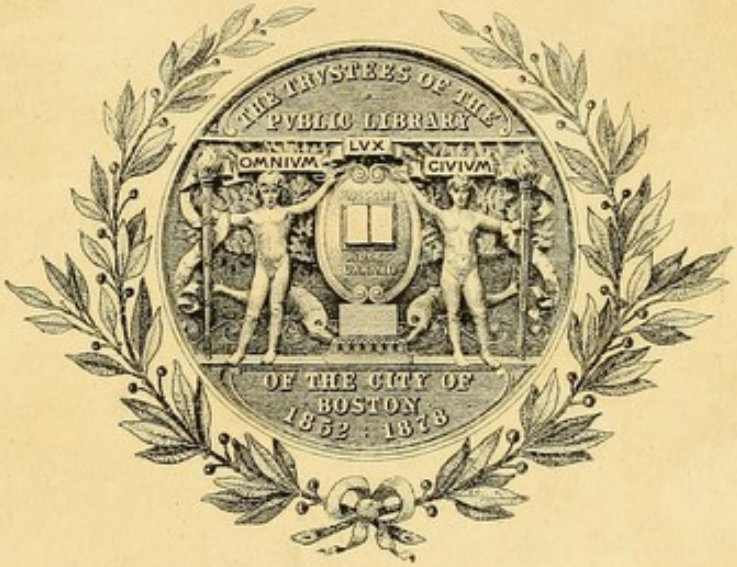
The span of gestation and the cause of birth : a study of the critical period and its effects in mammalia / by John Beard.



THE SPAN OF GESTATION AND THE CAUSE OF BIRTH.

A STUDY OF THE CRITICAL PERIOD AND ITS EFFECTS IN MAMMALIA.

BY

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"Was sich immer wiederholt, kann nicht vom Zufall oder vorübergehender Laune bedingt sein, sondern muss von einer Nothwendigkeit abhängen."

C. E. VON BAER.

JENA,
GUSTAV FISCHER.
1897.

Preface.

In the following pages a solution of the problem of the length of gestation in Mammalia and Man is essayed for the first time from the embryological standpoint. The question has often enough been examined by physiologists and gynecologists, but, if Harvey's attempts at its explanation be excepted, it has never yet received consideration as a problem of embryology. None the less, there can be no question, that all pertaining to the development of the embryo forms part of the science of embryology, unless this word mean but the study of the coming-into-being of the parts of the embryo, and not of the whole organism. Embryology, as usually understood, concerns itself at the present day almost exclusively with questions included under the former definition, and, unfortunate though it be, a science of the embryology of organisms hardly exists.

Yet no subject could be more interesting in its study, none more promising of results.

The coming-into-being — das Werden — of an organism is the most wonderful phenomenon in nature.

Our knowledge of this, even in the commonest animals, is lamentably deficient; while of subsidiary things, such as the fate of the blastopore, the nature of the mesoderm, the modes of formation of the germinal layers, etc., an immense literature has been created during the last thirty years.

Recapitulatory phases have been searched for in various forms during the greater part of the present century, and with what result? When embryologists survey the supposed evidences of the "biogenetic law", they must, surely, be impressed with their poverty — a scantiness out of all proportion to the time and energy expended in their pursuit!

What has recapitulation ever explained? What services has it at any time rendered to human knowledge? In its origin a mere flight of fancy, it came into being almost without apology, and in its subsequent career it has, if possible, given less and less reason for existence than in its infancy.

Although Oken was not the very first to enunciate it, he it was, who foisted it upon the science. In his writings it plays a large part, and at the present day it is, in fact, a fragment of the "Naturphilosophie" of Schelling and Oken.

When search is made for the facts, on which it may be supposed to have been founded, they are discovered to be only conspicuous by absence. Oken himself, remarkable man as he undoubtedly was, never made any discoveries, which by the wildest stretch of the imagination could be regarded as pointing to recapitulation. Beyond the discovery of the umbilical vesicle, and the recognition of the correspondence of it and the yolk-sac, the single

embryological fact, standing to his credit as an investigator, is the presence of a double loop of the gut projecting into the yolk-sac in the pig and other forms at certain periods of the development; but no upholder of recapitulation — unless it be Oken himself — has ever seen in this any evidence in its favour.

With so many embryologists still adherents of this ancient superstition, it is, perhaps, not wonderful, that the theory of an antithetic alternation of generations [1]) as underlying Metazoan development should be stigmatised as "wild and absurd".

A theory — like that of recapitulation, for instance — may be wild, if it be set up regardless of fact; it may be absurd, if the facts be notoriously opposed to it.

Antithetic alternation may be based on few facts — that is something, which a century's work would totally alter — but it was in its zoological birth based on some, and it has yet to be shown, which, if any, facts of the science are decisively against it.

And, if it should ever show signs of degenerating into decrepitude, and of inability to cope with and explain undoubted fact — a contingency, which its advocates need never fear — then will be the time to disown it, and to seek a better explanation.

Every advance is bound to meet with opposition, and even the trifling idea, that an antithetic alternation of generations may conceivably underlie, and explain, the peculiarities of Metazoan reproduction, can be no exception to the rule. Has it not almost always been absurd to

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1) A definition of this term is given in appendix c, p. 101.

suggest, that anything contrary to human experience might exist in fact?

The present writing, which is the natural sequel of "Certain Problems of Vertebrate Embryology", may be deemed by some to be quite independent of the theory of alternation of generations.

If it were granted, that, with the facts of the present contribution, the conclusions would naturally follow without antithetic alternation, it must be insisted, that some or other of these were revealed only by this latter as by a key, and that, if it did not underlie the development, these would necessarily be different from what they are. One might say, for example, that the functional period of the allantoic placenta in Eutheria was always some multiple of the normal life-span of the asexual generation or *phorozoon*.

Indeed, if the reproach be made me, that, in attempting to set up an antithetic alternation of generations as underlying the development, the facts have been strained, and do not bear at all the interpretation put upon them, the reply is not to seek.

What other meaning do they convey? If my reading of the facts be all at sea, it has still to be proved, that this is so. But it would then appear, that, in avoiding the alternation, Nature had made so suspicious an attempt to imitate it, that, had she adopted it, she could hardly have acted otherwise than she has done in her workings.

Probably by two or three years' further work and experiment the results of the present writing might have been much extended and strengthened; but delay in

publication has appeared undesirable for many reasons, not least of which is the pressure of other research, now far advanced towards completion.

The subject is too vast to allow of exhaustion by the work of one or two years, no matter how long previously prepared for, or how diligently carried out. Principles are the main things, and the exposition of these has alone been attempted. Greater detail and exactitude could only have been gained at an expenditure of time, money, and labour disproportionate to the end. And with what result? Mathematical accuracy in the conclusions would have only made firmer what is here already sufficiently established as fact. In the course of the investigation the former has continually asserted itself, and, finally, has become amply sufficient for present purposes.

If in most cases exactness to a day have been obtained in the various factors, wherein would lie the further gain in carrying-out precision to hours or minutes?

Others may find themselves in a far better position than the writer to follow up and explore these new regions. To them, and to the ever-increasing band of seekers after the modes of Nature's workings in development, this little volume may be commended, in the hope that they will examine it in an unbiassed spirit, and criticise its shortcomings impartially, not forgetting withal, that its author had but one aim — the discovery of Truth.

24th July 1897.

Contents.

"Nach ewigen, ehrnen,
Grossen Gesetzen
Müssen wir Alle
Unseres Daseins
Kreise vollenden."
Goethe.

Introduction.

In the lower animals, more particularly in those which live and reproduce themselves in water, the cause of birth, especially in the absence of uterine gestation, and the factors, which determine the ovulation period or periods, may possibly be in many cases not far to seek. A star-fish, for instance, may be said to be "born" from the moment that its parts are complete, i. e. as soon as it has obtained in its development such a state, that its individuality is an accomplished fact. Many animals come forth into the world long after the epoch is reached, the critical period, at which the organism, as the form at which the development has all along been aiming, has first actually obtained its full complement of organs, whilst others again begin their own free life at the critical period itself.

It is quite out of question to consider all of these cases here, even where the controlling conditions are known, or can be guaged. Our concern is solely

with the Mammalia, and with those of them, an overwhelming majority, in which uterine development has been adopted.

Something, some cause or causes, must govern the time at which the offspring is born into the world. Some law or laws must determine the period of gestation.

This latter, as is well known, is only variable within narrow limits in a given species. In certain cases the range of variation may extend apparently to a week or two, in others it may be limited to a day or less.

The period, then, is fairly, though not absolutely, constant [1]) for a given species, and, while it is often the same for closely allied animals, as in dog, wolf, fox, though perhaps not invariably so, as in rabbit and Guinea-pig, it varies within very wide limits, when the whole of the Mammalia are taken into account. Thus, while an opossum brings forth its young some 13 days after copulation and 8 impregnation, the period of gestation is almost 20 days in the mouse [2]), 30—31 in the rabbit, some 56 in the cat, 58—64 in the dog, 4 months in the pig, 5 months in the sheep, 12 lunar months in the horse, and so on, for even with a year the limitation of time is not reached.

As the period is practically constant for the species, and as it can be a different one even in allied forms, it may be suspected, that it is based on some law or laws, though it is, perhaps, not so obvious that the same law may govern all cases.

Attempts have more than once been made to reduce

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1) The variations observed will be considered, and an attempt may to reduce them, subsequently. (Compare appendix b.)

2) Sobotta's results confirmed by my own.

the gestation to correspondence with a given number of menstrual cycles or of ovulations, and there have even been those, who fixed the number for the Mammalia generally as 10. It will be presently shown that the ovulation-period is itself subject to a law, and further discussion of the question may be reserved for a subsequent section. At this juncture it is only necessary to remark that the view under consideration has never yet been made so convincing as to find any general acceptance.

Another very interesting problem is that of the ovulation-period. Naturally, this has not excited anything like the same amount of interest as that of the gestation. So far as my reading goes, hardly anyone would appear to have considered it at all, at any rate, for the Mammalia generally. The only theory generally held is admittedly one only of application to a few forms, in which the ovulation-period happens to coincide more or less approximately with a lunar epoch. Neither a morphological, nor a physiological explanation of its periodicity would seem to have been attempted, and, certainly, no one has ever conceived, or rather enunciated, the idea, that the law governing it might be one with an application to the Mammalia generally.

The slight attention this inviting problem has attracted may be gathered from the circumstance that, though comparative tables of the average length of gestation in various mammals have been drawn up, and I would particularise those of Tessier[1]), similar ones of the ovulation-periods, or of the heat-periods, are almost

1) Compare appendix a.

lacking. Of course, the interval has been determined with fair accuracy in some cases, but no attempt has been made to draw conclusions from their comparison. And, it must be admitted, none such could have been deduced without other data, hitherto lacking.

These, then, are the main questions to be considered in the present writing. In dealing with them we are, as will be seen, incidentally brought into contact with other problems, such as the meaning of menstruation. All these are connected together in a most curious fashion, and are thus ultimately all parts of one big problem, the mode of reproduction of Placental Mammals.

The present paper, containing what is offered as the solution of the problem, in so far as my attempts at unravelling it have as yet succeeded, may at the first glance strike the reader as of the nature of speculation.

A reproach of this kind, because not merited, would not touch the writer very deeply. It may be admitted that speculation, unaccompanied by research, may too often deserve reprobation. It is the method practised by Oken almost to the exclusion of research, and since his day it has had many adherents. Many supposed facts of zoology still find their only foundations in the dogmatic utterances of men, who never troubled to look and see, if their ideas received any confirmation in nature, and some of these dogmas are still upheld, even taught as facts of the science, although they came into being without proper, or, indeed, any credentials, and although the traces of their original parentage may have been lost, or forgotten [1]).

1) An instance of the kind of "research" which was wont to set up "facts" is afforded by the history of the swimbladder-

The investigations, which have resulted in the present paper, have been neither slight nor simple in character, although such that their issue could be stated in a few words.

The conclusions to be set forth depend primarily on what I have termed the critical period [1]) or phase of the development, its nature and its determination.

It was, of course, necessary to discover the critical phase itself, and, although the matter may now appear so simple and obvious, it was only towards the end of eight years of work that this revealed itself.

Once found, this key of many enigmas of Vertebrate embryology, renewed work was required to fathom, as far as possible, its nature and characteristics; and, though progress has been made, the opinion may be permitted, that all its peculiarities will probably require years of work and many observers for their complete elucidation.

To gain a fair knowledge of this period in the Mammalia the study of additional types has been a necessity, and five new ones, i. e. a Marsupial, *Trichosurus vulpecula,* pig, sheep, mouse and cavy have been more or less investigated.

Two other important points required to be cleared up. These were the period of formation of the allan-

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lung homology. Its origin seems to date to Oken, who simply in his dogmatic fashion wrote: — "Die Fischlunge ist die Luftblase oder Schwimmblase. Ich führe die Beweise nicht an. Wer den Bau kennt, dem ist es gewiss, wer aber daran zweifelt, der wähnt ihn nur zu kennen, und dann sind die Beweise vergebens." An error once planted on the science takes root and becomes a superstition. Not even the opposition of a Carl von Baer or a Johannes Müller has yet been able to eradicate the above dogma.

1) See appendix d.

toic placenta and the average length of time occupied by development to the critical period in various mammals. A year ago it was insisted that the allantoic placenta must first begin to be formed at, or only slightly before, the critical period. In pig, sheep, rabbit, and man the latter of these two alternatives has turned out to be correct. In this, as will subsequently appear, an important fact has been established; for from the known cases it may, and will, be concluded, that the period, when an allantoic placenta first comes into actual operation, is the critical phase in those cases, where the former is known, but where, from lack of suitable material, the latter has not been determined.

The importance attached to the average length of gestation from fertilisation to the critical period may, when he first reads the phrase, being an incredulous smile to the face of the reader.

He probably is, as the writer used to be, until his eyes were opened, impressed with the absolute irregularity of the early development in mammals. If he be not himself a worker in mammalian embryology, he may have read, for instance, the classic works of Bonnet and Keibel on the sheep and pig. And from these he may have gathered, among other impressions, that of variations in degree of development among embryos of the same age.

So far as the early development is concerned, i. e. that prior to the critical period, this conclusion apparently stands on a firm foundation of observation and fact.

It has long been, is still, and, notwithstanding all urgings to the contrary, may long continue to be, a cherished belief of embryologists, that everything of importance hap-

pens in the very earliest phases of the development. Moreover, what then takes place may be made, but erroneously, the measure for guaging the subsequent development.

How little there exists of a comparative embryology of later stages may be inferred from the circumstance, that the discovery of the existence of a corresponding phase of development, the critical phase, was only announced barely a year ago, although this phase has been governing the development of all sorts of Vertebrates for untold ages. And, again, the little attention later stages attract may be gathered from the prevalence of the curious idea, as yet totally unsubstantiated, that there may be several more critical phases, in a morphological sense, in addition to that already described.

On the nature of the critical phase itself more information will be given subsequently. At this juncture we are only concerned with the question of its relative fixity in time in mammalian development. It is one of the commonest experiences of an embryologist that the embryos contained in a given uterus, say of a pig or rabbit, exhibit variations in size, and, what is of more importance, in the degree of development, always provided that they be in phases prior to the critical one.

It is quite otherwise, when a uterus containing embryos of the critical phase comes into his hands. If one of the contained embryos be in the critical phase, as judged by its external characters, then the remaining embryos will either also be in the phase, or so near it, that it could have been a question of but one or two hours additional development and they, too, would have reached it. That is, of course, excluding abnormalities. von Baer, Bonnet,

and Keibel have noted the frequency of such in the pig, and my own experiences during the present year have been similar. Such abnormal embryos, so far as they have hitherto come under my notice, have invariably been such, that it was quite beyond their powers to have ever reached the critical phase [1]), and, therefore, they are, in respect to the time-question, negligible quantities.

All my experiences go to show, that in mammalian development the critical period is reached in any species in a space of time, which is relatively fixed for the species, though it varies in different species, and even in the individual, albeit in the latter case but slightly as a rule.

This conclusion was not arrived at suddenly. It is not of the nature of a leap in the dark. Neither is it according to the Okenian method [2]) of solving problems. The first suspicion of something of this kind arose, when last autumn the fact was noted, that the critical period of the rabbit was reached about the middle of gestation. This was the clue, which set agoing the inquiries, of which the present writing is a faithful report.

The thing was significant enough, but in itself it was only the sign-post of a very difficult and thorny path.

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1) The critical phase presents an insuperable barrier to most abnormal embryos. In all the hundreds of post-critical Vertebrate embryos (fishes and mammals), which I have seen, not a single one exhibited any great abnormality. In the phases just prior to the critical period they are in the pig very commonly met with.

2) From the fact, that mammals possess a double loop of intestine projecting into the yolk-sac at certain periods of development, Oken concluded that "all embryos must of necessity be *born* with an umbilical hernia". No attempt was made to see if this held in any case as a rule.

It was the index of the way at the beginning of the research, but at times this became a difficult maze, and sometimes the track seemed to give out entirely, or led into a cul-de-sac.

How many hours the writer has pondered over the difficult puzzles, with which his pursuit brought him face to face, how often he has had to commence the working out of some new point on his material, and what attempts at the gaining of new material have had to be made, all these need not be here detailed. The task would have been no labour at all; for the conclusions to be drawn would have been clear, had there existed in the literature of embryology full accounts of the development of various mammals, accounts neglecting no details, insignificant though they apparently might be, of time, size, or characters.

And this brings me once more to speak of one of the most glaring defects of practically all recent work on the history of the mammalian placenta.

Broadly speaking there are two sorts of Vertebrate embryologists. The one preserves and studies the embryo, throwing away the "membranes"; the other prizes the membranes and placenta, while rejecting the embryo. Possibly both are at fault, but the latter is by far the more serious transgressor. As a general rule he, who is interested in the placenta, seems to forget, that after all it is, so far as the foetal portion is concerned, only part of an embryo, and, what is more important, of a particular embryo with characteristics of its own. If it be recognised, it is, none the less, far too frequently ignored, that a given phase of placental development is in corres-

pondence with a certain phase in the characters of the embryo to which it belongs.

More than one prominent embryologist is now preaching the necessity of accuracy and detail in research, and this is no less desirable in the region of placental investigation than in general embryology. It cannot be said that an account of a given stage of placental development, however detailed and accurate it may be, is sufficiently so, if all mention of the embryo, of which it formed a part, be wanting.

To embryology in general a great service would be rendered, and much work in years to come would be rendered unnecessary, if to every placental description a brief account of its embryo were attached.

If this included the state of development of its chief organs, it would be all the more valuable; but, in many cases, it would suffice, if it included the external characters, age, when possible, and size. Half a loaf is better than no bread, but at present accounts of placental research are like stories half recounted, and — it is the unfortunate thing about it — stories which will have to be re-told sooner or later, because of their sins of omission.

Much labour would have been spared myself but for these omissions, and, possibly, additional evidence for my conclusions might have been gleaned, had those, who have gained laurels in the field of placental research, bestowed a little of their attention on the embryo, whose placenta they were describing.

The number of forms to be dealt with is somewhat limited. None the less representatives of several widely divergent genera of mammals are considered.

A larger number would have entailed very great expense, and their study would have required a very long time. Under the circumstances I have tried to do the best. A research of this kind, if carried out to the fullest extent possible, cannot be accomplished alone by one man, unaided by funds from external sources. To the works of others I am deeply indebted. If there be any value in my gleanings, it is to their labours, far more than to any of mine, that the result is due.

Lastly, let it be stated, that my conclusions would not have found themselves in print, if there had been any doubts in my mind as to their general validity. They have repeatedly been put to the test in the course of the work. Doubtless, there are mistakes of detail here and there in my conclusions, but the general thesis will — at any rate such is my belief — stand all tests.

I. The critical phase.

As the present writing depends entirely on the nature of what I have termed the critical phase [1]), it is of prime importance to consider this phase or period and its characteristics. For an account of the facts and factors, upon which the occurrence of the critical phase was first established in fishes, and its existence in the development then extended to include the opossum, rabbit, human embryo and other mammals, the reader may be referred to the work published last year [2]).

1) Compare appendix d.

2) Beard, J., On Certain Problems of Vertebrate Embryology, Jena 1896.

On the present occasion the characters of the critical phase, in so far as they relate to fishes, will be very briefly recalled, while more detailed consideration will be given to this period in the Mammalia.

The development of a fish, — or, indeed, of any Vertebrate, and of almost any Metazoan — is never, and can never be, a direct one. The fertilised ovum by repeated divisions gives rise to a great number of cells, but these neither become arranged to form directly an organism like the parent, nor do they as a whole become converted into the foundations of the adult body. An analysis of the development from the fertilised egg shows, that its a transient products first of all give rise to an organism, more or less simple in character. This organism in Invertebrate animals is very frequently represented by what we term a larva, such as a *Trochophore, Pilidium, Bipinnaria, Pluteus* &c. This larva, wherever found, may be spoken of as the *phorozoon* or bearing animal. It is an asexual organism, and, at the present day at any rate, the sole motive of its existence is to give rise to a sexual individual of metazoan rank, the gametozoon or sexual generation. In the formation of this latter the only part of the phorozoon habitually made use of is the original alimentary tract. The remainder of the gametozoon is formed from special cells set aside for the purpose, and these, like the cells of the sexual organs of a Metazoan, never form any real part of the phorozoon-body. Under the theory of an antithetic alternation of generations the continuity of the germ-plasm is as real a conception, as it is under the erroneous theory of direct development. The phorozoon is always very simply organised. It may, and often does,

develop sense organs, a nervous system, locomotor and excretory organs of its own, but neither morphologically nor physiologically do these attain any considerable degree of complexity.

Taking away all these special organs, — and in doing this we are only imitating Nature, for it is clear that under given conditions she reduces the phorozoon to the grade, of which we are about to treat, — taking away these special organs, what have we left? An organism, which is little or nothing higher than a simple gastrula. A greater reduction than this is impossible; for, if it could be carried out, it would yield something, which could not be regarded as at all of metazoan organisation. Even the very simplest phorozoon must present at least an arrangement of two layers of cells, an epiblast and a hypoblast. The latter is essential, because otherwise the organism would be unable to feed itself.

Wherever the development is such that no great amount of food is present in the fertilised egg, and where secondary conditions, like uterine development, do not obtain, a phorozoon or larval stage is always present.

But how the picture becomes altered, if a large store of food-yolk be present in the egg!

Here we no longer find an obvious phorozoon, and its existence can only be inferred from the identification of its parts.

The gulf between eggs with no food-yolk and eggs with a large bulk of this is a very wide one, and the change from the one sort of egg, and with that in many cases the passage from holoblastic to meroblastic cleavage, must have been a gradual one.

How has it been effected? Doubtless there is a great advantage to the developing organism in furnishing it with abundant nutrition, ready to hand; a usefulness still greater, when something is left over from the nutrition of the phorozoon to provide for the needs of the next generation, the gametozoon.

Are we to conclude that Nature recognised the utility, and set to work to realise it? Or shall we not surmise, that it was all something with a very small and almost accidental beginning, and with a start brought about by extrinsic circumstances, the intrinsic importance of the matter gradually becoming apparent, but only as it was slowly evolved?

It has, I think, been noted by others, that one of the most potent factors in reducing larvae or phorozoa has been the inclusion of the fertilised egg within a case or membrane, an egg-capsule in a wide sense, in which the early development could be effected. Probably, however, an egg-shell was not the primary structure in this procedure.

The first step in the series was, so it would seem, the deposition of a mass of eggs in a cocoon, and, thus, the egg-case of an *Arenicola* or of a worm, was the forerunner of an egg-shell[1]).

An examination of the purse or egg-capsule of a dogfish or skate, must always awaken feelings of admiration and wonder. A structure like this, so obviously designed to certain ends, so perfectly adapted to the needs of the organism cradled within it, is one of the marvels of creation.

