Early Ontogenetic Phenomena in Mammals and their Bearing on our Interpretation of the Phylogeny of the Vertebrates.

By

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With 160 Text-figures.

Preface.

In the present paper I have attempted to bring together the results of new investigations and recent reflections with such as had already been published on earlier occasions, but which, having appeared in very different periodicals and publications ('89, '90, '94, '95, '96, '99, '02, '05, '07), could not be easily brought into the necessary connection with each other by the reader.

I have to thank my friend Sir Ray Lankester for giving me the occasion to present this scattered material in a more concise form, and for his willingness to admit a profuse quantity of process figures into a Journal which, under his direction, has become justly famous for its excellent lithographic plates.

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CHAPTER I. THE Earliest Cell-layers.

Introductory.

The phenomenon of fecundation of the egg inaugurates the well-known series of cell-divisions which give rise in Amphioxus to a grouping of the first cleavage-cells into a hollow mulberry shape, whereas in cartilaginous fishes, in reptiles, and in birds the cleavage-cells are disposed in disc-shape at one point of the yolk, which latter, though originally part of the egg, will soon take the aspect of an appendage to the embryo. Again, in Amphibia and in certain more archaic fishes the yolk is much less considerably developed and the whole egg thus segmented in toto, whereas in the Teleosts there is an abundance of food-yolk, but a disposition of the parts somewhat different from what we find in cartilaginous fishes and in Sauropsids.

In Mammals again the whole of the egg-substance is segmented (holoblastic cleavage as against the meroblastic cleavage of the cartilaginous fishes and the Sauropsida), but the further development more and more resembles that of the reptiles in which a very considerable yolk is present, a fact that has given rise to the erroneous conclusion that the mammalian blastocyst was derived from the Sauropsidan by a process consisting in the gradual disappearance of the yolk, with retention of the other developmental characters. We will find occasion later on to discuss the value of this phylogenetic speculation.
We will in this chapter have to consider the earliest processes by which the cell-material consequent upon the cleavage of the egg comes to be arranged in the fundamental cell-layers out of which the different organs of the adult animal will gradually take their origin.

And we must in the first place call attention to numerous and important investigations that have taken place, more particularly concerning invertebrate animals, in which the cleavage-cells were followed as far as possible up to their final destination with respect to organogenesis (Wilson, '92, '97; Conklin, '97; Casteel, '04).

These researches concerning the "cell-lineage," as it has been called, have been carried on by the aid of such worms and molluscs that had eggs as transparent as possible, and, notwithstanding the evident high importance of the results obtained, there is for the present little chance of success for similar attempts with the opaque and yolk-laden or deeply hidden eggs of the Vertebrates. I mention this in order to point out that several questions in dispute might in this way be settled, and that more especially the mammalian egg with its holoblastic cleavage would here offer a most desirable object of study. There has been a tendency to suppose that the two primary cell-layers which are encountered in all vertebrate and invertebrate animals, the ectoderm and the endoderm, already become separated from each other when the two first cleavage cells arise.

Others have concluded that in this separation of the egg-cell into the two first cleavage cells the embryonic material was separated into the mother-cells of the right and the left half of the body or into the anterior and posterior half, as chance would have it (Roux). Experiments have even been carried out to prove this. At the present moment we are not in a position to say whether there is any general rule in this respect applicable to all vertebrates, and yet there seems to be hardly any doubt that both in Amphioxus and in man—the two opposite extremes in the phylum of the Chordata—the two first cleavage cells, if separated from each other,
may under favourable conditions each of them develop into a perfect, full-grown individual.

However this may be, the formation of the primitive cell-layers out of the cell-material derived from the segmenting egg-cells must now, in the first place, be considered, and, inverting the order generally followed, we will begin by considering the phenomena as they present themselves in the

A. Monodelphian and Didelphian Mammals.

As yet only a restricted number have been investigated with regard to the process of cleavage and the earliest formation of the layers, it being no easy matter to procure the material. As such I mention—

(1) Certain species of Primates, including both monkeys (Macacus, Cercocebius, a.o.) by Selenka (’89, ’90) and by Keibel (’04), and Tarsius by myself (’02).

(2) Lemurs (Nycticebus) by myself (’07). cfr.

(3) Carnivores (dog and cat) by Bonnet (’97) and Duval (’94, ’95).

(4) Chiroptera (diverse species of Vespertili) by E. van Beneden and Ch. Jullin (’99) and by Duval (’99).

(5) Insectivora (Talpa, Erinaceus, Gymnura, Sorex, Tupaj) by Heape (’89), Keibel (’88), and myself (’89, ’90, ’95, ’98).

(6) Rodentia (Lepus, Mus, Arvicolus, Cavia, Sciuers, a.o.) by Hensen (’73), E. van Beneden (’80), Selenka (’88, ’84), Frasch (’82), Masius (’89), Fleischmann (’91), Keibel (’80), Duval (’92), Robinson (’92), a.o.

(7) Ungulata (Ovis, Sus, Cervus) by Bonnet (’82), Keibel (’93), Assheton (’98), Wysse (’94), a.o.

(8) Dermoptera (Galeoepiheus) by myself.

(9) Edentata (Manes) by myself.

(10) Didelphina (Opossum, a.o.) by Selenka (’87).

1 Of the human subject as such early stages have as yet been brought to light, the earliest being those of Peters, von Heunekom, Bryce and Teacher.
Fresh eggs have served for the observation of the cleavage-processes in the rabbit to van Beneden and in the bat to van Beneden and Julin. Most of the other authors have made use of preserved specimens and of sections. A certain number of the figures given by different observers are here reproduced (Figs. 1—36).

I. The Mammalian Morula.

The compact mulberry stage (different in its compactness from the hollow mulberry of the holoblastic egg of Amphioxus alluded to above) contains about 36—72 cells. In the case of Tupaja and—judging from Bonnet's figure—of the dog the central cell or cells show a different reaction against staining reagents than the peripheral (Figs. 1, 2, 3). We will have occasion to discuss this phenomenon later on. Very soon fluid begins to accumulate between some of the constituent cells of this mulberry stage in mammalian development, and the solid mulberry then becomes converted into a hollow sphere, against the wall of which an accumulation of cells is visible which was already noticed by Bischoff ('42, '45) and other early authors.

Twenty-five years ago, when van Beneden published his remarkable researches above alluded to on the early development of the rabbit, the interpretation of these early phenomena was far from being satisfactory or uniform. The so-called megasphera of mammals, first described by van Beneden ('80), has since been abandoned by that author [though taken up again by Duval ('99, p. 64)]. We may, however, say that of late years a very general consensus of opinion has come to be established. In all the orders above-mentioned an early stage of the blastocyst has been observed corresponding to the phase just described in which an accumulation of cleavage-cells adheres at one point against an outer epithelial layer.¹

¹ E. van Beneden has ascribed the origin of the free space between the
Fig. 1. Cleavage stage of the dog (after Bonnet, '97). The mother cells (eb) of the embryonic knob, centrally situated, have stained more deeply than the trophoblast cells (tr). — Fig. 2 and 3. Sections through two different early cleavage stages of Tupaja javanica. In this case the trophoblast cells, tr are more deeply stained than the mother-cells of the embryonic knob eb. — Fig. 4 and 5. Sections through early stages of the opossum (after Seelos, '87). In Fig. 4 there are thirteen trophoblast cells tr and one mother-cell of the embryonic knob eb, in Fig. 5 the latter has given rise to a mass of cells which begins to project on the surface (eb) and in which the differentiation of entoderm cells has just commenced. — Fig. 6, 7, 8. Three sections of the development stages of the bat (after van Beneden, '99). In Fig. 6 the differentiation between trophoblast cells tr and embryonic knob is again expressed in the staining; in Fig. 7 the embryonic knob (eb) is not yet separated into ectoderm (eb) and entoderm (cm) as it is in Fig. 8.
This outer layer has been termed by me the trophoblast, that inner cell-mass: the embryonic knob or "Embryonalknoten" (86, p. 511; '89, p. 298). E. van Beneden, while recognising that the trophoblast is a separate layer ('99), does not as yet apply that name but calls it somewhat more circumlocutiously the "couche enveloppante."

The degree of independence existing between trophoblast and embryonic knob is subject to considerable variation. As the two only become segregated when the change of the morula stage into a vesicle comes about, there is generally at the outset no such very sharp distinction, and even in later stages this distinction is sharper in certain genera of mammals (Tupaia, Figs. 21, 29; Galeopithecus, Fig. 18; Cervus, Figs. 13, 14) than in others (Emu, Figs. 35—36; Tarsus, Fig. 19; Cavia, Fig. 24. Still there is reason to believe that in some it may be traced up to the very early stages of cleavage as are indicated by Figs. 1—3. The embryonic knob would then be represented by one or a few central cells, the trophoblast by the surrounding cleavage cells (as was already noticed above).

When the trophoblast is being distended into a vesicle the proliferation of the mother-cells of the embryonic knob is very much slower; the total number of cells of which the knob is built up rarely exceeding 24—30.

For the Opossum we have the data furnished by Selenka ('87), to which, however, I would put another interpretation. The central cell of Fig. 4, looked upon by him, without further proof, as a hypoblast cell, is undoubtedly the mother-cell of the embryonic knob as a comparison with Fig. 5 makes all the more evident. It is, of course, important to find this agreement between didelphic and monodelphic mammals.

epithelial outer layer and the inner mass to the extension of intracellular vacuoles ('99). His interpretation has found no support in the results obtained by Keibel and myself, nor in those of Selenka for the Opossum.
2. The Origin of the Entoderm.

Soon a most important process is inaugurated and from the inner cell-mass arises by delamination a separate lower layer which we designate as the entoderm of the embryo. These entoderm cells wander in radial direction along the inner surface of the trophoblast, which, in many cases, is thus soon transformed into a diermic structure. Sometimes, as for instance in Tarsius (Hubrecht, '62) the more important part of the delaminating entoderm (viz. that which remains situated below the rest of the embryonic-knob-cells) is present as a distinct cell-layer before this migration of entoderm cells towards the inner surface of the trophoblast commences (Figs. 8, 19); in other cases (Sorex, Lepus, a. o.) the entoderm cells migrate as soon as formed; whereas in Tupaja it is only after the entodermic vesicle has become nearly completed that the part of it which will remain in contact with the embryonic ectoderm is separated off from the latter by delamination (Fig. 29).

In certain mammals (Tarsius, monkeys, man) the entoderm cells never clothe the whole of the inner surface of the trophoblast, the entodermic vesicle remaining of smaller size than the trophoblastic sphere (Figs. 39, 40, 44—46, 62—65). To a certain extent this is explained by the fact that another vesicle (of which mention will be made later on) develops, at an uncommonly early period, fills up part of the vesicle formed by the trophoblast and prevents the entoderm cells from reaching the entire outer surface.¹

When the entoderm has separated off by delamination from

¹ It would seem that in Erinaceus a similar state of thing occurs temporarily; it having been observed by me ('89, Figs. 25, 36) that a closed entodermic vesicle, far smaller than the trophoblastic sphere which encloses it, is here noticed in very early stages (Fig. 34). Shortly after this (Figs. 35—38) the hedge-hog's blastocyst, is, however, a spherical trophoblast, against which the entoderm is everywhere adherent. The investigation of numerous early stages of the hedge-hog is, however, yet necessary to settle this point.
Fig. 8a. Section through an early bag's blastocyst (cf. Fig. 6 to 8); tr trophoblast; en entoderm. The ectodermic shield has not yet emerged out of its trophoblastic covering (after van Beneden, 99). — Fig. 9. Section through early stage of the bat (after Duval) cb embryonic knob, tr trophoblast. — Fig. 10. Section through early stage of the shrew (after Habrecht, 50). cb embryonic knob, tr trophoblast. — Fig. 11 and 12. Sections through early stages of the mouse, before and after fixation of the blastocyst to the uterine epithelium x. — Fig. 13 and 14. Two sections through the embryonic knob of Cervus (after Koebel, 50) before and after the development of the entoderm by delamination. The trophoblast (tr) is quite distinct from the embryonic ectoderm e; in Fig. 13 ectoderm and entoderm are yet united in the embryonic knob.
the embryonic knot, the remaining cells of the latter form the "embryonic ectoderm," which is thus situated between the entoderm and the trophoblast, and could for that reason easily deceive van Beneden (70) in regarding it as a third, mesodermic layer (Figs. 8, 11, 12, 15, 17, 18, 21—23).

3. Developmental phases of the Didermic Embryonic Shield.

The portion of the mammalian blastocyst where the embryonic ectoderm and its subjacent entodermal layer are situated may, already at this early stage, be conveniently termed the embryonic shield. This shield is sometimes slightly convex with the ectoderm on the convex side (rabbit, Fig. 23), sometimes it is bent the other way (Sus, Fig. 17; Tarsius, Figs. 20, 45), sometimes first one way (Figs. 20, 37, 53), and later [Figs. 50, 58] the other (Tarsius, hedgehog). Sometimes it is (Fig. 23) quite flat (Lepus, Sorex, a. o.).

A very instructive and in my opinion very archaic case among those above-mentioned is that in which the embryonic shield remains separated from the overlaying trophoblast by a space which arises simultaneously with the growing blastocyst. This space is from the outset a lenticular or crescentic cavity. Its appearance in Erimaeus is elucidated by the accompanying diagrams (Figs. 36—38). It represents the most typical instance of the manner in which the earliest amnion may have arisen as a protective water-cushion between the trophoblast and the embryonic shield, and we shall later on see that the space within the hedgehog's amnion is actually a later development of this early cavity. In the bat slight modifications of this simple arrangement occur, which seem to lead on to arrangements as we find them in Tarsius and in many Ungulates and Rodents, whereas on the other hand Pteropus (Figs. 22, 72), Galeopithecus (Figs. 41, 42), Cavia (Figs. 24, 25), monkeys and man (Figs. 39, 40) have developed
along another path, along which the amniotic cavity has from the first remained a closed vesicle.

A very important case is that of Tupaja in which the embryonic shield is originally quite bent upon itself (Fig. 30), convexity inwards, and gradually expands (under rupture and dehiscence of the trophoblast) into a flat surface with no trophoblastic covering above it (Fig. 32) by successive stages as they are reproduced in the accompanying diagrams. This arrangement possesses suggestive points of comparison with what has been called by Selenka ('00 a, p. 201) the "Entypie" of the embryonic shield, such as it exists in many rodents. All these cases are variations upon a similar theme as that of Tupaja, and not necessarily (as Selenka would have it) a consequence of the blastocyst undergoing its development in a cavity of exiguous dimensions, to the walls of which it had early adhered. Tupaja at once does away with this argument (Hubr., '99 a, p. 173), because here the blastocyst, while free from any attachment to the uterine walls, has yet the appearance of Figs. 30 and 31. The causes of the folded condition of the embryonic shield can hardly be so simply mechanical as Selenka supposed. They remain obscure for the present and will come anew under consideration when the origin of the amnion will be discussed.

The point to which the facts here brought forward have led us is the recognition that during the development of the mammalian blastocyst the trophoblast, which originally encloses the embryonic knob, behaves very differently in various mammals at the period that out of this knob arises the embryonic shield with its diericmic arrangement of the cells out of which the embryo is going to be built up. In the hedgehog (Figs. 37, 38), in Gymnura, in Pteropus (Figs. 07, 08), and in the other bats hitherto examined (Fig. 8a), in Galeopithecus (Figs. 41, 42), in many rodents (Arvicola, Mus, Cavia, Figs. 24—28), in monkeys, and (most probably) in man the trophoblast remains an entirely closed vesicle, inside of which the ontogenetic development of the embryonic knob will follow its course. In other genera of
Fig. 15. Section through a similar stage of Ammospermophilus. After a not yet published drawing of Prof. G. Loe of Mianopolis. Trophoblast or continued over embryonic ectoderm c, en endoderm. — Fig. 16. The same for the sheep (after Ascleriten, '88). — Fig. 17. The same for the pig (after Weyssen, '94). The endoderm has not yet opened out on the surface of the blastocyst (cf. Fig. 29-32). — Fig. 18. The same for Galeopithicus. — Fig. 19 and 20. The same for Tarsius. In Fig. 19 the endoderm c is in the very earliest phase of delamination (after Hubrecht, '92). In Fig. 20 there are yet remnants of the trophoblastic covering of the ectodermic shield. — Fig. 21. The same for Tupaj (after Hubrecht, '93). — Fig. 22. The same for Pteropus. In the ectodermal knob (e) a cavity will soon appear which becomes the amniotic cavity (after Selenka and Golre, '92) en umbilical vesicle.
mammals that part of the embryonic knob which is going to be the ectoderm of the embryonic shield rises to the surface, interpolates itself between the trophoblast cells, which then form no longer a closed sphere, but one that is discontinuous by the fact that at one pole this ectodermal shield has replaced what were originally trophoblast cells. This displacement may come about as it does in Tupaj (Figs. 29--32) where the unfolding of the embryonic shield bursts open the trophoblastic covering above the shield, thus increasing the surface of the vesicle by an area which is not trophoblast, but embryonic ectoderm. Or it may happen that a similar but less distinct process of dehiscence interpolates embryonic ectoderm in the trophoblastic vesicle in the way it comes about in the Opossum (Fig. 5), Tarsius (Fig. 20), Cervus (Fig. 13), Sus (Fig. 17), Ovis (Fig. 18). Or finally the trophoblast may continue to cover the embryonic ectoderm as in the case first named, but without the development of any cavity between it and the embryonic shield (Fig. 15). In this latter case, of which the classical example is the rabbit, as it was so clearly figured by Kölliker (Fig. 23), the trophoblast cells covering the embryonic ectoderm flatten out considerably, and finally disappear. Another example of this is the shrew (Hubrecht, '90; Fig. 26). These flat cells—superposed to the embryonic ectoderm—were for a long time designated as Ranber's cells, Ranber having been the first to direct attention to them. It was, however, not observed by Ranber, as it was later so clearly noticed by Kölliker, that this layer is merely the continuation of the peripheral trophoblast cells, but it remained for a long time an accepted, though erroneous interpretation, that the embryonic ectoderm was uninterruptedly continued in the peripheral trophoblast, and that Ranber's cells were an additional arrangement. This error was a natural consequence of a comparison, on a false basis, hereafter to be corrected, of the mammalian with the avian and reptilian blastocyst. The opinion of certain authors (Balfour,
Heape) that some of the Rauber cells become incorporated into the embryonic shield has not been well established nor been confirmed of late. I incline to believe in their final disappearance, and wish to call attention to the transition case which we may notice, for example, in Tarsius (Hubrecht, '02; Figs. 49a, b, 50b), where trophoblast cells can remain for yet a considerable time attached to the embryonic ectoderm, but also finally disappear. In this case the trophoblast opens up according to the type prevalent in the second group described above, and the permanence of an isolated trophoblast cell on the embryonic ectoderm is a matter of chance.

We may, in concluding this exposition of the varied relations in which trophoblast and embryonic ectoderm stand to each other in mammals, insist upon the fact that—if we except the Ornithodelphia, which will be discussed hereafter, and are as yet barely known as far as their early ontogeny is concerned1 (Caldwell, '87; Semon, '94; Wilson and Hill, '09)—all the Didelphio and Monodelphio hitherto investigated show at a very early moment the didermic stage out of which the embryo will be built up enclosed in a cellular vesicle (the trophoblast), of which no particle ever enters into the embryonic organisation.

4. The Mammalian Gastrula.

The didermic stage of the mammalian blastocyst just alluded to fully deserves the name of the "gastrula" stage as I have elsewhere attempted to expound ('02, p. 65—75; '05, p. 408). We should bear in mind, as was noticed in the introduction, that comparative ontogeny has come to a deadlock when attempting to fit in the mammals into the current interpretation of the early development of vertebrates. To

1 Just lately the more extensive paper of Wilson and Hill ('07) has appeared, in which figures are given (pl. 2, fgs. 4, 5), which allow us to accept quite similar arrangements for the Ornithodelphia (see text ffgs. 65—70).
Fig. 23. The same for the rabbit (after Kölliker '59). The trophoblastic peripheral wall of the blastocyst continues into the Rauher's cells $tr$ above the ectoderm. — Fig. 24 and 25. The same for Cavia (after Selenka). The reduction of the trophoblast is yet far more considerable. $a$ amnion cavity. — Fig. 26 and 27. Sections through two early stages of the mouse's blastocyst (after Selenka, '53). The trophoblast (ctv) is much further reduced in the second than in the first whereas that part of it ($pl$) which will form the placenta has proliferated much more considerably. $a$ amnion cavity.
express it in O. Hertwig's own words: "Die grössten Schwierigkeiten bereitet den Embryologen die Keimblattbildung bei den Säugethieren ... wegen der von anderen Wirbeltieren stark abweichenden Befunde" (06, p. 898).

As soon as we separate the phenomena of notogenesis, such as they are found in all vertebrates—Amphioxus included—from the phenomenon of gastrulation, recognising that the former follow upon the latter and bring about the formation of the notochord and the mesoblastic somites, the difficulties are considerably simplified.

Gastrulation is thus terminated in the mammalia when the didermic stage of the embryonic shield has come into existence. We have seen that this takes place not in consequence of any process of invagination but by means of a most unmistakable delamination of the entoderm, out of the embryonic knob.

This delamination gastrula of the mammalia generally enters upon the later phases of ontogeny which will be described hereafter without the appearance of a distinct blastopore.

Still to this there are a few notable exceptions that have gradually come to light, but have been mostly overlooked or misinterpreted in consequence of the erroneous views above alluded to. The most striking example is undoubtedly offered by the hedgehog, where the blastopore, a clearly visible perforation towards the hinder end of the embryonic shield, makes an evanescent appearance at one particular stage of the individual development (Fig. 53).

Along the lips of this opening the ectoderm and entoderm pass into each other, whereas these two layers, although genetically related, have up to this moment been separated and nowhere in confluence with each other. This latter fact is recognised by all observers. I am inclined to believe that the formation of the blastopore in the hedgehog is not only very evanescent, but that it does not necessarily appear in all hedgehog embryos, and that in exceptional cases the formation of notochord and somites may commence without the blastopore having become a visible opening.
In Tarsius on the other hand, where in an overwhelming number of cases the embryonic shield undergoes the changes consequent upon the first appearance of notochord and somites without any faint trace of a blastopore, one quite exceptional case came under observation (Fig. 52) in which what was evidently an atavistic attempt in that direction was noticed; all the more important because it helps us to fix the spot in the didermic gastrula at which the blastopore naturally occurs. Similarly blastoporic openings, or attempts at such a perforation in these early stages, have been noticed in the rabbit by Keibel ('89; Figs. 46, 47), in the mole by Heape (Fig. 54), in the opossum by Selenka (Fig. 55), in the shrew by myself (Figs. 56 and 57). In the diagrams a few of these observations have been reproduced.

The gastrula stage and the blastopore of the mammals are thus limited to the early phases and the simple phenomena here described. The blastopore becomes closed in all the cases above noticed, and after that a series of processes are initiated in which it would be utterly misleading further to use the word blastopore, Gastrulas mund, Ur mund, or Ur mund lippen. These structures in the further development that have been thus termed ought to be termed differently if we wish to put an end to the confusion that obscures these points at the present moment.

At the same time it should be noticed that one of the first features by which the formation of the notochord begins, viz., the formation on the embryonic shield of that median ectodermal proliferation, which I have called (90) the protochordal wedge (Primitivknötzen, Bonnet = Hensen'scher Knoten), takes place in the identical spot where the evanescent blastopore was or is situated (Fig. 52); and that from this point backwards a median region of proliferation extends which on O. Hertwig's example has been called the homologue of the "Urmund" and the "Urmundlippen," but which we ought to compare as I have elsewhere advocated (02, '05) with an elongated stomodeal slit, which even in the hypothetical ancestral forms was no longer a blastopore, but
Fig. 28. Section through an early blastocyst of the mouse (after Selenka, '83). & amnion, on the point of being constricted off. E. Endodermal shield. meo. mesoblast. en. ectoderm. tr. trophoblastic rudiment of placenta. — Fig. 29 to 32. Four successive stages in the early development of Tu-paja javanica. In Fig. 29 the trophoblast tr yet forms a solid closed sac round the embryonic Knob and endoderm, the latter only just beginning to split off from the embryonic knob as far as its embryonic portion is concerned. In Fig. 30 and 31 the bent embryonic ectoderm & commences to free itself from its trophoblastic covering; in Fig. 32 it has quite flattened out, forcing the embryonic shield on the top of the spherical blastocyst.
a dorsal mouth slit, a "Rückemund" (Fig. 160) of a vermicellar stage of development.

The mammalian blastopore, rudimentary, rare, and evanescent as it is, still reminds us of the blastopore of the invertebrates in this respect that in its immediate vicinity those cell proliferations commence which lead up to the formation of the so-called mesodermal structures.

5. Theoretical Speculations about the Origin of the Trophoblast.

The facts with which we have up to now become acquainted concerning the early development of didelphic and monodelphic mammals (the so-called marsupials and the placental mammals) fully justify the conclusion that the embryo already in its very earliest ontogenetic phases is provided with a larval envelope, an "Embryonalhülle." To this layer of cells we have given the name of trophoblast. Later on we shall see that this layer, though it is at first only one cell thick, can undergo the most varied proliferations in very divergent spots, and that such proliferations are at the basis of the whole phenomenon of placentation. The fact that to these proliferations and their significance for the early nutrition of the embryo, attention was first directed (Hubrecht, '88, '89) before the more general significance of the layer as a larval envelope had yet been fully appreciated was the cause that the name of trophoblast has been given to it. We will return to this when the phenomena of placentation will be discussed.

It cannot be denied that the consequences of considering the trophoblast as a larval envelope and of introducing this

1 It remains to be seen whether the name of "trophoderm," introduced by Sedgwick Mivart ('03) for that portion of the trophoblast which takes an active part in placentation, is a desirable innovation, or rather a synonymous circumvention. But even in the former case Duvall's proposal of the name of "seto-placenta" has the priority.
generalisation into the developmental history of vertebrates may be far-reaching.

Up to now foetal envelopes or membranes were only known in the ontogeny of reptiles, birds and mammals at somewhat later stages of their development. These membranes were respectively known as amnion, chorion, serous membrane, subzonal membrane (and in case of the Sauropsids and certain mammals, even allantois) so that Milne Edwards' subdivision of the vertebrates into Amniota, Allantoidea, as against the Anamnia, Amniatoidea, was based on the presence or absence of such membranes. Of the phylogenetic evolution of these foetal membranes no reasonable explanation has yet been offered, as is, for example, recognised, as far as the amnion is concerned, in an unbiased handbook of human embryology, as is that of Sedgwick Minot (p. 344, 1st edition). Now this obscure phylogeny would seem to become yet more complicated when we add to the already existing foetal membranes a new larval envelope, called trophoblast. The case is, however, quite the contrary. This early envelope, that we have seen making its appearance soon after the very first phases of segmentation of the mammalian ovum, instead of adding new difficulties, helps to explain old ones. It throws new and unerring light on the first origin both of the amnion and the chorion (respectively : serous membrane) and may prove to be a valuable key that may lead to a reasonable interpretation of much that is as yet obscure and incomprehensible. Out of this very earliest larval envelope the others seem to have gradually evolved; they may be looked upon as further differentiations of it and we have now to look out for the first origin of the trophoblast itself and see if we can furnish a hypothesis worthy of farther consideration. In that case the phylogeny of the other foetal membranes would a fortiori have been explained at the same time.

Now, I believe that we have only to assume that the ancestors of those Vertebrates in which a distinct trophoblast or the traces of it are found, were already possessed of a larval envelope in the antecedent stages of phylogeny, in order to
Fig. 33, 34 and 35. Sections of quite early stages of the hedgehog's blastocyst. Tr trophoblast, en entoderm, ce ectoderm yet firmly united with the trophoblast. — Fig. 36. A somewhat later stage in which considerable lacunae have originated in the proliferating trophoblast into which maternal blood penetrates. — Fig. 37. Section through a yet later stage in which the lacunae have developed all round the blastocyst and in which the amnion cavity (a) has arisen as a split between trophoblast and embryonic ectoderm (ce). — Fig. 38. Yet later stage of the hedgehog's blastocyst, in which the development of the embryo is further advanced and the amnion-well completed and externally clothed by mesoblast. uv umbilical vesicle, co coelen.
Fig. 39 and 40. Diagrammatic sections through two stages in the early blastocyst of man and the anthropomorpha, combined out of Selenka's ('96, '09) and Peters' ('09) drawings. c connective stalk, som & splan somatic and splanchnic mesoblast. Amnion and trophoblast as in the hedgehog — Fig. 41 and 42. A longitudinal and a transverse section of an early developmental stage of Galeoatherius culmen. In Fig. 41 the placenta is commencing to be formed on the upper surface of the blastocyst. Here too the amnionic cavity (a) has arisen by delification inside the embryonic knob. vm ventral mesoblast, connecting embryonic region with trophoblast. Fig. 42 belongs to a somewhat later stage in which a thickening in the entoderm (protodermal plate) has become visible. — Fig. 43. Transverse section through the ventral mesoblast of Galeophaenius. cc coelome, en entoderm, tr trophoblast.
obtain such a working hypothesis. Both Sauropsids and Mammalia are, ommium consensus, phylogenetically derived from very early Prototetrapods that lived about the Carboniferous period or even earlier, and which, in their turn, had aquatic and fish-like progenitors. These early, to us unknown, fishes have sprung from vermiform predecessors of coelenterate pedigree.

A tendency to exchange the radial for a bilateral symmetry and to separate the coelom from the enteron must at one time have characterised certain coelenterate ancestral forms, as has already been advocated by Sedgwick ('84) and by myself ('95) on earlier occasions. It is not straining the imagination to assume that in this line of descent closely-related forms may have developed, some with, others without a larval envelope, temporarily ensheathing the cellular elements that will build up the embryo itself and thus fore-shadowing the separation among their later, vertebrate descendants of such with and such others without a trophoblast.

We find examples of this amongst the Nemertean worms. In some of these the egg after segmentation develops straight away into the young worm, in others, which as far as the typical Nemertean characteristics go are very closely related, the cleavage results in a disposition of the embryonic material into (a) the first lineaments of the embryo itself and (b) a cellular temporary envelope of these, which is either more closely applied to (Desor's larva) or more distant from (Pilidium larva) the material that goes to build up the embryo.

And though I in no way want to infer that it is among the Nemertean or Gephyrea that we would have to look for the ancestral forms of the Vertebrates (nor either amongst any of the Annelids known to us) still it is an instructive fact that among different classes of worms (Gephyrea should also here be mentioned, see Fig. 129) the larval envelopes above alluded to are encountered in some but are absent in others.
This particularity may have passed on in the ancestral line of the chordata.

Now, if in our further phylogenetic speculations concerning the Prototetrapods and their descendants that live at the present time, we were to start from an oviparous aquatic animal, whose early developmental stages are provided with a larval envelope, we understand that, when any such animal came to adapt itself to inhabit the dry land it would doubtlessly score certain advantages if at the same time it became viviparous. Its adaptation would certainly be the more complete if, for its reproduction, it were independent of the aquatic medium. And towards the efficiency of this viviparous condition the larval envelope could immediately contribute by the mere change of its protective or locomotor significance into an adhesive one. This again would be facilitated if the larval envelope, increasing in surface, were to develop into a spherical vesicle prececdingly forestalling the further development of the mother-cells of the embryo of which this larval envelope had originally been an organ of protection and of locomotion. Subsidiarily this vesicular shape would contribute towards the retention of the developing egg for a longer time in the maternal genital ducts. And at the same time the possibility would arise of introducing through the wall of this swollen blastocyst not only fluid to increase the swelling, but also nutritive matter to further the growth of the dermoc "Anlage" contained in it.

All these circumstances accompanying the transition to an atmospheric environment would at the same time be unquestionable advantages of protection and nutrition to the embryo, such as are already sporadically obtained in certain fishes (Mustelus, Zoarces, and others). Besides this, however, another advantage might ensue, viz., the possibility of this larval and transitory layer becoming vascularized in aid of a yet more thorough system of nourishment at the expense of the maternal circulatory system.

And it is this what we actually observe in the mammals
Fig. 44—46. Three diagrams of the aspect of a longitudinal section through a Tardus blastocyst. In Fig. 44 the trophoblast yet covers the embryonic ectoderm. The cavities of the umbilical vesicle (u.v.) and of the extra-embryonic coelom (c.s.) in the ventral mesoblast entirely fill up the blastocyst; the connective stalk (c.s.) is formed and it is at this spot (cf. Fig. 62) that the attachment of the blastocyst to the maternal tissue comes about. In Fig. 45 the embryonic ectoderm has become exposed to the surface after desistence of the trophoblast; the entoderm in the embryonic region has thickened. In Fig. 46 protochordal plate pp and protochordal wedge pw have become differentiated (cf. Fig. 48): under the stalk of ventral mesoblast the amnian region of proliferating entoderm is once more cut longitudinally (a.); from here the vascularization of the connective stalk proceeds. — Fig. 47. The relative positions of ventral mesoblast (v.m.), trophoblast (t.v.) on its way to leave the embryonic ectoderm uncovered (cf. Fig. 20) and umbilical vesicle in a stage of about the same age as the following figure. — Fig. 48. A somewhat later stage in which a distinct ventral proliferation (p.p.0) of the ectoderm fuses with the entodermal proliferation (t.p.) of the entoderm. The protochordal wedge pw and the protochordal plate pp then become fused (cf. Fig. 52, 98, 99); the ventral mesoblast v.s. springs from the embryonic ectoderm just behind the protochordal wedge. ir trophoblast, p.m. splanchic mesoblast, u.v. umbilical vesicle.
Fig. 49. Longitudinal section of another Tarsius blastocyst in which the protocordal plate \( pp \) has become fairly established and the protocordal wedge is just in its very earliest phase, more so than in Fig. 48. The ventral mesoblast \( mw \) arises from the ectoderm, close behind \( mw \); the trophoblast \( tr \) is independent of both. — Fig. 50. Longitudinal section in about the same stage; the attachment of the blastocyst to the uterine wall commences about at the spot marked \( tr \); the corresponding proliferation of trophoblast \( tfr \) is not indicated in this figure (cf. Fig. 62); the ventral mesoblast \( mw \) springing from the ectoderm shows the extraembryonic coelom the wall of which is partly splanchic \( tfr \), partly somatic mesoblast \( smw \); \( pp \) protocordal plate. — Fig. 51. Transverse section of an early blastocyst of about the stage of Fig. 46 showing the proliferating protocordal plate.
Fig. 52. Longitudinal section of a Tarsius embryonic shield in which at the spot where the protochordal wedge ps has proliferated downwards a rudimentary attempt at a blastoporic perforation has quite exceptionally arisen. pp protochordal plate, ps protochordal wedge, vs ventral mesoblast, us umbilical vesicle. ee embryonic ectoderm; mres mesoblast, springing from protochordal plate. — Fig. 53. The early evanescent blastopore (%) of the hedgehog (after Hubrecht, 62). — Fig. 54. The same of the mole (after Heape); b blastopore, en endoderm.
Fig. 55. The same of the opossum (after Selenka): b blastopore, se urinal vesicle, ce endoderm, en entoderm, al albuminous layer, tr trophoblast. — Fig. 56, 57 and 58. Three longitudinal sections through an early histocyst of the shrew (Sorex) of which the embryonic shield is traced in the diagram of fig. 59. Fig. 50 and 57 are two succeeding sections through the posterior region where a rudimentary blastopore (b) pierces the embryonic shield, separating the proliferating endodermal region pe (proteochordal wedge) from the yet further posterior endodermal region which will give rise to the ventral mesoblast (cm), in which the posterior coelom will take its origin in crescent-shape as indicated in diagram 51 and 100. Fig. 58 is the longitudinal section through the endodermal proliferation pe of Fig. 50. Fig. 100 gives a longitudinal section through the posterior crescentic coelom of fig. 61. — Fig. 56. Superficial aspect of the early endodermal shield corresponding to the three preceding figures. The region of the proteochordal wedge is indicated by the posterior white, that of the proteochordal plate by the anterior shaded space.
from the Didelphia onwards, where either the omphaloidean or the umbilical arteries, or both, serve that purpose.

This then is my interpretation of the phylogenetic phases through which the trophoblast has passed. They cannot be said to be numerous or intricate, nor can the interpretation be looked upon as strained or artificial. The less so, because in all mono- and di-delphic mammals, which have as yet been examined, we do—as was noticed above—encounter a larval envelope—the trophoblast—which surrounds the formative cells of the embryo. Without exception the trophoblast undergoes the series of changes and physiological transformations here sketched, becoming first vesicular, then selective to certain nutritive matter, finally vascularised and locally strongly adhesive to and fused with maternal tissue.

B. Ornithodelphian Mammals and Sauropsida.

The segmented egg of Ornithorhynchus and Echidna, the two living representatives of the Ornithodelphian presents itself to us under a totally different aspect, as compared to the other mammals. The ornithodelphian egg does not cleave according to the holoblastic, but to the meroblastic type, and offers numerous points of comparison with that of reptiles and birds. However, our knowledge of it is as yet very scanty and limited to what Caldwell ('87), Semon ('94), and Wilson and Hill ('03, '07) have taught us. The egg is enclosed in a leathery shell. There is no, or hardly any, albumen, and this makes investigation of the earliest stages all the more difficult.

The formative protoplasm, accumulated at the upper pole of the yolk, breaks up into a number of cleavage-cells (Fig. 66) and at a very early stage the outer layer, already distinctly visible as such in the preceding stage (Fig. 67), has spread over the yolk as a membrane of flattened cells with flattened nuclei (Figs. 68 and 69). At the upper pole this layer covers—at the spot where the embryo is going
to be formed—the remains of the cleavage cells not as yet arranged in regular layers. I think we may safely compare this stage in the Ornithodelphian development with that of the higher mammals in which the, as yet undifferentiated embryonic knob is covered by the trophoblast, which has dilated into a vesicle. Although the interpretation here given differs from that of Semon, I feel confident that further and more detailed researches on the development of Monotremes will confirm this hypothesis, as well as the supplementary one which at present is not yet based on observation, viz. that the cells e.g. in Figs. 67 and 69, after a time arrange themselves into embryonic ectoderm and entoderm, the latter spreading out radially below the trophoblastic cell-layer, as indicated in Fig. 70. It is particularly to be regretted that the embryonic shield belonging to Semon’s Fig. 39 has come to grief, because it would no doubt have settled the point here under discussion.¹

The difference between the Ornithodelphia on one side and between Mono- and Di-delphia on the other would—if the interpretation here given were to be confirmed—consist in the fact that the trophoblastic vesicle of the former includes besides an embryonic knob a very considerable amount of food-yolk, the development of which will have gone parallel with the change in the ancestral line from viviparity to oviparity.

