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THEORIES OF EVOLUTION.

By EDWARD B. POULTON.

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In dealing with theories of evolution, I think that we shall all be agreed that we may leave out of consideration the question of the origin of life, and deal only with what has happened to life after its appearance, however that may have taken place. On this subject we shall probably most of us still agree with the opinion of Darwin[2], that we are not in a position to even speculate or think upon that question, — that any speculation about it is almost a waste of time. And this, I think, remains true in spite of the magnificent results of the organic chemists in producing chemical bodies by synthesis, which before had been regarded

[1] Read February 7, 1894.

[2] In Life and letters.

as capable of being made only in the laboratory of the living body. Many of these can now certainly be produced, but that is very different indeed from creating protoplasm endowed with life; and so far are we from achieving this by any chemical means, that I think we may venture to dismiss all consideration of the ultimate origin of life.

But granting the origin of living matter, these theories of evolution which we are considering and hope to discuss to-night can deal with it, and with their help we believe that we can account for what has subsequently happened; namely, the evolution of all forms of life, animal and vegetable, upon the surface of the earth.

The first of these theories which I propose to discuss is the well-known Darwin-Wallace theory of natural selection, with its three factors.

First, individual variation, — the fact that individuals differ, and that the differences are essential or inherent in the organism, so that even if animals were brought up alike, we know they would still be unlike, and so that, however much the offspring may resemble their parents, they are never exactly like their parents or exactly like each other. There is, then, first, individual difference, one of the most essential facts in the organism.

Secondly, the fact of heredity,— the fact that these inherent differences may be and are inherited. Although the hereditary transmission of acquired differences is disputed, the transmission of those that are inherent is certain. This stands before us as one of the most obvious and certain of conclusions, equally proved by the observation and experience of every one of us.

Thirdly, the fact that there must be a struggle for existence; that there are far more individuals born into the world in every species, even the most slowly increasing, than can possibly survive and reproduce.

These three factors must by logical necessity lead to a survival of the fittest among individual variations. It does not require a scientific mind to comprehend that, — to infer that some amount of evolution must ensue from the co-operation of those three factors, every one of which stands firm and undisputed. Among all the advocates of rival theories which have been brought forward to explain evolution, no one has ever ventured to attempt to disprove any one of these three factors. They stand unchallenged.

The politician, Henry Fawcett, saw, long before scientific people themselves understood what Darwin meant by natural selection, that logically some result must ensue from such co-operation. Fawcett said that natural selection must produce evolution as surely as a round stone will roll further than a square one. Some measure of evolution is simply the logical result of the co-operation of these three undisputed, abundantly proved factors.

Now, some writers have thought to undermine the theory of natural selection by arguing that the important and essential factor of individual variation is not explained by the theory which rests upon it. True, it is not; but for the theory of natural selection, the explanation does not signify. So long as individual variation is present, so long as it is hereditary, it does not signify how it is produced. There are, indeed, many theories professing to account for it; but biologists are not generally agreed as to the manner in which it is produced. But so long as it is there, it is available, and natural selection can make use of it.

It is interesting to note that, when Newton discovered the principle of universal gravitation, some people maintained that he had discovered nothing because he had not explained what gravity itself was. Now after two hundred years we can safely assert that universal gravitation stands out as one of the most triumphant discoveries of the human intellect; and yet we, even now, are just as much in the dark as to what gravitation itself is as when Newton wrote. Exactly so it is with regard to individual variation. So long as it is a fact essential to organic nature, that one individual must be different from another, and so long as these differences are hereditary, so long may natural selection have abundant material for its work, even though it is unable to explain how that individual difference is produced. I am very far from undervaluing the interest of such an explanation; on the contrary, I maintain that it forms one of the most interesting of biological problems now before the scientific world, or likely to be before it for many a day.

In fact, every successful attempt at scientific explanation only interprets down to a certain level of causation; and this is just as true of universal gravitation and natural selection as it is of smaller efforts. Down to a certain level of causation, natural selection explains at any rate some part of organic evolution. A more fundamental level would be to explain the factors upon

which natural selection itself depends; but because we have not yet reached that lower level, we have no reason for doubting, as some would believe, the complete efficiency, at its own level, of the explanation we do happily possess.

The theory which stands in contrast with natural selection, and which has been here supported more fully than in any other civilized country, with the exception of France, is the theory we usually attribute to Lamarck. Erasmus Darwin in England, however, has the priority, in that he first brought forward the principles which Lamarck more effectively supported. But to Herbert Spencer belongs the chief credit, because he has taken that part of the earlier theory which is acceptable to modern biological thought, and upon this basis has formed his great theory of evolution.

