

The Theory of Recapitulation : A Critical Re-statement of the Biogenetic Law. By WALTER GARSTANG, M.A., D.Sc.(Oxon), Professor of Zoology in the University of Leeds. (Communicated by Prof. W. BATESON, F.R.S., F.L.S.)

(With a Text-figure.)

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MORE than half a century has passed since Haeckel propounded his "fundamental Biogenetic Law" (1866). It played a great part in the campaign for the recognition of Evolution, has inspired and still inspires much good work in Palæontology, but, as a working hypothesis in Embryology, is admitted to have evoked little but controversy and confusion. This history alone renders it probable that the law is a mixture of sound and questionable elements, but the two have never been satisfactorily disentangled. The late Dr. C. H. Hurst (1893), Adam Sedgwick (1894 & 1909 (*a*)), and Geoffrey Smith (1911), Oscar Hertwig (1898 & 1896), and Morgan (1908), among others \*, have criticised particular aspects of it, but no one has presented a complete theoretical scheme capable of replacing Haeckel's as an explanation of the relations between ontogeny and phylogeny. Lately MacBride (1914 & 1917), from the embryological side, and Bather (1920), from the standpoint of palæontology, have revived the full Haeckelian doctrine ; and the former has even considerably extended it, though neither, so far as I can see, has refuted, or even appreciated, the force of the criticisms made by their predecessors. As it is not to the credit of science that Zoology should harbour a "law" which, like a creed, may be accepted or rejected at pleasure, and as I believe the basis of this law is demonstrably unsound, I venture to make a renewed attempt to define the points at issue. The most satisfactory way of doing this appears to be to re-state, in accord with modern knowledge, the theoretical relations of ontogeny to phylogeny, and then to subject the alternative theories to verification by test-cases. As the old law was essentially morphological, I exclude from present consideration all bionomical and ætiological questions not directly involved.

1. The two aspects of Haeckel's doctrine—the statement of fact and the theory of causation—were summed up by himself in the phrases : "Ontogenesis is the recapitulation of Phylogenesis" and "Phylogenesis is the mechanical cause of Ontogenesis." In these now familiar terms the new

\* Bateson's criticism of the law of von Baer, though not specially referring to Haeckel's modification of it, should be included here (1894, pp. 8-10).



conception of evolution was wedded, fifty years ago, to current ideas of ancestry, heredity, and development : Ancestors created, heredity transmitted, and development repeated the order of creation.

2. To Haeckel, phylogenesis meant "the chain of manifold animal forms which represent the ancestry" of an organism, *i. e.* the phyletic line of succession of adults. Ontogenesis was, and is, the succession of form-changes between zygote and adult of the same organism. The ontogenetic sequence was regarded as resembling, and actually caused by, the phyletic sequence of adults, which had preceded it.

3. But Haeckel overlooked the other evolutionary sequence, the phyletic line of succession of zygotes, running more or less parallel with the adult sequence, step by step, though steadily diverging. Every elaboration of adult form, even of its degree of pliability under environmental influence (for there are great differences among animals, as among plants, in this respect), was preceded by a corresponding elaboration of zygotic structure \*, nuclear or cytoplasmic or both, determining, under suitable conditions, the form and character of the ontogenetic changes and their result. Through the whole course of Evolution, every adult Metazoan has been the climax of a separate ontogeny or life-cycle, which has always intervened between adult and adult in that succession of forms which Haeckel terms "Phylogenesis." The real Phylogeny of Metazoa has never been a direct succession of adult forms, but a succession of ontogenies or life-cycles.

4. This was so from the very beginning, when zygote and adult were indistinguishable in form as ancestral Flagellate Protozoa. Zygosis must have been followed, then as now, by successive cell-divisions, corresponding to the cell-divisions of Metazoan ontogeny, though they led to no single multicellular adult. A stage further on, the corresponding cell-divisions gave rise to adherent colonies, fixed or free, arborescent or epithelial, each type established by its own ontogeny. The very first, most ancestral Metazoan of all—at whatever grade of evolution the dividing line may be drawn—must be admitted to have been built up by a full ontogeny from unicellular zygote to multicellular adult, so that, in the first, as in the latest Metazoan, ontogeny came first, leaving the first adult Metazoan as its original achievement. The next generation, through a new ontogeny, produced a second adult, and so on. In a word, Haeckel's causes and effects must be inverted. Phylogeny (in Haeckel's sense) is the product, the "record"—not the precedent cause—of successive ontogenies ; and neither the first, nor the second, of Haeckel's phrases can any longer express the basis of true biogenetic law. Ontogeny does not recapitulate Phylogeny : it creates it.

\* Cf. Hertwig (1906, i. p. 56) : "Die Eizelle z. B. eines jetzt lebenden Säugetieres ist kein einfaches und indifferentes, bestimmungsloses Gebilde . . . sondern . . . das ausserordentlich komplizierte Endprodukt eines sehr langen, historischen Entwicklungsprozesses."



5. Does this involve, then, the loss of the doctrine of Recapitulation? To which question I reply, first, with Goethe, "Was fruchtbar ist, allein ist

