PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Placentation of Hyrax capensis

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PHILOSOPHICAL TRANSACTIONS.

I.—*The Placentation of Hyrax Capensis.*

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Communicated by Prof. J. S. Gardiner, *F.R.S.*

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(Plates 1–4.)

The following account of the placentation of Hyrax is based on the examination of fifteen uteri that were obtained for the late Dr. Richard Assheton, Sc.D., F.R.S., by Mr. N. C. Thursby-Pelham and Mr. F. S. Delves Broughton in Nyasaland. Owing to pressure of work, Dr. Assheton was unable to make more than a cursory examination of one specimen. My results are necessarily very incomplete owing to the wide gaps between the different stages and the absence of any very early specimens.

I am indebted to Mrs. Richard Assheton for her kind permission to use the material, and also to Prof. J. Stanley Gardiner, F.R.S., the late Prof. MacAllister, F.R.S., and Prof. J. T. Wilson, F.R.S., for allotting me a grant from the Cambridge University Embryological Lectureship Fund. I wish to express my thanks for their unfailing assistance in providing me with every facility for carrying out the investigations. My thanks are also due to Prof. J. P. Hill, F.R.S., for his invaluable advice and assistance in the interpretation of the specimens, and for allowing me to examine the specimens procured by Mr. G. B. Haddon in the West Mali district of Northern Uganda and presented to University College by Dr. G. D. Hale Carpenter, of the Uganda Medical Service. Dr. G. S. Sansom, of University College, London, also gave me much help with sections and photographs. The completion of the work was rendered possible by the kindness of the Ministry of Agriculture and Fisheries in according me special leave for the purpose.

Through the kindness of the Superintendent of the Museum of Zoology of Cambridge University, I have also had access to the specimens referred to by Dr. Assheton in his paper on the "Morphology of the Ungulate Placenta" (1906).

The previous literature on the development of the Hyrax placenta is very brief. Home, Owen (1857), Milne Edwards (1844), Huxley (1864), George (1874), Turner (1876), and Assheton (1906) have described isolated specimens, but in none of their accounts are figured any histological details.

Their investigations may be summarized as follows:—

1. There is no trace of any lumen of the uterus in any part of the swelling; the trophoblast is equally developed on all sides of the blastocyst, both ends and sides.

At a stage equivalent to that of a 13 or 14-day rabbit the trophoblast remains as a highly vascularized investment completely surrounding the embryo and not attached to the mesoblast, which shows no signs of villous formation. The glands of the uterus take no further part in the nourishment of the fœtus.

For a considerable period both the yolk sac and allantois take nourishment from the spongy trophoblast saturated with maternal blood to the embryo. Later the spreading of the allantois forces the yolk sac away from the trophoblast, and the allantois is thereafter the sole intermediary between the trophoblast and the embryo. Both allantois and yolk sac lie closely apposed, but not in any way connected to the trophoblast layer. This inner surface of the trophoblast layer forms a cushion of thin-walled sinuses, containing, I suspect, arterial blood. The whole of the nutritive material for the embryo must at this time (approximately the 13-16-day rabbit stages) "be derived from these sinuses, carried therefrom by the vessels of both allantois and yolk sac, which lie in close *contact*, but not with any protoplasmic connection."

This is the summary given by Assheton (1906) from his examination of two specimens, the younger of which he regarded as equivalent to a 13-14-day rabbit and the older to a 16-day rabbit.

By comparison with what is known of other mammals, he further concluded that segmentation probably resembled that of Erinaceus, resulting in an "early easily separated trophoblast, leaving the yolk sac as a complete vesicle," and that, unlike Erinaceus, no decidua reflexa was formed, but that the embryo remained in the lumen of the uterus; "and after a great increase of the trophoblast layer has been effected, it then becomes attached at all points at once to the walls of the uterus, from which it may have been for a long time separated by a thick and persistent zona or albumen layer."

2. Owen (1857), Milne Edwards (1844), Huxley (1864), George (1874), and Turner (1876) described very much older specimens, and concluded that a full term or zonary placenta was formed with a persistent allantoic cavity but no yolk sac.

Owen regarded it as a "localized annular placenta with decidua, as in the elephant," but Milne Edwards thought it was non-deciduate, and Turner, who examined the same specimen, considered that there was an interlocking of the fœtal and maternal tissues like that in the placenta of the Carnivora, and that it further agreed with the cat in the large size of the allantoic sac, but that it differed "in the condition of the umbilical vesicle, which disappears in Hyrax apparently at an early period, but remains in Felis to the end of gestation."

The material from Nyasaland consisted of fifteen uteri with Fallopian tubes and ovaries attached; of these six were apparently non-pregnant and nine show placental swellings. In all the specimens there were never more than two fœtus, one in each horn of the uterus. They were all fixed in corrosive sublimate and afterwards preserved in 5 or 10 per cent. formalin, or else washed out with weak spirit after fixation and

gradually brought up to 75 per cent. alcohol. The histology of the material is good on the whole, but, owing to the mode of preservation, the material was exceedingly tough, so that it was difficult to obtain satisfactory series of sections.

Four of the uteri with no placental swellings were very small, but the other two (specimens 1 and 2) were larger. These were sectioned together with their Fallopian tubes and ovaries, in the hope that they might contain early ova, but none were found. The ovaries, moreover, showed no trace of ova having been recently dehisced, though in one specimen Graafian follicles that appeared ripe were present.

Non-Pregnant Uteri. (*Specimens* 1 *and* 2.)

External view.—The uteri are bipartite; the Fallopian tubes were much coiled at the upper ends and their dilated portions completely enclosed the ovaries.

Microscopical examination.—The two specimens presented such very different features that it is necessary to describe them separately.

Specimen 1.

This was slightly the larger of the two. Both horns of the uterus were sectioned, the one side transversely and the other longitudinally.

The mucosa is clothed by a columnar epithelium and is much folded (Plate 1, fig. 1), and contains numerous very large, thin-walled glands. They contain a small amount of coagulum but no leucocytes. The glands run a great length. They are especially large in the mid-region of the uterus; they are lined by columnar epithelium with large, round, lightly staining nuclei. The blood-vessels are small and scattered and the stroma consists of very attenuated cells. The whole uterus has an anæmic and uncongested appearance. The histology of the glands resembles that of Marshall and Jolly's (1906) figures of the dog and Hitschmann and Adler's (1910) figures of the human in the resting or anœstrus stage; by a comparison between them and with Specimen 2, I think this uterus may be regarded as in that condition. It differs, however, from the dog and the human uterus and also from the monkey, Heape (1894) in the enormous size and number of the glands.

Specimen 2 (fig. 2).

This is in a very different condition to the preceding. The uterine epithelium is much flattened, resembling the condition described by Heape (1894) in the case of the regenerated epithelium seen in the early post-menstrual stage in the monkey. The uterus contains much detritus, consisting of a coagulum in which degenerated leucocytes and blood corpuscles are enmeshed. The stroma has a very much more vascular appearance, numerous large vessels being present in the superficial zone of the mucosa below the uterine epithelium. In some places a quantity of blood has been extravasated and

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lies freely in the stroma. The blood contains a number of leucocytes and pigment granules like those described by MARSHALL (1906) in the post-menstrual stage in the dog.

The epithelium of the glands is very much thicker than in Specimen 1. Their lumen is much smaller, but they open more widely into the cavity of the uterus. Throughout their length they contain a coagulum similar to that in the uterus.

By comparison with the former specimen and the work of the author previously cited, there can be little doubt that the uterus is in the condition of œstrus, or "heat." It is therefore preparing for the reception of the ova.

The Fallopian Tubes.

These are much the same in both specimens. Their fimbriated extremities are much expanded and completely enclose the ovaries. The segment succeeding the opening is much coiled, and the epithelium contains numerous mucous-secreting cells similar to those in the rabbit. The middle straight portion has none of these mucoid cells, but has a ciliated columnar epithelium. Towards the posterior end numerous glands and blood vessels running parallel to the lumen are found in the stroma, but the glands do not open till they reach the uterus proper.

The ovaries of both specimens show no sign of any corpora lutea. There are one or two Graafian follicles lying close to the surface in Specimen 2. In these the membrana granulosa has almost disappeared and the ova are only partially surrounded by a single layer of cells. There is no sign that a discus proligerus would adhere to the ovum on the rupture of the follicle.

Pregnant Uteri.

Specimen 3. (Hyrax 5.)

Each horn showed a uterine swelling with an external diameter of 8 mm.—the diameter of the uterine lumen was 3 mm. This, the earliest pregnant stage that has so far been obtained, was not very well preserved, and the material proved so tough that a satisfactory series of sections was not obtained. The embryo was lost in both cases. The histology is not good and a detailed description need not be attempted. Fortunately, the next specimen is in better condition, and though at a more advanced stage than Specimen 3, the trophoblastic and maternal structures appear to be in substantially the same condition as in the latter. The general structure of the trophoblast and uterus can be made out in the sections, but the arrangement of the fœtal membranes is naturally conjectural.

Microscopical Examination (fig. 3).

Fœtal Tissue.—As in ASSHETON'S (1906) specimen, there is already a well-developed trophoblastic layer which is everywhere in contact with the uterine lining, both ends and

sides, and it is of an equal thickness throughout. There is no trace of any imbedding of the blastocyst. What I take to be the mesoderm of the chorion lies closely apposed to the inner surface of the trophoblast and consists of a single layer of attenuated cells.

The trophoblast has two very distinct parts—

1. An inner much thicker zone to which is attached the mesoderm of the chorion, in the form of a cellular network enclosing lacunæ containing maternal blood.
2. A continuous outer layer of cells that is in close contact with the maternal tissues and which is evidently phagocytic, as the mucosa is much degenerated and portions of it are being surrounded by this trophoblast. Both parts have a definite cellular structure and form, therefore, a *Cytotrophoblast*, but for convenience in description the outer invading layer will be referred to as the *Basal trophoblast* and the lacunalised portion as the *Inner trophoblast*. The portion of the Inner trophoblast on the fœtal side is very much attenuated and encloses large lacunæ. This is succeeded by a much more compact network with smaller lacunæ; between this and the Basal trophoblast are again many large lacunæ. These can be seen to be in direct communication with the maternal blood vessels which open through gaps in the Basal trophoblast.

The Maternal Tissues.

The uterus in transverse section shows the following structure :—

1. The *muscularis*, which is thick and contains many blood vessels.
2. A layer of somewhat loose tissue in which are the remains of the glands which were so evident in the non-pregnant uteri. They have diminished greatly in size and are found scattered here and there all round the uterus; their lumina are small and they are evidently taking no further part in the nourishment of the embryo.
3. There is a very thick compact layer of stroma (hereafter referred to as the *Decidua*) with many small and large blood vessels running in all directions. Some of the large channels can be traced running obliquely from the muscularis and turning through the stroma at right angles to the Basal trophoblast through which they pass to open into the lacunæ. They are lined by a syncytial layer throughout their course in the decidua; as stated above, the histology is not good, but there can be no doubt of this lining. Assheton (1906) described such vessels in his specimens and also the other vessels with no syncytial lining, and took them to be arteries and veins respectively. It is not possible to trace the other vessels with no syncytial lining very definitely here, and the question is deferred to a later section (*see* p. 9).

The structure of the decidua is more fully described in the next specimen but it can be stated that there is no trace of any uterine epithelium.

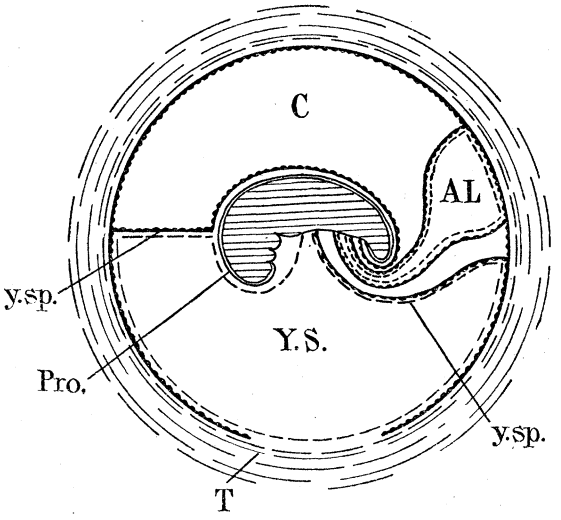
Specimen 4. (Hyrax 3.)

External diameter of the uterine swelling is 15 mm. *Internal* diameter 9 mm.

As can be seen from the dimensions, this was a very much larger specimen than the preceding. A placental swelling was opened and the embryo removed. The embryo lay within its amnion and the embryonic membranes which were closely apposed to the trophoblast, but had no firm attachment to it, as the whole formation could be removed without injury from the trophoblast shell.

The embryonic vesicle formation thus removed was sectioned, and from the preparation it was possible to get a fairly correct idea of the fœtal membranes.

The embryo is in much the same stage as the 11-day rabbit. It is covered by the amnion and the head bends down and is invested by the proamnion. The yolk sac cavity is large and its walls are extremely vascular (fig. 5, *Y.S.*). There is no sinus terminalis. I have not been able to trace the whole yolk sac in section, so am unable to say whether the blood vessels extend all over it; in a later stage, however, there is a small area at the antimesometrial pole where there are no blood vessels. In section the yolk sac wall appears as a thin-walled chain of blood vessels (fig. 5). The exact extent of the extra-embryonic cœlom could not be determined, but the accompanying text-fig. 1 is probably very fairly correct.



Text-fig. 1.—*C*, extra embryonic cœlom; *A.L.*, allantois; *Y.S.*, yolk sac cavity; *T*, trophoblast. The thin straight line denotes the ectoderm of the amnion; the thick indented line the mesoderm of the allantois, chorion and the yolk sac splanchnopleure; the thin broken line the endoderm; *Pro.*, proamnion; *y.sp.*, yolk sac splanchnopeure.

The allantois has grown out as a hollow sac and is fused with the mesoderm of the chorion at its lower end (*see* fig. 5 of Specimen 5). It is very vascular and has four large pairs of blood vessels which in surface view appear to meet together in the centre of the lower pole and appear rather like the seams of a football. Presumably, each pair

consists of a vein and an artery, but it is not possible to differentiate between them under microscopical examination.

The Trophoblast.

The *Inner trophoblast* is thicker than in the earlier specimen and the lacunæ are smaller. The *Basal trophoblast* is unaltered.

The Inner trophoblast is composed of polygonal cells with sharply-defined boundaries (fig. 4), except on the fœtal side, where the walls of the lacunæ that are apposed to the fœtal mesoderm are formed by a thin syncytial tissue with darkly staining flattened nuclei. With this exception the Inner trophoblast is anything from one to five cells thick. The nuclei are rounded and contain scattered chromatin granules; in a few a definite nucleolus can be found. I am unable to distinguish any mitotic figures. The maternal blood in the lacunæ is remarkable for the very large number of leucocytes it contains.

The *Basal trophoblast* is formed of columnar vacuolated cells of a somewhat lighter staining reaction than the Inner trophoblast. They have definite walls and form a continuous band all round the Decidua except where the maternal blood vessels pass through. On the fœtal side the Basal trophoblast is bounded by the polygonal cells of the Inner trophoblast, which appears to extend round the lacunæ nearly everywhere; but in places it is not possible to trace it, and there the Basal trophoblast would appear to be in direct contact with the maternal blood. It is difficult to be quite certain of this, as the Inner trophoblast is frequently drawn out into a very fine one-celled layer where it is in apposition to the Basal trophoblast. The nuclei of the Basal trophoblast are slightly larger and are more oval than those of the Inner trophoblast and, as a rule, have one or two nucleoli and deeply staining chromatin.

