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THE VASCULAR PATTERN OF THE PLACENTA IN FARM ANIMALS

(Horse, Pig, Cow, Sheep and Rabbit)

By

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I. INTRODUCTION

The importance of the placenta has been recognized for many years in embryology and physiology, but the physiology and morphology of the placenta are obscure in many points. Numerous studies of various kinds have been made on the placenta, in which, generally, the placentas of rat, mouse, guinea pig and rabbit were used, because their forms are similar to that of the human placenta. Studies on the other mammalian placentas are comparatively few; they were almost all done in the course of physiological rather than morphological experiments. In particular, the detailed vascular pattern of the placenta has been obscure in spite of the significance of the physiological function of the placenta with respect to the problem of placental transmission of various substances.

It has been considered that placental transmission is related to the tissue layers which lie between the maternal blood stream and fetal blood stream in the placenta: but it has become clear that the transmission is related not only to the part of the discoidal placenta which is the so-called "placenta", but also to the part consisting of fetal membrane, and that the relationship between the maternal blood stream and the fetal blood stream is not simple, histologically.

Generally, placentas in mammals have been classified by their shapes as "diffuse placenta", "polycotyledonary placenta", "zonary placenta" and "discoidal placenta." VON BAER (1928) and ROBINSON (1904) stated that placentas could be classified into two types, *viz*, the "apposed placenta" and the "conjoined placenta", according to the state of contact of fetal membrane with uterine mucosa. However, MOSSMAN (1937) pointed out that placentas of the same external form, but of very different internal structure, exist in many distantly related orders; and, furthermore, that some of the shapes ordinarily thought of as quite different are very closely related, while the external shape of the placenta is of little significance phylogenetically. In the classification by finer structure, there was HUXLEY'S classification (1864) in which he divided mammals between "Deciduata" and "Non-deciduata". STRAHL (1906) also divided mammalian placentas into two groups, *viz*., "Halb-placenta und Vollplacenta", while HUBRECHT (1908) and ASSHETON (1909) classified them as "plicate type" or "cumulated

type", based on the development of the trophoblast. GROSSER (1909, 1927) and MOSSMAN (1937) studied placentas histologically and classified them into the following five types according to the tissue layers lying between the maternal blood stream and the fetal blood stream: (1) the "epitheliochorial placenta", (2) the "syndesmochorial placenta", (3) the "endotheliochorial placenta", (4) the "haemocholial placenta", and (5) the "haemoendothelial placenta."

These above-mentioned methods of classification of plancentas were customarily combined and GROSSER's classification was applied to understand the problems of placental transmission. However, such application was made chiefly to the placentas of rodentia and humans and was based on the limited consideration that "placenta" meant something in which the chorion is vascularised from the allantois and actually fused with the uterine wall to form a fairly complex structure as described by AMOROSO (1952). To other parts, such as the fetal membrane or the intercotyledonary area, not much importance has been attached.

In the definition of the placenta, GROSSER (1933) stated, "Placentation may be defined as the intimate junction of the mucosa of the uterus with the chorion for the purpose of exchange of material between mother and offspring in both directions, but mainly in the sense of food supply for the latter…" FLYNN (1923) said, "The term placenta should be applied to all organs consisting of an intimate apposition or fusion of the fetal membranes with the uterine wall for the purpose of carrying out physiological processes destined for the well-being of the embryo." MOSSMAN (1937) said, "The normal mammalian placenta is an apposition or fusion of the fetal membranes to the uterine mucosa for physiological exchange." On the basis of these definitions, it is considered by the author that the fetal membrane and the part of the uterine mucosa which faces to the fetal membrane of the discoidal and zonary placenta, and the intercotyledonary area of the fetal membrane and the surface of the uterine mucosa of the polycotyledonary placenta, are all parts of the placenta. Physiological functions are carried on in these structures and there is fusion of the fetal membrane to the uterine mucosa in some cases. For example, BJÖRKMAN (1954) recognized that the overlying trophoblast of the intercotyledonary area in the bovine placenta is adherent to the uterine epithelium except over the glandular ducts, where areolae are formed. ASSHETON (1906) and WIMSATT (1950) states that the intercotyledonary area in the sheep placenta is in the same condition as in the cow. From the physiological standpoint, HAMMOND (1927) pointed out that the uterine milk was utilized by the fetus.

AMOROSO (1952) proposed that the exchange of oxygen and carbon dioxide is carried out principally in the cotyledon, while in the intercotyledonary regions,

on the other hand, the fetal vessels are related to the orifices of the glands, and appear to be concerned principally with the absorption of the less diffusible substances transmitted or secreted by the surface and glandular epithelium. According to BRUNSCHWIG (1927), in the white rat the passage of ferric and ferrocyanide irons from mother to nine-day embryo is effected not through the ectoplacental cone, but through the yolk-sac. On the placental trasfer of iron, WISLOCKI and DEMPSEY (1946) stated that in the human placenta, iron appears to be transmitted to the fetus through the syncytial trophoblast covering the chorionic villi; in carnivores, iron is absorbed by specialized areas of cytotrophoblast at the borders and at the base of the placenta (brown and green borders); in the sow, iron appears to be absorbed through all parts of the chorion, although mainly by the areolae. KIKUTA (1957) assumed that the passage way from fetus to mother of sodium rhodanide and xylose which were injected into the bodies of human fetuses, was not only as follows: fetus—umbilical cord—placenta—uterine wall—maternal blood, but also in the following way: fetus—transfusion of wall of umbilical cord—amniotic fluid—transfusion of fetal membrane—uterine wall—maternal blood. In the rabbit, where it is believed the bilaminar omphalopleur had disintegrated, opening up the yolk-sac cavity and exposing the yolk-sac splanchnopleur during placentation, antibodies do not transfer from the allantochorionic placenta and their transmission from mother to fetus is made from uterine wall to vitelline vessels *via* the uterine cavity (BRAMBELL and MILLS, 1947; BRAMBELL, HEMMINGS and ROWLANDS, 1947; BRAMBELL and HEMMINGS, 1949, MCCARTHY and KEKWICK, 1949; BRAMBELL, HEMMINGS, HENDERSON, PARRY and ROWLANDS, 1949; BRAMBELL, HEMMINGS and HENDERSON, 1951; BRAMBELL and HEMMINGS, 1960).

As noted above, many studies of the placenta have been made in humans and small animals, but studies with farm animals have been very few. Moreover, the researches on the placentas of cow and sheep were made mostly on the cotyledons only, while in the rabbit they were made on the discoidal placenta. In the presently described observations the author has employed the placentas of the horse, pig, cow, sheep and rabbit, and attempted to clarify the general morphological features, with special attention to the vascular patterns of these animals' placentas, which are closely related with the nutrition and respiration of the fetus.

The reports of researches on the placental vascular patterns in these animals may be briefly reviewed. In swine and horse, there are only a simple description and model pictures of TURNER (1875). HILLIGER (1958) observed the maternal vascular system in the cotyledon of the cow. In sheep, TURNER (1875) described the maternal vascular system of the cotyledon, BARCROFT and

BARRON (1942, 1946) the maternal and fetal vascular system of the cotyledon, and WIMSATT (1950) the fetal vascular system of the cotyledon and intercotyledonary area. In the rabbit, MOSSMAN (1926) observed the placental vascular pattern of the maternal and fetal blood vessels in detail.

As mentioned above, the studies on placental vascular pattern in farm animals are very few and incomplete in consideration of the definition of "placenta." In the present observations, the author has tried to overcome the deficiencies in the above-noted studies, to show the vascular pattern of maternal and fetal placenta, and to clarify the directions of blood flow in both parts.

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II. MATERIALS

All materials whether horse, pig, cow, or sheep were obtained from the Sapporo slaughter-house in Hokkaido during the period from 25th July, 1958 to 20th October, 1959. From these slaughtered animals, the pregnant uteri were collected and observed. The number of these materials and their breeds are as follows:

Species	No.	Breed
Horse	45	Percheron and Halfbred
Pig	29	Middle Yorkshire and its hybrid
Cow	49	Holstein-Friesian
Sheep	32	Corriedale

Seventeen pregnant rabbits which were bred in the First Farm of Hokkaido University were slaughtered and their uteri or placentas were studied. These materials are listed in Tables 1, 2, 3, 4, and 5.

TABLE 1. Horse Materials

No.	Date of Collection	Fetus				Treatments at Slaughter
		Sex	Body Weight (g.)	C.-R. Length (cm.)	Age estimated (months)	
7	25 Aug. '58	Female	44	10.5	2.5	Ut. / F.M. > A.I.P.—Alcohol
9	9 Sept. '58	"	80	12.8	3.0	Ut. —Latex—Form. / F.M.—Latex—Form.
14	3 Oct. '58	"	91	14.3	3.0	Form.
15	4 Oct. '58	"	178	17.0	3.5	F.M.—Latex / Ut. > Form.
18	8 Oct. '58	Male	255	19.0	4.0	Form.
8	28 Aug. '58	"	420	20.0	4.0	Ut.—Form. F.M.—Form.
16	4 Oct. '58	"	339	20.8	4.0	Form.
33	5 Nov. '58	Female	319	21.6	4.0	Ut.—Form. F.M.—Latex < Form. / HCl
3	19 Aug. '58	—	448	23.3	4.5	Ut. —Latex—Form. / F.M.—Latex—Form.
1	6 Aug. '58	—	533	24.0	4.5	Ut.—Latex—Form. F.M.—Form.
20	8 Oct. '58	Male	568	24.5	4.5	Form.
19	8 Oct. '58	Female	800	25.5	4.5	Ut.—Form. F.M.—Latex—Form.
47	20 Oct. '59	"	632	26.5	4.5	Ut.—Latex / F.M. > Form.
10	15 Sept. '58	Male	920	28.7	4.5	Ut.—Latex < Form. / HCl F.M.—Latex —Form.
11	22 Sept. '58	—	—	30.5	4.5	Form.
2	19 Aug. '58	—	1205	31.0	4.5	F.M.—Latex / Ut. > Form.
13	26 Sept. '58	Male	1253	32.0	4.5	Ut.—Form. F.M.—Latex—Form.
37	18 Nov. '58	Female	1387	32.0	4.5	Ut.—Form. F.M.—Latex < Form. / HCl
23	18 Oct. '58	"	1628	33.5	5.0	Form.
12	24 Sept. '58	"	1512	34.0	5.0	Ut.—Latex—Form. F.M.—Latex < Form. / HCl
48	20 Oct. '59	"	1950	33.5	5.0	Ut.—Latex—Form.
21	10 Oct. '58	Male	1818	37.0	5.0	F.M.—A.I.P. / Ut. > Alcohol.
38	18 Nov. '58	Female	2094	36.8	5.0	Ut—Form. F.M.—Latex < Form. / HCl.
24	18 Oct. '58	"	1969	38.0	5.0	Form.
25	18 Oct. '58	"	2386	39.0	5.5	Ut.—Form. F.M.—Form.
22	10 Oct. '58	Male	2420	39.0	5.5	Ut.—A.I.P.—Alcohol.

34	5 Nov. '58	Female	2870	42.0	5.5	$\overset{\text{Ut.}}{\text{F.M.}}$>Latex—Form.
17	8 Oct. '58	Male	2874	42.5	5.5	Ut.—Form. F.M.—Latex—Form.
30	4 Nov. '58	"	3280	42.7	5.5	Ut.—Form. F.M.—Latex—Form.
32	5 Nov. '58	"	2182	43.2	5.5	Ut.—Latex$<^{\text{Form.}}_{\text{HCl}}$F.M.—Latex$<^{\text{Form.}}_{\text{HCl}}$
31	5 Nov. '58	"	2940	44.0	5.5	F.M.—$\underset{\text{Ut.}}{\text{Latex}}$>Form.
39	18 Nov. '58	"	3350	44.5	6.0	$\overset{\text{Ut.}}{\text{F.M.}}$>Latex—Form.
35	5 Nov. '58	Female	4590	49.5	6.0	Ut.—Form. F.M.—Latex—Form.
42	13 Dec. '58	Male	6975	51.5	6.5	Ut.—Form. F.M.—Form.
29	4 Nov. '58	Female	5930	52.5	6.5	Ut.—$\underset{\text{F.M.}}{\text{Latex}}$>Form.
36	18 Nov. '58	Male	6038	53.5	6.5	Ut.—Form. F.M.—Latex—Form.
26	25 Oct. '58	"	6770	54.5	7.0	F.M.—$\underset{\text{Ut.}}{\text{Latex}}$>Form.
28	4 Nov. '58	"	6730	55.0	7.0	F.M.—$\underset{\text{Ut.}}{\text{Latex}}$>Form.
44	12 Jan. '59	"	12290	65.0	8.0	Ut.—Form. F.M.—Latex—Form.
41	13 Dec. '58	"	12975	66.5	8.0	Ut.—Latex—Form. F.M.—Form.
46	20 Feb. '59	"	13750	68.0	8.0	Ut.—Form. F.M.—Latex$<^{\text{Form.}}_{\text{HCl}}$
40	3 Dec. '58	"	13700	68.5	8.0	Form.
43	9 Jan. '59	"	16490	71.5	8.0	Ut.—Latex—Form.
45	30 Jan. '59	"	17805	77.5	8.5	Ut.—Form. F.M.—Latex$<^{\text{Form.}}_{\text{HCl}}$
27	28 Oct. '58	—	—	—	—	Ut.—Latex—HCl (macerated together with its fetus)

Ut. : Uterus.
F.M. : Fetal membrane.
Form. : Material was preserved in formalin solution.
HCl : Material was macerated by conc. HCl solution.
Latex : Neoprene-latex 601 A solution was injected into vessels.
A.I.P. : Mixture of sodium alginate, indigo carmine and Prussian blue was injected into vessels.
Alcohol : Material was preserved in alcohol solution.
C.-R. Length : Crown-rump length.

