On the Law of Development commonly known as von Baer's Law; and on the Significance of Ancestral Rudiments in Embryonic Development.

By

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The generalisation commonly referred to as v. Baer's law is usually stated as follows:—Embryos of different members of the same group are more alike than the adults, and the resemblances are greater the younger the embryos examined. It appears to be pretty clear that v. Baer held some such view as this,[1] and there can be no doubt that it is a view which is largely taught at the present day.[2] In fact, I think it is safe to say that all zoologists are brought up with this view as one of the fundamental postulates of their science.

It will be the object of the following pages to show that this view is not in accordance with the facts of development. V. Baer based his view mainly upon the study of Vertebrate embryos; and it will be convenient for us, in criticising him, to begin with an examination of this group. We may also, in the first instance, follow v. Baer in another point, viz. in limiting ourselves to the consideration of *embryos* as opposed to *larvæ*. Embryonic development and larval development take place under entirely different conditions, and in order to obtain clear ideas they must be considered apart in treating

[1] *Vide* 'Ueber Entwickelungsgesch. d. Thiere,' part i, pp. 221, 223, and 224.

[2] *Vide* Darwin in 'Origin of Species,' p. 364, 6th ed.; and Balfour 'Comp. Embryology,' vol. i, p. 2.

this subject. They have not as a rule been clearly distinguished, and facts based on a study of larvæ have sometimes been assumed to hold true for embryos without further examination; and this practice has, as I hope to show, given rise to errors which have prevented our arriving at a clear understanding of the subject.

It is, of course, impossible to examine fully all the stages of all Vertebrate embryos. In the comparison necessary for the criticism I am making it will be convenient to limit ourselves to typical cases, and I propose to consider (1) the embryos of animals widely divergent ; (2) the embryos of animals which are closely allied in the adult state. If it is found that in neither of these cases is the law of v. Baer followed, then I think we may reason that there is, to say the least of it, a strong probability that it will be found not to hold true for intermediate cases.

(1) Embryos of divergent classes of the Craniate phylum. The examples I have chosen are the fowl and dog-fish.

The fowl and the dog-fish in the adult state live under entirely different conditions; whereas in the embryonic phases the conditions are very similar, both being developed within an egg-shell at the expense of ovarian yolk and surrounding albumen.

According to the law of v. Baer these embryos ought to be closely similar in the young stage.

Do these embryos, developing under similar conditions, conform to the law? Superficially, clearly not. There is no stage of development in which the unaided eye would fail to distinguish between them with ease—the green yolk of the one, the yellow yolk of the other; the embryonic rim and blastopore of the fish, the absence of these in the chick; the six large gill-slits bearing gills on the one hand, the four rudimentary clefts on the other; the small head, straight body, and long tail, as opposed to the enormous head, cerebral curvature, short tail, and so on. A blind man could distinguish between them.[1] These embryos are not closely similar,

[1] I do not feel called upon to characterise the accuracy of the drawings of

but it is maintained that the law is justified by certain remarkable features of embryonic similarity which the adults do not exhibit, and of which the most important are the presence in the chick of pharyngeal clefts, a tubular piscine heart, and a similarity in the arrangement of the cardiac arterial system, a cartilaginous endo-skeleton, oro-nasal grooves, and a notochord. Now I freely admit that these are striking similarities, but I question whether they are sufficient to justify the law of v. Baer. By themselves, no doubt, they would be sufficient to justify that law; but are there no differences to set off against them? Are there no differences of a morphological value, as far-reaching and as striking as these similarities? Let us clearly understand the question at issue. V. Baer's law, as applied to the present case, may fairly be held to mean, if it has any meaning at all, that whereas the differences between the adults are large and important differences of class value, the differences between the embryos are slighter and unimportant, and of less than class value. Now in no single member of the group Craniata is the mesoderm of the head segmented. According to our present morphological knowledge, the discovery of an animal with cranial segments would be a very remarkable one, and would, we might confidently predict, require the establishment of a class at least separate from all other Craniate classes—such is our estimation of the importance of this feature. And if to this character was also added the presence of a cœlomic sac close to the eye, of another in the jaw, and of a third near the ear; of an aperture of communication between the neural canal and rectum, of kidney tubules opening into the muscle-plate cœlom as well as into the perivisceral cœlom, of a Müllerian duct opening into the front end of the Wolffian, I do not think that any anatomist would have any doubt about the matter. Now it is precisely in these points, amongst

embryos of different classes of the Vertebrata given by Haeckel in his popular works, and reproduced by Romanes and, for all that I know, other popular exponents of the evolution theory. As a sample of their accuracy, I may refer the reader to the varied position of the auditory sac in the drawings of the younger embryos.