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1) Not of all egg-cases, only of those secreted by some structure outside of the ovary.

Within the purse lies the egg itself, embedded in a semi-gelatinous mass, which in the lowly dog-fish or skate can have as its only function, — a nutritive one being out of question, — that of protecting the delicate egg from the effects of shock, until the blastoderm shall have enclosed it. This same egg-white, which has no appreciable nutritive value in fishes, becomes altered into a food-substance in higher forms.

In Elasmobranchs it remains semi-solid, until acted upon by the developing organism [1]), and then gradually, as the yolk gets enclosed, becoming fluid, it permits the yolk-mass to move about; and, finally, when completely fluid, it brings the interior of the shell into communication with the external medium by means of preformed apertures, which till then were blocked, and thus at the proper time water of respiration is admitted to the developing organism.

How much might be written, and how much will be one day, on the form of the capsule itself. It surely had a history, possibly not less interesting than that of the creature, with whose well-being it is united!

But to return to the cocoon, and to endeavour, however imperfectly, to trace how it was the forerunner of a skate-purse on the one hand, and of a large-yolked egg on the other.

A cocoon, such as that, in which *Arenicola* deposits its eggs, i. e. a very simple structure formed by a sexual duct, and containing a great number of small eggs with little food-yolk, may be looked upon as the beginning of the process.

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1) As established by Johannes Müller.

Larvae are hatched out within the cocoon, and live there, as long as they have yolk to consume. If they then find no other nutriment in this structure, they must emerge, and seek for food elsewhere. If there be unfertilised, or undeveloped eggs, or abnormal, or degenerated larvae along with them, these may serve as food for the others.

There are cases among the Mollusca, *Purpura* and *Buccinum*, in which this cannibalism is the normal course of events. A few of the eggs develop quickly, and become gastrulae with large mouths and muscular gullets. These few very soon use up their own food-yolk, and then proceed to devour their fellows, which have either not developed at all, or only gone a little way. If this were carried to an extreme, — and it is probable that such cases do occur, — it would end in there being only one phorozoon or larva left, gorged with food-yolk. The original cocoon, by the solidification of its outer walls, while the centre remains semi-fluid, will thus practically become an egg-case for one phorozoon. And this will be realised in fact, if the eggs to be consumed, instead of being deposited as separate entities within the cocoon, are joined to the one, destined to develop, while in the ovary. This is, of course, really what happens in a great many cases. The originally great number of eggs in the cocoon becomes reduced to one by the conversion of the rest into yolk-material in the ovary itself, and thus the cocoon becomes an egg-case for one egg. But, though such an egg contains a large amount of food-yolk, in many instances this cannot be retained within the cells of the phorozoon, and the latter must first of all reach the gastrula stage, before it can begin to enclose and grow round the yolk-mass, in order to annex it. Thus

it is, that the growth of a blastoderm, i. e. of a flattened gastrula over a yolk-sac, is exactly comparable to the devouring of yolk-masses by a *Purpura*-phorozoon. The end is the same, and probably the beginning was the same in both.

If uterine development be initiated, the phorozoon, formed from the fertilized egg, becomes a parasite.

There are two possible ways of nutrition open. If yolk be present, the phorozoon may grow over it and annex it, as it did, before the parasitism was initiated (e. g. *Acanthias, Mustelus vulgaris, Torpedo*). Or, with uterine development, the yolk may disappear; and, instead of feeding the phorozoon by means of a prepared yolk-store, its nutrition may be provided for as required by secretion from the uterine walls. In days gone by the phorozoon annexed the yolk, and fed upon it by means of a yolk-sac of epiblast and hypoblast. To do this the yolk-sac-covering had to be formed by the gastrulation [1]) in every development, and after the yolk became reduced or lost, the process was still gone through. Probably uterine nutrition of the phorozoon began towards the end of its life, and was gradually carried to earlier periods of the development.

If this were the case, the yolk-sac, i. e. the nutritive portion of the phorozoon or larva, would naturally be the part to become attached to the uterus and to form the original temporary placenta.

There are two things to be noted about this loss of the

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1) It will perhaps be admitted, that gastrulation is not complete in an Elasmobranch, until the blastoderm has grown over and enclosed the yolk. At any rate, it is not until that is done, that yolk-blastopore and neurenteric canal disappear (Sedgwick).

yolk. Firstly, that the portion destined for the nutrition to the critical phase, i. e. during the phorozoon-period, was probably lost in mammals subsequently to that portion set aside for post-critical nourishment; and, secondly, that with a yolk-sac containing yolk the hypoblast is the active medium for its absorption, whereas with the loss of yolk the absorptive activities become transferred to the epiblast of the yolk-sac, i. e. to the part in contact with the uterus.

The consequence is, that a yolk-sac placenta, ecto-placenta, or trophoblast is always ultimately referable, as was elsewhere insisted, to some part of the epiblastic covering of the yolk-sac. It is clear that this is the case in sheep, pig, and, especially, in the horse, and a shifting of position of such a trophoblastic ring as that on the yolk-sac of the horse would furnish the ectoplacenta of a rabbit, cat, or of any other mammal, where it is not diffuse.

This change in the activity of the yolk-sac epiblast, and its conversion into what we term the chorion, amply account for the fact of its separation from the hypoblast of the yolk-sac, whose importance has, in many cases at least, become largely diminished. While the embryo-mammal is in course of formation, while by a process of epigenesis its parts are being laid down on a phorozoon, (i. e. the blastoderm with its extensions, the yolk-sac and chorion), the nutrition of phorozoon, and through it of the embryo coming-into-being — des werdenden Embryos, to use an apt German phrase, — is effected by a placental attachment of the phorozoon, by an ectoplacenta, trophoblast, or yolk-sac placenta.

This continues so long as the embryo is only in course of arising, so long as its parts are incomplete. But, anon, there comes a period, and with it the critical phase, when the embryo has acquired its equipment, when its parts, though not yet fully elaborated, are all in existence, and when it is ready to become independent of its transient or larval foundation, of its foster-parent, the phorozoon.

This epoch, when the embryo is first completely there in all its parts, when it first *beginning* to be that, at which the development was aiming, this commencement of the critical period in a wide sense, corresponds also with the commencing degeneration of the phorozoon or larva. It is undoubtedly a problem for consideration, that of the co-incidence between these two factors.

There can exist no doubt whatever, that the initiation of the critical period in the development of any Vertebrate, brings with it the commencing degeneration of various important structures, of things, which have no place in the organisation of an embryo as a member of the sub-kingdom Vertebrata. It has been elsewhere demonstrated, that the commencing degeneration of the transient nervous system of various Elasmobranchii, of the hypophysis cerebri as the remains of a larval mouth, of the notochord, of the merocytes, of the yolk-sac itself, all date from this epoch, and the same is true of the yolk-sac of Mammals (e. g. mouse and rabbit)[1]), of the mammalian notochord, of the hypophysis cerebri, of the chorion, and, especially, of its trophoblastic portion. It is by no means probable that

1) Compare Duval, "Le placenta des rongeurs", and Arthur Robinson, "The nutritive importance of the yolk-sac", Journ. of Anat. and Physiol., 1892.

all the retrogressive changes, which then set in, have yet been recognised, but those already known appear to be of sufficient importance, more especially when compared with the progressive events of the same period, to rivet the attention and to demand explanation.

Why should these retrogressive changes take place at all, and why should they commence at a fixed epoch in the development, which is one and the same throughout the Vertebrata from the fishes to man himself?

Whatever may have been the course of events in ages past, the connection between the critical period and the commencing degeneration of the phorozoon is now not difficult to understand.

In former times it may have been, that there was at this period a miniature struggle for existence between the two generations, of such a nature that, other things being equal, the victory of the embryo or sexual generation, if only because of its better equipment, naturally ensued. Such a struggle may take place still in certain cases, where there is what, with no attempt at explanation, but with a tacit expression of ignorance, is termed "abrupt metamorphosis", such as in *Phoronis*.

There are in the normal development of a Vertebrate no signs of any decisive struggle at this time. The development apparently goes on as smoothly as clockwork at the period, when the sexual generation establishes itself, and provides for its own nutrition; and the degeneration of the phorozoon commences with the same mechanical regularity. If the precritical development be abnormal, the proper procedure at the critical period may be suspended, the development may be arrested, or it may, owing to non-

degeneration of parts of the phorozoon, become more abnormal. Even under the most favourable conditions, as will be shown subsequently, the embryo is some time, before it emerges from the phase, and before its own nutrition is properly established.

But, as a rule, the asexual generation or phorozoon prepares to leave the scene, and evinces not the slightest disposition to stand upon the order of its going.

Its task is accomplished, in that it has brought to a certain state of maturity the sexual form, which took its first origin in and upon it. Its purpose — if one may use the word, when necessity seems to be the more appropriate term — its purpose is fulfilled.

The course of its degeneration, particularly as seen in Elasmobranchii, reminds one of senile atrophy, and many of the phenomena, which I have already described in the development of *Raja,* tend to confirm this judgment of its nature.

If in the past the phorozoon possibly did not accept dismissal without a struggle, if in the present the length of time required for complete degeneration may be as prolonged as a year or longer in certain cases, its whole course from beginning to end points to symptoms, which are best explained as due to senile atrophy.

As in the course of ages the average life-time of the individuals of a species has been fixed by causes extrinsic to the single person, so here one may speak of a life-span, determined, not by the intrinsic capacities of one phorozoon, but by inexorable necessity, from which there is, and can be, no appeal.

An animal, no longer in possession of reproductive

powers, is from the point of view of Nature useless; but its continued existence may be tolerated, if it be not in the way. A phorozoon, which has safely carried a gametozoon to the critical period, is not merely effete, it cumbers the ground, and sooner or later must be suppressed.

"Eine Larve, welche die neue Generation erzeugt hat, hat ihre Aufgabe erfüllt und kann vergehen – die Entwickelung geht doch fort." (*C. E. von Baer.*)

II. The Critical Period in Mammalia.

As in other cases, the morphological and physiological critical phase is here reached, when all the parts of the embryo or sexual form have been laid down, and until that period the embryo is nourished by a yolk-sac placenta or trophoblast. As a general rule this is the only nutritive structure formed in the development of a marsupial. Such appears to be the sole apparatus of nutrition during uterine life in such marsupials as *Didelphys, Hypsiprymnus, Macropus* and *Trichosurus.* An allantoic placenta can have no functional period in these forms, for their uterine life is finished by the time, that it would begin to function. As in these instances there is in fact no such intra-uterine apparatus in existence, when the critical period is reached; the embryo or, following the terminology of His, the foetus, has nothing before it but starvation, if it remain *in utero*, and it follows, that it must be born into the world, in order to seek nutrition from

another source [1]). It has elsewhere been insisted, that a yolk-sac placenta or trophoblast can only function till the critical period, for it is part of a phorozoon, whose life-limit is then reached, and whose degeneration must then begin. Why *must* this be so? The answer to be given is, that the limit of the normal life of the phorozoon is reached, as shown by the facts, for in no mammal does a yolk-sac placenta or trophoblast continue to function after the critical period, and, wherever it is formed, it then begins to degenerate.

It can be proved with the requisite material, which, if of the proper age, need not be an extensive one, that non-placental mammals are born at the critical period. In the memoir, of which the present writing is a natural continuation, it was demonstrated that such was the case in *Didelphys* and *Hypsiprymnus*. Now, thanks to the kindness of Dr. R. Broom, the same facts can be established for *Trichosurus vulpecula* and rendered probable for *Macropus thetidis*. It was at first intended to describe the embryos, from which this result has been gathered, in the present paper; but, as figures are desirable for the illustration of certain points, it has been deemed better to publish the description of Dr. Broom's embryos elsewhere [2]).

In the former paper [3]) it was argued that, with the establishment of birth at the critical period in non-placental mammals, only the evolution of an allantoic placenta could inhibit this, and carry the birth over the critical phase to a later period. This was either demonstrated or shown to be exceedingly probable in certain instances, and since

1) Compare appendix r.
2) In the "Zoologische Jahrbücher", (Morphol. Abtheil.).
3) Certain Problems of Vertebrate Embryology, p. 41 et seq.

last year my endeavours have been directed to the firmer establishment of this thesis.

The existence of a critical period in a morphological sense, corresponding to that described in other cases, was set up for a number of placental mammals, but for one or two of them the evidences of a physiological one also were wanting. Since last spring these have been obtained in the cases of the sheep and pig.

It has been found, that slightly prior to the morphological critical period a beginning is made in the building up of an allantoic placenta. This is quite in agreement with all I have been able to gather from Duval's, Robinson's and Bonnet's researches, which taken together cover the development of the placenta in a very representative series of Eutheria. And, so far as can be made out from the literature and the few specimens in my own possession, it also holds good for man.

In fine, there does not appear to be the smallest doubt, that in all Eutheria the allantoic placenta commences to develop some little time, before the critical period is reached, and that this structure first enters upon its functions at or during the critical period.

As a preliminary to the formation of an allantoic placenta, the fusion of the allantois with the chorion takes place. This is, of course, a very old story. It is mentioned only to insist that, although this procedure affords the basis for a placental formation, in itself it is not any such thing. From it the placental formation proceeds apace, being brought about by the development of new blood-vessels, particularly capillaries, and new blood in connection with the allantois, or, to use an apt term employed by Bonnet

in his brilliant studies, it comes to pass by a vascularisation of the allantoic chorion.

The formation of these allantoic-chorionic capillaries begins some little time before the critical period. It must, however, not be assumed, that the *beginning* of such capillary formation and the *commencing development* of blood-cells within these yield in their first phases anything, which can be termed a placenta. Such a structure, small though it be, is first in actual existence, when some of the capillaries are complete and the blood-cells fully developed within them, when one can speak of a complete circulation, albeit still insignificant, in the allantoic chorion.

There is no nourishment to be gained from capillaries and blood-cells in course of development, the apparatus can first be of use, when some small portion of it is fairly complete. This condition is attained at the critical period, and then, although by no means fully formed, the allantoic placenta begins to function.

As a general rule, as it appears to me, the placenta at this period is very inadequate for its purposes. This may be concluded from its small size, and, still more, from the duration of the critical phase. This must be, as I have elsewhere insisted, comparatively of some length, for, especially in mammals, it is far easier to obtain embryos of the critical period, than of any other, from pregnant mammals taken at random.

The formation of an allantoic placenta thus leads to a postponement of birth until a later time, and the young is born in a stage of development, which is always an advance on the critical phase.

This is the case in *Parameles obesula* among mar-

supials. From Hill's statements, even without seeing the specimens, I am quite convinced that birth- and critical periods do not here coincide. To name one point only, in the newly-born *P. obesula* the lower jaw is ossified [1]), and this is the case at birth in no aplacental marsupial yet examined, and at the critical period in placental forms no part of the skeleton is ossified.

The introduction of an allantoic placenta was undoubtedly a circumstance bringing great advantages, but these were such, as could only be gained by making good use of the opportunities it afforded.

It led to prolonged uterine gestation, and, as the time of development to the critical period is always a comparatively short one, the length of the gestation and of the functional period of the allantoic placenta stand in intimate relation. Where the gestation is prolonged, the placenta enjoys a lengthy functional period, where it is short, there also the placenta has a brief activity.

The period must, according to Hill [1]), be very limited in *P. obesula,* and in the mouse it is only one of some 10 days. In the rabbit the placenta is in operation for 15 days, in the Guinea-pig for about 6 weeks, in the pig for 3 months, in the sheep for 4 months, in the horse for nearly 10 months, and in man for some 230 days.

It is evident that there must be some law governing its functional period in different species and in the members of the same species, for, even at a glance, it is seen, that the functional period of the placenta is always a certain fraction of the total gestation-length [2]).

1) From statements in Hill's letters to the writer.

2) But a different fraction in different species, i. e. $^1/_2$ in the mouse, $^2/_3$ in the cavy, $^3/_4$ in the pig, $^4/_5$ in the sheep, $^5/_6$ in man, and so on.

It is variable in length even in allied forms, for, while in the rabbit it is limited to about 15 days of uterine life, in the Guinea-pig it is in operation for 40 days or more. While variable in different forms, it is fairly constant, often very much so, in individuals of the same species.

Along with its variability in different species, and *a priori* dependent on this, the degree of development of the foetus at birth is widely different in different forms. Thus, in mouse, rabbit, cat, dog, &c. the new-born foetus is blind and helpless, while the Guinea-pig can see very shortly after birth, almost at once runs about, and begins to feed within 3 or 4 days after it is born.

This advanced condition of the young at birth is still more characteristic of Ungulata, as is well known. What is it that determines the degree of development, at which in a given species of mammal the young shall be born? What decides the length of gestation? Both of these may be described as under normal circumstances well defined and constant in the individuals of a given species.

Nature has no happy-go-lucky methods about her in her workings, and as von Baer sagely remarks, "was sich immer wiederholt, kann nicht vom Zufall oder vorübergehender Laune bedingt sein, sondern muss von einer Nothwendigkeit abhängen".

To elucidate and explain the necessity in these instances will be our task in the following pages.

III. Ovulation in Mammals.

Prior to the initiation of uterine gestation the species could be maintained, and the number of its individuals

increased without any great frequency of breeding seasons. It may even have been advantageous, that as many eggs as possible should be laid at one time, the number being limited by size and other causes. Into these it is not proposed to inquire here, for the research has been confined entirely to the Mammalia.

But it is quite clear, that the adoption of uterine gestation, even in marsupials, must have had a deeply reaching effect on the ovulation, in that it initiated a new periodicity [1]). It may well have been that a similar influence was exerted by the mammary function, for the mammae are subject to limitations in number, and thus in their nutritive powers, even in those instances in which they are most richly developed. It would require the resources of a Diana [2]) of Ephesus to provide for a number of young equal to the maximum still met with in *Didelphys* or the pig. It is quite likely, therefore, that the greatest number of mammae possible determined the maximum number of young, even before the uterine influence began to exert itself. But, that the limitations imposed by the mammae could not have been inexorable ones, is evident from the circumstance, that some forms at times still produce more young than can be suckled, i. e. *Didelphys*, the pig, and, occasionally, the rabbit. While there are

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1) Compare Pouchet appendix p.

2) Or Cybele, a goddess, daughter of Coelus and Terra. She is supposed to be the same as Ceres, Rhea, Bona Mater, Magna Mater &c. In Phrygia the festivals of Cybele were observed with the greatest solemnity. Among other forms "she is represented with many breasts, to shew that the earth gives aliments to all living creatures". (Lemprière's Bibliotheca Classica, 1801.) In ancient statues and pictures of her more than 20 mammae can be counted.

14—15 teats in *Didelphys*, there may be as many as 27 young in the uterus according to Selenka [1]), and the pig, with a maximum number of 12—16 nipples, may harbour in the womb as many as 20 embryos [2]).

It appears that usually this excessive number never reaches the birth-period, for in the pig my studies have shown me, that the critical period, or, rather, the period prior to it, is the great time for weeding-out, and only those embryos destined to be born, usually a reduced number, reach the critical phase.

Returning to the conditions created by uterine gestation, it must be noted that, under the most favourable conditions, the uterus can only retain, even for a short period, a restricted number of developing "eggs". It will hardly be necessary to survey the known cases in detail.

The largest known number is in the opossum, with 27 (Selenka), there may be 14 in the rabbit, and 20 in the pig.

The smallest possible number obtains as a rule, not free from exceptions, in numerous mammals, such as whale, man, bat, monkey, horse, and cow etc. Often the number is a variable one in different pregnancies and may be increased somewhat with the number of gestations, as in the cavy, where such an increase is the rule. The

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1) Compare appendix x.

2) Such numbers in these two forms could never be suckled, for in both each suckling has its own particular teat. In *Didelphys* under the conditions obtaining this is, perhaps, not wonderful, but it is a curious instinct, which reserves a certain teat for a given suckling in the pig. I have myself seen as many as 19 in the pig, and, more than once, 14 in the rabbit. The pig usually brings forth 8—14 according to Bonnet, and 5—8 is the normal number in the rabbit.

question thus naturally presents itself: what is the most favourable condition possible in the mammalian mode of reproduction, where the number of offspring to be produced at one birth is a very restricted one? At this stage the influences of climate and seasons, which undoubtedly tend to complicate matters, must be left out of account. According to competent opinion, thus of von Baer and other authorities, the original mammals must have arisen in a warm tropical climate without marked seasonal changes, so that at first the influence of climate on the periods of reproduction may have been far outweighed by other necessary conditions.

As to what happened before the birth (from the egg) was carried back to the critical period, as detailed in an earlier publication, it would at present be futile to inquire, for the requisite data are wanting. But in another of its aspects the effect of birth at the critical period seems capable of solution.

During gestation, even if the time elapsing between fertilisation and the critical period be brief, normal ovulation is suspended. It first becomes possible after birth, i. e. after the critical period.

Here consideration of the influence of lactation on the parent must be postponed.

It will probably be admitted that ovulation, if not exactly coinciding with the birth, yet following very shortly thereafter, is the most favourable condition for reproduction under the circumstances given. The mature female is then practically always pregnant. It is impossible to establish this thesis for any known marsupial at present, but this is explained by the circumstance, that so

very little is known as to the frequency of gestation in these. But, if it be allowable to cite instances from the Eutheria, and the sequel will, I think, justify this course, very convincing examples can be referred to.

Under favourable conditions the mouse [1]), rat, rabbit and Guinea-pig are practically always with young. In all of these a new copulation and fertilisation, i. e. a new gestation, follows at once, with only a very slight interval, upon the birth. All of these forms, as a rule and under proper conditions, are ready for a new pregnancy within at most a few hours after the cessation of the old one. An experienced rabbit-breeder informed me that a doe-rabbit may sometimes bear as many as 11 litters in a year.

In the absence of evidence from marsupials these instances are very significant, for rabbit and mouse possess a gestation-period of short length and equal to but double the length of the development to the original critical period.

From these facts alone the question intrudes itself what is the relation between the latter and the length of gestation? In most marsupials the two are of equal length, in the rabbit and mouse the latter is double the former. There is further the relation of the critical to the ovulation-interval, and one asks "is the critical interval [2]) equal to, or rather less than, the interval between two ovulations?"

The critical and the ovulation-intervals in rabbit and mouse would practically be equal in length, if the critical and birth-periods of these also coincided.

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1) Compare appendix v.

2) The interval from fertilisation to the critical phase.

In the rabbit the development to the critical period equals half of the period of gestation, and if the facts have been rightly observed, half of the ovulation-interval (roughly) also.

But let us consider the case of the mouse. If this form be not allowed to become pregnant again immediately after parturition, new factors are brought into play. The ovulation, which ensues some few hours after the birth, will be spent in vain, and ovulation will recur after an interval of about $9\,^5/_6$ to 10 days [1]).

But this time between two ovulations is, as Duval's. Robinson's and my own researches have shown, approximately equal to the length of time required by development to the critical period, or one may say, that the critical and ovulation-intervals are of approximately equal length. It is probable that in many mammals the critical and ovulation-intervals all but coincide in length, but the critical interval must always be a little shorter than the latter. It may be well to make this point clear, for, if it be ignored, one may be easily led astray, as the writer was for a time.

For the sake of argument let a hypothetical non-placental mammal, whose gestations form a practically uninterrupted series of such a kind, that the animal becomes pregnant again within a few hours of the birth of a litter, be assumed to exist [2]).

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1) For a discussion of this question in its relation to the cavy see appendix f.

2) This is only an assumption in that it relates to a non-placental mammal, a marsupial with this peculiarity not being at present known. But in these so little has been made out regarding the frequency of gestation, that there is little or no unlikelihood about the supposition, if it be borne in mind, that the conditions of gestation in more than one Eutherian mammal represent in fact what is here supposed, thus, mouse, rabbit, and Guinea-pig.

