SUPPLEMENT.

THE INHERITANCE OF ACQUIRED CHARACTERS.

President's Address, Delivered at the Annual Meeting of the American Ornithologists' Union, New York, Nov. 18, 1891.

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COLLEAGUES:—I desire at this time to bring to your notice a subject that does not seem to have greatly occupied the attention of ornithologists, although it has been the cause of much discussion among others prominent in different branches of science, and is so important that it strikes at the very root of the principles of evolution, and the causes that effect the variations exhibited by living creatures. This subject is comprised in the question, "Can acquired characters be transmitted by a parent to its offspring?" A school has arisen, under the leadership of Prof. August Weismann, of Freiburg University, which denies that acquired characters can be transmitted by their possessor, but attributes all variations that occur to the principle of natural selection, and Weismann asserts* that the inheritance of acquired characters has never been proved, either by means of direct observation or by experiments. This theory is of course in direct opposition to Lamarck's fourth law which those who do not agree with Prof. Weismann, accept as explaining their belief. This law, freely translated is as follows: "All that has been acquired, impressed, or altered in the organization of individuals during the course of their life, is preserved by generation, and transmitted to the new individuals which spring from those who have experienced these changes." Of course we receive this statement with a reservation, for it is not to be presumed that *all* characters, but only such would be transmitted, as would be necessary for the preservation or well-being of, or would be advantageous to, the offspring. Before discussing this subject it is very necessary to

*Essays upon Heredity, 2d ed. p. 81, English Translation.

ascertain what is meant by the expression "acquired characters." Weismann* defines these, as "no more than local or sometimes general variations which arise under the stimulus provided by certain external influences." Prof. Ray Lankester,† one of the most ardent as well as aggressive of Weismann's followers, explains the term as "new characters acquired by the parent as the direct consequence of the action of the environment upon the parental structure, and exhibited by that parent as definite measurable features."

Mr. Dyer‡ gives his view of this expression, in perhaps not quite so lucid a manner, as follows: "Acquired characters are those changes of hypertrophy, extension, thickening, and the like, which are obviously due to the direct physical action of the environment on the body of the individual organism." I would define this term, as seems most reasonable to me, as follows: Acquired characters are differentiations due to any cause, known or unknown, assumed by an individual or individuals during life, which render it or them recognizable as varying from the ancestral form. I do not profess to be able to produce proofs that are absolute, and show causes for these variations which may not be explained away by some unexplainable theory, any more than have Weismann and his followers been able to bring forward any that absolutely prove the position they have assumed to be correct, but I think evidence can be given, that may be called strongly circumstantial, if not direct, to show that characters have been acquired and then transmitted by a parent to its offspring. We will first consider the causes that, as has been asserted, produce these variations, and then cite some of the cases that would seem to show direct evidence of the power some of these causes, at least, have exerted in influencing these variations, and of their transmission from the parent to the offspring.

Weismann and his followers, as has been stated, assert that natural selection is all-sufficient to explain these phenomena. What is natural selection? For a reply I turn to Darwin, the originator of this theory, and read as follows: "The preservation of favorable variations, and the rejection of injurious varia-

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* Essays, p. 171.
† Nature, 1890, p. 315.
‡ Ibid. 1889, p. 128.

tions, I call natural selection.*....Some," he states, "have even imagined that natural selection induces variability, whereas it implies only the preservation of such variations as occur, and are beneficial to the being under its conditions of life"; and he farther says,† "unless profitable variations do occur, natural selection can do nothing"; also,‡ "unless favorable variations be inherited by some at least of the offspring nothing can be effected by natural selection," and this is reiterated farther on,§ "nothing can be effected unless favourable variations occur," and he goes on to say‖ "what applies to one animal will apply through all time to all animals — that is if they vary — for otherwise natural selection can do nothing." It will thus be seen that the author of this doctrine expresses himself in the most positive terms that the principle does not originate variation, but on the contrary is only effective when variation arising from some other cause has been produced. Let us consider some of the causes which, from the results, lead us to believe that they have originated variation, and first among these is environment. Darwin paid little or no attention to the influences of this cause, and in his letter to Moritz Wagner he says: "In my opinion the greatest error I have committed has been not allowing sufficient weight to the direct action of the environment, that is food, climate, etc., independently of natural selection. Modifications thus caused, which are neither of advantage or disadvantage to the modified organism, would be especially favored, as I can now see, chiefly through your observations, by isolation in a small area, where only a few individuals live under nearly uniform conditions. When I wrote the 'Origin of Species,' and for some years afterwards, I could find little evidence of the direct action of the environment. Now there is a large body of evidence."¶ It is, I think, the general belief, of ornithologists at all events, that a form to be successful in attaining a new development, must be isolated from other forms. This would seem to be self-evident; otherwise an individual that

*Origin of Species, 3d ed. p. 84.

†Ibid. p. 86.

‡Ibid. p. 107.

§Ibid. p. 114.

‖Ibid. p. 119.

¶Darwin's Life and Letters, Vol. III, p. 159.

should begin to vary from its type, no matter what its cause might be, would almost certainly have those variations extinguished by interbreeding with typical individuals. A reasonable supposition, why such individuals as above mentioned should be able to perpetuate their variations or acquired characters without isolation, would be that the influences producing the characters were so powerful as to extend over and include the majority of the members composing the group affected, and then it would naturally follow that the original type would gradually disappear (the same influences continuing with undiminished force), to be succeeded by the new form, which in its altered condition would be more fitted, as we may believe, to battle with its changing surroundings.

It is perhaps well that, before proceeding farther, I should here explain what I mean by 'type' and 'typical' forms, as those terms will be used by me frequently. Type simply denotes the *starting point.* Thus an individual first described is the starting point in our literature of what we call a species, with which all subsequently discovered forms are to be compared. The form represented by this individual may not be, and probably is not, the original source from which all its varieties have sprung, but merely, mainly from accidental circumstances, was first brought to our notice. Thus *Cyanocitta stelleri* is the type of its particular group, and it is customary to compare the allied forms with it. It does not follow that because the bird we recognize under this name was described first, that it was the source from which its races derived their existence, as one of the forms we call subspecies may just as likely have been the origin of all the races, *C. stelleri* included, but the latter, having been first known, is the starting point or 'type.' 'Typical' is that form which identically represents the type.

