CHAPTER VII

THE TRANSMISSION OF ACQUIRED CHARACTERS

"A right answer to the question whether acquired characters are or are not inherited underlies right beliefs, not only in Biology and Psychology, but also in Education, Ethics, and Politics."—HERBERT SPENCER.

"Il n'est pas démontré que les modifications acquises sous l'influence des conditions de vie soient généralement héréditaires, mais il paraît bien certain qu'elles le sont quelquefois. Cela dépend sans doute de leur nature."—YVES DELAGE. [This is the opinion of one of the acutest of living biologists, but we find ourselves forced to a negative position.]

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§ 8. *General Argument for the Transmissibility of Modifications.*

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§ 1. *Importance of the Question*

No one is at present entitled to rank the transmission of "acquired characters"—*i.e.* somatic modifications—among *the facts of inheritance*, and the logical place for a discussion of this subject should be beside other disputed questions, like the occurrence or non-occurrence of telegony. But we have given special prominence to a discussion of this problem because of its great importance both practically and theoretically, and because of the abundant debate which has been aroused over it.

Not a Merely Academic Problem.—The question as to the transmissibility of characters acquired during life by the body of the parent as the result of changes in environmental or functional influences is much more than a technical problem for biologists. Our decision in regard to it affects not only our whole theory of organic evolution, but even our every-day conduct. The question should be of interest to the parent, the physician, the teacher, the moralist, and the social reformer—in short, to us all.

If the particular results of changes or peculiarities in individual nurture, education, and experience do *not* directly and specifically affect the inherited nature of the offspring, there must be a revision of some current psychological and pedagogical opinions; but it must be borne in mind that man's rich *external heritage* of tradition and convention, custom and institution, law and literature, art and science, makes his case quite peculiar, for the results of man's external heritage are often such as might have come about if acquired characters *were* heritable.

If the particular results of changes or peculiarities in individual "nurture" do not directly and specifically affect the inherited nature of the offspring, there must be a revision of that theory of organic evolution which is usually called Lamarckian, in which it is a central postulate that whatever is acquired may also be transmitted.

Spencer's Estimate of the Importance of this Question.—After contrasting the two hypotheses of the transmissibility and the non-transmissibility of acquired characters, Herbert Spencer said: "Considering the width and depth of the effects which the acceptance or non-acceptance of one or the other of these hypotheses must have on our views of life, the question, Which of them is true? demands beyond all other questions whatever the attention of scientific men. A grave responsibility rests on biologists in respect of the general question, since wrong answers lead, among other effects, to wrong belief about social affairs and to disastrous social actions." This authoritative statement removes all need of apology for the prominence which we have given to the question.

An Interminable Question.—The attention of scientific men which Herbert Spencer demanded for this problem has not been grudgingly given. The subject has been keenly debated for many years; there are, as our bibliography will show, scores of papers and not a few books devoted to its discussion. Indeed, one of the most tolerant of biologists, Prof. W. K. Brooks, has spoken of it as "the interminable question." Those who give the affirmative answer have not succeeded in proving their case; as for the other side, how can they prove a negative? Therefore, while we have no hesitation as to the verdict of "non-proven" to which the evidence *at present available* points, we do not expect a satisfactory issue until many years of experimental work have supervened.

Why, then, if a satisfactory termination be not at present possible, and if no unanimity even among experts can be looked for, should we enter upon the discussion once more? Prof. Brooks states our warrant in a quotation from Berkeley's *Siris*: "It is Plato's remark in his *Theætetus*, that while we sit still we are never the wiser, but going into the river and moving up and down is the way to discover its depths and shallows. If we exercise and bestir ourselves we may even here discover something."

Experiment is doubtless most urgent, but misunderstandings in regard to the problem are still so prevalent that we take courage in attempting a re-discussion, from which we have tried to eliminate obscurity and prejudice.

§ 2. *Historical Note*

Doubt as to the transmission of acquired characters is certainly not novel, though Galton and Weismann deserve credit for defining the scepticism.

Brock has pointed out that the editor, whoever he was, of Aristotle's *Historia Animalium* seems to have differed from his master on this subject. Aristotle had referred to the transmission of the exact shape of a cautery mark, but the editor insinuated a doubt as to credibility of instances of this sort.

Kant.—In modern times Kant was one of the first to express a firm disbelief in the transmission of individual peculiarities; Blumenbach inclined to the same opinion; but neither seems to have defined precisely what he intended to exclude from the bundle of inheritance.

Prichard.—James Cowles Prichard (b. 1786), a well-known anthropologist, anticipated as early as 1826 some of the characteristically modern views on evolution. His importance has been pointed out by Prof. Edward B. Poulton. In the second edition of his *Researches into the Physical History of Mankind* (1826), Prichard stated the case in favour of the general evolutionist interpretation of animate nature, recognised the operation of natural and artificial selection, and not only drew a clear distinction between acquired and inborn peculiarities, but argued that the former were not transmitted. He was not rigidly consistent, however, and his convictions seem to have weakened in after years; yet his anticipation of one of Weismann's positions by more than half a century is very interesting.

In more recent times we find sporadic expressions of scepticism as to the transmission of acquired characters—*e.g.* by the morphologist His and the physiologist Pflüger; but, as we have said, the focussing of the question was due to Galton and Weismann.

Galton.—Thus Galton in 1875 stated his opinion that the current theory of the inheritance of characters acquired during the lifetime of the parents "includes much questionable evidence, usually difficult of verification. We might almost reserve our belief that the structural cells can react on the sexual elements at all, and we may be confident that at the most they do so in a very faint degree—in other words, that acquired modifications are barely, if at all, *inherited* in the correct sense of that word."

Galton's position at that time may be summed up as follows:

(1) In regard to climatic variations, Galton doubted the reality of any reaction of the "body" upon the germs, but believed that the germs are themselves *directly* affected.

(2) The same is true in regard to many diseases that have been acquired by long-continued irregular habits.

(3) The cases of the *apparent* inheritance of mutilations are outnumbered by the overpowering negative evidence of their non-inheritance.

(4) It is hard to find evidence of the power of the personal structure to react upon sexual elements that is not open to serious objection. That which appears the most trustworthy lies almost wholly in the direction of nerve changes, as shown by the inherited habits of tameness, pointing in dogs, and the results of Dr. Brown-Séquard's experiments on guinea-pigs.

Weismann.—But Weismann gave the scepticism an even sharper point. He denied *all* transmission of acquired modifications, partly because he found the evidence so flimsy and anecdotal, partly because he could not conceive of any mechanism whereby the transmission of a particular acquired modification could be effected, and partly because his whole theory of heredity and variation raised strong probabilities against the view that acquired characters were transmitted. On Weismann's view the sole fountain of specific change is in the germ-plasm of the sex-cells. It is true that the environment makes dints on the organism, but only upon its *body*; the reproductive cells, through which alone the change could be transmitted, are either unaffected or are not affected in such a definite way as to bring about the transmission of the parental modification. It is true that the results of changed function (use and disuse) are often very marked, and very important *for the individual;* but they are not transmitted as such or in any representative degree, and therefore are of no direct account in the evolution of the species. Thus the ground is taken from under the feet of Buffonians and Lamarckians, and the whole burden of organic progress is laid upon germinal variation and the processes of selection.

The following sentences indicate Weismann's original position:

(1) "Acquired characters are those which result from external influence upon the organism, in contrast to such as spring from the constitution of the germ."

(2) "Characters can only be inherited in so far as their rudiments ('Anlagen') are already given in the germ-plasm."

(3) "Modifications which are wrought upon the formed body, in consequence of external influences, must remain limited to the organism in which they arose."

(4) "So must it be with mutilations, and with the results of use or disuse of parts of the body."

(5) "No such modifications of the soma (affected by environment or by use and disuse) can be transmitted to the germ-cells, from which the next generation springs. They are, therefore, of no account in the transformation of the species."

(6) "The only principle that remains for the explanation of the transformation of the species is direct germinal variation."

On germinal variations natural selection operates in the usual way. The helpful subsidiary theory of germinal selection was afterwards suggested, and various saving clauses were added, which do not, however, affect the clearness and strength of Weismann's original position.

Lamarck's Laws.—It may be fairly said that the *fons et origo* of the affirmative position was Lamarck. Though he did not originate, he formulated and illustrated the theory of the inheritance of acquired characters. He maintained the transmissibility of modifications due to increased and decreased and changed use, and also of modifications due to environmental change, whether directly induced, or indirectly induced by altered function. The giraffe has attained its long neck by stretching it for many generations; swimming birds have got webbed feet because they stretched their toes in the water; wading birds have got long legs because they stretched them; the mole has very small eyes because it has ceased to use them; the whalebone whale has no functional teeth because it has acquired the habit of swallowing its food without mastication; and so on.

Lamarck's two laws of nature, which he said no observer could fail to confirm, were: *

(1) In every animal that has not passed beyond the term of its development, the frequent and sustained use of any organ strengthens it, develops it, increases its size, and gives it strength proportionate to the length of time of its employment. On the other hand, the continued lack of use of the same organ sensibly weakens it; it deteriorates, and its faculties diminish progressively, until at last it disappears.

(2) Nature preserves everything that she has caused the individual to acquire or to lose by the influence of the circumstances to which the race has been for a long time exposed, and consequently by the influence of the predominant use of certain organs (or in consequence of their continued disuse). She does this by the generation of new individuals, which are produced with the newly acquired organs. This occurs, provided that the acquired changes were common to the two sexes, or to the individuals that produced the new forms.

Prof. E. Ray Lankester has pointed out (1894) that Lamarck's

* I have taken the translation from T. H. Morgan's *Evolution and Adaptation* (1903), p. 226.

first and second laws are contradictory the one of the other. In correspondence with the normal conditions of the environment, organisms show "responsive" quantities in their parts; but change a young organism to an environment quantitatively different, and it shows *new* responsive quantities in the parts of its structure concerned, new or *acquired* characters.

"So far, so good. What Lamarck next asks us to accept, as his 'second law,' seems not only to lack the support of experimental proof, but to be inconsistent with what has just preceded it. The new character, which is *ex hypothesi,* as was the old character (length, breadth, weight of a part) which it has replaced—a response to environment, a particular moulding or manipulation by incident forces of the potential congenital quality of the race—is, according to Lamarck, all of a sudden raised to extraordinary powers." It is declared to be transmissible, that is, it alters the potential character of the species, so as to persist when other quantitative external conditions are substituted for those which originally determined it. But this has never been experimentally proved, and there is strong reason for holding it to be improbable.

"Since the old character (length, breadth, weight) had not become fixed and congenital after many thousands of successive generations of individuals had developed it in response to environment, but gave place to a new character when new conditions operated on an individual (Lamarck's first law), why should we suppose that the new character is likely to become fixed after a much shorter time of responsive existence, or to escape the operation of the first law? Clearly there is no reason (so far as Lamarck's statement goes) for any such supposition, and the two so-called laws of Lamarck are at variance with one another.

"In its most condensed form my argument has been stated thus by Prof. Poulton (*Nature,* vol. li., 1894, p. 127); Lamarck's 'first law assumes that a past history of indefinite duration is powerless to create a bias by which the present can be controlled; while the second assumes that the brief history of the present can readily raise a bias to control the future.'" (See E. Ray Lankester's *Kingdom of Man*, 1907, pp. 128–130.)

Lamarckism remains alive.—The Lamarckian position is still stoutly maintained—usually in more or less modified form—by many prominent naturalists, especially in France and America. It is often held along with a more or less half-hearted Darwinism, just as Darwin combined some Lamarckism with his own selectionist doctrine—even in spite of his protest, "Heaven forfend me from Lamarck nonsense of a tendency to progression, adaptations from the slow willing of animals, etc." Though Alfred Russel Wallace has said, "The hypothesis of Lamarck has been repeatedly and easily refuted by all writers on the subject"; though Huxley said, "The Lamarckian hypothesis has long since been justly condemned"; though Ray Lankester has said that perhaps the greatest step of progress in modern ætiology will be the complete removal of all taint of Lamarckism,—there remains a vigorous school of Lamarckians and a still more vigorous school of Neo-Lamarckians, who, whatever be the truth in regard to the transmission of acquired characters, have got a firm grip of the often-overlooked commonplace that *the organism is an active, self-assertive, self-adaptive living creature—to some extent master of its fate.*

§ 3. *Definition of the Problem*

A Protest.—Much time and energy have been wasted on the discussion as to the transmissibility or non-transmissibility of "acquired characters" or somatic modifications, through lack of precise definition of the terms. Usually, though not always, the fault has been with the supporters of the affirmative position, who have failed to observe the rules of the game by ignoring the definitions of those who find themselves forced to a negative conclusion. By all means let there be a critical discussion as to the best definition of "an acquired character," "a modification," "a somatic change induced on the body by environmental or functional influences"; by all means let there be a criticism of terms and categories—the minting of a perfectly unambiguous word for somatic modifications would be most welcome: but if the sheaves of facts and alleged facts are to be thrashed out with the end of getting at the wheat of truth, we *must* adhere to certain definitions—notably, of course, to those given by Weismann, who brought the problem in its modern aspect into focus. Even a sense of humour should hinder a young medical practitioner from thinking that he makes for progress by advancing an argument which has no cogency unless the biological dictionary be first re-edited. It should be evident that a discussion over which some of the wisest heads in Europe and America have pondered cannot be, as some have had the effrontery to declare it, a mere play of words. Is it too much to ask of those who are keen to break a lance with the Biologist of Freiburg that they should first at least read *The Germ-Plasm*?

What is an Acquired Character?—In our previous discussion of "heredity and variation" we have briefly expounded the distinction between germinal, blastogenic, constitutional, endogenous "variations," and bodily, somatogenic, acquired, exogenous "modifications." An acquired character, or a somatic modification, may be defined as a structural change in the body of a multicellular organism, involving a deviation from the normal, directly induced during the individual lifetime by a change in environment or in function (use and disuse), and such that it transcends the limits of organic elasticity, and therefore persists after the factors inducing it have ceased to operate.

Illustrations.—Dwarfing of Japanese trees, deformation of trees by the wind, blanching of plants grown in darkness, changes directly induced by transplantation, persistent sun-burning, change of colour after particular diet, callosities induced on the skin by pressure, *e.g.* those at first produced on the finger-tips of one who is learning to play the violin, dwarfing of animals in confined space, increased muscular development by exercise, atrophy of muscles through disuse, chronic fatigue of nerve-cells, alterations in the walls of the food-canal through particular diet, changes in the skeleton as the result of specialised activities, increased growth of hair, etc., after importation to a warm climate, accumulation of fat as the result of modified nutrition, and so on through a long list.

To understand the question clearly we must spend a little time and thought over it. Let us briefly consider the various relations between an organism and its surroundings.

1. **Relation of Dependence between Organism and Environment.**—It is a familiar fact that a living creature is dependent upon its surroundings. A great part of life consists in action and reaction between the organism and its environment. It is a profound commonplace that between the animate system—so incomprehensibly unified—and its inanimate milieu, there is a continual coming and going of matter and energy. On this life depends. The may-fly during its short aerial life must breathe even if it does not feed; the philosopher requires his dinner, just as his dog does. This may be called the relation of constant and normal environmental dependence—necessary to the development and to the continuance of the organism.

2. **Transient Adjustments.**—But surroundings are changeful, and the living creature changes with them. A great part of life consists of *effective responses* to external changes; consciously or sub-consciously the organism adjusts itself to changes in its environment, or works in the direction of adjustment. There is bright sunshine and our pulse beats more quickly; the external temperature rises and we perspire. Thousands of these changes are familiar, saving life from monotony. Yet in regard to many there remains no abiding result that can be detected. There are structural changes attendant on normal nerve-fatigue, but in rest and food we gain almost complete recuperation. No

doubt there is always *some* lasting impression, for even the bar of iron is never quite the same after it has been once struck; but the results of the slight organic changes we have been alluding to are usually lost as the sand-ripples are lost when the tide turns. They are the merely transient results of responses to frequently recurring environmental changes to which the organism is well accustomed.

3. **Adjustments which persist for a Considerable Time.**—Insensibly, however—for it is all a matter of degree—we pass from transient results to others which last for a considerable time. We are browned by the sun on our summer holiday, and the result may last far into the autumn. The change, though still very superficial, has taken a firmer hold. The world is full of illustrations—the increase in the child's weight after a month at the farm, the increase in the size of the muscles after a course of Sandow exercises, the warping of the plant-stem which has been illumined from one side only, the blanching of the banked-up celery. But these results do not last long after the inducing conditions have ceased to operate. Sooner or later there is a return to the normal. Like a bow unstrung, the organism rebounds approximately to its previous state. The stimulus ceases or the absent stimulus is restored, and the organism, as if at the command "As you were," returns to the *status quo*.

4. **Modifications.**—Insensibly, however—for it is still only a matter of degree—we pass from these temporary changes to others which are demonstrably permanent. For there are cases where the new stimulus provokes a structural change, which persists after the stimulus has ceased. As we have put it, metaphorically, the limit of organic elasticity has been transcended. These are what in technical language we call "acquired characters" or "modifications."

