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The fetal membranes of the aard vark

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With 4 plates

Introduction

The aard vark or Cape anteater, *Orycteropus*, is the only recent genus of the unique order *Tubulidentata*. Its phylogenetic affinities are uncertain. In spite of the fact that it is not a rare animal, and that it is also an extremely interesting one zoologically, little is known of its fetal membranes.

TURNER (1876) described the membranes of two almost identical near-term specimens (total lengths — 48 and 50 cm), but was uncertain as to whether or not the placenta was deciduate. DE LANGE (1931 and 1933) showed that it is endotheliochorial, and possesses a folded villous border chorion suggestive of the structure of the carnivore hematome. HORST (1949) described the membranes of an embryo of 8 mm CR in a gestation sac of 24 mm diameter. His is a careful account of this formative stage and contributes much toward an understanding of the late stages. Also his description of the ovaries points up the wide variety of conditions that occur in these organs in different mammalian groups, and the necessity of a comparative viewpoint in their interpretation. Although the aard vark is known to bear but a single young, HORST found five identical corpora lutea, two in the ovary of the pregnant side and three in the other, a situation indicating possible multiple ovulation followed by uterine «selection», as in *Elephantulus* (HORST, 1941).

The present specimen contributes information not given in TURNER's and DE LANGE's accounts of late stages, but it is imperative that more early stages be studied, if the nature of the aard vark membranes is to be thoroughly understood. This could greatly clarify the now puzzling phylogenetic position of the group.

Material

The pregnant aard vark uterus on which this description is based was loaned to the author by the Chicago Natural History Museum (Cat. no 56801) through the courtesy of Mr. D. D. DAVIS and Dr. KARL P. SCHMIDT. It was collected on June 5, 1930 at Maun (Shorobe), Bechuana-land, Africa by the Vernay-Lang Expedition. The pregnant horn had been dissected free of all other parts, unfortunately even of the ovary and most of the oviduct, and after a short slit had been made in the uterine wall, it had apparently been fixed in formalin and stored in alcohol. Histological preservation is fair, much better than usual in such collections which are too often merely «pickled» directly in alcohol.

Description

The pregnant horn formed an oval mass approximately $26 \times 17 \times 11$ cm, weighing, without the liquors, 1400 gms. The female fetus (Fig. 1) measures 24 cm CR, 43 cm total length (tail 12 cm), and weighs 1093 gms. The umbilical cord is 27 cm long. About 9 cm from the placental surface the allantoic duct begins to widen rapidly separating the cord vessels (Fig. 4). The cord proximal to this point averages about 8 mm in diameter and contains two arteries and one vein and a prominent allantoic duct with a lumen about 2 mm in diameter. It is moderately twisted, grooved between the vessels, smooth, and has no epithelial papillae.

The placenta (Fig. 4) is a broad, thin, incomplete zonary type, 31 cm in length, 17,5 cm in greatest width, 15 cm at its narrowest. Since the uterus is about 36 cm in internal girth, there is a gap in the placental girdle of about 5 cm at the antimesometrial border. Measured on its long axis the uterus extends about 4 cm beyond the placenta at the tubal end and 6 cm at the cervical end. The greatest thickness of the placenta, including the uterine wall, is 1 cm. The uterine wall is only about 2 mm thick so the greatest thickness of the placenta at a gyrus is 8 mm and its usual thickness about 4 mm. Its fetal surface is deeply grooved, especially centrally, producing long tortuous gyri usually about a centimeter in width and directed roughly circumferentially (Fig. 4). The main arborization of the allantoic vessels is on the fetal surface of the gyri. They often bridge the sulci, but frequently enter and are lost to sight in them for considerable distances. The single umbilical vein bifurcates about 10 cm from the placenta, each branch accompanying an artery for about 7 cm,

where each pair of vessels then divides again and begins its distribution to its half of the placenta. There is considerable overlap of distribution to the two halves near the cord attachment.