Weismann,* referring to environment, says, "I only know of one class of changes in the organism which is with difficulty explained by the supposition of changes in the germ; these are the modifications which appear as the direct consequence of some alteration in the surroundings," and he declines to consider the subject in detail because facts of sufficient precision are not known for a final verdict to be pronounced. But it may be seriously doubted if Prof. Weismann has been able to produce more facts

*Essays, 2d ed. p. 99.

of "sufficient precision" to prove the theory he advocates than those who as yet decline to accept his views can bring forward as practically substantiating their position. Neither side has proofs that can demand the pronouncing of a final verdict, and we can consider only which evidence produced is most likely to show the true solution of the problem.

Some of the evidence of variation produced, as we believe, by environment and isolation may be derived from various genera of birds containing numerous species with a wide dispersion, and of these I would cite *Ptilopus*, a genus of Fruit Pigeons. These birds are chiefly inhabitants of islands, and intercourse between them is impossible on account of the intervening sea. As an example of variations that are produced, I will select as a type *Ptilopus melanocephalus*, a thoroughly characteristic and well-marked form, known to and accepted by ornithologists as a species, and which is an inhabitant of Java, Lombock, Sumbawa, and Sulabessie. In the neighboring island of Flores is a form *Pt. melanauchen*, varying but slightly from the type as if just commencing to differentiate. To the north in the great island of Celebes is another variation called *Pt. melanospilus* differing in a narrower throat mark, and in having the crissum lemon-yellow washed with orange, instead of clear yellow. Sula and Ceram possess another form which has the occipital black band (present in all the forms cited) smaller, and the crissum orange yellow; and lastly in the island of Sanghir, farthest away, *Pt. xanthorrhous* is found, which has both abdomen and crissum orange, this color running upwards nearly to the breast, thus exhibiting the widest divergence from the type. It will be seen from this distribution that, as might have been expected, the variations in the forms living nearest to the type, and consequently with less change of environment, are the slightest, while as the separation becomes greater these differences are more pronounced, until in Sanghir appears a form which has departed so greatly from the type as to merit specific rank.

The probable cause of these differentiations in the members of *Ptilopus* may be explained as follows. The islands of the Eastern Archipelago doubtless are but the remains of what was once a continent, and this was not broken up simultaneously or always suddenly in its length and breadth, but sometimes gradually and at various periods. Therefore we should not be surprised that one species should inhabit various islands, between which are others containing distinct forms of the same genus. This may be accounted for in two ways. First, a species may have been widely dispersed over the continent; and when portions of this had disappeared beneath the waves, the fragments that remained above water at the outset were all inhabited by the same species; but the physical and other conditions of the environment at intermediate points were of a different character from those at the extremes, and in course of time the individuals, influenced by their environment, isolated on intervening islands, departed from their types, while others, though widely separated, retained their characters. Or, second, it may have been, on the breaking up of the continent, a portion of this inhabited by a strictly local form, but one surrounded by a more widely disseminated and typical species had not been submerged. This might explain the fact of why a distinct form should intrude itself on an island lying between others inhabited by a different one, the species with the greater range having been preserved at the extremes of its habitat which also had become islands. Thus isolation and environment had fulfilled their work, but the form remained true to its type, except where the environment had been changed.*

Other groups in the same genus present similar gradations of change and typical departures, but the above is sufficient for the present illustration. Now what has caused this variation? If, as we may suppose would be asserted by Weismann and his followers, it has occurred through natural selection and not by the parent transmitting its acquired characters to its offspring, how did the principle named act, if the environment was not sufficient to influence the change? Weismann acknowledges that the *germ-plasm*, that is, what he designates as the undying part of the organism contained in the germ-cells, may itself be modified through the action of the environment on the *soma*, that is, the body, increasing its nutrition, yet he denies that definite changes induced in certain parts of the *soma* by the action of the environment can be transmitted to a suceeeding generation. If, as granted by Weismann, the so-called 'immortal' part of the organism can be changed or modified by the influences of the environment, is it not reasonable to suppose that such modifications

*In this connection see Baur, 'Origin of the Galapagos Islands,' Am. Nat. 1891, p. 107.

would be exhibited by the germ-plasm upon the body of the individual's offspring, or must we believe that a modified or changed germ-plasm would produce the same results on succeeding generations that it did before it was altered from its original condition, no matter what the causes may have been to effect such modifications? But if such a modified germ-plasm did produce a modification in the offspring as presented by its parent, would not that be a transmission of acquired characters caused by the environment and not by natural selection?

If the influences of environment affect only the cells of the body, and these are unable to affect or modify the reproductive cells, would it not naturally follow that the offspring of an animal that was first changed by its environment, would not resemble its changed parent, but on the contrary would be what that parent was before it had acquired any new characters, and then the young would have to undergo in its life similar changes to those the environment had produced in its parent, and this would always be the case throughout all the generations of that species? In the young would always be produced the original appearance of the parent, never its alterations. But this, of course, is not so. The young bears a very close resemblance to its parent in the majority of instances, else the continuity of specific forms would be an impossibility. It is difficult to believe that the germ-plasm could be predisposed to all the infinite variations exhibited by the body in the many and totally different influences of its environment, and that the somatic cells exerted upon it no influence whatever. "If the body of the multicellular organism is thus, even according to Weismann's ideas, of secondary importance in comparison with the germ-plasm, if the latter corresponds to the unicellular organism, it follows that the multicellular is just as immortal or mortal as the unicellular. And thus it is impossible to see why, between the germ-plasm of the multicellular on the one hand, and that of the unicellular on the other, there should exist this profound difference, that the latter acquires characters during life and transmits them by heredity, the former not, — how the former any more than the latter can nourish itself and grow without being influenced in its nature by its nurture."*

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*Eimer, Organic Evolution, p. 71.

The germ-plasm, according to Weismann's theory, can produce body-plasm, but the latter can never originate germ-plasm. Germ-plasm is continuous, undying, the body-plasm is mortal. On this point Prof. Lloyd Morgan* remarks, "I cannot but regard his doctrine of the continuity of germ-plasm as a distinctly retrograde step. His germ-plasm is an unknowable, invisible, hypothetical entity. Material though it be, it is of no more practical value than a mysterious germinal principle. By a little skilful manipulation, it may be made to account for anything and everything. . . . . The fiction of two protoplasms, distinct and yet commingled, is, in my opinion, little calculated to advance our knowledge and comprehension of organic processes. For myself I prefer to stand on protoplasmic unity and cellular continuity."