The Englishman who works half his lifetime under a tropical sun may become so tanned that the result does not disappear during all the years in which he enjoys his pension at home. He has changed his skin, but he cannot by any means change it back again. Through prolonged disuse from early years a muscle may pass into a state of atrophy, and may so remain throughout life. Pressure on the little toe may so deform it, that even in the "easiest" shoes it can never right itself. A tree may be blown out of shape by the wind, and the crooked bough may never be straightened. Over-exertion may strain the heart permanently. A sudden shock may be followed by a whitening of the hair from which there is no natural recovery.

5. **Modifications and Variations.**—When we analyse *the observed differences* between fellow members of a species, we find that some of them can be definitely associated with peculiarities of function and environment. They can be more or less accounted for physiologically in terms of some change in surrounding influences or of some change in function thereby induced. They may not be hinted at in the young forms, but they begin to appear when the peculiar conditions begin to operate, and they are usually exhibited in some degree by all organisms of the same kind which are subjected to the same change of conditions. Furthermore, they can be experimentally brought about. These are "modifications."

By those who measure observed differences they are usually slumped along with true variations, but this appears to us to lead to confusion. *True variations are those peculiarities which remain when all the modifications are subtracted from the total of observed differences.*

It goes without saying that the distinction cannot *always* be drawn in practice. Often, however, it is quite apparent, and in any case the theoretical distinction is clear. Variations, in the strict sense, cannot be causally related to peculiarities in habit or surroundings; they are often hinted at in the earliest stages—even before birth; and they are very unequal even among organisms whose conditions of life seem absolutely identical. We refer them to changes in the germinal material before or during fertilisation. We call them endogenous, constitutional, blastogenic; and there is no doubt that they are transmissible, though they are not always transmitted.

Is there really an Antithesis?—Some subtle minds have found satisfaction in maintaining that the distinction between an acquired modification and an inborn variation is a distinction without a difference. In his interesting *Problems of Biology* Mr. George Sandeman points out that every acquired quality is congenital (*i.e.* there are in the organisation the rudimental possibilities of it), and that every congenital quality is also acquired (*i.e.* it requires to be nurtured by appropriate conditions if it is to develop). In this epigram there is undoubtedly truth, but is it relevant?

No doubt the possibility of the modification must be in the organism, just as the possibility of an explosion is in the barrel of gunpowder. The environment is not creative; yet, as a matter of fact, it seems possible to distinguish between the actual modification which we see and measure and the possibility of it which we presuppose.

Similarly, it is very true that the potentialities so marvellously embodied in the fertilised egg-cell require appropriate environing conditions if they are to be realised, for, as His observed long ago, "it is a piece of unscientific mysticism to suppose that heredity will build up an organism without mechanical means."

The common jelly-fish (*Aurelia aurita*) often has a pentamerous instead of a tetramerous symmetry. This is a variation of germinal, endogenous origin. Of course it requires an environment to develop in, but we cannot causally relate the structural peculiarity to any peculiarity in the environment. It seems to be logically quite distinguishable from a modification.

Discussing words is often indescribably tiresome, but it is better than misunderstanding them. "Inheritance of acquired characters" may be a most unfortunate phrase, but it has come to have a perfectly definite technical meaning and usage, which any normal person can understand in a few minutes. Prof. W. K. Brooks, in his *Foundations of Zoology,* says that he never uses the phrase "inheritance of acquired characters" except under protest, and this may be commendable restraint; but it seems to us inconsistent with his usual wisdom to go on to say, "If any assert that the dog inherits anything which his ancestors did not acquire, their words seem meaningless; for, as we use words, everything which has not existed from the beginning must have been acquired—although one may admit this without admitting that the nature of a dog is, wholly or to any practical degree, the inherited effect of the environment of his ancestors." But as the word "acquired" is now a technical term, meaning wrought out on the body as the result of changes in environmental or functional stimuli, we fail to see that, as we use the words, there is anything meaningless in the first assertion, or any warrant for the second.

Summary.—What forms the material basis of all inheritance, in all ordinary cases of sexual reproduction among multicellular organisms, is the fertilised ovum. The question under discussion is, physiologically stated, whether we can conceive that structural changes in the body of a parent, induced by changes in functional or environmental influence, can so specifically affect the reproductive cells that these will, if they develop, reproduce in any degree the modification acquired by the parent or parents. The question under discussion, logically stated, is whether there are any secure phenomena of inheritance which forcibly suggest the reality of the transmission of acquired characters; or whether, if such phenomena there be, a simpler interpretation may not be found. If, summing up in Galton's phrase, we call environmental and functional influences "nurture," our question is seen to be the exceedingly important one, May the results of peculiarities in parental "nurture" be as such transmitted, or is it the germinal "nature" alone that constitutes the inheritance?

§ 4. *Many Misunderstandings as to the Question at Issue*

The precise question is this: *Can a structural change in the body, induced by some change in use or disuse, or by a change in surrounding influence, affect the germ-cells in such a specific or representative way that the offspring will through its inheritance exhibit, even in a slight degree, the modification which the parent acquired?*

Before we pass to discuss the evidence pro and con it will be useful to notice some frequently recurring *misunderstandings*, the persistence of which would make further argument futile.

Misunderstanding I—*How can there be progressive evolution if acquired characters are not transmitted?*—Those who have not thought clearly on the subject often shake their heads sagely and remark that they "do not see how evolution could have been possible at all unless what is acquired by one generation is handed on to the next." To this we have simply to answer (1) that our first business is to find out the facts of the case, careless whether it makes our interpretation of the history of life more or less difficult, and (2) that in the supply of germinal *variations*, whose transmissibility is unquestioned, there is ample raw material for evolution. We know a little about the abundant crop of variations at present supplied; there is no reason to believe that it was less abundant in the past.

Misunderstanding II—*Interpretations are not facts.*—There are many adaptive characters in plants and animals which may be superficially interpreted as due to the direct result of use and disuse or of environmental influence. The Lamarckians have so interpreted them, and the Lamarckian way of looking at adaptations has become habitual to many uncritical minds. They see on modern flowers the footprints of insects which have visited them for untold ages; they speak of the dwindling of the whale's hind-limbs through disuse, of the hardening of the ancestral horses' hoofs as they left the marshes and ran on harder ground; they picture the giraffe by persistent effort lengthening out its neck a few millimetres every century, as the acacia raised its leaves higher and higher off the ground; and they say that animate nature is so full of evidences of the inheritance of acquired characters that no further argument is needed.

But all this is a begging of the question. It is easy to find structural features which *may be interpreted* as entailed acquired characters, *if* acquired characters can be entailed. Obviously, however, we must deal with what we can prove to be modifications, or with what we can plausibly regard as modifications because we find their analogues in actual process of being effected to-day.

It is easy to say that the blackness of the negro's skin was produced by the tropical sun, and that it is now part of his natural inheritance. It is easy to say this, but absolutely futile. Let us first catch our modifications.

The Golden Rod (*Solidago virgaurea*) growing on the Alps is precocious in its flowering when compared with representatives of the same species growing in the lowlands. Hoffmann found that Alpine forms transplanted to Giessen remained precocious, therefore the acquired precocity had become heritable. But there is no evidence that the precocity *was* acquired; it may have been the outcome of the selection of germinal variations.

The African Wart-hog (*Phacochœrus*) has the peculiar habit of kneeling down on its fore-limbs as it routs with its huge tusks in the ground and pushes itself forward with its hind-limbs. It has strong horny callosities protecting the surfaces on which it kneels, and these are seen even in the embryos. This seems to some naturalists to be a satisfactory proof of the inheritance of an acquired character. It is to others simply an instance of an adaptive peculiarity of germinal origin wrought out by natural selection.

Misunderstanding III—*Begging the question by starting with what is not proved to be a modification.*—There is no relevancy in citing cases where an abnormal bodily peculiarity re-appears generation after generation, unless it be shown that the peculiarity *is* a modification, and not an inborn variation whose transmissibility is admitted by all. Short-sightedness may recur in a family-series generation after generation, but there is no evidence to prove that the original short-sightedness was a modification. In all probability, short-sightedness is in its origin a germinal variation, like so many other bodily idiosyncrasies.

In regard to some diseases, such as rheumatism, it is often said dogmatically by those who know little about the matter that the original affection in the ancestor was brought about by some definite external influence—such as a cold drive or a damp bed; but it seems practically certain that in all such cases we have to do with an inborn predisposition, to the expression of which the cold drive or the damp bed was merely the liberating stimulus, comparable to the pulling of the trigger in a loaded gun. The liberating stimulus is, of course, of great importance, both in the case of the gun's discharge and the organism's disease, but it only goes a little way towards a satisfactory interpretation in either case. Not that we can explain the origin of rheumatism or shortsightedness or any such thing—there is no explanation in calling them germinal variations that cropped up; but we are almost certain that they never are modifications or acquired characters.

Herbert Spencer twits those who are sceptical as to the transmission of acquired modifications with assigning the most flimsy reasons for rejecting a conclusion they are averse to; but when Spencer cites the prevalence of short-sightedness among the "notoriously studious" Germans, the inheritance of musical talent, and the inheritance of a liability to consumption, as evidence of the inheritance of modifications, we are reminded of the pot calling the kettle black.

Over and over again in the prolific literature of this discussion the syllogism is advanced, either in regard to gout or something analogous—

Gout is a modification of the body, an acquired character;
Gout is transmissible;
∴ Modifications are sometimes transmissible.

It may be formally a good argument, but there is every reason to deny the major premiss. There is no proof that the gouty habit had an exogenous origin—that it was, to begin with, for instance, the direct result of high living; though it is generally admitted that excesses in eating or drinking may give a stimulus to its expression. "The conclusion I have arrived at," says Prof. D. J. Hamilton (1900, p. 297), "is that the gouty habit of body has arisen as a variation, and as such is hereditarily transmissible, and that excess of diet and alcohol merely renders the habit of body apparent." It may also be pointed out that gout and rheumatism and the like are rather *processes of metabolism* than structural modifications, though the latter may ensue.

After pointing out the irrelevancy of citing cases of the hereditary recurrence of polydactylism, hæmophilia, colour-blindness in man, or the absence of horns in cattle or of tails in cats, as instances of the transmission of acquired characters, Prof. Ernst Ziegler says (1886, p. 13): "Only that can be regarded as 'acquired' which is produced in the course of the individual life, during or after the period of development, exclusively under the influence of external conditions; the term is in no wise applicable to peculiarities which, as one says, arise of themselves from a predisposition already present in the germ."

Let us state the case once more. There is no doubt that the expression of a germinal variation during the lifetime of an individual may be sometimes definitely associated with a particular external stimulus. It may thus be mistaken for a modification, and mistakenly spoken of as "acquired." But the relation between the provoking stimulus and the expression of the innate tendency or predisposition is more or less arbitrary—various kinds of stimuli will have the same result; whereas the relation between an environmental influence and the induced modification is more or less constant—similar influences having similar results—and is more strictly causal. An external stimulus may provoke the expression of a germinal variation, as when a mouse provokes hysteria; but this is different physiologically from what occurs when the sun produces sun-burning.

A certain abnormal psychosis, which may not have been hinted at during early years, suddenly emerges under provocation. It is carelessly spoken of (even in the law courts) as due to that provocation—a fright, a wound, a debauch, a railway accident, a night's exposure, and so on, and it is carelessly thought of as "acquired"; it is recovered from, but it re-appears in the offspring: *therefore* an acquired character may be transmitted. But there is the strongest probability that what was called an acquired psychosis was primarily germinal, and might have emerged under quite different stimulation—for instance, under the normal events of puberty and parturition.

Another version of this misunderstanding is seen in references to the improvement of a breed in the course of generations, as the result, it is supposed, of functional modifications. Practice makes perfect in the individual, therefore also in the race. But we have seen no cases cited where the results were not hopelessly complicated by the occurrence of selection and elimination, which, by acting on constitutional variations, may quite well account for what is hastily referred to modification-inheritance.

Herbert Spencer was keenly aware of the misunderstanding which we have been discussing. "Such specialities of structure as are due to specialities of function are usually entangled with specialities which are, or may be, due to selection, natural or artificial. In most cases it is impossible to say that a structural peculiarity which seems to have arisen in offspring from a functional peculiarity in a parent is wholly independent of some congenital peculiarity of structure in the parent, whence this functional peculiarity arose. We are restricted to cases with which natural or artificial selection can have had nothing to do, and such cases are difficult to find."

Yet it is strange that he should point to such facts as the following: the bones of the wing in the domestic duck weigh less and the bones of the leg more in proportion to the whole skeleton than do the same bones in the wild duck ; in cows and goats which are habitually milked the udders are large ; moles and many cave-animals have rudimentary eyes. Cases like these may be in part regarded as instances of individually re-acquired modifications, but they are for the most part readily interpreted as due to the selection of germinal variations.

Misunderstanding IV—*Mistaking the reappearance of a modification for transmission of a modification.*—It is of little service to cite cases where a particular modification reappears generation after generation unless it be shown that the change recurs *as part of the inheritance,* and not simply because the external conditions which evoked it in the first generation still persisted to evoke it in those that followed. Reappearance is not synonymous with inheritance.

Illustration.—When Prof. Nägeli brought Alpine plants (*Hieracium,* etc.) to the Botanical Garden at Munich, many became in the first year so much changed that they were hardly recognisable as the same species, and their descendants in the garden were likewise quite different from their Alpine ancestors. The small Alpine hawkweeds became large and thickly branching, and blossomed freely. In some cases many generations were observed—even for thirteen years ; there was no doubt as to the *reappearance* of the acquired characters ; but it was not thereby proved that the reappearance was due to the inheritance. On the contrary, that the reappearance was due to the persistence of the novel conditions, to the changes which these directly impressed on each successive crop, was shown by the fact that when the plants were removed to poor, gravelly soil, the acquired characters disappeared, and the plants were re-transformed into their original Alpine character. " The re-transformation was always complete, even when the species had been cultivated in rich garden soil for several generations."

Misunderstanding V—*Mistaking re-infection for transmission.*—A particular form of the fourth misunderstanding has to do with facts so special that it may be conveniently treated of separately. It has to do with microbic diseases. It is admitted that a parent infected with tubercle-bacillus or with the microbe of syphilis may have offspring also infected. But such cases are irrelevant in the discussion. Infection, whether before or after birth, has nothing to do with inheritance. As Dr. Ogilvie says (1901, p. 1072), "Wherever the transmission of infectious disease from parent to offspring has been adduced to support the doctrine of the inheritance of acquired characters, it has been done in utter misconception of its meaning and scope."

Medical men have sometimes condescended to make a subtle distinction between "hereditary" and "congenital" syphilis—the latter manifested at birth, the former some time afterwards! It seems strange that they have failed to recognise that there is no reason to use the word "hereditary" at all in this connection. What occurs is an *infection*, and it is theoretically immaterial at what stage the infection occurs.* A microbe cannot be part of an inheritance.†

Misunderstanding VI—*Transmission in unicellulars is not to the point.*—It is not to the point to cite cases where unicellular organisms, such as bacteria or monads, have been profoundly and heritably modified by artificial culture, so that, for instance, the descendants of a virulent microbe have been made to lose their evil potency. It is irrelevant because in regard to unicellular organisms we cannot draw the distinction

* It may be the germ-cells that are infected—especially when the direct source of infection is the father; or it may be the embryo that is infected through the placenta: but the difference in the time of the infection is of no theoretical interest, nor can it be inferred from any difference in the outward symptoms, as these appear in the offspring.

† The egg of the green freshwater polyp (*Hydra viridis*) always contains little greenish corpuscles which are not present in the youngest stages of oogenesis. It is almost certain that these are minute unicellular Algæ (*Zoochlorellæ*). But no one can regard these useful symbions as actually part of the inheritance. The eggs of the silk-moth are often infected by a minute but fatal Protozoon which is present in the body of the moth. It seems uncertain at what precise point these pebrine organisms become associated with the egg, but however early it may be, the infection has nothing to do with inheritance. (See Ziegler, 1905, p. 5.)

between body and germinal matter, apart from which the concept of modifications is of no value. In artificial culture the whole character of the unicellular organism—its particular metabolism—is altered; it multiplies by dividing into two or more parts, which naturally retain the altered constitution. But this is worlds away from the supposed case of an alteration in the structure of the little toe so affecting the germ-cells that the offspring inherit a corresponding deformation.*

Prof. Adami (1901, p. 1319) says: "By subjecting a growth of pigment-producing bacteria to the action of a temperature just below that which will cause their death, we can bring about a loss of pigment production, so that the rapidly-succeeding generations are perfectly colourless; but gradually, in the course of time, the cultures made from the original (heated) tube regain the power of pigment production. This may be in two or three days, or, again, only after several transplantations at the end of two or three weeks; and when we remember that a bacillus divides and so forms a new generation in, on the average, something considerably less than an hour, it is seen that the acquired character may be impressed upon a race for some hundreds of generations. The more intense the alteration to which the bacillus is subjected, the longer and the more frequently the race is subjected to the altered temperature conditions, the longer it is before there is a sign of return to the normal."