In such a form the new ovulation, preceded by a short period of heat, must follow within a few hours of the birth. For the sake of illustration let it be supposed that, as in the rabbit, the new ovulation ensues 10 hours after parturition as a rule, the heat-period being confined to the interval from the 3rd to the 6th hour. As we are dealing with a non-placental marsupial, the young are born at the critical period. Copulation, resulting in the new gestation, will take place in the 3rd to the 6th hour after the birth. The new batch of eggs will be fertilised, and, thus, the new gestation will actually begin, some 10 hours after the birth. From this it follows, that the length of the development to the critical period, i. e. to the birth, will fall somewhat short of the interval between two ovulations, as a matter of fact, 10 hours short. Thus, if the period between any two ovulations be represented by 17 days 12 hours, the birth will take place in 17 days 2 hours, i. e. 10 hours before the new ovulation, and, therefore, the critical period will be reached in 17 days almost exactly, if 2 hours be allowed for the completion of the birth.

It is evident, that, if there be, as beyond doubt there is, a relationship between the length of development from fertilisation to the critical period and the ovulation-interval, the former must be somewhat shorter than the latter. It cannot be longer, for that would defer a new gestation to a still later ovulation, and would render an ovulation immediately before birth abortive.

The two cannot be exactly equal, for such a state of things might lead to a fatal delay in fertilisation [1]).

1) Unless, as may, perhaps, happen, the occurrence of the birth should serve to retard the coming ovulation.

IV. The Critical Unit.

The conclusion, as to the relationship between ovulation and the length of development to the critical period in the hypothetical case taken, is one, whose importance cannot be over-estimated. The bearings of the matter will be rendered obvious in the course of the following pages, and at this juncture it may be advisable to define an expression to be frequently employed in the sequel.

It is necessary to adopt some such term, as that about to be explained, if only for the sake of conciseness. But there is little or no doubt in my mind, that in its future career in mammalian embryology *"the critical unit"* will abundantly justify its existence.

In any given species of mammal, owing to the *original* necessities of the case in the non-placental ancestry, it was brought about, that there must be some close correspondence, as illustrated above, between the length of the development *in utero* (i. e. from fertilisation to the birth at the critical period) and ovulation. If either of them were variable to any extent, the ovulation could not be prepared in advance for the birth-period, and the birth might fall short of, or, what would be far more disastrous, rather overlap the succeeding ovulation, and thus render it abortive. If they were to go hand in hand, the one must control and determine the other. One of them must be fixed and the other must adapt itself to it. Now, as it appears to me, there can be no question, that it was the critical period, which *first* became fixed to happen at a certain time after the development commenced. As argued in

my former publication, æfter the initiation of the mammary nutrition, the birth was carried forward to the critical period, and the mammary nutrition was pushed backward to the same epoch, with resulting loss of the yolk, formerly set apart for post-critical nutrition [1]).

When the birth- and critical periods had thus been brought together, the ovulation-interval could adapt itself to this condition, as soon as it became stable. Thus, the original correspondence between the two was effected.

In all the forms, which have as yet come under my notice, it appears highly probable, that the length of time, elapsing between the fertilisation and the attainment of the critical phase, is fairly constant. To establish this with mathematical accuracy is almost impossible, for it would require a large series of very exact experiments on many forms, and, moreover, an absolutely accurate knowledge of the moment of fertilisation in every single case. It need hardly be said, that the latter could never be determined with any approach to mathematical correctness.

But, as will appear later on, if we accept as fairly fixed the interval of time mentioned above, no great error will have been made.

It is convenient, and even necessary, to define this interval; and, therefore, that period of time, which in any given species of Metatherian or Eutherian mammal represents the average duration of development, from the moment of fertilisation until with the critical period all the parts or foundations of the embryo have come into existence, may be termed *"the critical unit"*.

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1) For a fuller discussion the reader may be referred to pp. 54—58 of the above-cited memoir.

The term "critical unit" will be employed strictly in the above sense in the following pages, and it will be used as a measure, with which to guage the subsequent gestation, where this is prolonged beyond the critical period, as is the case in *Parameles obesula* and in all Eutheria.

V. Length of the Critical Unit.

The length of the critical unit in any given case has an important effect on the duration of uterine life, as will be explained later on, and it is now proposed to consider the variations of the unit, showing how they are related in different Eutheria. The shortest critical unit at present known is that of the opossum, where from fertilisation to birth the interval is about $7\,^3/_4$—$7\,^5/_6$ days (Selenka). It is probable, that short critical units are characteristic of marsupials, for in two other instances, *Macropus* and *Hypsiprymnus*, the gestation is also a very brief one [1]).

In the Eutheria, as yet studied by myself either from the literature or by actual research, the following table of approximate lengths has been drawn up:

	days		days
white mouse	$9\,^2/_3$—$9\,^5/_6$	pig [3])	28—30
rabbit (English)	$15\,^1/_4$—$15\,^1/_2$	sheep	29—30
cavy	21—22	cow	39—42 (?)
cat [2])	28	horse [4])	42
dog [2])	29—32	man	46—47

1) Compare appendices x and y.
2) Compare appendix i.
3) Compare appendix h.
4) Compare appendix g.

It will now be necessary to examine these numbers more closely, and to consider what reliance is to be placed on their being fairly constant.

Taking the latter point first of all, in view of the objections, which are certain to be raised against the notion, that the critical unit can be fairly constant for the species. The matter has been considered to some extent in the introduction, and besides the arguments there adduced, and which may be once more briefly recalled, others not less weighty must be brought forward.

As already stated, the experiences of some embryologists go to convince them only of the irregularity of the development and of the futility of expecting to find a certain stage of mammalian development in the embryos of a uterus of known period of pregnancy.

Against this idea, so far as it applies to Metatheria and Eutheria, the facts must be brought to bear. The rhythm of development in mammals is strong presumptive evidence against any great variation, for, in many cases at any rate, the birth is fixed to take place almost with clock-work-like regularity. This argument may be held not to amount to much, and for that objection I am quite prepared, for birth is apparently, though probably not really, subject to variation in time.

More weighty grounds are to be found in two considerations. It is one of the most characteristic peculiarities of uterine gestation, that it takes place under conditions of the most equable kind. The temperature of the uterus must be very uniform and constant in character under normal circumstances throughout the whole period, and

the variations, to which this is subject, must thus be very slight and regular in nature. It is, by the way, a curious fact, the bearings of which will have to be considered when dealing with the relative lengths of gestation in different species, that this temperature must be very similar throughout the mammalia, for in them the body-temperature in health is almost everywhere much the same.

A fixed, or but slightly varying, temperature is one of the first requisites for a regular rhythm in the development.

But the regularity of the development is rendered far more certain, when it is studied throughout the length of the critical unit in any given instance.

The greatest variations observed relate to the early stages, and — this is my experience — the earlier the stage examined, the greater will be the variations among the individual embryos. To much importance may not be attached to this, for many of the variations may be such, that only a very brief interval of time [1]) might be sufficient to rectify them, and some of them may be making for an abnormal condition, which ultimately would have been fatal.

As one approaches the critical period, the variations in degree of development become less marked, and among the embryos of one uterus, where some have reached the period, the remaining ones will either be in the critical phase also, or so near it, that only a very brief indulgence

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1) Compare appendix x.

in the matter of time would have enabled them to reach it, providing they were normal.

I possess several different batches of rabbit- and pig-embryos of the critical period. An abnormal rabbit-embryo has never yet met my eyes, probably, judging by pregnant uteri of earlier stages, they are suppressed and absorbed prior to the critical period.

In the rabbit one usually finds all the embryos of a given uterus in the critical phase, if any of them have reached it, but one or two cases have come under my notice, where a few of the embryos fell just short of the period, whilst the others had reached it.

In the pig the experiences are somewhat different, for here in several instances all the *normal* embryos were in the same phase, the critical one, where some of them had attained it. These are, perhaps, more important than the rabbit-examples, because of the much greater number of embryos as a rule in the pig.

Sometimes, however, one does find pre-critical embryos among critical ones in the pig, but they are invariably monstrosities, and those I have seen have been of such a nature, that they could never have reached the critical phase as anything but abnormalities, i. e. they could never have got to it at all.

Moreover, it must be again noted, that, when the critical period is reached, there is always a pause in the development, and that it is some time before this again advances. Thus, stragglers, if there be any, and this is doubtful, are given a further chance.

It may, therefore, be concluded that, in Mammalia, as is certainly the case in the Opossum from Selenka's

researches [1]), the critical phase is reached in a given length of time from fertilisation, and, thus, that the critical unit is for the species a fairly constant quantity, though probably subject to slight variation in the individuals of a species.

The wide differences in the lengths of the critical units of different species are remarkable circumstances, when it is considered, that the conditions of development do not vary to the same extent.

Temperature will not account for them at all, and in forms below the Mammalia it is the most potent factor in determining the rate of development.

The supposed influence of food-yolk, one of the superstitions of current embryology, does not here come into play [2]).

Marsupials have probably rather short critical units, but differences are even here to be encountered. While *Didelphys* and *Hypsiprymnus* have, according to Selenka [1]), almost identical critical units, Owen's observations [3]) on the kangaroo, with 38 days from copulation to birth, the fertilisation-point being unknown, indicate a fairly lengthy critical unit in this form, probably double or threefold that of the opossum.

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1) See appendix x.

2) The retarding effect of food-yolk is largely mythical, for it exerts nothing approaching the influence of temperature on the rate of development. A chick reaches the critical period in six days, when incubated at 40° C, whereas the corresponding phase of development in the rabbit is reached in 15 days, and in man in 45—47 days. It will appear, as a result of the above discussion, that the rate of the development is often due to some individual idiosyncrasy, and it is, and has been, determined by many factors.

3) Appendix y.

Among the mammals in the list on p. 36 the mouse is the only form with a very short critical unit. This is so little different from those of the two marsupials just referred to, that it appears likely to be a very old one, which has not undergone alteration.

The next two, of rabbit and of cavy, are not very different in dimensions. Moreover, that of the rabbit is about double that of the opossum, and as there are no grounds for assuming, that the development to the critical period could not, if necessary, take place in the same brief interval as in the opossum, it may be suspected, that possibly the original critical unit of rabbit has been doubled in its past history, and that of the cavy trebled. It is, however, impossible to establish this in these cases.

Now, it is remarkable, that in the mouse, and probably in the cavy [1]), the critical unit approximately equals the period between two ovulations, i. e. the ovulation-unit. The bearings of this will be presently evident. All the remaining forms of the list have much larger critical units, and these again are very much the same in the two Carnivora, a group, where, probably, the critical unit does not vary very much.

I pass over the cases of pig, sheep, and cow, because the facts regarding these animals appear to be similar to those to be noticed relating to the horse and human subject. In the two latter the critical unit is a large one, and, compared with that of the opossum, quite out of all proportion to the unit of time really requisite in a mammal for development to the critical period.

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1) Compare appendix f.

In the horse, and the same is true of the pig and sheep, so far as I can see, the critical unit no longer represents rather less than one ovulation-unit, but is now almost the equal of two.

This also holds for the human subject, if the time of the menstrual flow be not reckoned, and if one calculate, as it is proposed to do in the sequel, the ovulation-unit here as equal to $23—23\,^1/_3$ days.

The matter may be left in this position for the present and further discussion postponed until a subsequent stage.

The conclusions arrived at are: that originally the critical unit of any mammal was a short one, as it still is in the opossum, that it was then doubled or trebled, and, to keep up the correspondence, that the ovulation-unit was doubled or trebled also in Eutheria, and that in many Eutheria it has at some period or other been doubled a second time without any duplication of the ovulation-unit.

For the reasons of this procedure the reader may be referred to a subsequent section on "the duplication of the critical unit".

VI. The Length of Gestation in Eutheria.

It was insisted in a former publication, that the original allantoic placenta must have been formed at, or only very slightly before, the critical phase, and, as a matter of fact,

this is the epoch, at which it still begins to function. As we have seen, it *begins* to arise somewhat before the critical period, and it commences its functions at that time, while in a very incomplete condition, so that — and this is very clear from the researches[1]) of Duval, Bonnet, Hubrecht, and others — it is not a finished structure till long after the critical period. It somewhat resembles a machine, which, when first erected, is capable of fulfilling all demands upon it; but which, as these latter increase, has to undergo extensions, in order to fulfil its task. An allantoic placenta of a pig-embryo, which is a little beyond the critical period, doubtless suffices for the nourishment of an embryo of that size, but, with growth of the embryo, its placenta also must be increased and elaborated, to keep pace with the demands made upon it. This is, of course, all quite obvious. But with an allantoic placenta in operation a problem confronts us and demands solution. What determines the length of time, during which it shall function? What decides the period of gestation?

"Its formation would at once reverse the former order of events, and would carry the birth of the embryo to a later and later period of the development subsequent to the critical stage. And in this way it would conceivably come about, even in allied animals, like the rabbit and Guinea-pig, that in the one case the young might be born at a very much younger stage than in the other. As is well-known, the rabbit is born in a blind and helpless condition, and is fed by the milk-glands for a prolonged period, whereas the Guinea-pig comes into the world almost with

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1) My own researches on sheep, rabbit and pig, also lead to this conclusion.

its eyes open, and is soon able to run about, and very soon to feed itself" [1]).

So much could be written a year ago, but at that time there was only a shadow of a suspicion in my mind, that the length of gestation was determined by a law, and none, that the latter could be, even partially, made out. It was quite clear, that, if an allantoic placenta were evolved, its first effect would be to carry the birth beyond the critical period. This still happens everywhere among the Eutheria, and, also, in at least one marsupial, *Parameles obesula*. So certain is it, that it would be a miracle, if a species of mammal existed, in which, with an allantoic placenta, the birth still took place normally at the critical period.

With the knotty problem of the length of gestation there is also that of the birth-period bound up.

An embryo with an allantoic placenta is practically a parasite upon the parent, or, rather, upon the phorozoon, and *a priori* it is difficult to perceive what determines its expulsion *at the proper time*. Nor is it clear why the time, which is the fit one in some species, would, if adopted in others, lead to premature birth and the inevitable death of the foetus.

The fixed nature of the length of gestation has been explained by some authors as determined by the length of time, during which the placenta remains normal and healthy; and they have assumed, that, when it begins to degenerate, the birth-period is of necessity reached [2]).

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1) Vide "Certain Problems of Vertebrate Embryology", p. 56–57. A better contrast would have been rabbit and hare. (Compare appendix k.)

2) Under this theory abortion ought always to quickly follow the death of the foetus *in utero*, whereas it frequently does not.

Assuming the facts of this degeneration to be correct; although, like many other things, it is less based on fact than on fancy, under it no account is taken of wide differences in the gestation-periods of closely allied forms. Why should the placenta of the rabbit begin to degenerate after some 15 days of activity, while that of the cavy can remain normal for nearly three times that period?

What causes the degeneration assuming it to exist? But for the present I leave these conundrums and the cause of birth itself, in proceeding to set up a constructive theory of the basis of the gestation-length.

In dealing with this matter, though this is introduced, and only for purposes of illustration, at the close of the research and not at its beginning, let us once more take a hypothetical case, that of a non-placental mammal, whose critical- and birth-periods coincide, i. e. with a gestation-period of one critical unit.

The form we are dealing with must also be supposed at some time in its history to develop an allantoic placenta. The first influence of this will be, as we have seen, in prolonging the gestation beyond the critical period, and thus it will also lead to the suppression, or the rendering abortive, of the ovulation, which should have followed soon after the birth at the period [1]).

Can the gestation then be prolonged indefinitely? If it could, it might vary within the widest limits among the individuals of the species. In the first instance the result of prolonging the gestation by means of the allantoic placenta would ultimately lead to the birth happening shortly before the next ovulation-period at

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1) Compare appendix q.

latest. At first it may happen [1]) anywhere between the abortive ovulation above mentioned and the next one; but, if, as there undoubtedly is, there be an advantage in lengthening the gestation; when first prolonged, it will ultimately fall to be limited by the second ovulation after fertilisation. Thus, as the critical period was originally rather less than the interval between two ovulations, the gestation-period will come to include two critical units, and no longer one only, as was the case, when birth took place at the critical period. It will, thus, also come to correspond to two ovulation-units, though, as will be seen, this may later on no longer appear to be so [2]).

It is rather a matter of regret, that at the moment few forms, in which the gestation is probably rather less than two ovulation-units, can be referred to, but, unfortunately, hardly any attempts have been made to determine the ovulation-unit. It is either certain, or highly probable, that mouse, cavy, and rabbit, fall under this category. However that may be, it is beyond question, that there exist many Eutherian mammals, in which the gestation-period is composed of two critical units, and as examples may be mentioned mouse, rabbit, cat, and dog. In all of these cases, if proper allowance be made for the interval between copulation and fertilisation, starting from the latter point, the critical period is reached, and with it the first critical unit exhausted, as exactly as possible in the middle of the gestation [3]).

This is the principle, upon which the gestation-period

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1) Apparently, but there are reasons against it.
2) Compare appendix s.
3) Compare appendix i.

of any placental mammal was originally prolonged. When it was extended beyond the critical period, i. e. beyond the first critical unit, it naturally fell to be determined and ended before the next ovulation after the one missed, and thus as naturally came to include two critical units.

The advantages thereby won were undoubtedly great ones; the young could come into the world in a much more highly finished condition, than when born at the critical period, and the marsupium or pouch could be dispensed with [1]).

But, although a gestation of two critical units resulted in the birth of more mature progeny, the limit had by no means been reached. In all the cases one can think of, the new-born young, as in mouse, rabbit, cat, and dog, are still born in a blind, almost hairless, and helpless condition [2]). By again extending the gestation, to include one or more critical units, and, where necessary, by sacrificing some of the eggs or uterine embryos [3]), a still higher stage could be attained, and the young might come into the world in a yet better degree of development.

Before discussing this further prolongation and its complications in detail, it may be well to consider one other simple and instructive instance. The young of the cavy are born, as is well known, in a much more perfect condition than those of the rabbit. They can run about at once, and feed themselves in less than a week after birth, and, if not born seeing, they have open eyes

1) Compare appendix e.

2) Compare appendix k.

3) Such new extensions may be the actual causes of abnormalities among embryos *in utero* in certain cases. The adoption of a further critical unit in the pig, for instance, would be likely to entail a suppression of some of the embryos, which now normally develop.

before they are dry. *A priori* one would expect a much longer gestation, and this is the case. While there is not very much difference in the rate of development in the early stages between these two forms, their critical periods only differing by a week, the gestation-period of the Guinea-pig is quite double that of the rabbit, and it brings forth far fewer young. Ovulation- and critical units probably roughly correspond in the Guinea-pig, and, whereas the former is probably about 22 days, my experiments and Duval's placental researches show the critical unit to have a similar length.

The gestation-period of the cavy, therefore, includes three critical units, and thus the much more perfect state of the young at birth is explained [1]).

It is unfortunate, that at the present time no further examples of forms with a simple critical unit can be brought into the discussion, and that no attempt can be made at the moment, to show how forms with the same number of simple critical units in their gestation-periods, like mouse, rabbit, and possibly *Parameles obesula,* may quite conceivably correspond in the degree of their development at birth: that a difference in the number of critical units leads to differences at birth has been shown, though not in detailed form, in rabbit and cavy, and it will later on be as apparent in other instances.

What other forms with corresponding critical- and ovulation-units should be examined is not quite clear. They must be such, as would be easily obtainable, and readily furnish the facts required.

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1) More length of the gestation affords no explanation, for the degree of development, which is reached by a mouse in 10 days, requires 22 days in the cavy, 30 in the sheep, and 46 in man.

In short, to sum up the matter, no-one is more convinced than the writer, that the detailed working out of the lines of research suggested by the present writing would be very expensive, very difficult in many cases, and would entail a life-time of labour, but that it might, none the less, lead to interesting results.

It has been suggested, that, in the Eutheria already treated of, there has probably been a doubling of the original critical unit, and, with, it of the ovulation-unit also. This appeared probable from comparison with the short critical units of certain marsupials, but no other proof could be offered.

With a great many Eutheria matters stand in a different position. When the two units no longer correspond, the one being almost double the other, i. e. when the critical unit no longer corresponds to one ovulation-unit, but is *almost* the equal of two such, the duplication, probably a second one, needs no further proof. Such are the conditions met with in sheep, pig, horse, and man, where the critical unit is a long one, and almost the equal of two ovulation-units. Matters become further complicated here from the fact, that the gestation is far more prolonged, equals more critical units, and because the young, as is natural, are born in a more advanced condition.

The ovulation-unit of the sheep is given as 15 to 16 days, and the critical unit is almost the double of this, 29 to 30 days. In the horse the ovulation-unit is 21 days and the critical unit, as determined from Bonnet's researches on the placenta, and from the figures of Ewart's horse-embryos, is from 41 to 42 days, probably nearer

the latter than the former [1]). The human ovulation-period, as will appear from the subsequent discussion on the nature of menstruation, must be taken as equal to the interval, between the end of one menstruation and the beginning of a new one, i. e., according to the researches of Loewenhardt, as quoted by Hensen, about $23\,^1/_2$ days. The human critical unit, as estimated from the researches of His, is about 46 — 47 days, as nearly as can be judged.

In dealing with the gestation of these forms we have, therefore, two points to consider specially, and these are: the critical unit and its relation to the ovulation-unit, and the number of critical units in the gestation-period.

The latter point is much the simpler; for, as the critical period, and with it the critical unit, can be determined with greater or less accuracy, it then remains only a question of the average length of gestation, in order to decide by a simple division, what number of critical units must underlie, and determine, the gestation-period. It happens, that in the cases of horse, sheep, pig, and cow, the average length of gestation is pretty well known from the experiences of breeders, and, also, from the tables drawn up by Tessier in the year 1817 [2]).

It will, or ought to be, obvious, that no attempt can be made here to elucidate exceptional and out-of-the-way cases. Averages only can be our concern, and for the following reasons. In dealing with any individual gestation, to understand all about it we require the following

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1) Compare appendix g.
2) Compare appendices a and b.

data: the interval between copulation and fertilisation, the moment of fertilisation, the exact length of time to the critical period, the ovulation-period (also in accurate figures) and the number of days and hours in the total gestation. It would also be necessary for mathematical accuracy to be informed, whether or no the gestation was from beginning to end absolutely normal, and what was "the equation of error", as it may be termed, peculiar to the particular individual, and to the particular gestation of that same individual.

If all these factors were available, then, and then only, mathematical accuracy might be attainable. Thus, in the horse, while the average of 354 cases gave Tessier[1]) a mean period of from 341—346 days, he cites two instances where the gestation was over 400 days in length. The chief difficulty about these results is, that they afford no indication of the length of time between copulation and ovulation, and, as heat usually lasts in mares for a week, and moreover, as theoretically ovulation must be supposed to take place about the end of heat, or after it has ceased[2]), his figures must contain an error of several days at least. I shall, therefore, adopt 336 days as the average period in the mare, though well aware that this is subject to variation[3]).

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1) l. c., p. 25, 28. 226 mares served once only had an average gestation of 346 1/3 days, while 128 served several times gave an average of 341 2/3 days.

2) As in the rabbit.

3) With one or two critical units only greater accuracy in keeping to the time may be expected, as in the rabbit. Where the number is increased, and where, moreover, the critical unit approximates two ovulation-units, greater variation may be anticipated. It is curious and significant, that the observed variations should increase with a greater number of critical units in the gest-

But, in taking this as the average, one has the benefit of the experiences of horse-breeders.

The critical unit of the horse, as calculated from the condition of Ewart's embryos [1]) and from Bonnet's observations on the placenta, is about 42 days. It may fall somewhat short of this, but certainly does not exceed it. The horse-embryo of 7 weeks figured is too old, and that of exactly 6 weeks is slightly too young. But the latter is an embryo so near the critical period, that less than a day's further development would probably have sufficed for its attainment. This would give 43 days! Certainly, but it must not be forgotten, that the moment of copulation is not that of fertilisation, and, in allowing one day to elapse between the two, the assumption made is not too great. It is possibly too small, though probably only by a few hours.

