to say whether pollen grains capable of functioning ever result from those divisions where the chromosomes are irregularly distributed. The irregularities in reduction do not produce supernumerary pollen grains, such as have been described by Juel and Strasburger for *Hemerocallis,* for in all tetrads mature enough to show the separation of the pollen grains I have always counted four. One might expect an increase in number of pollen grains formed by one mother-cell, judging from the grosser manifestations of this abnormal factor. Functioning pollen is formed in quantity and no trouble at all is found in securing plenty of selfed seed of the abnormal strain.

Reduction phenomena in the ovule of the abnormal have so far been given only a superficial examination and the observations are not complete enough to report. Observations on the ripe capsules of selfed plants would lead one to believe that here, as in the case of the pollen, partial sterility is present, due to the abortive development of the ovules, but the latter is only a supposition, which further cytological study may or may not support.

Cytological examination of the anthers of the three classes of plants obtained from the abnormal × normal (304 × 402) was made. The conditions in the reduction divisions of the normal and homozygous abnormal segregates are identical with those present in the two grandparents. The heterozygote differs from the pure abnormal in degree only, having fewer sterile anthers and other abnormalities. Otherwise what has been said of the pure abnormal (300–309) applies also to the heterozygote.

In connection with this cross, it is interesting to note what bearing the nature of the reduction divisions in the ovule (300–309) might have upon the F_2 ratio. The abnormal class, although within the probable error, is always deficient. This is true also in the fasciated peas with which Mendel[27] worked and in one race of peas hav-

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[27] *Loc. cit.*

ing sterile anthers with which Bateson[28] experimented. While the number of plants has not been large in any of these cases, one wonders why it is always the abnormal (pure) class which is deficient. If the reduction phenomena in the ovules of the abnormal *Nicotiana* agree with the conditions present in the anthers, it seems not unreasonable to believe that there may be a relation between the mortality of the gametes carrying the factor for abnormalness and the deficiency in the ratio. Increased mortality of this class of gametes over the normal class would reduce the chances for combinations of the abnormal gametes, and as a consequence the normal and heterozygote combinations would be increased.

SUMMARY OF OBSERVATIONS

Concluding, one must bear in mind that the facts so far obtained seem to warrant the belief that some agent is at work on the internal structure as well as on the so-called external, and is of such a nature as to produce abnormalities in cell structure as well as in cell complexes or plant organs. The data, as a whole, raise a question as to the significance of chromosomes in inheritance.

Two strains of *Nicotiana tabacum* have been investigated, one being a sport from the other. The sport has been shown to differ from the normal in the possession of a unit character due to one Mendelian factor. When it is crossed with the normal, there results in F_2 a simple Mendelian ratio of 3:1 as regards normal and abnormal characters. The heterozygote is, with a little practise, distinguishable, making the ratio 1:2:1 with abnormalness partially dominant. The F_3 generation has proved these segregates to breed true. *Absolutely* clean normal segregates appear in F_2 and breed true. The abnormal character has been described in detail, and shown to affect practically all the structural parts of the plant individual, even to the germ cells. Both strains have the same chromosome number, 48 and 24, as a definite mode.

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[28] Bateson, W., and others, Reports to the Evol. Com., II, p. 91, 1905.

CHROMOSOMES IN RELATION TO MENDELIAN FACTORS AND A PHYSICAL BASIS OF INHERITANCE

Suppose we maintain the factor for the abnormal condition to be a particle of one chromosome. Gametes of the abnormal strain all contain the factor for abnormalness, as reciprocal crosses with the normal give the same results. In a cross a pollen grain of the abnormal strain unites with an egg of normal (402) parentage, and an intermediate is produced in F_1. The chromosome containing the factor for abnormalness is partly neutralized by pairing with a normal homologue. Gametes of two kinds are formed in approximately equal numbers in F_1, those containing the factor for abnormalness and those without it. But on a chromosome hypothesis, how are these gametes formed? There are two reduction divisions and 48 chromosomes, 24 of abnormal parentage and 24 of normal. According to current cytological investigation and interpretation, each chromosome separates from its homologue in its entirety during the first reduction division, so that, eventually, two kinds of gametes are formed as regards chromosomes. The factor for abnormalness or fasciation is in one chromosome, and chromosomes are believed to be in homologous pairs—one maternal with one paternal. The chromosomes of a homologous pair separate during the heterotypic anaphase, one going to each pole, it being contrary to current interpretation to believe that both members of a pair may go to the same pole. On this basis, according to the law of chance, approximately half the nuclei at the end of the heterotypic division will contain the chromosome carrying the factor for abnormalness and from half it will be absent.

Experimentally it has been shown that we have been dealing with only one pair of unit characters and that no complications are present. The various crosses have always given uniform results in F_1, even between species, and the fertile cross has given a close 1:2:1 ratio in F_2. Logically, then, one is led to believe that one out of the

24 chromosomes of abnormal parentage, and only one can contain the factor for abnormalness and produce the experimental results. If more than one contained it, the ratio in F_2 would be changed. For example, if it were present in two chromosomes, the ratio (as suggested by Emerson)[29] must be 15:1 or in this particular case where the heterozygote is distinguishable, 7:8:1. We might postulate its presence in all 24 chromosomes and believe, as Cannon[30] did, that parental chromosomes separate as a phalanx in the F_1 reduction division, each group going to one pole and thereby bringing about the formation of pure parental gametes. But the cytological investigations of Sutton, Rosenberg, Strasburger and others have brought to light evidence which precludes such a supposition. The experimental data from genetic researches are also opposed to this hypothesis, if one attempts to show a relation between the reduction division and Mendelian segregation. On a chromosome hypothesis, then, one *must* believe the factor for abnormalness to be present in only one chromosome out of the 48 concerned in the F_1 reduction phenomena, in order to be in agreement with the experimental results. This being the case, how is one to account for the abnormalities which occur during the reduction divisions in the anthers of the F_1 heterozygote? For they affect, not alone one chromosome, but all the nuclear and cell material concerned in the formation of the pollen grains. Can one postulate the influence of one chromosome to be so great, at times, as to bring destruction to its 23 associates of abnormal parentage, its 24 associates of normal parentage, as well as all the other organized contents of the mother-cell? Why, it may well be asked, if this destruction is the result of the activity of one chromosome does not it take place in the case of every anther and of every pollen mother-cell? Why should it affect only two or three

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[29] Emerson, R. A., "Genetic Correlation and Spurious Allelomorphism in Maize," 24th Ann. Rpt. Nebr. Agr. Exp. Sta., pp. 59–90, 1911.

[30] Cannon, W. A., "A Cytological Basis for the Mendelian Laws," *Bull. Torr. Bot. Club*, **29**: 657–661, 1902.

anthers in a flower containing 8 or 10? Not because it is absent from the other anthers, because the pollen from these anthers transmits the character. It is not a question of segregation then, but one of environment.

Evidently the gene is inactive or latent, for we know there is something present which for convenience we call a gene, and yet we can not see any of the visible signs of its presence, such as we see in the affected anthers. On a morphological conception it must be there; physiologically for the time being, so far as we can determine, it is non-existent. The inactivity we may suppose is due to a lack of a properly adjusted environment. This proper adjustment is only true of a few anthers in the F_1 plants. We believe this scarcity to be due to two kinds of latency —inactivity of the gene as in the pure abnormal and inactivity of the gene because of association with the cell materials that trace their lineage back to the sperm of the normal father. But latency is a vague term. In genetics, it is used to describe the period between the disappearance of a character and its reappearance. By pushing this conception to its logical conclusion it is clear that one can practically never prove the origin of a new character. Fasciation, while new to *Nicotiana,* is phylogenetically an old character. The production of purple fruits in *Rosa* would mean, phylogenetically, the reappearance of a latent character, for purple fruits are common to the *Amelanchiers* and to a species of *Pyrus.*[31]

The characters of the whole plant kingdom would be in a state of latency and patency, of inactivity and activity. To determine whether a character were new or not would involve a canvass of that part of the plant kingdom phylogenetically older than the family under investigation. Of course, we speak of segregation in phylogenetical lines, but the term has a different meaning in such cases. My F_2 normal segregates are pure and will breed true for absence of abnormalness, I believe, for any number of generations unless a new muta-

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[31] *Pyrus Niedwetzkyana.*

tion occurs. These recurrent mutations, Johannsen says, are rare in his experience, but they are admitted to occur in almost any long-continued pedigree line, and if fasciation should appear as a repeated mutation after 20 generations of plants involving 2,000,000 individuals had been grown, is one to infer that the gene was present all this time, but latent or inactive? Or is this a new gene produced by the same condition that brought about the original fasciation? Logically, if one defends the latency conception, he must believe that the original gene for fasciation was inactive in all these millions of plants, which in our present stage of knowledge is a ridiculous assumption, since the term is used to describe a somatic appearance. Applied to genetic problems in general, hopeless chaos would result. But on the supposition that a portion of a chromosome is responsible for the abnormality, it seems to me necessary to assume the chromosome to be capable of becoming active or latent without cause. For it seems probable that the anthers are all alike from a constitutional standpoint. How else can one account for the normal anthers and the abnormal ones, the normal pollen mother-cells and those affected by the abnormality?

The conception of latency is not necessary in the case of complete or incomplete dominance in F_1 hybrids, for in such cases there is evidence that a gene from one parent may be partially or completely inhibited in its expression by factors from the other parent, and this is probably what happens when we bring a line of chromosomes and cell materials from the normal (402) plants and associate them (by fertilization) with a line of cell materials from the abnormal (300–309).

While the phenomena of segregation described in the preceding pages may be capable of interpretation on a morphological basis, the gene for fasciation appears to me to lie deeper in sporogenesis than chromosomes. The abnormal character development appears most easily interpreted from a physiological standpoint. In

F_1 there is no break in the continuity of its manifestations between sporophyte and gametophyte, even though reduction and probably segregation have occurred. And should we not expect to see such a break if segregation by chromosomes took place in sporogenesis?

The evidence as a whole I think, warrants one in the suggestion that chromosomes are characters of the zygote and gametophyte, on the same footing in development with other plant characters. It is more difficult to comprehend this conception of these bodies, because they appear as characters in the development of the cell, rather than in the development of the larger unit, the individual organism. They are characters in the sense that they disappear and reappear at a place and time in the life history of the organism which we can predict. They can be transferred from one race of organisms to another provided fertile F_1 hybrids are possible. They are influenced in as definite a manner, by the underlying cause represented by the term factor for abnormalness, as are the zygotic expressions included in the word fasciation.

Concluding, I realize these speculations are largely negative in character, but they are in accord with a steadily growing skepticism among students of genetics as to the importance of chromosomes in inheritance, and their relation to segregating Mendelian characters. The impression has been distinctly gained from a study of this abnormal strain and its crosses with the normal that chromosomes are not the omnipotent creators of destiny, but characters on the same footing with other structures. The same dynamic forces, whatever they are, are changing and modifying these chromosome characters in the same capricious manner as those of a grosser nature. One would be inclined to ascribe these changes to an ultra-microscopic parasitic organism were it not for the experimental evidence in F_2, which precludes such a belief.

My warmest thanks are due Dr. E. M. East for suggestions and criticisms while engaged in this investigation.

July, 1912.

SHORTER ARTICLES AND DISCUSSION

HEREDITY IN A PARTHENOGENETIC INSECT (APHIS)[1]

STATEMENT OF PROBLEM

As is well known, Johanssen has found that in self-fertilizing strains of beans selection within the strain—selection in the "pure line"—does not change the mean of successive fraternities. If this conclusion holds generally we should expect it to hold among parthenogenetic species also. Among asexually reproducing animals Jennings (1909) finds that it is true for *Paramecium* and Hanel (1907) for *Hydra.*

Shull (1910) has found that strains of *Hydatina* from New York differ from a strain from Baltimore in the rate of production of males, and Whitney (1912) has found a similar difference in strains. For *Daphnia* (Woltereck, 1910) the persistence of the mode is less easily determined because of a high degree of variability depending on conditions.

Insects seemed to offer a new field for such studies, one in which we might expect external conditions to play a smaller rôle, and because of the well-known parthenogenesis of Aphids and their availability it was determined to test so far as it could be done in a few weeks of a summer, the suitability of plant lice for studies of this sort.

MATERIAL AND METHOD

After some experimenting it was decided to use *Aphis rumicis,* an aphid that commonly infests the poppies and nasturtiums about Cold Spring Harbor.

Potted poppies and nasturtiums were kept growing in the laboratory in large aquarium jars (about ½ meter high) covered with cheese cloth. Each plant was carefully inspected to make sure that there were no aphids upon it. Then one gravid female was placed on each plant and its movements and reproduction carefully watched. All young in these summer broods were produced parthenogenetically.

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[1] From The Biological Laboratory of the Brooklyn Institute of Arts and Sciences, Cold Spring Harbor, Long Island.

Brood No.	Mother				Offspring								
	Length		Ratio	Wings	1 12			2 13			3 14		
	3d Jt.	4th Jt.	3÷4		3d Jt.	4th Jt.	Ratio	3d Jt.	4th Jt.	Ratio	3d Jt.	4th Jt.	Ratio
1..	37	24	1.54	Absent	42	30	1.40	43	30	1.43	37	25	1.48
2..	37	23	1.61	Absent	42	29	1.45	45	26	1.73	46	30	1.53
					46	32	1.44	45	29	1.55	43	31	1.39
3..	—	—	—		38	25	1.52	38	26	1.46	37	26	1.42
4..	32	21	1.52	Absent	37	25	1.48	35	25	1.40	37	26	1.42
					39	29.5	1.32	39	29	1.34	41	30	1.37
5..	—	—	—		42	27	1.56	39	27	1.44	41	26	1.58
					41	24	1.71	41	27	1.52	39	29.5	1.53
5*a*.	35	24	1.46	Absent	29	19	1.53	28	18.5	1.51	26	17.5	1.49
					33	23.5	1.40	28.5	18.5	1.54			
5*b*.	33	27	1.22	Present	33.5	22.5	1.49	29	21	1.38	30	19	1.58
5*c*.	35	26.5	1.32	Present	24	15.5	1.55	23.5	15	1.57	28	16.5	1.70
6..	30	20	1.50	Absent	39	24	1.63	37	25	1.48	39	24	1.63
					34.5	24	1.44	37	26	1.42	32	22.5	1.42

Brood No.	Mother				Offspring								
	Length		Ratio	Wings	7 18			8 19			9 20		
	3d Jt.	4th Jt.	3÷4		3d Jt.	4th Jt.	Ratio	3d Jt.	4th Jt.	Ratio	3d Jt.	4th Jt.	Ratio
1..	37	24	1.54	Absent	41	27.5	1.49	37.5	27	1.39	38	22.5	1.69
2..	37	23	1.61	Absent	43	28.5	1.51	44	32	1.38	44	30.5	1.44
3..	—	—	—		35	24.5	1.43	33	23	1.43	36	26	1.38
4..	32	21	1.52	Absent	38	26	1.46	38	29	1.31	37	26	1.42
					35	25.5	1.37	35	24.5	1.43			
5..	—	—	—		40	27	1.48	39	25	1.56	36	25	1.44
					39	25	1.56						
5*a*.	35	24	1.46	Absent	27	18	1.50	29.3	19.5	1.50	30.5	20.5	1.49
5*b*.	33	27	1.22	Present	36	24	1.50	28	21.5	1.30	30	19	1.58
5*c*.	35	26.5	1.32	Present	26	16.5	1.58	27	17	1.59			
6..	30	20	1.50	Absent	31	22	1.41	36	27	1.33	35.5	26	1.37
					37	25	1.48	35.5	23	1.54	35	23	1.52

Offspring										
	4 15			5 16			6 17			
3d Jt.	4th Jt.	Ratio	3d Jt.	4th Jt.	Ratio	3d Jt.	4th Jt.	Ratio	Wings of These Offspring	Host Plant
41	24	1.71	41	27	1.52	40	25	1.60	Present	Shirley poppy (grew poorly)
43	30	1.43	44	29	1.52	44	30	1.47	Present	Opium poppy
44.5	33.5	1.33	42	29	1.45				(Winged)	
37	24	1.54	36	25.5	1.41	34	23	1.48	Absent (Wingless)	Shirley poppy
42	27	1.56	36	28	1.29	40	29	1.38	Absent	Nasturtium
40.5	29.5	1.37	36	26.5	1.36	36	26	1.38	(Wingless)	
45.5	28	1.63	40	27	1.48	39	26	1.50	Absent	Opium poppy
36	25	1.44	35	26	1.35	36	22.5	1.60	(Wingless)	
27	19	1.42	32	20	1.60	27.5	20	1.38	Absent (Wingless)	Opium poppy
20	16	1.25	31.5	20	1.58	32	23	1.39	Absent	Opium poppy
34.5	21	1.64	33.5	20	1.68	25	16	1.56	Absent	Opium poppy
35	23	1.52	36	24	1.50	36	25	1.44	Present	Opium poppy
35	22	1.59	37	24	1.54	38	26	1.46	(Winged)	

Offspring								
	10 21			11 22				
3d Jt.	4th Jt.	Ratio	3d Jt.	4th Jt.	Ratio		Wings of These Offspring	Host Plant
42	25	1.68					Present	Shirley poppy (grew poorly)
42.5	31	1.37	42.5	31	1.37		Present	Opium poppy
							Absent	Shirley poppy
38	27	1.41	39	30	1.30		Absent	Nasturtium
41	25	1.64	41	28	1.46		Absent	Opium poppy
29	18.5	1.57	28.5	20	1.43		Absent	Opium poppy
32.3	21.5	1.50	36	22	1.64		Absent	Opium poppy
							Absent	Opium poppy
35.5	22.5	1.58	36	23.5	1.53		Present	Opium poppy
36.5	22.5	1.62	36	24	1.50			

The characteristic whose inheritance it was finally decided to study was the ratio of the third antennal joint to the fourth antennal joint. This ratio offered the advantage of a fairly large range, *i. e.,* from 1.25 to 1.75; and the mode of a fraternity was soon observed to vary from about 1.35 to 1.55.

The measurements were made upon the mother at the same time with the offspring. The offspring were measured when it was obvious that they were mature and soon to breed. The insects were first etherized and the measurements were then made with a micrometer eyepiece, with a magnification such that the third antennal joint averaged about 32 units.

RESULTS

The following table gives the numerical data derived from the measurements made:

The ratios that are derived from measurements of the offspring are grouped into classes, and the frequency of the classes shown graphically in Figs. 1–7.

First, it appears that all aphids fall into two classes, winged and wingless. While the winged mothers had a smaller antennal ratio than the wingless mothers, the antennal ratio shows practically no difference in the winged and wingless *offspring.* Thus 10-winged offspring of a wingless mother give an average antennal index of 1.54, and 5 wingless offspring of the same mother give an average antennal index of 1.48. From a wingless mother with antennal index of 1.46 were derived 13 *wingless* offspring with an average index of 1.49, while from another wingless mother with antennal index of 1.50 were derived 22 *winged* offspring with an antennal index of 1.49. We may compare the antennal indices of the two lots of offspring whether they happen to be winged or not.

The nature of the food plant may be, on the other hand, of importance for the antennal index. Thus of two mothers with practically the same antennal index, one was fed on opium and the other on nasturtium. The progeny of the first finds its mode at 1.50 to 1.59; of the second at 1.30–1.39. It was not possible to determine from comparative studies whether there is uniformly a reduction of the index in the offspring of nasturtium-fed mothers, or whether this result was due to the fact that the nasturtium-fed mothers belonged to a special strain with a low index. In our ignorance it is clearly permissible to compare only offspring from similarly fed mothers. All data considered below are from offspring of opium-fed mothers.

To decide whether or not we have "pure lines" in *Aphis* it is necessary to breed two generations of offspring; it is better to breed more. It is necessary to breed two lines through these generations; it is better to breed three or more. The results so far obtained are inadequate since they continue only one line through two generations of offspring. The data obtained are as follows:

FIG. 1.
5
Opium poppy

FIG. 2.
5a
Opium
Mother, 1.46.

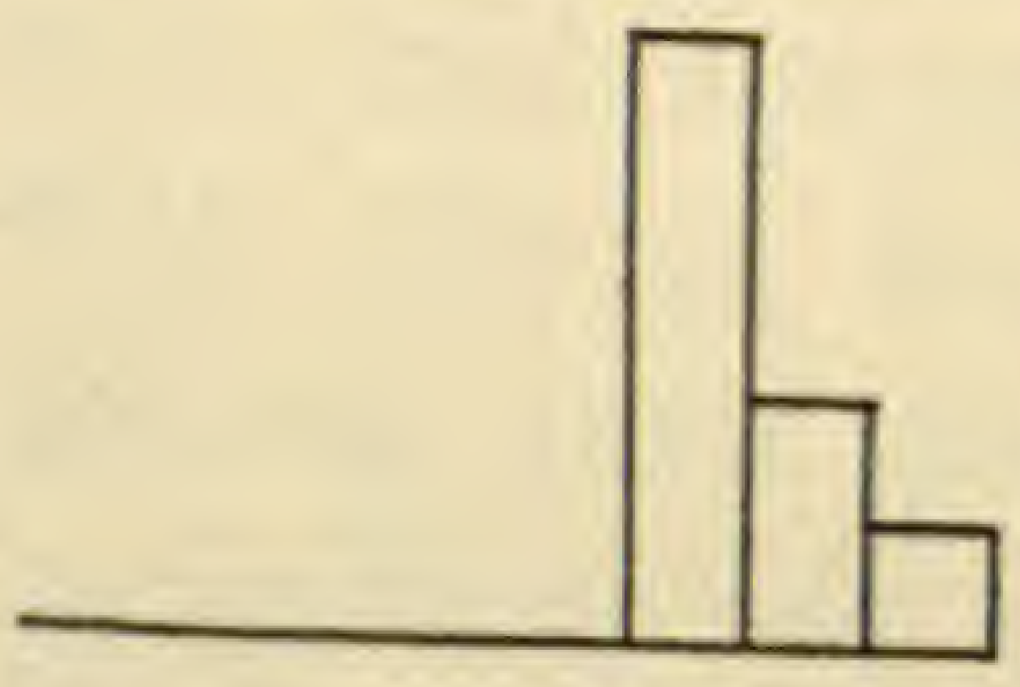
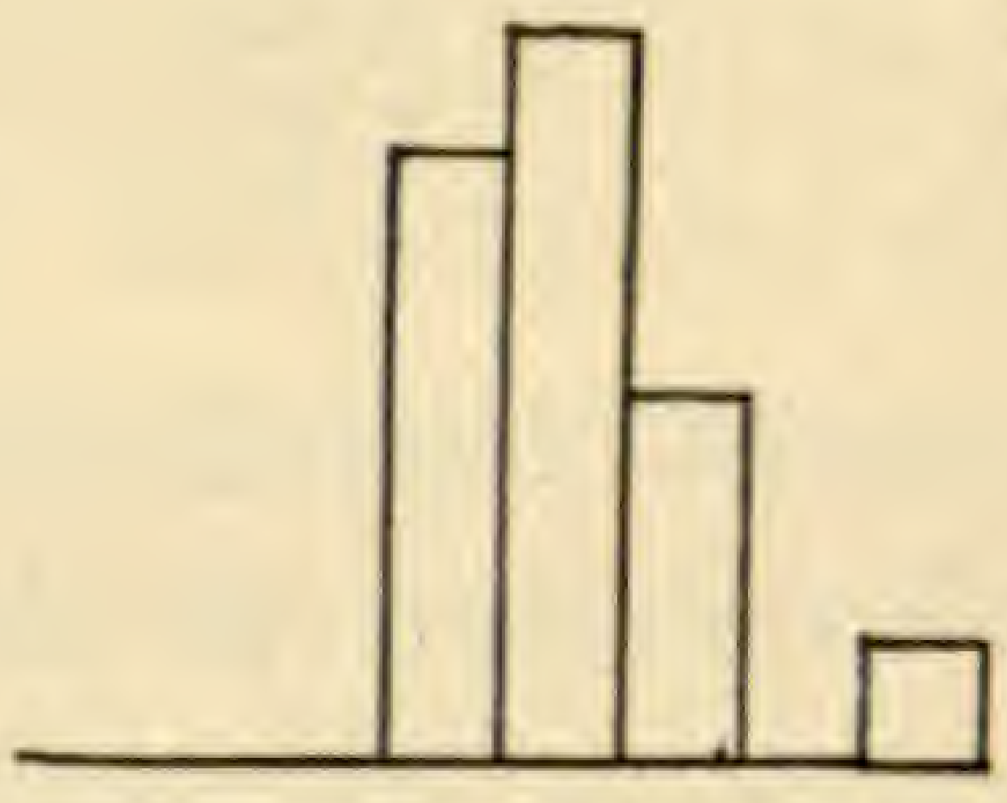


FIG. 3.
5c
Mother, 1.32.
Opium

FIG. 4.
5b
Opium



Mother, 1.22.
FIG. 5.
2
Opium
Mother, 1.61

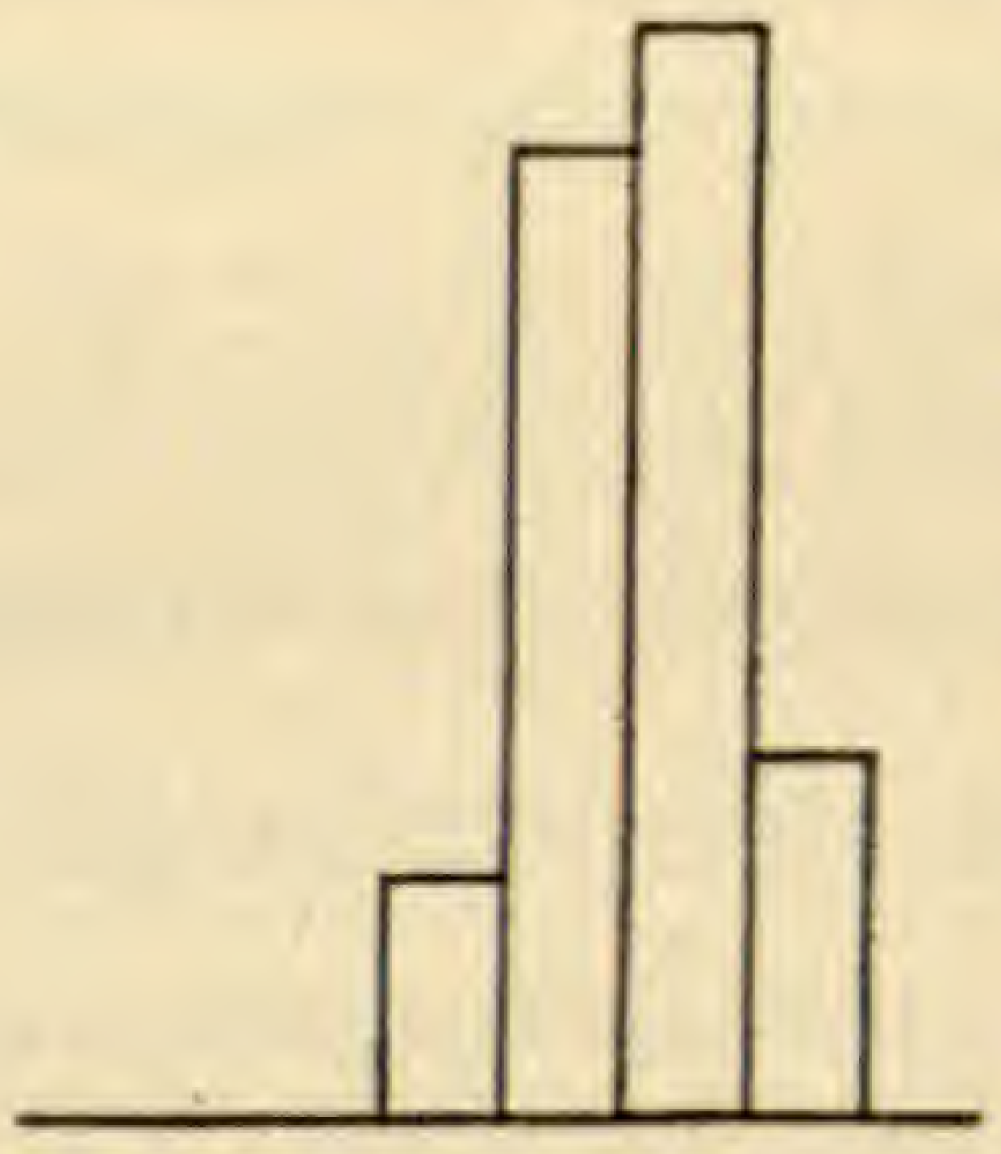


FIG. 6.
6
Opium
Mother, 1.50

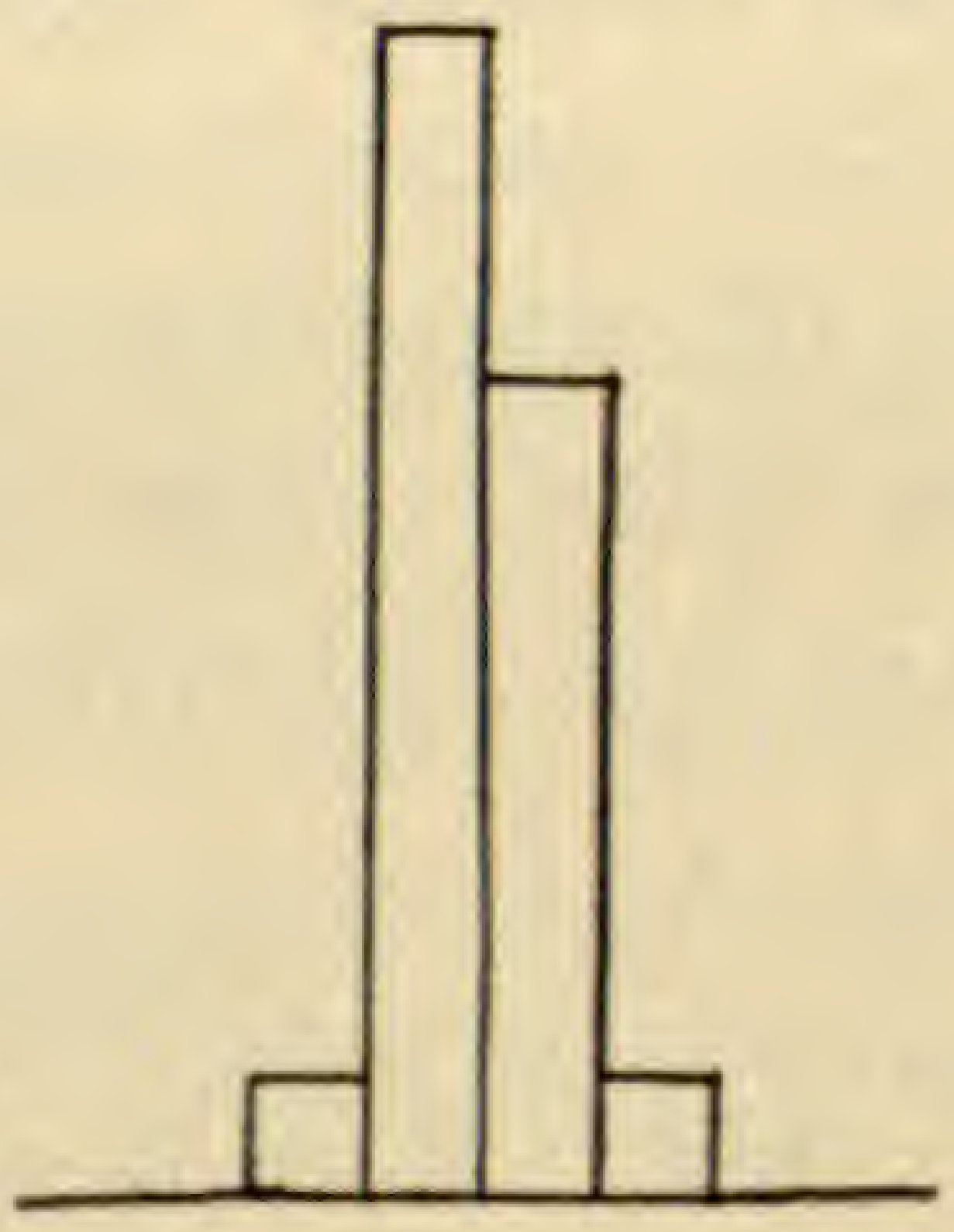


FIG. 7.
4
Nasturtium
Mother, 1.52

A wingless mother, whose antennal index was not obtained, was fed on opium poppy and produced 18 offspring. The distribution of the antennal ratios of these offspring is as given in Fig. 1. The mode is at 1.50–1.59, the average is 1.53. From this fraternity three individuals were now selected as mothers of the next. We may call them *5a*, *5b* and *5c* (Figs. 4, 5, 6). *5a* has the highest antennal ratio, 1.46. The mode of the progeny is at 1.55 (1.50–1.59) and the average ratio is 1.49. 5c has the next lowest ratio, 1.32. Her progeny also have the mode at 1.50–1.59. The third mother (*5b*) has a ratio of 1.22. The progeny is few in numbers and has two modes of which the major is at 1.50–1.59 like the two others; and the average is 1.47.

The foregoing series of facts may be tabulated as in Table *A*.

TABLE *A*

Family	Maternal Ratio	Offspring	
		Mode	Mean
5a	1.46	1.50–1.59	1.49
5c	1.32	1.50–1.59	1.61
5b	1.22	1.50–1.59	1.47

The table shows clearly that while the range in the maternal ratio is .24, the range in the means is only .14 and that there is no close relation between the order of the maternal ratios and the order of the fraternal means. In all the fraternities the mode stands in the 1.50–1.59 class.

CONCLUSIONS

In so far as this series goes, then, it speaks for the conclusion that, in the parthenogenetic *Aphis rumicis*, the progeny does not inherit the somatic idiosyncrasies of the parent but does inherit from the underlying germ plasm common to all; and hence progeny of somatically quite different sisters tend, on the average, to be alike. The somatic differences in the parthenogenetic line are not inherited.

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THE HIMALAYAN RABBIT CASE, WITH SOME CONSIDERATIONS ON MULTIPLE ALLELOMORPHS

IT has been shown by Castle ('06, '09), Hurst ('06) and Punnett ('12) that the Himalayan pattern in rabbits behaves as a simple recessive to self color, and as a simple dominant to albino. Thus, as Punnett points out, we might suppose self to be the double dominant, Himalayan a recessive in one factor, and albino a double recessive. But, to use Punnett's words:

The F_2 from self × albino should consequently contain Himalayans as well as true albinos. But among the large number of animals reared from such matings no Himalayans have hitherto been recorded, and for the present the relations between these various forms remain obscure.

If we suppose that albino may be either the second single recessive or the double recessive we avoid this difficulty, but are then unable to explain why albino × Himalayan should not, at least occasionally, produce selfs by recombination.

Now it seems to me that the facts of the case are fitted equally well by either of two hypotheses. In the first place, we may consider, as above, that Himalayan is a single recessive and albino a double recessive—if we suppose the two factors concerned to be completely linked. The gametic (not zygotic) constitution of the three types would then be represented thus; C being the color producer and S the factor changing Himalayan to self.

Self — CS
Himalayan — Cs
Albino — cs

If C and S be completely linked no cS individual can be obtained, and $CS \times cs$ would give no Cs in F_2.

On the other hand, we may consider the factor for self as allelomorphic to that for Himalayan pattern, and also to that for albinism. Then the three pure types might be represented thus (zygotic formulæ):

Self — SS
Himalayan — HH
Albino — AA

S, H, and A being allelomorphic each to itself or to either of the others, the crosses would result thus:

Self — SS
Himalayan — HH

F_1 SH — self

$$F_2 \left\{\begin{array}{l} \left.\begin{array}{l} SS \\ SH \\ SH \end{array}\right\} 3 \text{ self} \\ HH - 1 \text{ Himalayan} \end{array}\right.$$

Self — SS
Albino — AA

F_1 SA — self

$$F_2 \left\{\begin{array}{l} \left.\begin{array}{l} SS \\ SA \\ SA \end{array}\right\} 3 \text{ self} \\ AA - 1 \text{ albino} \end{array}\right.$$

$$\begin{array}{ll} \multicolumn{2}{l}{\text{Himalayan} \text{ — } HH} \\ \multicolumn{2}{l}{\text{Albino} \quad \text{ — } AA} \\ \hline F_1 & HA \text{ — Himalayan} \\ \hline F_2 & \left\{\begin{array}{l} \left.\begin{array}{l} HH \\ HA \\ HA \end{array}\right\} 3 \text{ Himalayan} \\ AA \text{ — } 1 \text{ albino} \end{array}\right. \end{array}$$

An explanation similar to the second one above has been given by de Meijere ('10) for Jacobson's results with *Papilio Memnon.* The evidence on this case is, however, very incomplete, and there are complications due to sex. Either triple allelomorphs or complete coupling would seem to cover the facts as we have them at present. Shull ('11) has also used a system of three allelomorphs for a case in *Lychnis dioica.* I shall refer to this case again.

It will be seen that triple allelomorphs may be substituted for complete coupling as an explanation of any case where only three of the four combinations possible on the complete coupling scheme are known. But if we have the double dominant, both single recessives, and the double recessive, then triple allelomorphism will no longer work. Thus, if a race of albino rabbits is discovered which produces self when mated to Himalayan, complete linkage will be the most likely explanation of the case.

There are certain other cases which fulfil the above requirements. Emerson ('11) has reported a case in beans (green leaves—green pods, green leaves—yellow pods, and yellow leaves—yellow pods are the three races concerned). The similar cases of complete linkage reported for corn by East and by Emerson are probably more easily explainable by linkage than by multiple allelomorphs, as, at least in some cases, all four possible races are found. Baur ('12) has a case in *Aquilegia,* where three types of leaves are found—green, variegated (green and yellowish green), and yellowish green. These behave toward each other in a manner exactly similar to that of the self, Himalayan and albino rabbits. Finally, Morgan ('12) has reported a case in *Drosophila ampelophila.* Red eye is a dominant to eosin and to white, and eosin is also a dominant to white. No two types ever give the third when crossed, either in F_1 or in F_2. The explanation which has been given in beans, columbines and flies has been that of two allelomorphic pairs, completely linked to each other.

The question as to which of these views is the more probable is closely bound up with the presence and absence hypothesis. On a strict application of this idea there is of course no possibility of more than two members of any given allelomorphic group. The presence and absence hypothesis as a universal principle has been criticized by Morgan ('13) in a recent paper, on what seem to me very strong grounds. It seems very unlikely that protoplasm (chromatin?) is such a simple substance that the only possible change in a given unit (molecule?) involves the loss of that unit. On the other hand, if a slight change takes place in a chemically complex gene, is it necessary to suppose that its allelomorphic relations must be upset? That very slight changes in the constitution of a gene might easily affect its behavior in ontogeny will, I think, be readily granted.

It is to be noted that in all the cases cited above the supposed three allelomorphs have similar ontogenetic effects. Thus the three in rabbits, in *Aquilegia*, and in *Papilio* all affect the distribution of pigment (and, in *Papilio*, also the shape of the wings), those in *Lychnis* the sex, those in beans the production of the same color in different organs, and those in *Drosophila* the production of different colors in the same organ. This may perhaps seem to be in favor of the view that we have here different modifications of the same gene, rather than two distinct genes and their absences.

The history of the red-white-eosin group of eye colors in *Drosophila* is interesting when considered from the viewpoint of the presence and absence hypothesis. The first white-eyed fly arose as a mutant in red stock. On presence and absence it must have been caused by the simultaneous loss of two factors, which were called *C* and *O* by Morgan. Then, in white-eyed stock there appeared an eosin-eyed fly. Here the factor called *O*, just lost, must have been put back again. Finally, in one of my own cultures, eosin has given rise to white by mutation.[1] In both these latter cases the flies had miniature wings, and in the white-to-eosin case they also had black body color. These characters give a check on the results, and make it extremely unlikely that any contamination had occurred. Further evidence to this effect is

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[1] After this paper went to press it was pointed out to me by Mr. H. J. Muller that there is another possible explanation of this case, which does not involve mutation from eosin to white. This interpretation can not be entered into until certain phenomena observed by Mr. C. B. Bridges have been more fully investigated.

given, in the eosin-to-white case, by the fact that the mutant fly was one of 127 obtained from a single pair, all of her brothers and sisters being of the expected classes (half of the females heterozygous for white), as were likewise the flies from six sister pairs.[2]

The presence and absence hypothesis involving a dropping out of whole genes or addition of entirely new ones does not offer as simple an explanation of this case as does the conception that we have here a relatively unstable gene, which does not drop out entirely, but undergoes various changes, that from white to eosin being reversible.

It should be noted that Shull ('11) has reported a case of what he calls reversible mutation in the sex-determining factor in *Lychnis*, which is very similar to the above red-eosin-white case. He has adopted a system of triple allelomorphs to explain it, though admitting that complete linkage will also cover the facts. He has also considered the bearing of the case upon the presence and absence hypothesis and upon the nature of mutation, reaching conclusions somewhat similar to those given above.

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January, 1913

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[2] There has been at least one case where eosin has seemed to arise as a mutant in red stock, but as there was no other character to serve as a check against contamination, the case does not carry very great weight.

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MENDELISM AND INTERSPECIFIC HYBRIDS

The complications of modern Mendelism have greatly increased the difficulty of discussing the practical applications of heredity. The word Mendelism itself has two essentially different meanings that are being used indiscriminately. A particular form of alternative inheritance is called Mendelism and the same name is applied to a general theory of heredity. It is true that the Mendelian theory was suggested by the Mendelian form of inheritance, but the facts are also capable of other interpretations. Many of the proposed applications of Mendelism to breeding and eugenics are in reality only inferences from the theory and are not in real accord with the facts on which they are supposed to be based.

An example of such a discrepancy may be found in the American Naturalist for July, 1912, in a paper entitled: "Evidence of Alternative Inheritance in the F_2 Generation from Crosses of *Bos indicus* on *Bos taurus.*" Though readers are evidently expected to believe that the hybrids are showing a typical Mendelian inheritance of the contrasted parental characters, the facts stated in the paper show that the behavior of the hybrids is not in accord with the Mendelian theory of heredity. Alternative inheritance is manifested in these bovine hybrids, but it is not the Mendelian form of alternative inheritance, with the contrasted parental characters behaving as independent units combined by the laws of chance. Instead of showing a Mendelian freedom of combination of the contrasted characters, these hybrids afford a much better illustration of a different principle of heredity, the coherence of characters derived from the same parental stock.

As the paper by Dr. Nabours seems to represent the only attempt that has been made to give a scientific account of a unique series of hybrids, it would be very undesirable to have the general conclusion regarding the application of Mendelism accepted without challenge. In addition to the scientific questions involved, the importance of finding the best way of securing a full utilization of the tick-resistant Brahma cattle in Texas will appeal to all who have had the pleasure of seeing Mr. Borden's imported animals and their hybrid offspring. But practical recommendations are hardly in order until the facts are better understood. To view these hybrids as a typical case of Mendelism is to overlook some of the distinctions which need to be recognized before correct applications can be expected.

ALTERNATIVE INHERITANCE

It seems to be taken for granted by Dr. Nabours, as by many other recent writers, that all forms of alternative inheritance represent the so-called Mendelian principle of heredity, that is, the alternative transmission of unit-characters in pure germ-cells. In reality the facts of alternative inheritance extend far beyond the field of Mendelism into regions where the Mendelian conception of alternative transmission can not be applied.[1]

The old assumption regarding hybrids and mixed races was that they represented intermediate combinations or averages between the contrasted characters of the parental stocks. A generation ago belief in "the swamping effects of intercrossing" was even more general among biologists than acceptance of Mendelism is now. But we have learned that the "swamping effects" were largely imaginary. The scientific world has its history of easily forgotten fads, no less than the world of politics or fashion.

The usual result of crossing is not the formation of an intermediate average, but the reappearance of the parental characters in the later generations of the hybrids, if not in the first. Recognition of the principle of alternative inheritance is having a revolutionary effect upon the science of heredity. The facts of Mendelism are of special interest because they represent extreme cases of alternative inheritance, but the interest is in no way dependent upon the Mendelian theory of heredity. Indeed, the theory often interferes with appreciation of the facts.

MENDELISM A THEORY OF ALTERNATIVE TRANSMISSION

Mendelism, as a theory of heredity, is an assumption that alternative inheritance is due to alternative transmission of independent particles or "units," which are supposed to represent the characters in the protoplasm at the time when the germ-cells are formed. If sufficient magnification could be applied, so that the structure of the protoplasm in the germ-cells could be fully

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[1] Cook, O. F., "Dimorphic Leaves of Cotton and Allied Plants in Relation to Heredity," Bulletin 221, Bureau of Plant Industry, U. S. Department of Agriculture, pp. 36–50.

shown, believers in the Mendelian theory would expect to find separate "gens" or discrete particles of some sort to represent the various characters of the adult animals or plants. The gens that represent the characters of different parents are supposed to remain entirely distinct and to find their ways into different germ-cells. Each germ-cell of a hybrid is supposed to receive only a single set of these hypothetical character-units or gens, representing the contrasted characters of the parents, and the sets are supposed to be made up by chance assortment. Thus the different germ-cells produced by a hybrid are supposed to represent all the combinations of the contrasted parental characters that are theoretically possible under the laws of chance.

The theory of Mendelism has greatly stimulated the study of cytology, in the hope of finding the supposed character-germs as actual, visible particles in the protoplasm. Some writers have argued that the chromosomes or chromomeres represent the characters, or at least the contrasted Mendelian characters, and have attempted to trace a definite relation between the behavior of the chromosomes and the inheritance of the characters. Other writers do not indulge in such speculations, but believe in alternative transmission for mathematical reasons. Typical cases of Mendelism are relied upon as affording sufficient proof of the theory of alternative transmission. The Mendelian theory accords with the numerical facts of Mendelism, but this is not a sufficient proof of its correctness, for it is not the only interpretation that the facts will admit. Elaborate Mendelian computations create in the casual reader an impression of mathematical certainty, but the same computations could be made under other theories of alternative inheritance.

ALTERNATIVE INHERITANCE AND NORMAL DIVERSITY

The facts of alternative inheritance are not at all confined to cases where the characters show the exact numerical proportions typical of Mendelism. Alternative inheritance is a general law that applies even in the vast and highly diversified groups of interbreeding individuals that constitute natural species. The typical Mendelian cases usually appear as results of previous artificial breeding of pure strains.[2]

The normal diversity (heterism) everywhere manifested among

[2] Cook, O. F., "Pure Strains as Artifacts of Breeding," THE AMERICAN NATURALIST, 43: 241, April, 1909.

the members of natural species is a result of alternative inheritance of contrasted parental characters, no less than the typical cases of Mendelism. If inheritance were not alternative, heterism would not be maintained. Each species or separate group of interbreeding individuals would gradually decline into a general uniform average. Under conditions of normal interbreeding among the representatives of different lines of descent there is no such tendency to uniformity. The offspring of the same parents differ normally among themselves in the same ways that the parents and ancestors have differed. Though each individual can bring into expression only one set of differences, other ancestral characters are likely to reappear in later generations. It is only by special methods of breeding in single or narrow lines of descent that conditions of uniform heredity can be established.

ALTERNATIVE EXPRESSION INSTEAD OF ALTERNATIVE TRANSMISSION

That characters are transmitted without being brought into expression is one of the best known facts of heredity, for which the theory of Mendelism makes no adequate provision. The idea of alternative expression of characters accommodates the numerical data of Mendelism as well as the idea of alternative transmission, and is in far better accord with other facts of variation. Diversity in natural species, and reversions that arise in select varieties and in hybrid stocks, afford adequate evidence for holding that alternative inheritance is due, not to alternative transmission of characters, but to alternative expression. When the facts of alternative expression are taken into account the theory of alternative transmission becomes unnecessary.[3]

COHERENCE OF CHARACTERS IN INTERSPECIFIC HYBRIDS

The contrasted characters of interspecific hybrids do not behave as independent Mendelian units, but tend to remain more or less united with others derived from the same parental stock. This coherence of expression often interferes with the formation of the combinations of characters according to the Mendelian theory of independent segregation of discrete units.[4]

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[3] Cook, O. F., "Transmission Inheritance Distinct from Expression Inheritance," *Science*, N. S., 25: 911, 1907.

[4] Examples of coherence of characters in cotton hybrids have been de-

Mendelian reactions are likely to be obtained when defective mutations, such as cluster cottons or hornless breeds of cattle, are crossed with normal varieties, but not when normal representatives of two species are crossed, like the Upland and Egyptian cotton or the cow and the zebu. Though there can be no question of the purity of the parental stocks with reference to many contrasted characters, interspecific hybrids seldom show the typical Mendelian behavior.

NON-MENDELIAN BEHAVIOR OF THE BOVINE HYBRIDS

The facts stated by Dr. Nabours regarding the bovine hybrids do not show that the behavior of the characters is essentially Mendelian. Even if the parental breeds were segregated in the same proportions as in simple Mendelian hybrids, the result would still be essentially non-Mendelian, for the parental types differ by many sharply contrasted characters. Such a segregation of "pure Brahma and pure Durham" would mean that there had been a complete coherence of all of the characters of the two parental stocks, instead of a Mendelian segregation and recombination of independent units. The actual facts appear to lie somewhere between complete coherence and complete segregation.

If the Mendelian conceptions of heredity applied to these bovine hybrids, the segregation of "pure Brahma and pure Durham," instead of appearing to be the rule, would occur only in extremely rare cases, because of the numerous differences of the parental types. Indeed, my own impression on this point is somewhat more Mendelian than the account given by Dr. Nabours. Though it was noticed that several individuals of the second generation were distinctly more Brahma-like and more Durham-like than any of the first generation, there were only two or three that suggested the idea of complete segregation of the parental types. The fact that impressed me was not that so much segregation of the contrasted parental characters had taken place in the second generation, but so little. The various colors and textures of hair and skin, the horns, humps and dewlaps were generally brought into coordinated, harmonious expression,

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scribed in several publications of the Bureau of Plant Industry, U. S. Department of Agriculture. Bull. 147, "Suppressed and Intensified Characters in Cotton Hybrids"; Bull. 156, "A Study of Diversity in Egyptian Cotton," and Cir. 66, "Cotton Selection on the Farm by the Characters of the Stalks, Leaves and Bolls."

instead of behaving as separate "units" combined by indiscriminate alternative transmission. Even the more complete reversions to the parental types may be considered as results of non-Mendelian coherence of characters in expression, rather than as examples of Mendelian segregation and recombination of independent "units."[5]

COMPARISON OF BOVINE HYBRIDS WITH COTTON HYBRIDS

The practical question to be determined is whether the Durham-like and Brahma-like individuals of the second and later generations are equal to the original parental varieties, and whether the intermediate individuals maintain the average of the first generation. In the second generation of interspecific cotton hybrids it is usual to find many degenerate plants with an obvious resemblance to one or the other of the parental stocks, though usually abnormal and inferior. But among the cattle the second generation hybrids seemed much less different from the first generation, both in constitution and in external features. No general tendency to inferiority in the second generation, as compared with the first, either in vigor or in resistance to ticks, had been detected by Mr. Borden. But the experiments have not continued long enough to afford adequate evidence on this point.

If the analogy of cotton should be found to apply with the bovine hybrids the Brahma-like and Durham-like animals that appear in the second and later generations will not prove to be equal to the Brahmas and Durhams that have not been hybridized, nor will the intermediate individuals show as high an average as the first generation. One of the usual results of crossing, even among varieties of the same species, is to destroy the effects of previous selection in establishing a uniform expression of the characters of the parent varieties. The fact that many of the second generation of Brahma hybrids are magnificent animals does not prove that equally superior hybrid varieties can be established. To increase the pure stock of Brahma cattle, and thus increase the possibilities of producing first generation hy-

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[5] In a more recent paper Dr. Nabours has recognized the divergence from typical Mendelism, in the following statement: "As a matter of fact, observations made this summer and to be described later, indicate that the segregation is not so simple as it at first appeared to be." See, "Possibilities of a New Breed of Cattle for the South", in American Breeders Magazine, **4**: 45, March, 1913.

brids, may be more important than the breeding of hybrid varieties. At least this is the suggestion to be drawn from the failure of many attempts to develop superior useful varieties of cotton and other seed-propagated plants from interspecific hybrids. As a barrier to a permanent union of two species degeneration in the second or later generations of a hybrid stock may be as effective as sterility in the first generation. It may prove very fortunate that Mr. Borden has imported Brahma cows as well as bulls, for this may make it possible to perpetuate the Indian breeds in Texas.

A tendency to deterioration in the later generations of hybrids is likely to be masked as long as hybrids are crossed back on one of the parental stocks, instead of being bred with each other. This is because even dilute hybrids share some of the stimulation effect shown in the first generation. But these questions of vigor and fertility, though of fundamental importance in practical breeding, lie outside of the range of the Mendelian theory. Vigor and fertility are phenomena of expression in the first generation, whereas the theory of Mendelism relates to the transmission of characters to the second and later generations. Mendelism has served a useful purpose in opening the way to a better understanding of the various forms of alternative inheritance, but the overshadowing Mendelian theory of heredity as a process of alternative transmission of character-unit particles needs to be cleared away.

This theory that alternative inheritance is due to alternative transmission does not lead to more correct ideas of the nature of heredity or to better methods of breeding. Instead of providing us with a simple method of making any desired combination of characters of different species, as writers on Mendelism have led the public to believe, the facts of alternative inheritance indicate that it is very difficult, if not altogether impossible, to secure permanent combinations of characters of different species. In plants that can be propagated from cuttings, hybrid combinations can be maintained, but this affords no assurance regarding types that are limited to sexual reproduction.

O. F. Cook

Bureau of Plant Industry,
U. S. Department of Agriculture,
December 27, 1912

ORDOVICIAN (?) FISH REMAINS IN COLORADO

DURING the past year Mr. P. G. Worcester, of the Colorado Geological Survey, has been investigating certain strata near Ohio City, Colorado, supposed to be of Ordovician age. The particular horizon under discussion contains *Receptaculites oweni* Hall (southeast of Fairview Mt.), *Halysites catenulatus* (L.) (basin east of north end of Fossil Ridge), *Platystrophia* (?) sp. (Fossil Ridge), and *Heliolites* (?) sp. with *Halysites catenulatus* at head of Alder Creek, west of Fossil Ridge. The *Heliolites* (?) is the same as that in the Cañon City Ordovician. These fossils were identified by Professor J. Henderson, and so far as it is possible to determine from them, the rocks should certainly be Ordovician. The first Devonian fossils were found about 100 feet above this horizon.

However, closely associated with the invertebrates cited, and certainly of the same age, are rather numerous fragmentary remains of fishes. These may be briefly described as follows:

1. A fragment of a plate exhibiting fine grooves with deep pits; resembling, so far as it goes, the plate of *Coccosteus disjectus* from the Old Red Sandstone, figured by A. S. Woodward, Cat. Fossil Fishes Brit. Mus., Part II, pl. VIII, fig. 1. The structure is also nearly identical with that of *Astraspis desiderata*, from the Ordovician of Cañon City, as figured by Walcott, Bull. Geol. Soc. Amer., Vol. 3 (1891), pl. 3, f. 7. Some of the other figures of *Astraspis* might well belong to Coccostean fishes.

2. A large fragment, having a diameter of over 30 mm., is covered with irregular obtuse vermiform ridges, and is *exactly* like the opercular plate of *Rhizodus ornatus* (Woodward, t. c., pl. xii, f. 5). so far as the sculpture goes. This particular species is lower Carboniferous, but Rhizodontid fishes also occur in the Devonian.

3. Numerous fragments of striated spines, some short, conical and straight; others more slender and curved. These appear to exactly correspond, so far as they go, with the spines of *Diplacanthus*, from the lower Old Red Sandstone. One of the supposedly Coccosteoid plates, 5 mm. thick, with the surface finely striate, with punctate more or less branching striæ or grooves, occurs in the same piece of rock as a supposed *Diplacanthus* spine, the two almost touching.

According to the available evidence, we seem therefore to have three families of fishes represented: (1) Coccosteidæ; (2) Rhizodontidæ; (3) Diplacanthidæ. The genera and species can not be precisely determined.

These fish remains, taken by themselves, would certainly be regarded as Devonian. Walcott's Ordovician species from Cañon City were said by Professor James Hall to have such a Devonian facies that he would certainly have referred them to the Devonian, but for the accompanying invertebrate fauna.

In general, when there is a conflict between the evidence from vertebrate and invertebrate fossils, the vertebrates must be allowed the most weight; but it is evident that the numerous and varied Devonian fishes had ancestors, so it is to be expected that types more or less like those of the Devonian will be found in older rocks. I understand from Mr. Worcester that there is no reason to believe that the Silurian is represented in the locality.

Schuchert ("Paleogeography of North America") remarks that in the Ordovicic or Ordovician, during the retreat of the sea,

> The first evidence of those peculiar heavily armored fishes belonging to the ostracoderms appears in cleanly washed beach sands and less abundantly in dolomites at three widely separated places in Colorado and Wyoming. They are now all fragmentary and seem to have been washed into the sea by the rivers. From this can it be inferred that during some earlier inundation the marine ancestors of these fishes were retained upon the land in relict seas, and under the stress of evanescent waters became modified into the armored double-breathing animals that gave rise later to the true fishes? Such being the interpretation, the marine fishes must then have been derived from land [freshwater] fishes, as suggested by Chamberlin and Salisbury.

The two localities in addition to the famous one at Cañon City are (Dr. Eastman in litt.) in the Big Horn Mts., and in the Black Hills uplift, in a bed lying above the Deadwood Formation. Both were discovered by Mr. N. H. Darton. These all agree in the character of their fish remains.

T. D. A. COCKERELL

UNIVERSITY OF COLORADO,
December 14

NOTES AND LITERATURE

SOME RECENT ADVANCES IN VERTEBRATE PALEONTOLOGY. II.

Waldemar Lindgren in a discussion of "The Tertiary Gravels of the Sierra Nevada of California,"[11] gives (p. 51) a brief review of the history of fossil mammals of the auriferous gravels of California. In this connection the author has touched on the age of the famous "Calaveras skull," which some have thought indicated a Tertiary age for man in California. The skull has in the past provoked much discussion and it is interesting to have new light brought forward. Mr. Lindgren, through his associate, Mr. J. M. Boutwell, interviewed some of the older residents of the region in which the "Calaveras skull" was found. One resident remembered the details of the "find" and stated to Mr. Boutwell that the mine in which the skull was found had been "salted" with the subsequently famous "Calaveras skull" as a practical joke by one of the neighborhood humorists. While this is not of very definite evidence for the non-Tertiary age of the "Calaveras skull" yet it fully sustains the important researches of Sinclair and Holmes, who could find no good evidence for the skull being other than that of the modern Indian.

The *Kansas University Science Bulletin* issued during the past summer contains three articles on fossil vertebrates. A new species of *Eryops* (*E. willistoni*) and the history of the development of our knowledge of the temnospondylous Amphibia is the subject-matter of one of the papers. The earliest known temnospondyle was described by Agassiz as a fish in 1777. The amphibian nature of the fossil was not noted until 1847 when it was correctly defined by Goldfuss and later by Jaeger. A list of 58 species is given, nearly or quite all of which belong with the Temnospondylia. The order Temnospondylia and the family Eryopidæ are defined and the geological range and geographical distribution given. The new temnospondyle (*Eryops willistoni*) is from the reputed Permian of Oklahoma. The species is quite distinct and the characters are shown in six plates of drawings of the skeletal remains.

An armored Dinosaur (*Stegopelta landerensis* Williston) is

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[11] **Prof. Paper 73, U. S. Geol. Surv.**

described in another paper[12] and illustrated in five plates. The material is in the University of Chicago. The form is one of the later, peculiar, armored, bizarre, stegosaurian dinosaurs allied to *Polacanthus* of England, *Stereocephalus* of Canada, *Hierosaurus* of Kansas Niobrara Cretaceous, *Ankylosaurus* of Montana and other widely distributed genera of armored dinosaurs. The dinosaur was found in a marine deposit associated with plesiosaur remains. A short sketch of the horizon, the Hailey shales of the Wyoming Cretaceous, is given.

The soft parts of Cretaceous fishes are described and figured in the other paper,[13] and a new herring from the Cretaceous near Waco, Texas, is described as *Thrissopater intestinalis,* so called on account of the preservation of the intestines. The form is allied to *T. magnus* of the English Cretaceous. Another form of fish, identified provisionally as *Empo nepaholica* Cope, is represented by the cast of the stomach, a portion of the intestine and a pectoral fin with a few scales.

Dr. S. W. Williston has reviewed the question of the homology of the *wing finger* of Pterodactyls[14] and has given a new restoration of a pterodactyl as it probably appeared in life. The restoration is based on Dr. Williston's previous restoration of the skeleton of *Nyctosaurus gracilis* Marsh published in Eastman's translation of Zittel's "Paleontology" (II, 255).

The question which has interested anatomists for nearly a century is whether the wing finger of the pterodactyls is the fourth or fifth. There have been many arguments for each determination. Cuvier was the first who correctly interpreted the homology of the wing finger, basing his determination on the phalangeal formula of other reptiles. Plieninger has recently raised the question as to whether the interpretation of the phalangeal formula, 2, 3, 4, 5, 3 for the hand and 2, 3, 4, 5, 4 for the foot, is the primitive one for the Reptilia. Dr. Williston answers this question conclusively in the affirmative and quotes as evidence newly acquired facts from the Permian vertebrates of Texas and New Mexico. To substantiate his claim he figures the entire arm of three genera of Permian reptiles, *Limnoscelis, Ophiacodon* and *Varanosaurus.* In all of these genera, known from nearly perfect material, the phalangeal formula is as given above.

The author gives further notes on the function of the pteroid

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[12] Vol. V, No. 14.

[13] Vol. V, No. 15.

[14] *Journ. Geol.,* XIX, 696–705, 4 figs.

bone, which has been interpreted as a vestige of the first finger. He considers it to be simply an ossified tendon supporting the patagial membrane running from the arm to the neck. He bases this conclusion on the relations of this structure in the well preserved skeleton of *Nyctosaurus* in the Field Museum fully described some few years ago by Dr. Williston.

In view of these facts there seems no longer to be any question that the wing finger of the pterodactyls is the *fourth*. The reduction of the phalanges of the wing finger from the primitive number of 5 to 4 is accounted for on the assumption that the claw of the finger has been lost as has the same structure in the bats. Further evidence is brought forth in the nature of the carpus to sustain the homology of the wing finger of the pterodactyls with the fourth digit of other reptiles.

The *Annals of the Queensland Museum*[15] contains two articles on fossil vertebrates by C. W. de Wis, former director of the museum. One of the papers describes a new species of bird, *Palæolestes gorei,* based on a single phalange. The specimen is carefully described, but the geological position is not given, the comparisons of the new form with other species of the same kind are not attempted so that one wonders just why the paper was published, since it really throws no new light on the subject excepting perhaps to extreme ornithological experts.

The same author in a few lines describes a new cestraciont fish from a single imperfect tooth. The form is insufficiently defined and no comparisons are given.

A new member of the theropodous Dinosauria has been described by Mignon Talbot[16] from remains discovered in an "erratic bowlder" of Connecticut Valley Triassic sandstone, which according to Talbot was carried two or three miles from its original source by the glacier. The stone contains the larger part of the skeleton of a small dinosaur of the carnivorous type, a member, undoubtedly, of those reptiles which made the so-called "bird-tracks" in the Connecticut Valley sandstone, so admirably described by Hitchcock, Lull and others. The find is a very unusual and exceedingly interesting one, since Triassic dinosaurs are not at all abundant. The animal when alive could not have been much larger than an ordinary-sized chicken, thus serving to restrain the common conception of dinosaur sizes.

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[15] Brisbane, Australia, No. 10, November, 1911.

[16] *Amer. Journ. Science,* June, 1911.

Portions of the hind limb, arm, skull, ribs, ventral scutellæ or abdominal ribs and portions of about thirty vertebræ are briefly described. The animal is compared with *Compsognathus,* to which it is closely allied and the new generic and specific terms, *Podokesaurus holyokensis,* are proposed. The specimen has been sent to Yale University Museum, where it will be prepared and further described by Dr. Lull.

Osborn[17] has given a discussion of the "Crania of *Tyrannosaurus* and *Allosaurus,*" illustrated with many beautiful figures, photographs and drawings. The discussion of the osteology of the skulls is based on the most recent nomenclature of the cranial elements and the various specimens are figured from many points of view, so that the reader gets an adequate notion of the appearance of the skulls of these remarkable dinosaurs. The figures (Plates III and IV) of the brain cavity, which is figured from the dorsal side in Fig. 17, will be of great interest to the general zoologist.

> Comparison of the intracranial cavity of *Tyrannosaurus* with the midsection of the skull of *Sphenodon* and brain *in situ* as figured by Dendy shows that the intracranial cravity in *Tyrannosaurus* corresponds with the outer surface and foldings of the *dura mater* and is thus merely a cast of the outer envelope of the brain, which gives us little idea either of the form or size of the brain itself. . . . The cast of *Tyrannosaurus* gives us a means of measuring the size of the *dura mater* envelope. It displaces 530 cubic centimeters of water. If the brain proper bore the same proportion to the *dura mater* envelope as that of *Sphenodon,* the bulk of the brain of *Tyrannosaurus* may be estimated at 250 cubic centimeters.

This sized brain in a skull 50 inches in length would not indicate a high degree of intelligence.

Further on in Part II of the same memoir the same author discusses "Integument of the Iguanodont Dinosaur *Trachodon.*" based on a marvelously complete "mummy" discovered in the Cretaceous of Converse County, Wyoming. The "mummy" and the impressions of the skin are figured in several excellent halftone plates, with explanatory line drawings. Osborn says of the skin:

> Properly speaking the skin is not squamate, or imbricating, as in the lizards, but is rather tuberculate. There is no evidence of a squamous overlapping, or of an imbricating arrangement of the scales anywhere.

Although this bipedal dinosaur when standing erect attained a

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[17] *Memoirs of the American Museum,* N. S., Vol. I, pt. 1, 1912.

height of 14 feet the individual tubercles are of very small size, never attaining a greater diameter than 5 millimeters. The paper closes with a reconstruction of *Trachodon mirabile* Cope in two attitudes, bipedal and quadrupedal and a discussion of a "Theory of Color Pattern" and "Habits of the Trachodonts." In regard to *Trachodon annectans* Osborn says:

> If the animals had spent any considerable part of their lives on dry land, even on the sands bordering the streams, the effect of the impact would certainly be observed in the retention of hoofs or ungues, in the coarsening of the palmar epidermis of the manus, because the fore limbs would certainly have been used occasionally, at least, in contact with the earth. There are no hoofs and the epidermal thickenings or pads are very lightly developed.

The conclusion then seems to be that the animals were largely aquatic.

The same author in Part III of the same series gives the attempts to arrive at some definite system of measurements for mammalian skulls with especial reference to the horse, in a paper entitled "Craniometery of the Equidæ." The author divides the discussion into (I) *Craniometric Systems, 1875–1912;* in which is given the results of the labors of Franck, 1875; Branco, 1883; Nehring, 1884; Tscherski, 1892; Salensky, 1902; Ewart, 1907; Bradley, 1907; and Osborn, 1912, the discussions being illustrated by figures and tables. (II) *Distinctions between Horses, Asses and Zebras.* (III) *Cytocephaly, the Bending of the Face on the Cranium,* the chief conclusions of which are: (1) in young animals the palatal and cranial lines are more nearly in the same plane; (2) in certain animals the deflection increases rapidly with age; (3) a horizontal and upward deflection is generally characteristic of primitive browsing types; (4) the downward deflection of the face and palate is highly characteristic of certain grazing types. (IV) *Craniometry and Odontometry in Paleontology.*

> In fossil skulls the *indices* lose value because the slightest degree of crushing or distortion seriously disturbs an index. Nevertheless the indices and ratios should be used wherever obtainable. Since fossil skulls and dental series are rarely complete or perfect, the paleontologist requires an additional series of detailed measurements of parts of the skull not needed by the zoologist.

Harold J. Cook in Volume 7, Parts 3, 4, and 5, of the Nebraska Geological Survey has given descriptions of a new genus and two new species of Miocene rhinoceroses and a "Faunal Lists of the Tertiary Formations of Sioux County, Nebraska." These formations extend from the Lower Oligocene to the Pleistocene and many species are listed, 11 pages being taken up with the lists. Peterson,[18] however, states that one of the above species was based on a deciduous dentition.

Dr. R. S. Lull in the *Yale Alumni Weekly* of November 8, 1912, gives a very interesting account of his expedition to Texas in search of the remains of early horses, which he found in abundance.

Broili[19] has described very carefully a new specimen of *Pterodactylus micronyx* H. von Meyer from the lithographic slates of Eichstaedt in Bavaria. The nearly complete animal is seen from the dorsal side as it lies in the stone.

The same author[20] describes and figures very fully the osteology of the skull of *Placodus* based on a series of specimens of this peculiar, primitive, yet highly specialized reptile. On page 151 are given four reconstructions of the dorsal, ventral, lateral and occipital views of the skull. The animal is very peculiar in many ways and of very uncertain relationship, being assigned to several reptilian groups by the various authors who have studied the species. The maxillary and palatine teeth have the unusual form of pavement crushing teeth, the palatine teeth are especially large and broad, the middle one of the three on each palatine measuring nearly one by two inches. That the animal was a feeder on molluscs or hard vegetation would seem quite probable. Zittel in his "Handbuch der Paleontologie" lists six species of this genus; the one described by Broili being *P. gigas* Ag. The animal possesses a single temporal opening in the skull and amphiplatyan vertebræ, with the nostrils located far back on the skull with the nasals reduced, indicating an aquatic habit of life.

In the *American Journal of Science* for November, 1912, S. W. Williston describes and figures further portions of the osteology of the peculiar Permian reptile *Limnoscelis* from New Mexico, together with a restoration of the skeleton of the species *L. paludis* Will. Nearly the entire osteology of the species is

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[18] *Science*, December 6, 1912, p. 801.

[19] *Zeitschrift der Deutschen Geologischen Gesellschaft*, Bd. 64, Jahrg. 1912, H. 3.

[20] Paleontographica, Bd. LIX, pp. 149–155, with figures and Taf. XIV.

known and much of it is preserved intact. Only a few caudal vertebræ and a few spines of the vertebræ are unknown, which for a fossil form is remarkable. In regard to the habits of the animal the author says:

> Taking into consideration the very short and stout legs with their broad flattened feet, the absence of claws, the elongate body and tail, it would seem not at all improbable that *Limnoscelis* was more or less at home in the water, though not strictly an aquatic animal. In much probability it lived in and about the marshes on the mud flats. . . .

From the press of the E. Schweizerbart'sche Verlagsbuchhandlung Nägle und Dr. Sprösser, Stuttgart, 1912, is a volume entitled "Grundzüge der Paleobiologie der Wirbelthiere," von O. Abel, professor of paleontology in the University of Vienna. The work comprises an octavo volume of 708 pages with 470 figures and a photographic reproduction of the skeleton of *Cryptocleidus oxoniensis* Phil. as mounted in the American Museum. The work is dedicated to Louis Dollo, professor of paleontology in Brussels. The work is divided into four sections as follows: (I) Geschichte und Entwickelung der Paleontologie, (II) Die Ueberreste der fossilen Wirbelthiere, (III) Die Wirbelthiere im Kampfe mit der Aussenwelt, (IV) Paläobiologie und Phylogenie. The work is too extensive for an adequate review in this place and it will suffice to say here something of the manner of treatment of the subject matter of the volume. The usual systematic method of compiling a paleontological work is not followed but the subject matter is presented from the standpoint of the adaptation of the animal to its environment and is thus very refreshing to the zoological paleontologists. Such items as the *auditory apparatus of the mosasaurs,* the *parietal organ, expansion of the thorax, dental reduction in the pterosaurs, convergence and parallelism, Todeskampf* are taken at random throughout the work to indicate the nature of the subject matter. Most of the figures are copied from the works of other authors but a few are new. Recent and extinct species are figured side by side when they illustrate the same biologic phenomenon, as for instance on page 438, the recent *Myliobatis aquila* is illustrated side by side with the silurian *Thelodus scoticus.* On page 214 he states that the present writer is mistaken in his correlation of the digits of the Branchiosauria and that the second finger has wrongly been regarded as the first. His reasoning is not adequate to support his contention. Why should we regard the first finger as having been lost? It would be interesting to have Abel's further views on this matter. The oldest amphibian has but four digits in the hand and they doubtless never had more, but we don't know. His discussion of the *origin of the thumb* is open to question as has been suggested by Doctor Matthew in a previous review of this work. The work as a whole is well printed; the illustrations are clear and show care in selection. The work is, I am sure, a welcome addition to our libraries.

Whatever we may think of the "Arachnid Theory" for the origin of the vertebrates, as outlined in Patten's "Evolution of the Vertebrates and their Kin," we must all acknowledge our debt to Professor Patten for the information on the oldest known vertebrates as outlined in Chapters XX and XXI of that work. Those of us especially who are engaged in the attempt of teaching something of the nature of the oldest known vertebrates must feel grateful to the author for the excellent discussions of these most interesting vertebrates, which he discusses and figures so fully and so beautifully. The text of these two chapters is illustrated with 33 exquisite drawings and photographs based on actual specimens or on the most authoritative works. The writer of these reviews feels a personal debt to Professor Patten for the figures of the left pectoral limb of *Eusthanopteron fordi* (Whiteaves) from the Devonian of Canada. He says of the limb that it

> indicates the way . . . in which the typical skeleton of the pectoral appendage of the tetrapoda has been derived from the biserial pectoral fin of fishes.

We should like to modify the sentence to say *may* instead of *has*, for no one knows whether or not this was the way of the origin of the tetrapodous limb. Restorations of *Cephalaspis, Lasanius, Birkenia, Thelodus, Lanarkia, Drepanaspis* and *Bothriolepis* are given, as well as two photographic pages of specimens of *Bothriolepis* as they occur in the rock; one slab containing nearly a dozen more or less complete specimens. By means of sections Professor Patten has arrived at some conclusions which seem to point, in his opinion, to the arachnoids. The structures he describes are certainly very interesting in their resemblance to arachnid structures. If his interpretation of their value is doubted he has the satisfaction of knowing that no better interpretation has been given. To say that they are characters due to parallelism is begging the question. If they do not indicate arachnid relationships what do they indicate?

Bertram G. Smith[21] gives a very interesting discussion of "Phylogeny" (in the Amphibia) in his valuable memoir on "Embryology of *Cryptobranchus.*" The keynote to his discussion is contained in the following sentence:

> In the present state of our knowledge it is impossible to reach an unqualified decision of the question under consideration. . . . Whatever light may be shed by future discoveries on the question of the derivation of the amphibia from the crossopterygia or the dipnoi it is clear that the point of origin is not far from either stock; in other words, that the three lines of descent have separated from a common stem at no very great intervals.

The discussion is illustrated by a figure of the pectoral limb of the crossopterygian *Sauripterus taylori* Hall, based on a specimen in the American Museum.

Louise Kellogg[22] has a very interesting paper on the "Pleistocene Rodents of California." The material described is from the cave deposits and the asphalt beds of California. The discussion is intended especially as an elucidation of the possible changes in climatic conditions during the Pleistocene as indicated by the rodent fauna. The species are listed according to the life zones which they indicate; the *Upper Sonoran, Transition* and *Boreal* all being indicated by several species; there being but slight indication of change since the time of deposition of the deposits. Two new subspecies are described.

ROY L. MOODIE.

UNIVERSITY OF KANSAS

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[21] *Journal of Morphology,* Vol. 23, No. 3, p. 540 ff.

[22] *Bull. of Dept. Geol. Univ. Calif.,* Vol. 7, No. 8, pp. 151–168.

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THE AMERICAN NATURALIST

A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with Special Reference to the Factors of Evolution

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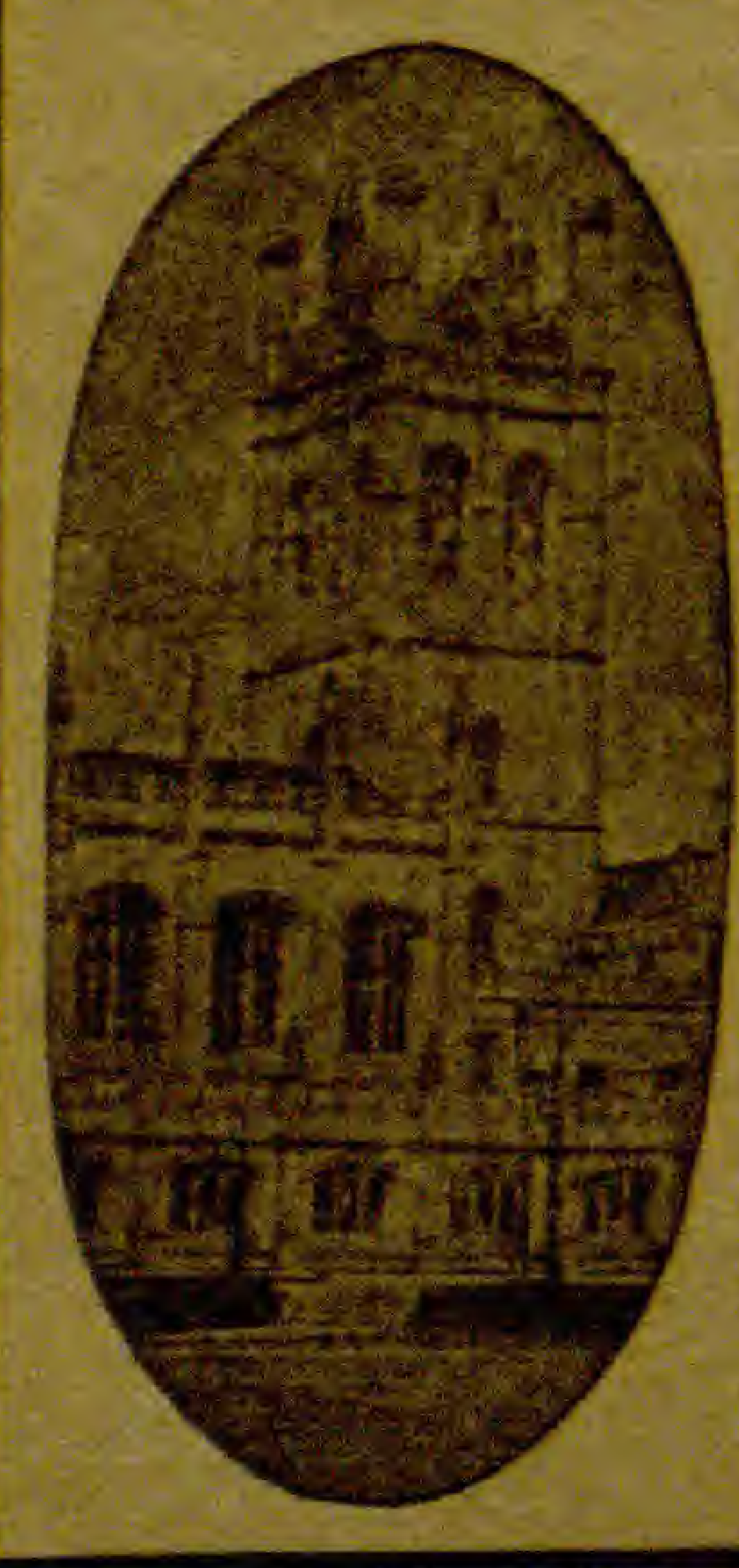

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THE
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INHERITANCE OF MAMMÆ IN DUROC JERSEY SWINE

PROFESSOR EDW. N. WENTWORTH

IOWA COLLEGE

THE relative fixity of character and definite methods of variation in the mammæ of swine make them a fruitful field for inheritance studies. The observations incorporated into this paper were made upon swine used in a feeding experiment at the Iowa State College. There were fifty-seven grade Duroc Jersey sows and five hundred and ten pigs of 1912 farrowing included in the investigation.[1]

The sows may be divided into two groups, one of forty two-year-old animals and the other of their yearling daughters, seventeen in number. In all, there are three generations for comparative study, a rare combination in such numbers among ordinary slow-breeding farm animals. There were two boars in use in the experiment. one a yearling, the other a two-year-old, both closely related as ordinary pedigree breeding is considered. From the standpoint of mammæ pattern, the boars were

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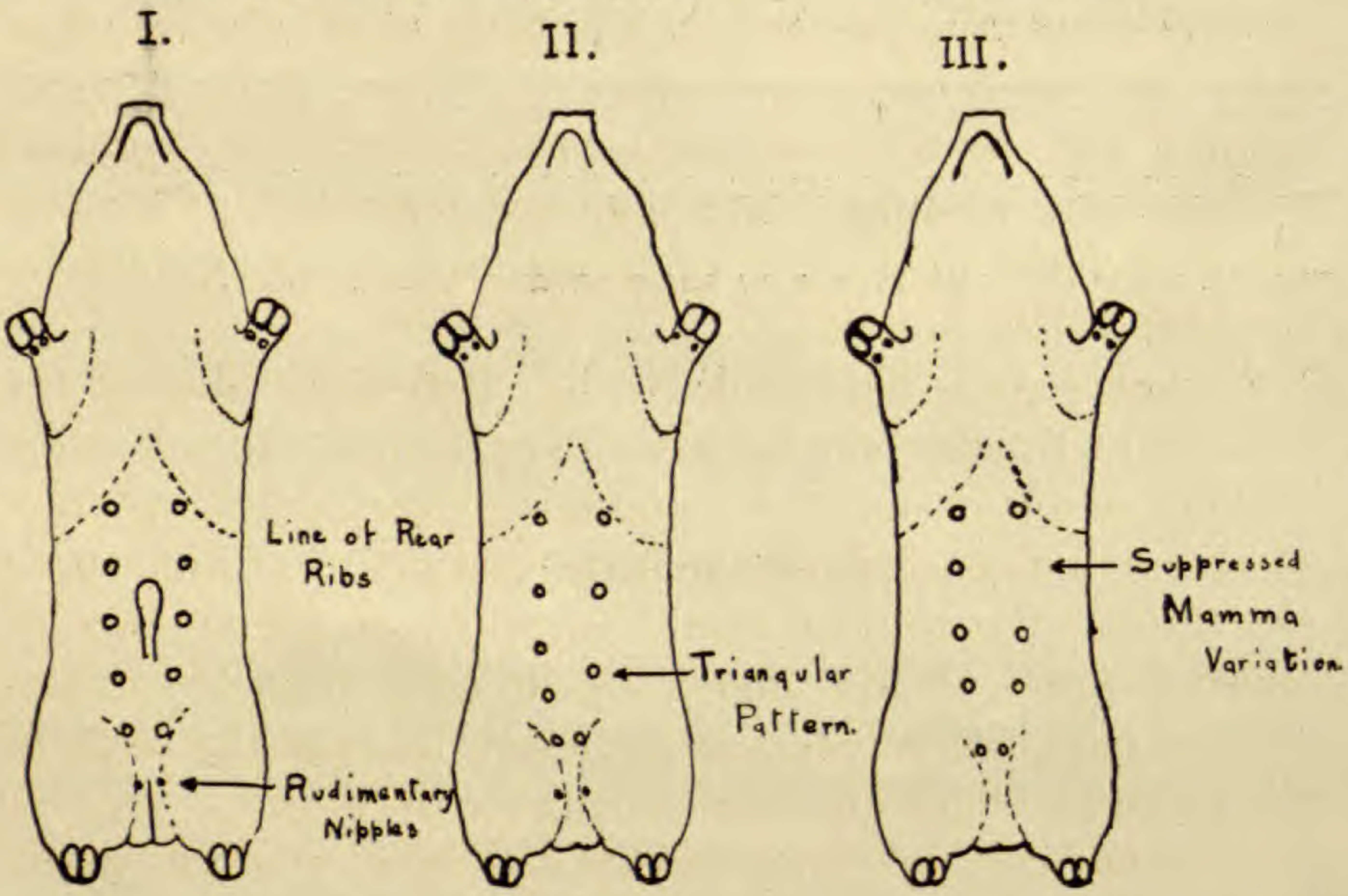
[1] The writer wishes to make acknowledgments to Professor John M. Evvard, of the Iowa Station, for the facilities he put at the writer's disposal and to Mr. A. R. Chappel, a senior student, for great assistance in the collection of data. But most of all, acknowledgments must be made to Dr. Castle, of Harvard University, for his assistance in the study of the data while the writer was working up his material at the Bussey Institution.

quite similar somatically, the only difference being that the asymmetry present occurred on opposite sides in the two animals. In the older boar the right nipple of the second pair was not developed, and in the younger boar the left nipple of the same pair was suppressed.



The Mammæ Pattern.—What may be termed the "normal" mammæ pattern consists in the occurrence along the ventral side of regularly placed pairs. The first pair lies just behind the junction of the ribs with the sternum. The last pair is inguinal in position, and its members lie close together near the median plane. The intermediate pairs are spaced about equally between, although a slightly greater distance separates the last two pairs. In the male with ten mammæ (five pairs), the sheath opening lies between the second and third pairs, while the fourth pair is about the same relative distance to the rear of the third. In the female the nipples are similarly placed, but less readily located in a definite manner, because of the absence of the sheath.

It has been assumed by some writers that the paired mammæ bear a relation to the metameric structure of the individual. Williams particularly contends for this view, claiming that each somite in the original ancestral condition possessed its pair of glands. He also invokes the theory of reversion to account for the definite places in which supernumerary nipples occur. Bateson, on the contrary, defines the position of the teats as occurring regularly on the "mammary lines." These lines diverge toward the axillæ and converge toward the inguinal region. He assumes that mammæ may appear at any point on these lines and apparently with only slight relationship to the somites.

Embryology.—Embryologically, Bateson's idea of the mammary lines seems to be well supported. In the swine embryo of 14–15 mm. the mammary ridges appear plainly visible in a dorso-lateral position. At about 17 mm. small elevations ("primitive teats") appear on the surface of these ridges. When about 19–20 mm. long, the intervening parts of ridges are resorbed, leaving the teats at the point in which they will normally develop.

This entirely precedes the formation of the true mammary tissue. In fact Creighton says that in the kitten the latter may not appear until after birth, although guinea pigs and swine show an earlier development. The factors that govern the transverse division of the lateral mammary tissue into mammæ, so far as the writer has been able to discover, are unknown. Most authors have insisted that metamerism has nothing to do with it, but offer little demonstrable in its place. Suffice it to say, however, there is some force that serves to maintain symmetry and regularity of division in the majority of cases. An attempt will be made to show some of its effects in the following study, even though it can not be definitely named and its action described.

Types of Variation.—The simplest type of variation in the number of mammæ consists of one more or one less pair than is the usual number. The writer has assumed the first pair and the inguinal pair constant, because of their definite position. On this assumption, the addition or substraction of a pair of mammæ must occur at some intermediate point. If a pair is added, it may be associated with a closer spacing of the teats, or possibly with a greater body length from the tip of the sternum to the border of the groin. If subtracted, the opposite condition would obtain. No observations were made on this point, and indeed it would be difficult to make them, because of the elastic nature of the tissue, the difficulty in handling the animals, and their marked variability in size and proportions.

There are two common sorts of asymmetry that may occur separately or together. These are the "suppressed nipple" and the "triangular" patterns. The former consists in the non-appearance of one member of a pair, while the latter shows one teat placed opposite two teats on the other side. The single teat is located at a point midway between the opposite two, and is always on the mammary line. The suppressed mamma variation appeared in 29.8 per cent. of the offspring and the triangle in 21.7 per cent.

The suppressed mamma variation may occur twice in the same animal, either on the same or opposite sides of the body, the two sorts of repetition being about equally frequent. But whenever the variation is repeated on the same side of the body, a normally placed pair of mammæ always intervenes. Less frequently a pair of mammæ seems to be omitted altogether, leaving an empty space where normally a pair of mammæ would occur. This may be interpreted as the suppression of two mammæ on opposite sides in one pair. The writer is rather doubtful of this interpretation, however, and does not include it in the 29.8 per cent. already mentioned. The omission of a pair was found in only 5 cases, or less than 1 per cent. of all.

The triangle pattern shows three or perhaps four types of compounding. Two triangles may appear with the single nipples on the same side and separated by one or more normal pairs, or they may be separated similarly, but have the single nipples on opposite sides. The third type is where no normal pair divides the two triangles and two mammæ on one side balance three on the other. In this case, where more than two triangles are present, three nipples on one side may balance four opposite or four may balance five. This last condition occurred in only two cases. The fourth type is doubtful and difficult to describe. It is as though the two triangles have their bases on opposite sides of the animal, but have one side in juxtaposition with the corresponding side of the other. In other words, two of the mammæ form the sides of two oppositely facing triangles and give a two-balancing-two effect. The mammæ on one side are opposite a point intermediate between those on the other. This effect may possibly be brought about by a combination of the suppressed nipple and triangle type as well. In seven individuals the triangle and suppressed nipple were found on the same animal, separated by one or more normal pairs.

There sometimes appears a pattern in which the mammæ of one side are set ahead of the points where they commonly occur, as though one lateral row were pushed slightly forward. This may be characteristic of the entire mammary series or of only one or two pairs. The arrangement is seldom so distorted that the identity of the pairs is lost, but occasionally it approaches the fourth compound type of triangle just discussed. A suggestion has been offered that this distortion may be due to the position of the fetus during pregnancy, so that when the abdominal walls grow together, the mammæ do not lie exactly opposite. An objection to this is that not only would the abdomen show the asymmetry, but also the ribs and sides. No observations were made on this point, but to the writer the explanation offered seems doubtful.

The Seat of Greatest Variation.—For convenience in description, the pairs of mammæ may be numbered from the most forward pair to the rear. Considering the first pair and inguinal pair as constant, the mammæ of the intervening region were tabulated by number. This method, of course, made the fifth and sixth pairs of much lower frequency than the other five, since so many animals had but ten mammæ. In figuring percentage frequencies for each position the total number of mammæ possible in all of the animals, if each had a pair in the position under consideration, was used as a basis for computation. The columns 1½, 2½, etc., show the frequencies of mammæ forming the apex of a triangle, in the position between pairs 1 and 2, 2 and 3, etc.

The total number of mammæ for each position which could occur if there were no variations is 1,138 for the first four and inguinal pairs. The constancy of the last named pair is particularly marked, only nine variations obtaining.

	Pair												
	1	1½	2	2½	3	3½	4	4½	5	5½	6	6½	Inguinal
No. nipples	1,112	25	989	37	1,088	14	1,095	19	649	28	127	7	1,129
Per cent. frequency mammæ	97.715	2.2	86.906	3.25	95.606	1.23	96.221	2.7	92.187	16.09	72.987	4.023	99.209
Per cent. frequency variations	2.285		13.094		4.394		3.779		7.813		27.013		0.791

Arranging the pairs in order of frequency of variation, the following sequence holds: 6th, 2d, 5th, 3d, 4th, 1st and inguinal. It is probable that the rank of the sixth is not significant, due to the lack of numbers in proportion to the others, but there is no question about the second pair being a leading seat of variation. In a former article on this subject the writer called attention to this fact without presenting figures. It is worth while noting that this variance in the second pair is perhaps not characteristic of swine as a whole, but simply due to the fact that both boars showed in this pair their variation from normal patterns.

The point of most frequent appearance of the triangular type is of interest, although possibly not significant. The rank is as follows:

	Per Cent.
Between 5th and 6th	16.09
Between 6th and 7th	4.023
Between 2d and 3d	3.25
Between 4th and 5th	2.7
Between 1st and 2d	2.2
Between 3d and 4th	1.23

Once more, if we discard the results between 5th and 6th, and 6th and 7th, because of small numbers, we find the high per cent. of variability at the second pair.

The point of appearance of the suppressed nipple variation was plotted in the same way and the following order of appearance was found:

	Per Cent.
6th pair	6.9
2d pair	6.3
5th pair	1.3
4th pair	1.1
3d pair	0.5
Inguinal pair	0.2
1st pair	0.0

Again the second pair is shown as the chief seat of variation. It may be well to mention that while there was a possibility of 1,138 mammæ appearing in the 1st, 2d, 3d, 4th, and inguinal pairs, only 704 mammæ could have appeared in the 5th pair and 174 mammæ in the sixth, because of the small numbers of animals having over ten and twelve mammæ, respectively.

No. Triangles	5 Prs.	6 Prs.	7 Prs.	f
1	4	53	23	79
2		8	10	18
3		2	1	3
4			1	1
f	4	63	35	101

Mean No. triangles = 1.267.
Standard deviation triangles = .5609.
Mean No. pairs mammæ = 6.3168.
Standard deviation pairs = .7889.
$r = .1666 \mp .065$.

Relation of Increased Pairs to the Common Variations.—A correlation was arranged between an increased number of pairs and the two common asymmetrical variations.

No. Suppressed Nipples	5 Prs.	6 Prs.	7 Prs.	*f*
1	1	91	24	116
2			9	9
	1	91	33	125

Mean of suppressed nipples = 1.072.
Standard deviation of suppressed nipples = .258.
Mean No. pairs = 6.256.
Standard deviation = .408.
$r = .5089 \pm .0447$.

While the correlation does not show a marked relation between the number of triangles and the increased number of mammæ, yet another method of plotting shows that there is a very significant relation between them and that the tendency to these variations may possibly be only a function of a large number of mammæ rather than a definitely heritable unit.

	No. of Pairs		
	5 Prs.	6 Prs.	7 Prs.
No. animals	217	296	56
No. each kind of animals with triangle	4	63	35
Per cent. animals of each class with triangle	1.84	21.28	62.5
No. animals of each class with suppressed mammæ	1	91	33
Per cent. animals of each class with suppressed mammæ	.46	30.74	58.93

The increased percentage of animals with the two types of variation among the animals with a larger number of mammæ speaks for itself.

This relation of the variations to the increased number of pairs, in connection with the fact that the variations appear most frequently in the pairs between the first, and inguinal, furnishes additional basis for the statement made earlier in the paper that the number of mammæ is increased by modifications between the first and inguinal pair.

Inheritance of the Two Forms of Variation.—The "triangles" show a marked degree of inheritance. Neither boar carried the triangular pattern somatically, but the offspring of the two were summarized separately to see if any difference developed in the offspring. Both boars possessed the "suppressed nipple" type, and, as might be expected, show little difference in breeding.

PIGS BY OLD BOAR

		Pigs with Triangle	Pigs with Suppressed Nipple	With Neither
Sows with triangle	No.	17	11	28
	Per cent.	30.00	20.00	50.00
Sows with suppressed nipple	No.	2	14	26
	Per cent.	4.7	33.3	62.0
Sows with neither	No.	45	60	169
	Per cent.	16.6	22.2	62.5

It is evident that a distinctly higher proportion of "triangles" appears in the pigs from sows of the same type. Also a distinctly greater percentage of pigs with the suppressed nipple comes from sows of the suppressed-nipple type, but the difference between the breeding character of the three classes of sows is not so marked with this variation, probably because the boar supplies the latter pattern with each mating.

PIGS BY YOUNG BOAR.

		Pigs with Triangle	Pigs with Suppressed Mamma	With Neither
Sows with triangle	No.	13	4	16
	Per cent.	39.394	12.121	48.485
Sows with symmetrical pairs	No.	9	23	62
	Per cent.	9.574	24.468	65.957

Combining the two tables, there appears a result which may be more significant than in either when separate. In this table in the cases where a pig possesses both variations, he is listed twice, so that the percentage runs slightly over one hundred. There is one duplication from sows with the triangle and four duplications in the offspring of the "normal" sows.

		Pigs with Triangle	Pigs with Suppressed Mamma	With Neither
Sows with triangle	No.	30	15	44
	Per cent.	34.091	17.045	50.000
Sows with suppressed mamma	No.	2	14	26
	Per cent.	4.762	33.33	61.905
Sows with even pair	No.	54	83	231
	Per cent.	14.835	22.802	63.461

It is of interest to note that each form of variation appears in about one third of the offspring of the mothers that bear the same variation. Where the mother does not possess either type, the triangle appears in about one-seventh of the offspring and the suppressed mamma in one fourth. It is possible that a three-factor Mendelian ratio would account for the results, but since the factors are unknown it is scarcely worth while to present it.

Two of the sows possessed both the triangle and the suppressed mamma, and are not listed above. A close agreement with the preceding table may be noted.

	Pigs with			
	Triangle		Suppressed Mamma	Even Pairs
Sows with both variations	No.	15	1	10
	Per cent.	31.25	6.25	62.5

The constancy of the per cent. of even pairs in the two tables is undoubtedly worthy of notice. Neither boar possessed the triangle. Sows with the triangle produced 39 pigs with the triangle and 69 without. Sows without the triangle produced 56 pigs with it and 349 without. The character is apparently inherited as a distinct entity even though it may be merely a function of an increased number of mammæ. The sows without the triangle may be divided on their breeding performance into two groups. The first produced only offspring without triangles (124 pigs) while the second produced 56 pigs with triangles, 225 without. The proportions here look significant. In the first group the ratio of those possessing triangles to those without is about 1:2. In the second it is $O:N$ and in the third 1:4. The relative frequencies of these three groups also look promising: 124 $(O:N)$:281 (1:4): 108 (1:2). The simple 1:2:1 ratio is approximated, although the excess of the second group is a little high. Records on next year's pigs are needed to prove the soundness of this method of division.

In a similar way the suppressed mammæ show a strong degree of inheritance. Both boars possessed the suppressed mamma pattern. Sows with the suppressed mamma produced 17 offspring with it and 49 without. Sows without it produced 94 with and 350 without. The ratios are approximately 1:3 and 1:3.7. Separating the sows without the character into two groups on the same basis as in the preceding case the following appears: 65 (1:3) from sows with the suppressed mamma, 388 (1:3) from sows without the suppressed mamma and 56 $(O:N)$ from sows without the suppressed mamma. The frequencies look like two 3:1 ratios combined in which the two groups of three and one group of one are similar, but it is not the normal ratio of 7:1. This also may be only apparent, however, and another year's test is needed to throw more light on the subject. It is beyond doubt, nevertheless, that these two forms of variation are distinctly inherited and the manner of inheritance only is that which remains to be demonstrated.

Evidences of Segregation of the Two Types of Variation.—The grand-dams were plotted against their pigs of the 1912 litters and the correlations were figured in comparison with the dams. The results were not enlightening, as the following table shows.

Correlation between No. triangles in grand-dams and 1912 pigs	—.0064 ± .0624
Correlation between No. triangles in dams and 1912 pigs	.2241 ± .0592
Correlation between No. suppressed nipples in grand-dams and 1912 pigs	—.0966 ± .0618
Correlation between No. suppressed nipples in dams and 1912 pigs	—.0052 ± .0624

In the negative correlations the probable error is either approximately equal to the coefficient or else far larger, so that no emphasis can be placed on the result. In arranging them according to per cent. of offspring bearing the same variation the following is obtained:

	Per Cent. of Pigs with Supressed Nipple
Grand-dams without suppressed nipple	23.00
Dams without suppressed nipple	22.22
Grand-dams with suppressed nipple	11.76
Dams with suppressed nipple	11.11

No difference shows between the two classes, so it is possible that the presence of the variation in the boars tends to even things up.

	Per Cent. Pigs with Triangle
Grand-dams without triangle	15.31
Dams without triangle	10.47
Grand-dams with triangle	16.66
Dams with triangle	29.03

In the case of the triangle, the grand-dams without the variation have a higher per cent. of offspring possessing it than do the dams, but where the triangle is present in the dams and grand-dams the younger generation seems to have the greater power of transmission. Since the old boar previously mentioned is the sire of the dams, and the young boar the sire of the 1912 pigs, there has been no point of entrance for the triangle somatically. The percentages show some sort of segregation of a recessive character, but further matings are necessary to clarify the matter.

Variation in Number of Mammæ.—There is quite a wide range in the number of teats that may be present. The smallest number found in these litters is nine, while in the litters of last year, elsewhere reported, one pig appeared with only eight. The highest number recorded on one animal was sixteen, these including a pair of rudimentaries to the rear of the inguinal pair. Of the mammæ on the mammary lines of the abdomen fourteen is highest number.

The relative frequency of occurrence of these different numbers among the swine studied is shown in the following table:

	Number Mammæ					
	9	10	11	12	13	14
Number pigs	4	195	135	127	33	15
Per cent. frequency	0.78	38.31	26.52	24.95	6.48	2.95

Nearly 90 per cent (89.8) of the pigs bear ten, eleven or twelve mammæ, and may therefore be considered the normal types of the Duroc-Jersey. In Bateson's data on Tamworth's and cross-bred Berkshires in his "Materials for the Study of Variation," he finds that twelve is the lowest number of mammæ occurring, fourteen is the mode and seventy-seven per cent. fall on thirteen, fourteen and fifteen. His numbers are much smaller (35), but it is highly probable that there is a difference in breeds as regards number of mammæ, particularly between those of bacon and lard type.

Correlation of Number of Mammæ between Dams and Pigs.—The coefficient of correlation for number of mammæ between the sows and pigs was not high (.2626 ± .028), yet it showed distinct inheritance. There was apparently no difference due to sex, as the boar pigs showed a correlation of .1734 ± .04 to their mothers, and the sow pigs were only slightly greater, .2133 ± .04. Since with the probable errors in consideration the two coefficients overlap, it seems doubtful if sex makes any difference in the inheritance.

Evidence of Segregation in Number of Mammæ.—The sows of the first generation were plotted against their grand-daughters giving the following results.

Grand-dams	Number of Mammæ of Pigs						
	9	10	11	12	13	14	Total
10		8	4	1			13
11	1	5	4				10
12		39	25	4			78
13		7	5	1			13
14		1			1	1	3
Total	1	60	38	16	1	1	117

Coefficient of correlation = .2962 ± .057.

The parents themselves showed a correlation to the offspring as follows:

Dams	No. Mammæ Pigs						
	9	10	11	12	13	14	Total
10	1	29	12	10			52
11		5	6				11
12		21	18	6			45
13		1			1	1	3
14		4	2				6
Total.......	1	60	38	16	1	1	117

Coefficient of correlation = .1418 ± .061.

The grandparents are much more closely correlated with the pigs (.2962 ± .057). Two explanations may be offered for this. Among the fifteen dams there were five pairs of sisters, so that there were only ten grand-dams to correlate. This would throw some of the litters into one class that were separated when correlated with the dams and so would modify the coefficient. An interpretation more satisfactory to the writer is that the higher coefficient between grand-dam and offspring represents the segregation of some mammary character the limits of which can not, at present, be defined.

Relation of Asymmetrical to Symmetrical Pattern.—An interesting point because of the constancy of the ratio lies in the relation of the symmetrical and asymmetrical patterns. In the pigs they occur in the ratio of 1:2, or 172 asymmetrical to 337 symmetrical. In the writer's paper of last year, already cited, the same ratio held and seemed unaffected by patterns in the parent. If divided according to sex, we find no difference, the boars showing 89 asymmetrical to 174 symmetrical and the sows showing 83 of the first to 163 of the second. The fact that both parents bear the asymmetrical pattern may influence the per cent. of asymmetry in the pigs, but this influence is very slight. Where boar and sows were asymmetrical the ratio was 50:85, while when the boar only was asymmetrical the ratio was 122:252. Putting them on the same basis, we find a ratio of 1:1.7 and 1:2.06. There may be significance in the difference between the two ratios, but the writer is inclined to think there is not, for last year's work gave 35 asymmetrical to 68 symmetrical pigs from two asymmetrical parents, and 33 to 62 from one asymmetrical parent.

Another method of plotting these ratios shows that differences may occur in connection with an increased number of pairs. When the animals have ten pairs, only four animals out of 199, or less than two per cent., show the variations. When the animals have six pairs, the number of animals having even pairs throughout are about equal with the number having the variation, 127 and 135, respectively. When the animals have seven pairs, the chances are about two to one that the animal will have one or the other variation (33:15). Placed on a percentage basis the following table results, showing that asymmetry is closely related to an increased number of pairs.

	Animals with		
	5 Prs.	6 Prs.	7 Prs.
No. animals	199	262	48
No. animals with the variations	4	135	33
Per cent. animals with the variations	2.01	51.52	68.75

Inheritance of Asymmetry.—The old boar possessed his asymmetrical nipple on the left side, the young boar on the right. The two boars were tabulated in their matings to sows possessed of each kind of asymmetry.

OLD BOAR (EXTRA NIPPLE ON LEFT)

	Pigs with Extra Nipples	
	On Left	On Right
Sows with extra nipple on left	18	16
Sows with extra nipple on right	4	6
Symmetrical sows	45	47

YOUNG BOAR (EXTRA NIPPLE ON RIGHT)

	Pigs with Extra Nipples	
	On Left	On Right
Sows with extra nipple on left	3	9
Sows with extra nipple on right	0	1
Symmetrical sows	11	25

With the older boar no evidence of the inheritance of unilateral asymmetry is shown. With the younger boar, however, there is a distinct excess of pigs showing the asymmetry on the same side as the father. Since there is no means of telling from the external appearance what recessive characters the sow may be carrying, it is possible that there is a marked difference in the lateral predisposition of the two boars.

An examination of the offspring of asymmetrical and symmetrical sows shows a slight tendency toward the production of asymmetry in the offspring of that kind of parents. Eighteen sows of this type produced 96 pigs with even pairs and 74 without. Thirty-nine symmetrical sows produced 215 pigs with even pairs and 125 without. Using the asymmetrical pigs as the base, the first ratio is 1:1.297 and the second is 1:1.72. While we are justified in assuming a degree of inheritance of asymmetry, we are not yet able to show the same by definite units.

Is Inheritance Lateral or by Pairs?—The embryological origin of the mammary tissue suggests that there may be a lateral inheritance. In order to determine this, the right side of the mother was correlated with both the right and left sides of the offspring, and the left side of the mother correlated in the same way. The offspring of the two boars were separated, since the old boar had six teats on the left side and five on the right, while in the young boar this relation was reversed.

The results were disappointing if one expected a high correlation.

	Pigs by Young Boar	Pigs by Old Boar
Right side dam to right side pig	.1196 ± .0353	.1601 ± .0346
Right side dam to left side pig	.0384 ± .0353	.2326 ± .0346
Left side dam to right side pig	—.0023 ± .0353	.1436 ± .0346
Left side dam to left side pig	—.0296 ± .0353	.2132 ± .0346

In the last three correlations in the pigs by the young boar, the probable error equals or exceeds the correlation, and in the pigs by the old boar, the probable error permits the correlations to just about meet each other or even overlap. In the pigs by the young boar the correlation between the same sides of sow and offspring exceeds that of the opposite sides, but in the offspring of the old boar the left side of the pig is more closely correlated to either side of the mother than is the right side of the pig. These contradictions lead the writer to believe that the inheritance is not lateral.

All of the offspring were tabulated as to number of pairs against their dams and the correlation was determined. The coefficient is .1994 ± .028, large enough to show some inheritance. As the animals included here possess the two common types of variation, or were from dams possessing those types, a second table was prepared of pigs with symmetrical pairs from sows of the same type. A larger coefficient resulted, .3588 ± .039, but even this is not satisfactory, as the boars possess the suppressed nipple, and of course, the offspring represent a selected group, although not selected from a standpoint that should favor the correlation.

Another method of tabulating may show the inheritance more graphically. The boars have six pairs, with one mamma suppressed.

No. Pairs in Sow	Av. for Offspring All Individuals	Av. for Symmetrical Individuals
5	5.57	5.27
6	5.76	5.48
7	5.90	5.65

There is a distinct increase in the means of the offspring as the number of pairs increases in the parent. The mating of the boars to the sows with the following number of mammæ is interesting:

Boars	Sows	Pigs with 5 Prs.	6 Prs.	7 Prs.
6 prs.	5 prs.	69	60	2
6 prs.	6 prs.	103	162	34
6 prs.	7 prs.	28	40	12

This corroborates the results above.

The foregoing tables lead the writer to believe that the method of inheritance is by the pair rather than the side, although the determination of the pair as a Mendelizing unit must be deferred until further study is made.

Rudimentaries in the Abdominal Series.—Bateson looks on rudimentaries that occur asymmetrically in the abdominal series of mammæ, as a sort of supernumerary organ systematically and different qualitatively from the normal mammæ. He so classifies them because of their visible differences and because of their ability to displace normal mammæ from the ordinary paired state. It seems to the writer that while this distinction may be all right from Bateson's standpoint, from the standpoint of heredity it is without weight. The factor that causes the transverse sectioning of the strips of mammary tissue is obviously separate from the forces that cause development of the glands. This factor operates irrespective of whether the gland be destined to develop or not, and it is very evidently this factor (probably complex) that is inherited.

At birth or shortly after it is difficult to tell whether a mamma will develop functionally or not. There are some that are so small and undeveloped that one may be positive as to their rudimentary state throughout life, but there are others for which prediction is very uncertain. The writer has left all doubtful cases out of consideration and has figured asymmetry due to a rudimentary nipple in relation to asymmetry produced by developed teats.

There are 89 asymmetrical males. One of these is asymmetrical from the presence of a rudimentary; two more possess a rudimentary each, but are asymmetrical through the presence of functional "triangles"; and two symmetrical boars possess rudimentaries as one member of a pair. It must be understood in connection with the foregoing that all of the mammæ of the male are really rudimentary, and that what the writer has termed rudimentary in the preceding statement refers to mammæ that are so much smaller as to occupy a relation similar to the rudimentary and normal mammæ in the young female.

Eighty-three asymmetrical sows show only one individual whose asymmetry is due to the presence of a rudimentary. One sow has a rudimentary, but is asymmetrical from a functional "triangle," and one symmetrical sow shows a rudimentary in one of her pairs.

Summarized this shows that only 1.123 per cent. of the asymmetrical males have their asymmetry caused by rudimentaries, and only 1.204 per cent. of the females. From this evidence it would seem that rudimentaries do not represent a step in the variation of the mammary linear series, but from the standpoint of heredity should be treated the same as normal teats, the lack of development being probably due to fluctuating somatic causes.

It is interesting to compare the variability of the nipples of the male, which are rudimentary throughout life, with the teats of the female, which are potentially functional. The coefficient of variability for the boar pigs is .1009 ± .003 and for the sow pigs it is .0943 ± .0028. The probable error permits a minimum separation of the two coefficients of only .0008, so that the difference between the two is probably not significant. In the litters of 1911, already referred to, the boar pigs were slightly more stable than the sows, which would further argue against a qualitatively constant significant difference.

The Rudimentaries to the Rear of the Inguinal Pair.—In the previous discussion no account has been taken of a pair of rudimentaries which occur on the lower forward part of the scrotum of the male, and well to the rear on the inner thighs of the female. The pair is entirely distinct from the others, and readily recognizable from its location and also from the fact that so far as the writer has observed it is always rudimentary. It seems probable that it lacks almost entirely the backing of mammary tissue found in the other mammæ. The writer has already described the inheritance of the character in another paper, so will simply summarize the results. The pair behave as a Mendelian unit character in heredity, dominant in males but recessive in females. That is, it is developed somatically in the male when either simplex (*Rr*) or duplex (*RR*), but develops in the female only in the duplex (*RR*) condition. The boars used were simplex from their behavior in breeding, while the sows embodied all three types.

BOAR (*Rr*)

Low Type	No. Sows		Boar Pigs		Sow Pigs	
			Absent	Present	Absent	Present
RR	9	Expectation	0	39	20	20
		Actual	0	39	27	13
		Expectation	17	51	66	22
Rr	16	Actual	23	44	64	24
		Expectation	60	60	95	0
rr	24	Actual	66	54	95	0

Fifteen of those recorded in the first two columns were daughters of some of the remaining. In each case the gametic composition assigned the young sows from their breeding performance confirmed the formula assigned the mother. There is some variation from the expectation particularly in the female pigs from the *RR* sows and the male pigs from the *Rr* mothers. The numbers are too small to permit of the deviation being significant, however, and the departure from expectation in the sow pigs in the first instance shows that the rudimentaries are not a distinctly feminine character. Attention should be called to the fact that in the male the deviations from expectation are on the same side.

The following table was plotted to see if the rudimentaries are a function of an increased number of mammæ, similar to the two common types of variation.

	Number of Mammæ per Animal					
	9	10	11	12	13	14
No. animals	4	181	131	135	36	16
No. animals with rudimentaries	3	59	58	52	10	1
Per cent. latter	75.00	32.59	44.28	38.52	27.77	6.25

The fluctuating percentages in connection with the fact that the two lowest percentages are recorded against the highest numbers of mammæ, would incline the writer to believe that the rudimentary mammæ of the scrotum and thigh are independent of the abdominal series, and furthermore that the Mendelian interpretation is correct.

Conclusions.—I. There are two common sorts of variation from the even paired type in the mammæ of swine, aside from the simple addition and subtraction of pairs. These are the "triangle" and "suppressed" nipple variations. Each shows a definite tendency to reproduce itself in the offspring, but both are apparently associated with an increased number of pairs.

II. The seat of the greatest variation in the animals under discussion is the second pair of mammæ. This is perhaps due to the type of variation in the sires.

III. There is apparently a breed difference in regard to the number of mammæ. Bateson shows that in Tamworths and Berkshires, 13, 14 and 15 mammæ are typical, occurring in 77 per cent. of the cases. The Duroc Jerseys studied show in 90 per cent. of the animals, 10, 11 or 12 mammæ.

IV. The ratio of asymmetrical to symmetrical patterns increases as the number of mammæ increase. With five pairs symmetry is almost constant; with six pairs, symmetry and asymmetry are equal. With seven pairs asymmetry outnumbers symmetry 2 to 1.

V. No evidence definitely showed that asymmetry is unilateral in inheritance. Asymmetry on one side of the parent does not, on the average, produce asymmetry on the same side only of the offspring.

VI. Sows differing in number of mammæ, when mated with the same boar, produce offspring variable in number of mammæ. In general, sows with a large number of mammæ produce more offspring of a corresponding sort than do sows with a small number of mammæ. The difference, however, is not great, and neither sort apparently breeds true. The correlation of mother and offspring in number of mammæ is measured by the coefficient .2626 ± .028.

VII. There is a distinct inheritance of the tendency to produce a greater number of pairs, the correlation being .3588 ± .034.

VIII. There is no evidence of lateral inheritance of the mammæ, the inheritance by pairs being a more probable hypothesis.

IX. No definitely Mendelizing units were found in the abdominal mammary series, but the relations between grandparents and offspring and parents and offspring, do indicate a segregation of some sort.

X. Rudimentaries in the functional mammary series have the same effect on the pattern as normal mammæ, and probably represent lack of development. There is no greater tendency to variation among the rudimentary nipples of the male than among the potentially functional nipples of the female.

XI. The paired rudimentaries to the rear of the inguinal pair behave as a simple Mendelian unit-character, sex-limited in inheritance.

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STUDIES OF NATURAL AND ARTIFICIAL PARTHENOGENESIS IN THE GENUS NICOTIANA.[1]

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EXPERIMENT STATION

PARTHENOGENESIS is a phenomenon that is known to exist in many widely separated genera of the higher plants. In but few cases does it seem likely that the regular reduction of gametogenesis with the subsequent nuclear fusion of fertilization never occurs, yet it is probable—from the frequent discovery of new examples—that it will ultimately be found that the ability to dispense with typical sexual reproduction is comparatively common. Should this prove to be the case, one would be forced to conclude that sexual reproduction was developed for reasons other than protoplasmic necessity, as Maupas and his followers would have biologists believe.

This is the fundamental problem toward the solution of which all data on parthenogenesis contribute, but pending the time when it can be discussed intelligently, there are sub-questions that are not without their interest. Loeb's researches have shown that the stimulus to development which is an attendant result of fertilization, is physico-chemical. Observations on several genera of parthenogenetic insects have shown that the presence or absence of sexual reproduction is largely dependent upon external conditions such as food, light, temperature, etc. Little is known of the rôle played by such stimuli in parthenogenesis in plants, however, although knowledge on the subject is of some import aside

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[1] Contribution from the Laboratory of Genetics, Bussey Institution of Harvard University.

from theory. For example, the geneticist is concerned, if, under any of the conditions likely to obtain in his experiments, plants ordinarily reproducing sexually should be incited to reproduce parthenogenetically.

This paper describes some facts on the subject obtained by experiments on the genus *Nicotiana*.

THE MATERIAL.

The material used in the investigation was turned over to me by Professor E. M. East, who had received it from various parts of the world. Each species had been cultivated in pure lines for at least three generations, so that it may be considered to be fairly well known. The specific names used are those accepted by Comes in his "Monographie du genre Nicotiana," Naples, 1899. To his descriptions, and to such figures as are published in the *Botanical Magazine,* the plants corresponded perfectly. To all intents and purposes, therefore, the plants may be considered wild, although they have been under cultivation several years.

The writer desires to express his thanks to Professor East, under whose direction the investigation was carried out, for the use of the pedigreed material and for much valuable advice. Certain unpublished data obtained in his own researches on *Nicotiana* are incorporated with his consent.

HISTORICAL.

For historical purposes it is only necessary to give a brief review of Hans Winkler's paper, "Über Parthenogenesis und Apogamie im Pflanzenreiche," published in 1908; and the less comprehensive paper, "Parthénogénèse des Végétaux Supérieurs," of L. Blaringhem, published in 1909. Blaringhem in his historical account of this subject, states:

> Déja Camerarius dans sa lettre célèbre sur le sexe des plantes (*De sexu plantarum epistola,* 1694) reconnaît que dans ses essais de castration du Maïs il obtient, malgré l'absence de pollen, le développement de graines fertiles sur les épis latéreaux femelles.

Among the early observers of parthenogenetic[2] qualities in plants are given Spallanzani (1767–1779), Henschel (1817–1818), Lecoq (1827), Girou de Buzareinques (1827–1833), Ramisch (1833–1838), Bernhardi (1834–1839), Tenore (1854), Gasparini (1846) and Naudin (1856). As a few of the plants cited by these authors are at the present time the object of research, Blaringhem gives a list of the observed plants with an indication of the more doubtful.

The list is given as follows:

(*a*) Plantes Dioiques.
- *Bryonia dioïca* d'après Naudin (confirmé en 1904 par Bitter),
- *Cannabis sativa* d'après Camerarius, Spallanzani, Henschel, Girou de Buzareinques, Berhardi et Naudin,
- *Datisca cannabina* d'après Wenderoth et Fresenius (très douteux),
- *Lychnis dioïca* d'après Henschel et Girou de Buzareinques,
- *Mercurialis annua* d'après Lecoq, Ramisch, Naudin et Thuret,
- *Pistacia narbonensis* d'après Bocconi et Tenore,
- *Spinacia oleracea* d'après Spallanzani, Lecoq et Girou de Buzareinques.

(*b*) Plantes Monoiques.
- *Cucurbita Melopepo, C. Citrullus* et autres espèces d'après Spallanzani, Sageret et Henschel,
- *Ficus Carica* d'après Gasparini,
- *Urtica pilulifera* d'après Henschel (très douteux).

Winkler, in his introduction, cites *Cœlebogyne ilicifolia* J. Smith, a diœcius member of the Euphorbiaceæ native to eastern Australia, which had been cultivated since 1829 at Kew in three "weiblichen Stocken," as the first mentioned case of seed production without the assistance of pollen grains. This observation led Smith to believe

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[2] No doubt many of these observations were incorrect, owing to imperfect control.

that pollen is not essential for the perfecting of Euphorbiaceæ seed. In 1857 A. Braun described *Chara crinita* Wallr. as a true case of parthenogenesis. In 1877, Strasburger with the aid of modern technique found that the embryos in *Cœlebogyne ilicifolia* were formed without fertilization, but that parthenogenesis was absent, as the embryos came not from unfertilized eggs, but from adventitious growths (Sprossungen) of the nucellus tissue. In 1900, Juel definitely proved its existence in *Antennaria,* thus establishing its presence in the higher plants.

As botanical investigators do not always agree in the use of the terms parthenogenesis and apogamy, Winkler divides all reproductive phenomena into three divisions, namely: Amphimixis, Pseudomixis, and Apomixis.

1. Amphimixis, which designates the normal sexual process.

2. Pseudomixis, which means the replacement of true sex-cell fusions by a false sexual process. Pseudomixis thus differs from amphimixis, essentially, only in the circumstance that the fusing cells are not differentiated as gametes. As an example of the pseudomictic (pseudomiktische) method of reproduction is cited *Lastrea pseudomas* var. *polydactyla* Wills, in which the sporophyte arises from a prothallium cell, its primordial nucleus fusing with a nucleus from a neighboring cell. Farmer and Digby (1907, p. 191) name this procedure "pseudo-apogamy." All non-sexual nuclear or cell fusions must not be considered as pseudosexual, however, for there is an asexual cell fusion in addition to the sexual and the pseudosexual, as, for example, the nucleus fusion described by Nemec (1902, 1903) in chloralized roots of *Vicia,* and also the frequently mentioned nucleus fusion in the young ascus of the Ascomycetes.

3. Apomixis, which is the replacement of sexual reproduction by another, an asexual process, which is not bound up with nuclear fusions. For it, there is already another term, namely that of apogamy. This latter term was applied by de Bary (1878, p. 479) for the fact, "dass

einer Species (oder Varietät) die sexuelle Zeugung verloren geht und durch einen anderen Reproduktionsprocess ersetzt wird." The word apogamy used with the meaning intended by de Bary covers the term apomixis of Winkler; but as all the recent authors use the expression apogamy in a new sense, the introduction of a new term seems justifiable.

Apomixis is subdivided into vegetative propagation, apogamy, and parthenogenesis:

(*A*) Vegetative propagation consists of the replacement of fertilization by vegetative formations (Ausläuferbildungen), arising of leafy (blattbürtiger) shoots, vivipary and similar examples of simple vegetative division and the adventitious embryo formation from nucellus cells.

(*B*) Apogamy, the origin through apomixis of a sporophyte out of vegetative cells of the gametophyte, is subdivided into (*a*) somatic apogamy, if the cell or the cell complex which produces the sporophyte possesses the diploid chromosome number, and (*b*) generative apogamy, if the mother cells of the sporophyte carry only the haploid chromosome number.

(*C*) Parthenogenesis, the apomictic origin of a sporophyte from an egg, is subdivided into (*a*) somatic parthenogenesis, if the egg possesses a nucleus with the diploid or unreduced chromosome number, and (*b*) generative parthenogenesis, if the nucleus of the egg is provided with only the haploid number of chromosomes.

Winkler remarks, it is probable that the relations between somatic apogamy and apospory are very close, as the former without the latter is surely not thinkable, while the latter (the primary proceeding) may exist without somatic apogamy. Examples of somatic apogamy are given, but no certain cases of generative apogamy are known; nevertheless, Winkler is very certain that their existence is possible.

Somatic parthenogenesis can be obtained in two ways: first, it can combine with apospory, that is, a normal sporophyte cell with the diploid number of chromosomes can grow directly into the gametophyte; second, the gametophyte can arise from the spores in the usual manner, except that the reduction division is discontinued. Examples are known for both cases. After discussing the cell division of the more interesting cases of somatic parthenogenesis, he sums up the families in which it occurs, as follows:

1. Polypodiaceæ (*Athyrium Filix-fœmina* var. *clarissima* Bolton and var. *unco-glomeratum* Stansfield; *Scolopendrium vulgare* var. *crispum Drummondæ*).

2. Marsiliaceæ (*Marsilia Drummondii* R. Br.).

3. Ranunculaceæ (*Thalictrum purpurascens, Th. Fendleri*).

4. Rosaceæ (*Alchimilla* § *Eualchimilla*).

5. Thymelæaceæ (*Wikstroemia indica*).

6. Compositæ (*Antennaria alpina, A. fallax, A. neodioica; Taraxacum; Hieracium* § *Archieracium* and § *Pilosella*, almost completely).

According to Juel (1900, 1904), Murbeck (1901), Guérin (1904) and Strasburger (1904, 1907), somatic parthenogenesis is simply a vegetative process, the egg being merely an ovate-shaped body cell of the sporophyte. Winkler disagrees with this opinion, for if it be true, the female individuals of parthenogenetic plants could produce only female offspring. But this is not the case, for from parthenogenetic seed of *Thalictrum Fendleri*, Day obtained seeds which yielded abundantly staminate and pistillate plants. Thus, it is conclusively proven that cells are not always equivalent, even though they are physiologically and morphologically alike.

Two theoretical cases of generative parthenogenesis are given as thinkable; first, the whole cycle of development could occur without a change in the number of chromosomes, that is, the haploid number is retained throughout; second, a regenerative doubling of the chromosomes could appear in the development of an egg with the haploid number into the sporophyte. No examples of the latter are known to occur in the plant kingdom.

Merogany (Merogonie) is given a brief notice. This expression was first used by Delage (1899), for the successful fertilization of a denucleated fragment of an egg by a spermatozoon. It was established in animals by O. and R. Hertwig (1887) and Boveri (1889) and in the plant *Cystosira barbata* by Winkler (1901).

Parthenocarpy is more fully discussed, as it has much in common with both parthenogenesis and apogamy, and is a great source of danger in investigations made to determine their presence or absence. Noll (1902) introduced the term, and defined it as the capacity of many plants, under exclusion of pollen, to form fruits outwardly normal, but in which seeds are absent or aborted. This condition was discovered by the elder Gärtner (1788) who named it *"frutificatio spuria"* and was for the first time critically investigated by the younger Gärtner (1844), who called it "Fruchtungsvermögen." Winkler thinks that it might be possible to separate the cases of stimulative parthenocarpy, in which the seedless fruits are produced only after pollination with their own or foreign pollen or in consequence of an insect prick or some other irritation; and the cases of vegetative parthenocarpy, in which the seedless fruits are formed without any pollination or other outer irritation. The latter phenomenon is thought to occur less frequently than the former. Noll in 1902 described it in the cucumber (Gurke) and mentioned the then known cases, the fig and the seedless medlar. Ewert[3] has found that several kinds of fruit can develop without the assistance of pollen. The best results were obtained when all the blossoms of an individual plant were protected from fertilization, as otherwise the fertilized flowers were so markedly favored in their development when compared with the remaining unfertilized ones, that the latter dropped while immature.

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[3] Ewert (1909, 1911) has noted the presence of parthenocarpy in the apple, pear, grape and gooseberry, and Kirschner (1900) has noted the same in the quince.

The relation between parthenocarpy and parthenogenesis of higher plants is very close, as all the known cases of parthenogenesis are associated with parthenocarpy, for not only embryos and seeds, but fruits develop at the same time without fertilization. Since both fruits and seeds which appear perfectly normal will develop, although they are without embryos, one can not be positive about parthenogenesis unless the presence of the embryo is ascertained.

In the discussion on the causes of parthenogenesis and apogamy, Winkler suggests the possibility of physico-chemical changes operating in a flower in consequence of non-pollination, and causing the parthenogenetic development of the ovules. Also, similar changes might be induced by the entrance of the pollen tube, even though fertilization did not take place, as when parthenocarpic fruits appear. If mutations occur which can supply the proper conditions for these physico-chemical changes, then it is possible to explain the inheritance of the parthenogenetic character after it has once appeared. Physical changes in the cytoplasm surrounding the egg, as well as changes in the osmotic pressure, are considered as only theoretical explanations for parthenogenesis. If they should be a cause, Winkler asks, why should these changes occur in some flowers and not in others; and if they appear in all flowers, why should not parthenogenetic embryo formations occur in all?

One who is not acquainted with Winkler's and Blaringhem's papers should refer to the originals, as it is impossible to give all the subject matter proper treatment in a brief review. The complete bibliographies appended to these papers are also well worthy of reference.

TESTS FOR THE PRESENCE OF NATURAL PARTHENOGENESIS IN THE GENUS NICOTIANA

The writer obtained no viable seed in his numerous castration experiments with the exception of one doubtful case of *N. plumbaginifolia.* The seed of this exception was secured in a field experiment conducted on the heavy clay loam of western New York, used as a check on the experiments of Professor East made on the light sandy loam of eastern Massachusetts. Since the seed from this one capsule of *N. plumbaginifolia* was all that was obtained from ninety-eight emasculated blossoms of this species, it is reasonable to treat it as the result of an experimental error.

The method of testing for parthenogenesis in these field experiments consisted simply in emasculating and covering the flowers. Both paper sacks and cotton batting were used to protect the stigmas from self or cross-pollination. When the latter covering was used the anthers were removed with the assistance of a small wire hook which minimized the injury to the corolla and the cotton wad was then fastened over the end of the corolla tube with the aid of a rubber band. The supposed advantage of the cotton batting was that it would interfere less with the photosynthesis processes, than the paper sack, as it excludes much less air and sunlight. The seed of *N. plumbaginifolia* was obtained from a capsule covered with the cotton batting; otherwise, no definite results were noted in favor of either covering. As the heavy rains and strong winds will break off the capsules covered with cotton, it is advisable to enclose them with netting sacks.

The extent of these emasculation experiments of Professor East and myself in which not a single seed was produced outside of the capsule of *N. plumbaginifolia* already noted, is already seen by referring to Table I.

Mrs. R. H. Thomas was much more fortunate in her emasculation work, as she obtained fertile seed with no apparent difficulty. Why parthenogenetic tobacco seed should develop so readily in England and so rarely, if ever, in the eastern part of the United States is difficult to understand. The explanation may be found in the differences of the soils and the climatic conditions of the two places, but this assumption is improbable. It seems more likely that new buds which escaped notice were developed in the course of her experiments. This explanation of these divergent results is very probable, as adventitious buds appear for several weeks after the formation of the first buds. Both self-fertilized and parthenogenetic blossoms produce offspring true to the mother species; and consequently an error, if it did occur, could not be detected.

TABLE I

FIELD CASTRATION EXPERIMENT

Species	Mass.			N. Y.		
	No. Buds	Treatment	No. Seed	No. Buds	Treatment	No. Seed
N. alata var. *grandiflora*	14	Emas. and covered	0		Emas. and covered	
N. attenuata				17	Emas. and covered	0
N. Bigelovii	12	Emas. and covered	0			
N. Forgetiana	20	Emas. and covered	0			
N. glutinosa	8	Emas. and covered	0			
N. Langsdorffii	12	Emas. and covered	0	54	Emas. and covered	0
N. Langsdorffii var. *grandiflora*	8	Emas. and covered	0	87	Emas. and covered	0
N. longiflora	16	Emas. and covered	0	45	Emas. and covered	0
N. paniculata	21	Emas. and covered	0			
N. plumbaginifolia	11	Emas. and covered	0	98	Emas. and covered	Several (1 capsule)
N. quadrivalvis	14	Emas. and covered	0			
N. rustica var. *brazilica*	14	Emas. and covered	0	16	Emas. and covered	0
N. rustica var. *humilis*	20	Emas. and covered	0	113	Emas. and covered	0
N. rustica var. *texana*	12	Emas. and covered	0			
N. suaveolens	10	Emas. and covered	0	13	Emas. and covered	0
N. tabacum (broadleaf)	10	Emas. and covered	0	11	Emas. and covered	0
N. tabacum (calyciflora)				83	Emas. and covered	0
N. tabacum (fasciated)	14	Emas. and covered	0			
N. tabacum (Havana)	28	Emas. and covered	0			
N. tabacum (Sumatra)	16	Emas. and covered	0	74	Emas. and covered	0
N. tabacum var. *fruticosa*				77	Emas. and covered	0
N. tabacum var. *macrophylla purpurea*				33		

EXPERIMENTS ON THE ARTIFICIAL PRODUCTION OF APOMICTIC SEED IN THE GENUS NICOTIANA

For the simplification of the following subject matter, the experimental procedures used in the attempted production of parthenogenetic seed have been divided into four classes, namely, the effects of foreign pollen, of mutilation, of fumigation, and of injections.

THE EFFECTS OF FOREIGN POLLEN

Gärtner (Burbidge, 1877), while making species crosses, obtained seed in a few cases which produced plants true to the maternal species and also true hybrids. Mrs. R. H. Thomas (1909) and Professor E. M. East have also observed the same phenomenon in their work. Professor East's results were as follows:

Seed was obtained which produced plants like the mother species and also true hybrids, from crosses *N. paniculata*[4] × *N. alata* var. *grandiflora, N. rustica* × *N. tabacum,* and *N. tabacum* × *N. Bigelovii;* seed which produced plants like the mother species and no true hybrids, from crosses *N. paniculata* × *N. Langsdorffii, N. paniculata* × *N. longiflora, N. paniculata* × *N. Forgetiana,* and *N. Bigelovii* × *N. sylvestris;* and seed which produced no true hybrids on one occasion but did produce true hybrids on other occasions, from cross *N. tabacum* var. *lancifolia* × *N. alata* var. *grandiflora.* These crosses gave per capsule from one to twenty-five good seeds that produced plants true to the mother parent, and many angular and undeveloped seed that produced very few hybrids. In the cases where no hybrids were produced, abortive seeds—probably hybrid in character—were present.

These seeds, true to the mother species, are thought by Professor East to be due to adventitious embryos arising from the tissue of the nucellus, for no case of seed formation after simple castration occurred in some hundreds of experiments, nor did seed giving maternal plants arise in any but wide species crosses giving sterile or nearly sterile progeny. If such be the case, parthenogenesis did not occur in these crosses.

Pollen grains of certain species in the plant kingdom are known to be capable of instigating the development of parthenocarpic fruits and of polyembryonic seed of foreign species, but whether they can cause the parthenogenetic development of ovules is still a question; even

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[4] The authorities for the specific names of the *Nicotiana* species used in these experiments are given on p. 23.

though varieties of *Vitis vinifera* have been noted by Millardet (1901) as giving only *Vitis vinifera* progeny, when pollinated by *Ampelopsis hederacea*. Examples of the parthenocarpic fruits, however, are common. The writer, while attempting to cross the tomato with the Jerusalem Cherry (*Solanum Pseudo-capsicum*) obtained parthenocarpic tomato fruits, but no fruit of any kind developed when the reciprocal cross was made. Parthenocarpic Seckel pear fruits were also produced by the application of Yellow Transparent apple pollen. In the crosses between *Nicotiana* species already mentioned, seed true to the mother parent was produced; but as in the case of the *Vitis vinifera*, there is no positive proof of a parthenogenetic development. What stimulatory effect is imparted by the pollen grain must be due either to an irritation caused by the entrance of the pollen tube or to the exudation of a "growth enzyme."

THE EFFECTS OF MUTILATION

The floral and axial organs of the plants were mutilated by emasculation, by the removal of the anthers, by decapitation, by the removal of both the stigmas and anthers, and by burning various portions of young buds, with the object of upsetting the normal functional processes in such a way as to incite the parthenogenetic development of seed. To simple emasculation and decapitation were added several modifications. Emasculated buds were covered with both paper bags and celluloid covers, but no advantages in favor of either covering could be detected. The decapitated buds were covered with the same two coverings, and in addition buds were left uncovered, but no differences in the results of these three methods were noted. Theoretically, the buds provided with the greatest amount of light and air should be favored in their development, but in this particular case, the results did not permit one to draw conclusions, since only negative results were obtained. Since capsules of *N. tabacum* were found to develop from pollinated flowers as well under the paper bags as under the celluloid covers, the latter covering was soon discarded. The advantages of the paper bags are, first, they cover a great many buds and, second, they are put on and removed very easily.

Clusters of buds that had been emasculated as well as those that had been decapitated were also ringed a few inches below the buds. The operation was performed with the hope that the food stored above the injury would upset the natural equilibrium of nutrition in such a way as to cause the development of the ovules. In these ringing experiments only negative results were obtained, although Ewert found that injuries to gooseberry branches favored the development of parthenocarpic fruits.

Neither the tickling of *N. tabacum* buds, varying in size from small to large, with a camel's hair brush every half hour for five consecutive hours, nor the cutting of the bases of *N. suaveolens* and *N. commutata* buds, with the point of a scalpel, gave results. Professor East has, however, produced a slight swelling in the capsules, but no seeds, by occasionally tickling the buds of the following species with a sharp-pointed instrument—*N. tabacum* (vars. fasciated, Sumatra, broadleaf, and Havana), *N. alata, N. Bigelovii, N. Forgetiana, N. glutinosa, N. Langsdorffii, N. Langsdorffii* var. *grandiflora, N. longiflora, N. paniculata, N. plumbaginifolia, N. quadrivalvis, N. rustica* (vars. *humilis, brazilica,* and *texana*).

Stimulation was also attempted, as already noted, by burning or rather singeing buds varying in development from very young to nearly mature, with a heated platinum wire. The hot wire was applied to various portions of the buds, namely, to the base, to the top of the ovary, the stigma, and to both the stigma and the ovary. When the pistils were not injured, the blossoms were covered with bags, but covering was not considered essential when the pistils were made functionless. *N. Langsdorffi* var. *grandiflora* and *N. plumbaginifolia* gave no results, but one capsule of *N. tabacum* produced fifty-six apparently normal seeds—none of which germinated after a period of several months' rest. The stage of maturity and the parts burned of each bud were not recorded and therefore the condition and exact treatment of this particular bud are unknown.

As a check on the uncovered decapitated pistils,[5] pollen from the same and other varieties was applied directly to the cut surface of the styles; in addition to pollen, cane-sugar solutions varying from 25 per cent. to 50 per cent. in strength,[6] stigmatic fluids, and in one instance nectar taken from the base of buds, were also applied. If the shortened pistils could be fertilized, it was thought that certain impossible crosses, as *N. alata* × *N. Forgetiana* and *Mirabilis Jalapa* × *M. longiflora* might be made, providing the difficulty existed in the extreme length of the styles. In one case, the applied stigmatic fluid and the pollen grains were taken from the same species. This precaution was used, as it was thought that the stigmatic fluid of one species might contain an enzyme or an inhibiting substance which would prevent the germination of foreign pollen grains. This supposition was supported by the growth of pollen grains in stigmatic fluids placed within Van Tieghem cells. For instance, the *N. glauca* pollen grains germinated and made good growth in the stigmatic fluid taken from *N. glauca* plants, while *N. suaveolens* pollen grains did not extend their pollen tubes in the stigmatic fluid taken from *N. Forgetiana*. If the tissue of the style contains an inhibiting agent, also, the germination of pollen grains on the cut style would be of no benefit. (This supposition may explain the negative results.[7])

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[5] Ewert (1909) quotes Gärtner who states that Henschel obtained seven ripe fertile seed from six blossoms of *Salvia sclarea* whose pistils had been destroyed, and four abortive seeds from three capsules of *Polemonium gracile* whose pistils had also been destroyed.

[6] A 33⅓ per cent. strength was used in the later work, as the pollen grains of *N. glauca*, *N. longiflora* and *N. tabacum* germinated readily and made good growth in this solution.

[7] The presence of one or more inhibiting agents might be used to explain the failure of grafts between plant species, for they may act like the antibodies, produced in animals by the transference of the blood of one species to that of another, and cause death.

Whether the pollen tubes in these experiments reached the ovules is not known, but probably not, since no fertile seed was produced. The production of numerous seed normal in appearance indicates, however, either that the pollen tubes must have stimulated the nucellus tissue in some way, or that normal seed development was started but not finished, for no seed of any kind was produced in the decapitated blossoms where pollen grains were not applied.

The total abortive seed produced by the pollination of the decapitated styles included two from *N. tabacum* where the stubs were covered with 50 per cent. cane sugar solution and self-pollinated, four from the same species where the stubs were covered with stigmatic fluid and self-pollinated, twenty-seven from *N. paniculata* where the stubs were covered with stigmatic fluid and self-pollinated, and fourteen from *N. tabacum* where *N. Forgetiana* pollen and no fluid was applied.

In connection with the decapitation experiments, an experiment on the grafting of pistils[8] was conducted. One hypothesis for the non-crossing of certain species, as has already been mentioned, is the extraordinary length of the style. By removing a portion of the style and grafting the stigma end of a pistil of either the same or another species to the stub, the style was shortened from one to one and a half inches. Immediately after grafting, the stigmas were pollinated. From one of the five grafted *N. tabacum* blossoms was produced one abortive seed. The development of this one seed may or may not have been due to the penetration of one or more pollen tubes, as in the cases where pollen grains were applied directly to the decapitated pistils.

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[8] The grafting technique is simple, nevertheless, the operation is difficult, owing to the small size of the styles. A light splinter was first attached to the base of the style by means of collodion, then the upper portion of the style was removed with a sharp knife. The end of the pistil to be grafted on the stub was cut off at the same angle and placed on the stub and made fast with the collodion.

MUTILATION EXPERIMENTS—FORCING HOUSE

TABLE II

Species	No. Clusters	No. Buds	Treatment	Stig. Fluid	Pollen	No. Seed	Remarks
N. alata var. *grandiflora*...	2		Decap.	Self	*N. Forgetiana*	0	
N. alata var. *grandiflora*...	1		Decap.	Self	*N. Sandaræ*	0	
N. alata var. *grandiflora*...	2		Decap.	Self	Self	0	
N. alata var. *grandiflora*...	2		Decap.	$33\frac{1}{3}$ per cent. sugar	*N. Forgetiana*	0	
N. alata var. *grandiflora*...	2		Decap.	$33\frac{1}{3}$ per cent. sugar	*N. Langsdorffii*	0	
N. alata var. *grandiflora*...	1		Decap.	$33\frac{1}{3}$ per cent. sugar	*N. Sandaræ*	0	
N. alata var. *grandiflora*...	1		Decap.	$33\frac{1}{3}$ per cent. sugar	Self	0	
N. Forgetiana............	1		Emas. and covered			0	
N. Forgetiana............	1		Decap.	*N. Langsdorffii*	*N. Langsdorffii*	0	
N. glauca...............	3	5	Emas. and covered			0	
N. glauca...............	2		Decap.			0	
N. glauca...............	1		Decap. and bagged			0	
N. glauca...............		3	Hot pt. wire and emas.			0	Singed stigmas.
N. Langsdorffii...........		5	Decap.	Self	*N. Forgetiana*	0	
N. Langsdorffii...........	1		Decap.	$33\frac{1}{3}$ per cent. sugar	*N. Forgetiana*	0	
N. Langsdorffii...........	2		Hot pt. wire and emas.			0	Singed base of buds.
N. Langsdorffii...........	1		Cut and emas.			0	Cut base of buds with scalpel point.
N. paniculata............	4	12	Emas. and bagged			1	Seed abortive.
N. paniculata............	5	5	Decap. and bagged			0	
N. paniculata............		3	Decap.	Self	Self	27	Seed abortive.
N. paniculata............	2		Decap.	25 per cent. sugar	*N. Tabacum*	0	
N. paniculata............	4		Hot pt. wire and emas.			0	Singed stigmas.
N. plumbaginifolia.......	2		Hot pt. wire and emas.			0	Singed base of buds.

TABLE II (*Continued*)

Species	No. Clusters	No. Buds	Treatment	Stig. Fluid	Pollen	No. Seed	Remarks
N. Sandarae	1		Decap.			0	
N. Sandarae	1		Decap.	Self	*N. Forgetiana*	0	
N. suaveolens		3	Decap.	Self	*N. Forgetiana*	0	
N. suaveolens	1		Cut and emas.			0	Cut base of buds with scalpel point.
N. tabacum	5	12	Decap. and covered			0	
N. tabacum	2		Decap. and bagged	0	*N. Forgetiana*	14	Seed contained in one locule.
N. tabacum	3	28	Decap. and bagged	0	Self	6	Three seeds in one capsule and one seed in other capsules.
N. tabacum	14	10	Emas. and covered			0	
N. tabacum	1	15	Emas. and ringed			0	
N. tabacum		8	Emas. and tickled			0	
N. tabacum	1		Decap. and grafted		Self	1	
N. tabacum	2	2	Decap. and ringed			0	
N. tabacum	1	1	Decap.	$33\frac{1}{3}$ per cent. sugar	*N. Forgetiana*	0	
N. tabacum	1	1	Decap.	50 per cent. sugar	*N. glauca*	0	
N. tabacum	1	2	Decap.	50 per cent. sugar	Self	2	Seed found in one capsule.
N. tabacum	1	1	Decap.	Nectar	Self	0	
N. tabacum		14	Hot pt. wire and emas.			56	Singed stigmas. Seed borne in one capsule.
N. tabacum	1	4	Hot pt. wire and emas.			0	Singed both stigmas and ovaries.

The mutilation experiments all proved to be valueless in the production of fertile seed; nevertheless, they were interesting, since they were the only methods, except where actual crosses were made and where chloroform gas was used, which caused any seed development.

(See Table II—Mutilation Experiments.)

EFFECTS OF FUMIGATION

Several species, the names of which are listed in Table III, were exposed before the plants had reached the flowering stage to gases given off by acetone, carbon tetrachloride, chloroform, ether, ethyl acetate, ethyl bromide, ethyl chloride, ethyl iodide, and formaldehyde. As in the previous experiments, the buds were emasculated and bagged. The object of this experiment, as of the one on mutilation of the plants, was to endeavor to upset the normal development of the floral organs in such a way as to cause the production of seed without the aid of fertilization.

The methods used in conducting this experiment were simple. Plants, growing in six-inch pots, were fumigated approximately one seventh of a cubic foot when drawn in at the top. The bags were closed either around the stems which had been previously surrounded with cotton batting or about the top of the pots, the method of treatment depending on the height of the plants. When everything was in readiness for fumigation, the gas was set free by the opening of the vial which was glued to the interior of the bag. Though the seams and the bottoms of the bags were sealed by melted paraffine, the retention of all the gas was not expected. A sufficient quantity was present, however, when acetone and formaldehyde were used, for the foliage of the plants, treated with these gases, to become noticeably injured.

TABLE III

FUMIGATION EXPERIMENTS—FORCING HOUSE

Species	Ht. Plant, In.	Liquid	C.c. per Cu. Ft.	Hrs. Exposed	No. Seed	Remarks
N. alata var. *grandiflora*...	3	Ethyl acetate	8	24	0	Leaves drooped, three capsules developed.
N. alata var. *grandiflora*...	1½	Ethyl acetate	12	24	0	Leaves drooped.
N. Bigelovii.............	4	Acetone	12	40	0	Several leaves injured.
N. Bigelovii.............	2¼	CCl_4	12	40	0	Slight injury.
Dewey's Sport No. 1......	5	Ethyl acetate	4	43	0	No injury.
Dewey's Sport No. 1......	9¾	Ethyl acetate	4	72	0	No injury, six capsules developed.
Dewey's Sport No. 1......	4¼	Ethyl acetate	6	43	0	No injury.
Dewey's Sport No. 1......	9¾	Ethyl acetate	6	72	0	No injury, three capsules developed.
Dewey's Sport No. 1......	5	Chloroform	2	43	0	No injury.
Dewey's Sport No. 1......	12¼	Chloroform	2	72	0	One capsule had six locules, six capsules developed.
Dewey's Sport No. 1......	4	Chloroform	4	43	0	No injury.
Dewey's Sport No. 1......	9⅝	Chloroform	4	72	0	No injury, one capsule developed.
Dewey's Sport No. 1......	6	Formaldehyde	4	43	0	
Dewey's Sport No. 1......	13½	Formaldehyde	4	72	0	Five capsules developed.
Dewey's Sport No. 1......	3¾	CCl_4	4	43	0	No injury.
Dewey's Sport No. 1......	9⅛	CCl_4	4	72	0	No injury, four capsules developed.
Dewey's Sport No. 1......	5½	CCl_4	6	43	0	No injury.
Dewey's Sport No. 1......	11¼	CCl_4	6	72	0	No injury, five capsules developed.
N. Forgetiana...........	1½	Formaldehyde	8	72	0	
N. longiflora.............		Ethyl chloride	12	24	0	Four capsules developed.
N. longiflora.............	Sessile	Ethyl iodide	12	24	0	
N. longiflora.............	Sessile	Ethyl iodide	12	24	0	Two capsules developed.
N. longiflora.............	2¾	Ethyl acetate	12	24	0	Two capsules developed.
N. longiflora.............	Sessile	Ethyl acetate	12	24	0	Four capsules developed.
N. paniculata............	4½	Ethyl bromide	2	22	0	No injury.
N. paniculata............	5	Ethyl bromide	4	22	0	No injury.
N. paniculata............		Ethyl bromide	6	20	0	Cover a bell-jar—not a paper bag.
N. paniculata............	6¾	Ethyl bromide	8	72	0	No injury.
N. paniculata............	6¼	Ethyl bromide	12	72	0	No injury, seven capsules developed.
N. paniculata............	6	Formaldehyde	4	20	0	
N. paniculata............	7	Formaldehyde	2	20	0	
N. paniculata............	5½	Acetone	2	22	0	Slight injury to foliage.
N. paniculata............	7	Acetone	4	22	0	No injury to foliage.
N. paniculata............	10½	Chloroform	1	22	2	No injury, one capsule developed.
N. paniculata............	10	Chloroform	2	22	0	No injury.
N. paniculata............	11	Ether	4	22	0	No injury.
N. plumbaginifolia........	Short	Ether	12	24	0	
N. plumbaginifolia........	Short	Ether	12	24	0	
N. plumbaginifolia........	10½	Ethyl iodide	8	24	0	
N. plumbaginifolia........	14½	Ethyl iodide	8	24	0	
N. plumbaginifolia........	1½	Ethyl bromide	12	40	0	One capsule developed.
N. quadrivalvis...........	8¼	Ethyl bromide	12	24	0	No injury, one capsule developed.

TABLE III (*Continued*)

Species	Ht. Plant, In.	Liquid	C.c. per Cu. Ft.	Hrs. Exposed	No. Seed	Remarks
N. quadrivalvis	9½	Ethyl bromide	12	24	0	No injury, two capsules developed.
N. quadrivalvis	8	Ethyl bromide	8	24	0	No injury, two capsules developed.
N. quadrivalvis	10	Ethyl bromide	8	24	0	No injury.
N. quadrivalvis	7	Ethyl chloride	12	24	0	Three capsules developed.
N. quadrivalvis	6	Ethyl chloride	12	24	0	Three capsules developed.
N. quadrivalvis	9	CCl_4	4	22	0	No injury.
N. quadrivalvis	12	CCl_4	2	22	0	No injury.
N. rustica var. *texana*	6¼	Acetone	4	43	0	No apparent injury.
N. rustica var. *texana*	20⅛	Acetone	4	72	0	Terminal growth injured, four capsules developed.
N. rustica var. *texana*	9	Acetone	6	43	0	Terminal leaves, slightly injured.
N. rustica var. *texana*	21¼	Acetone	6	72	0	One leaf injured, four capsules developed.
N. rustica var. *texana*	5	Ethyl bromide	4	43	0	No injury.
N. rustica var. *texana*	17	Ethyl bromide	4	72	0	No injury, seven capsules developed.
N. rustica var. *texana*	5¾	Ethyl bromide	6	43	0	One leaf slightly injured.
N. rustica var. *texana*	17½	Ethyl bromide	6	72	0	One terminal blossom leafy, six capsules developed.
N. rustica var. *texana*	7	Ether	4	43	0	No injury.
N. rustica var. *texana*	15¾	Ether	4	72	0	Terminal bud injured and produced leafy blossom. Eight capsules developed.
N. rustica var. *texana*	6¾	Ether	6	43	0	No injury.
N. rustica var. *texana*	18	Ether	6	72	0	No injury, thirteen capsules developed.
N. Sandaræ		Chloroform	8	24	0	No injury, three capsules developed.
N. Sandaræ		Chloroform	12	24	0	No injury, one capsule developed.
N. sylvestris	Sessile	Chloroform	12	24	0	Leaves (outer) turned yellowish after two days.
N. sylvestris	Sessile	Chloroform	12	24	0	
N. sylvestris	Sessile	Ether	8	24	0	
N. sylvestris	Sessile	Ether	8	24	0	
N. sylvestris	Sessile	CCl_4	12	24	0	No injury.
N. sylvestris	Sessile	CCl_4	12	24	0	No injury.
N. tabacum var. *fruticosa*	11	Ether	8	72	0	No injury.
N. tabacum var. *fruticosa*	5½	Ether	12	72	0	No injury.
N. tabacum var. *fruticosa*	7¼	CCl_4	8	72	0	No injury.
N. tabacum var. *fruticosa*	5⅜	CCl_4	12	72	0	No injury.
N. trigonophylla	5	Ethyl bromide	12	40	0	
N. trigonophylla	1½	Acetone	12	40	0	Leaves injured.
N. trigonophylla	3½	CCl_4	12	40	0	No injury.

Untreated plants of all of the above species were held as checks on the results of each test. A *N. rustica* var. *texana* plant produced one leafy terminal blossom, otherwise, all the plants were normal.

A *N. paniculata* plant treated with chloroform gave two abortive seeds, but none of the other species produced a seed. *N. rustica* var. *texana,* however, after two exposures to acetone vapor underwent very marked morphological changes in the structure of the terminal blossoms, both of the main and of the lateral stems. In other words, the most exposed buds suffered the greatest injury. As the ether, ethyl bromide, and check treatments produced one blossom apiece which was similarly affected, and no other species, even though treated with acetone, was injured in the same way, indicates that the *N. rustica* var. *texana* floral parts are somewhat unstable. This opinion is substantiated by Penzig who in his *Pflanzen-Teratologie* cites observations where *N. rustica* blossoms have been modified to such a degree that the petals have turned green and where five blossoms have been compressed into a common calyx. Perhaps the presence of a small amount of chlorophyll in the greenish yellow corollas is an indication of a close relationship of the petalous to the leafy condition. Even though the *N. rustica* blossoms are easily modified, it is very evident that the acetone vapor caused a disturbance in the natural development of the floral organs, for the two treated plants were affected in the same way and degree. The calyxes, corollas and stamens were modified markedly, while the carpels and pistils and most of the stamens were usually normal in appearance. For instance, in some cases the calyxes were fused together and enlarged to such a size that they resembled distorted and crinkled leaves. One blossom had three sepals fused to the corolla and two sepals located one half inch below the base of the blossom. The lower two had a node as distinct as any leaf on the branch, and within their axis were borne two small buds, which lacked calyxes. One of the upper three sepals also bore a similar naked bud in its axis. It may be that in this case the acetone vapor stunted the branches in such a way that many latent buds were present in a very small space. The corollas in some cases were entirely replaced by small green leaves—smaller than the sepals—and in other cases they were partially replaced by leafy tissue. A few stamens had their filaments flattened and their anthers replaced by a small green leaf. These changes might be advanced, as an evidence of the evolutionary development of the floral organs, if the theory that these organs are simply modified leaves and that reversions are frequently caused by injuries were not already so well substantiated. Whether any mutations might have occurred in the progeny produced from these blossoms is unknown, as fertilization of the ovules was not attempted. No parthenogenetic seed was obtained from these injured blossoms, and this might have been expected, since leafy formations in the blossoms are generally accompanied by sterility.

EFFECTS OF LIQUID INJECTIONS

The forcing of liquids into the plants was performed with the same object in view as in the preceding experiments, viz., to endeavor to stimulate cell division and thus possibly produce unfertilized seed. To certain liquids has been ascribed the power of being able to cause mutations when injected into the buds of certain plants, but in this experiment all the injections were made directly into stems of plants, eight to twenty inches in height.

The apparatus used was simple. Glass capillary tubes were connected by rubber tubing to glass tubes, about 30 inches long and about one quarter inch in diameter, which contained the liquids. The rubber tubing permitted the stems to lengthen without disturbing the operations. The end of the capillary tube was inserted from one eighth inch to one quarter inch into the stem, the distance depending upon the diameter of the stems and 1 inch to 15 inches below the terminal bud. An application of collodion held the capillary tube in place and stopped all leakage. After having supported the tube, the pinchcock—previously fastened to the rubber tubing—was released and the liquid flowed into the stem as rapidly as it could be used by the plant. The injection was assisted by the weight of its own column, and, in the most cases, by the addition of a short column of mercury, suspended by the surface tension of the liquid. The use of the mercury required considerable care, for when the surface tension was overcome by a jar, the mercury sank to the bottom and plugged the capillary tubes.

The treated species were: *N. tabacum* var. *fruticosa*, *N. paniculata*, *N. Langsdorffi* var. *grandiflora*, *N. Langsdorffii*, *N. alata* var. *grandiflora*, *N. attenuata*, and *N. Sandaræ*.

The materials used for the injections are: Sodium phosphate, butyric and valeric acids, ethyl acetate, acetone, benzol, chloroform, formaldehyde, methyl blue, saffranin and thiazin. The last three are simply stains and were used to trace the course of the liquids. The coloring matter was found to follow the vascular bundles of the stems and the leaves for several inches, and yet the slightest trace was not discovered in the buds. Acetone, butyric, and valeric acids of .5 per cent. strength caused severe injury, formaldyhyde at 2 per cent. caused a slight injury to the foliage, but no other liquid caused a noticeable disturbance.

All the treated plants, as in the previous experiments, had at least one cluster of buds emasculated and bagged, but all to no purpose, since not even one abortive seed developed.

SUMMARY

1. Seed giving plants true to the maternal species in the F_1 generation accompanied by aborted seed probably hybrid in nature, was found when certain *Nicotiana* species were cross-fertilized. Hybrid plants and plants purely maternal were obtained from the same capsules in other crosses.

2. The capsules of several *Nicotiana* species were

caused to swell slightly by merely tickling them with a sharp-pointed instrument, but no seeds were produced.

3. Abortive seed probably without embryos was produced by singeing young buds with a hot platinum wire, by the exposure of young plants to chloroform gas, and by cutting away a portion of the pistil and pollinating the stub both with and without the accompaniment of a germinative fluid.

4. Abortive seed was produced by shortening the pistils of a flower and grafting the stigma end of another pistil on to the stub and pollinating the same.

5. The ringing of the branches below a cluster of buds did not assist in the production of seed.

6. No seed was produced by the simple methods of emasculation and decapitation of blossoms, except in one doubtful case of *N. plumbaginifolia.*

7. It is likely that an agent inhibitory to the growth of pollen grains is present in the stigmatic fluids of certain species of the genus *Nicotiana;* at least, the pollen grains of *N. suaveolens* did not germinate in *N. Forgetiana* stigmatic fluid when placed within a Van Tieghem cell.

8. The exposure of young *N. rustica* var. *texana* plants to acetone gas caused the transformation of the corollas and the stamens of most of the terminal flowers into leafy tissue; otherwise, except in the mentioned case of the chloroform, no results were secured by the use of anaesthetic and toxic gases.

9. The injection of chemicals into the stems of tobacco plants was valueless in the production of seed.

10. As no unquestionable case of parthenogenetic seed was produced in the several hundred trials, it seems very improbable that parthenogenesis exists in the genus *Nicotiana*—at least in the species tested. The seed obtained in the crosses which came true to the mother species is probably polyembryonic—the stimulus of development being imparted either by the penetrating pollen tubes or by a substance exuded from the same.

NICOTIANA SPECIES USED IN THE EXPERIMENTS

- *N. alata* Lk. & Otto var. *grandiflora* Comes.
- *N. attenuata* Torr.
- *N. Bigelovii* Wats.
- *Dewey's Sport* No. 1.
- *N. Forgetiana* Sand.
- *N. glauca* Grah.
- *N. glutinosa* L.
- *N. Langsdorffii* Weinm.
- *N. Langsdorffii* Weinm. var. *grandiflora* Comes.
- *N. longiflora* Cav.
- *N. paniculata* L.
- *N. plumbaginifolia* Viv.
- *N. quadrivalvis* Pursh.
- *N. rustica* L. var. *brazilica* Schrank.
- *N. rustica* L. var. *humilis* Schrank.
- *N. rustica* L. var. *texana* Comes.
- *N. Sandaræ* Hort. (hybrid).
- *N. suaveolens* Lehm.
- *N. sylvestris* Speg & Comes.
- *N. tabacum* (broadleaf).
- *N. tabacum* (calyciflora).
- *N. tabacum* (fasciated).
- *N. tabacum* (Havana).
- *N. tabacum* L. var. *fruticosa* Comes.
- *N. tabacum* var. *lancifolia* (W.) Comes.
- *N. tabacum* L. var. *macrophylla purpurea.*
- *N. tabacum* L. (Sumatra).
- *N. trigonophylla* Dun.

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SHORTER ARTICLES AND DISCUSSION

SIMPLIFIED MENDELIAN FORMULÆ

I WAS somewhat surprised by Morgan's and Castle's suggestions for a simplification of Mendelian formulæ.[1] My surprise was not occasioned so much by the forms these suggestions took as by the fact that any pronounced changes were deemed necessary. I had not only employed the usual formulæ in my own work but had found no difficulty worth mentioning in understanding the formulæ used by most other workers in Mendelian fields. My experience with students in elementary courses in genetics had not prepared me for the idea that such formulæ were particularly difficult. Nevertheless I believe in simplifying the formulæ if some system can be found that will be applicable to all sorts of Mendelian inheritance. I believe, however, that I have no right to adopt formulæ for my own cases, no matter how simple they might be, if the same type of formula could not readily be applied to the materials with which other investigators are working. Such procedure on my part would result in no end of confusion if followed by any considerable number of workers each using his own special type of formula. The important question now is not whether I prefer a new style of formula that fits my case but whether it will fit all sorts of cases so that, if it is an improvement on the old style, it can be adopted by others and not necessitate the use of two styles where but one sufficed before.

Let us examine Morgan's and Castle's suggestions in the light of these remarks. Morgan's principal objection to the usual type of formula—that "it is not sufficiently elastic to allow the introduction of a new term in the series, unless a complete revision of the method is made each time that a new mutation in kind occurs"—seems to me to have little merit. Morgan uses eye color in *Drosophila* to illustrate his contention. Four eye colors had been designated as follows: red *PVO,* vermilion *pVO,* pink *PvO,* and orange *pvO.* A fifth color, eosin, arose and was found to produce red when crossed with orange, and hence was assumed to have the formula *PVo.* Morgan regards this as "inconsistent with the scheme already adopted because the small letter *o* stands for a character called eosin," whereas the capital letter *P* had been used for pink, *O* for orange, *V* for vermilion,

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[1] AMERICAN NATURALIST, 47: 5–16, and 47: 170–182, 1913.

etc. Morgan's trouble lies in the fact that he is attempting to force a letter to represent a *character* rather than merely one of the *factors* concerned in the development of that character or to represent the character and one of the factors. As a matter of fact, in the formula PVo, the character eosin is not represented by o but by PV when O *is absent* (with the addition, perhaps, of many factors as yet unknown). Similarly P does not stand for pink but for *one* of the factors concerned in the production of pink. One of the other factors concerned in the development of pink Morgan has identified and named O; there are probably other factors as yet unidentified. For orange he has identified only a single factor and that is this same O. No one has shown more clearly than Morgan that a character is not *determined* by a single factor. Why then should it be thought necessary to designate the first factor identified for any character, say pink, by the initial letter of that word? It is quite likely that P is no more important in the production of pink than is O. And it is equally probable that O is no more concerned in the development of orange than are perhaps a half dozen other factors not yet identified. The logical thing in such cases is to adopt Baur's $A \cdot B \cdot C \cdot$ designations, which fit in readily with current Mendelian usage. True, as Morgan insists, this necessitates the constant use of a key. But what system does not? What is there in Morgan's PVO, or even in his later PVE, to suggest red color?

It is fortunate that Mendelians "have not always taken the pains to state explicitly that the symbols represent both a factor and a residuum," for this, it seems to me, is not true. The residuum left when any factor is lost is usually not represented except by the few factors that have been identified in it. It is careless without doubt to leave so much to be taken for granted, but it would be cumbersome to have to write for pink

$$PvOX_1X_2X_3 \cdots X_n.$$

Perhaps we might use a single X to represent an unknown number of unidentified factors, or perhaps it would be as well to use UR for this unexplored residuum.

I am inclined to agree fully with Castle that Morgan's suggestion for a change in the current Mendelian formulæ is "confusion worse confounded," but here our agreement stops. I can see that it might be possible to do away with the use of small letters, since on the presence-and-absence hypothesis they represent nothing but the absence of factors designated by the corresponding capital letters. The designations of eye colors in

Drosophila (if we adapt Morgan's earlier scheme) would then become *PVO, VO, PO, PV* and *O,* instead of *PVO, pVO, PvO, PVo* and *pvO,* for red, vermilion, pink, eosin and orange respectively. The great difficulty in thus leaving out the small letters comes in distinguishing the heterozygous from the homozygous condition. True we can let *PVO* stand for the heterozygous condition of the three factors and *PPVVOO* for the homozygous condition. Then *PPVO* would indicate what is now commonly expressed by *PPVvOo.* But we now use the single letters when we wish merely to designate *phenotypic* differences or to indicate the factors in gametes, where of course all factors are simplex, and employ duplicate letters only when we desire to indicate *genotypic* differences. If then the small letters are discarded, we shall need to use some arbitrary sign to distinguish phenotypes from genotypes, else *PVO* might as now stand for a group of phenotypically like individuals or for a class having the genotypic constitution now commonly indicated by *PpVvOo.*

But Castle's suggestion is far from what is outlined above. He would use no letter to represent red eye color in *Drosophila* but merely write *normal.* For vermilion he would use *v,* for pink *p,* for pink-vermilion *pv,* etc. My first notion on reading the list of designations for eye color in fruit flies was that Castle used them only as abbreviations for the names of the colors, and *v* is really a better abbreviation for vermilion than is say Verm. or V'r'm'l'n. Now why, I thought, should one suggest such *character* abbreviations as a revised *Mendelian* terminology when Mendelism is concerned fundamentally with *gametic* factors and only incidentally with the *zygotic* characters that happen to develop through the interaction of particular combinations of gametic factors in a particular environment. But Castle's terminology is not concerned with mere abbreviations for characters, as witness:

> The revised terminology is more convenient than Morgan's in calculating the expected result of any mating, and is equally reliable. The results of every possible mating within the series can be readily computed without the confusing presence of the large letters.

Here I must frankly admit that I have experienced great difficulty in using Castle's terminology in calculating the expected results of matings in case of the eye colors in *Drosophila,* though this is probably due to some misunderstanding of just how Castle's formulæ are to be used. For instance, a cross of *v* (vermilion) with *p* (pink) should, if ordinary usage were followed, produce *vp* (vermilion-pink) whereas it actually produces red.

The use of capital letters for dominant factors and small letters for recessive ones, while it may work well in some cases, would be difficult of application in others. Brown color in beans is dominant[2] to yellow but recessive to black. Shall we then use *B* or *b*? True, Castle limits the use of the capital letter to the "factor responsible for a variation which is dominant in crosses with the *normal*" (italics mine), but who is to say what is the normal color of beans? The use of capital letters for some characters and small letters for others is, however, a minor matter and would not alone disqualify the proposed terminology.

When one is considering any new scheme, it is natural that he should try it out on material with which he is familiar. I have, therefore, attempted to apply Castle's suggestions to aleurone colors in maize. To make the matter as simple as possible, I will leave out of consideration color patterns and also the various dilutions or intensities of color and limit myself to the statement that aleurone may be purple, red, or white. In an account of certain crosses published last year[3] I made use of the symbols suggested by East and Hayes: *C* a general color factor, *R* concerned with *C* in the production of red, *P* resulting in purple when both *C* and *R* are present, and *I* an inhibitor of color development. I listed 14 kinds of white aleurone.[4] Now if we were to adapt Castle's formulæ for albino mice to these white maize types, we might use *wP* for whites transmitting purple in crosses, *wr* for whites transmitting red, and *wPr* for those transmitting both purple and red. But there are seven kinds of whites, all of which might yield purples in appropriate crosses with non-purples. How shall we distinguish between them? Of course we could add to *w* the letters *C, R, P, I* or such ones of these as might be necessary to indicate the factors latent in a particular white, but *wCRPI* is no improvement over *CRPI* from the standpoint of simplicity. Students in elementary courses in genetics who have used maize for laboratory material have had little trouble in calculating that when a white maize *CCrrPpIi* is crossed with another white maize *ccRRPpIi* there

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[2] On the presence-and-absence hypothesis it is hardly allowable to speak of the relation of two non-allelomorphic characters in terms of dominance. Brown is epistatic to yellow and hypostatic to black. Each is dominant to its own absence.

[3] AMERICAN NATURALIST, 46: 612–615, 1912.

[4] I now have much additional evidence for my assumption as to the different sorts of white aleurone.

should result, on the average out of every 16 grains in the first generation, 3 purple, 1 red and 12 white grains. I do not doubt that the calculation could be made with equal rapidity and accuracy if the small letters were omitted and the capital letters used in the same significance. The cross would then be: *CCPI* × *RRPI*. The greatest difficulty with this plan would come in designating the white now known as *crpi*, unless we employ a mere dash, ——. It is possible that there is some simple way of applying Castle's scheme to such a case as this, a way which I have stupidly overlooked or perhaps I have not understood the scheme at all. If there is some simple terminology that is workable, I shall be glad to use it, but I must confess to being suspicious of very simple formulæ for the complex phenomena of inheritance.

R. A. Emerson

University of Nebraska

THE INFLUENCE OF THE DEVELOPMENT OF AGRICULTURE IN WYOMING UPON THE BIRD FAUNA

Wyoming is an interesting field of inquiry for the zoologist, not only because it is new and unexplored, but because changing agricultural conditions in the state have unbalanced the fauna, so that new adjustments are taking place.

This is particularly true of the birds, and since going to the state two years ago, I have been collecting data from various sources to learn to what extent the former distribution of the birds has been affected.

The larger part of Wyoming remains practically unchanged as yet by the presence of man, but numerous towns have sprung up, with the attendant planting of shade trees, which furnish good nesting places for birds, and the same may be said of the ranches. It is in these restricted areas that the changes in adjustment may be expected to be most manifest.

Again the increased raising of grain in many localities has produced a more abundant food supply for birds which live largely upon seeds.

Old residents of the state, and collectors whose experience extends over a period of several years, are almost universally of the opinion that certain birds are much more abundant now than formerly. In their replies to circular letters sent out, they have frequently specified the species which have been affected in this way. It will be readily seen that those mentioned are the ones which would be expected to show the influences of the factors indicated above. Those most frequently mentioned as having increased in numbers include the robin, meadow lark, bluebird, mourning dove, crow, grackle and cow birds.

Many birds which were reported as rare in W. C. Knight's "Birds of Wyoming," published in 1902, are now reported by collectors as being fairly common. It seems, therefore, that Wyoming is rapidly becoming a more hospitable place for birds in general.

There is considerable evidence to show that the quail has only recently migrated into the state, and that its migration was from Nebraska up the valley of the Platte River. At present it has penetrated as far as the mouth of Horse Shoe Creek on the Platte and as far as Uva on the Laramie River, which is a tributary of the Platte. The quail seems to have appeared in Wyoming first about 1890, and one informant thinks that it dies off during the winters from lack of food, and is prevented from further migration into Wyoming only because of lack of seeds.

A similar evidence of the effect of food supply upon the presence of birds in the state is given by Stanley Jewitt, a government collector, who says:

> I have found some kinds [of birds] very common in the more cultivated sections of Idaho and Wyoming during the last three years that were almost, if not entirely, unknown a few years ago. Such birds as the bobolink, yellow-headed blackbird and lark bunting, follow the farmer as soon as irrigation systems are completed.

One of the most interesting points ascertained is in regard to the English sparrow. In reply to a query as to whether there are any isolated towns in Wyoming to which this sparrow has not yet found its way, Professor B. C. Buffum replied that there seem to be none of these sparrows in some of the smaller interior towns, such as Tensleep and Nowood.

About ten or fifteen species of birds new to the state have been reported since the publication of Professor W. C. Knight's book in 1902. It is hardly possible that these have all come into the state since that time. Most of them had probably been overlooked before, but however this may be, new birds can be expected to enter the state from time to time, and certain of those already there will become more numerous as conditions are made more favorable for their existence.

The quotations which follow are indicative of the source and reliability of the information from which the data of this paper were taken. They are extracts from letters received in reply to questions sent out by the writer. They are representative of the letters received from people who have had wide experience in the state. I think the conclusion that the changed conditions in the state in respect to increased raising of grain, tree planting and the irrigation of large tracts have been the direct cause of the increase in the number of birds, is justified. An increase which has been so marked that residents of the state in general have noticed and commented upon it.

QUOTATIONS FROM LETTERS RECEIVED

1. From William Richard, taxidermist, Cody, Wyo.:

> It has been my opinion for several years that the birds are on the increase, excepting the sage hens, ducks and eagles, which seem to be decreasing.

2. From Louis Knowles, forest supervisor, Sundance National Forest, Sundance, Wyo.:

> There has been a marked increase in the number of birds in this region during the last ten or fifteen years. The increase has been in numbers and not in species. The increase is undoubtedly due to the gradual increase of cultivated areas.

With Reference to the Quail

3. From John Hunton, one of the oldest and best informed citizens of Wyoming, Fort Laramie, Wyo.:

> The quail of the bob white species first made its appearance in the Wyoming section of the Platte Valley at the Wyoming-Nebraska line in the summer of 1890. They have gradually worked up the valley until reaching the vicinity of Guernsey. They have also worked up the Laramie River to the neighborhood of Uva. They are not and have not been numerous, being pioneers, as it were. During the winter of 1908–09 a covey of twenty-two frequented my yard here and fed with my chickens. On last Friday morning, June 14, I heard two bob whites on my meadow at Gray Rocks on the Laramie River, ten miles west of here. Occasional coveys are to be seen or heard along the valleys of both rivers as far as I have indicated. The quail evidently followed the course of the Platte Valley from Nebraska, and they are gradually working farther up the tributaries of the Platte as fast as the grain belt advances. I believe the cultivation of the soil to grains of various kinds is the only thing which has induced them to migrate west.

B. H. GROVE

UNIVERSITY OF WYOMING

NOTES AND LITERATURE

THE DEPTHS OF THE OCEAN[1]

The publication of this work marks an epoch in the advance of the science of oceanography second only to that initiated upon the return of the *Challenger* Expedition, but while the explorations of the *Challenger* were extensive and of necessity somewhat superficial, these later studies conducted by the *Michel Sars* are predominately intensive and thorough.

Not the least valuable of the lessons the book teaches us is the fact that through the skillful and courageous use of a small vessel by trained experts, results of the highest value to science may yet be achieved.

One admires the courage of the leaders of this expedition who ventured to cross and recross the Atlantic in a little steamer only 125 feet in length, and with a coal supply capable of carrying her only 3,400 miles at the economical speed of 9 knots.

The cruise was evidently conducted under the most auspicious conditions respecting its management, the Norwegian government providing the vessel, while Sir John Murray supplied the funds necessary for the expenses of the expedition; and it may be well to recall the fact that the most successful expeditions of the United States Fish Commission steamer *Albatross* were conducted under a somewhat similar arrangement between the late Dr. Alexander Agassiz and the government.

Thus the ripe experience of the veteran leader in this field of research, Sir John Murray, was enlisted to perfect the methods of such active young students of oceanography as Dr. Hjort and his able associates, Professors Koefoed, Gran, and Helland-Hansen, all of whom accompanied the expedition.

The cruise lasted from April until August, 1910, extending from Plymouth to Gibraltar, thence to the Canaries and then to the Azores, from which region a run was made into the Sargasso Sea and on to Newfoundland, and thence to Glasgow and Bergen.

The book before us is, however, far more than an account of this cruise, rich as its results are in achievement in new fields, for it is actually an epitome of all results hitherto attained in

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[1] A general account of the modern science of oceanography based largely on the scientific researches of the Norwegian steamer *Michel Sars* in the North Atlantic; by Sir John Murray, K.C.B., F.R.S., etc., and Dr. Johan Hjort, Director of Norwegian Fisheries, with contributions from Professor A. Appellöf, Professor H. H. Gran, and Dr. B. Helland-Hansen, xx + 821 pp., 575 figures. Macmillan and Co., Limited, London.

oceanography, and is thus comparable with Agassiz's "Three Cruises of the *Blake*" of 1888.

The first thing which strikes one upon reading this account of the cruise of the *Michel Sars*, however, is the enormous advance which has been made since Agassiz wrote his well-known work.

The book is written in that plain, honest English which the readers of Darwin learned to love so well. It is difficult to review because so crowded with facts of the highest interest, and it sparkles with that rare enthusiasm which characterizes the writings of those happy men of science to whom years and knowledge bring no lessening of youth's enthusiasm. At times the language seems quaint, for most of the chapters were written by students to whom English is not a native tongue; but this only adds to the readableness of the book. Indeed, it is a work which people of general culture as well as specialists may read with sustained interest from cover to cover. It is a fitting monument to the life-work of the great "Naturalist of the *Challenger* Expedition," Sir John Murray.

The historical chapter, and that upon the depths of the ocean are by Sir John Murray. Physical oceanography is written by Dr. Helland-Hansen, the phytoplankton by Professor Gran, the bottom fauna by Professor Appellöf, and the narrative, equipment, fishes of the sea bottom, pelagic animals and general biology are by Dr. Hjort, there being ten chapters in the book.

The signal success of this expedition was due to two factors: a corps of able, enthusiastic students already distinguished by high achievement in these studies, and the possession of exceptionally good apparatus provided through the generous support of the Norwegian government and of Sir John Murray.

Thus the ship carried a huge otter trawl, and a Petersen fish trawl, so efficient that in one haul they captured nearly as many individual fishes as the *Challenger* discovered in its twenty-five hauls between 1,500 and 2,000 fathoms. There were also large vertical closing nets 3 meters wide and 9 long, and hauls were at times made with ten nets and trawls out at various depths at one and the same time. The collections were thus exceptionally rich in species, some new and many rare forms such as *Spirula*, *Melanocetus krechi*, a remarkable genus allied to *Gastrostomus*, new Leptocephali, many larval fishes with telescopic eyes and a specimen of the giant squid.

But the results, important as they may be, will not be chiefly memorable for the new species and interesting forms discovered, for the intensive studies of the physics and chemistry of the sea, and the application of new methods made possible by improved apparatus has led to the dicsovery of certain general laws.

For example, Professor Gran, using a steam centrifuge capable of centrifuging 1,200 c.c. of sea water at a speed of 700–800 revolutions per minute, discovered the unsuspected fact that the smallest pelagic plants, the nannoplankton which pass readily through the meshes of an ordinary silk net, are far more abundant than are the larger forms. He found, also, that pelagic plant life is most abundant at depths of 10–20 meters, but becomes extremely scanty below 100 meters, and he confirms the conclusion of Nathansohn that marine plant-life thrives best where ascending currents bring upward a supply of nitrogenous compounds derived from the decomposition of organic matter in the deep sea. Gran concludes that in the tropics the phytoplankton consists of numerous species, most of which are rare, whereas in the colder waters there are few species but great aggregations of individuals.

Professor Helland-Hansen made use of a new form of photographic-plate photometer which he himself had invented. He was thus enabled to demonstrate that a good deal of sunlight penetrates to a depth of 1,000 meters, but at 1,700 meters his plates were unaffected by an exposure of 2 hours' duration. The sun's rays at a depth of 500 meters in clear tropical water still retain a definite direction, not having yet become diffuse. But the most important discovery is the fact that the red rays are absorbed more quickly than the blue. Thus little or no red light can penetrate into the depths and the dark red color so characteristic of the animals of the deep sea is explained by the fact that, there being no red light where they live, they appear black and are thus rendered invisible.

The ship was well supplied with oceanographic apparatus, having a number of Ekman's current meters, Richter's reversing thermometers, Petterson-Nansen's water bottle and Petterson's insulating deep-sea bottle, enabling one to bring samples of water to the deck and there determine the temperature which the water had when at the bottom of the sea.

The *Michel Sars* is certainly to be congratulated upon the success attending their skillful use of this apparatus. For example, the vessel ventured to anchor in a depth of 400 meters over a hard bottom in the straits of Gibraltar and then to make use of two Ekman current meters, one at a constant depth of 10 meters and the other at various depths down to the bottom. They achieved the first accurate quantitative determinations of the currents ever attained at Gibraltar and found that there is a surface current passing inward from the Atlantic to the Mediterranean, while at the same time a strong bottom-current of dense water passes outward into the Atlantic. The boundary between these two currents is usually at a depth of about 150 fathoms but this is greatly affected by the tidal conditions, for during one hour the current flowed outward toward the Atlantic even at the surface.

Other studies in the open Atlantic far from land enabled them to distinguish currents due to tidal action at the surprising depth of more than 1,000 fathoms. Indeed, a most interesting part of the book is devoted to the discussion of the physics of oceanic and tidal currents, and the expedition has achieved a hopeful purpose if it has done little more than point out the possibilities of research in the complex subject of the relation between tidal waves and tidal currents. The right-handed deviation of moving masses of water in the northern hemisphere due to the earth's rotation is clearly shown as a result of titration to determine the densities of sea water at various depths. Thus it is shown that the dense, relatively warm water of the Mediterranean spreads out in a great wedge in the intermediate depths of the Atlantic, and that most of this water moves northward off the coast of Portugal.

Through studies in density it is shown that the so-called "Gulf Stream" water overlies the cold water of Arctic origin.

But it is impossible to do more than merely indicate a few of the more important facts and laws presented in this remarkable book. In fact it is impossible to review a work which is itself a review of all previous studies as well as a medium for the presentation of newly discovered facts.

An appreciated feature of the book is the numerous charts, maps and hydrographic sections showing density and temperature gradients, the distribution of oxygen in the ocean, and the most recent results of exploration in soundings.

For example, it is shown that in 1910 the temperature at 400 fathoms in a certain place was 5° C. colder than in 1873 when the *Challenger* worked in the same region.

The area of the ocean is stated to be 139,295,000 square miles, of which 58.42 per cent. has a depth of between 2,000–3,000 fathoms, and about one sixth is less than 1,000 fathoms deep.

The hydrographic sections from the Sargasso Sea to Newfoundland, and from Newfoundland to Ireland, as well as the more intensive studies of the Spanish Bay and Gibraltar, and of the Wyville Thomson Ridge between the Faroe and Shetland Islands are especially interesting.

Other charts based upon the researches of Knudsen, Ostenfeld, and Brenneke show the distribution of dissolved oxygen in the Atlantic down to 1,500 fathoms between 60° N. and 50° S. latitude, proving that the higher the salinity and the temperature the less the absorption of oxygen, and hence the relative deficiency of oxygen in the surface waters of the tropics.

In a work of this magnitude there must needs be errors and omissions, but these are so infrequent and of such small moment that it seems ungracious to call attention to a few of the more noticeable. The impalpable chalky deposit found in coral reef regions is still referred to as "coral mud," although in 1910 Vaughan stated that it was a chemical precipitate, and this enabled G. Harold Drew, of Cambridge, to demonstrate that it is actually a precipitate caused by the action of a bacillus in depriving the warm tropical water of its nitrogen, thus enabling the calcium to combine with the dissolved CO_2 to form calcium carbonate.

In the table at the bottom of page 175, the statement "the number of grams of salts per *liter* of sea water" should read "the number of grams of salts per *1,000 grams* of sea water."

On page 187 "*purifying* sarcodic matter" should read "*putrifying* sarcodic matter." But such criticisms are really puerile, and are given chiefly to show the negligible character of the errors in the book, the editorial work upon which reflects great credit upon Messrs. James Chumley and Dr. Caspari.

