INHERITED VARIATION IN ANIMALS

Biologists are still divided upon an important question concerning Evolution. They cannot yet agree as to the part that the direct action of environment plays in the evolution of new species. Most biologists have already come to the conclusion that a haphazard, accidental, and therefore indefinite variability, which means that modifications in the size, the colours, the shape, and so on of a species of plants or animals appear in equal numbers round a certain average, is powerless to originate a new species. It could not do it, even if it were supported by Natural Selection in an acute struggle for life, because the modifications are always small at the outset, and have not in such case a life-saving value in the struggle for life; while the considerable modifications are few as a rule, and would be swamped by crossing; and so long as there is not some exterior cause, such as climate, food, etc., which acts during a number of generations for producing variation in a certain definite direction, there is no reason why the change should go on increasing.

Darwin saw as early as 1868 that such a conclusion had much in its favour, and modern research has rendered it unavoidable. Taking any variation-be it in the shape and the size of any organ, or in the colours and markings of an insect-it appears first as a small deviation from the normal size, shape, or colouring; and, in order that it should go on increasing from generation to generation, there must be some cause which for a number of generations affects most individuals of a given group in the same direction. Variation cannot be a collection of haphazard changes; it must be definite. And it must be cumulative, as Darwin said, which means that it must be inherited.

Suppose we take a group of small Crustaceans carried by an inundation into the underground waters of a dark cave. organs of smell and touch of these Crustaceans soon must be (and really are) so affected by life in the darkness that they take a greater development and increase in size, while the organs of sight deteriorate. And if the thus modified Crustaceans are going to originate a new race, the modifications they have acquired during their cave-life must be transmitted for a number of generations to their offspring before they acquire a certain stability.

But the hereditary transmission of the modifications acquired inder the influence of a new environment is precisely what a number of biologists will not admit. Consequently, after having examined first the theoretical considerations produced by Weismann and his followers in favour of the non-inheritance view, I summed up next the experimental evidence we possess in favour of the inheritance of variations produced in plants by the direct action of a changing environment.2 It appeared from this analysis that it is no more possible to maintain, as some botanists did a few years ago, that such changes are not inherited. They are transmitted from the parents to their offspring, and the doubts are now only about the mode of transmission of the changes from one generation to the next—not about the fact itself.

We must see now whether the same can be said of variation in animals. Having already examined in a previous paper 3 some of the profound changes that are produced in animals when they are placed in new conditions of life, we have now to see how far

these changes are inherited.4

Many instances of lower organisms undergoing inherited variations of structure when they are placed in new conditions of life are well known by this time. However, it is better not to introduce these cases into a discussion about the inheritance of acquired characters. When we deal with whole populations of Amoebae, Bacteria, or Infusoria, it is difficult to be sure that the change is not due to the survival of those individuals which accidentally—not under the influence of a modified environment may have got some features rendering them better suited to their new surroundings. Or else it may be suggested that the experiment was started with an already 'mixed population,' the general character of which changed in the new surroundings because those individuals survived which possessed features that were

² Ibid. October 1914.

¹ Nineteenth Century and After, March 1912.

³ Nineteenth Century and After, November and December 1910.

⁴ The literature of this vast subject is immense. Happily enough, there are some excellent works in which all the cases of such an inheritance and their bearing upon the theory of evolution have been critically examined by wellknown specialists. These works are: Dr. Paul Kammerer, Zuchtversuche zur Abstammungslehre, in Die Abstammungslehre, twelve lectures, Jena, 1911; Professor L. Plate, Selektionsprinzip und Probleme der Artbildung: ein Handbuch des Darwinismus, fourth, greatly enlarged edition of this most valuable, truly Darwinian work; and Vererbungslehre, being volumes I. and II. of Plate's Handbücher der Abstammungslehre, Leipzig, 1913; Dr. H. Przibram, Phylogenese: cine Zusammensetzung der durch Versuche ermittelten Gesetzmässigkeiten tierischer Artbildung, being vol. III. of his Experimental-Zoologie, Vienna, 1913; and Professor Richard Semon, Das Problem der Vererbung, 'Erworbener Eigenschaften,' Leipzig, 1912.

useful in the new conditions of life. For the time being it better therefore not to introduce such cases into the present discussion, the more so as we have more convincing experiment dealing with higher divisions of the animal world. I ought, how ever, to mention the experiments of M. Kaptereff on the disinter gration of the eye in certain species of Daphnia, reared in the dark, which represent an important continuation of the work of Viré, already analysed in this Review. But having seen only preliminary communication of the Moscow biologist, I prefer to leave this for another occasion.7

At the time when Darwin wrote his Origin of Species the naturalists found a great difficulty in explaining why grey and white colours should predominate in Arctic regions, tawny and yellow colouring in the deserts and the steppes, dusky colours among the insects on the maritime borders, a gorgeous coloration among the tropical birds, and so on. Darwin's explanation of this resemblance between the environment and its inhabitants was, as is known, Natural Selection. Those individuals—he wrote—have had the best chances of surviving in the struggle for life and leaving a progeny, whose colours, being in harmony with those of the environment, permitted those individuals to conceal themselves from their enemies, or to steal unnoticed towards their prey. As to the causes of the first appearance of protective colours, Darwin left the question unanswered in the earlier editions of his Origin of Species. He admitted that the direct action of environment might have been a cause of their appearance; but he preferred to describe such variations as 'accidental'that is, due to unknown causes, to be found out later on.

Since that time our knowledge of colours and markings in Nature has made a considerable progress. It was proved that they have a physiological origin, and that they are easily affected by a changing environment. On two occasions I have already summed up in this Review the main results of these studies,8 but a volume would be required to discuss them in full. However, our special purpose being to see now to what an extent the

⁸ Let me only mention the very careful experiments with a common Infusorium, the Slipper animalcule (Paramaecium), by the American Professor H. S. Jennings; those of the Leipzig Professor Woltereck on the little Water-Flea of our ponds, the Daphnia; and also those of Mr. E. Agar on the Simocephalus vetustus (communicated to the Royal Society on January 23, 1913), which have, however, to be continued before definite conclusions can be

⁶ Nineteenth Century and After, November 1910, p. 864.

