ON

GERMINAL SELECTION

AS A

SOURCE OF DEFINITE VARIATION

BY

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SECOND EDITION

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PREFACE.

The present paper was read in the first general meeting of the International Congress of Zoölogists at Leyden on September 16, 1895. Several points, which for reasons of brevity were omitted when the paper was read, have been re-embodied in the text, and an Appendix has been added where a number of topics receive fuller treatment than could well be accorded to them in a lecture. The address was first printed in *The Monist* for January, 1896, and afterwards in a German pamphlet.

The basal idea of the essay—the existence of Germinal Selection—was propounded by me some time since,[1] but it is here for the first time fully set forth and tentatively shown to be the necessary complement of the process of selection. Knowing this factor, we remove, it seems to me, the patent contradiction of the assumption that the general fitness of organisms, or the adaptations *necessary* to their existence, are produced by *accidental* variations—a contradiction which formed a serious stumbling-block to the theory of selection. Though still assuming that the *primary* variations are "accidental," I yet hope to have demonstrated that an interior mechanism exists which compels them to go on increasing in a definite direction, the moment selection intervenes. *Definitely directed*

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[1] *Neue Gedanken zur Vererbungsfrage, eine Antwort an Herbert Spencer.* Jena. 1895.

variation exists, but not predestined variation, run-
ning on independently of the life-conditions of the
organism, as Naegeli, to mention the most extreme
advocate of this doctrine, has assumed; on the con-
trary, the variation is such as is elicited and con-
trolled by those conditions themselves, though indi-
rectly.

In basing my proof of the doctrine of Germinal Se-
lection on the fundamental conceptions of my theory of
heredity, a few words of justification are necessary,
owing to the fact that the last-mentioned theory has
been widely and severely assailed since its first emer-
gence into light and even repudiated as absolutely
futile and erroneous.

In the first place, many critics have characterised it
as a "pure creation of the imagination." And to a
certain extent it is such, as every theory is. But is
it on that account necessarily wrong? Can not its
fundamental ideas still be quite correct, and it itself
therefore perfectly justified as a means of further
progress?

Surely my critics cannot be ignorant of the promi-
nent part which imagination has recently played in
the exactest of all natural sciences—physics? Are
they unaware that the English physicist Maxwell
"constructed from liquid vortices and friction-pulleys
enclosed in cells with elastic walls, a wonderful mech-
anism, which served as a mechanical model for electro-
magnetism"?[1] He hoped "that further research in
the domain of theoretical electricity would be pro-
moted rather than hindered by such mechanical fic-

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[1] See Boltzmann, *Methoden der theor. Physik,* Munich,
1892. (In the Catalogue of the Mathematical Exhibit.)

tions." And so it actually happened, for Maxwell found by means of them "the very equations, whose singular and almost incomprehensible power Hertz has so beautifully portrayed in his lecture on the relations between light and electricity." "Maxwell's formulæ were the direct outcome of his mechanical models." "These ideal mechanisms"—so relates Boltzmann in the same interesting essay—"were at first widely ridiculed, but gradually the new ideas worked their way into all fields. They were themselves more convenient than the old hypotheses. For the latter could be maintained only in the event of everything's proceeding smoothly; whereas now little inconsistencies were fraught with no peril, for no one can take amiss a slight hitch in a mere analogy.—Ultimately Maxwell's ideas were philosophically generalised as the theory that all knowledge consists in the disclosure of analogies."

But not only does it seem that there is little appreciation among biologists for the scientific import of imagination, they also appear to have little sense for the significance of theory. It is a favorite attitude nowadays to look upon theory as a sort of superfluous ballast, as a worthless survival from the epoch of decrepit "nature-philosophies." People pronounce with pride the miscomprehended utterance of Newton, *Hypotheses non fingo,* and place the value of the slightest new fact infinitely higher than that of "the most beautiful theory."[1] And yet theory originally

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[1] Of late this saying of Newton's is frequently quoted as if Newton were a downright contemner of scientific hypotheses. But if we read the passage in question in its original context, we shall discover that his renunciation of hypotheses referred solely to a definite case, viz., to that of universal

fashions science out of facts and is the indispensable precondition of every important scientific advance.

Heinrich Hertz,[1] the discoverer of electric undulations, had the same thought in mind when he said: "We form inward representations or constructs of outward objects, so constituted that the results that follow logically and necessarily from the constructs are in turn always constructs of the results flowing naturally and necessarily from the objects." "These constructs or mental images copied after familiar objects possessed of familiar properties, so constituted that from their manipulation effects result similar to those which we observe in the objects to be explained. Experience teaches us that the requirements here made can be fulfilled and that consequently such 'correspondences' between reality and the supposed images [or, as Hertz says, between nature and mind] actually exist. Having succeeded in extracting from the accumulated experience of the past, representative images or constructs fulfilling all these necessary requirements, we can then reproduce by them in a short space of time, as we might by models, results that in the outward world require a long space of time for their actualisation or can be produced only through our personal intervention," etc.

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gravitation, of whose character Newton could form no conception and hence was unwilling to construct hypotheses concerning it. Indeed, such a wholesale repudiation of hypotheses is antecedently incredible on the part of the inventor of the emission-theory of light, in which, to speak of only one daring conjecture, "fits" were ascribed to the luminous particles. Compare Newton, *Philosophiae Naturalis Principia Mathematica,* second edition, 1714, page 484.

[1] H. Hertz, *Die Principien der Mechanik.*

Such representative models, or constructs, now, in my theory of heredity, are the *determinants,* which may be conceived as indefinitely fashioned packages of units (biophores) which are set into activity by definite impressions and put a distinctive stamp upon some small part of the organism, on some cell or group of cells, evoking definite phenomena somewhat as a piece of fireworks when lighted produces a brilliant sun, a shower of sparks, or the glowing characters of a name.

The *ids*, also, are such representative models, and may be compared to a definitely ordered but variously compounded aggregate of fireworks, in which the single pieces are so connected as to go off in fixed succession and to produce a definite resultant phenomenon like a complete inscription surrounded by a hail of fire and glowing spheres.

Owing to the greater complexity of the phenomena in biology we can never hope to reach the same distinctness in our constructs and models as in physics, and the attempt to derive from them mathematical formulæ by the independent development of which research could be continued, would at present be utterly fruitless. In the meantime it seems preferable to have some sort of adequate model to which the imagination can always resort and with which it can easily operate, rather than to have to revert, in considering every special problem of heredity, to the mutual actions of the molecules of living substance and outward agents—processes which we know only in their roughest outlines. Or is any one presumptuous enough to believe we can infer from our slight knowledge of the chemical and physical constitution of the germs of a trout and a salmon the real cause

of the one's becoming a trout and of the other's becoming a salmon?

The fact is, we can make no show of accounting for the complex phenomena of heredity with mere *material* units; we can never reach these phenomena from below, but must begin farther up and make the assumption of *vital* units and *hereditary* units, if there is to be any advance in this field.

It is undoubtedly a splendid aim which the newly founded science of developmental mechanics has set itself of laying bare the entire causal line leading from the egg to the finished organism; yet, however much we may wish to see the success of this plan realised, we cannot disguise the fact that little or nothing is to be accomplished by it in the settlement of the problems of heredity. It is impossible to suspend the study of heredity until this mechanics is completed, and even if we could it would help us little, for the riddles of heredity are not concealed in the ontogenesis of types, or, to give an example, in the developmental history of man *as a race,* but in the ontogenesis of *individuals,* in that of a *definite and particular* man. This last ontogenesis exhibits the phenomena of variation, of reversion, of the predominance of the one or the other parent, etc., and no one is likely to believe that inductive evolutional inquiry alone will ever afford us knowledge of these minute and delicate processes, which, in their bearing on the total resultant development, phylogenesis, are after all the most important of all.

There is, accordingly, no choice left. If we are really bent on scientifically investigating the question of heredity, we are obliged perforce to form from the observed facts of heredity a highly detailed and elab-

orate theory, on the basis of which we can propound new questions, which will give rise in turn to new facts, and thus will exercise a retroactive influence on the theory, improving and transforming it.

This is precisely what I have sought to accomplish by my theory of Germ-plasm, as I stated in the Preface to the book bearing that name. It was never intended as a theory of life, nor, indeed, primarily, as a theory of evolution, but first and above all as a theory of heredity. I cannot understand, therefore, the animadversion, that my theory in no way furthers our insight into the mechanics of development. That is not its purpose; in fact, it takes the ultimate physical and chemical processes which make up the vital processes for granted; and inevitably it is constrained to do so. Its aim is to put into our hands a serviceable formula by means of which we can go on working in the field of heredity at any rate, and, if I am not mistaken, also in that of evolution. To me, at least, the newest results of developmental mechanics do not seem so widely at variance with the theory of determinants as might appear at first sight; so far as I can see, they can be quite readily made to harmonise with the theory, provided only the initial stage of the disintegration of the germ-plasm in the determinant groups be not invariably placed at the beginning of the process of segmentation, but be transferred according to circumstances to a subsequent period. The exact state of things cannot as yet be determined, so long as the mass of facts is still in constant flux.

In any event I still hold fast to the hope which I expressed in the Preface to my *Germ-plasm,* that despite the unavoidable uncertainties in its foundation my theory would yet prove more than a mere work

of imagination, and that the future would find in it some durable points which would outlive the mutations of opinion. It is possible that one of these durable gains is my much impugned idea of determinants, and in fact not only will the present essay be made to rest on this idea, but it will also defend it on new grounds, although primarily only as a representation of something which we do not as yet exactly know, but which still exists and on which we can reckon, leaving it to the future to decide the greater or less resemblance of our hypothetical construct to nature.

The real aim of the present essay is to rehabilitate the principle of selection. If I should succeed in reinstating this principle in its emperilled rights, it would be a source of extreme satisfaction to me; for I am so thoroughly convinced of its indispensability as to believe that its demolition would be synonymous with the renunciation of all inquiry concerning the causal relation of vital phenomena. If we could understand the adaptations of nature, whose number is infinite, only upon the assumption of a teleological principle, then, I think, there would be little inducement to trouble ourselves about the causal connexion of the stages of ontogenesis, for no good reason would exist for excluding teleological principles from this field. Their introduction, however, means the ruin of science.   AUGUST WEISMANN.

FREIBURG, Nov. 18, 1895.

GERMINAL SELECTION.

Numerous and varied are the objections that have been advanced against the theory of selection since it was first enunciated by Darwin and Wallace—from the unreasoning strictures of Richard Owen and the acute and thoughtful criticisms of Albert Wigand and Nägeli to the opposition of our own day, which contends that selection cannot create but only reject, and which fails to see that precisely through this rejection its creative efficacy is asserted. The champions of this view are for discovering the motive forces of evolution in the *laws* that govern organisms—as if the norm according to which an event happens were the event itself, as if the rails which determine the direction of a train could supplant the locomotive. Of course, from every form of life there proceeds only a definite, though extremely large, number of tracks, *the possible variations,* whilst between them lie stretches without tracks, *the impossible variations,* on which locomotion is impossible. But the actual travelling of a track is not performed by the track, but by the locomotive, and on the other hand, the choice of a track, the decision whether the destination of the train shall be Berlin or Paris, is not made by the locomotive, the cause of the variation, but by the driver of the locomotive, who directs the engine on the right track. In the theory of selection the engine-driver is represented by utility, for with utility rests the decision

as to what particular variational track shall be travelled. The cogency, the irresistible cogency, as I take it, of the principle of selection is precisely its capacity of explaining why fit structures always arise, and that certainly is the great problem of life. Not the fact of change, but the *manner* of the change, whereby all things are maintained capable of life and existence, is the pressing question.

It is, therefore, a very remarkable fact, and one deserving of consideration, that to-day (1895), after science has been in possession of this principle for something over thirty years and during this time has steadily and zealously busied itself with its critical elaboration and with the exact determination of its scope, that now the estimation in which it is held should apparently be on the decrease. It would be easy to enumerate a long list of living writers who assign to it a subordinate part only in evolution, or none at all. One of our youngest biologists speaks without ado of the "pretensions of the refuted Darwinian theory, so called,"[1] and one of the oldest and most talented inquirers of our time, a pioneer in the theory of evolution, who, unfortunately, is now gone to his rest, Thomas Huxley, implicitly yet distinctly intimated a doubt regarding the principle of selection when he said: "Even if the Darwinian hypothesis were swept away, evolution would still stand where it is." Therefore, he, too, regarded it as not impossible that this hypothesis should disappear from among

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[1] Hans Driesch, *Die Biologie als selbstständige Grundwissenschaft,* Leipsic, 1893, p. 31, footnote. The sentence reads: "An examination of the pretensions of the refuted Darwinian theory, so called, would be an affront to our readers."

the great explanatory principles by which we seek to approach nearer to the secrets of nature.

I am not of that opinion. I see in the growth of doubts regarding the principle of selection and in the pronounced and frequently bitter opposition which it encounters, a transient depression only of the wave of opinion, in which every scientific theory must descend after having been exalted, here perhaps with undue swiftness, to the highest pitch of recognition. It is the natural reaction from its overestimation, which is now followed by an equally exaggerated underestimation. The principle of selection was not overrated in the sense of ascribing to it too much explanatory efficacy, or of extending too far its sphere of operation, but in the sense that naturalists imagined that they perfectly understood its ways of working and had a distinct comprehension of its factors, which was not so. On the contrary, the deeper they penetrated into its workings the clearer it appeared that something was lacking, that the action of the principle, though upon the whole clear and representable, yet when carefully looked into encountered numerous difficulties, which were formidable, for the reason that we were unsuccessful in tracing out the actual details of the individual process, and, therefore, in *fixing* the phenomenon as it actually occurred. We can state in no single case how great a variation must be to have selective value, nor how frequently it must occur to acquire stability. We do not know when and whether a desired useful variation really occurs, nor on what its appearance depends; and we have no means of ascertaining the space of time required for the fulfilment of the selective processes of nature, and hence cannot calculate the exact number of such proc-

esses that do and can take place at the same time in the same species. Yet all this is necessary if we wish to follow out the precise details of a given case.