Also in the Sauropsida similar phenomena must have occurred of which, however, the traces are yet more difficult to establish than was the case in Ornithodelphia. The trophoblastic vesicle, which is in Ornithodelphia yet comparatively distinct, though as yet imperfectly known, is in many reptiles and birds distinguished with great difficulty from the embryonic shield because the phenomenon of the trophoblastic vesicle opening up at one spot, in order to let

¹ When this paragraph was first written Wilson and Hill’s latest extensive researches (’07) had not yet come into my hands. Their figures, here reproduced in the Figs. 68 and 70, seem to fully agree with the hypothetical interpretation here given, before these new facts had come to light.
Fig. 60 and 61. Two surface views of a yet later embryonic shield of the shrew. In fig. 60 the anterior zone of proliferating entoderm \( as \) is indicated as well as the primitive streak and the dotted outline \( mes \) of the mesoblast wings; in fig. 61 the notochord has begun to be formed; a neuraxial plate \( np \) is visible as well as extra embryonic posterior coelom, \( co \). (Fig. 56 to 61 after Hubrecht, 90.) — Fig. 62 to 65. Diagrams intended to demonstrate the gradual displacement in Tarsius of the embryonic shield from its original position (62) towards a position diametrically opposite the placenta (63). The zone \( c \) of fig. 16 is shown in fig. 63 as being at the same time the incipient allantois tube \( all \); in fig. 64 and 65 this becomes a posterior, cylindrical continuation of the anterior cavity \( N \), lengthening as the embryonic shield travels apicad. In 64 and 65 the placenta \( P \) has become a considerable trophoblastic proliferation in cushion shape (side Hubrecht, 90); in Fig. 65 the annion folds \( va, ka \) and the neuraxial canal \( as \) have made their appearance (cf. fig. 90); \( e \) extraembryonic coelom. \( H \) connective stalk, \( am \) annion (after Hubrecht, 97).
the embryonic ectoderm come to the surface, has become indistinct. It was above shown how perfectly distinct this is in monodelphian and didelphian mammals, and how there can be no doubt of its occurrence in Ornithodelphis (Fig. 70). Still this latter group helps us to explain how it was that it became indistinct and thus unrecognised in Sauropsids.

An outer trophoblastic layer has been described by Mehnert ('94, p. 214), who perfectly recognised its identity with the layer for which in Mammalia I had introduced the name of trophoblast, but who has created confusion by nevertheless proposing the new name of teloderm¹ (Grenzb.l.) and greater confusion yet by comparing heterogenous cell-layers as I will yet further indicate. Mehnert describes in detail how in the embryo of Emys interia the outer germ layer becomes dermion and produces two layers that are totally different from each other, of which the deeper layer furnishes the material for the definite epithelium of the tortoise and represents the primitive epidermis, whereas the outer layer of flattened cells, the trophoblast (Mehnert's teloderm), should be looked upon as a supra-epithelial layer. According to Mehnert the trophoblast can be quite easily separated from the epiderm (l. c., p. 213, Pl. IX, Fig. 8).

The growth of the trophoblast is said to be dissociated from that of the deeper epithelial layer. Mehnert claims to have established (on the authority of Mitsukuri's ('93) figures) the presence of a trophoblast in Clemmys japonica and in Trionyx japonica, in Lacerta muralis, Tropidonotus, and for birds in the duck, the chick, Larus, Sterna, Podiceps, Buteo, Aegialitis, Hirundo, Luscinia, and others. Now I must begin

¹ The reason he gives for substituting a new name and not applying the name of trophoblast is, "that it has not been proved that these cells participate in the first place towards the nutritive processes of the embryo." In this he is in full contradiction to Schauinsland ('08, p. 33) who holds it to be "sehr wahrscheinlich" that these very cells have a nutritive significance in reptiles. In the Mammalia, where the layer is ever so much more conspicuous, its phagocytic significance has been proved; but even if it had not, this seems hardly to justify Mehnert for over-burdening scientific nomenclature by the creation of a superfluous synonym.
by disclaiming the greater number of these cases. I feel convinced that in certain of the cases observed Mehnert and Mitsukuri have seen what is really the rudimentary plasmodi-trophoblast of reptiles, but that in others the first-named author has been misled and has confused what is really a superficial layer (distantly comparable to a mammalian epithelial layer) of later embryonic phases with trophoblastic elements that can only be noticed in certain early phases. I have published this disclaimer more than ten years ago ('95, p. 27, Anmerkung); I can here only repeat it. A real Reptilian trophoblast can, I think, be clearly detected in Mitsukuri's ('90) Fig. 59 of Clemmys, where we find a separate cell-layer of flattened elements accompanying the amnionfolds on their outer surface. This layer is not continued on the inner surface of the amnionfolds as Mehnert will have it in his case of Emys lutaria. Also in his coloured figures (l. c., 30a—37a) Mitsukuri seems to indicate, by a different tint of red, that he did not (as does Mehnert) see any continuity between this outer trophoblastic layer and the inner lining of the amnion.

If we were to adopt Mehnert's view—as I have perhaps been inclined to do more than I was justified to in 1895—then we would have to look not only upon the inner layer of the amnion as trophoblastic, but also upon the covering layer he describes in the duck, which forms a continuous supra-epithelial stratum both on the back and on the ventral surface of the embryo; and a comparison with what we have above described for the mammals ought to make us diffident in accepting this view as the real interpretation.¹

¹ It must be borne in mind that the phenomena here discussed are as yet only very partially known. And if we consider the very various methods which we have discussed above (p. 11), according to which the mammalian trophoblast disappears above the embryonic shield, we may also expect variations in the Sauropsida. If we suppose that an arrangement like that in the rabbit and other rodents (Figs. 15 and 23) where the Rauher Deckenschicht remains distinct for yet a longish time, were yet further protracted, we might obtain a state of things as that which is described by Mehnert for Emys and certain other forms. I should not mention this if it were not
Fig. 66 to 70. Five sections through the very earliest stages of Ornithorhynchus and Echidna. Fig. 66 earliest cleavage stage. Fig. 67 visible separation of trophoblast cells tr and of mothercells of the embryonic knob, ck. Fig. 68 and 69 this separation is yet far more clearly established: the trophoblast tr having travelled much further over the yolk surface, the embryonic knob (ck) being partly embedded in the yolk; Fig. 70 a yet further stage in which ecto- and endoderm (e and en) have become differentiated by de-lamination and in which the ectoderm has come to the surface; tr trophoblast.

(Fig. 66, 69, 70 after Wilson and Hill, '07; Fig. 67, 68 after Semon, '04.)
Fig. 71 to 73. Three figures of sections through the blastocyst of the frugivorous bat Pteropus after Selenka, Gähte. '92). In fig. 71 the embryonic ectoderm is yet a solid cell mass, in fig. 72 an amnion cavity (a) has appeared within it, in fig. 73 the final relations between trophoblast (tr), amnion (a), embryo and umbilical vesicle (uv) are established. — Fig. 74. Transverse section through amnion (a), embryo and umbilical vesicle (uv) of Hyllobates after Selenka, '00). spm the splanchic mesoblast on the umbilical vesicle (uv) which carries a very dense net of thickened remue in which haematopoetic processes occur. — Fig. 75. Surface view of the amnion-fold of Chlamydoe. Fig. 76. The same in transverse section, with proliferation of the anterior entoderm (pp). tr trophoblast separated into two layers. — Fig. 77. Transverse section of an embryo of Sphenodon with amnion nearly closed. The trophoblast is double layered. Fig. 75 to 77 after Schauinsland, '03.
EARLY ONTOGENETIC PHENOMENA IN MAMMALS.

A second author in whose investigations a reptilian plasmoditrophoblast has come to light is Schauinsland (103). In his figures of the young Chamaeleo (Fig. 76) and Sphenodon-embryo (Fig. 77), we notice that the rising folds of ectoderm, which are the first indications of the separate existence of amnion and sersna, are covered, externally, by a layer of varying thickness. The presence of this layer seems to me indicative of a similar process in reptiles as was noticed in mammals, viz. a differentiation of the region outside of the ectodermal shield (as such we encounter the trophoblast after the embryonic ectoderm has been interpolated in it) into a superficial and a deeper layer (plasmodi- and cytotrophoblast of v. Beneden and Hubrecht). And this differentiation arouses suspicion, further confirmed by the sharp distinction at the free border of the amnion fold between outer and inner layer (Figs. 76 and 77, that in reptiles the case may stand as in bats (Fig. 8a), and in the hedgehog (Fig. 38) where the outer surface of the amnion-fold is trophoblastic, whereas the inner is an upgrowth of the ectodermal shield (see also p. 77) and Duval (109, figs. 96, 102 and 117). The trophoblast of Sphenodon and Chamaeleo would thus be more than one cell thick even before the somatic mesoderm has made a diplotrophoblast of it. This trophoblast does not contribute to line the inner surface of the amnion cavity. Here only the embryonic ectoderm (see pp. 76—78) comes into play.

In this important respect Schauinsland thus sides, although not himself discussing the merits of the problem (which was not before his mind), with Mitsukuri and not with Mehnert. In Chamaeleon of which Schauinsland gives good illustrations (103, Pl. 26, figs. 184—180), which are very indifferently reproduced in Heetwig I, 2, p. 194, the same phenomenon is observed with quite as much distinctness (Fig. 76). After the amnion has closed in the very primitive fashion characteristic for Chamaeleon (Fig. 75) the "membrana serosa" consists of a double layer of trophoblast (Fig. 76).

desirable, from the very first, to keep an open eye for all the different possibilities that may help to elucidate these difficult points.
The facts above cited force us to the conclusion that, before the formation of the amnion in Sphenodon and in Chamaeleo begins, there must exist on the surface of the blastocyst a circular delimitation of a central region—what would be the actual embryonic shield of mammals—from a peripheral trophoblastic region. This delimitation is clearly indicated in another of Schauinsland’s figures (Pl. 46, fig. 117) for Sphenodon not reproduced in Hertwig, but here reproduced in Fig. 78. In Schauinsland’s text (‘03, p. 142) this is noticed in the following words:—“As it was repeatedly noticed (the trophoblast-cells) do not spread over the embryo proper, and thus the extra-embryonic and the embryonic portion of the ectodermal blastoderm can be sharply distinguished from each other.”

If we now restrict ourselves to the three cases here cited, a tortoise (Mitsukuri), Sphenodon, and the chameleon (Schauinsland), and purposely leave out of consideration all Mehnert’s cases, then we have three Sauropsida in which clear indications are noticeable that the mammalian trophoblast is after all also present in the Sauropsida.

Besides these indications there is, however, a strong a priori probability that views which are applicable to the embryonic membranes of mammals ought also to fit in with Sauropsids that have—because of these membranes—always stood in closer connection with the mammalia than with the lower vertebrates.

And we should not lose view of the fact that the comparison of Elasmobranch with Sauropsid ontogeny has always shown this incisive difference that there was never a membrana serosa nor an amnion in the former, so that a direct comparison in these two types of the process of the gradual inclosure of the yolk by radial expansion from the ectodermal shield was tainted by suspicion from the beginning: the whole of the serous membrane and the amnion being shed at birth in birds, reptiles and mammals; these being, in fact, larval layers.
Fig. 78. Another transverse section of Sphenodon after Schauinsland, '03, to show the differentiation of the twolayered trophoblast tr as against the ectodermal shield EP; pp proctochordal plate. — Fig. 79 to 82. Four longitudinal sections of frog embryos (after Brachet, '02). In Fig. 79 proctochordal plate pp and proctochordal wedge pw have become differentiated; in Fig. 80 the notochord (nch) is further developed and the ventral mesoblast pm makes its appearance; in Fig. 81 the segmentation cavity has coalesced with the enteric cavity that has become visible during notogenesis; in Fig. 82 notochord, somites and gut are formed, headfold has become visible, ventral mesoblast pm develops below and behind the entoderm cells.
And now that the interpretation of the facts in mammals has become comparatively easy (see also Chap. III) we should not shrink from resolutely interpreting the Sauropsidan development along the same lines.

A comparison of my own figures for early Eriaceus (59) and of van Beneden’s (90) for early Vesperitillo blastocysts with the figures above referred to of Schauinsland and Mitsukuri convinces us of the possibility of looking upon the double layer outside the formaire ectoderm—say of Sphenodon—as a duplication of the trophoblast. The two mammalian genera above mentioned, as also Sorex and others, show a duplication and even a more considerable thickening yet of the trophoblast immediately outside the embryonic ectoderm. And so it would not be a very strained assumption to say that in reptiles and birds—in which as we have seen Schauinsland admits of a sharp line of demarcation between the trophoblast and the embryonic shield on the surface (i.e., p. 142)—both layers that are outside of this line of demarcation are trophoblast-cells separated in an outer flattened and a deeper columnar layer. Even of this differentiation in shape the mammals offer the counterpart, as is seen, to the left side in Figs. 8 and 8a of van Beneden’s (90) early bats and Figs. 35–37 of the hedgehog here given.

We will, moreover, see in Chap. V that the trophoblast often differentiates into two layers that are known as the cytotrophoblast and the plasmotrophoblast. And so the assumption here advocated would oblige us to conclude that, in birds and reptiles, a circular patch of embryonic cells was separated—not visibly but potentially—from a peripheral region of trophoblast cells just as we have established this for Tupaia, Tarsius, and others, in which—after the embryonic shield has opened out—it is no longer possible to distinguish the line of demarcation between trophoblast cells and embryonic ectoderm cells, although we have noticed its actual existence in the successive ontogenetic stages. In most Sauropsida ontogeny would no longer clearly reveal this difference, but still the mutual relations would be the same, and exceptionally favourable cases as here described and figured (Ciemmys, Sphenodon, Glaucopsyche) would be all the more welcome confirmations.

Physiologically the outer layer of the serosa of Sauropsida is recognized to have undoubtedly (see p. 21, footnote) certain properties which we also encounter in the proliferating trophoblast of mammals. There is, for example, a very marked proliferation in the outer layer of the Serp, a viviparous lizard in which Studivani, Giacomini (91), and others have described both an allantoid and an amnionallantoic contact (placentation) between the serosa and the maternal tissues.

Similarly the action of the serosa of the chick in the region where Daval has described the “organie placentaire” gives rise to the same considerations.
But more extensive investigations ad hoc will have to be undertaken before
the isolated cases of the Reptilia above noticed will have obtained sufficient
lateral support to serve as a starting-point on which a theory on the modification
of the trophoblast in the Sauropsida—simultaneously with the formation
of an eggshell, etc.—may be based.¹

Of the part played by the Sauropsidan trophoblast in the formation of the
amnion we will have to speak in another chapter. Suffice it to add that no
certainties are as yet available to determine the exact moment at which the plasmodial-
trophoblast becomes distinguishable in the above-mentioned genera. Neither
Mitsukuri nor Schauinsland give any indications. Furthermore, it would be
important to know whether ontogeny gives any clue which would permit a guess
as to the question whether the trophoblast has, in the viviparous ancestors of
the Sauropsida, been as early differentiated from the remaining cleavage cells
as is the case in mammals,² or whether the differentiation has only set in later
as we find in the case of those Amphibia and fishes in which traces of an
outer larval layer are also present, and which we will more fully discuss in
the last paragraph of the next chapter.

C. Ichthyopterygia.

In the paragraphs A and B of this chapter we have attempted to show that beside the ectoderm and entoderm,
which by delamination establish the gastrula stage of mammals
and Sauropsida, there exists yet another very early cell-layer

¹ Recently Eternod has published an article, “La Gastrula dans la série
in text-fig. 16 and in fig. 26 on pl. 13, he attempts to homologise parts that
are in no way homologous, if we look upon the early developmental processes
of Mammalia and Sauropsida in the light above advocated. Eternod’s views
have already been successfully protested against by Schützer (“Anat. Zeit.,”
Bd. 31, p. 31). The latter author himself misses the mark, however, when he
says that “die epiblastische Schicht der Sauropsiden-keimblase der über die
Grenzen der Keimscheide hinausgewachsen embryonale Eioblast ist.” The
secondary degenerative stages of the trophoblast are here wholly misunder-
stood.

² The researches, above alluded to (pp. 12 and 20), of Wilson and Hill
seem to imply that in Ornithodolphia we have yet an important intermediate
stage, in which it is indeed possible, notwithstanding the yolk accumulation,
to distinguish the trophoblast from the mother-cells of the embryonic knob.
Semon’s ('94) figs. 33 and 34 allow of a similar interpretation.
to which the name of trophoblast has been given. This layer, phylogenetically subordinated to the ectoderm, was looked upon as a differentiation of the same order as the outer larval layer which in certain Nemertins, Gephyreae, and other worms often serves as a temporary envelope that is stripped off when the animal attains to a certain stage of development. In a later chapter it will be discussed whether the different faetal envelopes of the Amniota allantoida may not be brought into genetic relation with this layer, and whether we might be justified in thus tracing the faetal envelopes of the higher vertebrates as far back as the invertebrate ancestors provided with an ectodermal larval investment (Larvenhülle).

It would appear at first sight probable that in the Anamnia, Amallantoida (i.e. in the Ichthyopsida) traces of this larval cell-layer should not be met with, and that this very absence would help to explain the fact that here no amnion develops. However, the chance that the intrinsic differences between say Amphibia and Reptiles are not so incisive as this separation of the vertebrates in Amniota and Anamnia would make us believe, should also yet receive our consideration. And it is in this light that I intend to look upon the fact that in many amphibia certain ontogenetic stages reveal the presence of what has been called the "Deckschicht" of the larva. Numerous figures successively published by different authors show the extent to which such a layer has been actually observed. It should at the same time be noticed that in several other genera no trace of it has been found.

The more remarkable circumstance is, however, this—that not only in Amphibia such a "Deckschicht" makes its occasional appearance, but that similarly it is noticed during the development of certain Dipnoi and Ganoids (Fig. 87), and both more constantly and more unquestionably during that of all the Teleosts (Fig. 89) of which up to now the early development has been traced. Of these different groups the "Deckschicht" is here figured after the publications of different authors on the subject, and I will not here enter into further details, contenting myself with having shown that it is a
general feature in the development of Teleostomes, Dipnoi, and Amphibia.

Suppose for a moment that we are justified in looking upon the Deckenschicht of Amphibia and Teleostomes as being in reality homologous to the trophoblast of Mammalia and Sauropsids—homologous at least in that sense that what is a very active and most important layer during the development of the viviparous mammals is only a temporary, evanescent arrangement in the Ichthyopsids—then we must at the same time ask ourselves: is this homology, perhaps, indicative of an error into which we may have fallen when adopting Milne Edwards' distinction of the vertebrates in Amnian and Amniota? And should we not reconsider whether and how this error can be readjusted?

At all events the Elasmobranchs, the Cyclostomes and Amphioxus show in their early development no traces of a Deckenschicht and—as we shall see in a later chapter—no traces of other organs which are characteristic for the other vertebrates.

In this chapter I had to point to these facts; in Chapter III, p. 81, they will be more fully discussed, as also in Chapter VI, p. 150.

Chapter II. Further Development of the Two Germ-Layers of the Vertebrates up to the Appearance of the Somites.

I. Mammalia (Mono- and Di- delphia).


The participation of the entoderm towards the formation of tissue between the two primary layers in Mammals is denied by very high authorities as Kölliker, Selenka, Ziegler, Köibel, and others, who hold that material for mesoblastic
Fig. 83 to 86. Four longitudinal sections of Hypogeophis (after Brauer, '77). In Fig. 83 the downward proliferation of the ectoderm \( p_p \) protochordal wedge commences to fuse with the entoderm protochordal plate \( p_p \). In Fig. 84 the notogenesis has proceeded further; in Fig. 85 the segmentation cavity has coalesced with the enteric cavity; in Fig. 86 the ventral mesoblast \( v_m \) has also made its appearance and the entoderm \( e_n \) has spread below the notochord \( n_e \), \( y \) yolk.
structures is budded off only from the primitive streak, and who—some of them at least—even wish to derive the vascular system and the blood from the same source. Mesenchyme formation, so sharply distinguished by O. Hertwig from mesoblast formation [see his 'Lehrbuch,' ed. 1906, p. 218] is by many authors held to be of no significance whatever in mammals, although Bonnet, in his investigations on the sheep's development ('82, '89), has attempted to stem that current of thought in demonstrating for the sheep that the vascular region on the yolk-sac is a direct derivat of local proliferation of the entoderm. In his later publications on the dog, however, Bonnet has for that mammal denied the presence of a similar process, although from his plates ('01, Pls. XVII, XIX; fig. 6, and many others) another conclusion might certainly be drawn (Figs. 91 and 92). On the contrary for Sorex and Tupaja (as yet unpublished) the genesis of mesenchyme out of entoderm has been fully confirmed by myself, and the region in which the participation of the entoderm towards the formation of blood-vessels and blood occurs, has been figured in detail by me ('90, Figs. 58, 61). When seen from above the aspect is such as to warrant the designation of this region by the name of the annular zone of mesoblast-producing entoderm of the shrew and of Tupaja.

Since then the battle has been raging concerning this very difficult and yet very important question of comparative embryology round which many problems, connected with the interpretation of the germinal layers and the significance of mesoblast, centre.

Only very lately Rückert has given a remarkable digest—in co-operation with Mollier—in Hertwig's 'Handbuch,' Vol. I, p. 1244—1260, in which—starting from careful investigations—he draws important conclusions concerning blood-formation in all the Vertebrates, that go far to demolish part of the theoretical views held by Rabl on mesoblast formation, which latter have been largely accepted by the great majority of embryologists.
I need not here enter into a detailed exposition of this controversy, now that it has been so carefully done in the chapter just mentioned on "die erste Entstehung der Gefässe und des Blutes bei Wirbeltieren," in Hertwig's 'Manual.'

But I will pass on to a full description of what has already been observed and described in different mammals commencing with what, in 1890, I have called—

a. The Protochordal Plate.—This structure has at first been more or less ignored by many embryologists, later its significance has been recognised, but it has then been designated by a different name (Bonnet, '01, E.P.); this time I hope to establish definitely that I was not only justified to distinguish this protochordal plate as an independent anterior source of mesoblast in mammals, but that we ought henceforth to admit its presence under varied aspects also in Sauropsids and Ichthyopsids, as I will point out hereafter.

For mammals we have in the preceding paragraph described how in the didermic stage the entoderm cells under the ectodermal shield are considerably more massive than those that clothe the inner surface of the trophoblast, the latter being flattened and further apart. Figs. 8a, 14, 13, 30, 31 and 36 testify to this. As the didermic blastocyst increases in size there is a very marked phenomenon of further increase coupled with proliferating growth in that portion of the entoderm that lies under what will later be the anterior portion of the embryonic shield. I here re-figure this for Sorex after my own (Figs. 58, 59) for the sheep and dog, after Bonnet's (Figs. 91, 92) publications, and I add new figures indicating the same phenomenon in Tarsius (Figs. 48, 49, 50 and 51) Galeopithecus (Figs. 18, 42). For the pig it has been figured, although not viewed in this light, by Kieboel ('93, figs. 21—23).\(^1\)

\(^1\) Kieboel interprets his figures differently, and did not, in the paper above referred to, recognise the protochordal plate as a source of mesoblast, such as I had defined it three years before. Still the figures here cited leave no doubt of its existence in the pig.
In Sorex it was particularly interesting to be able to establish the independence of this early proliferation from any further source of mesoblast, although very soon after, the annular zone of mesoblast-producing entoderm connects this early protochordal plate with the mesoblast-producing regions at the hinder end of the embryonic shield. Seen from above this early phase is pictured in Figs. 59 and 60.

The entodermal proliferation here described has, in its earliest phases, the aspect of a mere thickening of the lower germ-layer, but very soon that aspect changes, and we notice that certain of the proliferated cells break away from their place of origin, and take up a situation between the two germ-layers. The extent to which the invasion by these mesenchyme cells of the space between ectoderm and entoderm spreads cannot always be very strictly determined for two reasons. Firstly, because the annular zone of mesoblast-producing entoderm, which becomes confluent with the protochordal plate (Fig. 60), starts its activity almost simultaneously, though, as Fig. 59 shows, just a bit later; secondly, because another invasion of this space—starting from the ectoderm—also begins to form about this time, and will be described below.

At a very early moment the cells derived from these three different sources intermingle, and it will prove a most intricate problem, which up to now has not yet been fully nor satisfactorily solved, nay, not even approached, to make out from which of the three starting points the various organic tissues have ultimately been derived.

In Sorex this was possible to some extent at a very early stage, because the anterior entodermal proliferation producing mesenchyme cells is inaugurated somewhat earlier than the process which starts from the posterior half of the ectodermal shield. In my paper on Sorex ('90) I have been able to sufficiently distinguish these early phenomena, although fully recognizing that after a time further discrimination becomes impossible. This latter fact may have contributed to bring so many of the best modern embryolo-
gists to follow Kölliker in his negation of the participation of the entoderm towards the production of mesoblast.

In Tarsius the distinction of the mesenchyme (derived from the entoderm) from other mesoblast-cells between the two germ layers is hardly feasible even in the earliest stages, because here the source of early entodermic mesoblast at the hinder end of the entodermic shield is in full flow at a very early period in consequence of the presence from the very outset of mesoblastic tissue, which I have called the ventral mesoblast. It forms a sac, partly applied against the umbilical vesicle from the very first, and encloses an extra embryonic coelomic space, which is thus present at a very much earlier moment than in other mammals with the exception of man and monkeys. Part of this ventral mesoblast will gradually become the connective stalk (Haftstiel, Bunchstiel) by which the embryo will be in vascular connection with the placenta and which will be fully discussed in a later chapter. But in this same Tarsius the entodermal proliferation above described for Sorex, and which I will continue to designate as the prochordal plate is all the more evident. It is figured in diagrams 48, 49, 50, and 51. The entoderm has here become two or three cell-layers thick. This region corresponds to what will later be the very front part of the head of the embryo, before the primordium of the heart has yet been folded in under that of the brain.

As to other mammals I do not dispose of quite as extensive data as for Sorex and Tarsius, but there is no doubt if we also consult the results of other investigators—even of those who deny the participation of the entoderm towards the formation of mesoblast—that this thickening of the entoderm occurs in all mammals. For Erinaceus, Gymnura, Talpa, and Tupaia I possess numerous convincing preparations already mentioned above. Also for Manis, Galeopithecus, Sciurus, Mus, Lepus. Several of these are here figured (Figs. 18, 37, 42). For the dog Bonnet gives very unmistakable illustrations ("01, Figs. 11—13, 31, 32), although he substitutes the name "Ergänzungplatte" for the older
one of "protochordal plate." Also in one of Ascheton's papers (96, Pl. 20, figs. 17 and 18) the author clearly figures the proliferating region in the entoderm here referred to.

b. The Annular Zone of Proliferation.—How the hind end of this entodermal protochordal plate comes to fuse with the front portion of a median entodermal downgrowth of the ectodermal shield I have described for Tarsius in a former paper (1902). It will again be discussed further down. It is, however, necessary first to establish a fact already formerly insisted upon both by Bouedt ('84) and myself ('90), viz., that when once the protochordal plate has made its appearance as a median, mesenchyme producing spot in the entoderm, the same mesenchyme producing properties become evident in peripheral regions of the entoderm. These regions have been named by Bouedt for the sheep the "Mesoblasthof"; shortly afterwar..." I have described them ('90) for the shrew as an elongated ringshaped zone of entoderm which is situated under and somewhat outside the border of the ectodermal shield (Fig. 69), and which, slanting backwards from the protochordal plate both right and left, meets under the hinder part of the shield in the region where the mesoblast has acquired that median thickening which is known as the primitive streak, continued in the Primates into the connective stalk (Haftstiel).

The presence of such an annular zone of mesenchyme producing entoderm has been very emphatically denied by such embryologists as Rabl, Koebel, and others, and in O. Hertwig's latest manual he makes no mention whatever of it in the chapter on the "Lehre von den Keimbättern." This is all the more to be wondered at, because we shall see that also in lower vertebrates a similar participation of the entoderm towards mesenchyme formation can as little be denied. It seems to me that the energy with which these facts are ignored must have its origin in the strength of certain theoretical considerations with which a multiple origin of mesodermal would clash.

1 For myself, I have on another occasion ('02, p. 64) expressed my sym-

There is no doubt that to a great extent the mesenchyme here described contributes towards the formation of blood-vessels and blood. The protochordal plate furnishes the endothelium of the heart, as I have elsewhere demonstrated for Tarsius ('02, Pl. IX, fig. 73, a and b), the annular zone produces the material for the area vasculosa on the umbilical vesicle. To that effect mesenchyme cells, which originated at an early stage in the annular region here alluded to, migrate over the surface of the umbilical vesicle and come to be situated between the layer of entoderm which forms its inner, and of splanchnic mesoderm which sooner (Primates) or later (other mammals) forms the outer wall of this vesicle. Besides these lateral portions of the annular zone the hinder portion of it, situated diametrically opposite to the protochordal plate, has yet an important part to play in the formation of blood-vessels and blood. From it the vascularisation of the Halстiel of the Primates is derived. From the distal end of this connective stalk vessels irradiate towards the whole inner surface of the diploctrophoblast (man and anthropomorphes) or only towards a restricted circular part of it (Tarsius). This vascularisation must phylogenetically have preceded (as we will discuss later on) that which comes about by means of a free allantois. The thickened entoderm in this hinder part of the ring is especially marked in Manis. After a comparatively short time the annular entodermal region has ceased to be a focus of mesenchyme production; henceforth the increase of the vasifactive tissue is left to mitoses of the cells already constituting it. We may after careful consideration of all the mammalian preparations at our disposal all the more safely conclude to the existence of such migration of vasifactive cells if we consider that in other vertebrates (Teleosta) this very phenomenon has been actually observed in the live embryo by Wunckebach ('86), Ziegler ('87), and others.

In how far yet other tissue than blood-vessels and blood pathies with Kleinenberg's ('80) drastic expression, "Es gibt kein mittleres Keimbrett."
spring from this entodermal proliferation will require very close investigation in all the different orders of Mammals.


I have on purpose postponed the discussion of the processes of proliferation in the ectoderm because in modern textbooks those in the entoderm are generally ignored or even denied, whereas as a matter of fact they are antecedent, at least in their very earliest appearance, to those which concern the ectoderm.

About the latter a very stately list of investigators, including many of the foremost embryologists, have published the results both of observation and of reflexion. Still we cannot say that at present a general consensus of opinion concerning these processes has been arrived at. They have been very ably summarised by O. Hertwig in his "Lehre von den Keimbältern" (93, pp. 918—940), and to that author I would direct those who are interested in the historical development of the different views held on this point.

This will give me occasion to skip at the present moment all controversial matter, and will allow me to put forward my own view of the case based on the examination of numerous early stages of different mammals. The point of divergence with other authors will then be noticed only afterwards.

a. The Protochordal Wedge.—At the time when the two germ-layers of the round or oval embryonic shield are not yet interlocked, but independent of each other, and when the future front region of that shield can already be distinguished by the proliferation in the endoderm noticed in the preceding paragraph, and many years ago designated by me (90) by the name of protochordal plate, a proliferation, directed downwards, of the ectoderm in the axis of the embryonic shield and somewhere in the posterior third of it, becomes visible. I have no hesitation in saying that this spot coincides with the anterior lip of what was described in Chapter II as the
evanescent blastopore of the didermic gastrula stage of mammals. However, only in some few mammals has this blastopore been shown to appear as an actual though very temporary and evanescent perforation of the embryonic shield (Figs. 53—57). The proliferation has been known by the name of its first observer as "Hensen's knob;" it has also been called the primitive knob (Bonnet, '89, pp. 38 and 40); for myself I wish to adhere to the name I have proposed for it many years ago ('90, p. 501) and call it "protochordal wedge," as I have called the entodermal proliferation "protochordal pinto." The point of importance in my wishing to stick to these names is that the next step in mammalian development is the firm fusion between these two independent proliferations that have arisen in quick succession in the two independent germ-layers, and that will henceforth be no more disconnected (Figs. 47, 48, 52, 57, 97—99). The notochord is built up of material situated in the axial line of these proliferations, hence the names.

Already Hensen has correctly observed ('76) that below the rounded knob which he found projecting downwards from the ectoderm, the degree of firmness with which entoderm and ectoderm cling together is at its maximum, and should be looked upon as an effective fusion of the two layers. This is fully confirmed both by transverse and longitudinal sections. I found the same in the shrew (Fig. 57) and more lately, in a yet higher degree, in Tarsius (Figs. 48 and 52).

In Tarsius where we have already seen on p. 32 how very massive the protochordal plate was, the protochordal wedge pushes downwards just behind it, over that part of the entoderm which again consists of flattened cells. The fusion between the proliferated endoderm and ectoderm cells, not yet effected in the section of Fig. 49, comes about immediately afterwards (Fig. 48). There is not the slightest evidence in Tarsius that the knob-like ectodermal proliferation which we have called the protochordal wedge undergoes any extension forwards which could be identified with what German authors
Fig. 87. Longitudinal section through an early embryo of Amia (after Bashford Dean, '96). This stage is comparable to that of Raia (Fig. 80) and of Hypogeophis (Fig. 89). $pp$ prochordal plate, $nch$ notochord, $vm$ ventral mesoblast, $st$ portion of intestine comparable with allantais region of higher vertebrates. — Fig. 88. Longitudinal section of early nuranoid embryo (after Boeke, '03). $pp$ prochordal plate, $pm$ prochordal wedge, $pc$ proliferation homologous to the ventral mesoblast. — Fig. 89. A section of the hinder portion of an older nuranoid blastodisk. $vm$ ventral mesoblast, $Kv$ Kupffer's vesicle; $nch$ notochord (after Boeke, '03). — Fig. 90. Longitudinal section of the hinder part of a Salmoid embryo with Kupffer's vesicle (after Ziegler, '02). — Fig. 91 and 92. Two sections through the anterior part of two different blastodisks of the dog (after Bemm, '01). The prochordal plate ($pp$) is proliferating in both of them.
have called the "Kopffortsatz." On the contrary, the moment the fusion with the protochordal plate has come about, a process of growth sets in of the tissues here considered, not in a proximal, but in a distal direction. As a comparison of Figs. 48, 52, 98, and 99 shows, the embryonic shield increases in length, and at the same time the distance between the spot where the protochordal wedge has originated and the front end of the ectodermal shield becomes more considerable. But during this process the situation of the point of fusion between protochordal plate and protochordal wedge may be said to be more or less constant (though not actually any longer discernible), whereas both plate and wedge have increased in length at a relatively equal rate (see Figs. 93—96). And so the protochordal wedge becomes undoubtedly lengthened, not, however, by its sending out any "Fortsatz," but by its being, so to say, "spun out" in consequence of the backward growth of the tissue that is going to be the notochord,\(^1\) thanks to new ectodermal proliferation being added to what had previously come into existence, and had fused with the entodermal protochordal plate. A thin canal is noted in mammals in the posterior part of the backward proliferation of this protochordal wedge (Figs. 98 and 99; \(ne, ca\)).

\(^{b}\) The Ventral Mesoblast.—We will now for a moment leave the protochordal wedge and inquire whether, besides this, any further contribution of the shield ectoderm towards the formation of tissues between it and the endoderm takes place.

In this respect Tarsius has proved to be a genus of mammals, which is of the utmost importance in throwing light upon these much disputed questions. Monkeys and man—

\(^1\) I am inclined to think that, if all these investigators that have stood up so decisively for a forward growth of the mammalian "Kopffortsatz" in other genera of mammals, were once more to look closely at their preparations, they would be willing to leave the possibility open that this forward growth may also in their case be an elongation, by material being added posteriorly, con-constantly with the increase in length of the shield.
as soon as we come to know their development in these same early stages—will, in all probability, fully confirm what Tarsius teaches us, considering that in so many other important points Tarsius is seen to resemble the other Primates most closely, and that in this very detail: the presence of an extra embryonic coelom at a stage ever so much earlier than in any other mammal, there exists perfect uniformity.

In Tarsius there is no doubt that before the appearance of the protochordal wedge (Hensen’s knob) in the posterior third of the ectodermal shield, another ectodermal proliferation has already preceded Figs. 47—50, etc.), the products of which have important parts to play in the constitution both of embryo and blastocyst, different, however, from those of the protochordal wedge.

This earlier ectodermal proliferation is primarily directed backwards (Fig. 49), whereas the protochordal wedge has a faint inclination forwards (Figs. 46 and 48). Like this, it is median and unpaired.

We will call this posterior proliferation the origin of the ventral mesoblast (Hubrecht, ’02, pp. 19 and 31), and we may emphasise that, whereas the wedge appeared in the hinder third of the ectodermal shield, this ventral mesoblast originates still further back (separated from the wedge by the potential blastopore) at the posterior extremity of the embryonic shield, there where the trophoblast is often quite sharply differentiated (cf. Figs. 48 and 49) from the embryonic ectoderm. We encounter this proliferation as soon as the entoderm after its delamination from the embryonic knob is busy forming a vesicle under the embryonic ectoderm (Figs. 44 and 62). This endodermal vesicle, as was seen in the preceding chapter (p. 8), never fills the whole of the blastocyst. Now the proliferation at the hind end of the embryonic ectoderm, which we consider as the primordium of the ventral mesoblast, hollows out at the very earliest moment, thus forming a second vesicle enclosed inside the trophoblast. The cavity of this vesicle should be classed as extra-embryonic coelom; its walls, where applied against the trophoblast
Fig. 93 to 96. Four surface-views of the embryonic shield of Turritus. In Fig. 93 the median concrescence of protochordal wedge and protochordal plate has come about and notogenesis has commenced; in Fig. 94 and 95 the region of the dorsal mouth (primitive streak) has become elongated simultaneously with the
early establishment of notochord and bilateral mesoblast; in Fig. 35 first indication of neurenteric plexus which in Fig. 36 has travelled backwards considerably. — Fig. 95a, b and 96c. Two further stages of Tursius development following upon those of Fig. 95-96. — Fig. 96a and 96b. Dorsal and ventral view of a blastodisk with about five somites. As Heindorf seen from below: ovum annionfold; all allantoideum tube, seen by transparency; ad/t allantoideum tube in umbilical vesicle; uc neurenteric plexus. — Fig. 96c. Later dorsal view, annion nearly closed. uc connective stalk, true part of trophoblastic wall of blastocyst. — Fig. 97, 98 and 99. Longitudinal sections of the embryonic shields respectively corresponding to Fig. 94 to 96. br trophoblast, vn ventral mesoblast, all allantoideum tube (present, but not indicated in Fig. 98). np proterochordal plate; nco neorcochord; uc, oc, uc neurenteric canal; ov anterior and posterior annionfold; per pericardium; h heart. Fig. 98 to 99 after Hurecht (82).
(which then becomes a diplotrophoblast or chorion) thereby render the peripheral blastocyst didermic, and may be styled parietal or somatic mesoblast; where applied against the endodermal vesicle they fall under the category of visceral or splanchnic mesoblast (cf. Figs. 45 and 63).

At the initial spot from whence the proliferation has started the ventral mesoblast is naturally more massive than in the peripheral, flattened portions, and may here be designated as the material out of which the primitive streak and the ventral stalk (Hafstiel, Ranchofret) of the Tarsius embryo takes its origin. This stalk-shaped connection between embryo and trophoblast is thus present in the very earliest stages of development (Fig. 62).

My conception of the ventral mesoblast in mammals has since been adopted by Rückert in his article above cited (1906, pp. 1248 and 1251). He compares it with the observations hitherto recorded of mesoblast formation in the same region in other Amniotes. From its posterior unpaired and median point of origin in Tarsius it gradually spreads forward right and left as the wings of mesoblast are known to do in other mammals ("Mesoderm-sichel"), and only later this vesicular mesoblast (vesicular, because the colon is there from the beginning, and does not, as far as the extra embryonic colon is concerned, originate by any uterine splitting process) also appears in front of the embryonic shield, and invades the space (cf. Figs. 62 and 63) where the anterior and superior ectodermal surface of the umbilical sac are yet in close opposition with the trophoblast (Hubrecht, '92, Figs. 48, 51c, as compared to 57c, c). The posterior median portion has simultaneously further developed into the incipient, as yet extremely delicate Hafstiel which as we saw is there from the very beginning, i.e. from the didermic stage downwards.
3. Mutual Relations between the Centres of Proliferation.

We must now consider the relation in which the embryonic shield the centre of proliferation of the ventral mesoblast stands to that which we have designated as the protochordal wedge. In general it may be said that in the earlier stages the former lies immediately behind the latter. We may add to this that if Tarsius were possessed of a blastopore in the didermic gastrula in the same way as Erinaceus is (and as are some other mammals) the situation of this blastopore would be such as to separate these two centres of proliferation. This becomes evident when we consider the exceptional case already noted above (p. 14) where the embryonic shield of a particular specimen of Tarsius was provided with a deep pit-like impression (Fig. 52) which cannot but be looked upon as an attempt at blastoporic perforation of atavistic significance, the very numerous stages of Tarsius of identical age which I have in my possession not revealing a trace of it.

