XV.

ON THE INHERITANCE OF ACQUIRED CHARACTERS IN ANIMALS WITH A COMPLETE METAMORPHOSIS.

By Alpheus S. Packard, M.D

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I. The Physical Basis of Heredity.

Before discussing our subject it may be well to give a brief historical sketch of the present views as to the physical basis of heredity.

As early as 1849, Owen, in his "Comparative Anatomy," suggested that there was a physical basis for heredity. Herbert Spencer, in his "Principles of Biology" (1866), based the phenomena of heredity on the supposed presence of "physiological units," which he conceived to be immensely more complex than chemical units or molecules. (Vol. I. p. 183.) But Darwin in 1868 brought the question to the front in his "Hypothesis of Pangenesis," which was disproved by experiments on the effects of transfusion of blood by Francis Galton,* who in 1875 published a theory of heredity which in some ways approached that of Jaeger.

Galton also claimed that acquired characters are only "faintly heritable," and he endeavors to explain the almost complete non-transmission of acquired modifications. †

The first, however, to suggest an objective and scientific basis appears to have been Dr. G. Jaeger, of Germany, who in 1876

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* Galton in 1875 suggested that each individual may properly be conceived as consisting of two parts, one of which is latent, and only known to us by its effects on posterity, while the other is patent, and constitutes the person manifest to our sense. "He also claimed that we are made up bit by bit of inherited structures, like a new building composed of the fragments of an old one, — one element from this progenitor, another from that, although such elements are usually transmitted in groups." — A Theory of Heredity, Journal of the Anthropological Institute, 1875. See also Contemporary Review, December, 1875.

† Contemporary Review, 1875, Vol. XXIII. p. 95.

made the following statement, as quoted by J. A. Thompson in his "History and Theory of Heredity." *

"Through a great series of generations the germinal protoplasm retains its specific properties, dividing in every reproduction into an ontogenetic portion, out of which the individual is built up, and a phylogenetic portion, which is reserved to form the reproductive material of the mature offspring. This reservation of the phylogenetic material I described as the continuity of the germ protoplasm. Encapsuled in the ontogenetic material the phylogenetic protoplasm is sheltered from external influence, and retains its specific and embryonic characters." †

In 1880 M. Nussbaum ‡ substituted a new hypothesis for Darwin's pangenesis. According to the view of this observer, the germinal cells from which the sexual products are derived are separated off from the other cells of the embryo very early, and undergo little alteration. Hence he concluded that some of the original germ substance is directly abstracted from the egg, and preserved without essential alteration to become, by giving rise to the sexual elements, the germ substance of another generation. Nussbaum also expressed his disbelief in the transmission of acquired characters. This belief, held by Darwin as well as by Lamarck, and almost universally adopted by medical men, had not before been called in question.

In 1884 Nägeli § took the ground that there are in every living cell two substances; one the nutritive plasm, and the other his hypothetical "idioplasma." This view was indorsed by Kölliker, who claimed that the sharp distinction between body and germ cells does not exist.

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* Proc. Royal Society Edinburgh, 1889, pp. 91–116. See also Brooks, "The Law of Heredity," 1883; Osborn, "The Cartwright Lectures," 1892; "Present Problems in Evolution and Heredity," Medical Record, New York, 1892; "The Present Problem of Heredity," Atlantic Monthly, March, 1891.

† Lehrbuch der algemeinen Zoologie, Leipzig, 1878, II. Abtheilung. In a previous book, published at an earlier date than the one quoted by Thompson, Zoologische Briefe, Wien, 1876, Jaeger writes thus: "Hier muss ich noch einmal den Gegensatz zwischen Darwin's Theory von der Pangenesis und meiner Theorie von der Continuität des Keimprotoplasmas hervorheben" (p. 326).

See also Weismann, "The Germ Plasm," p. 200. The author appears to have overlooked the statement of Jaeger in his Zoologische Briefe, wherein he explicitly, as shown by our quotation, refers to the "continuity of the germ protoplasm."

‡ Die Differenzirung des Geschlechts in Thierreich. Archiv für mikroskop. Anatomie, Bd. XVIII., 1880.

§ Nägeli, Mechanisch-physiologische Theorie der Abstammungslehre. München u. Leipzig, 1884.

In 1887 Minot* in a brief note suggested that Nägeli's hypothetical idioplasm is probably identical with the nuclear chromatin of morphologists; and that heredity is due to the transfer from parent to offspring of the nuclear substance.

Maupas,† in two memoirs published in 1889 and 1890, reaffirmed and extended this view, concluding that the chromatin of all cells is the bearer of heredity.

Meanwhile in 1885 appeared Weismann's epoch-making essays on heredity, his view being somewhat in the line of Jaeger's theory, but greatly expanded, and with many new and original suggestions. He stated that it was impossible to prove the existence of gemmules, and substitutes for pangenesis the now famous doctrine of "the continuity of the germ plasm," as affording a more rational basis than pangenesis or Brooks's modification of it. Weismann says: "The nature of heredity is based upon the transmission of nuclear substance with a specific nucleoplasm of the germ cell, to which I have given the name of germ plasm" (p. 180). As stated by Mr. E. B. Poulton,‡ an able commentator and exponent of Weismann's views, —

"The word 'continuity' expresses the theory that heredity depends on the fact that a minute quantity of this germ plasm is reserved unchanged during the development of the individual, and afterwards grows and gives rise to the germ cells. Hence the germ plasm is continuous from one generation to another in an unending succession, and from it the germ cells of each generation are produced.

"Parent and offspring resemble each other because both arise from the same substance, which develops rather later in the case of the offspring. Hence everything which is predetermined in the germ cell, every blastogenic character, may be transmitted, while somatogenic characters cannot be transmitted."

We will quote Weismann's definition of acquired and blastogenic characters: "We maintain that the '*somatogenic*' characters cannot be transmitted, or, rather, that those who assert that they can be transmitted must furnish the requisite proofs. The *somatogenic* characters not only include the effects of mutilation, but the changes which follow

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* Science, New York, VIII. 125.

† Sur la Multiplication des Infusoires Ciliés. Archiv de Zoologie expérimentale, sér. 2, VI. 165–278; Le Rajeunissement Karyogamique chez les Ciliés, VII. 149–517. See also Hartog, Quart. Journal Microscop. Science, December, 1891, and Osborn, *loc. cit.*, pp. 54–56.

‡ Theories of Heredity. Reprinted from the Midland Naturalist, November, 1889.

from increased or diminished performance of function, and those which are directly due to nutrition and any of the other external influences which act upon the body. Among the *blastogenic* characters, we include not only all the changes produced by natural selection operating upon variations in the germ, but all other characters which result from this latter cause." (p. 413.)

Weismann remarks that Nägeli has shown that even in so minute a space as $\frac{1}{1000}$ of a cubic millimeter such an enormous number (400,000,000) of "micellæ"[*] may be present that the most diverse and complicated arrangements become possible. It therefore follows that the molecular structure of the germ plasm in the germ cells of an individual must be distinguished from that of another individual by certain differences, although these may be but small; and it also follows that the germ plasm of any species must differ from that of all other species. (Weismann, p. 191.) It also follows, the author contends, that the molecular structure of the germ plasm in all higher

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[*] The existence of such primary elements as these, which are supposed to form the basis of organization of the protoplasm of cells, as well as the physical basis of heredity, is insisted on by nearly all of the biologists who have written on this subject. Professor Whitman, in an able article entitled "The Inadequacy of the Cell Theory," states that Ernst Brücke in 1861 first contended for the organization of the cell, and the existence of "smallest parts" as the basis of this organization, quoting him as follows. "We must therefore ascribe to living cells, in addition to the molecular structure of the organic compounds which they contain, still another and otherwise complicated structure; and this it is that we designate by the name organization." (Elementarorganismen, p. 387. Wiener Sitzungsberichte, October 10, 1861, Band XLIV. Heft 2, p. 381.)

Whitman then goes on to say that "we have seen similar ideas reappear in the 'physiological units' of Herbert Spencer, the 'gemmules' of Darwin, the 'micellæ' of Nägeli, the 'plastidules' of Elsberg and Haeckel, the 'inotagmata' [plasomes] of Wiesner, the 'idioblasts' of Oscar Hertwig, and the 'biophores' of Weismann."

Whitman contends that the secret of organization, growth, development, lies not in cell formation, "but in those ultimate elements of living matter for which *idiosomes* seems to me an appropriate name." He adds: "All growth, assimilation, reproduction, and regeneration may be supposed to have their seat in these fundamental elements. They make up all living matter, are the bearers of heredity, and the real builders of the organism." (Journal of Morphology, VIII. 639, 658, Boston, 1893. Compare also Weismann's "The Germ Plasm," Introduction.) Here should be quoted the striking remark of Herbert Spencer, "that sperm cells and germ cells are essentially nothing more than vehicles in which are contained small groups of the physiological units in a fit state for obeying their proclivity towards the structural arrangement of the species they belong to." (Principles of Biology, I. 254.)

animals must be very complex, and at the same time this complexity must gradually diminish during ontogeny.

In his latest work Weismann * thus states his mature and apparently final views: "All the phenomena of heredity depend on minute vital units which we have called *biophors*, and of which living matter is composed; these are capable of assimilation, growth, and multiplication by division." (p. 450.) He further discusses the nature and mode of action of these hypothetical bodies, which are contained in the nucleus, the latter serving as the "bearer of the biophors controlling the character of the cell." How these biophors are grouped into *determinants*, and how the latter form aggregates called *ids*, the nuclear rods (chromosomes) being aggregates of ids, called *idants*, is set forth in a very circumstantial way. He then states in the summary of his work: "The *germ plasm*, or hereditary substance of the Metazoa and Metaphyta, therefore, consists of a larger or smaller number of idants, which in turn are composed of ids; each id has a definite and special architecture, as it is composed of determinants, each of which plays a perfectly definite part in development." (p. 453.)