Lamarck believed in an innate tendency toward perfection in animals. Now, that is a view which very few zoologists at the present time, if any, would dare to sustain. In fact, an evolution due to an innate principle of perfection is not very much removed from the doctrine of special creation which preceded any theory of evolution. Herbert Spencer, therefore, rejecting all those elements of Lamarck, which the scientific world could not possibly accept, has taken that which has commended itself to science, and upon it has formed his great theory of evolution; so that the Lamarckian theory, as presented to the world to-day, comes before it in Spencerian language and in the closest relation to Spencerian thought. In saying this, however, I do not by any means intend to be understood as supporting Spencer's theories or the views upon which he bases them.

The Lamarckian theory, then, upon which Spencer has based his philosophy, is a theory of evolution dependent, not like natural selection upon three factors, but upon two. It depends first of all upon the effect wrought on the individual by that which happens during its lifetime. Instead of depending on those innate and essential differences upon which natural selection rests, this theory depends on those changes which are caused during the life of the individual,—the action of some external force upon it, the effect of its own will, the changes produced by the use and disuse of its own parts. The Lamarckian theory depends in fact on all those changes in an individual which we now call its acquired characters; that is, characters which the individual has

come to possess but which were not potentially present at the beginning of its separate life.

The first factor, therefore, is made up by changes that are wrought in this way. The second factor is heredity, by which it is supposed that these changes are transmitted; and it is certainly true that if such transmission is possible, some amount of evolution must result. You will all be prepared to admit that if these two factors represent facts, their co-operation must produce some amount of evolution.

It is important to remember, however, that both factors are not undisputed, as are the three factors of Darwinian evolution. Although we all admit the existence of acquired characters as the effect of external causes upon the individual during its life, yet biologists are by no means agreed that these effects are hereditary, and, if not, the acquired character ends with the individual in which it arose, and, not being handed on, can never become a character of the species. It is impossible for those who hold the Lamarckian or Spencerian view to escape from this. If it is true that such characters are transmitted, then the foundation of the theory is secure; but the transmission of acquired characters is by no means proved. Herbert Spencer has preferred to occupy himself in rearing a magnificent edifice upon this foundation, rather than employ his acute intellect in testing its firmness and security in every possible way.

So far as observation goes, all those characters which are believed by many to owe their origin to the Lamarckian principle, are present in the individual before the beginning of its active life, before the operation of those causes which were believed originally to account for the characters. According to the Lamarckian theory such characters have already become hereditary; and therefore it is of essential importance to the Lamarckian to prove that acquired modifications can be and are transmitted. Only in this way can he give good grounds for the opinion that such characters, when they occur ready-made in the individual, are to be explained by the action of external causes during the lives of ancestors.

These are the two main theories of evolution. There are several others, upon which I will dwell only for a moment because these two alone command any very large amount of attention at the present time.

In the first place, Lamarck's theory of the innate tendency towards progressive perfection in animals is not held in exactly that form, but some zoologists in this and other countries believe that they see evidence in the rise and fall of certain groups of fossil animals for the existence of a tendency towards extinction, or a tendency towards sudden growth, which lies within the animal itself and is not determined by any external cause. That is a very close approach to Lamarck's original principle of an innate tendency in one direction or another. I will not discuss it at any length, because I think that this evening if we get some idea and have some discussion on the merits of the two main theories of evolution, that will be as much as we can expect. I will only say with regard to the subject that arguments based upon fossil remains are apt to be somewhat dangerous, because we have, at least so far as the conditions of life are concerned, so small an amount of evidence. In certain parts of Africa, for instance, the presence of the tse-tse fly absolutely limits the existence of some of the larger quadrupeds. Wherever that fly is, the animal cannot exist. It is very possible that in future times skeletons will be found in specially large numbers on the borders of districts where the fly abounded, and any attempt to argue, from the appearance of the skeletons themselves, as to the causes of this great extinction will obviously be entirely false and misleading. We have in the skeleton of an animal so small an indication of the events of its life and the conditions of its death, that it is, except in very rare cases, most unsafe to argue as to the causes of its extinction.

Another theory of evolution is one which has been brought forward by Professor Geddes of Scotland. He believes that there is an innate tendency towards growth and towards that dissipation of matter which constitutes its reverse, — the anabolic and katabolic tendencies, as he calls them. But that view, although he argues it with much eloquence, has not been widely accepted, and I think it will be generally admitted that it does not yet rest on sufficient proof.

In addition to these, there are some who maintain the position that there is an unknown cause of evolution. They believe that these theories, although one or more of them may be of value, are yet insufficient to account for organic evolution. Those who take this line are of course logically bound to bring forward the

classes of facts with which no existing theory is, as they maintain, competent to deal.