Other cases in which the contiguity, but at the same time the mutual independence of the two centres of proliferation is evident were figured by me in a former publication (702, figs. 58b, 46d, 47, 48, 52, b and c).1 Out of them all (see also Figs. 47, 48, 49, and 50) I have constructed the semischematic diagrams, Figs. 44–46.

I need hardly explain that the presence, close to each other, of three centres of proliferation (one entodermal, two ectodermal) in the two germ-layers of the mammals, such as we have just described, combined with the fact that in each centre new cells are very actively developed which spread out in the only direction available to them, i.e. between these two germ-layers,

1 I will here notice that the mutual independence here insisted upon should be taken cum grano salis. The anterior and the posterior lip of the blastopore, being naturally connected by the lateral lips, it is not a material anatomical independence that is here meant, but an independent activity. On p. 44 this will be more fully entered into.
brings about a state of things in which it very soon becomes utterly impossible to say to which of the three centres a given cell or group of cells owes its origin. An intimate fusion, though withdrawing this question of cell-lineage out of the field of our powers of discrimination, does not, however, diminish the significance of the existence of such a cell-lineage,¹ and we will in future researches have to keep our attention directed to that point, even though we must recognize at the present moment that much of the confusion and of the erroneous notions that maintain such a hazy atmosphere round these important early phases of vertebrate development, is due to precocious generalisations on this head. It seems to me that the wish to uphold the reality of a third germinal layer, together with the ardent desire of not having to ascribe a multiple origin to it, is responsible for much theoretical dogmatism that will henceforth prove valueless.

The consequence of what we have here described for Tarsius is that the centres of proliferation which give rise to the prochordal wedge and to the ventral mesoblast are originally independent of each other. We shall by-and-by see that there is all reason to believe that the same holds good for all other Mammalia, aye, for all other Vertebrates. The principal difference between my own and the current views consists in the distinction which I wish to make between what was considered as the front portion of the primitive streak (Hensen's knob, of which even the anterior prolongation was called in full: "Kopffortsatz des Primitivstreifens") from the primitive streak material itself. This distinction, which is very soon effaced and could never be demonstrated in later stages, is, however, quite evident in the very early ones. And we will have to analyse, as acutely as we can, the differences this will call forth in our interpretation of the development of different tissues and organs concerned.

The ventral mesoblast at its very earliest appearance (also in Tarsius) may be said—as it springs from the hinder end of the ectodermal shield—to be more or less crescent- or fan-

¹ Vide E. B. Wilson (92, 97), as against Driesch and others.
shaped. We will again encounter this crescent (or "Sichel") shape in Sauropsids. But as the embryonic shield increases in length the centre of proliferation is equally stretched, and out of a crescent shape evolves a double wing-shape, the axis between the two symmetrical wings being in the axis of the embryo. Along this axis the ectoderm freely produces cell material penetrating downwards to the right and to the left between the germinal layers and forming what has often been designated as primitive streak-mesoblast continuing backwards in the median line as the connective stalk (Haftstiel).

Here we encounter an all-important phenomenon, which will be better understood when we have also considered it phylogenetically, and which consists in the substitution of what was at the outset the blastopore by what has later developed into the dorsal mouth-slit. The lengthening of the tissue which formed the lateral lips of the early blastopore has now set in, and the further proliferation of this tissue, concomitant with a process of coalescence of the right and left halves with reminiscences of the original lumen which was the slit-like cavity of the stomodeum (in the ccelenterate stage), brings our original centres of proliferation further apart. At the same time the continuity of the tissues is never interrupted.

The accumulation of cell material which represents the lateral lips of the dorsal mouth-slit (Rückenmünd) naturally causes an increase in length of the mammalian embryonic shield, during which the shape of the shield generally changes from a roundish to an oval or pear-shaped one (see Figs. 93—95). This lengthening is simultaneous with an increase in the extension of the lateral mesoblast wings (see Fig. 69). For Tarsius I have fully established this a few years ago ('02, Figs. 54, 57, 61, 72). And for other mammals it has been demonstrated by Bonnet ('97, Figs. 18, 19), Keibel ('93, '95), and others.

As soon as this accumulation of material that reveals itself in the increase in length of the embryonic shield has
reached a certain stage, an active process of transformation is inaugurated, which consists in the visible differentiation of all-important organs, notochord and somites, out of this matrix. The differentiation becomes first visible at the front end where our ectodermal proliferation, the protocordial wedge, has grown downwards and has coalesced with the protocordial plate. From this point backwards the notochord is now, so to say, spun out, the so-called primitive streak tissues—lateral lips of the dorsal mouth—at the same time diminishing in extent. Phylogenetically it corresponds to the origin and the coalescence of the lateral lips, not of the blastopore, but of the dorsally-situated stomodeum.

A comparison between Figs. 93—95 and 96 will at a glance reveal the effect of the new state of things. The protocordial wedge situated well forwards on the embryonic shield of Fig. 95 is no longer visible as such. The fine pore that was present just behind it (see the longitudinal section in Fig. 98) has undergone a displacement backwards, and has in Fig. 96 attained a position not far from the hinder end of the embryonic shield. This is due to a very marked process of elongation which becomes perfectly evident on the comparison of two longitudinal sections through these two embryonic shields (Figs. 98 and 99).

This process has been known to earlier observers, and has been described as the shortening of the primitive streak, going parallel to the formation of the earliest somites. How the cell material that has arisen as the paired wings of the ventral mesoblast and that which is spun out by the moving backwards of the protocordial wedge (producing the notochord in the median axis and the mesoblastic somites right and left of it) comes to arrange itself reciprocally and what changes are brought about in this material during this process is a very difficult and intricate question about which the various authors differ. I think we may safely say that by the rapid extension backwards of the differentiation process, as it is exemplified by Figs. 95 and 96, the dorsal region of the trunk is laid down in outlines (hence the word
neogenesis), whereas the derivates of the ventral mesoblast find employment in the construction of the posterior and postero-ventral portions of the embryo.

It will here suffice to state that the extra embryonic celom which is present in Tarsius (and undoubtedly in monkeys and man) in the ventral mesoblast at so very early a phase (extending as was described on p. 38 behind and below the endodermic vesicle and the ectodermal shield) first makes its appearance in the other mammals at a later period, but exactly in the same position, viz. behind the embryonic shield (Figs. 48, 61, and 100). From there it gradually extends in crescent shape right and left along the hind margin of the embryonic shield. This celom—considerably less spacious and less precocious than that of the Primates—is fully homologous to it, both as regards the place where it is found, the cell material in which it appears, and the relation in which it stands to the celom of the somites and lateral plates, as will be described later on. Bonnet's ('82, '89), Keibel's ('03), and my own ('02) observations on the appearance of this crescent-shaped celom are in perfect agreement with each other, as also those concerning the fact that this ventral celom only later fuses with the intra-embryonic celom (Keibel, '03, fgs. 39 and 40a; Hubrecht, '02, fig. 77d). The pericardial celom arises independently along the front border of the embryonic shield, and will also be more fully discussed later on (Hubrecht, '02, p. 37, fgs. 70, 78).

Summarising what we have here rapidly sketched we may agree to have seen that instead of a homogeneous median germ layer, instead of a mesoderm which has the same morphological importance as the two primary germ layers and originates from the coalescing lips of a blastopore, we find at least three foci of cell-activity in those primary germ layers. The appearance of these foci marks the end of the didermic stage of the blastocyst. In consequence of processes of proliferation and rapid mitosis there is started from these three centres a host of new cells, which, together, spread between
Fig. 106. Longitudinal section through the posterior end of the shrew's blastodisk with earliest appearance of posterior amnion fold (after Hubrecht, '00).

100. posterior portion, 101. ventral mesoblast, 102. trophoblast (cf. Fig. 59 and 61).
- Fig. 101, 102. Two sections through different blastodisks of Tarsius. Fig. 102 (375 and 180 Utr. coll.) in the posterior region of the primitive streak after Hubrecht, ('21).
Fig. 102 is in the more posteriorly situated, at the spot where the tubular (Schwanke's) and the allantoic tube (all), here situated ventrally of the former and on the point of diverging. The wall of both is actively proliferating vascular tissue. Between the lower border of the allantois and the umbilical vesicle a complex of yet more actively proliferating cells is present: this continues further backward (where the allantois and umbilical vesicle have become further severed) as a median proliferating raphe on the umbilical vesicle. In Fig. 101 lateral wings of mesoblast arise from the entoderm.
- Fig. 103. Transverse section through the hinder end of an early Tarsius embryo with tubular amnion (an) and allantois (all) in the already strongly vascularized connective stalk (st); see wall of the umbilical vesicle.
- Fig. 164. Longitudinal section of sparrow with early mesoblast in a stage of about Fig. 105 (after Schwankeal's, '03).
octoderm and entoderm in the shape of what appears naturally as a flattened layer of so-called mesoderm, but what is in reality the strictly grouped material for different organs and tissues. These have not sprung from the lips of any blastopore (Urmund), but have gradually come into existence in the same ontogenetical order as we must expect them to have arisen phylogenetically. The blastopore has lengthened out into the dorsal mouth. This lengthening has been accompanied by a dorso-ventral proliferation of ectoderm (protodermal wedge) out of which the stomodeum (notochord) arises, and during this time the dorsal mouth-slit has only been represented by vestiges. I have already discussed these processes elsewhere (’05). The dorsal, elongated mouth (Rückenmund, ’05, p. 363) may thus point to a vermaehtian-like ancestor (Fig. 160) in which the appearance of notochord and coelomic pouches was already foreshadowed by the stomodeum and the enteric diverticula to which the stomodeum gives access.

It is far outside the scope of this paper to establish in detail the cell-lineages as they may ulteriorly be found to exist, and which will some day allow us to ascribe to each of the three centres of proliferation here alluded to, its part in the formation of the Anlage of different organs and tissues between ecto- and entoderm. It should, however, be noticed that already in my publication of six years ago (’02, Pls. 8 and 9, figs. 59g and 75h) I have distinctly figured the fact that in the posterior region of the embryonic shield a very considerable part is played by the entoderm in the development of the lower half of wings of mesoblast of which the upper half springs directly from the ectoderm (Figs. 101—103).

These and many other phenomena will have to be minutely studied and established before we can commence our comparative analysis of these processes in Vertebrates.

But it should be borne in mind that the processes just alluded to have already been mentioned on p. 34, when the vascularisation of the "Hafistiel" was discussed. And that in the diagram, Fig. 46, the posterior source of proliferating
entoderm is clearly indicated as forming part of the ring that is figured for Sorex in Fig. 60.

The ultimate discussion upon this matter is postponed to a later publication, in which those stages of development which are inaugurated by the formation of the somites will be treated more fully.

II. Amphibia.

After this description of the early developmental processes of the Mammalia we will skip the Sauropsida, and first describe what is noticed in the Amphibia. This will afterwards afford us an occasion to compare the yolk-laden Sauropsida all the more rapidly both ways. And, above all, it will increase our confidence in the interpretation which we have founded on the Mammalia if we find it applicable as low down in the line of vertebrate descent as are the present Amphibia. It should, however, at the same time, be remembered that none of the three living stocks of Amphibia neither the Gymnophiones, nor the Urodeles, nor the Anura can be expected to stand in any way on the direct line of descent of our present mammals. Comparative anatomy has taught us (Fürbringer '00) that in very many respects the amphibians from Mammalia of the Palæozoic epoch must have been characterised by important points of difference from all the living remnants of that ancient stem. Still, if we find processes of early development that are in the main lines directly comparable to what we have described in mammals, and if they fit in well with the explanation which we have ventured to give for the Mammalia, we might say that the difficulties which have so often been complained of (p. 13) when attempting to establish the comparative ontogeny of the Vertebrates have greatly diminished.

We will, therefore, take the more important and careful descriptions of Amphibian development (to which we have no personal investigations of our own to add), and see whether the three centres of proliferation which we have noticed in
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the two germ-layers of the mammals are also present in the Amphibia, and whether the mutual relations of these proliferating centres and the further fate of the tissues and organs they produce also reveal close similarity.

We begin with the Gymnophiones, about the early phases of which A. Brauer ('97) has published an exceedingly lucid exposition based on the study of an extensive material.

We have successively to look out for a proliferation of the ectoderm corresponding to our prochordal plate, for an ectodermal proliferation representing the prochordal wedge, and for another ectodermal centre of growth which gives rise to ventral mesoblast. I will by means of copies of Brauer's figures show that all three are met with in Hypogeophis and that in their further relations and in the genesis of the organs produced by them the homology with the mammals is indubitable.

It should at the outset be remembered that the Hypogeophis egg is so saturated with yolk-material, that there is no holoblastic cleavage, but that the results of the cleavage process—as was noted in Chapter II—are found at one pole of the egg, and that a process of delamination transforms the fragmented ovum without delay into a gastrula with an endodermal lower layer (see Brauer, '97, Figs. A and B, pp. 403, 404).

More or less simultaneously a differentiation of ectoderm and endoderm becomes visible, which shows very great similarity with what was figured above (Fig. 19) for Tarsius. The point at which the ectoderm has commenced to proliferate, and at which its first change was a bend downwards (Fig. 83) is directly comparable to the primitive (Hensen's) knob on the mammalian ectodermal shield, and is no other than our prochordal wedge. The point at which the endodermal proliferation becomes evident is situated just in front of it and the two proliferations, as is so particularly clear in Brauer's fig. 43, here reproduced as Fig. 84, fuse in absolutely the same way as we see in the Tarsius, Fig. 48; with full confidence I indicate the corresponding regions in the Amphibian
by the letters \( P_{pp} \) (protochordal plate) and \( P_{wc} \) (protochordal wedge). Brauer's figure leaves not the least doubt that the cells indicated by \( P_{pp} \) are of entodermal, and the cells \( P_{wc} \) of ectodermal origin, nor do his own views on this point differ from mine as he calls the former "vegetative," the latter "animale Zellen."

The later transformation of this henceforth fused region of double proliferation (see Figs. 85 and 86), based on entirely the same plan as was noted not only in Tarsius but in very numerous other mammals, will be discussed later on. We must first look out for the third centre of proliferation. And we find this in Brauer's fig. 59, here copied in Fig. 86 where at a short distance behind the protochordal wedge and separated from it by an interval comparable to what we notice in the Tarsius, Figs. 48 and 48 (where the interval is at its minimum), the ectoderm is seen to undergo a new and very marked proliferation, which will give rise to tissues closely corresponding to the ventral mesoblast which we saw originating in this spot in mammals.

The difference between the case of Tarsius and Hypoglyphis is this, that in the former this posterior centre of proliferation is conspicuous first of all, whereas in the latter the two other centres have precedence. However, in this respect the other mammals side with the Amphibia, the protochordal plate and wedge being visible before or arising simultaneously with the proliferating centre for the ventral mesoblast.

Having thus established well-founded comparisons between Brauer's figures of early Gymnophiones (Coelidia) and our own for mammals, we will now turn to the Anura, and take as starting-point Brachet's figures ('03) of the frog.

In his earlier publication of the year 1903 (Figs. 6, 7, 39—47) we find that Brachet describes early stages both for the Axolotl and for the frog in which the presence of a protochordal plate can hardly be denied by any impartial observer. One of his figures, copied here in Fig. 79, leaves little doubt about the presence in the entoderm of the frog of a
particular spot of thickened entoderm situated at the very place where we would expect the protochordal plate at this earlier stage. His other figures, which are also copied here (Figs. 80—82) show the subsequent stages.

And as to the annular band of entoderm from which the blood-vessels and blood originate, we find it similarly disposed in the Amphibia according to Brachet, who for the frog writes (03, p. 686), “les endothélium vasculaires y compris l'endothélium endocardique et les futures cellules rouges du sang, procèdent de la portion du mésoblast... qui s'est séparée par délamination de la partie ventrale de l'endothélium gastruléen.” And further (03, p. 688), “de tout le vaste manchon mésoblastique qui se déline à la surface de l'endothélium gastruléen, la partie ventrale, sur une largeur plus ou moins grande selon les régions, se sépare complètement du reste à des stades relativement peu avancés, et, poursuivant dès lors une évolution spéciale, donne naissance à tout l'appareil vasculaire sanguin (endothélium vasculaires et cellules rouges du sang).”

The term manchon (muff) used by Brachet shows that he, too, has observed the region of the entoderm which produces the mesenchyme out of which the blood-vessels and the blood are developed in the shape of an annular peripheral investment of the region out of which the mediadorsal organs will develop.

With most laudable prudence Brachet does not generalize his results concerning the frog, but states expressly that for Triton he is inclined to stick to the conclusion he arrived at already in an earlier publication (08), and according to which also in Triton the vascular system is of entodermic origin, but that he all the same thinks a further confirmation of his observations desirable, whereas for Axolotl he makes all reserves, the study of the origin of the vascular cells being here very difficult. He is careful to add, however, that he cannot exclude the possibility that after all Axolotl may prove to fit into the same plan as the two others.

Other authors who, before Brachet, have come to similar
conclusions concerning the origin of the vascular system in the Amphibia are Goette ('75) and Schwink ('91). Both are convinced that all blood-cells are derived from the endoderm, as also the vessels. Brachet points out, however, that the stages on which Schwink bases his conclusions are already too far advanced.

It is important that Brachet, repeating Corning's ('99) observations, finds that in front of the notochord's anterior end the median protocordial-plate-material differentiates from behind forwards in this sense that mesoblast is seen to become isolated and to form a thin layer made up of one or two layers of cells that are interposed between the entoderm and the lower brain wall. In the beginning, he finds that the anterior end of the notochord reaches into this median mesoblastic band. Soon, however, it is separated out of it and the anterior extremity of the notochord becomes quite free. Later yet the median mesoblastic band thins out, breaks up and ultimately disappears, or is reduced to a few sparse cells that are distributed at random. The endoderm of the roof of the digestive tube is then closely pressed against the lower wall of the brain.

This would, ceteris paribus, also apply to the mammalia.

The next point we have to consider concerns the fusion described for mammalia by myself ('90) and others, and for Hypogeophis by Brauer of what we have called the protocordial plate with the protocordial wedge. Neither amongst Brachet's figures for Axolotl, nor among those for the frog, are the phenomena so self-evident as they were for Brauer's Hypogeophis. Still if we consider Brachet's figures of Axolotl and those for the frog no objection can reasonably be raised against my comparing the region which in all these figures I indicate by $P_p$ with that same region in Hypogeophis and in mammals. The fusion with the ectoblastic proliferation that is the protocordial wedge—although Brachet does not look upon it in that light—is inaugurated for Axolotl in Brachet's ('03) Figs. 4 and 5; for Rana in Fig. 79, here given. The ectodermal proliferation indicated as protocordial wedge is
thus located in the Amphibia (the same holds good for Hypogeophus) at the spot where the so-called dorsal lip of the blastopore makes its first appearance. And this proliferating spot (as was already noticed in Mammals and as Brachet [’02, ’03], Belloni [’84], and Lwoff [’94] have observed it for Amphibia), travels backwards a certain distance over the surface of the egg, spinning out at the same time both notochord and somites.

In the frog I have in the reproduction of Brachet’s figures indicated the corresponding regions by the letters $P_P$ and $P_W$. $P_P$ points to most decided entoderm which has by delamination become separated from the ectoderm situated above it. And the proliferation of entoderm marked $P_W$ and fused (more markedly yet than in the somewhat earlier phase of Axolotl) at the very outset of its proliferation with the protocoelard plate entoderm below it—about in the same way as we encounter the same phenomenon in Fig. 48 for Tarsius—has here already progressed a certain distance backwards. This distance has lengthened and the derivates of what was originally the protocoelard wedge have increased in Fig. 80 (Rana), and yet the letters $P_P$ leave no doubt that they are directed towards the original entodermal proliferation. So does $P_W$ show us what has become of the entodermal proliferating centre. We can quite understand that also concerning Amphibia dissensions have existed as to whether the notochord—first and foremost derivate of $P_W$—was of entodermal, mesodermal or ectodermal origin. And the different authors that have successively sided for the one or for the other of these solutions have pronounced themselves as best they could upon a material that is so far away from the extraordinary clearness with which these very early phenomena reveal themselves to us in Mammals. The continuity in which from the beginning ectoderm and entoderm pass into each other (Fig. 79) all along the ring-shaped zone of delamination (marginal zone of Goette), has contributed so extraordinarily to propagate and to strengthen the error of those who upheld that the phenomena which we have just seen
inaugurated are phenomena of gastrulation, instead of phenomena of notogenesis, that consequently all conclusions were naturally biased. However, the mammalia have come to show us the way out of the labyrinth and a reformation of our views must be the consequence.

Without for the present entering into further details concerning protochordal plate, protochordal wedge and their derivates in the frog, we will now see whether the third centre of proliferation which we also have recognised in Brauer’s Gymnophiones is as clear in the Urodeles and the Anura.

On this point Brachet’s researches, and those of other authors afterwards to be cited, leave no doubt whatever. The ectodermal centre of proliferation, hitherto known as the ventral lip of the blastopore is very clearly marked off (Figs. 80—82), and produces its mesoblastic derivates with perfect regularity, in a sequence that is immediately comparable to what we have found in and described for the mammals. Brachet writes about this third centre (703, p. 67) that it is: “Un épaississement notable de la partie toute inférieure de l’ectoblaste.” And further (l. c., p. 68): “Même épaississement considérable de l’ectoblaste qui vient par une large base se continuer avec les éléments du bouchon vitellin et cela à une certaine distance dans la profondeur de l’œuf.”

We have here before us the ventral mesoblast which in Tarsius (and the other Primates) arises so uncommonly early and stretches round the umbilical vesicle, creating a very early segregation of splanchnic as against somatic mesoblast.

When we take the Figs. 81 and 82 (copied from Brachet) we can immediately recognise the homology between the region marked cm and that of Figs. 46, 48, and 49, to which the same lettering is attached. We also see that if the mesoblast there produced in the Amphibia were to attain the early development it has in Tarsius and the cavity enclosed therein, this would similarly take the place of the so-called segmentation cavity, and be applied against the
cavity which in the mammal is styled the umbilical vesicle, and which is the so-called archenteron in the Amphibian. The concrescence between this and the segmentation cavity is the same as is noticed at the yet earlier stage of Tarsius (Fig. 19), in which the entoderm forms the roof of the trophoblastic cavity. But we will return to these possible comparisons later on.

It remains to be seen whether in other Amphibia than Rana and Triton the presence of a fourth focus from whence tissues are originated that take their place between ecto- and entoderm can be confirmed. In other words, whether anything corresponding to the annular zone of mesenchyme-producing entoderm (stretching backwards right and left from the protochordal plate and reuniting in the median line posteriorly under the ventral mesoblast) as it was figured in Fig. 60 occurs in Amphibia.

Although Brachet has not expressly stated that such an annular zone of entoderm was noticed by him, we may conclude from his descriptions that it does occur in his preparations. On p. 88 (’03) he writes about: "L'intense activité que l'on pourrait appeler mésoblastogène des cellules de la voute" (by which latter he means the roof of the archenteron); and on p. 89: "Les bandes mésoblastiques sont plus épaisses dans la région blastoporale que dans la région gastrale proprement dite ... Le mésoblaste péritônal est beaucoup plus abondant que le mésoblaste gastral (p. 90)."

From these citations I think we may conclude that the presence of an annular zone of mesenchyme-producing entoderm in Amphibia will in due time be yet more fully established.

Authors who have actually figured it in the posterior median line of the embryonic Anlage are Robinson and Assheton (’91, Figs. 14—17), where in the median region of the blastopore and behind it we notice an entodermal proliferation producing what the authors call "hypoblastic or inner layer of mesoblast of primitive streak," as against
the "epiblastic or outer layer of mesoblast of primitive streak." This investigation thus authorises a direct comparison of the phenomena figured in Figs. 101 and 102 for Tarsius, in which we have quite decisively recognised an epiblastic and a hypoblastic layer of mesoblast of the primitive streak, which is what was noticed in the frog by Robinson and Assheton.

It should yet be added that the annular zone of mesenchyme-producing entoderm may in the frog even commence as an unpaired ventral sheet, which only later becomes paired, and thus more or less annular. Brachet ('03, p. 686) expresses this as follows: "Il existe une phase du développement où les cellules vasculaires des futurs vaisseaux vitellins forment une couche continue imparie et médiane (Fig. 22) et la parité définitive est secondaire."

We have now seen that in the three subdivisions of the Amphibia we notice early processes of ectodermal and entodermal proliferation, which allow of direct comparison with what we have described for the Mammalia. And we may add that the continuity between the derivate of the prochordal plate and those of the annular zone is in Amphibia established even perhaps earlier yet, whereas the continuity of these latter derivate with those mesoblastic elements that originated right and left of the median dorsal line is again so very early established, that it cannot be wondered at that the Amphibia have not suggested to previous investigators the relative independence of these different sources from whence cells and tissues that will take their places between the two primary germ-layers arise.

When we will later recapitulate what are the farther lines of development of the products of the four proliferations above enumerated, the complete homology between Amphibia and Mammals will become yet more evident.
III. SAUROPSIDA AND ORNITHODELPHIA.

As to this class I have no observations of my own to offer. But we may glean from the researches hitherto published by others the following data which concern the participation of the entoderm in the formation of mesenchyme.

For the sparrow Schauinsland ('08) figures both a surface view, a longitudinal and a transverse section which leave no doubt about the presence in this bird of a very clearly defined protochordal plate, arising as a proliferation in the entoderm before any process of mesoblast formation has been inaugurated in the ectoderm. I here copy five of his figures (Figs. 105—109), adding that the region in the surface view which I have termed the protochordal plate is named by Schauinsland the "Entoblasthyl." Not only is its situation in perfect correspondence with the same region in Sorex, visible in Figs. 59 and 60, but the sections reveal the same constitution (Fig. 104 for the sparrow, Fig. 58 for the shrew), viz. a local thickening of the entoderm. And later when the ventral mesoblast (cf. p. 30) will have begun to make its appearance the surface view of bird and mammal will again be directly comparable, and the independent increase of tissues—intricately interwoven though deriving from different germ layers—undeniable.

Similarly in representatives of the reptiles there is no want of recent illustrations by various authors, showing that the median entodermal proliferation (protochordal plate) is present in early stages. I copy some of Passer (Figs. 104, 110), five of Sphenodon (Figs. 77, 78, 112—114), and two of Chameleo (Figs. 76, 111), all taken from Schauinsland. And I may add that Mitsukuri ('98), Mehnert ('92, '94), and Davenport ('06, Pt. VII) have revealed a similar state of things for tortoises, Strahl ('82, '84), Will ('90), and Corning ('99) for lizards, Voelzkow ('03) for crocodiles.

If the presence of a protochordal plate in Sauropsids may thus be looked upon as well established we have to look a
little more closely before affirming that the same can be said of
the annular mesenchyme-producing zone in the entoderm.
If we consult Mehnert's article in which he discusses the
origin and the development of the hemovascular tissue (area-
vasculosocrescent) in Emys and Struthio (96) we will then
find that for these two Sauropsids he accepts as the final
point of origin of the vascular tissue and the blood the ento-
derm. But he does more than that. He gives a detailed
account which in most points corresponds most exactly with
what we have above indicated for the mammalia, of the
origin in the hinder part of the "primitive streak" of a
decided entodermal proliferation which by many authors
has been incorrectly looked upon as ectodermal. I believe
that a careful re-examination of their preparations and a
comparison of those with the numerous section series of
Tarsius and Tupaja, which are always available for that
purpose, may convince even those who have formerly stuck
to the purely ectoblastic nature of the primitive streak, that in
the lower half of the primitive-streak-tissue a direct and
considerable proliferation of entoderm cannot possibly be
denied. This proliferating region is, as we have seen in
mammals, nothing else but the hinder median portion of the
ring of vasiformative tissue, which was above discussed and
figured (Figs. 46 and 60), and of which the protochordal plate
is the median frontal portion.

In the tortoise, Emys, Mehnert (96) gives detailed descrip-
tions as to how this ring of tissue has in the first place the
aspect of lateral outgrowths from the primitive streak; later
of crescent-shaped wings, and only finally of a ring. It
may be here remembered that also in the embryonic shield
of Tarsius the first origin of blood and blood-vessels is
observed in the hinder part, and that we notice a similar
wing-shaped advance in the distribution of the mesenchyme-
producing annular zone. At the same time it should be
borne in mind that once the primordium of the vascular
tissue having arisen out of the entoderm its further develop-
ment becomes independent of the region of its origin, so
Fig. 105 to 109. Five surface views of the early aspect of the sparrow's blastodisk (after Schamann, 63). In Fig. 105 there is as yet only an endodermal prooocordal plate pp (cf. longitudinal section of Fig. 104); in Fig. 106 a downwards growing prooocordial wedge pwo begins its fusion with the prooocordal plate; in Fig. 107 mesoblast has grown out from the borders of the elongated dorsal mouth; in Fig. 108 the ventral mesoblast vmb has made its appearance; in Fig. 109 the sickle-shape becomes visible in the posterior mesoblast, nch notochord.
that for example the fact that in Tarsius after a certain
time we find the whole umbilical vesicle thickly covered with
blood-vessels (Hubrecht, '02, Fig. 91) does not imply that
they have arisen in loco out of the entoderm. They have
become spread over this after they had once taken their
origin in the annular zone here more particularly alluded to.

I think it may here suffice to give the reference to
Mehnert's article in which he establishes the entodermal
origin of a ring of vasiform tissue both for a reptile and
for a bird, and not in this place to describe the process more
in full. The more so as it is well known how many differences
of opinion yet exist on this head between different authors.
The amount of difference can also be gathered from Mehner's
paper, who gives a tabular summary of the different opinions
held on this point by no less than thirty-six different authors,
grouped under the heads of six different possibilities for the
origin of blood and blood-vessels.

Having so wide a divergence to choose between, it is only
natural that I should feel inclined to side with Mehner
('96), O. Hartwig ('83, p. 319), Gaette ('74, '75), His ('00),
and Rückert ('05) in respect to the origin of the vascular
system now that different genera of mammals have pro-
vided me with perfectly trustworthy sections from which
to conclude to the existence of the annular mesenchyme-
producing zone of the entoderm. That for mammals,
Köllicker, Keibel, Heape, and others have denied the partici-
pation of the entoderm here advocated, and have derived the
whole vascular system from the mesoblast of the primitive
streak has no doubt its explanation in this fact that they
must have consulted later stages of development than those
in which the entodermic origin is evident. This latter stage
is very soon followed by one in which the participation of the
entoderm has come to a close, and in which the further deve-
lopment of the vascular system is now going on between the
two primary layers in the so-called mesoblast.

All the points here discussed have been sifted and care-
fully compared by Rückert and Mollier in the chapter which
they have contributed to Hertwig’s ‘Handbuch of Embryology.’ The student of their article will find no difficulty in accepting the generalisation above arrived at, that the entoderm is the mother tissue from whence the vascular tissue and the blood have taken their origin.

Rückeri writes concerning Geck (l.c., p. 1172): “Ich traf auf eine deutliche Ablösung der hier ziemlich dottorreichen ersten Gefäßanlagen von dem angrenzenden hohen und ebenfalls dottergefüllten Entoblast... Ihre entodermale Entstehung liegt daher klar zu Tage.”

Besides the protochordal plate and the annular zone of the entoderm from whence mesenchyme is produced we also find in the Sauropsida the ectodermal centres of mesoblast formation which we have noticed in the mammals.

The protochordal wedge is to some extent more marked than we found it in the Mammalia; it has of late been designated by O. Hertwig (’06) by the name of “Mesoderm-säckchen,” and it contains a cavity more spacious than the comparatively thin canal which we have encountered in mammals (Fig. 98). Also in this respect the exceptional case of Fig. 52 should be considered as throwing a side-light on these intricate processes both in mammals and Sauropsida.

The confluence between the earliest ectodermal downgrowth with the protochordal plate has up to now not been specially examined in reptiles. Still we may conclude from the figures here given, which I copy from other authors that it comes about in exactly the same way as we noticed it in Tarsius for mammals, and in Hypoglossus for Amphibia. Fig. 419, Hertwig (’06), shows us the earliest protochordal wedge in a snake as it fuses with the thickened entoderm; behind the protochordal wedge we notice the ventral mesoblast as a third focus of mesoblast formation. Figs. 427 and 429 are continuations of the same in somewhat later phases, and the correspondence with our Figs. 79, 80, 97, and 98, of Amphibia and Mammals is self-evident. In Hertwig’s Fig. 429 the source of ventral mesoblast has actually been shifted.
Fig. 110. Longitudinal section of a sparrow's blastodisk (after Schauinsland, 65); pp proteochordal plate, nch notochord, vmb ventral mesoblast. — Fig. 111, Longitudinal section of an early embryo of Chameleco (after Schauinsland, 65). pp proteochordal plate, pv proteochordal wedge, vmb ventral mesoblast, nc neurenteric canal, a amnion, tr two-layered trophoblast. — Fig. 112 to 114. Three sections through early blastodisks of Sphenodon (after Schauinsland, 65). In Fig. 114 (longitudinal section) proteochordal plate (pp), proteochordal wedge (pv), ventral mesoblast (vmb) and trophoblast (tr) are indicated. In this phase of notogenesis a long and distinct neurenteric canal (nc) is present. In Fig. 112, which is further anteriorly situated than Fig. 113, the proteochordal plate (pp) is transversely cut, as well as the anular zone of proliferating endoderm (ax) spreading backwards and contributing to the formation of the area vasculosa. In Fig. 113 the notochord (nch) has commenced its mediolongitudinal differentiation.
ventrally, and is found back by us in this same position, and at the same time quite marked in Fig. 111 for Chamaeleo.

For Lacerta all this is yet more distinctly brought before us in Wenkebach’s well-known figures (86) reproduced in Hertwig’s Figs. 437—441.

And as to birds Schwanzinland’s longitudinal section of the sparrow (Fig. 110) leaves no doubt whatever that the phenomena are, indeed, the same here as in reptiles and mammals. Protochordal plate, protochordal wedge, lateral lips of the dorsal mouth (primitive streak), and ventral mesoblast have each their proper position, and their adequate further development.

It is especially evident in this last-named section that the so-called Sichelrinne has the ventral mesoblast immediately behind it, and that in this region there is another thickening of the entoderm, preceding the formation of vasifactive tissue in this region as is indicated in the diagram of Fig. 46 that was more especially designed for mammals.

In finding all this amount of correspondence between Mammals, Amphibia and Sauropsids concerning certain general features of the very earliest development of mesoblastic structures it was, of course, a great desideratum to know in how far the oviparous mammals, the Ornithodelphia, agreed. This paragraph was already written, and the blank caused by our ignorance on this head was keenly felt by me when the very recent memoir by Wilson and Hill on Ornithorhynchus ontogeny appeared in the ‘Philosophical Transactions’ (‘07). This important paper furnishes us with the necessary data to fill up that blank, and I was only too pleased to have to re-model this paragraph as these data confirm in many respects the views here advocated, and accentuate a few points in my interpretation with quite unexpected decisiveness.

I may begin by remarking that a protochordal plate, of which mention has been made in the foregoing pages, is recognised by them as occurring in Ornithorhynchus, and is also designated by that name. However, the data concerning
the earliest appearance of this protochordal plate in Ornithorhynchus are too scanty than that I have ventured to mention it when in the preceding pages we discussed the protochordal plate. And it seems advisable on this point to await yet further researches on these rare mammals, of which it is so very difficult to obtain the required developmental stages.

As to the protochordal wedge and the ventral mesoblast of Sauropsida and Ornithodelphia some startling facts have been brought to light by Wilson and Hill, and will here be compared to what we find in reptiles, birds, and mammals higher than the monotremes.1

The most important discovery in Ornithorhynchus seems to be that mesoblast formation on the upper surface of what corresponds to the mammalian embryonic shield is started at two different spots lying in the median line. In other words the protochordal wedge and the ventral mesoblast, which we have followed in all the details of their earliest origin in Tarsius (p. 36), and which we have there found in closest proximity (see also Figs. 48, 49, and 50) are in Ornithorhynchus as wide apart as is indicated by Fig. 115. In Sauropsida, again, they have been found confluent by successive authors, but then in Ornithodelphia they become confluent soon after (Fig. 113), so that there is yet room for inquiry whether perhaps certain Sauropsids might not in very early stages conform with Ornithorhynchus.

The lesson should be drawn from the arrangements in

1 In passing, I may remark that Wilson and Hill's article is a very instructive example of the impossibility we have come to of retaining the current nomenclature, as this has gradually developed itself out of successive contributions of different authors. Only gradually can we attempt to obtain a more full comparative group of the subject here treated, and then such names as head-process, primitive knob and streak, and many other, prove to be a misleading commonplace. Already Wilson and Hill do not look upon the primitive streak of mammals and reptiles as a homologous structure ('07, p. 116), whereas they propose to drop "head-process" altogether (a point already advocated by myself and others). But then they add new ones, such as archenteric plate and others, the acceptability of which will yet have to be tested and seems to me questionable.
Fig. 115 and 116. Two surface views of early blastodisks of Ornithobranchus (after Wilson and Hill, '07). In Fig. 115 the protochordal wedge (pvw) and the neural mesoderm (vmw) are yet wide apart; in Fig. 116 they are fused in the median line and proliferation takes place along the whole length of the dorsal mouth, nch notochord. — Fig. 117 to 119. Three longitudinal sections through consecutive stages of neogenesis of Torpedo (after His, '09). In Fig. 117 ectoderm (ec) and endoderm (en) have been separated by delamination and notogenesis has commenced; in Fig. 118 the folding off of the head has proceeded further; in Fig. 118 and 119 part of the protochordal plate is being lifted up from the yolk. pp protochordal plate, nch notochord.
Ornithorhynchus—for the details of which I refer the reader to Wilson and Hill’s paper (‘07)—that in that particular region of the embryo, where notogenesis comes about, there are multiple centres of growth. What was in the pelagic vertebrate stage of the vertebrate ancestor (Fig. 160) the dorsal mouth-slit or "Rückennmund" (from which the stomodeum [notochord] continued downwards towards the intestine while the enteric chambers preceded the colon) has left in the early vertebrate embryo hereditary traces of its gradual extension backwards and of its closure.1 The proximal end of this dorsal mouth-slit is the earliest prochordal wedge, the distal end of it is our earliest growth-centre of the ventral mesoblast. Between these two there is (1) a backward growth of the prochordal wedge (above discussed for Tarsius and Amphibia); (2) a forward growth going to be confluent with the preceding and established by Wilson and Hill for Ornithorhynchus, as well as (3) lateral expansions from what may be called the lateral lips of the dorsal mouth-slit. What has been called the "Sichelrinne" is always situated at the distal end of this medio-dorsal region of proliferation, whereas what is originally the prochordal wedge (Hensen’s knob) is always at the proximal extremity in the original stage. It may be said to travel for a certain distance backwards before becoming unrecognisably united to the posterior proliferation.

What has sometimes been called the archenteric cavity in the prochordal wedge (which has been compared with the archenteron of Amphioxus by van Beneden, who has more especially studied it in bats (‘87)), what has been termed Mesodermssäckchen by O. Hertwig (‘06, p. 828), and what has been found as a transverse slit in Ornithorhynchus by Wilson and Hill, and as a decided cavity by many other authors, such as Will (‘90), Mitsukuri (‘93), Ballowitz (‘01), Weneckebach (‘86),

1 In this respect Hertwig’s views can be made to fit in very well with mine, only with the difference that the "Rückennmund" is not to be confused with an "Uramyd," and that "notogenesis" is not to be looked upon as "gastrulation."
Voeltzow ('99), Schauinsland ('08) in all orders of Reptiles seems to me to be the remnant of the space which has always been included in the coelenterate ancestors between the two lateral lips of the stomodeum of the elongating, actinian-like ancestral form. That from the wall of this cavity the notochord develops is only natural; that it communicates—be it even in a somewhat whimsical fashion and curiously intermittently—with the enteric cavity is also nothing but a hereditary reminiscence; that laterally it is inclined to tend towards communication with protosomites, as Wilson and Hill describe for Ornithorhynchus ('07) and Spee ('01) for Cavia, is again easily understood, if we remember that those portions of the primitive coelenterate enteron which must have become the precursors of a coelom (separated from an enteron) are in immediate continuity with the lower limit of the stomodeum (notochord).