others, that the embryo dogfish differs from the embryo chick. I am quite aware that arguments tending to reduce the classificatory value of the embryonic differences I have just enumerated might with more or less plausibility be adduced. But one thing at a time. I am at present dealing solely with the importance of the anatomical resemblances and differences between the embryos; and I think I have shown, as far as it can be shown, that they have, if judged by standards used when comparing adults, at least as great an importance as the resemblances between the same embryos—the differences, like the resemblances, relating solely to the embryos, and not existing in the adults. V. Baer's law then falls to the ground, and must be replaced by another law, which is as follows:—Embryos of different members of the same group often resemble one another in points in which the adults differ, and differ from one another in points in which the adults resemble; and it is difficult, even if possible, to say whether the differences or the resemblances have the greater zoological value (because we have no clearly defined standard of zoological value).

It will probably be urged here by my reader—Are you not beating the air in a vain warfare of words and unessentials of which we were all aware, and trying to kick up a cloud of dust by which to obscure the essential point, viz. that embryos pass through, incompletely if you like, stages of structure permanent in lower members of the same group? To such a one I reply, that I am as keenly alive to the importance of the essential point as he is, but that I differ from him in being dissatisfied with the explanation which is at present given of it, and that I am convinced that the form in which this phenomenon is referred to in v. Baer's law has led to the acceptance of an imperfect explanation of the embryonic phase in animal development.

(2) But before I come to that point I have to consider the case of the embryos of closely allied animals. If v. Baer's law has any meaning at all, surely it must imply that animals so closely allied as the fowl and duck would be indistinguishable in the early stages of development; and that in

two species so closely similar that I was long in doubt whether they were distinct species, viz. Peripatus Capensis and Balfouri, it would be useless to look for embryonic differences: yet I can distinguish a fowl and a duck embryo on the second day by the inspection of a single transverse section through the trunk, and it was the embryonic differences between the Peripatuses which led me to establish without hesitation the two separate species. But it is not necessary to emphasise further these embryonic differences; every embryologist knows that they exist and could bring forward innumerable instances of them. I need only say with regard to them that a species is distinct and distinguishable from its allies from the very earliest stages all through the development, although these embryonic differences do not necessarily implicate the same organs as do the adult differences.

If I have laid great stress—some may think undue stress—upon the inadequacy of v. Baer's law, I have done so because of the importance which is at the present day attached to this law by teachers of zoology. In support of this, I may quote the words of three of the greatest teachers of zoology of this or of any other age—words which show that they at any rate considered that the law correctly represented the facts.

Darwin, in the 'Origin' (p. 387, 6th ed.), says:—"So again it has been shown that generally the embryos of the most distinct species belonging to the same class are closely similar, but become, when fully developed, widely dissimilar. A better proof of this latter fact cannot be given than the statement by v. Baer that the embryos of Mammalia, of birds, of lizards, and snakes, probably also of Chelonia, are in their earliest states exceedingly like one another, both as a whole and in the mode of development of their parts; so much so, in fact, that we can often distinguish the embryos only by their size. In my possession are two little embryos in spirit, whose names I have omitted to attach, and at present I am quite unable to say to what class they belong. They may be lizards or small birds, or very young Mammalia, so complete is the mode of formation of the head and trunk in these animals."

This, I think, shows quite clearly Darwin's view of the matter.

Huxley, in his 'Man's Place in Nature,' says:—"The history of the development of any other Vertebrate animal—lizard, snake, frog, or fish—tells the same story. There is always, to begin with, an egg having the same essential structure as that of the dog; the yolk of that egg undergoes division or segmentation, as it is called, the ultimate products of that segmentation constitute the building materials for the body of the young animal; and this is built up round a primitive groove, in the floor of which a notochord is developed. Furthermore, there is a period in which the young of all these animals resemble one another, not merely in outward form, but in all essentials of structure, so closely, that the differences between them are inconsiderable, while in their subsequent course they diverge more and more widely from one another."

