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tables in "Directions for the use of the astrolabe", some simplification being introduced to enable it to be used for every year, leap-year or ordinary year alike.

It is most probable that the copies of the "Directions" and of ZACUTO's tables which have been found were preceded by older editions. In a letter written on May 1st 1500 by PEDRO ALVAREZ CABRAL's mate, reference is made to a determination of latitude in Brazil at south latitude 17°, which, as he writes, is made according to the rules of the astrolabe, and of which the results correspond entirely to the data in the tables of the Munich copy of the "Directions".

It cannot be ascertained with certainty from what source ZACUTO borrowed the tables referred to above, but BENSAUDE quotes a number of manuscripts, revealed by the researches of STEINSCHNEIDER, which were written after the preparation of the Alphonzine tables in 1252, upon astronomical subjects and instruments in Spain, Provence and Portugal, principally by Arabs and learned Jews of the 14th and 15th centuries. ZACUTO follows upon these writers, so that he was probably enabled to compile his tables from the data which they supplied.

It may therefore be concluded with the greatest probability, that the Portuguese owed their knowledge of the science of navigation at the time of their great discoveries, not to German scholars, but to the high scientific attainments of their own compatriots.

Zoology. — "*Critical and theoretical considerations about the origin of the primary foetal membranes in Vertebrates.*" By Dr. DAN. DE IJANGE. (Communicated by Prof. J. F. VAN BEMMELEN).

(Communicated in the meeting of March 25, 1916).

The presence of primary foetal membranes in *Sauropsida* and *Mammalia* has been considered for a long time as a characteristic of great systematic value and has led to the division of Vertebrates in *Amniota* s. *Allantoidea* provided with primary foetal membranes and *Anamnia* s. *Anallantoidea* without these membranes. Members of the last group (*Cyclostomata*, *Pisces* and *Amphibia*) are also named *Ichthyopsida*, since they live wholly or partly (as larvae) in an aquatic environment where they breathe by gills, gill-breathing never being present in the first group. Of course there exist *Amniota* which have become adapted to an aquatic life (turtles, marine Saurians and especially Cetaceans), but as in them lungbreathing has always been preserved and never been substituted by gill-

breathing, even in pelagic forms which never come ashore, this adaptation may be recorded as a secondary one. Thus we safely can suppose, as has been done by the majority of investigators, that the appearance of primary foetal membranes is to be considered as an adaptation to terrestrial life, an adaptation which makes it possible, that embryonic development takes place in liquid surroundings, though outside the water¹⁾.

Now the question is whether oviparity in *Sauropsida* may be deduced directly from oviparity in Amphibians, the holoblastic cleavage-type of the last group being changed simultaneously by accumulation of yolk in the meroblastic one of the first, the yolk-poverty of Mammalian eggs consequently being secondary, or whether the evolution has proceeded in a reverse direction. Most of the older and some modern investigators have declared in favour of the first alternative. According to them the mode of development of foetal membranes by folding up, so typical for the Sauropsidan egg is to be considered as primitive and the various modes of amnion-formation in Mammals are to be derived from this one. It is not my intention here to go into all the abortive attempts to explain the phylogenetic origin of the amnion, published before the year 1895, since HUBRECHT has criticized them sufficiently in his well known treatise on this subject²⁾, but it will suffice to summarize the conception of SELENKA³⁾, which combines the two older explanations.

SELENKA believes the amnion to be composed of two originally independent folds, growing together by chance, thereby closing the amnion-cavity and separating the embryo from its surroundings. These two folds are the headfold and the tailfold. The precocious segregation of brain and head, and the curving of these organs caused by this circumstance, push the head into the yolk, and in this way the headfold arises passively. It usually is at first a pro-amnion i.e. it consists of ectoderm and entoderm, the last being

¹⁾ I wish without delay to lay stress upon the fact that in my opinion the importance of the development within an amnion-cavity for terrestrial forms chiefly lies in the circumstance, that in this way the developing embryo is exposed on all sides to uniform pressure, while most writers think of protection against mechanical injuries from the outside. Tertiary e.g. coverings, already abundantly present in Amphibians, supply sufficient protection against these injuries. If mechanical pressure or shock can penetrate a bird's eggshell and glaircovering, they certainly will be able to pierce the thin chorion and amnion

²⁾ A. A. W. HUBRECHT Die Phylogenese des Amnions und die Bedeutung des Trophoblastes. Verhand. Kon. Akad. Wetensch. Amsterdam. 2e Sectie, D IV, N. 5.

³⁾ Vide E. SELENKA. Studien zur Entwicklungsgeschichte der Tiere. Bd. I, Heft 5, 1892: Zur Entstehungsgeschichte des Amnions. p. 186—189.

superseded afterwards by ingrowing mesoderm. SELENKA explains this phenomenon in a subtle manner by supposing the proamnion to have originally possessed mesoderm and bloodvessels. By the folding process the respiratory function of this part of the area vasculosa is in danger of being injured and therefore the mesoderm retires¹⁾. We shall revert to the subject later on, but the mere fact that in many Anamnia a proamnion-area is present in front of the enteron, without any folding process taking place, makes this explanation rather improbable.