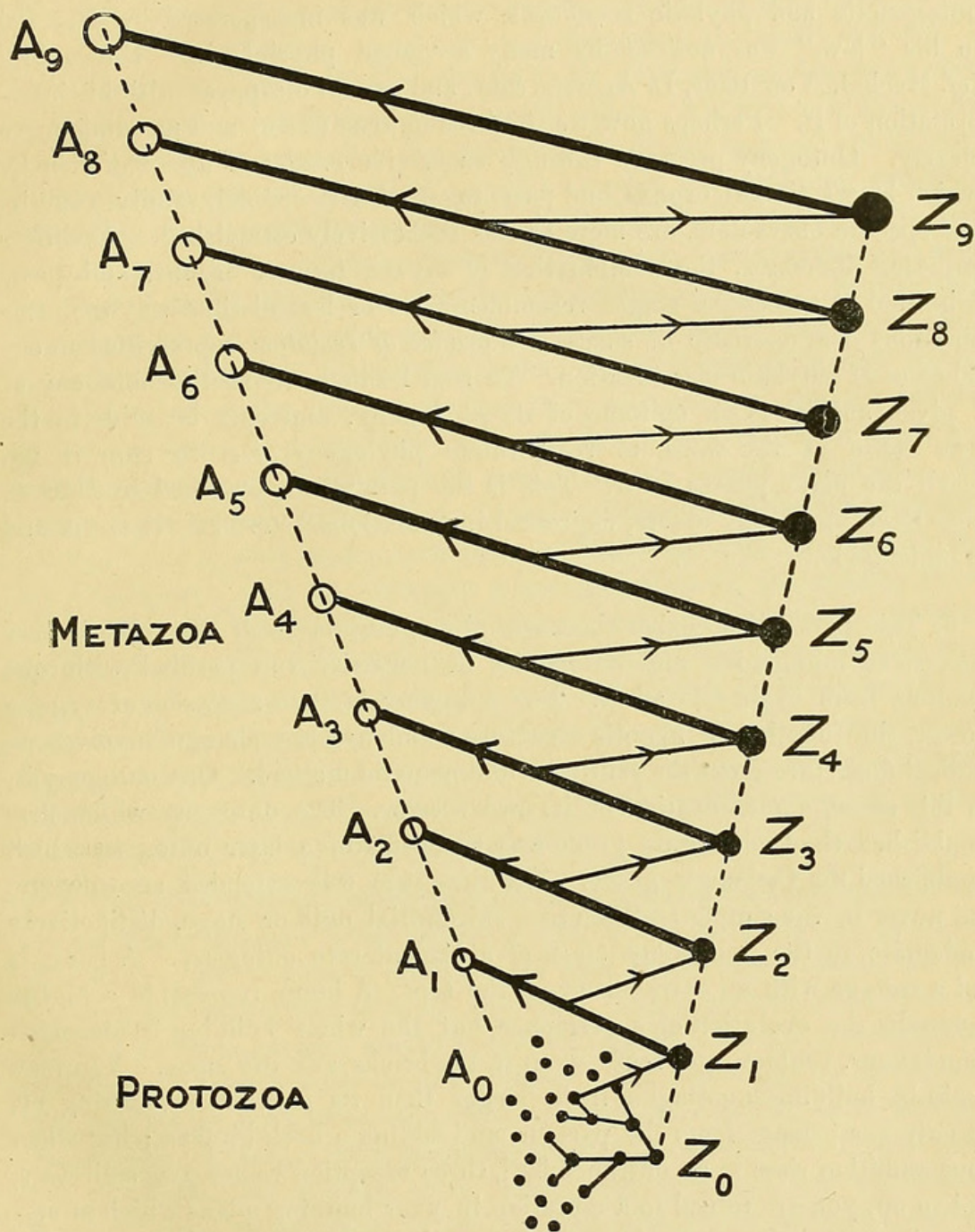


FIG. 1.—Diagram of the Relations between Ontogeny and Phylogeny.

$A_0$ - $A_9$  ..... the Phyletic succession of Adults.  
 $Z_0$ - $Z_9$  ..... do. do. do. do. Zygotes.  
 $Z_1$ - $A_1$  } ..... do. do. do. do. Ontogenies.  
 $Z_2$ - $A_2$  }  
 &c.

wahr," and, secondly, as Balfour wrote on another matter: "If the above position be admitted, it is not permissible to shirk the conclusions which seem



necessarily to follow, however great the difficulties may be which are involved in their acceptance" (1885, ii. p. 32). But the "parallelism" of ontogenetic and phyletic sequences, which was incorporated by Haeckel in his "law," was noticed by many a "good physiologist" before him (*cf.* Meckel, Von Baer, L. Agassiz, &c.), and cannot disappear with his interpretation of it. Perhaps now we shall see its true extent and meaning more clearly. Ontogeny proceeds through successive *grades of differentiation* by which layers, tissues, organs, and parts together with ordinal, family, generic, and specific characters, are more or less successively established. As differentiation increases, the combination of layers, tissues, organs, and parts exhibited at successive stages resembles more or less distinctively the combinations characteristic of successive *grades of evolution* represented in our schemes of phyletic classification. To that limited extent the ontogeny of a given animal is an epitome of its phylogeny, and may be said, in the true sense of the word, to recapitulate phylogeny, *i.e.* to sum it up, recall the main phases of it. This is the parallelism observed by Meckel, Von Baer, and many others, expressed in evolutionary terms. It exists and is undeniable.

6. This parallelism exists because phylogeny is itself the creation of successive ontogenies, and ontogenies of necessity run parallel with one another from zygote to adult. For ontogeny is the expression of zygotic power, the function of zygotic structure; and zygotic change involves no radical departure from the routine of ontogenetic method. One ontogeny is, in this sense, a modification of its predecessor. The ontogeny which first established the Cœlenterate grade was the basis of a later ontogeny which established the Cœlomate grade. The life-cycle was extended accordingly, but never by the simple addition of a substantial unit or stage, distinctively Cœlomate, to the final adult stage of a Cœlenterate ontogeny. A house is not a cottage with an extra storey on the top. A house represents a higher grade in the evolution of a residence, but the whole building is altered—foundations, timbers, and roof—even if the bricks are the same. You may begin by building a cottage a little larger than its predecessor, cutting off an entrance passage from the parlour, and adding a back kitchen; but when your ambition rises to an entrance hall, three reception rooms, two staircases, and so on, you are forced to a mutation in your building plans which affects operations from the start. The ontogeny of a Cœlenterate adds, in a certain sense, on a simple diploblastic base, certain effective, workaday, adult features by which it copes with the conditions of its life; but the replacement of these effective characters by others suited to the more adventurous career of a Cœlomate (*e.g.* development of prehensile mouth instead of tentacles) involves their disappearance altogether; and there remains of Cœlenterate organisation only that diploblastic residuum of differentiation out of which the Cœlomate may be economically and directly built up. Nor is the end of



the life-cycle alone effected. The Cœlenterate had a larva fitted both to distribute it and to build it up. It must be changed so as to perform this double function for a quite different creature, probably of very different size, habits, and requirements. And then the changes at the larval end must be fitted and co-ordinated with the changes at the adult end, so that every phase of the life-cycle is modified in some way or other. Yet it is only this much-pruned Cœlenterate sequence that survives as building material out of which a specifically Annelid ontogeny may give rise to a Crustacean, and so on. Inevitably the Cœlenterate sequence in the Crustacean's ontogeny is reduced to the simplest terms, and is as far from "mirroring" any functional Cœlenterate type, or the original mode of its formation, as possible. Nevertheless, the grades persist as stepping-stones from zygote to adult; and, having been successively pruned of unessentials as they ceased in turn to furnish directly the equipment of the adult stage, they have become very constant features of the ontogeny in a long line of evolutionary progress. For there is an irreducible minimum beyond which even ontogeny cannot abbreviate. The zygote is always unicellular, the larva multicellular and fitted for swimming, and the adult a multilaminar complex of interdependent parts; and even the Ctenophore, with its elaborate præ-organisation of the zygote, cannot escape the rule that  $8=4 \times 2$ . Ontogeny repeats the necessary successive grades of ancestral differentiation, but no ontogenetic stage is ever more than an immature adumbration of a particular adult type in the phyletic chain\*. It reproduces those successive grades, not because successive adult types have been included in it, but because each ontogeny is a modification, within limits, of its predecessor; and by those predecessors the phyletic chain of adults was organised and equipped.