The fact that this cavity, or slit, or porus offers a different extension and different shapes in different vertebrates; that in some it appears as a neurenteric canal, which in others is no more visible as an open space; that it undergoes a displacement backwards, and finally disappears, after having appeared in different parts of what will be the median plane of the back of the animal, shows that during ontogenesis this important discontinuity of tissue of phylogenetic significance has also that particular variability which very old and archaic portions of vertebrate organisation so often display (e. g. epiphysis, thyroid structures, etc.).

To look upon it, as van Beneden has attempted, as the archenteron, and to degrade the original entoderm to the

1 The very important question: in how far Wilson and Hill are right in stating ('07, p. 117) that the protosomites which they describe and figure "have nothing to do with the origination of the first definitive somites, nor are they in any way coextensive with the site of differentiation of the latter," will not here be entered upon as falling, as the superscription of this chapter indicates, outside the scope of this paper. Suffice it to say that my own preparations furnish me with most useful material for throwing light on these very obscure, but, nevertheless, all-important, points in the development of animals, to which I intend to devote full attention on another occasion.
value of a lecithophore, is an unwarranted hypothesis in the
take direction as that of the gastrulation in two phases, of
which Keibel and myself were the godfathers many years ago
(Keibel [89], Hubrecht [88]), but which we have both
abandoned since.

IV. Fishes.

The early developmental phases of the germinal layers of
the fishes have not been the object of personal observations
of any extension on my own part, although I possess a certain
number of section series both of Elasmobranchs and Teleosts.
And so I only intend, in the following pages, to give some
gleanings from the literature on the subject, which appear to
me to point to the possibility that the views to which in-
vestigations of the mammalia have led me may also hold good
for these lower vertebrates.

Beginning with Amphioxus, I need only allude to Legros' 
latest contribution to the ontogeny of this animal, from which
I have copied Fig. 120. In it we see the region marked \( pp \),
singled out by Legros as a part of the original entoderm
of the wide-mouthed gastrula, which in Amphioxus is formed
—in contradistinction to all other Vertebrates—by invag-
ation, and not by delamination (cf. p. 13).

Legros (07) and Cerfontaine (06) are willing to adopt the
essential points of Lwoff's interpretation, which has been so
fruitful in setting other observers to pause and reflect. The
part marked \( pv \) in the longitudinal section (Fig. 120) of a
stage of early metogenesis should thus be looked upon as the
median portion of what is Lwoff's "Dorsalplatte," and as an
essentially entodermal derivate which has come about in con-
sequence of the growth backwards of what was originally the
dorsal lip of the early blastopore (cf. for mammals with Figs.
48, 49, and 97—99 of Tarsius). During this backward growth,
which does not, as is the general belief, complete gastrulation
(see Hubrecht, '05), but which initiates metogenesis, the two
embryonic regions become distinguishable, which, also in
Amphioxus, we may term the essentially entodermic protoco-
chordal plate (\(pp\)) and the (ectodermic) protochordal wedge
\((pw)\).

In Elasmobranchs the comparison is not either difficult or
strained. We see in the Figs. 117—119 and 121—123, copied
from His and Rückert, that when once the separation of the
two primary layers has come about by delamination, a pro-
iferation in the entoderm makes its appearance (\(pw\) Fig. 122),
which here, too, deserves the name of protochordal wedge,
whereas the undoubted entodermal layer (\(pp\)) to the left of
the figure is, and remains, the homologue of what in the
mammals we have called the protochordal plate. In Fig. 123
notogenesis is in its incipient stage; in Fig. 117 it has con-
siderably advanced, and in 118 and 119, where the headfold
has made its appearance, part of what was the horizontally out-
spread layer (\(pp\)) has become lifted up from the yolk and is now
that part of the entoderm which lies in front of the anterior
end of the notochord, and which participates by means of its
surface that faces the ectoderm in the formation of the endo-
thelium of the heart (cf. Rückert and Mollier in 'Hertwig's
Handbuch,' Bd. I, 1; II, p. 10; 33, 34).

Perfectly similar occurrences were formerly described by
me (62, Pl. IX, figs. 72—74) for Tarsius, and Figs. 98, 99
should be compared with those here given for the Elasmo-
branchs.

As to the presence in Elasmobranchs of a ring-shaped
extent of entoderm which contributes to the formation of the
mesenchyme, out of which the vascular system is going to take
its origin, we find the most reliable data in Rückert and
Mollier's extensive treatise above cited. Their figure 777,
here reproduced as Fig. 124, is especially instructive, and it
will suffice to refer to that important article in 'Hertwig's
Handbook.' It will there be seen that also by the presence
of a circular region of mesenchyme-producing entoderm the
early Elasmobranch stages resemble the mammalian. Although
in Rückert's article a certain reluctance is unmistakable to
admit the value of his conclusion as to the entoblastic origin
Fig. 120. Longitudinal section of Amphioxus (after Legros, '95). Noto-
genesis has advanced considerably. At + Legros accepts a separation between the lower entodermal layer, originated by invagination and the layer to the right of + which he accepts as Wolff's example as a product of ectodermal proliferation. + would then separate; to the left: protochordal plate ++; to the right: the protochordal wedge ++, spun out. — Fig. 121, 122 and 123. Three longitudinal sections through blastodiscs of Pristurus (after Rückert, '06). In the two first gastrulation by delamination has come about; ++ ectoderm, ++ ento-
derm; in Fig. 122 the protochordal wedge ++ has fused with the entoderm ++; in Fig. 123 notogenesis has definitely commenced. + incipient gut cavity.
of the blood-producing mesenchyme, still de facto he is quite outspoken about it. His conclusion (l.c., p. 1095) that it is not of any importance, whether the blood anlagen of the Selachians are meso- or entoblastic is not ours, because we have in the first part of this chapter demonstrated that a precise analysis of the mesoblast formation also in mammals may considerably contribute to render comparison of the various classes more easy. That in Elasmobranchs, as in mammals, a very early fusion comes about between Rückert's peripheral and axial mesoblast, and that, after this has come about, an end is made to further unravelling is certainly true, but it may not withhold us from laying all the more stress on the necessity of comparing the very earliest stages with the utmost closeness.

The focus of proliferation corresponding to what we have called the ventral mesoblast in the Mammalia and the Amphibia must be sought for in the Elasmobranchs in the tail swellings. I do not intend to enter into further comparison here, but will postpone this to a later paper where the stages after the development of the mesoblastic somites will be discussed.

Among the Teleostomes we find developmental stages which have again a different character from what we noticed in Elasmobranch fishes. In many cases the eggs are not meroblastic, and then a more or less close comparison is possible between their development, and that of the Amphibia above discussed. So it is with the Sturgeon's eggs and with those of the Dipnoi: Ceratodus, Lepidosiren, and Protoperus (Fig. 125). Other comparisons with the development of the lamprey suggest themselves, and have already been pointed out by different authors. As to the external features of this development, the Rückenrinne, which Semon has figured for Ceratodus (Fig. 126), and which has also been noticed in Urodeles by Braun seems to me to be simply explained if we look upon it, not as any remnant of a blastopore (Urmund), as Semon (93, pp. 37—89) proposes, but as the last reminiscen-
ence of what was the ancestral "Räckenmund" of a more actinian-like ancestor.

In a later paper Semon ('01, p. 317) retracts his original comparison, arguing that the gastrulation process has already ceased before the "Nalö" becomes visible. Here again the false interpretation of the gastrulation process (see Hubrecht, '05) has misled Semon, whose original interpretation can be adhered to if we substitute notogenesis for gastrulation, and dorsal mouth (Räckenmund) for blastopore (Urmund).

Protochordal plate and protochordal wedge in their mutual relations may be considered identical with what we discussed for the Amphibia.

The ventral mesoblast, which, in Petromyzon, does not appear as so distinct a median and early proliferation of the ventral lip of the blastopore such as we meet with it in many amphibians, has not either that character at so early an age in Dipnoi and Ganoids; the homologue of it is found in the Schwanzknopf, as we also saw in Elasmobranchs. And Fig. 87, for Amia, indicates, moreover, if we compare it with Fig. 99 for Tarsius, that the intestinal continuation of both figures is of the same order, although in the mammal it is no slit, but has become a tube. Moreover, both of them may be brought into line with Kupffer's vesicle in Teleosts.

In many respects the development of the Teleosts offers peculiarities not met with in the Vertebrates hitherto discussed. The process of notogenesis has certain remarkable points of comparison with what we notice in many Amphibia. Ziegler has, in his 'Lehrbuch der vergl. Anatomie der modernen Wirbeltiere' (1898, Figs. 11—14) to accentuate the extent of this comparability, and says in his text (p. 182) : "The ventral border of the blastoderm advances quite in the same way as does the ventral point of transition between the smaller and the larger cells in Rana and Triton."

However, there are numerous points of divergence and the different authors who have of late occupied themselves with
Fig. 124. Transverse section of the right half of an early embryonic shield of Torpedo (after Römer and Malher, '06). The participation of a region of entoderm as towards the formation of blood and blood-vessels is here indicated. — Fig. 125. Longitudinal section of Lepidosiren (after Graham Kerr, '01). cf. Amphibia (Fig. 73). pp protochordal plate, pw protochordal wedge. — Fig. 126. The dorsal raphe (dorsal mouth, 'Riek- konrinne') dm of Ceratodus seen from above (after Sexson). Fig. 127 and 128. Two diagrammatic longitudinal sections of stages in the notogenesis of Amphibia (after Ziegler, '02). pp protochordal plate, pw protochordal wedge, vm ventral mesoblast.
Teleostean ontogeny are far from being in entire accordance on many points. Swaen and Brachet ('99, '04), H. Wilson ('91), Summer ('04), and Boeke ('02, '07) are among the authors who have lately considerably furthered our knowledge of Teleostean development. The latter author more in particular, who adopts my views concerning gastrulation and separates that process from what I have proposed to designate as notogenesis, gives certain figures which point in a direction that may finally lead to a more close comparison of the processes in Amphibia and Mammals on one hand, in Teleosts on the other. I copy a few figures from his latest papers in my Figs. 88 and 89 to elucidate how I imagine that it may perhaps later be possible to distinguish also in Teleosts a protochordal plate (pp) and a protochordal wedge (pwe) standing in the same relation to each other as in mammals.

The homologue of the protochordal plate can no doubt be detected in a portion of the periblast, to which layer, since Boeke's detailed investigations, participation in the formation of embryonic cells can no longer be denied. It is certainly striking that this participation is of a nature that would bring it in one line with those processes which we have above noticed, both in the protochordal plate and in the annular zone of entoderm, that is so closely allied with vasifastive phenomena. On the other hand the protochordal wedge, as a downward proliferation of the ectoderm increasing in length by a backward growth of the blastoderm and obtaining after some time a new coating of entoderm-cells below it, is quite exceptionally evident in Teleosts (Figs. 88, 89).

The focus of formation of the ventral mesoblast is in Teleosts originally far apart from the protochordal wedge, but fuses with it when the yolk has been entirely overgrown, and when what was at the outset the anterior ring of the blastodisc has coalesced from behind with the prostormial thickening. This prostormial thickening of Teleosts has since Boeke's researches ('02) to be looked upon as an entodermal (periblastic) proliferation, and is by me homologised with that proliferation in the entoderm of mammals which occurs
in the posterior region of the amnial zone described in Chapter II, paragraph 26, and diagrammatically represented behind the proctochordal wedge in Fig. 46. The fact that in and behind this entodermic proliferation Kupffer's vesicle is developed seems to further confirm that homology, as will be noted below. This vesicle becomes apparent when the yolk has become quite enclosed by embryonic tissue.

I have pleasure in noting that my identification of Kupffer's vesicle in Teleosts with the allantois in primitive mammals (a comparison which Kupffer himself did not fail to make) is accepted by Decker. A comparison between Figs. 90, 128, and 63 will further elucidate the chain of thoughts here implied. And I may call particular attention to Swaen and Brachet's article ('04) and their figures 58 to 77 (Pl. XV) of Trutta fario in order to show how these authors have established a close connection between this cylindrical posterior continuation of the entoderm, which goes by the name of Kupffer's vesicle, and the production of vascular tissue (Swaen and Brachet's Lame vasculaire, L.v.). I invite close comparison with what I have written about Tarsius on p. 45 and with Fig. 102 which was given of that mammal, and have no doubt that if we compare Kupffer's vesicle not with a free allantois of reptiles and most mammals, but with the incipient allantois met with in Primates, many apparent objections to such comparison will fall to the ground.

**Summary of Chapters I and II.**

Before the ectoderm and the entoderm have become differentiated from each other there is in mammals a distinct larval cell-layer surrounding (as soon as the cleavage of the egg has attained the morula stage) the mother-cells of the embryonic tissues. This layer, to which the name of trophoblast has been given, and which is, phylogenetically, an ectodermal derivative, contributes towards the formation of chorion and amnion, and is shed at birth. The mother-cells of ecko- and entoderm enclosed within the trophoblast, and at one point
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in immediate contiguity with it, separate into ecto- and entoderm by delamination.¹

The result of this delamination is the mammalian gastrula
—sometimes characterised by the temporary presence of an
actual blastopore—which very soon undergoes a series of
developmental changes (different from gastrulation) to which,
in this incipient stage, the name of notogenesis may be
applied. The tissues further forwards, that were the first
to appear, are simultaneously contributing to what may be
called kopallogenesis. The budding of the trunk from what
becomes the extreme forward region of the head is designated
by these two terms.

Before notogenesis has commenced, a posterior portion of
the ectodermal embryonic shield (immediately behind the
spot where the blastopore is actually or only virtually situated)
is told off as the mother-tissue of what will be the ventral
mesoblast. When notogenesis is inaugurated it does so by a
marked median and ventral proliferation of the ectoderm in
front of the posterior region just alluded to. This pro-
liferating downgrowth (the protochordal wedge) becomes
confluent with the entoderm and fuses with a proliferation in
it (the protochordal plate).

Both proliferations are centres of origin of mesoblastic
and mesenchymatic tissues. The antero-median entodermal
proliferation, called the protochordal plate, is in continuity
with a ring-shaped area stretching sideways and closing
behind, below the ventral mesoblast. This ring is the place
of origin of blood and blood-vessels. In certain mammals it
contributes in its hinder portion to a very early vascularisa-
tion of the trophoblast, thereby calling forth a connective
stalk (Bauchstiel), in which a remnant of entoderm, drawn
out in tube form, is the first indication of what in less
primitive arrangements has come to be the allantois.

¹ The two germ-layers (ectoderm and entoderm) of all the Vertebrates arise
by delamination; only in Amphioxus they owe their differentiation to a pro-
cess of invagination so common among invertebrates.
CHAPTER III. DIPLOTROPHOBLAST = SEROUS (SUBZONAL) MEMBRANE,
CHORION, AMNION, ALLANTOIS AND UMBILICAL VEIN IN
ONTOGENY AND IN PHYLOGENY.

In the second chapter of this treatise we have discussed
the facts that have convinced us, that the very early phases
in the development of mammals are characterised by the pre-

sence of what we look upon as a very early larval envelope:
the trophoblast. We have on p. 15 tried to imagine how
this larval envelope might have evolved out of arrangements
that are met with among invertebrates.

We have also hinted at a possible simplification of the
current views concerning the phylogeny of the fetal en-
velopes of the higher Vertebrates, views which, at present,
are neither satisfactory nor unanimously accepted.

But we have not yet given any detailed account as to how
we have to picture to ourselves the phylogenetic processes
by which out of this primitive trophoblast the different fetal
envelopes have evolved, and how it has come about that some
of these have been vascularised in diverse ways and have
thus laid the foundation for the phenomena of placentation,
so intimately related to the higher development which charac-

terises the Mammalia as against the lower Vertebrates.

I must begin by stating that much of what is going to be
brought forward in this chapter is an attempt at bringing
together in the light of an hypothetical interpretation facts
that have up to now been insufficiently understood or over-
looked. A solution that is anything else than hypothetical
can, of course, never be reached.

1. Chorion and Amnion.

The amnion is a membranous envelope which we encounter
in all Mammalia and Sauropsida and of which no traces are
found amongst Amphibia and Fishes, the two latter being
distinguished as Anamnia from the former, the Amniota.

Various views have been expressed concerning the phylo-
Fig. 129. Longitudinal section of a larva of Sipunculus nudus with its external larval layer $L$, which, later on, is shed; $m$ mouth, $e$ anus (after Hatschek, '84). — Fig. 130. Longitudinal diagrammatic section of an embryo of Dasyurus (after Hill, '90). $a l t l$ allantois, $a v$ area vesicularis umbilicalis, $a t r$ region in which the trophoblast shows phagocytic properties, $p r a$ pronucleus. — Fig. 131. Section through part of the "Deckeschicht" ($d s$) with local proliferation of same in the frog. $g s$ "Grundeschicht" (after Ashe, '96). — Fig. 132. Longitudinal diagrammatic section of the blastocyst of a Catarrhine monkey (Cercopithecus cynomolgus) with dorsal and ventral placenta (after Selenka, '91).
genesis of the amnion. And it must be recognised that the appearance— all of a sudden—of this useful and complicated fetal investment—though it is only present during the few weeks or months between early ontogeny and birth—is strictly comparable, both as regards its constituent layers and the way it comes into existence wherever we find it. This natural phenomenon must have its natural evolitional explanation for whosoever wishes to be guided by evolutionary principles in his interpretation of nature. The explanations given, and which we owe to Haeckel, van Beneden and others are, however, as we shall see, untenable. I have held this view long ago (85), and have made another attempt at solving this evolutionary riddle, but find that a repetition of my argumentation towards an alternative solution of this intricate problem may not seem out of place.

Now it is a very queer point that two of the fetal envelopes, the amnion and the serous membrane, seem to be so intricately interlocked with each other as far as their first appearance goes, that the serous membrane, as Schainland— the author of the chapter on fetal membranes in Sauropsida in Hertwig's new handbook—puts it, owes its origin to the outer plet of the amnion fold, but later increases in size by a process which splits it off from the umbilical vesicle. Of late the name amniogenic chorion (Bonnet) has been introduced for mammals in the place of serosa, thus underlining the supposition that it owes its origin to the amnion.

We would expect a fetal envelope of the importance of the chorion in Primates and of the subzonal membrane or serosa (diploscrophoblast) in other Mammalia and Sauropsida to have a phylogeny of its own and not to be a by-product of a folding process that is typical for the Sauropsida, but is absent in representatives of many orders of Mammalia.

A hypothesis which would separate the phylogeny of chorion (serosa) and of amnion would thus in itself appear to be more acceptable and might prove to be a better guide to the understanding of those mammals that have no amnion-folds (Cavia and other rodents, Pteropus, Galeopithecus,
Erinaceus, Gymnura, monkeys and man) than one which is obliged to derive the amniogenesis in the latter mammals from the phenomena which we notice in Sauropsida and a number of mammals by an obscure process of cenogenesis.

Such an alternate hypothesis I have advocated ('95a) more than thirteen years ago, and will here state it anew with certain additional facts in its support.

The starting-point for this hypothesis, which will enable us to admit a separate phylogeny for chorion and for amnion, was the fact that we have observed in all mammals the presence of an actual fetal envelope—the trophoblast—long before the appearance of anything like the amnion. And secondly the other fact that this early fetal envelope is bodily transformed into what is called the chorion, diploglamblast, serous membrane or subzonal membrane in later stages of development. There can thus be little doubt that we now have to turn the tables and must no longer look upon this outer envelope as a by-product of the amnion, but must, on the contrary, ask how has the amnion come to be developed out of or by the side of the older fetal membrane or embryonic envelope, the trophoblast?

Leaving aside the interesting, but at present quite unsolvable question whether vertebrates have ever existed in older geological times that possessed a trophoblast but were not yet provided with an amnion (a question which is justified as soon as we have established that the link between amnion and serosa is not as indissoluble as the modern embryological text-books will have it), we will now proceed to investigate such cases in which the independent development of chorion on one side, amnion on the other is yet particularly evident.

Of such cases I would cite some of those that have been already named above and that occur in different orders of mammals. We begin with an extreme case as is that of Cavia. The trophoblast and that proliferating portion of it which is known as the Träger are quite independent of the embryonic knob at a very early stage (see Figs. 24 and 25). In the embryonic knob, after the mother-cells of the
endoderm have become separated from it, a cavity arises, the lower surface of which becomes the entodermic shield, the upper surface the inner lining of the amnion, which is thus a closed cavity from the very beginning.

Cases of a less extreme nature are met with in other Rodents, and have been described in detail by Selenka (73, 74) and others. Thus for mouse and rat, for Articola and others, the cavity which in later stages is called the amnion is never in free communication with the space outside the trophoblast, but is always intra-trophoblastic. There is thus no necessity for a gradual meeting of folds in order to delimitate the amnion cavity which is an enclosed space from the very earliest (Figs. 27, 28). What is known and figured as the head-fold and tail-fold of the amnion in the mouse (Fig. 28) must be more fully investigated before comparing it with the same structures in Saurropsida. Moreover, these folds in the mouse, when once confluent, do not form a boundary between the amnion cavity and the outer world, but between two cavities inside the trophoblast, one of which is the amnion. Among the Rodents the case of Lepus is particularly instructive. I have already called attention to it in an earlier publication (75 a), and have there demonstrated that the so-called Rauber cells form part of the trophoblast, with which they are continuous (Fig. 23). In Lepus the trophoblast does not open out to bring the embryonic endoderm to the surface, but the trophoblastic cells above the latter flatten out and disappear in the way of the "Deckenschicht" of the Amphibia. This is not a primitive but probably a secondary arrangement, as may also be inferred from what Lee has found in another rodent (Anomospermophilus), which may be

1 In former publications (75 a, p. 25) I have more than once suggested that the amnion formation in man and monkeys (not known by actual observation) was probably of the same order as that of Cavia. While correcting this proof I became acquainted with the interesting early human ovum which was demonstrated at the Berlin Congress of Zoologists in April, 1906, by Drs. Bryce and Truelsen, and I feel confident that it goes a long way towards confirmation of this suggestion, if later finds will prove it to have been normal.
said (Fig. 15) to be intermediate between the entypie, such as it is represented in many rodents, ungulates, and insectivores (Figs. 13, 17, 29—32), and the flat embryonic ectoderm of Lepus, Sorex, and others.¹

A case which as far as the amnion is concerned offers great similarity to that of the Guinea-pig is that of the flying dog (Pteropus), where Selenka and Göhr (92) noticed a closed amnion from the very first. It develops into the definite amnion by a simple process of extension and moulding, and exists as a closed sac of ectodermal constitution long before a mesoblastic layer comes to duplicate its wall (Figs. 22, 71—73).

A very similar arrangement is met with in the yet much more primitive Galeopithecus (Figs. 41, 42), which, however, I have not yet found occasion to describe in detail.

Another very instructive case is that of Erinaceus and Gymnura. In one of these two genera we have described how the early blastocyst is characterised by the possession of an embryonic knob from which the ectoderm is so quickly separated off that the details of its earliest development have not yet come to light quite sufficiently. But at the same time the remaining embryonic ectoderm takes somewhat more time to become separated off from the trophoblast than in other mammals. And when it does it is by the appearance of a cavity between what is going to be the ectodermal shield and what will remain the trophoblast that the amnion-cavity is heralded into existence (Figs. 33—37). Here again it is a cavity that appears as such that strikes us as the dominant feature in the phenomenon. I have elsewhere demonstrated (95 a) that if we have to choose what is the more probable earliest appearance of the amnion, as a closed cavity or as set of folds by the meeting of which a cavity is going to be enclosed above the dorsal surface of the embryo, there is undoubtedly—speaking as an evolutionist—a heavy

¹ The exact details of the formation of the amnion in Anomospermophilus with respect to the exact derivation of its inner (epiblastic) layer should be looked forward to with interest.
balance in favour of choosing the first eventuality. Principally because only in case these have been the actual phylogenetic steps can we conceive that the amnion on its very first appearance was of immediate significance to the embryo, as a sort of water-cushion, shielding the embryonic rudiment—already at its very earliest appearance—from external pressure or mechanical insult. We have now seen that not only does the amnion appear as a closed sac from the very earliest in very numerous cases in different orders of mammals (to the list already given the monkeys and man should yet be added), but that in this case an explanation of its earliest origin is not far to seek. We have indeed admitted that the trophoblast is an early larval envelope by the presence of which a chorion or serous membrane is predestined to make its appearance sooner or later. From this larval envelope—also in the case of Nemertea and Gephyre (Fig. 129)—the embryonic ectoderm has to become segregated in one way or another, as also the amnion is being originated in different ways. We know from the examples we possess amongst Nemertea of the Filidium larva and the Desor’s larva that at one time this segregation takes the form of a splitting process (Desor’s larva) when (as is the case in the dorsal plate of that larva which I have formerly ['85, Figs. 58a, 95] described) the plate of future embryonic ectoderm provisionally remains attached to the larval envelope along a circular line of attachment much in the same way as we see the embryonic ectoderm of the hedgehog attached to the trophoblast (Fig. 37) with the closed amnion-cavity above it; whereas at another time (the lateral plates of the Desor larva or the embryonic plates of the Filidium) the separation of the definite ectoderm from the larval layer takes place by a process of invagination, during which that portion that is destined to become the outer wall of the embryo sinks away from the level of the larval surface into the cavity enclosed by that surface and develops further in this more sheltered position. In this latter case a circular fold ensures the continuity between larval and definite ectoderm, and only when the
folds meet has the surface of the Plidium become separated from the future body-wall of the embryo and are these two separated by a closed cavity which, also in the case of the Plidium larva, has for many long years borne the name of amnion cavity. It makes no difference that in the Plidium the process occurs at four different spots, the products of which fuse later. A. Willey (98) has speculated upon similar relations between arthropod embryos and their larval envelope, also designated as amnion in Peripatus, Lepisma, Gryllus, Foricula, and others; has rightly interpreted the direct comparability with the vertebrate trophoblast, and has looked upon it (as I have done [25 R] for vertebrates) as an adaptation to a viviparous habit acquired by the terrestrial descendant of an aquatic ancestor.

And so not only can we link in the larval trophoblast to cases met with amongst the invertebrates, but even for the development either of a closed amnion or of an amnion arising by circular folds (perhaps in the case of the invertebrates also a secondary modification) do we find examples in the invertebrate kingdom.

It seems to me that in the case of vertebrates we may be content to say: (a) that wherever an amnion is met with it is the sequence of the separation of the embryonic ectoderm from the larval envelope; (b) that this larval envelope (trophoblast, giving rise to chorion, diplophtrophia, or serosa) is always antecedent to and must be older than the amnion; (c) that the actual separation of the embryonic ectoderm from the trophoblast can be witnessed in those mammals where the amnion is from the first a closed cavity; and finally (d) that in those cases, both among mammals and Sauropsids where we do not notice a direct separation between embryonic ectoderm and trophoblast in consequence of which an amniotic space arises, we see the amniotic cavity appear at a later stage, thanks to a folding process, which may be entirely restricted to the ectodermal tissues, and for the formation of which the presence of mesoblast is in no way required.
Returning to the hedgehog for finding a reasonable explanation of how the folds may have arisen, when the amnion was no longer formed as a closed cavity ab initio, we see that here and in the bat a phenomenon occurs that does throw light on this point. We see (Fig. 38) that when a certain stage of development has been reached the circular rim of attachment of the ectodermal shield to the trophoblast shows a tendency to travel upwards. I have formerly ('95 b, p. 25) ascribed this to a splitting in the deepest trophoblastic layers. I now feel inclined—as I did in a yet earlier paper ('89)—to see the first step in this direction in a more direct co-operation of that rim of the embryonic ectoderm itself, which travels upwards along the surface offered to it by the massive blood-laden trophoblast (Hubrecht, '89 p. 374, Pl. 25, fig. 51). The annular zone of attachment thus becomes more and more restricted, and when finally it disappears a separation between amnion and trophoblast is at that same moment brought about. Whether mesoblast has occasion to extend itself in the region between these two is a question in no way of vital importance for the amniogenesis, as is also demonstrated by the peculiar way in which the amnion arises in Chamaeleon, a sauropod which, in this respect, undoubtedly reveals primitive characters. As such we reckon the fact that the amnion has, on starting, no lining of mesoblast, and that it has the shape of a ring-fold (Figs. 75, 76) closing about the middle by a uniform constriction not yet differentiated into head-fold, tail-fold, and side-folds.

This amnion fold of Chamaeleon has an outer plait of trophoblast, an inner plait of embryonic ectoderm, the two growing independently and passing into each other at the rim of the fold where—as in Sphenodon (see also Figs. 77 and 78)—lay in a somewhat earlier stage the potential line of demarcation between embryonic ectoderm and trophoblast alluded to above. These cases of reptiles are thus connected with that of the hedgehog above noticed and with that of the bats so very clearly figured by Duval ('99, Figs. 96, 102, 117,
123, 132). These latter figures, compared to Figs. 50, 57, 68, 73—76, 82, 85 on Duval's Pls. 2 and 3, make it clear to us how a case of closed amnion formation, as it is offered by Galeopithecus and Pteropus (and as it is virtually present in the very early bat stages (Duval's Figs. 50 and 57), can gradually become converted (in the other bats) in one in which the closed amnion only comes into definite existence through the gradual uprising of a rim, the outer wall of which is trophoblastic, the inner one a derivate of the embryonic ectoderm.¹

Many figures (8a, 13—17, 20, 23, 30—32, 37) have shown that the early separation between trophoblast and embryonic knob takes place in the most various ways. And that even in one and the same species, as, for example, Tarsius, the separation may come about earlier or later (cf. Hubrecht, '02, Pl. II, fig. 38, a—c; with Pl. VI, figs. 49, a, b, and 50 a—c). This later appearance calls forth a stronger resemblance between Tarsius and such cases as Pteropus or Cavia. At all events, it is this very early process of separation of what will be the embryonic tissues from the trophoblast that goes parallel to ontogenetic processes in the invertebrates to which we have called attention (Piliotium, Desor larva) as showing us the earliest cases of amniogenesis. Such cases as Tupaja (Fig. 30) and Cervus (Keibel, '09), and lately again Sus (Fig. 17) are particularly instructive. What Selenka has designated by the name of Eutypia is—from our point of view—no secondary phenomenon, but one which repeats very primitive features of separation between embryonic ectoderm and larval envelope in invertebrate ancestors.

The formation of a proamnion is a phenomenon which has no significance at all for our considerations concerning the phylogeny of the amnion in general. It is a temporary

¹ I call particular attention to Duval's ('99) Figs. 96 and 102, and feel too late, while correcting the proof, that I ought to have copied them in this paper, particularly because the independent growth of the trophoblastic (outer) and of the ectodermal (inner) plait of the amnion-fold is there so extraordinarily clear.
structure met with in many mammals and sauropsids where a circular region of the blastocyst in front of the head remains without mesoblast. Into this the front end of the embryonic body curves down and is temporarily sheltered. This envelope thus consists of ectoderm and entoderm only (Fig. 130). It is during further growth of the embryo gradually reduced; the head is withdrawn from it; mesoderm gradually appears between its layers, and when the embryo is ready it has entirely lost its proamniotic covering layer which is finally flattenned out. Thus the explanation of the amnion which appears furthest from the truth is that of Selenka ('91, p. 186), who has expressed the opinion that the amnion arose out of a double source, and that the two Anlagen of both amnion and proamnion were finally fused into one. The true interpretation must decidedly start from quite different considerations as were developed above.

1 The explanation of the first phylogenetic origin of a proamnion has not yet been attempted; generally it has been ascribed to rapidity of growth, which caused the embryo's head to become temporarily imbedded in its own umbilical vesicle. But then the Primates, who have undoubtedly the biggest heads—comparatively!—have no proamnion.

My own explanation is a very different one, and starts, not from yolk-laden eggs of Sauropsids, but from early viviparous prostetrapeds which must have preceded (see p. 15) both Sauropsids and Mammals. Some of these have obtained direct vascularisation of the trophoblast by umbilical vessels; a great many others have departed from this very direct line of perfect vascularisation, have given up the early "Haemiel" (the homologue of which reappears in the allantoic attachment), and have at an early stage utilised their area vascularis as the umbilical vesicle for establishing intercourse with the mother. T h e n e n e a temporary omphaloideal placentaion. A f t e r a time, however, the disadvantages of this system of vascularisation during the further increase in size of the embryo became evident. N o t , however, before arrangements had come into existence by which the omphaloideal placentaion could remain in function as long as possible. O f these arrangements the most important is no doubt the growth of the head down into the umbilical vesicle, with, as result, the formation of a proamnion. It reaches its maximum in the Didelphia which, after having given up allantoic placentaion (yet persistent in Perameles), enjoy omphaloideal attachment for a short time, and then come into the world under the same specialised conditions that are so characteristic for the Marsupials.
We can now understand how the particular mode of amnion development as we find it in birds, and more especially in the chick [which was naturally the type upon which all speculations concerning the amnion were originally based, no other being sufficiently known] has given rise to that erroneous conception of the amnion as the first cause of the production of the serous membrane. The error was all the more explicable, but at the same time all the more tenacious because in the chick the existence of the trophoblast as an extra larval envelope is not in any way evident (see p. 20). It is only by placing together all the transition stages from the more primitive mammals to the Ornithodelphia and the Sauropsida, that we can succeed in demonstrating how it comes about that the ectodermal layer of cells which in the latter gradually travels round the yolk and finally encloses it is not primarily the radial extension of the ectoderm, sensu strictiori, of the shield, but that it owes its origin to what we have learnt to distinguish as an enveloping layer, which has lost its significance in the oviparous sauropsids, and can only be seen in its full detail in mammals.

A yet further reduction, or, to put it more correctly, a reduction in yet another direction than what we notice in Sauropsida is presented by the trophoblast of the Amphibia. Not in all, but in very many of these the development is characterised by the fact that at a very early period the outer ectodermic layer of the young embryo is so visibly different from the subjacent ectodermal cell-layers that it is distinguished by the name of "Deckenschicht" from the latter which are termed the "Grundschicht." Moreover, the cells of the Deckenschicht proclaim their transitory and larval significance yet further by the fact that they disappear in later developmental stages, and that it is only into the constitution of peculiar larval organs that they play any part. So that of the sucking disc, and in that of what are considered as larval olfactory organs (Fig. 131).

This then is a decidedly transitory, we may even say larval layer. On a former occasion ('95) I have already committed
myself to a comparison between it and the mammalian trophoblast. I have since, in a recent publication ('07, p. 69), more distinctly accentuated that I would never look upon the Deckschicht of the Amphibia as having been the first starting-point of what afterwards becomes amnion and chorion of the higher mammals. We may safely say that Deckschicht and trophoblast are homologous and of similar descent, but we cannot at present fully picture to ourselves what has been the arrangement of the larval envelope in the common parent form from which both have derived. There is no doubt that the viviparity in those vertebrates that have become the higher mammals has contributed towards making the trophoblast ever so much more conspicuous. But whether for the Amphibia we may also assume that in past times the trophoblast was more conspicuous in very early stages and enclosed an embryonic knob, such as we notice in mammals, cannot be decided for the present. Suffice it to say that some few observations would seem to point in this direction. I do not, however, wish to develop these at present, considering the very hypothetical nature of the ground we are here treading on.

It should, however, be immediately observed that if we are willing to admit the homology of the amphibian Deckschicht with the mammalian trophoblast, we must then unhesitatingly go one step further.

For there is no reason why we should not consider in that same light the Deckschicht which we encounter in Ceratodus (Semon, '03, '01), in Lepidosteus (Dean, '95), in Acipenser (Salensky, '80, '81), representatives respectively of Dipnoi and of Ganoids; nay, we are thus insensibly led to consider the Deckschicht of the bony fishes (which is so well known a particularity of this class of Teleostomes) as also included in the group of phenomena about which we are here attempting to generalise.

And it then, of course, strikes us, supposing all these different outer covering layers during early larval life to be the remnants of an early larval envelope, of which we find no

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trace in Amphiornus, the Cyclostomes, and the Elasmobranchs, that the deep significance hitherto attached to the fetal membranes as a means of subdividing the vertebrates into the primary groups of Amniota and Amnienia runs great risks of losing much of its significance.

We have seen that the name Amniota, as against Amnienia, was not well chosen if we consider, as I have advocated, that not the amnion, but the chorion, is the primary fetal membrane, and that the name of Choriota, as against Achoria, would even have been better; that of Allantoidea as against Amnialantoidea being yet more defective, as we will see later on.

But now, considering that the chorion is only a derivative of the early larval envelope that we have called the trophoblast, and that of a trophoblast traces are met with among Amphibia, Dipnoi, Ganoids, and Teleostomes in general, the more important division should not come to lie, as is at present the case, between the Sauropsida on one side and the Amphibia on the other, but between those vertebrates in which a larval envelope, or traces of it, are found and those in which such traces are absent.

We have seen, by the example of birds and reptiles, that it is not always easy to detect traces of the trophoblast, which for various reasons is not always quite as distinct as it is in mammals. And so even when among vertebrates we have descended downwards as far as the Elasmobranchs and the Cyclostomes, the possibility of last traces of trophoblast and Deckelschicht having been obliterated cannot be denied. Still, on quite different arguments supplied by comparative anatomy, we must recognise that the line here drawn seems to correspond with certain distinctive characters of primary importance.

So within the realm of the last-named classes the phenomenon of ossification is wholly unknown. On the other hand, the ossification, as it has manifested itself in bony fishes, calling forth such bony pieces as the hyomandibular, the quadrate, the different pterygoids, the palatines, the maxillary
and premaxillae, the dentale, the angulare and the articulare, reveals itself by identical bony parts higher up in the scale of vertebrates. The general homology is even so close that we find no difficulty in comparing the elements of the skull and visceral arches of those bony fishes even in detail with the higher mammals and with man.

It will at all events be necessary to consider most carefully whether we had not better drop the primary division above noted of the Vertebrates into Amnia and Amniota, as this subdivision has not even contributed to help us to understand the amniot better, and has on the contrary kept apart certain classes which earlier naturalists, as Linnaeus and others, never thought of separating so widely. I expect that palaeontologists will also contribute willingly to efface a separation based on a distinctive character which could never be applied to the objects of their research. Whereas at the same time the other anatomical differences between Reptilia and Amphibia, for example, break down in the case of very numerous fossil forms of very great importance.

Having up to now discussed the fetal envelopes and appendages that are primarily of ectodermal origin, we have now to consider those in which the entoderm is the primary constituent. These are the umbilical vesicle and the allantois, of which the latter in many cases has actually assumed the shape of a vascularised embryonic envelope of respiratory or nutritive significance in Sauropsida and in many mammals.