According to the opinion of SELENKA the outgrowth of the tailfold is caused by the powerful growth of the allantois. The suppression of the free larval period and the development of the embryo within the eggshell render the emptying of the excretory products into the eggchamber impossible without at least serious injury to the normal metabolism of the embryo. Therefore the embryonic urine-bladder (allantois) expands and pushes between somato- and splanchnopleura of the yolk-sack. By this circumstance the respiratory function of the yolk-sack, already diminished by the liquefaction and shrinking of this organ, will be largely impaired. The allantois, if sufficiently provided with bloodvessels, can take over this function and the outgrowth of the tailfold is only a means for surface-increasing in connection with this new function.

Against both views serious objections may be raised. Without laying stress upon the rough mechanical conception of the sinking-down-hypothesis, we can state the fact that, along with the formation of the proamnion, no real sinking-in of the headregion occurs, but that principally the ectoderm and in second instance the entoderm actively grow over the embryo. Besides I never have found it mentioned that the proamnion fold contains yolk-material, a circumstance that seems to me a *conditio sine qua non* for the sinking-down-hypothesis.

The explanation of the outgrowth of the tailfold by the supposed tendency to surface-increasing of the allantois is *eo ipse* more plausible, but ontogenetic facts do not agree with it. The tailfold does not arise as an outgrowth of the allantois, but develops independently of this organ, and consists originally of ectoderm and mesoderm only, the true entodermal allantois following long afterwards, usually preceded by a so-called mesodermal one. Moreover the fact that the tailfold is wanting in many Sauropsida with a primitive type of development (*Sphenodon*, *Chelonia*) makes this explanation rather improbable.

¹⁾ SELENKA, l.c. 1892, p. 187.

Now against this point of view HUBRECHT opposed in the above mentioned treatise (1895) his own widely different one, which caused a sensation amongst the ranks of embryologists, and may be summarized in the following points:

1. If the real signification of the amnion is that of a protective water-cushion; it should originate as a closed bladder, otherwise one cannot understand its phylogenetic evolution.

2. This mode of development occurs in fact in certain Mammals (*Erinaceus*, *Galeopithecus*, *Pteropus*, *Cavia*, perhaps *Primates*), while the development by a process of folding, as most *Sauropsida* show it, differs very widely from it. Therefore it is obvious that the last method must be considered as a secondary one, but then we are obliged at the same time to derive the meroblastic yolk-laden eggs of *Sauropsida* from the holoblastic yolkless eggs of Mammals and the (secondary) oviparity of the first group from the more primitive viviparity of the last one.

3. The trophoblast i. e. the ectodermal covering of the embryonic fruit-bladder, to which the peripheral ectoderm-layer of the embryonic region sometimes may be added, plays an important part in the formation of foetal membranes and in the implantation of the embryonic vesicle into the wall of the maternal genital ducts. HUBRECHT considers the trophoblast as the most primitive of foetal membranes. In amphibian larvae, especially in tadpoles, it presents itself as the covering ectoderm-layer (Deckschicht), in Mammals with deciduous placentation it develops enormously in connection with its intensified nutritive function.

4. Originally the amnion-bladder develops as a cavity between trophoblast-covering and embryonic knob. In order to secure vascularisation the primitive amnion is divided by ingrowing vasoconductive mesoderm into two layers: the outer chorion and the inner amnion. In this way the amnion cavity is separated definitively from the outer trophoblast-layer and can increase along with the developing embryo, so that in later stages it fills up the greater part of the fruit bladder.

5. In some cases (most *Rodentia* with inversion of germ-layers e.g. *Muridae*) the mesoderm-folds do not penetrate the primitive amnion, dividing it into two layers, but grow into the primitive amnion cavity, and divide this cavity into the so-called false and true amnion cavities. This mode of development forms a transition towards the folding process which appears in all *Sauropsida* and in many Mammals with postponed attachment of the embryonic vesicle. In this case a merely ectodermal primitive amnion is never present, but the

definitive amnion¹⁾ develops immediately by outgrowth of mesoderm-containing folds.

The great merit of HUBRECHT's theoretical considerations in this question is to be sought partly in the searching criticism exercised on established ideas, e. g. on the axiom that amnion-development is eo ipse more primitive in Sauropsida than in Mammalia, partly in the widening of our mental horizon by opening new and unexpected perspectives which incite to new investigations. Therefore I feel obliged in honour of the memory of the great Dutch embryologist not to shrink from equitable criticism or from necessary correction and supplementation of his fertile ideas.

The premise mentioned sub 1 would be correct if the amnion-cavity really served in young stages as a protective watercushion. But this is by no means the case. In young mammalian foetera protection is furnished by what I will call here provisionally the trophoblast-bladder and the primitive amnion (archamnion RESINK) is only a means of pushing the embryonic knob into this protective watercushion. Therefore I am inclined with RESINK²⁾ to consider amnion-formation by entypy as primitive, whether this appears as a hollow invagination or as a solid ingrowth. I will revert to this point later on.