7. Thus Cœlenterate, Cœlomate, Protochordate, Gnathostome, and Tetrapod are successive grades of differentiation both in the ontogeny and phylogeny of a Frog; but at none of these grades does the ontogeny recall the form and structure of a possible adult ancestor. This is obvious enough in each of the first three grades; and in the fourth, which is held to "recapitulate" the Fish, the tadpole lacks dermal skeleton (both scales and fin-rays), paired fins, and biting jaws, which the adult ancestral Fish undoubtedly possessed. The tadpole, in fact, is not a modified reproduction of an adult Fish-ancestor, but a modification of the larva which that ancestral fish undoubtedly possessed—still recognisable, in less modified form, in the larvæ of *Polypterus* and *Dipnoi* to-day. In other words, the life-cycle of the Frog is a modification of the life-cycle of an ancestral freshwater Fish; and adjacent terms in the old life-cycle (larva and adult) have undergone parallel and correlated modifications, as well as some independent specialisations.

\* Cf. Von Baer (1828, p. 230): "Der Embryo geht nie durch eine andere Tierform hindurch, sondern nur durch den Indifferentzustand zwischen seiner Form und einer anderen."



8. That "recapitulation" does not require the reproduction of adult stages in the ontogeny in order to be exhibited is plainly seen in the development of many Geometrid moths. Everyone knows the Geometrid or "looper" type of caterpillar, provided with prolegs only on two of the hindmost abdominal segments (the 6th and last). This type is admittedly derived from a prototype which possessed the full Lepidopteran equipment of prolegs on segments 3 to 6, as well as the last, the prolegs on the three first segments having subsequently disappeared. But many Geometrid caterpillars possess vestiges of one or more pairs of these missing prolegs : in the March moth\* (*Erannis aescularia*, Schiff.) there are traces of the last pair (South, ii. pl. 125); in the common Brimstone (*Opisthograptis crataegata* (Linn.)) and Scalloped Hazel (*Gonodontis bidentata*, Cl.), clear rudiments of the last two pairs (*l. c.* pl. 115); while the Orange Underwing (*Brephos parthenias* (Linn.)) has the first two pairs rudimentary and the third pair fully developed and functional (Meyrick, 1895, and South, 1908, ii. pl. 39). In the Feathered Thorn, *Colotois* (*Himera*) *pennaria* (Linn.), the single pair of vestigial prolegs arises and disappears between the 1st and 4th moults (Buckler, 1897). Now, the time has long passed when it was possible to regard these prolegs as homologues and derivatives of the true legs of some Scolopendroid ancestor. They were "cenogenetic" larval features, adaptive interpolations, modifications of the middle stages of a life-cycle which originally, in the earlier phases of Endopterygote history, exhibited larvæ lacking prolegs altogether, as in Coleoptera. Yet these examples of vestigial organs are as reminiscent of ancestral (though larval) structure as the larval foot of the oyster, the larval stalk of *Antedon*, the transitory feet of the parasitic *Portunion*, or any other of the familiar examples that are held to prove the theory of adult recapitulation. They demonstrate, as Morgan has already urged (1919), that recapitulation is merely the static aspect of inheritance, and that, in this aspect, inheritance is not primarily the reproduction of adult characters, but the reproduction of the characters of each part of the whole life-cycle—the sequential expression of the full train of zygotic potencies.

9. It may be urged that such hereditary changes in the middle phases of the life-cycle do not affect the proposition that evolutionary changes usually take place at the end, and that the case for adult recapitulation rests on the evidence for this proposition. Nevertheless, to clear up the misunderstandings of the past, it is necessary to leave no margin for ambiguity. If "recapitulation," in the special sense of partial reproduction of the past, is hereby shown to be independent of the characters of adult ancestry, that is something gained : the axe is laid at the root of the tree. For much of the glamour of the old biogenetic law is due to its appeal to such idols of the market-place as the assumption that "like begets like," and that, as adults

\* Meyrick's classification and nomenclature are followed here, but the English names have been added for convenience of reference to South's figures.



only are capable of begetting, the thing begotten is built up of successive adults. That "cenogenetic" interpolations\*, without any adult ancestral significance, are a normal feature of almost every life-cycle, is often verbally admitted, though the recapitulationist rarely realises how profoundly such interpolations may affect his phylogenetic conclusions, and how dangerously subtle become his arguments when engaged in proving that such larvæ as the Trochosphere, the Nauplius, and other distributive stages of the life-cycle are at bottom "recapitulative." I propose to deal more fully with the origin and significance of such larval forms in another communication; but, to illustrate the principle, I may add one example of the origin of an interpolation in the most progressive of sequences known to us, viz. that of Vertebrates. There is no doubt that Birds are descended from Reptiles. It is beyond question that Reptiles are hatched in a form and with a somatic organisation which is that of a miniature adult Reptile in all respects. Yet the Bird is hatched in a form and with sundry details of organisation different from those of the adult, *e.g.* its downy plumage. Now, the "typical" down-feather is an open hollow tube, splayed out at its free extremity into a ring of soft barbs (or barbules) of equal size, and I ask if such a tubular feather is to be regarded as an intermediate stage in the phyletic derivation of feathers from scales. I submit that there is not a scrap of evidence, or of probability, that any adult ancestor of Birds, along the whole route from Reptiles to Sparrows, was ever clothed in anything except scales, feathery scales, and finally contour-feathers. The chick is an interpolation in the life-cycle of Birds, and its down is a "secondary" modification of complete contour-feathers. The Duck, the Fowl, and the Pigeon represent three successive grades of differentiation in the phylogeny of Birds. Anyone who will examine under a microscope the nestling-down of these three birds in the order mentioned, will see that they exhibit successive phases in the degradation (*a*) of the primitive rachis of a contour-feather and (*b*) of the barbs of such a feather, *i.e.* that the chick stage, with its peculiarities of organisation, has been evolved, step by step, within the group of Birds alone, and is an interpolation that has no relation with, and throws no light on, the præ-Avian adult ancestry, or on the way in which scales were transformed to feathers†.