A happy feature in the editorial arrangement of the book is the system of marginal notes which enable one quickly to discover the subjects of each paragraph. One regrets the absence of a bibliography, but the introduction of such a list would have perhaps too greatly enlarged the size of the book.

Apart from the purely scientific side which we have been considering the book indicates the possible practical value of these studies. For example, it is shown that the growth-rate of pine trees on the coast of Norway bears a direct relation to the temperature of the ocean water, and for six successive years when the amount of heat in the "Gulf Stream water" was great in the month of May the air temperature in Norway was high in the following winter. The water-temperature also bears a direct relation to the time of the blossoming of *Tussilago farfara* at Upsala. Also, Dr. Hjort shows that the southern limit of the valuable boreal food fishes everywhere coincides with the isotherm of 10° C. at a depth of 100 meters.

ALFRED G. MAYER.

THE GROWTH OF GROUPS IN THE ANIMAL KINGDOM

ANY one who makes an intensive study of many representatives of some organism becomes impressed by the fact that they form many slightly differing groups, and is led to ask how these diversities have arisen. This has been the experience of Lloyd[1] in studying the rats of India, in connection with the problem of plague prevention. He has therefore been moved to present in book form his impressions as to how the observed groups probably arise, together with the facts on which these impressions are based; and some general deductions from these impressions.

The facts observed in the study of the rats are of the following character: (1) Small groups of rats differing in some respects from the forms regarded as typical, occur frequently here and there. (2) Such groups, with the same exceptional characters, appear in various widely separated places, showing that the different small groups have arisen independently of each other. (3) "This is true, however, only in the case of groups whose peculiarity appears as a single character unit. Those groups whose peculiarity is made up of several uncorrelated characters arise on one occasion only" (p. 50). Descriptions and figures of many such cases are given; the account here is of much value and interest.

Such facts naturally lead the author to hold that groups of this sort have arisen by mutation: that is, by a dropping out or alteration of single unit characters, in the Mendelian sense; that the same character often drops out in different localities, giving rise to small groups of independent origin, yet having the same distinctive features. This part of the discussion would have been given more precision by consideration of the work on inheritance in rodents and other organisms, as carried on by Castle and others. Further, the pure line work with homozygotes and in vegetative reproduction might give definiteness to many of the author's rather vague views as to the nature of these groups. The conclusions of Lloyd along these lines will appear somewhat halting and loose to persons steeped in the experimental work in

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[1] "The Growth of Groups in the Animal Kingdom," by R. E. Lloyd, Longmans, Green and Co., 1912, 185 pp., $1.75.

the two fields mentioned. Lloyd's distinctive contribution is the demonstration that there exist in certain wild organisms the same conditions that are found in experimentation.

The author's interest lies mainly in bringing the work into relation with the species concept as employed in systematic zoology, and in showing its opposition to what he calls the "accepted" view that diverse groups of organisms arise gradually, by a process of selection among minute gradations. He shows that many of the so-called species of rats are distinguished from each other in the same way as are the small groups he has observed; therefore there is not ground for supposing all the members of such species to be descended from a common stock. "Animal species appear to be conventional rather than real" (p. 117). But among the author's fluctuating views on this point is the doubtful assertion that "there seems to be reason for believing that the distinction between specific and varietal characters which was recognized by De Vries in plants is also recognizable among higher animals" (p. 139); which would seem to imply that there is some sort of reality underlying the distinction of species. The matter is not analyzed with precision.

In a special chapter the author attempts to apply to certain problems of disease and abnormality in man the idea that new forms arise by mutation. Here again, those who have at hand such a work as Davenport's "Eugenics" will find the presentation vague, though tending in the same direction as in the work mentioned.

In a concluding chapter the author abandons empirical evidence for an attempt to criticize the theory of natural selection from a general and philosophical point of view. Much is made of the supposed requirement that variation should be "in all directions," the criticism depending "on the assumption that we can not imagine things varying in all directions" (p. 175). Further, adaptation is held not to be a phenomenon needing explanation. The rest of the discussion is of a similar character, showing less precision of analysis than any other part of the work.

The author states in the preface that the book is offered "as an assortment of opinions which may be of suggestive value." The observed facts in regard to the diverse groups of rats, however, make it more than this.

H. S. JENNINGS

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HEREDITY OF TRICOLOR IN GUINEA-PIGS

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WE undertook the following experiments with guinea-pigs in order to see whether the tricolor and bicolor conditions described by Galton for Basset hounds could be brought in line with modern Mendelian interpretation. According to his recent paper, Castle was led to study the same problem from the same point of view. He has published a brief and important statement summarizing his results.

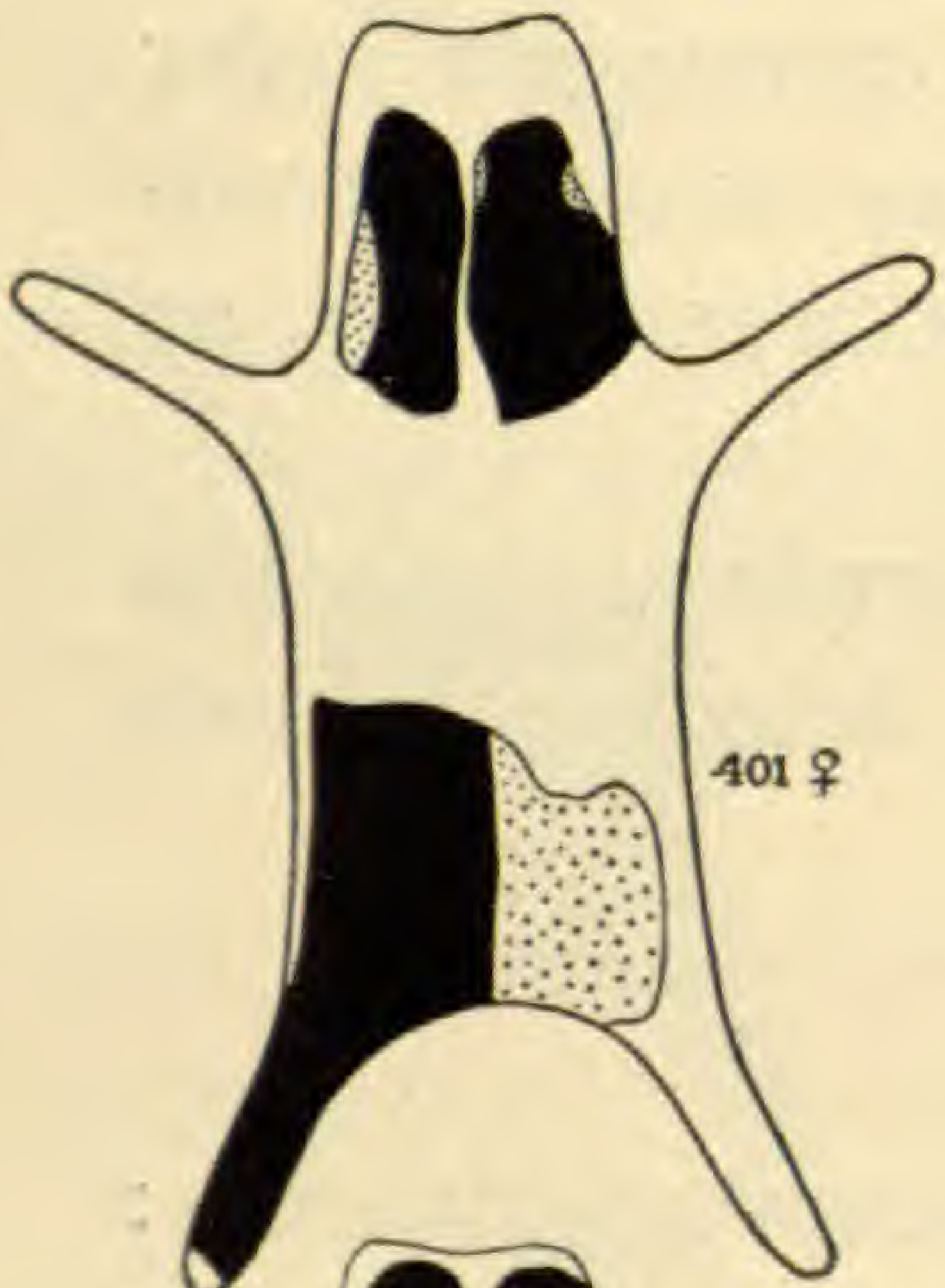
Our work was begun in 1908 and has gone on steadily, but slowly, since then, until a contagious disease destroyed the stock. It soon became evident that the problem is one of extreme complexity, and for its complete solution a much more elaborate and better planned series of experiments will be necessary. We hope that our results, fragmentary though they be, may serve to put on record the actual facts observed and that certain provisional suggestions that are made will be further tested.

The inheritance of color in guinea-pigs has been extensively studied by Castle. Animals with a coat of uniform color may be agouti, black, yellow (red) or albino. We are concerned here only with black, red and white (not necessarily albino). When black guinea-pigs are crossed to red ones the offspring are black, or black with traces of red. Castle points out that the F_1 black is not so dark as in the pure black strain, but shows evidence of the red. He states that the development of black does not hinder the development of some red pigment also in the hybrid, but the red so developed is concealed by the black. Black he regards as epistatic to red. Castle states in his recent book (1912) that in the F_2 generation three blacks to one red are produced.

Spotted animals contain white in patches. These patches may be very small in extent, or, at the other extreme, extend over the whole coat so that the eyes alone have dark pigment. These black-eyed whites, however, do not breed true, but produce spotted offspring, the spotting being variable. Black-eyed white mice give this result, and are to be sharply separated from albinos that have pink eyes and white hair. Albino guinea-pigs often have small patches of black, especially on the feet and ears, but this is not true for albino mice or rats.

In guinea-pigs the spotted animals may be black and white; or red and white. These races are said to breed true, or at least *certain* bicolor races of these kinds breed true. In addition there are races having red, black and white in their coats. These are the tricolors and it is with this race that we are here chiefly concerned. It has just been said that the tricolor is a distinct race, but this must not be understood to mean that they do not produce bicolor animals. In fact, amongst the offspring, bicolor animals continually crop out. It is this fact that has led Castle in his recent article to state that tricolors do not breed true. The bicolors produced in this way seem to differ from the pure races of bicolor in that they may produce tricolors again. For the present the question may be left open whether pure races of bicolors could be produced by selection of bicolors thrown by tricolor parents. Of course, if bicolor races had originally been incrossed, such a separation would be expected. In our experiments, at least, some bicolor individuals have appeared that seem to breed true, although the experiments are not extensive enough to settle the question.

In the following account, therefore, it should be under-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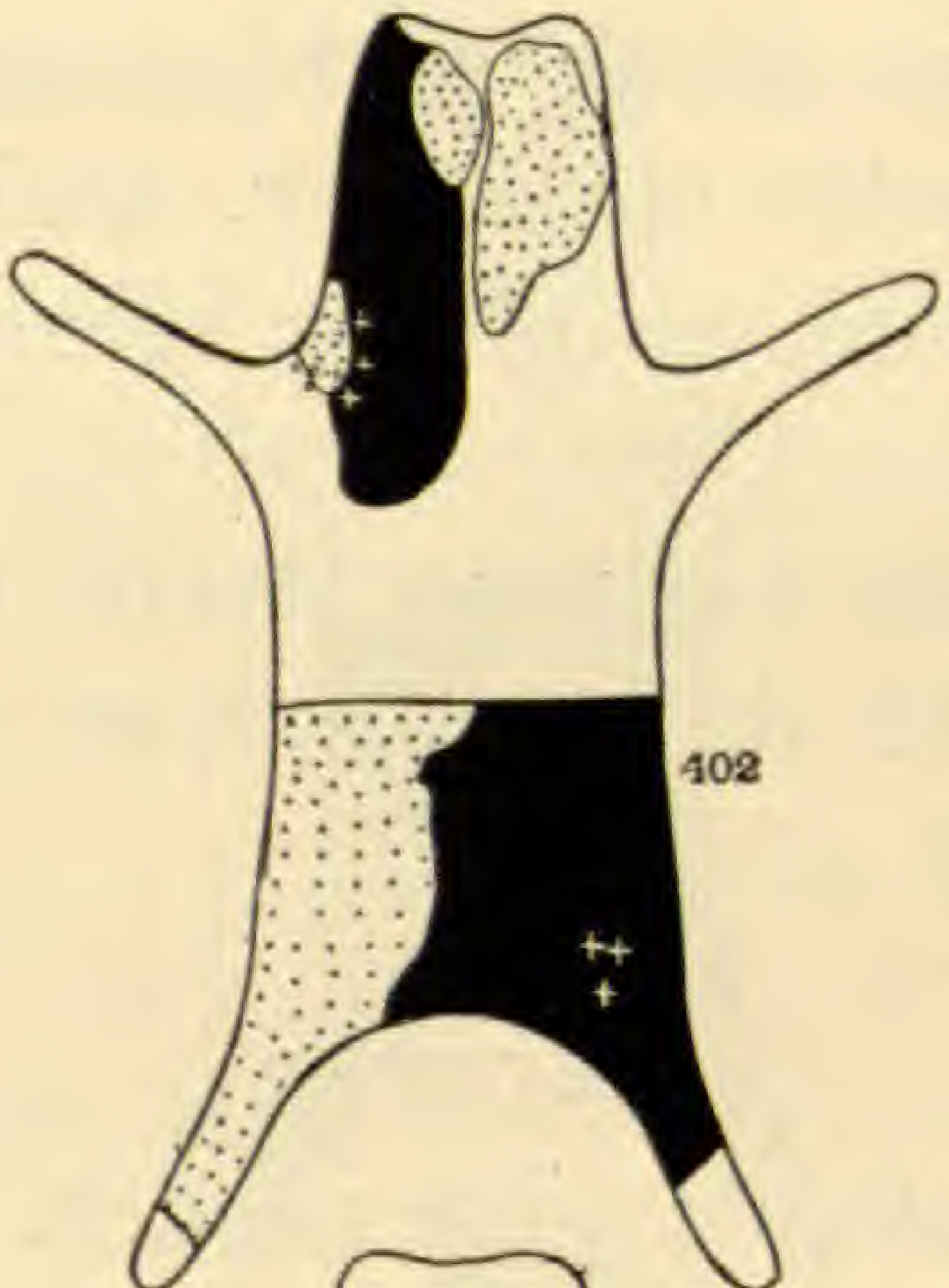
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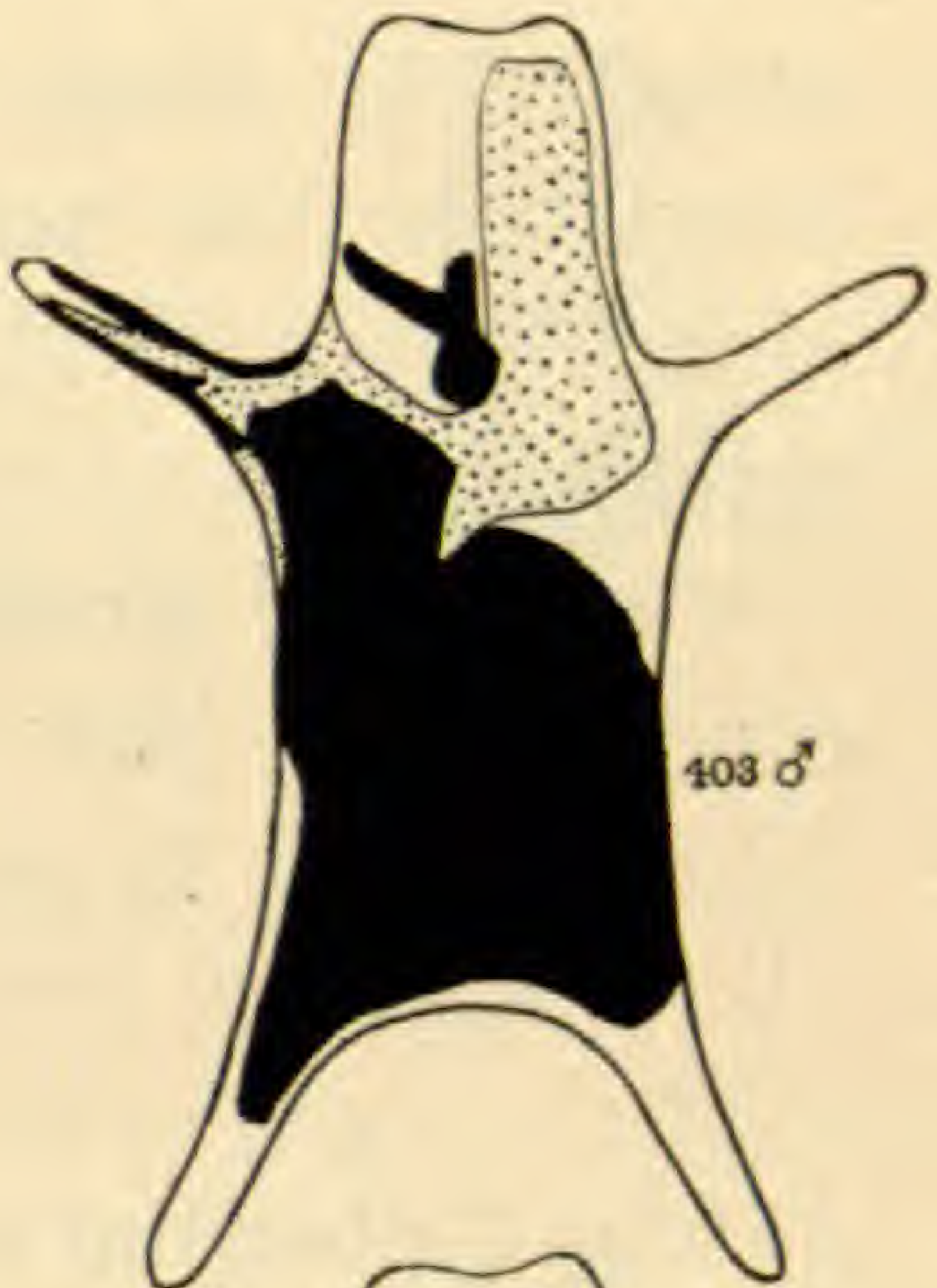
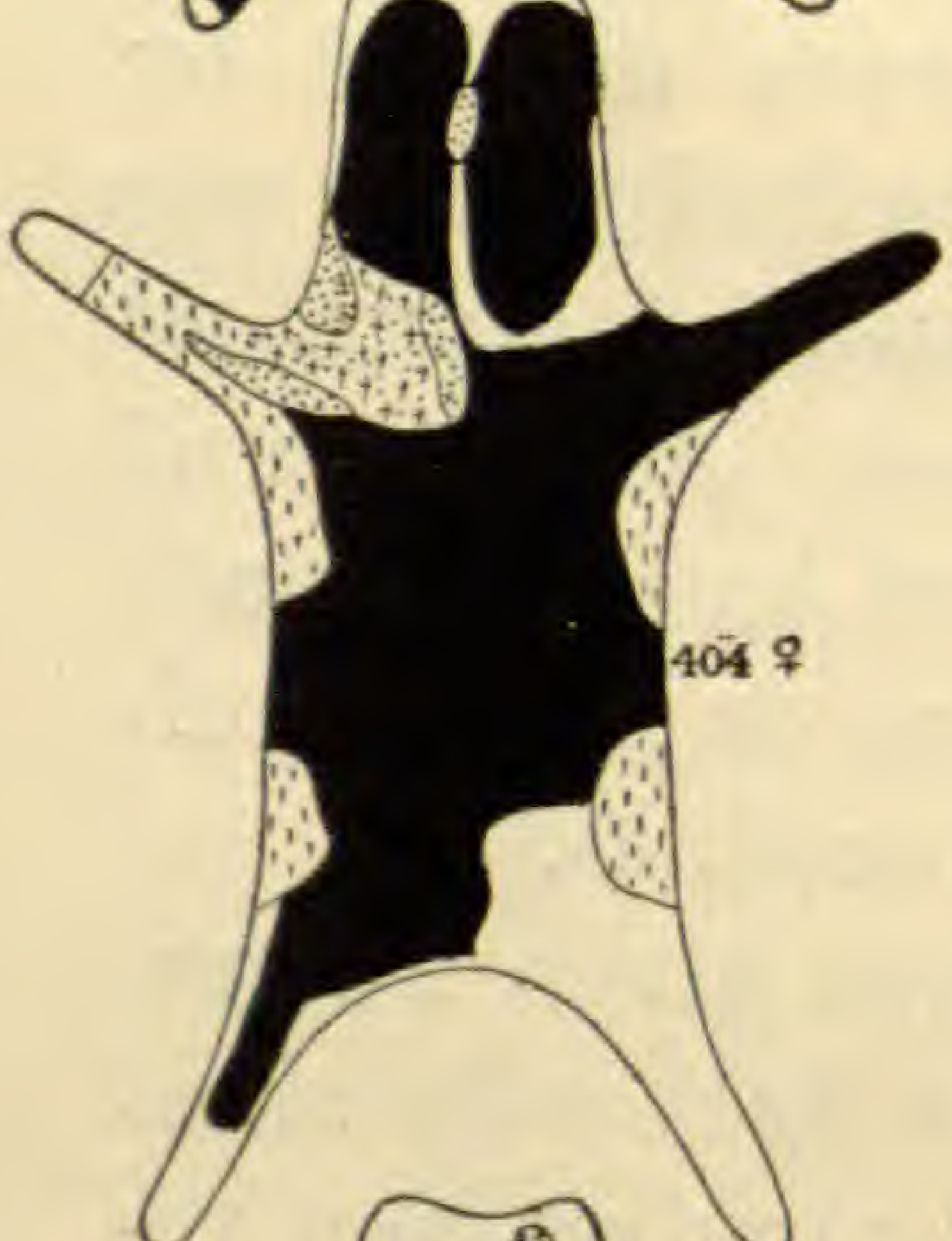

403 ♂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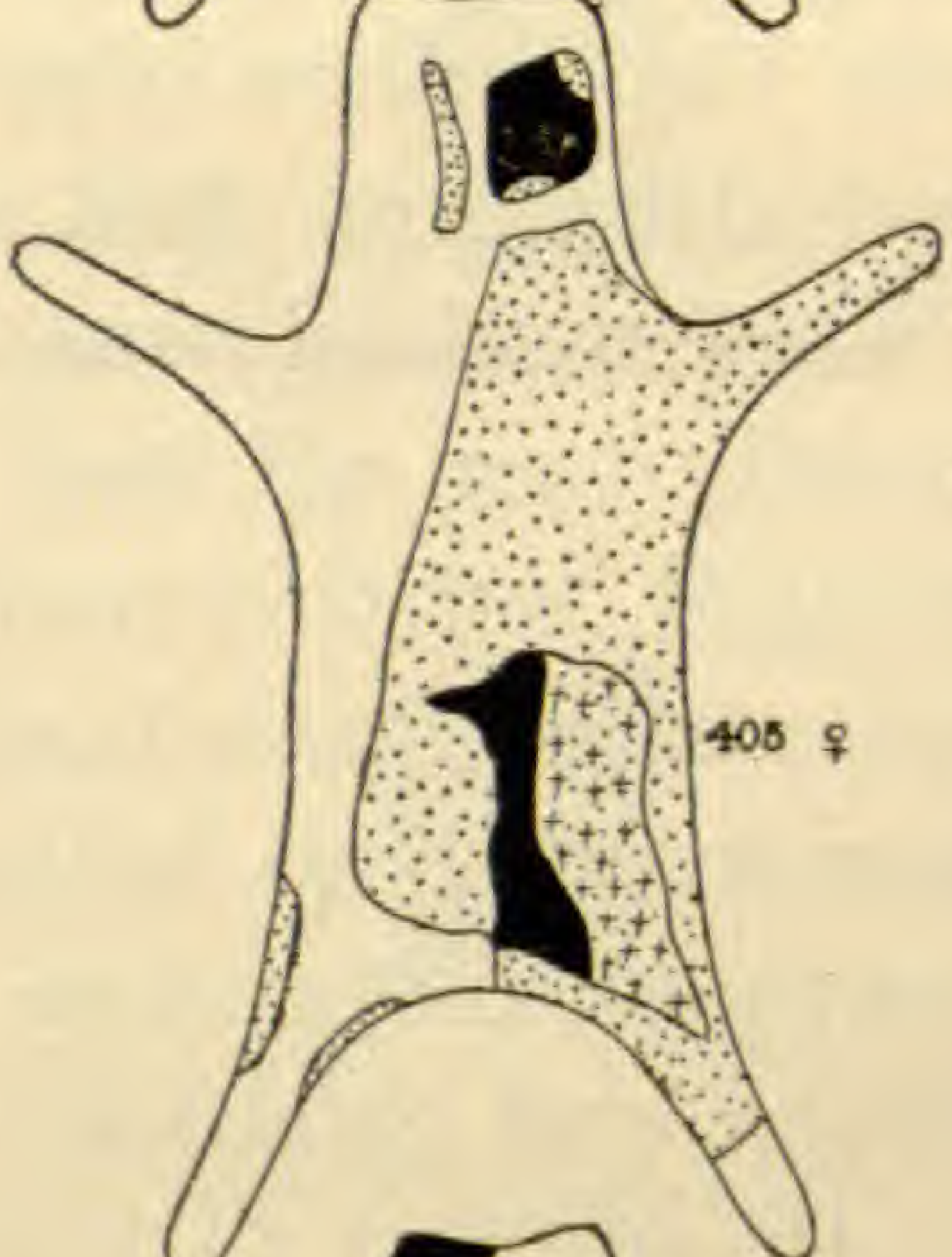
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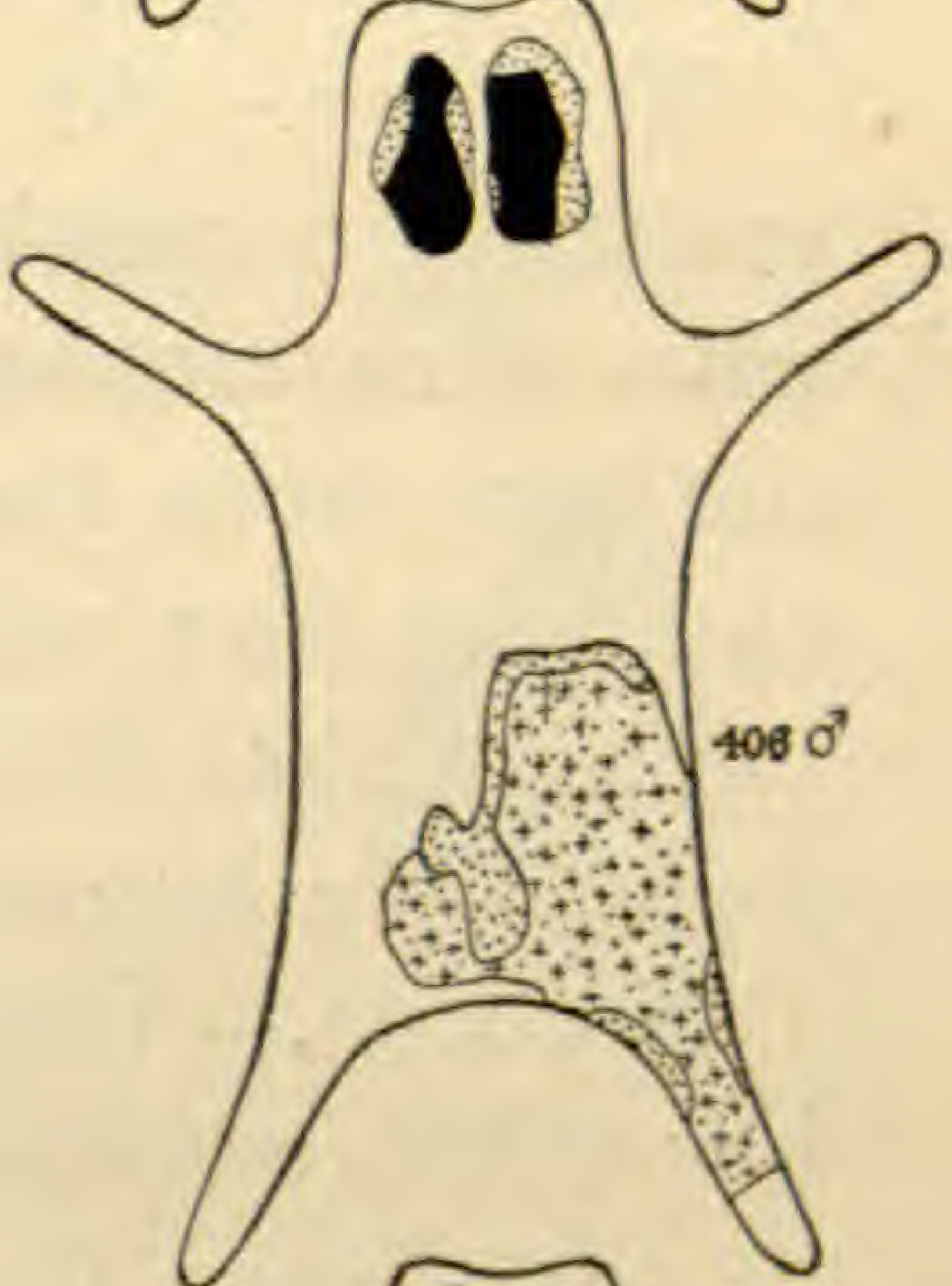
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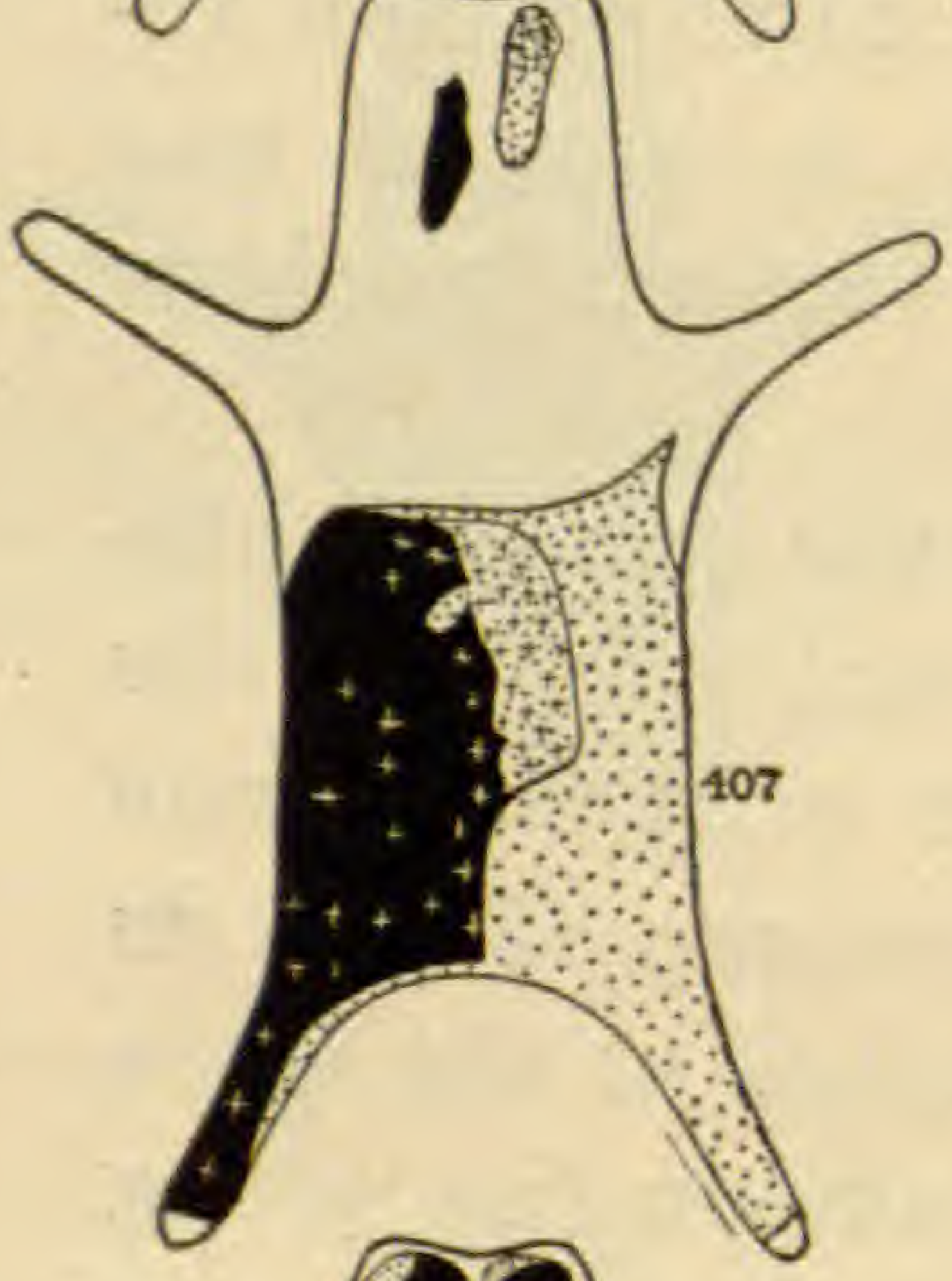
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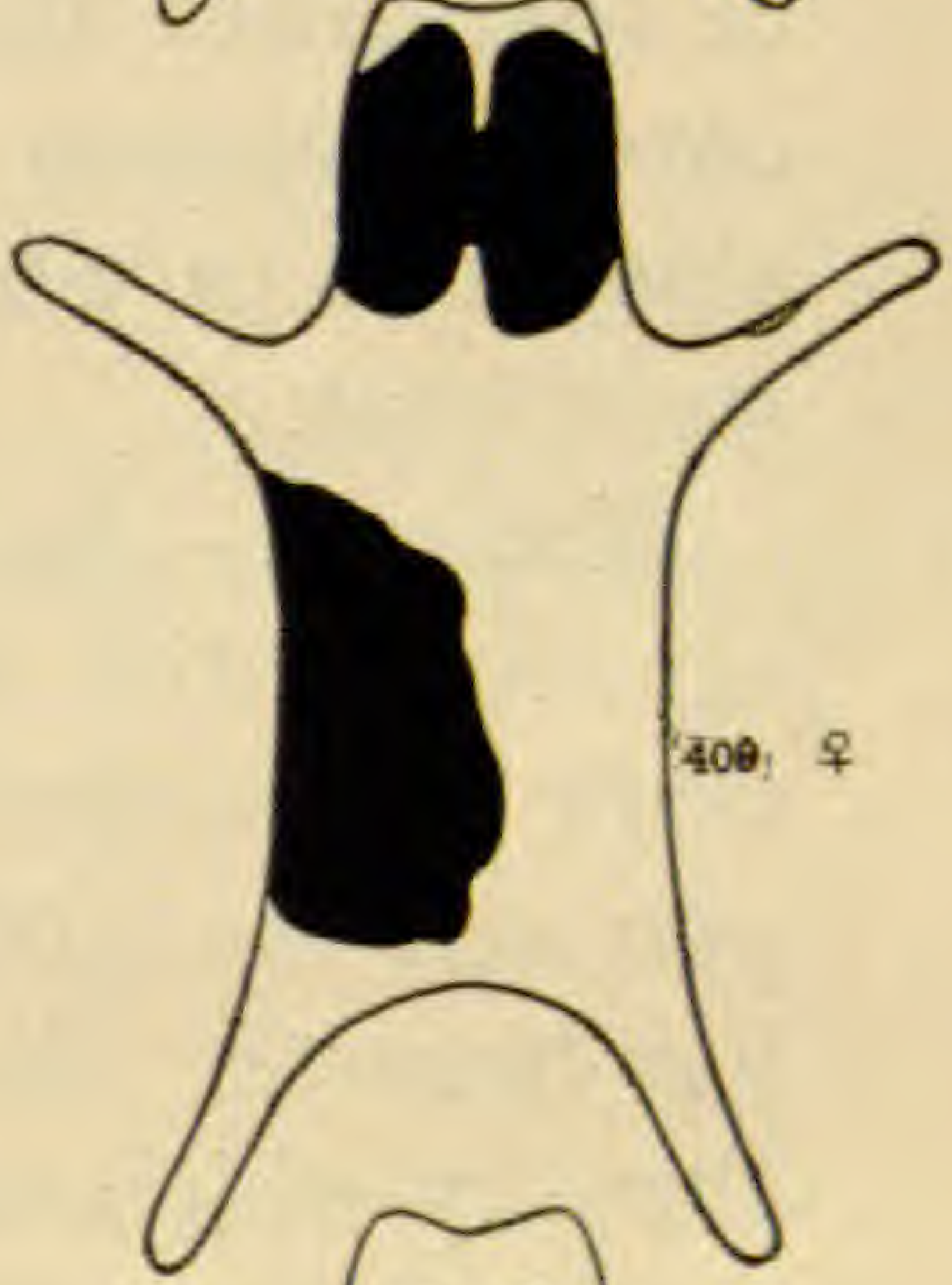
408 ♀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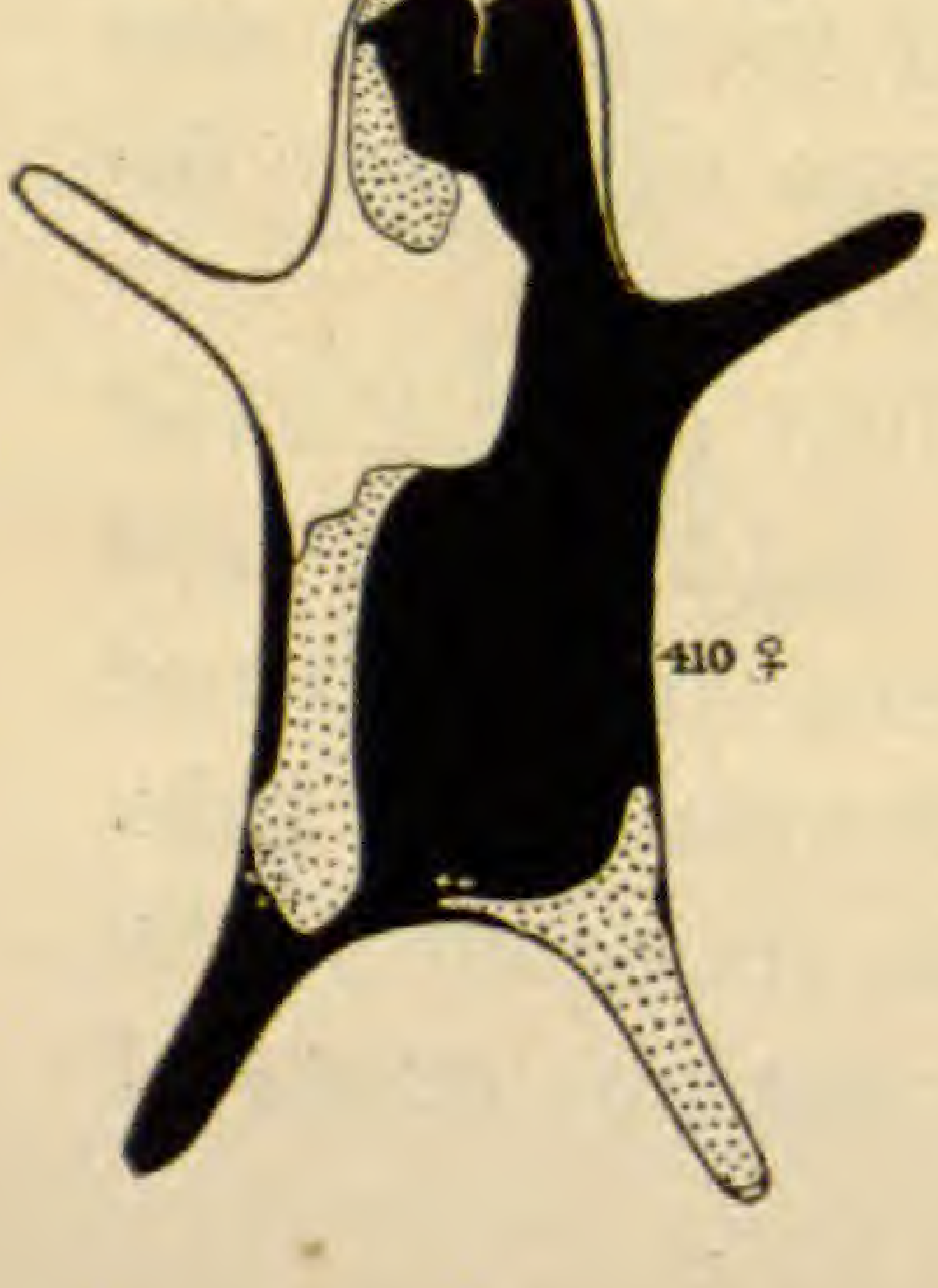

410 ♀


411 ♀


412

stood that when we speak of bicolored types we refer simply to the somatic character, and, as stated provisionally, we shall rank all of our bicolors, genetically, as tricolors.

Our chief problem resolves itself, therefore, into the question of how the different types of tricolor behave when mated to each other.

METHODS

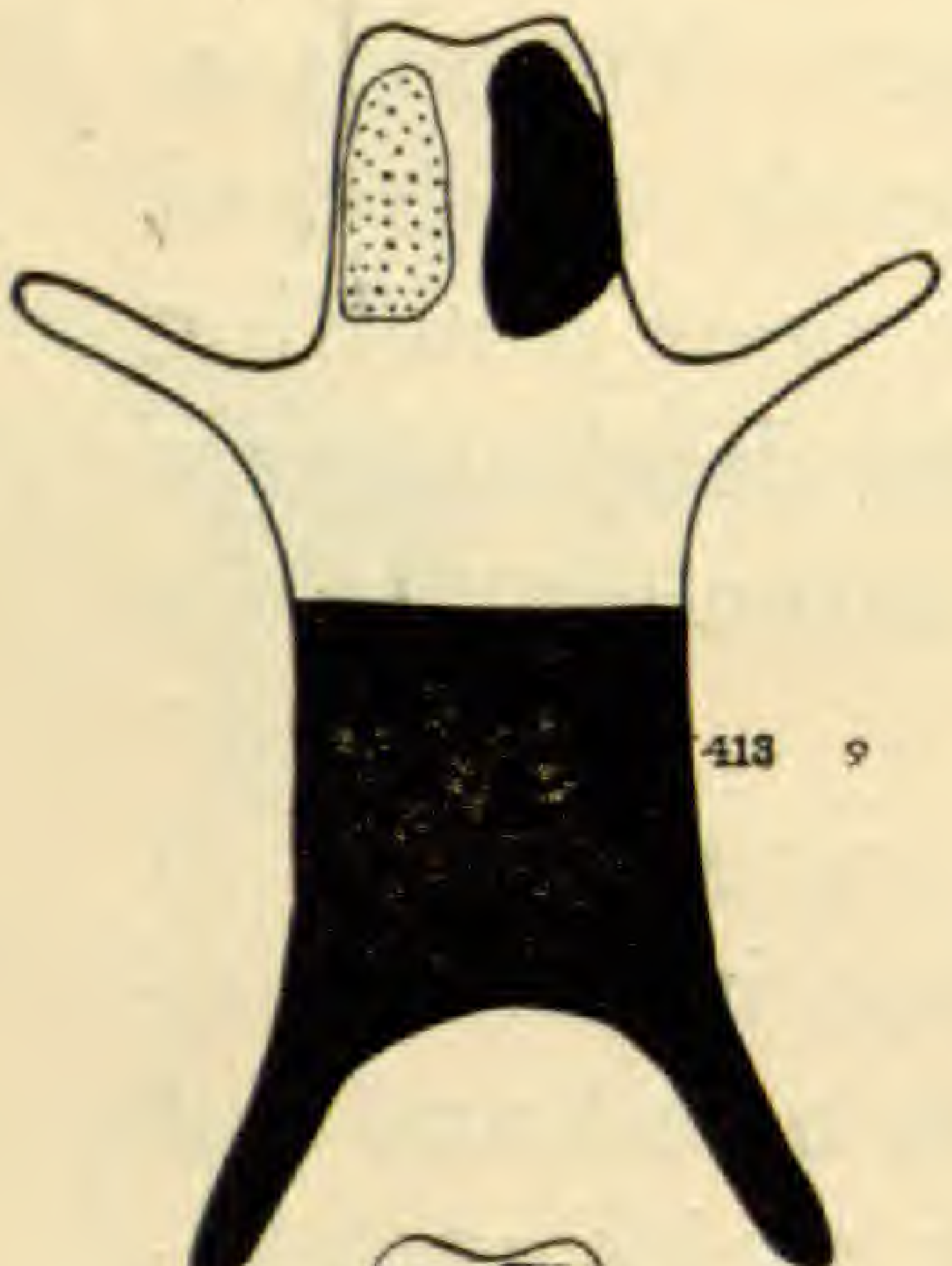
The following methods were used in these experiments:

Marking.—At first the guinea-pigs were marked by means of a numbered aluminum disk attached to the ear with wire staple. This method was unsatisfactory, as the tags were frequently torn off and lost. A system of ear holes was substituted, but this method had the disadvantage that the holes sometimes heal up in young animals. We know, however, of no better method.

Records.—The young animals were each given a number taken consecutively, and opposite the first individual of each litter the mother's and father's number was recorded together with the date of birth. A journal was also kept in which the records of the various matings were kept.

Matings.—As a rule several females were mated simultaneously with a single male. In the early part of the work the mothers were allowed to litter in the common pen and the mother identified by the presence of milk in her breasts. Sometimes two litters resulted at the same time, in which case it was impossible to assign the young to the proper mother. To avoid this, if more than one female seemed likely to litter at the same time, the females were isolated until after they had littered.

Charts.—A young individual was killed and skinned and the skin stretched just enough to hold it flat and then dried. From this a cardboard pattern was prepared and the outlines of all the sketches drawn from this. The midline of the sketch was divided into six equal parts, as an aid in locating the areas, and the various areas of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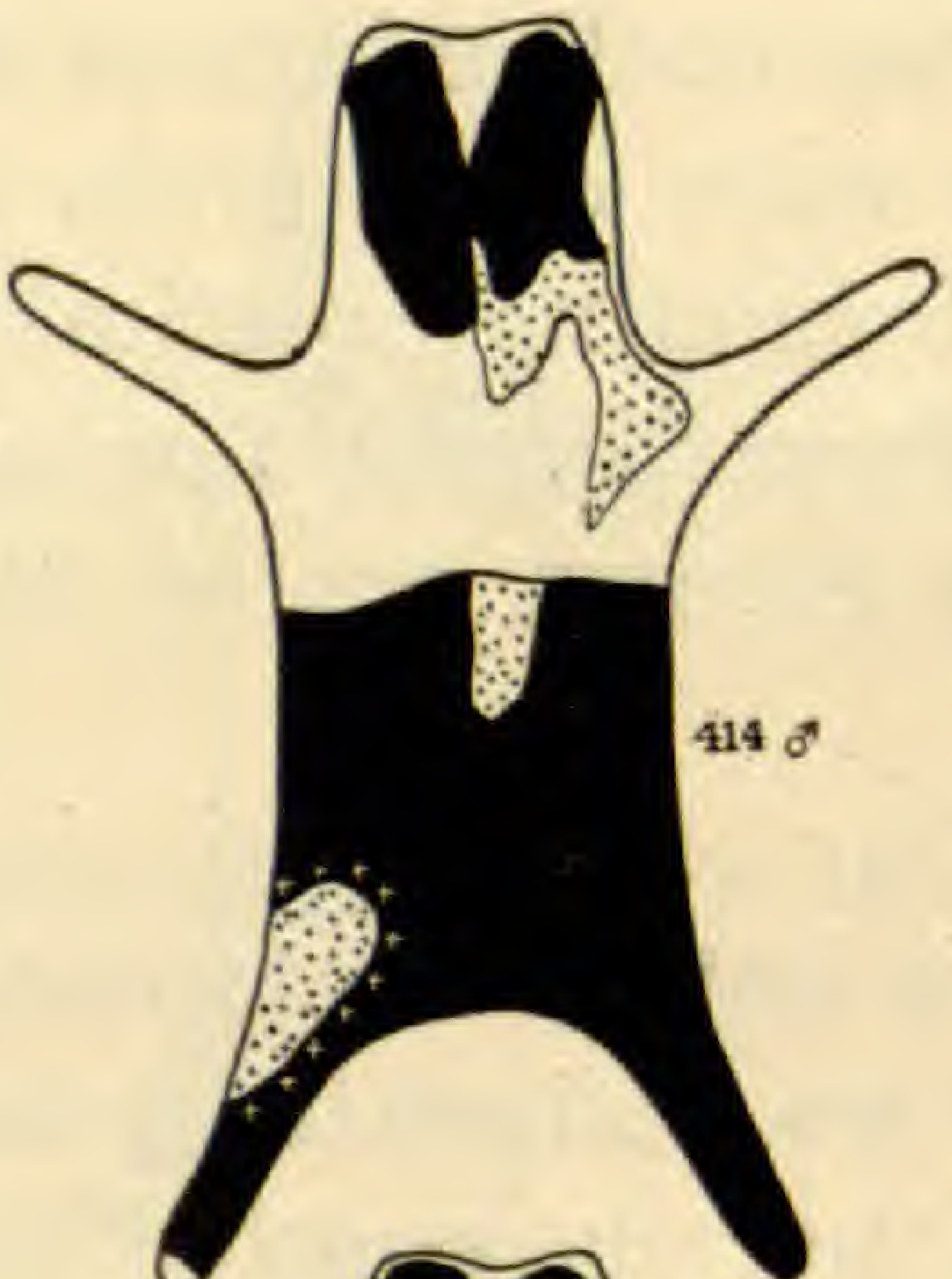
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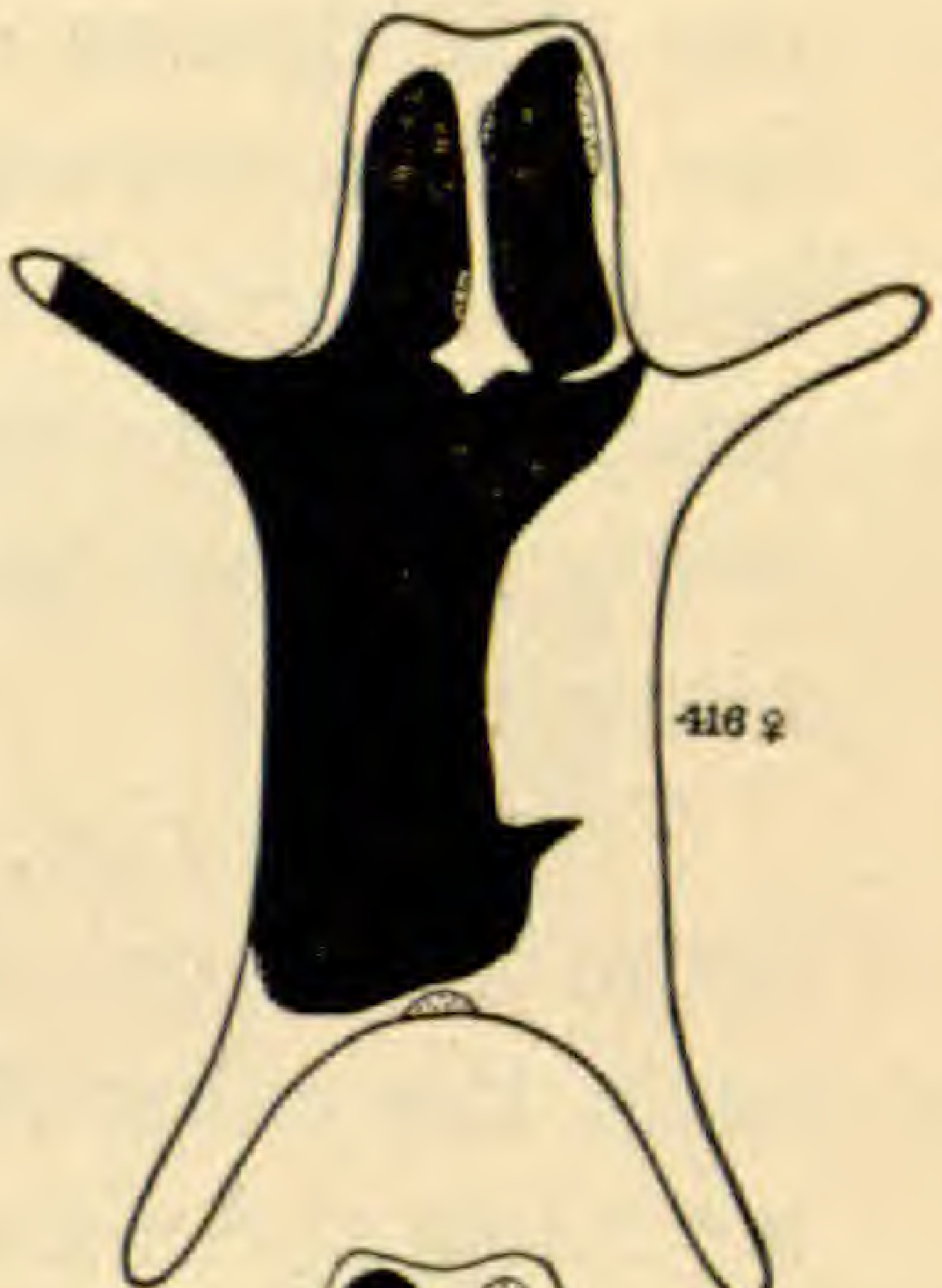
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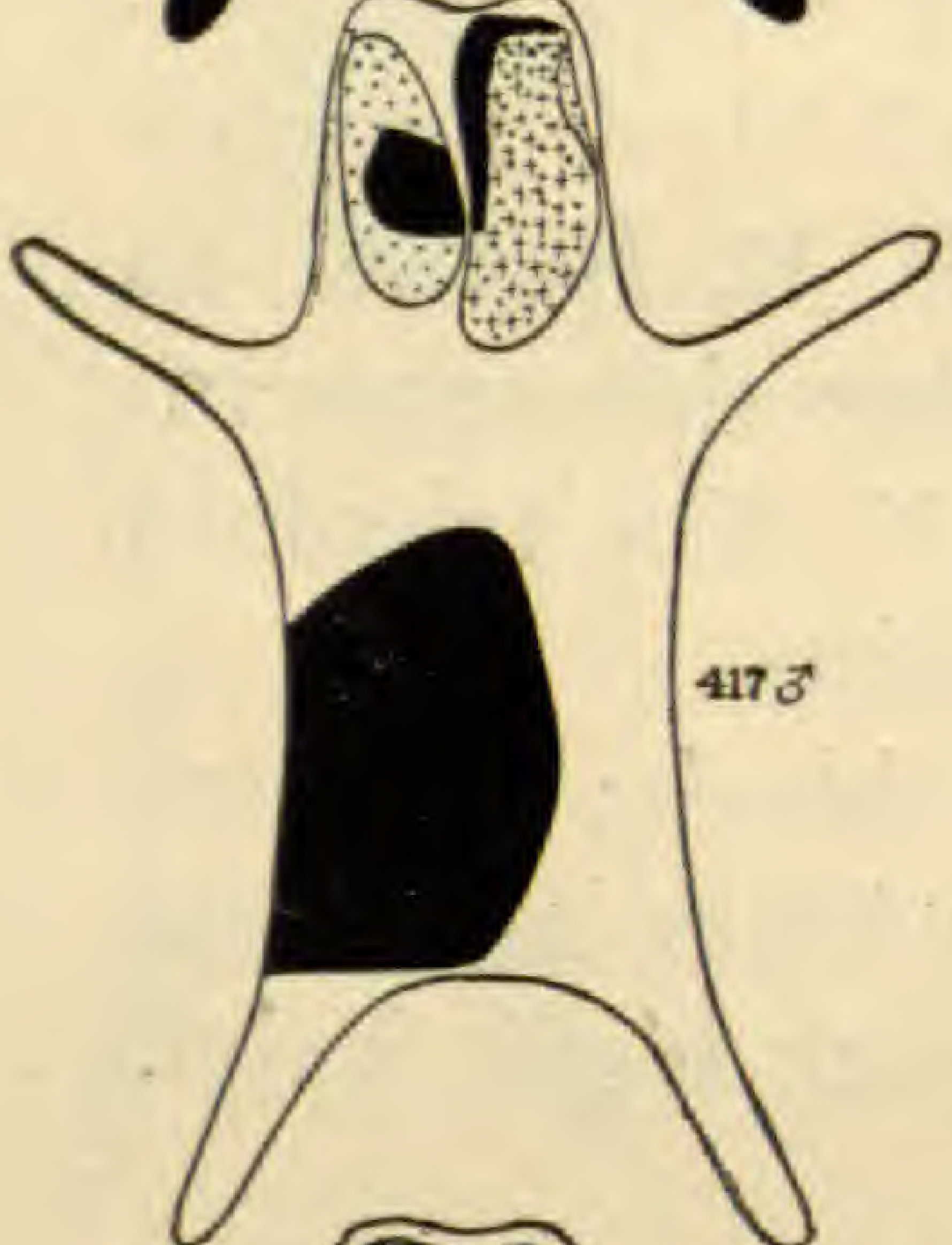
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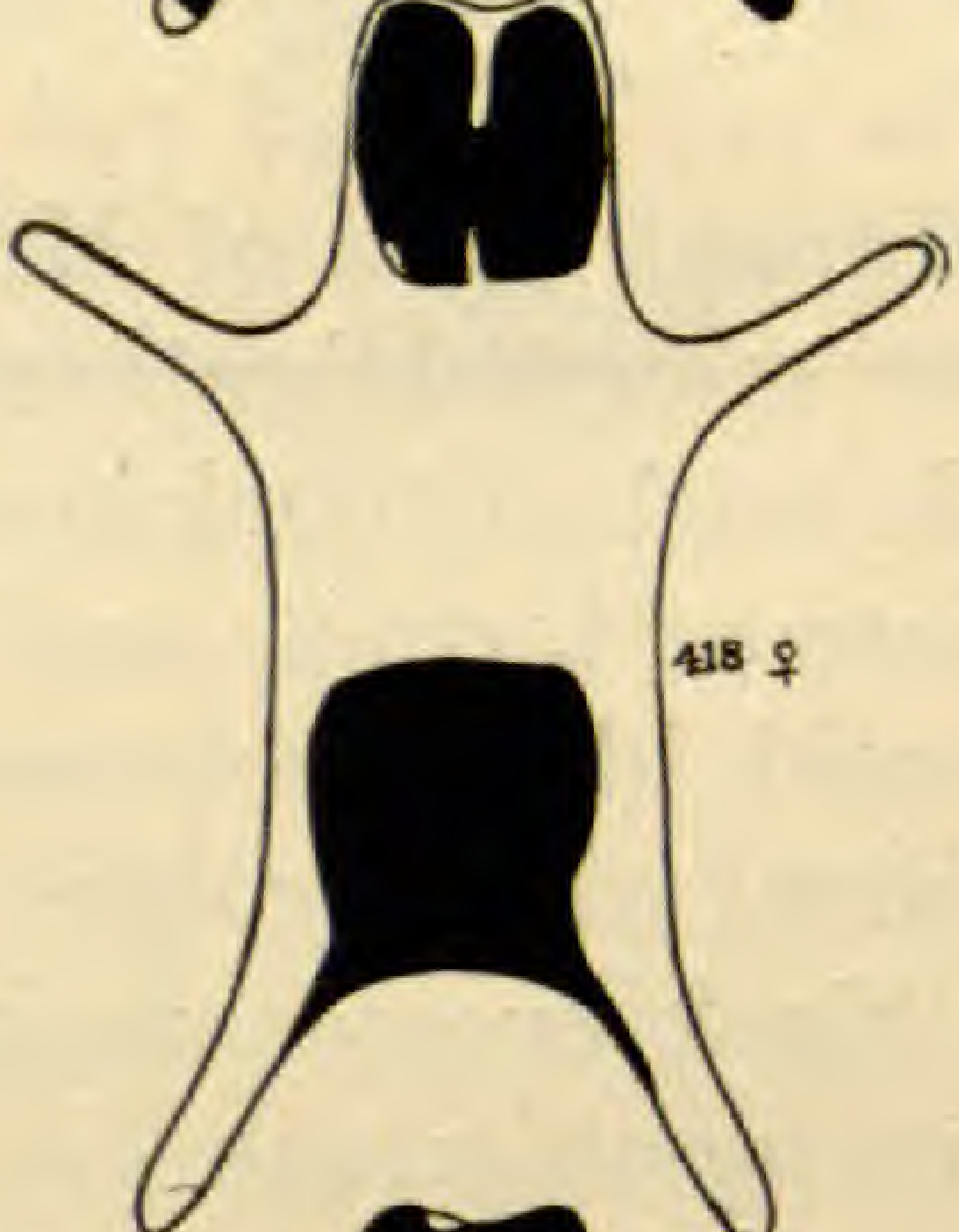
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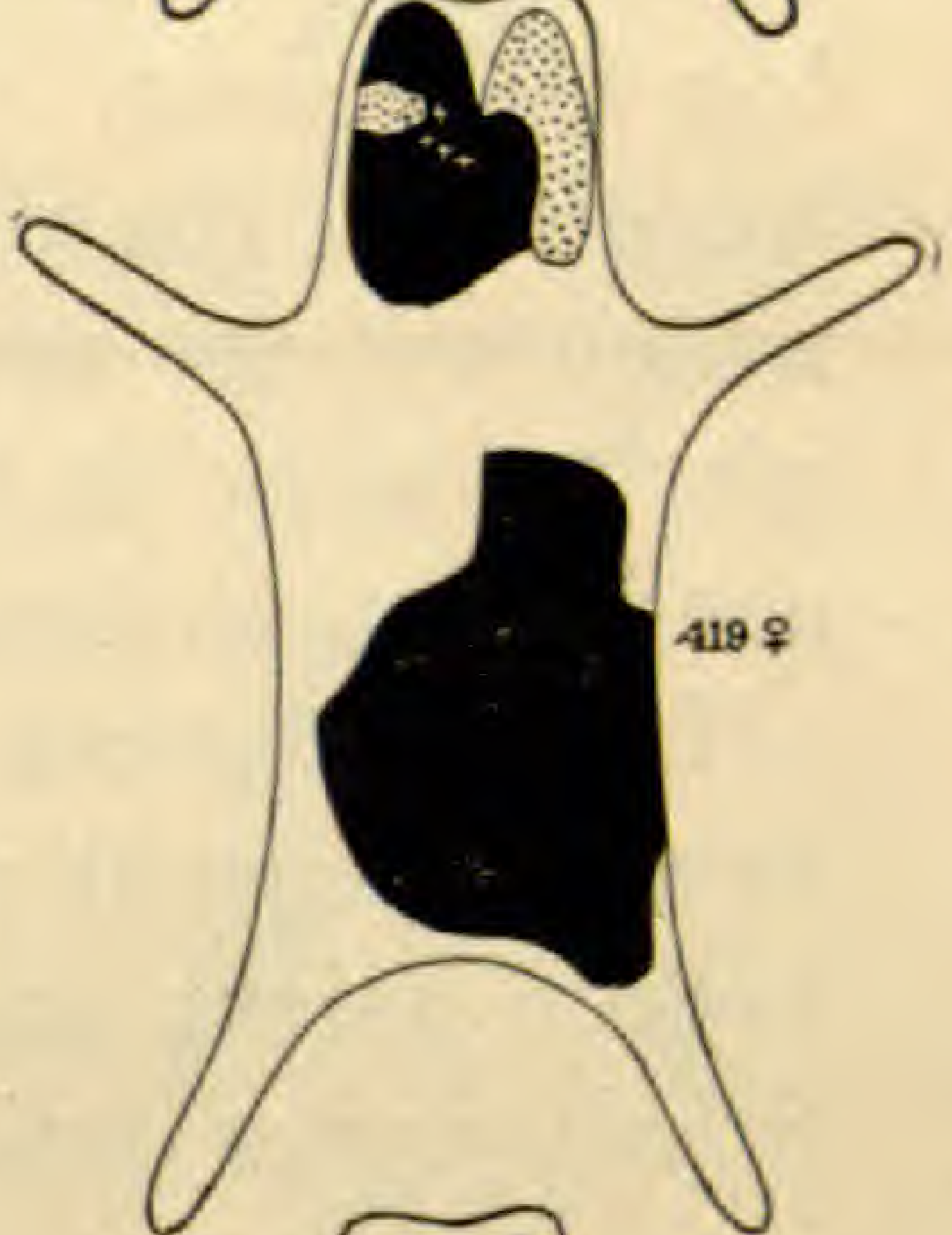
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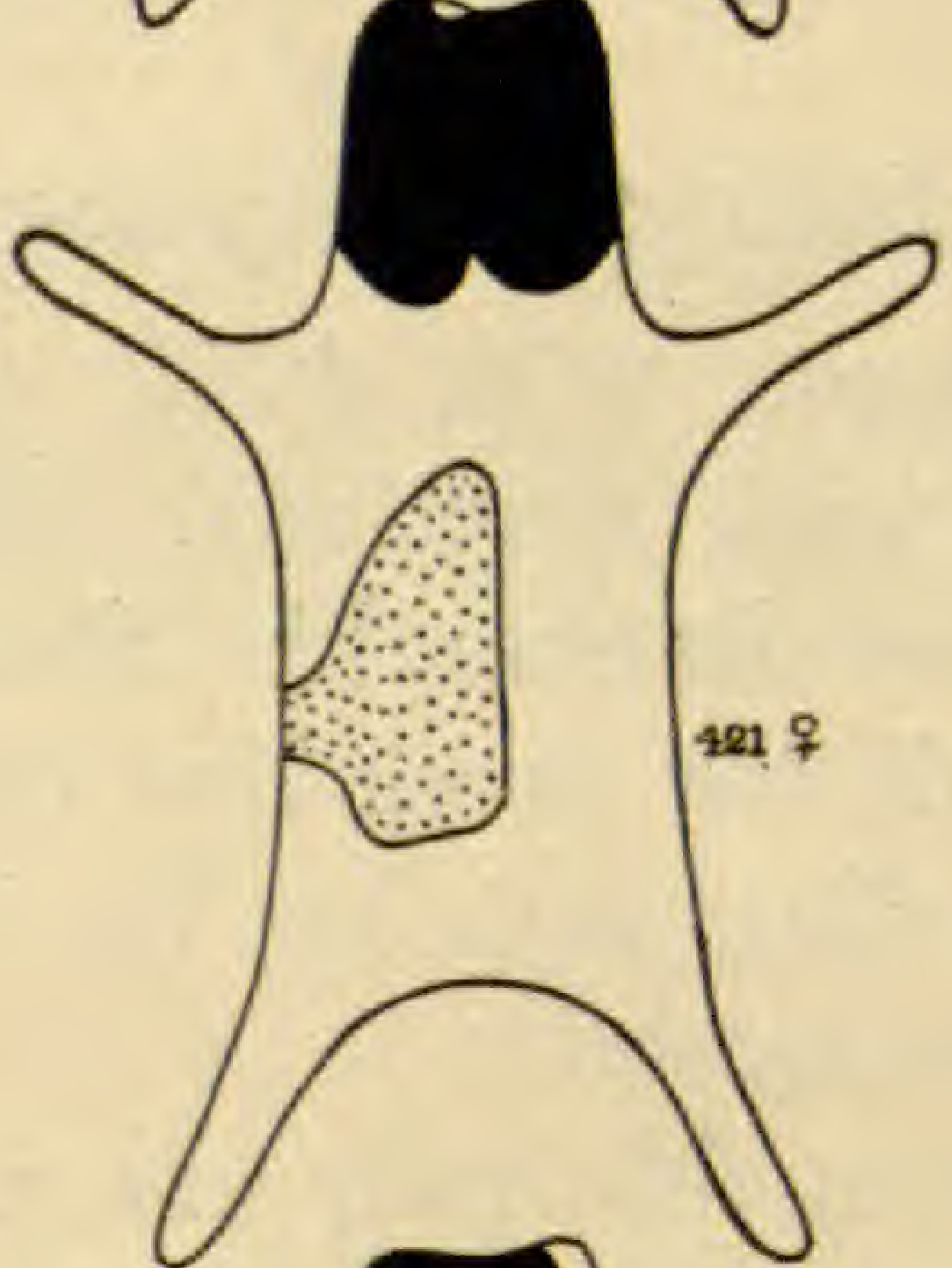
420 ♀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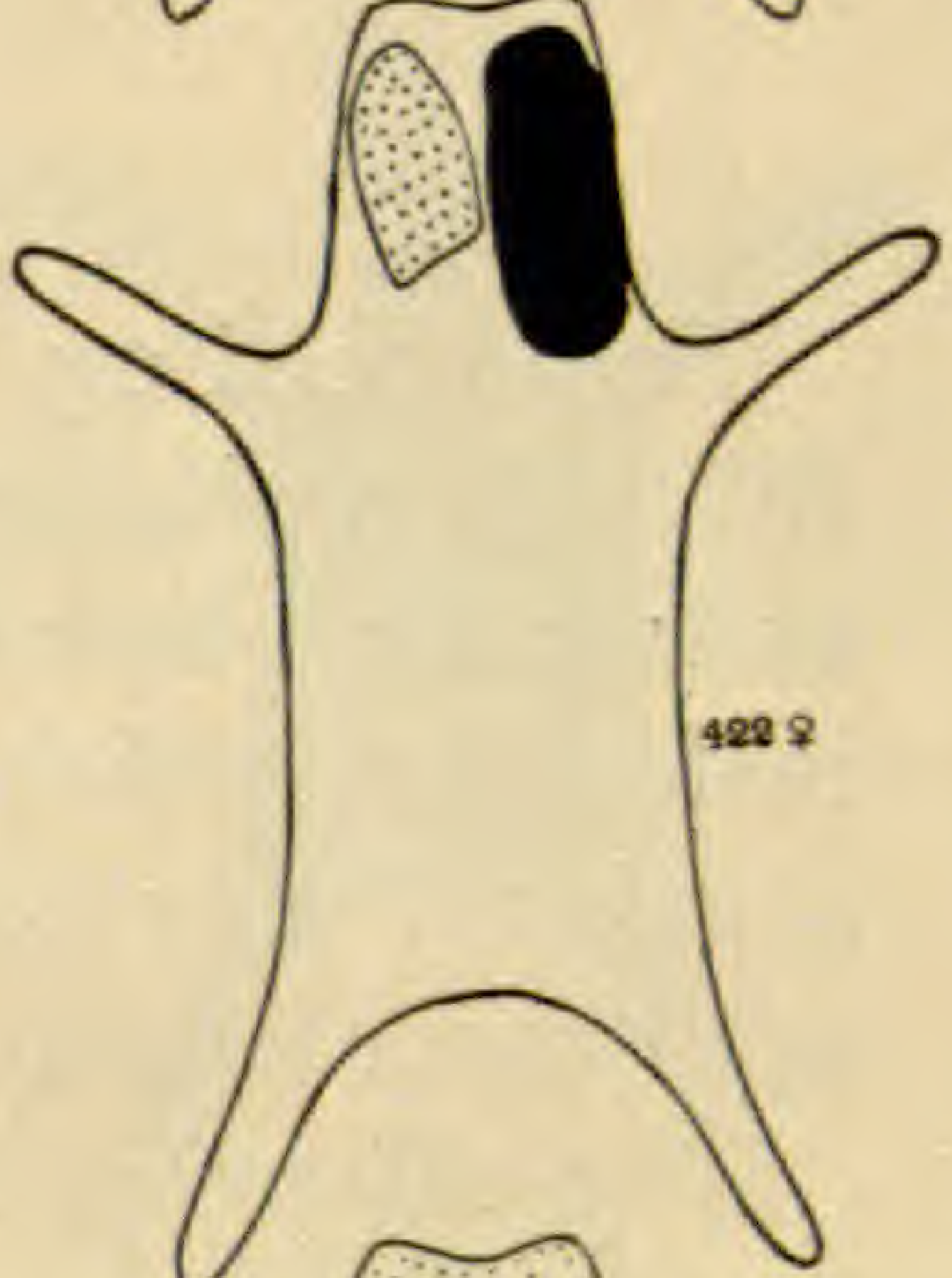
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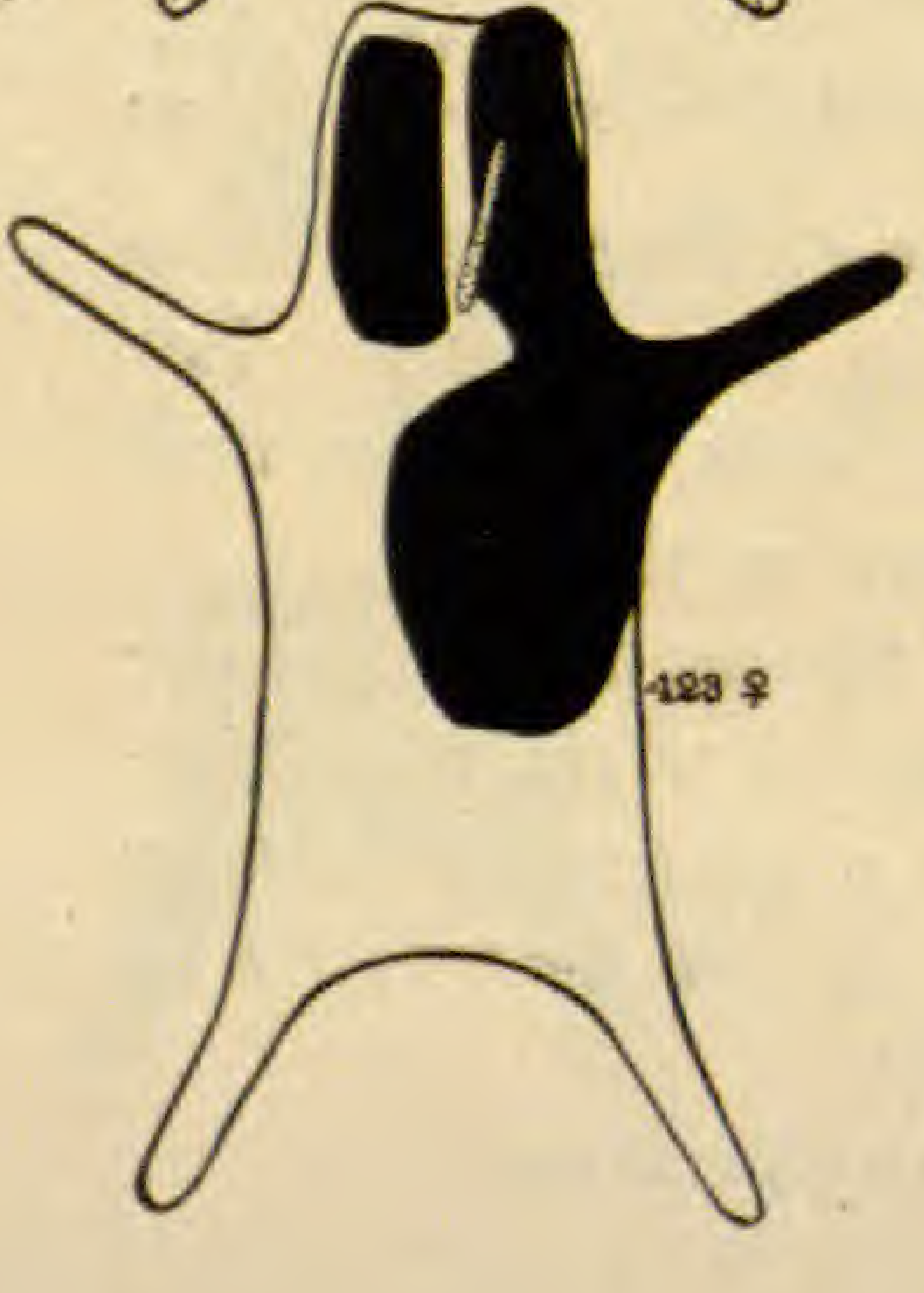
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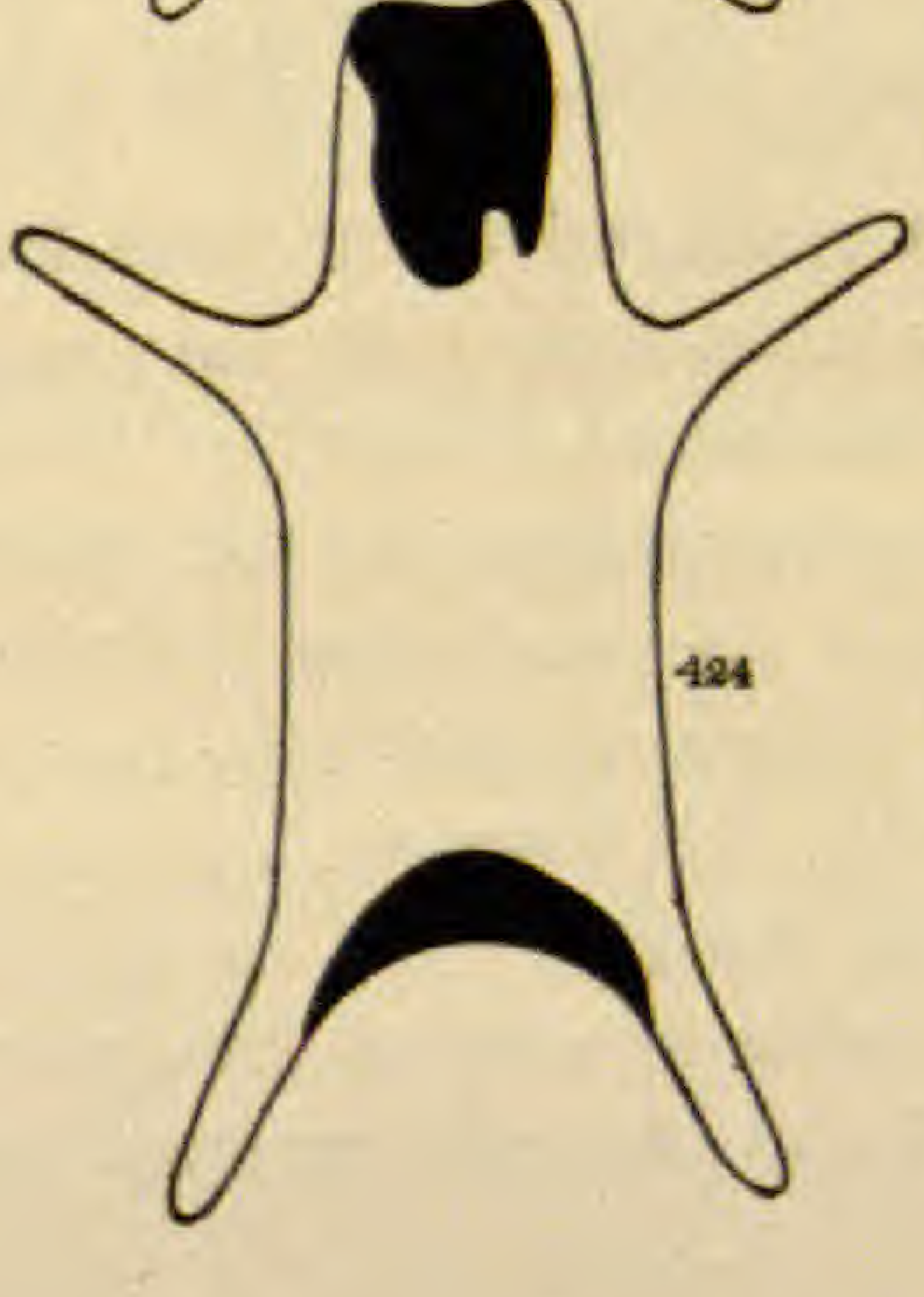
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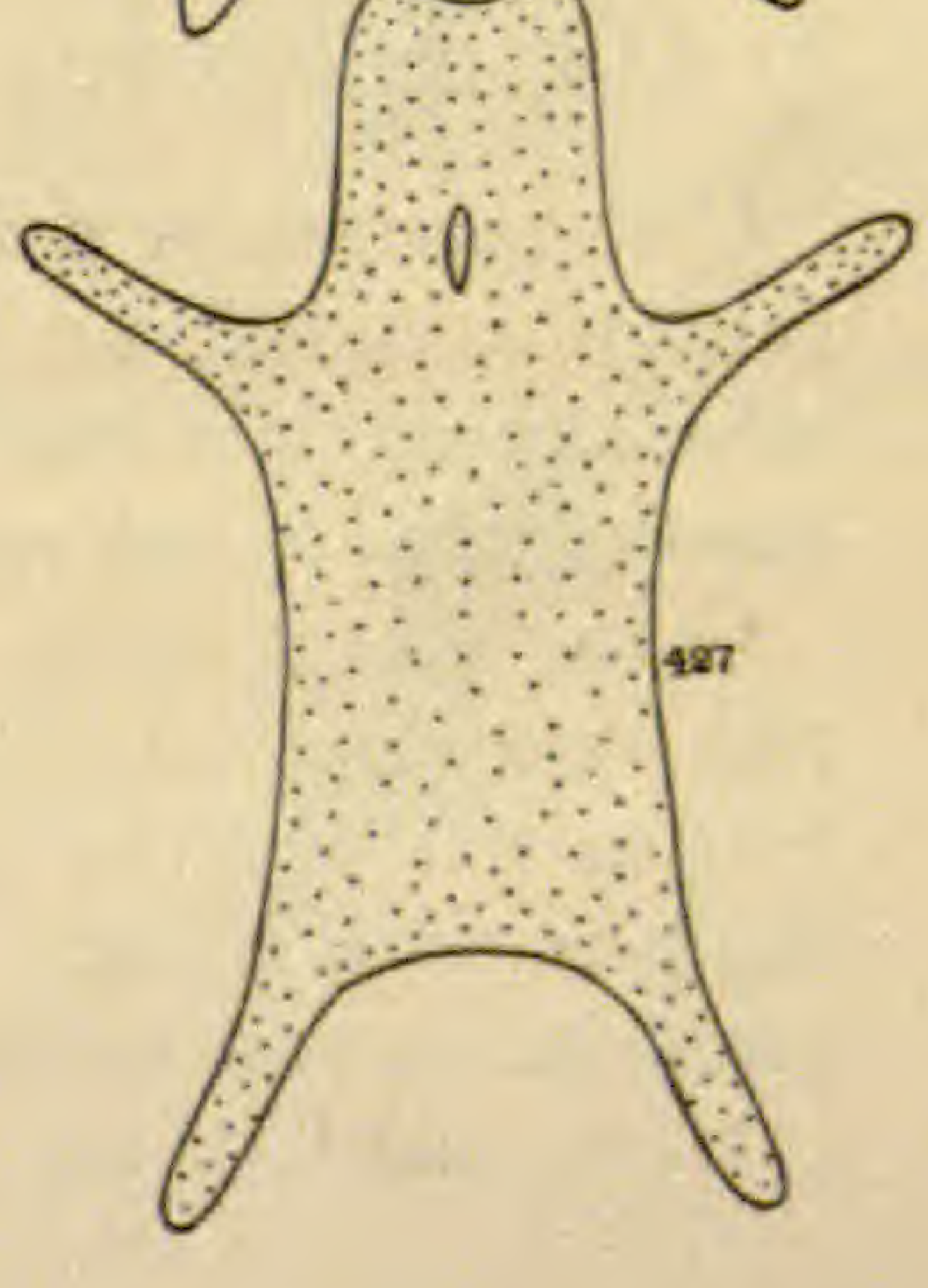
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the skin drawn on the outline in free hand.[4] The majority of the sketches were made from animals which had been preserved in formalin, sometimes in poor condition when put into the formalin. A few of the dead animals were lost by being thrown out by the attendant while cleaning.

The Material.—Our original tricolors were purchased from a dealer. It is important to note that in these animals the color that we designate as red is a red and not a yellow. Animals that are spotted black, white and yellow also occur. The self-colored red and black animals were from the pedigreed stock of Mr. B. B. Horton, to whom we are under many obligations for the opportunity to carry on this work at "Oakwood." The tricolors are known to fanciers as tortoise and white.

In the figures solid black represent black; stippled areas represent yellow; white crosses on black represent yellow hairs; and black crosses represent black hairs. Small circles indicate agouti areas.

BREEDING RECORDS

The breeding began with 401♀ (short-haired) and 402♂ (long-haired with rosettes). No. 401 we classify as tricolor black (see diagram).[5] She is the original female from which all the stock has descended. No. 402 also is tricolor (see diagram), but the black and red areas are nearly evenly balanced.[6]

The offspring from this pair are numbered from 403 to 414, inclusive; five, 405, 406, 407 (balanced), 408, 412,

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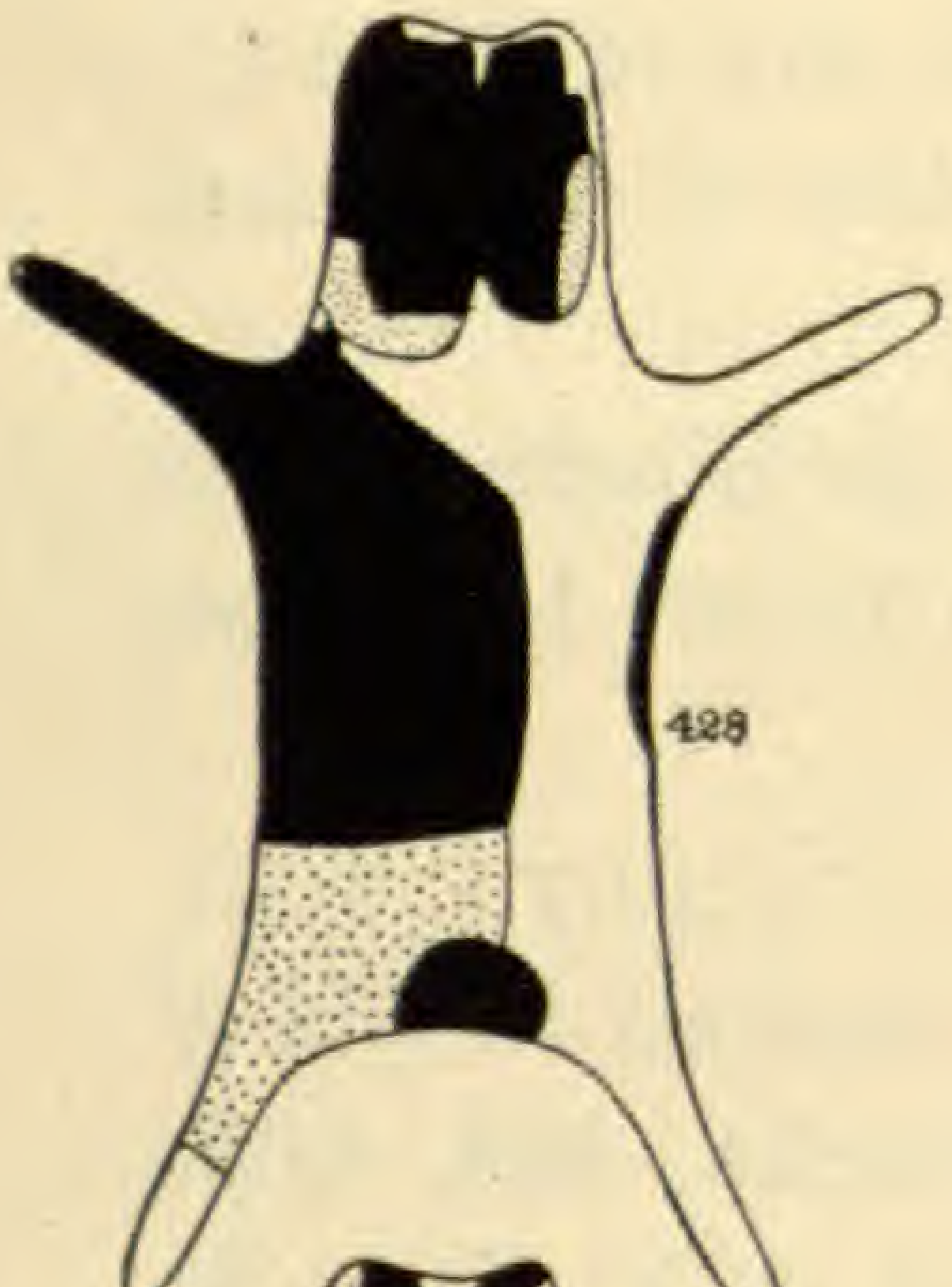
[4] The presence of a few scattered white hairs on the toes has been disregarded in classifying the animal as well as preparing the sketches. Ear color also has not been considered except for bicolor black, and then only when a patch of red was present here but not elsewhere on the body.

[5] After the pedigree chart was made the individual figures of the guinea-pigs were more carefully compared and in a few cases, in which the classification was doubtful (such, for instance, as whether a pattern in tricolor black is tricolor red) was changed; the designation in the text is to be preferred to that in the table in case of disagreement.

[6] Note that 401 and 402 are partially reversed as to color areas.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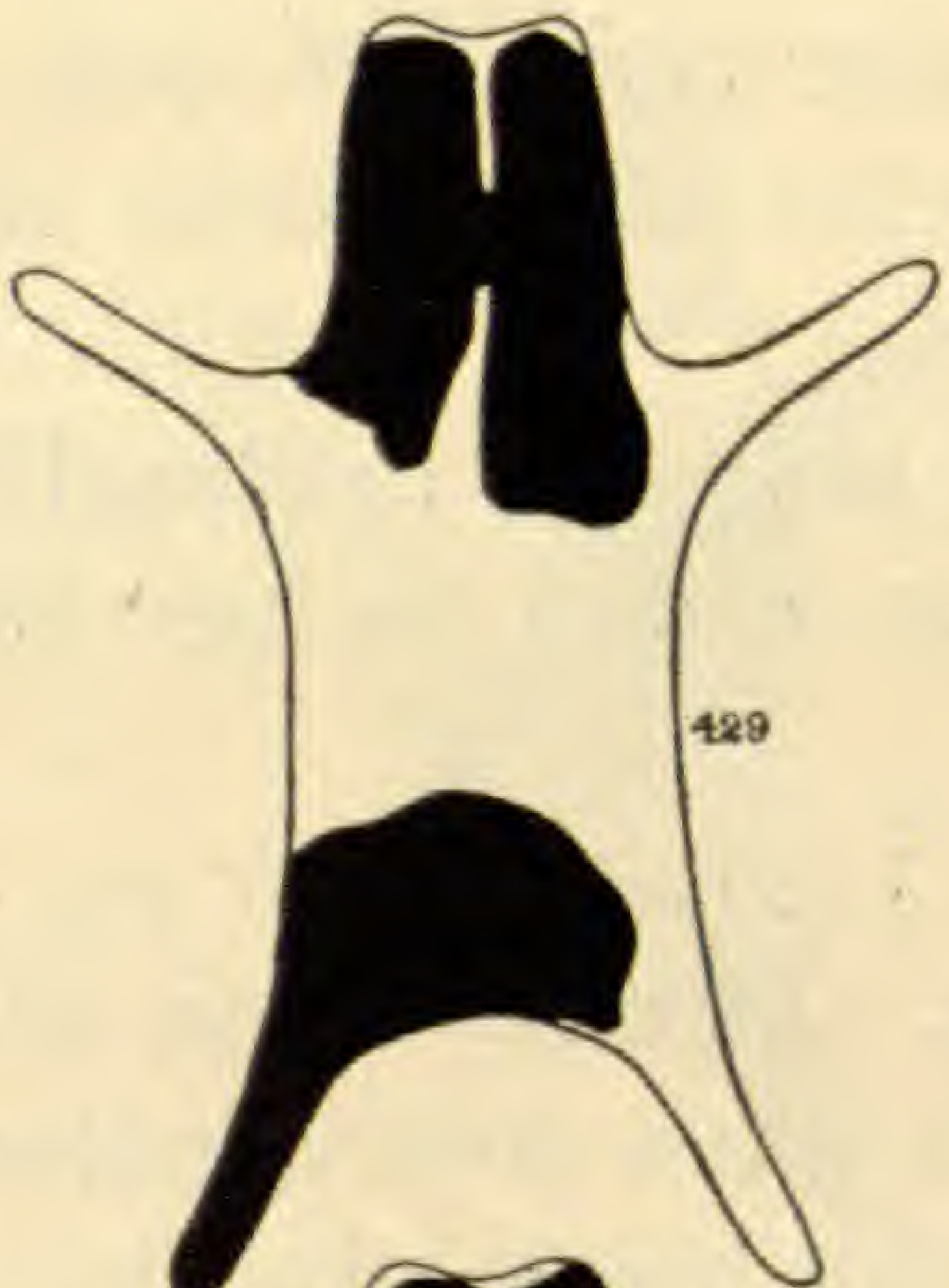
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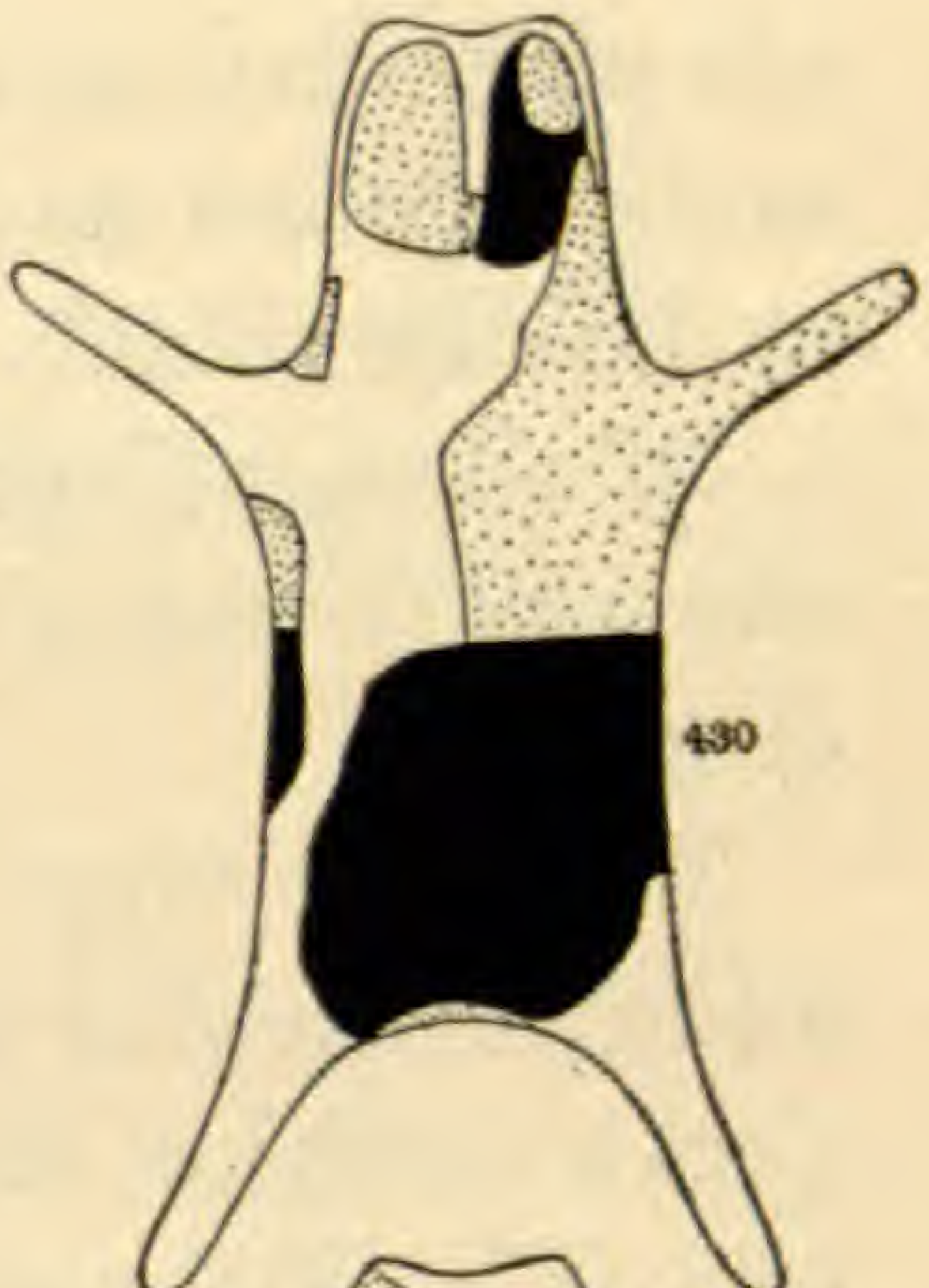
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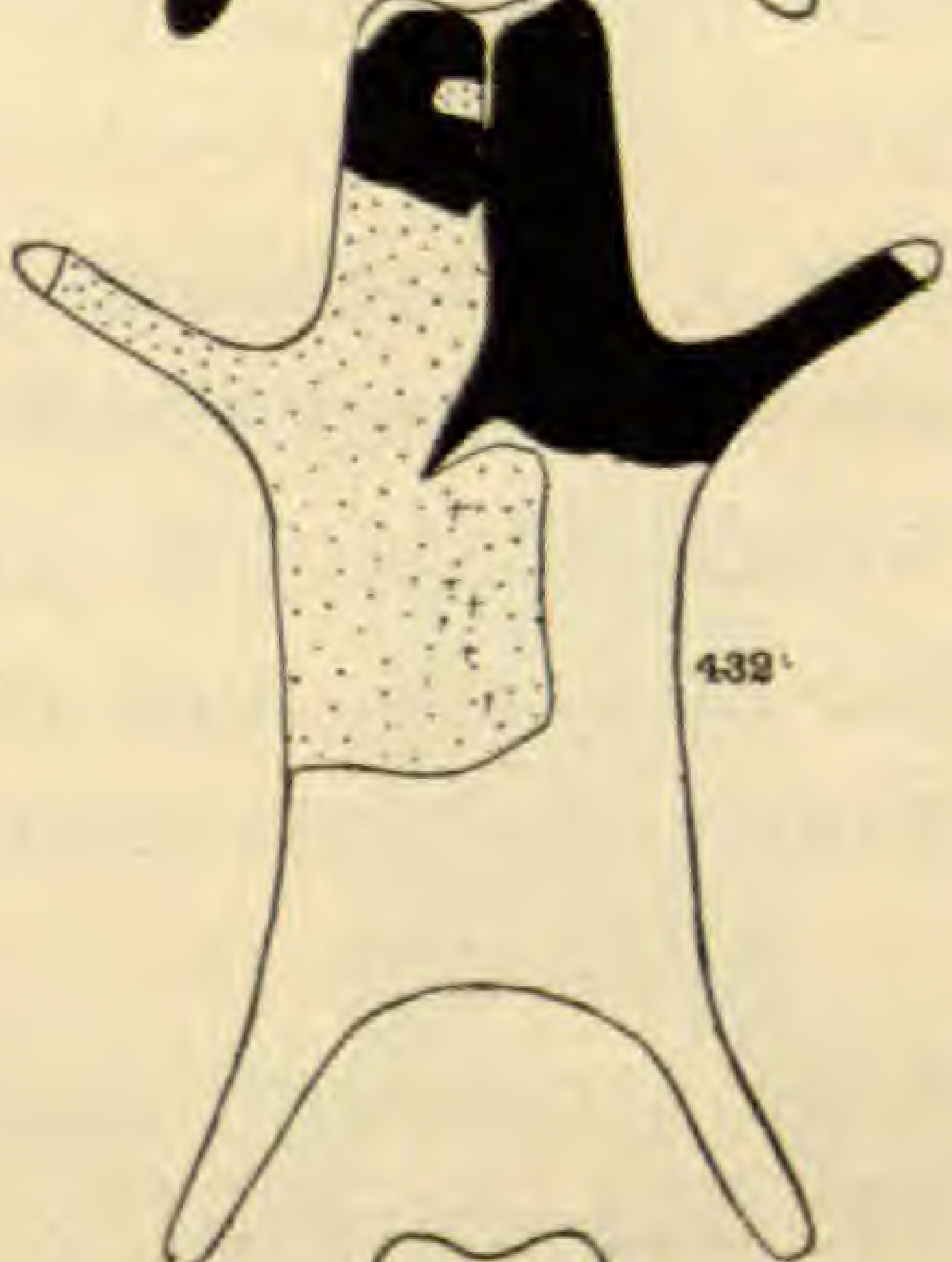
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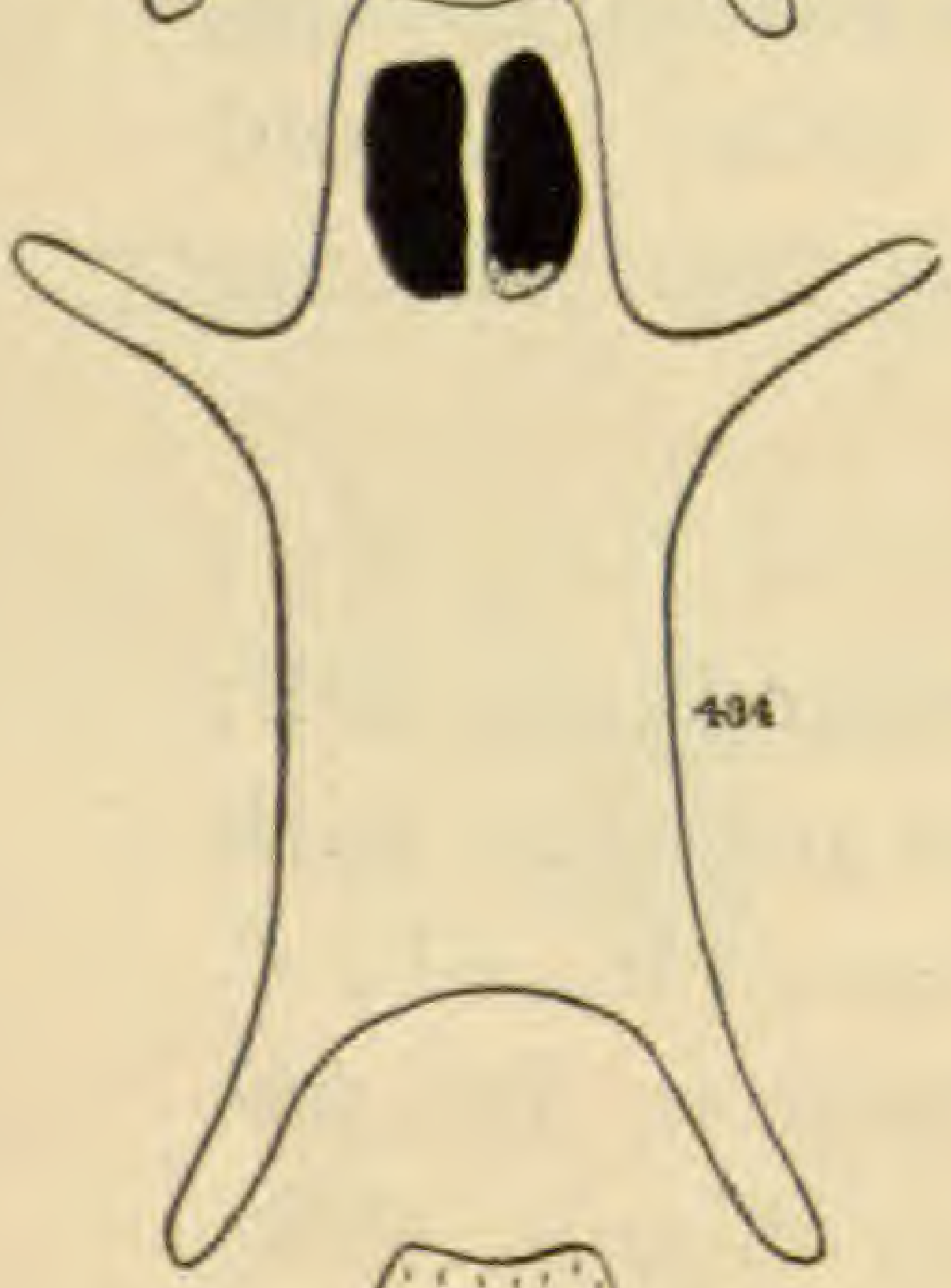
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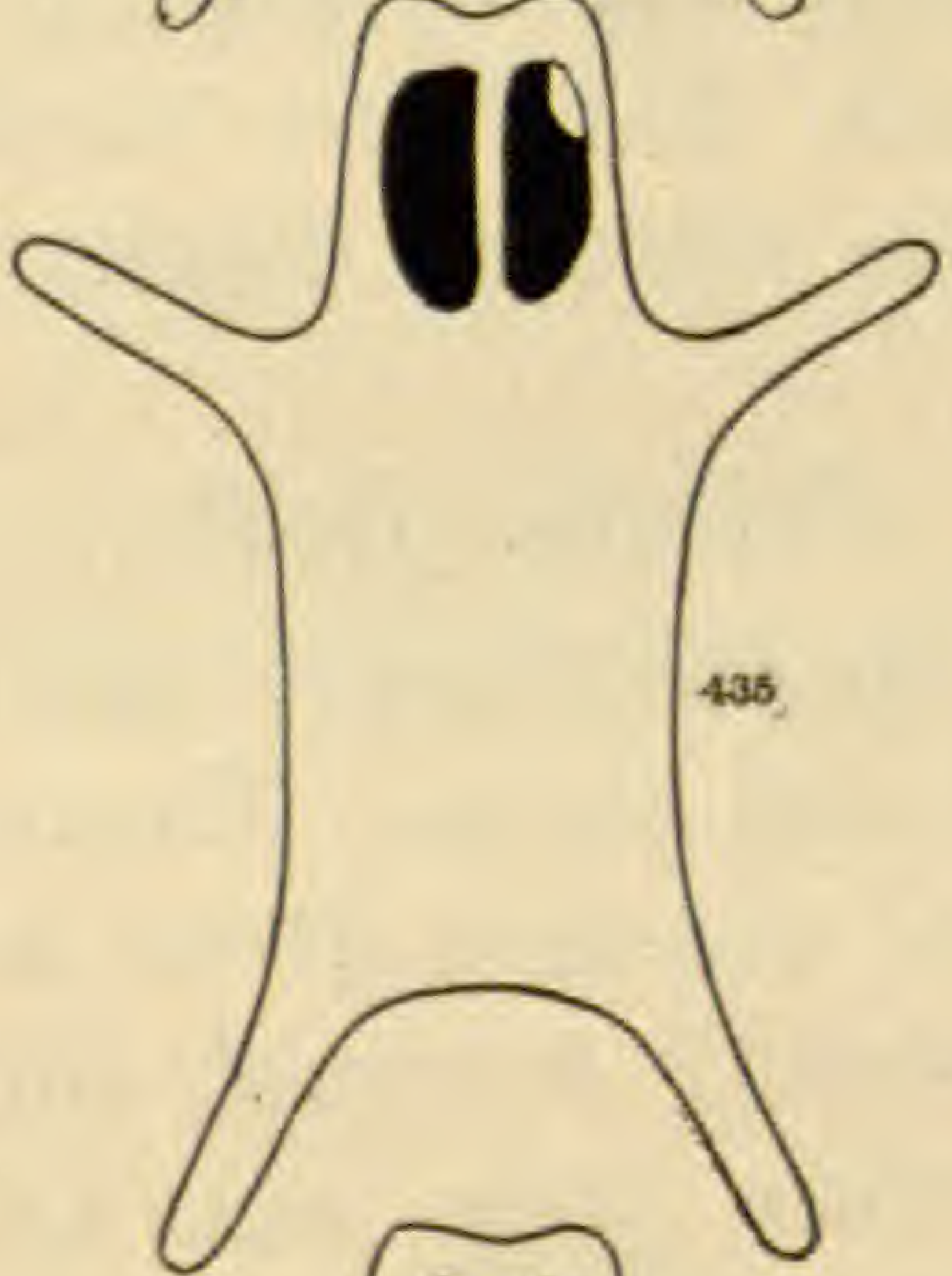
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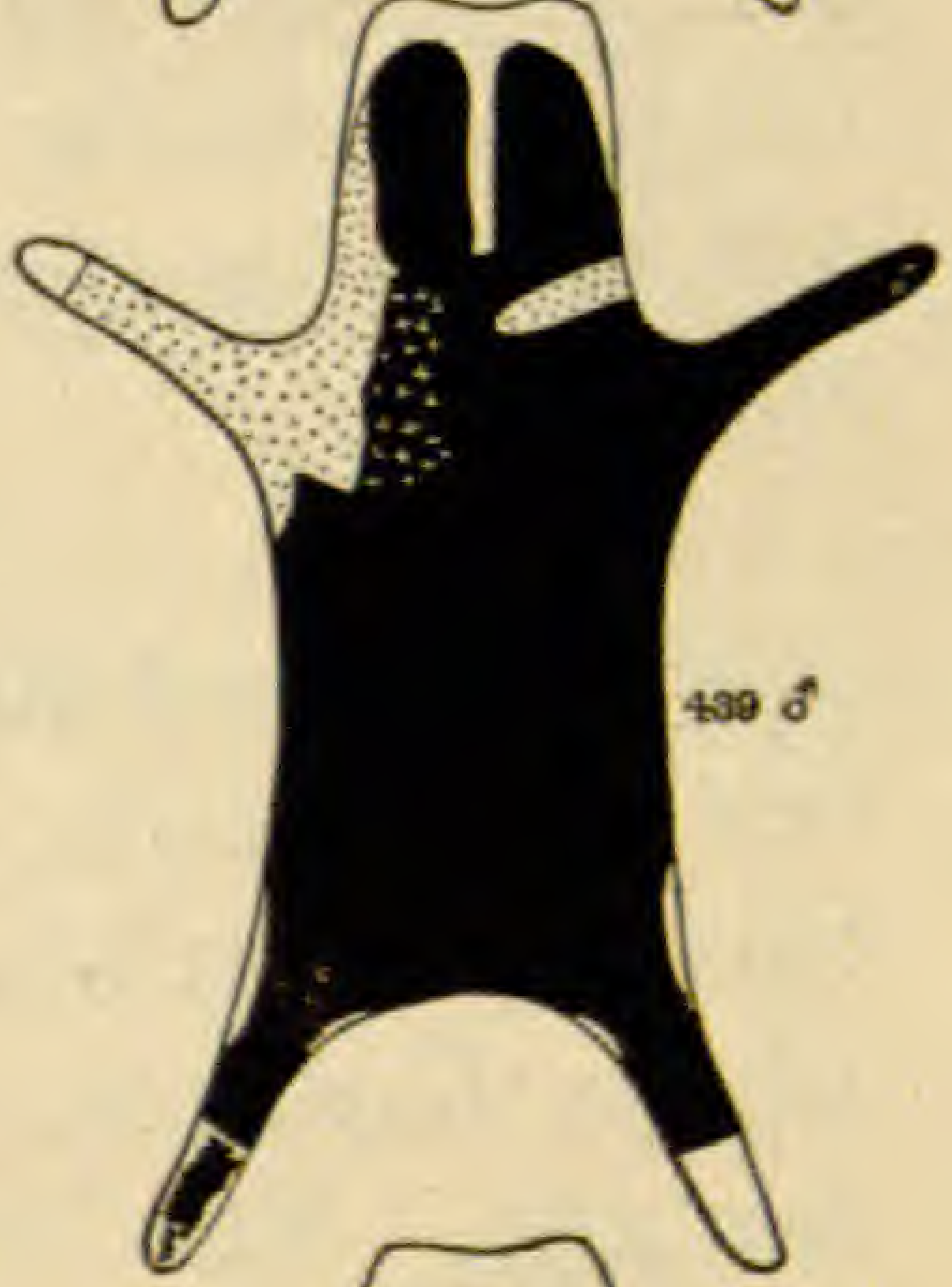
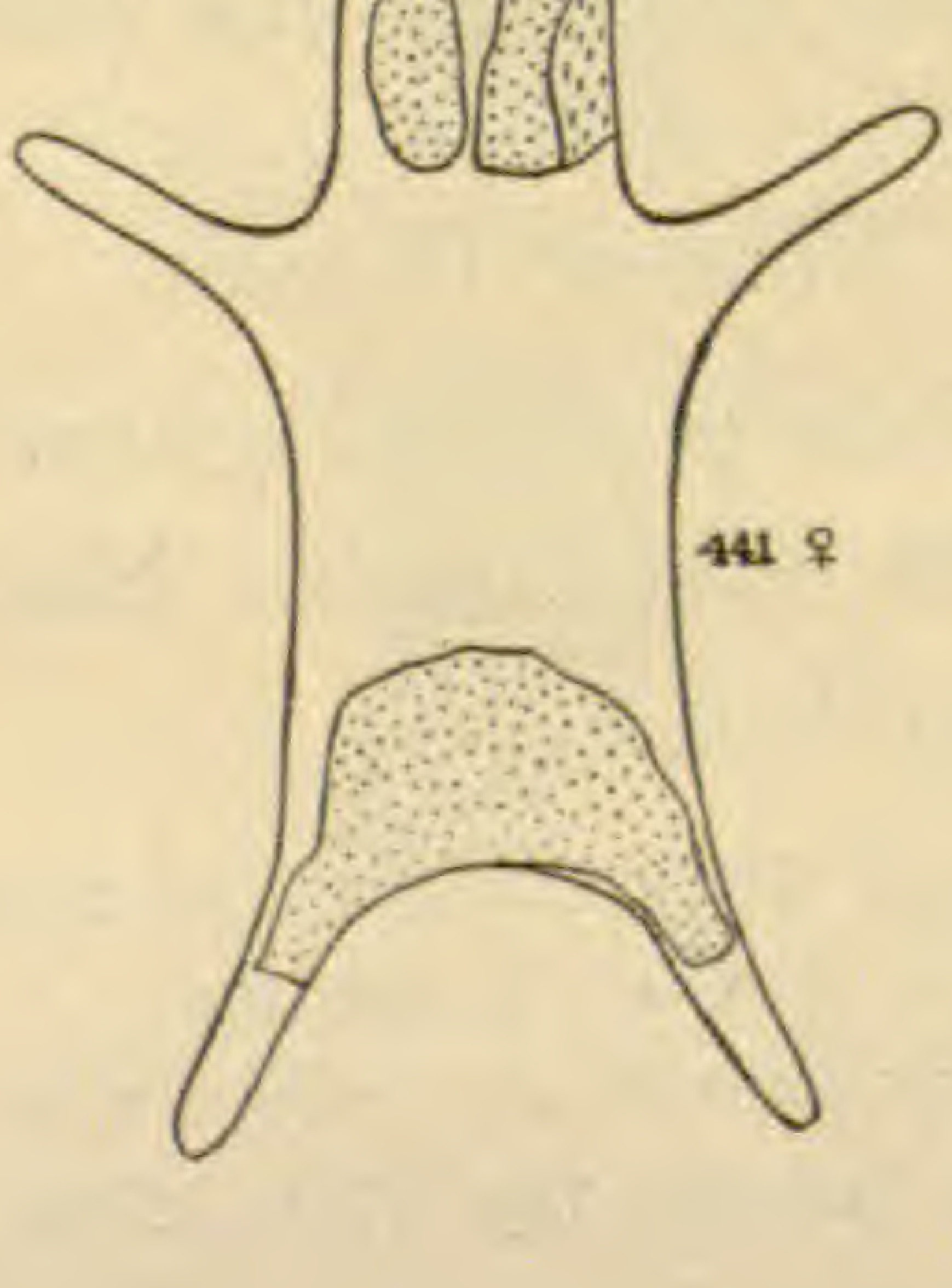
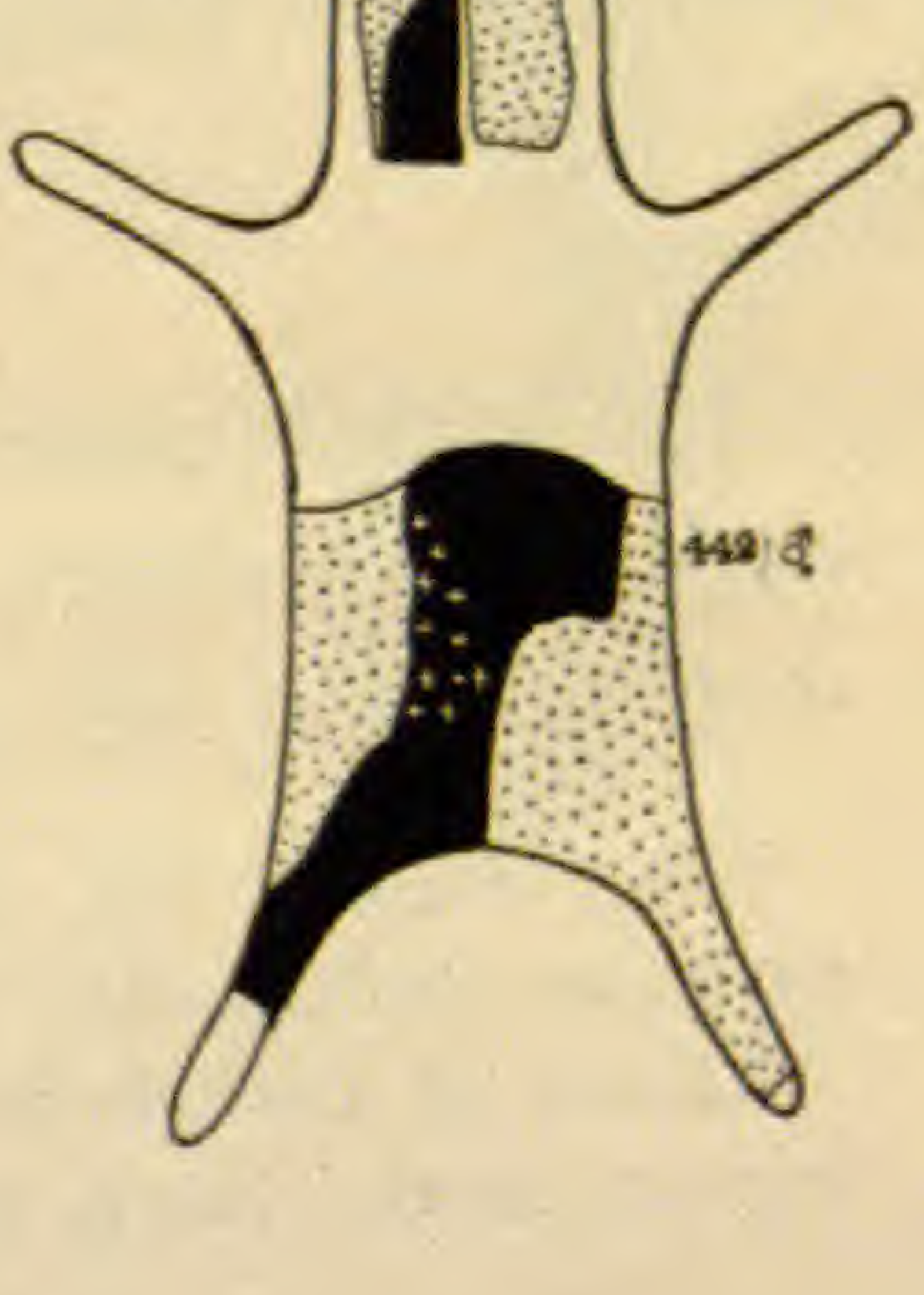

439 ♂


440


441 ♀


442 ♂

are classified as tricolor reds; 403, 404, 410, 411, 413, 414,[7] are classified as tricolor black, while No. 409 is classified as bicolor black.

Of these offspring only one is classified as bicolor, and she (409) has a trace of red on her right front leg (see diagram).

The next step was to mate, *inter se*, the tricolor blacks and the tricolor reds. For instance, 410 ♀ mated to 414 ♂ (both tricolor black) gave five tricolor blacks, 464, 465, 466, 507, 508, and three bicolor blacks—463, 475, 476. It is clear, in this instance, that tricolor blacks tended to produce the same color, *i. e.,* tricolor blacks.

Again, tricolor black 403 ♂ and 404 ♀ (she may be *413*), gave three tricolor blacks, 419, 420 and 428, and three intermediates, 421, 422 and 430, and four bicolor blacks, 418, 423, 424, 429. Four of these bicolor blacks have a trace of red.

No. 414 ♂ bred to 413 ♀ produced eight tricolor blacks: 452, 453, 490, 491, 439, 514, 515, 517; one intermediate, 516; one bicolor black, 513; two tricolor reds, 488 and 489. In this case the tricolor blacks gave two tricolor reds.

Tricolor Red[8]

Tricolor red 408 ♀ by 406 ♂ gave one intermediate, 442; two bicolor reds, 441 and 442 A. There was present with this female at birth of the next litter, another, viz., 412 ♂, which, however, probably was not concerned in its parentage. The offspring were one tricolor black, 493; two bicolor black, 494, 495, and one tricolor red, 492.

Bicolor Blacks

No. 409 ♀ (note red on leg) was mated to 520 ♂ and gave one intermediate, 554; two bicolor blacks, 552, 553 (reddish spot on left shoulder).

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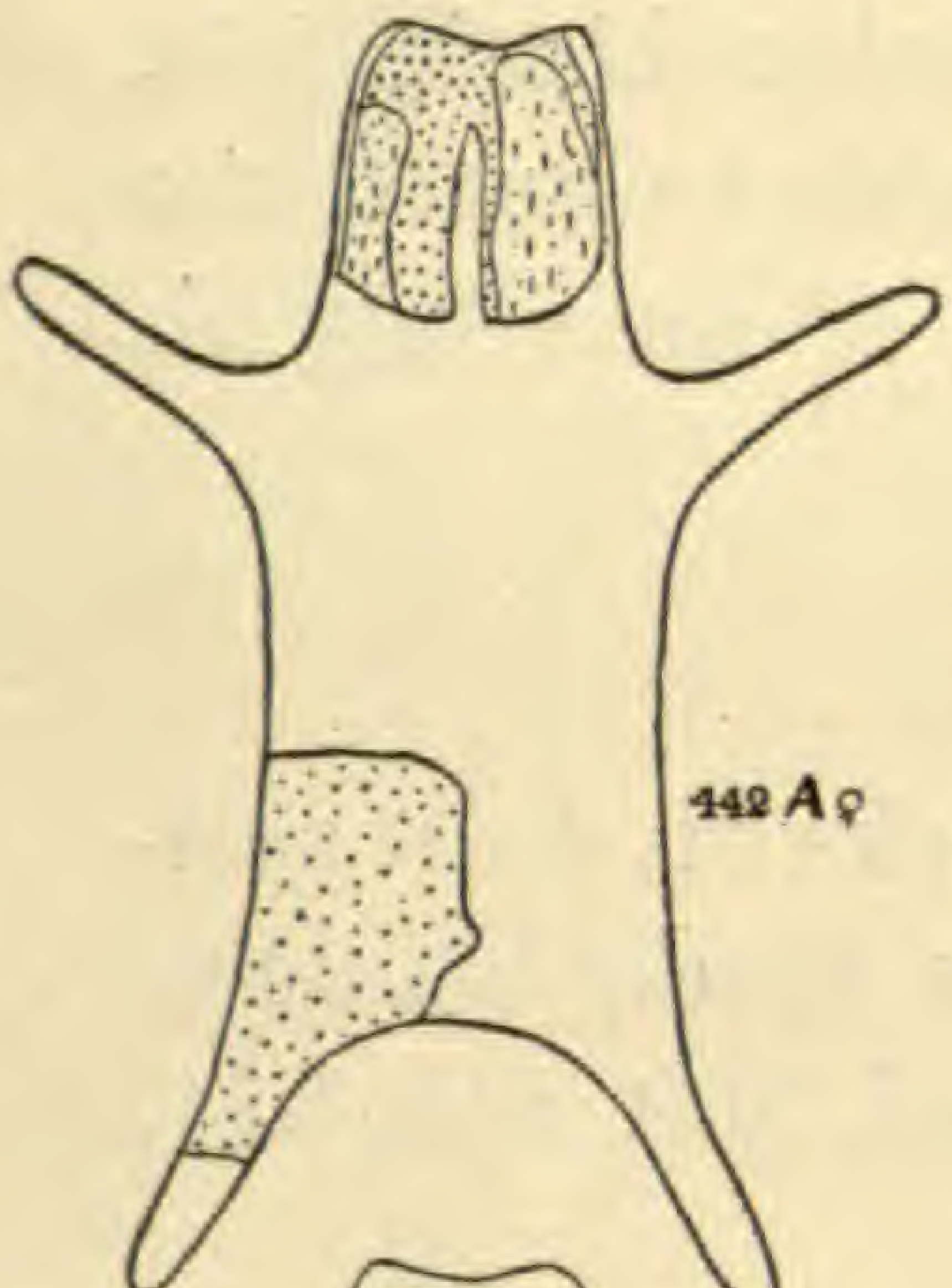
[7] The labels of 404, 410 and 413 were lost and thus the diagrams confused with one another, but not as to their parentage.

[8] Many of the tricolor reds contained much white and thus may have had more potential black, lying beneath the white, than was patent.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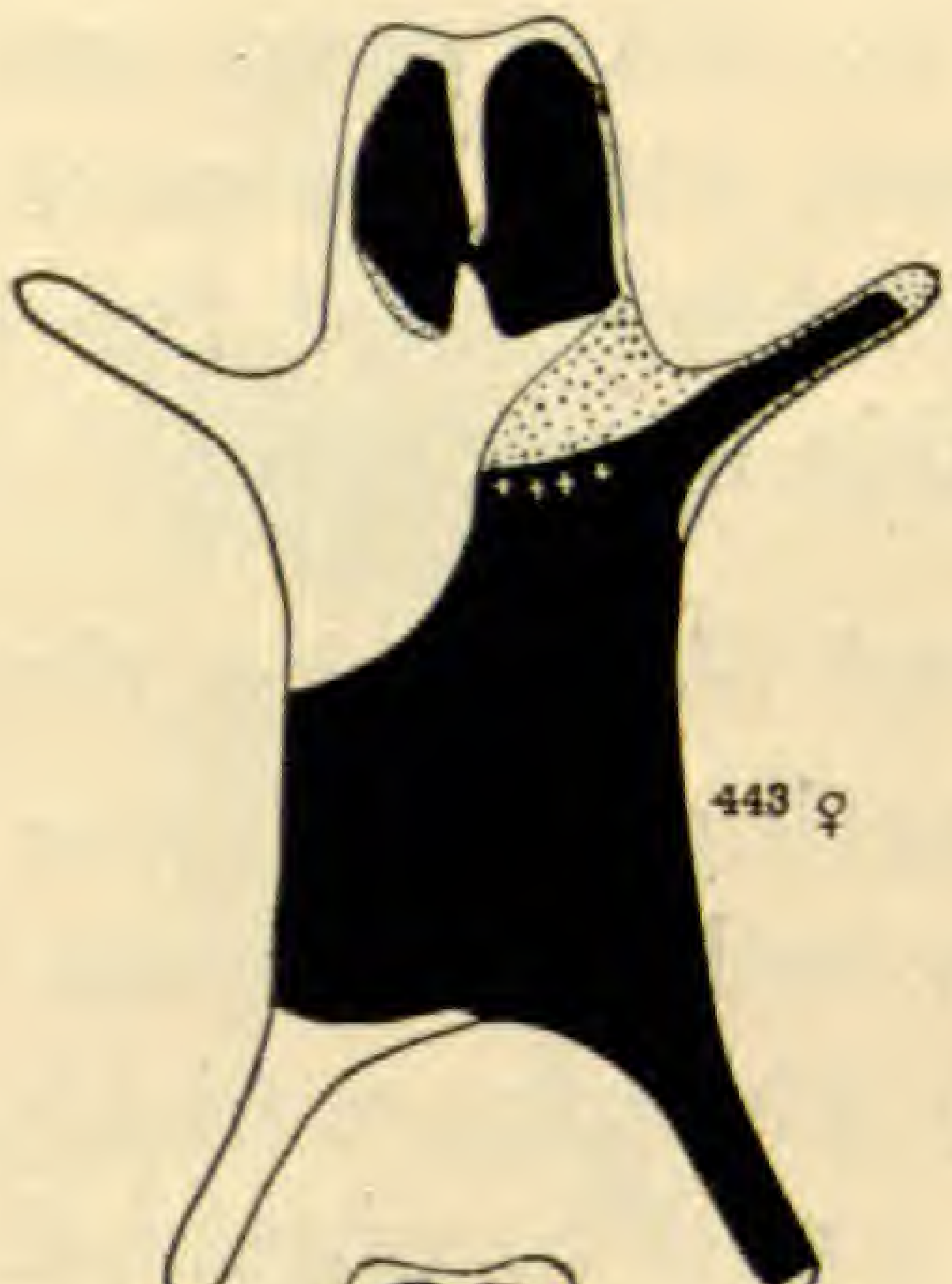
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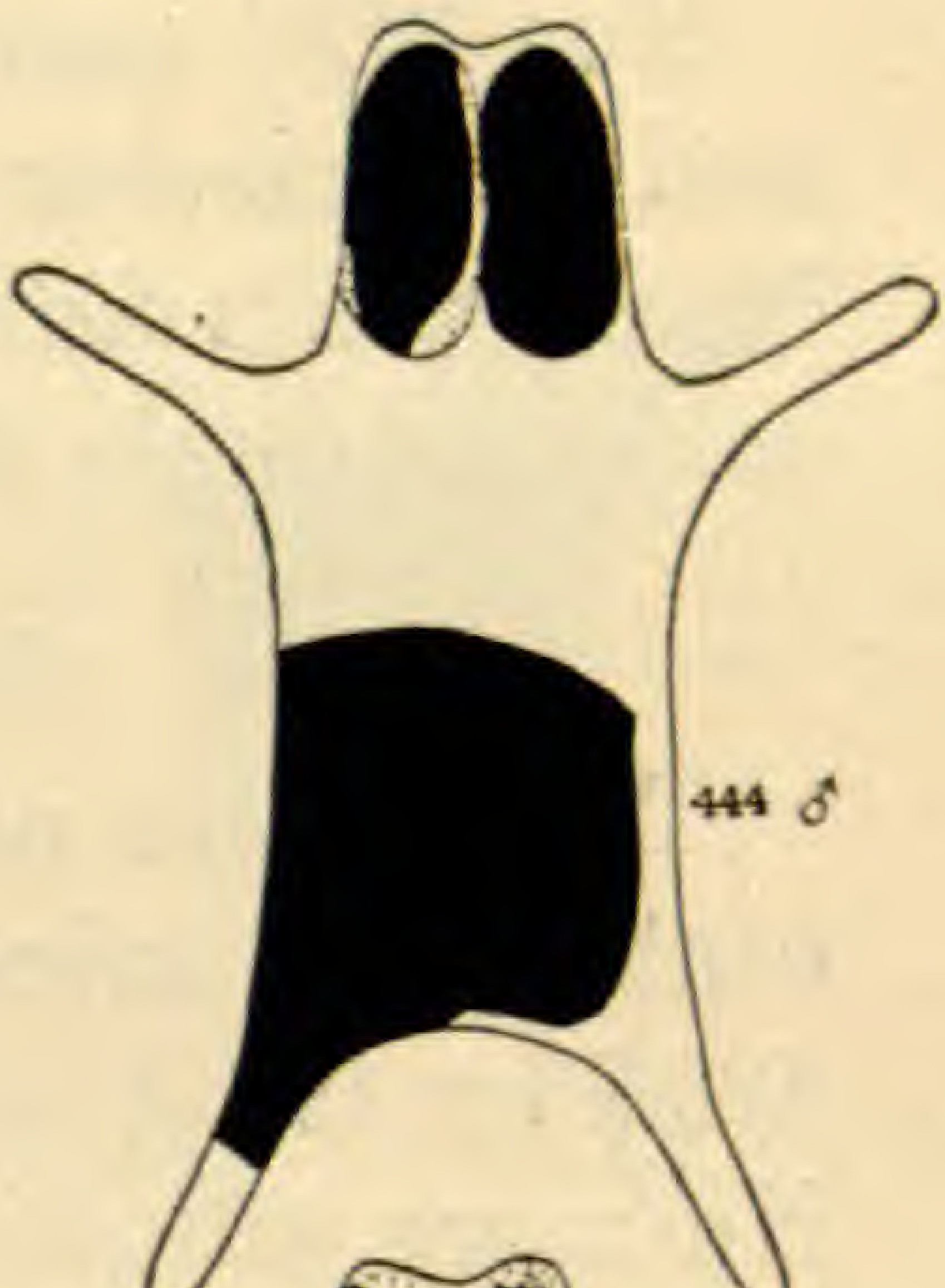
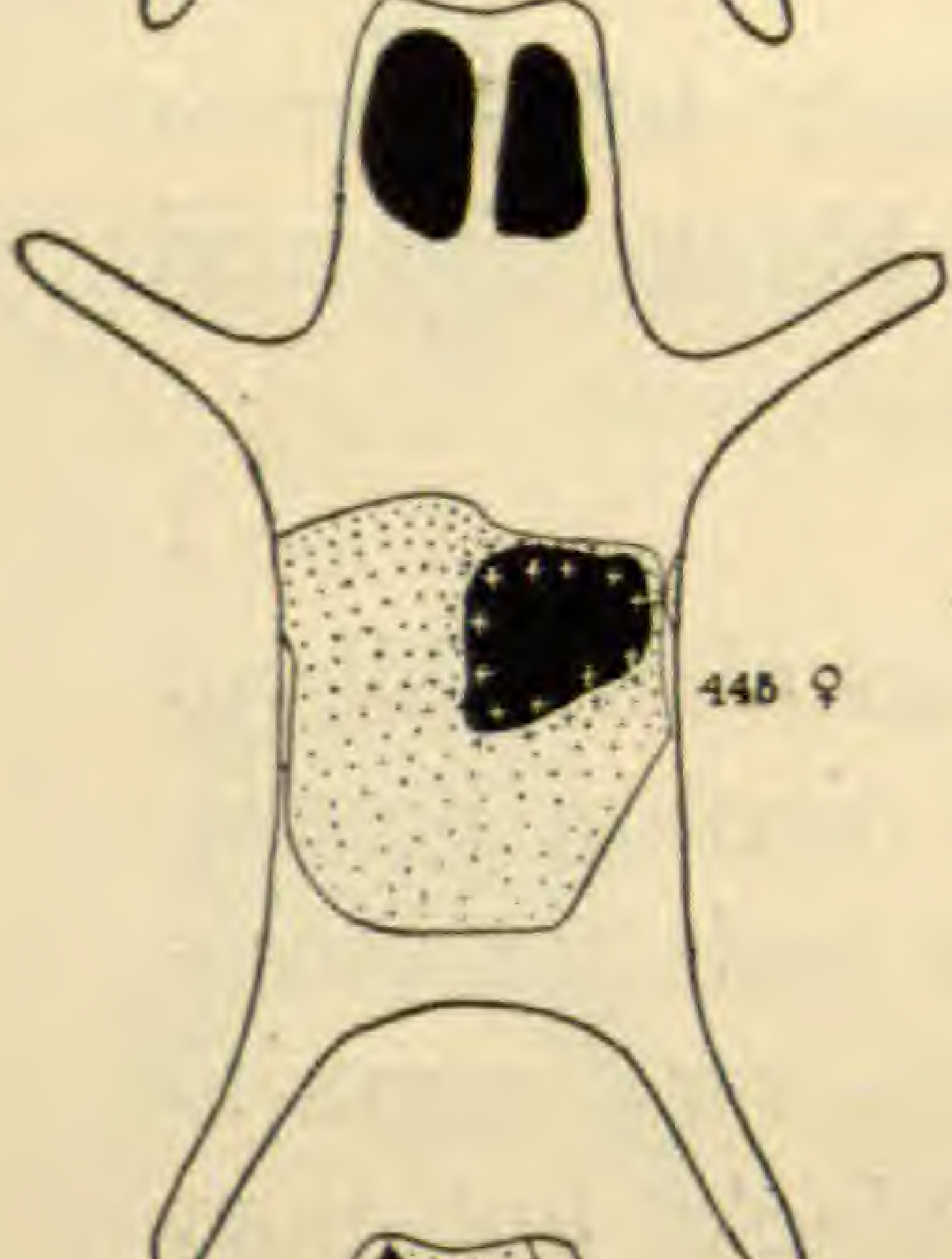
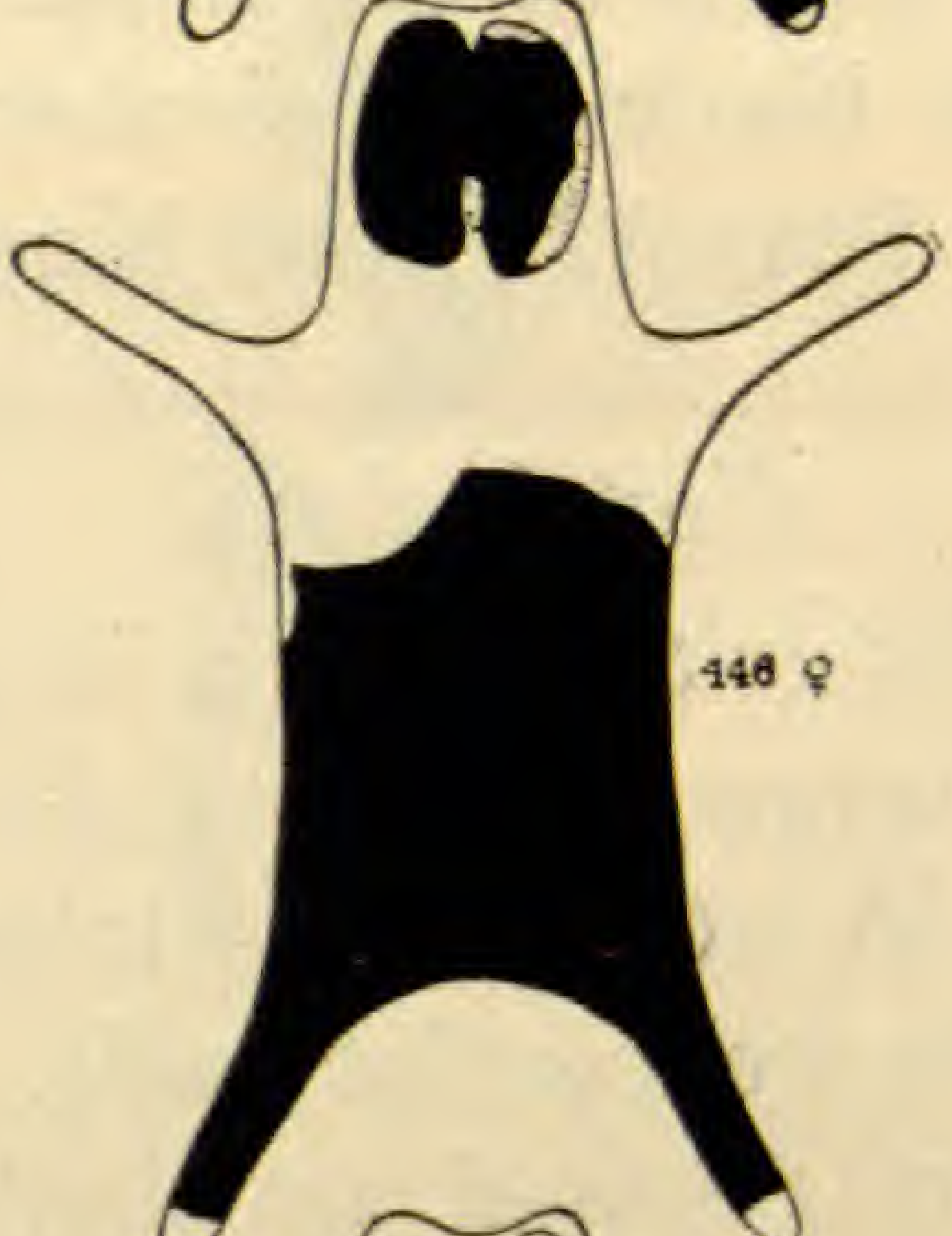

444 ♂


445 ♀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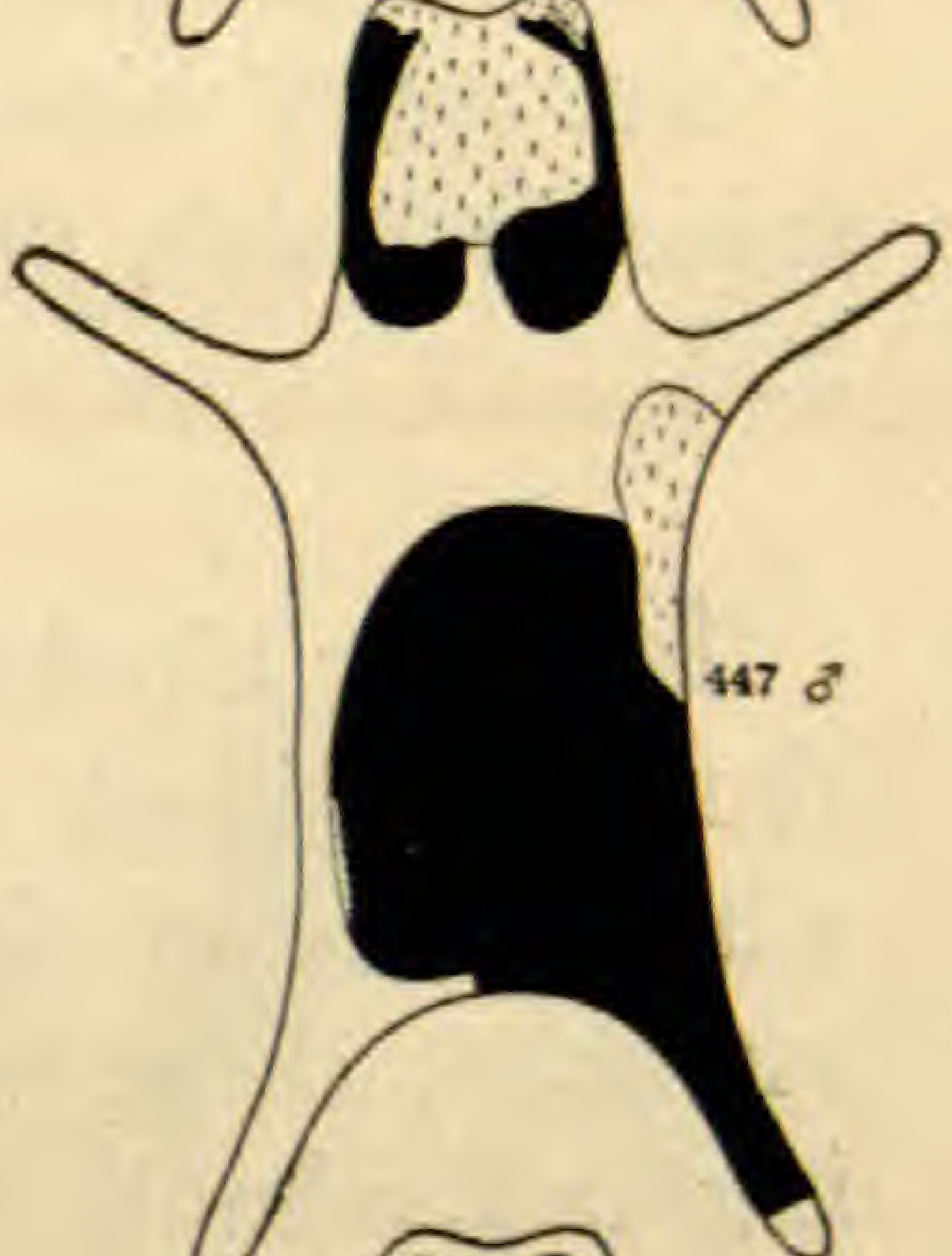
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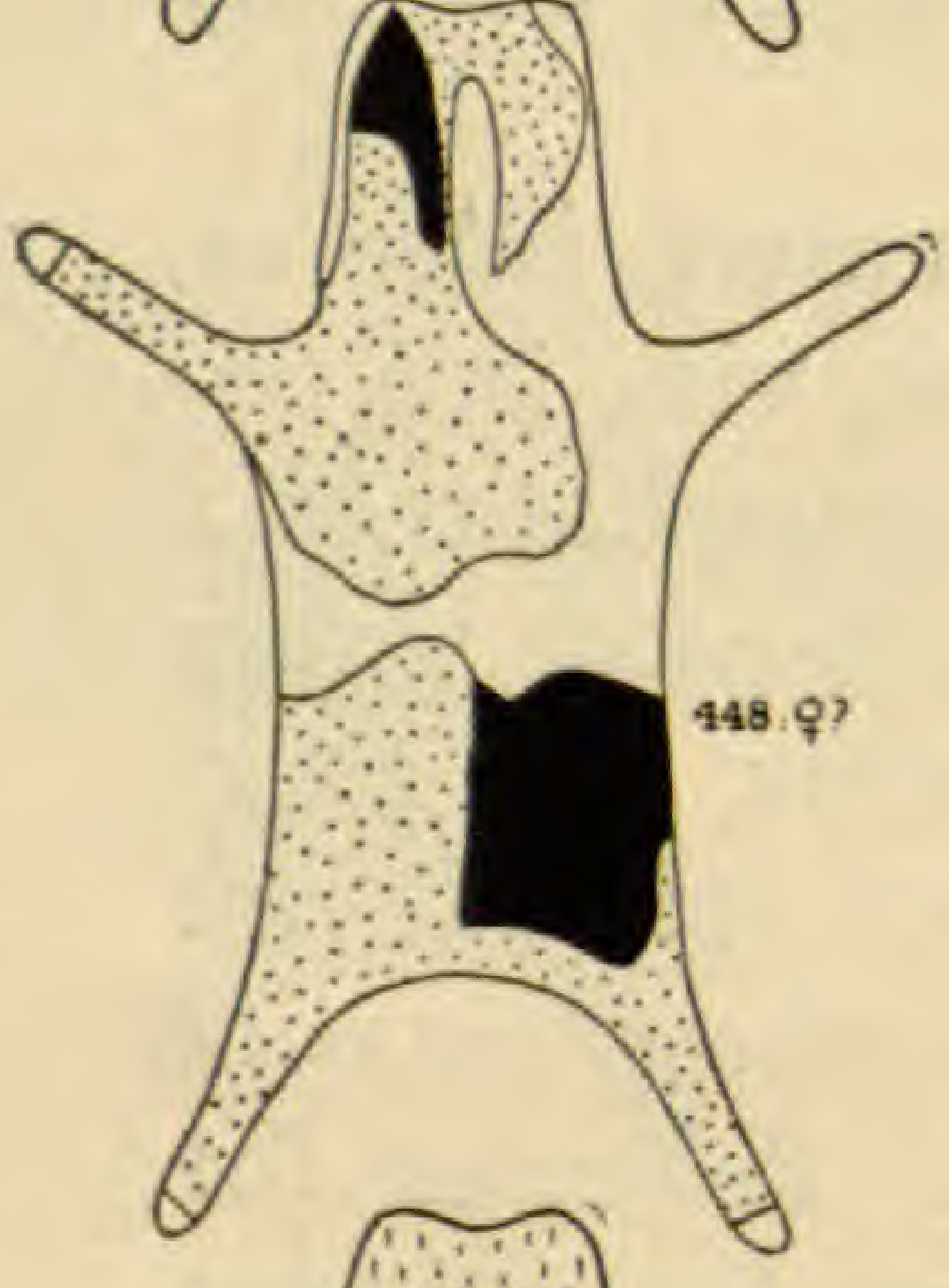
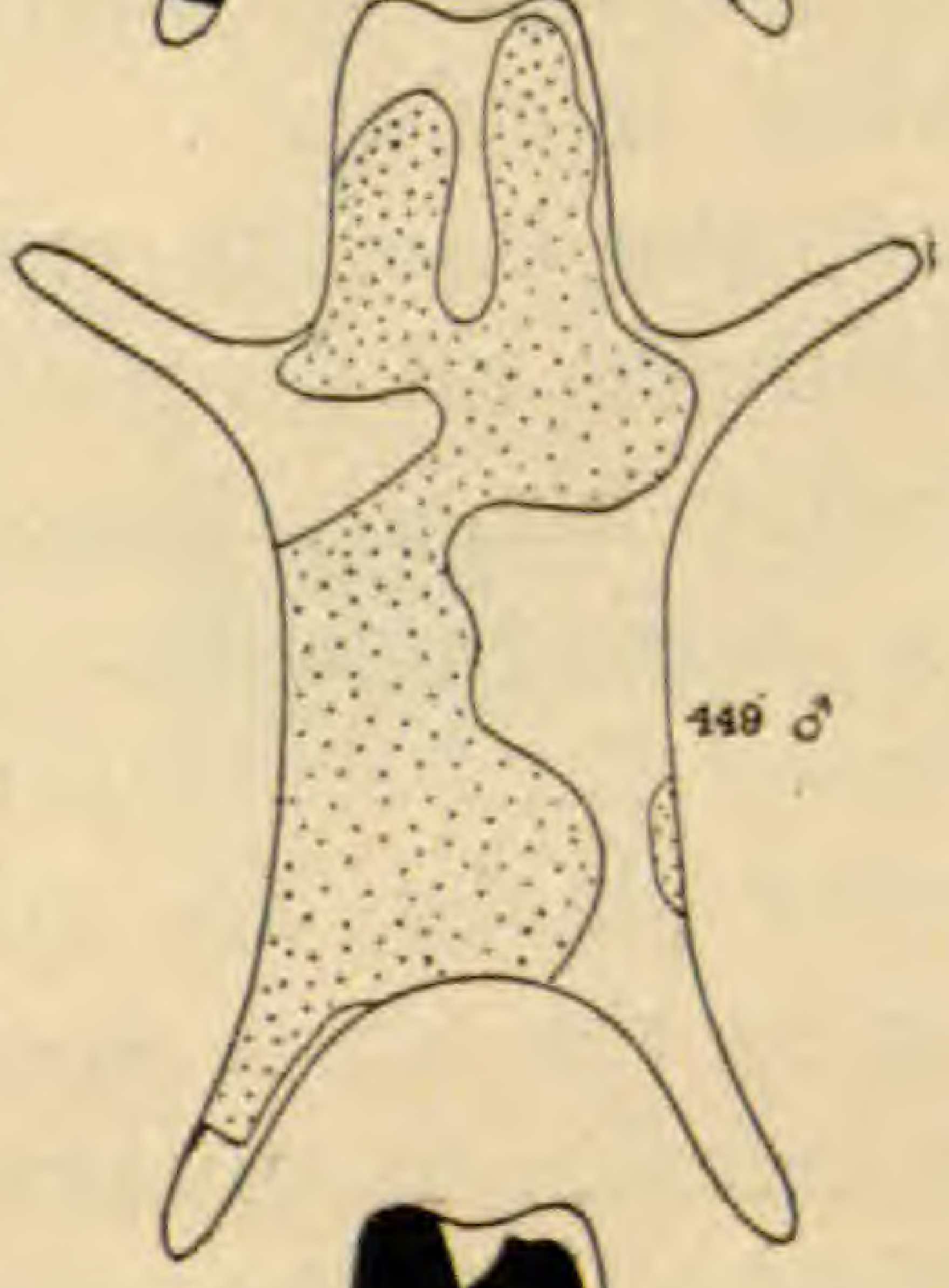
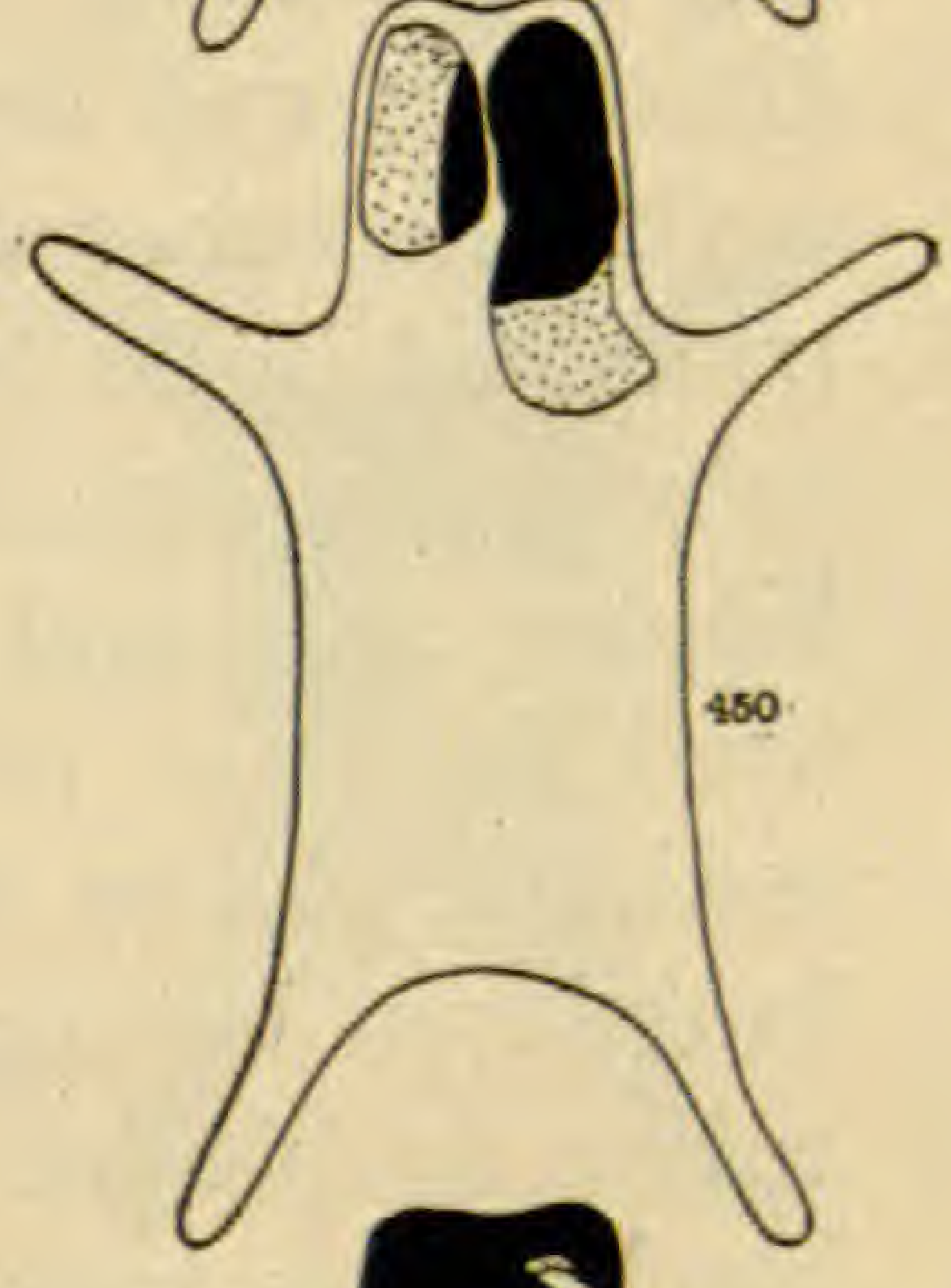

448 ♀?


449 ♂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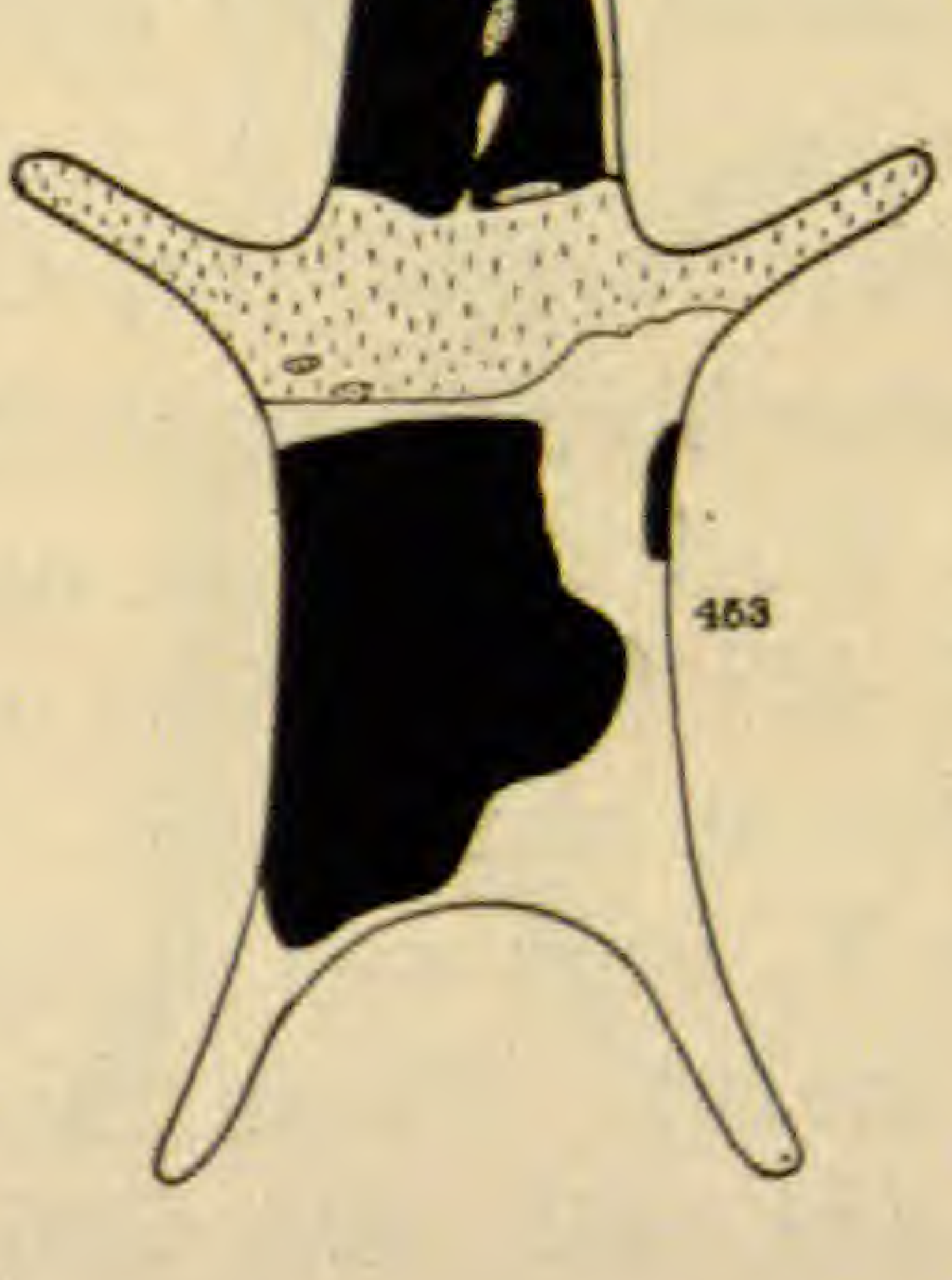
452 ♂


453


456

No. 409♀ mated to 503♂ gave one bicolor black, 533, and one tricolor black, 534. We were unable to breed the bicolor reds *inter se* because of the lack of an adult bicolor red male of this stock.

Second Generation Crosses

There were no matings of tricolor blacks in this generation. A tricolor red, black-cross, was made between 489♀ by 492♂ (son) which gave bicolor red, 509, 510, 511. No more offspring could be obtained.

No. 423♀ bicolor black by tricolor black 469♂ gave tricolor black, 504, 521, 522, and bicolor black, 503 and 520.

Conclusions

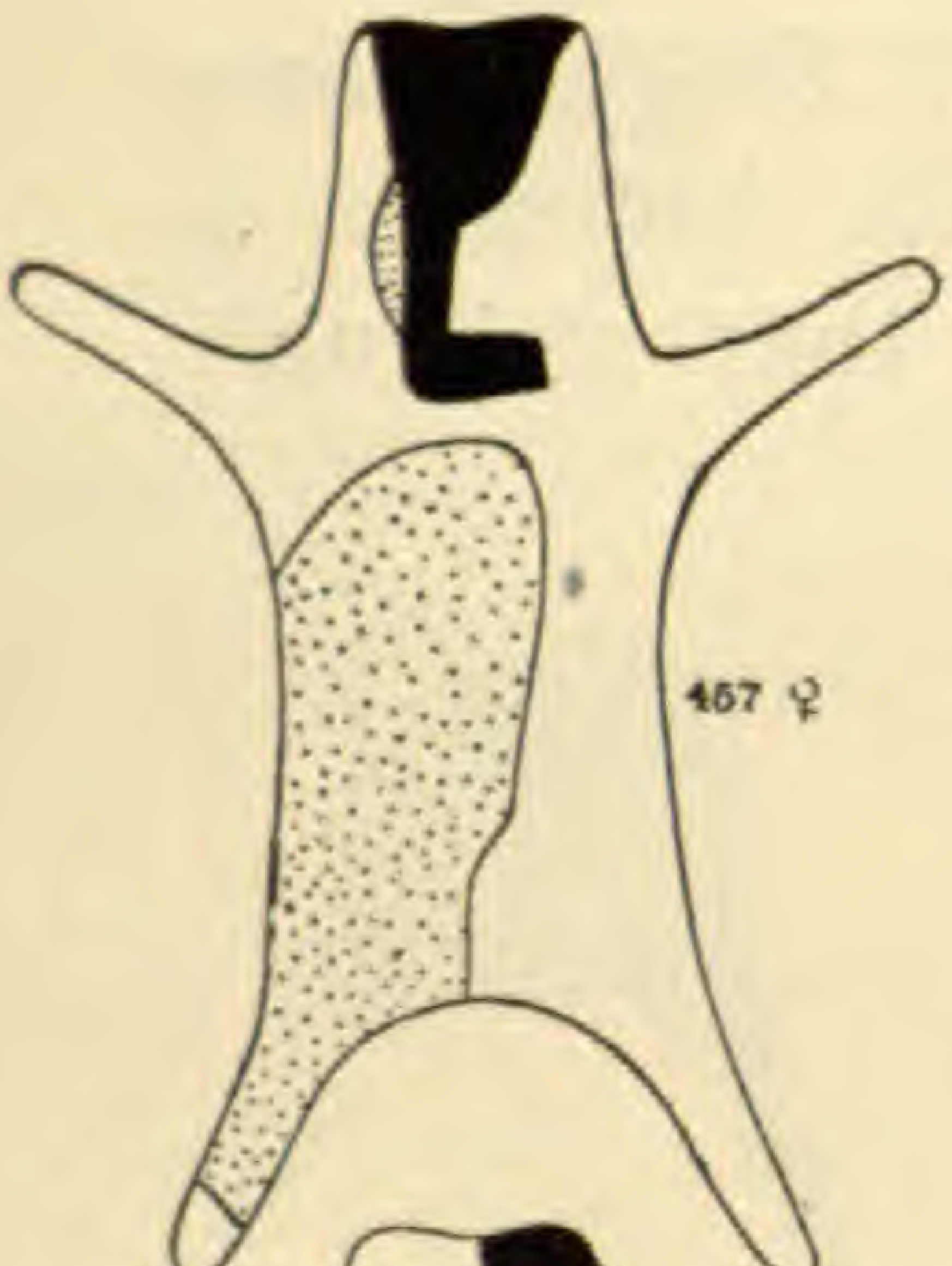
Tricolor blacks, *inter se,* gave a large number (21) of their own kind, a large number (14) of bicolor blacks, while 9 out of the 46 were either tricolor reds or intermediate; there were no bicolor reds. The two remaining individuals were classed as bicolor black, but may almost as well be called tricolor.

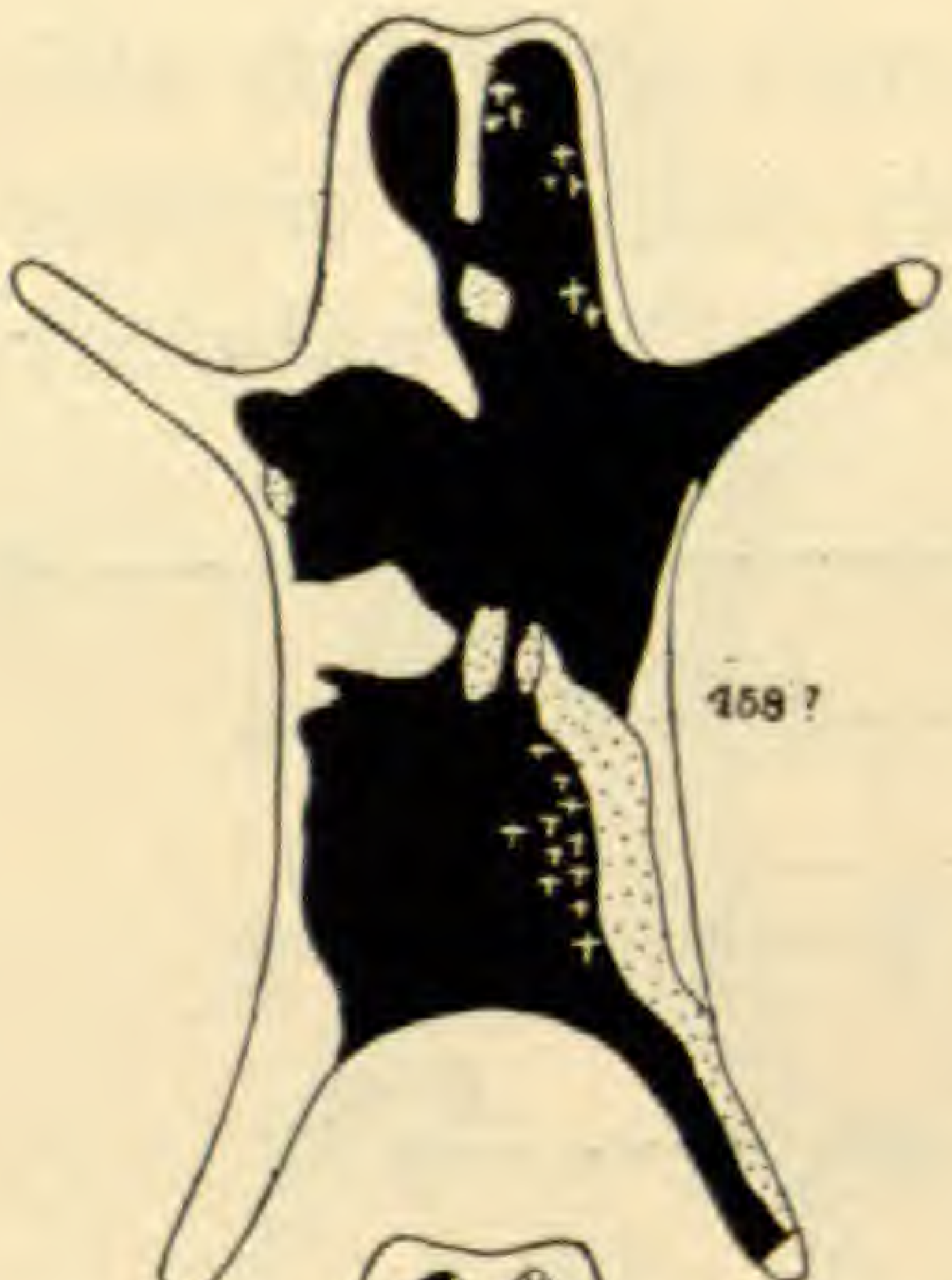
On the other hand, the tricolor reds mated, *inter se,* produced in 20 individuals all four classes, viz., two tricolor reds, two tricolor blacks, four intermediates, six bicolor reds and six bicolor blacks. The bicolor blacks bred, *inter se,* produced three tricolor blacks, one intermediate, eleven bicolor blacks, one tricolor red and one individual belonging to the black series, whose classification as bicolor or tricolor is uncertain. Selection for blacks gave more blacks, but the selection for red was inconclusive.

Spotted to Uniform Coat

The original tricolor black female, No. 401, was mated to a red male from Horton's stock and gave seven uniform reds, 425, 426, 427 (note white spot), 436, 437, 454 (minute spot of white on nose), 455.