In a second question the significance of the trophoblast, I also have a somewhat divergent opinion. I will not deny the important part played by this embryonic appendage in the amniogenesis of all Amniotes, but I am not convinced that it is already present as a larval envelope in Anamnia, or that it is represented by the covering layer of the epidermis (Deckschicht) of amphibian larvae. It is true that HUBRECHT has altered his opinion on this point in his later publications to a certain extent, but nevertheless he proposes to divide the Vertebrates in *Achoria* (*Cyclostomata* and *Selachii*, Vertebrates without trophoblast) and *Choriata* (all the rest, possessing this larval envelope)³⁾. In my opinion therefore I am fully justified in making some critical remarks on this point.

Of course the trophoblast of Mammals must have arisen from the ectodermal covering of anamniote larvae, one therefore is justified in saying that it is present potentially in the larval

¹⁾ I use the term 'amnion' in this case in a wide sense i.e. amnion s.s. + chorion resp. serous membrane.

²⁾ A. J. RESINK. Die Stamentwicklung der embryonalen Organe. Tijdschr. Nederl. Dierk. Ver. D. VIII, afl. 3, 1903.

³⁾ A. A. W. HUBRECHT. Ontogenetic phenomena in Mammals etc. Quart. Journ. Microsc. Sci. Vol. 53, 1908, p. 81—83.

epidermis, but HUBRECHT considers the outer ectodermal layer (Deckschicht) such as especially anuran larvae show it, as a separate organ, a reduced larval envelope. If this view were correct, we should expect this larval envelope to be developed in an obvious way in *Gymnophiona* and primitive tailed *Amphibians* such as *Amphiumidae* (*Megalobatrachus*, *Cryptobranchus*) and *Proteidae* (*Necturus*), whose eggs pass moreover through a long embryonic period, and this is in no way the case. In these forms the two layers of the epidermis bear exactly the same histological character. The solid ingrowth of cerebral ganglia seems to originate out of the deeper nervous layer only, but even this may be delusive. The invagination of the neural plate takes place before the differentiation of the two layers, or both participate in it. The extraordinary development of the "Deckschicht" in tadpoles may be partially ascribed to the fact that in these forms this layer forms a number of temporary organs possessing great importance for the subsistence of the larva, such as the suckers ventral to the gillregion and the larval sucking-mouth with its horny teeth, while perhaps the outgrowth of the operculum requires more material from the epidermis than in Urodelan larvae without this cutaneous fold.

Another weakness in HUBRECHT's theory is the fact that it gives no conclusive explanation of the differentiation of the holoblastic Amphibian egg into the embryonic knob and the exembryonic fruit-bladder of Mammals. As HUBRECHT starts from eggs without or with a small amount of yolk ¹⁾, this important question remains unsolved. HUBRECHT has paid little attention to this point. On p. 36 l. c. 1895 he writes:

„Nun lässt es sich denken, dass Formen welche in diese zweite „Kategorie gehört haben mögen, nebenbei eine starke bruchsackartige „Erweiterung der Bauchwand erlitten haben, und dass die Bildung „des Bruchsackes mit der eben erwähnten ringförmigen Einpflanzungs- „linie des primitiven Amnions zusammenfiel“.

p. 56: „Es ist viel wahrscheinlicher, dass die Protamnnoten vivipare „Amphibien gewesen sind, bei welchen, durch Flüssigkeitsansammlung „zwischen den Hypoblastzellen eine prall gefüllte, pseudomeroblastische „Keimblase zu Stande gekommen ist“.

¹⁾ I will remark on this point that in HUBRECHT's writings the terms "dotter-arm" and "dotterreich" are often used, when he really means holoblastic and meroblastic. Of course the existence of holoblastic eggs with an enormous amount of yolk such as in *Amphiumidae*, *Gymnophiones*, *Necturus*, *Dipnoi*, *Ganoïds* etc. and of meroblastic eggs with a rather small amount of yolk, such as pelagic Teleostean eggs, was known to him, but these eggtypes only play a subordinate part in his theoretical reasoning.

These are his only words upon the subject in his first great theoretical study. It cannot be denied that they contain in no way sufficient arguments for such a radical transformation and that in this respect the old-fashioned explanation is more conclusive than the modern one.¹⁾ The older conception starts from a yolkladen meroblastic egg. The exembryonic yolksack only serves to resorb the feeding material of the yolk and is shed after birth. Thus it is conceivable that a great amount of difference arises between the embryonic shield and the exembryonic part of the egg. With the transition of the sauropsidan oviparity into the mammalian viviparity the yolk material is lost, but the wall of the yolksack remains as the exembryonic part of the germladder.