The allantoic vesicle fills practically the entire exocoelom. It starts in the cord about 9 cm from the placental surface by rapid funneling out of the duct which reaches a diameter of about 5 cm at the region of vessel attachment to the placenta (Fig. 4). The umbilical vessels divide as they pass along this pyramid toward the placenta, producing the four artery and vein sets described above. These form the four edges of the pyramid and at its corners attach to the placenta. From these vessel attachments, delicate transparent allantoic septa about 1 cm high extend outward between the amnion and chorion (both placenta and chorion laevi), dividing the allantoic vesicle into four large lobes (Figs. 2 and 4). These liquorfilled lobes, which must average about 1 cm in thickness in the living, form an encircling cushion between the amnion internally and the chorion externally.

The septa and allanto-amnion are very thin, yet both contain a network of fine nutrient allantoic vessels. The non-placental portions of the chorio-allantoic membrane are also relatively avascular and thin.

From a point on the cord about 4 cm from the placenta, a delicate, somewhat nodular, whitish strand of tissue, 0,5 to 1,5 mm wide and 22 cm long passes between the layers of the allanto-amnion to the gap between the ends of the placenta at the antimesometrial side (Figs. 2 and 4). It ends in a slight dilatation at the junction of the four allantoic septa. There is a wrinkled and slightly thickened area of the chorion laevi about 1×3 cm at this place. This strand must be the vitelline duct. Its point of attachment to the chorion corresponds to the antimesometrial bilaminar yolk sac placenta described by HORST in his early stage. Thus the yolk sac of *Orycteropus* is probably very similar to that of *Equus* (AMOROSO, 1952).

In general structure the labyrinth (Fig. 5) is, indeed, as TURNER described it, much like that of the horse. The latter is epitheliochorial and contains many chorionic vesicles («areolae», «absorptive areas») and mucosal glands, while that of the aard vark is distinctly endotheliochorial and also has many chorionic vesicles, but few mucosal glands (Figs. 8 and 9). Yet, in both, the ridges and grooves of the allantochorion fit intimately into reciprocal grooves and ridges of the mucosa (Fig. 5). A labyrinth similar to that of *Orycteropus* would be formed in a placenta such as that of *Epuus*, if the uterine epithelium should disappear and the syn-

trophoblast should invade a thin zone of subepithelial stroma and engulf the maternal capillaries. It is conceivable that the endotheliochorial condition in *Tubulidentata* may have evolved in exactly this way from a primitive epitheliochorial condition.

The relatively simple nature of the aard vark endotheliochorial placenta is shown in Figure 8, where it is seen that the endothelial walls of the dilated maternal capillaries adjoining the mucosal stroma are often incompletely surrounded by trophoblast. Then too, stromal arterioles often retain their muscular and adventitial layers for some distance within the trophoblast. In poorly fixed and stained areas this simulates in appearance the hyalin membrane of certain carnivore placental tubules (*Mustela*, *Mephitis*, *Procyon*). However, the latter is probably a basement membrane produced by the maternal endothelium.

Although most of the placenta of *Orycteropus* is from 3 to 6 mm thick, the labyrinth proper has a thickness of only 0,2 to 0,5 mm (Fig. 5). This is far thinner than the labyrinths of other animals having fetuses of comparable or even smaller size; dog — 5 mm, racoon — 4 mm, cat — 4 mm, bobcat, *Lynx rufa* — 5 mm.

It seems proper to consider the labyrinth of the aard vark as of only the thickness of the trophoblastic layer because this layer so obviously simply coats the fetal surfaces of the broad, relatively undifferentiated stromal ridges and grooves of the mucosa. These are no more a part of the labyrinth than is the basal decidua of a rodent, or the basal gland layer of a carnivore.

The cores of these mucosal ridges are composed of simple areolar connective tissue, and contain the larger mucosal arteries and veins (Figs. 5 and 7). Their periphery consists of small rounded cells, presumably undifferentiated fibroblasts, together with a few larger cells whose nuclei resemble those of the trophoblast (Fig. 10). There is insufficient evidence in the material at hand to determine the origin of either of these cell types, and no statement can be made as to their homology with either trophoblastic giant cells or decidual cells.