7 Experimental Researches into the Influence of Darkness upon the Organs of Senses in the Daphnia,' preliminary communication by Paul Kaptereff, in Biologisches Centralblatt, vol. xxx., 1910, pp. 239-256, with drawings.

Recent Science,' in Nineteenth Century, September 1901, pp. 433-437, and April 1893, pp. 683-689.

langes in colour and markings produced by environment are therited, our remarks can be limited to those researches which with the changes of colours in certain butterflies and moths d certain Amphibians.

The Tortoiseshell butterfly, a very common inhabitant of our ardens and fields, has been a favourite subject of such studies. It was known long since to appear in two forms, described by entomologists as Vanessa levana and Vanessa prorsa, which formerly were considered as two different species. Later on it was found that these two forms were merely two different broods of the same pecies. The levana form, which is orange-brown, with blackishbrown spots on the upper side of the wings, lives through the winter as a chrysalis, to appear as a butterfly in the spring; while the eggs of the prorsa form, which has black wings with a white transverse band, are laid in spring, and it issues as a butterfly only later in the summer. It was natural, therefore, to suppose that the differences in the colours and markings of the two broods had something to do with the temperature under which their pupae had lived; and as early as 1864 Dorfmeister proved that the two forms of the Tortoiseshell butterfly (as well as an intermediate form occasionally met with) could be obtained by rearing their pupae in different conditions of temperature.10

A mass of similar experiments having been made since Dorfmeister opened the way, I shall mention only those of Mr. F. Merrifield and Professor Standfuss, both having dealt with a very great number of individuals.

Mr. Merrifield's experiments were made with the small Copper butterfly, 11 which also appears in two differently coloured forms, one of which is common in England and Germany, while the other is found in Southern Europe. These two forms were also considered as two separate local races. However, Mr. Merrifield obtained specimens very similar to the Southern form by rearing pupae of the Northern form in a higher temperature than the usual one in our latitudes, and vice versa.12

At the present time they are better known as Araschnia levana and A.

10 These experiments, repeated by many explorers, are quoted in all recent works on evolution, often with plates (among others in Przibram's Phylogenese, with coloured plates). Weismann having repeated Dorfmeister's experiments, confirmed them, but tried to explain them by a return to an ancestral form. There being no facts in favour of this supposition, while thousands of similar facts illustrating the action of environment are now known, the supposition had

11 Polyomatus phlaas ('The Effects of Temperature in the Pupal Stage on the Colouring of Pieris napi, Vanessa Atalanta, Chrysophanus phlaas, and Ephyra punctaria,' in Transactions of the Entomological Society of London, 1893, Pt. I., pp. 55-73, with coloured plate. Also 'The Colouring of Chr. phlæas as affected by Temperature,' in Entomologist, December 1893.

12 Same transactions, p. 65. The best effects were obtained during the period when the active part of the pupae stage had begun-great heat proA still wider series of experiments was made by Mr. Merrifold with the Tortoiseshell butterfly, studied by Dorfmeister, which also appears in two different seasonal forms, and the akin form Araschnia. These experiments were conducted for many year with great care, special attention being given to the study of the effects of an abnormal temperature at the different stages of the insect's life: the eggs, the larvae, and the pupae stage. The results of all these experiments were summed up by Mr. Men field himself, so I can give them in his own words:

'Without by any means doubting,' he wrote, 'that other influences that temperature, such as moisture, are, under some circumstances, more particularly in tropical and semi-tropical countries, 13 the determining cause I do assert that in species operated on by me, and, as I am convinced in many other species, the appropriate temperature, and nothing more applied in the right stage, is sufficient in itself to cause the insect belong to either phase, in all respects; that is to say, both as regards aspect, including size and therefore weight of mass, and life-habit; and even to divert the insect, after being launched in the direction of one phase, into the other.' The early larval stage being the period best suited to succeed in producing even the most difficult transformation, it is in the larval stage that the life-habits and mass of the two phases are, as a rule, determined, but in the pupal stage the facies may be materially affected, and even transformed.'

Another series of equally conclusive experiments relative to changes of colour in butterflies was made on a still greater scale by the Zurich Professor M. Standfuss, who himself summed up the results of his thirty years' researches, in 1905, before a Congress of Swiss Naturalists.¹⁵

voking duskiness, and moderate cold provoking vividness of colour in the coppery and the dark parts, smallness of spots and a considerable enlargement of the copper band in the hind wings. Having repeated the same experiments and obtained similar results, but not so pronounced as those of Mr. Merrifield, and having found later on, on the Ligurian coast, a zone where the same species had two seasonal forms. Weismann saw in this last fact a contradiction to the conclusion which he had to draw from his own experiments—namely, that the colour-variation must have been in this case 'cumulative' and inherited (Das Keimplasma, 1892, pp. 525-531). However, the hypothesis which he himself advocated later on—namely, that all the inherited 'determinants' of colour may not be modified at once—fully explains both the presence of two seasonal forms and the partial success of his experiments.

13 'In Southern Africa, for example, as shown by the experiments made by Mr. Guy Marshall.'

Dimorphism,' in Premier Congrès International d'Entomologie, Bruxelles, 1911, pp. 435-436. Besides, Mr. Merrifield entirely repudiates the idea that at least in the two species he experimented upon (Araschnia levana and Selenia bilunaria) the cause of differences between the two broods could be a congenital one, or that seasonal dimorphism should be a case of alternating generations (id. p. 436).

15 'Die Resultate dreissigjähriger Experimente mit Bezug auf Artbildung und Umgestaltung der Tierwelt,' in Verhandlungen der Schweizerischen Naturreprint).

To begin with, Professor Standfuss carried on, since 1873, most painstaking experiments upon 55,600 individuals belonging to thirty different species, in order to see whether it would not be possible to obtain by crossings a race capable of popagating itself. Having utterly failed in each case, Professor fandfuss began to look for other means to obtain new species namely, to variation. He studied therefore the fluctuating, indetermined variations, as well as the sudden variations or sports' (de Vries's 'mutations'); and after having obtained number of interesting results, too special to be discussed here, he came to the conclusion that neither the fluctuating variations for the 'sports' can be considered as originating new species. So there remained only to study the so-called local or climate laces, especially variation under the influence of different temperatures at the different periods of the individual's life.