\* *E.g.* Weismann's discussion of the evolution of markings in larvæ of Sphingidæ, much of which is probably sound, though unnecessarily complicated by the assumption that primitive longitudinal markings have been "shunted back" into earlier stages of the ontogeny, instead of being simply *replaced* in the later stages by patterns more suited to increased size or special conditions of exposure (1904, pp. 177-185).

† The subsequent publication of Prof. Cossar Ewart's valuable paper on "The Nestling Feathers of the Mallard" (P. Zool. Soc. 1921) renders this discussion inadequate and I hope to amplify it. In the meantime I would merely remark that, on the relation of feathers to scales, the association of several feather-germs with single scales on the foot of the Owl is no disproof of my thesis, since the feathers here represent a secondary extension, like that of the scales on the head of *Ceratodus*.



10. Let us now take an equally unambiguous case of evolutionary change at the adult end of the life-cycle. There is a group of genera of Geometrid moths in which the life-cycle terminates with normal winged males and more or less wingless females (*Apocheima*, *Hybernia*, *Theria*\*, &c.). It is an adaptive change, for, unlike their congeners which hibernate as pupæ and emerge in early summer, these moths emerge in winter when the trees are leafless, and the normal method of repose is much more dangerous. The males, like both sexes of other related genera, rest by day exposed with wings outspread on tree-trunks, palings, &c. The wingless females hide in the crevices of bark. Both are active at night, the females creeping out of their crannies, and the males hunting for them up and down the woods. In the Early Moth (*T. rupicapra*) and Dotted Border (*H. marginaria*), which emerge in February and March, the wings of the females are half as long as the body (South, ii. pl. 120); in the Scarce Umber (*H. aurantiaria*), which emerges as early as October or November, the wings are mere stumps (*l. c.* pl. 120); while in the Mottled Umber (*H. defoliaria*) and various other species the wings are completely lacking (*l. c.* pl. 122). The wings of the males are of full size throughout (Meyrick, and South, *l. c.*). Now here is a case of evolutionary change of the adult form, and in one sex only; but, with these facts before him, and with our knowledge of the origin and breeding of similar mutations in Morgan's *Drosophila* experiments, who can assert that this abnormal adult has been *added* to the life-cycle of its normally-winged ancestors, and that the old adult has been "pushed back" to an earlier phase of the life-history. The wingless female is the exact counterpart of the normal male, and, though I do not know if any change has already taken place in the pupal characters of the female, it is a safe deduction from our knowledge of the pupal condition in more extreme cases to assert that the only changes likely to ensue will be in the direction of still further reducing the size of the pupal wings. The ontogeny will be influenced *in the direction taken by the new adult, and without regard to the ancestral adult at all*. The new adult is just a modification of the old adult. There is no addition, no "tacking on" of a new stage; no "pushing back" or "tachygenesis" of the old adult stage—merely a substitution of one adult type for another, and, sooner or later, some correlated changes in the stage which immediately precedes it. Zygotic mutations have caused the changes; natural selection has controlled the breedings of successive generations; and heredity has perpetuated the results of the selection. Certain ancestral adult characters are disappearing from the ontogeny; and the condition of a flea, ontogenetically, as well as finally, without a trace of wings at any stage, is likely to be the end result.

11. I have selected this example, not because it is representative of all evolutionary changes that manifest themselves in the final stages of ontogeny, but because of its bearings on the most recent exposition of the theory

\* Meyrick's nomenclature (1895); English names and figures in South (1908).



of recapitulation from the embryological side. I have already shown that, in its original and general sense, recapitulation is a fact which was recognised long before there were any theories to account for it. But this generalised, or Meckelian, recapitulation needs to be clearly distinguished from the specifically adult recapitulation of Haeckel and his school, who could not understand the origin of the former except on a theory of catenary ancestral inheritance, each term in the ontogeny (except the last) being moulded after the likeness of a specific adult ancestor—though, of course, condensed, abbreviated, telescoped, and secondarily modified by adaptive changes. Now, the only way that I can see of establishing this theory by purely embryological methods, is to show that the penultimate stage of the ontogeny of a given type of adult resembles the final (adult) stage of the ontogeny of some theoretically ancestral type more closely than it resembles the corresponding penultimate stage of the same, and similarly with regard to the antepenultimate stage, and so on. I cannot find that this has been done, or even attempted, in any case—certainly not in any of the cases recently selected by MacBride for discussion. Yet this is his thesis: “When we assert that a Metazoan recapitulates in its life-history the past history of the race or stock to which it belongs, we mean that the stages intervening between the egg and the adult form resemble in some of their prominent features the *adult* animals which belonged to the same stock at different epochs in the past history of the race” (1917, p. 425); and he is concerned to show both that the adult stage of the ontogeny of a new species is an addition to the ancestral ontogeny (1914, pp. 23, 650), and that the adult stage of the ancestral ontogeny is reproduced (“recapitulated”) in the ontogeny of the new species as the last larval (or “neanic”) stage (*l. c.* pp. 21, 22). But his method of establishing these points is merely to select a number of cases in which the adult deviates considerably from the normal, and to show that “the young form resembles the type of the order to which the parent belongs and not the parental type itself” (1917, p. 428). “Thus the young Hermit-Crab swims freely about in the water and has a symmetrical abdomen like that of Shrimps and Prawns” [but so have the *young* stages of these creatures!]; “the young Flatfish swims with its ventral edge down and its dorsal edge up, and has an eye on each side of the head” [but so have the young of all Teleostei!]; “the young Comatulid is fixed to the bottom by a stalk like other Crinoids [and their young too, in all probability!]; and the young American Oyster possesses a foot like that of other bivalves by which it crawls about” [and, I may add, as the *young* of nearly all other Lamellibranchs crawl about!]. Nowhere does he show, or claim to show, that the young stages of any of these animals resemble the *adult more closely than the young* stage of typical members of their respective orders. He does not show it because he cannot. In every case that he discusses, whether the above, or the cases of the parasitic *Portunon*