Mr. Lucas† has shown how the change of habit in certain birds of the island of Guadalupe, due to their insulation, illustrates certain facts affecting skeletal variation. The descendants of migratory species having their habitat restricted, show the symptom of weakening flight in the decrease in the length of the sternum; later on a diminution in depth of keel takes place. Then follows a reduction in length of wing, beginning with the manus and fore-arm, the humerus apparently not being affected, until the rest of the wing is perceptibly lessened. Then the outer wing bones disappear, leaving only the humerus,—as in *Hesperornis*,—and finally the humerus itself may be wanting, as in *Dinornis giganteus.* But there are exceptions to this, and one is exhibited in *Salpinctes guadalupensis* which has gained in power of flight, both the wing and sternum exceeding in length those of the continental form, and this would seem to indicate that insulation does not necessarily cause degeneration. Mr. Bryant had shown that this Wren had become the most abundant species on the island, and in ten years had exhibited a slight increase in length of bill; and Mr. Lucas argues that in this species superior wing power would give superior ability to obtain food, to escape its enemies, and to prevent its being blown out to sea, and a superiority in these points would naturally lead to its increase. Why this bird should be an exception to the others on

*Anim. Life and Intell. p. 141,

†Auk, 1891, p. 218.

the island may be due to the fact that *Salpinctes*, being a genus whose members are feeble in flight, required a greater development of wing and sternum to place it on a par with other species whose wing power was naturally sufficient to successfully combat the influences of insular life, and which *Salpinctes* alone lacked.

But to draw my illustrations solely from island forms, may be objected to on the ground that the influences there exerted are more powerful and exceptional than in other geographical areas which have environments not so abruptly separated. I will therefore cite the effects we assume continental environments have upon a form of wide distribution, and take for my illustration the familiar species *Melospiza fasciata* Gmel. and its allies. This species and its subspecies are distributed throughout North America from the Atlantic to the Pacific, and from Mexico to Alaska, and its islands. The type is found in the form inhabiting the eastern States, and extends its range to Nebraska and Indian Territory, and is generally constant in its characters, the variations being scarcely noticeable, as would be expected from the similarity of the environment throughout this dispersion. New Mexico and Arizona present a form, *M. f. fallax*, that varies from the type in its extreme pale coloration and increase of size. This region possesses climatic influences of an arid character, very different from that with which the type has to contend, and in certain portions of the habitat, as in the region of the Gila River, these influences cause individuals to exhibit markedly different characters from those observed in the type. In Colorado, Utah, Nevada and northward occurs another form, *M. f. montana*, which in winter visits the neighborhood of Tucson in Arizona. This is darker in color than *fallax*, as might be supposed it would be from the greater humidity of its habitat, but the two forms seem to run into one another on the northern and southern limits, respectively, of their dispersion, and individuals thus intermediate present characters that are inconstant, and which are probably the result of interbreeding. The foothills of the Sierras, through the mountains, and in their western foot-hills, produce another departure from the type, *M. f. heermanni*, and here we have a form of a much darker shade of brown, and bill intermediate in size between those of the two forms first mentioned. In the neighborhood of Comondu, in Lower California, the physical conditions have differentiated another group, *M. f. rivularis*, distinguished from its New Mexico and Arizona relatives by darker color and greater size. Northward along the Pacific coast to the Columbian region another style is produced (*M. f. samuelis*), almost black in its coloration, and the smallest in size of all the subspecies. In the Columbian region a race, *M. f. guttata*, occurs, rufescent in hue, and with the bill more slender in porportion than any of the forms already mentioned. The typical home or central region of the dispersion of this form is the Columbia River region coastwise, but before reaching this point changes of an intermediate character in the color of plumage among individuals occur, foreshadowing the subspecies that ranges through the coast region of British Columbia, northward to Sitka. Thus migrants obtained in the fall and winter at Nicasio,* near San Francisco, are intermediate in coloration between the Pacific coast subspecies and that of the Columbian region, and individuals from the base of the eastern slope of the Cascades in Oregon exhibit gradations from that form which connect it by insensible stages with the subspecies of the Columbian region, *M. f. guttata.*

What is to be gathered from this mass of indisputable evidence, save that the variations of this widely dispersed form are caused primarily by the effects of environment, carried on, if you please, by natural selection, but not originated by it. The allied forms change with the localities they frequent. The different kinds of food, aridity, humidity, the elevation and depression of the earth's surface, producing mountain ranges and valleys, of various heights and depths, in short the many and potential physical and climatic influences that constitute what we call environment, have separately or together produced the various forms now existing, and that the characters acquired through these influences have been transmitted from parent to offspring. The various forms are isolated in the centre of their dispersion, as if on islands, from their allies, and when two of these are connected in the outlying portions of their dispersion, where the environment exerts influences derived from both neighboring regions, a new form is prevented from arising by the interbreeding of the two subspecies, even though the environment in the intermediate region could exert, if isolated, sufficient influences to produce and maintain

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*Henshaw, Bull. Nuttall Ornith. Club, 1879, p. 159.

another subspecies. It seems to me this deduction from the evidence is reasonable and more probable than to suppose that the germ of these various forms had a predisposition in some ancestor to produce them. We cannot actually prove that environment has caused these changes, with any more certainty, perhaps, than the theory of germ predisposition can be proved, but this we do know, that desert tracts contain light-colored species, and forests and districts with great rainfall have dark-colored species, and it is a fair assumption that these great differences are caused by environment; and granting this, have we not an explanation of causes of variation, in some degree at least?

Additional evidence of the presumed effects of environment in another genus of birds could be produced from Mr. Dwight's exhaustive paper on *Otocoris* or Shore Larks, with which you are all familiar, but my time is too brief to consider this portion of my subject any further. If natural selection were all sufficient to produce variations in any particular species, it is reasonable to suppose that it would effect such changes in others under the same environment. But our evidence seems to point the other way, and that environment causes variations, and natural selection only assists in their transmission.