I will not enter here into detailed objections to this reversion of the evolution. I think it improbable that the cellbuilt germladder of Mammals should have originated out of the amorphous yolk-mass of *Sauropsida* and later on I hope to demonstrate that the yolksack of Amphibians, the yolkmass of *Sauropsida* and the exembryonic germladder of Mammals are not quite homologous organs, but I will pass on to the more synthetical part of my treatise in which I will try to obviate by some slight alterations the above mentioned objections against HUBRECHT's theoretical conception.

Like HUBRECHT and his school, I am inclined to derive mammalian ontogenesis directly from the amphibian one without the intermediary of the meroblastic sauropsidan way of development, the latter being in my opinion far less primitive than the way in some Mammals. I therefore admit the secondary oviparity of Birds and Reptiles to have arisen out of a more primitive viviparity of the Protamniota, which of course is to be derived in its turn from the primary oviparity of anamniote ancestors. In opposition however to HUBRECHT's views I start from a yolkladen, holoblastic eggtype, such as is presented by the eggs of *Gymnophiones* and *Amphiumidae*.

Fig. 1 represents a median section through a diagrammatic embryo of this type. The large yolksack completely divided into cells passes gradually into the entoderm of the intestine and shows a continuous ectoderm covering. The mesoderm layer of the yolk, which originates chiefly from the ventral blastoporal lip, the so-called ventral mesoderm, has not yet reached the ventral and the anterior side of the yolksack. The latter part of the surface of the

¹⁾ It seems to me that the introduction of the term archomphalon by REŠINK (a somewhat modified notion of the yolksack) does not give any better solution of these difficulties.

yolksack which forms the anterior (resp. superior) wall of the liver-invagination, appears as a distinct organ, a crescentic area which I have called in connection with its topographic situation: praecerebral or terminal entodermarea. I here prefer using the term proamnion-area anticipating by this name its significance in Amniota.

The fact that the proamnion-area remains for a long time free from mesoderm is probably caused by the peculiar allogenic growing circumstances which prevail in the development of the yolkmesoderm, but it may be due to an autogenetic, morphological cause unknown to me. We have already mentioned the separate centre of proliferation of the yolk-mesoderm. This so-called ventral mesoderm arises in a slightly different way from the true somatic mesoderm.¹⁾

Now the fore-side of the yolk receives its mesodermal covering for the greater part from the ventral mesoderm, which arises on the hind side and for the lesser part from the cephalic mesoderm resp. from the pericard. The rapid outgrowth of the head region consuming a great mass of the cephalic mesodermal material, the ventral mesoderm being obliged to grow over the whole yolksack before reaching the fore-side, the consequence is that this side of the yolk will remain for a long time without mesodermal covering. What however may have been the real cause of the appearance of the proamnion-area, it may suffice here to state the presence of this organ in primitive Amphibians.

Now let us try to retrace the changes, which the amphibian ovum undergoes if the eggs are laid outside the water and the free larval state is consequently abbreviated or wholly abolished.

It may happen in this case that a more or less intense, internal nursing is provided, the embryo remaining during its whole development or during part of it in protective cutaneous folds or pits of the female (*Hyla goeldi* Boul., *Nototrema*, *Pipa americana* Laur., *Rhacophorus reticulatus* Günth. etc.), in the buccal cavity or in the oral sacs of the male (*Rhinoderma*) or in the genital ducts of the female (*Salamandra*, *Spelerpes*, *Typhlonectes*, *Dermophis thomensis* Boc. etc.). In the second place the parents may surround the synoion with a mass of froth, which dries up to a horny sheet

¹⁾ The ventral mesoderm does not arise as an epiblastic ingrowth like the somatic mesoderm (dorsal plate), but it proliferates from the ventral border of the blastopore (somatopore), where yolkcells pass into the epiblastic ones, grows in between the yolk and its epiblastcovering, and increases probably partly by delamination of peripheral yolkcells. It never divides into segments. Its character and development therefore recall that of the protochordal plate and that of the anterior head mesoderm or speaking generally that of the cephalic mesoderm I shall revert later on to its great importance in the mammalian fruitbladder.

and attach them to leaves or stones, in this way preventing or reducing evaporation (*Phyllomedusa*; *Hylodes martinicensis* Tschudi, many species of the genus *Rhacophorus*, *Rana opisthodon* Boul. etc.). In the third place the synoion may be deposited in damp, subterranean holes, the female curving around it for protection (many members of the family of *Gymnophiones* as: *Siphonops*, *Hypogeophis Ichthyophis* etc.).

In all these cases even in so-called viviparous forms the embryo remains surrounded by tertiary eggmembranes of colloid consistancy, the internal one liquefying in order to form an eggchamber, or by the fusing of many eggchambers a central cavity, filled up with an aqueous liquid. In this simple way Amphibians, which do not lay their eggs in the water, provide liquid surroundings for the developing embryo. It need not be said that these deviations from the normal way of development with a long larval period must be considered in most cases as the consequence of or as an adaptation to a non-aquatic life of the parents (usually to a burrowing life: *Gymnophiones*, and to an arboreal life, in the other examples)¹⁾.