Note : Age of the embryo was estimated from the crown-rump length and fetal body weight according to the figures in the reports of SCHMALTZ (1921), NISHIDA (1948), KUROSAWA (1948), ZIETZSCHMANN and KRÖLLING (1955), and SAKAI (1955).

TABLE 2. Pig Materials

No.	Date of Collection	Fetus						Treatments at Slaughter
		Litter Size			Average of Body Weight (g.)	Average of C.-R. Lengths (cm.)	Age estimated (months)	
		Male	Female	Total				
28	28 Oct. '58	—	—	8	—	1.7	1.0	Ut.—Latex F.M.—Form.
16	22 Aug. '58	—	—	12	—	1.8	1.0	Ut.—$\frac{\text{A.I.P.}}{\text{F.M.}}$>Alcohol
21	29 Sept. '58	—	—	7	—	2.3	1.0	Form.
23	13 Oct. '58	—	—	3	1.7	2.6	1.0	Ut.—Form.
29	19 Oct. '58	—	—	13	—	3.0	1.5	Ut.—Latex—HCl
1	25 July '58	—	—	6	—	4.3	1.5	Ut.—Latex—HCl
13	12 Aug. '58	7	0	7	10.3	5.1	1.5	Form.
2	27 July. '58	—	—	6	—	5.3	1.5	Ut.—Latex—Form.
22	13 Oct. '58	—	—	6	26.1	7.1	1.5	Form.
24	25 Oct. '58	6	6	12	25.7	7.6	1.5	Form.
6	4 Aug. '58	5	3	8	28.4	8.1	2.0	Ut.—Latex—Form. F.M.—Form.
12	12 Aug. '58	8	3	11	42.2	8.8	2.0	Ut.—Latex—Form. F.M.—Latex—Form.
31	6 Dec. '58	10	5	15	40.1	8.9	2.0	Ut.—Latex—HCl F.M.—Latex—Form.
34	4 Aug. '59	5	3	8	59.9	10.2	2.0	Ut.—Latex—Form.
7	5 Aug. '58	5	3	8	58.4	10.6	2.0	Ut.—Form. F.M.<$\frac{\text{Latex—Form.}}{\text{Form.}}$

8	5 Aug. '58	2	3	5	119.6	12.7	2.5	F.M.—Latex—Form. Ut.—Latex—HCl
33	12 Jan. '59	2	3	5	73.4	13.2	2.5	Ut.—Form. F.M.—Latex$<^{\text{From.}}_{\text{HCl}}$
36	4 Aug. '59	6	3	9	163	14.3	2.5	F.M.—Latex—Form.
3	30 July '58	—	—	9	188	14.4	2.5	Ut. —Latex—HCl F.M.—Latex<Form.
20	25 Sept. '58	7	3	10	244	16.9	2.5	$^{\text{Ut.}}_{\text{F.M.}}$>Form. F.M.—Latex—Form.
32	12 Jan. '59	0	5	5	287.4	17.4	2.5	Ut.—Form. F.M.—Latex$<^{\text{Form.}}_{\text{HCl}}$
35	4 Aug. '59	4	4	8	279	17.7	2.5	From.
30	6 Dec. '58	5	3	8	286.5	18.1	3.0	Ut.—Latex—From. F.M.—Latex—From.
5	1 Aug. '58	2	2	4	320	18.6	3.0	F.M.—$^{\text{Latex}}_{\text{Ut.}}$>Form.
18	23 Aug. '58	5	6	11	260	19.3	3.0	Ut.—A.I.P.—Alcohol F.M.—A.I.P.—alcohol
19	8 Sept. '58	2	0	2	626	23.5	3.5	Ut.$<^{\text{Latex—HCl}}_{\text{Form.}}$ F.M.—Latex—Form.
15	20 Aug. '58	4	3	7	881	24.4	3.5	Ut.—Form. F.M.—Latex—Form.
25	27 Oct. '58	3	7	10	765.7	25.0	3.5	Ut.$<^{\text{Form.}}_{\text{Latex—HCl}}$ F.M.—Latex—Form.
4	1 Aug. '58	—	—	4	1133	26.9	3.5	$^{\text{Ut. —Latex}}_{\text{F.M.—Latex}}$>Form.

Note: Age of the embryo was estimated from the crown-rump length and fetal body weight according to the figures in the reports of SCHMALTZ (1921), WARWICK (1928), NISHIDA (1948), ZIETZSCHMANN and KRÖLLING (1955) and SAKAI (1955).

TABLE 3. Cow Materials

No.	Date of Collection	Fetus				Treatments at Slaughter
		Sex	Body weight (g.)	C.-R. Length (cm.)	Age estimated (months)	
4	21 Aug. '58	—	—	3.0	1.5	Ut.—Latex—Form. F.M.—Form.
38	22 Nov. '58	Male	11	5.1	2.0	Ut.—Form. F.M.—Form.
30	5 Nov. '58	"	14	5.3	2.0	Ut.—Latex—HCl F.M.—Form.
37	22 Nov. '58	Female	16	5.9	2.0	Ut.—Latex—HCl F.M.—Form.
9	28 Aug. '58	Male	12.5	6.4	2.0	Ut.—A.I.P.—Alcohol
34	10 Nov. '58	Female	—	10.3	2.5	Ut.—Form. F.M.—Form.
2	8 Aug. '58	"	49	10.5	2.5	Ut.—Latex—Form. F.M.—Latex—Form.
49	20 Feb. '59	Male	68	11.7	2.5	Ut.—Latex—Form. F.M.—Form.
33	10 Nov. '58	"	65	11.8	2.5	Ut.—Form. F.M.—Latex—Form.
45	16 Jan. '59	"	72	12.5	2.5	Form.
20	30 Sept. '58	"	81	12.2	2.5	Ut. F.M. > Latex—Form.
27	24 Oct. '58	Female	77	12.7	2.5	Ut.—Latex—Form. F.M.—Latex—Form.
3	9 Aug. '58	"	95	13.2	2.5	Ut.—Latex—HCl F.M.—Latex—HCl
40	4 Dec. '58	Male	102	13.3	2.5	F.M.—Latex Ut. > Form.
21	1 Oct. '58	Female	110	14.0	3.0	Form.
35	10 Nov. '58	Male	121	14.0	3.0	Ut.—Latex F.M. > Form.
12	2 Sept. '58	"	122	14.0	3.0	F.M.—A.I.P. Ut. > Alcohol
1	29 July. '58	"	250	18.5	3.0	F.M.—Latex—HCl Ut.—Latex—HCl
13	3 Sept. '58	Female	320	19.5	3.5	Ut.—Latex < HCl / Form. F.M.—Latex < HCl / Fom.
24	9 Oct. '58	Male	305	19.7	3.5	Form.
48	9 Feb. '59	Female	400	20.5	3.5	Ut.—Latex—Form.
14	6 Sept. '58	Male	365	20.8	3.5	Ut.—Latex < Form. / HCl F.M.—Latex—Form.
54	11 Mar. '59	Female	556	22.5	3.5	Ut.—Latex—HCl
29	5 Nov. '58	Male	480	23.0	3.5	Ut. F.M. > Latex—Form.
16	17 Sept. '58	Female	560	23.5	3.5	Form.

41	6 Dec. '58	Male	1036	27.5	4.0	Ut.—Latex F.M.>Form.
		Female	895	26.5		
19	26 Sept. '58	Male	1088	28.0	4.0	Ut.—Latex—HCl F.M.—Latex—Form.
23	6 Oct. '58	"	1895	30.0	4.5	Ut. F.M.>Latex—Form.
22	1 Oct. '58	"	1113	30.5	4.5	Ut. F.M.>Latex—Form.
28	25 Oct. '58	Female	1760	34.0	4.5	Ut. F.M.>Latex—Form.
44	12 Jan. '59	"	3051	39.0	5.0	Cotyledon—A.I.P.—Alcohol Latex—HCl Form.
47	9 Feb. '59	Male	3542	39.0	5.0	Form.
52	2 Mar. '59	"	4200	41.3	5.0	Ut.—Form. F.M.—Form.
32	10 Nov. '58	"	4630	43.3	5.0	Ut. —Latex—Form. F.M.—Latex<HCl
50	27 Feb. '59	Female	3849	44.0	5.0	Ut. —Latex—Form. F.M.—Latex<HCl
25	15 Oct. '58	Male	5080	47.0	5.5	Form.
8	26 Aug. '58	Female	5069	49.0	5.5	Ut—Latex F.M—Latex>Form.
42	14 Dec. '58	Male	5996	50.5	6.0	F.M.—Latex—Form. Ut.—Latex—Form.
		Female	5676	50.5		
39	25 Nov. '58	Male	7662	54.0	6.0	Ut.—Latex—Form.
56	24 Mar. '59	Female	10705	63.0	6.5	Ut.—Form. F.M.—Form.
26	20 Oct. '58	"	11000	63.5	6.5	Form.
11	29 Aug. '58	"	11500	65.0	6.5	Ut.—A.I.P.—Alcohol
15	10 Sept. '58	"	12000	65.5	6.5	Ut. —Latex—Form. F.M.—Latex<HCl
55	24 Mar. '59	"	17655	66.5	6.5	Cotyledon—Form.
31	10 Nov. '58	"	14000	67.5	6.5	Cotyledon—Latex—Form.
43	12 Dec. '58	"	22550	72.0	6.5	Ut.—Form.
51	28 Feb. '59	"	22865	76.0	7.0	Cotyledon—Latex—Form.
46	21 Jan. '59	"	21750	85.0	9.0	Cotyledon—Latex<HCl Form.
10	28 Aug. '58	Male	30000	96.0	9.5	F.M.—A.I.P.—Alcohol

Cotyledon: Cotyledon portion was treated.

Note: The age of the embryo was estimated from the crown-rump length and fetal body weight according to the figures in the reports of RÖRIK (1908), SCHMALTZ (1921), BERGMANN (1922), HAMMOND (1927), NISHIDA (1948), KUROSAWA (1948) and ZIETZSCHMANN and KRÖLLING (1955).

TABLE 4. Sheep Materials

No.	Date of Collection	Fetus				Treatments at Slaughter
		Sex	Body Weight (g.)	C.-R. Length (cm.)	Age estimated (months)	
5	11 Oct. '58	—	1	2.0	1.0	Form.
3	9 Oct. '58	—	3.5	3.0	1.5	F.M.—Form. Ut.—Form.
		—	3.5	3.0		
35	11 Nov. '58	—	4.0	3.4	1.5	Ut.—Latex—Form.
		—	4.5	3.0		
21	7 Nov. '58	—	8.0	4.3	1.5	Form.
4	9 Oct. '58	Male	8.0	5.3	2.0	Ut.—Latex—HCl F.M.—Form.
27	5 Dec. '58	"	10	6.2	2.0	Ut.—Latex<HCl, Form.
		"	12	6.2		
26	5 Dec. '58	"	13	7.0	2.0	Form.
34	11 Nov. '58	"	17	7.3	2.0	Ut.—Latex—Form.
		"	13	7.0		
		"	15	7.1		
23	19 Nov. '58	"	18	7.7	2.0	Form.
18	7 Nov. '58	"	48	10.3	2.5	Ut.—Latex, F.M.—Latex>Form.
2	9 Oct. '58	"	57	11.5	2.5	Form.
28	5 Dec. '58	Female	60	11.7	2.5	Ut.—Latex—Form.
		"	54	12.0		
13	11 Oct. '58	Male	88	13.0	2.5	Ut.—Latex—HCl
15	11 Oct. '58	Female	103	13.7	2.5	F.M.—Latex, Ut.>Form.
		Male	112	13.5		
12	11 Oct. '58	Female	119	14.5	2.5	Ut.—Form. F.M.—Latex—Form.
7	11 Oct. '58	Male	134	14.7	2.5	Ut.—Latex, F.M.>Form.
		Female	123	14.5		
24	28 Nov. '58	Male	153	15.3	2.5	Ut.—A.I.P.—Alcohol
		Female	140	15.3		

19	7 Nov. '58	Female	180	16.0	3.0	F.M.—$\overset{\text{Latex}}{\text{Ut.}}>$HCl
17	7 Nov. '58	"	258	18.0	3.0	Form.
25	28 Nov. '58	Male	281	19.3	3.0	Cotyledon—Latex$<\overset{\text{Form.}}{\text{HCl}}$
9	11 Oct. '58	"	330	19.5	3.0	Ut.—Latex—Form.
		"	331	19.5		
30	14 Dec. '58	Male	280	20.3	3.0	F.M.—$\overset{\text{Latex}}{\text{Ut.}}>$Form.
		Female	251	19.0		
14	11 Oct. '58	Male	404	20.0	3.0	F.M.—Form. Ut.—Form.
		"	456	20.0		
11	11 Oct. '58	Female	353	21.0	3.0	Ut.—Latex—HCl
		"	325	21.0		
6	11 Oct. '58	Male	353	21.3	3.0	Form.
31	14 Dec. '58	"	370	21.8	3.0	Ut.—Latex—Form.
		"	383	21.7		
16	11 Oct. '58	"	619	23.5	3.0	F.M.—$\overset{\text{Latex}}{\text{Ut.}}>$HCl
10	11 Oct. '58	Female	584	23.7	3.0	F.M.—$\overset{\text{Latex}}{\text{Ut.}}>$Form.
		"	587	24.0		
8	11 Oct. '58	Male	586	24.3	3.0	Ut.—Latex—Form. F.M.—Latex—Form.
29	14 Dec. '58	Female	582	25.7	3.0	F.M.—Latex—Form.
		"	632	26.0		
33	18 Mar. '59	Male	1020	28.5	3.5	Cotyledon—Form.
32	9 Feb. '59	"	965	29.0	3.5	Ut.—Latex—Form.