But perhaps the most discouraging circumstance of all is, that in scarcely a single actual instance in nature can we assert whether an observed variation is useful or not—a drawback that I distinctly pointed out some time ago.[1] Nor is there much hope of betterment in this respect, for think how impossible it would be for us to observe all the individuals of a species in all their acts of life, be their habitat ever so limited— and to observe all this with a precision enabling us to say that this or that variation possessed selective value, that is, was a decisive factor in determining the existence of the species.

In many cases we can reach at least a probable inference, and say, for example, that the great fecundity of the frog is a property having selective value, basing our inference on the observation that in spite of this fertility the frogs of a given district do not increase.

But even such inferences offer only a modicum of certainty. For who can say precisely how large this number is? Or whether it is on the increase or on the decrease? And besides, the exact degree of the fecundity of these animals is far from being known. Rigorously viewed, we can only say that great fecundity must be advantageous to a much-persecuted animal.

And thus it is everywhere. Even in the most indubitable cases of adaptation, as, for instance, in that of the striking protective coloring of many butterflies,

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[1] *Die Allmacht der Naturzüchtung.* A Reply to Herbert Spencer. Jena, 1893, p. 27 et seq. [Also in the *Contemporary Review* for September, 1893.]

the sole ground of inference that the species upon the whole is adequately adapted to its conditions of life, is the simple fact that the species is, to all appearances, preserved undiminished, and the inference is not at all permissible that just this protective coloring has selective value for the species, that is, that if it were lacking, the species would necessarily have perished.

It is not inconceivable that in many species to-day these colorings are actually unnecessary for the preservation of the species, that they formerly were, but that now the enemies which preyed on the resting butterflies have grown scarce or have died out entirely, and that the protective coloring will continue to exist by the law of inertia[1] only for a short while till panmixia or new adaptations shall modify it.

Discouraging, therefore, as it may be, that the control of nature in her minutest details is here gainsaid us, yet it were equivalent to sacrificing the gold to the dross, if simply from our inability to follow out the details of the individual case we should renounce altogether the principle of selection, or should proclaim it as only subsidiary, on the ground that we believe the protective coloring of the butterfly is not a protective coloring, but a combination of colors inevitably resulting from internal causes. The protective coloring remains a protective coloring whether at the time in question it is or is not necessary for the species; and it arose as protective coloring—arose not because it was a constitutional necessity of the animal's organism that here a red and there a white, black, or yellow spot should be produced, but because it was advan-

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[1] That is, by the law of exceedingly slow retrogression of superfluous characters, which may be designated the law of organic inertia.

tageous, because it was necessary for the animal. There is only one explanation possible for such patent adaptations and that is selection. What is more, no other natural way of their originating is conceivable, for we have no right to assume teleological forces in the domain of natural phenomena.

I have selected the example of the butterfly's wing, not solely because it is so widely known, but because it is so exceedingly instructive, because we are still able to learn so much from it. It has been frequently asserted that the color-patterns of the butterfly's wings have originated from internal causes, independently of selection and conformably to inward laws of evolution. Eimer has attempted to prove this assertion by establishing in a division of the genus Papilio the fact that the species there admit of arrangement in series according to affinity of design. But is a proof that the markings are modified in definite directions during the course of the species's development equivalent to a definite statement as to the *causes* that have produced these gradual transformations? Or, is our present inability to determine with exactness the biological significance of these markings and their modifications, a proof that the same have no significance whatever? On the contrary, I believe it can be clearly proved that the wing of the butterfly is a tablet on which nature has inscribed everything she has deemed advantageous to the preservation and welfare of her creatures, and nothing else; or, to abandon the simile, that these color-patterns have not proceeded from inward evolutional forces, but are the result of selection. At least in all places where we do understand their biological significance these patterns are constituted and distributed over the wing exactly as utility would require.

I do not pledge myself, of course, to give an explanation of every spot and every line on a wing. The inscription is often a very complicated one, dating from remote and widely separated ages; for every single existing species has inherited the patterns of its ancestral species and that again the patterns of a still older species. Even at its origin, therefore, the wing was far from being a *tabula rasa,* but was a closely written and fully covered sheet, on which there was no room for new writing until a portion of the old had been effaced. But other parts were preserved, or only slightly modified, and thus in many cases gradually arose designs of almost undecipherable complexity.

I should be far from maintaining that the markings arose unconformably to law. Here, as elsewhere, the dominance of law is certain. But I take it, that the laws involved here, that is, the physiological conditions of the variation, are without exception subservient to the ends of a higher power—utility; and that it is utility primarily that determines the kind of colors, spots, streaks and bands that shall originate, as also their place and mode of disposition. The laws come into consideration only to the extent of conditioning the quality of the constructive materials—the variations, out of which selection fashions the designs in question. And this also is subject to important restrictions, as will appear in the sequel.

The meaning of formative laws here is that definite spots on the surfaces of the wings are linked together in such a manner by inner, invisible bonds, as to represent the same spots or streaks, so that we can predict from the appearance of a point at one spot the appearance of another similar point at another, and

so on. It is an undoubted fact that such relations exist, that the markings frequently exhibit a certain symmetry, that—to use the words of the most recent observer on this subject, Bateson[1]—a meristic representation of equivalent design-elements occurs. But I believe we should be very cautious in deducing laws from these facts, because all the rules traceable in the markings apply only to small groups of forms and are never comprehensive nor decisive for the entire class or even for the single sub-class of diurnal butterflies, in fact, often not so for a whole genus. All this points to special causes operative only within this group.

If internal laws controlled the marking on butterflies' wings, we should expect that some general rule could be established, requiring that the upper and under surfaces of the wings should be alike, or that they should be different, or that the fore wings should be colored the same as or differently from the hind wings, etc. But in reality all possible kinds of combinations occur simultaneously, and no rule holds throughout. Or, it might be supposed that bright colors should occur only on the upper surface or only on the under surface, or on the fore wings or only on the hind wings. But the fact is, they occur indiscriminately, now here, now there, and no one method of appearance is uniform throughout all the species. But the fitness of the various distributions of colors is apparent, and the moment we apply the principle of utility we know why in the diurnal butterflies the upper surface alone is usually variegated and the under surface protectively colored, or why in the nocturnal

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[1] *Materials for the Study of Variation with Especial Regard to Discontinuity in the Origin of Species.* London, 1895.

butterflies the fore wings have the appearance of bark, of old wood, or of a leaf, whilst the hind wings, which are covered while resting, alone are brilliantly colored. On this theory we also understand the exceptions to these rules. We comprehend why Danaids, Heliconids, Euploids, and Acracids, in fact all diurnal butterflies, offensive to the taste and smell, are mostly brightly marked and equally so on both surfaces, whilst all species not thus exempt from persecution have the protective coloring on the under surface and are frequently quite differently colored there from what they are on the upper.

In any event, the supposed formative laws are not obligatory. Dispensations from them can be issued and are issued *whenever utility requires it.* Indeed, so far may these transgressions of the law extend, that in the very midst of the diurnal butterflies is found a genus, the South American Ageronia, which, like the nocturnal butterfly, shows on the entire *upper* surface of both wings a pronounced bark-coloration, and concerning which we also know (and in this respect it is an isolated genus and differs from almost all other diurnal butterflies), that it spreads out its wings when at rest like the nocturnal butterfly, and does not close them above it as its relatives do. Therefore, entirely apart from cases of mimicry, which after all constitute the strongest proof, the facts here cited are alone sufficient to remove all doubt that not inner necessities or so-called formative laws have painted the surface of the butterflies' wings, but that the conditions of life have wielded the brush.

This becomes more apparent on considering the details. I have remarked that the usually striking colorations of exempt butterflies, as of the Heliconids,

are the same on both the upper and the lower surfaces of the wings. Possibly the expression of a law might be seen in this fact, and it might be said, the coloration of the Heliconids *runs through* from the upper to the under surface. But among numerous imitators of the Heliconids is the genus Protogonius, which has the coloration of the Heliconids on its upper surface, but on its lower exhibits a magnificent leaf-design. During flight it appears to be a Heliconid and at rest a leaf. How is it possible that two such totally different types of coloration should be combined in a single species, if any sort of *inner* rigorous necessity existed, regulating the coloration of the two wing-surfaces? Now, although we are unable to prove that the Protogonius species would have perished unless they possessed this duplex coloration, yet it would be nothing less than intellectual blindness to deny that the butterflies in question are effectively protected, both at rest and during flight, *that their colorations are adaptive.* We do not know their primitive history, but we shall hardly go astray if we assume that the ancestors of the Protogonius species were forest-butterflies and already possessed an under surface resembling a leaf. By this device they were protected when at rest. Afterwards, when this protection was no longer sufficient, they acquired on their upper surface the coloration of the exempt species with which they most harmonised in abode, habits of life, and outward appearance.

At the same time it is explained why these butterflies did not acquire the coloration of the Heliconids on the under surface. The reason is, that in the attitude of repose they were already protected, and that in an admirable manner.

That *exempt* diurnal butterflies should be colored on the upper and under surfaces alike, and should never resemble in the attitude of repose their ordinary surroundings, is intelligible when we reflect that it is a much greater protection to be despised when discovered than to be well, or very well, but never absolutely, protected from discovery.

It has been so often reiterated that diurnal butterflies, as a rule, are protectively colored on the under surfaces, that one has some misgivings in stating the fact again. And yet the least of those who hold this to be a trivial commonplace know how strongly its implications militate against the inner motive and formative forces of the organism, which are ever and anon appealed to. No less than sixty-two genera are counted today in the family of diurnal butterflies known as the Nymphalidæ. Of these by far the largest majority are sympathetically colored underneath, that is, they show in the posture of rest the colorings of their usual environment. In a large number of the species belonging to this group the entire surface of the hind wings possesses such a sympathetic coloration, as does also the distant apex of the fore wings. Why? The reason is obvious. This part only of the fore wing is visible in the attitude of repose. Here, then,—as a zealous opponent of the theory of selection once exclaimed,—there is undoubted "correlation" between the coloring of the surface of the hind wing and of the apex of the fore wing. Correlation is unquestionably a fine word, but in the present instance it contributes nothing to the understanding of the problem, for there are near relatives and often species of the same genera in which this correlation is not restricted to the apex of the

fore wings, but extends to a third or even more of their wings, and these species are also in the habit of drawing back their wings less completely in the state of rest, thus rendering a larger portion of them visible. There are species, too, like the forest-butterflies of South America just mentioned, the Protogonius, Anæa, Kallima species, etc., which have nearly the *whole* of the under surfaces of their fore wings marked according to the same pattern with their hind wings, and these butterflies when at rest hold their fore wings free and uncovered by their hind wings. Where are the formative laws in such cases?

Or, perhaps some one will say: "The covering by the hind wings hinders the formation of scales on the wing, or impedes the formation of the colors in the scales." Such a person should examine one of these species. He will find that the scales are just as dense on the covered as on the uncovered surface of the wing, and in many species, for example, in Katagramma, the scales of the covered surface are colored most brilliantly of all.

But the facts are still more irresistible, when we consider *special adaptations;* for example, the imitation of leaves, which is so often cited. It is to be noted, first, that this sort of imitation is by no means restricted to a few genera, still less to a few species. All the numerous species of the genus Anæa, which are distributed over the forests of tropical South America, exhibit this imitation in pronounced and varied forms, as do likewise the American genera Hypna and Siderone, the Asiatic Symphaedra, the African Salamis, Eurypheme, etc. I have observed fifty-three genera in which it is present in one, several, or in many species, but there are many others.

These genera, now, are by no means all so nearly allied that they could have inherited the leaf-markings from a common ancestral form. They belong to different continents and have probably for the most part acquired their protective colorings themselves. But one resemblance they have in common—they are all *forest-butterflies.* Now what is it that has put so many genera of forest-butterflies and no others into positions where they could acquire this resemblance to leaves? Was it directive formative laws? If we closely examine the markings by which the similarity of the leaf is determined, we shall find, for example, in Kallima Inachis, and Parallecta, the Indian leaf-butterflies, that the leaf-markings are executed *in absolute independence of the other uniformities governing the wing.*

From the tail of the wing to the apex of the fore wings runs with a beautiful curvature a thick, doubly-contoured dark line accompanied by a brighter one, representing the midrib of the leaf. This line cuts the "veins" and the "cells" of the wing in the most disregardful fashion, here in acute and here in obtuse angles, and in absolute independence of the regular system of divisions of the wing, which should assuredly be the expression of the "formative law of the wing," if that were the product of an internal directive principle. But leaving this last question aside, this much is certain with regard to the markings, that they are dependent, not on an *internal,* but on an *external* directive power.