Wherever free larval life is supplanted by an embryonic period within tertiary jelly-membranes, we may remark two characteristic phenomena; the presence of a large amount of yolkmaterial within the egg and the enormous development of respiratory organs. Both phenomena may be considered as necessary adaptations to the changed conditions of life of the young Amphibians.

If an aquatic larva capable of nourishing itself, is set free after a short embryonic period, the egg does not need to contain much reserve-material. If however development takes place wholly or for the greater part within tertiary eggmembranes, provision must be made for a more extensive victualling of the developing embryo. This explains the fact, so strange at first sight, that viviparous, terrestrial forms as *Salamandra atra* Laur. (and to a certain degree also as *S. maculosa* Laur.) possess eggs much heavier laden with yolk than the closely allied aquatic Tritons, which deposit their eggs into the water.

The considerable development of respiratory organs may be easily explained in the same way. In forms with a short embryonic period which is also passed, it is true, within tertiary eggmembranes, but where the greater part of the developing period is spent in the form of a free aquatic larva, the difficulties with which respiration meets, are far less serious than in forms where development takes place out of the water sometimes within folds, holes or internal cavities

¹⁾ An exception must be made for *Pipa*, a thoroughly aquatic frog.

of the parents. As in viviparous Amphibians the jelly membrane is preserved, there is no question of direct gas-interchange between parental and foetal blood and respiration must take place between the air in the parental breeding cavity (or the parental blood) and the foetal blood passing through the jelly membranes and the liquid contents of the eggchamber, not exactly a short way!

If development takes place out of the water, but not within parental breeding cavities, precautions have to be taken to reduce evaporation, which necessarily will limit the other interchanging processes. In all cases respiration is seriously impeded and in consequence of this circumstance respiratory organs increase enormously in size. External gills may act as such and acquire a much larger extent than in aquatic larvae (*Gymnophiones*, *Salamandra atra* Laur etc.), but the tail also may grow in length and show a very abundant vascularisation, in order to facilitate gas-interchanging processes (*Hylodes*, *Phrynixalis*, *Mantophryne* etc.), while in rare cases (*Rana opisthodon* Boul.) the whole skin and especially cutaneous folds on the side of the body supersede the other respiratory organs. We may conclude from these examples that widely different parts of the body may assume respiratory functions. Usually these organs possess at the same time a nutritive function the liquefying and absorption of the albuminous jelly membranes (hence the name allantoidean gills).

Now in my opinion anamniote ancestors of *Amniota* may have been viviparous in a manner such as I have sketched above, but in this case the yolksack may have assumed a respiratory function. The fact that the yolksack is always abundantly vascularized in yolk-laden eggs, since haemopoiesis chiefly takes place on the yolk surface and bloodvessels play an important part in absorbing and carrying off the reserve-material to the embryo proper, favours this proposition. The yolksack will show the same tendency to increase its surface as the above mentioned respiratory organs, but the less plastic yolk-cells will oppose. The consequence will be that somatopleura and splanchnopleura of the yolksack separate, the first carrying off part of the bloodvessels (allantoidean vessels) and exclusively taking care of respiration, while the splanchnic sheet will retain the umbilical bloodvessels, bloodformation and yolkabsorption being restricted to it. The somatic sheet which may be called pneumatoblast, once free from the impeding yolkmass, will rapidly enlarge its size and try to increase its surface by folding-up and by proliferating. Between somato- and splanchnopleura an extensive cavity: the exocoeloma will arise. The pneumatoblast also will assume a nutritive function:

the resorption of the jelly eggcoverings, and therefore we may use here without restrictions the term diplotrophoblast of HUBRECHT to which this organ answers morphologically and physiologically.

But evolution ¹⁾ does not stop at this point:

After resorption of the tertiary eggmembranes direct osmotic interchange of gasses and dissolved materials between foetal and maternal blood becomes possible and this method of respiration will be much more intense than the interchange between the aerial content of the oviduct and the foetal blood, which is obliged to pass the eggmembranes and the liquid of the eggchamber. Development therefore will show a tendency to secure as soon as possible the contact of diplotrophoblast and uterine wall. Thus this respiratory embryonic appendage will be precociously segregated ²⁾ and the tertiary eggcoverings will show a tendency to be reduced and to disappear. But then the eggchamber loses its significance as protective watercushion in which the embryo may develop under uniform pressure and it will be necessary to transfer this function to another organ.

Before treating this question further I must call the attention to the fact that by the precocious segregation of the diplotrophoblast the conditions of the fruitbladder in a hypothetical protamniote very much resemble those of the early mammalian fruitbladder (see fig: 2). On the ventral side of the vesicle a large watercushion is present, the wall of which shows all sorts of folds and proliferations and possesses respiratory and nutritive functions, while the still small embryonic area is situated on the dorsal surface of the fruitbladder. The comparatively large yolksack is attached to the ventral side of the embryonic area and is connected with the surface of the exembryonic fruitbladder by the proamnion-area. ³⁾

As the diplotrophoblast has only significance as an embryonic organ for respiration and nutrition, it is shed or resorbed at birth

¹⁾ For convenience sake I use in this paper the Neo-Lamarckian mode of expression, without assuming the Neo-Lamarckian mode of explanation with all its inferences.