Here the results were quite satisfactory. By rearing pupae at low temperatures, Professor Standfuss obtained the cold-season form out of pupae of the warm-season form, and partly he succeeded also in producing the reverse modification. More than that. Various races of several species were obtained, showing frequently a certain likeness, and occasionally a striking similarity, to the local races found in nature.¹⁸

And finally, in prosecuting further an experiment which gave an aberrant form of the Tortoiseshell butterfly (Vanessa urticae, L.), and rearing extremely modified individuals, he succeeded in transmitting the artificially altered aspect to a portion of the offspring.¹⁷ In these cases—Standfuss says—'we have a physiological fact; namely, a certain action was exercised upon the sexual domain, which produced the capacity for inheriting these newly acquired characters.'

It is impossible to give here all the details of Standfuss's experiments, or to analyse his conclusions. Suffice it to say that in his opinion the climate factors, especially temperature, are important, not only for modifying organisms, but also for originat-

¹⁶ From Araschnia levana, L., one can obtain the A. prorsa; from Polygonia c. album, L., the summer generation P. hutchinsoni, Robs.; from Chrysophanus amphidamas, Esp., the summer generation Chr. obscura, Rühl; and so on. Even those aberrant forms, strangely differing from the normal type, which occasionally are met with in nature, and whose origin was much discussed, were also obtained through the effect of an abnormal temperature of the environment.

17 Denkschriften der Allg. Schweizerischen Gesellschaft für die gesammte Naturwissenschaft, xxxvi., 1898, pp. 1-40, with tables; also Insektenbörse, xvi., 1899, and Przibram, l.c., tab. xviii. Taking one pair of the just-named butterfly, strongly altered after its pupae had been submitted to a high temperature, he obtained from this pair, under normal conditions, forty-three butterflies, four of which offered differences from the normal form nearly to the same extent as the parent form, while 'even amidst many thousands of normally bred butterflies grown under quite normal conditions similarly medified individuals never appear' (l.c., p. 22).

ing new independent species. And everyone who will study the work of Standfuss will agree that we see here precisely 'definite' variations, due to a changing environment, of Darwin spoke—these variations, if they affect a considerable number of individuals and continue to appear for a considerable number of generations, offering to Natural Selection the co tions under which it may consolidate a new variety, and

Π

Many more experiments were made to see whether changes in the colouring of butterflies and moths, due to modified confiltions of life, are inherited; but I shall mention here only those of E. Fischer with the beautiful reddish-brown Tiger moth (Arctic or Chelonia, caja), which gave the most positive results. nearly equal lots of pupae of that moth, fifty-four and form eight in number, were taken, and while the first lot was reared in normal conditions, the second was submitted to intermittent cooling down to 18° Fahr. The result was that while the first lot gave a normal offspring, the second lot gave darkened motify all of which were showing on their wings a more or less greater widening of their black spots. Professor Fischer succeeded next in rearing the progeny of a very much altered male and a rela tively well-altered female. He obtained from them 173 pupas and these pupae were reared at the ordinary temperature of room (64° to 75° Fahr.). The first moths obtained from this brood were normal, but the last seventeen were modified, both in colouring and the forms of their legs and wings, in the same sense as their parents had been modified, and some of them nearly to the same extent. 18 The modification produced by modified environment was thus transmitted to the next general tion, even though that generation was brought up under the normal conditions of life of the species.

Further experiments made by Professor Fischer with the Tortoiseshell butterfly gave the same results. The modification produced by an abnormal temperature was also transmitted to the next generation. And quite similar results were obtained in 1903 by Schröder, who experimented upon a common dweller in our gardens, the Magpie moth. 19 Individuals whose colouring was darkened by changes in the temperature of the surroundings

18 Abraxas grossulariata. Quoted by Przibram, I.c., pp. 60 and 184, plate xviii.; also R. Semon's Problem, p. 73.

musmitted the thus acquired characters, in a weaker degree, to of their offspring.

n speaking of these experiments Professor Plate makes a correct remark. We certainly have here cases of an intance of acquired characters; but the transmission having been ted for one generation only which was reared in normal condions, it can be explained in two different ways. It may be that modification of the body-cells was transmitted to the germcells; and it may also be, as Weismann suggested, that we have here a case of direct action of the abnormal temperature upon the gern-cells. But this has importance only for determining how modifications are transmitted. The fact of their transmission mains. Besides, it-must be said that the second suggestion mains improbable, so long as it has not been proved that the manges in the body-cells had no effect whatever on the germalls, even though the latter reproduced in the next generation xactly those changes that took place in the tissues and organs the parents. But nothing of the sort has ever been proved or ven attempted to be proved.

It is worth noting that moisture has the same effect as cold. A darker general colouring and darker markings were obtained by rearing pupae of the Magpie moth in a moist atmosphere. And when extreme heat was added (by Pictet) to a moist atmosphere. the front wings of the moth became quite dark: the effect was thus the same as if the pupae had been reared in a cold room. These changes were also inherited, although the offspring was brought up in a normal temperature.20

Altogether these experiments, as well as those of Mademoiselle de Linden and the latest experiments of Pictet, have fully proved that the whole process of formation of different colours is a physiological process, and, as such, it necessarily is influenced by the external conditions under which the butterfly or the moth is living. Consequently, little doubt remains as to the true origin of the seasonal forms of different butterflies and moths, as also the local forms limited to certain valleys, described by Pictet. They owe their origin, not to the immigration of new forms but to the inherited local actions of temperature, light, and altitude.²¹

¹⁸ The researches of Fischer date from 1895. The just-mentioned experiments were described in Allgemeine Zeitschrift für Entomologie, Bd. vi., 1901, with one plate. They have been summed up since in all recent works on heredity (Przibram's Phylogenese, p. 175, with coloured plate; Semon's Mneme, 1908, p. 83, and Problem, p. 72; Plate, and so on).

²⁰ When the pupae obtained from the thus modified individuals were reared under normal conditions, one-half of the seventy-eight moths issued from them inherited in a weaker degree the darker markings. And when a male darkened by hot surroundings was crossed with a normal female, it gave ten darkened moths out of a generation of forty-three.

