VII.—Studies on the Development of the Horse. I. The Development during the Third Week.

By J. Cossar Ewart, F.R.S., Regius Professor of Natural History, University of Edinburgh.

(MS. received June 7, 1915. Read June 7, 1915. Issued separately December 14, 1915.)

[Plates IX–XVIII and Twenty-one Text-figures.*]

CONTENTS.

A. Introduction and Review of Previous Work on Young Horse Embryos.

Soon after the publication of *The Origin of Species* it was realised by Huxley and others that convincing evidence of the fact of evolution might be obtained by a systematic investigation of the ancestral history and development of the Equidæ. From studying material in the British and other Museums Huxley announced at the end of the 'sixties that he believed "the Anchitherium, the Hipparion and the modern horses constitute a series in which the modifications of structure coincide with the order of chronological recurrence in the manner in which they must coincide if the modern horses really are the result of the gradual metamorphosis in the course of the Tertiary epoch of a less specialised ancestral form." † But this conclusion was soon profoundly modified. When in 1876 Huxley had the opportunity of examining the Yale and other collections of the fossil horses of America, he was satisfied that "we must look to America rather than to Europe for the original seat of the Equine series," ‡ and "that the European Hipparion is rather a member of a collateral branch than a form in the direct line of succession." §

Huxley directed his attention to the development as well as to the ancestral history. Convinced that modern horses passed through a three-toed stage, he

---

* The cost of reproduction of the plates and of certain of the text-figures has been defrayed by a grant from the Carnegie Trust for the Universities of Scotland.

† *American Addresses*, p. 83, 1877.

‡ *Loc. cit.*, p. 86.

§ *Loc. cit.*, p. 87.

examined the limbs of embryos hoping to find vestiges of the phalanges of the second and fourth digits. Unfortunately, he failed to discover in the specimens at his disposal evidence that in the modern horse the second and fourth digits are nearly as complete during the earlier weeks of development as they were in the three-toed Miocene horses. Since 1876, when HUXLEY lectured in New York on the evolution of the Equidæ, our knowledge of fossil horses has advanced so rapidly that we are now familiar with almost every link in the chain connecting the one-toed Pliocene horses with their remote four-toed Eocene ancestors. Further, we know that in modern breeds the second and fourth digits of the fore-limbs bear during development nearly the same relation to the third digit as in three-toed Miocene horses.*

But while some progress has been made during recent years in working out the development of the Equidæ, we still know surprisingly little of the phases through which the horse passes during the earlier weeks of gestation; as ASSHETON pointed out some years ago, "a thorough investigation into the development of Equus and its placenta has still to be made." †

It is doubtless true that HAUSMANN published in 1840 an account of the earlier stages of equine development,‡ and that in 1890 Prof. MARTIN of Zurich described a 21-days horse embryo; § but HAUSMANN'S views are no longer accepted, and there are good reasons for believing that MARTIN overestimated the age of his embryo.

That HAUSMANN'S contributions were of no great permanent value may be inferred from the statements made by BONNET in 1889, at the Berlin Conference of German Anatomists. When discussing at this conference the fœtal membranes of the Equidæ, BONNET pointed out that HAUSMANN'S account of the development during the earlier weeks had caused more confusion than enlightenment, and that his drawings of horse embryos are almost incomprehensible and worthless.

Though in 1889 BONNET was in a position to discuss at some length the fœtal appendages of a 28-days horse embryo, he was unfortunately unable to add appreciably to our knowledge of yet earlier stages; moreover, by asserting that the rate of development in the horse varied greatly during the earlier weeks, BONNET, like HAUSMANN, has caused confusion rather than enlightenment.||

In the Berlin paper BONNET relates that he received from a pupil a blastocyst taken from a mare 21 days after the first service, but that, owing to the rare specimen having been subjected to a preliminary examination before it reached his hands, he could only certainly make out that the blastocyst (fig. 3) had a globular form, measured 12 to 13 mm. in diameter, and was invested by a zona pellucida 4μ in thickness.

A year after BONNET'S paper was read at Berlin, Prof. PAUL MARTIN of Zurich

---

* EWART, "The Second and Fourth Digits in the Horse," *Proc. Roy. Soc. Edinburgh*, 1894; "The Limbs of the Horse," *Journ. Anat. and Physiol.*, Jan. and Feb. 1894.

† "The Morphology of the Ungulate Placenta," *Phil. Trans. Roy. Soc.*, vol. c, Ser. B, 1906.

‡ HAUSMANN, *Über Zeugung und Enstehung des wahren weiblichen Eier bei den Säugetieren*, Hanover, 1840.

§ PAUL MARTIN, "Ein Pferdeei vom 21 Tage," *Schweizer Archiv für Thierheilkunde*, Zurich, 1890.

|| BONNET, "Die Erhaute des Pferdes," *Verhandlungen der anat. Gesellschaft*, Jena, 1889.

published an account of a horse embryo, believed, like BONNET'S, to be 21 days old.* This embryo was obtained from an eight-year-old mare, served on the 2nd of April, and killed on the 23rd of the same month.

MARTIN'S blastocyst, instead of being, like BONNET'S, globular and 12 to 13 mm. in diameter, was egg-shaped (fig. 4) and measured 25 mm. by 35 mm. This blastocyst was very much smaller than a 28-days blastocyst figured by BONNET. Hence MARTIN came to the conclusion that the embryo from the eight-year-old mare had been arrested in its development. On the other hand, BONNET, on realising in 1891 that the blastocyst of his damaged embryo was very much smaller than MARTIN'S blastocyst, came to the conclusion that the rate of development in the Equidæ varies considerably during the earlier weeks, and unreservedly stated that in the horse the blastocyst at 21 days varies from 13 mm. to 35 mm.†

From the observations made during the last fifteen years, I have arrived at the conclusion that BONNET'S 13-mm. blastocyst (fig. 3) represents the stage reached at the end of the second week of gestation; that MARTIN'S 35-mm. blastocyst (fig. 4) represents the stage reached at the middle of the third week; and that at the end of the third week the blastocyst, in a breed about the size of the wild horse of Mongolia, measures at least 50 mm. (fig. 5). If I succeed in giving good reasons for these conclusions, in showing that BONNET'S so-called 21-days embryo is 14 or 15 days old, and that MARTIN'S so-called 21-days embryo is 17 or 18 days old, and that at the end of the third week a horse embryo is nearly as well developed as a 2-days chick and an 18-days sheep embryo, the more important facts about the development of the Equidæ during the first three weeks of gestation will have been established.

It is obvious that a difference between blastocysts and their contents may be due to several causes: *e.g.* to (1) arrested development, or (2) arrested growth, or (3) a difference in age. When in one of the two embryos derived from the same fertilised ovum progress is retarded, we have an example of arrested development; ‡ when, on the other hand, the embryos in one uterine horn, though as well developed, are smaller than those in the other horn, we have an example of arrested growth; § but when two embryos from, say, two different mares, belonging it may be to different breeds, differ in size, before assuming that the difference is due to arrested development or arrested growth, one must make sure that it is not due to a difference in age, to the large embryo being some hours, or it may be several days, older than the small one.

To be in a position to obtain horse embryos of a definite age during the earlier

---

* "Ein Pferdeei vom 21 Tage," *Schweizer Archiv für Thierheilkunde*, Band xxxiii, 1890.

† BONNET, *Grundriss der Entwickelungsgeschichte der Haussäugethiere*, Berlin, 1891.

‡ ASSHETON found a difference in the size and in the state of development in twin germinal areas of a sheep. *Journ. Anat. and Physiol.*, April 1898.

§ I once found in a rabbit doe eight young (alike in size) in the right uterus, and four young (also of uniform size) in the left uterus; but when the eight were placed in one scale of a balance and the four in the other, the four weighed a few more grains than the eight; nevertheless, the eight small fœtuses were as well developed as the four large ones. EWART, 27*th Report of the Bureau of Animal Industry, Dept. of Agriculture, U.S.A.*, 1911.

weeks of gestation, it is necessary to ascertain as accurately as possible when fertilisation of the ovum actually takes place. This implies, amongst other things that each mare used should be kept long enough under observation to admit of the normal length of the œstrous period being determined.

In a wild Prjevalsky mare (*Equus prjewalskii*) imported as a yearling from Mongolia, œstrus (the period of desire), first noticed during her third summer, lasted as a rule 6 or 7 days. Between the end of one period and the beginning of the next there was an interval of 14 or 15 days; *i.e.* in the wild, as in most domestic mares, the œstrous and anœstrous periods together as a rule occupied 21 days. The period of gestation in the wild mare, if one may judge from the Woburn and other records, averages 357 days or 17 diœstrous cycles of 21 days each. In the wild mare I had under observation œstrus set in 8 days after the birth of her first foal. She was served on the tenth and eleventh days after foaling, and the "period of desire" passed off before the morning of the twelfth day and never recurred until after her second foal was born.

In domesticated mares living under nearly natural conditions the length of the œstrous period varies considerably; and one occasionally hears of in-foal mares coming regularly "in season" during at least the first three months of the gestation period.* I have heard of a mare which proved in foal though the period of desire lasted under 24 hours,† and have had mares under observation which were continuously "in season" for 12 or more days.

In making a collection of embryos with a view to working out the development of the horse it would be a great advantage if one had definite information as to when ovulation takes place, how long the ovum, after escaping from the follicle, retains the power of effectively combining with a sperm, and also how long sperms retain their fertilising power after reaching the oviduct. Unfortunately, we have no definite information either about ovulation in the Equidæ or about the vitality of their ova and spermatozoa. But from my records made since 1895 it may, I think, be inferred (1) that there is in the mare an intimate relation between ovulation and the disappearance of œstrus—that in fact the period of desire as a rule terminates from 10 to 26 hours after ovulation; (2) that spermatozoa are usually stale 3 or 4 days after reaching the oviduct; and (3) that an ovum usually fails to develop unless it is fertilised within two days after escaping from its follicle. In support of these conclusions, it may be mentioned that when œstrus lasts from the seventh to the tenth day after foaling, the mare is likely to become again pregnant if served on the

---

* Mr C. M. DOUGLAS of Auchlochan informs me that Shetland pony mares sometimes take the horse regularly all through the period of gestation and yet produce a normal foal to the first service. Further, I am informed that in both Shetland and Clydesdale fillies œstrus may occur once and again during the earlier months of pregnancy without interfering with the normal development of the foal; and I have heard of a Clydesdale mare that came in season and was served three weeks before giving birth to a fully developed but dead foal.

† This mare belonged to a herd in the possession of the late Lord ARTHUR CECIL, a very competent and trustworthy observer.

eighth, ninth, or tenth day, but may fail to prove in foal if served on the seventh or not until the eleventh day. Service on the seventh day is in some cases of no avail, because the spermatozoa lose their fertilising power before the ovum escapes from its follicle on the tenth day, while service on the eleventh day is in some cases without effect, because the ovum has become stale before it is reached by the spermatozoon.* With a view to securing a 21-days embryo, five mares were kept under observation for several months. One of the five, a 13·2-hands Highland pony, came regularly "in season" every third week, and, as in the wild mare, œstrus lasted from 6 to 7 days. This Highland mare was served by a 14-hands Arab stallion at 2 p.m. on May 18, 1897, 7 days after she came "in season" (*i.e.* on the seventh day of œstrus). As she refused to take the horse on May 19, it may be assumed that an ovum escaped and was fertilised soon after the one and only service at 2 p.m. on May 18. On June 8, at 4 p.m. (21 days and 2 hours after service), the mare was killed and the pear-shaped 50-mm. blastocyst represented in fig. 5 was found in the left uterine horn (fig. 15). Obviously the age of the embryo found in the Highland mare may be under, but it cannot possibly be more than two hours over, 21 days.

BONNET'S 13-mm. blastocyst was taken from a mare 21 days after the first service. How often the mare was served is not stated. If served on the first day of œstrus, and again on, say, the third day, and if, as is quite possible, ovulation took place on the sixth or seventh day of œstrus, the age of the blastocyst (though removed 21 days after the first service) would only be 14 or 15 days. I am hence inclined to believe that the difference in size between BONNET'S so-called 21-days blastocyst (fig. 3) and the blastocyst from the Highland mare (fig. 5) was not due to either arrested development or arrested growth, but to a difference in age—to the ovum from which BONNET'S 13-mm. blastocyst was developed being fertilised 6 or 7 days after the first service.

MARTIN'S 35-mm. blastocyst was obtained from an eight-year-old mare, which had a foal the previous year. This implies that œstrus probably lasted 6 or 7 days. The mare was served at 1.30 p.m. on April 2, and killed at 8 p.m. on April 23. When œstrus set in and passed off is not mentioned. If ovulation took place on April 2 a few hours after service, the age of MARTIN'S embryo was in all probability 21 days; but if the ovum only escaped from its follicle on, say, April 6, the age would only be 17 days. The difference in size and number of somites between MARTIN'S so-called 21-days embryo (fig. 7) and my 21-days embryo (figs. 8 to 11) is considerable. Seeing that no information is given by MARTIN as to whether the mare which yielded his embryo was served at the middle or end of œstrus, I think it may be assumed that the difference between the embryos represented in figs. 7 and 8 is more likely to be due to a difference in age than to either arrested growth or arrested development. Taking these and other facts into consideration, I shall, I think, be justified in

---

* In all probability service sometimes induces ovulation; but, as a rule, no matter how often the mare is served, the follicle remains intact until the seventh or eighth day of œstrus.

regarding BONNET'S 13-mm. blastocyst as representing the phase reached at the beginning of the third week, and MARTIN'S 35-mm. blastocyst as representing the phase reached at the middle of the third week of development.*

1. *Bonnet's* 13-*mm. Blastocyst* (Pl. IX, fig. 3).

Sheep and goats are about as well developed and precocious at birth as foals. It might hence be assumed that the rate of development in Ungulates bears, as a rule, an intimate relation to the gestation period. In the Celtic pony the gestation period is approximately 366 days,† in sheep it seems to be about 150 days, and in the pig about 112 days; *i.e.* in the Celtic pony the gestation is practically three times that of the pig and 2·2 times that of the sheep. But the examination of a collection of Ungulate embryos clearly shows that the rate of progress, during at least the earlier weeks, bears little, if any, relation to the length of the gestation period, and especially that, though there is a family resemblance between the embryos of odd-toed and even-toed Ungulates, the fœtal appendages may differ profoundly.

Further inquiries will probably show that the blastodermic vesicle of the sheep at the end of the twelfth day agrees generally with the blastodermic vesicle of the horse at the end of the fourteenth day, and that a 15-days sheep embryo‡ differs but little from a 17- or 18-days horse embryo. But while at the outset horse embryos differ but little from sheep embryos, there seem to be, almost from the first, differences in the fœtal membranes. In BONNET'S 13-mm. horse blastocyst the zona pellucida was smooth, resistant, and elastic, and had a thickness of 4μ.§ Though in the sheep the blastocyst at the end of the twelfth day only measures about 1·5 mm., the zona pellucida has completely disappeared—according to ASSHETON the zona is greatly attenuated, if not actually absorbed, at or about the eighth day.|| Owing to the 13-mm. blastocyst having been injured, BONNET was unable to say anything about the embryo it contained—he was only able to note the presence of isolated nucleated polygonal cells adhering to the inner surface of the zona pellucida. In all probability further inquiries will show that a horse embryo at the end of the second week is at least as far advanced as a 10-days sheep embryo.

2. *Martin's* 35-mm. *Blastocyst* (Pl. IX, fig. 4).

MARTIN'S blastocyst not only differed from BONNET'S in shape and size, but also in having a 4-mm. thick albumen coat (fig. 4, *alb.*) within which was found no

---

* A 19-days horse embryo (text-fig. 19) in HAUSMANN'S collection had ten mesodermic somites. Seeing that MARTIN'S so-called 21-days embryo had only four somites, it was probably under rather than over 18 days.

† It is on record that the average gestation period for thirty-three thoroughbred mares of the Middle Park stud, Eltham, was 335·5 days; but in Shires and Clydesdales the gestation period seems to approach that of the wild horse of Mongolia (357 days), while in the ass it may run to 385 days.

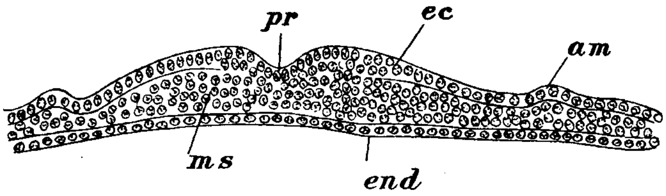
‡ ASSHETON has pointed out that in the sheep, goat, and pig "there is a close parallelism in time with reference to the development of the embryo." *Guy's Hospital Reports*, vol. lxii.

§ That the zona pellucida of a 13-mm. equine blastocyst has a thickness of 4μ wants confirmation.

|| ASSHETON, "Segmentation of the Ovum of the Sheep," *Quart. Journ. Micro. Sci.*, vol. xli, 1898.

trace of the zona pellucida. MARTIN thought the albumen coat was perhaps partly formed in the oviduct, and that it provided nourishment as well as protection. Though BONNET makes no reference to an albumen coat in his 13-mm. blastocyst, it is conceivable that the material for this coat is in part, as MARTIN suggests, provided by the oviduct; but in all probability the albumen is mainly derived, as in the mole, from the uterus.* On making sections through the albumen layer, MARTIN ascertained that it consisted of numerous strongly refractive delicate lamellæ, amongst which were groups of cells, free nuclei, and spermatozoa at various stages of disintegration.† There is no evidence that the albumen coat served to fix the blastocyst to the uterine mucous membrane.

MARTIN describes the blastodermic vesicle as consisting of two quite distinct layers—an ectodermal layer composed of columnar cells which seen from the surface appear polygonal, and an endodermal layer of flat polygonal cells between which are many gaps of a considerable size. In the neighbourhood of the embryo the blastocyst consisted of three layers, an outer, inner, and middle, the last made up of round cells continuous with the embryonic mesoderm. When the blastocyst was removed from the uterus, the embryo, being transparent, could not be detected, but as the fixing proceeded an oblong structure resembling the sole of a shoe made its appearance. As fig. 7 indicates, this embryo, rounded in front and pointed behind, had four somites and was separated by a narrow area pellucida from the area opaca. In a pig embryo with four mesodermic somites the amnion is represented by head, tail, and lateral folds, and there is a mass of mesoderm lying under the tail-fold which in course of time takes part in forming the allantois. Though MARTIN's embryo was 3·25 mm. in length, the amnion was apparently only represented by short inconspicuous lateral folds (text-fig. 1, *am.*), and there was no rudiment of an allantois.



TEXT-FIG. 1.—Transverse section of MARTIN's embryo. *am.*, amnion fold; *ec.*, ectoderm; *end.*, endoderm; *ms*, mesoderm; *pr.*, primitive groove. Compare with section of 21-days embryo (text-fig. 12).

That MARTIN's embryo represents a very early phase in the development of the horse—a phase reached in the pig on the fourteenth or fifteenth day—is made evident by the figures which illustrate his paper. In a dorsal view of the embryo (fig. 7) the primitive streak, the broad pointed primitive groove, the position of Hensen's node,

---

* HEAPE, "The Development of the Mole," *Quart. Journ. Micro. Sci.*, vol. xxiii, 1888.

† In Marsupials, as Professor HILL states, the ovum during its passage down the oviduct "becomes surrounded by a transparent layer of albumen ·015 to ·022 mm. in thickness, composed of very delicate concentric lamellæ, and having normally numbers of sperms embedded in it," and that this albumen layer is invested by a double-contoured membrane comparable to the shell membrane of the Monotreme egg. J. P. HILL, "The Early Development of the Marsupialia," *Quart. Journ. Micro. Sci.*, vol. lvi, December 1910.

and the narrow medullary groove with four somites at each side are indicated, while a transverse section through the posterior end of the primitive groove (text-fig. 1) makes it clear that the mesoderm in this region had not yet split into somatic and splanchnic layers, and especially that very little, if any, progress had been made in providing an amnion.

In a summary MARTIN directs special attention to the 35-mm. blastocyst being egg-shaped, to the presence of an albumen layer, and to the rudimentary condition of the amnion.

3. *Hausmann's* 19-*days Embryos.*

HAUSMANN, who had a stud including fifty-two mares, secured three 19-days embryos, viz. one 19 days 45 minutes after service, one 19 days and 7 hours, and one 19 days and 20 hours after service. HAUSMANN'S figures of these embryos are reproduced in text-figs. 19 to 21. Though it must be admitted that these figures are, as BONNET says, almost incomprehensible, they afford conclusive evidence in support of the view that MARTIN'S embryo, instead of representing the stage reached at the end of the third week, represents the stage reached on the seventeenth or eighteenth day of gestation. HAUSMANN'S 19 days 45 minutes embryo is characterised by ten or eleven mesodermic somites; MARTIN'S embryo had only four somites (fig. 7). As my 21-days embryo had over twenty somites (fig. 10), it may be safely assumed that MARTIN'S embryo represents the stage reached about the middle of the third week.

B. THE REPRODUCTIVE ORGANS AND FŒTAL MEMBRANES AT THE END OF THE THIRD WEEK.

1. *The Ovaries and Corpus luteum, Oviduct and Uterus.*

(1) *The Ovaries and Corpus luteum.*—The ovaries of the mare from which the 21-days embryo was obtained are represented in figs. 12 to 15. Up to the time ova begin to mature the ovaries in the mare are small and smooth, and more or less kidney-shaped; but as maturity is reached they increase in size, and eventually present a number of prominences each indicating the position of a growing ovarian follicle.*

A number of follicular prominences are seen in figs. 12 and 13, while sections through follicles, from which the contents escaped, are represented in fig. 15. Evidently, during the three months the Highland mare was under observation, a large number of ova were maturing with a view, doubtless, to giving her a chance

---

* Under normal conditions fillies reach maturity—begin to discharge ripe ova—about the end of the second or beginning of the third year, but under unfavourable conditions ovulation may only begin at the end of the third year. On the other hand, when fillies are well fed during their first winter, maturity may be reached at the end of the first or the beginning of the second year. Evidence of early maturity we have in a member of the Auchlochan herd of Shetland ponies. This pony, born on May 7, 1907, had a well-developed vigorous foal on May 23, 1909: assuming the gestation period was 336 days, this filly became pregnant at the age of 1 year and 45 days. Seeing that a heifer may become pregnant when only 5 months old, it is not surprising that a filly sometimes reaches maturity before she is a year old.

of eventually proving fertile even if she several times "broke service." Some of the follicles were under 5 mm., some were over 40 mm. in diameter, but even in a 6-mm. follicle (fig. 1) I found what appeared to be a well-advanced ovum (fig. 2). The largest follicle in the left ovary (fig. 15) doubtless contained a nearly ripe ovum. In the mare, up to the end of the sixth week the trophoblast is at the best only loosely connected to the uterine mucous membrane; it is hence mainly prevented from escaping from the uterine horn by internal hydrostatic pressure.* Had the blastocyst escaped from the uterus (*i.e.* had the Highland mare aborted, "broken service") during the third week, the large follicle seen in fig. 15 would have discharged an ovum on or about June 8, thus giving the mare a chance of again becoming pregnant without any loss of time. On the other hand, had the gestation in the mare been allowed to run its course, the maturation of ova would have been arrested and the size of the enlarged follicles in both ovaries gradually reduced. That the large follicle in fig. 15 would have remained intact is suggested by its outer wall being decidedly thicker than that of the wall of the large follicle in the ovary (fig. 16) of a non-pregnant mare which died on the second day of œstrus.†

The corpus luteum in the ovary of the mare which yielded MARTIN'S embryo was of a soft consistency, pale red in colour, and about double the size of a lentil. The corpus luteum found in the left ovary of the Highland mare is represented in fig. 18 natural size. The corpus luteum seen in fig. 17 occurred in the ovary of a mare which died three months after giving birth to a foal.‡

(2) *The Oviduct and Uterus.*—In the mare at the end of œstrus the trumpet-like expansion at the free end of the oviduct (fig. 19) lies near to, or in contact with, the follicle about to discharge an ovum. How long the "trumpet" retains this position after ovulation is not known—in the sheep the trumpet is said to adhere to the surface of the ovary for eight or nine days after service. The trumpet is lined with numerous lamellæ which converge to the ostium abdominale to become continuous with the interrupted ridges extending along the oviduct; it will be observed from fig. 19 that the lamellæ lining the trumpet are continued for some distance over its outer surface. The expanded upper part of the oviduct, immediately within the ostium, may play the part of a seminal receptacle—in a mare killed about 24 hours after service it contained numerous active spermatozoa. The oviduct opens into the uterine horn (fig. 19) by a minute aperture surrounded by the terminal portions of the lamellæ of the oviduct.

At birth the mucous membrane of the uterus presents few furrows and only

---

* Experiments by MARSHALL and JOLLY seem to show that the corpus luteum provides a secretion essential for the attachment of the embryo and for its nourishment during the first stages of pregnancy. "Contributions to the Physiology of the Mammalian Reproduction," *Phil. Trans.*, Ser. B, vol. cxcviii, 1905.