One pair of these F_1 reds was mated (lack of females preventing mating more). From this pair we obtained uniform reds, 483, 484, 495, 498, 528, 594, 595, and bi-


457 ♀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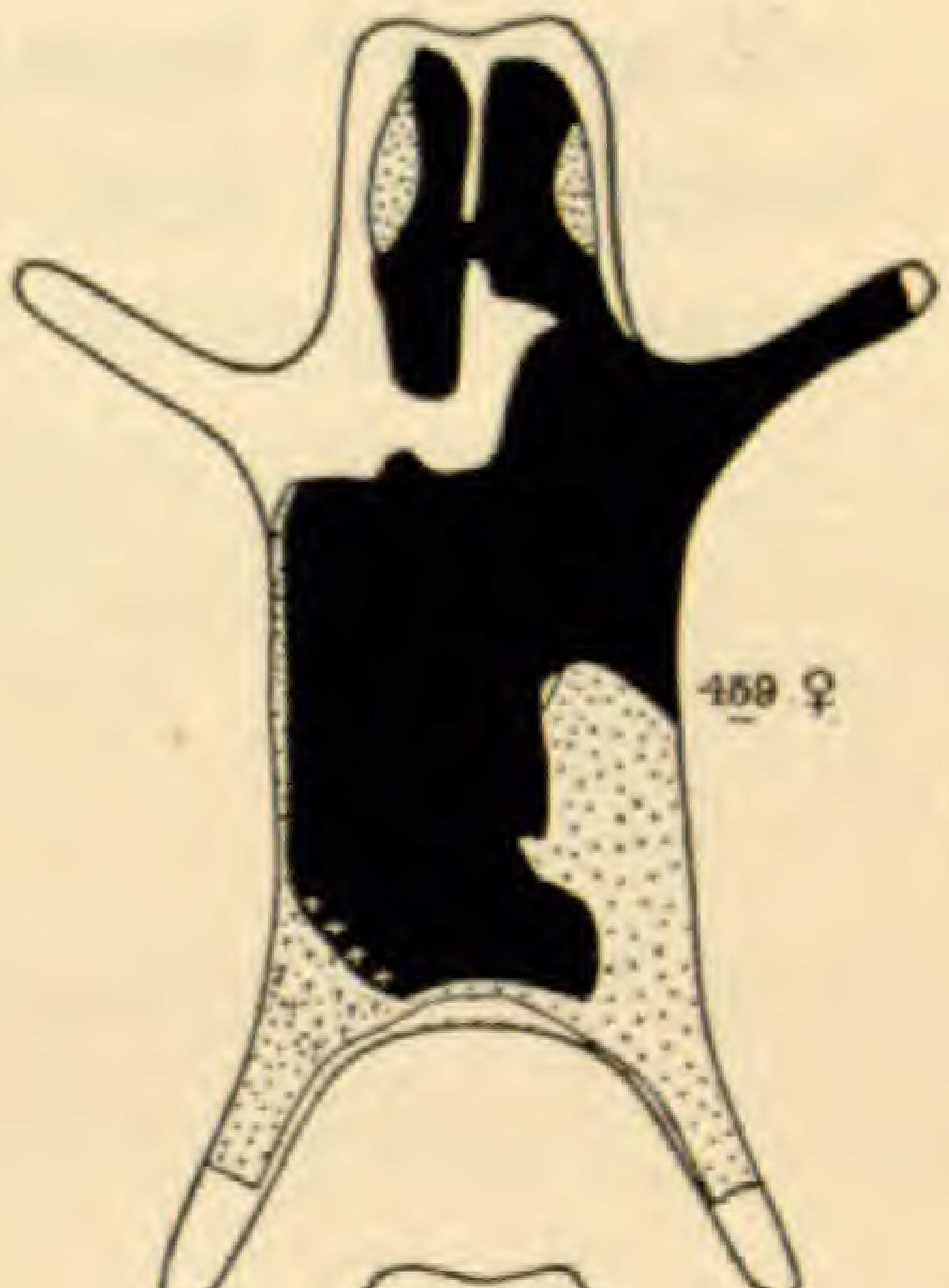
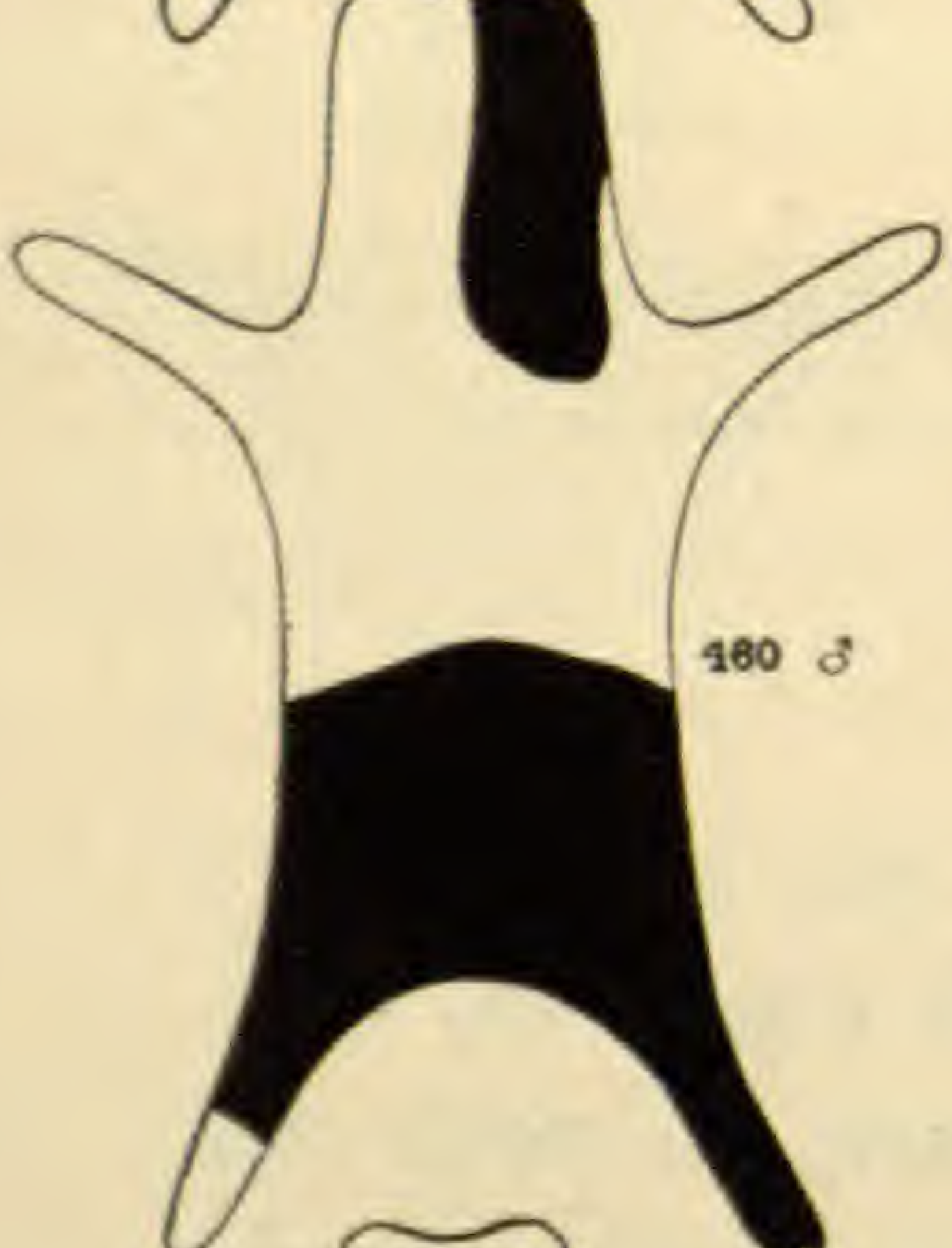

459 ♀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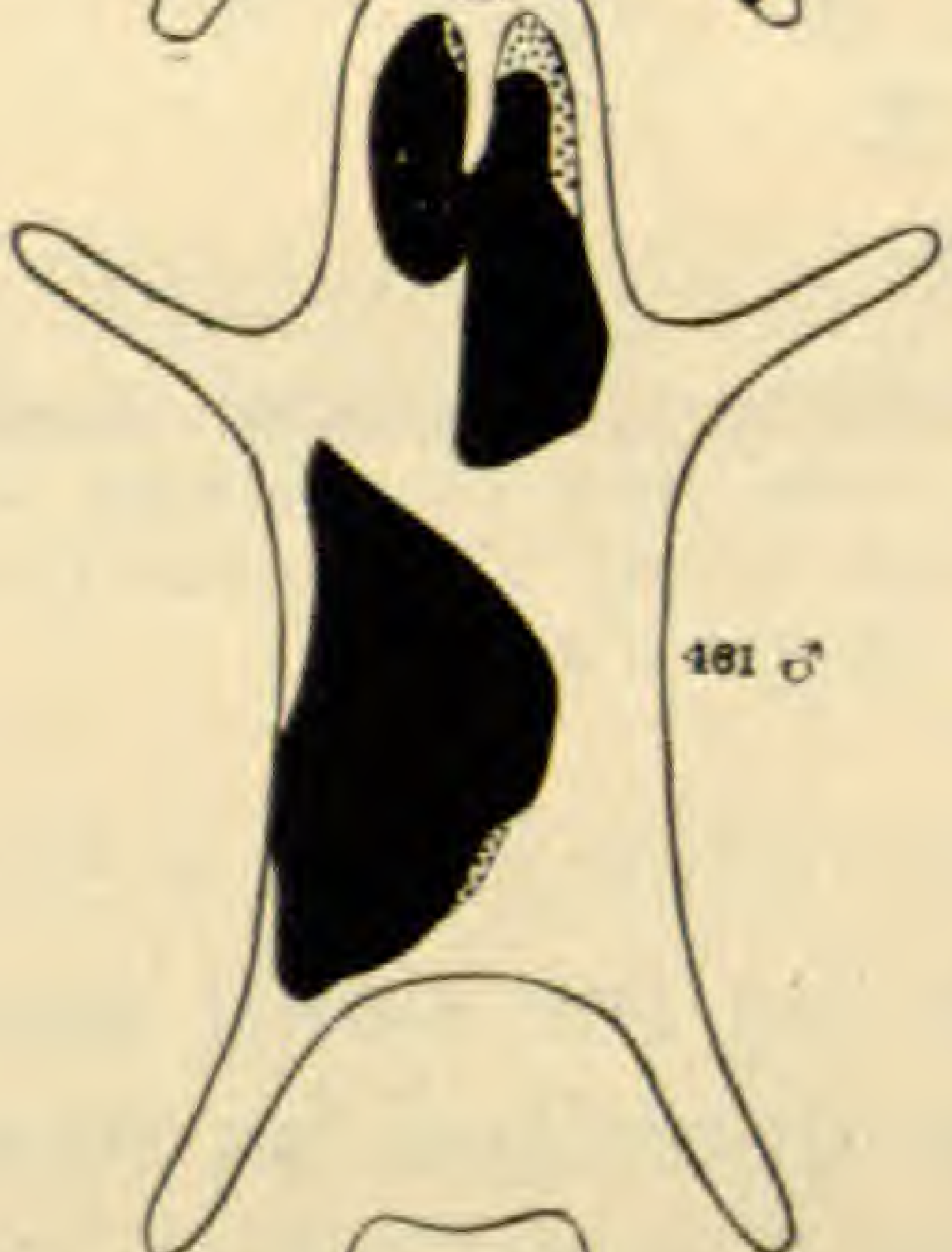
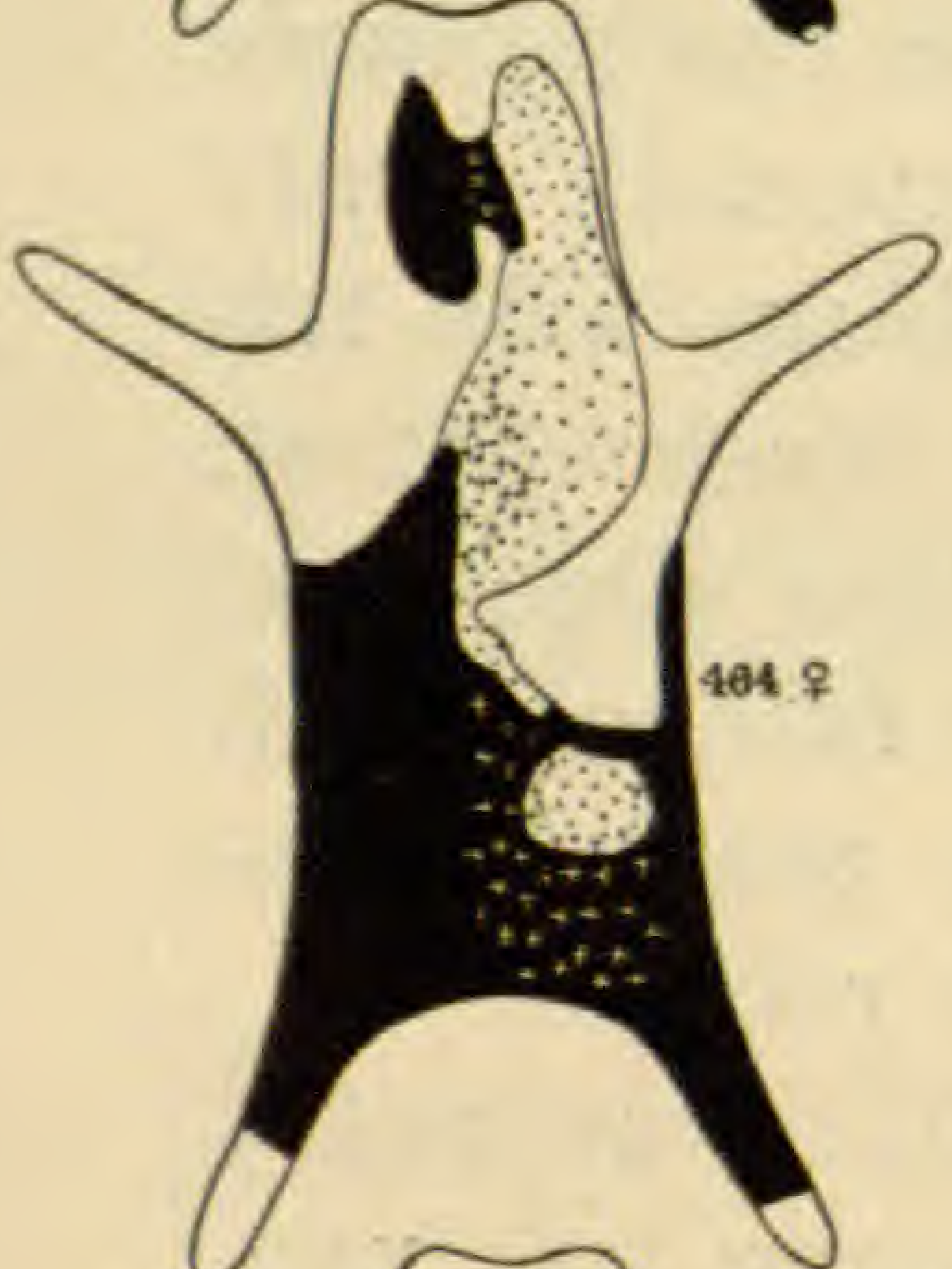

461 ♂


463 ♂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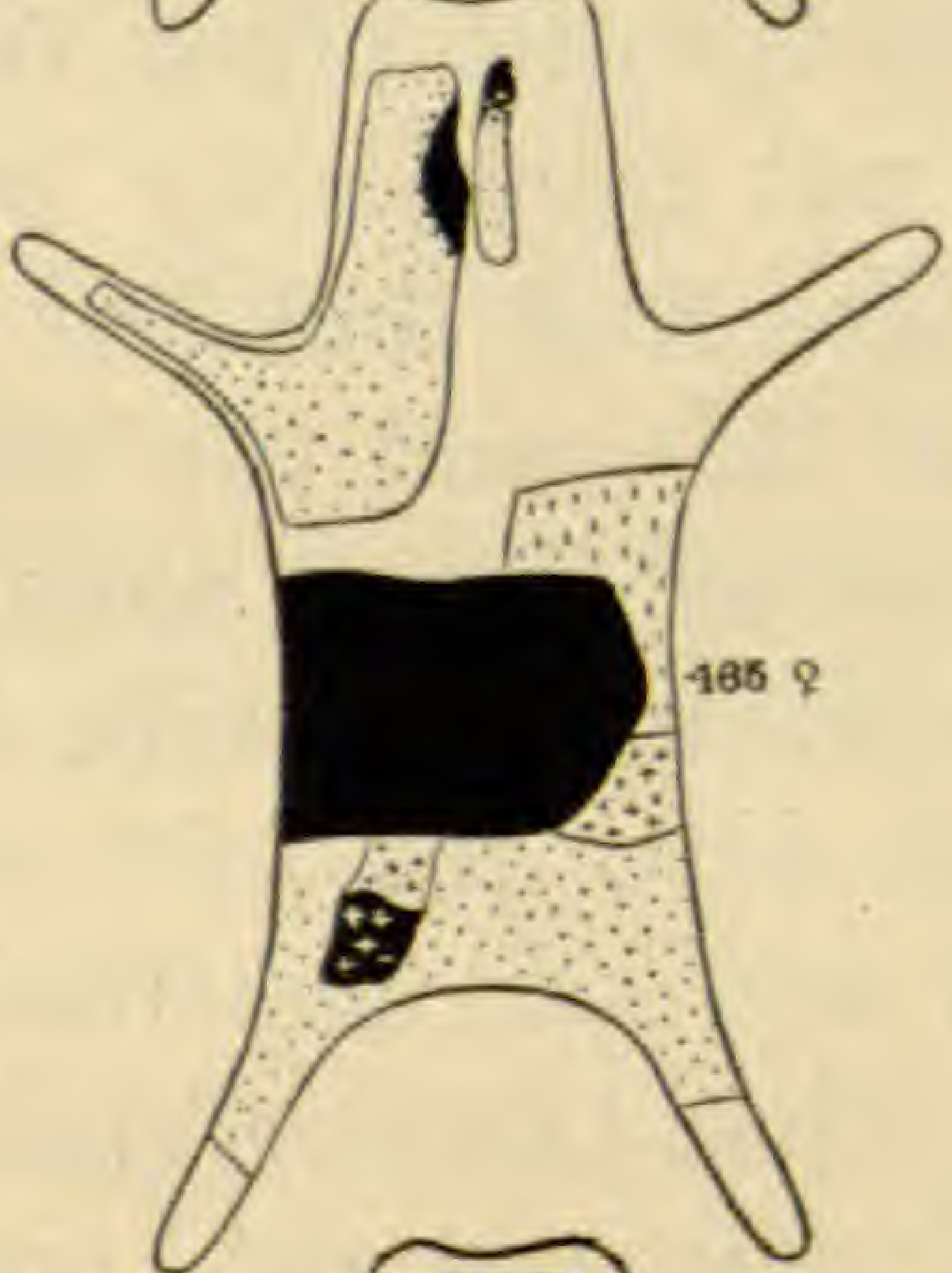
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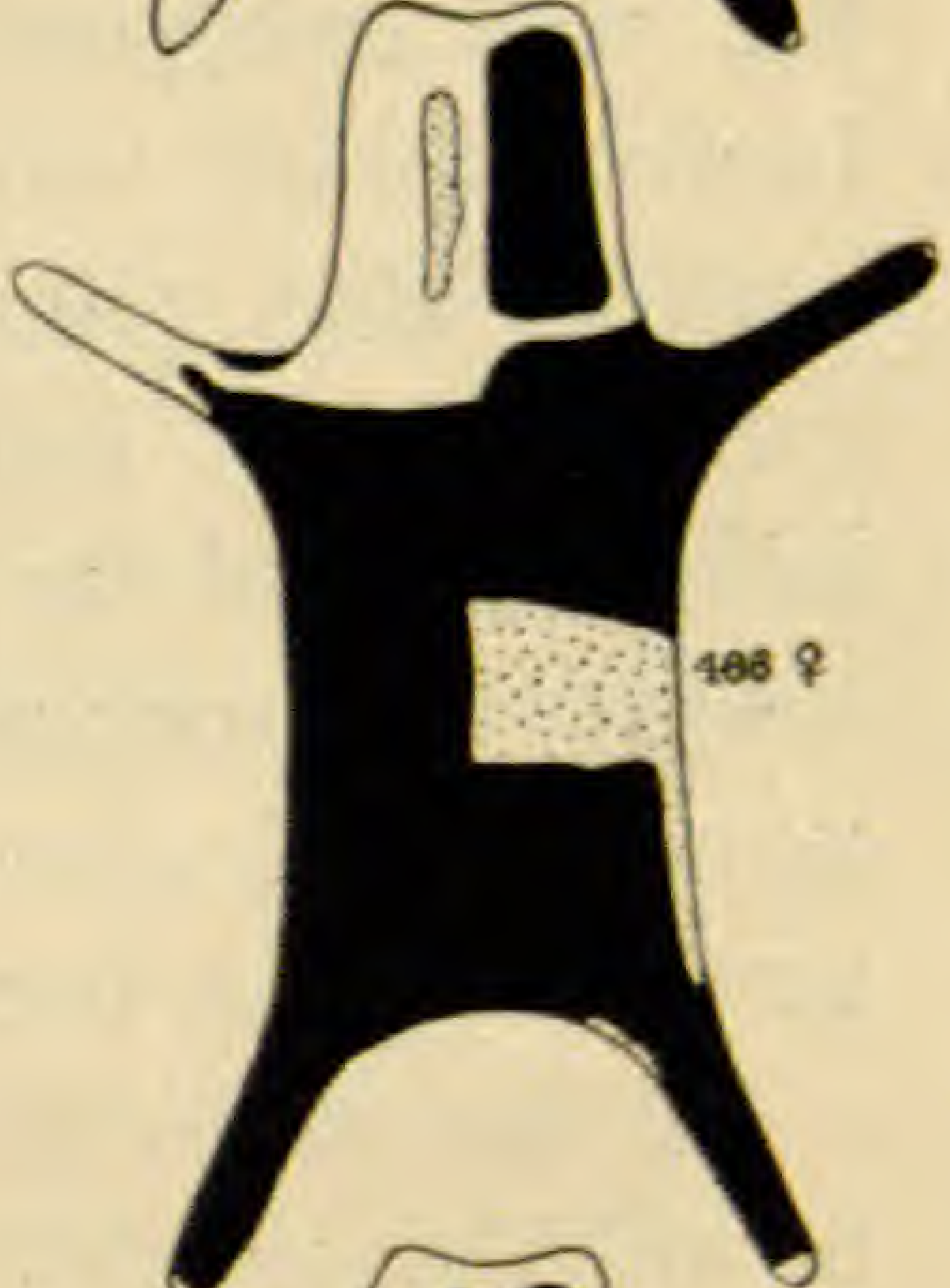
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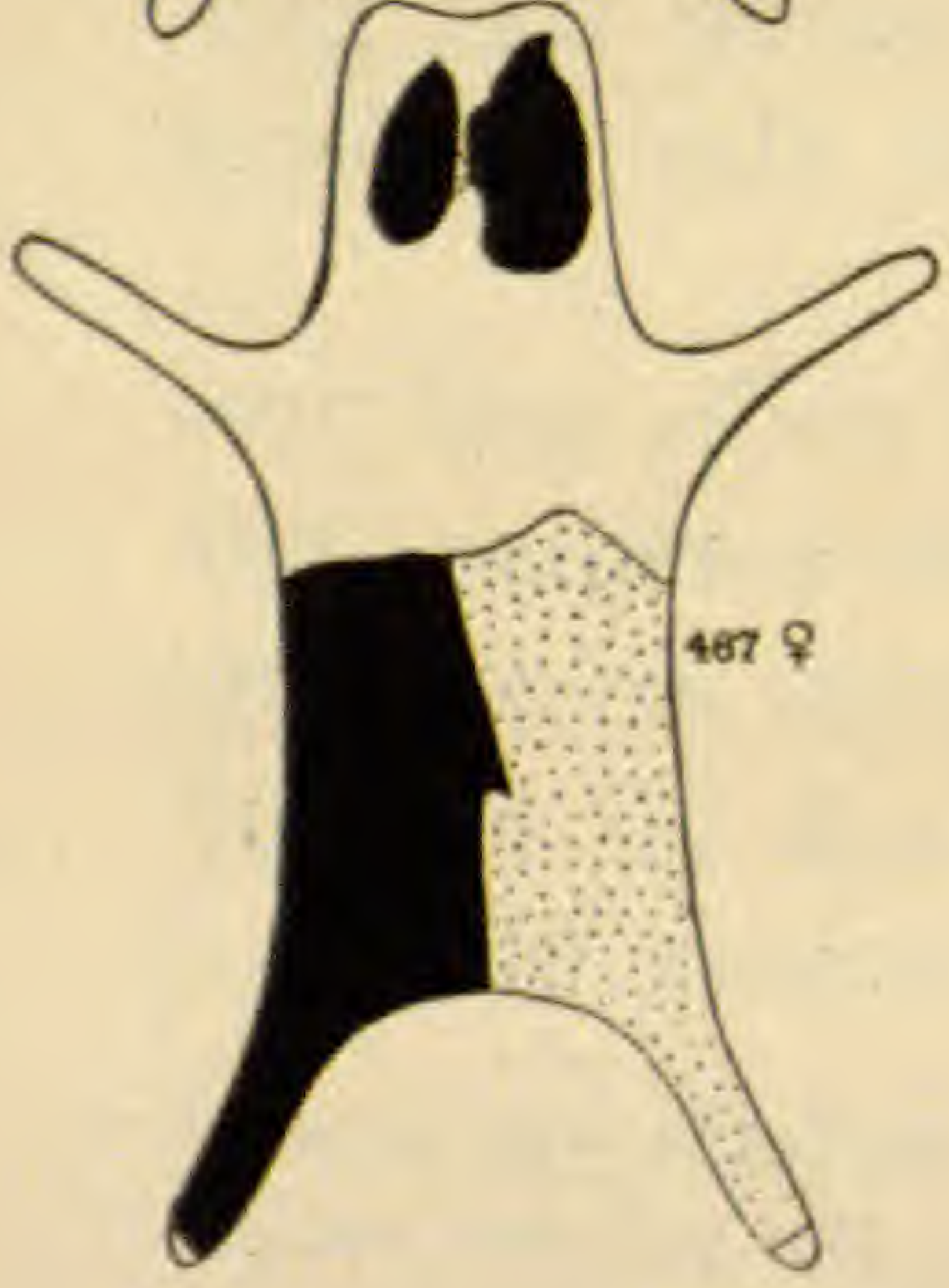
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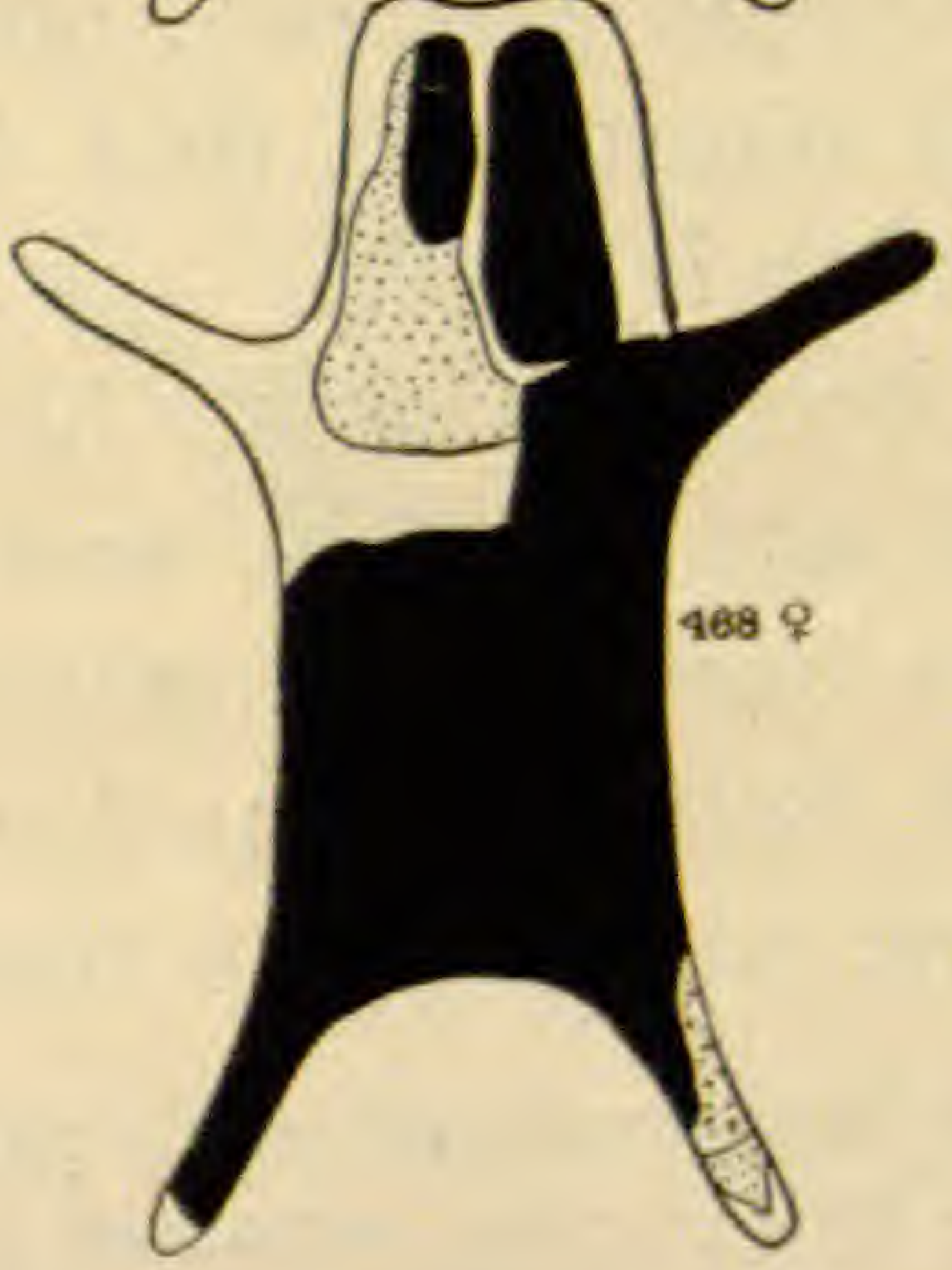
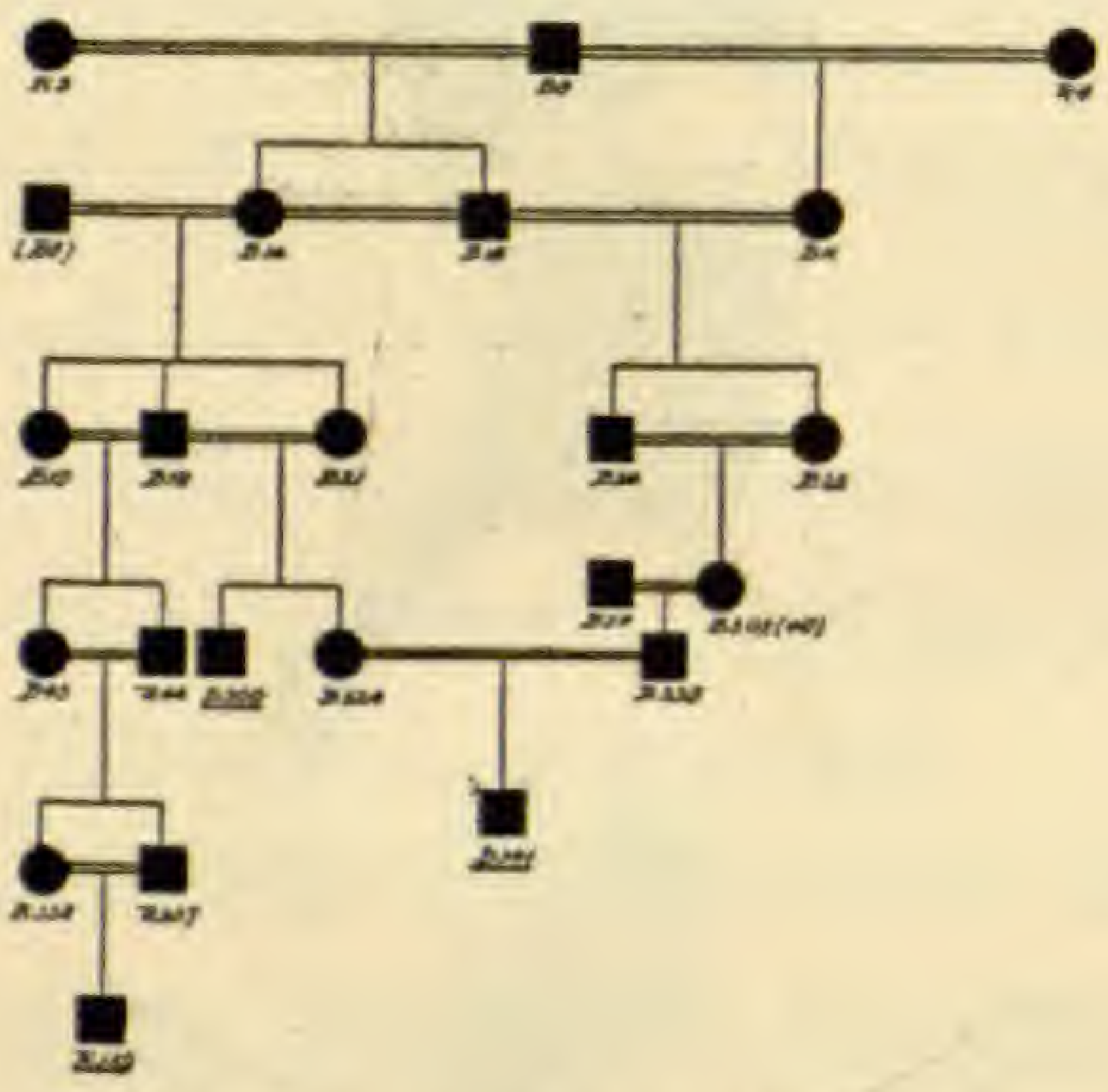

468 ♀


469 ♂

color reds[9] (mainly red), 482, 496, 497, 527, 596, and one individual, 526, much like the bicolor reds, but with a minute spot of black. It is noteworthy that although black entered into the original cross from one side it was not recovered except for the small spot of black on 526. Yet uniform black is described as dominant to red. If 401 was heterozygous for the black factor (as a single factor) black would not necessarily be expected. Only against this view is the fact that her matings with tricolor did not indicate this, and the small black spot on 526 could not be explained if this assumption were true.



Pedigree of "uniform" blacks and reds used in matings described in text. They came from Mr. Horton's stock.

One back-cross between 526 ♀ with her father, 427 ♂, gave one bicolor red, 576; and 577 (red, partially destroyed when found) and 578, classified as red.

On the other hand, when tricolor black 401 ♀ was mated to self black, 309 (Horton's stock), one young was produced, a self-colored black. In this case also uniform dominates, but the color is black.

No. 401 ♀ was also bred to another black male, and produced one black, 544, one red, 545, and one tortoise, 546. This male appears to have been homozygous as regards lack of spotted white, heterozygous for black (*B b*), and also heterozygous for some factor that causes black to

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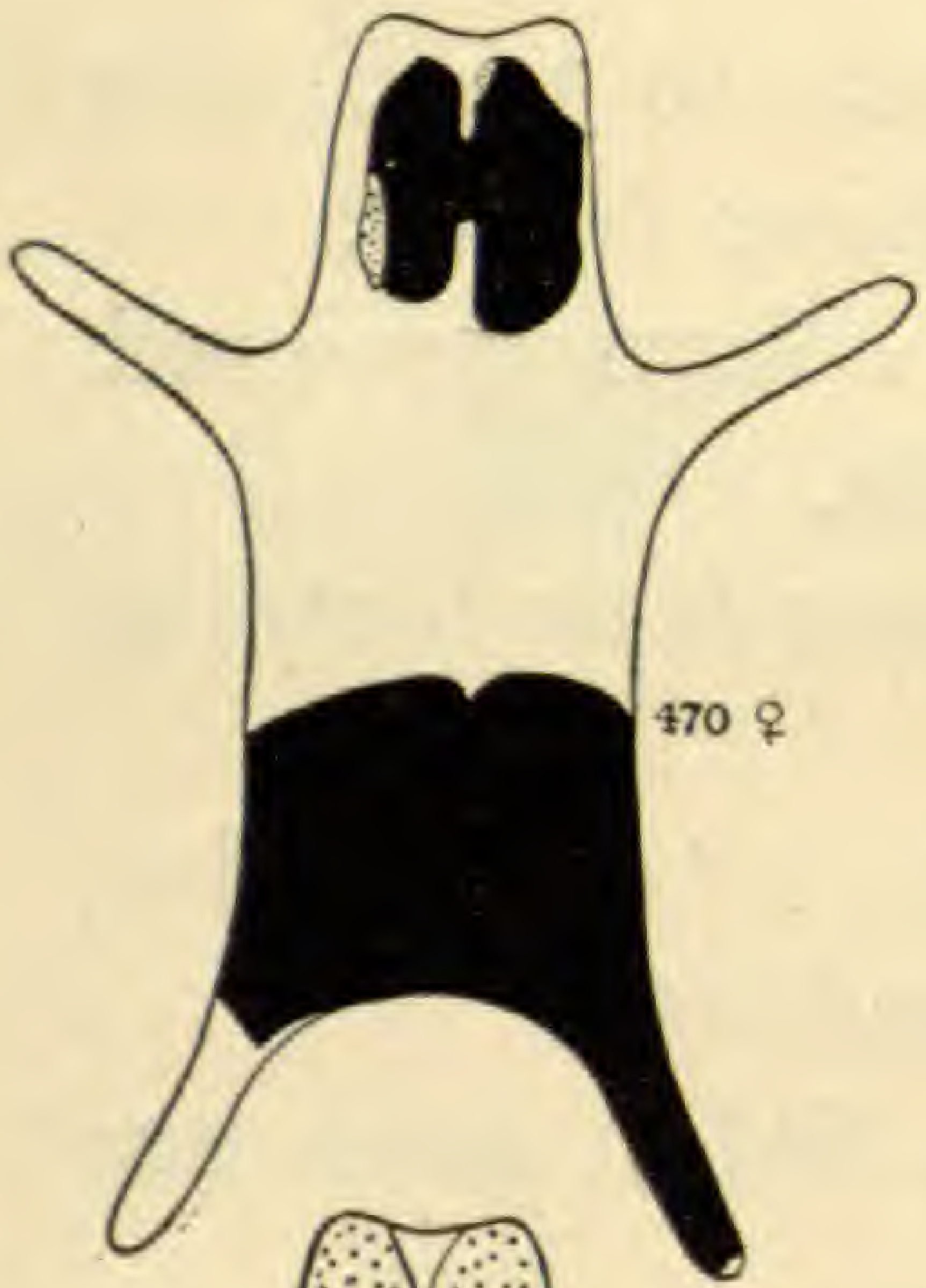
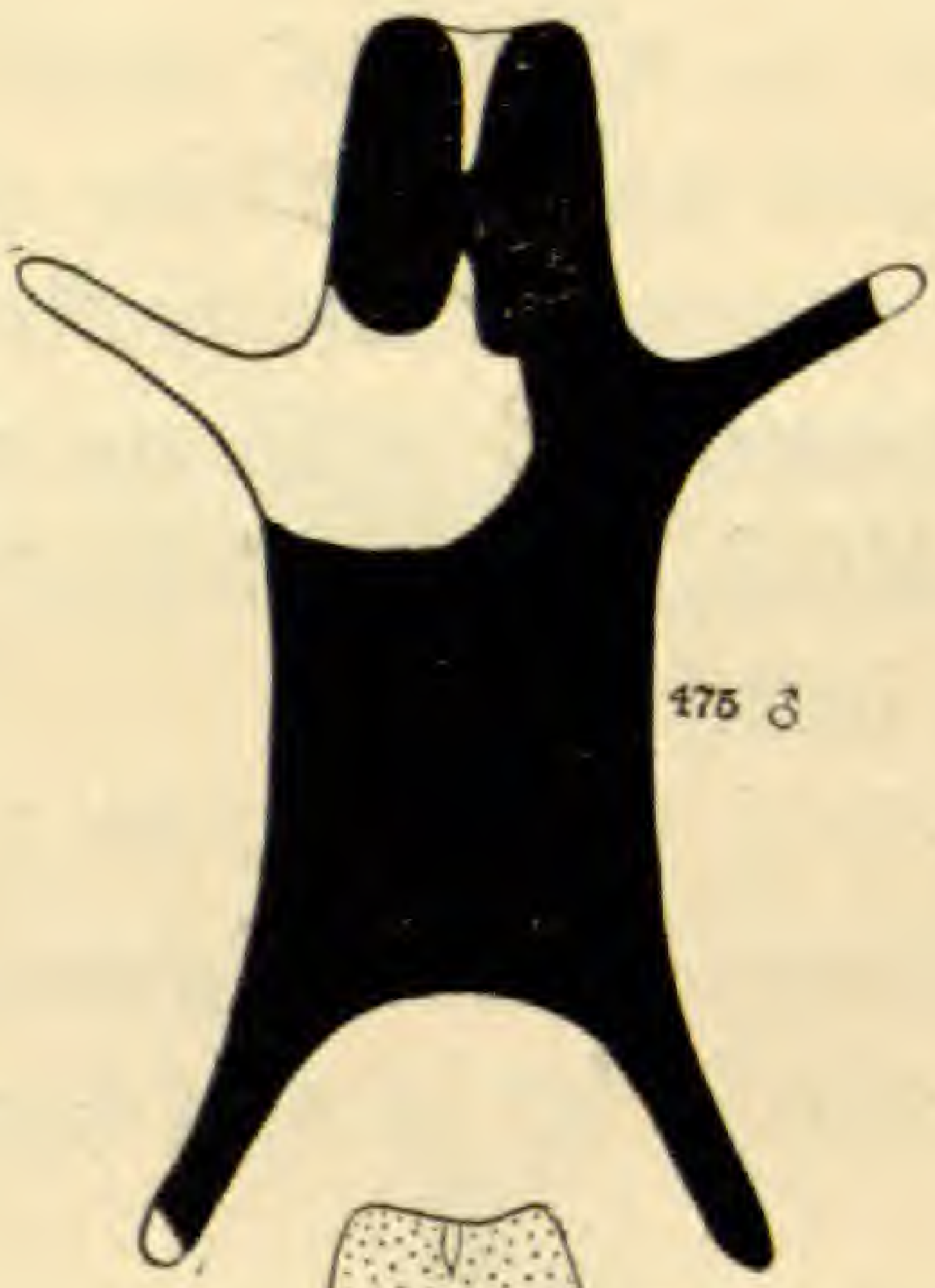
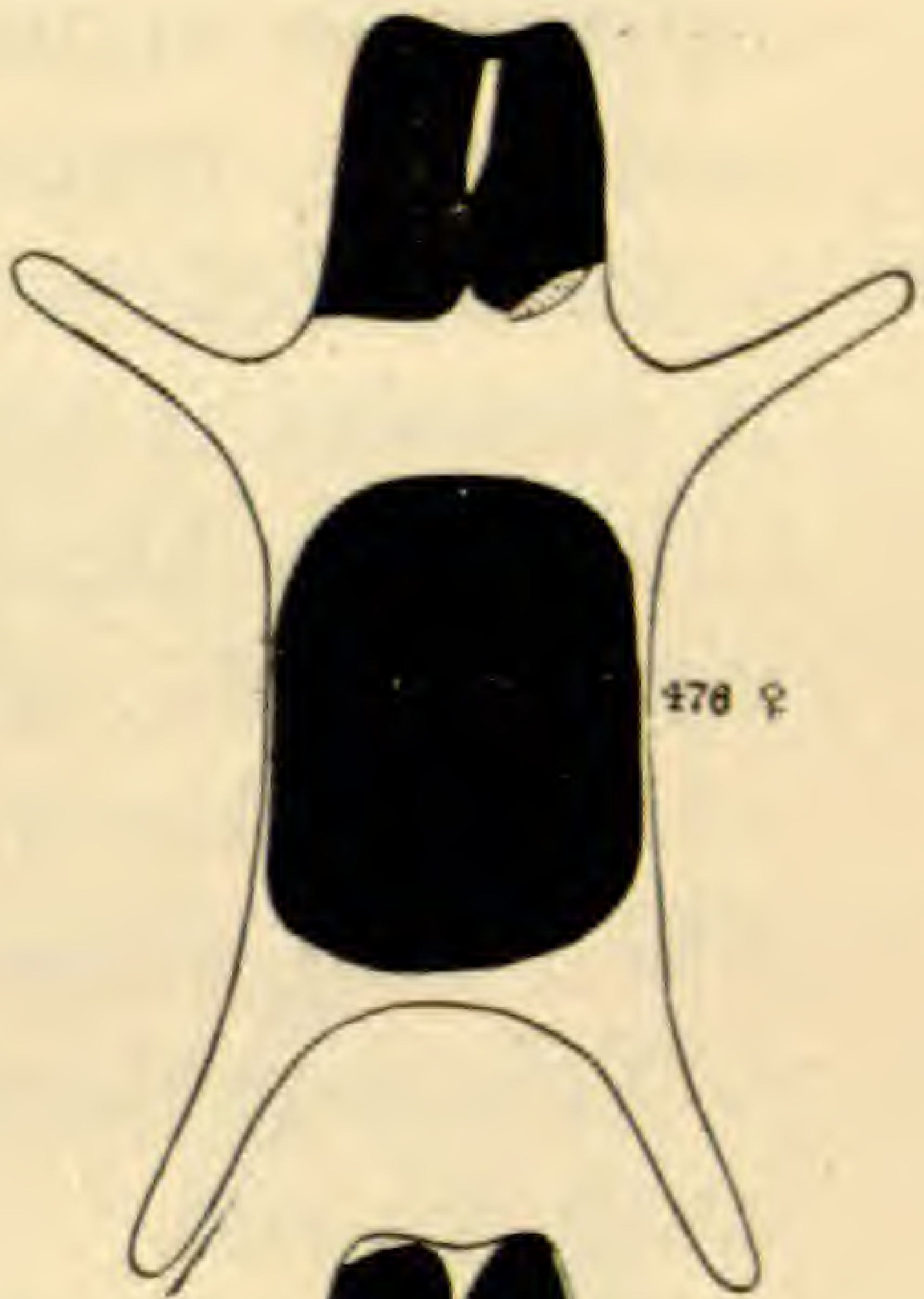
[9] On the whole the bicolor reds produced in F_2 when uniform was crossed in, had less white than the bicolor reds extracted from the tricolor series, and the white tends to occur on the anterior portion of the body.



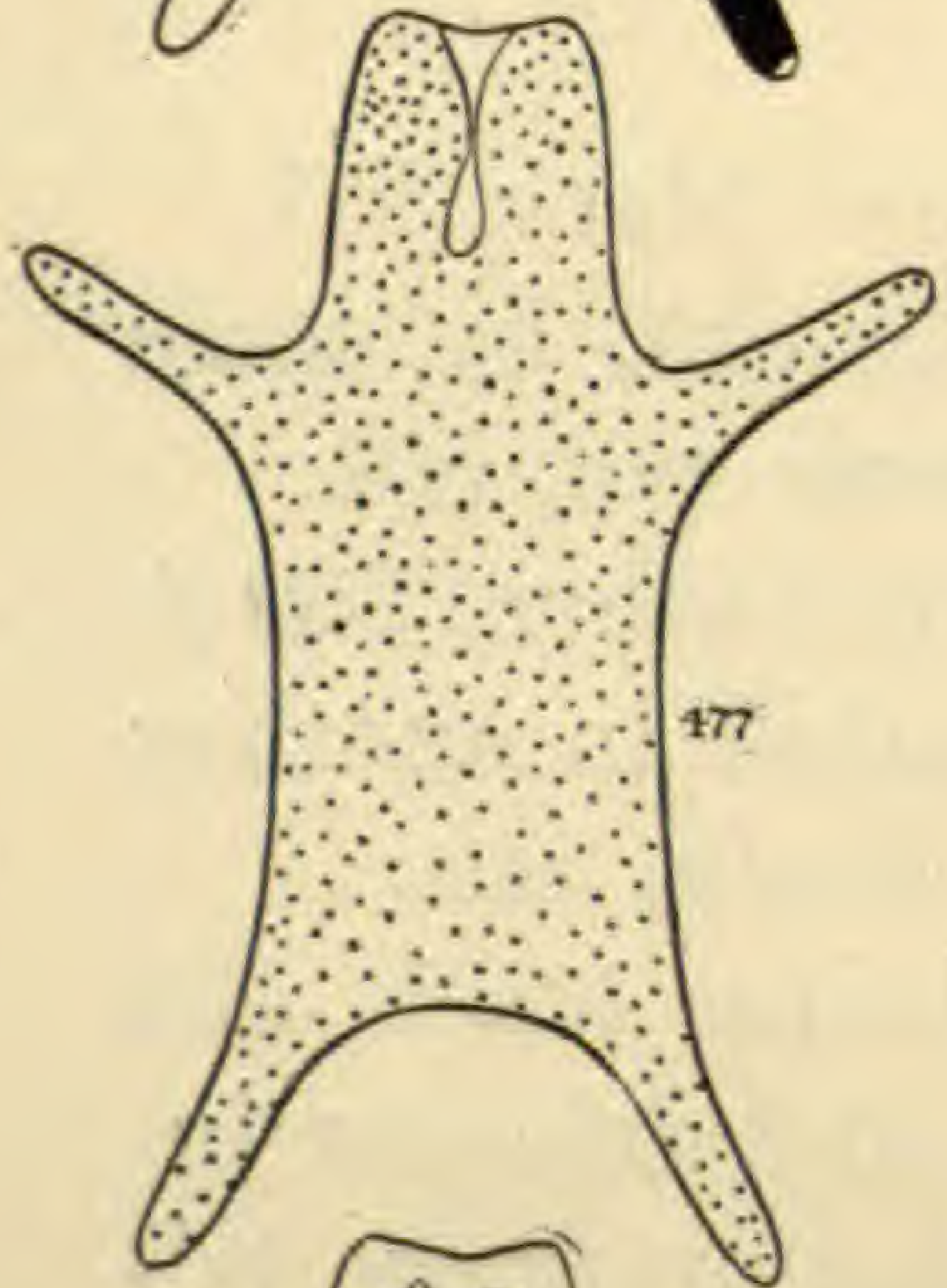
470 ♀



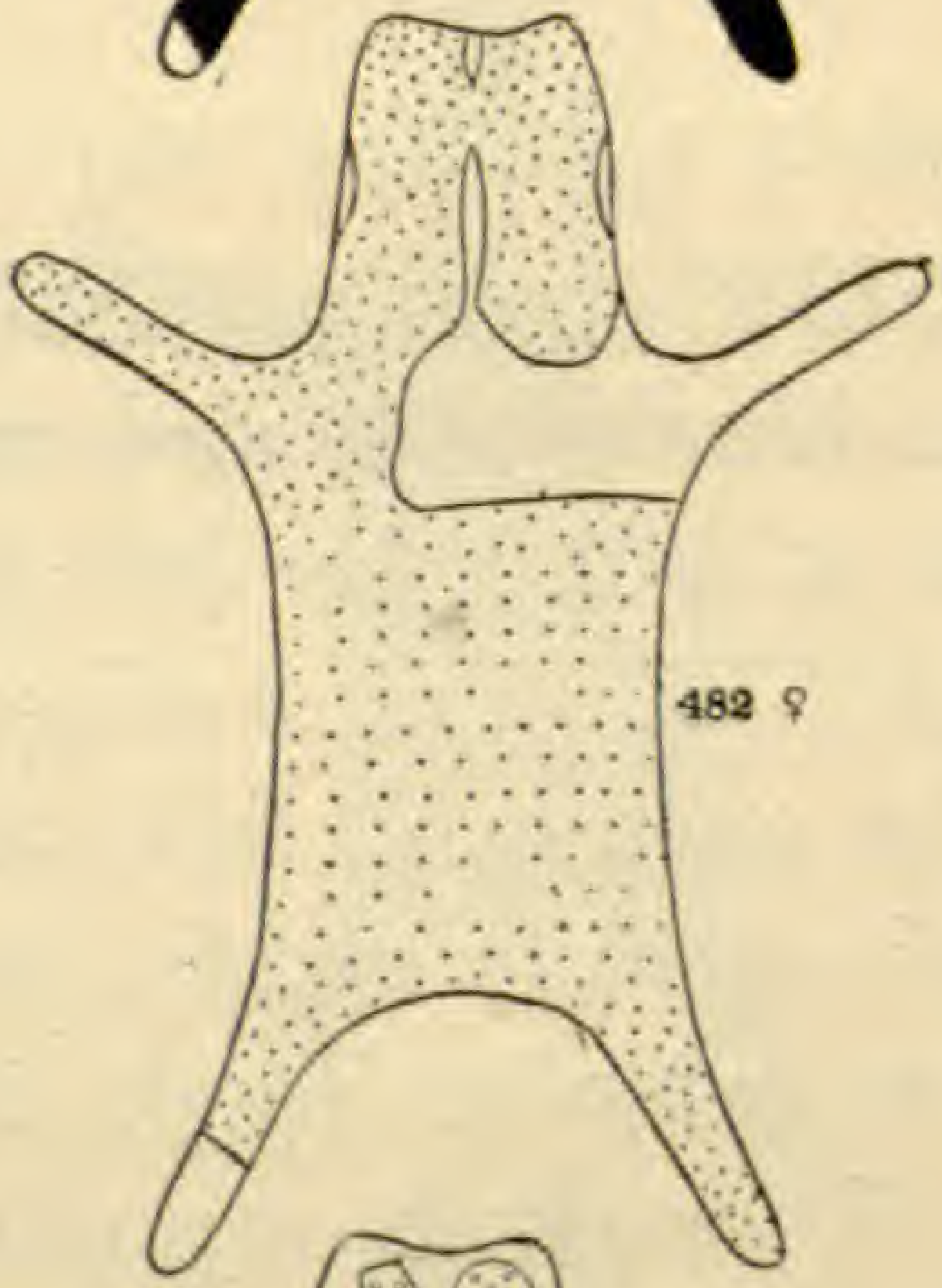
475 ♂



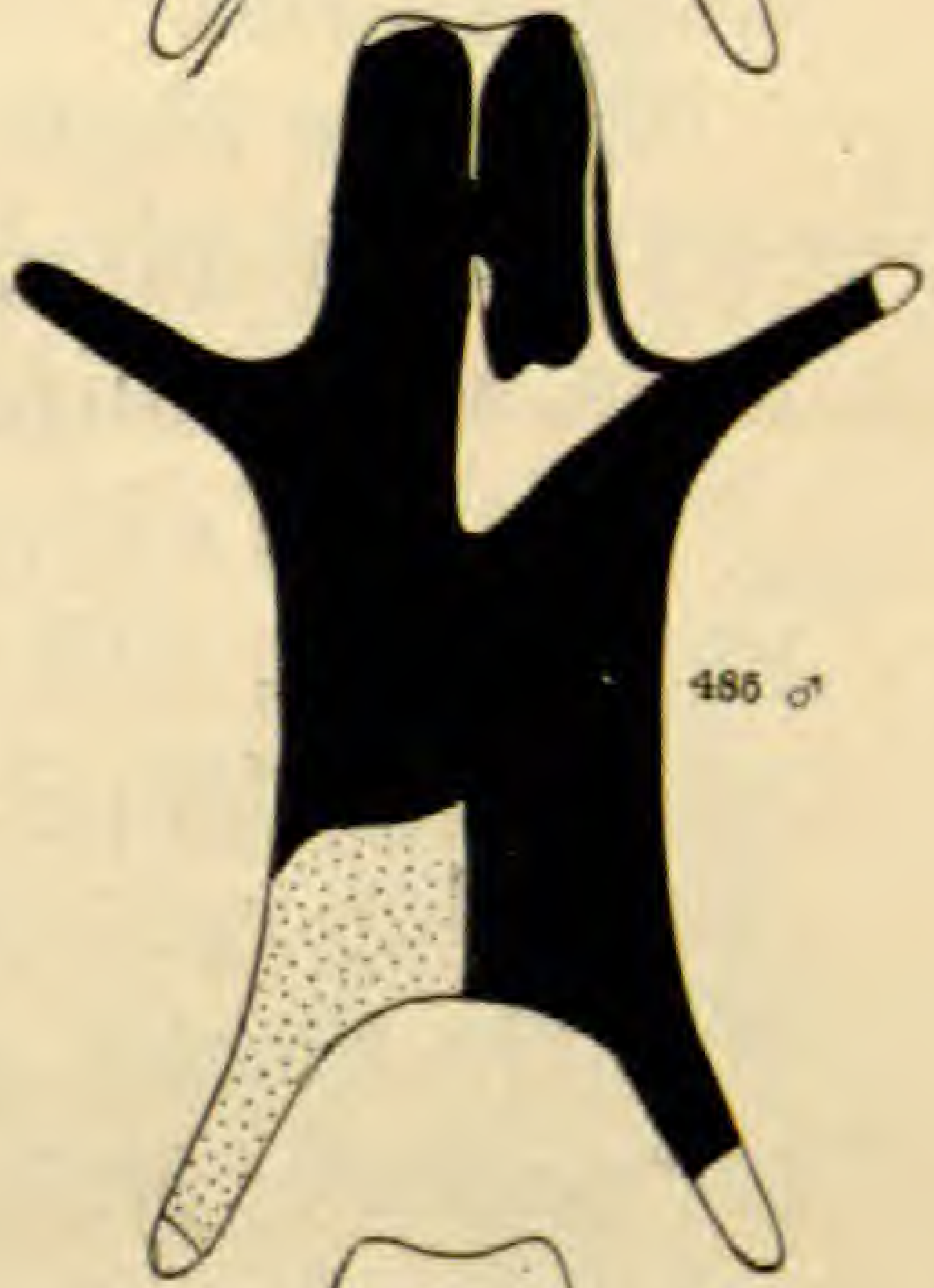
476 ♀



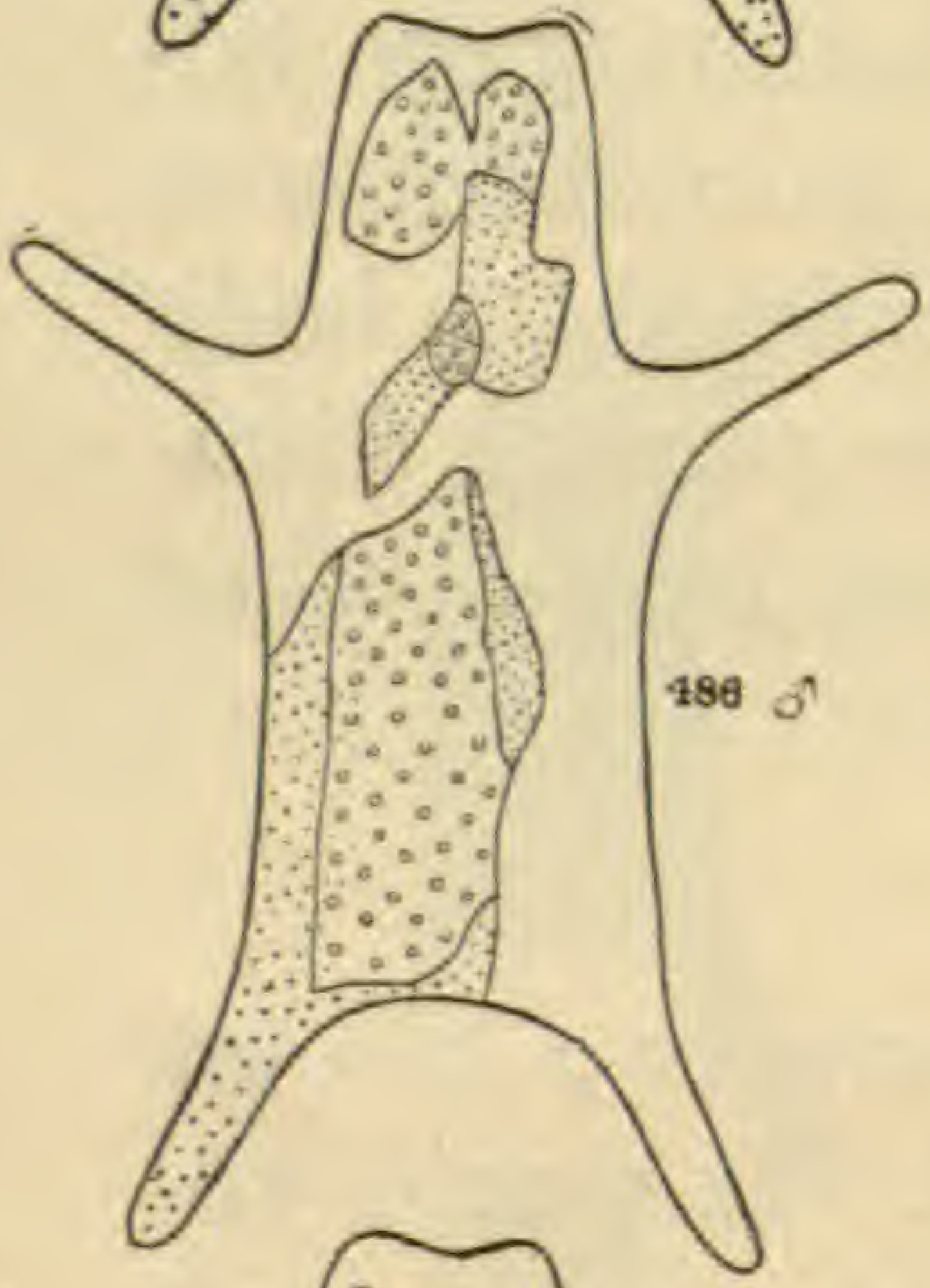
477



482 ♀



485 ♂



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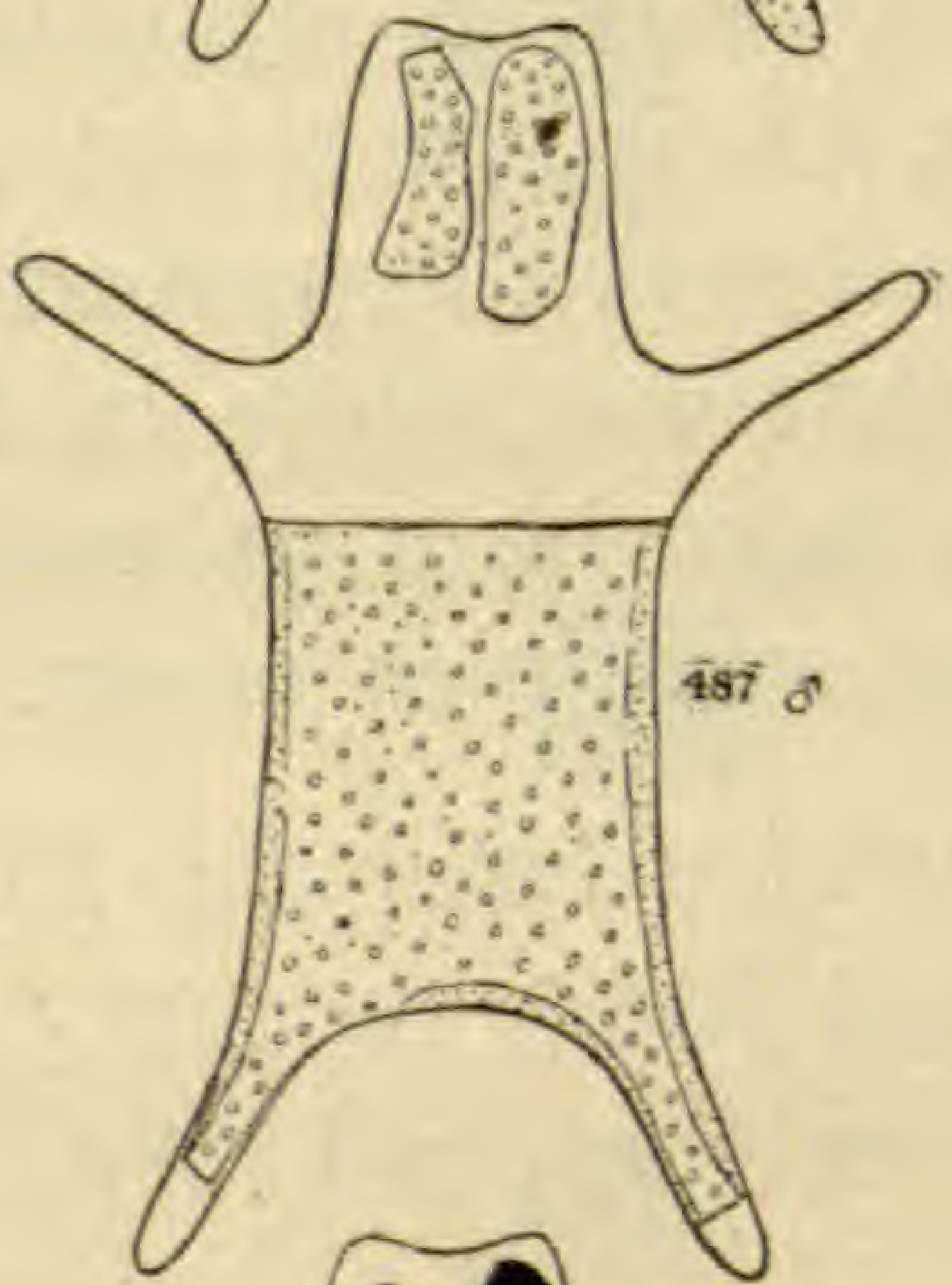

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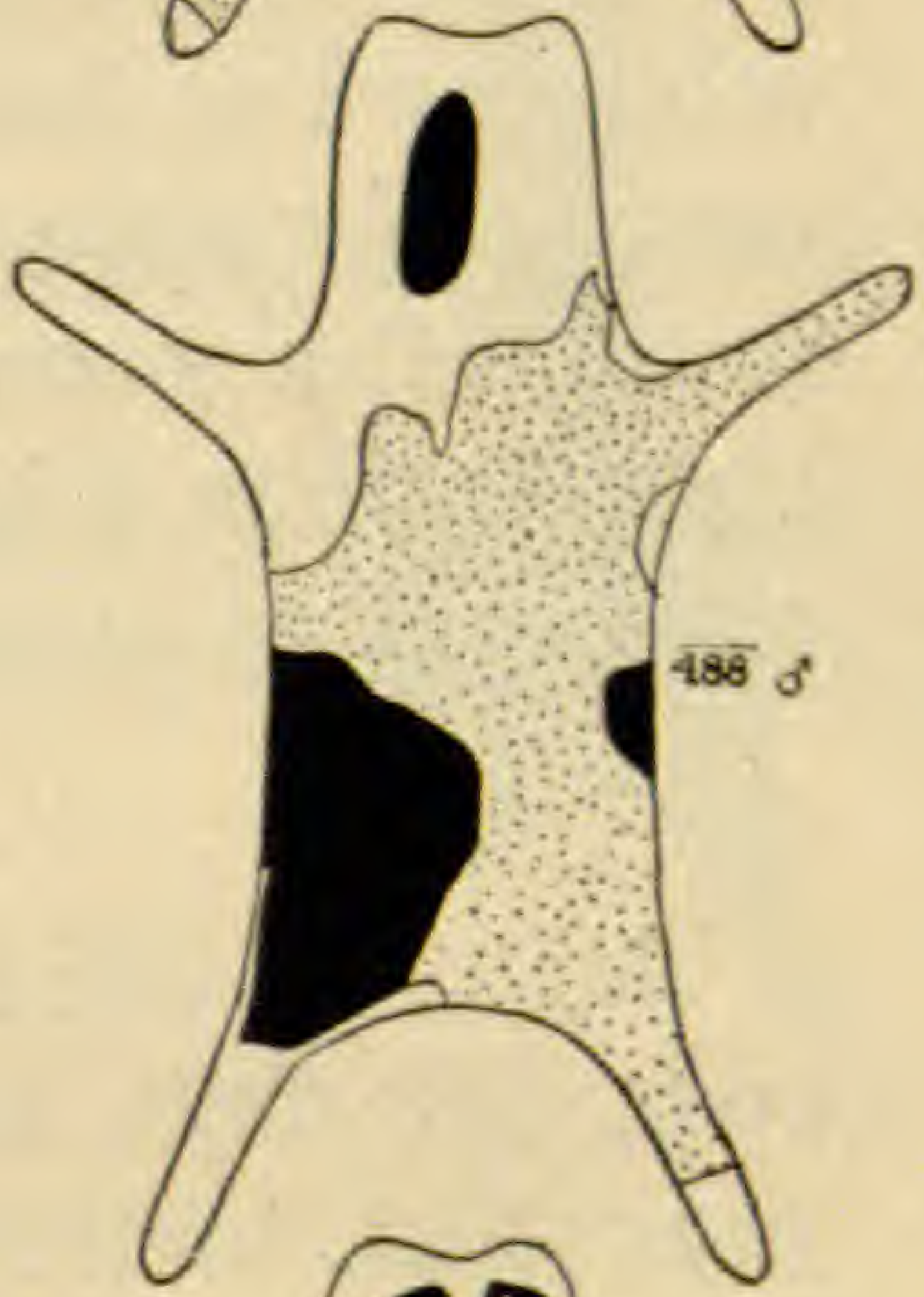

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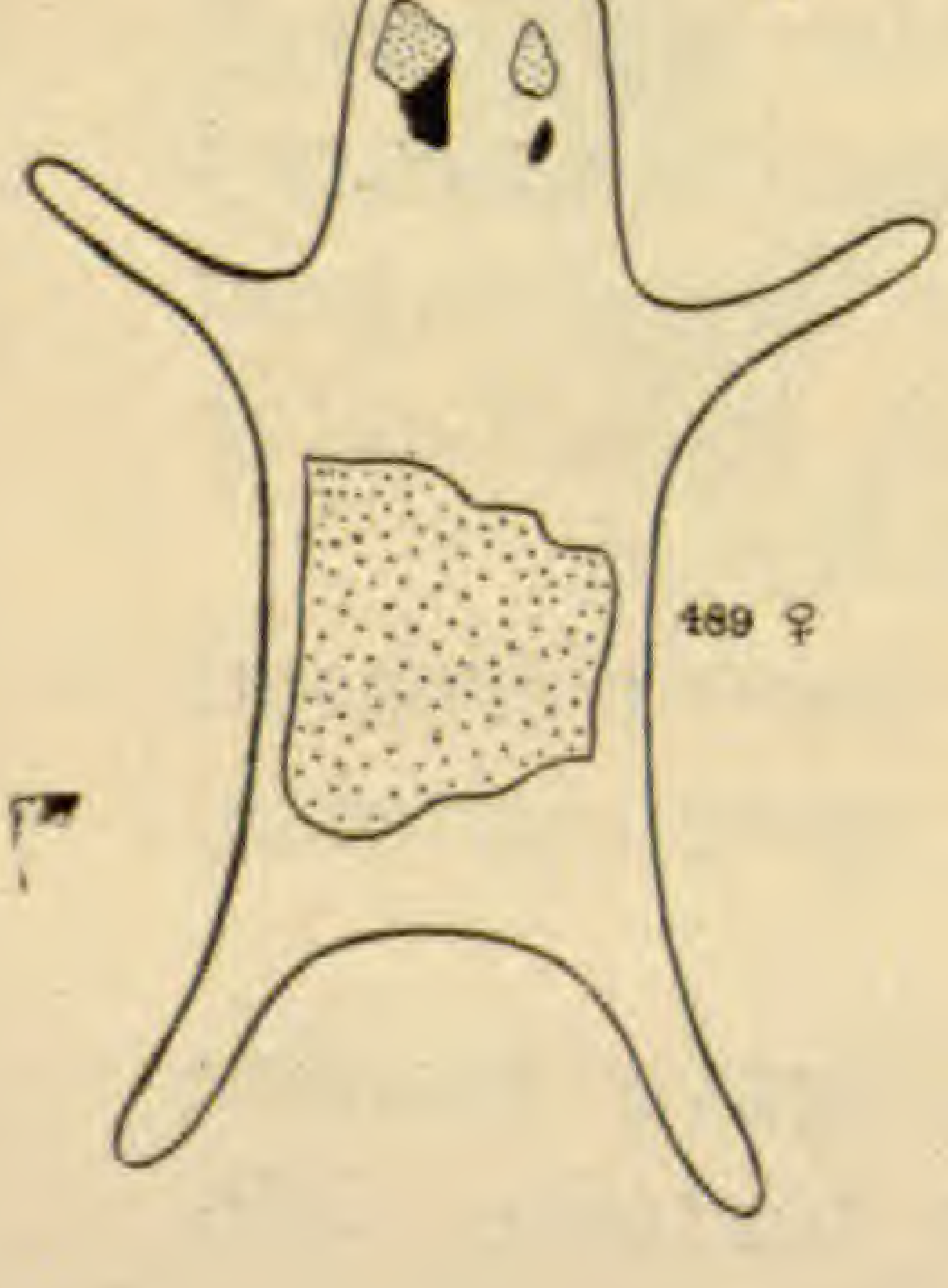
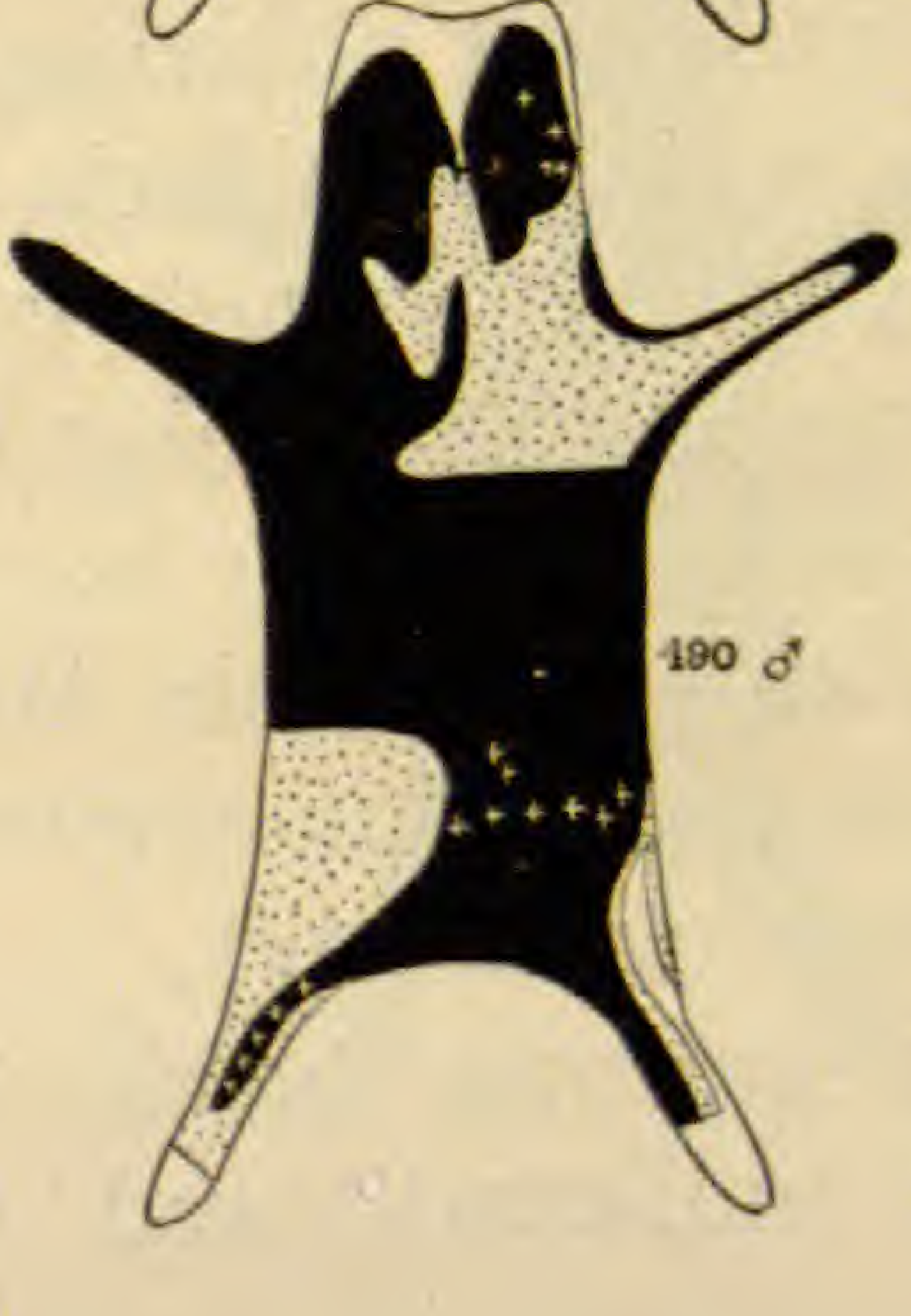


489 ♀



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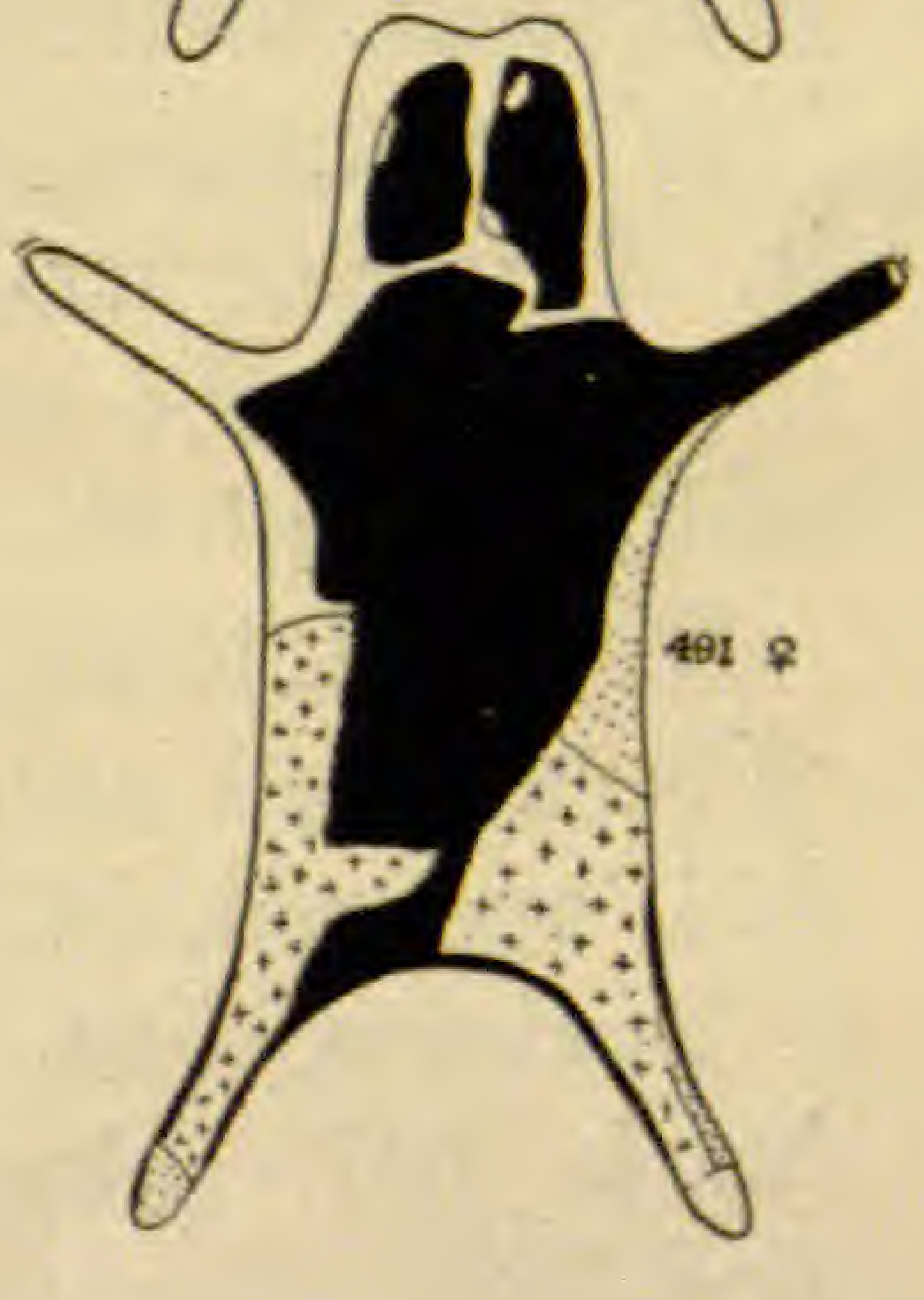


491 ♀

appear in spots, *i. e.,* a factor analogous to the factor commonly recognized as the white spotting factor.

In the following crosses some tortoise colors appeared. A tortoise is black-and-red with no white.

Tricolor black, 410 ♀, by red, 339 ♂, gave four tortoise, viz., 536, 537, 538, 539.

Bicolor black, 423 ♀, by red, 339 ♂, gave two tortoise, 540 (with white blaze—not in figure) and 541.

Tricolor black, 413 ♀, by a self-black, 341 ♂, gave one uniform red.

Tricolor black, 491 ♀, by same, 341 ♂, gave black, 551.

Tricolor black, 513 ♀ (nearly bicolor black), by same male, gave uniform black, 590, and uniform red, 591.

Black, 471 ♀ (out of 401 ♀, by 309 ♂), by father, 309 ♂, gave black, 518 and 519. Later when mated to another self black, 341 ♂, she gave red, 547, 548; black, 549.

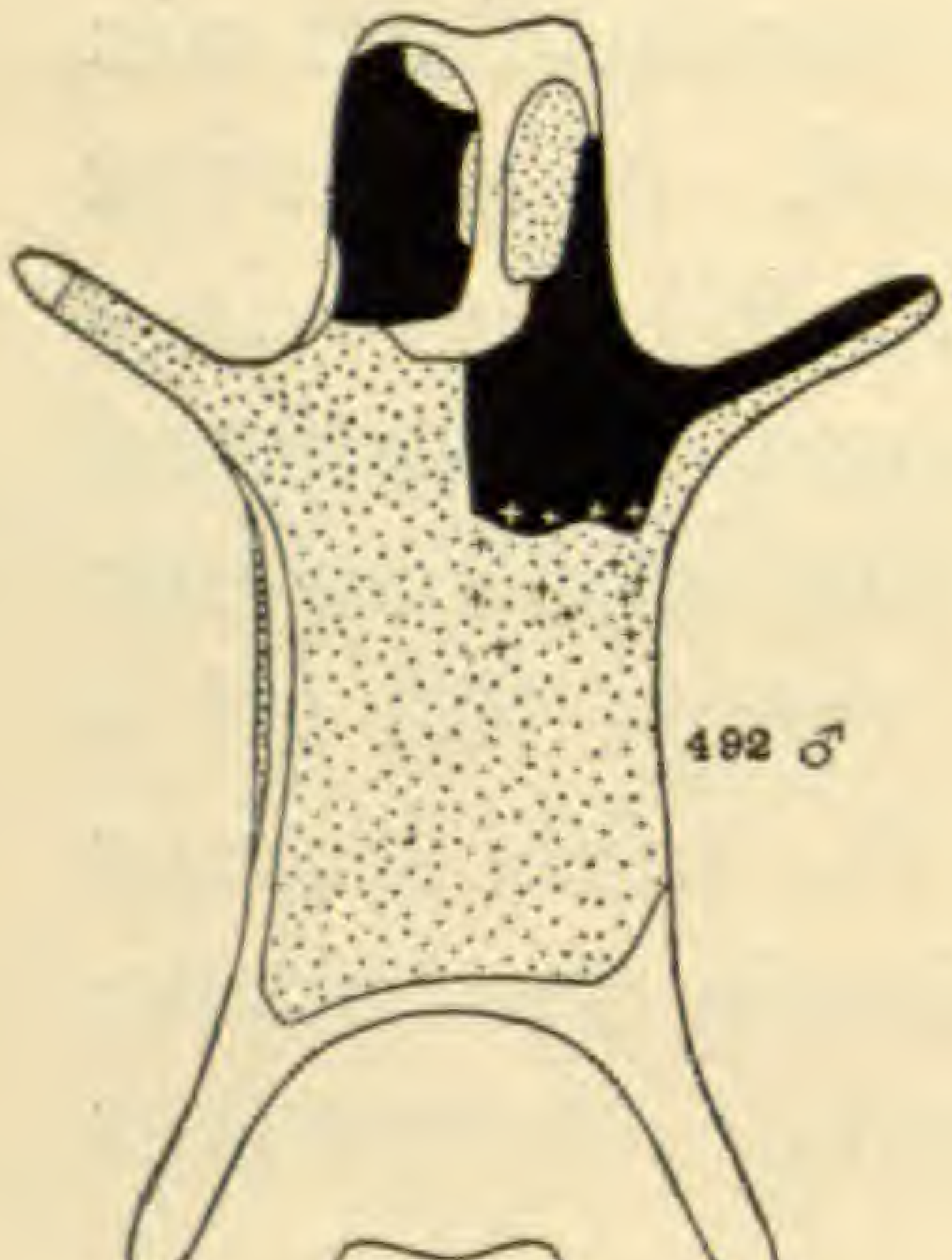
Bicolor red, 509 ♀ (nearly red?), by bicolor black, 535 (nearly black), gave tricolor black, 581, and tricolor intermediate, 532 ♂. These two opposite bicolors gave tricolors and so far as 502 is concerned two animals almost completely pigmented over the posterior half of the body produced a young that was white in these parts. Similar relations might have been pointed out in the other crosses; but reverse cases also occur.

Tortoise Inter Se, Etc.

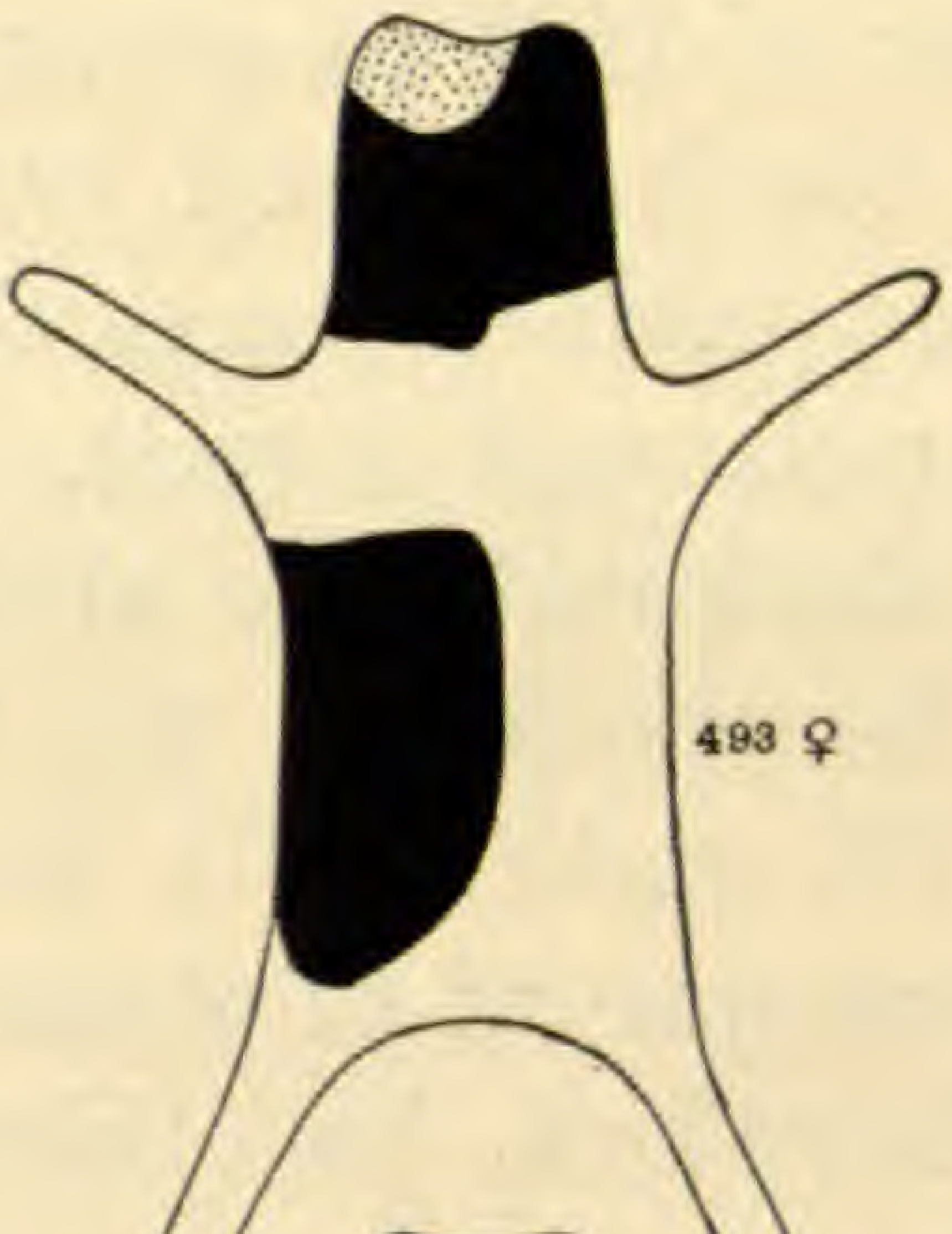
Tortoise, 538 ♀ and 536 ♀, by 537 ♂, gave two bicolor reds, 583, 580; two uniform red, 584, 585. It would appear that tortoise, while not showing white may carry it in the same way in which a uniform animal may carry it. It is also striking that the result is like that obtained in F_2 from the mating of 401 tricolor black, to self-color red, although the F_1 is somatically very different.

Tortoise, 524 ♀, by uniform black, 341 ♂ (never crossed with spotted animals as far as known), gave tortoise, 566, and red, 567 (not on charts).

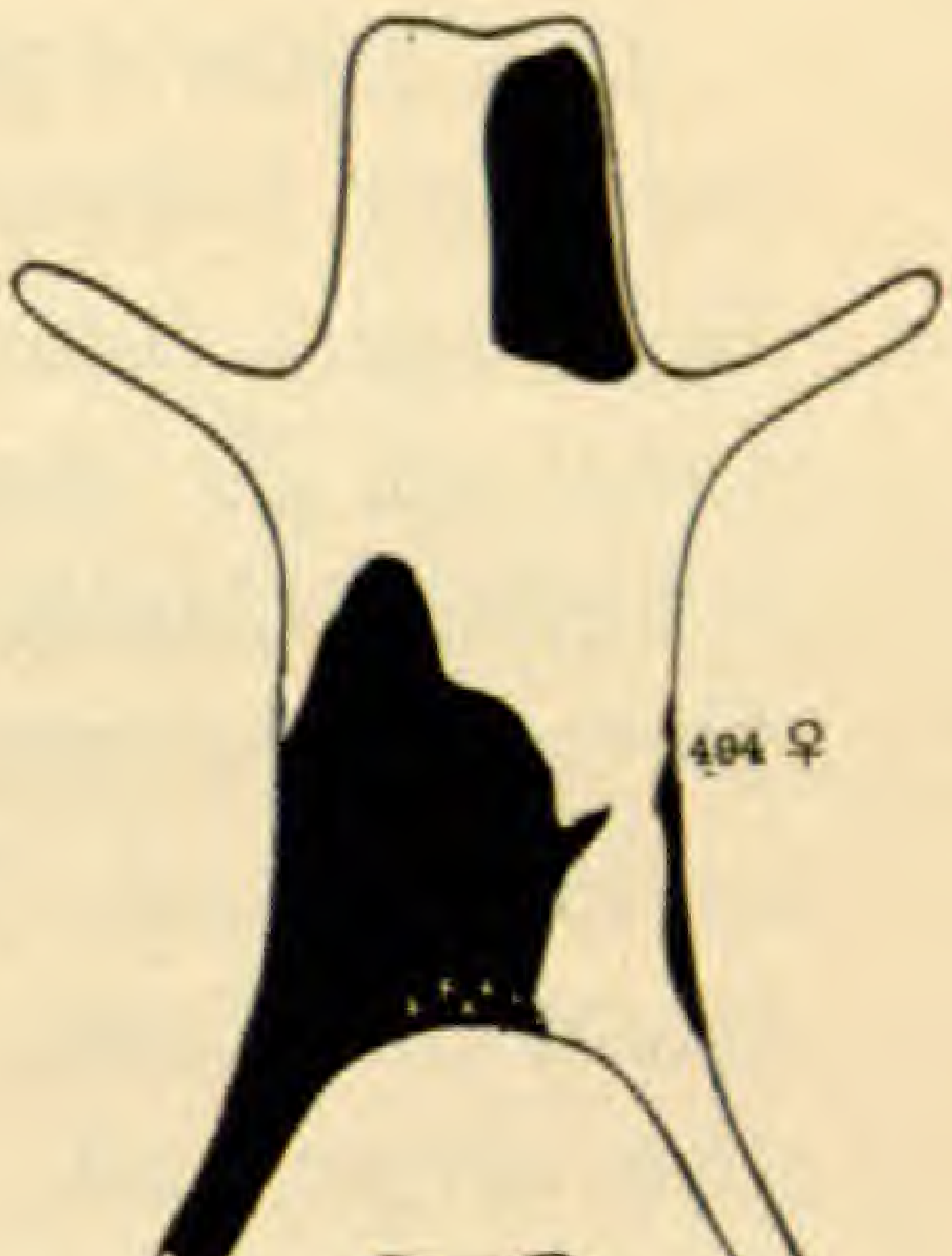
Tortoise, 524, by uniform black, 341, gave bicolor black, 587 (almost uniform), and two tortoise, 588 and 589.



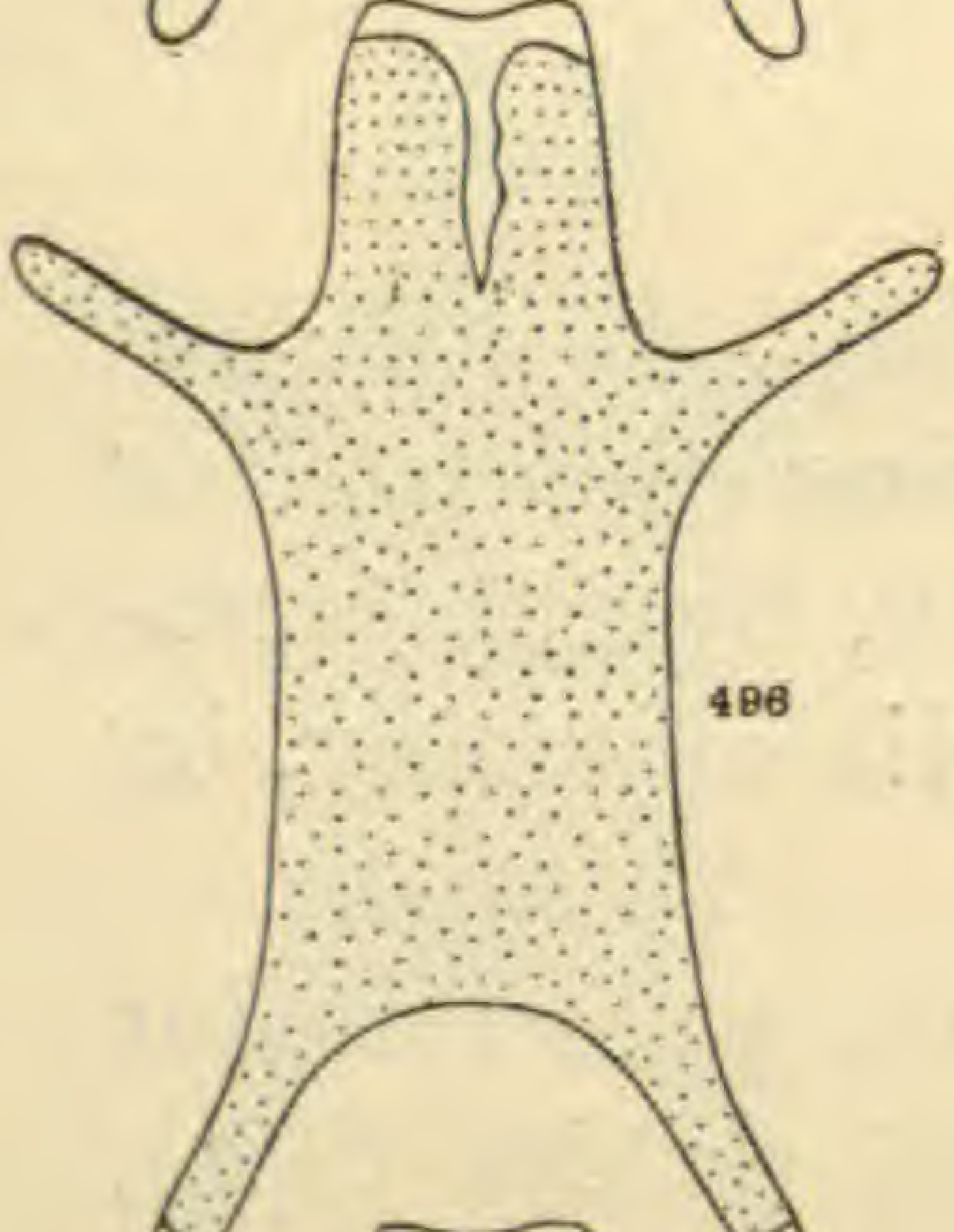
492 ♂



493 ♀



494 ♀



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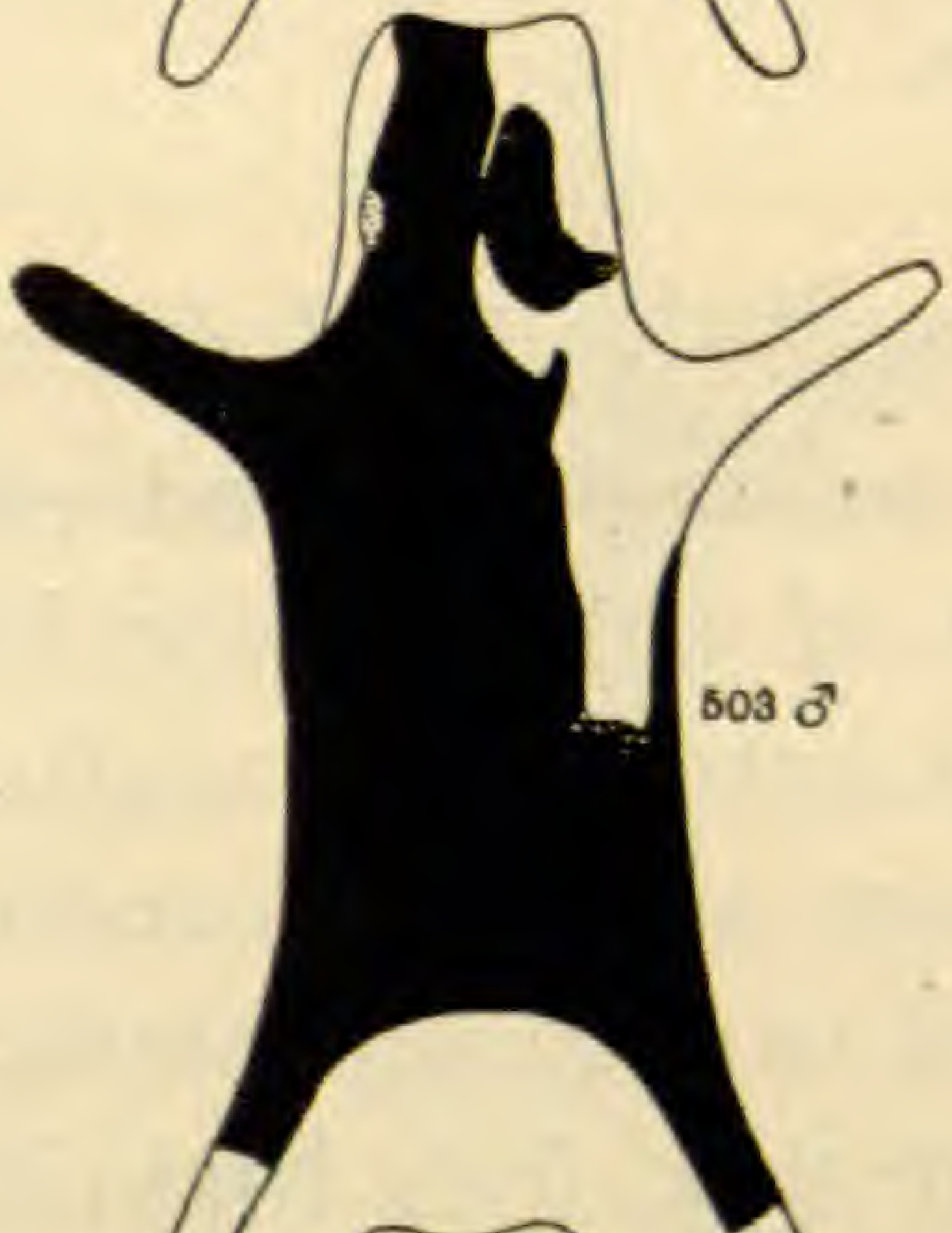
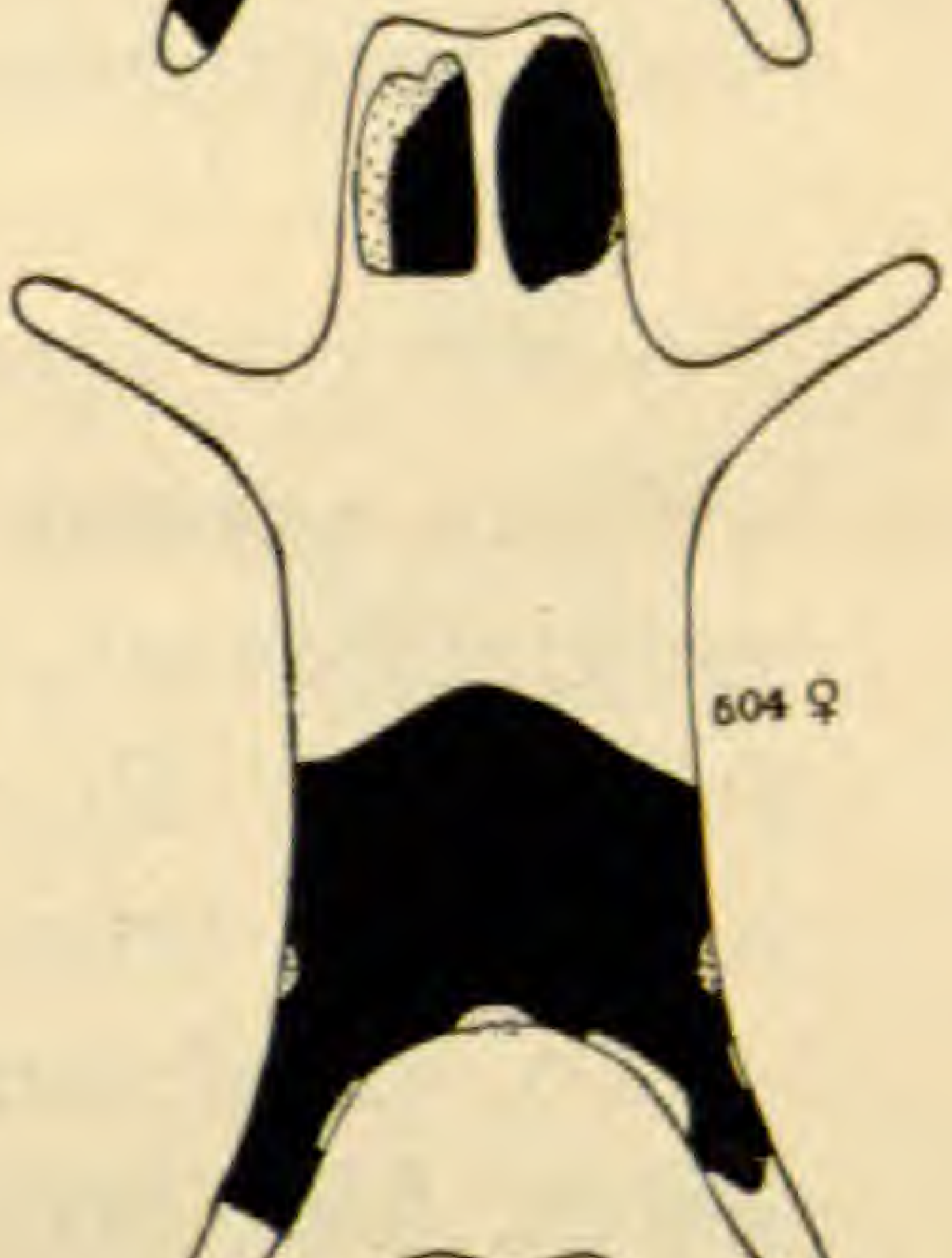


503 ♂



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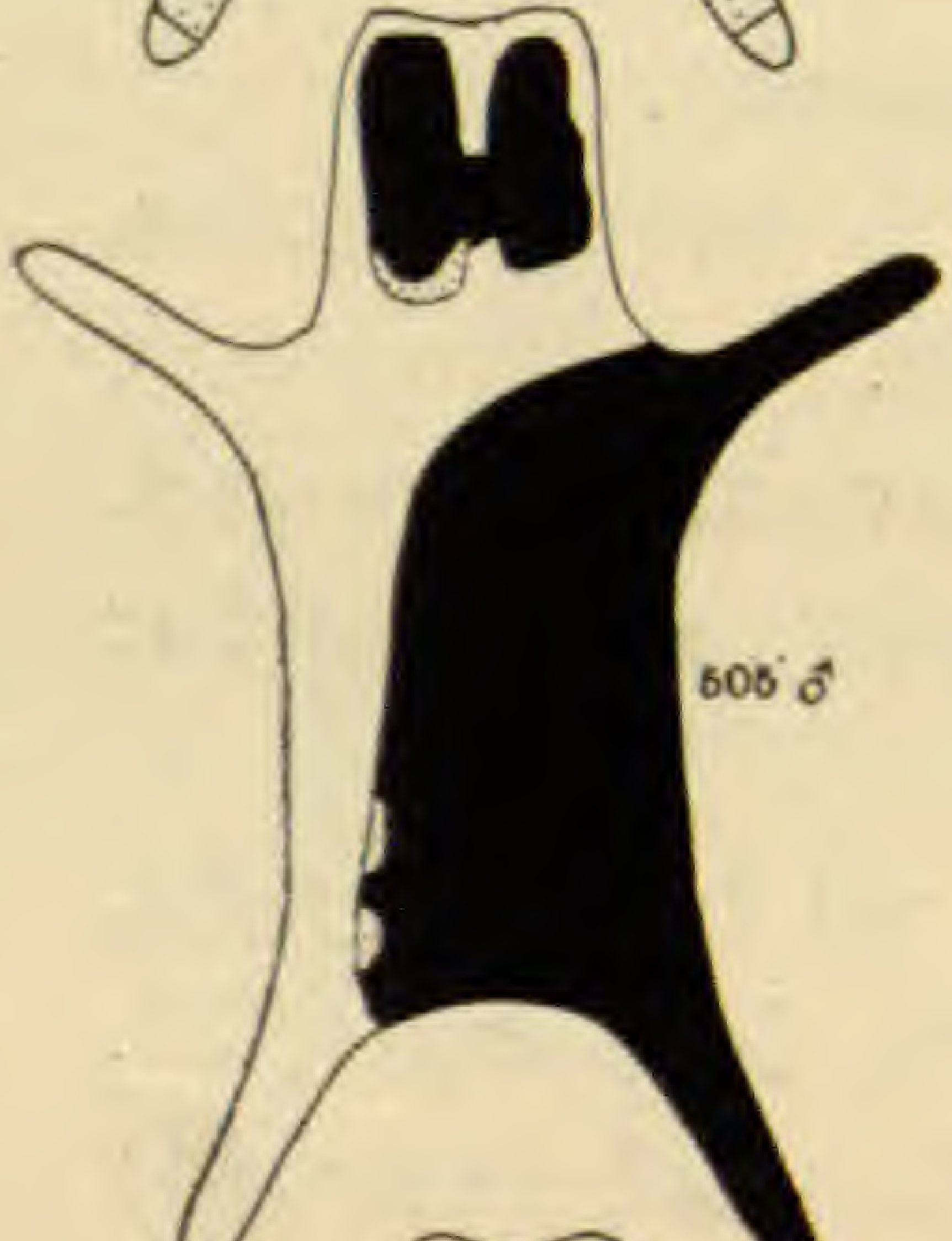
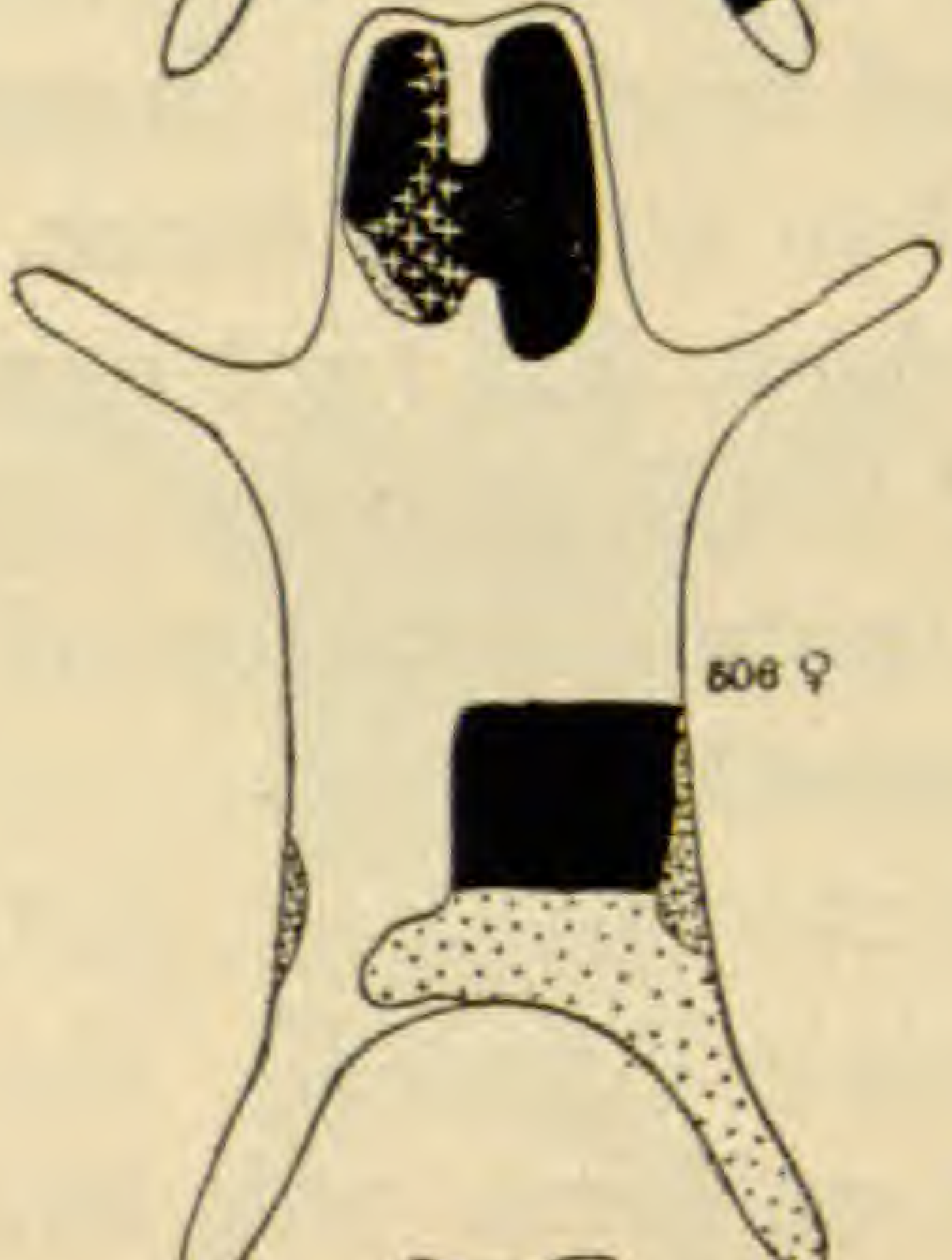


505 ♂



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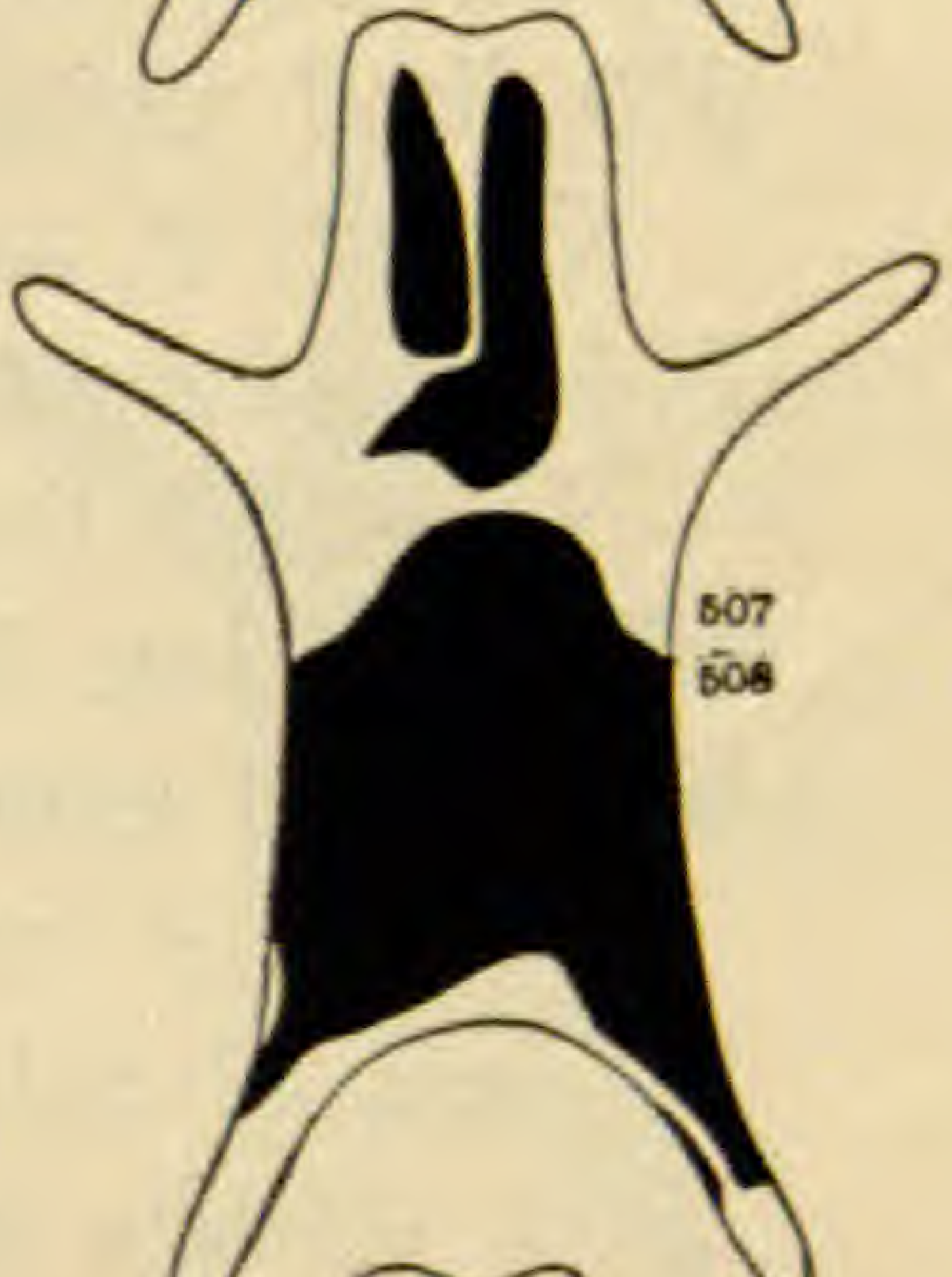

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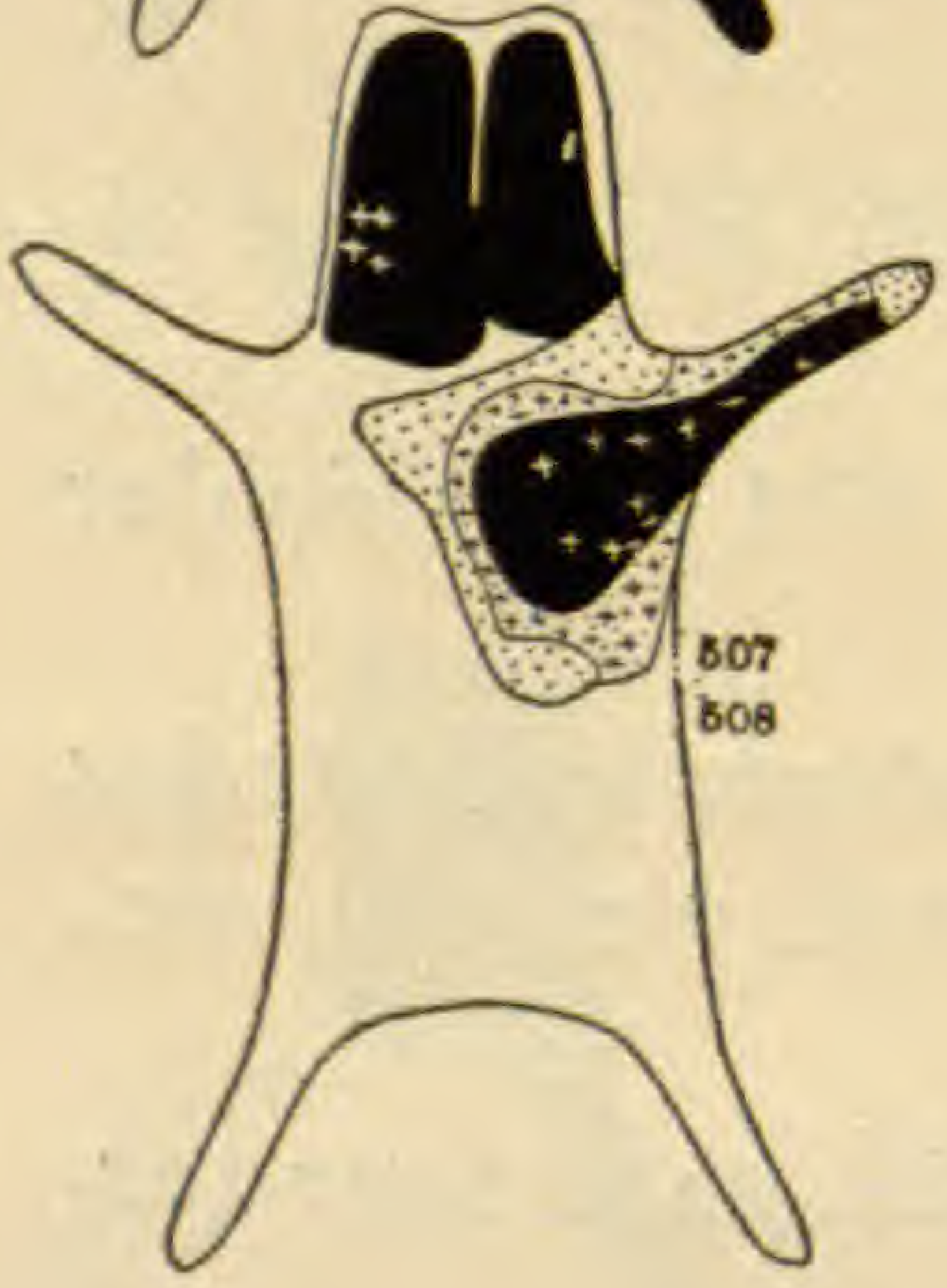

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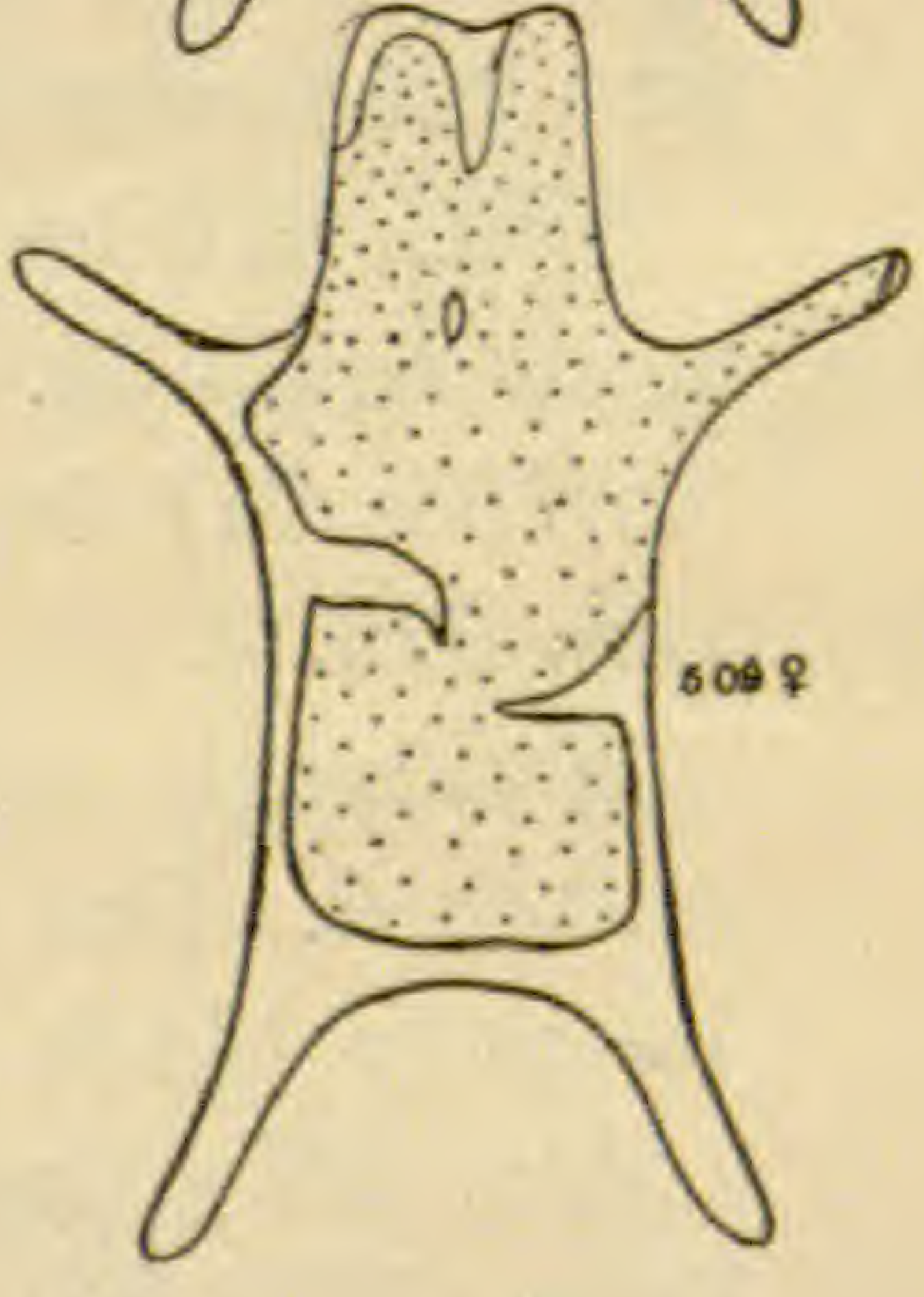


509 ♀

In Castle's paper of 1905 he gives the result of certain matings between black-red and black-red. Combining the result from two tables (pages 34 and 36) there is a total of 20 black-reds and 9 reds. It may be doubted whether Castle's black-reds are always the same as our tortoise, because he speaks in the text (page 32) of a reddish-black (1,179) and (1,180), but in the table stamps them as black. One parent of these animals was black; the other red. Therefore, his "black-reds" themselves were heterozygous.

Matings of 427 ♂

This animal is one of the red offspring (except for partial blaze), out of 401, tricolor black ♀, by 201 ♂ uniform red. He was extensively mated. His offspring, by his sister, have been already described.

No. 427 ♂, mated to tricolor black, 410 ♀, gave tricolor black, 558, tricolor red, 593, tortoise, 557 (white foot), 559 (had white hind toes), 592 (nearly black).

No. 427 ♂, mated to tricolor black, 522 ♀, gave tortoise, 574, and tricolor black, 575 (not charted).

No. 427 ♂, mated to tricolor red, 489, gave uniform red, 568, tortoise, 569 (note extension of black), and tricolor black, 570 (not drawn).

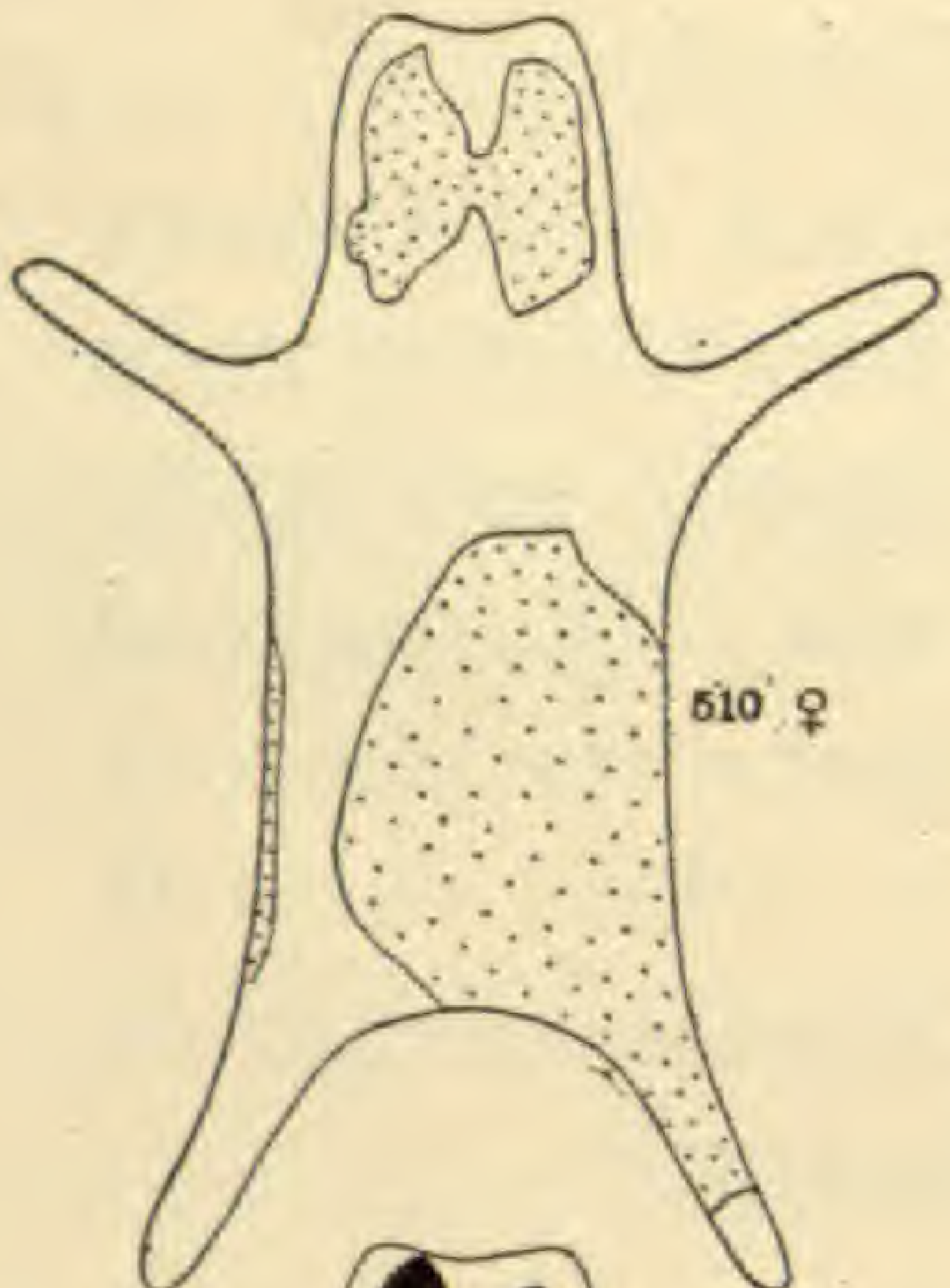
No. 427 ♂ was mated to three sisters, all bicolor reds, but not closely related to 427, viz., 509, 510 and 511. With 509 he gave uniform red, 562, 561 (not charted) and bicolor red, 562.

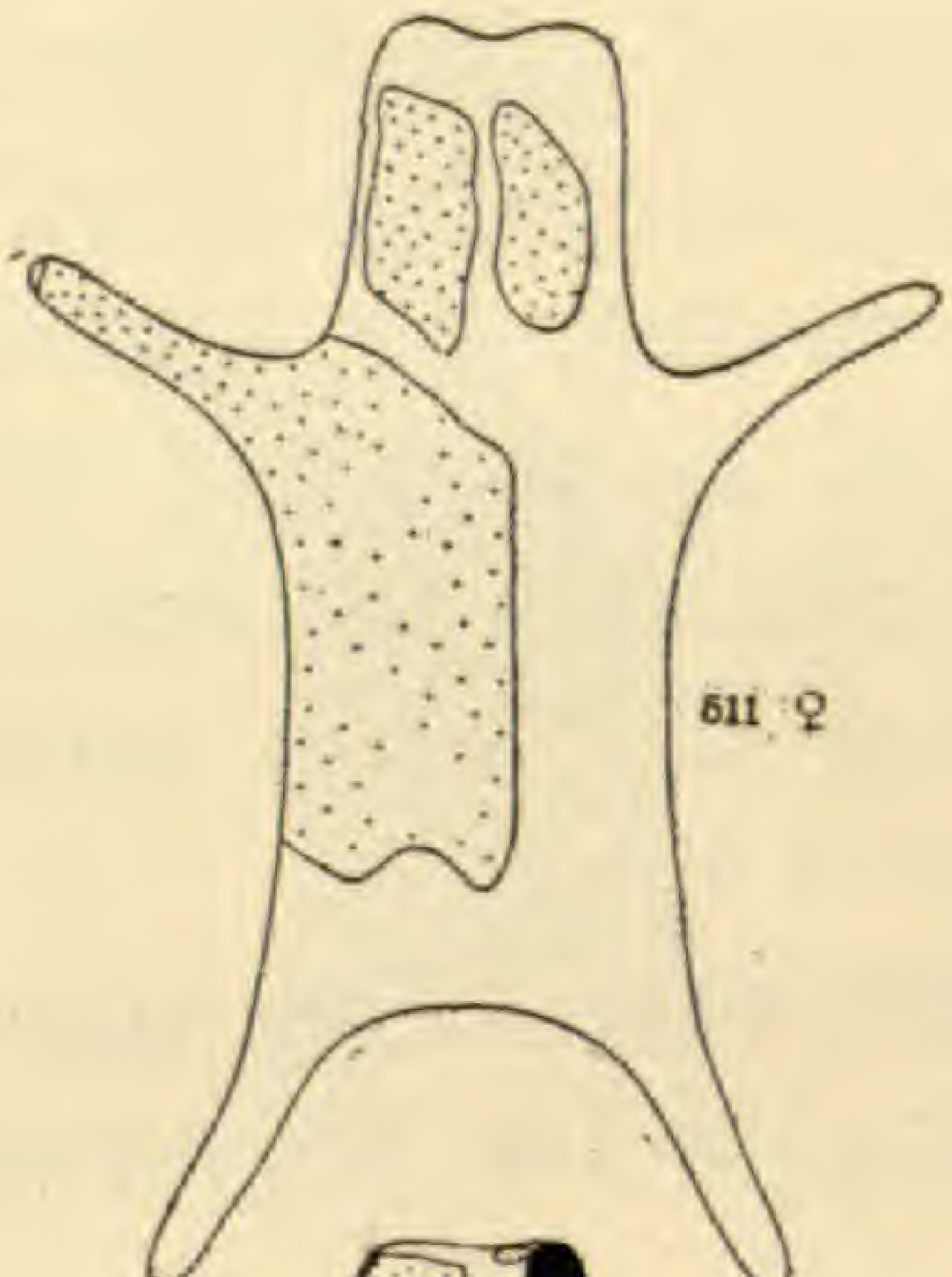
With 510 he gave uniform red, 563, 565, 565 *A*, and bicolor red, 564.

With 511 he gave uniform red, 571, 572, and bicolor red, 573.

Evidently 427 is heterozygous for uniform and carries no black. But when mated to black spotted, viz., 489, etc., he gave black spotted offspring.

No. 427 ♂, mated with bicolor black, 423, gave four tortoise, 579, 580, 597 and 598.


510 ♀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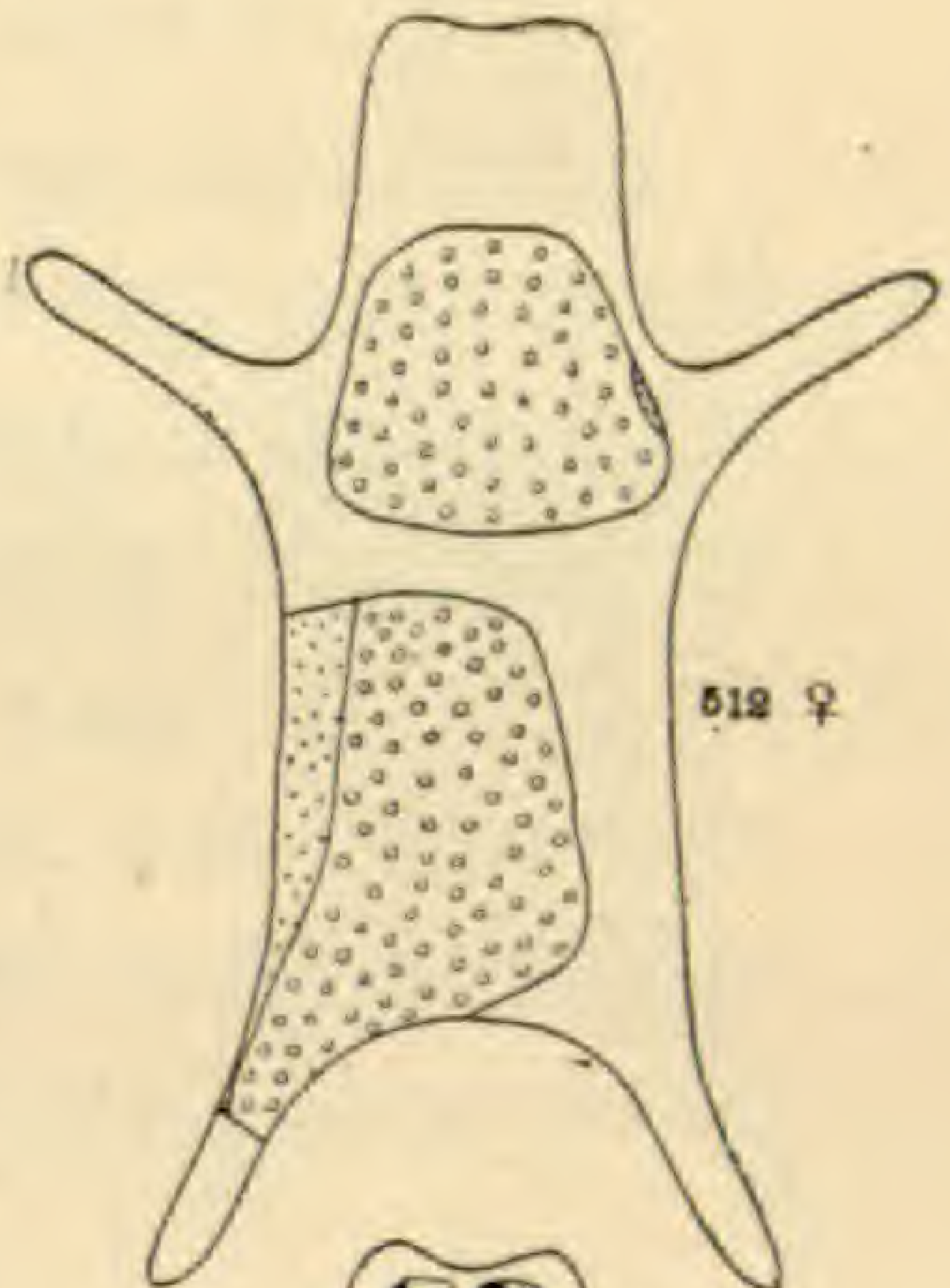
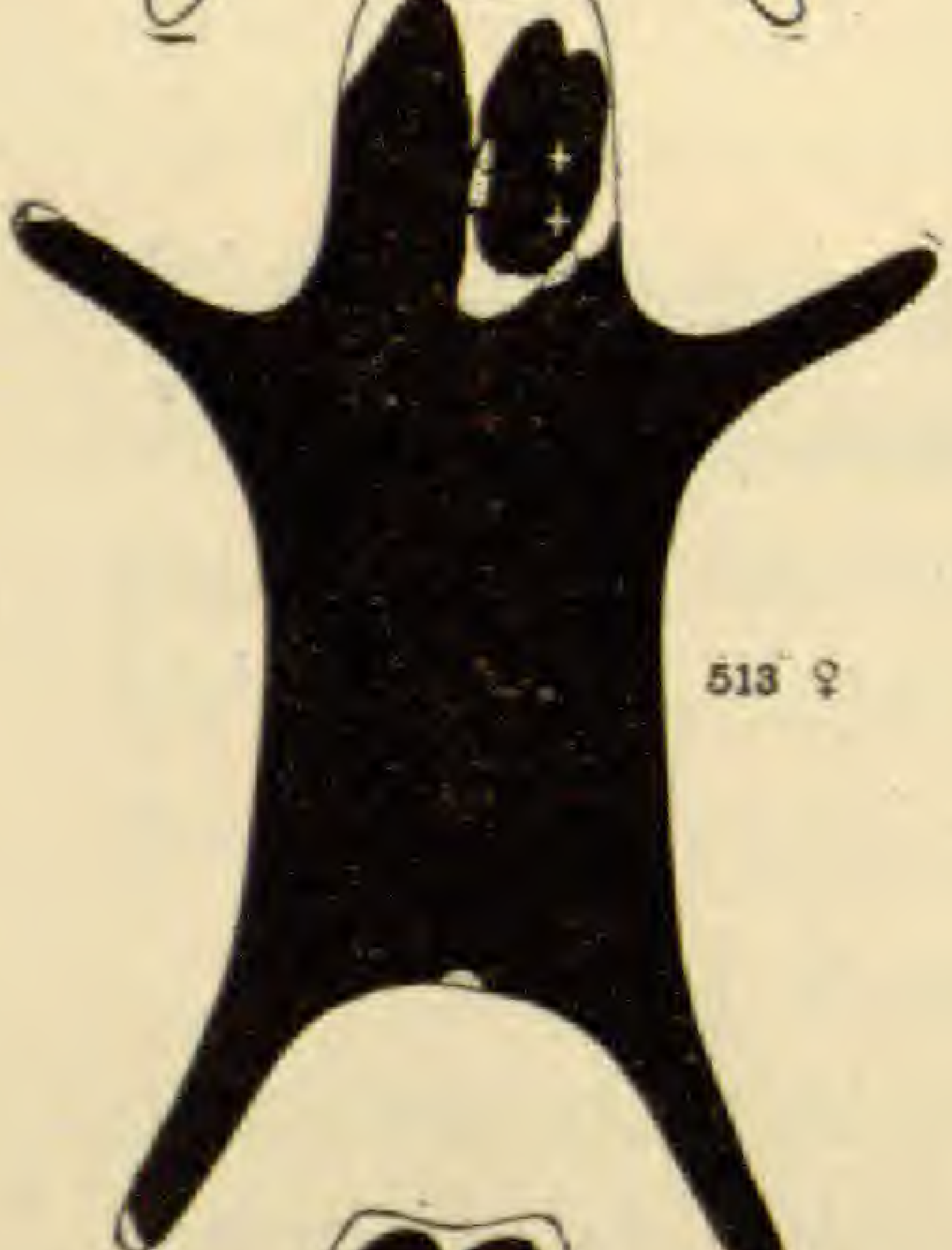
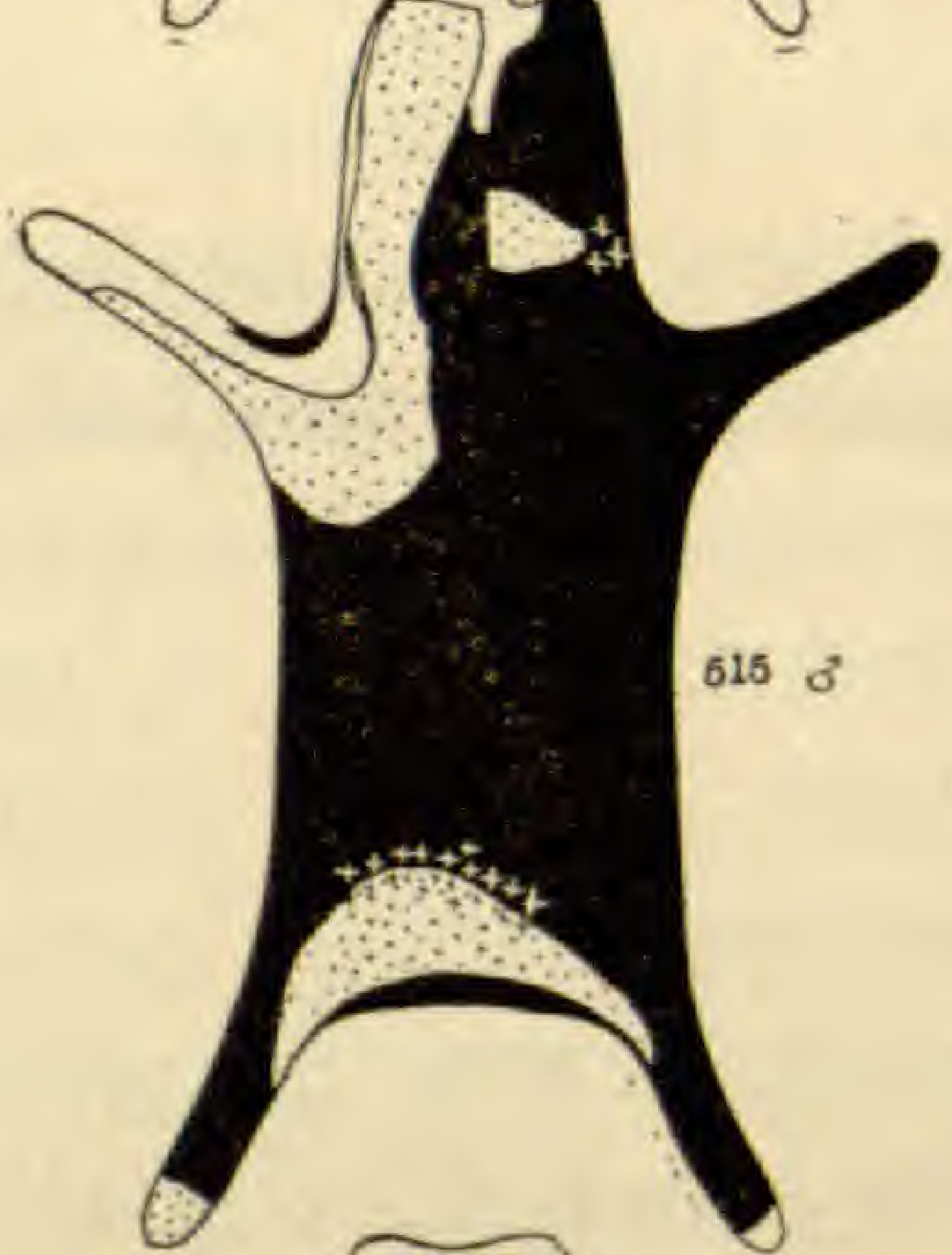
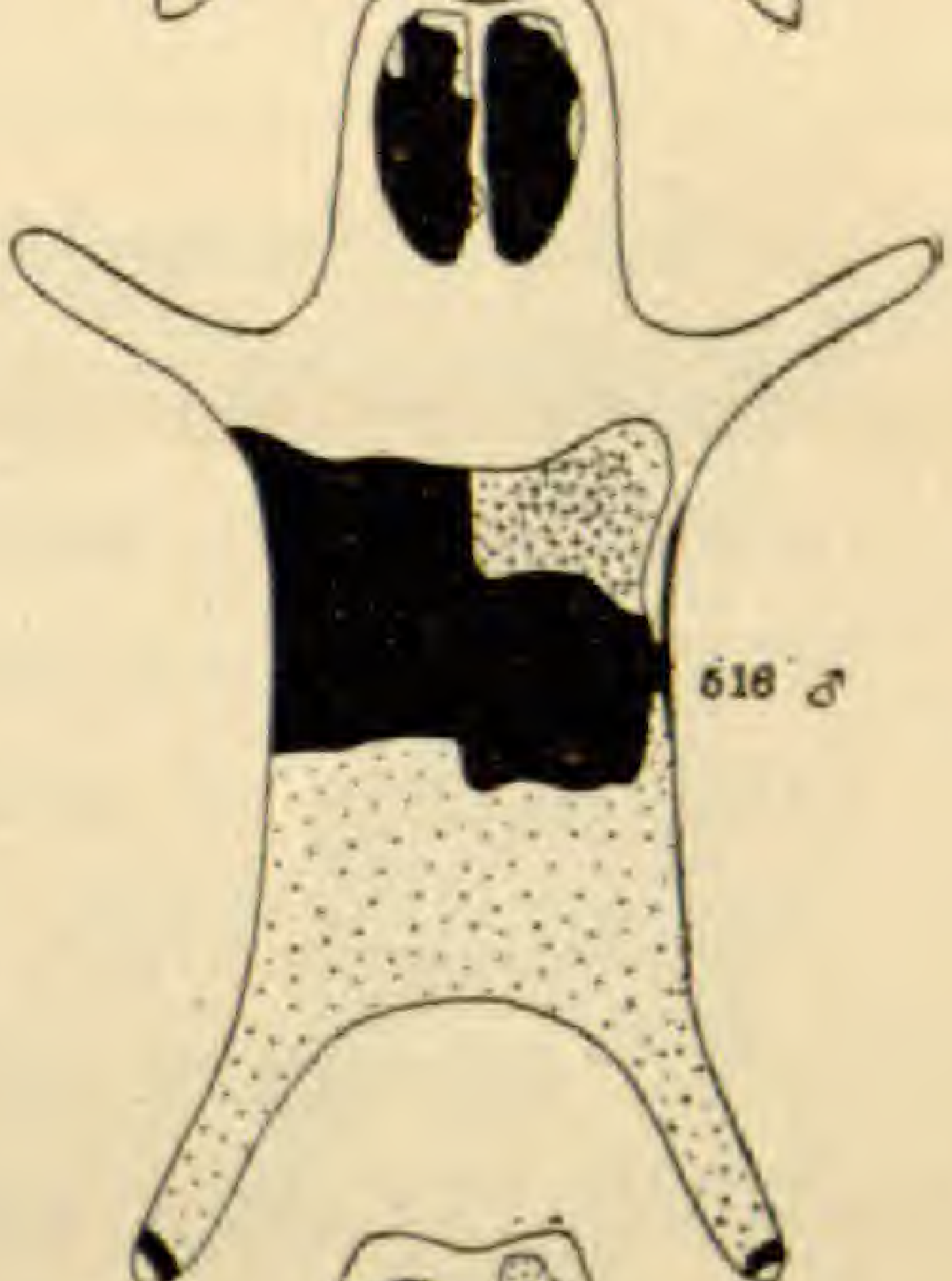

512 ♀


513 ♀


515 ♂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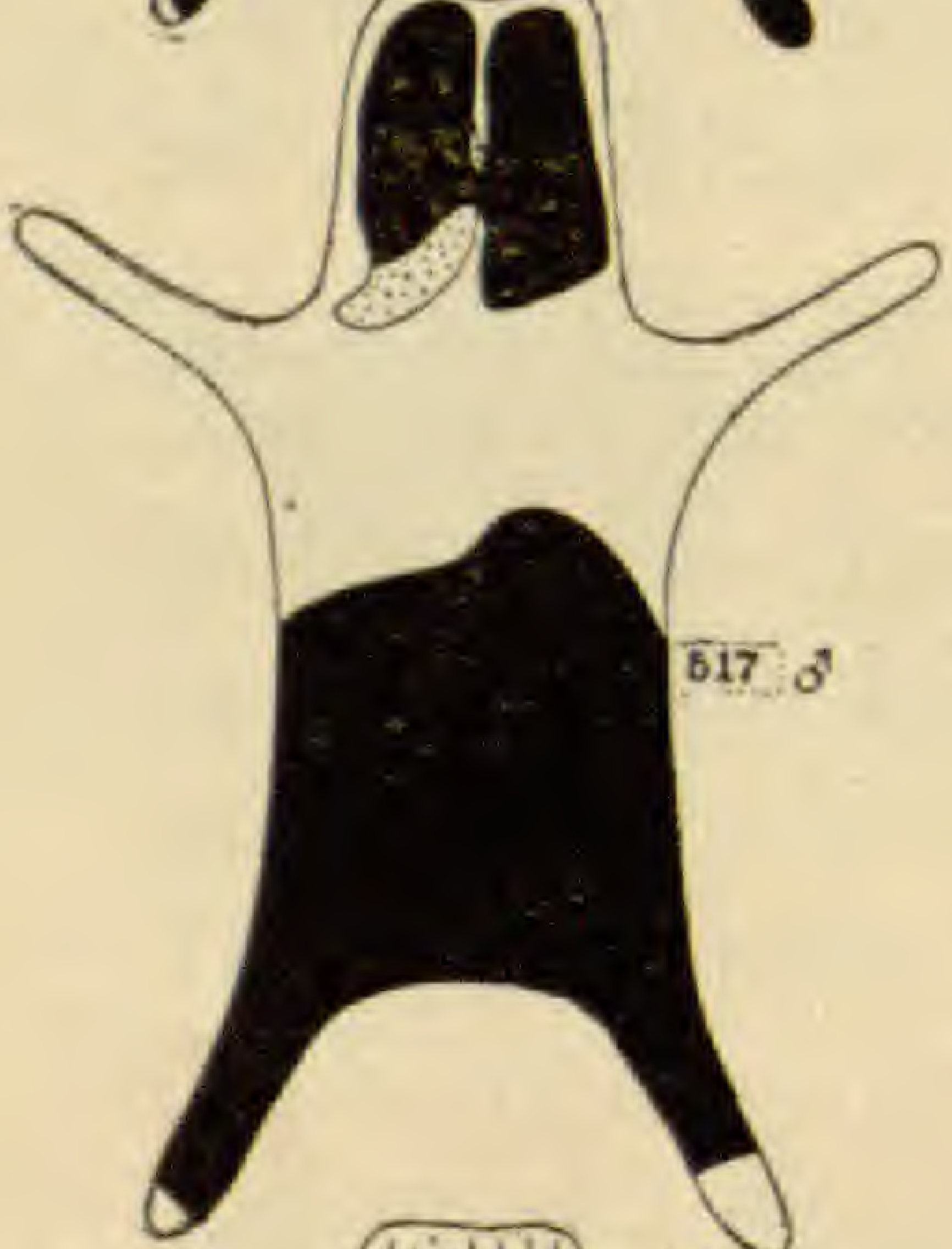
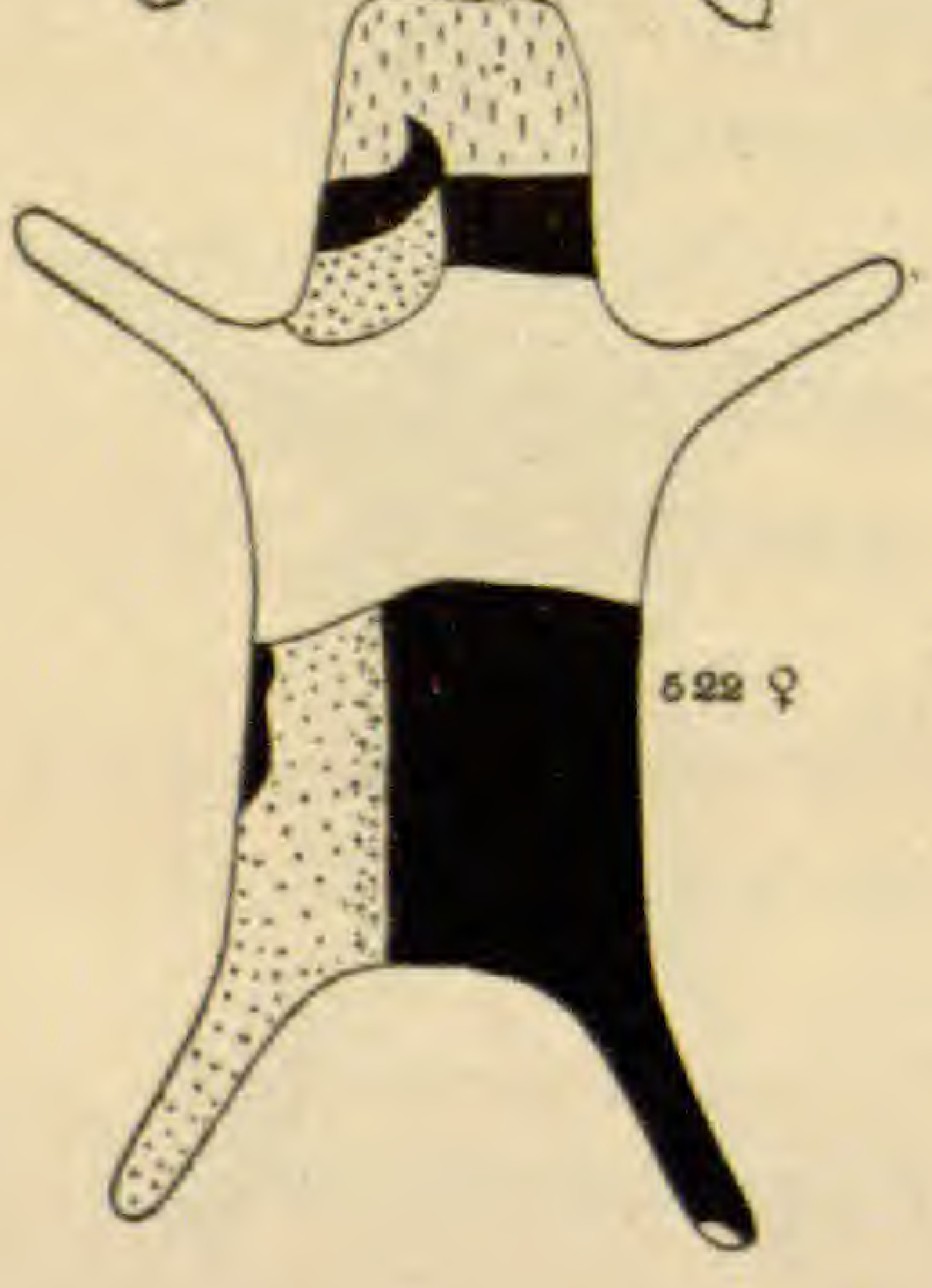
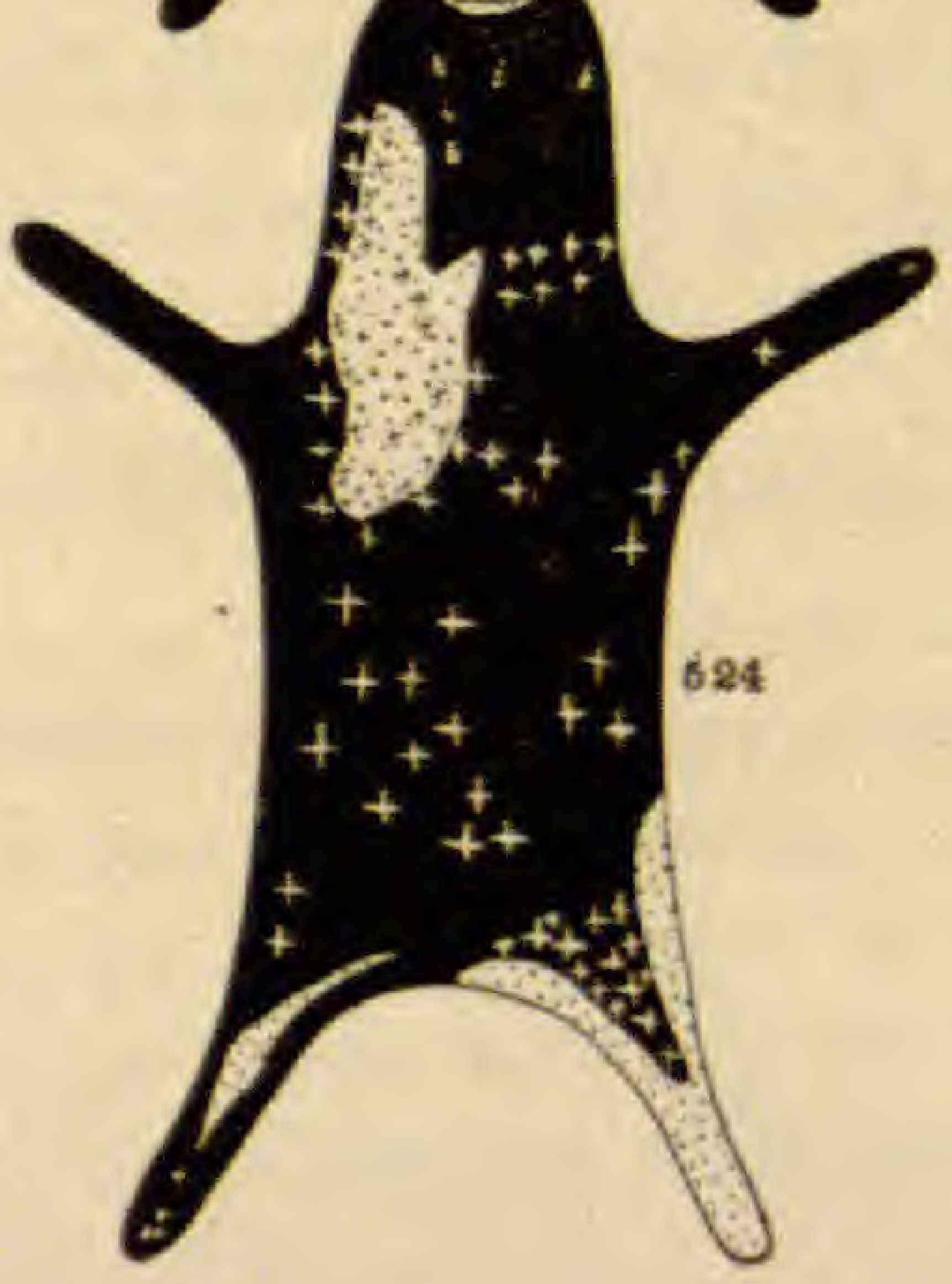

517 ♂


520 ♂


521 ♀


522 ♀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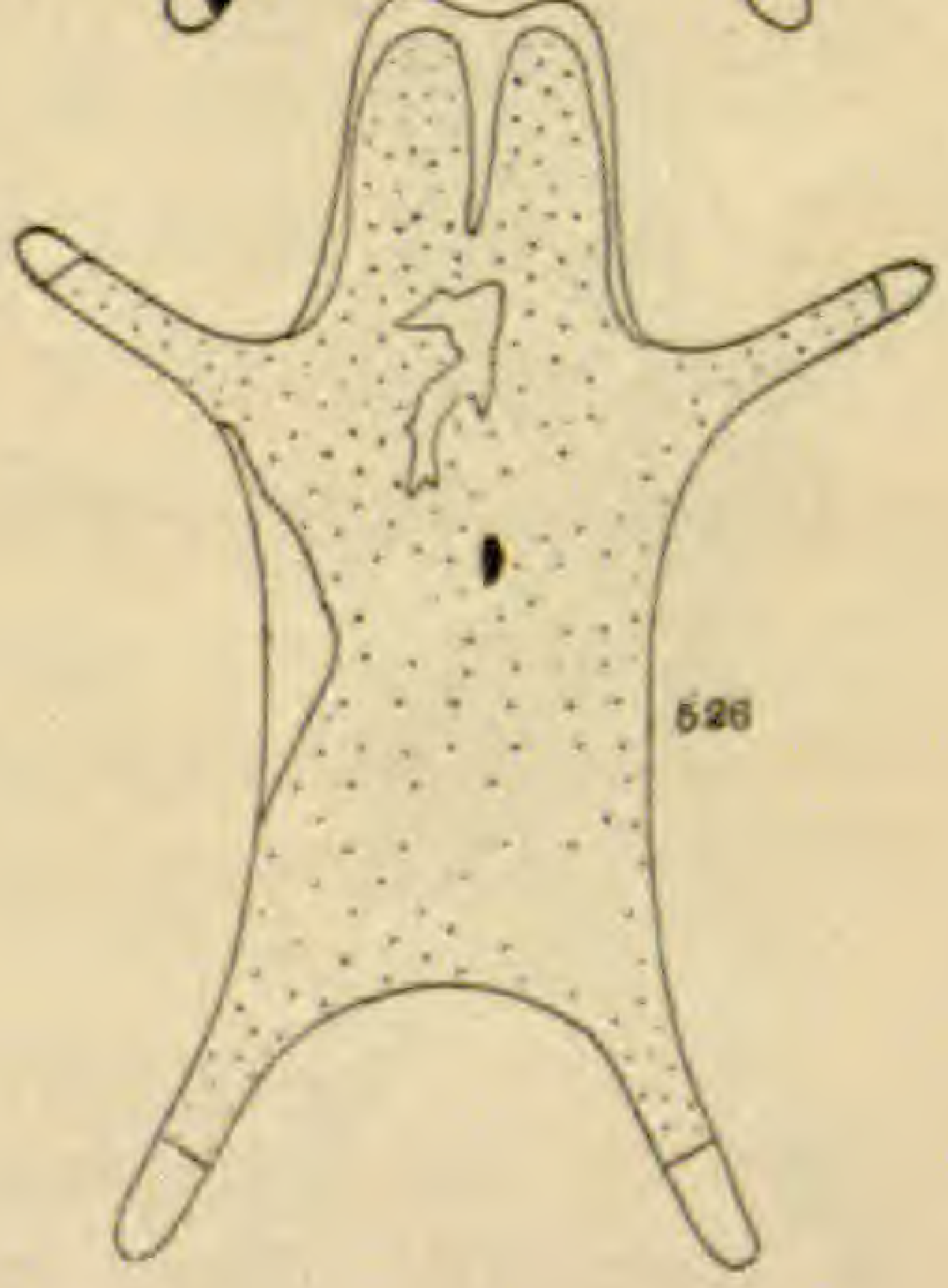
526

Agouti Spotted with White by Tricolors

A spotted agouti ♀ mated to tricolor black, 414 ♂, gave three tricolor blacks, 385, 499, 487, and two bicolor reds with agouti spots (*i. e.,* they had white spots, red spots and agouti spots), viz., 486, 487 and one, viz., 500, spotted agouti. It may seem that when agouti spots are present they take the place of the black. Castle's (1905) records support this suggestion. The agouti female seems to have been heterozygous for the agouti factor.[10]

DISCUSSION

It has been stated by Castle that when guinea-pigs with uniform coat are crossed to spotted guinea-pigs the offspring have uniform coats.[1] Our own limited experience confirms this statement. In the F_2 generation a variable offspring is obtained, ranging from uniform to much spotted. This question will be considered later.

A question of fundamental importance is whether the uniform coat can be treated as allelomorphic to spotted coat. This involves the question whether spotting is the product of one factor or of more than one.

In rats and in mice the same question has come up and Cuénot has handled the problem on the basis of a pair of allelomorphs. The main evidence on which the assumption of a pair of allelomorphs rests, is derived from the number of kinds of offspring in the F_2 generation. If uniform coat is treated as allelomorphic to spotted coat, the F_2 expectation is three uniform to one spotted, and this condition is the reported result for this generation.

On the other hand, if the spotted coat is due to more than one factor the situation becomes complicated, and the F_2 expectation is no longer three to one, unless we

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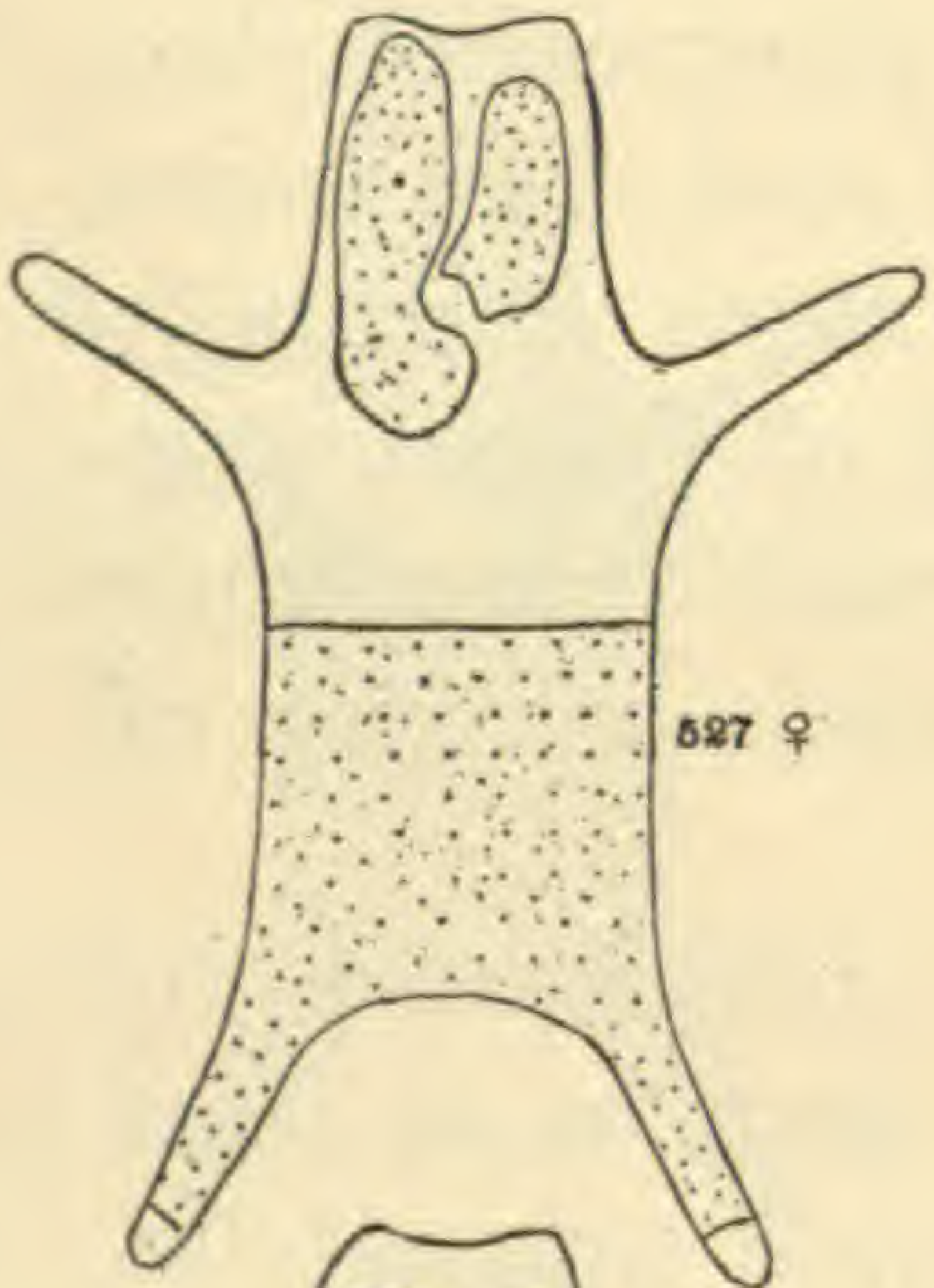
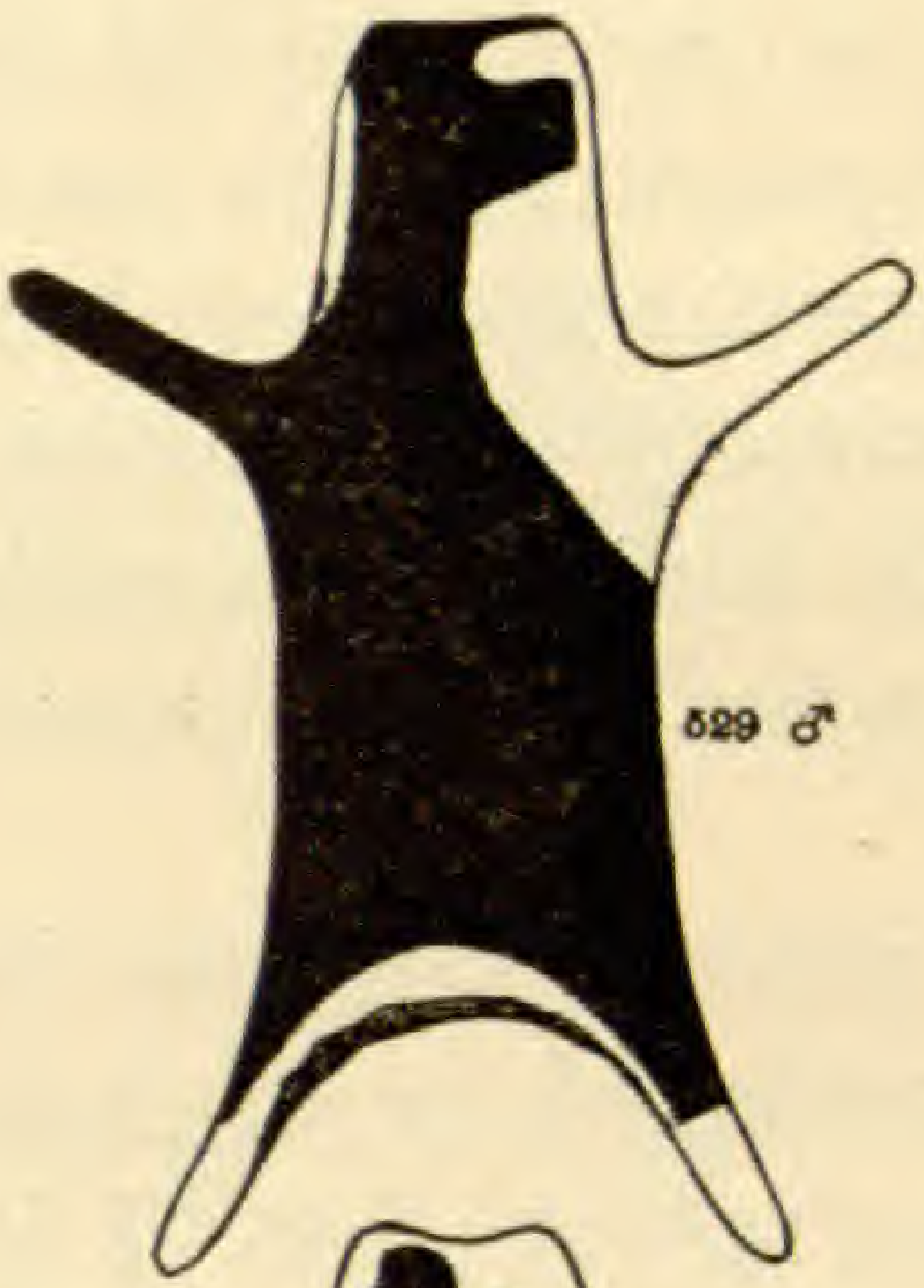
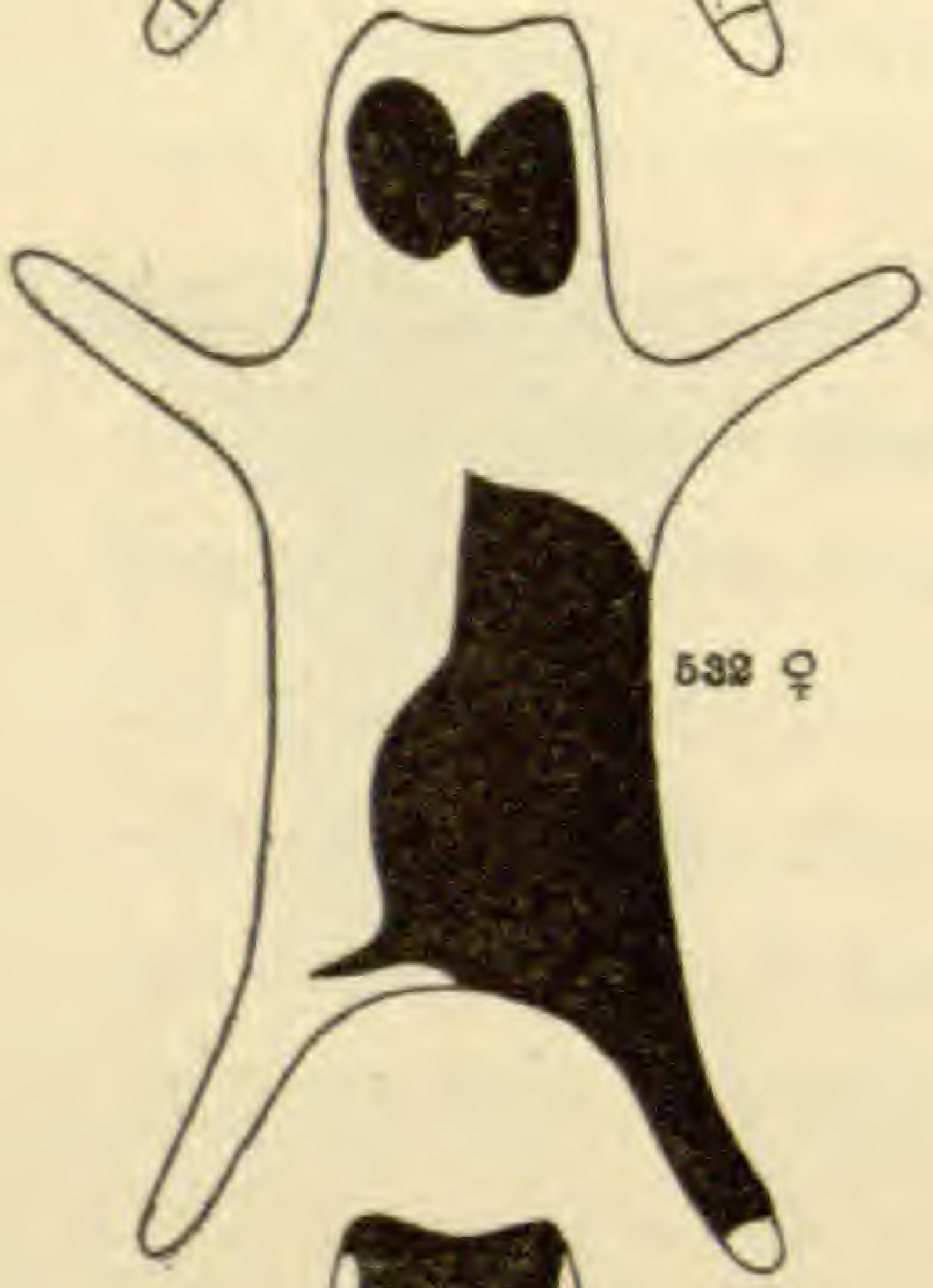
[10] One of the progeny of the mating of tricolor blacks, 469 ♂, by bicolor black, 423, calls for special attention. This individual, TB 521, had among the other pigmented hairs a great many that had a reddish base and a black tip. These recall, but are not identical with, agouti hairs.

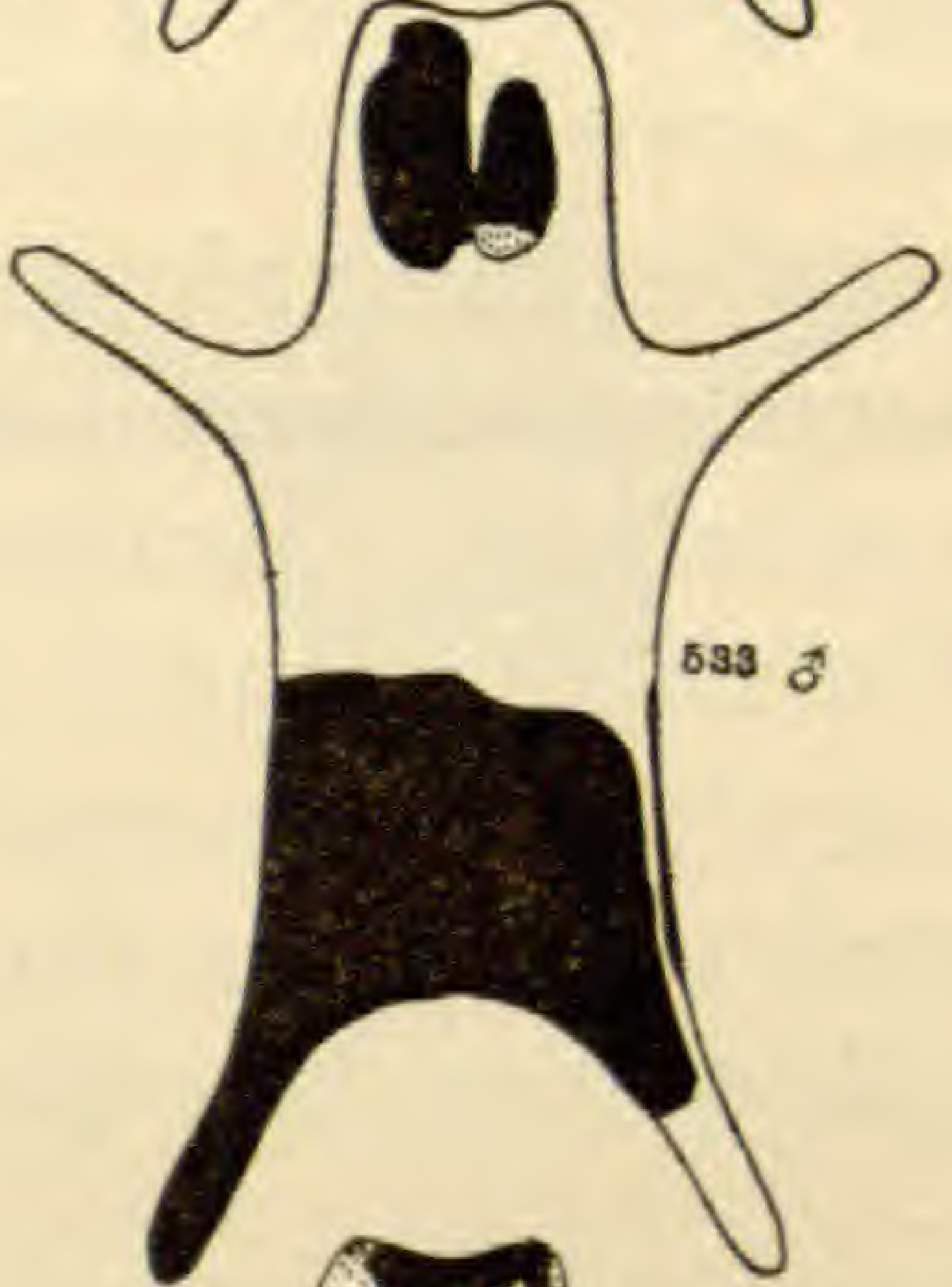
[1] Castle's mating shows in some cases apparent exceptions to the rule, but possibly the uniform animals were not entirely homozygous. Exceptionally a blaze may appear in the F_1's.

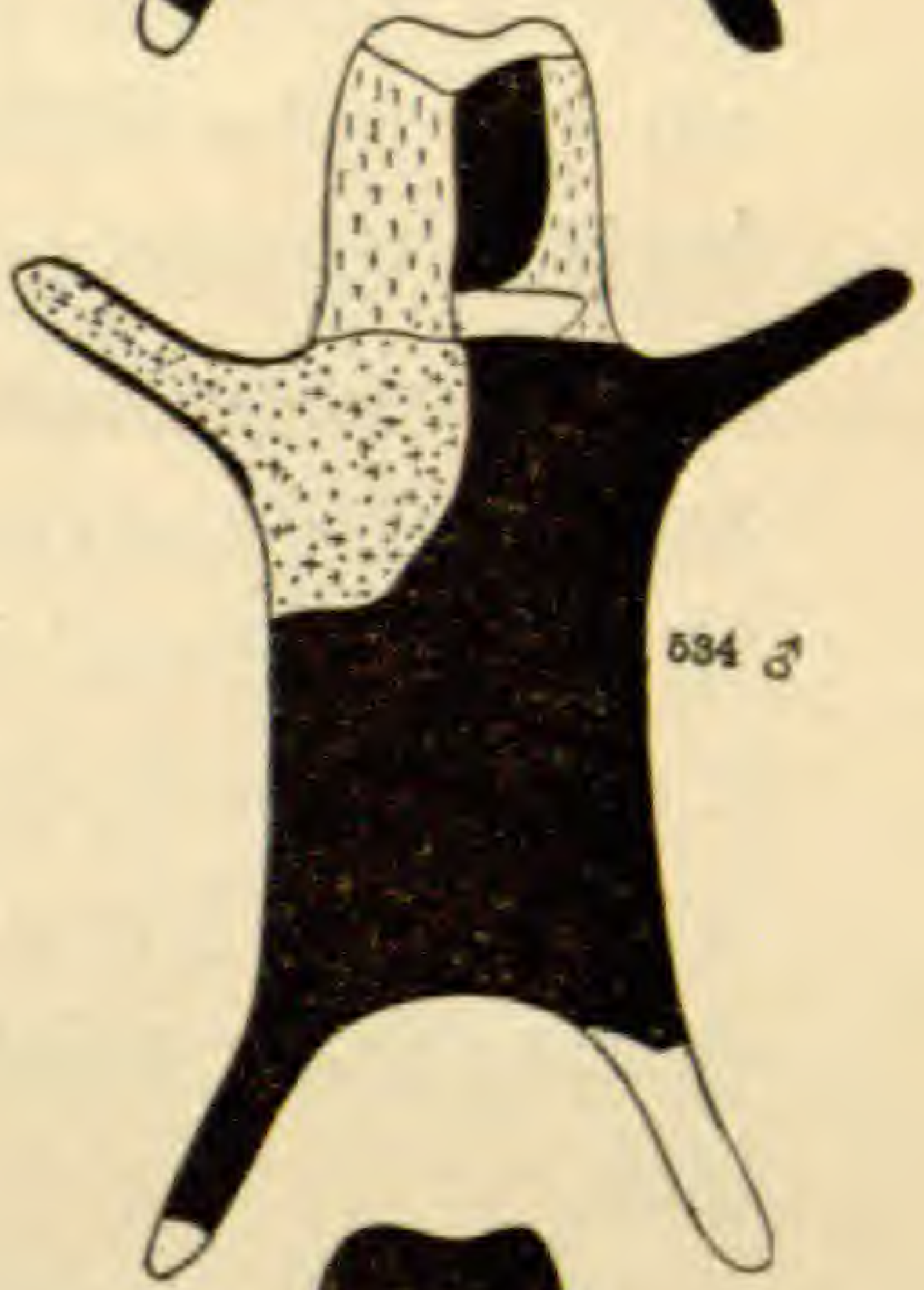

527 ♀


529 ♂

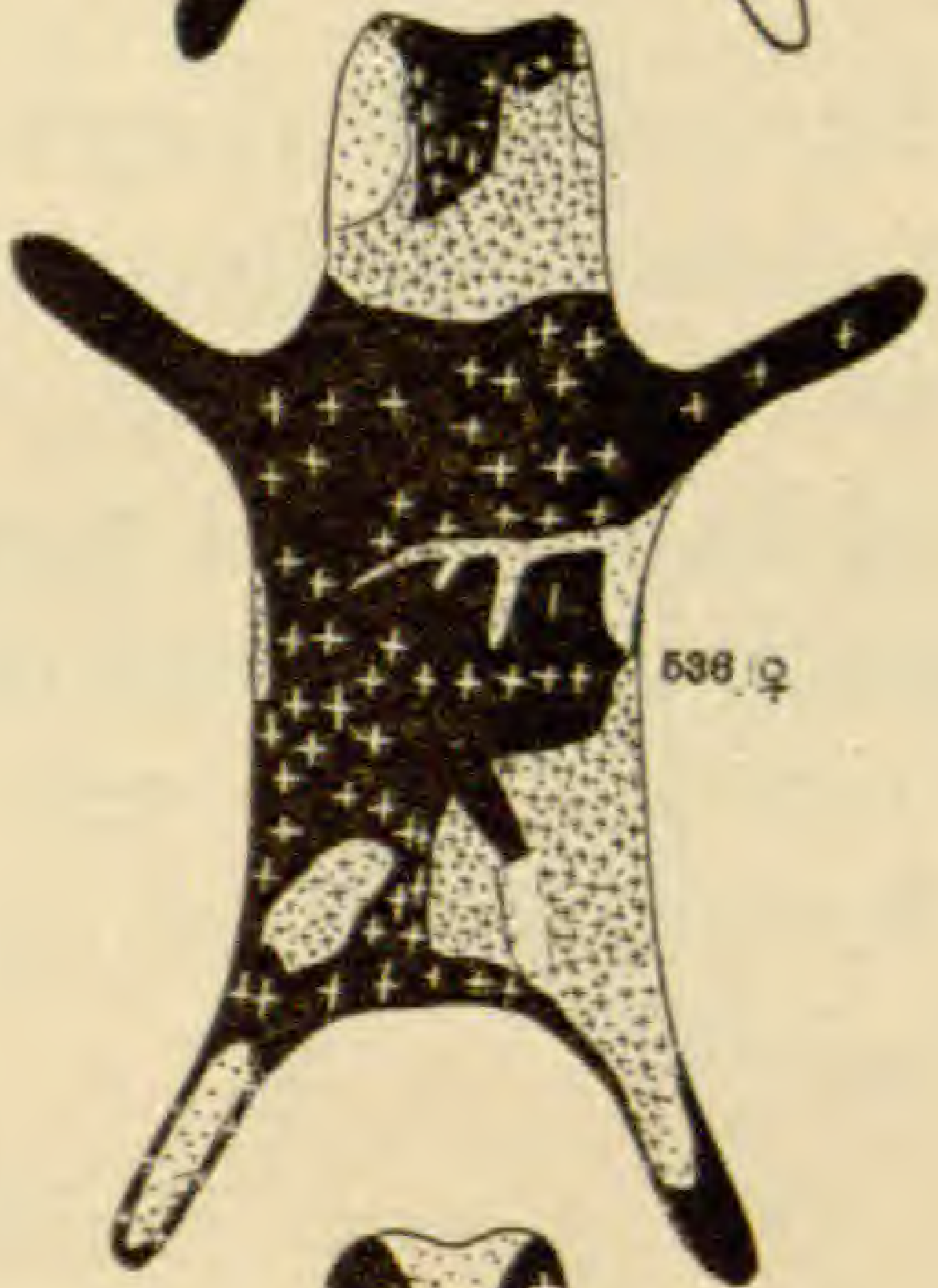

531 ♂


532 ♀


533 ♂


534 ♂


535 ♂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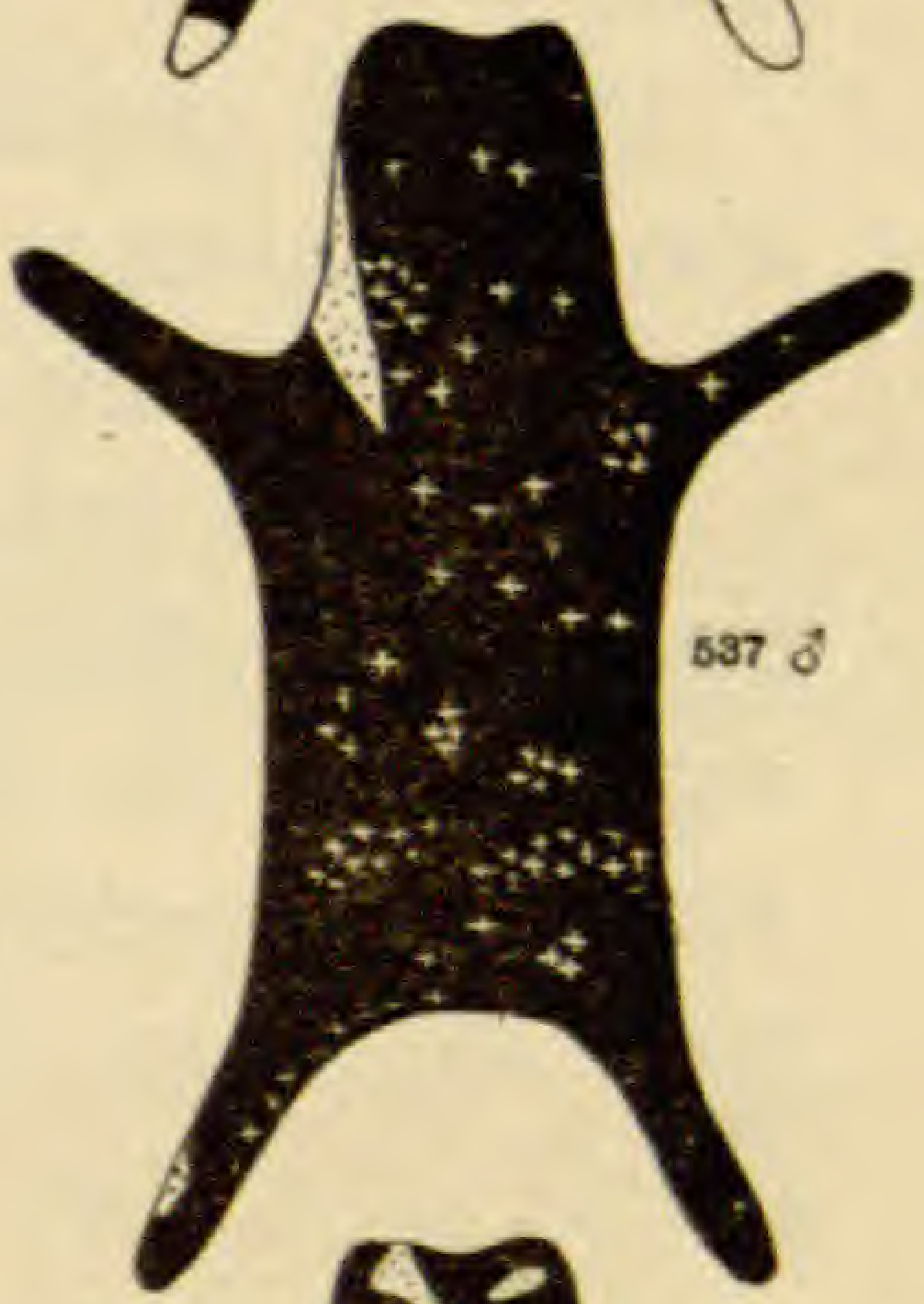
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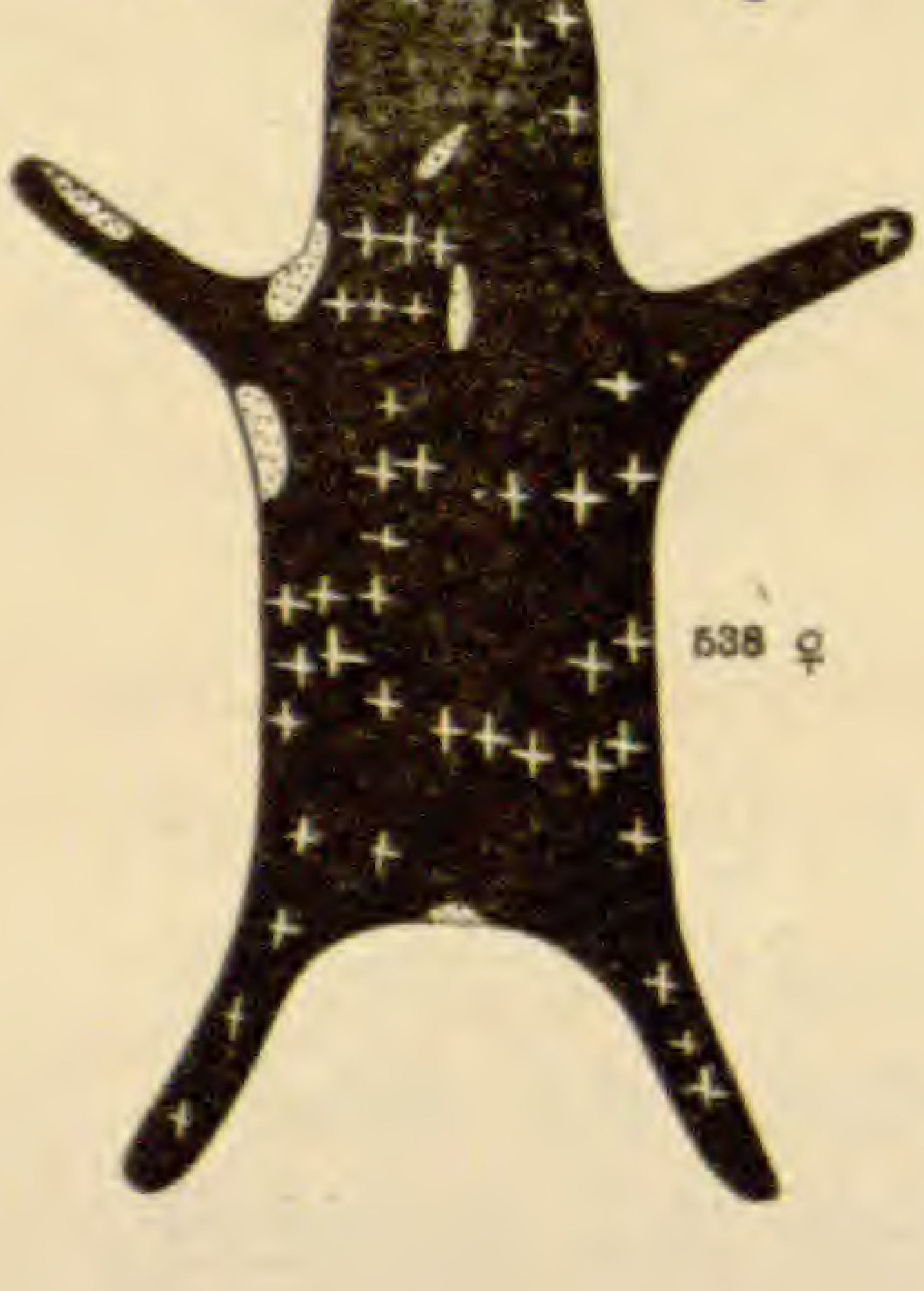
538 ♀


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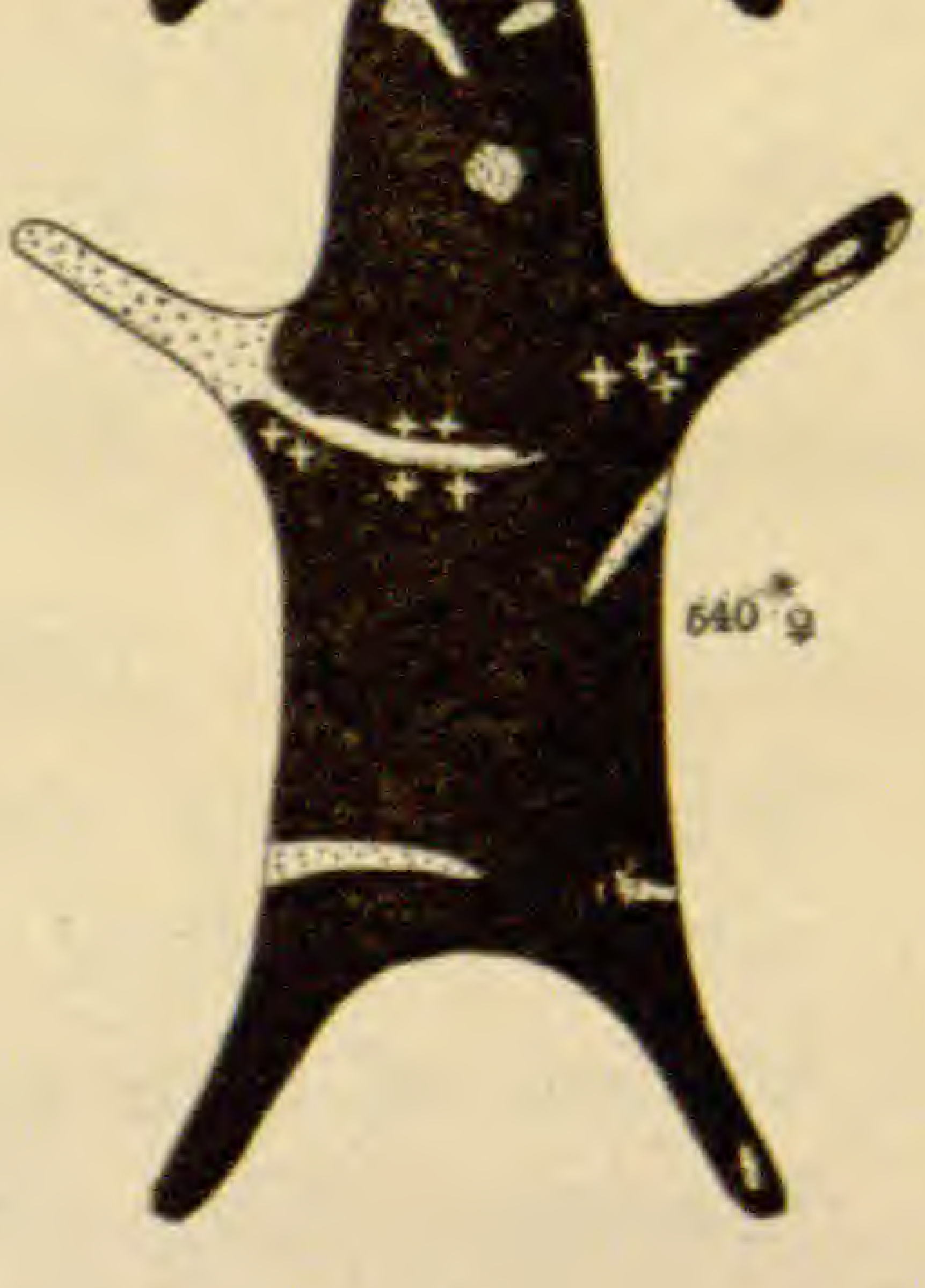

540 ♀

assume that there is one factor whose "absence" makes possible the development of the spotted coat. It seems to us that the experimental evidence, more especially the selection experiments of Cuénot and of Castle, suggest the possibility that the "spotted coat" is a very complex affair, depending presumably on a number of factors.