Should any one be still unconvinced by the evidence we have adduced, let him give the leaf-markings a closer inspection. He will find that the midrib is composed of two pieces of which the one belongs to the

hind wing and the other to the fore wing, and that
the two fit each other exactly when the butterfly is in
the attitude of repose, but not otherwise.   Now these
two pieces of the leaf-rib do not begin on correspond-
ing spots of the two wings, but on absolutely non-
identical spots.   And the same is also true of the
lines which represent the lateral ribs of the leaf.
These lines proceed in acute angles from the rib; to the
right and to the left in the same angle, those of the
same side parallel with each other.   Here, too, no
relation is noticeable between the parts of the wings
over which the lines pass.   The venation of the wing
is utterly ignored by the leaf-markings, and its sur-
face is treated as a *tabula rasa* upon which anything
conceivable can be drawn.   In other words, we are
presented here with a *bilaterally symmetrical* figure
engraved on a surface which is essentially *radially
symmetrical* in its divisions.

I lay unusual stress upon this point because it shows
that we are dealing here with one of those cases which
cannot be explained by mechanical, that is, by natural
means, unless natural selection actually exists and is
actually competent to create new properties; for the
Lamarckian principle is excluded here *ab initio,* see-
ing that we are dealing with a formation which is
only passive in its effects; the leaf-markings are ef-
fectual simply by their existence and not by any func-
tion which they perform; they are present in flight
as well as at rest, during the absence of danger, as well
as during the approach of an enemy.

Nor are we helped here by the assumption of *purely
internal motive forces,* which Nägeli, Askenasy, and
others have put forward as supplying a *mechanical*
force of evolution.   It is impossible to regard the co-

incidence of an Indian butterfly with the leaf of a tree now growing in an Indian forest as fortuitous, as a *lusus naturæ.* Assuming this seemingly mechanical force, therefore, we should be led back inevitably to a teleological principle which produces adaptive characters and which must have deposited the directive principle in the very first germ of terrestrial organisms, so that after untold ages at a definite time and place the illusive leaf-markings should be developed. The assumption of pre-established harmony between the evolution of the ancestral line of the tree with its pre-figurative leaf, and that of the butterfly with its imitating wing, is absolutely necessary here —a fact which I pointed out many years ago,[1] but which is constantly forgotten by the promulgators of the theory of internal evolutionary forces.

For the present I leave out of consideration altogether the question as to the conceivable extent of the sphere of operation of natural selection; I am primarily concerned only with elucidating the process of selection itself, wholly irrespective of the comprehensiveness or limitedness of its sphere of action. For this purpose it is sufficient to show, as I have just done, *that cases exist wherein all natural explanations except that of selection fail us.* But let us now see how far the principle of selection will carry us in the explanation of such cases—natural selection, I mean, as it was formulated by Darwin and Wallace.

There can be no doubt but the leaf-markings readily admit of production in this manner, slowly and with a gradual but constant increase of fidelity, provided a single condition is fulfilled: *the occurrence of the*

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[1] *Studien zur Descendenztheorie,* Leipsic, 1876. Vol. II, pp. 295 and 322.

right variations at the right place.   But just here, it
would seem, is the insurmountable barrier to the ex-
planatory power of our principle, for who, or what,
is to be our guarantee that dark scales shall appear at
the exact spots on the wing where the midrib of the
leaf must grow?   And that later dark scales shall
appear at the exact spots to which the midrib must be
prolonged?   And that still later such dark spots shall
appear at the places whence the lateral ribs start, and
that here also a definite acute angle shall be accurately
preserved, and the mutual distances of the lateral ribs
shall be alike and their courses parallel?   And that
the prolongation of the median rib from the hind
wing to the fore wing shall be extended exactly to
that spot where the fore wing is not covered by the
hind wing in the attitude of repose?   And so on.

If I could go more minutely into this matter, I
should attempt to prove that the markings, as I have
just assumed, have not arisen suddenly, but were per-
fected very, very gradually; that in one species they
began on the fore wing and in another on the hind
wing; and that in many they never until recently pro-
ceeded beyond one wing, in other species they went
only a little way, and in only a few did they spread
over the entire surface of both wings.

That these markings advanced slowly and gradually,
but with marvelous accuracy, is no mere conjecture.
But it follows that the right variations at the right
places must never have been wanting, or, as I ex-
pressed it before: *the useful variations were always
present.*   But how is that possible in such long exten-
sive lines of dissimilar variations as have gradually
come to constitute markings of the complexity here
presented?   Suppose that the useful colors had not

appeared at all, or had not appeared at the right places? It is a fact that in constant species, that is, in such as are not in process of transformation, the variations of the markings are by no means frequent or abundant. Or, suppose that they had really appeared, but occurred only in individuals, or in a small percentage of individuals?

Such are the objections raised against the theory of selection by its opponents, and put forward as insurmountable obstacles to the process. Nor are such objections relevant only in the case of protective colorings; they are applicable in all cases where the process of selection is concerned. Take the case of instincts that are called into action only once in life, as, for example, the pupal performances of insects, the artificial fabrication of cocoons, etc. How is it that the useful variations were always present here? And yet they must have been present, if such complicated spinning instincts could have taken their rise as are observable in the silk-worm, or in the emperor-moth. And they have been developed, and that in whole families, in forms varying in all species, and in every case adapted to the special wants of the species.

Particularly striking is the proof afforded of this constant presence of the useful variations by cases where we meet with the development of highly special adaptations that are uncommon even for the group of organisms concerned. Such a case, for example, is the apparatus designed for the capture of small animals and their digestion, found in widely different plants and widely separated families. On the other hand, very common adaptations, such as the eyes of animals, show distinctly that in all cases where it was necessary, the useful variations for the formation of

an eye were presented, and were presented further ex-
actly at spots at which organs of vision could perform
their best work: thus, in Turbellaria and many other
worms that live in the light, at the anterior extremity
of the body and on the dorsal surface; in certain
mussels, on the edge of the mantle; in terrestrial snails,
on the antennæ; in certain tropical marine snails in-
habiting shallow waters, on the back; and in the
chitons even on the dorsal surface of the shell!

But even taking the very simplest cases of selection,
it is impossible to do without this assumption, that
the useful variations are always present, or that *they
always exist in a sufficiently large number of individ-
uals for the selective process.* You know the thick-
ness and power of resistance of the egg-shells of
round-worms. The eggs of the round-worms of
horses have been known to continue their course of
development undisturbed even after they had been
thrown into strong alcohol and all other kinds of in-
jurious liquids—much to the vexation of the embry-
ologists, who wished to preserve a definite stage of de-
velopment and sought to kill the embryo at that stage.
Indeed, think of the result, if in the course of their
phylogenesis stout and resistant variations of egg-
shells had not been presented in these worms, or had
not always been presented, or had not been presented
in every generation and not in sufficient quantities.

The cogency of the facts is absolutely overpowering
when we consider that practically no modification
occurs *alone,* that every primary modification brings
in its train secondary ones, and that these induce
forced modifications in many parts of the body, fre-
quently of the most diversified, or even self-contra-
dictory, forms. Recently Herbert Spencer has drawn

fresh attention to these secondary modifications, which must always occur in harmony with the primary one, and has, as he thinks, advanced in this set of facts, a convincing disproof of the contention that such coadaptive modifications of numerous cofunctioning parts can rest on natural selection. Now, although I deem his conclusion precipitate, yet the very fact of a simultaneous, functionally concordant, yet essentially diversified modification of numerous parts, points conclusively to the circumstance that *something is still wanting to the selection of Darwin and Wallace, which it is obligatory on us to discover, if we possibly can,* and without which selection as yet offers no complete explanation of the phyletic processes of transformation. There is a hidden secret to be unriddled here before we can obtain a satisfactory insight into the phenomena in question. *We must seek to discover why it happens that the useful variations are always present.*

Herbert Spencer appealed to Lamarck's principle for the explanation of coadaptation, and it is certain that functional adaptation is operative during the individual life, and that it compensates in a certain measure the inequalities of the inherited constitutions. I shall not repeat what I have said before on this subject, nor maintain, in refutation of Spencer's contention, that functional adaptation is itself nothing more than the efflux of *intra-biontic* selective processes, as Spencer himself once suggested in a prophetic moment, but which it was left for Wilhelm Roux to introduce into science as "the struggle of the parts" of organisms.[1] I shall only remark that if functional adaptations were themselves inheritable, this would still be insufficient

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[1] Compare my essay, *Neue Gedanken zur Vererbungsfrage,* Jena, 1895, p. 10, second footnote.

for the explanation of coadaptation, for the reason that precisely similar coadaptive modifications occur in *purely passively* functioning parts, in which, consequently, modification *by* function is excluded. This is the case with the skeletal parts of Articulata; e. g., it is true of their articular surfaces with their complex adaptations to the most varied forms of locomotion. In all these cases the ready-made, hard, unalterable, chitinous part is *first* set into activity; consequently its adaptation to the function must have been *previously* effected, independently of that function. These joints, and divers other parts, accordingly, have been developed in the precisest manner for the function, and the latter could have had no direct share in their formation. When we consider, now, that it is impossible that every one of the numerous surfaces, ridges, furrows, and corners found in a single such articulation, let alone in all the articulations of the body, should hold in its hands the power of life and death over individuals for untold successions of generations, the fact is again unmistakably impressed upon our attention that the conception of the selective processes which has hitherto obtained is insufficient, that the root of the process in fact lies deeper, that it is to be found in the place where it is determined what variations of the parts of the organism shall appear—namely *in the germ.*

The phenomena observed in the *stunting,* or *degeneration, of parts rendered useless,* point to the same conclusion. They show distinctly that ordinary selection which operates by the removal of entire persons, *personal selection,* as I prefer to call it, cannot be the only cause of degeneration; for in most cases of degeneration it cannot be assumed that slight individual

vacillations in the size of the organ in question have possessed selective value. On the contrary, we see such retrogressions affected apparently *in the shape of a continuous evolutionary process determined by internal causes,* in the case of which there can be no question whatever of selection of persons or of a survival of the fittest, that is, of individuals with the smallest rudiments.

It is this consideration principally that has won so many adherents for the Lamarckian principle in recent times, particularly among the paleontologists. They see the outer toes of hoofed animals constantly and steadily degenerating through long successions of generations and species, concurrently with the re-enforcement of one or two middle toes, which are preferred or are afterwards used exclusively for stepping, and they believe correctly enough that these results should not be ascribed to the effects of personal selection alone. They demand a principle which shall effect the degeneration by internal forces, and believe that they have found it in functional adaptation.[1]

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[1] On the same day on which the present address was delivered at the International Congress of Zoölogists in Leyden, and on the same occasion, Dr. W. B. Scott, Professor of Geology in Princeton College, New Jersey, read a very interesting paper on the tertiary mammalian fauna of North America, in which, without a knowledge of my paper, he took his stand precisely on this argument and arrived at the opinion that it could not possibly be the ordinary individual variations which accomplished phyletic evolution, but that it was necessary to assume in addition phyletic variations. I believe our views are not as widely remote as might be supposed. Of course, I see no reason for assuming two kinds of hereditary variations, different *in origin.* Still it is likely that only a relatively small portion of the numberless individual variations lie on the path of phyletic advancement and so under

On this last point, now, I believe, they are mistaken, be they ever so strongly convinced of the correctness of their view and ever so aggressive and embittered in their defence of it.

Recently, an inquirer of great caution and calmness of judgment, Prof. C. Lloyd Morgan, has expressed the opinion that the Lamarckian principle must at least be admitted as a working hypothesis. But with this I cannot agree, at least as things stand at present. A working hypothesis may be false, and yet lead to further progress; that is, it may constitute an advance to the extent of being useful in formulating the problem and in illuminating paths that are likely to lead to results. But it seems to me that a hypothesis of this kind has performed its services and must be discarded the moment it is found to be at hopeless variance with the facts. If it can be proved that precisely the same degenerative processes also take place in such superfluous parts as have only *passive* and not active functions, as is the case with the *chitinous parts of the skeleton of Arthropoda*, then it is a demonstrated fact, that the cessation of functional action is not the efficient cause of the process of degeneration. At once your legitimate working hypothesis is transformed into an illegitimate dogma—illegitimate because it no longer serves as a guide on the path to knowledge but

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the *guidance* of germinal selection mark out the way of further development; and hence it would be quite possible in this sense to distinguish continuous, *definitely directed* individual variations from such as fluctuate hither and thither with no uniformity in the course of generations. The root of the two is of course the same, and they admit of being distinguished from each other only by their success, phyletic modification, or by their failure.

blocks that path. For the person who is convinced he has found the right explanation is not going to seek for it.

I can understand perfectly well the hesitation that has prevailed on this point in many minds, from their having seen *one* aspect of the facts more distinctly than the other. From this sceptical point of view Osborn has drawn the following perfectly correct conclusion: "If acquired variations are transmitted, there must be some unknown principle in heredity; if they are not transmitted, there must be some unknown factor in evolution."[1]

Such in fact is the case and I shall attempt to point out to you what this factor is. My inference is a very simple one: if we are forced by the facts on all hands to the assumption that the useful variations which render selection possible are always present, then *some profound connection must exist between the utility of a variation and its actual appearance,* or, in other words, *the direction of the variation of a part must be determined by utility,* and we shall have to see whether facts exist that confirm our conjecture.