These are interesting and reliable facts, but their citation as evidence of the inheritance of "acquired characters" is misleading, since no bacilli show any hint of the distinction between somatic and germinal material on which the definition of "acquired characters" depends, nor do they multiply except by division and

* It is surprising that even Prof. Oscar Hertwig (1898) supports his argument in favour of the transmissibility of somatic modifications by citing cases of inheritance in unicellular organisms. We are told that the irritability of certain Algae to light may be modified by exposure to strong light and to high temperature, and that "nobody would be surprised" if the progeny also showed "some similar property." But this is hardly evidence of the transmission of a modification! We are also told that under artificial conditions some bacteria may lose their toxic properties, and may transmit this somewhat negative character of lost virulence. This is admitted by all, but it is an *ignoratio elenchi*.

spore-formation. What occurred in the cases referred to was probably a temporary dislocation or disturbance of the characteristic organisation of the cells, with the result that pigment production was suppressed. When the inhibiting conditions were removed the original organisation recovered itself in the course of generations. But there is a great difference between such cases and, let us say, the transmission of sun-burning, or of specially strong muscles, or of a callosity on the skin, or a dwarfed form, which are instances of bodily modifications, technically called acquired characters. In the case of the bacilli the disturbed organisation was halved or multiplied in each reproductive process, and the effect originally induced was inherited from generation to generation, eventually disappearing as the restoration of normal conditions allowed the original organisation to re-assert itself in its integrity ; in the case of the supposed inheritance of a callosity we have to assume either that the influence which induced this, or the influence of it after it had been induced, also affected the germinal material in the reproductive organs in such a way that the contained germ-cells, when liberated, developed into an organism with more or less of the callosity. It must be evident, without further discussion, that the cases are not at all on a par, and that inheritance in unicellulars has not been considered with sufficient carefulness even by experts.

Prof. L. Errera (1899) reported an experiment with a simple but multicellular mould (*Aspergillus niger*), which adapted itself to a medium more concentrated than the normal. The second generation of the mould was more adapted than the first, and the adaptation to the concentrated medium was not wholly lost after rearing in the normal medium again. This looks like evidence of the inheritance of the acquired adaptive quality which was brought about as a direct modification. But the case does not really help us, since the distinction between *soma* and *germ-plasm* is not more than incipient in the mould in question. And even if the distinction were more marked, it would only show that the germ-plasm is capable of being affected *along with* the body, by a deeply saturating influence, which nobody has ever denied.

Misunderstanding VII—*Changes in the germ-cells along with changes in the body are not relevant.*—Another misunderstanding is due to a failure to appreciate the distinction between a change of the reproductive cells along with the body, and a change in the reproductive cells conditioned by and representative of a particular change in bodily structure. The supporters of the hypothesis that modifications may be transmitted point to the tragic cases where some poisoning of the parent's system, by alcohol, opium, or some toxin, is followed by some deterioration in the offspring. There is no doubt as to the fact; the question is as to the correct interpretation.

(1) In some cases it may be that the whole system of the parent is poisoned—reproductive cells as well as body; the effect may be as direct on the germ-cells as on the nerve-cells. These, therefore, are not cases on which to test the transmissibility of an acquired character—*i.e.* of a particular somatic modification. If a local poisoning had a structural effect on some particular organ, and if that structural effect was reproduced in any degree in the offspring, the case would be relevant; but when the whole organism is soaked in a poison the case is irrelevant. If it could be said that the sunshine, which brings about sun-burning in the skin, soaks through the organism even to its reproductive cells and specifically affects them, in a manner analogous to the saturating poison, we should have a physiological basis for expecting the inheritance of sun-burning. But we cannot make this assumption. We have no warrant for believing that the modification of a part re-echoes in a definite specific way through the organism until even the penetralia of the germ-cells reverberate.

(2) A parent organism is poisoned, and there are structural results of that poisoning. The offspring are born poisoned, and show similar structural peculiarities. This may be due to the fact that the germ-cells were poisoned along with the parental body; but it may also be due, in the case of a mother,

to a poisoning of the embryo before birth, in a manner comparable to pre-natal infection.

(3) In some cases—*e.g.* of alcoholism in successive generations—there may be poisoning of the germ-cells along with the body, there may be poisoning of the embryo before birth, and of the infant after; but it may also be that what is really inherited is a specific degeneracy of nature, an innate deficiency of control, perhaps, which led the parent to alcoholism, and which may find the same or some other expression in the child.

Cases are known in which the children of a dipsomaniac father and a quite normal mother have exhibited a tendency to alcoholism, insanity, and the like. In this case the possibility of poisoning the unborn child is eliminated, but there remain three possibilities of interpretation,—that there was specific poisoning of the paternal germ-cells; that what was inherited was the constitutional weakness which expressed itself as alcoholism in the father; and that there were detrimental influences in the early nutrition, environment, education—" nurture," in short—of the offspring.

But while we have admitted a good deal, we have not admitted the transmissibility of a particular structural modification brought about in the parental body as a result of the toxin.

An illustration of what we mean by the distinction " along with, but not through the body," is afforded by an experiment of Paul Bert's. He tried to acclimatise some Daphniæ (small fresh-water crustaceans) to salt water by gradually adding salt to the aquarium. At the end of forty-five days, when the water contained 1·5% of salt, all the adults had died; but the eggs in their brood-chambers survived, and the new generation arising from these flourished well in the salt medium (*cit.* Packard, 1894, p. 345). Packard sees in this case an argument for the heritability of a modification, but it seems to us merely an instance of the direct modification of the germ-cells or of the embryos. Cuénot, whom Packard cites, gives the correct interpretation: " This experiment shows with admirable clearness that the germ-plasm has, owing to the modification, become accustomed to the salt, causing it to produce a generation so different from the preceding."

Misunderstanding VIII—*Failure to distinguish between the possible inheritance of a particular modification and the possible inheritance of indirect results of that modification, or of changes correlated with it.*—At first sight this seems hair-splitting, but it is a crucial point. Through his vigorous exercise the blacksmith develops a muscular arm worthy of admiration ; the shoemaker acquires skeletal and muscular peculiarities less admirable. There are many permanent and profound modifications associated with particular occupations. Are we to believe, it is asked, that the occupation of the parents has no influence on the offspring ? Are we to believe, it is asked, that the children of soldier, sailor, tinker, tailor, are in no way affected by the parental functions ?

It would be interesting to have precise data in regard to this, but it is generally admitted that when parents have healthful occupations their offspring are likely to be more vigorous. The matter is complicated by the difficulty of estimating how much is due to good nurture before and after birth. It is not unlikely, too, that some profound parental modifications may influence the general constitution, may even affect the germ-cells, and may thus have results in the offspring. But unless the offspring show peculiarities *in the same direction* as the original modifications, we have no data bearing precisely on the question at issue.

A belief in the inheritance of modifications was perhaps expressed in the old proverb, " The fathers have eaten sour grapes, and the children's teeth are set on edge "—a proverb which Ezekiel with such solemnity said was not any more to be used in Israel. Now if " setting on edge " was a structural modification, and if the children's teeth were " set on edge " as their fathers' had been before them, there would be a presumption in favour of the transmission of this acquired character, though it would be still necessary to inquire carefully whether the children had not been in the vineyard too. But if, as Romanes said, the children were born with wry necks, we should have to deal with the inheritance of an indirect result of the parents' vagaries of appetite, and not with any direct representation in inheritance of the particular modification produced in the paternal dentition.

Misunderstanding IX—*Appealing to data from not more than two generations.*—It has often been pointed out that animals transported to a new country or environment may exhibit some modification apparently the result of the novel influence, and that their offspring in the same environment may exhibit the same modification *in a greater degree.* Thus sheep may show a change in the character and length of their fleece, and their progeny may show the same change more markedly.

But it is perfectly clear that if the evidence does not go beyond this, nothing is proved that affects the question at issue. It was to be expected that the offspring should show the modification in a more marked degree than their parents did, since the offspring were subjected to the modifying influences from birth, whereas their parents were influenced only from the date of their importation.

What would be welcome is evidence that the *third* generation is more markedly modified than the second; then there would be data worth considering. Only then would it be necessary to consider Weismann's somewhat subtle discussion as to the influence of climate.

§ 5. *Various Degrees in which Parental Modification might affect the Offspring*

It may seem, at first sight, unscientific to discuss various hypothetical degrees in which parental modifications might affect the offspring, when we do not know that modifications can be in *any* degree transmitted. But unless we are greatly mistaken, our theorem, if carefully attended to, will serve to make the issue clearer.

In regard to germinal variations, whose transmissibility is undoubted, it is well known that there may be different degrees of transmission, or, more cautiously stated, that the offspring's hereditarily determined reproduction of the parental variation may have diverse expressions. It seems just, therefore, to imagine that there might be different degrees in the transmission of modifications.

(1) The *first degree* of transmissibility would be illustrated if the offspring showed in any measure the same modification as the parent had acquired. If the sun-burnt parent had a congenitally swarthy child, that might be an indication of modification-transmission of the first degree of directness. It might be an illustration of what has been so carefully searched after—the transmission of *a particular acquired character*. We cannot too strongly emphasise that this and nothing else is what Weismann has denied; this and nothing else is the *crux* of "the interminable argument." And for the sake of argument, the possibility (1) must be kept quite distinct from the possibilities (2) and (3).

(2) If the offspring exhibited a new character, not the same as the parent's acquired modification, but affecting similar tissue, though in a different fashion, we might be justified in speaking of this as modification-transmission of the *second degree* of directness. It might be an illustration, not of the inheritance of a particular acquired character, but of something correlated therewith, if the much sunburnt parent of a thoroughly blond stock had a child with very dark hair on a very white skin. But the inference would not be certain.

(3) If the offspring exhibited a novel character, analogous to a modification, yet neither similar to the modification acquired by the parent nor affecting the same region of the body, it might be said that we had to deal with modification-inheritance of

the *third degree* of directness. It might be an illustration of the inheritance of an indirect effect of a parental modification if the sons of fathers who had eaten sour grapes had wry necks. But we should require many instances before admitting the hereditary nexus.

§ 6. *The Widespread Opinion in favour of Affirmative Answer*

It seems to be a widespread opinion that acquired characters may be transmitted, but often the opinion wavers when it is explained what this precisely means—namely, that a modification in the body, brought about by a change in function or environment, may so specifically affect the reproductive elements that when these develop there is in the offspring something corresponding to the parental modification.

Opinion of " Practical Men."—In fairness we must admit that the verdict of the *practical* man, whether physician or breeder, gardener or farmer, is still in many cases an unhesitatingly affirmative answer. One of the keenest of physicians has said that a few months in practice would dispel all doubt as to the inheritance of acquired characters; but there are equally keen physicians who have taken a different view. It may also be that the first had not freed himself from Misunderstandings V and VII.

Prof. Brewer, an American authority on breeding, who gives an emphatic affirmative answer, notes:

> " The art of breeding has become in a measure an applied science; the enormous economic interests involved stimulate observation and study, and what is the practical result? This ten years of active promulgation of the new theory has not resulted in the conversion of a single known breeder to the extent of inducing him to conform his methods and practice to the theory. My conclusion is that they are essentially right in their deductions founded on their experience and observations—namely, that ac-

quired characters may be, and sometimes are, transmitted, and that the speculations of the Weismann school of naturalists are unfounded."

But perhaps this widespread opinion does not mean so much as it seems; for it is very difficult to get busy practical men to take the trouble to appreciate an exact distinction such as is involved in the phrase, "the inheritance of an acquired character."

It may also be noted that many widespread beliefs are erroneous. There is a very widespread belief in telegony and maternal impressions, for which it seems difficult to find any scientific warrant. The distinguished name of Settegast may be cited as that of an authority on breeding—an exceedingly "practical man"—who believes neither in telegony nor in the inheritance of acquired characters.

Great Variety of Opinion.—There is little to be gained by a citation of opinions, for there are equally authoritative names on both sides. But there are some points of interest. Thus we have already noticed that the scepticism as to the inheritance of acquired characters is not a modern fad. It is also noteworthy that, while the majority of zoologists disbelieve in modification-inheritance, the reverse seems to be the case with botanists. Is this because modifications are even more marked and more recurrent in plants than in animals, or because the distinction between soma and germ-plasm is much less definite in plants than in animals?

But there is this use at least in noting the discrepancy of opinions, that we are warned from dogmatism. It cannot be an easy question when we find Spencer on one side and Weismann on the other, Haeckel on one side and Ray Lankester on the other, Turner on one side and His on the other, and so on.

Herbert Spencer was so convinced that he went the length of writing: "Close contemplation of the facts impresses me more strongly than ever with the two alternatives—*either there* *has been inheritance of acquired characters, or there has been no evolution.*" *

Haeckel is so convinced for the affirmative that he stakes his particular form of religion upon it, asserting that "belief in the inheritance of acquired characters is a necessary axiom of the monistic creed"; and what may sound to some even more serious is his declaration that, rather than agree with Weismann in denying the inheritance of acquired characters, "it would be better to accept a mysterious creation of all the species as described in the Mosaic account."

Sir William Turner has said that "to reject the influence which the use and disuse of parts may exercise, both on the individual and on his offspring, is like looking at an object with only a single eye"—which is not perhaps a very emphatic condemnation, since most microscopic research is monocular. Moreover, the doyen of British anatomists does not state the case with his usual precision.

Why is the Affirmative Position so widely held?—Even in regard to our own muscular and nervous systems, we are familiar with illustrations of the fact that practice increases capacity, and that desuetude is apt to be followed by loss of power. *À force de forger on devient forgeron.* Organs improve with the using and deteriorate in disuse. We are also well aware that changes in the environment or conditions of life, and notably in our food, cause changes in our body. It seems a "natural" assumption to suppose that these gains and losses and changes may be in some degree transmissible.

Apart from the "naturalness" of this assumption, there are probably four reasons why the affirmative position is so widely held:

(1) There are many facts which *suggest* modification-inheritance

* The italics are ours. See Herbert Spencer, "The Inadequacy of Natural Selection," *Contemporary Review*, February and March, 1893. Appendix B, *Principles of Biology*, 2nd ed. vol. i. 1898, p. 621

until they are examined critically. The late Duke of Argyll, in one of his scientific excursuses, said the world was strewn with illustrations of the inheritance of acquired characters, and Dr. W. Haacke, a very wide-awake evolutionist, has compared the evidences for the affirmative to the sand on the sea-shore for multitude, yet neither furnishes us, so far as we are aware, with a single case that will bear analysis. The affirmative may be an obvious interpretation of the results of evolution, but the obvious interpretation is seldom the right one. The sun does not go round the earth.

(2) The affirmative is an interpretation which seems to make the theory of organic evolution simpler; it suggests a more direct and rapid method than the natural selection of germinal variations. If to a growing and varying nature or germinal inheritance there were continually being added the results of peculiarities in nurture, the rate of evolution would be quickened, both upwards and downwards. But our first business is to find out whether the hypothesis actually consists with experience.

(3) We are so accustomed in human affairs to the entailment of acquired gains from generation to generation, to standing on the shoulders of our ancestors' achievements, that many find it difficult to refrain from projecting this on organic nature. They forget that the greater part of our entailing process comes about through our *social heritage*, which is altogether apart from our *natural inheritance.*

(4) A fourth reason is that many fictitious or anecdotal cases of the inheritance of acquired characters continue circulating. The inheritance of a letter branded upon the arm, which Aristotle notes, is still in the popular currency, though it is perhaps an extreme type of what His calls a handful of anecdotes. It is reported that Sioux Indians tattoo discs on the cheekbone prominences of their squaws, and it is said that similar marks may be seen on some new-born children (*Nature*, iii., 1870

p. 168). And besides fictitious cases there *are* some puzzling phenomena, which the supporters of the negative position are wont to dismiss as "coincidences"—which, it must be confessed, is never a very satisfactory way of dealing with difficult cases.

§ 7. *General Argument against the Transmissibility of Modifications*

Most of the evidence brought forward in support of the belief in the inheritance of acquired characters is terribly anecdotal; but apart from this Weismann was led to a position of entire scepticism by his realisation of the continuity of the germ-plasm.

The Apartness of the Germ-cells.—If the germ-plasm or the material basis of inheritance be something relatively apart from the body, and from its everyday metabolism, something often segregated at a very early stage in development, there is a presumption against its being readily affected in a specific manner by detailed exogenous changes wrought on the structure of the body.

It seems accurate to say that the reproductive cells which have the potentiality of becoming offspring never arise from differentiated body-cells. Whether they are recognisable as such, late or early, the germ-cells are simply those cells which retain in all its integrity the complex, definite, and stable organisation of the fertilised ovum from which the whole organism develops. They have their power of reproducing creatures more or less like the parents just because they are continuous, through an unspecialised cell-lineage, with the fertilised ovum from which the parental body arose. All the somatic cells are, of course, likewise the progeny of the fertilised ovum, but in their lineage there are differentiation and specialisation. We imagine that in them the numerous items or potentialities in the fertilised ovum are distributed and allowed to express themselves. In the germ-cell lineage they are kept concentrated and latent.*

In any case the germ-cells in the reproductive organs are not actively functioning elements of the body ; they are in a quite peculiar way apart from the general soma ; and Weismann has reasonably emphasised the difficulty of picturing any means whereby the modification of a particular corner of the body can react upon the germ-cells in a manner so specific that these can, when they develop, reproduce the particular parental modification or any approach to it. This argument, and the answers to it, must be carefully considered.