The bases of the mucosal ridges are connected to one another by the same two layers of stroma (Figs. 5 and 7), — the round cells adjacent to the trophoblast, and the outer areolar layer. Between the areolar layer and the myometrium there is often an even thinner zone containing coarse collagenous fibers and an occasional flattened gland remnant with cuboidal epithelium (Fig. 5). The collagenous layer does not enter the mucosal ridges; nor have any glands been seen within them. There is no

decidua in the sense of a layer of modified stromal cells laden with glycogen and lipid, and there is no spongy basal zone of hypertrophic glands as in carnivores. The fixed placenta separates easily from the uterine wall at the areolar layer, but it is unknown where the separation occurs at natural birth.

Throughout the placenta there are scattered chorionic vesicles. These are villous, nonsyncytial spots in the allantochorion, usually from 1 to 4 mm wide, presumably covering the mouth of a uterine gland, yet glands have not been seen in relation to them in the present specimen. HORST (1949) describes an early stage of these. They usually extend through the entire depth of the placenta and are therefore very similar to those of the pig, mare, and the moles (MOSSMAN, 1939).

For about 3 mm beyond the edges and ends of the placental zone the allantochorion is noticeably ridged and its trophoblast is high columnar. In this marginal area there is some extravasation of maternal blood and some phagocytosis of maternal red corpuscles by the trophoblast; therefore it is probably comparable to the carnivore hematome, but much smaller and without gross accumulation of maternal blood. The domestic cat has a similar relatively bloodless but globuliferous phagocytic border zone, and artiodactyls commonly show the same conditions at the margins of the cotyledons, but in all these forms this zone is much wider than that of the aard vark.

The chorion laevi is finely vascular and is covered by a low columnar trophoblast. No specialized areas have been seen in it. The uterine wall is so thin and conforms so closely with the chorionic surface, even at the tubal and cervical ends, that practically all portions of the chorion are in contact with uterine mucosa.

Discussion

The definitive membranes of *Orycteropus* are characterized by the persistence of a large allantoic vesicle. In this basic character they are like those of *Lemuroidea*, *Pholidota*, *Cetacea*, *Carnivora*, *Proboscidea*, *Hy-racoidea*, *Sirenia*, *Perissodactyla*, and *Artiodactyla*. Considering the allantois together with other conservative characters, such as those of the yolk sac and chorion, the resemblance is the closest to the *Perissodactyla* as represented by *Equus*; but unfortunately the membranes of neither the horse nor the aard vark are adequately understood. There is some resemblance to *Manis*, but to no other edentate.

The fact of the epitheliochorial condition in *Equus* and the endotheliochorial in *Orycteropus* does not indicate wide phylogenetic separation, as more than one GROSSER type is known to occur within orders, — endotheliochorial, hemochorial and hemoendothelial in *Rodentia* (MOSSMAN, 1956); within suborders, — endotheliochorial and hemochorial in *Microchiroptera* (WIMSATT, 1953); and even within families, — epitheliochorial and endotheliochorial in *Talpidae* (MOSSMAN, 1939). Furthermore, as pointed out previously in this paper, the labyrinthine condition of the aardvark placenta could conceivably have been derived relatively late, phylogenetically speaking, directly from an epitheliochorial type such as that of the mare by disappearance of the uterine epithelium and a very shallow invasion by trophoblast.

Although in the present state of our knowledge, these similarities between the fetal membranes of *Orycteropus* and *Equus* should be taken only as suggestive, they are strong enough to warrant further study of these two interesting genera. Such studies should be rewarding, especially if combined with a thorough investigation of the reproductive cycle and morphology of the ovary. (The history and significance of the multiple corpora lutea in these uniparous species is especially provocative.)

The synopsis of basic data which follows contains certain information which, although it has not actually been observed, can be deduced beyond any reasonable doubt from the facts that are known about this genus, and by comparison with the situations known to exist in other mammals. These items have been marked by an asterisk.