Weisman's reasons for not accepting the doctrine of transmission of acquired characters would appear to be purely hypothetical and *a priori*, as will be seen by the following extracts: "It is self-evident from the theory of heredity here propounded that only those characters are transmissible which have been controlled — i. e. produced — by determinants of the germ, and that consequently only those variations are hereditary which result from the modification of several or many determinants in the germ plasm, and not those which have arisen subsequently in consequence of some influence exerted upon the cells of the body. In other words, it follows from this theory that *somatogenic or acquired characters cannot be transmitted.* This, however, does not imply that external influences are incapable of producing hereditary variations; on the contrary, they always give rise to such variations when they are capable of modifying the determinants of the germ plasm. Climatic influences, for example, may very well produce permanent variations, by slowly causing gradually increasing alterations to occur in certain determinants in the course of generations. An apparent transmission of somatogenic modifications may even take place under certain circumstances, by the climatic influence affecting certain determinants of the germ plasm at the same time,

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* The Germ Plasm. A Theory of Heredity. Translated by W. N. Parker New York, 1893.

and when they are about to pass to that part of the body which they have to control. This is indicated by the climatic variations of the butterfly *Polyommatus phlæas*."

He then adds: —

"The primary cause of *variation* is always the effect of external influences. Were it possible for growth to take place under absolutely constant external influences, variation would not occur; but as this is impossible, all growth is connected with smaller or greater deviations from the inherited developmental tendency.

"When these deviations only affect the soma, they give rise to temporary non-hereditary variations; but when they occur in the germ plasm, they are transmitted to the next generation, and cause corresponding hereditary variations in the body." (pp. 462, 463.)

That the physical seat of heredity does exist in the nucleus has been wellnigh demonstrated, if not quite, by some remarkable experiments by Boveri at the Naples Zoölogical Station, so that what was a mere hypothesis has apparently become a matter of fact. Boveri's results appeared in 1889,* and a translation of his short paper has been published by Prof. T. H. Morgan in "The American Naturalist" for March, 1893.

Five years ago, by accident, the brothers Hertwig discovered that in consequence of shaking, certain eggs of sea-urchins fell to pieces; some of these pieces contained nuclei and others not. It was found that the non-nucleated pieces could be artificially fertilized as well as those containing nuclei, and that the bits of yolk underwent what is called segmentation.

Boveri, taking the hint suggested by these happy accidents, made the astonishing discovery that the enucleated bits of eggs could be fertilized, and that such bits developed into larvæ or young sea-urchins as completely formed as those growing from ordinary entire fertilized eggs.

The further experiments to prove the seat of heredity were to hybridize the fragments of eggs of one genus of sea-urchins with the sperm cells of another genus, and to rear them far enough along in life to determine whether the young showed the qualities of both species or one only. By cross fertilizing the enucleated egg fragments of Sphærechinus with the male germs of Echinus, Boveri produced an almost exact middle form, standing half-way between the two parents. He found however that a portion of the cross-bred larvæ agreed entirely

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* Ein geschlechtlich erzeugter Organismus ohne mütterliche Eigenschaften. Sitzung der Gesellschaft für Morphologie und Physiologie zur München. Sitzung am 16 Juli, 1889.

with the simple ordinary larva of Echinus, which he thinks must have been produced chiefly from enucleated fragments. This seemed to be proved by the fact that he could distinguish in a preserved and colored larva whether or not it had originated from a nucleated or enucleated egg by the size of its nuclei, which are considerably smaller in the larvæ derived from the enucleated bits of eggs. Hence all doubt seemed removed, and Boveri claims that he has proved that, by cross fertilization of whole eggs or bits of eggs having nuclei, larvæ are formed that are half-way between the larval forms of the parent species. On the other hand, larvæ arising from the *enucleated* bits of eggs have entirely the characteristics of the parent (male) species. Hence, if his experiments are correct, he demonstrates the law that the nucleus alone is the bearer of hereditary qualities. Thus the hypothesis that the substance of the nucleus of reproductive cells is the physical basis of heredity seems provisionally at least placed on a foundation of fact.

On the other hand reference should be made to the recent papers of Driesch and of O. Hertwig,* who from researches on the phenomena of cleavage and the formation of organs in the embryo of the frog regard the egg as isotropic, its first cells as qualitatively alike, the development of the embryo being the result of an epigenetic formation of organs, the process being one of interrelation of the cleavage cells. Hence in place of the mosaic theory of Roux and the germ plasm theory of Weismann, Hertwig substitutes the theory of the controlling inter-adjustments of the embryonic cells and later of the tissues and organs.

II. HEREDITY OF CHARACTERS ACQUIRED DURING THE LIFETIME OF THE INDIVIDUAL.

It would appear that many, if not most, of our leading anatomists and cytologists agree that there may be a physical basis for heredity, and that this basis is afforded by the germ plasm of the nucleus, a portion of which is continuous in succeeding generations. They do however disagree as to whether acquired or "somatogenic" characters can be transmitted by heredity, and whether the contents of the nuclei of germ cells are influenced or not by whatever affects the body in general.

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* O. Hertwig, Archiv für Mikroskop. Anatomie, 22 December, 1893, XLII. 662–794. See Abstract by E. A. Andrews in the American Naturalist, March, 1892, pp. 272–278.

Perhaps the ablest objector to this phase of Weismann's theory of heredity is Kölliker,* who (1) denies that there is any fundamental difference between body and germ plasm; and (2) claims that in the various cellular changes the characters of the original germ plasm may be either wholly retained, or degenerate, or be wholly lost.

Sir William Turner † and other medical men also favor the theory of the transmission of acquired characters. He suggests that the more subtle processes of generation may be transmitted where mutilations may not.

Detmer ‡ likewise opposes Weismann's view on the following grounds: —

1. The intimate histological influences of external conditions on the organism.

2. The importance of correlation in allowing an influence to saturate from one part to another, and thus to the sexual cells.

3. The suggestiveness of the persistence of certain phenomena (in plants) after the inciting conditions have ceased.

The criticisms of Kölliker have been ably discussed by Weismann in his Essays upon Heredity.

The views which have had weight with us, and which seem to oppose Weismann's theory that acquired traits cannot be transmitted, are the following: —

1. The laws of correlation (*a*) of growth, and (*b*) of organs in the mature organism.

If one part or organ of the body is removed, aborted, or changed, the rest may, in certain cases, be either temporarily or permanently affected by the change.

2. Whatever affects the body in general would tend to affect the germ plasm, since the tissues and cells of the ovaries and testes are supplied with blood, and are innervated like other parts and organs of the body; hence the plasm of the nuclei of these cells, though it may exist in a temporarily indifferent state is nourished, or at least preserved from degeneration, and is thus influenced by whatever affects the body.

3. The operation of castration in either sex, as is well known, re-

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* Das Karyoplasma und die Vererbung. Zeitschrift für wissens. Zoologie, XL. iv. 228, 1886, and Anat. Anzeiger, III., 1888.

† Report of the British Association for the Advancement of Science for 1889, pp. 756-771. 1890.

‡ Zum Problem der Vererbung. Archiv für die ges. Physiologie, XL. 1887.

sults in a profound modification of the physical, intellectual, and moral nature of the subject operated upon.

4. It has not yet been satisfactorily disproved that new characters, or the tendency to the heredity of such characters, are not the result of a change of external environment, however slight. This appears to be the primary cause of all changes in organisms.

5. As blastogenic or congenital characters are not invariably transmitted, with much less reason may somatogenic or acquired characters be invariably transmitted, especially at the present day.

6. The transmission of acquired characters may have been more frequent and regular in early geological ages, during the period of the origin of family, ordinal, and class ancestral types, and when such forms were more plastic than now owing to more wide-spread and rapid changes in the physical geography of the earth's surface than occur at present. During palæozoic times somatogenic characters may have greatly preponderated over blastogenic characters; for at certain critical periods in geological history there were wide-spread extinctions of certain species of plants and animals, followed or accompanied by profound modification of others, which led to the origination of new types. Hence a study of the origin and subsequent modification and disappearances of organs in series of extinct animals will afford weighty facts.

7. If congenital characters are the only ones which can be inherited, they must have in the beginning originated from those acquired during the lifetime of the individual, or if not in the first, in the second or third, or a later generation.

8. Can we always draw the line between congenital and acquired characters? It seems to us to be often not only very difficult, but well-nigh impracticable, except in animals with a metamorphosis.

9. The results of the cultivation of fruits and of the domestication of animals, as well as the experiments of Brown-Séquard, Bert, and others, strongly suggest that the characters acquired during the lifetime of such organisms are capable of transmission.

10. If there were no such thing as the transmission of characters, either anatomical, physiological, or mental, originating during the lifetime of an organism, how should we have any evolution resulting in the different groups of organisms? Does not the denial of the fact of transmission of acquired features either in the past or present cut away the support for either phase of evolution, whether Lamarckism or Darwinism?

If the processes of heredity have to be begun over again with the birth of each individual, then we shall have to invent a new term for what is ordinarily understood to be progressive or continuous evolution. The assumed peculiar property of the germ plasm is its continuity from one generation to another, and its capability of receiving with each new generation the impress resulting from a change in the environment, or tendency to such change. Were this not so, then the offspring would be simply a repetition of the parents, instead of being like them with a difference, and there would be neither any fixed variation nor any individuality in organisms. Take the subject of human education. Does it wholly depend on the permanence of the intellectual enviroment, or is there an inherited capacity or aptitude for learning which runs in families or strains, and which is the result of the education of one or several generations, whether the training be for business, for the learned professions, or even for criminal pursuits? Unless we are much mistaken, all human progress in learning, or in the arts and sciences, is based on the conception that in the long run mankind will increase in mental intelligence and capacity for learning. The history of science shows that a new department of learning may arise and each succeeding generation work more easily on the foundation laid by the previous generation. The work does not have to be begun *de novo*, but some degree of capacity for the new cult is inherited by successive generations; certainly the intellectual environment may be said to change with each generation.

All progress in humanity appears to be due, not only, in the first place, to our maintaining the present intellectual environment, with the manifold and many-sided stimuli of our present social structure, but also to the unceasing efforts of the leaders in advanced thought in many different departments of mental training and effort to open up new fields of research in natural, physical, and mental science, and their applications, to gain new and higher points of view in sociology and morals as well as in statecraft, and in short to perfect and hasten the development of the ideal man. Unless this progress, which is an historic fact, has been due not only at the outset, but all through human history thus far, to this principle of the inheritance of mental traits, causing the intellectual efforts of one generation to pass down and thus to have finally a cumulative effect, how could there be any progress in human society? *

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* Herbert Spencer states in his Principles of Biology: "Certain powers which mankind have gained in the course of civilization cannot, I think, be accounted for, without admitting the inheritance of acquired modifications." Vol. I. p. 249.