† Further inquiries may show that in the case of mares that come in use during the period of gestation ovulation may occasionally take place.

‡ The function of the corpus luteum in the mare is dealt with in *The Physiology of Reproduction*, by F. H. A. MARSHALL, Longmans, 1910.

rudiments of glands, but by the third month a number of deep furrows extend along the horns and along the greater part of the body of the uterus. By the end of the first year the uterine mucous membrane, from a short distance within the cervix up to the ends of the horns, is folded longitudinally to form narrow nearly parallel ridges separated by deep furrows. Eventually these ridges are cut transversely into numerous tongue-shaped processes (figs. 14 and 21). The condition of the uterine mucous membrane at the end of the third week is indicated in figs. 25 and 26. With the exception of the cervix the uterus is lined by a layer of columnar epithelium beneath which is a somewhat dense layer of connective tissue traversed by numerous capillaries (fig. 24). At a deeper level the connective tissue of the uterine wall forms an irregular network the meshes of which are traversed by blood-vessels of various sizes, and by the numerous uterine glands (fig. 26).

Before proœstrum sets in—*i.e.* during the period of rest (anœstrum)—the uterine mucosa is of a pale colour and coated with a thin layer of mucus; but as proœstrum advances it becomes more and more congested, with the result that the glands become more active. When the œstrous phase is reached the tongue-like processes making up the uterine ridges (figs. 14 and 21) are red and swollen; this is partly due to congestion of the capillaries, and partly to the engorged condition of the glands. An indication of the condition of the mucous membrane during œstrus will be gained from figs. 23 and 24, which represent sections of a uterine ridge about 24 hours after œstrus set in. The sections, though affording no evidence of the escape of blood into the cavity of the uterus during proœstrum, show at places extravasated blood in the connective tissue and in the lumen of the glands. It will be noticed that amongst the extravasated blood corpuscles bodies resembling hæmatoidin crystals (fig. 24) are fairly common; there is, however, an absence of pigment such as usually occurs in sheep.*

Martin states that the mucous membrane of the uterus from which his 35-mm. blastocyst was obtained was swollen and spotted. There was no spotting or evidence of congestion in the uterine horn which contained my 21-days embryo; in fact, at the end of the third week, as during anœstrum, there is neither marked congestion nor evidence of unusual activity of the uterine glands nor yet of destruction of the uterine epithelium. In the absence of signs of unusual activity in the uterine mucous membrane during the earlier weeks of gestation the mare evidently differs from the sheep and pig, in which, in addition to an increase of the interglandular tissue, there is considerable degeneration of the lining epithelium. An indication of the difference between the uterine mucosa at the end of the third week and during œstrus will be gained from figs. 23 to 26; in figs. 25 and 26 the mucous membrane of the uterine horn containing the 21-days embryo is represented, in figs. 23 and 24 the mucous membrane at the end of the first day of œstrus.

Notwithstanding the absence of marked congestion of the mucosa at the end of

---

* Marshall, "The Œstrus Cycle in the Sheep," *Phil. Trans.*, Ser. B, vol. cxcvi, 1903.

the third week, there was—if one may judge by the presence of leucocytes and fat globules—abundance of the uterine milk so essential during the earlier weeks for the nourishment of the embryo.

2. *The Blastocyst.*

It has already been mentioned that the blastocyst is globular in form and measures 13 mm. at the beginning of the third week; that it is ovoid and has a length of 35 mm. at the middle of the third week; and that by the end of the third week it is pear-shaped and measures 50 mm. (fig. 5).

Though the blastocyst is not, as BONNET stated in 1889, spherical up to the seventh week, a globular form is retained longer in the Equidæ than in even-toed Ungulates;* in an embryo pig, at the same phase as a 21-days horse, the blastocyst, instead of measuring 50 mm., may reach a length of 1000 mm. BONNET believed there was still a trace of the zona pellucida at the end of the fourth week, but MARTIN failed to find any evidence of the zona in his 35-mm. blastocyst, and there was no vestige of a zona at the end of the third week. As soon as the 21-days blastocyst was exposed the embryo was seen at the broad rounded end (fig. 5), and there were faint indications of the vitelline vessels and the sinus terminalis. Immediately beyond the sinus it was possible to detect minute circular projections (trophoblastic discs), and still nearer the small end shallow semi-opaque depressions (fig. 34).

3. *The Trophoblast.*

The isolated nucleated polygonal cells seen by BONNET adhering to the inner surface of the zona pellucida of his 13-mm. blastocyst doubtless belonged to the trophoblast. The trophoblast of MARTIN'S 35-mm. blastocyst apparently consisted throughout of epiblastic cells almost tall enough to rank as columnar cells; as is often the case with trophoblastic cells, the nucleus was nearer the inner than the outer end. In my 50-mm. blastocyst, in the absence of the albumen coat present in the 35-mm. blastocyst, the trophoblast lay in direct contact with the lining of the uterus. As in this embryo the amnion was complete and the unsplit mesoderm highly vascularised, I expected to find the trophoblast at least as highly specialised as in Marsupials at a corresponding stage of development.

Sections through the blastocyst in the embryonic area, in the region of the sinus terminalis, and in the non-vascular distal end made it evident that three kinds of epiblastic cells took part in forming the trophoblast, viz.: (*a*) typical columnar cells, (*b*) very tall columnar cells, and (*c*) columnar cells ending in free sac-like processes. The greater part of the trophoblast consisted of cells of the first category, *i.e.* of fairly tall typical polygonal columnar cells in contact with each other along their entire length, with deeply placed nuclei and nearly square-cut outer ends

---

* Figures of the blastocyst at the end of the fourth, fifth, sixth, and seventh weeks are given in the writer's pamphlet, *A Critical Period in the Development of the Horse*, A. & C. Black, 1897.

(fig. 28, *tr.*). Cells of this type, with cells of the non-vascular somatic mesoderm of the embryonic area, formed the true chorion (text-fig. 12, *ch.*), and they made up the trophoblast forming the outer wall of the space containing the unsplit highly vascular mesoderm which extended from the exocœlom to a short distance beyond the sinus terminalis (fig. 34, *s.t.*). Typical columnar cells also occurred beyond the sinus; they occupied, *e.g.*, spaces between the trophoblastic discs (fig. 34, *t.d.*) and between the shallow depressions scattered over the pointed end of the blastocyst.

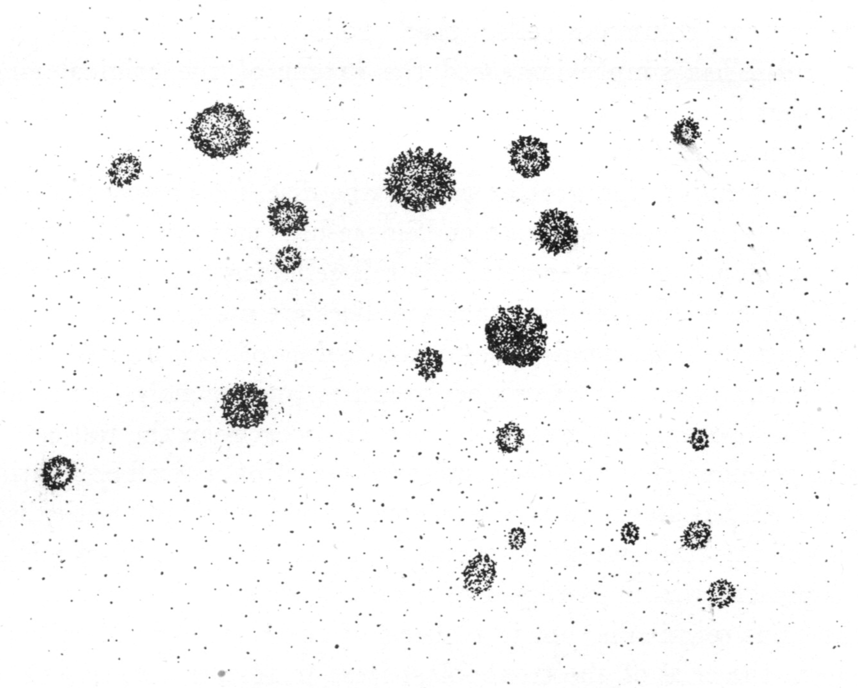
Though the simple columnar trophoblastic cells in the embryonic area are in contact with the somatic mesoderm (fig. 34), and the corresponding cells beyond the sinus terminalis are in contact with the yolk-sac endoderm (fig. 30), the cells forming the trophoblast between the exocœlom and the sinus terminalis are not in contact with the unsplit vascularised mesoderm. Evidence of this we have in fig. 28. From this figure it is evident that there is a space between the trophoblast (*tr.*) and the yolk-sac endoderm (*y.e.*), in which is suspended the rich plexus of vitelline vessels carrying blood to and from the embryo.

There is no evidence at the end of the third week that any of the cells of the trophoblast up to the sinus terminalis are either phagocytic or in any way adapted for fixing the blastocyst to the lining of the uterus. In all probability the simple columnar trophoblastic cells simply imbibe the fluid portion of the uterine milk in much the same way as the cells lining the intestine of the adult horse absorb the fluid constituents of the food in the alimentary canal. This fluid on reaching the space between the trophoblast and the yolk-sac endoderm has a chance of at once entering the capillaries of the unsplit mesoderm and being conveyed to the embryo by the vitelline veins. Taking into consideration the relatively great extent of the vascularised mesoderm, it is extremely probable that the trophoblast extending between the exocœlom and the sinus terminalis is the chief means by which nourishment is secured for the embryo at the end of the third week.

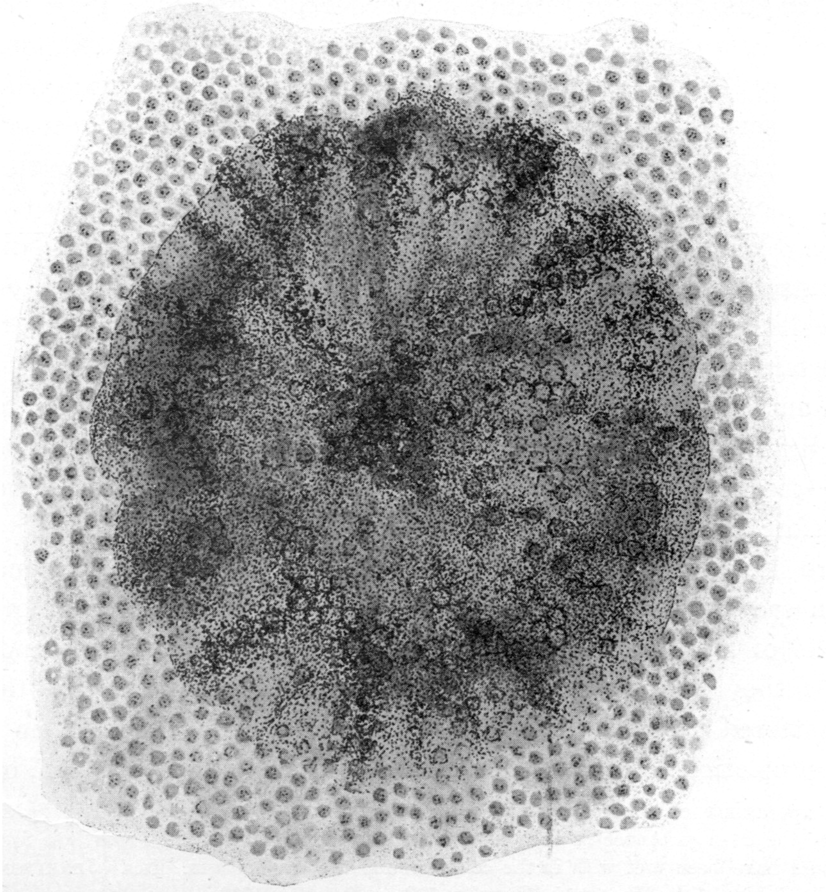
The second, or very tall, cells only occur in the fully developed trophoblastic discs. These discs (text-fig. 2) are especially numerous near the edge of the vascularised mesoderm which extends beyond the sinus terminalis (fig. 22 and text-fig. 4)—in an area near the sinus measuring 10 by 3 mm. I counted 27 discs at various stages of development. A disc 300 times enlarged is given in text-fig. 3, and a similar disc, on a smaller scale, viewed from within, is given in text-fig. 4; sections of discs are given in figs. 29 and 30. The majority of the sections of any given disc contain so many nuclei (fig. 29A) that one is apt to assume that the peculiar trophoblastic projections from the 21-days horse blastocyst consist of several layers of cells, are in fact formed by a heaping up of cells, and are hence akin to the heaps of cells met with in the trophoblast of Manis.* But sections carried through the centre of a disc (fig. 29) clearly prove that even the largest discs consist of a single

---

* Max Weber, "Beiträge zur Anatomie und Entwickelung der Genus Manis," *Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien*, Leiden, 1892.



TEXT-FIG. 2.—Group of trophoblastic discs near sinus terminalis at various stages of development. ×28.



TEXT-FIG. 3.—A full-grown trophoblastic disc seen from without. ×300.

layer of long, narrow, columnar cells; that proliferation, instead of leading to a heaping up of cells, has simply increased the extent of the original single layer, with the result that it has bulged outwards to form a dome-like projection with a relatively small central cavity.

The long cells forming the greater part of the disc, *i.e.* the part in contact with the lining of the uterus, never seem to end in sac-like processes, but such processes are usually seen protruding from some of the tall cells forming the edge of the discs (fig. 29). It might hence be inferred that the discs are only, or at least mainly, concerned with fixing the embryonic sac to the lining of the uterus. If, however, sections of a disc are carefully examined, granules, and vacuoles containing one or more deeply stained bodies, are invariably seen in or between the tall cells (fig. 29); hence it may be assumed that the discs subserve nutrition as well as fixation.*

As it happens, all the stages in the development of the trophoblastic discs are met with at the end of the third week. Nothing of the nature of a basement membrane or coagulum is present within the layer of simple columnar cells forming the trophoblast up to the sinus terminalis, but in sections of the 50-mm. blastocyst beyond the unsplit mesoderm the cells of the trophoblast seem to rest on a basement membrane. As offshoots from this apparent basement membrane extend up between the trophoblastic cells, and as the layer reaches a considerable thickness under the developing and completed discs (figs. 29 and 30), it is evidently formed out of material taken in by the epiblastic cells forming the trophoblast beyond the sinus terminalis. Under the large disc represented in fig. 29 the coagulated material reaches a considerable thickness, but under the developing disc given in fig. 30 the amount of the coagulum is still limited. Sometimes a band connects the coagulum of one disc with that of an adjacent disc. Whether the thickening of the coagulum at certain definite points is due at the outset to increased activity of the cells under which it lies, or to a zone of phagocytic cells around those destined to form the disc, I am unable to say. It is, however, certain that as the coagulum increases in amount the cells lying over it increase in number, and especially in length.

It is well to bear in mind that these trophoblastic discs are only present for a short time—they are not yet developed at the middle of the third week, and they disappear before the end of the fourth week.

The third kind of trophoblastic cells, instead of ending in square-cut ends, terminate in sac-like processes separated from each other by more or less distinct spaces. Cells of this type are always found in the grooves surrounding the discs (fig. 30, *pc.*); they also occur in patches between the discs and line the shallow depressions scattered over the distal end of the blastocyst. There is no evidence that the sac-like projections of these cells either adhere to, fit in between, or destroy the

---

From the appearance of some of the round bodies seen in the disc represented in fig. 29 it is extremely probable that had the 21-days blastocyst been fixed with osmic acid, fatty globules like those found by JENKINSON n the sheep would have been met with in the cells forming the trophoblastic discs. JENKINSON, "Notes on the Histology and Physiology of the Placenta in Ungulata," *Proc. Zool. Soc.*, 1906.

cells of the uterine mucosa. While the simple columnar cells of the trophoblast are probably mainly concerned with taking in nutritive fluids, the cells with sac-like processes seem to be truly phagocytic. In one of the cells in fig. 30 minute bodies are seen in the sac-like projection.

It is probable that, after the albumen layer (text-fig. 11) disappears, phagocytic cells are comparatively common, but that, as the sinus terminalis migrates towards the distal pole, their number is gradually reduced. Seeing that a membrane-like coagulum is not present within the layer of simple columnar cells forming the trophoblast up to the sinus terminalis, it may be presumed that the coagulum under the trophoblast beyond the sinus is mainly formed from material taken in by the epiblastic cells with sac-like processes.

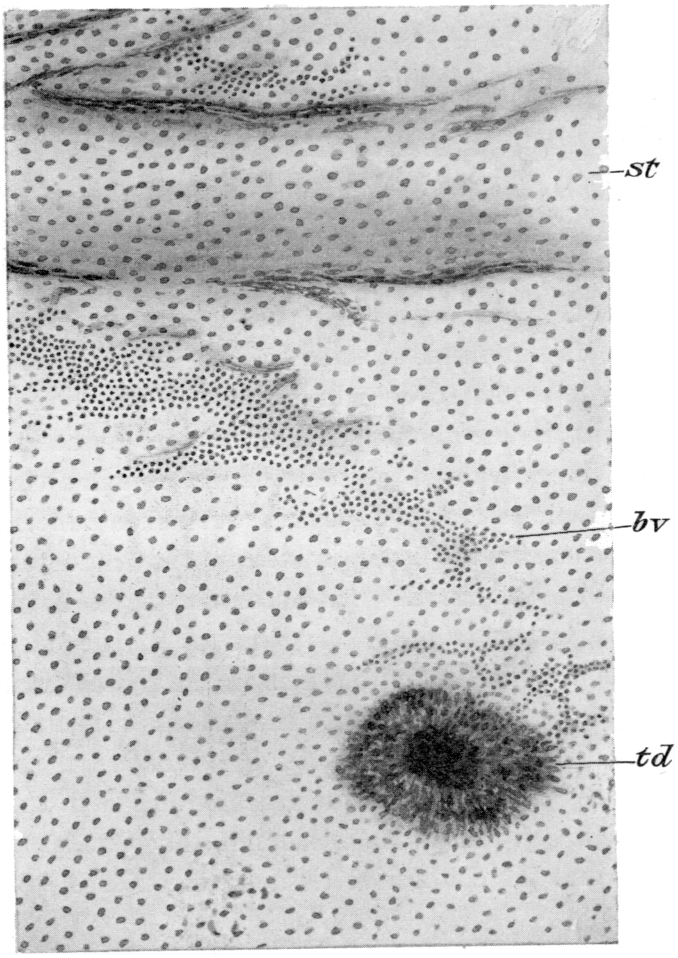
Though the trophoblastic discs and the internal hydrostatic pressure may together be sufficient at the end of the third week to retain the blastocyst in the same position in the uterine horn, they are evidently not able to prevent it escaping from the horn when by accident or otherwise the passage leading to the uterus becomes dilated. At the end of the third, as at the end of the sixth week, the moment the blastocyst is exposed it seems to detach itself from the lining of the uterus; to what extent this result is due to uterine contractions induced by incisions made to expose the embryo it is difficult to say, but the fact remains that until the allantoic villi begin to appear at the end of the seventh week such adhesions as exist between the blastocyst and the uterus are easily broken down. Structures at all comparable to the trophoblastic discs of the 21-days horse blastocyst have not, as far as I am aware, been met with either in other Eutheria or in the Marsupialia. The discs differ from the irregular epiblastic villi which in the rabbit during the second week of gestation acquire a close attachment to the mucous membrane of the uterus and thus aid in fixing the blastocyst. They differ still more from the multinuclear *giant cells* which in some cases erode the uterine mucosa, and from the large trophoblastic masses (syncytia) which, *e.g.* in Spermophilus, not only penetrate the epithelium but extend some distance into the connective tissue of the uterus.

4. *The Yolk-sac.*

Just as a typical amnion consists of an inner layer of ectoderm and an outer layer of somatic mesoderm, a typical yolk-sac consists of an inner layer of endoderm and an outer layer of splanchnic mesoderm. In the horse at the middle of the third week the extra-embryonic endoderm consists of polygonal epithelial cells separated by many gaps of a considerable size. In the absence of mesoderm, except in the vicinity of the embryo, this imperfect layer of endoderm lies in direct contact with the trophoblast. Hence at the middle of the third week the yolk-sac, except in the neighbourhood of the embryo, consists only of an imperfect layer of endoderm.

Before the end of the third week is reached the mesoderm has greatly increased, and, more important still, has split within and for some distance beyond the embryo (fig. 33

and text-fig. 12) into somatic and splanchnic layers, thus giving rise to cœlomic and exocœlomic spaces. Owing to this partial splitting of the mesoderm the part of the yolk-sac nearest the embryo is complete, *i.e.* it consists of a layer of endoderm and a layer of splanchnic mesoderm. But beyond the exocœlom (fig. 34 and text-fig. 12) the yolk-sac at the end of the third week is not yet provided with its mesodermic coat, for up to a line slightly beyond the sinus terminalis it simply consists of a single layer of endoderm which forms the inner boundary of a space occupied by the unsplit mesoderm; beyond this line the endoderm is intimately related to the trophoblast (fig. 28).* The cells of the yolk-sac endoderm around the opening into the yolk-stalk, like the cells lining the stalk, are columnar in form (fig. 50); but within a short distance of the yolk-stalk, right up to the sinus terminalis, the yolk-sac endoderm consists of a single continuous layer of flat polygonal cells (fig. 31, *a*) some of which



TEXT-FIG. 4.—Sinus terminalis (*s.t.*) of a 21-days embryo and trophoblastic disc (*t.d.*) seen from within. *b.v.*, blood-vessels on growing margin of unsplit mesoderm beyond sinus terminalis. × 90.

---

* In the sheep and pig the mesoderm is soon completely split into somatic and splanchnic layers. The result of this splitting is the formation of a free yolk-sac vesicle (text-fig. 13). The yolk-sac is nearly, but never quite, a free vesicle in the horse.

are connected by protoplasmic bands with the vessels of the unsplit mesoderm (fig. 28).

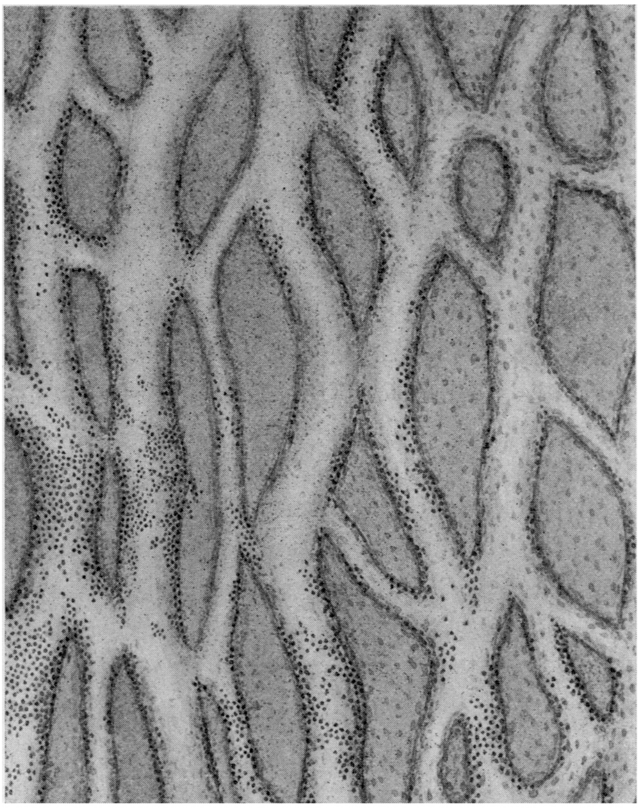
Except within the trophoblastic discs, the endoderm beyond the margin of the unsplit mesoderm also consists of a single layer of polygonal cells (fig. 30), but opposite the discs the endoderm cells proliferate to form tubercles which project into the cavity of the yolk-sac (figs. 29 and 32).

The first indication of a trophoblastic disc is a local thickening of the coagulum lying between the trophoblast and endoderm, presumably the result of the increased activity of a group of trophoblastic cells (fig. 30). The first indication of a yolk-sac tubercle is an ingrowth from the thickened coagulum which causes the endoderm to bulge into the cavity of the yolk-sac (figs. 31 and 31A). The endoderm cells in contact with the globular ingrowth from the coagulum stain more deeply and are decidedly more granular than the surrounding cells (fig. 31A). It may hence be inferred that the coagulum is attacked by the endoderm cells in its immediate vicinity. As the coagulum expands and projects further into the cavity of the yolk-sac it acquires an almost complete investment of endoderm cells with relatively large nuclei. A section through the centre of a growing tubercle (still connected by a short stalk with the subtrophoblastic layer of coagulum) is represented in fig. 32, while fig. 32A represents a section through the edge of the same tubercle.

If, as is usually the case, the coagulum forming the kernel of the tubercle reaches a considerable size, the capsule of endodermic cells ruptures, with the result that the coagulum projects freely into the cavity of the yolk-sac (fig. 29). Just as it is impossible to say to what extent the uterine milk is modified as it passes through the trophoblastic discs to form the coagulum, it is impossible to say how the contents of the tubercles are modified by the endodermic cells forming their capsules.