Synopsis of basic data
Orycteropus (*afer?* and *capensis*)

Aard Vark

Implantation:

Orientation (disc): mesometrial *

Orientation (first attachment): probably antimesometrial *

Depth: probably superficial *

Decidua: no capsularis; no typical decidual cells; manner of placental detachment unknown

Amniogenesis: unknown

Yolk-sac:

Bilaminar omphalopleure: temporary; large and highly specialized — trophoblast invades deeply surrounding maternal capillaries

Chorio-vitelline placenta: unknown

Vascular splanchnopleure: unknown

Chorio-allantoic placenta:

Shape: incomplete zonary, very broad and thin

Type: labyrinthine, labyrinth much thinner than placenta

Finer morphology: endotheliochorial

Accessory placentae: rudimentary marginal hematome-like zone only a few millimeters wide and with little maternal blood. Many chorionic vesicles 1—4 mm in diameter

Location: mesometrial and lateral

Allantoic vesicle: large, permanent, four-lobed

Authorities: TURNER; DE LANGE; HORST; author

Summary

The fetal membranes of a 43 cm (total length) aard vark (*Orycteropus afer*?) fetus are described and compared with previous descriptions by others of three late fetuses and one early embryo. The total information indicates that implantation is superficial with a mesometrially oriented embryonic disc and no decidua. The bilaminar omphalopleure is temporary, but large and highly specialized. The chorioallantoic placenta is a very broad and thin zone, incomplete antimesometrially, labyrinthine, endotheliochorial, and with a rudimentary marginal hematome-like zone. It contains many chorionic vesicles formed earlier at the mouths of dilated glands. The allantois is large, four-lobed and permanent.

In so far as the basic characters of each are known, there is more resemblance of the membranes of *Orycteropus* to those of *Equus* than to any other genus.

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Figure Legends

Fig. 1 Aard fark (*Orycteropus afer?*) fetus: 24 cm CR, 43 cm total length. x $\frac{1}{4}$.

Fig. 2 Diagrams of the interior of the aard fark membranes to show the extent of the chorio-allantoic placenta, the four lobes of the allantois, and the position of the yolk stalk. ch. l. = chorion laevi; p. = placenta; v. d. = vitelline duct; 1, 2, 3, 4 = allantoic septa separating the four lobes of the allantoic vesicle. Cervical end at right.

A. Mesometrial half showing the four septa (numbered) leading to the base of the pyramidal dilatation of the allantoic duct (center).

B. Antimesometrial half showing the four septa converging at a point between the ends of the incomplete zonary placenta. This point apparently also marks the position of the atrophied yolk sac, as the vitelline duct leads from here to the umbilical cord.

Fig. 3 Interior of pregnant horn of uterus opened after fixation. In order to flatten it for photography it was necessary to incise it deeply at several places. Most of the allanto-amnion was cut away to show the septa (see Fig. 4). Since the yolk stalk lies between the allantois and amnion it is attached only at its ends to the allanto-chorion and umbilical cord. Note the long pyramidal funnel of the allantois in the placental end of the cord. x 2.1.

Fig. 4 Same as Figure 3 but with a strip of black paper inserted between the yolk stalk and placenta. The allantoic septa are marked by ink lines and are numbered to correspond with Figure 2. The placental margins are indicated by dots. The cervical end is at the bottom. Lettered areas indicate portions removed for sectioning. x 2.1.

Fig. 5 Vertical section through area «A», showing the placental labyrinth applied to the stroma of the mucosal folds. Note that the labyrinth is relatively thin and that this type of placenta is actually only a step removed from the epitheliochorial condition. Some of the relatively rare flattened glands can be seen next to the inner muscular layer. x 27.

Fig. 6 Vertical section through a large chorionic vesicle or absorptive area of area «A». x 36.

Fig. 7 Vertical section through a thicker portion of the placenta, area «C», showing deep interfolding of the labyrinth and the mucosal stroma and a narrow section of a chorionic vesicle. x 36.

Fig. 8 Detail of a portion of the labyrinth showing the trophoblastic tubules lined with endothelium and filled with maternal corpuscles (black). Note how the maternal vessels are not completely engulfed by the syncytial trophoblast at their mucosal margins (lower right). x 270.

Fig. 9 Detail of the walls of a trophoblastic tubule, showing the syncytial trophoblast and the lining of maternal endothelium. x 735.

Fig. 10 Detail of the mucosal stroma. The upper two-thirds shows mainly the cell types adjacent to the labyrinth (upper left), the lower one-third shows the looser central stroma. Note that there are at least two, probably three cell types near the labyrinth, but that none appear to be clearly either decidual cells or trophoblastic giant cells. x 735.

