

The Fœtal Membranes of the Vertebrates.

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By

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I WAS honoured by the request of the Executive Committee to give an address at the first meeting of the Embryological Section of the Seventh International Zoological Congress.

I hope that in choosing for my subject the present state of our knowledge concerning the fœtal membranes of vertebrates I can avoid the disadvantages of too much special detail, and can at the same time call your attention to the fact that these fœtal membranes offer a very wide field for theoretical speculation, that may in its turn influence our views concerning certain important phylogenetic problems.

The fœtal membranes of vertebrates are known to occur in reptiles, birds, and mammals. The embryological hand-books tell us that they are absent in amphibians and fishes.

In consequence, a primary subdivision of the vertebrates has been instituted, those with fœtal membranes being classed as Amniota allantoidea, those without them as Anamnia analantoidea. From this nomenclature any close observer, even when he is not a zoologist, may safely conclude that one of the fœtal membranes carries the name of amnion, the other

¹ At Professor Hubrecht's request this address is here reprinted. It will assist readers in apprehending the conclusions which Professor Hubrecht holds to be rendered probable by the large memoir published in this Journal in November, 1908.

the name of allantois. An older, now more obsolete, subdivision into Achoria and Choriata reveals the presence of a third membrane, the chorion, about which we will have more to say hereafter, and which will explain how this third membrane came to fall—so to say—between two stools, when the division into Amniota and Anamnia was established.

If we now take into account that neither chorion nor amnion nor allantois was ever detected in fishes or in amphibians, then we must recognise that the problem, how these foetal membranes of the vertebrates did arise, is one well worthy of full consideration.

Up to now attempts to explain their gradual evolution have utterly failed. So, for example, the suggestion of van Beneden and others that the amnion, as a protective membrane, arose in consequence of the early embryo sinking into the yolk-sac, which closed up above it, has long since been abandoned. Also Haeckel's idea that the allantois arose by a precocious segregation of the urinary bladder of an early amphibian which took the habit of carrying blood-vessels, at a very early stage, to the outer wall of the blastocyst, must be dropped by all who object to predestination in evolutionary processes. Whenever an explanation offers itself which does afford a clue to a more logical sequence of events, it should be preferred.

And turning finally to the outer layer, the chorion, who can be satisfied with the lame explanation that the appearance of this membrane is a necessary sequel to the formation of the amnion, which we find inside of it, and which later, in so many orders of mammals, never even arises by folds, which, however, in their turn are necessary to explain the chorion's appearance?

The subsidiary explanation of all the three embryonic envelopes, which I am going to offer you on this occasion, seems to me to have the great advantage of simplifying matters; especially in this sense, that henceforth we can link them all three to one simpler and earlier stage (which must have preceded in the Carboniferous and in earlier geological

epochs) without having to look for incipient stages of any of them among our present ichthyopsids. Nay, we may even say that of this earlier, archaic starting-point evident traces have been preserved in the teleostomes, the dipnoi, and the amphibians, so that we have to reconsider most seriously whether it will be wise to go on subdividing the vertebrates into the two subdivisions of those that have and those that have not the foetal envelopes above mentioned.

Now let us consider the facts as they present themselves to us, when we want to test the question whether one single original foetal envelope could not after all be at the bottom of the three complicated involucra we have just mentioned. As far as I can see, we are only in need of this one assumption, that an invertebrate ancestor was possessed of what we call an exterior larval layer (such as are not uncommon among different worms, and as we find them, with certain further complications, in some arthropods), to be able to explain how, in their vertebrate descendants, chorion, amnion, and allantois gradually came into being.

Part of this hypothetical assumption we see actually realised under our eyes wherever one of the mammals goes through its normal stages of development.

We find that the cell-material out of which the embryo is going to be built up is surrounded by an expanded cell-layer, which takes no part whatever in the composition of the future embryo. Here we actually have our single larval layer that will be stripped off later, and that surrounds what are going to be the formative cells.

In all mammals it is this very larval layer which will become the outer wall of the blastocyst, what we have above called the chorion.

But before following it in its further transformations, we have to ask ourselves, what can be the reason that this outer larval layer, this trophoblast, is so far away from the formative cells of the embryo which adhere to it only at one point?

We have only to recall the fact of the pilidium larva, in which, similarly, the distance between the outer layer and the

cell-material, which is going to be the new worm, is also very considerable, to remove the objection that in this respect mammals would stand isolated. And we may go one step further and say that it is easy to understand why this considerable extension of the outer larval layer has come into existence. When we look back along the line of phylogenetic descent we can imagine that at the period when, for the first time, aquatic animals became inhabitants of the land, four-footed instead of four-finned, and adapted for aerial breathing in addition to their respiration by the aid of gills, it may have been a great advantage to them to become viviparous at the same time, i. e. to keep their developing eggs inside of them, where they are better protected and can be better nourished than outside of the mother. The atmosphere and the dry land offer less favourable conditions for the development of that small amount of protoplasm that forms the primordium of each new being than does the water, and so viviparity is likely to have been a parallel phenomenon to the exchange of the aquatic for the terrestrial existence.