Although this possibility has been repudiated by Castle and not considered by Cuénot, it may be at least worth serious examination; for, if it should prove true, an entirely different appearance will be given to the selection experiments referred to above. Now, the fact that the modal class changes when much spotted (with white) and little spotted (with white) animals are selected, and the fact stated by Cuénot that much spotted behaves like a dominant to little spotted, suggests that we may be dealing here with a mixed population that may be treated in conformity with a Mendelian interpretation of the problem.

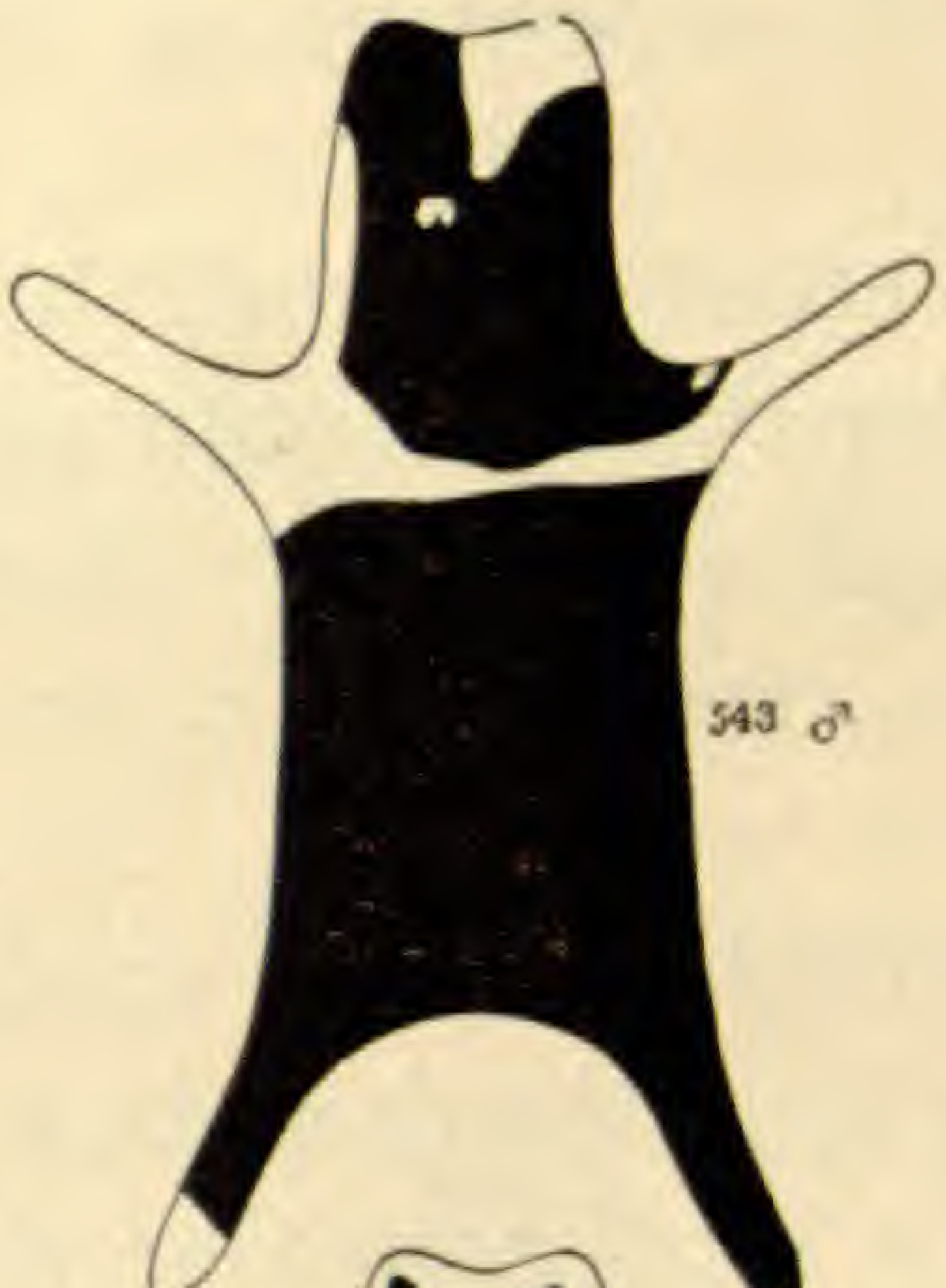
If much spotting has arisen through a series of progressive mutations, the following hypothesis may serve at least to put the facts in a new light.

It may be expresed in a general way as follows: If one special condition must be realized before any spotting can occur (the first realized stage may be simply due to a recessive spotting factor *ss*. Such an animal, mated to pure uniforms, will give:

$$\begin{array}{lll}
S & S & \text{Uniform} \\
s & s & \text{Spotted} \\
\cline{1-2}
S & s & \text{F}_1\,\text{♀} \\
S & s & \text{F}_1\,\text{♂} \\
\cline{1-2}
SS & Ss & \\
 & Ss - ss & \\
\cline{1-2}
\multicolumn{2}{l}{1SS - 2Ss - 1ss} & \text{F}_2
\end{array}$$

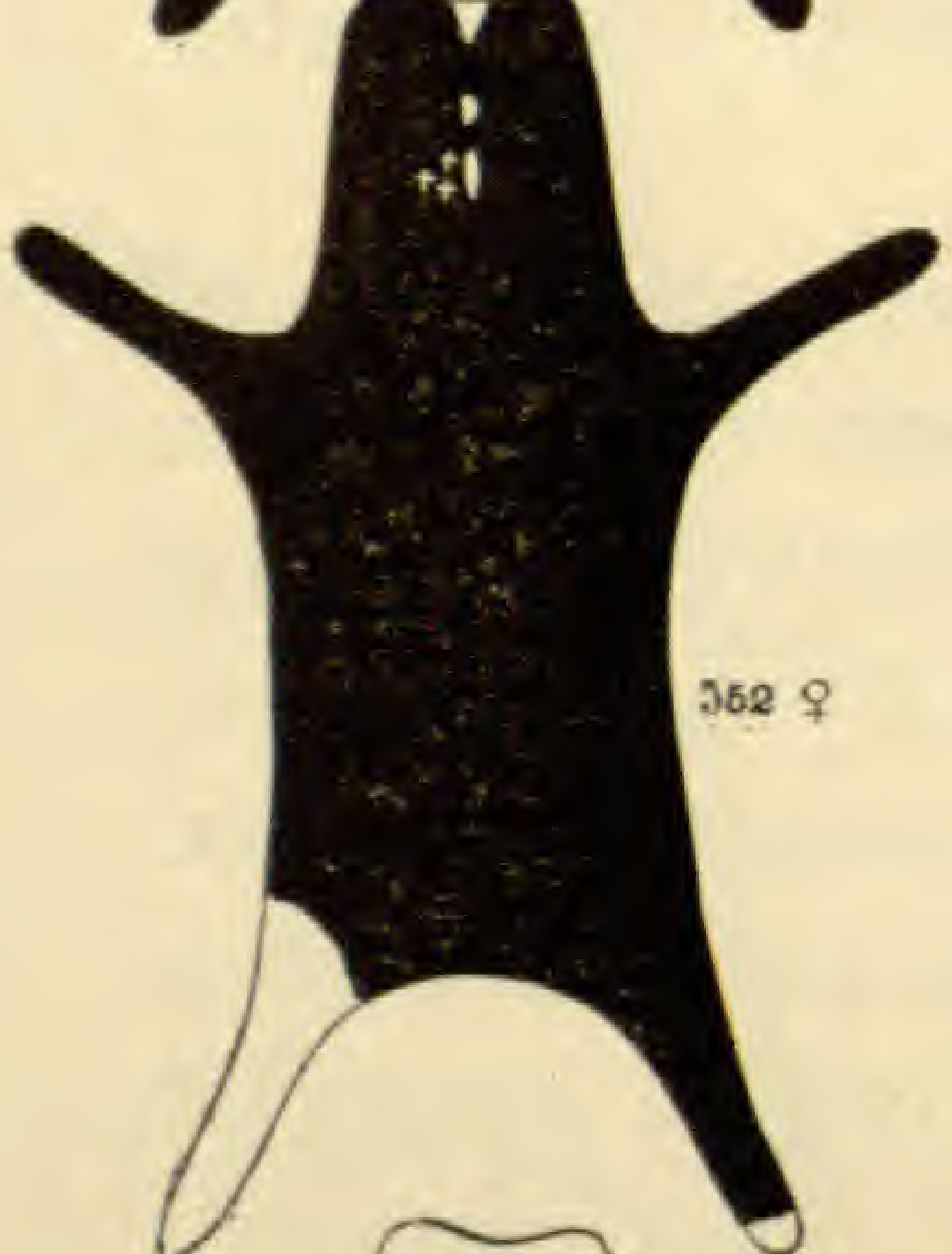
which is the simple Mendelian ratio of 3:1. In other words, the first realized stage of the spotted is a modification of the original factor and therefore its allelomorph. This means that in all *ss* animals the spotted

541 ♂

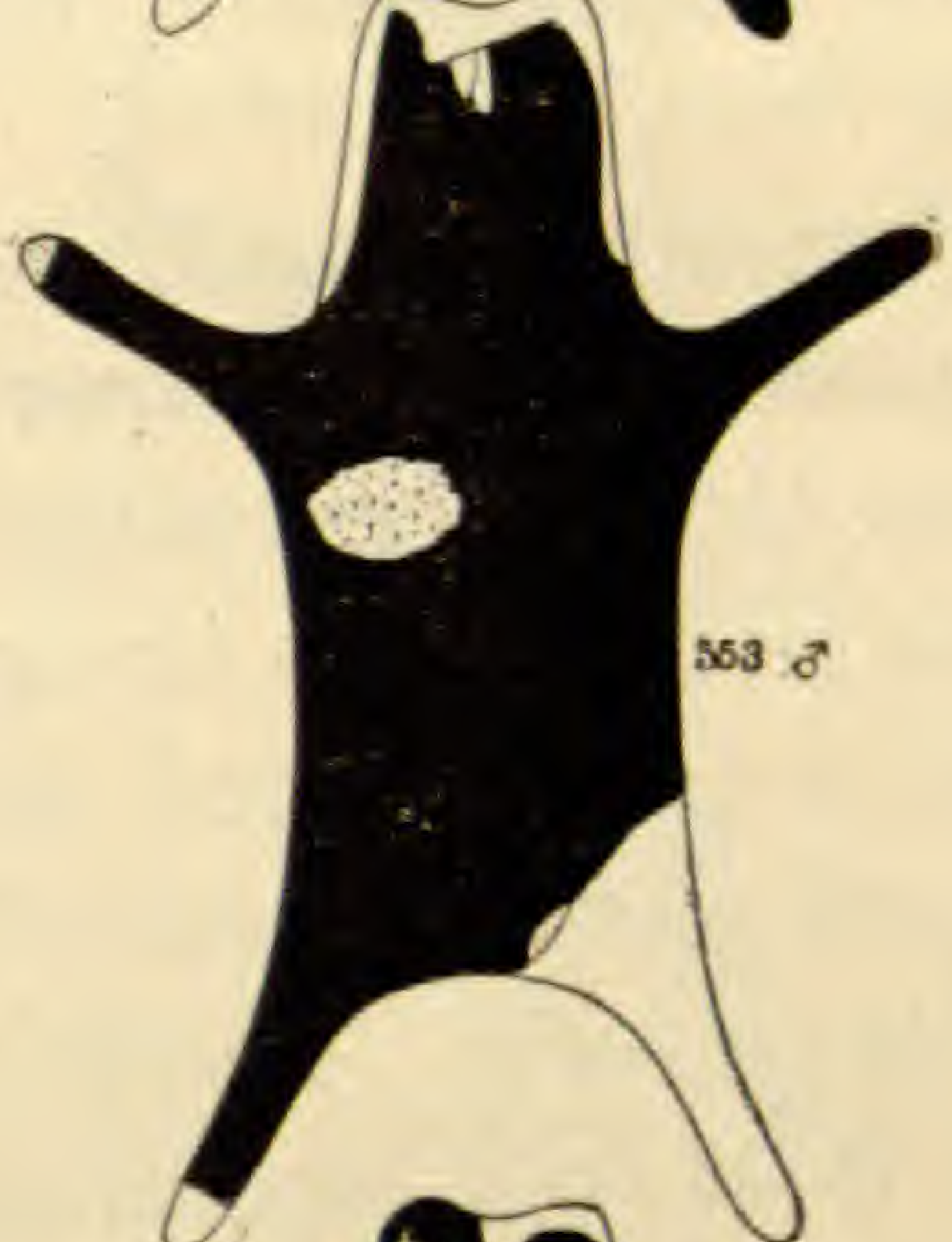


543 ♂

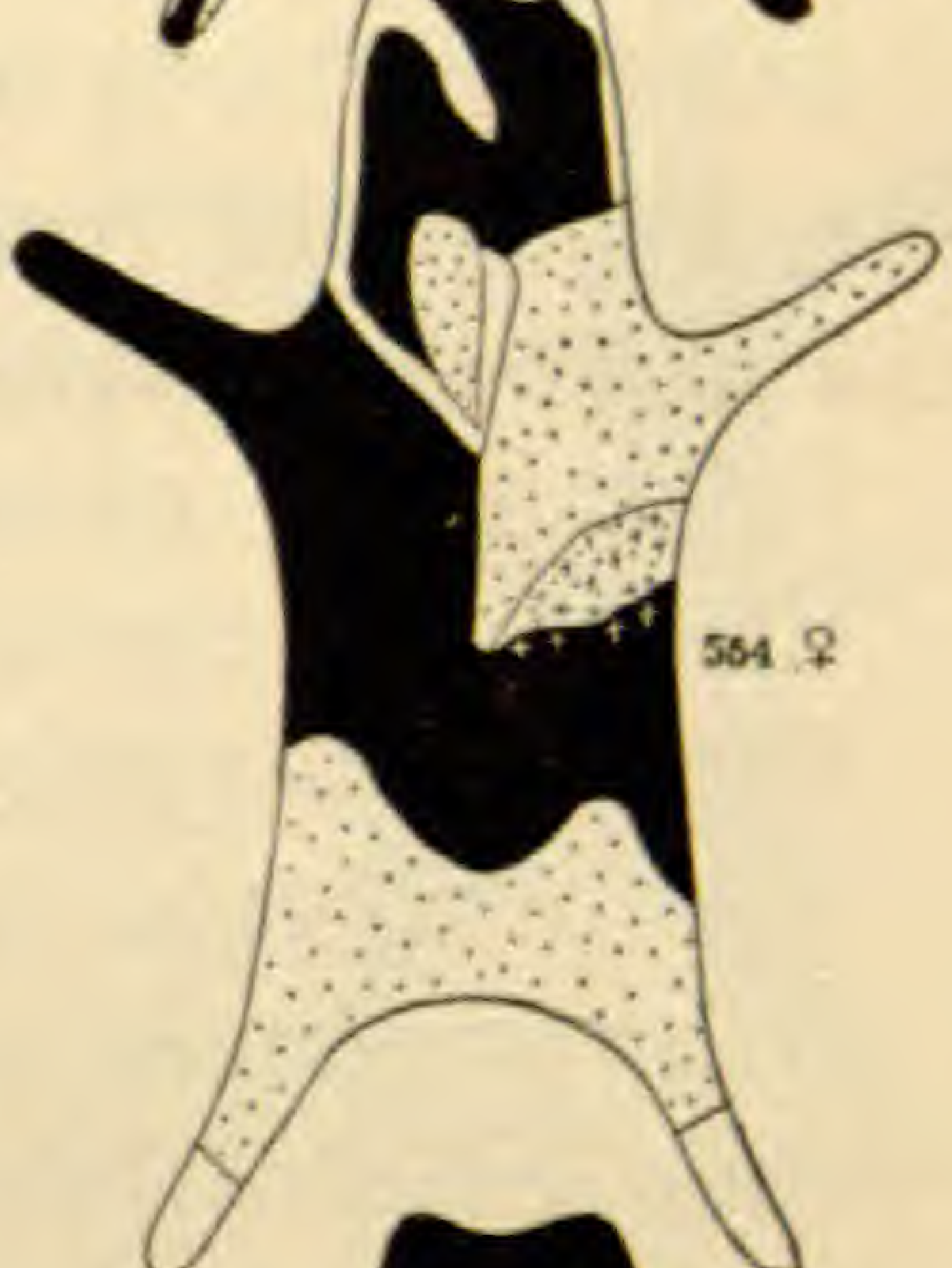
546 ♂



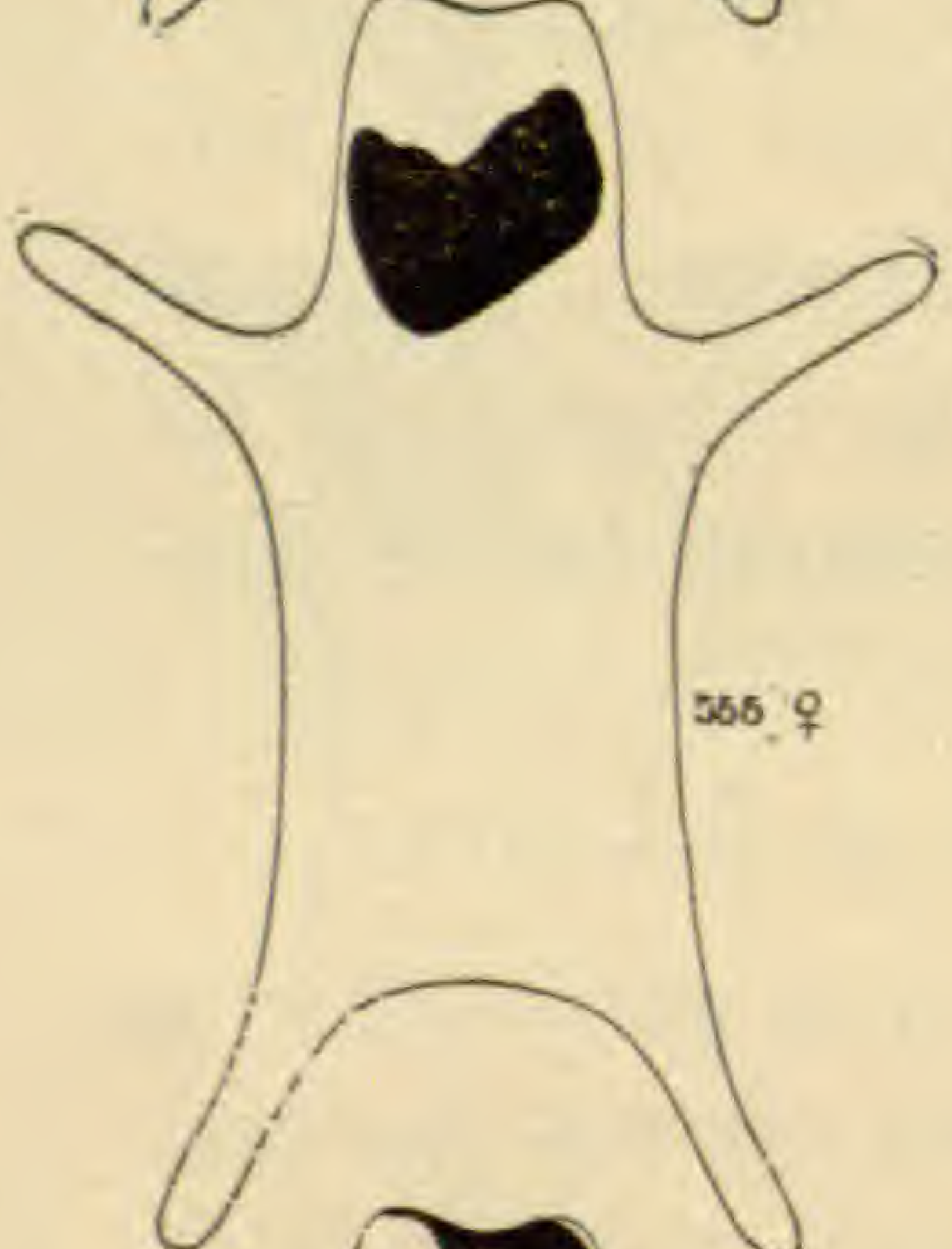
552 ♀



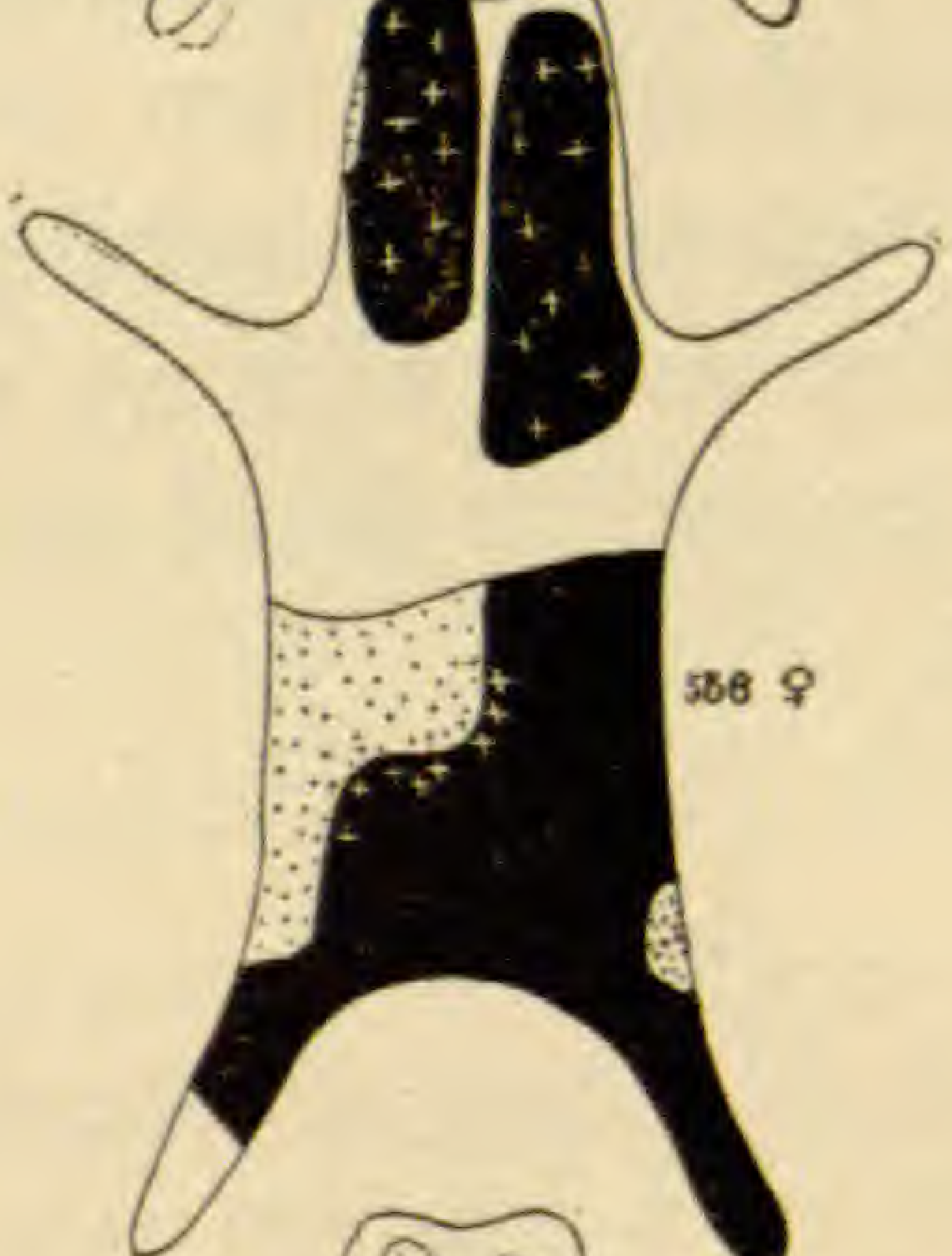
553 ♂



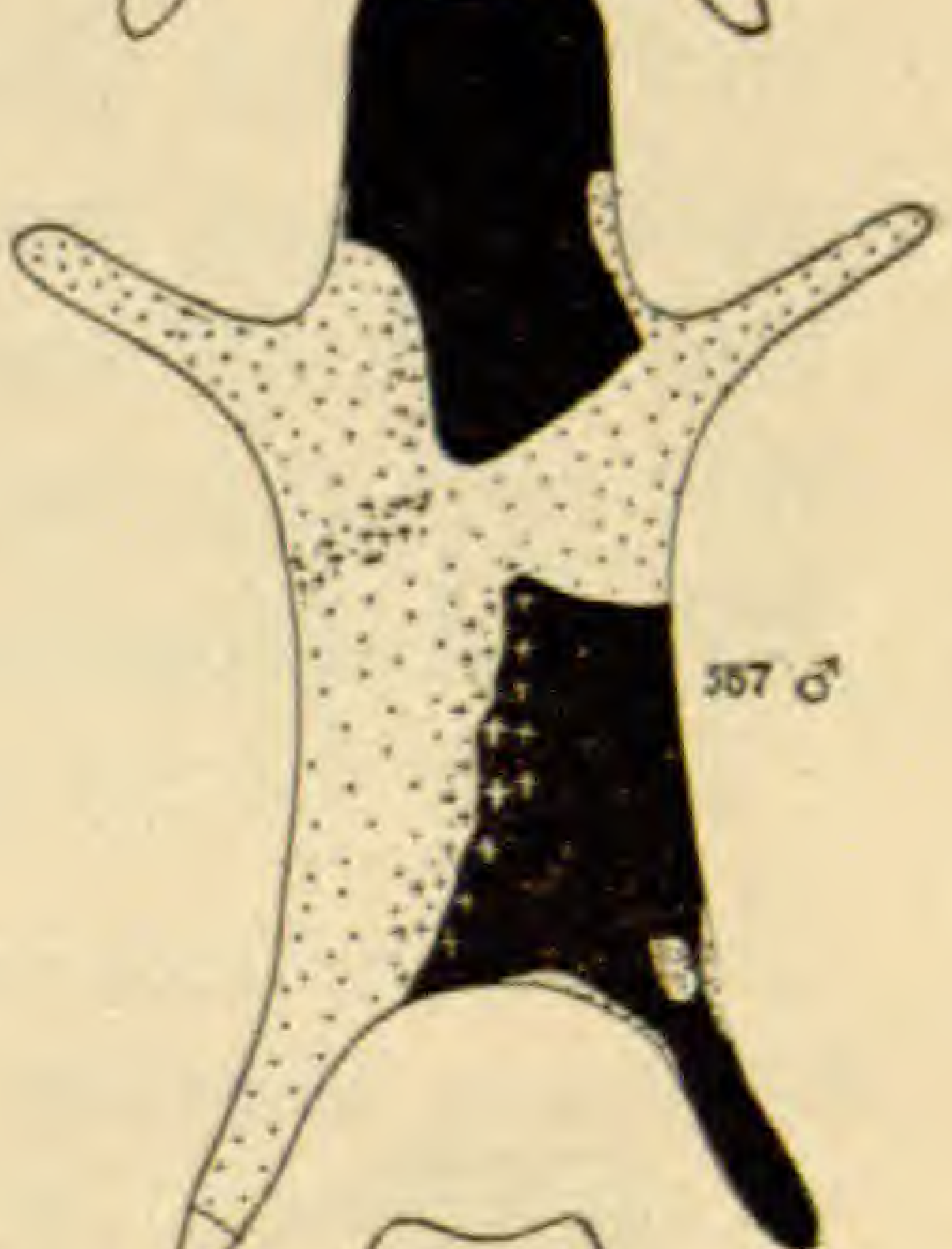
554 ♀



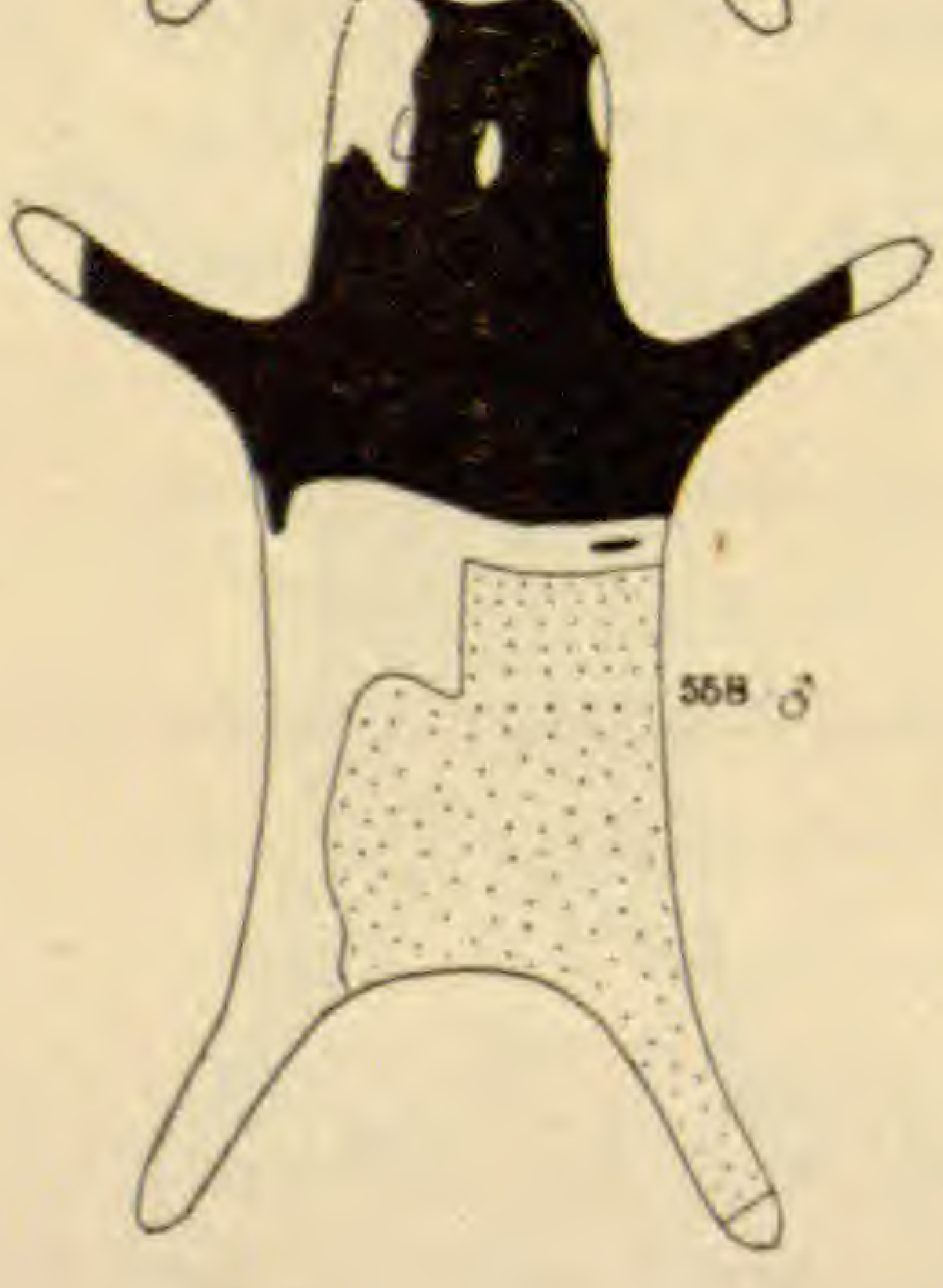
555 ♀



556 ♀



557 ♂



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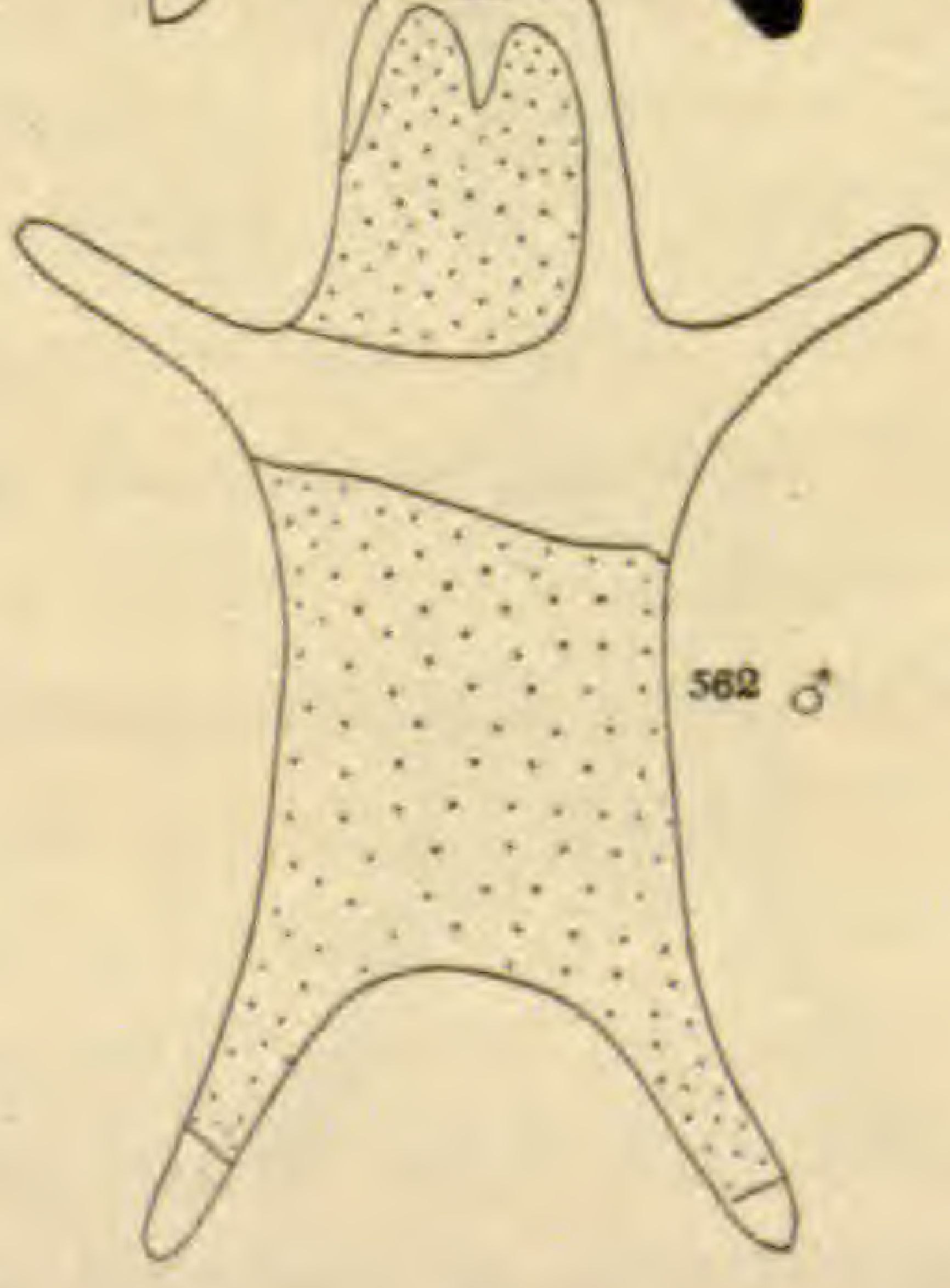

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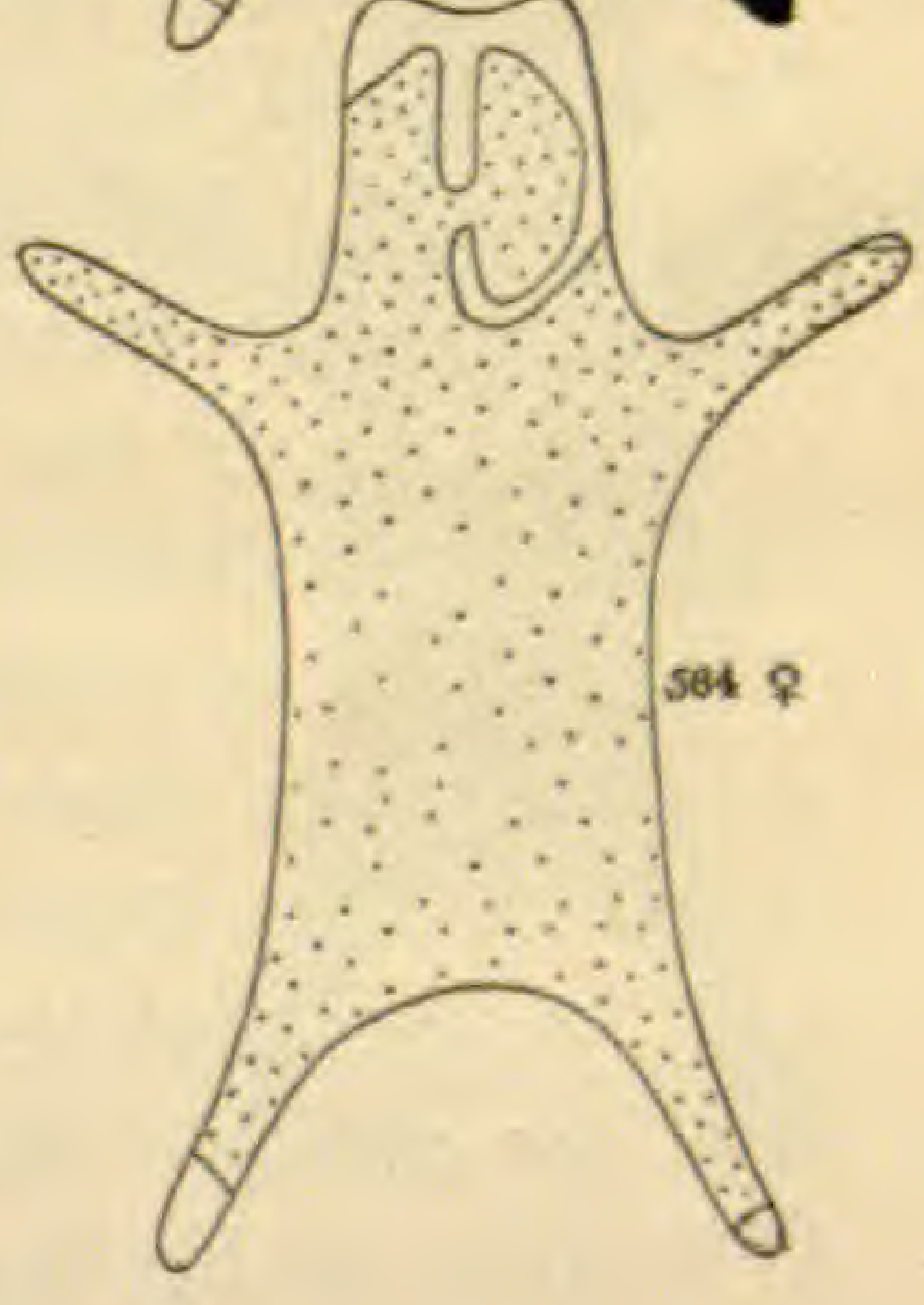

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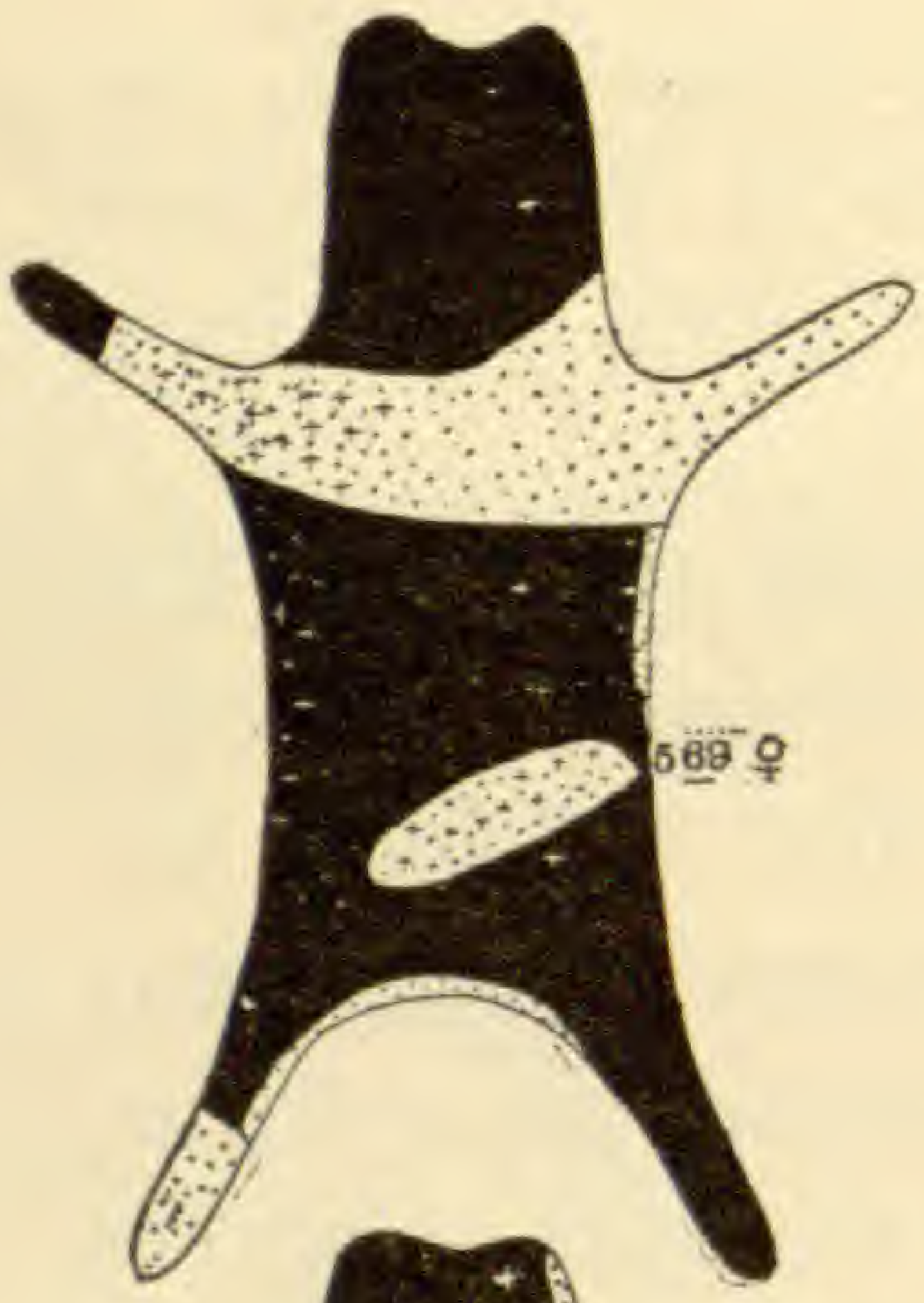
condition appears, its extent being determined by other factors.

The extension of spotting would be considered as due to successive mutations which could only be *realized* after the first stage *ss* had occurred. Such stages would be represented by sss_1s_1, sss_2s_2, sss_3s_3 or complexes of these, namely, $sss_1s_1s_3s_3$ or $ssS_1s_1S_3s_3$, etc. Selection would then consist in eliminating from such combinations different factors. The hypothesis is in a sense complex, but so are the facts. We shall consider this hypothesis later after our facts have been presented.

Castle has recently pointed out that there are cases of yellow-and-white-spotted guinea-pigs that breed true. In these he assumes that a chromogen factor (the one that makes any color possible) is irregularly distributed. Hence, wherever color is produced that color is yellow. Where no color is produced, because of the absence of the color producer, white results. Black-and-white races, if such exist (Castle does not specifically mention such races except black-and-white from tricolors of the tricolor series), would fall under a similar scheme. Yellow-and-black animals also exist with no white (Castle). In this case the color factor for *black* is assumed to be distributed irregularly.

Castle's explanation for the tricolors is as follows:

> Now the tricolor race is a yellow one spotted both with white and with black, *i. e.*, it results from irregularity in distribution through the coat of two different chemical substances, the color factor and the black factor. These two factors are known to be independent of each other in heredity. See Castle (1909). It is therefore not to be supposed that they will commonly coincide in distribution. If the black factor extends over all the colored areas, the animal will be black-and-white. If the black factor falls only on areas which lack the color factor, it will produce no visible effect, and the animal will be yellow-and-white. If, finally, the black factor falls on some of the colored areas but not on all of them, those in which it falls will be black, the others yellow, and the uncolored areas of course white. Hence a tricolor will result. But the gametic composition of these tricolors will not be different from that of the black-and-whites or red-and-whites produced by the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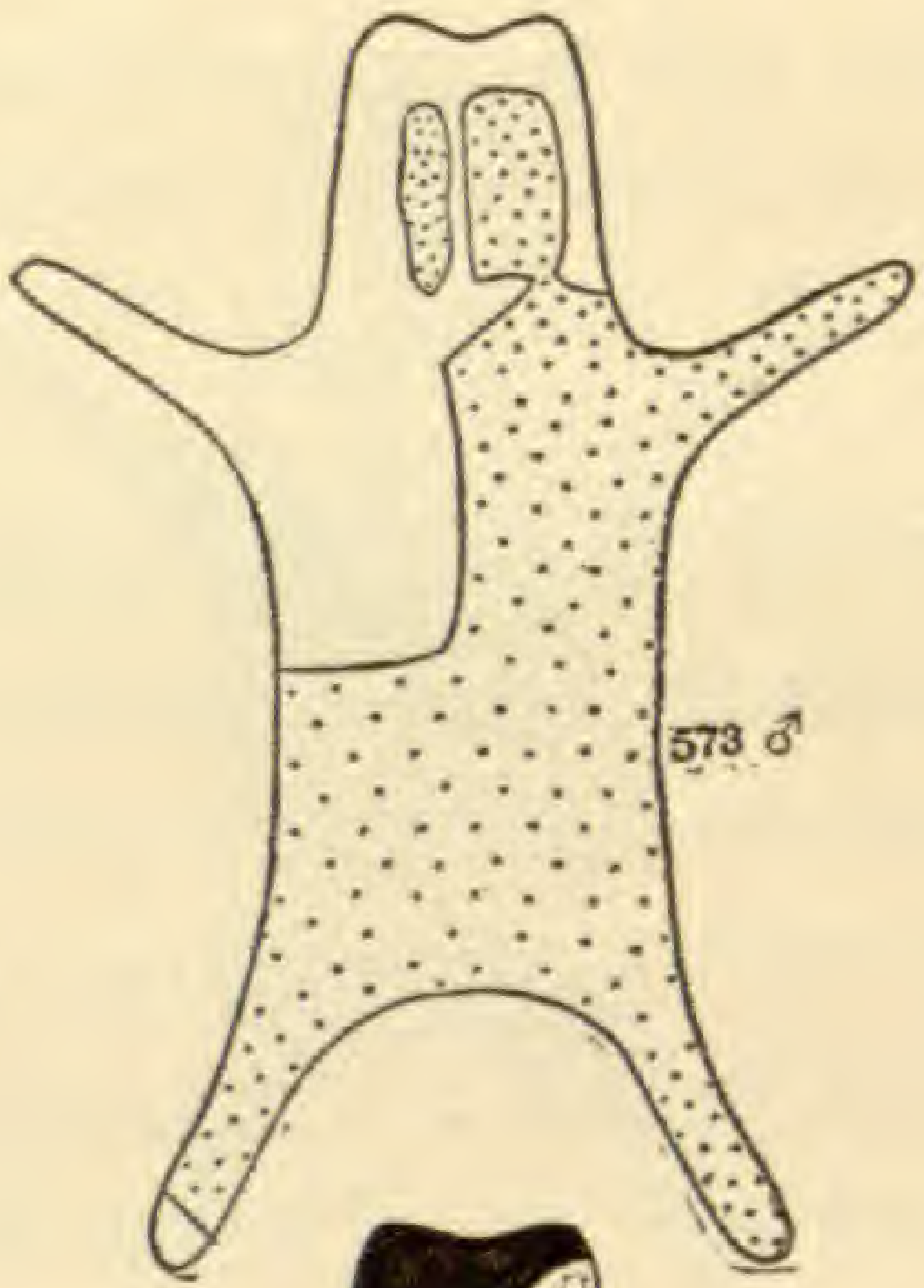
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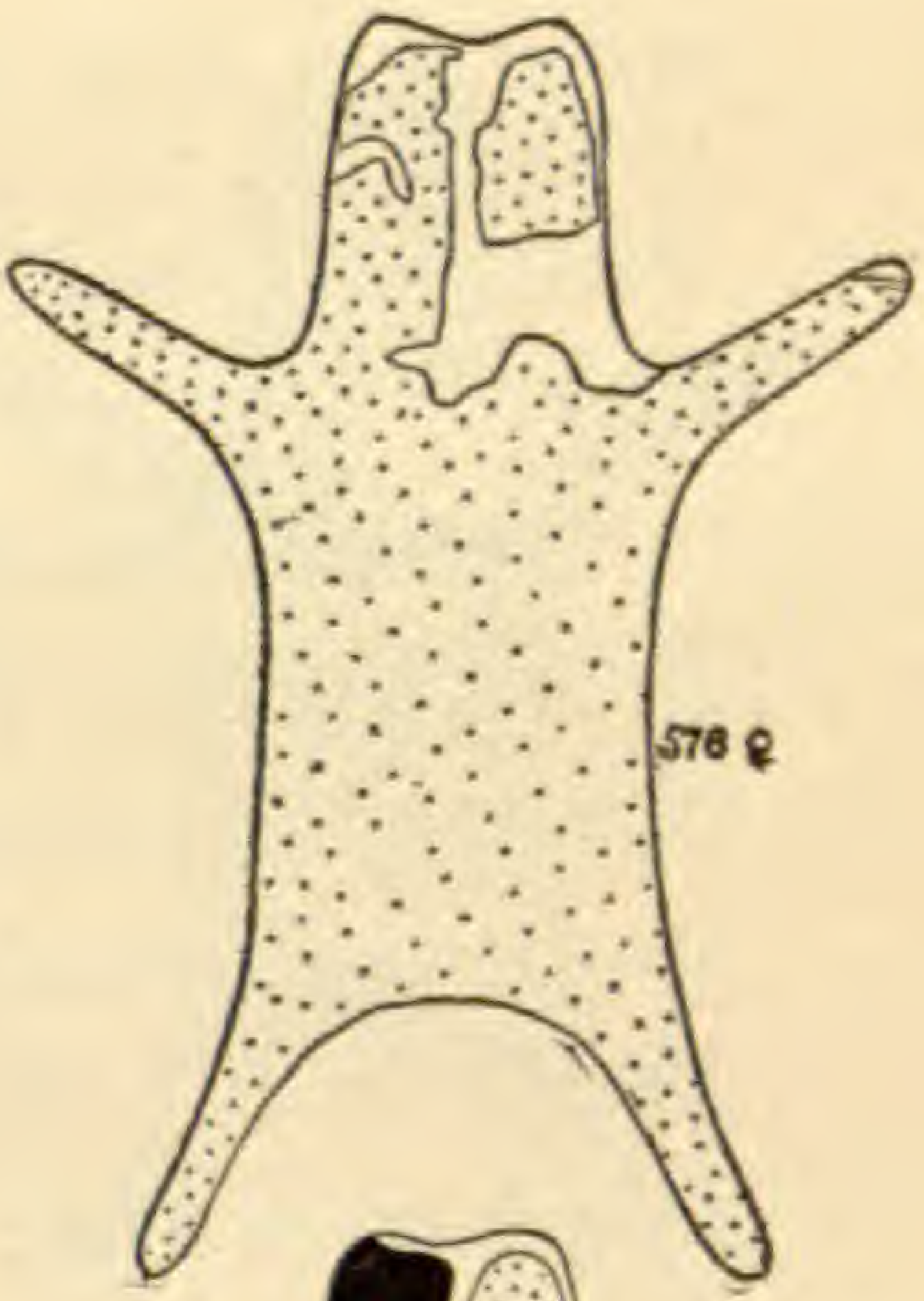
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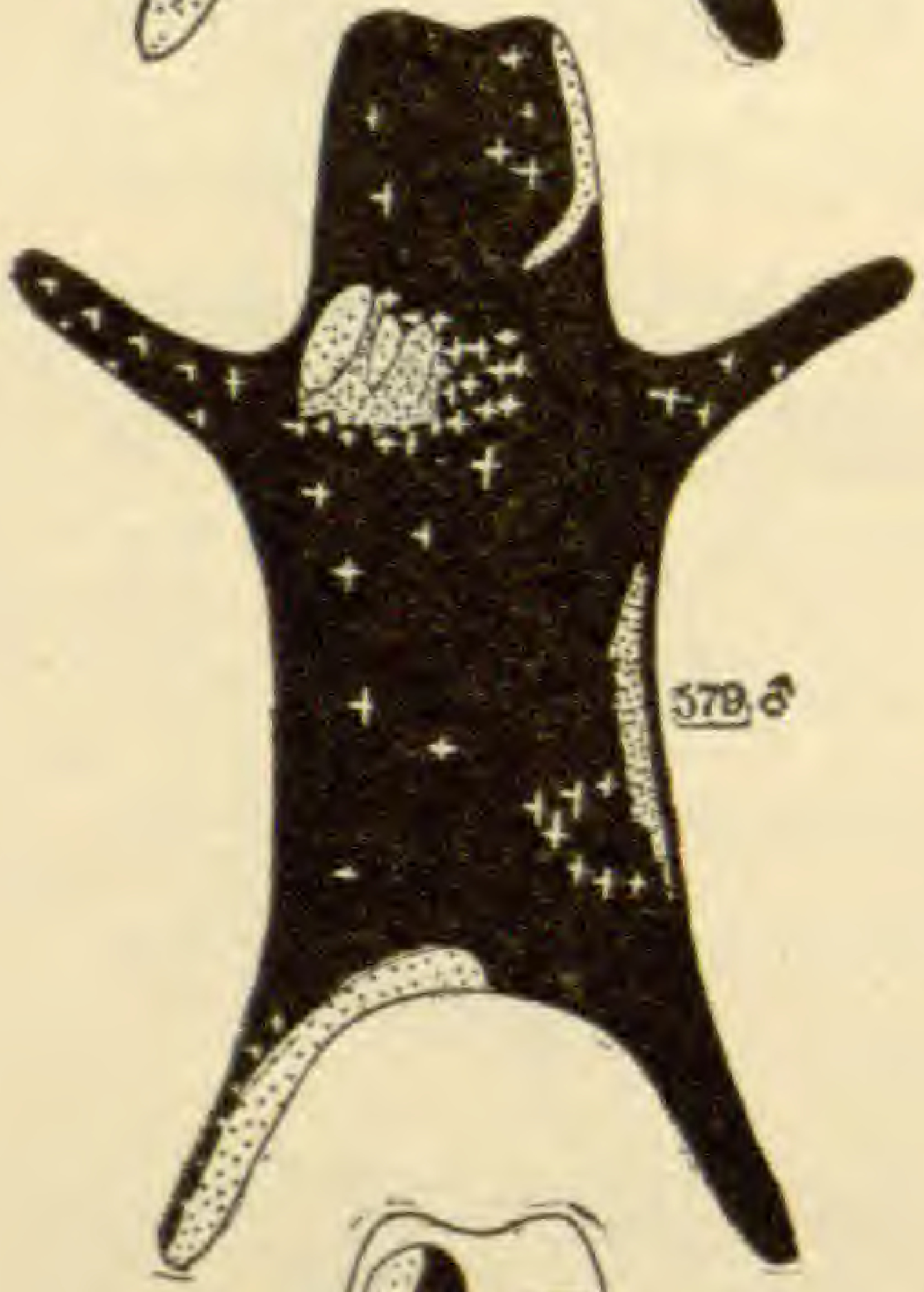
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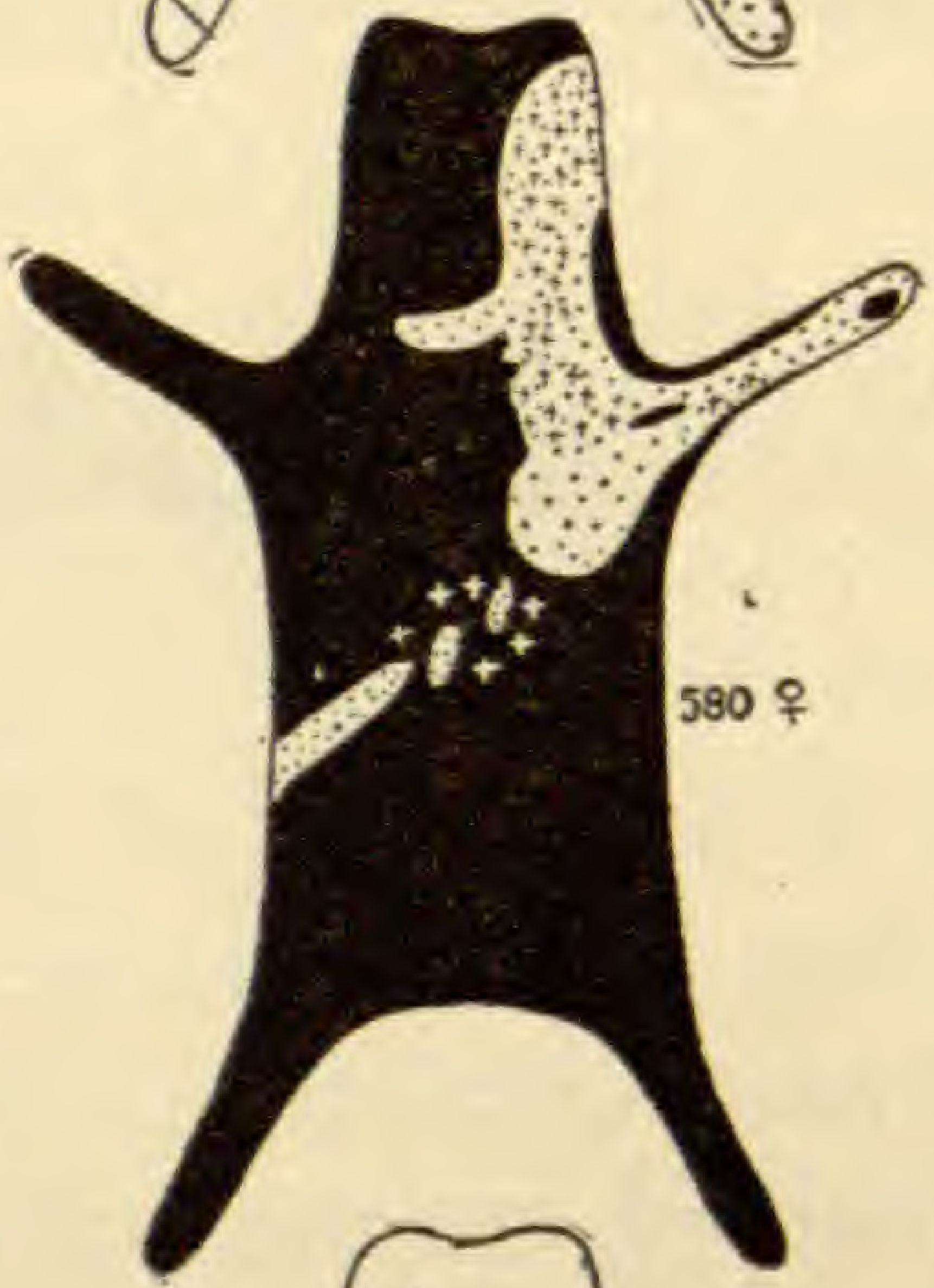
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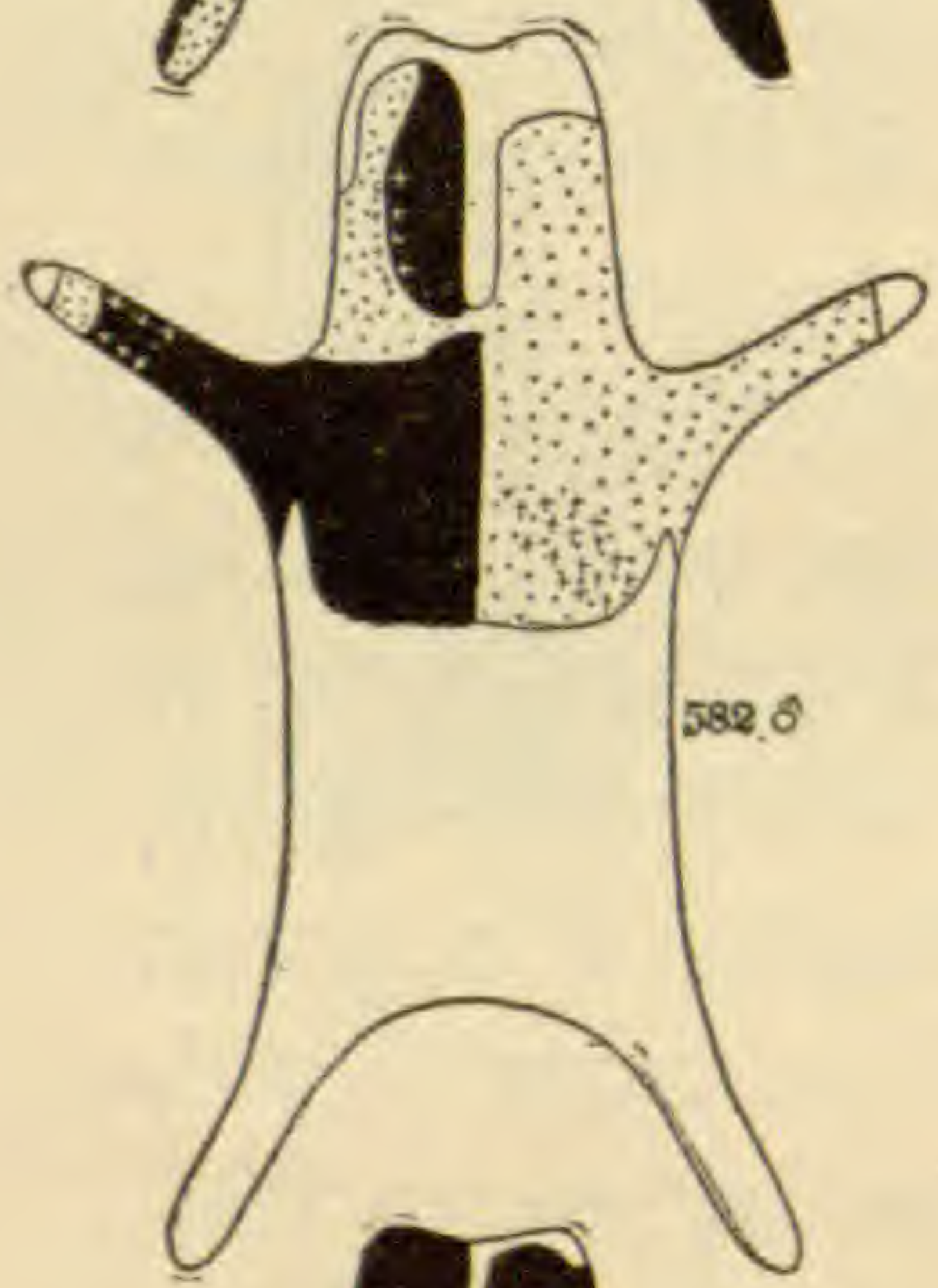
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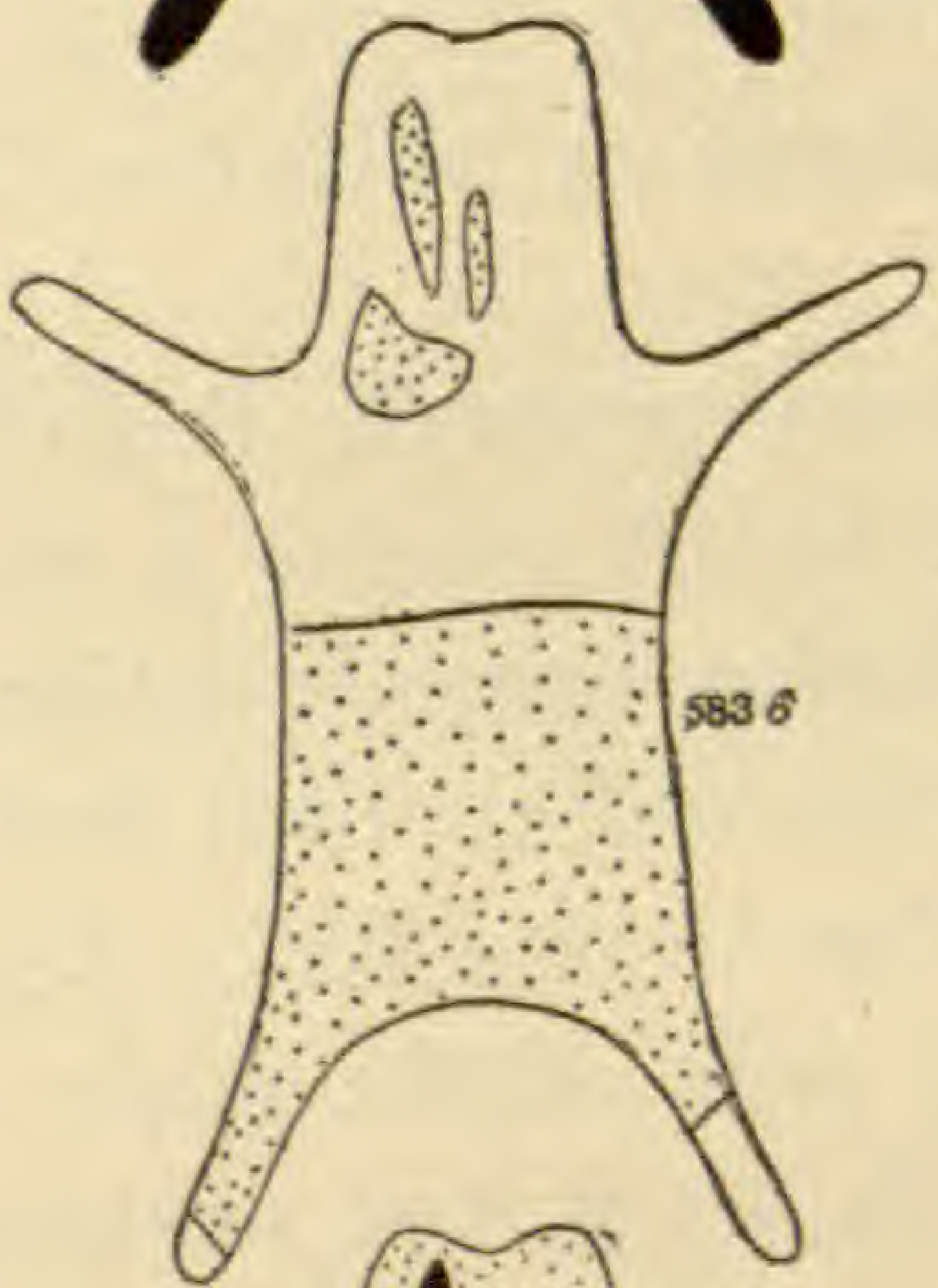
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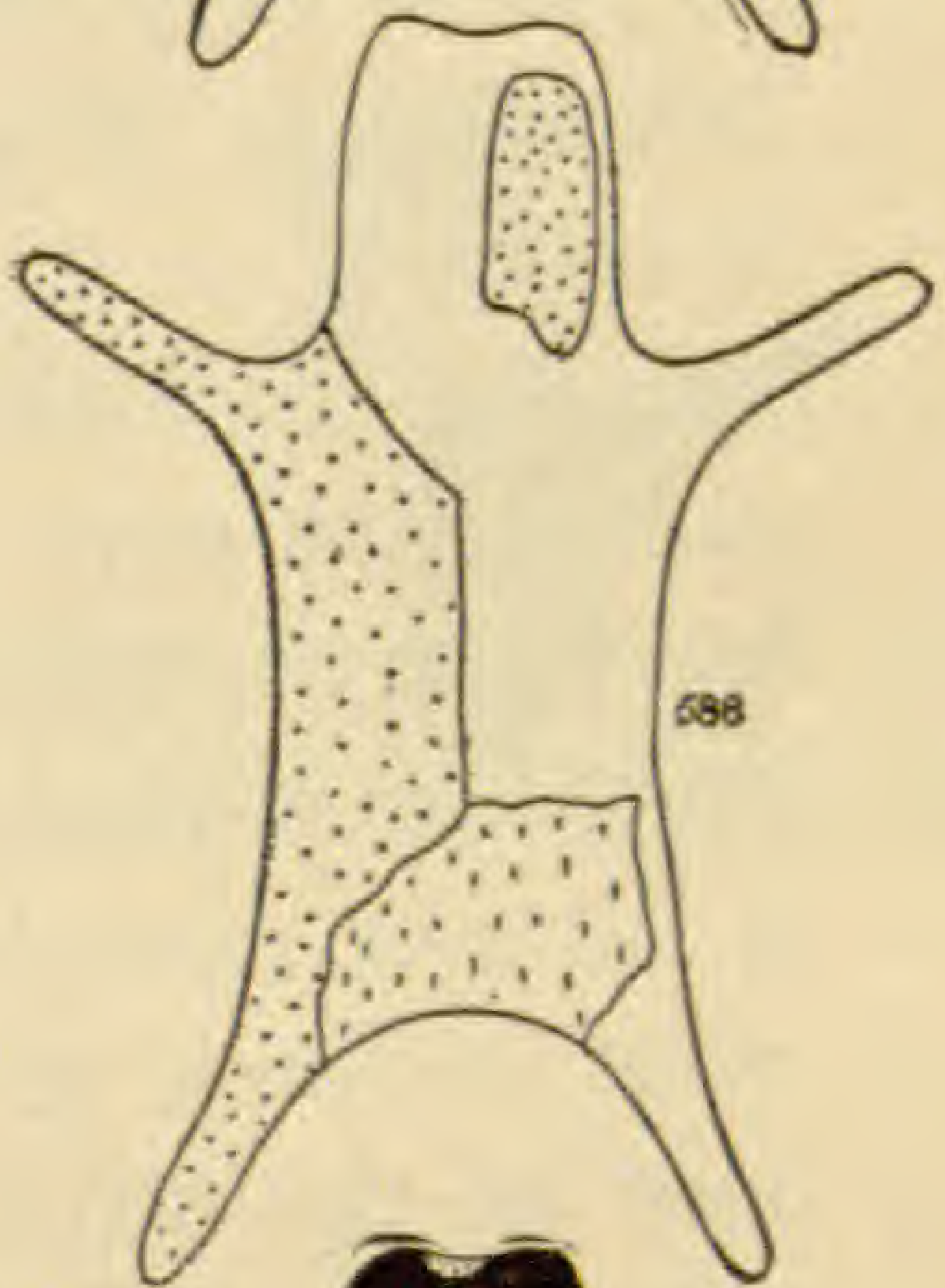
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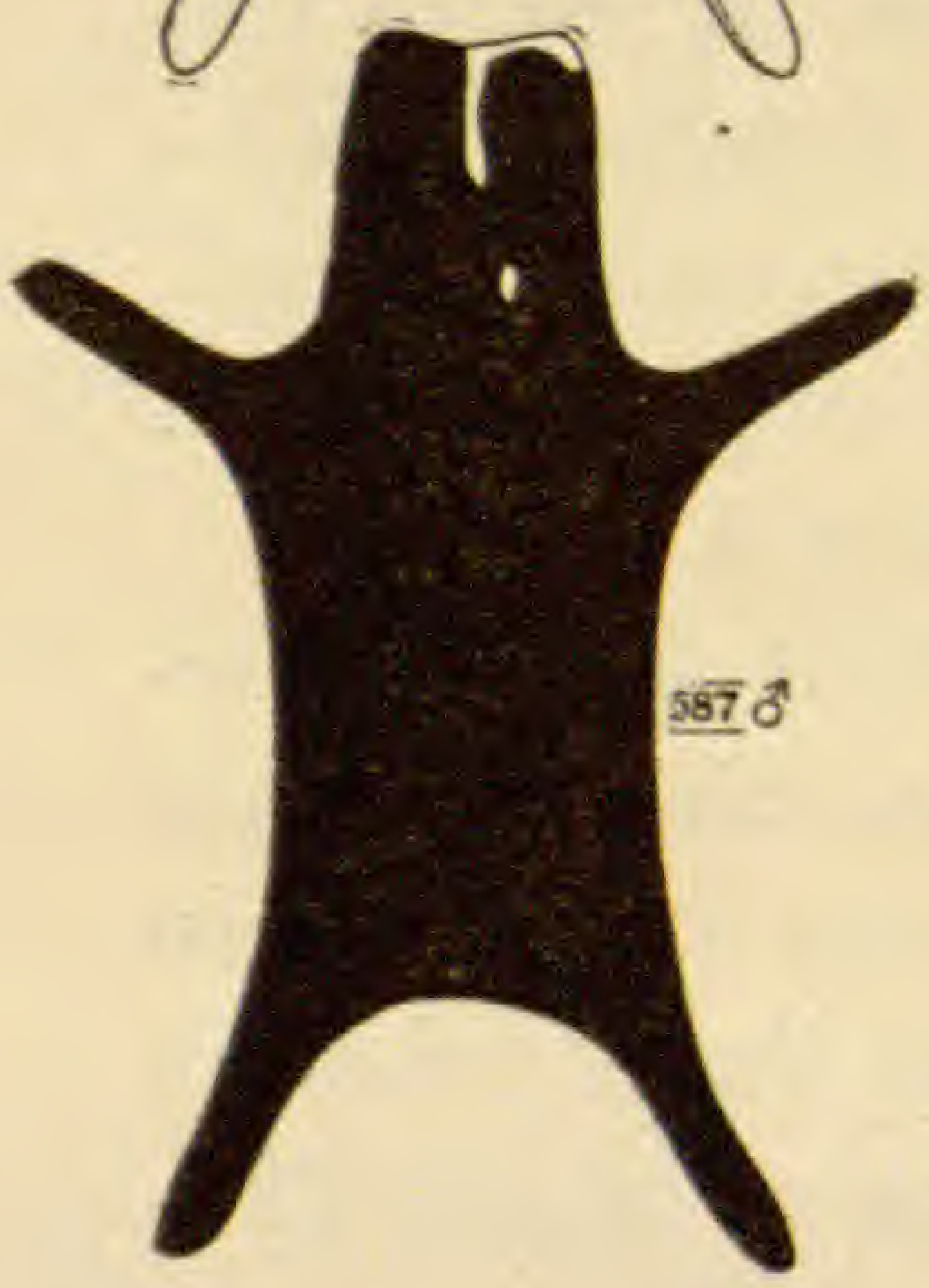
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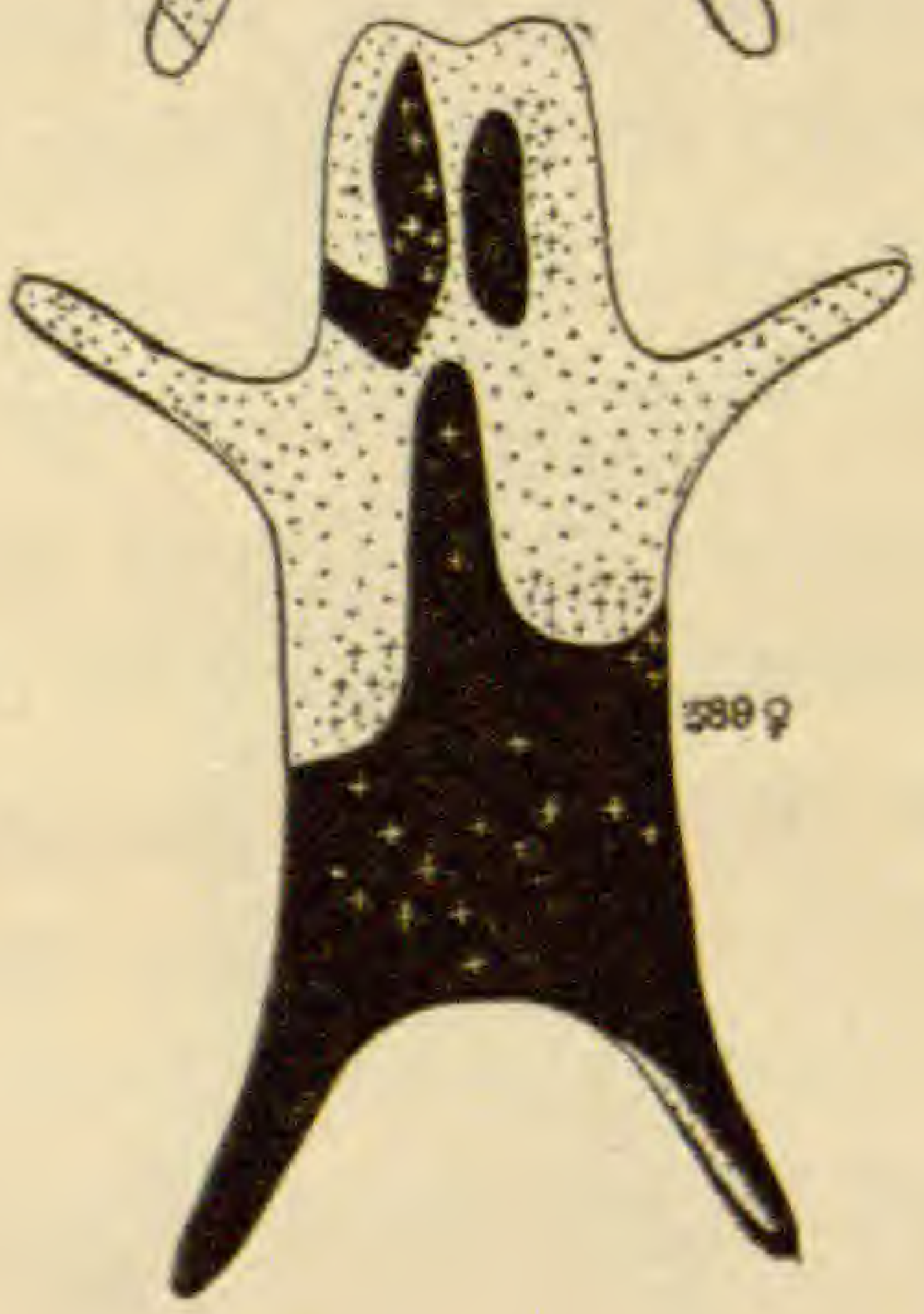
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same race, since all alike will be characterized by irregularity in distribution of the same two factors A tricolor race on this hypothesis should be unfixable, as has up to the present time been found to be true.

It will be observed that this hypothesis rests on the fact that two characters are irregularly distributed, viz., black and white, and on the assumption that yellow is always uniformly distributed. What is meant by irregularity in the distribution of a character except as a statement of a fact is not clear. The words suggest somatic distribution of *factors,* at least the factors for black and for white, that have come from the germ-cell. On the other hand, it may be that the heritage of every cell is like that of all the others; and regional differences give rise to difference in pigment development. But on the last view the irregularity in distribution of the character is not explained by referring it to regional differentiation, for the question is left as uncertain as before.

There may be involved, moreover, the question of the inheritance of a pattern or patterns, for, if the spots are localized, as Castle says in his earlier papers, or, at least, if *spot-areas* are present, the distribution of black and white may not be so simple a problem as indicated by the hypothesis under consideration. Furthermore, if spotting is due not to one or two, but to several factors, a further complication is present. And finally, if a given spot is black on one side of the body and its mate is yellow on the other side, even the assumption of many factors will have difficulty in explaining the results unless a somatic segregation of the factors is assumed. Until these questions have been cleared up the explanation of the inheritance of spotting is likely to remain obscure.

Hagedoorn has recently[2] pointed out that for the occurrence of spots in rabbits and in certain other animals (cats, goats), Castle's explanation may not apply. He concludes that the distribution of color in these tricolor animals must depend upon the cooperation of many fac-

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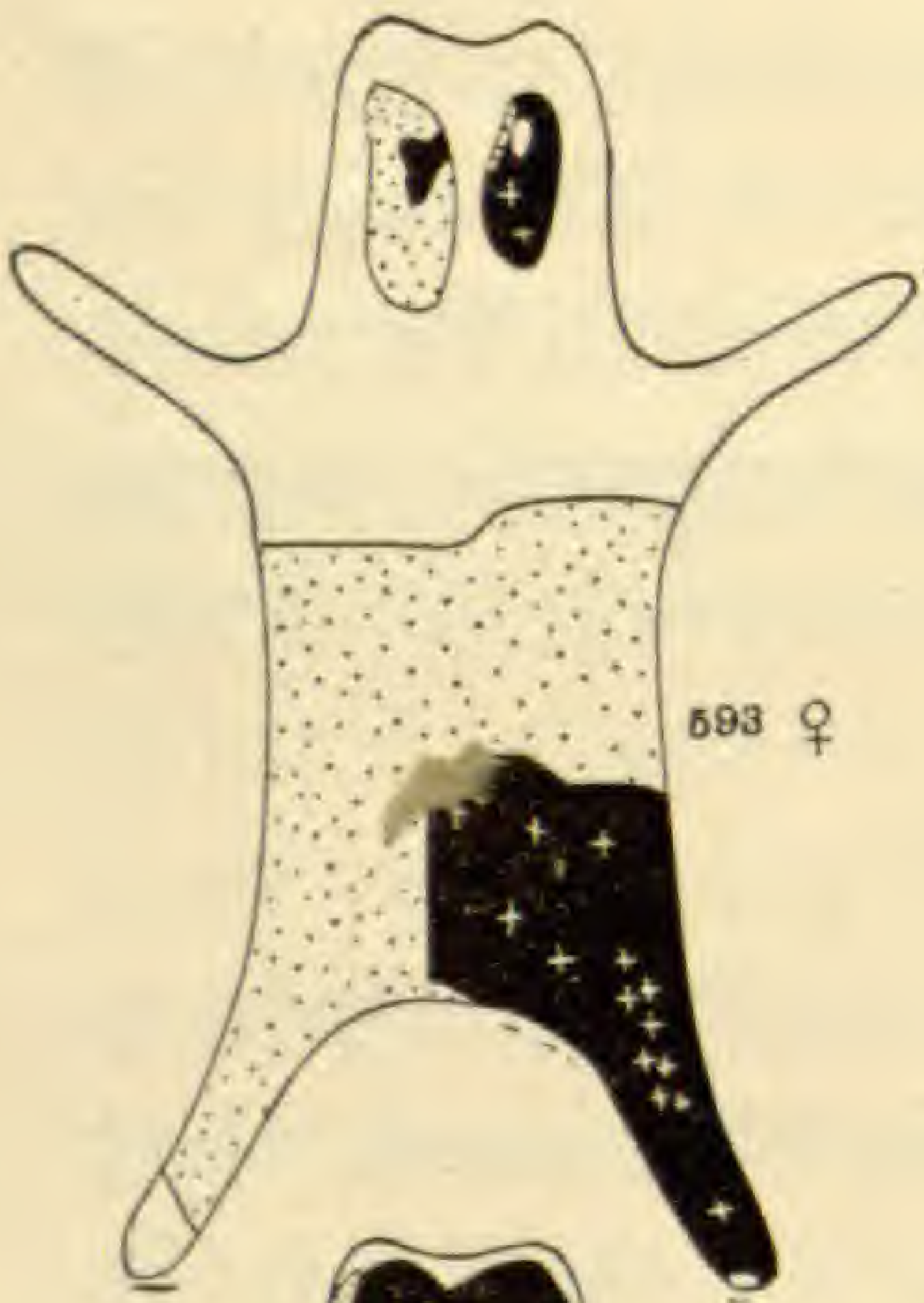
[2] AMER. NAT., November, 1912.



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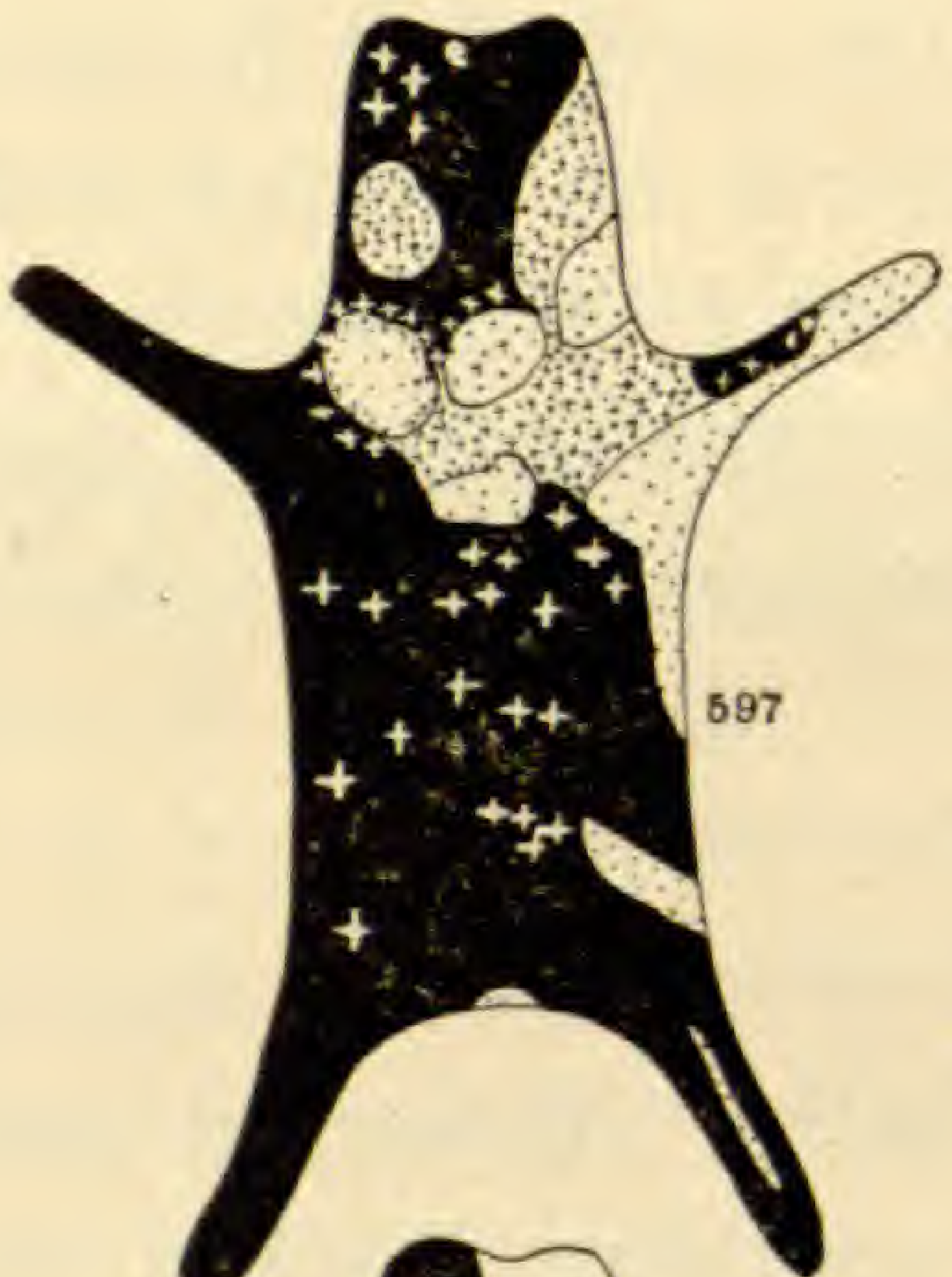

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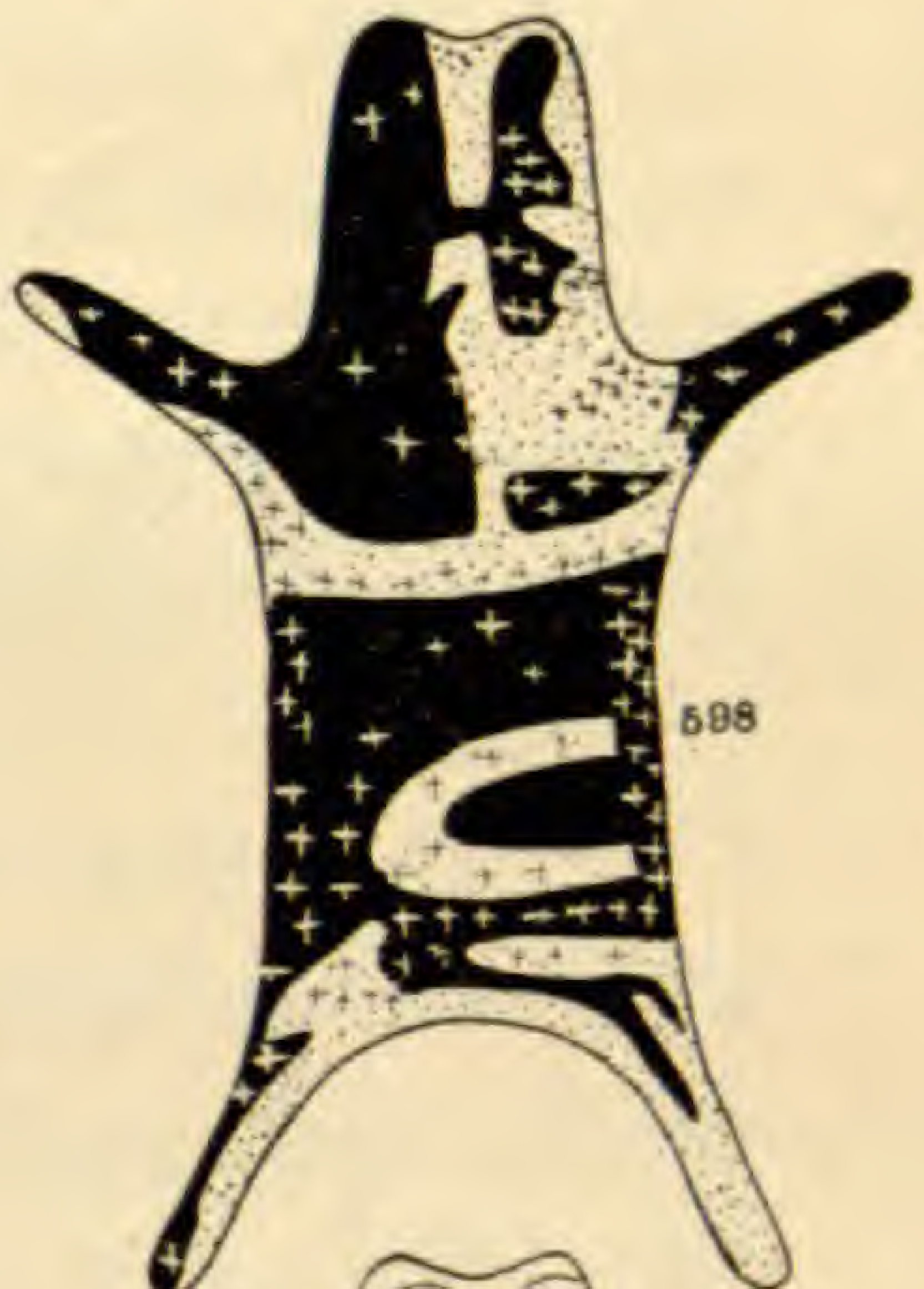

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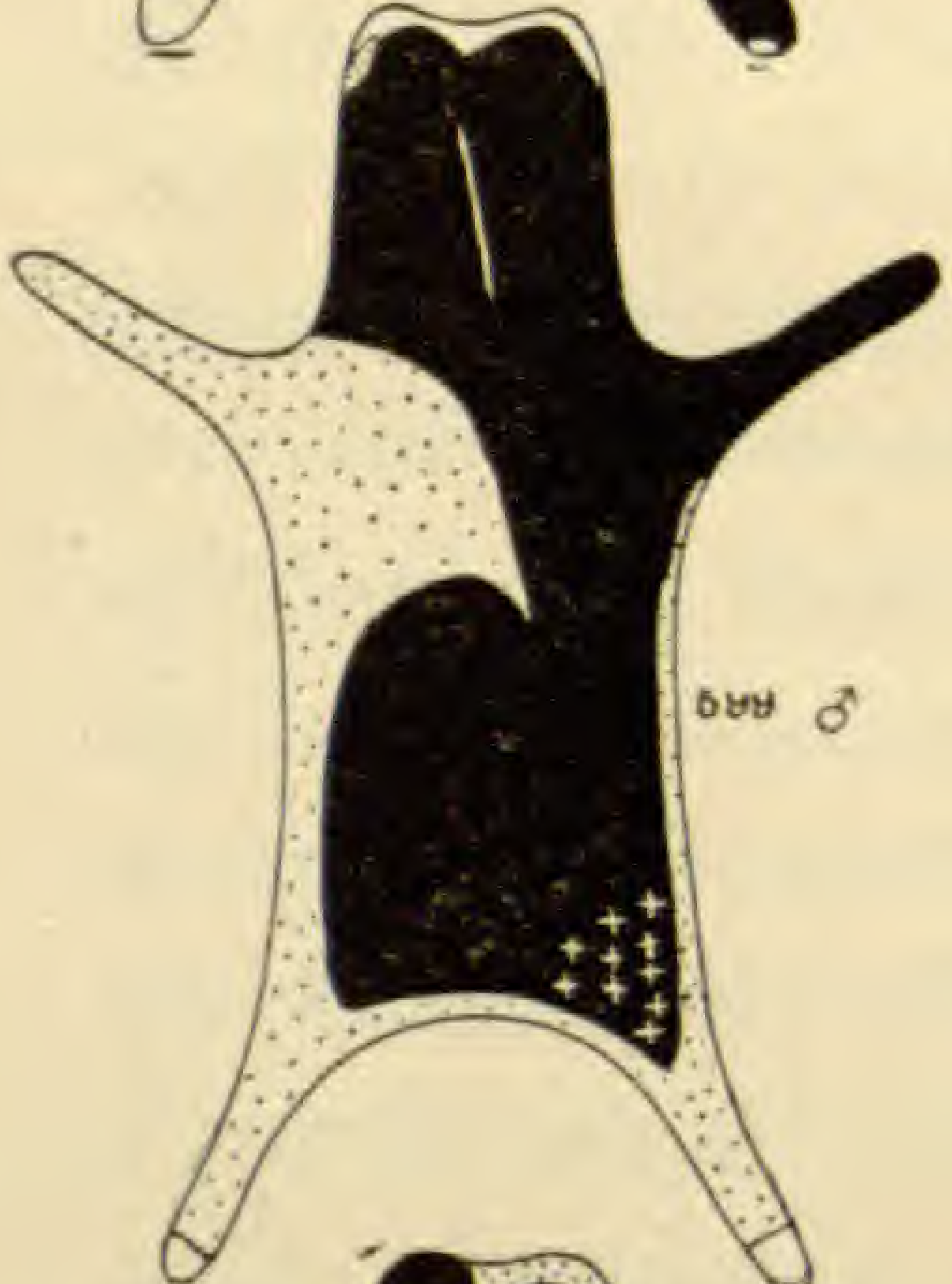

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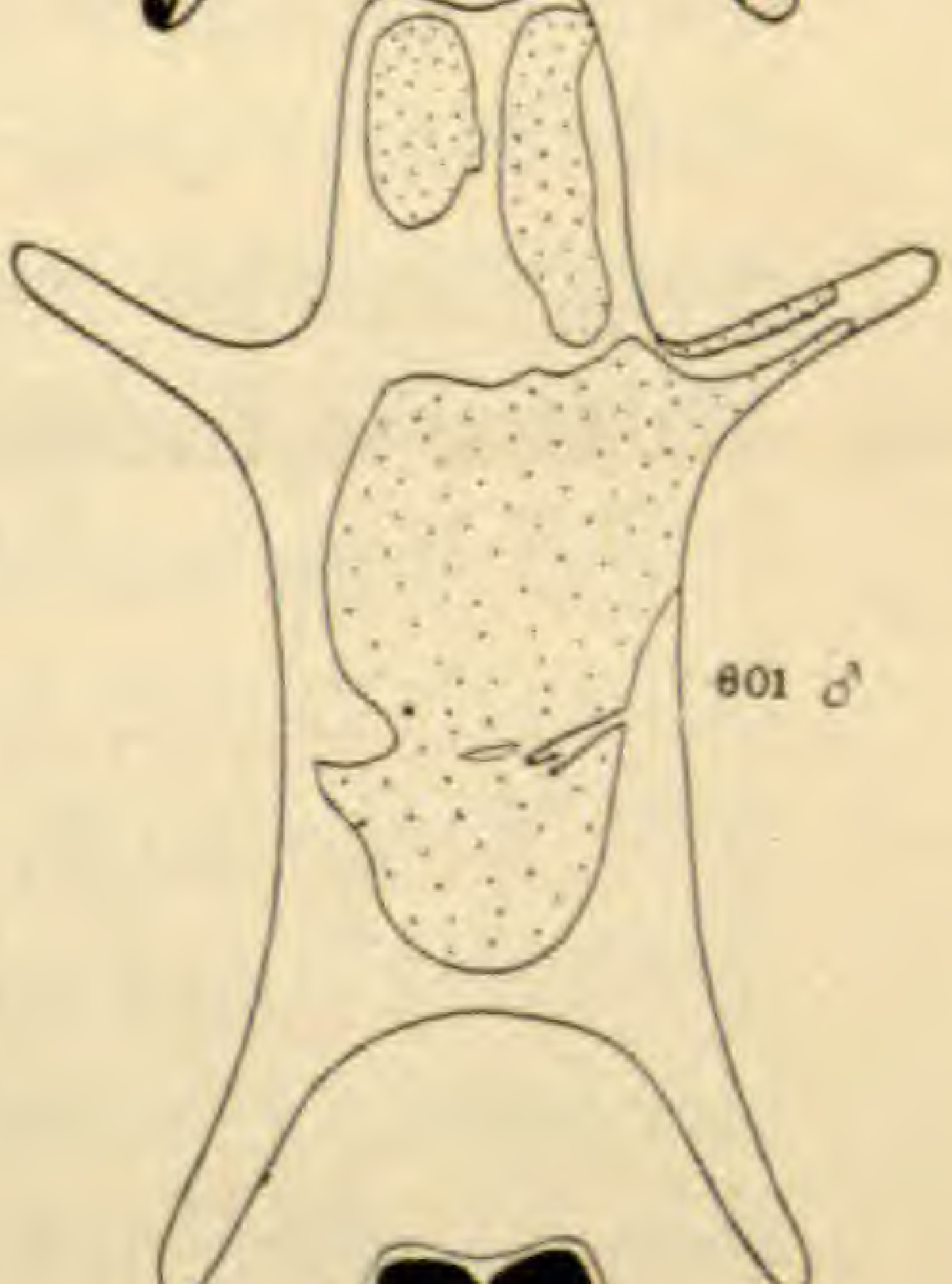

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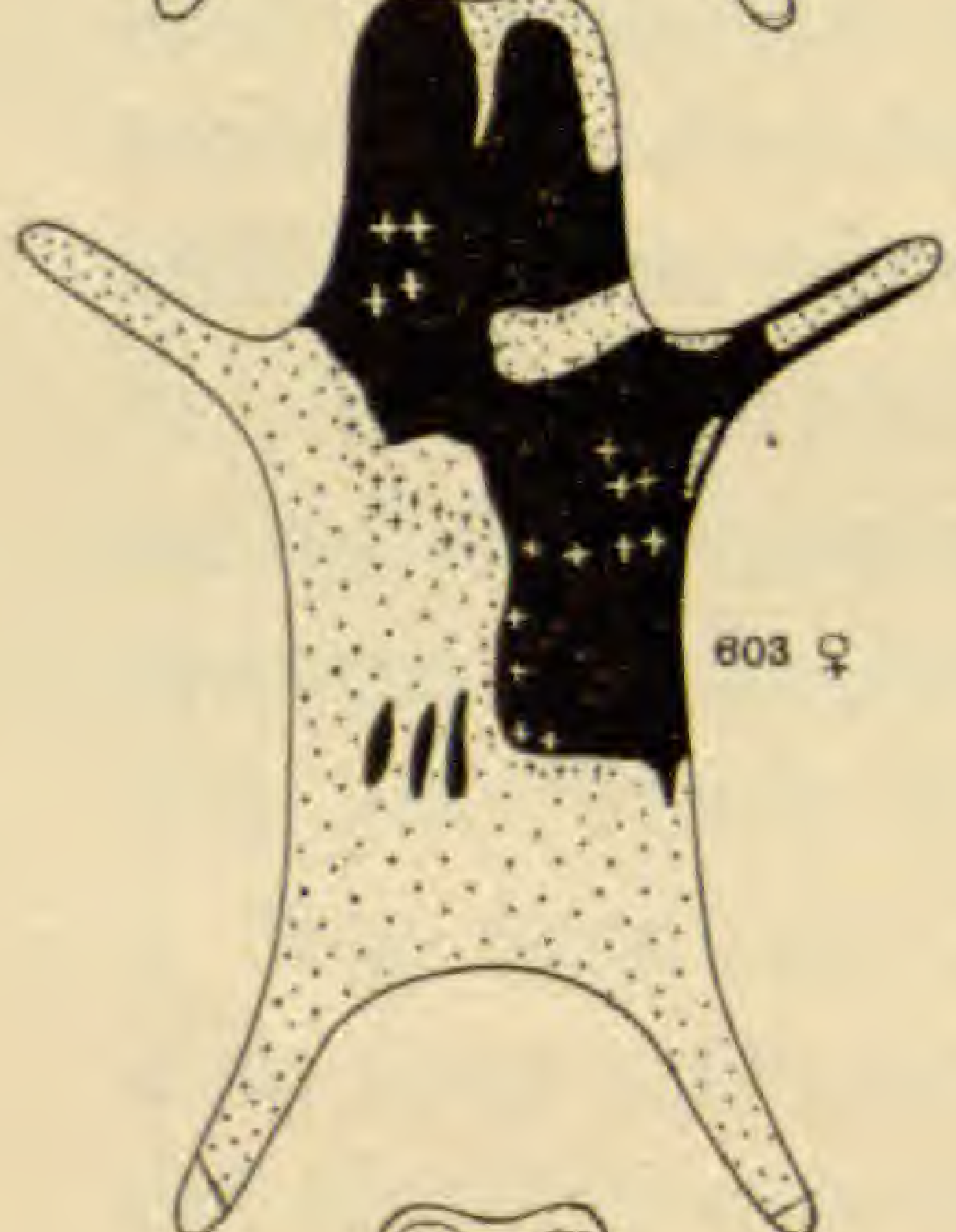

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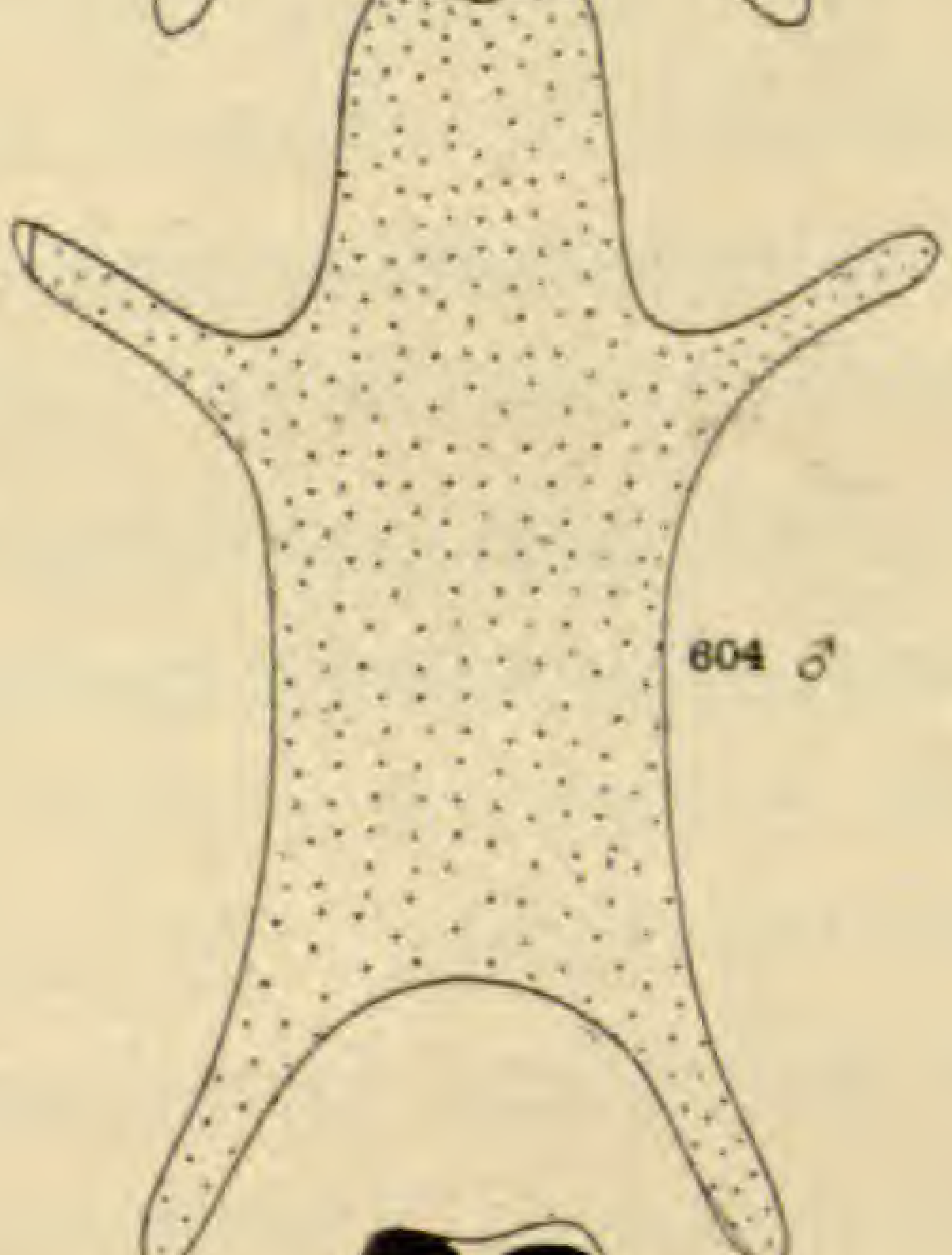

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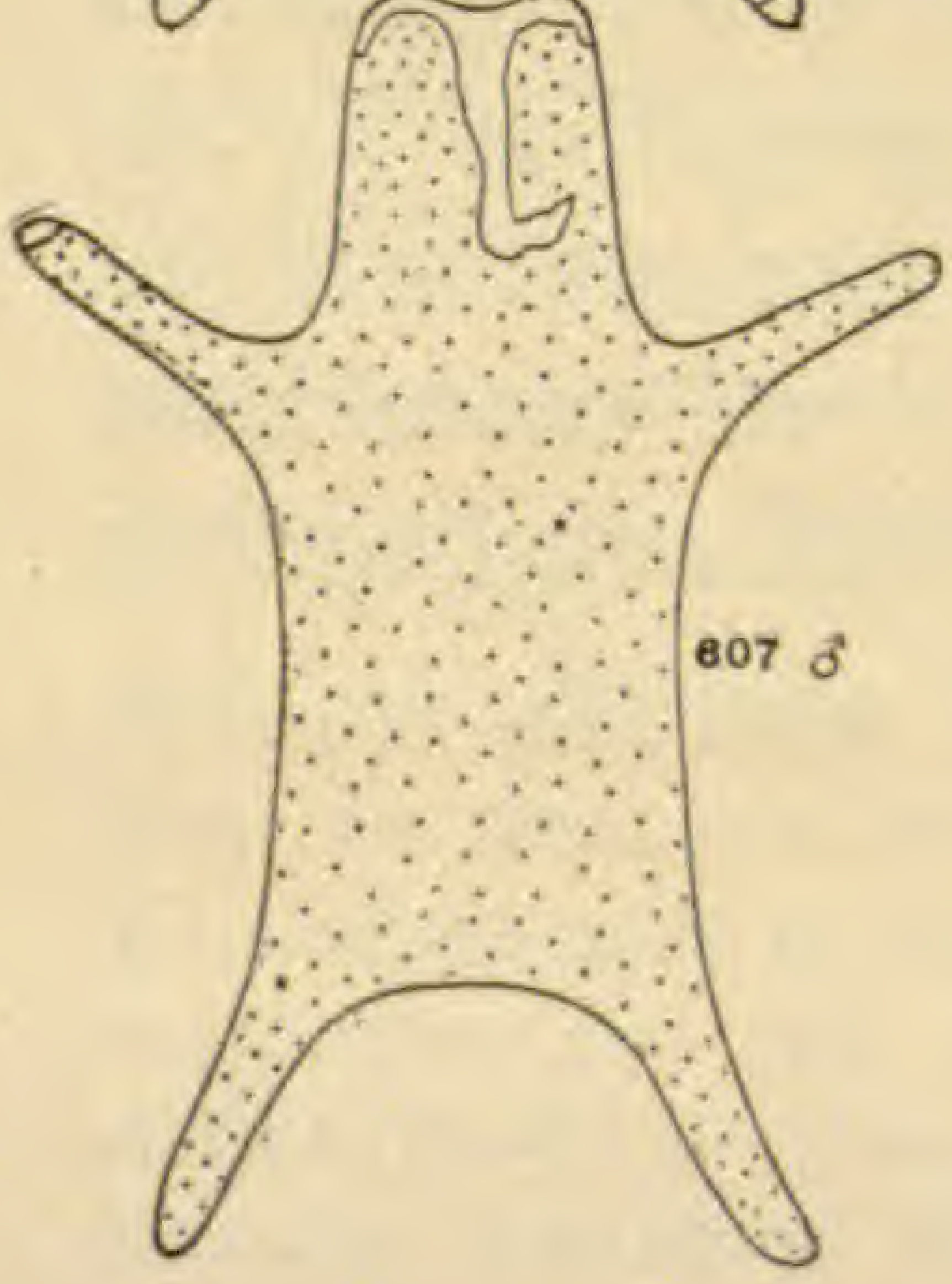

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tors. He also points out that in tricolor dogs a spot, if on the back, is black; if on the leg, yellow. If this view is correct it would seem to follow that regional differences determine the color that develops, or that somatic segregation of color factors is definite in respect to body regions.

In the case of the Norway rat, a wild gray bred to a spotted animal gives offspring that generally contain a white spot on the belly. It would seem, in this case, that the "factor" for spotting in this region of the body is dominant over the uniform coat—the other spotting factors may be recessive, and for their development depend on the *ss*-factor.[3]

So long as these questions remain on such an unsatisfactory basis we can do little more than adopt provisionally some such view as Castle's, or else describe the facts without regard to any special theory. In the following account, therefore, we shall attempt little more than a description of the results that we have obtained. Our description resolves itself, therefore, into the question of the heredity of black-and-white somatic areas. The question of whether these are overlapping areas as Castle assumes or else spot centers in which color or no color may occur, or both is left undecided. It is certain that a spot may be large or small, and, therefore, the realized pattern is variable. Possibly we may get a clearer idea of this question if we look upon the spot as a center from which color, if present, is more likely to spread, and, if we assume somatic segregation in an early stage of the embryo the extent of the spot will be a measure of the extent to which a given cell containing the color factor multiplies as compared with neighboring

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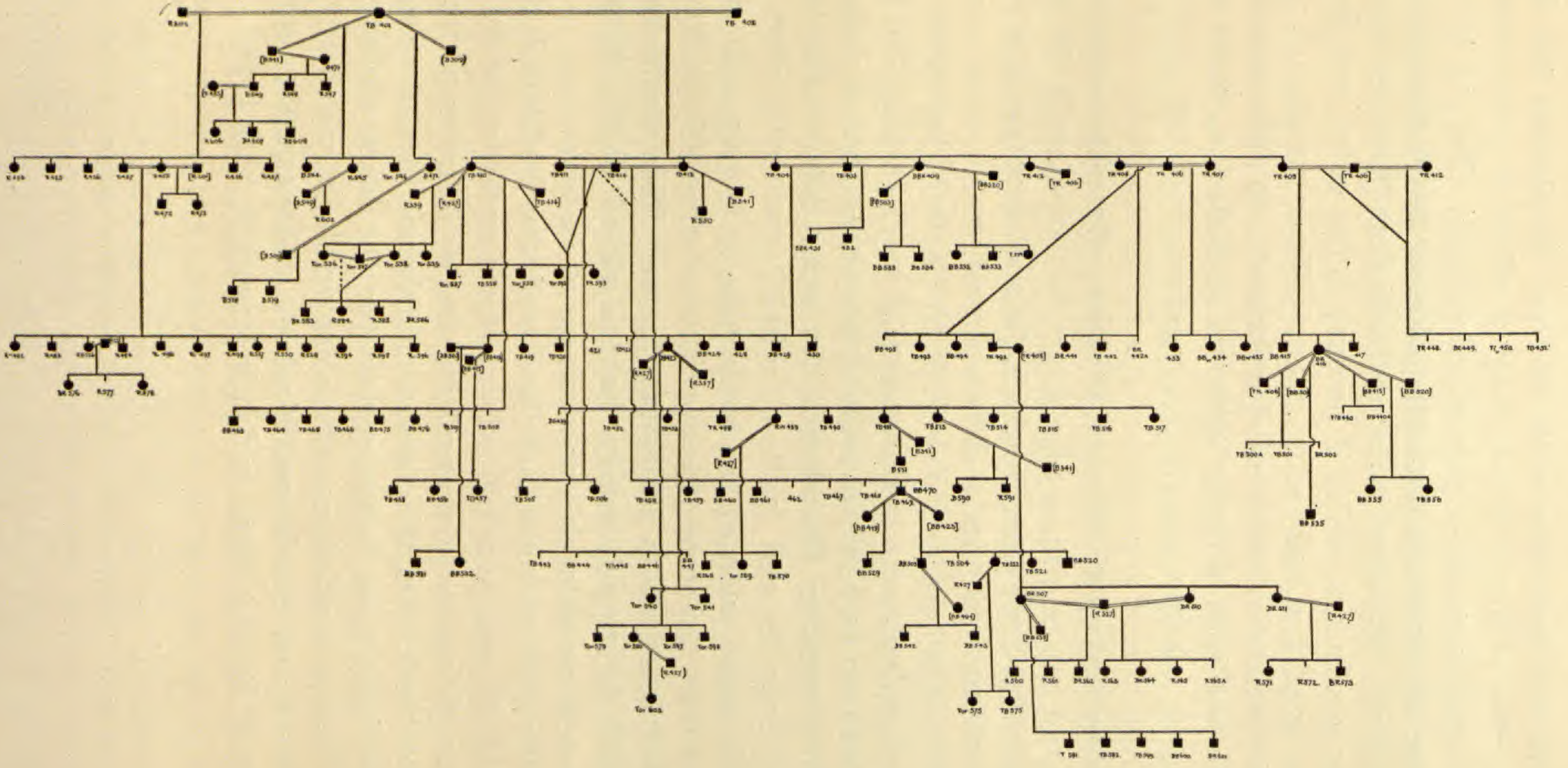
[3] We may conceive of spotting factors in two ways: Each area or center may be supposed to have a representative in the germ and each of these representatives to be entirely independent of each other in inheritance. Or there might be several factors of different sorts, such that one produces a certain pattern, another a different pattern, a third factor a third pattern and so on. The overlapping of these various patterns would still produce spotted animals.

areas that have the white factor. In pigeons the dark wing-bar of some breeds may be white in other breeds, although pigment is present, elsewhere. We can not assume, of course, a pigment producer to be absent from the germ. It seems more probable that there are special color producers, which if present in the germ, and therefore in all the body cells, give a definite reaction in that region where a white band is formed. In this case there is no *localization* factor inherent as such, *i. e.*, there is no need to assume somatic segregation, but only germinal segregation of a particular special factor that is realized in a special part. The substitution of a white area for a colored one in guinea-pigs might be looked at in the same way. But the extent to which the spot develops is a more difficult and perhaps a different problem.

The most obvious objection to Castle's hypothesis of overlapping areas is the excess of bicolors recorded both in his own and in our results, assuming that no true bicolors were in the stock. An exact lap of the black area over the red (yellow) could happen only when the black spots were of the same size or larger, and occur in exactly the same places as the red area left by the distribution of white producing factor. This would be expected to happen rarely, but, as stated above, tricolors throw a considerable percentage of bicolors.

Our matings show that the distributor for black is dominant, as seen in tricolor by uniform and tortoise by uniform giving tortoise; and tricolor by tricolor giving bicolor black. On this basis our original race of tricolors must have been heterozygous for the black distributor, and hence could throw some bicolor blacks which are real bicolors, not overlapped bicolors. This explains our excess of bicolor black which belonged to both types.



CAUSES AND DETERMINERS IN RADICALLY EXPERIMENTAL ANALYSIS

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EVEN where the experimental situation is clear, disagreement often exists as to the causes or determiners of given phenomena. For clearing the mind on such matters, as well as for guiding experimentation, the writer has found useful two rules of thought, which are here submitted. The bald statements of the rules will be followed by a commentary with illustrations.

Rule 1. Radically Experimental Thinking.—Test all questions or doubtful propositions as to causation, determination, explanation, by seeking mentally an experiment which, if carried out, would decide the matter. If no such experiment is conceivable, the question is one with which science can not deal.

Or: Reduce all questions to an experimental situation.

Rule 2. Causation of Differences.—In seeking causes or determiners, compare two cases and discover to what is due the difference between them. A cause or determiner is that which brings about the difference between two specifiable cases.

1. RADICALLY EXPERIMENTAL THINKING

What sort of knowledge is sought in the questions: How is this phenomenon caused or determined? How can we understand or account for this?

One of the things we desire to know is this: What conditions can be found which, if supplied, will produce the thing we are trying to understand; if changed or altered will change or do away with it? Finding conditions is called observation; supplying, altering or removing them is called experiment; this question therefore asks for conditions discoverable by observation and experiment. The search for and formulation of such conditions makes up a large part of the work of science; does the search for other sorts of conditions form any part of its work?

Men do indeed infer certain things confessedly not discoverable by observation or experiment, but these evidently deserve, and commonly receive, a classification by themselves, as something else than science; otherwise science itself would require division into experiential and non-experiential, the former including what is commonly practised as science. Our rule is the test for this classification; a question that could not be answered by any conceivable experiment (or series of experiments) does not belong to (experiential) science.

But what does "conceivable experiment" include and exclude? An experiment is a change in one or more of a given set of conditions; ideally carried out it involves the presence of two similar systems, known to act in the same way; on one of the systems a certain condition is then altered, and the difference this brings about is observed. In cases where this ideal can not be fulfilled, it forms the standard for mental reference with relation to the experiment as actually tried. The possibility of experimenting comes from the observed fact that conditions which sometimes occur or act together need not always do so. Now, a proposition to separate such conditions as are in the nature of things inseparable would not be a conceivable experiment. Is such a proposition involved in the question whether psychic processes affect physical ones?

But often a change in some one of a given or specified set of conditions is conceivable where it is not practicable. This may be for technical reasons; we have not obtained control of the conditions. Or the system under consideration may belong to past time. But in both these cases, when we assert that a specified condition is the cause of a certain result, we mean that if this condition could be or had been altered, as is done in experimentation, the result would have been different.

It is this mental reference to an experimental situation that is the essential point for clearing one's thought. Two diverse cases that require this clearing are of frequent occurrence. (1) A question expressed in general terms is so conceived by one person as to require for its answer a certain experiment, while another person understands it in such a way that it requires another experiment; thence arises argumentation at cross purposes. Clear statement of the problem as an experimental situation reveals at once that two diverse questions are under discussion, and gives either immediate agreement, or a method of solving the difficulty by experimentation.

(2) Questions or propositions as to causality or explanation are frequently so framed that they exclude an answer by any conceivable experiment in changing conditions. The attempt to state them as an experimental situation at once reveals that they do not belong to (experiential) science. Questions expressed in general terms are frequently so understood that no experiment or series of experiments could answer them, though the same questions may be so interpreted that they are answerable by experiment. When one side of a discussion understands the question in one of these ways, the other side in the other way, the resulting confusion is dispelled by the attempt to formulate the question as an experimental situation. Our second practical rule aids powerfully in clearing up such matters; it will therefore be taken up before passing to illustrations.

2. Causation as the Production of the Difference between Two Specified Cases

Nothing in science appears so productive of confusion and disagreement as attempts to state causes or determiners of things. Clearing of thought results if one adopts, at least as a preliminary measure, the rule to search for the causes or determiners of the *difference between two specified cases.*

The production of an event or a result requires, as a rule (at least in biology), the previous occurrence of a great number of conditions, alteration of any of which would change the result. Consider, for example, what an infinity of conditions must be fulfilled for the production of the brown color of a human skin or of a human eye; or for the swimming of an organism toward a window. Hence many minds revolt against the assertation that any particular thing x (a chromosome; a nucleus; a single physical agent, such as light) is the determiner or the cause for this result:—for it takes much more than the "determiner" to produce it. But other minds, apparently equally sane, persist in speaking of particular determiners or causes for exactly such cases. The difference is due neither to stupidity on one part or the other, nor to disagreement as to the experimental situation, but to a different conception of what is implied experimentally by "determiner" or "cause." One party thinks, when speaking of determination, of *everything necessary in order that the given result shall be produced;* so that "a determiner" would to him mean something supplying all these required conditions. The other means by a determiner *that which brings about the difference between a case that gives this particular result, and another which does not.* The first view insists that many things are necessary in order to produce the result; the second insists that if the "determiner" x is altered, the result is altered or done away with. Both are correct.

If one is seeking to understand, rather than to criticize or confute, the solution of the apparent disagreement lies in clearly distinguishing these two things, and in noting the meaning which underlies the proposition examined. The difference between a person with brown eyes and a similar person with eyes not brown may be decided or determined by something which by no means supplies all the conditions necessary for the production of the brown color. It takes an entire state to go to war, but a very small difference in the conditions may determine whether war or peace shall prevail. It might indeed be clearer if for the word *determiner* in such a meaning, some such name as "decider" were used, but it is important not to confuse a criticism of linguistic fitness with a denial of experimental facts. All the "determiners" spoken of in the formulations of Mendelian inheritance appear clearly to be such in the sense only of "deciders."

Conclusions deducible only from discovery of all the conditions necessary to produce a certain result must, of course, not be drawn from experiments showing a determiner only in the sense of "decider" between two possibilities; this appears not infrequent. Such illegitimate conclusions are perhaps most usually drawn when persons understanding determination in the first sense examine the statements of those that use the word in the second sense; this is a source of polemics.

Since to produce almost any result an indefinitely great number of preceding conditions, of diverse sorts, must have been fulfilled, and since neither thought nor practical investigation can handle all these at once, it becomes necessary to so analyze our problems that at a particular juncture only one cause or determiner (and that a definite one) need be sought. The key for this is the following principle:

A single sufficient determining factor can be found only for the difference between two cases.

With relation to this, several points must be grasped.

1. Evidently two cases may be so chosen that the difference between them is not due to a single determining cause. But by proper analysis problems can be brought (at least usually) to a situation where but a single determining cause *is* required; this is done by comparing cases that differ only in certain defined features; and in bringing the two cases closer and closer together, till finally the difference between them is due to but a single experimental cause.

2. For the difference between two cases that are di-

verse even in several respects, a relatively simple and unequivocal complex of causes can, as a rule, be discovered, so that the problem for investigation becomes clearly limited. But to search for all the causes of anything taken by itself is (in biology at least) a hopelessly indefinite and unlimited task.

3. Search for a single definite and unequivocal cause or determiner of a given result or characteristic has meaning only when there is at least implicitly a comparison with something else, for nothing is in itself completely and exclusively determined by any single preceding condition. What cause or determiner will be found depends upon what comparison is made. When the comparison is not specified, it may be made with diverse things by different minds; thence arise apparent disagreements. The cause or determiner of brownness of skin in man is some peculiarity of the germ cell, when we compare a given brown individual with a white one that has lived under the same conditions; it is exposure to sun when we compare a brown individual that has lived in the open with his in-door brother; if some other comparison is made, the cause is still different. It is really the difference between the two cases that we account for, and *both members of the comparison must be considered before the cause can be given.*

4. When seeking the cause of a given result, it may be unnecessary to state what we are comparing it with, because that is evident. But much obscurity and disagreement would be avoided if that were always made clear; the investigator himself should at least have thought through the comparison carefully.

5. While it is helpful if in experimentation the two cases compared can both be concretely present, for clearness of thought this is not indispensable. One of them may be supplied mentally.

6. By successively comparing our given case with others, taking first those which differ from it but little, and passing then to cases which differ from it in other re-

spects, and in a greater number of ways, the causal analysis may be carried to any extent desired. In this way is reached, so far as it can be reached, that complete statement of all the things on which a given process or result depends, with its accompanying ''mental model'' of the process,—that is commonly set forth as the aim of scientific investigation. At the same time, by classifying all the various sorts of preceding differences (''causes'') and the corresponding succeeding differences (''effects''), we obtain general rules or laws.

7. But the statements or mental models of given processes referred to above can never be really complete in the sense of specifying everything that must have occurred in order that the given result should appear. For all differences between cases we find preceding differences, and so backward indefinitely. If this infinite regress appears unsatisfactory, it is the constitution of nature that is at fault. But any given investigation seeks, for definite purposes, to trace the determining differences back only to a certain stage. The investigator commonly finds that after a time the preceding difference of conditions passes into a field through which he is not interested in tracing it; as when a biologist finds a result to be due to a preceding difference in temperature.

8. Expressed accurately, the principle underlying all this is: *Every succeeding difference in perceptual conditions is experimentally bound up with a preceding difference in perceptual conditions.* This may be called *the* postulate of experimental analysis. Cause or determiner, and effect or thing determined, are both *differences* between specifiable cases. In common usage the term cause or determiner is loosely employed to express that which is added, or that which is subtracted, to produce one case from the other; it may, therefore, as well be the absence of something as the presence of something. Thus, the determiner for blueness of eyes, as compared with brownness of eyes, is, loosely, but con-

veniently expresed, the *absence* of something present in the germ cell that produced the brown eyes. The apparent absurdity of saying that something is determined by nothing disappears when we understand that this merely means that the *difference* between the given case (blue eyes) and some other (brown eyes) is due to the lack in the former of something present in the latter. This sort of analysis is necessary for all statements regarding determiners in Mendelian inheritance, and when properly carried out it reveals their true meaning and rids them of offense.

9. The question may be raised whether this way of looking at causation is a mere practical device for clearing thought in particular cases, or whether it has a wider significance. Is all causation only of differences? Is it only of differences that a causal explanation can properly be given? Is causal formulation inapplicable to things taken by themselves, without differentiation or comparison? Does all causal formulation necessarily imply comparison? It appears that all this might be affirmed; here the matter is raised merely as a question.[1]

3. ILLUSTRATIVE QUESTIONS FOR RADICALLY EXPERIMENTAL ANALYSIS

A. Some assert that a certain chromosome is a determiner of sex; others dissent.

What experiment or experiments would decide? Or has the word determiner here no experimental meaning? The positive assertion is evidently absurd if it is taken to mean that the chromosome contains all the conditions necessary for the production of the sex characteristics (male or female). Interpreted in accordance with our two rules, it means merely that if two similar eggs side by side produce animals of the same sex, and if from one of these a certain chromosome could be removed (or

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[1] Mills's "method of differences" set forth in his "Logic" is not the search for the causes of *differences between cases,* recommended above, but merely the examination of differences, as an aid to causal investigation of things taken by themselves.

to one a certain chromosome could be added), this egg would now produce an animal of the other sex. The question is thus purely an experimental one. Of the enormous number of conditions necessary for the production of the sexual characteristics, this assertion specifies one, which happens to be practically interesting to us. We trace the *difference* in sex between two individuals back to a *difference* between the two eggs from which they came. We may then trace the difference between the eggs back to differences between the sperms; the latter to differences between the chromosome groups of the parents, and the process of tracing back is limited only by our knowledge. All these preceding differences (and any others that may yet be found to cause a *difference* of sex) are equally sex determiners; the discovery of one kind of sex determiner (in our sense of determiner) does not preclude the discovery of a thousand others.

B. Some assert that the brown color of the skin (or some other color characteristic) is hereditary; others dissent, asserting that it is due to oxidation of a certain chemical compound, or to exposure to the sun.

Applying rule 2, when we compare individuals that have lived under the same conditions and find one (*a*) dark, the other (*b*) white, we must conclude that the difference is hereditary, in the sense of determined by a *difference* in the germ cells. But this difference in the germ cells may be of such a nature as to prevent oxidation in one case, while permitting it in the other; it is then likewise true that the cause for the color is oxidation. The same individual *a* that is dark might perhaps not be so if not exposed to the sun; it is then true that exposure is the cause of the color. All these statements as to causes are elliptical, and all are equally true; at which one we arrive depends on what comparisons are made; what *differences* we are accounting for.

C. Some assert that the nucleus is the "bearer of the hereditary qualities"; others deny this with ridicule.

Making precise by means of our two rules this loose and obscure proposition, it means the following experimental situation. If two eggs side by side were identical in cytoplasm and in environmental conditions (throughout), but differed in their nuclei, the specified "hereditary qualities" produced would differ. If the assertion is that the nucleus is the *exclusive* "bearer," it further means that if two eggs side by side were identical in nucleus and in environmental conditions, but differed in cytoplasm, the specified "hereditary qualities" produced would *not* differ. The questions are experimental ones, of the highest interest, on which much work has been done.

But if the assertion is understood to mean that the nucleus contains all the conditions necessary for the production of the hereditary qualities; or if it means that the characters produced are independent of the environment—of course experiments already tried show its incorrectness. Only by reducing it to an experimental situation does it become a profitable question.

D. Some assert that the development of muscular tissue or of nervous tissue (or the like) is determined within the cells; others dissent.

This means that if the two cells were kept under same conditions, one would still produce muscle, the other nerve. It does not mean that the cell contains within itself all the conditions necessary for the production of muscle (or nerve); and it leaves open the question what the two cells would produce if they were kept under diverse conditions.

E. Some assert that the movement of a given organism is unequivocally determined by some external agent (as light); others dissent.

If the assertion is only that when two organisms are alike in internal and in other external conditions, a difference in the light on the two may unequivocally determine a difference in movement, it is correct. If, on the other hand, it asserts that when two organisms are subjected to the same conditions of light, an internal difference of condition may not equally unequivocally determine a difference in the movement (so that one may, for example, move toward the source of light while the other does not), it is incorrect. What is unequivocally determined is always a difference between two cases; what determines the difference depends on the comparison made.

F. Some assert that physical conditions affect psychic states, and *vice versa;* that the physical and psychical interact; others dissent.

To assert that physical conditions affect psychic states can mean only, from a radically experimental point of view, that a preceding alteration in an exclusively physical condition results in a change in a psychical condition (pain, sensation). The experiment appears to occur frequently, and to give as unequivocal results as any experiments in science (unless we suspect all physical changes to be accompanied by psychical ones, in which case we drop the radically experimental standpoint). (It will be observed that experimentation can have nothing to say on the question sometimes discussed as to whether the physical and psychic conditions occurring *at the same time* have a relation of cause and effect; this is a typical example of a question that can not be reduced to an experimental situation.)

The converse assertion is that a change in an exclusively psychical condition produces a change in physical conditions. The experimental situation is not a conceivable one, unless psychical changes *do* occur unaccompanied by physical ones.

G. Some assert that entelechy is required for determining what happens in development; others dissent.

The bearing that experiment can have on this question is to discover whether there ever occur cases in which two systems alike in all perceptual respects act in two perceptually different ways. If no such cases occur, no additional agent is experimentally demanded. If such cases do occur, the question whether entelechy is to be brought in is a non-experimental one.

4. RELATION OF RADICALLY EXPERIMENTAL ANALYSIS TO OTHER FORMULATIONS

Radically experimental analysis thus reduces all questions to an experimental situation; seeks for every existing perceptual difference between cases to find a preceding perceptual difference on which the later one experimentally depends; and results in a formulation or explanation which includes only perceptual factors.

We often find, particularly in biology, formulations or explanations which are based on non-perceptual factors. This non-perceptual character is not always realized, nor readily detectible; it will be brought out by applying to the doctrine in question the two rules set forth above. In other cases the formulation confessedly includes non-perceptual factors; such is the vitalism of Driesch.

For clear thinking as to all such doctrines, confessed or unconfessed, a grasp of their relations to radically experimental analysis is essential. The crucial questions are: Can radically experimental analysis be carried through all parts of science, even biology? That is, can experimental causes be found for all that occurs? If so, are other sorts of causes likewise required? Is recourse to formulations including non-perceptual factors due to (1) a supposed lack of experimentally perceptible determining differences for all differences in results; or (2) to a mental need for some other conditions, *in addition* to the perceptual ones, to show perhaps "why" the perceptual conditions produce the results they do? Supplementary non-perceptual theories of the first sort, based on an assumed lack of perceptual determining factors, tend to discourage experimentation or the search for perceptual determining factors; while supplementary theories of the second sort have nothing to do with experimental science.

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CLONAL VARIATION IN PECTINATELLA

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THE freshwater Bryozoan *Pectinatella magnifica* produces, as is well known, lenticular statoblasts or winter buds that carry at the margin hooks whose number varies from 11 to 26. The statoblasts develop in the funiculus of the zooids. The zooids arise by budding from embryonic tissue which is laid down even in the statoblast-embryo of the preceding generation. The zooids of a colony are thus related as closely as possible, being developed parts of one and the same germplasm. The zooids of a colony are found in branches or twigs that radiate from a center and, in *Pectinatella,* are thick, short and blunt, forming a stellate colony. Many of these corms lie in contact with each other on the surface of a more or less spherical mass of jelly that is secreted by the colony. The colonies are in close contact like the facets of a compound eye. As the gelatinous mass increases so does the area available for the colony and thus additional space is allowed for their growth.

Whence come the colonies that lie on the surface of any one of the gelatinous masses? In part they arise by fission of preexisting colonies. A given colony gains an elliptical shape and then constricts in the short axis; the periphery of the colony is increased and room made for new branches and new young buds. If all colonies on the surface of a given mass arose thus we could refer the origin of them all to the original colony that came from the statoblast. But, unfortunately, things are not so simple. For two statoblasts may germinate in close proximity to each other on the same substratum and, under such circumstances, the masses of jelly they secrete will flow together and form parts of a single mass. Thus the gelatinous masses in nature are of two sorts:

simple, all of whose colonies (and included statoblasts) carry the same germplasm and *compound,* those whose colonies and statoblasts carry more than one kind of germplasm. These can not, in general, be distinguished by gross appearance.

Recent studies have shown that parts of organisms that are derived from the same germplasm (without the intervention of sexual reproduction) are much more constant in their morphological features than parts of organisms that, however closely related, are each the product of the union of two germ cells. For germ cells are necessarily more or less unlike, and may be very unlike, and, consequently, their progeny will be variable. We should expect then (to return to the *Pectinatella* masses) to find them of two kinds, (*a*) with a relative constancy in the modes of the distributions of the statoblast-hooks, and (*b*) with two or more modes (centers of variation) of statoblast-hooks in different colonies from the same mass.

HISTORICAL

The first statistical study of variation in the number of hooks per statoblast made was, in 1900, by one of us. In 1906, Miss Alice W. Wilcox showed that a *Pectinatella* mass is derived from statoblast-embryos the products of which repeatedly divide, move from each other and, as they enlarge, come in contact again. Her study makes it probable that a mass may be derived either from one or from two or more independent statoblast-colonies. Braem (1911, pp. 321, 323) refers to a mass derived from about 80 statoblasts, but the product of a great proportion of them perished. He has also a mass derived from only one statoblast. Braem points out that the number of hooks per statoblast tends to increase with the age of the colony and of the whole mass. He considers a possible difference in heredity tendencies inside the different colonies and concludes that this factor is small as compared with other factors, above all, temperature of the water.

Thus he finds that, in one and the same colony, the mean number of hooks increases with the temperature of the colony when the hooks are being formed and, in support of this contention, gives tables of his countings from the same mass between July and October. Some of his data support this conclusion strongly, as shown in Table I.

TABLE I

Braem's Serial Number.	Date of Examination.	No. of Statoblasts Counted.	Average Number of Hooks.	Description of Mass.
24	Aug. 23	30	14.33	Derived from 5 statoblasts. First statoblast June 28.
25	Sept. 14	12	17.50	From peripheral zone.
26	Sept. 14	34	18.47	An offshoot from the same mass.
18	Sept. 6	145	14.12	Derived from 2 statoblasts.
19	Sept. 24	441	14.69	Oldest portion.
20	Sept. 24	302	15.44	Peripheral (younger) zone.
21	Sept. 24	81	16.65	Youngest zone.
22	July 16	3	13.33	First statoblast.
23	Aug. 3	56	15.52	

In other cases the hypothesis is not sustained as shown in Table I*a*.

TABLE I*a*

Braem's Serial Number	Date of Exam.	No. of Statoblasts Counted	Average Number of Hooks	Description of Mass
10	Aug. 7	32	12.94	Mass from 1 statoblast, 1st statoblast.
11	Aug. 31	287	14.21	Same mass.
12	Sept. 10	235	13.82	Same mass.
13	Oct. 5	440	14.47	Same mass.
14	Aug. 31	258	14.56	
15	Sept. 15	365	14.30	

The remaining series have determinations at two dates only and are less significant, though supporting the hypothesis, so far as they go.

INFLUENCE OF AGE ON THE NUMBER OF HOOKS

In our work, colonies of *Pectinatella* were grown on a clean board kept at the dam, lowest lake, Cold Spring Harbor, and examined daily. The first young colonies that attached themselves to the board in June were doubtless statoblast colonies (although the shell of the statoblast was not found) as no embryos were seen until July. None of the colonies formed statoblasts during June, but began to form them early in July. At various dates some of these elementary colonies were removed from the board and the hooks of their statoblasts counted. Later the separate colonies grew together and their origin became confused, but it is certain that the sets of statoblasts given in Table II are each derived from a single statoblast-ancestor. All statoblasts that possessed well-developed hooks were counted—there was no selection.

TABLE II

DISTRIBUTION OF FREQUENCIES OF NUMBERS OF HOOKS PER STATOBLAST IN EACH OF SEVERAL COLONIES, COUNTED AT DIFFERENT DATES

Date, 1912	Number of Hooks										Average
	12	13	14	15	16	17	18	19	20	21	
July 6			5	9	5	1					15.1
July 9			1	2	2	1					15.5
July 9			3	3	4	2	1			1	16.0
July 17[1]	1	1	3	6	7	6					15.5
July 17[2]			4	27	16	6					15.5
July 19		1	9	24	5	5					15.1
July 19	1	4	10	10	6	2					14.7
Aug. 8			2	14	9	3	1				15.5
Aug. 8[3]			3	4	1	1					15.0
	2	6	40	99	55	27	2	0	0	1	

Our studies, though not made on one and the same simple mass at successive periods, have been made on several colonies early in the season (beginning July) and at the end of the season (October). Counts on 241 statoblasts from 13 colonies made in July average 15.3 hooks; 7,255 statoblasts of one mass made in October gave an average of 15.6 hooks; 5,593 statoblasts from a probably

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[1] Many undeveloped.

[2] Few, if any, undeveloped. The two colonies taken on the 17th were small, adjacent and attached to each other. Probably from the same statoblast.

[3] Colony in full life and vigor; immature statoblasts on funiculi.

complex mass counted at the same time in October gave an average of 16.0 hooks. Thus the difference between two sets of counts made in the same month on two distinct masses is greater than between the July and October counts. The highest average number of hooks found in any mass during October was in Mass *B*, 3,802 individuals, with an average of 16.6 hooks.

Comparing with Braem's, it appears that our counts run much the higher. The average of all counts made by Braem is 14.34, which is decidedly lower than our July average (15.3); and in one colony he obtained an average of 12.94 hooks. A great mass found at Jackson Park, Chicago, in August, 1898, gave an average of 13.78 hooks. It is clear, accordingly, that however important the temperature factor may be,[4] it is secondary in importance to some other factor that determines the variation in the number of hooks.

The number of hooks is determined by the number of pocket folds arising in the membrane that secretes the chitinous covering of the statoblast; and the question now transfers itself to the reason why in some statoblasts few, in others many, such folds occur. At one time we entertained the hypothesis that there was a causal relation between thickness of membrane and the size of and distance between pocket folds, such that a thin membrane permits smaller and more numerous folds. Unfortunately, it was not feasible to measure the thickness of the setigerous membrane, for by the time the number of eventual hooks can be determined the membrane has become relatively thin and very irregular in thickness. Our study did serve to indicate that the number of hooks can not be determined in a mechanical way by the thickness of the membrane, but that, on the contrary, the folds follow, and their number is determined by, the number

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[4] Unfortunately, we made no thermometric determinations of the temperatures of the lake water. The lake is spring fed and shaded around the edges. As a guess, it rarely exceeds 20° C. in temperature; the July temperature is probably about 18°.

of centers of cell keratinization. In some statoblasts the number of these centers is small; in others great.

To test the hypothesis that the size of the cells in the setigerous membrane covering the statoblast influences the number of folds arising in it, we measured the diameter of the facets on the disc and on the float of statoblasts with 20 hooks and those with 12 hooks. The average diameter of a facet on the disc in 25 measurements (each based on a row of facets) was, in statoblasts with 20 hooks, 8.37 μ; in statoblasts with 12 hooks (14 sets of measurements) 8.25 μ. On the float, in statoblasts with 20 hooks, 9.54 μ, in statoblasts with 12 hooks, 9.40 μ. It results first, that the facets (cells?) of the float are slightly larger than those of the disc, but that the difference in size of the facets in statoblasts with many and those with few hooks is neglible.

Since there seems to be nothing in the interrelation of parts to determine that the number of hooks shall be great or small one is naturally led to suspect that in these varying statoblasts we are actually dealing with distinct biotypes. We turn, consequently, to that phase of the question. The ideal conditions for an answer to the inquiry whether there are distinct biotypes in respect to number of hooks are these: To plant several statoblasts (with varying number of hooks) from each of the several independently arisen colonies and count the number of hooks on the statoblasts that are produced therefrom. We have not abandoned the hope of meeting these conditions, but our attempts to do so have hitherto been frustrated. Of nine statoblasts affixed (by shellac) to submerged wood none hatched. Also, colonies observed daily from hatching were eaten up by the larvæ of caddis flies (*Hydropsyche*). Finally after we had secured a good development of colonies free from predaceous insects all our work was brought to naught by the destruction of our floats.

We have, however, sought to get the required information in a more indirect way. We have studied the number of hooks on statoblasts from different masses in order to see if there was less variation inside of one mass than between different masses. This method has its clear limitations; for one does not know whether a given mass is simple or compound in origin. If, in any large mass, the modes, or the average, of the number of hooks varies greatly between colonies, that is evidence of the compound nature of the mass. If, on the contrary, the averages of all the different colonies of a mass are closely alike that indicates the homogeneity and probably simple nature of the mass—its origin from one statoblast.

TABLE III

MASS 1

Colony No.	*N*	11	12	13	14	15	16	17	18	19	20	21	Average
1	460		4	22	148	324	272	165	48	10	7		15.62 ± 1.26
2	884		2	37	145	303	259	173	46	26	8		15.66 ± 1.36
3	828		1	33	165	320	243	155	72	9	1	1	15.58 ± 1.30
7	720		6	31	136	324	283	132	76	7	4	1	15.62 ± 1.30
8	523		2	41	166	296	249	166	63	11	4	2	15.59 ± 1.33
10	361			31	155	335	241	161	69	8			15.59 ± 1.25
12	508		2	30	189	319	242	120	59	35	4		15.57 ± 1.39
13	337			39	134	305	258	130	92	39	3		15.75 ± 1.42
14	288			63	180	270	230	139	104	4			15.57 ± 1.43
17	326			28	150	337	240	153	77	15			15.63 ± 1.28
18	401		3	45	207	331	217	154	30	10	3		15.36 ± 1.26
20	348		3	26	155	313	273	152	69	9			15.60 ± 1.25
21	560			39	179	332	257	146	43	4			15.44 ± 1.19
22	439	2	2	18	158	291	265	164	87	11	2		15.70 ± 1.32
24	272			26	143	298	268	180	63	18	4		15.71 ± 1.30

TABLE IV

MASS 2

Colony No.	*N*	12	13	14	15	16	17	18	19	20	21	26	Average
1	689		20	130	251	282	190	101	23	3	1		15.91 ± 1.35
4	284		10	67	240	278	240	144	18	4			16.19 ± 1.27
6	679	2	25	113	260	299	205	83	10	3			15.88 ± 1.27
10	646		14	128	243	274	189	108	43				15.99 ± 1.37
16	501	6	12	106	281	291	192	84	26	2			15.89 ± 1.30
20	387		26	109	299	307	163	80	13	3			15.78 ± 1.25
24	277			83	220	310	238	116	25	7			16.18 ± 1.25
26	354		11	79	198	308	249	127	23	3		3	16.23 ± 1.36
30	367		16	93	237	308	250	85	11				15.98 ± 1.20
31	250		8	84	260	260	232	112	44				16.14 ± 1.31
33	240		8	75	283	237	230	154		13			16.13 ± 1.30
34	308		16	117	253	263	214	123	10	3			15.97 ± 1.31
35	205		15	98	230	351	205	63	34	5			15.99 ± 1.26
36	308		10	71	198	341	257	84	26	13			16.19 ± 1.25
40	259		12	16	286	305	220	93	15	4			16.02 ± 1.20

In any case the data collected have an interest of their own and are herewith put on record.

TABLE V

Mass 3

Colony No.	N	11	13	14	15	16	17	18	19	20	Average
1	646		15	70	271	280	210	121	28	5	16.10 ± 1.30
3	746	1	11	101	243	291	213	111	16	13	16.06 ± 1.33
4	708		20	105	196	253	237	151	30	8	16.20 ± 1.41
5	513	2	16	94	270	311	214	72	14	8	15.92 ± 1.24
8	362	5	22	77	254	293	207	105	25	11	16.04 ± 1.37
9	282		7	85	262	252	227	124	39	4	16.15 ± 1.33
15	442	5	32	152	290	265	167	66	18	5	15.66 ± 1.35
17	421	2	7	71	195	237	197	207	59	26	16.53 ± 1.51
18	297		10	125	266	226	215	128	30		16.02 ± 1.36
22	488		4	82	240	305	195	131	33	10	16.18 ± 1.33
24	271		11	92	214	262	196	148	63	15	16.31 ± 1.47
25	419	2	7	88	224	344	215	86	31	2	16.06 ± 1.24
26	279		7	50	172	211	283	168	79	29	16.68 ± 1.45
31	236		8	47	170	343	280	102	42	8	16.36 ± 1.23
32	221		5	68	172	240	231	190	77	18	16.59 ± 1.45

TABLE VI

Mass 4

Colony No.	N	12	13	14	15	16	17	18	19	20	21	Average
1	342		12	73	208	292	237	123	50	6		16.27 ± 1.34
2	278	4		25	97	255	238	212	94	50	25	17.11 ± 1.54
3	269		4	41	119	197	204	290	104	41		17.05 ± 1.47
5	356		6	45	180	213	225	188	82	56	6	16.81 ± 1.58
6	559	2	16	140	265	286	170	89	29	4		15.85 ± 1.35
7	537			30	132	276	238	212	73	30	9	16.86 ± 1.40
8	231			39	126	177	307	230	78	43		16.97 ± 1.40
10	268		4	26	134	231	250	220	93	34	8	16.44 ± 1.44
12	299	3	10	94	291	271	211	101	13	7		15.95 ± 1.27
13	158			25	171	241	234	228	82	13	6	16.80 ± 1.37
14	254			31	134	217	272	225	71	51		16.94 ± 1.41
15	253			24	174	245	170	253	87	39	8	16.91 ± 1.49
16	156			32	141	160	320	192	109	45		17.01 ± 1.43
17	198		5	40	136	227	237	177	116	51	10	16.96 ± 1.57
18	132			30	167	258	212	250	68	15		16.75 ± 1.34

Note.—Each of the Tables III–VIII, gives for a number of separate colonies of one and the same mass the frequency of occurrence of each number of hooks to a statoblast. The actual number of statoblasts counted is given in the column headed N; the columns to the right of N are for the entries corresponding to the number of hooks named at the top of the column; the frequencies are reduced to 1,000 statoblasts per colony. The column at the extreme right gives the average number of hooks for each colony together with the standard deviation of the distribution.

TABLE VII

MASS 5

Colony No.	N	12	13	14	15	16	17	18	19	20	21	22	Average
1	239			13	104	268	242	214	101	50	8		17.08 ± 1.41
2	572		5	24	113	217	217	230	144	45	5		17.14 ± 1.50
7	213				75	263	258	282	70	28	19	5	17.19 ± 1.33
8	179			22	112	223	330	196	61	45	11		16.98 ± 1.38
9	177			6	85	237	305	237	85	45			17.12 ± 1.26
11	107		9	56	141	150	234	196	159	56			17.05 ± 1.64
15	116			17	76	190	268	319	104	26			17.21 ± 1.26
16	78				103	244	308	218	90	24	13		17.08 ± 1.29
20	163		6	12	61	203	203	320	98	85	6	6	17.44 ± 1.48
21	337			15	83	160	297	210	142	74	18		17.42 ± 1.48
22	323		25	99	235	272	189	118	53	9			16.11 ± 1.46
24	336		3	77	223	283	202	122	63	24	3		16.36 ± 1.46
31	272		7	66	239	280	184	165	52	7			16.31 ± 1.38
32	357	6	53	216	289	240	126	62	8				15.38 ± 1.33
34	333	18	69	222	291	228	102	54	12	3			15.24 ± 1.41

TABLE VIII

MASS 6

Colony No.	N	12	13	14	15	16	17	18	19	20	21	22	23	24	26	Average
1	461		2	20	128	260	217	215	74	48	13	13	7	2	2	17.11 ± 1.72
2	617		20	110	306	298	183	70	10	2						15.77 ± 1.20
5	484		12	105	277	351	161	72	17	4						15.85 ± 1.21
6	531	2	19	158	335	258	149	60	19							15.61 ± 1.25
12	470		26	68	215	274	228	157	28	4						16.22 ± 1.36
14	492	8	37	173	260	211	185	96	26	4						15.72 ± 1.48
20	252		16	64	190	266	238	159	52	12	4					16.40 ± 1.42
25	45			44	67	178	222	378	89	22						17.18 ± 1.32
31	650	2	37	142	317	283	154	58	6	2						15.58 ± 1.24
47	171	6		76	111	251	263	175	99	18						16.70 ± 1.47
49	322		6	146	280	295	193	62	16	3						15.79 ± 1.23
50	278	14	58	212	330	205	126	51	4							15.25 ± 1.31
51	200				65	185	225	275	100	120	20	10				17.65 ± 1.53
52	280	4	25	125	310	250	186	89	7	4						15.75 ± 1.30
53	340		3	50	217	282	209	170	47	18	3					16.45 ± 1.38

From Tables III to VIII it appears that certain *Pectinatella* masses are characterized by a great constancy in the modal and the average number of hooks in a colony. Thus, in Table III the range in the average is only from 15.36 to 15.75, or 0.4, and the modal number of hooks is constantly 15 in all colonies of the mass. So, too, in Table IV with one exception the mode of the 15 colonies is 16 despite the fact that the average for the whole mass is near the dividing line between 15 and 16, viz., 16.03. The remaining masses show a greater or less commingling of biotypes. Thus, in Table V the empirical mode varies from 15 to 17 and the range of the average number of statoblast hooks to a colony is .76. In Table VI the mode ranges from 15 to 18 and the range of the average is 1.20. Tables VII and VIII show masses 5 and 6 to be even more variable with a range of 2.40 hooks in the averages.

Examining the standard deviations, we find no evidence that, except for the fact that, as is usually the case, the standard deviation tends to increase with the average, the great variability of masses 5 and 6 is due to a corresponding variability inside the individual colony.[5] We conclude, consequently, that the difference in variability between masses 1 and 2, on the one hand, and masses 3 to 6, on the other, is due to the fact that the former are simple in origin and the latter are compound; the former represents one biotype, the latter two or more biotypes. Compare the pairs of distributions in Table IX for mass 1 and mass 6—the most unalike having been selected in each case.

TABLE IX

COMPARISONS OF TWO UNLIKE DISTRIBUTIONS IN

MASS 1

No. of Hooks	12	13	14	15	16	17	18	19	20	21	22	Average
Colony 13		39	134	305	258	130	92	39	3			15.75 ± 1.42
Colony 21		39	179	332	257	146	43	4				15.44 ± 1.19

MASS 6

Colony 50	14	58	212	330	205	126	51	4				15.25 ± 1.31
Colony 51				65	185	225	275	100	120	20	10	17.65 ± 1.53

[5] The highly exceptional colony 1 of mass 6 being neglected. Unfortunately, we have no data concerning the position on the mass of this remarkable colony. In a paper just received from Braem (1913) a similarly highly variable colony is described.

The difference between the members of the first pair is chiefly in the scattering of the distribution—in the variability—inside the colony. The difference between the members of the second pair is a difference of mode—of type. These latter two distributions, and others in Table VIII, have little in common; they are the product of distinct biotypes.

Inside of a single biotype—inside of a single colony—there is a great variability in the number of hooks. Why is this? Unfortunately, we do not know. The query is one with others concerning the cause of variability, upon which we hope to shed some light.

Our study suggests that the difference in the average number of hooks in mid and late summer statoblasts is not due merely to the differences of age, temperature and food conditions in these two seasons, but probably also to the circumstance that the biotype that forms many hooks is one that develops later in the season than the others. Our study has, indeed, solved few problems, it has rather shown what a fine field for investigation is offered by the remarkable variation of the hooks on the statoblasts of *Pectinatella.*

COLD SPRING HARBOR, N. Y.,
February 25, 1913

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SHORTER ARTICLES AND DISCUSSION

SIMPLICITY VERSUS ADEQUACY IN MENDELIAN FORMULÆ

IN this journal for March, 1913, Professor William E. Castle discusses and criticizes in a friendly spirit certain suggestions concerning Mendelian nomenclature that I brought forward in the January number of the same journal. There are so many essential points on which we agree and so few on which we disagree that I should like to make clear the necessity of having for our work on *Drosophila* a dual set of symbols. Castle finds, on the other hand, that for mice and for guinea-pigs a single set of letters, *abc*, suffices to make clear his results and to cover his theoretical ideas.

There are three reasons why in certain cases it seems necessary to use more than a single system of lettering for factors.

1. Castle's scheme gives us no way of adequately representing heterozygous forms. In dealing with such combinations it is an essential both to the author and to the reader to have the heterozygote represented with its constituent allelomorphs. Instead of making the system more cumbersome the dual set of symbols is helpful.

2. We are dealing in *Drosophila* with about one hundred mutations, of which forty-five have been sufficiently studied to show that they fall into three groups. Within these groups the factors concerned show linkage to each other, but no factor of one group shows linkage with any factor of any other group. Linkage means some sort of relation which we interpret in terms of a linear series. We further interpret this series in terms of chromosomes, but even if the series is taken merely as an abstract principle the need of a dual system of letters to express the order of the factors in a paired linear series is imperative, so that we may represent interchanges between the pairs. To take the sex-linked group of factors, for example. In a heterozygous female there are two linear series present, corresponding to her duplex condition, or, as we think, to the two homologous sex chromosomes. Any factor in the one series has a correlative factor in the other series (in the other chromosome) in a corresponding position, and in order to treat the linkage of the factors we must have some method of representing and of distinguishing them. If from the mother the factors *aBcdE* enter the combination and from the father *AbCDe*, the heterozygous female is represented by the two groups:

$$\begin{matrix} aBcdE \\ AbCDe \end{matrix}$$

In all problems relating to crossing-over of the factors from the one series to the other the location of each factor (and its allelomorph) is expressed by the formula just given, whereas one in which even the *duplex* condition is represented by small letters in a single line (*abcde*) fails to indicate the order of the factors in their mutual relations in the two series.

3. In cases in which sex-linked factors are involved the half formula of the female will sometimes suffice (if thought of in duplex), but in the male the half formula will not suffice when some of the factors are sex-linked and others not. If *a* and *b* are sex-linked, then the formula *abcde* fails to represent the condition in the male, for only *cde* are present in duplex.

In contrasting his scheme with mine Castle (page 176) uses the full formulæ for my cases and the abbreviated formulæ for his own, to the apparent advantage of the latter. If he tried to express in his formulæ what I have expressed in mine, and had omitted from my formulæ what he omits from his own, the advantage would have appeared differently. For shorthand purposes the most abbreviated form of any system will be employed in each particular case, except where for special reasons the comparative formula, in spite of its length, gives a clearer idea of the relations involved. When representing eye colors, for instance, we put into the formulæ only the symbols for the particular eye colors under consideration, but not, of course, the symbols for other eye colors that are not being used. Castle gives the impression that I would use all the known symbols for eye color each time I wrote out the formula for the eyes, but obviously nothing of the sort is intended, for we have other eye colors that do not appear in papers that are not concerned with them.

Castle uses small letters for the recessive mutants, as I also propose to do in exactly the same sense. He scores a point—admittedly—when he says that in my formulæ the factor *B* which he reads as black is the only factor that is not present in the black fly. There is just one unfortunate line on page 13 that gives Castle the opportunity to make this jibe, while the whole spirit of the paper goes to show that the small letter stands for the factor carried by the recessive mutant. In order that no misunderstanding of this sort may again arise let me state that small *p* is the factor for pink; small *b* the factor for black; small *v* the factor for vermilion; small *m* the factor for miniature. The allelomorphs of these factors in the normal flies are dominant and are represented by the capital letters *P, B, V, M.*

These are the allelomorphs that I assume to have changed in some way to give the factors for the mutations in question.

I do not understand, after the very explicit statement in my paper, why I failed to make clear what I meant by "residuum" and as I can not hope to make the matter any clearer I shall not attempt here to discuss it further.

In writing my original paper I had considered the question as to the manner of representing the dominant mutant, but since that paper dealt mainly with the presence and absence theory, in which absence meant the recessive condition, I decided not to complicate the discussion with the treatment of the dominant and did not mention dominant except in a footnote on page 13. Castle has called attention to the necessity for considering this matter and has pointed out a distinct weakness in my scheme, if the aforesaid footnote be made the basis for the case of dominants. I gladly avail myself, therefore, of this occasion to further develop this topic. Agreeing that at times it is important to distinguish in the same formula between the dominant mutant factors and the dominant normal allelomorphs of recessive mutant factors, I would suggest that in such cases the letter standing for dominant mutant factor be primed:[1] $D'E'F'$. The allelomorphs of these factors that occur in the normal type can be most conveniently represented by $d'e'f'$. The entire scheme will be:

Recessive mutants	abc
Their allelomorphs	ABC
Dominant mutants	$D'E'F'$
Their allelomorphs	$d'e'f'$

In many cases it may not be necessary to distinguish whether the dominant is the normal or the mutant form. In this, as in all cases, abbreviated formulæ that readily suggest themselves as occasion arises will be employed, and in general, of course, only as much of the scheme will be used as is essential for the matter in hand. But when more complicated questions arise than can be discussed on Castle's curtailed formula, the plan here suggested may, I hope, be found both simple and convenient.

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[1] Or in more general terms; if the factor is named after the dominant character, prime the allelomorphs. Since in the case of *Drosophila* we always take the symbol from the name of the mutant the above statement is equivalent to saying, if the mutant is dominant, prime the allelomorphs.

THE POSSIBLE ORIGIN OF MUTATIONS IN SOMATIC CELLS

THAT mutations are accompanied by some change in the germ-plasm is, I take it, indisputable. Have we, however, any reason to suppose that the change takes place within the germ cells? I am not sure, as a matter of fact, that geneticists in general regard the gametes as the place of origin of mutations. It is true, however, that experiments in the artificial production of mutations in plants[1] have been limited largely to treatments of the ovaries from about the time of the reduction division to about the time of fertilization. This suggests a belief on the part of investigators that mutations are most likely to be induced in the gametes or in the stages of the plant closely associated with gamete formation. MacDougal (*loc. cit.*) considered it most probable that mutations take place just prior to the reduction division.

The very uniqueness of the reduction division has perhaps suggested the likelihood of the occurrence of chance irregularities in it resulting in the production of mutations. Davis[2] has interpreted the occurrence of 21 chromosomes in *semi-gigas* forms of *Œnothera* as possibly brought about by a pushing forward of the premature fission of the chromosomes from the anaphase to the metaphase of a heterotypic mitosis followed by another fission before the metaphase of the following homotypic mitosis, resulting in the production of gametes with 14 chromosomes, which are supposed to unite with normal gametes (with 7 chromosomes). The *gigas* forms of *Œnothera,* with their 28 chromosomes, however, seem more readily explained by the assumption of a double fission of chromosomes in some mitosis after fertilization. Otherwise we must assume that both male and female gametes with 14 chromosomes are produced at about the same time and that two such gametes happen to meet in fertilization—certainly a rare chance.

The heterozygous condition of the new character in some mutations and the frequent appearance of mutations as seed-sports rather than as bud-sports may, at first thought, make it seem reasonable that they might have their origin in the gametes or at least at about the time of gametogenesis. Neither of these occurrences, however, affords any real evidence for placing any such limit upon the time of origin of a mutation. The reason for this statement will become apparent later.

East[3] has called attention to the asexual production of varia-

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[1] MacDougal, D. T., *Pop. Sci. Mon.,* 69: 207–225, 1906; Carnegie Pub. 81: 61–64, 1907. Gager, C. S., *Mem. N. Y. Bot. Gard.,* 4: 22, 1908. Humbert, E. P., *Zeit. ind. Abst. Vererb.,* 4: 161–226, 1911.

[2] Davis, B. M., *Annals of Botany,* 25: 959, 1911.

[3] East, E. M., Ann. Rpt. Conn. Agr. Expt. Sta., 1910, p. 139.

tions in the potato that are known to mendelize in sexual reproduction, but has regarded these occurrences as a segregation of characters in somatic cell divisions (of a heterozygous plant?) rather than as a change in genetic factors, which alone can be regarded as a true mutation.

The interpretation that I have given to the results of a study of the inheritance of a recurring somatic variation in maize have some interest in this connection.[4] The results in brief are these: (1) The more red there is in the pericarp of the seeds of variegated-eared maize ("calico" corn), the more likely is the progeny of these seeds to have self-red ears and the correspondingly less likely to have variegated ears. (2) Red ears thus produced behave like F_1 red ears produced by crossing self-red races with variegated races or self-red races with white races, depending upon whether the variegated parent ear was homozygous or heterozygous and upon whether it was selfed or cross-pollinated. (3) Red ears that behave exactly like crosses between pure reds and pure whites occasionally arise from the seeds of white races crossed by pollen from variegated races.

My interpretation of these results postulates the presence of a genetic factor for self-color, *S*, in occasional gametes instead of the ordinary variegation factor, *V*. The presence of *S* in female gametes is apparently due to a change of *V* to *S* in somatic cells from which these gametes arise and this change in genetic factors apparently manifests itself in the development of red pigment in such pericarp cells as are directly descended from the original modified cell. The larger the mass of modified cells the more red appears in the pericarp and the more likely are the female gametes to carry the *S* factor. But since red never develops in the pericarp until the seeds are nearly mature, it happens that the somatic variation does not become visible until weeks after the gametes are formed and until still longer after the change in factors occurs. It is reasonable to suppose that the presence of the *S* factor in the male gametes is due to the same sort of change in the somatic cells from which they arise as that responsible for the presence of *S* in the female gametes. This somatic variation, however, never becomes visible because the staminate inflorescence dies very soon after the pollen is shed. It is quite possible indeed that such a somatic change would never become apparent even if the tassel did not die too early, for a color limited principally to the cob and to the pericarp of the seeds could scarcely be expected to appear in the tassel.

It seems possible that the production of self-colored plants

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[4] These results were presented at the Cleveland meeting of the American Society of Naturalists, January 2, 1913. The paper will be printed later.

from variegated ones as here outlined[5] bears more than a superficial resemblance to mutation. The comparative frequency of the change in factors from V to S in variegated plants is perhaps the most striking dissimilarity between the two. Mutations must certainly result from the loss or gain or the modification of genetic factors. They must arise potentially whenever a change in genetic factors takes place, whether in the somatic cells or germ cells of the parent or in the early somatic cells of the mutant offspring. It is conceivable that many mutations may arise in a manner similar to the origin of red-eared maize plants from the male gametes of variegated maize—similar in the sense that the change in genetic factors may occur in somatic cells without any visible modification of those cells or of any part of the plant body arising from them.

East has shown (*loc. cit.*) that Mendelian characters of potato tubers sometimes arise as bud-variations. If the same characters should be found to appear as seed-sports, that fact would not, in some cases at least, preclude the possibility of their having had their potential origin in somatic cells of the parent plant. If a change of genetic factors having to do with tuber shape should occur in the growing point of an underground stem, the change would doubtless manifest itself in any tubers that grew from the modified cells of that stem (provided that the new character were a dominant one or that the change affected both of the like genetic factors of the modified cells) and the change would at once be recognized as a bud-sport. But if exactly the same change should occur in the growing point of an aerial stem, the new tuber shape obviously could not manifest itself in the parent plant and would appear, if at all, only among the seedlings of that plant where it would of course be classed as a "seed-sport."

Whether or not mutations do arise as suggested here, the possibility seems great enough to warrant the extension of experiments in their artificial production to include the treatment not merely of plant ovaries but of all growing parts from which gametes may be expected eventually to arise. In animals of course treatment would have to be aimed at the germinal tissue but with the higher plants in general almost any meristematic tissue is potentially germinal tisue.

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[5] Correns has reported results with *Mirabilis* similar to my results with maize (Correns, C., *Ber. Deutsch. Gesel.*, 28: 418–434, 1910). There is little doubt also that de Vries's results with *Antirrhinum*, listed by him as ever-sporting variation, are to be interpreted in the same way (Vries, H. de, "Species and Varieties," pp. 315–322, 1905).

NOTES AND LITERATURE

VALUATION OF THE SEA[1]

It is very interesting to see a small country like Denmark lead so prominently in several lines of ecologic study. The nestor of plant ecologists, Warming, has done his work here. The ecology of fresh-water animals, particularly the plankton, has been studied by Wesenberg-Lund; the marine animals have been persistently studied by Dr. C. G. Joh. Petersen, and the ecological interrelations of the vegetation and the animals (particularly the fish) have been studied recently by the plant ecologist Ostenfeld. And although this is not all that has been done, it shows very clearly the network of problems on sea and land which has been studied from a modern ecological standpoint.

The paper now under consideration is one of the latest ecological contributions to a study of the conditions of life upon the sea bottom. The senior author, Dr. Petersen, has been at work on these problems since 1883. This long interval affords him a splendid opportunity to observe the character of the changes on the sea bottom. He says: "The impression of the fauna as a whole remains, however, unchanged within such a short period of time as one generation. This holds good for the Kattegat and the Baltic, thus for comparatively open and large stretches of water." Through his studies of the fishes, particularly the plaice, he came to the conclusion that, "To understand the distribution of animals right on the bottom, we must study the occurrence of each species throughout the whole of its life." When he learned that the plaice from the western part of Limfjord were inhibited in growth for 8 months, but when transported to its central part they increased four to five times their original weight, he concluded that serious attention must be given to their food. The cause for this difference he thought was due to the relative amounts of food present—but how was this to be determined? This led to a long series of experiments in methods of

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[1] "Valuation of the Sea. I. Animal Life of the Sea-Bottom, Its Food and Quantity" (quantitative studies). By C. G. Joh. Peterson and P. Boysen Jensen. Report of the Danish Biological Station to the Board of Agriculture, Vol. XX, pp. 1–76, Plates VI, 1911. Translated from "Fiskeri-Beretning for 1910." Copenhagen.

taking bottom samples by means of an apparatus attached to a long pole. By means of such methods he and his former assistant compared the number of animals per square meter. Dahl (1893) had made quantitative studies of the sea bottom at low tide by digging and the quantitative investigations by Petersen are believed by him to be the first made off shore. To improve these bottom studies a new apparatus was devised for work in deeper waters and the results of the present study are the first product of this new device, which permits samples of the bottom to be brought up in their natural position. Detritus collectors were also used in these studies. With the new sampler it was found that when food was abundant on the bottom there was a surface layer of *brown* or gray, and when the food was scanty this layer was black and malodorous. In view of the fact that the digestive tube of most of the animals which were not vegetable feeders or predaceous, contained a substance much like the surface *brown* layer, Petersen decided to investigate this subject more fully. The bottom layer he calls the "dust-fine detritus." This layer in addition to its inorganic parts consists of plant and animal remains, including some plankton organisms. Here then is a very much neglected source of food, and he remarks: "We have so long and so often heard of the rôle the plankton is considered to play in the economy of the sea, that we almost forget the other sources of food, which, however, at any rate in the smaller waters, certainly have even greater importance."

The dependence of animals upon plants for nutrition is just as intimate in the sea as upon the land. Therefore to understand the transformation of substance in the sea from the inorganic to the various kinds of animals one must begin with the marine plants. This phase of the subject was investigated by Jensen. In addition to the plankton plants there are those attached to the bottom, the algæ and grass wrack *Zostera*. The plankton of the North Sea is more abundant than in the more enclosed waters of the Kattegat. This plankton is not an important source of organic material; the main supply on the bottom is therefore either the algæ or the *Zostera*. Jensen shows that a characteristic feature of the metabolism of the sea is that the organic materials do not remain where they are formed but tend to become widely distributed, more or less uniformly over large areas. This might well be called Jensen's law. The vegetation of the sea, on account of its very limited range, except the vegetable plankton (and bacteria), is in marked contrast with that on land. And if it were not for the broadcast scattering of plant remains "the greater part of the bottom of the sea would be bare, not only of vegetation, but also of the animal life dependent on the vegetation." The source or sources of bottom deposits was now investigated in detail. In this connection the origin of the bottom deposits in Danish lakes is instructive. Wesenberg-Lund has found a considerable amount of organic materials on the bottom of these lakes. This layer is eaten by animals and a bottom soil is formed which has passed through the digestive systems of animals. This material is called *gytje* and is "formed in pure clean water chiefly by the excremental agency of the bottom-fauna." These organic materials are derived from the land, the littoral zone, or from the plankton. In deep lakes the plankton materials are dissolved before they reach the bottom, but in shallow lakes the soft parts of the plankton are also added to this layer. This condition naturally calls to the reviewer's mind the activity of earthworms in the soil, and Dall's[2] discussion of the banks of excrement formed by fish on the borders of the continental slopes.

Returning now to the bottom deposits in Danish waters, it is interesting to note the character of the organic bottom layer. This forms a brown layer from 1–2 mm. thick, composed of fluffy fine materials, both organic and inorganic. When tested for cellulose but little was found, but large amounts of pectose were present and similar relations resulted in tests of *Zostera,* thus supporting the view that *Zostera* was an important source of this organic material. Below this upper layer is a dark blue one, and both layers are free from odor. This kind of bottom is found in depths of more than 6 meters. When these bottom samples are examined it is found that the amount of carbon is greater when *Zostera* is abundant, rather than when plankton is abundant, and therefore Jensen concludes that the "main source of organic matter in the sea bottom must be due to the *Zostera* belt and not to the plankton organisms." Bottom samples taken out at sea show that there is a progressive diminution of carbon with distance from the shore, and therefore he again concludes that: "the organic matter in the sea bottom is mainly derived from the benthos formation at

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[2] *Pro. Biol. Soc. Wash.*, Vol. 5, pp. 10–11, 1890.

the coasts. . . . The result of these investigations is, therefore that the plants of the *Zostera* belt and not the plankton organisms constitute the principal source of the organic matter in the sea bottom.'' And this is in harmony with Petersen's contention that *Zostera* ''is certainly the plant, which for a great part conditions the fish-wealth of our coasts and attracts the fishes from the open and deeper waters into the shallow, enclosed bays and fjords.'' These are very important conclusions and deserve the careful consideration of students of marine animals in other localities. These investigations may well serve as models for investigators in many other regions, and this point of view should also be applied to lakes and streams.

When the black, foul-smelling bottom layer is examined it is found to contain much methane or marsh gas, probably due to the activity of bacteria, small amounts of oxygen and carbon dioxide. The black color is mainly due to ferrous sulphide, which in fresh water is mainly due to the reduction of sulphates by anerobic bacteria. These black muds contain the greatest amounts of organic materials. These soils are most abundant in the inner fjords, and they represent an early stage of the conditions, which in its extreme development is found in the Black Sea. Jensen states that he does not know of a similar condition of affairs in fresh water where he is inclined to think such a condition is prevented by humic acid. This recalls the phenomenon of ''stagnation'' which Whipple and others have studied in American lakes, and which is even occasionally found in rivers heavily charged with sewage. He concludes this chapter with this striking sentence: ''We may therefore, to a certain extent, regard the large oceans as the lungs of the sea, which supply the water-masses of the inner seas with oxygen and remove the superfluous organic matter.''

Jensen next considers the transportation of the organic materials from its course near the shores to the bottom. The winds are found to be an important agent in the process, as is shown by the presence of a larger amount of débris in the water after storms. By centrifuging this material is removed from the water, and when examined microscopically it is found to be composed mostly of materials so finely divided that it is not possible to recognize its source. Examined chemically, as well as microscopically, it is found to be ''completely identical with the uppermost brown layer on the sea bottom.''

The food of the animals of the Danish fjords is discussed by Petersen. The oyster has commonly been considered as a plankton feeder, although the materials found in its digestive tube are indistinguishable from the surface brown layer of the bottom and Petersen believes that the oyster feeds, in the main, upon the organic parts of the dust-fine detritus. The growth of oysters on objects raised from the bottom has been supposed to support the view that they were plankton feeders, but now since it is known, through the use of the centrifuge, that "pure" water contains the dust-fine detritus which is everywhere available, it also supports the view that the oyster feeds upon this as well. Petersen remarks that Lohmann was the first to recognize this detritus as an essential source of food for plankton animals, and now Petersen gives it much greater extension and importance. Thus in the past a clear distinction has not been made between the ordinary plankton and detritus feeding animals. Such feeders may be divided into two classes, those which filter the material out of the water, and those which take it off the bottom. In addition to the oyster the food of several other animals is considered, such as Echinoderms, shrimp and *Cardium*. He observed in an aquarium that the long-siphoned bivalve *Abra* sucks in through the siphon the surface layer of detritus and he suggests that the short-siphoned bivalves probably take their detritus directly from the water. To the reviewer it seems that here are several important suggestions for the students of our American Unionidæ. These molluscs are probably detritus feeders also, rather than wholly plankton feeders, and this may be a factor in their greater development in streams, compared with ponds and lakes, on account of the superior powers of streams in transporting detritus and other food.

Instead of taking up the food relations of each species, Petersen decided upon a larger unit, the animal community of Limfjord, Thisted Bredning, and he studied the mass of animals living on a square meter of the soft bottom. A review of the food relations of such a sample area showed that it was "*a detritus-eating Lamellibranch-worm community with its predatory animals.* This animal community forms the basis for a great part of the fish-life there." There are other communities. Thus nearer the shore in about 5 meters and less of water the *Zostera* zone begins, and this is a region which has not been investigated quantitatively. Here the dominant animals are small gastropods, *Rissoa, Littorina*, Nudibranchs, *Mytilis*, Amphipods, Isopods and numerous animals which abound in *Zostera*. Shoreward from this zone is the sand bottom, and finally the strand, each with its characteristic animals and food habits. Such a study calls to mind Möbius's description of the oyster bank as a biocœnose. In discussing the food relations of these communities Petersen adds a word of caution to those who in the future use the word plankton. They should not use it without stating exactly what is meant, whether plankton captured by a net, that which is small enough to pass through the net, and the detritus plankton. In summing up the general relation of these communities Petersen remarks: "All seems to me to indicate, that the greatest mass of the bottom-fauna per square unit is to be found in the smaller waters, where the bottom-flora occurs at least in the neighborhood, whilst the bottom of the oceans is as a rule to be regarded as waste regions. . . . One thing is certain, at any rate, the great, rich fisheries are not prosecuted on the open oceans, but always in more or less close proximity to the coasts or in the smaller waters."

For a detailed study of the productivity of the different kinds of bottom Petersen found it necessary to devise various forms of bottom samplers, so that the mass of life for a unit area of bottom might be determined. His investigations in this line were begun in 1896, but his earlier results were not published. His latest invention is a bottom sampler which permits one to secure a specimen of soft bottom, with the layers of mud in their natural position, from an area of about one tenth of a square meter. The animals are taken from this sample and their rough weight and dry weight are determined. The dry weight is believed to be the most precise estimate of the amount of life which a given unit area of bottom can produce. The many difficulties encountered in making such determinations are discussed fully, because he was eager to make, if possible, some calculation of the annual production of such a bottom. The fish are estimated to consume about 3 grams per square meter, and the whelks and starfish may eat twice as much food substance as the fish, or about 6 grams dry weight per square meter. For the Thisted Bredning, he estimates that the total amount of dry matter on the bottom is about 30 grams per square meter. He estimates that the bottom fauna reproduces its own mass each year, and consumes its own weight of food several times during the same period. Of course these estimates are provisional.

A very interesting and unique feature of this report is the series of four large diagrams which show the relative density of the population of the sea bottom. Each diagram represents one fourth of a square meter and its population. The drawings are natural size and show the average fauna. The suggestion is made that such quantitative pictures of the sea bottom would be suitable for museum exhibits, and progressive curators will no doubt utilize this idea.

This is a paper of more than usual interest, and one which will appeal to a variety of students. The general physiologist will be particularly interested in it for its bearing on the problem of the metabolism of the sea, the ecologist for the mutual food relations of the plants and animals, the economist and fish culturalist for its bearing on the problem of increasing the economic productivity of the sea, and the paleontologist, the geographer and the oceanographer each in turn will find much of interest.

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DOCTRINES HELD AS VITALISM

PROFESSOR H. S. JENNINGS

THE JOHNS HOPKINS UNIVERSITY

1. A well-known zoologist remarks that before certain papers had elucidated vitalism, he had had a personal meaning for the word, but after, he did not know at all what vitalism means.[1] Are not many of us in this case? And is not the remedy more papers on vitalism, such as we have recently had from Lovejoy, Ritter, Glaser, Woodruff, MacDougall and others—in order that we may know what is in each other's minds? In the obscurity, persons holding the same views are rallying to different battle cries, while those with diverse views march in supposed alliance. The following has arisen in the course of an attempt by the writer to clear his own mind on the matter, and particularly to discover for practical purposes whether the principles underlying the work of the biologist are essentially diverse from those of the rest of science.

The papers of Lovejoy[2] have been of the greatest value in distinguishing and classifying the views commonly held as vitalism, but there appear to be still certain important distinctions that need emphasis before the obscurity is quite dissipated.

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[1] "V. L. K.," in *Science*, October 20, 1911, p. 520.

[2] *Science*, November 26, 1909; April 21, 1911; July 21, 1911; November 15, 1912.

TWO DIVERSE GENERAL CLASSES OF VITALISTIC DOCTRINE

2. Two fundamentally diverse questions are dealt with in discussions of vitalism, often as if they were the same. The two questions bear respectively upon (*A*) the need for the division of science into two contrasted parts; and (*B*) the nature of science.

A. The doctrine perhaps most commonly signified by vitalism is that there is a deep-lying distinction of some sort between what occurs in the living, and what occurs in the non-living; with a correlative deep-lying distinction between the sciences that deal with the two; so that science must on this account be divided into two kinds, vitalistic and non-vitalistic.

B. Vitalism is sometimes used to signify merely the doctrine that mechanistic formulation is not adequate for giving an account of nature. In place of it there must then be put some other formulation, and this is at times called vitalistic. The clearest statement I have found of this is given by Rádl:

> One either banishes completely the idea of causality from science, or one distributes it in quantitative elements present everywhere, whose origin one holds not to be open to investigation; or one conceives the elements to be qualitative entities. The first view leads to geometry, the second to mechanism, the third to vitalism.[3]

3. It is clear that this "vitalism" *B* is the doctrine held for physics and chemistry under the name of "energetics" by such men as Ostwald. It is not presented by Rádl as characterizing a difference between the living and the non-living; it merely holds that science is necessarily non-mechanistic. It would be equally valid if there were no living things as objects of study.

4. Lack of clear distinction as to which of these two doctrines is meant by vitalism results in discussion at cross-purposes, one party dealing with the doctrine *A*, the other with *B*. Not infrequently indeed the two questions appear to be confused in the mind of a single

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[3] Translation from Rádl, "Geschichte der Biologischen Theorien," Bd. 1, p. 81.

thinker, the grounds he gives for vitalism tending merely to show that nature can not be explained mechanically, while the conclusion he draws is that there is a distinction between the living and the non-living; though he may also hold that the non-living can not be explained mechanically. In this way it is evident that no difference in principle is made between the living and non-living.[4]

5. To clear up this matter one may propose to himself the following:

Test Question.—Suppose it were demonstrated that mechanical formulation[5] is not adequate for living things, would that establish vitalism, *without a correlative demonstration that it is adequate for non-living things?*

If one answers this question affirmatively, his vitalism is of the class *B*, not requiring any difference in principle between the living and the non-living.

6. My own "personal meaning" for vitalism had been that set forth under *A;* I had supposed it an irreducible minimum for a vitalistic doctrine that it should make a deep-lying distinction of some sort between the science of the living and that of the non-living; but the arguments for vitalism adduced by various authors show that not all share this idea. It appears clear that the doctrine *B*, that mechanism is not adequate to nature in general, has no distinctive interest for the biologist; he shares his interest in such a question on an equal footing, theoretical and practical, with the physicist. Many persons who do not call themselves vitalists hold that the mechanical formulation of nature (as simply masses moving in space and time, and the laws of such movements, with nothing

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[4] A grosser form of the same confusion is at times seen in the proposition that science can not "explain" life. These statements as a rule imply such a meaning of the word *explain* that it is equally true that science can explain nothing whatever—so that again no distinction is made between the living and the non-livng. See the excellent development of this point by Glaser, *Pop. Sci. Monthly,* July, 1912.

[5] For our purposes it is immaterial just what is understood by mechanical formulation, provided the meaning is the same when applied to the living as when applied to the non-living.

else) has not demonstrated itself adequate for nature, organic or inorganic; and perhaps incline to the view that it will be shown inadequate. Such, for example, is the position taken by Bütschli, in what he considers to be an attack on vitalism,[6] such also is the position of the present writer. "Vitalists" that hold to nothing more than this will avoid classification with a totally different set of theorists if they pronounce themselves clearly on this question; and the same is true for "non-vitalists." Do you or do you not hold that there is a deep-lying distinction between the science of the living and that of the non-living? Do you hold that mechanism is or is not adequate to nature? These questions are not identical.