The Significance of Ancestral Rudiments in Embryonic Development.

The existence of a phase at the beginning of life during which a young animal acquires its equipment by a process of growth of the germ, is of course intelligible enough. We see such a phase in the formation of buds, and in the sexual reproduction of both animals and plants. The remarkable point is that while in most cases this embryonic growth is a direct and simple process—e.g. animal and plant buds, embryonic development of plant seeds—in some cases—e.g. most cases of sexual reproduction of animals—it is a circuitous one, and the embryonic phase shows stages of structure which seem to possess a meaning other than that of being merely phases of growth.

As is well known, the explanation which is given of this circuitous course of embryonic development is that we are dealing with a special case of the law of heredity—"each organism reproducing the variations inherited from all its ancestors at successive stages in its individual ontogeny" ('Comp. Emb.,' vol. i, p. 3).

"These two principles, namely, that slight variations generally appear at a not very early period of life, and are inherited at a corresponding not early period, explain, as I believe, all the above specified leading facts in embryology." (Darwin, 'Origin,' p. 392, ed. vi.)

But this explanation, though good as far as it goes, is not entirely satisfactory, because it fails to explain (without further qualifications) the majority of cases (animal and plant buds, embryonic development of seeds) in which ontogeny presents no ancestral traces; it is at variance with the fact that in many cases variations which affect the adult have affected the whole of embryonic development (see below); and it does not enable us to understand why some organs, e.g. gill slits, have been retained in embryogeny, whereas other organs which have much more recently disappeared, e.g. teeth of birds, fore-limbs of snakes, have been entirely lost. It assumes that the repetition of ancestral characters in embryogeny is the intelligible rule; and that their omission is the exception which requires explanation whenever it occurs. This assumption is not warranted by the fact above indicated that in the vast majority of ontogenies there are no phylogenetic traces, nor by the consideration that a number of important organs, such as teeth and hand-claws in birds, limbs in snakes, gill-clefts in fishes, have recently disappeared without leaving a trace in ontogeny.

In fact the balance of evidence appears to me to point most clearly to the fact that the tendency in embryonic development is to directness and abbreviation and to the omission of ancestral stages of structure, and that variations do not merely affect the not-early period of life where they are of immediate functional importance to the animal, but, on the contrary, that they are inherent in the germ and affect more or less profoundly the whole of development.

I am well aware that in holding this opinion I am running counter to the great authority of Darwin. In the chapter from which the above quotation was taken he gives many facts and arguments in favour of the view that slight variations generally appear at a not very early period of life, and are inherited at a corresponding not early period. He admits that larger variations—monstrosities—do affect the embryo at a very early period, but he thinks that slight variations do not. Without considering the difficult question as to where the line should be drawn between a slight variation and a monstrosity, I may merely point out that Darwin's evidence is largely based upon the experience of breeders that it is impossible to tell until some time after birth what will be the merits or demerits of their young animals. In mitigation of the force of this fact it must be remembered that a successful breeder is a highly skilled man—that he possesses powers of observation greater than the ordinary—that his success depends upon his ability to see points which escape the eye of other people. If the points for which the mature animal is selected are thus difficult of observation, can we wonder if it is beyond the power of man to see them when the animal is immature, and the relative sizes of the parts of the animal, and its whole appearance, are so different? In support of this way of looking at the matter I would urge that when the variation is large and of a nature to be easily observed, it can—in a great many instances at any rate—be detected all through development.