and *Actheres* (1914, pp. 22, 206), the young resemble the young stages far more closely than they resemble the adult stages of their respective "normal" relatives\*. The symmetrical larva of Pleuronectids is scarcely distinguishable from many Teleostean larvæ of other families: it is distinct from any existing or fossil *adult* Teleost. It is the adult Oyster which has lost its foot, not the young Oyster which has acquired it. It is the adult *Portunion* which has lost its legs, not the young *Portunion* which has acquired them by tachy- (or any other kind of) genesis from its adult ancestors! These cases are all in the same category as the case of the wingless Moths already discussed. No new stage has been *added* to the life-cycle. One adult stage has been transformed into another, but the penultimate stages remain as before. The protagonist has missed his point, and the riposte is obvious. It was not his task to prove that Oysters were Mollusks, that Hermit-Crabs were Crustacea, or Pleuronectids Fishes. Comparative Anatomy did that long before the science of Embryology staked its claim. His province was to show that by virtue of Haeckel's Biogenetic Law he could reconstruct the prominent features of an *adult* ancestor from a developmental stage. All he has done is imperfectly to confirm Von Baer's præ-Haeckelian doctrine, that animals resemble one another more closely in their young stages than in their adult stages†. For his own illustrations show how greatly the adult may differ from the larva. He has merely shown the resemblance between the larvæ of a given class. It follows that, for all he has shown to the contrary, the "typical" or "normal" larvæ, which the Pleuronectid larva resembles, might have grown into Cod, Mackerel, or any other type of Teleost, and that the *adult* ancestors of Pleuronectids, so far from being "normal," may have carried themselves upside down like a *Remora*, or stood on their tails like Pipefishes. If no more relevant evidence than this is forthcoming, I claim that the old Biogenetic Law of adult recapitulation is dead, and that Morphology is henceforth free from a delusive and cramping hypothesis. Ontogeny is not a lengthening trail of dwarfed and outworn gerontic stages. Youth is perennially youth and not precocious age.

12. It is true that ontogeny could not exhibit its normal progressive differentiation of structure if evolution had always been of the type exhibited by these examples of metamorphic Insects, Lamellibranch Mollusks, parasitic Crustacea, and Pleuronectid Fishes. Evolution within these groups to-day partakes mostly of the nature of an adaptive radiation of the various types, whereas the general lines of ontogeny correspond rather with that kind of evolution which involves morphological and physiological progress. Although a detailed examination of any of these various advances falls

\* Note especially the absence of the 8th pair of thoracic limbs in *Epicarid*, as in all other *Isopod* larvæ.

† "Im Grunde ist also nie der Embryo einer höheren Tierform einer anderen Tierform gleich, sondern nur ihrem Embryo" (1828, p. 220).



outside the purview of the present communication, the slightest survey of Vertebrate evolution shows a series of triumphs over limiting environments of medium, temperature, space and time which has been based as much on the substitution of new for old organs as on the continuous elaboration of particular ones. When a given organ is wholly transformed in the course of evolution, it rarely shows traces in ontogeny of the original steps of its transformation (*e.g.* bony scales to fin-rays, horny scales to feathers, lobate fins to pentadactyle limbs, pentadactyle limbs to wings). The final form alone is inherited and develops directly. But when originally separate organs are ultimately united into one organ, some stages of the process of amalgamation are necessarily repeated (*e.g.* branchial arches to hyoid, vertebral elements to vertebræ, muscle-buds for paired limbs, anchylosis of limb-bones, segmental tubules of kidney, &c.). And when a new organ has arisen in intimate dependence on an old organ, the old organ may still remain necessary for the development of the new (Kleinenberg, 1886). Thus backbone replaces notochord, and bone replaces cartilage in present as, doubtless, in past ontogeny, for the former organ or tissue is still necessary as scaffolding for the later one; and the constant development of gill-slits in the ontogeny of terrestrial Vertebrates is but another illustration of the same phenomenon, as Sedgwick has already pointed out (1894)—for a complex double circulation that has been elaborated along channels determined by a branchial circulation cannot readily depart from the phyletic steps of its formation. It is this formative dependence of one organ, or set of organs, on another that confers on Vertebrate ontogeny its marked recapitulative character.

13. But it is equally clear that the whole succession is explicable without recourse to the theory of successive adult incorporations, and that the ontogenetic stages afford not the slightest evidence of the specially adult features of the ancestry. So far as notochord and gill-slits are concerned, they make their appearance in the earliest larval stages of every animal that presents them, including *Amphioxus* itself. Their phyletic origin is still wrapped in obscurity. The case is hardly different as regards cartilage, bone, scales, feathers, hairs, lungs, limbs, and all the other organs concerned. No example can be adduced of any of these organs *arising* in an adult stage of ontogeny. Until that evidence is produced, it is idle to claim that recapitulation which involves any of these organs is a repetition of specifically adult ancestral features. Moreover, it is impossible to overlook the fact that some of the most pregnant changes in the characteristics of the higher Vertebrates are directly or indirectly traceable to changes in the earliest stages of the ontogeny. The elaboration of the brain in Birds and Mammals, and the development of their social and æsthetic senses, are connected with the interpolation of the helpless chick, puppy, or baby stage in the ontogeny, which from the simplest beginnings has led to the development of educability and



preferential action in place of the limited range of reflex and automatic mechanisms of more primitive types. That "little twist of brain," which distinguishes one philosopher from another, is not more striking in its effects than are those trifling touches to the structure of the heart which transformed the cold-blooded Reptile and Stegocephalan into the warm-blooded Bird and Mammal respectively. Yet these are changes which, however graduated through successive generations at the outset, were not of a character to have been completed, or even initiated, in any adult stage of ontogeny. They must have been first manifested as a series of embryonic mutations, subjected continuously to selective tests of their relative physiological efficiency. Age bears the buffets of the world, but youth regenerates it.

14. It is, however, the palæontologists who are the real defenders of the Biogenetic stronghold. With them the Law is a faith that inspires to deeds, while to the embryologist it is merely a text for disputation. The difference is striking and worth defining. When the embryologist sets up his larval images and worships them as præ-Cambrian ancestors, the real ancestors cannot be produced to demonstrate his folly. But the palæontologist's aim is to trace lineages directly, and he is not satisfied until he has produced his ancestors, or at least the most substantial remnants of them. I confess that I have been tempted many times before to-day to attack a theory which has led so many of us into blind alleys, but always Hyatt's Ammonites recurred to present an unanswered, and seemingly unanswerable case for Haeckelian recapitulation. *A priori* it seems absurd that senile characters should be the beginnings of a line of evolution (Hyatt, 1897, p. 221 &c.), but the formidable array of evidence, the wide range of unfamiliar material to be studied, and, not least, our ignorance of the habits and conditions of life of this type of Mollusk, have all conspired to render these Ammonites to me a real obstacle. The following case, however, has recently impressed me with its remarkable analogies, and justifies me, I hope, in presenting a general argument without directly tackling the Ammonite problem itself, at any rate for the present.