5. *The Mesoderm.*

At the middle of the third week the mesoderm is in the act of splitting in the region of the mesodermic somites; at the end of the third week, as already mentioned, the splitting of the mesoderm into somatic and splanchnic layers has extended some distance beyond the embryo (fig. 34 and text-fig. 12). The inner portion of the space resulting from the splitting becomes the cœlom, the outer forms the exocœlom (text-fig. 12). As fig. 34 and text-fig. 12 indicate, the greater part of the mesoderm at the end of the third week is still unsplit, and lies between the endoderm and trophoblast. This unsplit mesoderm is in contact neither with the trophoblast nor the endoderm; it occupies a space between these layers, and supports the vitelline vessels carrying blood to and from the embryo. The blood comes direct from the two aortæ by the two vitelline arteries (text-fig. 7). The left artery (*l.v.*), very much larger than the right (figs. 27 and 35), eventually bifurcates and encircles the blastocyst as the sinus terminalis (fig. 34); the left artery, before bifurcating to form the sinus, gives off numerous branches, some of which anastomose with branches from the small right artery. These branches, together with many others from the sinus terminalis, form an arterial network (fig. 34). From the network small veins proceed which unite ultimately to form the large vitelline veins, by means of which the blood from the yolk-sac is poured into the sinus venosus. The large left and small right vitelline arteries and the large vitelline veins are seen in fig. 35. The general scheme of the yolk-sac circulation is given in fig. 34, while fig. 22 and text-fig. 5 represent on a larger scale the network formed by branches proceeding from the sinus terminalis.



TEXT-FIG. 5.—Portion of vitelline network near sinus terminalis. × 90.

In the case of the rabbit and other mammals in which the lower polar region of the blastocyst is never invaded by mesoderm, blood-vessels never occur beyond the sinus terminalis; when, however, as in the sheep, the mesoderm extends throughout practically the whole of the lower portion of the blastocyst, no definite sinus terminalis appears. In the horse at the end of the third week, though a sinus has been established, it does not, as in the rabbit, mark the limit of vascularisation, for, as fig. 22 and text-fig. 4 indicate, blood-vessels or blood-islands extend some distance beyond the sinus. But by the end of the fourth week there are neither blood-vessels nor blood-islands beyond the sinus terminalis; hence the yolk-sac circulation in the horse has even a different history from that of the pig, in which a temporary sinus is followed by general vascularisation.

6. *The Amnion.*

In MARTIN's embryo the amnion was only represented by indistinct lateral ridges (text-fig. 1, *am.*); in my 21-days embryo the amnion was complete (figs. 33, 34, and text-fig. 12). In the sheep and pig the amnion, well advanced on the fifteenth day, may be complete on the sixteenth day, *i.e.* at the stage characterised by from 8 to 10 mesodermic somites. As there are neither head nor tail folds in the horse on the seventeenth day, the amnion is probably only completed on the twenty-first day, *i.e.* at the stage characterised by about twenty somites. It may hence be assumed that the amnion appears relatively later in the horse than in the sheep and pig—the early development of the amnion in even-toed Ungulates is doubtless correlated with the early disappearance of the zona pellucida. Whether in the Equidæ the amnion is mainly derived from a head fold, as in the chick, or from a tail fold, as in the rabbit, will doubtless be ascertained when a more complete series of embryos is available. But seeing that the head is sharply bent backwards (fig. 33) at the end of the third week, the probability is that in the horse, as in the pig, the head fold contributes most. In a longitudinal section of the 21-days embryo the amnion (in contact at its origin with the allantoic diverticulum) is seen to arch upwards and forwards over the external opening of the spinal cord (fig. 33). In a transverse section on a level with the minute diverticulum (fig. 33, *cl.*) which seems to represent the cloacal chamber, the crescent-shaped amniotic cavity is seen to lie immediately above the lateral extensions of the allantoic diverticulum (fig. 50, *al.d.*). In the semi-diagrammatic drawing of the blastocyst (fig. 33) the amnion is represented as having a large cavity. As a matter of fact, there is very little amniotic fluid at the end of the third week, with the result that in transverse sections the amnion is seen to be only separated by a narrow space from the embryo (fig. 8).

The structure and relations of the amnion and the extent of its cavity will be gathered from figs. 36 to 53. It will be observed that in the horse, as in the sheep and pig, the amnion is directly continuous with the somatopleure, and that in some of the sections the mesodermic layer of the amnion is thrown into more or less distinct longitudinal ridges (fig. 45). It will be further observed that owing to the head projecting into the amnion as into a cowl or sac, the facial portion of the embryo is completely enveloped by the amnion (figs. 36 and 37).

In front of the vitelline veins (figs. 39 and 40) the amnion again assumes the form of a sac or hood, with the result that in the most anterior part of the flexed embryo the dorsal portion of the amniotic cavity is no longer separated from the ventral portion. It will be noticed that many of the sections figured suggest that the one and only object of the somatopleure is to provide a water-jacket over the back of the embryo.*

* With a water-jacket (the amnion) above and a water-bed (the yolk-sac) underneath, the embryo horse is as well protected from jars and pressure as a chick all but completely surrounded by amniotic fluid.

7. *The Allantois.*

In the rabbit the allantois is represented on the eighth day by a mass of mesoderm cells at the posterior end of the embryo. On the ninth day a diverticulum from the hind-gut extends into this cell mass and soon expands to form the allantoic vesicle. In the pig and sheep a similar diverticulum (which extends into a mass of mesoderm on or about the fifteenth day) gives rise at a comparatively early stage to a long compressed allantoic vesicle (text-fig. 15). If the allantois appeared relatively as soon in the horse as in the sheep, one would expect to find allantoic mesoderm investing the posterior end of MARTIN'S embryo (fig. 7), but, as already stated, there is no indication of an allantoic diverticulum at the middle of the third week.

In the 21-days embryo the caudal end was surrounded by a large fin-like expansion (fig. 11), mainly composed of mesoderm, into which extended a diverticulum from the hind end of the intestine (fig. 33). From the series of transverse sections of the 21-days horse embryo it was impossible to make out the exact form and relations of either the allantoic diverticulum, the heart, or the pharynx. These difficulties, together with the difficulty of accounting for the difference between BONNET'S and MARTIN'S so-called 21-days embryos and the still greater difference between MARTIN'S embryo and my 21-days embryo, ultimately led to a deadlock. Repeated attempts to obtain 14-days horse embryos failed; nevertheless, progress eventually again became possible. With the help of information gained from breeding experiments I was in course of time able to account for the differences between my 21-days embryo and the so-called 21-days embryos of BONNET and MARTIN, and at an opportune moment my colleague Professor ROBINSON was good enough to offer to have a model of my 21-days embryo constructed by the wax-plate method.

This model was in due time completed in the Anatomical Department of the University of Edinburgh by Mr A. GIBSON, M.B.*

In the description of the model of the 21-days embryo,† Professor ROBINSON, in the section dealing with the fœtal membranes, points out that "the allantoic diverticulum is a narrow-necked sac (fig. 33) so flattened dorso-ventrally that its cavity is reduced to the dimensions of a narrow cleft" (fig. 52). He further states (*a*) that the diverticulum expands as it passes caudally into the somatic mesoderm beneath the caudal part of the amnion fold, until it attains a width of 235μ; (*b*) that "the endodermal diverticulum is surrounded laterally, ventrally, and caudally with mesoderm (fig. 33), but dorsally it lies in relation with the ectoderm in the region of the caudal end of the amnion"; and (*c*) that "the allantoic blood-vessels consist of a number of dilated capillaries which form a coarse network on each side. Each lateral network

---

* Mr GIBSON, before leaving Edinburgh to occupy the Chair of Anatomy in the University of Winnipeg, was good enough to place at my disposal notes and drawings of the model he made under the supervision of Professor ROBINSON.

† "Description of a Reconstruction Model of a Horse Embryo Twenty-One Days Old," *Trans. Roy. Soc. Edin.* vol. li, by ARTHUR ROBINSON, M.D., Professor of Anatomy, University of Edinburgh.

receives two branches from the caudal end of the dorsal aorta of the same side, and it terminates at the caudal end of the allantoic mass in a terminal transverse sinus from which the umbilical veins take their origin" (text-fig. 7).

That the endodermic diverticulum from the hind-gut (fig. 33, *al.d.*) is allantoic and not simply a portion of the cloacal chamber is suggested by its narrow neck, its relation to the vascular and capillary plexus of blood-vessels in the allantoic mesoderm, and by its agreement with the diverticulum recognised as the rudiment of the allantois in the sheep and pig.

In the chick the allantois, a small diverticulum at the close of the second day, is flask-shaped and half the length of the embryo on the fifth day, while on the ninth day it almost completely surrounds both embryo and yolk-sac. In the sheep and pig (in which the fœtal appendages appear relatively sooner than in the horse) the allantois has the form of a small two-horned diverticulum on the sixteenth day and of a large double-horned sac on the eighteenth day (text-fig. 15). Nevertheless, the time of appearance of the allantois in the horse may be said to closely coincide with that in the chick, for, though small at the stage characterised by about twenty-two somites, it surrounds two-thirds of the embryo on the twenty-eighth day and nearly invests the entire yolk-sac on the sixty-third day, *i.e.* at the stage in the horse which may be said to correspond with the ninth day in the chick.

C. The Embryo at the End of the Third Week.

1. *Size and External Conformation.*

Martin's embryo (fig. 7), which represents the phase reached in the horse at or about the middle of the third week, had a total length of 3·25 mm., and the greatest breadth was 1·3 mm. The 21-days embryo, instead of lying, like Martin's, at right angles to the long axis of the blastocyst (fig. 4), occupied a position nearly parallel to its long axis (fig. 5). Measured round the curve this embryo had a length, when fresh, of 11 mm., *i.e.* it was more than three times the length of Martin's embryo. The length of the dorsal portion of the trunk seen in fig. 10 was 6·25 mm. The length of the head and the adjacent part of the trunk seen in fig. 11 was 3·25 mm., and the greatest breadth 2 mm.

If Martin's embryo represents the stage reached in the sheep at the fifteenth day of gestation, the 21-days horse embryo probably represents the stage reached in the sheep at the end of the eighteenth day. In the 21-days embryo horse one especially notices :—(1) the curving downwards and backwards of the head and front portion of the trunk round the inner ends of the vitelline veins (fig. 8); (2) the large pericardial sac lying in the space between the branchial region and the vitelline veins (fig. 8); (3) rudiments of the external gill slits and of the gill pouches, between the branchial arches (figs. 8 and 9); (4) the openings into the otic sacs (fig. 11); (5) the absence of a maxillary process from the mandibular arch; (6) the absence of nasal sacs and of limb rudiments; (7) the presence of a broad fin-like expansion at the caudal end of the embryo (fig. 11); (8) the external opening from the posterior end of the spinal cord (fig. 10); (9) the broad yolk-stalk connecting the embryo with the yolk-sac (fig. 33); and (10) the mouth (fig. 33) between the fronto-nasal process and the first pair of branchial arches (fig. 9).

2. *The Nervous System and Sense Organs.*

At the middle of the third week the nervous system is represented by a medullary groove, shallow at its origin immediately in front of the primitive groove, but deep in the region of the mesodermic somites (fig. 7). This groove communicates by means of a neurenteric canal with the rudiment of the hind-gut. Before the end of the third week the medullary groove is converted into the medullary or neural canal. Though at the end of the third week the neural canal still opens to the exterior at the caudal end (fig. 33), it is closed in front and the cerebral vesicles are already modified to form rudiments of the fore-, mid-, and hind-brain. The fore-brain, separated by a shallow groove externally and a faint ridge internally from the mid-brain, occupies the greater part of the obliquely directed fronto-nasal process (fig. 33). The transverse sections through this process show amongst other things the original cavity of the anterior cerebral vesicle and the primary optic vesicles (fig. 36). The mid-brain, small and indistinctly separated from the hind-brain, has a relatively large oval cavity. In fig. 37 the large cavity of the mid-brain is seen also, the notochord lying between the mid-brain and the diverticulum (Seessel's pouch), which for a time projects from the roof of the fore-gut immediately within the bucco-pharyngeal membrane.

The hind-brain (figs. 38 to 40), long and tubular, is neither distinctly separated from the mid-brain nor the spinal cord. After curving backwards and downwards the hind-brain forms a dorsal curve which probably marks the beginning of the spinal cord. The chief interest of the hind-brain at the end of the third week is its relation to the otic vesicles. These vesicles (fig. 38) lie close to the hind-brain, nearly on a level with the second branchial pouch.*

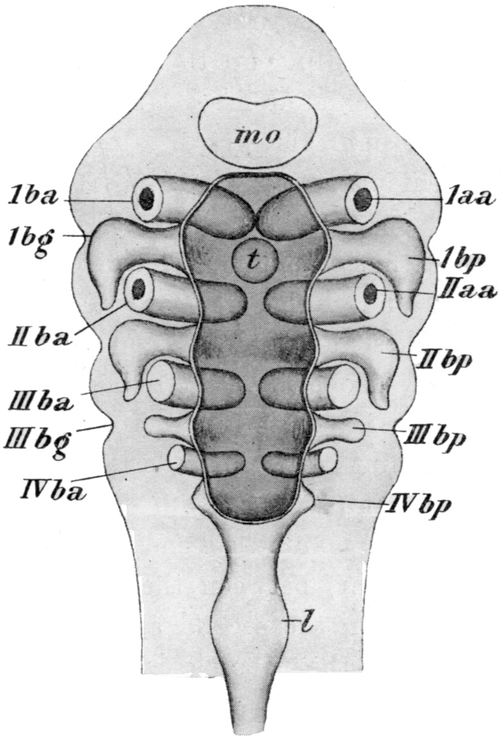
The spinal cord, in the form of an ectodermic tube with a distinct lumen, extends from the hind-brain to the caudal end of the embryo to end in a mass of cells with which the notochord and the cloacal diverticulum are intimately related. The relation of the spinal cord to the notochord and hind-gut, and the opening of its canal to the exterior, are indicated in fig. 33, while in fig. 52 a section of the cord immediately in front of the external opening is represented. From the figures of transverse sections of the embryo it will be observed that the spinal cord assumes a triangular form in the caudal region (figs. 50 to 52), but a more or less oval form throughout the greater part of the trunk (figs. 41 to 49).

---

* Owing to the slight obliquity of the section, only the external opening of one of the vesicles is seen in the figure.

3. *The Alimentary Canal.*

At the end of the third week the alimentary canal is closed in front and behind, but the middle portion is in free communication with the yolk-sac (fig. 33). An ectodermic involution in front of the fore-gut represents the mouth, while an endodermic outgrowth from the hind-gut represents the allantois (fig. 33). The mouth (stomodæum) is an irregular deep pit between the naso-frontal process and the first (mandibular) pair of branchial arches (fig. 8). The floor of the pit which separates the embryonic mouth from the pharynx consists of only two layers (fig. 33), a layer of ectoderm and a layer of endoderm, the latter intimately related to the notochord and the mandibular arches. Immediately behind this partition (the bucco-pharyngeal membrane) between the mouth and the pharynx a diverticulum projects upwards towards the notochord (fig. 37), which Professor Robinson regards as Seessel's pouch.



Text-fig. 6.—Diagram of branchial pouches and branchial arches. I.*b.p.* to IV.*b.p.*, the four branchial pouches; I.*b.a.* to IV.*b.a.*, the four branchial arches; I.*b.g.* and III.*b.g.*, the first and third branchial grooves; I.*a.a.*, first aortic arch; II.*a.a.*, second aortic arch; *mo.*, mouth pit; *l.*, possible lung rudiment; *t.*, tuberculum impar.

The Fore-gut.—At the end of the third week the pharyngeal part of the fore-gut is especially interesting because of the presence of branchial or gill pouches and their related branchial arches. In the chick there are during development four pairs of pouches and five pairs of arches, and for a time each of the three foremost pouches opens to the exterior and thus gives rise to imperfect gill clefts. In man at the end of the third week there are four pairs of branchial arches and four pairs of branchial pouches, but only the first two pairs of pouches and the first two pairs of arches (the mandibular and hyoid) are well developed, and even the large first pouch has never been found opening to the exterior.

In the 21-days horse the branchial pouches and arches generally agree with the corresponding structures in man. The first pouch (figs. 9 and 33 and text-fig. 6) projects outwards and upwards between the first (mandibular) and second (hyoid) arches until it is only separated from the first branchial groove (fig. 8 and text-fig. 6) by a thin partition (consisting of endoderm and ectoderm) which eventually takes part in forming the tympanic membrane. The second branchial pouch (fig. 9 and text-fig. 6), though smaller than the first, extends outwards and then upwards towards the otic sac (fig. 38), thus filling up the greater part of the space between the second (hyoid) and third branchial arches. On the way it approaches the second branchial groove (text-fig. 6); but this groove is neither as long nor as deep nor yet as intimately related to its pouch as the groove between the mandibular and hyoid arches.

The third branchial pouch (figs. 9 and 39), decidedly shorter and narrower than the second, extends outwards and slightly upwards towards the space between the third and fourth branchial arches (text-fig. 6) to end some distance from the shallow third indication of a branchial groove (fig. 8). In the horse, as in man, there is only a minute diverticulum (text-fig. 6) representing the fourth branchial pouch of the chick, and only at the most a faint indication of a branchial groove lying behind the rudimentary fourth branchial arch (text-fig. 6).

In the floor of the pharynx of man at the end of the third week there is a small mesial tubercle (tuberculum impar) between the mandibular and hyoid arches, a forked elevation (furcula) between the second and third arches, and furrows leading into the branchial pouches; the tubercle is the first indication of a tongue, while the furcula gives rise to the epiglottis. In the 21-days horse there is a small mesial prominence in the floor of the pharynx between the first and second branchial arches (text-fig. 6), and furrows leading to the branchial pouches, but no rudiment of either larynx or epiglottis. It may be mentioned that the fore-gut expands behind the fourth branchial pouch and gives off at each side a shallow diverticulum (text-fig. 6). These diverticula may represent rudiments of the respiratory system.

The Mid-gut and the Hind-gut.—The mid-gut, together with the anterior part of the hind-gut, communicates with the yolk-sac by means of a broad yolk-stalk (fig. 33 and text-fig. 12). In the region of the yolk-stalk the cavity of the hind-gut has the form of a narrow channel (fig. 50), but behind the yolk-stalk it assumes the form of a wide flattened tube (fig. 51), the end of which projects upwards into the mass of cells occupying the space between the notochord and the terminal portion of the spinal cord: this dorsal diverticulum (figs. 33 and 52) seems to represent the cloacal chamber. From the ventral aspect of the hind-gut the allantoic diverticulum (fig. 33) extends backwards and upwards into the thick layer of mesoblast surrounding the caudal end of the embryo.

4. *The Notochord.*

From MARTIN'S statements it may be assumed that the notochord in the horse agrees in its origin with that of the mole. As in the mole, the endoderm cells underlying the medullary canal in front of the primitive streak are enlarged and arranged first to form a groove and then a cord (the chorda dorsalis), the thickened posterior end of which may contain a canal continuous with the neurenteric canal. At the middle of the third week large cells, continuous with ectodermic and endodermic cells at the anterior end of the primitive streak, form a groove immediately under the medullary groove. At the end of the third week the place of this groove is occupied by the notochord. In the last fifteen sections through the tail end of the embryo there is no indication of a notochord, but in the sixteenth section (fig. 52) the notochord, nearly one-third the size of the spinal cord, is seen to the right of the middle line: like the spinal cord, it has a distinct central canal.* Though eccentric in position near its origin, the notochord soon occupies the middle line and lies immediately below the spinal cord. If the drawings of transverse sections through the trunk (figs. 43 to 52) are referred to, it will be observed that the notochord and its canal vary both in shape and size. The sections through the head and pharynx (figs. 37 to 40) show that the notochord varies in shape and size and is intimately connected with the endoderm of the anterior third of the roof of the pharynx (figs. 33 and 39) and with the hind-brain.

5. *Heart and Blood-vessels.*

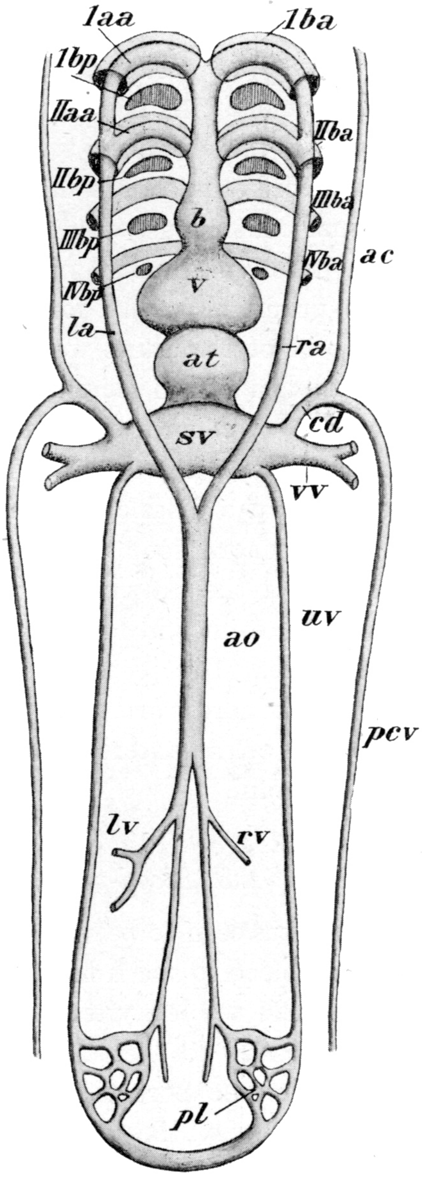
The embryo when first exposed was seen to be surrounded by a countless number of blood-vessels engaged in carrying blood to and from the yolk-sac (figs. 5, 34 and 35). Of these vessels the most obvious were the left vitelline artery, the sinus terminalis, and the large vitelline veins proceeding to the large bulging heart occupying the space between the pharynx and the middle portion of the trunk (fig. 33). The heart in the horse at the end of the third week, like the heart in a 3-days chick, consists of a sinus venosus, an atrium, a ventricle, and a truncus arteriosus.† In a 3-days chick, as in man about the end of the third week, there are five pairs of aortic arches, but in the 3-weeks horse only the first two pairs of arches (text-fig. 7) have made their appearance. There were neither rudiments of a heart nor yet of blood-vessels in MARTIN'S embryo; hence it may be assumed that in the horse during the second half of the third week there is (1) the vascularisation of the yolk-sac and the formation of the vitelline veins; (2) the fusion of these veins to form a single tubular

---

* The notochordal canal, unlike the neural canal, is closed, does not open into the amniotic cavity.

† Professor ROBINSON in his description of the model recognises (1) a sinus venosus, (2) a sinu-atrial canal, (3) a ventricle, (4) an atrio-ventricular canal, (5) a bulbus cordis, and (6) a truncus aorticus.

heart; (3) the elongation and folding of this heart so that it assumed the form of the letter "S"; and (4) its constriction into four more or less distinct chambers.



Text-fig. 7.—Diagram of heart and blood-vessels. *v.v.*, right vitelline vein; *s.v.*, sinus venosus; *at.*, atrium; *v.*, ventricle; *b.*, bulbus arteriosus; I.*a.a.*, first aortic arch; II.*a.a.*, second aortic arch; *l.a.*, left aorta; *r.a.*, right aorta; *a.o.*, dorsal aorta; *l.v.*, left vitelline artery; *r.v.*, right vitelline artery; *pl.*, plexus in allantoic mesoderm; *a.c.*, anterior cardinal vein; *p.c.v.*, posterior cardinal vein; *c.d.*, duct of Cuvier; *u.v.*, umbilical vein; I.*b.a.* to IV.*b.a.*, four branchial arches; I.*b.p.* to IV.*b.p.*, four branchial pouches.