VITALISM AS THE DOCTRINE THAT THERE IS A DEEP-LYING DISTINCTION BETWEEN THE SCIENCE OF THE LIVING AND THAT OF THE NON-LIVING

7. Leaving aside such "vitalism" as is merely a general alternative to "mechanism," and understanding by it the doctrine that there is a deep-lying distinction between the occurrences in the living and those in the non-living (which I believe is the idea that at least lurks in the background in most minds, even though the grounds discussed may not directly bear upon it)—then its validity is open to the following:

8. *Test.—Examination to determine whether the characteristics of living things, or of the science of living things, that are urged as ground for vitalism, are really distinctive of the living, as contrasted with the non-living. If both living and non-living are found to possess them, these characteristics furnish no ground for vitalism.*

Much clearing of the atmosphere would result if we could so much as get a general expression of opinion as to whether this is a valid test. In the following I propose to examine by the aid of this test the common vital-

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[6] Bütschli, O., "Mechanismus und Vitalismus," Leipzig, 1901, pp. 7–8.

ism of class *A*. Different grounds may be urged, and have been urged, for making a deep-lying distinction between the living and non-living; we shall take up the main classes of these.

"DESCRIPTIVE" VITALISM

D. 9. Descriptive and more or less superficial differences of course exist between the living and the non-living; this is the basis for distinguishing "biology" from "physics" or "geology." The question of vitalism is, whether there are deeper lying distinctions than those so expressed, such as to require the division of science into two contrasted parts, vitalistic and non-vitalistic. Many distinctions may be admitted to exist, and to be of interest, without their being considered ground for such a division of science.

10. It is of course difficult or impossible to state *a priori* what sort of a difference would be sufficient ground for holding science divisible into two contrasted parts. The following seem to be fair propositions: (1) The burden of showing that there exists a difference of sufficient depth to require the division of science into two contrasted parts is upon those that make the positive claim that there *is* such a difference; (2) the difference must be one as to the nature and laws of the *occurrences* in the two fields.

11. The most plausible descriptive ground for vitalism would be that which maintained that since living things have consciousness, while others, so far as we know, do not, we have here, *eo ipso,* a deep-lying difference between the two fields; and this quite independently of the question whether the activities of living things require consciousness for their explanation. Besides the impossibility of demonstrating the presence of consciousness in living things generally, and its absence in the non-living, such vitalism appears quite sterile, since all that it would express is now expressed by using the word consciousness.

Quite a different matter would be the contention that the fact of consciousness in organisms requires us to use in accounting for their activities different principles from those employed in the inorganic; this comes up at a later point.

12. Other descriptive differences are sometimes urged, such as the fact that only among living things exist bodies that have both individualized forms and complex structure. Few, however, consider such differences to actually constitute ground for vitalism, though they may be held to serve as indices to other differences, that do constitute such ground. Such essential differences fall in one of the two classes, *E* and *F*, set forth in following paragraphs:

VITALISM BASED ON THE OCCURRENCES IN LIVING THINGS

13. The differences in *occurrences* that are seriously proposed as a basis for distinguishing vitalistic from physical science appear to fall into two general classes:

E. Vitalism based in some way on the appearance of new laws of action in living things, although these new modes of action depend experimentally on the perceptual[7] conditions there found.

F. Vitalism based on the doctrine that the activity of some non-perceptual[7] agent must be considered in accounting for what occurs in living things, so that the perceptual conditions alone do not furnish unequivocal determining factors for what occurs ("experimental indeterminism").

14. It may aid in understanding the drift of what follows to state first the conclusion to which the analysis comes. This conclusion is that theories of the sort mentioned under *E* do not make any valid distinction between the science of the living and that of the non-living, even

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[7] By perceptual or physical condition is meant any condition which could be detected by any sort of physical tests, *beyond the single effect from which its presence is first assumed*. This point is analyzed in detail in my paper in *Science* of June 16, 1911.

if we admit that what they state for the living is correct; this conclusion results from a consideration of the nature and method of science. Those mentioned under *F*, on the other hand, if admitted for living things, make a real difference of fundamental character between the two fields (unless we admit experimental indeterminism for the non-living also).

E. Vitalism Based on New Laws of Action in Living Things

15. This "doctrine of organic autonomy"[8] is well expressed by Lovejoy as follows:

> What the vitalist maintains is that, even given a complete knowledge *both* of all the laws of motion of inorganic particles and of the actual configuration of the particles composing a given body at a given cross-section of time, you could not from such knowledge deduce what the motion of the particles, and the consequent action of the living body, would be.

Lovejoy later continues:

> Again, such a view would not, in itself, deny that the behavior of organisms is a function of the number and configuration of the material particles composing them.[8]

16. Now, with regard to all theories fulfilling these conditions, the essential question is as follows:

Even if it be granted that under the conditions found in living things, the laws of action are diverse from those observable in the non-living, does the science of living things therefore bear a relation to the rest of science differing from that borne by the parts of inorganic science to each other? Or would this be merely one example, out of many, that from a knowledge of what happens under given conditions, it is frequently not possible to predict what will happen under other conditions?

17. An affirmative answer to this latter question will take away the ground for dividing science into two divisions, vitalistic and non-vitalistic, on such a basis. In the following it is proposed to examine the main sup-

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[8] *Science*, April 21, 1911.

posed grounds for vitalism falling under E, to discover whether they do make distinctions between the sciences of the living and the non-living that are essentially diverse from the internal differentiations of inorganic science.

The answer to this question will depend to a certain extent at least upon one's views as to the nature and method of progress in science; the way scientific generalizations ("laws") are reached. The questions of vitalism come back so directly to this that the best method of exposition will be to take up the nature and method of science explicitly.

18. *Formulation of the Work of Science.*—To understand the nature of science it is necessary to look at it in process of formation: to consider the condition of affairs before a given part of science is formulated, and to observe how the formulation occurs. To look upon science as something done and fixed, in order to grasp its character, is most misleading. Yet it is not uncommon. Bergson says, for example, that we necessarily treat the living like the inert, "carrying over into this new field the same habits that have succeeded so well in the old; and it is right to do so."[9] But if we look on science as *forming* habits (rather than as exclusively a thing with habits formed), there will appear no reason why it should not have the same direct and original relation to the living as to the non-living, forming its habits on the former as well as on the latter.

19. Viewing the matter in this way, we may say that science is a name for humanity's process of making a survey of the universe, with an attempt to formulate the results of this survey. So far as it deals with occurrences, we may say that it is an attempt to determine the conditions under which things happen. So far as it formulates its results, it gives "a series of propositions asserting what under given conditions our experience

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[9] "Creative Evolution," p. 195.

would be."[10] Or, since all "conditions," so far as we can deal with them, are experiences, what science tries to formulate reduces to propositions of the following form: "When you have such and such experiences, you will have such and such other experiences."[11]

Thus science is a process of getting varied experiences, including the experience of discovering how diverse experiences are interconnected, and of formulating these experiences, particularly the interconnections.

20. Generalizations, laws, are formulations, of the sort characterized above, that cover many experiences or things at once. The possibility of generalizations depends upon the fact that things which differ in some respects may be (or act) alike in other respects. This is what makes science as a system possible. Everything distinguishable is unique in some respect; otherwise, it would not be distinguishable; it differs at least in place or in time, and so in its relation to the rest of the configuration of the universe, from everything else. But it is found that certain of the differences between things do not affect certain of their properties or actions, so that we do find uniformities in nature. The study of how things or processes are determined is largely a study of what antecedent differences do, what do not, alter the particular succeeding difference in which we are interested; or just what succeeding differences they do make. But *whether a given diversity does affect a given property or action is determinable, in the first instance, only by experience.*

21. *Interruption of the Exposition in Order to Make the Application of this Point to Certain Doctrines Proposed as Vitalistic.*—The fact that two things which differ in some respects act alike in some respects is certainly nothing peculiar to living things. On this ground I can not see anything vitalistic in any sense, in one of

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[10] Balfour, "Defense of Philosophic Doubt," p. 181.

[11] This formulation of what science tries to do leaves quite open the underlying question of how it happens that we should have the experiences we do, and so appears to be valid whatever one's metaphysics.

the so-called vitalistic doctrines set forth by Lovejoy. This doctrine Lovejoy characterizes as follows:

> There is, however, a doctrine which goes beyond this mere assertion of organic autonomy, and declares that (in part) the action of living bodies *is not strictly a function of the number and spatial configuration of the particles composing them at any given instant.* In other words, organisms not only have unique laws of their own, but these laws can not even be stated in terms of the number and arrangement of the organism's physical components.[12]
>
> It is the doctrine that certain vital phenomena are not dependent upon "any fixed configuration of material parts existing in the organism or cell at the moments at which the phenomena take place"—*i. e.,* that the same phenomena occur in a given organism in spite of profound modifications of the composition and configuration of the parts, through a sort of redivision of labor and redistribution of functions among the parts that remain.[13]

22. In a former paper[14] I interpreted the proposition quoted above, that the laws of organisms "can not even be stated in terms of the number and arrangement of the organism's physical components," as a statement of Driesch's view, that the organism's physical components fail to include the factors necessary for the determination of the diversities that occur, so that the same set of perceptual components may act in different ways at different times (as determined, according to Driesch, by a non-perceptual factor), thus giving experimental indeterminism. It appears, however, from the discussion in Lovejoy's later papers[15] that he meant merely the fact "that the same phenomena occur in a given organism in spite of profound modifications of the composition and configuration of the parts." But this can be asserted equally as a positive fact for both living and non-living. With this interpretation we could in the first of the two statements quoted above substitute "bodies" for "living bodies," and have a proposition that holds for things in general. An iron body of a certain form moves toward the earth. We may change the form in most

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[12] Lovejoy, *Science,* April 21, 1911. Italics in original.

[13] Lovejoy, *Science,* July 21, 1911.

[14] *Science,* June 16, 1911.

[15] *Science,* July 21, 1911, and November 15, 1912.

varied ways; it still moves toward the earth. We may change the material, substituting lead, brass, stone, wood; it still moves toward the earth. We may change both form and material in most radical ways; it still moves toward the earth. In a clock that keeps time we may substitute iron wheels for brass ones; we may remove a number of the wheels, and substitute others in different number and form and made of different material, and still have the clock keep time. A stream that flows to the sea will still flow to the sea though its bed be altered in many ways; if obstacles are interposed, it will dig beneath, or overflow, or go around, or carry the obstacle away, and finally reach the sea. A microscope bringing light to a focus may be made of lenses of different materials, in different forms, in different arrangements. A diffraction grating may be substituted for a prism, in order to separate the rays of light of different velocities.

23. In all these cases it is evident: (1) that the particular changes made are such as do not affect radically the particular action in question; (2) we *could* make changes that *would* alter this action; (3) furthermore, in most cases at least, the process gone through does differ in certain respects after the change is made, although the general result remains the same. Now, precisely these same three statements can be made for the phenomena in organisms. When we remove a part of the egg of the sea urchin, or otherwise alter it, and it continues to develop, it is evident (1) that the change made is one that does not radically affect the development; this is a mere statement of the observed facts. But (2) we can readily make an alteration that will prevent the characteristic action, just as we can in the clock. No one, of course, denies this: all that is necessary is to remove the nucleus, or destroy its characteristic structure; and other changes will accomplish the same result. Again, (3) the processes after the egg has been altered are somewhat different from what they were before (as no one denies), though the development takes in its main features the

same course as before. The parallel appears to be complete between what happens when the organism is changed in ways not essential to its characteristic action, and what happens when the same thing is done for an inorganic combination.

24. I therefore quite agree with Lovejoy that when so interpreted "it is surprising that this, of itself, should be regarded as violating the rule of causal uniformity."[16] It appears equally surprising that it should be regarded as exemplifying something not common in the inorganic. To formulate the laws of what happens "in terms of the number and arrangement of the physical components" requires, for organic and inorganic equally, that we should recall that different sets of physical components often give the same laws (at least in main features); and the scientific procedure, in both fields, is to determine experimentally what alterations do, what do not, make a difference in the particular feature in which we are interested. Such an experimental analysis is (in large measure at least) equally practicable in the non-living and the living, and it has been successfully carried far in the latter. I therefore do not see how vitalism of any kind can be based on this state of affairs.

25. The vitalism of Driesch is based, not on the general principle, as interpreted above, but upon certain very special conditions which he believes can be demonstrated to exist in organisms, and which, *in their special nature,* render it impossible that the organism should continue to act in the "normal" way after division, except as some non-perceptual agent of a peculiar character acts as a determining factor. The concrete reasoning leading to this view is summarized in section 42 of the present paper.

26. *Resumption of the Exposition of the Work of Science.*—After we have had certain experiences of things and their interconnections, we can use these in prediction; indeed, the formulated scientific statement is in most

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[16] Lovejoy, *Science,* July 21, 1911.

cases essentially a prediction, for it says that if you get one set of experiences, you will have another also. But the prediction is made on the basis of experience already had. It could not be predicted without experience that the union of C, H and O in certain proportions will give the characteristic properties of the alcohols. There is no *a priori* reason that can be given for the appearance, in the first instance, of these characteristics. Yet we can use the experienced fact that they do appear in further prediction or explanation of what occurs under certain conditions. We learn by experience in the alcohol series what effect is produced by adding certain radicals; *after this* we can predict what effect such addition will have, *provided other conditions do not alter the case.* Whether any given set of the other conditions will alter the case can again be determined, in the first instance, only by experience.

This is certainly typical for the actual process of building up a large part of science. For such parts the fact of special importance here is the one last stated: *Whether any given change in the conditions will alter the action can be determined, in the first instance, only by experience.* This is exemplified in multitudes of instances by physical science, especially in the cases of "critical points." By numerous observations it is determined what progressive change in the properties of a substance is made by a certain amount of change in some condition, as temperature. A general law can be deduced which, since it works regularly so far as observed, would naturally be extended to include changes in parts of the scale not observed. But this would give false results, for at a certain point the characteristics suddenly change, becoming totally diverse from what they were, as in solidifying or vaporizing. Such sudden changes are most marked in chemistry. We have two substances mixed together, as H and O. We observe and formulate the changes they undergo as certain conditions are gradually changed. But at a certain point in this gradual change of conditions, the characteristics of the two substances alter radically, in a way quite diverse from that which our formulation hitherto has given us; in place of the two gases H and O there appears, for example, water. The science of chemistry deals with multitudes of these sudden changes, which are quite out of line with what is observed before precisely the necessary conditions are reached for producing them.

27. Now, among the things which have to be learned empirically are the effects of *configurations*. This is true even on the most strictly mechanistic view. The laws of the motion of a body when the configuration is such that forces from two other bodies act upon it at right angles had to be learned by experience, before they could be used in prediction. By varying the position of the bodies, the angles of the directions of the forces, the number of bodies or forces, etc., the laws of such variations were worked out, till now we have an extensive system that can be used in prediction. In chemistry we have a set of rules as to the effects of configuration that are not apparently continuous with the rules obtained in the way just set forth; the rules for the results when H and O are in one combination or another; when C, H and O, are in one configuration or another, had to be learned by experience in each case. We have thus in this direction a large store of propositions regarding configurations, that may be used in prediction. But for what will happen under any configuration never before experienced the only test is experience. It would have been quite impossible, for example, from a knowledge of what happens in the configurations given by the compounds of copper to predict the laws for the configurations given by compounds of carbon.

28. *Application to the "Doctrine of Organic Autonomy."*—This asserts, as we have seen, that with a knowledge of "all the laws of motion of inorganic particles and of the actual configuration of the particles compos-

ing a living body," one could not deduce the action of the living body.

Now, the configurations in living things are either the same as those in the non-living or they are different. If they, and all other conditions, are the same, and yet we get different results from them, then the uniformity of nature fails, and we drop into indeterminism. On the other hand, if they are different, then according to precisely the principles and practise of inorganic science, this different configuration is a matter whose consequences are to be learned only by experience. After it has been learned by experience it is a datum to be employed in prediction, exactly as are the corresponding data of inorganic science. The process of acquiring and using the knowledge is the same as that employed throughout the rest of science. To divide science into two divisions because the processes are the same in the two appears contrary to reason.

29. The thing that would show that the occurrences proceed on different principles in the two cases would be to discover that the *same combinations* acted differently in the two fields, for the fact that things in one configuration do not behave as they do in another is illustrated thoroughout inorganic science. The arguments for vitalism appear to lead, if maintained in a form such as to show a real difference in principle between living and non-living, almost always thus directly to indeterminism.

30. The strict mechanical theory holds that when we have gained an acquaintance with the elementary particles and with certain of the laws of their movements, combinations and interactions, we have experienced in principle everything that may occur, so that anything else which occurs can be expressed in terms of what we have already discovered. Thus, if we could be informed of the nature of the elementary particles and of their configuration in a living body, we could predict its action without acquiring further empirical knowledge.

31. But suppose that we discovered and could demon-

strate that in some of the configurations shown by living things, the particles move differently from their movements in the configurations dealt with hitherto in mechanics. This would simply show that the theory was in error which held that all possible effectively different configurations had in principle been experienced. It would leave us in the same condition that science would have been in if men had tried to predict the results of all configurations before the effects produced when two forces act at right angles had been experienced. To make the experience fuller, so that prediction would be possible, would require merely the extension of the same process used in getting the fundamental data of mechanics. The fact that some men supposed that they had gotten all the possible different sorts of experience when they had not seems no ground for dividing science into two contrasted parts; particularly when the second supposed part is built by a continuation of the process that produced the first.

32. While the considerations just set forth appear the decisive ones, certain other points may be noticed. The mechanical theory that from our knowledge of inorganic particles, their combinations and movements, we could predict behavior under all conditions that can be stated is one that, as matter of fact, can not be verified either for the inorganic or the organic. It may be held that perhaps the reason for this is that we do not yet know the conditions accurately enough to apply the laws of mechanics. But this answer can be given with equal force for the organic and the inorganic. To make exceptions to the mechanical theory largely destroys its *raison d'être;* for it is commonly held, not because it can be demonstrated, but because it furnishes a theoretically universal formula. If we fall back on the empirical evidence, we find difficulties of exactly the same character in applying the mechanical view to chemistry as to biology. There appears in the evident fact that the mechanical theory is as yet equally inadequate in the two fields

no ground for making a fundamental distinction between them.

33. A very subordinate additional possible ground for vitalism may be mentioned here. It may be held that combinations which have in fact never been produced before are frequently appearing in living things. This idea seems possibly in part the basis of Bergson's vitalism. Owing to the almost infinite number of variable factors involved in biological processes, it appears not improbable that this state of affairs actually holds. This might make it quite impossible to predict some of the things that will occur in biology, even with a knowledge of everything that had gone before; since the only test for what a new configuration will produce is experience. Does this constitute a basis for division of science into vitalistic and non-vitalistic? Apparently not. Suppose that a given previously unpredictable thing occurs, as a result of a configuration that had not before been realized. Suppose this be therefore accounted a vitalistic process. Now, suppose that after the lapse of time the same configuration recurs, and thus the same thing happens. It would now be no longer vitalistic. But the mere difference between a process that occurs once and the same process if it occurs again can hardly be considered sufficient for separating science into two divisions differing in fundamental principles. Just how many times a thing occurs seems rather irrelevant to the nature of the process, or to the nature of the science with which it deals.

On the other hand, if the same combination later recurred and did not give the same results, then indeed would we have a new principle involved; at the same time we should have to follow Bergson into indeterminism, the natural terminus of vitalistic theories.

34. *Psycho-vitalism and Finalistic Vitalism.*—These two doctrines differ, but for our present purposes they may be dealt with together. The former holds that the fact of consciousness in organisms requires us to use dif-

ferent principles for explaining what occurs in them from those employed in the inorganic; maintaining that in explaining movements consciousness must be substituted on the same footing of effectiveness for physical determining factors. Finalistic vitalism makes a similar claim for the employment of the end or purpose of a process, in explaining what happens.

In regard to both these doctrines, it appears that we are confronted with the same dilemma that we meet in other cases. Either for all diversities in physical action we can find antecedent physical diversities which are uniformly connected with the succeeding ones, so as to furnish a causal explanation for the latter, or we can not. In the former case a complete account or explanation of the processes can be given on the same principles as in all experimental science, so that there is no ground for separating off these processes in a special division of science. In the latter case we fall again into physical and experimental indeterminism; from the same physical conditions diverse physical results may follow, depending upon diversities in some factor not physical. This I should admit to be valid vitalism; it illustrates the way a vitalistic argument appears to wind up almost inevitably at experimental indeterminism.

F. VITALISM BASED ON THE DOCTRINE THAT A NON-PERCEPTUAL AGENT TAKES AN ACTIVE PART IN THE PROCESSES IN LIVING THINGS, ALTERING WHAT THE PERCEPTUAL CONDITIONS ALONE WOULD PRODUCE

35. The doctrine that a non-perceptual vital agent (as consciousness, purpose, entelechy) actively intervenes in the processes of organisms is at once the archetype and culmination of vitalistic doctrine; the one fully worked out exemplar of this type is the system of Driesch.

36. My analysis leads me to agree fully with Driesch that only by such active or dynamic vitalism is a real difference in principle made between the science of the oc-

currences in organisms and that for the inorganic. The change of Driesch's views on this point is worth sketching, as the type of the logical development of an attempt to establish a valid difference in principle between the living and the non-living. Driesch's earlier attempts in this direction (in his "Die Biologie als selbständige Grundwissenschaft" (1893), and the "Analytische Theorie der Organischen Entwicklung" (1894)), consisted in the advocacy of a "static teleology" for development; holding that purposiveness is shown, but this is "given" in the original structure of the egg, as that of a machine may be said to be given in its structure. But for the detailed analysis of the changes that occur, in the egg as in the machine, he held that perceptual determining conditions could be found for everything that happens:

> We even expect from the future that these analyses will be constituted of entirely clear and definitely perceptual (*greifbaren*) chemical, physical and structural elements, and that within the analysis there will not be found even the slightest appearance of the teleological view-point.[17]

37. But later Driesch became convinced that by such a descriptive or static theory the autonomy of life processes is not demonstrated, and he thereupon turned to an active or dynamic vitalism, in which the vitalistic agent alters the physical processes occurring. The steps by which his opinion on this matter became changed are fully and explicitly set forth in the paper on "Die Maschinentheorie des Lebens" (1896) and that on "Die Lokalisation morphogenetischer Vorgänge" (1899). In the former paper he remarks that in his earlier theoretical papers, "I saw the specifically biological feature of organic processes in a *given* order or structure, as I called it; in something 'static'; biology was for me in this sense tectonics."[18] In the latter paper, after stating this point again, he remarks, "I hardly need to emphasize the fact that I have now abandoned this standpoint"

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[17] Translation from "Analytische Theorie der Organischen Entwicklung," 1894, p. 149.

[18] "Die Maschinentheorie des Lebens," *Biol. Centralbl.*, 16 (1896), p. 363.

(p. 36); he insists on the need, if vitalism is to be demonstrated, of showing that a vitalistic agent is at work at *particular steps* of the occurrences. In a general theoretical paper of 1902 he says, "But such a descriptive teleology as I have myself formerly held has nothing to do with the assertion of real autonomy of the life processes."[19] This distinction between static and dynamic theories has been maintained by Driesch ever since; it is emphasized in "The Science and Philosophy of the Organism" (II, p. 136, etc.), static teleological[20] theories not leading to vitalism, while dynamic theories do so.

> The true problem is: *by what single acts* does the restoration of "equilibrium" take place here, especially in those cases in which it is proved that entelechy is at work, and that physicochemical diversities and potentials are not able to offer a sufficient explanation of what happens.[21]

Driesch answers this question by holding that a non-perceptual vitalistic agent may actively intervene at certain steps in the processes, altering what would otherwise occur. The method by which this agent operates we shall take up in a moment.

38. Now, it results from the occasional[22] active intervention of such a non-perceptual agent that the same physical combination may give sometimes one physical result, sometimes another, depending upon whether, and

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[19] "Zwei Beweise für die Autonomie von Lebensvorgängen," Separatabdruck aus: Verhdlg. des V. Internat. Zool. Congress, p. 2.

[20] It is to be noted that Driesch's vitalistic doctrines are throughout teleological; it is only the difference between "static" and "dynamic" that determines whether a given one of these doctrines asserts "a real autonomy of the life processes."

[21] "Science and Philosophy of the Organism," II, p. 177.

[22] Driesch does not hold that this agent is active in all the processes in organisms—so that it is by no means a mere name for the aggregate or unity or consequence of the physical conditions present. "We know already that not every event that takes place during morphogenesis and metabolism is the direct outcome of entelechian acts" ("Science and Philosophy of the Organism," II, p. 150). He does to death "any theory which tries to make entelechy arise as a new elemental consequence of some constellation" of physical conditions: "entelechy can not be regarded as arising from material conditions of any sort" (*ibid.*, p. 254).

how, the non-perceptual agent takes part in the process. This being so, it would evidently be impossible from a complete knowledge of all the physical or perceptual conditions to predict what would result from a given situation, even after one had once experienced it. In a previous paper,[23] I have characterized as experimental indeterminism this condition of affairs, in which, in the words of Driesch "Two systems absolutely identical in every physico-chemical respect, may behave differently under absolutely identical conditions, in case that the systems are living systems";[24] and have pointed out that for the work of the investigator experimental indeterminism presents the same practical situation as would absolute indeterminism.

39. It would certainly be difficult to imagine a more fundamental difference, either theoretical or practical, between two divisions of science, than that resulting from the acceptance of experimental indeterminism, along with the determining activity of a non-perceptual agent, for the living; science might well be divided into two contrasted parts, vitalistic and non-vitalistic, on such a basis.[25] Furthermore, as I have already set forth, this appears to me the form to which all vitalistic doctrines come, if they make any really valid distinction in principle between the sciences of the living and the non-living. It is perhaps worthy of note in this connection that the two most influential systems of vitalism at the present time—that of Driesch and that of Bergson—are avowedly such systems of indeterminism, either experimental or absolute.[26]

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[23] *Science*, June 16, 1911.

[24] See Jennings, *Science*, October 4, 1912.

[25] Unless indeed it be maintained that such indeterminism holds also for the inorganic—certainly not a widespread doctrine.

[26] Bergson's views are not, like those of Driesch, put in such clear form that it is easy to perceive just wherein the indeterminism lies, or whether the word as he employs it has any precise meaning. Apparently, however, the ground for Bergson's indeterminism is the idea that time makes a change in the action of things, without at the same time necessarily changing the physical substratum of such action. This appears to give the equivalent of experimental indeterminism.

40. The inquiry remains as to the grounds for this proper form of vitalism, based on the active intervention of a non-perceptual agent, and involving experimental indeterminism. Many doctrines of this character appear as mere general reflections, with no attempt at precise formulation of grounds and consequences; to the critic they are intangible. Driesch deserves the gratitude of all students of such matters for working out in full such a doctrine; for showing us whither such a road leads. The complex hierarchy of non-corporeal entities at which Driesch arrives, and which appears so fantastic to some critics, is the logical result of this full working out; persons who hold to the intervention of a non-perceptual agent, but refuse to draw the further consequences of such a doctrine, have no just ground for criticism until they have shown how such intervention can intelligibly produce the results it does without such a system as Driesch sets forth.

41. With the details of that system we shall not deal, but examine only the basis for the fundamental assumption. What ground is there for supposing that situations do occur which involve experimental indeterminism, and consequently the activity of a non-perceptual agent?

42. The concrete grounds which Driesch sets forth may be summarized as follows, taking the argument from development as a type. Driesch holds (1) that in order that what is produced should be determined by physical factors, it can be demonstrated that the egg would have to be a complex machine, with 'typical' diversities in the three directions of space, these diversities being necessary for the production of organisms differentiated in the three directions of space; (2) that a machine with such necessary typical diversities can not be divided in any plane you please and the pieces continue to act as did the whole machine (for the pieces would of course lack some of the necessary typical differentiations). Therefore (3) what the egg produces can not be determined (alone) by physical diversities in

space, but must be determined by the differentiations of some complex, but non-spatial, non-perceptual agent (for, being non-spatial, such an agent is not altered by division, as the physical machine is).

43. The further development of Driesch's system consists in working out logically, with extreme acuteness and subtlety, the characteristics of this complex, non-spatial agent, to which Driesch gives the name entelechy. We may take his conclusions as showing to what doctrines such a view leads. What we are now interested in is this; just where and how would arise situations involving experimental indeterminism?

44. Driesch sets forth that a physical system without entelechy acts differently from the same system with it: "a material system in space left to itself will behave differently from what it would if controlled by entelechy;"[27] "without entelechy there would be other chemical results,"[28] etc.

45. Now, precisely how does entelechy take hold to alter the action that would otherwise occur? So long as a vitalistic theory remains vague and refuses to specify the precise difference between the action if it holds and the action if it does not hold, we lack the essential point for forming a judgment of it. Driesch deserves the highest credit for recognizing this, and refusing to take refuge in vagueness; he attempts to show just how the vitalistic agent may act.

The general condition for anything to happen in the universe is, that uncompensated differences of intensity (of energy, etc.) exist; if two unequal "forces" act against each other, movement occurs in the direction of the greater, etc.

Now, just what entelechy does, according to Driesch, is to compensate some of the existing differences of intensity—thus holding back the action that would occur—and later to release that which was held back. This is

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[27] "Science and Philosophy of the Organism," II, p. 336.

[28] *Ibid.*, p. 254.

said to happen mainly or only "in the spheres of chemical and of aggregative events,"[29] these of course comprising most of what happens within organisms.

> But entelechy *is* able, so far as we know from the facts concerned in restitution and adaptation, to *suspend* for as long a period as it wants any one of all the reactions which are *possible* with such compounds as are present, and which would happen without entelechy. And entelechy may *regulate* this suspending of reactions now in one direction and now in another, suspending and permitting possible becoming whenever required for its purposes.[30]

This is the *only* thing that entelechy can do.[31]

46. It requires little thought to perceive how powerful such an agent would be. In a cell containing chemicals *a, b, c, d,* etc., all of which tend to interact, it could allow *a* and *c* to unite, but prevent *a* and *d,* etc. If our four chemicals were H_2SO_4, HCl, NaOH and KOH, such an agent could restrain the union of H_2SO_4 and KOH, and of HCl and NaOH, permitting the rest; as a result we should get a certain set of compounds. Or, if entelechy restrained others, we should get a different set of compounds from the same chemicals. If an organism swallowed poison, or if poison were in any way produced within its tissues, this agent could hold back the action of the poison on the tissues, so that the organism would be unharmed, until it had had time to eliminate these poisons through its excretory apparatus. If one of the two cells of an egg contained all the conditions required for producing both the anterior and the posterior part of the body, such an agent could hold back one set of processes and permit the other, thus deciding which part of the body should be produced. Or if the egg contained all conditions necessary for producing both a starfish and a sea urchin, such an agent could in this way decide which animal should be produced. If an organism contained the conditions necessary for producing

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[29] *L. c.*, p. 181.

[30] *L. c.*, p. 180.

[31] *L. c.*, pp. 178, 180, 185, 187, etc.

any of the actions of which men are capable, this agent could determine which actions would occur.

47. In such suspension of action entelechy transforms kinetic energy into potential energy; stopping a movement, the energy of the latter becomes potential (instead of being dissipated as heat, as is usual in stoppages that occur through other agencies). Later the movement can continue again, the potential energy being reconverted into kinetic.[32] Thus there is no offense to the principle of the conservation of energy; this is the reason why the action of entelechy is to be conceived in this precise way. Driesch takes up the case of a moving element having a mass *m*, and shows just how the process would work; the kinetic energy "is transformed into an equivalent amount of 'potential' energy located at the place of *m* and kept there till it is set free, that is, transformed into kinetic energy"[33] again.

48. Now, this portrays clearly the situation that involves experimental indeterminism. Consider this mass *m*, moving at a certain speed. It is stopped in a certain position by entelechy; its kinetic energy is converted into potential. Another body of the same mass lies in the same relative position; it has not been stopped by entelechy. The two masses are alike in all respects, but one contains a great amount of potential energy, the other none. There is no way of calculating from the position and the mass the amount of energy contained. If we studied one and determined its potential energy experimentally, we could tell nothing as to the potential energy of the other, though the two were perceptually alike in all respects. One would lie quiet; the other, on being released by entelechy, would proceed on its way with all the energy that it had before possessed.

This situation would be striking in the case of chemical reactions. Two substances, *a* and *b*, are in juxtaposition, under given external conditions. They do not

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[32] *L. c.*, pp. 219–221.

[33] *L. c.*, p. 220.

unite, being restrained by entelechy. Again, the same two substances are in juxtaposition, under the same conditions. This time they do unite, not being restrained by entelechy. If we have several chemicals in juxtaposition, the variety of results obtainable as a result of selective suspension by entelechy would be very great. By studying what happens under given conditions in one or several cases, one could discover no rule that would hold, as to what would happen under the same conditions in another case.

49. It is evident that the conditions set forth by Driesch for the operation of entelechy are present in every organism, and in every cell of every organism. Thus if the experimenter on organisms reaches different results in different cases, he may be quite on the wrong track in searching for some perceptual difference in the two cases; the diversity of results may be due to the diverse operation of entelechy on perceptually identical systems. This Driesch fully recognizes, as the quotation given in section 38 shows; other statements to the same effect, such as: "I reject absolute indeterminism, but accept experimental indeterminism," are quoted in a former paper.[34]

50. It will be observed that the acceptance of experimental indeterminism is a necessary consequence of the exposition of the work of entelechy given in the "Science and Philosophy of the Organism." But apparently this is an undesigned consequence; what the author attempted to establish is the activity of the non-perceptual agent, and he is merely compelled to accept experimental indeterminism into the bargain, apparently with some reluctance. He has not, so far as I know, touched in his published works upon the difficulty for experimentation induced by this condition of affairs.[35] He now,

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[34] *Science*, October 4, 1912.

[35] The quotations from Driesch on experimental indeterminism given in this and former papers are from letters, and are published with his permission. (But see note at end of this paper.)

as Lovejoy has recently set forth,[36] endeavors to minimize the difficulties presented to the experimenter by this condition of affairs, holding that "practically experimental indeterminism is not a great danger for science."

51. Certainly such a conclusion can not be deduced from the arguments advanced by Driesch while endeavoring to establish the activity of his non-perceptual agent. "Chemical and aggregative events," which he holds to be the sphere of operation of entelechy, comprise most of the events taking place in organisms, and if "entelechy is able . . . to suspend for as long a period as it wants any one of all the reactions which are possible with such compounds as are present, and which would happen without entelechy," etc., no experiment in biology fails to present the conditions for the interference of entelechy. Hence the experimenter must always be in doubt as to whether it is worth while to search for preceding perceptual differences determining different results in two experiments. Just so far as it does present such difficulties for experimentation, and no farther, is there basis for such a determining activity of a non-perceptual agent as set forth in Driesch's vitalism.

52. But is there reason to believe that if we could actually perceive all potentially perceptual diversities, we should really ever find that two systems identical in all perceptual factors behave differently? To me it appears that there is none; and that, so far as development goes, it can be asserted that for every case cited in support of vitalism in which diversities of development arise, definite preceding perceptual diversities can be pointed out, which experimentally determine the later diversities. I question whether any one would attempt to cite a case in which this can not be done. If this be the state of the case throughout, then empirical demonstration of experimental indeterminism is impossible, for no case of it ever arises.

53. If this be true, it seems important for forming a

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[36] *Science*, November 15, 1912.

judgment of the validity of this sort of vitalism. Now, it appears to me that in his recent attempt to show that such vitalism does not seriously affect experimental science—in the letter quoted by Lovejoy—*Driesch in effect admits this; pulls the empirical foundations from beneath his theory,* so far as they depend on the occurrence of any particular cases in which two perceptually similar systems behave differently, and is left in the position of maintaining in general what he denies for all particular cases; at least he saves himself from this position only by the expedient of asserting the "very great probability" of certain conclusions, in place of their certainty. The passage lends itself so fully to the arguments of those convinced that any doctrine involving experimental indeterminism has no sound basis that I should have hesitated to make use of it until similar statements were incorporated into some formal publication by Driesch, save for the fact that, with Driesch's permission, it has already been given currency by Lovejoy.[37] The passage is as follows:

> Practically, we may say that complete knowledge of the physico-chemical constitution of a given egg in a given state and of the behavior following this constitution in one case implies the same knowledge for other cases (among the same species) with a very great probability. But this is a probability *in principle* and can never be more. It would not even be a probability in the case that we did not know the origin (or history) of the "given egg in a given state," viz.: that this egg is the egg, say, of an ascidian. But to know this "history" or "origin" *is, of course, already more than simply to know* "the physico-chemical constitution" and its consequences in one case (which suffices in the realm of the inorganic).
>
> It *may* be that the eggs of fishes, echinoids and birds are the same in all *essentials* of the physico-chemical constitution. There happens something very different in the different cases on account of the different "entelechies."
>
> In spite of this; we know what will happen with great probability from one case, if you know that this egg "comes from a bird" and that the other "comes from an Echinoid." (I, intentionally, leave out of account here the existing differences in size, shape, etc., of the eggs in question; these *may* be *not* among the "essentials.")

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[37] *Science,* November 15, 1912. (See note at end of the present paper.)

Therefore: *practically* " experimental indeterminism " is not a great danger for science.

54. There are here two main points that are of interest in the present connection.

(1) In the case of comparing eggs *from the same organism,* evidently the situation resulting in experimental indeterminism never arises so far as the "very great probability" is realized. Thus the differences in the development of different cells of the sea urchin egg, or of fragments of *Tubularia,* or of the ascidian, on which Driesch bases so largely his vitalism, are all due experimentally to perceptual differences in the conditions, so that so far as experimental explanation goes, they are accounted for in the same sense that any diversity of action is accounted for in the inorganic world.

The only escape from this lies in Driesch's substitution of "very great probability" for *certainty.* The special grounds for this substitution are not evident. Even with regard to inorganic events, no man can say absolutely that what has happened under given conditions will "certainly" always happen under the same conditions; for the only test of this is experience, and some cases are not yet experienced. But no distinction along this line between organic and inorganic is evident, when once a "very great probability" is admitted for the organic.[38]

Those who begin by assuming intervention by a nonperceptual agent might argue that under the same conditions throughout, the purposes of entelechy would always be the same, hence it would always cause the same things to be done under the same conditions. But this is merely another way of admitting that no cases showing experimental indeterminism ever occur.

(2) With regard to eggs from diverse organisms there are two main points:

(*a*) The distinction made between knowing the history or origin, and knowing the physico-chemical consti-

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[38] But see note at the end of this paper.

tution signifies the following experimental situation. If an experimenter could have the egg of a starfish and another of a sea urchin presented to him, knowing nothing of their origin, could examine each so thoroughly as to perceive all the perceptual characters, all the physical diversities well known to exist between the two, and could observe that one develops into a starfish, the other into a sea urchin—*he could not predict, when a similar pair are again presented, which would produce a starfish. which a sea urchin* (although it is admitted that he could if he knew the origin of the two). Is there any plausible ground for such a proposition?

(*b*) As between these eggs from different organisms, the assertion is that the diversities in what occurs are not due to the present and observable differences in physical constitution, these differences being supposedly "not among the essentials."

Now, this abandons experimental evidence and *all possibility of such*, for it is well known that the eggs of different organisms do show differences in constitution, and that these differences are followed regularly by differences in what happens, which is all that experimental science can discover.

55. The result of these two admissions is then to leave without any possible empirical basis the idea that two perceptually identical systems can give diverse results, save only if there are ever cases with eggs of the same organism where the "very great probability" spoken of is not realized. All admit that the eggs of diverse organisms *are* perceptually diverse; Driesch admits that the eggs of the same organism always do the same thing under the same conditions "with very great probability." Nothing then is left, so far as development is concerned, but the substitution of this "very great probability" for "certainty," as a basis for the idea that an experimental, perceptual, cause is ever lacking for any diversities in result; and so for that kind of vitalism which requires and depends upon experimental indeterminism.

SUMMARY

In conclusion, the point of view developed in the foregoing may be briefly characterized and compared with that presented in certain other discussions. It agrees, I take it, with Lovejoy, Spaulding, and others, in admitting the possible validity of a "vitalism" that makes no distinction between the science of the living and that of the non-living, holding merely that mechanistic formulation is not adequate to nature in general; such "vitalism" being synonymous with "energetics" or "temporalism," or some similar doctrine. Confusion of such a doctrine with a vitalism that holds to a deep-lying distinction between the science of the living and that of the non-living is a common source of misunderstanding.

As to doctrines which attempt to make such a deep lying distinction, dividing science into two contrasted kinds, vitalistic and non-vitalistic, it farther admits (with, I judge, Lovejoy, Bergson, Woodruff, Ritter, Spaulding, Glaser and others) that configurations perhaps exist in the living, whose laws of action are not predictable from a formulation of what happens in configurations occurring in the non-living. But this is held to be merely an example of a general principle, equally well exemplified when diverse inorganic configurations are compared: from formulating the action of one configuration, that of another can not be predicted with certainty, until its action has also been experienced; this continual recourse to observation and experiment being one of the essential features of science in general. Hence it holds that such facts present no ground for dividing science into two divisions, vitalistic and non-vitalistic; but also that study of the organic configurations of matter gives results that are as fundamental as the study of inorganic configurations; results which no exclusive study of the latter could ever supply. Parts of biology are therefore "antonomous" in the same sense, and in no other sense, that the science of the compounds of carbon is autonomous in comparison with that of the compounds of copper.

It thus holds, in agreement with Driesch, that any "static" doctrine, in which admittedly the perceptual conditions determine what happens in the living system, does not make a difference in principle between the laws of the living and those of the non-living; but that to make such a difference, it must be held that the *same conditions* may act diversely in the two fields; thus giving rise to experimental indeterminism (and perhaps to the assumption of a non-perceptual factor for determining the diversities not otherwise accounted for, as in the vitalism of Driesch). But it holds (I take it with Lovejoy, Glaser, Woodruff, Spaulding, Sumner and perhaps most investigators) that we do not have grounds for supposing that such a condition exists; and that even Driesch's presentation results in the non-existence of any actual cases of experimental indeterminism.

Note.—Since this paper was written Driesch has published an article ("Ueber die Bestimmtheit und die Voraussagbarkeit des Naturwerdens," *Logos*, Bd. 4, 1913, pp. 62–84) in which he (1) states clearly his acceptance of experimental indeterminism for the organic (p. 65); and (2) attempts to show that the grounds for substituting *very great probability* in place of *certainty* are stronger for the living than for the non-living. The argument on this second point is a somewhat abstruse one, based on certain consequences held to flow from the concept of individuality.

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THE PRESENCE OF THE BARRED PLUMAGE PATTERN IN THE WHITE LEGHORN BREED OF FOWLS[1]

DR. PHILIP B. HADLEY

IN connection with certain inheritance studies, which were undertaken primarily with another purpose in view, a quantity of data are at hand which relate to the constitution of the White Leghorn breed of fowls. In the course of the studies mentioned many crosses were made between the White Leghorn (♂) and females belonging to a variety of black breeds, such as Black Hamburg, Black Minorca, Black Java and Black Spanish. In F_2, and later generations, there appeared a proportion of birds which possessed over the entire body a typical barred plumage pattern. This circumstance led to an inquiry regarding the source of this character in the cases mentioned, and the results of this study appear to warrant the conclusions presented in this paper.

EXPERIMENTAL RESULTS IN F_1

The stock used in these experiments was the best that could be obtained from reliable breeders who had bred the respective varieties for a long period of years. In all the crosses to be mentioned the White Leghorn ♂ was used with black ♀♀. First will be described the results obtained from the mating: White Leghorn ♂ × Black Hamburg ♀.

In the first generation from this cross nothing but white birds was obtained (110 individuals). No birds were, however, pure white. All showed black fleckings which were apparent in some cases only upon close observation. In a small proportion of birds, both males and females, there were present from one to three

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[1] Contribution No. 18 from the Biological Laboratory of the Rhode Island Agricultural Experiment Station, Kingston, R. I.

FIG. 1. White Leghorn ♂.

wholly barred or more often partly barred feathers. These usually occurred either among the wing coverts or the tail coverts, although they were occasionally seen in the primary and secondary wing feathers or on the neck. The barring on these feathers was always most distinct at the distal end of the feather, but was never of so good a quality as seen in the Barred Plymouth Rock breed. The "under color" was usually dark. For these F_1 results two series of matings were made and 110 chicks reared. In each series a different White Leghorn ♂ was used, but the results were the same in both cases.

EXPERIMENTAL RESULTS IN F_2

Of the F_1 fowls raised in 1910 one cockerel and five pullets were bred together in 1911. The cockerel was hatched as a pure white bird with no trace of black down feathering. When adult, a single feather showing a buff-yellow bar appeared among the coverts of each wing. Among the saddle feathers were a few showing some buff.

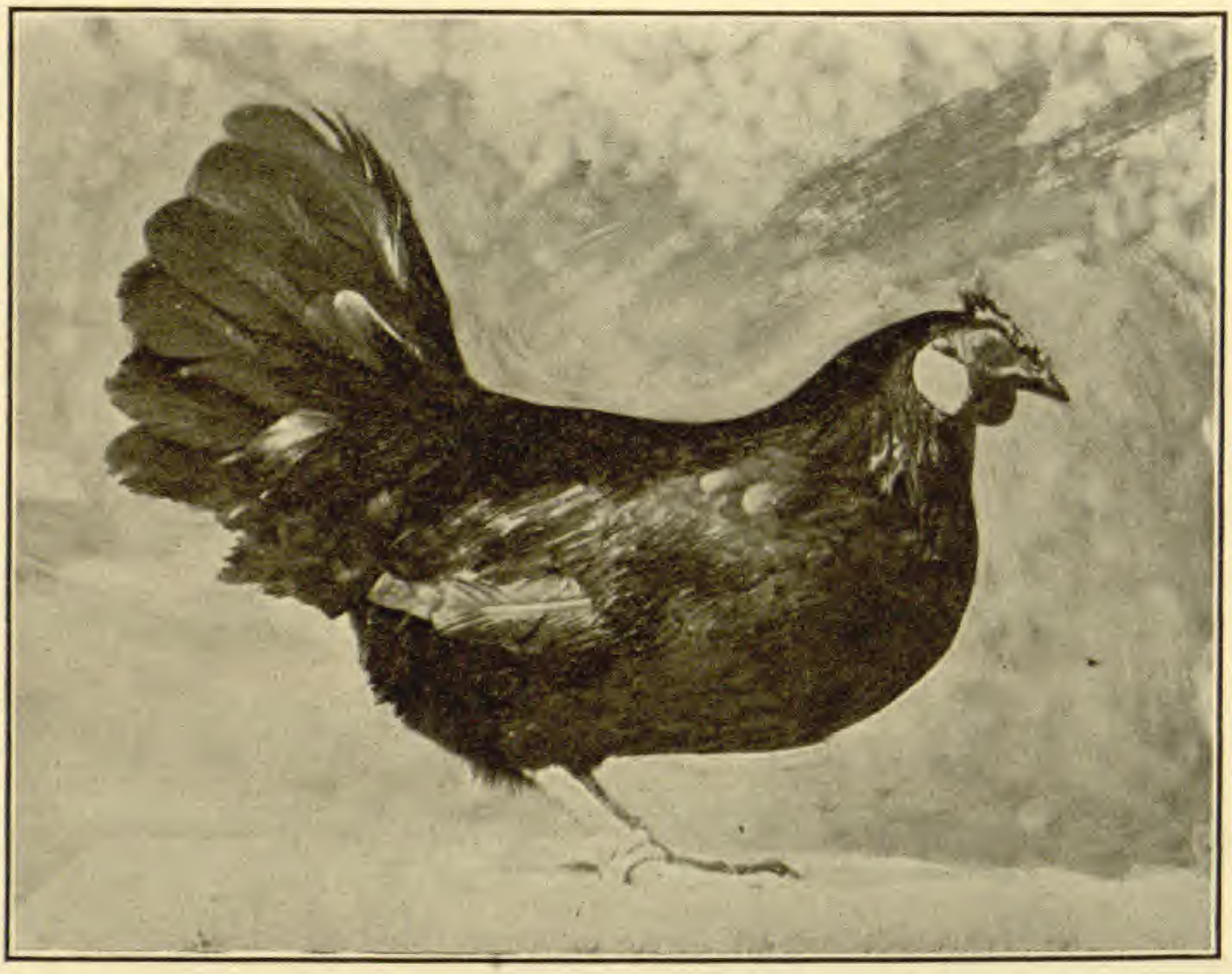

FIG. 2. Black Hamburg ♀.

Of the F_1 females employed in 1911, 201 *G* was a nearly pure white bird but showed a few splashes of black in the saddle feathers and wing coverts. Hen 201 *L* was hatched with a large patch of black down on the back, but eventually became a pure white bird. Hen 202 *G* showed many black splashed feathers on back and wings, while 211 *B* and 211 *V* had a small amount of black ticking. Hen 211 *K* was almost pure white.

The results of these matings showed blacks, grays, whites, splashed whites and barred birds. The blacks possessed as good color as in the original parent stock; the grays appeared as dilute blacks. Some of the whites were pure whites while others showed black ticking. The splashed individuals showed many grades, some being heavily splashed, some slightly. In the barred birds the barring covered the entire body. It was often indistinct, owing to the dark under color, which was never so light as in pure-bred Barred Plymouth Rocks. The barring appeared to correspond fairly well, however, with the barring depicted in early illustrations of years

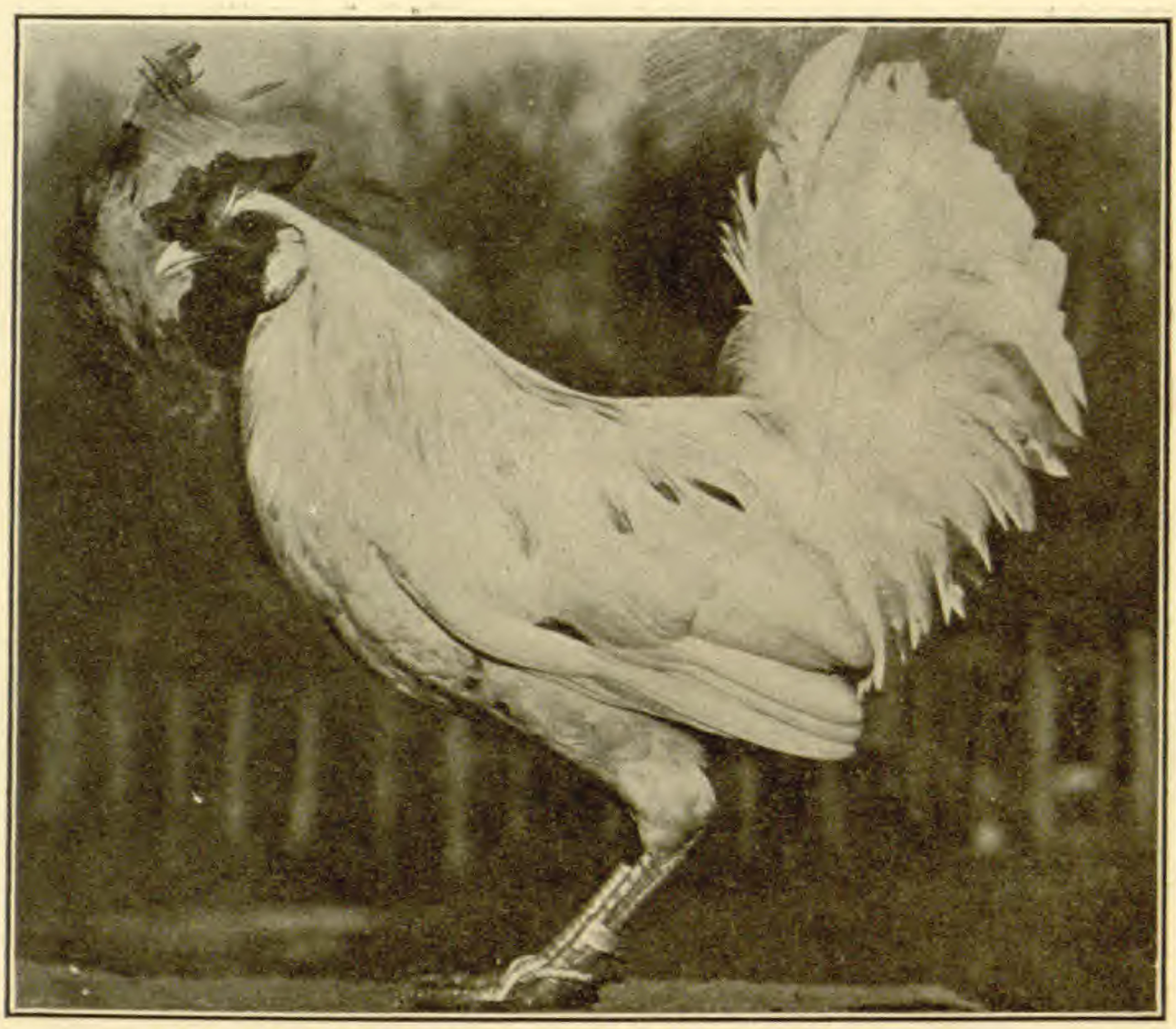

FIG. 3. F_1 Cross-bred ♂.

ago, before the Barred Rocks had been developed to the present state of perfection. The proportions in which these different types appeared in the 1911 series is shown in the accompanying table (Table I).

TABLE I

RESULTS IN 1911 FROM MATING

♂(W. L. ♂ × B. H. ♀) × ♀(W. L. ♂ × B. H. ♀).

Mating	Mother	Total Number	White	Black			Barred			Gray
				♂	♀	?	♂	♀	?	
314	201 *G*	30	21	0	6	0	2	0	1	0
315	201 *L*	22	16	0	1	0	2	0	3	0
316	202 *G*	6	5	0	1	0	0	0	0	0
317	211 *B*	17	15	0	1	0	0	0	1	0
340	211 *K*	23	18	0	0	2	0	0	0	3
341	211 *V*	19	15	0	0	1	0	2	0	1
Totals		117	90	0	9	3	4	2	5	4
Expected......		117	$87\frac{3}{4}$	0	$7\frac{5}{16}$		$14\frac{10}{16}$	$7\frac{5}{16}$		
Totals		117	90		16			11		
Expected......		117	$87\frac{12}{16}$		$7\frac{5}{16}$			$21\frac{15}{16}$		

[2] Includes the four gray fowls.

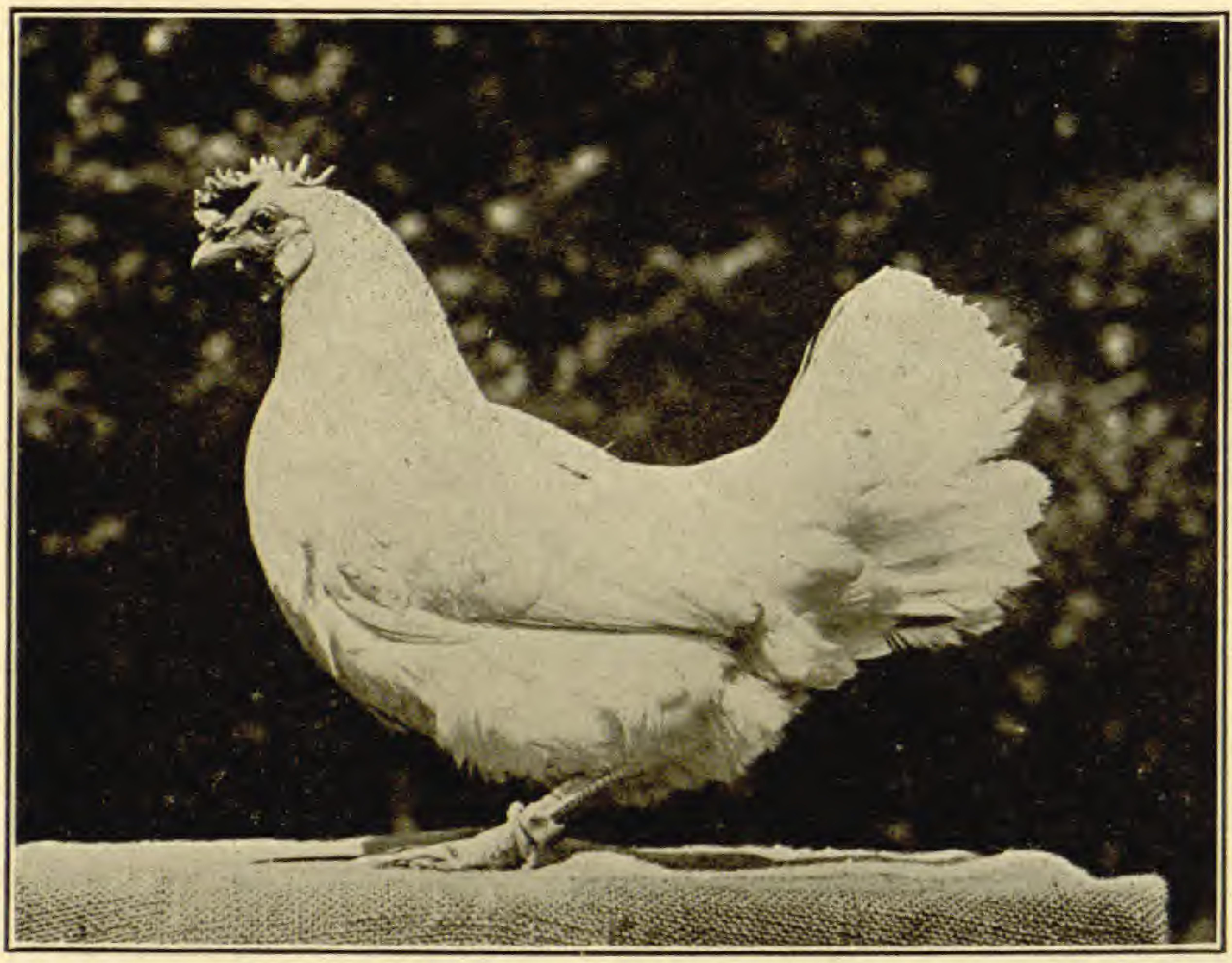

FIG. 4. F_1 Cross-bred ♀.

Before discussing this case, the results of a similar mating of other F_1 birds, in 1912, may be presented. The F_1 male was 8 *L*, mated with his sisters, 8 *B*, 8 *G*, 8 *H* and 8 *I*, all of which resembled the F_1 females in the 1911 series.

TABLE II

RESULTS IN 1912 FROM MATING

♂(W. L. ♂ × B. H. ♀) × ♀(W. L. ♂ × B. H. ♀).

Mating No.	Total No.	White	Black			Barred		
			♂	♀	?	♂	♀	?
456	18	13	0	1		2	1	1
457	13	8	0	1		3	0	1
458	14	10	0	1		2	1	0
459	25	21	0	0		2	1	1
460	67	54	0	3	1	5	3	1
Totals	137	106	0	6	1	14	6	4
Expected		$102\frac{12}{16}$	0	$8\frac{9}{16}$		$17\frac{2}{16}$	$8\frac{9}{16}$	
Totals	137	106	7			24		
Expected		$102\frac{12}{16}$	$8\frac{9}{16}$			$25\frac{11}{16}$		

DISCUSSION

It may now be asked how the presence of the barred

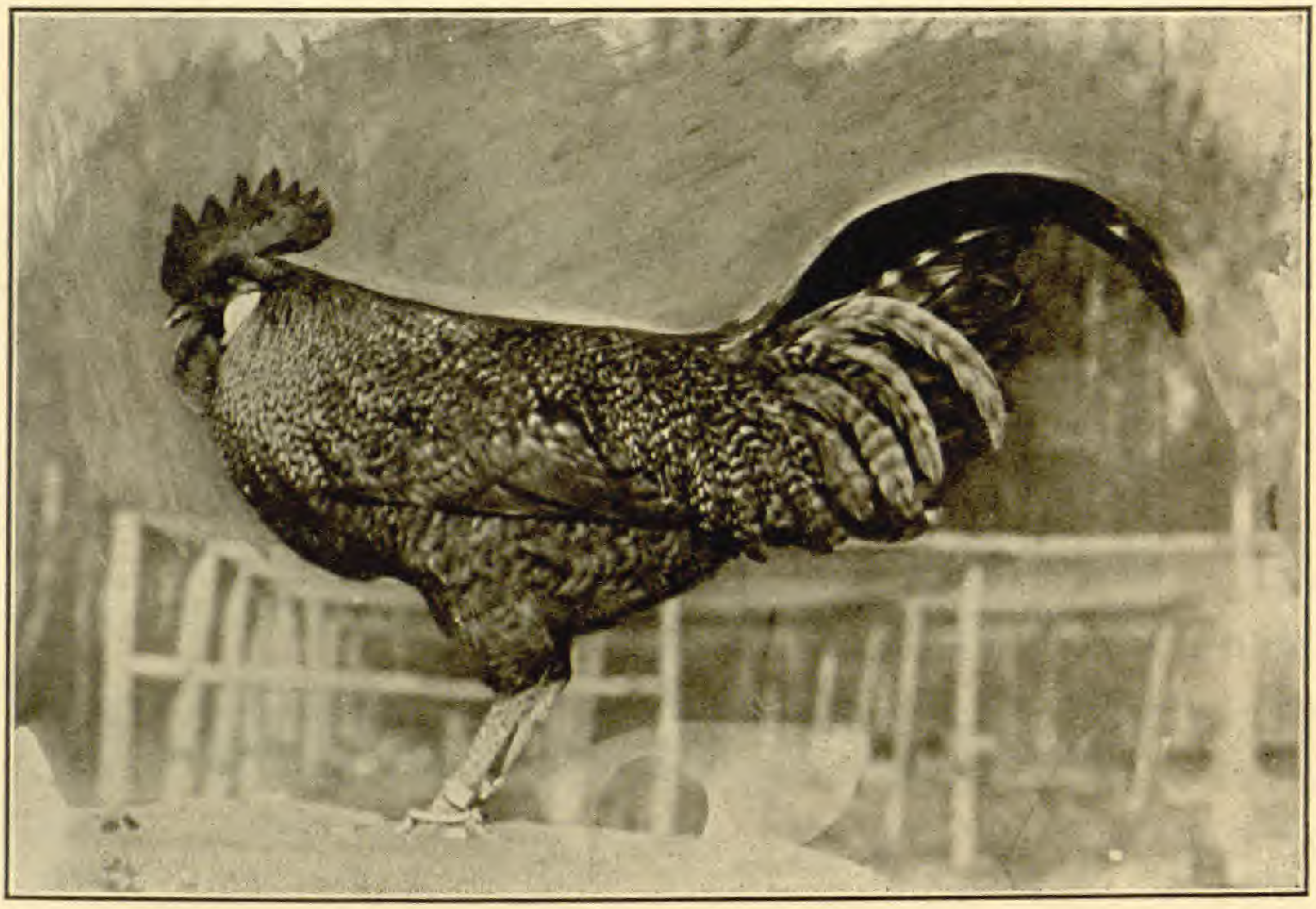

FIG. 5. F_2 Barred ♂.

birds is to be explained. Since it would be impossible for the Black Hamburg females to carry the barring factor, unless they also possessed an inhibition for barring, the obvious conclusion is that this pattern came from the White Leghorn. We may tentatively assume then that the W. L. ♂ is homozygous for barring, and attempt to ascertain to what extent the experimental results agree with the expected results in such a case.

First, it may be said that the W. L. breed in all probability carries a factor for black pigmentation (N), and also a factor which inhibits the manifestation of black in the plumage (I). Furthermore we may assume that it possesses a color factor C, and that the male is homozygous for the absence of the female sex factor, F, for which the females are heterozygous. In addition to this we may assume that in gametogenesis the barring factor, B, is repelled by F. There is no reason for assuming that the W. L. ♂ is other than homozygous for I. We may then write the zygotic formulas of the W. L. ♂ as:

FIG. 6. F_2 Barred ♀.

$$C_2B_2N_2f_2I_2$$

forming gametes

$$CBNfI \cdot CBNfI.$$

As to the zygotic constitution of the Black Hamburg ♀♀ there is no reason for supposing that they contain either B or I, although they do contain C and N; also they may be looked upon as heterozygous for F. We may therefore write their zygotic formula as

$$C_2b_2N_2Ffi_2$$

forming gametes

$$CbNFi \cdot CbNfi.$$

But, since, in all probability, none of the birds in these experiments lacks the factors C or N, we may leave these out of consideration, thus writing the W. L. ♂ formula:

$$B_2f_2I_2$$

forming gametes

$$BfI \cdot BfI,$$

and the B. H. ♀ formula as

$$b_2Ffi_2$$

forming gametes

$$bFi \cdot bFi.$$

The mating then becomes

W. L. *BfI* *BfI*
B. H. *bFi* *bFi*

B_bf_2Ii = white ♂♂, heterozygous, for barring and inhibiting factor.
$BbFfIi$ = white ♀♀, heterozygous, for barring and inhibiting factor.

In other words, the F_1 from mating of W. L. ♂ × B. H. ♀ gives birds that are all white, but heterozygous for *B* and *I*. The fact that some F_1 birds put up barred feathers may be explained on the ground that the dominance of the inhibiting factor (*I*), in heterozygous condition, was not complete. Where a little black was permitted to show, there it filled the pattern of an already barred feather.

What now takes place when the F_1 whites are mated among themselves? The F_1 males with the zygotic constitution *BbffIi* form gametes *BfI Bfi bfI bfi*. The F_1 females with the zygotic constitution *Bb Ff Ii* form gametes *BfI bFi Bfi bFI*. The mating of the F_1 stock may therefore be represented:

♂ *BfI* . *bfi* . *Bfi* . *bfI*
♀ *BfI* . *bFi* . *Bfi* . *bFI* giving in F_2

$$\text{♂♂}\left\{\begin{array}{lll} B_2f_2I_2 & (1) & \text{White, homozygous for } B \text{ and } I. \\ Bbf_2Ii & (2) & \text{White, heterozygous for } B \text{ and } I. \\ B_2f_2Ii & (2) & \text{White, homozygous for } B\text{; heterozygous for } I. \\ Bbf_2I_2 & (1) & \text{White, heterozygous for } B\text{; homozygous for } I. \\ Bbf_2i_2 & (1) & \text{Barred, heterozygous for } B\text{; no } I. \\ B_2f_2i_2 & (1) & \text{Barred, homozygous for } B\text{; no } I. \end{array}\right.$$

$$\text{♀♀}\left\{\begin{array}{lll} Bb\ Ff\ Ii & (2) & \text{White, heterozygous for } B \text{ and } I. \\ bb\ Ff\ i_2 & (1) & \text{Black, no } B \text{ nor } I. \\ Bb\ Ff\ I_2 & (1) & \text{White, heterozygous for } B\text{; homozygous for } I. \\ bb\ Ff\ Ii & (2) & \text{White; no } B\text{; heterozygous for } I. \\ Bb\ Ff\ i_2 & (1) & \text{Barred, heterozygous; no } I. \\ bb\ Ff\ I_2 & (1) & \text{White, no } B\text{; homozygous for } I. \end{array}\right.$$

The data presented above may be summarized as follows:

Characters	♂	♀	Total
White	6	6	12
Black	0	1	1
Barred	2	1	3
Totals	8	8	16

In other words, among every 16 birds in F_2 we might expect to find 12 whites, 3 barred and 1 black. The whites should be equally divided between the sexes; of the three barred birds, two should be male and one female; the one black should be a female. Moreover, one of the barred males should be homozygous for this factor, while the other male and the female should be heterozygous. Other birds, including both males and females, should carry the barring factor but not manifest the pattern since they will also be either homozygous or heterozygous for the inhibiting factor, *I*.

Having thus outlined what we should expect to see result in F_2, provided the original W. L. cockerel was actually homozygous for barring and also possessed factors *C, N* and *I,* we may now attempt to ascertain to what extent these theoretical results agree with the experimental data and furnish an interpretation for them.

First, referring back to Table I, it is apparent that the expected 3:1 ratio of a white × black cross is fairly closely realized among the 117 birds included in this table. Actual results were 90 white: 27 dark, while the expected are 88 white: 29 dark. Whereas we should expect only 7 + blacks, all females, we actually have 12 blacks (16 including the grays), including 9 females and 3 of undetermined sex. In part explanation of the discrepancy it may be said, however, that in very young chicks it is impossible to distinguish the blacks from the barred. In case chicks die during the first week of life, all those which would later develop barring must be described as black. It therefore can not be doubted that several of the birds described as black were actually barred. The only way to avoid this difficulty is to embody in the tables no chicks which die under three weeks of age. This plan was adhered to in the collection of data presented in Table II.

Regarding the barred birds, it is clear that more are called for than actually appeared; but, as already explained, the number would probably have been made up by addition of birds from the blacks, if these chicks had lived long enough to develop their barring. It is apparent, however, that the ratio of males to females is in the right sense.

Turning now to the results of similar matings presented in Table II, it is apparent that the experimental results conform more closely to the expected. In this case all the chicks were over three weeks old when described. The obtained ratio of whites to blacks is 106:31, while the expected is 102:35. The actual ratio of black to barred birds was 7:24, while the expected was 8 + : 25 +. As was to be expected, no black males appeared, while the number of barred males was approximately twice the number of the barred females (14:6), the expected being 17 + : 8 +.

It is thus clear that when only chicks over three weeks old are included in the tables, the actual and the expected ratios find close agreement, and appear to demonstrate the correctness of the view that the male White Leghorn fowl is homozygous for the barred plumage pattern. Evidence similar to that presented above has been secured from matings of White Leghorn ♂ with Black Minorca, Black Java and Black Spanish hens. Crosses involving the White Leghorn ♀ have not yet been made, but it seems likely that these fowls are heterozygous for the barred character, which probably follows lines of inheritance similar to the barring of the Barred Plymouth Rock breed. In the White Leghorn breed, of which several different males have now been tested, the barred pattern appears to exist as a cryptomere, much as in the breed of

White Plymouth Rocks, the chief difference in these two races being that whereas the white of the White Rock is a "recessive white," occasioned, in all probability, by the dropping out of a color factor, the White Leghorn is a so-called "dominant white," determined by the presence of an inhibitor acting upon one or both of the color factors, which also appear to be present in this breed.

CONCLUSIONS

These results serve to confirm suggestions made by Davenport[3] regarding the presence of barring in some of his White Leghorn stock, and also to explain some of the results obtained by Hurst[4] in matings, which involved the White Leghorn breed. They also help to explain some of those cases known to many poultrymen[5] in which barring (the "cuckoo marking") has resulted from the crossing of black (or dark) with white breeds in which the presence of the barred plumage pattern was not suspected.

Obviously this work has no bearing upon the *origin* of the barred pattern. It merely indicates that the White Leghorn breed of fowls, as studied, carries factors for both black and barring. The failure of the black to show depends upon the action of the inhibitor, *I*, while the barred pattern can appear only in the presence of the uninhabited *N* or *C*.

March 4, 1913

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[3] Davenport, C. B., "Inheritance in Poultry," Publication No. 52 of the Carnegie Institution of Washington; Papers of the Station for Experimental Evolution, No. 7, 1906.

"Inheritance of Characters in the Domestic Fowl," Publication No. 121 of the Carnegie Institution of Washington; Papers of the Station for Experimental Evolution, No. 14, 1909.

[4] Hurst, C. C., Report II to the Evolution Committee of the Royal Society, London, England, 1905.

[5] Wright, L., "New Book of Poultry," London (Cassell), 1905.

NOTES ON THE GEOLOGIC WORK OF TERMITES IN THE BELGIAN CONGO, AFRICA

THE following notes were taken during 1911 in the region about seventy-five miles west of Lake Tanganyika between latitudes 4° 15′ and 5° south. This region lies along the western base of the great mountain system which passes to the west of Lake Tanganyika.

The Loami River Region.—The gentle slope between the base of the mountain and the swamp of the Loami river is pretty generally covered with termites' nests averaging about ten feet in height and forty feet in diameter at the base. Some of the mounds are much larger, but they are generally composed of two nests which were started so close together as to grow into one mound. They are very much rounded by weathering, but a few of them have newly formed pinnacles projecting from near the tops.

In many well-drained places as many as five hills to the acre may be counted, but this is more than are ordinarily found. One may walk for three or four hours, however, through country averaging more than one nest to the acre. The most favorable places for the nests seem to be where the soil is deep and well drained.

Methods of Construction.—The newest nests recognized were small slightly raised mounds about three feet in diameter with two or three small chimney-like pinnacles rising from them. Before there was anything to attract attention above the surface of the ground, the termites had made a nest below the surface and had mixed the surrounding soil with excrement from their bodies to form a stiff clay. From this base, they then built small chimneys about a foot in diameter, with passages about two inches in diameter leading from the nest. It is up through these openings that the mounds are built, the small white ants carrying up little balls of soft clay and plastering them around the tops of the chimneys. This is the only work in which I have seen the workers expose themselves to the sunlight.

The chimneys are continually being washed down by the storms, forming large rounded mounds with passageways about two inches in diameter leading through them and down below the surface of the ground. These passageways are enlarged at irregular intervals into spherical chambers about four inches

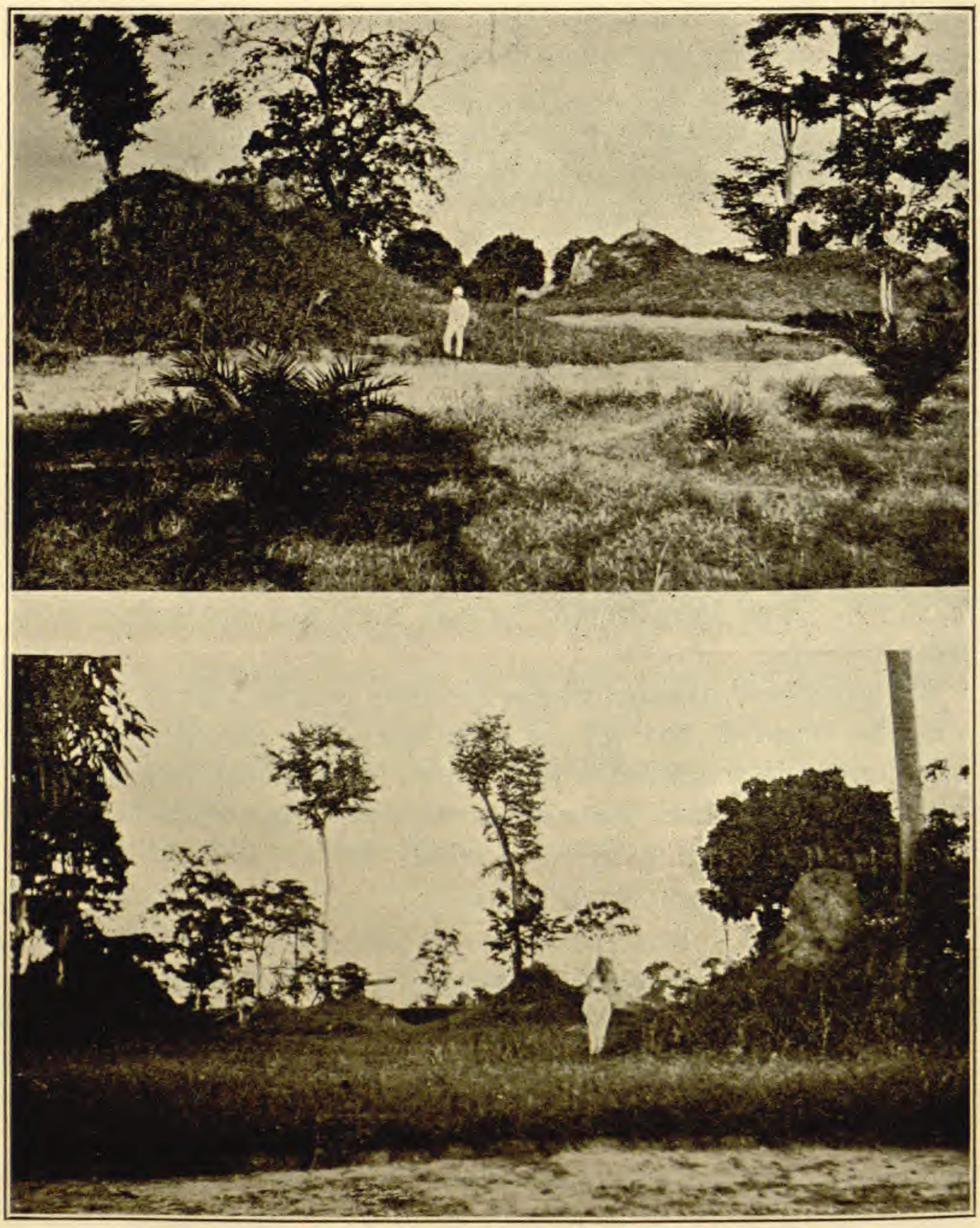

FIG. 1. Termites nests in Stanleyville. Photos. by D. Steel.

in diameter, and in each chamber a cellular ball of chewed-up vegetation is made to fit loosely. The eggs are stuck to the walls of the cells and are presumably hatched by the heat from the organic matter. A ball freshly dug and containing the eggs is always noticeably warm.

I have never seen the eggs being put in place, but have been told that they are carried from the queen and put in place by the workers.

Fig. 1 gives a section through an ant-hill as shown in an excavation made to get clay for plastering the walls of a house.

I have seen a termites' nest excavated for this purpose to a depth of five feet, but further than this I have no evidence as to the depth of their work. Laterally their passageways seem to underlie vast areas, as it is seldom that one can put a wooden box on the ground so far from a foraging route that the insects will not find it out in a few days.

The Stanleyville Region.—There are a great many termite nests in the forest country around Stanleyville, but they are of a slightly different character from those previously described. The newer portions of the Stanleyville nests, instead of being chimney-like structures, resemble the white ants' nests of Brazil as described by Dr. Branner. They are built of earth, in many cases containing grains of sand and masticated vegetable matter. This is built on in a plastic condition leaving no external openings and hardens on exposure.

The walls of these nests wash down, forming rounded mounds and in time form mounds similar to those described from the Loami valley.

A general idea of the age of the nests can occasionally be obtained in this region from the size of some of the trees which are found growing on the mounds. Fig. 2 shows the stump of a camwood tree which grew on a mound near Stanleyville. Camwood is a hard, red wood much resembling rosewood in appearance, and this stump is thirty inches across the top.

Along the Kasai River.—Still another variety of termite nest is found in the drainage of the Kasai river. This variety does not show the aversion to poorly drained localities that was noted in the Loami valley, but seems rather to prefer the clayey soil of the lowlands to sandstone hill areas.

The nature of the above-ground portions of the nests is illustrated in Figs. 3 and 4. While these termites have extensive underground foraging trails similar to those mentioned above, there seems to be much less of the nest below the general surface of the ground.

The live part of the nest is a dome-shaped chamber at or slightly above the surface of the ground. This chamber ordinarily has walls about six inches thick of firmly cemented sandy clay and enclosing a cellular mass consisting mostly of masticated vegetation. Fig. 3 shows one of these chambers which has been broken open. It also shows a portion of the cellular mass within.

The largest of these nests reach a height of about twelve feet

Fig. 2.

Fig. 3.

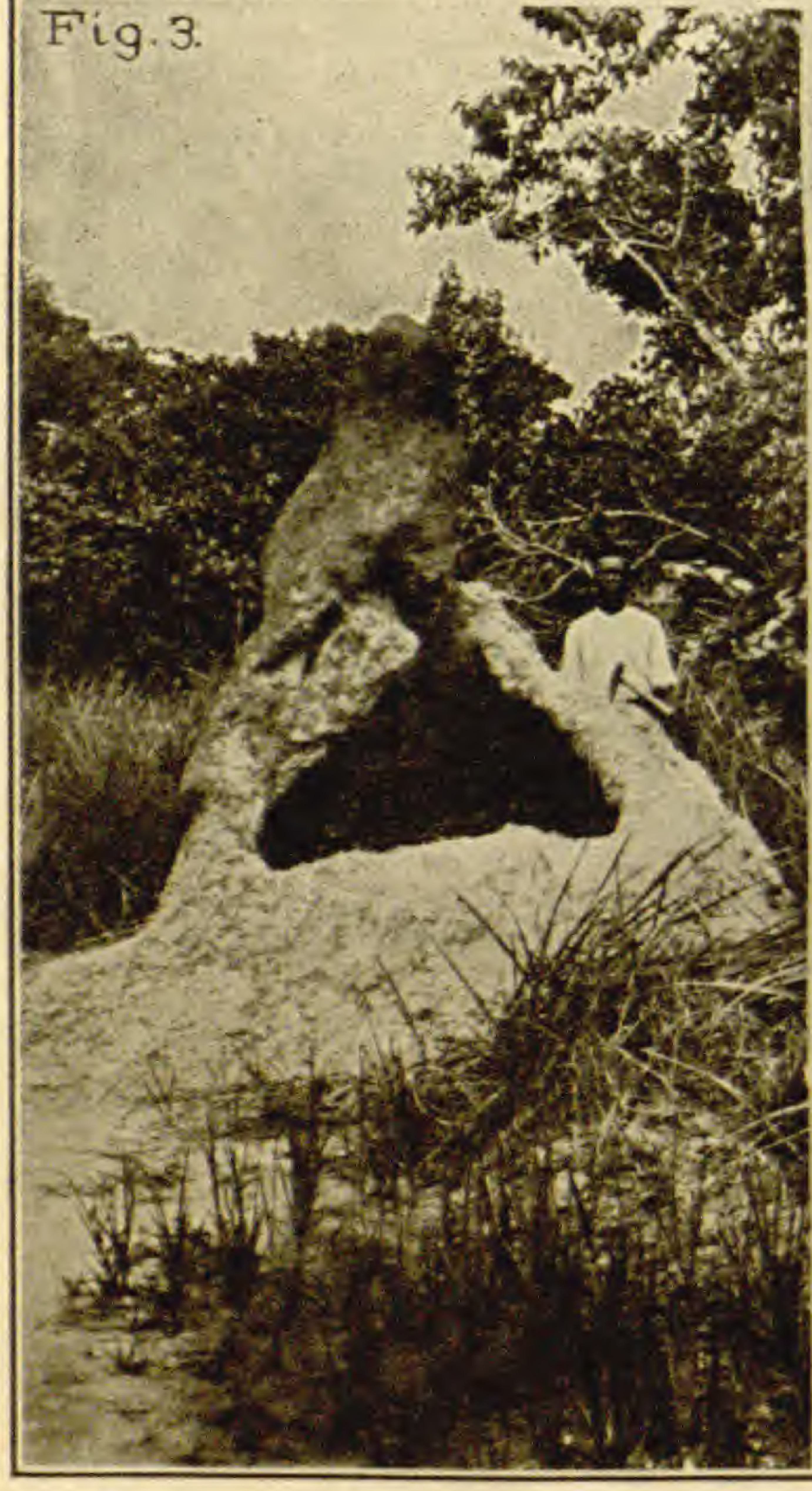

Fig. 4.

Fig. 2. A termites nest in Stanleyville.
Fig. 3. A broken termites nest near Dima on the Kasai River.
Fig. 4. A termites nest near Dima. Photos. by D. Steel.

and have a diameter at the base of ten or twelve feet. They have no visible openings.

Habits of African Termites.—While the ants of equatorial Africa do not seem to be nearly so numerous or of nearly so much importance to man as those of tropical America,[1] the termites and their work are evident throughout practically the entire Congo basin. They are not a serious pest, however, as their habits are known, and only simple precautions are required to prevent their ravages.

Termites seldom expose themselves to the light, so if an object is placed on supports so far from the ground that they can not easily fill up the intervening space with earth, it is practically safe from their attacks. If, on the other hand, the object happens to be an especially palatable piece of wood, a bale of cloth, or a leather case, and is placed directly on the ground, it is remarkable how soon the termites will find it and begin their attack. A box left in this way seldom suffers much damage the first day, but if left for several days, the bottom may be pretty completely eaten away.

I have never known termites to do any damage farther than about two feet above ground, but there is another insect, a small beetle, which will often eat away the entire inside of building timber leaving nothing visible of their work but the small holes where the insects enter the stick and finely powdered wood which they throw out through those holes.

There are several species of timber, however, which are not attacked by either insect. The walls of practically all of the buildings of the Congo are supported by timbers driven into the ground, and where these timbers are selected by natives who understand the habits of the insects, they are seldom eaten away.

Termites as Food.—I noticed one evening that termites were swarming from all of the nests around our camp. A cry went up among the natives, and the women and children ran with dishes of water and seated themselves around the openings in the nests. They then caught as many of the insects as they could, and either put them into the water so that they could not fly away, or ate them at once. Those which were put into the water were afterwards dried and were considered a delicacy.

DONALD STEEL

OROVILLE, CALIF.

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[1] J. C. Branner, "Geologic Work of Ants in Tropical America," *Bull. Geol Soc. Amer.*, XXI, 444–496.

NOTES AND LITERATURE

WORK ON GENETIC PROBLEMS IN PROTOZOA AT YALE

Two ideals are commonly represented in the practise of university laboratories. Some concentrate upon a unified set of problems, endeavoring thus to make a definite mark upon science; others cultivate breadth, the different workers taking up problems lying in diverse fields. The work done in recent years at the Yale Zoological Laboratory by Professor L. L. Woodruff and his associates is an interesting example of the former type; the present is an attempt to give a unified survey of this work, which has been directed with concentration and effectiveness upon the general questions of reproduction in unicellular animals.

The work on these matters may be represented as a tree with a single trunk and diverging branches. The trunk consists of the study of Woodruff's culture of a single line of *Paramecium,* begun in 1907, to test the hypothesis that death is a necessary consequence of continued reproduction without conjugation. This study was itself an outgrowth of an investigation (the seed of the tree) made by Woodruff as a student under the direction of the investigator who has been chiefly responsible for the recent revival of work on the more general problems of reproduction in the Protozoa, Professor Calkins, of Columbia University. This first investigation (1) led to results in agreement with the views of Maupas and of Calkins, that continued reproduction without conjugation results inevitably in death.

> All the cultures give incontestable proof that the species studied [*Oxytricha fallax, Pleurotricha lanceolata,* and *Gastrostyla steinii*] pass through cyclical periods of general vitality. The periods of depression lead to death if the culture is subjected to the same environment. Minor fluctuations also occur which may be called "rhythms."
>
> A rhythm is a minor periodic rise and fall of the fission rate, due to some unknown factor in cell metabolism, from which recovery is autonomous.
>
> A cycle is a periodic rise and fall of the fission rate, extending over a varying number of rhythms, and ending in the extinction of the race unless it is "rejuvenated" by conjugation or changed environment (1, page 627).

Woodruff, however, felt that the matter needed further test, particularly with relation to the part played by environmental conditions, as compared with that dependent upon internal factors. Suspecting that the ultimate death might be due rather to the constancy of the conditions than to anything inherent in the process of living, he set in progress on May 1, 1907, a line derived from a single individual of *Paramecium aurelia,* keeping it under varied conditions. That is, the culture medium was altered from day to day. This line was found to reproduce actively, without degeneration and without conjugation. From time to time Woodruff has published brief papers showing the progress of this line and the relation of the facts to general problems. Such bulletins have been issued at the 465th generation (5); then at generations 490 (3), 1,185 (6), 1,238 (7), 1,795 (9), 2,121 (10), and 3,029 (22). The culture at last accounts had been in progress five years, during which time the animals had reproduced 3,029 times without conjugation; the potential number of progeny produced being represented by 2 raised to the 3,029th power (a number composed of 912 integers), and constituting a volume of protoplasm equal to 10^{1000} times the volume of the earth (22, page 123). Woodruff well concludes:

> I believe this result proves beyond question that the protoplasm of a single cell may be self-sufficient to reproduce itself indefinitely, under favorable environmental conditions, without recourse to conjugation, and clearly indicates that senescence and the need of fertilization are not primary attributes of living matter (22, page 123).

This conclusion has been supported by the work of other investigators (notably by that of Enriques), but all will agree that the mainstay of this most important generalization is this work of Woodruff.

Under varied conditions the reproductive power of this line thus showed itself to be indefinitely great. Now arose the question whether the variation of the conditions was the essential point, or whether the death in a constant hay infusion may not be due to a lack in the hay of elements essential to the prolonged life of the cultures; in other words, whether it may not be a case of slow starvation. To test this, Woodruff and Baitsell (15) on October 1, 1910, separated from the line living under varied conditions a set which was kept in a constant medium of ¼ per cent. beef extract. After seven months the authors report that this was "practically as favorable a medium for the reproduction of this pedigree culture of *Paramecium aurelia* as the 'varied' environment, and therefore . . . it appears fair to conclude that it is the 'composition' of the medium rather than the changes in the medium which is conducive to the unlimited development of this culture without conjugation or artificial stimulation" (15, page 141).

From this basic investigation, giving conclusive results on an ancient and fundamental problem, have grown branch studies by Woodruff and his associates on a large number of diverse factors affecting reproduction. This work has been done mainly on *Paramecium*, as a contribution to the general effort to get the genetic physiology of one type animal fully cleared up, but other infusoria have likewise been dealt with. We may divide these studies into (1) those on internal factors and (2) those on external factors.

1. *Internal Factors.*—In his first paper (1) as we saw, Woodruff distinguished certain small changes in the reproductive rate, which he called rhythms. The question comes up as to whether these, like the changes resulting in death, may not be due to something in the environmental condition, perhaps to fluctuations in these conditions. This problem was attacked by Woodruff and Baitsell (16). Their result was that practically constant conditions of the environment tend to bring out the rhythms more clearly, from which it is concluded that they are due to causes within the organism. A possible chance for doubt of this conclusion arises from the question whether the precautions taken to keep the bacterial content of the cultures uniform were adequate; certain work done in the Zoological Laboratory of the Johns Hopkins University indicates that they were not—in which case the fluctuations in the reproductive rate might be due to variations in the bacterial content of the medium.

Baitsell's study (13, 23) of the effects of conjugation between closely related individuals in *Stylonychia pustulata* belongs here. It was found that after such conjugations the animals do not continue to reproduce. Baitsell summarizes as follows:

> The experiments show conclusively, it is believed, that conjugation is induced by *external* conditions affecting the organisms, and bears no relation, in this form at least, to a particular period of the life cycle.
>
> It is suggested that infertility of syzygies in these cultures is the result of the fact that the gametes had an identical environmental history (23, page 74).

With regard to the second suggested conclusion, doubt may be raised, since it was not shown that under the conditions gametes with diverse environmental history give more fertile pairs; possibly conjugation involves regularly the death of a large proportion of the gametes.

Here perhaps belongs also the study by Woodruff (14) showing that *Paramecium caudatum* and *Paramecium aurelia* are distinct species:

> Since one of the crucial tests of a species is its ability to breed true to type indefinitely, *aurelia* and *caudatum* have adequately met this test during more generations than any other animal under observation (14, page 237).

2. *External Factors.*—Studies of the effects of a long list of external factors on reproduction have branched out from the main trunk given by the study of the life cycle. In his "seed paper" of 1905 (1), Woodruff had included a number of experiments with various chemical and physical agents, showing particularly that Protozoa are extremely sensitive to solutions of electrolytes. He followed this up in 1908 (4) with a study of the effects of alcohol. This showed that:

> (1) Minute doses of alcohol will decrease the rate of division at one period of the life cycle and increase it at another period of the life cycle. (2) When alcohol increases the division rate the effect is not continuous, but gradually diminishes and finally the rate of division falls below that of the control. . . . (4) Treatment with alcohol lowers the resistance of the organisms to copper sulphate (4, page 104).

Woodruff and Bunzel (8) further undertook a precise study of the directly destructive effects of various salts and acids on Paramecia taken from the pedigree culture serving for the trunk experiments. The results of this work, not bearing directly on reproduction, lie a little to one side of the main stream of experimentation; the conclusion is:

> Considered as a whole, the results of the experiments indicate a marked parallelism between the order of toxicity of the various cations toward *Paramecium* and the ionic potential of the ions employed (8, page 194).

A considerable number of studies (11, 12, 17, 18, 19, 20, 21) are devoted to analysis of the effects of the environmental conditions to which the animals are subjected in their natural lives, —the culture media—upon reproduction and vitality. A paper by Woodruff (12) on "The Effect of Excretion Products of *Paramecium* on its Rate of Reproduction" concludes:

> (1) The rate of reproduction of *P. aurelia* and *P. caudatum* is influenced by the volume of the culture medium, within the limits tested [*i. e.*, 2, 5, 20 and 40 drops of varied environment medium] and the greater the volume the more rapid is the rate of division. (2) *Paramecia* excrete substances which are toxic to themselves when present in their environment, and these substances are more effective when the organisms are confined in limited volumes of the culture fluid. (3) The excretion products of *Paramecium* play an appreciable part in determining the period of maximum numbers, rate of decline, etc., of this animal in hay infusions (12, page 581).

A careful study of the effects of changes of temperature on reproduction made by Woodruff and Baitsell (17) showed that the temperature coefficient (factor by which the rate of reproduction is multiplied when the temperature is raised ten degrees) is approximately 2.7, so that the rate of cell division is influenced by the temperature in a manner similar to that for a chemical reaction.

These studies of environmental action had shown Woodruff that different races of *Paramecium* are adapted to different conditions, and that this throws light on the diverse results reported by different observers. In a paper of 1911 (18), he concludes:

> (1) The discrepant results of various workers on the longevity of *Paramecium* are in all probability due to variation in the cultural demands of the race isolated for study. (2) It is probable that most, if not all, normal individuals have under suitable environmental conditions, unlimited power of reproduction without conjugation or artificial stimulation (18, page 65).

In this second statement much is involved in the word "normal"; the experience of the Johns Hopkins Laboratory is that some lines die out after a time, even though they may at first multiply in the usual way.

The study of cultural action was next made general and extended to the other organisms in the infusorian cultures, by a careful examination of the source and sequence of development of the organisms usually found in the cultures of decaying vegetation. The conclusions are of practical interest for the laboratory worker. Woodruff finds that Protozoa are rarely introduced from the air; and that *Paramecium* is not introduced dry, on hay or otherwise.

> Air, water, and hay are all sources from which Protozoa are derived, and increase in importance in the order given. Of these three, however,

air is practically a negligible factor in seeding infusions (19, page 263).

The order in which different common forms most frequently appear, reach their maximum, and disappear in hay infusions is shown in the following list (taken from 19, page 243).

APPEARANCE	MAXIMUM	DISAPPEARANCE
1. *Monads.*	1. *Monads.*	1. *Monads.*
2. *Colpoda.*	2. *Colpoda.*	2. *Colpoda.*
3. *Hypotrichida.*	3. *Hypotrichida.*	3. *Hypotrichida.*
4. *Paramecium.*	4. *Paramecium.*	4. *Amœba.*
5. *Vorticella.*	5. *Amœba.*	5. *Paramecium.*
6. *Amœba.*	6. *Vorticella.*	6. *Vorticella.*

As hay infusion is the typical culture medium for such organisms, a study was made by Fine (20) of its chemical properties, with particular relation to the acidity, the purpose being to correlate, so far as possible, the chemical conditions with the protozoan sequence. The paper concludes:

> The acidity of hay infusions is essentially due to bacteria, their efficiency in producing acid being governed by the concentration of the infusion in acid-yielding materials. The protozoa play a relatively small part in the production of acid.
>
> The sequence of protozoa and the course of the titratable acidity possess no intimately mutual relation. Either may vary within wide limits without appreciably influencing the course of the other.

This line of work is evidently still under active treatment, since we note that the *Journal of Experimental Zoology* promises a paper by Woodruff on "The Effect of Excretion Products of Infusoria on the Same and on Different Species, with Special Reference to the Protozoan Sequence in Infusions."

The problems of reproduction, age and death are bound up in recent theories with those of the size of cells and nuclei; a paper on this aspect of matter in the same journal is likewise promised from Woodruff.

Among the laboratories of this country which have made a definite mark on some unified problem of general interest (and such are happily now becoming numerous), certainly a most honorable place must be accorded to this work done at Yale by Woodruff and his associates.

A. R. MIDDLETON

ZOOLOGICAL LABORATORY OF THE JOHNS HOPKINS UNIVERSITY

CHRONOLOGICAL LIST OF PAPERS

(In the above review the papers are referred to by the serial numbers here given in parentheses. The papers in the *Proceedings of the Society of Experimental Biology and Medicine* and in *Science* are merely short abstracts on work published in full in other papers.)

(1) *Woodruff, L. L.,* An Experimental Study on the Life History of Hypotrichous Infusoria, *Journ. Exp. Zool.,* 2: 585–632, November, 1905.—(2) *Id.,* Variation During the Life Cycle of Infusoria and its Bearings on the Determination of Species, *Science,* 25: 734–735, May 10, 1907.—(3) *Id.,* The Life Cycle of *Paramecium, Proc. Soc. Exp. Biol. and Med.,* 5: 124, May 20, 1908.—(4) *Id.,* The Effect of Alcohol on the Life Cycle of Infusoria, *Biol. Bul.,* 15: 85–104, 1908.—(5) *Id.,* The Life Cycle of *Paramecium* when Subjected to a Varied Environment, AMER. NAT., 42: 520–526, August, 1908.—(6) *Id.,* Studies on the Life Cycle of *Paramecium, Proc. Soc. Exp. Biol. and Med.,* 6: 117–118, May 26, 1909.—(7) *Id.,* Further Studies on the Life Cycle of *Paramecium, Biol. Bul.,* 17: 287–308, September, 1909.—(8) *Woodruff, L. L., and Bunzel, H. H.,* The Relative Toxicity of Various Salts and Acids toward *Paramecium, Amer. Journ. Physiol.,* 25: 190–194, December, 1909.—(9) *Woodruff, L. L.,* On the Power of Reproduction without Conjugation in *Paramecium, Proc. Soc. Exp. Biol. and Med.,* 7: 144, May 18, 1910.—(10) *Id.,* Two Thousand Generations of *Paramecium, Archiv f. Protistenkunde,* 21: 263–266, 1911.—(11) *Id.,* The Effect of Culture Medium Contaminated with Excretion Products of *Paramecium* on its Rate of Reproduction, *Proc. Soc. Exp. Biol. and Med.,* 8: 100, April 19, 1911.—(12) *Id.,* The Effect of Excretion Products of *Paramecium* on its Rate of Reproduction, *Journ. Exp. Zool.,* 10: 557–581, May, 1911.—(13) *Baitsell, G. A.,* Conjugation of Closely Related Individuals of *Stylonychia, Proc. Soc. Exp. Biol. and Med.,* 8: 5, May 17, 1911.—(14) *Woodruff, L. L., Paramecium aurelia* and *Paramecium caudatum, Journ. Morphol.,* 22: 223–237, June, 1911.—(15) *Woodruff, L. L., and Baitsell, G. A.,* The Reproduction of *Paramecium aurelia* in a "Constant" Culture Medium of Beef Extract, *Journ. Exp. Zool.,* 11: 135–142, July 5, 1911.—(16) *Id.,* Rhythms in the Reproductive Activity of Infusoria, *Journ. Exp. Zool.,* 11: 339–359, November 20, 1911.—(17) *Id.,* The Temperature Coefficient of the Rate of Reproduction of *Paramecium aurelia, Amer. Journ. Physiol.,* 29: 147–155, December 1, 1911.—(18) *Woodruff, L. L.,* Evidence on the Adaptation of *Paramecium* to Different Environments, *Biol. Bul.,* 22: 60–65, December, 1911.—(19) *Id.,* Observations on the Origin and Sequence of the Protozoan Fauna of Hay Infusions, *Journ. Exp. Zool.,* 12: 205–264, February 10, 1912.—(20) *Fine, M. S.,* Chemical Properties of Hay Infusions with Special Reference to the Titratable Acidity and its Relation to the Protozoan Sequence, *Journ. Exp. Zool.,* 12: 2, February 10, 1912.—(21) *Woodruff, L. L.,* The Sequence of Protozoan Fauna in Hay Infusions, *Proc. Soc. Exp. Biol. and Med.,* 9: 65–66, February 21, 1912.—(22) *Woodruff, L. L.,* A Five-year Pedigreed Race of *Paramecium* without Conjugation, *Proc. Soc. Exp. Biol. and Med.,* 9: 121–123, May 15, 1912.—(23) *Baitsell, G. A.,* Experiments on the Reproduction of the Hypotrichous Infusoria. I. Conjugation between Closely Related Individuals of *Stylonychia pustulata, Journ. Exp. Zool.,* 13: 47–75, July 5, 1912.

NOTES ON ICHTHYOLOGY

THE most imposing work in ichthyology for the year is Dr. C. H. Eigenmann's "Fresh Water Fishes of British Guiana," published in the *Memoirs of the Carnegie Museum,* No. 5. This paper contains a very full discussion of the different species of the region concerned, with synonymy and notes of various kinds. It is also accompanied by an excellent series of maps and figures, with an illuminating discussion of the fauna of British Guiana and northern Brazil. This paper is the result of a most important expedition made by Dr. Eigenmann under the auspices of the Carnegie Museum at Pittsburgh.

Another work of very great importance is the "Résultats des Campagnes Scientifiques" of Albert the First, Prince of Monaco. In Fascicule XXXV of this splendidly printed series, Dr. Eric Zugmayer gives the results of the work of the Yacht Princesse-Alice for the ten years from 1901 to 1910. Many species, old and new, are described, with a series of admirable plates representing deep sea fishes of the Mediterranean which the learned and indefatigable prince has brought to light.

In the *Ann. and Mag. Nat. Hist.,* 1912, Mr. C. Tate Regan discusses the relations of the various families of eels.

In another paper he discusses the relations of the Blennioid fishes which, following Gill, he divides into numerous families, the Brotulids with the Fierasfers and Zoarces being regarded as among these Blennioid families. In another paper Mr. Regan discusses the affinities of the Mailed Cheek fishes. Following Cuvier and Jespersen, he assigns the sticklebacks to this group, contrary to the views of all other recent systematists. I can not believe that the sticklebacks have any affinity with the mailed cheek fishes, the ossified skin on the cheek being an analogy only.

In another paper Mr. Regan discusses the hag fishes of the genus *Heptatretus.* The different groups characterized by the number of gill openings, ranging from 6 to 14, are not regarded as separate genera.

In another paper the anatomy of the Discocephali is under discussion. He regards these fishes, in spite of the singular sucking disc on the head, as allies of the perch-like fishes, perhaps not far removed from *Naucrates.*

In another paper Mr. Regan discusses the family of Caristiidæ which he regards as allies of *Beryx*. He compares *Caristius* with *Platyberyx*, lately described by Zugmayer from Cape St. Vincent. He thinks that the two belong to the same genus and are perhaps not even specifically distinct. In this he is apparently wrong; *Platyberyx* seems related to *Beryx* but *Caristius* is, as I have already indicated, closely related to the Bramidæ. It is still nearer to *Pteraclis* from which it is mainly distinguished by the short anal fin, the anal fin in *Pteraclis* being nearly as long as the dorsal fin. The species described from Japan by Bellotti, as *Pteraclis macropus*, belongs also to this group and is in fact a second species of the genus *Caristius*.

Regan also describes in *Ann. and Mag.* and in the *Proc. Biol. Soc.* a large number of species from the rivers of South America with valuable notes and figures.

In the *Records of the Canterbury Museum*, Edgar A. Waite gives additions and modifications of the basic list of the fishes of New Zealand.

In the *Trans. New Zeal. Inst.* are given a number of valuable notes on New Zealand fishes. The grotesque *Aegeonichthys appelli* of Clarke is figured and also the extraordinary *Oreosoma atlanticum*, which has not been seen since the original specimen of Cuvier. The fish has seven ventral rays like others referred to the family of Zeidæ.

In the Indiana University Studies, 1912, Dr. Eigenmann describes a number of new species from the rivers of northern Colombia and in the *Ann. Carn. Mus.*, 1911, he describes numerous Characin fishes from rivers of northern South America.

In the *Proc. Linn. Soc. N. Y.*, Mr. J. T. Nichols gives a list of the fishes known to occur within fifty miles of New York, 237 in number, with figures of several.

In the *Bull. Amer. Mus. Nat. Hist.*, Mr. Nichols describes a new frog fish from Barbadoes, *Antennarius astroscopus*. He also gives a figure of the little known *Pseudomonacanthus amphioxys*.

In another paper Mr. Nichols gives notes on Cuban fishes. *Siphostoma torrei* and *Xystæma havana* are described as new.

In the *Proc. Biol. Soc. Wash.*, E. W. Gudger gives notes on fishes from Beaufort, North Carolina.

In the *Proc. Biol. Soc. Wash.*, T. D. A. Cockerell gives valuable notes on the scales of flounders, soles, codfish and other forms.

In the *Proc. U. S. Nat. Mus.,* Dr. C. H. Gilbert and C. V. Burke describe a number of new snail-fishes from the waters of Japan.

In the same proceedings Charles V. Burke describes additional species of snail-fishes or Liparids, including the new genus *Polypera* based on *Neoliparis greeni. Cyclogaster bristolense* is described from Bristol Bay, *C. megacephalus* from Bering Sea, *Careproctus gilberti* from Kadiak Island, *Paraliparis deani* from Alaska, *Paraliparis garmani* from New England and *Rhinoliparis attenuatus* from Bering Sea.

In the same proceedings Barton A. Bean and A. C. Weed describe an important collection of fishes from Java.

In the same proceedings Lewis Radcliffe describes 29 new species allied to the codfishes, from the Philippines. A new genus, *Macrouroides inflaticeps,* is made type of a distinct family.

In the same proceedings D. S. Jordan and C. W. Metz describe two new species from Hawaii.

In the same proceedings Professor J. O. Snyder enumerates the fishes collected by him in the Riu Kiu Islands, with numerous figures of interesting forms. The fauna of these islands is strictly tropical, in many regards not very different from that of Samoa but with some characteristic Japanese species.

In the same proceedings Professor Snyder enumerates the species obtained in the *Albatross* expedition of 1906 in the waters of Japan. Many new species are described and figured.

In the *Proc. Biol. Soc. Wash.,* B. W. Evermann and H. B. Latimer describe a collection obtained from the Olympic Peninsula in the state of Washington. In the proceedings of 1908 B. W. Evermann and W. C. Kendall describe and figure a European pipe fish, *Nerophis æquoreus,* obtained in the western Atlantic, the first American record of this species.

In the *Bull. Bur. Fish.,* 1910, Gilbert and Burke describe the fishes collected in Alaska by the steamer *Albatross* on its way to Japan. About forty new species were obtained in this expedition.

In the same bulletin W. C. Kendall describes a new flat fish from the Georges Bank, off New Foundland, under the name of *Pseudopleuronectes dignabilis.*

In the *Mitteil. Naturh. Mus. Hamburg,* 1912, Georg Duncker discusses the genera of the pipe fishes.

In the *Ann. Mus. Zool. Univ. Napoli,* J. Pellegrin describes fishes in the Museum of Naples, mostly obtained by an expedition to the Red Sea.

In the Report of the British Antarctic Expedition of Shackleton, Mr. Edgar R. Waite describes the fishes taken in the Antarctic, four species only, all of the family of Nototheniidæ.

In the *Bull. Americ. Mus. Nat. Hist.,* L. Hussakof describes eight Chimæroids of the Cretaceous of North America.

In the *Ann. N. Y. Acad. Sci.,* R. D. O. Johnson describes an extraordinary climbing catfish, *Arges marmoratus,* from Colombia. In connection with this, Dr. Bashford Dean remarks that "it is hardly to the credit of our cloth that these observations on fishes should be first made by a mining engineer."

In the *Zoologischen Anzeiger,* 1912, Dr. L. F. de Beaufort describes new Gobies from Ceram and Waigeu.

In the *Zool. Jahrb.,* L. S. Berg describes the origin of the fishes of the basin of the river Amur.

Under the title of "Faune de la Russie," Dr. Berg describes and catalogues the fishes of Russia, a valuable paper, accompanied by good descriptions, which unfortunately for most of us are mainly in Russian.

In the *Bull. Mus. d'Hist. Nat. Paris,* 1912, Dr. Pelligrin enumerates fishes from the New Hebrides with the description of *Callechelys guichenoti,* hitherto imperfectly known.

In the *Bull. Inst. Oceanog.* of the Prince of Monaco, Dr. Zugmayer describes numerous deep-sea fishes obtained by the prince.

In the *Bull. Soc. Zool. de France,* 1912, Dr. Louis Fage describes a collection of fishes from the coast of Morocco.

Under the head of "Figures and Descriptions of the Fishes of Japan," Mr. Shigeho Tanaka, lecturer in the Imperial University, continues his series of excellent descriptions and figures of Japanese fishes, the text being both in Japanese and in English. Of this series ten fascicules have been published. When it is finished it will give a most complete and valuable account of the fishes of Japan. No attempt is made to classify these species, one being taken up after another in the order which the author finds most convenient, a matter of necessity under the circumstances of publication.

In the *Journal Coll. Sci. Imp. Univ. Tokyo,* H. Ohshima describes in detail the luminous organs of various fishes, among them the small deep-water sharks of the coast of Japan.

In the *Proc. Roy. Soc. Queensland,* A. R. McCulloch describes some new Atherinidæ from Australia.

In the *Rec. West. Austr. Mus.,* Mr. McCulloch publishes notes on various fishes from western Australia.

In the Records of the Canterbury Museum, Mr. Waite describes the many species, some of them of remarkable interest, obtained by the trawling expedition of New Zealand.

In the *Revue Institute d'Agronomie,* Montevideo, Professor André Bouyat gives popular accounts in Spanish, with photographs, of the principal food fishes of the coast of Uruguay.

In the *Zoologischen Anzeiger,* George Wagner discusses the possibility of the existence of the species of Gar pike described from a Chinese drawing under the name of *Lepisosteus sinensis.* No naturalist has ever found a gar pike in China and the question of where this specimen was obtained from which this drawing is made is still uncertain.

In the *Bull. Soc. Zool. de France,* Mr. F. Priem describes the fossil fishes of the Argentine Republic.

In the *Field Mus. Nat. Hist.,* Dr. Seth E. Meek describes new fishes of numerous species from the rivers of Costa Rica. Dr. Meek and S. F. Hildebrand also describe a number of new species from Panama.

In the *Trans. Amer. Fish Soc.,* at St. Louis, are numerous valuable papers relating chiefly to the culture or to the diseases of fishes. One of the many papers of practical value is an account of the fur seal herd of the Pribilof Island and the prospects for its increase, by C. H. Townsend. The sole cause of the reduction in numbers of these animals has been the killing of females at sea, known as pelagic sealing. In the early Russian days before the present methods of removing the bristles from seal skins, leaving the soft underfur, was discovered in London, the most valuable fur was that of the young animals at the age of four months when they change the black coat for the silver gray of the first year. In those days these silver-gray pups were killed indiscriminately on land without regard to sex, a matter which naturally rapidly reduced the herd. But so long as the females are protected, both on land and sea, there is no reason why the herd should not enormously increase, probably in time with proper management on the land, so as to yield even more than the 100,000 skins of superfluous males which were taken each year during the lease of the Alaska Commercial Company.

In the *Publ. Leland Stanford Jr. Univ.*, Professor E. C. Starks describes the skeletons of various families of mackerel-like fishes. In a general way he finds that the real relations of these forms, as indicated by their skeletons, correspond very nearly to the impressions made by their external characters. Among other things there is no immediate relation between the genus *Gerres* and the genus *Leiognathus*. These have some superficial resemblances, and have been placed in the same family by Dr. Boulenger.

In the Bureau of Fisheries documents Dr. G. H. Parker discusses the effect of explosions of motor boats and guns on fishes. These sounds under water are extremely faint and have little effect on the animals. Some of the noises made by the fishes themselves seem to have a certain attraction to others of their kind.

In the Biennial Report of the Commissioners of Fisheries of Wisconsin is a valuable discussion of the brook trout disease in the hatcheries of Wisconsin, the disease in this case being due to a parasitic crustacean, a small copepod, *Lernæopoda edwardsii*. This creature is a parasite on the eastern brook trout but not on the other species of trout reared in Wisconsin. The best remedy seems to be to clean up the hatcheries, scraping the ponds, and introducing the sand filter. It is also suggested that the old trout, most usually affected, be got rid of early and that the copepods may be drawn apart by means of electric lights.

In the *Bull. Bur. Fisher.*, G. H. Parker discusses the sense structures of a small shark.

In the *Fishing Gazette*, Dr. Hussakof describes the spoonbill cat fishery of the lower Mississippi.

Under the head of Dogfish, D. E. Lane, of Bellingham, Washington, attempts to show that the species of *Squalus* have a great commercial value, the oil from the livers being capable of many uses through purification, and the bodies susceptible of being made into a high-grade fertilizer.

In the *Zool. Soc. Bull.*, F. B. Sumner describes in detail the adaptive colors among fishes and the changes which some of them undergo. In a certain species of turbot from the Bay of Naples marked all over in life with gray and dark spots of different shades and sizes, it is found that this fish placed on different bottoms adapts itself not only to the general color tone, but to the texture and pattern as well.

In the *Bull. Inst. Oceanog.*, Dr. Fage discusses the attempts to introduce the salmon in the Mediterranean, thus far unsuccessful.

In several papers in the *Anatomischen Anzeiger*, E. P. Allis, Jr., describes the blood vessels and other structures of many species of sharks and other fishes.

In the *Proc. 7th Internat. Zool. Cong.*, Professor H. F. Nachtrieb describes the lateral line of the paddlefish. Another paper is in the *Journal of Experimental Zoology.*

In the *Bulletin* of the Bureau of Fisheries, XXXII, for 1912, under the head of "The Age at Maturity of the Pacific Salmon of the Genus *Oncorhynchus*," Dr. Charles H. Gilbert gives a detailed account of his investigations of the scales of the salmon, following a method begun by Johnston in his studies of the salmon of Scotland. In this paper he shows that the age of the salmon can be determined by its scales and because the salmon of the Pacific Coast runs periodically, this information thus secured may be of great commercial importance. A few years ago a similar study was undertaken by Professor J. P. McMurrich. Unfortunately this work, which was otherwise well done, rested on an initial mistake. The red salmon, which was taken by him to be a four-year old, was actually five years of age.

Summing up, Dr. Gilbert presents the following conclusions:

1. The sockeye spawn normally either in their fourth or fifth, the king salmon either in their fourth, fifth, sixth or seventh year, the females of both species being preponderatingly four-year fish.

2. The young of both sockeye and king salmon may migrate seaward shortly after hatching, or may reside in fresh water until their second spring. Those of the first type grow more rapidly than the second, but are subject to greater dangers and develop proportionately fewer adults.

3. Coho salmon spawn normally only in their third year. The young migrate either as fry or yearlings, but adults are developed almost exclusively from those which migrate as yearlings.

4. Dog salmon mature normally either in their third, fourth or fifth years, the humpback always in their second year. The young of both pass to sea as soon as they are free swimming.

5. The term "grilse," as used for Pacific salmon, signifies conspicuously undersized fish which sparingly accompany the

spawning run. They are precociously developed in advance of the normal spawning period of the species. So far as known, the grilse of the king salmon, coho and dog salmon are exclusively males, of the sockeye, almost exclusively males, except on the Columbia River, where both sexes are about equally represented. The larger grilse meet or overlap in size the smaller of those individuals which mature one year later at the normal period.

6. Grilse of the sockeye are in their third year, of the king salmon in their second or third year, of the coho and the dog salmon in their second year.

7. The great differences in size observed in spawning runs are closely correlated with age, the younger fish averaging constantly smaller than those one year older, though the curves of the two may overlap.

This article is also printed in the *Pacific Fisherman.*

F. L. Landacre in the *Jour. Comp. Neur.* discusses certain ganglia of the gar pike and their relations and significance.

In the *Bur. Fish. Doc.,* A. B. Alexander discusses the halibut fishing grounds of the Pacific Coast.

In the *Rapp. Cons. Internat. de la Mer,* Professor D. W. Thompson, of Dundee, describes the distribution of the cod and haddock.

In the *Bull. Soc. Géol. de France,* Mr. Priem discusses the fossil fishes of the Upper Tertiary in southern France and also the Mezozoic fishes of the same region.

In the *Bull Amer. Mus.,* Dr. Hussakof describes a sawfish embryo.

In the *Bull. Bur. Fish.,* Professor J. O. Snyder describes under the name of *Salmo regalis,* the royal silver trout of Lake Tahoe. It is one of the most remarkable of the many American species of trout, being of beautiful steel blue and silver with very few spots. It is probably older and more primitive than any of the other trout, doubtless being part of the original fauna of Lake Lahontan.

DAVID STARR JORDAN.

The American Naturalist

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GENETICAL STUDIES ON ŒNOTHERA. IV

THE BEHAVIOR OF HYBRIDS BETWEEN *Œnothera biennis* AND *Œ. grandiflora* IN THE SECOND AND THIRD GENERATIONS[1]

DR. BRADLEY MOORE DAVIS

UNIVERSITY OF PENNSYLVANIA

THOSE who have followed the reports of my genetical studies on *Œnothera* (Davis, '10, '11 and '12*a*) must have noted that I have obtained during the past four years a series of hybrids from the cross *grandiflora* × *biennis* with various points of strong resemblance to forms of *Œnothera Lamarckiana* De Vries. I say forms of *Œ. Lamarckiana* because it is, I think, clear (Davis '12*a*, p. 383) that this species has within itself a number of biotypes which, although in most respects essentially similar, differ from one another in the size of the petals, in the height of the stigma relative to the tips of the anthers, and, to a lesser degree, in some other characters. These biotypes may be segregated by critical selection and cultivation through pure lines and I venture to believe that the *Lamarckiana* of De Vries's cultures was less pure when he began his studies twenty-five years ago than it is to-day. At the present time a very large-flowered type (petals 4–4.5 cm. long) is generally thought

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[1] An abstract of this paper was presented before the American Society of Naturalists at its meeting in Cleveland on January 2, 1913.

of when this plant is discussed. *Lamarckiana* then, like many species, has its minor strains which may be isolated.

Heribert-Nilsson ('12) in his recent extended analytical studies on *Œ. Lamarckiana* reaches the same conclusion that *Lamarckiana* is not a simple species but, on the contrary, polymorphic. His investigations are the first serious attempts to bring forward evidence that will explain the "mutants" and minor varieties as derivatives from a hybrid through the segregation and recombination of characters on Mendelian principles. These studies form a very important contribution to the research upon this interesting plant.

I have not as yet among my hybrids of *biennis* and *grandiflora* obtained any plant that matches in all respects any one of the biotypes of *Lamarckiana*. On the other hand, there is, I believe, no important character of taxonomic value presented by *Lamarckiana* through its various biotypes that has not appeared in some of my hybrids. I have, as it were, surrounded the group of *biotypes,* which we call the species *Lamarckiana,* with a circle of hybrids that in various characters agree with the plants that have come down to us through the cultures of De Vries. If the group of biotypes of *Lamarckiana* is enlarged to include certain of its so-called "mutants" the number of my hybrids with points of resemblance to this larger assemblage is correspondingly increased.

My studies have now reached a stage where I have data to present on the behavior of hybrids between *biennis* and *grandiflora* in the F_2 and F_3 generations. These later hybrids have a two-fold interest; first with respect to their possible interpretation in relation to Mendelian principles of inheritance, and second, with respect to the behavior of certain types in the F_2 generation, which types repeat in the F_3 the history of the F_1 parent hybrid in throwing the same marked variants, and thus exhibit a behavior similar to that of *Lamarckiana* when in successive generations it produces a series of similar "mutants."

There has come to light during the past year a historical matter of interest which bears very directly on the problem of the origin of the *Lamarckiana* of De Vries's cultures. This is the determination of Lamarck's plant, *Œnothera Lamarckiana* Seringe (1828), grown in Paris at about 1796 or somewhat earlier, as a form of *Œ. grandiflora* Solander (1789) = *Œ. grandiflora* "Aiton." The evidence for this determination (see Davis, '12*b*) is very convincing and there can be, I think, no doubt but that De Vries ('01, Vol. I, pp. 316, 317) was mistaken when he identified the material of his cultures with the type specimen of *Œ. Lamarckiana* Seringe, the sheet upon which Lamarck (?1798) based his description in the Encyclopédie Méthodique Botanique. It should be remembered that Professor De Vries made this identification some years before the rediscovery of *Œ. grandiflora* at its original habitat in Alabama in 1904, and consequently before there was available our present information on this species.

Œnothera Lamarckiana Seringe (1828) now becomes a synonym of *Œ. grandiflora* Solander, described in Aiton's "Hortus Kewensis" (1789), and the material of De Vries's cultures can not bear the name *Lamarckiana* with Seringe as an authority. I have suggested, however, in the paper cited above (Davis, '12*b*, p. 530) that the plant of De Vries's cultures retain the name *Lamarckiana* to be written in the form *Œ. Lamarckiana* De Vries. A change of name for this plant would be most unfortunate, since it would result in endless confusion in the literature of experimental morphology. The evidence indicates that *Œ. Lamarckiana* De Vries has come to us as the product of the garden through a long history of cultivation and that its parentage is far from pure; in short, that it is of hybrid origin. As a garden plant we are seemingly justified in giving it the name *Œ. Lamarckiana* De Vries by Article 50 of the code formulated by the International Botanical Congress held in Vienna in 1905.

The effect of the separation of *Œ. Lamarckiana* De Vries from Lamarck's plant of about 1796 is to make far more tangible the problem of its origin. In former papers in the NATURALIST (Davis, '11, p. 226; '12, p. 379) I have criticized adversely the attempts that have been made to place the appearance of *Lamarckiana* De Vries in Europe at dates previous to 1778 when *Œ. grandiflora* Solander was introduced at Kew. In a recent contribution Gates ('13, pp. 17–19) admits that the presence of *Lamarckiana* in Europe previous to 1760 is not established and thus abandons his former position when he sought to prove its very early introduction from America. With Lamarck's plant (*Œ. Lamarckiana* Seringe) removed from the discussion we are brought to periods where we may hope for more direct evidence on the history of *Lamarckiana* De Vries than that furnished by old accounts and figures. This matter will be further discussed at the end of this paper in the section entitled, "The Problem of the Origin of *Œ. Lamarckiana* De Vries."

The material of this paper will be arranged under the following headings: (1) F_3 Generations in the Family from the F_1 Hybrid 10.30*La*, (2) F_3 Generations in the Family from the F_1 Hybrid 10.30*Lb*, (3) Hybrids of *grandiflora B* × *biennis D* in the F_2 Generation, (4) A Discussion of the Behavior of the Hybrids in the Second and Third Generations with Reference to the Stability of Mendelian Factors, (5) The Habit of "Mutation" in *Œ. Lamarckiana* De Vries considered with Reference to the Behavior of the Hybrids between *biennis* and *grandiflora*, (6) The Problem of the Origin of *Œ. Lamarckiana* De Vries.

1. F_3 GENERATIONS IN THE FAMILY FROM THE F_1 HYBRID 10.30*La*

The F_1 hybrid plant designated 10.30*La* has already been described and figured (Davis, '11, pp. 211–213, Figs. 9, 10, 11), and a brief account of its F_2 generation was given in my last paper (Davis, '12*a*, pp. 410–413). The plant was the result of the cross *grandiflora B* × *biennis A*, the latter parent being a rather small-flowered race of *biennis* from Woods Hole, Massachusetts. The F_2 generation from 10.30*La* consisted of 1,451 plants, among which could be readily selected at an early stage of development a group of 141 rosettes much smaller than those constituting the mass of the culture and sharply distinguished by their strongly etiolated leaves of a narrower form. From these etiolated rosettes developed a class of dwarfs, the later foliage of which outgrew the etiolated peculiarities of the young plants and became green. The normal green rosettes constituting the mass of the culture presented a remarkable range of form, but inclined more towards the female parent of the cross, *grandiflora B*.

A large proportion of the plants, at maturity, were fairly close to the F_1 hybrid plant 10.30*La*, but there was presented a wide variation from this form with a markedly greater tendency towards the *grandiflora* parent type. Although the range of variation clearly indicated a process of segregation in this F_2 generation, it was a segregation modified by a general progressive advance in the size of the plant organs. Thus, with respect to flower size, the culture gave a large number of plants (about 50) with flowers as large as or larger than the *grandiflora* parent, while the smallest flowers represented were 2–4 times larger than those of the *biennis* parent. The leaves throughout the mass of the culture were, as a whole, larger than those of the parents of the cross and generally distinctly crinkled.

It should be recalled (see Davis, '12*a*, p. 412) that a number of remarkable forms appeared in the F_2 culture in addition to the segregates, forms which no taxonomist would think of relating to either parent of the cross or to the F_1 hybrid plant 10.30*La*. Some of these forms were sterile, but the 141 peculiar dwarfs from etiolated rosettes and the extreme types showing progressive evolution were fertile, as was the culture, as a whole.

The problem which I outlined for study through the F_3 generation was two-fold: (1) Would extreme types of the F_2, such as the dwarfs, hold their characteristics, and (2) Would a selfed plant representative of the mass of the F_2 produce an F_3 progeny with points of similarity to the F_2 generation? If this proved true there would be presented a behavior analogous to that of *Lamarckiana*

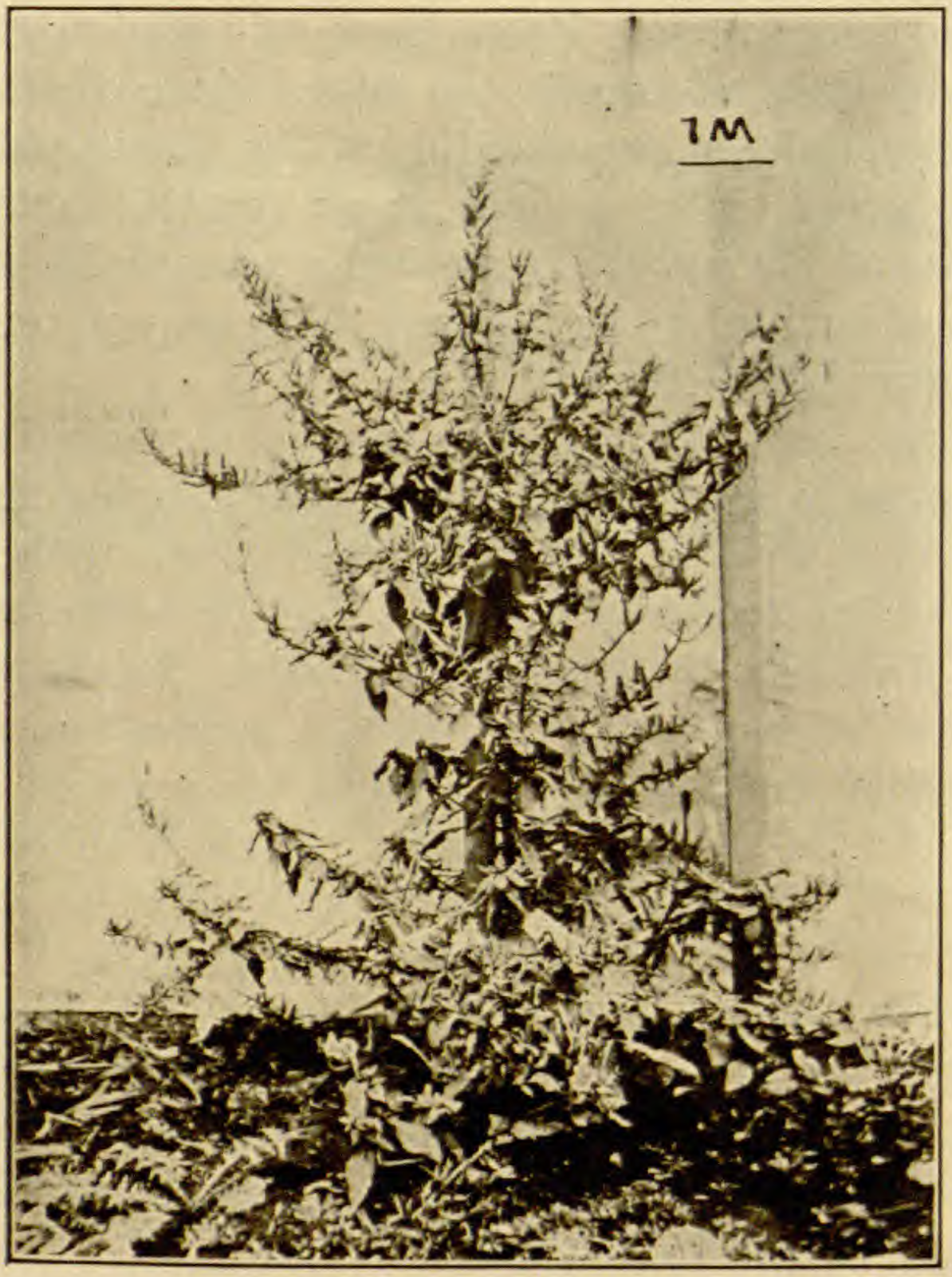


FIG. 1. Dwarf, 11.41*ra*, in the F_2 from the F_1 plant 10.30*La*, hybrid of *grandiflora B* × *biennis A*. This plant came from an etiolated rosette and shows the irregular branching characteristic of these dwarfs.

FIG. 2. Dwarf, 11.41*ra*, in the F_2 from the F_1 plant 10.30*La*, hybrid of *grandiflora B* × *biennis A*. The inflorescence and two leaves from the lower portion of the plant illustrate the varied forms of the leaves.

which throws off in successive generations marked variants which hold true when self-fertilized.

A plant, 11.41*ra*, was selected as being representative of the F_2 dwarfs from etiolated rosettes (Davis, '12*a*, p. 413) and, being selfed, became the parent of an F_3 generation (culture 12.53). The stunted growth and irregular branching characteristic of these dwarfs was well illustrated by this plant, 11.41*ra* (Fig. 1), as was also the varied form of the leaves (Fig. 2). The peculiarities of the etiolated rosettes from which the dwarfs come are well shown by the two plants at the bottom of Fig. 4.

From the F_2 dwarf, 11.41*ra,* 243 seeds, the contents of a single selfed capsule, were sown (culture 12.53). These produced 116 seedlings, the leaves of which, following the cotyledons were strongly etiolated in the lower half in the manner characteristic of these dwarfs; 69 rosettes were potted and carried to an advanced stage of development; 48 plants were brought to maturity. The rosettes were all etiolated, in some cases over three fourths of the basal portion of the leaves, in others somewhat less; the leaves were narrow and long-petioled. The F_3 generation (culture 12.53), from the F_2 dwarf, 11.41*ra,* was then absolutely true to the characters of the etiolated rosettes, one of which is shown in Fig. 4, 12.53*a*. The 48 plants brought to maturity presented the dwarf habit with ir-

Fig. 3. A type, 11.41*c,* in the F_2 from the F_1 plant 10.30*La,* hybrid of *grandiflora B* × *biennis A*. This plant represented closely the character of the mass of the F_2 generation and was similar to the F_1 parent 10.30*La* except for a progressive advance in leaf and flower size.

regular branching and varied leaf form characteristic of the F_2 parent, 11.41*ra*; these plants also outgrew later the etiolated peculiarities of their rosettes. The flower size among these 48 plants of the F_3 varied greatly, a further point of similarity to the group of dwarfs in the F_2 generation. It appears then, as far as this culture in the F_3 gives evidence, that the dwarfs from etiolated

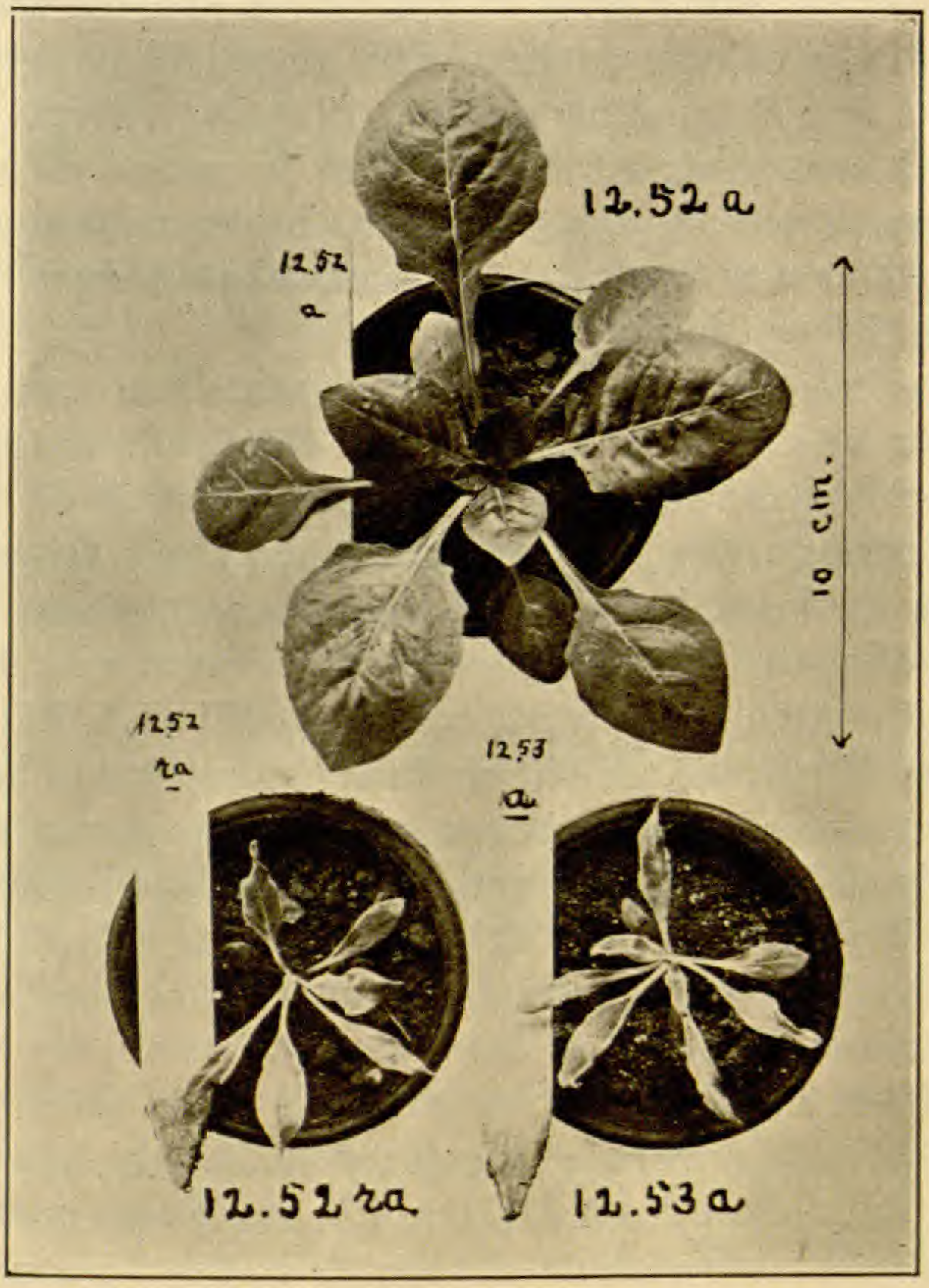


FIG. 4. 12.52*a* and 12.52*ra*, rosettes in the F_3 from the F_2 plant 11.41c (Fig. 3), the first, representative of the green rosettes constituting the mass of the culture, the second, one of 18 etiolated rosettes that developed into dwarfs. 12.53*a*, one of the etiolated rosettes in the F_3 from the F_2 dwarf 11.41*ra* (Figs. 1 and 2); it holds perfectly the characters of its F_2 parent, and is shown for comparison with 12.52*ra*.

rosettes in the F_2 generation constitute a group of plants very stable and perhaps homozygous with respect to their most striking peculiarities.

The second part of my study of this family concerned the behavior in the F_3 of a plant representative of the mass of the F_2 generation. The individual chosen, 11.41*c* (Davis, '12*a*, p. 412), was a large plant (Fig. 3) with long branches from the base and a foliage of conspicuously crinkled leaves. The type was represented by about 170 plants in the culture and, intergrading with other forms, stood close to the center around which the mass of the culture varied. This plant, 11.41*c*, was similar to the F_1 parent hybrid, 10.30*La*, except that it showed something of the general progressive advance throughout the F_2 generation in the broader and more crinkled leaves and in the somewhat larger flowers (petals 2.5 cm. long).

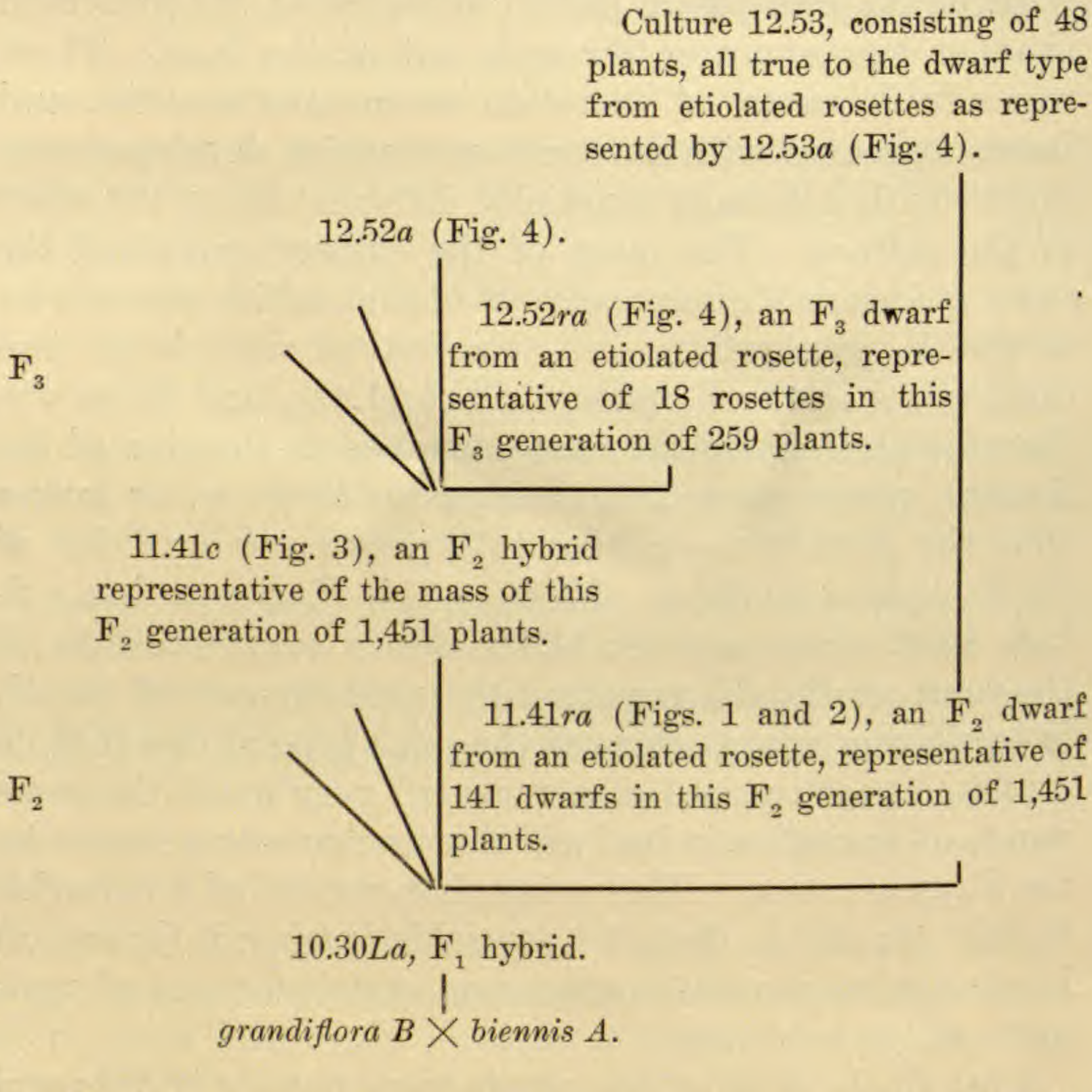
From the plant 11.41*c* an F_3 generation was grown (culture 12.52). There were sown 411 seeds, the contents of 3 selfed capsules and 285 rosettes developed. Among the seedlings 18 plants at once caught my attention as having etiolated leaves following the cotyledons. These 18 seedlings developed into small rosettes with narrow, strongly etiolated leaves, which could not be distinguished from the etiolated dwarfs that have been described above. The contrast between the green rosettes of this culture, 12.52, and these etiolated dwarfs, is illustrated in Fig. 4, which shows sister plants, 12.52*a* green and representative of the mass of the culture, and 12.52*ra* one of the 18 etiolated dwarf types. By the side of 12.52*ra*, for comparison (see Fig. 4), is shown one of the 48 etiolated dwarfs in culture 12.53, which, although an F_3 individual from 11.41*ra*, illustrates accurately the appearance of the etiolated dwarfs in the F_2 generation. It will be noted that the two dwarfs, 12.52*ra* and 12.53*a*, are of the same type.

The 18 etiolated rosettes of the F_3 culture 12.52 grew into dwarfs indistinguishable in all essentials from the 48 plants of the F_3 generation 12.53 and the 141 plants in the F_2 represented by 11.41*ra* (Figs. 1 and 2). They outgrew the etiolated condition of the younger stage, but remained dwarfs, branching irregularly and presenting varied forms of leaves; there was also exhibited the same wide range of flower size. The evidence was then clear that in this family an F_2 plant of a type close to the mass of the F_2 culture could throw off in the F_3 the same class of dwarfs that appeared in the F_2 generation.

The normal green rosettes constituting the mass of the culture 12.52 (see Fig. 4, 12.52*a*) inclined strongly towards the *grandiflora* parent of the cross, but presented broader leaves not so strongly cut at the base. There was a wide range of variation among the rosettes, and forms appeared with narrow leaves which developed into plants with a foliage markedly different from the mass of the culture. The mass of the culture presented the same evidence of progressive evolution which was shown in the F_2 generation, *i. e.*, the leaves were large and crinkled as in the F_2 parent plant 11.41*c*, and there was likewise maintained the same advance in the size of the flowers, which ranged from types as large as or larger than the *grandiflora* parent to types as small as that of the F_1 hybrid 10.30*La*. In short, this F_3 generation, culture 12.52, from a plant 11.41*c*, fairly representative of the mass of the F_2, repeated the performance of the F_2 in exhibiting a large class of the same type of dwarf from etiolated rosettes and also repeated very much the same range of variation in leaf and flower characters shown by the F_2 generation. There was then presented a behavior closely parallel to that of *Lamarckiana* when it throws off in successive generations the same marked types of variants, which hold true.

Late in the season two plants were noted (12.52*fa* and 12.52*fb*) upon which a large number of flowers were 5-merous, *i. e.*, the flowers had 5 sepals, 5 petals, 10 stamens, and as far as noted 5 cells in the ovary. I am not aware that this character has before been noted in the genus *Œnothera*. These flowers were not restricted to particular branches and were found in the same inflorescence with normal flowers. The 5-merous flowers, were not observed by me until October, too late in the season to self-pollinate with the hope of obtaining seed. Open-pollinated seed was, however, collected from these two plants and will be sown in the hope that this interesting sport may be followed in later generations.

The genealogy of the family from the F_1 hybrid 10.30*La,* in so far as it refers to the production of dwarfs, is presented in outline as follows:



Culture 12.53, consisting of 48 plants, all true to the dwarf type from etiolated rosettes as represented by 12.53*a* (Fig. 4).

12.52*a* (Fig. 4).

F_3

12.52*ra* (Fig. 4), an F_3 dwarf from an etiolated rosette, representative of 18 rosettes in this F_3 generation of 259 plants.

11.41*c* (Fig. 3), an F_2 hybrid representative of the mass of this F_2 generation of 1,451 plants.

F_2

11.41*ra* (Figs. 1 and 2), an F_2 dwarf from an etiolated rosette, representative of 141 dwarfs in this F_2 generation of 1,451 plants.

10.30*La,* F_1 hybrid.

grandiflora B × *biennis A.*

2. F_3 GENERATIONS IN THE FAMILY FROM THE F_1 HYBRID 10.30*Lb*

The F_1 hybrid designated 10.30*Lb* was a sister plant to 10.30*La* and, therefore, also the product of the cross *grandiflora B* × *biennis A.* It has been described and figured in the earlier paper (Davis, '11, pp. 213–216, Figs. 12, 13 and 14), and a brief account of its F_2 generation will be found in my last contribution (Davis, '12*a*, pp. 413–415). From the F_2 generation of 992 rosettes, culture 11.42, a group of 147 were sharply distinguished by their uniformly small size and narrow leaves. These developed into a class of very remarkable dwarf plants (Davis, '12*a*, p. 415, 11.42*r*) which at maturity were from 3–4 dm. high, rarely branched, and bore medium-sized flowers (Fig. 5). The leaves of the rosettes and mature plants were fully green; there was no etiolation so characteristic of the group of dwarfs from the sister F_1 hybrid 10.30*La*. The character of the young dwarf rosettes is shown in Fig. 7 and Fig. 9, 12.59*a*, in comparison with rosettes (shown above) similar to forms representative of the mass of the culture.

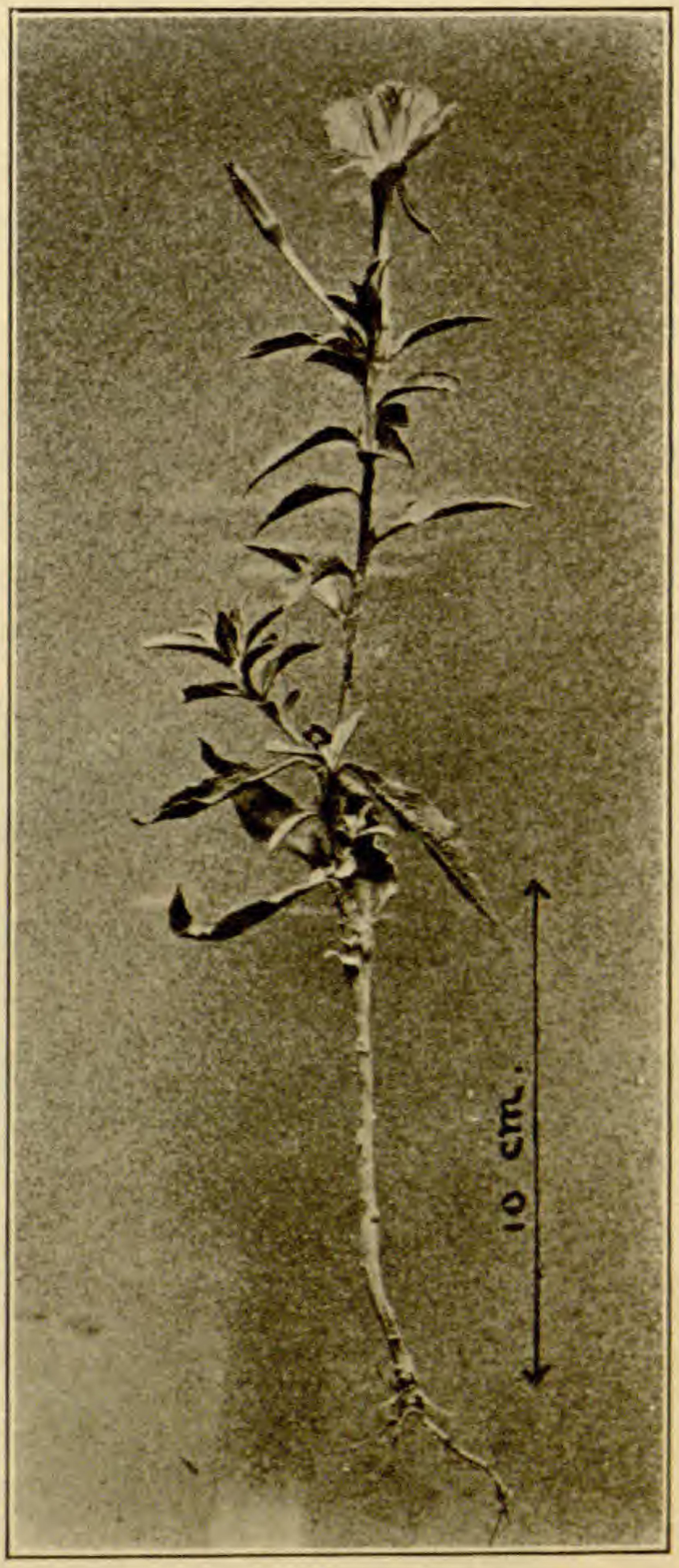


FIG. 5. Dwarf, 11.42*r*, in the F_2 from the F_1 plant 10.30 *Lb*, hybrid of *grandiflora B* × *biennis A*. This plant came from a rosette similar to that shown in Fig. 7, 12.59*a*.

The rosettes constituting the mass of the culture exhibited a wide range of form with the extremes approaching the rosettes of the *biennis* and *grandiflora* parents; there was not shown a clearly defined tendency towards either parent of the cross. From these rosettes a much more varied culture developed than the F_2 generation from the plant 10.30*La*.

There was more evidence of segregation towards the respective parents, but the same progressive advance in flower size. Many plants bore flowers as large as or larger than those of the *grandiflora* parent, while no plant presented flowers as small as those of the *biennis* parent. The foliage was extremely varied, ranging from lanceolate leaves to broadly elliptical or ovate leaves with well-defined crinkles.

A larger number of remarkable forms appeared in this culture, 11.42 (see Davis, '12*a,* p. 415), than in the one from the plant 10.30*La,* forms that would rank as types specifically distinct from either parent of the cross and from the F_1 hybrid plant 10.30*Lb*. Among these we shall refer to (1) the dwarf type 11.42*r* (Fig. 5), (2) a small-leaved type 11.42*f* (Fig. 6), (3) a large-flowered type with large crinkled leaves 11.42*g* (Fig. 8), rather common and fairly representative of the mass of the culture, (4) a medium-flowered type remarkable for its broad-much-crinkled leaves 11.42*l* (Fig. 14), and (5) a plant with very narrow leaves and very small flowers, anthers sterile 11.42*j* (Fig. 15).

The same problem lay before me in the study of the F_3 generations from these types in the F_2 of the plant 10.30*Lb,* as in the family which has just been described from the sister plant 10.30*La*. Would the extreme types such as the dwarfs hold their characters, thus proving to be homozygous, and would selfed plants more or less representative of the mass of the F_2 repeat in their F_3 generations something of the history of the F_2?

Of the 147 dwarf rosettes in the F_2 from 10.30*Lb* there were brought to maturity 90 plants. These constituted, as stated above, a very uniform group with characters well shown in Fig. 5. One of these, 11.42*ra,* was selected and selfed to become the parent of an F_3 generation. The contents of one capsule, 196 very small seeds, were sown and gave culture 12.59, comprising 66 rosettes, all similar and dwarf. One of these rosettes is shown in

Fig. 7 and Fig. 9, 12.59*a*, and it should be noted that the specimen is not a seedling, but a half-grown rosette comparable in point of age to the large rosettes (shown above) which represent closely the normal form and size. The dwarfs are delicate plants, very sensitive to drought, and I was able to bring only 46 individuals to maturity. These proved to be in all respects similar to the dwarfs of the F_2 generation, except that they were even smaller in stature and flower size; this further dwarfing was, however, probably due to less favorable cultivation. From the behavior of this F_3 we may, I believe, safely conclude that the dwarfs of the F_2, representing an extreme type, are stable, or homozygous, with respect to their most important characteristics.

There will now be described the F_3 generation from a small-leaved plant, 11.42*f* (Fig. 6), about 1 m. high, with

FIG. 6. A type, 11.42*f*, in the F_2 from the F_1 plant 10.30*Lb*, hybrid of *grandiflora B* × *biennis A*. A form characterized by small leaves, medium-sized flowers, and large capsules.

medium-sized flowers and large capsules (3.3 cm. long). This type (Davis, '12*a*, p. 415, 11.42*f*) was represented by several plants in the F_2 from 10.30*Lb*. It illustrated an extreme combination of small leaves with large capsules, but must not be regarded as representing a class since its characters intergraded through numbers of plants into the mass of the culture. The contents of one selfed capsule, 219 seeds, were sown as culture 12.55; these produced 75 seedlings from which 62 rosettes developed.

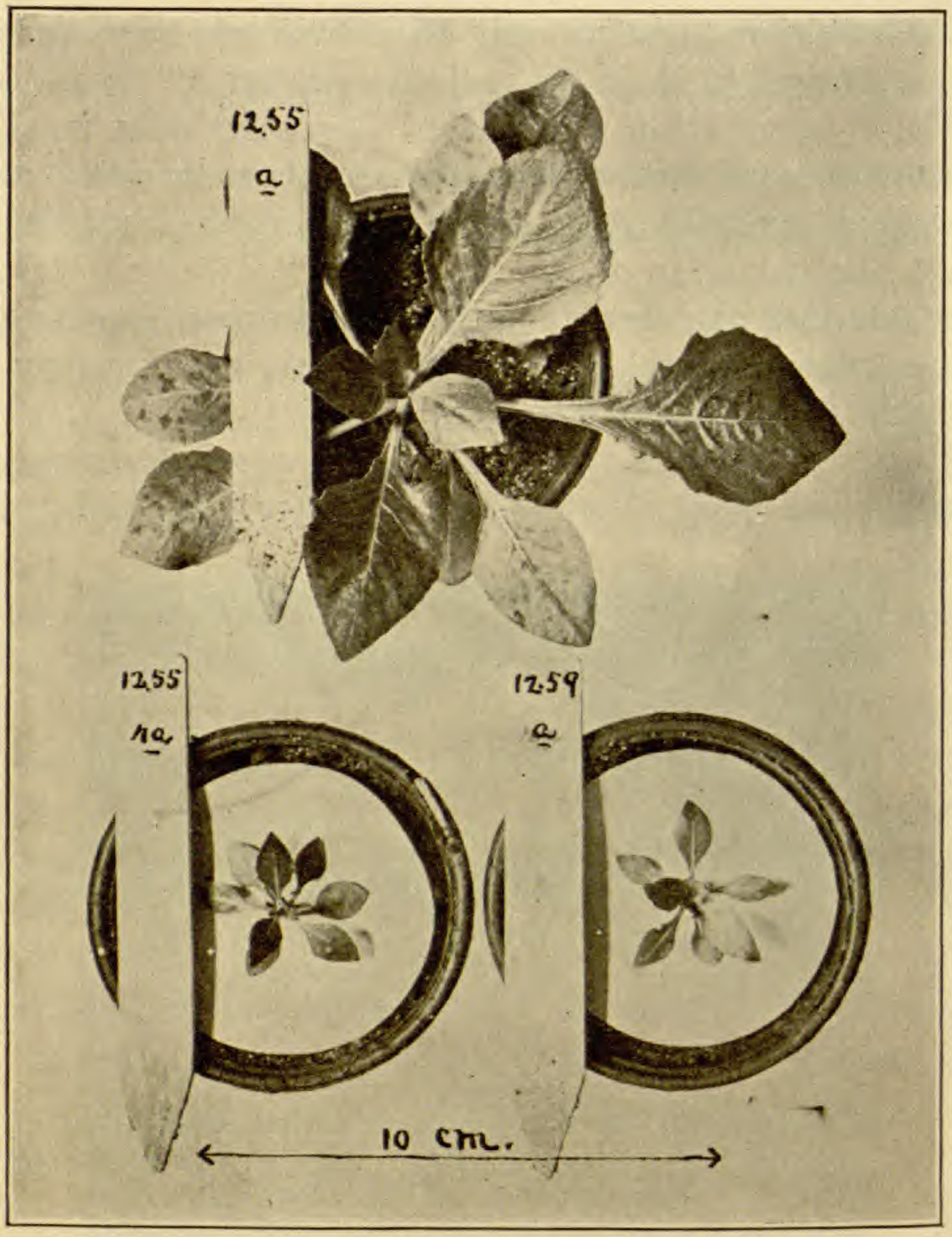


FIG. 7. Rosettes in the F_3: 12.55*a* representative of the mass of the culture from the F_2 plant 11.42*f* (Fig. 6); 12.55*ra* a sister rosette, one of 8 dwarfs in the same culture; 12.59*a* a rosette from a plant similar to 11.42*r* (Fig. 5).

From the mass of rosettes with characters as illustrated in Fig. 7, 12.55*a*, a group of 8 dwarfs (Fig. 7, 12.55*ra*) was quickly recognized. One can hardly imagine a much sharper contrast between rosettes in the same culture than is shown in this illustration (Fig. 7, 12.55*ra* compared with 12.55*a*). By the side of the dwarf 12.55*ra* is a rosette, 12.59*a*, of the F_3 from one of the dwarfs of the F_2, 11.42*ra* (similar to Fig. 5). A comparison will show how perfectly the F_2 type 11.42*f* (Fig. 6) has repeated the behavior of its parent hybrid F_1 plant 10.30*Lb* in throwing off a class of similar dwarfs. The 8 dwarfs of the culture 12.55 were set out under conditions ill-suited to their constitution and I had great difficulty in saving 5 plants from a period of drought. These are now in the hot house, where it is hoped that they may be brought to maturity.[2]

The normal rosettes of the F_3 culture 12.55, excluding the 8 dwarfs described above, developed a fairly uniform set of plants which at maturity exhibited a foliage of broader and more crinkled leaves than those of the F_2 parent hybrid 11.42*f*. This progressive advance in foliage was also supplemented by a greater vigor and size of the plants, although the flowers remained without marked change. Summarizing the behavior of the F_2 plant 11.42*f* in the F_3 generation, the most striking points were the repetition of the behavior of the F_1 parent hybrid 10.30*Lb* in throwing off the same types of dwarfs, and a much greater uniformity among the normal plants with apparent advance in leaf size and vegetative vigor.

The next form to be considered is a plant, 11.42*g*, which was fairly representative of the mass of the F_2 generation from 10.30*Lb*. This plant (Davis, '12*a*, p. 415, 11.42*g*) was 1.5 m. high and characterized by large flowers (petals about 4 cm. long) and large crinkled leaves (Fig. 8). It was a type rather common and intergrading with other forms of the culture. It exhibited a decided progressive advance in flower and leaf size over the F_1

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[2] Of the 5 dwarfs 3 are now (June 1, 1913) almost full grown and true to the type.

parent plant 10.30*Lb*, but stood close to the center around which the mass of the F_2 culture varied.

From this plant, 11.42*g* (Fig. 8), the contents of two capsules, about 900 seeds, were sown (culture 12.56) and 377 rosettes developed. Among the rosettes a group of 20 dwarfs very shortly defined itself. The characters of the dwarfs are illustrated in Fig. 9, 12.56*ra*, where they may be compared with those of a normal rosette, 12.56*a*, shown above. The same sort of contrast is here exhibited as that illustrated by Fig. 7 for the culture from 11.42*f*. By the side of the dwarf 12.56*ra* is again figured the

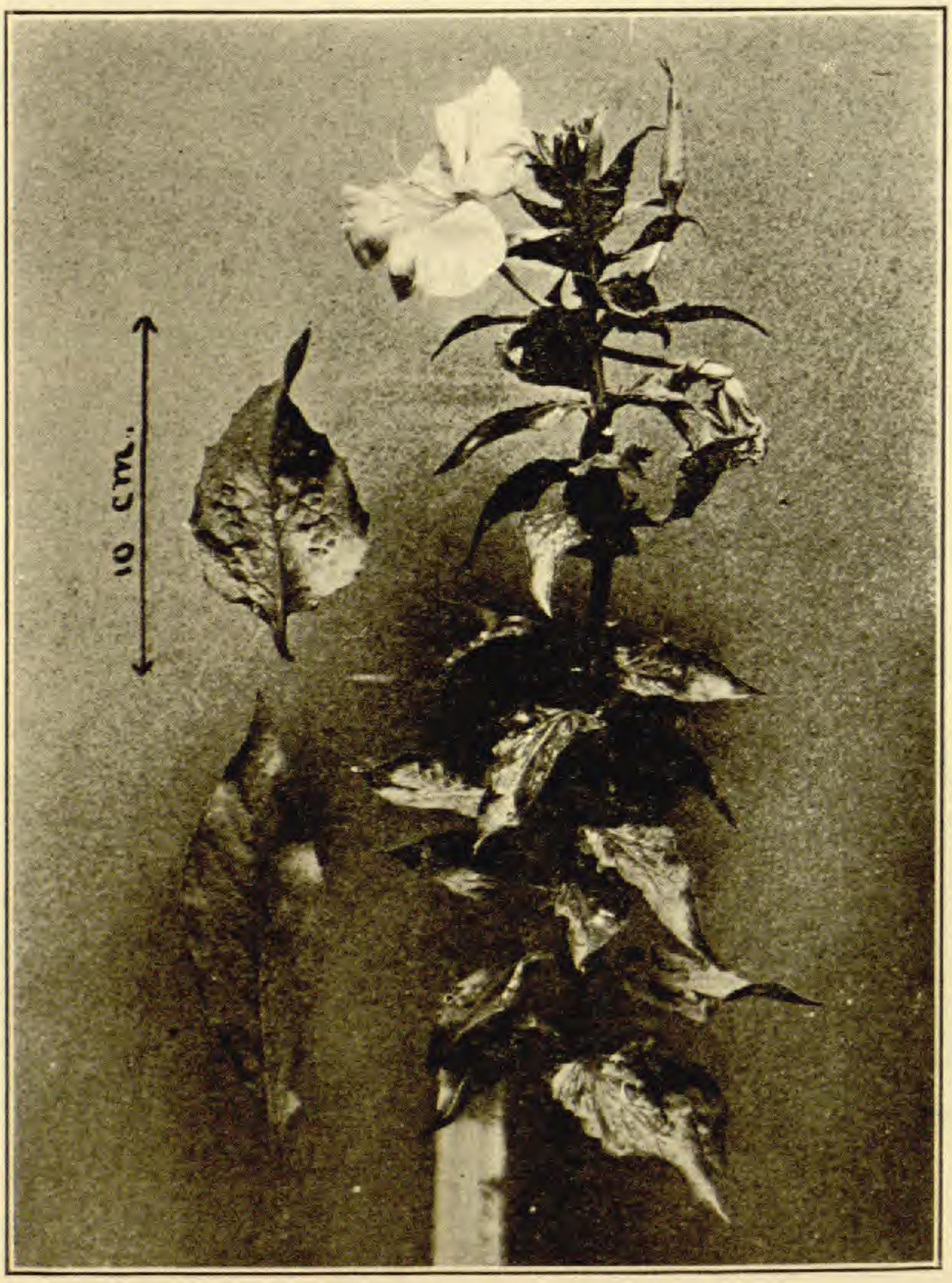
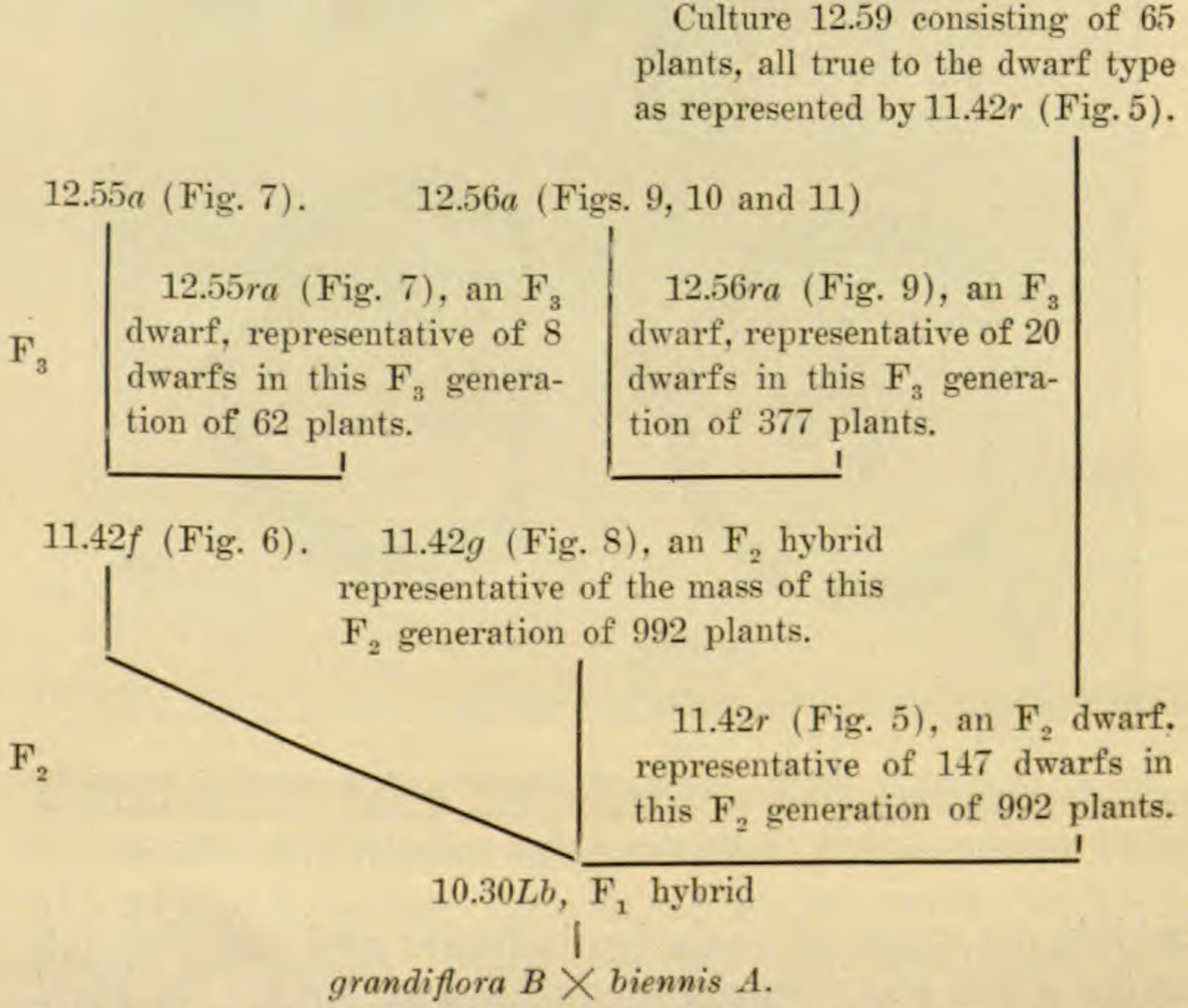


FIG. 8. A type, 11.42*g*, representative of the mass of the F_2 generation from the F_1 plant 10.30*Lb*, hybrid of *grandiflora B* × *biennis A*. A form characterized by large, crinkled leaves and large flowers (petals 4 cm. long).

rosette 12.59*a* (compare Fig. 9 with Fig. 7) of the F_3 from one of the dwarfs in the F_2, 11.42*ra* (similar to Fig. 5). Figs. 7 and 9 then illustrate the same behavior, in the first case that of the F_2 plant 11.42*f*, and in the second case that of the F_2 sister plant 11.42*g*, and both plants have produced a class of dwarfs similar to that which appeared in the F_2 11.42*r*, the type shown in Fig. 5. I had the same difficulty with the 20 dwarfs from 11.42*g* as with the 8 from 11.42*f* and was only able to save 7 plants from a period of drought. These at the present writing are also in the hothouse, where they bid fair to reach maturity.[3]

An outline of the genealogy of the sets of dwarfs produced by the family from the F_1 hybrid 10.30*Lb* will make clearer its complications. The important feature is of course the close parallelism of this history with the behavior of *Lamarckiana* when it produces in successive generations a marked variant that breeds true.



Culture 12.59 consisting of 65 plants, all true to the dwarf type as represented by 11.42*r* (Fig. 5).

12.55*a* (Fig. 7). 12.56*a* (Figs. 9, 10 and 11)

F_3

12.55*ra* (Fig. 7), an F_3 dwarf, representative of 8 dwarfs in this F_3 generation of 62 plants.

12.56*ra* (Fig. 9), an F_3 dwarf, representative of 20 dwarfs in this F_3 generation of 377 plants.

11.42*f* (Fig. 6). 11.42*g* (Fig. 8), an F_2 hybrid representative of the mass of this F_2 generation of 992 plants.

F_2

11.42*r* (Fig. 5), an F_2 dwarf, representative of 147 dwarfs in this F_2 generation of 992 plants.

10.30*Lb*, F_1 hybrid

grandiflora B × *biennis A.*

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[3] Of the 7 dwarfs 4 are now (June 1, 1913) almost full grown and true to the type.

Of the 357 normal green rosettes in culture 12.56 from 11.42*g,* 128 plants were set out and brought to maturity. A single interesting rosette with leaves sharply streaked with white failed to live. The rosettes consisted of unusually broad, ovate or elliptical leaves, loosely arranged (see Fig. 9, 12.56*a*). The group of plants at maturity exhibited a range of variation in flower and leaf size, but on the whole was remarkably uniform except for the plant 12.56*x* to be described later.

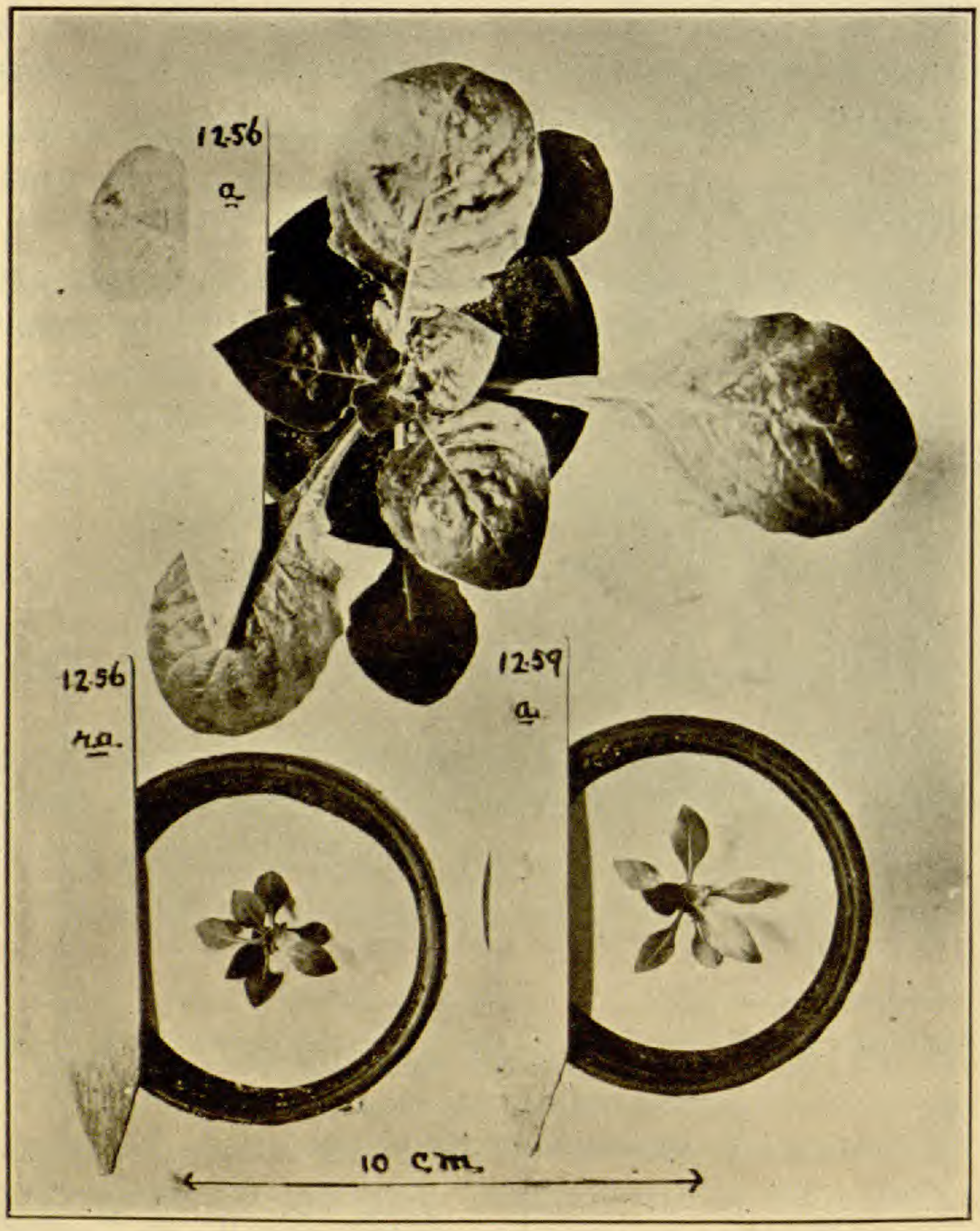

FIG. 9. Rosettes in the F_3: 12.56*a* representative of the mass of the culture from the F_2 plant 11.42*g* (Fig. 8); 12.56*ra* a sister rosette, one of 20 dwarfs in the same culture; 12.59*a* a rosette from a plant similar to 11.42*r* (Fig. 5).

The type characteristic of this group (culture 12.56) is one of the most interesting among my hybrids and will be briefly described. It is a large plant, 1.5–2 m. high, with long branches from the base (Fig. 10), stem green above, reddish below, leaves much larger and thicker than in *grandiflora,* and strongly crinkled. Inflorescence (Fig. 11) *grandiflora*-like, very dense on the main branches, bracts persistent. Buds 8–9 cm. long, cone circular in section, sepals green, their tips attenuate. Petals about

FIG. 10. Mature plant, 12.56*a,* from the rosette 12.56*a* (Fig. 9), representative of the mass of the F_3 generation from the F_2 hybrid 11.42*g* (Fig. 8). A form remarkable for the size and thickness of the leaves, size of flowers and general vigor.

4 cm. long. Stigma 5–8 mm. above the tips of the anthers. Capsules 2.8 cm. long.

Although this type presented many of the peculiarities of the *grandiflora* parent, there was evident a remarkable degree of progressive evolution in the size and thickness of the leaves, size of the flowers, and general vigor. These progressive advances introduce characteristics of

Fig. 11. Flowering side branch of the F_3 hybrid 12.56*a* (Fig. 10), showing the *grandiflora*-like inflorescence and broad crinkled bracts. At the right is a leaf from the lower portion of the main stem.

Lamarckiana and make this type a very favorable one for back crossing with certain races of *biennis* which in certain respects (*e. g.*, stem coloration, rosette characters, etc.) are closer to *Lamarckiana*. Such a back cross was made last summer with *biennis D* and should result in a further advance towards the synthesis of *Lamarckiana*-like hybrids between *grandiflora* and forms of *biennis*.

The single plant, designated 12.56*x* in the culture de-

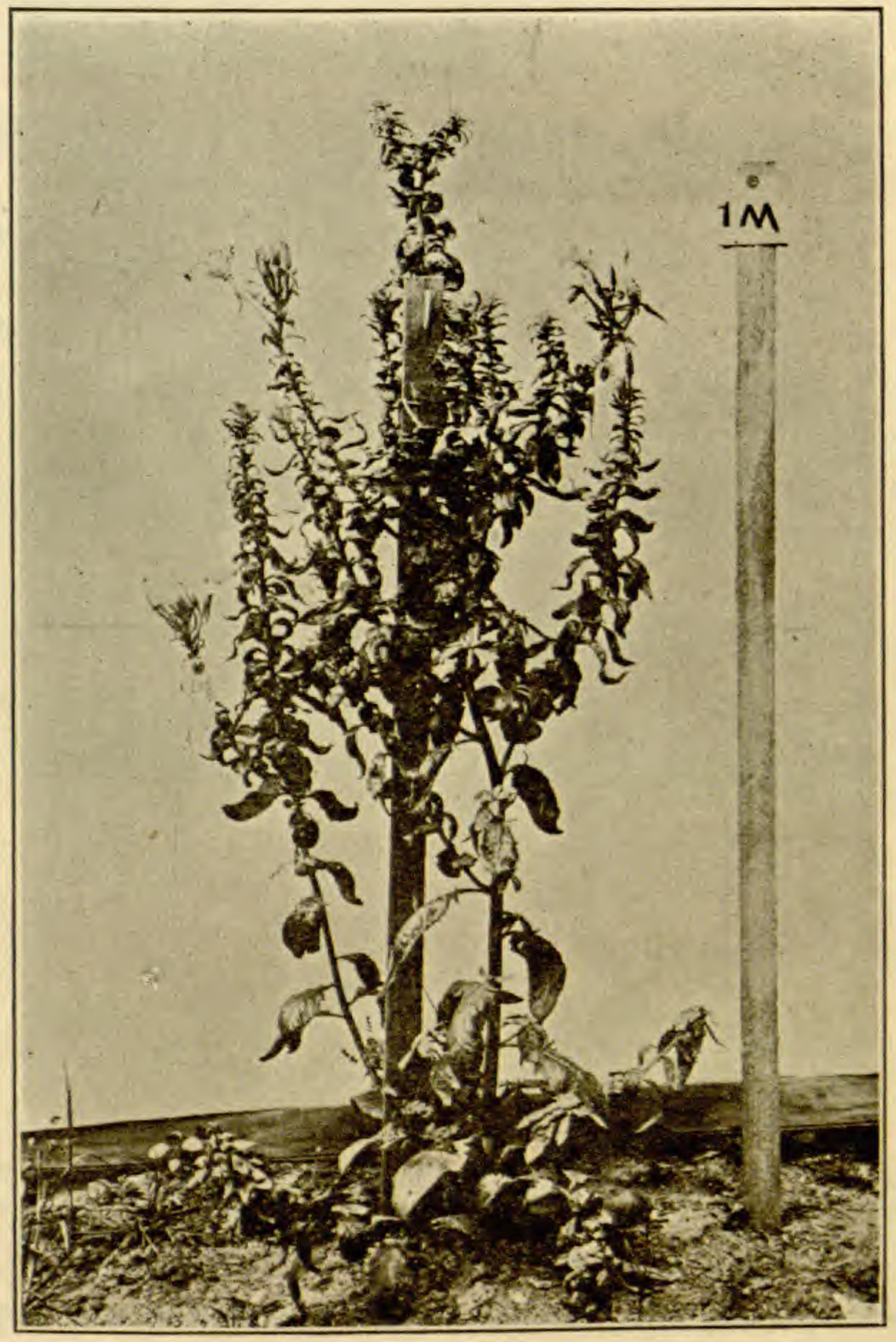

FIG. 12. Mature plant, 12.56*x*, a remarkable type represented by a single individual in the F_3 from the F_2 hybrid 11.42*g* (Fig. 8). A form distinguished by its stocky habit and very large thick leaves. The plant had at least 21 chromosomes, the triploid number.

scribed above, presented characters that distinguished it from the mass in much the same way that *gigas* is distinguished from *Lamarckiana*. In the rosette stage the plant was marked because of the exceptional thickness and large size of the leaves. The mature plant, somewhat more than 1 m. high (Fig. 12), was much shorter and more stocky (*gigas*-like) than the average of the culture; the leaves were even thicker. The inflorescence (Fig. 13) was more dense because of the shorter internodes so that the top appeared flattened as in *gigas*.

FIG. 13. Flowering side shoot of the F_3 hybrid 12.56*x* (Fig. 12), showing the four-angled buds, and dense inflorescence, flat-topped because of the short internodes. At the right is a leaf from the lower portion of the main stem.

The buds, 8–9 cm. long, presented a stouter cone, 4-angled, and the sepal tips were less attenuate and thicker. The petals were about 4 cm. long, the hypanthium was shorter, and the stigma lobes, 4–6 mm. above the tips of the anthers, were thicker than in the type representative of the mass of the culture. The capsules, 1.8 cm. long, were shorter and stouter. So many of these points of difference suggest the characteristics of *gigas* that it was not surprising to find the chromosome count to be above 14, the normal diploid number for *Œnothera*. It is difficult to determine the exact number, but from counts made this spring at the growing points of seedlings from this plant I am certain that the chromosome count is at least as high as 21, the triploid number. It will be remembered that the triploid number has been determined by both Miss Lutz ('12) and Stomps ('12) for "mutants" derived from *lata* and *Lamarckiana* to which Stomps has given the name *semi-gigas*. We have then in this plant (12.56*x*) a variant from the parent hybrid which probably corresponds closely to the "triploid mutants" of *Lamarckiana* or its derivatives.

There will now be briefly described the F_3 generation from a type 11.42*l*, represented by a single plant in the F_2 from 10.30*Lb* (Davis, '12*a*, p. 415, 11.42*l*). This plant, about 1 m. high, was remarkable for its broad, entire, much-crinkled leaves (Fig. 14); the flowers were medium-sized (petals 2 cm. long). The contents of two capsules, 222 seeds, were sown, from which 117 plants were obtained and brought to maturity (culture 12.58). The mass of the rosettes consisted of broad elliptical leaves, crinkled and loosely arranged. Several rosettes were *grandiflora*-like, intergrading, however, with the mass, and 8 presented a long narrow form of leaf. The culture at maturity was very well graded from plants 1.6 m. high, with flowers as large as those of *grandiflora* (petals 3.5 cm. long) to plants the counterpart of the F_2 parent hybrid 11.42*l*. The foliage of the culture as a whole continued the progressive advance of 11.42*l* as shown by larger leaves which were more strongly crinkled. The plants from the 8 rosettes with narrow leaves also had at

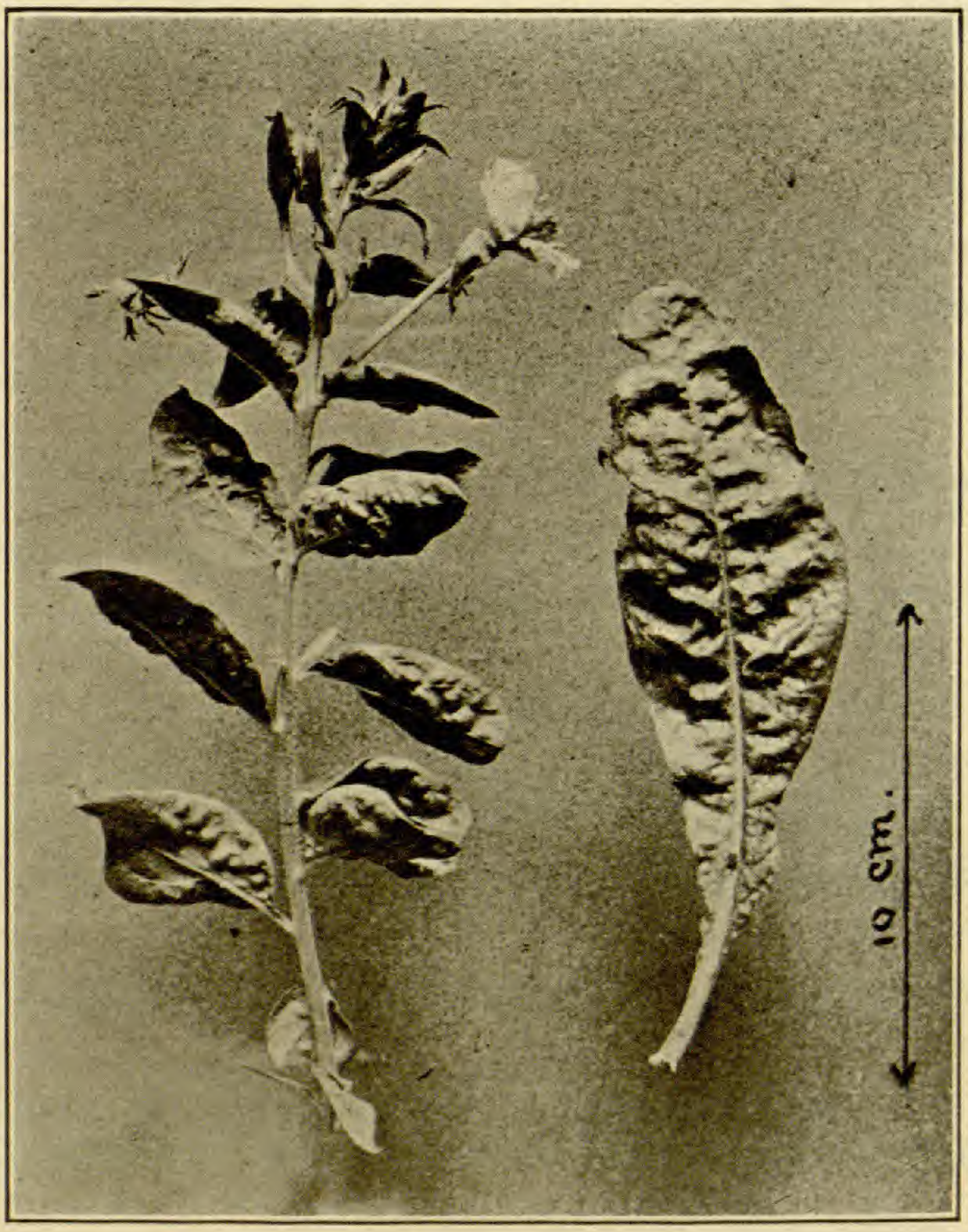

FIG. 14. A type, 11.42*l*, in the F_2 from the F_1 plant 10.30*Lb*, hybrid of *grandiflora B* × *biennis A*, represented by a single plant. A form characterized by its broad, entire, much crinkled leaves and medium-sized flowers (petals 2 cm. long).

maturity smaller and narrower leaves; the flowers were medium-sized (petals 2.5 cm. long). They constituted a clearly defined group but could not be called dwarfs. It is interesting to note that an F_2 type so clearly defined as 11.42*l* may, nevertheless, be strongly heterozygous and consequently may be very far from representing a stable segregate in the F_2.