The curious Prosobranch Gastropod *Lamellaria*, which mimics and devours Compound Ascidians, produces veliger larvæ of a unique type known as *Echinospira* (Krohn, 1853, 1857). The hyaline shell first produced is dilated so that it is far larger than its occupant—resembling in this respect the gelatinous house of an Appendicularian. It is coiled like the shell of an Ammonite, being in some species discoidal, with perfect symmetry, in others spiral, and in the related *Onchidiopsis* more simple and sac-like (Bergh, 1887). The larva can withdraw himself completely, or, with his mantle-edge clasping the mouth of the shell, he can protrude a large 4- or 6-lobed velum, and swim about with it on his excursions with wonderful grace and ease. The mouth of the shell is regularly extended at its margin, the successive additions being marked by transverse lines of growth and generally by one or two pairs of longitudinal (spiral) rows of tubercles or spines as well.



Inside this rapidly growing house (the roof of earlier whorls being periodically destroyed to make room for their successors), the larva secretes a second flatter shell (the rudiment of the adult shell) which fits his visceral hump and adheres to it, but is temporarily fixed in the cavity of the outer shell until he shifts his position, when it is carried forward—as though he were trying to improve on an Ammonite's arrangements by the device of a portable septum \*. Now, the point of the analogy is this: that the spiral rows of tubercles on the outside of the shell are variable in different species, and that in the same individual they may go through a cycle of changes exactly like the progressive changes of an Ammonite. The shell may pass through a smooth stage, a unituberculate stage (the outer row of tubercles), a dituberculate stage (with both rows developed), a spiny stage, and lastly a ribbed stage, in which cross-ribs join the tubercles of the two rows together. Unfortunately for the completeness of the analogy, *Echinospira* does not (so far as I have yet seen) present a gerontic stage, for, being only a larva, and usually very lively and vigorous, he quits his cage before old age comes over him, and transforms himself into a torpid Ascidian-eating *Lamellaria*. I hope to publish shortly some figures of the remarkable process of metamorphosis, of which I was lucky enough to be an eye-witness last year at Plymouth, as well as some further details of the growth of the larval shell; but for my present purpose I refer to Simroth (1885, text-fig. 5; Taf. xvi. figs. 1 & 2; xviii. figs. 1-2, 6-8), whose excellent figures sufficiently illustrate my immediate points. Meanwhile I submit (1) that the characters of the larval shells of *Lamellaria* and its allies are purely cenogenetic, with no relationship to the characters of any adult ancestors; (2) that gradual and progressive changes in the shell of the same individual, from one type of "ornament" to another, occur regularly, and are apparently determined by the constitution, size, and vigour of the larva under the particular conditions of its existence; and (3) that different degrees of the power of tubercle- and spine-formation characterise the larvæ under different conditions of existence.

In this case, from which all specific influence of adult ancestry is excluded, there is no escape from the conclusion that the power to perform these variously graduated operations, and the extent of that power, are essentially functions of the zygotic constitution, though there is a considerable margin for the direct influence of conditions. I conclude that, if this is so for the "cenogenetic" larvæ of *Lamellaria*, it is not likely to have been different for the "palingenetic" stages of Ammonites.

15. I return to the keynote with a direct comparison between the ontogeny and phylogeny of an animal in which the skeleton has been an important index of racial structure throughout geological time—the Crinoid *Antedon*.

\* The two shells correspond to the two layers of an ordinary Molluscan shell, dislocated from their original union. The outer or larval shell, corresponding to the prismatic layer, is formed by mantle-edge alone; the inner or adult shell, corresponding to the nacreous layer, is formed by the visceral surface of the mantle alone.



In selecting this type from the few that fulfil the necessary conditions, I have naturally not overlooked the fact that in the two most doughty advocates of Haeckel's law in this country, we also possess two of the foremost experts in Echinoderm embryology and Crinoid palaeontology respectively. If I err in my selection, or statement, of facts to be brought into prominence, they will know, I think, that it is from inadvertence and not from intention. The test of palaeontology cannot, of course, be brought to bear on the origin of the stalked condition, or at present, at any rate, of the primal torsion of the internal organs of Echinodermata; but I regard it as established by the form-sequences which Bather and his colleagues have traced, that radial symmetry was imposed upon the skeleton of an original pear- or sac-shaped body by the extension of superficial food-grooves leading to the mouth from food-collecting tentacles—a view which I understand is shared by MacBride (1911, p. 248). The hypothesis that Cystoid, Blastoid, and Crinoid were successive and independent offshoots from an unknown stock that lacked a skeleton seems to me to involve the negation of precise morphological evidence.

Accepting as my basis Bather's masterly sketch (1900) of the phyletic classification of these groups, and bearing in mind his own cautions (*l. c.* p. 138), as well as the slenderness of the geological record of Permian and Triassic forms, the main outlines of the adult ancestry of *Antedon* cannot have deviated far, I think, from the following sequence (the Roman numerals in brackets refer to certain figures of special significance in Bather's work):—

(?) Præ-Cambrian.—Præ-brachiote ancestors, first Cystoid, with numerous irregular thecal plates, then reduced and approximating to Blastoid regularity. Finally an immediate ancestor of Cysto-Blastoid structure exhibiting an ill-defined separation between calyx and stalk (*cf.* Cystoidea, viii., xviii.), but with fixed pentameral symmetry and composition of the firm cup, as in Blastoids\*, from the Basals upwards (*Stephanocrinus*, ii.). From such an ancestor, after development of arms, the Monocyclia and Dicyclia, distinguished at first only by the exclusion, or inclusion, of Infra-Basals in the cup (*i. e.* the position of the growth-zone), diverged. I pursue further only the Dicyclia series, and neglect the Camerata.

Cambrian.—The primitive Inadunate: 5 simple arms, distinct from the cup; disk firmly plated with 5 Deltoids (Orals), supporting ambulacra above their conjoined edges (*cf.* *Hybocrinus*, xxxvi.). Slightly modified, this type survived among Ordovician Cyathocrinoids (*Porocrinus*, lxxxvi.): Anal plates (X & RA) present in the circlet of Radials; Posterior Oral, the only madreporite.

\* The stereotyped monocyclic constitution, sharply separated stalk, and late geological development of Blastoids suggest that this group may be composed, in reality, of *pædo-genetic Crinoids*, and it would be worth while to extend this hypothesis to some of the Cystids themselves.



Ordovician.—Dendrocrinoid modification. Arms still non-pinnulate, but dichotomously branched; the disk now flexible by interpolation of small plates between Orals and Radials, but Ambulacra remain suprategminal. Anals as before, supporting a great anal turret (xxvi.). Madreporite lost.

Silurian.—Dendrocrinoid arms forked and pinnulate (*Dendrocrinus*, iii.).