Note: The age of the embryo was estimated from the crown-rump length and fetal body weight according to the figures in the reports of ASSHETON (1906), SCHMALTZ (1921), CLOETE (1939), WALLACE (1945), NISHIDA (1948) and ZIETZSCHMANN and KRÖLLING (1955).

TABLE 5. Rabbit Materials

No.	Date of Collection	Fetus				Treatments at Slaughter
		Litter Size	Average of Body Weight (g.)	Average of C.-R. Length (cm.)	Age (days)	
1	27 July. '57	7	—	—	27	Ut.—Latex—Form.
2	22 July. '57	4	—	—	24	Ut.—Latex—Form.
3	26 July. '57	7	—	—	28	India ink was injected in the uterine vessels.
4	24 July. '58	8	—	—	20	Ut.—Latex<Form. HCl
5	28 July. '58	10	—	—	24	Ut.—Latex—HCl
6	18 Aug. '58	6	—	—	25	F.M.—Latex<HCl Form.
7	11 Sept. '58	5	26.6	7.4	26	Ut.— Latex<HCl F.M.—Latex—Form.
8	24 Sept. '58	6	—	—	21	Ut.—Latex—Form.
9	21 Oct. '58	1	50	9.8	29	Ut.—A.I.P.—Alcohol
10	3 Sept. '59	2	—	6.0	22	Ut.—Latex—HCl
11	8 Sept. '59	5	28.8	8.8	27	F.M.—Latex—Form.
12	1 Oct. '59	3	12.3	5.4	23	Ut.—Latex F.M.—Latex>Form.
13	2 Nov. '59	9	12.6	6.6	24	Ut.—Latex F.M.—Latex>Form.
14	5 Nov. '59	7	11.8	6.3	23	F.M.—Latex—Form.
15	6 Nov. '59	3	—	7.9	25	Ut.—Latex—Form.
16	6 Nov. '59	6	35.8	8.7	27	Ut.—Latex—Form.
17	17 Nov. '59	5	41.3	9.3	28	F.M.—Latex—Form.

III. METHODS OF OBSERVATION

1. REVIEW OF THE METHODS FOR STUDIES OF THE VASCULAR SYSTEM

Researches on the vascular patterns in various organs have been numerous, but the methods may be summarily stated as being of three kinds; (1) making histological preparations, (2) making cast specimens, and (3) by X-ray radiation.

(1) The method of making histological preparations

The technique employed commonly consists of intravascular injections of opaque or colored materials, study of thick sections of extirpated organs, and

preparation of models of the blood vessels by means of making serial sections. Many workers have employed these methods, for example, JOHNSTON (1900), MALL (1904), GOLDMANN (1912), MATSUZAWA (1924), STAFFORD (1930), BRAMBEL (1933), IWANE (1935), DARON (1936), RAMSEY (1949), BURR and DAVIES (1951), BARLOW (1951), ANDŌ and YAMASHITA (1952 a, b), SAKAI (1952), MORIZAKI (1953), KAWADA (1953), PRICHARD and DANIEL (1954), TANAKA and TSUGAWA (1956), HIGUCHI (1956) and others.

(2) The method of making cast specimens

Materials such as latex, celloidin, synthetic resin and others are injected into the vessels and the cast specimens are made by maceration with concentrated HCl or NaOH solution.

It is said that the first cast specimen made in dental gum was by STEIN (1898). Later, PERNKOPF (1928 a, b), BURT (1928) and others advocated the convenient use of rubber as material for intravascular injection. Recently, as an improvement on rubber, neoprene latex has been employed as an important material for making vascular casts (BARCROFT and BARRON, 1946; CHRISTENSEN, 1952; ROSS, 1952; PRICHARD and DANIEL, 1954). TAKAHATA (1955) illustrated the method of using neoprene and stated that the use of neoprene is very easy; the material can be injected into a very small vascular cavity and the cast is very elastic, strong, not sticky, and can be preserved perfectly. TAKAHATA et al. (1956, 1957) succeeded in making very fine neoprene latex cast specimens of the vascular arrangement in the kidneys of various species.

Many kinds of synthetic resin are also used. RAMSEY (1949), KAZZAZ and SHANKLIN (1951), BURR and DAVIES (1951) and others used vinyl acetate; ELIAS and PETTY (1952), JULIAN (1952), CHRISTENSEN (1952), SAKAI (1952) and others vinylite resin; ŌTA and TAJIRI (1954), KOBAYASHI and SAKAMOTO (1956), WATABIKI (1957), YAMAMOTO (1958) and others used various kinds of acrylics.

Celluloid and celloidin are also used commonly.

(3) The method of X-ray radiation

A contrast medium such as sodium iodide is injected into the vessels, and observations are made either directly or from film (ROSS, 1952; TRABUCCO and MARQUEZ, 1952; and others).

The synthetic resin cast specimens, generally, are suitable for stereometric observations, but the injection of resin into fine and intricate vascular systems, such as in the placenta, may be neither complete nor easy, and in many cases the specimens cannot be used for observation on account of brittleness of the resin. The neorprene latex cast specimens, on the contrary, are elastic and

soft, the material is preserved in its original form, the specimens can be cut at one's will, and the injection of the neoprene latex solution can be completed at low viscosity and high liquidity. Accordingly, the auther used the neoprene latex solution, chiefly, although he used a solution of pigments and india ink in a few cases. Paraffin sections were made to check the results of observation of these neoprene latex casts and injected specimens.

2. METHODS EMPLOYED IN PRESENT OBSERVATIONS

Treatment at time of sampling are shown in tables 1-5. The treatments were carried out by three methods: (1) the untreated materials were preserved in 10% formalin solution, (2) neoprene latex was injected into the vessels of the materials, and (3) pigments were injected into the vessels of the materials. The crown-rump length and body weight of fetuses were measured at sampling, and those figures were used to estimate the fetal age.

(1) Treatment by means of 10% formalin solution

Samples treated thus were used for macroscopic and histological observations. Paraffin sections were prepared and stained with hematoxylin-eosin. For fixation, the pregnant uteri were cut to open the uterine cavity. After removing fetuses, these materials were placed in 10% formalin solution in most cases. But in many cases of horses and pigs, fetal membranes came off easily from the uterine mucosa, and then, in a few cases, concentrated formalin solution was injected directly into the allantoic cavity through the uterine wall.

(2) Treatment by means of injection with neoprene latex solution

The material injected was neoprene latex 601 A solution which was diluted 3-4 times with water; water-dispersible colors for use in latex were also used. For injection, the needle of a Meyer's injector, with the tip of the needle made dull, was inserted into the vessels and ligated to the vessel wall. The injection was made chiefly into the middle uterine arteries and veins in each side. In the rabbit, however, the injection was made into the aorta and vena cava because the vessels on the broad ligaments of the uterus are very fine.

For injection, all vessels except that in which the latex was injected were ligated to prevent leakage of the neoprene latex solution. The injected uterus was kept in running water about 1-2 hrs., then the following procedure was carried out; namely, some materials were placed in concentrated HCl solution for maceration, and others were preserved in 10% formalin solution. On the other hand, the injection into the fetal vessels of the allanto-chorion was made via the umbilical cord after cutting open the uterine cavity and fetal allantoic cavity. The procedure of injection was the same as above, and after it the

materials were treated in the same way.

From the materials which were macerated in concentrated HCl solution for several days, the tissues were removed in the water tank and neoprene latex cast specimens were thus obtained; the specimens were preserved in 10% formalin solution. These specimens were used for macroscopic and microscopic observations directly in the water.

The materials fixed in formalin solution were sliced in sections with a razor by hand. These sections were observed in intact state or in transparent state by histological procedure. Some materials were macerated with concentrated HCl solution and neoprene latex cast specimens were obtained. These specimens were illuminated from above or below, and observed microscopically.

(3) Treatment by means of injection with other materials

The method devised by TANAKA and TSUGAWA (1956) was applied in a few cases. A mixture of sodium alginate, indigo carmin and Prussian blue was injected into the vessels. The proportions in the mixture were as follows:

(i) 0.5% sodium alginate solution is made with water and the solution is filtered through gauze.

(ii) To the solution, 1.5% indigo carmin and 1.5% Prussian blue are added and mixed.

This mixture was injected into the vessels. The materials were placed in absolute alcohol saturated with aluminium chloride, sliced in sections by hand and were made into transparent specimens.

In one case of rabbit, india ink diluted with saline solution was injected in the uterine vessels.

Many specimens were prepared in this study. They were chiefly observed for the vascular pattern under low power of the microscope. Many photographs were taken.

IV. FINDINGS

A. RESULTS OF OBSERVATIONS ON THE PLACENTA OF THE HORSE

The placenta of the horse is classified as the diffuse epitheliochorial type. There are numerous tufts of villi over the surface of the allanto-chorionic membrane; the filiform villi of the tufts occupy the crypts in the uterine mucosa; the fetal membrane is in contact with the uterine mucosa. In reference to the time of attachmant, the blastocyst in the mare lies relatively unattached in the uterus until a comparatively late stage of development. The time

at which the villi develop and attach to the uterine mucosa tightly is about 10 weeks after fertilization (KOLSTER, 1902; SCHAUDER, 1912; EWART, 1915; CATCHPOLE and LYONS, 1934; AMOROSO, 1952; and HARVEY, 1959).

Most of the available descriptions concerning the developed placenta will be found in the papers by TURNER (1875), CATCHPOLE and LYONS (1934), YAMAUCHI (1947, 1948), AMOROSO (1952) and HARVEY (1959). Concerning the endometrial cups, which are known to secret gonad-stimulating hormone, there are descriptions by SCHAUDER (1912), COLE and GOSS (1943), KAWAHARA and SHINOZAWA (1943), YAMAUCHI (1947, 1948), CLEGG, BODA, and COLE (1954), AMOROSO (1951, 1952) and others. The author did not observe endometrial cups in detail, because they are present only during early pregnancy and are not recognizable after the 5th month in pregnancy.

1. Macroscopic observations of the horse placenta

Generally, most of the fetal body lies in the cavity of the uterine body, while a small part of it lies in the cavity of the pregnant uterine horn. The pregnant uterine surface is smooth. The branches of the uterine arteries are distributed all over the uterine horns and body. Many anastomoses of the branches of the uterine arteries within the opposite broad ligament are recognized on the surface of the uterine body. The ovarian vein is large and anastomoses with the ovarian vein of the other side, running over the upper part of the uterine body.

In many cases, the allanto-chorion in the horse is easily removed from the uterine mucosa and can be pulled out with the fetus by cutting open the uterine wall. In a few cases, formalin solution was directly injected into the allantoic cavity and the pregnant uterus was preserved in formalin solution. In these materials, the allanto-chorion was fixed on the endometrium (Fig. 1). The fetus wrapped with amnion is mainly in position with the head of the fetus facing the uterine cervix. The umbilical cord is twisted and attached to the allanto-chorion at the transitional portion from the uterine body to the uterine horn. The amnion, including the fetus together with amniotic fluid, is closed around the umbilical cord. The umbilical cord is divided into two parts, the amniotic and the allantoic portions; in the amniotic portion, turning is shown. The endometrial cups were present as circular folds which are separate from each other and surround the transitional portion from the umbilical cord to the allanto-chorion in the first half of a pregnancy, but they could not be seen in the latter half. They appeared as gray tubercular projections, and corresponded to the many other endometrial folds in the state of fixation.