The facts do indeed exist and lie before our very eyes, despite their not having been recognised as such before. All *artificial selection* practised by man rests on the fact that by means of the selection of individuals having a given character slightly more pronounced than usual, there is gradually produced a general augmentation of this character, which subsequently reaches a point never before attained by any individual

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[1] H. F. Osborn, "The Hereditary Mechanism and the Search for the Unknown Factors of Evolution," in *Biological Lectures delivered at the Marine Biolog. Lab. at Wood's Holl in the Summer Session of 1894.* Boston, 1895.

of this species.   I shall choose an example which seems to me especially clear and simple because only one character has been substantially modified here.   The long-tailed variety of domestic cock, now bred in Japan and Corea, owes its existence to skilful selection and not at all to the circumstance that at some period of the race's history a cock with tail-feathers six feet in length suddenly and spasmodically appeared.   At the present day even, as Professor Ishikawa of Tokio writes me, the breeders still make extraordinary efforts to increase the length of the tail, and every inch gained adds considerably to the value of the bird.   Now nothing has been done here whatever except always to select for purposes of breeding the cocks with the longest feathers; and in this way alone were these feathers, after the lapse of many generations, prolonged to a length far exceeding every previous variation.

I once asked a famous dove-fancier, Mr. W. B. Tegetmeier of London, whether it was his opinion that by artificial selection alone a character could be augmented.   He thought a long time and finally said: "It is without our power to do anything if the variation which we seek is not presented, but once that variation is given, then I think the augmentation can be effected."   And that in fact is the case.   If cocks had never existed whose tail-feathers were a little longer than usual the Japanese breed could never have originated; but as the facts are, always the cocks with the longest feathers were chosen from each generation, and these only were bred, and thus a hereditary augmentation of the character in question was effected, which would hardly have been deemed possible.

Now what does this mean?   Simply that the hered-

itary diathesis, the constitutional predisposition (*Anlage*) of the breed was changed in the respect in question, and our conclusion from this and numerous similar facts of artificial selection runs as follows: *by the selection alone of the plus or minus variations of a character is the constant modification of that character in the plus or minus direction determined.* Obviously the hereditary *diminution* of a part is also effected by the simple selection of the individuals in each generation possessing the smallest parts, as is proved, for example, by the tiny bills and feet of numerous breeds of doves. We may assert, therefore, in general terms: a definitely directed progressive variation of a given part is produced by continued selection in that definite direction. This is no hypothesis, but a direct inference from the facts and may also be expressed as follows: *By a selection of the kind referred to the germ is progressively modified in a manner corresponding with the production of a definitely directed progressive variation of the part.*

In this general form the proposition is not likely to encounter opposition, as certainly no one is prepared to uphold the view that the germ remains unchanged whilst the products proceeding from it, its descendants, are modified. On the contrary, all will agree when I say that the germ in this case must have undergone modifications, and that their character must correspond with the modifications undergone by its products. Thus far, then, we find ourselves, not on the ground of the hypothesis that has been lately so much maligned, but on the ground of facts and of direct inferences from facts. But if we attempt to pierce deeper into the problem, we are in need of the hypothesis.

The first and most natural explanation will be this
—that through selection the zero-point, about which,
figuratively speaking, the organ may be said to oscil-
late in its plus and minus variations, is displaced up-
wards or downwards.   Darwin himself assumed that
the variations oscillated about a mean point, and the
statistical researches of Galton, Weldon, and others
have furnished a proof of the assumption.   If selec-
tion, now, always picks out the plus variations for
imitation, perforce, then, the mean or zero-point will be
displaced in the upward direction, and the variations
of the following generation will oscillate about a
higher mean than before.   This elevation of the zero-
point of a variation would be continued in this manner
until the total equilibrium of the organism was in
danger of being disturbed.

There is involved here, however, an assumption
which is by no means self-evident, that every advance-
ment gained by the variation in question constitutes
a new centre for the variations occurring in the fol-
lowing generation.   *That this is a fact,* is proved by
such actual results of selection as are obtained in the
case of the Japanese cock.   But the question remains,
Why is this the fact?

Now here, I think, my theory of determinants gives
a satisfactory answer.   According to that theory every
independently and hereditarily variable part is repre-
sented in the germ by a *determinant,* that is by a de-
terminative group of vital units, whose size and power
of assimilation correspond to the size and vigor of the
part.   These determinants multiply, as do all vital
units, by growth and division, and necessarily they in-
crease rapidly in every individual, and the more
rapidly the greater the quantity of the germinal cells

the individual produces. And since there is no more reason for excluding irregularities of passive nutrition, and of the supply of nutriment in these minute, microscopically invisible parts, than there is in the larger visible parts of the cells, tissues, and organs, consequently the descendants of a determinant can never all be exactly alike in size and capacity of assimilation, but they will oscillate in this respect to and fro about the maternal determinant as about their zero-point, and will be partly greater, partly smaller, and partly of the same size as that. In these oscillations, now, the material for further selection is presented, and in the inevitable fluctuations of the nutrient supply I see the reason why every stage attained becomes immediately the zero-point of new fluctuations, and consequently why the size of a part can be augmented or diminished by selection without limit, solely by the displacement of the zero-point of variation as the result of selection.

We should err, however, if we believed that we had penetrated to the root of the phenomenon by this insight. There is certainly some other and mightier factor involved here than the simple selection of persons and the consequent displacement of the zero-point of variation. It would seem, indeed, as if in one case, *videlicet,* in that of the Japanese cock, the augmentation of the character in question were completely explained by this factor *alone*. In fact, in this and similar cases we cannot penetrate deeper into the processes of variation, and therefore cannot say *a priori* whether other factors have or have not been involved in the augmentation of the character in question—other characters, that is, than the simple displacement of the zero-point. There is, however, another class of phyletic modifications, which point

unmistakably to the conclusion that the displacement of the zero-point of variation by personal selection is not and cannot be the only factor in the determination and accomplishment of the direction of variation. I refer to *retrogressive development,* the gradual degeneration of parts or characters that have grown useless, the gradual disappearance of the eye in cave-animals, of the legs in snakes and whales, of the wings in certain female butterflies, in short, to that entire enormous mass of facts comprehended under the designation of "rudimentary organs."

I have endeavored on a previous occasion to point out the significance of the part played in the great process of animate evolution by these retrogressive growths, and I made at the time the statement that "the phenomena of retrogressive growth enabled us in a greater measure almost than those of progressive growth to penetrate to the causes which produce the transformations of animate nature." Although at that time[1] I had no inkling of certain processes which to-day I shall seek to prove the existence of, yet my statement receives a fresh confirmation from these facts.

For, in most retrogressive processes *active* selection in Darwin's sense plays no part, and advocates of the Lamarckian principle, as above remarked, have rightly denied that active selection, that is, the selection of individuals possessing the useless organ in its most reduced state, is sufficient to explain the process of degeneration. I, for my part, have never assumed this,

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[1] In 1886. See my paper on "Retrogression in Nature," published in English in Nos. 105, 107, 108, and 109 of *The Open Court,* and also in my essays on *Heredity,* Jena, 1892.

and I enunciated precisely on this account the *principle of panmixia.* Now, although this, as I still have no reason for doubting, is a perfectly correct principle, which really does have an essential and indispensable share in the process of retrogression, still it is not *alone* sufficient for a full explanation of the phenomena. My opponents, in advancing this objection, were right, to the extent indicated and as I expressly acknowledge, although they were unable to substitute anything positive in its stead or to render my explanation complete. The very fact of the cessation of control over the organ is sufficient to explain its *degeneration,* that is, its deterioration, the disharmony of its parts, but not the fact which actually and always occurs where an organ has become useless—viz., *its gradual and unceasing diminution continuing for thousands and thousands of years culminating in its final and absolute effacement.*

If, now, neither the selection of persons nor the cessation of personal selection can explain this phenomenon, assuredly some other principle must be the efficient cause here, and this cause I believe I have indicated in an essay written at the close of last year and only recently published.[1] I call it *germinal selection.*

The principle in question reposes on the application, made some fifteen years ago by Wilhelm Roux, of the principle of selection to the *parts* of organisms—on the *struggle of the parts,* as he called it. If such a struggle obtains among organs, tissues, and cells, it must also obtain between the smallest and for us invisible vital particles, not only between those of the body-cells, strictly so called, but also between those of the

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[1] *Neue Gedanken zur Vererbungsfrage,* Jena, 1895.

germinal cells. Roux himself spoke of the struggle
of the molecules, by which he presumably understood
the smallest ultimate units of vital phenomena—ele-
ments which De Vries designated pangenes, Wiesner
plasomes, and I *biophores,* after Brücke's ingenious
conception[1] of these invisible entities had been almost
totally forgotten, or at least had lain unnoticed for
thirty years. No struggle, as that is understood in
the theory of selection, could take place between real

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[1] Delâge, in *La structure du protoplasma et les théories sur
l'hérédité,* etc., Paris, 1895, is mistaken in attributing to Her-
bert Spencer the merit of having first pointed out the neces-
sity of the assumption of biological units ranking between the
molecule and the cell. Brücke set forth this idea three
years previously to Spencer and established it exhaustively
in a paper which in Germany at least is famous ("Elemen-
tarorganismen," *Wiener Sitzungsberichte,* October 10, 1861,
Vol. XLIV., II., p. 381). Spencer's *Principles of Biology* ap-
peared between 1864 and 1868; consequently there can be
no dispute touching the priority of the idea. Strangely
enough Delâge cites Brücke's essay in the Bibliographical
Index at the end of his book correctly, although Brücke's
name and views are nowhere mentioned in the book itself.
It is to be observed, however, that the elementary organisms
of Brücke are not merely the precursors of Spencer's "phys-
iological units," but repose on much firmer foundations than
the latter, which, as Delâge himself remarks, are at bottom
nothing more than magnified molecules and not combinations
of different molecules of such character as to produce neces-
sarily phenomena of life. He aptly remarks on this point:
"the physiological units of Spencer are only chemical mole-
cules of greater complexity than the rest, and as he defines
them they would be regarded as such by every chemist. He
attributes to them no property *essentially* different from
those of chemical molecules." Assimilation, growth, propa-
gation, in short the attributes of life, are not attributed by
Spencer to his units, while Brücke by his very designation
"elementary organisms" expresses the idea of "ultimate living

molecules, for molecules are neither nourished, subject to growth, nor propagated.

The gradual degeneration of organs grown useless may be explained, now, by the theory of determinants very simply and without any co-operation on the part of active personal selection, as follows.

Nutrition, it is known, is not merely a passive process. A part is not only *nourished* but also actively *nourishes* itself, and the more vigorously, the more powerful and capable of assimilation it is. Hence powerful determinants in the germ will absorb nutriment more rapidly than weaker determinants. The latter, accordingly, will grow more slowly and will produce weaker descendants than the former.

Let us assume, now, that a part of the body, say the hinder extremities of the quadruped ancestors of

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units," to use Wiesner's phrase. Of course this particular aspect of the vital units was not emphasised by Brücke with the same distinctness and sharpness as by recent inquirers, who took up Brücke's ideas thirty years after. I refer to the conception that the union of a definite combination of heterogeneous molecules into an invisibly small unit, forms the cradle or focus of the vital phenomena. This was first done and apparently on independent considerations by De Vries, and soon after by Wiesner, and subsequently by myself (De Vries, *Intracelluläre Pangenesis,* Jena, 1889; Wiesner, *Die Elementarstructur und das Wachsthum der lebenden Substanz,* Vienna, 1892; Weismann, *Das Keimplasma,* Jena, 1892). Let me say at the close of this note that it is not my intention in thus defending the rights of a great physiologist, to censure in the least the distinguished author of *L'hérédité* who has set himself a remarkably high standard of exactitude in such matters. Certainly, when we consider the enormous extent of the literature that had to be mastered to produce his book, embracing as it did all the various theories of recent times, such an oversight is quite excusable.

our common whales, are rendered useless.   Panmixia
steps in, *i. e.,* selection ceases to influence these organs.
Individuals with large and individuals with small hind
legs are equally favored in the struggle for existence.

From this fact alone would result a degradation of
the organ, but of course it would not be very marked
in extent, seeing that the minus variations which occur
are no longer removed.   According to our assumption,
however, such minus variations repose on the weaker
determinants of the germ, that is, on such as absorb
nutriment less powerfully than the rest.   And since
every determinant battles stoutly with its neighbors
for food, that is, takes to itself as much of it as it
can, consonantly with its power of assimilation and
proportionately to the nutrient supply, therefore the
unimpoverished neighbors of this minus determinant
will deprive it of its nutriment more rapidly than was
the case with its more robust ancestors; hence, it will
be unable to obtain the full quantum of food corre-
sponding even to its weakened capacity of assimilation,
and the result will be that its ancestors will be weak-
ened still more.   Inasmuch, now, as no weeding out of
the weaker determinants of the hind leg by personal
selection takes place on our hypothesis, inevitably the
average strength of this determinant must slowly but
constantly diminish, that is, the leg must grow smaller
and smaller until finally it disappears altogether.   The
determinants[1] of the useless organ are constantly at

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[1] I speak here of determinants, not of groups of determi-
nants, which is the more correct expression, merely for the
sake of brevity.   It is a matter of course that a whole
extremity, such as we have here chosen, cannot be repre-
sented in the germ by a single determinant only, but requires
a large group of determinants.

a disadvantage as compared with the determinants of their environment in the germinal tenement, because no assistance is offered to them by personal selection after they have once been weakened by a decrease of the passive nutrient influx. Nor is the degeneration stopped by the uninterrupted crossing of individuals in sexual propagation, but only slightly retarded. The number of individuals with weaker determinants must, despite this fact, go on increasing from generation to generation, so that soon every determinant that still happens to be endowed with exceptional vigor will be confronted by a decided overplus of weaker determinants, and by continued crossing therefore will become more and more impoverished. Panmixia is the indispensable precondition of the whole process; for owing to the fact that persons with weak determinants are just as capable of life as those with strong, owing to the fact that they cannot now, as formerly, when the organ was still useful, be removed by personal selection, solely by this means is a further weakening effected in the following generations—in short, only by this means are the determinants of the useless organ brought upon the inclined plane, down which they are destined slowly but incessantly to slide towards their completed extinction.