These figures give eight as the number of critical units in the gestation [2]).

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ation. They are minimal in the opossum with one critical unit, they vary within a day in the rabbit (two critical units), 3 or 4 days in the cavy (three critical units), they are greater in the pig with four compound critical units, larger in the cow with still more critical units and a longer gestation, and are largest in the horse with a prolonged gestation. In fine, the variations observed are proportionate to the length of the gestation, to the number of critical units, and, naturally, also to the length of this unit.

1) Compare appendix g.

2) In the cow the ovulation immediately succeeding birth does not lead to a new gestation. The mare does not begin a new gestation, until some days after the birth has taken place. This might have the appearance of putting a difficulty in the way of view, that the ripening-up of an egg or eggs was the direct cause of birth. It is, however, no such thing; for, although the approach of birth cannot inhibit ovulation, the fact, that a birth has happened, may probably delay it, just as menstruation does, as will appear subsequently.

For the cow there are no exact data to go upon, and. unfortunately, no funds have been at my disposal to use in testing the matter.

In this instance the only thing approximately known is the ovulation-unit, which, from our knowledge of other cases, points to a critical unit of 40—42 days at most. Taking the critical unit as 39—42 days, with seven such critical units in the gestation, 94 % of Tessier's cases are accounted for, and a slight individual variation of only two days in a very few instances would dispose of the remaining 6 %.

The sheep is far more accurately known: from Bonnet's statements of ages it is easy to determine these exactly in my embryos, and as the result we get a critical unit of 29—30 days. As the gestation of this animal only varies between 145 and 152 days [1]) we obtain with great accuracy five critical units as characteristic of the sheep.

The pig has a much shorter gestation of 109—123 days [1]): several considerations, which are discussed in an appendix [2]), point to a critical unit of 28—30 days, and these numbers give us a gestation of four critical units.

The figures and statements of His regarding human embryos, when looked at in the light of "critical-period-morphology", point to a critical unit of 46—47 days, and a case, the details and embryo of which I possess, agrees with this conclusion. Taking the length of human gestation [3]) as 276—282 days we find that it must include six critical units.

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1) Tessier, Bonnet, and other authors.
2) Appendix h.
3) Compare appendix m.

Broadly, it may be stated, that increases in the number of critical units are in association with a more advanced development at birth on the part of the foetus. Thus, the four critical units of the pig do not give as great a degree of development at birth, as do the five of the sheep, the seven of the cow, or the eight of the horse.

The helpless condition of the human foetus at birth may seem to be militate against this result, but this exception is more apparent than real.

The condition of a form at birth is not always revealed by its degree of helplessness. This undoubtedly shows its physiological state; but, what we are concerned with, is not so much the physiological, as the morphological, degree of its development. The human foetus at birth may be, and probably is, morphologically as far advanced as, if not further than, a new-born sheep or Guinea-pig, and the apparent difference is probably to be set down to a different mode of life on the part of the parent. A form, which has acquired the habit of carrying its young about with it, if at first only while suckling them, has initiated a mode of life for the young during lactation, which is bound to leave its impress upon them, if for no other reason than because it introduces panmixie.

Special cases, like that of the human foetus, do not, however, tend to controvert the rule, that an increased number of critical units in the gestation will result in a more advanced degree of development at birth. Mere length of gestation does not attain this end, for a mouse, or rabbit, at birth is probably as far advanced, as a dog with a threefold or double length of gestation.

The importance attached to the number of critical

units, apart from their length, may at first sight appear to be overrated, but a little consideration will show, that this is not so.

What can be accomplished in a certain interval of time might be supposed to be always an equivalent quantity, did not our experience contradict this. It has already been pointed out, that under very similar conditions a certain degree of development, reached in the opossum in 8 days, requires 15 in the rabbit, 30 in the sheep, 42 in the horse, and 46 in man. The reason of the greater degree of development with an increased number of critical units in the gestation lies much deeper, and it is to be sought in the circumstance, that forms with gestation-periods of several critical units must in their ancestral history have passed through conditions, in which the number was smaller. In fine, they must have started with a gestation-period of one critical unit, and have gradually increased this number. Whilst it may be, that, owing to divergent evolution, forms with a similar and large number of critical units in the gestation do not bring forth their young, unless more or less allied, in corresponding phases of development [1]); where the gestation is made up of one or two critical units, it is probable, if not certain, that such a correspondence obtains [2]).

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1) None the less this remains to be proved.

2) This must not be confused with recapitulation as understood in current embryology. Although at the close of like units, 2, 3, 4 and so on, two embryos of different species may possibly be in a like grade of development this, if true, would not be connected with the so-called "biogenetic law". Compare "Certain Problems of Vertebrate Embryology", Jena 1896, p. 34—37.

VII. The Duplication of the Critical Unit.

The points, here under discussion, naturally bring up another question, which has already been indicated.

We have considered the relation of the critical to the ovulation-unit in those instances, where the former was termed "simple". But there remain other cases, where the critical unit is a large one, and where its relation to the ovulation-unit, because it much exceeds this, is not so clear. It is improbable, that there are very many of the lower orders of Mammals, if any, in which anything of this kind is to be encountered. It probably does not occur, or only rarely, in Marsupials, Insectivora, or Rodentia, but it may turn out to be the rule in all the higher ones. The actual instances, which at present have cropped up, are horse, cow, sheep, pig, cat, dog, and man, representatives of three of the most important orders of mammals.

A peculiarity about these cases is, that, with a large critical unit, we have, except in cat and dog, a long gestation-period made up of several critical units.

The rule, so far as it can be made clear from the facts available, appears to me to hold here also. There is a relationship between critical- and ovulation-units of the same *kind*, as that ascribed to other cases, but it is rather different in one important respect. In the above instances the critical unit no longer falls rather short of one ovulation-unit, it exceeds it, and in such a way, that it now is rather less than two ovulation-units.

This is shown by the following short table:

	critical unit	ovulation-unit
sheep	29—30 days	15—16 days
pig	28—30 „	15—18 (?) „
cow	40—41 „	21 „
horse	42 „	21 „
man	46—46 $^{2}/_{3}$ „	23 $^{1}/_{3}$ „

Here, once more, we are face to face with a problem requiring solution. Why should the simple relation between the two units, obtaining in rabbit, mouse, or cavy, have been altered? What advantage, or advantages, are to be gained by the new procedure?

It is, probably, sufficiently clear, that one of the main objects in prolonging the gestation of the higher mammals has been the bringing of the young into the world in a more advanced degree of development. This explanation is a very obvious one, and has been urged by others [1]); but, as we have seen, mere length of gestation will not effect this, for it is conceivable, that one might have a very prolonged gestation of two, or even of one, critical unit, and in such a case the new-born young would be brought forth in a more or less immature condition. If it be correct, that the gestation-period of the kangaroo has a length of some 38 days, as Owen stated, it follows, that the comparatively prolonged gestation in this instance fails to accomplish more, than is reached in 8 days by the opossum, or in 10 days by the mouse, while it falls far short of the

1) The name of Robert Chambers, author of the celebrated "Vestiges of the Natural History of Creation", is sometimes cited in this connection, but he seems to have regarded the effect of increase of gestation-length as causing the passage from a lower to a higher genus.

degree of development arrived at by the rabbit in several days fewer than 38, or by the mouse in little more than half the time. It must, therefore, be accepted, that mere length of gestation, apart from the influence of other factors, does not determine the degree of development at birth. And this can be rendered more certain by other considerations.

We have seen, that in certain cases, rabbit, cavy, and mouse, the critical unit is a very short one, and, moreover, that it must be considered as originally falling just short of an ovulation-unit.

Now, the critical unit is, as we have stated, the average time requisite in a given form for development to the critical period, and this unit, owing to its relations to the ovulation-unit, governs the gestation-length in such a fashion that the latter must always be some multiple of the former, the degree of development attained by the time of birth being determined by the number of critical units in the gestation.

There appears no reason to doubt, that a simple critical unit, like that of the mouse, i. e. one approximately equal to an ovulation-unit, could, if necessary, suffice as the unit of such forms as man, horse, sheep, or pig. What the cavy, or mouse, reaches in a period of probably rather less than an ovulation-unit ought, so it would seem, to be possible of attainment by a human, sheep-, pig-, or horse-embryo in a like interval.

There is no doubt whatever, to my mind, that in bygone days this held true, but at the present time double this interval, i. e. almost two ovulation-units, is the period required; or in other words, as already stated, the critical unit in these forms is somewhat less than two ovulation-units.

Before inquiring further into the matter, it may be well to see what would happen, if in man, pig, sheep, and horse the critical unit corresponded approximately to one ovulation-unit, whilst the number of the former in the whole gestation-period were to remain as at present.

The obvious result would be a shortening of the gestation, and in each instance it would be reduced to half of its present length. Thus, in man it would be 138—140 days, in the horse 168—175 days, in the sheep $72^1/_2$—76 days and in the pig $54^1/_2$—$61^1/_2$ days.

It would follow from this, that, if the milk-nutrition of a preceding litter did not interfere, the number of offspring produced would in the long run be double what it is at present.

The reverse of the picture is this; that, when by the addition of new critical units the gestation-period most advantageous for the species had been reached, i. e. that with which the young came into the world in the condition [1]) of development most suited to the needs of the species, when no further advance in uterine development was desirable, or needful, if it became necessary, or useful, to further prolong the gestation without altering the degree of development at birth, this could only be attained by increasing the critical unit.

In a cavy an increase of 10 days in this would yield a further prolongation of gestation for 30 days. In a form with a critical unit of 21 days and a gestation of 7 such units, an increase of 20 days in the unit would lengthen the gestation by 140 days. But, in enlarging the critical

1) Not the highest degree of development possible, for, theoretically, that would coincide with sexual maturity!

unit Nature could act in no such haphazard a fashion. She had also to take the ovulation-unit into account, and either prolong this in a corresponding degree, or else adapt the new critical unit in such a manner, that it would correspond approximately to two ovulation-units. If she had adopted the former course in any instances, we should not be able to point to evidences proving it, and could only suspect it from the conditions in other forms, in which it had not happened [1]).

That she chose the latter in the higher mammals is demonstrated by the fact, that in man, pig, sheep, and horse, the critical unit is rather less than two ovulation-units.

In the present discussion we are less concerned with the objects of certain phenomena, than with the things themselves. It is, indeed, sufficient for the end in view, to determine the facts, without troubling much about purposes. But the arrangement just noted and its results are of so curious a nature, that one is tempted to inquire into their possible meaning.

If, as here maintained, the critical unit governs the length of gestation in such a fashion, that the latter is always some multiple of it — and the truth of this does not appear to be in the least doubtful — the one obvious result of a duplication of the critical unit must be a doubling of the whole gestation-period. As we have seen, the number of critical units in the gestation determines the degree of development at birth, the length of the unit having absolutely no influence in this matter.

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1) As already indicated, the comparison of the short critical unit of *Didelphys* with the nearly two-fold one of *Lepus* leads one to suspect, that once upon a time this eventuality also was realised.

It follows from all this, that the doubling of the whole gestation-period, brought about by a duplication of the critical unit, can have no effect whatever on the degree of development, attained by the time the birth-period arrives; and, therefore, some other reason must be at the bottom of the matter.

A very obvious consequence is, that the number of gestations possible in a given time will be reduced by half.

There would appear to be no conceivable advantage to the species in a Malthusian arrangement leading to this: indeed, some compensation for this loss of possible progeny might seem called for under it.

Apparently, the solution must be sought for elsewhere. When the forms are studied, in which the critical unit is "simple", i. e. in which it approximates to one ovulation-unit, it is noticed that they are all of small size, for example, mouse, rabbit, cavy, mole, and hedgehog [1]).

Those, on the other hand, which have a compound critical unit of approximately two ovulation-units, are, in the adult condition, usually much larger in size, as for example, man, horse, cow, sheep, and pig [2]).

In all these cases it may be assumed, that at corresponding periods of uterine or post-uterine life the young of the latter set must be much larger, than those of forms with simple critical units.

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1) That mole and hedgehog must be placed in this category appears to me to be certain from the circumstance, that, with a short gestation-period of either one, or two (according to some), months, the young are born in a very helpless condition.

2) Something of the same kind possibly prevails in the marsupials, and it may account for the longer gestation of the kangaroo (recorded by Owen), as contrasted with the much shorter one of the opossum, or kangaroo-rat.

So far as the actual sizes of the various embryos at the critical period itself are concerned, there is, perhaps, not so much difference, but even then it is marked, and, whereas a rabbit-embryo of the critical period measures about 12—13 mm (greatest length) [1]), one of a pig is then between 19 and 20 mm in length [2]).

Thus, the only reason [3]), so it would appear, which can be assigned for this duplication of the critical unit, must depend on an increase in size having taken place in the course of the evolution of the higher mammals. This has been proved by Marsh, Cope, and others in the case of the horse, *Phenacodus* not being larger than a sheep [4]) and the other known ancestors in proportion.

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1) See appendix t.

2) In marsupials at the critical period *Trichosurus* measures 14 mm, *Macropus thetidis* probably under 20 mm, and *Macropus major*, according to Owen, 25 mm.

3) But it is by no means suggested, that other possible and reasonable explanations should be excluded. Geddes and Thomson note regarding the length of gestation that "it also depends on size, being about 280 days in the cow and 150 in the sheep". (Evolution of Sex., p. 247.) Compare also the following: „So sind nehmlich eben die Thiere, bei denen sich eine geringere Fruchtbarkeit zeigt, auch solche, die eine grössere Zusammensezung ihres Körpers haben, und bei denen die Jungen nach der Geburt weit ausgebildeter erscheinen, und so sind's ferner sie, zu deren Hervorbringung die Natur bei weitem am meisten Zeit braucht; um einen Elephanten zu bilden, dingt sich die Natur bei dem unfruchtbaren Elephanten zwei Jahre aus, während wenige Wochen zur Bildung einer Ratte hinreichen", u. s. w. (C. F. Kielmeyer, Ueber die Verhältnisse der organischen Kräfte etc. Eine Rede, den 11. Februar 1793 — — gehalten. Stuttgart 1794, p. 29.)

4) One species being as big as a bull-dog.

VIII. The Influence of Lactation.

Discussion of this important matter has been postponed until now because of its complexity. The subject is a very big one, and, undoubtedly, one of the very many awaiting the attentions of coming comparative physiologists. It is rather strange, that it should hitherto have attracted so little notice, for in the human subject the problem is one, that is constantly intruding itself upon the gynecologist. Leaving the conditions in man on one side, it is certainly the fact that there are many mammals, in which the milk-nutrition, and it alone, suffices for the suppression of ovulation for certain periods, varying in length in different species, and, even, in some cases in the individuals of a species, though this is of rarer occurrence.

At this juncture, and with the slight material available from my own incidental observations, and from what can be gathered from books, very little can be done towards elucidating the question.

In some animals the milk-nutrition appears to have absolutely no influence on the ovulation, and, unquestionably, this must be regarded as the primitive mammalian condition. In such a case, as we have seen, the female is practically always pregnant, for a new ovulation and gestation ensue almost immediately after the birth.

Under favourable conditions of nourishment this appears to be the state of affairs in cavy and mouse.

My own experiences with the breeding of these animals are too limited, to enable me to exclude the possibility,

that suckling may have a disastrous effect on a new gestation; but, certainly, from my reading no evidences of its having had such an influence have been encountered [1]). Moreover, they both appear to ovulate with strict regularity throughout the greater part of the year.

As a rule, the same may be said to hold good for the rabbit also, and a breeder of rabbits informed me, that it was not at all uncommon for a rabbit to have eleven litters in a year.

Some years ago, for the space of a year, the breeding of rabbits on a large scale was attempted in Freiburg i/B., with a view to the acquisition of a complete series of embryos. The experiment came to sudden and unanticipated close owing to the acceptance of an appointment in Edinburgh.

Interesting observations were, however, made: in some cases too interesting, because of their negative properties in helping the collection of material.

In order to keep up the stock, the young of many rabbits were allowed to live, when it was intended, that the mother should be sacrificed at an early interval after the birth, to obtain the embryos of a gestation following on the birth. This meant, that while the mother was supposed to be pregnant, the young were allowed to suckle.

Many such suckling females were sacrificed at dates from the eighth to the fourteenth day of gestation, and in some of them it was found that, while the mother had certainly

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1) Since the above was written, experiments with mice have been made to test the matter, and it has turned out, that lactation may in this animal lead to the suppression of a new gestation.

ovulated within the usual period of twelve hours after birth as determined by Bischoff, the resulting embryos had been unable to hold their own against those suckling, and had died, before advancing very far in their development. This was proved by their remains. Since then many such cases have come under notice.

In such instances it was clear, that the mother had been unable to satisfy the demands of two sets of young, those outside the body at the mammae, and those *in utero,* and, that lactation was responsible for the starvation of the latter.

The nutrition of the mother could not have been the cause, or, rather, only indirectly, for it was possible, that the abundant nutriment furnished to her had enabled her, to bring forth a greater number of young, than that, which she could nourish, as well as a new set *in utero.* This suppression of a gestation, already commenced during a milk-nutrition, is probably fairly common in the rabbit, but it is very far from being the rule in this animal.

In the pig, on the other hand, ovulation, and with it gestation, entirely ceases during the lactation-period, which here, remarkably enough, is about equal to the length of gestation, i. e. four months. About the end of this time the young are weaned, ovulation and heat ensue, and the sow may again enter upon a new gestation.

Much the same sort of thing happens in the cat and the dog, the difference here being due to a shorter gestation, and, thus, the lactation-period is almost equal to that of two gestations.

It is a curious fact, that the cat especially seems to have divided up the whole year in such a way, that two

gestations can occur, with prolonged lactation-periods, mainly filling the intervals.

In pig, dog, and cat, the effect of the lactation in suppressing, or rendering ovulation abortive, and with it gestation, is very apparent.

In man, though naturally the exceptions are now, perhaps, far more numerously represented, than cases conforming to the rule, one can again note an average lactation-period, about equal to that of pregnancy.

In the sheep [1]), on the other hand, with its single gestation during winter, we encounter the influence of climate, rather than that of lactation, and the same thing probably holds in a great many cases. But so little is known with reference to this, that it would be futile to attempt its discussion [2]).

Summing up the matter, it must be concluded, that originally lactation had no influence on gestation, and that this is still so in many cases, but that in others it has acted as a check on a new gestation, and still does so. Where this obtains, the lactation-period will normally correspond to one or more gestation-lengths, i. e. it will keep up the rhythm of the gestation and ovulation.

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1) Bonnet (Arch. f. Anat. u. Entwickl., 1884) makes the following interesting citation: — "Franck giebt an, dass das sich durch grosse Fruchtbarkeit auszeichnende chinesische Ong-te (a variety of sheep) kurze Zeit nach der Geburt wieder trächtig werde und zweimal im Jahre Junge bringe" (p. 172).

2) According to Ryder, the diversion of nourishment from the ovary during the period of gestation tends to starve the remaining ovarian ova, and this check to fertility is further prolonged during lactation. This citation is taken from the writings of my friend, J. Arthur Thomson, and it was noted too late to find the exact reference.

IX. The Special Case of Man.

On account of the difficulties and complications, which beset the elucidation of the gestation-period of the human subject, including under these ovulation- and fertilisation-epochs, as well as menstruation, it is no doubt convenient to consider this instance by itself in all its bearings.

Of the factors involved, except the birth-period itself and the menstruation-interval, no exact information is obtainable. The data, upon which the age of any particular embryo can be fixed, are always deficient; and, thus, it happens that, given an embryo of the critical period, its age can only indirectly be calculated.

The date of copulation may be left out of account, even though it be accurately known; for, while in certain animals the time of fertilisation can be approximately reckoned from that of copulation, it would be idle to suppose, that in man similar information could be made at all a certain basis for the calculation of the moment of fertilisation. The most important factor is only approximately known, and this is the time of ovulation. There is no doubt, that in any instance, where this is known, and where the relationships between ovulation and copulation can be stated in days or hours, the problems remaining will turn out to be very easy of solution.

But the most vital points in the case of man are the determination of the ovulation-unit and of the time of ovulation. The ovulation-unit is, however, not far to seek, and almost by common consent — whether rightly or

wrongly remains to be discussed — it has been set down as 27—28 days.

It may, indeed, be taken as the general opinion, that, whatever be the relationship between menstruation and ovulation, there is a correspondence between the two, of such a kind, that the interval of the one is equal to that of the other.

But, before an attempt can be made to estimate the probable time of ovulation, it is necessary, that the phenomena of menstruation should be studied. This study is all the more forced upon us by the circumstance, that not only is the gestation-period, as a rule, calculated from the occurrence or non-occurrence of a menstruation, but the time of fertilisation also.

X. The Meaning of Menstruation.

It is hardly necessary to say, that this is a subject, about which much has been written. For one, who is not at all versed in gynecology, and who has no observations of his own to put forward, it may appear presumptuous to venture an opinion. But there are numerous facts available, and to the writer it has, rightly or wrongly, appeared, that the things, he has fallen in with regarding the critical period, and the critical unit, etc. do have bearings on the problem of menstruation.

It is not proposed in this place, either to recite the various theories of menstruation, or to attempt to disprove them. Most of them can hardly be termed explanations at

all, for they are either far-fetched and largely hypothetical, or they leave in mystery as much as they profess to solve.

The points, which mainly concern us, are the phenomena of menstruation, its average-interval, and its connection, or non-connection, with ovulation.

Regarding its correspondence to the heat-period or rut of mammals, as supposed by Tyler Smith and others, very little is required in disproof. The mere fact, that heat in mammals is the time of sexual intercourse *par excellence*, while menstruation in those few forms, in which it occurs, is just the exact opposite of this, sufficiently illustrates how untenable this position is[1]).

Of the various theories of menstruation a critical account has recently been given by J. C. Webster[2]), and to this, as also to the memoirs of Walter Heape[3]), the reader may be referred.

The facts, as laid down by others, and as Heape's researches on the menstruation of *Semnopithecus* and *Macacus* have proved them to be, will be made the basis of the following discussion.

Menstruation is a periodic process, occurring in the majority of cases with great regularity in cycles of $27\,^1/_3$ to 28 days, though subject to variations.

Some individuals have a period of greater or less

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1) If a heat-period ever existed in human ancestry, the lengthening of the menstrual flow has sufficed to extinguish it.

2) Webster, J. C. The Biological Basis of Menstruation. (Reprinted from the Montreal Medical Journal, April 1897, pp. 19.)

3) See appendix w. Heape concludes that "the primary cause of menstruation remains unexplained".

amount than the above, and, even in healthy women, the flow may recur irregularly, so that, as quoted by Hensen from Loewenhardt, of 46 and 50 consecutive menstrual periods of two women, these occurred at intervals of 16, 21, 22, 23, 24, and 32 days (once), 25 days (nine times), 26 days (eight times), 27 days (twenty-one times), 28 days (seventeen times), 29 days (fifteen times), 30 days (eight times), 31 days (five times), 33 days (thrice), 34 days (four times). The average is $27^1/_3$ days, and it is worthy of notice, that more than half the cases closely approach the mean.

In a menstrual cycle four stages are recognised [1]):

1) The constructive stage, resulting in the formation of a menstrual decidua, and lasting approximately 7 days.

2) The destructive stage, including the whole period of the catamenial flow, and usually embracing 5 days.

3) The stage of repair, during which the uterus is recovering from the destructive changes. To this period 3 to 4 days are assigned.

4) The period of quiescence, of 12—14 days duration.

