On certain problems of vertebrate embryology / by John Beard.

ON CERTAIN PROBLEMS
OF
VERTEBRATE EMBRYOLOGY.

BY

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"Eine Larve, welche die neue Generation erzeugt hat,"
"hat ihre Aufgabe erfüllt und kann vergehen — die"
"Entwickelung geht doch fort."

C. E. VON BAER.

JENA,
GUSTAV FISCHER.
1896.

Preface.

Twelve months ago, in a paper published in the "Anatomischer Anzeiger" and in the Annals of Botany in conjunction with J. A. Murray, it fell to my lot to point out the bearings of the doctrine of an antithetic alternation of generations (as underlying reproduction and development) on the phenomena of the reduction of the chromosomes during oogenesis and spermatogenesis, and on the meaning of the processes involved in the conjugation of the Infusoria.

Twelve months later circumstances have brought me, in the course of similar enquiries, to an examination of the bearings of this theory on the developmental processes of the higher Vertebrates, the Mammalia and man himself.

The rapidity with which the whole series of enquiries, including those into the transient nervous apparatus of various Ichthyopsida and into the history of the yolk-sac and contents, has been, and is being, effected, is more apparent than real.

It has, in truth, required eight years of hard work, often performed under discouraging external circumstances, and interrupted by exacting duties, to attain a standpoint

from which tangible results could be grasped at and secured.

The starting-point for my researches was an investigation of the early development of *Lepidosteus*, and, notwithstanding the novel character of some of the results of a preliminary study of that, the writer has been blamed for deserting the original subject for "fresh fields and pastures new".

But the line of research has since its commencement in September 1888 shaped its own course, and, often starting off anew at a tangent, it has carried the observer along in its current. When zoologists and anatomists read the present paper along with a recent memoir of mine on *Raja* and other forthcoming ones on *Scyllium* and other forms, they may judge for themselves as to whether the end has justified the means: as to whether or not embryological science has been better served by the postponement of a fuller account of the development of *Lepidosteus* in favour of other themes.

The simplicity of the results contained in the present paper is their best recommendation. The reader may often be astonished at the elementary and obvious nature of the explanations offered of various things; loss of yolk, immature birth of Marsupials, allantoic placenta etc.; but he may be asked to bear in mind that, but for the arduous labours of many embryologists, labours that withal often appeared to yield only results disproportionate to the time expended upon them: but for my own long struggles with the history of the transient nervous apparatus; and but for the circumstance that the theoretical fate of the yolk-sac, its contents and the merocytes, found an actual confirm-

ation in fact, the present paper, which appears to furnish natural explanations of so many things of which previously nothing was known, could not have been written.

The merit, if there be any, is not mine. It was all dependent on the unearthing of the master-key of antithetic alternation, and on the unmasking of a fixed and corresponding critical stage in the development in various animals.

As often happens, such a master-key has been found to open many locks, and none, as yet tried with it, has failed to yield to its gentle pressure.

This master-key is probably, as was elsewhere indicated, one that can be universally applied in all but the very lowest forms of life.

All that it has been attempted to prove for the Vertebrates can, in my opinion, be established, *mutatis mutandis*, for most, if not for all, of the Invertebrata. In Coelenterata an antithetic alternation of generations is very generally obvious, but it is not quite similar in its details to that which would appear to obtain in the higher Metazoa above them. Regarding these, the general principles, enunciated in various recent publications of mine, will, I am convinced, be shown to hold good here also; for, as an instance, and as significant of the existence of a critical stage, does not Kleinenberg write concerning *Lopodorhynchus* that the suppression of the larva begins when the "Anlagen der Organe des Annelids eine gewisse Selbstständigkeit erreicht haben"?

So it is in the Vertebrata at the critical stage, and so it will prove to be in the majority of the Invertebrata.

With many of its devotees current embryology has largely degenerated into a wild-goose chase after homologies between holes and spaces in various animals, in utter disregard of the boundaries of these. To those who have had a surfeit of this kind of embryological research, which satisfies only where a very little makes for contentedness, the newer embryology of antithetic alternation may require no commendation. Embryological work carried out on the new basis, whatever else it does, yields *new facts*. Once the standpoint is reached, where an antithetic alternation becomes recognised, facts come with amazing rapidity.

We have, indeed, in embryology reached a parting of the ways, where a decision, as to the path along which future work shall lie, must be taken.

There is, so it appears to me, only one course open to future research, and that is along the track of antithetic alternation. It is the goal which the two great Masters of embryology, Carl Ernst von Baer and Johannes Müller, almost reached, and, if we revert to the point at which they left off, our increased knowledge of the phenomena of development will infallibly reveal to us the narrow trail leading thence to the well-defined track of alternation of generations.

26th June 1896.

Contents.

"Today I saw the dragon-fly
Come from the wells where he did lie.
An inner impulse rent the veil
Of his old husk: from head to tail
Came out clear plates of sapphire mail.
He dried his wings: like gauze they grew:
Thro' crofts and pastures wet with dew
A living flash of light he flew."

Tennyson — The two voices.

Introduction.

There exists a period in the history of every belief when it is held less on evidence than on faith. Sooner or later mens' minds begin to inquire into the basis of fact on which the conclusion was originally formed and if there was, as may happen even in science, no original groundwork of fact for the views in question, they proceed to search, as diligently as may be, for something which may serve as a reason for their belief. In such cases the result may vary, and more often than not the original view has to undergo fundamental modification, even if it escape total abandonment. Such a belief in zoological science is the so-called recapitulation-theory.

Originally enunciated at a time when Embryology as a science barely existed, it commenced to grow and expand, until it soon extended far beyond the narrow ground of fact on which it was first planted, and, instead

of receiving nutriment for its new branches from fact, it was diligently fed by the fancies of those who presided over its early life, and, ultimately, its branchings and foliage became so rich, that for a time people forgot to seek for the sources of these.

But among the ardent disciples of the „biogenetic law" there were those who sought to give it a firm foundation in fact by extended researches on as rich and abundant a material as could be obtained. The sequel has, so far as such fundamental researches have been carried out, not been of a kind favourable to the theory.

Is this to be looked upon us at all unexpected? We have indeed had "phylogenies" and "histories of the evolution" of this or that group, or even of the whole animal kingdom, but these, in so far as they have been presented in detailed fashion, and in as far as they have been, or may be supposed to have been, based on the facts of Comparative Embryology, although they have emanated from the pens of eminent zoologists, have usually not been written by embryologists versed in knowledge of the actual processes of development.

It is surely of much significance to note that in the group where a knowledge of the course of the phylogeny would be of most interest, i. e. in the Mammalia, no embryologist versed and skilled in Mammalian embryology is prepared to come forward and enunciate from his own and from existing work on the embryology of Mammals a phylogenetic history which would bear examination!

The recapitulationists are more inclined to devote their oracular deliveries to generalities, and, more often than not, where their statements relate to a particular animal, or to

a small group of such, they are wrapped up in vague terms and leave unsaid things of far more importance than those actually enunciated [1]).

Of the ancestry of the Vertebrata, or, as they are more usually termed where phylogeny is in question, the "Chordata", there exists an extensive choice of theories, and hardly a single invertebrate group, small or large, remains which has not had *nolens volens* the parentage of the Vertebrata thrust upon it.

The Vertebrate morphologist lives in a state of constant apprehension, lest the discovery of some new and curious Invertebrate should also unearth a new claimant towards the honour of being the only true Vertebrate ancestor. He knows only too well from experience that his consent to the parentage will not be asked, and that probably all that he and his fellow workers have laboriously unearthed in the actual embryology of the Vertebrata will either be ignored, or, if made use of, then in a manner which must excite his profound astonishment. He may learn that the tongue-bars of the gills of *Amphioxus* represent the thymus, he may, with amazement, hear that, before animals were Vertebrates, their stomach lay in that holy of holies, the brain, and he may witness the gradual — no, the sudden, evolution of two new sets of reproductive organs to replace an original ovary or testis, which was presumably too much imbued with Invertebrate traditions to be able to continue to function as the starting point for a new race of animals with backbones.

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1) Many of the strongest supposed proofs of recapitulation have relation only to organs and not to organisms.

But enough of phylogenetic theories. When a skilled embryologist sets to work on a vast material to examine into the application of the "biogenetic law" to his own particular animal, then, whatever the result may be, his procedure commands respect and approval.

A hypothesis, and in this case the biogenetic law is a hypothesis, is always justifiable until it be proved to be contrary to fact. When, as in the instance held in view, the investigation results unfavourably for the hypothesis, we can but conclude, either that the hypothesis was wrong, or that the author's results are false. If the latter alternative, as in Keibel's case, is to be put out of court, there remains but the former. And it is that which Keibel urges as the proper conclusion, for, as he emphatically remarks [1]): "Bei Säugern kann man, wenn man den gegenseitigen Entwickelungsgrad der Organe im Organismus ins Auge faßt, von einer Wiederholung der Phylogenie in der Ontogenie durchaus nicht sprechen; das "biogenetische Grundgesetz" wird hier, wenn man so sagen darf, nur durch Ausnahmen bestätigt, d. h. mit einem Wort, von einer Geltung des biogenetischen Grundgesetzes kann für die Säuger in der angedeuteten Hinsicht überhaupt nicht die Rede sein".

In the preceding remarks phylogenetic history has only been referred to, because, in the form of recapitulation, it was supposed to be more or less written into the life-histories and development of animals, and hence seemed to explain all the mysterious processes and transformations, which may occur during these.

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1) Keibel, F., Studien zur Entwickelung des Schweines, II. Morph. Arbeiten, Bd. V, p. 76.

Recapitulation was thus looked upon as the ultimate cause of the processes of development, for in the words of one author [1]) "every animal is obliged to climb its own genealogical tree, seeking its pedigree in the course of its own development".

If this be not the case, it follows that some other explanation of development must be sought for.

There may possibly be several methods, which *a priori* might serve as explanations of the developmental history. I confess to no desire to enumerate these, or to weigh their claims. Having myself been gradually forced by the facts unearthed in the long slow course of research to adopt an antithetic [2]) alternation of generations as underlying the development of several members of the various divisions of the Ichthyopsida, and believing there to be no escape from the conclusion that all the higher Vertebrates had a piscine ancestry, and finally, from repeated examination of the facts available regarding Invertebrate development and that of Vertebrates above fishes, having been led to a recognition of numerous facts favourable to such a conclusion for nearly every group of the animal kingdom, it has seemed to me a natural and reasonable course to endeavour to obtain recognition for this probable law of development among zoologists and anatomists.

It is a reasonable view to take, if only because it is the acknowledged mode of development of a great portion of animate nature, viz all the higher plants [3]).

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1) The late Prof. A. Milnes Marshall.

2) As opposed to a homologous alternation.

3) To prevent prejudice what has been already said elsewhere may be once more repeated, viz. that my own adoption of

It is a natural view, because, as it seems to me, the facts only admit of such an explanation, and, until it be proved to be untenable, it must to myself and to those who have mastered, understood, and accepted it, appear to be the only reasonable and natural explanation of Metazoan development.

I. The characters of the critical stage in the Elasmobranch Fishes.

Among my recently published results of the investigation of the transient nervous apparatus of *Raja batis* [1]), to my mind, one of the most striking was the discovery that the degeneration of the transient system was always initiated at a fixed point in the development, and this has been found to hold good for *Scyllium, Pristiurus, Lepidosteus, Salmo, Triton* and other forms.

So sharply characterised was this stage that it soon became a matter of comparative ease to pick out an Elasmobranch embryo of this period, and then to find the external diagnosis confirmed by the microscopic examination of sections.

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an antithetic alternation of generations originally came about from the factors of animal development, and was never influenced in the slightest degree by any consideration whatever as to the nature of that of plants.

1) Beard, J., The history of a transient nervous apparatus in certain Ichthyopsida, Pt. I, *Raja batis*. Zool. Jahrb., Morph. Abtheil., Bd. IX.

What are the constant features which every Elasmobranch embryo presents when degeneration in the transient system is initiated? These characters of the embryo were only incompletely enumerated in the part of my work already published. More recently the examination of the "critical stage" in *Scyllium canicula,* followed by renewed study of the skate sections, has furnished a greater precision to the definition of the stage in question. It was soon found that, when a direct comparison between the two forms, the Selachian and the Batoid, was made, the correspondence was exact in almost every particular, and that in the two cases practically all the organs of the embryo of the fish were in corresponding stages of development, nay more, that practically, — for as yet I know of no exception to this statement, — all the organs of the fish were laid down and histological differentiation had begun in all. The stage, then, was seen to be a constant one, and in all the cases examined it was found to be bound up with a series of constant characters [1]) in the various organs of the embryos of the different fishes studied. As to the points that mark this period in the development, they are the following: —

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1) These only vary in minor respects in different oviparous fishes, thus scale-formation has not then been set about in *Lepidosteus, Salmo*, and, of course, *Petromyzon*. And in these three divisions of the fishes it does not appear that the sex of the organism is decided. All this is due, at least so I believe, to the acquisition of a sort of secondary larval life on the part of the young fish comparable to the tadpole stage of the Amphibian. Miall's explanation of this latter (comp. Nature, Dec. 19, 1895) is one with which I entirely agree, and I would extend it to Ganoids, Teleostei and Marsipobranchii.

The embryo is rapidly acquiring the adult form of body, and this is especially the case in the head, snout, and fins. It is then first actually distinguishable as the embryo of a certain species of animal, and from this moment it is rapidly making for the adult form of body. The chorda is becoming intravertebrally constricted by the formation of cartilaginous vertebral centra, and the neural arches are developing. Of great importance, as absolutely fixing the period, and because it was the very first fixed point to be established (as long ago as 1888), is the commencing formation of the posterior fissure leading to the establishment of the permanent central canal in the spinal cord.