A remarkable plant, 11.42*j*, appeared in the F_2 from 10.30*Lb* (Davis, '12*a*, p. 415, 11.42*j*) which in habit and

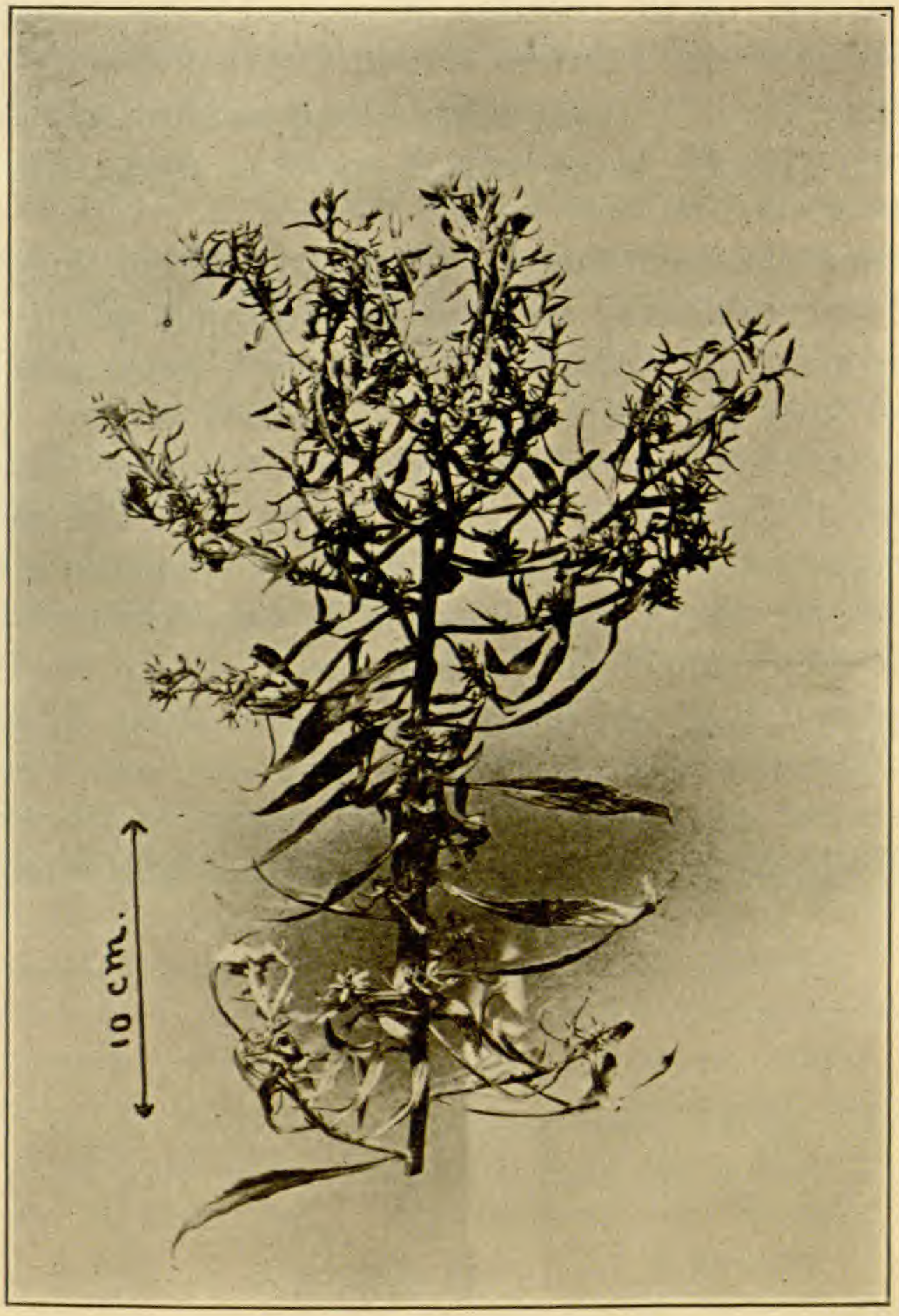

FIG. 15. A type, 11.42*j*, in the F_2 from the F_1 plant 10.30*Lb*, hybrid of *grandiflora B* × *biennis A*, represented by a single plant. A remarkable form with a foliage of very narrow leaves, and with very small flowers (petals 6 mm. long), anthers sterile. This plant in its habit and foliage matched closely De Vries's "mutant" *Œnothera elliptica*.

foliage agreed very closely with the "mutant" *Œnothera elliptica* obtained by De Vries ('01, vol. I, pp. 280–284) from *Lamarckiana*. This plant, 7 dm. high, developed from a rosette with narrow leaves and at maturity presented a foliage of very narrow leaves well illustrated in Fig. 15, which shows the top of the main stem. The flowers, however, were very small (petals 6 mm. long) and the anthers as far as observed were completely sterile. Since this plant apparently could not be selfed, I pollinated it from a large sister plant of the F_2 with *grandiflora*-like flowers. The result was 154 seeds from several capsules which gave 46 plants in the F_3 generation (culture 12.57). Of the rosettes, 40 proved to be large-leaved, exhibiting much variation, but with several plants similar to *grandiflora;* 6 rosettes bore long narrow leaves.

From the 40 large-leaved rosettes there developed plants 1.2–1.5 m. high with a foliage of crinkled leaves, and medium-sized flowers (petals 2–2.5 cm. long). Of the 6 narrow-leaved rosettes, 5 developed plants which agreed with the "*elliptica*" type and 1 became a broad-leaved form similar to the 40 described above. The 41 large-leaved plants of the culture evidently took their characteristics largely from the pollen parent of the cross and represented something of a blend. I am at a loss to account for the five individuals of the "*elliptica*" type unless they came from apogamously formed seed. The "*elliptica*" type has since appeared in other F_2 generations from the cross *grandiflora* × *biennis,* and it appears to be a not uncommon expression of one of the extreme forms which may be thrown in the F_2 of this cross.

(*To be continued*)

THE INFLUENCE OF PROTRACTED AND INTERMITTENT FASTING UPON GROWTH

DR. SERGIUS MORGULIS

In an earlier paper on inanition[1] I pointed out the significance of the period following a prolonged fast in investigating the problem of growth. Prolonged starvation—notwithstanding the exhaustion which it produces—seems to exercise a rejuvenating effect upon the assimilative capacity of the organism, which builds itself up again with surprising rapidity as soon as feeding is resumed. It was also shown there, that the increase in weight of the animal does not necessarily correspond to the quantity of ingested food, being somewhat greater than the latter, which is due to absorption of water from the surroundings. Whereas inanition causes a relatively greater loss of dry substance than of water, it was found that "the effect of resumed feeding (upon the salamander) is to increase the water content more relatively than the dry substance" (p. 213).

Since those results were published I had an opportunity of collecting more material bearing upon this topic. The experiments were made with the salamander *Triton cristatus,* and strengthen my former observations on *Diemyctylus viridescens.* In the subjoined Table *A* the data as to the weight of nine salamanders with the exact amounts of food taken during 7 to 14 days after starvation are summarized. The renewal of feeding after several weeks of privation does not generally proceed smoothly, the animals either taking sick or refusing the food, hence the relapses with the diminution of the body weight which may be seen occasionally throughout the table.

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[1] Morgulis, S., "Studies of Inanition in its Bearing upon the Problem of Growth," I, *Arch. f. Entw.-Mech.,* Bd. 32, 169–268, 3 plates, 1911.

That the rate of growth is independent of the amount of nutrition is revealed by these experiments in a striking manner; they show rather the reverse, namely, the utilization of the food by the organism according to the need of its tissues and cells. The impulse to grow plays the leading part here, not the quantity of food brought into the digestive organs, and in this respect the growth after starvation has much in common with embryonic growth.

TABLE A

No.	1		2		3		4		5		6		7		8		9	
Days of Feeding	Weight of Animal	Amount of Food in Gms.	Weight of Animal	Amount of Food in Gms.	Weight of Animal	Amount of Food in Gms.	Weight of Animal	Amount of Food in Gms.	Weight of Animal	Amount of Food in Gms.	Weight of Animal	Amount of Food in Gms.	Weight of Animal	Amount of Food in Gms.	Weight of Animal	Amount of Food in Gms.	Weight of Animal	Amount of Food in Gms.
1	0.631	.0450	0.631	.1020	0.755	.1125	1.067	.0580	0.882	.0480	0.889	.0870	0.826	.0920	0.887	.1300	0.821	.0843
2	0.679	.0368	0.749	.0790	0.865	.0565	1.093	.0620	0.917	.0610	1.077	.0870	0.967	.1460	1.084	.1300	0.929	.0736
3	0.729	.0535	0.872	.0490	0.959	.0590	1.102	.0910	1.025	.0610	0.977	.0870	1.169	.1460	0.978	.1300	0.969	.0631
4	0.780	.1215	0.897	.0590	0.973	.0590	1.207	.0570	0.988	.0625	0.937	.1450	1.122	.1270	0.909	.1300	0.969	.0953
5	0.922	.0920	0.977	.0520	0.923	.0525	1.231	.0655	1.041	.0690	1.109	.1450	1.206	.1270	0.909	.1300	1.058	.0662
6	1.077	.0920	0.977	.0520	0.923	.0525	1.251	.0690	1.104	.0540	0.887	.1210	1.146	.1270	0.864	.1520	1.055	.0990
7	0.941	.0920	0.961	.0725	0.919	.0740	1.251	.0690	1.104	.0540	0.978	.0890	1.140	.1270	1.063	.1070	1.000	.0856
8	0.898	.0920	1.001	.1100	1.011	.0930	1.308	.0960	1.037	.1000	1.020	.0890	1.090		1.146	.1070	1.064	.0998
10	0.898	.0920	1.001	.0770	1.011	.1170	1.308	.0800	1.037	.0980	1.020	.0890	1.090		1.146		1.064	
12	0.898	.0920	0.937	.0700	1.107	.0665	1.308	.1070	1.037	.0870	1.020	.0890	1.090		1.146		1.064	
13	0.898	.0920	0.937	.0700	1.107	.0665	1.351	.1030	1.157	.0780	1.020	.0890	1.090		1.146		1.064	
14	0.898	.0920	0.937	.1580	1.107	.1270	1.351	.1030	1.157	.0780	1.020	.0890	1.090		1.146		1.064	
15	1.011	.0920	1.227	.1580	1.227	.1270	1.399	.1030	1.263	.0780	1.120	.0890	1.243		1.200		1.211	

Food offers merely a greater or less scope to the inherent growth-tendency of the organism, and, like so many other factors, may either increase or decrease its effect. It is possible that the reduction in size of the cells, or rather the diminished ratio between cell-body and nucleus, has something to do with the observed processes of intense growth, and that the rejuvenescence of the organism is analogous to the condition in the embryo, where the cell-body is likewise small in relation to its nucleus. There is certainly more than mere superficial resemblance between the two phenomena of growth from the point of view of the protein metabolism. Already in the eighties

Kahan[2] observed that after seventeen days of inanition (when the body had suffered a loss of 31 per cent.) rabbits gained 56 per cent. in weight on a diet even less sufficient than that, which could just maintain them in a state of equilibrium under normal conditions. The retention of protein by the cells, as their principal building material, is greater than usual, and along with it goes the retention of water.

If the growth of the body as regards weight corresponded to the amount of food taken for that period of time, then the coefficient of growth should be equal, $G/F=1$. According as to whether a larger or smaller portion of the food is transformed into body substance, *i. e.*, participates in growth, the coefficient ought to vary from 0 to 1. Furthermore, when the increase in weight of the animal exceeds the quantity of ingested food, the coefficient will rise above 1. In the following Table B we give the records of the body weights for consecutive days, the amount of food ingested and the corresponding coefficient of growth of four animals.

TABLE B

ANIMAL 1

Date	Nov. 3	December							Total for 7 Days
		22	23	24	25	26	27	29	
Body weight in grm.	.910	.631	.679	.729	.780	.922	1.077	.898	
Difference in weight....		−30.6%	+.048	+.050	+.051	+.142	+.155	—	+.267
Amount of food given (in grm.) on previous day.......			.0450	.0368	.0535	.1215	.0920	—	.3488
Ratio between increase in weight and amount of food......			1.07	1.36	.95	1.17	1.68	—	.77

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[2] Kahan, J. A., "Der Einfluss des Hungerns auf das Körpergewicht bei der Auffütterung von Tieren mit einer beschränkten Nahrungsmenge nach einem überstandenen Hunger," *Russ. Medizin*, Nr. 17–19, 1885.

ANIMAL 2

Date	Nov. 8	January								Total for 7 Days
		3	4	5	6	7	8	9	10	
Body weight in grm....	.892	.631	.749	.872	.897	.977	?	.961	1.001	
Difference in weight....		−29.3%	+.118	+.123	+.025	+.080	?	−.016 (?)	+.040	+.370
Amount of food given (in grm.) on previous day......			.1020	.0790	.0490	.0590	.0520	——	.0725	.4125
Ratio between increase in weight and amount of food......			1.16	1.56	.51	1.36	?	?	.56	.89

ANIMAL 3

Date	Nov. 8	January								Total for 7 days
		3	4	5	6	7	8	9	10	
Body weight in grm....	1.064	.755	.865	.959	.973	.923	—	.919	1.011	
Difference in weight....		−29.0%	+.110	+.094	+.014	−.050	—	−.004	+.092	+.256
Amount of food given (in grm.) on previous day......			.1125	.0565	.0590	——	.0525	——	.0740	.3545
Ratio between increase in weight and amount of food......			.98	1.67	.024	?	?	?	1.28	.72

ANIMAL 5

Date	Nov. 14	January								Total for 7 Days
		2	3	4	5	6	7	8	9	
Body weight in grm....	1.140	.882	.917	1.025	.988	1.041	1.104	—	1.037	
Difference in weight....		−22.7%	+.035	+.108	−.037	+.053	+.063	—	−.067	+.155
Amount of food given (in grm.) on previous day......			.0480	.0610	——	.0625	.0690	.0540	——	.2945
Ratio between increase in weight and amount of food......			.73	.177	——	.85	.91	?	?	.53

The animals were weighed both before and immediately after feeding, so that the amount of food consumed could be ascertained accurately by subtracting the former weight from the latter. After twenty-four hours the animals were weighed again, the difference between this weight and that of the previous day giving the growth for twenty-four hours. In some cases the increase is only a fraction of the quantity of food which the animals received; not infrequently, however, it has been even greater than that quantity. In the case of the four salamanders recorded above there are ten out of eighteen determinations, which show an excess of growth over the amount of ingested food. We find that the coefficient of growth never falls below 0.5 (the one instance where it is only 0.24 is obviously accidental); in other words, as regards weight the increase of the body is never equal to less than one half of the quantity of ingested material, and the average coefficient for all four animals for a seven-day period of renewed feeding is 0.73. This fact is particularly significant when we compare it with the condition found in continually fed specimens. In the case of other four control salamanders it was found that the coefficient of growth was only 0.26, *i. e.,* only about 26 per cent. of the food had gone to the building up of the body substance.

When the growth occasioned by a return to a normal diet after a protracted starvation is studied from the point of view of the body dimensions instead of the body weight, it appears that it is exceedingly slow during the first two weeks, showing that during that time primarily the internal organs undergo reparation, the enlargement of the musculature and of the skeleton ensuing subsequently.

Salamanders fed intermittently did not become as heavy nor as large as the control specimens; that is to say, their growth has been retarded from the point of view of both weight and size. The coincidence of the results of measuring both weight and length of the body strengthens our conclusion that frequently repeated starvation affects unfavorably the vitality of the organism. The conclusion concurs with that of Kahan,[3] who subjected pigeons two or three times to hunger, feeding them very abundantly in the periods between, and found that their power of resistance declines with each new experience of starvation.

> Der nach vorhergegangenem Hungern bei unbeschränkter Nahrungsaufnahme aufgefütterte Organismus zeigt die Folgen der früheren Nahrungsentziehung, . . . und bei wiederholter Nahrungsentziehung rascher verfällt, als der gesunde (p. 277).

Seland[4] experimenting with chickens got quite different results. He allowed his birds to reach a state of equilibrium in body weight, when food was withdrawn for periods of one to two days, and then they were again fed. He discovered that the periodically fasting birds grew heavier than the control, although they were actually getting less food. According to von Seland, the increase is not caused by a deposit of fat, but by an accumulation of albuminous material, and the periodic fasting has the effect of making the body heavier, stronger and more solid. Von Seland's assertion, however, regarding the increase in quantity of the albuminous substances lacks the proof of chemical analysis.

We saw in the foregoing that after a period of protracted starvation, when about one fourth of the body weight has been lost, growth is very intense and the per cent. of the consumed food which becomes converted into the substance of the organism is nearly three times as large as in the continually fed salamanders. The impulse to grow determines the degree of utilization of the nutriment, the rate of growth being regulated by the particular state of the cells of the organism, which in turn is probably occasioned by the relation of the nucleus to the

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[3] Kahan, J. A., "Mit Auffütterung abwechselnde akute experimentelle Inanition," *St.-Petersburger med. Wochenschr.*, Nr. 30, 275–277, 1886.

[4] V. Seland, "Ueber die Nachwirkung der Nahrungsentziehung auf die Ernährung," *Biol. Centralbl.*, Bd. 7, 145–158, 184–192, 214–224, 246–256, 271–281, 1887.

cell-body. We shall attempt now to demonstrate this point further by comparing the results obtained for long periods with differently nourished animals. The data which are given in the subjoined tables are so arranged that the number of times when either the starved or the periodically fasting salamanders received food is just one half of the number of feedings of the control specimens for some definite length of time. We take the *number* of feedings which could be obtained from the individual records as indicating the approximate amount of consumed food, since the actual quantities—except in a few instances—have not been measured directly. It is clear, of course, that animals fed *ad libitum* do not always take the same quantity of food, nor is it likely that different animals consume each similar amounts, but in the run of weeks it may be expected that the positive and negative variations will compensate for each other. We may, therefore, accept the *number* of times at which the animals received food as a measure for the *total quantity* of food consumed during a certain period. Furthermore, to make the weights of the different animals comparable with one another they have been computed on the assumption that the initial weight of all animals was one gram.

In Table *C* we have the data of four groups of starved salamanders and of their corresponding controls. The first two groups, each comprising four individuals, are compared at the end of 112 days, during which period the control specimens were fed 96 times, while the others (after 7–8 weeks of complete inanition) were fed 48 times. The ratio between the number of feedings being 1 ÷ 0.5, it follows that by the end of 112 days the control animals have probably consumed twice as much food as the starved animals. The final body weight at the close of this period was 3.823 g. and 4.265 g. (1st group), and 3.092 g. and 3.694 g. (2d group), respectively. Taking the mean of these two groups, we get 1 ÷ 1.165 as the ratio between the final weights, and 1 ÷ 2.45 as the ratio between the daily increase in the control and starved animals. Examining the data of the third and fourth groups where in the course of 84 days the control specimens were fed 72 times and the starved ones only 36 times we encounter practically the same result.

TABLE C

	Group	Control Animals (A)	Animals Fed after Protracted Starvation (B)	Ratio Between A and B ($A = 1$)
Number of feedings	i	96	48	1 ÷ 0.5
	ii	96	48	1 ÷ 0.5
	iii	72	36	1 ÷ 0.5
	iv	72	36	1 ÷ 0.5
Body weight (Initial wt. = 1 gr.)	i	3.823	4.265	1 ÷ 1.116
	ii	3.092	3.694	1 ÷ 1.195
	iii	2.557	2.170	1 ÷ 0.849
	iv	3.040	2.635	1 ÷ 0.867
Daily increase in body weight	i	0.029	0.068	1 ÷ 2.345
	ii	0.022	0.056	1 ÷ 2.545
	iii	0.022	0.033	1 ÷ 1.500
	iv	0.028	0.046	1 ÷ 1.643

The fact that in the case of these last two groups the starved individuals have not reached the same weight as the corresponding controls, whereas in the former two groups they even became by one-sixth heavier than the controls, must be attributed to the shorter duration of the feeding-up of these animals. We find thus that a fasting experience enables the organism to attain almost the same weight (or even a greater weight) which animals that did not have such an experience attain, upon half the quantity of their food supply, because the rate of growth after starvation is considerably greater.

We may proceed now in a similar fashion to compare the effect of continual and of intermittent feeding upon the growth of the body. These data are recorded in Table *D*, and are likewise calculated for an initial weight of one gram. The ratio between the number of feedings of these two kinds of animals being 1 ÷ 0.5, the respective body-weights have not become 0.5 of that of the control specimens, but 0.57–0.81; in other words, the intermittently fed animals have increased somewhat more than the control animals would have done with the same quantity of food. Taking the average for all four groups together, we find that the intermittently fed specimens with one half the amount of food reach a little over two thirds of the body weight of the continually fed ones.

TABLE D

	Group	Control Animals (A)	Periodically Fasting Animals (C)	Ratio Between A and C ($A=1$)
Number of feedings	i	120	60	1÷0.5
	ii	120	60	1÷0.5
	iii	120	60	1÷0.5
	iv	108	54	1÷0.5
Body weight (Initial wt. = 1 gr.)	i	4.395	2.520	1÷0.573
	ii	3.550	2.885	1÷0.813
	iii	3.520	2.490	1÷0.708
	iv	3.616	2.501	1÷0.692
Daily increase in body weight	i	0.028	0.025	1÷0.893
	ii	0.022	0.032	1÷1.455
	iii	0.021	0.025	1÷1.191
	iv	0.024	0.028	1÷1.167

Assuming the values for the normally fed animals equal to 1, we may sum up the results of our comparison of the growth in weight of continually fed individuals (*a*) and those starved (*b*) or intermittently fasting (*c*) in the following formulæ:

a	*b*	*c*	
1	0.5	0.5	Quantity of food.
1	2.01	1.18	Daily increase in weight.
1	1.01	0.70	Final body weight.

The results of the above study are obviously at variance with those of von Seland who found that his periodically fasting birds have been faring best. This difference in our results may, of course, be accounted for by the circumstance that the periods of fasting of my salamanders have been rather long (one to three weeks; also in Kahan's experiments the periods were from one and a half to two weeks) whereas von Seland's chickens have never fasted more than 12 to 48 hours at any time.

Why does the intermittent feeding produce such an inhibiting effect upon the growth of the body in weight? Before attempting to answer this question it should be recalled that these animals utilize a larger portion of their food in building up their tissues than normally fed salamanders do, the rate of their growth being likewise about one fifth greater. We also pointed out that the animals remained smaller in size and lighter in weight than the controls. We meet, thus, in the case of the periodically starved salamanders two contrary phenomena: on the one hand, we observed and directly measured on a number of individuals their deficient growth; on the other hand, we found that the growth activity has not been impaired, but even somewhat greater than in the case of the control Tritons. In the paper, already referred to in the beginning of this article, I showed that the water content of the organism increases 4 per cent. when salamanders are returned to a normal diet after protracted starvation. The water content probably comes back to the natural level when the animals have again reached their normal state. In the case of the intermittently fasting salamanders this may not happen, if the fast is repeated before the effect of the preceding inanition has been overcome. If we recall that the per cent. of water in the organism of starved individuals is also somewhat higher than the usual (by 1.5 per cent.) it becomes quite probable that water may be accumulating in the tissues of intermittently starved specimens to the extent of being a hindrance to their growth.

Acute hunger has an entirely different effect. It may even exhaust the organism for a time, but so long as degeneration has not set in—degenerative changes appear generally in the advanced stages of starvation—inanition may produce an invigorating influence upon the organism, which has its parallel in the embryonic growth only. The temporary relief which the organs of digestion get may contribute much towards improving their capacity, but the resulting rejuvenation of the organism is a composite effect of the activity of all its cells. The chief reason for the revitalization of the organism is in the enhanced need of the cells for nourishment. The cells become "avaricious," if we may say so, and the increased proportion of the nucleus in the cell organization may perhaps in a measure be responsible for that.

From all that has preceded the conclusion can be drawn that periodic starvation is more detrimental to the organism than acute starvation followed by a liberal supply of food. In the former case the individual remains below the level of the normally fed animals; in the latter case, on the contrary, provided the inanition has not been carried too far, the restorative process may go even beyond the limit attainable under normal conditions. From the viewpoint of practical application this conclusion is evidently of importance, suggesting to those who have made the problem of social welfare their own the dangers to the health and vigor of mankind which lurk in the more commonly occurring underfeeding and chronic starvation, especially of the young and growing generation.

CAMBRIAN HOLOTHURIANS[1]

AUSTIN H. CLARK

Preface.—In a recent number of *Science*[2] Dr. Hubert Lyman Clark published a most interesting and valuable summary of the literature on the fossil remains of the Holothuroidea, accompanied by critical remarks. The greater part of his paper is devoted to a consideration of Dr. Charles D. Walcott's contribution to the knowledge of Cambrian geology and paleontology in which there are described as holothurians, under the new generic names *Eldonia, Laggania, Louisella* and *Mackenzia,* four new forms from the Middle Cambrian of British Columbia.[3]

Dr. Clark reaches the conclusion that *Laggania* can not positively be assigned to any invertebrate phylum, for he sees "nothing beyond the probable form of the body, and the terminal mouth, to suggest a holothurian, and these characters are equally suggestive of actinians;" *Louisella* he does not believe is a holothurian, though he can offer no suggestion as to its proper systematic position; *Mackenzia* he does not consider a holothurian; he hints that it may be an actinian, though he hastens to emphasize the fact that he does not positively make that assertion; *Eldonia* he is sure is not a holothurian, but he does not place it in any phylum.

To sum up Dr. Clark's criticism, he is sure that none of the four genera established by Dr. Walcott really belong to the Holothuroidea, but he is quite unable to suggest a more logical resting place for any of them.

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[1] Published by permission of the secretary of the Smithsonian Institution who, however, does not hold himself responsible for any of the views expressed.

[2] *Science,* Vol. 35 (N. S.), No. 894 (February 16, 1912), p. 274.

[3] Smithsonian Miscellaneous Collections, Vol. 57, No. 3, pp. 41–58.

Dr. Clark remarks that in Fig. 2 on plate 13 (representing *Mackenzia costalis*) "the terminal mouth surrounded by a jointed or notched ring is distinctly shown; in the specimen I was unable to make out these points satisfactorily"; I can personally vouch for the presence of the "notched ring"; but after the specimen was photographed Dr. Walcott tells me that it was subjected to an acid bath in order to remove a deposit of calcite, and while it was in that bath the ring seems to have disappeared.

Dr. Clark laments that "if *Eldonia* is a holothurian, it becomes virtually impossible to define the class except in terms of the alimentary canal; indeed, if *Eldonia* is a holothurian, the echinoderms themselves can be defined in no other terms, for *Eldonia* lacks every single character which justifies the customary view that holothurians are echinoderms." I can not agree that *Eldonia* lacks every characteristic echinodermal character; but even if it did and we were forced to define the class Holothuroidea on the basis of the digestive tube the Holothuroidea would merely be brought into line with very many of the other animal groups. I would like to see Dr. Clark draw up a definition which would successfully differentiate the Trichoptera from the Lepidoptera, or the Orthoptera from the Neuroptera, or a definition which would include all the members of the Diptera, but exclude all other insects. The more we learn about the various types of animals the more it is impressed upon us that the dividing lines between them are purely arbitrary, and that there is a fundamental unity covering the whole field of zoölogy.

Introduction.—My study of the specimens upon which these new genera and species were based was entirely independent of that made by Dr. Walcott, and, on account of our entirely different previous training, I approached the problems presented in an entirely different way. Excepting *Eldonia,* I did not examine any of the genera in detail until after his paper was in press. After its publication the bearing of these new genera from the Cambrian upon certain phases of marine biology, especially on the probable age of the deep-sea fauna, led me to examine all of them with the greatest care in order to determine to my complete satisfaction whether the classification made by Dr. Walcott was beyond doubt justified by the available facts.

Dr. Clark and I examined the material together during a visit which he made to Washington; but we did not discuss the classification or the systematic position of the genera.

After the publication of Dr. Clark's article, as my examination of the material had led me to conclusions quite different from those at which he had arrived, it seemed advisable to put on record the results of my studies so that those to whom the material is not accessible may have, in addition to the published figures, which are wonderfully good and leave little to be desired, the conclusions of three entirely independent investigators, each with a very different previous training, and each entirely uninfluenced by the conclusions arrived at by the others.

Before taking up the discussion of these forms in detail it is advisable to give a brief outline of the general principles of deduction by which my conclusions regarding them have been reached.

The characters by which animals are identified are of two classes, the fundamental, or characters of prime systematic importance, and the correlative, or characters of prime practical importance, though often of no systematic importance whatever.

In the exceedingly rapid work, often under the most unfavorable conditions, demanded in the identification of organisms brought up by the dredge at sea one has no chance to look for fundamental characters. The general shape of the organisms, coupled with a few other obvious features, alone are depended upon. Thus a shell with a more or less polished surface and perfect bilateral symmetry is at once known to be a brachiopod, regardless of whether it possesses a stalk or not; a soft and flabby, more or less shiny, tubular object, with or without body processes, is at once identified as a holothurian, no matter whether tentacles are visible or not, and quite regardless of its symmetry. In deep-sea work one soon gets to know the representatives of the various phyla by characters never mentioned in systematic treatises, and never even dreamed of by the laboratory student; yet the identification by these characters after practise is quite as sure as the identification by the features of real classificatory significance.

The identification of many fossils calls for essentially the same mental processes as the rapid identification of animals brought up by the dredge; one must be prepared to grasp at once the salient correlative features if the fundamental characters are obscured. Unfortunately this method of work has often yielded deplorable results when applied by paleontologists unacquainted with the practical side of the work of the marine biologist; but this is no reason why it should not lead to perfectly reliable conclusions when logically applied.

The chief of the correlative characters in any group of animals is the general body form taken in connection with the size. Thus in differentiating echinoderms from other organisms at sea we rely entirely upon size and shape; there is no time to look for radial symmetry; we probably take this in subconsciously, though it may be to a large extent mentally ignored.

When any member of a group of animals adopts a mode of life entirely different from that of all the other members of the same group we must be prepared to encounter extraordinary, sudden and unexpected changes in its organization which are not connected with the more usual type of organization by any intermediates; and it must be remembered that such changes affect first of all the general body form. Among such animals we almost always find the group characters developed in a most erratic manner; some structures will be very highly specialized, sometimes specialized far beyond what is seen in any other member of the group, while others will be in a very rudimentary or primitive state of development, or even absent altogether.

The echinoderms differ very abruptly from the crustacean line of descent from which they took their origin and, similarly, each echinoderm class differs very abruptly from all the others. We see in all the echinoderms to-day most perplexing combinations of primitive and highly specialized characters associated in all sorts of ways, and this leads us naturally to the assumption that there was no definite intergrade between the echinoderms and the barnacles, but that the former sprang from the latter or, more strictly speaking, from the same phylogenetic line which may be traced by easy stages to the latter, by a broad saltation in which the assumption of the free habit and the correlated assumption of pentaradiate symmetry combined to make the existence of intergrading forms impossible, while at the same time it resulted in the formation by the echinoderms, at the very moment of their origin, of two widely diverse stocks, the heteroradiate (including the Pelmatozoa, the Echinoidea and the Holothuroidea) and the astroradiate (including the Asteroidea and the Ophiuroidea) between which there are, and can be, no intergrading forms.

Thus in dealing with the echinoderms we must be ever on the alert to detect sudden saltations. We must also be prepared to eliminate from our minds all ideas of hypothetical ancestors from which all echinoderms are commonly supposed to have been derived, but which probably never existed; and, along with the hypothetical ancestor myth, to banish from our thoughts all ideas of fundamental echinodermal structures, equally non-existent. No echinodermal structure is of such fundamental importance in the economy of the animals that it can not be either profoundly modified or even dispensed with altogether under special conditions, reverting to a type more or less characteristic of some other phylum. The pentaradiate symmetry is often brought forward as a character of the highest importance; but it is the result not of a class peculiarity, but of simple mechanics: the somatic divisions in the echinoderms are marked by lines of weakness; hence the divisions of the body must be uneven in number, so that no line of weakness will go straight through the body, thus subjecting the animal to danger through a shearing strain; when the somatic divisions are by lines of extra strength, as in the cœlenterates, the divisions are always equal, as in this case the continuation of a line of strength directly across the body gives added rigidity.

We know enough about organic life at the present day to be somewhat sceptical when new phyla are proposed to include problematical forms. If we can not allocate an animal on the basis of some supposedly fundamental character, or if it falls on the basis of a single character in a phylum from all the groups in which it differs in all the others, we ignore that character entirely and take up another. In every group each character has a definite and restricted application, beyond the limits of which it is quite valueless. The echinoderms are commonly said to be pentaradiate, and the great majority certainly are; but certain genera, entirely or in part, possess three, four (like most medusæ), six, seven, eight or ten rays; we recognize them as echinoderms just the same. Specimens of the genus *Limnocnida* are commonly pentaradiate; but we instantly recognize them not as echinoderms, but as hydromedusæ. The echinoderms we say have abundant calcareous deposits in the skin, and often also in the deeper parts of the body; the genus *Pelagothuria* has no trace of any calcareous deposits whatever, but no one doubts that it is an echinoderm.

These few obvious cases are selected from an almost unlimited choice; they show conclusively that any character, no matter how fundamental it may be, may suddenly become quite worthless, forcing us to depend entirely upon other characters which in other cases are more or less ignored. Thus, to take two instances from the fossil crinoids, in the genus *Marsupites* the only feature which can possibly give a clew to its true affinities is the arm structure, which is that of an ordinary comatulid; and in the allied genus *Uintacrinus* the arm and pinnule structure alone are found to be reliable.

Eldonia.—In *Eldonia* there are only two structures upon which we can hope to base our deductions concerning its systematic position: (1) the bell-like general shape, and (2) the coiled digestive tube with two tentacle clusters at the anterior end.

1. The bell-like shape suggests the cœlenterates, and such forms as *Trochosphæra* or trochophore larvæ.

The highly specialized digestive tube at once negatives the supposition that *Eldonia* may be a cœlenterate.

Trochosphæra has a general form and an internal structure which is certainly suggestive of *Eldonia;* but there are many reasons why it is not possible to connect the two. In the first place there is the question of animal mechanics; the size of the members of each group of animals is limited by physical and mechanical considerations due to the requirements of fundamental structure, etc. Thus we do not find butterflies as large as ordinary birds, nor cetaceans so small as the average fish; their structure is not adaptable to the limitations imposed by such sizes. *Trochosphæra* is surrounded by a band of cilia, just below which is the mouth, and below that another band of cilia. Ciliated bands do not transform into broad body fringes such as we see in *Eldonia;* they are more or less uncertain structures, and are present as ciliated bands, or are absent altogether. *Trochosphæra* has a powerful retractor muscle attached to the posterior portion of the alimentary canal; powerful retractor muscles are a feature of all the rotifers; there is no trace of any retractor muscle in *Eldonia.*

In *Trochosphæra,* and in the so-called trochophore larvæ, the anus opens at the pole determined by the ciliated band as the equator, while the mouth is just below the chief ciliated band. In *Eldonia* the mouth is the more central, and there appears to be a possibility that the anus is on the dorsal surface above the fringed border. The ciliated bands of *Trochosphæra* have a very definite connection with the mouth, a connection not evident between the fringed border of *Eldonia* and the mouth, the relationships in the latter being almost exactly like the relationships between the digestive tube and the expanded brim in such holothurians as *Euphronides tanneri.* Although the superficial resemblance between *Eldonia* and *Trochosphæra* (including trochophore larvæ) is certainly striking, I can not see the slightest reason for connecting the two; the relation between them is precisely similar to that between certain of the pteropods and the nautilus, which, on account of their remarkable similarity, were for a long while placed in the same genus.

2. Certain "worms" have a digestive system suggesting that of *Eldonia;* but such worms are never provided with oral tentacles, possessing instead a tough protrusible proboscis; nor do they ever have the digestive tube differentiated as in *Eldonia;* nor do they ever have the body of a type which, on account of the structure of the body wall and the general internal anatomy, particularly the type of muscular investment, could by any stretch of the imagination be supposed to assume a bell-like form.

Certain heteroradiate echinoderms, as some holothurians belonging to the family Elpidiidæ, a few echinoids, and the (recent) endocyclic crinoids, have a digestive tube resembling very closely that of *Eldonia,* and in the holothurians there are always tentacles about its anterior end. Moreover, in many of the Elpidiidæ, as, for instance, in *Euphronides tanneri,* the body is entirely surrounded by a broad brim with marginal lappets, just as it is in *Eldonia.*

Judging from all the evidence which we have—and the specimens of *Eldonia* are among the most wonderfully preserved fossils which have ever come to light—*Eldonia* can be nothing else than a heteroradiate echinoderm, and among the heteroradiate echinoderms a holothurian, in which class it comes nearest to certain of the Elpidiidæ.

Affinities of Eldonia.—In *Eldonia* the body is medusa-like, circular, bordered with a broad *Euphronides*-like brim of uniform width; the mouth and anus are near together, the mouth being nearer the center; the general configuration of the digestive system is very similar to that seen in the endocyclic crinoids; there are two large many-branched tentacles, one on either side of the mouth.

Eldonia seems to me to be a pelagic derivative from some elpidiid type; the body has shortened so that the mouth and anus have become closely approximated; the brim surrounding the body has become laterally extended and uniformly developed, so that a swimming bell has resulted. *Eldonia* is therefore an elpidiid holothurian which has become flattened dorsoventrally and at the same time laterally expanded into a circular form resembling that of the medusæ.

We are familiar with just such a transformation in the echinoids; *Dendraster, Echinarachnius, Arachnoides,* etc., are flattened, circular and disk-like, though derived from ovoid, globular or more or less spherical types. In these the flattening has been in the direction of the radial symmetry so that the oral pole is at or near the center of one surface and the aboral pole at or near the center of the other. In *Eldonia* the flattening has possibly, though not certainly, been in a plane at right angles to this so that the oral pole is at one edge of the circular disk and the aboral pole at the other. This is only a slight advance over the conditions seen in *Benthodytes typicus,* so that it need occasion no surprise.

The reduction of the number of tentacles in *Eldonia* to two possibly indicates a suppression of three of the radial systems, leaving only two of the original five. Many of the crinoids show a more or less complete reduction of two or three of the radial systems; indeed, in *Tetracrinus* one is invariably absent.

In certain forms among the Comasteridæ, as, for instance, in *Comatula micraster,* ambulacral grooves, nerves and tentacles may be entirely absent from six out of the ten arms, or from three out of the five rays, leaving, as in *Eldonia,* only two of the original five divisions functioning normally, and these two may be three times as large as the others.

If we can assume that the two tentacles of *Eldonia* indicate a suppression of three of the original five radial systems, or a carrying out to completion of the condition already far advanced in many of the Elpidiidæ, a reasonable explanation of the structure of *Eldonia* becomes a relatively simple matter.

If we take a form like *Scytoplanes typicus* or *Euphronides tanneri* and shorten the body so as to bring the mouth and anus near together, giving the digestive tube exactly the same shape that it assumes in the so-called endocyclic crinoids, the two radial muscles would form a circular band of concentric muscle fibers just beyond the enteric canal, exactly as we see them in *Eldonia.*

Ordinarily among the echinoderms the mouth is at one pole of the radial symmetry and the anus is at the other. In the recent crinoids the anus has become entirely dissociated from the aboral radial pole and has migrated to a position near the mouth. It is thus evident that the connection between the anus and the aboral pole is not absolutely unchangeable.

The water vascular system centers, in all echinoderms, in a ring about the œsophagus, from which (usually) five radial canals are given off. How then can we account for the small central ring in the center of *Eldonia,* far removed from the mouth? The first question to be answered is whether the arrangement of the water vascular system about the mouth is really fundamental, or whether it is merely a matter of mechanical convenience when the mouth happens to be, as it usually is, at or near one of the apices of the pentamerous symmetry.

Now among the crinoids there are two families, the

Comasteridæ and the Uintacrinidæ, in which the mouth, instead of being as usual in the center of the ventral surface of the disk, is lateral, situated typically on the very edge of the ventral surface of the disk, between the bases of two of the arm groups. In these families the tubes of the water vascular system, above which ambulacral grooves usually, though not always, run, instead of converging in five large vessels to the circumoral ring lead from the arms to a large trunk vessel which runs around the periphery of the disk with the anal tube instead of the mouth as its center. This large peripheral ring, is interrupted posteriorly, and the mouth passes through it anteriorly; but it indicates a tendency for the water vascular system to transform from a ring about the mouth to a ring about the anal tube, or more correctly, into a ring about the ventral pole of the body regardless of the position of the mouth. In this connection it would be interesting to determine if in the Comasteridæ the so-called stone canals were confined to the circumoral ring, or if they showed a tendency to migrate secondarily along the peripheral water tube.

With the assumption by *Eldonia* of the circular form and the spiral digestive tube the muscles assumed a concentric arrangement. Probably at the same time the water tubes, following the course of the muscles, also attained the form of a peripheral canal, after the same manner as we see almost consummated in the Comasteridæ. The peripheral water tubes in *Eldonia* serve largely as braces to bind the animal together, just as they serve as braces in the marginal brim of *Euphronides tanneri*. This function would, for mechanical reasons, induce a diminution in the diameter of the central ring, in order that they might function to the best advantage; but the muscular ring, in order to preserve a maximum availability for expansion and contraction, would remain with the greatest possible diameter. Thus we should theoretically reach a condition precisely like that seen in *Eldonia;* a very large concentric muscular ring, and a very small, also concentric, apical water vascular ring with exceedingly long tubes reaching out into the marginal tube feet, fused together into a broad and uniform marginal brim.

In *Eldonia* the radial canals so-called are the canals of the podia transformed into a system of braces, exactly as they are transformed into a system of braces in *Euphronides tanneri, Benthodytes typica,* and many similar forms; in these species, which live supported upon ooze and have developed a broad brim about their body so that they will not sink into it, the ring canal of the water vascular system retains its original position about the œsophagus, while in *Eldonia,* which floats free in the water, and possesses a medusoid body form, the canals have become enormously elongated and of uniform length all around, serving as body supports (like the ribs of an umbrella) instead of merely as supports for an expanded brim; and, as a necessary result of the change in the mechanics of the body, the central ring of the water vascular system has migrated from its original position about the gullet to an apical position in the center of the apical portion of the animal, equidistant from the border on every side.

The entire dissociation of the water vascular system from the mouth is the most difficult thing to explain in *Eldonia.* But, after all, this is not without a parallel. In the bilaterally symmetrical invertebrates one of the most fundamental structures is the nerve ring about the œsophagus, consisting of the supraœsophageal ganglion, the two circumœsophageal ganglionic connectives and the subœsophageal ganglion. The relationship of these nerves is entirely changed in the crinoids; here we find a circumœsophageal ring consisting of the supraœsophageal ganglion alone, the subœsophageal ganglion at the dorsal pole, with its continuation directly downward at right angles to the plane of the digestive canal instead of parallel to and directly beneath it, and the circumœsophageal ganglionic connectives resolved into numerous nerve strands parallel to, instead of passing horizontally around, the gullet. Surely if such a fundamental rearrangement can take place in the nervous system we can not be surprised in seeing the water vascular system become entirely dissociated from the mouth.

Pelagic animals tend to become delicate and translucent, and if belonging to groups with a more or less calcified (or chitinous) skeleton, to reduce that skeleton to a minimum or to dispense with it entirely. Thus the entire absence of any trace of a skeleton in *Eldonia* does not prevent us from suggesting an affinity with the holothurians, more especially as the recent pelagic holothurian *Pelagothuria* has no trace whatever of calcareous elements.

Dr. Clark remarks that the oral tentacles of *Eldonia* are suggestive of the marginal clusters of *Lucernaria* and its allies, or perhaps are not fundamentally different from those of some rhizostomous medusæ. This would naturally be the case no matter to what group *Eldonia* belonged. The tentacles of *Eldonia* undoubtedly are subject to the same mechanical and physical forces as are those of the pelagic medusæ, and this would be amply sufficient to induce a strongly marked parallelism, no matter what their ultimate origin might have been.

The body of *Pelagothuria* is tubular, with the mouth at one end and the anal opening at the other; its alimentary canal is in loops (a long-drawn-out spiral); the swimming organ is merely an expansion of the oral disk. *Pelagothuria,* therefore, though similarly pelagic, is radically different from *Eldonia,* derived from a radically different stock.

The embryology and metamorphosis of the echinoderms lead us to believe that they were derived from phyllopod crustacean ancestry through the barnacles as a result of the sudden suppression of one half of the body and the consequent assumption of a circular body form. Since there are only two tentacles in *Eldonia,* we might suggest the remote possibility that *Eldonia* may have arisen from a form like *Scytoplanes typicus* by a further sudden suppression of half of the body and the dropping out of three of the rays, the rest of the body curving about so as to form again a circular animal from one originally pentamerous, though ultimately derived from bilateral ancestors.

Louisella.—No marine animal is known except among the Elpidiidæ with a body form resembling that of *Louisella pedunculata.* A comparison between this fossil and such recent species as *Scotoplanes insignis* shows a similarity that can not but be more than superficial.

Dr. Clark in speaking of *Louisella* says that "none of the podia are sufficiently defined to enable one to make out even the form, let alone the structure, whereas if they were really like those of *Scotoplanes* and other elasipods, their rigidity would have caused them to be as well defined as any part of the body outline." Every one who has collected specimens of certain of the species of Elpidiidæ knows that they are as delicate and as difficult to preserve as are many, if not most, medusæ; even when hardened in alcohol the podia of such forms as *Deima pacificum* are extremely soft and flabby. If any species of the group adopted a pelagic habit this character would naturally be greatly accentuated.

Laggania.—It is difficult to see how *Laggania cambria* can be interpreted otherwise than as a holothurian of the elpidiid type, a form related to such species as *Benthodytes sanguinolenta,* or especially to *B. sibogæ.*

Circumstantial Evidence Suggesting the Possible Occurrence of the Elpidiidæ in the Palæozoic.—As I understand the three holothurians from the Middle Cambrian described by Dr. Walcott (*Eldonia, Laggania* and *Louisella*), they all fall within, or are closely related to, the family Elpidiidæ. Now the Elpidiidæ are preeminently creatures of the deep sea, and represent possibly the most strictly abyssal group to be found among marine organisms. The *Siboga* dredged one species in 31 fathoms, and the first species to be described was found in

50 fathoms in the Arctic Ocean; but the great majority of the species occur below 1,000 fathoms, extending downward to 2,900 fathoms.

Now in forms confined to the deep sea, or to exceedingly high latitudes, or subjected to widely varying temperatures or salinities, or occurring in highly saline, alkaline or acid water, or under unnatural conditions generally, the geological age of the maximum virility of the genera or families may be guessed by the amount of difference between the chemical and physical surroundings among which they now live, and the conditions obtaining slightly below low-tide mark on a tropical coast bathed by ocean water free from any admixture of fresh, and containing the normal proportion, in amount and in kind, of salts. Such forms as *Artemia,* occurring in salt pans, *Xiphosurus, Tachypleus* and *Carcinoscorpius* (*"Limulus"*) occurring in more or less foul and muddy situations, and the Elpidiidæ, characteristic of great depths, we therefore suspect of being relics of the earliest geologic times, representing what were once the dominant types in their respective groups, possessed of such vigor and adaptability that, forced by internal specific pressure, due to increase in the number of the individuals, they were able to accommodate themselves to these conditions. When these types began to wane new and vigorous forms arose in the tropical littoral which extirpated them from all the more desirable locations, allowing them to persist only in such unnatural situations as those into which they had intruded when in the prime of their vigor.

There is not the slightest reason for supposing that any markedly new animal type ever originated in the deep sea, or under conditions differing much from those found just below the low-water mark.

If we are ever to discover any recent representatives of such groups as the trilobites, the eurypterids, the blastoids or the cystids we shall find them not in the tropical or temperate littoral, but living under some highly abnormal conditions, in the deep sea, in highly saline, alkaline or acid water, in the regions of excessive cold or excessive heat (such as hot lakes), in stagnant pools in the ocean bed, in brackish underground lakes or streams, or in comparable situations; but apparently none of these groups were highly adaptable; though very abundant, they flourished through comparatively small extremes in their physical and chemical environment, from which subsequent vigorous types with the same or a greater economic radius promptly ousted them.

The disappearance of a group in a given horizon, it should be pointed out, does not at all mean that the group really vanished at that time; it means merely that at that time it disappeared from the littoral. Most groups undoubtedly persisted long after they ceased to occupy a habitat which is now a geological stratum, under locally unfavorable conditions, finally dying out at a time long subsequent to the last record in the rocks.

Not only does the deep-water habitat of the Elpidiidæ betoken a very ancient origin, but the group to-day is evidently senescent. The extraordinary shapes assumed by most of the species can only be interpreted as a result of an explosion of the characters induced by extreme age.

Thus, reasoning backward from a study of the recent fauna alone, we should expect to find the Elpidiidæ and *Artemia,* or very closely allied forms, in the early paleozoic rocks, representing the littoral in the age when they were at the height of their ascendancy, and we should be greatly surprised should they appear in any post-paleozoic formation.

Lorenzinia.—Lorenzinia, mentioned by Dr. Clark, is undoubtedly the cast of part of a medusa, as any one acquainted with the literature on the fossil medusæ can see.

Mackenzia.—The two specimens assigned to the genus *Mackenzia* appear to me to be undoubtedly mud-living actinians of the family Edwardsiidæ, closely related to the *Edwardsia,* for the following reasons. In a semi-desiccated synaptid the longitudinal lines marking the longitudinal muscles become gradually obsolete, and the digestive tube, more or less distended with inorganic matter, becomes more and more prominent, so that finally we see an elongated worm-like object with a prominent digestive tube which bears a collar about the anterior end; longitudinal markings become obliterated and lost in the irregular foldings which take place, while these also obscure the other more flaccid internal organs; a soft mud-living actinian, on the other hand, is reinforced internally by numerous mesenteries; on desiccation these tend to lie flat, and to raise the body wall at the lines of attachment slightly, giving a fluted or pleated appearance, just as is shown in *Mackenzia.* No trace of a tubular digestive tube is visible in *Mackenzia,* nor is there any other internal differentiation, but there are prominent, regular and numerous parallel pleats; these pleats are four in number in the upper part of the body, but apparently five in the lower part, so that there are probably eight mesenteries represented; there appear to have been sixteen tentacles, two in each intermesenterial space; the contracted lower portion of the body suggests the physa of *Edwardsia;* it is probable, therefore, that *Mackenzia* is an actinian, and that it should be placed in the family Edwardsiidæ near the genus *Edwardsia.* Some of the preserved specimens of *Edwardsia farinacea* in the National Museum collection are almost identical with the specimen of *Mackenzia costalis* figured by Dr. Walcott, the similarity of the contracted anterior portion of the body being especially striking.

Systematic Position of the Genera Discussed.—When a biologist, especially a zoogeographer, undertakes to deal with fossils, he becomes of necessity somewhat of an iconoclast. The faunas of the several horizons represent to him not so many distinct and separate successive faunas each derived directly from that preceding, but so many distinct faunal regions, each equidistant from the center, the center representing the phylogenetic starting point of organic life. In certain limited genera or in certain small groups an extraordinary progressive development is undoubtedly traceable through a greater or lesser extent of geologic time; but in general there is a balance between the organisms in each horizon which is strikingly similar to the balance between the organisms in every other horizon and between the organisms in each of the present faunal regions, so that, taking into consideration the circumstances under which the animals in each horizon lived, we are not able to say with any degree of accuracy that, phylogenetically speaking, any one fauna, zoogeographic or paleontologic, is *in toto* more primitive than any other.

Keeping this in mind and speaking solely as a biologist, I would suggest the following disposition of the genera described by Dr. Walcott:

- Holothuroidea
  - Family Elpidiidæ
    - Genus *Laggania*
    - Genus *Louisella*[4]
  - Family Eldoniidæ (near the Elpidiidæ)
    - Genus *Eldonia*
- Zoantharia
  - Family Edwardsiidæ
    - Genus *Mackenzia*

Summary.—*Eldonia* is a free-swimming holothurian, and is most closely related to the species of the family Elpidiidæ.

In body form alone does *Eldonia* resemble a medusa; this general resemblance may therefore safely be disregarded as a parallelism resulting from a similar pelagic habit.

In the general shape of the body as well as in the course of the digestive tube *Eldonia* approaches *Trochosphæra* (and trochophore larvæ); but the enormous dis-

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[4] Both of these genera can probably be referred, with a reasonable degree of probability, to subfamilies in this family; but it seems best to leave them, for the present at least, unassigned.

crepancy in size, the broad fringe about the body, the large tentacles on either side of the mouth, the absence of muscles of the group type characteristic of the rotifers, and the submarginal anus, seem to negative the idea that the two can be in any way related.

The medusoid body form, the absence of a protrusible proboscis and the presence of a large branched tentacle on either side of the mouth appear to offer conclusive evidence that *Eldonia* can not be a "worm."

The digestive tube of *Eldonia* resembles that of the heteroradiate echinoderms, and especially that of certain holothurians; the tentacles on either side of the mouth suggest an affinity with the holothurians; the radial canals, leading to a central ring, are comparable to the radial canals and the central ring of the holothurians; the broad circular muscle about the body suggests a modified longitudinal holothurian muscle, and is of the group type characteristic of the echinoderms; the broad brim about the body is strikingly similar to the brim developed in certain elpidiid holothurians, such as *Euphronides tanneri* and *Scytoplanes typicus*. A pelagic holothurian is known as an inhabitant of the recent seas; though very different in origin and in affinities from *Eldonia*, it demonstrates that a pelagic habit is not impossible in the group. The species of the family Elpidiidæ are preeminently inhabitants of the deep sea; this suggests that the fossil representatives of the family should be found in very early geological formations.

Therefore *Eldonia* is a pelagic holothurian, related to the species of the family Elpidiidæ.

No marine animals are known outside of the holothurian family Elpidiidæ which have a body form like that of *Louisella pedunculata* in all its details; but this species agrees in every particular with one or other of the species in that family. We can not, therefore, escape the conclusion that *Louisella pedunculata* should find a place in the family Elpidiidæ along with all the recent animals which in any way resemble it.

By exactly the same reasoning *Laggania cambria* is assigned to a position in the same group.

The type specimen of *Mackenzia costalis* shows a pleated structure which can only be interpreted as due to longitudinal mesenteries, probably eight in number; there appear to have been sixteen processes around the mouth which probably indicate tentacles retracted before preservation; the distal portion of the body resembles closely the distal portion of the body in the genus *Edwardsia*. Thus, as *Mackenzia costalis* presents characters not found outside of the Zoantharia, and in that group peculiar to the family Edwardsiidæ, it seems necessary to assign it to a position in the family Edwardsiidæ, near the genus *Edwardsia*.

SHORTER ARTICLES AND DISCUSSION

VIABILITY AND COUPLING IN DROSOPHILA

In the course of work done in the college year, 1911–12, under the direction of Dr. Castle, at the Harvard Zoological Laboratory, Cambridge, Mass., an experiment was performed to test the relative viability of the red-eyed and the white-eyed stock of *Drosophila ampelophila* Loew. The white-eyed race was obtained from Professor Morgan, while the red-eyed material was reared from banana exposed near the laboratory.

A large glass jar well supplied with fermenting banana and tightly covered with a double layer of closely woven cheese-cloth was used for the experiment. Five pairs of flies from the red-eyed stock and five pairs from the white-eyed stock were introduced on November 29, 1911. After a few weeks the jar was well supplied with flies of both eye-colors, but the red-eyes considerably surpassed the whites in number. Fresh food was introduced once and on February 12 a number of the flies were drawn off and counted.

Let us consider here what the expectation of the ratio between reds and whites would be, after the culture had been running indefinitely. Assuming equal viability of the two races, we should expect equality of reds and whites among the males, and three reds to one white among the females. This appears from the following combinations based upon Morgan's formulæ. The mutation producing white eyes, being recessive to the wild type, has been denoted by a small letter as suggested by Castle.[1]

Red female gives gametes x and x.

White female gives gametes wx and wx.

Red male gives gametes x and —.

White male gives gametes wx and —.

The combinations will then be as follows:

$$\begin{array}{ll}\begin{array}{l} 2wx\,\text{—} = 2\text{ white males,}\\ 2x\;\;\text{—} = 2\text{ red males,}\end{array} & \left.\begin{array}{l}1\;x\;\;x\\2\;wx\;x\end{array}\right\} = 3\text{ red females,}\\ & 1\;wx\;wx\;\;= 1\text{ white female.}\end{array}$$

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[1] "Simplification of Mendelian Formulæ," American Naturalist, XLVII, 555, March, 1913.

It is evident upon inspection of these formulæ that although the red females have gained over the whites, this is due solely to the formation of two heterozygotes where at first we had a pure red and a pure white. Since the ratio of the three types of gametes does not change, we may expect the above recorded ratios of red and white flies to persist indefinitely.

Let us now observe the results of counts and compare these with the theoretical ratio. The count of February 12 gave 129 red males, 202 red females, 21 white males and 3 white females. Instead of equality in the males, we have 6 reds to 1 white, and instead of 3 to 1 in the females, we have 67 reds to 1 white.

On March 13 flies were again drawn off from the jar and counted, giving 303 red males, 514 red females, 36 white males and 2 white females. The males are now 8.42 reds to 1 white and the females 257 reds to 1 white.

On April 12 a count showed 1,341 red males, 1,363 red females, 95 white males and 24 white females, or 14.1 reds to 1 white among the males, and 56.8 reds to 1 white among the females.

In general these results show that the reds are outrunning the whites. Disregarding sex we expect a ratio of 5 reds to 3 whites to persist in the population. On February 12 we get 14 to 1; on March 13, 21.5 to 1 and on April 12, 22.7 to 1. On April 12 there are more white females than would be expected, an irregularity which can apparently be explained only by chance. The great excess of females in the first two counts probably denotes that the lethal factor clearly demonstrated by Morgan[2] was present in the stock and the equality of the sexes in the last count denotes that the lethal factor has been bred out.

Among the flies examined in the last count were a few reds in which the eyes were reduced to about one fourth the normal diameter, and also a spotted-eyed fly which was not counted in the numbers recorded. The latter had the right eye red with a white patch four ommatidia in diameter near the vertex, and the left eye white with a red spot eight to twelve ommatidia in diameter with a few smaller red spots below it near the posterior margin. Later examinations of the culture were made in the hope of obtaining a spotted-eye fly alive, but these were without success.

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[2] "The Explanation of a New Sex Ratio in *Drosophila*," *Science*, N. S., XXXVI, 934, November, 1912.

Small-eyed flies were obtained from the same stock and further work is now being done with these.

The association of the differential factor between colored and white eyes, *w*, with the differential factor between long and miniature wings, *m*, was tested. Matings were made between white-shorts and red-longs, and between white-longs and red-shorts and in both cases the long-red female offspring were paired to short-white males. In this way the F_2 progeny gave directly a measure of the classes of gametes produced by the long-red F_1 females, except as they may have been affected by differences of viability. When white-shorts were mated with red-longs, the female offspring were of composition, *wmx—x*, giving excess of white-shorts and red-longs over the other two possible combinations; and when white-longs were mated with red-shorts, the female offspring were of composition, *wx—mx*, giving excess of white-longs and red-shorts.

Daughters of white-shorts by red-longs gave 3,371 red-longs, 1,136 red-shorts, 1,571 white-longs and 2,064 white-shorts.

Positive association of *w* and *m* is given by the equation

$$\frac{\text{red-longs} + \text{white-shorts}}{\text{red-shorts} + \text{white-longs}} = \frac{5{,}435}{2{,}707} = 2.$$

Greater viability of the longs is shown by the equation

$$\frac{\text{longs}}{\text{shorts}} = \frac{4{,}942}{3{,}200} = 1.54.$$

Greater viability of the reds is shown by the equation

$$\frac{\text{reds}}{\text{whites}} = \frac{4{,}507}{3{,}635} = 1.24.$$

Daughters of white-longs by red-shorts gave 1,047 red-longs, 1,116 red-shorts, 1,651 white-longs, 671 white-shorts.

Negative association of *w* and *m* is given by the equation

$$\frac{\text{red-longs} + \text{white-shorts}}{\text{red-shorts} + \text{white-longs}} = \frac{1{,}718}{2{,}767} = 0.62.$$

According to previous work on these factors this equation should have given 0.50, and we may suppose that larger numbers would have corrected this discrepancy.

Greater viability of the longs is shown by the equation

$$\frac{\text{longs}}{\text{shorts}} = \frac{2{,}698}{1{,}787} = 1.51.$$

In this case the whites appear in excess of the reds.

$$\frac{\text{reds}}{\text{whites}} = \frac{2{,}163}{2{,}322} = 0.931.$$

Dividing the sum of all the reds bred by the sum of all the whites bred we get an excess of reds—6,670 : 5,957 = 1.12.

These counts add nothing new to the theory of association, but are in agreement with Morgan's ratios.

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A DISCUSSION OF THE RESULTS OBTAINED BY CROSSING ZEA MAIS L. (MAIS DJAGOENG) (—REANA LUXURIANS DUR.—TEOSINTE) AND EUCHLÆNA MEXICANA SCHRAD[1]

The author prefaces his discussion of the hybrids of maize and teosinte with a minute study of the male and female spikelets of both plants, showing the similarity between them.

After reviewing the work of Harshberger with the cross maize ♂ × teosinte ♀, he takes up the result of his own reciprocal cross, maize ♀ × teosinte ♂. He shows that the first generation hybrids by the latter cross were uniform and agree closely with those from the reciprocal cross made by Harshberger.

The plants of the second hybrid generation of the cross, maize ♀ × teosinte ♂ form a diverse series, of which the different individuals differ widely in stooling and branching ability, as well as in the structure of the ear. A complete reversion, however, to either one of the parent types never occurs. The series tends more towards the maize than the teosinte type, and it is shown that associated with the stronger development of the maize type, is a reduction in the number of branches, a reduction in the number of ears per plant, a less horny texture of the axis and of the calyx-glumes, and a reduction in the depth of the pits of the axis. The nature of the diversity in the second hybrid generation argues against the absolute purity of the sex cells.

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[1] "A Discussion of the Results Obtained by Crossing *Zea mais* L. (*Mais Djagoeng*) (*-Reana luxurians* Dur. *-teosinte*) and *Euchlæna mexicana* Schrad," by J. E. van der Stok, in *Teysmannia*, Vol. 21, 1910, p. 47–59. The translation upon which this abstract is based was made by Karle Lotsy, Bureau of Plant Industry, U. S. Dept. of Agriculture, Washington, D. C.

Another cross was made with two varieties of Java maize, Madoera and Menado, using pollen from the first hybrid of the maize × teosinte cross. The resulting plants varied widely regarding the stooling ability and structure of the ears. This is not surprising in view of the inequality of the sex cells of the hybrid.

Seed from the second generation hybrids were sown and that again from the resulting plants, thus securing fourth generation hybrids. These hybrids (fourth generation) while differing widely from each other, remained within the limits of the most different types which appeared in the second generation hybrids. The practical result of these crosses, maize × teosinte, are not very satisfying. The resulting hybrids are far inferior to teosinte for fodder, and although the seed can be more easily harvested from the hybrids than from teosinte, it is not nearly so valuable as that from good varieties of maize.

The author closes by calling attention to the fact that teosinte is immune from the chlorosis disease of maize which is very prevalent in Java, but the hybrids of maize and teosinte showed no decrease in sensitiveness to the disease.

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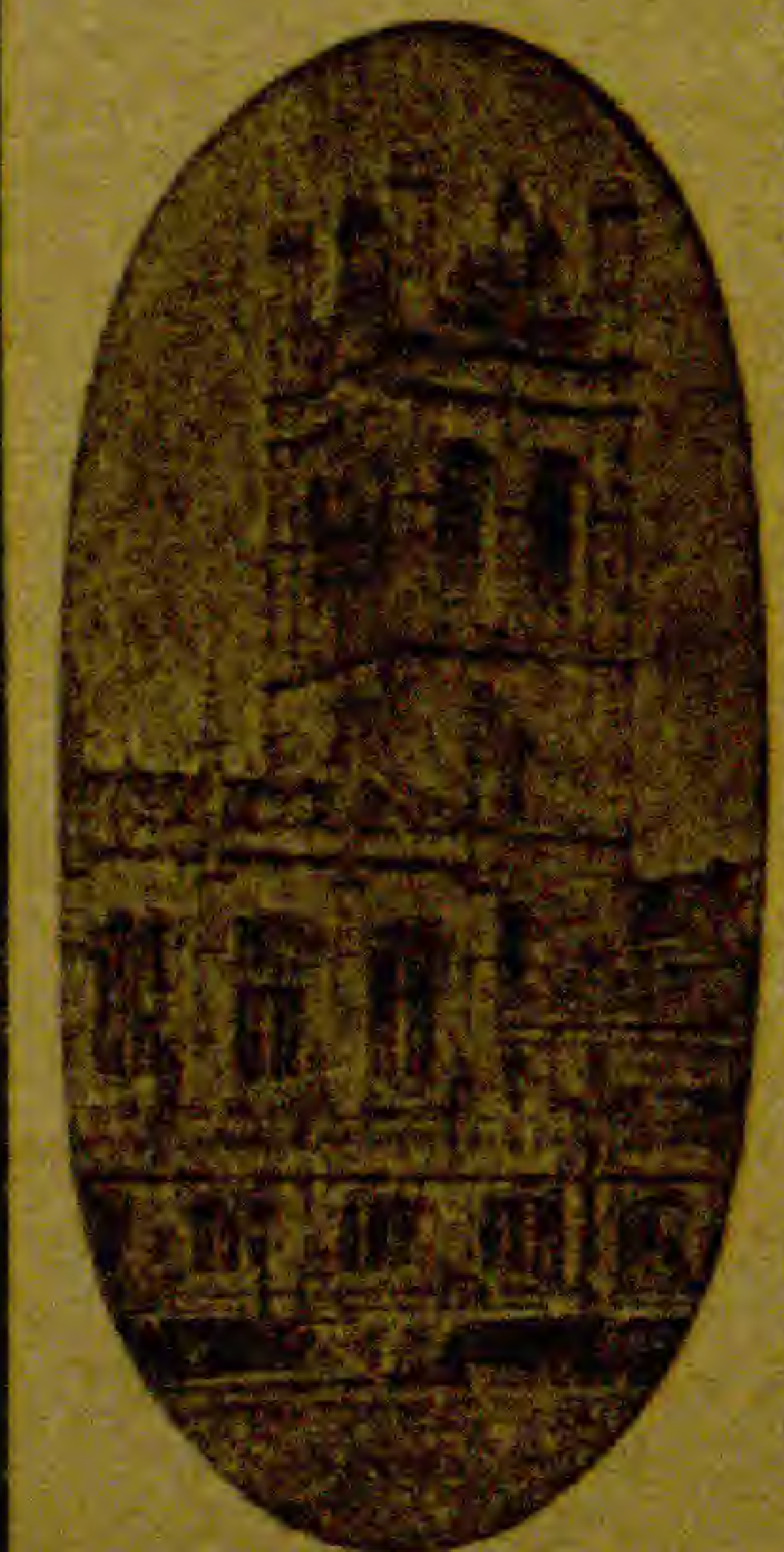

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A MONTHLY JOURNAL

Devoted to the Advancement of the Biological Sciences with
Special Reference to the Factors of Evolution

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THE

AMERICAN NATURALIST

VOL. XLVII *September, 1913* No. 561

THE NATURAL HISTORY OF THE NINE-BANDED ARMADILLO OF TEXAS

PROFESSOR H. H. NEWMAN

THE UNIVERSITY OF CHICAGO

FOR some years past the writer has been engaged in a study of various phases of the biology of the Texas armadillo and has published a number of papers, some of them in collaboration with J. T. Patterson and some of them alone, dealing with matters of development, cytology, sex and heredity. There now appears to be a demand for a brief, non-technical summary, giving the gist of the findings discussed in detail in these papers. The present account will furnish such a summary and will in addition deal with certain matters not yet published.

NOMENCLATURE AND AFFINITIES

In the publications thus far issued the armadillo of Texas has been referred to under various generic titles (*Dasypus*, *Tatusia* and *Tatu*) and it would be well to come to a final decision as to nomenclature. The systematists seem to have finally settled upon the name *Dasypus novemcinctus texanus*. They recognize two other subspecies of this form in North America, viz., *D. novemcinctus fenestratus*, the common Mexican armadillo, and *D. novemcinctus hoplites*, a type described by Allen from the hills of Grenada. These three subspecies are probably no more than local varieties of which many others could no doubt be discovered were one inclined to make a careful survey of the range of the species. There is scarcely a doubt that the North American armadillos are all derivatives of the Peba armadillo (*Dasypus novemcinctus*) of South America, a species of wide range, occurring from Panama to Paraguay. The mulita of the Argentine and Kappler's armadillo of Surinam were formerly classified as species of *Dasypus,* but the former is now *Cryptophractus hybridus* and the latter *Tatusia kappleri.* Nothing is known about the development of the latter, but the preliminary paper of Fernandez shows that the mulita is strikingly like our species in the details of polyembryonic development. Such a fundamental resemblance would seem to indicate that the two species are very closely related and should be classed in the same genus. About a dozen other species of armadillo, assigned to several other genera, are native to South America. About their natural history little is known.

RANGE, DISTRIBUTION AND FUTURE OF THE ARMADILLO IN TEXAS

In his "Biological Survey of Texas" Bailey (1905) states that

> The armadillos are strictly Lower Sonoran, but in the rough country between Rock Springs and Kerrville they range fairly into the edge of the Upper Sonoran Zone. As a rule they do not extend east of the semiarid or mesquite region, nor to any extent into the extremely arid region west of the Pecos, but occupy approximately the semiarid Lower Sonoran region of Texas north to near latitude 33°.

Bailey lists many localities from which armadillos have been taken or authentically reported. To this list I should like to add the following localities, which I have visited and from which I have obtained considerable numbers of specimens: Boerne (over 100), Comfort (nearly 200), Fredericksberg (about 40), Kerrville (about 25), Ingram (90), Helotes (3). Many of those reported from Boerne, Comfort and Ingram were brought from distances of twenty miles or more. At the towns of Boerne and Comfort we find a flourishing industry in which the armadillo furnishes the raw material. Many thousands of the adult animals are slaughtered annually for their armor, which is shaped into baskets and sold all over the world as curios. Armadillo hunting has come to be a recreation and a source of additional income for large numbers of young American and Mexican farmers. When they come to town to sell produce and purchase supplies they bring also many armadillo baskets which they have learned to make in an expert fashion and for which there is a ready market. One dealer with whom I am well acquainted claims to have shipped no less than 40,000 baskets during the last six years. At least two other firms have been almost equally active. In spite of this extensive slaughter the animals seem to be increasing in numbers, for I had no difficulty in obtaining in about two weeks nearly two hundred pregnant females. Those used in my work would have been slaughtered for their armor alone, so I felt no compunction about destroying so many unborn young. Hunters and dealers generally have the idea that the range of the armadillo is extending rapidly

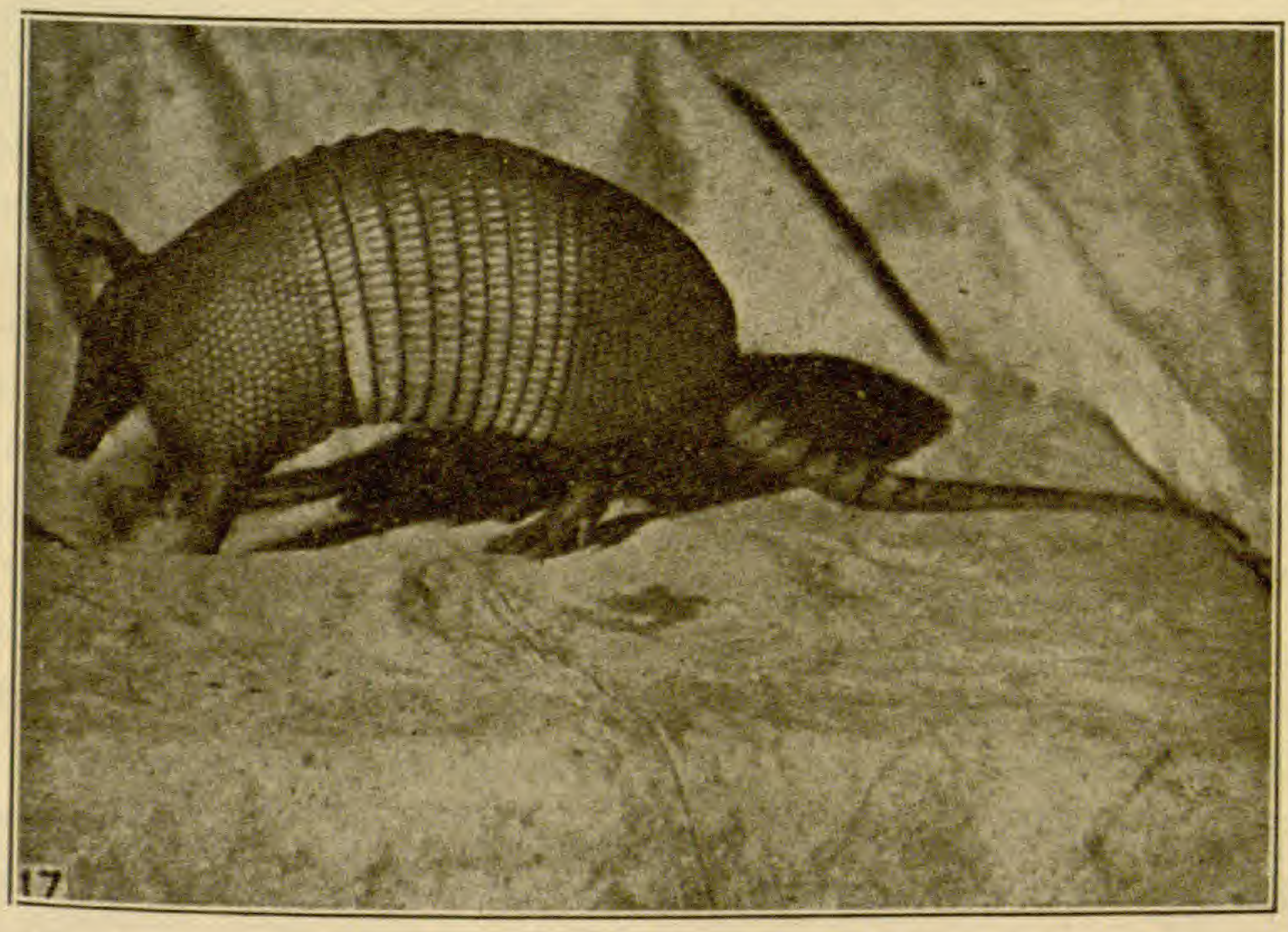


FIG. 1. Photograph of a living armadillo showing the complete armor and the usual resting attitude. The head is usually withdrawn between the two flaps of the shoulder shields when the animal is feeding in the thickets.

northward and eastward. There seems to be no reason to doubt that the species is multiplying and spreading, for I have it on good authority that in the regions where it is now most plentiful it was almost unknown 20 years ago. Its range is, however, strictly circumscribed by definite ecological conditions as I shall proceed to show.

Ecology and Habits

The armadillo spends its life on the defensive and its defensive equipment consists of structural and functional adjustments to a very special environment. Of the structural adaptations the armor (Fig. 1) is the most obvious, but its use is not what it is commonly supposed to be. While the carapace doubtless serves partially to protect the animal when it is attacked by large carnivors, the fact that dogs often bite through the bony plates and seriously damage the shell shows that for this type of enemy the protection is very inadequate. In fact it is the experience of hunters that, when closely pressed by dogs, the harassed animal turns on the back and strikes most effectively with the powerful claws. The armor has a much more important significance in that it enables the animal to invade the dense, thorny thickets of cactus and chapperal, etc., that characterize its normal habitat. When pursued it is possible for the armadillo to plunge headlong into a mass of thorny vegetation that would be totally inaccessible for an unarmed enemy. Then too they can penetrate all sorts of underbrush in search of insect food without danger from thorns or spines. In some regions of the country the animals take advantage of the rough and rocky character of the hillsides and river banks, seeking shelter from enemies by retreating into holes and crevices among the rocks that are just large enough to admit them but too small for their enemies. Armadillos living in these regions have the armor much worn from rubbing and scraping against the angles and sharp edges encountered in the rocky passages of their retreats. If one is able to reach the tail of an armadillo concealed in a rock pile the animal braces the armored back against the roof or sides of the hole and holds so hard that the tail will come off before the body can be moved. Thus in divers ways the armor serves a protective function other than the primary one connoted by the name. Still further, there can be no doubt but that the carapace serves as a reducer of surface evaporation, an important factor in making life possible in the semiarid regions, for there are many periods of extreme drought during which it must be of vital importance to conserve moisture. It is possible, indeed probable, that the armor is phylogenetically older than the particular conditions comprising the present environment of the armadillo, hence we can scarcely claim that the armor is in any strict sense an adaptation. It seems far more likely that in the exercise of its prerogative of choice of habitat the species has selected an environment affording an unpreempted food area and an adequate shelter from enemies.

The armadillo is preeminently insectivorous, although in captivity it appears practically omnivorous. Stomach examinations of freshly caught wild animals show the remains of insects, chiefly ants, together with much earth and more or less vegetation. In captivity they eat meat of all kinds, even exhibiting canibalistic propensities under certain conditions, for when shipped in crates or boxes the stronger ones kill and disembowel the weaker, and mothers devour their own new-born offspring. Hunters and basket dealers justify the extensive slaughter of the armadillo by giving to the animal a bad name. It is said, on how good authority I am unable to state, that the "'dillo" is a robber of newly made graves and a destroyer of vast numbers of the eggs of such ground birds as wild turkeys and quails. They are also said seriously to damage the grazing value of certain territories by rooting up quantities of grass. I am of the opinion that much of the destruction of bird eggs and of grass might more justly be blamed upon the Texas peccary, which has a range quite similar to that of *Dasypus*.

Armadillos are essentially nocturnal in habit, although one may encounter them at dusk. On warm nights they spend their time rooting about in the dry leaves and ground vegetation after the manner of hogs. Their grunting, snuffing noises are heard at some distances on quiet evenings. The strong burrowing claws are used to a considerable extent in digging for food, but their primary function is that of burrowing. Burrows may be for temporary or permanent shelter. A permanent burrow may be dug six or seven feet deep with a chamber at the bottom about two feet in diameter, which is filled loosely with dried leaves and grass. This is the winter retreat of the armadillo, where he undergoes partial hibernation during the periodic cold spells. Buried in the grass and leaves, the animal defies its worst enemy, cold. In this connection it may be said that there is probably no mammal so sensitive to cold as the armadillo. In captivity they shiver at temperatures when other mammals are warm, and often die during the night if insufficiently bedded down with straw. Their further spread northward will no doubt be blocked by temperature barriers. Temporary burrows are made as a retreat from enemies when other shelter is unavailable. Hunters claim that an armadillo will dig a hole in ordinary soil in a minute or two, disappearing even after having been sighted.

They seem to have their regular haunts and do not ordinarily go far from their burrows or caves. From the smoothly worn mouths of these retreats beaten paths lead to thickets, pools and streams. Bailey has seen evidences that they, after the manner of pigs, enjoy a mud bath. The trail of the tail along the paths is a ready means of distinguishing the haunts of the "'dillo," for it leaves a mark like that of a dragging rope.

In captivity the animals display the utmost gentleness and tractability so long as one does not attempt to lay hands upon them. If one attempts to hold one of them by the shell he will realize how strong and active is its resistance, for it bucks vigorously like a broncho and throws off all holds. The tail is the weak point in its defence, as it offers a perfect handhold, but, even when grasped by the tail, it furnishes an interesting struggle by violently rotating the body and often succeeds in twisting free from the enemy's grasp. Then one is surprised at the speed of which the animal is capable, its galloping gait being apparently unhindered by its armored cuirass.

Of the senses, that of smell is the only one upon which the animals seem to rely. When feeding they frequently raise the snout on high and sniff the air in all directions. The eyes are rudimentary and practically useless. If disturbed an armadillo will charge off in a straight line and is as apt to run into a tree trunk as to avoid it. That the hearing is not at all keen is evidenced by the fact that one may approach them on the leeward side even if the approach is somewhat noisy.

Breeding Habits

Information as to mating and care of young has come indirectly through hunters, among whom there is a considerable degree of consensus of statement. It is claimed that armadillos pair for life or at least for the season. It is very common to capture a male and a female together or to dig a pair out of a burrow. The period of œstus comes early in the autumn, extending over a variable period of time. A large proportion of the females taken in October show the early stages of pregnancy, but early stages have been found as late as December. It seems probable that the young "does" of the previous season's crop reach maturity late in the autumn, for the largest females are almost invariably pregnant in October while many of the smaller females are nonpregnant at that time. The young are for the most part born in March, although births during April are not rare.

From these observationts it may be estimated that the period of gestation averages from the middle of October to the middle of March, a period of five months or 150 days, an extended gestation period for so small a mammal. The young are fully formed at birth, with eyes open and with a complete though not very hard armor. They are able to walk in a more or less uncertain fashion within a few hours after birth.

Copulation occurs with the female turned on the back, this position being necessary on account of the armor and the ventral location of the genitalia.

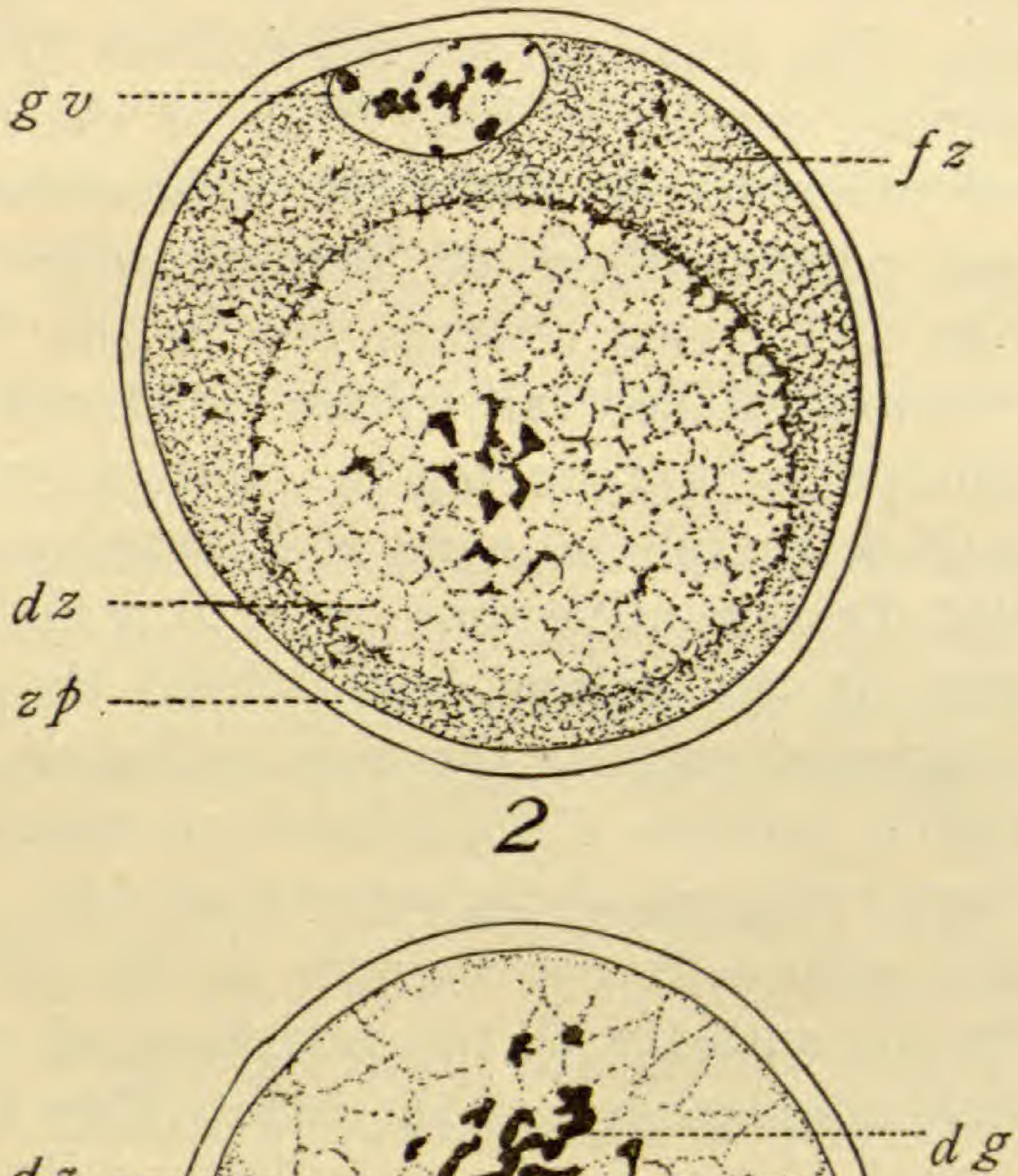
POLYEMBRYONIC DEVELOPMENT

Our earliest observations dealing with the development of the Texas armadillo revealed the facts that the four embryos are enclosed in a common chorion and that these monochorial quadruplets are always unisexual. These early observations stimulated an investigation of the embryological and cytological conditions that underlie polyembryony and sex-determination. The published accounts carry the history of development through the period of ovogenesis up to the time of fertilization and from the primitive streak stage to birth. The hiatus between fertilization and the formation of the primitive streak is almost completely filled by two sets of observations, one by Patterson, who has secured late cleavage stages and all of the history up to the primitive streak, and the other by the writer, who has described the early cleavage of parthenogenetically developing ova. The observations of Patterson were reported at a meeting of the central branch of the American Society of Zoologists at Urbana in 1912; the paper on parthenogenetic cleavage is now in press and will no doubt appear before the present contribution. By piecing together the subject matter of these separate investigations the writer is able to offer the following account of the development.

Ovogenesis and Fertilization

The early phases of ovogenesis are in no way peculiar and in themselves offer no clue as to the physiology of polyembryonic development. A detailed study of the growth period of the ovocytes and of folliculogenesis shows that in normal ovaries there is only one ovocyte to the follicle and that in ovulation only one egg is given off at a time. The details of maturation are like those of other mammals, especially like those of the marsupial *Dasyurus* as presented by Hill ('10). The growth period involves an accumulation of deutoplasmic material, which in the full-grown ovocyte lies in the form of a coarsely vacuolated central sphere containing deeply staining granules. Surrounding the deutoplasmic sphere is a fairly thick peripheral zone of homogeneous protoplasm, called the formative zone (Fig. 2), which is somewhat thicker at the animal pole where the germinal vesicle is flattened against the zona pellucida. During the maturation process a remarkable reorganization of the cytoplasmic regions of the ovocyte occurs. The fluid deutoplasmic sphere forces its way to the surface and comes to lie in contact with the periphery of nearly the whole animal hemisphere of the cell. This forces the formative protoplasm to the vegetative pole where it assumes the form of a cap thick at the pole and thin at the equator, having a crescentic outline in meridional section (Fig. 3). The maturation spindle, forced from its normal position at the animal pole, lies as near the latter as possible without leaving the formative protoplasm, and assumes a position tangential to the nearest periphery of the cell, but nearly parallel to the primary axis of the latter.

The two maturation divisions occur without disturbing this new arrangement and no other radical change seems to take place until after fertilization, at least so one must conclude from the fact that a tube egg in a late phase of fertilization still shows the formative and deutoplasmic zones arranged as in Fig. 2. This one fertilization stage (Fig. 4) shows two polar bodies and the male and female pronuclei lying close together in the thickest part of the formative zone. There is nothing in maturation nor in fertilization to suggest or account for polyembryony. Their chief evidential value lies in the fact that they demonstrate the fact of polyembryony and show that the latter is not due to any



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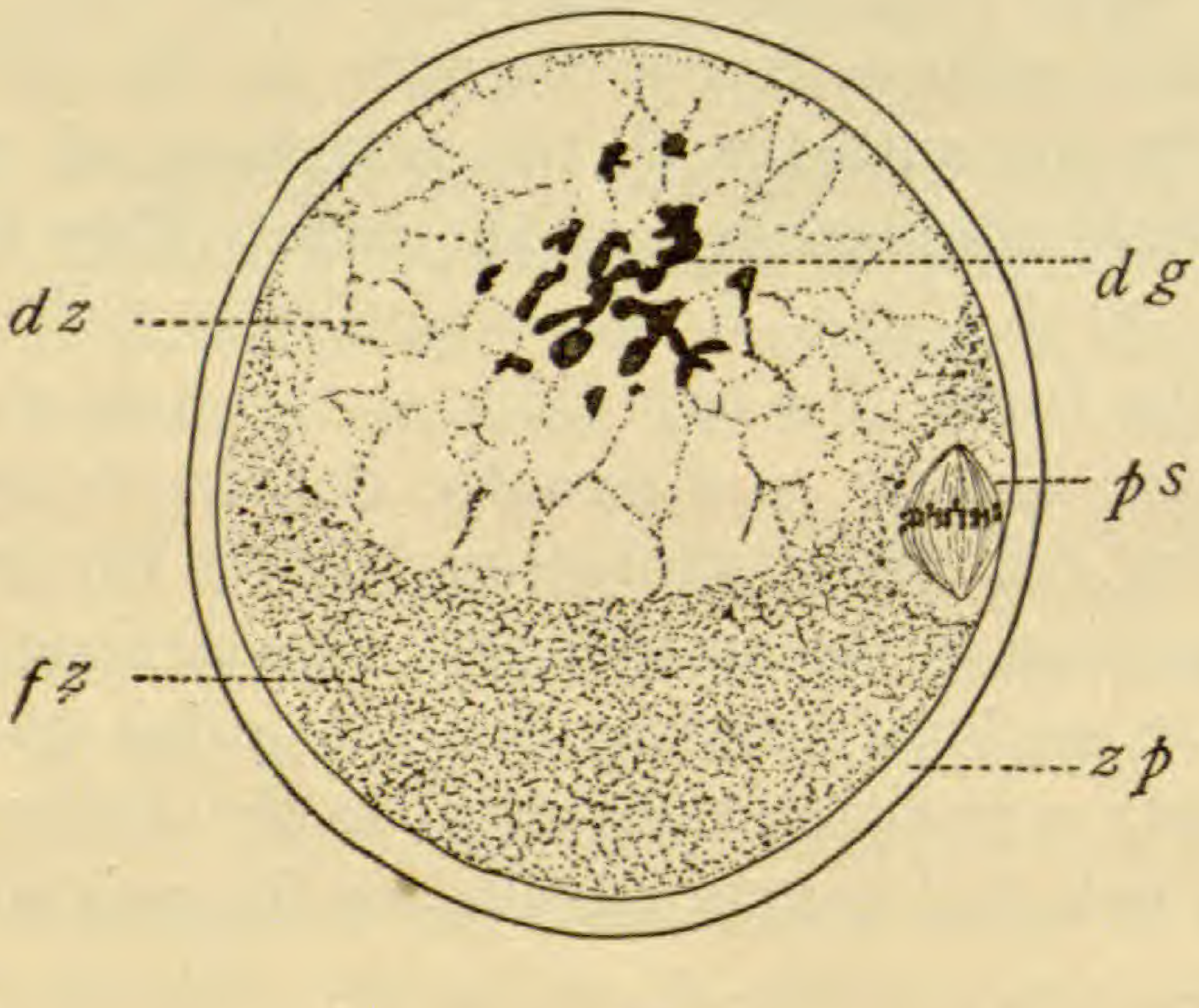

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Fig. 2. A section through a full-grown ovocyte before the changes incident to maturation have taken place. Note the peripheral formative zone (*fz*), in which lies the flattened germinal vesicle (*gv*). The deutoplasmic zone or sphere (*dz*) lies in the center. The zona pelucida (*zp*) is a dense shell-like membrane.

Fig. 3. An ovocyte during the first maturation division, showing the reorganized cytoplasmic zones. The polar spindle (*ps*) is situated far from the animal pole. The deutoplasmic granules (*dg*) are conspicuous at this period. Other lettering as in Fig. 2.

morphological peculiarity of the germ cells. In brief the egg is a simple egg with one nucleus and is fertilized by a single spermatozoon. Hence the embryo starts out as a single and not as a multiple individual.

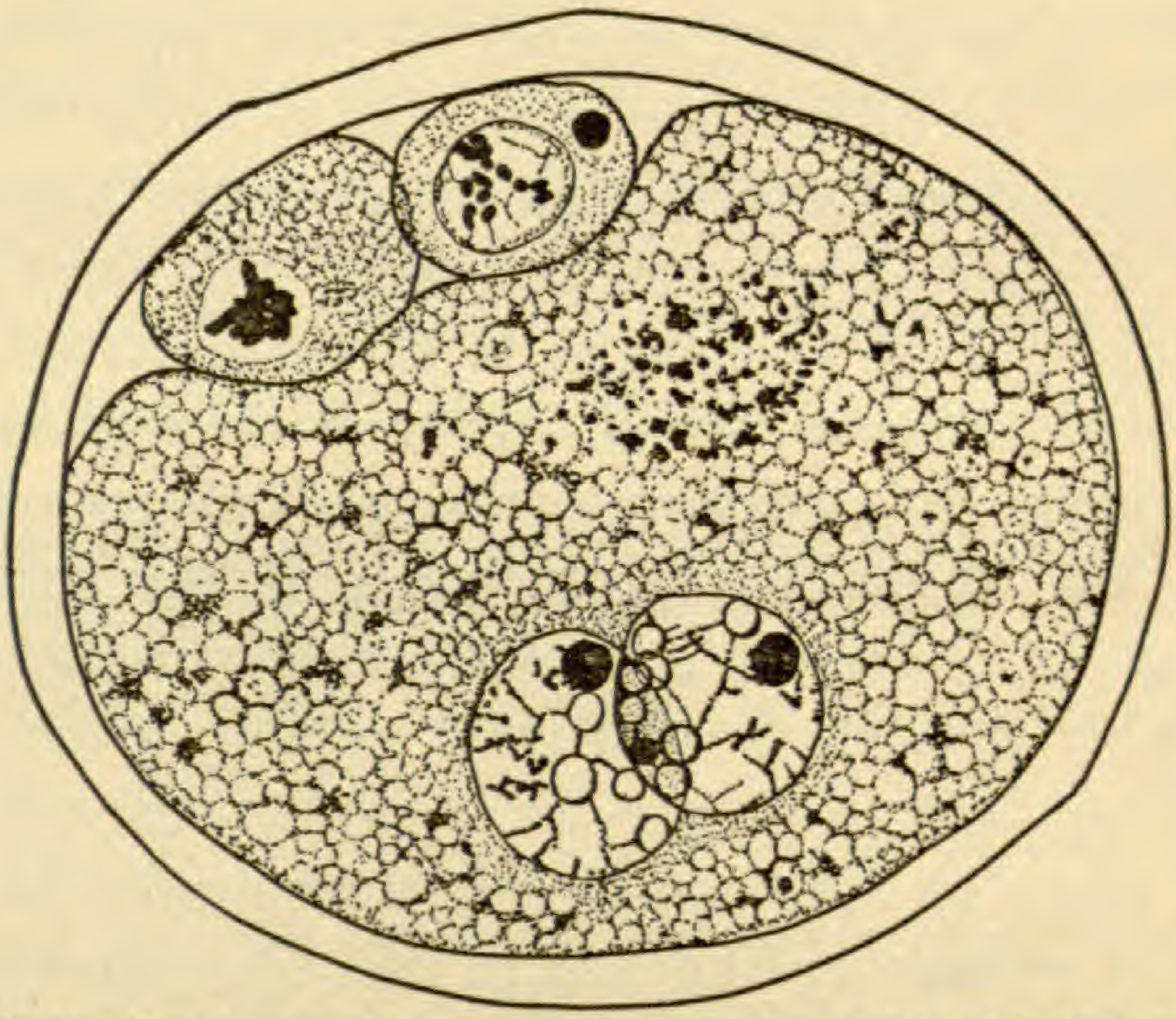

FIG. 4. A fertilized egg found in the fallopian tube, showing the male and female pronuclei in contact and occupying the thickest part of the formative protoplasm. There are two polar bodies. The deutoplasmic zone does not appear in this section.

The claim of Rosner ('01), based on an examination of one pair of ovaries inadequately preserved, that the four embryos are the result of the fusion of several follicles and the subsequent fusion of the several eggs or vesicles given off by the rupture of a compound follicle, is completely refuted by the present studies. It may be of interest to show how Rosner came to fall into so serious an error. The writer after the examination of a large number of normal ovaries chanced upon one pair showing substantially the conditions described by Rosner. These ovaries were from a very large, old female and when examined cytologically showed many multiple follicles, containing from two to eight or more ovocytes in various stages of development. Everything about these ovaries, however, is atypical and there can be no doubt as to their pathological character. That Rosner should by chance have stumbled upon such an ovary and that he drew a general conclusion as to the normal condition from so slender an evidential basis constitutes a biological comedy of errors scarcely equaled in our literature.

Cleavage

Nothing is at present known of the early cleavage stages of the fertilized egg and I shall offer here as a tentative substitute facts dealing with the parthenogenetic cleavage of eggs in atretic follicles. The first step in the development of such eggs is the elimination of the deutoplasmic material, which probably is thrown out of the protoplasm by a rupture of the plasma membrane of the egg. The formative protoplasm of the egg in this way unburdens itself of a considerable volume of inert and probably deleterious material, which, although outside of the egg-cell proper, remains within the zona pellucida and more or less completely surrounds the egg in the form of pseudo-epithelium of cell-like masses, which I have called cytoids. The egg now consists of a homogeneous, clarified protoplasm and there is every reason to suppose that the elimination of byproducts of metabolism has served to rejuvenate the cell so that its normal processes of growth and reproduction may be resumed. The nucleus, which, previous to and during maturation, had ceased to carry on metabolic exchanges with the cytoplasm, now evinces renewed activity in that astral rays, entirely absent during maturation divisions, now penetrate the entire cytoplasm and a typical cleavage spindle appears. Two-, four- and eight-cell stages occur in fairly regular fashion, but even at the eight-cell stage unmistakable signs of degenerative changes manifest themselves, which bring about a rapid dissolution of embryonic integrity and inhibit further progressive changes. There is no evidence in this material that parthenogenetic development proceeds to the formation of teratoma or tissue formation; in fact, the total lack of cleavage stages later than about the eight-cell stage argues strongly against the possibility of the development of any such structures. This study serves two purposes, that of affording a critical demonstration of parthenogenetic development of mammalian ova, and that of furnishing a clue as to what we may expect to find when we come to know the facts about the early cleavage of normally developing eggs. In the latter connection it is of interest to note that in *Dasyurus,* whose developmental peculiarities up to the time of cleavage parallel those of the armadillo, there is, as a preliminary to cleavage, an elimination of the deutoplasmic material almost precisely like that shown in our parthenogenetic material. This fact lends support to the conjecture that, in essential features, parthenogenetic cleavage parallels that of normal development and may be used as a substitute for the latter, at least up to the eight-cell stage.

For the sake of rendering the present account as nearly complete as possible I shall make a statement regarding the late cleavage and early embryology, based partly on Patterson's observations. The earliest stage shown by the latter at the Urbana meeting was an inner-cell-mass stage, like that of any ordinary mammal. Such a vesicle becomes attached by its animal pole to the very apex of the fundus of the uterus, where it lies in a position predetermined for it at a point where two grooves in the uterine mucosa cross each other, the one running laterally between the openings of the fallopian tubes and the other at right angles from mid-dorsal to mid-ventral aspects of the uterus. This position at the crossing of these grooves enables the investigator to locate with certainty even the excessively minute earliest stages of the developing vesicle. As it expands the vesicle becomes depressed in the groove and elongates laterally into an ovoid form with the long axis running from the right to the left sides of the uterus. As soon as it gains attachment to the uterine mucosa the vesicle undergoes germ-layer inversion like that seen in the rodents, the result being that two secondary vesicles are produced, an inner complete ectodermal vesicle and an outer endodermic vesicle, incomplete at the area of attachment where the primitive placenta or Träger arises. Up to this time there is no sign of polyembryony. The first step in the direction of a division of the single embryonic vesicle into four embryonic rudiments is seen in connection with mesoderm formation. The mesoderm arises at two points, to wit the extreme right and left sides of the laterally elongated vesicle, and soon assumes the form of two hollow pouches that subsequently expand and fuse together in the median lines into a common extraembryonic body cavity. This mode of origin of the mesoderm shows that the embryo is no longer developing as a unit, but that there has arisen a bilateral duality of function, due probably to the partial physiological isolation of the right and left sides of the mesoderm. The possible cause of this isolation will be discussed presently. The first recognizable rudiments of the embryos appear as two blunt processes or

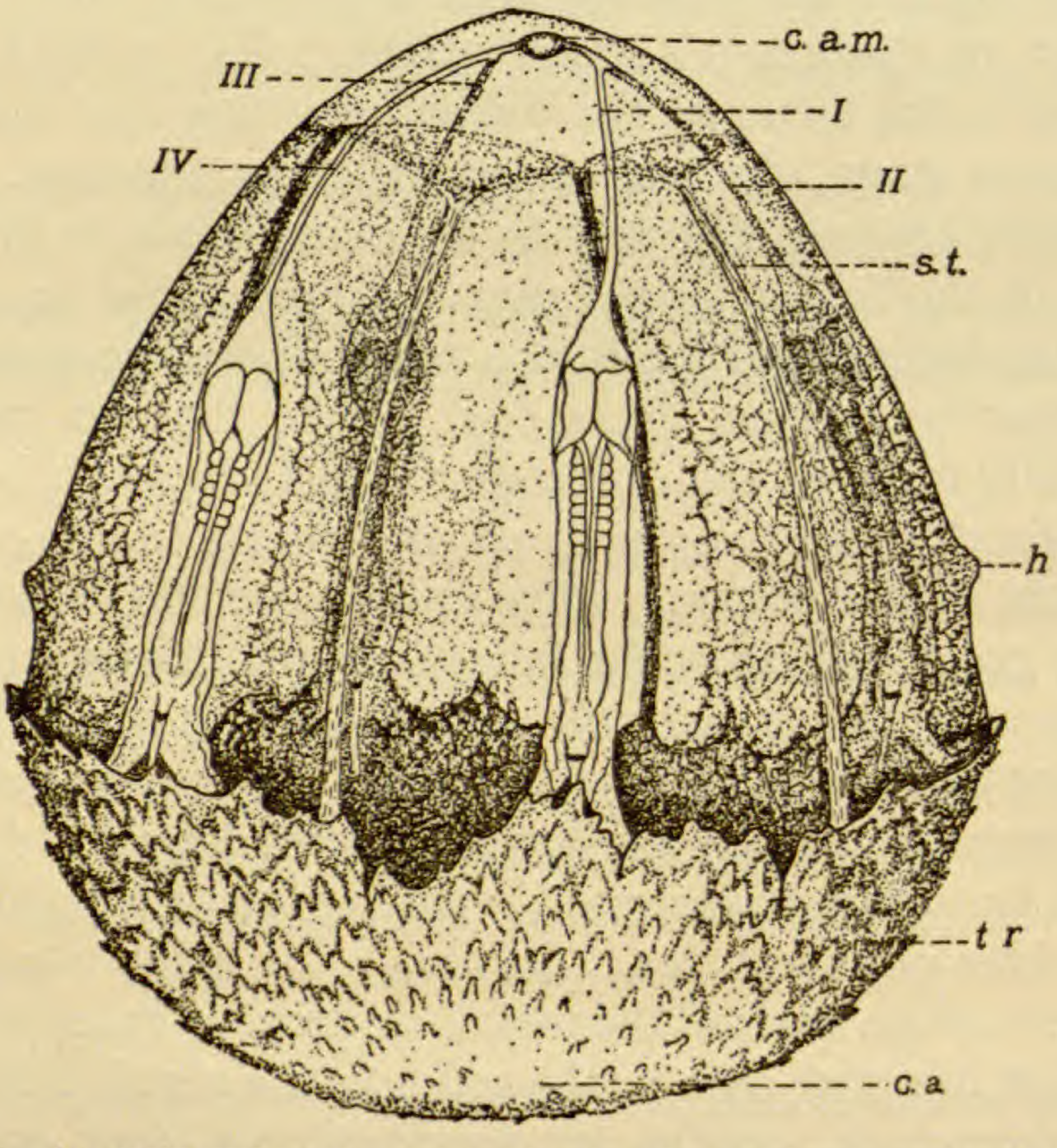

FIG. 5. An early embryonic vesicle showing four embryos enclosed within a common chorionic membrane. The small common amnion (*c. am.*) still retains its connection with the separate amnia of the embryos by means of the slender amniotic connecting canals (I–IV). The four embryos are attached to a common discoid primitive placenta, the Trager (*tr*), by belly-stalk bands.

thickenings of the ectodermal vesicle. These two primary embryonic buds arise in connection with the dual centers of origin of the mesoderm, each appearing directly beneath a primary mesodermal pouch. These two primary buds elongate and soon divide at the tip into paired outgrowths, which constitute the primordia of the two pairs of embryos. The embryos develop on the inside of the inner vesicle and are consequently in a common ectoderm-lined, fluid-filled cavity, which is a sort of common amnion. Subsequently the separate embryos sink into the floor of the common amnion and retain their connection with the latter only by slender amniotic connecting canals, which gradually shrivel up and disappear. An early somite stage with the common amnion and the connecting canals still intact is shown in Fig. 5, which also illustrates the attachment of the four fœtuses to the Träger by means of the allantois and the belly-stalk bands which constitute the primitive umbilicus. The saucer-shaped Träger or primitive placenta develops from the part of the trophoblast which originally formed the point of attachment for the vesicle. This area has not been invaded by the entodermal vesicle, but is reinforced directly by mesoderm, which invades the maternal mucosa and produces primitive villi, that are at first in the form of blunt ridges, but later take on the form of flat scales (see Fig. 5), and subsequently assume the typical arborescent form of definitive placental villi. The subsequent development of the embryos is of little interest except to the specialist and need not be referred to here. The history of the placenta, however, is of unusual interest in that it illustrates the futility of attempting to use the special types of placentation as criteria of animal affinities. The early placenta as shown in Fig. 5 is a single discoid structure. Subsequently the points of attachment of the four umbilical cords become areas of rapid placental development and the parts of the Träger in between them almost lose their villi. At this stage the placenta consists of a set of four separate discs. As these villous regions expand they come into contact at their margins and apparently fuse into a lobate zone, which had been called a compound zonary placenta. Finally the zone separates along the dorsal and ventral lines to form two lateral notched discoid placentæ, to which we need scarcely apply a name. It is obvious that there is nothing to be gained by attempting to classify such a placental complex or by comparing it with those of other groups of mammals, for the peculiar conditions seen here are obviously merely very special adjustment to the peculiar conditions arising from polyembryonic development within a single chorion. The fœtuses after they have once been separately outlined are distinct, complete units and are associated scarcely more closely than are the embryos of other forms of mammals where several individuals develop simultaneously in a single uterus, for they have their own separate amnia and separate placentation, and there is absolutely no admixture of fœtal blood.

Without further burdening the reader with an elaboration of embryonic details and relations we may briefly summarize the situation in-so-far as the question of specific polyembryony is involved. The ovogenesis is normal; a single egg is fertilized by a single spermatozoon; the cleavage is apparently normal and gives rise to a blastodermic vesicle similar to that of other mammals, especially the rodents; germ-layer-inversion affords an easy mechanism for producing several embryos in a single chorion, for the quadruplets arise by means of dichotomous budding of the inner ectodermic vesicle without affecting the enveloping membranes of the vesicle, which form the common chorion; the subsequent embryonic development of the several embryos is as independent as it can be under monochorial conditions, since each individual has its own separate amnion, allantois, umbilicus and placenta. This in brief is the polyembryonic situation, a consideration of which offers for solution several problems peculiar to the material. What are the physiological causes of polyembryony? What factors determine the definite bilateral orientation of the embryos in the vesicle, or what factors are responsible for pairing of embryos? What light does the situation throw on the problem of sex determination? Does the condition give us any fulcrum on the problem of predetermination and epigenesis? What are the modes of inheritance peculiar to polyembryony? Does the polyembryonic situation offer any new facts bearing on the general problems of genetics? These problems will be discussed in the order given.

THE CAUSES OF POLYEMBRYONY

In a previous paper (Newman, '12) were listed a series of seven possible explanations of polyembryony, nearly all of which assumed some abnormality in ovogenesis, maturation or fertilization. The discovery that all of these processes are normal in the armadillo served to eliminate all but the last suggestion, which was to the effect "that the cause of specific polyembryony may lie in factors strictly external to the ovum, among which one of the most probable is in some way associated with the bilaterality of the uterus." At that time no discussion of that possibility was attempted. The discovery of a specific parasite within the armadillo egg, together with a consideration of certain unpublished data presented orally by Patterson, leads me to hazard the following hypothesis.

A careful examination of many ovaries and many thousands of ovocytes has revealed the universal presence of what I consider to be a protozoan parasite in the egg cytoplasm. This parasite is a large body as compared with the size of the host cell and must have a deleterious effect on the egg, probably weakening it or lowering its vitality. Such a depressed egg, in which the parasite has grown and multiplied, develops into a vesicle of some size before the effects of a lowered vitality become apparent. When, however, under the pressure exercised by the transverse groove in the uterine mucosa, the vesicle becomes elongated laterally so that its right and left sides come to be separated a maximum distance from each other. In such a depressed and weakened vesicle unity of functioning ceases to exist and two new centers of growth arise at points where the pressure is less severe, viz., the opposite ends of the elongated vesicle. We have seen that mesoderm forms at two lateral points and that the embryonic buds of the ectodermal vesicle follow suit. The rebudding of the primary buds must be due in like manner to the establishment of two growing points in each primary bud. Such an explanation of polyembryony involves the whole problem of the physiology of budding, about which there is great diversity of opinion. According to Professor Child's theories of development and reproduction, any part of a system which, through a lowering of the rate of metabolism of

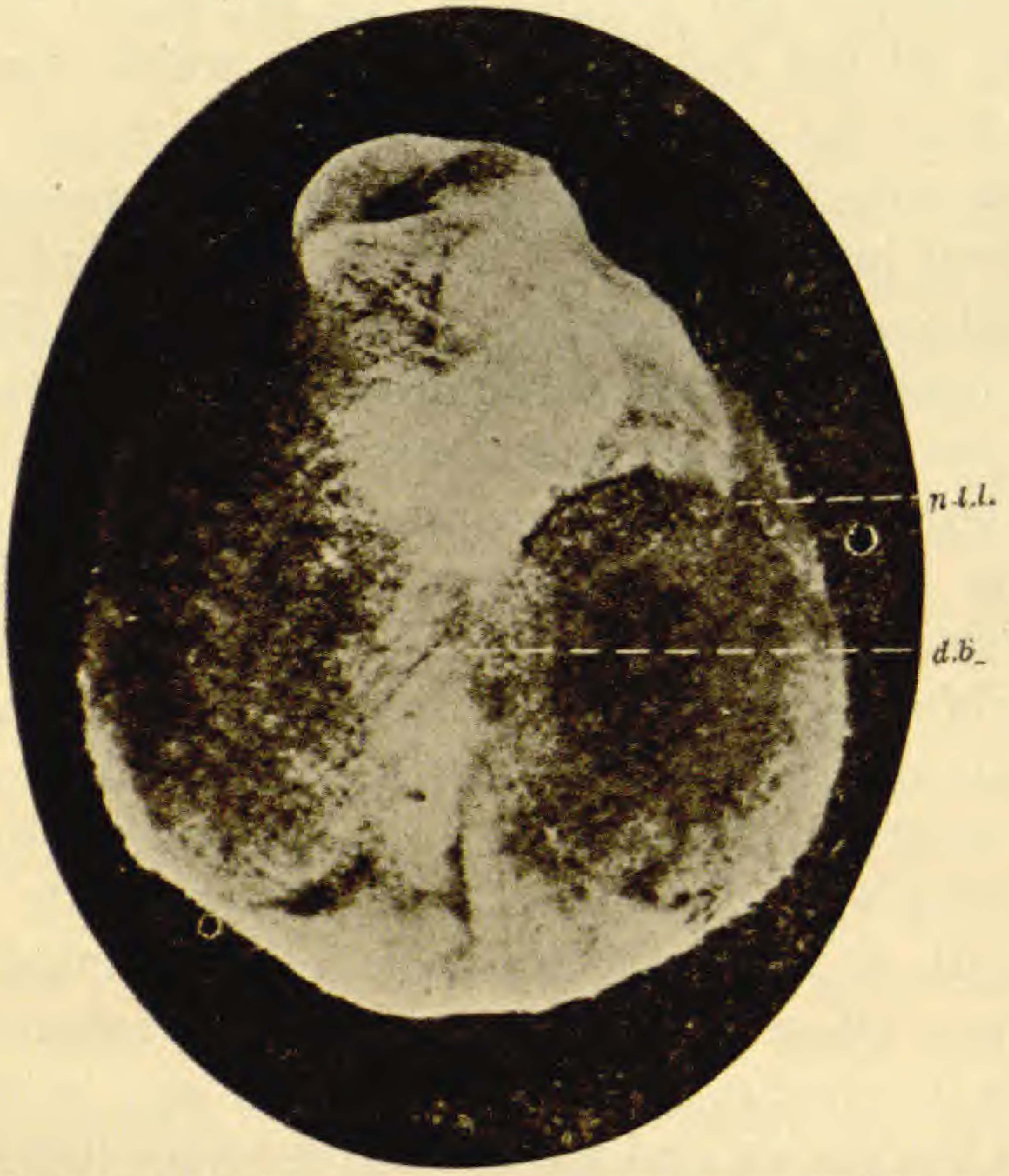

FIG. 6. Photograph, about one half natural size, of an embryonic vesicle just before birth, showing the two lateral placental areas, attached to the right and left sides of the maternal uterus, separated from each other by an area practically free of villi. The outlines of the four fœtuses may be seen through the transparent, non-villous areas of the common chorionic vesicle.

the controlling part of the system, say the animal pole of the blastodermic vesicle, is liable to physiological isolation of parts at certain distances from the dominant region. When such isolation of parts occurs new centers of control arise, which produce buds capable of establishing whole new systems like the original. Thus in the particular case under discussion the rate of metabolism of the whole vesicle is lowered by parasitism to such an extent that the dominant growth center of the system no longer is able to hold the various subsidiary growth regions under control, and new centers of control arise at points determined by secondary pressures exercised by the uterine grooves, as explained above. Further complexities in development are of the nature of adjustments of four separate fetuses compelled to carry on growth and differentiation within a common chorion which had already been established before physiological isolation of the four embryonic rudiments had taken place. According to current theories, reproduction is a result of senescence and, on this basis, it may be assumed that the young blastodermic vesicle, weakened by the ravages of parasites, is precociously old, and therefore tends to reproduce by a process of dichotomous budding. Later, when the parasite completes its active period and goes into encystment, and when the embryos begin to gain new vigor through the absorption of the maternal nutrient fluids, general rejuvenation occurs, the rate of metabolism increases, so that no further isolation of parts occurs. In this connection it is of interest to note that in the mulita armadillo of the Argentine budding goes one or two steps further than in our species and from eight to twelve fetuses result. The writer recognizes the extremely hypothetical character of the explanation of polyembryony here offered and would welcome any suggestion that would lead to a more satisfactory theory. It would be of interest, however, to know whether there is an egg parasite in the mulita, and the writer intends to test this possibility in the near future. If this should prove to be the case the hypothesis here offered would receive a striking support. A detailed description of the life history of the parasite here discussed is in preparation and will no doubt soon appear in print.

THE PROBLEM OF THE ORIENTATION OF THE COMPOUND VESICLE IN THE UTERUS AND THE ORIGIN OF PAIRS

One of the most striking facts that came to light in the early stages of the present studies is that the vesicle is distinctly a bilateral object and that this bilaterality is strictly in accord with the bilaterality of the uterus. It was noted that one pair of fetuses was attached to the right and the other to the left placental disc. It was furthermore discovered that this pairing is not merely a mechanical adjustment of the fetuses to the shape of the uterus, but involves resemblances in stage of development, size and the minutiæ of inherited peculiarities. To explain this condition we offered the conjecture that each

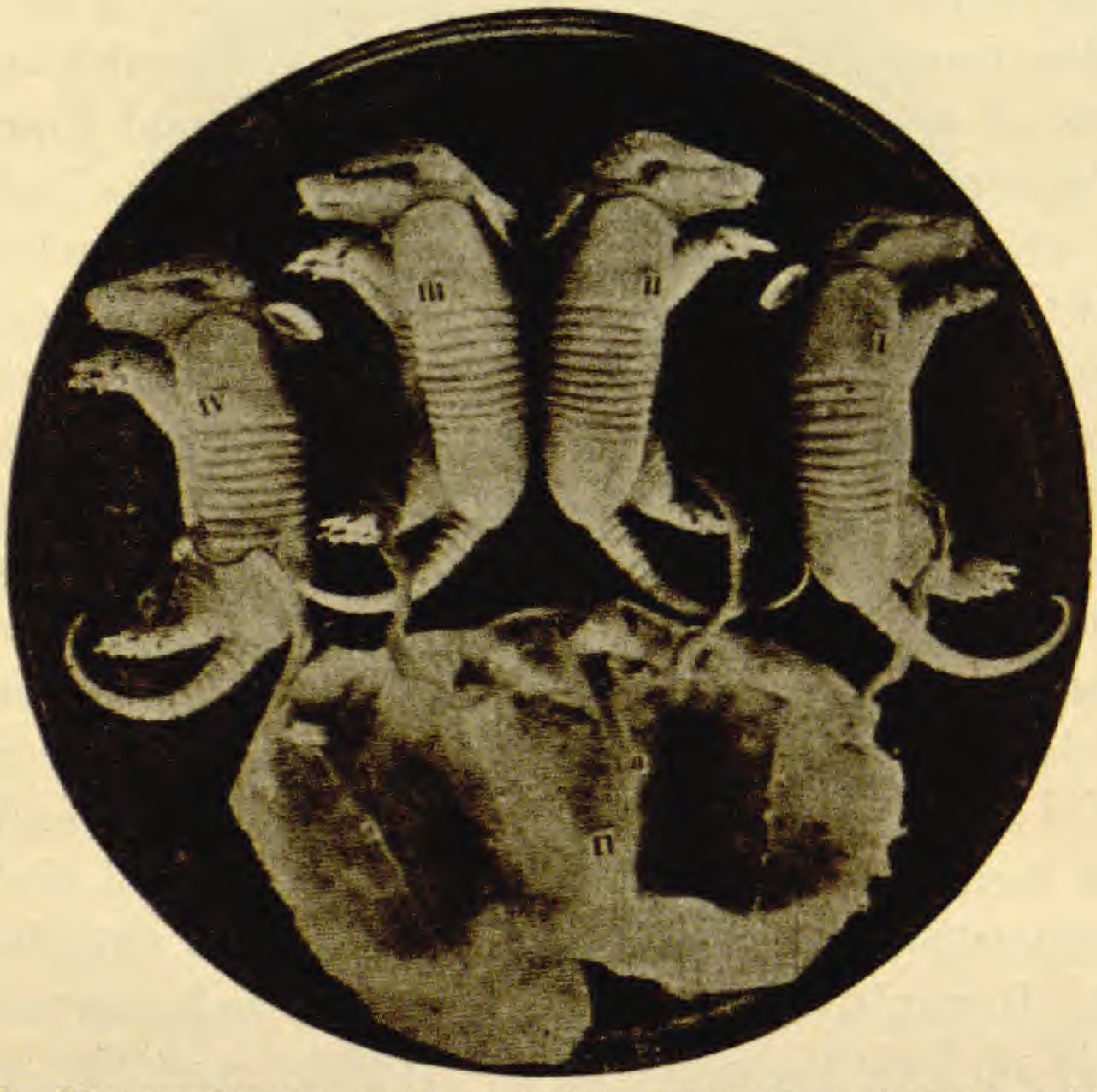

FIG. 7. Photograph of a vesicle a little younger than that shown in Fig. 6, split open along the mid-ventral line, showing the umbilical attachments of the quadruplets.

pair is derived from one of the first two cleavage blastomeres, an idea borrowed from the literature on human duplicate twins. Such a theory, however, involves the difficulty of explaining how the cell descendants of one blastomere would come to occupy a position with reference to one or the other lateral halves of the uterus. The axial orientation of the vesicle is determined by the fact that it always becomes attached by an area of trophoblast at the animal pole, but there is no mechanism for preserving a bilateral orientation. There is on the other hand good evidence, as brought out in the last section of this paper, that the definitive bilaterality of the compound embryonic vesicle is imposed upon it by certain definite bilateral conditions within the uterus, which result in the vesicle being pressed dorso-ventrally and elongated laterally so as to acquire a bilaterality in conformity with that of the uterus. Thus bilaterality and pairing of fetuses are strictly secondary results and bear no relation to any axes of the egg or planes of cleavage. The closer resemblances between the individuals of pairs and their closer placental association are due to their common origin from one primary bud, which means that they are genetically more closely related than are the members of opposite pairs. Mirrored-image effects are also made more intelligible by our knowledge of the mode of origin of a pair from a single primary bud, in that when an inherited peculiarity on the right margin of one individual of a pair is found on the left margin of its partner, it means that some median primordium of the primary bud has been split by the secondary budding, so that the resultant character is found repeated on the adjacent sides of the two fetuses. Dichotomies of primordia of this sort also serve to explain the distribution of many peculiarities inherited by the quadruplets from the parents.

SEX RATIOS AND SEX DETERMINATION

In a collection of 182 sets of fetuses sufficiently advanced to determine with certainty the sex there has appeared no exception to the rule that all fetuses in a set or litter, whether the number of individuals in a set be 2, 3, 4 or 5, are of the same sex. Of these 182 sets 88 were female and 94 male, which would seem to indicate that the two sexes are about equal in numbers. A total of 210 sets have come under the writer's observation, and of these four showed 5 fetuses, four showed 3 normal and 1 degenerate individuals, and in one case twins were born, due probably to the degeneration of a pair of fetuses. There are no authentic cases of less than four embryos being produced, but there are four cases, or less than 3 per cent. of the total number, in which there is exhibited a tendency toward an increase in the normal or typical quadruplet condition. This may be a progressive tendency and might conceivably result in numbers of fetuses resembling those produced by the mulita. The fact that the individuals of a polyembryonic litter are invariably of the same sex supports certain current views regarding the problem of sex determination. In particular it shows clearly that sex must be determined prior to the separation of the embryonic materials from which the four fetuses arise. Since, from the standpoint of cell lineage, this separation must take place at least as early as the cleavage stages, it would appear practically certain that sex is predetermined in the undivided oosperm. It has been claimed that the data with reference to sex in the armadillo might as readily be used as evidence of the control of sex by environment; for it is claimed that the environment of the four fetuses in a common chorion is as nearly identical as it could be made under controlled conditions. I claim, however, that there is no greater environmental uniformity here than exists in cases where several fetuses develop simultaneously in a single uterus. In both cases the individual fetuses have separate amnia, separate placentæ and unmixed fetal blood. The enclosure within a common chorion is a matter of secondary importance since each fetus is isolated completely in the really important ways just mentioned. Moreover it is certain that pronounced differences in nutrition and rate of development frequently occur, as is evidenced by the facts that one pair of fetuses is often strikingly larger than the other. If sex is capable of being altered by nutritive factors one would expect to note some differences of sex within a set in which some fetuses have evidently had a much less favorable developmental environment than others. There are in my collection several sets of quadruplets in which one pair of fetuses is very decidedly larger and more advanced than the other. A condition of this sort is probably to be traced back to a very early period, as early as that shown in Fig. 5, where it is readily seen that one pair is distinctly in advance of the other. Patterson has also stated that it is not uncommon to find one of the primary bud primordia dividing in advance of the other. If sex is capable of being influenced by metabolic inequalities of any sort, there should be opportunity here for the operation of such influence. Yet there is not a single instance in which there is any diversity of sex within a set of fetuses derived from a single germ cell.

Cytological studies of the germ cells are in strict accord with current chromosomal hypotheses of sex determination. The female diploid number of chromosomes is 32 and the haploid 16; the male diploid 31, producing two kinds of spermatozoa, one with 15 and the other with 16 chromosomes. There occurs in the reduction division an odd chromosome like that described for other vertebrates, notably the birds and man as shown by Guyer. The presumption is that this odd chromosome plays the same rôle in the determination of sex as it is assumed to play in an extensive array of animals. The character of the evidence is the same in all cases. On this basis it may be claimed that in the armadillo an egg fertilized by the 15 chromosome type of spermatozoon produces a male and one fertilized by a 16 chromosome type, a female. Environmental factors are powerless to alter the sex thus determined.

ANALYSIS OF PREDETERMINATIVE VERSUS EPIGENETIC FACTORS IN DEVELOPMENT

According to the proponents of the pure line hypotheses the genotypic constitution of an individual is fixed at the time of fertilization of the ovum. On this assumption the fertilized egg of the armadillo has a fixed and definite hereditary potentiality and, unless inequalities of some sort are introduced during development, *i. e.*, epigenetically, the four fetuses should be identical. The degree of difference then that actually exists among the individuals of a given set of quadruplets should be a measure of the potency of the epigenetic factors of all kinds, while the degree of correlation among the individuals of a set should serve as a criterion of the relative strength of the predetermining factors. It has been customary to employ the data derived from comparisons of human duplicate or identical twins as a measure of the extent of predetermination, but such data are unreliable for two reasons. It is impossible, on the one hand, to be sure whether or not such twins are the product of one egg, and in practically all cases the measurements and comparisons are made comparatively late, so that the two individuals may have had a divergent environmental experience. In both of these respects the armadillo quadruplets offer superior advantages and should in the future take the place of human twins as material illustrating the potency of predeterminative factors in development, for not only do we know for certain that each set of quadruplets is the product of a single egg, but the amount of material is thoroughly adequate for statistical treatment, and the individuals are compared before birth, so that their pairing and placental relations are known. Coefficients of polyembryonic correlation have been determined for a very large number of characters, such as the numbers of plates or scutes in the various regions of the armor, and these have ranged from 0.92 to 0.98. These coefficients are strictly of the order of those determined for antimerically paired structures of the same individual. In other words, these quadruplets resemble one another as closely as do the right and left sides of single individuals. One might readily make the claim that the quadruplets are simply four parts of one individual, since they have been derived by a process of asexual budding from a single embryonic vesicle. The closest of ordinary blood relations have coefficients of correlation of a decidedly lower order, that of brothers being about 0.5; hence the polyembryonic relation is much closer than a mere fraternal one. We may conclude then that the predetermining mechanism works accurately up to from 91 to 98 per cent. and that epigenetic disturbances or inequalities effect alterations in the end result ranging from 2 to 8 per cent. One of the most fundamental postulates of the sciences of taxonomy and phylogeny is to the effect that degrees of resemblance are criteria of blood relationship. This postulate is strongly supported by the facts just given, since the closest resemblances ever found to exist between individuals are here the result of the closest possible blood relationship; for no closer genetic relationship could well be conceived than that involved in the known origin of these armadillo quadruplets.

A subsidiary question arises as to what kind of epigenetic factors operate in inducing dissimilarity among the polyembryonic offspring of a set. Studies of the heredity of certain characters and of the distribution of certain units among the quadruplets lead to the conclusion that the most important differences are due to imperfections in the mechanism for distributing germinal materials, a mechanism which has visible expression in the mitotic complex of cleavage. It seems probable that certain materials which condition the development of certain characters are not distributed with exact equality to the first two blastomeres. This would make one half of the embryonic vesicle different in potentiality from the other. A similar inequality might exist in the second cleavage and in subsequent cleavages. Mere differences in nutriment, position, etc., are impotent to influence any but dimensional characters, such as length, weight and relative position of units. Inherited characters are affected only by changes in the germinal materials, and such changes might readily be due, as indicated, to inequalities in the distribution of material particles during cleavage.

Modes of Inheritance in Polyembryonic Offspring

The material for the study of inheritance consists of nearly two hundred sets of quadruplets and the armor of the mothers. Without breeding in confinement, which is not at present practicable, no data concerning paternal inheritance are available. Since, however, there is no sex dimorphism with regard to the characters studied, and since males and females inherit alike from the mothers, one can discover all the essential laws of inheritance governing the polyembryonic relationship from a comparison of individuals in sets and of quadruplets with their mothers. After an exhaustive study of this large mass of material the chief general laws discovered are to the effect that single meristic variates, such as particular scutes, and also aggregates of these elements, as for example the total numbers of these units in a given region of the armor, are inherited in the alternative fashion and show only a minor degree of blending. This is an unexpected result in view of the fact that it has been the general impression that meristic variations usually exhibit blended inheritance and substantive variations obey the laws of Mendelian inheritance. In this material it has been found that single scutes, recognizable through some marked peculiarity, such as a tendency to split or to fuse with a neighboring element, is inherited as a Mendelian dominant character. If the mother has the character unilaterally or in one band of the armor, one or more of the offspring invariably exhibit the character either unilaterally or bilaterally, either in one band or reduplicated in two or more bands. Again a single scute peculiarity in the mother may be inherited by one, two or all of the offspring, as a row of peculiar scutes starting at the place where the one peculiar element occurs in the mother. Such fluctuations in the expression of a type peculiarity may conceivably be due to epigenetic factors, and suggest duplication of factors of the neo-mendelian sort.

One of the problems of this material is to determine why one individual or one pair inherits a dominant peculiarity from the mother, while the others do not. They all have the same germinal constitution at the beginning and that some should inherit the character and others not seems to imply that there must have occurred a segregation of maternal and paternal inheritance factors during cleavage. The distribution of the characters so as to produce mirrored image effects, together with this segregation of parental characters, seems to imply a sort of dichotomous distribution of some material basis that conditions the development of the characters so segregated and distributed. Such determiners need not be conceived of as Weismannian elements, but that they have corporeal existence appears to the writer as an unavoidable conclusion.

The data upon which these conclusions are based are of highly complex character and have not yet been published in extenso. The demonstration of the tenability of the conclusions can be made only by the use of much more illustrative material than can be presented in a paper of this sort. In conclusion it may be said that, although the inheritance phenomena have occupied more time and attention than any other phases of the armadillo work, the conclusions reached are less precise and less satisfactory than those in other fields. Yet it is imperative that we should find out just what new light this unique material and unparalleled genetic situation may be able to throw upon the general problems of inheritance. The detailed data and conclusions regarding these intricate problems are being elaborated for publication in the near future.

DARWINISM IN FORESTRY

RAPHAEL ZON

U. S. FOREST SERVICE

THE centennial anniversary of the birth of Charles Darwin was the occasion for many interesting reviews of what Darwinism has done for the biological sciences. In all these reviews, however, scarcely any reference is made to forestry. Yet historically and inherently there is a most remarkable and unique connection between Darwinism and forestry.

On April 10, 1860, soon after the appearance of the first edition of the "Origin of Species," Darwin wrote to his friend C. Lyell:

> Now for a curious thing about my book, and then I have done. In last Saturday's *Gardeners' Chronicle,* a Mr. Patrick Matthew publishes a long extract from his work on "Naval Timber and Arboriculture," published in 1831, in which he briefly but completely anticipates the theory of Natural Selection. I have ordered the book, as some few passages are rather obscure, but it is certainly, I think, a complete but not developed anticipation! One may be excused in not having discovered the fact in a work on Naval Timber.[1]

And three days later, on April 13, 1860, he wrote to J. D. Hooker.[2]

> *My dear Hooker*—Questions of priority so often lead to odious quarrels, that I should esteem it a great favor if you would read the enclosed. If you think it proper that I should send it (and of this there can hardly be any question), and if you think it full and ample enough, please alter the date to the day on which you post it, and let that be soon. The case in the *Gardeners' Chronicle* seems a little stronger than in Mr. Matthew's book, for the passages are therein scattered in three places; but it would be mere hair-splitting to notice that. If you object to my letter, please return it; but I do not expect that you will, but I thought that you would not object to run your eye over it.

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[1] "The Life and Letters of Charles Darwin," by F. Darwin, 1898, New York, Appleton & Co., p. 95.

[2] *Ibid.*, pp. 95 and 96.

The statement to which Darwin referred in his letter to Hooker appeared in the *Gardeners' Chronicle* on April 21, 1860 (page 362), and is this:

> I have been much interested by Mr. Patrick Matthew's communication in the number of your paper dated April 7th. *I freely acknowledge that Mr. Matthew has anticipated by many years the explanation which I have offered of the origin of species, under the name of natural selection.* I think that no one will feel surprised that neither I, nor apparently any other naturalist, *had heard of Mr. Matthew's views,* considering how briefly they are given, and that they appeared in the *appendix to a work* on *Naval Timber and Arboriculture.* I can do no more than offer my apologies to Mr. Matthew for my entire ignorance of this publication. If another edition of my work is called for, I will insert to the foregoing effect.[3]

In the Historical Sketch[4] which he added to the later editions of his book Darwin gives Matthew credit for the Nature's law of selection in the following words:

> In 1831 Mr. Patrick Matthew published his work on "Naval Timber and Arboriculture," in which he gives precisely the same view on the origin of species as that (presently to be alluded to) propounded by Mr. Wallace and myself in the *Linnean Journal,* and as that enlarged in the present volume. Unfortunately, the view was given by Mr. Matthew very briefly in scattered passages in an Appendix to a work on a different subject, so that it remained unnoticed until Mr. Matthew himself drew attention to it in the *Gardeners' Chronicle,* on April 7th, 1860. The differences of Mr. Matthew's view from mine are *not of much importance:* he seems to consider that the world was nearly depopulated at successive periods, and then re-stocked; and he gives as an alternative, that new forms may be generated "without the presence of any mould or germ of former aggregates." I am not sure that I understand some passages; but it seems that he attributes much influence to the direct action of the conditions of life. *He clearly saw, however, the full force of the principle of natural selection.*[5]

In a letter written by Darwin to J. L. A. de Quatrefages on April 25, 1861, he referred to Patrick Matthew's explanation in a postscript as follows:

> I have lately read M. Naudin's paper, but it does not seem to me to anticipate me, as he does not show how selection could be applied under

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[3] *Ibid.*

[4] "The Origin of Species," 1878, p. xvi—Historical Sketch.

[5] *Ibid.*

nature; but an obscure writer on forest trees, in 1830, in Scotland, most expressly and clearly anticipated my views—though he put the case so briefly that no single person ever noticed the scattered passages in his book.

Grant Allen in his biography of Darwin (1888) calls Patrick Matthew the unconscious author of the principle of natural selection which he applied in his book on naval timber to the entire Nature.

Here then is a most interesting fact which seems to me of deep significance to foresters. The first Darwinian, who twenty-nine years before Darwin formulated the law of natural selection, was a forester. I shall not attempt here to compare Darwin's and Matthew's views on natural selection. Matthew's book, the full title of which is "Naval Timber and Arboriculture, With Critical Notes on Authors Who Have Recently Treated the Subject of Planting," is accessible in the Congressional Library. The chapter on Nature's Law of Selection I hope can be reprinted in the next issue of the *Proceedings of the Society of American Foresters,* so that every one will be able to draw the comparison for himself.

In bringing together this evidence I am very far indeed from any desire to detract in the least from the great service which Darwin rendered to science. It was Darwin who first gave flesh and blood to the idea of natural selection. It was his wonderful interpretation of all biological facts in the light of natural selection that made the latter the universal law applicable to the entire organic world. Before this accomplishment the claims of all others must sink into obscurity.

My purpose in assembling these records is twofold: *First,* to restore the memory of one who ploughed the same fields as we do now, the name of a forester whose idea, although it did not perish, slumbered almost unknown for nearly thirty years until another and bigger man brought it to life and general recognition; and *second,* to offer an explanation of the reason why a forester above all others should be the one to observe and formulate the law of the struggle for existence as the basis for natural selection and the origin of new species.

My first purpose, I hope, has been accomplished by quoting extracts from Darwin's correspondence. The second still remains.

There is nothing accidental, in my opinion, in the fact that a forester should be the first to observe the struggle for existence and its bearing upon the development of the new varieties, because there is no other plant society in the world which presents a more striking example of the struggle for existence and of natural selection than the forest. Nowhere else, also, can the law of this process be more fully studied.

The regular decrease in the number of trees on a given area with increase in age forms one of the earliest observations of the foresters, who, at a time antedating Darwin, properly gave this process the name of the struggle for existence, the struggle for the necessary growing space. The foresters have discovered the laws governing this process, a process in which almost 95 per cent. of all trees that start life in the stand perish, and in the form of yield tables have expressed it quantitatively, have measured and weighed it. They have shown how this struggle for existence varies with the species, climate, drainage and soil conditions, and age of the stand; that it is more intense, and consequently the differentiation into dominant and suppressed classes occurs earlier with light-needing species than with shade-enduring ones. In a climate most suitable to the species and on favorable situations this struggle again results in more rapid differentiation into dominant and suppressed trees than when the species grow outside of their optimum range and on poor soils. These are elementary and fundamental facts known to foresters for many years.

The foresters have not only observed these facts, but they have also furnished an explanation for them. The more favorable the conditions of growth, the greater is the development of the individual trees; the earlier, therefore, begins the struggle for space and the differentiation into dominant and suppressed, with the subsequent dying out of the latter. They have followed this process throughout the entire life of the stand, have established its various degrees of severity, and have discovered its culmination during the period of the most rapid growth in height. This struggle for space and light is the basis of the forester's operations, as only by utilizing and controlling it is he capable of producing wood of high technical qualities, tall cylindrical boles, free of branches, and wood with uniform annual rings possessing great elasticity. Without this struggle there is no forest, there is no production of valuable timber, save firewood.

The struggle for existence in a forest stand is not confined to individual members of the same age or the same story, but the forest, as a whole, battles for its existence against the adjoining meadow, swamp or shrub vegetation; the old trees against the young growth that comes up under them; groups of trees of different species or of different ages against each other. In this struggle the forest accomplishes what no other vegetation does; namely, it actually changes the climate over the area occupied by it, and makes it inhospitable for its enemies. The forest creates its own interior environment to which its own members are completely adapted, but in which other species find either too much or too little light, the humus too scant or too deep, or too acid, the temperature too high or too low. Whatever it may be, the forest's competitors are eliminated through the changed environment. To change this environment, however, there must be a close stand, there must be present the struggle for existence among the individual members of the stand. Through interior struggle among its own members the stand secures resistance against invasion by other vegetation. How manifoldly broad and deep, then, is the struggle for existence in the forest.

When we come now to natural selection nowhere else is it expressed in such fullness and so strikingly as in the forest. The forest is a natural breeding place in which constantly only the trees best adapted to the climate and the situation are allowed to remain. In the forest only the conquerors in the struggle for existence are the ones which produce seed in abundance. During a seed year the dominant and co-dominant trees produce seed in large quantities; the intermediate trees, which may properly be called the candidates for suppression, participate but little, and then only in exceptionally good seed years, while the oppressed and suppressed do not bear seed at all. With what rigidity, then, must the natural selection go on in a forest, if we consider *first* what a small percentage of trees in a stand of the same generation come to be conquerors in the struggle for existence; *second,* the great age reached by trees; *third,* the numerous generations of trees that have succeeded each other in the same forest; and *fourth,* the relatively limited capacity of tree seeds for dissemination. With each generation the forest trees must become more and more delicately adjusted and adapted to the given conditions of growth. The new generation inevitably arises from seed sown by the best developed trees, from those which have withstood the long and intense battle not only against Nature alone, but against Nature in the presence of competitors. Of this possibly only 1 per cent. or less will reach maturity and be able to continue the species. No wonder, therefore, that in spite of search for new species all over the world so few forest trees have been successfully introduced into new countries and so little progress has been made with the artificial improvement of them. So perfect is the natural selection in the forest, so fine is the adjustment between the environment and the forest trees, that it is almost impossible for man to approach it. I do not mean the introduction of trees for park purposes or breeding new varieties for some other purpose than timber; I have in mind only the establishment of natural forests and the production of timber.

The natural selection forms also the basis of the forester's operation in selecting trees for seeding purposes, in making regeneration cuttings, in collecting seed for reforestation and so on.

These few facts are enough to show with what fullness and force the principles advanced by Darwin are expressed in the forest. If agriculture furnished Darwin with many examples of artificial selection upon which he built by analogy his principle of natural selection, the forest, of all plant formations, furnishes the most striking examples and proof of the latter. *As a matter of fact, forestry as an art is nothing else but the controlling and regulating of the struggle for existence for the practical ends of man; forestry as a science is nothing else but the study of the laws which govern the struggle for existence.*

Is there anything strange, therefore, that it was a forester who first formulated the principles of natural selection? Is there anything strange, also, in the fact that it was also foresters who have laid the foundation for what has come to be known as ecology, which is the logical development of Darwinism? Because of the fact that the forest is the highest expression of plant life, the foresters occupy the strategic position from which they command vistas accessible only with difficulty to other naturalists. In this lies the strength of forestry, its peculiar beauty, and the debt which science owes to it.

GENETICAL STUDIES ON ŒNOTHERA. IV

II

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3. HYBRIDS OF *grandiflora B* × *biennis D* IN THE F_2 GENERATION

In my last paper (Davis, '12*a,* pp. 392–406) there was described an especially interesting F_1 generation, culture 11.35, of the cross *grandiflora B* × *biennis D.* The *biennis* male parent of this cross (Davis, '12*a,* pp. 385–389, Figs. 1–3) was of a race with the stem coloration characteristic of *Lamarckiana, i. e.,* the papillæ or glands at the base of long hairs were colored red on green portions of the stem. The *grandiflora* female parent bears the same type of papillæ, but they follow the color of the stem and therefore lack the red over green portions of the stem. The *biennis* parent then presented a character, the red coloration of the papillæ, that might be expected to be present or absent in the F_1, and to present an alternative inheritance in the F_2 generation.

It will be remembered that in the F_1 generation of this cross, *grandiflora B* × *biennis D,* consisting of 180 plants, two sharply contrasted classes appeared (Davis, '12*a,* p. 395). Class I was represented by 12 plants which had the stem coloration of the *biennis* parent (red papillæ on green portions of the stem). Class II was represented by 168 plants with the stem coloration of the *grandiflora* parent (stems above clear green). Other peculiarities of these classes are described in the paper cited above, but we are concerned at this time chiefly with the behavior of this color character. The mixed conditions in this F_1 generation naturally suggested the probability that the male *biennis* parent was heterozygous with respect to the red coloration of the papillate glands and that it formed two classes of gametes with and without the factor responsible for this character.

Although it is true that the form *biennis D* in later generations has been uniform as to the stem coloration described above it by no means follows that the original plant of 1910, which furnished the gametes of the cross, was homozygous for this character. I have already noted the fact (Davis, '12*a*, p. 386) that types occur wild similar to *biennis D* except for their clear green stems. Consequently the original plant may have been heterozygous with respect to factors for red papillæ and in my later generations I may have isolated a homozygous line.

Last summer I grew the reciprocal of the cross described above, *i. e.*, a cross *biennis D* × *grandiflora B* which involved the same parent plants as in the first. The F_1 generation of 103 plants, culture 12.11, was brought to maturity and consisted of the same two clearly defined classes. Class I, consisting of 87 plants, presented the stem coloration of the *biennis* parent (red papillæ on green portions of the stem). Class II, consisting of 16 plants, presented the stem coloration of the *grandiflora* parent (stem above clear green). There was a disproportion of the numbers as in the previous case, but in the reciprocal cross the plants with red papillæ were in a large majority, 87:16, instead of being in a small minority, 12:168, present in the first cross. Other peculiarities of these classes were the same as in the first cross. Again the mixed conditions in the F_1 reciprocal cross suggested the probability that the *biennis* parent, in this case female, was heterozygous with respect to the red coloration of the papillate glands and that it also formed two classes of gametes with and without the factor responsible for this character.

The two classes of hybrids in the F_1 generation described above appear to present a phenomenon similar to the "twin hybrids" of De Vries ('07) which result when *Œ. biennis* or *Œ. muricata* are pollinated by *Lamarckiana* or by one of its derivatives (*e. g., rubrinervis, brevistylis* or *nanella*). Critics have pointed out that this behavior indicates that *Lamarckiana* is heterozygous or hybrid in character since it must form at least two different types of male gametes. De Vries apparently believes that the "twin hybrids" in my crosses show that the *grandiflora* parent is in a condition similar to that of *Lamarckiana* and that the "twin hybrids" are due to the mutations of *grandiflora*. My interpretation of the behavior is quite the opposite, for, as will be shown, the evidence indicates that the *biennis* parent, with respect to the characters concerned, is heterozygous and that the race of *grandiflora* is stable. If this is true the evidence does not indicate that the race *grandiflora B* exhibits with respect to these characters the habit of mutation as claimed by De Vries ('12, p. 30).

Among some 300 plants of *grandiflora* grown from wild seed and 200 more grown in isolated lines none have presented red-colored papillæ over green portions of the stem. All green-stemmed forms of *biennis* have proved perfectly true to this character. One of the best known types of green-stemmed *biennis* is the Dutch plant extensively grown by De Vries and Stomps, and this, as far as I know, is constant. Furthermore, all green-stemmed F_1 hybrids have in later generations proved constant to this form of coloration. There is thus much evidence that the absence of red in papillæ over green portions of the stem constitutes a homozygous condition. The type *biennis D,* as stated before, can not be distinguished in other respects from wild plants which lack the red coloration in their papillæ, and it seems probable that this assemblage is a mixed population in which some plants are heterozygous with respect to the character of their stem coloration.

Although I can not as yet present experimental proof that the red coloration of papillæ is a character dominant to its absence, we should expect this to be the case because anthocyan coloration is obviously a character in addition to that of the green and because its inheritance appears to be alternative. It is on this hypothesis that I shall treat the red coloration of papillæ as a dominant character when for convenience employing a Mendelian notation in the accounts that follow.

It became a matter of interest to determine how representatives of Class I and Class II would behave in the F_2 when selfed and how they would behave when crossed reciprocally. Therefore I selected a plant, 11.35*m* (Davis, '12*a*, Figs. 6 and 7), as representative of Class I, and a plant, 11.35*a* (Davis, '12*a*, Figs. 5, 8 and 9), as representative of Class II, and according to my plan (Davis, '12*a*, p. 399) carried these in pure lines into an F_2 and also grew the crosses 11.35 $m \times a$ and 11.35 $a \times m$. Furthermore, a large F_2 generation was grown from an especially interesting plant 11.35*La* (Davis, '12*a*, Figs. 10, 11, 12 and 13), also representative of Class II, which resembled *Œnothera Lamarckiana* closely in certain particulars. These cultures will now be briefly described.

1. *The F_2 Generation from 11.35m.*—From this plant, with red papillæ on green portions of the stem as in the parent *biennis*, the contents of one capsule, 413 seeds, were sown. The culture, 12.43, produced 180 seedlings, of which 166 plants were brought to maturity. Among these, 86 plants presented the stem coloration of 11.35*m* and the *biennis* parent of the cross, and 80 plants presented the stem coloration of the *grandiflora* parent.

Let us assume the formula for the *biennis* parent to be *Rr* (*R* standing for the presence of the factor responsible for the red color of the glands and *r* for its absence); *i. e.*, the *biennis* parent is held to be heterozygous for this character and to form two classes of gametes, viz., *R* and *r*. Let us assume that the formula for the *grandiflora* parent with respect to this character is *rr*. The F_1 hybrid plant 11.35*m* would then be expected to have the formula *Rr* and to produce gametes *R* and *r*. These gametes in chance combinations should give F_2 hybrids in the proportions $1RR:2Rr:1rr$, which would be a 3:1 ratio with respect to the appearance of the character *R* (red papillæ). I lay no stress on the fact that in my small cultures the numbers were $86R:80r$, but merely wish to note the point that in this F_2 generation two classes appeared sharply distinguished by the presence or absence of the character under discussion.

I was unable to differentiate in this F_2 other characters on the plants 11.35*m* and 11.35*a* associated with the presence or absence of the red papillæ (see Davis, '12*a*, p. 395). There was a wide variation in habit, leaf, form, inflorescence, flower proportions and flower size (petals 2.2–3.9 cm. long), a variation that seemed unrelated to the presence or absence of red papillæ. In this culture also appeared a group of 15 dwarfs, recognizable when young rosettes, which at maturity were from 5–6 dm. high, sparsely branched, and with a foliage of narrow leaves; 6 of these dwarfs had the stem coloration of the *biennis* parent (red papillæ) and 9 that of *grandiflora*.

Among the plants with red papillæ on the stems I selected an individual, 12.43*g*, which among my hybrids with the stem coloration of *Lamarckiana* most resembled that form. I shall make this plant the starting point of a pure line with the hope that in later generations I may find variants still closer to the *Lamarckiana* type which may be isolated by selection. Whether the plant is homozygous with respect to the red coloration of the papillate glands is a point to be determined by the next generation.

2. *The F_2 Generation from 11.35a.*—From this plant with the stem coloration of the *grandiflora* parent (papillæ green over green portions of the stem), the contents of one capsule, 432 seeds, were sown. The culture, 12.42, produced 165 seedlings of which 147 plants were brought to maturity. These presented uniformly the stem coloraion of the F_1 hybrid plant 11.35*a* and of the *grandiflora* parent. It seems then safe to conclude that such a plant as 11.35*a* is homozygous as to its stem coloration with possibly the formula of a recessive (*rr*) lacking the factor that produces the red color in the papillate glands. This position is supported by the evidence from the much

larger F_2 generation grown from the sister plant of the same Class II, 11.35*La,* where 532 plants agreed in having this same type of stem coloration characteristic of *grandiflora.*

The culture was remarkable for the length and breadth of its leaves, which far surpassed that of the parents of the cross and for its general vigor. In these respects there was marked progressive evolution. The flower size, however, was below the *grandiflora* type, the petals ranging from 1.5 to 2.8 cm. long (those of *grandiflora* being about 3.3 cm. long). Since none of these plants appeared to present the possibility of developing the stem coloration of *Lamarckiana,* I have not considered it worth while to follow the family further.

3. *The Cross 11.35 m × a and its Reciprocal 11.35 a × m.*—These crosses were made to determine whether or not the peculiarity of the red glands with the other correlated characters was in any sense or degree sex-limited. Thus if these characters were carried by the male gametes from the plant 11.35*m,* the progeny of the cross 11.35 *a* × *m* should have the peculiarities of Class I, while the progeny of the cross 11.35 *m* × *a* should have the peculiarities of Class II. A behavior of this general nature has been described by De Vries ('11) in his paper on double reciprocal crosses.

From the cross 11.35 *m* × *a* the contents of one capsule, 276 seeds, were sown. The culture, 12.45, gave 143 plants which were brought to maturity. Of these, 50 plants presented the red-colored papillæ characteristic of 11.35*m* and of the *biennis* parent, and 83 had the coloration of 11.35*a* and of the *grandiflora* parent. On the hypothesis developed through the cultures previously described the plant 11.35*m* should have the constitution *Rr* and the plant 11.35*a* should have the constitution *rr.* The female gametes of 11.35*m* should then have been of two sorts (*R* and *r*), the male gametes from 11.35*a* should have been all similar (*r*), and the plants of the culture distinguished as 50*Rr* and 83*rr.* The expected ratio of the two classes would be 1:1, provided that the female gametes R and r were formed in equal numbers and mated in equal proportions with the male gametes (r). It is at least clear from this culture that the factor for red glands (R) is in this case carried by a certain proportion of the female gametes and that the female gametophytes for the plant 11.35m must be of two sorts (R and r).

The plants of this culture, 12.45 (11.35 $m \times a$), failed to exhibit consistently the other differences associated with the presence or absence of red glands as illustrated by the two F_1 types 11.35m and 11.35a. There was a marked progressive advance over the parent species, *biennis* and *grandiflora,* in leaf size and general vigor, but not in flower size, the petals ranging from 1.5 to 3.2 cm. in length.

From the cross 11.35 $a \times m$ the contents of one capsule, 223 seeds, were sown. The culture, 12.44, gave 142 plants which were brought to maturity. Of these 23 plants presented the red-colored papillæ characteristic of 11.35m and of the *biennis* parent, and 119 had the coloration of 11.35a and the *grandiflora* parent. The proportions of these two types (23:119) is far from the expected ratio 1:1 on the hypothesis considered above, but it should be noted that the total number of plants in the culture (142) is small. The main consideration is, however, clear, viz., that the factor for the red papillæ is in this case carried by a certain proportion of the male gametes and that the male gametophytes from the plant 11.35m must be of two sorts (R and r). Thus in both crosses (11.35 $m \times a$ and 11.35 $a \times m$) the character of the red papillæ is represented in certain of the gametes both male and female and the character is not sex-limited.

The plants of the culture 12.44 (11.35 $a \times m$) also failed to show consistently the other differences associated with the presence or absence in the F_1 of red papillæ. There was a similar progressive advance over the parent species in leaf size and vigor, and likewise no advance in flower size, the petals ranging from 1.3–3 cm. in length.

4. *The F_2 Generation from 11.35La.*—This plant, 11.35*La* (Davis, '12*a*, pp. 401–406, Figs. 10, 11, 12 and 13), was one of the most interesting of my hybrids because of its strong resemblance to *Lamarckiana* in buds and foliage. The coloration of the stem was, however, that of Class II, *i. e.,* it was *grandiflora*-like in the absence of red in the papillæ on green portions of the stem. I had no means of knowing, when this plant was selected as the parent of a second generation, that its type of stem coloration was probably recessive to that of the red papillæ as found on the *biennis* parent, and that I should be disappointed in my hope of obtaining in an F_2 some plants with the stem characters of *biennis D* and *Lamarckiana*. I now believe that such a form is unable to produce in later generations plants with red papillæ, and, since this is an important character of *Lamarckiana,* my efforts with this particular line of hybrids will be discontinued. The F_2 generation from this plant, however, from the genetical standpoint proved to be one of the most interesting that I have grown and well merits a brief description.

The contents of 14 capsules, containing 2,217 seeds, were sown, and after eight weeks gave a culture, 12.41, of 623 seedlings. An unusual mortality, apparently in a class of dwarfs, reduced the culture finally to 532 plants. The rosettes before they were half grown presented an extraordinary range of variation and it became possible to group them although this preliminary classification required considerable revision later. A large group of more than 100 rosettes presented broad closely clustered and crinkled leaves of the *Lamarckiana* type. Many of these rosettes when half grown were indeed indistinguishable from those of *Lamarckiana* at the same age. A smaller group of about 20 consisted of rosettes with narrow leaves; most of these developed into dwarf forms. Finally, the remainder, constituting what might be called the mass of the culture, contained rosettes ranging on the one hand from a number somewhat *grandiflora*-like to a few rosettes somewhat close to the *biennis* type, and between these extremes was an assemblage of intermediates impossible of classification. In short, this portion of the culture presented an excellent illustration of a relative segregation of characters, with the extremes, however, quite far from the pure parent types. As the culture grew to maturity a reclassification of the types became necessary and finally five groups were separated as described below.

Group *A* consisted of 132 plants which had the *Lamarckiana*-like foliage and short internodes (Fig. 16) of the parent F_1 hybrid 11.35*La*, together with the 4-angled buds and flower form of this plant. These plants developed from the group of rosettes with broad crinkled leaves of the *Lamarckiana* type. The size at maturity ranged from plants 1.3 m. high to dwarfs 4 dm. in height; the habit and leaf size exhibited great variation. The extreme types of dwarfs (13 in number) had very much the habit of *nanella*. The flowers varied greatly in size, petals 3.5–1 cm. long, with the stigma both above and below the level of the anthers. There was, therefore, in this group a decided segregation of flower size. A peculiar feature of these flowers was the very common cutting of the petals at the edge into narrow segments as in laciniate varieties of flowers. This is, as far as I know, a new character in the genus *Œnothera*. The greatest development of leaf size and extent of crinkling observed in this group is illustrated in Fig. 17, which shows two rosette leaves of one of the hybrids, 12.41*Lp*, compared with the rosette leaves of the parent types of *biennis* and *grandiflora*.

Group *B* contained 5 dwarfs, 3–4 dm. high, sparsely branched or not at all, and with narrow leaves. The buds and flowers were *grandiflora*-like in form, but the petals were only about 1.8 cm. long. These dwarfs were very delicate and presented the characters of *Œnothera* reduced in size to about the simplest terms. They recalled the class of dwarfs in the F_2 from the plant

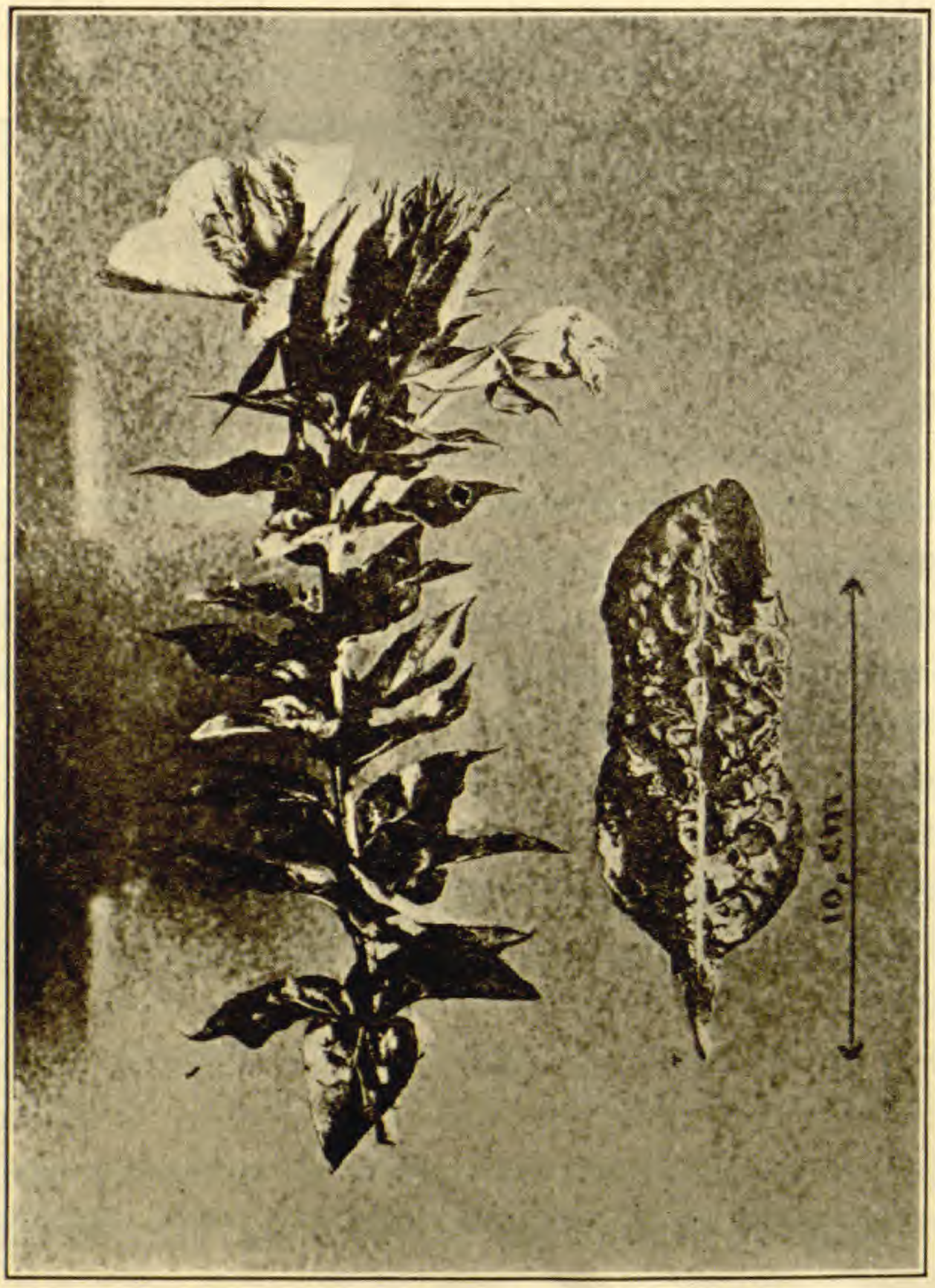

FIG. 16. A type, 12.41*Li*, in the F_2 from the F_1 plant 11.35*La*, hybrid of *grandiflora B* × *biennis D*, representative of Group *A*. A form similar to *Lamarckiana* in foliage, four-angled buds and fairly large flowers (petals 3 cm. long), but the stem coloration was the type of *grandiflora*, and the internodes were short as in *gigas*.

10.30*Lb* (Fig. 5), but were present in very much smaller proportions.

Group *C* comprised 7 plants having the habit of *grandiflora* with long branches from the base, but with narrow lanceolate leaves. The flowers were *grandiflora*-like (petals 3 cm. long), but the plants were not so high (about 8 dm.). The plants were distinguished with difficulty from certain forms in group *F*.

Group *D* consisted of 3 plants, short and very much branched and with revolute leaves, very narrow above. The plants failed to flower.

Group *E* included 23 plants with a stiff upright habit and much-crinkled leaves. They resembled most closely the larger forms in group *A*, but were without the short internodes characteristic of those plants.

Group *F* contained the mass of the culture, 362 plants, after the separation of the groups described above. As a group it presented the best illustration of the relative segregation of characters that I have so far met in an F_2 generation. There was a very wide range of variation in flower size, habit and leaf form. A few types resembling *grandiflora* could be picked out at one end of the series, while at the other end were plants much closer to the *biennis* parent than have usually been found.

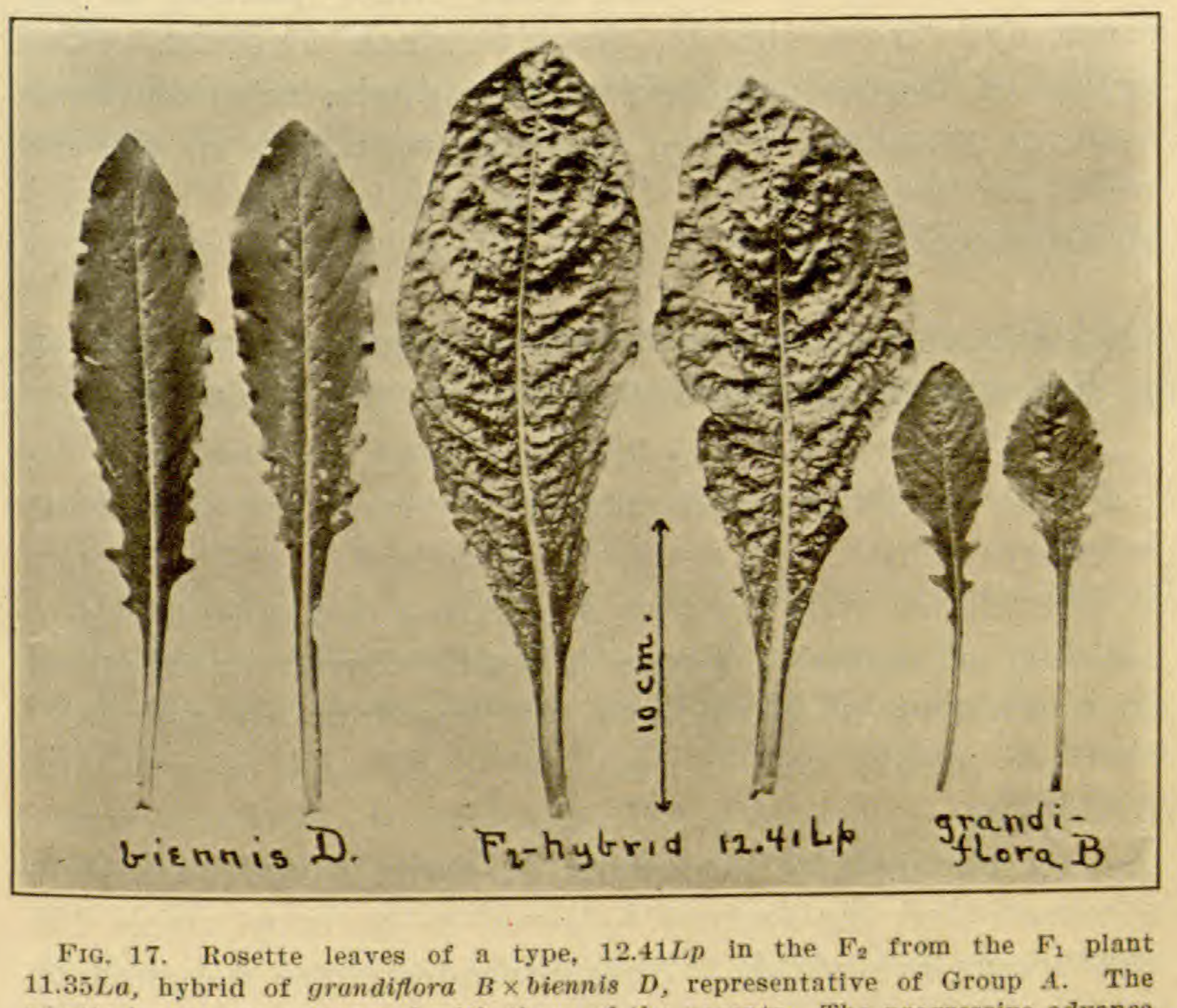

FIG. 17. Rosette leaves of a type, 12.41*Lp* in the F_2 from the F_1 plant 11.35*La*, hybrid of *grandiflora B* × *biennis D*, representative of Group *A*. The rosette leaves are contrasted with those of the parents. The progressive advance in leaf size and crinkled texture is very striking. The dry weight of the two leaves of the hybrid (1.65 *g.*) was more than twice that of the two leaves of *biennis* and more than nine times that of the two leaves of *grandiflora*.

Curiously the tendency in this group appeared not to be progressive as to the size of flowers and other plant organs, but, instead, retrogressive. There were no plants with flowers larger than those of *grandiflora,* but in contrast a large number had flowers (petals 1–1.5 cm. long) much smaller than those of the *biennis* parent type (petals about 2 cm. long). The general tendency throughout this group, as well as that of group *A,* was distinctly downward as regards the size of the plant's organs. This is the first time that I have met with such a phenomenon in my observations on second generation hybrids of *Œnothera.*

Considering the culture, as a whole, it presented the same sort of extreme variation that has appeared in other F_2 generations. Many types were present which were taxonomically distinct from either parent of the cross and from the F_1 hybrid plant 11.35*La.* The groups of dwarfs included few individuals, but these were quite as puzzling in their extreme reduction in size as were the dwarf types described from the F_1 plants 10.30*La* and 10.30*Lb.*

4. A Discussion of the Behavior of the Hybrids in the Second and Third Generations with Reference to the Stability of Mendelian Factors

I wish briefly to point out what seem to me difficulties in interpreting the F_2 generations described in this paper in accordance with a strict Mendelian conception of the stability of factors. These difficulties are not presented as a criticism of Mendelism, for the data are not sufficient to justify conclusions, but it is well to note the problems.

As I understand the tenets of strict Mendelism it is assumed that the factors believed to be responsible for characters are stable. New characters are believed to appear either by the loss of factors or by their recombination in the gametes, with possibly the occasional introduction of new factors or modification of the old to give "mutations." The process of segregation, of course, adds or subtracts nothing from the sum total of the factors but merely distributes them variously to the gametes that are formed. The increase or loss of factors in the offspring of a hybrid results from the mating of gametes which carry a greater or less number of factors.

Mendelism in its extreme expression may then be said to rest in large part on a law of *the conservation of factors.* This means that factors could never disappear from a genetic line of development if all of the gametes were mated and if all of the zygotes matured. It follows that the factors contained in an F_1 hybrid must all come out in an F_2 generation if that generation is sufficiently numerous.

The most striking specific problems brought forward by the data presented in this paper are:

1. The explanation of the large groups of dwarfs thrown off in the F_2 generations and repeated by certain plants in the F_3.

2. The explanation of the well-defined progressive evolution, excluding the dwarfs, exhibited by these same cultures.

With respect to the dwarfs the ratio of their production in the most striking of the F_2 generations is as follows:

The F_1 hybrid 10.30*La* gave 141 dwarfs in a culture of 1,451 plants (ratio about 1:9).

The F_1 hybrid 10.30*Lb* gave 147 dwarfs in a culture of 992 plants (ratio about 1:5.7).

These are large ratios, considerably above the 1:15 which might be expected if the range of size depended upon so simple a matter as the presence or absence of two factors. It must be remembered that the dwarfs were very much smaller than either parent, as best shown in the dwarfs from the plant 10.30*Lb* (Fig. 5), where the proportion, about 1:5.7, was the largest. These small plants (Fig. 5), 3–4 dm. high, came from parents, *biennis* and *grandiflora,* about 10–15 dm. and 15–20 dm.

high, respectively. It is difficult to imagine fertile hybrids of such parentage much more reduced in their vegetative expression than are these dwarfs. Furthermore, the reduction was apparently a complete loss in the power of a greater growth, as was indicated by the dwarfs breeding true in the F_3 generation.

If the dwarfs were to be interpreted in so simple a manner as recessives from a cross where two factors for size were allelomorphic to their absence the ratio of the dwarfs to the mass of the culture should have been as 1:15. Why then in the mass of the culture, dwarfs excluded, was there no evidence of other classes? The two factors assumed must be of large value if their absence is to make the difference between the size of the dwarfs, 3–4 dm., and the size of the parents, an average of about 15 dm. There might be expected a class of giants to balance the class of dwarfs and in the ratio of 1:15. There should have been several other classes ranging between these giants and the dwarfs. With only two factors for size concerned, and these of such large value, it seems impossible that the fluctuating variations could conceal the presence of such classes. Yet the mass of the culture failed to exhibit them, and only the dwarfs could be separated as a class sufficiently distinct to warrant its designation. The mass of the culture ranged in size approximately between the limits of the parents; the gap between them and the dwarfs was not bridged by intermediates.

I am aware that the dwarfs might be explained as resulting from the presence of an inhibiting factor introduced into the cross, but again there should have been evidence of other size classes together with the dwarfs according as the inhibitor was present in a full or in a lessened amount or was entirely absent. These difficulties are in themselves of sufficient weight, let alone the general improbability of such a situation.

The explanation of the progressive evolution of an F_2 generation in which the culture with respect to certain characters appears to advance as a whole presents the second problem to be considered. This phenomenon was also best exhibited by the F_2 generations from the hybrids 10.30*La* and 10.30*Lb*. A large number of plants in these cultures bore flowers with petals 1 cm. longer than those of the *grandiflora* parent (petals about 3.3 cm. long), and the smallest flowers were, for the most part, two or more times larger than those of the *biennis* parent (petals about 1.3 cm. long); between these extremes was a very perfect range of intermediates. An explanation for the advance in flower size over that of *grandiflora* may, of course, be offered as a recombination of factors for large size on the hypothesis of multiple factors for the size of petals, but why was there not a balancing group of plants with flowers as small as or smaller than those of *biennis?* Even the dwarfs of these cultures had flowers larger than those of the *biennis* parent. The only plant having smaller petals was the extraordinary form 11.42*j* (Fig. 15). What had become in these cultures of the factors responsible for small size?

A similar situation was presented by the character of the foliage most markedly exhibited by the F_2 generations from 10.30*La* and 11.35*a*. The leaves throughout the mass of these cultures were much larger than those of the parents of the cross and much more crinkled. There was thus a marked progressive advance in leaf size with the absence of small-leaved classes of plants unless such were represented in the F_2 from 10.30*La* by the dwarfs. Admitting that possibility, the same problem must be faced as was discussed for the explanation of the dwarfs themselves which were present in a ratio of about 1:9, suggesting the 1:15 ratio with the presence of two factors for leaf size. Thus two factors for leaf size should give through the culture other classes besides those of the recessives, and these were not evident. Applying the hypothesis of multiple factors for leaf size one is compelled to enquire what has become of the factors or combination of factors that should give classes of small-leaved plants to balance the mass of the culture with its progressive advance in leaf size and degree of crinkling.

I present these problems not altogether as a criticism of the hypothesis of multiple factors which has been so ably applied in the recent *Œnothera* study of Heribert-Nilsson ('13), and by East, Hays and other investigators in various groups. This hypothesis has amply justified the confidence of its advocates, but it does not seem to me to be established as wholly satisfactory. There has been abundant evidence in my cultures of a segregation of size in the F_2, but my question is whether this segregation may not be accompanied by a modification of factors whereby new sets wholly, or in part, take the place of the old. I do not think that East ('12) quite met the problem in his recent discussion of my data.

It has been suggested to me that the marked progressive advance in the size of organs in an F_2 generation may result from the continuance of the stimulus of heterozygosis (East and Hays, '12) apparent in the F_1. Is it not, however, possible to view the phenomenon in the F_2 as the direct modification of the factors for size as a result of the cross? One of the most extreme illustrations that I have observed of such an advance is illustrated in Fig. 17, which shows rosette leaves of a certain F_2 hybrid plant (12.41*Lp*) in comparison with those of its parents. This plant failed to mature flowers and its study could not be continued. There was certainly indicated very profound changes in its vegetative organization.

Advocates of the hypothesis of multiple factors for size allelomorphic to their absence may claim the possibility of selective fertilization in the formation of zygotes preceding an F_2 or later generations. This possibility can not be disregarded, but we have no data for the œnotheras. There has been, however, in my experience usually a high degree of sterility in the seeds of *Œno-*

thera hybrids following the F_1 for which no adequate explanation is known.

In one F_2 generation I have noted a distinct retrogression in the size of the flowers. This was the F_2 from the plant 11.35*La* briefly described in this paper. It contained no plants with flowers larger than those of *grandiflora* and a large proportion of the culture bore flowers as small as or smaller than the flowers of the *biennis* parent. The *biennis* parent in this cross was a rather large-flowered type (*biennis D,* petals about 2 cm. long) which made the retrogression appear the more marked.

A striking feature of the F_2 generations here considered has been the diverse progeny from F_1 sister plants of the same culture. Thus the F_1 hybrids 10.30*La* and 10.30*Lb* were sisters of the cross *grandiflora B* × *biennis A* and the F_1 hybrids 11.35*m,* 11.35*a* and 11.35*La* were sister plants of the cross *grandiflora B* × *biennis D.* Each plant gave its own peculiar set of types in the F_2 with peculiarities so pronounced that the blood relationship was much obscured. This is difficult to understand except on the theory that the parent stock was heterozygous; yet there has appeared no evidence of this in the cultures of the pure species. It is, however, clear that I have been working with complex material and it is not certain that the species of *Œnothera* employed in my crosses have been homozygous to the degree demanded for experimentation on the behavior of unit factors. For this reason I have endeavored to discuss the problems with full caution and I hold my point of view tentatively.

5. THE HABIT OF "MUTATION" IN *Œnothera Lamarckiana* DE VRIES CONSIDERED WITH REFERENCE TO THE BEHAVIOR OF THE HYBRIDS BETWEEN *biennis* AND *grandiflora*

Perhaps the most important observations on these hybrids of *grandiflora* and *biennis* in the second and third generations have been those showing a close parallelism of their behavior to that of *Œnothera Lamarckiana*. Thus the hybrids have thrown off marked variants of new specific rank as does *Lamarckiana*. Certain of these new forms have held true and others have continued to throw variants as do some of *Lamarckiana's* "mutants." One form (12.56*x*) appeared with a marked increase over the normal chromosome number (14) and apparently corresponds closely to the triploid "mutants" from *Lamarckiana* or its derivatives (Lutz, '12; Stomps, '12*a*). A most striking feature has been the production in successive generations of classes of dwarfs, plants which contrast sharply with the mass of the culture and which are stable.

This behavior of the hybrids appears to me to be of quite the same character as the "mutations" of *Lamarckiana*, but the results, here concerned with crosses between distinct species, are clearly of the sort that were to be expected from their hybrid association. It is not fundamental to my position that the various forms of the variants in the F_2 and F_3 generations should match the "mutants" from *Lamarckiana*. Since the F_1 hybrids were not themselves the counterpart of *Lamarckiana*, they should not be expected to give the same progeny as this latter plant. It is sufficient for my purpose to point out the essential parallelism between this hybrid behavior and that of *Lamarckiana* when it gives rise to its "mutations."

De Vries ('12, p. 30) has questioned the stability of my *grandiflora* stock, apparently believing that my hybrids exhibit, at least in part, a mutating habit inherited from the *grandiflora* parent. This view is based on the appearance of two classes of hybrids (twin hybrids) in the F_1 from the cross *grandiflora B* × *biennis D*. The evidence, however, indicates that this peculiarity is connected with the *biennis parent*, which may not have been homozygous for the character of stem coloration at the time the cross was made, although in later generations the form has held true.

I am perfectly willing to admit the complexity of my stock material of *grandiflora* and *biennis,* and also the possibility that the forms may not have been strictly homozygous at the time the crosses were made. It was in no wise necessary for the purposes of my experiments that they should be strictly homozygous. My only concern was that the material should be American types of *Œnothera* without the possibility of contamination through crosses with *Lamarckiana.* That my forms of *biennis* and *grandiflora* had these qualifications there can, I think, be no doubt. They have, as a matter of fact, bred true in the small cultures which have been carried through two generations for *biennis A* and *biennis D* and four generations for *grandiflora B.*

An abstract of my argument is as follows: (1) Since hybrids of *biennis* and *grandiflora* show points of strong resemblance to *Lamarckiana* and, (2) since the behavior of these hybrids in the F_2 and F_3 parallel closely the behavior of *Lamarckiana* when it gives rise to "mutants," (3) therefore, there are strong reasons for believing that the "mutations" of *Lamarckiana* are due to instability of its germinal constitution resulting from a hybrid origin. The fact that *Œnothera Lamarckiana* is not known as a component of any native *Œnothera* flora and the fact that its known history has been entirely as a cultivated plant or as a garden escape naturally greatly strengthen the force of the above argument.

It does not seem to me that these arguments are answered by a supposition that the behavior of my hybrids involves a habit of mutation inherited from the parental types. On the contrary, are we not justified in asking of the mutationists evidence from material the status of which, as representative of a wild species, is beyond question? Stomps ('12*b*) has apparently endeavored to meet the situation by a study of a cross between the *biennis* and *cruciata* of the sand dunes of Holland. From the cross he obtained in the second generation a *biennis nanella* and a *biennis semi-gigas.* Both of these new forms are regarded by Stomps as "mutants" in the De Vriesian sense in the belief that *biennis* and *cruciata* have an identical germinal constitution, except for factors that determine floral structure and, therefore, with respect to other characters may be crossed as though they were homozygous. Applying these conclusions to the problem of the status of *Œ. Lamarckiana,* Stomps reasons that since *biennis* mutates and since *biennis* is an older species than *Lamarckiana,* it follows that mutations among the œnotheras are older than *Lamarckiana* and consequently the mutations of this species can not be the result of hybridization.

In a recent discussion (Davis, '13) of the conclusions of Stomps I have taken exception to the assumption that his *biennis* and *cruciata* have exactly the same germinal constitution except for floral characters. This I can not believe probable, for the reason that, whatever may be the relation between the two species, they have certainly had a long period of independence. *Cruciata* has never appeared in the extensive cultures of the Dutch *biennis* that have been grown by De Vries and Stomps, and there is no experimental evidence that it has been recently derived from the latter form. From my point of view Stomps really made a cross between two species and obtained two marked variants due to some germinal modification as a result of the cross.

It seems to me fair to ask: Why did Stomps find it necessary to cross *biennis* and *cruciata* to obtain these "mutants" *biennis nanella* and *biennis semi-gigas?* If they have the same germinal constitution except for floral characters, Why should not *biennis* alone or *cruciata* alone give the "mutants"? There is no form of *biennis* better known to the workers in the experimental gardens than this Dutch plant. It is believed to have been on the sand dunes of Holland since pre-Linnæan times and Bartlett ('13) has recently presented strong reasons for believing the plant to be the form known to Linnæus as *Œnothera biennis* and consequently to be regarded as the type-form of the species. No species of *Œnothera* is perhaps so free from suspicion as to its gametic purity. It Stomps can obtain mutations from tested material of the Dutch *biennis* grown in pure lines he will have the basis of a strong argument, but this seems to me lacking in the conclusions drawn from his cross of *biennis* with *cruciata*.

I do not believe it at all probable that the Dutch *biennis* will be found to "mutate" under normal conditions to a degree worthy of serious consideration for the mutation theory of De Vries. The plant has already been made the subject of extensive cultures and its characters are known to a number of workers with œnotheras. Yet I am far from taking the stand that environmental conditions may never induce a modification of germinal constitution and still leave the organism vigorous. The possibility of direct modification of germ plasm, independent of sexual mixing, presents one of the most inviting fields of genetical research. However, if such research gives affirmative conclusions we should be most cautious in applying them to the conditions that normally surround a species and to the process of organic evolution.