2. The Umbilical Vesicle.

The umbilical vesicle in mammals may be grouped according to some few modifications, of which we will have to discuss the respective value and genesis. The first is that which we find in man, monkeys, and Tarsius. In these mammals the umbilical vesicle from the very first remains smaller than the trophoblast, never filling the whole of it. We have seen on p. 44 how the rest of the trophoblast comes to be lined by
ventral mesoblast at very early stages. On the surface of the umbilical vesicle of both man, monkeys, and Tarsius a very intricate net of bulky blood-vessels is developed. To a certain extent these blood-vessels may contribute to bring about exchanges between the fluids contained in the cavities both of the umbilical vesicle and the extra-embryonic colon outside of it (which is shut off from the exterior by the diplotrophoblast) and between the embryonic blood. It is, however, not known whether these fluids contain nutrient that might be of use to the developing embryo, as is the nutrient contained in the yolk-sac, say, of Sauropsida. Nor is it known whether the uterine lumen of Tarsius contains anything resembling uterine milk which could be transferred by a special action of the trophoblast cells inside the blastocyst, and from thence by the blood-vessels of the umbilical vesicle be transported towards the embryo. And also for the catarrhine monkeys we are yet in the dark as to whether the annular zone of non-proliferating trophoblast, which separates (see Fig. 132) the dorsal from the ventral placenta is utilised in the same direction, and whether in that case the vascular net of their umbilical vesicle would effectuate osmotic absorption and transportation of materials that had passed from the uterine lumen into the extra-embryonic colon of the blastocyst. For man and the anthropomorphs such a process would be in any case excluded, their blastocyst being enclosed in a decidua basalis, and not possessing the ring-like zone just mentioned for lower monkeys.

Under these circumstances considerable doubt must be entertained as to the efficiency of the vascular area of the umbilical vesicle for nutritive or respiratory purposes among the Primates. A suggestion which I published some years ago (Hubrecht, '89), and which has been independently brought forward by Saxer ('96) and Spee ('96) should then be considered more closely, viz. that this very fine-meshed net of considerable calibre has, in the first place, a hematopoietic significance. ¹ There is no reason for wonder

¹ It should be borne in mind that the bone-marrow as focus of hemato-
that the surface of the umbilical vesicle should, during the embryonic period, play an active part in this direction, if we remember how copiously blood formation is going on during embryonic life in another derivate of the entoderm, viz. the liver, not to mention the increased significance which we have to ascribe to the entoderm as the primary source of blood and blood-vessels, since the recent researches of Räckert and Mollier ('06). One of the main arguments of Ed. van Beneden ('99, p. 333) for not accepting my views on the phylogeny of the Mammalia was this, that the presence and the considerable development of the umbilical vesicle of the Mammalia could according to him only be explained, if for mammals we accept a reptilian ancestor with meroblastic, yolk-laden eggs. Van Beneden's reluctance might dwindle away if this hematopoietic significance of the surface of that part of the entoderm which has grown out into an embryonic appendage, and has been styled the umbilical vesicle, was found to be its chief "raison d'être."

That this hypothesis is not specially intended to stand as an argument against van Beneden's criticism follows from Spee's independent advocacy ('96) of the hematopoietic significance of this dense, vascular, network on the human (and simian) umbilical vesicle (Figs. 74, 156, 157).

The question once again arises if this significance of the vascular area on the umbilical vesicle of the higher Vertebrates is not older than that other property which it has assumed in the meroblastic eggs of Sauropsida, viz. the hematopoietic processes is not yet present, and that also the liver cannot be said as yet to furnish a sufficient number of blood-corpuscles for assisting in the metabolic processes of the Primate embryo. And so the development and the increase of an extensive hematopoietic network on part of the intestinal surface (which from the very first had its significance as matrix for vasificactive mesenchyme) is quite natural. Thus, a hernia-like expansion of part of the gut would first have had a hematopoietic significance (Reptiles), would then have secondarily acquired significance in amnioidian placentaion (many mammals), and would finally have cooperated (Sauropsida) towards the transport of a reserve of yolk-oxidase, which in these cases had become accumulated against the inner surface of this network.
porty that these vessels of the area vasculosa, ramifying over
the yolk, as they did before the endoderm cells have become
yolk-laden to that extent, carry this reserve-food towards the
embryo.

That the blood-vessels of the umbilical vesicle in mammals
can attain a high calibre (Fig. 74) and that nevertheless
the enclosed blood-cells have all the appearance in sections of
not yet being freely suspended and movable I have noticed
on earlier occasions (89, 90). I have since found this con-
formed in Tarsius, Tupaja, and others. And it would certainly
not advocate against the haematopoietic significance of these
blood-vessels, that also in Teleosts Wenekebach (86) and
Ziegler (87) have shown that a solid chord may gradually
develop into a vessel with a wide lumen and with blood-cor-
puscles that originally appeared as the inner core of the
Anlage of the blood-vessel.

Having started from the consideration of the small um-
bilical vesicle of the Primates, we must now consider the case
we find in the majority of mammals where the entoderm
clothes the whole inner surface of the trophoblast at a very
early period. So it does in Ungulates, but in those it
becomes severed from the trophoblast comparatively soon
again. This takes place when the mesoblast has developed and
has become split into a somatic and a splanchnic layer. The
splanchnic layer always remains very small as compared to
the somatic in consequence of the enormous distension of the
diplotrophoblast (Fig. 133). In other mammals, as in many
Insectivores (Fig. 38), the separation between the umbilical
vesicle and the diplotrophoblast is not so rapid, and sufficient
time elapses before it comes about, so as to allow the vascular
area that has in the meantime developed on the umbilical
vesicle to become not only a centre of haematopoiesis, but
now also a vehicle for a very appreciable exchange in a
region which has been termed the omphaloidean placenta.
I have elsewhere (89, Pl. 18, fig. 32; Pl. 24, fig. 44) given a
detailed description of this for the hedgehog and also for
the shrew (94A, figs. 7—11, 51, 83).
Fig. 133. The blastocyst of Tragulus, opened, to show the small umbilical vesicle ov, the amnion ov, and the incipient allantoid cdl, dt diploblastic (after Scholza, '91). — Fig. 134. Trophoblastic proliferations tr with lacuna /d in which albuminous fluid is being absorbed (after Selenka, '87).

—Fig. 135, 136 and 137. Sections through three stages of adhesion between uterine epithelium and trophoblast in Tapajä (after Hubrecht, '99). tr trophoblast; on ectoderm; u uterine epithelium.
A strongly developed vascular network on the umbilical vesicle is also found in many Didelphia (Fig. 130), where the vascular area is undoubtedly in a high degree of nutritive significance during the short stay of the blastocyst in the uterus.

In the Ornithodelphia viviparity has been replaced by oviparity. There is no voluminous albumen layer, and the yolk-laden blastocyst is narrowly enclosed in the egg shell, a detail which renders the safe handling of the early embryonic shield exceedingly difficult. I believe this meroblastic arrangement in the Ornithodelphia to have been preceded by viviparity and by a relation of the spacious trophoblast to the formative ectoderm such as it was described and discussed above, the evolution of the allantois having come about during this viviparous phase. Perhaps we may yet regard the aberrant way in which the area vasculosa spreads over the yolk sac as a primitive character. Instead of being restricted to a circular region, the blood-vessels of Echidna invade the total surface of the umbilical vesicle (here: yolk sac) although they do not form so dense (Semon, ’94, Figs. 619 and 61s) a network as they do in the Primates.

In the Sauropsida the phenomena of yolk-increase, and specialisation in the area vasculosa have varied in different directions.

3. The Allantois.

We now come to discuss the last of the embryonic appendages or foetal membranes, which are looked upon as characteristic for Sauropsida and Mammalia, viz. the allantois. This again was naturally first known in the chick, and what was revealed about it by this venerable archetype of vertebrate embryology was applied and adapted as best could be to the other higher vertebrates.

In the didelphic and monodelphic mammals its function could not be, as in birds, an extension against the egg-shell for respiratory purposes. But even in these it is seen soon
to spread out against that portion of the blastocyst-wall, where the placenta is going to be formed. Thus, in mammals the allantois was both anatomically and physiologically the homologue of what was designated by that name in Sauropsida.

One difficulty was this, that in man no free allantois was ever detected, the (involuntary!) attempt of a German embryologist to let a chick-embryo stand for an early human foetus, only serving—once the fraud detected—to emphasize the existing difficulty. Moreover, further investigations showed that in no monkey, and not either in Tarsius spectrum was any free allantois present.

It seems to me that the confusion even now yet rampant concerning the phylogeny of the allantois would not have arisen if evolutionary principles had been more logically adhered to in the attempts to trace that phylogeny.

Observation shows that the main significance of the allantois in the developmental history of the higher vertebrates is a nutritive one, thanks to the strong vascularisation of its walls and the close contact into which these are brought either with vessels of the maternal mucosa (many Ungulates, Lemurs, and others) or with blood-spaces in the trophoblast, to which maternal blood gains admittance, thanks to the transitory arrangements furnished by the trophospongia (most other placental mammals).

Vascularisation of the diplo-trophoblast or of the chorion (as I have proposed in 1896 and 1898) to continue calling the outer embryonic envelope only in Primates) is thus the outcome of the developmental phenomena noticed in what has been called the allantois. And there is reason to believe that such mammals as have attained this aim most completely and at the earliest moment will be safer guides for teaching us how the arrangement may have come about phylogenetically than those in which the appearance of this vascularisation is for one reason or another retarded.

Now the Primates, who have no trace of omphaloidean placentation, but whose trophoblastic attachment to the
maternal mucosa in the region where the placenta will later appear is most precocious and elaborate, are decidedly in the first case.

And still there is here no free allantois at all. We must consequently try to analyse whether the method, according to which the vascularisation of the trophoblast comes about in the Primates, points in the direction of secondary changes by which the formation of a free allantois was precociously forestalled, or whether, on the contrary, the phenomena are such as to make it probable that the vascularisation is here brought about in a yet simpler, more direct, and more primitive way. In the latter case comparison with those mammals that possess a free allantois is none the less necessary, but then we may expect to meet a free allantois in its earliest incipient stages, only in the Primate stem in geological periods so far back that we can safely say that it will never actually reveal itself to us. These Primates, reaching back into the mesozoic and palæozoic epochs, had evidently better be called Proprimates, or even Protetrapods. As soon as a free allantois arose a step was taken in the direction of one of the numerous sidebranches: Sauropsida, Ornithodelphia, Monodelphia, etc.

At the same time we will then have to look out for transition forms which may serve to explain how, out of the more primitive arrangements of the Primates the free allantois of other mammals, and of the Sauropsida has come to evolve.

Now of the Primates that have no free allantois, man and the monkeys have not yet furnished a material of sufficient extension to study the very early stages of their vascular attachment in detail. For this we have to fall back upon Tarsius, which I have been able to investigate on this point ('02) in sufficient numbers to enable us to emit a constructive hypothesis with respect to what is called the "Haftstiel" or "Bauchstiel," i.e. the connective stalk by which the embryo communicates with the vascularised trophoblast, without any free allantois having preceded it.
And so we must just recapitulate what we notice in Tarsius. The very small blastocyst of about .08 mm. diameter has only just become attached to the maternal uterine epithelium. That portion of its trophoblast which serves for the attachment proliferates considerably, and enters into firm union with the correspondingly proliferating trophospongia (Hubrecht, '09, Figs. 13, 55, 56).

The blastocyst thus attached has only just passed through the phase (see p. 12) in which the trophoblast has opened out above the ectodermal shield (in a few cases I even found this process somewhat retarded: '02, Figs. 40, 50). This shield is by no means situated diametrically opposite the point of attachment (Fig. 62), but on the contrary so as to bring the hinder end of the ectodermal shield in the most immediate vicinity of the place of attachment to the maternal mucosa (Hubrecht, '07, Fig. w', w'). From this hinder end of the ectodermal shield we have seen in a former chapter (p. 38) that the so-called ventral mesoderm proliferates backwards and downwards, at the same time becoming extended into a vesicle of extra-embryonic celom. In this vesicle the direct and axial prolongation of the original starting-point of the proliferation is encountered as a raphe of tissue, a thickened ridge of only a few hundredths of a millimeter in length. This raphe is already in this very early phase the “connective stalk” by which the embryonic shield is in communication with the proliferating trophoblast that inaugurates the placenta. There is not the least reason to look upon it as an eventual precocious segregation of anything like a free allantois; it is early mesoblast, neither yet splanchnic nor somatic by which the embryo is from the very earliest connected with that portion of the surface that is going to be the placenta. There is as yet no question of its being vascularised. And it is the method by which this vascularisation is going to be brought about which will show us the way to an interpretation of the allantois, quite different from that contained in the text-books. At the same time more satisfactory, because it is an explanation of the phylogeny of
the allantois based on facts that are not only furnished by the higher but also by the lower vertebrates.

In studying the problem how the vascularisation of this early raphe or connective stalk of mesoblast is brought about we must bear in mind that in a former chapter (p. 89), we have established that the starting-point for the vascular system, as we find it outside and inside of the embryo, is an annular zone of entoderm, which, at an early stage of the development of Tarsius, lays the foundation both of the blood-vessels and of the blood.

We saw the endothelium of the heart derive from the entoderm cells in the anterior portion of the protocordal plate ('02, Fig. 73, a, b), we saw the blood-vessels on the entodermal wall both in the intra- and in the extra-embryonic vascular regions take their origin out of the entoderm ('02, Fig. 59, c—f), as this was also observed for Petromyzon by Goette ('88, '90); for Selachians, by Swaen and Rückert; for Teleostei, by Swaen et Brachet ('99); for Amphibia, by Goette ('75) and Brachet ('02, '03); for birds, by Balfour and Deighton; for mammals (sheep, Tupaje, Sorex), by Bonnot ('84, '89) and myself ('99).

Moreover, the most intense manifestations of the production of blood-vessels in Tarsius is given in the hinder region, where the annular zone of mesenchyme-producing entoderm underlies the median zone of the ventral mesoblast ('02, Fig. 59, g—k). In earlier stages it is this posterior median zone ('02, Fig. 54, g—k) which commences vascularisation of the mesodermal raphe we are here discussing, thus laying the foundation of the blood-vessels in the "connective stalk." Now in this region of the stalk we can imagine the vasifactive phenomenon to have become exceptionally active if we remember that vascularising the "stalk" means at the same time the possibility of direct vascularisation of the diplo-trophoblast. This direct vascularisation would undoubtedly constitute so great an advantage to those mammals possessed of it (see pp. 84 and 102) that we can well imagine a vascular hypertrophy arising. Also in somewhat later stages
evident proof of this has been forthcoming (’02, Fig. 75, i.; 77, h—h).

Now considering the two facts (a) that the first source of the vasactive tissue is always the entoderm, and (b) that the stalk necessarily increases in length with the growth of the embryo (yet more so in Tarsius than in monkeys and man, because in Tarsius it bends round towards the surface of the blastocyst opposite to the embryo), then we cannot wonder that active entodermal tissue is left behind in the stalk even when the rest of the intestinal wall undergoes the folding processes by which its definite tubular shape is gradually brought about. This entoderm, of which I have been able to follow even the very earliest appication (’02, Figs. 56, 57, 59--61) takes the shape of a tubular extension in the lengthening stalk. I have particularly called attention to the fact that it does not grow into the stalk actively, but that it has spun out (’02, Fig. 11, a-c, Taf. XII) passively, as we saw was the case with the lengthening of the notochord (p. 37), and similarly with the thickening of the placenta (p. 125).

It is not suggested here that, when once the connective stalk is thoroughly vascularised and the vessels carried by it have spread out on the inner surface of the placenta and have provided branching capillaries for the vascularisation of the embryonic placental villi, any further vasactive processes go on or start from the endodermic epithelial tube.

1 This expression should be understood cum grano salis. It is not the stalk that bends down, or has during its lengthening process bent down towards that opposite surface, but it is the embryonic shield that has, so to say, crept upwards (as I have elsewhere described [’02, p. 19; ’07, Figs. w1—w2]) along that surface of the blastocyst, which is opposite to the placental attachment (Figs. 62—63). The shield region is originally situated quite close to the surface of attachment; later, when the amnion folds are being formed, it is found diametrically opposite to the latter. This change in the situation of the embryo with respect to the placenta does not occur in monkeys and man, hence the connecting stalk in their case is much shorter than in Tarsius. At the same time they have for this reason their backs turned towards the placenta, Tarsius, on the contrary, its ventral surface.
which represents in this stalk what will in other mammals
and in the Sauropsida be the inner cavity of the allantois.
This epithelium is only a remnant of what in earlier
stages was a proliferating vasiformative region of the endoderm,
and which, after being yet active for some time (02, Fig. 61,
65, 66), finally lapses into the position of a residuary structure
ending blindly and being in the umbilical cord of the later
fetal stages only difficulty recognisable as a string of cells of
quite a rudimentary character.

We have now followed the connective stalk of Tarsius and
the endodermal epithelial tube within it, which we will call
allantois, in its entire development. It is, in the present
state of our knowledge, no unfair assumption to say that
the genesis of the connective stalk of man and monkeys,
with its epithelial endoderm tube, which there also is design-
nated as allantois, must correspond in its principal character-
istics with what we have just described. And we may now
emphatically affirm that the Primates have no free allantois,
but that the stalk-like connection between embryonic shield
and embryonic envelope is of so early a nature, and can be so
perfectly explained without having recourse to any endo-
dermic outgrowth, that we are justified in looking upon this
peculiar arrangement of the connective stalk of the Primates
as more primitive than the free allantois of any
other of the higher Vertebrata.

Now let us for a moment try to realise how those who take
the free allantois as the more primitive have to picture for
themselves the phylogenetic origin of it. I have elsewhere
(07, p. 58), in discussing this question, expressed myself
as follows:—‘‘We could not possibly imagine that the allan-
tois arose as an independent vesicle spontaneously growing
out from the hind gut. At what stage of phylogenesis would
this have been inaugurated? Has ever any amphibian-like
animal been struck by the happy thought that it might allow
its urinary bladder to undergo a so much earlier development,
in order that it might obtain a so much more considerable
size and such a copious vascularisation? And that in this
way that most important larval organ, the allantois, all of a sudden originated, the organ by which nutrition and respiration is brought about, and which has become reduced in man, the monkeys, and Tarsius to the connective stalk?"

I doubt whether any embryologist will be found willing to adhere to this conception.

I continue to cite from the Normentafel publication (07, p. 56):—"We may yet further point out that the very latest and very thorough going investigation of Peter (05) describes and figures certain (Taf. I, figs. 9-11; II, figs. 14-18) details which also Strahl (81, '82, '83) and Corning ('95, Figs. 4, 7, 9) had noticed before. According to these investigations, the allantois of Lacerta originates so very early as a solid Anlage in the hinder axis of the embryo (the cavity appearing only later, and yet later opening out into the gut) that the respective relations could not have been different if the allantois of Lacerta, instead of being derived from a free outgrowth of the gut, had on the contrary evolved out of an earlier and solid connective stalk in the axis of the embryo.

The relations between the allantois of Tarsius and Nycticebus are further yet illustrated by Figs. 21-3 and 221-3 of the Normentafel (07). From them we learn that what is called the allantois of Tarsius belongs to the very oldest parts of the gut, and that the caudal gut (Schwanzdarm) only originates later as a protrusion directed dorsally. If we consider how matters stand in Nycticebus 92, 148 and 289 ('07, Tabelle 2, 3, and 4), then we see that the hinder elongation of the gut, which we notice in the caudal extremity above the umbilical vesicle, might be considered to resemble remains of a connective stalk as much as anything else. The ventral portions are already strongly vascularised in Nycticebus 92, more yet in 148, and it can, for 289, just as well said that the caudal gut develops, as in Tarsius, as a dorsal protrusion from the posterior (connective stalk) portion of the gut, as that one should conform to the current view and look upon the protruding allantois as a free vesicle.
which has been later evolved. And yet it is also in Nycticebus that out of this early primordium the comparatively spacious allantois originates, which spreads against the diplostrophoblast in the well-known way. However, nothing would prevent us, neither in Nycticebus nor in Lacerta mentioned before, to look upon the particular features of the formation of their allantois as so many reminiscences of an earlier connective stalk.

I have reason to believe that many hesitate to accept my conclusions concerning these embryonic phenomena, because for them the derivation of the mammalian blastocyst out of a yolk-laden sauropsidan egg, as it has since a long series of years been taught in all manuals of embryology, seems too well established, all the more so because the Ornithodelphia appear to be such typical transitions.

It is, however, my conviction that in the Ornithodelphia—as in the Sauropsida—a profusion of yolk and ovi-parity have both arisen only after viviporous ancestral forms had preceded, in which a larval envelope (trophoblast) and its respective derivatives (diplostrophoblast, ammon) were already present. Rapid vascularisation of the trophoblast by means of umbilical vessels (as it must have existed in those ancestors) was replaced in those descendants that obtained a considerable increase of yolk by an early vascularisation of the wall of the yolk-sac (area vasculosa). Only later the palaeogenetic vascularisation of the larval envelope (trophoblast) again comes to

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1 It is certainly striking that both from Corning's figures (95) of Lacerta and from those of Bennett (§84, 96) of the sheep, it follows that also, according to these authors, the allantois appears earlier than the caudal gut; and that thus the conception of the allantois as the older, posterior, axially situated elevation of the intestine (cf. Kühnert, '02, xx. figs. 5 and 7), that has acquired great importance for the vascularisation of the equally primitive connective stalk, appears quite valid. Moreover, by this conception the phylogeny and the ontogeny of the allantois are more easily reconciled than by that other, which sees in the allantois only a later vesicular formation which protrudes ad hoc.
the front and co-operates to bring about favourable conditions for respiration."

If we try to find out whether among living mammals there are such that would yet exemplify transitional stages, as they must have existed between such ancestral forms that possessed (as do yet the Primates) a more primitive "connective stalk" and such that have come to evolve a free allantois, we must conclude that such forms are few. However, where they are found—among the Rodents and in Galeopithecus—we must recognise that we have one of the lower orders before us. In the Insectivores, where we might have expected to find traces, those that have hitherto been examined all possess a free allantois, but then they vary so considerably among themselves that we have reason to look forward hopefully to those Insectivores whose ontogeny has not yet been traced.

Among Rodents are Cavia and the different mouse genera, where the allantois offers peculiarities that might here be adduced. These cases are, however, the same in which the phenomenon of the so-called inversion of the germinal layers occurs, and one might be doubtful as to whether this latter phenomenon were not rather responsible for the peculiarities of the allantois. However, I have attempted (on pp. 74, 75) to connect this phenomenon with primitive features also noticed in the development of invertebrates. We must for the present suspend our judgment and recognise that the whole process of inversion has still much that is obscure and can on no account be explained by apparently simple mechanical explanations as Selenka has attempted (’84, p. 70). An early circumseribed attachment of the blastocyst to the maternal uterine wall was in his estimation the cause which rationally explained that the embryonic shield becomes bent upon itself (entypio). He neglected to consider that in a case of very early "entypio" as it is found in Tupaja and was fully discussed above (p. 10, Figs. 29—32), the blastocyst is during all these phases perfectly free and unattached in the much wider lumen.
EARLY ONTOGENETIC PHENOMENA IN MAMMALS.

On the other hand an embryonic shield, if curved in this way and then developing an early ventral mesoblast by proliferating ectoderm at the hinder end of the embryonic shield (cf. p. 92), would be very favourably situated for an early vascularisation of the trophoblast, all the more so if a decidua reflexa—as is also met with in many Rodents—co-operated. And so it would not seem impossible to turn the argument the other way, and to pretend that the very inversion was in some way connected with an earlier presence of a vascular "connective stalk." I do not, however, wish to press this argument, as I feel the ground is as yet too uncertain. I have only wished to call attention to those rodents and eventual insectivores where the first rudiment of the allantois is in no way an outgrowth from the hind wall of the gut, but simply a proliferation in a very early stage of vasiformative tissue at the hinder end of the embryonic shield.

I may call attention to the fact that very many years ago I have already suggested (89, p. 375) that potentially the possibility of the development of a connective stalk was present in the hedgehog, and was only perhaps retarded by the fact of the omphaloidean placenta having acquired considerable significance in early stages.

Summarising we may say that the allantois, such as we find it in Sauropsida and in many mammals and which has erroneously been looked upon as being primarily a urine-reservoir during embryonic life, is not the fit starting-point for phylegetic speculations about its evolution, but that the more subordinate position in which we find it in the Primates offers a clue for the explanation of its earliest appearance. At the same time it makes us understand so much better, that the favourable conditions under which the Primates succeed in establishing an early and very thorough vascularisation of their trophoblast, has contributed largely to their exceptional development in regard to the central nervous system.

We can safely say, as I wrote recently (07, p. 60), that the different orders of mammals represent so many attempts
by which nature, starting from simple methods of vascularisation of the external embryonic membrane, has tended to create a very wide range of adaptation to all the different possibilities of nutrition which are offered to the embryo. The uncommon diversity which we observe in the endless varieties in the arrangement of the fetal membranes of the mammals would be as good as inexplicable if we held on to the derivation of the monodelphian mammals out of yolk-laden ancestors with ornithodelphian characters. And since, after Hill's ('97) investigations, we must assume that the didelphian mammals are not descended from Ornithodelphia but from monodelphian, placental ancestors, they no longer form an imaginary transition between Ornithodelphia and Monodelphia.

Thus a more direct phylogeny of the latter should form the object of diligent research, towards which the present paper is a first attempt.

CHAPTER IV.—The part played by the Trophoblast in the Nutrition and the Attachment of the Embryo.

In Chapter II we have discussed the trophoblast as a larval layer which is of great importance in monodelphian and didelphian mammals, but which, in the Sauropsida, has diminished both in importance and in distinctness parallel to the development of oviparity, and of which we may presume that even among lower vertebrates rudiments are yet retained.

Suggestions have been thrown out on p. 18 that the original significance (protective, locomotor, or otherwise) of the ancestral larval layer may have gradually become converted into an adhesive and a nutritive one. For this I want in this chapter to adduce all the evidence available.
Fig. 138 and 139. Two sections through two successive phases of placentation of Perameles. *all* allantoic vessels, *tr* trophoblast, *ts* maternal trophospongia (after Hill, '97). — Fig. 130. Section through the placenta of the bat (after Nolf, '96). *ts* maternal trophospongia, *tr* embryonic trophoblast, yet including remains of the endothelia of maternal capillaria which in other places have disappeared by resorption. *av* allantoic vessels with embryonic bloodcorpses.
1. Didelphinae Nonplacentalia.

An important case is that of the opossum, in which we notice in Selenka's figure here copied (Fig. 134) how a considerable proliferation occurs in the trophoblast at a yet very early age, and how in this proliferation cavities or sinuses appear in which the surrounding nutritive fluids contained in the uterus lumen and partly enclosing the egg as a sort of albumen layer can penetrate. There is no doubt that this nutritive matter, when once it is surrounded by trophoblast cells, many of which undergo special proliferation, can be absorbed in an accelerated and intensified fashion, and is then utilised for the benefit of the developing embryo, most probably by its passing in some form or other inside the cavity of the umbilical vesicle.

We have not to go higher than these same Didelphinae to find that also properties of adhesiveness are characteristic for the trophoblast cells. In the genus Perameles it has been made known by J. P. Hill ('97) that far from being aplacental—as was the current opinion concerning all Didelphinae—the blastocyst of this genus possesses a very well developed adhesive surface, by which it fuses with the maternal uterine mucosa, and against which after a time allantoidean blood-vessels become applied, thus forming a full-fledged allantoidean placentation.

The trophoblast at those points of adhesion between blastocyst and maternal epithelium undergoes marked changes, as can be concluded from Hill's Figs. 138 and 139. About the nature of the fusion between maternal epithelium and trophoblast we will have something to say further on (p. 115)\(^1\); here it may suffice to state that the changes are only brought about in those trophoblast cells which partake in the placentation process, not in those which are present over the

\(^1\) I may here add that I differ from Hill in the interpretation of the later stages of the Perameles placenta, and that I am inclined to ascribe a much more considerable part to the proliferating trophoblast than he does.
remaining surface of the blastocyst, which does not adhere to
the maternal mucosa.
A second most instructive case of attachment of the
didelphian blastocyst to the maternal tissue we also owe to
Hill when he described the early stages of Dasyurus (100).
He finds the allantoideal diploctrophoblast in full retreat and
degeneration, the allantois itself hardly vascular and evidently
abdicating. The contact with the maternal nutritive matter
is brought about during the eight days of gestation by a
ring-shaped zone (ar, Fig. 190) where the omphaloideal vessels
form a vascular ring, which undoubtedly facilitates the respira-
tion of the embryo, while below this ring another ring of
peculiarly developing trophoblast constitutes still another sur-
face upon which nutritory processes are inaugurated (atr, Fig.
130). This lower ring is about one and a half the width of
the vascularised omphaloideal ring, and is also distinguished
from the latter by the much more considerable activity
of the trophoblast cells that form the outer layer of this
omphaloideal diploctrophoblast. Hill describes in detail how
the trophoblast cells surround and destroy part of the maternal
uterine epithelium, how they then reach maternal sub-
epithelial capillaries, how they envelope these and gradually
develop into a syncytium of undoubted nutritive significance
for the embryo. It is interesting to note that at birth the
embryonic proliferations are not shed (nor is any maternal
tissue), but that they are absorbed in situ, as I have described
it for the mole (contradeciduate type of placentation, p. 124).

2. Monodelphia.

Passing on to the monodelphian mammals, we find an
endless variety in the adaptation of the trophoblast to early
phenomena of adhesion, of nutrition, and of phagocytosis, the
latter leading up to an actual embedding of the blastocyst in
maternal tissue, thus ensuring an all the more extensive
possibility of mutual osmotic interchange between the
maternal and embryonic vascular systems.
Fig. 141. Longitudinal section through an early human blastocyst with annion (am) neuro- 
enteric canal, connective stalk (es) and 
alveolar tube (after Spec). 
Vascularized trophoblastic 
wall of blastocyst with villi only partially 
represented. N umbilical 
vesicle. — Fig. 142. 
Diagrammatic section 
through the blastocyst 
and early placental 
attachment of a catarrhine monkey (after 
Schonau, '00). CE uterine epithelium, E vessels 
in maternal trophospongia, JF lacunae in 
trophoblastic tissue, filled with maternal blood.
Between the extremes such as we find them on one hand in the Ungulates, where the young blastocyst undergoes an immense increase in size before the processes described in Chapter III are inaugurated, and on the other hand in certain Primates, Insectivora, and Rodentia, where the blastocyst is yet uncommonly small when these processes are started, every possible gradation has already been observed in different orders of Monodelphia. It may in general be said that in the first-named case, when there is an enormous initial increase in surface, the changes which the trophoblast undergoes and the proliferations to which some of its cells are subject are much less considerable, whereas in the second case those changes and proliferations are ever so much more intense.

I have no hesitation in saying that the new functions to which the trophoblast must have become adapted, simultaneously with the gradual development of the amphibious Prototrapod ancestors into monodelphian mammals, were—each in its special significance—of the utmost importance for the different lines along which this development could proceed. The highest degree of development has been reached by those descendants whose trophoblast exhibits a maximum of activity, and in whom we at the same time find a maximum of useful adaptations in the blastocyst, by which the latter can have the full profit of the advantages thus offered by the proliferating trophoblast. This combination is not always present. Thus we find among primitive monodelphia the hedgehog and Gymnura with a very intense proliferation of the trophoblast (Figs. 36—38), but deficient in the way in which the blastocyst responds to and utilises the facilities thus offered. On the contrary, in man and the Anthropomorphae the trophoblastic preparations resemble very closely to what the hedgehog shows us, but here the development of the blastocyst itself has followed a totally different line, and has reached a degree of early completeness and differentiation (Figs. 39, 40, 141, 143, 144), which secures to the developing embryo, during pregnancy, a combination of the most favour-
able circumstances as far as the conditions of nutrition are concerned. It cannot well be doubted that this has been very conducive to allowing the central nervous system to reach that stage of higher development and complication by which the human brain is so widely separated from that of other mammals.¹

More than once the mammalian blastocyst, when it actively attacks the maternal tissues, reminds one of a temporary internal parasite. It is clear that the more perfect the arrangements are by which the temporary parasite obtains its food from the mother-host, the more intense and perfected can be its nutrition and growth during life in utero.

a. Hedgehog (Erinaceus).—We will now select a few examples out of the numerous cases offered by all the different orders of mammals.

We begin by what may at the same time be looked upon as a primitive, as a full-fledged and a very instructive case, viz., the hedgehog, in which we find the above-said resemblance with the higher Primates, as was admitted by investigators of early human blastocysts, such as Siegenbeek van Henkelom ('08), and Peters ('09).

The blastocyst, at a period when the entoderm is not yet clearly separated from the embryonic knob (cf. p. 8), and when the cavity inside of the trophoblast is not either very spacious, is found in the lumen of the uterus at the bottom of a comparatively deep pit which has originated preparatory to pregnancy by a proliferation of the maternal tissue, which was fully described elsewhere by myself ('09, p. 312), and by Resink ('02). We find the trophoblast of the very young embryo closely applied against the maternal epithelium of the pit; then against the denuded subepithelial

¹ In connection with this I may just call in mind the curious fact that in other mammals, who, beside man, share those favourable adaptations of the blastocyst (Tarsius being the best known of them), a very unexpected increase in the volume of the central nervous system in its very earliest stages is noted. This increase has been more fully described and figured by me elsewhere ('07, p. 80, figs. 1–9).
mucosa, the maternal epithelium being eroded just where the trophoblast is in contact with it, and finally becoming embedded in this mucosa, the mouth of the pit in the maternal tissue being at the same time closed by extravasating blood and by cell proliferation. There can be no doubt that in these three early stages the action of the trophoblast cells, both towards the maternal epithelial and subepithelial tissues, is strongly corrosive (perhaps chemically) or phagocytic (cf. '39, Pl. 22a, 23, figs. 39a, 41). Nor that in the now following stages (during which the trophoblast shows a very extensive proliferation all around the whole blastocyst) it eats its way yet further into the tissues of the maternal trophospongium, and locally destroys the endothelium of fine capillaries which then shed the blood they contain into the lacunar spaces of this trophoblastic proliferation. These lacunar spaces are not of an irregular sponge-like shape. When seen in transverse section they are disposed (as cup-shaped arcades filled with maternal blood) round the internal cavity contained in the blastocyst (Figs. 35 and 37), which, as soon as the entoderm has come to line the inner surface of the trophoblast, will have become the cavity of the umbilical vesicle. Into this cavity the maternal blood which circulates in the lacune of the trophoblast can now with great facility give off such substances as may be selected by the trophoblast cells that form the separating wall between the maternal blood and the cavity of the umbilical vesicle. Between the contents of this cavity and the trophoblast cells there is only a thin layer of entoderm cells. Later the extra embryonic vascular

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1 The same trophospongium, which I introduced nineteen years ago ('39), is here taken in the sense in which I have used it since 1899 ('99, p. 460), and in which my pupil Resiak ('92) has applied it to the hedgehog. It indicates maternal cell-proliferation, especially intended for the fixation of the blastocyst, and shows a different histological evolution in different genera (Sorex, Lepus, Topaja, Tarsus, etc.). In the hedgehog I formerly called this proliferation the decidual swelling ('39, p. 311). For the hedgehog the amount of fetal trophoblast is thus seen to be yet more considerable than I dared to suppose originally, when I mistook part of the embryonic trophoblast for maternal trophospongium.
network (area vasculosa) of the umbilical vesicle will come to develop on this very surface. Conditions will thus arise that are yet more favourable for an interchange between the maternal blood, slowly circulating in the trophoblastic lacunae, and the embryonic blood-corpuscles winding their way along the paths of this area vasculosa of the hedgehog (Fig. 38). And later yet at another spot of this massive trophoblastic spongework, soaked with circulating maternal blood, the allantois of the hedgehog will find occasion to attach itself and to lay the foundation of the allantoideal placentation by which the earlier but provisional endodermal placentation (as the region of osmotic interchange above noticed is sometimes called) is succeeded. This will be further discussed in Chapter VI.

During the very considerable proliferation of the trophoblast in the hedgehog here alluded to, a further specialisation of the different parts of it becomes apparent very soon. The outer layer comes to produce very large cells with big nuclei which in a former publication (88, p. 323) I have termed deciduous trophoblast, and which seem to have a further phagocytic effect on the surrounding maternal tissues. Up to now the hedgehog’s trophoblast has retained the character of a massive spherical outer layer of the blastocyst, which is surrounded on all sides by maternal tissue (decidua capsularis), thanks to the closure of the mouth of the deep pit into which it has found its way in the earlier stages (p. 102). As development proceeds this capsularis thins out consider-
Fig. 143. Section through a very early human blastocyst imbedded in the maternal mucosa (after Peters). *tr* trophoblast, *tes* maternal trophospongia, *de* decidua capsularis, *E* Embryo. — Fig. 144. The same of Hylobates (after Solouka, '90). *tr* vascularized villi with trophoblastic outer layer, *l* lacuna, *c* extraembryonic coelom.
ably on one side, viz., the surface that is contiguous with the uterine lumen. This thinning out goes parallel to, and is largely caused by, the increase in size of the growing blastocyst. The natural consequence is, that also the trophoblastic investment of the blastocyst is simultaneously considerably flattened as far as it is covered by the decidua capsularis. The maternal investment retains its thickness only along a saucer-shape zone furthest from the original uterine lumen. It is in this part of the trophoblastic proliferation that the allantoidean placenta comes about and reaches its maximal development; a saucer- or disc-shaped placenta, which I have fully described in a former publication (89), is the final outcome.

b. Primates.—The investigations of Peters (99), Siegenbeck van Heukelom (98), Selenka (00), Straub (02, '04), Spee (96), Kollmann (92), and, quite lately, Bryce and Teacher ('08) have revealed to us that the early trophoblast of man and the anthropoid monkeys is very similar (Figs. 39, 40, 143, 144) in its general line of development to that of the hedgehog. The very early stages and the exact way in which the human blastocyst comes to be imbedded in the maternal mucosa are, however, yet insufficiently known. Moreover, as we will see in Chapter VI, the placental lacunae are more spacious and the villi partially free and floatingly suspended in the maternal blood that circulates in these trophoblastic lacunae (Figs. 141, 144).

In the catarrhine monkeys, which differ from the Anthropomorphice and from man by the absence of a decidua reflexa (capsularis), the trophoblastic proliferation is no longer equally distributed over the whole surface, but is restricted to two regions opposite to each other, and corresponding to what will later become the dorsal and the ventral placenta (Figs. 132, 112). There is thus a circular zone along which there is hardly any proliferation of the trophoblast. I hold this arrangement to be secondarily derived from the complete enclosure present in man and the anthropoids. Again in Tarsius, which I have also classed with the Primates on the
very pressing grounds which have already been discussed in preceding chapters, the proliferation of the trophoblast only takes place on a restricted portion of the spherical surface of the trophoblast, as I have demonstrated elsewhere (‘94, b, ’96, ’99). It is by this restricted portion that the blastocyst first adheres to the maternal uterine epithelium, and it is here that proliferations arise which become fused with other proliferations of the maternal trophospongia in a way analogous to what we noticed for the hedgehog. Thus a vascular spongework is brought about, against which the developing placenta comes to be attached (Figs. 147, 150). The details of the trophoblastic differentiation of Tarsius I have described in my former paper (‘99); it may here suffice to say that besides the development of lacuna and large giant-cells with very peculiar nuclei, I have noticed an interesting phenomenon in these trophoblastic and also in maternal trophospongian cells.

This phenomenon, which will have to be inquired into also in other mammals, consists in the production of red blood-corpuscles out of these cells, or rather out of the nuclear matter, which undergoes a series of most remarkable changes and transformations. Those red blood-corpuscles, devoid of a nucleus, would thus be derived from nuclear matter of certain trophoblast cells. This is certainly less astonishing, since it has been shown by me in a former paper (‘99) that the definite red blood-corpuscles of the embryo also arise by nuclear transformation in the nucleated blood-mother-cells.

The production of blood-corpuscles by the cells of a larval envelope is surely an unexpected histological phenomenon. Still, the details of differential segregation during the successive stages of cell lineage are not yet well enough known to justify any apodictic negation. The possibility is not excluded that at the first cleavage (suppose this to separate trophoblast from embryonic knob) certain potentialities of hematogenesis may be passed on to this trophoblast mother-cell.