The vacuoles contain a certain amount of detritus presumably of maternal decidual origin. Long protoplasmic processes extend into the Decidua and surround small masses of the Decidual tissue (fig. 4).

The Maternal Tissues (fig. 4).

The thick Decidual tissue is very vascular as in the earlier specimen. It changes very much in character as it approaches the fœtal side. On the maternal side it has a very definite cellular structure of long spindle-shaped cells, with small deeply-staining nuclei. This is gradually replaced by a mass of cells with irregular boundaries, the nuclei becoming larger and lighter as the cellular structure becomes more indefinite until at the innermost edge, where it touches the Basal trophoblast, the cellular structure has disappeared altogether, and irregular rounded masses of cytoplasm containing one to several nuclei are found. They much resemble the megalocaryocytes described by Jenkinson in the mouse, but they are almost certainly of maternal origin. These giant cells are being surrounded by the processes of the Basal trophoblast, and what I take to be their degenerated nuclei may be found in the vacuoles of the columnar cells.

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The maternal blood vessels have not been easy to follow in the sections taken and their consideration is deferred to a later stage.

Specimen 5. (Hyrax 11.)

External diameter of the uterus 17 mm. Internal diameter 9 mm.

This is a very slightly older specimen than the last, and the allantois is a little bigger, but there is very little difference between the two.

The Inner trophoblast is somewhat thicker (compare figs. 4 and 6), and the lacunæ are smaller. The Basal trophoblast has the same structure histologically, but has a more irregular outline, and is advancing into the decidua in great tufts.

The decidua has been reduced greatly as compared with Specimen 3 and is rather narrower than in Specimen 4.

Specimen 6. (Hyrax 7.)

External diameter of the uterus 17 mm. Internal diameter 9 mm.

The Embryo and Fœtal Membranes.

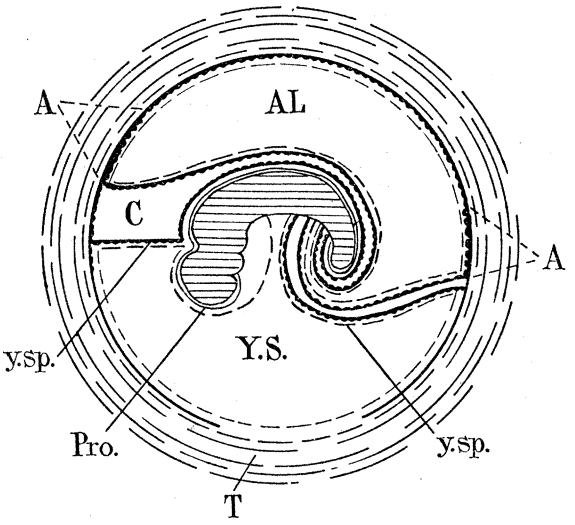
One of the two horns of the uterus was cut open and the embryo removed, as in the previous specimens there was no firm attachment between the allantochorion, *i.e.*, mesoderm and the trophoblast. The allantois has grown out considerably. The embryo is in a slightly more advanced stage than the youngest specimen described by Assheton (1906). The head is still bent down into the proamnion. The drawing (fig. 15) shows the embryo with the proamnion pushed back from the head which it envelops in reality.

The other horn of the uterus was sectioned transversely with the embryo *in situ*. Unfortunately the yolk sac and allantoic cavities collapsed in imbedding so that the whole uterus is somewhat folded. It is, however, possible to trace the arrangement of the fœtal membranes which are shown diagrammatically in text-fig. 2.

It will be seen that the allantois has grown out and fused with the mesoderm of the chorion nearly over the whole extent. There are no outgrowths from the allantoic mesenchyme, but in transverse section of the entire uterus the mesenchyme is seen to have thickened in two places indicated in text-fig. 2 by *A*—*A*. This thickening is probably the beginning of the zonary annular band from which the allantoic placenta is formed (as seen in the next specimen). Elsewhere the allantois possess a thin richly vascular wall which lies close against the fœtal surface of the Inner trophoblast. The allantoic endoderm is a thin layer of squamous cells. Over the lower hemisphere the wall of the embryonal formation is still formed by the Omphalopleure. It is very vascular except for a small area on the mesometrial side.

The *Inner trophoblast* is slightly thicker than in the previous stage, and the *Basal trophoblast* has penetrated still further into the decidua. Their histological structure

is the same as in the preceding stage. The decidua is still further reduced and the giant cells somewhat larger and more numerous.



TEXT-FIG. 2.—Diagram to show Fœtal Membranes in Specimen 6.—*C.*, extra embryonic cœlom; *A.L.*, allantois; *Y.S.*, yolk sac cavity; *T*, trophoblast; *Pro.*, proamnion; *y.sp.*, yolk sac splanchnopleure; *A—A*, thickened allantoic mesoderm. The thin straight line denotes the ectoderm of the amnion; the thin broken line denotes endoderm; the thick indented line the mesoderm of the allantois, the chorion and the yolk sac splanchnopleure.

Maternal Blood Vessels.

The two varieties of maternal blood channels described by ASSHETON are evident in this specimen. The one variety is lined by a syncytial endothelium with large round nuclei (*see* fig. 11 of Specimen 8). The vessels in question pass through the Basal trophoblast and penetrate the Inner trophoblast, and in a very few cases can be traced right through the Inner trophoblast into the lacunæ on the fœtal side. This syncytial lining appears to form a partial lining to the lacunæ. But the majority of these blood vessels only penetrate a portion of the Inner trophoblast. On the maternal side of the Basal trophoblast the syncytial lining cannot be traced for more than a short distance through the decidua. The channels do not seem to arise from any large blood vessels, but from several small sinuses that appear as slits in the outer part of the decidua. From this specimen alone it would be difficult to say whether the syncytial endothelium was of maternal or fœtal origin. There is no evidence either way, but from the examination of the youngest stage (p. 5) where the endothelium could undoubtedly be traced through the whole thickness of the decidua, there can be little doubt that it is of maternal origin. ASSHETON in his specimen thought that this was probable and that the channels conveyed the arterial blood stream.

The other channels are bounded by a squamous endothelium with small darkly staining nuclei. They can be traced from the large blood vessels which run parallel to the Basal trophoblast in the decidua near the muscularis; they run obliquely through

the decidua and pass through the Basal trophoblast to open directly into the lacunæ, just internal to that layer. They lose their endothelium as they pass through the Basal trophoblast. They are probably the maternal veins.

Specimen 7. (Hyrax 12.)

External diameter of the uterus 23 mm. Internal diameter 15 mm.

The uterus contained the customary two embryos, but the placental swelling of one horn was very much smaller than the other, and on examination the fœtus of the smaller horn was found to be in a degenerate condition, and was evidently undergoing absorption in the manner as is so frequently observed in the rabbit.

The uterus of the other horn was cut open and a thick zonary band round the middle of the uterus was seen. To this the allantois adhered closely, but the connection between the allantois and the trophoblast elsewhere was of so loose a nature that it was not possible to cut sections of the two together.

The entire maternal muscularis was very elastic and invariably curled away from the decidua, so that it was not possible to obtain satisfactory sections of the maternal tissues.

The *embryo* is in a very much more advanced stage than Specimen 6 and corresponds to about a 16-day rabbit. It appears to be slightly older than the elder of Assheton's two specimens. His, however, was in a very imperfect state of preservation, which makes a comparison difficult.

The placentation is also far in advance of that of the preceding stage, the establishment of the definitive zonary allantoic placenta through the formation of allantoic villi has made considerable progress, whilst the yolk sac now appears as an independent small vesicle, as the result of the extension of the extraembryonic cœlom into the mesoderm of the omphalopleure and the consequent separation of the latter into yolk sac wall and chorion. The allantois, moreover, has greatly increased in size, and envelops not only the yolk sac but also the embryo enclosed in the amnion.

On cutting through the allantois what I take to be a large allantoic cavity is found partially divided into four chambers, which open to one another below the embryo, as in Assheton's specimen. His observation that " The blood vessels which pass from the umbilicus to the chorion are attached along their whole course to the proximal wall of the allantois, and do not partake of the enveloping process which has occurred in the allantois itself, so that the cavity of the allantois is partly divided by bagging between the vessels," is borne out by the arrangement in Specimen 7.

The bagging of the allantois, which has grown out as a hollow sac, takes place on either side of the zonary band, where the attachment of the allantois to the trophoblast is first and most firmly effected; and to again quote Assheton, " subsequent expansion takes place so as to envelop the embryo as one might imagine the inner folds of the inner net to pass through the trammels of a larger one and so envelop whatever were below." The cavities of the four chambers are thus divided from one another above

and on each side of the embryo, but are continuous below it. The interpretation of these cavities is, however, a very difficult one, and the matter is discussed further when dealing with older specimens.

Placenta—Zonary Area.

The material has somewhat shrunk, as may be seen in fig. 7, but it is very evident that the allantoic villi (that is to say, the allantoic mesenchyme with the mesoderm of the chorion) are pushing their way into the trophoblast between the lacunæ. The Inner trophoblast is less thick than in the previous specimen, and the large inner lacunæ of maternal blood are enclosed by a thin syncytial layer where they are being surrounded by the allantoic villi; here the polygonal cellular structure has been lost, but it still persists in the region where the allantoic villi have not extended though the cell boundaries are less sharply defined.

The Basal trophoblast also retains its columnar structure. The decidual syncytial masses or giant cells described in Specimen 4 are found in much greater abundance, the cytoplasm is in bigger masses and contains more nuclei. They are seen both within as well as outside the Basal trophoblast, and are found even within the Inner trophoblast, having evidently been engulfed by the Basal trophoblast.

The allantoic mesenchyme is bounded on the fœtal side by the thin squamous allantoic endoderm; the mesenchyme forms a thick band of connective tissue from which the allantoic villi grow out as blunt processes bearing numerous allantoic capillaries. On the fœtal side of the allanto-chorion are many large blood vessels which are readily distinguishable as veins and arteries by their walls.

Assheton described the allantoic villi as being equally well developed over the entire surface of the allantois. There is no doubt that this is not the case here, where the development of the villi is exclusively confined to a zonary band. There is little difference in the size of the blastocysts, and it is difficult to understand the discrepancy. Both in this and in Specimen 6 there is an early indication of the zonary arrangement which is so prominent a feature of the later placentation. Until more uteri have been procured it is not possible to say whether there is ever a "diffuse" allantoic placentation. In the Nyasaland material, as far as allantoic villi are concerned, there is no evidence of it. Assheton's material was received in an imperfect condition as "the muscular layer . . . of a uterus from which had been removed . . . the placenta stripped from the muscle coats and containing the embryo," and it is possible that owing to the imperfections a correct interpretation was not obtained. I have examined his sections (very few were cut of this stage). They all appear to have been taken from the middle of the placenta—that is, from the same region as my zonary area. The villi are about the same length, but there is the curious difference that the Inner trophoblast is much thicker. It is possible that the thickness may vary in different animals, or that it is more apparent than real, and the thinner trophoblast is merely due to loss of blood and shrinkage in preservation.

Perizonal Area.

The difference between the zonal and perizonal regions can be appreciated by a comparison between figs. 7 and 8. The Basal trophoblast alone has the same appearance. The Inner trophoblast is much narrower though the lacunæ are large. The allantoic mesenchyme appears as a thick layer which lies closely apposed to the lacunæ; its capillaries may be found separated by their walls alone from the thin-walled lacunæ, and it is possible that there is some interchange between the products of the maternal and fœtal blood, and to that extent it might be possible to speak of a "diffuse" allantoic placenta.

Maternal Tissue.

As far as can be gathered from the imperfect sections, the decidua is very largely reduced as compared with the previous stage in the zonal and perizonal areas.

Specimen 8. (Hyrax 16.)

This is a very much older specimen than those already described. The uterus measures 35 mm. in length and 31·5 mm. in diameter. The mesometrial blood vessels were tied, so that there was no excessive loss of blood and the preservation is good.

On cutting through the uterus the embryo, in its amnion, is found to be entirely surrounded by what I take to be the allantois. As in the last specimen, the allantois is only adherent over the now broad zonary placental band. It is divided into four compartments by septa which run between the allantoic wall carrying the four main pairs of allantoic vessels and the allantoic wall investing the amnion. The two central chambers are co-terminal with the placental area, and are divided from one another by a septum which runs parallel to the back of the embryo. The other two much larger compartments occupy the poles. All four compartments open into one another below the embryo, where the four pairs of blood vessels divide. Blood vessels which can be traced back to the four main trunks run all over the unattached walls of the allantois, but are not very numerous. The arrangement of the allantois is thus a peculiar one, and it is difficult to understand how it is brought about. The condition that might have been expected is that the allantoic cavity would have been confined to the zonary placenta, and that the compartments on either side would have been extraembryonic cœlom, but this is certainly not the case. All four compartments are clearly continuous with one another, and the blood vessels are undoubtedly allantoic. The uterus presented by Dr. Hale Carpenter of Uganda was opened with the hope that it would throw more light upon the matter. It is a younger specimen than Specimen 8, and except for some slight difference in the position of the septa, shows the same structure. In neither specimen was any remains of the yolk sac to be seen definitely, though in the Uganda one there was a very small outgrowth at the umbilicus which might be the last remnant.

The Fœtus (Specimen 8, fig. 17) is deeply pigmented except for a small diamond-shaped patch on the back which marks the position of the Dorsal gland. It is covered with very fine small hairs, and in certain places long vibrissæ are well marked.

The Placenta (fig. 9).

A section taken through the zonary band shows a very advanced stage of placental development. The zonary band measures 23 mm. in breadth. Approaching from the fœtal side is seen first the thin allantoic endoderm, which is closely apposed to a broad band of allanto-chorionic mesoderm. From this allanto-chorionic villi have grown out to a great length; they are invested all round by thin layers of syncytial trophoblast and are much branched and interlocked, forming a *Labyrinth*, which is bathed on all sides by maternal blood. It is not easy to differentiate between the trophoblastic and allantoic tissues, but it is evident that the allantoic "core" is composed of very thin cells with flattened deeply-staining nuclei, whereas the trophoblast (fig. 12) has somewhat more rounded nuclei. Allantoic capillaries can be seen here and there in the centre of the villi, and they can be followed back to the allantoic vessels which run in the thick layer of allanto-chorionic mesoderm, but as a whole the fœtal blood circulation in the villi is not conspicuous. The trophoblastic walls of the villi are connected at frequent intervals to the walls of the next villus by fine protoplasmic strands forming a complicated system of lacunar channels in which maternal blood is circulating.

The allantoic villi do not penetrate through the entire thickness of the Inner trophoblast, and between their ends and the Basal trophoblast there is still a purely trophoblastic network enclosing blood lacunæ. This network has lost its cellular structure and is now syncytial and may, therefore, be called, to use ASSHETON'S term, a Plasmoditrophoblast (fig. 10). Indeed, the entire Inner trophoblast has now become converted into Plasmoditrophoblast. The Basal trophoblast still retains its columnar cellular structure, and is seen to be surrounding large giant cells (fig. 10).

The Maternal Blood System.

The maternal blood circulation can be followed clearly in this specimen. The two kinds of channels already referred to (pp. 5 and 9) are very distinctly seen.