As mentioned above, a fetus can be pulled out with its fetal membrane

from the uterine cavity (Fig. 2). The surface of the fetal membrane is smooth in early pregnancy, but it become rough with the development of villi according to the stage of pregnancy. In the fully developed allanto-chorion, the size of villi at the top of the uterine horns and at the *orificum internum uteri* is less than in other portions.

Two arteries and one vein pass through the umbilical cord; the vein is bifurcated in the amniotic portion of cord. On the inner surface of the amnion, the arteries and veins connected with the umbilical vessels are distributed, showing complex curves and branchings and many anastomoses. The outer surface of the amnion (the side of the allantoic cavity) is smooth while the inner surface is uneven on account of the blood vessels.

The vessels of the umbilical cord are surrounded by the umbilical sheath; at the portion of connection with the allanto-chorionic membrane the umbilical vessels branch into several vessels along the surface of a small coniform cavity, and then they disperse radially on the inner surface (the side of the allantoic cavity) of the allanto-chorionic membrane. The first main branching occurs at a short distance from the point in transition from the umbilical cord connected with the allanto-chorionic membrane in early pregnancy, but it occurs at a greater distance in later pregnancy. These branched vessels are not distributed in parallel, but they give off many branches. At the tips of those vessels, small vessels are arranged like a fern leaf and the tops of arteries and veins are adjacent to each other like the teeth of a comb (Fig. 3). There is no anastomosis macroscopically visible in these vessels.

2. Microscopic observations on the vascular pattern in the villi of the horse placenta

On the surface of the allanto-chorionic membrane (the side facing toward the uterine mucosa), numerous tufts of villi are present like flowers which are tightly arranged independently of each other. Capillaries exist on the surface and in the center of each villus (Figs. 4–5).

The villi, generally, are small and simple and arranged irregularly during early pregnancy, but with the advance of pregnancy the villi become larger and form tufts. The capillaries on the surface of villi form a network; they come together in the axial vessels which connect with the branches of the umbilical vessels. The allantoic vessels which are branched from the umbilical vessels are distributed plainly on the side of the allantoic cavity (Fig. 6), and from these vessels many tributaries are given off into the villi on the side of the uterine mucosa. The villi form tufts and each villus of the tuft is arranged radially (Fig. 7). The villi, which show two or three branchings at their tips,

are covered with a capillary net and the capillaries of each villus are gathered gradually at their axes (Figs. 8–10). It was recognized that a capillary exists which reaches to the top of a villus, running through the center of the villus from the root. In the specimens which were injected sufficiently with latex, the villi were covered with a network of latex, and the inner structure of villi was unclear; the central capillary of a villus could be observed only by signs of its existence such as shown in Figure 11. However, the relationship between artery and vein could be established by observing the various specimens which were subjected to injections in various proportions. From these observations, it was learned that the arterial tributary, which is connected with the branch of the umbilical artery, runs through the axis of the tuft of villi, and gives off branches in each villus. Those branches reach to the top of each villus, running through the central portion of each villus. On the way to the top, the axial arterial tributary gives off many lateral twigs which connect with the superficial capillary net of each villus (Figs. 12–13).

These conclusions are based on observations of the allanto-chorion, itself, which was pulled out from the uterine cavity. In the observations of the villi in the uterine crypts in the natural state, it was clear that the villus is not always single, but usually has two or three small branches (the secondary villi) at the top, which are given off from the same shaft-like villi (the primary villi). The axis of the tuft of villi is projected vertically to the surface of the allanto-chorion, and the primary villi are attached radially to the axis. The tufts of villi show a flask-like shape and they are very closely fitted into the crypts in the uterine mucosa (Figs. 14–16). In these specimens, the arterial tributary penetrates into the axis of villi and branches radially into the center of each villus, and finally disperses to the superficial capillary net (Fig. 17). The capillaries which cover each villus converge at the roots of the primary villi and connect with the 4–5 venous tributaries which surround the axial artery. These venous tributaries meet with the venous tributaries of the other tufts of villi, and connect with branches of the fetal vein.

It is also clear in the cross sections of the villi that arterial tributaries exist in the central portion of each villus (Fig. 18).

3. Microscopic observations on the vascular pattern on the surface of uterine mucosa

The surface of the uterine mucosa of the mare which has reached an advanced stage of pregnancy is subdivided into a multitude of irregular polygonal areas, varying in diameter, by slender ridges which anastomose with each other so as to present a reticulated appearance. Each area is subdivided into many

crypts, which penetrate deeply into the mucosa. That is to say, some crypts form a group, and numerous groups of crypts are spread all over the uterine mucosa (Figs. 19–20). In injected specimens it could be seen that small blood vessels occupy the ridges, and break up into small branches which end in a compact capillary plexus situated in the walls of the crypts. In the central portion of figure 20, a large vessel is seen rising to the surface of the uterine mucosa, with its branches running to four groups of crypts, which are arranged surrounding the central vessel. These groups are fomed by smaller crypts in their inner portions.

In the observations of the surface layer of uterine mucosa, a labyrinthine layer, which was torn off from the uterine mucosa, was viewed by illuminating the tissue from the back side of the uterine mucosa. The arterial tributaries appear among the groups of crypts, disperse radially into the surrounding crypts, and connect with the capillary net on the walls of crypts (Figs. 21–22).

Those described above were recognized clearly in the specimens of neoprene latex casts. The surface of the uterine mucosa forms a vascular layer of about 1 mm thickness. This vascular layer is constructed of numerous globes of compact capillary plexi, which are arranged in a row. At the upper surface of the globes, holes open irregularly; they are empty and include many cylindrical spaces in their interior. In the spaces among the globes, arteries run to the surface of the uterine mucosa; their branches are connected with the capillaries of the globes at their tops (Figs. 23–24). It is clear that one globe of a capillary plexus encloses one tuft of villi and forms a so-called cotyledon, and that the filiform villi of the tuft fit into the small cylindrical spaces of the globe. On the ridges of the top of a globe of the capillary plexus, the arterial tributaries run transversely and form the edges of the openings of the crypts and extend into the capillary net on the walls of the crypts (Fig. 25).

Observing from the back side of the globes, one sees that the globes are held by the network of capillaries surrounding the outside of each globe. Each globe is independent and connects with the venous tributary at its bottom (Figs. 26–28). Looking at the side of globes, one sees that each globe connects with the arterial tributary at the top and is connected with the venous tributary at the bottom; the inner structure which has the cylindrical sections is seen (Fig. 29).

These cylindrical sections of globes are more clear in the transparent preparations. The venous tributaries connect with the globes at their bottoms; the globes (cotyledons) are open at their upper surface and are partitioned into many chambers by septa which run longitudinally in the globe. It was recognized, by changing the focus of the microscope, that the maternal capillary net

of each septum forms many cylinders (Figs. 30-32). In the intercotyledonary spaces, arterial tributaries run up to the surface of the uterine mucosa (Fig. 33). They disperse into the crypts from their upper portions (Figs. 34-35) to form cylindrical capillary nets and connect with the uterine venous tributaries at the bottoms of the globes (Fig. 36). In the transverse sections of the cotyledons, round rings of capillaries show in the central portion of the cotyledon, and in the surrounding portion the capillaries are arranged irregularly. This means that the crypts open radially in the cotyledon.

In early pregnancy, it should be noted, the surface of the uterine mucosa is very irregular, and does not form cotyledons.

4. Histological observations of the horse placenta

In the fully developed placenta, the tufts of villi are interlocked with correspondingly shaped pockets of the mucosa, forming characteristic morphological units as cotyledons, and the placental labyrinth is formed (Fig. 37). A thin layer of dense connective tissue separates the placental labyrinth from the deeper-lying glandular zone of the mucosa, and the muscular layer lies under it. Connective tissue exists among the neighboring cotyledons as the septa. Uterine glands run up to the surface through these septa and open to the areolae (Fig. 38). Uterine vessels, also, run to the surface through these septa (Fig. 39).

In the cotyledons, the arrangement of villi is very regular, and the maternal septa lying between the villi are very thin (Figs. 40-41). The lining of the maternal crypts in the cotyledon consists of a flattened cellular layer of uterine epithelium which is closely applied to the cuboidal cellular epithelial investment of the villi. In the longitudinal section of the cotyledon, two kinds of capillaries are recognized in the villus; one of them runs through the central portion of the villus longitudinally, the other exists on both sides of the central capillary surrounding it. In the cross sections, maternal crypts in the cotyledon show round irregular spaces and the walls of the crypts, which are covered with epithelium of various thicknesses, are very thin (Figs. 42-43).

The capillaries in the maternal septa surrounding the crypts are seen intermittently. In most places cross sections of the capillaries, of which the diameters are about enough to contain one or two blood cells, can be recognized, but longitudinal sections of them are few. This predominance of capillary cross sections is the same in either cross or longitudinal sections of septa. This means that the maternal capillaries in the septa are distributed in a winding fashion and form networks. The connective tissue layer in the wall of maternal crypts is very thin so that the capillaries are directly in contact with the epithelium. At the central portion of a villus the capillary is always visible in

cross sections. This capillary is arterial as already described and surrounding this capillary the sections of capillaries are arranged irregularly. These sections of capillaries are cross sections in many cases and the capillaries are in contact with the epithelium; but no invasion of these capillaries into the epithelium was recognized. In the longitudinal sections, the capillaries of the villus run in parallel to the central artery on both sides of it. These capillaries appear intermittently and they run wanderingly as compared with the straight-running central arterial capillary. It is believed, from these facts, that the capillaries surrounding the central arterial capillary form a network.

The cotyledons are separated from the glandular zone of the mucosa by a thin layer of connective tissue. The arteries run through the connective tissue among the cotyledons to the surface of the mucosa. The uterine venous tributaries connect with the bottoms of the cotyledons (Fig. 44).

5. Summary of observations on the placenta of the horse

Most of the available descriptions concerning the placental structure of the horse concern histological observations on the cellular layers which exist between the maternal blood stream and fetal blood stream. Descriptions concerning the vascular pattern of the villi and maternal cotyledons of the horse cannot be found, except in TURNER's paper (1875) in which he presented a model picture of the placenta of the horse and gave a simple explanation of it. Therefore, the present writer tried to demonstrate the vascular pattern of the horse placenta using the method of injection of neoprene latex solution, a method which has never previously been applied to the horse placenta. The results are summarized as follows:

One or two arterial tributaries penetrate into the axis of the tufts of villi from the allanto-chorionic membrane, and the axial arterial capillary gives off branches radially into the center of each villus; the small central arterial capillary of a villus reaches to the top of the villus. A villus shows an irregular and cylindrical shape; the top has 2 or 3 branches in many cases. The central arterial capillary of a villus, which reaches to the top of the villus, gives off many short lateral twigs which connect wtih the superficial capillary net. Then the arterial blood which is flowing through the central arterial capillary to the top of the villus pours into the superficial capillaries at the top and side of the villus, and the surface blood, running through in the capillaries to the root of the villus, is gathered gradually and drained into the few venous tributaries surrounding the axial arterial capillary.

On the other hand, on the surface of the uterine mucosa, the capillaries in a layer of labyrinth form the numerous small globes of the compact capillary

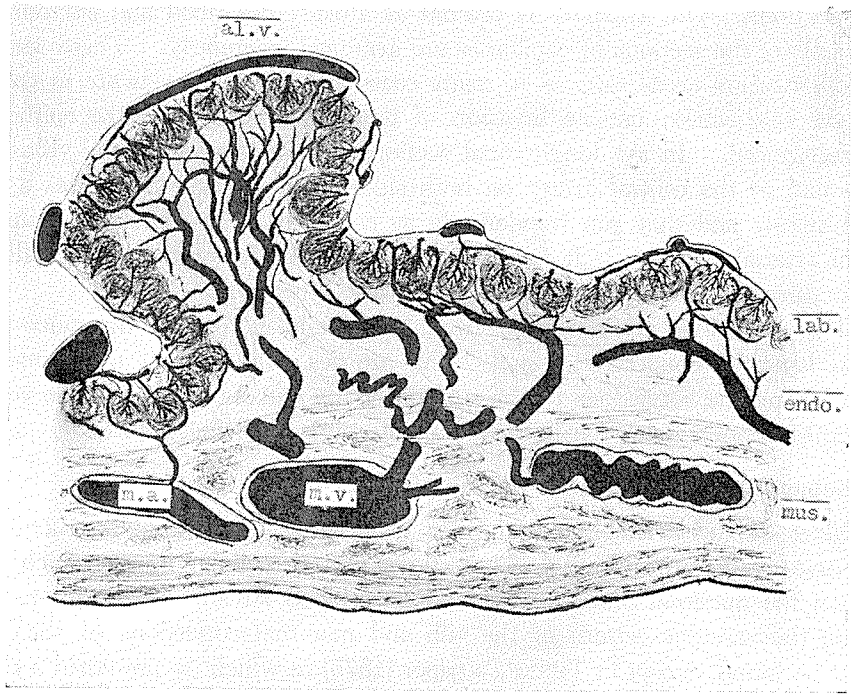

Diagram 1. Vascular pattern of the horse placenta.
al. v.—allantoic vessel, lab.—labyrinth, m. a.—maternal artery, m. v.—maternal vein, mus.—muscular layer, endo.—endometrium.

plexus. They are arranged in a row and surround each tuft of the villi respectively. Each globe (cotyledon) is covered smoothly by a capillary net which has regular polygonal or round meshes as a result of anastomosis of capillaries. Uterine arterial tributaries run up vertically to the surface of uterine mucosa among the globes and are dispersed radially along the ridges of surface to the tops of the globes; they connect with the capillary net which covers the crypts in the globes. At the upper surface of the globe, comparatively large holes open irregularly surrounding the axes of the villi; on the inner side of the globes many cylindrical crypts are formed which contain the villi. The septum, or wall of the crypt, is very thin and contains a layer of capillary net. The maternal blood which is flowing in these capillaries reaches the somewhat large capillaries which cover the surface of each globe and drains into the few venous tributaries at the bottom of the globe.