The vitelline veins, which play so important a part during the earlier weeks, are seen in figs. 34, 35, and 43 approaching the embryo. Fig. 43 also shows the lateral portions of the sinus venosus in the pleuro-peritoneal canals. The intimate relation of the sinus to the fore-gut is made evident by fig. 42. The sinus venosus, though formed from the vitelline veins, receives blood from the allantois and the embryo as well as from the yolk-sac. The allantoic (umbilical) veins (text-fig. 7), one at each side, spring from a transverse sinus in the allantoic mesoderm at the caudal end of the embryo (text-fig. 7). The blood from the embryo reaches the sinus by the short Cuvierian veins formed by the junction of the anterior and posterior cardinals. Each anterior cardinal (primitive jugular) vein (text-fig. 7) begins near the mandibular arch; as it runs backwards it approaches the first two visceral pouches and the otic vesicle. Each posterior cardinal vein (text-fig. 7) runs forwards from the caudal end of the embryo; on the way it is intimately related to either the pronephric duct or the Wolffian body. The blood flows from the sinus (text-fig. 7) by a wide opening into the atrium; the atrium, separated by a constriction from the sinus, opens by a valved aperture into the ventricle—portions of the atrium and ventricle are seen in figs. 38 and 40. While the sinus and atrium occupy the uppermost and left portion of the space between the pharynx and the middle curved portion of the trunk, the ventricle occupies the middle and right portion and lies in contact with the floor of the fore-gut and the yolk-stalk (fig. 33). The truncus (bulbus) arteriosus springs from that part of the ventricle lying in contact with the floor of the pharynx, and runs forwards in contact with the atrium (fig. 39) to reach the middle line and give off two pairs of aortic arches (text-fig. 7), a pair to the mandibular arches and a pair to the hyoid arches.* As text-fig. 7 indicates, the first aortic arch on the left side proceeds backwards in front of the first branchial pouch to meet and unite with the smaller second aortic arch and thus form the left aorta. In a like manner the first aortic arch on the right side unites with the second arch to form the right aorta. The two dorsal aortæ as they proceed backwards lie one at each side of the notochord (fig. 42), and are also more or less intimately related to the pharynx and gill pouches, the spinal cord and otic sacs, the pleuro-peritoneal sinus and the anterior cardinal veins (figs. 38 to 41). On nearing the sinus venosus the two aortæ approach each other and completely fuse, but they again separate when a point about 3 mm. from the caudal end is reached (text-fig. 7).

As the two aortæ proceed backwards through the posterior third of the trunk they are intimately related to the notochord and the mesodermic somites. On reaching the posterior border of the yolk-stalk the distance between the aortæ (text-fig. 7) becomes greater, and it continues to increase until they end in the allantoic mesoderm. As the aortæ proceed backwards the left gives off the large left vitelline artery (text-fig. 7), which eventually bifurcates to form the sinus terminalis (fig. 34); the right gives off the small right vitelline artery (text-fig. 7). Before ending blindly each aorta gives off branches to the hind-gut; some of these branches give rise to a plexus with which the allantoic (umbilical) veins communicate (text-fig. 7).

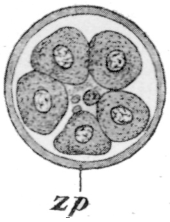
---

* In only having two pairs of aortic arches the 21-days horse agrees with a human embryo of about 15 days figured by His. In a figure by His of a human embryo of about 3 weeks all five aortic arches are present. If the age of these human embryos is approximately accurate, the aortic arches appear later in the horse than in man.

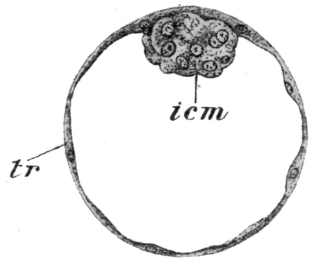
D. Early Developmental Stages in the Horse and Sheep.*

If horses are descended from ancestors allied to Hyracotherium of the London Clay, ample time has elapsed to admit of prenatal as well as postnatal variation in directions different from those followed by even-toed Ungulates. It is hence probable that almost from the outset horse embryos will differ from sheep embryos at a like stage in the life-history.

The Ovum.—In the Eutheria the ova, though always small, vary considerably; they may be under ·1 mm. or over ·3 mm. in diameter. For example, in deer the ovum may only measure ·07 mm.; on the other hand, the human ovum varies from ·22 to ·32 mm. In sheep the ovum, exclusive of the zona pellucida, measures ·15 mm.; in the horse it probably never exceeds ·18 mm. In the ripe ovum of the sheep, figured by Assheton, there is no indication of a perivitelline space; but even in the unripe ovum shown in fig. 2 from a 6-mm. ovarian follicle of a mare there is a distinct space between the vitellus and the zona pellucida.



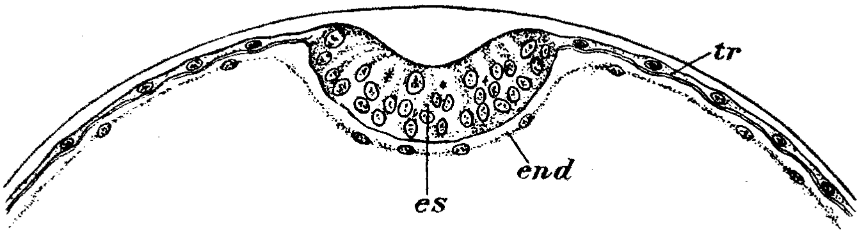
8.



9.

Text-fig. 8.—Segmenting ovum of sheep with distinct zona pellucida (*z.p.*).

Text-fig. 9.—Blastodermic vesicle of sheep. *tr.*, trophoblast; *i.c.m.*, inner cell mass. Note absence of zona pellucida. (After Assheton.)



Text-fig. 10.—Ovum of deer. The inner cell-mass (text-fig. 9) has differentiated to form (1) the embryonic shield (*e.s.*) continuous with trophoblast (*tr.*), and (2) the endoderm (*end.*). At the corresponding stage in the horse there is still a zona pellucida—the line external to the shield and trophoblast represents the zona in the horse. (After Keibel.)

In the sheep the zona (text-fig. 8, *z.p.*), attenuated at the end of the first week, ruptures and disappears about the ninth day of gestation. As the amnion is only completed at the end of the second or beginning of the third week, it follows that

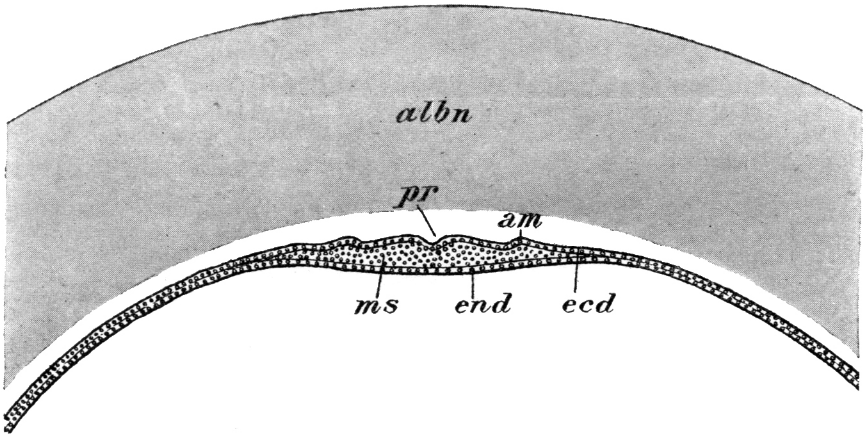
---

* For information about the development of the sheep I am mainly indebted to papers by Assheton and Bonnet, more especially to "The Morphology of the Ungulate Placenta," Assheton, *Phil. Trans. Roy. Soc.*, 1906; "The Segmentation of the Ovum of the Sheep," Assheton, *Quart. Jour. Med. Sci.*, 1898; "Beiträge zur Embryologie der Wiederkäuer," R. Bonnet, *Archiv f. Anat. u. Physiol.*, *Anat. Abth.*, 1889.

for some days sheep embryos come into intimate relation with the lining of the uterus.

In the horse the zona pellucida, according to Bonnet, has a thickness of 4μ when the blastocyst measures 13 mm. (fig. 3), *i.e.* at the end of the second week. Further, during the first half of the third week the blastocyst acquires an albumen coat, which at the middle of the third week has a thickness of 3 or 4 mm. (fig. 4, *alb.*).

In the sheep as segmentation proceeds it soon becomes evident that certain cells will give rise to the trophoblast (text-fig. 9, *tr.*), and that others will form the inner cell-mass (text-fig. 9, *i.c.m.*) which is eventually differentiated into endoderm and embryonic shield. In text-fig. 10 the embryonic shield (*e.s.*), trophoblast (*tr.*), and endoderm (*end.*) of a deer are represented. Like differentiations and phases in all probability occur in the Equidæ.



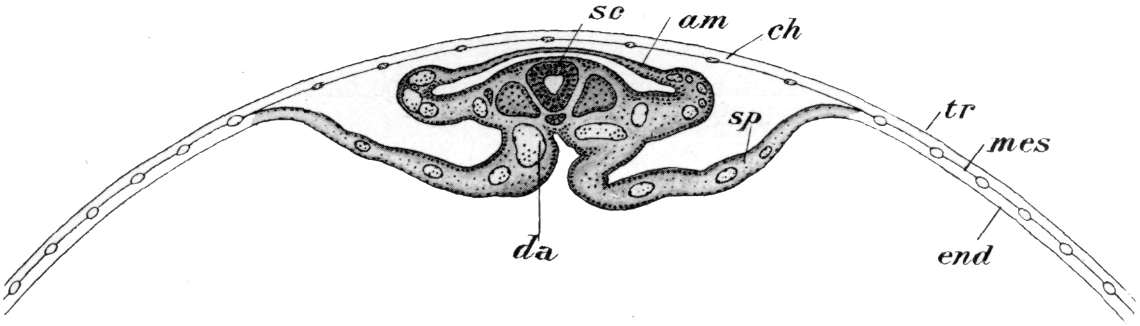
Text-fig. 11.—Diagram to indicate the stage reached in the horse about the middle of the third week. *albn.*, thick (3–4 mm.) albumen coat; *am.*, amnion fold; *ecd.*, ectoderm; *end.*, endoderm; *ms.*, mesoderm; *pr.*, primitive groove. Albumen layer is lost before end of third week.

The Blastocyst.—In the horse the blastocyst, nearly spherical at the end of the second week (fig. 3), is egg-shaped at the middle of the third week (fig. 4) and pear-shaped at the end of the third week (fig. 5). At this stage it has a length of 50 mm., and occupies the lower part of one of the uterine horns (fig. 15).

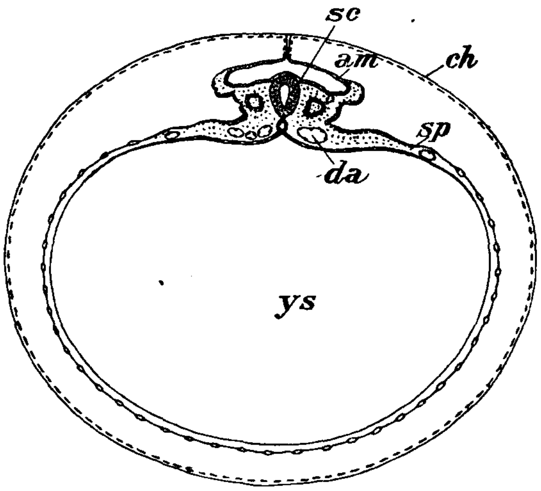
In the sheep soon after the rupture of the zona pellucida the blastocyst loses its spherical outline (text-fig. 13) and soon elongates into a narrow tube which occupies both uterine horns. This tubular blastocyst may have a length of 240 mm. at the end of the twelfth day, and measure 400 mm. (nearly 16 inches) at the end of the third week (text-fig. 16).

The Trophoblast.—In the horse up to the middle of the third week the trophoblast, except in the vicinity of the embryo (text-fig. 11), is in contact with the endoderm, but by the end of the third week, over and immediately beyond the embryo, it is in contact with non-vascular somatic mesoderm (text-fig. 12). Beyond the exocœlom up to the sinus terminalis the trophoblast forms the outer wall of a space (fig. 28) occupied by the unsplit highly vascular mesoderm; beyond the sinus it is in contact with the yolk-sac endoderm (fig. 34).

In the sheep, up to the appearance of the amnion folds, the trophoblast, except under the embryonic shield, is in contact with a thin imperfect layer of endoderm.



Text-fig. 12.—Drawing to indicate the stage reached in the horse at the end of the third week, after the albumen coat as well as the zona has disappeared. *am.*, amnion, now complete; *ch.*, chorion, made up of a layer of trophoblast and a layer of somatic mesoderm; *s.c.*, spinal cord; *d.a.*, dorsal aorta; *sp.*, splanchnopleure; *tr.*, trophoblast; *mes.*, unsplit vascularised mesoderm; *end.*, endoderm.



Text-fig. 13.—Drawing to indicate the stage reached in the sheep about the middle of the third week. In the 21-days horse the mesoderm is only split in the vicinity of the embryo. In the sheep at a corresponding stage the splitting of the mesoderm is complete; the inner (splanchnic) layer has united with the endoderm to form a free yolk-sac vesicle (*y.s.*), the outer with the trophoblast to form the chorion (*ch.*). *am.*, amnion; *s.c.*, spinal cord; *d.a.*, dorsal aorta; *sp.*, splanchnopleure. (After Bonnet.)

As the splitting of the mesoderm proceeds, the exocœlom extends in all directions, with the result that the trophoblast is completely separated from the endoderm and provided with a lining of non-vascular mesoderm (text-fig. 13).

In the horse the trophoblast at the end of the second week seems to consist of simple polygonal nucleated cells. At the middle of the third week the cells are cubical, but by the end of the third week they are long enough to rank as columnar cells. Up to the sinus terminalis there are simple columnar cells (fig. 28); beyond the sinus, in addition to typical columnar cells, there are very tall columnar cells forming the larger trophoblastic discs (fig. 29) and cells with sac-like processes (fig. 30), some of which surround the discs, while others line the shallow areas scattered over the distal end of the blastocyst. Up to the end of the third week the trophoblast in the horse consists of a single layer of cells, which are either quite free or loosely connected with the uterine epithelium.

In the sheep the trophoblast at the outset consists of a single layer of simple polygonal cells; by the tenth day the cells are wedge-shaped, and by the fourteenth cubical. By the eighteenth day the cells which roughly correspond to the cotyledonary burrs projecting from the lining of the uterus, have assumed a columnar form.* These columnar cells develop minute ridges which by fitting into slight grooves in the cells of the burrs may assist in fixing the blastocyst.

The Uterus.—In the sheep, when the ovum reaches the uterus "the mucous membrane is that typical of an anœstrous period"; but as development proceeds there is a general increase in the complexity of the glands, with increased secretion, an invasion of the epithelium by leucocytes, and towards the close of the third week a thickening of the stroma. These changes are accompanied by a destruction of the uterine epithelium over the cotyledonary areas by means of binucleate trophoblastic cells insinuating themselves between the cells of the uterine epithelium to form a layer between the epithelium and the sublying stroma. The nourishment for the embryo, which mainly consists of "uterine milk," is taken up by the cells of the trophoblast lying between the cotyledonary burrs.

In the mare, even at the end of the third week of gestation the mucous membrane is still that typical of the anœstrous period. The glands at the end of the third week may be more active, and leucocytes may be more numerous in the uterine cavity, but of this there is no evidence, neither is there any indication of erosion of the uterine epithelium or of changes in the sublying stroma.†

Martin states that the mucous membrane of the uterus from which his embryo was obtained was congested and spotted. There was neither congestion nor spotting of the lining of the uterus from which I removed my 21-days embryo. In all probability, in the Equidæ at the end of the third week the whole of the trophoblast takes part in procuring nourishment for the embryo.

Amnion.—In the sheep the lateral folds are conspicuous on the fourteenth day, and extend well over the embryo on the following day. By the end of the sixteenth day the amnion is complete and connected by a cord to the inner surface of the chorion (text-figs. 13 and 14).

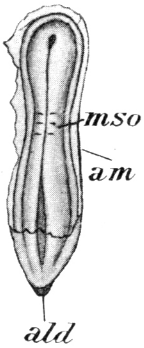
Though in the sheep the amnion is well advanced on the fifteenth day, at the stage characterised by two pairs of mesodermic somites (text-fig. 14), there is no indica-

---

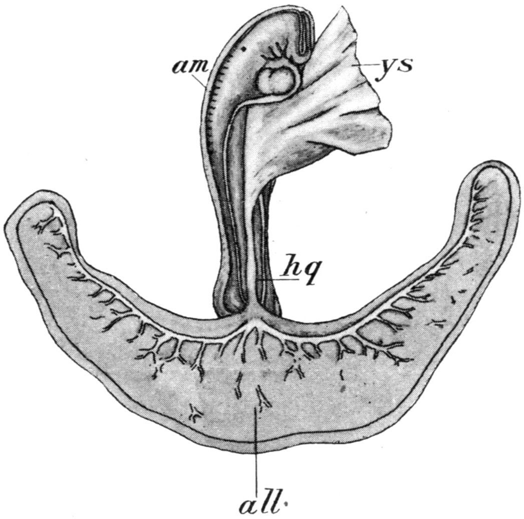
* Opposite the cotyledonary burrs Assheton says the trophoblast perhaps consists of two layers.

† The pig closely agrees with sheep during the earlier weeks of gestation. The blastocyst begins to elongate on the eleventh day. As it increases in length it is thrown into transverse folds, with the result that, though apparently of no great length, it may measure when extended over 1000 mm. at the middle of the third week. The uterine epithelium begins to degenerate on the fourteenth day, and is reduced to a thin layer by the eighteenth day.

tion of the amnion in the horse until the middle of the third week. Even when four pairs of somites are present the amnion in the horse is only represented by very slight lateral ridges (text-fig. 1), but by the twenty-first day the amnion is complete.



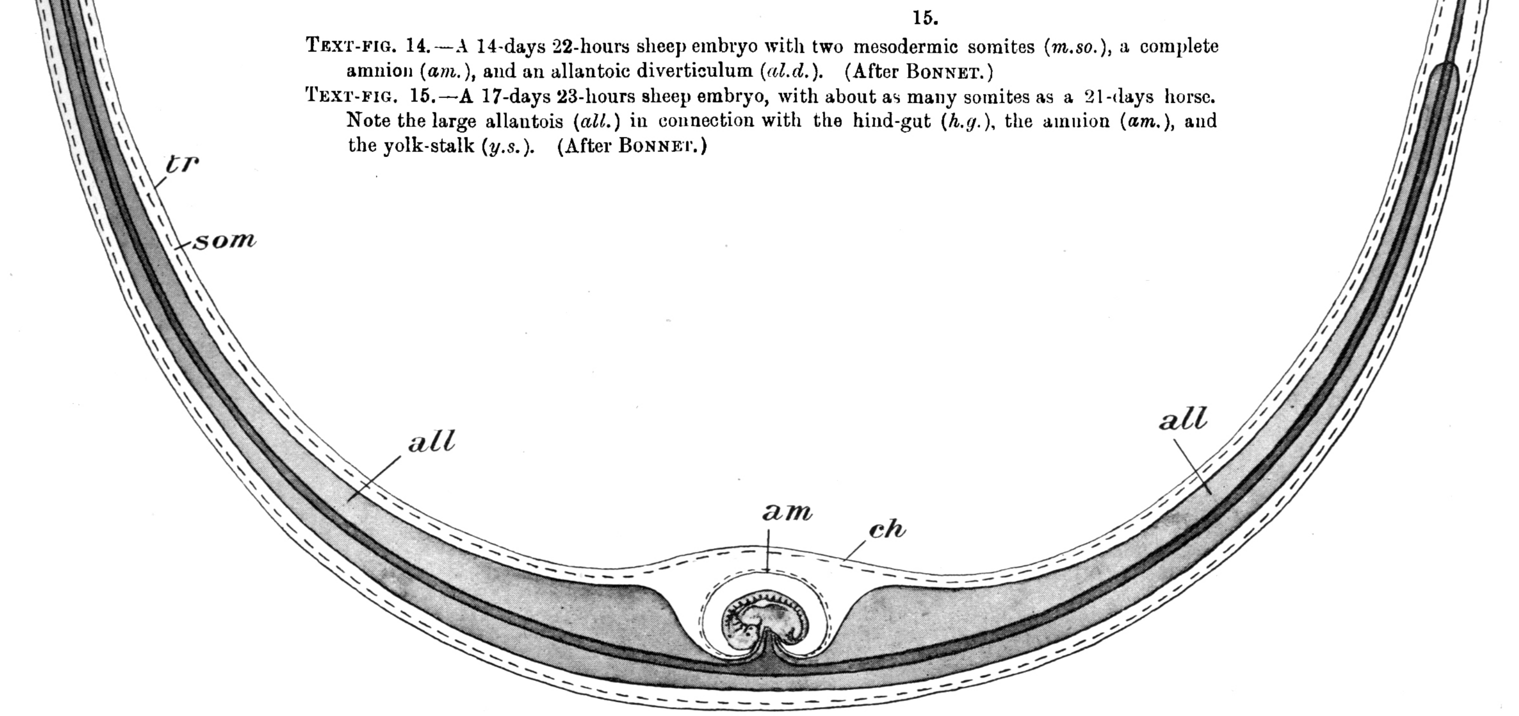
14.



15.

TEXT-FIG. 14.—A 14-days 22-hours sheep embryo with two mesodermic somites (*m.so.*), a complete amnion (*am.*), and an allantoic diverticulum (*al.d.*). (After BONNET.)

TEXT-FIG. 15.—A 17-days 23-hours sheep embryo, with about as many somites as a 21-days horse. Note the large allantois (*all.*) in connection with the hind-gut (*h.g.*), the amnion (*am.*), and the yolk-stalk (*y.s.*). (After BONNET.)



TEXT-FIG. 16.—Diagram of a 21-days sheep embryo and its membranes. Compare with diagram of a 21-days horse embryo (fig. 34). A 21-days sheep is at about the same stage of development as a 28-days horse. *am.*, amnion ; *ch.*, chorion consisting of a trophoblast (*tr.*), and somatic mesoderm (*so.m.*) ; *y.s.*, yolk-sac ; *all.*, allantois.

The early rupture of the zona pellucida and the absence of an albumen layer may perhaps account for the amnion appearing at an earlier phase in the sheep than in the horse.

Yolk-sac and Mesoderm.—In the sheep the splitting of the mesoderm already begun at the end of the twelfth or the beginning of the thirteenth day is completed at or about the end of the sixteenth day. When the yolk-sac endoderm is completely invested by splanchnic mesoderm a typical yolk-sac (*i.e.* a free vesicle separated by a distinct space from the chorion) is the result (text-fig. 13). As the blastocyst assumes a tubular form the yolk-sac elongates: by the twenty-first day it may reach a length of over 350 mm. (14 inches) (text-fig. 16). As the mesoderm splits the splanchnic layer undergoes vascularisation, *without, however, a sinus terminalis being established.*

In the horse the splitting of the mesoderm begins on the seventeenth or eighteenth day, but proceeds so slowly that it has only extended a short distance beyond the embryo on the twenty-first day (text-fig. 12). As the unsplit mesoderm extends between the trophoblast and endoderm it undergoes vascularisation, and the left vitelline artery bifurcates at an early stage to form a sinus terminalis (fig. 34).* As the splitting of the mesoderm is never complete in the horse, the most distal part of the yolk-sac endoderm retains throughout fœtal life a slight connection with the trophoblast. This implies that the yolk-sac in the horse is never, as in the sheep, a free vesicle.

In the horse at the end of the third week tubercles project into the cavity of the yolk-sac (fig. 32), each endodermic tubercle being related to a trophoblastic disc. There are apparently neither trophoblastic discs nor endodermic tubercles in the sheep.

Allantois.—In the sheep there is a rudiment of the allantois at the end of the second week (text-fig. 14); a like stage is not reached in the horse until the end of the third week (fig. 33). On the sixteenth day the allantois in the sheep is a two-horned sac 2·7 mm. in width; on the seventeenth day it measures 16 mm. (text-fig. 15); the following day the width is nearly double; and on the twenty-first day, as text-fig. 16 shows, it has a length of nearly 300 mm. (nearly 12 inches).

In the horse at the end of the third week the allantois is still a minute diverticulum 235μ in width; in the sheep at a corresponding stage of development the width between the horns is over 30 mm.

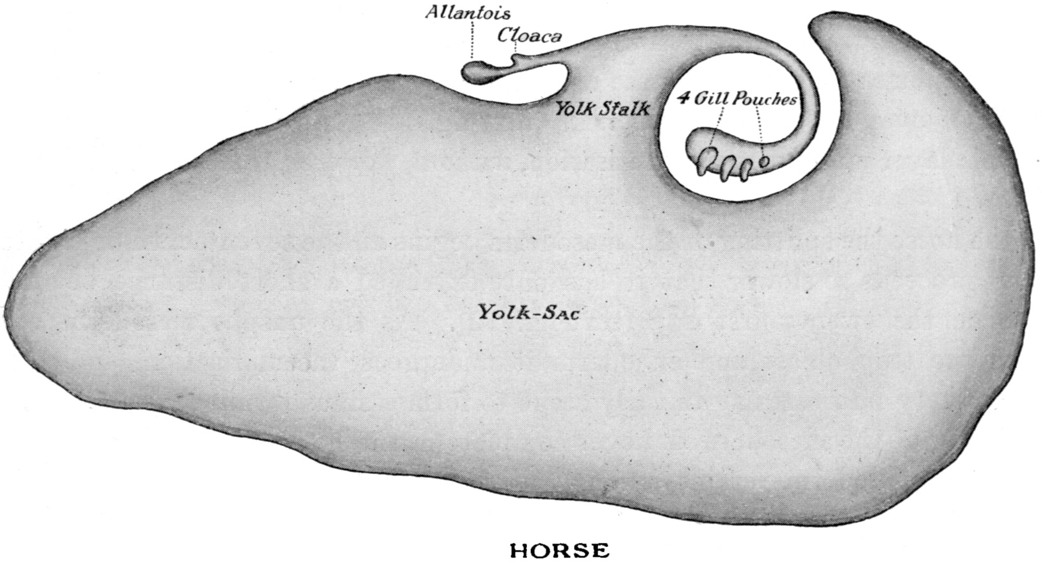
The Embryo.—The youngest sheep embryo figured by Bonnet was 3 mm. in length (text-fig. 14). It represents the phase reached 14 days and 22 hours after service, and is characterised by two pairs of mesodermic somites. In Bonnet's figure (text-fig. 14) the mesodermic somites, primitive streak, neural groove, allantoic rudiment, and parts of the amnion are represented.