6. The Problem of the Origin of *Œnothera Lamarckiana* De Vries

As stated in the introduction to this paper, we are no longer in our problem of the origin of *Œnothera Lamarckiana* De Vries concerned with Lamarck's plant (*Œ. Lamarckiana* Seringe, 1828) of about 1796. This plant (Davis, '12*b*) was with little doubt a form of *Œ. grandiflora* Solander, 1789, introduced at Kew in 1778. It had no relation to the cultures of Carter and Company, of about 1860, which were the starting point for the distribution among seedsmen of the plants known in cultivation as *Lamarckiana* (an incorrect determination of Lindley) from some of which De Vries's material was derived.

The historical side of the problem then largely centers on the history and composition of these cultures of Carter and Company. We have the statement of this firm that their seeds were received unnamed from Texas. This suggests that *Lamarckiana* De Vries may have in it the blood of some of the large-flowered œnotheras with an upright habit that are known to be present in the southwestern United States. There are a large number of such forms which frequently pass under the name of *Œnothera Hookeri* and have not as yet been properly segregated in the experimental garden. I am working with several of these types to determine whether any of them may prove to be more favorable than *grandiflora* as forms to cross with *biennis* in my attempts to synthesize *Lamarckiana* as a hybrid. (See note at end of paper.)

It must, however, be borne in mind that we have at present no confirmatory evidence that such plants as Carter and Company describe or the *Lamarckiana* of De Vries's cultures grow in Texas. It is possible that Carter and Company obtained their plants from some part of England, as from the sand hills of Lancashire, where large-flowered œnotheras were reported at dates earlier than 1860 and where at the present day *Œ. Lamarckiana* is successfully established. We must look to British botanists for investigations which will make clear the history of such *Œnothera* floras as that of Lancashire, and it is to be hoped that collections will be thoroughly searched for evidence on their probable development.

With respect to the composition of the cultures of Carter and Company we have some strong evidence from the specimens grown by Asa Gray in 1862 that their plants differed in some important respects from the *Lamarckiana* of De Vries. These specimens have been figured and described (Davis, '12*a*, pp. 417–422) and it seems probable that the plants were not more than one or two generations removed from the original cultures of Carter and Company. The specimens have characters in part those of De Vries's *Lamarckiana* and in part those found in *grandiflora,* and undoubtedly present in some of the large-flowered œnotheras of the west and southwest. If the plant of Dr. Gray was representative of the cultures of Carter and Company the evidence indicates that their forms became greatly modified during the quarter century before the time when De Vries began his studies, at about 1886, and isolated the type which we know to-day as *Œnothera Lamarckiana* De Vries.

On the experimental side of the problem of the origin of De Vries's *Lamarckiana* we have evidence of its hybrid nature from various sources. The recent analytical studies of Heribert-Nilsson ('12), previously mentioned, show that certain characters of *Lamarckiana* behave in a manner suggesting their association in a complex hybrid that is still throwing off segregates. His conclusions that *Lamarckiana* is a polymorphic species is supported by my own experience in isolating certain biotypes from material of De Vries. The "twin hybrids" produced when *Lamarckiana* or certain of its derivatives furnish the pollen of a cross with *biennis* or *muricata* indicate, as suggested by several critics, that different types of gametes are formed by *Lamarckiana.*

My own studies on hybrids between forms of *biennis* and *grandiflora* have reached an interesting point. I have not been able to synthesize by direct crosses, from wild stock so far obtained, any hybrid with all of the characters of *Lamarckiana* in the same plant, although I believe that all of the important taxonomic characters of *Lamarckiana* have been represented in some of my hybrids. It is, however, probable that more favorable parental types will in time come to hand. For example, a form, with the habit and foliage of the Dutch *biennis* and with the stem coloration of *Lamarckiana,* which the Dutch *biennis* apparently has not, would furnish very favorable material. In the meantime I have the possibility of crossing my hybrids back with certain wild species and of crossing the hybrids with one another. In this way it may be possible to bring into one plant all of the characters of *Lamarckiana*. It is of course in no way essential to the hypothesis of the hybrid origin of *Lamarckiana* that the plant should have arisen as the product of a simple cross. With Lamarck's plant eliminated from the problem of the origin of De Vries's material, the importance of *grandiflora,* on historical grounds, is materially lessened and we may consider other large-flowered types of more recent introduction into Europe as possible parents in a cross.

The resemblance of my various hybrids to *Lamarckiana* and the parallelism of their behavior in the F_2 and F_3 to that of *Lamarckiana* give in themselves sufficient reasons, in my opinion, to justify the belief in its hybrid character and to point to the probability that this plant arose as a cross between distinct forms of *Œnothera*. *Lamarckiana* thus would not be representative of a wild species of essentially stable germinal constitution and its "mutations" are most simply interpreted as the behavior of a hybrid.

UNIVERSITY OF PENNSYLVANIA,
April, 1913

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NOTE ADDED AUGUST 10, 1913

It is a satisfaction to announce that this summer (1913) I have obtained an F_1 hybrid generation with, I believe, all of the essential taxonomic characters of the small-flowered forms of *Œ. Lamarckiana* De Vries. The cross was a large-flowered, undescribed species of *Œnothera* from California pollinated by the Dutch *biennis* (*Œ. biennis* Linnæus). The hybrids differ from the small-flowered *Lamarckiana* only in relatively small plus or minus expressions of certain of its distinctive characters. It is not unreasonable to expect that generations from these hybrids in the F_2 will give material for future selection towards the large-flowered *Lamarckiana* of De Vries.

SHORTER ARTICLES AND DISCUSSION

NOTES ON A DIFFERENTIAL MORTALITY OBSERVED BETWEEN TENEBRIO OBSCURIS AND T. MOLITOR

I RECENTLY had occasion to subject some meal worms for short periods of time to a temperature considerably higher than that of the laboratory. Although the experiment was begun with a different purpose in view, there has been one feature noted which seems worth recording at this time.

The meal worms used consisted of the larvæ of *Tenebrio molitor* Linn. and *T. obscuris* Fabr. These larvæ are very readily distinguished from each other by the fact that the pigment in the integuments of *T. molitor* is yellow to orange-brown, while that of *T. obscuris* is almost black. In other features the larvæ resemble each other to a remarkable extent.

EXPERIMENTS WITH ELEVATED TEMPERATURE

The worms were placed in large Stender dishes containing a little meal and the dishes were then placed in a large, constant temperature incubator, being insulated from the bottom of the incubator by a cork ring and care being taken that the glass sides of the dishes did not come in contact with the copper sides of the incubator. The temperature was frequently noted through the glass door of the incubator and was also recorded on a maximum and minimum thermometer placed inside of the incubator and likewise insulated from contact with the copper sides or floor.[1]

Three major experiments were made after a probable differential mortality had been observed. These experiments are summarized below.

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[1] A much higher temperature is obtained if contact with the walls or floor is allowed. When an experimental dish was not insulated from the floor all of the larvæ which it contained were dead when larvæ in an insulated dish were still active.

Experiment 1.—104 larvæ (53 *T. molitor* and 51 *T. obscuris*). Kept at a temperature of 43° C. for 3 hours. These were the survivors of a previous heating at 41°–42° for 4 hours in which no record was kept of the number dying. Count made 24 hours after last heating.

	T. molitor	*T. obscurus*
Normal or nearly normal	2	44
Sluggish	13	6
Barely alive	13	1
Dead	25	none
Per cent. dead	47.17	—

Experiment 2.—50 larvæ (25 *T. molitor* and 25 *T. obscuris*). Heated 3 hours at 43° C. Not previously heated. Count made 24 hours later

	T. molitor	*T. obscurus*
Normal or nearly normal	none	none
Sluggish	none	none
Barely alive	none	12
Dead	25	13
Per cent. dead	100	52

Experiment 3.—441 larvæ (204 *T. obscuris* and 237 *T. molitor*). Heated at 41.5°–42° for 3.5 hours.

	Count in 24 Hrs.		Count in 48 Hrs.		Count in 96 Hrs.	
	T. mol.	*T. obs.*	*T. mol.*	*T. obs.*	*T. mol.*	*T. obs.*
Normal or nearly normal	none	176	none	164	none	164
Sluggish	none	7	none	7	21	6
Barely alive	195	15	160	21	128	10
Dead	42	6	77	12	88	24
Per cent. dead	17.72	2.94	32.50	5.88	37.14	11.77
Per cent. barely alive	82.28	7.35	67.50	10.29	54.01	4.90

Inasmuch as these experiments show a remarkable differential mortality, two other series of experiments were undertaken, in one of which the external influence used was exposure to cold for a long period of time and in the other set, exposure to an atmosphere of pure carbon dioxide.

EXPERIMENTS WITH COLD

Two experiments were made on the influence of cold as affecting the death rate. Two large Stender dishes, each of which contained 50 *T. molitor* and 50 *T. obscuris,* were placed inside of a battery jar, together with a maximum and minimum thermometer, the top of the jar was closed with a sheet of rubberized cloth to keep out moisture, and the whole was then fastened outside a laboratory window, in such a manner that the bottom rested upon a concrete slab, but the remainder of the jar was not in contact with the laboratory walls. The experiment ran from December 28, 1912, to March 9, 1913.

Unfortunately for this experiment, the winter at Cold Spring Harbor was unusually mild and the minimum temperature recorded in the jar was only —10° C. with a maximum of + 11°.

The jar was then taken into the laboratory and after standing at room temperature for 24 hours a count was made. A second count was made six days later with the results given below.

	First Count				Second Count	
	Experiment 1		Experiment 2		Exps. 1 and 2 Combined	
	T. obs.	*T. mol.*	*T. obs.*	*T. mol.*	*T. obs.*	*T. mol.*
Alive	40	47	33	44	50	91
Dead	10	3	17	6	50	9
Per cent. dead	20	6	34	12	50	9

EXPERIMENTS WITH CARBON DIOXIDE

In the third set of experiments, the influence of carbon dioxide on the differential mortality, approximately 75 larvæ of each species were placed in each of three gas wash bottles (E. & A. No. 3,658). The wash bottles were connected together with rubber tubing and carbon dioxide from a Kipp generator (limestone and hydrochloric acid) was slowly passed through the apparatus during the entire course of the experiment. The carbon dioxide was first washed through a saturated solution of sodium bicarbonate and then through distilled water before passing to the bottles containing the larvæ.[2]

The stream of carbon dioxide was started at 12 M., December 19. At 12:05 P.M. the jar nearest the generator (Jar No. 1) showed no movement of *T. molitor* but the *T. obscuris* were still very active; at 12:07 P.M. only a few *T. obscuris* were moving in jar No. 1 and nearly all of the *T. molitor* in jar No. 2 were dormant; at 12:09 all of the *T. molitor* in each of the three jars were in a state of "suspended animation" but a few *T. obscuris* were

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[2] I have already shown (*J. Biol. Chem.*, **10**, p. 90, and AMER. NAT., **45**, pp. 749–750) that it is possible to keep insects in pure carbon dioxide for hours without causing death, although to all appearances they are dead within a very few minutes after being subjected to the action of the gas.

still moving in jar No. 1; 12:11 P.M. "some movement in each jar but only of *T. obscuris*"; 12:20 P.M. "There are still a few *T. obscuris* moving in each jar, these have bubbles at their mouth"; 12:25 "Still a slight movement of a few but the 'suspended animation' is practically complete"; 12:30 P.M. "No movement in any."

An analysis of the gas passing through the apparatus was made at 3 P.M., December 19, and it was found to consist of 98.92 per cent. by volume of carbon dioxide (absorbed by KOH) and 0.27 per cent. of oxygen (absorbed from the residual gas by alkaline pyrogallol). Another analysis was made at 11 A.M., December 20, showing 99.15 per cent. of carbon dioxide and 0.04 per cent. of oxygen.

At the end of each experiment the last wash bottle of the chain was detached from its mate, a rapid current of air was drawn through it for several minutes, and then the larvæ were shaken out into a large open dish and allowed to remain fully exposed to the air. Counts were made at intervals. The results of the experiment are shown in the table below.

THE EFFECT OF CARBON DIOXIDE ON DIFFERENTIAL MORTALITY

	Jar No. 3		Jar No. 2		Jar No. 1	
Hrs. in CO_2	23.5		46.5		51.5	
Date Removed	Dec. 20, 11:30 A.M.		Dec. 21, 10:30 A.M.		Dec. 21, 3:30 P.M.	
	T. mol.	*T. obs.*	*T. mol.*	*T. obs.*	*T. mol.*	*T. obs.*
Count made Dec. 21, 9 A.M.:						
Alive	66	51				
Dead	10	24				
Count made Dec. 21, 10 A.M.:						
Alive			64[3]	30[3]	48[3]	8[3]
Possibly alive			5	15	21	35
Certainly dead (discolored)			5	31	6	35
Count made Dec. 28:						
Alive	60	38	66	26	59	10
Dead (discolored)	16	37	9	50	16	68
Per cent. dead	21.05	49.33	11.99	65.80	21.33	87.18

SUMMARY

The exposure of larvæ of *Tenebrio molitor* and *Tenebrio obscuris* to elevated temperature for a few hours causes a much greater mortality among the larvæ of *T. molitor* than among those

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[3] None able to crawl as yet. The feet only are moving.

of *T. obscuris;* 37.14 per cent. of *T. molitor* are dead after 3.5 hours at 42° as contrasted with 11.77 per cent. deaths of *T. obscuris.*

Exposure to cold for a long period of time causes a differential mortality in the opposite direction, nearly all of *T. molitor* (91 per cent.) remaining alive while 50 per cent. of *T. obscuris* died.

Subjecting a mixture of the larvæ to an atmosphere of pure carbon dioxide for 24 to 51 hours causes a differential mortality in favor of *T. molitor,* only 21.33 per cent. dying after 51.5 hours in the carbon dioxide as contrasted with 87.18 per cent. of *T. obscuris.*

It has been my experience, and I understand that owners of bird stores have noted the same fact, that there is a relatively high death rate among the larvæ of *T. obscuris* under natural conditions, while almost none of the larvæ of *T. molitor* die before pupating.

ROSS AIKEN GORTNER

THE CARNEGIE INSTITUTION OF WASHINGTON

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A CONTRIBUTION TOWARDS AN ANALYSIS OF THE PROBLEM OF INBREEDING[1]

DR. RAYMOND PEARL

THE effect of inbreeding on the progeny is a much-discussed problem of theoretical biology and of practical breeding. It has been alternately maintained, on the one hand that inbreeding is the most pernicious and destructive procedure which could be followed by the breeder, and on the other hand, that without its powerful aid most of what the breeder has accomplished in the past could not have been gained and that it offers the chief hope for further advancement in the future. While there is now, among animal breeders at least, a more widespread tendency than was formerly the case towards the opinion that inbreeding *per se* is not a surely harmful thing, nevertheless this opinion is by no means universally held and in any case does not rest upon a definite and well-organized body of evidence. Aside from a relatively small amount of definite experimental data one's judgment in the matter (so far as it is not wholly speculative) is finally formed on the basis of his interpretation of the vast accumulation of material comprised in the recorded experience of the breeders of registered (pedigreed) livestock.

This material recorded in the books of registration far exceeds in amount and in diversity any which could possibly be obtained experimentally on the same forms of life. It must be said, however, that the discussion of it

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[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 47.

with a view to an analysis of the effects of inbreeding, though undertaken at greater or less length by a number of men including Lehndorff, von Oettingen, Bruce Low, Hocsch, Chapeaurouge, Bunsow, Stranz and others, has not led to results characterized by the precision or the definiteness or the quality of getting at fundamentals demanded in the present state of the science of genetics.

The lack of precision and fundamental character in the studies alluded to is not primarily to be attributed to any inherent defect in the material. In the breeding of all of the domestic animals inbreeding has been practised; in many instances to a very marked degree. Further the manner in which the inbreeding has been done (the types of relationship-matings) exhibits a most intricate diversity, from which different types may be picked out for analysis in any reasonable quantity. The records are accurate within their limitations, to a high degree. Probably no experimentalist's records *of descent* are more accurate, considering the relative numbers involved in the two cases.

The real need, I venture to think, has been for an appropriate and valid method of pedigree analysis, which possessed generality, and could on that account be depended on to give comparable results when applied to two (or more) different pedigrees. Specifically, there seems not to have been worked out any *adequate general method of measuring quantitatively the degree of inbreeding which is exhibited in a particular pedigree.* Without such a measure it is clearly impossible to proceed far in the analysis of the kinship aspect of inbreeding.

It is the purpose of this paper to present a method for measuring and expressing numerically, in the form of a coefficient, the degree of inbreeding which exists in any particular case, and to show by illustrations the manner in which these coefficients may be computed. I shall endeavor to show that the method is (*a*) *unique*, in the sense that the values obtained in any particular instance can only be affected by the degree or amount of inbreeding which has been practised in the line of descent under consideration and (*b*) *general,* in the sense that it is equally applicable to all pedigrees and to all degrees and types of inbreeding.

PRELIMINARY DEFINITIONS

In attempting any general analysis of the problem of inbreeding from the theoretical standpoint one is confronted with the necessity for a definition of inbreeding, which shall be at once precise and general, that is, such as to include all of the many diverse ways in which this sort of breeding may be practised. A great number of definitions of the concept "inbreeding" have been proposed in the literature of genetics. I shall not attempt to review these definitions here, since to do so would serve no useful purpose in the present connection. A careful consideration of them is bound, I think, to lead one to the conclusion that they have been, in general, based on grounds of practical expediency, rather than critical biological analysis.

Clearness and simplicity of thinking will be gained by approaching the problem *de novo.* Leaving aside for the moment all consideration of details as to how a particular piece of inbreeding is done it is clear that underlying all definitions of inbreeding is to be found the concept of a *narrowing* of the network of descent as a result of mating together individuals genetically *related* to one another in some degree. Let us take this as our basic concept of inbreeding. It means that the number of potentially *different* germ-to-germ lines, or "blood-lines " concentrated in a given individual animal is *fewer* if the individual is inbred than if it is not. In other words, *the inbred individual possesses fewer different ancestors in some particular generation or generations than the maximum possible number for that generation or generations.* This appears to be the most general form in which the concept of inbreeding may be expressed.[2] In whatever way the

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[2] This, of course, looks at the matter primarily from the standpoint of kinship. This is all that is intended here. The discussion of the justification for this method of treating the subject, and of gametic relationships

mating of relatives is accomplished, or whatever the degree of relationship of the individuals mated together, the case in last analysis comes back to the above statement, namely that there are actually in the pedigree of the inbred individual fewer *different* ancestors in some particular generation or generations than the maximum possible number.[3]

The idea suggested in the foregoing paragraph may be expressed symbolically as follows. If there is absolutely no collateral relationship between any of the individuals in a pedigree, the number of different individuals in succeeding ancestral generations will be given by the series

$$x \leftrightarrow (1)2 \leftrightarrow (2)4 \leftrightarrow (3)8 \leftrightarrow (4)16 \leftrightarrow (5)32 \leftarrow \cdots \rightarrow (n)2^n, \qquad \text{(i)}$$

where the numbers in parenthesis denote the numbers of the ancestral generations (1 = parents, 2 = grandparents, 3 = great-grandparents and so on), and the free figures denote the maximum possible number of different ancestors in the indicated generation. If in any generation in the series relatives are bred together the same individual will appear more than once in the ancestral series, and the number of different individual ancestors in the higher terms will be accordingly diminished below the maximum number as given in (i). The series will then become

$$\begin{aligned} x \leftrightarrow (1)2 \leftrightarrow (2)4 - y_1 \leftrightarrow (3)8 - y_2 & \\ \leftrightarrow (4)16 - y_3 \leftrightarrow (5)32 - y_4 \cdots, & \end{aligned} \qquad \text{(ii)}$$

where $y_1, y_2, y_3, \cdots$ may, in the nth generation have any value not greater than $2^n - 2$, in the case of organisms in which two individuals must cooperate in the process of reproduction. The final limiting case is, of course, self-

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in inbreeding (heterozygosis in the sense of East and Hayes, etc.), will be undertaken in a later section of the paper (p. 605).

[3] This generalized concept of inbreeding seems to me to be in essential (though not entirely in verbal) agreement with that of O. F. Cook, whose interesting general discussions of this and related problems are summarized in a recent paper ("The Superiority of Line Breeding over Narrow Breeding," U. S. Dept. Agr., Bur. Plant Ind. Bul. 146, 1909). I use "inbreeding" as a generic term, while Cook regards it as a species of "line breeding." This seems to me to be a purely terminological difference, and not of great consequence.

fertilization, where the number of ancestors reduces to 1 in each generation.

THE MEASUREMENT OF THE DEGREE OF INBREEDING

This brings us to a consideration of a practical and general measure of the degree of inbreeding exhibited in a particular pedigree. This problem has been attacked by a number of other investigators, but so far as I have been able to learn all previous measures have been modifications in one form or another of the scheme of Lehndorff. This plan[4] took account, as a measure of inbreeding, only of the number of generations intervening between that generation in which relatives were bred together, and that generation in which their first common ancestor was found. Thus Lehndorff says:[5]

> I am of opinion, that a horse should only be termed *in-bred,* when in sum total less than four degrees lay between its parents and their common ancestor; in other words, when the children or grandchildren of a stallion or a mare are mated, I call their produce *in-bred;* but this term does not apply to the produce of great-grandchildren of the common ancestor. We must not forget that in the pedigrees of horses the word brother or sister often means half-brother or half-sister, and that here the definition borrowed from the human family connection is not applicable.
>
> As breeding within *moderate relationship* I reckon the mating of stallion and mare that are removed from their common ancestor four, five or six degrees. It is indifferent whether they are on both sides equidistant from, or one of them nearer to the male or female progenitor than the other.

Von Oettingen used a measure exactly the same in principle as this of Lehndorff's. The system of Bruce Low, though somewhat differently stated, comes to essentially the same thing, so far as I am able to determine from abstracts, this author's original writings not having been accessible to me.

All systems based on the number of "free generations" alone do not furnish a precise or reliable measure of the real intensity of inbreeding. The essential reason for this failure, stated baldly, is that they do not take account

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[4] Cf. Lehndorff, G., "Horse-breeding Recollections," Philadelphia, 1887.

[5] *Loc. cit.*, p. 49.

of the composition of the generation to which the "common ancestors" of an inbred pair belong. This can be most clearly shown by comparison of two hypothetical pedigrees. In these pedigrees letters will be used to designate animals.

PEDIGREE TABLE I. (*Hypothetical*)

Alpha	*a*	*c*	*g*	*o*
				p
			h	*t*
				u
		d	*i*	*v*
				w
			j	*x*
				y
	b	*e*	*k*	*z*
				1
			l	2
				3
		f	*m*	*o*
				q
			n	*r*
				s
Ancestral Generation	1	2	3	4

PEDIGREE TABLE II. (*Hypothetical*)

Omega	a_1	c_1	g_1	o_1
				p_1
			h_1	o_1
				p_1
		d_1	i_1	o_1
				p_1
			j_1	o_1
				p_1
	b_1	$_1$	k_1	o_1
				p_1
			l_1	o_1
				p_1
		f_1	m_1	o_1
				p_1
			n_1	o_1
				p_1
Ancestral Generation	1	2	3	4

Now it is plain that in both of these pedigrees the number of "free generations" between the mating of the parents of Alpha and Omega respectively (generation number 1) and this common ancestor—*o* in one case, and o_1 and p_1 in the other case—*is the same,* namely 2. Yet every one would agree that the inbreeding involved in the breeding of Omega is much more intense than that involved in the breeding of Alpha. In the second pedigree it is assumed that there were only two *different* individuals in the fourth ancestral generation. In other words, *all* the individuals in generation 3 of this pedigree II are brothers and sisters, though different animals (*i. e.,* produced, by hypothesis, at successive matings of o_1 and p_1). A condition in considerable degree approaching this is very frequently found in livestock pedigrees. On the other hand in pedigree I all of the individuals of the fourth generation are different and are assumed to be absolutely unrelated, with the single exception of individual o, which appears twice in this generation. The point I think is clear: according to the Lehndorff measure both of these pedigrees show the same degree of inbreeding (free generations $=2$), whereas actually there is a wide difference between the two.

In developing a general measure of the intensity of inbreeding we may well start from the conception set forth in the preceding section, namely that the inbred individual possesses fewer different ancestors than the maximum possible number. Besides this factor account must be taken of the generation or generations in which the reduced number of different ancestors is found, and the extent to which these generations are removed (in the sense of Lehndorff discussed above) from the individual or generation under consideration. In other words the two factors which must be included in a general measure of the intensity of inbreeding are (a) the *amount* of ancestral reduction in successively earlier generations, and (b) the *rate* of this reduction over any specified number of generations.

Both of these demands are met, I think, by taking as a measure of the intensity of inbreeding in any generation the proportionate degree to which the actually existent number of different ancestral individuals fails to reach the maximum possible number, and by specifying the location in the series of the generation under discussion.

This statement is amplified and made more precise in the following propositions.

1. The production of the individual must be the point of departure in any analytical consideration of inbreeding, leading towards its measurement. That is, the question to which one wants an answer is: What degree of inbreeding was involved in the production of this particular animal?

2. It is therefore necessary practically to *start* with the individual and work *backwards* into the ancestry in measuring inbreeding, rather than to start back in the ancestry and work down towards the individual.

3. In the genetic passage from the $n+1$th generation to the nth, or in other words the contribution of the matings of the $n+1$th generation to the total amount of inbreeding involved in the production of an individual, the degree of inbreeding involved will be measured by the expression

$$Z_n = \frac{100(p_{n+1} - q_{n+1})}{p_{n+1}}, \tag{iii}$$

where p_{n+1} denotes the maximum *possible* number of different individuals involved in the matings of the $n+1$ generation, p_{n+1} the *actual* number of different individuals involved in these matings. Z_n may be called a *coefficient of inbreeding*. If the value of Z for successive generations in the ancestral series be plotted to the generation numbers as a base, the points so obtained will form a curve which may be designated as the *curve of inbreeding*.

It will be noted that the coefficient of inbreeding Z is the percentage of the difference between the maximum possible number of ancestors in a given generation, and the actual number realized, in the former. The coefficient may have any value between 0 and 100. When there is no breeding of relatives whatever (that is, in the entire absence of inbreeding) its value for each generation is 0. As the intensity of the inbreeding increases the value of the coefficient rises.

4. The above measure of inbreeding has to do primarily with the *relationship* aspect of the problem. The theoretical bearings of this fact will be discussed in a later section.

5. Since the only possible infallible criterion of relationship between individuals is common ancestry in some *earlier* generation, we are led to the practical rule, in measuring the degree of inbreeding in a pedigree, to regard all different individuals as entirely unrelated until the contrary is proved by the finding of a common ancestor. This no doubt appears at this stage of the discussion as an exceedingly obvious truism. The reader is urged to accept it as such, and hold fast to it, because it will help him over some apparent paradoxes later.

The method of calculating coefficients of inbreeding, and their real significance will be made much clearer by the consideration of illustrative examples of their application. To these we may therefore turn.

THE CALCULATION OF COEFFICIENTS OF INBREEDING

We may first consider some simple hypothetical pedigrees, before attacking the more complicated ones actually realized in stock-breeding.

Illustration I. Continued Brother × Sister Breeding

Let us begin with the most extreme type of inbreeding possible, namely the mating of brother with sister for a series of generations. Pedigree Table III gives the pedigree of an individual so bred.

PEDIGREE TABLE III. (*Hypothetical*)

To Illustrate the Breeding of Brother × Sister, out of Brother × Sister, Continued for a Series of Generations

x	*a*	*c*	*e*	*g*
				h
			f	*g*
				h
		d	*e*	*g*
				h
			f	*g*
				h
	b	*c*	*e*	*g*
				h
			f	*g*
				h
		d	*e*	*g*
				h
			f	*g*
				h
Ancestral Generation	1	2	3	4

Let us now proceed to the calculation of the coefficients of inbreeding Z_0, Z_1, Z_2 and Z_3. For Z_0 we have

$$p=2,$$
$$q=2,$$

whence

$$Z_0 = \frac{100(0)}{2} = 0.$$

In the same way

$$Z_1 = \frac{100(4-2)}{4} = 50.$$

$$Z_2 = \frac{100(8-2)}{8} = 75.$$

$$Z_3 = \frac{100(16-2)}{16} = 87.5.$$

These results may be expressed verbally in the following way: In the last two ancestral generations x is 50 per cent. inbred; in the last three generations it is 75 per cent. inbred; and in the last four generations it is 87.5 per cent. inbred.

This pedigree table and the constants will repay further consideration, since the case is a limiting one. With the table at hand it is possible to grasp a little more clearly the precise meaning of the coefficients of inbreeding. Thus it is seen that what the value of $Z_1=50$ really signifies is that because the individuals a and b were brother and sister the number of different ancestors which x can possibly have in any ancestral generation can not be *more* than 50 per cent. of the total number theoretically possible for the generation. That is, x's sire and dam having been brother and sister means that x can not have had more than 2,048 different great-great-great-great-great-great-great-great-great-grandparents, instead of the possible 4,096. He may have had fewer than 2,048, but $Z_1=50$ tells us that he could not have had more. Similarly $Z_2=75$ indicates that since c and d, the grandsire and grand-dam of x were brother and sister, x can not have in any ancestral generation more than 25 per cent. of the theoretically possible number of ancestors for that generation. And so on for the other values of Z.

In the limiting case of the closest inbreeding possible the successive Z's will have the values given in the following table.

TABLE I

VALUES OF THE SUCCESSIVE COEFFICIENTS OF INBREEDING (Z_0 TO Z_{15}) IN THE CASE OF THE MOST INTENSE INBREEDING POSSIBLE (BROTHER × SISTER OUT OF BROTHER × SISTER CONTINUED)

Coefficient of Inbreeding	Ancestral Generations Included	Numerical Value of Coefficient
Z_0	1	0
Z_1	2	50
Z_2	3	75
Z_3	4	87.5
Z_4	5	93.75
Z_5	6	96.875[6]
Z_6	7	98.4375
Z_7	8	99.21875
Z_8	9	99.609375
Z_9	10	99.8046875
Z_{10}	11	99.90234375
Z_{11}	12	99.951171875
Z_{12}	13	99.9755859375
Z_{13}	14	99.98779296875
Z_{14}	15	99.993896484375
Z_{15}	16	99.9969482421875

From this table it is apparent that while the narrowing or exclusion of the possible different source lines of descent proceeds very rapidly in the first few generations of brother × sister breeding, only relatively little change is made by further generations of this sort of breeding. Thus in seven generations of brother × sister breeding all but about 1.5 per cent. of the potentially different ancestral "blood-lines" will have been eliminated. After 16 generations of this sort of breeding (a number easily attainable in ordinary breeding experiments) an individual so bred can by no chance possess more than 3/1000 of one per cent. of the different lines of ancestral descent which are theoretically possible. This table strongly suggests that if, in an experiment to test the influence of inbreeding, no particular effect is observed during ten gene-

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[6] There is, of course, no further point in the retention of all the decimals in these coefficients than to make plain the law of their formation. In the case of maximum inbreeding here illustrated, the Z's are the successive terms of a series in which any term is equal to the preceding term plus one half the difference between the preceding term and 100, or in which the successive differences are halved.

rations of brother × sister breeding, it is extremely improbable that any effect will be produced by a further continuation of the same method of breeding. If an apparent effect should suddenly appear some time later than the tenth generation the case would need the most critical scrutiny, to determine whether the observed effect had really been due to the inbreeding, rather than to some other unsuspected cause.

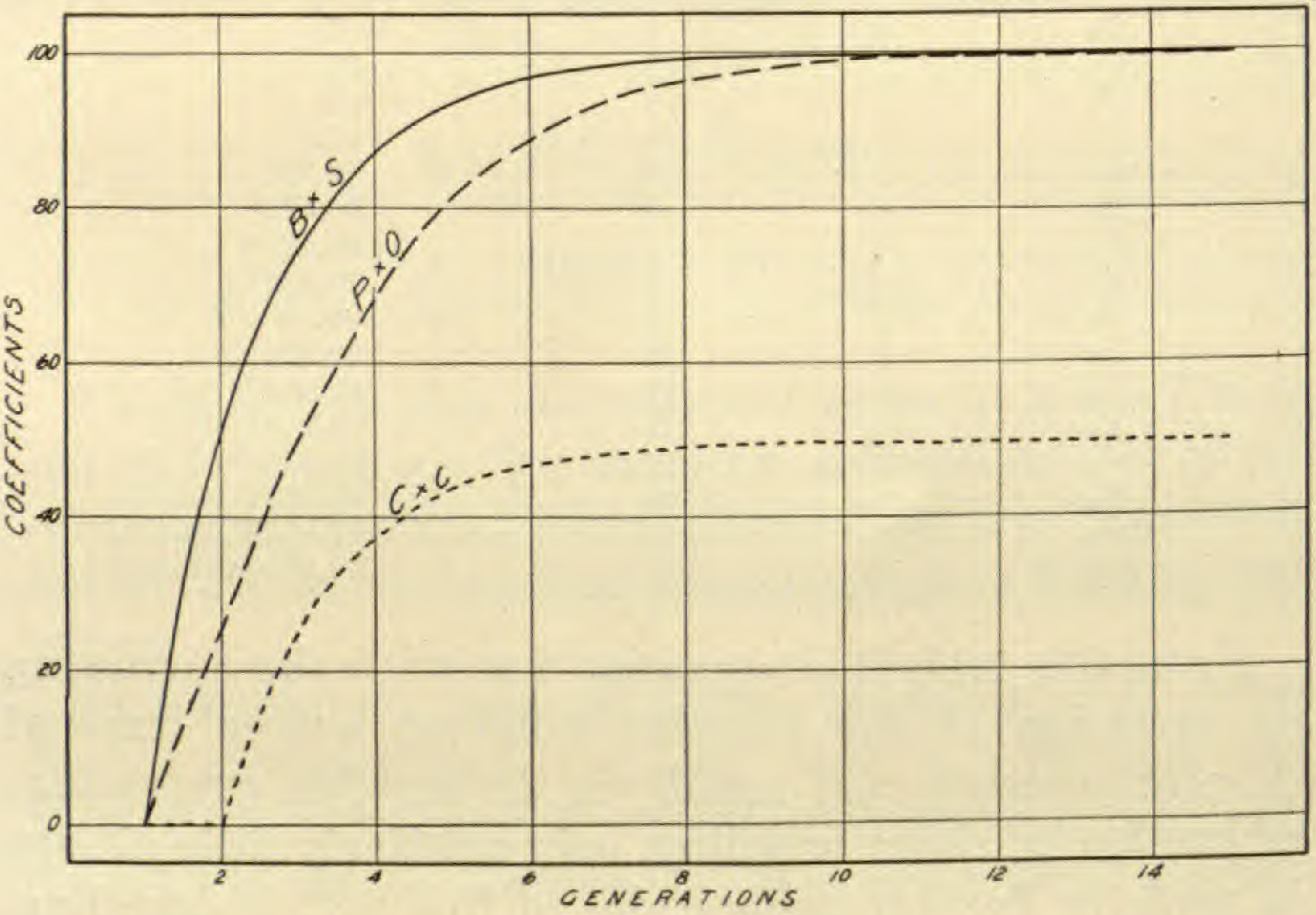

FIG. 1. Curves of inbreeding, showing (*a*) the limiting case of continued brother × sister breeding, wherein the successive coefficients of inbreeding have the maximum values; (*b*) continued parent × offspring mating; and (*c*) continued first-cousin × first-cousin mating.

The values of the Z's in Table I are maxima: No particular coefficient of inbreeding can have a higher value than that given in the table. It is not possible, for example, so to breed any animal (having an obligate bisexual type of reproduction) that its pedigree on analysis will give $Z_3 > 87.5$. If, therefore, the coefficients of Table I are plotted the result will be the maximum limiting *curve* of inbreeding. This curve is shown in Fig. 1.

In all actually realized pedigrees except those in which there has been continued brother × sister breeding the curve of inbreeding found will lie wholly or in part below the maximum curve shown in Fig. 1.

Illustration II. Parent × Offspring Breeding

The next illustration of the application of coefficients of inbreeding will be the general case of back-crossing, that is, the mating of parent × offspring. Such a case is illustrated in the hypothetical pedigree Table IV..

PEDIGREE TABLE IV. (*Hypothetical*)
To Illustrate the Breeding of Parent × Offspring

y	a	d	f	m
				n
			g	f
				l
		e	d	f
				g
			i	d
				o
	b	a	d	f
				g
			e	d
				i
		c	a	d
				e
			k	a
				s
Generation Number	1	2	3	4

Here it will be seen that b, the dam of y, is a daughter of a, who is also the sire of y and that in each preceding generation every daughter is bred back to her sire. Proceeding as before to calculate the coefficients of inbreeding we have, first,

$$Z_0 = \frac{100(2-2)}{2} = 0.$$

In forming the expression for Z_1 we are met by the fact in determining q_{n+1} for generation 2 that the individual a has already appeared once and been counted as a "different" ancestor in generation 1. Therefore it will not be counted a second time in generation 2, and we have

$$Z_1 = \frac{100(4-3)}{4} = 25,$$

and by the same process,

$$Z_2 = \frac{100(8-4)}{8} = 50,$$

$$Z_3 = \frac{100(16-5)}{16} = 68.75,$$

$$Z_4 = \frac{100(32 - 6)}{32} = 81.25,$$

and so forth.

The values of the successive coefficients for parent × offspring breeding for 16 ancestral generations are given in Table II.

TABLE II

VALUES OF THE SUCCESSIVE COEFFICIENTS OF INBREEDING IN THE CASE OF CONTINUED PARENT × OFFSPRING MATING

Coefficient of Inbreeding	Ancestral Generations Included	Numerical Value of Coefficient
Z_0	1	0
Z_1	2	25
Z_2	3	50
Z_3	4	68.75
Z_4	5	81.25
Z_5	6	89.06
Z_6	7	93.75
Z_7	8	96.48
Z_8	9	98.05
Z_9	10	98.93
Z_{10}	11	99.41
Z_{11}	12	99.68
Z_{12}	13	99.83
Z_{13}	14	99.91
Z_{14}	15	99.95
Z_{15}	16	99.97

By comparison of this table with Table I it is evident that while the increase in intensity of inbreeding is not so rapid in the first few ancestral generations by this parent × offspring type of breeding as with the brother × sister type, by the time the tenth ancestral generation is reached the values are for practical purposes the same.

The curve of inbreeding for continued parent × offspring breeding is shown in Fig. 1.

Illustration III. First-Cousin × First-Cousin Breeding

As a third illustration may be taken the case of continued cousin mating. Such breeding represents the next step in decreasing intensity of inbreeding beyond the parent × offspring type.

In this pedigree it will be seen that in each mating the sires of the individuals bred together are brothers. In other words, each individual is mated with its first-cousin.

PEDIGREE TABLE V. (*Hypothetical*)

To Illustrate the Continued Breeding of First-Cousin × First-Cousin

Generation Number	1	2	3	4	5
A	*a*	*c*	*g*	*m*	1[7]
					2
				n	3
					4
			h	*o*	1
					2
				p	5
					6
		e	*i*	*m*	1
					2
				n	7
					8
			j	*q*	1
					2
				r	9
					10
	b	*d*	*g*	*m*	1
					2
				n	11
					12
			h	*s*	1
					2
				t	13
					14
		f	*k*	*m*	1
					2
				n	15
					16
			l	*u*	1
					2
				v	17
					18

The values of the successive coefficients of inbreeding for this case are given in Table III. The calculation of these is carried out in accordance with the same principles as have been illustrated in the previous cases. We have

$$Z_0 = \frac{100(2-2)}{2} = 0,$$

and

$$Z_1 = \frac{100(4-4)}{4} = 0,$$

since in generations 1 and 2 there are two and four *different* ancestors respectively.

$$Z_2 = \frac{100(8-6)}{8} = 25,$$

---

[7] Owing to the limitation of the alphabet resort is had to numbers to designate individuals in this generation.

since in generation 3 the two individuals g and h each appear twice, and by our rule any ancestor is only counted once.

$$Z_3 = \frac{100(16-10)}{16} = 37.5,$$

since in generation 4 the individuals m and n appear four times and are only counted as different ancestors once each.

TABLE III

VALUES OF THE SUCCESSIVE COEFFICIENTS OF INBREEDING IN THE CASE OF CONTINUED FIRST-COUSIN × FIRST-COUSIN MATING

Coefficient of Inbreeding	Ancestral Generations Included	Numerical Value of Coefficient
Z_0	1	0
Z_1	2	0
Z_2	3	25
Z_3	4	37.5
Z_4	5	43.75
Z_5	6	46.88
Z_6	7	48.44
Z_7	8	49.22
Z_8	9	49.61
Z_9	10	49.80
Z_{10}	11	49.90
Z_{11}	12	49.95
Z_{12}	13	49.98
Z_{13}	14	49.988
Z_{14}	15	49.994
Z_{15}	16	49.9969

It will be seen from this table that the upper limit of intensity of inbreeding approached by continued cousin matings is 50 per cent. In general, cousin mating is one half as intense a form of inbreeding as brother × sister mating, with a lag of one generation behind. That is Z_3 for cousin matings is one half as large as Z_2 (not Z_3) for brother × sister matings.

The curve of inbreeding for cousin matings is given in Fig. 1.

Illustration IV. The Pedigree of the Thoroughbred Horse, Postumus

Leaving now the hypothetical cases we may consider some actually realized pedigrees, and measure the degree of inbreeding exhibited. I have chosen as a first case of this sort a very simple one in which there is little inbreeding. This is the pedigree for five ancestral generations of the thoroughbred horse, *Postumus*. This pedigree is given by Bunsow,[8] and is here reproduced without change of arrangement, although the plan used of placing the dam above the sire instead of below is contrary to the general American and continental usage.

PEDIGREE TABLE VI

Showing the Breeding of Postumus

Postumus	Pontoon	Pontillon	Maid of Wye	Euxine	Varna
					King Tom
				×Vedette	×Mrs. Ridgway
					×Voltigeur
			Fernandez	Isola Bella	Isolene
					Stockwell
				Sterling	Whisper
					Oxford
		Orvieto	Napoli	Sunshine	Sunbeam
					Thormanby
				Macaroni	Jocose
					Sweetmeat
			Bend Or	Rouge Rose	Elleen Horne
					×Thormanby
				Doncaster	Marigold
					×Stockwell
	St. Simon	St. Angela	Adeline	Little Fairie	Lacerta
					Hornsea
				Ion	Margaret
					Cain
			King Tom	Pocahontas	Marpena
					Glencoë
				Harkaway	Fanny Dawson filly
					Economist
		Galopin	Flying Duchess	Merope	Velocipede's dam
					Voltaire
				Flying Dutchman	Barbelle
					Boy Middleton
			Vedette	Mrs. Ridgway	Nan Darell
					Birdcatcher
				Voltigeur	Martha Lynn
					×Voltaire
Gen. No.	1	2	3	4	5

In this pedigree every animal that has already appeared in a lower ancestral generation is marked with an "X," indicating that it is to be "counted out," that is, can not be regarded again as a *different* ancestor.

We then have for the successive coefficients of inbreeding the following values:

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[8] Bunsow, R., "Inheritance in Race Horses," *Mendel Journal*, Vol. I, pp. 74–93, 1911.

$$Z_0 = 0,$$

$$Z_1 = \frac{100(4-4)}{4} = 0,$$

$$Z_2 = \frac{100(8-8)}{8} = 0,$$

$$Z_3 = \frac{100(16-15)}{16} = 6.25,$$

$$Z_4 = \frac{100(32-27)}{32} = 15.625.$$

From these results it is possible to make a precise statement as to how much *Postumus* was inbred. In the five ancestral generations, to which the pedigree extends, he was inbred to an extent (15.6 per cent.) which represents approximately three fifths of the intensity of inbreeding involved in once mating first cousins. In other words, if in the first ancestral generation, a mating of first cousins had occurred, and there had been no other mating of relatives whatever, Postumus would in that event have been nearly twice as much inbred as he actually was.

In the first three ancestral generations Postumus was not at all inbred, and in the first four only 6.25 per cent., an intensity equal to about one fourth of that involved in once mating parent × offspring.

These figures are definite pedigree constants for the horse Postumus, which are directly comparable with similar constants for other animals.

Illustration V. The Pedigree of the Brown Swiss Bull, Saxton (2668)

We may next consider a more complex case, in which the intensity of inbreeding is greater, and in which the calculation of the coefficients is not so simple a matter because of the length of the pedigree. On this account the method of computation will be illustrated in detail. As before the "X" with an animal's name indicates that it has appeared at least once before in the lower ancestral generations and can not therefore be counted again. The pedigree of Saxton, a bull of the Brown-Swiss breed of cattle, is given as Pedigree Tables VII–XVI.

PEDIGREE TABLE VII

Showing the Breeding of Saxton

Gen. No.	1	2	3	4	5	6
Saxton	Ole Bull	Otis	Burton	Shamrock	Humbert	Jethro. Go to pedigree Table VIII.
						Ivy. Go to pedigree Table IX.
					Hannah F	● Elmo
						● Hannah
				Norman	Dermot Tell	Lester Tell. Go to pedigree Table X.
						Mildred. Go to pedigree Table XI.
					Rena	Increase Tell. Go to pedigree Table XII.
						Hester. Go to pedigree Table XIII.
			Salome	● Hamlet	×Marshall Jewell	× ——
						×Muotta
					×Suecica 2nd	× ——
						×Suecica
				Hannah	Frederick Schiller (Imp.)	——
						——
					Frances	Albert Tell (Imported).
						Geneva (Imported).
		Winona Rice	Nate Rice	Eddy Bonaparte	The Grove	● Bonaparte (Imported).
						Blanche (Imported)
					Alis	Nig Tell. Go to pedigree Table XIV.
						Elwerdess (Imported)
				Pattie	● The Grove	×Bonaparte
						×Blanche
					Rigi (Imported)	——
						——
			Lillian Rice	Burleigh	Bonaparte (Imported)	——
						——
					Schoni (Imported)	——
						——
				Florine	Philip Tell	Charlie Tell. Go to pedigree Table XV.
						Jungfrau. Go to pedigree Table XVI.
					Fraülein	Wm. Tell (Imported).
						Gretchen (Imported).

PEDIGREE TABLE VII—*Continued*

Gen. No.	1	2	3	4	5	6
Saxton	Sheba 2d (Dam of Saxton)	Elmo	Gold Dust (Imported in dam)	—	—	— —
					—	— —
				Brunnen (Imported)	—	— —
					—	— —
			Muotta (Imported)	—	—	— —
					—	— —
				—	—	— —
					—	— —
		Sheba	Hamlet	Marshall Jewell (Imported in dam)	—	— —
					● Muotta	× ×
				Suecica 2nd (Imported in dam)	—	— —
					Suecica (Imported)	— —
			Selma (Imported)	—	—	— —
					—	— —
				—	—	— —
					—	— —

Pedigree Table VIII—*Continuation of* VII

Jethro	● Gold Dust	× —	× —
			× —
		×Brunnen	× —
			× —
	● Hannah	×Frederick Schiller	× —
			× —
		×Frances	×Albert Tell (Imp.)
			×Geneva (Imp.)
Gen. No.	7	8	9

Pedigree Table IX—*Continuation of* VII

Ivy	● Marshall Jewell	× —	× —
			× —
		×Muotta	× —
			× —
	Lola	David G. Tell	● Albert Tell (Imp.)
			● Geneva (Imp.)
		● Minnie	×Wm. Tell (Imp.)
			×Gretchen (Imp.)
Gen. No.	7	8	9

Pedigree Table X—*Continuation of* VII

Lester Tell	Conrad Tell	● Increase Tell	×Albert Tell	× —
				× —
			×Brinlie (Imported)	× —
				× —
		Josie	● Wm. Tell, Jr.	×Wm. Tell (Imp.)
				×Zurich (Imp.)
			Myra	● Wm. Tell (Imp.)
				● Geneva (Imp.)
	Ada	Forest Tell	● Wm. Tell	× —
				× —
			Lissa (Imported)	—
				—
		Cowslip	● Robert Tell	×Wm. Tell (Imp.)
				×Brinlie (Imp.)
			Estelle	● Wm. Tell (Imp.)
				● Lissa (Imp.)
Gen. No.	7	8	9	10

In dealing with this pedigree it will be assumed, in the absence of information on the point and the impossibility of acquiring any, that any imported animal was not inbred to any degree whatsoever. This is probably not often strictly true, but, on the other hand, some assumption must be made, and this puts all individuals on an equal footing. It is in accord with the principle laid down earlier (p. 585) that in pedigree analysis all individuals

Pedigree Table XI—*Continuation of* VII

Mildred	George Tell	● Albert Tell	× —	× —
				× —
			× —	× —
				× —
		● Ethel	×Wm. Tell	× —
				× —
			×Lucerne (Imp.)	× —
				× —
	Metta	● Wm. Tell, Jr.	×Wm. Tell	× —
				× —
			×Zurich (Imp.)	× —
				× —
		Daffodil	● Robert Tell	×Wm. Tell (Imp.)
				×Brinlie (Imp.)
			● Estelle	×Wm. Tell (Imp.)
				×Lissa (Imp.)
Gen. No.	7	8	9	10

Pedigree Table XII—*Continuation of* VII

Increase Tell	● Albert Tell (Imp.)		
	Brinlie (Imp.)		
Gen. No.	7	8	9

Pedigree Table XIII—*Continuation of* VII

Hester	Henry Clark Tell	● Wm. Tell	× —
			× —
		Verona (Imported in dam)	—
			● Brinlie Imp.
	Minnie	● Wm. Tell	× —
			× —
		● Gretchen	× —
			× —
Gen. No.	7	8	9

must be considered to be unrelated until the contrary is proven by the evidence of their ancestry. After all, the only thing we can possibly measure is the inbreeding shown in the *recorded* pedigree. All that has happened prior to the beginning of the record must be a matter of assumption. The same assumption should, however, be made for all cases. What this assumption really means practically is that, in all cases of analysis of actual pedigrees, which are bound after a time to come to an end, the values of the coefficients of inbreeding obtained are *lower limiting values*. They signify that the intensity of inbreeding in a particular case could not have been *less*

PEDIGREE TABLE XIV—*Continuation of VII*

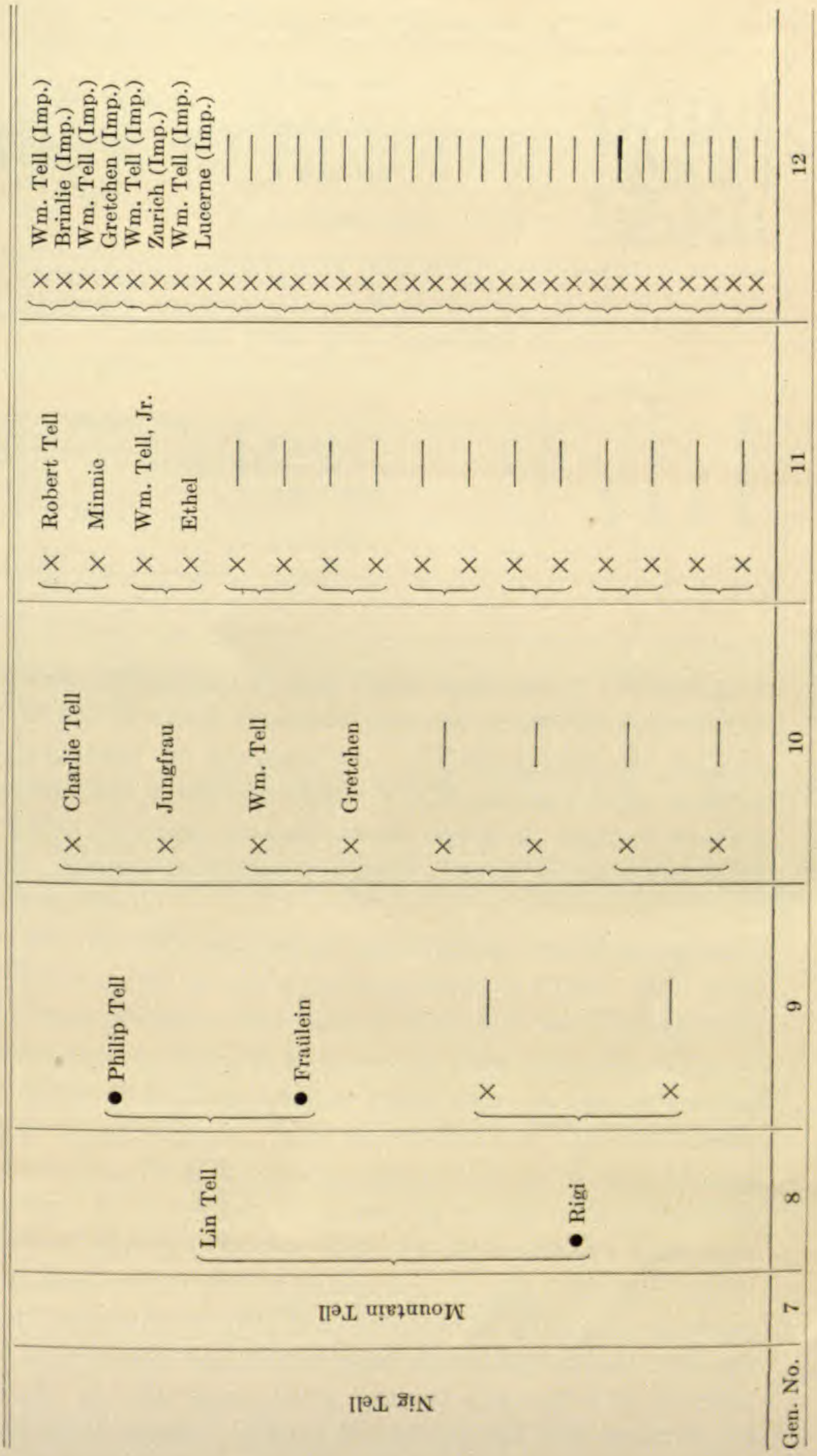
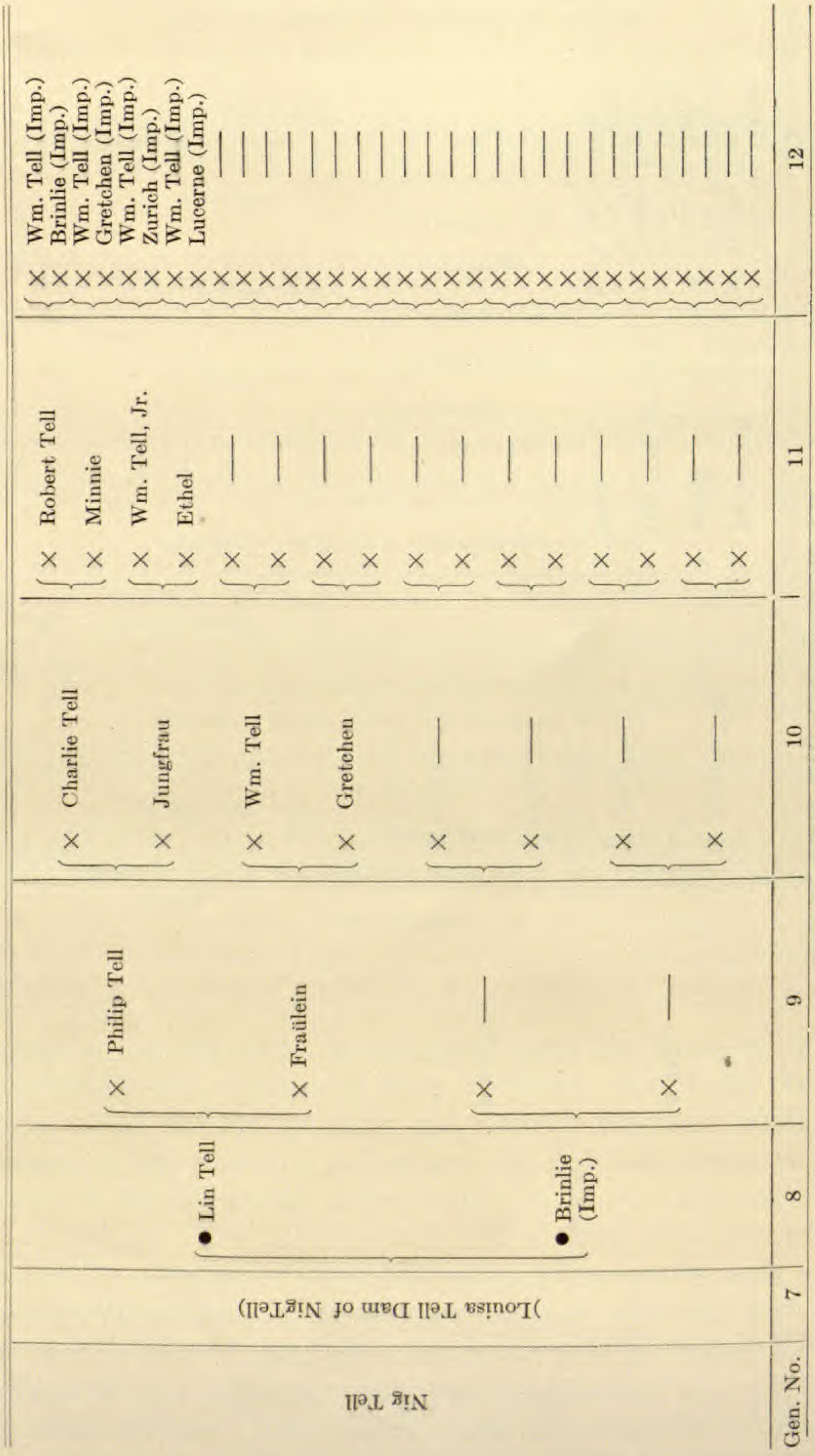


TABLE XIV—*Continued*



PEDIGREE TABLE XVI—*Continuation of* VII

Jungfrau	Wm. Tell, Jr.	● Wm. Tell	×	—
			×	—
		Zurich (Imp.)		—
				—
	Ethel	● Wm. Tell	×	—
			×	—
		Lucerne (Imp.)		—
				—
Gen. No.	7	8	9	

PEDIGREE TABLE XV—*Continuation of* VII

Charles Tell	Robert Tell	● Wm. Tell	×	—
			×	—
		● Brinlie	×	—
			×	—
	● Minnie	×Wm. Tell	×	—
			×	—
		×Gretchen	×	—
			×	—
Gen. No.	7	8	9	

than that indicated; it may have been more. Whether it was or not is not a question open to scientific determination but only to speculation. Furthermore, of course, experimental breeding with "wild" animals is on exactly the same footing as herd-book work in regard to this point. Every experiment must *begin* somewhere with unknown stock.

In the twelfth ancestral generation the theoretically possible number of different ancestors is 4,096. In a relatively long pedigree like that of Saxton it would obviously be an extremely tedious business to determine the value of q by direct counting, as has been done in the preceding simpler illustrations. The calculation of the coefficients of inbreeding may be greatly simplified in the case of long pedigrees by a system of counting which makes the *line of descent* the unit rather than the individual. This system is used in the above pedigree. While each individual animal which is eliminated because of previous appearances in a lower ancestral generation is marked with an X, those at the apex of a line of descent are marked with a solid circle. These latter are all that need to be counted directly. Their elimination automatically eliminates their own ancestors. Thus the bull Hamlet first appears in the third ancestral generation as the sire of Sheba. He next appears (here marked with a solid circle) in the fourth generation as the sire of Salome. He will, by the general rule for coefficients of inbreeding, not be counted as a "different" ancestor in the fourth generation. But this automatically eliminates his two parents in the fifth ancestral generation, his four grandparents in

TABLE IV

WORKING TABLE USED IN CALCULATING THE COEFFICIENTS OF INBREEDING FOR PEDIGREE TABLE VII

Animal	Ancestral Generation								
	4	5	6	7	8	9	10	11	12
Hamlet	1	2	4	8	16	32	64	128	256
The Grove		1	2	4	8	16	32	64	128
Muotta		1	2	4	8	16	32	64	128
Elmo			1	2	4	8	16	32	64
Hannah			1	2	4	8	16	32	64
Bonaparte			1	2	4	8	16	32	64
Gold Dust				1	2	4	8	16	32
Hannah				1	2	4	8	16	32
Marshall Jewell				1	2	4	8	16	32
Albert Tell				1	2	4	8	16	32
Minnie				1	2	4	8	16	32
Minnie					1	2	4	8	16
Increase Tell					1	2	4	8	16
Albert Tell					1	2	4	8	16
Ethel					1	2	4	8	16
Wm. Tell, Jr.					1	2	4	8	16
Wm. Tell					1	2	4	8	16
Wm. Tell					1	2	4	8	16
Gretchen					1	2	4	8	16
Rigi					1	2	4	8	16
Lin Tell					1	2	4	8	16
Brinlie					1	2	4	8	16
Wm. Tell					1	2	4	8	16
Brinlie					1	2	4	8	16
Wm. Tell					1	2	4	8	16
Wm. Tell					1	2	4	8	16
Albert Tell						1	2	4	8
Geneva						1	2	4	8
Wm. Tell, Jr.						1	2	4	8
Wm. Tell						1	2	4	8
Robert Tell						1	2	4	8
Robert Tell						1	2	4	8
Estelle						1	2	4	8
Brinlie						1	2	4	8
Philip Tell						1	2	4	8
Fraulein						1	2	4	8
Wm. Tell							1	2	4
Geneva							1	2	4
Wm. Tell							1	2	4
Lissa							1	2	4
Totals	1	4	11	27	69	148	300	600	1200

the sixth generation, and so on until in the twelfth generation 256 ancestors of Hamlet will be so eliminated. The same consideration applies in every other like case.

Practically then the method of dealing with a pedigree of this sort is first to go through and indicate in a distinctive way every *primary*[9] reappearance of individuals. Then form a table on the plan of Table IV, the character of which is so obvious as not to need detailed explanation.

This table is to be read in the following way: Because of the reappearance of Hamlet in the fourth ancestral generation Saxton has 1 fewer ancestors in that generation than he would have had in the entire absence of inbreeding; 2 fewer in the fifth generation and so on. The totals of the columns of this table are the values, for each generation, of

$$p_{n+1} - q_{n+1}$$

in (iii). These totals, multiplied by 100, have then merely to be divided by p_{n+1} in order to obtain the successive Z's. The whole operation may be very quickly carried out. It is not in fact necessary to fill out the whole of the later columns of the table, the entries may be cumulated.

For the present pedigree we have

$$\begin{aligned} Z_0 &= 0, \text{ as always,}^{10} \\ Z_1 &= 0, \\ Z_2 &= 0, \\ Z_3 &= 6.25 \text{ per cent.}, \\ Z_4 &= 400/32 = 12.50, \\ Z_5 &= 1{,}100/64 = 17.19, \\ Z_6 &= 2{,}700/128 = 21.09, \end{aligned}$$

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[9] By "primary" reappearance in the pedigree is meant a reappearance as the sire or dam of an individual which has not itself appeared before in the lower ancestral generations. Thus Wm. Tell makes a *primary* reappearance in the tenth ancestral generation as the sire of Myra, a cow which is not found in any generation below the ninth.

[10] The apparent paradox implied in the fact that Z_0 must always be zero, or, in other words, that in the first ancestral generation, considered *alone*, there is no inbreeding will be cleared up, if it strikes the reader as paradoxical, by a reconsideration of the general principle numbered 5 on p. 585. The point, of course, is that it is impossible to say whether the parents are or are not related to one another until something is known of *their* parentage, or, in other words, until a *second* ancestral generation is considered.

$$\begin{aligned} Z_7 &= 6{,}900/256 = 26.95, \\ Z_8 &= 14{,}800/512 = 28.91, \\ Z_9 &= 30{,}000/1{,}024 = 29.30, \\ Z_{10} &= 29.30, \\ Z_{11} &= 29.30. \end{aligned}$$

From these values it is seen that, so far as the ancestry is known the bull Saxton is 29.3 per cent. inbred. The curve of inbreeding, Fig. 2, shows that this intensity was gradually and steadily attained, by slight additional inbreeding in each generation. In the end (always within the limitation of the *known* ancestry) Saxton is some 4 per cent. more closely inbred than he would have been had his dam been his sire's daughter, without other inbreeding in the ancestry. In the first five ancestral generations Saxton is less intensely inbred than Postumus.

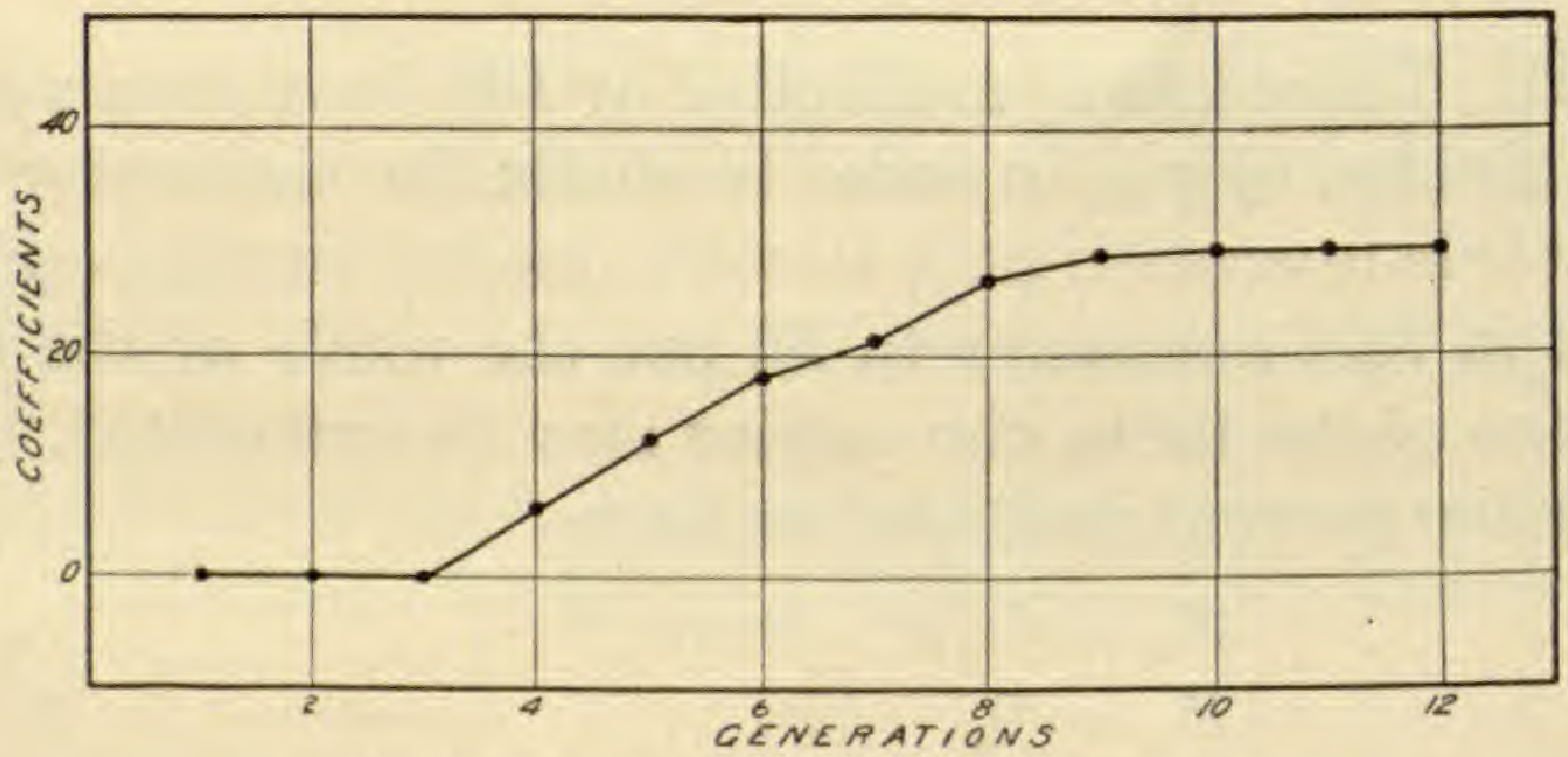

FIG. 2. Curve of inbreeding of the bull Saxton.

COEFFICIENTS OF INBREEDING AND THE GAMETIC CONSTITUTION OF THE INDIVIDUAL

Up to this point the whole discussion has looked at the problem of inbreeding solely from the standpoint of the kinship of mated individuals. Nothing whatever has been said about the germinal make-up of the individuals. This method of treatment was not accidental, or due to any oversight of so important a phase of the problem, but was deliberately planned to bring out clearly that the development of the coefficient of inbreeding was quite independent of any theory of the mechanism of the hereditary process. These coefficients measure a real and definite attribute of a pedigree.

But is the thing measured worth measuring? Does any significance attach to knowing how much an animal is inbred in the kinship sense? I think there is no doubt that every breeder of the larger domestic animals would answer this question in the affirmative. The question, however, demands careful consideration, because of the suggestion recently advanced that the effect of inbreeding, if there be any, depends entirely upon the nature of the combinations of hereditary units (genes) formed. Thus, for example, we have the suggestion of Bruce[11] to the effect that the vigor of the individual increases as the number of dominant elements in its hereditary make-up increases, while an increase of recessive elements connotes a decrease in physiological vigor. A thorough and far-reaching discussion of the problem of the relation between the gametic constitution of the individual and its physiological characteristics is to be found in the very valuable paper by East and Hayes[12] on heterozygosis. The most significant conclusions of that paper in the present connection are these:[13]

> Stimulus to development is greater when certain, or possibly all, characters are in the heterozygous condition than when they are in a homozygous condition.
>
> This stimulus to development is cumulative up to a limiting point and varies directly with the number of heterozygous factors in the organism, although it is recognized that some of the factors may have a more powerful action than others.

These conclusions appear to be supported beyond any chance of doubt or question, for certain characters of plants subjected to self-fertilization, by the experimental evidence set forth in the paper. Inbreeding tends, according to these authors, to isolate homozygous strains "which lack the physiological vigor due to heterozygosity. Decrease in vigor due to inbreeding lessens with decrease of heterozygosity and vanishes with the isolation of a completely homozygous strain. Moreover, these homo-

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[11] *Science*, N. S., Vol. 32, pp. 627–628, 1910.

[12] East, E. M., and Hayes, H. K., "Heterozygosis in Evolution and in Plant Breeding," U. S. Dept. Agr., Bur. Plant Ind. Bulletin No. 243, pp. 1–58, 1912.

[13] *Loc. cit.*, p. 8.

zygous strains can be quite different from each other in actual inherent vigor. . . . Thus we see the true explanation of the apparent degeneration that so many observers have attributed to inbreeding per se'' (p. 37).

As has been said the experimental data of East and Hayes are derived solely from the results of self-fertilizing plants. Self-fertilization is in one sense the closest of all possible forms of inbreeding (since $q_{n+1}=1$), but it involves at least one difference *in principle* from the closest inbreeding which it is possible to accomplish in obligate bisexual forms. This difference is in the fact that while, on the one hand, if a population is subjected to self-fertilization generation after generation the proportionate number of pure homozygotes in the population automatically increases,[14] *there is,* on the other hand, *absolutely no such automatic increase in the proportion of homozygotes necessarily following any other sort of inbreeding except self-fertilization.*

The proportion of homozygotes can only be increased during continued inbreeding other than by self-fertilization, *if there is at the same time a continued selection* (*assortative mating*) *of gametically like individuals.*

While this point seems to have been quite generally overlooked the proof of these above statements is very simple, and anyone can work it out for himself. It follows, indeed, directly from Pearson's[15] demonstration that the individuals of the segregating generation, if they breed at random *inter se,* will ''continue to reproduce themselves in the same proportion as a stable population.''[16] Pearson, at the conclusion of his analytical proof, says: ''It is thus clear that the apparent want of stability in a Mendelian population, the continued segregation and ultimate disappearance of the heterozygotes, *is solely a*

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[14] As has been shown incidentally by East and Hayes (*loc. cit.*), and in a very clear and detailed manner by Jennings (AMER. NAT., Vol. XLVI, pp. 487–491, 1912).

[15] Pearson, K., *Phil. Trans. Roy. Soc.* (A), Vol. 203, pp. 59 and 60, 1904.

[16] G. H. Hardy (*Science,* N. S., Vol. XXVIII, pp. 49–50, 1908) has given a proof of this same point. Cf. also Spillman (*ibid.,* Vol. XXVIII, pp. 252–254, 1908).

result of self-fertilization;[17] with random cross-fertilization there is no disappearance of any class whatever in the offspring of the hybrids, but each class continues to be reproduced in the same proportion." This is exactly the point of distinction made above between self-fertilization and all other forms of inbreeding.

The objection will at once be raised that inbreeding is not "random cross-fertilization." But *gametically* it *is,* unless prevented from so being by some sort of associative mating on a gametic basis. As I have shown in an earlier section the most general form of the concept of inbreeding possible is that of the diminished number of different actual ancestors in proportion to the maximum number possible. But surely the *existence* of relatively few ancestors in itself can involve no necessary implication as to the gametic constitution of those ancestors, so far as concerns homozygosis or heterozygosis.

Analytically the proof is as follows: Let us start with the condition of complete heterozygosis, and consider what will be the result of the closest possible inbreeding (aside from self-fertilization), namely the continued breeding of brother × sister, in a population all the individuals of which are heterozygous with reference to one alternative character pair A and a, these characters being, by hypothesis, not sex-linked. All the individuals will then have the constitution Aa. This will be true of all males and all females whether they stand in the relation to each other of brother and sister or not. Let all matings be of the brother × sister type. The offspring of the next generation will be in no wise affected by this fact, of course, but only by the constitution of the individuals mated. We shall then have the population of *male* progeny constituted as follows:

$$Aa \times Aa = \left\{ \begin{matrix} AA \\ Aa \\ aA \\ aa \end{matrix} \right\} \text{males.}$$

The population of *female* progeny will evidently exhibit exactly the same distribution, namely

---

[17] My italics, R. P.

$$Aa \times Aa = \left\{\begin{matrix} AA \\ Aa \\ aA \\ aa \end{matrix}\right\} \text{females.}$$

Now since the above expressions give not only the probable distributions of the characters in the whole progeny population, *but also the probable distribution of these characters within any single family,* it necessarily implies that the constitution of the sister of any male is equally likely to be any one of the four possible combinations. Or, in other words,

The constitution of any particular sister of any particular AA ♂ is equally likely to be either AA, or Aa, or aA, or aa.

The constitution of any particular sister of any particular Aa (or aA) ♂ is equally likely to be either AA, or Aa, or aA, or aa.

The constitution of any particular sister of any particular aa ♂ is equally likely to be either AA, or Aa, or aA, or aa.

This clearly means that the progeny of the next generation produced, by hypothesis, from the mating of brothers × sisters of this generation will be gametically such a progeny as it produced by mating at random a male population of the constitution

$$AA + 2Aa + aa$$

with a female population of the same constitution, namely

$$AA + 2Aa + aa.$$

But, as Pearson[18] first showed, this results in a progeny

$$16AA + 32Aa + 16aa.$$

There is *no* increase in the proportion of homozygotes, which was the point to be proved. Of course the same reasoning obtains in regard to the next and any number of other generations. In other words the proof is general and complete that *no increase of the proportion of homozygotes in the population follows inbreeding save under one or the other of two special conditions,* viz.

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[18] *Loc. cit.*

(*a*) *Continued self-fertilization.*

(*b*) *Some form of gametic assortative mating which increases the natural probability of like gametes uniting to form zygotes.*

Really, of course, (*a*) is only one special form of (*b*). Not only is self-fertilization the closest sort of inbreeding possible when conceived in the sense of the idea of inbreeding defined and developed in this paper, but also it is necessarily the most extreme form of *homogamy* possible. No other kind of inbreeding is necessarily homogamic. It of course may be, and in actual practise very often is homogamic, but to make it so *selection* of some sort is necessary.

The above proofs deal with but one character pair, *A, a*. By induction the proof could be extended to any number of such pairs. There is a point which needs to be kept in mind here, however. This is that the whole reasoning applies only to such genetic differences as are left in the strain after the operation of inbreeding. As will be shown presently the number of original genetic differences in a stock is reduced by inbreeding in a manner which is precisely measured by the coefficients here proposed.[19] But there is no tendency for continued inbreeding to increase, the proportion of homozygotes, *with respect to those characters in regard to which there are genetic differences left after any particular inbreeding operation.* Further it should be understood that the elimination of genetic differences from a strain is not through homozygosis, but by the dropping out entirely from the network of descent of individuals which potentially may bear such differences.

The above discussion makes it evident that there is a fundamental distinction between inbreeding in general and the special case of self-fertilization. Before leaving this phase of the matter it seems desirable to discuss in a little more detail certain terminological usages of workers in the field of plant breeding together with their

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[19] See p. 612 *infra*.

implications.[20] The custom has grown up (notably in the work of Shull and East) of using the term "inbreeding" when self-fertilization is really meant. I think it would be difficult, in view of the considerations already set forth in detail, to justify this usage on general grounds. In any event it is clear that when the term inbreeding is used in the sense of self-fertilization it is not used in its ordinary sense. The plant-breeder rarely carries out a mating which is *strictly* comparable with the matings which the animal breeder makes when he inbreeds. The closest inbreeding possible with animals is the continued mating of brother and sister. How often does the plant-breeder make a mating which is *objectively* exactly this? It is assumed, specifically and implicitly, by the plant-breeder that his method of inbreeding by self-fertilization is *equivalent* to methods of inbreeding practised in animals. On the basis of that assumption he compares the results in the two cases. Can such a comparison be regarded as a strictly just one, until it has in fact been proven to be so by concrete evidence? I think it can not, because it rests on an assumption which is not only unproven, but which, as I have endeavored to show, is contrary to fact.

On just this ground, it seems to me, the section of the paper of East and Hayes devoted to an "Extension of the Conclusions to the Animal Kingdom" is weakened. From this section I have been unable to understand precisely what the concept in the minds of these authors as to inbreeding in animals really is. They nowhere sharply define their concept of inbreeding. Throughout the portion of the paper dealing with plants it appears

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[20] In taking the paper of East and Hayes as the text for the following discussion there is not the slightest implication of a desire to criticize that most excellent piece of work in general. In the writer's opinion it must be regarded as the most fundamental and enlightening investigation on one particular phase of the problem of inbreeding which has yet appeared. Upon the experimental work and so much of the conclusions as directly relate to the actual experiments I have no criticism whatever to make. The only point in regard to which the paper seems to me possibly open to criticism is the treatment of the problem of inbreeding in animals. Even here it is possible that I have not correctly understood the authors' position,

clearly enough that *practically* they make inbreeding synonymous with self-fertilization. But here it is not so clear. The discussion in the first two paragraphs on p. 41 of the paper seem to me to indicate that in animals East and Hayes would make homozygosity the criterion of inbreeding. Thus they say:

> But let us confine the discussion to the lower animals. If this is done there are two things to consider, the closeness of matings and their result. The statement is often made that self-fertilization in plants is a much closer sexual relationship than can obtain in bisexual animals. With a germ-to-germ transmission conception of heredity it is doubtful if this is true. Thus it is perfectly clear that it is not kinship of the organisms furnishing the sex cells that determines the closeness of the mating, but the similarity of the constitution of the cells themselves.
>
> On this account the statement must be made very emphatic that investigations such as studies of cousin marriages in the human race amount to nothing. A cousin marriage may be a wide cross, it may be very narrow.

But surely to make homozygosity, either of mated individuals or of progeny, a *criterion* of inbreeding is an untenable position. It is the easiest of matters to do either of the following things:

(*a*) To produce homozygous offspring from the mating of heterozygous parents (one half of all the offspring of such parents will be homozygous).

(*b*) To produce heterozygous offspring from the continued mating of brother × sister.

(*c*) To produce homozygous offspring in any numbers, indeed to found and perpetuate a strain purely homozygous with reference to any desired character or characters, without ever mating together even distantly related individuals, not to mention brother and sister.

If all of these things are possible, as they certainly are, what becomes of any attempt to make homozygosity a criterion of inbreeding? All *effects* hitherto attributed to inbreeding may conceivably be due to homozygosity. I am sure, however, that even East and Hayes themselves would not contend that this had been proven experimentally for animals. But even granting this to be so it

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but if so no harm will be done by a further clarifying discussion of so important a problem.

would not mean that the mating of brother and sister was not inbreeding, or that it was the equivalent of self-fertilization.

The position of East and Hayes, as indicated in the quotations given, seems to me to amount to a proposition to throw away entirely as meaningless all kinship elements in genetic descent. Is this not a bit premature? It is true that "a cousin marriage may be a wide cross, it may be very narrow." But does this fact justify from the standpoint of experimental science, and in the present state of knowledge, the generalization of the preceding sentence: "the statement must be made very emphatic that investigations such as studies of cousin marriages in the human race amount to nothing?" Is not the real task of science here to investigate and compare cousin marriages which are wide crosses and cousin marriages which are narrow ones? In other words, there would appear to be *two* variables here, not one. I can not regard the results of East and Hayes, important as they are, as justifying the closure of a field of experimental science in which as yet very little has been done.

Returning now to the main problem it may be inquired: What, if any, is the relation of the coefficients of inbreeding to zygotic constitution? Do the coefficients tell us anything regarding this matter? A little consideration shows that they do. The successive coefficients of inbreeding indicate the rate and degree to which the *possible* number of *different* heredity unit factors present in the ancestry is subsequently reduced as a result of inbreeding. They give no indication, as has already appeared, of the condition in which the *remaining* factors are present (*i. e.,* whether in homozygous or heterozygous condition). The meaning here will be clear if a concrete example is considered. When one brother and sister mating is made 50 per cent. of the maximum possible number of different ancestors is eliminated. It is at least readily conceivable, if indeed it can not be said to be highly probable, that no two individuals among higher animals and plants are *exactly* alike in zygotic constitution when *all* hereditary characters are taken into account. This means, in last analysis, that each individual must differ from every other by at least one unit factor, possibly more. Once mating of brother and sister will diminish the number of such differences by 50 per cent. from what it would have been had no such mating occurred. The number of homozygous individuals *with respect to the hereditary differences remaining*, however, will not increase. This is practically equivalent to saying that while self-fertilization increases the proportion of *individuals* homozygous with reference to all characters, the closest inbreeding other than self-fertilization, if continued, increases the proportion of *characters* with respect to which all individuals are homozygous. Then while both processes tend towards uniformity in the progeny, it is a different kind of uniformity obtained in a different way, in the one case from what it is in the other.

While in the above discussion only brother × sister mating is mentioned it is clear that the same reasoning applies regarding the meaning of the coefficients of inbreeding in all other types of mating.

There are other theoretical relations of inbreeding coefficients which are of interest, but to discuss them in detail here would take us altogether too far afield in the analytical side of determinantal inheritance theories.

CONCLUDING REMARKS

In this paper has been presented a general method of measuring the intensity or degree of the inbreeding practised in any particular case. The method proposed is shown to be perfectly general. It is based on no assumption whatever as to the nature of the hereditary process. On the contrary, it is founded on the most completely logical and comprehensive definition of the concept of inbreeding that it seems possible to formulate. This is, in simplest form, that the fundamental objective criterion which distinguishes an inbred individual from one not inbred is that the former has fewer different ancestors than the latter. It is believed that the proposed coefficients of inbreeding may be made extremely useful in studies of the problem of the effect of inbreeding, whether in relation to its purely theoretical aspects, or in the practical fields of stock-breeding and eugenics. In discussing the relation of the proposed coefficients of inbreeding to the zygotic constitution of individuals it is shown that the common assumption, that (*a*) self-fertilization, and (*b*) the closest inbreeding possible with obligate bisexual organisms (brother × sister breeding), are equivalent processes, is not well founded in fact. The automatic increase of the proportion of homozygotes which necessarily follows continued self-fertilization does not necessarily follow inbreeding of any other sort. Inbreeding of any other type than self-fertilization, unless accompanied by selection, does not change the proportion of homozygotes and heterozygotes (with reference to any possible genetic differences) in the progeny populations. Inbreeding reduces the number of different hereditary factors in the stock.

THE INHERITANCE OF COAT COLOR IN HORSES

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In May, 1912, I published a paper on "The Inheritance of Coat Color in Horses." It was based on a study of the American saddle horse. I knew at the time of my investigation that A. H. Sturtevant, of Columbia University, N. Y., had in the hands of the printer a manuscript which gave a summary of all papers published to date on the subject. It was my agreement with him, made at Cold Spring Harbor, N. Y., in 1911, that when his paper was published I was to draw on its material for another summary of the problem involved. Sturtevant's paper, "A Critical Examination of Recent Studies on Colour Inheritance in Horses," was published in the *Journal of Genetics,* Vol. II, No. 1, Cambridge, England.

Sturtevant had published, August, 1910, in the *Biological Bulletin,* his study of the "Inheritance of Color in the American Harness Horse." Hurst, of England, had based his conclusions on a study of the English thoroughbreds. Wilson had tabulated the color of the Shire, Clydesdale and thoroughbreds; while Harper had given his attention to the French percherons. To these five breeds I am now able to add the records of the saddle horse. It is my purpose to combine the figures and draw some conclusions from them.

My apology, if one be necessary, for devoting so much time to the color of the horse is, that this is only a part of a larger study, the determination of the unit characters of the horse. I hold that we can make poor progress in this larger work until we have solved the most obvious ones of these characters. If there is a law governing the transmission of color, may we not infer that a law of somewhat like nature will govern the transmission of the more essential qualities of the horse? If it can be proved that colors are unit characters and their inheritance obeys the Mendelian Law of dominants and recessives, I believe one very important step will have been taken to solve the whole problem of breeding horses.

This problem of breeding horses is a very large one. No other animal is quite so valuable as the horse. Immense sums of money are invested in farms and studs for his production. The value of the horses themselves mount up to over a thousand million of dollars. In number the horses in this country are over twenty million. The large farmers may have automobiles, engines and other mechanical devices, but they have horses and use them in large quantities. The small farmer's most valuable possession is the faithful family horse. Yet, how little is known about the scientific breeding of this valuable animal. Hogs and cattle we are producing to order, but the production of the horse is still a haphazard business. I believe that any effort that will aid the breeder in producing better horses will be an effort well spent.

In going through the American Saddle-Horse Register I secured the color in 3,913 matings, which involved the color of 11,739 horses. To these numbers I am now able to add from Sturtevant's tables 8,464 matings, giving a total of 12,377 matings or the color of 37,131 horses. This number is sufficiently large, it seems to me, to enable proper deductions to be drawn, unless it is in the case of the rare colors.

The tabulated matings and the resulting foals are:

Chestnut × Chestnut

Breed	Chestnut	Black	Brown	Bay	Authority
Thoroughbred......	1095	9 (bay or brown)			Hurst
Shire.............	44	1	1	5	Wilson
Trotter...........	69	0	0	0	Sturtevant
Saddle............	224	0	0	0	Anderson
Total...........	1432 99%	16 not chestnut 1%			

Chestnut × Black

Saddle............	77 32%	52 22%	13 6%	98 40%	Anderson

Chestnut × Brown

Saddle	44 24%	24 12%	23 12%	102 52%	Anderson

Chestnut × Bay

Saddle	318 34%	36 4%	27 3%	536 59%	Anderson

Black × Black

Percheron	0	49	2 not black		Harper
Shire	2	39	0	3	Wilson
Clydesdale	0	36	2	0	Wilson
Trotter	2	34	4	2	Sturtevant
Saddle	5	114	4	0	Anderson
Total	9 3%	272 91%	12 4%	5 2%	

Black × Brown

Thoroughbred	0	8	20	12	Wilson
Shire	4	39	36	19	Wilson
Clydesdale	1	61	106	34	Wilson
Trotter	1	11	9	5	Sturtevant
Saddle	6	69	38	40	Anderson
Total	12 2%	188 35%	209 42%	110 21%	

Black × Bay

Thoroughbred	14	1	27	33	Wilson
Shire	19	39	43	125	Wilson
Clydesdale	7	40	67	104	Wilson
Trotter	7	16	31	48	Sturtevant
Saddle	54	141	77	261	Anderson
Total	101 9%	237 22%	245 21%	571 48%	

Brown × Brown

Breed	Chestnut	Black	Brown	Bay	Authority
Thoroughbred	11	6	114	78	Wilson
Shire	2	7	27	20	Wilson
Clydesdale	0	32	165	34	Wilson
Trotter	0	5	7	7	Sturtevant
Saddle	0	12	19	14	Anderson
Total	13 2%	62 11%	332 59%	153 28%	

Bay × Brown

Thoroughbred	123	10	365	744	Wilson
Shire	5	23	56	133	Wilson
Clydesdale	5	25	254	206	Wilson
Trotter	8	9	31	81	Sturtevant
Saddle	25	47	85	223	Anderson
Total	166 7%	114 5%	791 32%	1387 56%	

Bay × Bay

Thoroughbred	270	1	125	1295	Wilson
Shire	28	13	18	287	Wilson
Clydesdale	5	6	59	243	Wilson
Trotter	9	1	3	46	Sturtevant
Saddle	122	58	58	660	Anderson
Total	434 13%	79 2%	263 8%	2531 77%	

Gray × Not Gray

	Gray	Not Gray	
Thoroughbred	73	56	Wilson
Shire	146	186	Wilson
Clydesdale	9	15	Wilson
Trotter	141	142	Sturtevant
Saddle	49	89	Anderson
Total	418 46%	488 54%	

Gray × Gray

All breeds	47 72%	18 28%	

Chestnut	Black	Brown	Bay	Gray	Roan
9	2	2	9	1	13

Roan × Black

1	11	3	1	0	15

Roan × Brown

1	5	16	18	1	28

Roan × Bay

9	5	12	38	1	50

Roan × Gray

0	0	3	0	5	7

Roan × Roan

0	0	0	3	2	9

It will be seen from the foregoing that out of 1,438 matings of chestnut with chestnut all the foals are chestnut except 16. Sturtevant gives from 69 such matings all chestnut foals. In like manner I report 224 chestnut matings producing chestnut foals. This makes a total of 293 foals from chestnut matings among the two breeds, trotter and saddle horse, without an exception. It is true that I found in the records two bay colts reported from chestnut sire and dam. The breeder of them is still living and informs me that it is a typographical mistake in the record. I have made diligent effort in the last few months to find a living colt from chestnut parents that is not chestnut itself. My efforts have been in vain, although I have asked in the breeding journals for the information so as to give it the widest publicity.

I have no doubt that either mistakes in the record or in the reports for registration are numerous enough to account for the 16 exceptions given in the above tabulation. There are those chestnut horses whose color is so close to that of a light bay that it would be marvelous if mistakes were not made in reporting the color for registration. Then, too, it is not always easy to determine the color the horse is to be by examining the young foal. As a rule the colt that has the dark mane and tail and dark legs will shed out to be a bay, while that one which has the light mane, tail and legs will shed to be a chestnut.

There is a tendency to blend in bay and chestnut. While the blend is not complete by any means, its tendency is apparent and at times gives trouble to foretell the color of the mature horse. I have examined a bay stallion that had on his ankle a small space covered exclusively with chestnut hairs. It is these animals on the border line that are so liable to be registered bay when in fact they are chestnut. I find numerous errors in all the registration records which I have been able to examine. The color of the horse has always been a minor consideration in registration, the pedigree being considered the important thing. Often the pedigree is mutilated by typographical mistakes. Why should we not expect the color to be changed in the same way?

The other writers on this subject have not given any figures showing the behavior of chestnut when mated to bay, brown and black. I find that black to chestnut gives: 32 per cent. chestnut, 22 per cent. black, 6 per cent. brown, and 40 per cent. bay. Brown to chestnut gives: 24 per cent. chestnut, 12 per cent. black, 12 per cent. brown, and 52 per cent. bay. Bay to chestnut results in: 34 per cent. chestnut, 4 per cent. black, 3 per cent. brown, and 59 per cent. bay. The behavior of bay with chestnut is just what is to be expected if chestnut is recessive, as it seems to be. But it is in the matings of chestnut with black and brown that the real difficulty is encountered. Why should chestnut and black matings give 40 per cent. bay, and with brown it gives 52 per cent. bay. I must confess that up to this time I have not found an explanation to this. With these exceptions chestnut certainly behaves as a recessive to all other coat colors in horses.

Another strong evidence of the hypostatic position of chestnut is found in the matings in which it is not involved in the color of either the sire or the dam. Black × black matings give 3 per cent. chestnut foals. Black × brown gives 2 per cent. chestnut. Black × bay gives 9 per cent. chestnut. Brown × bay gives 7 per cent. chestnut. Brown × brown 2 per cent. chestnut. Bay × bay gives 13 per cent. chestnut. Here are six classes of matings with no external evidence of chestnut in the animals mated, yet regularly there come from them chestnut foals. This certainly is the way a unit-character should behave, and to behave this way it must be recessive. A striking example of the recessive nature of chestnut is to be found in The Theorist, a chestnut trotting bred stallion. I gave his color pedigree in *The Horseman* of December 17, 1912. The three generations immediately before him are of solid colors other than chestnut. The fourth generation has one chestnut individual, and the next generation two. If this is not the behavior of a unit-character I am unable to state how a recessive character should behave.

There are some stallions that are homozygous for their own colors and are unable to produce even from chestnut mares any chestnut foals. The two trotting stallions are Bingen and Alcyo, who, I have found, do not produce any chestnuts, although each one has had numerous mares who to other stallions do produce chestnut foals.

Black is dominant to chestnut and hypostatic to brown, bay, gray and roan. The percentages are from a total of 298 black × black matings: 91 per cent. black, 3 per cent. chestnut, 4 per cent. brown, 2 per cent. bay. The brown and bay from black matings are very small, not enough to vitiate the conclusion that black is hypostatic to these two colors as well as to gray and roan. Under the present methods of registration there can be no sharp line of demarcation between black and brown. I am confident that as the records are now made up enough errors have crept in, by registering browns black, to account for the exceptions above mentioned. From true black horses mated to true black only black and chestnut will be obtained, in my opinion. The percentages of black colts from the cross of black and brown and black and bay are 35 per cent. and 22 per cent., respectively; just about the figures that the Mendelian law would justify.

In regard to brown and bay no little difficulty is encountered. Wilson says:

> The relative positions of bay and brown remain to be settled; and although there is evidence in favor of brown being dominant to bay, this conclusion is not clearly established. It must be remembered these are the colours breeders have the greatest difficulty in discriminating; and errors effect sires and dams and foals. In regard to sires it has been possible to correct the registered colors in several cases; and while every correction has increased the evidence in favor of brown being dominant, it is still possible there may be other explanations, as, for instance, that bay is a diluted brown.

Wilson's conclusion is that brown is dominant to bay, although he expresses a doubt as to the correctness of his own conclusions.

In his interpretation of the figures, Sturtevant goes the line of least resistance. He says:

> I am unable to agree with Wilson that bay and brown can satisfactorily be separated I base this upon my own observation, upon the frequent changes from bay to brown and *vice versa* which he (Wilson) mentions finding in the Clydesdale records, and the similar changes which I have observed among Harness Horse records, and upon the frequent recording of English Thoroughbreds as "bay or brown." My conclusions, then, are that brown and bay are not distinct, brown being merely a dark bay.

I do not believe that either Wilson or Sturtevant is correct. I reached the conclusion in my first paper, based on the records of the saddle horse alone, that brown is dominant to chestnut and black and hypostatic to bay. With all the figures before me now, I am still of the opinion that brown is recessive to bay. When bay is mated with brown the product is: 56 per cent. bay, 32 per cent. brown, 5 per cent. black and 7 per cent. chestnut. The total number of horses produced by this mating is 2,460, a number large enough to show that the percentages can be relied upon. Bay × bay produces: 77 per cent. bay, 8 per cent. brown, 2 per cent. black and 13 per cent. chestnut.

Brown × brown gives: 2 per cent. chestnut, 11 per cent. black, 59 per cent. brown and 28 per cent. bay. It is this 28 per cent. bay that is the greatest obstacle in the way of the interpretation which I have given to the results. If brown is a recessive to bay there should be no bay foals from brown sire and brown dam. Yet such matings yield a large per cent. of bay. I spent much time during the summer of 1912 studying the color of horses in the field. I believe that I have found an explanation for the above difficulty.

There is a brown horse that is called by horsemen the seal brown. The seal-brown horses appear to be almost black, and can easily be mistaken for black. The top line is all black, as is the mane and tail. The legs, except for possible white markings, are black up to the body. The body is very dark brown, in some cases showing a lighter shade near the flanks, and back of the nostrils a little of the lighter shade of brown is found. This is the true brown horse and only such should be recorded as brown.

There is a class of so-called brown horses known as the mahogany browns. These horses have black mane and tail, black legs, the top line of the body and sometimes the under line are black. The sides of the body have many bay hairs mingled with the black hair. Some blotches, usually near the flanks, seem to be exclusively bay. It seems to me that this horse is on the border line between bay and black, or is an example of the incomplete dominance of the bay over the black.

If this theory be true, such mahogany brown horses are not, from the standpoint of reproduction, brown at all. No true brown foals should come from them unless the factor for brown be latent in their germ cells. They are examples of the simplex bay and when mated should give bay and black foals.

When it is remembered that the records have all these so-called mahogany browns recorded as browns, and no possible way to separate them, it becomes a very difficult matter to properly interpret results. I should be inclined to agree with Sturtevant that no separation of brown and bay can be made, were it not that I have found these two classes recorded as brown, while one class is a brown and the other class is a bay. Brown × brown matings, when a per cent. of genetically bay individuals enter into such matings, would have to give some bay foals. Twenty-eight per cent. of bay foals is none too large to expect from the number of simplex bays recorded as browns.

Another solution of this matter of black, bay and brown was suggested by A. B. Cox in a letter to me under date of May 14, 1912.

> Might it not be possible that bays, browns and blacks should be considered as a unit and that their appearance could be controlled by an independent factor; something on the same principle of the dilute factor in rabbits' color as set forth by Professor Castle? We have different shades of chestnut and also of gray roans, might not these different shades also be controlled by this dilute factor? Should we not divide the colors in three classes: (1) Gray roans; (2) bay, brown and black; (3) chestnut of different shades? Each class to be controlled by one factor, and then the different shades of these units to be controlled by an independent factor.

It is no little temptation to adopt this short series as it relieves at one stroke so many difficulties. Black, (seal) brown and bay are just as distinct colors as are chestnut and gray. This being so, I believe that each must have a separate factor, even though it may make the factors for color very numerous in the germ cells. For example, from gray × bay matings there are produced gray, bay, brown, black and chestnut, five colors; showing that in the germ cells of a gray horse there must be the factors for five colors. In view of all the evidence which I have I adhere to my first interpretation, adopt the long series and place brown recessive to bay. Bay I place between brown and the two colors which are dominant to it, gray and roan.

That gray and roan are dominant to bay there can be no doubt. Nine hundred and six foals from matings gray × not gray produce 46 per cent. gray and 54 per cent. not gray. It is known that homozygous gray when mated with any of the four popular colors will always produce a gray. It is only from a heterozygous gray that other than a gray can be produced. Roan behaves exactly the same way. I have no records that would indicate the comparative strength of roan and gray. For the present I place them at the top of the series as of coordinate strength. It is just possible that there is a white that is dominant to both the gray and roan, but this has not come under my observation. Nor do I have any data to enable me to place dun in a series.

The cause of the different shades of roan, bay and chestnut must be left to another paper, as well as the interesting behavior of the white markings to be found on most horses, and also the dappled condition of certain grays, bays and chestnuts.

Sturtevant has suggested that C represent the factor for chestnut; H for black; B for bay (or brown); G for gray; R for roan, and W for white. I now suggest this change: Add the factors for brown, Br, and dun, D, and change black to Bl. The series then becomes: C, hypostatic to all others. Bl epistatic to C but hypostatic to Br, which in turn is hypostatic to B. G and R are both epistatic to B, and perhaps are hypostatic to W. This leaves D (dun) unplaced except that it is known to be near the top of the series with G and R.

THE VARIATIONS IN THE NUMBER OF VERTEBRÆ AND VENTRAL SCUTES IN TWO SNAKES OF THE GENUS REGINA

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It has been asserted that the number of large scales on the ventral surface in snakes is the same or nearly the same as the number of vertebræ. Gadow (1901, p. 582) asserts that the "skeleton segments correspond in number to the ventral and transverse scales of the skin," but Jourdran (1903, pp. 25–26) has failed to find an exact correspondence between the total numbers of scutes and vertebræ in many specimens. According to the counts published by the latter writer (1903, pp. 25–26), the discrepancy may vary from 25 less to 53 more scutes than vertebræ, and he concludes,

> On peut donc conclure qu'il n'y a qu'une concordance tres relative entre le squelette interne et la metamerisation externe des teguments.

Unfortunately a study of Jourdran's paper seems to show that his counts of the vertebræ can not be relied upon. Some of the skiagraphs are so poor that it is doubtful if careful counts could be made from them, many of the numbers given are estimates, the tail in some of the specimens is broken, the disposition of the vertebræ is not indicated, except when the number of ribs is given, and the number of ribs given is in some cases much greater than shown in the skiagraphs, apparently indicating that the long transverse processes of the proximal tail vertebræ have been counted as ribs. We believe that Jourdran's work shows only that some discrepancy between the number of vertebræ and the number of scutes may occur. Grosser (1905, pp. 57–61) has pointed out that there is a metameric arrangement of the ventral scales except in the neck, anal and tail regions, so that discrepancies must be confined to these regions.

On the assumption that the belly scales and body vertebræ are the same, Bateson (1894, p. 123) has pointed out that there must be considerable variation in the number of vertebræ in this region, and Ruthven (1908) has shown that if the number is the same in both series in the genus *Thamnophis* closely related species when differing in relative size also differ in the number of body and tail vertebræ, since they do so vary in the number of scutes.

In view of the fact that there may be a discrepancy in the number of vertebræ and ventral scutes, general conclusions based on the correlation between the two series are of little value until the method, amount and place of variation has been determined. As is well known a pronounced sexual variation in the scutes occurs in at least some species, the males having on the average fewer belly scutes and more subcaudal scutes than the females. It might very well be that while the total numbers of scutes and vertebræ are not the same, the number in each whole series is about the same in the two sexes, the variation simply affecting the relative number on the body and tail, or there may be more or less scutes than vertebræ on the body and less or more scutes than vertebræ on the tail, so that the total number in the two series is close together, or the number of scutes may vary independently of the vertebræ sufficiently to bring about the observed sexual differences, the number of vertebræ remaining the same, and the relation between the number of members in each series may be different in different forms.

It has been the purpose of this study to determine the correlation that exists between the number of belly scales and body vertebræ and between the number of subcaudal scales and caudal vertebræ in two species of snake, and from this to discover if the sexual and individual differences in scales are associated with differences in the total number of vertebræ or are merely in the relative number on the body and tail.

The results embodied in this paper were in part obtained by Mr. Charles Obee, in 1910, under the direction of the senior writer, and were submitted by him in the form of a thesis to the faculty of the department of literature, science and the arts, University of Michigan, in partial fulfillment of the requirements for the degree of Master of Arts. The work was completed by the junior writer in 1912. The skiagraphs were made by Dr. E. T. Loeffler, of the department of dentistry, University of Michigan, and we gratefully acknowledge his untiring efforts to provide us with satisfactory plates of the rather difficult material, without which the work could not have been completed.

The methods used in this study are simple. Two closely related species belonging to the North American genus *Regina* (*Natrix* in part or *Tropidonotus* in part of some writers), *R. leberis* (L.) and *R. grahami* (B. & G.) were used. Most of the work was done on *R. leberis*. In a series of specimens the sex and the number of ventral (belly and subcaudal) scales was determined, and skiagraphs were made of each specimen from which the vertebræ were counted. Before making the skiagraphs a pin was thrust through the body at the anus so that the position of the last few body vertebræ would be revealed, and it was determined by dissection which pair of the short anterior ribs is the first to reach a ventral scute and the number of this scute.

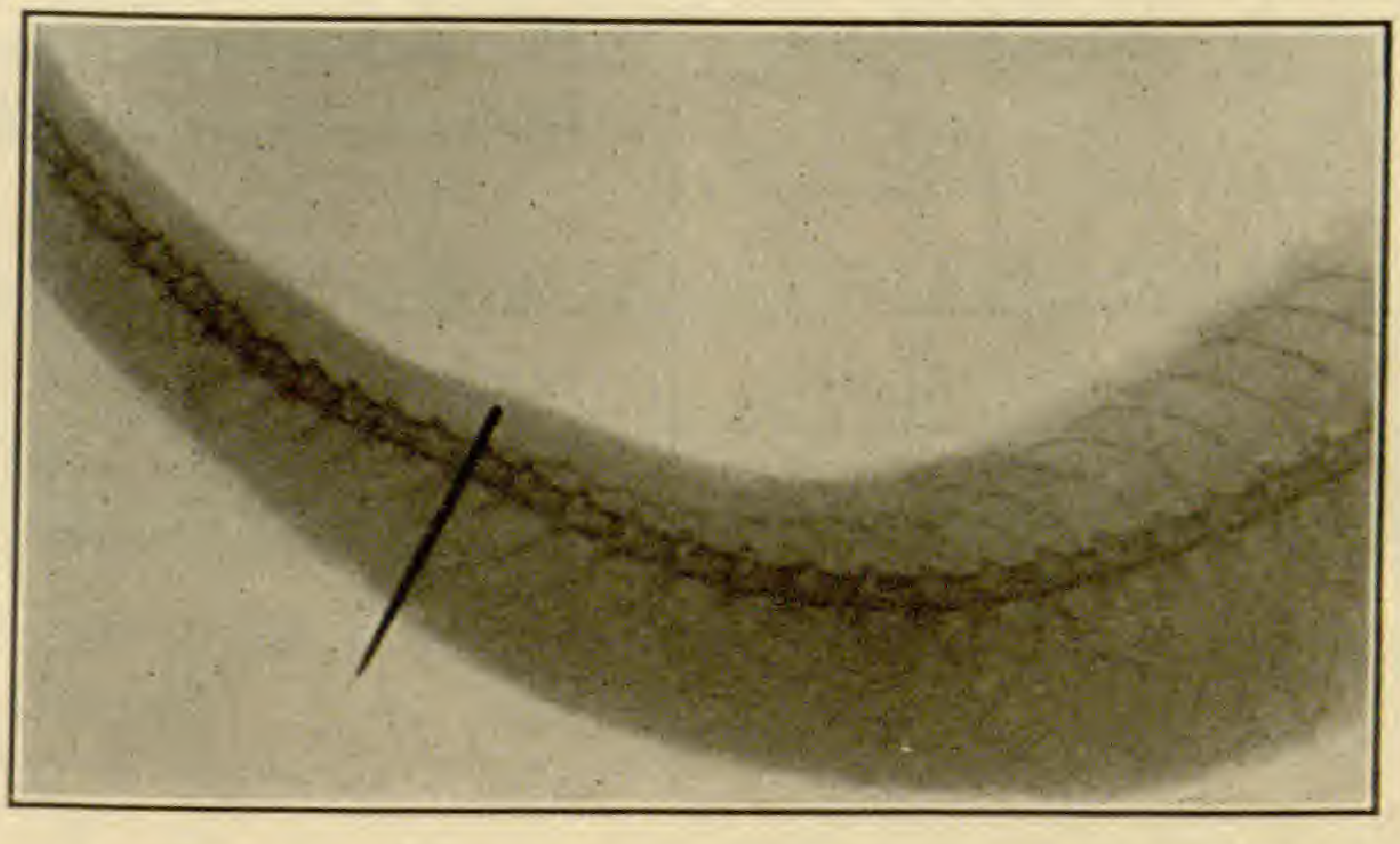

FIG. 1. Skiagraph of anal region of a specimen of *Regina leberis* (L.) to show position of last three vertebræ. The pin lies in the anal opening.

General Relations of Vertebræ and Scutes.—It is first to be stated that in the few specimens dissected it is the third or fourth pair of anterior ribs, on the fifth and sixth vertebræ, that first extends to the belly scutes, and the scute reached is the eighth. This makes three or two scutes more than vertebræ in the neck region, and there is probably a slightly greater difference than this in some specimens, as there is a difference in the extent to which the gular scales encroach upon the region occupied by the first scutes. On the other hand, it is to be noted, as shown by the skiagraph (Fig. 1), that it is the ribs of the fourth from the last vertebra that connect with the last scute in front of the enlarged anal plate, the antepenultimate pair terminating distally opposite the anal plate (which has thus been considered a part of the belly series), and the two last pairs of ribs extending into the base of the tail. Counting the anal plate, then there would be, barring the discrepancy anteriorly, two more body vertebræ than scutes, but as there are about two or three scutes in excess of vertebræ anteriorly the two extra ribs reduce the discrepancy to one or nothing in the specimens dissected. That this is about the normal condition is shown by the variations in the series studied, and it may be concluded that when the differences are more or less than this number the discrepancy is due to the addition or loss of a belly scute or two under the chin.

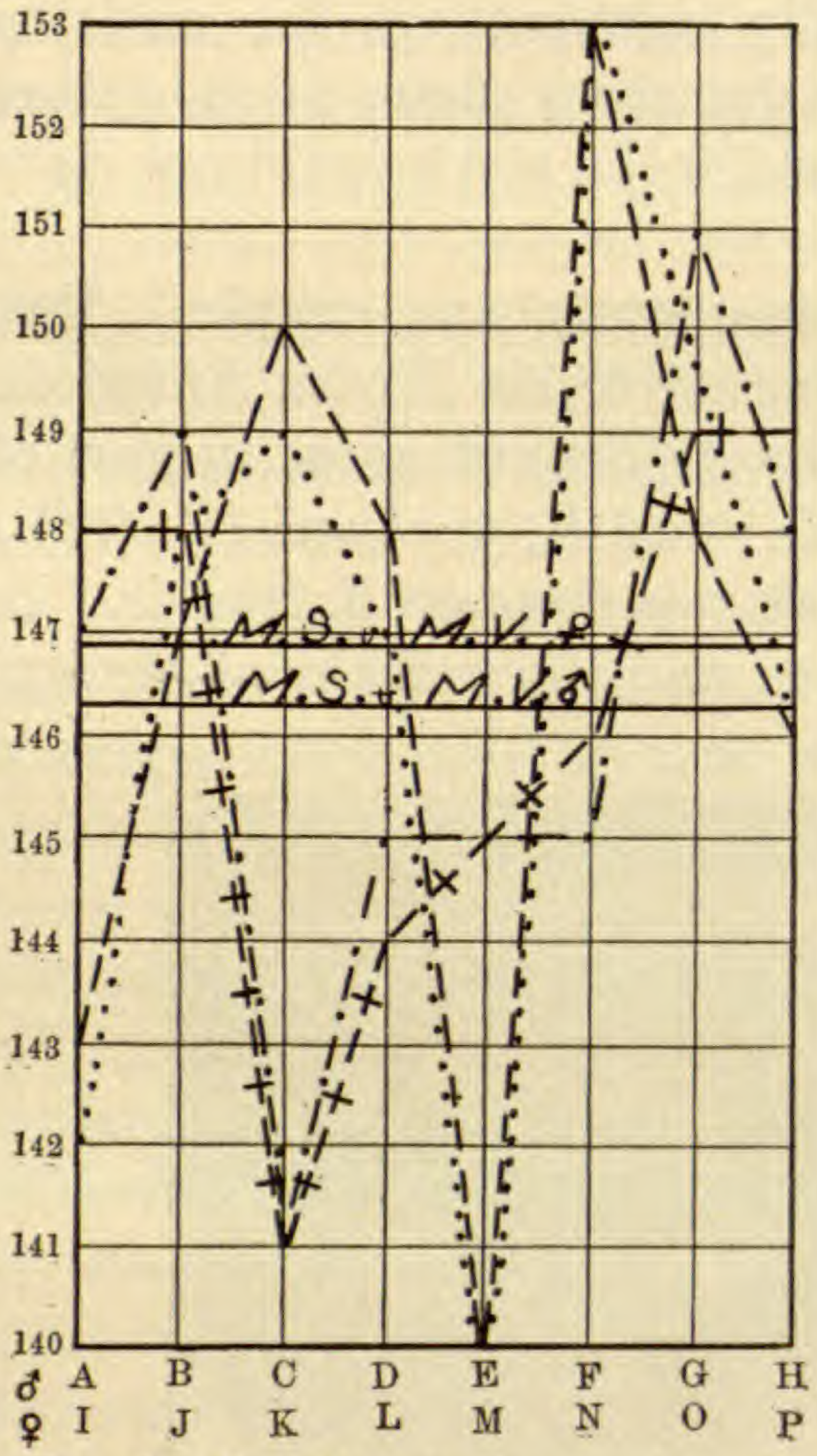

Fig. 2. Variation in the number of body vertebræ and belly scales in *Regina leberis* (L.). ————, variation in vertebræ, females; —+—+—+, variation in vertebræ, males; . . . ., variation in scutes, females; —.—.—., variation in scutes, males; M.V., mean number of vertebræ (146.25 ♂, 146.87 ♀); M.S., mean number of scutes (146.37 ♂, 146.75 ♀).

Variation in R. leberis.—In the diagrams (Figs. 2, 3, 4) the variations in sixteen specimens of *R. leberis* are shown graphically and in such a way as to illustrate their nature and the correlation that exists between the different series. The results appear to be as follows. There is a variation

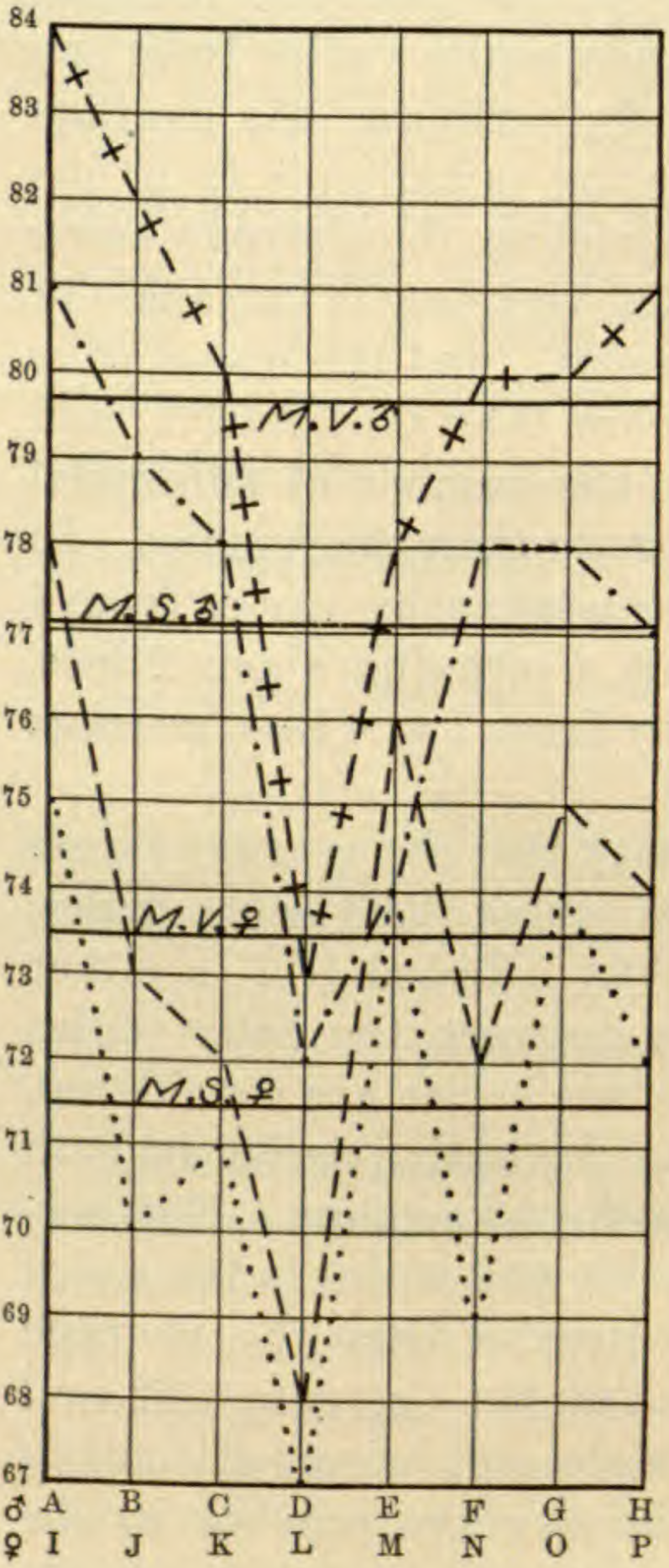

Fig. 3.

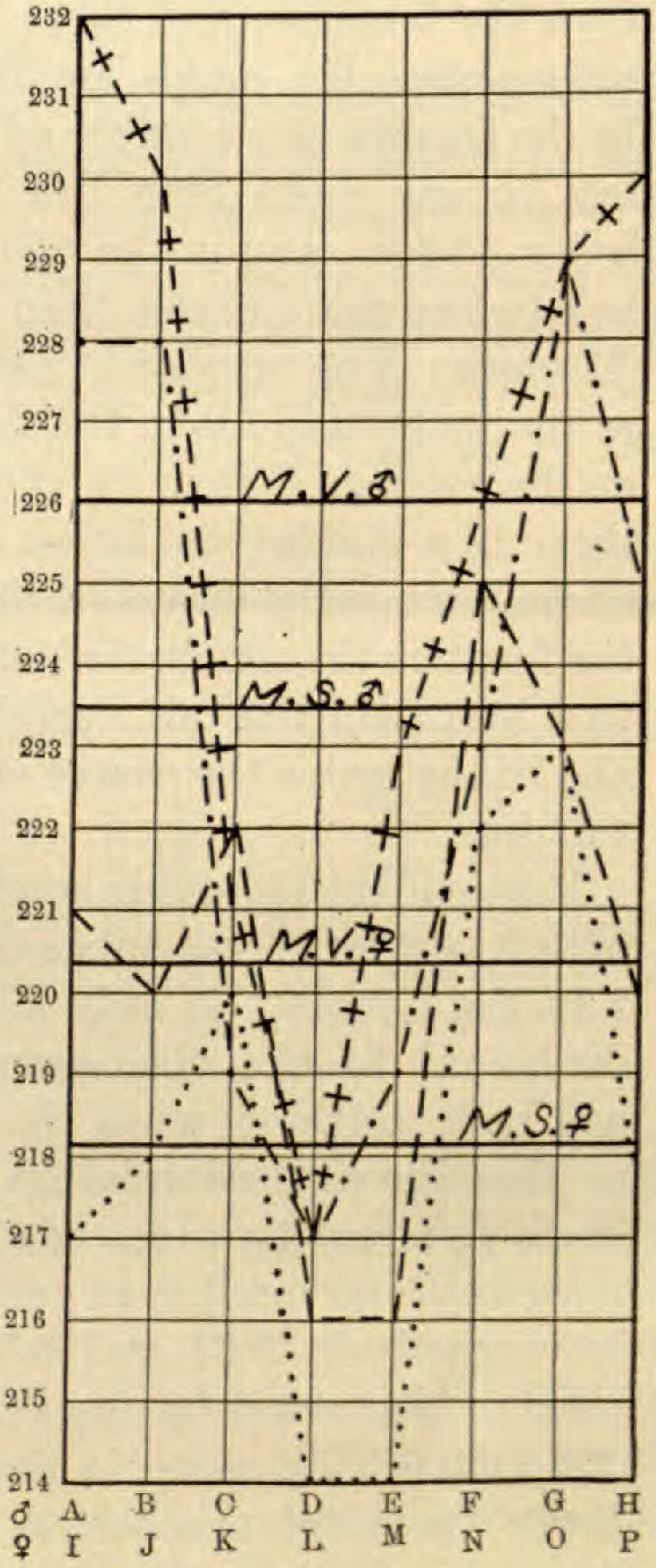

Fig. 4.

Fig. 3. Variation in the number of caudal vertebræ and subcaudal scales in *R. leberis* (L.). ————, variation in vertebræ, females; —+—+—+, variation in vertebræ, males; . . . ., variation in scutes, females; —.—.—., variation in scutes, males; M.V., mean number of vertebræ (79.75 ♂, 73.50 ♀); M.S., mean number of scutes (77.12 ♂, 71.50 ♀).

Fig. 4. Variation in the total number of vertebræ and ventral scutes in *R. leberis* (L.). ————, variation in vertebræ, females; —+—+—+, variation in vertebræ, males; . . . ., variation in scutes, females; —.—.—., variation in scutes, males; M.V., mean number of vertebræ (226 ♂, 220.37 ♀); M.S., mean number of scutes (223.50 ♂, 218.25 ♀).

in the number of body vertebræ (8 in the males and 13 in the females), and the males have on the average .62 less than the females; and there is a similar variation in the belly scales, the males having .38 less than the females. In the females the number of belly scales varies from one less to one more than the body vertebræ, the average being .12 less, and in the males the variation is from one less to two more scales than vertebræ, the average being .12 more. The number of caudal vertebræ is variable (11 in the males and 10 in the females), and the males have on the average 6.25 more vertebræ than the females; and there is a similar variation in the number of subcaudal scutes,[1] the males having 5.62 more than the females. In the females the number of subcaudal scales varies from 1 to 3 less than the tail vertebræ, averaging about 2 less, and in the males the scutes vary from 1 to 4 less, average 2.63 less.

It is evident from this summary that the average excess of tail vertebræ over subcaudal scutes (2.63 in the males, 2 in the females) is only slightly affected (.12 in either direction) by the discrepancy between the belly scutes and body vertebræ when the whole series are considered, so that the normal relation in the entire series in both sexes is about two less scutes than vertebræ. Furthermore the total number of vertebræ and scutes in the males is respectively 5.63 and 5.25 greater than the average number possessed by the females, the decrease (.62 and .38) in the body series in the males not being sufficient to lower the total number to the average number in the females. Still further, a pronounced variation in the total number of vertebræ and scutes in each sex is revealed. This variation amounts to 15 vertebræ and 12 scutes in the males and 9 vertebræ and 9 scutes in the females, and is of course due to the fact that deviation from the mean in one member is not compensated by a corresponding deviation from the mean in the opposite direction in the other member. Thus in the 16 specimens the variation on the body and tail is in the same direction

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[1] It should be stated here that the subcaudal scutes are paired, and that references to the number always refer to the pairs.

in 6 specimens, and while in different directions in the remaining 10, in only 5 do the deviations in the two members approach equality and in four of these the deviation from the average is very small in both series.

Variation in R. grahami.—From the above results one may conclude that if the same correspondence in the number of ventral scutes and vertebræ prevails in nearly related forms the form with the most scales will have the most vertebræ. To test this point in the genus studied a small series of males (all that were available) of *R. grahami* were examined. The results are shown in the following table:

THE NUMBER OF VERTEBRÆ AND VENTRAL SCUTES IN THREE SPECIMENS OF *Regina grahami* (B. & G.)

Body Vertebræ	Body Scales	Tail Vertebræ	Tail Scutes	Total Vertebræ	Total Scutes
177	178	68	62	245	240
167	170	64	63	231	233
177	178	62	64	244	242
Average 173.66	175.33	66.3	63	240	238.3

Body scutes > body vertebræ = 1.67. Tail scutes < tail vertebræ = 3.3.
Total vertebræ > total scutes = 1.66.

It will be noted that the same close correspondence in scutes and scales is indicated in *R. grahami* as has been demonstrated for *R. leberis,* and that notwithstanding the fewer vertebræ in the tail the former species has a decidedly larger number of vertebræ and scutes. There is no reason to believe that the females of *R. grahami* will not show a similarly higher number of scales and the same relation between scutes and vertebræ.

SUMMARY AND CONCLUSION

The variation in series of *R. leberis* may be summarized as follows:

1. The number of belly scutes is practically the same as the number of body vertebræ, and the number of subcaudal scutes is between two and three less than the number of caudal vertebræ.

2. The sexual differences consist of an average of less

than one body vertebra and belly scale more and between five and seven caudal vertebræ and subcaudal scales less in the females than in the males.

3. There is considerable variation in the total number of vertebræ and scales in the two sexes, variations in the series of one member rarely equaling opposite variations in the series of the other.

It goes without saying that the extent of variation in the two series is probably not indicated in the small amount of material used, but the relations of the numbers in the different series are so little variable that there can be but little doubt that the above summary expresses the general conditions.

It is not known at present just how widespread this close correspondence in the number of vertebræ and ventral scutes is among snakes, but it is conservative to say that there is probably a correlation between the two series in most, if not all, forms, and that in some groups this correlation approaches close correspondence in the number of parts. It follows from this that, as in *R. leberis* and *R. grahami,* the species with most numerous ventral scales have more vertebræ than others in which the same correspondence prevails, and the opposite, and, as the senior writer has shown that variations in size in groups of related species in the genus *Thamnophis* are associated with differences in the number of scutes, the larger forms having more scales than the smaller, it may be assumed, tentatively at least, that difference in relative size in such a group of closely related species is a deep-seated modification that affects the number as well as the size of the metameres.

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SHORTER ARTICLES AND REPORTS

THE SIMULTANEOUS MODIFICATION OF DISTINCT MENDELIAN FACTORS

IN another paper[1] on the inheritance of a recurring somatic variation in variegated ears of maize, it was shown that the amount of red color developed in the pericarp of variegated seeds bears a definite relation to the development of color in the progeny of such seeds. The relation is such that the more color there is in the pericarp of the seeds planted the more likely are they to produce plants with wholly self-red ears and correspondingly the less likely to produce plants with variegated ears. Self-red ears thus produced behave just as if they were hybrids between self-red and variegated races or self-red and white races, the behavior in any given case depending upon whether the parent variegated ears were homozygous or heterozygous for variegated pericarp and whether they were self-pollinated or crossed with white.

To interpret these facts I have suggested that perhaps (1) a Mendelian factor for variegation, *V*, is changed to a self-color factor, *S*, in a somatic cell, (2) that all pericarp cells directly descended from this modified cell develop red color, and (3) that of the gametes arising from modified cells one half carry the *S* factor and one half the *V* factor.[2] Whether it ever happens that more than one half of such gametes carry *S* is unknown, but it is certain that a considerable part of them carry *V*. This is shown by the fact that self-red seeds from a variegated ear that has been cross-pollinated by white-eared maize produce a considerable percentage of variegated-eared plants. Evidently in such cases the duplex condition of the factors is changed to the simplex condition by the change of one *V* factor to an *S* factor, so that the zygotic formula *VV* becomes *VS*.

Now it often happens that a considerable patch of self-red grains occurs on an otherwise variegated ear. The cob immediately beneath such a patch is sometimes variegated, just like

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[1] Not yet in print.

[2] This hypothesis was noted in my discussion of the possible origin of mutations in somatic cells. AMERICAN NATURALIST, 47: 375–377, 1913.

that beneath the variegated grains of the same ear, and sometimes self-red, the red cob spot corresponding exactly with the patch of red grains. Yet the wholly red ears arising from such self-red seeds invariably have wholly red cobs without respect to whether the parent seeds were from a red or variegated cob spot. It seems possible that in some cases the change from V to S occurs earlier in the life of the plant than in other cases. In some plants the change may, it seems possible, occur soon after the cob is laid down, in which case all the cells of the glumes as well as of the pericarp over a considerable area will be red. In other plants it appears that the change from V to S occurs independently in the rudiments of several grains, but not until after the glumes associated with them have been laid down. But in either case, it must be remembered, the red ears produced from such red seeds always have wholly red cobs as well as wholly red grains and cob and pericarp colors are coupled in all later generations. Evidently, whatever is responsible for the change from variegation to self-color always affects both cob and pericarp colors.

This would occasion no surprise if it were known that red cob color and red pericarp color are due to identical factors. But I have presented, in another place,[3] evidence that cob and pericarp colors are dependent upon distinct genetic factors which are either coupled or allelomorphic in inheritance. Even if it should be shown that the red color of the cob is due to identically the same pigment as the red color of the pericarp, it must nevertheless be assumed that there are distinct genetic factors that influence the distribution of this pigment. The factor S_c that has to do with the determination of self-pattern of cob color can hardly be the same as the factor S_p that has to do with the same pattern in the pericarp, for, if it were the same, a cross of a strain having variegated cob and variegated pericarp with a strain having self-red cob and colorless pericarp should produce progeny self-red in both cob and pericarp, whereas such a cross actually produces ears with self-red cobs and variegated pericarp. We are practically driven, therefore, to the conclusion that there must be distinct factors for self-color of the cob and self-color of the pericarp, S_c and S_p, respectively. It seems reasonable then to suppose that the same is true of the variegation pattern and that there are both V_c and V_p for variegated cob and variegated pericarp, respectively.

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[3] Ann. Rpt. Nebr. Agr. Expt. Sta., 24: 59–90, 1911.

If this is true, we are confronted with the problem of explaining the apparently universal occurrence of self-red cobs in connection with self-red ears arising in F_1 from variegated-eared parents. Why, in short, should V_c and V_p, if they are really distinct, always change together to S_c and S_p, whenever either one changes? This seems the more unaccountable when considered in connection with the fact that the change often, or perhaps always, affects only one of the two like (duplex) factors of a homozygous somatic cell, so that $V_cV_p \cdot V_cV_p$ becomes $S_cS_p \cdot V_cV_p$.

In my former paper (*loc. cit.*) I accounted for perfect coupling of cob and pericarp factors in certain crosses by the assumption that the two factors were located in the same chromosome, and explained perfect allelomorphism of the same factors in other crosses by the assumption that the two factors were located in homologous chromosomes. This was on the further assumption that homologous chromosomes separate at the reduction division exactly at the plane of their union in synapsis. If in place of this last assumption, however, we accept Morgan's[4] suggestion, based upon cytological evidence presented by Janssens, that homologous chromosomes may become spirally twisted together in synapsis and that the plane of separation may not always coincide exactly with the plane of union, we must also accept his further suggestion that the linear position of factors within a chromosome has much to do with the degree of coupling and allelomorphism, "linkage." To me Morgan's hypothesis seems the most reasonable interpretation of the facts of partial coupling and "repulsion," and it also affords a satisfactory explanation of perfect coupling and allelomorphism.

In accordance with Morgan's hypothesis, we must suppose, not only that the factors V_c and V_p are located in the same chromosome as I had done before, but in addition that they are situated very close together in this chromosome, since their linkage seems to be perfect. Similarly we must suppose, not only that V_p and S_p are in homologous chromosomes, as I had previously done, but that they are in almost exactly homologous positions in these chromosomes, since their allelomorphism appears to be perfect. This second supposition follows of course as a corollary of the first one if S is produced through a modification of V.

Now we might suppose further that the two factors, V_p and

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[4] *Science*, N. S., 34: 384, 1911.

V_c are located side by side in the same chromosomes not only at the time of the reduction division but also in all nuclear divisions and even perhaps that they remain in fairly close proximity in the more diffused chromatin of the resting nucleus. Then if homologous chromosomes or their chromatin masses are not closely associated in somatic cells, it would seem possible that whatever causes the change of a V_p factor into an S_p factor might at the same time affect the V_c factor of the same chromosome changing it into an S_c factor, while the V_p and V_c factors of the homologous chromosome remain unchanged.

It is of course recognized that a rather formidable number of hypotheses, with subsidiary assumptions, have been marshalled here to account for what may be very simple phenomena, but, if they do not do too great violence to the known facts of cytology, we are justifiable in accepting them tentatively as an attempt at a consistent interpretation of what otherwise seem inconsistent genetic facts.

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THE FOURTH INTERNATIONAL GENETICS CONFERENCE[1]

IN a subject developing so rapidly as that of genetics, the delay of one and one half years in the publication of the results of an investigation is a serious matter. It is therefore to be regretted that the publication of the proceedings of the Fourth International Conference on Genetics has followed the common fault of international congresses in this respect. In many cases results which were new at the time of the conference have been anticipated by other work. In other cases the results of later experiments have no doubt served to modify opinions expressed at the conference. A portion of this delay is inherent in the nature of an international meeting. However, it is hoped that for the coming conference, steps will be taken to insure the more rapid publication of the proceedings.

The present volume of 570 pages consists of two parts. Part I (pages 1 to 79) contains the matter of historical interest relat-

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[1] "Comptes Rendus et Rapports de IV^e Conférence Internationale de Génétique." Edités par Ph. de Vilmorin. x + 571 pp. Masson et Cie, Paris. 1913.

ing to the conference. It includes the general organization; the list of members and adherents; an account of the various scientific and executive meetings and finally an account of the numerous receptions and excursions arranged for the entertainment of the members.

The membership of the conference totaled approximately 250, representing twenty different countries. Of these about 150 attended the conference. There were five sessions for the reading of papers and the transaction of business.

As the members registered each received an addressed envelope containing the program of the conference and printed slips giving in French a brief summary of each paper to be presented. In addition there were the invitations to the various receptions, excursions and entertainments, and finally an elegant bronze medal commemorative of the conference and bearing upon its reverse the name of the member. This medal, which was designed by R. Benard, bears on its face the likeness of Mendel. On the reverse in addition to the member's name is the artistic representation of pea flowers and pods and the inscription "*Rerum cognoscere causas.*" This elegant souvenir was provided through the generosity of M. Ph. de Vilmorin.

Of the many enjoyable excursions arranged for the conference, especial mention should be made of the day spent at Verrières-le-Buisson in visiting the experimental gardens of Vilmorin, Andrieux et Cie. An account of the more interesting cultures seen on this excursion is given on pages 44 to 56. At l'Institute Pasteur de Garches, in addition to the work of serum production, the members were shown the extensive plant for the breeding of guinea-pigs. In a visit to the Pasteur Institute at Paris the members were welcomed by Professor Metchnikoff and were enabled to see much of his work. During this trip Professor Blaringhem exhibited specimens and spoke of his work on traumatism with maize. The conference closed with a complimentary "Banquet de Clôture" at L'Hôtel Continental.

Any account of this conference would be incomplete without an appreciation of the royal entertainment given to the visiting members. For this the conference was chiefly indebted to the able secretary, M. Ph. de Vilmorin, to whose untiring efforts were due both the success and pleasure of the meeting.

Part II contains the fifty-eight scientific papers presented at the conference. These are printed either in French or English and in each case there is a brief summary in the alternate language. This is a great convenience to the French and English reading public but it is not clear why German should have been so rigidly excluded. A number of the papers were presented in German but in each case these have been translated into French with an English summary.

Of the papers which attracted most attention at the conference probably that of Miss Saunders on "The Breeding of Double Flowers" held first place. Miss Saunders's results have since been published elsewhere but their interest is sufficient to be noted very briefly here. In the genus *Matthiola* there are two kinds of single flowers—(1) the double-throwing and (2) the non-double-throwing. The doubles are always sterile, so that doubles must always come from single parents. Miss Saunders showed that singleness is due to two factors, X and Y, and that in the non-double throwing type these two factors are linked together. Doubleness is due to the absence of either or both of these factors. Now it further appears that in the double-throwing strains all four possible combinations of these factors occur in the ovules but "the pollen appears unable to carry X and Y either alone or together." Thus we have in addition to the coupling or reduplication a case of sex-linked inheritance which so far as the writer is aware was the first case to be reported among plants.

In a brief paper Professors Bateson and Punnett pointed out that what they had formerly termed "coupling" and "repulsion" are in reality phases of the same phenomenon. In each case the results are produced by a "reduplication" of those gametes which represent the parental combinations. This is another case of results which were new at the time of the conference but which have become familiar to students of genetics through other publications.

A number of papers deal with the heredity and breeding of cereals. Of these there may be mentioned one by Dr. Jesenko upon a fertile hybrid between wheat and rye. This cross has been made a large number of times but in every instance the F_1 plants were sterile. Dr. Jesenko succeeded in finding one plant partially fertile and from this, F_2 and F_3 generations have been grown. The interest in this work lies in the fact that the F_2 and F_3 plants were fairly fertile. In this connection should be noted the paper by Mr. Sutton, of England, on hybrids between the wild pea of Palestine and the common commercial pea. In this species-cross the F_1 plants were also nearly all sterile, but from a large number of crosses a few seeds were obtained and the F_3 and succeeding generations were quite fertile. A very similar result was reported by M. Bellair in the case of certain tobacco hybrids. It is possible that these investigations may point the way to a better understanding of sterility in species crosses.

The communication of M. Boeuf on the stability and variation of characters in pure strains of cereals points again to the conclusion that selection within a "pure line" is without effect. The author cites a large number of experiments to support his thesis.

The observations of Dr. Trabut upon the origin of cultivated oats will be of interest to students in this field.

Two papers deal strictly with the inheritance of quantitative characters, a subject of so much interest at the present time. Professor Bruce, of London, concludes that "It can not be affirmed with certainty that Mendelian laws apply to such characters." Professor Balls, of Egypt, presents a large amount of interesting data regarding quantitative characters in cotton hybrids. However, he believes the fluctuating variations are so large and due to so many causes that it is not possible to show that such characters are controlled by segregating factors. The rapid advance in this field of genetics within the past year would hardly support these conclusions.

An important paper by Nilsson-Ehle on Mendelism and acclimatization gives us a somewhat different view of acclimatization than that usually held. This author holds that increased resistance to cold, for example, is not obtained by the simple isolation of a more resistant type already present in a variety. Further such types do not arise by mutations in the ordinary sense of the word. He says in his summary (p. 156):

> On the contrary, all my researches tend to show that the numerous types which can be distinguished, both in the characters of resistance to cold, precocity, and other quantitative characters, are produced by various combinations of certain Mendelian factors.

To those biologists who are still skeptical as to the validity of the factorial concept as a means of interpreting the facts of heredity we would recommend the paper by Professor von Tschermak. In experiments on the recrossing of hybrid peas which have extended over eight years and in which "some thousands of individuals have been recorded" he is able to "confirm the factorial theory in the most complete and satisfactory manner.'' In more recent papers he has given the details of these extensive experiments of which only a summary is presented in the above paper.

While the majority of the papers deal with plants there are several upon the animal side. Of these, there may be mentioned one by Walther on the coat color of horses. He considers that there are two principal colors in horses' coats, viz., yellow and red. These he says are allelomorphic to each other with yellow dominant. These colors may be modified by supplementary markings such as black marks, white hairs, etc. Thus such colors as brown, bay and dun would depend upon multiple factors.

Papers by Chappellier on duck hybrids, by Noorduyn on canaries and by Houwink on fowls contain points of interest.

Papers by Crouzon and by Drinkwater deal with phases of human inheritance.

Several papers by de Vilmorin and by Mrs. Haig-Thomas as well as those by Blaringhem, von Ruemker, Collins and Kempton, Johannsen, Hurst, Salaman, Swingle, and others contain many interesting points which it is not possible to mention in this brief account.

The volume is well printed on good paper and the numerous illustrations are well executed. A welcome feature of the volume is the reproduction of photographs of the participating members of the conference so far as these could be secured.

In general the editorial work is good. However, in spite of the fact that two proofs were submitted to the authors a considerable number of typographical and grammatical errors are to be found. This is particularly true in some of the English summaries (cf. for example p. 130). The services of an English editor would have made these much more readable.

The volume contains a wealth of observation which well repay reading. It will form a welcome addition to the library of students of heredity.

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The American Naturalist

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Special Reference to the Factors of Evolution

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THE EFFECT ON THE OFFSPRING OF INTOXICATING THE MALE PARENT AND THE TRANSMISSION OF THE DEFECTS TO SUBSEQUENT GENERATIONS

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It is a thoroughly demonstrated fact that the fertilized egg may be so treated or modified during development as to cause it to give rise to abnormal embryos of definite types. Experiments on the unfertilized egg or female germ cell are not nearly so numerous, are more difficult to perform, and the results are not so decided. The treatment of the male germ cell, or spermatozoon, so as to modify it and to cause a modified development of the egg which it subsequently fertilizes, is an experiment which has rarely been performed with success. In the present communication we wish to consider rather briefly the various methods of treating or modifying the spermatozoon or male germ cell and the result of this modification on the embryo which arises when such a spermatozoon fertilizes an egg. In order to fully appreciate the results obtained by experiments on the sperm it becomes necessary to refer from time to time to the effects derived when the egg is similarly treated.

Since the positive literature bearing on the artificial modification of the sperm is not extensive, I shall first consider it in a general way, and devote the latter part of the paper to the results obtained in a set of experiments which have been conducted on guinea-pigs for the last few years.

The spermatozoön is more difficult to treat experimentally than is the ovum, on account of the fact that the treatment so often renders it inactive or cripples it in such a way that it is unable to penetrate and to fertilize an egg. The spermatozoon, although apparently delicate, is more or less resistant, so that a mild treatment gives no effect. The difference between the upper non-effective dose of treatment and the fatal or "paralyzing" dose is slight, yet it is the precise treatment between these two points which yields results.

Little has been done in treating chemically the spermatozoa of invertebrates, though some of the hybridization experiments furnish indirect evidence as to what might occur. Herbst's experiment of starting the development of an egg by parthenogenesis and then fertilizing one blastomere with a foreign spermatozoon offers splendid opportunity for investigating the influence of strange substances introduced by the sperm. The spermatozoa of the sea urchin have been subjected to the action of radium emanations by Günther Hertwig, who found that after intensive treatment for several hours such spermatozoa subsequently disturb the processes of division in the eggs which they have fertilized. Paula Hertwig found that fertilized ascaris eggs treated several hours with radium preparations gave pathological division figures; the chromatin bodies showed a tendency to break down and disintegrate; division was slow and the karyokinetic figures were finally completely deranged.

Investigations on vertebrates have been more extensive. The most beautiful results have been obtained on fish and amphibians through the radium experiments of Oscar Hertwig, his son Günther and his daughter Paula. The outcome of these experiments is so striking and is of such serious importance that I shall dwell somewhat upon their significance. About three years ago O. Hertwig published the results of his first radium experiments in the *Proceedings of the Prussian Academy of Sciences.* At that time he showed that when the unfertilized eggs of a frog are treated for a certain time with radium rays, these eggs, after being fertilized by normal spermatozoa, develop abnormally. Hertwig also found that when the milt or semen of the frog was exposed to the action of radium for a certain time the spermatozoa swimming in it were injured. When eggs were fertilized by these sperm they always developed abnormally. The general type of the abnormalities was the same whether the eggs alone had been treated before fertilization or whether the sperm was treated. When both eggs and sperm were treated the developmental modifications were still more pronounced, though Hertwig claims that the deformities were of a similar type to those which occurred after treating only one of the cells.

Since that time Oscar Hertwig with his son and daughter have extended and analyzed these experiments in a comprehensive fashion. When the sperm of a number of amphibians, frog, toad and salamander, are exposed for five minutes to 5.3 mg. of radium bromide, normal eggs fertilized by such sperm give defective embryos, the defects being generally shown by the central nervous system. They are really of the nature of developmental arrests or degeneration.

If the spermatozoa are exposed for fifteen minutes the effects on development are still more marked. When, however, the sperm in salt solutions are treated intensively for 2 and 3 hours between two mesothorium capsules, the results are most surprising. In one experiment almost all the eggs fertilized by such sperm went *normally,* and in other experiments they went almost normal but slow, yet they were extraordinarily better than eggs that were fertilized by sperm that had been treated for only five minutes. After three weeks the radium larvæ were still behind the control. Hertwig concluded that the spermatozoon had been so injured by the intensive treatment that it could no longer take part in development, although it could penetrate the egg and cause it to develop parthenogenetically.

A number of important experiments were tried to test the correctness of this conclusion. The most striking of these were those performed by Günther Hertwig in crossing different species.

It is well known that the sperm of the frog will fertilize the egg of the toad or of another species of frog, but the resulting development proceeds for only a short time and the egg usually dies in the blastulæ stage. Günther Hertwig decided that if the influence of the sperm in development was really destroyed by the intensive radium treatments then such a spermatozoon would merely serve as a parthenogenetic agent and the egg should develop in a normal manner, yet be parthenogenetic. He used the eggs of *Bufo vulgaris* (the common toad) and of *Rana veridis* (the green water frog), and the sperm of *Rana fusca*. He ran two sets of each kind of eggs; one set was fertilized by normal *R. fusca* sperm; the other by sperm which had been treated for two or three hours between two capsules of mesothorium. The eggs fertilized by normal sperm did not develop beyond the blastular stage as was expected, while those fertilized with the radiumized sperm developed about normally and hatched from the jelly and gave rise to swimming tadpoles. O. Hertwig repeated this experiment by crossing the eggs of *Triton vulgaris* with the sperm of *Salamandra maculata*. The sperm were treated for 2¼ hours between two strong mesothorium preparations. Poll had found that this cross proceeded only as far as the blastular stage and Hertwig confirmed this.

When, however, the semen was treated for 2¼ hours a different result was obtained. Many eggs failed to become fertilized, some showed polyspermy, and only six went normally. The chromatin of the sperm was thought to be destroyed and the eggs went by parthenogenesis. Loeb has found in the remarkably wide crosses he has made on invertebrates and vertebrates that the products of part of the foreign sperm finally act as a poison and cause the eggs to develop abnormally. The types of monsters in these crosses are similar to those produced by treating the eggs with chemical poisons. In many cases these sperm take no part in development but initiate the process by serving as a parthenogenetic agent. Hertwig takes the same position, and further finds, that when the foreign sperm is treated with radium the injurious substance contained in it is killed or destroyed so that the spermatozoon initiates development by parthenogenesis without later causing the development to be abnormal. Bataillon's method of sticking eggs with fine platinum needles to give artificial parthenogenesis is similar, Hertwig thinks, to the use of sperm intensively treated with radium. The treated spermatozoon plays the rôle of the platinum needle in Bataillon's experiment. The male chromatin can no longer combine with the female chromatin, there is no amphimixis. Bataillon, by his sticking method, obtained from 10,000 *R. fusca* eggs only 120 hatched tadpoles, and but three metamorphosed, while in some of Hertwig's radium experiments almost all hatched from the jelly.

The radium experiments of Hertwig give us the first method of artificial parthenogenesis which offers promise for use with mammals. Hertwig suggests that since artificial fertilization is possible in many mammals, one might fertilize with semen which had been intensively treated with radium so that the chromatin was destroyed, and with such sperm artificial parthenogenesis in mammals could be accomplished. Two years before Hertwig made this suggestion Dr. Congdon was trying the effects of radium on the spermatozoa of mice and rats in the anatomical laboratory at Cornell and is now continuing these experiments in the anatomical laboratory at Stanford University; up to now he has not succeeded in obtaining fertilization with the modified spermatozoa, though of course much experimentation is necessary in order to establish the proper intensity of the treatment.

These experiments of Hertwig also afford interesting data as to the nature and importance of the part played by the chromatin in development. The cells of the embryos which resulted from eggs fertilized by intensively treated sperm were found by O. Hertwig, P. Hertwig, and Poll, to contain the reduced number of chromosomes showing that the paternal chromatin had been destroyed by the treatment. Günther Hertwig found the nucleus volume in radium larvæ to be one half the size of the nucleus in the control; he measured the mass of nuclei of nerve cells, liver cells, blood corpuscles, embryonic muscle cells, etc. The entire larva was smaller. P. Hertwig found the male pronucleus derived from intensively treated sperm to be modified in the first and second divisions of the frog's egg and Opperman found the same in the trout. O. Hertwig found in *Triton* eggs that the intensively radiumized male chromatin took no part in the developmental process and the soma cells contained one half the chromosome number. The male chromosome set falls out of the development and the soma nuclei contain only the female set.

Finally, Hertwig obtained another most striking result which may be mentioned, although it is not entirely in line with the present subject. When eggs instead of the spermatozoa were subjected to intensive treatments of 2 to 5 hours with radium, the chromatin of the female pronucleus was found to be broken down and destroyed. If eggs, after such intensive treatment, were fertilized by normal sperm, it was found that they developed almost normally, although when eggs were treated from 15 minutes to $\frac{1}{2}$ hour they always developed abnormally though fertilized with normal spermatozoa. Hertwig, therefore, concludes that the intensively treated eggs fertilized by normal sperm develop by the process of merogony; that is, the egg nucleus being destroyed by the treatment, the sperm nucleus enters the egg and causes development to proceed in the same way that the female pronucleus acts in parthenogenesis. Only one set of chromosomes, either the paternal or maternal, is necessary for development of the egg.

During the summer of 1912 I treated the spermatozoa of fish with various salts and organic substances with negative results. When the treatment was sufficiently strong to affect the spermatozoa it rendered them incapable of fertilizing the eggs. A method could no doubt be devised for modifying fish spermatozoa with various chemicals and of course radium does modify the fish sperm as Opperman found.

Only a few experiments have been performed in attempting to modify the offspring of birds by injuring the male. Todde found that the offspring from alcoholized roosters were not quite normal and that the roosters did not succeed as well as usual in fertilizing eggs. Lustig's experiments showed that by inoculating fowls with abrin the offspring were rendered less resistant to inoculations of abrin than were control animals of the same age. This result followed the inoculations of either parent, the male as well as the female.

A more extensive literature bears upon the actions of poisons on the male germ cells of mammals, though most of the cases are uncontrolled observations. The treatment of the germ cells of mammals is a more complex proposition than the experiments on those lower forms in which the fertilization is external and where, for this reason, the eggs and spermatozoa may be treated directly. In mammals the stimulus must be applied through the animal body and the case is thus complicated since it is often impossible to differentiate between the direct action of the substance applied and the secondary effects due to the responses of the parental body to the treatment. With certain treatments, however, the case is not so complex as would appear at first sight, since the substances may pass into the blood stream and the lymph and act directly on the germ cells just as they do on other tissues and cells of the body.

In experiments to modify the germ cells of mammals the first proposition becomes then, to determine whether the substances used reach the germ cells directly. One of the best substances for such experiments is alcohol, since its action and distribution in the body has been largely studied and since it acts so decidedly to modify the developmental processes, as many workers have found on invertebrates, and as I have shown by treating fish eggs with this substance.

It is a well known and generally accepted fact that alcohol does cause changes and degeneration in many of the tissues of animals and man. The question arises, how, then, can the reproductive tissues, the ova and spermatozoa escape? Nicloux and Renault have found that alcohol has a decided affinity for the reproductive glands. In the testicular tissues and the seminal fluid an amount of alcohol is soon present which almost equals that in the blood of an individual having recently taken alcohol. The proportion of alcohol in the testis as compared with that in the blood was as 2 to 3, and in the ovary of female mammals as 3 to 5. From these observations it must follow that alcohol may act directly on the ripe spermatozoon shortly before it fertilizes the egg, and if this substance injuriously affects the germ cells, then one should expect to find an indication of the injury in the resulting development as Hertwig has found from his radium treated spermatozoa.

There are a number of observations on human beings bearing on this point, though they probably all need confirmation by experimentation on lower mammals. Lippich claims to have observed 97 children resulting from conception during intoxication. Only 14 of these were without noticeable defects. Twenty-eight were scrofulous, three had "weak lungs," three showed different atrophic conditions, one watery brain, four feebleminded, etc. Sullivan reported seven fairly authentic cases of drunkenness during conception; six of the offspring died in convulsions after a few months, and the seventh was stillborn.

Rösch was the first, in 1837, to study the reproductive glands of alcoholics and found degeneration of the testicles. Lancereaux described a parenchymatous degeneration of the seminal canals. Simmonds (1898) found azoospermie (spermatozoa without tails) in 60 per cent. of cases of chronic alcoholism; 5 per cent. of these men were sterile. Kyrle reported three cases of total atrophy of the testicular parenchyma in which death had resulted from cirrhosis of the liver due to alcohol. He attributed the atrophy of the testicle to the cirrhosis of the liver and not to chronic alcoholism.

Bertholet (1909) has made an extensive examination of the influence of alcohol on the histological structure of the germ glands, particularly on the testicles of chronic alcoholics. He found testicular atrophy in alcoholics with no cirrhosis of the liver. Bertholet observed partial atrophy of the testicles in the majority of 75 chronic alcoholics. The men died between the ages of 24 and 57 years, the greatest mortality being between 30 and 50 years. In 37 cases, excluding syphilitics, a microscopical examination showed a more or less diffuse atrophy of the testicular parenchyma and a sclerosis of the interstitial connective tissue. The canals were reduced in size and their lumina obliterated. Spermatogonia were atrophic. It was generally impossible to differentiate spermatocytes or spermatids. There were no dividing cells and no spermatozoa. These conditions with slight variations were found in 24 cases. Such atrophic structures were present in one drinker only 29 years old. In 4 cases of cirrhosis of the liver the testicular atrophy had not progressed very far and spermatozoa were still present.

The extreme conditions of atrophy of the testicles were only found in alcoholics. Observing the testicles of nonalcoholics that had died of various chronic illnesses, such as tuberculosis, no atrophy of the testicles or thickening of the membrana propria was found. Two old men of 70 and 91 years still possessed spermatozoa in the canals.

Bertholet concluded that the atrophy he observed was not due to old age, cirrhosis of the liver, or other systemic conditions, but to the effects of chronic alcoholism on the reproductive glands. Weichselbaum has confirmed the observations of Bertholet.

It is certain, however, that the chronic alcoholic is not so often rendered sterile as Bertholet's study would lead one to believe. It is not rare to find alcoholics with large families. My experiments on mammals may not be of sufficient duration at the present time, yet I have male guinea-pigs that have been almost intoxicated on alcohol once per day for six days a week for a period of 32 months, which are still good breeders. Thirty-two months of a guinea-pig's existence is proportionately equal to a good fraction of a human life. A number of these animals have been killed and their testicles examined microscopically and found to be normal. In some cases where the male had failed to succeed in impregnating the female for several times, one of his testicles was removed and studied microscopically; the testicle was found to be normal and the male later gave offspring by other females. Ovaries have been similarly examined and in no case has the alcoholic treatment caused a visible structural change in the reproductive glands. The actual physiological proof of the efficiency of the organs is shown by the ability of the animals to reproduce. Although there is no visible structural change in the germ cells, nevertheless, they have been modified by the treatment to an extent sufficient to cause them in most cases to give rise to defective embryos or weakened individuals which die soon after birth.

Nicloux has carefully demonstrated on dogs and guinea-pigs the passage of alcohol from the blood of the mother into the tissues of the embryo. After a short time the amount of alcohol in the blood of the fetus is about equal to that in the blood of the mother, while there is really slightly more alcohol in a given weight of the tissues of the fetus than is to be found in an equal weight of liver tissue from the mother. The reality of the passage of alcohol from the mother to the fetus demonstrates the possibility of the intoxication of the fetus.

There is an abundance of data bearing on the effects of parental poisoning on the human offspring, yet almost all of it is complicated. The question arises whether the defects of the offspring are actually due directly to the parental poisoning or to the often degenerate condition of the parent. With lower mammals this question may be controlled, since vigorous individuals with no physical weaknesses may be selected for study. One of the most interesting human cases is that Forel cites as recorded by Schweighofer. A normal woman married a normal man and had three sound children. The husband died and the woman married a drunkard and gave birth to three other children; one of these became a drunkard; one had infantilism, while the third was a social degenerate and drunkard. The first two of these children contracted tuberculosis, which had never before been in the family. The woman married a third time and by this sober husband again produced sound children. This is a logical experiment, the female was first tested with a normal male and gave normal children; when mated with an alcoholic male the progeny were defective. She was later tested again with a normal male and found to be capable of producing sound offspring. A number of such cases are on record but all are open to the question whether the defective offspring are actually due to the effects of the poison on the parent, or to the fact that the parent may have been weak and degenerate from the beginning.

Other substances than alcohol seem to act directly on the germ cells of man and mammals, and these actions are more important since there is no reason to believe, for some of them at any rate, that they accompany a degenerate condition. Constantine Paul long ago pointed out that the children of lead workers were often defective.

He made the interesting observation that when the father alone was employed in such work his children were affected. In 32 conceptions with such fathers 12 resulted in premature labor and stillbirths, 20 living births occurred but only 3 children survived. Eight died the first year, 4 the second, and 5 the third year.

Mairet and Cambemale in 1888 were the first to experiment on the influence of alcohol on the mammalian offspring. They treated a dog for 8 months with absinthe (11 gr. per day per kilo of animal weight) and paired this alcoholized dog with a normal bitch. Twelve young resulted; 2 were born dead, 3 died within 14 days, and the others died between 32 and 67 days of intestinal catarrh, tuberculosis, etc. In a second experiment, both parents were mated while normal, then the female was treated for 23 days (2.75 to 5 gr. of absinthe of 72 per cent. per day per kilo). Of 6 young 3 were stillborn, 2 had normal bodies though of weak intelligence, while one was very sluggish. The evident criticism against this experiment is that an insufficient number of animals was used and there was no control. It is very difficult to rear pups in a laboratory; when apparently perfectly normal, they often die shortly after birth.

Hodge, in 1897, obtained similar results. From one pair of alcoholic dogs he observed 23 pups, 8 were deformed, 9 were born dead, while only 4 lived. In a control set, 41 individuals lived, 4 were deformed, but there were no stillbirths.

Nice has recently published results of treating mice with alcohol. He finds little, if any, effect of the treatment on the offspring. Considering his method of administering the alcohol and the results obtained, the doses used were probably insufficient to produce effects. It may also be possible that mice are more resistant to alcohol than are other mammals. I have discussed these experiments in a previous communication.

EXPERIMENTS

Three years ago a series of experiments were begun on guinea-pigs with the hope of modifying the type of embryo in mammals so as to produce definite monstrosities as one is able to do with lower vertebrates. This primary object has not been fully accomplished, yet the experiments have demonstrated several significant points and have shown that an alcoholized male guinea-pig almost invariably begets a defective offspring even when bred to a vigorous normal female.

Normal, healthy animals are selected for the experiment, and in all cases they are first tested by a normal mating in order to establish their ability to produce vigorous offspring. After such a test the treatments are begun. During the experiments the treated males and females are mated from time to time with normal animals, and in addition, control matings of normal individuals are made. Some of the specimens are treated with alcohol and ether. These substances were used since they readily act upon animal cells and since I had studied their effects on the development of fish embryos and found them to cause rather definite and easily recognizable defects in the central nervous system and organs of special sense.

METHOD AND TECHNIQUE

In the beginning of the experiments alcohol was given along with the food, but the animals ate less and the food did not apparently agree with them. It was then administered in dilute form by a stomach tube; this method disturbed digestion and seemed to upset the animals considerably. It is certain that alcohol given to animals through the stomach deranges their digestion and appetite to such an extent that the experimenter is unable to determine whether the resulting effects are due to the alcohol, as such, or to the general deranged condition of the animal. When given in the drinking water they take little or none of the water and the treatment is insufficient. For these reasons an inhalation method of treatment has been resorted to which, as far as experience goes, has no serious disadvantages and does not complicate the conditions of the experiment.

A fume tank of copper is made of sufficient size to supply breathing space for 4 or 5 guinea-pigs at one time. The tank is arranged with four outlets, so that definite amounts of the fumes may be passed through in a given time and the ventilation controlled. In this way each animal could be given about the same amount of the substances. The individuals, however, differ so in their resistance to the treatment that it has been found better to treat all to about the same degree of intoxication. This physiological index is more reliable as each animal is thus affected in a similar fashion each day. For this purpose they are placed in the fume tank on a wire screen, and absorbent cotton soaked with alcohol is placed beneath the screen, and the animals inhale the fumes. The tank was described and illustrated in a previous article.

Ether is given in a similar manner, except that the animals are much more readily overcome and must be carefully watched while inhaling even the most dilute doses.

In order to avoid handling the females during late pregnancy, a special treating cage is devised. An ordinary box-run with a covered nest in which the animal lives is connected by a drop-door with a metal-lined tank, having a similar screen arrangement to that of the general treatment tank. The pregnant animal may be driven daily into the tank and thus treated with alcohol fumes throughout her pregnancy without being handled in any way that might disturb the developing fetus.

DIRECT EFFECTS OF THE TREATMENT ON THE ANIMALS

Many of the animals have now been treated almost to the point of intoxication for six days per week for nearly three years. They are affected by the alcohol fumes in different ways; certain ones become drowsy and stupid, while others become excited and sometimes vicious during the treatment, constantly fighting and biting at others in the tank. One male always had to be treated alone on this account. The fumes are inhaled into the lungs and pass directly into the circulation, so that the animals show signs of intoxication very soon after being put into the tank, yet the intake of alcohol is so gradual that they may remain for one hour or more without becoming totally anesthetized. The mucosa of the respiratory tract is considerably irritated during the first few days or weeks of the treatment, but later becomes hardened and little effect can be noticed. The cornea of the eye is greatly irritated and often becomes milky white and opaque during the first few months; but later this clears up in most of the specimens and the animal is able to see perfectly, though one male that has been treated for 32 months is now entirely blind. The general condition of the animals under the treatment is very good; they all continue to grow if treated before reaching their full size, and become fat and vigorous, taking plenty of food and behaving in a normal manner in every particular.

Certain of the animals have been killed at different times during the experiment and their organs and tissues studied microscopically; all have seemed entirely normal. The tissues of one female were examined after she had been treated for over a year, and the heart, stomach, lungs, liver, kidney, etc., were all normal. She was generally fat but there was no fatty accumulation in the parenchyma of any of the organs except possibly a slight excess in the adrenal glands.

As mentioned above several of the animals, both males and females, have been partially castrated during the experiments and the ovaries and testis have been found to be in healthy condition.

The treated animals are, therefore, little changed or injured so far as their behavior and structure goes. Nevertheless, the effects of the treatment are most decidedly indicated by the type of offspring to which they give rise, whether they are mated together or with normal individuals.

EFFECTS ON THE OFFSPRING

The animals have been mated in various combinations. First, treated males have been paired with normal females, the paternal test; this is the crucial test of the influence of the treatment on the germ cells. In this case the chemically modified or weakened spermatozoon can alone be responsible for the defective offspring, since the egg is normal and develops in a normal environment in the healthy mother.

Second, treated females are paired with normal males, the maternal test. This combination offers two chances for injuring the offspring. Either the ovum may be defective as the result of the treatment which the mother has undergone, and may thus give rise to a defective individual; or secondly, the developing embryo may be affected directly by the alcohol in the system of the mother, since Nicloux has shown that this substance may pass from the blood of the mother into the tissues of the fetus. Thus the intoxication of the embryo may modify its forming structures in the same way that a fish embryo develops deformed organs and parts when in sea-water to which alcohol has been added.

The third combination is the mating of two alcoholic individuals. This is the most severe test and offers the greatest chance for defective offspring.

Before the experiment or treatment begins the guinea-pigs are all tested by normal matings and are found to give normal vigorous offspring. They continue to give normal offspring until the treatment has lasted for some time. The effect accumulates slowly and is not noticed at once. A number of experiments in which the treatment of a female was commenced at the beginning of pregnancy have so far given rather indefinite results, although a slight effect may be indicated.

In all 124 matings of treated individuals have been made. One hundred and three of these have reached full-term and are recorded. Twenty-one matings are not yet due. From the 103 full-term matings only 52 young have survived and most of these are somewhat under size and show their affected condition in the type of offspring to which they give rise. Yet their parents were all unusually large and originally strong animals.

From 35 control matings 56 healthy offspring have been derived which continue to produce normal animals in the following generations, in a few cases now to the fourth generation.

A tabulated summary of the results may be arranged as indicated in Table 1. The conditions of the animals in the mating pairs are shown in the first column of the table and the total results of the matings are indicated in the following columns.

The first horizontal line gives the record when alcoholic males are paired with normal females. Fifty-nine such matings have reached term, 25 of these gave negative results or early abortions. Some embryos were aborted during very early stages and were generally in such poor condition when found in the cages that little could be learned from them. They were partially or completely eaten by the mother in most cases. The males were always kept with the females during favorable periods for a number of days, usually about three weeks, and conception should have occurred in all cases, as it did with the control matings.

Thirty-four of the 59 matings resulted in conceptions which ran the full term. Eight, or about 24 per cent. of these, were stillborn litters, consisting in all of 15 individuals. Most of these were somewhat premature; in a few cases their eyelids were still closed and the hair was sparse on their bodies. (A normal guinea-pig at birth is well covered with a hairy coat, its eyelids are open and it very quickly begins to run about.)

Twenty-six, or only 44 per cent., of the matings produced litters of living young. These litters contained in all 54 individuals. Twenty-one, or almost 40 per cent., of these young guinea-pigs died within a few days or less than four weeks after birth, while 33 of them survived. *Thus, out of 69 full term young, of which 54 were born alive, only 33 have survived, and many of these are small and excitable animals, and although not treated themselves have since given rise to defective offspring in several cases where they have been mated with one another.* On the other hand, 35 control matings have produced 32 living litters consisting of 60 individuals, only 4 of which have died and 56 are perfectly normal animals.

It is of interest that the young animals before dying show various nervous disturbances, having epileptic-like seizures, and in most cases die in a state of convulsion.

The important fact in the above case is that the father only was alcoholic, the mother being a normally vigorous animal. *This experiment clearly demonstrates that the paternal germ cells may be modified by chemical treatment to such a degree that the treated male will beget abnormal offspring even though he be mated with a vigorous female.* A reconsideration of the figures in the first line of the table shows really how decidedly the injured spermatozoon expresses itself in the fate of the egg with which it combines.

For comparison the second line of the table shows the results of matings between alcoholized females and normal males. These matings might be expected to give more marked results than the previous ones, since in the treated female not only the germ cells may be affected, but the developing embryo itself may be injured by the presence of alcohol in the blood of the mother.

There are 15 matings between alcoholized females and normal males. Three of these, or 20 per cent., gave negative results, or were possibly aborted very early. Three stillborn litters were produced consisting of nine individuals, while 60 per cent. of the matings gave living litters. This result is better by 16 per cent. than that obtained when alcoholized males were paired with normal females. The proportion of surviving individuals is, however, less from the treated females than from the treated males. The 9 living litters contained 19 young, 9 of which died soon after birth and 10 survived. Thus out of 28 full term young only 10, or about 36 per cent., survived, while 64 per cent. of the offspring were lost; in the above cases where the male alone was alcoholic almost 48 per cent. of the full term young survived.

TABLE I

CONDITION OF THE OFFSPRING FROM GUINEA-PIGS TREATED WITH ALCOHOL

Condition of the Animals	Number of Matings	Negative Result or Early Abortion	Stillborn Litters	Number Stillborn Young	Living Litters	Young Dying Soon After Birth	Surviving Young
Alcoholic ♂ by normal ♀....	59	25	8	15	26	21	33
Normal ♂ by alcoholic ♀....	15	3	3	9	9	9	10
Alcoholic ♂ by alcoholic ♀..	29	15	3	6	11	7	9
SUMMARY..................	103	43	14	30	46	37	52
Normal ♂ by normal ♀.....	35	2	1	4	32	4	56
2d generation by normal.....	3	0	0	0	3	0	4
2d generation by alcoholic....	3	0	2	5 1 def.	1	0	2
2d generation by 2d generation	19	7	0	0	12	6 1 def.	13
Female treated during pregnancy..................	4	0	0	0	4	1	7

The third horizontal line indicates the results of pairing alcoholized males with alcoholized females. The effects of the treatment in this case are slightly more marked than in either of the above lines. Twenty-nine such matings gave in 15, or more than 50 per cent., of the cases negative results or early abortions. Three stillborn litters occurred, each consisting of two individuals. Only 11 living litters were produced. These contained 16 young, 9 of which survived while 7 died soon after birth.

A comparison of this combination with the control matings given in the fifth line shows in a decisive manner the really detrimental effects of the treatment. In the one case only 9 surviving young were obtained from 29 matings, while in the other the control animals gave 56 surviving young from 35 matings.

The fourth line summarizes the results of the matings made with treated individuals. A total of 103 matings have run the full term; 43, or almost 42 per cent. of these, have given negative results or early abortions; while 35 control matings failed in only two cases to yield a full term litter. Fourteen, or 13½ per cent., of the matings gave stillborn litters consisting of 30 individuals. Only one stillborn litter occurred in the 35 control matings; this was a large litter of 4 young and the mother seemed almost unable to carry them. The 103 matings of treated animals gave only 46 living litters, about 45 per cent., while 32 living litters, or 91½ per cent., were produced by the 35 control matings. The 46 living litters from the alcoholic individuals contained 89 young, 37 of which died shortly after birth and 52 survived. The 32 living litters from the normal animals consisted of 60 individuals, only 4 of which died while 56, or 93 per cent., of these survived.

Of 119 full term young, 30 of which were stillborn, produced by the alcoholic animals, only 52, or less than 44 per cent., survived as against the 56, or 87½ per cent., survivors among the 64 full-term control offspring.

The bottom line of the table shows that 4 normally mated females treated with alcohol during the period of gestation gave 4 living litters, consisting each of 2 young. One out of the 8 young died soon after birth. These few cases would seem to indicate that the treatment, when started at the beginning of gestation, was not particularly injurious to the embryos developing *in utero*.

ARE THE EFFECTS ON THE OFFSPRING TRANSMITTED?

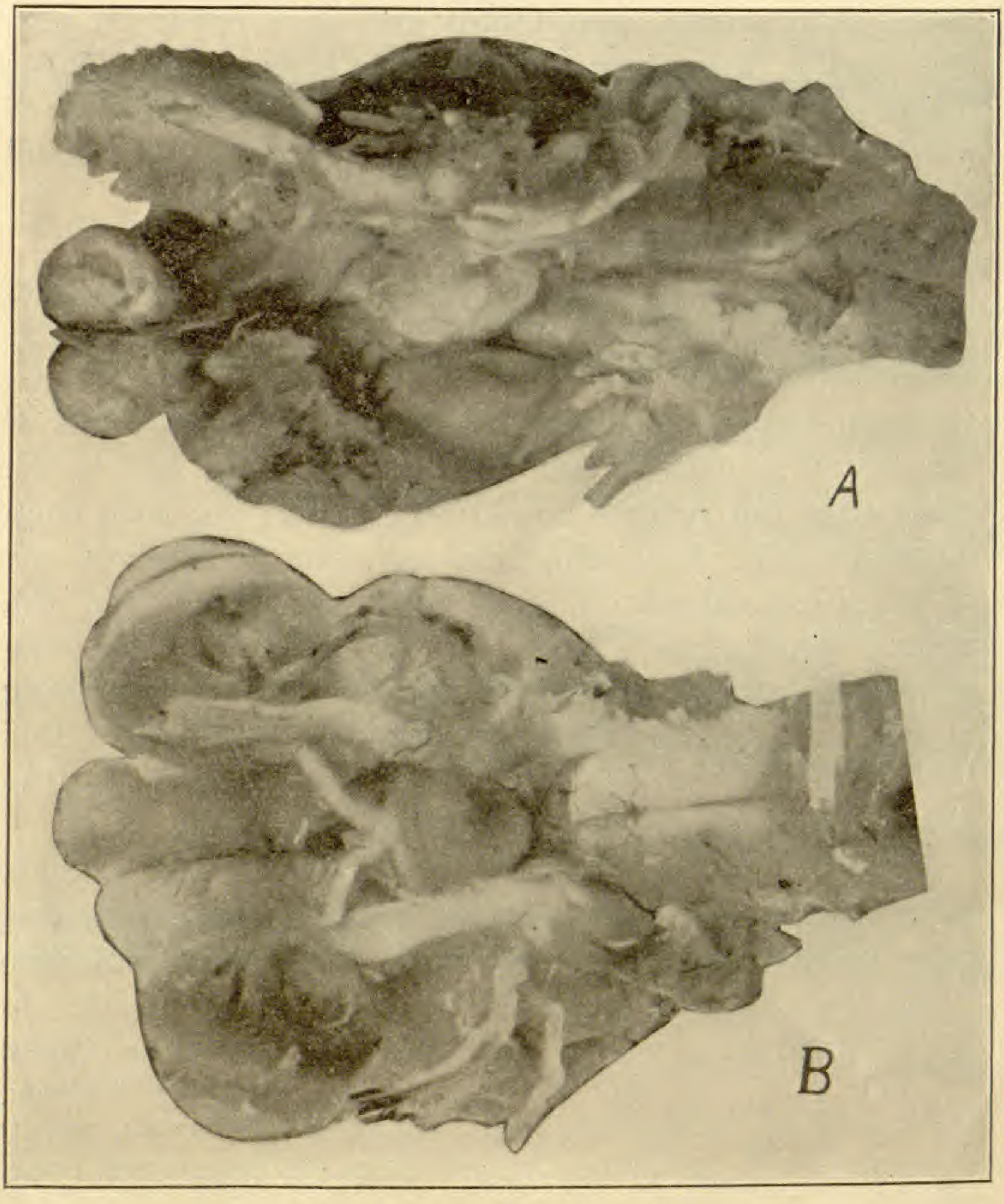
The offspring derived from the alcoholic individuals are termed second generation animals, and were not treated with alcohol. The sixth, seventh and eighth lines of the table represent the data obtained from the few full time matings that have been made with these guinea-pigs.

In three cases second generation animals have been mated with normal individuals and have produced perfect results, though the litters have been small. Three litters are recorded containing a total of 4 young, all of which survived. It might seem as though the normal mate counteracted any defect which may have been present in the second generation animals.

The mating of second generation individuals with alcoholized guinea-pigs gave decidedly different results. The seventh line shows that 2 out of 3 such matings produced stillborn young. In one of these cases the female was of the second generation and the male alcoholic, and in the other case the reverse condition existed; yet both combinations gave dead offspring, one litter of two and one of three individuals. One of these specimens from the second generation female by the alcoholic male was grossly deformed. The third mating gave two surviving young. At present there are too few matings of this combination from which to draw conclusions, yet the results obtained are the most disastrous of all.

Nineteen matings between second generation animals have been made. The outcome in these cases compares very unfavorably with that from the control matings, while the data are much of the same type as those obtained from the alcoholic combinations. Seven, or almost 37 per cent., of the matings gave negative results. Twelve living litters were born consisting of 19 individuals, 6, or about 32 per cent., of which died very soon after birth and showed various nervous disorders. One was entirely eyeless and decidedly deformed.

From the number of records available one might conclude that the effects of the alcoholic treatment were as pronounced upon the offspring of the second generation animals, although they had not been directly treated, as they were upon the offspring of alcoholized individuals. The poison acts upon the cells and tissues of the body, the germ cells as well as other cells, and an offspring derived from the weakened or affected germ cell has all



EXPLANATION OF PLATE

Ventral surfaces of two guinea-pig brains. *A*, the brain of an animal which was entirely eyeless, no optic nerves or tracts are present. *B*, the brain from another member of the same litter. This animal was defective and died shortly after birth, but possessed normal eyes as the photograph shows and the optic nerves are clearly seen passing medially to form the chiasma and from there the optic tracts are shown along the anterior margins of the tuber cineria. All of these optic structures are missing in the brain above.

the cells of its body, both soma and germ, defective since each of the cells is a descendant of the injured germ cell combination.

These are the initial experiments with mammals to show *that an injury of the germ cells may express its effects on the offspring and be passed through subsequent generations.*

The actual outcome of the experiments may be more fully recognized by a consideration of one of the most striking cases. A large normal female, weighing about 700 grams, had given two normal young by a control mating and had since given non-viable young by a mating with an alcoholic male. She was then mated with another large strong alcoholic male which weighed 740 grams and which had given before this mating apparently healthy offspring by normal females. The mating resulted in the production of 4 young, all small and rather excitable in their behavior. These individuals from the normal mother and the alcoholized father grew slowly, although they ate freely and appeared to be well. They remained small and below the average in weight. Three were males and one was a female.

One of the males was mated with a normal female and two normal young resulted. He was then mated with a female from an alcoholic father and she gave birth to two small young; one of these offspring was only half size and very excitable. He was then mated with a female from an alcoholic mother and one small young was produced.

A second one of the three males was mated with a normal female which produced one large apparently normal offspring. He was then mated with a female from an alcoholic father and two small young resulted, one of which died within five days and the other is weak and nervous. He was again mated with a normal female and one normal young was produced.

The third male was mated with his sister and she gave birth to 3 young. One of the young died when one day old, having been in a constant tremor since its birth; another lived for nine days but whenever it attempted to walk it was seized with spasmodic contractions; the third specimen exhibited the same nervous manifestations and was completely eyeless. This animal died eight days after birth and an examination of the brain showed an entire absence of optic tracts, as may be seen in Plate 1*A*.

In the development of this animal it is probable that the optic vesicles were suppressed and never arose from the brain. Thus, no eyes, optic nerves, or optic tracts could have formed. This particular eyeless condition in these experiments is of interest since one is readily able to suppress the origin of the optic vesicles in fish and chick embryos by similarly weakening the embryo with treatments of alcohol, ether, etc.

The mother of these offspring was remated with her brother, but she died six weeks later, not becoming pregnant. She was in an emaciated condition but had always been less than half normal weight.

The three extremely weak and defective offspring were doubtless due to the fact that both of their parents had similarly weakened or injured constitutions, having resulted from a single mating of a normal female with an alcoholized male. The eyeless offspring and the other two nervous non-viable individuals should not be interpreted as due merely to the fact that their parents were brother and sister. Several normal matings of brother and sister have been made during the experiment and perfectly healthy offspring have been produced. In the studies of heredity conducted on guinea-pigs brother and sister are crossed with impunity, in no way weakening their offspring. The significant point in the present consideration is that the two animals coming from the same mother and treated father may have had similar weaknesses or defects and the combination of two such individuals resulted in offspring which exhibited these defects to a more decided extent. The three animals were far more defective than their parents and owed their defects to the modified condition of the germ cells of the grandfather from which they descended.

CONSIDERATION OF INDIVIDUAL MATINGS AND RESPONSES

Studying the data of individual animals, another point of some importance presents itself. This is the fact that the same male often yields very different results when bred to different females, although the females are similar so far as the experiment goes, being either all normal or alcoholic. This may be due to the varying degrees of resistance or hardiness possessed by the germ cells of different individuals. A part of this difference may be due to the fact that as the treatment advances the germ cells are more affected and the results do actually become more pronounced.

Male No. 5 that has been treated with alcohol for two and one half years, has been mated 25 times. Eleven of these matings have yielded negative results; 4 were with alcoholic females and 7 were with normal. Three of the matings gave stillbirths, 2 with normal females and one by an alcoholic female. Only 11 of the 25 matings gave living litters, 4 of these were non-viable and 7 litters survived. Five of the 7 surviving litters were from normal females and 2 from alcoholic mothers. *This alcoholic male has, therefore, begotten only 7 surviving litters out of the 14 full term litters born and out of a total of 25 matings.*

Alcoholic male No. 6 shows a still worse record. Out of a total of 21 matings, 10 have given negative results, 5 by normal and 5 by alcoholic females. Two matings gave stillborn litters, one from a normal female and one from a second generation female. Nine living litters resulted from the 21 matings, 3 from alcoholic females and 6 from normal. Five of the nine litters born alive were non-viable, the young dying soon after birth. *Only 4 litters survived out of the 11 reaching term and out of the total of 21 matings.* Three of these surviving litters were from normal females and one was from an alcoholic mother.

Alcoholic male No. 43 has been mated 10 times. Three of the matings gave negative results, two by alcoholic females and one by a normal. One stillborn litter resulted from a mating with an alcoholic female. Six living litters came from the 10 matings. The young in 3 of these litters died soon after birth and 3 litters survived.

Alcoholic male No. 45 has now been treated about one and one half years and has been mated 9 times. One mating with a normal female gave a negative result. One mating with a normal female gave a stillborn litter. Seven living litters were produced, 5 of which survived, 2 from alcoholic females and 3 from normal females. The data in this case appear slightly better than in the foregoing but this is due to the fact that only a few matings have been made and most of these during the early stages of the treatment, when the effects are not so pronounced.

All of the other alcoholized males in the experiments show comparable records.

A reference to Table I shows that with three exceptions 35 matings of normal males with normal females gave living litters containing in all 60 individuals, only 4 of which failed to survive. This record stands in striking contrast to the data recorded above from the 4 alcoholic males, and it shows convincingly that the alcoholic treatment has affected the germ cells of these males so that they are no longer capable of producing entirely normal offspring even though they be mated with normal females.

The outcome of the successive matings of fifteen different females is tabulated in Table II. The varying ways in which the same individual has responded in different matings is noticeable. Number 15, a normal female, shows an instructive record. Mated with alcoholic male No. 6 she gave two stillborn young; mated with alcoholic male No. 5 a negative result; remated with No. 5, two young were born and both died of convulsions during the fourth week; then mated with a normal male a normal vigorous offspring was produced; mated again with alcoholic male No. 5 an apparently normal guinea-pig was born; mated with No. 43, an alcoholic male, she gave 2 young which only lived for two days; then mated again with a normal male she produced 2 vigorous offspring and finally mated with No. 69, an etherized male, 2 young were born, one of which died at birth. Thus, out of the 8 matings, 2 with normal males gave perfectly normal offspring, while 5 out of the 6 matings with treated males gave disastrous results and only one of these matings resulted in the production of an apparently normal young.

Number 56, a normal female, mated to a normal male, No. 48, gave 2 normal young; with alcoholic male No. 45 gave 3 premature stillborn fetuses; again to a normal male No. 80 gave 3 normal offspring; and finally again to alcoholic male No. 45 she gave one very small young.

Normal female No. 63 gave two normal individuals by a normal mating and then three successive matings with an alcoholic male failed to produce a viable offspring; one mating resulted negatively, one gave three young dying shortly after birth, and in the third case two late fetuses were aborted. She was then mated again to a normal male and produced two vigorous offspring.

Normal female No. 50 was mated alternately with normal and alcoholic males for 4 matings, with alternately good and bad results.

Animals 19, 30, 54 and 58, all normal females, show records closely similar to the ones just mentioned. (In a former table of successive matings the first mating of No. 19 has been recorded incorrectly; it should read by a normal male giving two normal offspring as in the present Table II, instead of by alcoholic male No. 4 with a negative result.)

Alcoholic female No. 64 gave two normal young by a normal male before her treatment was commenced. Mated to alcoholic male No. 6 she gave two young; one died at birth and one survived; with alcoholic male No. 5 she gave an apparently normal young; finally, by alco-

TABLE II

RESULTS OF THE SUCCESSIVE MATINGS OF FIFTEEN FEMALES.