All we shall have time for to-night is briefly to compare natural selection, the Darwinian interpretation of evolution, with the Lamarckian theory. It is interesting to note that, although they are so essentially distinct one from another, in earlier times these two theories appear to have been entirely confused. Lamarckian evolution, Spencerian evolution, appeals to the mind of man far more strongly than Darwinian evolution. Any one of us, were we to have created the organic world, would certainly have created it according to Lamarck. We should have made evolution by use and disuse of parts, and not by natural selection. However, we are not concerned with the sort of world that we should have created. The question before us as scientific men is not what might have happened, but what has happened. Nature, as I have heard Prof. Michael Foster say, has a very queer way of going by roundabout paths and refusing to take the roads we should lay out for her ourselves, and which we look upon as the most direct and obvious. The fact that the general aspect of the Lamarckian theory commends itself to the human mind affords no reason for looking upon it as the correct one, as opposed to the Darwinian theory.

The Duke of Argyle, who is still strongly antagonistic to natural selection, a few years ago wrote an article in the Nineteenth century called "The power of loose analogy." By this title he intended to imply that those who believe in natural selection have been led away by the specious character of the words themselves. I suppose that the Duke feels himself bound to account in some way or other for the fact that people believe in natural selection, while he does not, and accordingly he suggests that the seductive power of the title employed by Darwin has misled the scientific mind into a belief in the process itself, — only rare and subtle intellects like his own being proof against such an allurement. *Natural:* a word expressive of familiar objects and processes always around us. *Selection:* a process with which we are all familiar. In this way it seems reasonable to the Duke of Argyle to suppose that men have been misled by the seductive nature of the terms employed by Darwin. The terms applied to processes familiar to every one, and therefore every one accepted them at once, without inquiring what they

really meant. This is, of course, an explanation eminently satisfactory to the single writer who was not to be convinced by "the power of loose analogy." But when we proceed to test this ingenious suggestion, and look into the history of the times to which it applies, when we read Darwin's letters, we find that he continually complains that people do not understand what he means by natural selection, and he almost regrets having used these words. He says more than once that he wishes he had used Herbert Spencer's term, the survival of the fittest, because his own title, natural selection, is comprehended with such difficulty.

When we look to another class of evidence we find equally sure ground for the conviction that natural selection was driven into men's minds with the very greatest difficulty, and by no means with the ease which the Duke of Argyle assumes. It is very interesting to consult the various skits written between twenty and thirty years ago, and in which the writers supposed that they were making fun of Darwin's theory. If you will read them, you will be struck by one very remarkable fact: their authors are all making fun of Lamarck when they believe they are making fun of Darwin.

I remember once seeing a picture in Punch, representing the evolution of the power of flight by the human species. It represented a man standing upon the roof of a house and waving his hands, which, in consequence of the use to which they were put during his individual life, grew somewhat in size. Passing down to the next generation, his son was found waving rather larger hands, and the waving made them still larger. In the course of generations the descendants acquired large wings and flew down from the roof of the house. That was supposed to be a parody on evolution according to Darwin. I have called it a skit, but you will see at once that you cannot get a better illustration of Lamarckism. It *is* Lamarckism. It is not making fun of it; it is a description of the process itself.

Then Lord Neaves wrote a song in which he attempted to make great fun of Darwin's theory. It was a very long song, many verses of which were skits upon Lamarck, while supposed to be skits upon Darwin.

> "A deer with a neck that was longer by half
> Than the rest of its family's — try not to laugh —
> By stretching and stretching became a giraffe,
> Which nobody can deny."

This is pure Lamarckism. The evolution was supposed to be caused by stretching without any selection at all.

The best example of all, however, is given by Mr. Courthope, in his "Paradise of birds." I commend his account of the evolution of birds and mammals to those who believe the Lamarckian theory. He tells us there about the Ornithorhynchus, which he commends as a very prudent beast:—

"For he saw in the distance the strife for existence,
That should his grandchildren betide,
And resolved, as he could, for their ultimate good,
A remedy sure to provide;
With that, to prepare each descendant and heir
For a separate diet and clime,
He laid, as a test, four eggs in his nest,
But he only laid two at a time.
On the first he sat still, and kept using his bill,
That the head in his chicks might prevail;
E'er he hatched the next young, head downwards he slung
From the branches, to lengthen his tail.
Conceive how he watched till his chickens were hatched,
With what joy he perceived that each brood
Were unlike at the start, had their dwellings apart,
With distinct adaptations for food.
From the bill, in brief words, were developed the birds,
Unless the tame pigeons and ducks lie;
From the tail and hind legs in the second-laid eggs,
The apes and—Prof. Huxley."

If we now turn to the skits on evolution written at the present day we find they are very different. Miss May Kendall, in writing her "Ballad of the Ichthyosaurus," only a few years ago, says:—

"E'er man was developed, our brother,
We swam and we ducked and we dived,
And we dined as a rule on each other;
What matter? The toughest survived."