Concerning the relationship between the maternal and fetal blood streams in the contact surface on both sides of the tissue layers, the maternal blood

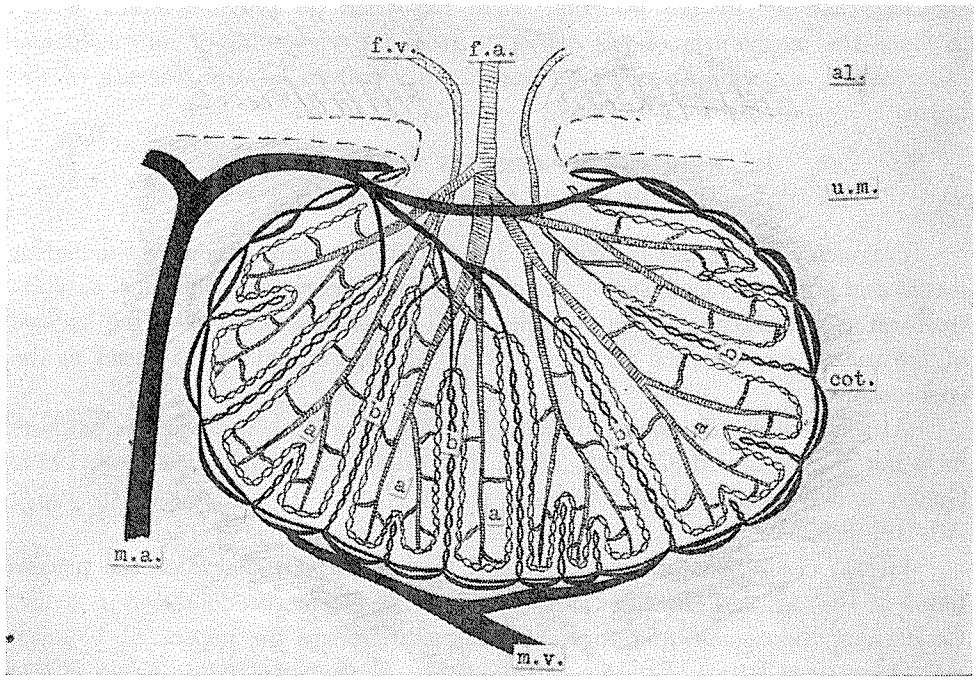

Diagram 2. Vascular pattern in the cotyledon of the horse placenta.
f. a.—fetal arterial vessel, f. v.—fetal venous vessel, al.—allanto-chorion, u. m.—uterine mucosa, cot.—cotyledon, m. a.—maternal arterial vessel, m. v.—maternal venous vessel, a—villus, b—maternal septum.

flows from the fetal side of the uterine mucosa towards the outer surface of the uterus, while the fetal blood flows in the opposite direction to that of the maternal blood stream. This is clear in the histological observations, too. The epithelium exists on both the fetal membrane and on the uterine mucosa.

From the above observations, a diagram of uterine mucosa and allanto-chorion is drawn on page 396.

In short, the capillaries which are distributed to the surface of the villi are venous capillaries and connect with the umbilical cord; they receive oxygen from the maternal blood and transport it to the fetus. The capillaries which are distributed to the maternal septa are arterial capillaries connected with the uterine arterial tributaries, and they carry oxygen to the fetal capillaries of the villi, after which they drain to the uterine venous tributaries. A diagram of the vascular pattern in the cotyledon is shown on this page.

Though the essential meaning of the relationship between the capillaries of villi and the capillaries of the walls of the crypts is surmised from the gas

exchange activity in the placenta, there has been no previous study which explains the mechanism of gas exchange from the viewpoint of morphological observations, especially concerning the vascular pattern in the placenta of the horse.

B. RESULTS OF OBSERVATIONS ON THE PLACENTA OF THE PIG

Pregnancy in the pig is multiple and the embryos are generally situated in the central portion of each sac. The sac, or allanto-chorionic membrane, exhibits fusiform shape, and numerous club-like small projections occur over the surface of the sac, except on the necrotic tips of allanto-chroion; it is faced to the endometrium.

Attachment occurs about 15 days after fertilization, though various workers have not always agreed (CORNER, 1921; WINTERS, GREEN and COMSTOCK, 1942; GREEN and WINTERS, 1945; GREEN, 1946; HITZIG, 1949; AMOROSO, 1952; AUSTIN, 1959).

HITZIG (1949), AMOROSO (1952) and HARVEY (1959) described the placentation of the pig, and HUGHES (1928) observed the freemartin condition in swine. Concerning the uterine migration of fetuses, there are the papers of CORNER and AMSBAUCH (1917), CORNER (1921, 1923), WARWICK (1926), KUDŌ (1951) and others. TURNER (1875), FRAENKEL (1898), GOLDSTEIN (1926), WISLOCKI and DEMPSY (1946), AMOROSO (1952), and DEMPSEY, WISLOCKI and AMOROSO (1955) observed the fully developed pig placenta; and ABROMAVICH (1926), BRAMBEL (1933) and HITZIG (1949), especially, made mention of the areolae.

However, there has been no detailed description of the vascular pattern in the pig placenta and no reported experiment using neoprene latex casts prior to this study.

1. Macroscopic observations of the pig placenta

The pregnant uterine horns do not arrange plainly, but each pregnant portion which contains a fetus overlaps, because they are long and bulky with their contents, and complexly curved. The uterine body is very small. The large ovarian vein, which runs across the central portion of the broad ligament, connects with the ovarian vein on the opposite side via the uterine cervix. The large branches of this vein run to the uterine horn, and these branches give off many small veins, which run over the surface of the uterine horn vertically and extend to the mucosa at the mesometrial side of the uterine horn. The uterine artery, also, gives off several branches at the central portion of the broad ligament. These arterial branches run directly to the mesometrial

side of the uterine horn, divide right and left, and anastomose with each other along the proximal portion of the uterine horn. From these vessels, many branches are given off on the surface of the uterine horn (Fig. 45).

The fetal membranes can be readily stripped off from the uterine mucosa by cutting open the uterine wall in most pregnant uteri. The pregnant portions of the uterus can be identified by observing the appearance of the uterine horns because the pregnant portions are voluminous and the portions which separate the fetuses are contracted. The uterine mucosa forms a wrinkled surface and each fold of the mucosa runs vertically to the central axis of the uterine horn. However, these folds are not arranged in parallel, but rather radially because the dorsal surface of the uterus is expanded more than the ventral surface in each pregnant portion.

Each allanto-chorion with its contained embryo is a distended, fusiform sac and has allantoic diverticula at the tips of the allanto-chnrion. These allantoic diverticula are sharply marked off from the main body by an annular thickening and show a thin, yellow-brown-colored membranous sac. The cavity of a diverticulum is connected to the allantoic cavity through a narrow pathway in the part of annular thickening (Fig. 46).

Fetuses are oriented with the ventral side of the body always facing to the mesometrial side of the gestation sac. The top of the umbilical cord, also, is attached to the allanto-chorionic membrane on the same side. The amniotic sac is in contact with the allantoic sac on one side of a fetus, while the other side is free in the allantoic cavity. The amniotic membrane is transparent, colorless, and thin, and the vascular system can not be recognized clearly.

Two arteries and a vein run through the umbilical cord; the arteries turn to the left and right, respectively, at the mesometrial side of the allanto-chorionic sac and distribute to each half of the fetal membrane; the umbilical vein parts right and left at the mesometrial side. These vessels run longitudinally in parallel on the central portion of the allanto-chorion to the mesometrial side of the gestation sac. These axial vessels give off many branches at right angles on the way, but radially to the annular portion.

The capillaries at the tips of the allanto-chorion are focused to the annular portions and the arterial capillaries anastomose with the venous capillaries at these annular portions.

In early pregnancy, each allanto-chorionic sac is separate, but as gestation advances the adjacent chorionic sacs become fused. However, the fusion is not very tight.

Many large folds of the fetal membrane are formed according to the formation of the folds of the uterine mucosa (primary folds); and villi which

are matched by corresponding uterine depressions, according to microscopic observation, form numerous small folds over the fetal membrane in parallel to the primary folds. Moreover, many areolae, which show round spots of varying diameter, but averaging 1–2 mm, are scattered on the surface of the chorion. By the injection of colored latex into the umbilical vessel, these areolae are rendered recognizable as white spots compared with the surrounding colored spaces (Fig. 47). The areolae are classified as regular in type in most cases; irregular areolae are very few and it is necessary to observe carefully to discover their existence.

2. Microscopic observations on the vascular pattern of the allanto-chorion of the pig placenta

The surface of the fetal membrane can be divided into two parts, areolar and interareolar areas. The secondary folds of the allanto-chorion develop as far as the villi, each of which shows a simple club-like shape when observed separately. The attachment between the fetal membrane and uterine mucosa is formed by the interlocking of the villi and uterine crypts. The areolae have minute central depressions surrounded by villi which are the terminal villi of a group of ridges; these villous ridges are arranged radially to each central areola (Fig. 48).

(a) Interareolar area

In the early stage of the secondary folds, the capillaries are distributed close together only on the surface of the projections, forming a network. The vascular relationship between the separate folds is very irregular. The projections of the folds are so inconspicuous that the vascular system on the surface of the fetal membrane appears only as a vascular layer of capillary network on the whole (Fig. 49). In the later stages of pregnancy, however, the folds become complicated and each projection in the folds is almost covered with a network of capillaries (Fig. 50). The capillaries covering the surface of the complicated secondary folds run transversely along each fold; the relationship of the vessels between adjacent folds is not very close. Near term, the projections in the folds become clear and larger to form the villi which show a club-like shape in each projection (Figs. 51–53). Each villus is covered with the capillary net over almost all of its surface; the capillary net is constructed with small square, pentagonal, or hexagonal meshes of capillaries. In some villi, an arterial branch, somewhat larger than the capillaries, runs up from the root of the villus to the top along the side surface of the villus, and disperses to the capillaries at the top of the villus. The shape of the top of a villus is not always round, but like a broad bean which has become depressed at the

central portion, or like a heart of which the top is made round. The arterial twig on the surface of such a villus runs up along this depression to the top. Though this artery disperses to the capillaries covering the surface of a villus, the superficial capillary net not only covers the surface of a villus, but also covers the adjacent villi around it. However, in some cases such an arterial twig is not recognized.

In a vertical section of the fully developed allanto-chorion, the club-like villi are seen to be closely arranged in a row facing the uterine mucosa, and the fetal tributaries are distributed along the side of the allantoic cavity. From these tributaries, many branches are given off which reach to the root of each villus. These branches connect with the capillaries of the villus, either after running up vertically to the top of the villus on its surface, or immediately at the root of the villus. Sometimes such branches elongate obliquely on the surface of a villus and are distributed on several villi, and the capillary net on the villus connects frequently with the capillary net of adjacent villi (Figs. 54–56).

Generally, the ends of the arterial branches connect with the superficial capillaries of the villi, while the capillaries connect with the tips of venous tributaries at the roots of villi. The capillary net does not always entirely cover the surface of a villus; in some portions of the surface of some villi there is no vascular distribution (Fig. 57). In such a villus, the edge of the capillary net is rendered smooth by a linear capillary. Parts which are lacking in vascular distribution are usually seen on the side of each villus.