We can see clearly that once an embryonic envelope, one cell-layer thick, being present (on our original assumption, as far back as the invertebrate ancestor), that this one-layered larval envelope could obtain high efficiency for the incipient viviparity if only it bulged out as much as possible, thereby—

(1) Preventing the egg from passing through the genital ducts rapidly and being deposited, so to say, accidentally.

(2) Enabling the egg to adhere in various ways to the maternal tissues, either as a simple mechanical improvement of what was attained (1), or at the same time inducing phagocytotic attacks on that maternal tissue.

(3) Creating the occasion for individual trophoblast cells of this outer layer to absorb fluids either from the uterine cavity or accessory to the phagocytic processes alluded to under (2), and thus accumulating nutritive material inside the blastocyst.

Furthermore, it is equally clear that, once the viviparity having been established, and the surface extension of the

trophoblast going parallel with it, a yet more efficient mode of nutrition than the one alluded to above under (3) might be obtained if the embryonic vascular system, which was slowly coming into existence on the hereditary plan of development, succeeded in spreading out, in one way or another, on this outer trophoblastic layer, and would enter into osmotic interchange with maternal blood.

Finally, the protection of the embryonic shield during its further development by some sort of appliance resembling a water cushion would, in these incipient viviparous animals, undoubtedly have been a most efficient variation, for the earliest origin of which we have simply to go back to the early stage in which we noticed the formative cells of the embryo adhering to the larval layer, the trophoblast, in one spot only. Suppose that in further development this sessile attachment to have become converted into a circular adhesion—by fluid accumulating between the trophoblast cells and the formative cells, as we see it happen under our eyes in *Erinaceus* and *Gymnura*—we then find that the water-cushion, in *casu* the amnion, took its origin in a most simple fashion, whereas the chorion is in no way dependent on it, but has preceded it as an earlier formation.

The rapid summary here given shows us that the assumption of a single monodermic larval layer is quite far-reaching enough to allow us to understand how, out of it, chorion, amnion, and allantois (the latter as representing one form of early vascularisation of the trophoblast) have gradually come about.

The only change we have to make, in what I might designate the present "fashion" in comparative embryology, is that we look upon the earliest ancestors of mammals not as oviparous, yolk-laden vertebrates, but that we acknowledge them to have been viviparous animals with blastocysts that obtained vesicular shape from quite other motives than an eventual "loss of yolk," such as Rabl has attempted to prove. Here, then, is the place for an appeal to palæontologists. They have no shadow of direct interest in fœtal envelopes which are

never met with in the fossil condition ! But they may, nevertheless, be all the more impartial judges when we have to choose between two different assumptions: the one given in the hand-books, according to which mammals must, through the Ornithodelphia, be derived from some oviparous sauropsidian ancestor, or the one here advocated, according to which a viviparous Prototrapod, provided with an adhesive and distending larval layer diverged into various directions, some of the descendants utilising the conditions of growth and development (such as they find them) with the highest degree of intensity and becoming primates, others applying their trophoblast to nutritive purposes in more diverse and less direct ways, becoming the ancestors of most of our other Monodelphia and Didelphia. Others, again, going a certain distance with the preceding, but then acquiring yolk-laden eggs (Ornithodelphia), whilst yet other very effective branchings off in various directions gave rise to the primitive sauropsidian ancestors.

The difference between the sauropsidian and the amphibian descendants of the protetrapods need no longer be so incisive—as those zoologists that divide the Vertebrates into Amniota and Anamnia would make it. The hypothesis here brought forward proposes to look upon what we know as the Deckschicht of the early larval Amphibia and Dipnoi, and even of the teleostomes, as a last remnant of the very larval layer from which we started in trying to explain the foetal membranes of vertebrates according to what seems to me a simple plan.

We have now to look a little closer into certain details, by which we may be enabled to judge of the greater or smaller degree of tenability of some of the views here brought forward.

We notice that all the Mammalia-monodelphia, that have up to now been observed in very early stages, fully confirm the strong antithesis which in those early stages prevails between the trophoblast and the embryonic cells strictiori sensu. We also notice this in the Didelphia, as far at least as Selenka's figures for the opossum go, although he himself has not interpreted the facts he brought to light in the same

way as I do. Similarly, Wilson and Hill, in their latest paper on the development of the duck-bill, give us figures of sections which make it probable that the distinction between trophoblast and formative cells holds good here, even though the development of yolk has obliterated the sharp outlines of the process.