The horse embryo figured by Martin (fig. 7) differs but little from Bonnet's 14-days 22-hours sheep embryo (text-fig. 14). Martin's embryo, which represents the stage reached at the middle of the third week, measured 3·25 mm. in length and had four mesodermic somites. Though in this embryo the primitive and neural grooves

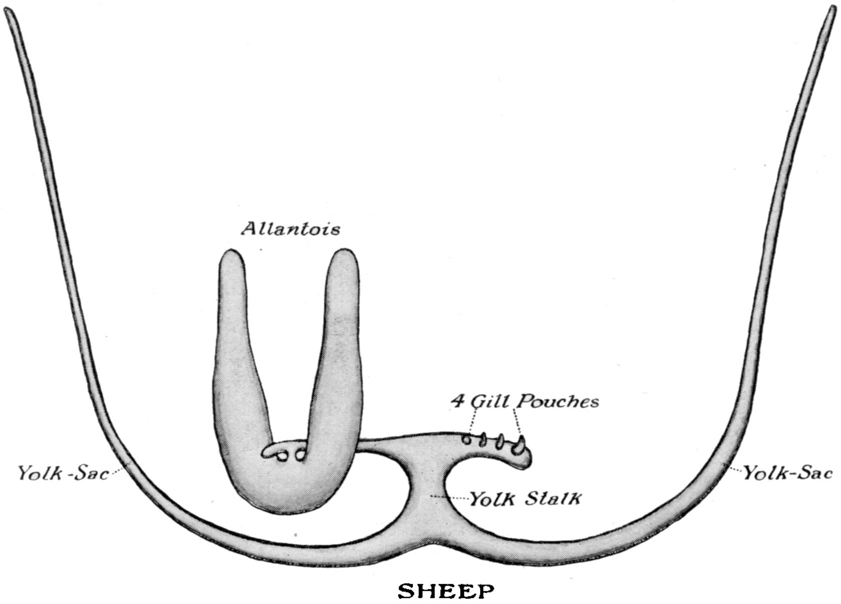
---

* In the pig, in which the yolk-sac is a free vesicle as in the sheep, there is a temporary sinus terminalis followed by general vascularisation; hence in a sense the arrangement of the yolk-sac vessels in the pig is intermediate between that of the sheep and that of the horse.

are distinct, there is no rudiment of an allantois, and the amnion is represented by two hardly perceptible lateral ridges; as the mesoderm is not split under these ridges, one is perhaps hardly justified in regarding them as rudiments of the amnion. Martin and Bonnet believed this 3·25 mm. embryo was 21 days old, but I have given reasons for regarding it as representing the stage reached on the seventeenth or eighteenth day of gestation.



Text-fig. 17.—Diagram of the endoderm of a 21-days horse embryo. Note the gill pouches in connection with the fore-gut, the wide yolk-stalk leading into the pear-shaped yolk-sac, the cloaca, and the minute allantoic diverticulum projecting from the hind-gut.

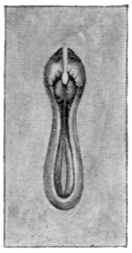


Text-fig. 18.—Diagram of the endoderm of a sheep at about the same stage of development as a 21-days horse. Note the large crescent-shaped allantois and the long tubular yolk-sac which extends into both uterine horns.

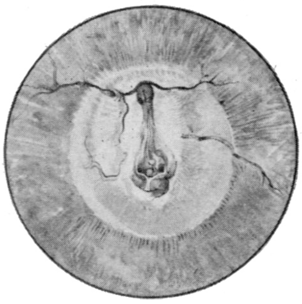
During the fifteenth and sixteenth days marked progress is made by sheep embryos. The 16-days 22-hours embryo figured by BONNET has ten mesodermic somites, a long deep neural groove, rudiments of the fore-, mid-, and hind-gut, and two branchial arches; the primitive streak is still distinct, the amnion is complete, and there is a crescent-shaped allantois.

In 1840 HAUSMANN figured a 19-days horse embryo with ten or eleven mesodermic somites. While generally agreeing with BONNET'S 16-days 22-hours sheep embryo, HAUSMANN'S 19-days horse embryo (text-fig. 19) has apparently no rudiment of an allantois, and very little progress has been made in the development of either the nervous system, gut, or branchial arches.*

In a 17-days sheep embryo there are over twenty somites, the greater part of the neural groove is converted into a canal, and there are indications of otic as well as of cerebral vesicles; the fore- and hind-gut have assumed a definite form, and the allantois has a width of 16 mm.; further, there are branchial arches, a three-chambered heart, two aortæ, and a rudiment of the notochord (text-fig. 15).


19.


20.


21.

TEXT-FIG. 19.—HAUSMANN'S figure of a 19-days 45-minutes horse embryo.
TEXT-FIG. 20.— ,, ,, 19-days 7-hours ,,
TEXT-FIG. 21.— ,, ,, 19-days 20-hours ,,

In a sheep embryo at the beginning of the nineteenth day there are more than twenty mesodermic somites, and the development of the nervous system has advanced so far that the three regions of the brain are easily recognised; there are distinct optic as well as otic vesicles, a three-chambered heart, a maxillary process from the first visceral arch, and a large allantois in connection with a well-developed hind-gut.

The 21-days horse embryo is in some respects intermediate between a 17-days and a 19-days sheep embryo, but it obviously differs in shape, in the less-developed condition of the hind-gut, and especially in the blastocyst, yolk-sac, allantois, and the structure of the trophoblast.

For some years it has been assumed that the rate of development in the horse varies greatly during the first three weeks. This assumption is the result of BONNET stating in 1891 that a 21-days blastocyst varies from 13 mm. to 35 mm.† Now

---

* HAUSMANN'S 19-days horse embryo lends strong support to the view that MARTIN'S so-called 21-days embryo represents the stage reached at the middle of the third week.

† "Eier vom 21-Tage schwanken zwischen 1·3 cm.–3·5 cm. Länge," BONNET, *Grundriss des Entwickelungsgeschichte*, 1891, p. 240.

that a 21-days blastocyst 50 mm. in length has been described, presumably BONNET would state that in the horse the blastocyst at the end of the third week varies from 13 mm. to 50 mm.

By studying the œstrous period in the mare and the condition of the ovaries before and after service, I arrived at the conclusion that the difference between my 50-mm. blastocyst and BONNET'S 13-mm. blastocyst was not due to arrested development but to a difference in age—a conclusion supported by drawings of horse embryos (text-figs. 19–21) published in 1840 by HAUSMANN.

Further, it has been taken for granted that during the earlier weeks the horse closely agrees in its development with other typical Ungulates. It is conceivable that up to the end of segmentation, perhaps up to the formation of the embryonic shield, there may be almost complete agreement between even-toed and odd-toed Ungulates; but by comparing young horse embryos with sheep embryos at a corresponding stage, evidence has been obtained in support of the view that from the time the mesodermic somites make their appearance the two main groups of the modern hoofed mammals follow different routes—the sheep, pig, and other even-toed Ungulates especially differing at the end of the third week from the horse in the form of the blastocyst, yolk-sac, and allantois, and in the structure and relations of the trophoblast.

E. SUMMARY.

During the last fifty years so much progress has been made in clearing up the pedigree of the horse that we are now familiar with every chapter in the ancestral history between the 14-inch four-toed *Hyracotherium* of the London Clay and the 60-inch *Equus sivalensis* of the Indian Pliocene.

But while our knowledge of the remote ancestors of the Equidæ is well-nigh complete, we still know surprisingly little about the more interesting chapters of the life-history of the horses now living under domestication. We are acquainted with the ancestral history because COPE, MARCH, OSBORN, SCOTT, and other American palæontologists made a systematic and exhaustive study of "fossil" horses; we know little about the more interesting phases of the life-history of the living Equidæ because embryologists have not yet succeeded in working out the development of either horses, asses, or zebras.

In America several expeditions have been sent out in search of material for the study of extinct horses, but until recently only one serious attempt seems to have been made to obtain material for a systematic study of the development of recent horses.

Unfortunately, this attempt (made in Hanover by HAUSMANN some eighty years ago) yielded meagre results. Professor BONNET of Giessen, famous for his memoirs on the development of domestic animals, when referring in 1889 to previous work on the fœtal membranes of the horse, pointed out that about the first stages of development we have nothing to depend on except the statements and drawings of HAUSMANN, who had a stud including fifty-two mares at his disposal for his researches. These statements, which relate to the development at the end of the third week, owing to the mistaken views of their author about the ovum and its membranes, BONNET points out, have caused more confusion than enlightenment, while the drawings which illustrate HAUSMANN'S contributions are almost incomprehensible and worthless.

In the home of the thoroughbred racehorse no systematic attempt has been made by embryologists to work out the life-history of the Equidæ, and sporadic attempts to elucidate special points in the early history have hitherto been well-nigh as fruitless in England as the ambitious attempt made in the 'thirties of last century in Hanover.

From first to last the difficulty in England has been lack of material. This was especially true of an attempt made by HUXLEY to find rudiments of the second and fourth digits. When preparing the lecture on fossil horses delivered in 1876 in New York, it occurred to HUXLEY that strong evidence in support of the fact of evolution would be forthcoming if it were proved that the modern horse passes through a *Hipparion* or 3-toed stage during development.

Armed with all the available material Sir WILLIAM FLOWER could place at his disposal, HUXLEY proceeded to search for rudiments of the phalanges of the second and fourth digits. To HUXLEY'S great disappointment the search was in vain. HUXLEY failed, not because the 3-toed stage is absent in the recent horse, but because it appears, comes and goes, much earlier than he expected. Up to the end of the Miocene period all horses had throughout life three complete toes both in front and behind. For this reason it seems to have been assumed that the 3-toed phase, if it actually occurred in the modern horse, would persist for a considerable time and be preceded by a 5-toed phase. As a matter of fact, as I shall show in a subsequent paper, the abbreviation in the development in the Equidæ is so marked that the 3-toed stage is reached during the fifth week of gestation and practically comes to an end during the seventh week.

It seems to have been taken for granted that during the earlier weeks horse embryos develop along the same lines as other Ungulates. I find, however, that from the second week onwards the horse follows a route different from that of all the other mammals hitherto studied.

Since 1891 it has been assumed that during the earlier weeks the development of the horse is retarded in some cases, accelerated in others. In the roe deer the development is arrested as soon as the cleavage stage is reached, with the result that little or no progress is made for several months. There is, however, no evidence that at any stage the development is arrested in the horse. The belief that in the horse progress is sometimes retarded is based on a statement by BONNET, who in 1891 asserted without any reservation that the blastocyst at the end of the third week varies in length from 13 mm. to 35 mm., *i.e.* from half an inch to over 1·5 inches. BONNET arrived at the conclusion that a 21-days blastocyst may vary from 13 mm. to 35 mm. because he received in 1889 a 13-mm. horse blastocyst taken from a mare twenty-one days after the first service, while in 1890 PAUL MARTIN of Zurich obtained a 35-mm. blastocyst also taken twenty-one days after service. I find that at the end of the third week of gestation, *i.e.* twenty-one days after service, the blastocyst measures 50 mm.; that BONNET'S so-called 21-days embryo probably represents the stage reached at the end of the second week; and that MARTIN'S so-called 21-days embryo represents the stage reached at the middle of the third week of gestation. The age of BONNET'S and MARTIN'S embryos having been dealt with, attention is next directed to the condition of the ovaries, oviducts, and uterus at the end of the third week, and to the position of the 50-mm. (21-days) blastocyst in the uterine horn (fig. 14). The trophoblast at the end of the third week is unusually interesting; in several essential points it differs from that of the sheep and pig and other Ungulates hitherto examined. Up to the sinus terminalis it consists of typical columnar cells (fig. 28); beyond the sinus there are (1) groups of very tall columnar cells arranged to form trophoblastic discs (fig. 29) which probably help to fix the blastocyst to the lining of the uterus, (2) groups of columnar cells in the act of elongating to form additional discs (fig. 30), and (3) columnar cells with sac-like processes (fig. 30)—these phagocytic cells occur around the margins of the discs and in the grooves surrounding the discs, but especially in shallow depressions beyond the sinus terminalis which probably lie opposite the openings of the uterine glands and are concerned in taking up the more solid particles of the "uterine milk."

In the region of the embryo the trophoblast by uniting with the somatic layer of mesoderm forms the outer wall of the exocœlom (text-fig. 12). From the exocœlom to a short distance beyond the sinus terminalis the trophoblast forms the outer wall of a narrow space occupied by highly vascular but still unsplit mesoderm (fig. 28). The distal portion of the trophoblast is intimately related to the yolk-sac endoderm (fig. 34). Sections of the blastocyst afford no evidence that solid particles penetrate the cells of that part of the trophoblast extending between the embryo and the sinus terminalis, but they afford abundant evidence that granules of various sizes enter both the tall columnar cells of the discs and the cells with sac-like processes which form a considerable part of the trophoblast beyond the sinus terminalis (figs. 29 and 30). The sections further demonstrate the presence of a continuous sheet of coagulum between the trophoblast and the yolk-sac endoderm (fig. 30). Between the discs this coagulum (which probably consists of nutritive material derived from the "uterine milk") resembles a basement membrane, but under the discs it reaches a considerable thickness and is continuous with similar coagulated material entering into the formation of yolk-sac tubercles (fig. 32).

In the vicinity of the embryo the yolk-sac consists of endoderm and a layer of splanchnic mesoderm, but from the exocœlom to the sinus terminalis it is only represented by endoderm (text-fig. 12). Beyond the sinus the yolk-sac endoderm is intimately connected with the trophoblast (fig. 34). Except opposite the discs the yolk-sac endoderm consists of a single layer of cells; opposite the discs, where it takes part in forming the yolk-sac tubercles, the endoderm may consist of two layers of cells (fig. 32).

At the middle of the third week the splitting of the mesoderm is only beginning, and the amnion is only represented by indistinct lateral ridges (text-fig. 11). At the end of the third week the amnion is complete and the mesoderm is split so as to form a cœlom and a small exocœlom (text-fig. 12). The outer (somatic) layer of mesoderm together with a layer of ectoderm forms the amnion; further, by uniting with the trophoblast the somatic mesoderm gives rise to the chorion of the embryonic area (text-fig. 12). The inner (splanchnic) layer of mesoderm by uniting with endoderm forms the yolk-stalk and the upper free and only complete part of the yolk-sac.

The unsplit mesoderm (text-fig. 12) which extends from the exocœlom to the sinus terminalis is highly vascular; it receives blood from the embryo by the vitelline arteries and returns it to the embryo by the vitelline veins (fig. 34).

There is no indication of an allantoic diverticulum at the middle of the third week, but at the end of the third week there is a considerable mass of vascularised allantoic mesoderm at the caudal end of the embryo, into which extends from the hind-gut a small allantoic diverticulum (fig. 33 and text-fig. 17).

Martin's embryo, the age of which is almost certainly 17 or 18 days, has four pairs of mesodermic somites (fig. 7). Hausmann's 19-days embryo (text-fig. 19) has probably ten somites, but the 21-days embryo has over twenty somites (figs. 10 and 11). Martin's embryo in shape resembles the sole of a shoe; my 21-days embryo is hook-shaped (figs. 7 and 8). That this strongly bent embryo is older than Martin's so-called 21-days embryo is indicated by its size, by the phase reached in the development of the nervous, alimentary, and circulatory systems, and especially by the complete amnion and the allantoic diverticulum. The nervous system is represented by a fore-brain with optic vesicles, by an indistinct mid-brain, by a hind-brain adjacent to which are otic vesicles, and by a spinal cord completely closed except at the caudal end, where it opens by a neuropore into the cavity of the amnion (fig. 33).

The alimentary system consists (1) of a fore-gut from which branchial pouches project outwards towards shallow branchial furrows (text-fig. 6) lying between branchial arches, (2) of a mid-gut which communicates by a yolk-stalk with a large yolk-sac (fig. 34), and (3) of a short hind-gut from which a cloacal rudiment projects upwards and an allantoic diverticulum extends backwards (fig. 33 and text-fig. 17).

The circulatory system is represented by a sinus venosus, an atrium, a ventricle, and a bulbus arteriosus; by two pairs of aortic arches, two dorsal aortæ, and by vitelline and other arteries, vitelline, cardinal, umbilical, and other veins (text-fig. 7).

A notochord (fig. 33) and branchial arches (text-fig. 6) represent a skeleton, and excretory organs are represented by Wolffian bodies and pronephric ducts.

In a comparison between horse and sheep embryos it is pointed out that even at the stage characterised by four pairs of mesodermic somites the horse differs from a sheep at the corresponding phase in its life-history, and that, as development proceeds, the differences, more especially in the fœtal appendages, become more pronounced.

EXPLANATION OF PLATES.

Plate IX.

Fig. 1. Ovarian follicle of a mare containing an unripe ovum; this follicle only measured 6 mm. The large follicle in fig. 16, which contained a ripe ovum, measured 37 by 33 mm.

Fig. 2. The unripe ovum seen in fig. 1. × 300. This ovum measured ·11 mm. exclusive of the zona pellucida; the average size of the ripe ovum of the mare, exclusive of the zona pellucida, is probably ·18 mm. In the sheep the ovum is about ·15 mm. In deer the ovum may be under ·1 mm.; in Dasyurus it averages ·24 mm.; while the human ovum varies from ·22 to ·32 mm.; hence the ovum in the horse, as in the sheep, is relatively large. Between the ovum and the zona pellucida (*z.p.*) is the perivitelline space (*p.s.*); the cells external to the zona form the corona radiata (*c.r.*). The egg of amphioxus only measures ·12 mm., yet it contains sufficient deutoplasm to provide all the energy required for development up to the gastrula stage. It may hence be assumed that the ovum of the mare contains all the nutrient required for development up to at least the morula stage.

Fig. 3. This figure indicates the actual size of Bonnet's so-called 21-days blastocyst—it probably represents the phase reached at the end of the second week. Bonnet states that the blastocyst was invested by a zona pellucida 4μ thick.

Fig. 4. Martin's so-called 21-days blastocyst, natural size, invested by a thick (3 to 4 mm.) albumen layer (*alb.*). This 35-mm. blastocyst probably represents the stage reached at the middle of the third week. After Martin.

Fig. 5. The blastocyst, natural size (50 mm.), taken from a Highland mare 21 days and 2 hours after the one and only service on the seventh day of œstrus. Note the difference in the size and position of the embryo from the embryo in fig. 4, the left vitelline artery, the sinus terminalis, and the vitelline veins.

Fig. 6. A section through the lower end of the left uterine horn. The blastocyst is kept in contact with the tongue-like processes of the uterine mucosa by hydrostatic pressure. Natural size.

Fig. 7. A dorsal view of Martin's so-called 21-days embryo. Note the four pairs of mesodermic somites, the primitive streak, and the primitive and neural grooves. × 15. After Martin.

Fig. 8. The 21-days embryo seen in fig. 5. This hook-shaped embryo is three times the size of, and much further advanced in its development than, Martin's so-called 21-days embryo. Note the right vitelline vein (*v.v.*) on its way to the relatively large heart (*ht.*), the fronto-nasal process (*f.p.*), the four branchial arches (*b.a.*) and branchial grooves, and the depression between the first arch and the fronto-nasal process, which represents the mouth or stomodæum (*s.*). Only the front part of the amnion (*am.*) is represented. × 15.

Fig. 9. Part of the same embryo with its amniotic investment. Note the swelling near the end of the fronto-nasal process due to the optic vesicle (*o.ve.*); the mouth between the fronto-nasal process and the first pair of arches (1 *b.a.*); and the cavities of the three branchial pouches (*b.p.*). × 15.

Fig. 10. A dorsal view of the same embryo. Note the mesodermic somites and the neural canal with its opening to the exterior at the caudal end (*n.p.*). × 15.

Fig. 11. The same embryo seen from below, the anterior part surrounded by the amnion (*am.*). Note the openings of the otic vesicles (*o.v.*), the great width of the pericardial chamber, the somites, and the fin-like caudal expansion which consists in part of allantoic mesoderm. × 15.

PLATE X.

Figs. 12 and 13. The right and left ovaries of the Highland mare from which the 21-days embryo was obtained. Natural size.

Fig. 14. The uterus, oviducts, and ovaries of the same mare, half natural size, with part of the wall of the body of the uterus and of the left uterine horn removed to expose the 21-days blastocyst. Note the longitudinal folds of the uterine mucous membrane cut by transverse furrows into tongue-like processes, and the opening leading from the right uterine horn.

Fig. 15. The left uterine horn, blastocyst, and oviduct, and the ovary sectioned to show ovarian follicles at various stages of growth. Had the blastocyst escaped about the end of the third week the large follicle on the right (*o.f.*) would have discharged a ripe ovum on or about the day the mare was killed. Had the gestation gone on to full time the size of the large follicles would have been gradually reduced. There is no evidence of erosion of the lining of the uterus by trophoblastic cells, or of epiblastic processes from the trophoblast projecting into the spaces between the cells of the uterine mucosa. Natural size.

PLATE XI.

Fig. 16. Section through the ovary of a mare which died on the second day of œstrus. Note that the outer wall of the large follicle (*o.f.*) is thinner than in the large follicle in fig. 15. Had this mare survived four or five days longer this follicle would have doubtless discharged a ripe ovum. Natural size.

Fig. 17. Section through the ovary of a mare which died three months after giving birth to a foal. Note the corpus luteum (*c. lm.*) above the circular follicle near the middle of the ovary. Natural size.

Fig. 18. The corpus luteum found in the left ovary of the mare from which the 21-days embryo was taken. Natural size. The corpus luteum in the mare from which MARTIN obtained his so-called 21-days embryo was about double the size of a lentil.

Fig. 19. The "trumpet" of the oviduct and upper end of the left uterine horn represented in fig. 14. Note the small opening (*o.i.*) leading from the horn into the oviduct, the numerous lamellæ lining and extending over the edge of the trumpet, and the interrupted lamellæ lining the expanded part of the oviduct adjacent to the trumpet. Natural size.

Fig. 20. Transverse section through the upper end of the left uterine horn represented in fig. 14. Natural size.

Fig. 21. Part of the left uterine horn in contact with the 21-days blastocyst represented in fig. 15. It shows the appearance assumed by the ridges when the horn is pinned out on a flat surface. As the horn expands the ridges become less prominent and the spaces between the ridges are gradually increased. Natural size.

Fig. 22. Part of the sinus terminalis (*s.t.*) taking an irregular course through the unsplit mesoderm of the 21-days embryo: *v.a.*, vessels proceeding from the sinus towards embryo; *b.v.*, vessels in mesoderm beyond the sinus; *t.d.*, trophoblastic disc. × 28.

PLATE XII.

Fig. 23. Section showing the highly congested condition of the uterine mucosa on the second day of œstrus. × 40.

Fig. 24. Part of the same more highly magnified, showing congested capillaries, distended glands, and yellow bodies resembling hæmatoidin crystals. There was no evidence of the escape of blood corpuscles into the cavity of the uterus or of destruction of the uterine epithelium. × 250.

Fig. 25. Section through a ridge from the uterine horn containing the 21-days embryo. × 14.

Fig. 26. Part of the same section more highly magnified (× 100). At the end of the third week of gestation the glands are decidedly less active and there is less congestion than is the case during œstrus.

Fig. 27. The 21-days embryo, 15 times natural size. The head and front portion of the trunk are bent backwards round the large heart. *v.v.*, the large vitelline veins reaching the sinus venosus from the yolk-sac; *r.v.a.*, small right vitelline artery; *l.v.a.*, large left vitelline artery; the left aorta and the proximal part of the left vitelline vessel (text-fig. 8) are not represented in the drawing.

PLATE XIII.

Fig. 28. Section of the blastocyst immediately beyond the sinus terminalis. *tr.*, trophoblast consisting of columnar cells—note that the cells are in contact with each other along their whole length, have square-cut ends and deeply placed nuclei; *md.*, unsplit mesoderm lying in a space between the trophoblast and the yolk-sac endoderm; *md.e.*, growing edge of mesoderm, in contact with inner surface of trophoblast; *y.e.*, yolk-sac endoderm, in contact with the trophoblast, immediately beyond the growing edge of the mesoderm; *b.v.*, a blood-vessel beyond the sinus terminalis.