The effect of climatic influence is shown in the changes exhibited by the blue butterfly, *Lycæna agrestis*.* This occurs in three forms. A and B alternate in Germany as winter and summer forms; B and C are the winter and summer forms in Italy. The form B occurs in both climates, but appears in Germany as the summer, in Italy as the winter, form. The German winter form A, however, is completely wanting in Italy, while the Italian summer form (var. *allous*) does not occur in Germany.

Duration of life, among individuals, we also regard as a prominent factor in the development of species, and cause of variation; and the longest-lived creatures evolve new forms or variations the slowest. This would seem to be almost paradoxical, for it would appear that the longer an animal was exposed to the influences of its environment the more its immediate offspring would be impressed by and illustrate those influences. This might be so if reproduction and development were equally rapid in all creatures. But of course this is not so. The longest-lived creatures produce the fewest young, and naturally maturity is

*Eimer, Organic Evolution, p. 126.

slow in arriving. It is difficult to ascertain the age to which wild creatures are capable of attaining, but as the results of our only means of observation, viz., animals in captivity, it is found that Eagles live nearly one hundred years.* Ravens live nearly as long. Parrots have reached nearly one hundred years. Magpies live twenty years, and small birds, as the Nightingale, Blackbird, etc., from ten to twenty years. As a rule birds of long lives lay but few eggs at a time, and allowing for the destruction of the eggs from numerous causes, and the mortality among the young, it is estimated by Weismann,† arguing on the lines of Darwin and Wallace, that given the fertility and average of life of a species, a calculation can be made of the number of those reaching maturity. A species living ten years and laying twenty eggs each year, only two of its young in that time will reach maturity, if the number of individuals in the species is to remain constant. Or if the duration of life of an eagle is sixty years, and it reaches maturity at ten years, and then lays two eggs a year, out of the one hundred eggs laid only two will develop into adult birds. Weismann considers that this calculation rather under- than over-estimates the proportion of mortality among the young. However this may be, or whether we may altogether accept his calculations as correct, or warranted by recorded data, it appears to be a recognizable fact that the greater the age of an animal the slower it reproduces, and is the less able to originate divergences from those characters it received at its birth. The influences of the environment would be slower in their effects on a long-lived individual, and changes from its type, or starting point, correspondingly delayed. We must therefore look for variations and departures from the types more among those species with shorter lives, and greater number of offspring, where the influences of environment and natural selection are able to produce their legitimate effects in the briefest periods of time.

What is the result of the effect of environment on individuals? It provides them with the means of succeeding in the struggle for life. Dwellers of deserts, or desert-like districts, are pale in coloration and assimilate the ground, and so escape detection. Humidity and rainfall cause a melanistic phase of plumage,

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* Brehm, Leben der Vögel, p. 72. Weism. Essays, p. 37.

† Duration of Life, Essays, 2d ed. p. 13.

witness the birds of Florida or those of the Northwest Coast, as compared with similar forms in drier sections of our country, and evidence is given upon this point in 'The Entomologist' as stated by Cockerell* that moisture is the cause of a certain phase of melanism, especially among lepidoptera. We may believe that the climatic changes of boreal regions influence the appearance of animals that are found within their limits, witness the white covering, affording, during the lengthened winter, an additional means of protection through concealment amid snow and ice. All such evidence strengthens us in the belief that the environment originates variation. Additional evidence of this I obtained in the clever paper† of my friend, Mr. F. M. Chapman, on a collection of birds from British Columbia, obtained on the coast and in the interior. The former is visited by a rainfall heavier than that observed in any other portion of North America, resulting in a dense forest-growth; the interior has a minimum of rainfall and vegetation comparatively desert-like in character. "The effect of this rainfall is the production of forms that are darker, more richly colored, or more heavily barred or streaked than any other representative of their respective genera." As a proof of this, thirty-one birds are enumerated from the coast, all of which present these distinguishing characters, when contrasted with their representatives from the interior, which are paler in every instance.

An acquired character resulting from the influence of environment will be inherited as long as the causes that produced it remain the same, but will be extinguished or changed with a changing environment, provided sufficient time has not elapsed for the character to become fixed. In the latter case heredity would probably cause the appearance of the character for several generations at least, even under a changed environment. Baur‡ has shown that Hoffman by isolating the wild carrot and bringing it under different conditions changed it considerably, and this change was inherited. Alpine plants removed to a botanical garden acquire new characters. The green Parrot (*C. festiva*),

* Nature, Feb. 27, 1890.

† Bulletin Am. Mus. Nat. Hist. III, No. 1, 1890, p. 127.

‡ Amer. Nat. 1891, p. 312.

as mentioned by Darwin,* when fed with the fat of siluroid fishes became variegated with red and yellow feathers, and the natives of Gilolo, in an analagous manner, alter the colors of the *Lorius garrulus* into the *L. rajah.* These characters will reappear if the causes that produced them continue, but not otherwise. The effect of food is illustrated in bees. The larvæ of worker bees, royally fed, develop into queens; and the workers raise queens when from any cause these are not present in the hive. The faculty enabling the workers to attain the wisdom to accomplish this cannot be inherited from their parents, queen and drone, but must exist in germ in worker larvæ, and be developed into mental characters either of queen or workers, according to the nourishment provided. This can only be explained by the inheritance of acquired characters, and by correlation, and not by the continuity of the germ-plasm, or by panmixia.†

In his essay on heredity Weismann asserts‡ that "from an Eagle's egg an Eagle of the same species is developed, and not only are the characteristics of the species transmitted to the following generation, but even the peculiarities. The offspring resemble the parents among animals as among men"; and again in the same essay, when speaking of the reproductive power of the germ-cells, he says: "Each of these can, under certain conditions, develop into a complete organism of the same species as the parent, with every individual peculiarity of the latter produced more or less completely." This is the position he would naturally take for his line of argument, and although those who differ from his views, might and do agree with him to a certain degree, they are not willing to go with him to the full extent such assertions would naturally carry them. Like does beget like, but not always. There are restrictions. It does in the sense that an Eagle can only produce an Eagle, and not a Swan, and a Grouse can only produce a Grouse, and not a Crow, but both forms can and do often produce young that vary from their parent in essential characters, such as color of plumage, size, and other attributes that form their complete organization. If this were not so, if like only could beget like, in its restricted sense,

*Animals and Plants. Domest. II, p. 269.