The evidence is of this kind :—(1) Organs which we know have only recently disappeared are not developed at all in the embryo. For instance, the teeth of birds, the fore-limbs of snakes, reduced toes of bird's foot (and probably of horse's foot), the reduced fingers of a bird's hand. These are instances which readily occur; I have no doubt that many others might be quoted by anyone giving attention to the matter. (2) Organs which have (presumably) recently become reduced or enlarged in the adult, are also reduced or enlarged in the embryo. Many examples of this might be given, and it is a most important point as showing the manner in which variations have affected the whole of embryonic development. As examples I may mention the small outer toes on the feet of the pig and probably of other Ungulates, the large digit of the ostrich's foot and of the kangaroo's foot, the spiracle of Elasmobranchii,[1] the rudimentary character of the phalanges of the bird's hand. I have no doubt that many other instances will occur to my reader. (3) Organs which have been recently acquired may appear at the very earliest possible stage; e.g. the double hallux present in some breeds of fowls makes its appearance as soon as the other digits; the webbing of the duck's foot is not preceded by a stage in which the digits are separate. In short, the evidence seems to indicate that in a great number of cases adult variations of any part are accompanied by precedent similar alteration of the same part in the embryo. I do not mean to affirm that the alteration of the organ in

[1] The spiracle of Elasmobranchii is a reduced gill-cleft, and in correspondence with its reduction in the adult it is found to be reduced also in all stages of its development from its very first appearance, which takes place after the hyobranchial cleft—not before it, as would be expected from its position as the anterior member of a series (see Self, "Notes on Elasmobranch Development," this Journal, vol. xxxiii, p. 572). It would be excessively interesting in this connection to ascertain whether any trace of the spiracle is present in the embryos of those Elasmobranchs in which it is absent in the adult. In fact, an account of the spiracular cleft throughout the Vertebrata is much needed. Is it present in embryo in Teleosteans and in Lepidosteus? Balfour asserts that it is present in the former ('Comp. Embryology,' vol. ii, p. 77, mem. ed.), but I am unable to find his authority for the statement. He also states that it is present in the embryo Lepidosteus as a double layer of cells without a cavity (Balfour and Parker on 'Anatomy and Development of Lepidosteus,' mem. ed., pl. xxxvii, fig. 43), but, so far as I am aware, his interpretation of this structure has not been confirmed. In Amniota—throughout which the pharyngeal clefts present a very remarkable constancy—the spiracular cleft is as large, if not larger, than the succeeding one, and appears first in development. This is an exceedingly interesting fact, which has not been sufficiently noted. It tends to show that the Amniota have arisen from aquatic forms independently of the terrestrial Amphibia, in which group the spiracular cleft is not formed at all—though a slight rudiment of it does appear for a short period. In fact, we may take it as a fact of systematic value that the spiracular cleft is absent or rudimentary in all Ichthyopsida while it is present in relatively normal development in all Amniota.

the embryonic stage[1] is the same as it is in the adult. It may be altered relatively more or it may be altered relatively less; the point is that it is altered in the same direction as the adult organ. And this is surely what we should expect when we remember that embryonic development is the preparation of the free form in the most perfect state and at the least expense. If this view is correct that variations are present in the embryo—that an organ which is enlarged, diminished, or suppressed in the adult is correspondingly, or nearly so, enlarged, diminished, or suppressed in the embryo,—then I ask, how are we to account for those cases which most undoubtedly occur in which records of previous states of structure are present in the embryonic history, e. g. the pharyngeal slits of Sauropsids, the tubular heart, the vascular arches, the embryonic kidney of the same group, and many such. The point is this: organs which have been recently altered show a similar alteration in the embryo, whereas some organs, like the gill-slits, which must have been altered very far back, do not show a corresponding embryonic alteration, but persist more or less in their old form without discharging the original functions or being of any use to the embryo. In other words, some ancestral organs persist in the embryo in a functionless rudimentary (vestigial) condition and at the same time without any reference to adult structures, while other ancestral organs have disappeared without leaving a trace. The latter arrange-

[1] It appears that in some cases, at least, it is less in the embryo. E. g. sternal ribs of ostrich are generally five in adult, rarely six; in embryo, they appear always to be six. In birds the fibula reaches the tarsus in embryos, but very rarely does so in adults.

A case of this kind which might be investigated is this:—In the golden plover the hallux is entirely absent, whereas in other plovers it is present. Has the golden plover any trace of it in the embryo?