²¹ Arnold Pictet, 'Influence de l'alimentation et de l'humidité sur la variation des papillons,' in Mémoires de la Société de Physique et d'Histoire Naturelle de Genève, vol. xxxv., 1905, Introduction. In this Introduction Pictet mentions the excellent summings-up of the whole question by Countess Marie von Linden (Biologisches Centralblatt, xxiv., 1904), G. Agassiz (Etude sur la coloration des

Important modifications of size and colouring, which also reappear in the next generation, were obtained moreover by lead ing the caterpillars of different moths with food which we the habitual food of the species. Thus, taking a common of our hedges, the Ocneria (or Liparis) dispar, whose caterpil usually feed on the leaves of the oak, if they were fed with le of the walnut-tree, the moths to which they gave origin were smaller size, their black markings became less distinct, and the general colouring had a tendency towards whitening (albinism) Doubtless signs of an inheritance of these changes were seen in the second generation, even though the caterpillars of the last were fed with their normal food of oak-leaves. It is interesting to note that after the caterpillars of the same moth had been with sainfoin (Onobrychis sativa) they gave origin to a new form; and that after walnut-tree, oak, and sainfoin leaves had been given in succession to each one of three generations, the new form produced in this way bore distinct traces of the this sorts of food.²² These changes, too, were inherited to a certain

I can also mention a work, by Mr. Roswell H. Johnson, on Determinate Evolution in the Color-Pattern of the Lady Beetles,23 the conclusions of which are in favour of the inherit ance of a determinate variation, chiefly dependent upon the climate conditions prevailing in different parts of the United States. By determinate variation the author understands variation tion in a definite direction going on in the germ-plasm, 'cither with or without external influence,' along several development. lines 'which are called into activity here and there as the environment sets one or another into play.' Both inherited and uninherited variation having taken place in these experiments, the former is hypothetically explained by the author as a case of so-called 'parallel action' of the outer modifying agencies on the germ-plasm and on the body-cells, so as to reproduce in the offspring the same changes as took place in the body-cells of the parents. Here, again, two possible interpretations are suggested; but the fact of transmission of changes acquired in one generation

Finally, the interesting experiments of MM. Lambert and Kamensky on aberrant forms of silkworms obtained by

Papillons, Lausanne, 1903), and the lectures of F. Henneguy (Les Insectes,

their caterpillars with different sorts of leaves ought to mentioned here, together with the experiments of Professor and Mrs. Bell,24 who obtained 'a diminutive but still The le race of Lilliputian silkworms' by feeding the silkworms for mee successive generations with gradually diminished rations of mulberry-tree leaves.

to would be impossible to mention here all the important results obtained by a great number of biologists who have studied effects of sunshine, humidity, abnormal food, various gases. features preventing free circulation, and so on, on the size, the oms, and the colouring and markings of quite a number of fisects, as also the inheritance of new instincts acquired by caterollars when they were given a new sort of food. So I must efer the reader to the excellent summary of all such works given Professor Przibram in his Phylogenese, which, let us hope, at last be translated into English, as well as the works of Kammerer, Plate, Goebel, and Semon.²⁵

III

That modifications produced in the colours and markings of butterflies, moths, and beetles by changes of temperature, moisture, and food are inherited in the next generation, is thus no more a matter of doubt. Even if the modifying agencies have acted for one generation only, their effects will often re-appear in the next generation. And the question arises, 'What is inherited in such cases?'

We know by this time that the colours and the markings of animals are not 'accidental.' They are determined by certain physiological functions. And we conclude therefrom that if a changed environment modifies the colours or the markings, these modifications are the consequences of certain changes in the functions of some organs.26 The experiments of Standfuss, Fischer, and many others 27 fully confirm this view. They show that the same variation in the colouring of butterflies and moths can be obtained by rearing their pupae in cold, or in very hot surroundings; and that the same modifying agency at different

²⁴ O. L. Kellogg and K. G. Bell, 'Variations induced in Larval, Pupal, and Imaginal Stages of Bombyx mori,' in Science, N.S., vol. xviii., 1904. Summed up in Appendix to 'Inheritance in Silkworms, I.' (Stanford University, 1908,

pp. 79-80). Also in Przibram's Phylogenese, pp. 181-182.

25 Two interesting cases of an inherited modified instinct, observed by Arnold Pictet, might also be mentioned. See 'Quelques exemples de l'hérédité des caractères acquis,' in Archives des Sciences physiques et naturelles, t. xxviii., 1910, pp. 504 seg.; and 'Un nouvel exemple de l'hérédité des caractères acquis, in same Archives, t. xxxi., pp. 561 seq.

20 This is also the conclusion to which Arnold Pictet was brought by his

27 Ruhmer, F. Urech, Mademoiselle von Linden, Federley, Pictet for Lepidopters; Tower for the Colorado Beetle; and so on.

²² Arnold Pictet, l.c., and 'Des Variations des Papillons provenant des changements d'alimentation de leurs chenilles et de l'humidité,' in Comptes Rendus du VIe Congrès International de Zoologie, Session de Berne, 1904, pp. 499 seq., where several other interesting facts are mentioned. ²³ Carnegie Publications, No. 122, Washington, 1910.

degrees of intensity (a warm temperature, as well as a very high temperature) may produce both a darker and a paler variety. Thus in Lizards, while a moderately warm temperature moisture produce an increase of black pigment, the same causes when their intensity goes beyond a certain limit, produce a destruction of the black pigment.²⁸

It was found, moreover, by Pictet that, apart from a exceptions, discovered by Mademoiselle von Linden, changes the colouring of the wings of butterflies and moths were most due to an increase or a decrease in the quantity of pigment deposited under the microscopic scales with which the wings Lepidopters are covered, like a roof with tiles—and not to change in the chemical composition of the pigment.²⁹ Besides the scales themselves, which decompose white light owing to the fine microscopical striae with which they are covered, may be diminished in numbers; they also may be dwarfed and deformed and show other signs of defective development, if the pupae have been submitted to excesses of temperature, or other noxious outside influences.³⁰

In all these cases it can thus be said that important changes in the colouring and markings, the size of the moth, and the shape of some of its organs were changes in its general vigour

The importance of this conclusion is self-evident. It does not mean, of course, that the differences in the general colouring and the markings upon which entomologists base the division of a species into a number of sub-species or varieties should be mere individual differences of vigour. But they show that acquired differences of general or local vigour may weaken or reinforce certain physiological functions which result, in their turn, in important changes of size, colours, reproduction, and so on. They alter the functions of vital organs, and, through them, those characters which have a specific value are modified. Such changes cannot be but inherited for a number of generations, just as a predisposition for tuberculosis, or a weak heart is inherited.³¹