†See Eimer, Organic Evolution, p. 267.

‡Essay, pp. 72, 73.

there could be no advancement towards a more perfect development, and the creature of today would be the same creature it was at its creation, and it would remain the same throughout its existence. John. T. Gulick* has defined this principle in a manner that seems most satisfactory, and nothing that I have yet seen advanced by the advocates of natural selection as the all-sufficient cause, is able to controvert his conclusions. Mr. Gulick explains: "1st. Unlike to unlike, or the removal of segregating influences, is a principle that results either in extinction through failure to propagate; or in the breaking down of divergences through free crossings. 2d. Like to like, when the individuals of each inter-generating group represent the average character of the group, is a principle through which the stability of existing types is promoted. 3d. Like to like, when the individuals of each group represent other than the average character of the group, is a principle through which the transformation of types is effected."

In exemplification of these principles this author illustrates them somewhat in this way. Sexual and social instincts often bring in groups like to like together that do not cross, and when the different groups occupy the same area, and are guided by the same habits in the use of the environment, divergences occur even without a diversity of natural selection. He farther explains the way in which this divergence arises. A partial change of plumage or development of plumes results from a local segregation; and through social segregation, the principle that causes animals to associate with those whose appearance has become familiar to them, these variations are prevented from being submerged by intercrossing. Then when the invisible instinct and visible character lead individuals thus characterized to associate together, the new characters are intensified, because any individual of the community not imbued with the desire to remain with animals thus changed, will stray from them and fail to breed. He calls this process social selection. Then sexual selection steps in and preserves and accumulates peculiarities of color or plumage, for any individual deficient in these characteristics would be less likely to breed and produce offspring. He concludes as follows: "Varieties thus segregated may often develop divergent habits in

* Nature, XLII, 1890, p. 536.

their use of the environment, resulting in divergent forms of natural selection, and producing additional changes, but so long as their habits of using the environment remain unchanged, their divergencies cannot be due to natural selection." From these deductions, it is very obvious that we can only accept the dogma that 'like begets like,' with reservations. The offspring may be like its parent, but not always, nor in all respects. There are too many and too complex influences at work to hinder and prevent this. Natural selection cannot prevent a character from diverging from its accustomed path, and subsequently reappearing with modifications. Nothing, I believe, has yet been adduced to prove that natural selection can cause variation; it is merely the vehicle by means of which variation is continued. It takes what it finds already prepared and assists its transmission to succeeding generations. Selection, to employ the phraseology of a well-known naturalist, Prof. E. D. Cope,* "cannot be the cause of those conditions which are prior to selection"; in other words, selection cannot explain the origin of anything, and to this fact, even so strong an anti-Lamarckian as Prof. Lankester subscribes, for in his rather heated reply to Prof. Cope's article, he asks† "Who has ignored this? When and where?" If then it is conceded, even by this ardent follower of Weismann, that selection does not originate, or cannot cause variation, what becomes of their theory? We must look for some more potent factor to explain the origin and transmission of acquired characters, and this we believe we find in the influences exerted by isolation and environment.

Another fact requiring investigation, and its influence in the transmission of acquired characters, is the use or disuse of any particular organ. Prof. Romanes‡ explains the effect of this as follows: "If any structure which was originally built up by natural selection on account of its use, ceases any longer to be of so much use, in that degree will the prominence before set upon it by natural selection be withdrawn. And the consequences of this withdrawal of selection as regards that particular part, will be to allow the part in a corresponding measure to degenerate through successive generations." Weismann calls this principle

*Nature, XLI, 1889, p. 79.

†Ibid. p. 129.

‡Ibid. p. 437.

Panmixia, but Prof. Romanes terms it Cessation of Selection. The first-named author contends that this cessation of selection is capable of inducing degeneration down to the almost complete disappearance of a rudimentary organ, but Prof. Romanes argues that unless assisted by some other principle it can at most only reduce the degenerating organ to considerably above half or even one quarter its original size; because although no longer sustained by natural selection, it is by heredity, and as long as this force is unimpaired, the withdrawal of selection cannot reduce the organ much below the efficient level above which selection maintained it. But he farther argues that the force of heredity must fail, because a useless organ absorbs nutriment, occupies space, etc., and then natural selection not only ceases, but becomes reversed, and hastens the degeneration of the organ until a point of balance is reached, and the organ being no longer a source of detriment remains as a rudiment, and so it would remain forever if heredity were everlasting, which is not reasonable to suppose, and that the eventual disappearance of the organ would be caused by this failure of heredity. Prof. Weismann at first argued that the degeneration of an organ from disuse could be effected by panmixia alone, until it was reduced to five per cent of its original size, or in his words* "the complete disappearance of a rudimentary organ can only take place by the operation of natural selection; this principle will lead to its elimination, inasmuch as the disappearing structure takes the place and the nutriment of other useful and important organs;" not that the organ is transmitted from parent to offspring in a continued diminished state until it disappears, not from a failure of heredity itself, but by the influence of selection exerting a deteriorating effect. This he modifies, however, in his reply to Prof. Vine's criticism† when he says, "organs in disuse become rudimentary, not through the direct action of disuse, but because natural selection no longer sustains them." Therefore these disused organs which have become 'acquired characters,' transmitted from parent to offspring through undiminished conditions, disappear not through the failure of heredity but by selection withholding its sustaining power, or as Prof. Romanes has argued, acting in an opposite degree.

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*Essays, 2d ed. p. 89.

†Nature, Oct. 24, 1889.