On the one hand, let us imagine a cessation of the operation of this principle. Suppose all the forces and stimuli of modern society to be removed, and the human organism to live like blind beetles in a cave, or a savage tribe isolated in the midst of an otherwise uninhabited continent, with a total uniformity of conditions, physical, social, and moral, the effects of disuse would at once set in. Heredity without this vivifying principle of cumulative transmission, as it might be called, would be retrogressive in its action, and the race would by reversion return to the status of prehistoric times. Or, on the other hand, if the present intellectual environment were maintained without the cumulative action of the principle of inheritance of acquired characters, the social organism would become stagnant, and the race would be semi-fossilized, or in a state of arrested development, like the Chinese.

As we have already suggested in the beginning, blastogenic or acquired characters may have greatly preponderated over the somatogenic, and in fact the former or acquired characters may have constituted the fundamental elements of heredity in general when life forms had only got as far as the Monera and lowest Protophytes. Then as the life forms became more differentiated there may have ensued a corresponding specialization into both blastogenic and somatogenic characters. It seems most probable, as Kölliker suggested, that there is no fundamental difference between the body and germ plasm, and such a difference if it exists may be incapable of physical demonstration.

Apropos of the view that whatever affects the body in general must have some effect, however slight, on the germ plasm in it, we would cite the following facts and considerations.

Mr. Herbert Spencer in a powerful article in the Contemporary Review for March, 1893, entitled "The Inadequacy of 'Natural Selection,'" after quoting the facts regarding Lord Morton's hybrid between a male quagga and a chestnut mare seven eighths Arabian, and the results of crossing English and French breeds of sheep, and Giles's "sow and her produce," as fatal to Weismann's theory of the non-transmission of acquired characters, contends that these facts demonstrate "that the somewhat different units of a foreign germ plasm permeating the organism permeate also the subsequently formed reproductive cells, and affect the structures of the individuals arising from them."

He then quotes Professor Sedgwick's letter to himself, dated December 27, 1892, referring to the continuity of the cells composing the tissues of animals, so that the protoplasm of the whole body is continuous, in which he states "that the connections between the cells of adults are not secondary connections, but primary, dating from the time when the embryo was a unicellular structure." Hence Spencer maintains that "the alleged independence of the reproductive cells does not exist." Thus the *soma* is a "continuous mass of vacuolated protoplasm, and the reproductive cells are nothing more than portions of it separated some little time before they are required to perform their functions."

In his "Monograph of the Development of Peripatus Capensis," Mr. Adam Sedgwick, F. R. S., Reader in Animal Morphology at Cambridge, writes as follows: —

"All the cells of the ovum, ectodermal as well as endodermal, are connected together by a fine protoplasmic reticulum." (p. 41.)

"The continuity of the various cells of the segmenting ovum is primary, and not secondary; i. e. in the cleavage the segments do not completely separate from one another. But are we justified in speaking of cells at all in this case? *The fully segmented ovum is a syncytium, and there are not and have not been at any stage cell limits.*" (p. 41.)

He then states in his letter to Mr. Spencer: —

"It is becoming more and more clear every day that the cells composing the tissues of animals are not isolated units, but that they are connected with one another. I need only refer to the connection known to exist between connective tissue cells, cartilage cells, epithelial cells, etc. And not only may the cells of one tissue be continuous with each other, but they may also be continuous with the cells of other tissues." (pp. 47, 48).

"Finally, if the protoplasm of the body is primitively a syncytium, and the ovum until maturity a part of that syncytium, the separation of the generative products does not differ essentially from the internal gemmation of a Protozoön, and the inheritance by the offspring of peculiarities first appearing in the parent, though not explained, is rendered less mysterious; for the protoplasm of the whole body being continuous, change in the molecular constitution of any part of it would naturally be expected to spread, in time, through the whole mass." (p. 49.)

"Mr. Sedgwick's subsequent investigations confirm these conclusions. In a letter of December 27, 1892, passages which he allows me to publish run as follows: —

"'All the embryological studies that I have made since that to which you refer confirm me more and more in the view that the connections between the cells of adults are not secondary connections, but primary, dating from the time when the embryo was a unicellular structure. . . . My own investigations on this subject have been confined to the Arthropoda, Elasmobranchii, and Aves. I have thoroughly examined the development of at least one kind of each of these groups, and I have never been able to detect a stage in which the cells were not continuous with each other; and I have studied innumerable stages from the beginning of cleavage onwards.'"

As regards plants, De Vries [*] and other botanists believe that all or the greater number of cells in the plant body contain the total heredity characters of the species in a latent condition.[†]

In this connection should be noted an observation of Maupas, who saw the cytoplasm of an infusorian pouring into the nucleus until its bulk was increased eight times.

Hoffman observed the transmission of acquired characters in the poppy, etc., as the result of deficient nutrition.[‡]

In 1890 Van Bemmelin [§] gave a useful and very exhaustive account of the doctrine of heredity, with especial reference to the question of heredity of acquired characters, stating the views of various pathologists, anthropologists, and physiologists. In conclusion he makes some objections to the view that the germ plasm is independent of external influences.

I am indebted to Prof. G. W. Field for the statement that MM. Charrin and Phisalix [‖] cultivated *Bacillus pyrocyaneus* for several successive generations at 42.5° C. with the result that it lost its chromogenic property. This non-chromogenic character apparently thus acquired was retained upon cultivation under most favorable circumstances, and it seemed to show no tendency to recover the chromogenic property.

"Laurent modified the chromogenic function of the Kiel water bacillus by exposing it to direct sunlight for a limited time. The suppression of this peculiarity was transmitted from generation to generation, so that a perfect albinotic variety was formed. The color property was also lost when cultivated at blood heat, and was not

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[*] Intracellülare Pangenesis, Jena, 1889.

[†] Osborn, *loc. cit.*, p. 62.

[‡] Biol. Centralblatt, 1887, p. 667; Botan. Zeitung, 1887, pp. 260, 772, 773.

[§] De Erfelijkheid van verworven Eigenschappen. 's Gravenhage, p. 279. (See abstract by V. Haecker in Biolog. Centralblatt, Bd. X. pp. 641–652, 686–694. Also a brief abstract in Zoologischer Jahresbericht für 1890, Alg. Biologie u. Entwick., p. 23.)

[‖] See Comptes Rendus, 1892, CXIV. 1565–1568.

regained when continued cultivation was carried on at lower temperatures." *

In still more recent experiments Gley and Charrin † have vaccinated a certain number of male rabbits against the effects of the bacillus of blue pus (*Bacillus pyocyaneus*) by injecting into them attenuated cultures. These males then mated with females while in heat. The greater number of the offspring died before birth or soon after; those which lived were atrophied, more or less deformed, but in some cases endowed with an immunity from the effects of the bacillus of blue pus.

"It is evident," says Cuénot, in commenting on this experiment, "that the attenuated infection communicated to the fathers by vaccination had profoundly deranged the structure of the male germ plasm; hence the numerous abortions and malformations of their descendants. It is exactly the same as in the case of females alone which have before fecundation received injections of poisons; they either abort, or the young do not grow and die at an early age."

That the effects of alcoholism and other forms of intoxication with poisons, etc., produced on individuals are inherited by the next generation is allowed by M. Cuénot. Whether the effect upon the system saturates through and affects the germ plasm or not does not affect the fact that such lesions are acquired during the lifetime of the individual. As he says: —

"Intoxication of the organism which is not fatal likewise reacts on the germ plasm, which may undergo profound modifications. Alcoholism, for example, which exaggerates in a way so characteristic the diatheses of parents (insanity, cirrhosis, etc.) also alters the sexual cells. The children of parents both affected with alcoholism, when born, are sickly, unhealthy, presenting a special predisposition to consumption and to nervous troubles."

It is possible, adds Cuénot, that the celebrated observations of Brown-Séquard, confirmed by Dupuy and Obersteiner, on the heredity of epilepsy produced in guinea-pigs, is also explained by a partial in-

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* Bacteriology in its General Relations. By H. L. Russell. Amer. Naturalist, December, 1893, p. 1060.

† Gley et Charrin, Influences héréditaires expérimentales. Comptes Rendus de l'Académie des Sciences, Paris, CXVII., 1893. Quoted from L. Cuénot in "Revue gen. des Sciences, pures et appliquées," 15 Fév., 1894. This and other cases are cited by M. Cuénot in favor of Weismannism, but we think they directly prove the contrary; they illustrate the direct action of a change of environment during the lifetime of the individual, the changes being inherited by the succeeding generation.

toxication of the germ plasm. The guinea-pigs are rendered epileptic by different procedures, i. e. section of the spinal cord, of the sciatic nerve, of the great sympathetic, etc. The young to which they give birth after these operations often present (17 times in 30) a general feebleness, and various nervous affections; motor paralysis of the fore or hind legs, or trophic paralyses, which result in the loss of toes, of the cornea, etc.;* in 32 young born of epileptic parents two have shown symptoms of epilepsy. "The transmission of nervous troubles cannot then leave the shadow of a doubt, although in no case has *the mutilation which has been the cause of it in the parents been reproduced in the descendants.*" Cuénot then adds, "We are still in the presence of an infection of the germ plasm, due perhaps to bacteria as in the case of syphilis (an opinion sustained with much force by Weismann), perhaps also to poisons secreted by epileptic parents, which carries us back to the case of alcoholism."

Another case is the result of experiments by Paul Bert,† who attempted to acclimatize some Daphniæ in salinated water by adding from day to day a little salt in the water of an aquarium. At the end of 45 days, when it contained 1.5% of salt, all the Daphniæ had died, but the *eggs contained in their brood-sac survived,* and the new generation of Daphniæ to which they had given birth flourished perfectly well in the same medium. "This experiment," adds Cuénot, "shows with admirable clearness that the germ plasm has, owing to the modification, become accustomed to the salt, causing it to produce a generation so different from the preceding." We should interpret these facts as showing that the Crustacean had been so profoundly affected in the lifetime of the individual as to produce young perfectly adapted to a changed environment; the germ plasm may have been the vehicle, all the same, but the experiment is a case in favor of the Neo-Lamarckian principle.

Other authors who have advocated the views that acquired characters may be transmitted are Cope,‡ Ryder,§ Osborn, Vines,‖

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* It appears that, if the young are born with tails, an even more important lesion, the loss of toes and of the cornea, etc., results. Why should not these cases strongly confirm the Lamarckian principle of the inheritance of characters acquired during the lifetime of the individual?