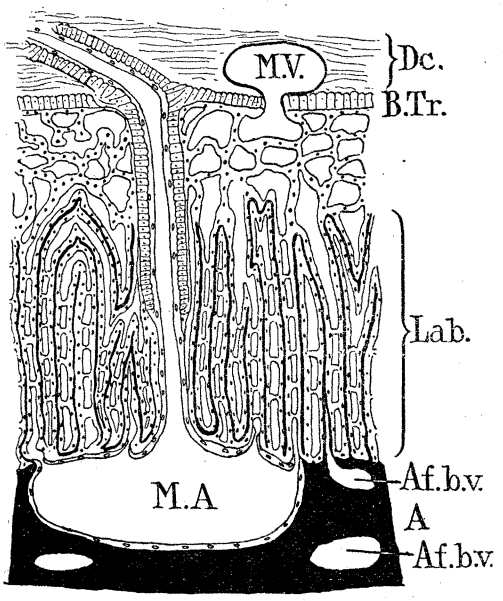
Firstly, there are wide channels, presumably arteries, bounded by a syncytium. They pass through the Basal trophoblast and the labyrinth and widen out into large lacunæ which lie between the broad band of allantoic mesoderm and the labyrinth. These lacunæ have numerous openings into the spaces between the villi. The maternal endothelium is continuous all round the lacunæ and for a very short distance up the sides of the villi. The basal layer of trophoblast follows the endothelium for a considerable distance into the decidua and also through the labyrinth (fig. 11).

Secondly, there are wide thin-walled vessels, presumably veins, with a squamous endothelium which pass through the Basal trophoblast and open into the lacunæ of the

plasmoditrophoblast. Their endothelium is not visible further than the Basal trophoblast.

On the assumption that these two kinds of vessels are arteries and veins respectively, it is evident that the maternal arterial blood is carried direct to the bases of the villi and percolates back through the lacuna channels bounded by the trophoblast. During its passage through these channels osmotic interchanges are effected with the fœtal blood circulating in the capillaries in the villi, and it finally returns to the veins by way of the lacunæ in the plasmoditrophoblast.

The blood system is illustrated diagrammatically in text-fig. 3.



TEXT-FIG. 3.—Diagram illustrating the Maternal and Fœtal blood system in the Placenta. Allantoic tissues are shown by solid black. Trophoblastic tissues, white with black dots. Basal trophoblast columnar cells with dots (*B.Tr.*). Endothelium to maternal artery, white with clear oval dots. *D.C.*, decidua; *Lab.*, labyrinth of allanto-trophoblastic villi; *Al.b.v.*, allantoic blood vessels; *A.*, allantois; *M.V.*, maternal veins; *M.A.*, maternal artery.

Maternal Tissues.

The muscularis is somewhat thicker and the blood vessels larger than in the younger stages. The decidua is reduced to a very thin layer, except where it surrounds the arteries, where it is of a considerable thickness. The giant cells are larger and more numerous.

Perizonal Area.

The allantois is here very thin and is slightly vascular. The maternal uterine epithelium is now restored and forms an even syncytial layer with round lightly-staining nuclei. Flattened glands are present here and there and large blood vessels run between the mucosa and the muscularis parallel to the epithelium.

Specimen 9. (Hyrax 13.)

This is a more advanced specimen than the last. The uterus measures 85 mm. in length and 45 mm. in diameter.

The embryo (fig. 18) is closely covered with dark brown hair and has all the appearance of the adult. The fœtal membranes are the same as in the previous specimen.

The Placenta.

The zonary band is 23 mm. in width. There is but little difference between this and Specimen 8. The villi have elongated greatly; the basal layer of allantoic mesoderm is thicker and its blood vessels larger. Fig. 13 shows clearly the openings of a lacuna of maternal blood into the intervillous spaces and an allantoic vessel passing into a villus.

Specimen 10. (Hyrax 15.)

This uterus was of an unexpectedly large size in comparison with the size of the mother and also with Specimen 9. It measures 110 mm. in length and 70 mm. in diameter at the head end and 65 mm. in diameter across the zonary area.

The embryo appears much the same as in Specimen 9. The zonary area is the same breadth (23 mm.), and it is difficult to understand why gestation has been so prolonged when to all appearance the embryo of Specimen 9 was at full term.

The difference in size may, however, be merely an individual one, and the specimens at the same stage of gestation.

There is no difference in the structure of the placenta, which need not, therefore, be described again.

Summary.

The early development of Hyrax is still unknown, but it is clear that there is no imbedding of the blastocyst, the latter undergoing its development in the uterine lumen.

Before pregnancy the uterus is exceedingly glandular and the glands open into the uterine cavity.

1. In the earliest stage studied (Specimen 3) the maternal mucosa forms a thick band of decidual tissue which is devoid of any epithelium. All over its extent the trophoblast has already undergone marked differentiation, and is in process of attacking the decidual tissue; it consists of (1) a basal phagocytic layer (= "*Basal trophoblast*") composed of columnar cells actively engaged in invading and destroying the superficial decidual tissue, and (2) a much thicker zone of "*Inner trophoblast*" overlying the basal zone and composed of a cellular network, the meshes of which form lacunæ occupied by maternal blood. The embryo and fœtal membranes, apart from the trophoblast, were lost in this specimen.

2. The next two specimens (Specimens 4 and 5) are at much the same stage of development, the embryos are approximately comparable to an 11-day rabbit.

The arrangement of the fœtal membranes is shown in text-fig. 1 (p. 6). The head end of the embryo is bent down and enclosed in the amnion. The extraembryonic cœlom is large and the allantois has grown out as a small vesicle, and has become attached to the mesoderm of the chorion over a very small area. The yolk sac cavity is large, and the unsplit mesoderm of its omphalopleural wall is richly vascularised by the vitelline vessels of the vascular area (except possibly over a small area at the lower pole), as in the next stage. A sinus terminalis is absent. The vitelline vessels of the omphalopleure lie in close contact with the attenuated walls of the lacunæ in the cytotrophoblast. The nourishment of the embryo is therefore probably effected by an interchange of products between the fœtal blood circulating in the vitelline vessels and maternal blood circulating in the trophoblastic lacunæ. The placentation up to this stage is therefore a diffuse *omphalopleural* or *omphaloidean* placentation.

3. An older specimen (Specimen 6) shows that the allantois has markedly increased in size, and has nearly obliterated the extraembryonic cœlom (text-fig. 2). Its walls are thin and very vascular, and its outer wall has now spread over and united with the mesoderm of the chorion practically over the entire extent of the latter. The allantois exhibits a marginal thickening (shown at *A*—*A*, in text-fig. 2), which extends all round the allantois forming a thickened band which is probably the forerunner of the zonary placenta. The omphalopleure of the yolk sac has the same relations as in the earlier specimens. There is a small area at the antimesometrial pole which is not vascular. The embryo is probably nourished at this stage partly by the products conveyed by the yolk sac vessels and partly by the allantoic vessels through the interchange of products between the blood in their vessels and the maternal blood in the lacunæ.

4. In the next specimen (Specimen 7) the omphalopleure of the yolk sac has become split into yolk sac splanchnopleure and chorion. The allantois has grown out and enveloped the amnion and embryo. It is much thickened round the mid-region of the uterine swelling, and there forms a zonary band from which allanto-chorionic villi are pushing their way in between the lacunæ of the Inner trophoblast. Elsewhere the connection between the allantois and the trophoblast is very loose. The allantois is partially divided into four chambers by septa between its blood vessels and its proximal walls. These chambers open into one another below the embryo, but are divided from each other above it and on each side of the zonary band. The placentation at this stage and henceforth is entirely *Allantoidean*.

5. Three older specimens (Specimens 8, 9 and 10), all approaching full term, show a great development of the allantoic villi in the zonary area. They have grown out very greatly and form an elaborate labyrinth sheathed on either side by fine layers of trophoblast, in between which are the lacunæ occupied by maternal blood. The trophoblast has lost its cellular character, except at the outermost edge, where the Basal trophoblast persists and is still attaching the maternal decidua. Maternal arteries penetrate the whole thickness of the labyrinth and open into lacunæ on its

inner border. The maternal veins open into lacunæ immediately within the advancing cytotrophoblastic edge.

The arrangement of the fœtal membranes is the same as in the fourth stage; the allantois in the perizonal area is very thin and bears a few blood vessels. The uterine epithelium is restored in the perizonal area. Gestation is evidently very prolonged, the oldest specimen being very large in proportion to the size of the mother. It is covered with hair and is fully developed.

Conclusions.

The study of the development of the placenta of Hyrax as seen in the material available beyond demonstrating that the definitive allantoic placenta is zonary and of the hæmo-chorial type, throws but little light on the much-discussed question of the affinities of Hyrax. This mammal has been variously described as related to the Rodentia, the Ungulates and Elephas. The placentation certainly bears no resemblance to any Ungulate so far investigated, and although it agrees with that of rodents in being hæmo-chorial it is sharply distinguishable by its zonary form and the detailed character of its trophoblast. At first sight there would appear to be some resemblance to the full-term placenta of Elephas, as described by Assheton and Stevens (1905). There is the same zonary arrangement and a comparable great complexity in the arrangement of the allantoic villi, but in Hyrax there is no syncytial layer of maternal tissue such as is said to surround the villi in the elephant. Were the placentation of Elephas better known, however, it is possible that resemblances might be found, but as far as our knowledge extends at present, it is not possible to make any definite statement. In fact, the placenta of Hyrax, whilst conforming to the hæmo-chorial type typical of the Rodentia, Insectivora, etc., is of so unusual a type, and presents such unique features of its own, that all one is justified in saying is that our present knowledge of the placentation of Hyrax rather tends to emphasise the isolated position which the order occupies in the series of the Eutheria.

GLOSSARY.

1. *A.B.v.* Allantoic blood vessel.
2. *Al.* Allantois.
3. *Al.c.* Allantoic capillary.
4. *Al.e.* Endoderm of allantois.
5. *Al.v.* Allantoic villi.
6. *Am* Amnion.
7. *B.Tr.* Basal trophoblast.
8. *B.V.* Blood vessel.
9. *B.v.al.* Allantoic blood vessel.
10. *Coa.* Coagulum.
11. *Cœ.* Extra embryonic cœlom.
12. *C.U.* Cavity of uterus.
13. *Dc.* Decidua.
14. *Emb.* Embryo.
15. *G.c.* "Giant cell."
16. *Gl.* Glands.
17. *H.G.* Hind gut.
18. *I.Tr.* Inner trophoblast.
19. *L.* Labyrinth of allantoic villi trophoblast.

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GLOSSARY—(*continued*).

20. *Lac.* Lacunæ containing maternal blood.
21. *Leu.* Leucocytes.
22. *M.* Muscularis.
23. *M.A.* Maternal artery.
24. *M.b.v.* Maternal blood vessel.
25. *M.ch.* Mesoderm of chorion.
26. *Mes.* Mesometrium.
27. *M.v.* Maternal vein.
28. *P.tr.* Plasmoditrophoblast.
29. *P.Z.* Perizonal area.
30. *Sy.* Syncytial lining to maternal artery.
31. *Sy. Tr.* Syncytial Trophoblast.
32. *Y.S.* Yolk sac.
33. *Z.P.* Zonary placenta.

DESCRIPTION OF PLATES.

Plate 1.

Fig. 1.—Transverse section through the uterus of a non-pregnant Hyrax (Specimen 1). × 20.

Fig. 2.—A transverse section through a portion of a non-pregnant uterus (Specimen 2). Here the stroma has enormously increased compared with Specimen 1. The glands have very much thicker walls and the stroma is very much more vascular. × 200.

Fig. 3.—Transverse section through the whole width of the uterus and trophoblast of Specimen 3. The maternal glands are reduced greatly in size and lie close to the muscularis. The mucosa has thickened and is very vascular. The region Dc. shows the extent of the decidual maternal tissue.

The figure shows two maternal blood vessels with a definite syncytial lining; that on the right-hand side is beginning to pass through the Basal trophoblast. The Inner trophoblast forms a network of lacunæ containing maternal blood. To avoid confusion the blood corpuscles have been omitted. × 100.

Fig. 4.—A transverse section through the decidua and the trophoblast (Specimen 4). The columnar Basal trophoblast is surrounding the "Giant cells" in the decidua. The maternal blood in the lacunæ, which are surrounded by the cubical Inner trophoblast, contains numerous leucocytes. × 190.

Plate 2.

Fig. 5.—A transverse section through the embryo and fœtal membrane of Specimen 5 showing the attachment of the allantois to the mesoderm of the chorion. × 50.

Fig. 6, Specimen 5.—A transverse section through the entire thickness of the uterus and trophoblast. The decrease in extent of the decidua and the increase of the trophoblast, as compared with Specimen 3, can be realised, as they are drawn to the same scale. The blood corpuscles in the smaller lacunæ are omitted for the sake of clearness. × 100.

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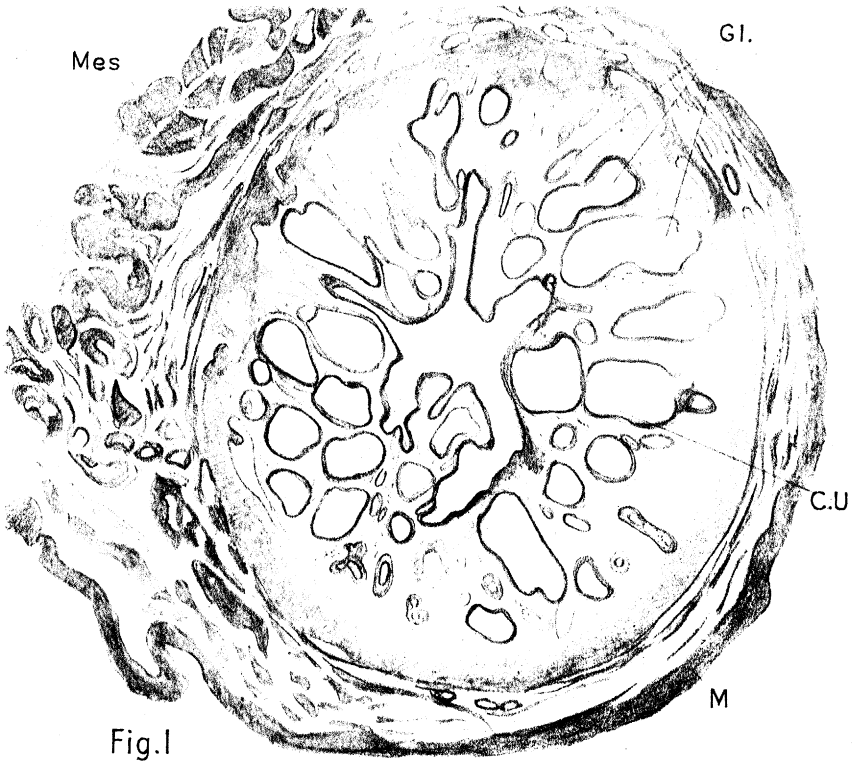