Now what is heredity, how did it originate, and how can it cause individual variability? An explanation cannot be found in the higher organisms, but must be sought for, according to Weismann, in unicellular organisms, or those in which no distinction exists between body and germ-cells; and which reproduced by fission, or division, when the two descendents of an individual are nothing more than the two halves of that individual. It is undisputed and acknowledged* by Weismann, that unicellular organisms are acted upon by external influences, and that these cause variations of size, color, form and number or arrangement of cilia, and these resulting characters are transmitted to the offspring, and he remarks "We are thus driven to the conclusion that the ultimate origin of hereditary individual differences lies in the direct action of external influences upon the organism," and that when individual difference had been attained by unicellular organism, "it necessarily passed over into the higher organisms when they first appeared." Does it not seem reasonable then to suppose that when these latter organisms received these inherited characters, they also obtained the power of transmitting direct adaptations derived from their environment? Regarding the evolution from cells of one kind (Protozoa) to cells of two or more kinds (Metazoa) coöperating in the same organism, Prof. Lloyd Morgan† argues that "Whenever and however this occurred the new phase of developmental reproduction must have had its origin. And if in cell-division there is any continuity of protoplasmic power, the faculty of producing diverse coöperating cells would be transmitted. On any view of the origin of the metazoa, this diverse or developmental reproduction is a new protoplasmic faculty; on any view it must have been transmitted, for otherwise the metazoa would have ceased to exist." But Weismann claims that in multicellular or higher organisms these variations could not originate and be transmitted, and illustrates this by citing* the improbability of a pianist, who by practice had developed the "muscles of his fingers so as to ensure the highest dexterity and power," being able to transmit this power to his offspring, because, according to his view, the effect would be entirely transient, as it would be unable to produce any

*Essays, 2d ed. pp. 285, 286.

†Anim. Life and Intell. p. 143.

change in the molecular structure of the germ-cells, and could not therefore produce any effect upon the offspring. This, however, does not seem to be a proper illustration of the subject, for the son of a pianist, even if capable, might not choose to become a pianist, and although the muscles his parent developed, might, if exercised, easily acquire an equal power to them, more easily probably than the offspring of a parent who had not so developed them, yet if disused they would remain in an only partially develloped condition. Such may also be the answer to the similar illustration of Mr. Dyer,* of the blacksmith and his muscular arms. It does not follow that the son of a blacksmith must, or will, himself be a blacksmith; and until this acquired development has been observed in a line of blacksmiths descending from father to son for generations, it would be impossible to ascertain whether the abnormal muscular development could be transmitted or not. In this connection it may be stated that Mr. Arbuthnot Lane (as quoted by Lloyd Morgan)† has shown that certain occupations, such as shoe-making, coal-heaving, etc., produce recognizable effects upon the skeleton, the muscular system, and other parts of the organization. And he believes that such effects are inherited, being very much more marked in the third generation than they were in the first. And it might also be pointed out that the extreme development of the thigh muscles in the Ostrich is continued from parent to offspring, and although this is now an inherited character through long periods of time, it must have been at one stage of the bird's existence a character acquired from use, and its unusual development began when the wings became modified and its changed habits caused the individual to rely for defence and safety more upon its legs.

We may therefore say with Prof. Eimer that "every character which must have been formed through the activity of the organism, is an acquired character. All characters, therefore, which have been developed by exertion are acquired, and these characters are inherited from generation to generation. The same holds for all organs atrophied through disuse — the degree of atrophy is acquired and inherited. In the first class we see especially the

*Nature, XLI, 1890, p. 247.

†Anim. Life and Intell. p. 169.

‡Organic Evolution, p. 86.

action of direct adaptation, in the second the results of the cessation of this action. A third class of acquired characters is to be traced simply to the immediate action of the environment on the organism, and originally, at the commencement of their appearance, all characters must have belonged to this class."

Let us now consider other characters that are transmitted. Myopia is a deterioration of the powers of the eye, and this has become so prevalent in certain portions of Europe as to be almost a national characteristic. That its effects are and have been transmitted from parent to offspring is undeniable. Natural selection can have had nothing to do with it, otherwise this would be to assert that this principle, in this instance at least, had transmitted a character having an injurious effect, and thus enabling its possessor to be less fitted for the struggle for life, or exactly the opposite of the theory of the survival of the fittest. Weismann attempts* to meet the difficulty of this evident transmission of this acquired character by attributing it to an "accidental disposition on the part of the germ, instead of to the transmission of acquired short-sightedness," or to the "greater variability of the eye, which necessarily results from the cessation of the controlling influence of natural selection," or panmixia. Or, in other words, that some progenitor of these myopic-inflicted generations may have had a congenital disposition to myopia, and have developed weak sight from an original predisposition which he naturally transmitted, not as an acquired character. And again, eyesight in a European, unlike that of a savage, is no longer under the preserving influence of natural selection, and the European, therefore, to make up for this deficiency and render himself the equal of any, uses spectacles. On this explanation Prof. Osborn well remarks† that "the latter example shows how Weismann's followers are put on the defensive when they try to explain the introduction of a new character without the Lamarckian principle, and solely by ingenious application of the Darwinian principle." Another instance of transmission of acquired characters, though perhaps old and often referred to, is that of a puppy, the offspring of parents trained to hunt birds, which, though untrained itself and never having seen other individuals of its species at work in the fields, suddenly stops and, without

*Essays, 2d ed., pp. 90,91.

†Atlantic Monthly, 1891, p. 360.

knowing the effect of a shot, springs forward, barking, to seek for game when the gun is discharged. Weismann endeavors* to explain this by saying that the dog has not inherited from his forefathers a certain association of ideas,—shot and game,—but rather he has inherited a reflex mechanism which impels him to start forward on hearing a report, and that it is not the effects of training, but some predisposition on the part of the germ, which has been increased by artificial selection. But this reasoning, even if capable of proof, which of course it is not, would not explain the fact of a puppy suddenly coming to a stand and remaining motionless in an uncomfortable attitude in the same manner as was the habit of its parent, unless this character of the breed so displayed had been transmitted by its parent. The first pointer undoubtedly possessed the instinct, or inherited the habit of hunting. It is not to be imagined it also possessed the trait of stopping and remaining stationary when it had found the object it sought, for that would have enabled the game to escape, but this additional trait was added by man to utilize and make more efficient its other powers, and assist him in obtaining game, and this habit so acquired by the dog was transmitted to its offspring, and continued by succeeding generations. If this had not been so, each offspring of every parent would have been obliged to acquire the same habit in the same way independently. Prof. Eimer† cites instances of pointer puppies belonging to him, which had never been trained, and never had seen a Partridge, "pointing a covey perfectly correctly, standing motionless with head outstretched, fore paw lifted, and tail stiffly erected." These, he says, "are thorough-bred pointers which require no training at all, but have completely inherited the habits to which their ancestors were educated." He also cites an instance of a *Wildbodenhund*, a dog "used to drive game towards the sportsman by barking." It was about two weeks old when he obtained it, and as soon as it grew up, although it was never taken out shooting, began to drive game on its own account, and in spite of punishment, extended its operations every day. Another instance of acquired characters being transmitted is that of a pure-blooded female pointer or setter which had produced offspring by mating

*Essays, p. 94.