This is true natural selection. The authoress understood what she was talking about. And even long ago, at the time when those mistaken parodies were written, intended for Darwin and really applying to Lamarck, we find an acute mind like that of James Russell Lowell, in the Biglow papers, making fun of Darwinian evolution:—

"Some flossifers think thet a fakkilty's granted
The minnit it's proved to be thoroughly wanted,
Thet a change o' demand makes a change o' condition,
An' thet everythin' 's nothin' except by position;
Ez, fer instance, thet rubber-trees fust begun bearin'
Wen p'litikle conshunces come into wearin',
Thet the fears of a monkey, whose holt chanced to fail,
Drawed the vertibry out to a prehensile tail."

That is a most ingenious and interesting parody, making the theory of natural selection apply to the individual instead of to the species. The writer pretends to suppose that a quality is gained in the course of the individual life, because of the individual need; whereas under natural selection it is gained in the course of many generations by a need which is imperative enough to cause the extinction of individuals without the quality, or with it in a comparatively slight degree.

Another interesting question has been raised by Mr. Lloyd Morgan, as to whether the phrase "natural elimination" would not be a more correct one than "natural selection." The process is, of course, selection by and through elimination. The survival of the fittest means the elimination of the unfittest.

The relation between selection and elimination has been put in a very striking way by Mr. Samuel Butler, who says that according to natural selection we are what we are, not by the successes of our fathers and mothers, but by the failures of our uncles and aunts. The question is, shall we dignify with the title of this important cause of evolution those who have failed in the struggle, and do not happen to be the ancestors of any living species, or those who have succeeded in the struggle and are now abundantly represented by descendants? I think that "natural selection" forms on the whole the best term for the process. It has the advantage, also, of being the historic term proposed by Darwin.

Another important point in favor of "natural selection" as a term, is that it suggests a parallelism or comparison with the process of artificial selection. Yet another point is the fact that you may find in the words themselves all the three factors obviously suggested; for selection would be impossible without individual difference, and it would be useless unless these differences were hereditary; and, furthermore, selection implies something which selects; that is to say, the conditions of nature,

the rate of increase with its result, the struggle for existence. So that the three factors of natural selection are implied by the very words themselves.

Now I want very briefly to bring forward the chief objections that have been urged against natural selection. In the first place, if natural selection be true, all the varied characters of animals and plants must prove to be useful to the possessor in the struggle, or to have been useful at some time in its history.

We are only required, however, to prove utility as regards undoubted characters of the species, and these are hereditary, and we must put on one side certain characters which are confined to the individual in which they appear. For instance, if it were proved that the Mollusca of any one river differed from those of the same species in another river, but that the differences were confined to the individuals in which they occurred, so that if these Mollusca were placed when young in the second river, they would come to resemble those which were proper to it, then we should not be concerned with characters of the species at all. The language spoken by a nation similarly is not a character of the human species, for we know that a child of another nation would acquire it perfectly together with the particular modes of thought and expression tortuous or direct which are associated with it. These results of environment are not characters of the human species. The individuals of the human species come into the world with a certain elasticity, a certain power of being developed in various directions. But although the elasticity itself is a character of the species, and is inherent, the particular quality in which it may result when operated upon is certainly not a specific character.

The more we work on the characters of animals in general, even though we at first can see no utility, the more we come to admit this principle, and to believe that either now or in some past time, the characters have been useful. I can certainly say of many characters which I have studied in some of my investigations, that at first they seemed to be meaningless, but afterwards appeared to be of much importance in the struggle for existence. I think we may safely assume with regard to many characters of which we can now see no explanation that by and by the explanation will be forthcoming.

Being unable to prove utility does not invalidate natural selection. If inutility could be proved for any large class of characters, the theory would certainly be destroyed as a wide-reaching and significant process. I do not think, however, that any such evidence has been forthcoming. I shall be interested in the discussion which follows this paper to hear whether those who believe in the Lamarckian theory have any such evidence to produce, whether they can prove that any one great class of characters has been useless in the past and remains useless in the present.

Another class of objection has been urged long ago, and is still urged to-day. Why do we not find in the paleontological series the records of failures? Now, as regards the individuals of a species we cannot expect to find any such evidence. What is failure? Failure means, according to natural selection, the failure to produce offspring. The individual which comes into the world and dies young has failed. The individual which is represented in the generations of the future has succeeded. Natural selection has set its stamp upon that individual. But it is impossible to say whether or not this is true of any particular fossil. We have not got the facts before us by which we can form any conclusions.

Furthermore, we know the struggle for existence is excessively complicated. The skeleton *alone*, though of the highest value in association with the rest of the organism, has been the turning point in the struggle in a comparatively small number of cases. When it has been the turning point in association with other parts, these latter are absent. We have only a very small part of the problem before us, and never can expect any more.