1. **The Germ-cells may be affected by the Body.**—In the first place, it has been answered that the body does undoubtedly, in some cases, exert some influence on the gonads, so that the difficulty is reduced to this : Can a modification of part of the body exert a specific or representative influence on the germinal material ?

But what is the precise nature of the alleged influence of the body on the gonads ? It is pointed out that nervous changes can excite the reproductive organs, that food-stuffs may increase their activity, that alcohol and other stimulants may influence them, and so on. But there is a great difference between any such excitation of the gonads and the propagation of a particular modification, let us say, from the skin to the germ-cells. And there is a great difference between a poisoning of the germ-cells along with the body, and the influencing of them in a manner so specific that they can, when they develop, reproduce the particular parental modification. (*See* Misunderstanding VII.)

* In certain conditions, as yet unknown, certain body-cells may revert to a primitive mode of behaviour—like some kinds of criminals in society. Thus the cells which develop into cancerous growths behave in some ways like germ-cells, especially in their mode of division. (See the researches of Farmer, Walker, and Moore.) But such cases need not lead us to Hertwig's extreme conclusion that every cell is potentially a germ-cell.

2. **Hypotheses as to Possible Mechanism of Transmission.**— In the second place, attempts have been made to construct hypotheses by aid of which we might conceive how a modification of, say, the skin, can exert a specific or representative influence on the germinal material.

Thus, Darwin suggested his provisional hypothesis of pangenesis, according to which the parts of the body give off gemmules which pass as samples to the germ-cells. But his suggestion remains a pure hypothesis—and an unnecessary one unless new facts come to light—and is nowadays maintained by no one except in extremely modified form—*e.g.* in the Pangen-theory of De Vries.

Spencer deserves credit for at least facing the difficulty of conceiving a *modus operandi* whereby a particular modification in, say, the brain or the thumb, can specifically affect the germinal material in such a way that the modification or a tendency towards it becomes involved in the inheritance. Briefly stated, his theory is as follows:

Spencer's Theory of the Mechanism of Transmission.—Spencer made the legitimate postulate that, intermediate between the biological unit or cell and the chemical molecule, there were "constitutional units," the vehicles of specific characters, ancestral and parental traits, and the individual peculiarities of the organism itself.

He supposed that they were very stable in their "fundamental traits," but plastic as regards their "superficial traits."

He supposed that they had "such natures that while a minute modification, representing some small change of local structure, is inoperative on the proclivities of the units throughout the rest of the system, it becomes operative in the units which fall into the locality where that change occurs."

He supposed "an unceasing circulation of protoplasm throughout an organism," such that, "in the course of days, weeks, months, years, each portion of protoplasm visits every part of the body"—a wild assumption.

Finally, "we must conceive that the complex forces of which each constitutional unit is the centre, and by which it acts on other units while it is acted on by them, tend continually to re-mould each unit into congruity with the structures around, superposing on it modifications answering to the modifications which have arisen in these structures. Whence is to be drawn the corollary that in the course of time all the circulating units—physiological, or constitutional, if we prefer so to call them—visit all parts of the organism; are severally bearers of traits expressing local modifications; and that those units which are eventually gathered into sperm-cells and germ-cells (*i.e.* egg-cells), also bear these superposed traits."

Thus the constitutional units are supposed to circulate and to visit one another throughout the body. When they come to a modified structure and visit its modified constitutional units, they are supposed to be themselves impressed; thus impressed, they are supposed to be gathered into the germ-cells, which thus come to bear the "superposed traits" resulting from modifications.

If we were sure that modifications were ever transmissible, we might be glad of this hypothetic interpretation of the business. But it is a difficult hypothesis to think out, and it would hardly be tolerable even if there were facts which it was needed to interpret. In particular, the conception of "an unceasing circulation of protoplasm," so that "each portion of protoplasm visits every part of the body," seems not only unwarranted, but contradicted by well-established facts.

3. **A Mechanism may exist though it remains Unknown.**—In the third place, we must recall Prof. Lloyd Morgan's warning that although we cannot imagine how a modification might, as such, saturate from body to germ-cells, this does not exclude the possibility that it may actually do so. Oscar Hertwig also maintains that our ignorance of any mechanism which could secure the transmission of an acquired character is not a good argument against the possibility of its occurrence. There are, he says, many facts in biology which are quite secure, though no causal nexus can be worked out at present (*Allgemeine Biologie*, 1906, p. 621). It must be noted, however,

that, so far as we can understand, *a very complex and special mechanism* would be necessary if a modification in, say, the eye is specifically to affect the germinal material.

Dr. George Ogilvie (1901) writes: "In a subject so involved in obscurity the present incomprehensibility of certain relations can hardly serve as an argument against their existence. The development of the apparently uniform germ-plasm into the infinite differentiation of a complex cell-state is, although no longer a matter of doubt, perhaps not less inconceivable." But this illustration is not altogether appropriate, since our inability to conceive the precise "how" of development rests on our inability to restate in simpler terms any of the fundamental facts of life, such as growth, assimilation, or reproduction, whereas the supposed relation between soma and germ-cells is inconceivable in rather a different sense.

A better illustration, it seems to us, would be found in the difficulty of exactly stating how particular changes in the gonads are correlated with particular changes in the body—*e.g.* in the changes associated with puberty, conception, ovarian and testicular disease. Yet here we can at least imagine what the general nature of the physiological nexus may be—in terms, for instance, of internal secretions.

A Concrete Case: Spencer's Hands.—It may illumine the abstract argument to take a concrete case. Why had Herbert Spencer small hands? He says that it was because his grandfather and father were schoolmasters, who did little manual work from day to day, save in wielding the pen and sharpening the pencil. Through disuse of the sword and the spade their hands were "directly equilibrated" towards smallness. But since Mr. Spencer senior was "a combination of rhythmically acting parts in moving equilibrium," the dwindling of the hands and the moulding of the physiological units thereof reverberated through the whole aggregate; a change towards a new state of equilibrium "was propagated throughout the parental system—

a change tending to bring the actions of all organs, reproductive included, into harmony with these new actions," or inactions. The modified aggregate impressed some corresponding modification on the structures and polarities of the germ-units. And this was how Herbert Spencer had small hands. At least, so he tells us.

Disuse of Parts.—It seems "natural" to suppose that organs have dwindled *pari passu* with their disuse, and *because* of their disuse. But the two statements are not synonymous. The dwindling may be due to germinal variations in the line of reduction, which are appropriate because of some change in the animal's habits and environment. It may even be that the organism meets an endogenous reduction of certain parts by itself changing its habits and habitat. Moreover, it is important to notice, as Emery, Kennel, and Ziegler have pointed out, that there has probably been a "Kampf der Theile im Organismus" (a struggle of parts within the organism) not merely in individual ontogeny, but also in the racial phylogeny. Dwindling of one part occurs when some adjacent part attains increased differentiation. "Thus snakes have not lost their limbs because they did not use them, but because of their evolution in the direction of exceptionally large trunk and tail musculature. In man the strong dentition of his Simian forebears has become weaker, not through disuse, but because the extraordinary increase of the brain has been correlated with a weaker development of other parts of the head" (H. E. Ziegler, 1905, p. 3).

§ 8. *General Argument for the Transmissibility of Modifications*

The Germ-cells are not Insulated.—While it must be admitted that the germ-cells have a certain apartness from the daily life of the body, and that they are unspecialised cells that have not shared in the differentiation characteristic of the body-cells, is there not some risk of exaggerating the distinction between somato-plasm and germ-plasm?

In many simple animals, such as sponges and hydroids, the germ-cells simply make their appearance at certain times of year among the commonplace somatic cells. In many plants the distinction between body and germ-cells can hardly be drawn until the period of reproduction sets in. Thus Spencer refused to accept the contrast between *body*-cells and *germ*-cells as expressing a fact, and referred to the numerous cases in which small pieces of a plant or a polyp may grow into entire organisms.

To this objection Weismann answers,—(1) that the distinction between somatic cells and germ-cells has been gradually emphasised in the course of evolution, and that in the simpler multicellular organisms it is still incipient; (2) that it is quite conceivable that, even in some complex organisms, the body-cells, though differentiated, may retain some residual unused germ-plasm; and (3) that there may be a quite definite and distinct germ-*plasm,* though there is no demonstrably distinct lineage of germ-*cells*.

Again, however, we must remember that the blood, or lymph, or other body-fluids form a common medium for all the parts of the animal, gonads included; the results of changes in nutrition may saturate throughout the body and affect the germ-cells *inter alia.* The nervous system makes the whole organism one in a very real sense; in plants there are often intercellular bridges of protoplasm binding cell to cell, and this is true in not a few cases among animals. Moreover, there are subtle, dimly understood correlations between the reproductive organs and the rest of the system. If changes in the reproductive organs can effect changes in remote parts, such as the larynx and the mammary glands, why may not there be reciprocal influences? In short, the organism is a unity, and to divide it up, in any hard-and-fast way, into soma and germ-cells may land us in the same fallacy as parcelling the mind into separate faculties.

It must be admitted, therefore, that it is quite erroneous to think of the germ-cells as if they led a charmed life, uninfluenced by any of the accidents and incidents in the daily life of the body which is their bearer. But no one believes this, Weismann least of all, for he finds the chief source of germinal variations in the stimuli exerted on the germ-plasm by the oscillating nutritive changes in the body.

Weismann's Concessions.—There are some who find in this "a concealed abandonment of the central position of Weismann," and who say: "If the germ-plasm is affected by changes in nutrition in the body, and if acquired characters effect changes in nutrition, then acquired characters or their consequences will be inherited." But it is quite illegitimate (§ 5) to slump acquired characters and their consequences as if the distinction were immaterial. The illustrious author of *The Germ-Plasm* has made it quite clear that there is a very great difference between admitting that the germ-plasm has no charmed life, insulated from bodily influences, and admitting the transmissibility of *a particular acquired character*, even in the faintest degree. The point, let us repeat, is this: Does a structural change in a part of the body, induced by use or disuse, or by change in surroundings, influence the germ-plasm in such a specific or representative way that the offspring will thereby exhibit the same modification that the parent acquired, or even a tendency towards it?

Determination of Sex.—In this connection reference has been made to experiments such as those of Yung, who was able, by altering the nutrition of tadpoles, to raise the percentage of females from a normal of about 50 to about 90. Have we not here an instance of an environmental influence playing in the first place on the nutritive system, affecting the blood and lymph, saturating through the body, and reaching the reproductive system? If the experiments are reliable, some tadpoles which would have become males in natural conditions became females under the stimulus of altered nutrition.

It must be noted, however, that what was effected was not the transmission of a modification, but an alteration of the natural proportions of the sexes. The immature reproductive organs, while in a state of "sexual indifference," were biassed towards femaleness. Thus the case does not do more than show that the gonads are reachable by somatic influences, which no biologist has ever denied.

The Real Difficulty.—Even when we recognise, as fully as we can, the unity of the organism, that each part shares in the life of the whole, it is very difficult to think of any *modus operandi* whereby a local modification can specifically affect the germ-plasm. The argument that we can as little understand the *modus operandi* whereby an influence passes from the gonads to distant parts of the body is not really sound. For we know that in some cases the reproductive organs, besides being areas for the multiplication of germ-cells, are organs of internal secretion, producing specific substances which are carried away by the blood-stream, and serve as the stimuli awakening the dormant potentialities of distant parts.

Nor does the fact that morbid processes in a particular part may result in a diffusion of toxins, which saturate even the germ-cells, help us much in our attempt to picture how a modification could become transmissible. For there is not the slightest reason for supposing that the ordinary modifications in which naturalists are interested, which experimental evolutionists can bring about, are associated with the formation of specific toxins which might diffuse through the whole system.

Spencer's Statement of the a priori *Argument.*—As Herbert Spencer was perhaps the keenest and most convinced upholder of the affirmative position, it seems just to give his statement of the *a priori* argument. We have made a comment on each of the steps.

(1) "That changes of structure caused by changes of action must be transmitted, however obscurely, appears to be a deduction from first principles—or if not a specific deduction, still, a general implication."

"For if an organism, A, has, by any peculiar habit or condition of life, been modified into the form $A,^1$ it follows that all the functions of A^1, reproductive function included, must be in some degree different from the functions of A."

"An organism being a combination of rhythmically acting parts in moving equilibrium, the action and structure of any one part cannot be altered without causing alterations of action and structure in all the rest."

Comment.—(*a*) It is not denied that some deeply saturating modifications of the body, affecting the nutritive stream, may affect the reproductive organs. This is not the point at issue. (*b*) How far a modification is likely to affect the reproductive organs must be determined by observation and experiment. The appreciability of the change will depend on the amount and nature of the modification, and on the intimacy of the correlation subsisting in the organism. Dislodging a rock may alter the centre of gravity of the earth, but it does not do so appreciably.

(2) "And if the organism A, when changed to A^1, must be changed in all its functions, then the offspring of A^1 cannot be the same as they would have been had it retained the form A."

Comment.—This is logical, but is it true? The change from A to A^1 may be important, it may appreciably alter the metabolism, but it does not follow that it can appreciably alter the architecture of the germ-plasm. Spencer's assumption that the change in the constitutional units of the body must affect the constitutional units in the germ-cells remains an assumption.

(3) "That the change in the offspring must, other things equal, be in the same direction as the change in the parent, appears implied by the fact that the change propagated throughout the parental system is a change towards a new state of equilibrium—a change tending to bring the actions of all organs, reproductive included, into harmony with these new actions."

Comment.—It seems to us to pass the wit of man to conceive how or why an improved equilibrium in, let us say, the use of the hand should involve any corresponding or representative change of equilibrium in the germinal material.

The drawback to abstract biology based on first principles is that it enables its devotees to develop arguments which seem plausible until they are reduced to the concrete.

§ 9. *Particular Evidences in support of the Affirmative Answer*

The question is whether modification-inheritance does or does not occur, and we must no longer postpone our consideration of the concrete evidence used to support the affirmative position. Our reason for not placing this section in the foreground of the chapter is mainly that a multitude of misunderstandings have had to be cleared away before the so-called direct evidence could be profitably considered. When one naturalist, Dr. W. Haacke, declares that instances of modification-inheritance are as plentiful as sand on the shore, and another, Prof. E. Ray Lankester, declares that the Lamarckian position has its only remaining defence, and that no secure one, in Brown-Séquard's experiments, we have obvious justification for our preliminary discussion.

The instances adduced as evidence of modification-inheritance might be classified according to the errors involved, but we have arranged them rather in reference to the general nature of the modifications discussed, whether environmental or functional, whether tending to increase or decrease, and so on. The alleged inheritance of the direct effects of mutilations, injuries, and the like is discussed separately in §§ 10 and 11.

Improvement in Trotting Horses.—Over a hundred years ago (1796) the utmost speed of the English trotter was stated at a mile in 2 min. 37 sec. Since 1818, accurate records have been kept, which show a gradual increase decade after decade in the speed and in the percentage of swift trotters. The standard has risen and the breed has improved. The mile can now be run in 2 min. 10 sec., or less. It is claimed by Cope and others that we have here direct evidence of the transmission of the structural results of exercise.

Brewer (*cit.* Cope, 1896, pp. 426-30) relates that about 1818 the record speed of the trotting horse was 3 min. to the mile; in 1824 it was reduced to 2 min. 34 sec.; in 1848, to 2 min. 30 sec.; in 1868, to 2 min. 20 sec.; in 1878, to 2 min. 16 sec.; in 1888, to 2 min. 11½ sec.; and finally to 2 min. 10 sec. "The gain in speed has been cumulative. . . . It has gone on along with systematic exercise of special function in successive generations; . . . there is nothing that would lead us to even suspect that the changes due to exercise of function had *not* been a factor in the evolution; . . . there is every appearance and indication that the changes acquired by individuals through the exercise of function have been to some degree transmitted, and have been cumulative, and that this has been one factor in the evolution of speed."

It is impossible to prove the negative above suggested—namely, that function has *not* been a factor; but the affirmative position is robbed of all cogency by the admitted occurrence of rigorous artificial selection. The improvement supposed to be entailed may not have been a modification at all; but, supposing it was, the interpretation of the result simply by the hypothesis of use-inheritance gives a false simplicity to the case. It overlooks the selective breeding which increases the constitutional swiftness, and the process of elimination which persistently weeds out the less swift from the stud. And even apart from artificial selection and elimination there may be a progressively cumulative succession of *variations* making for greater and greater swiftness. We may even picture how this might come about, if we adopt Weismann's conception of germinal selection.