† P. Bert, Sur la Cause de la Mort des Animaux d'Eau douce qu'on plonge dans l'Eau de Mer. Comptes Rendus de l'Académie des Sciences, XCVII., Paris, 1883.

‡ Origin of the Fittest, 1887, and minor papers.

§ A Physiological Hypothesis of Heredity and Variation. Amer. Naturalist. January, 1890, pp. 85–92.

‖ Lectures on the Physiology of Plants. Cambridge, 1886.

Eimer,[*] Geddes and Thompson,[†] Brown-Séquard,[‡] and Giard,[§] as well as Henslow, Lloyd Morgan, and others.

Eimer's work is entirely based on the view that the inheritance of acquired characters is a fundamental law of organic growth, though he allows "that the permanent action of external conditions on the body of the organism in most cases is not immediately perceptible. From physiological principles this is not in general possible." He thinks that more time than even Darwin supposed to be necessary must be invoked. He adds: "Every character which must have been formed through the activity of the organism is an acquired character. All characters, therefore, which have been developed by exertion, are acquired, and these characters are inherited from generation to generation. The same holds for all organs atrophied through disuse; the degree of atrophy is acquired and inherited. In the first class we see especially the action of direct adaptation, in the second the results of the cessation of this action. A third class of acquired characters are to be traced simply to the immediate action of the environment on the organism, and originally, at the commencement of their appearance, all characters must have belonged to this class." (p. 87.)

At present it seems the better course, now that the hypothesis has been so fully discussed, to wait for more facts, and to very thoroughly test the cases which seem to favor or to oppose the doctrine.

Some of the discussions held on this subject have savored of the metaphysics of the Middle Ages, and quite artificial distinctions, with the invoking of "natural selection" by authors whose natural selection is quite a different doctrine from the natural selection of Darwin; and other occult causes have been given undue prominence.

Meanwhile we feel justified from the facts now known in holding the view that characters acquired in the lifetime of the individual, as the result of functional activity in certain regions of the body or in certain organs, may under favorable conditions be more or less com-

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[*] Organic Evolution as the Result of the Inheritance of Acquired Characters, etc. Translated by J. T. Cunningham. London, 1890.

[†] Evolution of Sex, 1890. See also Dr. O. von Rath's Criticisms of some Cases of Apparent Transmission of Mutilations. Translated by Prof. H. B. Ward, Amer. Naturalist, with the bibliography at the end of the article, January, 1894.

[‡] Faits nouveaux établissant l'extrême Fréquence de la Transmission par Hérédité d'États organiques morbides, produits accidentellement chez des Ascendants. (Comptes Rendus de l'Académie des Sciences, 13 Mars, 1882.)

[§] L'Hérédité des Modifications somatiques. Revue Scientifique, Tom. XLVI. No. 23, 6 Déc., 1890.

pletely transmitted; or at least the tendency to such transmission, if latent in one generation, may appear in a succeeding one. And in the earlier geological ages this principle may have been much more active than at present. The hypothesis seems to be a good working one to account for phenomena which cannot be otherwise explained, and should not in consequence of adverse, though often very able and candid criticism, be set aside. On the contrary, if as the result of Weismann's criticisms it be only provisionally adopted, should it not lead to further experiments in the laboratory, and to further and more thorough studies of the metamorphosis of animals, with a view to ascertain how far they are correlated with changes of habit and function?

The lines of future investigation in this field appear to lie mainly in four directions: —

1. In the domain of comparative cytology.
2. In the study of the life histories or metamorphoses of animals.
3. In the further observation of the facts of heredity as observed in the raising of plants, in the breeding of domestic animals, and that of the different races of mankind, and especially by laboratory experiments like those of Semper, Bert, and others, in changing the surroundings of organisms.
4. In the study of the gradual modification and specialization of some organs in forms now extinct, with the degeneration and loss of others, a subject so fully worked out by Professor Osborn as regards the teeth of mammals.

III. Inheritance at corresponding Periods of Life.

But perhaps the crucial cases will be found to occur in animals with a complicated metamorphosis, because in such instances we can draw the line between characters which are congenital and those which are acquired. As regards the characters which appear in post-embryonic life, it is not difficult to see that they have originated in response to stimuli brought about by changes in the environment.

My attention has been turned to this subject while studying the complicated life histories of some of the Bombycine moths, in which there are usually five distinct larval stages, and sometimes as many as nine, not to mention the pupal and imaginal stages. Now in each and all of these stages the organism is as a rule adapted to some more or less temporary change in its environment. It seems, the more closely we observe the habits of some of these caterpillars, almost capable of demonstration that the different temporary colors, markings, organs, and structures developed, and for the time being useful only to become at a later stage useless and therefore discarded, as new and dissimilar conditions of life arose, — it seems almost self-evident that such markings and structures were the result of the responses of an organism in its most plastic time of life to changes in its habits, such changes being due either to changes in its surroundings, or to the effort to repel the attacks of insects, birds, etc.

However such stages arose, they are at the present epoch transmitted from parent to offspring with wonderful certainty. Among the Arctians, and in other caterpillars, the number of moults is known to vary, either from artificial breeding or from other unknown causes, possibly lack of nutrition. This form of heredity was called by Darwin* "Inheritance at corresponding Periods of Life," and by Haeckel† "Homochronous Transmission." Darwin thus describes the phenomenon: "When the embryo leads an independent life, that is, becomes a larva, it has to be adapted to the surrounding conditions in its structure and instincts, independently of those of its parents; and the principle of inheritance at corresponding periods of life renders this possible." (p. 51.) Again: "On this principle of inheritance at corresponding periods, we can understand how it is that most animals display from the germ to maturity such a marvellous succession of characters." (p. 60.)

Examples of this law are the complicated metamorphosis of certain free, but more especially the parasitic worms, notably the fluke worms and the Cestodes, the complicated metamorphoses of the Echinoderms, of the Mollusca, the Crustacea, and the metamorphic insects, and more especially such insects as the Meloidæ, Rhipiphoridæ, and Stylopidæ, in which there is a hypermetamorphosis.

It is not altogether improbable that the phenomena of alternation of generations is primarily due to changes in surroundings, and hence of habits, resulting in new needs which were met by adaptation to the new surroundings, the different stages being finally fixed by homochronous heredity. Take the case of the Hydroids, where the generation of fixed hydra-like individuals gives rise by budding to the free-swimming, egg-producing medusa form. The hydra-like individuals are the result of direct inheritance, while the medusa is prob-

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* The Variation of Animals and Plants under Domestication, II. 51.

† History of Creation, I. 217, 218. See also Giard, who, referring to the laws of heredity, remarks: "Plusieurs de ces lois, et en particulier la loi de l'hérédité homochrone, fournissent aussi, nous le verrons, de bons arguments en faveur du principe de Lamarck." Revue Sc., 6 Déc., 1890.

ably a secondary product, the result of adaptation to a free-swimming mode of life; all its organs in a so much higher scale of perfection than those of the generalized hydra-form ancestor having resulted from the manifold stimuli of a changeable environment. The same may be said of the Aurelia, with its free Scyphistoma larval stage.*

The alternation of generations in the Trematodes is apparently likewise the result of adaptation to a change of hosts bringing about homochronous heredity. It is evident that alternation of generations is the extreme of a series, beginning (1) with simple direct growth; (2) an incomplete metamorphosis (the lower winged insects); (3) genuine metamorphosis; (4) the hypermetamorphosis of Meloidæ, Rhipiphoridæ, and Stylopidæ; the 5th and last term being the cases of alternation of generations. It seems difficult to account for these sets of individuals or generations, unless we resort to the principle of inheritance of characters acquired during the lifetime of the ancestral forms, which gave rise to these interrupted or alternate series of forms.

On the other hand Weismann in order to account for alternation of generations carries us out of the sphere of observation and induction into speculative regions, and assumes that "*two kinds of germ plasm exist in those species in which alternation of generations occurs*, both of which are present in the egg cell as well as in the bud, though only one of them is active at a time and controls ontogeny, while the other remains inactive. The alternating activity of these two germ plasms causes the alternations of generations." † Are not over-nutrition and changes in station and habits the more appreciable and potent causes?

The complicated metamorphosis of the Crustacea is the result of the adaptation to variations in the environment. It is not improbable that the Nauplius of the primitive Crustacea, the Branchiopoda (including the Phyllopoda), was a secondary and not a primary form. The proof would seem to be the non-existence of any adult Arthropod with such a form and structure as that of the Nauplius. The earliest Crustacean was probably a naked, shelless Cladoceran or Phyllopod-like form, with a few or many definite segments, bearing unjointed or imperfectly jointed lamellate swimming legs, derived from the flattened parapodia

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* In his suggestive book entitled "A Theory of Development and Heredity" (1893), Prof. H. B. Orr accounts for alternation of generations by secondary changes of the environment which favored the hydroid stage and the perfect medusa stage, and at the same time tended to eliminate the intermediate stages. In other cases the secondary changes of environment destroyed the hydroid stage, as we find Medusæ without any hydroid stage. (p. 225.)

† The Germ Plasm, p. 457.

of some ancestral Annelid worm. The cylindrical rowing appendages of the Nauplius appear to be secondary and adaptive characters, fitting it for its free-swimming surface life.

The Zoëa larva of the Decapoda, with its body composed of head and abdomen alone, without thoracic segments and appendages, is also an adaptive stage, a differentiated or farther advanced Nauplius.

The Megalops stage of the Brachyura, or crabs, induced at the end of the free-swimming life of the zoëa, and intermediate between the zoëa and crab stage, the thorax and thoracic appendages being present, is likewise an adaptation to the transition period connecting the free-swimming or surface life and the creeping and bottom life of the adult.

These different stages, the result of adaptation, are signal examples of the inheritance of characters at corresponding periods of life, and would appear to have been originally the result of the inheritance of characters originated or acquired during the life of the individual; i. e. the ancestor of the existing decapodous Crustacea.

On the other hand, in groups where a metamorphosis is the rule, there are exceptional forms in which development is abbreviated or direct. Such cases are the direct development of the starfish, *Leptychaster kerguelenensis* Smith, while *Pteraster militaris* is viviparous; and the direct development of *Anochanus sinensis* and of *Hemiaster cavernosus* among Echinoids. The lobster and crayfish are exceptions to other macrurous Crustacea, in which there is a complicated metamorphosis, their development being condensed or abbreviated, and limited to embryonic life. So with the crabs of several species living in the Black Sea, whose direct development was traced by Rathke.