The sense organs, except that they are only in course of histological differentiation, are practically those of the adult animal. The lateral line reaches to the tail-end, and in its course the sense organs are mapped out and have openings on the surface of body. The ampullae &c. in the head region are rapidly developing and the main groups are laid down. The naso-buccal groove is established and the Schneiderian folds are present, or, in other words, the nose is like that of the adult. In the eye the lumen of the lens has practically disappeared and some little time previously pigmentation of the retina had set in. In the auditory organ the semicircular canals are completely established and the organ is practically that of an Elasmobranch. In the mouth the beginnings of a dental ridge are encountered. The alimentary canal is rapidly taking on the adult form. The oesophagus is still closed, but the re-opening is slowly in operation. The pancreas, is formed, and very shortly afterwards begins [1])

1) see appendix d.

to function. The cloaca has just opened. The thymus is laid down or almost completely so [1]).

In the urinogenital system the permanent kidney [2]) is in connection with the ureter, the Müllerian ducts almost reach the cloaca, and the sex is for the first time definitely established and, more particularly, internally by ovary or testis and by the diameter of the Müllerian ducts, and externally in the male by the differentiation of the claspers. In the skin, apart from Mayer's "parapodoids", which are transitory structures, the first beginnings of scale-formation are in evidence in the form of a segmental row of papillae along each side of the back [3]), as P. Mayer showed [4]). The slight ossifications of ripe embryos are

1) Whereas at this period the 5 thymus elements of *Raja* are completely separated off from the branchial epithelium, in *Scyllium* this is not usually the case, for here some or all of them are still connected with the place of origin. This is, however, no difficulty, for, as was shown elsewhere (Anat. Anz., Bd. IX, pp. 476—486) the thymus is to be regarded as a specialised portion of the gills, and it would not be surprising to find a Vertebrate animal in which it remained attached to the gill-epithelium throughout life. The main point is, however, that thymus-elements are present.

2) Those embryologists who maintain the existence of various "generations" of renal organs and evolve the second and third of these out of — nothing, overlook the fact that Semper long ago proved that the so-called "metanephros" of Elasmobranchs was only the posterior portion of the "mesonephros".

3) The single point of difference between *Raja* and *Scyllium* in this stage concerns the position in which the first rudiments of scales are developed.

4) Mayer, P., Die unpaaren Flossen der Selachier. M. Z. S. Neapel, Bd. VI, p. 227. Mayer remarks "sie treten ganz früh auf" and figures them in a *Scyllium canicula* of 38 mm, but they are first visible in embryos of about 32 mm. An explanation of Mayer's parapodoids and of their early appearance is attempted in another communication in which analogous structures in *Raja* are recorded and described.

as yet entirely absent, i. e. the skeleton is entirely cartilaginous [1]), so far as it is formed.

Finally, apart from many minor details, there remains one event of far-reaching and fundamental importance to be recorded. In stating this I should like to be permitted to lay unwonted emphasis upon its gravity. At this period the embryo annexes the contents of the external yolk-sac [2]), an internal yolk-sac is formed and the yolk is gradually drawn into it and thence into the gut, where, during the rest of the development within the egg-case, and for some time afterwards, it serves for the nourishment of the young fish and is digested by the cells of the gut. Prior to this stage the embryo only obtained nourishment from the yolk-sac by means of the yolk-sac circulation, and not even directly through this, but indirectly by the intermediation of the "yolk-hypoblast" and the specialised parts of this, the merocytes. Taking the whole of these characters into account, the embryo is now for the first time a young fish, and it is independent of its transitory, or larval, or asexual foundation, it can set about feeding itself, and it is powerful enough to begin the task of suppressing the transient foundation, including the transient nervous

1) This point only becomes important in the sequel.

2) As will be shown elsewhere (Anat. Anz.), in a paper already written, in *Scyllium* and *Raja* the epiblastic and mesoblastic coverings of the external yolk-sac shrivel up and are absorbed (this is hardly new). The hypoblastic lining breaks up as the yolk leaves it, degenerates and is absorbed. The merocytes degenerate and atrophy. In *Lepidosteus* there is a peculiar "self-sacrifice" of the merocytes, which results in their break-up and digestion. (see appendix a.)

apparatus, the merocytes and yolk-hypoblast, the notochord [1]) and other evanescent structures.

The starting nature of the whole discovery in *Raja batis* and *Scyllium canicula* naturally led to the investigation of other cases among the Ichthyopsida [2]), and in all of those examined, apart from minor differences, which, as will be demonstrated elsewhere, are never insuperable difficulties, in all cases this critical period, where the embryo first begins to be what the development is aiming at, could be fixed upon with ease from the then existence in the embryo of the majority of the above characters.

II. On modifications in the characters of the critical stage in certain Ichthyopsida.

Marsipobranchii, Ganoidei, Teleostei and some, if not all, Amphibia present certain typical departures from the characteristic points of the critical stage of *Scyllium*. This stage is undoubtedly present in all these forms, and it

1) The question as to whether the notochord belonged to the larva or to the adult has been long and anxiously considered. Here is not the place for weighing the pros. and cons. of the matter, but its fate at the critical stage in the vast majority of the Vertebrata seems to leave no escape from a conclusion as to its larval nature. The result is not an unwelcome one, for it leads to a closer association of the Vertebrate and Ascidian *larvae*. The remark may also be permissible that in my opinion Kleinenberg's substitution of organs is not usually really any such thing but that it has its basis in a substitution of organisms.

2) see appendix 1.

presents certain of the more important features that define the same period in *Scyllium* or *Raja*. But, along with these, certain other characteristics have not yet developed.

The most important of these differences is the as yet non-differentiation of sex, and, often along with it, there may be the absence of scale rudiments (Ganoidei, Teleostei) and of paired limbs (Amphibia).

Thus, it becomes of importance to enquire into the reasons which explain the apparent anomalies.

My task here is lightened or, indeed, the burden largely if not entirely removed from my shoulders, by the existence of a valuable paper [1]) by L. C. Miall.

Although Miall's publication professes by its title to deal solely with the transformations of Insects and with the nature of the so-called insect larva or caterpillar, it also contains a valuable and exceedingly interesting discussion of the supposed larval nature of the tadpole stage of Amphibians.

Miall's arguments (p. 153) cannot be reproduced here: any condensation of them would destroy something of their cogency. One passage only need be quoted and it runs as follows: —

"Adult transformation [2]) is rare among free-living animals, though parasites furnish many examples. The Ctenophora, instead of settling down early, maintain a pelagic life, and become specially modified thereto in a late stage of development. The secondary sexual characters assumed by some birds and mammals at the time of

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1) Miall, L. C., The transformations of Insects. Nature, Dec. 19, 1895, pp. 152—158.

2) As opposed to "larval transformation".

sexual maturity, such as the train of the peacock or the antlers of the stag, are analogous facts. But the closest parallel to the transformation of insects is to be found in the Amphibia. Frogs and toads, having already as tadpoles attained the full development of the more primitive Amphibia, change to lung-breathing, tailless, land-traversing animals.

. . . . . It is by virtue of their adult transformation that both the amphibian and the insect are enabled to wander from the place of their birth, to seek out mates belonging to other families and to lay their eggs in new sites.

In those Amphibia which undergo transformation, the stage added to the life-history of the more primitive forms is not the tadpole, but the frog or toad. In those insects which undergo transformation, complete or incomplete, the winged state is the new addition. If a pupa appears in the life-history, it results indirectly from the acquisition of wings by the adult. Hence it seems to me that in Amphibia and insects the peculiar change, which renders possible all the rest, belongs to the adult condition, i. e. these animals undergo an adult metamorphosis" [1]).

Agreement may be expressed, in the main, with Miall's arguments, and, entirely, with his conclusions. It can easily be shown that the tadpole is not — and Miall states that it is not — a larva in the sense in which we speak of an Invertebrata larva. It is not an asexual form upon which a sexual generation arises: The true alternation and the true larval phase here, as in insects

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1) loc. cit. p. 153.

and as in other forms, happen at an earlier period of the development.

But owing to this secondary adult metamorphosis, which it is Miall's service to have pointed out, the sexual characters, the development of limbs, and some few other things get carried forward from the true critical stage to a far later period when the adult transformation occurs.

Mutatis mutandis, for every case may differ in some slight details, the same is true of Marsipobranchii, Ganoidei and Teleostei, in which, so far as can at the moment be seen, the establishment of sex, and, it may be, the development of skin scales, (while teeth may then be developed!) are transferred from the critical period to the later adult metamorphosis [1]). In another connection many of these cases may be considered elsewhere, and here it will only be insisted that in all of them the critical stage is a very marked one, and that the apparent deviations are explained by considerations relating to an adult transformation very like what Miall ascribes to insects and Amphibia.

III. As to the existence of a critical stage above the Ichthyopsida.

It then became an interesting enquiry, that as to the existence or non-existence of such a stage in forms above

1) The asymmetry of flat-fishes is also probably brought to pass by a similar secondary adult transformation.

the Ichthyopsida. It had some years ago been insisted [1]) that the alternation of generations which was believed to underlie the development of the Ichthyopsid must, albeit in reduced form, be also existent in the higher Vertebrates. Certainly there was little or no hope of finding a larval or transient nervous apparatus [2]) in these at any stage, for, with the cessation of development in water, and again, with the initiation of uterine development, there was no longer a free existence for the larva, and thus no *raison d'être* for a larval nervous system. But in all these higher forms the embryo arises on a blastoderm, it has transitory structures in the form of an amnion, and, it may also be, an ectoplacenta and an external yolk-sac, full or empty, are formed. This yolk-sac obtains a covering by the growth of the blastoderm, and all these structures together may be taken as representing the asexual generation or larva. Hubrecht [3]) has most ingeniously derived the trophoblast and amnion from the outer layer of the epiblast of Amphibians. My own view is in entire agreement with his, for I have long regarded

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1) Beard, J., On a supposed law of Metazoan development. Anat. Anz., VIII, 1892, pp. 27—29.

2) As a matter of fact such a larval nervous apparatus always tends to become suppressed with development on land. No such thing is known among the Insecta, for I agree with Miall (Nature, Dec. 19, 1895) that the caterpillar stage is not a true larval stage at all, but that the caterpillar is a young insect with an adult metamorphosis. At the same time there is, as Kennel has tried to prove, a larva, or rather the remains of such, in the form of amnion, serosa, and, I would add, indusium. In fact, as an attempt to prove will be made elsewhere, the alternation is apparent even here.

3) Hubrecht, A. A. W., Die Phylogenese des Amnions etc. Verhandl. K. A. Wiss. Amsterdam, 2. Ser., Theil 4, No. 5, pp. 1—66.

this layer in the frog-development as a larval epiblast and have definitely stated it regarding that stratum in *Lepidosteus* [1]). The resolve to make a search for something equivalent to the critical stage in higher Mammals was already made, when, through the kindness of the author, a copy of Keibel's monograph on the development of the pig, Part II, came into my hands [2]).

Quite apart from my own particular idea the monograph was exceedingly interesting on account of the arguments concerning and culminating in the rejection of any attempt to establish the recapitulation theory for the higher Vertebrates. But of far more import was the fine series of pictures of pig-embryos which Keibel gives. These arrested the attention, and it soon became clear that in all probability my sought-for critical stage, if existent, must either be among them, or very near to one of those depicted.

Bearing in mind what had been made out concerning this stage in *Scyllium*, as before detailed, it became an easy task to pick out the embryo from the figures of pl. VII which must represent my quest. This figure was fig. 68, and it was recognised that either the critical stage must be here, or in some undepicted stage between it and fig. 67.

The matter could, of course, be solved by a reference to the normal table of the characters of various embryos, a table which Keibel has, to his credit, so laboriously and so well compiled.

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1) Beard, J., The early development of *Lepidosteus osseus*. P. Roy. Soc. Lond., Vol. XLVI, p. 111.

2) Keibel, F., Studien zur Entwickl. des Schweines, II. Morph. Arbeiten, Bd. V, pp. 17—168, 7 plates.

At this juncture one material remark may be permitted. It may rightly be demanded that any stage in a higher Vertebrate presumed by me to fulfil the conditions of a "critical stage", such as that described for *Scyllium*, shall fit into the scheme without compulsion. This is like the requirement which His makes for a normal human embryo, viz: — that, without being forced in, it shall fit into the series of normal embryos. By and by it may be possible to make, from my own researches and from those of others, a normal table of the "critical stage" in an extensive series of Vertebrate embryos from fishes up to and including man, and in such a table [1]) no embryo must be figured and recorded which does not in the main, without distortion, fulfil all the requirements.

Returning to the matter under discussion, the characters of stage 68, as given on p. 66—67, showed themselves to be such that there could be no question that there was other than a very close agreement between this stage in the pig and the critical stage in *Scyllium*. This is revealed in the appended table [2]),

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1) A preliminary table of this sort is that appended to the present communication.

2) In the table all statements not taken directly from my own observations or from what is said by Keibel or Selenka for particular embryos are marked by enclosure in brackets. The headings have been taken from Keibel's work on the pig already cited. One or two slight alterations have been made partly with a view to saving space, and partly to render the comparison a little more complete. Thus, the limbs are dealt with under the heading "form of body", and the notochord and vertebral column are taken together. The ear-column is omitted, not because this organ fails to fit into the scheme, for it does so perfectly in my own material of fishes, birds and mammals, but simply from the

where the more important statements of Keibel concerning stage 68 may be compared with my finds for *Scyllium* and *Raja*.

There are only two points in which observations appear at first sight to be at variance in the two cases. These are both important.