But while we cannot expect to find evidence of the survival of the fittest among the individuals of a species, we may expect to find it in the supplanting of classes by classes, of groups of species by groups of species. Some of the facts which have been brought forward as evidence in this direction do, to my mind, very strongly support the theory of natural selection by paleontological evidence. Consider especially the case of the large mammals preceding those which gave rise to the quadrupeds now upon the earth. So far as we can judge of these huge forms by their skeletons, they appear to have possessed a bodily structure as well fitted to survive as that of many now living in the world;

but they differed from these latter in that they had extremely small brains. We can easily understand that inferiority of intellect would cause them to be worsted by animals which were in other respects no better endowed.

Exactly parallel is the relation of man and the apes. In bodily structure the difference is insignificant. In the brain, however, we meet an important and essential distinction. It would appear here that natural selection has taken one particular part of the organism of paramount importance in the struggle, and has developed that rather than made a change along the whole line.

We see the same relationship in the gigantic reptiles of the secondary period as compared with the mammals of the Tertiary. The latter with their larger brains and higher intelligence were able to supplant the former, just as they have in turn been supplanted by the still larger brained animals whose descendants now people the earth. All this seems to me to afford very strong support to the theory of natural selection.

Passing now to another class of objections: natural selection, it is said, can never account for the beginnings of things. Until an organ is raised to a useful level, selection can have nothing to do with it. At first sight that is a serious objection, but it suggests its own answer; viz., that an organ so rarely develops *ab initio*. Organs are not formed anew in an animal, but they are formed by the modification of pre-existing organs; so that, instead of having one beginning for each organ, we have to push the beginning further and further back, and find that a single origin accounts for several successive organs, or at any rate several functions instead of one.

The typical vertebrate has four limbs. These in fishes are used for swimming, while in terrestrial forms the same limbs are modified and used for walking. New organs are not introduced, but the old are modified for a new purpose. When the terrestrial form again becomes aquatic, the limb that was used for terrestrial progression is modified back into a functional fin; and again, when flight becomes necessary, the same organ is used for the new function. So that whatever the changes in the mode of progression, we need no new organ at all; for the old organ is used for the new purpose. It is very much easier to understand how a useful level can be attained in that way than by organs starting *ab initio*. But of course we must come down to a true

beginning if we push our inquiries far enough. In attempting this, we are carried to those remote times in which the ancestors of vertebrates arose. Upon these forms we can do no more than speculate, but it is at any rate impossible to prove that four bud-like projections from the body may not have been useful, from their very beginning, to a slender worm-like animal in pushing its way through mud or thick weeds. Dr. E. B. Tylor has told me that he believes that the same thing holds with regard to human weapons. He said that, in examining ancient weapons, he was often struck with the fact that a weapon or implement had ultimately turned out to be so very much more useful for a new purpose rather than that for which it was originally formed. Here, then, one origin apparently accounts for several forms of implement.

Another objection raised against natural selection is that a selective cause is never a true cause. Professor Cope means to imply that when he speaks of the "*Origin* of the fittest." But Darwin's argument on this point is perfectly sufficient. He says that when a man drops iron into sulphuric acid, he does not originate the chemical force that operates, but he may be fairly said to make sulphate of iron. So natural selection does not itself originate the factors upon which it depends, but it is so essential to the result that it may be fairly looked upon as the true cause (at that level of causation). In Galton's work we have a most complete inquiry into human variation and its inheritance, and he shows us that such variation by itself, unguided by selection, can never advance to anything. Even if you start with ancestors who are remarkable for any intellectual or structural feature, their descendants, although some of them may partake of their parents' peculiarities, sometimes even to an increased extent, will ultimately return to the pattern of the race. There is always a "recession towards mediocrity." Hence, unguided variation can never explain the "origin of the fittest." Such a view is entirely contradicted by the results of Galton's researches. Any marked change in the direction of fitness can only become a character of the species by accumulation through many generations, and this can only take place by natural selection. Variation unguided by selection can never advance on the increase of fitness present among the individuals of a single generation; and even these improvements, if relatively marked, can never become

a character of the species without selection, but by recession will tend to be lost in the subsequent generations.

I have briefly touched on some of the chief difficulties which are advanced against natural selection. I now propose to devote the remaining part of my time to the difficulties which seem to me to apply to the Lamarckian theory.

Lamarckian evolution, as I have mentioned before, depends upon acquired characters. A good deal of misconception has arisen from this use of the word "acquired." An acquired character has sometimes been interpreted to mean any character that an animal has come to possess; hence, inherent and acquired characters have been confused. The word "acquired," as used by biologists, must be understood to have a limited and special application, meaning only those characters which have been produced in the organism by the incidence of external forces, or by the action of its own forces, use and disuse of parts, and so on, during its life. Weismann has suggested the term "blastogenic" for characters potentially present in the germ at the very beginning of life, and "somatogenic" for those which appear afterwards and are not potentially present in the germ. Here blastogenic is the equivalent of inherent, and somatogenic of acquired.