²⁾ The mesodermal covering of the diplotrophoblast arises out of the ventral mesoderm. In consequence this also will show a tendency to precocious segregation. Sometimes it appears even before there is question of mesodermformation in the embryo proper. In some orders of Mammals (SCHLATER *Anat. Anz.* Bd. 30 and 31, 1907) e.g. in Primates, but especially in polyembryonic armadillos (PATTERSON, *Anat. Anz.* Bd. 41, 1912) this phenomenon is most striking.

³⁾ Since the proamnion-area does not possess a mesodermal covering, it cannot perform any respiratory function and it cannot be divided into a somatic and a splanchnic yolk sheet. Hence the yolk sack will be connected with the surface of the fruitbladder at this spot.

just as commonly happens with other embryonic respiratory organs of Amphibians. The differentiation of the amphibian embryo or larva — built up of more or less equivalent cells — into a small embryonic shield forming exclusively the young animal and a large exembryonic fruitbladder, being shed at birth, may be sufficiently explained in this way.

This situation once obtained, it will suffice for the protection of the small embryonic area to invaginate the latter into the large trophoblastbladder and in this manner a fruitbladder with entyped embryonic area has arisen. As the proamnion area is situated at the foreside, invagination of this part of the fruitbladder does not reduce the respiratory surface and one can understand that this process will take place chiefly at this side, setting aside the consideration that the precocious development of the headregion may serve as an ontogenetic (not as a phylogenetic) causal moment for this phenomenon.¹⁾

At the backside the entypy will take place exactly at the spot where the ventral mesoderm grows out i.e. at the spot where from the beginning the connection between embryonic and exembryonic mesoblast and between embryonic and exembryonic bloodvessel-systems are present. Now entypy withdraws at this point a part of the respiratory diplotrophoblast from the surface of the fruitbladder, but on the other side the connection between embryonic and exembryonic vesselsystem is thus maintained in a very intimate way. I think that in this manner the peculiar circumstance that the connective stalk (Haftstiel) of so many mammalian germbladders (e.g. in Primates) is always found at the caudal side of the embryo is conclusively explained. I therefore cannot agree with RESINK, who supposes the amnionstalk to be originally uniformly vascularized and I think I have demonstrated that important arguments can be brought forward for considering the appearance of the connective stalk at the caudal side of the embryo and at the back of the archamnion as a primitive characteristic.

¹⁾ HUBRECHT considers the proamnion a formation without morphological significance (see p. 79. 1908, note) and ascribes the lack of mesoderm and bloodvessels to the rapid growth of the headregion. His arguments on this point are however somewhat contradictory and the fact that the proamnion is present in nearly all groups of *Amniota* and is especially well developed in archaic *Sauropsida* (*Sphenodon*, *Chelonia*) makes it rather improbable that this organ should not possess an important morphological signification. Moreover its presence in *Amphibia* strengthens my opinion in this matter. Thus I consider strong development of the proamnion as a primitive feature. In *Sauropsida* it represents the last remainder of the original entypy.

Now if the germladder remained free in the uterine cavity the growing embryo would soon evolve the original entypy, a phenomenon which is realized in some Mammals (e.g. in *Tupaja*) under somewhat altered conditions. When however osmotic interchange between maternal and foetal blood has been settled, it is plausible that the embryo tries to profit from this relation as much as possible, and that foetal and maternal bloodvessels approach each other very closely. Trophoblast-outgrowths therefore attack the mucous membrane of the uterine wall, penetrate into the latter and pierce the wall of the maternal vessels so as to fill up the gaps and cavities of the trophoblast with maternal blood. The corrosion will chiefly take place at the embryonic pole of the germladder i.e. at the spot of the original entypy since in this manner the connection between foetal and maternal circulation by way of the connective stalk becomes as intimate as possible. The maternal tissue will answer to this attack of the foetal vesicle by overgrowing it in all directions, enveloping it totally in order to avoid bleeding to death. Now in the attached fruitbladder, totally enveloped by maternal tissue there cannot be question of evolving the original entypy.

We may imagine the original entypy as a hollow invagination and may then call the cavity with RESINK archamnion-cavity and its wall archamnion. On the other hand no serious objection can be made to imagining the stalk which pushes the embryonic knob into the trophoblastvesicle to be originally solid. In the first case the archamnion cavity will pass continually into the definitive amnioncavity. The ectodermal archamnion will become separated from the trophoblast by ingrowing mesodermfolds as I have already mentioned in explaining HUBRECHT's theory. This happens in most Rodents with so called inversion of germ layers. In the second case the amnion cavity arises by delamination in the tissue of the solid amnionstalk and forms from the beginning a closed waterbladder above the embryonic region. This manner of development, occurring in *Erinaceus*, *Galeopithecus*, *Pteropus*, *Cavia* and perhaps in *Primates*¹⁾, has been the starting point of HUBRECHT's theoretical considerations. I hope to have made it clear that in my opinion this difference is