Of special import is the point as to the very first commencement of the formation of the posterior fissure and central canal of the spinal cord. Keibel does not mention it, which, in view of the excessive importance to be attached to this phenomenon, in view of the fact that this marks, as was long ago recognised, the initiation of

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difficulty of filling in the details of cases cited from other authors. Thus Keibel makes no statement as to the semicircular canals, though these must be already existent in stage 68 of the pig. The hypophysis cerebri is not included, because it is at best a rudimentary structure, but, it must be added, what I have noticed regarding the beginning of "Sprossenbildung" in other cases is quite on all fours with Keibel's results. In fact, it may be briefly but emphatically declared that not the slightest attempt has been made to "improve" the table by leaving out awkward things. None such have been encountered.

In addition to the five forms, *Sus*, *Scyllium*, *Raja*, *Didelphys* and *Homo*, it is proposed to include five others in the table. Two of these, *Talpa* and *Lepus*, are now ready and, like the remaining three, their critical stages will be briefly defined in the table only. As they confirm all that has been said, further discussion at the moment is unnecessary. *Gallus*, *Anas*, and *Lacerta* are being investigated, and the results will be added before publication of the paper. For my own material additional characteristics could have been noted in the table under other headings, but they would, in my opinion, have been mostly unimportant ones. The best tribute to the excellence of Keibel's tables is the adoption of his headings &c. One very striking thing about Mammalian embryos of the critical stage may be here mentioned, and that is the extraordinary similarity of the transverse sections through corresponding regions of the body in various cases (see also appendices b, c, and l).

degeneration of the larva, and of its nervous system, and the period when the embryo begins to be independent of the larva, is in one respect unwelcome, whilst in another it is acceptable, because it affords an opportunity of controlling the comparison.

The exact determination of this point may not be as easy in a Mammalian embryo as in an Elasmobranch one, for the diagrammatic mode of development of the latter is of the two far the easier to follow. But a re-examination of the embryo may be looked for with the utmost confidence, and I feel sure that, if all else fails, a comparison with stages 67 and 69 will completely establish the truth of my prophecy that, while in stage 68 the commencement of the formation of the posterior fissure has only just been started, the process has gone an appreciable distance in stage 69.

The remaining point concerns the sex of the embryo. This, I hold, though perhaps difficult to determine, is probably already established. Keibel himself doubtless recognises the difficulty there often exists in fixing the period in embryos of higher Vertebrates when the sex is first established. He was able to definitely state the sex in the next stage, and I feel quite convinced that in stage 68 also it is already determined in the embryo.

But now, it may be asked, assuming that all this is so, what does it prove? If there be anything in the comparison of the two stages, if stage 68 in the pig really represent a "critical stage" in the sense of that of *Scyllium*, where is the evidence of the beginning suppression of a larva or asexual generation? What does it all signify?

To this it may be, with all deference, replied, that

if a corresponding stage can be shown to exist in practically all Vertebrates, or good reason offered for an apparent exception, — and this can, I think, be done — something — nay much — is surely gained, for in all the years, during which the recapitulation theory has ruled, it has never been able to yield anything like it!

So far as the particular case, the pig, is concerned, the only evidence of commencing degeneration to be seen, apart from the yolk-sac and amnion, which only leave the scene at a very much later period, is in the notochord [1]).

From theoretical considerations one would expect, as the absence of a larval nervous system is accounted for, that, at any rate, there would be some change in the mode of nutrition of the embryo comparable to the annexation of the contents of the yolk-sac in *Scyllium*.

The same sort of thing is here quite out of question, for the yolk-sac, though existent, is quite empty, and it would only afford the embryo a Barmecide feast.

A suspicion appeared warranted that here some important alteration in the mode of nutrition of the embryo by changes in the placentation was inaugurated, but unfortunately at present we know too little of the history of the placenta [2]) in the pig to be able to say any thing at

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1) And in another larval structure, the *hypophysis cerebri*.

2) The same difficulty regarding the placental changes crops up again and again in dealing with different Mammals. One main reason of this is that, in describing a particular phase of the placenta, observers have not seen fit to give a picture of the embryo to which it refered, or to describe the state of the organs of the embryo. It is much to be hoped that in this respect a new era in embryology may be now initiated.

all definite and decisive about the matter. It may be frankly confessed that I was in a dilemma, but — — — not for very long! Changes must, if there was anything in the correspondence, have at some epoch or other in the past have been carried out at this period of the development, and these changes must have ultimately led to the evolution of the placenta and its original formation at the critical period.

IV. Correspondence of the critical stage in *Scyllium* with the birth-period in *Didelphys*.

Where should one look for light upon the matter? At once it was recollected that the Marsupials are described as being born in a very immature condition, and that in connection with this fact they have generally no allantoic placenta. The existence of a yolk-sac placenta was no difficulty, for it had long been recognised that such a connection was merely larval in nature.

Why should the Marsupials, it was asked, be born into the world in an immature condition? What is the meaning of it all? And — *in what stage are they born?*

The latter question was the crucial one. The enquirer said to himself, "if you are right as to the meaning of the critical stage, and as to its existence in the Mammalia, then in all probability the Marsupials with no allantoic

placenta **are born at the equivalent of the critical stage of *Scyllium* and *Sus***".

Selenka's magnificent monograph was at once consulted and, fortunately for the theorizer, it was abundantly evident **that in practically every essential point, as may be seen from the normal table of comparisons, confirmation of the theoretical answer was to be found.** An examination of Selenka's figures and text will convince the sceptical reader that everyone of the statements in the table concerning the Opossum is in one form or other really contained in Selenka's memoir [1]). There are no particulars given as to the first development of teeth, but C. Röse (Anat. Anz., Bd. VII p. 639 et seq.), who worked out the tooth-development of *Didelphys* in Selenka's sections, records the find of the first trace of a dental ridge in an embryo of $6^1/_2$ days, and states that in the new-born [2]) Opossum it is "stellenweise kolbig angeschwollen" (p. 642).

Thus, a momentous result is obtained — momentous in its bearings on the Eutheria, viz: — that in the Opossum and probably also in other non-placental Marsupials, the

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1) In a more recent memoir (Studien &c., Heft V, 1891) Selenka describes the developmental history of *Hypsiprymnus*, and on p. 185 he describes the newly born young of this form as "sehr ähnlich" to the new-born Opossum, but it is only right to add that he also states that the former "in der Ausbildung des Körpers und der Organe hinter" the Opossum "etwas zurücksteht". It may, in view of the close resemblances noted, be doubted if this is at all seriously the case. The figures do not go to prove it, and the facts stated are on all-fours with corresponding facts in the Opossum-memoir.

2) The reader may be reminded that, according to Selenka, the Opossum is born when barely eight days old.

young Mammal is born as soon as, by developing hair and the presence of mammary glands, (not to speak of other characters), it is recognisable as a Mammal, that its sex is then first established, **that a new mode of nutrition by means of mammary glands is initiated, and that this stage corresponds with an exactness that is marvellous with the stage in *Scyllium* or *Raja* when the embryo is able to set about the suppression of its larval foundation.** In the latter case the embryo is first recognisable as a fish, in the former, the Opossum, it has then by its hair and mammary glands revealed its Mammalian nature.

V. An enquiry as to the existence of a "critical stage" in human development.

When it thus became apparent that the "critical stage" of the Ichthyopsidan development had its representative in two such typical Mammals as the Opossum and the pig, an extension of the enquiry was urgently called for.

On the one hand an attempt had to be made to find this phase in representative Sauropsida, such as the lizard and chick, while on the other confirmation for a general thesis had to be looked for in the highest Mammals as represented by man.

As a sufficient material of lizard- and chick-development was either in store, or could be easily obtained, it

was argued that, given sufficient stages, it ought *a priori* to be a matter of ease to pick out the embryos of importance, for they would be those which first showed a strong and marked tendency towards the adult type. At the time of writing this several embryos of these two forms have been photographed, and an examination of the sections can shortly be made. At the present moment any very detailed search among embryos of various Mammals, except in the case of *Talpa* and *Lepus*, is, in my own case, a matter of impossibility. Rich and abundant as is my collection of embryos of Ichthyopsida —, so rich that, outside of the Zoological Station of Naples, there probably exists no other collection approaching it in number and variety, — it is correspondingly deficient in representatives of the group of Mammals.

This would not be a matter of very great regret to me personally, if there existed in the literature of embryology accounts of the development of various Mammals containing tables of the state of the organs and pictures of the embryos at various periods of the development.

Apart from the monographs of His on the human embryo, Selenka on the Oppossum, and Keibel on the pig, such detailed accounts have at the moment hardly any existence.

The older memoirs of Remak, Bischoff and von Baer, valuable though they be, are too full of gaps and deficiencies to be of service in the enquiry.

Naturally, wherever possible. I prefer to pick out my embryo from a series [1]) described by some other observer,

1) In this connection Bonnet's researches on the development of the sheep would have been of service had the results been published to a sufficiently late stage.

for such a course has the advantage of placing the comparison beyond the suspicion of subjectively having read into it things having no existence anywhere else than in the imagination.

There remains then, from the observations of others, only the case of the human embryo to be dealt with.

It is an unfortunate circumstance that, excellent as are the accounts in existence concerning various human embryos, more particularly those contained in the classic researches of His, the tables of characters of these embryos, where they are to be had at all, are lamentably deficient. And this is so much so, that regarding no single human embryo, which might be expected to fulfil the conditions requisite for insertion into the comparative table, could information be obtained throwing light upon the state of development of some of the most important organs, and this without considering the placenta, for, as it happens, our knowledge of the changes of this structure during the 7th week of development is at the present time very limited in extent.

From His' normal table it is a matter of comparative ease to pick out the stage which ought theoretically to fulfil the conditions required of a "critical stage".

This would lie somewhere about fig. 22 and fig. 23. These are the earliest embryos which are distinctly Mammalian and human in form. The normal length of the embryo (XCI) of fig. 22 is given by His as 16 mm, that of fig. 23 (*Ltz*) as 17.5 mm.

It may interest the reader, as bearing out my argument, to hear what His himself writes concerning this

period of the development. In the introduction to the Chapter on embryos of the second mouth he says: —

"Mit Absicht nenne ich das junge Geschöpf am Schluss des zweiten Monats bereits Fötus und nicht mehr Embryo. Wenn diese beiden Ausdrücke überhaupt einen getrennten Sinn haben sollen, so kann es doch offenbar nur der sein, dass wir den werdenden Organismus Embryo nennen, so lange derselbe noch eine provisorische, nur zur Einleitung der definitiven dienende Gliederung besitzt. So sind z. B. Urwirbel, Schlundbogen, Wolff'sche Leiste u. s. w. embryonale Organe, welche später in unveränderter Form nicht persistiren. Von einem Fötus reden wir dagegen da, wo die Gliederung bereits den Charakter der bleibenden angenommen hat. Vollzieht sich auch die Umwandlung des Embryo in den Fötus nicht mit einem Male, so können wir doch constatiren, dass von einem gewissen Zeitpunkte [1]) ab der sich entwickelnde Körper eine Form angenommen hat, die über seine Natur keinen Zweifel mehr lässt. Noch bei einer Länge von 12—13 mm sieht ein menschlicher Embryo so aus, dass nur der erfahrene Forscher ihn unbedingt als solchen erkennen wird. Bei einer Länge von 16 mm dagegen wird die Form auch dem unerfahrensten Auge als die eines werdenden Menschen kenntlich sein. Der Uebergang vom Embryo zum Fötus fällt demnach beim Menschen ungefähr in die Entwickelungsstufe von 13—16 mm. Nach Ueberschreitung dieser Stufe sind die Gestalt des

1) The period here mentioned can now be more exactly defined as that in which the embryo, passing through the critical stage, emerges, in the terminology of human embryologists, as the foetus.

Kopfes und die Gliederung der Extremitäten definitiv menschlich geworden"[1]).

The embryos assigned to this period, i. e. the 7th week of development, have as yet not been described, so far as I am aware, by His.

Fortunately, however, in a recent valuable memoir [2]) Keibel has recorded certain important characteristics of human embryos previously to, in, and subsequent to the 7th week.

The statements are nothing like as full as could have been wished, but the sections still exist, and from them, no doubt, fuller information will shortly be forthcoming. In seeking for the equivalent of my critical stage among Keibel's embryos the one held in view was that in which the first beginning of a posterior fissure-formation could be established. I had previously had the privilege of examining some sections of a fine human embryo of fully 8 weeks, of which Dr. Berry Hart is the fortunate possessor, and had satisfied myself that here the posterior fissure-development had progressed to a considerable distance. Therefore, it was concluded that the stage looked-for was earlier than this, and probably in the sixth or seventh week. Of these periods Keibel's memoir contains particulars of several embryos, and, although for a short time it looked as if the end of the sixth week would yield the phase in quest, this conclusion quickly gave place to a certainty that the "critical

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1) His, W., Anatomie menschlicher Embryonen, II, pp. 44—45.

2) Keibel, F., Zur Entwickelungsgeschichte des menschl. Urogenitalapparates. Arch. f. Anat. u. Physiol., Anat. Abtheil., 1896, pp. 55—156, 5 plates.

stage" must be sought after in embryos of the commencement of the seventh week. Keibel's text-figure 70 of a transverse section of the trunk-region of embryo *H. s. Brn.* put an end to further search; for the eye experienced in the observation of posterior fissure-formation recognised without difficulty that here the process was just initiated. This embryo is stated by Keibel to lie between figs. 22 and 23 of His' normal table and its age is given as 45—47 days, normal length 17 mm[1]). From the text and figures of Keibel's memoir it became quite clear that information concerning many of the more important characteristics of an embryo of this period could be obtained. So far as these have been gathered from Keibel's work and, more particularly, so for as they relate to embryo *H. s. Brn.*, they are noted without the addition of brackets in the annexed table.