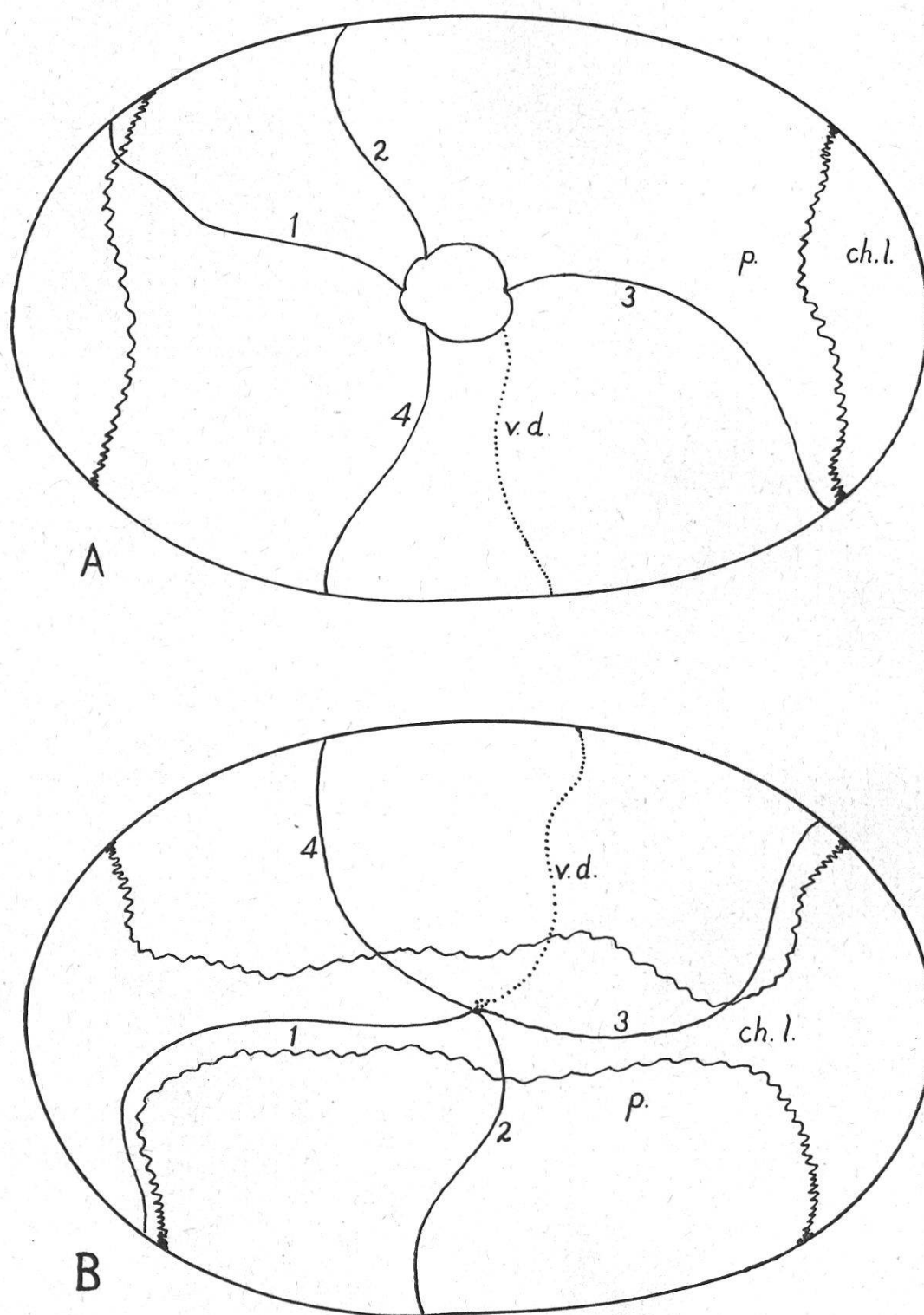


Fig. 2

Plate 1

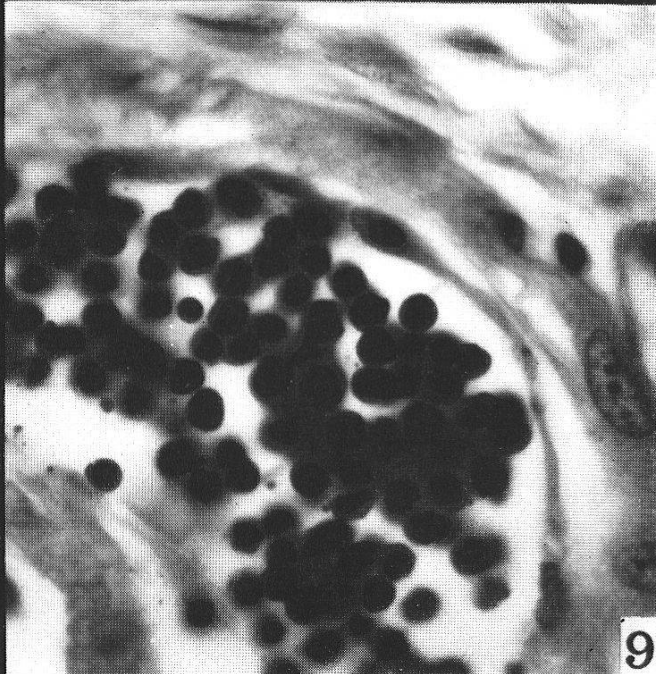