The foregoing explanation will be probably accepted as satisfactory *in a purely formal regard,* but it will be objected that, even granting this, it has not yet been proved to be the correct one. In answer I can of course adduce nothing except that it is at present the only one that can be given. It may be that the actual state of things in nature is different, but if it can be shown that a self-direction of variation merely from the need of it is at all conceivable by mechanical means,

that in itself, it seems to me, is a decided gain. It must also not be forgotten that some process or other *must* take place in the germ-plasm when an organ becomes rudimentary, and that as the result of it this organ, and only this organ, must disappear. Now in what shall this process consist, if not in a modification of the constitution of the germ? And how could the effect of such a modification be limited only to *one* organ which was becoming rudimentary if the modification itself were not a local one? These are questions which it is incumbent on those to answer who conceive the germinal substance to be composed of like units.

Applying, now, the explanation derived from the disappearance of organs to the opposed transformation, namely, to the *enlargement* of a part, the presumption lies close at hand that the production of the long tail-feathers of the Japanese cock does not repose solely on the displacement directly effected by personal selection, of the zero-point of variation upwards, but that *it is also fostered and strengthened by germinal selection.* Were that not so, the phenomena of the transmutation of species, in so far as fresh growth and the enlargement and complication of organs already present are concerned, *would not be a whit more intelligible than they were before.* We should know probably how it comes to pass that the constitutional predisposition (group of determinants) of a *single* organ is intensified by selection, but the flood of objections against the theory of selection touching its inability to modify *many* parts at once would not be repressed by such knowledge. The initial impulse conditioning the independent maintenance of the useful direction of variation in the germ-plasm must rather be sought

in the utility of the modification itself, and this also seems to me intelligible from the side of the theory. For as soon as personal selection favors the more powerful variations of a determinant, the moment that these come to predominate in the germ-plasm of the species, at once the tendency must arise for them to vary *still more strongly* in the plus direction, not solely because the zero-point has been pushed farther upwards, but because they themselves now oppose a relatively more powerful front to their neighbors, that is, actively absorb more nutriment, and upon the whole increase in vigor and produce more robust descendants. From the relative vigor or dynamic status of the particles of the germ-plasm, thus, will issue spontaneously an ascending line of variation, precisely as the facts of evolution require. For, as I have already said, it is not sufficient that the augmentation of a character should be brought about by uninterrupted personal selection, even supposing that the displacement of the zero-point were possible without germinal selection.

Thus, I think, may be explained how personal selection imparts the initial impulse to processes in the germ-plasm, which, when they are once set agoing, persist of themselves in the same direction, and are, therefore, in no need of the continued supplementary help of personal selection, *as directed exclusively to a definite part.* If but from time to time, that is, if upon the average the poorest individuals, the bearers of the weakest determinants, are eliminated, the variational direction of the part in question, now reposing on germinal selection, must persist, and it will very slowly but very surely increase until further development is impeded by its inutility and personal selection

arrests the process, that is, ceases to eliminate the weaker individuals.

In this manner it becomes intelligible how a large number of modifications varying in kind and far more so in degree can be guided *simultaneously* by personal selection; how in strict conformity with its adaptive wants every part is modified, or preserved unmodified; how a given articulation can undergo modifications, causing it to disappear on one side, to grow in volume on another, and to continue unaltered on a third. For every part that is perfectly adapted, although it can fluctuate slightly, yet can never undergo a permanent alteration in the ascending or descending direction because every plus and every minus variation which has attained selective value would be eliminated by personal selection in the course of time. Therefore, a definite direction of variation cannot arise in such cases and we have also reached, as it seems to me, a satisfactory explanation of the *constancy* of well-adapted species and characters.

Hitherto I have spoken only of plus and minus variation. But there exist, as we know, not only variations of size but also variations of *kind;* and the coloration of the wings of butterflies, which we chose above as our example, would fall, according to the ordinary usage of speech, under just this head of variations of quality. The question arises, therefore, Have the principles just developed any claim to validity in the explanation of *qualitative* modifications?

In considering this question it should be carefully borne in mind that by far the largest part of the qualitative modifications falling under this head rest on *quantitative* changes. Of course, chemical transformations, which usually also involve quantitative altera-

tions, cannot be reduced to the processes of augmentation described, inasmuch as these, by their very nature, can be effected only in living elements capable of increase by propagation; but the interference of selection does not begin originally with the constitutional predisposition (*Anlagen*) of the germ, i. e. with the determinants, but with the ultimate units of life, the *biophores.*

A determinant must be composed of heterogeneous biophores, and on their numerical proportion reposes, according to our hypothesis, their specific nature. If that proportion is altered, so also is the character of the determinant. But disturbances of this numerical proportion must result at once on proof of their usefulness, or as soon as the modifications determined thereby in the inward character of the determinant turn out to be of utility. For fluctuations of nutriment and the struggle for nutriment, with its sequent preference of the strongest, must take place between the various species of the biophores as well as between the species of the determinants. But changes in the quantitative ratios of the biophores appear to us qualitative changes in the corresponding determinants, somewhat as a simple augmentation of a determinant, for example, that of a hair, may on its development appear to us as a qualitative change, a spot on the skin where previously only isolated hairs stood being now densely crowded with them, and assuming thus the character of a downy piece of fur. The single hair need not have changed in this process, and yet the spot has virtually undergone a qualitative modification. The majority of the changes that appear to us qualitative rest on invisible *quantitative* changes, and such can be produced at all times and *at all stages*

of the vital units by germinal selection.   In a similar
manner are induced the most varied qualitative
changes of the corresponding determinants and of the
characters conditioned thereby, just as changes in the
numerical proportions of atoms produce essential
changes in the properties of a chemical molecule.

In this way we acquire an approximate conception
of the possible mechanical *modus operandi* of actual
events—namely, of the manner in which the useful
variations required by the conditions of life *can* al-
ways, that is, very frequently, make their appearance.
This possibility is the sole condition of our being able
to understand how different parts of the body, abso-
lutely undefined in extent, can appear as variational
units and vary in the same or in different directions,
according to the special needs of the case, or as the
conditions of life prescribe.   Thus, for example, in the
case of the butterfly's wings it rests entirely with
utility to decide the size and the shape of the spots
that shall vary simultaneously in the same direction.
At one time the whole under surface of the wing ap-
pears as the variational unit and has the same color;
at another the inside half, which is dark, is contrasted
with the outside half which is bright; or the same con-
trast will exist between the anterior and posterior
halves; or, finally, narrow stripes or line-shaped
streaks will behave as variational units and form con-
trasts with manifold kinds of spots or with the broader
intervals between them, with the result that the picture
of a leaf or of another protected species is produced.

I must refrain from entering into the details of such
cases and shall illustrate my views regarding the color-
transformations of butterflies' wings by the simplest

conceivable example—viz. that of the uniform change of color on the entire under surface of the wing.

Suppose, for example, that the ancestral species of a certain forest-butterfly habitually reposed on branches which hung near the ground and were covered with dry or rotten leaves; such a species would assume on its under surface a protective coloring which by its dark, brown, yellow, or red tints would tend toward similarity with such leaves. If, however, the descendants of this species should be subsequently compelled, no matter from what cause, to adopt the habit of resting on the green-leafed branches higher up, then from that period on the brown coloring would act less protectively than the shades verging towards green. And a process of selection will have set in which consisted first in giving preference only to such persons whose brown and yellow tints showed a tendency to green. Only on the assumption that such shades were possible by a displacement in the quantitative proportions of the different kinds of biophores composing the determinants of the scales affected, was a further development in the direction of green possible. Such being the case, however, that development *had to* result; because fluctuations in the numerical proportions of the biophores are always taking place, and consequently the material for germinal selection is always at hand. At present it is impossible to determine exactly the magnitude of the initial stages of the deviations thus brought about and promoted by the sexual blending of characters; but it may perhaps be ascertained in the future, with exceptionally favorable material. Pending such special observations, however, it can only be said *a priori* that slight changes in the composition of a determinant do not necessarily condi-

tion similar slight deviations of the corresponding character,—in this case the color,—just as slight changes in the atomic composition of a molecule may result in bestowing upon the latter widely different properties.   As soon, however, as the beginning has been made and a definite direction has been imparted to the variation, as the result of this or that primary variation's being preferred, the selective process must continue until the highest degree of faithfulness required by the species in the imitation of fresh leaves has been attained.

That the foregoing process has actually taken place is evidenced not only by the presence of the beginnings of such transformations, as found for example in some greenish-tinted specimens of Kallima, but mainly by certain species of the South American genus Cato-nephele, all of which are forest-butterflies, and which, with many species having dark-brown under surfaces, present some also with bright green under surfaces— a green that is not like the fresh green of our beech and oak trees, but resembles the bright under surface of the cherry-laurel leaf, and is the color of the under surfaces of the thick, leathery leaves, colored dark-green above, borne by many trees in the tropics.

The difference between this and the old conception of the selection-process consists not only in the fact that a large number of individuals with the initial stages of the desired variation is present from the beginning, for always innumerable plus and minus variations exist, but principally in the circumstance that the constant uninterrupted progress of the process after it is once begun is assured, that there can never be a lack of progressively advantageous variations in a large number of individuals.   Selection,

therefore, is now not compelled to wait for accidental variations but produces such itself, whenever the required elements for the purpose are present. Now, where it is a question simply of the enlargement or diminution of a part, or of a part of a part, these variations are always present, and in modifications of quality they are at least present in many cases.

This is the only way in which I can see a possibility of explaining phenomena of *mimicry*—the imitation of one species by another. The useful variations must be produced in the germ itself by internal selection-processes if this class of facts is to be rendered intelligible. I refer to the mimicry of an exempt species by two or three other species, or, the aping of *different* exempt patterns by *one* species in need of protection. It must be conceded to Darwin and Wallace that some degree of similarity between the copy and the imitation was present from the start, at least in very many cases;[1] but in no case would this have been sufficient had not slight shades of coloring afforded some hold for personal selection, and in this way furnished a basis for independent germinal selection acting only in the direction indicated. It would have been impossible for such a minute similarity in the design, and particularly in the shades of the coloration, ever to have arisen, if the process of adaptation rested entirely

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[1] That this is not so in all cases has recently been shown by Dixey from observations on certain white butterflies of South America which mimic the Heliconids and in which a small, yellowish red streak on the under surface of the hind wing has served as the point of departure and groundwork of the development of a protective resemblance to quite differently colored Heliconids. "On the Relation of Mimetic Characters to the Original Form," in the *Report of the British Association for 1894.*

on personal selection.   Were this so, a complete scale
of the most varied shades of color must have been
continually presented as variations in every species,
which certainly is not the case.   For example, when
the exempt species *Acræa Egina,* whose coloration is
a brick-red, a color common only in the genus Acræa,
is mimicked by two other butterflies, a Papilio and a
Pseudacræa, so deceptively that not only the cut of
the wings and the pattern of their markings, but also
that precise shade of brick-red, which is scarcely ever
met with in diurnal butterflies, are produced, assuredly
such a result cannot rest on accidental, but must be
the outcome of a *definitely directed,* variation, pro-
duced by utility.   We cannot assume that such a col-
oration has appeared as an *accidental* variation in just
and in only these two species, which fly together with
the *Acræa* in the same localities of the same country
and same part of the world—the Gold Coast of Africa.
It is conceivable, indeed, that non-directed variation
should have accidentally produced this brick-red *in
a single case,* but that it should have done so three
times and in three species, which live together but
are otherwise not related, is a far more violent and
improbable assumption than that of a causal connexion
of this coincidence.   Now hundreds of cases of such
mimicry exist in which the color-tints of the copy are
met with again in more or less precise and sometimes
in exceedingly exact imitations, and there are thou-
sands of cases in which the color-tint of a bark, of
a definite leaf, of a definite blossom, is repeated *exactly*
in the protectively colored insect.   In such cases there
can be no question of accident, but *the variations pre-
sented to personal selection must themselves have
been produced by the principle of the survival of the*

fit! And this is effected, as I am inclined to believe, through such profound processes of selection in the interior of the germ-plasm as I have endeavored to sketch to you to-day under the title of germinal selection.

I am perfectly well aware how schematic my presentation of this process is, and must be at present, owing mainly to our inability to gain exact knowledge concerning the fundamental germinal constituents here assumed. But I regard its existence as assured, although I by no means underrate the fact that eminent thinkers, like Herbert Spencer, contest its validity and believe they are warranted in assuming a germ which is composed of *similar units.* I strongly doubt whether even so much as a *formal* explanation of the phenomena can be arrived at in this manner. So far as direct observation is concerned, the two theories stand on an equal footing, for neither my dissimilar, nor Spencer's similar, units of germinal substance can be *seen* directly.