I am aware that it is often held—Darwin held it—that rudimentary organs are, relatively to the adjoining parts, larger in the embryo than in the adult. But unless this fact can be shown to be universal, it has but little value because it applies to many other organs in the embryo which are not rudimentary, e. g. brain, eye, heart, and kidney. This difference in relative size is probably simply owing to the fact that the bulk of the skeletal, muscular, and connective tissues of the embryo is relatively less than in the adult.

ment seems to be the rule, the former the exception. How are we to account for the exception? The key to the position is, in my opinion, to be found by comparing the conditions of larval and embryonic development. In larvæ the organs are functional and the animal is getting its own living during the development, whereas in embryos the development takes place under the protection of egg membranes, the pupal case, or the uterine wall, and the organs are for the most part functionless, special arrangements being made for the supply of nutriment. These two developments have generally not been properly distinguished by naturalists writing on this subject.

In embryos the organs are for the most part functionless and without relation to the maintenance of life; consequently there is nothing to counteract the tendency to the appearance of a variation at all stages in the life of an organ. In larvæ, on the other hand, the organs are functional and the conditions of life may be different from those of the adult. They have to maintain themselves during the various phases of their development; consequently if a variation of an organ at one stage is injurious to the same organ at a previous or subsequent stage, it will be eliminated at the stages at which it is injurious. In this way, as will be readily seen, natural selection will compel the limitation of variations in an organ to particular stages in the development of that organ; the power of natural selection will inevitably prevent a variation useful at one stage from affecting another stage of the same organ in which its presence would be injurious to the larva. Thus there must be in larvæ a tendency to the inheritance of variations at corresponding periods, and to the elimination of them at other periods when they would be harmful to the organism. Thus it must happen that if variations occur which enable the adult to change its condition of life, and if at the same time the old habits of life are retained by the last larval stage, then the old arrangement of organs will be retained by the larva. In this way, as the adult form gradually progresses in evolution, not only one but a whole series of larval stages might become established, each one being based upon some ancestral stage of structure and retaining some ancestral habit of life. But of course these larval stages are liable to vary and are subject to the natural selection engendered by the struggle for life. So they may themselves become modified and the ancestral habits and structure which they have inherited may also become modified. It thus becomes apparent that larvæ will often retain traces more or less complete of ancestral stages of structure, and that they will do this in virtue of the operation of the force of heredity and of natural selection. And the retention of ancestral features by the larvæ will be the more complete the more completely the ancestral habits of life are retained by them. There is, then, in larvæ a tendency to the inheritance of variations at corresponding periods, and in this respect larvæ differ from embryos.

To sum up, I would maintain that ancestral stages of structure are only retained in so far as they are useful to the free-growing organism, i. e. to the larva in its free development. Or, to put the matter in another and more recondite form, modifications appearing in and affecting the adult structures will similarly affect the same structures all through the development of the offspring unless the old structural arrangements are called into being in the development of the offspring by the application of the old stimulus, viz. the same external conditions of life.

In embryos, on the other hand, the organs are for the most part functionless, and there appears to be no reason for the retention of ancestral conditions of structure. On the contrary, as I have shown above, most organs when modified in the free-living state are similarly modified in the embryo. And, as I have already insisted, this is what we should expect when we remember that embryonic development is the preparation of the free form in the most perfect state and at the least expense. How is it, then, that we do get in embryos in certain cases a most remarkable preservation of ancestral organs and conditions of structure which have been lost in the adult? I think it can be shown that the retention of ancestral organs by the larvæ after they have been lost by the adult is due to the absorption of a larval or immature free stage into embryonic life.

Let us take an example. Let us try to picture to ourselves the steps by which the tadpole stages of the frog might be lost, so that the adult frog arose direct from the egg. The larval organs of a tadpole cannot disappear one by one independently of one another. If the gill slits disappeared before the heart had become double and the lungs had developed, the tadpole would die of asphyxia. In order to completely obliterate the piscine stage from the tadpole, you require a number of nicely co-ordinated variations affecting different organs in very different ways—all tending to the atrophy of those organs which adapt it to an aquatic life and to the development of the organs required for terrestrial life. Such a combination of suitable variations as is here required—such an inversion of the original evolutionary changes —is very unlikely to occur,[1] especially when the same object can be obtained, namely the obliteration of the piscine phase in the frog's life, by a simple single variation—that is to say, by the mother becoming viviparous and retaining its young within its uterus or oviduct until the piscine stage of development has been passed through; or by the ovarian ovum developing a greater amount of yolk, so that the whole development up to the close of the piscine stage can take place before hatching at the expense of the yolk. That larval stages do disappear and embryonic stages arise in this way is shown by the case of the viviparous salamander (Salamandra atra), in which the gills, &c., are all developed but never used, the animal being born without them. Here, therefore, is an actual case in which the larval phase has disappeared by becoming embryonic and therefore functionless, and therefore largely removed from the direct action of natural selection; once em-