At any rate, we have no right to say that it is 'incomprehenhow a certain change in the colours of the wings of a buttergen be transmitted to its germ-plasm. It is transmitted; and then we have studied in detail this fact, we shall learn that is transmitted, and how. Moreover, we know already that the germ-plasm does not live the isolated life it was supposed to five under the hypothesis of Weismann and his followers. That the germ-plasm of the reproductive cells and that of the nuclei of the body-cells stand in a close intercourse is no more a matter of doubt for those who have studied heredity.32 It is also well known by this time that both in plants and animals there exists a connexion between most cells, by means of fine threads of protoplasm. So that, instead of speaking of the 'isolation' of a group of cells in the organism, we must speak now of the close intercourse that exists between all the organs of living beings, and study them, after having wasted so much time on the discussion of the hypotheses accumulated by Weismann in support of his hypothesis of prae-determined evolution.

IV

In the experiments on variation in the Colorado beetle, which have been made by W. L. Tower at the Chicago University Station for Experimental Evolution, we have another series of researches dealing with the same subject of colouring and markings, and leading to some important conclusions. The researches of Mr. Tower lasted for several years; an immense material (more than 200,000 beetles) was handled; and the results were embodied in a bulky volume, rich in valuable data. Unfortunately the American explorer wrote his work under a strong influence of the Weismann hypotheses, and therefore we find in it, by the side of an important experimental material, conclusions which are hardly justified by the explorer's own data.

To begin with, Mr. Tower confirmed two observations, already made by Merrifield, Standfuss, Mademoiselle von Linden, and

is sometimes characteristic of a weak heart, it is in all probability some defect of such an important organ as the heart which is inherited and determines the shape of the nails.

⁸² Professor Plate, in his monumental Selektionsprinzip (4th edition, pp. 451-453), after having shown that we must admit the existence of a continual intercourse between the germ-cells and the body-cells, adds: 'The question as to the nature of these communication-ways must for the time being remain unanswered. Most of the cells being connected with each other by inter-cellular plasm-bridges, and all the organs of both animals and plants standing in a correlative mutual dependency, I do not consider the existence of germ-plasm inter-communication threads as an "unimaginable auxiliary theory."'

38 An Investigation of Evolution in Chrysomelid Beetles of the Genus Lepti-

notarsa. Washington, 1906 (Carnegie Publications).

²⁸ P. Kammerer, 'Künstlicher Melanismus bei Eidechsen,' in *Centralblatt für Physiologie*, xx., 1905, pp. 261-263; 'Die Wirkung äusserer Lebensbedingungen auf die Organische Variation,' in Roux's *Archiv*, xxx., i. pp. 381-383, 388-390.

²⁰ Pictet, Recherches sur le mécanisme, etc., p. 8.

of Vanessa Io. This colour is due to the white scales being placed upon black ones acting as a screen. When the blue spots, modified by temperature, become green, this is due to the fact that white scales (blue to our eye) are placed upon yellow scales. And so on (Recherches sur le rôle des écailles, pp. 11-12).

of the hand, is inherited. This does not necessarily mean, however, that a specially modified 'pangen' or 'determinant' of every nail is inherited. The nails in this family being of that flattened shape which, as medical men know,

many others in their experiments on butterflies and months. Colour-modifications, obtained by the effects of cold on the of the Colorado beetle, could also be obtained by excessive in moisture, and a different composition of the surrounding And from this fact Mr. Tower concluded that 'there is no specific response (variation) following any given stimulus '; 'the response (variation) following stimulus is entirely determined within It appears, however, from the just-mentioned researches of Pictet—posterior, it must be said, to the work of Mr. Tower—that the fact may have a quite different meaning. both cold and extreme heat can produce discolouring, the reason of it is that both depress the vitality of the beetle—the cone quence being in both cases the elaboration of a smaller amount Many other cases of similar physiological effects being produced by different stimuli could also be pro

Another observation, which already had been made with regard to inherited variation in butterflies and moths, is also confirmed by Mr. Tower with more precision with regard to the Colorado beetle. In order that a colour-modification should be transmitted to the offspring, the modifying agency (cold, excess sive heat, moisture, and so on) must be acting at a certain definite period of the beetle's life; namely, during the period of growth of the germ-cells. It is during this short period of a few days that the modifying cause is able to produce an effect that

The fact that the germ-cells can be influenced by the outer agencies only during a short period of a few days certainly is, as Professor Semon says, an important fact which explains several hitherto unexplained freaks in the inheritance of variations. But the conclusion which Mr. Tower draws from it is apparently too wide; and when he repeats over and over again in his work that somatic variations (variations in the structure of the body and the functions of its organs) are not inherited; that 'in these beetles the only variations of permanence are germinal' (and by 'germinal' he understands that they are produced directly on the germ-plasm, and not through the body-cells); and when he concludes that 'the only possibility of evolution is through germinal

quation' (understood in this sense),37 he maintains something is not yet proved by his experiments.

It is self-evident that in order to be inherited every variation must in some way or another affect the germ-cells. No biologist gas ever believed that any inheritance may take place otherwise through the reproductive cells. But if the sensibility of these cells is different at different times of their development, and if the modification in the body-cells takes place at a time when the ferm-plasm is not yet sensitive enough for receiving the impresfion of the modifying agencies; or if no stimulus goes out from the cells of the body at the time when the germ-plasm is especially sensitive—then there can be no inheritance. This is precisely— Professor Semon thinks—what happened in the cases observed by Mr. Tower. The external agencies produced a deposit of pigment in the outer cuticula of the pupae; but this modification could have no influence on the germ-plasm, because the cuticula had no channels connecting it with the latter.38 At the same time the possibility was not excluded for other external stimuli (which alter the size of the insect, or the form and functions of its organs) to act upon the germ-plasm.39

All that can therefore be concluded from the remarkable experiments of Mr. Tower is, in Professor Semon's opinion, that there are cases when the external modifying agencies act only on the body-cells, without influencing the germ-plasm; but till now we have not yet the certitude that there are cases when such agencies act only on the germ-plasm without producing any modification in the tissues and organs of the body.