The events of the constructive phase are compared with those, occurring in the placental lobes of the rabbit's uterus from the fourth to the eighth day of gestation, and for a fuller account the reader may be referred to other sources [2]). The phases of repair and quiescence require no elucidation, but it is obvious, that the events of the period of repair may be regarded as similar in kind to those, which succeed birth or an abortion.

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1) Compare Heape, appendix w.

2) Compare appendices u and w.

There remain, then, the actual phenomena of the catamenial period itself for explanation.

Prior to the appearance of the menses the uterus has formed a decidua, which is regarded as equivalent to that, which would arise, when a fertilised egg became affixed to the uterus. If an egg were affixed in this position, and if then menstruation took place as usual, we should regard this as an abortion[1]).

Indeed, the whole of the phenomena of the constructive, destructive, and repair-periods point, to the conclusion, that menstruation is an abortion of a decidua at a time, when the "egg" ought to have become fixed to the uterine wall, but where this was impossible, because of the failure of fertilisation. It is an abortion of something prepared for an egg given, off at or after the close of the preceding menstruation, and it takes place, because this egg has escaped fertilisation.

If there be, as I hold there is, any truth in the doubling of the former simple critical unit in man, it is an abortion which in its period corresponds to this latter.

It represents an abortion at the old critical period, and is one, in which the decidua belongs to a missing $22^1/_2$ to $23^1/_2$ days embryo, and, thus, in all its phenomena it resembles a parturition, as first noted by Burdach, and is, in fact, an abortive one. This view of the matter is one, which is in agreement with all the facts[2]), and, so far as my reading goes, it is the only explanation covering all the

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1) As a matter of fact medical experts have long been of opinion, that early abortions of the first month of pregnancy are very often unnoticed, because they are taken to be normal menstruations.

2) For Minot's views compare appendix u.

phenomena. If this conclusion be right, it follows, that menstruation and ovulation cannot, as a rule, coincide; or, to put the matter more exactly, that ovulation cannot be connected in such a way with menstruation, as to happen just before or during this, any more than that birth and ovulation could exactly coincide in rabbit, mouse, or cavy. This is confirmed in the strongest possible manner by Heape's researches[1]), as well as by the observations of Bischoff, Kölliker, Coste, and others on the bodies of women, who had died during menstruation.

The explanation of the nature of menstruation just given has thus far been based solely on the interpretation of the phenomena before, at, and after the catamenial period, but in the sequel it will be manifest, that other facts can be drawn upon in support of this conclusion.

Menstruation is, thus, a phenomenon, which, as others have noted, lies on the borderland of pathology. It probably dates from a time, when the reproductive rhythm was such, that the mature female was always pregnant, and, possibly, when pregnancy was far shorter, than it now is. It persists, probably, because its existence is entangled in the reflex mechanism of ovulation.

Ovulation cannot be supposed to occur during the constructive stage, for that would assume the preparation of a decidua for the reception of an egg, before it was fertilised, and the analogy of other cases is entirely against this.

Again, in other animals, like mouse, cavy, rabbit, or horse, the period of quiescence of the uterus is not that of ovulation, but it ensues in these very soon after a birth

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1) Compare appendix w.

has taken place, and, of course, at other fixed intervals, when the animal has not just borne young.

This leaves us with the periods of destruction and repair, embracing some 8 or 9 days, in which ovulation may happen. If menstruation be comparable to an abortion, it cannot be supposed, as we have seen, that, *as a rule,* it and ovulation will coincide; for, again, the analogy of other forms favours the idea, that ovulation cannot happen, until the (premature) birth or abortion is complete.

If the abortion of the decidua, prepared for an unfertilised egg, only occupied a very brief interval of two or three hours, in other words, an interval comparable in length to the birth-time of the rabbit or cavy, ovulation could, as in these animals, ensue within a few hours of the end of this. But at the present time menstruation is a process extending over several days, and an egg, released from the ovary during the earlier part of menstruation, would require to wait a long time for fertilisation.

From these considerations it appears, that the most likely time of ovulation must be, as a rule, towards the very end of the menstrual flow.

This result is also in agreement with, among others, the opinion of Hensen. He writes: — „die bisher vorliegenden Thatsachen sprechen zu Gunsten der älteren Ansicht, dass nämlich die Follikel *in der Regel* [1]) gegen Ende der Menstruation platzen“ [2]).

The experiences of Hyrtl, Bischoff, Kölliker, and Coste, as cited by Hensen, support this view.

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1) Italics in the original.

2) Hensen, V., Zeugung. Handb. d. Physiol., 1881, p. 75.

Apparently opposed to it are the majority of the examples of embryos, whose histories have been recorded by His [1]), and in these it must be assumed, either that the menstrual flow was slight, and had been overlooked — a likely and an unlikely thing — or that an unusual ovulation had happened [2]). This appears to be the more likely explanation.

There seems to be no reason for doubting, that sometimes an egg may be given off at unusual times in the middle of a menstrual cycle; and upon the views of the nature of mammalian development advanced in the present writing, it is far more reasonable, than the supposition, that ovulation might just precede menstruation. The experiences of Heape and others are also opposed to this latter. The fertilisation of such an egg would suppress the menstruation, and with it the ensuing ovulation would be rendered obortive, and its egg or eggs would degenerate in the ovary. This, if correct, is a very important conclusion, for the fertilised egg would develop, as if it belonged to the succeeding suppressed ovulation, and, thus, the phases of its subsequent uterine life would not chime in dissonance with the rhythm, which must of necessity underlie mammalian reproduction.

It will be taken, then, that, as a rule, ovulation slightly succeeds menstruation, and the question now arises "what is the ovulation-period"?

The answer to this is not so simple, as it would appear to be. At the first glance it looks, as though its interval were equal to that of menstruation.

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1) His, W., Anatomie menschlicher Embryonen, II, p. 74 etc.

2) See the latter part of appendix m (on "Length of pregnancy in man") for a fuller discussion.

The acceptance of 27—28 days as the ovulation-unit fails to establish anything about the pregnancy beyond its supposed correspondence to ten menstrual periods, which I hold to be erroneous.

Quite apart from the circumstance, that on this assumption no correspondence between it and the critical unit can be set up, as I know full well at the cost of much wasted labour, it must be noticed, that the menstrual interval is often different in different women, and even in the same individual at different times.

Hensen cites two interesting examples drawn up by Loewenhardt: "So betrug bei zwei Frauen die Zeitdauer von 46 und 50 sich folgenden Perioden 1 mal 16, 21, 22, 23, 24 und 32 Tage, 9 mal 25, 8 mal 26, 21-mal 27, 17 mal 28, 15 mal 29, 8 mal 30, 5 mal 31, 3 mal 33, 4 mal 34 Tage. Diese Schwankungen traten sehr unregelmässig ein" [1]). From what follows, I am convinced, that a far greater regularity would have appeared, if the intervals, from the end of 'one menstruation to the beginning of the next, had been noted and recorded. Such an interval on the average must be equal to about $23\,^1/_2$ days.

A few of the lower numbers seem to be against this, but it by no means follows, that, because there is a "show" externally, the menstruation has not really ceased internally [2]). Without allowance for something of this sort, a post-menstruation, it is nevertheless curious to note, that about half of the cases approach the mean, i. e. $27\,^1/_3$ days.

If menstruation, as already indicated, correspond to

1) loc. cit., p. 64—65. Previously quoted in English on p. 70.
2) As long ago urged by the gynecologist, Dr. Tyler Smith.

an abortion, its effect, if prolonged, is to delay the ovulation ensuing upon it.

It may be concluded, that originally menstruation was very much shorter than it now is, so short at first as to occupy a very brief interval of time, possibly only an hour or less. There seem to be no grounds for assuming, that its present average duration was fixed at its initiation, or that it was then longer than it now is. If it were very brief, the interval between any two periods would be equal to the present average time, between the end of a menstruation and the beginning of the next.

Moreover, if we carry the menstrual cycle over into the period of gestation, calculating the latter as equivalent to ten of the former, we fail to remark, that during pregnancy, where the menstrual flow is suppressed, the beginning and the end of a menstruation are the same thing. And — so it appears to me — there can be no reason for including a certain number of days in each cycle for a process, which varies in length in the non-pregnant individual, and which has no actual dimensions at all in pregnancy.

I conclude, therefore, that, as nearly as one can guage it at present, the human ovulation-unit has a length of about $23\,^1/_3$ days, or perhaps rather more, though hardly 24 days. It will be seen, that on this estimate a satisfactory measure of the length of pregnancy may be made, and, what is quite as important from my point of view, a perfect relationship, between it and the critical unit, can be demonstrated.

XI. The Human Critical Unit [1]).

From the researches of His, as recorded in the three parts of the "Anatomie menschlicher Embryonen", from the conditions presented by Keibel's human embryo H. s. Brn., as demonstrated in a former publication [2]), and from the data concerning a human embryo now in my own possession, it is quite clear, that the critical period is reached in human development in 45—47 days.

From the facts recorded by His and Keibel concerning embryos of about 17 mm (Nackenlänge) this is as near an estimate of the critical unit, as can be made, but of the embryo in my possession, which I owe to the great kindness of Dr. Anderson of Stonehaven, a more exact determination can be arrived at.

As this embryo and its history are of vital importance for the line of inquiry in hand, as the specimen is almost the exact counterpart of another, given me without its history by a former pupil, Dr. Martin Corry, and, finally, as the membranes of these two are typical of a number of such, which, *minus* embryos [3]), have passed through my hands, it appears desirable to note this particular case in detail.

The Stonehaven embryo is of the critical period. The grounds, on which this conclusion is based will, be given elsewhere, here the fact and the history of the embryo alone concern us. The patient last ceased a menstruation

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1) Compare also appendices n and o.

2) Certain Problems of Vertebrate Embryology, p. 27—32.

3) To be more exact, either without, or with crushed and distorted embryos, or only parts of such.

before becoming pregnant on Dec. 1st 1896, and the abortion took place on Jan. 17th 1897.

Assuming the ovulation to have occurred at the end of the catamenial flow, and to have been followed by almost immediate fertilisation, the embryo has an age of at most 46—47 days. As already indicated, its position in the normal table agrees with this.

But of special interest, in their bearings on the results of the preceding section, are the following considerations. If, following Harvey, Tyler Smith, and others, we estimate the gestation as equivalent to ten menstrual periods, and if in this special instance we seek for the occurrence of a menstrual period at this abortion, as Tyler Smith was wont to do, we find, that the latter falls some 4—5 days short of the second catamenial period.

But if, on the other hand, the mode of reckoning the menstrual period during pregnancy, advocated in the present writing, be adopted, a very different and rather surprising result is arrived at.

Calculating from the end of the last menstrual period on Dec. 1st to the beginning of the next (suppressed) menstruation with an interval of $23^1/_3$ days, the date of Dec. 24th is obtained, as that of the latter. As in pregnancy it is impossible to assign any length of time for the duration of the flow, the next cycle must be taken as beginning on the same day.

A further interval of $23^1/_3$ days brings exactly the date of the abortion, Jan. 17th. It is impossible to overestimate this result. Important for us, though, possibly, insignificant compared with its other bearings, is the proof of the equivalence of the human critical unit to rather less than two ovulation-units.

XII. Abortions.

In a former publication the importance of the critical period as one, at which abortions might be expected to be of frequent occurrence, was commented upon. It was insisted, that, owing to the mode of development, and to the absolute necessity of completion of all the parts of the embryo by the time the critical period was reached, failure to comply with the unwritten, but, none the less, inexorable, rules of the development prior to the critical period, was bound to revenge itself and result in abortion. Whilst any intention of assigning these factors as the causes of all early abortions must be disclaimed, everything since met with in the research has tended to strengthen the conviction, that a large percentage of abortions in man, and mammals generally, can be traced to causes, connected with the critical period, the critical unit, or the ovulation-unit. The instance described in the preceding section is a very significant one, and it is undoubtedly typical of a great many others.

Although abortions [1]) are of daily occurrence, it is very difficult to get at the facts concerning them.

Whitehead of Manchester, as quoted by Tyler Smith, found, that of 2000 women, patients at the hospital, 37 % had aborted before reaching the age of 30, and Tyler Smith himself estimated, that of the women, who had lived in wedlock, and passed through the child-bearing period, 90 % had aborted once or oftener.

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1) In the present section no distinction will be made between abortions and miscarriages.

It must be stated, that there is absolutely no novelty, in the idea, that abortions might be connected with the periodicity of ovulation and menstruation.

Klein and Burdach early in the 19th century noted, that abortions, where not due to external causes, appeared to be of most frequent occurrence, at what ought to have been menstrual periods.

Tyler Smith remarks: — "there is, in fact, in all women a tendency to abort at the times represented by catamenial periods" [1]).

And further on he adds: — "I have observed in cases of abortion, occurring at what would have been a catamenial period, that menstruation has appeared at the end of a lunar month from the abortion, as if it were dating itself from a simple menstruation" [2]).

In many standard works, such, for instance, as Tanner's [3]), tables exist of the frequency of abortions at various periods of pregnancy, but these are drawn up in such a way, as to be absolutely useless for detailed examination. Whitehead's table, dealing with 602 cases, classifies the data by the number of months of pregnancy, but "each figure in the first column (number of cases of each particular month) embraces a period of four weeks, extending from a fortnight before to the same length of time after the month indicated". It will be apparent, that of a table of this sort no exact analysis is possible.

But from this and other tables certain things can be deciphered.

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1) Smith, W. Tyler, Parturition etc., London 1849, p. 115.

2) loc. cit., p. 119. — A very significant statement in the light of the conception of menstruation here advocated.

3) Tanner, Diseases of Pregnancy, 3rd Ed. 1867.

For various reasons[1]) it might be anticipated, that abortions would be most frequent at the critical period and at some multiple of it in the human subject[2]), thus, 1) at the 46th—47th day, when a menstrual period should recur; 2) at the end of the third month; 3) at about the end of the 20th week; 4) towards the end of the 27th week; 5) at 33 1/2 weeks; and, lastly, 6) towards the end of the 40th week, i. e. the end of pregnancy.

Of these the first and second are unquestionably periods, when abortions are very apt to occur.

My own material proves this for the first (the critical period), and the common testimony of gynecologists, as well as Whitehead's table[3]), speaks emphatically regarding the second, whilst the sixth is the actual normal birth-period.

Thus, even with the meagre data available, three of the six hypothetical periods can be established.

But, probably, there are other intervals of importance. In mammals generally actual ovulation appears to be suspended during gestation. If it were to come into operation during that epoch, it would certainly lead to abortion.

It is highly probable, that during pregnancy the ovaries, with their nervous mechanism, mark the time with the regularity of clockwork, and that no period,

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1) Briefly these are: — a) owing to a certain degree of abnormality in the embryo, or in the "membranes", b) failure in the proper formation of a placenta, c) reversion to an ancestral birth-epoch, d) and owing to ovulation. The two latter are closely connected, and they might come into play not only at the critical period, but at some multiple of the critical unit.

2) And for similar reasons in other higher Eutheria also.

3) In this out of 602 cases, extending from the second to the eighth month, no fewer than 275 are assigned to "three months".

which ought to be one of ovulation, is allowed by them to elapse without notice, without some inner change. The ovary, with its nervous apparatus, from the moment of puberty to the time, when its functions naturally cease, may, indeed, be compared to a clock [1]), wound up at the start, and striking the hours with extreme regularity by periodic emissions of one or more eggs. During pregnancy the clock does not cease to run; it still strikes the hours, but in muffled fashion, so that, if all goes well, the sound is not heard outside of the ovary. And, just as some clocks are so arranged, as to give an indication of the approach of the hour shortly before the arrival of the striking-period, so the ovary announces the normal advent of birth some little time before the ovulation, due soon after the birth-period. What form the muffled strikings take during gestation is a problem for exact investigation, but it is not unlikely, indeed, highly probable, that they are represented by abortive ovulations of eggs, which degenerate in the ovary. Only in this way can regularity in the functionings of the ovary be conceived as being maintained.

In this connection the *corpus luteum* and its history during Mammalian gestation afford interesting material for reflection.

This structure appears to be entirely absent below the mammalia, and its increase in size during gestation would appear to be a contrivance for diminishing the

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1) von Baer remarks somewhere, that natural processes have any number of times been likened to the movements of a clock, but it is the only convenient machine, appearing to "go" of itself with rhythmic movements, to which one can refer.

nutrition of the ovary and ova, and, thus, of preventing a normal ovulation [1]).

After the initiation of gestation the striking of the clock first becomes audible again soon, often immediately, after birth [2]). This is the case in mouse, rabbit, cavy, horse, cow, and other ruminants, and probably in some form, i. e. as a wasted or an abortive ovulation, in man, cat, dog, pig, and sheep, in which a new gestation does not shortly ensue on the birth.

The muffled strikings during gestation, the normal periods of ovulation, may then, as Tyler Smith and others have insisted, be frequent times of abortion; if, for no other reason, then because the development is going on wrongly, and this is the best way of putting an end to it, and of obtaining a new start.

In this connection cases of death of all the embryos *in utero* at early stages of the gestation in rabbit and cavy must be mentioned. During the last nine years many such have been encountered in my work. When in such instances all the young have died at an early stage, owing to the influence of lactation, or to some other unknown cause, they must either be absorbed or aborted prior to the next ovulation due. Usually, if not too large, they are disintegrated and absorbed *in situ*, but, if this does not happen, there can be no doubt, that an abortion must shortly precede the next ovulation.

There would appear to be no advantage in drawing up a list, of what ought to be abortion-periods, corresponding to suppressed ovulations included in human pregnancy, as

1) Compare appendix q.
2) Compare appendix v.

there are no data available at the present time, upon which to decide the matter. But it may once again be insisted, that during pregnancy they must be counted, not as intervals of 27—28 days, but of 23—23 $^1/_3$ days, or thereabouts.

What holds good for man will, *mutatis mutandis*, be found true of other placental mammals. I am firmly of the conviction, that to many with prolonged gestation-periods, such as horse, cow, sheep, etc., the considerations, outlined above, with due regard to the ovulation- and critical units, will be found to apply.

Thus, as an instance, may be mentioned certain statements regarding sheep, which were made to me by Prof. Wallace of Edinburgh University. It is said, that shepherds find, that sheep, which have been served, often refuse the ram at the next ovulation- (more exactly rutting) period, and then receive him at the next following one. Shepherds believe these sheep to have aborted, and describe them as having "held", and then failed to "hold". These facts agree well with abortion at the critical period followed by a new fertilisation at the ovulation almost immediately succeeding.

XIII. The Cause of Birth.

Although this question figures largely in the title of the present writing, although the whole of the latter has worked up to it as to a climax, and although it has hitherto been wrapped up in a mystery, which resisted all attempts at unveiling, its resolution does not appear to be anything like so important, or so interesting, as the

solving of the riddle of the duration of uterine life. Its explanation comes, it is true, as a culmination, but it is so simple, that little acumen is now necessary for its perception.

Wheresoever one seeks information regarding this physiological problem, little else is found, than an admission, that absolutely nothing is known concerning it.

In a standard work on physiology we read: — "we are utterly in the dark as to why the uterus, after remaining apparently perfectly quiescent (or with contractions so slight as to be with difficulty appreciated) for months, is suddenly thrown into action, and within, it may be, a few hours gets rid of the burden it has borne with such tolerance for so long a time; none of the various hypotheses, which have been put forward, can be considered as satisfactory. And until we know what starts the active phase, we shall remain in ignorance of the exact manner in which the activity is brought about" [1]).

Werth, in Hensen's „Physiologie der Zeugung", remarks: — "der Eintritt der als *Wehen* bezeichneten Uteruscontractionen gehört zu denjenigen Processen, welche in Bezug auf die veranlassenden Momente den Erklärungsversuchen einen hartnäckigen Widerstand entgegengesetzt haben. Im Ganzen treten die Wehen ziemlich präcise 40 Wochen nach der letzten Menstruation auf etc." [2]).

According to Tanner, "we are really unacquainted with the exciting cause of parturition" and he proceeds to comment on "the devout remark of the Arabian physi-

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1) Foster, M., Text-book of Physiology, 2nd Edition 1878, p. 554. In later editions the existence of the problem is still admitted.

2) loc. cit., p. 279.

cian, Avicenna — that at the appointed season labour comes on by the command of God" [1]).

Spiegelberg is no more explicit. He writes: "— die Schwangerschaft ist eine periodische Function, und es ist wie bei anderen periodisch ablaufenden Vorgängen ganz müssig, nach der immanenten Ursache der Periodicität, ihrer Dauer, hier also nach der Ursache des Eintritts der Geburt zu fragen; die Art der Periodicität ist eben durch die Organisation bestimmt, nur die Bedingungen, unter denen sie in die Erscheinung tritt, sind uns zugängig" [2]).

Explanations have been offered, but, as yet, they have not carried conviction.

Thus, Harvey, as cited by Tanner, after making some observations on the way, in which "prudent matrons calculate", proceeds to say, that they, "after ten lunar months have elapsed, fall in labour, and reap the fruit of their womb the very day, on which the catamenia would have appeared, had impregnation not taken place" [3]).

It is interesting to note, how here a kernel of probable truth is wrapped in a thick husk of error. The period of pregnancy does not correspond to ten menstrual cycles; for, as we have seen, these are variable in different individuals, and in the same person at different times. Moreover, Hensen, with other authorities, estimates 281.86 days as "wohl zu hoch" for the duration of pregnancy. And, although at the time of birth a men-

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1) loc. cit., p. 178.

2) Spiegelberg, O., Lehrbuch d. Geburtshülfe, 1878, p. 125.

3) The works of William Harvey, M. D. Translated for the Sydenham Society by Dr. Willis, London 1847, p. 529.

strual period is undoubtedly due[1]), it is not the tenth period, but the twelfth from the initiation of pregnancy. Finally, since menstruation must be regarded as in a certain sense an abortion, the birth itself is the menstrual period due[2]).

Another author, Dr. Tyler Smith[3]), like Pouchet, regarded heat or rut and menstruation as the same thing, and he looked upon the birth as a heat-period, in which, instead of the passage of an unfertilised ovum, that of a fully developed one took place. Although he noted, that in many animals an ovulation ensued soon after birth[4]), one searches in vain for a statement, that the approach of this is the cause of birth.

It would be of no service to continue these citations, as they would but needlessly extend this paper.

Harvey would have been quite right, apart from the wrong number of menstrual cycles and the failure to notice the correspondence of pregnancy to a certain number of ovulations, had he compared menstruation and parturition more closely together, showing, that in a sense they were identical.

Tyler Smith went to the other extreme, in making menstruation, abortion, and parturition the equivalents of

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1) Harvey, Naegele, Rigby, and Berthold have all insisted on the supposed correspondence of the duration of pregnancy to some multiple of a menstrual period.

2) Compare appendix u.

3) Considerable pains have been taken to grasp the full significance of Tyler Smith's views, more particularly, because of some superficial resemblances certain statements of his, when studied apart from their context, bear to conclusions of mine. In appendix l quotations at length are given from his two chief works, and it remains only to say, that in their essence his arguments and conclusions, because based on what appear to be false premisses, are diametrically the opposites of those contained in this paper.

4) Compare p. 112.

rutting periods. In doing this he explained neither the one nor the other. It is no explanation to say, that menstruation, abortion, and parturition are all comparable to heat-periods, or that in this sense "parturition is essentially a menstrual period". Tyler Smith thought, that he had interpreted menstruation, in concluding its equivalence to heat in animals, and, thus, felt entitled to reduce parturition to the same thing. In another direction Tyler Smith was obviously on the right track, for he was apparently the first to assign the exciting source of parturition to the ovary, whilst failing to perceive, that a coming ovulation must be the real cause.

In concluding this discussion it is possibly a work of supererogation to treat of the cause of birth in detail.

From the results of preceding sections the reason of the climax of pregnancy, parturition, must be apparent.