But on several points nothing could be stated definitely regarding Keibel's embryo, and for these it was necessary to search in the literature relating to human embryos of the 7th week. This quest also was as successful as could have been desired, and, as the result, one can confidently say that, except in one respect only, the presence of hair development, a human embryo towards the beginning or middle of the 7th week can without distortion be included in a comparative table of the "critical stage" in the Vertebrata.

The statements in brackets in the table are those not at present recorded for embryo *H. s. Brn.* and in each case an authority is quoted for the developmental fact

1) The passage from His previously cited was only noticed after this conclusion had been arrived at.

ascribed to a typical human embryo of the beginning or middle of the 7th week.

As the case of the human embryo has its special importance, it may be well to record more fully the characters which establish the existence of the equivalent of the critical stage in it during the 7th week.

Keibel states that his embryo *H. s. Brn.* lies between figs. 22 and 23 of His' normal table. The reader will remember that, as quoted previously, His ascribes to human embryos of this period a marked human form, so marked that even a tyro would have no difficulty in recognising it. As its characters show, such an embryo is then for the first time a Mammal, and is becoming for the first time distinctly human. If there existed species of animals very closely allied to man, it is probable that just before this period even a skilled embryologist might have difficulty in distinguishing between a human embryo of the 6th week and a corresponding embryo of a nearly related species [1]). And this absence of very near relatives is, I take it, the ground, which explains the comparative ease with which observers are able to distinguish a human embryo as such even earlier than the 7th week. But, no matter how many near relatives among animals man might possess, by the middle 7th week the human embryo would differ from all corresponding ones of other species, for, not only had it then obtained its class-position as a Mammal, but, like the skate and dog-fish, it was beginning to put on something of the species to which it belonged, and for which its development had been making.

1) A comparison of chick- and duck-embryos just prior to the critical stage will prove the truth of this remark.

From the normal table[1]) it is clear that in an embryo in the stage of fig. 22—23 the face, head, and external ears are those of a human being. The limbs are advanced in development and the digits are mapped out. It is probable that the first rudiments of nail-formation are present, as, according to Hensen, these begin to develop in the 7th week[2]). The chorda, as seen in Keibel's text-figure 70, is intravertebrally constricted by marked cartilaginous centra, and cartilaginous neural arches are developing. From the same text-figure it can be made out that the formation of the posterior fissure leading to the establishment of the permanent central canal is initiated.

Keibel's memoir contains no references to the sense organs of this embryo, but in the literature, more especially in His' great work, the following facts as to these may be found. The human retina commences to be pigmented "towards the end of the second month". The semicircular canals are completely formed and the whole ear, externally and internally, is that of a Mammal in general and of the human species in particular. Jacobson's organ is developed, the choana is open, and the nasal organ is of the adult type. In the mouth the salivary glands are, according to His, laid down, and, as Röse[3]) showed, the first appearance of a dental ridge

1) Keibel has not figured the external appearance of embryo *H. s. Brn.*

2) see appendix o.

3) Röse, C., Ueber die erste Anlage der Zahnleiste beim Menschen. Anat. Anz. Bd. VIII, 1893, pp. 29—32. Description of dental ridge in Hochstetter's human embryo of 11 mm (? N. L.) i. e. free epithelial papilla of tooth described as becoming the dental ridge of the 15 mm N. L. embryo previously recorded by him.

can be detected in a human embryo several millimetres smaller than *H. s. Brn.* According to Keibel the urino-genital sinus is open to the exterior but, — and this is peculiar — the anus is still closed [1]). The same author records that the permanent kidneys are present, that the Müllerian ducts are formed for part of their course, and this is the earliest embryo whose sex he records as definitely established.

Concerning the typical Mammalian structures, mammary glands and hair, there are no particulars as yet available with reference to embryo *H. s. Brn.*, but it is stated by Rein [2]) that the former were first found [3]) in a human embryo of 16 mm N. L. which would correspond to fig. 22 of the normal table. Hair-development does not appear to have been observed in human embryos as early as the 7th week. In the embryos of other Mammals, such as pig, rabbit, and mole, they first appear at or just before the "critical stage" in the form of papillae on the snout, cheeks, and above the eyes. The first hairs to arise in the human embryo ought thus to be those that will form components of the eye-brows, as none are to be expected on the cheeks and snout. The hair-coat of the human species is, however, in such a rudimentary condition, and varies so much at all periods of life in various individuals, that the presence of hair-follicles as a cha-

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1) More recently it has been found that in many cases the anus opens just after this period, i. e. when it is first needed.

2) Rein, G., Untersuchung. über die embryologische Entwickelungsgeschichte der Milchdrüse. Arch. f. mikrosk. Anat., Bd. XX, p. 456 (compare also appendix b).

3) As distinct structures apart from a mammary ridge (comp. appendix b).

racteristic of the „critical stage" may quite conceivably have been lost.

The other characters, when taken together, far outweigh this deficiency, and even negative any judgment adverse to the presence of the "critical stage" in human development [1]).

VI. Probable general occurrence of the critical stage in Vertebrata and its characteristics.

From all that has been described in the preceding pages and in the comparative table it may be concluded that there is abundant evidence tending to prove the existence [2]) of a "critical stage" in the development of every Vertebrate embryo, and that this important phase is represented by equivalent characters in embryos of the various classes. In

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1) At the moment it is impossible to state with certainty of any known human embryo that it is in the "critical stage", and this is so for reasons already mentioned. Given a fair series of embryos of an Elasmobranch, Sauropsid, or Mammal, it is not difficult to pick out two embryos one of which must represent, as judged by its external characters, the stage or phase sought for. An artillerist requires two trial shots before making a hit, the embryologist can be satisfied with one. The first trial of the latter will probably be beyond the mark, but in the second he can make this failure good. Certainly His' fig. 23 of the normal table is of an embryo slightly beyond the phase, and the actual stage is either represented by the embryo of fig. 22, or by Keibel's embryo *H. s. Brn.*, or by both.

2) There are some cases, such as the Amphibians, where this statement only becomes justifiable after a fuller consideration of the special facts.

general terms it may be stated that the stage [1]) in question is the one in which the embryo first reveals itself to be what it has been aiming at becoming, in that it then first can be definitely assigned to its own particular class, and in that it is beginning to acquire a something setting it down as the young of some particular form, and marking it decisively off from those of even allied species.

Its organs are then all laid down, and only the histological differentiation is as yet lacking in many of them. It has, generally speaking, revealed the class to which belongs by the initiation of the development of bony scales, horny scales, feathers, or hair and mammary glands. It has, as a rule, established its own individuality by taking on the characters of the one sex or of the other.

Only of this stage in the various divisions of the Vertebrata can one institute a table of comparisons of embryos of various species, showing a close similarity in characters, which are those common to Vertebrate animals in general; a marked dissimilarity in embryos of different classes in those features, which distinguish the class; and another difference in embryos of different species but of the same class in those traits, which typify genera or even species.

The general resemblance among all the various embryos of this period is a striking one only in so far as it relates to characteristics of Vertebrate animals in general,

1) The stage or phase is not one which is very quickly passed through. It has some duration, but it marks a very decisive turning-point in the development, for, once it is passed, the embryo rapidly puts on the characters of the species, histological differentiation progresses apace, and the embryo increases quickly in size.

it becomes sharply reversed into absence of likeness, whilst maintaining similarity in the degree of development, in points which define class from class, and, again, we find a general likeness in minor characters among the embryos of a single class in this stage united with generic and even specific distinctions in the embryos of various genera and species.

The circumstance that, while the "critical stage" is a corresponding one throughout the Vertebrata, and, indeed, one in which the sum-total of the development of the various organs in any one case is *about* the equivalent of the sum-total of this development in any other instance — that, while this is so, there are class- and generic distinctions, and even specific ones, coming into existence, which sharply define the various embryos, proves that there is here no recapitulation in the sense in which that word has been generally understood, or, in other words, that any Vertebrate embryo does not climb any part of its own genealogical tree in its development.

If there be anything in recapitulation, an embryo must in the course of its individual development pass through some one or more stages of its ancestry. Thus, if it be a Mammalian embryo, it must pass through, among others, a piscine stage.

No zoologist or embryologist would for a moment maintain that it must pass through a stage in which in all its characters it was a fish, but there are those who still believe that a piscine stage, vaguely defined, can be encountered somewhere or other during the development. Usually this phase is supposed to be present when the branchial arches and clefts are developed, but, as Keibel

has proved, there is no correspondence between the two at this period, and in the preceding pages it has been demonstrated that at the only epoch of the development, when a close similarity can be shown to exist between the Mammalian and the piscine embryo, this resemblance, as evidence of recapitulation, is rendered null and void by the presence of typical Mammalian features in the one embryo along with typical piscine traits in the other. In other words, paradoxical though it may sound, a Mammalian embryo only resembles a fish in a number of its characters, when it is already a Mammal!

In the same way the absence of any other of the lower stages in the development of a higher Mammal can be conclusively proved. I would even venture to deny the presence of a Monotreme stage in the ontogenetic history of man, a stage of whose existence Keibel[1]) speaks, notwithstanding his rejection of the applicability of recapitulation to the Mammals.

When the embryology of the Monotremes shall have been worked out, and this, fortunately, is approaching accomplishment, it will doubtless be evident that the only true stage of comparison between Monotreme and human, or other Mammalian, embryo is the equivalent of the critical stage in the two cases. But here again the human or other Mammalian embryo, while generally resembling a Monotreme embryo of the "critical stage", will be seen to differ from it in those characters which assign it to the position occupied by its progenitors in the Vertebrate scale.

1) loc. cit. p. 147.

That the organs may to a greater or less degree individually recapitulate their phylogeny is something that I, for one, have never denied. But this confirms the truth, not of the recapitulation theory, but of the maxim "*omne organum ex organo*".

If this be Keibel's meaning when speaking of a Monotreme stage, i. e. if he limit it to the existence of a cloaca along with a certain condition of rectum and urinogenital organs — and this appears to be so — no objection can, at present at any rate, be offered to the validity of this view.

Any supposed recapitulation of various stages permanent in lower forms in the ontogeny of, say, a higher Mammal can easily be disposed of by a simple "*reductio ad absurdum*".

For the sake of argument let such a series of hypothetical stages as those suggested by Haeckel be taken; although, as must be admitted, it would be unfair to Vertebrate embryologists to assume that any one of them had announced his adhesion to this scheme.

But, unfortunately, there is no other series that can be got hold of, for no one else, except Oppel[1]), has committed himself to anything at all definite. The actual existence of any such series in the development of a higher Vertebrate is disproved by the circumstance that, when the embryo may be supposed to be in any one of

1) While rejecting the applicability of the recapitulation theory to the Vertebrata, Oppel, as cited by Keibel, still thinks the existence of a "Vorfischstadiums, eines Fischstadiums, eines Landthier- und eines Proamniotenstadiums" possible during the development of a Mammal! (Oppel, A., Vergleichung des Entwickelungsgrades der Organe. Jena 1891). Comment is quite superfluous.

the stages, *it is at the same time in them all, and is also a Mammal.* When it resembles most one of the supposed ancestral stages, then, and only then, it resembles them all to a degree varying directly with their grade of evolution in the Vertebrate scale.

VII. On actual and probable changes in the nutrition of the Vertebrate embryo at the critical period.

It has been established that in the embryo of an Ichthyopsid, probably of all Ichthyopsids, important alterations in the mode of nutrition take place at the period coinciding with the commencement of degeneration of the transient nervous apparatus and the first attempts at the formation of a permanent posterior fissure to the cord. In this group these changes may be classified in two categories. In those forms, in which there is a marked yolk-sac, more particularly in the Elasmobranchii and, in a modified way, in the Ganoidei, as represented by *Lepidosteus*, it is then for the first time that the embryo, or sexual form, is enabled to annex the yolk-sac, in order to feed upon the contents of this structure during the remaining portion of its development, until the time shall arrive when it will be in a position to obtain food for itself. And again, in those forms in which the segmentation is complete, i. e. more particularly most of the Amphibia, and probably

the Dipnoi, and in which therefore no true external yolk-sac is formed, it is then that, for a longer or shorter period varying with the available supply, the embryo feeds upon the yolk-cells, which from my point of view are to be regarded as parts of the larva.

It may be added that the conditions in *Lepidosteus* [1]) connect the two extremes, and for a fuller discussion of the facts the reader may be referred to a forthcoming paper. In view of all that happens in the embryo leading up to this degeneration of larval structures and annexation of the yolk-sac, and in view of the close correspondence in the phenomena even in the highest Vertebrates, phenomena whose completion marks the critical stage, it appeared only reasonable to expect parallel, though possibly not always the same, changes in the nutrition of the embryo at this period throughout the Amniota, including man.

With the special cases of the Sauropsida no proper attempt to deal can be made here. It is exceedingly probable that important changes [2]) take place in the case of the chick, and *a priori* some of these might be supposed to be represented by what Duval [3]) has described in connection with the absorption of the albumen or white of the egg. The process, however, is stated to commence at the tenth day of development, and this is far beyond the critical period.

But in the mode of absorption of the yolk some

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1) see appendix a.

2) see appendix c.

3) Duval, M., Sur les annexes des embryons d'oiseau. Journ. de l'Anatomie etc., 1884, pp. 201—241.

alteration may come about, though it would require a new research to establish this [1]).

In the Reptiles too little is known about the later development to allow of any statements whatever at the present moment.

And, therefore, not without regret, one must leave the actual conditions for future investigation. The reader may, perhaps, think that the writer might reasonably be expected to work out and prove the actual existence of things about which he speaks so confidently. Undoubtedly this ought to be done, but there are limits to possibilities, and, moreover, at the risk of a certain incompleteness I prefer to judge for myself, of which problems solutions are at the moment most urgently called for.

And, as is elsewhere in this paper insisted, if the extremes agree, the forms between them cannot present insuperable difficulties.