Fig. 1

Fig. 2

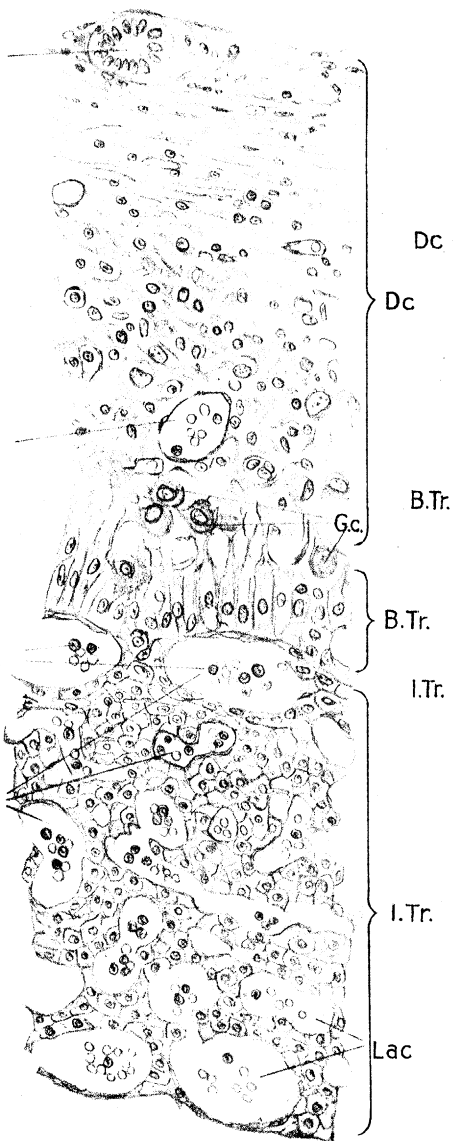

Fig. 4

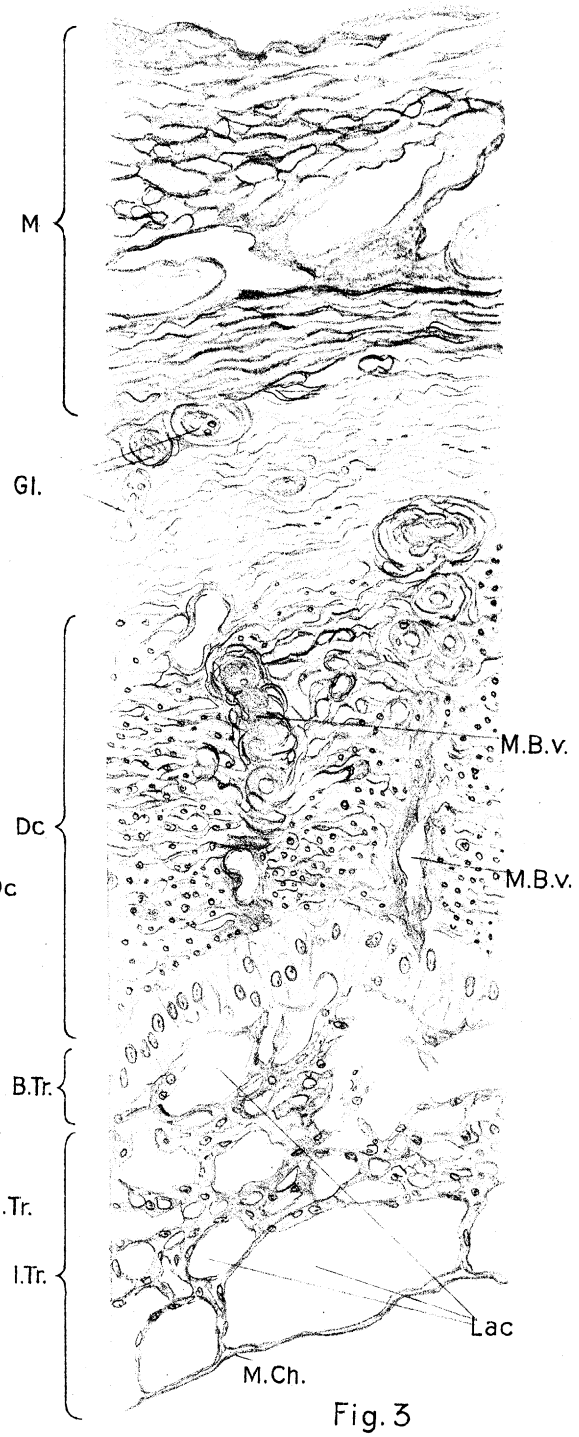

Fig. 3

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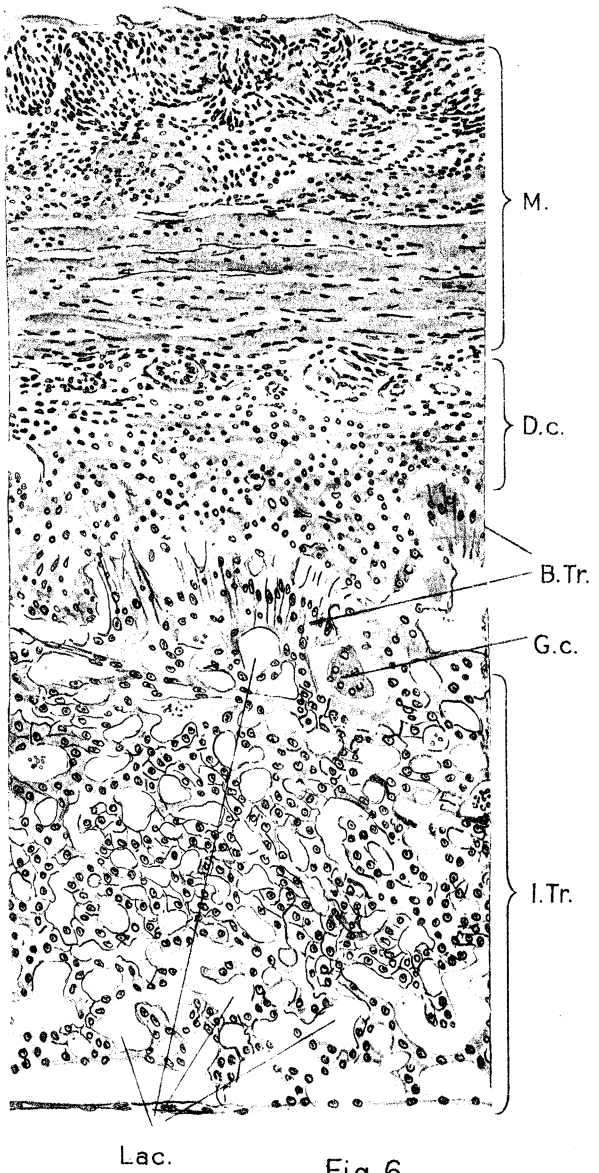

Fig. 6

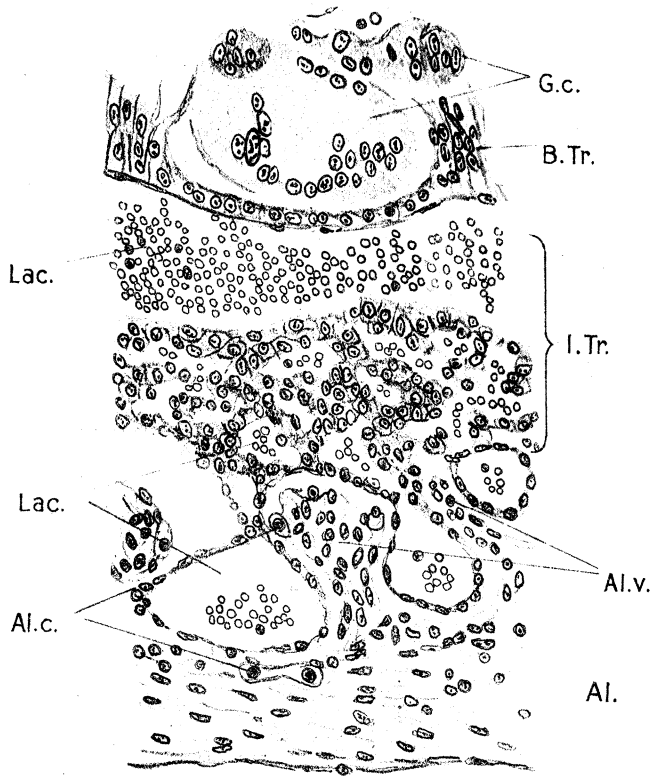

Fig. 7

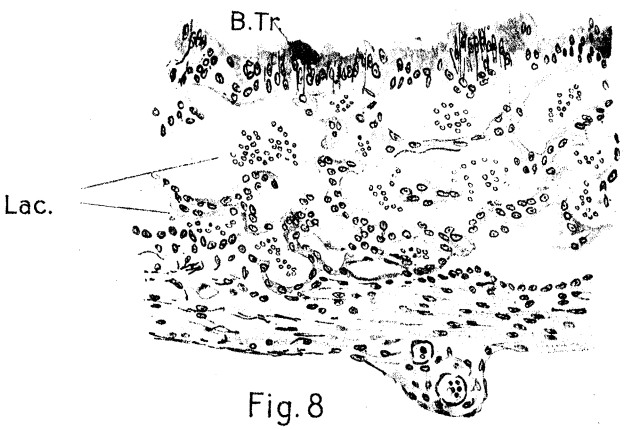

Fig. 8

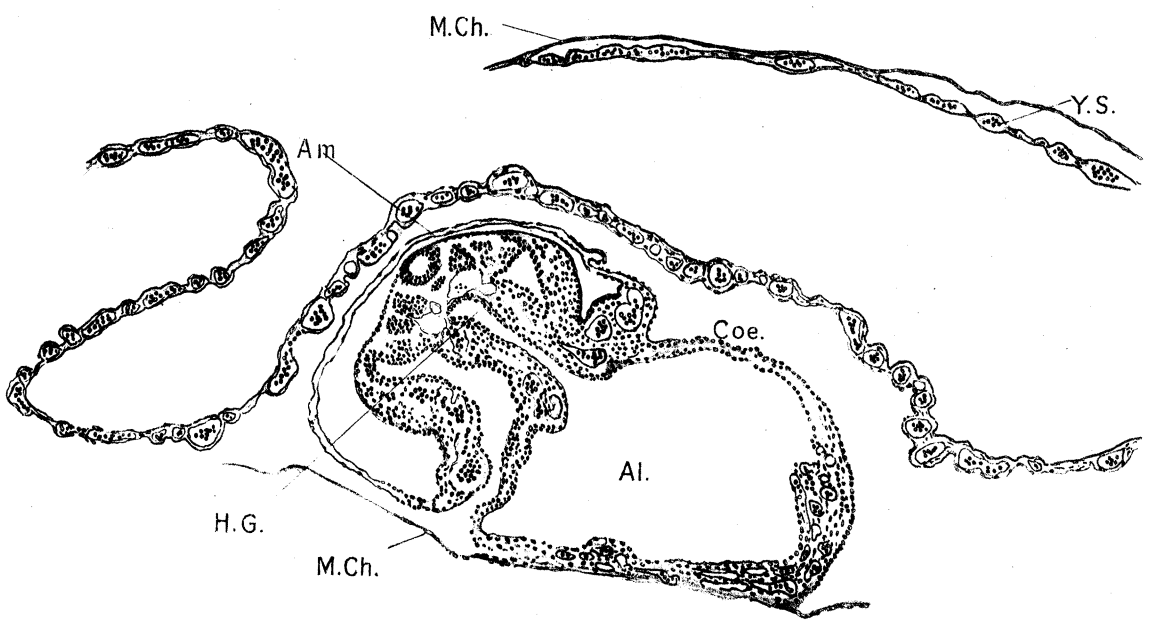

Fig. 5

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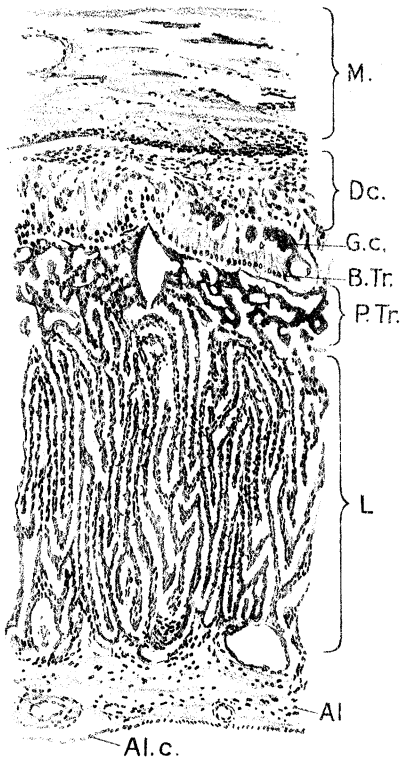