In such exceptional cases as these, the phenomenon of direct development will undoubtedly be found to be caused by some change in the conditions of existence.

Attention should also be here drawn to the fact that the term congenital is an elastic one. Mammals, at least the placental ones, are only born after a long uterine life, but fish and tadpoles, as well as the higher nesting birds, are born in a more premature condition, and congenital characters in these animals have quite a different significance from those of mammals. So it is in a less degree with the larvæ of insects, the degree of inequality in the perfection of the larva being very great in different groups, especially in the parasitic Hymenoptera and Coleoptera.

IV. Homochronous Heredity in Insects with a Hypermetamorphosis.

The hypermetamorphoses of the Meloidæ, Rhipiphoridæ, and Stylopidæ very strikingly illustrate the principle we are endeavoring to emphasize and establish. The facts are given in the writings of Newport, Fabre, Westwood, Siebold, Valery-Mayet, Riley, and others.

In Meloë the freshly hatched larva, or "triungulin," is an active Campodea-like larva, which runs about and climbs up flowers, from which it creeps upon the body of bees, such as Anthophora, who carries it to her cells, wherein her eggs are situated. The triungulin feeds upon and destroys the eggs of its hostess. Meanwhile its inactive life in the bee's cell reacts upon the organism; after moulting, the second larval form is attained, and now the body is thick, cylindrical, soft, and fleshy, and it resembles a lamellicorn larva, with three pairs of rather long thoracic legs. This second larva feeds upon the honey stored up for the young or larval bees. After another moult, there is another entire change in the body; it is motionless, the head is mask-like without movable appendages, and the feet are represented by six tubercles. This is called the semi-pupa or pseudo-pupal stage. This form moults, and changes to a third larval form, when apparently, as the result of its rich concentrated food, it is overgrown, thick-bodied, without legs, and resembles a larval bee.

After thus passing through three larval stages, each remarkably different in structure and in the manner of taking food, it transforms into a pupa of the ordinary coleopterous shape.

The history of Sitaris, as worked out by Fabre and more recently by Valery-Mayet, is a similar story of two strikingly different adaptational larval forms succeeding the triungulin or primitive larval stage. The first larva is in general like that of Meloë, the second is thick, oval, fleshy, soft-bodied, and with minute legs, evidently of no use, the larva feeding on the honey stored by its host. The pseudo-pupal stage is still more maggot-like than in the corresponding stage of Meloë, and the third larva is thick-bodied, with short thoracic legs.

In the complicated life history of another Cantharid, *Epicauta vittata*, as worked out by Dr. C. V. Riley, we have the same acquisition of new habits and forms after the first larval stage, which evidently were at the outset the result of an adaptation to a change of food and surrroundings. The female Epicauta lays its eggs in the same warm, sunny situation as that chosen by locusts (Caloptenus) for depositing their eggs. On hatching, the active minute carnivorous triungulin, ever on the search for eggs, on happening upon a locust egg gnaws into it, and then sucks the contents. A second egg is attacked and its contents exhausted, when, owing to its comparatively inactive habits and rich nourishing food after a period of inactivity and rest, the skin splits along its back, and at about the eighth day from beginning to take food the second larva appears, with much smaller and shorter legs, a much smaller head, and with reduced mouth-parts. This is the Carabidoid stage of Riley. After feeding for about a week in the egg a second moult occurs, and the change of form is slight, though the mouth-parts and legs are still more rudimentary, and the body assumes " the clumsy aspect of the typical lamellicorn larva." This Riley denominates the Scarabæidoid stage of the second larva.

After six or seven days there is another transformation, the skin being cast, and the insect passes into another stage, " the ultimate stage of the second larva." The larva, immersed in its rich nutritious food, grows rapidly, and after about a week leaves the now addled and decaying locust eggs and burrows into the clear sand, where it lies on its side in a smooth cell or cavity, and where it undergoes an incomplete ecdysis, the skin not being completely shed, and assumes the semi-pupa stage, or coarctate larval stage of Riley.

In the spring the partly loose skin is rent on the top of the head and thorax, and then crawls out of it the " third larva," which only differs from the ultimate stage of the second larva " in the somewhat reduced size and greater whiteness." The insect in this stage is said to be rather active, and burrows about in the ground, but food is not essential, and in a few days it transforms into the true pupa state.

These habits and the corresponding hypermetamorphosis are probably common to all the Meloidæ, though the life history of the other species has yet to be traced.

In the genus Hornia described by Riley, the wings of the imago are more reduced than in any other of the family, both sexes having the elytra as rudimentary as in the European female glow-worm (*Lampyris noctiluca*). These, with the simple tarsal claws and the enlarged heavy abdomen, as Riley remarks, "show it to be a degradational form."

Its host is Anthophora, and the beetle itself lives permanently in the sealed cells of the bee, and Riley thinks it is subterranean, seldom if ever leaving the bee gallery. The triungulin is unknown, but the ultimate stage of the second larva, as well as the coarctate larva, is like those of the family in general, the final transformations taking place within the two unrent skins, in this respect the insect approaching Sitaris.

It appears, then, that as the result of its semi-parasitic mode of life the Campodea-form or triungulin larva of these insects which have free biting mouth-parts like the larvæ of Carabidæ and other carnivorous beetles, instead of continuing to lead an active life and feed on other insects, living or dead, and then like other beetles directly transforming into the normal pupa, moult as many as five times, there being six distinct stages, before the true pupal stage is entered upon. So that there are in all eight stages including the imaginal or last stage.

One cannot avoid drawing the very obvious conclusion that the five extra stages, constituting this hypermetamorphosis, as it is so well styled, were structural episodes, so to speak, due to the peculiar parasitic mode of life, and were evidently in adaptation to the remarkable changes of environment, so unlike those to which the members of other families of Coleoptera, the Stylopidæ excepted, have been subjected. The fat overgrown body and the atrophied limbs and mouth-parts are with little doubt due to the abundant supply of rich food, the protoplasm of the egg of its host, in which the insect during the feeding time of its life is immersed. Since it is well known that parthenogenesis is due to over, or at least to abundant nutrition, or to a generous diet and favoring temperature, there is little reason to doubt that the greatly altered and abnormally fat or bloated body of the insect in these supernumerary stages is the result of a continuous supply of rich pabulum, which the insect can imbibe with little or no effort.

The life history of the Stylopidæ is after the same general fashion, though we do not as yet know many of the most important details. The females are viviparous, hatching within the body of the parent, as I once found as many as 300 of the very minute triungulin larvæ issuing in every direction from the body of what I have regarded as the female of *Stylops childreni* in a stylopized Andrena caught in the last of April. The larvæ differ notably from those of the Meloidæ in the feet being bulbous and without claws, yet it is in general Campodea-like and in essential features a triungulin. The intestine ends in a blind sac, as in the larvæ of bees, and this would indicate that its food is honey. The complete life history of no Stylopid is completely known. It is probable that, hatched in June from eggs fertilized in April, the larvæ crawl up on the bodies of bees and wasps; finally, after a series of larval stages as yet unknown,* penetrating

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* Westwood in his excellent account of this group remarks " Hence, as well as from the account given by Jurine, it is evident that the pupa of the Stylops is enclosed in a distinct skin, and is also in that state enveloped by the skin of

within the abdomen of its host before the latter hibernates, and living there through the winter. The females, owing to their parasitic life, retain the larval form, while the free males are winged, not leading in the adult stage a parasitic life, though passing their larval and pupal stages in the body of their host, and are so unlike ordinary beetles as to be referred by good authorities to a distinct order (Strepsiptera).

The triungulin stage of these insects corresponds in general to the form of the larval Staphylinidæ and allied families, such as the Tenebrionidæ, which are active in their habits, running about and obtaining their food in a haphazard way, often necessarily suffering long fasts. In these external-feeding, less active coleopterous larvæ, like the phytophagous species, which have an uninterrupted supply of nutritious food, we see that the body is thick and fleshy. So also in the larvæ of the Scarabæidæ, Ptinidæ, and the wood-boring groups. In internal feeders, like the larval weevils and Scolytidæ, which live nearly motionless in seeds, fruits, and the sap-wood of plants and trees, with a constant supply of nourishing, often rich food, the eruciform body is soft, thick, and more or less oval-cylindrical. So it is with the larvæ of Hymenoptera, especially in the parasitic forms, and in the ants, wasps, and bees, which are nearly if not quite motionless, at least not walking about after their food.

Now the change from the active triungulin stage to the series of secondary nearly legless, sedentary, inactive stages is plainly enough due to the change of station and to the change of food. From being an independent, active, roving triungulin, the young insect becomes a lodger or boarder, fed at the expense of its host, and the lack of bodily exertion, coupled with the presence of more liquid food than is actually needed for its bare existence, at once induces rotundity of body and a loss of power in the limbs, followed by their partial or total atrophy.

That this process of degeneration may even occur in one and the same stage of larval existence is very well illustrated by what we know of the life history of the wasp parasite of Europe, *Rhipiphorus paradoxus*. Thanks to the very careful and patient observations of Dr. T. A. Chapman, we have a nearly complete life history of this beetle, the representative of a family in many respects connecting the Meloidæ and Stylopidæ.* Where Rhipiphorus lays her eggs is un-

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the larva, contrary to the suggestion of Mr. Kelly." Class. Insects, II. 297. This is all we know about the supernumerary larval stages.

* Some Facts towards a Life History of Rhipiphorus paradoxus. Annals and Magazine of Natural History for October, 1870.

known. Dr. Chapman however found a solitary specimen of the young larva in the triungulin stage. He describes it as "a little black hexapod, about $\frac{1}{50}$ inch (.5 mm.) in length, and $\frac{1}{120}$ inch in breadth, broadest about the fourth segment, and tapering to a point at the tail; a triangular head with a pair of three-jointed antennæ nearly as long as the width of the head, with legs very like those of *Meloë* larvæ; the tibiæ ending in two or three claws, which are supported and even obscured by a large transparent pulvillus or sucker of about twice their length; this was marked by faint striæ radiating from the extremity of the tibiæ, giving it much the aspect of a lobe of a fly's proboscis. Each abdominal segment had a very short lateral spine pointing backwards; the last segment terminated by a large double sucker similar to those of the legs; and the little animal frequently stood up on this, and pawed the air with its feet, as if in search of some fresh object to lay hold of."