Just now the case of the Mammalia offers the greatest interest to me personally, on practical and theoretical grounds alike. On the one hand, because of the bearings of the matter on the evolution of the placenta, and on theoretical ones, because what is found to hold good for the Mammals and fishes will probably, *mutatis mutandis*, be also valid for the Sauropsida. If the extremes agree, the remainder are hardly like to be very exceptional.

When the close parallelism between the critical stage of *Scyllium* and stage 68 of the pig was noted, there remained one puzzling point in which it was apparently absent.

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1) see appendix c.

The yolk-sac [1]) of placental Mammals is an empty bag [2]) and the annexation of its empty cavity would not help the embryo in the least. Hence, the change in the nutrition, which was theoretically called for, had to be searched for elsewhere. So far as one could see from a cursory review of what is known of the placenta, there appeared to be no marked change in the mode of nutrition of the embryo Mammal at this period.

But the point is, as will be seen, difficult to decide in almost any case, and specially so in that of the pig. The details of the placentation have hardly been worked out at all in the pig, and even in such instances as the rabbit it is difficult to bring a certain stage of the embryo into close correspondence with its equivalent grade of placental development. And this arises simply and solely from the circumstance that, when a particular stage of placental development has been described, the observer has concerned himself too little, if at all, about the state of the organs of the embryo to which it belonged. There are exceptions, but these are few and far between. A picture of the embryo is not sufficient, for, unless the series described be a very complete one, it is easy to mistake the actual embryonic phase sought for.

So far as it went, my search in the literature was for a time very unsatisfactory in its results, and a final conclusion seemed remote. But the certainty of important

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1) On my theory a good part of the larva in Mammals and its presence, therefore, explicable. On any other theory merely the remnants of a formerly meroblastic egg, a useless luxury, and its continued existence, therefore, quite inexplicable.

2) see appendix e.

changes at this epoch appeared to be so clear to the observer, that the problem was tenaciously held on to.

Then the Marsupials were recollected, and the common statement that they were born in a very immature condition was called to mind. They, also, have an empty yolk-sac, and the idea arose "what if they are born in the critical stage"? "They must be born at this period, for otherwise there seems no good reason for the anomaly." As described in the preceding pages, this turned out to be exactly as had been guessed. For once, at any rate, a hypothesis had justified itself!

The young of the Opossum, then, are born at the critical period, at the stage which corresponds to that in which the embryo of *Scyllium* annexes the contents of the yolk-sac and begins to feed upon them. The young Opossums have no allantoic placental attachment, and they possess a yolk-sac [1]), which is then quite empty; therefore at this stage they are born, transferred to the pouch, and nourished by the milk of the mammary glands. If an allantoic placenta were formed, there would be no need for this premature birth, i. e. to put the words in another way, if at this period an allantoic placenta were formed, the birth would not take place so prematurely. There can, I think, be no possible doubt that, if such a placental attachment were to be initiated in the Marsupials, it would be established at the equivalent of the critical stage, i. e. just before the embryo is now born into the world. The original allantoic placenta must have been formed at, or only slightly before, this period.

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1) see appendix e.

Among Marsupials the only instance known of the existence of an allantoic placenta is in *Parameles obesula*, as recently recorded by my friend and former pupil J. P. Hill[1]).

It is unnecessary to dilate on the importance of the discovery, which Hill has been so fortunate as to make. So far he has not been in a position to determine at what stage this placental connection comes to pass, but it may be expected that, it will not be formed much, if at all, before the stage in which the young of the Opossum leave the maternal uterus. It appears quite certain that this will turn out to be the case.

Actual observations of placental formations, or of changes in a trophoblast or ectoplacenta[2]) leading to the formation of an allantoic placenta, at what *a priori* would appear to be the critical period in various Eutherian Mammals, even if they exist in print, are difficult of access.

Limited as the time at my disposal has been, owing to the pressure of University duties, many important memoirs on the development of the placenta have been perused with but little actual result. Indeed, it may be stated that the recognition of such changes as relating to the critical period is only possible when the observer either gives a picture of the embryo, or when its age or other characters are described in such a way that a mental image can be formed of it.

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1) Hill, J. P., Prel. note on the occurrence of a placental connection in *Parameles obesula* etc. Proc. Linn. Soc. N. S. W., Vol. X, pp. 578—581, 1895.

2) see appendices f and n.

There exists therefore no wish to ignore the valuable researches on placenta-development, which we owe to the labours of such morphologists as Sir William Turner, Waldeyer, Ercolani, Selenka, Frommel, Bonnet, Strahl, van Beneden, Julin, Hubrecht and others, but a conviction that at the present time it would be a hopeless task on the part of an outsider and onlooker to attempt to find in the published researches on the placenta of diverse Mammals something pointing in every case to a change in the mode of nutrition of the embryo at the equivalent of the critical period.

I believe, — and consider that the facts recorded in the preceding pages furnish good grounds for such a belief, — that originally the formation of an allantoic placenta took place at the critical period, and that this point lies at, or immediately before, the time when in *Didelphys* the young is born.

An attempt will now be made to illustrate the above remarks by concrete examples.

In the first place as to a actual formation of an allantoic placenta at the critical period. In Bonnet's text-book of the embryology of the "Haussäugethiere" (p. 82) there is a figure (fig. 75) of a sheep embryo of the 30th day.

No doubt exists in my mind, from comparison of this embryo with corresponding ones of the pig and rabbit, that it somewhere about represents the critical stage. Absolute certainty could only be obtained by a direct comparison with older and younger stages, and, more especially, from an examination of the grade of development of its organs.

In the chapter dealing with the "Eihüllen im Besonderen" we read the following significant passage [1]):

"Die Verwachsung der Allantoisoberfläche mit dem amniogenen Chorion, und damit die Bildung des Allantoischorions tritt gewöhnlich am 30. Tage ein (Schaf)."

Assuming that the embryo of fig. 75 is at the critical period, and this identification was made before the above statement was noted, the change postulated in the mode of nutrition is abundantly verified in this instance [2]).

According to Duval [3]) in the rabbit important changes take place in the placenta from the 15th to the 20th day of the development, and these lead to the gradual replacement of the ectoplacenta, or trophoblast, by the permanent, or definitive, allantoic placenta, which had, indeed, begun to be formed at a much earlier period, i. e. the 12th day. At present an investigation of the time of occurrence of the critical stage is in progress, and all that can at this juncture be stated is that it is probably reached about the 15th day of the development. Since the above was written, it has been found that **in the rabbit the critical stage is reached during the 15th day, and thus the change postulated is here actually realized.** It is now impossible to add more to the text, and for further information the reader may be referred to appendices b, f, and i.

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1) loc. cit. p. 250.

2) It is possible that the "Umwandlung einer gürtelförmig angelegten in eine doppelt-scheibenförmige Placenta" described by Strahl in *Mustela* (Anat. Verhandl. München 1891, p. 121) may be a case of development of an ectoplacenta previous to the critical period and its replacement at this epoch by an allantoic placenta.

3) Duval, M., Le placenta des Rongeurs, p. 352 et seq.

VIII. The practical importance of the critical stage in the embryology of man.

It is now fitting to consider the case of the human embryo. And in this connection it may be of interest, and even of importance, to take a somewhat wider survey of the matter than we have yet had reason to do.

In the earlier pages and in the table of comparisons the critical stage has been described as being in all probability reached at the very end of the sixth week or early in the seventh [1]). The changes that may be expected at this period in the human, as in any other Vertebrate, embryo, may be grouped under two heads. In the first place we have to consider probable changes in the nutrition of the embryo, when, in the words of His, it ceases to be embryo and becomes foetus. In the second place it may be of practical importance to consider the actual effects of the period on the embryo itself, more especially in their pathological aspects.

Our knowledge of the placenta at this period appears to be somewhat deficient, but it is such that one can form an idea that very important things are taking place. This appears clear from a passage quoted by His from a publication by the renowned gynecologist Hegar. The quotation runs as follows: —

"Der Zeitpunkt, in welchem die Fehlgeburt zu Stande kommt, ist ein ziemlich bestimmter, es ist das Ende des

1) The difficulty of determining the actual age of a human embryo is too well recognised to need any comment here.

zweiten und der Anfang des dritten Monats, also der Termin, in welchem die Placenta in einem raschen Entwickelungsprocess begriffen ist" [1]).

Had it not seemed, during the writing of the present memoir, that the human placentation formed an exception, greater emphasis would have been laid on the probability, amounting almost to certainty, *that in the Eutheria the critical period was always marked by the initiation of the formation of an allantoic placenta.* But "was uns als Ausnahme erscheint, ist in der Regel" and the case of man is no exception to the rule.

An allantoic placenta is never, and can never be, developed much, if at all, before the critical period is reached, for it is then that the embryo can and must first begin to make provision for its own nourishment.

And now briefly to consider the case of the human embryo.

The villi of the human chorion of four weeks have been described by E. van Beneden [2]) as representing a trophoblast or ectoplacenta [3]).

These villi are stated to persist until the second half of the second month, i. e. probably until the critical period; when part of them are replaced by the allantoic placenta, which then arises, while the rest disappear [4]).

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1) Hegar, A., Monatsschrift für Geburtskunde, Bd. XXI, Suppl.-Hft. p. 34.

2) Duval, M., Placenta des Rongeurs, pp. 11—12.

3) It may be also mentioned that Duval, whose opinion on such a point carries great weight, expresses his cordial agreement with van Beneden's conclusion.

4) Schultze, O., Grundriss der Entwickelungsgesch. des Menschen etc., 1896, p. 148.

Thus, even the conditions in the human embryo appear to agree with those, which, on *a priori* grounds, might have been predicted. The first-formed placenta is a trophoblast or larval structure, and, as stated above, this, at a period which most probably corresponds to the critical stage, is replaced, or substituted, by an allantoic placenta.

From what has been recorded concerning the placentation of the rabbit, sheep, horse and man it may safely be concluded that **at the critical period in Eutherian Mammals a change of nutrition is invariably brought to pass by the commencing formation of an allantoic placenta and the suppression of a trophoblast or yolk-sac placenta.**

And now, as to the actual effects of this period on the embryo itself. Hegar's words and the following quotation from His[1]) need no comment on the part of an outsider. His writes: — "Der zweite, und wohl noch ein Theil vom dritten Monat der Schwangerschaft scheint den Zeitraum zu umfassen, während dessen der Uterus sich Alles dessen entledigt, was nicht entwickelungsfähig ist. Aus späteren Fötalperioden sind mir schlecht genährte, hier und da auch angefaulte Fötus durch die Hände gegangen, aber keine Produkte, von denen man nicht hätte annehmen dürfen, bei günstiger Ernährung hätten sie auch bis zum Geburtstermin ihr Leben weiter führen können." The whole of the short chapter on "das Vorkommen missbildeter Formen" may be perused with advantage.

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1) His W., Anatomie menschlicher Embryonen. Theil II, p. 16.

If the equivalent of the critical period of *Scyllium* or *Raja* exist also in the human embryo, and that this is so the weighty words of His and Hegar, when read along with the facts of my table of comparisons, go to prove; if here, as in *Scyllium* it is bound up with an antithetic alternation of generations, in which the sexual form arises on a reduced larva, it appears possible to explain the frequency of abortions of monsters at the time mentioned in the passages previously quoted.

In such a mode of development there is always the possibility that, should the embryo or sexual generation fail to exhibit itself in a normal manner at the period, when it ought to begin to acquire a certain independence and to set about the suppression of the larva or asexual generation, in and on which it had previously slumbered, the necessary procedure at the critical stage may be omitted, and, as a consequence, the victory of embryo, which ought naturally to ensue, may be lacking, and this may lead to its destruction.

Prior to this stage it matters little how its organs behave in their development, and this, as Oppel, Keibel and Mehnert have shown, is true of individuals or species as compared with each other or with other species. Keibel, in particular, has shown the immense variation that may exist in the degree of development of various organs in early periods of the development *prior to my critical stage*, and the facts are matters of every day observation to every diligent embryologist.

All sorts of malformations of the embryo may be tolerated before the momentous stage is reached, when the roll-call is made. Until then the embryo is only coming

into being, it is incomplete, and it lies in the very essence of the early development that deficiencies in the embryonic body should be suffered to exist. It is only at the critical period that deficiencies in the embryonic body become of importance, and, if they be serious ones, it is too late to make them good, when all the chief organs and systems of organs should be already laid down, and when a direct and immediate advance towards the adult position ought to be made.

The nature of the critical stage premises a certain state of the embryo, if in grave respects this latter be found wanting, though it may linger for a time, its doom is ultimately certain.

It may be concluded from the observations of His, Hegar and others, that, even if the abortion be not immediate, the failure to comply with the rules of the development prior to the critical period will, as a general rule, revenge itself by an early casting out of the monster.

Other cases of abortion, where the embryo is not malformed, may be covered by failure of the changes postulated as occurring in the placentation at the critical period. Others again may find their explanation in one or other of the causes assigned to the phenomena by His. All that is here attempted is to point out one great cause of the frequency of the abortion of monsters at the period assigned by His and Hegar.

IX. Yolk-sac, mammary glands, and placenta.

It is perhaps now possible to form some idea of the course of events in the history of the Vertebrata in past ages leading to the evolution of the allantoic placenta of the Eutherian Mammals. In what follows only a very brief sketch of the matter can be given. A fuller account, and the actual establishment of the same on a solid basis of fact, must inevitably be postponed, until the time requisite for putting the results together can be gained.

In reading the sketch the reader will kindly bear in mind that, contrary to what he might suppose, facts are far more welcome to me than theory. There is only one theory in question, that of an antithetic alternation of generations as underlying Metazoan development, and this formed the starting-point for the discovery of the facts of this and other papers now about to be published elsewhere. Wherever suppositions have otherwise been made, they have been such as could be verified by observation, and some have been justified by facts in the preceding pages.