It is part of the same necessity, whose conditions we have studied, which dominates the developmental history of Metatheria and Eutheria from the moment of fertilisation of the egg, through the time of the building-up of the future animal, to the end of its uterine life, and it is the inevitable and rhythmical sequel of all, that has gone before. The length of gestation in any given species of placental mammal is fixed by a certain characteristic number of critical units, and this determines the degree of development, probably, in general terms, that most favourable for the species, at which the young shall be born. A critical unit corresponds to either one or two ovulation-units in different species. And, as in the Marsupial ancestry the ovulation-period was fixed by birth at the critical phase, so now necessity

forces any form, in which the gestation has been lengthened to embrace two or more critical units, even when these latter have been doubled, still to carry out the extension in such a way, that it shall keep strictly rhythmic step with the periodicity of the ovulation. Thus, the gestation is prolonged so as to fall just short of a given number of ovulation-units.

During pregnancy the ovary is still marking time, and in muffled tones striking the hours. When the natural term of the gestation approaches, the warning, that the time-limit is nearly run out, comes from the ovary, and, in obedience to this intimation, which is of the nature of a command, birth takes place "at the season appointed", in order that a new ovulation, which may, or may not, be expended in vain beyond inducing the birth, shall be carried into effect, and Nature's law observed.

XIV. The Rhythm of Reproduction in Mammalia.

A Summary.

The problems dealt with in the preceding pages have of necessity been treated of singly; and, now that the main facts have been cleared up, there may be, at any rate for the reader, a certain convenience in bringing the whole together in a connected and brief form. In this way it will be easier to comprehend the order and rhythm of reproduction in the Mammalia.

The following lines may also serve the purpose of a

summary, of what has gone before in the preceding pages. Of certain theoretical items, i. e. the origin of an egg-case and large yolked-egg, no outline will be given, but the reader may be referred to the section, in which they are treated of [1]).

The inquiry really begins with an examination of the conditions, under which reproduction can be, and is, effected, when uterine development and nutrition of offspring by means of mammary glands are initiated.

In the memoir, "on certain Problems of Vertebrate Embryology", published last year, among other things it was demonstrated, that the evolution of mammary glands and the initiation of lactation had been the primary factors in reducing the yolk in the egg of ancestral mammals. This reduction, due to the mammae, could, however, be carried no further back than the critical period, i. e. than the epoch, at which the embryo, being first complete in all its parts, could, and must, provide for its own nutrition. The mammary organs could not, and cannot, begin to function prior to that time. If, as has happened, a yolk-sac placenta, or trophoblast, be developed, it, as a structure forming a part of the phorozoon, can only function until the critical period, when it must begin its degeneration, for its normal life-span is reached.

The combined workings of these two factors, mammary and trophoblastic nutritions, from opposite points, the one beginning at the soonest at the critical period, the other ending at the latest at this important epoch, have brought it about, that, where no allantoic placenta is developed, there uterine life is only possible until the critical period, when

1) p. 13—18.

the young must, perforce, be born. This is probably the case in all aplacental marsupials, and it certainly holds in *Hypsiprymnus, Didelphys, Trichosurus,* and *Macropus,* as either demonstrable, or already established.

Once the birth was fixed to take place at the critical period in ancestral Metatheria and Eutheria, an alteration of this arrangement could only be brought to pass by the evolution of an allantoic placenta.

If this happened, the birth could be postponed to a later time, for the nutrition of the foetus beyond the critical period[1]) was then provided for.

Before an allantoic placenta had been, so to speak, invented, the coincidence of birth- and critical periods had led to deeply-reaching effects on the ovulation.

Prior to all these changes, evolution of mammae, trophoblast, etc., ovulation may have occurred at regular periodic intervals, but of this there is no evidence available as yet in the developmental history of mammals[2]). However this may be, and it is a matter of no apparent import, the initiation of birth at the critical period put restrictions upon ovulation, if none previously existed.

Ovulation was rendered impossible during gestation, and under the most favourable circumstances it could only recur shortly after every birth. Under the conditions imposed by uterine gestation the number of offspring is at the best a restricted one, no case being known, in which

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1) The critical period is one of starvation rather than, as suggested by Houssay, of asphyxiation (compare Houssay, F., Le rappel ontogénétique d'une métamorphose chez les Vertébrés, Anat. Anz., Bd. XIII p. 33—39).

2) The conditions in Monotremes might be interesting in this connection.

the uterus can normally harbour more than 27 developing embryos, the average number being much smaller, even in the most prolific forms. It, therefore, became necessary, to repeat the ovulation as often as possible under the limitations of frequency and number of eggs imposed.

Thus, it arose, that the ovulation-period became almost equal to, but actually a little longer than, the interval of time necessary for development to the critical period, or, in other words, to the birth.

This latter interval may be termed "the critical unit" in any given case, and in the same way the period of time between any two ovulations may be described as "the ovulation-unit". It is probable, that the critical unit first fixed the ovulation-unit; or, at any rate, that the interaction of the two led to a correspondence, such that the latter always very slightly exceeded the former. Owing to this it resulted, that a coming ovulation, i. e. a reflex message from the ovary, was the direct cause of birth. Tyler Smith in 1849 almost foresaw this; but, though he assigned the cause of birth to the ovary, he failed to recognise, that a coming ovulation was at its basis.

When an allantoic placenta was initiated, with consequent prolongation of the gestation, the correspondence and relationships of the critical- and ovulation-units determined the conditions, under which this prolongation might take place. It could only be extended in the first instance by being made to embrace two critical units instead of one so as to maintain the correspondence of the critical- and ovulation-unit, i. e. so that birth might still be induced and succeeded by a new ovulation.

The carrying-out of this extension of gestation to two

critical units afforded the passage from the Metatherian to the Eutherian stand, and it led to the loss of the marsupium, as a structure no longer required.

This type of gestation of two units is still in existence in many of the lower Eutheria, as mouse, rabbit, etc., and, probably, in mole and hedgehog. A gestation of two units, although it gave an advance on the condition at birth, characteristic of forms, whose gestations were made up of one unit only, did not yield the advantages to be gained by a still further prolongation of the gestation to include three or more critical units. These advantages were seized upon in course of time by various mammals, and utilised to varying extents, their gestations gradually coming to include a greater number of critical units.

But, wherever further prolongation was acquired, it was always still effected under the rules originally laid down as to a correspondence between the length of gestation and a certain number of critical- and of ovulation-units. By a curious coincidence, for it is nothing more, in the appended table (p. 98) forms with from one to eight critical units in the gestation are included.

An examination of the list will make it clear, that, as a rule, forms with a greater number of such units in the gestation are born in a condition more advanced than those with a less.

Mere length of gestation does not effect this, for a mouse attains in 20 days a degree of development as advanced as a rabbit in 30, or as a dog in 62; or, again, an opossum reaches in 8 days, the stage of development arrived at by a rabbit in 15 days, a cavy in 22, a sheep in 30, a horse in 42, or a human embryo in 46 days.

The reason of a greater degree of development at birth with an increased number of critical units lies deep, and is to be sought in the circumstance, that forms with gestation-periods of several critical units must, in their ancestral history, have passed through conditions, in which the number was smaller. They must have started with a gestation of one critical unit, and have gradually increased this number.

While many of the lower Eutheria still maintain very conservative traditions, among the higher ones in certain orders, thus, in Ungulata and in man, a rather different state of affairs obtains, probably as a secondary condition. Even in the lower forms, such as rabbit and cavy, it is rendered likely, from a comparison with the short critical unit of the opossum or *Hypsiprymnus*, that the critical unit, and with it the ovulation-unit, has been doubled, or trebled.

However this may be, something of the same sort has taken place without affecting the ovulation-unit in Ungulata and man. In horse, sheep, pig, and man the critical unit is no longer the equivalent of one ovulation-unit, but almost of two such. This is interpreted as meaning, that the gestation-length has been doubled without altering the grade of development at birth, and it is put into association with a probable increase of size in the course of the ancestral history, without excluding the possibility, that other factors may have come into play.

In all mammals ovulation during gestation is either abortive or suppressed: and this is necessary, for normal ovulation during gestation would lead to abortion.

The *corpus luteum* is probably a contrivance for the suppression or rendering abortive of ovulation during gestation.

The commencing degeneration of this structure some little time before the end of the gestation (like its rapid atrophy, where fertilisation has not taken place), allows of preparation being made for a new ovulation. As already indicated, the approach of this ovulation is, in a reflex manner, the direct cause of birth [1]).

In preceding chapters consideration is given to the causes of many abortions in various mammals and to the nature of menstruation.

It has been insisted, as was already done in the memoir "on certain Problems of Vertebrate Embryology", that the critical period (with the consequences following in its train), multiples of this, and the ovulation-periods, normally-suppressed during gestation, must be very frequently times of abortion in various mammals, particularly in those, like horse and man, where the gestation is a prolonged one of several units.

Menstruation is comparable to an abortion prior to a new ovulation, and it is an abortion of a decidua prepared for an egg, which was given off subsequent to the preceding menstrual period, and which has escaped fertilisation.

It is an abortion corresponding in its periodicity with a former critical unit, which obtained before the present one arose by a duplication. Thus, it is comparable to an abortive birth at a former critical period.

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1) See appendix q.

So far it has appeared, that, under the conditions governing it, gestation in Metatherian and Eutherian mammals is, like their ovulation, dominated by a rhythm, and a similar and connected one really underlies lactation. This latter originally, and even now in many cases, had no effect on gestation, and a female, suckling young, could, and in some species can, become pregnant again immediately after the birth of a litter. This, as is well known, holds true of the mouse, rabbit, and cavy. But in others the effect of lactation has been either to destroy the fruit of the new succeeding gestation, or to render the ovulation ensuing on the birth useless, beyond inducing the latter.

When a new gestation now no longer follows on the birth of a litter, one can in many cases make out, that lactation still keeps up the rhythm of the gestation in corresponding to one or more gestation-lengths. It has to do this in the mouse and rabbit; and, regarding the former, Sobotta has put it on record, that lactation finishes only a day or two before a new litter is born [1]). But in the pig lactation suppresses a new gestation [2]), lasting as long as the latter would have done, i. e. about four months, while in cat and dog the lactation-period is equal to about two gestation-lengths.

Thus, ultimately, lactation, gestation, the ovulation- and critical units are all connected together in a remarkable way, and their relations are such, that they all typically conform with the rhythm of reproduction in the Mammalia.

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1) In the work cited in appendix v.
2) And occasionally in mouse and rabbit.

This latter is of such a nature, that without it there would be no regulated course for the gestation, no periodicity in the ovulation could be maintained, and the birth of offspring would be a matter of chance and accident, instead of one of law and necessity.

In mammals the uterine development from beginning to end, gestation, birth, ovulation, and, in many cases at least, lactation, all obey one rhythm, whose basis is in the ovary.

By ovulation this rhythm is proclaimed throughout the reproductive life of the female, in gestation the same rhythm is maintained, but in a modified fashion; and, as the span of uterine life draws to a close, it again asserts itself, and induces birth.

Harmony and law reign in the reproductive life of Mammalia, and, where previously chance and chaos appeared to rule in this, there we have learnt to recognise "a certain seeming order", the dominion of necessity and the action of regulated change.

What the visible universe would be without the law of gravitation, holding the planets in their orbits and dictating to each its "vorgeschrieb'ne Reise", that on a far smaller scale the microcosmos in the uterus of a pregnant mammal would present without the domination and sway of an iron necessity.

The reign of law prevails in the infinitely little no less, than in the immeasurably vast, and, that this should be, is probably not less momentous and vital for human existence, than that the law, which moulds a tear, should guide a planet in its course.

Comparative Table of Gestation-periods, Critical Units, etc.[1]).

Name	Ovulation-unit in days	Critical unit in days	Number of critical units in gestation	Average gestation in days
Opossum *(Didelphys virginiana)*	—	$7\frac{5}{6}$	1	$7\frac{5}{6}$
Kangaroo *(Macropus major)* .	—	—	1	38
White mouse *(Mus musculus)* .	$9\frac{5}{6}$—10	$9\frac{2}{3}$—$9\frac{5}{6}$	2	$19\frac{1}{3}$—$19\frac{2}{3}$
English rabbit *(L. cuniculus)* .	31—32 (?)	$15\frac{1}{4}$—$15\frac{1}{2}$	2	$30\frac{1}{2}$—31
Dog *(Canis familiaris)*[2]) . . .	—	29—32	2	58—64
Cat *(Felis catus)*[2])	—	28	2	56
Cavy *(Cavia porcellus* var. *domesticus)*[3])	21—22 (?)	21—22	3	63—66
Pig (*Sus scrofa* var. *domesticus*)[4])	15—18	28—30 (?)	4	112—120
Sheep *(Ovis aries)*[5])	15—16	29—30	5	145—150
Cow *(Bos taurus* var. *domesticus)*	21	40—41 (?)	7	280—287
Horse *(Equus caballus)*[6]) . .	21	42	8	336
Man *(Homo sapiens)*[7]) . . .	23—$23\frac{1}{3}$	46—$46\frac{2}{3}$	6	276—280

1) For remarks on the table see appendix b.
2) Compare appendix i.
3) Compare appendix f.
4) Compare appendix h.
5) Compare appendix z.
6) Compare appendix g.
7) Compare appendix m.

Appendices.

a) Tessier, Recherches sur la durée de la gestation et de l'incubation dans les femelles de plusieurs quadrupèdes et oiseaux domestiques. Mémoires de l'Acad. des Sciences, Paris, Année 1817, p. 1—40.

The memoir contains observations on the apparent gestation-lengths in 575 cows, 442 mares, 912 sheep, 25 sows, and 161 rabbits.

Of the cows[1])	544	(94,6 %)	had an average gestation of				$282^{11}/_{17}$	days
Of the mares served once	272	(81,6 %)	„	„	„	„	„ $346^{1}/_{3}$	„
Of the mares served oftener	128	(75 %)	„	„	„	„	„ $341^{1}/_{4}$	„
Of the sheep	912	(100 %)	„	„	„	„	„ $151^{1}/_{8}$	„
Of the sows	25	(100 %)	„	„	„	„	„ $115^{1}/_{2}$	„
Of the rabbits	161	(100 %)	„	„	„	„	„ $31^{1}/_{3}$	„

b) Remarks on the table and on Tessier's results. As stated in the text, no attempt can be made to do more than illustrate general averages. In many, nay, almost all, of the animals included in the list exceptions to the rule will readily be found. Each such exception would have to be considered on its own merits, and to do this it would first of all have to be demonstrated, that it did not really conform with the rule. Obviously, to prove this certain data are requisite.

Since in all such cases the time of birth is known, the actual duration of the gestation can only be stated, if the approximate time of fertilisation be obtainable. Now, although, in dealing with averages, it can be determined with sufficient nicety from that of copulation, this is by no means to be taken for granted, when an irregular and anomalous instance is under discussion. In such cases various factors may come into play. Thus, the ovulation may have been delayed, resulting in a postponement of the moment of fertilisation; the individual may have an abnormal, as compared with the usual, ovulation-unit, and with this an unusual critical unit. Mares are known, in which heat and probably ovulation return every 14 days, and analogous cases have been met with in the human female. Tyler Smith remarks, that an unusual type

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1) Earl Spencer found in 764 cows an average gestation of 285 days.

of menstrual cycle appears in his experience to be associated with a departure from the normal duration of pregnancy.

This is quite what one might expect from general morphological considerations and from the intimate relationship, which, as we have seen, must always subsist between the critical- and ovulation-units [1]). What applies to the species must with even greater force hold good in the individual. Unless in any given individual the two units be in agreement in the mode described in the text, it is difficult to see how the rhythm of the development can be maintained. Moreover, although this point was not mooted in the general memoir, it has not been overlooked, that, even at the present day, there may be a tendency in certain species to a still further lengthening of the gestation. This may, or may not, influence the critical- and ovulation-units, it may be met with in few, or in nearly all, of the individuals of a species.

In the same way a shorter gestation-period in some individuals of a species may be due either to conservatism, or to a reversion to a nearer or more remote former such period.

One cannot be expected to solve an equation, if two or more of its factors be unknown quantities, unless it be so stated that these can be guaged.

In all such unusual instances of longer or shorter gestations all the factors, except the moment of birth, are unknown. Given these, there would in all probability in most of them be no problem left to be solved, for all the difficulties would then disappear.

From Tessier's work it appears clear, that in more than one of the domesticated animals (cow, and horse) a prolongation of the gestation, not accounted for by a delayed ovulation, does take place. Without all the details concerning these it is out of question to explain them. Some of them may be such, that the underlying anomaly influenced all the factors, ovulation- and critical-unit etc. in the same way, while others may be determined by some other reasons. It may be — and this agrees with what must have happened in the past, when at one time gestations were shorter, and only gradually got longer by the annexation of a new critical unit — it may be, that some, at any rate, are explicable as the result of the adoption of a further such unit. The gestation-periods of children born with teeth might be interesting in this respect.

But the matter has in the case of man important medico-legal aspects, and these are dealt with elsewhere [2]).

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1) The ovulation-periods of pig and sheep have been quoted simply as given by many authorities, but it may be stated that if properly investigated a much more exact and stable number would probably be found in each.

2) See appendices n and o.

Reverting to Tessier's observations. In the cow he found, that out of 577 cases no fewer than 544 had a gestation of 270 – 299 days.

Ovulation-units of 20—21 days and critical units of 39 – 42 days would give, with the multiple of 7, 273—294 days for the gestation, or, in other words, a variation of one day in the ovulation- and of 3 days in the critical unit account for rather more than 90% of his examples. An ovulation-unit of 22 days, with the critical one in correspondence, covers all Tessier's highest cases but one, and his single very exceptional instance of a gestation of 321 days may be disposed of by the assumption of an ovulation unit of 23 days. In the above it has, thus, not been necessary to introduce a further critical unit. Similarly, in the horse almost all of Tessier's cases would be embraced in ovulation-units of 20—23 days with corresponding critical units, and by far the great majority by an ovulation-unit of 21—22 days.

In the sheep Tessier's records do not show so great a divergence as in the cow and horse, and the slight variation in the table suffices. (Compare also appendix z.)

Finally, it may once more be insisted, that these statistics give no clue at all as to the moment of fertilisation. In the horse and cow the interval between copulation and fertilisation may frequently be one of several days, and these would fall to be deducted from the gestation. In this connection it is significant to note, that the average of mares served several times, given by Tessier, is, as might have been expected, smaller, than in those served once only; and, whereas the latter exceeds 346 days, the former is little over 341. Even this is probably too high.

c) Antithetic *versus* homologous alternation of generations. More than one morphologist of standing has expressed to me his inability to understand, in what sense the term "antithetic alternation" is used. As elsewhere remarked, botanists, never having been pestered with the recapitulation nightmare, have made far greater advances with their (simpler) embryological problems, than have zoologists.

The distinction between the two kinds of alternation is a botanical one, but, none the less, it is demonstrably applicable to animals. It was first made in 1874 by Celakovsky (Sitz. d. Gesell. d. Wiss. Prag 1874, p. 30), and the Annals of Botany (Vol. 4, 1889—91) contains an able exposition of it from the botanical side by F. O. Bower.

Homologous alternation is what has long been known in zoology, it is, in fact, what Chamisso originally described in *Salpa*.

In it the two, or more, generations from egg to egg, though only one of them is sexual, are homologous organisms. The sexless chain-producing *Salpa* is just as much a Tunicate and a *Salpa*, as is the sexual form.

Where, however, two distinct generations, sexually and asexually-produced respectively, occur in a life-history, and, where the two are neither homologous in their parts nor in their entirety, there we deal with a case of *antithetic alternation*.

To treat of the subject adequately a book would need to be written. But, as an instance, comparing together an Annelid and its *Trochophore*, it is noted, that the two organisms are not homologous, for, though the one is a segmented worm, the other is not.

If only so much could be said, the thing might seem to many embryologists to be a mere quibble; for, although they look upon the *Trochophore* as an ancestral form, it is to them at the same time a young Annelid. At one and the same time it is an ancestor and also a descendant of an ancestor — a contradiction in terms only to be explained away by Okenian metaphysical reasoning! But, looking at the organisation of the two, it is clear, that no homology subsists between their parts; for the nervous, excretory, locomotor, and sensory organs of the *Trochophore* are not those of an Annelid, neither do they become converted into those of the sexual form. If they be new formations, not in their origin parts of the Annelid, they must have arisen as temporary structures out of nothing!

d) The critical phase or period. In my work of last year, "Certain Problems of Vertebrate Embryology", the terms, critical stage, phase, and period, were used somewhat indiscriminately, in the present writing only the two latter are employed. The grounds for this course of action cannot be detailed here, since they have arisen out of a very extensive and minute series of observations on the development at this epoch in *Scyllium canicula*. A full account of the facts, obtained from the study of a great number of embryos, will probably be published, as soon as the material has been exhausted.

On the present occasion it only remains to state, that this epoch of the development, termed the critical one, is in reality a phase, lasting some little time, and not a stage. In *Scyllium canicula* it begins with embryos of 32 mm (measured after preservation in alcohol), and it is ended by the time the embryo is 34 mm in length. Very similar conditions have been noted in the sheep and pig, and in these also the critical phase persists, whilst the embryo increases somewhere about 2 mm in length.

It may also be mentioned here, that, as nearly as one can

judge, the critical phase has in mammals a longer duration than any other phase of the development, for it is far easier, by trusting to chance, to obtain embryos of this period than of any other.

Thus, if a dozen pregnant uteri of pig or sheep be obtained from the slaughter-house, two or three of them are almost sure to contain embryos of the critical period.

It may be well to note briefly the external characters by which one can detect an embryo of this period. They are as follows: — the embryo is *first beginning* to look like the form, whose offspring it is. The lachrymal groove has disappeared, the eyeballs are no longer rounded but somewhat oval, the fore-limbs are flexed, the digits of the hand are just indicated, the mammary line has just completely disappeared (if one be at any time present), and the "milk-points" are quite distinct and separate. Hair-follicles are usually visible on cheeks, snouts, or over eyes. Internally, there are many characters, but the best and surest guide is the condition of the spinal cord. At the beginning of the phase the formation of the posterior fissure or septum of the cord is just initiated, at the end of the phase it has progressed a very slight distance.

e) Eutherian *versus* Metatherian gestation-arrangements. The advantages of a gestation even of but two critical units over that of a single unit are curiously exemplified by the facts resulting from the introduction of the rabbit into Australia, into the midst of a fauna, almost all of which belongs to the one-unit-series.

These rodents have done far more than hold their own against marsupials in the struggle for existence, not only against food-competitors, but also against enemies.

Mr. Begg, a resident for 31 years in Victoria, recently informed my friend and colleague, Dr. Gregg Wilson, that in his experience the rabbit had mainly been answerable for clearing out "kangaroos" in this colony, and others have assured me, that, where rabbits flourish in Australia, there herbivorous marsupials are now wanting.

It is easy to perceive the great advantages these lowly Eutheria would have in this struggle. A rabbit will doubtless breed all the year round in such a warm climate as that of Victoria, will produce many young at a birth, and suckle for less than a month. Marsupials breed seldomer — they cannot help themselves in the matter — many bring forth only one or two young[1]), and, according to Owen, *Macropus major* suckles for 10 months! By

1) In Dr. Broom's rich collection of marsupial embryos of some ten or more genera there were not more than a couple of cases, where the minimum did not obtain.

the time this animal, with its one offspring, is ready to begin a second gestation, the number of young rabbits, offspring of one mother, and able to feed themselves, might well be a hundred. The rabbit, with a gestation of two units and a short lactation-period, has an immense advantage[1]) over a kangaroo (*M. major*) with a single rather long critical unit and a lactation-time of 10 months. If a *Macropus major* bred continuously, it must at the expiration of every new critical unit turn out the pouch-young, and this or these would be in a very ill-developed condition.