The attempt has been recently made to discredit my *Anlagen,* or constitutional germ-elements, on the ground that they are simply a subtilised reproduction of Bonnet's old theory of preformation.[1] This

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[1] Oscar Hertwig, *Zeit- und Streitfragen der Biologie,* Jena, 1894. It is customary now to look upon the preformation-theory of Bonnet as a discarded monstrosity, and on the epigenesis of K. F. Wolff as the only legitimate view, and to draw a parallel between these two and what might be called to-day "evolution" [i. e. unfoldment] and epigenesis. The evolution, or unfoldment, of Bonnet and Harvey, however, was something totally different from modern doctrines of evolution, and Whitman is quite right when he says that even my theory of determinants would have appeared to the inquirers of the last century as "extravagant epigenesis."

impression is very likely based upon ignorance of the real character of Bonnet's theory. I will not go into further details here, particularly as Whitman, in several excellently written and finely conceived essays, has recently afforded opportunity for every one to inform himself on the subject. My determinants and groups of determinants have nothing to do with the preformations of Bonnet; in a sense they are the exact opposites of them; they are simply *those living parts of the germ whose presence determines the appearance of a definite organ of a definite character in*

Biologists in that day were concerned with quite different questions from what they are at present, and although now we probably all share the conviction of Wolff that new characters do arise in the course of evolution, yet the acceptance of this view is far from settling the question *as to how these new characters are established in the germ-substance*—for in this substance they certainly must have their foundation. When, therefore, O. Hertwig laments over my regarding evolution and not epigenesis as the correct foundation of the theory of development, his sorrow is almost as naïve as is the statement of Bourne that epigenesis is a fact and not a theory ("a statement of morphological fact," *Science Progress,* April, 1894, page 108), or, as is the latter's unconsciousness that facts originally receive their scientific significance from thought, i. e. from their interpretation and combination, and that thought *is* theory. And when S. Minot, as the leader of the embryologists, carries his zeal to the pitch of issuing a general pronunciamento against me as a corruptor of youth, in which he declares it to be a "scientific duty to protest in the most positive manner against Weismann's theory," I wonder greatly that he does not suggest the casting of a general ballot in the matter. (See the *Biologisches Centralblatt* of August 1, 1895.) We see how with these gentlemen the wisdom of the recitation-room regarding the infallibility of epigenesis has grown into a dogma, and whoever ventures to disturb its foundations must be burnt as a heretic.

the course of normal evolution. In this form they appear to me to be an absolutely necessary and unavoidable inference from the facts. There *must* be contained in the germ parts that correspond to definite parts of the complete organism, that is, parts that constitute the reason why such other parts are formed.

It is conceded even by my opponents that the reason why one egg produces a chicken and another a duck is not to be sought in external conditions, but lies in a difference of the germinal substance. Nor can they deny that a difference of germinal substance must also constitute the reason why a slight *hereditary* difference should exist between two filial organisms. Should there now, in a possible instance, be present between them a second, a third, a fourth, or a hundredth difference of hereditary character, each of which could vary from the germ, then, certainly, some second, third, fourth, or hundredth part of the germ must have been different; for whence, otherwise, should the heredity of the differences be derived, seeing that external influences affecting the organism in the course of evolution induce only non-transmissible and transient deviations? But the fact that every complex organism is actually composed of a very large number of parts independently alterable from the germ, follows not only from the comparison of allied species, but also and principally from the experiments long conducted by man in artificial selection, and by the consequent and not infrequent change of only a single part which happens to claim his interest; for example, the tail-feathers of the cock, the fruit of the gooseberry, the color of a single feather or group of feathers, and so on. But a still more cogent proof is furnished by the degeneration of parts grown use-

less, for this process can be carried on to almost any extent without the rest of the body necessarily becoming involved in sympathetic alteration. Whole members may become rudimentary, like the hind limbs of the whale, or it may be only single toes or parts of toes; the whole wing may degenerate in the females of a butterfly species, or only a small circular group of wing-scales, in the place of which a so-called "window" arises. A single vein of the wing also may degenerate and disappear, or the process may affect only a part of it, and this may happen in one sex only of a species. In such cases the rest of the body may remain absolutely unaltered; only a stone is taken out of the mosaic.

The assumption, thus, appears to me irresistible, that every such hereditary and likewise independent and very slight change of the body rests on some alteration of a *single* definite particle of the germinal substance, and not as Spencer and his followers would have it, on a change of *all* the units of the germ. If the germinal substance consisted wholly of like units, then in every change, were it only of a single character, *each* of these units would have to undergo exactly the same modification. Now I do not see how this is possible.

But it may be that Spencer's assumption is the *simpler* one? Quite the contrary, its simplicity is merely apparent. Whilst my theory needs for each modification only a modification of *one* constitutional element of the germ, that is, of *one* particle of the germinal substance, according to Spencer *every* particle of that substance must change, for they are all supposed to be and to remain alike. But seeing that all hereditary differences, be they of individuals, races,

or species, must be contained in the germ, the obligation rests on these similar units, or rather the capacity is required of them, to produce in themselves a truly enormous number of differences. But this is possible only provided their composition is an exceedingly complex one, or only on the condition that in every one of them are contained as many alterable particles as according to my view there are contained determinants in the whole germ. *The differences that I put into the whole germ, Spencer and his followers are obliged to put into every single unit of the germinal substance.* My position on this point appears to me incontrovertible so long as it is certain that the *single* characters can vary hereditarily; for, if a thing can vary independently, that is, *of its own accord,* and *from the germ,* then that thing must be represented in the germ by some particle of the substance, *and be represented there in such wise that a change of the representative particle produces no other change in the organism developing from the germ than such as are connected with the part which depends on it.* I conceive that even on the assumption of my constitutional elements (*Anlagen*) the germ-plasm is complex enough, and that there is no need of increasing its complexity to a fabulous extent. Be that as it may, the person who fancies he can produce a complex organism from a *really* simple germinal substance is mistaken: he has not yet thoroughly pondered the problem. The so-called "epigenetic" theory with its *similar* germinal units is therefore naught else than an evolution-theory where the primary constitutional elements are reduced to the molecules and atoms— a view which in my judgment is inadmissible. A *real*

epigenesis from absolutely *homogeneous* and not merely *like* units is not thinkable.

All value has been denied my doctrine of determinants[1] on the ground that it only shifts the riddles of evolution to an invisible terrain where it is impossible for research to gain a foothold.

Now I have indeed to admit that no information can be gained concerning my determinants, either with the aided or with the unaided eye. But fortunately there exists in man another organ which may be of use in fathoming the riddles of nature and this organ which is called the brain has in times past often borne him out in the assumption of invisible entities—entities that have not always proved unfruitful for science by reason of that defect, in proof whereof we may instance the familiar assumptions of atoms and molecules. Probably the biophores also will be included under that head if the determinants should be adjudged utterly unproductive. But so far I have always held that assumptions of this kind *are* really productive, if they are only capable of being used, so to speak, as a *formula,* whereby to perform our computations, unconcerned for the time being as to what shall be its subsequent fate. Now, as I take it, the determinants have had fruitful results, as their application to various biological problems shows. Is it no advance that we are able to reduce the scission of a form of life into two or several forms subject to separately continued but recurrent changes,—I refer to dimorphism and polymorphism,—that we are able to reduce such phenomena to the formula of male, female, and worker determinants? It has been, I think, ren-

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[1] Oscar Hertwig, *Zeit- und Streitfragen der Biologie,* Jena, 1894.

dered conceivable how these diverse and extremely minute adaptations could have developed side by side in the same germ-plasm, under the guidance of selection; how sterile forms could be *hereditarily* established and transformed in just that manner which best suits with their special duties; and how they themselves under the right circumstances could subsequently split up into two or even into three new forms. Surely at least the unclear conception of an *adaptively* transformative influence of food must be discarded. It is true, we cannot penetrate by this hypothesis to the last root of the phenomena. The hotspurs of biology, who clamor to know forthwith how the molecules behave, will scarcely repress their dissatisfaction[1] with such provisional knowledge—forgetful that *all our knowledge is and remains throughout provisional.*

But I shall not enter more minutely into the question whether epigenesis or evolution is the right foundation of the theory of development, but shall content myself with having shown, first, that it is illusory to imagine that epigenesis admits of a simpler structure of the germ, (the precise opposite is true,) and secondly, that there are phenomena that can be understood only by an evolution-theory. Such a phenomenon is

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[1] Nor will those, who demand a demonstration of "how the biophores and determinants are constituted in every case, and must be arranged in the architecture of the germ-plasm." (O. Hertwig, *loc. cit.,* p. 137). As if any living being could have the temerity even so much as to guess at the *actual* ultimate phenomena in evolution and heredity! The whole question is a matter of symbols only, just as it is in the matter of "forces," "atoms," "ether undulations," etc., the only difference being that in biology we stumble much earlier upon the unknown than in physics.

the *guidance of variation by utility,* which we have considered to-day. For without primary constituents of the germ, whether they are called as I call them, determinants, or something else, *germinal selection,* or guidance of variation by personal selection, is impossible; for where all units are alike there can be no struggle, no preference of the best. And yet such a guidance of variation exists and demands its explanation, and the early assumptions of a "definitely directed variation" such as Nägeli and Askenasy made are insufficient, for the reason that they posit only *internal* forces as the foundations thereof, and because, as I have attempted to show, the harmony of the direction of variation with the requirements of the conditions of life subsists and represents the riddle to be solved. *The degree of adaptiveness which a part possesses itself evokes the direction of variation of that part.*

This proposition seems to me to round off the whole theory of selection and to give to it that degree of inner perfection and completeness which is necessary to protect it against the many doubts which have gathered around it on all sides like so many lowering thunder-clouds. The moment variation is determined substantially though not exclusively by the adaptiveness itself, all these doubts fall to the ground, with *one* exception, that of the utility of the initial steps. But just this objection is the least weighty. Without doubt the theory requires that the initial steps of a variation should also have selective value; otherwise personal selection and hence germinal selection could not set in. Since, however, as I have before pointed out, *in no case can we pretend to a judgment regarding the selective value of a modification, or have any*

experience thereof, therefore the assumption that in a given case where a character is transformed the original initial steps of the variation did have selective value, is not only as probable as the opposed assumption that they had none, but is *infinitely more probable,* for with this we can give an intelligible explanation of the mysterious fact of adaptation, while with that we cannot. Consequently, unless we are resolved to give up all attempts whatsoever at explanation, we are forced to the assumption that the initial steps of all actually affected adaptations possessed selective value.

The principal and fundamental objection that selection is unable to create the variations with which it works, is removed by the apprehension that a germinal selection exists. Natural selection is not compelled to wait until "chance" presents the favorable variations, but supposing merely that the groundwork for favorable variations is present in the transforming species, that is, supposing merely that in the constitutional basis of the part to be changed are contained components which render favorable variations possible by a change of their numerical ratio, then those variations *must* occur, for the reason that quantitative fluctuations are always happening, and they must also be augmented as soon as personal selection intervenes and permanently holds over them her protecting hand. Not only is the marvelous *certainty and exactitude* with which adaptation has operated in so many individual cases, rendered intelligible in this manner, but what is more difficult, we are able to understand the *simultaneity* of numerous and totally different modifications of the most diverse parts co-operant towards some collective end, such as we see so frequently occur,

for example, in the simultaneous rise of instincts and protective similarities, or in the harmonious and simultaneous augmentation of two co-operant but independent organs, as of the eye and of the centre of vision, or of the nerve and its muscle, etc.

The "secret law," of which Wolff prophetically speaks in his criticism of selection, is in all likelihood naught else than germinal selection. This it is that brings it about that the necessary variations are always present, that symmetrical parts, for example, the two eyes, usually vary alike, but under circumstances may vary differently, for example, the two visual halves of soles; that homodynamic parts, (for instance, the member-pairs of Arthropoda,) have frequently varied alike, and not infrequently and in conformity with the needs of the animal, have varied differently. It brings it about also that conversely species of quite different fundamental constitutions occasionally vary alike, as instances of mimicry and numerous other cases of convergence show us. As soon as utility itself is supposed to exercise a determinative influence on the direction of variation, we get an insight into the entire process and into much else besides that has hitherto been regarded as a stumbling-block to the theory of selection, and which did indeed present difficulties that for the moment were insuperable—as, for example, the like-directed variation of a large number of already existing similar parts, seen in the origin of feathers from the scales of reptiles. The utility in the last-mentioned instance consisted, not in the transformation of one or two, but of *all* the scales; consequently the line of variation of *all* the scales must have been started simultaneously in the same direction. A large part of the objections to the theory of selection

that have been recently brought forward by the acut-est critics, as for example by Wigand, but particularly by Wolff,[1] find, as I believe, their refutation in this doc-trine of germinal selection. The principle extends precisely as far as utility extends, inasmuch as it creates, not only the direction of variation for every increase or diminution demanded by the circumstances, but also every qualitative direction of variation attain-able by changes of quantity, so far as that is at all pos-sible for the organism in question.

Considering also the contrary process, the degenera-tion of useless parts by the cessation of selection in re-gard to the normal size of that part, a clear light is shed on that whole complex system of ascending and descending modifications which makes up most of the transformations of a living form, and we are led to understand how the fore extremity of a mammal can change into a fin at the same time that the *hinder* ex-tremity is growing rudimentary, or how one or two toes of a hoofed animal can continue to develop more and more powerfully, whilst the others in the same de-gree grow weaker and weaker until finally they have disappeared entirely from the germ of most of the individuals of the species.

Possibly some of that large body of inquirers, most-ly paleontologists, who till now have considered the Lamarckian principle indispensable for the explanation of these phenomena—perhaps some, I say, will not utterly close their eyes to the insight that germinal selection performs the same services for the under-standing of observed transformations, particularly of

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[1] "Beiträge zur Kritik der Darwin'schen Lehre," *Bio-logisches Centralblatt,* Vol. X., p. 449. 1890.

the degeneration of superfluous parts, that a heredity of acquired characters would perform, without rendering necessary so violent an assumption. I have always conceded that many transformations actually do run parallel to the use and disuse of the parts,[1] that therefore it does really look as if functional acquisitions of the individual life were hereditary. But if it be found that *passively functioning parts,* that is, parts which are not alterable during the individual life by function, obey the same laws and also degenerate when they become useless, then we shall scarcely be able to refuse our assent to a view which explains both cases. It certainly cannot be the physiological function which provokes modifications in the individual, which are then subsequently transmitted to the germ and in this way made hereditary, if *functionless parts also change* when they become useless. It is precisely this *uselessness,* then, from which the initial impulse emanates, and the primary modification is not in the soma but in the germ.