Fig. 29. Section through the centre of a trophoblastic disc. The disc consists of very tall cells, devoid, except round the margin, of sac-like processes. Some of the cells contain one or more round bodies derived perhaps from the "uterine milk." The cavity of the disc is occupied by a deeply stained coagulum continuous with a membrane-like coagulum (*cm.*) lying between the trophoblast (*tr.*) and endoderm (*end.*). The endoderm between the discs consists of a single layer of cells, but opposite the discs it sometimes consists of masses of cells in contact with a lightly stained material which projects into the cavity of the yolk-sac. Many of the cells surrounding the disc end in sac-like processes (*pc.*).

Fig. 29A. Section through the edge of a disc. In such sections, owing to the presence of many nuclei, the disc seems to have resulted from a heaping up of cells. Many of the endoderm cells (*end.*) seen in this section differ from the typical endoderm cells in figs. 30 and 31.

Fig. 30. This section represents an early stage in the development of a disc. On the left of the section are nearly typical columnar cells (*tr.*); then come cells with sac-like processes (*pc.*), apparently in the act of taking in food particles; then cells which by proliferating and elongating eventually form the disc; cells with sac-like processes (*pc.*) also occur on the right of the elongating cells. In the region of the developing disc the coagulum is thick and irregular; beyond this region it has the appearance of a basement membrane. Further, within the developing disc the endoderm has undergone proliferation and lies in contact with a lightly stained coagulum.

PLATE XIV.

Fig. 31. A minute coagulum lying between the trophoblast and the endoderm. This represents the first stage in the development of a trophoblastic disc and of a yolk-sac tubercle; *tr.*, trophoblast; *end.*, endoderm; *cm.*, coagulum. × 400.

Fig. 31A. The coagulum in fig. 32 seen from the cavity of the yolk-sac. The cells in contact with the coagulum are more granular and more deeply stained than the surrounding endoderm cells. × 400.

Fig. 32. A later phase in the development of a yolk-sac tubercle. The coagulum (*cm.*), now larger, is invested by highly granular endoderm cells (*end.*) × 400.

Fig. 32A. Section through same tubercle beyond the margin of the coagulum. × 400.

Fig. 33. Diagram of longitudinal section of 21-days embryo and its membranes. Note the complete amnion (*am.*), the small allantoic diverticulum (*al.d.*) embedded in the allantoic mesoderm (*al.m.*), the wide yolk-stalk (*y.s.*), that the mesoderm (*md.a.*) except in the immediate vicinity of the embryo is still unsplit, and that the spinal cord opens at its caudal end (*c.n.*) into the amniotic cavity (*am.c.*); *at.*, atrium; *cl.*, cloaca; *d.a.*, dorsal aorta; *ecd.*, ectoderm; *end.*, endoderm; *exo.*, exocœlom; *f.b.*, fore-brain; *h.b.*, hind-brain; *m.*, "longitudinal growth-centre of embryo"; *m.b.*, mid-brain; *md.*, mesoderm; *mo.*, mouth; *nc.*, notochord; *ne.c.*, canal of spinal cord; *p.o.v.*, optic vesicle; *s.c.*, spinal cord; *s.v.*, sinus venosus; *t.*, tuberculum impar; *v.*, ventricle; *y.sa.*, yolk-sac; 1, 2, 3, 4, internal branchial slits. *Circa* 15 times natural size, 21-days embryo.

Fig. 34. Semi-diagrammatic drawing of the 21-days blastocyst with part removed to show the embryo. Note the complete amnion (*am.*), the yolk-stalk (*y.s.*) leading into a large yolk-sac, the left vitelline artery (*v.a.*), the sinus terminalis (*s.t.*), and the right vitelline vein (*v.v.*), that the greater part of the mesoderm is still unsplit (*md.a.*), and that the non-vascularised distal portion of the blastocyst consists only of trophoblast (*tr.*) and endoderm (*end.*). Beyond the sinus, dots (*t.d.*) represent some of the trophoblastic discs. *am.c.*, amniotic cavity; *exo.*, exocœlom; *md.*, mesoderm. *Circa* 3 times natural size.

Fig. 35. The 21-days embryo as it appeared when the chorion was removed. Note the large left vitelline artery (*v.a.*), the large right and left vitelline veins (*v.v.*), and the rich plexus of vessels in the vicinity of the embryo.

PLATE XV.*

Fig. 36. Section through fronto-nasal process of the 21-days embryo. *am.*, amnion; *am.c.*, amniotic cavity; *f.b.*, cavity of fore-brain; *p.o.v.*, primary optic vesicle.

Fig. 37. Section through head end of notochord (*nc.*). *m.b.*, mid-brain; *f.g.* fore-gut; *s.p.*, Seessel's pouch; *sto.*, stomodæum; 1 *a.a.*, first aortic arch.

Fig. 38. Section through otic vesicles (*o.v.*). *h.b.*, hind-brain; *d.a.*, dorsal aorta; *f.g.*, fore-gut, from which notochord projects upwards towards floor of hind-brain; 2 *b.p.*, second branchial pouch; *d.a.*, dorsal aortæ formed by union of first two aortic arches; *at.*, atrium; *b.co.*, bulbus cordis; *pc.*, pericardium.

Fig. 39. Section through third branchial pouch (3 *b.p.*). *at.*, atrium; *a.v.c.*, atrio-ventricular constriction; *b.co.*, bulbus cordis; *d.a.*, dorsal aorta; *h.b.*, hind-brain; *pc.*, pericardium; *v.*, ventricle.

Fig. 40. Section through fourth branchial pouch (4 *b.p.*). *at.*, atrium; *at.v.*, atrio-ventricular valve; *b.co.*, bulbus cordis; *d.a.*, dorsal aorta; *h.b.*, hind-brain; *v.*, ventricle.

PLATE XVI.

Fig. 41. Section through anterior part of sinus venosus (*s.v.*). *am.*, amnion; *d.a.*, dorsal aorta; *f.g.*, fore-gut; *nc.*, notochord; *pp.c.*, pleuro-pericardial cavity; *s.c.*, spinal cord; *v.v.*, vitelline vein.

Fig. 41A. Section through middle part of trunk in a line with above. *m.g.*, mid-gut; *m.p.*, muscle plate; *p.d.*, pronephric duct; *u.v.*, umbilical vein; *w.b.*, Wolffian body. Other abbreviations as before.

Fig. 42. Section through trunk and middle portion of sinus venosus (*s.v.*). *d.c.*, duct of Cuvier; *lu.*, lung; *v.v.*, vitelline vein; *c.v.*, branch of vitelline vein. Other abbreviations as before.

PLATE XVII.

Fig. 43. Section through posterior part of sinus venosus (*s.v.*) and the terminal portions of vitelline veins (*v.v.*). *pc.*, pericardium. Other abbreviations as before.

Fig. 44. Section through middle part of trunk in region of yolk-stalk. *sp.*, splanchnopleure. Other abbreviations as before.

Figs. 45 and 46. Sections through posterior third of trunk. Note that the amnion (*am.*) is folded to form longitudinal ridges. *c.v.*, posterior cardinal vein. Other abbreviations as before.

Fig. 47. Section near the point where the dorsal aorta divides in two. Abbreviations as before.

PLATE XVIII.

Figs. 48 and 49. Sections nearer caudal end than fig. 47, showing two aortæ (*d.a.*). Abbreviations as before.

Fig. 50. Section through hind-gut (*h.g.*) immediately in front of posterior wall of yolk-stalk. Note the triangular form of the spinal cord (*s.c.*), the mesodermic somites (*m.p.*), cardinal veins (*c.v.*), and the two aortæ (*d.a.*).

Fig. 51. Section through the posterior wall of the yolk-stalk (*y.st.*). *al.b.*, allantoic branches of aorta; *h.g.*, hind-gut. Other abbreviations as before.

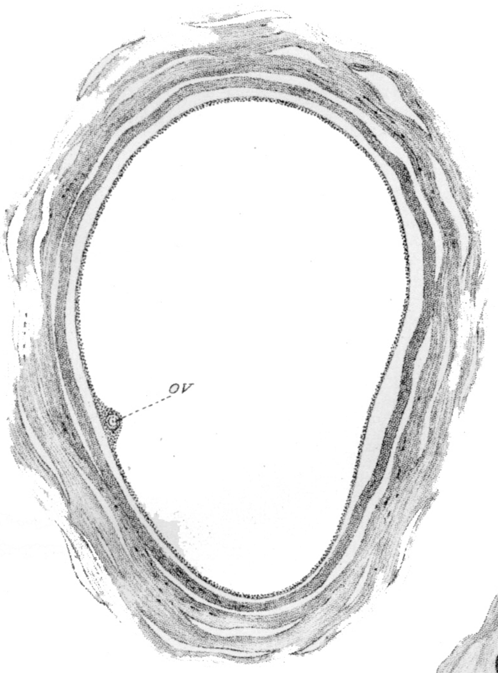
Fig. 52. Section through cloaca (*cl.*) immediately in front of opening of spinal cord into amniotic cavity. The notochord *nc.*, is tubular, and lies at one side of the middle line. Note the wide allantoic diverticulum (*al.d.*) and the crescent-shaped amniotic cavity (*am.c.*). Other abbreviations as before.

Fig. 53. The tenth section from the caudal end of the embryo. *am.*, amnion; *am.c.*, amniotic cavity; *al.d.*, terminal portion of allantoic diverticulum; *c.n.*, caudal neuropore; *s.c.*, spinal cord; *sp.*, splanchnopleure; *u.v.* umbilical vein.

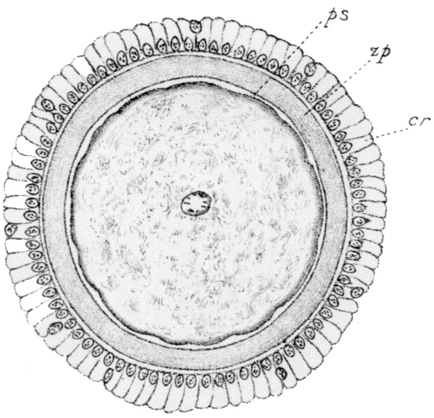
---

* The figures in Plates XV–XVIII are all magnified 75 diameters.

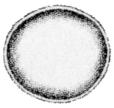
Ewart: Development of the Horse.



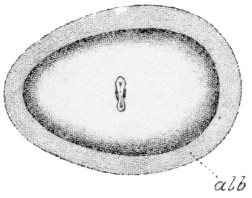
1



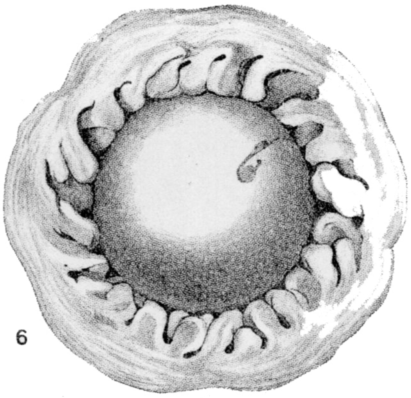
2



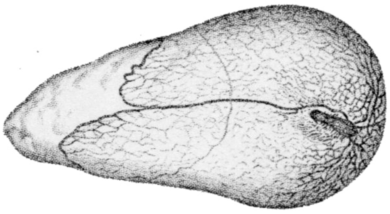
3



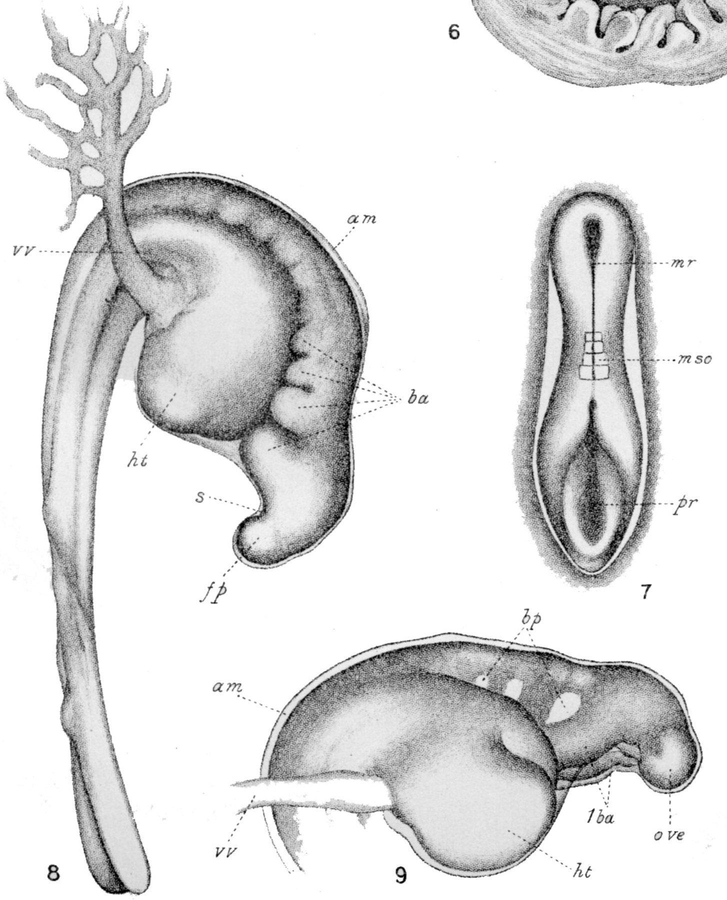
4



6



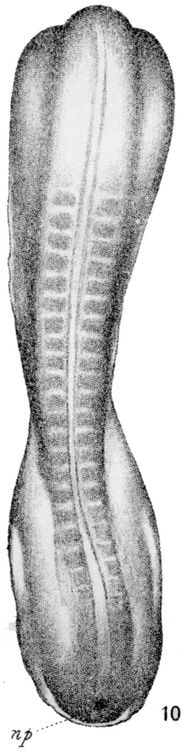
5



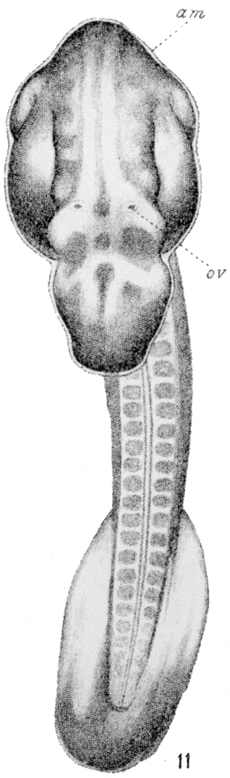
8

9

7



10

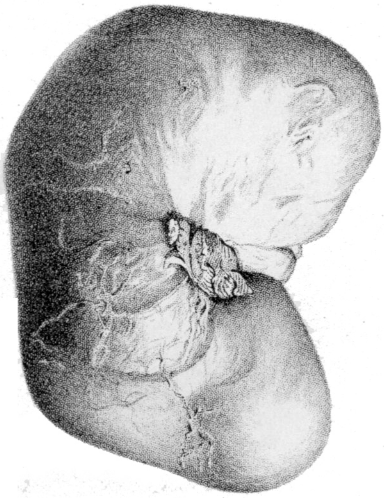


11

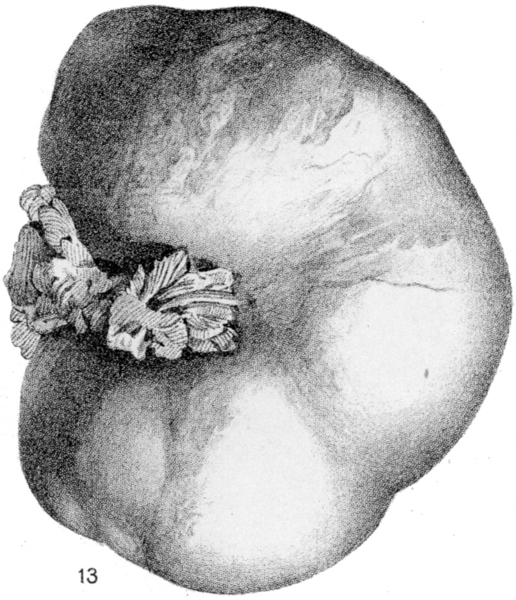
Figs. 1-3 by Augusta Lamont,
4-11 by Fiddes Watt.

McFarlane & Erskine, Lith. Edin.

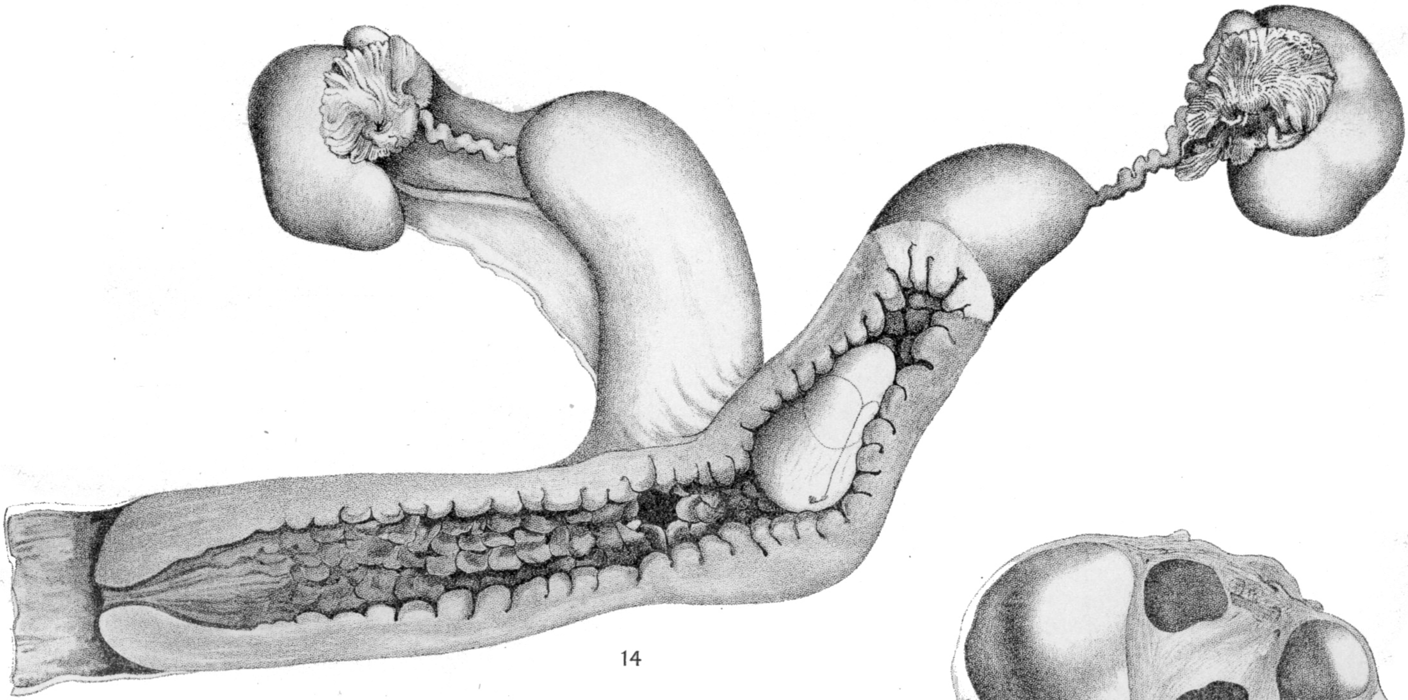
Ewart: Development of the Horse.



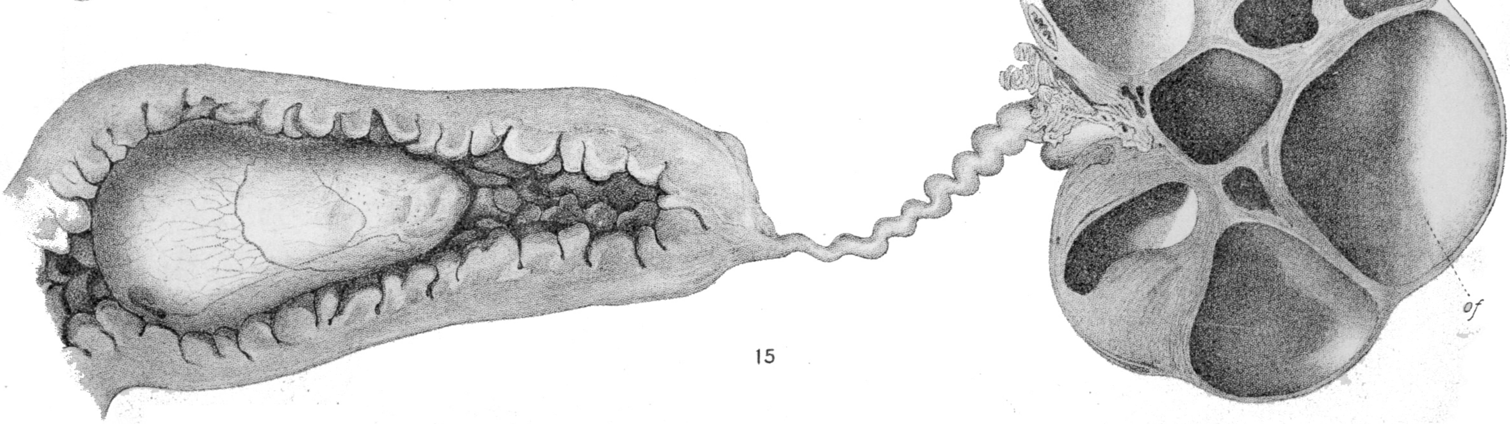
12



13



14

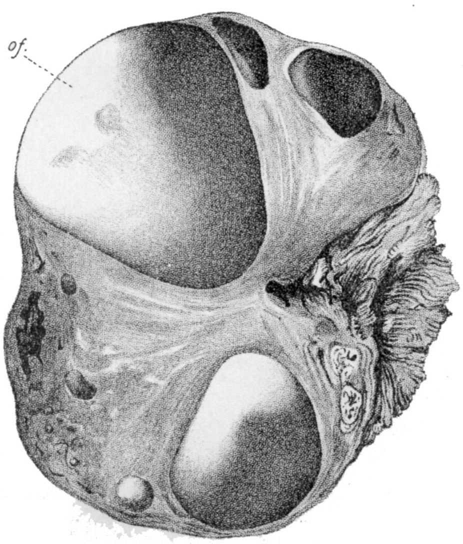


15

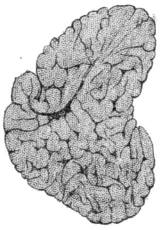
Fiddes Watt, del.

McFarlane & Erskine, Lith. Edm.

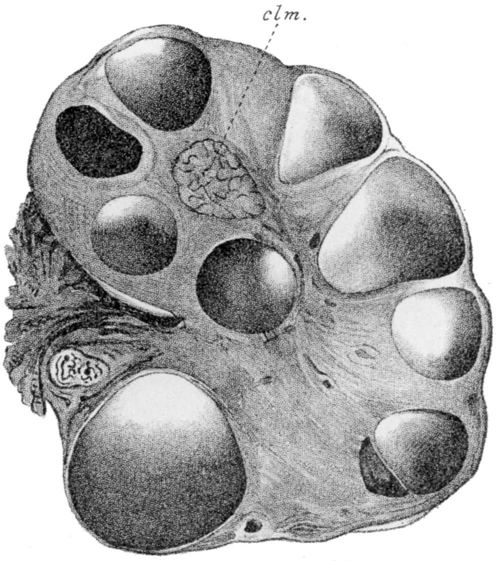
Ewart: Development of the Horse.