Besides the cases of trophoblastic proliferation, preparatory
Fig. 145. Transverse section through uterus and foetus of Hynax. *m* muscularis, *c* uterine gland, *an* *av* maternal uterine artery and vein, *tv* trophoblast with blood lacunae and surrounding allantoic villi; *cla* entodermal lining of allantois; *E* embryo; *amn* amnion. — Fig. 146. The allantoidean diplotrophoblast of Nycticebus looked into after removal of the embryo and of the left half. — Fig. 147. The non-vascular diplotrophoblast of Tursius looked into after removal of the embryo. The presence of a connective stalk has led up to the formation of a discoidal placenta. — Fig. 148. Diagram of Nycticebus during the formation of allantoidean diplotrophoblast. *c* extraembryonic coelom. — Fig. 149. The same for the Primates, where the trophoblast is directly vascularised by means of the connective stalk *M*.
Fig. 150. Side view of reconstruction of blastocyst of Tarsius with placenta \( P \), connective stalk \( c \), amnion \( a \), allantois and umbilical vesicle \( uv \) (after Hubrecht, '96). — Fig. 151. Embryo of Chiromys madagascariensis yet for the greater part enveloped in its allantoidean diploidrophoblast, showing exactly the same features of placentary arrangements as other Lemures (Nycticebus, Galago). Original specimen in the British Museum. — Fig. 152. Nycticebus tardigradus. Transverse section of uterine wall (\( mew \)) with honey-combed inner surface against which the trophoblastic and vascularized embryonic villi fit. \( all \) allantoic tissue vascularizing the villi (after Hubrecht, '96).
to placentation, which have here been alluded to, we find the
same in very diverse form among insectivora, Rodentia, Carni-
vorata, and others, and it would lead us too far to give a
detailed account of all the possible variations known up to now.
We can already conclude from a comparison of the hedgehog
and certain Primates that the trophoblast's specific modifica-
tions are all the more considerable the more extensive the
surface is over which the blastocyst comes into contact with
and fixes itself in the maternal tissue. Tarsius, which had a
comparatively limited surface of attachment, retains an un-
modified trophoblast over a very considerable portion of the
growing blastocyst.

c. Rodentia and Carnivorata.—Among Rodents we similarly
notice that besides cases in which the rapidly-enlarging
blastocyst is only very partially attached to the mucosa (as is,
for example, the case along a hoof-shaped part of the surface
close to the embryonic shield in the rabbit), there are others
in which the (generally comparatively much smaller) blasto-
cysts disappear partially or wholly in the maternal tissue, and
become in the latter case enclosed in a decidua capsularis, there
being valid grounds for looking upon this latter process as
the more primitive. The mouse, Arvicola, the guinea-pig are
examples of this. Selena ('83, '84), Duval ('87), Jenkinson
('02), Disse ('06), and others have given detailed descriptions
of the very considerable modifications which the trophoblast
cells undergo after the blastocyst has become definitely lodged
in the maternal subepithelial tissue. They increase very
considerably in size, become confluent for the formation of a
syncytium, contribute towards the formation of spacious
incisions for the reception of maternal blood in the immediate
vicinity of the developing blastocyst; in short, they are of
great significance for the welfare of the young embryo. In
many Rodents the trophoblastic proliferation assumes a
different character according to the part of the surface which
we examine, F. Muller ('07), and in those where the embryo
becomes wholly surrounded by maternal tissue the tropho-
blast does not necessarily behave as it does in the hedgehog,
where its proliferation is equally strong all over the surface. On the contrary, in the mouse, in Arvicola, Cavia, and others, there is a very marked centre of proliferation, which will afterwards become the placental attachment, and which already, in the very early stages, consists of an accumulation of trophoblast cells to which Selenka has given the name of Träger (supporter) (Figs. 24—28).

The phenomena recorded in this chapter are not considered in the same light by all authors. Notably Strahl's interpretations contained in his extensive researches on this subject ('89 to '92) and in his chapter on mammalian placentation to Hertwig's Handbuch, differ considerably from my own. He is inclined to ascribe a much more considerable significance to the part which maternal tissue plays in the full-grown placenta. Many of the trophoblastic proliferations described in this chapter are by him considered to be of maternal origin. The latest author, however, who has thoroughly investigated the subject and who has published a very lucid exposition of his results, Schoenfeld ('03), adopts my views (l. c., p. 814), and differs both from Strahl and from Donnet ('97—'01). The latter, though also studying the dog, as did Schoenfeld, has probably declined to accept the possibility ("le fait pouvant paraître bizarre" Schoenfeld) of the existence of a mixed plasmodium in which both foetal and maternal elements are represented. Such a plasmodium was detected by myself in Tarsius ('99, Figs. 92—64) and Tupaja ('99, Figs. 51—54), by Schoenfeld in the dog (l. c., Pl. 24, fig. 6), and enabled the latter author to establish the real nature of the placentas of the Carnivora, towards the interpretation of which the views of Duval ('94, '95) and Strahl ('90a, '94) presented conflicting interpretations.

I may add that Schoenfeld's results according with and confirming those which I had obtained in Insectivores and Primates (and equally applicable to the rabbit, which was also personally investigated by Schoenfeld) seem to me to open up a line of research by which we will be able better to understand the placentation of those Ungulates and Lemurs,
in which, as was hinted at above, we might be tempted to deny the presence of any placenta, and which yet, for several reasons, I do not consider as primitive in respect to placenta. The so-called diffuse placenta has been looked upon by Strahl and the older authors as the necessary starting-point from which more complicated and more specialised systems of placentation should be derived. In this they were wrong. The presence of this diffuse placentation in such orders as Lemures, Cetacea, Edentata, and Ungulates, which anatomically are widely separated, as well as its absence in the placenta-facous Didelphia are facts that should render us diffident in pronouncing the diffuse arrangement to be archaic, and that should encourage us to consider whether perhaps it might not be degenerative or secondary simplified, similarly as the emphaloidean placentation of the opossum is most probably a secondary simplification of arrangements such as we find them in Perameles.

In order to develop this more fully I will go back to Schoenfeld's latest contribution to the subject. In his comparative resumption of the facts established for the rabbit and the dog he says ('03, p. 813):

"In comparing the results obtained in these two mammals considerable analogies can be detected in the genesis of their placentas. I wish to throw full light on the absolutely passive part that is played by the epithelium of the uterine and by the uterine glands. Those elements are destroyed in the rabbit and the dog; they give rise to débris which in the rabbit are resorbed by the plasmodium, but especially by maternal leucocytes and by decidual elements (glycogen cells), which in their turn degenerate and are resorbed by the fetal plasmodium; in the dog the débris of the glandular cells are resorbed either by the fetal plasmodium or by the trophoblast cells of the terminal plates.

1 So they are, according to my own experience, in Erinaceus, Tarsius, Tupaj, Sciurus, Sorex (after a temporary proliferation of the maternal epithelium, which thus offers a more extensive pabulum to the destructive trophoblast cells; cf. Hubrecht, '94a), Talpa, Galeopithecus, Vespertilio, monkeys and man."
A second point which they have in common concerns the important part that is played in both cases by the fetal plasmodium. By its presence it brings about the destruction of the epithelium and of the glands; both in the rabbit and the dog it penetrates in the connective-vascular decidual tissue and reaches the maternal vessels, which it separates from their adventitial (decidual) cells.

If, however, in these two animals, the presence of the egg in the uterine cavity can somehow provoke a reaction on the part of the connective tissue that has become decidual, which is characterised by an active proliferation of its elements, then—at the same time there exists a considerable difference between the two species with respect to the evolution of the decidual cells. In the rabbit these last named are destroyed wherever they come in contact with the fetal tissue, particularly with the plasmodium; in the dog, on the contrary, the connective tissue-cells are not destroyed; they take part in the constitution of the plasmodium, they fuse with it, and give rise to a mixed plasmodium. The connective tissue-cells of the rabbit succumb in the struggle with the invading fetal elements, whereas in the dog they resist and associate themselves with the latter. The same is the case for the endothelium of the blood-vessels; it disappears in the rabbit, it persists in the dog. . . . The placental trophoblast (Hubrecht's trophoblast) is thus differentiated into a cytotrophoblast (inner) and a plasmoditrophoblast (outer layer). The plasmoditrophoblast adheres at a given moment against the uterine epithelial synplasma and brings about the disappearance, the destruction of the latter. The plasmoditrophoblast then penetrates into the modified uterine connective (decidual) tissue, which in Hubrecht's terminology is known as the trophospongia.

In invading the trophospongia, the plasmoditrophoblast brings about the destruction of the latter in the rabbit, whereas in the dog it associates itself with it into a mixed plasmodium."

I have given this long citation because it is such a clear
resumption of the facts as they present themselves to those who are unwilling to fall in with Strahl's views, and because it allows us to group the other Insectivores and Rodents as far as known with the rabbit, whereas those carnivores, besides the dog, that have been carefully investigated up to now (cat, Putorius, fox) as well as most probably the bats (Fig. 140) all belong to the second category. Now if we remember the numerous points of comparison which the paleontologists have taught us to notice between early Carnivora (as have been the Creodonta) and early Ungulates (as were the Condylarthra), then we are induced to consider whether in respect to placentaation the arrangements which on this head are characteristic for the living representatives of both orders also merge into each other.

A very strong argument in favour of the view here advocated is furnished by Asheton's researches (706) on the placentaation of Hyrax (vide Fig. 145.) Here we have a mammal that in many respects offers archaic peculiarities, and that has been placed not far from the Rodents (Procaviidae), from elephants, and from Ungulates by different

1 Cretaceous tritubercular Creodonta are considered (vide Weber, 1904, p. 538) as having been parent forms, both of Condylarthra and of other ungulate families beside these, and I presume that it was during this process of evolution that the early placental arrangement underwent the simplification which so naturally leads from the arrangements as we know them for living Carnivora to those so-called diffuse placentals, but in reality apical, arrangements of the Ungulates in general.

Parallel phenomena of placental simplification occurred in two other great phyla of nonodelphian mammals, most probably, however, at a yet much earlier period. This led up to the Lemurine so-called diffuse placenta on the one hand, to that of Maasis (among Edentates) on the other. Cetacea, Proboscidea, Sirenia equally seem to be examples of a placentaion, which, like that of the Carnivora (resp. early Creodonta), finds itself on the road towards simplification. I presume there is great probability that in their ancestral forms all these orders more closely resembled the present Insectivora and Primates, as far as the complication of their placenta went, but that their considerable increase in size favoured extension with simplification of the placental area, as this is more evident yet in Ungulates and Lemurs.

More details are given further on p. 144.
authors, and that—as far as its early placental characters go—resembles man, the anthropomorph, and the hedgehog, types whose placenta we were willing to regard as corresponding to primitive arrangements. The fact that modern paleontology (vide Weber, ’04, p. 715) admits relationship between Hyrax and the fossil Condylartha (Monocotteridae), and even (“in einer entlegen Wurzel”) with the South American fossil Toxodontia, brings the importance of the Hyrax placentaion in general yet more to the front.

It should simultaneously be kept in view that the living Ungulates are ever so much further specialised from the Condylarths than are the living Carnivores from the Creodons. This, of course, affords an à priori probability that the Carnivores have as yet less far departed from the original arrangement than have the Ungulates.

And with this à priori conclusion before our minds we will now consider the facts of the case.

II. Other Insectivores, Ungulates, Edentata, and Lemures.—In the Insectivores, also distantly related to Creodons and Carnivores, but in many respects more primitive than the latter, we find a state of things in which the destructive faculties of the trophoblast come into play more fully yet than in the Carnivores, whereas in the Primates (Tarsius, monkeys, and man) that destructive faculty is present in quite unabated energy. If we look upon what Schoenfeld has above so well depicted for the dog as a modified, more benign process, originally derived from the first, but in which the endothelium of the maternal capillaries is spared by the destructive phagocytic trophoblast, while certain other maternal elements of the syncytium are also allowed to associate with the trophoblast without being destroyed, then we can imagine the same process yet further restricted. We would then have, for example, a denudation of the maternal mucosa, local or general, by the destruction of the maternal epithelium through the activity of the trophoblast, but the trophospongian reactions in the subepithelial maternal tissue might be reduced to a minimum, say to the
production of certain distinct cellular (decidual) elements, which might approach the denuded surface and eventually fuse with or pass through the adherent trophoblast cells. The maternal capillaries would then not either be eaten into, but also have preserved their endothelium, consequently the interaction between the maternal and the embryonic blood would be a little less direct, but this might be balanced by this somewhat less direct interaction taking place over a considerably extended surface, consequent upon the so much more considerable size of the blastocyst. Now if we consult the very recent paper by Ciro Barbieri ('06) on the placentation of Tragulus memiana we find a state of things there described which approaches closely to what was sketched above, viz. a denuded mucosa, an active trophoblast of which vascularised villi penetrate into denuded crypts, decidual maternal elements which pass from the mucosa into the trophoblast, thus forming an association of maternal and embryonic elements as in the dog, not, however, localised, but transitory.

The fact that the surface of the interchage between the Tragulus fetus and its mother has a more considerable surface extent than that in the dog and very much more than in any Insectivore should also not be lost sight of, especially when we consider that other species of Tragulus examined by Selonka ('91) and by Strahl ('05) show, again, further diminution of the destructive trophoblastic activity, because in these the maternal epithelium does not disappear in the crypts. The maternal and embryonic blood is in these cases separated by fully two epithelial strata, and the passage of decidual elements through the trophoblast was not noticed. There is, of course, not the least difficulty in passing from these latter stages on to those which we find both in Ruminants and in such Ungulates as the horse and the pig, which latter have always been looked upon as the prototype of the diffuse placentas.

Suppose this to have been the real phylogenetetic development of the arrangement of the so-called "placenta" of Ungulates—which would thus in reality be a secondarily
simplified process in which the trophoblastic activity had considerably subsided—we would then have no difficulty in understanding that similar simplification and change of function, leading to parallel results, had occurred in other orders of mammals. As such we may count certain Edentata (Manis) and the Lemurs, although our actual acquaintance with the former is yet very scanty.

We know that in Myrmecophaga and Dasypus there is a discoid micrallatoidean placenta, that in Orycteropus capensis the placenta is zonary (as yet very imperfectly known), that in the sloths it has a more cotyledonary character, whereas in Manis more recent investigations (also extended to histological detail) of Max Weber ('01) have made us acquainted with a placentation very much like that of the simplified Ungulates, but at the same time with very marked vestiges of trophoblastic proliferation (Fig. 155). Considerable maternal proliferation of the uterine mucosa, such as was also figured for Manis by Weber, suggests the probability of descent with simplification from ancestors with more complicated arrangements. But the delicate question whether this latter proliferation is, indeed, maternal or—as has been proved in similar cases in other orders—trophoblastic will first have to be solved.

At all events, for the Edentata more extended researches on all the living genera should elucidate the question whether simplification in the direction of a so-called diffuse placenta is the real explanation of many of the facts here encountered. It should be borne in mind that any direct comparison of Dasypus on one hand and Manis on the other may be as misleading as that between Lemurs and Primates, because also on palaeontological grounds the old order of Edentata is being split up into two or three independent ones, comprising, one, the Nomartha (by Max Weber ('04) again sub-divided into the separate orders of Pholidota and Tubulidentata), the other the Xenarthra.

And now, in the third place, the Lemurs. Their so-called diffuse placenta, of which I gave figures fourteen years ago
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(194 a, Figs. 31, 39, 40), is here represented by Figs. 146 and 152. It has since then also been studied by Strahl ('99), and offers different points by which it is differentiated from that of the Ungulates, as, for example the presence of capsular spaces (Fig. 152) which have been discussed by Strahl in his contribution to Hertwig's Handbuch. Chiromys (Fig. 151) has the same arrangement. We cannot for the present indicate the intermediate steps by which the simplification of a placenta of the Insectivorous or Primate type down to that of the present Lemurs was brought about and we may safely affirm that this secret has been taken into the grave by very old, probably mesozoic, Mammalia. But I hope that all the considerations we have discussed above may have sterilized any attempt to place Ungulates and Lemurs on one line, viz. that of the so-called primitive placentation. We are in no way justified to evolve the ever so much more intricate and perfectioned placental arrangements of Primates and Insectivores out of them.

3. Didelphia Placentalia.

We must now for a moment consider more closely the place which the placentiferous Didelphia have to occupy in this line of argumentation.

Without it being necessary to recapitulate the details furnished by comparative anatomy we may take it for granted that these mammals, which are now restricted to Australia and America (but in the tertiary period also spread over Europe), ought to be looked upon as an early side-branch of the mammalian stem, which has undergone very numerous adaptations to food and surroundings in its recent home, and which is characterised by peculiar points, both osteological and odontological, but more particularly by the curious physiological process of short pregnancy and very early birth that is followed by a protracted period of passive adhesive-ness to the maternal nipple, generally inside a ventral brood-pouch.

Besides scanty details about their development which we
owe to Owen and others, our knowledge of their ontogeny has recently been furthered, in the first place, by Selenka ('87) and Hill ('97). And the researches of the latter, that have already been alluded to above more than once (p. 3), have shattered the old notion that this specialised group of mammals was intermediate between the Ornithodelphia and the Monodelphia. They have furnished most weighty data from which we must conclude that—previously to the very quaint modifications which have taken place when the growth of the foetus was in part transferred from the uterus to the marsupium—these animals were more closely related to monodelphian contemporaries than they are now. Most of them have now, during the short period of pregnancy, a well-developed area vasculosa on the umbilical vesicle, which, thanks to a quite extraordinary development of the proamnion (Fig. 130), can most efficiently serve as a means of osmotic exchange between the foetal blood and the maternal, which circulates in deep folds of the uterine mucosa. At the same time most of them show an allantois which lies hidden in a recess of the umbilical vesicle, and does not in any way come to the surface or partake in nutritory exchanges.

Hill's researches ('97, 1900) on Perameles and Dasyurus, and what Caldwell ('87) found many years ago in Phascolarctos, show that this passiveness of the allantois and its ineffective and hidden situation are not the general rule. In the genus Perameles the allantois partakes in a very effective placentation, histologically corresponding to what we observe in the Monodelphia; in Phascolarctos we notice a first step in a degenerative direction, the allantois yet touching in one circular spot the outer wall of the foetal vesicle, but not entering any more into vascularised connection with the mother.

We must now more fully discuss the earliest phenomena that are described by Hill for his Perameles blastocysts, more particularly as far as the proliferation of the trophoblast is concerned.

Hill comes to the conclusion ('97)—and Strahl ('06, p. 277)
has fully accepted this—that at the spot where in Perameles
the allantois gives rise to the placental attachment the tropho-
blast—which in an early stage can be most sharply (Fig. 138)
distinguished from the maternal trophosphongian syncytium
(into which the maternal epithelium has been converted)—dis-
appears entirely in a later stage, presumably phagocyotically
destroyed by the maternal syncytium, thanks to which (Fig.
139) the maternal blood is now brought into very close con-
tact with the embryonic blood circulating in the allantoic
vessels.

Now a phenomenon of this nature which, as even Strahl
acknowledges, would be unique among the Mammals, is far
from being firmly established in Hill's paper. In many of
his figures, which have not been copied by Strahl, and which
may be said to represent transitory stages between his
figs. 149 and 150, we see the trophoblast cells of fig. 149
becoming converted into much larger cellular elements (our
Fig. 138), which, instead of being attacked and resorbed by
the maternal syncytium, penetrate into this and very freely
mix with it in a way which corresponds most closely with
what Schoenfeld has so well described for the dog. I have
no doubt that also Perameles offers a very good example of a
syncytium with a double, mixed character, in which both
maternal and fetal (trophoblastic) elements exist side by side
of each other, and by which the endothelium of the maternal
vessels is not attacked or eroded. Thus in the height of
development of the Perameles' placenta (Fig. 139) we clearly
recognise the presence of the trophoblastic elements yet in
full activity, which at other spots are so mixed up with the
maternal syncytial cells as to have given rise to the erroneous
conclusion accepted by Strahl of the trophoblast's disappear-
ance.¹ The name of semiplacenta avillosa by which Strahl
designates it will have to be dropped. The Perameles' pla-
ca may be said to be somewhat simpler—because

¹ I have to thank Mr. Hill for sending me some of his original preparations
of the placenta of Perameles in different stages, by which I have been enabled
to confirm the contradictory opinion here formulated.
thinner—form of placenta than that of the Carnivora, but at the same time to approach most closely to that type, whereas amongst the Insectivora, Sorex provides us with an example (Hubrecht, '94, Fig. 74) of a yet more extensive proliferation of the maternal uterine epithelium before the allantoidean attachment of the blastocyst comes about than even Perameles. At all events, the placentation of Perameles, characterised by so intimate a fusion between fetal and maternal elements, should never be classed amongst those forms of placenta which are either primarily primitive (as yet unknown to us) or secondarily simplified (Ungulates, Lemurs, Cetacea, etc.).

Chapter V.—Different Aspects and Details of Placentation.

1. Embryonic (Trophoblastic) and Maternal (Trophospongian) Preparatory Processes.—We have in the preceding chapter followed the mammalian blastocyst in its very varied attempts to remain attached to the wall of the maternal mucosa; and we have seen that either part of or—in some exceptional cases—all the trophoblast-cells bring about this fixation by peculiar modifications. We once find the blastocyst attached either by its surface diametrically opposite the embryonic shield (Tarsius) or by the surface contiguous to the embryonic shield (Lepus, bats, mole, Perameles among Didelphia) or by both these surfaces together (catarrhine monkeys). Or, again, the blastocyst may be fixed in a zonary or ring-like shape, and the axis of this ring may be perpendicular to and below the embryonic shield (Sorex), or it may run parallel to the shield (Carnivores), or finally a double batch of proliferating trophoblast may be present, not, as in the catarrhine monkeys, above and below the developing embryo, but right and left of it (Tupaj). Again, the blastocyst may be fully enclosed in maternal tissue, and the trophoblastic activity may then
reveal itself all round (Ectrinaceae, man, and Anthropoidea, many rodents), or the attachment of the blastocyst to the maternal mucosa may be so superficial that the trophoblastic proliferations (Fig. 134) serve other purposes than fixation (Opossum). Finally, in certain cases no trophoblastic proliferation is noticed at all (many Lemurs, Sus, Equus).

At all events, the trophoblastic fixation of the embryo is something essentially different from the fixation by means of a placenta, although in all cases the definite placenta becomes established at a spot where trophoblastic proliferation has paved the way, but by no means on all the spots where such proliferation has preceded. Some of these regions, as we have seen for the hedgehog, and as holds good for other mammals, serve the purpose in the form of the so-called omphaloideal placenta, others never come in direct contact with any vascular area of embryonic origin.

That part of the trophoblastic proliferation which corresponds with the spot where the definite placenta is going to be developed may be indicated on Duval's example as the ectoplacenta, so that in catarhine Monkeys and Tupaia there is a double ectoplacenta, whereas in the hedgehog we might distinguish a ring-shaped omphaloideal and a disc- or saucer-shaped allantoideal ectoplacenta.

Placentation, properly speaking, only becomes a fact when this ectoplacenta which is vascularised by embryonic vessels and soaked by maternal blood, circulating in vessels or in lacunar spaces, has entered into such intimate fusion and concrescence with maternal trophospongian proliferation that the two tissues can no longer be distinguished, much less be separated from each other. In this way there is much to say in favour of denying the existence of such a thing as has been called "the diffuse placenta." Maternal and embryonic tissues being in that case so perfectly free and independent from each other, that at birth they separate as easily as a finger does out of a glove, a placenta cannot possibly be said to be present. Fusion of embryonic with maternal tissues is its condition sine qua non; and so we must admit
a placenta in case of certain Didelphins (Perameles) and deny it to certain Monodelphins (Equus, Sus, Nycticebus, Galago, and others). Attempts at systematic arrangements based on placental characters having never been very successful up to now, there is no objection to this somewhat radical change in our conceptions.

And so in order to understand the final constitution of the placenta it is not sufficient to be acquainted with the very varied changes in the trophoblast which precede it, but it is also necessary to study most closely the diverse modifications and proliferations which take place in the maternal mucosa preparatory to the coalescence with distinct regions of the embryonic trophoblast. It would fall outside the scope of this paper to enter into a full and detailed description of all these varied modifications. I will only select a few examples in order to call attention to the extreme width of variation which this series of maternal preparatory arrangements for the confluence with the semi-parasitic trophoblastic tissues can undergo in different genera of mammals.

But before entering upon those details I wish to have formulated a generalisation to which a close comparison of all the facts observed in this whole field of inquiry necessarily leads us. Those facts then have established that the quintessence of the respective changes that become apparent in the maternal tissue consists in: (a) degeneration and destruction—sooner or later—of the uterine epithelium and of the uterine glands in the region of the future placenta; (b) increase of the vascular supply in that region; (c) production of tissues histologically resembling as closely as possible those which the trophoblast produces; fusion and concrescence being thus facilitated; (d) arrangements by which extravasation of blood in other directions than that of the trophoblastic lacunae is rendered difficult or impossible; (e) in certain cases development of haemato poetic properties, the blood-corpuscles thus formed being set free in the maternal blood as are those produced by haemato poetic processes in certain trophoblast cells; (f) arrangements by
which, when once the regular passage of maternal blood into the trophoblast has been firmly and safely established, all these preparatory processes as far as the mother is concerned come to a standstill, the further elaboration of the placenta being exclusively a function of the trophoblast and of the embryonic blood-vessels or vascular allantoic villi, which gradually have become imbedded in and ensheathed by the trophoblast.

In short, we may say that the mutual relations between maternal trophospongia and embryonic trophoblast are such that the maternal trophospongia leads up to the formation of a hemorrhage, and that the embryonic ectoplacenta (itself a trophoblastic proliferation), succeeds in surrounding this hemorrhage most thoroughly and in utilizing it most fruitfully. It was Duval (‘89—‘92) who first established this comparison.

a. Insectivora.—For the hedgehog we have in the preceding chapter given a full account of the phenomena accompanying the attachment of the blastocyst. We will here add a few facts concerning the maternal preparation for the placental attachment.

Already on p. 102 the local swelling was noticed into the median pit-like cavity of which the early blastocyst disappears. These swellings arise after impregnation but independently of a local stimulus caused by the blastocyst, as I have more than one preparation in which the swelling is present but does not include a blastocyst. Another detail which proves the relative independence of these swellings is the very fixed and regular appearance of a limited hemorrhage occurring at the lips of the swellings such as have been described by myself and by Resnik, and by which the final closure and the completion of the decidua reflexa is brought about. Characteristic features of the trophospongian swellings here described are yet the following. They arise in the antimesometrial half of the mucosa and have the aspect of a spherical knob with an incisure on its free surface, the direction of which is parallel to the axis of the
uterus horn. A transverse section of this longitudinal incision, the lips of which coalesce when the decidua reflexa comes to be established, and shows the aspect given in Figs. 2, 3, 37 of my paper of '89. The cavity is thus not so much a cylindrical one (as it would seem to be if only one section is examined) but a slit-like one.1

And the swelling itself is evidently one of inter glandular, non-epithelial vascular tissue of the mucosa. Numerous fine capillaries transverse the swollen region in which the uterine glands and their lumen rapidly degenerate and disappear (cf. Hubrecht, '89, figs. 37 and 38), sometimes even (i.e. fig. 39) the remains of the glands being phagocytically disposed of by the activity of the trophoblast cells. The endothelium of these maternal capillaries is generally swollen; their opening up and the extrusion of the blood-fluid into the trophoblastic lacunae after their having been eroded by the action of the trophoblastic cells has already been described above. The swelling continues to enlarge simultaneously with the enlarging blastocyst inside of it. The part of it which will contribute towards the constitution of the reflexa is the part which protrudes in the uterine lumen; it becomes thinner and its elements more stretched and fibrous as pregnancy goes on; finally it becomes, together with the trophoblast, a thin membrane, which ruptures at birth.

The remaining saucer-shaped portion of the maternal trophospongia takes part in both these successive phenomena of growth and of distension, but as it is applied against the antimesometrical wall of the mucosa it does not share the vicissitudes of the reflexa, but constitutes what has been called in human embryology the decidua serotina. It flattens

1 It will be very interesting to learn whether in man the closure of the decidua capsularis occurs about in the same way. It has as yet not been definitely established, although it seems very probable. N.B.—This footnote was already in print when, during the proof correction, I became acquainted with Bryce's and Teare's sections of a very early human blastocyst ('08) which, even more than Peters' specimen, establishes the similarity which in this respect exists between man and the hedgehog, a similarity which I have ventured to predict in an earlier publication ('89).
out more and more, the trophoblast applied against it undergoing a series of modifications, fully described by me elsewhere ('89, Pl. 26), and thus forming the bulk of the placenta, in which allantoic villi form an intricate network supporting embryonic vessels. The blood contained in the latter is thus bathed by the maternal blood circulating ever since the beginning in the intervening meshes of the trophoblastic meshwork.

The full-grown discoid placenta of the hedgehog is thus nearly exclusively a product of embryonic (trophoblastic) activity, and has gradually become evolved out of what was originally a thick spherical coating of trophoblast, closely comparable to what we notice in man (Fig. 143). When at birth it comes to be severed from the maternal mucosa and to be expelled as "afterbirth," a certain, though in no way considerable quantity of maternal tissue comes with it, the puerperium being accompanied by phenomena which have been more fully described by Strahl ('07).

After the hedgehog we will yet successively discuss of Insectivores, Sorex and Tupajæ; of Chiroptera, Vespertilio; of Carnivores, the dog; of Rodents, Lepus and Cavia; of Primates, Tarsius and man.

In Sorex the maternal trophospongian proliferation is exceptionally not in the first place subepithelial but epithelial. As I have described elsewhere ('94A), a considerable cushion of mucosal proliferation brings about the nearly cylindrical swelling against which (i.e., Figs. 8—11) the omphaloidean circulation of the embryo fits, whereas at the spot, diametrically opposite to the mesometrium, where the allantoidean placenta will later be situated, a very marked epithelial proliferation sets in. This proliferation soon becomes provided with crypts, which may on no account be confounded with the original glands, of which traces are co-existent with them. Into these crypts trophoblastic proliferations become en-sheathed (Hinbr., '94A, Figs. 74—81), and for a time maternal and embryonic proliferation are equally represented in this region until the embryonic becomes dominant,
when once the basis has been established for an intimate relation along a considerable surface between the maternal blood-corpuscles circulating in the trophoblast and the embryonic ones also present in it. In this way, again, the placenta becomes established, the allantoic villi and their trophoblastic sheaths being spun out centripetally and not centrifugally. The massive dome-shaped placenta is thus in its full-grown condition, essentially again an embryonic structure in which maternal blood circulates (Hubr., '94a, Figs. 11–15); the maternal epithelial proliferation has gradually been reduced to flat remnants in the region where the maternal blood enters the trophoblastic lacunae. Also in Sorex the placenta is expelled as afterbirth, and the regeneration of the mucosa comes about so quickly that young embryonic stages are often met with in a uterus which yet carries the unmistakable signs of the puerperium.

Tupaja is an example amongst Insectivores in which the disappearance of uterine glands in the region which will serve for the attachment of the placenta is not postponed till pregnancy has commenced and the formation of a maternal trophospongia has actually been inaugurated. Even in the virginal uterus of Tupaja that region can already be distinguished by the absence of glands. As Tupaja has a double placenta, right and left of the developing embryo, which is always situated with its head turned towards the ostium uteri and with its belly facing the mesometrical attachment of the uteruse, and as moreover Tupaja never produces neither more nor less than two young at a time (Hubrecht, '95, p. 10) these predisposed spots are situated very symmetrically in the two uterine cornua. When pregnancy commences a general swelling of the uterine tissues is noted,

1 One word may here be added concerning the mole’s placenta (see Verhout ['94] and Strahl ['90, '92]), which is not expelled as an afterbirth, but which is resorbed is loco, embryonic trophoblastic tissue serving thus as a pabulum to maternal histolytic processes; the placenta, instead of deciduate, being thus, as I have termed it, cont radeciduate, which term has been accepted by Hill ('98, p. 424) for Perameles.
Fig. 153. External aspect of the villiferous blastocyst of the pig (after Strahl, '06). — Fig. 154. The elongated early blastocyst of the sheep (after Bonnet). — Fig. 155. The tropoblast of Manis with local proliferations (after Weber).
and the two spots here alluded to become very marked. They protrude with cushion-like convexity in the uterine lumen, and are covered by a pallisade epithelium, against which the blastocyst becomes attached. The trophoblast proliferates, as was noted above (Huber, '99, PIs. 5 and 6), and as soon as the blastocyst has come to adhere to the two spots just mentioned the maternal epithelium is destroyed, and processes of mutual interlocking between the subepithelial maternal proliferation and the trophoblastic proliferation now ensue.

Here, again, as in Erinaceus and Sorex, the embryonic proliferation becomes very soon dominant when once the passage of maternal blood into trophoblastic spaces has been brought about by the aid of the maternal trophospongia, and now the allantoideal villi, ensheathed by trophoblast, continue by their farther mutual growth to considerably thicken the incipient placenta. This thickening takes place here again in a centripetal direction. It should be remarked as a very wide difference between what is observed in Tupaja and what occurs in the hedgehog and the shrew, that the two pairs (one pair for each fetus) of cushion-shaped spots of Tupaja, described above, first serve for an allantoideal placentation, but that after a certain time the vascular area on the umbilical vesicle is dislodged out of its situation, its place being then taken by the allantois, which develops the villi ensheathed by trophoblast that were above alluded to.

The two placentas right and left are of course identical. They seem to be rarely expelled as afterbirth in toto, but rather to be broken up partially, perhaps even partly to be subject to a resorption in loco, as was noticed for the mole's placenta. These data I owe to Dr. Miss M. v. Herwerden ('06), who has lately looked through a series of preparations of puerperal Tupaja uteri.

b. Chiroptera, Carnivora, Rodentia.—In the Chiroptera the placentation has been studied by Frommel ('88), v. Beneden and Julin ('84), Göhré ('92), Nolff ('95), Duval ('90), and others. Here, too, there is a considerable amount of maternal trophoscopic proliferation, which in many cases
invests as much as three-quarters of the surface (Fig. 159) of the blastocyst, but does not close up to a full decidua capsularis. The sequence and the histological detail of the phenomena are to a great extent comparable to what we saw in the hedgehog; for the details the authors above cited should be consulted.

For the Carnivora, Duval ('94, '95), Bouver ('97, '01), Schoenfeld ('03) and others have furnished us with reliable data. Here, again, the definite placenta is a structure of embryonic derivation, which partly cuts its way in the symplasmata resulting from the degeneration of the epithelium of the uterine glands. More so than in other orders of mammals certain maternal elements persist (see above, p. 108), though enclosed by the trophoblastic syncytium; it is even stated that the endothelium of the maternal capillaries is not destroyed, as is the case in so many other mammals. In this respect the arrangement in Erinaceus is more thorough.

Coming to the Rodents, Schoenfeld ('03), whose important researches have been alluded to above, has lately compared the rabbit with the dog, and comes to the conclusion that they have very much in common; the rabbit's placenta being, however, discoid, the dog's sonary. As to the histological differences, both show trophosphongial (maternal) and trophoblastic (embryonic) preparatory processes before the blastocyst becomes attached to the uterine wall; after that the maternal epithelium is destroyed in the rabbit yet more fully than in the dog, also as concerns the endothelium of the maternal capillaries, which in the rabbit decidedly disappears under the destructive agency of the trophoblast-cells or their derivatives.

In the other Rodents we have already noticed the so-called Träger as a particular trophoblastic proliferation against which, after certain further cellular intermingling with maternal trophosphongial elements the allantoideal placenta comes to be developed. The combined action of trophoblast and trophosphongia brings about spacious lacunae round the blastocyst in the earlier stages of pregnancy. In these lacunae
Fig. 153. External aspect of the villiferous blastocyst of the pig (after Strahl, '05). — Fig. 154. The elongated early blastocyst of the sheep (after Bonnet). — Fig. 155. The tropoblast of Manis with local proliferations (after Weber).
Fig. 156 and 157. Two stages in the development of the connective stalk and the umbilical vesicle of Hylloboes concolor and H. rafflesii (after Selenka, '05). The proliferating network on the umbilical vesicle is strongly developed and of haematopoietic significance. Vascularized trophoblastic villi are visible in Fig. 157. *w* connective stalk, *c* placental trophoblastic villi, *v* vascular network on the umbilical vesicle, *vit* allantoic tube, *nc* neurenteric canal.

Fig. 158. Section through the stalked discoid placenta of Cavia (after Strahl, '06).
maternal blood circulates freely; later the nutritive processes are more concentrated in the placenta.

3. Primates.—Of Primates I will just yet touch upon the placenta of Tarsius and man. The first is the result of a limited trophoblastic proliferation simultaneous with a trophospongian process by which interglandular mucosal tissue prepares a surface with which the trophoblastic proliferation very soon forms a most intricate concrescence, in which maternal blood freely circulates, and which attains to comparatively considerable thickness before embryonic vessels have yet become ensheathed between the trophoblastic proliferations (Hb., '99, Pl. 11, fig. 67). Soon after this latter process begins, further increase only occurs in this trophoblast and its enclosed embryonic vessels, the trophospongia remaining active only in the zone where the placenta will separate from the maternal tissues, this zone being in the latter half of pregnancy only a stalk (Fig. 147) through which arteries and veins have access to the placental blood-spaces.

Such a stalked condition of the placenta is also characteristic (Fig. 158) for certain Rodents (mouse), and to a certain extent for Sorex, whereas in the squirrel, the hedgehog, in man, in Galeopithecus, and others the discoid placenta may be termed sessile over its whole proximal surface. Haemato-poietic processes occurring in Tarsius during placentaion have been noticed by me elsewhere ('99, p. 368, Pl. 14).

The placenta of man has already been alluded to on p. 101. There is no doubt that in it trophoblastic elements play quite an overwhelming part, much more so than was recognised by earlier observers (Figs. 142, 143). Thanks to the investigations of von Henkelom ('88), Peters ('99), and Bryce and Teacher ('05) we have now also become acquainted with part of the trophospongian arrangements in man, and a prediction of mine ('89) that the early, then as yet unknown stages of the human placentaion, would offer close resemblance to what we find in the hedgehog has been fully confirmed by the authors alluded to.

One of the most notable differences between the placenta
of man and the hedgehog consists in the greater freedom and
greater extension of those villi in which the embryonic blood
circulates, bathed by the maternal blood in the trophoblastic
lacuna. These villi are in no way to be looked upon, as
many of the text-books yet have it, as so many ingrowths
which the chorion has sent out to penetrate into the maternal
tissue. They are in man, and also in monkeys and Tarsius,
growths not of a centrifugal but of a centripetal nature, as
we have also had occasion to describe the corresponding
structures in the hedgehog, in Sorex, Tupaja, etc. The
freedom with which they float about in the maternal blood is
another characteristic of man and the monkeys (Figs. 141, 142).
In Tarsius and in the hedgehog their arrangement is more that
of a suspension in a very delicate and at the same time most
intricate trellis-work formed by the trophoblast cells that have
come spun out into this. When the connecting trabeculae of
this trellis-work are suppressed, as we see it in the higher
Primates, the surface available for osmotic interchange is
naturally increased, and the free movements of the villi may
also be considered as an advantageous circumstance
(Fig. 144).

About the histological details of the placenta of man and
monkeys certain points are yet in dispute, and such investiga-
tors as Selenka ('00a) and Strahl ('02, '04) seem to be
willing to put to the account of maternal proliferation more
than they are justified to. An agreement will, I expect,
soon be reached, and the latest researches on these and other
orders of mammals (Bryce, '08) seem to point in the direction,
which Duval ('88) and myself ('88) have been indicating for
the last twenty years, viz. final destruction of the maternal
epithelium and circulation of the maternal blood in tropho-
blastic lacuna.