Case of Squatting Punjabis.—It has been stated that the Punjabis of India show certain peculiarities of musculature and skeleton which are associated with the frequency with which these people assume on all possible occasions the squatting posture. It is asserted that the peculiarities of structure are due to the peculiarities of function, but this requires definite proof (Misunderstanding III). They may be adaptations originating in germinal variations. It is necessary to know whether the peculiarities are in any degree represented on new-born Punjabi babies, but even then it would be simpler to regard them as variations than as transmitted modifications. There can be no conclusiveness in regard to peculiarities whose first appearance is hidden in obscurity. If squatting increased from generation to generation, and if the structural peculiarities increased *pari passu*, the case would be interesting; but even then we should have to inquire whether we were not dealing with a progressive variation.

Peculiarities of Occupations.—In his interesting paper on the anatomy of the shoemaker, Dr. Arbuthnot Lane describes the peculiarities induced by this occupation, which tends to form a distinct anatomical type. The same is true of the tailor. "The bent form, the crossed legs, thumb-and-forefinger action, and peculiar jerk of the head while drawing the thread, are the main features of the sartorial habit," and they are associated with permanent changes in muscles, insertion surfaces, and articulations. These are indubitable modifications: what of their transmission? No one, Dr. Lane says, would expect any perceptible changes in the first generation, but he thinks that he has observed inherited effects in the third.

We can only say that this line of inquiry deserves to be followed up, especially since our minute acquaintance with the human body and the accumulation of facts in regard to its variations make a discrimination between modification and variation more secure than is possible in many other cases. It should be remembered, however, that if the shoemaker's sons and grandsons and subsequent descendants all "stuck to the last," there might tend to be an accumulation of general constitutional peculiarities—*e.g.* of meditativeness and of the physical effects of persistent sedentary work, which might dispose the organism to re-acquire particular modifications in a more marked degree.

Large and Small Hands.—Darwin (*Descent of Man*, p. 18) refers to the alleged fact that the infants of labourers have larger hands than those of the children of the gentry; but this, and many similar cases of which it is a type, may be sufficiently accounted for by interpreting the observed differences as constitutional characteristics of different stocks probably accentuated by various forms of selection. Spencer notes, "That large hands are inherited by those whose ancestors led laborious lives, and that those descended from ancestors unused to manual labour commonly have small hands, are established opinions." But if we accept the "opinions" as correct, it is easy to interpret the size of the hands as a stock character correlated with different degrees of muscularity and vigour, and established by selection. The hands of Japanese are in many details anatomically different from the hands of Europeans, but there is no warrant for regarding these detailed differences as other than constitutional racial differences of germinal origin accentuated modificationally in the individual lifetime.

Dwindling of Little Toe.—The alleged dwindling of the little toe has been repeatedly cited as a case in point—proving the inheritance of a modification produced by tight boots. But precise data are wanting; a dwindling has also been observed in savages who do not wear boots; it is possible that there may be in man, as there was in the ancestors of the modern horse, a constitutional variation in the direction of reducing digits; and there are other possible explanations of the rather vague assertions. It need hardly be pointed out that unless there is a measurably *progressive* dwindling with similar boots in the course of generations the case has no point. A control experiment comparing the toes in sets of brothers respectively booted and bootless would be interesting.

Results of Pressure.—Darwin (*Descent of Man*, p. 18) regards the thickened sole of even unborn infants as due to "the inherited effects of pressure during a long series of generations."

But here again it is impossible to exclude the interpretation that a variation in the direction of thickened solar epidermis might have selection-value from very ancient days, to the arboreal ape as well as to the bootless man. H. H. Wilder, in a paper in which he gives a detailed comparison of the palms and soles of Primates and Man (*Anat. Anzeig.* xiii. (1897), pp. 250-6), distinctly refuses to commit himself to a Lamarckian theory, believing that the facts may be equally well interpreted in terms of variation and selection.

Bollinger (1882) suggests that the weak development of the breasts in women of the Dachauer district is due to the old-established fashion of wearing tight corsets which are pressed flat on the breasts. It is necessary to inquire (*a*) whether the peculiarity is not a modification inflicted on each successive generation, or whether it is ever exhibited by a Dachauer woman who does not wear a corset; and (*b*) whether the same peculiarity does not occur where the fashion is entirely different.

Climatic Changes.—Virchow and others have laid stress on the fact that many peculiarities in races of men and of other living creatures are climatic in origin, and yet are now part of the natural inheritance. But acclimatisation is usually a slow and gradual process, involving selection of germinal variations, and it is difficult to get clear-cut cases of climatic modifications. It must also be remembered that Weismann expressly admits that climatic influences, especially if long-continued, may influence the germ-plasm along with whole system, and may induce germinal variations that come to stay; but this "has certainly nothing to do with the view that functional modifications of any particular organ can cause a corresponding change in the germ-plasm." (See *The Germ-Plasm*, 1893, p. 408.)

In adjacent areas with different climatic and other environmental conditions we not infrequently find closely related species or local races. It seems impossible to doubt that these are blood-relations, derived from a common ancestor. Are they not due to the environmental differences? In some way, surely, the organismal differences are causally correlated with the environmental differences, and it is granted by all that peculiarities of climate induce changes in the nutrition, respiration, circulation, and so on. If so, the germ-plasm may be affected and variations may be provoked, some of which are adaptive. But the result of these variations may be something different from and much more profitable than the modifications directly induced. They may be expressed in relation to quite different organs. Thus it seems quite unnecessary to believe in the transmission of climatic modifications as such, or in any representative degree. Moreover, we must never forget that the active organism must be credited with the power of seeking out environments which suit its inborn nature—variations included.

Plants in New Environment.—Much has been made of the changes which follow a radical change of environment. When a plant is transferred to a new soil and climate it may undergo a very marked change of habit; its leaves may become hairy, its stem woody, its branches drooping. "These," Herbert Spencer said, "are modifications of structure consequent on modifications of function that have been produced by modifications in the actions of external forces. *And as these modifications reappear in succeeding generations, we have, in them, examples of functionally established variations that are hereditarily transmitted.*" But this is a *non-sequitur*, since the modifications may reappear merely *because they are re-impressed directly* on each successive generation. It is Misunderstanding IV.

At the same time it should be noted that radical change of environment may induce germinal variations or mutations which breed true. These must be distinguished from modifications, as already explained, since we cannot interpret them physiologically as the direct somatic results of the environmental change.

Experiments on Brine-shrimps.—Reference is often made to the observations and experiments of Schmankewitsch (1875) on certain brine-shrimps belonging to the genus *Artemia.* By lessening the salinity of the water he was able to transform one type, *Artemia salina,* in the course of generations into another type, *Artemia milhausenii.* By increasing the salinity, he was

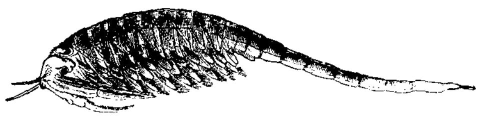

FIG. 27.—Side view of male *Artemia salina* (enlarged). (From Chambers's *Encyclopædia.*)

able to reverse the process. Although he did not himself make any such claim, his work has often been referred to as an illustration of changing one species into another, and of the inheritance of acquired characters.

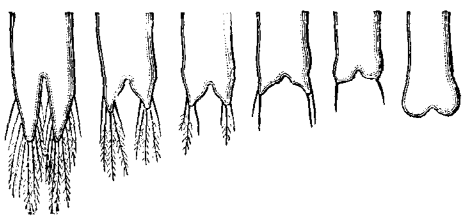

FIG. 27*a*.—Tail-lobes of *Artemia salina* (to the left) and of *Artemia milhausenii* (to the right); between these four stages in the transformation of the one into the other. (From Chambers's *Encyclopædia*; after Schmankewitsch.)

It seems very doubtful, however, whether we have here to do with modifications at all. Schmankewitsch did not modify any one *Artemia salina* into *Artemia milhausenii*; with a progressively changing environment and in the course of generations he observed a transition of the population from the one type to the other; it is probable that the change of salinity operated directly on the eggs. This seems the more likely since the differences between the two types (in shape of tail, details of bristles, etc.) are not such as we can interpret as the natural direct results of altered salinity. It is well known that slight alterations in the physico-chemical composition of the water have sometimes a great and mysterious influence on eggs and developing embryos. Furthermore, the species of *Artemia* seem to be very variable, and there is a series of intermediate forms connecting *Artemia salina* and *Artemia milhausenii.* Perhaps the altered salinity simply pulled the trigger of variability.

But if the changes were somatic modifications, it is still open to the critic to point out that Schmankewitsch experimented with a progressively changing environment on a series of generations, and that the results were due to modifications hammered afresh on each successive generation, without there being any inheritance of these modifications.

A Typical Case.—An often-quoted and typical instance was communicated to Darwin by Moritz Wagner. Some pupæ of a Texan species of *Saturnia* were brought in 1870 to Switzerland. In May, 1871, the moths emerged and were entirely true to type ; they had young, and these were fed on the leaves of *Juglans regia* (the Texan form feeding on *Juglans nigra*); these young developed into moths so different in colour and form from their parents that some entomologists referred them to distinct species. This was a well-marked individual modification, but the story stops just where it was beginning to be interesting. We are not told about the subsequent generations. If they, too, were fed on *Juglans regia*, and reared in Switzerland, they probably reproduced the new type, but this would simply mean that the modification was re-impressed on successive generations. The same seems to be true in regard to most of the climatic changes of which we have authentic information.

Experiments on Butterflies.—Some very interesting experiments have been made, especially by Standfuss and Fischer, who subjected pupæ of butterflies to abnormal temperatures, observed the subsequent modifications on the fully formed insects, and showed that these were repeated in their progeny.

Standfuss reared the pupæ of the common *Vanessa urticæ* at a lower than the normal temperature, and obtained a northern type (var. *polaris*); he reared them at a temperature higher than the normal, and obtained a southern variety (var. *ichnusa*). In the progeny he found a very small percentage (all males) which showed a change in the same direction as the parents.

Fischer worked with *Arctia caja*, reared the pupæ at 8° C., and obtained some unusually dark forms. Two of these were paired and their progeny was reared at the normal temperature. A small percentage of these—the last of the brood to emerge from the pupa-state—showed the same kind of melanistic peculiarity as the parents had shown.

Fischer pointed out, however, that the colour-aberration in the offspring was not a repetition of the parental peculiarity, though it was in the same direction and sometimes went farther. He did not regard the case as illustrating the transmission of a specific modification, but agreed with Weismann's interpretation that the germ-cells had been prompted to vary by the lowered temperature. It should also be noted that in many butterflies there is a strong constitutional—*i.e.* germinal—tendency to melanistic variation, that the aberration does not occur in all the individuals subjected to the low temperature, that it occurs in very diverse degrees, and that the experimenter *selected* two forms to pair together.

Americanisation of Irishmen.—Herbert Spencer thought that the best examples of inherited modifications occur in mankind. "Thus in the United States the descendants of the immigrant Irish lose their Celtic aspect, and become Americanised. . . . To say that 'spontaneous variation,' increased by natural selection, can have produced this effect is going too far." If the vague statement as to the Americanisation of the Irishman be correct, and if it be true that intermarriage is rare, it remains probable that the Americanisation is a modificational veneer impressed afresh on each successive generation.

Breeders' Evidence.—The evidence given by breeders in support of the theory of modification-inheritance, which is a tacit or an avowed belief of many, if not of most, appears to us in most cases too full of vagueness and misunderstanding to be of significance; but it has been often adduced by expert biologists, notably by Cope (1896), who cites his cases from Brewer (1892–3), an acknowledged agricultural authority. The first argument relates to the inheritance of characters due to nutrition, and is as follows: The size of domestic animals is often of much practical importance, and has been attended to for many years with all the carefulness which a pecuniary stake ensures. It used to be said that "feed is more than breed," but it is now recognised that "heredity or 'breed' is the more important." There is also, of course, careful selection, "but no breeder claims that a breed is or can be kept up to extra size by selection alone." "Breeders do not believe that the characters acquired through the feeding of a single ancestor, or generation of ancestors, can oppose more than a slight resistance to that force of heredity which has been accumulated through many preceding generations, and is concentrated from many lines of ancestry. Yet the belief is universal that the acquired characters due to food during the growing period have *some* force, and that this force is cumulative in successive generations. All the observed facts in the experience with herds and flocks point in this direction." The breeding of small and delicate Alderney cows was furthered by systematic underfeeding of the calves. Large-sized breeds have originated in regions of abundant food, and smaller breeds in districts of scantier forage. "This can hardly be due to accident." In short, "if these acquired characters are in no degree whatever transmitted, then certain practices of breeders, which are founded upon the contrary belief, are delusive and expensive mistakes."

We have given this argument at some length, since it deals with a subject of great practical importance, and since it is presented to us with the double authority of Cope and Brewer. It is, however, on every count most disappointingly inconclusive. If the size is a function of four variables,—(*a*) the inheritable constitution of the stock (statistically determinable in certain of its expressions at the beginning of a period of observation); (*b*) the individual modifications produced by altered nutrition (approximately determinable by control experiments and observations); (*c*) the possible occurrence of modification-inheritance; and (*d*) the amount of discriminate selection within a given period (also admitting of more or less precise statement),—then the only feasible way of reaching a conclusion as to the importance of any one factor—say the third in this case—is to eliminate the others one by one.

As to the Alderney cows, it is admitted by all that the skilful breeder can breed small or breed large, either by relying wholly on the selection of a sufficiently variable stock, or by assisting selection by modification kept up for each generation; but this does not touch the question at issue.

And if it be a fact that large-sized races always come from regions of abundant nutrition, and *vice versâ*, it is plainly consistent both with natural and artificial selection.

As to the argument that unless modification-inheritance be a fact the practice of breeders is an expensive mistake, one is tempted to retort that the latter is at least as likely as the former; but the sufficient answer is that breeders, even though they may think they do, never put their stake on the doubtful card.

Finally, it may be noted, though this is a point rather for the biologist than for the breeder, that experiments on increased size of parts are more decisive than those which refer only to the size of the whole.

Manly Miles gives two cases to illustrate what seems to him a general fact, the occurrence of modification-inheritance in breeding: "The fashion of raising lambs by nurses of other breeds, and drying up the dam at once to keep her in show condition, resulted in seriously diminishing the inherited capacity for milk production in the females of the family as treated." "Cows on short pastures and under careless management will form the habit of 'going dry' early in the season, and this habit of giving milk for a short period is not only transmitted, but becomes a marked peculiarity of the females of the family that is persisted in under better conditions of food supply."

But these and numerous similar cases only show, what is universally admitted, that a nutritive disturbance in the mother is apt to affect the nutritive vigour of the offspring.

Brewer (cited by Cope, 1896, p. 436) reports what may be called a good case. Sheep taken from a favourable region to one with alkaline or salt soil, dry climate, and corresponding forage plants, acquire a certain harshness in the wool. The change begins immediately, "but is more marked in the succeeding fleeces than in the first. It is also alleged that the harshness increases with succeeding generations, and that the flocks which have inhabited such regions for several generations produce naturally a harsher wool than did their ancestors, or do the new-comers." Of course, the second generation would naturally have harsher wool than the new-comers, but if harshness really *increases* with succeeding generations, the case is one of the best as yet brought forward.

Immunity.—Another typical line of evidence is based on the study of immunity. To this very important, but very difficult, subject we have referred in another chapter, but the particular point here may be briefly stated. It is well known that some natives are relatively immune to yellow fever; this is now a heritable quality; the question is whether it can be regarded as originally an acquired character. Was it in origin a modification of the bodily metabolism subsequent upon the disease? It seems very difficult to adopt this interpretation, and most authorities incline to the other alternative of regarding immunity as a constitutional variation which has become dominant in the race by the elimination of those members who were not immune.

It may be objected, however, that there are cases where a mother rabbit or guinea-pig has been artificially rendered immune to certain diseases, and has afterwards had young born immune. This may be due to a kind of infection before birth, some anti-toxin or other having probably passed from the mother to the unborn young. (Misunderstanding No. V.)

Medical Arguments.—A medical argument which has convinced many is somewhat as follows. Its cogency rests on the difficulty of drawing hard-and-fast defining lines.

It is alleged that a pregnant woman with smallpox may infect her unborn offspring—a clear case of intra-uterine contagion.

A tubercular mother may have an offspring without tuberculosis, but with something wrong with its heart. Here a constitutional diathesis, stimulated by a bacillus, is followed by a result in the offspring quite different from the condition in the parent.

Toxins produced by bacterial disease in the parent may affect the offspring without inducing any special disease, but by weakening its constitution and power of resistance.

Toxins produced, apart from bacterial disease, by a saturation of the parent with alcohol, opium, and the like, may affect the offspring both functionally and structurally, with the result that there are diseases and malformations.

It has been shown experimentally that toxins (hydrocyanic acid, nicotin, alcohol, etc.) may, directly injected into the eggs of fowls, affect the development so that malformation results. It is stated that the effects of lead-poisoning on the offspring may be wholly due to the father. Therefore it seems legitimate to infer that toxins produced in the body may have a direct effect upon the germinal material.

It is not shown, however, that the effect on the offspring is the same as that induced in the parent—which is the biological point under discussion—and it is a wild hypothesis that an ordinary modification liberates anything comparable to a toxin.