The Lamarckians were right when they maintained that the factor for which hitherto the name of natural selection had been exclusively reserved, viz., *personal* selection, was insufficient for the explanation of the phenomena. They were also right when they declared that panmixia in the form in which until recently I held the theory was also insufficient to explain the degeneration of parts that had grown useless, but they

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[1] Poulton has adverted to the fact that this is nevertheless not always the case; for example, it is not so with the teeth, whose shape it had also been sought to reduce to the mechanical effects of pressure and friction. See "The Theory of Selection" in *The Proceedings of the Boston Society of Natural History,* Vol. XX., page 389. 1894.

erred when they ascribed hereditary effects to the se-
lection-processes which are enacted among the parts
of the body (Wilhelm Roux) and which are rightly
regarded as the results of functioning. And they did
this, moreover, as they themselves admit, not because
the facts of heredity directly and unmistakably re-
quired it, but because they saw no other possibility of
explaining many phenomena of transformation. I am
fain to relinquish myself to the hope that now after
another explanation has been found, a reconciliation
and unification of the hostile views is not so very
distant, and that then, we can continue our work
together on the newly laid foundations.

That the application of the Malthusian principle was
thoroughly justified is now clear. *The entire process
of the development of living forms is guided by this
principle.* The struggle for existence, *videlicet,* for
food and propagation, takes place at all the stages
of life between all orders of living units from the
biophores recently disclosed upwards to the elements
that are accessible to direct observation, to the cells,
and still higher up, to individuals and colonies. Con-
sequently, in all the divers orders of biological units
lying between the two extremes of biophores and
colonies, the modifications must be controlled by se-
lective processes; therefore, these govern every change
of living forms no matter what its significance, and
bring it about that the latter fit their conditions of
life as wax does the mould; and the various stages of
these processes, as enacted between the divers orders
of biological units, in all organisms not absolutely
simple, are involved in incessant and mutual inter-
action. The three principal stages of selection, that of

personal selection[1] as it was enunciated by Darwin and
Wallace, that of *histonal* selection as it was estab-
lished by Wilhelm Roux in the form of a "struggle
of the parts," and finally that of *germinal selection*
whose existence and efficacy I have endeavored to sub-
stantiate in this article—these are the factors that have
co-operated to maintain the forms of life in a constant
state of viability and to adapt them to their conditions
of life, now modifying them *pari passu* with their en-
vironment, and now maintaining them on the stage
attained, when that environment is not altered.

Everything is adapted in animate nature[2] and has
been from the first beginnings of life; for adaptiveness
of organisation is here equivalent to the power to exist,
and they alone have had the power to exist who have
permanently existed. *We know of only one natural
principle of explanation for this fact—that of selection*

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[1] As the highest stage of selective processes must be re-
garded that between the highest biological units, the colonies
or cormi—a stage, however, which is not essentially different
from personal selection. In this stage the persons enact the
part that the organs play in personal selection. Like their
prototypes they also battle with one another for food and in
this way maintain harmony in the colony. But the result of
the struggle endures only during the life of the individual
colony and can be transmitted through the germ-cells to the
following generation as little as can histological changes
provoked by use in the individual person. Only that which
issues from the germ has duration.

[2] This statement has often been declared extravagant, and
it is so if it is taken in its strict literalness. On the other
hand, it would also seem, by a more liberal interpretation, as
if there existed non-adaptive characters, for example, rudi-
mentary organs. Adaptiveness, however, is never absolute
but always conditioned, that is, is never greater than outward
and inward circumstances permit. Moreover, an organ can

of the picking out of those having the power to exist from those having the power to originate. If there is any solution possible to the riddle of adaptiveness to ends,—a riddle held by former generations to be insoluble,—it can be obtained only through the assistance of this principle of the self-regulation of the originating organisms, and we should not turn our faces and flee at the sight of the first difficulties that meet its application, but should look to it whether the apparent effects of this single principle of explanation are not founded in the imperfect application that is made of it.

If I am not mistaken the situation is as follows : We had remained standing half way. We had applied the principle, but only to a portion of the natural units engaged in struggle. If we apply the principle throughout we reach a satisfactory explanation. Selection of *persons* alone is *not sufficient* to explain the phenomena ; *germinal* selection must be added. Germinal selection is the last consequence of the application of the principle of Malthus to living nature. It is true it leads us into a terrain which cannot be submitted directly to observation by means of our organs of touch and by our eyes, but it shares this disadvantage in common with all other ultimate inferences in natural science, even in the domain of inorganic na-

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only disappear gradually and slowly when it has become superfluous; yet this does not prevent our recognising every stage of its degeneration as adapted when compared with its precursor. Further, it does not militate against the correctness of the above proposition that there are also characters whose fitness consists in their being the necessary accompaniments of other directly adapted features, as, for instance, the red color of the blood.

ture: in the end all of them lead us into hypothetical regions. If we are not disposed to follow here, nothing remains but to abandon utterly the hope of explaining the adaptive character of life—a renunciation which is not likely to gain our approval when we reflect that by the other method is actually offered at least in principle, not only a broad insight into the adaptation of the single forms of life to their conditions, but also into the mode of formation of the living world as a whole. The variety of the organised world, its transformation by adaptation to new, and by reversed adaptation to old conditions, the inequality of the systematic groups, the attainment of the same ends by different means, that is, by different organisations, and a thousand and one other things assume on this hypothesis in a certain measure an intelligible form, whilst without it they remain lifeless facts.

And so in this case, I may say, that again doubt is the parent of all progress. For the idea of germinal selection has its roots in the necessity of putting something else in the place of the Lamarckian principle, after that had been recognised as inadequate. That principle did, indeed, seem to offer an easy explanation of many phenomena, but others stood in open contradiction to it, and consequently that was the point at which the lever had to be applied if we were to penetrate deeper into the phenomena in question. For it is at the places where previous views are at variance with facts that the divining rod of the well-seekers must thrice nod. There lie the hidden waters of knowledge, and they will leap forth as from an artesian well if he who bores will only drive undaunted his drill into their depths.

APPENDIX.

I. THE REJECTION OF SELECTION.

Many years ago Semper[1] denied the power of selection to create an organ, declaring that the organ must have previously existed before selection could have increased and developed it. More recently Wolff[2] has distinguished himself by the vigor with which he has attacked the "task" of "setting aside the dogma of selection." Henry B. Orr[3] is also of opinion that selection is not the real cause of improved organic states; he regards it as a factor checking growth in certain directions, but not as a cause producing growth. Likewise Yves Delâge,[4] in his recent voluminous but in many respects excellent work, regards natural selection solely as a subordinate principle which is devoid of all power to create species (p. 391), although he grants to it certain functions, and even characterises it

[1] Semper, *Die natürlichen Existenzbedingungen der Thiere,* Leipsic, 1880, pp. 218-219.

[2] Wolff, "Beiträge zur Kritik der Darwin'schen Lehre," *Biolog. Centralblatt,* Vol. X., Sept. 15, 1890, and "Bemerkungen zum Darwinismus mit einem experimentellen Beitrag zur Physiologie der Entwicklung," *Biolog. Centralblatt,* Vol. XIV., Sept. 1, 1894.

[3] Henry B. Orr, *A Theory of Development and Heredity,* New York, 1893.

[4] Yves Delâge, *La structure du protoplasma et les théories sur l'hérédité et les grands problèmes de la biologie générale,* Paris, 1895.

as "an admirable and perfectly legitimate principle" (p. 371). A more pronounced opponent of selection, of any kind, as a principle creating species, is the Rev. Mr. Henslow,[1] whose views we shall discuss later, in Division VII. of this Appendix.

Finally, must be mentioned the name of Th. Eimer, as that of a pronounced and bitter enemy of the theory of selection. I shall leave it to others to decide whether he can properly be called an "opponent" of the principle, in the scientific acceptance of the word. I can see in the blind railings of the Tübingen Professor nothing but a reiteration of the same unproved assertions, mingled with loud praises of his own doughty performances and captious onslaughts on every one who does not value them as highly as their originator.[2]

The lack of confidence latterly placed in the theory of selection even by professed adherents of the doctrine, is well shown by such remarks as the following

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[1] Henslow, *The Origin of Species Without the Aid of Natural Selection, A Reply to Wallace.* 1894.

[2] If any one should deem these words too severe, let him read the sarcastic passages in which Eimer has dispatched the late unfortunate Eric Haase who had been presumptuous enough to oppose the Tübingen Professor's deliverances on certain points. Haase, as we all know, fell a victim to the climate of the tropics, shortly after resigning the post of Director of the natural science collections in Bangkok, in order to return to Germany and to work out the fruits of his tropical sojourn. The unfortunate end of this accomplished man who had rendered important services to science had no effect in mollifying the resentment of Herr Eimer at the opposition which his views had encountered; and in twenty printed pages he takes him to task in the most personal and rancorous manner for this affront, remarking at the close: "In the meantime Herr Haase has died. Nevertheless I owe

from Emery,[1] who says: "Some pupils of Darwin have gone beyond their master and discovered in natural selection the sole and universal factor controlling variations. Thus there has arisen in the natural course of things a reaction, especially on the part of those who, while they accept evolution, will have naught to do with natural selection or Darwinism as they call it." Emery then professes himself a Darwinian, although not in the sense of Wallace and "other co-workers and pupils of Darwin." For him "natural selection is a very important factor in evolution, and in determining the direction of variation plays the highest part; but it is far from being the only factor and is probably also not the most efficient factor." Not the most efficient factor but plays the highest part!

II. CHEMICAL SELECTION.

If we refer adaptation to selection, we have also to trace back to this source the origin of the organic combinations which make up the various tissues of the body and which go by the collective name of muscular, nervous, glandular substance, etc. Lloyd Morgan has prettily likened the vital processes to the periodic formation and discharge of explosive substances.[2] Unstable combinations are upon the application of a

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it to myself, in spite of this occurrence, to make public the foregoing facts, in order," etc. Any one who is interested in knowing the motives of Herr Eimer's excuse may find them in his book *Artbildung und Verwandtschaft bei den Schmetterlingen,* Part II., p. 66.

[1] "Gedanken zur Descendenz- und Vererbungstheorie." *Biolog. Centralblatt,* July 15, 1893.

[2] C. Lloyd Morgan, *Animal Life and Intelligence,* London, 1890-1891, p. 30-33.

stimulus suddenly disintegrated into simpler and more stable compounds; through this disintegration they evoke what is called the function of the disintegrating part—for example, certain changes of form (muscular contractions) or the excretion of the disintegrated products, etc.

Now how is it possible that such unstable chemical combinations, answering exactly to the needs of life, could have arisen in such marvellous perfection if the *useful* variations had not always been presented to the ceaselessly working processes of selection? or, if the constantly increasing adaptation to the constantly augmenting delicacy of operation of physiological substances had depended in its last resort on *accidental* variations? Hence, not only with regard to the "form" of organs, but also with regard to the chemical and physiological composition of their materials, we are referred to the constant presence of appropriate variations.

III. VARIATION AND MUTATION.

I have still to add a few remarks on the subject touched on in the footnote at page 31. The view there referred to was discussed by Professor Scott before in an article published in the *American Journal of Science,* Vol. XLVIII., for November, 1894, entitled "On Variations and Mutations." Following the precedent of Waagen and Neumayr, Scott sharply discriminates between the inconstant vacillating variations which it is supposed [?] produce simultaneously occurring "varieties," and "mutations," or the successively evolved *time*-variations of a phylum, which constitute the stages of phyletic development. The facts on which this view is based are those already

adduced in the text—the *Zielstrebigkeit* (to use K. E. von Bär's phraseology) displayed in the visible paleontological development, the directness of advance of the modifications to a final "goal." "The direct, unswerving way in which development proceeds, however slowly, is not suggestive of many trials and failures in all directions save one." And again, "The march of transformation is the resultant of forces both internal and external which operate in a *definite manner* upon a changeable organism and similarly affect *large numbers of individuals.*"

The two points which I have here italicised are actually the facts which separate phylogenetic from common individual variation: the definite *manner* of the change, repeated again and again without modification, and its occurrence in a *large number of individuals.*

Still the two are not solely a result of observation, deduced from paleontological data; they are also *a consequence of the theory of selection*, as was shown in the text. If the theory in its previous form was unable to fulfil this requirement, it is certainly now able to do so after germinal selection has been added, and it is not in any sense necessary to assume a difference of *character* between phylogenetic and ontogenetic variations. Bateson and Scott are wrong in imagining that I ask them "to abrogate reason" in pronouncing the "omnipotence of natural selection." On the contrary, the theory seems to me to accord so perfectly with the facts that we might, by reversing the process, actually construct the facts from the theory. What other than the actual conditions could be expected, if it is a fact that selection favors only the useful variations and singles them out from the rest by producing them in

increasing distinctness and volume with every genera-
tion, and also in an increasing number of individuals?
The mere displacement of the zero-point of useful
variations alone must produce this effect, especially
when it is supported by germinal selection. It is im-
possible, indeed, to see how considerable, that is per-
ceptible, deviations could arise at all on the path of
phyletic development if in each generation a large
number of individuals always possessed the useful,
that is, the phyletic variations?   In fact, by the as-
sumption itself, the difference between useful and
less useful variations is merely one of degree, and
that a slight one.