Devonian. } Dendrocrinoids lose RA, and then X from cup (*Graphio-*  
Carboniferous. } *crinus* and *Erisocrinus*, c); their arms become biserial;  
Infrabasals reduced and covered by stem.

Trias.—From Graphiocrinidæ arise Pentacrinidæ: cup (patina) shallow, the disk bulging up between the arms; no persistent proximal columnal as yet; stem cirriferous, its ossicles changing from round to pentagonal, with petaloid furrows and radiating ridges; no Anal; arms (again?) uniserial. Various members of the family swim about, and re-anchor themselves by distal cirri of stem. Obscurely leading to *Flexibilia Pinnata*, but exact links missing (cf. *Bathycrinus*, with bi-fasciate stem-ossicles, like *Bourgueticrinidæ* and *Antedonidæ*, figs. xlix., cxv.).

Jurassic.—The first “Pinnata,” with persistent proximal columnal and reduced Basals; stem-ossicles of modified Pentacrinid or Bathycrinid types. *Millericrinus* (no cirri) broke away from bottom of its stalk for swimming, the stem being slowly absorbed (lii.). *Thiolliericrinus*, the first Antedonid, with cirriferous compound Centrodorsal, fairly stout stem, and bifasciate joints of stem-ossicles.

Lias.—*Antedon* and later types break away from top of stalk early in life.

With this sketch of the adult ancestry of *Antedon* before us, let us now see how it is recapitulated in the ontogeny. Certain sequences of form-change take place in the same order. The larva on fixation exhibits successively an armless (“Cystid”) stage, and stages with simple arms, forked arms, and pinnulate arms respectively; the Oral plates at first are co-extensive with the disk, as in Blastoids\* and Cyathocrinoids, and then a peripheral growth-zone (perisome) is established between them and the Radials as in Ordovician Dendrocrinoids; an Anal plate appears within the circlet of Radials, rises above it and disappears, as in Carboniferous Dendrocrinoids; the Infra-Basals arise separately and then fuse with one another and the proximal columnal, marking the change from Dendrocrinoidea to *Flexibilia Pinnata*.

\* Another Blastoid or pre-Crinoid relic appears to be involved in the abortive attempt of the 5 primary tentacles to branch and grow as radial canals in the vestibulate stage, each peristomial tentacle (in spite of its lack of food-grooves and skeleton) representing a Blastoid brachiole. If Blastoid brachioles are homologous with Crinoid pinnules, the view that simple unbranched arms are primitive in Crinoids becomes untenable.



Now note the discrepancies. Except possibly in the anal interradius, there is no trace of præ-Cambrian irregularity in the number and arrangement of the skeletal plates, of the earlier acquisition of radial symmetry by the ambulaera and its later imposition upon the plates of the calyx; no sign of the derivation of the stalk by constriction of a pyriform base; no evidence of the oral plates having originally formed a solid disk, above the sutures of which the ambulaera ran. Except for certain additional dislocations to be referred to in a moment, it is just as in the development of the skeleton of a Vertebrate limb: the number of the skeletal elements is fixed from the beginning (even the pattern of the stem-joints) and ontogeny reveals no signs of their past history—with two exceptions: the migrations of the Anal plate and the composition of the Centro-dorsal. The former is a precious record of the change exhibited by the ancestral Dendrocrinoids, when, as arm-structure changed and flexibility increased, the diminishing anal chimney (fig. iii.) no longer required a buttress in the calyx wall to support it. But its retention in the ontogeny of *Antedon* is no proof of the normality of so precise a record of ancestral change: rather is it the exception which proves the rule of absence of such records. It is comparable with the "useless" notochord of the Vertebrate embryo. It has no part to play in the adult, because, as growth proceeds, the bases of the arms take over the main support of the body; but in the larva the patina is the sole support, and, as an Anal plate (and a Radial as well) was a constant inherited element of the cup through nearly the whole of Palæozoic time, it is scarcely surprising that it should be retained in that part of the life-cycle where it is still conceivably useful. On the other hand, it is squeezed out of the cup as soon as the anal tube, by remaining small, withdraws any demand for its retention, and when the flexible incorporation of the five arm-bases in the cup sets up a counter-demand for strict pentameral symmetry. This demand, so far as the Radial is concerned, has long since been met by the complete elimination of that plate from the ontogeny. "One thing at a time" is nature's rule. Similarly the ontogenetic history of the Centrodorsal is a physical necessity if one plate is to be made by the amalgamation of a number (*cf.* development of vertebræ, pore-plates of *Echinus*, &c.); and the other recapitulative features of the ontogeny (arm-development &c.) are examples of other necessities of differentiation, since you cannot get 2, except by duplicating 1. Adult recapitulation demands that the arm-branches should extend to the full length of the arms (as in Cyathocrinoids) before they reduce themselves alternately to the dimensions of pinnules. This they do not do. They take the shortest route to their goal, so far as constitution, not ancestry, will allow them.

But these discrepancies with phylogeny are trifles beside the phenomena of development of the Oral and Radial plates. In the whole series of adult ancestors from Cambrian times to the present, not one possessed Oral plates



which rested on the Basals; nor, if we overlook this developmental modification, did one of those ancestors in its adult condition ever possess Orals which were hinged to the Radials on the edge of the cup, capable of opening and shutting over the entire disk like the valves of a trap-door (Bather, fig. xxxiii.; MacBride, 1914, figs. 408-410). Where does the sure, frail "Ariadne-thread" conduct us now? If no fossil evidence were available, anyone who should attempt to reconstruct the ancestral Crinoid on the common embryological assumption that the stalked larva of *Antedon* represented an ancestral adult stage would go inevitably astray, as many have done already in spite of palæontological knowledge\*. For the remarkable thing is that several existing Crinoids possess an arrangement of oral valves in the adult precisely or closely similar to that of the larval *Antedon* (*Holopus*, l.c. xxxiv.; *Hyocrinus*, Sedgwick, 1909, fig. 209; *Thaumatoocrinus*, Carpenter, 1884, pls. iii., vi., lvi.). The relations of the oral plates in *Antedon* to the vestibular roof of the larva, as well as the temporary suppression of Radials, are clearly "cenogenetic" features. If a vestibule was a feature in the development of the earliest Crinoids, the oral plates must have been deposited beneath its floor, and not in its roof. Their relation to the roof (which alone enables them to split apart and function as valves) is an embryonic mutation. It is, therefore, scarcely open to doubt that the condition of the oral valves in the adult *Holopus* (and *Hyocrinus*?) is due to the retention of a feature that was purely embryonic, not adult, in origin, and that, in this respect, these interesting Crinoids are as "pædomorphic" as any Perennibranchiate Amphibian.