Alcoholism.—Habitual drunkenness in a parent or in the parents produces familiar modifications, and may be followed by dire results in the offspring. But before drawing the hasty conclusion that definite structural results of alcoholic poisoning on the parent's body are in the strict sense transmitted to the offspring, we do well to consider—(1) that the intemperate habits of the parent may be the expression of an inherited psychopathic disposition, and it is this which is transmitted to the offspring; (2) that the saturation of the body with alcohol may have a direct effect on the nutrition and developmental vigour of the germ-cells; (3) that the children of drunkards often become accustomed to alcohol as part of their food, from the days of suckling onwards.

Nervous Diseases.—Prof. Binswanger of Jena, a famous student of psychiatry, has expressed his inability to find evidence that a mental or nervous disease acquired during the individual life is, as such, or in partial expression, inherited by the offspring. There are, he of course allows, numerous cases in which an inheritance of mental or nervous diseases can be traced from one generation to another; but his difficulty was to find a case where it could be securely maintained that the first occurrence of the disease was due to external influence.

It may, of course, be urged, though it seems an untenable extreme, that mental and nervous diseases never have an exogenous origin, but are always referable to germinal defect. If so, it simply forces us to say that this line of argument is closed as far as the question of the transmissibility of modifications is concerned.

Modifications of Habits and Instincts.—Many animals are very plastic in their habits, and some show some plasticity even in their instincts. It seems an interesting line of experiment to try to determine whether there is any evidence of transmission of peculiar *individually modified* habits. For an expert discussion of the subject we must refer to Principal Lloyd Morgan's *Habit and Instinct.*

There are obviously many difficulties. The experimenter must be sure that the original change of habit is really *modificational,* not an inborn idiosyncrasy. He must be careful to eliminate the possibility of the offspring learning by imitation or suggestion. He must also exclude the possibility of selection. He must remember that the offspring are probably as docile, as plastic, as adaptable as their parents, or perhaps more so. Mountaineering mules come to have an extraordinary power of adapting themselves to peculiar exercises, but mule does not inherit from mule!

A hen becomes an adept in rearing ducklings: will her own children, put to a similar task, be less fussy than she was at first? House-martins have learned to build beneath the eaves: has there been any hereditary transmission of this acquired habit, or is it merely "the result of intelligent adaptation through the influence of tradition"? Have grouse inherited the habit of flying so as to avoid telegraph wires? Is it indubitably the case that the kittens of a cat "taught to beg for food like a terrier" may spontaneously exhibit the same peculiar habit? These are some of the cases which Lloyd Morgan discusses, and his conclusion is that the evidence for the transmission of acquired habit is insufficient.

§ 10. *As regards Mutilations and the Like*

When we think of the bellicose activities of our ancestors, it seems almost absurd to discuss the question of the transmissibility of the results of mutilations, wounds, and other injuries. Moreover, it is well known that dishorning of cattle, docking of horses' tails, curtailing of sheep, cropping of dogs' ears, and similar practices, have been continued for many generations without any known hereditary effect. The circumcision of the children of Jews and Mohammedans has gone on for many centuries, but there is no demonstrable structural result. Yet the question is one of *possibilities*, and there is a huge literature of observations and experiments.

Few Useful Results.—The net result, it must be confessed, is very disappointing, and the reasons for this are not far to seek.

(1) Many of the experiments and observations have failed to conform to the ordinary canons of scientific method. Many of them overlook the probability of coincidence, identify *post hoc* with *propter hoc*, mix up observation and inference, or base a conclusion on a small number of instances. It may be noted that cases suggesting the transmission of the results of mutilation and injury are most abundant in the older, less critical literature. What may be called good cases have been very scarce of recent years, though many observers have been on the watch for them.

(2) Some of the kinds of experiment—*e.g.* the amputation of large parts or of portions of internal organs, such as the spleen—are evidently of a kind which must be rare in nature. Therefore, though such "fool's experiments," as Darwin would have called them, may have some indirect value, they tend to be of little significance to the evolutionist.

(3) The experimental repetition of those mutilations and injuries which *are* common in nature is of little value, since nature's experiment shows with sufficient clearness that the results are not transmitted. If they were there would be but little now left of man and other combative organisms. As Hartog says, "The tendency to transmit the mutilation itself would be so ruinous as to rapidly extinguish any unhappy race in which it was largely developed" (*Contemp. Rev.*, v. 64, p. 55). As a matter of fact, even in the individual lifetime the results of mutilation are very often repaired by regeneration, which in its specialised expression is probably the adaptive outcome of prolonged selection.

(4) If the results of mutilation can be in any degree transmitted, they must affect the germ-cells in some specific way. The improbability of this is very great in the case of many mutilations, such as lopping off a tail. The amputation has often little demonstrable effect beyond a slight irritation of the tissues at the cut surface; the organism's reaction bears little relation to the actual effect produced; a considerable part of the body has been lost, but there is no constitutional disturbance—the

reaction is a mere scar. Why should one expect the offspring to have a shorter tail because its parent has been curtailed ? Might one not as reasonably expect a longer tail ? No one has ever observed that the descendants of much-pruned fruit-trees or decorative shrubs are any the smaller in consequence. The length of the hair in offspring is not known to be affected by the frequent cropping, clipping, or shearing of their parents. In fact, the structural results of most mutilations are not modifications in the usual sense.

(5) But there are cases in which the removal of a part has deeply saturating effects. Thus the removal of a thyroid gland may have an influence on many parts of the body. In such cases, therefore, the possibility of the germ-cells being influenced is more conceivable. But, unless the change in the offspring—supposing that there is some change—corresponds to the direct change wrought upon the parent, we have not to deal with modification-inheritance of the first degree, which is the only question under dispute.

(6) Since the structural change due to a mutilation is not on the same plane as the ordinary modifications which occur in nature, we do not expect useful results from further mutilation experiments. We may refer, however, to the suggestion made by Dr. J. W. Ballantyne,* that in this connection, as with other modification experiments, investigators err by beginning at too late a stage, after the organism is firmly set. It may be that experiments on early stages would yield more positive results. It may be that the germ-cells in their early generations are more reachable by, or sensitive to, somatic influences.

Illustrations.—In our brief discussion of this well-worn subject, we shall for convenience distinguish three categories : (A) amputations, such as docking the tail ; (B) wounds, such as the rupture of the hymen ; (C) deformations, such as the compression of the

* "Discussion on Heredity in Disease," *Scottish Med. and Surg. Journal*, vi. (1900), p. 312.

Chinese lady's foot. Under each category we shall notice merely a few typical cases, which may be added to as the reader pleases by referring to the literature cited, or by consulting the great work of Delage.

Amputations repeated Generation after Generation.—Circumcision among Jews and Mohammedans, docking horses, dogs, and sheep, cutting off parts of the ears of dogs, dishorning cattle, are cases in point, and there is no evidence of transmitted result. Darwin (1879) does indeed cite Riedel to the effect that a shortened prepuce has been induced among the Mohammedans of Celebes, but Delage notes the inconclusiveness of Riedel's observations. Haeckel (1875) and Leidesdorff (*Wien. med. Wochenschr.* 1877) have also stated that a rudimentary prepuce occurs more frequently in races who practise circumcision, but other statistics do not bear this out. As Ziegler says (1886, p. 27), "There is in this respect no difference between Jews and Christians; among the latter a defective development of the prepuce is as frequent as among the former." See also Roth, *Correspondenz-Blatt f. Schweizer Aerzte*, 1884.

Weismann cut off the tails of mice for nineteen generations, Bos for fifteen, Cope for eleven, Mantegazza and Rosenthal likewise, but in no case was any inherited result observed. An American record of the production of a tail-less race almost certainly illustrates an unscientific use of the imagination.

The tails of fox-terriers are often cut, and pups with short tails are sometimes observed. The following case is representative of a number of records. A fox-terrier, whose tail had been cut, had four pups, one with a full-length tail, one with a rather short tail, and two with quite short tails. But the short tails had the usual tapering vertebræ (D. E. Hutchins, *Nature*, lxx., 1904, p. 6).

Delage cites Tietz (1889) to the effect that kittens with an atrophied tail are *frequent* in the Eiffel, where the peasants habitually curtail their cats—in mistaken kindness, for they believe that there is a worm at the root of the tail which keeps them from catching mice! If abortive tails are unusually common in that district, the fact is of much interest, and Delage does not find sufficient explanation in the suggestion of Dingfelder (1887), that, as the peasants leave short-tailed kittens alone, an inborn variation towards short tails has been allowed to diffuse itself. It is, of course, easy to appeal to an innate tendency to shortening of the tail, but it is curious that the examples should be found so generally among domesticated animals, like cats and dogs, sheep and horses, which are so often artificially docked.

Amputations not repeated throughout Generations.—These form what we may call the "curtailed cat" type, the point being that a she-cat whose tail has been cut off accidentally or otherwise has been known to bear kittens, some or all of which have tails shorter than the normal. The cogency of such cases is annulled when we remember,—(1) the existence of a Manx and Japanese breed of tail-less cats; (2) the occasional occurrence of tail-less or short-tailed kittens as "sports" in the litters of quite normal parents; and (3) the frequently observed variability of the tail region in many mammals. In all such cases at least two inquiries are imperative: (1) some estimate of the probability of coincidence, since the *post hoc* may be no *propter hoc*, but merely a variation which happens to resemble more or less the result of the mutilation; and (2) an investigation into the pedigree of both parents, since there may be in either or in both an innate tendency towards a shortening of the tail. These inquiries are not usually made.

A number of very interesting cases are given by Delage (1903), and it is difficult to dispose of them except by calling them "mere coincidences." One of my colleagues has told me of a case of a child with a peculiar bare patch among the hair, corresponding to a similar area on the mother's head, where the bareness was due to ringworm. The child's patch was bare save for a narrow streak of short hair, stretching about half way across. The patch was a little in front of the mother's, but was similarly situated above the left ear. What can one say but "coincidence"? Or may one suggest that the ringworm found out a hereditarily weak spot?

Wounds repeated Generation after Generation.—We do not aim at any surgical precision in distinguishing amputations from wounds. Our point is simply that there is a difference between the effect of an amputation which may be almost negative, and the effect of a wound which disturbs the relations of parts. The classification is borne out by the fact that whereas there is not a grain of evidence, so far as we know, to lead one to believe in the inheritance of the results or any results of amputations, except when very important organs are operated upon, the same cannot, at first at least, be said in regard to the effects of wounds.

The typical case here is the rupture of the hymen in the first sexual intercourse—a trivial lesion, perhaps, but one which has occurred in every generation, and one of which no inherited results are known. Like circumcision, it is in one respect not a quite satisfactory negative case, being limited to one sex. Among savage peoples, however, ear-boring, nose-boring, and the like, have been practised by both sexes for many generations; and it need hardly be said that no inherited result has ever been observed.

Casual Wounds.—Darwin cites the case of a man whose thumbs were badly injured in boyhood, as the result of frost-bite. His oldest daughter (S) had thumbs and thumb-nails like the father's; his third child was similar as to one thumb; two other children were normal. Of the four children of S, the first and the third, both daughters, had deformed thumbs on both hands. The cogency of this case depends on whether there was or was not any previous family tendency to thumb-deformity. It may have been that the frost-bite was really an unimportant incident. Darwin gives another case of a man who, fifteen years before marriage, lost his left eye by suppuration. His two sons had left-sided microphthalmia. Here we have probably to deal with an innate eye-defect in the father.

Bouchut * reports the case of a man of twenty-five who injured his hands and feet by a fall from a scaffold. Of five children only one was normal. His son had one finger on each hand and two toes on each foot. A daughter (M) had two toes on each foot, one finger on the right hand, and two on the left. She married a normal man, and of her four children the oldest was normal, the others like herself.

Cases like the last may seem puzzling to those unaccustomed to deal critically with the facts of inheritance. But in reality they are in most cases merely illustrations of the familiar fallacy of confusing *post hoc* and *propter hoc*, of mixing observation and inference (Ziegler, 1886, p. 26). Bouchut does not say that the children showed the same deformity as their father acquired; he does not tell us about the ancestry of the father and mother, an indispensable fact if a case is to be considered seriously, since inborn malformations are common in some families; finally, the frequency of inborn malformations of the fingers and toes must be borne in mind, and the possibility of coincidence allowed.

Ziegler (1886, pp. 29, 30) discusses a number of cases where defects

* *Nouveaux Éléments de Pathologie générale,* Paris, 1882. Cited by Ziegler, *1886, pp. 3, 4.*

in the eye occurred in the offspring of animals whose eyes had been operated on, injured, or infected. But experiments in which the eyes are infected with tubercle or the like are not relevant until all possibility of the offspring being infected is excluded; and as for cases such as those given by Brown-Séquard (1880), where the extirpation of the eye-bulb in the parent was followed in the offspring by the loss of one eye or of both, or by corneal obscuration, it is necessary to compare the results with the statistics as to the frequency of various kinds of innate eye-defects.

Deformations.—We do not know all that we should like to know in regard to the artificially deformed feet of Chinese ladies, but there is no evidence that the long-continued deformation has resulted in *any* hereditary change.

For untold ages the herdsmen in some parts of the Nile valley have artificially deformed the horns of their cattle, making them bend forwards, twist spirally, and so forth; but no effect on offspring has ever been observed (R. Hartmann, *Die Haussäugethiere der Wildländer. Ann. Landwirthsch.*; Berlin, 1864, p. 28).

The Rook's Bill-feathers.—Settegast and others have referred to the bristle-like feathers about the nostrils and the base of the bill in the young rook. They are said to disappear mechanically when the bird begins to bore with its beak in the ground, yet they are always present in the nestling. To cite this as an example of the *non-transmission* of a deformation-effect is probably quite erroneous, for there is no proof that the disappearance is causally connected with burrowing. It is probably a constitutional peculiarity that these feathers should be moulted and not replaced. They disappear even if the rook is not allowed to bore (*see* Oudemans and Haacke, cited by Delage, 1903, p. 223). On the other hand, to start from the fact that the bristles disappear even if there is no boring in the ground, and to cite this as an instance of the transmission of a deformation-effect, is equally fallacious. There is no evidence that it was a deformation-effect to start with.

Some Puzzling Cases.—While the argument based on the apparent transmission of the results of mutilation appears to us very weak, it must be admitted that there are some cases which, if accurately recorded, are puzzling. It is desirable that any fresh cases, similar in nature to those which we propose to illustrate, should be studied carefully and without prejudice. Though they may not prove modification-inheritance, they may lead to interesting results.

Prof. Haeckel * records that a bull on a farm near Jena had its tail squeezed off at the root by the accidental slamming of the byre-door, and that it had thereafter a tail-less progeny. This is very interesting, but we are bound to ask—(1) how often tail-less cattle arise apart from curtailing by the byre-door; (2) whether the bull had any tail-less offspring before it was curtailed; (3) how many tail-less offspring it actually had, and so on. It may be that the answers to these questions would be quite satisfactory, but, to make the case cogent, the questions should have been forestalled.

In 1874 Herr W. Besler, in Emmerich on the Rhine, wrote to Prof. L. Büchner (1882, p. 24) to report the following case. At Döbeln, in Saxony, at Eichler's Hotel there, he saw a young dog apparently bereft of ears and tail. When he remarked that the beast had been far too much cut, he was told that this was not the case, for it and its brother had been born so, out of a litter of four. The mother was normal, the father was an "Affen-Pinscher," whose ears and tail had been cut. The same condition had occurred once in a previous litter. Supposing that this was more than an ostler's yarn, we should have to inquire into the ancestry of the father and mother to see whether inborn shortness of ears and tail had ever manifested itself in the family.

Prof. Büchner also relates that in the autumn of 1873 a building-contractor, K——, in Westphalia, bought a duck whose right "wing-bone" had been broken and had mended in a crooked fashion. Next spring the duck had four ducklings, two of which showed on the right wing, and two on both wings, an extra feathered wing (4-5 in. in length), protruding immovably at an angle of 45° above the otherwise normal wing. But this duplicity, if such it was, bore no precise relation to the original injury, and probably was quite unconnected with it.

Büchner gives a number of other instances. Thus Williamson saw dogs in Carolina which had been tail-less for three or four generations, one of the ancestors having lost the tail by accident.† But tail-lessness is also known as a germinal variation.

Bronn ‡ describes the case of a cow which lost one horn by ulceration; it had afterwards three calves which showed on the same side

* *Schöpfungs-Geschichte*, ed. 1870, p. 102.
† Waitz, *Anthropologie der Naturvölker*, i. p. 93.
‡ *Geschichte der Natur*, 1871, p. 96.

of the head no true horn, but a small nucleus of bone hanging to the skin. It may have been that an inborn weakness, which led to the ulceration of the mother-cow's horn, took a slightly different expression in the calves.

Dr. J. W. Ballantyne quotes Kohlwey's experiments on pigeons: "He cut off the posterior (first) digit of the foot, and the mutilated bird got into the habit of turning the fourth digit backwards and using it in perching; he got no descendant of these mutilated birds without a posterior digit, but he got a descendant of one of the pairs with its fourth digit turned backwards like the first. The mutilation was not transmitted, but the physiological adaptation to meet it was." Is it sufficient to regard this simply as a coincident variation?