Fig. 9

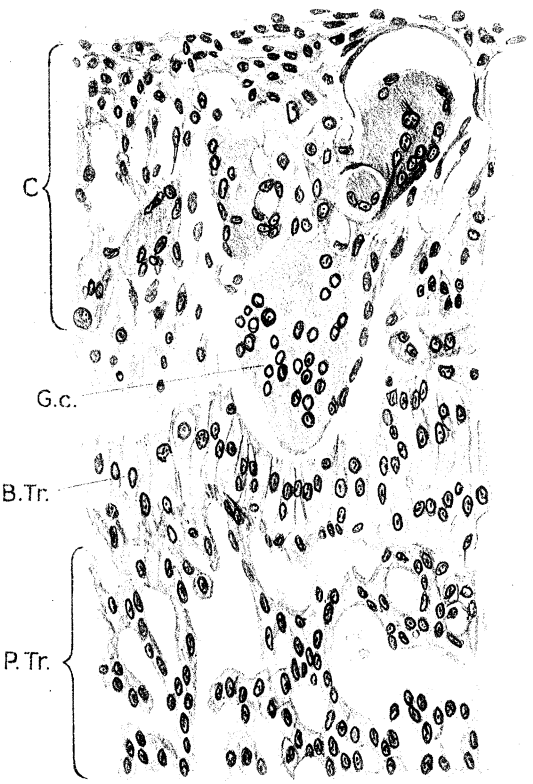

Fig. 10

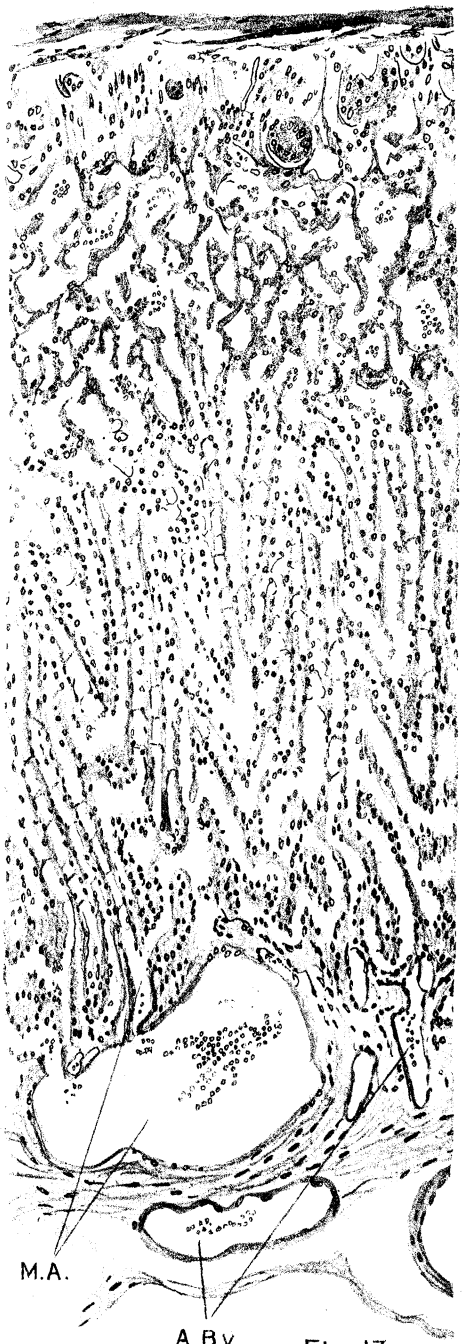

Fig. 13

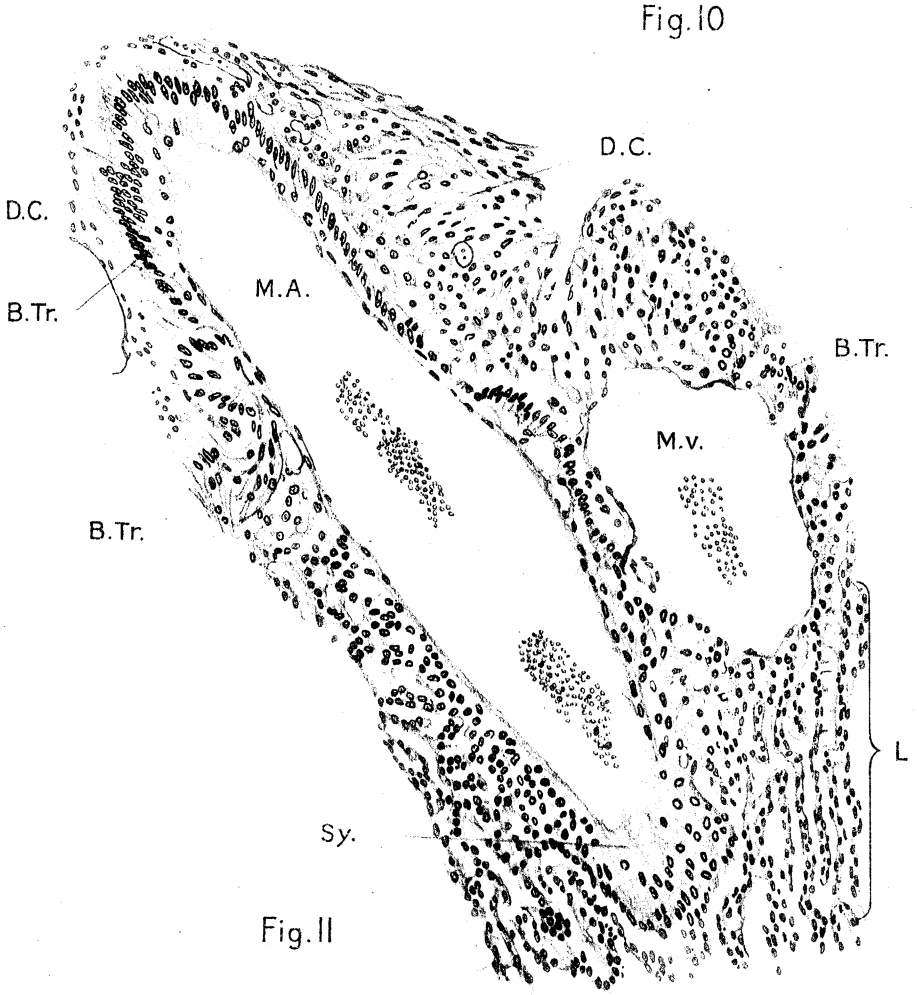

Fig. 11

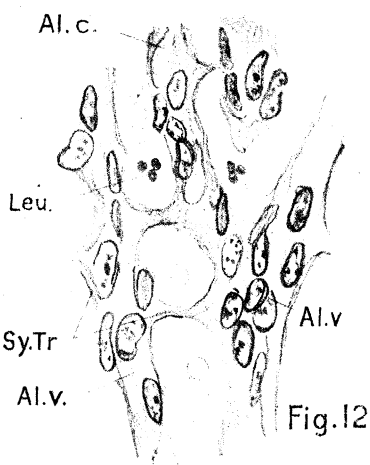

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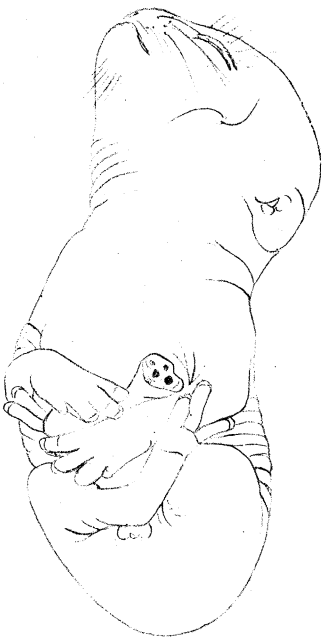
Fig. 14.



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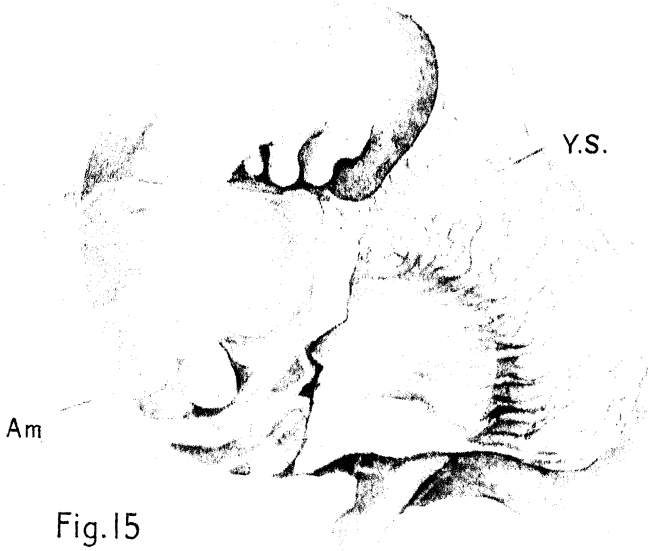

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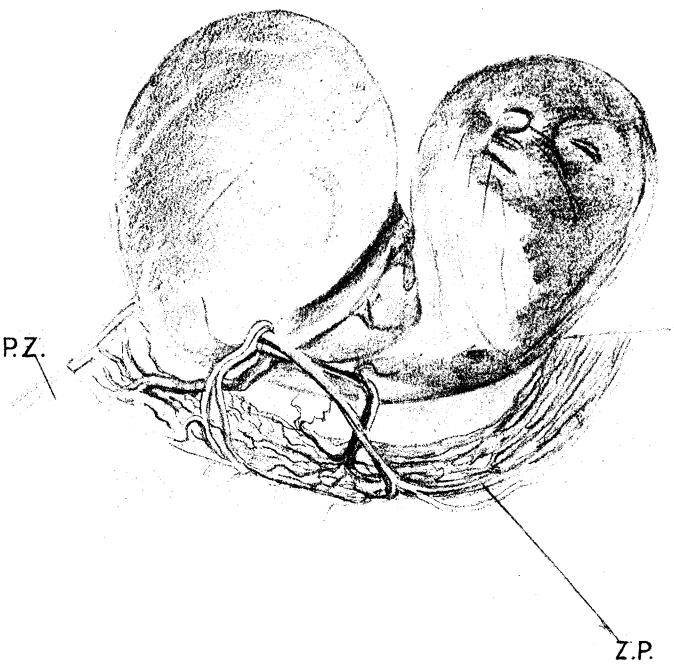

Fig. 18

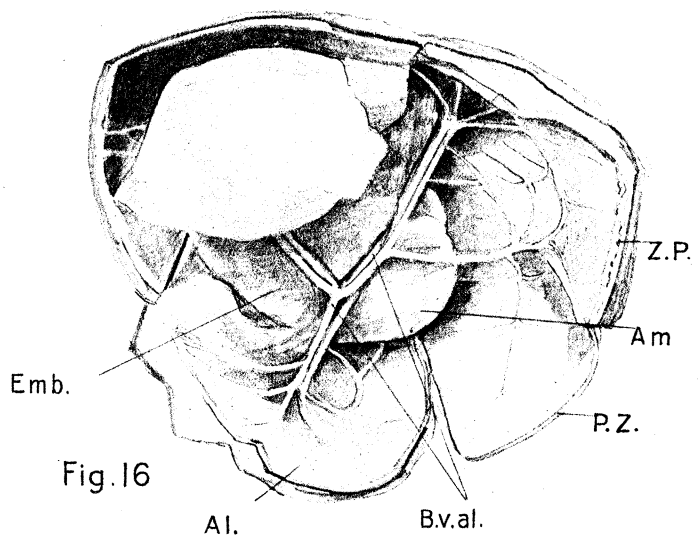

Fig. 16

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Fig. 7, Specimen 7.—A transverse section through the zonary region of the allantoic placenta and the trophoblast. Allanto-chorionic villi can be seen growing in between the lacunæ in the Inner trophoblast. The Basal trophoblast is surrounding a large "Giant cell." × 190.

Fig. 8, Specimen 7.—A section through the perizonal region of the allantois and trophoblast. The drawing is of a lower magnification than fig. 7. × 100.

Plate 3.

Fig. 9, Specimen 8.—Transverse section through the allantoic placenta showing the labyrinth formed by the interdigitation of the allantoic villi and trophoblast. × 60.

Fig. 10, Specimen 8.—Transverse section through a portion of the Decidua, the Basal trophoblast and the Plasmoditrophoblast. The Basal trophoblast is seen to be surrounding a "Giant cell." × 135.

Fig. 11, Specimen 8.—A transverse section through a portion of the maternal tissue and the labyrinth to show the different kinds of maternal blood vessels. The vessel on the left (presumably an artery) is bounded by a syncytial lining and is passing through the labyrinth, where it will eventually open into a large lacunæ. At its upper end the Basal trophoblast has followed its course right up to the Decidua. The vessel on the right (presumably a maternal vein) has just passed through the Basal trophoblast and has opened into a lacunæ in the plasmoditrophoblast. × 85.

Fig. 12, Specimen 8.—A section through a portion of the labyrinth. × 670.

Fig. 13, Specimen 9.—A transverse section through the allantoic placenta, illustrating the fact that the scheme of placentation is essentially the same as in Specimen 8. × 100.

Plate 4.

Fig. 14, Specimen 5.—A surface camera drawing, much magnified, of the embryo enclosed in membrane. The head may be seen to be dipping down into the proamnion and the allantois is grown out.

Fig. 15, Specimen 6.—A much magnified camera drawing of the embryo with the yolk sac folded back.

Fig. 16, Specimen 7.—A dissection of the uterus. The embryo is seen in its amnion lying beneath the four large pairs of allantoic blood vessels. The difference in thickness of the allantois between the zonal and perizonal areas is clearly indicated. The septa between the allantoic blood vessels divide the allantoic cavity into four partially closed chambers. This cannot, however, be very clearly seen in the drawing.

Fig. 17, Specimen 8.—Embryo natural size.

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Fig. 18, Specimen 9.—Natural size. The embryo, covered thickly with fine brown hair, lies within the amnion. The allantoic vessels leading to the placenta have been shown by pushing the embryo slightly to one side.

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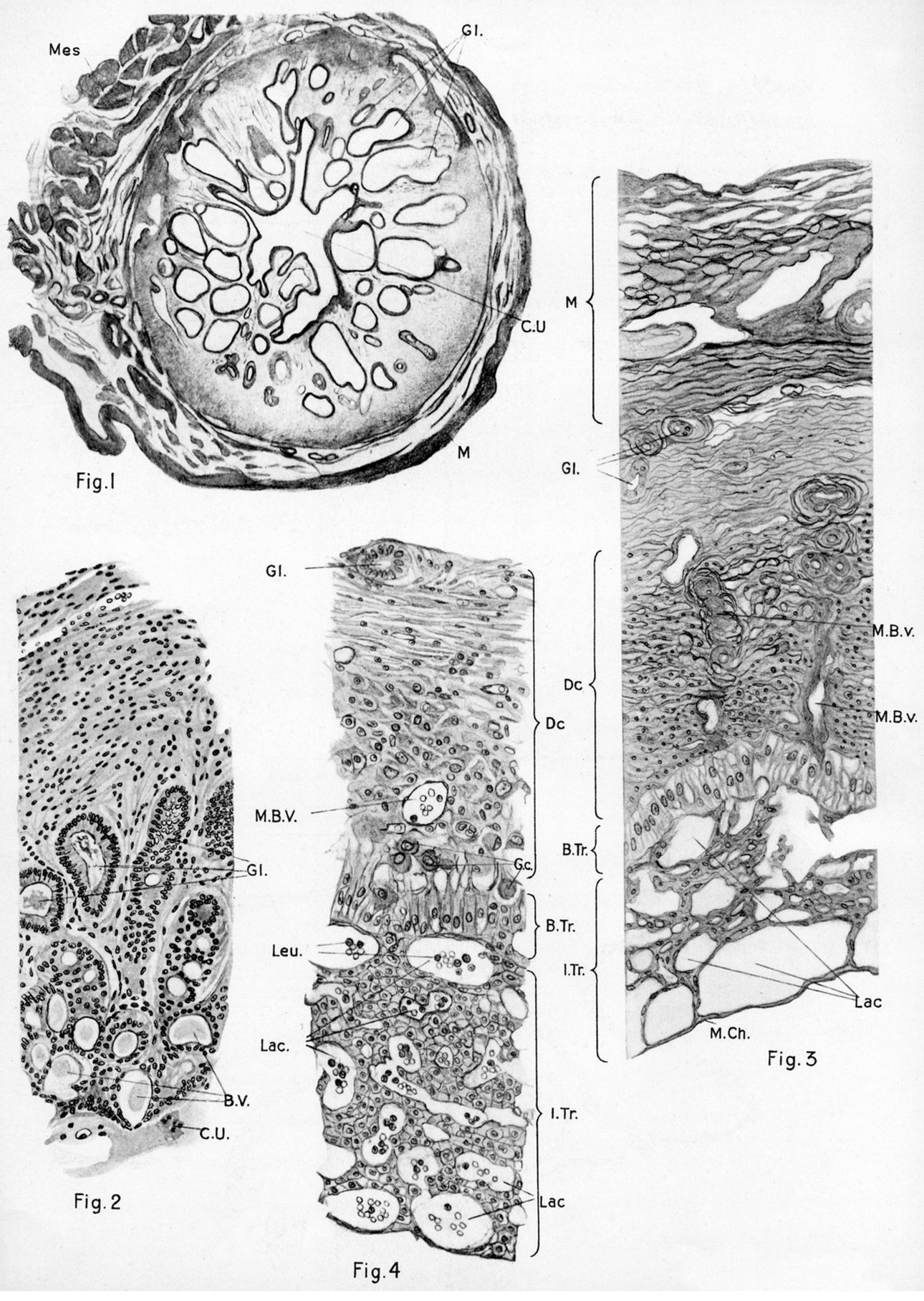

PLATE 1.

Fig. 1.—Transverse section through the uterus of a non-pregnant Hyrax (Specimen 1). × 20.

Fig. 2.—A transverse section through a portion of a non-pregnant uterus (Specimen 2). Here the stroma has enormously increased compared with Specimen 1. The glands have very much thicker walls and the stroma is very much more vascular. × 200.

Fig. 3.—Transverse section through the whole width of the uterus and trophoblast of Specimen 3. The maternal glands are reduced greatly in size and lie close to the muscularis. The mucosa has thickened and is very vascular. The region Dc. shows the extent of the decidual maternal tissue.

The figure shows two maternal blood vessels with a definite syncytial lining; that on the right-hand side is beginning to pass through the Basal trophoblast. The Inner trophoblast forms a network of lacunæ containing maternal blood. To avoid confusion the blood corpuscles have been omitted. × 100.

Fig. 4.—A transverse section through the decidua and the trophoblast (Specimen 4). The columnar Basal trophoblast is surrounding the "Giant cells" in the decidua. The maternal blood in the lacunæ, which are surrounded by the cubical Inner trophoblast, contains numerous leucocytes. × 190.