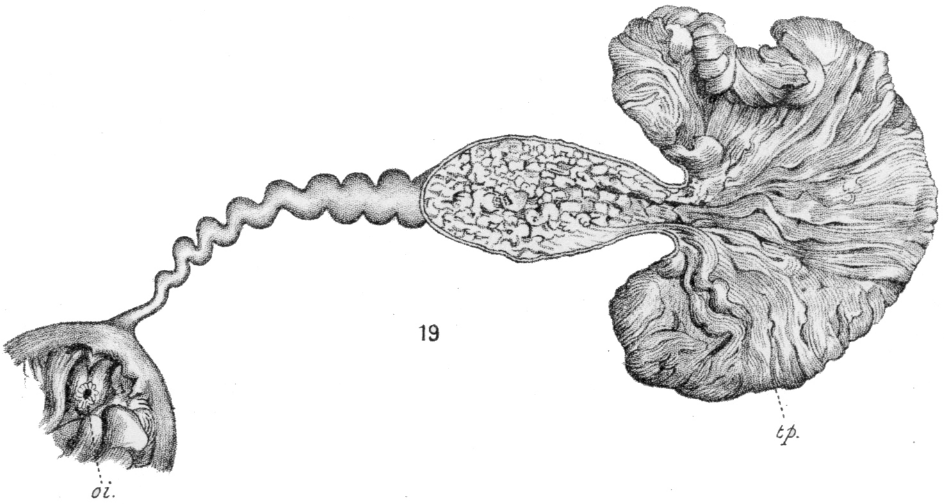
16



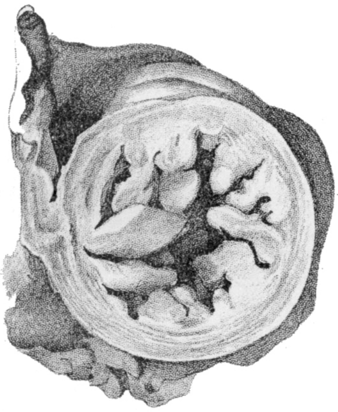
18



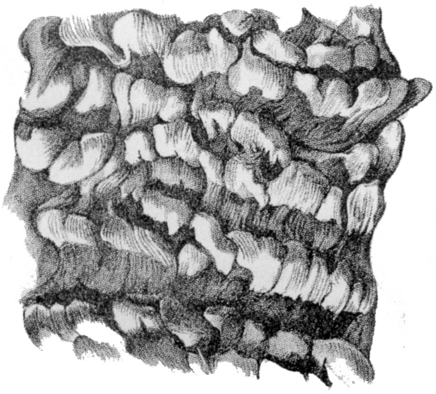
17



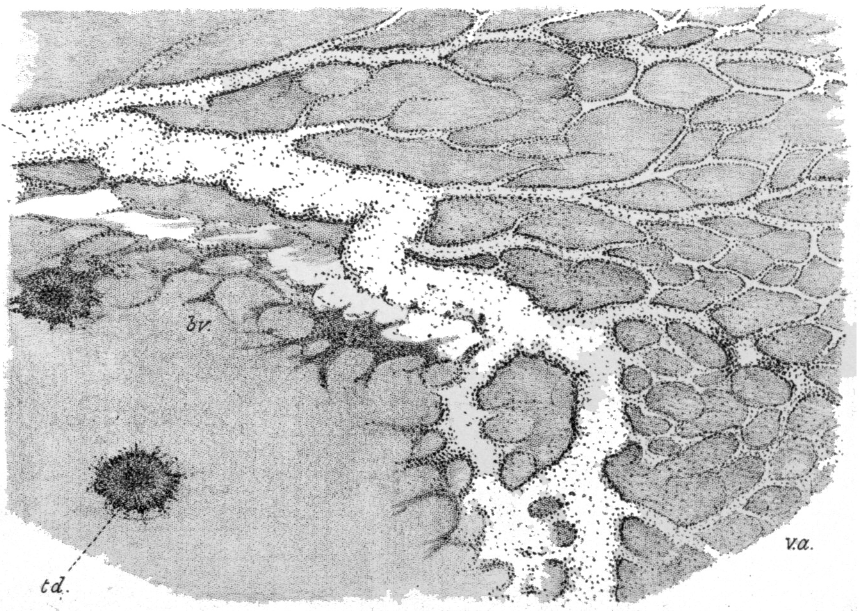
19



20



21



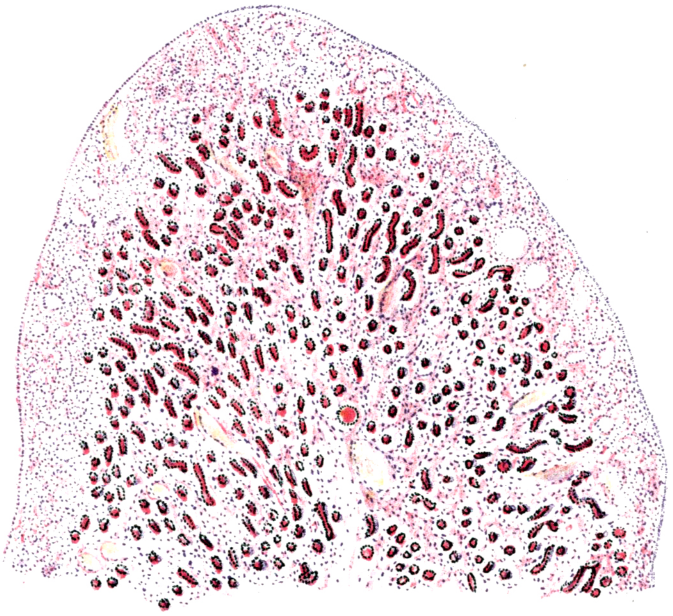
22.

Figs. 16–21 by Fiddes Watt. 22 by Augusta Lamont.
McFarlane & Erskine, Lith. Edin.

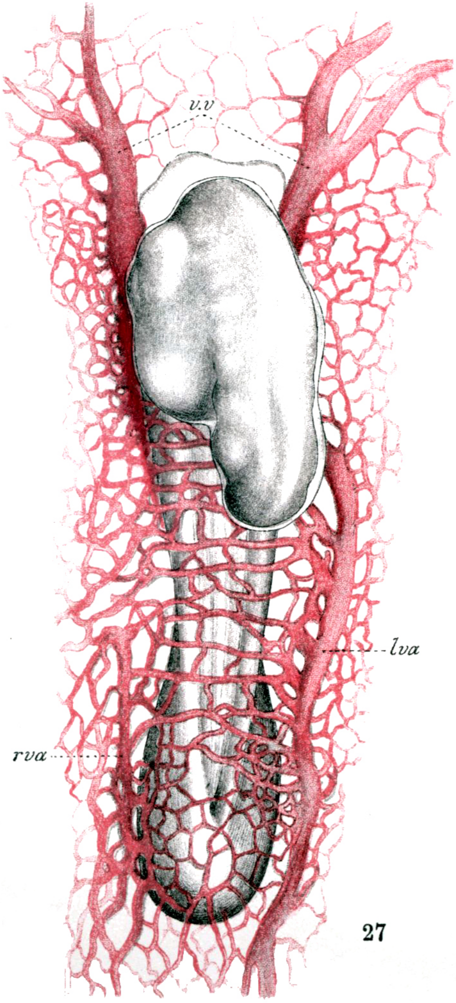
Trans. Roy. Soc. Edinr. Vol. LI.

EWART: DEVELOPMENT OF THE HORSE.—PLATE XII.

24

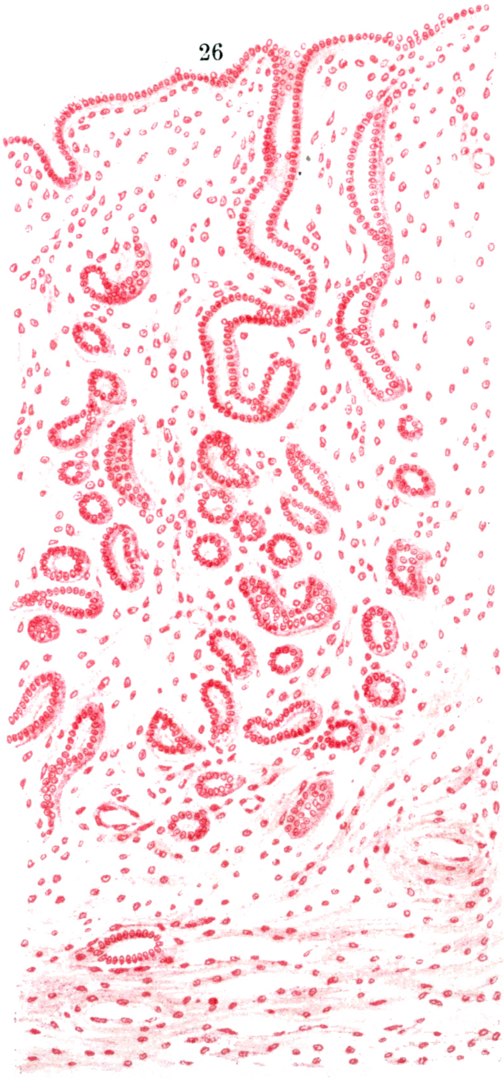


23



27

25

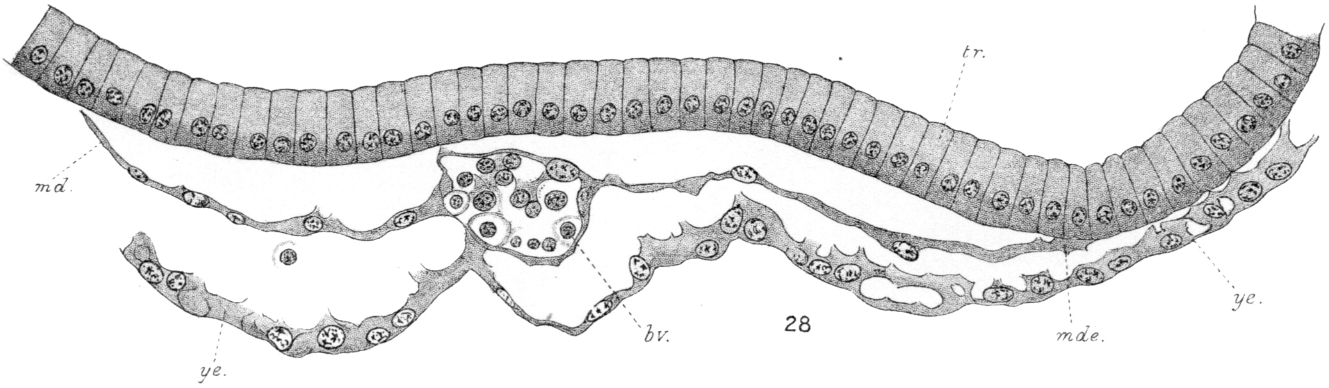


26

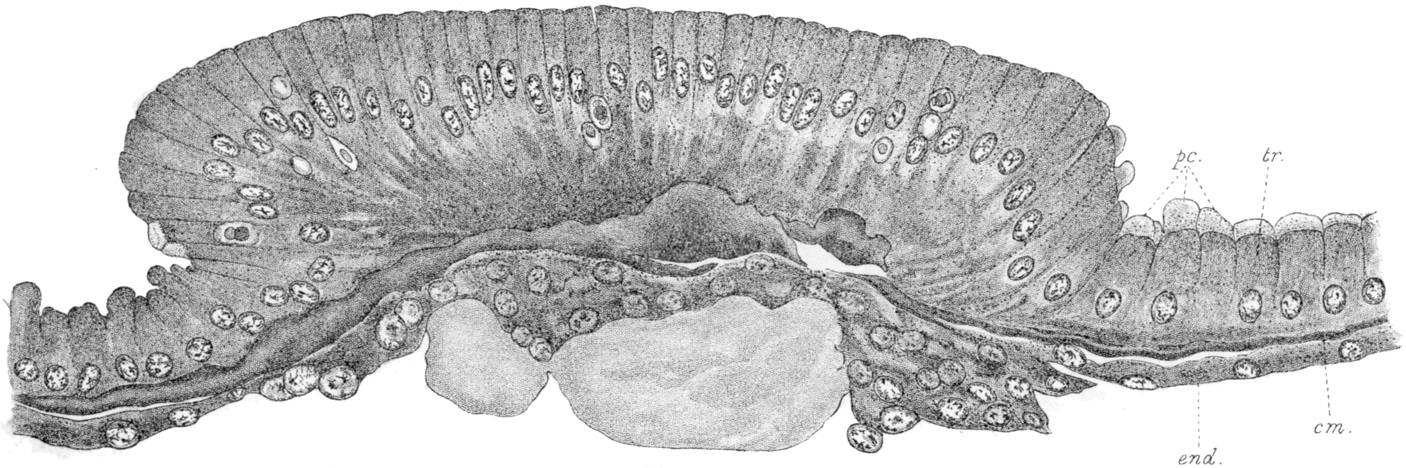
Figs. 23–26 by Richard Muir; Fig. 27 by Fiddes Watt.

M'Farlane & Erskine, Lith., Edin.

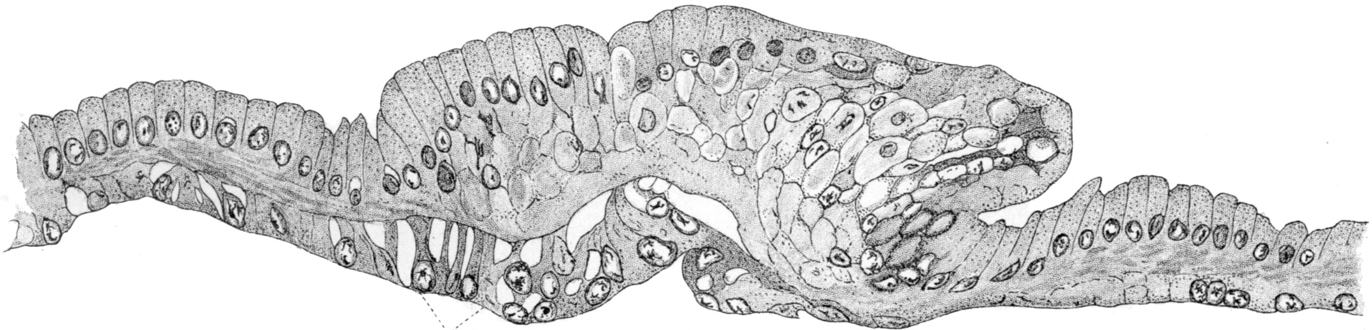
Ewart: Development of the Horse.



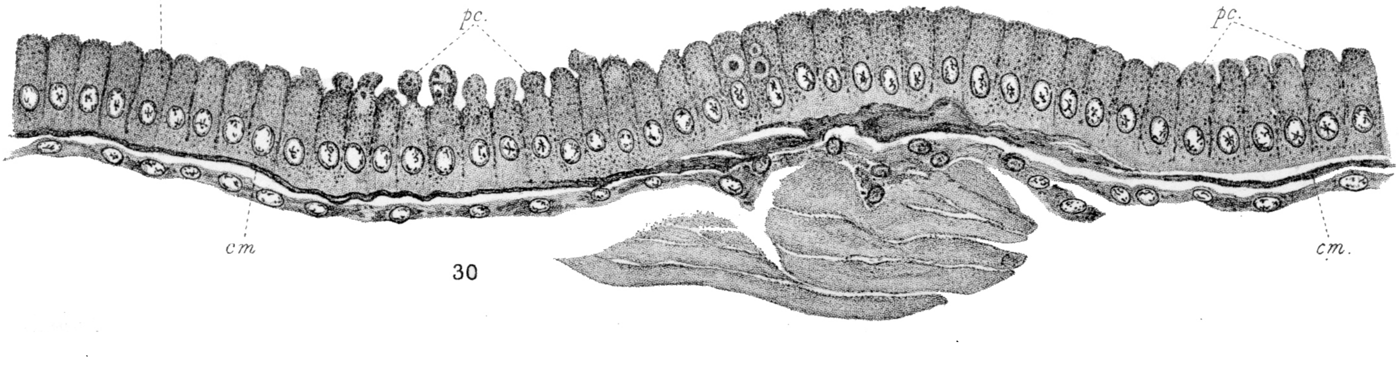
28



29



29A

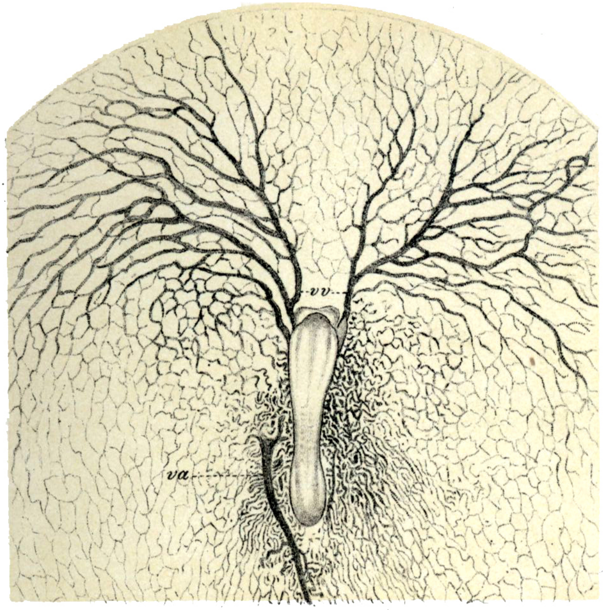


30

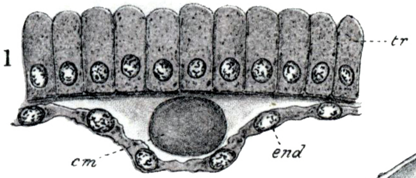
Augusta Lamont, del.

McFarlane & Erskine, Lith. Edin.

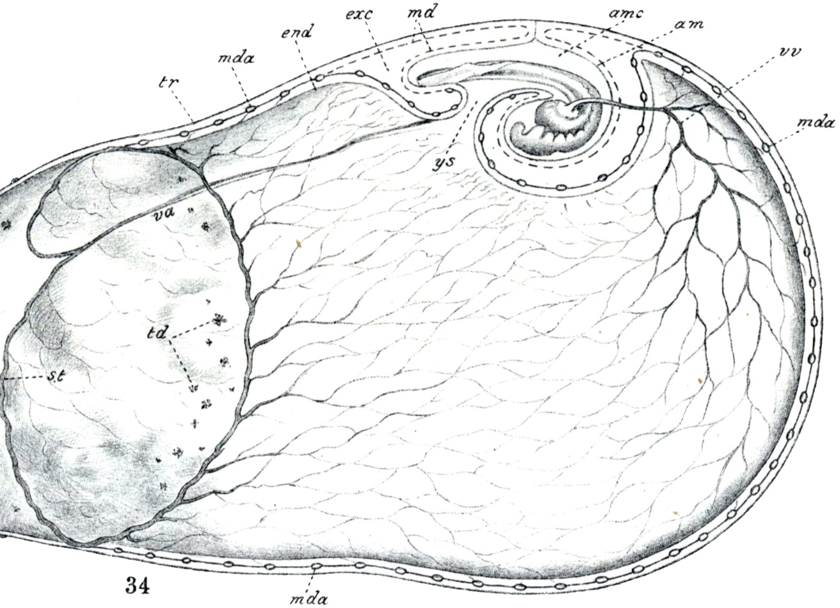
EWART: DEVELOPMENT OF THE HORSE.—PLATE XIV.



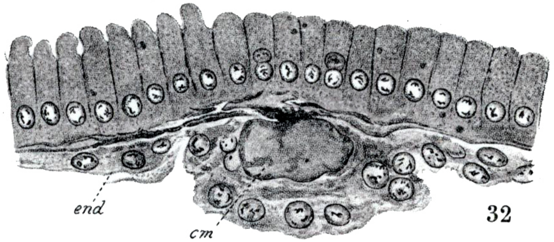
35



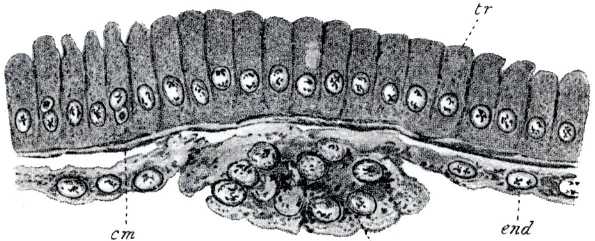
31



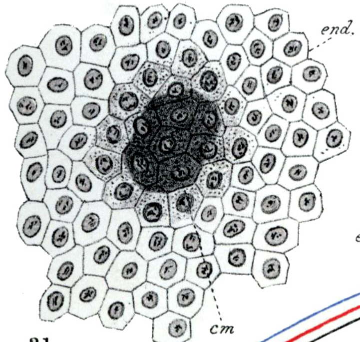
34



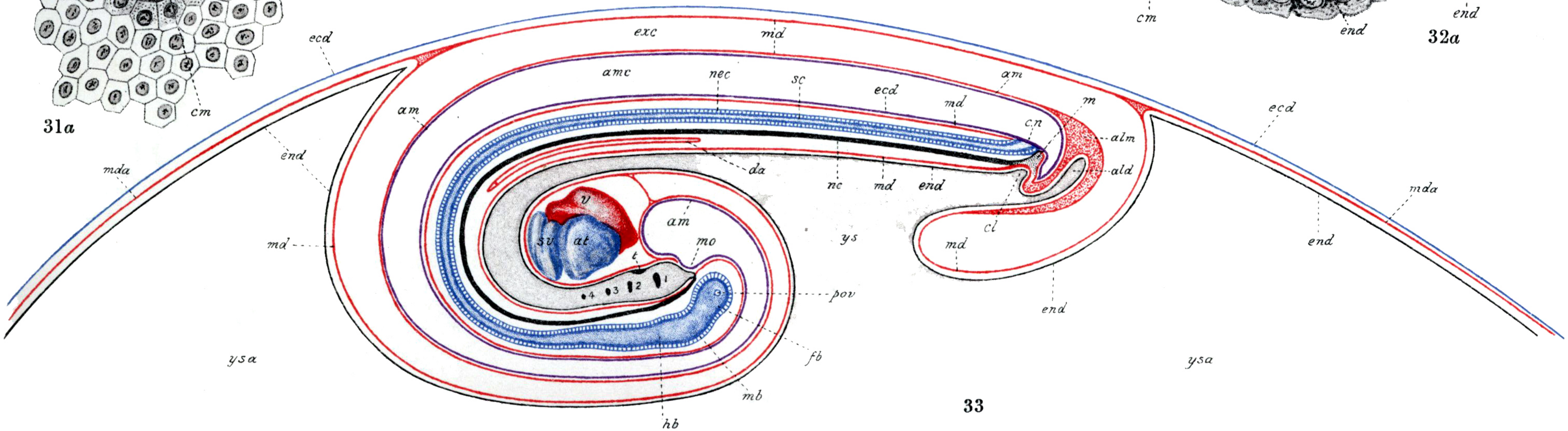
32



32a



31a



33

PROFESSOR J. COSSAR EWART: "Studies on the Development of the Horse."—PLATE XV.

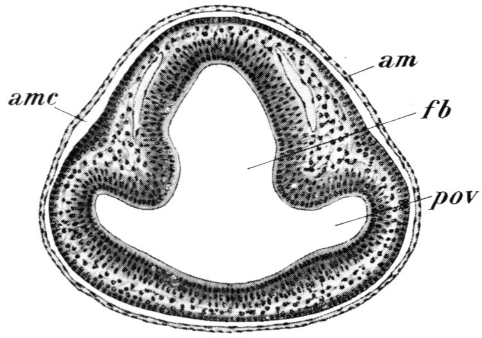


FIG. 36.

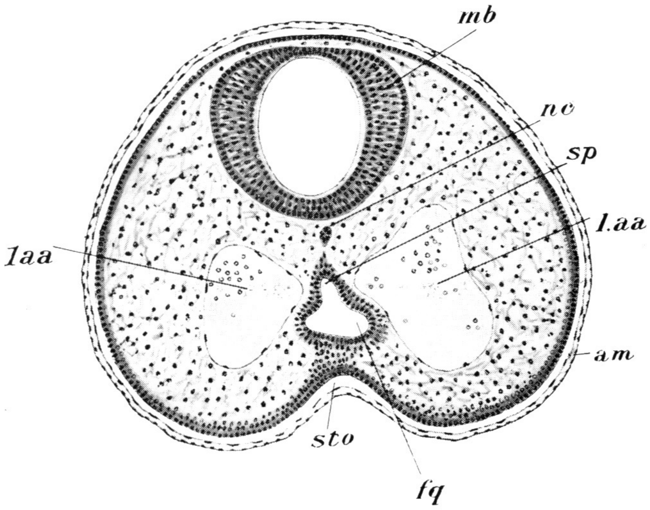


FIG. 37.

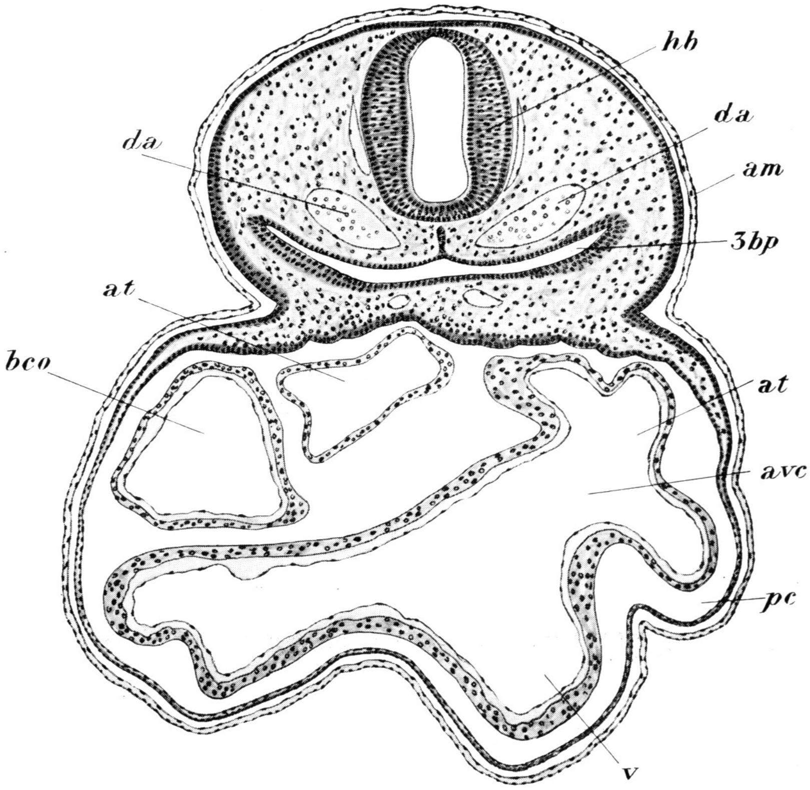


FIG. 39.