The reappearance in the offspring of modifications produced in the parents by exterior agencies, which has been observed in moths, butterflies, and beetles, has also been established for

37 Variations are inherited, Mr. Tower says; 'all inheritable variations behave alike; and in no case is there any evidence to show that there is a fundamental difference between "mutants" and any other inheritable variation. (p. 308). But 'there exists at present not one single fact to show the inheritance of acquired somatic variations or their incorporation in the germ-plasm' (p. 310); the inherited variations 'are direct responses in the changed constitution of the germ-plasm to stimuli' (p. 312). As already shown by Professor Semon, in his Problem der Vererbung 'Erworbener Eigenschaften,' pp. 108-115, these assertions are not proved by Mr. Tower's experiments.

38 'Precisely in these cases observed by Tower all possibility of a stimulus occasioned by the colour-modification is excluded. Because these modifications consist in deposits of pigment in the outer cuticula, which has no pore-canals, and therefore its deeper part, where the pigment deposits are, stands in no sort of stimulus-conducting connexion with the irritable substance of the organism and its germ-cells (R. Semon, Das Problem, p. 111).

³⁰ Das Problem, p. 113.

⁸⁴ Loc. cit., p. 302.

ss In chapter viii. of Semon's Das Problem der Vererbung Erworbener Eigenschaften' the reader will find an excellent discussion of the conclusions

^{38 &#}x27;Of considerable importance,' Mr. Tower writes, 'is the strong evidence which points to the general conclusion that these permanent variations arise during the growth periods of the germ-cells, and do not appear to arise before or after this period. Just what this signifies is at present difficult to determine, further experiments and cytological studies being necessary before we shall be able to arrive at a more complete understanding of it ' (l.c., p. 296).

certain divisions of Vertebrates. In a previous article to it shown that substantial changes can be produced in the colour and the habits of Amphibians and Reptiles by rearing them unwonted conditions of life. Now we can say that such modifications are inherited.

One of such cases was observed in the newt-like creature the Mexican lakes, known as Axolotl, or Siredon, which nothing else but a well-known terrestrial Salamander, t Amblystome, in its yet undeveloped larval stage, when it has not yet lost its external gills and has not yet acquired internal lungs It is known that the undeveloped Amblystome, or Axolotl, is however, capable of reproducing itself in that larval stage, and therefore it was considered for some time as a separate species until it was proved that young Axolotls can be transformed into Amblystomes by rearing them on land, with an abundance of food, or in an imperfectly aërated water.41 Further experi ments about the inheritance of this acquired character have been made by Madame Marie de Chauvin, and it appeared that the descendants of the thus modified Axolotls retained a tendency towards an early accomplishment of the metamorphosis, even if they were brought up in conditions that are normal for Axolotla As to those descendants of Axolotls which for the last five-andtwenty years or so were kept in such conditions as to reproduce themselves in the larval stage, it becomes more and more difficult to provoke in them the Amblystome metamorphosis-much more than it was in individuals freshly brought from the Mexican lakes, where, on account of the frequent drying up of the lakes, the Axolotls were breeding in continually changing surroundings.42

In the same article I also mentioned Kammerer's experiments with the eel-shaped, flesh-coloured, and nearly transparent amphibian, the *Proteus anginus* of the Austrian caves. When it was placed into tanks opened to a broad daylight it began to be covered with brown and black spots—the experiment succeeding best with young, well-fed males kept in warm water. The darker colouring was lost when the animal was taken back to dark surroundings, or was poorly fed; but it reappeared in favourable conditions. In his earlier experiments Kammerer failed, however, to obtain a progeny from the modified individuals.

Bit he succeeded next year. 43 The thus acquired character was transmitted to the next generation, whenever some time field passed between the development of the black patches in the parents and the birth of their offspring. Moreover, the dark colouring appeared in the latter, whether the young ones were born in well-lighted surroundings or in the dark. The same result was obtained if the father alone had black spots. Consequently—Professor Semon remarks with full right—this is not a case of passive transmission of the black pigment from the parent to the ovum. It is a case of inheritance of an acquired character. 44

In another series of experiments Dr. Kammerer came to still more decisive conclusions, ⁴⁵ and I have already analysed in the just-mentioned article the inheritable modifications he obtained in the mode of reproduction of the Spotted or Fire Salamander. Similar results were obtained next with the colouring of the same Salamander. When it was kept for several years on a yellow clay its yellow markings considerably increased at the cost of its fundamental black colouring. When the offspring of the thus modified individuals, coloured yellow to a great extent, was divided into two lots, one of which was kept on a yellow ground, and the other on a black ground, the abnormal yellow colouring was retained to a great extent in the second lot, and increased in the first. Contrary effects were produced when the Salamanders were reared on a black ground, and the acquired darkening was also retained to a certain extent. ⁴⁶

43 P. Kammerer, 'Experimente über die Fortpflanzung, Farbe, Augen und Körper-Reduction bei Proteus anginus, Laur,' in Archiv für Entwickelungsmechanik, Bd. xxxiii., 1912, pp. 349-425.

⁴⁰ Nineteenth Century and After, December 1910.

All Experiments of Mme. Marie de Chauvin, Shufeldt, and Winterbret. See Nineteenth Century and After, December 1910, pp. 1047-1049.

p. 188. Besides, it was found that cannibalism produced in the males an increased size of head and teeth.

⁴⁴ R. Semon, Das Problem, etc., p. 76. As to Kammerer he sums up this part of his experiments as follows: 'An inheritance of acquired characters in its general wide sense is by all means to be noted, and this is what imports most for the explanation of the phylogenetic process. Whether this acquired character can be described in the strict Weismann's sense of Somatogene remains undecided.' The transparence of the body of the Proteus offers, of course, favourable conditions for making new characters appear in the germplasm through a direct action of light upon the latter. But this is again only a question as to how the character acquired by the body reappears in the offspring, but does not impair the fact of its reappearance, which is the main point for explaining the evolution of new forms possessed of precisely those new characters which have been produced by a new environment.

⁴⁵ Roux's Archiv für die Entwickelungsmechanik, vols. xvii., xxv., and xxviii.