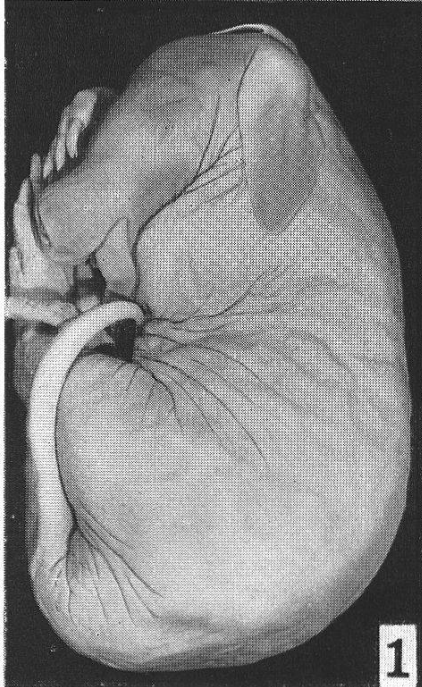
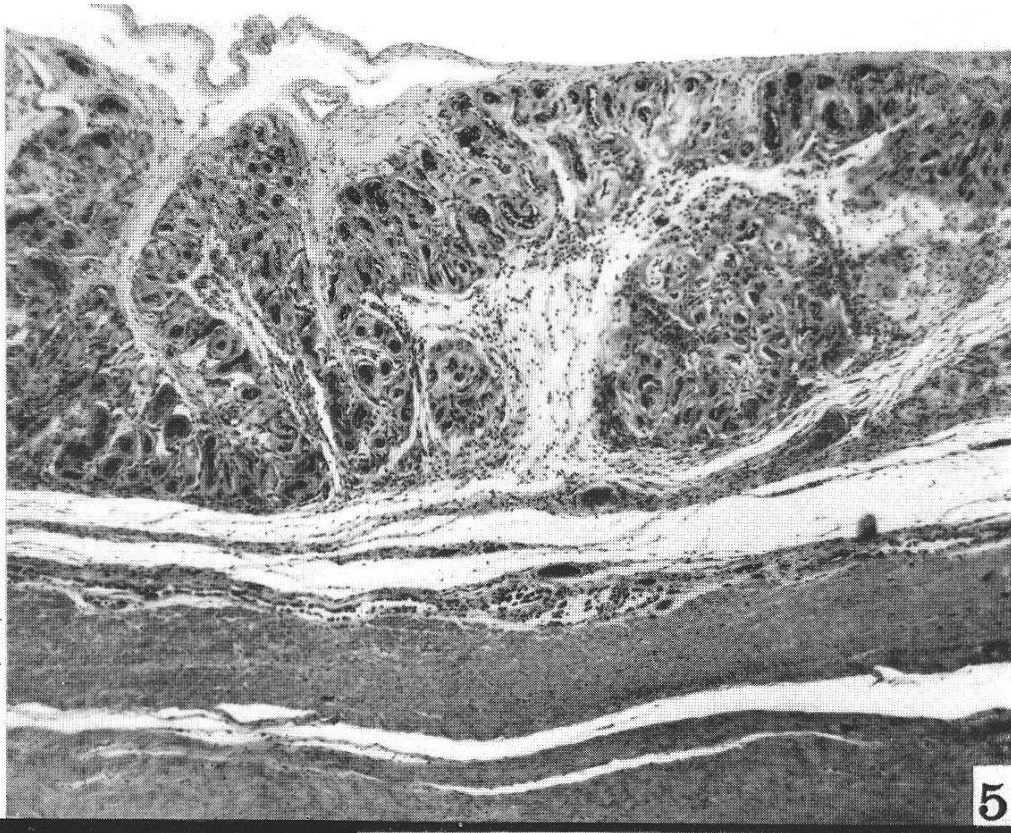