Against this the rabbit, with a short gestation, can place in the scale its two critical units and continuous breeding, such that at the end of a new gestation-period the young of a preceding one are able to take care of themselves. This fatal conservatism of the majority of marsupials, in clinging to a gestation of one critical unit, would appear to have had in past times, and to have at present, more influence in leading to their extermination in various parts of the world than any other causes, not excluding that usually assigned, the evolution of the Carnivora. But it must not be forgotten, that the tendency of recent research, that of Semon, Klaatsch, O. Schultze, Fleischmann and mine[2]), goes to prove a marsupial ancestry for the Eutheria. Therefore, in past times, when some forms attained the Eutherian stand, those still Metatherian had, probably, a "Hobson's choice" between following suit and extinction.

f) Ovulation in the cavy. It may be admitted, that the non-establishment of the ovulation-period of this animal weakens any arguments based upon this particular case. For this reason the mouse has been used as an illustration, where my preference would have been the cavy, had the facts all been made clear regarding it. For a long time, though not without misgivings, the period mentioned by Hensen was accepted as correct. His opinion in its wording does not bear a ring of certainty about it, it runs: — "Meerschweinchen mit 66 Tage dauernder Trächtigkeit scheinen eine Brunstperiode alle 17½ Tage zu haben". If this be taken to mean, that rut, and with it ovulation, recurs in the non-pregnant cavy every 17½ days, it requires little consideration to see, that this is impossible. During my recent experiments with cavies it only became certain, that there must be some different period of rut, when it was too late to establish this during the present summer.

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1) Rabbits are said to crop the herbage so closely, that no herbivorous marsupial can find food, where they are numerous. And an allantoic placenta is a far more efficient nutritive organ than a mammary apparatus.

2) One might add also the placental work of Duval, Hubrecht, Selenka, and others.

But it is intended, that the actual ovulation-unit should be found out, as soon as the necessary experiments can be made.

Reasons may be given for doubting the correctness of Hensen's statement.

I believe the probabilities to be, that usually the critical unit of the cavy is rather less than 22 days and the gestation-period, as given by Hensen, 66 days, and these numbers will be used in the following discussion.

If $17^1/_2$ days, or any number very near this, be the ovulation-unit of the cavy, there can be no correspondence, such as there is in the mouse, between it and the critical unit, or the total gestation.

By no amount of ingenuity can $17^1/_2$ be divided into 66, or 67, or even 68 without remainder. Now, it is quite certain, that Guinea-pigs ovulate within a few hours of the birth of a litter (compare Bischoff, Entwickelungsgesch. des Meerschweinchens, p. 12), and, unless the ovulation-unit correspond to the gestation-length, it must, in conformity with what we know of the mouse and other cases, when multiplied by some simple number, almost equal the gestation-length.

If the latter be divided by 4, we get a number $16^1/_2$, which is too small, for it is considerably smaller than the critical unit. In the same way, half the gestation-length is too large, and the number, giving a relationship between critical- and ovulation-units, is 3, which yields 22.

Information has been sought on this subject from all sorts of sources, scientific and "practical". Two experienced breeders of prize-cavies assured me, that these animals could become pregnant at any time. In need hardly be said, that I declined to believe them.

The only figures found are given by Bischoff. They are as follows: —

Birth of Litter	Next copulation	Interval
May 27	July 6	41 days
June 17	Aug. 7	50 „
June 17	Aug. 6	48 „
June 25	Aug. 15	50 „

The first of these numbers points to an interval of 22 days, or thereabouts, assuming one period to have been missed either by the cavy or by the observer, while the others indicate a much larger unit and one too large for the facts. It must, however, be pointed out, that, as the cavy, and the same, unfortunately, is true of the other forms mentioned in this work, lives under the artificial conditions of domestication, the ovulation rule may be sometimes more honoured in the breach than in the observance. Cases of mice,

which apparently failed to ovulate until 2 or 3 days after the birth of a litter, have come under my notice.

Whatever else they establish, Bischoff's figures[1]) show this, that cavies do ovulate oftener than every 66 days, and than every 41—50 days, for otherwise, if the latter held good, there would be no correspondence between birth and ovulation.

Founding on the facts relating to the development of the Guinea-pig and its critical unit, on those concerning the ovulation in the mouse and other forms, as set forth in this work, and on the above discussion, it may be stated that the normal ovulation-unit of the cavy is probably somewhere about 22 days. He, who would impugn the correctness of this conclusion, ought, if logical, to deny entirely the periodicity of ovulation in mammals. At any rate, to such a critic the words of Pouchet would find an apt application, for he would undoubtedly be one "de ceux qui, dominés par leurs anciennes études, préfèrent nier l'évidence plutôt que de s'adonner à de nouveaux travaux".

g) The critical period of the horse. A year ago this was fixed, though not with certainty, as lying towards the end of the seventh week of gestation. A re-examination of the evidence as yet available has led me to alter this conclusion. In the first instance the result was arrived at from a misconception of Bonnet's statements, regarding the formation of the placenta and the change in shape of the egg. These were understood to happen towards the end of the seventh week; whereas, as a matter of fact, in his text-book he assigns them to the end of the sixth week.

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1) Hensen's well-known researches could only be referred to long after the above was written. He states (Beobachtungen über die Befruchtung und Entwickelung des Kaninchens und Meerschweinchens, Zeitschr. f. Entwicklungsgesch., Bd. I p. 217), that if, after the birth of a litter, the female cavy escape fertilisation, the period, from the birth to the next ovulation, was found to be 17, 18, 35, and 37 days. The only observation to be made regarding these figures is, that they show at most the time of a new rut, and not, of a fresh ovulation. The date of this could be best determined by obtaining and estimating the age of the embryos, from comparison with known cases, at some period of the subsequent gestation. It may be added that the average of Bischoff's and Hensen's figures gives a probable ovulation-unit of almost exactly 21 days, or allowing for a days interval between copulation and fertilisation, one of 22 days.

Hensen also writes on p. 215: — "bei den Meerschweinchen erfolgt (die Copulation) in der Regel 0 bis 3 Stunden nach dem Gebären, und die Ovulation richtet sich nach letzterem".

Regarding the latter it may be insisted, that just the very opposite is the case, i. e. that parturition adapts itself to the ovulation and not *vice-versâ*.

Figures of Ewart's horse-embryos have now been published (J. C. Ewart, A critical Period in the Development of the Horse, London, A. & C. Black, 1897), and from them the following points can be made out. By the kindness of Prof. Ewart I have also had more than one opportunity of inspecting the original specimens of 4, 5, 6, and 7 weeks from copulation. The embryo of 49 days is decidedly beyond the critical phase; for it is not merely *beginning* to resemble a horse, it is one, as the author notes.

The 42 days embryo just borders on the critical phase, for the lachrymal groove is still present, and the head is not much raised. But its fore-limbs are flexed, the eye is oval, the snout is just commencing to lengthen and one or two hair-follicles are visible above the eyes. It is, however, so near it, that a few hours further development, and certainly not more than 24, would accomplish what is lacking.

As mentioned in the text, this would give 43 days at most but only on the assumption, that copulation and fertilisation were identical. If to the time given the interval between copulation and fertilisation be added, a sufficient span of time would be obtained to bring the embryo to the critical period. In fine, the embryo falls short of the critical period by some hours, but this deficiency is made good, if the interval between copulation and fertilisation be allowed for. It may be added, that neglect to make this allowance, which is usually an unknown quantity and often of some dimensions, accounts for many of the differences between embryos from different uteri, but apparently of the same age.

h) The critical unit of the pig. I had hopes of being in a position, through the kindness of Mr. J. P. Glendinning of Overshiell, Mid-Calder, N. B., to settle this question by actual observation. This gentleman placed a sow at my disposal for the purpose, but unfortunately, when the killing-time arrived, it turned out, that she was not in young. As there is no likelihood of my being able to test my theoretical conclusions for some time to come, it may be well to indicate here the grounds, on which they are based. In Edinburgh, and probably in most large towns, it is quite easy to obtain pig-embryos of many stages in a perfectly fresh condition from the slaughter-house. During the past winter and spring Mr. J. A. Murray and myself got together a very representative series in this way, but, though we have three or four different sets of critical embryos, the age of none of them is known.

In estimating the probable length of the critical unit of the pig the data available were: — 1) the average length of the gest-

ation, 2) somewhat wide statements of the rut-interval, 3) Keibel's valuable researches on the development, with ages of embryos until the 22nd day, 4) Bonnet's researches on the pig and sheep, but especially on the latter, and 5) his statements on the correspondence in the rate of development in the two animals.

The average gestation is 112—120 days, and the only numbers of possible critical units, which need be considered, are 3, 4, and 5.

The last of these (5) is decidedly too high an estimate; for, when divided into the gestation-length, it gives 22—24 days as the critical unit. A glance at Keibel's figures of 22 day-embryos is sufficient to disprove this number, for such embryos are far younger than critical ones. The number 3 gives a critical unit of 37—40 days. From what follows, as also from the circumstance, that 37—40 days is more than double an ovulation-unit, this possibility must be rejected.

We are left with 4 as the remaining possible number of units in the gestation, and with this a critical unit of 28—30 days is obtained. I believe this to be the correct one. With 28—30 days as the critical unit this latter is somewhat less than two ovulation-units. Bonnet (Entwickelungsgeschichte, p. 247) remarks, that pig and sheep show "so grosse Uebereinstimmung" in their early development, that they can be treated of together.

A comparison of Bonnet's and Keibel's figures demonstrates the truth of this, for until the 22nd day stages of the two, almost corresponding in age and characters, can be found.

Where differences are noted, the advance may be in either form, i. e. at a certain precritical stage there may be a day or so of difference in either of them, sometimes the pig is ahead, at others the sheep[1]). I conclude, therefore, that this correspondence lasts until the critical period, i. e. for 6—8 days longer than it is known to obtain, and that the critical unit of the pig is, as nearly as can be judged without further experiment, about equal to that of the sheep.

i) The critical units of dog and cat. As no embryos of this period have as yet fallen into my possession, it is needful, that the reader should be informed, upon what data the estimates given in the table are based. Much time has been spent in seeking definite statements in the literature, and the only ones of service have been encountered in Duval's series of memoirs on "Le

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1) Due, probably, to differences in the actual time of ovulation and fertilisation.

placenta des Carnassiers" (Journ. de l'Anatomie, Vols. 29, 30, and 31). If in these any description of the embryos had been given, the conclusions to be drawn would have been perfectly clear; for very definite and precise statements could then have been made.

Regarding the dog Duval remarks, that the replacement of the ectoplacenta or "l'angioplasmode" by the allantoic placenta commences towards the 30th to the 32nd day — "c'est-à-dire vers le milieu de la gestation, qui est, chez la chienne, de cinquante-huit à soixante-quatre jours" (Journ. de l'Anat., Vol. 29, p. 663).

Similar, though not so precise, statements are made concerning the cat in other papers, and other evidence, supporting the estimate of 28 days as the critical unit of the cat, will be found in O. Schultze's "Entwickelungsgeschichte", 1896, p. 84.

It will be noticed, that, particularly in the dog, Duval comments upon the fact, that the allantoic placenta begins to replace the trophoblast *at about the middle of the gestation.*

If any part of the argument of the work were really based on our knowledge of the development of dog and cat, it might be admitted, that the conclusions rested on insufficient data. But the results of the present writing stand quite independently of what we know of these animals, and they have only be introduced to show, that, so far as our knowledge extends, these two forms exhibit only evidences of conforming with the rule.

k) The gestation of the hare. In many works consulted it is stated, that hare and rabbit have equal gestation-lengths. According to Flower and Lydekker, "the rabbit is sharply separated from the hare by the fact, that it brings forth its young naked, blind, and helpless; to compensate for this, it digs a deep burrow in the earth in which they are born and reared, *while the young of the hare are born fully clothed with fur, and able to take care of themselves in the 'form' in which they are born*" (Mammalia, 1891, p. 494).

They also give the gestation of the hare as about 30 days, i. e. like that of the rabbit.

There is, of course, no doubt about the condition of hare and rabbit at birth. But, either the gestation of the hare is longer than that of the rabbit, or its critical unit is shorter. From our knowledge of the state of the young at birth in mouse, rabbit, and cavy, it may be taken as certain, that the hare has at least three critical units in its gestation, and this would point either to a longer gestation, or, what is quite as likely, to a shorter critical unit than in the rabbit. If current statements be correct, the latter alternative must be the true one.

I have felt bound to cite this case, because throughout the research difficulties have always been sought for under the idea, that from these more was to be learnt than from simple facts. The instance of the hare cannot be regarded as a crucial one, unless the facts, when better known, should turn out to be at variance with the argument. This contingency is highly improbable, even impossible.

1) Smith, W. Tyler, Parturition and the Principles and Practice of Obstetrics, London 1849.

p. 85. "The catamenial fluid is most probably, I may say, certainly, intended as an envelope for the ovule escaping from the ovarium, but unless impregnation takes place, no relation ever occurs between the uterus and ovule."

p. 85. "Menstruation is, in fact, the unimpregnated oviposition, while conception is the impregnated oviposition of the human subject."

p. 85. "Menstruation — — is the parturition of the *ovule*, instead of the parturition of the *ovum*; and it represents, with the exception I have already dwelt upon, the whole of parturition in birds, and in many fishes and amphibia."

p. 114. "In those animals of which we know the order of the oestrual periods, as the rabbit, the horse, and cow, the duration of pregnancy is a multiple of an oestrual period. Doubtless this law is as extensive as periodic oestruation itself. Not only is gestation a multiple of the oestrual period, but the time of parturition is positively an oestrual period. The maturation of ova, which has ceased during utero-gestation, is resumed, and the sexual instinct is predominant, just as though the uterus did not contain the product of a former ovulation and conception."

p. 115. "There is, in fact, in all women, a tendency to abort at the times represented by catamenial periods."

p. 118. Parturition is essentially a menstrual period. The author then goes on to state that "the sanguineous appearance called the 'show', which indicates the coming on of labour", is not due to rupture of certain vessels, but is really the beginning of a menstruation. So far as can be gathered, he regards the foetus as the ripe egg belonging to this menstruation, which only differs from any other flow as indicated above.

p. 119. "I have observed, in cases of abortion occurring at what would have been a catamenial period, that menstruation has appeared at the end of a lunar month from the abortion, as if it were dating itself from a simple menstruation."

p. 122. "When the ovum is expelled as a mature embryo, it is still ovarian excitement, at the return of an ovarian period, which brings about its delivery from the uterus. Under this point of view, the dehiscence of an ovule from the most simple ovarium is analogous to the complex function of human parturition."

A Course of Lectures on the Theory and Practice of Obstetrics by W. Tyler Smith, Lancet, 1856, Vol. I. Also as a separate work: — A Manual of Obstetrics, London 1858. — The paging below is from the "Lancet".

p. 86. "In the human female, it is believed that in ordinary cases the ovule escapes towards or shortly after the termination of the menstrual flow, through the pore or fissure found in the peritoneal surface of the ovary."

p. 113. "In women who menstruate two or three days only, the interval, between the cessation of one period and the beginning of another, is longer, and in those who are many days unwell, shorter, the length or brevity of the discharge does not usually affect the time of its return."

p. 114. "The cause of menstruation must be referred to the ovaria."

p. 276. "Many years ago I drew a comparison between menstruation, abortion, and parturition" — to the effect that all three were the equivalents of rutting-periods.

p. 276. "The tendency of abortion to occur at the catamenial dates has long been a matter of observation."

p. 232. "In 1851 Mr. Coleman, of Surbiton, drew my attention to the following circumstance: — Two ladies, patients of his, were married on the same day, and both were delivered within ten hours of each other. The marriages took place on the 7th of May, 1850, and one was confined on the afternoon of Febr. 8th, 1851, and the other at 2 a. m. on the 9th, or 276 days from the date of the marriage."

The author proceeds to support the table of Dr. Reid, according to which the average duration of pregnancy is 275 days.

On p. 332 the question, why parturition should occur at the tenth, rather than at any other, catamenial period, is raised, and he asks why the menstrual period itself should consist of twenty-eight-days. "The only answer is, in fact, that these particular periodicities do occur." He also states that he has noted, that in women with longer or shorter menstrual periods "the duration of pregnancy is more irregular than usnal".

p. 333. "I have thus advanced, and I trust impartially, the arguments and facts for and against the theory of the ovarian cause of

labour, which I believe I was the first to propound. I have for many years taught that the ovaria, acting at or near the tenth period from the time of the ovulation which has ended in impregnation, excite in the uterus those changes which lead to the expulsion of the ovum. I have also compared the show which accompanies parturition, and the lochial discharge which follows it, to the menstrual discharge. It has appeared to me, that the changes in the uterine portion of the membranes are similar to the changes which occur in menstruation, and that the contractions of the uterus resemble those more imperfect contractions which occur in many women at the catamenial periods, and which we do not hesitate to refer to the ovaria. I believe there are some facts, which do not admit of explanation upon the supposition, that the cause of labour depends on the maturity of the ovum; as for instance, the occurrence of uterine contractions at the end of gestation in cases of extra-uterine foetation. I believe, on the contrary, that the facts which appear to militate against the ovarian theory, most of them admit of explanation."

Tyler Smith's conclusions have been quoted at some length, because, on a superficial reading, they seem to resemble some of the views advanced in the present writing. A more careful study of his works will, however, lead to a different conclusion. He regarded heat and menstruation as the same thing, and he looked upon parturition as a heat-period, in which, instead of the passage of an unfertilised ovum, that of a fully-developed one took place. Although he noted, that in many animals an ovulation ensues soon after parturition[1]), one searches in vain for a statement that the approach of this is the cause of birth. In spite of his mistakes, all honour to his memory; for, like Pouchet and Bischoff, he was a pioneer-worker at a very difficult question, which could not at that time be solved, because the data were insufficient.

m) Length of pregnancy in woman. It is quite beyond the scope of this work to consider at length the conflicting testimony on this subject. It is discussed in detail from the points of view of the anatomist, physiologist, and gynecologist in the works of His, Hensen, Spiegelberg, Tanner, Tyler Smith and others. The only course open to the writer was to examine their testimony from his own standpoint, and so endeavour to come to a decision.

The conclusions drawn as to its average duration are given in the table as 276—280 days, and after much consideration of the

1) With Sobotta I hold that this happens in all mammals.

matter there seems no good ground for altering this result. Many striking cases and more than one list of instances are on record supporting this view.

The two births cited by Tyler Smith (see p. 111) are very significant, and Hensen's citations and arguments appear to me to carry conviction.

It would, as more than once admitted, be very easy to bring forward numbers of exceptional instances totally at variance with the law, but what would they prove? Take the Gardner case, with a suggested gestation of 304—311 days, as an example. The only thing known about this is the date of birth; of the other factors, date of last menstruation, fertilisation, and length of menstrual cycle, there is not a particle of information available.

If most of the factors of supposed abnormal cases were revealed, possibly the abnormality would disappear. In the lower mammals, where the date of fertilisation can be approximately gathered from that of copulation, the length of gestation varies only within the narrowest limits; more especially in those forms, which, as a rule, produce a number of young at a birth. The apparent variations are largest (1) where the rut-period is long, (2) where the normal gestation-period is a prolonged one, and (3) where the number of young at a birth is usually the minimum. I am inclined to lay much emphasis on the latter point, for it is in the horse, cow, and human subject, where the variations are most pronounced; whereas in rabbit, sheep, and pig, in which as a rule two or more eggs are fertilised, they are of a trifling character. (Compare also latter part of appendix z.)

If a single egg be fertilised at a certain time, it by no means follows that it will develop. In almost every gestation of rabbit, cavy, and pig some of the fertilised eggs quickly abort, while others of the same batch live through the gestation. In horse, cow, and the human subject such an early death and absorption of the "egg" must be of very frequent occurrence, while living spermatozoa may be left in possession for some considerable time. As Burns sings:

"The best laid schemes o' mice and men gang aft a-gley."

Although, as a rule, the ovulation-unit of any form is a fixed one, the possibility of an unusual ovulation must not be lost sight of. In the higher forms (where alone such irregularities seem to occur and, perhaps, frequently) it would be an exception of a kind proving the rule, instead of controverting it.

As the horse and human subject are those, in which these apparent difficulties crop up, our study of the matter may be confined to them.

It has been shown, that in these at the present day the critical unit corresponds to two ovulation-units instead of to one only, as must have been the case in past times. If such a duplication of the one unit can take place, a change in the other is rendered *a priori* possible, more especially, when it is noted, that the lower mammals, and especially certain marsupials, appear to have very small units.

In both man and the horse it appears highly probable, that a doubling, or even a trebling, of the ovulation-unit has happened in the ancestral history, for it is more than double that of the mouse in both cases, and, if one may guage the ovulation-unit of *Didelphys* from its critical unit, the ovulation-period of the two Eutheria is nearly threefold this. Thus, in the horse and man we may occasionally have to deal with irregular reversions to a former ovulation-unit of 7 or 14 days in the former, and, in round numbers to 8, 12, or 16 days in the latter.

The reader may also be reminded, that, just as certain women possess the peculiarity of regularly-occurring short menstrual periods, and thus necessarily of briefer ovulation-units than usual, so also there are mares, which "come into season" every 14 days, instead of every 21.

To illustrate the matter by examples. A mare may have ovulated at a certain date and the egg may have been fertilised. If this egg were to quickly succumb — and my experiences of the past ten years would not lead me from analogy to regard this as unlikely to happen [1]) — an irregular ovulation at some ancient ovulation-period might conceivably lead to a new fertilisation without a new copulation, and, as likely, this would apparently result in a gestation of unusual type.

In the human subject one might have to deal with a reversion to an old ovulation-unit of 8, 12, or 16 days [2]); and, if the egg given off at the normal period had, in the meantime, died or missed fertilisation, the egg of the irregular and unusual ovulation might be fertilised, before there had been time to form a menstrual decidua, and thus the next menstruation would be suppressed. But the embryo of such an egg would be bound to adapt itself to the rules of the development, or have these modified to suit it.

1) It is a much more likely thing, that a gestation after its initiation should be suppressed, than that ovulation should fail to happen at the proper time.

2) It is impossible at present to decide with certainty, if in man's ancestry former ovulation-units were 8 and 16 days, or 12 days.

If they were not altered, its early development until the critical period would require to be abnormally slow, otherwise it would reach the critical period at too early a date to admit of agreement with the *normal* ovulation-rhythm.

If harmony were absent, the embryo would certainly be aborted, and this probably very frequently happens: if all were brought to chime in, its development would proceed.

But — and this is the significant point — the gestation would probably be apparently longer than usual, and might, by some three weeks, or even more, exceed the normal time.

This matter has been discussed, not only because of its bearings on the length of gestation, but also with reference to those human embryos, whose probable ages date not from the last menstruation but from the first missed menstrual period. Several instances of such are given by His[1]).

In dealing with these we are bound to conclude, that ovulation and fertilisation took place, before the missed menstrual period was due; otherwise, of course, it would not have failed to appear.

As others have remarked, there would seem to be no grounds for assuming, that an ovulation immediately prior to a menstruation could arrest the latter. We must, therefore, conclude, that the ovulation probably occurred from 7—14 days before the menstruation was due, that is, before the menstrual decidua was formed. I incline very strongly to the conviction, that the most likely time for such an unusual ovulation would be half way between the end of one menstruation and the beginning of the next, and, in fact, at a ancient ovulation-period, which obtained before the present one was acquired.

As stated above, the egg of such an ovulation would probably act, as if it belonged to the normally-succeeding one, on account of the necessity of obedience to certain rules. And, thus, if later on aborted, its apparent age would date from the latter.

His' cases can, I believe, be best explained in this way, assuming that they really relate to embryos dating from suppressed menstruations.