Again, in reptiles and birds traces of the larval layer have, in later years, been unmistakably noticed. Schauinsland, Mitsukuri, and Mehnert were among the foremost to contribute facts in this direction, although at the same time they failed to see the essential points of comparison with the mammals. This failing on their part is all the more explicable as the bird's egg, which has always served as the prototype even of mammalian development, does not clearly bring out the fundamental distinction that exists between trophoblast and formative matter of the embryo.

The gradual obliteration of this distinction may, perhaps, be ascribed to the fact that in these sauropsids, as in the ornithodelphia, a shell has developed, which naturally tends to relegate any outer larval layer to the pension list.

Concerning the yolk accumulation in the sauropsidian egg, there is no trouble at all to suppose that the vesicular blastocyst of an early viviparous ancestor has gradually become yolk-laden. The contrary assumption, found in the handbooks, that the mammalian egg, while totally losing its yolk, has yet preserved the identical developmental features as the sauropsid, is, in reality, much more difficult to reconcile with sound evolutionary principles.

We have seen that a simple clue to our understanding of the complicated fœtal envelopes of the sauropsids and the mammalia is the assumption of a simple larval layer, one cell thick, among the invertebrate ancestors.

We must be ready to admit that this one factor has undoubtedly given rise to an endless number of variations and modifications in those innumerable families, genera, and species which have come and have gone, ever since the time when viviparity and terrestrial life became an established fact

in the vertebrate kingdom. What is preserved to us in the recent fauna inhabiting this planet is only the faintest echo of the multitudinous and protean changes that have, during the course of time, succeeded one another. And it has been our mistake to attempt to co-ordinate the present stages of development with each other in such a sense that they were expected to represent, in lineary arrangement, the successive evolutionary stages of those foetal envelopes.

How false the conclusions may be to which this method may lead us is best exemplified by what is at present often taught concerning, e.g., placentation, a phenomenon in which the outer larval layer, the trophoblast, plays such a prominent part. You will find in the text-books that this was started by what is called the diffuse placentation as it is at present met with in many ungulates, in the lemurs, and in certain Edentates. It is my conviction that this doctrine is utterly false. The diffuse placentation is no placentation at all! The horse and the lemur are, by birthright, aplacental animals, much more so than marsupials, such as *Perameles* and *Dasyurus*, which have hitherto ranked among the *Mammalia aplacentalia*. And still, by careful comparison of various data, we can soon discover that the diffuse placentation, and that variety of it which is styled the polycotyledonary, far from being archaic or primitive, is, on the contrary, very largely a secondary modification. Among the living *Carnivora* we find several intermediate stages, not in the sense that these have been phylogenetic transitions, but in that wider sense that these *Carnivora* demonstrate the possibility how more intricate placental structures may finally have led up to a diffuse placentation, as that of the horse and the pig, consequent upon an increase in the area of surface contact between mother and foetus. What was originally a small surface of intense interchange (*Procavia*) has then gradually become an extended surface, along which two epithelial layers, one maternal and one foetal, between the blood of the mother and the blood of the embryo, offered no impediment for a sufficient interchange of nutritive matter and of oxygen.

If we do not accept the starting-point in the placentation-process to be represented in the ungulate arrangement, a proposal which the systematic position of the Ungulata would in itself render doubtful, we must then look for another phylogenetic sequence which will help us to rightly interpret that momentous process of placentation. And here the important results of Hill's investigation of very intense placental phenomena in some marsupials, such as *Perameles*, have great weight.

We may fairly conclude that kangaroos, phalangers, opossums and other marsupials have only gradually become aplacental, parallel to those other formidable changes which must have accompanied the elaboration of that peculiar type which we call our recent *Didelphia*, in which the dentition, the lactation, and those adaptations of the new-born animals for nutrition during their life inside the marsupium form such distinctive characters.

And so if the *Didelphia* are in reality erratic *Monodelphia* secondarily modified and with an allantois that has been thrown out of the line of its normal development, with the exception of *Perameles*, *Dasyurus*, and in part *Phascolarctos*, then we have again to look, not amongst them, but amongst the *Monodelphia*, for such forms that can give us an indication as to what may have been the primitive stage of placentation.

And I may here state that my own researches on the placentation of both primates and of insectivores have led me to the conclusion that we should look in quite another direction than the one alluded to above, which starts from diffuse placentation. In the earlier part of this address I have considered those early phylogenetic stages when, in viviparous, air-breathing tetrapods, the larval layer, the trophoblast, found the most diverse possibilities open to it.