This almost microscopic larva finds a wasp grub and bores into its body, probably entering at a point near the back of the first or second segment behind the head. Dr. Chapman succeeded in finding the larva of the beetle within that of the wasp, before the latter had spun up. "Assuming that the wasp larva lives six days in its last skin before spinning up, I should guess that the youngest of these had still two or three days' feeding to do. The *Rhipiphorus* larvæ were but a little way beneath the skin of the back, about the fourth and fifth segments [counting the head as the first], and indifferently on either side. The smallest of these was $\frac{1}{16}$ inch in length, and, except its smaller size, was precisely like the larger ones I am about to refer to, having the same head, legs, plates, etc. These were of the same size as those of the larger larvæ, the difference in size of the latter being due to the expansion of the intermediate colorless integument."

After the wasp grub has spun the silken covering of its cell the larva of Rhipiphorus may be still detected in some of them, being rendered visible by its black legs and dark dorsal and ventral plates. "On extracting this larva, it bears a general resemblance in size and outline to the youngest larva of Rhipiphorus that I had found feeding externally on the wasp grub, but with the very notable exception of the already mentioned black marks. These are, in fact, a corneous head, six-jointed legs, and a dorsal and ventral series of plates. I immediately recognized the head and legs as identical with those of the little black mite already described, but presenting a ludicrous appearance in being widely separated from each other by the white skin of the larva. I have no doubt that the dorsal and ventral series of black marks are the corresponding plates of the mite-like larva floated away from each other by the expansion of the intervening membrane. By measurement also they agree exactly in size, although the larva extracted from the wasp grub is ten times the length and six times the width of the little *Meloë*-like larva. In length it is $\frac{1}{6}$ inch (4.5 mm.) and $\frac{1}{28}$ inch in breadth."

The remarkable changes thus described in the larva of this beetle after it has begun its parasitic life within the body of its host are especially noteworthy because the great increase in size and difference in shape, as well as in habits, all take place before the insect has moulted. The rapid development in size, and consequent distention of the body and the separation of the sclerites of the segments behind the head, are paralleled, as Chapman says, by the greatly swollen abdominal region of the body in *Sarcopsylla penetrans* and in the female of the Termitidæ. In those insects this distention is due to the enlargement of the ovaries and of the eggs contained within them, but in the Rhipiphorus it is due to the comparative inactivity of the larva, and to its being gorged with an unending supply of rich food, the blood and fat of its host. It follows, then, that if a sedentary life, and over, or at least abundant nutrition, will have this effect within the short period covered by the single first larval stage of the Rhipiphorus, it is reasonable to infer that the hypermetamorphosis is also due to the same factors.

Chapman then goes on to say, that finally, within six hours of the time of spinning up of the wasp grub, the Rhipiphorus larva at the end of Stage I., which is "usually in motion, and for its situation might be called tolerably active, is seen to lay hold of the interior of the skin with its anterior legs, and keeps biting and scratching with its strong and sharp jaws until it is able to thrust through its head, when, in less than a quarter of an hour, it completely emerges by a vermiform movement; and at the same time it casts a skin, together with the black head, legs, plates, etc."

The larva, now in its second stage, passes forward and seizes hold of the upper or lateral aspect of the prothoracic segment of the wasp grub. On emerging it becomes shorter and thicker, "and very soon loses length by that curving forward of its head which is so marked in the full-grown larva, and which does not exist before its emergence." The larva is now found "lying like a collar immediately under the head of the wasp grub, and is attached to it by the head, though not very firmly. At this stage the feeding of the young Rhipiphorus is rather sucking than eating.

When about 6 mm. in length it moults a second time, and the full-grown larva closely though superficially resembles a Crabro or Pemphredon larva, the small head being bent over forwards. By the time it is ready to pupate it has wholly eaten the wasp larva, and the temperature of the cell being high, a larva 5 mm. long grows large enough in two days to fill the top of the cell of its host, and the larva is ready to pupate about a week after hatching, so that its development is very rapid. The beetles themselves do not live in the cells. Chapman thinks they hibernate, and that the eggs are laid in the spring or summer.

We thus have in this insect three larval stages, the triungulin, and two later stages, the great differences between the first and the last two being apparently due to their parasitic mode of life, the larva spending its second stage within its host, involving an existence in a cell with a high temperature, an uninterrupted supply of rich, stimulating food, and a comparatively sedentary mode of life compared with that of the triungulin at the beginning of its existence. It is quite obvious that the hypermetamorphosis is primarily due to a great change in its surroundings, i. e. the parasitic mode of life of the beetle, habits of very rare occurrence in the Coleoptera, numerous in species as they are.

In the Proctotrypidæ there is also a hypermetamorphosis.*

In a species of Platygaster which is parasitic in the larva of Cecidomyia, the first larva (Cyclops stage) is of a remarkable shape, not like an insect, but rudely resembling a parasitic Copepod crustacean. In this condition it clings to the inside of its host by means of its hook-like jaws, moving about, as Ganin says, like a Cestodes embryo with its well known six hooks. In this stage it has no nervous, vascular, or respiratory system, and the digestive canal is a blind one.

After moulting the insect entirely changes its form, it is thick oval cylindrical, nearly motionless, with no appendages, but with a digestive canal and a nervous and vascular system.

After a second moult the third and last larval stage is attained, and the insect is of the ordinary appearance of ichneumon larvæ.

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* Metschnikoff, Embryologische Studien an Insecten. Zeitschrift für wissens. Zoologie, XVI. 389–500, 1866.

Ganin, Beiträge zur Erkenntniss der Entwickelungsgeschichte bei den Insecten. Zeitschrift für wissens. Zoologie, XIX. 381–451, 1869.

Ayers, On the Development of Œcanthus niveus and its Parasite, Teleas. Memoirs Bost. Soc. Nat. Hist., III. 225–281, 1884.

For an abstract of the work of Ganin, see Balfour's Comparative Embryology, I. 345–348; also Packard's Our Common Insects, 1873, pp. 161–167.

Not less striking is the life history of Polynema, which lays its eggs in those of a small dragon-fly (*Agrion virgo*). The first larval stage is most remarkable. It hatches as a microscopic immovable being, entirely unlike any insect, with scarcely a trace of organization, being merely a flask-shaped sac of cells. After remaining in this state five or six days it moults.

The second stage, or Histriobdella-like form, as Ganin names it, is more like that leach-like worm than an insect.

The third larval form is very bizarre, though more as in insects, having rudimentary antennæ, mouth-parts, legs, and ovipositor. In this condition it lives from six to seven days before pupating.

The strange history of another egg parasite (Ophioneurus) agrees in some respects with that of the foregoing forms. It is when hatched of an oval shape, with scarcely any organs, and differs from the genera already mentioned in remaining within its egg membrane, and not assuming their strange shapes. From the cylindrical sac-like non-segmented larva resembling the second larva of Platygaster it passes directly into the pupa state.

A fourth form, Teleas, is an egg parasite of Gerris, and in America one species oviposits in the eggs of Œcanthus.

The spindle-shaped larva in its first stage roughly resembles a trochosphere of a worm rather than the larva of an insect so high in the scale as a Hymenopter. It is active, but after moulting the second larva is oval, still without segments. Dr. Ayers gives a profusion of details and figures of the first and second stages of our Teleas, the second strongly resembling the Cyclops stage of Ganin. He describes three stages, and though he did not complete the life history of the insect he thinks it changes to an ovoid flattened form which succeeds the Cyclops stage in other Pteromalidæ, and that there are at least four ecdyses.

It is difficult to account for these strange larval forms, unless we suppose that the embryos, by their rich abundant food, have undergone a premature development, the growth of the body walls being greatly accelerated, the insects so to speak having been, under the stimulus of over-nutrition and their unusual environment, and perhaps also the high temperature of the egg, hurried into vermian existence on a plane scarcely higher than that of an active ciliated gastrula.

Further observations, difficult though they will be, are needed to enable us to account for the singular prematurity of the embryo of these parasites. That these stages are reversional and a direct inheritance from the vermian ancestors of these insects is not probable, but the forms are evidently the result of adaptation in response to a series of stimuli whose nature is in part appreciable but in part unknown.

It may be noted, however, that the appearance of a primitive band in the second larval stage indicates the origin of these forms, as well as that of insects in general, from a Peripatus-like, and again from an earlier leach-like Annelid ancestor. Hence the first larval or Cyclops stage is due to a precocious development caused by the unusual environment, and is simply adaptational, and not of phylogenetic significance.

V. On the Inheritance of Acquired Characters in Lepidoptera.

Perhaps in no other group of animals may we study the subject of the inheritance of acquired characters with more success than in the Lepidoptera. In these insects the four stages of existence, the egg, larva, pupa, and imago, are definite and fixed, and during each of the last three the organism is, so to speak, a different creature, with distinct and separate shape and structure external and internal, and during each stage leads a different life. Family, generic, and specific characters are inherited at each of these stages, and at each there is a combination of congenital and acquired characteristics, some of both classes of which, i. e. the least marked, are difficult to separate from one another. The following is an attempt at a rough grouping of such features at the last three stages.

We omit the egg stage, for though they more or less vary in shape and ornamentation, this is perhaps due more to difference in the structure of the lining of the oviduct of the female than to the action of external circumstances on the egg after it has been laid. Yet this should be said with some reservation, because we are not aware that any one has discussed the probable mode of origin of the specific differences in the shape and color of the eggs of birds, or the shape and markings of the eggs of insects; though undoubtedly the agency of external causes together with natural selection has something to do with the variation.*

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* It has seemed to us that the relation of specific and generic characteristics in the eggs of insects is a most difficult problem. Yet it should be observed that, while the differences in ornamentation and shape are primarily due to the impression on the shell received from the lining of the oviduct, yet the wonderful diversity we see in the eggs of insects is often readily seen to be correlated with the external conditions in which they exist, after having been deposited by the parent. As regards the eggs of birds, the thick solid shell and conico-

In the larval histories already published we have endeavored, where they have been observed with sufficient completeness, to discriminate between the congenital and the acquired characters.

1. *Larval State.* — A. In this state we have the inheritance of congenital characteristics.

B. Inheritance of what were originally acquired characters, the results of attacks of enemies. Examples are the tubercles armed with spines and sometimes with a singular kind of easily detached spines which are hence called caltrops (*Empretia*, etc.), stripes, spots: all apparently inherited at different periods of larval life; the least important specific and varietal characters probably having been originally acquired during the life of an individual.