What is said in the sequel regarding the mammary glands and placenta is, however, not of a nature that can be directly proved by observation; it can only be shown to be exceedingly probable.

There can be no question that originally Vertebrate animals possessed eggs with little food-yolk and that thus, though it may be disputed that the quantity of food-yolk

absolutely determines the kind of segmentation [1]), no external yolk-sac is formed. In all such cases it may be taken as probable that there was originally a free larval stage, with a larva rather like that still existing in some Ascidians [2]). As a free-living organism, uncontaminated with the germs or rudiments of the sexual generation or true Vertebrate form, which ought to arise later, instead of, as is the case, very early upon it, such a larva no longer exists. It has, as I have attempted to show elsewhere, always the future generation, in a very imperfectly developed condition, upon it from the start.

When the egg became meroblastic, as was stated some years ago, the larva or phorozoon became [3]) reduced to a blastoderm upon which the sexual generation, gametozoon, or true Vertebrate, arose.

The blastoderm grows over and encloses the yolk [4]),

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1) As witness many of the Teleostei where the egg with meroblastic segmentation may be far smaller than an Amphibian egg with holoblastic divisions.

2) As far as can be seen at present this Ascidian larva has resemblances to the one that can be mentally pictured as still underlying the development of many Ichthyopsida, but the statement may be permitted that in saying this nothing is asserted regarding the ancestry of Vertebrates. Of all the theories of the latter no one is, or can be, in my opinion, justified by embryological fact.

3) By the word "phorozoon" or the "bearing-animal" it is intended in future to indicate the asexual generation or the equivalent of the sporophyte-generation in plants. In many of the Invertebrates it represents what is generally termed a larva, e. g. Trochophora, Actinotrocha &c. but it does not represent what is called a larva in Insects or Amphibians. I agree with Miall's judgment of these latter.

4) It may be as well to point out for the benefit of possible critics that the yolk-sac is not there from the start in a meroblastic egg, it always has to be formed during the early development.

and this may be interpreted as the annexation of the yolk by the phorozoon or larva. Thence, until the critical period the gametozoon or future Vertebrate is only nourished through the intermediation of the phorozoon from the yolk.

At the critical period the gametozoon begins to suppress the phorozoon, and, as will be described elsewhere, it annexes the contents of the yolk-sac in one or other of a few ways. The parts of the larva atrophy and are either absorbed, starved to nothingness, or digested.

In those cases where there is no proper yolk-sac and only yolk-cells (parts of the phorozoon or larva) these latter from the critical period onwards break down and degenerate and are digested, while in the same instances other parts of the phorozoon atrophy.

Such is, in brief, the history of events in the Ichthyopsida so far as I have yet followed it.

Leaving the Sauropsida [1]) out of account, the history of the yolk-sac in Mammals may now be considered.

Formerly, as all embryologists believe, all the Mammals possessed a large yolk-sac full of yolk.

Now such a well-filled yolk-sac only exists in the Monotremata. The remaining Mammals develop a rather large, but always quite empty, yolk sac [2]). Why do they

1) It might have been supposed that the case of the chick would have received fuller consideration. Although we possess what professes to be a very complete account of the yolk-sac of the chick, i. e. that of Hans Virchow, and although fully recognising the laboriousness and industry with which Virchow has built this up, I regret that it cannot be used, for it is by no means clear from it what takes place during the 6th day i. e. during the critical period in the chick. (Compare also appendix c.)

2) Compare appendix e.

do this? It never forms any part of the adult body! The embryo or gametozoon develops on a blastoderm, and this blastoderm encloses a space in which there ought to be yolk.

Why does the Mammalian embryo arise on a blastoderm and why does an empty yolk-sac develop, unless blastoderm and yolk-sac together represent parts of a reduced larva, or phorozoon, upon which the adult form takes its origin?

How has it come about that the Mammalian yolk-sac is an empty one? In the opinion of embryologists generally uterine development accounts for the emptiness of the yolk-sac. This used also to be my opinion, but it is no longer so. When the uterine development is very short, as in Marsupials, it may account for a small part [1]) of the loss, but not for the greater portion. Such an explanation is, however, superfluous.

The direct cause of the total loss is perhaps to be seen in the formation of a pouch, for the reception of the young [2]), and in the evolution of mammary glands for the nutrition of the young when hatched out within the pouch.

The mode in which this was probably effected is shown by the conditions in Monotremes in which there

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1) Compare appendix e.

2) It is difficult to decide if the pouch was first formed for the young or for the incubation of the egg. Either appears to be possible, but I incline to the opinion that the former was the original reason and that the latter followed, because of the advantage thereby gained. As Klaatsch has proved, the mammary glands are the forerunners of a pouch, which arises in connection with the former.

exist and function a large yolk-sac full of yolk and mammary glands [1]).

It may be as well to recall the course of events in the development of a Monotreme. The large egg, covered by an egg-shell, is laid just as is usually the case in Sauropsida. After the egg is laid a blastoderm is formed which gradually encloses the yolk and forms an external yolk-sac. It may be presumed that in one way or another — for the modes vary — at the critical period the embryo annexes the yolk-sac and feeds upon its contents, until it is born. During this time in *Echidna* the egg lies in the pouch, the young is born within the pouch and thence onwards is fed by the secretion of mammary glands [2]).

If anything happened to cause the young Mammal to quit the egg-shell at an earlier period than usual, it would probably all the sooner get to the mammary secretion. If this adoption of the milk-nutrition got carried further and further back to earlier stages of the development, while the laying of the egg got more and more postponed, ultimately the egg would be laid at the same time that the embryo was due to be born, i. e. to leave the egg-shell, and thus an egg-shell would soon become an un-

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1) Compare appendix k.

2) It may be confidently anticipated that Gegenbaur's view of the two-fold origin of mammary glands will shortly be proved to have been an error. Klaatsch tacitly homologises the mammary pockets of the milk glands and the marsupium of Monotremes and Marsupials, (Verhandl. Anat. Gesellsch. Basel 1895, p. 147) a conclusion from which there is, indeed, no escape. It appears to me to be neither reasonable nor conceivable that the mammary glands should have had a two-fold origin, and in the present discussion their homology throughout the Mammalia will be assumed.

necessary luxury, and this is the case in Marsupials, where none is formed.

But the carrying backwards of the beginning of the milk-nutrition to earlier stages can go no further than the critical stage i. e. than the stage in which the embryo first begins to feed itself. This is again realized in *Didelphys* and *Hypsiprymnus*, where the young one is born in the critical stage, and the same is probably true of all those Marsupials, i. e. the majority, in which no allantoic placenta is formed.

But, as we have seen, this is, according to all tradition, the period at which the young Marsupial ought to begin to feed on the contents of a well-filled yolk-sac, and this it probably, nay certainly, originally began to do at the critical period. A well-filled yolk-sac and actively secreting milk-glands ready for the embryo would be a superfluity of nourishment, and, if the embryo took to the one, it must, perforce, reject the other. It must, however, be remembered that the carrying-back of a milk-nutrition to an earlier period of the development was, in all probability, a gradual process, and that *pari passu* the contents of the yolk-bag would be diminished [1]).

But the result is clear. As soon as the birth was carried back to the furthest limit, to the critical stage, the yolk of the yolk-sac became unnecessary, and, although the bag itself could not be dispensed with, for it was part of the reduced phorozoon on which the embryo arose, its contents became useless, and disappeared. And thus it

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1) Compare appendix k.

came about that all the Mammals above the Monotremata possess an empty yolk-sac [1]).

The whole of this argument shows, I think, something else, about which more must be written.

It proves that the mammary glands are far older in time than an allantoic placenta.

If this be correct, it is easy to perceive what was the subsequent evolution from the stage in which the majority of Marsupials still remain.

It is not proposed in this place to discuss the yolk-sac placenta or the ectoplacenta (trophoblast). These are without doubt appendages of the larva or phorozoon, and all their history goes to prove this [2]).

Reverting to the allantoic placenta. This, as Hubrecht and Duval have demonstrated, is brought to pass through the intermediation of a temporary (larval) placental attachment, the ectoplacenta or trophoblast. Assuming an allantoic placenta to be once introduced, its formation, as was previously stated, must have first occurred at or only very slightly before the critical stage. Probably at this stage for reasons which have been already mentioned.

Its formation would at once reverse the former order of events, and would carry the birth of the embryo to a later and later period of the development subsequent to the critical stage. And in this way it would conceivably come about, even in allied animals, like the rabbit and guinea-pig, that in the one case the young might be born at a very much younger stage than in the other. As is well-known, the rabbit is born in a blind and helpless

1) Compare appendix e.
2) Compare appendix n.

condition, and is fed by the milk-glands for a prolonged period, whereas the guinea-pig comes into the world almost with its eyes open, and is soon able to run about, and very soon to feed itself [1]).

There is certainly an advantage in many cases, as others have noted, in the young being born in an advanced condition of development, and this is particularly so in those forms which have to avoid enemies by running away. Such an advantage is only to be attained by lengthening the period of uterine gestation, and this inevitably results in the shortening of the time of milk-nutrition, for the two are in inverse proportion.

Thus, as it appears to me, it can be concluded: —

1) that the earliest mode of nutrition of the Mammalian embryo subsequent to the critical stage was by means of the yolk of a well-filled yolk-sac:

2) that the yolk disappeared and the yolk-sac became an empty receptacle subsequent to the formation of milk-glands and a marsupial pouch, and the carrying backwards of the period at which the embryo was born to earlier stages, until the limit was reached at the critical period:

3) that then for a time, and this condition is still existent in the majority of the Marsupials, the mammary glands came into function at the critical period, which coincided with the birth of the embryo:

4) that the mammary glands are thus older than the allantoic placenta, and after the loss of the yolk, they remained

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1) The young of many Ungulata begin to eat grass within a day or two of birth.

the sole organs of nutrition of the embryo or foetus after the critical period, until the placenta began to be formed:

5) that the allantoic placenta was first formed at the critical period and that this is probably still the case in all orders of Eutherian Mammals (e. g. sheep, rabbit, Man):

6) that with an allantoic placenta in formation the birth of the embryo at the critical stage ceased to be necessary: that the marsupial pouch originally formed to receive an immature embryo ceased to be of value and disappeared:

7) that, with the advantage derived from a prolongation of uterine gestation, the embryo in many cases came to be born in a more and more advanced condition, and thus made smaller and smaller demands on the mammary secretion:

8) that, once uterine gestation with an allantoic placenta was initiated, the original importance of the mammary glands became diminished in this way, and, as their functional period is in an inverse ratio to that of uterine gestation, that they are in many Eutherian Mammals being gradually rendered useless, and will thus in all probability and given a sufficient period of time, finally, like the yolk of the Mammalian yolk-sac, in certain cases ultimately entirely disappear.

X. On von Baer's laws of development and on a new law of Vertebrate development.

It appears to be advisable, if only in order to emphasise a different view of the matter, to refer to what is known as von Baer's law. But, as a matter of fact, the term "von Baer's law" is incorrect, for on p. 224 of von Baer's well-known work four laws are established, and von Baer's law according to Haeckel is quite a different version to that great embryologist's law according to some other zoologists. The Haeckelian version [1]) is far the more correct as an interpretation of what von Baer actually wrote, though in its application Haeckel diverges widely from the views von Baer held, for the latter zoologist in the 3rd law distinctly states that "jeder Embryo einer bestimmten Thierform, anstatt die andern bestimmten Formen zu durchlaufen, scheidet sich vielmehr von ihnen" [2]).

The commonly accepted account, on the other hand, is not one of the four laws stated by von Baer, though it is not disputed that it fairly represents certain of his views.

It is not proposed to discuss the actual meaning, or the justification, of the commonly accepted version of von Baer's law. All that is here intended is to quote

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1) Haeckel, E., The evolution of man. Engl. edition. Vol. I, p. 57.

2) von Baer, C. E., Entwickelungsgesch. d. Thiere. I. Theil, p. 224.

the four actual laws written on p. 224, and to indicate how they appear to require amendment.

They are as follows: —

1) "Dass das Gemeinsame einer grossen Thiergruppe sich früher im Embryo bildet, als das Besondere."

2) "Aus dem Allgemeinsten der Formverhältnisse bildet sich das wenige Allgemeine und so fort, bis endlich das Speciellste auftritt."

3) "Jeder Embryo einer bestimmten Thierform, anstatt die andern bestimmten Formen zu durchlaufen, scheidet sich vielmehr von ihnen."

4) "Im Grunde ist also nie der Embryo einer höhern Thierform gleich, sondern nur seinem Embryo."

To the third law no objection whatever can be offered, while all four appear to require a restriction to the phases of development at and subsequent to the critical stage.

So far as these laws apply to the Vertebrata, and it was in study of these that von Baer established them, they may, to an extent varying with the interpretation one should put upon them, be replaced by the following: —

There is a stage[1]) in the development of every Vertebrate embryo, during which, and only then, it resembles the embryo of any other Vertebrate in a corresponding stage in certain general features. But, while it thus agrees exactly with any other embryo in this stage in characters which are common

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1) In this memoir referred to as "the critical stage".

to all Vertebrate animals, it differs from the embryo of any other class in certain special class-features, and also from any other embryo of the same class but of a different order in other and ordinal characters. Immediately before this stage is reached, it begins to put on generic and specific characters, and thus it then begins to differ from all other embryos in these.

This is the sole point in the development, in which it is possible to find any series of constant resemblances between embryos of different Vertebrates, but it is also characterised by the existence of certain fixed and definite differences.

The whole of this has its explanation in an antithetic alternation of generations as underlying the development; for it is the stage at which the embryo first has acquired such an independence as will enable it to set about the task of suppressing the larval or asexual foundation, the phorozoon [1]).