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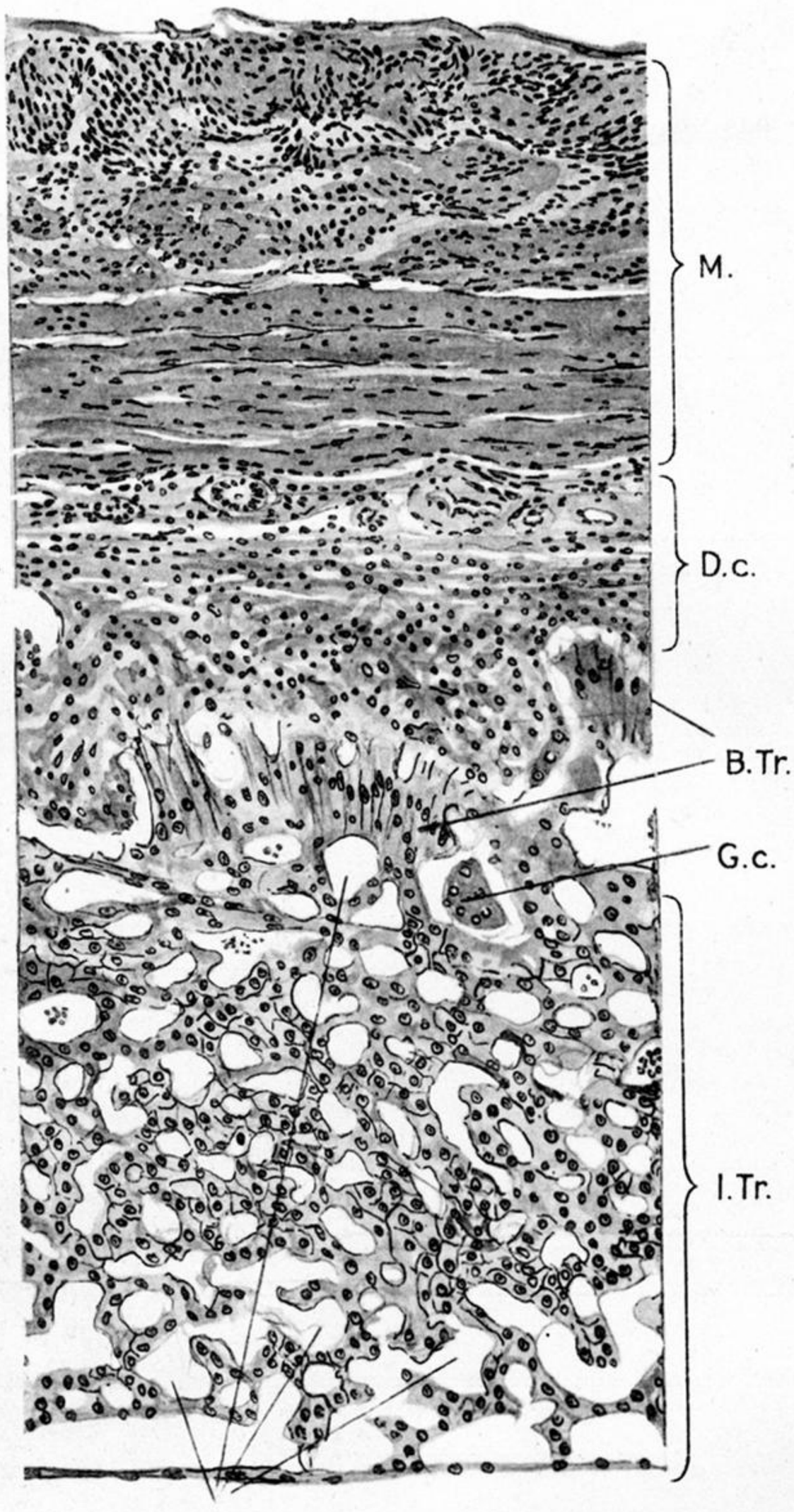

Fig. 6

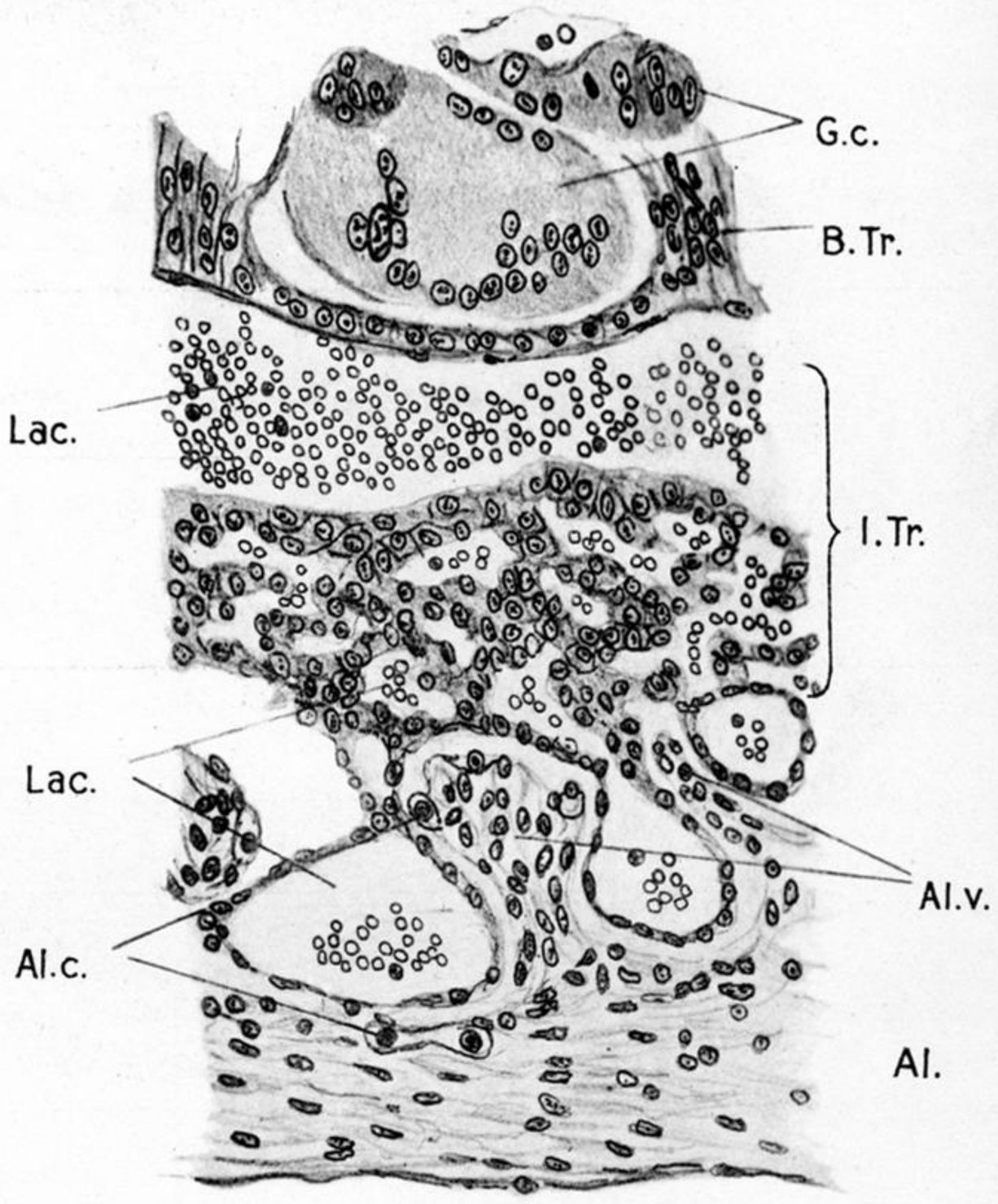

Fig. 7

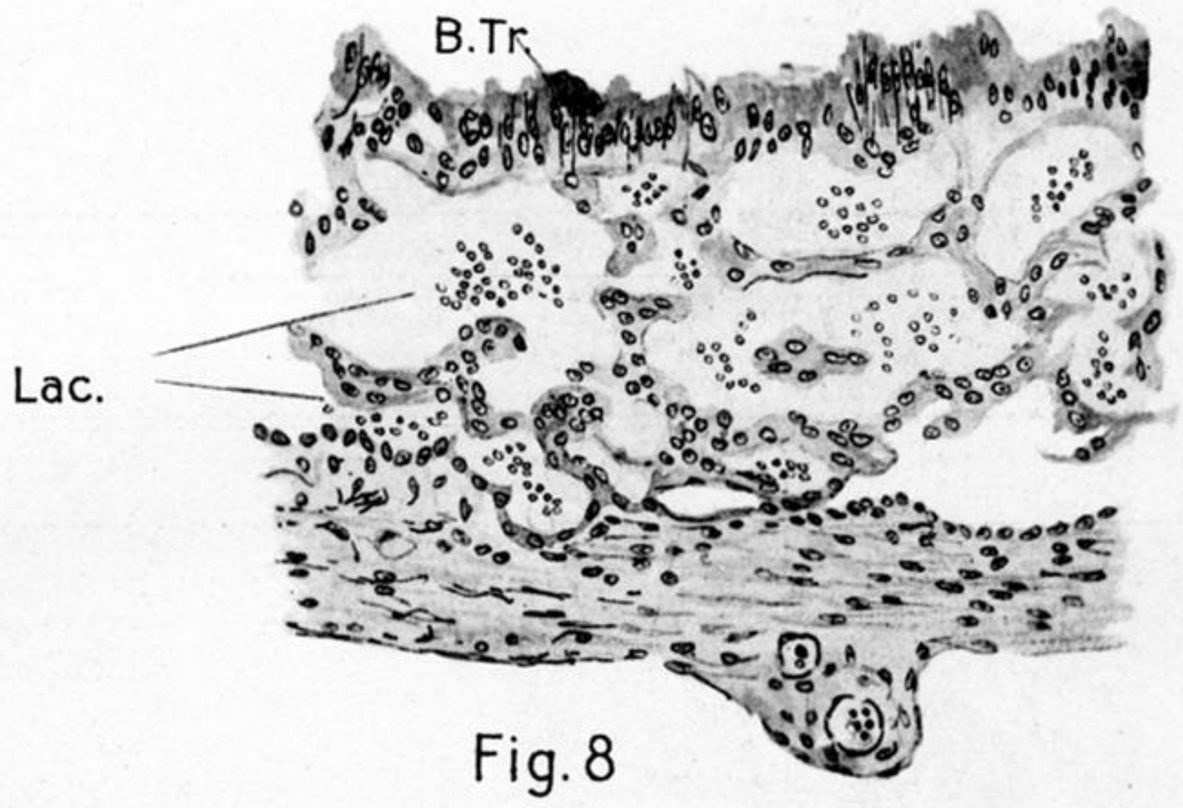

Fig. 8

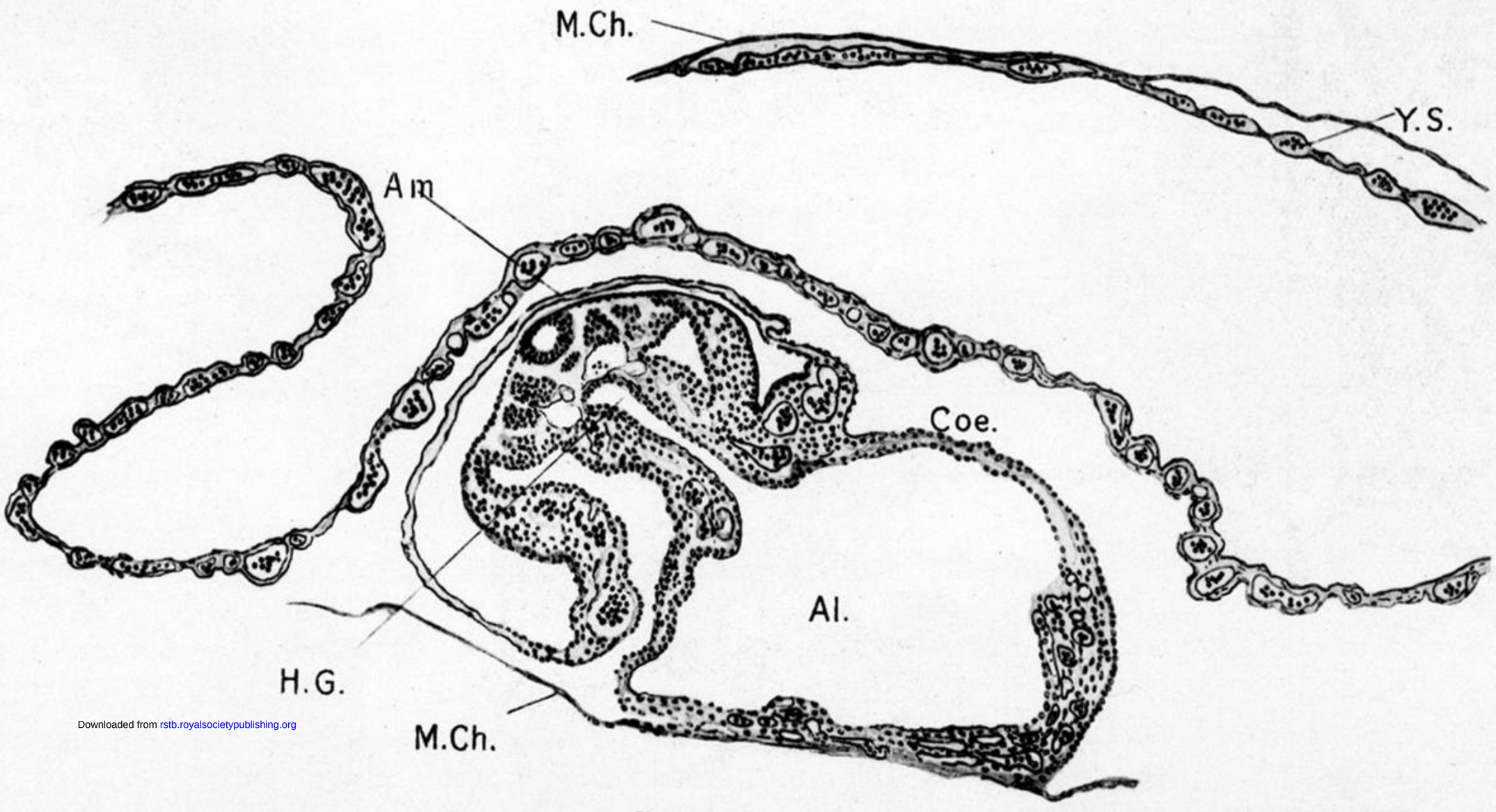

Fig. 5

PLATE 2.

Fig. 5.—A transverse section through the embryo and fœtal membrane of Specimen 5 showing the attachment of the allantois to the mesoderm of the chorion. × 50.

Fig. 6, Specimen 5.—A transverse section through the entire thickness of the uterus and trophoblast. The decrease in extent of the decidua and the increase of the trophoblast, as compared with Specimen 3, can be realised, as they are drawn to the same scale. The blood corpuscles in the smaller lacunæ are omitted for the sake of clearness. × 100.

Fig. 7, Specimen 7.—A transverse section through the zonary region of the allantoic placenta and the trophoblast. Allanto-chorionic villi can be seen growing in between the lacunæ in the Inner trophoblast. The Basal trophoblast is surrounding a large " Giant cell." × 190.