Plate 2

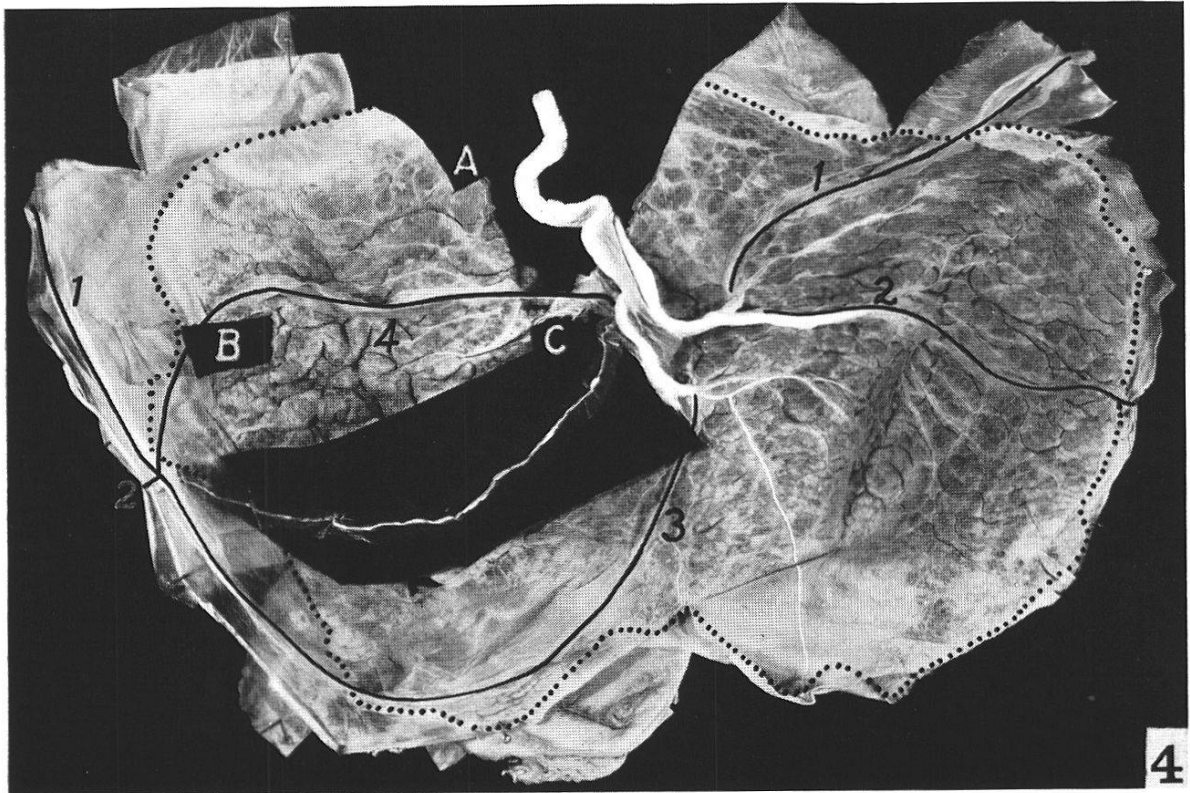