In transparent specimens it is recognized, also, that the arterial tributaries attach to the roots of villi, and the branches are given off to the tops of villi, running up along the surface of each villus, and disperse to the capillary net on the surface of the villus on their way, or immediately at the root of each villus. On the other hand, the venous tributaries, also, connect with the superficial capillary net at the roots of villi; therefore, it is hard to distinguish whether the tributaries are arterial or venous. There are, however, tendencies for the venous tributaries to be larger than the arterial ones, and for the positions in which the venous tributaries connect with the capillary nets of the villi to be in the chorionic fossa portions in many cases. In a few cases there are arterial and venous branchlets which run up the surface of a villus in parallel; in such a villus they are distinguished only by the color of injected materials. It is certain from the cross sections that there is no central vessel in a villus (Fig. 58).

In short, the relationship between the arterial and venous vessels, distributed on the surface of villi, is not very regular in most cases. But, as a general tendency, in many villi a branch artery runs up along the surface from the

root to the top, and disperses to the capillaries which form the network covering the villus either on the way or at the top of a villus. It is also frequently recognized that the capillaries connect with the tip of the arterial tributary immediately at the root of a villus. These capillaries form a network and entirely cover the surface of a villus, except sometimes for a small portion on the side of a villus. The capillary net of the villus connects with either the tips of the venous tributaries at the root of a villus or with the capillaries of adjacent villi. However, in a few cases there are branch veins which distribute to the villi in the same manner as the arterial twigs.

(b) Areolar area

Regular areolae are scattered all over the fetal membrane, and each has a round or oval shape. An areola has a depression in the central portion and many papillate projections which are arranged radially from the center and are different in appearance from the surrounding villi (Fig. 59). The secondary folds surrounding an areola elongate and extend into the areola radially (Fig. 60). The capillaries of the villi in each fold gather in a few capillaries near the end of a fold and connect with the capillaries distributed in the papillate projections of an areola. The capillaries in the papillate projection may or may not form a network, and disappear at the bottom of the central depression of an areola (Fig. 61). There are a few capillaries which run along the circumference of an areola and connect with the capillaries in each fold. But, in a few cases, such a surrounding capillary is not recognized.

In the vertical sections of an areola, the capillaries which entered from the villi of the folds into the papillate projections immediately rise up to the tops and then run down in reverse direction to the bottom of the depression, then are gathered into a few large vessels connected directly with the large venous tributaries (Figs. 62–63). The venous tributaries, however, give off branches to the surfaces, not only of the areolae, but of the villi surrounding the areolae. It is more clear by means of observation from the allantoic side of the allantochorion that the capillaries of the villi of folds are gathered at the bottoms of the areolae and connect with the venous tributary (Fig. 64).

Irregular areolae are very few and flat on the surface; their shapes and sizes are various; they have no papillate projection (Fig. 65). The capillary net covers the surface of an irregular areolar area flatly and connects with the tributaries of the artery and vein; especially large branches of veins connect with these capillaries. It is estimated that these irregular areolae have the same function as the regular areolae.

3. Microscopic observations on the vascular pattern on the surface of the uterine mucosa of the pregnant pig

(a) The area corresponding to the interareolar area of the allanto-chorion

On the surface of the uterine mucosa, many secondary folds are arranged vertically to the uterine horn. These folds are small in the middle of pregnancy, but near term they become very large and complicated (Fig. 66). A layer of capillary net covers the entire surface of the uterine mucosa, which is constructed with numerous crypts interlocking with the tips of the villi (Fig. 67). In longitudinal section of the uterine mucosa, it appears that the secondary folds are very thin in contrast to the broad crypts, and that the tributaries of arterial and venous vessels running tangentially along the bottoms of the crypts do not penetrate into the secondary folds (Figs. 68–70). The tops of the tributaries connect directly with the capillaries on the surface of the uterine mucosa at the roots of folds or at the portions where the bottoms of the crypts usually approach the roots of the folds.

It is clear, upon observation of the surface layer of the mucosa from the reverse side, that the capillary net layer covers the surface of the uterine mucosa and shows many round, bamboo basket-like shapes arranged close together all over the surface in rows. The bottom of each basket is depressed, and many arterial and venous tributaries run in complicated fashion along beneath this layer of capillaries. The rims of the "bamboo baskets" correspond to the folds, while the bottoms of the baskets correspond to the bottoms of crypts. The tributaries of uterine vessels are distributed along the ditches formed by the junctions of baskets on the reverse side of the mucosa, and the tips of these branches connect with the surface capillaries, usually near the roots of folds, but a few at the bottoms of crypts (Figs. 71–73). In a few cases, anastomosis between the arterial and venous tributaries is recognized beneath the superficial capillary net.

Concerning the relationship between arterial and venous vessels, it seems at a glance that their arrangement is irregular. But there are no cases in which the tops of these arterial and venous tributaries connect with the surface capillaries in the same location. However, blood circulation from arterial to venous vessels via the capillaries must occur. This is proved by more delicate observations. The tips of the arterial tributaries disperse to the capillaries of the crypt at one side of the round bottom of the crypt, and the tip of the tributary vein connects with the capillaries of the same crypt at the opposite side. Generally, there are many such connections between arteries and veins through the capillaries which cover a few continuous crypts. In such a combination

of artery and vein, the blood stream does not flow in a constant direction, but moves irregularly in many directions. This fact shows that there are many small local circulatory arrangements on the surface of the uterine mucosa.

(b) The area corresponding to the areolae of the allanto-chorion

As mentioned above, many folds are arranged on the uterine mucosa and many round spots showing shallow depressions are scattered on the uterine surface at the areas corresponding to the areolar areas of the allanto-chorion (Figs. 74–75).

In the central portion of each spot a mouth of a uterine gland is seen as a small hole. The secondary folds surrounding these spots are arranged radially to the spots and the surface of the spot is flat without papillate projections. The surface capillaries in this spot, which connect with the capillaries of the surrounding folds, are very rough and form a network with large meshes. They connect with a few more large vessels which are the uterine venous tributaries (Fig. 76). This relationship is also clearly seen in the vertical sections of a spot (Fig. 77), and upon observation from the reverse side of the uterine mucosa (Fig. 78).

It is clearly indicated, then, that the blood flowing in the superficial capillary net of the uterine mucosa is drained in part from these spots to the venous tributaries.

(c) The relationship of the fetal and maternal vascular systems in the interareolar area

Generally, it is hard to obtain a good specimen in which the fetal and maternal vascular systems can be observed simultaneously, because of the loose contact of the fetal membrane and uterine mucosa. But in a few specimens it was recognized that the capillary nets of the fetal and maternal sides form parallel double planes and that they are curving and interlocking with each other (Fig. 79).

4. Histological observations of the pig placenta

The fetal membrane is attached to the uterine mucosa histologically, but in many histological specimens the villi of the allanto-chorion and the folds of uterine mucosa are shrunken to the extent that they appear to be separated.

In early pregnancy, no secondary fold of the uterine mucosa is formed (Fig. 80); the uterine epithelium is a single layer of low columnar cells, while the trophoblast is a single layer of columnar cells; large nucleated erythrocytes are recognized in the fetal vessels. The maternal and fetal capillaries and distributed beneath their respective epithelia. However, with the advance of

pregnancy, villi are formed and the contact surfaces of both maternal and fetal tissues become highly irregular curving (Figs. 81–82). The uterine epithelial cells become cuboidal, while the epithelial cells of a villus are columnar, though their shapes are various. Generally, the cytoplasm of the uterine epithelial cells is basophilic, while the cytoplasm of the chorionic epithelial cells, which have a thin layer on their upper portions which is strongly eosinophilic, takes the eosin stain. The capillaries of both sides spread out in immediate contact with the epithelial cells and, moreover, on the fetal side many capillaries penetrate into the epithelium of the top and side of a villus.

Although columnar or cuboidal epithelial cells cover the top of a villus, chorionic epithelial cells at the root of a villus and at the chorionic fossa are more high-columnar and have lighter cytoplasm compared with the former, and are vacuolated in many instances.

The capillaries of villi are distributed mainly in the subepithelial area. At the top or side of a villus many intraepithelial capillaries are seen, but few occur in the chorionic fossa portions. At the central portion of a chorionic fold there are few capillaries (Figs. 83–84). The interareolar area can be divided into two parts, then: the intraepithelial capillary nets which cover the chorionic folds, and the relatively avascular parts which are found at the chorionic fossae. Often the intraepithelial capillaries come to lie so near the surface that only a very thin layer of epithelial cytoplasm separate the blood vessels from the maternal tissues. An areola shows a large depression and has large papillate projections on the surface. The epithelial cells are mostly single-high-columnar in nature, and their nuclei are arranged irregularly because of numerous vacuoles in the cells. There are no intraepithelial capillaries in this part (Figs. 85–86).

On the surface of the uterine mucosa, numerous folds are recognized, except in the spots corresponding to the areolae. The spots are flat on the surface and fit over the areolae. The epithelial cells are uniformly cuboidal or flat. Uterine capillaries are densely distributed in the subepithelial layers, but never in the intraepithelial layers. In the subepithelial layer, near the roots of folds, rather large vessels exist.

5. Summary of observations on the placenta of the pig

On the surface of the interareolar area of the allanto-chorion, primary and secondary folds are formed fitting the folds of the uterine mucosa. The secondary folds of the allanto-chorion develop as far as the villi, which show a simple club-like shape in each case; the villi interlock with the uterine crypts. A network of small meshed capillaries covers the surface of the villi, and shows a long zonary shape along the secondary folds. The relationship of vessels in

each fold is not close. The arterial and venous tributaries which are distributed in this area reach to the roots of the villi and disperse to the surface capillaries of the villi. The correlation between the arterial and venous tributaries which are distributed on the surface of villi is not clear, but irregular. Generally, however, the arterial branches which are given off from the arterial tributaries at the roots of villi run up to the tops along on the surface of the villi, and disperse to the superficial capillary nets of the villi on their way or at their tops; the capillaries connect with either the venous tributaries at the roots of villi or with the capillaries of adjacent villi. It can be supposed that numerous small and limited local circulations occur in this area, and that another blood stream which flows along the surface of a secondary fold exists. This supposition is confirmed by the existence of numerous areolae which are scattered on the surface of the allanto-chorion. The superficial capillaries of the secondary folds of the allanto-chorion, surrounding the areolae, elongate and extend into the areolae radially; these capillaries connect with the venous tributaries finally. Then, it is reasonable to suppose that the arterial blood is pushed up into the superficial capillaries of the villi at the interareolar area through the numerous arterial twigs and tributaries, that the exchanges between fetal blood and maternal blood occur at the surface of these villi, that the blood in the capillaries is drained in part by the numerous venous twigs and tributaries in the interareolar area, and that some of the blood in the capillaries is drained by the venous tributaries in the areolae.

The same relationship can be seen on the uterine side. The surface of the uterine mucosa, which has many secondary folds, is covered with a capillary net which is seen, by observation from the reverse side, to be an arrangement of many round "bamboo baskets" in rows, due to the formation of secondary folds and crypts. The tops of the numerous arterial and venous tributaries connect with this capillary net chiefly at the roots of folds, and no vessel runs up to the top through the central portion in a secondary fold. The tip of an arterial tributary connects with the capillaries at one side of the round bottom of a crypt, and at the other side of the crypt connects with the tip of the venous tributary. Many such oppositions of the arterial and venous tributaries through the superficial capillary net, which covers a few continuous crypts and folds, occur in various ways. Moreover, in the areas corresponding to the areolae of the allanto-chorion, there are many flat spots which contain the mouths of the uterine glands in their central portions. The surface capillary net of such a spot connects with the capillary net of the villi and with the venous tributaries. It is surmised, then, that the fetal and maternal streams flow under the same conditions along the contact surfaces of the fetal and

maternal tissues.