Fig. 8, Specimen 7.—A section through the perizonal region of the allantois and trophoblast. The drawing is of a lower magnification than fig. 7. × 100.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

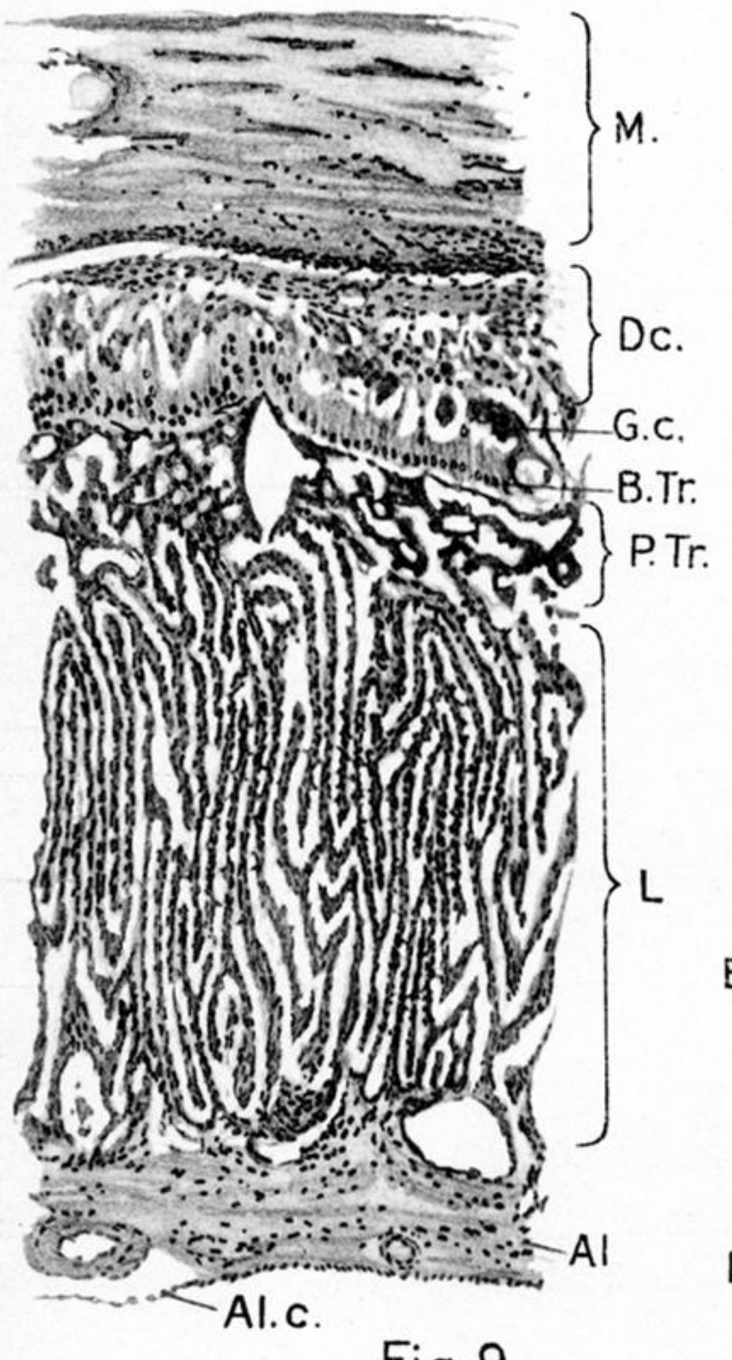

Fig. 9

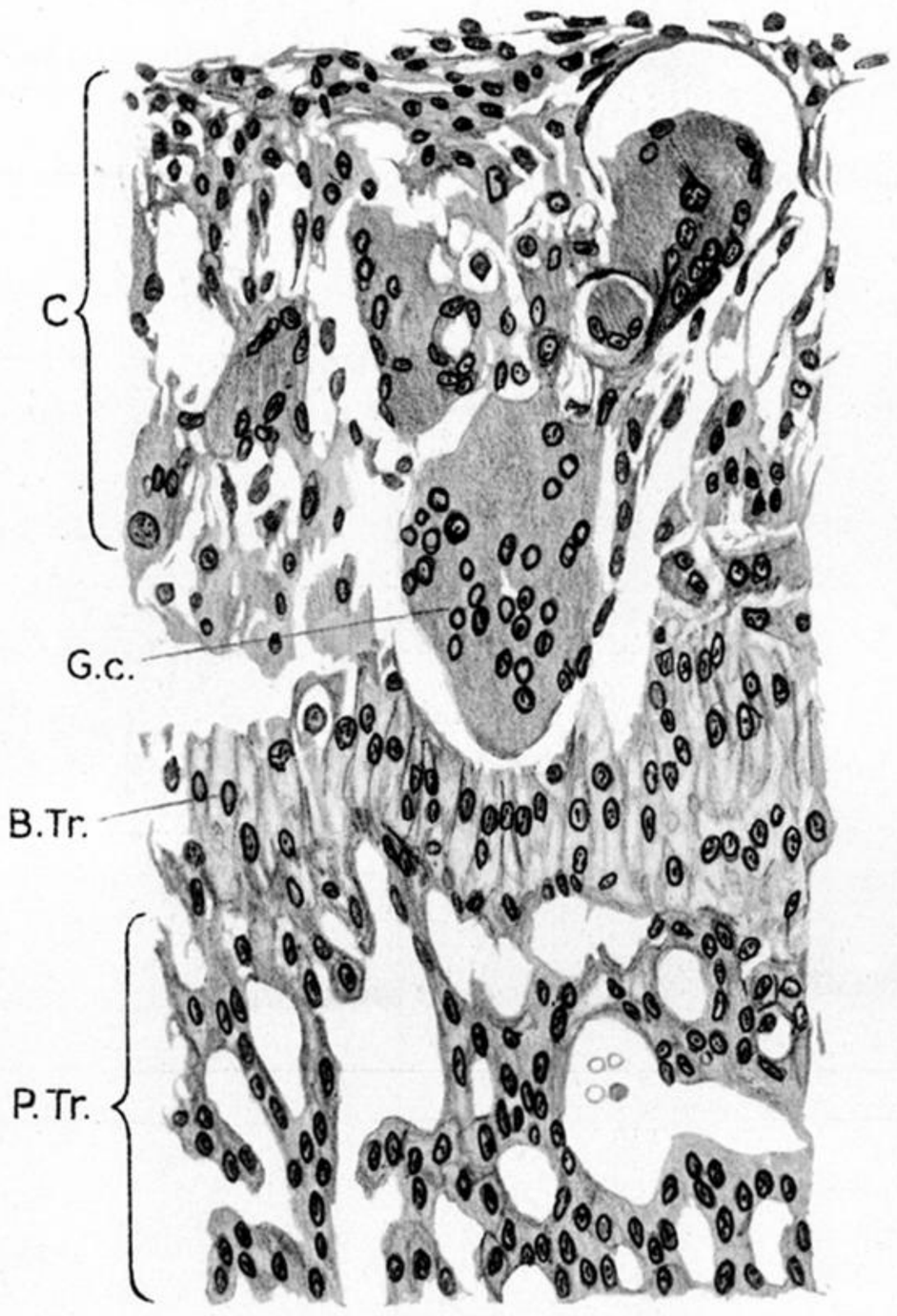

Fig. 10

Fig. 13

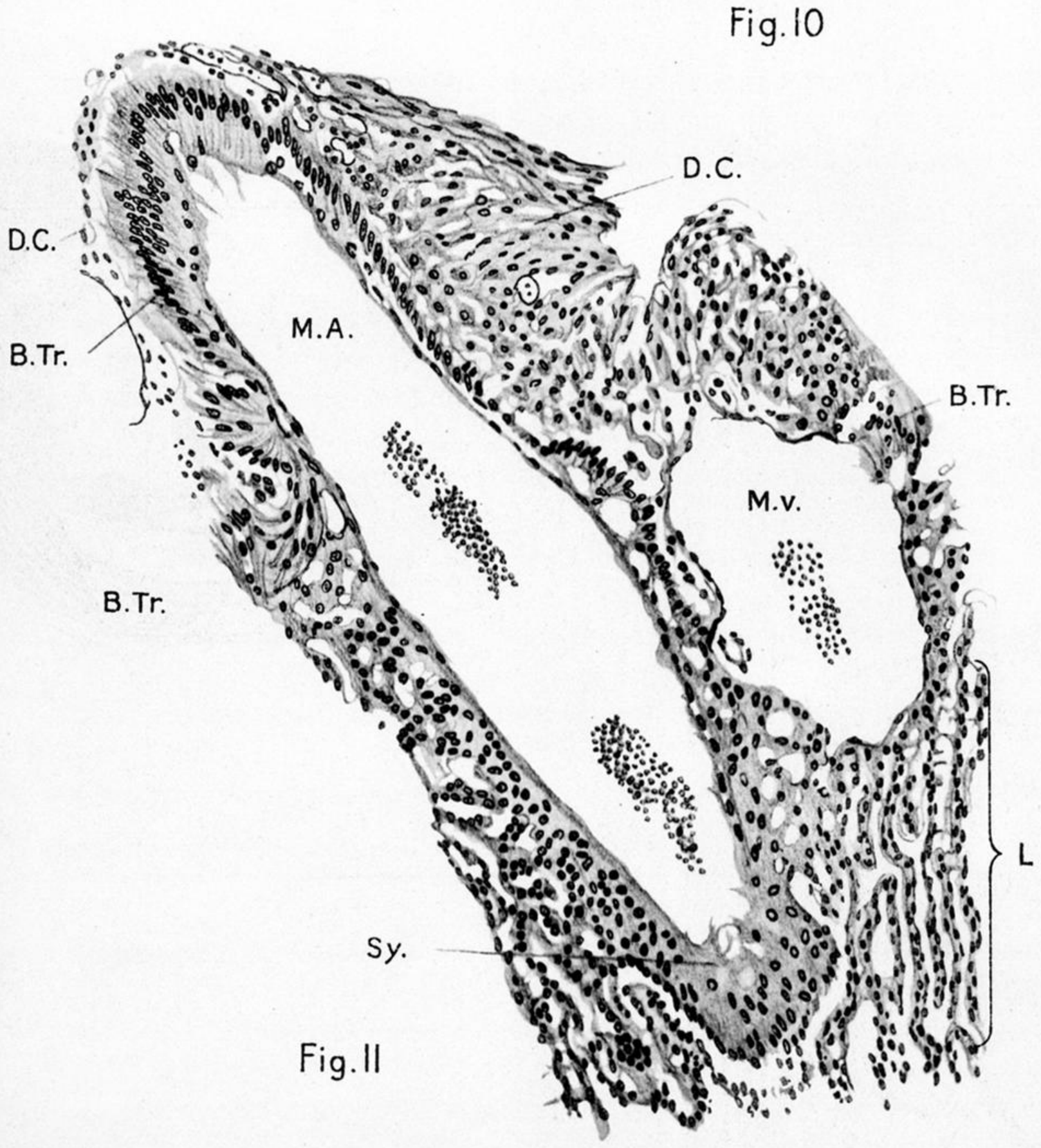

Fig. 11

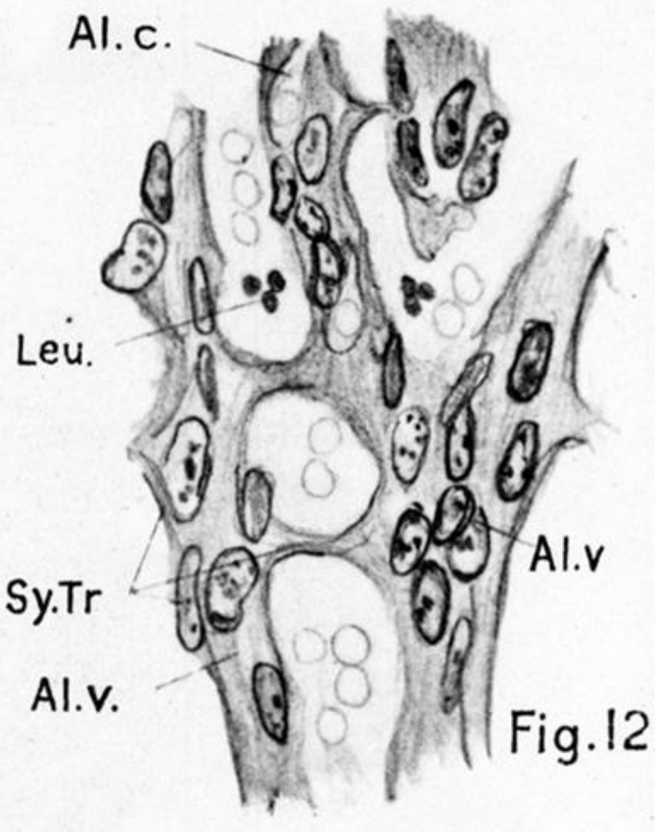

Fig. 12

Plate 3.

Fig. 9, Specimen 8.—Transverse section through the allantoic placenta showing the labyrinth formed by the interdigitation of the allantoic villi and trophoblast. × 60.

Fig. 10, Specimen 8.—Transverse section through a portion of the Decidua, the Basal trophoblast and the Plasmoditrophoblast. The Basal trophoblast is seen to be surrounding a "Giant cell." × 135.

Fig. 11, Specimen 8.—A transverse section through a portion of the maternal tissue and the labyrinth to show the different kinds of maternal blood vessels. The vessel on the left (presumably an artery) is bounded by a syncytial lining and is passing through the labyrinth, where it will eventually open into a large lacunæ. At its upper end the Basal trophoblast has followed its course right up to the Decidua. The vessel on the right (presumably a maternal vein) has just passed through the Basal trophoblast and has opened into a lacunæ in the plasmoditrophoblast. × 85.

Fig. 12, Specimen 8.—A section through a portion of the labyrinth. × 670.

Fig. 13, Specimen 9.—A transverse section through the allantoic placenta, illustrating the fact that the scheme of placentation is essentially the same as in Specimen 8. × 100.

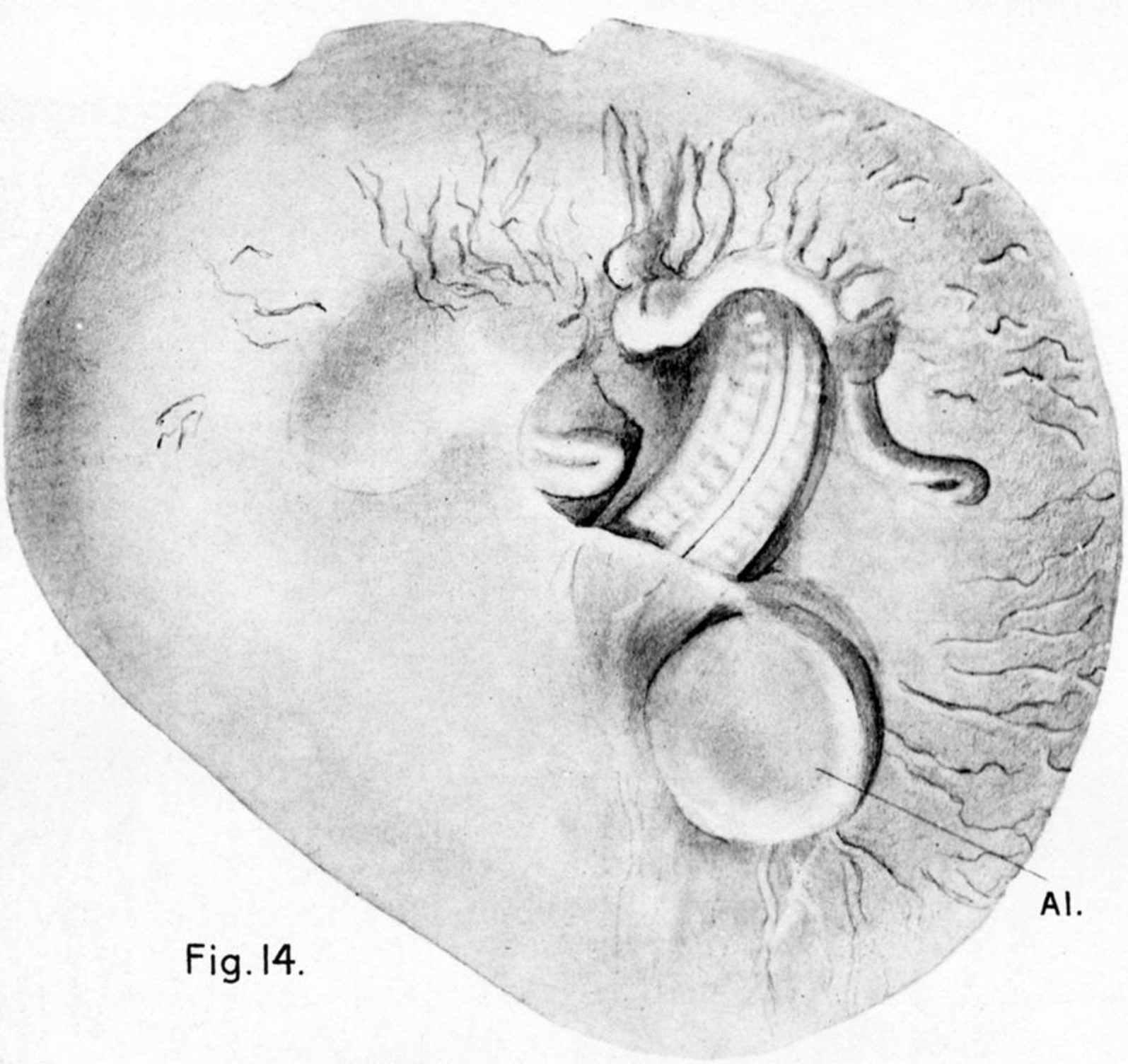

Fig. 14.