I believe that those forms of which the embryonic trophoblast actually attacked the maternal uterine mucosa phagocytically were the pioneers towards the formation of what has later become the discoid placenta. In some forms, even among our recent mammals, that phagocytic attack is com-

bined with a penetration of the whole blastocyst inside the maternal tissue, e. g. man, anthropomorphæ, hedgehog, *Gymnura*, and many rodents. This was naturally a far higher position of vantage than any peculiar fixation inside the lumen of the uterus, for now, when once the blastocyst was encapsuled inside its mother's tissues, it could be most thoroughly bathed in maternal blood without any extravasation into the uterine lumen. To take three examples of this we may allude to the guinea-pig, the hedgehog, and man. Still, all these utilise the favourable conditions offered to them, thanks to their situation inside a capsula or decidua capsularis, in a very different manner.

There is a most remarkable amount of similarity between the hedgehog and man, as far as the conditions are concerned, which the mother offers to the young. But then the embryo of itself of man has seen its way to much more intense utilisation of these favourable conditions than the hedgehog embryo has. Principally because the vascular system of the hedgehog develops in a sequence of stages, which serve to bring its area vasculosa on the umbilical vesicle in primary contact with the profusion of maternal blood by which the blastocyst is surrounded.

On the contrary, in man this area vasculosa on the umbilical vesicle is not in contact at all with the maternal circulation. In man it is more devoted to hæmatopoietic functions, i. e. to the formation of new blood-corpuscles for the embryonic circulation. But in another respect the human blastocyst has got far ahead of that of the hedgehog, in so far as the developing embryo has succeeded in vascularising its outer larval layer, its trophoblast, at a quite exceptionally early moment, without the aid of any allantoic outgrowth, and simply in consequence of a very early segregation of certain portions of the mesoblast, into which the entoderm sends both blood-vessels and blood-corpuscles. This very early vascularisation of the trophoblast leads to a most intense osmotic interchange between the blood of mother and child—far more intense than what obtains in the hedgehog, where an ompha-

loidean placentation precedes an allantoidean one, the allantois being a vesicular outgrowth, as it is in so many mammals and in all sauropsids.

I cannot refrain from looking upon the vascularisation of the outer larval layer or trophoblast, such as it occurs in man, in the monkeys, and in *Tarsius*, as the more primitive arrangement of the two. And in that case the presence of a connecting stalk (*Haftstiel*) and the absence of a free allantois in man, monkeys, and *Tarsius* is not a secondary simplification, but a primary fact of high importance. What is known as the allantois tube inside the so-called *Haftstiel* or *Bauchstiel* of man, monkeys, and *Tarsius*, is not the remnant of what was once a vesicular allantois, but a remnant of that part of the entoderm which has served towards the vascularisation of the trophoblast. It is this portion of the entodermal surface which will become the free allantois in those other descendants of the primitive tetrapods, which have not adhered to the very direct line of utilising most fully and as early as possible all favourable circumstances. This most direct line leads up straight to the primates. Less direct lines, in which conditions of different or of slower vascularisation have come to the foreground, are, however, represented in various orders of monodelphian mammals, and further in the *Didelphia*, the *Ornithodelphia*, and in the different subclasses of sauropsids. In the latter the allantois has grown to the dignity of a separate fetal membrane, which co-operates to the further ensheathing of the developing embryo, and which carries the blood-vessels for respiratory purposes to the inner surface of the egg-shell, whereas, in the ancestral viviparous forms, the same vessels were more directly distributed over the inner surface of the outer embryonic larval layer, in order to improve the nutritory conditions which had been inaugurated by phagocytic action of the trophoblast cells on the maternal tissues.

This, then, is a short sketch and a rapid review of how the fetal membranes of the vertebrates may be looked upon if we make certain changes in the interpretations that have

been hitherto adhered to, but by which latter nobody has as yet succeeded in clearing up the actual phylogenesis of these foetal membranes.

Full and extensive investigations of all those numerous genera of mammals that have not yet been examined will, I hope, in due time give us occasion to complete or to modify the views here advocated.

It was a great pleasure to me to offer them, tentatively, in an address which I was invited to give in the section of embryology of this Seventh International Congress—a section which, with good right, has been called into life for the first time at this meeting in Boston. Embryological problems have been attacked by American investigators with wonderful results, and the lucidity of exposition that is characteristic of so many of your embryological workers is only equalled by the beautiful transparency of the eggs of those marine animals on which so many important researches on cell-lineage have been conducted.

That I have been less clear is not only a congenital defect, but is parallel with the utter hopelessness of our expecting that we shall ever be able to follow the cell-lineage in the deeply hidden and exceedingly small mammalian eggs. Still, a full knowledge of that very cell-lineage would be eminently decisive for many of the questions that have occupied us in the course of this address, to which you have listened with so much patience.