Moreover, it must be noted that they are all abortions, and this indicates that there was something wrong about the development. As the embryos themselves are normal, the abnormality must lie either in the placental changes, or with the mother. In most of them the cause is to be sought in the maternal organism, and this is in agreement with the conclusion we have arrived at. If no other cause can be assigned for the abortion, something connected

1) His, loc. cit. II. p. 74 etc.

with the suppressed menstruation may possibly underlie it. So far as I can see, the thing must likely to bring about the suppression of a menstruation, apart from sickness or disease, would be an unusual ovulation in the middle of the menstrual cycle, before a decidua had been formed, and followed by fertilisation. The uterus is then in a state of rest, and its subsequent changes may be influenced by the existence of the fertilised egg.

n) The critical unit of man in its medico-legal aspects. According to the law of England, and possibly of other countries, the embryo *in utero* is not alive until "quickening" appears in the sixteenth to seventeenth week of pregnancy. The importance attached in law to this sign has relation to the procuring of abortion and to pregnant women condemned to death. It is not necessary to cite here, what the law lays down regarding these points: every-one interested in the matter knows in what works to seek for information. But the only person, whose right it is to decide, at what period of its development the child may be said to live, is the embryologist. Now, it may be admitted at once, that, if embryological opinion were asked for on this subject, the majority would hold to the view, that the child was alive and in existence from the moment of fertilisation of the egg.

Such is not the conclusion, which anyone, who has read this memoir and its predecessor, has the right to draw. One thing, which stands out clearly as the result of these studies of Vertebrate, mammalian, and human development, is, that, until the critical period is reached, the embryo, as that of a certain species of animal, has no complete existence. It is only coming into being and its parts are not all present until the critical period. Thence onwards its individuality is established, and, whereas its early development was in its essence an epigenesis, from the critical period this becomes an evolution or unfolding of parts already in existence. Thus, to be consistent and to be in accord with the results of science, the law ought to consider the child to be alive, from the moment the critical period is reached; and, certainly, from the end of the seventh week of intra-uterine life.

o) Medico-legal aspects of the length of gestation. From time to time, but naturally somewhat rarely, cases involving the question of prolonged pregnancy come before the courts. A celebrated one is that of the Gardner peerage, cited by Tanner, and another is referred to by Tessier (p. 176). In the former the main point to be decided was whether or not a certain pregnancy could have been as prolonged as 304 to 311 days. Seventeen medical men were examined, of whom "five supported the view,

that the period of human utero-gestation was limited to nine calendar months, or from 270 to 280 days. The remaining twelve seemed to maintain the possibility, that pregnancy might be protracted to nine and a half, ten, or even eleven calendar months; and so, of course, to 311 days, the alleged term of gestation".

Looking at the matter from the point of view afforded by the results of the present work, it is readily seen, that without the addition of a further critical unit — and the assumption of this ought in any case to be our last resort — an ovulation-unit of 26 days, with the critical unit in correspondence, would give in the human subject a period of pregnancy of 312 days. In such an instance the only justification for the adoption of such a unit would, so it appears to me, depend on the existence in the particular individual of a regular menstrual cycle of 30 days or more. If this obtained, the abnormality of so prolonged a gestation would appear to be explicable: without it and without other data no certainty on the matter could be arrived at. It must be mentioned, that Cederschjöld "has tried to show that the duration of gestation is influenced by the length of the intervals between the catamenial periods". (Tanner, loc. cit., p. 193.)

p) Pouchet, F. A., Théorie positive de l'ovulation spontanée et de la fécondation des mammifères et de l'espèce humaine, Paris 1847.

The book is apparently a revised edition of an earlier work published in 1842. The latter has not been available for reference on the present occasion. Pouchet's work is a very important one, and to realise this one has to remember, what was held regarding the ovulation of mammals prior to 1840. It was considered, that ovulation only occurred as the result of sexual congress, and to have disproved this is one of the chief merits of Pouchet's work. He showed conclusively, that in various mammals, but more particularly in the pig, rabbit, and in man, ovulation takes place at characteristic periodic intervals quite unconnected with copulation. Thus, Pouchet was the pioneer, upon whose foundation more than upon any other the slight advances contained in the present writing are laid.

It seems to us so natural now to recognise the regular periodicity of mammalian ovulation and its independence of copulation, that it is difficult to appreciate the great advance, which, in the first instance, we owe to him. His results were confirmed, independently of him and of each other and within a short period after their first publication, by Bischoff and Raciborski.

Pouchet, and not Tyler Smith, would appear to have

been the founder of the view of the correspondence of rut and menstruation. That the times of occurrence of the two, i. e. just prior to ovulation, are alike there can be no doubt, but that the two things themselves are identical is quite out of question. It need only be repeated here that the sole similarity between the two is that mentioned above. But they may both in their first origin have arisen ont of the same phenomena. (Compare Heape appendix w.)

q) The corpus luteum. Bonnet, in his excellent "Entwicklungsgeschichte der Haussäugetiere", p 19, remarks that during gestation, as he repeatedly observed, the ovary becomes "blutarm", and that the *corpus luteum* persists till shortly before the birth. The indifferent blood supply of the ovary and the growth and nourishment of the *corpus luteum* during the greater part of the gestation, such that in the mare it may come to equal in size the rest of the ovary (Bonnet), are factors which must result in either the suppression or the rendering abortive of ovulation during gestation. If the growth of the *corpus luteum* be not a contrivance to this end, why does it not go on growing to the very finish of the gestation? Why does it stop short some time before the close, unless it be to render an ovulation just after birth possible?

It must be noted here, that P. Mingazzini and E. Giacomini have described what they consider to be true *corpora lutea* in reptiles, amphibians, and selachians. This is a satisfactory result, for it removes any difficulties about a first and sudden appearance of this structure in mammals. Whether it possesses any functional importance in lower Vertebrates, and whether its functions in these, if any, are everywhere similar, remains to be seen.

For recent work on the *corpus luteum* in the mouse and rabbit the reader may be referred to Sobotta's memoirs in the Arch. f. mikrosk. Anat., Bd. 45, 1895, and in Anat. Hefte, Heft 26, 1897.

r) Changes in the mammary glands at the critical period. The reviewer of my "Problems of Vertebrate Embryology" in "Natural Science" for January 1897 first directed my attention to the fact, that changes in the mammae are among the earliest symptoms of pregnancy. It became of interest to learn whether, like other things, these were in association with a certain phase of the gestation; whether, in fact, the mammae still retained their ancient sympathetic connection with the critical period, at which, as shown last year, they begin to function in non-placental Marsupials. It is very clear from works on midwifery, such as Spiegelberg's, that this is the case in the human subject, where changes in them begin from the seventh week.

Tanner (Diseases of Pregnancy, 1867, p. 75) remarks: — "and, finally, it may be laid down as a law, that, when a woman is gravid for the first time, and has missed two monthly periods a drop or more of milk may be expressed from the breasts."

And in Dalziel's "British Dogs" p. 468 the author writes: — "it is not easy to tell whether the bitch is in pup before the fourth week has passed; by that time the teats begin to enlarge, and there is a ridge-like swelling between them." The critical period is given in the table as 29—32 days, and it probably varies with the breed of dog.

s) Is the ovulation-unit ever approximately equal to the gestation-period in Eutheria? For some time during the course of the experiments and investigations of the present work the possibility of this being the normal rule in certain cases had to be considered. If current statements were trustworthy, it appeared undoubtedly to hold good for mouse, rabbit, and cavy. But, although the periodicity of ovulation was established by Pouchet and Bischoff more than 50 years ago, since then no appreciable advance towards an accurate knowledge of the subject has been made. In more than one point I found current beliefs either vague or utterly at sea, and thus began to doubt the existence of exact information even regarding the true ovulation-units of the three common animals mentioned above, all of which, by the way, are bred by fanciers in countless numbers every year, whilst books on breeding agree in complete silence regarding the periods of ovulation.

Concerning the case of the cavy, as mentioned in another appendix, time has not been available, in which to clear the matter up.

But the true facts have, I think, been established regarding the mouse: an exceedingly satisfactory result, because of its lowly position in the Eutherian scale.

Fleischmann has commented upon the agreement of rodents and marsupials in respect of certain developmental arrangements. The mouse, especially, exhibits this to a great degree. Even its new-born young are exceedingly like young Metatheria, of which Dr. R. Broom has shown me a large number from different species.

As in marsupials the yolk-sac of the mouse plays a considerable rôle in the early development (Robinson). And the gestation is a short one of only two critical units, i. e. but one more than in non-placental marsupials.

Now, with all these agreements it might have been anticipated, that the mouse would exhibit a correspondence and agreement between ovulation- and critical units. As detailed elsewhere, this has turned out to be the case. Exceptions are, however, met with, and in some white mice, when not pregnant, there may be a failure to ovulate some ten days after a birth, or the ovulation may be abortive. Which of these is the correct explanation can only be settled by observation.

Thus, the mouse must be removed from the list of those placental forms, in which, if current belief be correct, the ovulation-unit corresponds to the length of gestation.

Such an arrangement cannot hold good for the cavy either. A correspondence of the ovulation in this case to two critical units would be disastrous, for it would throw the arrangements for inducing the birth out of gear, an ovulation not being due until 22 days after the event. As described on p. 104 — 106, it is quite out of question that the ovulation-unit can equal the gestation in the cavy. It cannot do anything other than rather exceed one third of the latter.

There remains, then, the rabbit, and here there are no experiments to offer. None the less, from the known lengths of critical unit and of gestation there can, to my mind, be no particle of doubt, that the ovulation-unit here has a length of $15^1/_2$ to 16 days. In fact, if one except cases, like cat and dog, in which breeding has become restricted to certain periods of the year, wheresoever there is a periodic rut with ovulation, these recur at intervals approximately equal to, or half the length of, the critical unit of the species.

t) Sizes of embryos of the critical period. The measurements given below are taken from embryos killed with corrosive sublimate and brought up to 90 % alcohol, i. e. they are of embryos measured *when preserved.* I have made a considerable number of measurements of embryos before, during, and after preservation, and have found, that the main shrinkage with sublimate preservation takes place in the alcohol, and even in a weak solution of it. The figures will be published elsewhere in another connection. The most surprising result was the trifling extent of the shrinkage in corrosive sublimate both in mammals and fishes.

The total shrinkage, the final measurement being made when the embryo had reached 90 % alcohol, was on a fairly constant average rather under $11^1{}_2$ % of the live-length. In five critical embryos of one rabbit the following are very exact measurements of the lengths in the preserved condition: —

Greatest length in mm	Nacken-Länge in mm
12	11
12½	11½
12	11
13	12
12	11

Thus far three pig-uteri with embryos of the critical period have been obtained. They are lettered F, FA and FB.

The embryos of F and FA are in very much the same position in the critical phase, whilst those of FB are almost emerging from it. The lengths are given in millimetres:

Series F		Series FA		Series FB	
G. L.	N. L.	G. L.	N. L.	G. L.	N. L.
20.5	17	19	17	20.5	18
19.5	17	17	15	21	19
19.5	17	19.25	17	20	17.5
18	15.3	18.5	17	21.5	19
20	17	17	15	20.5	18
20	18	18	17	20.5	18
19.5	16.5	18	16.5	20	18
19	17	17.5	15	20.5	18.5
21	18	17.5	15.5	and three monsters.	
19	17	18	16		
and two monsters.		18.5	16.5		
		17	15		
		18.5	16.5		
		18	16		
		no monsters.			

Of critical embryos of the sheep but two sets have as yet been obtained, they are both cases of twins. The measurements are G. L. 16, 16, 16.75, and 16 mm. Guinea-pig embryos of the critical period are rather smaller than corresponding rabbit embryos.

u) Minot, C. S., "The changes of the uterus during menstruation and gestation are homologous, the menstrual cycle being prolonged and modified by pregnancy." Uterus and Embryo. Journ. of Morph., Vol. II, p. 437.

With almost prophetic instinct Minot writes concerning the cause or causes of parturition: — "we evidently have to do with a progressive maturation of the uterus — a series of changes we cannot explain, but which is, as already pointed out, closely similar to the series of changes during menstruation. Hence it is probable that there is a common cause for the ending of the series (the casting off of the superficial part of the mucosa *in both cases*) etc." Human Embryology, p. 27.

"The menstrual and gravidital changes follow the same cycle, and differ from one another essentially only in two points: 1) the

time occupied, and 2) the extent of the changes. In fact the alterations, though of the same character, are greater in extent and occupy a longer period during gestation than during menstruation. These considerations force us to the conclusion that the gravid uterus is passing through the menstrual cycle prolonged and intensified. The function of gestation is a direct modification of the function of menstruation, and the two are physiologically homologous. The deduction is so evident that I have been surprised not to have yet encountered it clearly enunciated in any of the authors I have consulted." Human Embryology, p. 25.

The above extracts from the writings of Minot appear to me to indicate a certain amount of agreement between his view of menstruation and that adopted in the text. How much further one may go is not very clear; for the meaning of more than one of his phrases is anything but obvious.

No attempt is made to explain the cause either of birth or of menstruation, and the opinion, that "the function of gestation is a direct modification of the function of menstruation", looks very much like an inversion of matters. We know what gestation and parturition are, and why certain phenomena accompany them. From these, and other facts, as we have seen, menstruation and the menstrual cycle can be explained. But how gestation and parturition can be obtained as direct, or indirect, or any sort of modification of a menstrual cycle and of menstruation, passes comprehension. If parturition and the gestation-cycle be explained in terms of menstruation and the menstrual cycle, we must first know what the latter really are, and regarding their meaning Minot supplies no information whatever.

It is, of course, quite true, that there is an association between the two, as Minot insisted, and it is such that, if an embryo were present in connection with the decidua formed before a menstruation, the menstrual cycle would be "prolonged and intensified" through the ensuing gestation.

But menstruation is a modification of gestation and not *vice-versa.*

In stating, that "the changes in the uterus during menstruation and gestation are homologous", Minot really goes no further than did Tyler Smith, for the latter distinctly recognised this, and only differed from Minot in assigning an erroneous cause to the two, whereas the latter attempts to explain neither. He merely states, that "it is probable there is a common cause for the ending of the series", but does not say what this is, though the cause of the casting-off of the superficial part of the mucosa at parturition

is not far to seek: it has played its part, and is no longer required.

A view quite similar to Minot's is "clearly enunciated" in Burdach's Die Physiologie als Erfahrungswissenschaft[1]), where it is written: — "Die Menstruation ist in ihrem Beginnen durch Blutandrang, Auflockerung, und Herabsenkung ein Vorbild der Befruchtung und Schwangerschaft, in ihrem Ausgange aber durch Zusammenziehung und Blutergiessung ein Vorbild des Gebärens."

Undoubtedly to some extent agreement subsists between Minot's views on menstruation and the menstrual cycle and those adopted in the text, and as these, so far as they are similar, date back to Burdach in 1830, if not to an earlier writer, there is not much novelty about them. The one new point is the recognition in the present writing, that menstruation is an abortion of the decidua prepared for a missing embryo, which ought to have arisen from an egg given off after the preceding menstruation, and that this abortion happens at a time corresponding to the end of a former critical unit, and prior to a new ovulation.

v) Sobotta, J., Die Befruchtung und Furchung des Eies der Maus, Taf. II—VI, p. 15—93. Arch. f. mikrosk. Anat., Bd. XLV, 1895.

p. 27. "Die Brunst tritt bei der Maus wie beim Kaninchen, Meerschweinchen, Hund und wahrscheinlich allen Säugern unmittelbar nach dem Wurf auf, wie von den verschiedensten Untersuchern gefunden wurde. Auch ist von Bischoff sicher festgestellt worden, dass Eier unabhängig von der Copulation ausgestossen werden."

p. 28. Trächtigkeitsdauer fast 20 Tage.

Ovulation (apart from that soon after birth i. e. on the day of birth) ensues 21 days later.

"Dass zwischen dem 1. und 21. Tage post partum noch ein oder mehrere Ovulationstermine liegen, kann ich nicht mit Bestimmtheit bestreiten, möchte es indess auf Grund einiger daraufhin angestellter Untersuchungen vorläufig in Abrede stellen." Copulation takes place 3 hours after birth, and may be repeated 24 hours later. p. 35. Lactation lasts nearly 3 weeks. p. 28.

As mentioned in the text the only point, in which my experiments have led to a result different from the above, relates to the frequency of ovulation. The ovulation-unit of the mouse is not 20 or 21 days, as hitherto supposed, but it corresponds to the critical unit, and, as nearly as can be guaged, it is $9^5/_6$ to 10 days. A "normal" mouse, which has given birth to a litter, does not first

1) 1830, Bd. III, p. 6.

ovulate 20—21 days later, if not allowed to become pregnant at once, but under this latter condition after the ovulation following the birth, it ovulates in $9^5/_6$ to 10 days. Thus ovulation- and critical units are approximately equal, the latter being very slightly less than the former.

w) Heape, Walter, The Menstruation of *Semnopithecus entellus*. Phil. Trans. London, Vol. CLXXXV, Part I B, pp. 411—471, with 7 plates.

— The Menstruation and Ovulation of *Macacus rhesus*. Proc. Roy. Soc. Lond., Vol. LX, 1896, pp. 202—205.

Since the results of the two works are, as Heape himself states, very much the same, only the first will be cited.

The work contains a list of literature treating of menstruation and a discussion of various views, which have been held.

p. 462. Heat or rut and menstruation are concluded to be analogous processes.

p. 462. "A substantial periodic growth of the (uterine) mucosa is arrested by degenerative changes when a fertilised ovum is not present". This is a pithy summary of what the phenomena of menstruation are.

Ovulation was not often encountered in menstruating apes, and (p. 443) the ripening of the ovum was found to be independent of the process of menstruation. "Ovulation is neither the cause nor the necessary result of menstruation." „It is possible, however, that the increased blood supply to the generative organs during menstruation may induce ovulation, when a sufficiently ripe ovum is present."

p. 461. "The primary cause of menstruation remains unexplained."

x) Selenka, E. Studien über Entwickelungsgesch. d. Tiere, Heft IV, I, 1886: Das Opossum.

The interval from copulation to birth in *Didelphys virginiana* is given by Selenka as not quite 13 days, and that from fertilisation to the end of gestation as $7^5/_6$ days.

p. 105. "Die Zahl der in den beiden Uterushörnern aufgefundenen Embryonen schwankte zwischen 7—27, betrug aber meistens 12—16; da sich im Beutel des Weibchens aber nur 8—15 Zitzen vorfinden, so möchte ich glauben, daß das reichliche Futter und der Mangel an Bewegung die Veranlassung werden zu dieser überraschenden Fruchtbarkeit."

p. 106. — "Alle Eier im Uterus des trächtigen Weibchen stehen immer auf gleicher Entwickelungsstufe; nur zuweilen findet man

einige Eier in ihrer Entwickelung den übrigen vorausgeeilt oder hinter ihnen zurückgeblieben, aber das Alter differirt doch kaum um mehr als 1—2, sehr selten bis 8 Stunden."

— Studien über Entwickelungsgesch. d. Tiere, Heft V, I 1891: Beuteltiere u. Kängaruratte.

p. 173. From copulation to fertilisation the following intervals are given: —

Hypsiprymnus	11 days
Phalangista	13 „
Dasyurus	14 „

p. 175. In *Hypsiprymnus* 8 days elapse from fertilisation to birth, i. e. almost the same as in *Didelphys*.

y) Owen, R., The length of gestation in the kangaroo, *Macropus major*, was determined as 38 days from *copulation* to birth. If an allowance of 14 days, as the possible interval between copulation and fertilisation, were made, as in *Dasyurus*, we should obtain an actual critical unit of 24 days. This, however, would be merely a surmise. But the actual gap between the two is hardly likely to be as small as in the opossum (5 days) and it may be equal to or exceed that in *Dasyurus* (14 days).

Owen's results are given in, among other places, Todd's Cyclopaedia of Anatomy and Physiology, 1839-47, Vol. III, p. 322.

z) Bonnet, R., Beiträge zur Embryologie der Wiederkäuer, gewonnen am Schafei. Arch. f. Anat. u. Entwickl., 1884, pp. 170—230, 3 Plates.

p. 171. The "Brunst", on which Bonnet made no investigations himself, is stated to be short, lasting for 24, 16, or 20—30 hours.

p. 172. The gestation of the merino-sheep is given as 150 days, rut returning 7 months later and then recurring at intervals of 17 days (Rueff). The rut-periods happen in spring and autumn.

While this work was in the press, an opportunity of consulting the following important communication arose, but too late to permit of reference in earlier pages.

Nathusius, H. von, Ueber einen auffallenden Racenunterschied in der Trächtigkeitsdauer der Schafe. Zool. Garten, Jahrg. 3, 1862, p. 102—105.

This short, but exceedingly interesting and important, paper records observations, extending over 4 years, on the average gestation-lengths of over 200 merino and about 100 Southdown sheep, and the former are stated to have been imported originally from Spain, the latter from England. On p. 103 the author remarks

"trotzdem tragen die Merinos constant die Frucht durchschnittlich sechs Tage länger als die Southdowns".

On p. 104 there is a table of the results of the experiments. In the 4 years the gestation-length varied in the merinos from 149.3—151 days, and 872 cases gave 150.3 days as the average gestation-length. In the same period it varied in the Southdowns between 143—144.3 days, and the average of 442 cases was 144.2 days.

In crosses between the two breeds remarkable results were obtained, thus:

$\frac{1}{2}$ merino, $\frac{1}{2}$ Southdown = 146.3 days average gestation
$\frac{1}{4}$ „ $\frac{3}{4}$ „ = 145.5 „ „ „
$\frac{1}{8}$ „ $\frac{7}{8}$ „ = 144 „ „ „

Here no allowance is made for the interval between copulation and fertilisation. Even without allowing for this, if we calculate theoretical gestation-lengths for the crosses on the basis of 150 days average gestation in the merino and 144 in the Southdown, with the proper fractions of these numbers we obtain:

$\frac{1}{2}$ merino, $\frac{1}{2}$ Southdown = 147 days,
$\frac{1}{4}$ „ $\frac{3}{4}$ „ = 145.5 „
$\frac{1}{8}$ „ $\frac{7}{8}$ „ = 144.75 „

As Nathusius distinctly denies any attempt at accuracy in noting the gestation-lengths within half a day or more in many of the cases, this result is a very remarkable one, and the observed gestation-length so closely approaches the calculated one (the discrepancies being probably due to "errors of experiment") as to warrant the conclusion, that it is a fixed quantity for the variety, and that it is determined in the cross by the relative percentages of the two races contained.

To summarise the matter, Nathusius's figures serve to support the contention, that the span of gestation is, as a normal thing, practically a constant quantity for the individual and for the variety, but that it may differ within certain limits in different varieties of a species; and, moreover, that in crosses between varieties the gestation-length tends to approach the mathematical mean.

Index.

Errata.

p. 6 line 16 *for* being *read* bring.
p. 12 line 13 „ an „ a transient.
p. 25 last line „ *Parameles* „ *Perameles.*
p. 33 line 7 „ marsupial „ mammal.
p. 36 line 5 „ *Parameles* „ *Perameles.*
p. 44 line 10 „ *Parameles* „ *Perameles.*
p. 48 line 20 „ *Parameles* „ *Perameles.*
p. 88 line 30 „ Marsupial „ non-placental.
p. 125 line 5 „ Beuteltiere „ Beutelfuchs.
p. 127 2nd column *for* cannabalism *read* cannibalism.

p. 2 line 18 *following* 8 *insert* after.
p. 12 line 12 *delete* a transient.
p. 15 line 3 „ the comma.
p. 16 line 4 „ the first comma.
p. 18 line 27 *before phorozoon insert* the.
p. 18 line 29 *delete* the comma.
p. 49 line 9 „ the comma after "with".
p. 71 line 10 „ the comma after "point".
p. 71 line 15 „ the comma.

Jena, printed by Hermann Pohle. — 1717