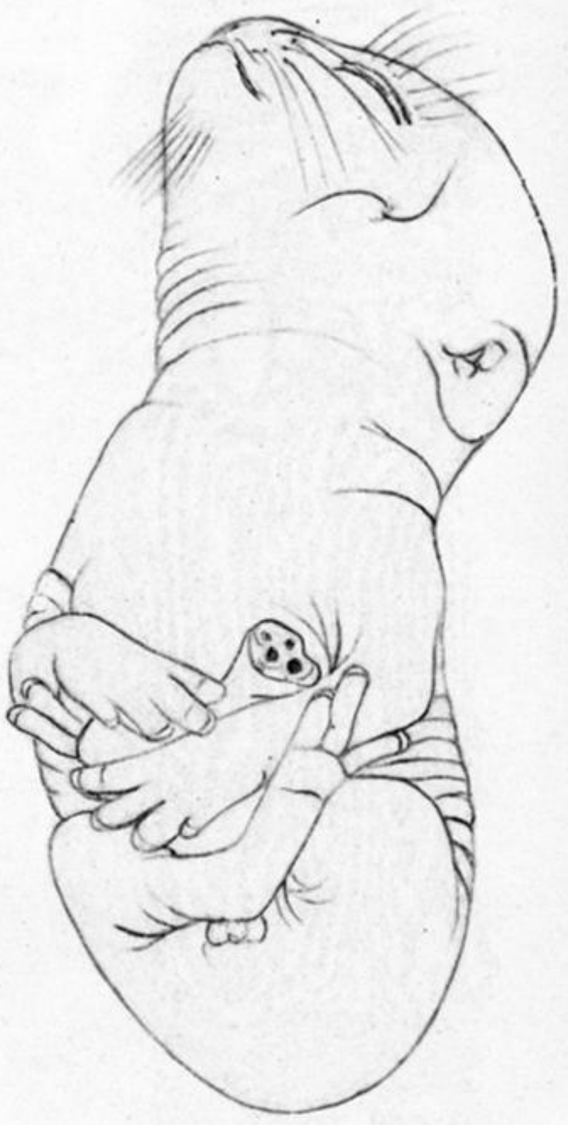

Fig. 17

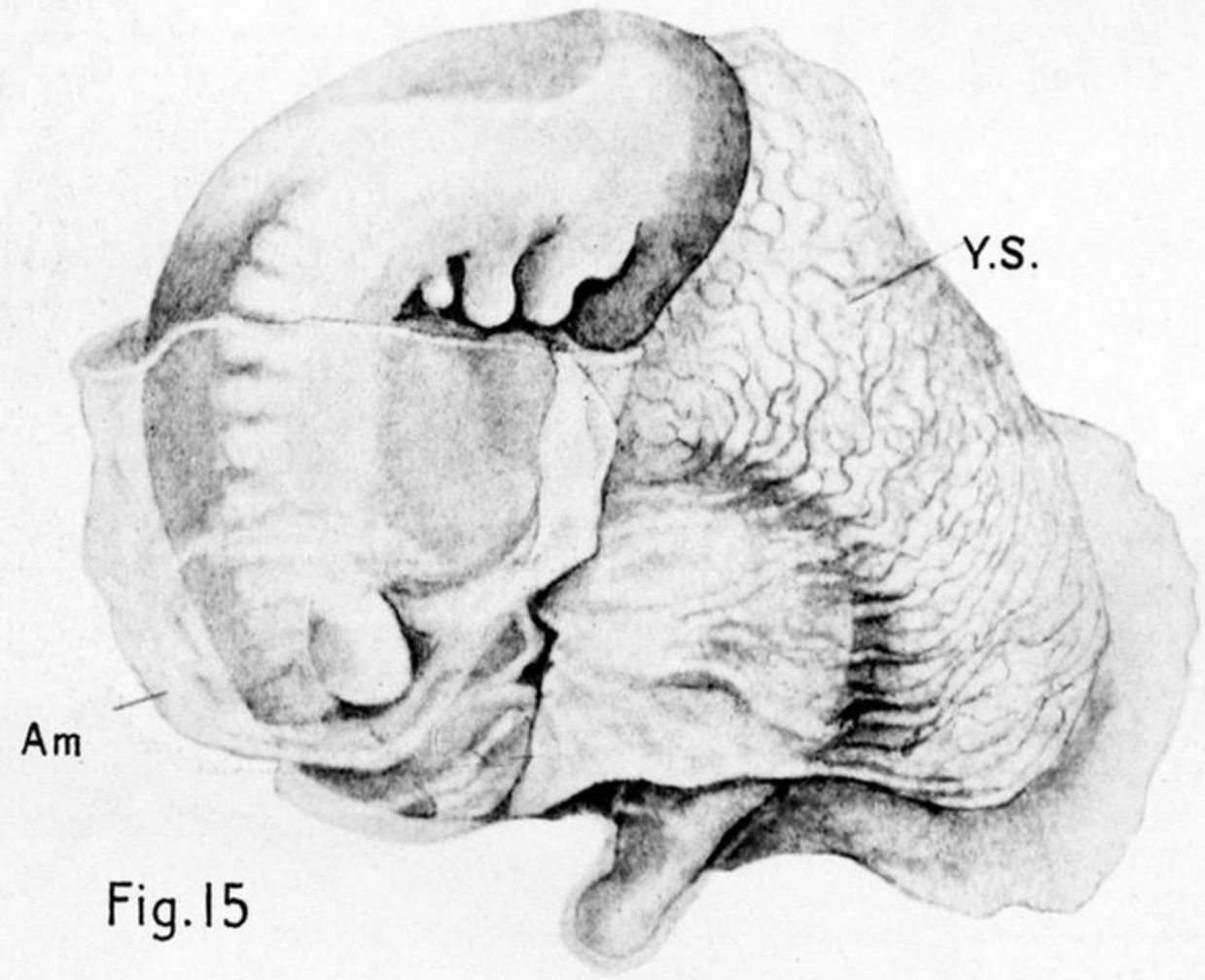

Fig. 15

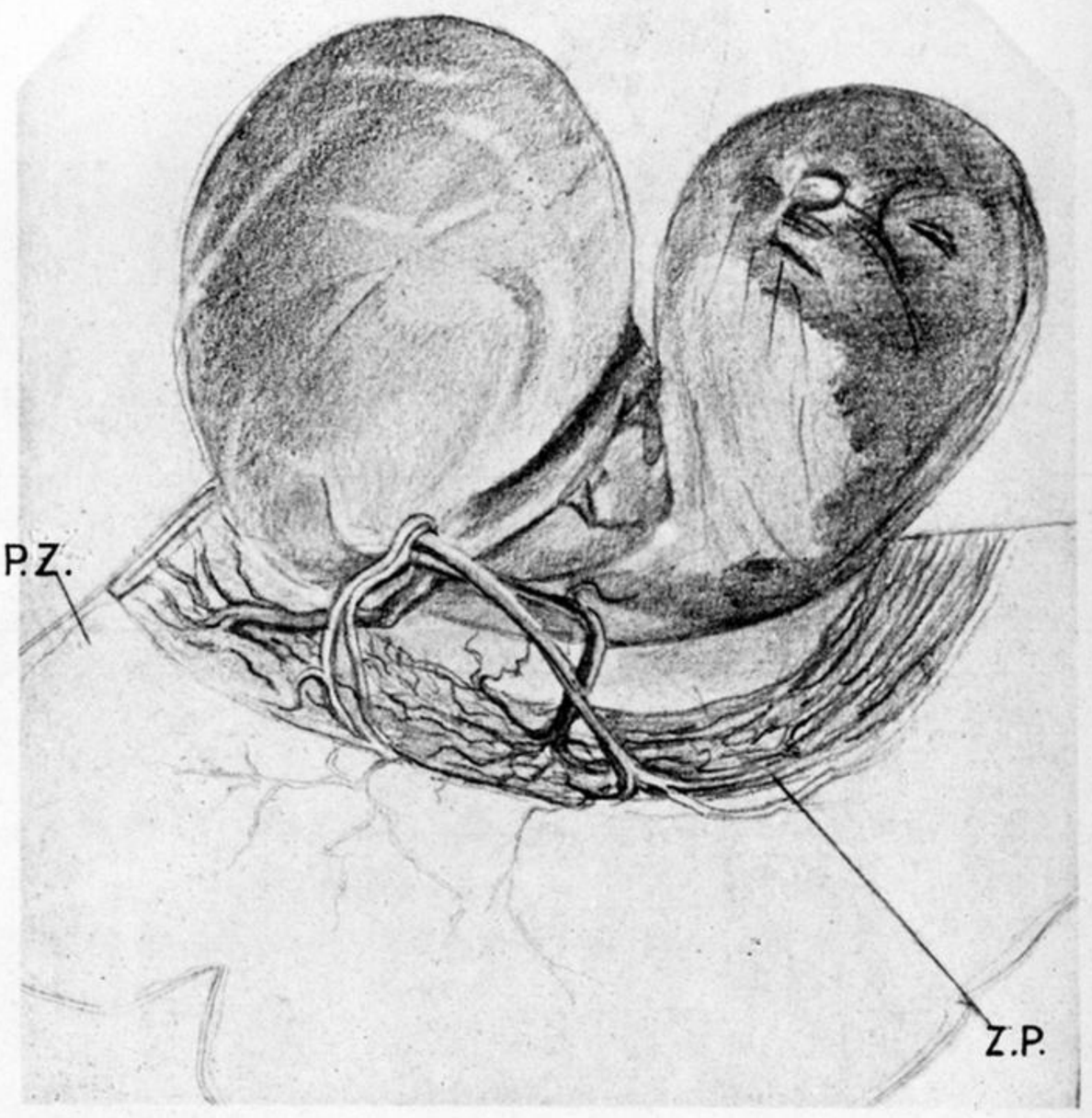

Fig. 18

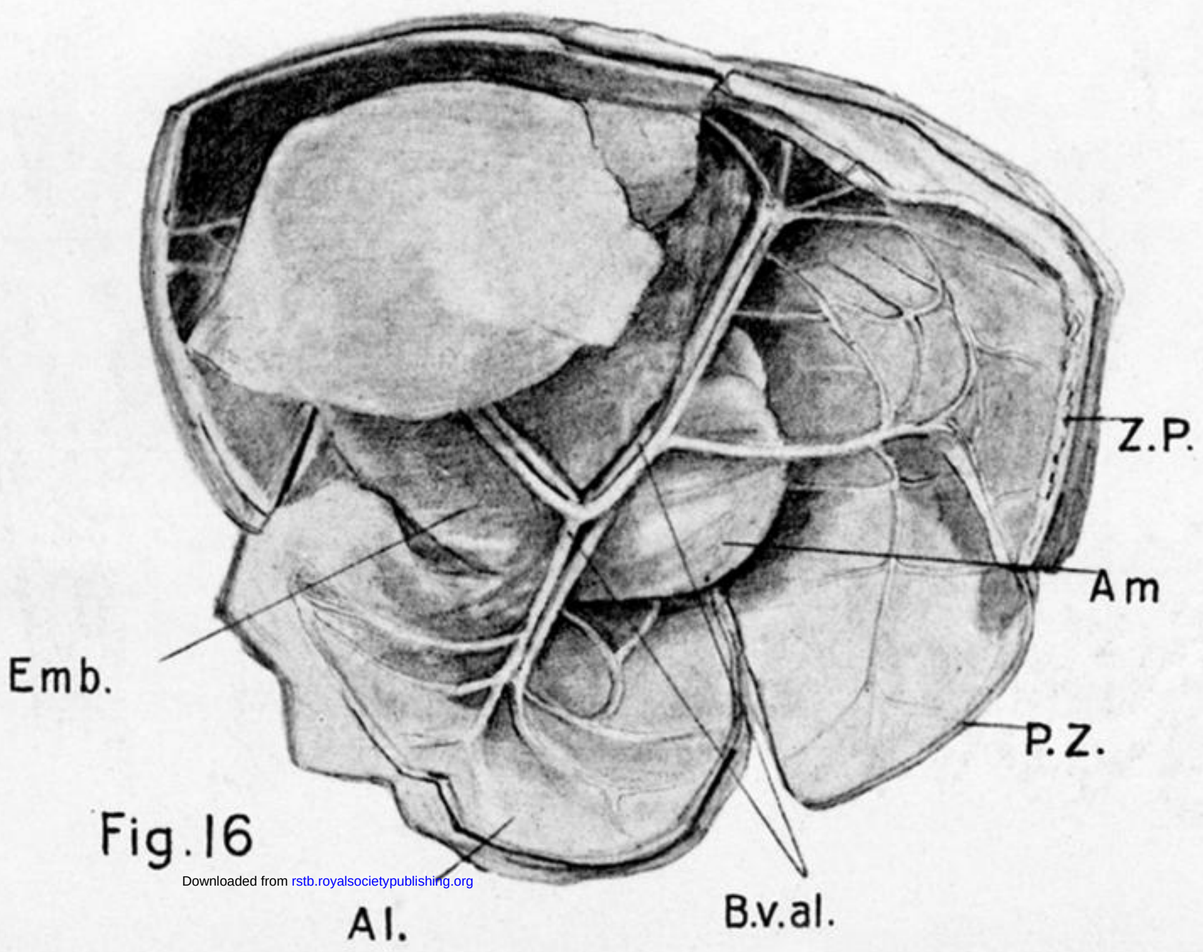

Fig. 16

Plate 4.

Fig. 14, Specimen 5.—A surface camera drawing, much magnified, of the embryo enclosed in membrane. The head may be seen to be dipping down into the proamnion and the allantois is grown out.

Fig. 15, Specimen 6.—A much magnified camera drawing of the embryo with the yolk sac folded back.

Fig. 16, Specimen 7.—A dissection of the uterus. The embryo is seen in its amnion lying beneath the four large pairs of allantoic blood vessels. The difference in thickness of the allantois between the zonal and perizonal areas is clearly indicated. The septa between the allantoic blood vessels divide the allantoic cavity into four partially closed chambers. This cannot, however, be very clearly seen in the drawing.

Fig. 17, Specimen 8.—Embryo natural size.

Fig. 18, Specimen 9.—Natural size. The embryo, covered thickly with fine brown hair, lies within the amnion. The allantoic vessels leading to the placenta have been shown by pushing the embryo slightly to one side.