These structures of the placental vascular system are considered to be thus arranged functionally for the exchange between fetus and mother, because there is a tendency for the density of any substance involved in the exchange to be kept constant. The capillaries of both fetal and maternal sides are supplied with fresh blood by numerous arterial branches everywhere in the interareolar area; on the contrary, the blood leaves in part through the superficial capillaries, while the surface blood is flowing to the areolae or to the areas corresponding to the areolae, which are connected with the venous tributaries. The system is also suitable for the exchange in that the capillaries at the tops or sides of villi are distributed in the intraepithelial layer, and the distance be-

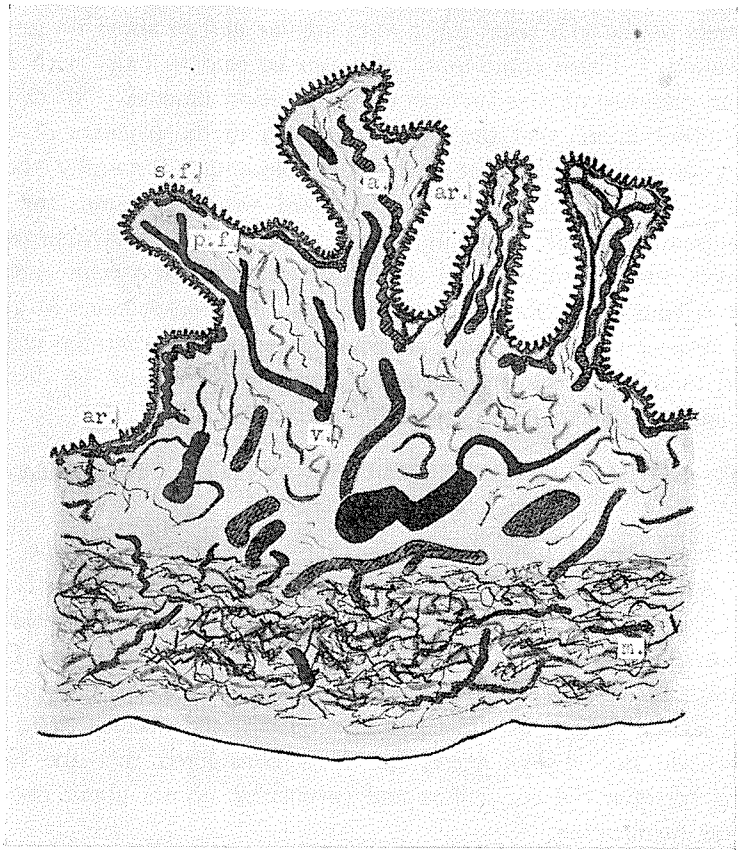

Diagram 3. Longitudinal section of the uterine mucosa in the pregnant pig.
ar.—areola, a.—uterine arterial vessel, v.—uterine venous vessel,
p. f.—primary fold, s.f.—secondary fold, m.—muscular layer.

tween the two blood streams becomes very small.

A diagram of the vascular system in the uterine mucosa is drawn on page 407.

To put it briefly, the villi of the pig placenta are formed by the development of the folds. Though the pig placenta is classified as a diffuse epitheliochorial placenta like the horse's, the arrangement of the villi in the pig placenta is very irregular and their structure is primitive in comparison with the villi of the horse. In the horse placenta, the villi form cotyledons and are arranged regularly on the surface of the fetal membrane.

In the case of the horse, the tufts of villi form cotyledons and the arterial tributaries run up to the tops of each villus through their central portions. The venous capillary net, which covers the surface of the villi, surrounds the axial arterial tributaries. But in the pig's fetal membrane, the arterial and venous vessels of the villi seem to be very similar and to show no great degree of specialization. These conditions, also, can be said to exist with respect to the vascular patterns of the surface of the uterine mucosa. It may be said from these observations that the vascular pattern in the placenta of the pig is primitive in comparison with that of the horse placenta. Generally, the placenta is an organ which has developed a specialized vascular system for exchange between fetus and mother. But in the pig placenta, special structures, areolae, are developed, and no complicated structure forms between fetal and maternal tissues. It is considered, then, that the pig's placentation remains in a primitive stage with respect to the placental structure and the fact that the uterine milk is absorbed mainly by the areolae. The pig placenta must be distinguished from the placenta of the horse on these points.

C. RESULTS OF OBSERVATIONS ON THE PLACENTA OF THE COW

It has been known for a long time that many swollen uterine caruncles, which are specialized non-glandular areas, exist on the surface of the endometrium of the pregnant cow. The development and attachment of the fertilized ova has been studied by HAMMOND (1927), WINTERS, GREEN and COMSTOCK (1942), KINGMAN (1948), MELTON, BERRY and BUTLER (1951), CHANG (1952), FOLEY and REECE (1953), MARION and GIER (1958) and others. The results of their studies do not always agree, but it is considered that the first actual interlocking between the cotyledons and carunculae occurs about one and half months after fertilization.

The histological changes in the fetal and maternal cotyledons during pregnancy have been described by FRAENKEL (1898), ASSHETON (1906), JENKINSON (1906), KOLSTER (1909), ANDRESEN (1927), HAMMOND (1927), KINGMAN (1948),

AMOROSO (1952), CHANG (1952), WEETH and HERMAN (1952), FOLEY and REECE (1953), WEETH (1953), BJÖRKMAN (1954), ZIETZSCHMANN and KRÖLLING (1955) and others. TURNER (1875), also, offered a simple description of the fully developed placenta in the cow.

Concerning the vascular pattern of the cow placenta, KRONACHER (1927) showed a diagram of the vascular system in the villus of the cotyledon, and HILLIGER (1958) observed the vascular system in the maternal cotyledons. HILLIGER (1958) sought out the vascular relationship between the uterine vessels and the caruncular vessels by the method of injection with plastoid-korrosion into the pregnant uterine vessels. But, according to the figures in his paper, the injections into the carunculae were insufficient and the fine structure of the vascular system does not show in detail.

Dealing with the accessory cotyledons, there are papers of KOLSTER (1903), JENKINSON (1906), RÖRIK (1907) and HAMMOND (1927).

As already indicated, the endometrium of the cow is subdivided into two parts, the uterine carunculae and the intercaruncular areas. TURNER (1875), KOLSTER (1903), HAMMOND (1927), WEETH and HERMAN (1952), AMOROSO (1952) and BJÖRKMAN (1954) observed these intercaruncular areas. Histochemical studies of the placenta in the cow were undertaken by HÖPPING (1937), WEETH and HERMAN (1952), WEETH (1953), FOLEY, REECE and LEATHEM (1954), BJÖRKMAN (1954) andothers. LILLIE's papers (1916, 1917) about the freemartin in the cow are classical.

As noted above, studies of the cow placenta have been made by many investigators, but investigations on the vascular pattern of the placenta are very few, and described only by HILLIGER (1958). Therefore, the present author undertook to study the vascular pattern of the fully developed placenta of the cow, making use chiefly of neoprene latex cast specimens.

1. Macroscopic observations of the cow placenta

The large pregnant uterine horns, which are fixed to the vertebral side of the body at three points, the vagina and the ovaries, are suspended in the abdominal cavity. Uterine arteries and veins run along the mesometrial side of the uterine horns on broad ligaments and give off many branches on the uterine surface vertically to the dorsal side of each uterine horn. On the surface of the endometrium, many large cotyledons are arranged, and the thick, short umbilical cord is connected with the allanto-chorion on the mesometrial side of the uterine mucosa. The amnion is in contact with the chorion on one side of the fetus, while the other side of the amnion is free in the allantoic cavity. Four large fetal vessels run through the umbilical cord. The arrangement of

the umbilical vessels in a cross section at the portion near the umbilicus shows as a square or trapezoid; the front rank vessels are arteries and the rear rank vessels are veins. These two umbilical arteries are anastomosed with each other by a somewhat thick and short vessel near the allanto-chorionic membrane. The umbilical arteries are easily distinguished from the veins by ascertaining the existence of this anastomosis.

The arrangement of the cotyledons is linear, parallel to the uterine axis, and in four series on the whole; although there is a tendency for the linear arrangements to be in five series at the broadest part of the uterus (Fig. 87). The allanto-chorion covers the surface of the endometrium and cotyledons; at the cotyledons it is tightly attached to the maternal cotyledons by their villi, and the fetal membrane in the uterine cavity can be stripped off by tearing the fetal cotyledons away from the maternal cotyledons. The villi on the surface of the allanto-chorion are located, in the form of round or oval tufts of villi, at the places corresponding to the maternal cotyledons. When the fetal sac is taken out intact from the uterine cavity and left on a plate, the arrangement of the fetal cotyledons is linear and in parallel to the inner side of the fetal sac, mesometrial side, and they are larger at the central portion of the fetal membrane than at the top. The cotyledons in the inner ranks are larger than those in the outer ranks. The umbilical arteries and veins turn to the right and left, respectively, at the mesometrial side of the uterine horn, and run together in parallel to the top of each side of the fetal sac along the central axis of the uterine horn. These axial vessels on their way give off many branches at right angles, but radially to the tops of the fetal membrane. At the main portion of the fetal membrane, the branches are distributed to the fetal cotyledons in the inner series at first, while the more elongate branches reach to the cotyledons in the outer series, and other branches are distributed to the intercotyledonary area. One or two large branches of the axial artery and vein reach to the surface of a cotyledon, the allantoic side, and are distributed evenly all over the cotyledon, with additional small branches, but no anastomosis can be recognized on the surface of a cotyledon. It was observed that the neoprene latex solution, injected into the artery, reached to the small branches covering the surface of the cotyledon, which penetrate vertically into the inner portions of the cotyledon. Then, before long, the injected solution appears again on the surface from the inner parts of the cotyledon and drains into the branches of the veins.

The maternal cotyledons, when the fetal cotyledons covering them are removed, show spongy projections which have many crypts and pits of various sizes. Accessory cotyledons occur irregularly among the cotyledons as large

wart-like projections. The formation of the folds on the uterine mucosa is not very remarkable in comparison with those in the horse and pig, but small folds are formed at right angles to the uterine axis. Small depressions, about 1–3 mm. in diameter, are scattered on the surface of the endometrium. These depressions correspond to the areolae, which are scattered in the intercotyledonary area on the surface of the fetal membrane. The areolae are small ovoidal projections, about 3–4 mm. in diameter at the largest, oriented parallel to the uterine folds.

On the surface of a cotyledon the fetal blood vessels form a vascular covering of fetal arteries and veins; many vascular tufts of villi, about 1–2 cm. or more long in a large one, attach to the outer side of the fetal membrane; they are inserted into the pits and crypts of the maternal cotyledon centripetally (Fig. 88). The fetal cotyledon is subdivided into two parts, the villi and the surface portion.

The tributaries of uterine arteries and veins reach to the bottom of the cotyledon, running through the pedicle to its top, and penetrate into the maternal cotyledon and disperse to the many branches which run straight up to the surface of the cotyledon through the maternal septa. Among these axial branches in the maternal cotyledon, the tufts of capillaries are seen (Fig. 89).

In vertical sections of the cotyledon, it is seen to be connected to the uterine mucosa by a narrow pedicle which penetrates into the cotyledon as far as the central portion and has an umbrella-like shape at the top. The cotyledons cover the outer surfaces of these pedicle tops; they are constructed of the club-like tissue groups which contain the maternal vessels in their central portions and have the fetal vessels at their boundaries; they are arranged transversely and tightly (Fig. 90).

2. Microscopic observations on the vascular pattern in the cotyledon of the cow placenta

(a) Fetal vascular system

The cotyledon presents an uneven surface. Several fetal tributaries penetrate into a villus from each depression of the cotyledon, while many small branches of fetal vessels are distributed on the convex portions (Fig. 91). These fetal tributaries are rather large and penetrate vertically into the cotyledon as axial arterial and venous vessels of the villus, and usually they reach to the bottom of the cotyledon running through the villus. The small branches distributed on the surface of the cotyledon occupy the intervillus areas, which are called "chorionic arcades."

The axial arterial and venous tributaries extend straight in parallel through

the villus to the top, giving off not only a few main branches on the way, but also many small capillaries surrounding the axial vessels. Though the capillaries surrounding the axial vessels of the villus are connected with the capillaries in the arcade, the vascular distributions in villi and arcades are different (Fig. 92). The capillaries, which are given off directly from the axial tributaries, form a multitude of minute tufts which do not become very elongated, and which enter and occupy the crypts surrounding the main stem of each villus (Figs. 92–97). The minute villi forming these tufts are slender and leaf-like in shape; the axial tributaries become narrow as they approach the top of villus and show a single capillary loop at the top, like the minute tufts surrounding the axis of the villus. These minute tufts are arranged like leaves on the branches of tree and each contains a flat, irregular capillary net. But it can be said that this capillary forms a single loop rather than a capillary net; it connects with the axial arterial tributary in one end at the root of a minute tuft and with an axial venous tributary or a neighboring capillary loop in the same end at the root of the minute tuft (Figs. 95–96). The minute tufts are projected vertically or somewhat obliquely to the top of a villus from the axis into the crypts and radially only at the top of villus. A capillary runs smoothly along the edge of each leaf, showing a U-shaped turn at the top of leaf, and then returns to the root. The leaves vary in shape and size, but are narrow at the root and become wide over the middle portion to the top. The edges of the leaf-like minute tufts are chiefly wavy, but sometimes straight. However, a simple and irregular capillary net is formed on the leaf (Figs. 94 and 96).

These facts become more clear in cross sections of the villi. The small capillary tufts are projected radially surrounding the axis of a villus and a few arterial tributaries are situated in the central portion of the axis; directly from this artery many capillaries of each leaf-like minute tuft are given off. Each villus displays round, oval or rhombic partitions which are surrounded by the maternal septa. The central portion in each partition is the axis of a villus and in the surrounding portion of this axis the maternal and fetal tissues are mingled with each other (Figs. 98–99).

In the arcade, the surface of fetal tissues facing the maternal tissues is irregular and rough, and sometimes shows small villus-like projections. The small branches of the fetal arterial branches penetrate vertically and directly into the fetal tissues of the cotyledon almost to the surface of the chorionic side; then they disperse to the many capillaries returning to the surface on the side of the allantoic cavity. These capillaries form an irregular network and are connected with the fetal venous tributaries on the surface of a cotyledon

(Fig. 100). There is a close relationship between the villous capillaries and arcade capillaries; the capillaries of the villi connect with the capillaries in the arcades, and some branches which are given off from the villous axial tributaries extend to these areas (Fig. 101).