Some of the best cases are those in which a morbid change was associated with the loss or injury of a particular structure. A cow loses its left horn by suppurative inflammation; it has subsequently three calves in which the left horns were abortive (Thaer, 1812). But it may be that the original loss was due to a weakness of germinal origin.

Prof. W. H. Brewer (1892–3) is responsible for launching a large number of rather unseaworthy instances of modification-inheritance. *Inter alia*, he tells the story of a pure-bred game-cock who lost an eye in a fight, and transmitted his loss. While the wound was very malignant, he was turned into a flock of game-hens of another strain, and "a very large proportion of his progeny had the corresponding eye defective." "The chicks were not blind when hatched, but became so before attaining their full growth. The hens afterwards produced normal chickens with another cock."

Of great interest is the statement made by some botanists that some peculiar effects on trees due to mites, ants, etc., are transmitted. Thus Lundström says that the little shelters (acarodomatia) produced on the leaves of lime-trees, etc., by mites, may appear when there are no mites. But are there ever no mites?

But, admitting that there are some puzzling cases, we cannot avoid the general conclusion that as regards mutilations, amputations, wounds, and deformations, the case for the affirmative is not strengthened by further inquiry.

§ 11. *Brown-Séquard's Experiments on Guinea-Pigs*

In recent discussions of modification-inheritance much prominence has been given to the experiments made by Brown-Séquard, Westphal, and others on the apparent transmission of artificially induced epilepsy in guinea-pigs. The reason for this prominence is that the case is not without cogency, and that a record of precise experiments (although of a somewhat ugly character) comes as a relief amid anecdotal evidence. Prof. E. Ray Lankester goes the length of saying (1890, p. 375), "The one fact which the Lamarckians can produce in their favour is the account of experiments by Brown-Séquard, in which he produced epilepsy in guinea-pigs by section of the large nerves or spinal cord, and in the course of which he was led to believe that in a few rare instances the artificially produced epilepsy was transmitted." As the case has been often discussed—*e.g.* by Romanes (1895, vol. ii. chap. iv.)—we shall treat of it briefly.

What the Experiments were.—Through a long series of years (1869-91), Dr. Brown-Séquard, a skilful and ingenious, if somewhat impetuous, physiologist, experimented on many thousands of guinea-pigs. He made a partial section of the spinal cord in the dorsal region, or cut the great sciatic nerve of the leg; he observed that the injury was followed after some weeks by a peculiar morbid state of the nervous system, corresponding in some of its features to epilepsy in man; he allowed these morbid animals to breed, and found that the offspring were frequently decrepit, and that a certain number had a tendency to the so-called epilepsy.

Results of the Experiments.—If it be understood that we have omitted or altered a few difficult technicalities, we may call the following statement Brown-Séquard's summary of his results. The inverted commas are ours:

(1) "Epileptic" symptoms appeared in the offspring of parents who had been rendered "epileptic" by an injury to the spinal cord.

(2) "Epileptic" symptoms appeared in the offspring of parents who had been rendered "epileptic" by section of the sciatic nerve.

(3) An abnormal change in the shape of the ear was observed in the offspring of parents in which a similar change followed a division of the cervical sympathetic nerve.

(4) Partial closure of the eyelids was observed in the offspring of parents in which that state of the eyelids had resulted either from section of the cervical sympathetic nerve, or the removal of the superior cervical ganglion.

(5) An injury to the restiform body (associated with the medulla oblongata) was followed by a protrusion of the eye (exophthalmia), and this reappeared in the offspring sometimes through four generations, even affecting both sides, though the lesion in the parent had only been on one of the corpora restiformia.

(6) An injury to the restiform body near the nib of the calamus was followed by hæmatoma and dry gangrene of the ears, and the same conditions reappeared in the offspring.

(7) After a section of the sciatic nerve, or of the sciatic and crural, some of the guinea-pigs gnawed off two or three of the toes, which had become anæsthetic; in the offspring two or three toes were absent. Sometimes, instead of complete absence of the toes, only a part of one or two or three was missing in the young, although in the parent there was a loss not only of the toes, but of the whole foot (partly eaten off, partly destroyed by inflammation, ulceration, or gangrene).

(8) As effects of an injury to the sciatic nerve, there followed various morbid states of the skin and hair of the neck and the face, and similar alterations in the same parts were observed in the offspring.

When the sciatic nerve had been cut in the parent, the descendants sometimes showed a morbid state of the nerve. There was also a similarity in the successive appearance of the phenomena, described by Brown-Séquard as characteristic of the periods of development and of abatement of the "epilepsy," especially in the appearance of the epileptogenic area and the disappearance of hair around that area whenever the disease showed itself.

Muscular atrophy of the thigh and leg followed section of the sciatic nerve, and this was also observed in the offspring.

After cutting the restiform body one eye suffered deterioration; this was seen in the offspring in one eye, or even in both.

In general, the morbid conditions may affect both sides in the parents and only one in the offspring, or *vice versâ*, or the side affected may be different.

One generation may be skipped, but the duration of transmission was in some cases traced through five or even six generations.

The females seemed better able to transmit morbid states than the males.

As to the frequency of transmission, some inherited result was observed in more than two-thirds of the cases.

Brown-Séquard's results were partly confirmed by his assistants, Westphal (1871) and Dupuy (1890), by Obersteiner (1875), and by Romanes (1895). Dr. Leonard Hill divided the left cervical sympathetic nerve in a male and a female guinea-pig, and thereby produced a droop of the left upper eyelid. Two offspring of this pair exhibited a well-marked droop of the upper eyelid. "This result is a corroboration of the series of Brown-Séquard's experiments on the inheritance of acquired characters."

Facts to be noted, which dispose of a Number of Criticisms.—It is stated that the so-called "epileptic" state may also be induced in the dog by injury to the cerebral cortex, and may, in this case also, reappear in the offspring. If this be so it shows that we have not to deal with a tendency *peculiar* to guinea-pigs.

It is stated that the "epileptic" condition does not occur spontaneously—*i.e.* apart from injury to the nervous system—in guinea-pigs. Therefore the interpretation of the apparent inheritance as being due to a fresh variation which happened by coincidence to resemble the parental state, is inadmissible.

As the tendency to "epileptic" fits (which do not last long) was seen only in the offspring of animals which had been operated on, and was manifested only after appropriate stimulus, especially after irritating an "epileptogenic" zone behind the ear on the same side as the original injury, we must pass by Galton's suggestion (1875) of the possibility of reappearance through imitation. Even if it be allowed that there is a certain infectiousness in "fits," this would not apply to the loss of toes, the diseased state of the ear, the protruding eyes, and so on.

It is stated that the morbid condition of the parents was also induced by bruising the sciatic nerve without cutting the skin, or by striking the animals on the head with a hammer. If this be so it seems to show that the result may occur without any associated microbe influence, and possible infection of the offspring thereby (Weismann's criticism, in part). The hypothesis of microbes does not seem to be supported by any definite facts, but we note that it is not entirely excluded by Ziegler in his review of possible explanations (1886, p. 29).

Brown-Séquard experimented with both males and females, and although he got more striking results with the latter, he did not fail with the former. This seems to lessen the force of the criticism that the offspring were affected during gestation, and therefore not, in the strict sense, hereditarily.

Criticisms.—(1) The original modification was cutting, bruising, or destroying part of the nervous system ; the subsequent result was the "epileptic" state, and the various other diseased conditions mentioned. It need hardly be said that the mutilation or injury inflicted on the parent was never reproduced in the offspring, though the subsequent results sometimes were.

(2) The conditions exhibited by the offspring were very diverse—general feebleness, motor paralysis of the limbs, trophic paralysis resulting in loss of toes, cornea, etc., other nervous and sensory disorders, and in some cases the particular "epileptic" state. In a number of cases the condition of the offspring was so different from that of the parent, that the only common feature was that in both cases there were abnormal neuroses. Romanes, while regarding his results as corroborations of those of Brown-Séquard, admitted that the epileptic condition was only rarely transmitted.

(3) Even numerically there was no small diversity in the results. Thus in one set of experiments (Obersteiner, 1875), out of thirty-two young ones born of "epileptic" parents, only two showed symptoms of "epilepsy" and paralysis, three were paralytic, and eleven were only weak. Romanes did not find that any of the offspring of parents who had eaten their toes off showed, even in six generations, any defect in these parts. Even Brown-Séquard only observed this peculiar "transmission" in about 1 or 2 per cent. of cases.

(4) Prof. Ziegler's criticism is partly based on the allegation that guinea-pigs (as we keep them in captivity) are pathological and nervous animals, very readily thrown into an epileptic state. On

making a slight cut in the skin, on the occasion of a small operation on the neck, Ziegler sent an apparently healthy guinea-pig into a severe epileptic fit. But there seems considerable difference of opinion as to this nervousness of captive guinea-pigs.

(5) It seems to us that the original modification was too violent to afford satisfactory data in connection with the present discussion. No matter how neatly the operations were effected, the partial section of the spinal cord, the cutting of the sciatic or of the cervical sympathetic nerve, the removal of the superior cervical ganglion, the injuring of the restiform body, imply very serious injuries, and it is hard to believe that others were not implied in some of the experiments—*e.g.* on the restiform body. But if a modification is violent it may disturb the whole organism, nutritive * and reproductive † functions alike, and it may naturally lead to abnormality in the offspring. Especially may it lead to general decrepitude, which, it seems to us, was the most frequent result. At the same time this hardly touches the most distinctive feature of the experiments, that sometimes there appeared in the offspring morbid conditions precisely similar to the results of the injury inflicted on the parents. It may be, however, that only particular parts of the body are susceptible to the influence of the original disturbance.

Prof. T. H. Morgan (1903, p. 257) directs attention to the experiments of Charrin, Delamare, and Moussu, which have an interesting bearing on some of Brown-Séquard's results. After the operation of laparotomy on a pregnant rabbit or guinea-pig, the kidney or the liver became diseased, and the offspring showed similar affections. The experimenters suggested that some substance set free from the diseased kidney of the mother affected the kidney of the young in the uterus. "May not, therefore, Brown-Séquard's results be also explained as due to direct transmission from the organs of the parent to the similar organs of the young in the uterus?" But this would not be inheritance in the strict sense. It should be noted, however, that what has been just said does not of course apply to those cases in which Brown-Séquard experimented on the male parent. Charrin maintains on experimental grounds that "cytotoxins" may pass not only from the mother to the fœtus, but from either parent to its germ-cells—ova or spermatozoa (see *Revue générale des Sciences*,

* Dupuy, while confirming Brown-Séquard, laid emphasis on the alterations of nutrition after the experiments.

† Sommer notes a diminution of fertility after the experiments.

Jan. 15, 1896). Moreover, Voisin and Peron have found evidence that in epilepsy a toxin is produced which causes convulsions when injected into animals (see *Archives de Neurologie*, xxiv., 1892, and xxv., 1893, and Voisin's *L'Épilepsie*, Paris, 1897, pp. 125–133). It is thus not a mere speculation to suppose that a toxin was produced in the guinea-pig epilepsy, and that this affected the germ-cells of both sexes. This suggestion is made by Prof. Bergson in his remarkable book *L'Évolution Créatrice* (1907), and he adds to the suggestion the query, May not something of the same sort be true in those cases where acquired peculiarities are transmitted ?

Prof. T. H. Morgan (1903, p. 255) also notes an interesting fact. " While carrying out some experiments in telegony with mice, I found in one litter of mice that when the young came out of the nest they were tail-less. The same thing happened again when the second litter was produced, but this time I made my observations sooner, and examined the young mice immediately after birth. I found that the mother had bitten off, and presumably eaten, the tails of her offspring at the time of birth. Had I been carrying on a series of experiments to see if, when the tails of the parents were cut off, the young inherited the defect, I might have been led into the error of supposing that I had found such a case in these mice. If this idiosyncrasy of the mother had reappeared in any of her descendants, the tails might have disappeared in succeeding generations. This perversion of the maternal instincts is not difficult to understand, when we recall that the female mouse bites off the navel-string of each of her young as they are born, and at the same time eats the after-birth. Her instinct was carried further in this case, and the projecting tail was also removed.

" Is it not possible that something of this sort took place in Brown-Séquard's experiment ? The fact that the adults had eaten off their own feet might be brought forward to indicate the possibility of a perverted instinct in this case also." On the other hand, this interpretation cannot apply to some other results which Brown-Séquard observed.

Sommer's Experiments far from corroborating Brown-Séquard's.— In experiments the results of which were published in 1900, Max Sommer repeated some of those which Brown-Séquard and others had made, but without corroborating them.

The so-called " epilepsy " was induced by cutting the sciatic nerve on one side or on both sides ; the tendency to " fits " occurred some days or some weeks after the operation ; they were brought on by rubbing particular areas of the body (the epileptogenic zones) ; whether they ever occurred spontaneously remained doubtful, since any friction on the appropriate spots—*e.g.* when the animal scratched itself—served to bring them on. After some months the tendency to the attacks disappeared, and irritation of the appropriate areas was followed by only a slight fit or by none. (This is a noteworthy fact.)

The fertility of the " epileptic " guinea-pigs was lessened.

Twenty-three young ones were reared (a small number compared with those in Brown-Séquard's experiments)—six from two pairs in which the father was " epileptic," six from four pairs in which the mother was " epileptic," and seven from five pairs in which both parents were " epileptic." *In no case did " epilepsy " appear in the offspring.* Even paralysis of one or more of the extremities was not demonstrated, though most carefully looked for.

In the parents there were several defects in the toes or ulcerations of the hind extremities, but *in no case was there reappearance of the defects or ulcerations in the offspring.*

Two of the young were decrepit, and in one there was a clouding of the cornea; but there is no warrant for associating this directly with the " epilepsy " of the parents.

Sommer's conclusion is as follows : " As regards the hereditary transmission of epilepsy in guinea-pigs, or of other accidentally acquired pathological symptoms—*e.g.* defects in the toes—we have obtained an absolutely negative result; we have not been able to confirm the experiments of Brown-Séquard and Obersteiner; and we do not think that these can any longer serve as a support to the doctrine of the inheritance of acquired characters." *

Before leaving the subject of these disagreeable experiments we may be permitted to express our opinion that, altogether apart from convictions as to the ethical limits of scientific inquiry, a sound biology is not likely to gain much from experiments the conditions of which are so utterly different from those occurring in the state of nature. It seems to us that they are entirely

* Sommer also points out that the guinea-pig's " epilepsy " does not correspond to true epilepsy in man, but rather to the so-called reflex epilepsy which follows from peripheral nerve-injuries.

different from experiments on decapitated earthworms, curtailed lizards, crabs with lost limbs, and the like, for there the investigator is in touch with injuries which frequently occur in natural conditions.

The case is certainly a difficult one, but from what we have said it must be evident that it cannot be cited without qualification in support of the thesis that somatic modifications are transmissible. It is illegitimate to conclude, as Debierre does (1897, p. 4): "Il est donc incontestable que des caractères acquis artificiellement pendant l'âge adulte de l'animal ou acquis naturellement pendant la vie embryonnaire peuvent être transmis par l'hérédité."

Our general conclusion is that the results of Brown-Séquard's experiments do not strengthen the affirmative position; and that their probable interpretation is that the artificially induced epilepsy liberated a toxin which affected the germ-cells in some cases, the germ-cells and the fœtus in other cases.

§ 12. *Negative Evidence in favour of the Affirmative Answer*

In support of the affirmative answer Herbert Spencer adduced what he called *negative* evidence—namely, those "cases in which traits otherwise inexplicable are explained if the structural effects of use and disuse are transmitted."

(1) First he referred to the co-adaptation of co-operative parts. With the enormous antlers of a stag there is associated a large number of co-adaptations of different parts of the body, and similarly with the giraffe's long neck and the kangaroo's power of leaping. Spencer argued that the co-adaptation of numerous parts cannot have been effected by natural selection; but that it might be effected by the hereditary accumulation of the results of use.

It must be admitted that co-adaptations are difficult to account for in terms of the ordinary selection formula, but it is also difficult to accept the use-inheritance interpretation. We do not really know to what extent deep-seated co-adjustment can be effected by exercise even in the course of a long time, and the theory requires such data before it can be more than a plausible interpretation, with certain *a priori* difficulties against it.

Another interpretation may be suggested. If an animal suddenly takes to leaping, many individual adjustments to the new exercise may arise; if the animals of successive generations leap yet more freely, they may individually acquire more thorough adjustments. Meanwhile there may arise constitutional variations making towards adaptation to the new habit, and under the screen of the individual modifications these may increase from minute beginnings till they acquire selection-value (Mark Baldwin, Lloyd Morgan, and Osborn). Nor should it be forgotten that variations in different parts of the body are often correlated. The subsidiary theory of germinal selection is also helpful. Finally, it is possible that in some of these cases the result was not due to the gradual accumulation of minute variations, but was originated by one of those sudden discontinuous changes which are now called mutations.