[1] It has suggested to me here that this combination of variations must have taken place in phylogeny, otherwise the terrestrial animal could not have been evolved; why not then in the larva? To this I reply: there is no necessity for the long and laboured changes to be gone over again in inverted order in the case of the tadpole, because the object can be obtained by the simple inclusion of the tadpole stage within the embryonic period.

bryonic only, the conditions of its existence are totally altered. Its disappearance is no longer a matter of importance to the organism, because the embryo being protected from the struggle for existence the presence of rudimentary functionless organs is unimportant to it. They therefore persist, and it is this persistence which has given rise to von Baer's law. But von Baer's law is imperfect, because it omits to take cognisance of the fact that embryonic features are no more constant than are the adult characters; that indeed they vary with the adult characters, so that no adult character is changed without some precedent alteration of all the previous embryonic phases. The embryonic life is a connected whole, and it is impossible that an isolated alteration of one particular stage can have taken place. All variations must run through the whole development; they may come out strongly at one particular stage, but they must have been led up to and followed by variations in all other stages.

Embryonic variations are not for the most part acted upon by natural selection, because they concern rudimentary organs only; but when free life is reached, and the organs become functional, the same variations continued (for continue they must) are put to the test, and the organism stands or falls by them. The constancy of development in the same species proves this point; for if the embryonic stage could vary without the free stages being at all affected, then, as natural selection does not act upon rudimentary embryonic organs, the embryonic organs would run riot, and we should expect to find the greatest diversity in embryonic development of the same species, and this we do not find; and this applies not only to organs which persist into the adult, but also to organs which disappear before the adult stage is reached. These purely embryonic structures must have some nexus with structures which succeed them in development, and a variation in them must be accompanied by variations in these later appearing persistent organs. In fact, it seems to me most important to remember that the various stages in the development of an animal are just as much correlated as are the different organs of the adult animal with one another. I repeat, the constancy of development in the same species proves this point, as do the small but constant differences between the embryonic phases of slightly different but distinct species.

Granting that embryonic rudiments do vary, of which I do not think there can be any doubt, then it would appear that the variations must be selected, not with regard to their intrinsic[1] merits at the moment as is the case with variations in functional organs, but with regard to the effect of their descendent or correlated variations in the adult. So it comes about that the embryonic rudiments in one group of animals, though resembling generally those of another group of the same class or phylum (just as the functional adult organs resemble one another generally), yet differ from them in minor points, so that the group has its own individual character with regard to that particular rudimentary organ, just as it has its own individual character with regard to any adult functional organ.

The conclusion here reached is that, whereas larval development must retain traces (it may be very faint) of ancestral stages of structure because they are built out of ancestral stages, embryonic development need not necessarily do so, and very often does not; that embryonic development, in so far as it is a record at all, is a record of structural features of previous larval stages. Characters which disappear during free life disappear also in the embryo, but characters which though lost by the adult are retained in the larva may ultimately be absorbed into the embryonic phase and leave their traces in embryonic development.

[Throughout the above discussion I have, to avoid complication, treated all embryonic organs to be functionless; but it

[1] By intrinsic merits at the moment, I mean the effect on the organism as a whole at any particular moment. A variation in a rudimentary functionless organ of an embryo can have no effect upon the welfare of the embryo (excluding secondary effects—if any—of interfering with functional organs, e. g. blood-vessels); its utility can only be judged when the free state is reached.

must not be *forgotton* that some of them are functional and that these resemble organs of larvæ in retaining ancestral features, e. g. the ductus arteriosus, &c.]