The histological details of the placenta of the catarrhine
monkeys resemble very closely those of man and the Anthro-
ponomorphae. Whether their double placenta (Fig. 132) is a
primitive or—as I hold it to be—a secondary arrangement
(derived from an ancestral decidua capsularis) must be solved
by later comparative investigations of the more primitive Platyrhines and Arctopithec. Only lately Strahl ('06a) has recognised the presence of a decidua capsularis in Myeces, a platyrhine monkey!

2. The Classificatory Value of the Placenta.

The short account of diverse placentas in different orders of mammals in this and the preceding chapter can have convinced us of the inadequacy of judging about the more or less close agreement of these different placentas by their outward shape, as was done in the second half of the last century when the distinction of zonary, diffuse, and discoid placentas was first proposed, and when at the same time the new obsolete subdivision of the Mammalia placentaria into Deciduata and Indeciduata came into use.

The discoid placenta of the mole out of which at birth allantoic villi are retracted like so many fingers out of a glove and which is further resorbed in situ; the discoid placenta of Galeopithecus in which at the outset enormous lacunae are filled with maternal blood and which at a later period is quite imbedded in the uterine wall; the discoid placenta of the rabbit and of Ursus which, when full grown, is attached to the mother by a stalk of much smaller diameter than the placenta itself; the discoid placentas of the hedgehog and of man, the latter with its loose and floating villi as against the dense trellis-work of villi and trophoblast in the former; all of them are most intricate and very variously specialised, and at the same time essentially very temporary productions of these different mammals, the discoid shape being of no value whatever when considering their respective affinities.

To allow of the arrangement of the different types of placenta in anything like phylogenetic sequence the placentation of all living mammals should first be investigated and made known, and even then it will be very questionable whether the mutual relationship can be established to its full
extent now that the number of fossil mammals, about whose placentation we will never know anything, is so very much more considerable than that of the living representatives of the Mammiferi.\(^1\) Especially the very early stages in the formation of the placenta and the mutual relation as well as the details of maternal trophospongia and embryonic trophoblast should guide us in comparing placentas and in deciding about their amount of similarity and homology.

And we will then certainly not be inclined to adopt Strahl’s latest scheme for the arrangement of the different plans of structure of the placenta\(^5\) (‘06). The amount of blood-relationship which comparative anatomy (in its other chapters than that concerning placentation) enables us to establish between the different families of the mammalian stem obliges us to reject his plan of classification.

\(^1\) The attempt lately made by Strahl (‘05) to introduce a new classification, with a corresponding novel terminology for the mammalian placentas, is decidedly premature, and as such detrimental to real progress on this line.

\(^5\) It condemns itself, where Strahl adduces (‘06, p. 275) in its favour, “Dass wir nach diesen die bisher bekannten Placentalformen gut gegen einander abgrenzen können. Wir brauchen keine Übergangsformen zu notieren ...” and further, “Ausserdem scheint ich dabei vorläufig einige seltenere, mir aus eigener Anschauung nicht bekannte Placentalformen aus, wie sie gewissermassen als Specialitäten in einzelnen Tieren vorkommen.”

This immature attempt may appear satisfactory to its author—who in a later publication (‘07, p. 19) has, however, already proposed certain corrections—but it breaks down (independently of the general considerations just brought forward) in the very primary subdivision into Half-placenta (Semi-placenta) and Full-placenta (Placenta), when we consider that, according to Strahl’s own definition, the node ought to be removed from the second, Paraemers from the first subdivision.

The principles of Strahl’s system are decidedly artificial, and may satisfy the anatomist who has to consider the human placenta in the light of comparative anatomy. But the zoologist, who considers only the phylogenetic development—so very difficult to construct—as a trustworthy guide to classification, will prefer to abide for the present, and to look forward for new data, before proposing a new classification for the so diverse phenomena of placentation.

\(^2\) As, for example, where he classes together as Mammalia chorina C. semiplacenta diffusa: Cetaceae, Suinae, Equidae, Canidae, Manis, Tapir, Hippopotamus, Lemures.
3. The Phylogeny of the Placenta.

Although it may yet be too early to venture upon the attempt of sketching a phylogeny of the placenta, different from that in which the diffuse placenta is looked upon as the starting-point such as we find it generally accepted in textbooks, still I may be allowed to bring forward certain considerations which ought to be kept sight of whenever that sketch is drawn up.

In the first place the old and catching comparison between the very early villiferous state of the human blastocyst, which in the phase of, for example, the so-called Reichert’s ovum was said to pass ontogenetically through a diffuse phase to which the discoid stage only succeeded later, ought to be definitely got rid of, as I have already suggested long ago (’89, p. 330). The fact is that this so-called villiferous stage of the human ovum does not resemble the diffuse placenta at all because (1) Reichert’s ovum is incomplete, and if complete would not have a villiferous but a sponge-like aspect, the so-called villi being actually transversely connected superficially (cf. Figs. 36—40); (2) in consequence of the presence of a decidua reflexa (capsularis) it is not freely suspended in the uterine cavity as are the blastocystas which show the so-called diffuse placentation; (3) there are no maternal crypts clothed with epithelium into which the villi fit, but these are directly bathed by maternal blood.

Once this comparison being discarded, we ought to look the question in the face whether the diffuse placentation as we find it in the horse, the pig, and the lemur, does really represent the first step on the road that finally leads to the very complicate placentorial arrangement of man and other mammals. The three examples just named are in themselves sufficient to arouse a certain a priori suspicion. We could hardly expect that the most primitive type of placentation should be retained in an animal that is so eminently specialised as the horse. Nor in an order such as the Lemurs that
is by some looked upon as closely related to monkeys and man, but of which the placentation is so utterly different. And so we will have to look out for a probable eocenogenetic explanation of these cases of so-called diffuse placentation, which were already discussed above (p. 113).

The first condition that should be fulfilled by a natural scheme of placental phylogeny is this, that the different families and orders of mammals should fit into it according to the degrees of relationship that have already been established by means of the other systems of their organisation. And in making an attempt in this direction it is natural that we should first ask what is the nature of the placentation in those mammals that may be looked upon as representing the more primitive types—the Didelphia, the Insectivores, the Rodentia, the Primates? We then find, as we have already in part discussed above, that the Didelphia furnish very conclusive evidence of their being very specialised descendants of the placental mammals, that, even in those, in which there is no more any real placentation as in the Opossum, there is yet a very active proliferation of the trophoblast, and that in those which do retain placentation, or the traces of it, this placentation can be omphaloidean (Dasyurus) or allantoidean (Perameles). Finally that in this latter case intimate fusion on a phagocytic basis comes about between embryonic and maternal tissue.¹

If we examine the two other orders of more primitive Mammalia, that have been submitted to a more extensive inquiry as to their placentation, the Insectivores and the Rodents, we are immediately struck by a fact of prominent importance as compared to what we find in the so-called higher orders, the Carnivores, Ungulates, Chiroptera, etc., viz. a most considerable amount of diversity, both in the general outlines and in the details of placentation. This is well

¹ This holds good, whatever view we may be inclined to share: J. P. Hill's that the trophoblast is destroyed by the maternal synechiae, or my own that the trophoblast is the more active part, remnants of the maternal tissue being, however, persistent, as was also noted in many carnivores.
calculated to confirm us in our judgment that these orders are more primitive, and that in them the phenomenon of placentation has not yet come to be normalized to a particular type. Still, this conclusion is only of partial value, as we will by and by see that the diversity here alluded to is in one case characterized by high specialization, in another by the appearance of peculiar characteristics, which throw light on certain general problems of placentation, whereas in others, again, types are represented which might furnish an argument to those who wish to subdivide the order of Insectivores in two or more independent orders.

At all events, we must conclude from the facts before us that the really simplest and earliest form of placentation is no more represented in any living genus of mammals, and we have to attempt to disentangle out of all the numerous data at our disposal the phylogenetic evolution which has gradually brought about the numerous forms now known to us.

When discussing the trophoblast on p. 18 of this treatise, we saw that a change of function, which must have occurred at a very early period, when this larval envelope contributed towards the retention of the blastocyst inside the genital ducts of the henceforth viviparous Protetrapod, in the first place developed adhesive qualities by which the blastocyst remained fixed to the uterine wall. We have supposed that a second parallel phenomenon was an increase in size of the larval trophoblast, precursory to the further development of the embryo proper. In consequence of this the adhesive surface would become of more considerable extent, and could be pressed more firmly against the maternal mucosa. If, at the same time, phagocytic properties became developed (which are now generally recognized to be characteristic for ever so many mammalian trophoblasts), then in addition the trophoblast layer might serve to hand over into the cavity enclosed within it material elaborated by it, which might in its turn serve towards the growth and nutrition of the embryonic cells (s. stv.). For it is sufficiently known that both in the
glandular products contained in the lumen of the uterus, in its epithelium, in its subepithelial layers, and in its blood-vessels matter is available which can be easily transformed into such nutritive material for the embryo the moment a means of transport and elaboration of this material is available. That the trophoblast does serve as such is also recognised by all observers.

Now I hold it probable that the first and strongest claim to which the blastocyst had to answer, when viviparity gradually came about, was that of fixation. We will find a proof of that by and by when we come to discuss the phenomena in Lemures. The most natural arrangement for the attachment of a growing blastocyst that is passing outwards through a cylindrical uterus was the zonary attachment which would be the simplest possibility by which the two surfaces might adhere together. This has been retained in the Carnivora and some other mammals (Elephas, etc.), and as such seems to have a primary significance. When firm attachment could be combined with phagocytosis it would be a safer arrangement than phagocytical absorption of elements contained in the uterus lumen without firm attachment; in this latter case expulsion of the growing blastocyst might be a dangerous possibility. And so the firm zonary attachment, combined with destruction and digestion of the maternal uterine epithelium, might be the next step which we also find realised in the Carnivora, to which then and there is added further extension of the phagocytosis by the diverse processes which have been so carefully analysed and so lucidly described by Bonnet ('02). The maternal tissue—whether we accept Stehli's, Bonnet's, or Schoonfeld's views concerning the maternal epithelium and the trophoblast—is universally recognised to undergo catalytic changes, and to pass into a symplasma, towards the composition of which superficial epithelium, proliferated epithelium of crypts and glands, subepithelial connective tissue, lacoocytes, and blood have all largely contributed. This symplasma, thus prepared, is thereby made fit for the phagocytic absorption by the
trophoblast cells, who again pass the food thus obtained either to the embryonic blood-corpuscles or into the cavities inside the trophoblast, be this umbilical sac or extra-embryonic culom.

The details of these physiological and complicated nutritive processes are still out of our grasp, and nevertheless they have undoubtedly very important significance by the side of more simple osmotic phenomena. Bonnet recognizes (\textit{ibid}, p. 489) that the actual feeding of the trophoblast cells on albuminiferous syrnplasmata, on fat, and on the morphotic substances of the maternal blood, as it takes place under our eyes, considerably facilitates our understanding how the proteids which diffuse with so much difficulty pass from the mother into the embryo. Similarly the supply of iron in the mammals which have no ferruginous yolk to fall back upon, and which nevertheless must take place in utero, becomes explicable in this manner.

I feel confident that these researches of Bonnet and others on the nutritive resources of the Carnivores are of the highest importance for a full understanding of the placentation process, of which the starting-point would then be the combination of adhesive and of phagocytic properties in the trophoblast cells. The same investigator, Bonnet, has in an anterior publication made us acquainted with the presence in the sheep's uterus of a substance which he has named "uterine milk."

It is in reality the product of catalytic processes of the same sort as those that were described above, and it differs from the material produced in the Carnivores only in this respect, that it has been set free into the uterus lumen. A transition stage between the two is, perhaps, that case of the Tragulus embryo (another Ungulate already cited on p. 118), in which formed elements were seen to pass out of the maternal connective tissue, through a layer of trophoblast into the embryonic tissues. At all events, there is an a priori probability that the arrangement in which organic detritus in the uterine lumen is being absorbed by the embryonic trophoblast is a later development from that in
which the primarily adhesive trophoblast began to combine phagocytosis with mere adhesiveness. As the total surface of the blastocyst increased, and as the adhesion became localised in the maternal carunculi and embryonic cotyledons, the remaining surface of the blastocyst developed such properties that the uterine milk was easily absorbed by its trophoblastic outer layer. Such a process seems to have been further again specialised in the pig and the Lemurs, in which certain sac-like receptacles (Figs. 152 and 153) serve for the reception of foodstuffs prepared by the maternal mucosa, and hoarded by the embryo in these pouches. But I continue to maintain that these were not primitive arrangements, but derived from those where, as in Carnivores, the foodstuffs were sought for yet inside the uterine mucosa (and not in the uterine lumen) by the proliferating phagocytic trophoblast.

Besides by the direct phagocytic process, nourishment and then especially oxygen is yet furnished to the embryonic blood-vessels by the osmotic processes which take place between the maternal blood and the embryonic; and we may perhaps say that there has been a certain amount of competition between the two systems as to which of them should be foremost in providing for the requirements of the internal parasite, the embryo. So differentiation and adaptation has run along very different lines, now specialising in one, now in the other of these two directions, but in some combining the effects of both. It is probable that in these latter the beneficial effect obtained was the maximum, and that this has at the same time revealed itself by higher development of the embryo in general. And if we try to class the mammals according to this principle I think we may arrive at making a very fair bid for a natural arrangement both as far as placental and other anatomical characters are concerned.

The early Carnivores have been united by paleontologists in the fossil order of Creodonts, relationships between these and the early Ungulates being recognised. Many recent Insectivores also reveal by different points their more primi-
tive character. And, as was hinted at above (pp. 108, 126), it is among Carnivores that we find, both as to fixation of the blastocyst and histological details of the placenta, what may be looked upon as yet undifferentiated arrangements. The phagocytic phenomena are in full swing. Osmotic exchanges between maternal and embryonic blood are possible on an extensive scale, both on the omphaloidean and on the allantoidean plan.

Now among Insectivores many placentas, which, as we know (see p. 132), are here so very varied, also come under this definition. The omphaloidean placenta of Erinaceus follows its course, and plays for some time an important part in bringing about osmotic exchanges. After some time it is stopped by removal of the area vasculosa that becomes folded up, and it is replaced by the allantoidean placenta. In the very earliest stages of the blastocyst phagocytosis has taken place on a most extensive scale and with undeniable intensity, eroding the maternal capillaria and digesting glandular and uterine epithelium in a manner which only finds its parallel among monkeys and man.

Still it remains an open question whether the hedgehog’s placenta should be cited amongst the more primitive types. In the mole we find certain characteristics which in another direction seems to be primitive. Vermhout’s investigation (‘94) has brought to light a very extensive phagocytosis in the early stages of placentaion. At the same time we notice in the mole what I have termed the contra-deciduate type (vide Hill, ’97, p. 424) of placentaion. In the mole the act of parturition has a very peculiar character by itself through the fact that the embryo is expelled out of the mother’s womb only enveloped in the allantois with the fully extracted villi forming a woolly covering to that fetal involucrum. The trophoblast and all its proliferations, which have carried on such active phagocytosis, remains adherent to the uterine mucosa, and is neither wholly nor partially shed but gradually resorbed in situ by the mother’s tissues, causing the external aspect of the uterus during the puerperium to have a similar
aspect as during pregnancy, only in the inverted sequence; the uteri with the smallest swelling being the furthest puerperal stages.

In this case the properties of fixation and phagocytosis characteristic for the mammalian trophoblast have been able to come into play on an extensive scale without occasioning any hemorrhage in the mother, even leaving a certain pabulum behind of embryonic origin, the digestion of which may rather be of some advantage to the mother than the contrary. There is some reason to believe this arrangement in which there is no question yet of an afterbirth, but rather the contrary (hence the name of contra-decidua) should be looked upon as a primitive arrangement. The more so as a similar phenomenon has been noticed by Hill in Perameles where the allantois, however, is not expelled together with the embryo as we saw was the case in the mole, but where in addition to the trophoblast the allantois also appears to be absorbed by the maternal tissue, thanks to the activity of migratory leucocytes described and figured by Hill. Having advocated ('95 p. p. 118) the archaic significance of the arrangement in the mole, already before Hill found a similar phenomenon in a didelphian mammal, I must naturally emphasise my original contention after Hill’s discovery in a mammalian order which, however much specialised it may have become, certainly contains representatives of an old stock. Since then the peculiar contra-deciduate characters have been noted for Tapajá (to a limited extent at least) by Dr. M. van Herwerden ('06).

In these early types we thus see that maternal phagocytosis in the placental regions keeps pace with embryonic phagocytosis. Nutrition by osmotic exchange has undergone a very marked reduction in the Didelphia as was discussed above (pp. 100, 115), the genera Perameles, Phascolarctos, and to some extent Dasyurus being perhaps yet the last in which the earlier arrangements have been preserved. In all the others the allantois has in a greater or lesser degree been reduced both in size and in amount of extension against the trophoblast.
The intra-uterine nutrition is no longer accompanied—as in the more primitive Perameles—by fixation of the blastocyst against the uterine wall, and there is only a very loose connection between vascular maternal folds of the mucosa and the vascularised surface of the umbilical vesicle. Moreover, this connection is only of a very short duration, parturition taking place after eight to fourteen days, and the peculiar specialised nutrition in the marsupium coming into play immediately after. Still the early blastocyst of the Opossum shows the spongous proliferation of the trophoblast (Fig. 134), of which we may certainly say that it can contribute towards the absorption and elaboration of fluid material contained in the uterine lumen. It does not reveal marked propensities towards direct phagocytical action. Selenka found its lacunae (187) filled with liquid which it most probably derived from the contents of the uterine glands that had found their way into the uterine lumen.

Summarising what we find in the Didelphia we may say: (1) in the more primitive forms: a well-fixed blastocyst which is united by a proliferating trophoblast to the syncytium that arose out of the maternal uterine epithelium. The blastocyst is nourished by the combined results of phagocytosis and of osmotic exchange between on the one hand an allantoic and an omphaloideal vascular network with, on the other hand, a maternal lacunar circulation in a syncytium of mixed derivation, the embryonic parts of which are resorbed by the maternal after parturition; (2) in the secondarily specialised forms: a blastocyst very loosely held between numerous and intricate maternal folds with which it enters into osmotic exchanges by means of an omphaloideal circulation on the faintly convex surface above the embryo without any villi corresponding to the maternal folds. Moreover, an early trophoblastic proliferation in which probably absorption of fluid material, taken from the uterine lumen, is of more importance than eventually additional phagocytotic phenomena.

In all existent genera of Didelphia the early ontogenetic
events and the different phases in the mutual relations of blastocyst and mucosa ought to be fully known in order to furnish us with all the data that can be brought to bear upon this important question. And it is to be fervently hoped that those genera that are very rapidly diminishing in number in their native land, some of them even on the verge of disappearance, may yet be fully investigated before they have been exterminated, and have thereby become as mute on this important point as are their fossil predecessors.

Turning back to the Monodelphus we notice that among the Insectivores another genus than the mole, above discussed, furnishes particular points of comparison with certain Didelphus. The genus I here allude to is Sorex, in which a localised strong proliferation of the uterine epithelium has been described by me (94a, Figs. 74 and 80) into which allantoidean villi fit, which in that early stage very much resemble those that have been figured by Hill (98, Pl. 33, figs. 28, 29) for Perameles. If the pregnancy of Sorex were to be brought to an early close in this very stage by a series of new adaptations as have occurred in the Didelphus the resemblance on general points between Sorex and Perameles would be certainly remarkable. The maternal epithelial proliferation of Sorex, however, does not give rise to a syncytiunz as in Perameles, but to a cellular agglomeration in which crypts appear, each of which harbours a trophoblastic villus with its core of vascularised allantoidean tissue.

The parallel cases which we have been able to institute between Didelphus on the one hand, certain Insectivores and Carnivores on the other hand, seem to encourage us when we pretend that a similar stage must have been the average degree of complication to which the earliest mammalian placentation corresponded, and that the so-called diffuse placentation which up to now has been looked upon as representing an early starting-point has wrongly usurped this place, as we will by-and-by demonstrate when we will advocate that the latter arrangement is an example of a
much specialised lateral offshoot in the line of development. To our picture of the eventual earliest arrangement we must yet add that the blastocyst itself must in that ancestral form have been characterised—on account of what we have so fully discussed in Chapter IV—by a very early local or total vascularisation of the trophoblast by means of a connective stalk which formed an ab initio connection between the embryonic shield and the trophoblast. No free allantois can have been present in the very earliest cases; this must have made its appearance only gradually, probably in consequence of the vascularisation of the connective stalk having been temporarily overtaken by the vascularisation in the anterior four-fifths of the annular zone of entoderm, where blood and vascular tissue was being formed out of the latter (cf. p. 34). The vascular area on the umbilical vesicles was thus brought at an early period in close contiguity with the vascular maternal mucosa and an early omphaloidean placenta may have been called forth out of what had primarily been a surface of haemato poetic significance in the ancestors.

At the same time the direct chorionic placenta came to be retarded. Later, however, overtaking the precocious omphaloidean placenta, again it supplanted the latter in the later phases of development. This gave rise to the first appearance of a free allantois.

That the partial vascularisation of the trophoblast by means of a primitive connective stalk is not merely a hypothetical possibility is proved by Tarsius, which corresponds to a transition stage as here imagined, its blastocyst being moreover situated in the uterine lumen.

The great advance which has been made by the other Primates (monkeys and man) is that in these the blastocyst becomes attached to the uterus by a more considerable surface, and that the resulting placenta—be it single or double—is not stalked as in Tarsius but sessile, whereas in the Anthropomorphæ and in man the very considerable difference from Tarsius is this, that the blastocyst quite disappears within the maternal tissue, and is by the formation of a
decidua reflexa quite removed out of the uterine lumen (Fig. 149). This phenomenon of encapsulation inside the mucosa has appeared independently in more than one order of mammals, and can be observed in all its transition stages in different genera [Vespertilio [Fig. 150], Rodents, etc.).

The question may be raised—but cannot yet be solved for the present—whether perhaps the placentation of the catarhine monkeys has not arisen by secondary modification out of one in which a distinct decidua reflexa existed. Different details seem to point in this direction; the investigation of the placentation of more genera of monkeys than have up to the present been subjected to research on this point is very desirable.

The removal of the developing blastocyst out of the uterine lumen and its total enclosure by a decidua capsularis is a phenomenon of all the more primary importance, as by it the phenomena of osmotic and of phagocytotic nutrition can be over so much more intensified. It is clear that the removal out of the uterine lumen may mean a most profuse extravasation of blood all round the blastocyst, combined with constant renewal and circulation of this maternal blood, which is absolutely impossible as long as the blastocyst remains situated in the lumen of the uterus. Man and the man-apes, different genera of Rodents, as well as the hedgehog (Erinaceus) and Gymnura have realised this arrangement, of which later investigations may yet bring to light new examples. We are certainly justified to say that this phenomenon of the formation of a decidua capsularis must have made its first appearance already in a very early moment of the phylogeny of the placental arrangements.

Diametrically opposed to the intensification of both phagocytotic and osmotic processes, as it is presented to us wherever a decidua capsularis has come to be developed, is another phenomenon which, by the very nature of it, excludes the combination of it with encapsulation, viz. the early increase in size of the blastocyst, by which its total surface, in comparison to that of the actual embryonic surface, becomes ever
so much more extensive, and offers more copious opportunities for the absorption of nutritive material either out of the uterine lumen or, more indirectly, out of the vascularised mucosal surface, be this provided with an epithelium or deprived of it.

This state of things we find realised in Ungulata, in Cetacea, and in certain Edentates. Both for the sheep and the pig Bonnet and Keibel, and earlier authors before them, have made us acquainted with a most considerable growth in size of the sometimes even tubular blastocyst (Figs. 153 and 154), on the surface of which the embryonic shield only occupies a hardly visible space (total length of blastocyst 21 cm., breadth 1½ mm.; length of corresponding embryonic shield 1 mm.). This considerable surface increase, which is also found in the Equidae and other Ungulates which have hitherto been ranked as representatives of diffuse and polycotyledonary placentation, is thus seen to go parallel to a certain extent to a not inconsiderable increase in the size of the adult animal, with a corresponding increase in the size of the, generally bicorneate, uterus.

The conditions in which we find the free allantois in these Ungulata show that the considerable enlargement of the blastocyst has only commenced after the free allantois had already been evolved out of the earlier arrangements. Before the allantois has spread out against the inner surface of the diploctrophoblast, the outer trophoblastic investment has full occasion to be very active in elaborating and transporting the detritus in the uterine lumen, which has been termed "uterine milk," inside the cavity of the blastocyst. After the allantoic vascularisation of the diploctrophoblast has come about the latter becomes applied against the maternal surface, where at numerous, but independent, spots (so-called caruncles), the tissue has been prepared by the formation of so-called cotyledons, into which fit groups of allantoic villi. In other Ungulates no cotyledons are present, but the maternal surface is thrown into a dense network of folds and crypts, into which corresponding folds or villi of the blasto-
cyst fit. In the case of the polycotyledonary placentation, osmotic and phagocytic absorption is yet combined, in that of the diffuse placentation of the horse it would seem as if the osmotic interchange between the maternal and embryonic blood (which takes place all over the extensive surface where the villi interlock in the crypts) has by far superseded phagocytic nutrition. There is an intact double epithelial layer, one maternal, one trophoblastic, that everywhere separates the two blood-fluids; nevertheless the considerable surface over which the two circulatory systems are in such very close proximity seems to make up for what is lost in exiguity of the separating membranes. And so the placentary arrangements, as we find them in the horse, appear to me as an extreme state of specialisation of what in Carnivores, some Insectivores, and in Didelphus was a more primitive but a more complicated arrangement. The fixation of the blastocyst by means of adhesive and phagocytotic properties of the trophoblast cells seems to have been reduced to a minimum; the phagocytosis, which was certainly more active in the Artiodactyla, where also the fixation by means of the cotyledons was somewhat more firm, is in no way prominent in the horse, but the possibility of osmotic processes between large surfaces of maternal and foetal vascularised tissue has reached a higher degree of development.

The polycotyledonary arrangement has thus retained more hereditary points in common with the primitive placentation described above, than the diffuse. Tragulus meminna has already been cited (p. 113) in support of this. Also the less considerable degree of specialisation, which we find in the skeletal parts of the limbs, would correspond with the smaller amount of placental specialisation. The sequence in placental complication would thus have to be reversed; it is not the polycotyledonary arrangement that represents an advance as compared to the diffuse, but it is the diffuse that should be looked upon as the last rung of a ladder of simplification which the placental processes have undergone in the Ungulates, starting from the arrangements above alluded to, which,
though more complicated, were yet more archaic. The primitive earliest stages are unknown to us, and probably meant to remain unknown for ever, as so many transition forms that must have existed in the palaeozoic epoch.

The "diffuse" placentation of the Lemurs should be looked upon as a second case of a simplified arrangement leading to a very similar result, as in the horse, but not necessarily, though not impossibly, along the same phylogenetic track. There is no reason why this simplification should not have arisen more than once; also in the Edentata, Manis, as has already been expressed above, gives another example of it.

That in Lemurs the evolution of the diffuse placenta has been different can be in part made probable by the fact of a very curious early phenomenon noticed in Nycticebus. We have already described in Insectivores, Rodents, and Carnivores the very early and very effective adhesion of the youngest blastocysts to the uterine wall, and the phenomena of placentation consequent upon this. Nycticebus has fecal investments which, in the latter half of the period of pregnancy, can, together with the enclosed fetus, be quite easily washed out of the maternal crypts, the trophoblastic villi not being in any way confluent with maternal tissue. There are two intact layers of epithelium between the maternal and the embryonic blood (Figs. 146 and 152). We would thus expect that the early blastocyst cannot either boast of any strong adhesion to the uterine wall, but would agree with the horse, pig (Fig. 153), sheep (Fig. 154), etc. Nycticebus, however, wholly differs from these latter by the fact that in those early stages, when the blastocyst has a diameter of 5–11 mm., it is very firmly kept in its place in the uterine horn, in which we find it, by another peculiarity. The horn (and the blastocyst inside of it) have, namely, undergone a quite unusual degree of distension; the median portion of the genital ducts, however, is not in any way comprehended in this enlargement. Consequently the blastocyst is kept in its place very effectually, although there is no surface adhesion whatever, and
although there are two intact epithelial surfaces in contact with each other, the uterine and the trophoblastic, which do not show as yet any wrinkling or any villi. Considering the presence of uterine glands, one might expect the surfaces to be lubricated by the secretion of these glands, and expulsion of the early blastocyst would undoubtedly follow had the swelling and extension not become limited to the horn only, in which, as I have described elsewhere (07, p. 35), it is consequently generally very difficult to find the exact situation of the embryonic shield.

The difference in these early arrangements authorises us to keep the diffuse placentation of Lemurs apart from that of Ungulates. It was not necessarily obtained along the same hereditary line of development.

We have now sufficiently discussed the maximum degree of simplification which the placentary phenomena undergo in Ungulates, Lemurs, and Edentates, to which attention had also already been called in the preceding chapter. In all of them an osmotic exchange between the contents of the capillary (not lacunar) circulation in the maternal mucosa and the fetal capillaries in the trophoblastic villi is obtained. The total surface over which this osmotic interchange takes place has become very considerable, and at the same time any concrescence between trophoblast and uterine epithelium has been quite given up, two intact epithelial layers separating the maternal from the embryonic blood.

We must now discuss some of the principal deviations from the central plan of placentation from which we started in opposite directions, viz. in such as bring about, instead of an extension of surface for the osmotic exchanges an intensification of the process over a restricted surface. This may, of course, be expected in those mammals which have not by an increase in the size of the adult (as in many Ungulates), so to say, created favourable conditions for surface extension in the placentary processes. And, indeed, it is in Rodents, but especially in Insectivores and Primates, that we find intensified conditions as are here alluded to.
It has been noticed above (p. 163) that for such intensification of the osmotic exchanges the removal of the blastocyst out of the uterine lumen and its total inclusion within the mucosa by the formation of a so-called decidua reflexa or capsularis is very essential. The two most striking, and, at the same time, most perfect cases of this are presented (as was also already mentioned) by the hedgehog and by man. Still the two cases are in many respects different, but resemble in this respect that, whereas our primitive placental cases show a combination of phagocytosis and osmosis during a comparatively considerable portion of the period of pregnancy, in the hedgehog and in man the phagocytosis is of great intensity in the beginning, but is followed by a second period in which the osmotic interchange is considerably perfected. This latter perfection is noticeable along two lines. First, the tissue separating the maternal and the embryonic blood is most considerably reduced, and while we yet noticed two epithelial and two endothelial layers between maternal and embryonic blood in many Ungulates, we see that in Insectivores and Primates it may become reduced to a simple membrane of maximal tenuity. We need not insist upon the very great difference this makes for rendering osmotic interchange ever so much more effective, and we are then no doubt justified in saying that the Primates and certain Insectivores represent a step in advance on our archaic type, just as well as the Ungulates represented a retrograde step.

A second improvement by which intensification of the osmotic processes is being brought about, concerns the extent to which embryonic vascular surface is brought in contact with maternal blood. Here, too, we see that man and to a somewhat lesser extent the monkeys undoubtedly represent a maximum of intensification of the osmotic process. The allantoic villi, exceedingly numerous and finely branched and covered only by the excessively thin layer of tissue above alluded to, present an all the more considerable surface for the osmotic processes because they are freely suspended in the maternal
blood and thus bathed on all sides; whereas, for example, in
Tarsius, in the hogs hog, and in other insectivores, although
there is only a very thin membrane separating maternal and
fetal blood, still the section shows a very fine sponge-work
of the finest membranous structures between which the allan
toic villi are densely distributed. As they are, however, not
freely suspended, but stretched between and supported by
the meshwork here alluded to, the total surface available for
osmotic interchange must necessarily be relatively less.

It would seem as if, in the human placenta, there is still
left a certain margin for phagocytyotic processes, brought
about by the so-called “syncytial cells,” which are present
here and there on the villi, and are nothing but remnants of
a plasmodiotrophoblast (cf. Bryce and Teacher, ’08). An
important fact which was mentioned on p. 111 is the discovery
by Assheton (’06) of the early placentary stages in a primitive
Ungulate as is Hyrax. It adds considerably to the probability
that the simplification which was above suggested as having
occurred in the phylogeny of the Ungulate placenta is indeed,
the actual explanation of the phenomena such as we notice
them.

4. Summary of Chapters IV and V.

In concluding this and the preceding chapter I wish to
emphasise that we have established an undeniable activity in
the trophoblast of monodelphian and of didelphian mammals
preceding and accompanying placentation, and that we have
at the same time shown that those orders where such activity
was insignificant or absent (Lemurs, certain Edentates and
many Ungulates) must in this respect be looked upon as
having been secondarily modified by various circumstances.
Direct indications of this retrograde process are not wanting.

This being the case and the well-known and apparently
natural starting-point which the so-called diffuse placenta
offered us for establishing the phylogeny of placentation
having thus broken down, we have attempted to establish
that phylogeny—about which palaeontology will never be able to instruct us—on quite another basis.

This basis is far from being complete. Too little is yet known of the histological detail of the placentaion process in the greater majority of mammals, and even when we will be fully acquainted with all those details as far as the recent mammals are concerned, even then we will perceive that the clue to many questions of phylogenetic importance lies amongst the extinct genera.

We may, however, say, that if on the one hand placentaion details will help us to establish natural affinities in the grouping of the mammals, on the other hand no phylogeny of the placenta should be considered admissible if it would lead to any artificial grouping of naturally allied or naturally diverse mammals such as was discussed on p. 139.

Viviparity and placentaion have gone hand in hand with the development of allantois and amnion. And only after the two latter had appeared in the early viviparous tetrapods of the palaeozoic period did certain side lines of development diverge from that which led up to modern Mono- and Didelphia.

In those side lines oviparity again came to the front, and on them we meet the parent forms of the Ornithodelphina, the Reptilia, and the birds.

Chapter VI.—Reflections on the Phylogeny and the Systematic Arrangement of Vertebrates.

We have in the preceding chapters attempted to establish that certain fundamental conceptions concerning the embryonic envelopes and the placentaion of the higher vertebrates are much in want of a renewed critical analysis. We have some time ago ('02, '05) come to a similar conclusion with respect to gastrulation in vertebrates.1

1 Keibel ('05) and Brenchet ('05) have expressed their conviction that these
I will in this chapter attempt to draw the conclusions concerning the systematic arrangement of the vertebrates as such, to which due consideration of all the facts here considered must lead us, giving at the end a short sketch, partly already contained in earlier publications ('02, '05), of what may be considered as the most probable hypothetical invertebrate ancestors to which all these views point.

We have then first to take into account that the primary subdivision of the vertebrates is that into the two great groups sharply defined against each other as the Amniota (Mammalia, Sauropsida) and the Anamnia (Ichthyopsida). It has long been known that parallel and identical to this subdivision another is possible into Allantoidea and Anallantoidea, and that the fact of the existence of this double character increased our faith in the significance of this primary subdivision of the vertebrates.

However, we have since seen that it would be difficult to pretend that the Primates are true Allantoidea, a free allantois not being present in this order. And on the other hand we have seen that of even more importance than either amnion or allantois is the outer embryonic layer, the trophoblast; in itself a larval envelope of very great antiquity.

The trophoblast, which is most marked in mammals, is ever so much more hidden in Sauropsida, and its presence can here only be recognised by a careful comparison of all the variations which we notice in its relations to the embryonic epiblast respectively in Mono-, Di-, and Ornithodelphia.

Clearer, however, than in most Sauropsida are certain reminiscences of the trophoblast in many Amphibia, Dipnoi, and Teleostomi. They consist in the presence, during early larval life, of an outer, generally somewhat more strongly pigmented, and also generally flattened layer of cells, which disappear when development proceeds, and which correspond, as far as modified views seem to them to be more acceptable than the current opinions on the vertebrate gastrulation. This agreement is all the more welcome as Keibel, by his comprehensive article in the "Ergebnisse der Anat. und Entw. gesch.," vol. 19, has an authoritative voice in the matter.
their situation in relation to the rest of the embryo is concerned, with the trophoblast of mammals. In the Amphibia, Dipnoi, and Teleostomi, however, the layer does not in any way participate in the formation of an amnion or of a fetal envelope, nor does it remain at a distance from the developing embryo, protecting it in some way or other. Its significance as a transitory outer membrane is, however, undeniable, even when its participation in the formation of certain superficial, mostly larval, structures is remembered. And we are forced to consider whether we should not, for that reason, be justified in saying that, together with mammals and Sauropsida, these vertebrates have a common descent from ancestors in which a transitory larval envelope played a prominent part. We yet notice a similar occurrence in different classes of Vermes (Nemertea, Gephyrea) where certain groups have definite larval layers which are absent in others.

In that case a second consideration is this: do the cartilaginous fishes stand apart in that respect, and what about the Cyclostomes and Amphioxus?

About the absence in the latter genus of anything like an outer larval layer there can be no reasonable doubt after the numerous investigations concerning its early development which we owe to such a considerable number of trained embryologists. As to the sharks and rays, we can be equally positive that none of those who have studied their embryology up to now have cited any fact which would support the notion that anything like the "Dachsicht" of Teleostomes, Dipnoans, or Amphibia is present in any of them. We have, of course, the example of the Sauropsida to make us rather careful concerning cases in which there is an apparent absence of a trophoblastic layer. But then in this case the difference on many other points of comparative anatomy as between the cartilaginous fishes and the higher vertebrates is so considerable (as has already been partly pointed out above on p. 82) that it seems advisable to leave it open that the Selachians may very well have descended from ancestors without an outer larval layer.
For Cyclostomes the same reasoning holds good, although there are certain indications that in this group we have before us animals in which degeneration and regression with considerable modification has gone on to such an extent that it would perhaps not be impossible to link them on later to higher vertebrate ancestral forms as yet unknown.

And so the question presents itself:—Are we justified in displacing the dividing line which in vertebrate classification is almost generally adhered to, and which separates Ichthyopsidea from Sauropsida and Mammalia? Or is it necessary to accept a primary division which brings together on one side the Cyclostomata and the Elasmobranchii, and on the other the Teleostomes, Dipnoi, Amphibians, Sauropsida, and Mammals?

I am well aware that I would not be justified in proposing such a radical change only on the strength of the arguments which I have brought forward in this paper, and by which I have attempted to show that the second group is characterised by the more or less distinct presence of an additional larval layer, the trophoblast, whereas in the first group no traces of this have up to now been found.

But if we penetrate somewhat more deeply into the question by considering whether there are yet additional characteristics by which this dividing line might be strengthened, because also on other points the two groups are equally distinct from each other, then we may arrive at a firmer foundation in support of such a radical change.

In my opinion there are even two different lines of argument along which to advocate the new dividing line here proposed.

The first is offered by that series of organs which are so intimately connected with respiratory processes, and which we call the lungs and the air-bladder (swimming-bladder). After Spengel’s (‘04) and Goette’s (‘04) lucid articles there

1 I must make an exception for Ray Lankester’s article on Vertebrata in the ‘Encyclopaedia Britannica,’ in which, with prophetic insight, he entirely ignores this subdivision.
can hardly be any more doubt but that we may look upon all the diverse modifications of lungs and swimming-bladder (the latter either double, ventral, or single and dorsal) as derivatives of what were originally a pair of posterior gill-pouches, in which change of function was slowly inaugurated parallel to preparatory steps by which an adaptation to terrestrial life was rendered possible.

Now the structures here alluded to are found in the Teleostomes, the Dipnoi, the Amphibia, Sauropsida, and Mammals, and never was any trace of them found in the Elasmobranchs or the Cyclostomes; so that here we have a concomitant argument to the one derived from the trophoblast in further justifying the new line of demarcation.

And I would call the attention of those who hesitate to introduce this new barrier between cartilaginous and osseous fishes to a set of other considerations which in my opinion have not been sufficiently looked into up to now.