Some years ago I suggested that the terms "centripetal" and "centrifugal" might be employed to express this acquired difference, acquired characters being centripetal, because they are impressed upon the body or one of its parts from without; inherent characters being centrifugal, because, arising from within, due to the essential nature of the organism itself, in the course of development they come to appear, as it were, on the surface as visible features.

When we now consider the transmission of acquired characters, upon which the Lamarckian theory certainly depends, we are led first of all to inquire whether it is possible to frame a theory of heredity within which such transmission can be included. If, for instance, there is a change in the brain of an animal, owing to the exercise of some part of it, how can such a change in the brain-cell be transferred to the germ-cells of the animal, so as to be transmitted to its offspring? It may be objected, if you can prove that such transmission does take place it is no matter how it takes place. Quite true, if the evidence is sufficient and indisputable. But we must remember that the amount of evi-

dence required in order that there may be sufficient, depends upon the probability or improbability of the thing to be proved. This view is extremely well put by Professor Huxley in his memoir of Hume, where he says that if any one came to him and stated that he had seen a piebald horse in Piccadilly he would be prepared to believe it; that he might require confirmatory evidence if the statement were that a zebra had been seen; but that if even the friend in whom he trusted told him he had seen a centaur trotting down that eminent thoroughfare, he should emphatically disbelieve it, and that nothing short of a monograph on the anatomy of the centaur by a comparative anatomist of the stamp of Johannes Müller would convince him that the observation was correct. We are compelled to admit that the amount of evidence we require does to a great extent depend upon the inherent probability or improbability of the conclusion to be sustained. If it appears to us to be almost impossible to conceive of a mechanism whereby an acquired character can be transmitted from the outlying parts of the organism to its germ-cells, then we have every reason for scrutinizing most carefully any evidence that is alleged to prove such transmission.

Let me first of all give you a concrete example which is frequently brought forward by those who believe in the Lamarckian theory in this country, and have chiefly studied the skeletons of Mammalia. They say the joint of an animal possesses just the sort of shape that would be produced by the motion of the joint itself, and they urge that the joint as we see it has arisen from the hereditary effects of that motion. They look upon this as a very satisfactory explanation, because they consider it to be so obvious and fundamental. You do not require anything further, selection is unnecessary and even the individual variation—so mysterious a factor of the Darwinian theory—is here entirely explained.

But is the interpretation valid? In the first place, it is clear that such an hypothesis can never afford a wide or general explanation. There are a great many parts of the animal body which are not modified in their use. You cannot thus explain the growth of hair, or the color upon the surface of the organism. For these and other useful but passive structures, the Lamarckian interpretation will not hold at all. Hence we may divide the organism into two sections, to one of which the Lamarckian

theory might be held to apply, and to the other the Darwinian alone.

But upholders of the Darwinian theory consider that it applies to the other section as well. They point out, that while the form of the joint is the sort of form that would be produced by the motion, such a form is the only one which admits of convenient motion, that motion has been essential to the life of the organism, that alert and rapid movements have been a necessity in the struggle for existence, and that any form which would prevent or clog the movements would be at once destroyed by the operation of natural selection. Natural selection they hold to be competent to explain these parts which the Lamarckians also claim to explain, while it offers the only explanation of the other parts.

If we suppose that Lamarckian evolution in part explains the actively used organs, and Darwinian evolution in part, we should expect that modification would take place more quickly in that section of the organism where the two principles were at work than in the other section where only one principle—the Darwinian—can play a part. But there is no evidence of such especially rapid evolution. It seems to me that we are in a position to use the old principle of cutting off superfluous causes. No unnecessary cause should ever be introduced into an explanation, and if Lamarckism, untenable in the one section, is superfluous in the other, it should be removed, unless there is very clear evidence proving that it has been at work.

Furthermore, in certain cases, such as the protective attitudes and appearances assumed by many animals, we meet with clear evidence that the two kinds of parts—those that are effected by their use and those that are not affected—have undergone development together, suggesting strongly that their evolution has been under the direction of one set of forces, and not of two sets which have little in common.

Having now brought forward certain general objections to the Lamarckian position, let me take exception to one or two special cases.

Certain animals, such as lobsters and crabs, have the power of very readily parting with some of the most important of their members. The large claws are easily thrown off, and this may be of great advantage in the struggle of life, because when an

individual is attacked by an enemy and seized by the claw, it has a chance of escaping. In the case of the lobster, the dismembered claw may not let go of the enemy although the enemy may let go of the claw. The claw may take charge of the enemy while the lobster escapes.