2. *Pupal State.* — A. Cocoon: the absence or presence of a cocoon was doubtless originally due to differing external conditions: while the dense, perfect cocoon is characteristic of the spinning moths (*Attacidæ, Lasiocampidæ*, etc.); the Ceratocampidæ make none at all, but, like the Sphinges, the larvæ simply bury themselves in the earth before pupation. In the Arctiidæ and the Liparidæ the cocoon is chiefly composed of the barbed larval hairs, with a little silk to fasten them more firmly together: in the Geometridæ certain larvæ spin a loose thin web. In such cases the spinning of a cocoon is intimately associated with a change of larval habits, and is with little doubt an acquired habit, originally formed by a single individual.

B. The shape of the pupa is often dependent on the presence or absence of a cocoon. In the Notodontidæ the cremaster is often absent in genera (Gluphisia, which spins a very slight cocoon, and Lophodonta which spins no cocoon) which do not spin a cocoon,

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oval shape of the murre's eggs seem due to the unprotected manner in which they are left on rocks and shelves from which they are liable to fall. Here might be cited the suggestive essay of Prof. John Ryder, "The Mechanical Genesis of the Form of the Fowl's Egg," (Amer. Phil. Soc. Philadelphia, 1893, XXXI. 203–209,) in which he attempts to show that "the configuration of the outline of the hen's egg is determined by mechanical means, while the egg membranes and shell are in process of formation within the oviduct." We may contrast with the murre's egg that of the robin, in which the shell is thin and uniform in color, since it is protected from harm by being contained in a nest; so also the color of murres' eggs may be due to the action of protective mimicry, the spots assimilating them to lichen-grown or variously tinted rocks, by which they escape the observation of their natural enemies, the fox, the mink, and other egg-devouring animals. So the eggs of Chrysopa, of lice, of many bugs, etc., are in shape and mode of attachment beautifully adapted to prevent them from being seen by egg-destroying animals.

and are closely allied to those which do. In Cerura there is no spine on the rudimentary cremaster, because the pupa lies in a very dense cocoon. The cremaster affords excellent generic and specific characters. In the subterranean pupa of Datana it is present, and is of use in aiding the pupa to reach the surface of the ground. It is very large and acute in the subterranean pupæ of Ceratocampidæ and Sphinges. It is evident that in the presence or absence of a cremaster, and in its shape, and in the number of hooks and their shape, we have a set of very plastic characters, whose variability and plasticity are due to the varying habits of the pupa, whether living above or under ground, whether protected by a very thin loose netlike cocoon, or by a solid double one like that of Cerura or of the silk-worms. Also whether the thread is continuous and can be readily reeled, as in *Bombyx mori*, or whether the thread is often interrupted at the anterior end, as in *Platysamia cecropia*, is a feature which was probably the result of a slight change of circumstances, and may have been inaugurated as the result of variation in a single individual, during a single lifetime, becoming eventually fixed by homochronic inheritance.

III. *Imago Stage.*—It is easier to select what may have been acquired characters in caterpillars than in butterflies and moths, and yet the last have a complicated series of what may originally have been acquired characters. It should be borne in mind that, while caterpillars live for weeks and even months, are subject to frequent moults, are active and dependent on a proper supply of their food, usually this or that plant, butterflies and moths perish directly after mating, taking little or no food. Of course, acquired characters are most marked in the parts which are most used, as the maxillæ, wings, and external genital armature.

The absence of maxillæ, or their very rudimentary condition, in Bombycine moths, is with little doubt a recently acquired character. The very arbitrary distribution in Lepidoptera of scent-organs (androconia, etc.) is apparently a character recently acquired. The wonderful variations in the markings of the wings, due to a variety of slight causes, may often arise during an individual's lifetime and become a matter of inheritance, the result of sudden changes in temperature, moistness or dryness, and changes in food of the larva. By subjecting individual pupæ to prolonged cold or heat, varieties, and a greater or less number of broods, may be produced artificially, and this may illustrate how seasonal varieties have arisen in nature.

Many species are only separated by differences in the male genital armature. These, as is well known, are subject to great individual variation, and why should not the characters peculiar to a distinct variety, or even species, arise during the lifetime of two individuals when mated? Many individuals die without being mated; an unusually vigorous polygamous butterfly may have some new congenital extra development of hooks and processes, and by frequent use develop the muscles controlling these to the extent of providing an acquired character, which may be, if useful, inherited in the next and succeeding generations.

But an especially interesting and fruitful field of investigation would be a study of wingless Lepidoptera, such as the canker-worm, the autumn moths allied to it, the tussock moths (Orgyia), and especially the sac-bearers or Psychidæ.

The loss of wings in these cases seems originally to have been due to disuse in certain individuals more sluggish than others, and with little doubt has been the result of inheritance of what were originally acquired characters. It is easy to imagine how this has been induced by a study of a series of forms beginning with certain European genera in which the wings of the female are very small, and passing to those in which they become simple pads, as in the Orgyia, and ending with those, such as Anisopteryx, in which their reduction is still further carried out. And then examples like those should be compared with certain of the Ephemeræ, whose hind wings are so much reduced; with Pezzotettix and other Orthoptera with aborted wings, and certain Hemiptera in which the wings are aborted, ending with the great order of Diptera, comprising a vast number of species in which the hind wings have not only undergone a great reduction, but have been transformed through change of function into balancers, with their extraordinary sense-organs. It is not difficult to see that the disuse of wings may have begun in the life of a single individual, which, losing its wings, having perhaps inherited a tendency to this lesion through corpulency and other bodily changes, became inactive, averse to flight, and finally transmitted the peculiarity or the tendency to such peculiarity to its offspring.*

In a paper in the Proceedings of the Boston Society of Natural History (XXIV. 482) on the life history of *Drepana arcuata*, I have described the different stages of this moth, and at the end recapitulated the congenital characters, and finally given a synopsis of the chief

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* L. Knatz (Archiv für Naturgeschichte, LVII. 49–74, 1 pl., 1861) mentions 183 instances of reduced wings, and states that the reduction in wings is accompanied by an enlarged abdomen and an increase in the size of the ovaries, with greater fertility. Journ. Royal Microscopical Society for 1891, p. 462.

steps in the evolution of the adaptational characters which appear after the first exuviation. It seems very probable that these later features were the result of the action of external stimuli, both physical and biological, and that they were acquired not only during the lifetime of the larva, but at certain distinct stages or periods during the growth of the creature. The changes are both colorational and structural, and during the different stages the larva was adapted for different surroundings, and thus at each important stage was virtually for the time being a distinct animal.

During the pupa stage special and unusual structural adaptations arose; the cremaster being unusually developed, and also a pair of cephalic hooks, serving to entangle the head in the web of the cocoon, so that the pupa cannot be thrown out of the curled leaf which remains in the first brood on the tree. These I regard as characters acquired by the insect after birth, and in response to the exigencies of life at different stages. The reader is also referred to the conclusions given in that paper.

Acquired Characters in the Notodontidæ. — In the systematic portion of my work on this group I have given a number of life histories of the family from papers recently published, and with more or less detail pointed out the later adaptational, as distinguished from the congenital characters. I have called attention, in late articles, to the varying shape of the tubercles and setæ in the larvæ of the Bombyces and other of the higher Lepidoptera, and to their probable mode of origin, and why they appear on certain segments in preference to others. The attention of the reader is called to the summary or recapitulation of changes especially in the life history of *Datana integerrima*, *Apatelodes torrefacta*, *Symmerista albifrons*, *Macrurocampa marthesia*, and several species of Cerura, while there is a summary of the steps in the assumption of the adaptive characters at the different larval stages of Schizura. The steps in the evolution of what may be regarded as acquired characters in Schizura, and in *Dasylophia anguina*, Hyparpax, Heterocampa, etc., are readily seen by an examination of the plates in the monograph referred to.

The Notodontians are remarkable in general for the humps, tubercles, and spines of their larvæ, some of which are congenital, while others appear at different stages after birth. Still some larvæ of this group are entirely without them, and remain so throughout their larval life. And this is an argument that the various processes of the cuticle or outgrowths of the entire integument are characters originally acquired during the post-embryonic life of the young insect.

Take, for example, the larval *Nadata gibbosa;* this, like the caterpillar of Gluphisia and of Lophodonta is a smooth-bodied larva, ornamented with lines, but entirely unarmed. The life history of *N. gibbosa* shows that it is born with a smooth body, without any rudiments of tubercles or enlarged bristles, while no traces of the yellowish subdorsal lines appear until at the end of the second stage. This form is therefore a primitive one, and this fact would seem to demonstrate that the humps, tubercles, and spines, so frequently observed in the group, arose within recent geological times, and were acquired during the postembryonic stages of the larvæ of different genera, in response to various changes in the surroundings of different species, these finally becoming fixed and regularly transmitted along various lines of development, definite when the changes in the environment are definite, and resulting in a series of forms constituting the present genera of the family.

One of the most notable cases in the family is that of the loss at about the middle of the larval life of the remarkable antlers of *Heterocampa biundata.* During the three earliest stages the larva bears on the prothoracic segment a pair of enormous antlers, each with four tines. At the second moult these are discarded, and in the last two stages are represented by a pair of conical, rounded, polished, piliferous knobs. The rest of the partly grown body of the larva is smooth. After casting its horns the larva assumes a new set of colorational markings, so that in its last two stages it is a totally different creature in appearance from the earlier stages.

I have also observed the wonderful changes undergone by the caterpillar of *Heterocampa guttivitta,* representing five stages, nearly every one of which presents notable differences. In the first, directly after hatching, the reddish larva has not only a pair of enormous antlers with four tines on the first thoracic segment, but a pair of long antler-like spines on abdominal segments 1 to 6, and also 8 and 9; those on segments 1 and 8 being about three times as large as the others. It is certainly one of the most singular larvæ of the family.

Now this bizarre armature is entirely discarded at the first moult, excepting that the prothoracic antlers are represented by a pair of knob-like tubercles, the other segments, however, showing no trace of the former existence of spines. Also, while the body was not striped in Stage I., it is now paler red with a more brownish tint, and is marked with four yellowish stripes. At the end of this stage the lines become effaced, and the body grows more yellowish on the sides. In the third stage the tubercles still persist, but the markings differ very much, as reddish dorsal patches appear in the middle and near the end of the body, and there are anticipations of the markings of the fully grown caterpillar. In the present stage the insect closely resembles the mature larva, having bright crimson markings on the thoracic segments, and on the third and fourth and on the fifth and sixth abdominal segments, these bright spots becoming somewhat less decided and conspicuous in the final stage.