¹⁾ The occurrence of the so called tubes of Selenka in Primates (RESINK, l. c. p. 179; H. STRAHL und R. BENECKE. Ein junger menschlicher Embryo. Wiesbaden 1910; O. GROSSER. Über hypothetische Frühstadien menschlicher Entwicklung. Zentralbl. Phys. Bd. XXII, 1908) which may be considered as remains of an open archamnion-cavity, makes it doubtful whether they do not belong to the first group.

not of great importance. The main fact is that the embryonic knob is pushed into the protective trophoblastbladder, either by invagination or by solid proliferation. Moreover in how many cases do not these two processes take each other's place, without it being possible to settle which mode of development is the more primitive one?

After being definitely separated from the diplotrophoblast the amnion cavity may increase along with the growing embryo, without being impeded by its connection with the surface of the fruitbladder. Gradually the room of the latter will be filled up for the greater part by the amnioncavity and in this way the latter takes upon itself the protective function exercised in the beginning by the trophocoel or by the exocoeloma.

In this paper I will not digress on the changes in the method of development of the primary egg membranes within the class of Mammals, since I should be obliged to repeat many things, which have been set forth in so excellent a manner by HUBRECHT and his pupils. I cannot avoid however making a few remarks upon the other foetal appendages:

1. *Allantois*. We have seen that in early stages of (phylogenetic and ontogenetic) development the connection between the embryonic area and the respiratory and nutritive diplotrophoblast is secured by the caudal connective stalk. This stalk arises at the ventral side of the blastoporus and turns dorsal to the surface of the germbladder. As the amnion-cavity grows ventral, it is turned also to the ventral side and may be called with His ventral stalk (Bauchstiel).

If the connection between maternal and foetal circulation is very intimate, the osmotic interchange between these systems is intense enough to remove obnoxious excretory products out of the foetal circulation, a condition realised e.g. in Primates. If the connection between mother and fruit loosens or if implantation takes place at a later period, the excretory products must be stored up in a way that will not cause inconvenience to the embryo. For this purpose the embryonic urine-bladder, the allantois increases. As this organ is situated near the point of attachment of the connective stalk to the embryo, it is plausible that it will grow along the stalk in order to remove as soon as possible from the embryo and gain the surface of the fruitbladder where the opportunity for osmotic interchange is greatest. In this way the allantois will come in contact with the bloodvessels of the connective stalk and the diplotrophoblast (allantoidean vessels, see above) and will assume a respiratory and nutritive function. The fact that in most cases the so-called mesodermal allantois (in my opinion a relic of the connective stalk)

grows out much earlier than the true entodermal one, the latter penetrating into the former, is an indication that the evolution of the allantois may have taken place in the way outlined above.

2. The *yolksack*. Our starting point has been an organ containing a large amount of yolk but divided completely into cells, such as occurs in many Amphibian larvae and embryos. If viviparity has led to the attachment of the germbladder to the uterine-wall, the deposition of reserve-material in the cells of the yolksack becomes superfluous and thus the amount of yolk will diminish in the course of evolution and finally disappear. The yolkfree umbilical bladder will retain however some importance as a haemopoietic organ, while in some cases respiratory and nutritive functions may be also retained to a certain degree. This condition leads in some cases to omphaloid placentation (*Marsupials*, young stages of horse). Though I have not been able to remove all difficulties encountered in this point, I am inclined to consider the micromphaloid germbladder of *Primates* as primitive and the macromphalon especially if connected with omphaloid placentation, as a secondary phenomenon.

Now as the trophoblast bladder increases in size and thus the umbilical vesicle relatively diminishes in extent, two possibilities present themselves. The wall of the umbilical vesicle may separate on the whole surface from the diplotrophoblast, with exception of the proamnion-area (the entyped forewall of the germbladder). In this case the typical fruitbladder of *Primates* appears, where the embryonic rudiment with the small and free yolksack is suspended in the large trophoblastbladder by an archamnion-stalk. If however the umbilical vesicle remains attached to the diplotrophoblast at various points, its wall, being outdistanced in growth by the latter, will be torn to pieces as the wall of the fruitbladder increases in extent. This happens in Rodents with inversion of germ layers, where the yolk-entoderm remains in connection with the trophoblast-layer. In this case it presents a continuous layer below the embryonic shield only, but it is not able to coat the wall of the whole germbladder on the inner side¹⁾. Consequently the cavity of the yolksack opens into the trophocoel.

I think we may start from similar conditions, if we wish to understand the phylogenetic evolution of the sauropsidan egg. We have only to imagine that in the common umbo-trophocoel yolk-material is deposited, as the primitive viviparity of Protamniotes changes into the secondary oviparity of Prosauropsida, that further

¹⁾ See esp. SELENKA, l.c. H. I, 1883, p. 16, T. I and II and H. III, 1884, T. XI and XII.