Hence, as I before remarked at page 31, I see no
reason for assuming two kinds of hereditary variations,
distinct as to their origin, such as Scott and the other
palæontologists mentioned have been led to adopt, al-
though with the utmost caution.   I believe there is
only one kind of variation proceeding from the germ,
and that these germinal variations play quite different
rôles according as they lie or do not lie on the path
of adaptive transformation of the species, and conse-
quently are or are not favored by germinal selection.
To repeat what I have said in the footnote to page 31
only a relatively small portion of the numberless in-
dividual variations lie on the path of phyletic ad-
vancement and so mark out under the *guidance* of
germinal selection the way of further development;
and hence it would be quite possible to distinguish
continuous, *definitely directed* variations from such
as fluctuate hither and thither with no uniformity in
the course of generations.   The origin of the two is
the same ; they bear in them nothing that distinguishes
the one from the other, and their success alone, that

is, the actual resultant phyletic modification, permits their being known as phyletic or as vacillating variations. Uncertain fluctuations along the path of evolution are what the geologists would be naturally led to expect from the theory of selection, but which they were unable to discover in the facts; it is evident, however, that these fluctuations are not a logical consequence of the theory of selection as that is perfected by germinal selection, and there seems to me to be no reason now for attributing "variations" to the union of changing hereditary tendencies, while "mutations" are ascribed to the effect "of dynamical agencies acting long in a uniform way, and the results controlled by natural selection."

The idea which the Grecian philosophers evolved of the thousands of non-adaptive formations that nature brings forth by the side of adaptive ones, and which must subsequently all perish as being unfit to live, is certainly correct in its ultimate foundations. But it is in need of far more radical refinement than it underwent in the hands of Empedocles, or than it seems likely to undergo at the hands of many contemporary inquirers. We know now that nature did not produce isolated eyes, ears, arms, legs, and trunks, and afterwards permit them to be joined together just as the play of the fundamental forces of love and hatred directed, leaving the monsters to perish and granting permanent existence only to harmonious products. Yet there is a weak echo of this conception, although infinitely far removed from its prototype, in the question as to where all the non-adaptive individuals are preserved that have perished in the struggle for existence and been eliminated from development by selection? Where, for example, are the fossil remains

of the rejected individuals in the line of the Horses? Certainly they should be forthcoming in far larger numbers than the individuals lying directly in the path of development, for by our very assumption the latter were greatly in the minority in every generation. Doubtless the question would be a proper one if our eyes were sufficiently keen-sighted to assign the life-value of the various minute differences that distinguish the "better" from the "worse" individuals of every generation. But this is a task which we can accomplish at best only with selective processes which are artificially directed by ourselves, as in the case of doves and chickens, and even there only with the utmost difficulty and only with reference to a single characteristic and not with any species which to-day exists in the state of nature. Picture, then, the difficulties attending such a task as applied to the meagre fossilic bones of prehistoric species, touching which the richest discoveries never so much as remotely approach to the actual number of individuals that have lived together for a *single* generation in the same habitat. If the differences between good and bad in a single generation were striking enough to be immediately remarked *as such* in fossil bones, the development of species would take place so rapidly that we could directly witness it in living species.

IV. REMARKS ON THE HISTORY OF DEFINITELY DIRECTED VARIATIONS.

As to the attempt here made to apply the selective process to the elements of the germinal substance (the idioplasm) and thus to acquire a foothold for definitely directed variation not blind in its tendency but pro-

ceeding in the direction of adaptive growth, it is re-markable that the same was not made long ago by some one or other of the many who have thought and written on selection and evolution.

Allusions to a connexion between the direction of variation and the selective processes are to be found, but they remained unnoticed or undeveloped. I have been able to find at least two such observations, but would not wish to assert that there are not more of them hidden somewhere in the literature of the subject. One of them is old and comes from Fritz Müller. It was appended by his brother Hermann as a "Supple-mentary Remark" to his book *Die Befruchtung der Blumen durch Insecten* (1873) and is dated Novem-ber 24, 1872. We read there: "My brother Fritz Müller communicates to me in a letter which reached my hands only after the bulk of the present work had passed through the press, the following law discovered by him, which materially facilitates the explanation by natural selection of the pronounced characters of sharply distinguished species: 'The moment a choice in a definite direction is made in a variable species, progressive modification from generation to genera-tion in the same direction will set in as the result of this choice, wholly apart from the influence of ex-ternal conditions. Transformation into new forms is thus greatly facilitated and accelerated.'"

The facts on which F. Müller based the enunciation of his law, are the results of several experiments with plants, the numbers of whose grains (maize), or styles, or flowering leaves, were, by the exercise of choice in the cultivation, made to change in definite directions. Accurately viewed their significance is the same as that of numerous other cases of artificial selection, for

example, that of the long-tailed Japanese cock which was laid at the foundation of the theory in the text, although the numerical form of the observation gives more precision and distinctness to the reasoning based on them, than is to be observed in cases where we speak of characters as being simply "longer" or "shorter."

F. Müller's opinion regarding the increase of characters by selection is expressed as follows: "The simplest explanation of these facts appears to be that every species possesses the faculty of varying within certain limits; the crossing of different individuals, so long as no choice is effected in a definite direction, maintains the mean round which the oscillations take place at the same points, and consequently the extremes also remain unaltered. If, however, one side is preferred by natural or artificial selection, the mean is shifted in the direction of this side and accordingly the extreme forms are also displaced towards that side, going now beyond the original limit. However, this explanation does not satisfy me in all cases."

It is not known to me that F. Müller ever returned to this conception subsequently to the year 1872 or gave further developments of the same, nor have I been able to discover that it has been mentioned by other writers or incorporated in previous notions regarding selection.

The second naturalist who has approached the fundamental idea of my doctrine of germinal selection, is a more recent writer. I refer to the English botanist Thiselton-Dyer, a scientist whose occasional utterances on the general questions of biology have more than once evoked my sympathetic approval. In an article, "Variation and Specific Stability," which appeared in

Nature for March 14, 1895, this author enunciates twenty theses touching this subject, many of which appear to me apposite and correct, particularly the following: In every species there is a mean specific form round which the variations are symmetrically grouped like shots around the bull's eye of a target. As soon as natural selection comes into play and favors one of these variations it must shift the centre of density. Variations arise by a change in the outward conditions of life and can be useful or indifferent; only in the first case will natural selection obtain control of them and "the new variation will get the upper hand and the centre of density will be shifted."

This is not germinal selection, but it is the same as what I have referred to in this and in the preceding essay as displacement of the zero-point of variation. Thiselton-Dyer did not draw the conclusion that a definitely directed variation answering to utility resulted from this process, which variation alone must cause the disappearance of useless parts, for the reason that he never attempted to penetrate to the causes of the shifting of the zero-point of variation. Neither Fritz Müller, whose utterances Thiselton-Dyer was obviously ignorant of, nor Thiselton-Dyer himself pushed his inquiries beyond the thought that the shifting in question resulted entirely in consequence of personal selection. There is no gainsaying that the degeneration of useless organs cannot be explained by personal selection alone, seeing that though the minus variations may possibly have a selective value at the beginning of a degenerative process, they certainly cannot have such in the subsequent course of the same, when the organ has dwindled down to a really minimal mass of substance as compared with the whole

body. Of what advantage would it be to the whale if his hinder leg, now concealed in a mass of flesh and no longer protruding beyond the skin, should still be reduced one or several centimetres in size? (Spencer.) If the minus variations have no selective value, how can the upper limit of the variational field be constantly displaced downwards, as actually happens? It is unquestionable but something different from personal selection must come here co-determinatively into play.

V. HISTORICAL REMARKS CONCERNING THE ULTIMATE VITAL UNITS.

(For this Appendix which is marked "Appendix V." in the German edition of *Germinal Selection* see the footnote at page 40.)

VI. THE INITIAL STAGES OF USEFUL MODIFICATIONS.

In characterising as "least" weighty the old objection that the variations are too small at the start to be useful and to be selected, I find myself diametrically opposed to many writers of the present day, who have taken up with renewed vigor this old stumbling block to the principle of selection. Bateson[1] regards the deficient proof of the utility of initial stages as the most serious objection that can be made to natural selection. New organs must in the necessity of the case have first been imperfect; how, then, could they have been selected since imperfect organs cannot be useful? Answers from various quarters have already been

[1] *Materials for the Study of Variation with Especial Regard to Discontinuity in the Origin of Species,* London, 1895, p. 16.

made to this and to similar objections, and Darwin
himself has referred to the fact that even the smallest
variations may have selective value; Dohrn, too, has
urged his principle of change of functions, which with
regard to this question of the utility of initial stages
has certainly a wide significance. Still, every trans-
formation and new structure in the narrow sense of
the word does not rest on change of function, and
neither Darwin nor Wallace, nor any other more re-
cent champion of the principle of selection, can ever
succeed in demonstrating in *every* case the selective
value of an initial stage. One reason why this cannot
be done is because *in no case of morphological varia-
tion do we really know what these initial stages are.*
To say that "new organs were at first necessarily im-
perfect" appears obvious enough, but it is at bottom a
meaningless assertion, for it is not only possible but
certain, that "imperfect" organs may still have selec-
tive value, and in by far the most cases have had se-
lective value. The fact that we see to-day a long grad-
uated line of forest-butterflies which possess resem-
blance to leaves and by this means are able in a meas-
ure to conceal themselves from prying eyes, yet that
this resemblance in many species is very imperfect, in
others more perfect, and in a very small number very
perfect, simply proves that even "imperfect" forma-
tions may be of utility. The word "imperfect" in this
connexion is itself very imperfect, for it is utterly an-
thropomorphic and estimates the biological value of a
structure by our own peculiar artistic notions of its
faithfulness to a leaf-copy, whilst we are really con-
cerned here only with its protective value for the
species in question, which is by no means dependent
merely on the faithfulness of the copying, on the faith-

fulness of the imitation, but on numerous other factors, such as the frequency and sharp-sightedness of the enemies of the species, the fertility of the species, their frequency and persecution in earlier developmental stages, and so forth, in brief, on their need of protection on the one hand and on their other means of protection on the other.

Now all this cannot be exactly calculated in any given case, and it will be better, instead of haggling about individual cases concerning which we can never judge with certainty, to take the position adopted in the text and say: Since the utility of the initial stages *must* be assumed unless we are to renounce forever the explanation of adaptation, let us then take it for granted. No contradiction of facts is involved in this assumption; in fact, even individual variations exist whose eventual utility can be demonstrated, for example, the invisible differences enabling Europeans of certain constitutions to resist the attacks of tropical malarial fevers,—or the differences of structure, likewise not directly visible, which enable palms from the summits of the Cordilleras to withstand our winter climate better than palms of the same species from along the base-line of the mountains; and so on.

VII. THE ASSUMPTION OF INTERNAL EVOLUTIONARY FORCES

Definite variation was not only postulated in the last decade by Nägeli and Askenasy, but has also been repeatedly set up in recent years by various other authors. The Rev. George Henslow, in his book *The Origin of Species Without the Aid of Natural Selection,* 1894, regards the variations occurring in the state

of nature as always definite and not with Darwin as indefinite, and meets the objection that modification but not adaptation to outward conditions of life can be inferred from this fact, by the bold assumption that it is precisely the outward conditions of life or the environment which "induces the best fitted to arise." He further concludes that natural selection has nothing to do with the origin of species. At the basis of his conviction lies the naturally correct view that the summation of *accidental* variations is insufficient for transforming the species, but that definitely directed variation is necessary to this end. But concerning the way in which external conditions are always able to produce the fit variations, he can give us no information—if I am not mistaken, for the simple reason that such is not the fact, that the outward conditions only apparently determine the direction of variations whilst in truth it is the adaptive requirement itself that produces the useful direction of variation by means of selectional processes within the germ.

C. Lloyd Morgan also has recently expressed himself in favor of the necessity of definite variation, though likewise without assigning a basis for its action, and without being able to show how its efficacy is compatible with the plain fact of adaptation to the conditions of life. He seeks to find the origin of variation in "mechanical stresses and chemical or physical influences," but this conception is too general to be of much help. He has, in fact, not been able to abandon completely the heredity of acquired characters.

Emery[1] likewise sees only the alternative of a "de-

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[1] "Gedanken zur Descendenz- und Vererbungstheorie," *Biolog. Centralblatt,* 1893, Vol. XIII., p. 397.

finitely directed variation" from internal causes and of
a summation of "accidental" variations.   He says:
"A summation of entirely accidental variations in a
given direction is extremely difficult," because "natural
selection thus always awaits its fortune at the hands
of accident whereby it is possible that the little good
thereby produced will be swept away by other accidents
(disadvantages of position) or obliterated in the fol-
lowing generations by unfortunate crossings."   We
can, therefore, continues Emery, well conceive "how
many scientists look upon the whole theory of selection
as a fable, or else throw themselves into the arms of
Lamarckism."   Unquestionably Emery has   here
singled out the insufficient points in the assumption of
a selection of "accidental" variations ; he has recog-
nised the necessity of operating, not with single varia-
tions, but with "directions of variation."   He has not,
however, attempted the derivation of directed ten-
dencies of variation from known factors ; he apparently
thinks of them as of something which has sprung from
unknown   constitutional   factors   and   consequently
ascribes to them the capacity of shooting beyond their
mark, so to speak, that is, of acting beyond and ahead
of utility, and so of producing modifications which may
lead to the destruction of the species.

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