Kammerer, Zuchtversuche zur Abstammungslehre, in the collection of papers of different authors published in Jena, in 1911, under the title Die Abstammungslehre, pp. 107, 110 seq. For Kammerer's experiments in rearing Salamanders on yellow and black paper (to avoid the influence of moisture) see his communication to the Graz Congress of Zoologists, analysed by Przibram (Phylogenese, p. 193), and his contribution to the Zeitschrift für induktive Abstammungs- und Vererbungslehre, Bd. iv., 1911, mentioned by Semon (Das Problem, p. 75). In this series of experiments the acquired characters were also inherited.

Similar effects, similarly inherited, were obtained with Water Newt, one species of Frogs, and some Lizards. 47

VI

Finally, biologists know a considerable number of inherited variations which cannot be explained by the selection of accidental modifications, and in all probability represent the effects of the use or disuse of different organs. In chapter xxiv. of Variation Darwin mentioned many such instances. Changes in the length of the digestive tube in domestic animals, which must be attributed to a changed diet; the drooping ears of many domesticated species—the more striking as there is only one wild species with drooping ears, the elephant; the superiority of our cows and certain goats for yielding considerable quantities of milk, which must be attributed, of course, to selection, but also, as Darwin wrote, 'partly to the inherited effects of the increased action, through man's art, of the secreting gland'; inherited short-sightedness, and so on; all these belong to the same category. 48

It is also known that Herbert Spencer, in the first edition of his Principles of Biology, and still more so in his discussions with Weismann (published in separate pamphlets and reproduced in the second edition of the Principles), pointed out a number of similar inherited modifications due to the use or disuse of different organs. One of them was the more perfect development of the sense of touch in those parts of the human skin which are exposed to a frequent contact with the exterior world, and especially in the tip of the tongue and the tips of the fingers. It was known indeed from the experiments of Weber on the sense of touch that tactile perceptiveness is far more developed in the breast of man than in his back, and still more so in his forefingers—there being a series of gradations

Lizard (Lacerta serpa) and the Lacerta fumana, the changes of colouring, pronext; but they were retained only in the same degree as the first generation back to the normal ones.

The direction of hair in animals and man may also be mentioned. In an elaborate work on this subject (The Direction of Hair in Animals and Man, London, 1903, with numerous illustrations) Mr. Walter Kidd shows that if natural selection must have been an important factor for determining the general direction of hair from the tip of the snout to the end of the tail, which is now seen in the otter and must have been the primitive type, the same cannot be said of the modifications of this type in various animals, and especially in man. Part of these modifications are certainly due to the form of the animal; but there are many variations of the hair-slope (reversed areas of hair-tufts, cohorts, 'featherings,' and 'crests') which Mr. Kidd can only explain by the effects of new habits and the hereditary transmission of the thus acquired new features in the distribution of hair and its different slopes.

hetween these two extremes, and the gradations corresponding to the frequency of contact of our skin with utensils and the like. Spencer continued these experiments upon two compositors, whose organs of touch at the tips of their fingers are continually exercised during their work. The experiments confirmed his previsions. Spencer found that with these two compositors the factile perceptions of the forefingers were far more refined than they are in persons engaged in other occupations. 49

It is self-evident that such differences in the sense of touch cannot be attributed to natural selection. They must be the results of a determinate variation, due to the use of certain nerves in excess of the others.

No experiments having yet been made upon the sense of touch in different parts of the body in new-born infants, we have no direct proofs of the inheritance of the thus acquired developed sense of touch. But it is known, and was mentioned by Darwin, 50 that in infants, 'long before birth, the skin on the soles of the feet is thicker than in any other part of the body' -a fact about which Darwin said that 'it can hardly be doubted that this is due to the inherited effects of pressure during a long series of generations.' 51 This observation having been contested lately by Mr. Shattock, 52 Professor R. Semon made the necessary anatomical researches to verify it,53 and they fully confirm the fact (noticed already by Bernhard Albin in 1754) that the development of the skin on the plant of the foot and the palm of the hand, long before the birth of the infant, progresses in advance of its development in other parts of the body. Besides, during nearly the whole of the first year of the infant's life a horny layer is developed on the plant of the foot, much thicker than everywhere else, excepting the palm of the hand, although during the first year of the child's life the sole is not yet subjected to external pressure. After a careful discussion of the whole subject, Professor Semon confirms the conclusion of Darwin to the effect

⁴⁰ Using a pair of compasses Weber had found that they had to be opened to the extent of two and a half inches before the middle of the back could distinguish between two points and one. At the same time the end of the forefinger distinguished the two points when the points of the compasses were only one-twelfth of an inch apart. All possible gradations between these two extremes were found in different parts of the skin. In his experiment on skilled compositors, Spencer found that their forefingers distinguished the two points when the distance between them was only one-seventeenth of an inch. (The Inadequacy of Natural Selection, London, 1893. Reprinted in Principles of Biology, second enlarged edition, London, 1898, vol. i.)

⁸⁰ On the authority of Paget's Lectures on Surgical Pathology, 1853, vol. ii., p. 209.

51 The Descent of Man, 1901 edition, p. 91.

⁵² S. G. Shattock, 'Lamarckism and Callosities' in Proceedings of the Royal Society of Medicine, vol. iv., London, 1911; quoted by Semon.

⁵³ Die Fussschle des Menschen,' in Archiv für Mikroskopische Anatomie, Bd. lxxxii., Abth. ii., 1913, pp. 164-211, with plates.

that the just-mentioned development of a horny layer in infant can only be a consequence of an inherited modification due to the pressure that was exercised upon the plant of the feet during a very long period of time, since our remote ancestors began to walk in an upright position. If equally conclusive results have not been obtained in our experiments upon the effects of the use and disuse of different organs, it is because we have not such numbers of generations upon which the modifying agency would have acted as we have in this case.

Altogether, it is high time that the whole of the subject of inherited variations due to the use or disuse of organs, to which Spencer gave such an importance in his *Principles of Biology* should be studied as seriously as Professor Semon has studied if for the plant of the foot.

VII

We thus see that, taking into consideration the results obtained lately by experimental research, we have no right to maintain that the modifications produced in both plants and animals by the direct action of a changed environment are not inherited. We must recognise, on the contrary, that there are proofs, both inductive and experimental, that such modifications are inherited. Even if the modifying influences have acted for a very limited number of generations—and both Lamarck and Darwin pointed out the importance of a prolonged action—it was found in nearly all carefully made experiments that traces of the modifying influences to which the parents had been submitted were found in the offspring.