The things that define this stage have been discussed and described in the preceding pages, and, in concluding, it may once again be urged that only on the view of an antithetic alternation as underlying the development do the phenomena we have been considering admit of a reasonable interpretation.

To many zoologists the idea of an antithetic alternation of generations as underlying Metazoon development appears to be nonsensical and absurd, in total for-

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1) Compare appendix m.

getfulness of the fact that such an alternation is bound up with the reproduction of a large part of animate nature, i. e. all but the lowest plants.

If the things described here and in recent and forthcoming publications of mine can be solved on any other theory, surely the time has come, when that solution should be forthcoming?

But . . . . . *it will be sought after and called for in vain!*

XI. Concluding remarks.

The history of the yolk-sac and its contents has only possessed special interest to me personally on account of its obvious bearings on the mode of development by an antithetic alternation of generations.

There is one general conclusion that can now be drawn, and it is that in no Vertebrate does the yolk-sac, where one is present, find any utilisation in building-up or forming a part of the embryonic body. It also appears certain that in no case do the yolk-cells or merocytes become members of the embryonic body, but, as here recorded for *Scyllium* and *Lepidosteus* [1]), there comes a period in their history when they begin to degenerate, and, in one way or another, they are afterwards absorbed.

Even in those Amphibians in which there are yolk-cells within the gut in early stages, these, from the criti-

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1) See appendix a.

cal period, as appears to be clearly established by the researches of many embryologists, and, as is confirmed by some I have myself made, degenerate, break-up and are digested, much in the same manner as the yolk-laden cells of *Lepidosteus* do, once they are within the gut.

What is the meaning of it all? Why do the yolk-cells of Amphibians first begin to be used up at the critical period with the initiation of degeneration of the larval nervous system? Why are there any yolk-cells in the Amphibia? It is quite unusual to find such a mass of cells, which apparently on any currently accepted explanation are only what some pathologists term "rests" [1]). Why should the yolk first come into the alimentary canal of a *Scyllium* embryo at the critical period?

Why should the whole of the yolk-sac, epiblast, mesoblast and hypoblast, be absorbed? Why should the merocytes degenerate and disappear in *Scyllium*: why in *Lepidosteus* should they laden themselves with yolk, then degenerate, break up and be digested?

Why should there be a few merocytes, limited only to early stages, in *Gallus*, (H. Virchow) and soon disappearing?

Why should the Mammalia, except Monotremes, have a perfectly empty [2]) yolk-sac, which, useless as it is in the light of any generally accepted explanation, is always

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1) That this term is justified embryologically is more than doubtful.

2) This "emptiness" is only meant to apply to stages later than the critical period. Yolk may, to some extent, be present before then, but by that epoch it will be found to have been used up. See also appendix e.

formed, often grows to a large size, and is then rejected from the development, in other words is not made use of in forming the body of the embryo?

Any embryologist who should undertake to answer **the whole** of these questions will probably find himself immersed in a sea of troubles, unless he should see fit to adopt the only reasonable view, that of an antithetic alternation of generations as underlying the development.

But, supposing him to be so fortunate as to find some other explanation of the whole, let him then attempt to grapple with the history of the nutrition of the mammalian embryo, let him then consider how the large mass of yolk was lost, which of the two was first formed, mammary apparatus or allantoic placenta.

Let him try to explain how it comes about that the embryo of *Didelphys* is born at the critical period, and why it then corresponds to a *Scyllium* embryo of 32 mm, which is just beginning to take yolk into its intestine, or why it is then in a stage of its development, in which it resembles a rabbit-embryo of the 15th day, or a sheep-embryo of the 30th day, or a human-embryo of the seventh week, or a horse-embryo of near the end of the seventh week, either of which is just forming its allantoic placenta.

Let him further consider the meaning of a yolk-sac placenta, or of a diplotrophoblast or ectoplacenta.

Let him ponder over the general occurrence of a corresponding critical stage throughout the Vertebrata.

When he has done all this; when he has satisfactorily accounted for all these things; when he has explained away the larval and transient nervous system of *Raja,*

Scyllium, Lepidosteus and other oviparous Ichthyopsida: and when, finally, he has shown that the degeneration of the larval nervous apparatus in uterine development, or in development on land, requires no former connection with a larval existence in water to account for it; when all this has been done, then, and then only, good reason for doubting the existence of an alternation of generations in the development of all Vertebrates will have been shown.

What we dignify by the name of a law in embryology must always be something with which the facts can be shown to be in conformity.

The only "law of development" generally accepted is not worthy of the name, for there are hosts of facts with which it is not in agreement, and some of those, who formerly believed in it, are deserting it, because their researches prove its falsity.

The terms "nonsensical and absurd" regarding the antithetic alternation as applied to Metazoa may, perhaps, have point and be in place, when the thing has been proved to be so. If an embryologist be *a priori* of that opinion, it may be humbly suggested to him that it is his bounden duty to sit down and, as carefully as may be, examine the facts for himself. But it will not suffice to make a few desultory observations on the transient ganglion-cells of the first best Teleost, and then, when he has logically (?) concluded that they are merely cells of the spinal ganglia, assume that he has explained everything, or, indeed, anything.

All the things mentioned above, and many more, are in agreement with the view of an antithetic alternation

as underlying Metazoan development, and — where are the **facts** that are opposed to it?

And echo answers — *"where?"*

Appendices.

a) The mode of absorption of the yolk in *Lepidosteus* subsequent to the critical period is briefly as follows. A fuller account will presently be published in the Anatomischer Anzeiger. The merocytes or cells of the yolk-hypoblast form a hillock leading into a deficiency or gap in the ventral wall of the gut, i. e. a "yolk-bay" in Hans Virchow's terminology. From this point they form a protoplasmic network extending some distance into the yolk. The threads of this appear to draw yolk-plates to the merocytes. These fill themselves with yolk, proliferate off into the gut-cavity, their nuclei break up into small deeply-staining particles, the yolk-plates are broken up within the cell, the latter then breaks down and releases a sort of emulsion of fine yolk-particles and remains of nuclei, and this mass is digested. The whole process is very curious, and requires illustrations for its proper comprehension. It may be described as a "self-sacrifice of the merocytes".

b) The age assigned to the rabbit-embryo described in the table, i. e. 15 days, was determined as follows. It was labelled 17th day, but, like most of the rabbit-embryos in my possession, the age was marked according to the statements of the dealer who supplied the animals. Anyone, who has had dealings with such people, will know how unreliable their assurances are.

The actual age can, however, be fixed. O. Schultze, in his paper on "die erste Anlage des Milchdrüsenapparates" (Anat. Anz. VII, p. 269), writes: "bei Embryonen des 15. Tages sind die zwischen den einzelnen Anlagen gelegenen ursprünglichen Verbindungsbrücken vollständig zurückgebildet, und finden sich jederseits 3—4 'Milchpunkte'."

A pregnant rabbit, recently obtained, contained six young. Four of these were in exactly the same stage, (i. e. the critical stage) as the one in the table, while the other two had not yet reached this period. This was evident in, among other things, the

partial existence of connections between the posterior "milk-points" of Schultze. As the other four had just completed the formation of their "milk-points", it appears clear that they represent 15 days embryos, and this conclusion therefore applies to the embryo in the table.

c) H. Virchow's publications on the yolk-sac are the following: — 1) Der Dottersack des Huhnes. Festschrift f. R. Virchow, Berlin 1891, pp. 223—353. 2) Das Dotterorgan der Wirbelthiere. Z. W. Z., Bd. LIII, Suppl. 3) Same title Arch. mikrosk. Anat., Bd. XL. p. 39. 4) Dotterzellen und Dotterfurchung bei Wirbelthieren. Verhandl. Anat. Gesellsch. Wien 1892, p. 209. — In no one of these are changes at a period, which might be supposed to correspond to my critical stage, described. So much may be admitted for the benefit of those who may believe such changes to be mythical, but he, who feels disposed to uphold this thesis, should first make investigations for himself in any form he may choose. If the chick be chosen for the research, the investigator will find, in all probability, that Virchow's researches are incomplete, and that, while the annexation of the yolk-sac by the embryo-chick is not the same in its details as that to be described by me for *Scyllium* and *Lepidosteus* in a forthcoming number of the Anatomischer Anzeiger, the phenomena are only variations rung upon the same theme. If they are not to be found, that will, in the first instance, only prove that the observer could not find them. So much is certain: there is in the chick as marked and characteristic a critical stage as in *Scyllium* or *Raja*, and, unless all written here and elsewhere be due to pure chance, or be an invention of the devil, it is then in the chick-development that the embryo must begin to annex the yolk. Notwithstanding Virchow's objections to O. Hertwig's statement that the yolk-sac of the chick is in retrogressive metamorphosis during the latter part of the development, such must be the case from the 6th day onwards.

The critical period is reached in the chick in the course of the sixth day of development. It appears probable that the change in the mode of nutrition postulated in the text is effected by the complete enclosure of the yolk-sac and the establishment of a complete hypoblastic covering which, in the way described by Hans Virchow, thence onwards provides for the assimilation of the yolk. As merocytes, according to the author just cited, are only rudimentary structures in the chick, it appears likely that the yolk-hypoblast of the chick in late stages is not the homologue of the yolk-hypoblast of *Scyllium* prior to the critical stage: the former may belong to the embryo, the latter is larval. The early dis-

appearance of merocytes in the chick is very significant in this connection.

d) It has been recorded that the pancreas in *Scyllium* begins to enter upon its functions with the introduction of yolk into the gut at the critical period. It is probable that the critical period marks the time in all Vertebrates when this secretory structure first commences its functions.

e) The considerations advanced in the text only account for the absence of yolk in the Mammalian yolk-sac at and after the critical period. If it be entirely empty of yolk prior to that epoch, the formation of a yolk-sac placenta or of a diplotrophoblast must be the cause of the disappearance of this portion. At the critical period in Mammalia above Monotremes the embryo invariably finds itself in possession of an empty yolk-sac.

To prevent misconception, it may be stated definitely that from the standpoint taken up in this paper the presence of yolk in the yolk-sac of an Eutherian Mammal in early stages of the development would offer no obstacle to the validity of the views here set forth — there may be Mammalian eggs which do contain even a fair amount of food-yolk, but this will never be found to be sufficient in Marsupials and Eutherian Mammals to take the embryo beyond the critical period, and rarely or never in Eutheria will its amount be sufficient to enable a temporary yolk-sac — or diplotrophoblastic placenta to be dispensed with. It would not surprise me to learn that the yolk-sac placenta formed a substance of a yolk nature.

f) The yolk-sac placenta and the ectoplacenta of Duval or diplotrophoblast of Hubrecht are both temporary and evanescent structures. Both, if formed, arise at a very early period of the development, and out of structures which never form components of the gametozoon or sexual organism. They are therefore to be regarded, as already indicated, as parts of the phorozoon or larva.

When such a structure is developed, the period of its functional activity can never be prolonged beyond the critical period, for it is then that the embryo succeeds to its inheritance, and proceeds to suppress the whole of the transitory foundation, upon which it arose. The yolk-sac placenta must then commence its degeneration, the diplotrophoblast, where formed, will then in all the Eutheria begin to be replaced by an embryonic structure, the allantoic placenta (compare appendix n).

g) Immediately after this paper was sent to the press the question of the period during which the embryonic oesophagus was closed was recalled.

The meaning of this closure was discussed on p. 87 of part I of "the history of a transient nervous apparatus", where it was concluded that the closure takes place because the larval gut required to be, as it were, re-built before it could serve as the gut of a Vertebrate. In *Scyllium*, *Raja*, *Lepidosteus*, *Lacerta*, *Gallus* and other lower Vertebrates it is at the critical period still closed, though, as can easily be proved by counting the sections in which the lumen is occluded and comparison with earlier stages, it is slowly re-opening. As the Opossum begins to be fed by milk as soon as it is born, it follows that in this case the oesophagus must at birth have re-opened. These being the facts relating to *Scyllium*, the Opossum &c., it becomes of importance to find out the state of affairs in other Mammals. If the line of argument in the text be correct, if all Mammals were fed by milk-glands before an allantoic placenta was formed, if the placenta had gradually displaced the mammary glands, in fine, if the birth at the critical period in Marsupials once held for the ancestral Eutheria, then probably the oesophagus of Mammalian embryos has re-opened by the critical period. An examination of the sections of *Talpa* and *Lepus* showed that this hypothesis was correct; *in them the whole oesophagus has obtained a well-marked lumen by the time the critical period is reached.*

h) The reader, if he be an embryologist, is not likely to fall into the error of concluding that the "critical stage" in any given case is invariably reached with a given size of embryo, or a given period of uterine gestation, or incubation &c. The sizes and periods given in the text and tables are only meant to be approximate, and in some instances they only refer to particular embryos. A good illustration of the caution necessary in dealing with ages and sizes arose soon after the manuscript was completed. From a rabbit, pregnant probably 15 days, six embryos were taken. Four of these were quite alike in external characters, but they varied within a millimeter or so in length. All four were recognisable as just in the critical stage, and as corresponding exactly in external appearance with the rabbit-embryo described in the table. The remaining two, on the other hand, at first sight appeared to be abnormal, and my curiosity was excited, for among the great number of rabbit-embryos, which had passed through my hands, an abnormal case had never been encountered. They seemed to be abnormal, because the lachrymal groove had not yet disappeared, but a closer examination of the em-

bryos proved that the limbs had not reached the stage of those of the other four, the mammary ridges were still evident, and the formation of hairs on the eyebrows and snout was not well initiated. In fine, while the other embryos had just reached the critical stage, these two had not yet done so.

i) The conditions in the horse will probably turn out to agree with those in the sheep. In fact, since the text was written it has become increasingly evident that in all Eutherian Mammals *the actual formation of an allantoic placenta will be found to take place at about the equivalent of the critical period.*

In the case of the horse, it may confidently be anticipated that the critical period will be found to occur towards the end of the seventh week of development. It is then that, according to Bonnet (Verhandl. Anat. Gesellsch. 1889, p. 28), the "egg" ceases to be rounded and takes on the form of a two-horned sac, it is then that the actual allantoic placenta begins to be established, and the retrogressive metamorphosis (p. 32) of the yolk-sac placenta dates from this period.