It is this, that while nobody objects to the Cetacea being looked upon as the descendants of terrestrial Mammalia, nor to the Sauropterygia and Ichthyopterygia as having sprung from Reptilia that were air-breathing land-animals, the question has not enough been looked in the face whether many of our Dipnoi, Ganoids, and Teleostes may not also perhaps have had terrestrial ancestors? I fully recognise that we are here entering a field of wild and hypothetical speculation, but on the other hand insist on the necessity of testing this heuristic assumption. If we admit that air-breathing, hairy, and milk-producing quadrupeds originally lived on the dry land and have been able secondarily to adapt themselves in the most marvellous way to a life absolutely bound in all its functions to the high seas as that of the whales, how could we then wonder that in the palaeozoic epoch, when for the first time life on the dry land became possible and weird amphibious protetrapods left the water and managed to adapt themselves to this atmospheric environment, on many an occasion side branches of these earliest land-animals turned back to purely aquatic life
carrying certain hereditary stigmata which pointed to the fact that once they had been air-breathers already.

Up to now we only know such a ridiculously small portion of all the fossil animals that have lived in the palæozoic period, that it is not foolhardy to predict that very numerous remains may yet in future be unearthed in which this question presents itself.

And if we think of those innumerable series of species, genera, families, and orders of which at present we know nothing, is it then improbable that in those earlier periods of the world's history the same phenomenon of a secondary return to the aquatic medium has presented itself over and over again?

If I were allowed to point to one example I would select Polypterus, and ask if its paired and ventral air-bladder might perhaps not have served as effectual lungs to a more fully air-breathing ancestor, and if Klatsch's hypothesis (96) of the phylogeny of its limb-skeleton might not easily be turned the other way round so that the central plate with the two longer bones right and left of it should not be looked upon with Klatsch as an incipient carpus with lateral radius and ulna, but as an adaptation of what had already functioned as a supporting limb-pair in a terrestrial ancestor to a re-assumed aquatic life?

Similar questions might be put concerning the Dipnii, who in the Devonian epoch appear to have lived—judging from footprints—five-toed tetrapod contemporaries. Even in Teleosts (Saccobranchus and Anabas scandens) evolutionary processes are going on even now which tend to an exchange of the aquatic for the atmospheric life and vice versa.

The air-bladder in the Teleosts—which by common consent is now generally derived from arrangements such as they are now possessed e.g. by Polypterus, and not vice versa—has this other curious particularity that in certain closely allied species of the genera Scomber, Sebastes, Umbrina, Thynnus, Chironectes, it may be totally absent in the one, present in the other. Thus according to Stannius, 'Zootomie der Fische,' 2e
Aufl., 1854, S. 22, Scomberesox Camperi has an air-bladder,
Scomberesox Rondeletii has none. In other families,
Squamipennes, Tenioidei, Siluroidei, Cyprinoides, Cichlidae,
etc., the same is noted. I hold this to be an argument for
looking upon the air-bladder as an organ that is fairly on the
way to become rudimentary. Certainly not as an organ that
is yet very essential to the life of many Teleost fishes in
their present environment.

At the same time the fact of the existence of such a very
great number of Teleost species is certainly no argument
that the whole of their pedigree must necessarily lie in the
aquatic medium.¹

I will not go so far as to say that all Teleostomes and
Dipnoi have descended from terrestrial, air-breathing tetra-
pods, because the material upon which to base a similar
conclusion is by far too scanty; but on the other hand I will
not either for the same reason anathemise any naturalist
who feels inclined to go as far as that. It should certainly
be kept in view that the incipient aeropneustic conditions
which ensued upon the adaptation of posterior gill-crests to
aerial respiration need not necessarily have been accom-
panied by a terrestrial life. Still it will certainly have
contributed to render further adaptations to a terrestrial or
rather amphibious existence easier.

I must, however, yet allude to one argument which goes
parallel to that derived from the air-bladder and lung-
arrangement.

It is an osteological argument and calls our attention to
the fact that the mutual relation of the ossifications on the
skull and visceral arches of the Teleostomes are to such a

¹ While correcting the proof of these pages Aschelom’s ‘Development of
Gymnarchus niloticus’ (the Budget Memorial volume, 1868) came into
my hands, in which I find the possibility of similar inverse relations discussed
on arguments derived not only from lung and air-bladder, but on further
developmental details concerning the vascular system and the gills, brought
together under ten heads (l.c., p. 407). Gymnarchus belonging to a primitive
family of Myxocysterygii, it is only natural that I should welcome support
obtained independently along a perfectly different chain of reasoning.
very great extent homologous both in number, in sequence, in position, and in development to similar ossifications in the Amphibia, the Sauropsida, and the Mammalia.

Confining ourselves to the comparative osteology of the head we may say that the conformity is very suggestive, and that, where nobody advocates any direct descent of the land-animals from Teleostomi, this conformity might certainly plead for the possibility of the inverse proposition.

This proposition to be taken in the sense above alluded to, viz. that great attention should be given to the evident probability that the return to an aquatic environment may have been by polyphyletic lines of descent and at different periods of the earth's history.

There is no doubt that we must look towards paleontology for furnishing us with the arguments that will have decisive weight in deciding these delicate questions of phylogeny, for which we can never hope to possess arguments derived from splanchnological or from developmental sources.

And we may at all events expect that as more and new fossil finds come to increase our knowledge of the paleozoic epoch, some of them will certainly prove to have a bearing on the points here in dispute.

A division of the vertebrates in the superclasses of Cyclostomata, Chondrophora, and Osteophora might suggest itself, Amphioxus remaining yet more isolated in its superclass of Cephalochordata.

The Chondrophora would then contain the Elasmobranchs, the Osteophora all the other higher vertebrates.

In further subdividing the Osteophora the existent grouping into Teleostomi, Dipnoi, Amphibia, Sauropsida and Mammalia might remain, although it will have to be carefully considered whether the recent, most considerable progress of palaeontology will not allow of a more satisfactory reclassification in the borderland between Amphibia and Reptilia, now that we have reason to believe that the very sharp distinction which in later days was upheld between these two according to the
presence or absence of amnion and allantois is to a great extent artificial.

When embryology no longer forces us to go on extending the distinction between the so-called Amniota and Amniaria into the paleozoic period, certain lines in comparative anatomy may perhaps suggest a new grouping in which also that other inadequate test, the double or single occipital condyle, is relegated to its real value. But then the palaeontologist who will go deeper into this matter should bear two other points in mind which both this investigation and numerous other researches in comparative anatomy have brought to light of late years, viz. that the mammalian characteristics bring us down to a point where comparison with the lower Amphibia—as Fürbringer (100) has more especially advocated—is more ad rem than comparison with the more specialized reptiles; secondly that the Ornithodermia should be looked upon as a sub-class by itself, small at present, but perhaps more extensive long ago (Multituberculata), in which sauropsidian and mammalian characters are curiously combined but which was never in the direct line of descent of Mono- and Didelphia.\(^1\) Then, again, that these latter may be said to be a very specialised side branch of ancestors that were

\(^1\) I wish here to refer to a passage in an interesting article by Wortman ('00) on the origin of mammals (l. c., p. 429). He says, "Early in the mesozoic there appeared small, mammal-like forms, which were widely distributed over both the northern and southern hemispheres. Representatives of these species continued throughout the Cretaceous, and finally disappeared in the early stages of the Tertiary. . . . Many of them are classified in the group Multituberculata, which, without much doubt, finds its nearest living representative in the Dugong of Australia. . . . In one instance a fairly complete skull is known (Tridyodus) from the Karoo-beds of South Africa. The teeth of this species are astonishingly like those of many types in the northern hemisphere, and hitherto it has always been classified in this group. Seeley has shown that the organisation of the skull presents so many reptilian characters as to cause him to refer it to the Reptilia. If this reference is correct, then, in the absence of any fact to the contrary, it is highly probable that all the multituberculates are as much reptile as mammal. Indeed, it is not easy to say, at first glance, upon which side of the line living monotremes should be placed. There can be little doubt that, when more
already placental Monodelphia, so that the Mammalia s. str. are no more broken up into three stems but in reality contain only one, the course of which through the corridors of time will have to be established by the palaeontologists, who will undoubtedly finally be able to trace it far into the carboniferous, nay, perhaps, even into earlier geological epochs, simultaneously with the first evolution of air-breathing vertebrates of Protetrapodian structure.

Then, again, if we take these Monodelphia, their respective subdivision into natural orders will awaken all the more interest as they bring us closer to the phylogenetic development of man himself, one of the problems about which the human mind will never be wholly at rest; and here comparative anatomy, embryology and palaeontology ought to cooperate more intensely than it has hitherto generally done. Only of late—thanks, in the first place, to efforts of American palaeontologists—this is brought home to us and is beginning to be realised.

Here, too, however, a very broad and very modern spirit ought to prevail. And though recognising that only of the recent Mammalia the embryology can be traced, and that there is not the least chance of ever obtaining positive facts concerning the embryology of fossil groups, still, it ought to be fully realised that when once the ontogeny of all the existing genera of mammals is known—and this is a goal that ought to be taken in view without delay—we will have in those facts indications of great delicacy for determining degrees of consanguinity. The details of ontogeny and fully known, these ancient fossil types will present every conceivable gradation between these two great divisions of the Vertebrata."

Now, this is the very point which, on repeated occasions ("05, "09), I have advocated, viz. that the recent Ornithodelphia are one of the many offshoots into which the Protetrapodan ancestors have subdivided themselves, when once they had commenced to adapt themselves to life on dry land and to aerial respiration. The stems that remained viviparous are yet represented by the living Mammalia, those that have become oviparous diverged into the Ornithodelphia, and—further off yet—into numerous Reptilia, and have never given rise to viviparous descendants.
placentation will prove to be a very subtle instrument (as it has already shown itself to be with respect to the Primates) by which wide deviations in external habitat may be spanned and by which important generalisations may thus be reached.¹

Already have the voices of anatomists of different countries repeated what I have ventured to express more than ten years ago, viz. that among mammals the Primates have actually retained many very primitive characters. And the voices alluded to go even further and say that among the Primates the same may be said, in very many respects, concerning man as compared to the other Primates. Always with this one all-important reserve that his specialisation (a) in respect to brain development (including cerebral circulation) and brain power, (b) to adaptation of the forelimbs to the most diverse uses, and (c) of the larynx and tongue to articulate speech is quite out of comparison as regards importance with any other series of specialisations that are, however, so numerous amongst the different orders of mammals.

The order of the Insectivora will have to be broken up, and many of the small fossil mammals that may yet be brought to light will have to be carefully tested as to their relations to the different orders into which the Insectivora will be subdivided. Already Wortman has proposed to transfer the Hyposcodidae (hitherto considered as Primates) to the Insectivora.

¹ I may here once more repeat, what I have already stated elsewhere, that placentation is so delicate a touchstone, because it was a phenomenon that appeared and evolved ever so much later than other processes or structures in the vertebrate organisation, and that this comparative youth must decidedly contribute to retain small differences, which in older organs have been worn away by the effect of time. On the other hand, the details of the very early blastocyst must undoubtedly be of pre-eminent importance, just because they come to light at such a very early stage of development. The different characteristic details of very early stages must be all-important for determining hereditary affinities one way or the other, as they are undoubtedly least of all affected by influences that call forth adaptations in the organs of the adult animals.
And Tarsius will have to be definitely removed from the Lemurs, as has also already been done by myself ('96, '00, '02) and by Wortman ('03, '04, p. 167), who unites it with monkeys and man in the order of the Anthropoidea, differentiated from the Lemurs, in addition to the characters derived from the blastocyst and the placentas, discussed above, by the arrangement of the ento-carotid circulation, which in the Lemurs more closely approaches to the peculiar plan of the Insectivores.

Wortman's subdivision of his suborder of Anthropoidea in the three superfamilies

(a) The Acretopithecini, including as single family the Hapalidae;

(b) Palæopithecini, including, besides Anapithecus and Tarsius, yet Necrolemur and (perhaps) Microchærus;

(c) The Neopithecini, man and the living monkeys, besides the fossil family of Adapidæ,

is the embodiment of what I have stood up for since my publication in Gegenbaur's Festschrift ('96), and has, of course, my full sympathy.

I must, however, differ from Wortman when he considers "the Primates a perfectly natural and homogeneous order, including the Lemurs, monkeys and apes, as well as man himself" (l. c., p. 163). I hold his suborder of Anthropoidea, above named and very fully discussed in his paper ('03), to be in reality a full-rank order, which should retain the time-honoured name of Primates. The two other suborders which Wortman combines with his Anthropoidea, viz. the Lemuriidea and the Chironyidea, should be ranked together as suborders of the distinct order of Lemurs. I will discuss this point somewhat more fully with reference to the contents of the previous chapters.

Chiromys madagascariensis has a typical diffuse placenta, of which I here give a figure (Fig. 151) taken by myself from a Chiromys fetus in the British Museum kindly lent to me for the purpose by the trustees. This placenta, which, as dis-
cussed on p. 115, can hardly be called a placenta at all, corresponds with the villiferous diploblast, with massive villi of Nycticebus in all respects, and I have no doubt but that also the relation between diploblast and allantois, etc., in Chiromys will be of the same type as that of Nycticebus (Fig. 148), so that really nothing is in the way of following Wortman's suggestion and placing these two suborders of Chiromyidea and Lemuroidea together; selecting for the order which comprises them the name of Lemures as above stated. Besides the recent Chiromys madagascariensis, Wortman adds the fossil genera Mixodectes, Cynodontomys, Microsyops Smilodectes, and Metachiromys, in all of which the dentition has acquired that peculiar Rodent-like aspect which is so characteristic for the recent genus. I prefer Wortman's views to the proposal which Osborn has made, viz. to unite the six American fossil genera into a suborder of the Rodentia, which Osborn calls the Proglires. Wortman states that what is known of the skeleton betrays the same Primate stamp with equal distinctness, as does the skeleton of Chiromys. And as to the modification of the incisors which is complete in the living Madagascar species, it is progressive but incomplete in the American genera. Wortman adds that "these are the only representatives of the Primates in which the slightest tendency towards such modification is shown. That so distinctive and profound a change could have originated twice independently in the same order is so highly improbable as to be unworthy of serious consideration". The group is of pretorial origin, Mixodectes, its oldest representative being already highly modified in the second stage of the lower Eocene.

The Lemuroidea, which may be united with the Chiromyidea into the order of Lemures are characterised by Wortman in the following manner:

"Limbs elongate, prehensile, and adapted to an arboreal habit; incisors of lower jaw reduced in size, pectinate and procumbent in position; anterior lower premolar very generally enlarged and functioning as a canine; ento-carotid canal..."
not traversing the petrosynaptic molar and lachrymal very generally in contact on anterior rim of orbit; fourth digit of the manus the longest of the series."

He adds: "Some . . . are inclined to deny the genetic connection of this group, as well as that of the Chiromyoides with the true monkeys, and assign to them a separate and independent ordinal rank. This, however, is manifestly incorrect." After a page devoted to internal anatomy and placentation, Wortman concludes: "It seems by far the safest plan to rely largely if not solely upon osteological evidence for our conclusions respecting the affinities and evolution of the various groups of theMammalia." And then he finishes by brushing aside the objections I have raised to connecting Lemures and Primates in one and the same order.

In once more vindicating the position which I have taken up in this question twelve years ago [96] I may begin with remarking that the last citation, however comprehensible the idea there developed may seem from a purely paleontological point of view, is not justified in this particular case. Rarely have differences of such importance concerning internal anatomy been established as is the case between the two suborders of the Lemurs on the one hand—Tarsius, monkeys, and man on the other.

Wortman seems to have grasped these differences only partially, and writes: "It is difficult to decide what value is to be attached to the placentation in estimating affinities." In the preceding chapters we have repeatedly shown—as had been already done by me before Wortman published his paper—that it is certainly not only on arguments drawn from the placentation that Lemurs and Primates ought to be separated, although the placentation as such is, indeed, profoundly different in the two cases. But the difference between the evolution of the blastocyst, the part played by endoderm and mesoderm in coating the inner surface of the trophoblast, and the way in which the diplo-trophoblast is vascularised in a greater or lesser degree in the Primates, with the permanent retention of what we have called the
connective stalk, is so utterly different from what we find in Lemurs, and on the other hand so closely homologous if we take forms so wide apart as Tarsius and man, that we must frankly recognise that if ever, then here is a case in which these details of internal anatomy, as revealed by ontogeny, must weigh very heavily in the scale.

Wortman has not taken the least notice of the very important differences in the early blastocyst, and takes it easy with the placental differences as we have seen by the citation on p. 162. He even commits himself to the following statement (l.c., p. 403): "While it is probably true that these characters derived from the soft anatomy indicate a wide distinction between existing monkeys and lemurs, yet it is much to be doubted whether these distinctions would not assume very small proportions or completely disappear, did we have an Eocene monkey with which to make the comparison." Now this piece of reasoning is very lame indeed. We have an Eocene monkey to compare with Tarsius, viz. Anaptomorphus. On p. 213 of another publication ('04) Wortman (who places both in the same suborder as monkeys and man) enumerates eleven points of resemblance between Tarsius and Anaptomorphus: (1) in size, (2) in brain development, (3) in relation of brain to foramen magnum, (4) in absence of sagittal crest, (5) in shortened face and large orbits, (6) in situation of internal carotid canal, (7) in dentition, (8) in structure of molars and premolars, (9) in shape of bulla, (10) in lacrimal bone and lacrimal opening, (11) in relations of lacrimal and malar.

Now, where these numerous points of resemblance exist it would be most illogical to presume, without strong positive evidence, that blastocyst and placentae of the Eocene Anaptomorphus as compared to the living Tarsius, were as wide apart as is that of a true Lemur like Nycticebus from that of Tarsius, as Wortman would have us believe. Moreover, this would not be an advance in any respect, because we do not see our way to derive the arrangements in Tarsius from those present in Nycticebus.
And so both the facts and the reasoning, that is brought to bear upon them, convince us that there is an immense amount of probability, that already in the Eocene did those fundamental ontogenic differences exist between the Primates as represented by Anaptomorphus and between the then existing Lemurs, which we now notice between Tarsius and the modern Lemurs, Ungulatos, etc.

I hope to have established in the preceding chapters my full right at exacting the application of all data we dispose of, both osteological and ontogenetical, to the settlement of questions of affinity between Mammalia. That in very many cases, when groups that are exclusively fossil come under consideration, we will have to go by the osteological characters only, is, of course, self-evident. But it does not diminish our conviction that if there, too, we could have had ontogenetical evidence in addition to go by, our conclusions would be yet more emphatically trustworthy.

In the case of the Primates it is all the more necessary to insist upon the ontogenetical characters being allowed to have their full weight for several reasons. Firstly, because a careful consideration of these characters makes it evident that man, the monkeys, and Tarsius are more primitive in the possession of their connective stalk than are the Lemuroids with their free alantois, whatever may up to now have been said of the latter’s placentation being more primitive, a point which in Chapter V I have endeavoured to reduce to its true proportions. Secondly, because the osteological characters seem to be such as to induce most palaeontologists to incline towards a perfectly gradual passage from the lemuroid to the anthropooid type. The facts of ontogeny, however, should force them henceforth to look out for additional characters by which Wortman’s Anthropoidea (already represented in the Eocene by Anaptomorphus, for which there is no reason at all to suppose that its blastocyst was not as similar to that of Tarsius as its dental and skeletal characters are) can yet additionally be distinguished in older formations from those forms which must have led up to the
present lemurs. That Wortman unites the Adapidae to the Primates s. str. and gives them not a subordinal rank but classes them as a family of equal value as the Cebidae, the Cercopithecidae, the Simidae, and the Hominidae is an important step, the justification of which can be better appreciated by trained palaeontologists than by myself. But if Wortman is right in thus separating the Adapidae from the Lemuridae, Nesopithecidae, and Megaladapidae, which are the super-families in which he subdivides his Lemuridae, then he and others will have to trace downwards the line by which, on the one hand, these latter families and, on the other, the Primates (Adapidae included as above stated) are connected to earlier mammals of the Mesozoic in which the deep cleft which ontogeny demonstrates between the two may have been less, but traces of which must be deciphered out of osteological details. Perhaps that problem may prove to be too arduous, but even then we are in no way justified to follow Wortman when he proclaims his sole faith in osteological characters and voluntarily suppresses ontogenetic evidence where it exists, because in so many cases it does not exist or rather can never any more be brought to add its testimony to what osteology reveals us.

I must in conclusion yet refer to a citation which Wortman gives from Flower and Lydekker's "Mammals, Living and Extinct." Wortman is quite justified in thereby (I. c. '03,

1 Nesopithecus of Forsyth Major is an instructive example in this respect. Dr. Forsyth Major, from the unusually high development of the skull, and its many resemblances to the higher apes, concluded that it was an Anthropoid. Lydekker preferred to class it as a highly developed Lemur. Wortman followed him in this, undoubtedly after careful consideration of both Major's and Lydekker's argumentation, and instituted the super-family of Nesopithecidae above referred to. Now, I have no doubt that the ontogenetical details of Nesopithecus would immediately have settled this question. As it is, it seems to me that only a most careful examination of the entire skeleton, wherever available, will furnish material for a definite judgment.

In the meantime we should, in this and other cases of so delicate and yet so important a nature, suspend our judgment, however much I would in the present case be willing to accept the validity of Lydekker's opinion.
p. 463) giving his reader the impression that the value of
the deciduate and non-deciduate type of placenta has been
overrated. Not only that, but since then among the so-called
deciduate placentary mammals some have been detected
(Hubrecht, Hill) in which the placenta instead of being
deciduate might even be termed contra-deciduate, in this
sense that no maternal tissue is being expelled after parturi-
tion, but that embryonic tissue is undergoing a process of
resorption on the part of the mother.

And so I will not deny that the value which we ascribe to
particular points in the placentaion and in the puererium
of mammals may vary according to the greater or lesser
acquaintance we possess of their details. But I cannot over-
look that even Flower and Lydekker in the same citation
maintain that "the characters and arrangements of the fertil
structures . . . will form, especially when more completely
understood, valuable aids in the study of the natural
affinities and evolution of the mammals."

On p. 159 I have developed the idea that in certain cases
the "character and the arrangement of the fertil structures"
will even prove to be a discriminating re-agent both delicate
and powerful. And I must emphatically repeat that the case
of the ordinal separation of the Lemures from the Primates is
one of crucial importance, and that, whatever inconvenience
may in the present state of our knowledge be caused by it to
palaeontologists, we should on no account surrender or
acquiesce to the proposal of so eminent an authority as
Wortman, but should determine (1) to keep separated the
two orders of the Primates and the Lemures, and (2) to use
all our ingenuity and acuteness in order to trace, as new
fossil remains come to light, remains belonging to the one
and to the other order by osteological details only. But
then of course such finds which bring us teeth or even teeth
and skulls only, may in some cases be misleading, and only
complete skeletons can have full demonstrative weight.

This new and more exacting method of dealing with fossil
remains is in the nature of things in the first place applicable
to Primates and Lemures, because we have concluded from the facts discussed in the preceding chapters that, more even than Huxley ('81) supposed the Insectivores to be, the Primates come under our consideration as containing the more primitive types of mammals. And it is only natural that they and their nearest allies will be more difficult to differentiate from each other than other mammals, who, even though archaic in some respects, were well specialised in others, as are many of the earlier Condylarthc, Ungulates, and Creodonts.

Wortman, in his remarkable discussion on the origin of the Primates ('03, pp. 419—436) shares this opinion when he says: "It is true that the Insectivora furnish a type of cerebral circulation which might easily have passed into that of the Anthropoides, through the suppression and disappearance of the stapedial branch of the onto-cotid, but, as we have already seen, this character is shared by the Rodentia, and probably by other groups as well. At the same time it does not form a type of cerebral circulation from which that of the Lemurs could have been evolved (l. c., p. 436)."

We here have a most instructive example of that differential treatment of the most delicate marks visible on the base of the skull of fossil mammals by which their ordinal grouping may be influenced. And it is exactly this delicate discrimination which I have been advocating in the preceding pages. The example is all the more instructive as it shows us points of agreement in angiological and osteological detail between Insectivora, Rodentia, and Primates, s. str., between which orders (all of them primitive) we have discussed so many points of comparison referring to the placenta, the blastocyst, etc. At the same time Wortman denies a similar degree of direct comparability on this particular point between Insectivores and Lemurs (see also l. c., p. 167), which, as he says, "are sufficiently distinct to afford reliable diagnostic characters." Now we have seen that also with respect to their peculiar placentation (which, as I have said, is not necessarily as primitive as it has always been looked upon)
the Lemurs differ considerably from Rodents, Insectivores, and Primates, but have again great similarity with Perissodactyles and Artiodactyles (Equus, Sus, Tapirus) and others. Here, then, is a point to which paleontologists should try to give particular attention. They might then help us to get hold of a clue by which to differentiate the early mesozoic pedigree of Ungulates and Lemurs from that of the Primates, Insectivores, and Rodents, and by that contribute to restore their own belief in the value of ontogenetical characters as guides to problems of classification.

I finally wish to cite the last phrases of Woriman's so exceedingly suggestive paper just alluded to, in which he finds it difficult—and I am here in full accordance with him—to derive the Primates from the Insectivora. He says: "The greatest difficulty in the way of deriving the Primates from any form or forms of the Insectivora at present known consists in the total lack of prehensile powers of the manus or pes. Any group which is placed ancestral to the Primates must of necessity be one in which some distinct approach to this condition is made, since its possession is one of the chief requisites of fundamental importance. With the single exception of Lophiomys among the Rodentia, the only other living mammals which exhibit prehensile extremities are found among the Marsupials, and the evidence points very conclusively to the fact that all of them, even those with highly modified limbs for terrestrial progression (as the kangaroos), are descended from ancestors with grasping hands and feet. It is, therefore, not beyond legitimate supposition to assume the existence of a very considerable group of ancient Metatherians living within the arctic circle during cretaceous time whose manner of life had already become arboreal. If such a group did exist it is far more likely that the Primates were derived from it rather than from the Insectivora or any other group now living."

Now the prehensile power of the manus or pes lacking in the Insectivora as far as known to us re-appears again, at least in the shape of an opposable thumb in certain Amphibia
Fig. 159. Section through uterus and early embryo of Pteropus (after Gehre). There is no entire decidua capsularis. The placenta will be of the staked type. $d_a d^t$ the free borders, which, if united, would form a closed decidua capsularis. — Fig. 160. Diagrammatic representation of a vermiculian stage in the phylegony of vertebrates; the notochord $n c h$ developing out of the stomodaeum, the coelomic diverticula $y o$ some becoming split off from the enteron (after Hubrecht, '02).
and even the fossil amphibian, known only by its footprints, Chirotherium, is supposed to have possessed this distinctive character of the Primates. So here, again, we find an indication that in trying to bridge the distance between Primates and the lowest Tetrapods the road is rather via an amphibian ancestor than via reptilian-insectivorean transitional stages.

We now come to the final paragraph of this chapter, in which we have to give our attention to the continuation of the Vertebrate (Chordate) pedigree among the invertebrate phyla.

I have on a former occasion (05A) expressed myself on this subject, but will here once more restate my own views.

The diagrammatic type for a representative of the vertebrate phylum would be a bilaterally symmetrical, segmented, coelomate animal, with the gut below, the central nervous system above the axial notochord. Following Sedgwick in his proposal to derive this type from an elongated, actinian-like starting-point, I have constructed a diagrammatic figure, which I here reproduce (Fig. 160), and in which I suppose the circumoral nerve-ring of the actinian-like ancestor to have become the central nervous system, the stomodaeum to have become the notochord, the coelom to have arisen out of the peripheral parts of the coelenteron. The original actinian-like dorsal mouth-slit (itself a differentiation of what was the blastopore of the gastrula-larva) is only evanescently reproduced during vertebrate development by the communication between outer world and enteron, which travels backwards and separates the two halves of the concrescent notochord. The anus and the anterior neuropore may be two remnants of this slit; the vertebrate mouth is a neoformation, as are the gill-slits and the coelomopores. In how far openings in the lateral body-wall, by which in certain living actinians the coelenteron communicates with the exterior, belong to the same category as the openings just mentioned cannot for the present be definitely settled; nor can we know how many coelomic pouches were present at the starting, nor how
metamerism has finally increased after the gastrula stage had been passed and the phenomena of kaphalogenesis and of notogenesis had begun to show themselves.

For an eventual comparison of the larval coelomic pouches as they were described for Balanoglossus by Bateson ('36) with what we know about the coelomogenesis in Vertebrates the indications at the present moment are only of the very slightest, too slight for making any further mention of them here.

The presence of an outer larval layer (of ectodermal derivation) in the worm-like transition-form that stood between this archaic starting-point and the predecessors of our osteophororous vertebrates, its absence in that which led up to the Cephalochordata, the Cyclostomes, and the Chondrophora was discussed on p. 151 of this paper.

A comparison of these hypothetical and intermediate stages between the coelenterate and the vertebrate phyla with the conclusions to which Woltereck has come, when he, too ('04), has stated that in Annellid development phases occur which seem to agree with what I have designated by the terms of kaphal- and notogenesis, had better be put off to a later publication, this last paragraph being more of a recapitulative than of a constructive significance.

I finally call attention to the fact that the unsatisfactory state in which our modern comparative embryology leaves a number of important phylogenetic problems—I may here call attention to O. Hertwig's own words on p. 898 of vol. 1, 1, 1. of his new handbook—may partly find its explanation in the circumstance that up to now the comparative embryology of Vertebrates has been principally founded on what we know of the chick, supplemented by what Kowalevsky and Hertwig taught us about Amphioxus, Balfour about Blasmbbranch fishes. Now that we have proposed to accentuate the distinction between Chondrophora and Osteophora I may be allowed to invite younger embryologists to tackle wherever they can the early developmental stages of mammals or
Amphibio in preference to the cartilaginous fishes or to Amphiopus, however much more easy the latter material can be obtained.

I have no doubt that in mammalian embryology very many surprises are yet in store for us.

REFERENCES REPEEED TO.


—— '08.—"An Account of a Blastodermic Vesicle of the Sheep of the seventh day with Twin Germinal Arcs," 'Journ. Anat. and Phys.'

—— '06.—"The Morphology of the Ungulate Placenta," 'Phil. Trans. R.S. London,' vol. 198.

Ballwitz. '01.—"Die Gastrulation der Ringelnatter," 'Zeitsch. f. wiss. Zool.,' Bd. 70.

Babéni. '06.—"Intorno alla placentà del Tragulus fuminus, Erxl.," 'Anat. Anz.,' Bd. 29.


van Beneden. '80.—"Recherches sur l'embryologie du lapin," 'Arch. de Biol.,' vol. 1.

—— '88.—"De la Fornation et de la Constitution du placenta chez le Murin (Vesperitilio murrinus)," 'Acad. de méd. de Belgique,' Série 3, t. 15.

—— '99.—"Recherches sur les premieres stades du développement du murrin (Vesperitilio murinus)," 'Anat. Anz.,' Bd. 16.

et Julius. '00.—"Observations sur la maturation etc., de l'eau chez les Gastropodes," 'Archives de Biologie,' vol. 1.

Binzoff. '42.—"Entwickelungsgeschichte des Kaninchenba.," Braunschweig.
Bischop. '85. — Die Entwicklungsgeschichte des Hundekeiles, Braunschweig.

'83. — Entwicklungsgeschichte des Meerschweinchens, Giessen.

'84. — Entwicklungsgeschichte des Robes, Giessen.

'84. — Recherches sur la formation des annexes fœtales chez les Mammifères, Arch. de Biologie, vol. 5.


'05. — "Gastrulation et formation de l'embryon chez les Caudés," Ant. Amt., Bd. 27.


EARLY ONTOGENETIC PHENOMENA IN MAMMALS. 173


Cerfontaine. '06.—"Recherches sur le développement de l'Amphioxus," "Arch. de Biol.," T. 22. F. 2.


Dean, Bashford. '95.—"The Early Development of Garpix, and Sturgeon," "Journal of Morphology," vol. 11.


EINSTEIN. '01.— "Embryologische Untersuchungen," Heft 2.

1. "Die Stammesgeschichte der Nagetiere."


— '75.— "Entwicklungs geschichte der Uake.


EARLY ONTOGENETIC PHENOMENA IN MAMMALS.

HERTWIG, O. '06.—"Die Lehre von den Keimblättern," 'Handb. der vergl. u. experim. Entwicklungslehre der Wirbeltiere,' 1 Bd., 1 Th., 1 Hälfte.


— '00.—"On the Fetal Membranes, Placentaion, and Parturition of the Native Cat (Dasyurus viverrinus)." 'Anat. Anz.,' Bd. 18.


HURBRECHT. '85.—"Entwickelungsgeschledes der Lineus obscurus," 'Utr. Gesellsclap.'


— '96.—"Die Keimblaste von Tarsius, ein Hilfsmittel zur schärferten Definition gewisser Säugehierodaeuungen," 'Festschrift für Gegenbor.'


— '98.—"La formation de la decidua reflexa chez les geaeres Erinaceus et Gymnura," 'Annales du Jardin botanique de Bâlenzorg,' Suppl. 11.

HUBRECHT. '00 a.—"Blatthäutung im B der Affen?" "Biol. Centr.," Bd. 10.
— '03 a.—"Gastrulation der Wirbeltiere," "Anat. Anz.," Bd. 26, und
— '05 a.—"Die Abstammung der Anneliden und Chordaten und die
Stellung der Ctenophorae und Platthelminten im System," "Jen.
Zoolog. Jahrb.," Bd. 32.

und KEIBEL. '07.—"Nomentafeln zur Entwickelungsgeschichte des

JENKINS. '02.—"Observations on the Histology and Physiology of the

KEIBEL. '88.—"Zur Entwickelungsgeschichte des Igel," "Anat. Anz.,"
Bd. 3.
— '89.—"Zur Entwickelungsgeschichte der Chorda bei Säugern (Meesel.
und Kaniachen)," Leipzig.
— '93—'94.—"Studien zur Entwickelungsgeschichte des Schweines,"
'Morph. Arb.," Bd. 3 und 5.
in Tübingen.
Jena," Vers. 18.

KERK, J. GEMAN. '01.—"The Development of Lepidosiren paradoxa,"

KLAATSCH. '96.—"Festschrift für Gegenbaur," Bd. 1.

KLEINENBERG. '85.—"Die Entstehung des Annelids aus der Larve des
Lepidochirius," "Z. W. Z.," 44.

KÖLLiker. '88.—"Die Entwicklung der Keimbäder der Kaniachen,
Festschrift Würzburg.
— '83.—"Über die Chordahöhle und die Bildung der Chorda beim

KOLLMANN. '02.—"Beiträge zur Embryologie des Affen," "Arch. Anat. und

LEGROS. '07.—"Sur quelques cas d'asynestrie blastoporeale chez l'Amphi-

LWOFF, B. '74.—"Die Bildung der primären Keimbäder und die Entste-
hung der Chorda und des Mesodermes," Moskau.
EARLY ONTOGENETIC PHENOMENA IN MAMMALS. 177

MAURUS. '89.—"De la genese du placenta chez le Lapin," 'Arch. de Biologie,' vol. 9.


—'94.—"Ueber Entwicklung, Bau und Funktion des Amnions und Annienzangens nach Untersuchungen an Emys lutaria taurica (Maralı)," 'Morph. Arb.,' Bd. 4, H. 2.


—'96.—"Etudes des modifications de la muqueuse uterine pendant la gestation chez Vespertilio murinus," 'Arch. de Biol.,' 14.

NUEL. '91.—"Quelques phases du developpement du Petromyzon planeri," 'Arch. de Biol.,' T. ii.


—'95.—"Uber die Einbettung des menschlichen Eies und das fruhesten bisher bekannte menschliche Placentationsstadium,' Leipzig und Wien.

PETER. '05.—"Normentafeln uiiber die Entwickelung der Wirbeltiere," H. 4.


VOL. 53, PART 1.—NEW SERIES.
ROBINSON and ASHETON. '31.—"The Formation and Fate of the Primitive Streak, etc. of Rana temporaria,"  'Quart. Journ. Micr. Sci.,' vol. 32.


— '81.—"Recherches sur le développement du Sterlet,"  'Arch. de Biol.,' T. ii.


— '03.—"Beiträge zur Entwicklungsgeschichte und Anatomie der Wirbeltiere, 1—111.,"  'Zeitschr. f. wiss. Zool.,' Bd. 16.


SCHWENKEL. '03.—"Contribution à l'Étude de la Fixation de l'œuf des Mammiferes dans la Cavité utérine, et des premières Stades de la Placentation,"  'Arch. de Biol.,' 19.


SEGUIN and MINOT. '03.—"A Laboratory Text-book of Embryology.

SCHULNDKA, E. '83.—"Keimblätter und Primitivorgane der Maus;"  'Untersuchungen über Entw. gesch. der Tiere,' 1.

— '84.—"Die Blätterumkehrung im Ei der Nagethiere,"  'Untersuchungen über Entw. gesch. der Tiere,' iii.

— '87.—"Das Opossum;"  'Untersuchungen über Entw. gesch. der Tiere,' iv.

— '91.—"Beutelsuchs und Känguruhratte; zur Entwicklungsgeschichte der Amnion der Kantjil (Tragulus javanicus); Affen Ost-Indiens,"  'Untersuchungen über Entw. gesch. der Tiere,' H. 5, Erste Hälfte.
EARLY ONTOGENETIC PHENOMENA IN MAMMALS


'00 a. "Vermessungen," Heft 3.


'01. "Die ektochondale Medinannahme des Ceratodus," 'Arch. f. Entw. mech.' Bd. 11.

SIEGENDORF V. HEUCKELM. '98. "Uber die menschliche Placentation," 'Arch. für Anat. und Phys.'


'52. "Beiträge zur Entwickelung von Lacerta agilis," 'Arch. f. Anat. und Phys.'


99.—“Der Uterus gravidus von Gaingo agisymphallus,” Schriften der Senckenb. naturf. Ges. zu Frankfurt-a.-M.

03.—“Der Uterus gravidus des Orang Utaus,” Anat. Anz., Bd. 22.


03.—“Die Embryonalhülle der Säuger und die Placenta,” in Hertwig’s Handbuch der vergl. Entw. Geschichte, Bd. 1, Th. 2.


SUMMER. 94.—“A Study of Early Fish Development—Experimental and Morphological,” Arch. für Rütw. mech., Bd. 17.

SWAN und FRANCETT. 09.—“Études sur les premières phases du développement des organes dérivés du mésoblaste chez les Poissons tétracténés,” Arch. de Biol., T. 16.


VONHOUT. 94.—“Ueber die Placenta des Maulwurfs (Talpa europaea),” Anat. Hefte, Bd. 5.


EARLY ONTOGENETIC PHENOMENA IN MAMMALS. 181

WEBER, MAX. '01.—"Beiträge zur Anatomic und Entwicklung der Geraus Manis," 'Zoologische Ergebnisse einer Reise in Niederl. ost-indien.'

—— '04.—"Die Singethiers," Jena.

WESCHER. '86.—"De embryonale ontwikkeling van de Amajoris (Ent-

—— '90.—"Zur Entwicklungsgeschichte des Greyko,' 'Biol. Central-

WILLET, A. '60.—"Trophoblast and Serosa: a Contribution to the Mor-


—— '97.—"Considerations on Cell-lineage and Ancestral Raminenceses,


WILLIAMS and HILL. '03.—"Primitve Knot and Early Gastrulation Cavity

—— '07.—"Observations on the Development of Ornitho-

WOLFFERAK. '04.—"Wurmkopf, Wurmnas und Trecephora," 'Zool.

WORTHMAN. '03.—"Studies of Eocene Mammalia in the Marsh Collection,


—— '02.—"Lehrbuch der vergleichende Entwicklungsgeschichte der niederen Wirbeltiere," 'Jenn, Fischer.'