†Organic Evolution, pp. 168, 169.

with a dog of another breed. These puppies would be mongrels showing traits of both parents. Now if this female is again mated with a pure-blooded dog of its own species, the offspring will be pure, but occasionally in some of the litters, it may be years afterwards, there will appear in some of the offspring characters belonging to the breed to which the first dog belonged. These having been received by the female, were retained and transmitted to her offspring, though apparently they may have been dormant for considerable periods of time.

Birds acquire habits not possessed by their parents. I cite an instance. Currituck Sound, in North Carolina, where wild fowl are accustomed to pass the greater portion of the winter, is a great resort of sportsmen, who pursue the birds in every way to accomplish their destruction. This at length was carried to such a degree that the fowl had no place left for them to rest during the day. Some years ago the gunners were surprised to find that whenever the weather permitted, as soon as a gun was fired in the early morning, the birds would rise and betake themselves to the ocean, and remain congregated on the water, just beyond the line of the breakers, and would not return until night closed in. This custom was acquired by birds of succeeding years, until the habit has become apparently established. Now it may be said that this is not an *acquired* habit, but the result of example, the old birds leading the young to the sea. But this would be to assume that the majority of the birds which commenced this habit had survived and returned to this locality every winter. And even if the young, without at first comprehending the reason for so strange a proceeding, merely followed the old birds, is it reasonable to suppose they would remain in such an unusual locality throughout the day, deprived of their food, which could be obtained in profusion on the other side of the narrow beach? It must have been something more powerful than the mere example of the flight of the old birds to the ocean, witnessed by the young for the first time, which compelled them to remain. Can we not more reasonably presume that it was the knowledge acquired by the parents that this was a secure method to escape from a threatened danger, and transmitted to the young who assumed the habit as part of their nature?

Instances of transmission of acquired habits are found in the change of nesting among birds. Geese proverbially make their nests upon the ground, but in certain localities arboreal nidification is adopted. This is witnessed in various parts of the Yellowstone, and upper Missouri regions, as related by Coues,* where the birds build in the heavy timber along the larger streams, and transport their young to the water in their bills, corresponding with the habits of the Wood Duck, some of the Mergansers and other Ducks. This character of change of habits is also exemplified in the Herring Gull (*L. a. smithsonianus*), caused mainly by persecution, and to escape from its enemy, man. Audubon† gives a striking instance of this. On arriving at White Head Island in the Bay of Fundy, he was surprised to see individuals of this species nesting in trees, and the owner of the island, a Mr. Frankland, informed him that this habit had been acquired *within his recollection.* When he first came to the island all the nests were placed on the moss in open ground, but as the eggs were collected for winter use, the old birds began to nest in trees in the thickest part of the woods, and their young followed this habit when their time of breeding arrived. Audubon also states that on neighboring islands to which fishermen and eggers have free access, this Gull breeds altogether on trees, and their original habits have been entirely given up. A remarkable effect of this transmission of an acquired character is that the young hatched in the trees do not leave the nest until they are able to fly, while those hatched in nests on the ground run about in less than a week and conceal themselves at the sight of man among the moss and plants. Some of the nests he saw in the trees were placed at a height of more than forty feet, those in the thickest part of the woods were about ten feet from the ground, and placed close to the stem, and were to be seen with difficulty. The species of the genus *Colaptes* build in holes in trees, either natural cavities, or enlarged to suit their needs. But *C. cafer* is known to breed in the banks of streams, where the absence of trees renders such a proceeding necessary, and like a Kingfisher, readily excavates a burrow. This fact has been observed by Mr. Henshaw‡ in New Mexico and Arizona, and is also mentioned by Dr. J. A. Allen§ as occurring along the Ogden and

*Birds of the North-west, 1874, p. 554.

†B. of Am. Vol. VII, p. 163.

‡Ornith. Wheeler Survey, p. 401.

§Bull. Mus. Comp. Zoöl. III, p. 169.

Weber Rivers in Utah. In the latter instance, it being September, the time for breeding had passed, but the birds were dwelling in the holes, were frequently seen sitting in them, and the author's observations led him to believe they had nested in the holes, there being no trees in the vicinity.

The evidence of variations produced by use and disuse of special organs also tends to confirm our views that acquired characters are transmitted. The modifications of the wing in various families of birds, when through disuse the power of flight has been lost, and this member has become either rudimentary, or else changed both in form and size so as to serve more like a fin, giving its possessor additional powers for the pursuit of its prey under water, are numerous; and to attribute these modifications to the principle of selection, or predisposition of the germ and to deny that use or disuse has produced hereditary effects, as Prof. Weismann asserts,* is to argue from a mere assumption that lacks evidence to establish even its probability.

Migration preserves a species true to its type, in that migratory birds keep together in flocks, and select localities in which to remain, having similar environments to those where they were reared. But if a species ceases to migrate for any cause and remains isolated in its habitat, then differentiation occurs, and the variations that appear are reproduced in their offspring. Thus it may not be supposed that the Great Auk was always incapable of flight, but that it migrated, even if only to a limited extent, while its wings were fully developed. This is a reasonable supposition, because all its relatives, the Divers and Auks, are birds of great wing-power and migrate at the present time. From some cause, unknown to us, but possibly from its ability to procure food throughout the year in the region it inhabited, it gradually ceased to migrate, and its wanderings becoming less and less, its wings were employed chiefly under water in pursuit of its natural food. The wings therefore being used in a different manner from that when the bird was flying, would be modified and reduced in size until they reached the form and dimensions most suited to assist the species in swimming beneath the surface, but which in their reduced condition rendered flight no longer possible. These modifications were transmitted to its offspring, rather, we would

*Essays, p. 92.

suppose, from the production of hereditary effects than to a predisposition of the germ, or selection, for there is no reason to suppose that this especial species of Auk, the largest and most powerful of the family, should have been in any way more predisposed to a degeneration of any of its organs than were any of its relatives, which have not degenerated, and which from their structure were no better fitted for the struggle for existence.