Furthermore, it may be gathered from Duval's magnificent monograph on „le Placenta des Rongeurs" that there are strong grounds warranting the suspicion that in rat, mouse, and guinea-pig the replacement of the ectoplacenta by an allantoic placenta begins to be effected in all at the equivalent of the critical period of the rabbit, *Didelphys*, or *Scyllium*. For further particulars the reader may refer to Duval's book.

k) In Monotremes, according to R. Semon, at hatching the yolk-sac is not taken into the body as in Sauropsida, but withers and is cast off. This illustrates the influence mammary glands have exercised on the disappearance of yolk in the eggs of Mammals.

l) To save space it has not been thought needful to describe the critical stages of *Torpedo*, *Pristiurus*, *Lepidosteus*, *Salmo* and *Triton*, though these have been fixed and studied.

m) In all Vertebrates, and in Invertebrate forms above Coelenterata, important events will be found to happen at the equivalent of the critical period.

n) A yolk-sac placenta, an ectoplacenta and a trophoblast seem to be at bottom identical, even though for descriptive purposes one may apply to them different names according to the points on the blastocyst from which they are developed. There can,

indeed, be only one kind of temporary or larval placenta, and that is one which is formed from a different part of the blastoderm from that on which the embryo itself arises. When there is a "yolk-sac placenta" this is developed directly from the part of the blastoderm which grows over the yolk-sac and encloses it. An ectoplacenta or trophoblast is also ultimately referable to the blastoderm. It would be convenient to apply to all such temporary placental formations, which have arisen from parts of the blastoderm (i. e. from the larva or phorozoon), the generic name of blastocystic placenta, but, as the term Hubrecht has introduced is now in very general use, it may be better to extend its application to all temporary placental attachments of the blastocyst apart from an allantoic connection.

o) Although for a time it seemed as if the beginnings of nail-formation might be a characteristic of the critical period in Mammals, more recent observation has taught me that such is not usually the case.

XII. Tables of comparison of th

Name	Measurements	Form of body	Chorda dorsalis and vertebral column	Nervous system	Eye	Nose
The pig *Sus scrofa domesticus* Keibel's stage 68.	Gr. l. 18,6 mm, normal length 16,8 mm.	The embryo is acquiring pig-characters, more especially by the formation of a snout. In hand and foot the digits are mapped out. Obvious rudiment of external ear.	The chorda begins to be intravertebrally constricted (i. e. formation of vertebral column).	(Probably commencing formation of post. fissure and of permanent central canal.)	No lumen in lens. Lachrymal duct has reached nasal chamber. Pigmentation in retina began in stage 65.	In prece ing sta choana op (Jacobso organ de loped i. adult form nasal org established
Scyllium canicula (several embryos of both sexes).	32 mm [1]) in length.	The embryo is acquiring form of dog-fish, more especially from snout-formation, from shape of paired fins, and from differentiation of unpaired fins from continuous fin.	The chorda is becoming intravertebrally constricted by marked cartilaginous vertebral centra. The neural arches are developing.	Commencement of degeneration of transient apparatus. Commencing formation of post. fissure and of permanent central canal.	No lumen in lens. Pigmentation in retina began some little time before this stage.	Adult for of olfacto organ.
Raja batis (two embryos, male and female).	About 71 mm.	The embryo is making for the adult form. It is flattening form above downwards, and its anterior fins, which have more or less the adult shape, are growing forwards. Unpaired fins are differentiated.	The chorda is becoming intravertebrally constricted by marked cartilaginous vertebral centra. Cartilaginous neural arches are developing.	Commencing degeneration of transient apparatus. Commencing formation of post. fissure and of permanent central canal.	No lumen in lens. Pigmentation in retina began some little time before this stage.	Adult for of olf. orga

1) Compare appendix h.

ical stage in various Vertebrates.

pophysis	Mouth	Alimentary canal &c.	Urogenital system	Skin and skeleton	Nutrition
rst sug-on of dding rossen-dung).	Dental ridge laid down.	Thymus elements of the two sides have become approximated caudally. Anus open.	In the permanent kidney tubuli contorti and first beginning of glomeruli (i. e. permanent kidney pretty well established). Müllerian ducts developed for a short distance. Sex established in stage 69 (probably here also). (Probably also externally by external genital organs.)	Mammary glands completely differentiated from mammary ridges. Rudiments (Anlagen) of hair (i. e. the embryo now a Mammal). No ossifications in skeleton.	(Probable first formation of allantoic placenta.)
ications dding.	Dental ridge laid down.	Thymus almost completely developed from upper wall of gill clefts, but still connected therewith. Cloaca open.	Kidney completely established. Müllerian ducts almost reach cloaca. Sex established, internally by ovary or testis, by size of Müllerian ducts, and externally by the claspers in the male.	First rudiments (Anlagen) of scale formation (i. e. the embryo is now a fish). Skeleton cartilaginous so far as it is formed.	Embryo annexes external yolk-sac, — an internal yolk-sac is formed and yolk drawn into it and thence into gut. Then or soon afterward pancreas comes into function. Prior to this stage the embryo only obtained nourishment from yolk-sac by means of the yolk-sac circulation.
	Dental ridge laid down.	Thymus elements separated from upper wall of gill-clefts. Cloaca open.	Kidney completely established. Rest of characters as in *S. canicula* above.	Rudiments of a dorsal row of scale papillae along the tail, i. e. future spines.	As in *S. canicula*.

	Measurements	Form of body	Chorda dorsalis and vertebral column	Nervous system	Eye	Nose
The Opossum *(Didelphys virginiana)* after Selenka. Age 8 days.	Greatest length 11,25 mm.	The embryo has progressed far towards the adult form of body. The snout has adult characters. The limbs are quite as far advanced as those of the pig-embryo described above. The digits are well marked and those of the fore-limb bear claws.	The chorda (as seen in fig. 4 t. 29) is intravertebrally constricted by marked cartilaginous centra. Cartilaginous neural arches are developing.	As the figure cited shows, probable commencement of formation of post. fissure and of permanent central canal.	Pigmentation of retina set in during the last hours of foetal life.	Jacobs… develope… (wrongly… med in fi… t. 29). Ch… open (fi… t. 29) i… adult for… olfactory… gan.
Human Embryo. Keibel's Embryo *H. s. Brn.* Age 45—47 days.	Normal length 17 mm.	The embryo is clearly recognisable as human in form, it is stated by Keibel to lie between fig. 22 and 23 of His' normal table. Thus, judged by either of these, one may say of it, that the face and head are those of a human being. The limbs are advanced in development, and the digits are obviously mapped out. (The external ear is human in form. His.)	The chorda, as seen in Keibel's text-figure 70 is intravertebrally constricted by marked cartilaginous centra. Cartilaginous neural arches are developing.	As the same text-figure shows, the formation of the post. fissure and of the permanent central canal is initiated.	(Human retina commences to be pigmented towards end of second month [Marshall]). (Condition of lens probably as in the pig cited above.)	Jacobs… organ d… loped, … ana oper… i. e. a… form of n…
Mole. *Talpa europaea* Embryo A. ♂.	Greatest length along one straight line 10,5 mm.	The body is distinctly mole-like in form. Head & snout are specially so, limbs and digits are in an advanced state of differentiation. Obvious rudiment of external ear.	The chorda is being intravertebrally constricted by the formation of a cartilaginous vertebral column. Neural arches developing.	Commencing formation of post. fissure.	The retina is completely pigmented. No cavity in the lens. Lachrymal duct reaches nose.	Jacobs… organ d… loped. (… ana open… adult for… olf. orga…

1) Compare appendix g.

...physis	Mouth	Alimentary canal &c.	Urogenital system	Skin und skeleton	Nutrition
	In Selenka's embryos C. Röse found the "erste Spur einer Zahnleiste" in one of $6^1/_2$ days, and thus, though rather more advanced, it is present in this embryo.	Cloaca open [1]).	Permanent kidney small. No statement as to Müllerian ducts. Sex established. Well-marked penis in male.	Mammary glands completely differentiated (fig. 6, t. 27). First hair papillae on snout (i. e. embryo is now a Mammal). No ossifications in skeleton.	Embryo born and a new mode nutrition (by mammary glands) initiated. (No yolk in yolk-sac and thus unless a placenta were formed no further nourishment to be obtained in utero.)
	(The first trace of a dental ridge is stated by C. Röse to be present in Hochstetter's embryo of 11 mm (? N. L.). It has the form of a free epithelial papilla and is described as becoming the dental ridge of the 15 mm embryo previously recorded by him. Salivary glands laid down. His.	(Thymus formed.) Urinogenital sinus open. Anus closed.	Permanent kidney laid down. Müllerian ducts formed for part of their course. Sex established internally and externally.	(Rein describes the first traces of the mammary glands as visible in an embryo of 16 mm N. L., thus corresponding to fig. 22 of His' normal table.) (No hair - development has yet been observed as early as the 45th day.) No ossifications in skeleton.	(Commencing formation of allantoic placenta.)
...cations ...rossen- ...igen".	Dental ridge laid down.	Thymus elements of the two sides have become approximated caudally. Anus appears to be on the poinit of opening.	Permanent kidney established and Malpighian bodies formed. Müllerian ducts formed for part of their length. Sex established (probably slightly before this stage). Externally marked by penis.	Mammary glands completely differentiated from mammary ridges. Numerous small hair-follicles on snout and a few above eyes. In fore- and hind-limbs the epidermis (Malpighian layer) is thickened at the ends of the digits but as yet no true nail formation.	Probable first formation of allantoic placenta.

	Measurements	Form of body	Chorda dorsalis and vertebral column	Nervous system	Eye	Nos
Rabbit. *Lepus cuniculus* Embryo A. ♂ aged 15 days [1]).	Greatest length along one straight line 13 mm.	The body is very like that of a rabbit in form, and this is especially so in the head and snout. The limbs and digits are in course of differentiation, but the digits, though mapped out, are not free from web. Obvious rudiment of external ear.	The chorda is being intravertebrally constricted by the formation of cartilaginous vertebral centra. Neural arches are developing.	Commencing formation of post. fissure.	The retina is not much pigmented. No cavity in lens. Lachrymal duct reaches nose.	Jacob organ loped. ana ope adult fo ol'. org
Lizard. *Lacerta agilis* Embryo D. ♀.	G. l. head to root of tail, about 10 mm.	The embryo is acquiring the adult form of body and this is particularly noticeable in form of snout. In the limbs the digits are defined but still completely connected. Lachrymal grooves have disappeared.	The chorda is becoming intravertebrally constricted by the formation of cartilaginous centra. Cartilaginous neural arches are developing.	Commencing formation of posterior fissure leading to formation of permanent central canal.	The retina is pigmented. The lumen of the lens has practically disappeared.	Jacob organ loped. ana ope
Chick. *Gallus bankiva* var. *domesticus*. Embryo D. ♂ aged 5 days 10 hours. (Incubated at 40° C.)	G. l. about 13 mm.	The embryo is acquiring the adult form of body and this is especially seen in formation of beak-like snout. Three digits are distinguishable in the fore-limb, but they differ as yet little in size and are still connected, as are also those of foot. Lachrymal grooves have disappeared.	The chorda is becoming intravertebrally constricted by the formation of cartilaginous centra. Cartilaginous neural arches are developing.	Commencing formation of post. fissure.	The retina is pigmented. The lumen of the lens is disappearing Lachrymal duct reaches nose.	Choa oper No trac Jacobs organ none d oped brids.
Duck. *Anas boschas.* Embryo A. ♂ aged 7 days (incubated at 40° C.).	G. l. 13,25 mm.	The embryo only differs from the preceding form in shape of snout, which is rounded.	As in chick.	As in chick.	As in chick.	As in c

1) See appendix b.

ophysis	Mouth	Alimentary canal &c.	Urogenital system	Skin and skeleton	Nutrition
lications prossen- ngen".	Dental ridge laid down.	Thymus elements of the two sides have become approximated caudally. Anus still closed but near point of opening.	Permanent kidney established and Malpighian bodies formed. Müllerian ducts partly formed. Sex established. Externally marked by penis.	Mammary glands completely differentiated from mammary ridges. Numerous hair-follicles on snout and some above eyes. In the fore-limbs thickenings at ends of digits. None as yet in hind-limb.	(According to Duval commencement of replacement of trophoblast by allantoic placenta.)
lications prossen- ngen".	Dental ridge laid down.	Thymus completely formed. Anus appears to be just opening.	Müllerian ducts partly formed. Permanent kidney developed. Sex established.	Indications of scale-formation as thickenings of Malpighian layer along sides of body. No ossifications in skeleton.	Probable annexation of contents of yolk-sac.
rked in- ions of rossen- ngen".		Thymus completely formed. Anus on the point of opening. Gizzard formed. Lungs begin to bud out air-sacs.	Müllerian ducts partly formed. Permanent kidney developed. Sex established.	Indications of feather-formation as thickenings of Malpighian layer along sides of body and near bases of wings. No ossifications in skeleton.	Probable annexation of contents of yolk-sac.
n chick.		As in chick.	As in chick.	As in chick, but feather-indications more marked along a line below limbs.	See chick.

Jena, printed by Hermann Pohle. — 1572

Errata.

p. 43	line 20	*instead of*	a actual	*read*	an actual.
p. 48	line 17	„	„ of embryo	„	of the embryo.
p. 51	line 2	„	„ is formed	„	was formed.
p. 60	line 19	„	„ in study	„	in the study.