(2) Secondly, Spencer dwelt upon the notably diverse powers of tactile discrimination possessed by the human skin, and sought to show that while these could not be interpreted on the hypothesis of natural selection or on the correlated hypothesis of panmixia, they could be interpreted readily if the effects of use were inherited. But the difficulty again is to get secure data. It is uncertain how much of the inequality in tactile sensitiveness is due to individual exercise and experience, though it is certain that tactility in little-used parts can be greatly increased by use. Nor is it certain how much of the apparent unlikeness in tactility is due to unequal distribution of peripheral nerve-endings and how much to specialised application of the power of central perception. As Prof. Lloyd Morgan says: "We do not yet know the limits within which education and practice may refine the application of central powers of discrimination within little-used areas. The facts which Mr. Spencer adduces may be in a large degree due to individual experience, discrimination being continually exercised in the tongue and finger-tips, but seldom on the back or breast. We need a broader basis of assured fact." Nor, it may be added, is the action of selection to be excluded.

(3) Spencer's third set of negative evidences was based on rudimentary organs which, like the hind limbs of the whale, have nearly disappeared. Dwindling by natural selection is here out of the question; and dwindling by panmixia—*i.e.* the diminution of a structure

when natural selection ceases to affect its degree of development—"would be incredible, even were the assumptions of the theory valid." But as a sequence of disuse the change is clearly explained. Prof. Lloyd Morgan replies : "Is there any evidence that a structure really dwindles through disuse in the course of individual life ? Let us be sure of this before we accept the argument that vestigial organs afford evidence that this supposed dwindling is inherited. The assertion may be hazarded that, in the individual life, what the evidence shows is that, without due use, an organ does not reach its full functional or structural development. If this be so the question follows : How is the mere absence of full development in the individual converted through heredity into a positive dwindling of the organ in question ?" Moreover, the convinced Neo-Darwinian is not in the least prepared to abandon the theory of dwindling in the course of panmixia, especially in the light which Weismann's conception of germinal selection has thrown on this process.

§ 13. *The Logical Position of the Argument*

Before we state what appears to us at present the inevitable conclusion, it may be useful to indicate briefly the logical position of the argument.

Weismann has pointed out that there are two possible methods by which the affirmative position—that modifications are transmissible—might be established. In the first place, there might be actual experimental proof of such transmission ; in the second place, there might be a collection of facts which cannot be interpreted without the hypothesis of modification-inheritance.

Experiment.—The experimental method has not been followed as often as might have been expected, and where it has been followed the results are far from conclusive. But it is important to remember that although a few good cases of the inheritance of an acquired character would prove the possibility of such inheritance, hundreds of failures to demonstrate the transmission experimentally do not prove that it is impossible.

The Neo-Lamarckian believes that when new conditions of life operate in an approximately similar way for many generations, they will produce definite and slowly cumulative effects upon the organisms subjected to them. He is by no means committed to the belief that every change of conditions will produce appreciable hereditary effects in a few generations. The point is not whether modifications are fully and completely transmitted, but whether *any trace* of them may be transmitted. Still less is the Neo-Lamarckian bound to admit that any given change of conditions, more or less arbitrarily selected by any one as being convenient for experimental purposes, will produce recognisable results in the following generation. Thus the fact that most of the experimental results are inconclusive or negative does not disprove the Lamarckian belief.

Interpretation.—As to the second method, that of the interpretation of facts, it cannot be very conclusive either, since both sides have to prove a negative in order to establish their case. The Neo-Lamarckians have to show that the phenomena they adduce as illustrations of modification-inheritance cannot be interpreted as the results of selection operating on germinal variations. In order to do this to the satisfaction of the other side, the Neo-Lamarckians must prove that the characters in question are outside the scope of natural selection, that they are non-utilitarian and not correlated with any useful characters—a manifestly difficult task. The Neo-Darwinians, on the other hand, have to prove that the phenomena in question cannot be the results of modification-inheritance. And this is in most cases impossible. Thus we seem to reach a logical dead-lock.

Cases where the Theory of Modification-Inheritance is inapplicable.—It is true, however, that there are certain characters of certain organisms, in regard to which it may be said with some security that they could not have arisen by the inheritance of acquired characters. Thus many insects and the like have adaptive characters in their cuticular structures—knobs suited for crushing, saws suited for cutting, gimlets suited for boring, and so on. But these cuticular structures are non-cellular, non-living parts of the external investment of the body; they are made and re-made (after moulting), by the underlying living skin. How then can they be interpreted in terms of modification-inheritance? The matter becomes even more difficult when we consider cases in which the adaptiveness is in the colour or markings of these inert cuticular parts. Weismann has argued that, since there are some adaptive characters which cannot be interpreted in terms of modification-inheritance, this hypothetical factor need not be assumed in attempting to interpret the origin of other adaptations, similar to the former, except that the factor in question is not by the nature of the case apparently excluded from having any connection with them.

But it cannot be said that this application of the "law of parsimony" is altogether successful. It may recoil on those who use it. It might be argued that there are some adaptive characters which cannot be readily interpreted in terms of natural selection (as is implied in the appeal of some Neo-Darwinians to "intra-selection," "germinal selection," and so on), and that therefore natural selection cannot be regarded as a generally acting factor. Moreover, the Neo-Lamarckian is at liberty to reply, that he does not regard the modification-inheritance theory as applicable to all possible cases.

Antecedent Probabilities.—If we turn to the antecedent probabilities of the two beliefs, we find that the assumptions of either side are equally improbable to the other, according to their respective points of view. Thus, the supporters of the negative answer may say that they cannot conceive how a particular local modification of the body can so affect the germ-cells that, when these develop into offspring, the acquired character shall re-appear. The supporters of the affirmative answer may say that they find it impossible to believe in the selectionist interpretation of many of the adaptive characters which make up an organism, impossible to believe that the little items of improvement which are added generation after generation—say in a cricket's musical instrument—can have had selection-value. There are other difficulties on both sides, and it is likely to remain for a long time a matter of opinion which side has the greater difficulties to face.

A Matter of Fact.—It is plain, however, that what we have to ask is whether interpretations in terms of modification-inheritance have any basis in present-day experience, such as selectionist interpretations have, for instance, in domestication on the one hand and variation-statistics on the other. And our survey seems to indicate that it is very difficult to find any empirical basis whatsoever for the affirmative position.

If modification-inheritance were known to be a fact it would in nowise exclude interpretations in terms of natural selection and other factors, for even the most thorough-going Neo-Lamarckian will hardly maintain that his hypothesis, if verified, would be an all-sufficient ætiological factor, and even the most convinced Neo-Darwinians could not refuse to recognise an additional factor if that were verifiable. There is no need to pit one theory against the other in this fashion; the more factors in evolution that are discovered the better!

The question resolves itself into a matter of fact: Have we any concrete evidence to warrant us believing that definite modifications are ever, as such or in any representative degree, transmitted? It appears to us that we have not. But to say dogmatically that such transmission is impossible is unscientific. In regard to that, the truly scientific position is one of active scepticism (*thätige Skepsis*).

§ 14. *Indirect Importance of Modifications*

Importance of Nurture.—Scepticism as to the transmission of acquired characters does not imply that we under-rate the importance of "nurture." We have seen (1) that an appropriate environment is the necessary correlate of a normal inheritance, otherwise the organism cannot realise itself in development; (2) that changes in environment and function may provoke variations in the germ-plasm; (3) that the individual is often very plastic and readily acquires adaptive modifications which may be of great individual importance, and may even preserve the life; (4) that the secondary effects of modifications may, in certain cases, reach and influence the germ-cells; (5) that the state of the maternal constitution is very important in cases where there is an intimate connection between the mother and the unborn young.

Selection and Stimulus.—In two other ways changes in the conditions of life are of great importance: they form part of the mechanism of selection, whereby the relatively less fit variants are quickly or slowly, roughly or gently, eliminated; and they act as a stimulus to the intrinsic self-assertiveness and "endeavour after well-being" which characterise living creatures. We must advance beyond the conventional view that the environment is like a net closing in upon passive victims, which can only escape if they have been fitted by germinal variation (or acquired modification) to pass through some of the meshes; we must recognise as a fact of life, what Lamarck and many others have seen with clearness, that organisms actively assert themselves against this closing net, and by active endeavour (also, of course, a variational character when traced back) may win their way through.

Indirect Importance of Modifications.—But there is another important consideration, which has been stated independently by Profs. Mark Baldwin, Lloyd Morgan, and H. F. Osborn—namely, that adaptive modifications may act as the fostering nurses of germinal variations in the same direction. We have referred to this elsewhere, but it may give greater completeness to our survey if we quote a brief statement of the idea as expounded by Lloyd Morgan (*Habit and Instinct*, 1896, p. 319):

"Persistent modification through many generations, though not transmitted to the germ, nevertheless affords the opportunity for germinal variation of like nature.

"Suppose that a group of plastic organisms is placed under new conditions. Those whose innate plasticity is equal to the occasion are modified and survive. Those whose plasticity is not equal to the occasion are eliminated. . . . Such modification takes place generation after generation, but, as such, is not inherited. . . . But any congenital variations similar in direction to these modifications will tend to support them and to favour the organism in which they occur. Thus will arise a congenital predisposition to the modifications in question.

"The plasticity still continuing, the modifications become yet further adaptive. Thus plastic modification leads, and germinal variation follows; the one paves the way for the other.

"The modification *as such* is not inherited, but is the condition under which congenital variations are favoured and given time to get a hold on the organism, and are thus enabled by degrees to reach the fully adaptive level."

§ 15. *Practical Considerations*

We have seen that the scientific position in regard to the *transmissibility* of modifications should be one of active scepticism, that there seems to be no convincing evidence in support of the affirmative position, and that there is strong presumption in favour of the negative.

A modification is a definite change in the individual body, due to some change in "nurture." There is no secure evidence that any such individual gain or loss can be transmitted as such, or in any representative degree. How does this affect our estimate of the value of "nurture"? How should the sceptical or negative answer, which we believe to be the scientific one, affect our practice in regard to education, physical culture, amelioration of function, improvement of environment, and so on? Let us give a practical point to what we have already said.

(*a*) Every inheritance requires an appropriate nurture if it is to realise itself in development. Nurture supplies the liberating stimuli necessary for the full expression of the inheritance. A man's character as well as his physique is a function of "nature" and of "nurture." In the language of the old parable of the talents, what is given must be traded with. A boy may be truly enough a chip of the old block, but how far he shows himself such depends on "nurture." The conditions of nurture determine whether the expression of the inheritance is to be full or partial. It need hardly be said that the strength of an (inherited) individuality may be such that it expresses itself almost in the face of inappropriate nurture. History abounds in instances. As Goethe said, Man is always achieving the impossible. Corot was the son of a successful milliner and a prosperous tradesman, and he was thirty before he left the draper's shop to study nature.

(*b*) Although modifications do not seem to be transmitted as such, or in any representative degree, there is no doubt that they or their secondary results may in some cases affect the offspring. This is especially the case in typical mammals, where there is before birth a prolonged (placental) connection between the mother and the unborn young. In such cases the offspring is for a time almost part of the maternal body, and liable to be affected by modifications thereof—*e.g.* by good or bad nutritive conditions. In other cases, also, it may be that deeply saturating parental modifications, such as the results of alcoholic and other poisoning, affect the germ-cells, and thus the offspring. A disease may saturate the body with toxins and waste-products, and these may provoke prejudicial germinal variations.

(*c*) Though modifications due to changed "nurture" do not seem to be transmissible, they may be re-impressed on each generation. Thus "nurture" becomes not less, but more, important in our eyes.

"Is my grandfather's environment not my heredity?" asks an American author quaintly and pathetically. Well, if not, let us secure for ourselves and for our children those factors in the "grandfather's environment" that made for progressive evolution, and eschew those that tended elsewhere.

> "Was du ererbt von deinen Vätern hast
> Erwerb es, um es zu besitzen."

Are modifications due to changed nurture not, as such, entailed on offspring? Perhaps it is just as well, for we are novices at nurturing even yet! Moreover, the non-transmissibility cuts both ways: if individual modificational gains are not handed on, neither are the losses.

Is the "nature"—the germinal constitution, to wit—all that passes from generation to generation, the capital sum without the results of individual usury; then we are freed, at least, from undue pessimism at the thought of the many harmful functions and environments that disfigure our civilisation. Many detrimental acquired characters are to be seen all around us, but if they are not transmissible, they need not last.

(*d*) The plasticity of the organism admits of definite modifications being re-impressed on successive generations of individuals, and this is the more important when we consider what has been said in the section on "The Indirect Importance of Modifications." They may serve as modificational screens until coincident variations in the same direction can emerge and establish themselves. This also cuts both ways in human societies, where natural selection is interfered with, and where naturally prejudicial deviations from the norm are not necessarily punished by elimination.

(*e*) Of particular importance is the fact that man, in contrast to other creatures, has developed around him an external heritage, a social framework of customs and traditions, of laws and institutions, of literature and art—by which results almost equivalent to the organic transmission of certain kinds of modifications may be brought about.

(*f*) Is there not some result of the long-drawn-out controversy on "the inheritance of acquired characters," if we are thereby freed from indulging in false hopes, but are forced to the conviction that "nurture" is more important than ever? Although what is "acquired" may not be inherited, what is not inherited may be acquired. Thus we are led to direct our energies even more strenuously to the business of re-impressing desirable modifications, and therefore to developing our functions and environments in the direction of progress.

It may be, however, that our methods must change with the change in our expectations. For though we can by modification directly influence the individual, and in some measure even control the expression of his inheritance, it is not through modifications that we can hope directly to influence posterity. Man is a slowly reproducing, slowly varying organism. What is above all precious is the conservation of good stock. No number of veneering modifications—superficial screens of organic defects—can atone for allowing a deterioration of the germinal inheritance to diffuse itself or accumulate. For progress which is really organic—for progress, that is, in our natural inheritance—we must wait, or rather work, patiently. The quest after *Eutopias* and *Eutechnics* must be associated with an enthusiasm for *Eugenics*.

Inheritance of Moral Character.—In the development of "character," much depends upon early nurture, education, and surrounding influences generally, but how the individual reacts to these must largely depend on his inheritance. Truly the individual himself makes his own character, but he does so by his habitual adjustment of his (hereditarily determined) constitution to surrounding influences. Nurture supplies the stimulus for the expression of the moral inheritance, and how far the inheritance can express itself is limited by the nurture-stimuli available just as surely as the result of nurture is conditioned by the hereditarily-determined nature on which it operates. It may be urged that character, being a product of habitual modes of feeling, thinking, and acting, cannot be spoken of as *inherited,* but bodily character is also a product dependent upon vital experience. It seems to us as idle to deny that some children are " born good " or " born bad," as it is to deny that some children are born strong and others weak, some energetic and others " tired " or " old." It may be difficult to tell how far the apparently hereditary goodness or badness of disposition is due to the nutritive influences of the mother, both before and after birth, and we must leave it to the reader's experience and observation to decide whether we are right or wrong in our opinion that quite apart from maternal nutritive influence there is a genuine inheritance of kindly dispositions, strong sympathy, good-humour, and good-will. The further difficulty that the really organic character may be half-concealed by nurture-effects, or inhibited by the external heritage of custom and tradition, seems less serious, for the selfishness of an acquired altruism is as familiar as honour among thieves.

It is entirely useless to boggle over the difficulty that we are unable to conceive how dispositions for good or ill lie implicit within the protoplasmic unit in which the individual life begins. The fact is undoubted that the initiatives of moral character are in some degree transmissible, though from the nature of the case the influences of education, example, environment, and the like are here more potent than in regard to structural features. We cannot make a silk purse out of a sow's ear, though the plasticity of character under nurture is a fact which gives us all hope. Explain it we cannot, but the transmission of the raw material of character is a fact, and we must still say with Sir Thomas Browne: " Bless not thyself that thou wert born in Athens; but, among thy multiplied acknowledgments, lift up one hand to heaven that thou wert born of honest parents, that modesty, humility, and veracity *lay in the same egg,* and came into the world with thee."

The study of inheritance leaves a fatalistic impression in many minds, and to some extent this is justified. We cannot get away from our inheritance. As the poet Heine said half bitterly, half laughingly, " A man should be very careful in the selection of his parents." On the other hand, although the organism changes slowly in its heritable organisation, it is very modifiable individually; and this is man's particular secret—to correct his internal organic inheritance by what we may call his external heritage of material and spiritual influences.

CONCLUSION

If there is little or no scientific warrant for our being other than extremely sceptical at present as to the inheritance of acquired characters—or better, the transmission of modifications—this scepticism lends greater importance than ever, on the one hand, to a good " nature," to secure which is the business of careful mating; and, on the other hand, to a good " nurture," to secure which for our children is one of our most obvious and binding duties: the hopefulness of the task resting especially upon the fact that, unlike the beasts that perish, man has a lasting external heritage, capable of endless modification for the better, a heritage of ideas and ideals, embodied in prose and verse, in statue and painting, in cathedral and university, in tradition and convention, and above all in society itself.