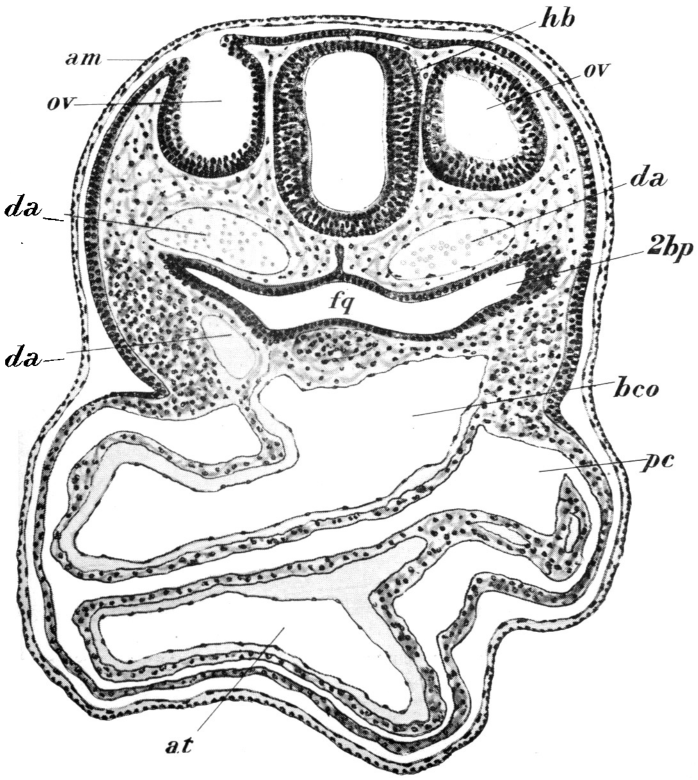


FIG. 38.

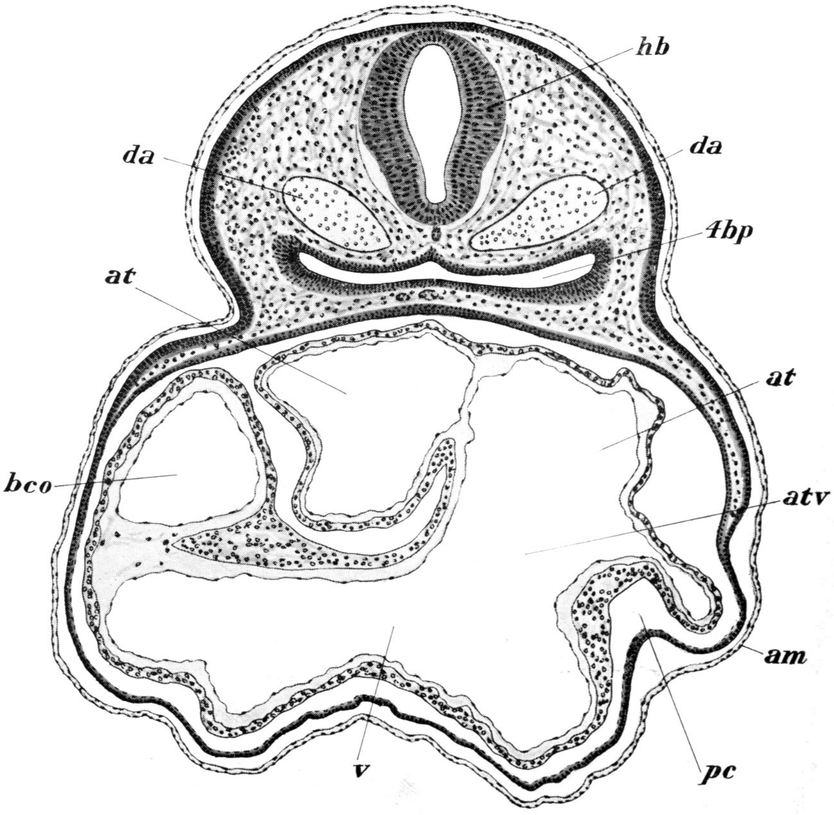


FIG. 40.

RICHARD MUIR DEL.

Neill & Co., Ltd., Edin

PROFESSOR J. COSSAR EWART: "Studies on the Development of the Horse."—PLATE XVI.

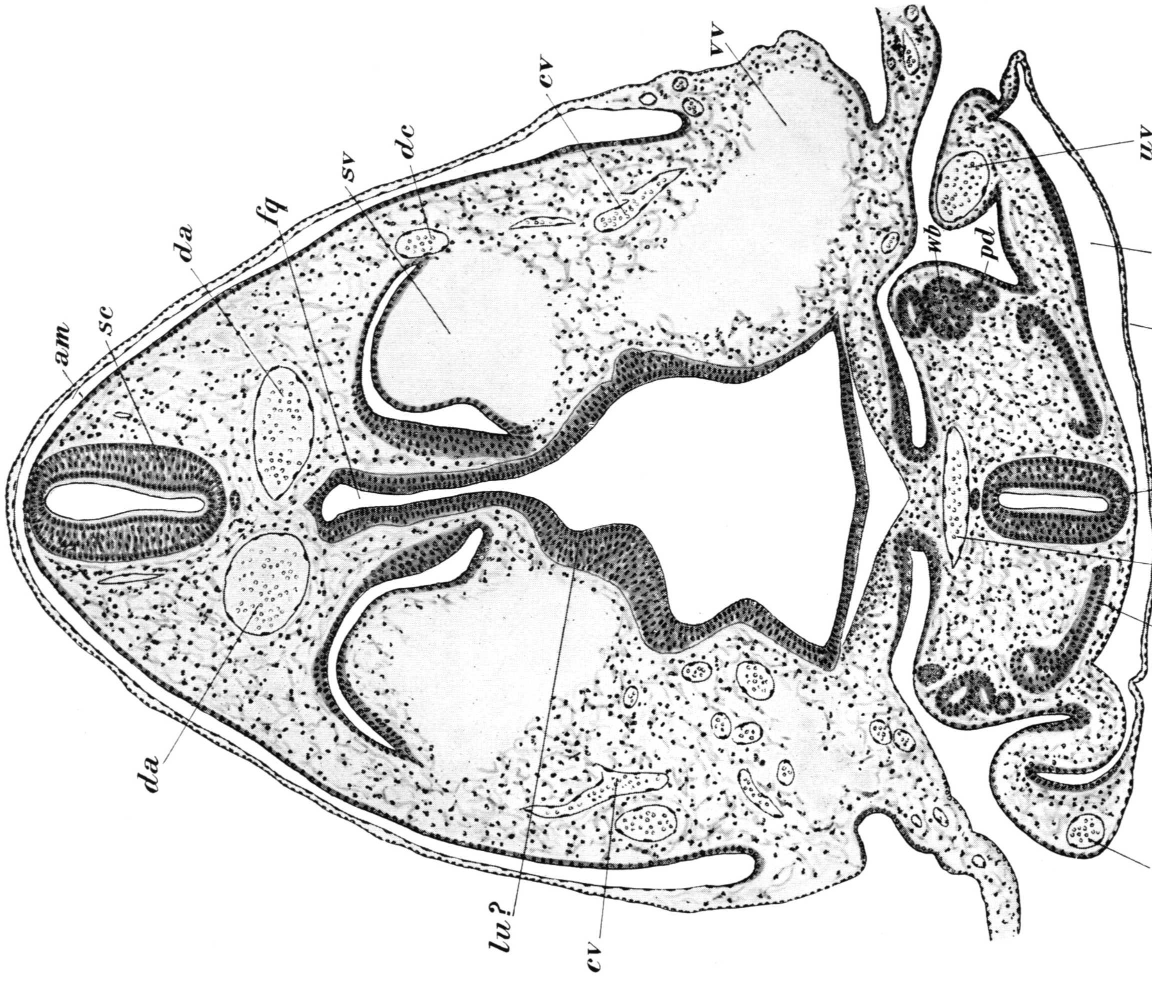
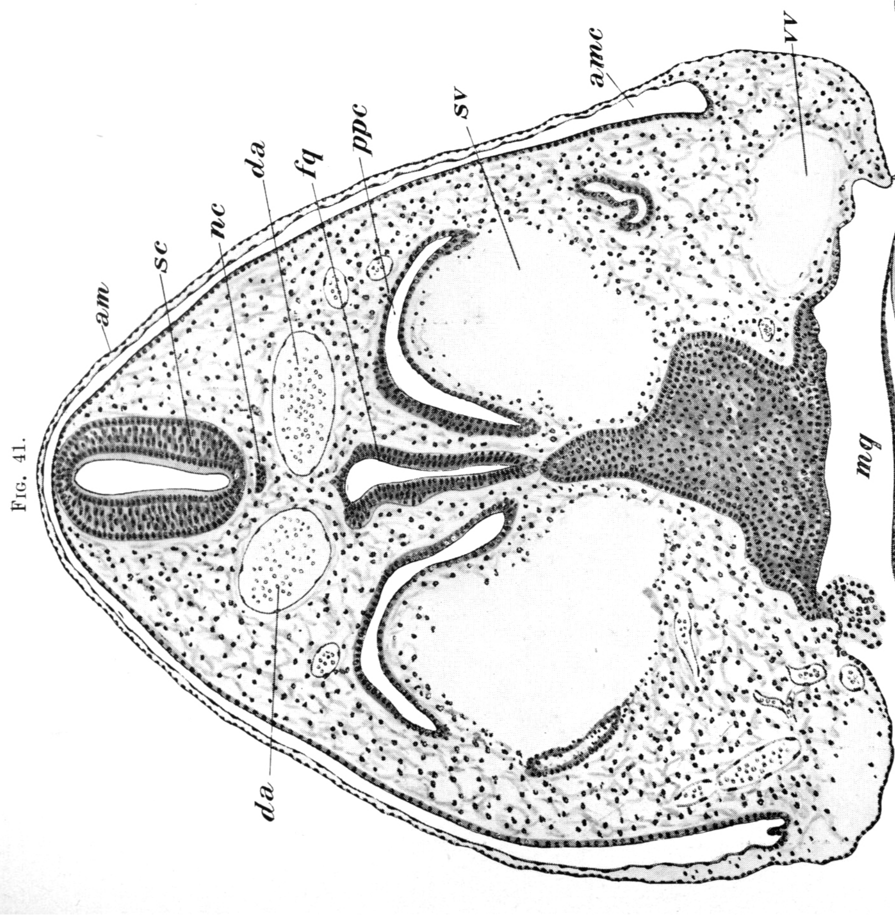


FIG. 42.

Neill & Co., Ltd., Edin.

FIG. 41.



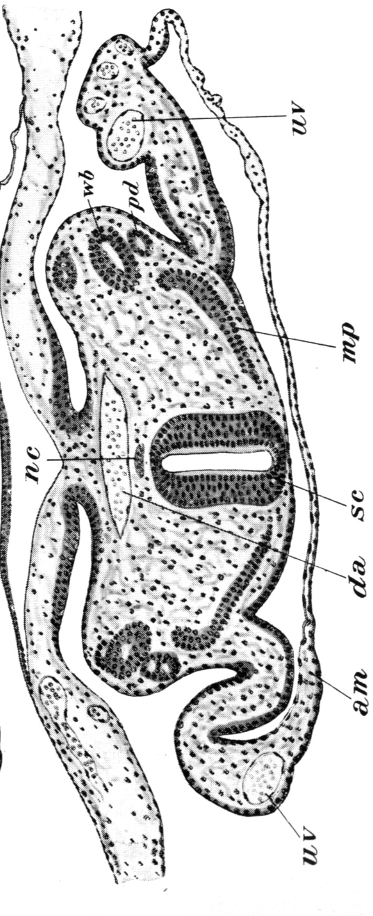


FIG. 41A.

RICHARD MUIR DEL

PROFESSOR J. COSSAR EWART: "Studies on the Development of the Horse."—PLATE XVII.

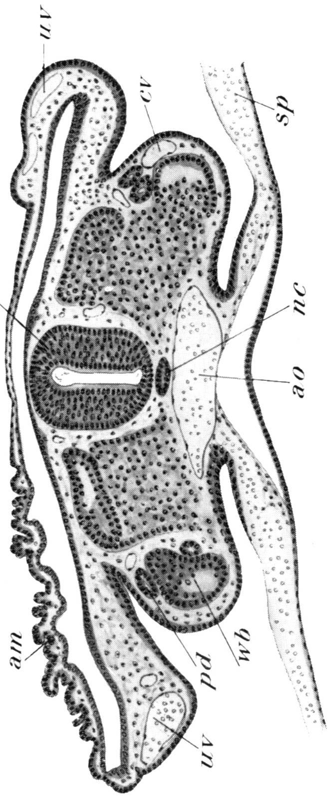


FIG. 45.

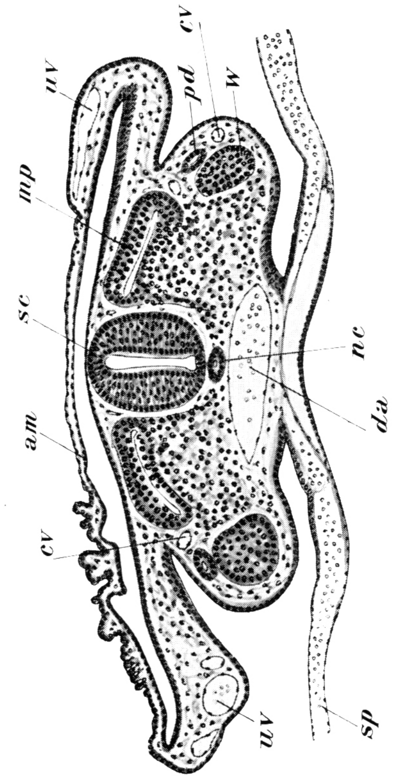


FIG. 46.

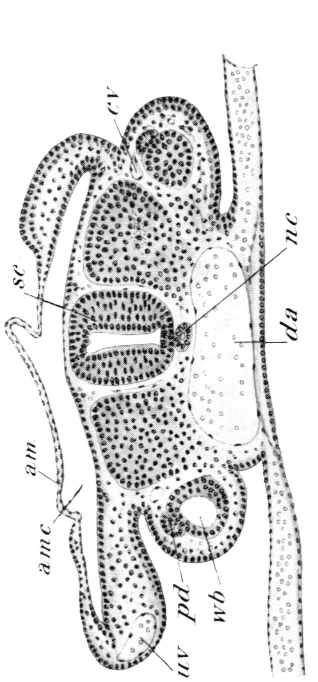


FIG. 47.

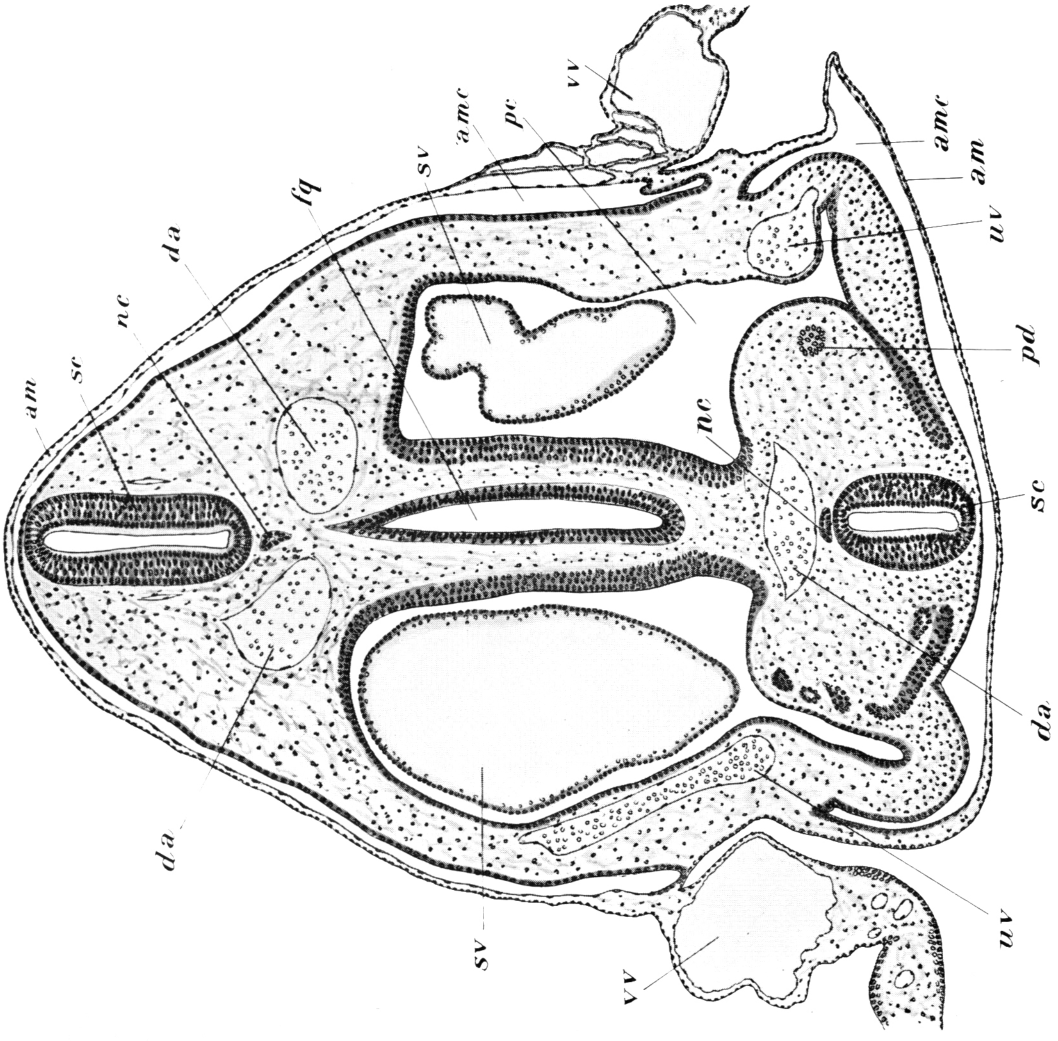


FIG. 43.

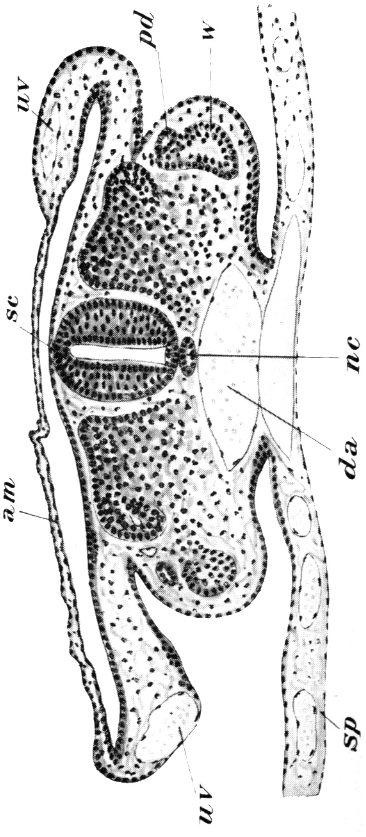


FIG. 44.

RICHARD MUIR DEL.

Neill & Co., Ltd., Edin.

Trans. Roy. Soc. Edin. VOL. LI.

PROFESSOR J. COSSAR EWART: "Studies on the Development of the Horse."—PLATE XVIII.

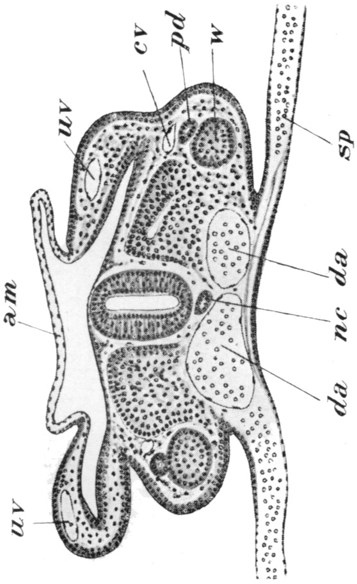


FIG. 48.

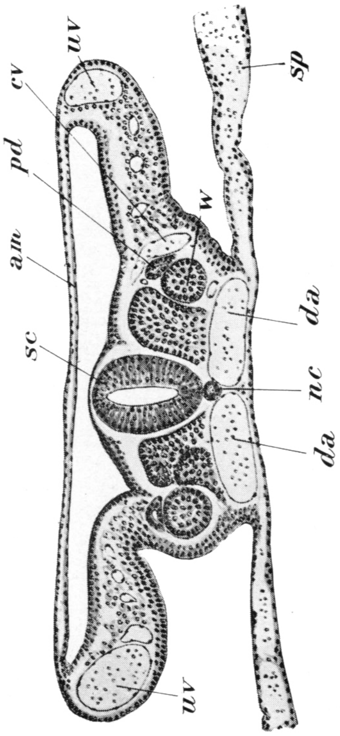


FIG. 49.

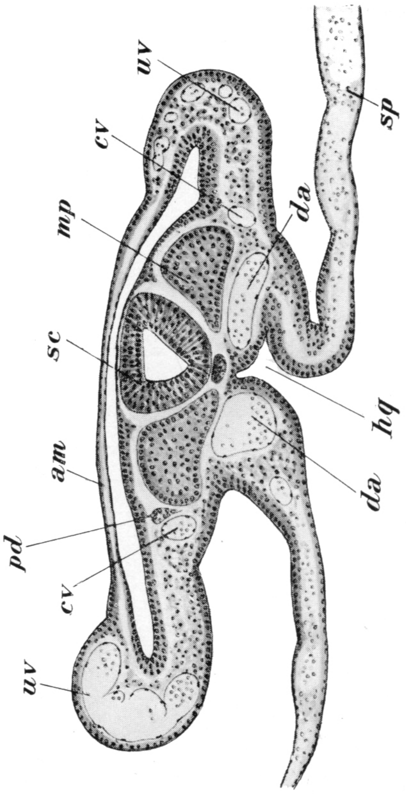


FIG. 50.

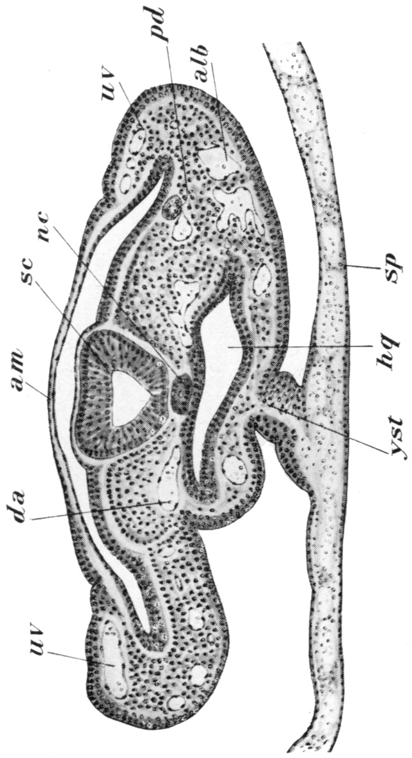


FIG. 51.

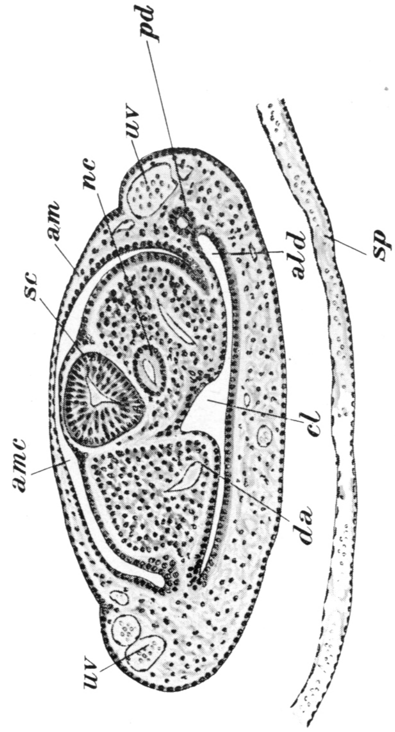


FIG. 52.

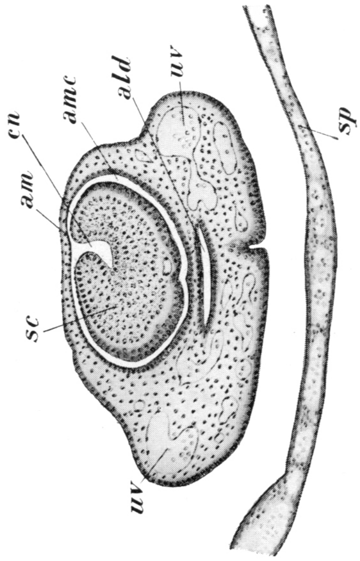


FIG. 53.

Neill & Co., Ltd., Edin.

RICHARD MUIR DEL.