The Ostrich probably has descended from ancestors capable of flight, but they, we may suppose, did not possess so great a stature because a bird of that size would require such an expansion of wing that it hardly would be available to any creature other than a pelagic species. This ancestor was also a ground-feeding bird, and it is to be supposed that from physical changes occurring in its habitat it was obliged to rely more upon its legs than on its wings in order to procure a sufficiency of food, or escape from its enemies. Then the wings became reduced in size and the thighs correspondingly increased, and the legs not only were a means to enable the bird to travel with great swiftness, but also became a powerful weapon of offence or defence. Although the Ostrich is unable to fly at the present day, yet the manner in which it uses its wings when running, elevating them, and keeping them stationary as a bird does when sailing in the air, may be regarded as a trait derived from its flying ancestor, the only one appertaining to flight which its rudimentary wing permits it to retain.

I have by no means exhausted the evidence derived from birds, which strengthen us in the belief that acquired characters may be inherited; and I think the majority of ornithologists will agree with Prof. Lloyd Morgan* when he says: "I confess when I look round upon the varied habits of birds and mammals, when I see the Frigate Bird robbing the Fish Hawk of the prey that it has captured from the sea, the bald-headed chimpanzee adopting a diet of small birds, a *Semnopithecus* in the Mergui Archipelago eating crustacea and mollusca, and the Koypu, a rodent, living on shell fish; when I consider the divergence of habits in almost every group of organisms, the Ground Pigeons, Rock Pigeons and Wood Pigeons, seed-eating Pigeons and fruit-eating Pigeons; the carrion-eating, insect-eating, and fruit-eating Crows, the aquatic and terrestrial Kingfishers, some living on fish, some on

*Anim. Life and Intell. p. 446.

insects, some on reptiles; the divergent habits of the Ring Ouzel and the Water Ouzel; and the peculiar habits of blood sucking bats; — when I see these and a thousand other modifications and divergences of habit, I question whether the theory that they have all arisen through the elimination of those forms which failed to possess them may not be pushed too far; I am inclined to believe that the inheritance of acquired modifications has been a coöperating factor. It is not enough to say that these habits are all useful to their possessors. *It has to be shown that they are of elimination value* — that their possession or non-possession has made all the difference between survival and elimination."

Other branches of zoölogy also afford striking evidences of this transmission difficult to explain away. Moritz Wagner has shown that a species of *Saturnia*, transferred from Texas to Switzerland acquired new characters and transmitted them to its offspring of the first generation. A number of pupæ were brought over, and the moths developed out of the coccoons exactly resembled the Texan species. Their young were fed on leaves of *Juglans regia*, and the moths were different, both in form and color, and were considered by entomologists as a distinct species. The polymorphic snail *Helix nemoralis*, was introduced from Europe into Lexington, Virginia, a few years ago. Under its new conditions it varied to a greater extent than it had been known to do elsewhere, and one hundred and twenty-five varieties have been observed, of which no less than sixty-seven are new or unknown in Europe, its native country.*

The shrimp *Artemia salina* lives in brackish water, and the *A. milhausenii* in water much salter. By altering gradually the saltness of the water, either of them can be transformed intc the other in the course of a few generations, and the change of form is maintained, the altered conditions remaining the same.†

Vertebrate paleontology furnishes evidences that acquired characters are transmitted, and that the majority of these occur alone from use and disuse, and Weismann argues that these variations are quantitative, and are acted upon by natural selection. But in tooth evolution, as pointed out by Prof. Osborne,‡ there are ex-

*Cockerell, Nature, Feb. 27, 1890.

†Lloyd Morgan, after Schmankewitsch, Anim. Life and Intell. p. 164.

‡Am. Nat. 1891, p. 16.; ibid. Nature, XLI, 1890, p. 227.

amples that are qualitative, or "rise of structures that are essentially new, and not simple modifications of pre-existing forms."

One of them is the addition of new cusps, which do not rise at random points and disappear, but successive cusps are added to the simple conical crown at the point of the maximum wear. There are rare exceptions to this fact, however, which will require subsequent research to explain whether or not they are in conformity with the laws of individual adaptation. A very striking instance of the effects of use and disuse is cited also by Prof. Osborne* derived from the ancient pedigree of the American horse, where we are (to use the Professor's words) in before the birth, so to speak, and the modifications in the leg from the four-toed *Hyracotherium* to the eocene *Mesohippus* were caused, as proved by various investigators including himself, by the strain arising each time the foot was placed upon the ground producing infinitesimal alterations in all the bones of the leg, and "during the early geological periods these strains were constantly changing *pari passu*, with the gradual decrease of the lateral, and increase of the central digits." And in view of this evidence we may all say with the writer of the article from which I have quoted that "it is hard to believe with the new school, these invariable sequences of race adaptation on individual adaptation are not instances of cause and effect. If they are, they afford absolute proof of the transmission of acquired characters. If not, all our pains-taking researches and vast literature lead to no result."

I have thus as briefly as possible, though fully conscious of having occupied more time than I ought, brought this extremely important subject before you for your earnest consideration. It will be readily perceived that I have merely touched upon a few of the points that would naturally arise for discussion, in connection with the transmission of acquired characters but my object, in drawing your attention more particularly to this question, is to excite your interest, in the hope that by your own individual investigations and experiments you may be able to throw some light on so much that now is obscure and impossible of explanation. We none of us have the temerity, I trust, to say with a distinguished botanist† that "the questions at issue with regard to evolution are now thoroughly understood by biologists," but

*Atlantic Monthly, 1891, p. 362.

†Dyer, Nature, XLI, 1890, p. 315.

rather approach our task with a full appreciation of its enormous difficulties, and in the words of the Duke of Argyll* "conscious above all thing of the ignorance of man." The subject I have discussed offers a new field for ornithologists to explore, one of a higher plane, and permitting a wider vision than many of those they are accustomed to tread. I submit it to my younger colleagues, who have time and opportunities before them, as of infinitely more importance than the discovery and naming of new forms, which is by no means the beginning and end of ornithology, but rather, if I may so term it, the A B C of the science; and then by their contributions towards the elucidation of my theme, they will benefit not only those who are devoted to our own branch but also all scientific men throughout the world.

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*Nature, XLI, 1890, p. 367.