Now that is a very interesting adaptation. We find the claw so formed that it can be thrown off, but even when thrown off it continues to be of much use to the organism. Its nervous and muscular mechanism is so arranged that mutilation actually stimulates it to contract, and it continues to hold the enemy. In the case of certain crabs, the dismembered claws keep snapping and jumping about. The same is true of the tails of many lizards, which, when thrown off, will jump about in the most active way, distracting the attention of the enemy, while the lizard makes its escape. Here, too, mutilation stimulates the nervous and muscular mechanism in tail and claw.

In these cases of actively used parts of the organism the Lamarckian interpretation is absolutely at fault. You cannot apply it. It is impossible to explain upon the theory of the transmitted effects of use and disuse. No activity manifested by the tail after it has ceased to be part of the lizard can ever be transmitted. Not only that, but all development undergone by the tail from the effects of use and disuse, etc., up to the time of its severance, is also lost to the individual, and cannot be hereditary. And so with the claw. The large claw is the most important appendage of the lobster, and yet it is probable that most lobsters lose it many times and grow a new one. We have here a very specialized organ with very remarkable functions continuing in ever an increased degree after severance from the animal; all this is readily explained by the Darwinian theory, but cannot be explained by the Lamarckian.

The same inadequacy of the Lamarckian theory is forced upon us when we look a little more deeply into the nature of the process which is supposed to occur. The Lamarckians attempt to explain joints and some other structures by the effects of stress and pressure, but when we look into the matter a little, we find that the explanation is not so complete as it is supposed to be.

For instance, it has been believed in this country by many distinguished biologists that the complex shape of mammalian teeth is due to pressure produced by mastication. As the pressure

has been applied to the tooth, so has the tooth grown. But would pressure produce such an effect upon a tooth? That is certainly not our experience. Pressure and friction have an unfortunate way of wearing a hole in the tooth, rather than causing it to grow an elevation. As a matter of fact we know that the shape of teeth is predetermined long before they are cut in the soft dental matrix beneath the gum. It is not a question of the transmission of acquired characters, but the supposed transmission of a character which the parent cannot by any means acquire. Teeth, so far as they react to pressure or friction can only react by wearing away. With regard to the joint, we are told by some Lamarckian writers, that pressure and friction produce the reverse effect and wear away cavities rather than cause new growth.

I was reading a most interesting paper by Dr. Wortman of New York, the other day, attempting to explain the occurrence of a furrow in a joint, owing to the pressure of a corresponding ridge. The pressure of the ridge, it was said, produces a furrow in the opposite side of the joint. It seems to me that in this we are going a little beyond what physiology and histology teach us. It seems to me to be a blind appeal to mechanical forces unsupported by any adequate investigation of the physiology and histology of the tissues concerned. Is it likely that a bone would react to intermittent pressure by producing a furrow? It is far more probable that the reverse effect would tend to be produced.

I will only ask one more question with regard to this matter of use and disuse, and that is, why, if you are going to explain any of these parts by pressure and friction, should the process be stopped when a useful level is reached? If the pressure does cause such effects and they are hereditary, how are they prevented from increasing beyond all bound in the course of generations? Why should pressure on teeth cease to produce further growth, when the tubercle has reached its proper height? It seems to me that the fact that all these shapes of bones and teeth just reach and stay at an adaptive level is the strongest evidence that they are not produced by the operation of mechanical forces, but by natural selection.

We now pass to the consideration of indirect evidence: that it would be impossible to explain evolution without the Lamarckian theory.

Time will permit me to deal with only one class of characters, and that is associated with the nervous system and manifested as instinct. These instinctive actions are generally thought to be the strongest evidence in favor of Lamarckian evolution. It has been argued that we cannot explain the instinctive action of animals — the wonderful instincts which are due, as we know, to modifications of the nervous system, — except by supposing that animals have intelligently modified their actions in consequence of experience and observation, and that the result has then been transmitted and has become the non-intelligent instinct of their offspring. If we had no other explanation of instinctive action, such an interpretation would constitute a strong support to the Lamarckian theory.

I do not, however, believe that this is the only, or, indeed, the correct explanation of instinct. In considering this question, we must distinguish between the instinct manifested by many of the higher invertebrate animals and much that we are apt to call the instinct of the vertebrates. A great many actions which are put down to instinct in the higher vertebrates, such as birds and mammals, are not instinctive at all, but merely the result of observation during the life of the individual. We see an example of this in the action of the seal which, as Nansen tells us, took up a position on the outer ice-floes to escape the dangers of the polar bear, and afterwards incurred this very danger on the inner floes to avoid the greater peril from the hunter. This is a clear case of reasoning from the results of observation, and no instinctive avoidance of danger. So also with a bird which flies away if you have a gun in your hand, but allows you to come near when you have a walking-stick. This is the result of reason and not merely instinct; and we must carefully distinguish between a lesson learned by the individual, however well learned and easily repeated it may be, and a true instinctive action which was never learned at all but sprang fully formed into existence. Such true instincts certainly occur in the higher vertebrates, such as the act of sucking performed so perfectly without any education or practice by the newly born mammal. In the lower animals such true instincts are relatively far more numerous and play a most prominent part in the life of the individual. In these cases of true instinct I would suggest that we are dealing with actions which have never been intelligent at any time in the past history

of the species, and which have been due to the operation of natural selection upon the nervous system. Certain cases which are most strongly held to be the outcome of the transmission of gained experience and the acquired results of practice certainly cannot be explained in this way.