This brings me to my last point. When the common argument is urged that the stalked larva of *Antedon* "recapitulates" the adult stage of its stalked ancestors, it seems to be forgotten that every type of Pelmatozoan, from præ-Cambrian Cystids to the present time, must also have possessed a tiny fixed stage of simple structure following a free-swimming larval life, and that the main features of the skeleton must have been laid down in that, or a still earlier, stage of its ontogeny. It follows from what has been said that the modern Pentacrinoid larva of *Antedon* is a modification of the corresponding stage of the ancestral ontogeny, not of the adult stage, and that the adult *Antedon* is not an addition to the ontogeny of any preceding Crinoid, but just a modification of the adult phase of the same ontogeny—partly by loss (*e.g.* anal turret and plates, Oral plates, stalk, &c.), partly by

\* P. H. Carpenter (1884, p. 145) compared the vestibulate condition of *Antedon* with the Camerate condition of *Haplocrinus* (Bather, xxxv.) and the Platycrinidæ (l.c. xl.). It is a tempting suggestion, especially as the Carboniferous Platycrinidæ possessed bifasciate oval stem-ossicles. But these types are Monocyclic; the relations of the "Orals" are only superficially similar, and it is very doubtful if these plates are other than enlarged "proximal ambulacrals" (see Bather, pp. 127-129, and fig. xli.).



elaboration of pre-existing structures (arms, stem-ossicles). Nature does not build up a new type by addition or abstraction of "stages," but of organs, or parts of organs \*. Moreover, when she makes a change, she does not do so by altering these organs, or parts of organs, when fixed or rigid, but when plastic and growing. In particular cases this may be late in life, but it is not usually so, and it is not likely to have been so with respect to the patinal skeleton of the Crinoids under consideration. The Anal plate within the circlet of Radials is a feature inherited from earliest Silurian ancestors. It is claimed to "recapitulate" an adult feature of those ancestors. I submit that no Anal or other plate was ever interpolated within the patina except in the formative stage of growth when the Radials themselves were loose and unsutured. The first Anal plate that entered the Radial circlet from the disk (if that was its origin) must have done so as the result of an embryonic, not an adult, mutation. Once let the towering anal chimney of an adult Dendrocrinoid (*cf.* Bather's fig. iii.) effect a breach in the wall of the patina, and the whole cup would split asunder. Nature underpins when it is safe to do so. She usually builds the foundation first and the superstructure afterwards.

16. The following summary, omitting illustrative detail, recapitulates in closer logical sequence the chief points of this attempt to re-define the foundations of Morphogenetic Law.

#### RECAPITULATION.

- I. Ontogeny is the sequential expression of zygotic powers of cell-division through simple to complex grades of cell-grouping and differentiation.
- II. Phylogeny is the procession of ontogenies along a given phyletic line of modification. It is expressed in terms of adult structure, but the zygotes of successive ontogenies have also undergone a parallel elaboration of nuclear or cytoplasmic structure, or of both, which determines the sequence of the ontogenetic form-changes.
- III. The phyletic succession of adults is the product of successive ontogenies. Ontogeny does not recapitulate Phylogeny: it creates it.
- IV. An individual confronts the world before his ontogenetic processes are completed, and often at a very early period of his life-cycle. Only those individuals reproduce who have survived the ordeal of larval conditions. Adaptation of the larva accordingly plays a prime part in determining the modification of successive ontogenies.

\* *Cf.* Weismann (1904, ii. p. 174): "... it is impossible to compare a particular *stage* in the embryogenesis of a species with a particular ancestral form. Only the stages of *individual organs* can be thus compared and parallelized."



- V. The life-cycle is extended, not by addition of a new adult stage at the end of the old adult stage, but by further differentiation of organs or parts of organs. Old adult characters are eliminated from the ontogeny unless required as temporary bases for the new characters.
- VI. As the individual, through all the form-changes of his life-cycle, is an evolutionary and functional unity, modifications manifested in his larval or adult phases involve co-ordinating changes in the more passive and formative phases (embryonic, post-larval, pupal stages).
- VII. Thus, while a given ontogeny, under normal conditions, tends to repeat the form-sequences of its predecessors, it is liable to changes in every part of the life-cycle—positively, by equipping the larval and adult stages for the changing conditions of their various careers, or with greater efficiency for the same conditions, and negatively, by abbreviating the formative processes to the uttermost.
- VIII. The idea that form-changes in ontogeny were preceded by similar changes in adult ancestry is an illusion, since adult Metazoan ancestors never directly gave rise to their successors, but to gametes; and these, blended with other gametes, were the real heralds of successive ontogenies. Plainly the first Metazoan was not produced by a Metazoan. He was the result of a Protozoan ontogeny, the *tour de force* of a genius among Protozoan zygotes. The first Bird was hatched from a Reptile's egg. We can speak of earlier and later, original and modified, ontogenetic processes; but the possibility of a distinction between ancestral and ontogenetic processes is out of the question. All changes are ontogenetic.
- IX. In the same way the contrast between "palingenetic" (repetitive of adult ancestry) and "cenogenetic" (foreign or non-repetitive) characters, which was originally based by Haeckel on an assumed hereditary difference between adult changes and embryonic adaptations, has lost its significance. Both types of character were of ontogenetic origin, and equally hereditary, but the one set arose earlier in the phyletic history than the other. Morphology will not recover exactitude of outlook until it is entirely freed from the hypnotic influence of Haeckel's terminology. I propose in future to use *palaeogenetic* and *neogenetic* when referring to ontogenetic processes, and *palaeomorphic* and *neomorphic* when contrasting primitive and modified types of structure.
- X. There is a general correspondence between the successive grades of differentiation in ontogeny and the successive types of organisation which characterise the steps of phyletic progress (Meckel's law). This general correspondence exists because each series—the ontogenetic and the phyletic—was preceded and caused by the same



phylogenetic series of ontogenies. The outcome of each successive ontogeny was an adult representative of one of the successive types of organisation. The last ontogeny of the whole series is the one under consideration. Inevitably there is recapitulation of successive grades of differentiation, but repetition of adult ancestral stages is necessarily and entirely lacking. Ontogeny is not an animated cinema show of ancestral portraits; but zygotes may be likened to conjurers playing the old tricks for the most part, and occasionally opening a surprise packet—nor do they always keep their novelties back until the end of the performance, as *Antedon* and *Holopus* bear witness.

In other articles I propose to deal with the origin and significance of larval forms, and to draw attention to some further examples of the influence of larval characters upon adult organisation, to which I apply the term “Pædomorphosis.”

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