Now it seems natural to suppose that the disappearance of the armature of this insect with the first moult was due to the lack of need for it by the caterpillar, which gradually became adapted to a life on the under side of an oak leaf, where it assumed a simple spindle-shaped body, extended when at rest along the midrib, in which position we have found such caterpillars, its body glaucous green, and so marked with yellowish lines and reddish spots, as well as with dashes and lines, as to be wonderfully assimilated to the greenish, reddish, and whitish hues and shades of the leaf under which it was sheltered.

It also seems reasonable to suppose that these adaptational colorational features were acquired by the ancestors of the present forms during the different stages succeeding the first ecdysis. And thus we are warranted in assuming that this and multitudes of other cases of adaptation to the change in habits and modes of life, and special situations, were acquired originally at different periods after birth during an earlier geological period than this, when the ancestors were fewer in number and more plastic than now. Otherwise, how can we have had the differentiation of a few ancestral forms into the present series of genera, subfamilies, and families, represented by such a great number of species?

Indeed, it seems difficult to account for the evolution of the vast hordes of existing species of insects unless we assume that there was going on throughout the entire process the rise and perfecting of post-natal acquired characters, such characters becoming fixed by heredity, and reappearing with unerring certainty at different stages in the life of the individual; while in some animals whose postnatal metamorphosis through some environmental change became suppressed, we have the more salient stages epitomized during the life of the embryo.*

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* For many additional facts in the ontogeny of the Bombycine moths bearing on this subject the reader may be referred to my papers in the Proceedings of the Boston Society of Natural History, XXIV. 510-560, 1890; Journal of the

In his Chapter XIII. of "The Germ Plasm," Weismann gives an interesting example of the inheritance of climatic variation in butterflies. After an account of his recent experiments on *Polyommatus Phlæas*, he states: "Both experiments, however, prove the correctness of the old assumption of lepidopterists that the action of heat on a single generation is capable of giving the German form of a blackish tint; and since, moreover, it is clear that the development of a single generation at a lower temperature can render the color of the Neapolitan butterfly less black, it appears that the two varieties may have originated owing to a gradual cumulative influence of the climate, the slight effects of one summer or winter having been transmitted and added to from generation to generation. *This would then seem to be an instance of the transmission of acquired characters.*" He then adds, that he does not believe that this is the correct interpretation of the facts; on the contrary he insists: "The theory of determinants will I believe supply a very simple explanation of this apparently complicated case, which I consider of great value, because it confirms this theory. Instead of supporting the doctrine of the transmission of somatogenic characters, this example shows how *such a process may apparently be brought about*, and on what it depends. A somatogenic character is not in this case inherited, but the modifying influence — the temperature — *affects the primary constituents of the wings in each individual*, — i. e. a part of the soma — *as well as the germ plasm contained in the germ cells of the animal.* It modifies the *same* determinants in the rudiments of the wings of the young chrysalis as in the germ cells, namely, those of the wing scales," etc.

We certainly prefer the more simple explanation first given, but only to be rejected, by Weismann, since it appears to be really based on observed facts, and to be a natural and logical induction from such facts, and is thus a more scientific explanation. The same process of reasoning will apply to the inheritance of acquired characters in the ontogeny of the Lepidoptera and that of other groups, such as we have endeavored to set forth in this essay.

It is, moreover, a simple and natural inference, such as in the case of the butterflies experimented on by Weismann, and would be the

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New York Entomological Society, I. 22–28, 57–76; Proceedings Amer. Phil. Soc. Philad., February, 1893, pp. 83–108, March, 1893, pp. 189–192; Proc. Amer. Acad. Arts and Sciences, Boston, 1893, XXVIII. 55–92; Annals New York Acad. Sci., May, 1893, VIII. 41–92. Also Monograph of the Bombycine Moths of North America, Part I., in course of publication in the Memoirs of the National Academy of Sciences, Vol. VII.

first explanation which would suggest itself to any observer. On the other hand, the extremely complicated speculative and *a priori* second explanation of Weismann, based as it is on pure assumptions, does not carry conviction, and thus is not an efficient working hypothesis to explain inheritance at corresponding periods of life.

It is noticeable that in his writings Weismann does not touch upon homochronous heredity, though his earlier work, "Studies in the Theory of Descent" (1876), which is largely based on Lamarckian views, afterward abandoned by the author, is a storehouse of the most suggestive facts.

In seeking to explain the causes of a metamorphosis in animals, one is compelled to go back to the primary factors of organic evolution, such as the change of environment, whether the factors be cosmical (gravity), physical changes in temperature, effects of increased or diminished light and shade, under or over nutrition, and the changes resulting from the presence or absence of enemies, or of isolation. The action of these factors, whether direct or indirect, is obvious, when we try to explain the origin or causes of the more marked metamorphoses of animals. Then come in the other Lamarckian factors of use and disuse, new needs resulting in new modes of life, habits, or functions, which bring about the origination, development, and perfection of new organs, as in new species and genera, etc., or which in metamorphic forms may result in a greater increase in the number of, and an exaggeration of the features characterizing the stages of larval life.

VI. The Adequacy of Neolamarckism.

It is not to be denied that in many instances all through the ceaseless operation of these fundamental factors there is going on a process of sifting or of selection of forms best adapted to their surroundings, and best fitted to survive, but this factor, though important, is quite subordinate to the initial causes of variation, and of metamorphic changes.

Neolamarckism,* as we understand this doctrine, has for its founda-

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* In 1885, in the Introduction to the "Standard Natural History," we proposed the term Neolamarckianism, or Lamarckism in its modern form, to designate the series of factors of organic evolution, and we take the liberty to quote the passage in which the word first occurs. We may add that the briefer form, Neolamarckism, is the more preferable.

"In the United States a number of naturalists have advocated what may be called Neo-Lamarckian views of evolution, especially the conception that in tion a combination of the factors suggested by the Buffon and Geoffroy St. Hilaire school, which insisted on the direct action of the *milieu*, and of Lamarck, who relied on the indirect action of the environment, adding the important factors of need and of change of habits resulting either in the atrophy or in the development of organs by disuse or use, with the addition of the hereditary transmission of characters acquired in the lifetime of the individual.

Lamarck's views, owing to the early date of his work, which was published in 1809, before the foundation of the sciences of embryology, cytology, palæontology, zoögeography, and in short all that distinguishes modern biology, were necessarily somewhat crude, though the fundamental factors he suggested are those still invoked by all thinkers of Lamarckian tendencies.

Neolamarckism gathers up and makes use of the factors both of the St. Hilaire and Lamarckian schools, as containing the more fundamental causes of variation, and adds those of geographical isolation or segregation (Wagner and Gulick), the effects of gravity, the effects of currents of air and of water, of fixed or sedentary as opposed to active modes of life, the results of strains and impacts (Ryder, Cope, and Osborn), the principle of change of function as inducing

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some cases rapid evolution may occur. The present writer, contrary to pure Darwinians, believes that many species, but more especially types of genera and families, have been produced by changes in the environment acting often with more or less rapidity on the organism, resulting at times in a new genus, or even a family type. Natural selection, acting through thousands, and sometimes millions, of generations of animals and plants, often operates too slowly; there are gaps which have been, so to speak, intentionally left by Nature. Moreover, natural selection was, as used by some writers, more an idea than a *vera causa*. Natural selection also begins with the assumption of a tendency to variation, and presupposes a world already tenanted by vast numbers of animals, among which a struggle for existence was going on, and the few were victorious over the many. But the entire inadequacy of Darwinism to account for the primitive origin of life forms, for the original diversity in the different branches of the tree of life forms, the interdependence of the creation of ancient faunas and floras on geological revolutions, and consequent sudden changes in the environment of organisms, has convinced us that Darwinism is but one of a number of factors of a true evolution theory; that it comes in play only as the last term of a series of evolutionary agencies or causes; and that it rather accounts, as first suggested by the Duke of Argyll, for the *preservation* of forms than for their origination. We may, in fact, compare Darwinism to the apex of a pyramid, the larger mass of the pyramid representing the complex of theories necessary to account for the world of life as it has been and now is. In other words, we believe in a modified and greatly extended Lamarckianism, or what may be called Neo-Lamarckianism."

the formation of new structures (Dohrn), the effects of parasitism, commensalism, and of symbiosis, in short the biological environment; together with geological extinction, natural and sexual selection, and hybridity.

It is to be observed that the Neolamarckian in relying mainly on these factors does not overlook the value of natural selection as a guiding principle, and which began to act as soon as the world became stocked with the initial forms of life, but he simply seeks to assign this principle to its proper position in the hierarchy of factors.

Natural Selection, as the writer from the first has insisted, is not a *vera causa*, an initial or impelling cause in the origination of new species and genera. It does not start the ball in motion; it only so to speak guides its motions down this or that incline. It is the expression, like that of "the survival of the fittest" of Herbert Spencer, of the results of the combined operation of the more fundamental factors. In certain cases we cannot see any room for its action; in some others we cannot at present explain the origin of species in any other way. Its action increased in proportion as the world became more and more crowded with diverse forms, and when the struggle for existence had become more unceasing and intense. It certainly cannot account for the origination of the different branches, classes, or orders of organized beings. It in the main simply corresponds to artificial selection; in the latter case, man selects forms already produced by domestication, the latter affording sports and varieties due to change in the surroundings, that is, of soil, climate, food, and other physical features, as well as education.

In the case also of heredity, which began to operate as soon as the earliest life forms appeared, we have at the outset to invoke the principle of the heredity of acquired characters during the lifetime of the lowest organisms.

Finally, it is noticeable that when one is overmastered by the dogma of natural selection he is apt, perhaps unconsciously, to give up all effort to work out the factors of evolution, or to seek to work out this or that cause of variation. Trusting too implicitly to the supposed *vera causa*, one may close his eyes to the effects of change of environment or to the necessity of constant attempts to discover the real cause of this or that variation, the reduction or increase in size of this or that organ; or become insensible to the value of experiments. Were the dogma of natural selection to become universally accepted, further progress would cease, and biology would tend to relapse into a stage of atrophy and degeneration. On the other hand a revival of

Lamarckism in its modern form, and a critical and doubting attitude towards natural selection as an efficient cause, will keep alive discussion and investigation, and especially, if resort be had to experimentation, will carry up to a higher plane the status of philosophical biology.