# WEISMANN AUGUST

# ON GERMINAL SELECTION AS A SOURCE OF DEFINITE VARIATION

August Weismann

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# Содержание

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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 variation exists*, but not predestined variation, running on independently of the life-conditions of the organism, as Naegeli, to mention the most extreme advocate of this doctrine, has assumed; on the contrary, the variation is such as is elicited and controlled by those conditions themselves, though indirectly.

In basing my proof of the doctrine of Germinal Selection 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 emergence 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 prominent 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 mechanism, which served as a mechanical model for electromagnetism"?[2] He hoped "that further research in the domain of theoretical electricity would be promoted rather than hindered by such mechanical fictions." 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

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

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

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."[3] And yet theory originally fashions science out of facts and is the indispensable precondition of every important scientific advance.

Heinrich Hertz,[4] 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.

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?

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[3] 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 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.

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

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 elaborate 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,"[5] 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 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

[5] 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."

*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 processes 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.[6] 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, 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 today 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[7] 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 advantageous, 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.

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

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

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[8]—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

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

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 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 corresponding 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 surface 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*, seeing that we are dealing with a formation which is only passive in its effects; the leaf-markings are effectual simply by their existence and not by any function 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.

# Конец ознакомительного фрагмента.