This is an important result. True, it is said now by the followers of Weismann that in such cases of inheritance as are mentioned in the preceding pages it was not proved that there had been a real inheritance of acquired characters. not proved, they say, that the modifications produced in the body of the plant, or the animal, had called forth such changes in the germ-cells that they reproduced in the offspring the changes which took place in the parent stock. The germcells may have been affected directly. There may have been a parallel action in the body of the modified organism and its germ-cells. But there is no reason either why the latter hypothesis should be preferred to the former. The main argument of those who pronounce themselves in favour of a 'parallel induction ' in the germ-cells is the argument which Spencer spoke of in the second edition of his Principles of Biology. We cannot imagine, they say, how a change which took place in a muscle or a nerve can effect a corresponding change in that part of the germ which will have to produce a corresponding part in the

offering.⁵⁴ But it is evident that this argument, as the Milan Pofessor Eugenio Rignano remarks in his most valuable work on the transmission of acquired characters (after having candidly wined that he himself for some time was influenced by it) has little logical value as the argument of those who refused to recognise universal gravitation because they saw no means by which the attraction of the sun could be transmitted through space to a planet.⁵⁵

Besides, the more we advance in our studies of heredity, the more we learn that the germ-plasm does not lead the isolated life it was supposed to lead when Weismann first framed his germ-plasm and amphimixis hypotheses. This conception has been proved to be quite false, and many years ago Romanes pointed out how Weismann himself had changed his opinions on this point in the second volume of his Essays. But since that time we have had more and more researches showing that the bodycells and the germ-cells stand in a close intercourse.

To take a few instances only: the researches of Sitowski demonstrate that, if the caterpillars of the small moth *Tineola bisseliota* are fed with wool containing the aniline colour Soudan III, not only the bodies of these caterpillars become coloured in red, but also the cells enclosing the eggs in the moth and the larvae obtained from these eggs show 'a characteristic red tint' '6'; similar results were obtained with other insects and other aniline colours; and many well-known cases of infection of the germ-cells by bacteria developed within the body-cells are also cases in point. Of course, there is a great difference between the infection of germ-cells by grains of a colouring matter or the spores of a fungus, and a modification of the germ-cells by the influence of the body-cells. But these facts show how unscientific it was to affirm, or even to suppose, that the germ-cells cannot be affected by changes going on in the body-cells because we,

reproduced some lines from the letter of a Cambridge professor, who wrote as follows: 'Many zoologists, most of us here at Cambridge, are intensely opposed to the doctrine of the inheritability of acquired variations. Even assuming that the developmental power of a germ is determined by its molecular structure (and I for one would question this), we still fail to conceive any means by which, for instance, a change in the development of a muscle or a nerve can effect a corresponding change in that part of the germ which is destined to produce a corresponding part in the descendant.' In reproducing these lines Professor J. T. Cunningham, in his work Sexual Dimorphism in the Animal Kingdom (London, 1900), added the quite true remark that this was 'an extremely unscientific attitude' (p. 421).

⁵⁵ La transmissibilité des caractères acquis, Paris (Alcan), 1908, p. 2. ⁵⁶ Sitowski, in Bulletin International de l'Académie des Sciences de Cracovie, 1905, and Science, September 1909, analysed by A. Drz. in Revue Scientifique, 1909, ii. p. 660. Also Weismann, Studien über die Descendenztheorie, second edition, ii. 59.

with our total ignorance of all these processes, could not see this action could take place. Now that we know how cells the body are closely connected with each other by means of interest cellular protoplasma threads and wandering cells, we ought say, on the contrary, that we cannot imagine how a germ-plasm which grows in immense proportions at certain periods and fed by the body-cells, can remain uninfluenced by the processes going on in the organs of the body. The very hypothesis of parallel induction,' by which Weismann tried to explain the facts of transmission of modifications and mutations to the offspring, is a recognition of that mutual influence. The same statement of the same statement

However, it may be asked, 'If the inheritance of variations due to the action of environment is widely spread in Nature (a it must be if the external influences play an important part in evolution), why is it that we have so few cases where the transmission of acquired characters is proved by direct experiment? This is certainly an important question, and in a subsequent article I shall try to answer it, as well as to analyse the general conclusions that can be drawn as regards the Direct Action of Environment and Evolution.

P. KROPOTKIN.

THE PEASANT SONGS OF RUSSIA

In happened some years ago in Southern Russia that a gang of labourers digging on the open Steppe came upon the walls of an ancient burial vault. An entrance was made, and then a strange sight was revealed. Upon a bier in the centre of the chamber lay the body of a queen, apparently untouched by decay. Her robes of royal purple were spangled and fringed with gold, a diadem set with jewels lay on her dark hair; a golden mask covered her face. At her feet lay vessels of gold and silver and the bones of slaves.

But even while the workmen stood and wondered a change took place. The purple draperies faded and fell into dust. The mask of gold slipped down. In the passing of a few hours light and air had done the work of time.

That scene, as I read of it, seemed to me symbolic of the changes taking place in the Russia of to-day. Bit by bit the walls of mistrust and prejudice that separated Russia from Western Europe are breaking down. Modern ideas and manufactures are penetrating the towns and even the villages. Those who have known Russia in the past are aware that the primitive handicrafts, the ancient rites and customs, have begun to pass away, and that as they come into closer contact with industrial progress they must eventually disappear. But the peasant still possesses a national heirloom which has suffered little change or loss in the course of centuries in the vast uncounted store of folk-songs and the 'bylinys' or epic chants, whose historic value has only lately been realised, even in Russia.

Like precious manuscripts lying unheeded on the shelves of a sequestered library, this treasure of the humble has survived through stormy periods of devastation and war. It has been handed down from one generation to another by word of mouth, accompanying and commemorating every stage of the moujik's life, from the cradle to the grave. In these religious festivals, marriage-songs, dance-songs and songs of love, of invocation and lament, there lies a master-key to the inner life of Russia, and a clue to much that appears at first sight strange and incomprehensible in that land of contrasts and extremes.

Przibram's Experimental Zoologie, 1909. Analysed in Roux's Archiv, xxvii. 4,