For instance, how upon any such hypothesis can you explain the wonderful structure of the cocoon spun by the larva of an insect? The view would be, I suppose, that the ancestral larva spun a cocoon which was not much of a success and was in consequence attacked by enemies; that the larva observed these attacks, and accordingly improved its cocoon. But that is not the way in which the struggle for existence is waged with insects. If the larva failed, it failed, and that would be the end of the matter. It has no chance of improvement; it has no opportunity of learning by experience. Its only chance of survival is to avoid experience of foes altogether; experience is the most dangerous thing in the world to an edible insect. This becomes still more obvious when we remember that failure or success is almost always determined long after the cocoon is made. The caterpillar perhaps spins the cocoon in autumn, but the real stress of competition will come in winter, when insect-eating animals are pressed hard with hunger and search high and low for food. But the caterpillar by this time is a chrysalis and of course has no opportunity of improving the cocoon. The selective test is applied long after the operation has been performed, and when there is no possibility of gaining by experience. We are thrown back, then, solely upon natural selection, which acts on the nervous system of the caterpillar, and thus compels it to make the cocoon in a certain way. In other words, those caterpillars which are impelled by their nervous system to make ill-formed, conspicuous cocoons have no chance of living, and in future stages producing offspring. Hence, the selection caused by the keen sight of foes first raises and then maintains at a high level the standard of cocoon-making.

This contention as to the uselessness and danger of experience applies to the whole of those smaller defenceless animals which have no chance of fighting with their enemies or of escaping when once they have been detected.

Another special kind of instinct has been greatly relied on by Romanes as evidence for the Lamarckian theory of transmitted

experience. Certain Hymenoptera allied to wasps possess an instinct which leads them to sting larvae and store them up in their nests as food for their young. It is generally believed that the larva is stung in the central part of the nervous system so that it can no longer struggle. I say "generally believed" because it has been pointed out to me by so distinguished an observer as Dr. Peckham of Milwaukee, that certain facts are opposed to the generally received account. It is to be hoped that the observations which are chiefly due to Fabre will be repeated and tested as minutely as possible. The prey is stored up in the mud-tube or burrow of the hymenopteron, and keeps perfectly fresh because it is alive, although completely paralyzed. Larvae stored up in this way appear to live much longer than those which, in the full possession of their faculties, are deprived of food.

Now this is a very wonderful instinct, and it has been argued that here is a case which cannot be explained except on Lamarckian lines. I maintain, on the contrary, that it is a case which cannot by any possibility be explained on Lamarckian lines.

The wasp-like insect has no opportunity of learning by experience because it can never know whether the larva stored up is a failure or a success. If the larva had not been stung, or, accepting the received accounts, had been stung in the wrong place, it would struggle and perhaps kill the young grub; or dying of starvation it might dry up and be useless as food. But the hymenopteron never goes back to inquire. It makes all the difference to the young grubs whether the food provided for them is in an appropriate condition or not, but it makes no difference whatever to the parent insect. The latter seals up the chamber in which its eggs have been laid and never opens it again; it has no chance of noting the failure or success of the food it has provided. It is clearly a case like that of the cocoon which cannot be explained on the Lamarckian theory and must be explained on the Darwinian. And this latter interpretation is easy: those insects which possessed the nervous mechanism impelling them to provide food in an appropriate condition gave to their offspring the opportunity of surviving and inheriting the same instinct. While others, impelled to perform less efficient actions, were thereby cut off from any representation in the next generation.

If the origin of wonderful and complex examples of instinct such as these cannot be explained by the Lamarckian theory but readily by the Darwinian, why should not natural selection also offer an adequate explanation of all other cases?

I have already taken up a great deal too much of your time. I much hope to have the opportunity to-night of hearing many stronger arguments in favor of the Lamarckian theory than it has been my opportunity to hear hitherto.

Note.— In revising the short-hand transcript for publication, I have not made any changes which alter the character of the address. It remains the record of a spoken address, the sequence and continuity of which were maintained by the use of brief notes. I have not verified the quoted opinions and words of others, and there are probably verbal errors. I believe, however, that in every case the true meaning of the author has been preserved. —E. B. Poulton. Oxford, May 21, 1894.