Dr. DAN. DE LANGE Jr.: "Critical and theoretical considerations about the origin of the primary foetal membranes in Vertebrates".

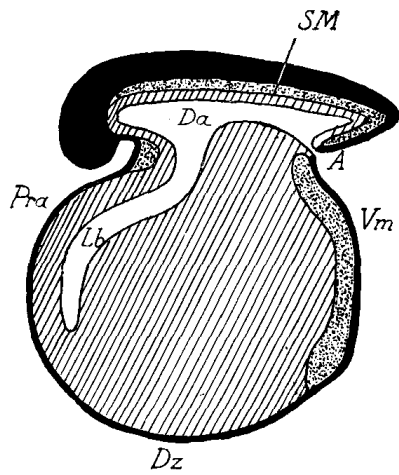


Fig. 1.

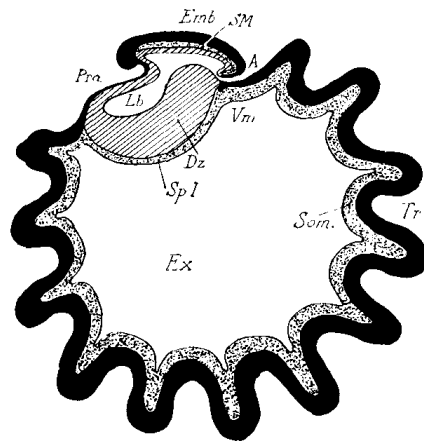


Fig. 2.

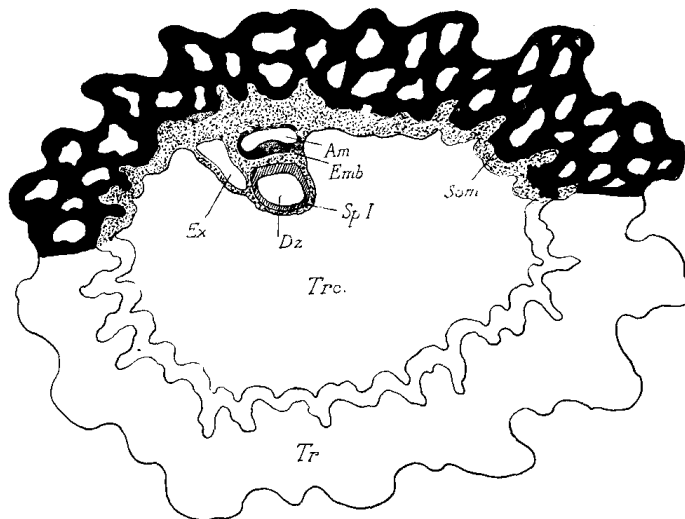


Fig. 3.

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the reduction of the yolk-entoderm at the anti-embryonic pole is continued and is followed by that of the trophoblast cells, the latter losing for the greater part their respiratory and nutritive function and the scheme of the Sauropsidan egg is realised. Even in Rodents there is already an indication of this reduction of trophoblast cells at the anti-embryonic pole¹).

EXPLANATION OF THE PLATE.

Common abbreviations.

A. anal aperture. *Am.* amnion cavity. *Da.* intestine. *Dz.* umbilical vesicle resp. yolk-sack. *Emb.* embryonic area. *Ex.* exocoeloma. *Lb.* liver-outgrowth. *Pr* proam-nion-area. *SM* segmented body mesoderm (somatic mesoderm). *Som.* somatopleura. *Spl.* splanchnopleura. *Tr.* trophoblast. *Vm.* ventral mesoderm.

Fig. 1. Diagrammatic median section through an amphibian larva with large yolk-sack.

Fig. 2. Hypothetic transitional form between a yolkladen amphibian larve and the germbladder of viviparous Protamnota (median section).

Fig. 3. Diagrammatic median section through a germbladder of a Primate with ectoplacental proliferations on all sides.

In all the figures ectoderm is shown in black while mesoderm is dotted and entoderm hatched.

Chemistry. — “*Chemical actions in the subsoil of the dunes.*”

By Dr. J. VERSLUYS, M. E. Communicated by Prof. J. BOESEKEN.

(Communicated in the meeting of March 25, 1915).

In the dunes and the sub-soil thereof water containing the principal ions of sea-water is as a rule found at a slight depth but in quite a different proportion, as the ions Ca and HCO₃ are very predominant therein.

Still, the concentration of the Ca-ions, which in proportion to the other ions occur in very large quantities, is smaller therein than in sea-water. At a greater depth water is generally found in which the ions occur in about the same concentration and the same mutual proportion as in sea-water.

The water of the first class will in future be called the normal fresh water, the other the normal salt water.

As chief ions may be mentioned

Na, Mg, Ca, Cl, HCO₃ and SO₄.

In the normal fresh water, the concentration of all the ions is

¹) See SELENKA, l.c. H. I, 1883, Fig. 21, 24 and 25, T. II, and H. III, 1884, Fig. 9, T. XI, Fig. 13, T. XIII, Fig. 30, T. XIV and Fig 44, T. XV.