Animal	1st Mating	2d Mating	3d Mating	4th Mating	5th Mating	6th Mating	7th Mating	8th Mating
No. 64 alc.	Nor. ♂, 2 nor. young	Alc. ♂ 6, 2 young, 1 died	Alc. ♂ 5, 1 nor. young	Alc. ♂ 43, 2 foetuses, died *in utero*, killed mother	....	....	....	....
No. 59 alc.	Nor. ♂, 3 nor. young	Nor. ♂ 44, 2 young, 1 died	Alc. ♂ 43, 0	Alc. ♂ 43, 0	Nor. ♂ 69, 3 yg., died *in ut.*, killed mother	....	....	....
No. 30 nor.	Nor. ♂ 25, 2 nor. young	Alc. ♂ 45, 2 nor. young	Alc. ♂ 5, 1 nor. young	Alc. ♂ 5, 2 foetuses, died *in utero*, killed mother	....	....	....	....
No. 15 nor.	Alc. ♂ 6, 2 stillborn	Alc. ♂ 5, 0	Alc. ♂ 5, 2 young, both died in convulsions	Nor. ♂, 1 nor. young	Alc. ♂ 5, 1 apparently normal	Alc. ♂ 43, 2 young, both died 2d day	Nor. ♂ 70, 2 nor. young	Ether ♂ 69, 2 young, 1 died
No. 19 nor.	Nor. ♂, 2 nor. young	Alc. ♂ 6, 1 stillborn	Alc. ♂ 6, 0	Alc. ♂ 5, 4 small, ½ size young	Alc. ♂ 45, 2 young, 1 died	Alc. ♂ 6, 0	Alc. ♂ 6, 3 young, 2 died	
No. 63 nor.	Nor. ♂ 44, 2 nor. young	Alc. ♂ 5, 0	Alc. ♂ 5, 3 young, all died	Alc. ♂ 5, 2 late foetuses aborted	Nor. ♂ 93, 2 nor. young	....	....	....
No. 50 nor.	Nor. ♂ 46, 3 nor. young	Alc. ♂ 43, 2 young, both died	Nor. ♂ 69, 2 nor. young	Alc. ♀ 43, 0	....	....	....	....
No. 54 nor.	Nor. ♂ 44, 2 nor. young	Alc. ♂ 6, 2 young, both died	Nor. ♂ 72, 2 nor. young	Alc. ♂ 43, 1 young	....	....	....	....

Animal	1st Mating	2d Mating	3d Mating	4th Mating	5th Mating	6th Mating	7th Mating	8th Mating
No. 55 alc.	Nor. ♂, 2 nor. young	Alc. ♂ 6, 0	Nor. ♂ 47, 2 young, both died	Alc. ♂ 6, 1 young	....	....	....	....
No. 56 nor.	Nor. ♂ 48, 2 nor. young	Alc. ♂ 45, 3 premature, stillborn	Nor. ♂ 80, 3 nor. young	Alc. ♂ 45, 1 young, very small	....	....	....	....
No. 58 nor.	Nor. ♂ 46, 2 nor. young	Alc. ♂ 6, 2 nor. young	Alc. ♂ 43, 1 young, died at birth	Alc. ♂ 6, 0	....	....	....	....
No. 60 alc.	Nor. ♂ 46, 3 young, all died	Nor. ♂ 44, 2 nor. young	Alc. ♂ 45, 1 stillborn	Alc. ♂ 43	....	....	....	....
No. 62 alc.	Nor. ♂ 47, 2 nor. young	Nor. ♂ 46, 2 small young	Alc. ♂ 6, 2 young, died 2d day	Alc. ♂ 45, 2 young, died 2d day	....	....	....	....
No. 65 nor.	Nor. ♂, 2 nor. young	Alc. ♂ 5, 2 small young	Alc. ♂ 6, 2 small young	Nor. ♂ 83, 2 young, 1 died, ♀ treated during pregnancy	....	....	....	....
No. 66 alc.	Nor. ♂, 1 nor. young	Nor. ♂ 44, 2 nor. young	Alc. ♂ 5, 0	2d gen. ♂ 102, 3 fetuses aborted	2d gen. ♂ 102, 2 small young	....	....	....

holic male No. 43 she produced two fetuses which died *in utero* and killed her.

Female No. 59, alcoholic, has a similar record and was also finally killed by 3 fetuses dying *in utero* and poisoning her.

Alcoholic females 55, 60, 62 and 66 all show very poor records in the production of viable offspring.

During the course of the experiments four females have been killed by the death of fetuses *in utero*. In three of the cases this occurred after the females had been treated with alcohol for a number of months and were becoming more and more affected by the treatment. No. 61 died after she had been given alcohol for four months with three fetuses *in utero* which had apparently been dead for several days. No. 64 had been treated with alcohol for over one year and finally, while in a late stage of pregnancy by alcoholic male No. 43, she became stupid and refused to eat. On examination the fetuses showed no signs of life and were quite hard; they were removed by operation and had been dead several days. The mother had become so intoxicated by this condition that she was unable to recover after the removal of the fetuses.

Female No. 59 had been treated with alcohol for thirteen months when, after being mated with a normal male, she was operated upon in order to remove three dead fetuses. She failed to recover.

The fourth case of young dying *in utero* was that of a normal female, No. 30, that had been mated with an alcoholic male. The almost full term fetuses died and produced the same symptoms in the mother as those in the cases above; she was also operated upon and failed to recover.

It is a perfectly easy operation to remove the ovaries or uterus from a normal guinea-pig. I have not tried to remove living fetuses. There is little doubt, however, that it is the accumulated toxins owing to the presence of the dead fetuses which prevented the females from recovering after the operation in these three cases.

The death of the late fetuses *in utero* is to be expected merely as a step in the series. A number of early abortions of embryos have occurred, and the table shows the enormous fatality among the young shortly after birth, as well as the frequent occurrence of stillborn litters. When the young happen to die shortly before birth instead of after birth, the female in some cases is unable to expel them from the uterus.

A consideration of a few of the notes made from the individual matings will further serve to illustrate the actual response of the animals to the treatment as shown by the outcome of the matings. For this purpose we may take two random groups.

First a group of eleven matings made on October 30 and 31, 1912, resulted as shown in the following notes:

Oct. 30, Nor. ♀ No. 30 × Alc. ♂ 5 = Jan. 9, 1913—One normal young, No. 123 ♀.

Oct. 30, Nor. ♀ No. 29 × Alc. ♂ 45 = Jan. 20, 1913—Three very small young, Nos. 134 ♂, 135 ♀, and 136 ♀.

Oct. 30, Nor. ♀ No. 58 × Alc. ♂ 6 = Jan. 15, 1913—Two normal young, Nos. 129 ♂, 130 ♀.

Oct. 30, Alc. ♀ No. 62 × Nor. ♂ 46 = Jan. 9, 1913—Two small but normal young, Nos. 121 ♀, 122 ♀.

Oct. 30, Alc. ♀ No. 59 × Alc. ♂ 43 = 0.—*Only one of the eleven matings that did not take.*

Oct. 30, Alc. ♀ No. 60 × Nor. ♂ 44 = Jan. 17, 1913—Two apparently normal young, Nos. 131 ♂, 132 ♂.

Oct. 31, Nor. ♀ No. 68 × Nor. ♂ 69 = Jan. 21, 1913—Three normal young, Nos. 137 ♂, 138 ♂, 139 ♂.

Oct. 31, Nor. ♀ No. 71 × Nor. ♂ 72 = Jan. 10, 1913—Two small normal young, Nos. 126 ♂, 127 ♂.

Oct. 31, Nor. ♀ No. 73 × Nor. ♂ 70 = Jan. 19, 1913—One large young, No. 133 ♀.

Oct. 31, Nor. ♀ No. 74 × Nor. ♂ 79 = Jan. 11, 1913—One large young, No. 128 ♀.

Oct. 31, Alc. ♀ No. 55 × Nor. ♂ 47 = Jan. 9, 1913—Two small and weak young, Nos. 124 ♀, 125 ♂, both died when one month old.

In the group of 11 matings, 4 were between normal males and normal females, control matings, three were between alcoholic males and normal females, and three between normal males and alcoholic females. All of these produced offspring as noted, while the single mating between an alcoholic male and an alcoholic female gave a negative result although the animals were kept together as long as the individuals of any of the other pairs, 17 days.

One of the alcoholic females gave two young which died within a month.

A second group of 18 matings made during November, 1912, are recorded as follows:

Nov. 4, 2d Gen. ♀ 100 × 2d Gen. ♂ 92 = 0.—Together very long, though failed to take.

Nov. 4, 2d Gen. ♀ 101 × 2d Gen. ♂ 99 = 0.—Together very long, though failed to take.

Nov. 15, 2d Gen. ♀ 91 × 2d Gen. ♂ 92 = Feb. 18, 1913—One large young, apparently normal, No. 170 ♂.

Nov. 15, 2d Gen. ♀ 98 × 2d Gen. ♂ 99 = 0.—Failed to take, though together six weeks.

Nov. 16, 2d Gen. ♀ 76 × 2d Gen. ♂ 77 = Jan. 28, 1913—Three defective young, one eyeless, all died within 10 days.

Nov. 16, Nor. ♀ 88 × 2d Gen. ♂ 78 = Feb. 20, 1913—One large young apparently normal, No. 171 ♂ (long gestation).

Nov. 16, Alc. ♀ 66 × Alc. ♂ 5 = 0.

Nov. 16, Nor. ♀ 87 × 2d Gen. ♂ 75 = Jan. 27, 1913—Two normal young, Nos. 140 ♀, 141 ♂.

Nov. 16, Nor. ♀ 19 × Alc. ♂ 6 = Jan. 30, 1913—Three small weak young, two died shortly after birth, one No. 146 ♂ survived.

Nov. 16, Nor. ♀ 34 × Alc. ♂ 43 = Feb. 4, 1913—Two normal young, Nos. 156 ♀, 157 ♂.

Nov. 16, Nor. ♀ 49 × Alc. ♂ 45 = Jan. 31, 1913—Three normal young, Nos. 147 ♂, 148 ♀, 149 ♀.

Nov. 16, Nor. ♀ 33 × Nor. ♂ 46 = Jan. 30, 1913—Two fine young, Nos. 144 ♂, 145 ♀.

Nov. 23, Nor. ♀ 50 × Nor. ♂ 69 = Feb. 5, 1913—Two large young, Nos. 160 ♂, 161 ♀.

Nov. 23, Nor. ♀ 15 × Nor. ♂ 70 = Feb. 4, 1913—Two large young, Nos. 158 ♀, 159 ♂.

Nov. 23, Nor. ♀ 54 × Nor. ♂ 72 = Feb. 3, 1913—Two large young, Nos. 150 ♂, 151 ♂.

Nov. 23, Nor. ♀ 56 × Nor. ♂ 80 = Feb. 3, 1913—Three normal young, Nos. 152 ♂, 153 ♂, 154 ♀.

Nov. 23, Nor. ♀ 52 × Nor. ♂ 81 = Feb. 12, 1913—One large young, 167 ♀.

Nov. 23, Nor. ♀ 53 × Nor. ♂ 48 = Feb. 3, 1913—One large young, 155 ♂.

To summarize these 18 pairings: 7 were normal control matings all giving vigorous young. Three were alcoholic males by normal females, all gave young. Two litters consisted of small animals, while the third litter was very weak, two of its members died just after birth.

Five of the matings were made between untreated animals which came from alcoholic parents, second generation animals. One litter of 3 individuals was born, all were weak and defective, one being eyeless and the 3 died within ten days. One other litter consisted of only one individual which was born after an unusually long period of gestation. Three of the matings gave negative results. Thus 3 out of 5 second generation matings failed to take, one gave non-viable young, and only one litter of viable young was produced from the 5 matings, as against 7 viable litters from the 7 control matings.

There were two matings of second generation males by normal females. Both of these gave viable young, though one of the females had an unusually long gestation period. The normal mates seemed to have counteracted the weakened condition of the second generation males.

The one mating between two alcoholic individuals again gave negative results.

Thus 4 of the 18 matings failed to take, 3 of these were between second generation animals and the fourth was the double alcoholic mating.

Fourteen matings were successful, in five cases one member of the pair was normal and in seven cases both were normal. In the remaining two cases both animals were of the "second generation," though themselves untreated, one litter was non-viable and but a single litter of one young survived.

These sample notes from 29 pairs out of the total of 167 full term matings contained in Table I, gives a fairly clear idea of the manner in which the individual animals respond.

CONCLUSIONS

Finally, in conclusion, we may consider the type or nature of the injury produced by the treatments and the manner of transmission or inheritance involved. The treated animals themselves show no effects of nervous or systemic injuries in their general health or behavior. It is only when such individuals are bred that they prove to be inferior to the untreated animals. This inferiority is shown both by a slowness or failure in many cases to conceive, although they copulate normally, and by the poor quality of the offspring to which the successful conceptions give rise. That this poor quality of offspring is due to an injury inflicted by the treatment on the germ cells of the alcoholic animals is shown by the fact that when the male alone is treated the offspring he begets are decidedly inferior. The germinal taint is still further demonstrated by the fact that the offspring from treated parents although themselves not treated produce equally or more defective young than do the treated animals.

The defects shown by the offspring of alcoholic parentage are general in type, not definite or specific. The central nervous system and special sense organs are apparently most affected, and this is true also in embryos developing in unfavorable environments. I have found that fish embryos when developed in a large number of unusual environments, including alcohol and ether, always show marked abnormalities of the nervous system and special sense organs, particularly of the eyes and ears. When chick embryos are subjected to similar environmental conditions, it has been found in experiments performed during the last two winters, that they respond in a manner similar to the fish. Many chick embryos show different degrees of cyclopia and the degeneration or absence of one eye of the normal pair is a common defect in the chick as it is in the fish where many grades of monophthalmicum asymmetricum were described in my communications on the subject. In this connection the eyeless guinea-pig derived from untreated animals that had an alcoholic father becomes of special interest, and the general nervous symptoms, spasms, epileptic-like seizures, etc., shown by animals of two generations gain importance.

All defects of the nature of those mentioned may be considered as due to weakened development or developmental arrest. Any environment which weakens or retards the early stages of development will cause such conditions. How, then, are they transmitted by the alcoholic male, or by the untreated offspring of alcoholic parentage?

When the animal is treated with alcohol, lead or almost any poison for a long period of time, the poison acts to weaken or injure all of the body tissues with which it comes in contact through the circulation, the liver and other glandular organs usually show the effects in particular. The reproductive glands are injured as well as others and all the cells and tissues of such an organ are below normal. When such a male animal is paired with a normal female, the resulting offspring contains in every cell of its body elements derived from the weak or injured male pronucleus. Unless the vigor of the normal parent is sufficient to overcome the injured condition, the offspring is defective.

The important thing in considering this defective offspring is the recognition of the fact that not only its soma cells but its germ cells as well are defective, since all were derived from the modified spermatozoon of the injured father. When this offspring with injured germ cells is paired with a similar individual, as has been frequently done in the experiments described, the resulting animal body is constituted of cells, all of which are the result of proliferation or division from the primary injured egg and sperm cell; thus all of the cells are of a similar inferior nature. Therefore, the young derived from the second generation should be, leaving out of consideration the power of a cell to recover from such poisoning, equally as defective as those derived from the treated parents.

This might be construed to show the transmission of acquired characters, but it can not be properly interpreted in such a sense. There is in this case no transmission of new or strange characters strictly speaking, merely a weakened or injured cell gives rise to other weak cells. The term ''weak'' is employed for the lack of a better one, meaning that the cells are below normal in reaction, respond slowly or in a deranged manner and often die or wear out early in their career.

It may be that in nature such defects as hare-lip and cleft palate are transmitted in a fashion similar to the method just suggested. These defects run in families and are said to be inherited. Their character, however, is clearly that of a developmental arrest. Such defects are very probably not truly inherited at all, that is, they are not definite characters or qualities as hair and eye color are, but are due to the fact that the germ cells from which the deformed individual arose, or the uterine environment in which it developed, were not fully normal in vigor. A more careful study of the inheritance of such defects will doubtless reveal the fact that other deformities and developmental arrests are also common in the same families. In other words, weak germ cells or the poor developmental environment runs in the family, and hare-lip and cleft palate are merely the external expressions of these conditions.

The interpretation may be concretely expressed as follows: Mammals treated with injurious substances, such as alcohol, ether, lead, etc., suffer from the treatments by having the tissues of their bodies injured. When the reproductive glands and germ cells become injured in this way they give rise to offspring showing weak and degenerate conditions of a general nature, and every cell of these offspring having been derived from the injured egg or sperm cell are necessarily similarly injured and can only give rise to other injured cells and thus the next generation of offspring are equally weak and injured, and so on. The only hope for such a line of individuals is that it can be crossed by normal stock, in which case the vigor of the normal germ cell in the combination may counteract, or at any rate reduce, the extent of injury in the body cells of the resulting animal. By continually introducing normal mates into such a line the defects might be entirely eliminated, but the continued interbreeding of animals with defects or systemic injuries will doubtless result in the death of the race.

The offspring from a diseased father derives all of its cells from the poor sperm, thus each cell is poor in part and is so passed from generation to generation.

The present experiments are being continued and a large number of matings between second and third generation animals are now made. Various combinations of second generation animals are being tried in order to compare the effects resulting from paternal and maternal treatments, as well as the doubled effects. Two animals, both derived from alcoholic fathers, are mated, others from alcoholic mothers, and the various crosses between these classes are tried. In other cases second generation sisters are mated one with a normal and the other with an alcoholic male, and subsequently these matings will be reversed in order to study the power of the normal mate to counteract the injured condition, as well as the tendency of new alcoholic cells to augment the condition.

SUMMARY

Three years ago a series of experiments were begun with guinea-pigs in order to test the possibility of modifying the type of development in mammals, so as to produce definite monstrosities, as had been accomplished with lower vertebrates. This primary object has not been fully attained at the present time, yet the experiments have demonstrated several points concerning injury of the germ cells, and have shown that an alcoholized male guinea-pig almost invariably begets defective offspring even when mated with a vigorous normal female.

A method has been devised for administering the alcohol by inhalation. The animals inhale the fumes of 95 per cent. alcohol which are readily taken into the pulmonary circulation, and very soon cause a state of intoxication. By this method the stomach is not injured and the general metabolism of the animal is maintained in a healthy condition. Few changes are produced in the tissues of the animals, even after a treatment given six times per week has extended over almost three years. Yet the actual effects upon the reproductive glands are indicated by the inferior quality of the offspring to which the alcoholized individuals give rise.

The animals have been mated in various combinations. First, alcoholized males are paired with normal females, the paternal test, and also the crucial test of the influence of the treatment on the germ cells. Fifty-nine such matings have reached term. Twenty-five of these gave negative results or early abortions. Thirty-four of the fifty-nine matings resulted in conception which ran the full term. Eight, or about 24 per cent., of these were stillborn litters containing in all 15 dead individuals. Many of them were somewhat premature. Twenty six, or only 44 per cent., of the matings produced litters of living young, containing a total of 54. Twenty-one, or almost 40 per cent., of these young animals died within a few days or less than four weeks after birth and only 33 of them survived. Many of the 33 survivors are small excitable animals and though not treated themselves have usually given rise to defective offspring in the several cases where they have been mated with one another.

The second combination is between alcoholized females and normal males, the results of which are interesting in comparison with the above. In this combination there are two chances to injure the offspring; in the first place it may arise from a defective egg cell, or secondly, it may be injured by an abnormal developmental environment within the body of the alcoholized female. Fifteen such matings have been made. Three of these, or 20 per cent., gave negative results, or were possibly aborted very early. Three stillborn litters of nine individuals were produced. Sixty per cent. of the matings gave living litters, as against 44 per cent. in the first combination between treated males and normal females. The proportion of surviving young is, however, less from the treated females than from the treated males. Of 19 living young, 9 died soon after birth and 10 survived.

The third combination was between alcoholized males and females. Twenty-nine such matings gave in 15, or more than 50 per cent., of the cases negative results or early abortions. Three stillborn litters occurred, each consisting of two individuals. Only 11 living litters were produced containing 16 young, 9 of which survived while 7 died soon after birth.

All of the matings of the treated animals may be combined and compared with control matings as follows: In a total of 103 full term matings, 43, or almost 42 per cent., have given negative results or early abortions, while 35 control matings failed in only two cases, or about 6 per cent., to yield a full term litter. Fourteen, or 13½ per cent., of the matings gave stillborn litters consisting of

30 dead individuals. Only one stillborn litter occurred in the 35 control matings; this was a large litter of 4 individuals and the mother seemed almost unable to carry them. The 103 matings gave only 46 living litters, about 45 per cent., while 32 living litters, or 91½ per cent., were produced by the 35 control matings.

The 46 living litters from the alcoholic matings contained 89 young, 37 of which died shortly after birth and 52 survived. The 32 living litters from the normal animals consisted of 60 individuals only 4 of which died while 56, or 93 per cent., of them survived.

Of 119 full term young, living and stillborn litters, produced by the alcoholic animals only 52, or less than 44 per cent., survived as against the 56, or 87½ per cent., survivors among the 64 full term control offspring.

The offspring derived from the alcoholic individuals are termed second generation animals and were not themselves treated with alcohol. In three cases second generation individuals have been mated with normal and have given perfect results, although the litters have been small. It might seem as though the normal mate possessed a strong tendency to counteract any defect which may have been present in the second generation animal.

Mating second generation individuals with alcoholized guinea-pigs gave very different results. Two out of three such matings produced stillborn young, one of which was grossly deformed. The third mating gave two surviving young.

Nineteen matings have been made between second generation animals, the outcome of which compares very unfavorably with that from the control matings, while the data are closely similar to those obtained from the alcoholic matings. Seven, or almost 37 per cent., of the matings gave negative results. Twelve living litters were born consisting of 19 individuals, 6, or about 32 per cent., of which died very soon after birth and showed various nervous disorders; one was entirely eyeless and decidedly deformed.

From the number of records available one might conclude that the effects of the alcoholic treatment were as pronounced upon the offspring of the second generation animals, although they had not been directly treated, as upon the offspring of alcoholized individuals. The poison injures the cells and tissues of the body, the germ cells as well as other cells, and the offspring derived from the weakened or affected germ cells have all of the cells of their bodies defective, both soma and germ, since each of the cells is a descendant of the injured germ cell combination. In this manner the defects or degenerate conditions are transmitted or passed to subsequent generations.

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SUPPLEMENTARY STUDIES ON THE DIFFERENTIAL MORTALITY WITH RESPECT TO SEED WEIGHT IN THE GERMINATION OF GARDEN BEANS

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I. INTRODUCTORY REMARKS

In an earlier paper[1] I have shown that in field cultures the mortality of seeds of *Phaseolus vulgaris* is not random, but selective with respect to seed weight.

From the available data it appeared that both the upper and lower weight classes are more heavily drawn upon in the mortality than is the modal region of the seed weight distribution. So delicately balanced is this mortality of the two extremes in the particular series of experiments that the mean weight of the survivors in the long run differs not at all from that of the population from which they are drawn, while their variability, either absolute as measured by the standard deviation or relative as expressed by the coefficient of variation, is distinctly less than that of the original population.

Now while these results are deduced from such large and representative series of data, that their general validity for the specified conditions seems beyond much question, their substantiation has appeared to me for two reasons most desirable:

(*a*) The demonstration of selective elimination was somewhat indirect. Comparisons could not be made between the physical constants of the seeds which developed and those of all exposed to risk, or between the constants of those which actually failed and those which actually developed, but were necessarily drawn between the constants of the general population from which the seeds were taken for planting and those of the seeds

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[1] Harris, J. Arthur, "On Differential Mortality with Respect to Seed Weight Occurring in Field Cultures of *Phaseolus vulgaris*," AMER. NAT., 46: 512–525, 1912.

which developed to maturity. The method is perfectly legitimate, providing the samples planted be drawn in a purely random manner (as they were in these experiments), but the probable error of random sampling is a two-fold one, and this increases the difficulty of determining the statistical significance of a given constant.

(*b*) The result seemed, *a priori*, improbable. Other studies[2] had demonstrated a moderately low but consistently positive correlation between the weight of the seed planted and the number of pods on the plant produced. It seemed reasonable to assume that since the larger seed produce the heaviest plants they are in general more vigorous, and hence should be more viable.[3] If the seeds increase in vigor and viability from the smallest to the largest, one would anticipate an increase in the mean of the survivors and a decrease in their variability resulting from the mortality in the lower part of the range of variation instead of a reduction in variability without a change in type (mean). These were the biological hypotheses which led me to question the generality of the statistical findings. Further work was therefore undertaken along various lines. Additional field cultures in which it will be possible to compare the constants of the seeds developing with those of the seeds failing, were made.[4] Such cultures can only substantiate, refute or modify the conclusions drawn from the experiments already carried out, but will not advance our knowledge of the proximate causes of the differential mortality. To this end, physiological (including chemical and physical) studies must be instituted.

The purpose of this paper is to discuss the results of

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[2] Harris, J. Arthur, "On the Relationship between the Weight of the Seed Planted and the Characters of the Plant Produced," *Biometrika*, 9, pt. 1, 1913; also "The Size of the Seed Planted and the Fertility of the Plant Produced," *Amer. Breed. Mag.*, 3: 293–295, 1912.

[3] Providing of course that the correlation between size of seed planted and size of plant produced is not merely the result of extra reserve food in the larger seeds.

[4] The results of these and of other data from experiments made long since, but as yet in a raw condition, should be ready in a few months.

one of these physiological experiments, in as far as they bear upon the questions of the existence of a differential mortality and of its consequences in the population. The evidence which they afford concerning the causes underlying the differential death rate is a question too complicated both biologically and statistically to be discussed in the limits of this paper.

For a fair understanding of the portions of the data which are placed before the reader, it will be necessary, however, to state briefly the general purposes which led to the adoption of the particular methods employed.

On the assumptions that the vigor of the seeds increases from the lower to the higher weight classes,[5] one might expect a mortality of seeds in the lower portion of the range of variation due to innate incapacity for development. One must then seek some other factor to account for the mortality of the heavier seeds.

One of the simplest *a priori* assumptions is that the larger seeds require longer to germinate and that they are in consequence longer exposed to the vicissitudes of germination—to death by excessive moisture or by excessive draught before or shortly after expanding their leaves.

Now nothing whatever is here stated or implied in favor of any of these suggestions. For the present, they stand purely and simply as the first of a series of hypotheses to be tested in the quest of the true interpretation of an observed phenomenon. They are mentioned here solely to explain why a particular series of experiments was set up in the way in which it was.

II. METHODS

The first thing needful in testing these hypotheses is to determine the relationship between the size of the seed and the time required for its germination. To do this, while at the same time securing data for a further test of

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[5] The chief evidence in support of this view is that afforded by the results already mentioned for the correlation between the weight of the seed planted and the characters of the plant produced. But of course this correlation may be due solely to stored food materials.

the existence of a selective mortality, one must work with as large numbers of seeds as possible in order to obtain a reliable measure of selective mortality as well as decisive constants for the relationship between seed weight and time required for germination, if it be of the low or moderate order that one might expect. It is desirable that the germination tests be made under conditions as uniform as possible. The technique adopted must also be practical—that is, in the case of the present study, the work was necessarily done at a season of the year when it would not interfere with other experiments; the seeds had to be germinated so that each of the many hundreds or thousands of pots could be examined without too great back or eye strain every three hours throughout the twenty-four during the whole period of germination; finally, the expense of setting up and maintaining the experiment had to be kept within reasonable limits.

These requirements seemed, after careful consideration, best met by planting the seeds separately in three-inch pots of moderately fine sand. To facilitate handling, the pots were filled with slightly moist sand which was generally allowed to dry before the seeds were planted. The whole experiment was then watered at the same time. In a few instances, it was impossible to have the sand of all the pots perfectly dry when the seeds were planted, but I believe this introduces only a small source of error, for in these cases the planting was rushed through as rapidly as possible, and the individually labeled seeds were always thoroughly shuffled before planting to counteract, in as far as might be, the heterogeneity of environmental conditions afforded by different parts of the greenhouse. The space on the benches was filled to the level of the top of the pots with sand to prevent too great evaporation.[6] The labels were com-

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[6] In a few earlier experiments, fine bench gravel was used, in the later ones, sand of the same kind as that in the pots. The gravel was employed at first, since I thought it might be feasible to water indirectly by flooding the gravel and allowing the sand to absorb it through the sides of the pots. This proved entirely impracticable. Not only was the method of watering unsuccessful, but the gravel permitted an enormous amount of evaporation.

pletely sunk in the sand so that the series number and the weight of the seed were quite unknown at the time of recording the results. Thus personal equation as far as it implies any bias with regard to the material was absolutely excluded.

At the outset, I must emphasize the fact that this technique (which I still believe is the best possible under all the requirements) falls far short of what one would desire. The germination of bean seeds under glass on a large scale is a rather difficult process. If a sufficient supply of moisture can be held in the soil from the beginning to the end of the experiment and the temperature be kept fairly high, the problem of good germinations in the greenhouse is solved. But when one is doing the work during the period of hot days and cool nights coming in the early fall, the question of maintaining proper soil moisture and temperature is a very serious one. It is remarkable how heterogeneous the environment of a single section of a greenhouse system is! This is especially noticeable in the drying out of the pots in sand cultures. Just here lies one of the greatest difficulties. The germinating bean seedling is very sensitive to watering, especially in connection with low temperature. I imagine this is particularly true of old seeds which have nearly lost their viability. Probably the considerable irregularity in our percentages of germination is very largely due to the impossibility of controlling closely enough the soil moisture.[7]

In classifying, three groups were recognized: (*A*) seeds germinating normally, (*B*) seeds germinating but producing seedlings more or less abnormal, (*C*) seeds failing to germinate.

On general grounds, the recognition of the three classes seemed desirable; for purposes other than those of this paper, it was essential. They can, of course, be combined

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[7] The effect of this inability to control moisture sufficiently was, when present, always in the direction of a reduction of the percentage of germination through the rotting of some of the seeds, for in all cases the amount of water was finally sufficient to bring about germination.

at pleasure for comparisons. The distinction between *A* and *C* or *B* and *C* allows of practically no difference of opinion. Personal equation probably plays considerable part in distributing the seedlings between those which germinated normally and those which were somewhat abnormal, for there is no clear line of distinction between the two. Practically all the cases were decided by myself. The abnormalities were in small part teratological and in part physiological or pathological—*i. e.,* curved hypocotyls failing to bring the plumule promptly to the surface, cotyledons failing to free themselves from the seed coat, blighted primordial leaves, etc. The results of this study seem to indicate the need of more precise consideration of aberrant seedling in future experiments.

III. Materials

This research and the one which preceded it are inbetween seed weight and seed mortality in *Phaseolus vulgaris* as a whole,[8] and at the same time lay up data which when sufficiently supplemented by others of various kinds shall enable one to determine whether (and if so, why) the relationship between seed weight and seed mortality differs from variety to variety, or whether it is dependent upon the conditions under which the seeds planted were grown or those under which they were germinated, or upon the age of the seeds.

Five characteristics were, therefore, deemed desirable in the seeds used. (*a*) They should be known from breeding tests to belong to strains as uniform as possible. (*b*) They should represent several distinct varieties. (*c*) Different lots should have been grown under as diverse environmental conditions as possible. (*d*) Different ages of as nearly as possible comparable seed should be investigated. (*e*) Comparison with the results of field experiments should be easily carried out.

[8] The materials are, however, for technical reasons limited to the dwarf varieties.

These conditions were most satisfactorily met in the seeds held over from various pedigree experiments made during the last several years. Coupled with the favorable points of these are some obvious disadvantages,[9] which practically are of relatively small weight in view of the fact that it would require several years work to secure a better series.

It is unnecessary to devote space to the description of these materials, since the key letters used are those employed in previous papers, in which a large amount of quantitative information concerning them may be obtained.

Altogether thirteen "experiments" were made. That is, a greenhouse or a section of a greenhouse was filled thirteen times. These experiments are numbered *A* to *M*, and the letters separated from the pedigree formulæ by dashes in the tables refer to them. As a glance at the tables will show, several different series of seeds often went into a single experiment—the capacity of the small greenhouse being about 3,000 and that of the large greenhouse about 8,000 pots. The specific details of these experiments seem at present irrelevant.

[9] Chief among these is the age of some of the seeds—resulting in very low percentages of germination. This is possibly a very important factor. The field cultures were grown in 1908, 1909 and 1910. The sand cultures, made in large part from samples of the same lots of seeds as used in the various field experiments, were carried out in the summer of 1912. Any one who takes the ratio of the seeds germinating to those actually planted for the individual samples will be impressed by the very low percentages of germination in these experiments. This is largely attributable to differences in age of seed, but in addition it will be noted that the seeds were grown under different environmental conditions and that they were germinated under conditions which could not be maintained the same from experiment to experiment. Inability to control temperature and substratum moisture may account for considerable differences.

Now it is clear that in these experiments it has not been possible to differentiate between the deaths which occurred in the seed envelopes and those which have taken place under the vicissitudes of field or sand culture conditions. This problem can not be profitably discussed until experiments under varying and carefully controlled conditions can be made with seed identical except for age. For such experiments one should start with large quantities of pedigreed seed and follow it through its period of viability. Material was bred for this purpose in the summer of 1912.

IV. Analysis of Data

The distributions of seed weight are shown in the conventional units of .025 gram range.[10] Tables I–II give those for the seeds germinating normally, Tables III–IV for those which germinated but produced more or less abnormal seedlings,[11] Tables V–VI those for seeds which failed to germinate.

From these the three more essential physical constants (mean, standard deviation and coefficient of variation) have been deduced and are presented with their probable errors in Tables VII, VIII and IX.[12]

TABLE I

Weight of Seeds Germinating Normally

Series	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Totals
NHD–J	—	2	4	8	14	18	12	9	3	6	—	1	—	—	77
NHD–M	—	2	3	14	23	58	37	25	5	2	1	—	—	—	170
NHH–J	1	—	—	7	29	38	71	27	16	13	6	—	—	1	209
NHH–M	—	—	5	30	88	158	186	120	50	19	11	6	3	—	676
NHHH–J	—	7	33	120	215	252	122	45	16	5	—	—	1	1	817
NHHH–M	2	12	47	176	389	456	218	88	25	5	1	—	—	—	1,419
NHDD–J	—	1	8	42	140	233	225	142	51	17	8	—	—	—	867
NHDD–M	1	5	20	59	202	344	318	175	58	16	5	6	—	—	1,209
NDH–D	—	—	4	7	48	56	43	16	2	—	—	—	—	—	176
NDH–E	—	1	1	31	65	87	54	16	3	—	—	—	—	—	258
NDD–D	—	3	2	10	21	19	16	13	3	1	—	—	—	—	88
NDD–E	—	—	4	5	16	17	12	3	—	—	—	—	—	—	57
NDDD–D	—	1	8	62	108	122	60	22	4	—	—	—	—	—	387
NDDD–E	—	—	6	67	106	98	53	35	7	—	2	1	—	—	375
NDHH–D	1	7	17	66	144	153	98	25	2	1	—	—	—	—	514
NDHH–E	—	4	10	50	122	154	81	24	6	—	—	—	—	—	451
FSS–I	5	56	202	268	121	34	14	—	—	—	—	—	—	—	700
FSS–L	2	63	328	467	252	59	9	—	—	—	—	—	—	—	1,180
FSH–C	—	—	8	51	183	164	52	11	3	—	—	—	—	—	472
FSD–C	—	7	43	104	52	19	7	—	—	—	—	—	—	—	232
FSHH–C	4	34	178	317	223	89	20	2	—	—	—	—	—	—	867
FSDD–C	1	27	107	259	175	89	20	2	—	—	—	—	—	—	680

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[10] Class 1 = 0.000–0.025 gram, class 2 = 0.025–0.050 gram, etc. Thus to pass from the constants (means or standard deviations) in units to those in grams subtract .5 and multiply by .025.

[11] In some of these series, N is insignificant, but it has seemed best to lay the whole data before the reader. The degree of trustworthiness of the constants is indicated by their probable errors. In some cases, too, lots of material are combined.

[12] Tables of constants for $(A + B)$ and $(B + C)$ are not given, although they enter into some of the comparisons. They can be derived from the original tables of data or calculated from the constants for A, B and C by appropriate formulæ.

TABLE II

Weight of Seeds Germinating Normally

Series	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	Totals
USS–I . . .	—	1	1	1	13	39	106	142	162	176	135	120	78	47	18	21	9	4	3	3	3	1	1	—	—	1	—	—	—	—	—	1,085
USS–K . . .	—	—	—	2	5	16	41	90	141	167	206	181	107	88	37	10	3	3	—	—	—	—	—	1	—	—	—	—	—	—	—	1,098
GGH–F . . .	—	1	—	—	—	—	—	2	6	17	27	51	81	94	86	78	57	39	27	18	7	2	1	—	—	—	—	—	—	—	—	594
GGH–G . . .	—	—	—	—	—	—	—	—	—	3	10	16	33	32	32	23	17	14	4	2	3	—	1	—	—	1	—	—	—	—	—	191
GGH–K . .	—	—	—	—	—	1	—	2	6	13	20	41	57	60	60	61	54	29	14	10	4	1	1	1	—	—	—	—	—	—	—	435
GGH$_2$*–F* . .	—	—	—	—	—	1	1	3	1	8	22	29	76	77	58	55	45	26	10	8	5	—	—	—	—	—	—	—	—	—	—	425
GGH$_2$*–G* . .	—	—	—	—	—	—	2	5	2	4	19	20	41	38	41	23	16	19	7	7	3	1	—	—	—	—	—	—	—	—	—	248
GGH$_2$*–K* . .	—	—	—	—	—	—	—	2	7	6	12	27	30	51	50	44	54	29	15	6	4	1	3	—	—	—	—	—	—	—	—	341
GGD–F . . .	—	—	—	—	1	4	5	12	34	34	41	39	20	13	9	6	2	—	—	1	1	—	—	—	—	—	—	—	—	—	—	222
GGD–G . . .	—	—	—	—	2	3	2	13	11	27	17	22	5	5	9	2	1	—	1	1	—	—	—	—	—	—	—	—	—	—	—	121
GGD–K . . .	—	—	—	1	1	4	9	18	47	41	32	31	21	13	8	6	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	237
GGD$_2$*–F* . .	—	—	—	1	1	1	2	12	19	42	70	77	64	44	29	16	12	8	3	—	—	—	—	—	—	—	—	—	—	—	—	401
GGD$_2$*–G* . .	—	—	—	—	—	1	2	11	22	23	58	43	61	33	25	9	11	1	2	—	—	—	—	—	—	—	—	—	—	—	—	302
GGD$_2$*–K* . .	—	—	—	—	2	2	2	11	25	34	47	68	54	55	54	25	21	5	6	1	1	—	—	—	—	—	—	—	—	—	—	413
GGHH–F .	—	—	—	—	—	—	—	1	5	8	14	38	48	56	41	28	18	22	20	2	—	1	1	—	—	—	—	—	—	—	—	303
GGHH–G .	—	—	—	—	—	—	—	1	1	5	7	8	18	28	15	12	9	6	4	1	1	—	—	—	—	—	—	—	—	—	—	116
GGHH–K .	—	—	—	—	—	—	—	1	5	9	16	28	54	62	38	29	16	15	12	3	2	2	—	—	—	—	—	—	—	—	—	292
GGDD–F .	—	—	—	—	4	1	2	8	16	28	61	37	59	51	35	8	9	1	2	—	—	—	—	—	—	—	—	—	—	—	—	322
GGDD–G .	—	—	—	—	1	—	1	1	6	16	22	22	22	17	9	7	5	2	3	—	—	—	1	—	—	—	—	—	—	—	—	135
GGDD–K .	—	—	—	—	1	2	3	7	22	36	65	63	52	30	22	16	5	3	1	1	—	—	—	—	—	—	—	—	—	—	—	329
LL–A	—	—	—	—	6	6	5	3	8	10	18	8	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	69
LL–B	—	—	—	—	—	3	1	4	9	5	2	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	26
LLS–A . . .	—	—	4	11	13	25	33	51	37	48	37	43	24	13	9	10	4	1	—	1	1	—	—	—	—	—	—	—	—	—	—	365
LLS–B . . .	—	—	3	8	9	13	24	29	17	30	24	16	12	8	3	2	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	200
LLS–H . . .	1	3	10	34	75	165	207	272	299	303	259	204	153	87	51	40	26	13	2	3	—	—	—	—	—	—	—	—	—	—	—	2,207
LLS–K . . .	—	—	1	6	8	10	22	35	38	43	26	22	12	8	6	3	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	243
W–K	—	—	—	—	—	1	2	7	14	20	39	42	57	60	56	61	55	34	33	19	13	10	11	6	3	2	2	1	—	—	1	549
GGS–L . . .	—	—	—	—	—	—	—	—	1	3	5	10	20	11	29	27	22	19	11	10	4	6	1	—	—	—	—	—	—	—	—	179

TABLE III

WEIGHT OF SEEDS MORE OR LESS ABNORMAL IN GERMINATION

Series	4	5	6	7	8	9	10	11	12	13	14	15	Totals
NHD–J	—	1	4	6	9	14	12	4	—	3	—	—	53
NHD–M	—	1	—	5	18	24	26	11	3	1	—	—	89
NHH–J	—	—	—	1	13	13	16	11	4	—	—	—	58
NHH–M	—	—	—	1	17	42	39	26	14	6	1	2	148
NHHH–J	1	—	2	7	7	15	6	2	1	—	—	—	41
NHHH–M	1	1	2	7	10	17	8	7	—	—	—	—	53
NHDD–J	—	1	2	6	14	9	12	5	5	—	—	—	54
NHDD–M	—	—	—	4	12	24	10	3	2	2	—	—	57
NDH–D	—	—	—	10	32	28	30	11	—	—	1	—	112
NDH–E	—	—	1	17	27	40	26	10	4	1	—	—	126
NDD–D	2	1	2	4	9	19	8	6	—	—	—	—	51
NDD–E	—	—	1	3	10	9	10	2	3	—	—	—	38
NDDD–D	—	—	1	11	15	15	11	3	1	—	—	—	57
NDDD–E	—	—	2	8	9	4	5	1	—	1	—	—	30
NDHH–D	1	—	3	6	22	14	11	4	1	—	—	—	62
NDHH–E	—	—	1	6	6	14	12	1	1	—	—	—	41
FSS–I	1	7	24	28	6	1	—	—	—	—	—	—	67
FSS–L	—	8	30	33	24	11	4	—	—	—	—	—	110
FSH–C	—	—	—	12	39	39	24	10	2	—	—	—	126
FSD–C	—	5	10	28	12	1	—	—	—	—	—	—	56
FSHH–C	—	5	8	21	12	6	—	—	—	—	—	—	52
FSDD–C	1	2	7	20	13	3	1	—	—	—	—	—	47

Any conclusion concerning selective mortality must rest upon a comparison of these constants.

The method of making these tests demands a word of explanation. In the previous study, the comparison was necessarily drawn between the constants of the seeds which actually produced fertile plants and those of the general population from which they were drawn; the constant for the general population was subtracted from that of the sub-sample. The positive or the negative sign of the difference showed whether mortality had tended to raise or to lower mean or variability.

In these greenhouse experiments, on the other hand, we have the constants for samples (A) normally germinating, (B) germinating abnormally and (C) failing to germinate. (B) may possibly be regarded as intermediate between (A) and (C).

If we take the difference between the constants

Survivors *less* failed

we shall have plus differences of the mean if selection has tended to raise the general average by eliminating the

TABLE IV

WEIGHT OF SEEDS MORE OR LESS ABNORMAL IN GERMINATION

Series	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	Totals
USS–I	—	—	—	—	7	4	7	9	9	4	2	5	2	—	2	—	—	—	1	1	—	—	—	—	—	—	—	53
USS–K	—	1	1	—	3	2	10	8	15	16	17	7	10	4	—	—	—	—	—	—	—	—	—	—	—	—	—	94
GGH–F	—	—	—	—	—	—	1	2	1	2	7	14	26	30	16	19	13	8	2	2	—	—	—	—	—	—	—	143
GGH–G	—	—	—	—	—	—	1	1	—	3	4	4	11	13	6	9	5	1	3	1	1	—	—	—	—	—	—	63
GGH–K	—	—	—	—	—	—	2	1	1	2	5	9	14	15	6	14	10	4	3	2	1	—	—	—	—	—	—	89
GGH_2–*F*	—	—	—	—	—	—	—	—	—	—	1	2	3	4	3	4	1	5	1	1	—	—	—	—	—	—	—	25
GGH_2–*G*	—	—	—	—	—	—	—	—	—	—	3	2	3	3	6	2	1	—	2	1	1	—	—	—	—	—	—	24
GGH_2–*K*	—	—	—	—	—	—	—	1	—	1	—	—	1	—	1	—	2	—	—	—	—	—	—	—	—	—	—	6
GGD–F	—	—	—	—	1	9	13	16	30	29	9	5	7	1	1	—	1	—	—	—	—	—	—	—	—	—	—	122
GGD–G	—	1	—	—	1	1	9	15	13	23	15	8	9	2	2	1	—	—	—	—	—	—	—	—	—	—	—	100
GGD–K	—	—	—	—	3	4	23	41	54	44	27	15	9	4	4	—	—	—	—	—	—	—	—	—	—	—	—	228
GGD_2–*F*	—	—	—	—	1	1	2	3	2	3	6	6	3	—	1	—	—	—	—	—	—	—	—	—	—	—	—	28
GGD_2–*G*	—	—	1	1	—	—	—	3	2	3	1	6	4	3	1	2	—	1	—	—	—	—	—	—	—	—	—	28
GGD_2–*K*	—	—	—	—	—	—	—	2	2	1	4	5	2	1	2	—	1	—	—	—	—	—	—	—	—	—	—	20
GGHH–F	—	—	—	—	—	—	—	1	1	—	1	2	1	7	1	1	1	3	—	—	—	—	—	—	—	—	—	19
GGHH–G	—	—	—	—	—	—	—	—	—	—	2	1	3	1	1	1	2	—	—	—	1	—	—	—	—	—	—	12
GGHH–K	—	—	—	—	—	—	—	—	2	1	1	—	—	1	1	1	1	—	—	—	1	—	—	—	—	—	—	9
GGDD–F	—	—	—	—	—	—	1	2	1	—	—	1	4	1	1	—	—	—	—	—	—	—	—	—	—	—	—	11
GGDD–G	—	—	—	—	—	—	—	—	1	—	2	2	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	8
GGDD–K	—	—	—	—	2	—	1	—	1	—	2	3	1	1	—	—	1	—	—	—	—	—	—	—	—	—	—	12
LL–A	—	—	—	—	1	2	4	8	11	8	14	2	6	3	—	—	—	—	—	—	—	—	—	—	—	—	—	59
LL–B	—	—	—	—	1	2	2	10	4	4	6	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	33
LLS–A	—	1	—	1	3	4	4	8	10	14	6	15	13	19	13	5	7	4	2	2	—	—	—	—	—	—	—	131
LLS–B	—	—	—	2	—	2	1	6	4	9	6	2	4	9	4	2	2	2	—	—	—	—	—	—	—	—	—	55
LLS–H	4	2	7	13	12	34	44	47	73	77	80	119	109	101	49	40	34	20	12	2	6	1	—	—	—	—	—	886
LLS–K	—	1	1	3	3	5	10	6	16	10	16	20	18	13	12	7	3	3	—	—	—	—	—	—	—	—	—	147
W–K	—	—	—	—	—	—	1	1	3	3	6	3	1	3	9	6	3	4	4	7	2	—	1	—	2	—	1	60
GGS–L	—	—	—	—	—	1	—	2	4	1	16	21	22	42	38	36	34	17	10	2	2	2	—	1	—	—	—	251

TABLE V

WEIGHT OF SEEDS FAILING TO GERMINATE

Series	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Totals
NHD–J......	—	15	75	180	370	338	205	90	22	6	1	1	—	—	—	1,303
NHD–M.....	—	10	82	213	397	442	277	92	33	5	—	—	—	—	—	1,551
NHH–J......	—	—	7	26	157	329	359	222	97	31	11	4	—	—	1	1,244
NHH–M.....	—	3	6	36	157	384	463	289	108	33	12	5	3	1	—	1,500
NHHH–J....	2	7	23	82	164	201	95	31	15	3	1	—	—	—	—	624
NHHH–M...	1	6	16	30	50	62	35	14	3	1	—	—	—	—	—	218
NHDD–J....	—	2	10	33	92	116	112	69	24	7	2	—	—	—	—	467
NHDD–M....	—	1	9	21	55	65	32	17	4	2	1	—	—	—	—	207
NDH–D.....	1	1	17	67	141	145	102	1	13	2	—	—	—	—	—	490
NDH–E......	—	3	16	75	196	214	123	55	11	1	—	—	—	—	—	694
NDD–D......	2	6	24	95	162	137	75	20	10	—	—	—	—	—	—	531
NDD–E......	1	3	32	84	147	137	75	27	5	—	—	—	—	—	—	511
NDDD–D....	—	2	8	33	64	65	51	15	5	1	—	—	—	—	—	244
NDDD–E....	—	3	8	35	73	60	31	16	—	1	1	—	—	—	—	228
NDHH–D....	—	1	13	53	101	91	52	23	2	—	—	—	—	—	—	337
NDHH–E....	—	1	10	23	73	74	39	21	—	—	—	—	—	—	—	241
FSS–I.......	13	164	254	264	92	21	3	2	—	—	—	—	—	—	—	813
FSS–L.......	13	104	298	243	143	50	11	1	—	—	—	—	—	—	—	863
FSH–C......	—	1	6	57	139	144	52	13	4	1	—	—	—	—	—	417
FSD–C......	4	44	164	197	91	27	3	—	1	—	—	—	—	—	—	531
FSHH–C.....	1	12	62	114	93	31	10	3	—	—	—	—	—	—	—	326
FSDD–C.....	—	24	92	113	72	20	7	2	1	—	—	—	—	—	—	331

smaller seeds; we shall have negative differences for standard deviations and coefficients of variation if there is a mortality of both the larger and smaller seeds—thus increasing the variability in the eliminated sample and decreasing variability in the surviving population.

Hence, regarding the abnormal germinations (tentatively) as intermediate between normal development and failure, we take our differences:

$(A)–(C)$, or normally germinating *less* failed,

$(B)–(C)$, or abnormal *less* failed,

$(A)–(B)$, or normally germinating *less* abnormal.

Since the number of individual experiments is fairly large, the comparisons may be made by merely noting the sign of the differences—*i. e.*, by taking the gross results of the individual experiments. Or one may treat the data from a more numerical view-point, taking averages of the actual differences. Both methods will of course be used.

In considering the differences between the constants of the three classes of seeds dealt with for the whole experi-

TABLE VI

WEIGHT OF SEEDS FAILING TO GERMINATE

Series	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Totals
USS–I	—	—	2	3	6	18	25	46	73	69	53	54	51	16	15	9	4	3	—	1	—	—	—	—	—	—	448
USS–K	—	—	—	2	3	3	9	27	20	40	47	50	30	20	9	6	3	1	1	—	—	—	—	—	—	—	271
GGH–F	—	—	—	—	—	—	1	4	2	4	10	17	15	31	34	31	29	20	29	8	5	—	2	—	—	1	243
GGH–G	—	—	—	—	—	—	—	4	3	9	11	18	25	44	40	42	29	25	9	7	3	3	4	—	2	—	278
GGH–K	—	—	—	—	—	—	—	2	2	3	7	13	16	30	31	36	25	12	5	7	4	1	1	1	1	—	197
GGH_2–*F*	—	—	—	—	—	1	—	—	1	—	4	7	12	6	8	6	8	5	1	2	1	—	—	—	—	—	62
GGH_2–*G*	—	—	—	—	—	—	1	3	—	—	4	9	3	13	21	12	10	5	2	—	2	—	—	—	—	—	85
GGH_2–*K*	—	—	—	—	—	—	—	1	—	2	—	5	2	10	13	8	8	4	2	1	1	—	—	—	1	—	58
GGD–F	—	—	—	2	2	—	5	4	16	16	13	16	7	1	—	1	—	—	1	—	—	—	—	—	—	—	84
GGD–G	—	—	—	2	2	6	13	21	24	28	27	21	20	14	5	2	1	2	—	—	—	—	—	—	—	—	188
GGD–K	—	—	—	1	—	5	7	12	26	38	37	23	22	7	6	2	1	—	—	—	—	—	—	—	—	—	187
GGE_2–*F*	—	—	—	1	—	—	3	1	5	4	9	7	14	3	3	—	—	—	—	—	—	—	—	—	—	—	50
GGD_2–*G*	1	—	1	2	5	1	2	9	6	7	5	18	25	15	9	1	4	4	—	—	—	1	—	—	—	—	116
GGD_2–*K*	—	—	—	—	—	—	2	5	2	7	6	13	7	8	6	3	3	—	1	—	—	—	—	—	—	—	63
GGHH–F	—	—	—	—	—	—	—	1	—	1	1	10	9	8	15	3	3	—	1	3	1	—	—	—	—	—	56
GGHH–G	—	—	—	—	—	—	—	—	—	—	5	3	8	5	6	7	2	3	2	3	1	—	—	—	—	—	45
GGHH–K	—	—	—	—	—	—	—	—	—	—	3	5	2	10	2	4	7	1	4	1	1	1	—	—	—	—	41
GGDD–F	—	—	—	1	—	—	2	2	2	3	3	10	—	4	1	1	—	—	—	—	—	—	—	—	—	—	29
GGDD–G	—	—	—	—	1	—	1	1	2	8	9	8	12	2	3	3	1	1	—	—	—	—	—	—	—	—	52
GGDD–K	—	—	—	—	1	—	—	2	5	9	8	5	2	6	3	1	—	1	1	1	—	—	—	—	—	—	45
LL–A	—	—	2	6	9	14	30	29	51	66	65	42	30	24	18	5	4	1	—	—	—	—	—	—	—	—	396
LL–B	—	—	—	—	7	16	41	55	68	85	86	57	42	16	9	—	1	3	1	—	—	—	—	—	—	—	487
LLS–A	—	—	3	2	4	9	9	9	8	10	8	9	9	7	8	5	1	1	—	—	1	1	1	—	—	—	105
LLS–B	—	—	3	9	9	16	28	24	36	26	37	23	24	25	23	16	11	10	4	2	—	1	—	—	—	—	327
LLS–H	—	—	3	15	18	24	15	34	34	46	43	43	49	56	61	44	38	21	13	12	5	4	—	3	—	—	581
LLS–K	—	—	—	3	1	3	3	4	3	3	2	3	3	7	7	9	2	3	1	—	1	—	—	—	—	—	58
W–K	—	—	—	—	—	1	1	3	5	6	9	3	6	5	14	7	9	8	5	8	4	—	2	—	2	—	98
GGS–L	—	—	—	—	—	—	1	1	6	6	5	28	41	64	86	92	86	66	53	25	15	19	9	2	3	1	609

TABLE VII

Physical Constants for Seeds Germinating Normally

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
NHD–J	9.247 ± .154	2.006 ± .109	21.696 ± 1.233
NHD–M	9.276 ± .074	1.435 ± .053	15.464 ± .579
NHH–J	10.029 ± .078	1.678 ± .055	16.731 ± .567
NHH–M	9.889 ± .041	1.595 ± .029	16.132 ± .303
NHHH–J	8.649 ± .033	1.388 ± .023	16.049 ± .275
NHHH–M	8.686 ± .023	1.300 ± .017	14.792 ± .194
NHDD–J	9.597 ± .032	1.416 ± .023	14.753 ± .244
NHDD–M	9.465 ± .028	1.437 ± .020	15.187 ± .213
NDH–D	9.040 ± .057	1.123 ± .040	12.426 ± .454
NDH–E	8.849 ± .048	1.134 ± .034	12.812 ± .387
NDD–D	8.955 ± .116	1.618 ± .082	18.073 ± .948
NDD–E	8.649 ± .109	1.216 ± .077	14.055 ± .905
NDDD–D	8.628 ± .041	1.184 ± .029	13.719 ± .339
NDDD–E	8.739 ± .048	1.379 ± .034	15.781 ± .398
NDHH–D	8.607 ± .037	1.254 ± .026	14.565 ± .313
NDHH–E	8.732 ± .038	1.188 ± .027	13.610 ± .311
USS–I	14.215 ± .056	2.730 ± .040	19.208 ± .288
USS–K	14.911 ± .045	2.226 ± .032	14.930 ± .220
FSS–I	6.860 ± .027	1.057 ± .019	15.407 ± .284
FSS–L	6.947 ± .019	.950 ± .013	13.678 ± .193
FSH–C	8.521 ± .030	.959 ± .021	11.259 ± .250
FSD–C	7.232 ± .044	.996 ± .031	13.769 ± .439
FSHH–C	7.243 ± .025	1.083 ± .018	14.955 ± .248
FSDD–C	7.378 ± .028	1.094 ± .020	14.822 ± .277
GGH–F	18.841 ± .073	2.629 ± .052	13.953 ± .278
GGH–G	18.796 ± .119	2.446 ± .084	13.016 ± .457
GGH–K	18.790 ± .085	2.622 ± .060	13.956 ± .325
GGH$_2$*–F*	18.635 ± .078	2.396 ± .055	12.855 ± .302
GGH$_2$*–G*	18.440 ± .117	2.720 ± .082	14.749 ± .456
GGH$_2$*–K*	19.170 ± .096	2.633 ± .068	13.734 ± .361
GGD–F	15.140 ± .108	2.377 ± .076	15.699 ± .515
GGD–G	14.942 ± .160	2.601 ± .113	17.406 ± .864
GGD–K	14.776 ± .106	2.423 ± .075	16.398 ± .521
GGD$_2$*–F*	16.354 ± .079	2.347 ± .056	14.349 ± .349
GGD$_2$*–G*	16.275 ± .087	2.253 ± .062	13.844 ± .387
GGD$_2$*–K*	16.847 ± .086	2.593 ± .061	15.391 ± .370
GGHH–F	18.459 ± .097	2.511 ± .069	13.602 ± .380
GGHH–G	18.319 ± .149	2.381 ± .105	12.997 ± .585
GGHH–K	18.298 ± .096	2.439 ± .068	13.328 ± .379
GGDD–F	16.379 ± .087	2.311 ± .061	14.106 ± .382
GGDD–G	16.681 ± .150	2.588 ± .106	15.513 ± .652
GGDD–K	16.106 ± .083	2.243 ± .059	13.929 ± .373
LL–A	13.522 ± .193	2.380 ± .137	17.604 ± 1.042
LL–B	13.115 ± .247	1.866 ± .175	14.224 ± 1.357
LLS–A	13.759 ± .109	3.097 ± .077	22.511 ± .590
LLS–B	13.280 ± .140	2.943 ± .099	22.157 ± .783
LLS–H	13.772 ± .042	2.902 ± .030	21.068 ± .223
LLS–K	13.638 ± .116	2.671 ± .082	19.587 ± .622
W–K	19.329 ± .108	3.753 ± .076	19.417 ± .410
GGS–L	19.972 ± .141	2.799 ± .100	14.013 ± .509

TABLE VIII

PHYSICAL CONSTANTS FOR SEEDS MORE OR LESS ABNORMAL IN GERMINATION

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
NHD–J	8.906 ± .159	1.714 ± .112	19.251 ± 1.307
NHD–M	9.325 ± .933	1.305 ± .660	13.993 ± .901
NHH–J	9.603 ± .109	1.229 ± .077	12.794 ± .814
NHH–M	10.047 ± .080	1.445 ± .057	14.387 ± .576
NHHH–J	8.537 ± .155	1.469 ± .109	17.209 ± 1.319
NHHH–M	8.679 ± .141	1.526 ± .200	17.578 ± 1.187
NHDD–J	9.019 ± .150	1.633 ± .106	18.107 ± 1.213
NHDD–M	9.175 ± .115	1.284 ± .811	13.933 ± .901
NDH–D	9.045 ± .076	1.198 ± .054	13.244 ± .607
NDH–E	8.984 ± .078	1.296 ± .055	14.429 ± .626
NDD–D	8.667 ± .151	1.601 ± .107	18.477 ± 1.275
NDD–E	9.105 ± .151	1.382 ± .107	15.180 ± 1.202
NDDD–D	8.649 ± .111	1.245 ± .079	14.395 ± .928
NDDD–E	8.333 ± .186	1.509 ± .131	18.111 ± 1.628
NDHH–D	8.444 ± .148	1.740 ± .105	20.609 ± 1.290
NDHH–E	8.902 ± .128	1.215 ± .091	13.647 ± 1.035
USS–I	14.019 ± .302	3.257 ± .213	23.236 ± 1.602
USS–K	14.766 ± .167	2.403 ± .118	16.275 ± .821
FSS–I	6.507 ± .071	.860 ± .050	13.219 ± .784
FSS–L	7.110 ± .076	1.184 ± .054	16.647 ± .778
FSH–C	8.896 ± .068	1.123 ± .048	12.628 ± .545
FSD–C	6.892 ± .077	.859 ± .055	12.468 ± .807
FSHH–C	7.115 ± .100	1.068 ± .071	15.004 ± 1.014
FSDD–C	7.170 ± .104	1.125 ± .074	14.792 ± 1.051
GGH–F	19.279 ± .130	2.310 ± .092	11.980 ± .485
GGH–G	19.238 ± .227	2.674 ± .161	13.899 ± .851
GGH–K	19.382 ± .197	2.759 ± .140	14.237 ± .734
GGH_2–*F*	20.400 ± .317	2.349 ± .224	11.514 ± 1.113
GGH_2–*G*	19.833 ± .375	2.721 ± .265	13.718 ± 1.360
GGH_2–*K*	18.333 ± .933	3.389 ± .660	18.485 ± 3.720
GGD–F	14.295 ± .123	2.007 ± .087	14.041 ± .618
GGD–G	14.950 ± .150	2.228 ± .106	14.903 ± .727
GGD–K	14.491 ± .085	1.896 ± .060	13.083 ± .420
GGD_2–*F*	15.321 ± .295	2.316 ± .209	15.114 ± 1.393
GGD_2–*G*	16.464 ± .422	3.311 ± .298	20.109 ± 1.884
GGD_2–*K*	16.750 ± .344	2.281 ± .243	13.619 ± 1.479
GGHH–F	18.947 ± .420	2.711 ± .297	14.308 ± 1.597
GGHH–G	19.417 ± .544	2.795 ± .385	14.396 ± 2.023
GGHH–K	18.556 ± .872	3.878 ± .617	20.897 ± 3.464
GGDD–F	16.363 ± .541	2.660 ± .383	16.259 ± 2.399
GGDD–G	16.875 ± .339	1.423 ± .240	8.435 ± 1.132
GGDD–K	15.667 ± .669	3.434 ± .473	21.921 ± 3.160
LL–A	14.932 ± .183	2.080 ± .129	13.927 ± .881
LL–B	14.152 ± .223	1.899 ± .158	13.420 ± 1.134
LLS–A	17.153 ± .209	3.550 ± .148	20.693 ± .898
LLS–B	16.473 ± .303	3.327 ± .214	20.194 ± 1.351
LLS–H	16.652 ± .080	3.538 ± .057	21.244 ± .355
LLS–K	16.244 ± .185	3.327 ± .131	20.482 ± .839
W–K	20.683 ± .384	4.410 ± .272	21.321 ± 1.371
GGS–L	19.900 ± .110	2.594 ± .078	13.038 ± .401

TABLE IX

PHYSICAL CONSTANTS FOR SEEDS FAILING TO GERMINATE

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
NHD–J	8.594 ± .026	1.413 ± .019	16.443 ± .223
NHD–M	8.659 ± .023	1.357 ± .016	15.675 ± .194
NHH–J	9.864 ± .027	1.397 ± .019	14.166 ± .195
NHH–M	9.905 ± .024	1.379 ± .017	13.917 ± .175
NHHH–J	8.654 ± .037	1.363 ± .026	15.752 ± .308
NHHH–M	8.491 ± .069	1.505 ± .049	17.723 ± .590
NHDD–J	9.351 ± .046	1.476 ± .033	15.781 ± .357
NHDD–M	8.821 ± .066	1.401 ± .046	15.878 ± .540
NDH–D	8.624 ± .038	1.239 ± .027	14.367 ± .316
NDH–E	8.804 ± .032	1.237 ± .022	14.050 ± .259
NDD–D	8.411 ± .038	1.314 ± .027	15.617 ± .331
NDD–E	8.444 ± .039	1.307 ± .028	15.484 ± .334
NDDD–D	8.746 ± .058	1.336 ± .041	15.275 ± .477
NDDD–E	8.531 ± .059	1.322 ± .042	15.499 ± .501
NDHH–D	8.564 ± .045	1.237 ± .032	14.444 ± .383
NDHH–E	8.701 ± .053	1.211 ± .384	13.917 ± .450
USS–I	14.435 ± .085	2.664 ± .060	18.451 ± .430
USS–K	15.092 ± .101	2.453 ± .071	16.251 ± .483
FSS–I	6.422 ± .025	1.066 ± .018	16.606 ± .285
FSS–L	6.693 ± .026	1.147 ± .019	17.134 ± .286
FSH–C	8.565 ± .035	1.073 ± .025	12.521 ± .297
FSD–C	6.779 ± .034	1.168 ± .024	17.235 ± .367
FSHH–C	7.331 ± .042	1.123 ± .030	15.317 ± .414
FSDD–C	7.018 ± .042	1.143 ± .030	16.284 ± .438
GGH–F	19.584 ± .129	2.979 ± .091	15.210 ± .476
GGH–G	19.194 ± .119	2.934 ± .084	15.285 ± .447
GGH–K	19.330 ± .131	2.729 ± .093	14.116 ± .489
GGH_2–*F*	18.597 ± .235	2.745 ± .116	14.761 ± .913
GGH_2–*G*	18.718 ± .184	2.583 ± .134	13.798 ± .727
GGH_2–*K*	19.328 ± .238	2.688 ± .168	13.906 ± .887
GGD–F	14.286 ± .172	2.334 ± .121	16.335 ± .872
GGD–G	14.500 ± .128	2.598 ± .090	17.920 ± .643
GGD–K	14.690 ± .106	2.141 ± .075	14.578 ± .519
GGD_2–*F*	15.400 ± .216	2.262 ± .153	14.688 ± 1.012
GGD_2–*G*	15.827 ± .218	3.483 ± .154	22.005 ± 1.020
GGD_2–*K*	16.302 ± .223	2.628 ± .158	16.122 ± .994
GGHH–F	18.321 ± .221	2.451 ± .156	13.378 ± .868
GGHH–G	18.978 ± .270	2.687 ± .191	14.157 ± 1.027
GGHH–K	19.341 ± .294	2.787 ± .208	14.412 ± 1.095
GGDD–F	15.103 ± .325	2.591 ± .229	17.154 ± 1.563
GGDD–G	16.019 ± .225	2.406 ± .159	15.020 ± 1.016
GGDD–K	15.822 ± .293	2.918 ± .208	18.442 ± 1.355
LL–A	14.356 ± .070	2.704 ± .050	18.832 ± .467
LL–B	14.154 ± .070	2.280 ± .049	16.106 ± .357
LLS–A	14.571 ± .266	4.036 ± .188	27.698 ± 1.384
LLS–B	15.036 ± .142	3.794 ± .100	25.233 ± .706
LLS–H	16.480 ± .117	4.169 ± .082	25.295 ± .531
LLS–K	16.362 ± .376	4.240 ± .266	25.914 ± 1.728
W–K	19.092 ± .282	4.140 ± .199	21.683 ± 1.093
GGS–L	20.350 ± .078	2.867 ± .055	14.088 ± .278

ment, it is necessary to note that, except for the coefficients of variation, these constants are in absolute values. Clearly enough a difference of .254 unit in mean or of .197 in S.D. for White Flageolet beans with an average weight of 6.755 units and a S.D. of 1.071 units is not comparable with a difference of the same absolute amount in Golden Wax or Burpee's Stringless with a mean weight of, say, 18.401 and a scatter in weight of 2.544 units.

TABLE X[13]

PHYSICAL CONSTANTS FOR GENERAL POPULATION

Series	*N*	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
NHD.....	6,630	8.529 ± .012	1.458 ± .009	17.099 ± .103
NHH.....	7,334	9.774 ± .011	1.421 ± .008	14.537 ± .082
NHHH...	5,601	8.609 ± .012	1.338 ± .009	15.543 ± .101
NHDD....	5,029	9.417 ± .014	1.484 ± .099	15.763 ± .109
NDH.....	3,227	8.852 ± .015	1.555 ± .011	14.089 ± .121
NDD.....	2,362	8.487 ± .019	1.377 ± .014	16.218 ± .163
NDDD....	1,946	8.649 ± .020	1.315 ± .014	15.210 ± .168
NDHH ...	2,433	8.604 ± .017	1.252 ± .012	14.549 ± .144
USS......	3,271	14.640 ± .030	2.519 ± .021	17.205 ± .148
FSS......	3,740	6.755 ± .012	1.071 ± .008	15.854 ± .126
FSH......	2,122	8.516 ± .016	1.092 ± .011	12.826 ± .135
FSD......	1,989	6.956 ± .016	1.034 ± .011	14.858 ± .161
FSHH....	1,788	7.225 ± .017	1.080 ± .012	14.953 ± .172
FSDD....	1,643	7.213 ± .019	1.127 ± .013	15.623 ± .188
GGH......	2,828	18.919 ± .034	2.674 ± .024	14.131 ± .177
GGH_2.....	1,284	18.799 ± .049	2.608 ± .034	13.873 ± .188
GGD......	2,140	14.972 ± .036	2.498 ± .026	16.681 ± .193
GGD_2.....	1,419	16.379 ± .046	2.577 ± .033	15.732 ± .204
GGHH....	1,329	18.401 ± .047	2.544 ± .033	13.824 ± .184
GGDD....	1,093	16.298 ± .048	2.395 ± .044	14.700 ± .216
LL........	1,070	14.206 ± .050	2.443 ± .036	17.197 ± .260
LLS......	5,305	14.826 ± .033	3.570 ± .023	24.077 ± .167
W........	707	19.412 ± .099	3.888 ± .070	20.032 ± .374
GGS......	1,039	20.176 ± .059	2.800 ± .041	13.876 ± .209

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[13] These constants are, except for the *LL*, *LLS* and *GGS* series, calculated directly from the data tabled for the general populations. In the case of the *LL* series the seeds were already a selected class—the heavier and lighter having been drawn for the planting giving rise to *LLS* plants. Hence in this case the constants were based on the summed seriations for the seeds failing, producing abnormal seedlings and producing normal seedlings in the two lots. They will differ somewhat from those of the whole population of seeds weighed. In the *LLS* and *GGS* series the tables for the general population were not yet prepared, hence the seriations of the seeds of classes (*A*)–(*C*) were summed for the various experiments and served as the basis for the general population constant.

Hence these absolute differences must, for the sake of convenience and of strict comparability, be reduced to relative terms. The best way of doing this is to express them in percentages of the general population values for the same constant, where "general population" means the whole mass of the particular strain and series of seeds from which the seeds for the individual experiments were drawn.

In the discussion of the whole series of experiments both absolute and relative values will be taken into account. In the preparation of the diagrams for differences in mean and S.D. the relative (percentage) values only will be used.

Table X gives the physical constants for the general populations, and the numbers of seeds upon which they are based.

I now turn to the various comparisons. It would be desirable to place before the reader the individual differences and their probable errors, but since these number 750 their publication is precluded by lack of space, and the small summary tables must suffice. All these differences may, of course, be derived by the reader caring to check the arithmetic from the tables of fundamental constants.

(To be concluded)

RECIPROCAL CROSSES BETWEEN REEVES'S PHEASANT AND THE COMMON RING-NECK PHEASANT PRODUCING UNLIKE HYBRIDS

MANY sex-linked characters have been described in birds (fowls, pigeons, canaries and doves). The pheasant hybrids to be described, however, show merely a different appearance of male sexual plumage characters in the F_1 hybrids of a reciprocal cross between Reeves's pheasant and the common ring-neck pheasant (*P. torquatus*). These hybrids are sterile, and therefore the experiment ends with the first cross, although Cronau[1] stated that the offspring from a Reeves's cock and common pheasant hen were occasionally fertile. Poll,[2] however, who studied the spermatogenesis of numerous pheasant crosses, found the hybrids between Reeves's and the common pheasants and between Reeves's and Sommerings's pheasants always sterile.

The Reeves's pheasant was originally given generic recognition by Wagler under the name *Syrmaticus reevesi.* This distinction it certainly deserves, although later writers have often placed it under *Phasianus.* The ring-neck pheasant, so called, refers to the common stock pheasant which is now practically pure *torquatus.*

In the fall of 1911 two hens were mated as follows: Pen D contained a ♂ Reeves's with two ring-neck hens; pen H a ♂ ring-neck with two Reeves's hens. These were all birds of the season. The Reeves's were from the same clutch of eggs from a single pair, and the ring-necks from a strain of which large numbers have been bred on the farm. The Reeves's never, to my knowledge, shows any variation of plumage in captivity. The strain of ring-necks is practically constant, though the white neck ring sometimes differs in its width.

It is therefore fair to suppose that the somatic difference of the hybrids to be described is a constant feature, although from pen D only two males were reared to maturity, and from pen H only four. The six birds, however, immediately fall into two classes. They have all the appearance of two well-marked species. Hens were reared only from pen H.

---

[1] Cronau, C., *Zool. Garten.*, 1899, p. 99.

[2] Poll, H., *Gesellschaft Natur.-Freunde,* 1908, p. 127.

A large number of eggs from these two pens was set, but from pen D only five chicks were hatched; from pen H, ten. These two lots of chicks were noted as differing both in down and in first plumage in the following way: those with the Reeves's father and ring-neck mother, pen D, were lighter-colored than the birds of the reciprocal cross. No detailed observations were made. On maturity this same difference was found to hold. On comparing the adult specimens dorsal side up, there is at once seen to be a constant difference involving all the feather regions. In general, it may be said that in cross D the Reeves's father transmitted to his hybrid offspring more of his own characters than the female Reeves's transmitted to her offspring in cross H. This is especially shown in the almost pure Reeves's head pattern of cross D, and in the general lighter tone of the whole upper parts and flanks.

On the other hand, the stronger tail barring of Reeves's pheasant, as contrasted with the ring-neck, has been transmitted to cross H by the Reeves's hen, and has not been carried to the same extent by the male Reeves's in the other cross.

The plate shows the difference, and needs no explanation. The other differences are briefly as follows:

Cross D, feathers of mantle with reduced and irregular black band.

H, feathers of mantle with broad black band.

D, feathers of mantle tending to sub-terminal bar of buckthorn brown (Ridgway, 1912).

H, brown bar absent.

D, general color of mantle more tawny and less dark than in H. Back and rump much lighter than in H, with also an entirely different feather pattern. Upper tail coverts lighter in D than in H. Barring of tail reduced in D to basal third and not heavy. In H, heavy barring of whole tail, becoming blotchy and obscured towards terminal third.

Scapulars, greater and lesser wing coverts, and even primary quills different in the two crosses; and tending to more rich browns and larger light areas in D than in H. First primary with larger and more distinct light bars on inner web in D than in H.

Flanks lighter and with tawny sub-terminal bars in D, which are not present in H.

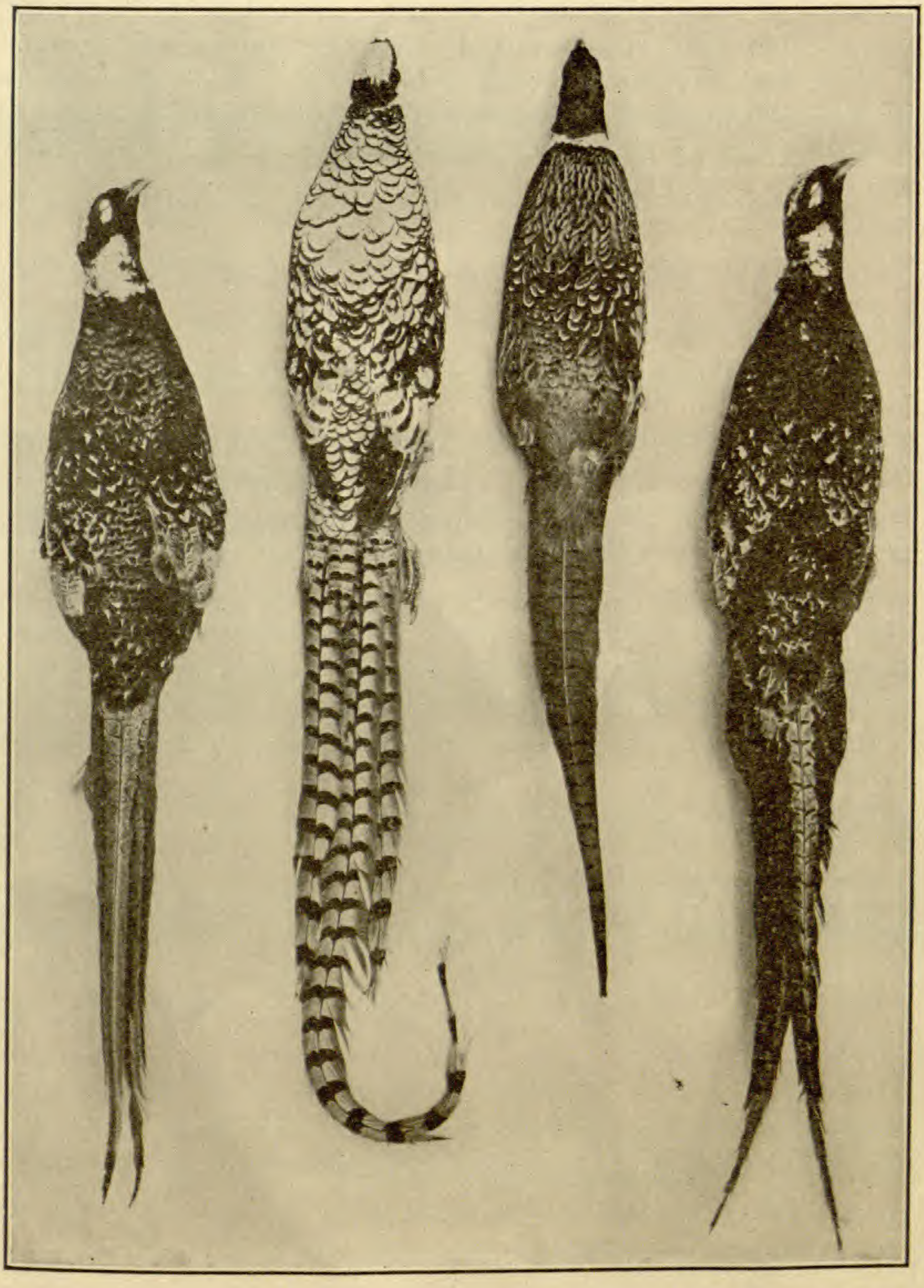

FIG. 1. Male hybrid from a mating of a male Reeves's with a female ring-neck pheasant.

FIG. 2. Male Reeves's pheasant.

FIG. 3. Male ring-neck pheasant.

FIG. 4. Male hybrid from a mating of a male ring-neck with a female Reeves's pheasant.

Breast and lower throat slightly darker in H than in D, but very similar. Rest of lower parts about the same in both crosses.

Three hen birds were reared from pen H. They all showed strong tail barring and other well-marked Reeves's characters.

The females of the two species involved are quite different, and it is therefore to be regretted that there are no specimens from both crosses for comparison.

SUMMARY

That this somatic difference between reciprocal crosses in other pheasants is not always present, is shown by the uniform F_1 generation in the two crosses, Amherst × Gold, of the genus *Chrysolophus,* bred by myself. In the work of Professor Allesandro Ghigi and Mrs. Haig-Thomas on pheasants no reciprocal crosses have apparently been made.

The significance of the present case is not clear, and it is desired simply to put it on record. Further work is necessary to prove that reciprocal crosses between Reeves and the true pheasants always give different results.

It is interesting to note that the differences which have been described are rather subtle ones and quantitative rather than qualitative.

JOHN C. PHILLIPS

The American Naturalist

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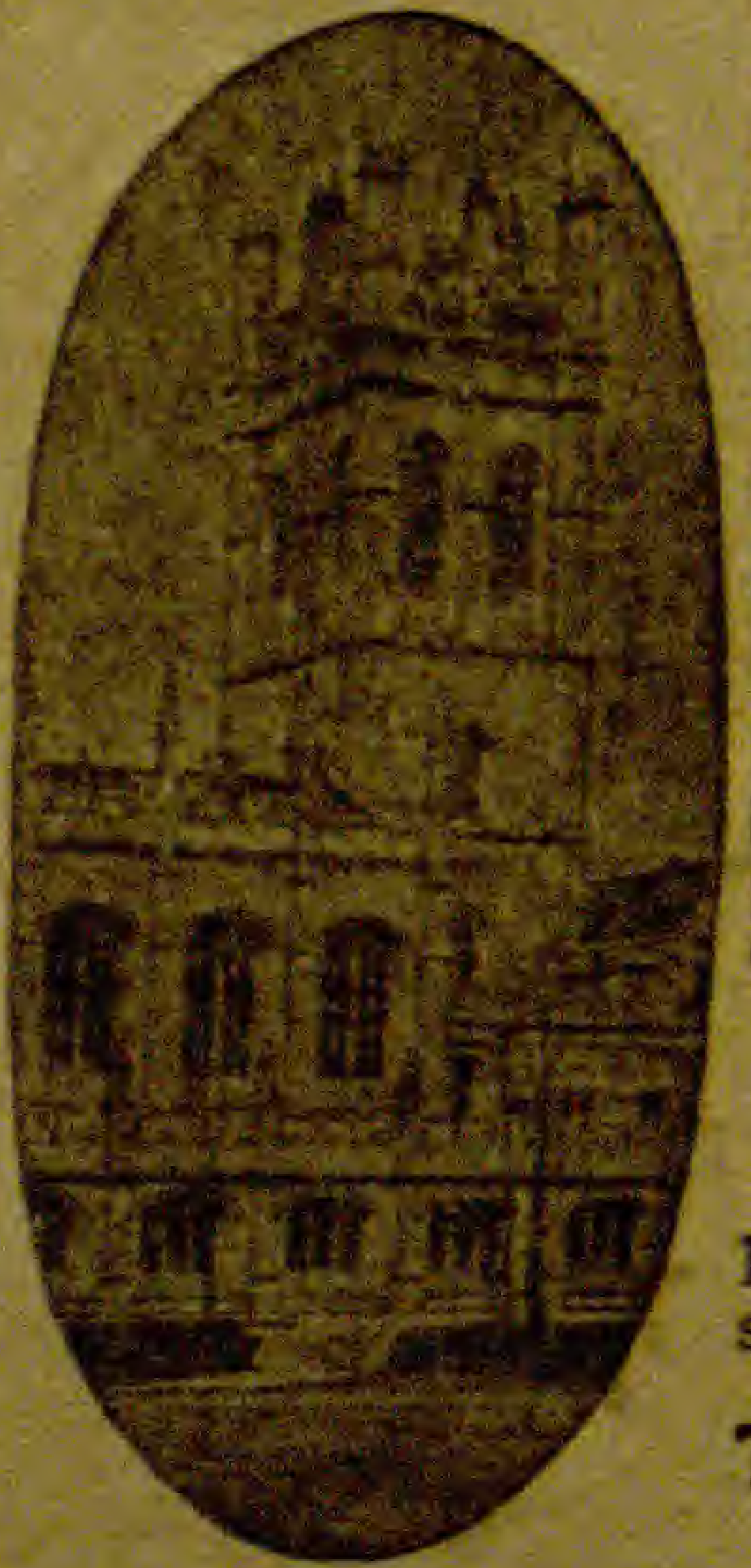

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THE
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THE FIXATION OF CHARACTER IN ORGANISMS[1]

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THE segregation of animals and plants into those groups which we call species, genera and families and the arrangement of such groups in a natural system of classification are made possible by the fact that during the evolution of any group there are always characters which have varied comparatively little and, from their constancy throughout large numbers of otherwise different individuals, are therefore of great value in determining relationships. Should all the characters of an individual be equally subject to change in the passage from one generation to another such chaos would result that anything but the most arbitrary classification would be quite impossible. It is of great importance to the taxonomist, the experimental morphologist and the student of evolution in general to ascertain, if possible, what are the causes for these differences in degree of variability and to attempt a formulation of the laws under which they appear.

The first attempt at a scientific explanation of this problem was put forward by the theory of Natural Selection. In its extreme form this theory assumes that all conservative characters, known to be very ancient because of their occurrence throughout large groups of organisms, are characters of supreme importance in the

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[1] Graduate Bowdoin Prize Thesis in Biology, Harvard University, 1913.

struggle for existence, which have consequently been firmly standardized and kept rigidly true to type by the action of natural selection in continually eliminating those individuals which showed a tendency to depart from the normal condition. The invariable presence of segments in the Articulata, of tracheæ in insects, of the backbone in vertebrates, of gills in fishes, of feathers in birds, of roots in the vascular plants, of seeds in the spermatophytes and of vessels in the wood of the angiosperms, all of which are characters of universal occurrence in the groups which they distinguish, is explained as due to their supreme importance for survival. The frequent variability of rudimentary or obviously useless structures is laid to their unimportance in the struggle for existence and their consequent removal from the standardizing influence of natural selection. This belief in the dependence of structural conservatism on functional utility is widely held to-day and has been stated by Montgomery as follows: "A character which persists through a very long racial period must do so by virtue of being of particular value for the economy of the organization or for the perpetuation of the race. Structures of less value are more readily modified, substituted or even lost."[2]

A strict application of the selection hypothesis, however, evidently fails to explain many facts which a study of phylogeny brings forward. Can we imagine, for example, that either the number five, on which echinoderms are built, or the number three, which is characteristic of all hexapod insects, are or ever have been of critical value in the struggle for existence? Is it logical to suppose that the position of the protoxylem with reference to the later-formed elements of the vascular axis, a position which is extremely constant throughout the main groups of vascular plants, has been definitely determined by natural selection, or that the precise number of floral parts or the

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[2] Montgomery, T. H., "On Phylogenetic Classification," *Proc. Philadelphia Acad. Sci.*, Vol. 54, 1902, p. 214.

particular degree of coalescence or adnation exhibited between them, is of great functional importance? Many structures, insignificant and in all probability quite useless, are extremely constant throughout large groups of animals and plants. Must we believe that all these conservative characters and structures are of immense importance in the struggle for existence, but that such features as size, shape, color and texture, which are comparatively inconstant, are of much less survival value? It is true that certain discoveries of modern physiology have lent some support to the oft-repeated defence of the selection theory that structures of apparently little importance may be in reality of much significance to the organism. Our knowledge of vital processes is as yet so slight that it is quite impossible to pronounce any particular feature as certainly of great or of little value for survival, but the mass of such information as we have acquired from a study of anatomy, physiology and ecology points decidedly to the conclusion that it is precisely those characters of little importance to the organism which are usually most conservative.

It is also very doubtful if the constancy of such apparently more essential characters as the vertebral column of vertebrates, the feathery covering of birds, or the floral reproduction of seed plants is due to the supreme importance of these characters in the struggle for existence, as the selection theory postulates; for it is evidently not the mere presence of a backbone or of feathers or of flowers *per se* which is of great significance to the individual, but the presence of these structures in very specific size, shape, texture, color and other respects. The vertebral columns of a shark and of an elephant could not be exchanged without disaster, nor could the feathers of a duck and an ostrich or the flowers of a pine and an orchid. The "conservative" character is useful only as it is associated in each individual with many other "variable" ones. The most fundamental and unalterable distinction between a fern and a flowering plant resides in their respective methods of reproduction; but in a competition between the two it is not primarily this difference which decides the outcome. Differences in vegetative characters, as well, and in the general vigor and adaptability of the two plants determine which shall survive. One of the most conservative and deeply-seated distinctions between a mammal and a bird is the possession of hair by one and of feathers by the other, but in the struggle for existence between a bat and a night-hawk this difference is of very slight importance. The victor in such competitions is that individual all of whose bodily parts in their size, shape and general structure are so well coordinated as to produce an organism with the greatest degree of hardiness and adaptability.

The conservative characters in each family or larger group—its most important distinguishing features—provide a general plan of structure, a theme, on which are produced the modifications of genera and species. It is these modifications, involving the plastic and least conservative characters, which are of most importance in adaptation and therefore in survival. The general plan is of comparatively little significance in a contest—about as much as is the particular make of modern rifle used by an army or the special type of construction of a racing car. A satisfactory interrelation and coordination of parts is the important thing, and the degree of perfection with which this is attained, on almost any plan, determines success or failure. It is true that after very long periods of time in organic evolution slight differences in value between two general plans of structure will sometimes make themselves felt and the best will finally become dominant. Seed plants have little by little overcome vascular cryptogams and mammals have superseded reptiles. A highly adaptable organism, however, constructed on an "inferior" plan will often supplant one which belongs to a generally superior type but is lacking in versatility and vigor. The common bracken fern, for example, a cryptogamous plant, is of almost universal distribution and is much more successful than most seed plants. The great majority of fundamental distinctions and conservative characters seem to be of as little survival value as is pentamery to the echinoderms or the presence or absence of stipules to any family of the dicotyledons.

The theory of natural selection, at least in its extreme form, can not therefore well be regarded as a satisfactory explanation for structural conservatism. Darwin himself frequently called attention to the fact that "the physiological importance of an organ does not determine its classificatory value"[3] and cited many examples of organs or characters obviously insignificant or useless which are nevertheless very constant and of great value in determining relationships. Darwin voices the general defence of selectionists on this point, however, when he states that "the importance, for classification, of trifling characters mainly depends on their being correlated with other characters of more or less importance."[4]

If the conservatism of a useless character depends on its correlation with one of great functional value which is continually preserved through the action of natural selection, it ought to be possible to discover this essential character and to use it in classification. A search for such universal and vitally important distinctions, however, is strangely fruitless, for in most families the only characters which we can definitely point out as common to all the individuals are precisely those which seem utterly insignificant for survival. This fact becomes increasingly obvious as we consider still broader groups where the number of common characters becomes smaller and smaller until there are but one or two features of absolute diagnostic value. The two great divisions of the amniotes, for example, the Sauropsida on the one hand and the Mammalia on the other, can be rigidly distinguished from one another only by the presence, respect-

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[3] "Origin of Species," 6th ed., p. 431.

[4] *Loc. cit.*, p. 433.

ively, of one or of two occipital condyles or joints between skull and backbone. The two largest families of living conifers, the Abietineæ and the Araucarineæ, are roughly separable on several characters, but the only distinction to which no exception has been found is the presence or absence of "bars of Sanio," minute bands of pectose on the walls of the wood elements. Similarly, the monocotyledons and dicotyledons, the two great divisions of the higher seed plants, are ultimately separable, as their names imply, by the number of the cotyledons in the embryo. It can not well be claimed that any of these characters or many others which are common to wide groups of animals and plants are in themselves physiologically important but it is equally impossible to distinguish others, of great value for survival, with which these are correlated.

Darwin frequently calls attention to the fact, now so generally admitted, that a classification based on one or a few distinctions is of much less value than one which takes into account a large number of correlated characters. Such a group of characters, however, corresponds to what we have mentioned as the general plan or type of structure and consists, at least in the broader groups of organisms, of features which are mainly unimportant for survival.

It is possible to maintain that the success or failure of an organism depends more on some deeply seated property of its protoplasmic make-up, such as its powers of resistance or adaptability, than on any external and visible structures. But if there is a correlation of such fundamental abilities with features of structure, is it not more reasonable to suppose that it would occur with characters of great functional importance rather than with those which are of no physiological significance? The fact that so often in the same family, all of whose members possess the typical conservative features of the group, there are some individuals which are dominant and successful and others which are unsuccessful and are being exterminated seems to prove that there is no correlation between the vigor and adaptability of the organism and its conservative structural characters.

Darwin maintains that the constancy of useless features "chiefly depends on any slight deviation not having been preserved and accumulated by natural selection which acts only on serviceable characters";[5] but if all the characters and structures of any particular group were originally variable in the same degree, a supposition which the theory of natural selection is usually regarded as making, it is surely impossible to suppose that variations will not be most strikingly manifest in just those features which are not subject to the eliminating action of natural selection.

Simple and plausible as the selection theory is, we must admit that it offers by no means a complete solution of the problem of fixity since, in general, the conservatism of a structure or character seems to be inversely rather than directly proportional to its survival value. To reach a better understanding than such a theory gives as to why variation does not occur with equal frequency and extent throughout all parts of an organism, we must first of all endeavor to formulate, from the great mass of facts at hand, such general laws of variability and conservatism as we may be able to discover empirically and must then try to explain them as well as we may. A survey of the fields of taxonomy and comparative anatomy shows the possibility of discovering in the evolutionary development of organisms the presence of numerous uniformities and the operation of many general principles of phylogeny, some of which are of universal occurrence, or nearly so; others valid throughout large groups of animals and plants, and still others applicable only to particular orders or families. The formulation of such principles and a thorough application of them is the great task before the taxonomist and the phylogenist, if they are to establish their sciences on a sound and rational

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[5] *Loc. cit.*, p. 431

basis as something more than mere collections of facts. The purpose of the present paper is to set forth a few of the more important of these evolutionary principles, with their significance in the general process of evolution, and to suggest a possible explanation for the fixation of character which shall be more satisfactory than that proposed by the selection theory.

In our search for such principles of conservatism, it is primarily apparent that in the main those features which are slow to change in one family are slow to change in others also, and that consequently there are certain rather definite categories of characters which throughout all animals and plants show an inherent tendency to be conservative and slow to change, and others which are fundamentally plastic and variable. The conservative categories are, in general, those of number, relative position and general plan, characters usually of little functional significance; whereas the commonly variable features are those of more importance for survival and include such distinctions as size, shape, color and texture. The essential difference between these groups of categories is not at all in their absolute degree of conservatism or plasticity, but rather in their general tendency to become fixed or to remain plastic. Number, position and plan are not always constant, by any means, but they tend to become so during the course of evolution, whereas size, shape, color and other commonly variable characters are almost always changeable and rarely become stereotyped.

The conservatism of number is everywhere apparent. The two great groups of radially symmetrical animals, the cœlenterates and the echinoderms, are constructed (with a few exceptions) on the plans of six and of five, respectively. Insects, on the other hand, display almost invariably a scheme of three or its multiples in the number of body regions, segments, appendages and many other structures. Among fishes the number of gills, of visceral arches, of fins and of fin rays varies little throughout large families; and in the higher vertebrates, the number of teeth, of vertebræ, of digits, of aortic arches, of brain lobes, of cranial nerves and of countless other structures is very conservative and is characteristic of large groups of animals. In the plant kingdom the fixity of number is even more noticeable. Throughout gymnospermous plants the number of sporangia to a sporophyll, in both the male and the female cones, varies but slightly. The two great groups of angiosperms, the dicotyledons and the monocotyledons, can be separated on but one constant character, the number of cotyledons in the embryo. The numerical plan of the flower in both series is also very constant, being almost invariably four or five in the dicotyledons and three in the monocotyledons. Most angiosperm families, or genera, at least, have a characteristic number of sepals, petals, stamens and carpels, which is of great importance in classification. Similar instances could of course be multiplied almost indefinitely.

Conditions of relative position and of insertion of parts are also notably conservative and of value in determining relationships. In the higher invertebrates, for example, the nerve cord is always ventral to the digestive tube and chief blood vessels, whereas in the vertebrates it is invariably dorsal. The mass of the liver may be disposed almost anywhere, but its attachment is always on the ventral side of the digestive tube. The source of the nerve supply to many organs is exceedingly slow to change and is of much importance in determining the primitive position of structures which have been moved from their original situation. Among plants, the relation of bud to leaf is very constant, and the particular relative positions of sporangium and sporophyll, of protoxylem and later-formed wood elements, and of parenchyma cells and vessels are very characteristic for each of the main groups of vascular plants. The degree of coalescence between the members of the same floral circle and the method of insertion of each of the floral circles upon the axis or upon one another are admitted to be of the greatest diagnostic value.

The character of general plan, or type, which really includes those of number and position, is of the utmost importance for the discovery of relationships. In every natural group of organisms, no matter how dissimilar its members may appear, there is always a specific plan or theme which is common to all and upon which the structure of each individual is built. The two-layered or three-layered body plan, the presence or absence of segmentation, the definite type of arthropod or vertebrate appendage which is so constant throughout its endless modifications, the plan of the central nervous system in the vertebrates, and the precise and unvarying character of the epidermal structures in the different classes of that phylum, are a few of the innumerable examples of the conservatism of type in the animal kingdom. In the case of plants the same fact is no less evident. The general topography of the vascular system, the presence or absence of leaf-gaps, the degree of differentiation in the structure of the wood and the open or closed character of the leaf venation are all extremely constant. The notable conservatism of type in the reproductive organs of all plants is well known and is universally used in classification. The almost complete uniformity throughout animals and plants of many cytological characters, such as those concerned with mitosis, might also be cited as striking examples of the conservatism of plan or type.

Plastic and variable characters, no less than conservative ones, are separable into categories, the most important of which are size, shape, color and texture, of which the inconstancy is so notorious that any broad classification based upon them is very rarely a natural one.

But even if we admit that certain characters are essentially more slow to change than others, it is very evident that this difference is not an absolute one, but that "conservative" features may display a greater or a less degree of constancy in certain parts of the organism than in others. These differences in local variability, however, like those between general categories of characters, are not random and entirely unpredictable ones, for we are able to distinguish certain definite parts of the plant and animal body which throughout larger or smaller groups of organisms are characteristic seats of conservatism, and others which are everywhere subject to continual change. The urinogenital, nervous and skeletal systems of vertebrates, and to a certain extent of invertebrates as well, are typically conservative and subject to comparatively slight alteration during evolutionary development. Certain definite regions of the body, such as the skeleton of the mammalian neck, are more definitely stereotyped than others as to the number and arrangement of parts. The extreme conservatism of the reproductive organs of all plants has of course long been recognized and has been proven by a study of internal as well as of external structure. More recently it has been demonstrated, that the woody axis, as well, is the seat of firmly fixed and therefore ancient characters. Each main division of the vascular plants has a fundamental stelar plan, and every subordinate group has its peculiar and specific type of wood structure which is exceedingly constant in individuals otherwise very different and, as a diagnostic character for families and sometimes smaller groups, is therefore of much value. The axis of the root is especially conservative and has remained practically unchanged in its general plan throughout the entire evolution of woody plants. The vascular system of the leaf, especially at the node where the leaf and stem unite, has many times been found to display primitive features wholly lost elsewhere. In such conservative systems and regions it is not *all* the characters which have become constant, but only those which we have called typically conservative, such as number, position and plan. Variable characters are variable anywhere.

Not only are certain regions of the body characteristically more conservative than others, but it is also true that particular stages, notably the earlier ones, in the life history of the individual are much less subject than the rest to variation and change. The law of recapitulation, which declares that ontogeny repeats phylogeny, is now accepted in a more or less modified form by almost all zoologists, and despite differences in the interpretation of embryology as a guide to a knowledge of ancient animals, it is generally agreed that early developmental stages are much more conservative than are later ones.

Not as many striking examples of recapitulation are known among plants as among animals, but Darwin long ago noticed resemblances between the leaves of certain seedlings and of their supposed ancestors, and others have cited many similar instances. Attention has more recently been called, particularly by Jeffrey, to the fact that the internal structure of the young plant or of a first annual ring of the mature plant, even more clearly than their external form, is slow to change and therefore frequently displays primitive characters. The woody axis of one of the higher ferns begins in the sporeling as a solid rod, which, after forming a medullated cylinder, gives rise to the complicated vascular system of the adult, the various steps of its development representing stages through which its ancestors doubtless passed and which now characterize the more primitive living families of ferns. In the first annual ring of certain conifers occur resin canals, "bars of Sanio," parenchyma cells and other structures present throughout the wood of more primitive and presumably ancestral types. The first few annual rings of many angiosperms, as well, show in the structure of their rays and vessels characters which are undoubtedly ancient. On an abundance of such evidence as this it must be admitted that the validity of the law of recapitulation has been demonstrated for plants almost as thoroughly as for animals.

We have seen that conservative characters vary considerably in their constancy according to the part of the body or the stage of development with which they are associated. Still more notable cases of differences in fixity are evident in similar characters occurring in different families. A feature which is conservative and of diagnostic value in one group may be variable and worthless in another. The number of teeth and vertebræ, for example, is much less constant among fishes than among mammals. The general floral plan is far from uniform throughout the Rosaceæ, but in such families as the Cruciferæ it is exceedingly constant. This introduces still another principle of conservatism which is really the crux of the whole problem of fixation of character and seems to be a fundamental law of evolution—the principle that the progressive evolution of any character or structure, whether involving reduction or increased complexity, is attended by a continual decrease in its tendency to change. Differentiation and specialization are followed by increasing fixity.

It is a well-known biological fact that the more primitive families of animals and plants, those which still maintain an ancient type of organization, are much more variable in their characters than are those which have progressed far from such a primitive condition. The lower Arthropoda, for example, display great variety in the number of body segments and appendages and in many anatomical features, but the highly specialized hexapod insects, despite their enormous numbers, wide distribution and extreme variation in size, shape and color, have become rigidly stereotyped with regard to almost all characters of number and general plan. In the ascending vertebrate series from cyclostomes to mammals there are also many instances of the increasing fixation of what we have called conservative features, for it is well known that the characters which make up the mammalian type are much more definite and sharply circumscribed than those pertaining to the lower groups of vertebrates where there is much latitude in the distinguishing features. Likewise, the most advanced and highly specialized families of plants, such as the Compositæ and the Orchidaceæ, are characterized by a stereotyped floral plan which is invariable throughout all the members of these dominant groups, whereas in plant orders admittedly lower in the scale, such as the

Rosaceæ, Caryophyllaceæ, Cyperaceæ and Gramineæ, the floral type is very much more various both in number and in relative position of parts. The evolution of the gametophyte from its gymnospermous to its angiospermous condition is a continual progress from simple and variable structures to those which are fixed and highly specialized. The same principle is evident as well among vegetative structures, for the lower and more "generalized" families, both among conifers and dicotyledons, show a greater diversity in their wood structure than do the higher groups.

This progressive evolution from a primitive variable condition to one which is fixed and specialized is always attended by a reduction in the number of similar parts. Multiple structures are characteristic only of the lower types of organization. Other characters tend to show a similar phylogenetic change from the complex to the more simple, with the result that a structure in its highly developed state is very often less complex than is its more primitive homologue. Evolution more often involves reduction than amplification.

These four general principles of conservatism—that there are definite categories of fundamentally conservative and fundamentally variable characters; that certain organs or regions of the body are more conservative than others; that early stages in ontogeny are more constant than later ones, and that advance in evolutionary development involves an increase in fixity, are established on a large and continually increasing mass of observed facts and may well demand recognition from all biologists. Many other principles, such as those concerned with reversion and orthogenesis, are gradually being formulated and it is only a matter of time and more extended observation before the science of phylogeny will be placed on a much more uniform and exact footing.

To establish these laws on a sound basis of observed facts is a matter of some labor, but it is a much less difficult undertaking than to provide a reasonably complete explanation for their existence. This task must ultimately be left to the sciences of physiology and genetics, and in the meantime it is possible only to make suggestions and conjectures as to what are the causes which underlie the facts of conservatism.

The very difficulties in the way of the explanation of fixity proposed by the theory of natural selection suggest a possible solution of one of the most conspicuous problems—why it is that just those characters of least physiological importance and survival value are most conservative. May it not be true that the tendency toward progressively increasing fixity, which seems to be almost universal in organic evolution, has succeeded in rendering comparatively invariable those features which are of little significance for survival, but that in the case of vitally important characters this tendency has been overcome by the opposing action of natural selection in eliminating individuals which are not sufficiently plastic and adaptable, and in thus maintaining or increasing the variability of all characters important in the struggle for existence?

If this conception of the matter is a true one, the function of natural selection is almost precisely the reverse of what it is ordinarily supposed to be, for instead of operating to fix characters and preserve types intact its action results in their elimination, in so far as they interfere with success, and in the placing of a premium on versatility. Selection, in other words, is made for general adaptability under varying conditions rather than for the possession of any particular characters or structures. The great variability of dominant organisms, long ago noticed by Darwin, should be regarded on such a hypothesis as a cause rather than a result of their dominance. Fixity is tolerated by natural selection only so long as it affects characters of little or of no functional importance. Such characters thus become very conservative and furnish the taxonomic "type." This conception of organic evolution as the result of the continual interaction of these two great factors—progressive fixation, which is ever tending to make characters constant and to decrease variability; and natural selection, which operates in eliminating individuals which have become too rigid in their vitally essential features, and thus in encouraging those which display superior adaptability—is at least helpful in presenting a clear picture of the process of evolution.

The marked conservatism which we have noticed in particular structures or organs may perhaps be explained in a similar way as due to their comparative unimportance in the economy of the individual. The fact that the reproductive organs in all plants and in many animals are especially conservative may possibly be taken to indicate that the particular method of reproduction is of less vital concern to the race than are its other activities. The conservatism of other structures, such as the root, is evidently due to the comparative constancy of their surroundings. Internal structures in general are apt to be more conservative than external ones because of their exposure to a less varied environment.

Various attempts have been made to explain those phenomena of conservatism which have been grouped under the head of recapitulation. De Vries has maintained that the seedling characters of plants are just as dependent on the action of natural selection as are those of the adult and that ancient features persist in youth only when they happen to be of survival value for the early stages of the plant. The same position has sometimes been maintained on the zoological side. To attribute functional importance to all embryological characters, however, and to explain the numberless cases where there is close correspondence between ontogeny and ancestry as due simply to the operation of natural selection, is to burden that hypothesis beyond all necessity.

The theory of formative stimuli, which explains the persistence of structures in the embryo of animals on the assumption that their presence is absolutely necessary as a "stimulus" for later development, meets with difficulties in the case of plants. Here development is not due to interstitial growth, as in animals, and does not involve progressive differentiation of almost all the cells of the body, but is brought about by the activity, at a growing point, of a small group of undifferentiated, continually dividing cells, from the innermost of which are laid down tissues which almost immediately become fixed and unalterable in size and shape. The influence, upon such a distant growing point, of structures previously laid down must be slight as compared with the effect of already formed structures, in animals, upon growth in which they themselves are taking an active part.

The facts of recapitulation can perhaps be understood better on the principle, which we have already discussed, that certain categories of characters are inherently more conservative than others. It may be said that, theoretically, every individual tends to inherit all the peculiarities of its ancestors; but since life is short and history is long, most of the chapters have to be omitted. It is only reasonable to suppose that those features will disappear first during evolutionary advance which are least conservative and least firmly fixed in the constitution of the race; and such we find to be the fact, for it is not characters of size, shape, color and texture which are usually preserved in ontogeny, but the less plastic ones of number and plan. The presence of gills and their associated skeletal and circulatory structures became rigidly implanted in the primitive vertebrate stock and the general outline of these structures still persists in the embryos of modern terrestrial forms. It is not a functional gill which is repeated, however, nor one of definite shape or special construction, but simply a gill cleft, with the vestiges of its ancient skeleton and vascular supply. It is as though what the geneticist would call the factor for the gill openings had persisted unchanged, but that the factors for the shape, size and structure of the gills had been widely altered or disappeared altogether. The developing axis of a woody plant repeats little of the histological features of its predecessors, but it does recapitulate the general vascular topography of successive ancestral forms. The developing organism has concentrated within it an essence, so to speak, of the most conservative and therefore the most salient characters which distinguished the ancient members of its line. The fact that all plastic and highly variable features have been swept away enables these historical landmarks to stand out distinctly, and gives to the structure of the animal embryo and of the young plant a very important significance in the science of phylogeny.

The principle that fixity of character increases with differentiation, which we have regarded as of so much importance in evolution, is easier to establish than to explain. It is possible to regard the matter from the viewpoint of genetics and to imagine that a "variable" species is a "mixed population," the members of which are continually intercrossing, and that the appearance, in certain individuals, of definite discontinuous variations isolates such individuals from the rest of the species and causes the partial or complete establishment of each as a distinct "pure line" with more closely defined characters. The more numerous such discontinuous variations were, the more complete the isolation of a given line would become and the more purely, therefore, would it reproduce itself until finally its characters became very sharply fixed. In other words, fixity may be due to germinal segregation and may depend directly on the proportion of factors which are in a homozygous condition in the germ plasm of the two parents. Complete homozygosity in both would ensure complete fixity of parental characters in the offspring.

A comparison also suggests itself between the effects of differentiation in ontogeny and in phylogeny. Experimental work has shown that in the more primitive animals, where the power of regulation is best developed, any part of a tissue or elementary organ, so long as it remains undifferentiated, is able, upon necessity, to give rise to all structures that the whole tissue would normally have produced. A sufficiently large group of cells from any portion of the blastula of an echinoderm, for example, will produce a normal larva; but the moment the process of gastrulation begins, this power of producing the whole animal is definitely lost by those very cells which possessed it but a few hours previously; for, now that differentiation has begun to take place, a piece which shall give rise to a normal larva must include a little of both the primitive ectoderm and entoderm and can not be taken at random from anywhere in the embryo. Any portion of the primitive gut, which later develops, is able to produce the cœlomic pouch, should the normal region of origin of that structure be removed, but this "equipotency" lasts only so long as there is no differentiation, for if the pouch once begins to develop and then is removed it can never be produced again even by the cells which a short time previously had the power to form it. This process of ontogenetic segregation results in the continual loss of potentialities, in the progressive narrowing down of the possibilities at the command of every living cell. The situation in phylogeny is very similar, for the possibilities before a simple, plastic and comparatively undifferentiated organism—the lines of evolution along which its descendants may go—are much greater than those before one which is highly developed and sharply specialized. Increased differentiation is followed so regularly by decreased plasticity, both in phylogeny and ontogeny, as to suggest the possibility of a common cause.

There is also a similarity between structural fixation and certain psychological phenomena. The performance of an action is always uncertain and variable at first, but constantly tends to become stereotyped and habitual. The simpler types of animal activity are directed by instincts which are comparatively changeable and plastic, but where behavior has become highly specialized and complex, instinct has attained a high degree of precision and invariability. In the same way, a person whose activities are of wide range and comparative simplicity is much more adaptable than one who has become habit-bound through a life of intense specialization. As an organism's "experience mass" becomes continually greater and more complex the formation occurs of that system of habits which in man we call a mental character, and this process, like that of ontogenetic and phylogenetic development, involves the continual elimination of potentialities and consists in the progressive fixation, with advancing age, of characters which during youth were variable and inconstant. It so much resembles the establishment of an organic structural type by the elimination of variability through advance in specialization as to suggest that perhaps both phenomena are manifestations of the same cause.

Such attempted explanations of the differences in fixity which occur between organic characters are of course incomplete and highly unsatisfactory. The very fact, however, that it is possible at all to formulate principles of conservatism and variability, unexplained though they may be, which shall be of application throughout the animal and plant kingdoms or which shall at least be operative in certain definite groups of organisms, is of great significance and value to the biologist, for it enables him to place all branches of his science on a somewhat more exact and uniform basis. It must of course be borne in mind that such principles as these are not invariably operative, for exceptions to all of them are frequently found. Biological laws undoubtedly exist, but they seem to belong to quite a different category from the invariable ones of the physical sciences.

The science of taxonomy will perhaps receive the greatest benefit from a general recognition of the fact that there are such things as laws of phylogeny, for a united effort by all biologists to define these laws more clearly and to apply them more widely will result, through the establishment of much more precise taxonomic criteria, in a clearing up of many difficulties and disputes as to relationships and in the construction of a truly natural classification on a more logical and consistent basis.

A knowledge of phylogenetic principles is also of value to the general student of evolution, for through it a better conception of the development of organic structures may be obtained than is set forth by the selection theory. A recognition of the facts that fixity increases with differentiation and that there are inherent differences in variability between functionally important characters and those which are useless for survival makes possible a much clearer understanding of the evolutionary history of any particular group.

The evolution of the hexapod insects is a case in point. The primitive insects seem to have been air-breathing arthropods with an indeterminate number of body segments and appendages. The ancestors of our modern hexapods achieved their first success through some advance in specialization over this more primitive type, but the improvements which gave them ascendancy and which enabled them to found a distinct and dominant group were certain unknown changes, doubtless in plastic and functionally important characters which were of great value for survival at the time, but which, having isolated the family and put it on its feet, so to speak, continued to change and may be possessed by few or no living descendants. The progressive increase in specialization, however, which caused the success of the primitive hexapods resulted in the gradual fixation of certain functionless characters, such as the number of segments and appendages, which finally became rigidly stereotyped as we see them to-day, so that they now distinguish *all* hexapods, whether successful and dominant species or those which are being beaten and exterminated. The conservative features have progressed steadily but slowly to their present condition, but the plastic characters, during the same time, have doubtless passed through wide and unrecorded ranges of variation and in so doing they have, as it were, caught and fixed into the advancing and increasingly specialized hexapod type the particular conservative and functionless characters which happened to distinguish those fortunate individuals which founded the present family. As a result our modern hexapods, as a whole, like all other natural orders, have as constant characters certain peculiarities of number and plan, whereas the subordinate groups of the order are still distinguished, in many cases, by the functionally important features to which they owe their successful establishment, but which in future evolution are doubtless destined to vary much.

Similarly, in that ascending group of animals which were to give rise to the higher vertebrates, the primitive archipterygium became stereotyped into the pentadactyl appendage, with its definite skeletal plan; but the particular improvements which caused the primitive pentadactylous stock to succeed at the start and to become segregated as a new and distinct order were doubtless concerned with such plastic but functionally important characters as size and shape and with the general vitality and adaptability of the race, and had little or nothing to do with the particular number of digits or arrangement of bones in the appendages. These characters, originally variable, simply happened to belong to a successful and progressive group of organisms and became fixed and stereotyped as specialization took place.

The ancestors of the grasses doubtless varied much as to nodal structure, but the particular group which through its success became the dominant and distinct modern family happened to be characterized by the possession of leaves whose bases formed an open sheath around the stem and were provided with a small membranous structure, the ligule. These characters, which are doubtless not the ones to which the family owes its success, since they are present alike in dominant and in unsuccessful species, became so firmly fixed during the progressive evolution of the Gramineæ that they now distinguish all members of the family.

All conservative and stable characters which are common to large groups of organisms have thus reached their present condition through slow but steady progress during the same time that plastic and functionally important features were changing and moulding themselves in adaptation to every new demand of the environment.

Organic evolution in general, including that of human civilization, seems to have resulted from the opposing actions of the two great factors which we have so often mentioned: on the one hand, the tendency toward fixation, which results in the stereotyping of structures and of habits and social customs, and which gives rise to mental as well as physical conservatism; and, on the other, the action of natural selection in weeding out such physical characters as tend to make the organism unadaptable and such customs, institutions and even societies as have become too firmly stereotyped through habit and precedent or too bound by tradition to maintain themselves in the advance of civilization. Natural selection does not interfere with useless or harmless characters which therefore become firmly fixed and are of great value in determining relationships between organisms and between civilizations and in deciphering the path of evolutionary advance.

This biological principle that trivial but conservative characters which happen to distinguish the beginnings of a successful evolutionary line become closely associated with all its subsequent development has therefore many suggestive parallels in human history. Any great movement is always colored by the circumstances surrounding its inception. The fact that our first popular translation of the Bible happened to be written in the seventeenth-century English does not account for the enormous subsequent spread of the Scriptures, but nevertheless the now archaic phraseology of the King James Version, a "conservative character" like all religious phraseology, and "unimportant for survival," has persisted almost unaltered throughout the history of the Protestant churches, and, surviving numberless changes of ritual, creed and theology, has stamped itself indelibly upon religious expression everywhere.

The whole subject of organic conservatism is so vast and so little understood as to be far beyond satisfactory treatment within the limits of such a paper as the present one. An extensive correlation of the mass of facts already in our possession and the discovery of a multitude of new ones will be necessary in order to formulate laws of phylogeny with any degree of accuracy. The essential point in the whole matter is the indication that evolution of animals and plants is not a random and fortuitous process, dependent on the caprice of external, inorganic nature, but that it is subject everywhere to certain definite and discoverable laws. Such a point of view, of course, is essentially an orthogenetic one and emphasizes the importance of the evolving organism rather than the creative power of the environment. By establishing the essential uniformity of vital processes everywhere it also tends to elevate biology from a mere subsidiary of the physical sciences to an independent position of its own.

SUMMARY

1. The construction of a natural classification of organisms is made possible only by the fact that certain characters of every individual are more conservative and less subject to variation than others during evolutionary development.

2. The explanation of conservatism propounded by the theory of natural selection is unsatisfactory since, so far as we are able to determine, characters which are most firmly fixed are in general those of least importance for survival.

3. From a study of phylogeny it is possible to formulate certain general principles of conservatism which are valid throughout more or less extensive groups of organisms.

4. The principal categories of conservative characters are those of number, position and plan.

5. Particular organs or regions of the body, throughout large groups of animals and plants, are less subject to change than others and hence are seats of primitive characters.

6. The early ontogenetic stages of animals and plants repeat those characters which were most conservative and firmly fixed in their ancestry.

7. Evolutionary advance and increase in differentiation tend to result in the decrease of variability. This is analogous to the loss of potentialities during ontogeny and is also comparable to the formation of habit.

8. Organic evolution is dependent on the action of two opposing factors: that of progressive fixation. which tends universally toward greater rigidity and conservatism in all characters during evolutionary advance; and that of natural selection, which tends to maintain or increase the variability of those characters important for survival by eliminating individuals where such characters have become so fixed that the organism fails to possess a necessary degree of adaptability. Natural selection is not concerned with harmless and trivial characters which consequently tend to become very conservative and are of much value in classification.

9. Such general principles of phylogeny as these, if thoroughly established and defined, will make possible the construction of a truly natural classification of organisms on a logical and uniform basis. They also present a clearer conception of the general method of evolution than is set forth by the theory of natural selection alone.

The writer is much indebted to Professor Herbert W. Rand, of Harvard University, for suggestions and information.

INHERITANCE OF LEFT-HANDEDNESS[1]

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Introduction.—The fact that left-handedness "runs in families" has probably attracted the attention of many observers, yet the method of inheritance has not been fully studied. Many people imagine the condition to depend entirely upon training or imitation. There is thus much of guesswork concerning the true nature of the condition.

Literature.—A considerable bibliography of left-handedness has recently been cited by Professor H. E. Jordan.[2] Most of his references are, however, to articles of little value, especially since nearly all of them were written previous to the modern period of genetic study. Professor Jordan puts forth the tentative opinion that left-handedness is a recessive character. Unfortunately the data which he presents consist chiefly of a few selected pedigrees from which the reader can obtain very little information. He suggests more than once that some of his cases are examples of the spontaneous appearance of left-handedness in a family. If such spontaneous development were so frequent the whole population would, in a few generations, be left-handed. The appearance of a left-handed child in a family without left-handed ancestors for three or four generations is not to be considered remarkable, for this is the way in which recessive characters frequently behave.

Method of Obtaining Data.—At the beginning of a course of lectures on heredity in the University of Colorado in 1911 I distributed papers calling for informa-

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[1] An earlier paper, entitled "Mendelian Proportions and the Increase of Recessives," which grew out of my studies on inheritance of left-handedness was published in the AMERICAN NATURALIST, Vol. XLVI, pp. 344–351, June, 1912.

[2] *Breeders' Magazine,* Vol. II, pp. 19–29 and 113–124, 1911.

tion from the students in regard to right- and left-handedness in their own families or in other families with which they might be quite familiar. Each student noted down the parents and every child in the family. Since the students who reported are from nineteen to twenty-five years of age, the probability is that their families are now complete as to the number of children. Similar data were collected from another set of students in 1912. In addition to these collections of statistics, I have also studied the affection in a family of four generations, including about thirty people. Since this material offers nothing especially different from that gathered from the students, I have not included it in the present study.

TABLE I

STATISTICS OF PARENTS AND CHILDREN

	Number	Per Cent. Observed	Per Cent. Expected $4RR:4Rr:rr$	Per Cent. Expected $9RR:12Rr:4rr$
Total parents..........	610			
Right-handed parents...	561	91.94	89.99	84.00
Left-handed parents....	49	8.06[3]	11.11	16.00
Total children.........	1,130			
Right-handed children ..	953	84.34	89.99	84.00
Left-handed children....	177	15.66[3]	11.11	16.00

Value of Different Data.—Since the young people from whom the information was obtained would be much more likely to know of left-handedness among their brothers and sisters than in their parents, the reports for children are probably more accurate than those for parents. It is easy to see how a child would report a parent as right-handed unless the person were very definitely left-handed. A child would not know about the early history of his father or mother. On comparison of the number of left-handed individuals among parents and children left-handedness seems to be about twice as common among the children. This is, of course, a manifest absurdity and is

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[3] Since the proportion of left-handed children is nearly twice that of the left-handed parents it is evident that left-handedness among the parents is greatly under-reported.

TABLE II

Statistics of Families

	Number	Per Cent. Observed	Per Cent. Expected $4RR{:}4Rr{:}rr$	Per Cent. Expected $9RR : 12Rr : 4rr$
Total families	305			
Families with both parents reported as right-handed	258	84.59	79.01[4]	70.56[5]
Families reported as having one parent right-handed, the other left-handed	45	14.75	19.74[4]	26.88[5]
Families reported as having both parents left-handed	2	0.66	1.24[4]	2.56[5]
Families reported as having all children right-handed	174	57.05	69.13[4]	59.04[5]
Families with some or all children left-handed	131	42.95	30.87[6]	40.96[7]
Average number of children per family in the population (families 305, children 1,130)	3.7			
Average number of children among families showing some left-handed children (families 131, children 548)	4.1			

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[4] The expected number of matings of any particular sort, or the matings resulting in particular types of offspring, in a population of $4RR : 4Rr : rr$ may be calculated from the following table:

1. $4RR \times 4RR = 16$
2. $4RR \times 4Rr = 16$
3. $4RR \times rr = 4$
4. $4Rr \times 4RR = 16$
5. $4Rr \times 4Rr = 16$
6. $4Rr \times rr = 4$
7. $rr \times 4RR = 4$
8. $rr \times 4Rr = 4$
9. $rr \times rr = 1$

$\overline{81}$

Matings 1, 2, 4 and 5 have both parents right-handed; adding $16 + 16 + 16 + 16 = 64 \div 81 = 79.01$ per cent. Matings 3, 6, 7 and 8 are each of a right-handed and a left-handed parent. Mating 9 is of two left-handed parents; this type may be expected once in 81 times, or $1 \div 81 = 1.24$ per cent. Only right-handed children will appear in matings 1, 2, 3, 4 and 7; left-handed children are to be expected in 5, 6, 8 and 9. These last make $16 + 4 + 4 + 1 = 25 \div 81 = 30.87$ per cent.

[5] The expected number of matings of a particular sort, or the matings resulting in particular types of offspring, in a population of $9RR : 12Rr : 4rr$ may be calculated as suggested in the previous footnote. Here it is necessary to use the following table:

1. $9RR \times 9RR = 81$
2. $9RR \times 12Rr = 108$
3. $9RR \times 4rr = 36$
4. $12Rr \times 9RR = 108$

to be accounted for as just stated. Probably the most valuable parts of the statistics are the figures showing families with left-handed children and also the total number of left-handed children in the population.

Natural and Acquired Left-handedness.—Most right-handed people can be taught to use the left hand for many purposes, and conversely left-handed people may learn to write and perform various acts of skill with the right hand. But aside from these rather unusual cases there are many individuals who are naturally right-handed and do most of their work with the right hand. Others are left-handed by nature. Left-handedness seems to be connected with a more highly developed condition of the right cerebral hemisphere. Evidence in support of this view is found in a number of cases of aphasia connected with left hemiplegia. The left motor area of the cortex, as is well known, is associated with speech in most individuals. Hence a lesion of this area results in aphasia and paralysis of the right side of the body. When similar

$$\begin{array}{lllr}
5. & 12Rr \times 12Rr & = & 144 \\
6. & 12Rr \times 4rr & = & 48 \\
7. & 4rr \times 9RR & = & 36 \\
8. & 4rr \times 12Rr & = & 48 \\
9. & 4rr \times 4rr & = & \underline{16} \\
 & & & 625
\end{array}$$

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[6] Only in the following matings could left-handed children appear:

$$\begin{array}{lrl}
4Rr \times 4Rr = & 12 & \text{right-handed, } 4 \text{ left-handed} \\
4Rr \times rr = & 2 & \text{right-handed, } 2 \text{ left-handed} \\
rr \times 4Rr = & 2 & \text{right-handed, } 2 \text{ left-handed} \\
rr \times rr = & 0 & \text{right-handed, } 1 \text{ left-handed} \\
 & \overline{16} & \qquad\qquad\quad \overline{9}
\end{array}$$

The children in these families would then be expected in the ratios of 16 : 9, or 64 per cent. right-handed, 36 per cent. left-handed.

[7] Only in the following matings could left-handed children appear:

$$\begin{array}{lrl}
12Rr \times 12Rr = & 108 & \text{right-handed, } 36 \text{ left-handed} \\
12Rr \times 4rr = & 24 & \text{right-handed, } 24 \text{ left-handed} \\
4rr \times 12Rr = & 24 & \text{right-handed, } 24 \text{ left-handed} \\
4rr \times 4rr = & 0 & \text{right-handed, } 16 \text{ left-handed} \\
 & \overline{156} & \qquad\qquad\quad \overline{100}
\end{array}$$

The children in these families would then be expected in the proportion of 156 right-handed to 100 left-handed, or 61 per cent. right-handed and 39 per cent. left-handed.

TABLE III

STATISTICS OF FAMILIES REPORTED AS HAVING BOTH PARENTS RIGHT-HANDED

	Number	Per Cent. Observed	Per Cent. Expected[8] $4RR:4Rr:rr$	Per Cent Expected[8] $9RR:12Rr:4rr$
Total families in the group	258			
Families within this group having all children right-handed	165	63.95[9]	75.00[10]	67.35[11]
Families within this group having some children left-handed	93	36.05[9]	25.00[10]	32.64[11]
Total children in the group	953			
Right-handed children reported in the group	837	86.74	93.75[12]	91.84[13]
Left-handed children reported in the group	116	13.26	6.25[12]	8.16[13]
Children in those families in which all children are right-handed	555	58.24[9]	75.00[10]	67.35[11]
Children in those families in which some children are reported as left-handed	398	41.76[9]	25.00[10]	32.65[11]
Right-handed children in those families in which part of the children are left-handed	282	70.85[9]	75.00	75.00
Left-handed children in those families in which part of the children are left-handed	116	29.15[9]	25.00	25.00

[8] See footnotes 4 and 5 to Table II.

[9] The figures show that some of the alleged right-handed parents are really left-handed.

[10] The population considered in this table is made up of matings 1, 2, 4 and 5 given in footnote 4 to Table II, thus:

$$\begin{array}{ll} 1. & 4RR \times 4RR = 16 \\ 2. & 4RR \times 4Rr = 16 \\ 4. & 4Rr \times 4RR = 16 \\ 5. & 4Rr \times 4Rr = 16 \\ & \overline{\ 64} \end{array}$$

Obviously, only mating 5 will show left-handed children. This constitutes $16 \div 64 = 25$ per cent. of the families.

[11] The entire population considered in this table is made up of matings 1, 2, 4 and 5 in footnote 5 to Table II, thus:

$$\begin{array}{ll} 1. & 9RR \times 9RR = 81 \\ 2. & 9RR \times 12Rr = 108 \\ 4. & 12Rr \times 9RR = 108 \\ 5. & 12Rr \times 12Rr = 144 \\ & \ 441 \end{array}$$

The families showing left-handed children would be only those in mating 5. This constitutes $144 \div 441 = 32.65$ per cent.

[12] The only left-handed children will be in mating 5, viz.: $4Rr \times 4Rr$. They will constitute one fourth of the children in this mating, or one sixteenth of all the children $= 6.25$ per cent.

[13] The only left-handed children will be in mating 5, viz.: $12Rr \times 12Rr$. They will constitute one fourth of the children in this mating. Hence: $\frac{1}{4} \times 144 \div 441 = 8.16$ per cent.

lesions of the right cerebral cortex result in paralysis of the left side and also in aphasia, it is sometimes found that the persons thus affected were naturally left-handed. I am informed by my colleague, Dr. O. M. Gilbert of the department of medicine of this university, that this connection of left-handedness with a speech center on the right side of the cortex is well attested.

A certain number of persons consider themselves to be "ambidextrous" and claim that they are not naturally either right-handed or left-handed. It is, however, difficult for one to know his own original condition with regard to the use of the hands, since in most homes the child is taught early the use of the right hand in taking up a spoon or cup. I suspect that the "ambidextrous" persons are really left-handed by nature.

Mendelian Explanation of Heredity of Left-handedness.—A study of the accompanying tables will suggest that left-handedness is a Mendelian recessive. It belongs to that group of characters which may show themselves in families where neither parent is affected, and sometimes in families with no affected ancestors for a number of generations. In the 305 families there are only two reported as having both parents left-handed. If the condition is a Mendelian recessive the children in these families should all be left-handed. According to the report, however, one child is right-handed. Of course it is possible that one of the parents was by nature right-handed. Possibly some heterozygous (simplex) persons may easily learn to use the left hand.

Presentation of Material.—The material collected has been classified in such manner that it can be made use of by others who may be studying the subject. In some of the tables I have indicated the expected percentages if the population were to consist of the three Mendelian types of individuals in the following proportions, viz.:

(*a*) $4RR : 4Rr : rr$,
(*b*) $9RR : 12Rr : 4rr$.

TABLE IV

BOTH PARENTS REPORTED AS RIGHT-HANDED, BUT WITH SOME OF THE CHILDREN LEFT-HANDED (FAMILIES 93, RIGHT-HANDED CHILDREN 138, LEFT-HANDED CHILDREN 116).[14]

Name of Person Reporting	Right-handed Children	Left-handed Children	Name of Person Reporting	Right-handed Children	Left-handed Children
Ahr	2	1	Max	1	1
Ba	0	1	Mer (*a*)	1	1
Bar	3	1	Mer (*b*)	2	1
Bat	3	1	Milb	1	1
Ben	3	1	Mill. L.	3	1
Br. F.	1	1	Mill. W.	6	2
Br. H.	3	1	Mur	4	1
Br. N.	2	3	N	8	1
Bu	3	1	Ol	4	1
Bur	2	1	Ow	1	1
Chr	3	1	Pe	9	3
Con	1	1	Po	2	1
Cou	1	1	Pu	7	1
D	0	1	Re	1	1
Don	4	1	Rid (*a*)	2	2
Dou	5	1	Rid (*b*)	0	1
Ed	4	1	Rid (*c*)	2	2
F (B)	3	1	Ro	4	1
F (C)	5	1	Roberts	6	2
Fl	1	2	Rbtn (*a*)	4	1
Fur	1	1	Rbtn (*b*)	2	1
Ga	4	1	Rbsn	2	1
Gi	3	2	Sa	6	3
Goo (*a*)	1	1	Salb	4	2
Goo (*b*)	2	2	Sc (M)	3	1
Gr	1	3	Sc (P)	1	1
Ha (P)	5	2	Schm	6	2
Har	2	1	Shee	3	2
He	2	1	Sheld	1	1
Hi	2	1	Sm	0	1
Hu	2	1	Smi (B)	4	1
Hun	3	1	Smoth	3	1
Is	8	1	Spra	2	1
J (M)	3	1	Stream	1	1
J (R)	6	2	Sul	3	1
Joh	3	2	T	3	1
Jon	1	2	Tay (R)	7	1
Ka	3	1	Tenn	2	1
Kei	3	1	Terw	3	1
Kel	5	1	Warn	2	1
Ken	3	1	Web (H)	4	1
L	4	1	Weim	1	1
Li	7	2	Wh (E)	2	1
Mac	5	1	Wh (H)	2	1
McNab	4	1	Wilh	4	1
McPh	4	1	Wr	4	1
Ma	3	1			
				138	116

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[14] The percentage of left-handed children is 45.67. According to Mendelian rules the expectation is 25 per cent. As noted before it is apparent that many of the parents reported as right-handed are really left-handed. Hence the large excess of left-handed children.

In the above ratios RR is pure right-handed, Rr is heterozygous right-handed and rr is left-handed. I have taken these particular proportions because they are stable and they approximate to a degree the actual condition in the population studied. As is noted in the table, the number of left-handed persons is probably greater than the reports indicate. Some families reported as having both parents right-handed evidently belong with the group of one left-handed and one right-handed. Some reported in this latter group belong, no doubt, with those having both parents left-handed.

TABLE V

ONE PARENT RIGHT-HANDED, THE OTHER LEFT-HANDED

A. Right-handed Parent Evidently Heterozygous (Families 36, Right-handed Children 88, Left-handed Children 55).

Name of Person Reporting	Right-handed Children	Left-handed Children	Name of Person Reporting	Right-handed Children	Left-handed Children
Ba..........	1	1	Li (*b*)........	1	1
Bi...........	2	1	McD........	2	1
Br...........	2	1	McF.........	3	1
Bra..........	3	1	McK........	3	1
Ca..........	3	4	Mal.........	2	1
Ch..........	2	2	Mil..........	2	1
Cu..........	4	2	Mit..........	3	2
D'A.........	0	1	Ols (*a*).......	1	1
Di...........	2	1	Ols (*b*).......	1	2
Fra..........	4	1	Or...........	0	1
Fre..........	1	1	Re..........	3	1
H (*d*)........	4	3	Ri...........	2	1
He..........	4	1	Str..........	2	1
Hea.........	2	3	Wa (*a*).......	2	1
Hi...........	2	2	Wa (*b*).......	1	1
Ho..........	5	2	Web.........	2	1
Kei..........	5	3	Wei.........	5	2
Li (*a*)........	2	2	Wil..........	5	3
				88	55

Fecundity of Left-handed Families.—It is well known that in certain species of animals races showing particular recessive traits have less vitality and perhaps less reproductive ability than the ordinary members of the species. From the studies herein recorded, especially in Table II, it is seen that the left-handed families are quite as fertile as the normal ones.

Summary.—The foregoing pages are given to a study of left-handedness among 610 parents and 1,130 children, the data being collected from students at the University of Colorado. It is concluded that left-handedness is a Mendelian recessive. The condition probably exists in about one sixth of the population. A suggestion is made that the three Mendelian types of individuals may exist in some such proportion as 9 *homozygous right-handed*: 12 *heterozygous right-handed*: 4 *left-handed*.

B. Right-handed Parent Probably Homozygous (Families 9, Right-handed Children 27, Left-handed Children 0).

Name of Person Reporting	Right-handed Children	Left-handed Children	Name of Person Reporting	Right-handed Children	Left-handed Children
Ba..........	5	0	Nau........	2	0
Be..........	4	0	Pi..........	3	0
Bl..........	1	0	Spr.........	2	0
Du..........	4	0	Sto.........	3	0
Mi..........	3	0		27	0

TABLE VI

BOTH PARENTS REPORTED AS LEFT-HANDED

Name of Person Reporting	Number of Right-handed Children	Number of Left-handed Children
McN	1	2
P	0	4
	1[15]	6

[15] Mendelian expectation requires that all the children of these families be left-handed. It is possible that one of the parents in the McN family was naturally right-handed and that the left-handedness was only acquired. If this is not the case then there seems no explanation to offer for the appearance of the right-handed child.

SUPPLEMENTARY STUDIES ON THE DIFFERENTIAL MORTALITY WITH RESPECT TO SEED WEIGHT IN THE GERMINATION OF GARDEN BEANS—II

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Comparison of Means

Take first the most stringent comparison—that between the constants of the seeds germinating normally and those of the seeds failing to germinate, *A–C*. The frequencies and mean magnitudes are:

	f	Absolute Values	Relative Values
Plus differences	29	+.396	+3.50
Minus differences	21	−.702	−4.62
All differences	50	−.065	+0.09

Or considering only differences which are at least 2.5 times their probable error:

	f	Absolute Values	Relative Values
Plus differences	15	+0.541	+5.42
Minus differences	9	−1.355	−8.84
All differences	24	−0.170	+0.07

For the 18 cases in which the differences are at least 4 times their probable errors the results are:

	f	Absolute Values	Relative Values
Plus differences	12	+0.536	+ 5.73
Minus differences	6	−1.634	−10.93
All differences	18	−0.187	+ 0.17

These facts in a somewhat different form are made clear to the eye in Diagrams 1 and 2.[14]

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[14] Two types of graphs seem most suited to bring out clearly these results. In both, the signs and magnitudes of the differences between the normally developing and the eliminated series are shown by the direction and lengths of a series of lines. The solid lines falling below the zero bar show on the scale to the left the magnitude of the negative differences—*i. e.*, of those

The first of these graphs shows the values reduced to percentages of the constants for the general population of seeds from which the samples used in these experiments were drawn, *i. e.*, the constants given in Table X. The second shows the ratio of the differences to their probable errors.

The impression given by both of these charts is that the mean weight of the surviving seeds has been increased by the mortality, although there are one or two conspicuously large negative values in each case. This impression is borne out by the numerical result, if we confine our attention to the signs, merely. Of the 50 experiments, 29 show an increase and 21 a decrease in seed weight, whereas if there were no relationship between mean seed weight and viability, the deviations would be expected to be equally divided between positive and negative, except for the error of random sampling which would be given by $.6745\sqrt{50 \times .5 \times .5}$. Thus in the present case for the whole fifty experiments, the deviation from the equality which we should expect if there were no relationship between mean seed weight and mortality is 4 ± 2.38 series. Surely this can not be regarded as a trustworthy difference, but we note that the difference has the same sign and is relatively larger as we reduce our number of cases by disregarding those comparisons which are less

in which the seeds failing were heavier or more variable than those which developed, in which selection decreased mean weight or variability. The broken lines extending above the zero bar show the number and the magnitude of the differences indicating an increase in mean or in variability as the result of selective elimination. The length of these bars may be determined in three different ways. They may simply represent the absolute differences (in units of .025 gram). They may represent percentage difference, on the basis of the constant for the whole population, as explained above. They may be in terms of the ratio of the difference to its probable error.

The first is the method used in the diagrams of the earlier paper. It is of no advantage here where the number of entries is too numerous to enable absolute values for individual series to be conveniently read from them. The second has the merit of presenting to the eye all the values in comparable terms. The third shows at a glance the statistical significance to be attached to the differences represented. The two latter are used.

probably statistically significant with respect to their probable errors. Thus if we throw out the 26 cases which are less than 2.5 times their probable error, we find that 15 are positive and 9 negative, a deviation of 3 ± 1.65.

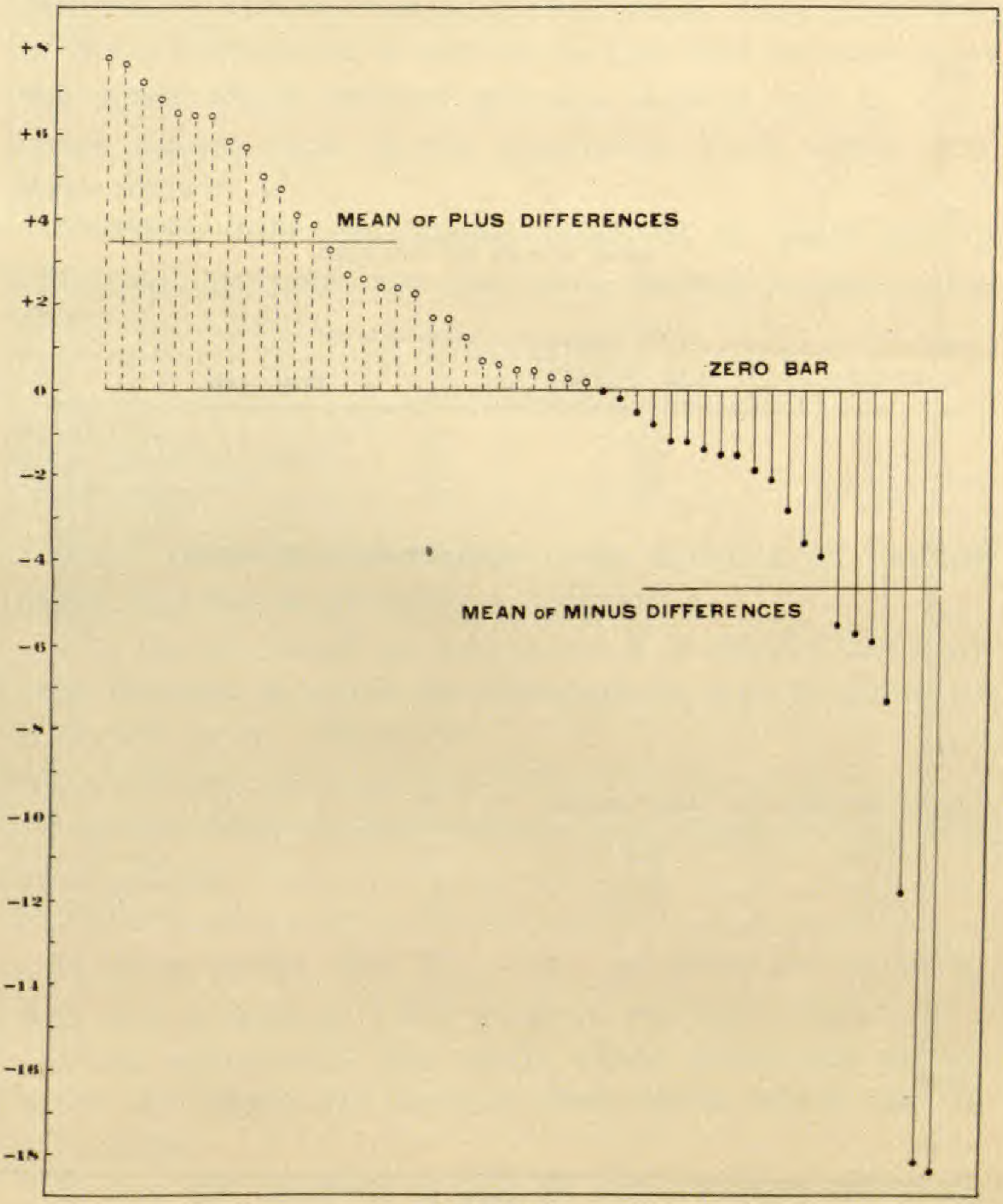

DIAGRAM 1.

If we consider only differences which are four times their probable error, we find 12 positive and 6 negative, a deviation from equality of 3 ± 1.43.

When, however, we turn to the averages—both absolute and relative—we see very little support for the view that there is a tendency for the weight of surviving seeds to be heavier than those which fail. Sometimes, the general average is positive and sometimes it is negative in sign; it is always insignificant in magnitude. Nor, to return to the question of the more qualitative classification of the experiments, can any great weight be attached to such inequalities in the number of positive and negative differences as we have secured.

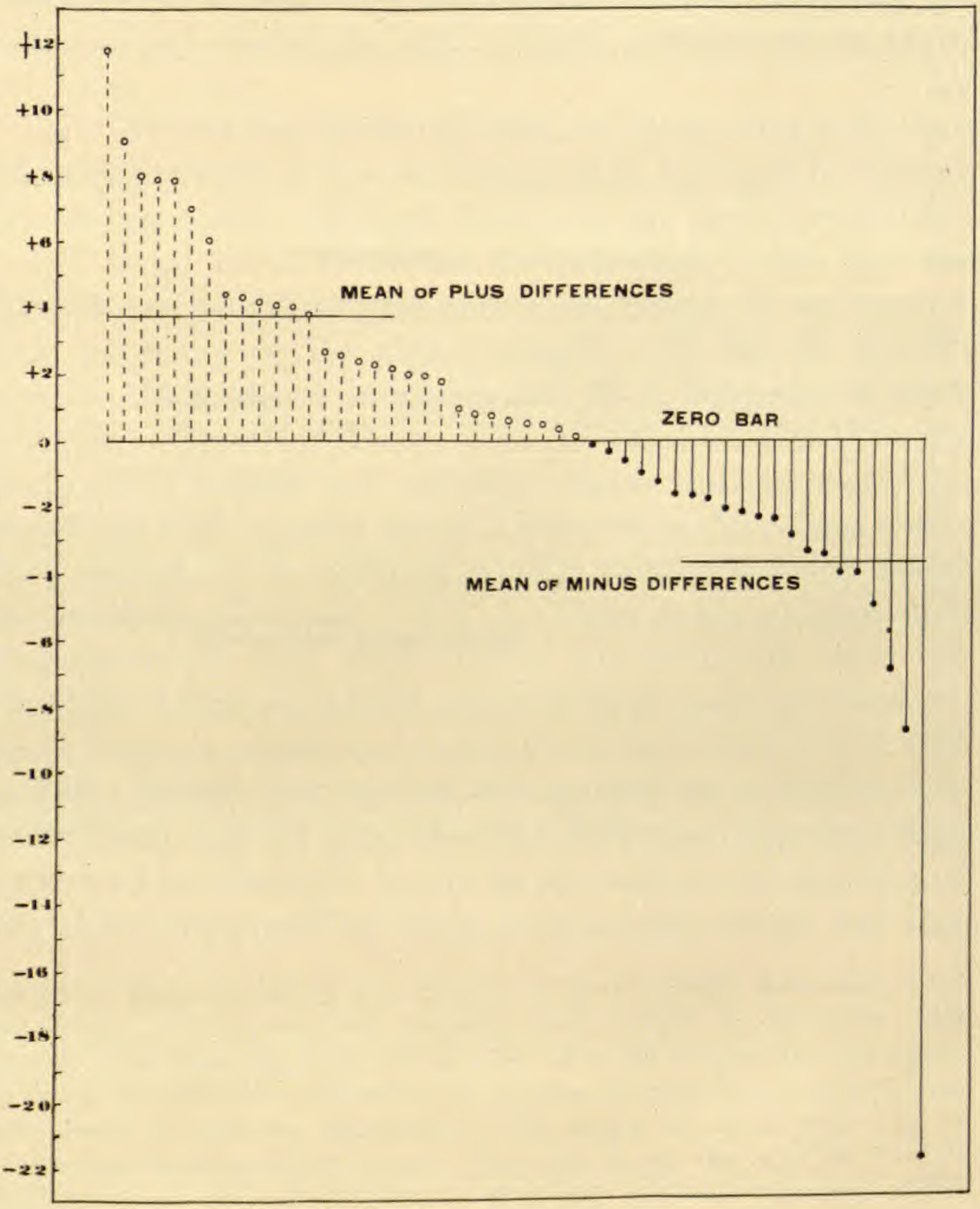

Diagram 2.

The mean values of the ratios of the differences, *A–C,* to their probable errors have also been struck. The 21 negative cases give a mean ratio of 3.70 while the 29 positive values give 3.75. These substantial averages taken in connection with the number of rather high individual ratios certainly suggest that there are real biological differences between the samples of seeds. One expression of these differences is seen in the fact that in some cases the seeds which survive average heavier and in other cases lighter than in the population from which they were drawn.

Consider now the weight relations of seeds giving abnormal germinations and those failing to germinate, *B–C:*

	f	Absolute Values	Relative Values
Plus differences	32	+.581	+4.34
Minus differences	18	−.287	−2.08
All differences	50	+.268	+2.03

Thus there is a deviation from equality of 7 ± 2.38 cases, and this is probably significant.

For the abnormal germinations N is small; there are only 12 cases in which the difference is over 2.5 times its probable error. These are:

	f	Absolute Values	Relative Values
Plus differences	11	+1.026	+7.39
Minus differences	1	−0.450	−2.23
All differences	12	+0.903	+6.58

In seven series, diff. $E_{\text{diff.}} > 4$. *All these are positive;* they give a mean of 1.093 *absolute* and 8.47 *relative.*

Thus, apparently, the seeds which germinate abnormally are distinctly heavier than those which fail to germinate.

If now we combine A and B and compare all seeds which germinated with all those which failed, we have:

	f	Absolute Values	Relative Values
Plus differences	31	+0.360	+3.25
Minus differences	19	−0.513	−3.26
All differences	50	+0.028	+0.77

For the cases which are 2.5 or more times their probable error:

	f	Absolute Values	Relative Values
Plus differences	17	+0.510	+4.92
Minus differences	7	−1.035	−6.44
All differences	24	+0.060	+1.60

Thus by combining normal and abnormal germinations there is stronger evidence for an increase in mean seed weight by a selective death rate than when the normal germinations alone are considered. This point will be taken up again.

Just here it is necessary to point out that in this series merely the capacity for germination of the seeds in sand is taken into account, whereas in the former study only those were considered viable which had produced fertile plants. In combining normal and abnormal seedlings and contrasting them with those which failed to germinate at all, we are undoubtedly considerably overestimating the capacity for survival in nature.[15]

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[15] From personal experience in the handling of the plants I have no doubt whatever that had germination taken place in a substratum less easily displaced than sand (*e. g.*, in a stiff clay soil) a number of the seeds classified as abnormal in germination would not have succeeded in unfolding their primordial leaves to the light. Again, I believe there is not the slightest question that of those which did reach the surface a higher proportion would fail to develop into mature plants than of the seedlings classified as normal. In fine, there is probably a post-germination as well as pre-germination mortality, and this mortality is probably selective. Indeed for morphological variations it has been shown to be so. (Harris, J. Arthur, "A Simple Demonstration of the Action of Natural Selection," *Science*, N. S., 36: 713–75. 1912). My general impression from working with the seedlings of both sorts is that there is likely to be a larger difference in mortality between the normal and abnormal seedlings of this paper than between the normal and abnormal seedlings of the study of the death rate of normal and morphologically aberrant seedlings.

It is possible, therefore, that such differences in mean weight as are found between the results of the two investigations may be in part due to a somewhat different elimination during germination and in part due to a selective mortality occurring beyond the point at which the census for the later series of experiments was necessarily closed. Thus it appears that when the abnormal germinations are grouped with the normal to give the comparison $(A + B) - C$ the evidence for an increase in mean seed weight through selective mortality of the lighter seeds is strengthened. A comparison of the two classes of seedlings also suggests that the seeds giving rise to those which are abnormal may be heavier than those germinating

Ideally, to obtain results valid for individuals attaining reproductive maturity one should take a small proportion of the seeds germinating normally and a much higher proportion of those giving rise to abnormal seedlings and combine them with the seeds failing to germinate. There is no possible way of estimating the proportion of A and B which should be classed with C. If one wishes to make the comparison which shall be at the opposite extreme of that in which all seeds germinating at all are compared with those failing to germinate, he may combine the seeds germinating abnormally with those which do not germinate. Thus $(A+B)-C$ and $A-(B+C)$ will give us the upper and lower possible measures of the influence of mortality of abnormal seedlings on seed weight.

Turning to the comparison of means for $A-(B+C)$:

	f	Absolute Values	Relative Values
Plus differences	27	+0.371	+3.46
Minus differences	23	−0.745	−4.81
All differences	50	−0.142	−0.35

Restricting comparisons to differences at least 2.5 times their probable error:

	f	Absolute Values	Relative Values
Plus differences	14	+0.524	+5.28
Minus differences	13	−1.192	−7.73
All differences	27	−0.302	−0.99

Or restricting still further to those which are at least $4E$:

	f	Absolute Values	Relative Values
Plus differences	12	+0.515	+ 5.46
Minus differences	8	−1.599	−10.64
All differences	20	−0.331	− 0.98

Certainly, there is in these figures no trustworthy indication of an increase of mean weight as a result of selective mortality.

normally. If this is true, and if the abnormal seedlings have a higher post-germination mortality, it is clear that some of the increase in mean observed in these experiments would have disappeared if the plants had been required to develop to maturity under field conditions.

Somewhere between this minimum value and the one given above by $(A + B) - C$ probably lies the true measure of the change in mean weight as it would occur if the plants were required (as they would be in nature) to grow to reproductive maturity.

I now turn to the individual varieties. This demands, for results which shall be at all trustworthy, the combination of both sets of experiments.[16]

The accompanying table gives the results for the relative differences in mean weight (differences expressed as percentages of the general population constant).

Varieties	f	Relative Values
NAVY:		
Plus differences	18	+2.461
Minus differences	6	−1.134
All differences	24	+1.562
NE PLUS ULTRA:		
Plus differences	5	+1.122
Minus differences	3	−1.962
All differences	8	−0.022
WHITE FLAGEOLET:		
Plus differences	9	+1.787
Minus differences	3	−0.247
All differences	12	+1.276
BURPEE'S STRINGLESS:		
Plus differences	10	+1.244
Minus differences	16	−1.048
All differences	26	−0.167
GOLDEN WAX:		
Plus differences	0	———
Minus differences	7	−2.087
All differences	7	−2.087
FLAGEOLET WAX:		
Plus differences	1	+0.263

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[16] The method of rendering the result of these sand cultures most nearly comparable with the field experiments is to draw the comparison between the germinated seed and the general population from which they were drawn. Of course, the errors of random sampling in the drawing of the seeds would be overcome by comparing the constants for the seeds actually planted $(A + B + C)$ with those failing to develop, but this would not give differences comparable with those from field culture work where $(A + B + C + \ldots)$, not $(A + B + C)$, is known.

Anyone who cares to do so may make this comparison numerically for the whole material by taking the physical constants for $(A + B)$ and subtracting from them the general population constants given in Table X. It has already been made graphically in a paper on "Current Progress in the Study of Natural Selection," in *Pop. Sci. Mo.*, in press.

I believe that the purely statistical differences between the two sets of

This anaylsis of means by varieties is most suggestive. Leaving out of account Flageolet Wax for which there is only a single experiment, it appears that in Navy and White Flageolet there is a distinct increase in mean weight of survivors, that in Ne Plus Ultra and Burpee's Stringless there is no marked change in mean weight, while in Golden Wax there is a pronounced tendency for the survivors to be lighter than the general population.[17]

It is clear that such a condition as this would give, with a proper combination of strains, precisely the general result that we have found for the means: that is, an average of no change by selective elimination but significantly positive differences in some experiments and significantly negative differences in others. Here is a problem requiring further analysis—which, however, can be profitably undertaken only when larger bodies of experimental evidence are at hand.

COMPARISON OF ABSOLUTE VARIABILITIES

For the standard deviations for seeds germinating normally and seeds failing to germinate, *A–C*, in the whole material the results are:

experiments are not sufficient to be of material importance. Much greater weight is probably to be attached to certain experimental and biological factors. These are to be seen in both (*a*) the possible influence of the two types of substrata, and (*b*) the fact that in the field cultures viability was measured in terms of capacity to produce mature fertile plants, while in the sand cultures it was (necessarily) measured in terms of the capacity for (normal or abnormal) germination only.

[17] Possibly these results are due merely to the unavoidable errors of experiment and of sampling. Only far wider series of data can settle this point; until then no stress whatever is to be laid upon it. But *a priori* there is nothing unreasonable or improbable in such results. These varieties differ widely in the characteristics of their seeds and there is nothing surprising in the indication that in one variety the death rate is more concentrated toward the lower end of the range of variation, in another it is more restricted to the upper limit, while in a third both extremes are decimated. This seems especially probable in view of the fact that in this as in other cultivated species the varieties have been developed to suit the fancy of man and not to meet the requirements of the race in competitive life in nature.

	f	Absolute Values	Relative Values
Plus differences	17	+.145	+ 8.67
Minus differences	33	−.351	−13.77
All differences	50	−.183	− 6.14

These relationships are made clear by Diagrams 3 and 4. The first of these shows the differences in standard deviations expressed as percentages of the population S.D. The second shows the ratio of the differences to their probable errors.

The distribution of the differences which are at least 2.5 times their probable errors may be summarized:

	f	Absolute Values	Relative Values
Plus differences	5	+.335	+21.81
Minus differences	15	−.569	−21.64
All differences	20	−.343	−10.78

Thus of the 17 positive differences, 12 or about 71 per cent. are statistically untrustworthy (*i. e.*, $< 2.5E$) while

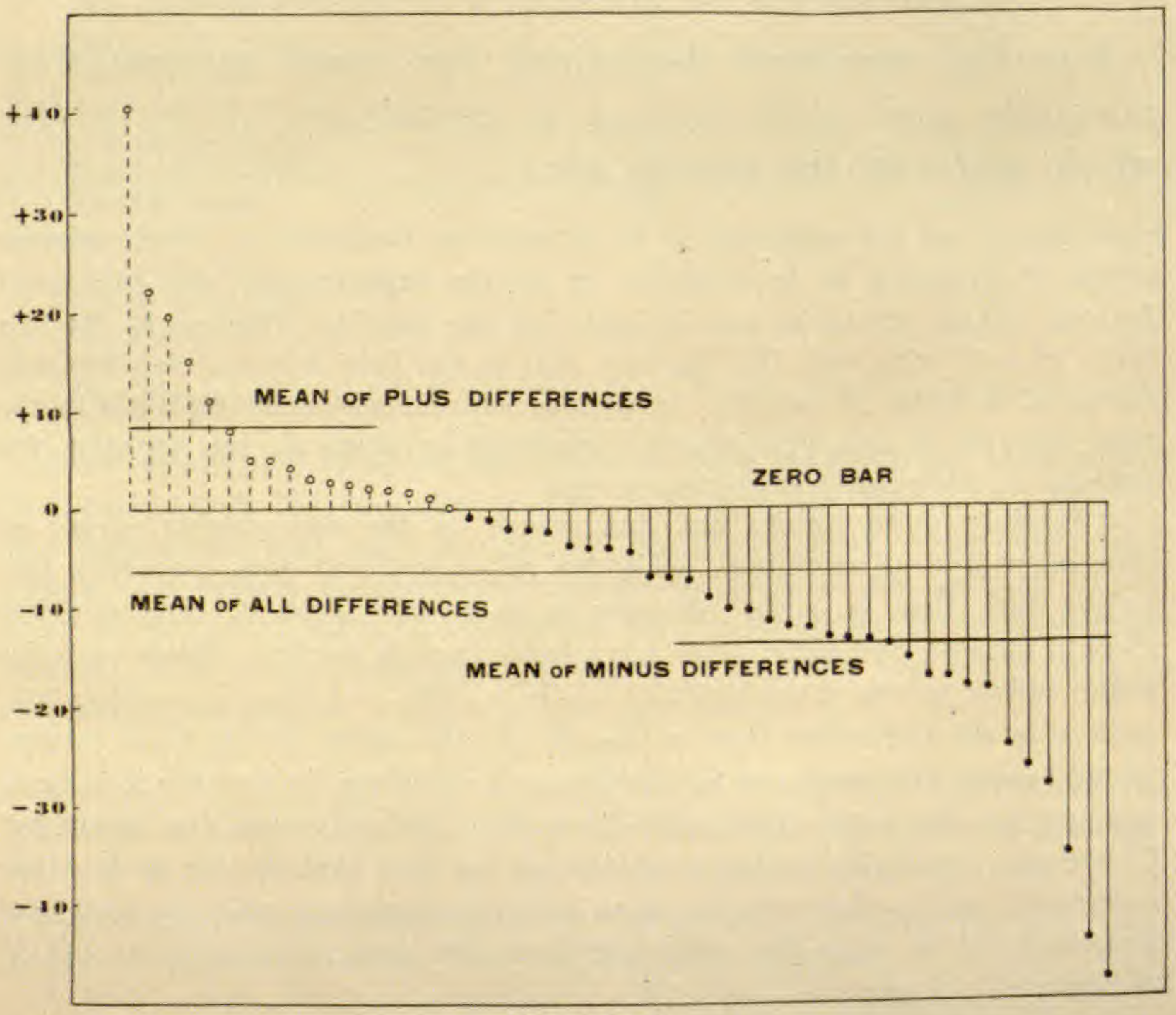

DIAGRAM 3.

of the 33 negative differences, only 18 or roughly 55 per cent. are not statistically significant. The deviations from equality are 8 ± 2.38 for the whole material and 5 ± 1.51 for the 20 series which are more probably statistically significant.

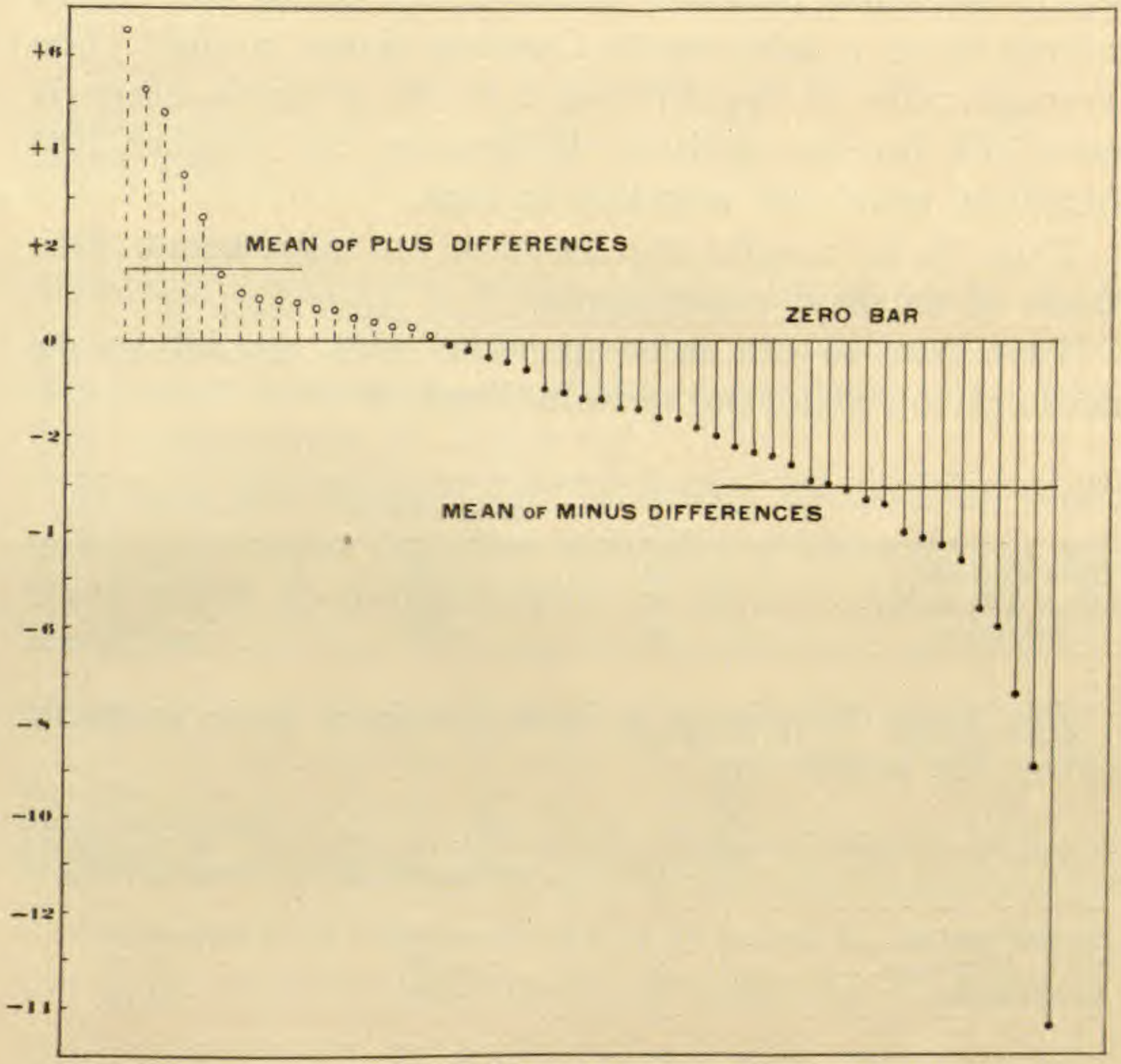

DIAGRAM 4.

Only 12 individual differences are over four times their probable error:

	f	Absolute Values	Relative Values
Plus differences............	3	+.363	+25.22
Minus differences..........	9	−.769	−27.31
All differences.............	12	−.486	−14.18

These results can leave no doubt as to the reduction in the absolute variability when the seeds which produce normal seedlings are selected out from those which fail to develop. The number of negative differences is significantly higher than the number of positive differences. The mean of the negative differences is larger numerically than that of the positive differences. The proportion of negative differences is higher among the constants which are more probably trustworthy, being only 1.5:1 among those $< 2.5E$ but 3:1 among those $> 2.5E$. The average ratio of the difference to its probable error is only 1.65 for the positive differences, but reaches 3.04 for those which are negative in sign.

Thus these results are in excellent agreement with those of the field experiments.

Turn now to the same question with regard to the seeds giving abnormal germinations, *B–C:*

	f	Absolute Values	Relative Values
Plus differences	23	+.235	+12.14
Minus differences	27	−.331	−15.32
All differences	50	−.071	− 2.69

For those differences at least 2.5 times their probable error, the results are:

	f	Absolute Values	Relative Values
Plus differences	3	+.466	+28.14
Minus differences	11	−.501	−21.75
All differences	14	−.294	−11.06

Perhaps the evidence for a reduction in variability is not so strong when seeds germinating abnormally are compared with those not germinating at all. This is precisely what one would expect if such seeds may be regarded as in some degree intermediate between those which produce perfect seedlings and those which produce no seedlings at all.

I now turn to the question of a possible reduction in variability as one passes from seeds germinating abnormally to those germinating normally. The answer is given by the comparison *A–B:*

	f	Absolute Values	Relative Values
Plus differences	19	+.273	+13.78
Minus differences	31	−.366	−15.95
All differences	50	−.123	− 4.66

For differences 2.5 or more times their probable errors:

	f	Absolute Values	Relative Values
Plus differences	6	+.505	+24.41
Minus differences	9	−.560	−25.08
All differences	15	−.134	− 5.29

It is clear that in passing from the seeds producing abnormal seedlings to those germinating normally there is in general a reduction in absolute variability of weight. This point will be discussed in greater detail when relative variabilities are taken up.

If now the comparisons be drawn between all seeds which germinate (whether normally or abnormally) and those which do not germinate at all, *i. e.*, $(A+B)-C$, we have:

	f	Absolute Values	Relative Values
Plus differences	15	+.136	+ 8.37
Minus differences	35	−.266	−11.18
All differences	50	−.146	− 5.32

Or restricting the comparison as usual to those which are more probably statistically trustworthy $(>2.5E)$:

	f	Absolute Values	Relative Values
Plus differences	4	+.297	+20.85
Minus differences	13	−.475	−19.12
All differences	17	−.294	− 9.72

The comparison involving the other extreme in the treatment of the abnormal seedlings is $A-(B+C)$. For all the series this gives:

	f	Absolute Values	Relative Values
Plus differences	17	+.160	+ 9.13
Minus differences	33	−.331	−13.45
All differences	50	−.164	− 5.77

For cases at least 2.5*E*, the results are:

	f	Absolute Values	Relative Values
Plus differences	5	+.352	+22.21
Minus differences	16	−.521	−20.26
All differences	21	−.312	−10.15

Thus the treatment of the abnormal germinations does not materially affect the general results for reduction in variability.

It seems unnecessary to consider both absolute and relative variabilities for the individual varieties. The results will be summarized for the coefficients of variation.

COMPARISON OF RELATIVE VARIABILITIES

As demonstrated in the preceding sections, mortality is so related to seed weight that absolute variability is reduced in passing from seeds which fail to germinate to those which produce seedlings. Possibly, too, there is a change in type. Such changes in mean, even if due only to the errors of sampling, may somewhat affect absolute variabilities. It is desirable, therefore, to reduce all these to relative terms—to express them as ratios of the absolute variabilities (× 100) to the means.

The coefficients of variation, being already in relative terms, give only one set of means to consider.

For *A–C*, all series, the results are:

	f	Averages
Plus differences	12	+1.45
Minus differences	38	−1.95
All differences	50	−1.13

Thus we have a deviation from the 25:25 ratio of 13 ± 2.38 which must certainly be regarded as significant.

For cases at least 2.5 times their probable error:

	f	Averages
Plus differences	3	+3.45
Minus differences	16	−3.26
All differences	19	−2.22

Only 8 are 4 or more times their probable error. Of these, 3 are positive, averaging + 3.34, while 5 are negative, averaging — 4.45.

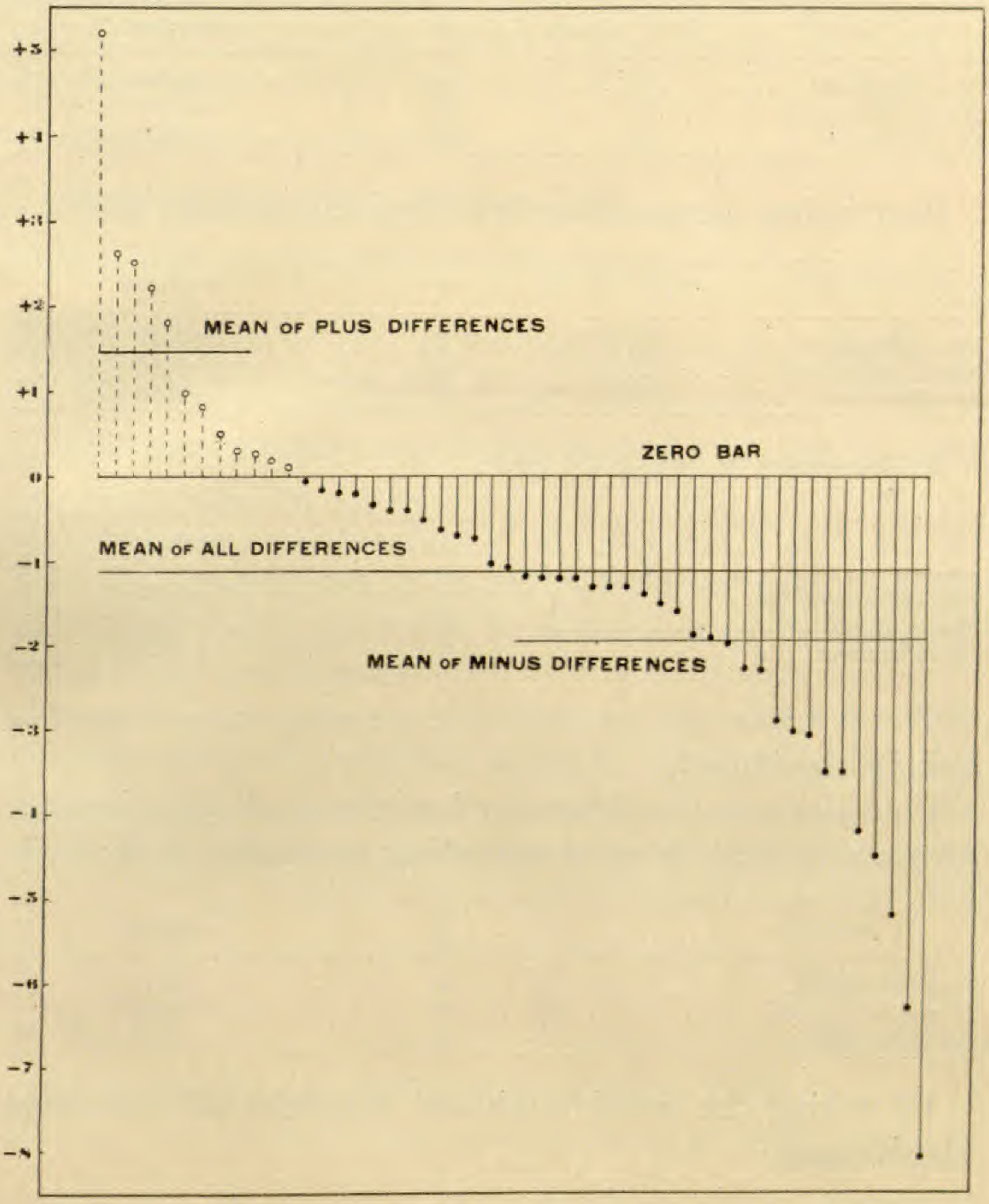

Diagram 5.

The differences for *A–C,* all material, are shown in Diagram 5. Note by comparison with Diagrams 3 and 4 that the evidence for selective mortality becomes stronger when variabilities corrected for size of the means are substituted for absolute values.

Comparison of the relative variability in weight of seeds giving abnormal germinations with that of those failing to germinate at all, *B–C*, gives:

	f	Averages
Plus differences	18	+2.24
Minus differences	32	−2.35
All differences	50	−0.70

Restricting comparisons to differences at least 2.5*E*:

	f	Averages
Plus differences	2	+5.47
Minus differences	10	−4.74
All differences	12	−3.04

Differences at least 4*E* are:

	f	Averages
Plus differences	1	+6.17
Minus differences	6	−4.56
All differences	7	−3.03

The reduction in variability in passing from *C* to *B* is clearly significant.

Consider now the difference between seeds germinating abnormally and those germinating normally, *A–B*:

	f	Averages
Plus differences	21	+2.11
Minus differences	29	−2.27
All differences	50	−0.43

Or taking the usual minimum standard of statistical significance:

	f	Averages
Plus differences	7	+3.42
Minus differences	5	−5.32
All differences	12	−0.23

There is no certainty of any reduction in relative variability here. But turning back to the standard deviations we find that there were fair indications of a lowering of variability.

This apparently contradictory result finds an explanation when the means are taken more fully into account. Consider these, *A–B:*

	f	Absolute Values	Relative Values
Plus differences	23	+.331	+2.96
Minus differences	27	−.899	−5.96
All differences	50	−.333	−1.86

Restricting to those at least 2.5*E:*

	f	Absolute Values	Relative Values
Plus differences	6	+0.596	+ 5.43
Minus differences	12	−1.703	−11.02
All differences	18	−0.937	− 5.54

The mean weights are higher in series *B* than in series *A*. *The relative variabilities for B are, therefore, reduced by the higher values of the means.* Thus when we take the comparison *A–B* for relative variabilities, the reduction which we noted in dealing with the absolute values does not appear.

Consider now the result of combining all seeds which germinated at all (whether normally or abnormally) and comparing their coefficients of variation with those of the seeds which failed to germinate, $(A+B)-C$:

	f	Averages
Plus differences	12	+1.29
Minus differences	38	−1.71
All differences	50	−0.99

Or restricting to differences at least 2.5*E:*

	f	Averages
Plus differences	4	+2.74
Minus differences	13	−2.69
All differences	17	−1.41

Thus we have for all the material a deviation of 13 ± 2.38 cases from the equality to be expected if there were no selective mortality tending to reduce variability. In 38 cases out of 50 the variability of the seeds which germinated is lower than that of those which failed.

In this comparison, all seeds which germinate at all have been considered viable—although it is practically certain that many of the abnormal ones would not have been able to reach maturity. If one wishes to take the other extreme, he may throw all the seeds producing abnormal seedlings with those which failed to germinate at all and compare with those germinating in a perfectly normal manner, $A - (B + C)$.

	f	Averages
Plus differences	12	+1.52
Minus differences	38	−1.69
All differences	50	−0.92

Or for differences $> 2.5E$:

	f	Averages
Plus differences	4	+3.13
Minus differences	16	−2.65
All differences	20	−1.49

Thus the disposition of the abnormal seedlings makes relatively little difference in the end result.

Variety	f	Mean Difference
NAVY:		
Plus differences	9	+1.253
Minus differences	15	−0.796
All differences	24	−0.028
NE PLUS ULTRA:		
Plus differences	4	+0.878
Minus differences	4	−1.833
All differences	8	−0.478
WHITE FLAGEOLET:		
Plus differences	2	+0.031
Minus differences	10	−0.683
All differences	12	−0.563
BURPEE'S STRINGLESS:		
Plus differences	3	+0.637
Minus differences	23	−0.669
All differences	26	−0.518
GOLDEN WAX:		
Plus differences	1	+0.175
Minus differences	6	−1.356
All differences	7	−1.137
FLAGEOLET WAX:		
Minus differences	1	−0.283

I now combine the differences $(A + B) - (A + B + C + \cdot \cdot \cdot)$ for the 50 experiments of the present paper with the 28 given by the field test, as already done for the relative means. The little table gives the results.

For every variety except Ne Plus Ultra the differences are exclusively or preponderantly negative. For each of the six varieties the general average is negative in sign, although sometimes very low. Such results give additional force to the conclusion that there is a reduction in variability due to a differential mortality.

V. Recapitulation and Discussion

1. This paper embodies a portion of the data of a second study of the relationship between seed weight and seed viability in *Phaseolus vulgaris*. The constants are based on greenhouse plantings in sand of some 46,000 individually weighed seeds, chiefly of the pedigrees employed in the field experiments.

Bearing in mind the various sources of error sufficiently emphasized in the body of the paper, the following may be said of the findings.

2. In general the results of the first study are fully confirmed. In certain particulars, however, the narrower analysis made possible by the wider materials now available suggests some modification and considerable extension of conclusions.

3. The statement concerning means was:

> This selective death rate is of such a nature that the mean of the available seeds remains practically the same as that of the original populations, while the variability is reduced. In short, both large and small seeds are less capable of developing into fertile plants than are those which do not deviate so widely above or below the type.

This was all that could then be said, for while many thousands of individually weighed seeds were involved, the number of series was too low to justify analysis into the individual varieties or into groups by age of seed or conditions of growth. Examined in the same manner, these data show *in the long run* some indication of an increase in the mean weight of the survivors, but no uncontrovertible evidence of a change in mean weight as a result of selective mortality. But *individually considered,* more differences in mean weight are from two to four or more times their probable errors than can possibly be attributed to experimental or sampling errors. Some of these differences are positive, others are negative. There seems in view of these facts, no escape from the conclusion that there is a real biological relationship between weight and viability of such a nature that in some experiments the heavier and in other experiments the lighter seeds are most heavily drawn upon in the mortality. This seems clear from the greenhouse experiments in whatever way the differences are taken. There are indications of the same condition in field cultures, although here the criterion of statistical trustworthiness is, because of the dual errors of sampling, less dependable.

There is strong evidence for varietal differences with respect to mortality. In some strains the heavier, in others the lighter, seeds seem less capable of development. The reason for these differences may be sought in the inherent characters of the stocks used or in the environments to which they have been subjected. This question is, however, so complicated that larger and more diverse series of data must be gotten together for its final solution.

4. Consider now the variabilities. There can be no question whatever concerning the reality of the reduction in variability, either absolute or relative, as a result of differential mortality. The following conditions seem to prevail for the individual comparisons which may be made.

There is probably a reduction in absolute variability, and there is certainly a reduction in relative variability, in passing from seeds which fail to germinate to those which produce abnormal seedlings.

There is probably also a reduction in standard deviation in weight in passing from seeds which give abnormal seedlings to those which germinate normally. This reduction is not so evident in the coefficients of variation, probably because of changes occurring in mean weight.

There is clearly a lowering of both absolute and relative variabilities between seeds which fail to germinate and those which germinate normally, or those which germinate at all, either abnormally or normally. The disposition which is made of the seeds which give rise to abnormal seedlings does not affect the conclusion concerning a reduction in variability due to a differential death rate.

To what extent this reduction is incidental to a change in mean through elimination preponderantly from one end of the range, as compared with elimination from both the extremes without change of type, must be determined on wider series of data, and probably by the use of statistical methods not yet applied to the problem.

5. The constants of this paper, taken in connection with data made directly available from other published studies by the key letters, can be used towards the solution of a number of problems not touched upon here. These have been purposely left out of account because they were aside from the present main purpose and because I hope to have much more extensive materials for their solution later.

6. Concerning the causes of the differences in viability no conclusions can be drawn. I have shown[18] that in general the larger seeds require longer for germination, but the precise relation, if any, of this phenomenon to selective mortality, as well as its explanation in more general physical and chemical terms, are still to be worked out.

Tumamoc Hill, Tucson, Ariz.,
April 3, 1913

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[18] Harris, J. Arthur, "A First Study of the Relationship between the Weight of the Bean Seed, *Phaseolus vulgaris*, and the Time Required for its Germination." In press.

SHORTER ARTICLES AND DISCUSSION

A CROSS INVOLVING FOUR PAIRS OF MENDELIAN CHARACTERS IN MICE

THE present experiment was planned as a control upon more detailed work being carried on at the Bussey Institution. It has, however, a distinct value, as demonstrating from a single cross the existence of four independent pairs of Mendelian characters in the color inheritance of mice.

That the yellow and agouti factors are not inherited independently of each other has been demonstrated by Sturtevant.[1]

The four pairs of characters under consideration here were recorded by Castle and Little[2] and are briefly as follows:

A = agouti, a = non-agouti.
B = black, b = no black (brown).
D = density, d = diluteness.
P = dark eye, p = pink eye.

In each case the character represented by the small letter is recessive in combination with its allelomorph, designated by a large letter.

To obtain all possible combinations of these four pairs of characters, a single pure wild gray mouse was mated with several pink-eyed dilute brown females from a homozygous stock bred at the Bussey Institution and shortly to be reported upon by one of the writers.

Wild gray mice possess the dominant members of all four paired characters mentioned above, and consequently have the gametic formula ABDP. The pink-eyed dilute brown mouse, on the other hand, exhibits the recessive conditions of the same factors and is of the formula abdp. It is in appearance a very pale lilac color and in Miss Durham's classification is described as "Silver Champagne."[3]

The F_1 individuals resulting from this cross (wild ♂ × pink-eyed dilute brown ♀) were all, as expected, similar to the wild

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[1] AM. NAT., 1912, p. 368.

[2] *Science,* 1909, p. 312.

[3] *Journal of Genetics,* 1911, p. 159.

parent in color. They were mated *inter se* and disposed so as to raise as large a number of F_2's as possible.

In this F_2 generation we should expect to find sixteen visibly different types of color, in the proportions indicated in Table I. Table I also shows the results actually obtained in the experiment.

TABLE I

Color	Formula	Observed Numbers	Expected Numbers	Theoretical Proportion	Observed Proportion
Black Agouti	ABDP	436	373.4	81	94.5
Black	aBDP	127	124.5	27	27.5
Brown Agouti	AbDP	103	124.5	27	22.3
Dilute Black Agouti	ABdP	130	124.5	27	28.2
Pink Eyed Black Agouti	ABDp	103	124.5	27	22.3
Brown	abDP	40	41.5	9	8.7
Dilute Brown Agouti	AbdP	31	41.5	9	6.7
Dilute Black	aBdP	37	41.5	9	8.0
Pink Eyed Black	aBDp	35	41.5	9	7.6
Pink Eyed Brown Agouti	AbDp	38	41.5	9	8.2
Pink Eyed Dilute Black Agouti	ABdp	38	41.5	9	8.2
Dilute Brown	abdP	11	13.8	3	2.4
Pink Eyed Brown	abDp	12	13.8	3	2.6
Pink Eyed Dilute Brown Agouti	Abdp	15	13.8	3	3.3
Pink Eyed Dilute Black	aBdp	17	13.8	3	3.7
Pink Eyed Dilute Brown	abdp	7	4.6	1	1.5
Total		1,180			

If we consider each allelomorphic pair of characters separately, the following results are observed (Table II):

TABLE II

Characters	Observed Numbers	Expected Numbers	Theoretical Proportions	Observed Proportions
A	894	885	3	3.12
a	286	295	1	1
B	923	885	3	3.59
b	257	295	1	1
D	894	885	3	3.13
d	286	295	1	1
P	915	885	3	3.45
p	265	295	1	1

It will be seen that there is in each case a slight excess of animals possessing the dominant character. Further, in Table I there was an excess of black agouti (gray) animals, which possess all four dominant characters.

This last excess, however, is not sufficient, in the opinion of the writers, to support any theory of coupling, especially in the absence of significant differences in the other classes.

The excess of grays may better be explained on the basis of selective elimination of the various recessive animals, for the F_2 young could not be graded satisfactorily until nearly four weeks old, and no account was kept before this time.

A minor error may have occurred in recording the pink-eyed dilute brown young, as they resemble closely the intense pink-eyed brown and no breeding test was undertaken.

To summarize the results of this mating, it is obvious that we are dealing with four clear-cut pairs of Mendelian characters as described by Castle and Little in 1909, among which no coupling or association can be detected.

C. C. LITTLE
J. C. PHILLIPS

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