To put the matter in another and more general way, the only functionless ancestral structures which are preserved in development are those which at some time or another have been of use to the organism during its development after they have ceased to be so in the adult. In this way I should be inclined to explain the hair of the human fœtus and the teeth of the fœtal whale—that is to say, I should be inclined to suppose that the possession of the lanugo is due to the fact that there was a time in the evolution of man when the babe required this protection against the cold after the necessity for it had disappeared in the adult, and that the young whale in the days when whalebone was first acquired still retained the ancestral habits which required teeth. It is, however, possible that these and other similar cases of the retention of rudimentary organs in late embryonic life have another explanation, and it becomes necessary to collect and examine as many cases as possible of the undoubted retention, as embryonic rudiments, of organs which we have reason to know have recently disappeared from the adult stage.

The retention of such organs in the embryo may, as I have hinted, be due to the fact that they have been retained functionally by the young animal after they have been lost by the adult; but another explanation is possible, which is that organs which are becoming functionless, and disappearing at all stages, may in some cases disappear unevenly; that is to say, they may remain at one stage after they have totally disappeared at another. In this manner we might get an organ which had become quite functionless and had quite disappeared in the free stage, still persisting, though with a much reduced development, in the embryo. It is possible that the lanugo and the teeth of fœtal whales may be explicable in this manner. But that such a retention of organs in the embryo is not an important or permanent one is shown by the fact of their comparative scarcity in embryonic histories. This is a most important subject, and I propose in a future paper to collect and examine as many cases as I can find of the retention in the embryo of organs which have lately disappeared in the adult.

There is another aspect of the same question which is suggested by the above considerations, viz. if an organ can disappear unevenly there is no reason in the nature of things, so far as I can see, why it should not disappear in its devoloping embryonic stages before it does so in the adult, so that there would still be found in the adult a persistent useless rudiment of it after all trace had gone in the embryo. And we may even go further than this, and maintain that if organs can disappear unevenly it is conceivable that traces of an ancient organ might appear and disappear more than once in the course of development. Of the last-suggested phenomenon I know of more than one instance, but I know of no instance of an organ disappearing in its embryonic stages while still persisting as a rudiment in the adult. As an example of the repeated appearance and disappearance of a rudimentary organ in embryonic development I may mention the neurenteric canal of certain species of birds as described by Gasser,[4] and quoted by Balfour in the 'Comparative Embryology' (vol. ii, p. 162, mem. ed.). The anterior neuropore of Ascidians, which appears twice in the development, is another example of the same phenomenon. Although I know of no instance of an organ disappearing in the embryo before it totally disappears in the adult, I do know of instances of rudimentary embryonic organs which have disappeared in their earlier stages while still present at a later stage, e.g. the muscle-plate cœlom of Aves, the primitive streak of Amniote blastoderms, and the neurenteric canal of Aves; and I have no doubt that many instances of this might be collected.

From the application of the principles set forth in the preceding pages it becomes apparent to us why it is that in the

[1] Gasser, "Der Primitivstreifen bei Vogelembryonen," 'Schriften d. Gesell. zur Beförd. d. gesammten naturwiss.,' zu Marburg, vol. ii, sup. 1, 1879.

higher animals it is the early stages of development which have the greatest interest for us, the later stage having been added at a time when, as now, the immature stages of free life were but little marked, and consequently there was but little chance of the incorporation of any ancestral features in the embryonic development. It also helps us, I think, to understand why the most interesting of the ancestral embryonic features were related to the passage from the aquatic to the terrestrial condition, because when this took place in phylogeny there must have been a most pronounced aquatic larval stage, such as we find to-day in Amphibia.

Appendix.

Mr. J. J. Lister has pointed out to me as confirmatory of the views set forth in the preceding pages that there is at least one exception to the rule that animals produced by budding show no ancestral rudiments in their development, viz. the sexually mature medusoid spore-sacs. These organisms present in their development traces, as is well known, of many organs which they must formerly have possessed in a functional condition, e. g. the umbrella cavity, the marginal tentacles, the circular canal, &c.; but, as Mr. Lister points out, these spore-sacs differ from other buds in this important fact that they have most undoubtedly had quite recently a free life during the maturation of the generative products; and it may be that it is the impress of this ancestral free life which has given rise to the ancestral features in the development.