Plate 3

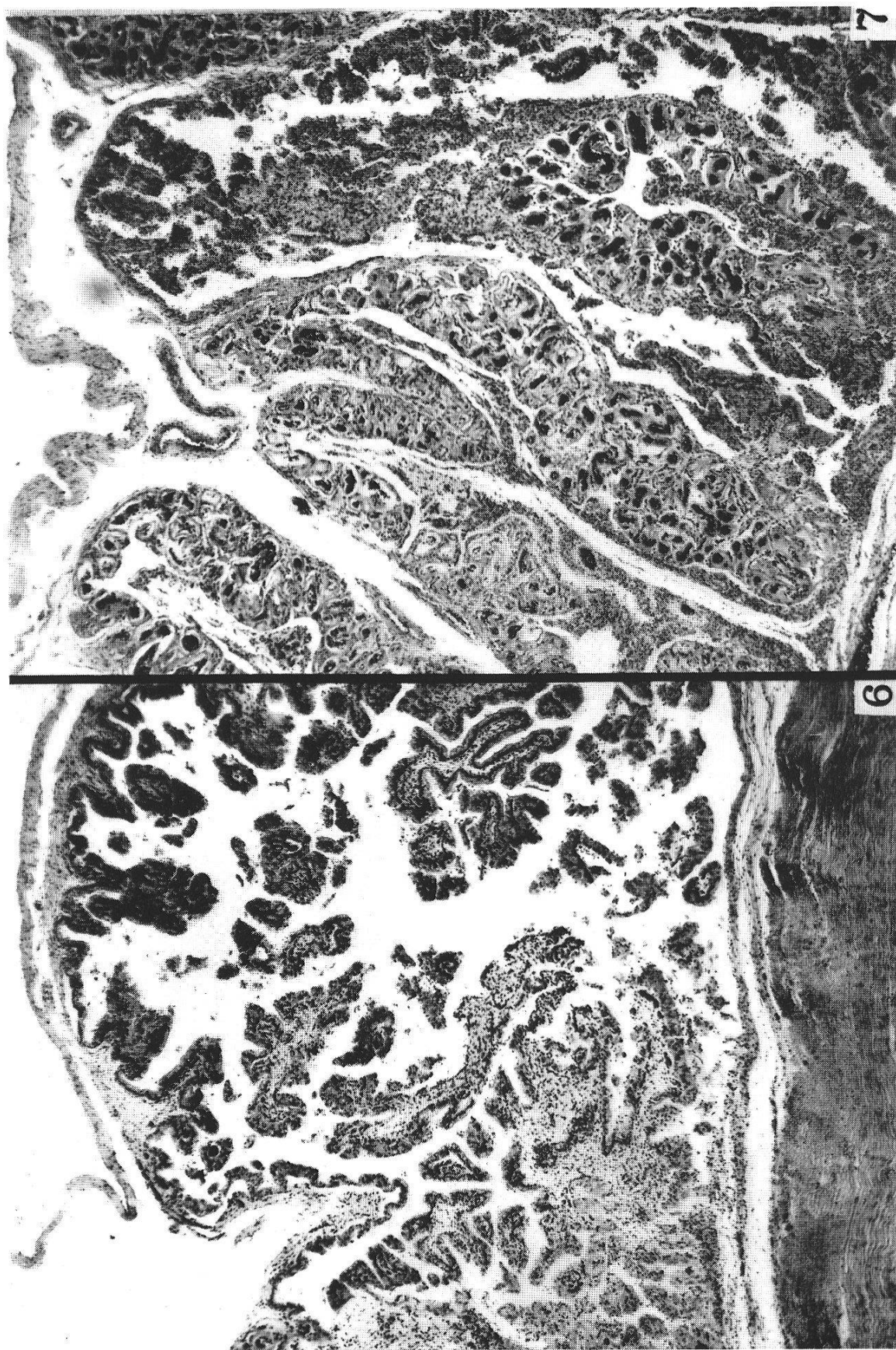


Plate 4