(b) Maternal vascular system

Many arteries which reach to the bottom of a cotyledon through the pedicle are coiling and penetrate into the maternal septa of the cotyledon. These tributaries run up directly to the surface of the cotyledon; near the surface they turn and run along the surface of the maternal cotyledon, giving off many small branches, and sometimes their tops turn to the bottom of the cotyledon along the crypts. Generally, the maternal capillaries are distributed tightly on the surface of the maternal cotyledon and sparsely on the inner portion of the cotyledon (Fig. 102).

All over the surface of the maternal cotyledon, many papillate projections are formed. Those projections which contact the fetal tissues are covered with an irregular capillary net which is connected the tributaries or branches of an artery or vein at their roots, and continue to the capillary net on the neighboring projections (Fig. 103). The arterial tributary which runs along the surface of the maternal cotyledon connects with these capillaries. The cavity of the crypt gradually becomes narrow; the papillate projections of the wall of the crypt become attached tightly to each other near the bottom of the crypt and their projections become joined to those on the opposite side. It is recognized that the surface maternal blood of the cotyledon flows through these capillaries covering the papillate projections from the arcades to the bottoms of the crypts. These capillaries run through the maternal cotyledon to the bottom, sometimes forming tributary veins in the maternal cotyledon, and connect with the main veins in the pedicle.

In the inner part of the maternal cotyledon the vascular distribution is sparse compared with that on the surface. The capillaries in the inner part of the cotyledon form a network which shows irregular, polygonal, large meshes (Fig. 102). These capillaries, which fill up the maternal cotyledon like cotton between the large maternal arterial and venous tributaries in the neoprene latex cast specimens (Fig. 104), connect with the uterine venous tributaries at the bottom of the cotyledon (Fig. 105), or in the cotyledon (Fig. 106). It is clear from cross sections that the maternal tributaries, chiefly, run through the junctions of maternal septa in the cotyledon, and few arterial and venous branches are given off in the surrounding areas (Fig. 107). The capillaries in the maternal tissue, which are mingled with fetal tissues, are arranged in

a single row, never in two rows. The capillary meshes are polygonal in cross section and also in vertical section. On the other hand, in the sections of the top of a minute villus, the fetal tissue, which is covered with the somewhat opaque maternal tissue, is flat and contains one to three capillary sections which are arranged linearly (Fig. 108).

3. Microscopic observations of the vascular pattern in the intercotyledonary area of the cow placenta

(a) Fetal vascular system on the surface of the allanto-chorionic membrane

Many areolae are observed on the surface of the allanto-chorion facing the uterine mucosa. Generally, the surface of the inter-areolar area is comparatively even and smooth, though small folds are formed in a direction perpendicular to the uterine axis. A layer of capillary net covers the surface of the inter-areolar area (Figs. 109–110); this capillary net connects with many branches of fetal arteries and veins.

An areola is recognized as a small elliptical projection, which is constructed of more small papillate projections (Fig. 111). These papillate or villus-like projections are covered with an irregular capillary net which is connected with the capillary net on the surface of the inter-areolar area and with the fetal branch veins which run through the axes of these papillate projections (Fig. 112). On the back side of these areolae, the fetal venous tributaries are always distributed directly (Fig. 113). It is believed that fetal blood on the surface of the allanto-chorion is drained in part from the areolae.

(b) Maternal vascular system on the surface of the uterine mucosa

Many small depressions, which correspond to the areolar area of the allanto-chorion, are scattered on the surface of the uterine mucosa (Figs. 114–115). In the area corresponding to the inter-areolar area, numerous capillaries are closely arranged in parallel (Fig. 116) and run straight along the surface of the uterine mucosa in a direction perpendicular to that of the axis of the uterine horn. These capillaries anastomose with each other in complicated fashion to form a network, and connect irregularly with many branch arteries and veins of the uterus (Fig. 117). The surface of these uterine depressions is covered with a capillary net which connects with the surrounding capillary net, and the venous tributaries connect with the capillary net at the bottom or on one side of each depression (Fig. 118). It can be supposed that the vascular relationship on the surface of the uterine mucosa possesses the same character as that on the allanto-chorion.

4. Histological observations of the cow placenta

The fetal cotyledon is subdivided into two parts, *viz.*, villi and arcade. Each villus is independent of the maternal septa which surround the villus and each villus is fitted into a crypt. At the arcade, the maternal tissues show papillate or branched projections reaching to the allanto-chorion (Fig. 119). The large maternal vessels in the cotyledon extend straight through the maternal septa to the surface (Fig. 120). Generally, a crypt is surrounded by the maternal septa and has a pot-like shape which becomes narrow near the bottom. In the central portion of the crypt, the villous axis extends longitudinally, and from this axis of a villus many small branches are given off vertically into the surrounding crypt; these branches are mingled with the maternal tissues. In the central portion of the villus axis, large fetal vessels are recognized. In cross sections of the cotyledon, the axis of a villus show a starfish-like shape and is surrounded by the maternal septa (Fig. 121). In the central portion of the axis of a villus, a few large arteries and veins are recognized. The maternal septum rises vertically on the bottom of the cotyledon and runs directly to the surface. The septum increases its thickness near the surface of the cotyledon and shows a slender club-like shape in vertical section. Many branches are given off vertically from the side of a septum to the central portion of the crypt and they are mingled with the villous tissues. But the branches of the fetal villus and maternal septum are arranged chiefly in parallel and tightly piled upon each other (Fig. 122).

Generally, in the cotyledon, the cells of the fetal tissues are larger than those of the maternal tissues, and scantily stainable. In the crypt zone of the cotyledon, as it is called by BJÖRKMAN (1954), the crypts are lined mostly with a simple cuboidal epithelium, but partly with a simple squamous or columnar epithelium. The cells of the epithelia are comparatively small and arranged tightly, and their stainability is intermediate, but in a few cells the nuclei are highly stainable. Most nuclei lie in the upper portion of the epithelial cells, and show round or transversely elliptical shape; but they are longitudinally elliptic in the columnar epithelial cells. In the subepithelium the maternal connective tissue is dense and its cytoplasm show high stainability. The maternal capillaries are distributed in these connective layers, sometimes directly beneath the epithelium (Fig. 123), but no intraepithelial capillaries are seen in this part. The most characteristic cells in the epithelium of the crypts are binucleate or mononucleate giant cells which are scattered in the epithelium and contain large round or elliptical nuclei; the cytoplasm is of varying size and is highly stainable in most cells.

The trophoblastic cells of villi are generally cubic and many binucleate or mononucleate giant cells intervene among them. The arrangement of the trophoblastic cells is very irregular on account of the various vacuolations in the trophoblastic cells. The ordinary cubic cells of the trophoblast contain round nuclei in their central portions, but sometimes the nuclei show various shapes because of the vacuolation of the poorly-staining cytoplasm. The connective tissue under the trophoblast is rough and stained only weakly. Fetal capillaries are recognized in the layer of this connective tissue and directly beneath the trophoblast, though sometimes in the trophoblast (Fig. 124). The intraepithelial capillaries of the villi are separated from the maternal tissues by only a thin cytoplasmic layer in some places.

In the arcade zone, the epithelium of the crypts is degenerated and the connective tissue layer is adjacent to the fetal tissue in most place. There are many erythrocytes, free cells and masses of degenerated matter in the spaces between fetal and maternal tissue. But the degenerated epithelium, which is arranged irregularly and has deeply-stained cytoplasm, remains in some places. On the fetal side of an arcade, many small and short villi which show uniform features are recognized. Generally, the fetal epithelial cells in these areas are columnar, weakly stainable, and strongly vacuolated. At the roots of villi, the epithelial cells are high-columnar, strongly vacuolated, and arranged irregularly. In the epithelium, many giant cells occur. Numerous fetal capillaries are distributed beneath the epithelium.

In the intercotyledonary area the uterine epithelial cells are narrow-columnar or cubic, but in some areas the epithelium is stratified or entirely lacking. The uterine capillaries are distributed more in the *lamina propria* than in the *stratum compactum*, and it can be said that the *lamina propria* forms a vascular layer. The chorionic columnar epithelial cells are single pseudo-stratified and their arrangement is very irregular because comparatively large and ellipticall cells, which have weakly staining cytoplasm, intervene among them (Fig. 125).

In an areola, small villus-like projections are crowded, and their epithelium exhibits the same features as the surrounding chorionic epithelium. Many fetal capillaries are distributed under the epithelium, forming a vascular layer (Fig. 126). Intraepithelial capillaries are not recognized in this area on either side.

5. Summary of observations on the placenta of the cow

Generally, the placenta of the cow has been called a cotyledonary placenta. Studies of this placenta have been focused mainly on the cotyledons in the past, and those concerning the intercotyledonary area are very few. In the present study the author observed the vascular pattern both in the cotyledon and in the

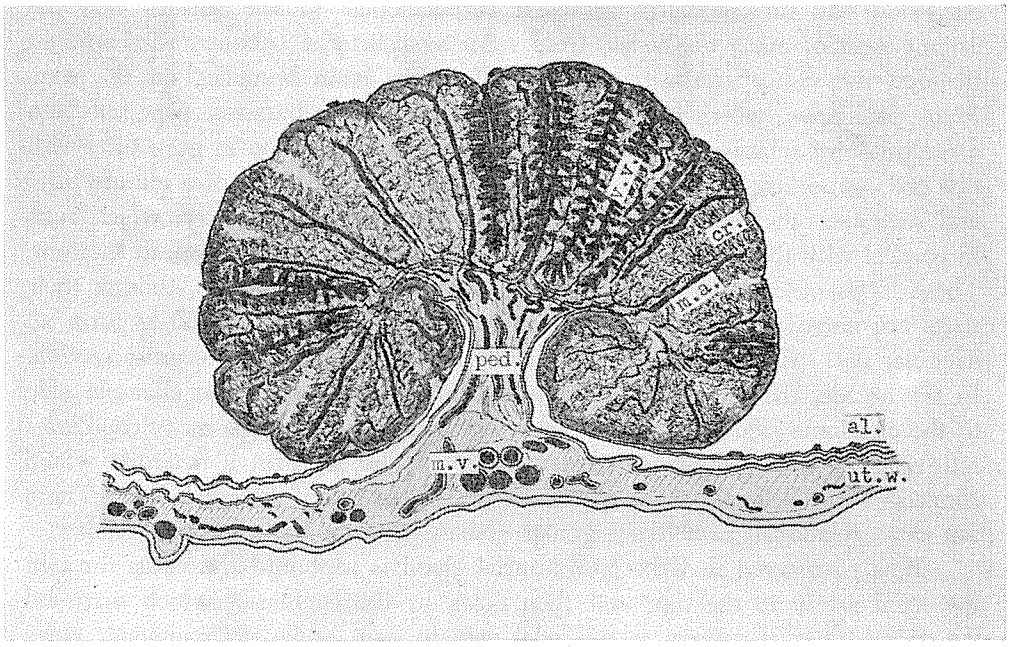

Diagram 4. Vascular pattern of the cotyledon in the cow placenta.
ut. w—uterine wall, ped.—pedicle, al.—allanto-chorion,
m. v.—maternal vessel, v. v.—villous vessel, cr.—crypt,
m. a.—maternal arterial vessel.

intercotyledonary area.

A digram of the vascular system in the cotyledon is shown above.

The cotyledon is joined to the uterine mucosa by the pedicle and it shows an umbrella-like or button-like shape surrounding the pedicle. The surface is not even. In vertical section an arrangement of club-like tissue groups is observed. These contain longitudinal maternal vessels in the central portion and have fetal vessels which have penetrated from the surface depression of the cotyledon at their boundaries. Many uterine arteries and veins run up in parallel through the pedicle to its top, and they penetrate into the cotyledon with coiling and branching at the bottom. The arterial tributaries extend up to the surface of the cotyledon through the central portion of each club-like tissue group, and turn transversely along the surface, giving off capillaries to the surface. Sometimes they anastomose with other arterial tributaries on the surface; sometimes their tips turn along the crypt to the bottom of the cotyledon and disperse to the capillaries.

The villi penetrate the cotyledon from the surface to the bottom of the

cotyledon and are regularly arranged perpendicular to the surface like the arrangement of many needle-leaf trees. An axial arterial tributary runs straight through the villus to the top, giving off a few main branches on the way. Many capillaries, which are given off from the axial tributaries, penetrate into a multitude of minute tufts. A capillary forms a single loop in each tuft, with one end connecting with the axial arterial tributary in the root of a minute tuft; and with the other end connecting with an axial venous tributary, which runs in parallel with the axial artery, or with a neighboring capillary loop, in the root. These loops of capillaries aer wavy and become wide at the tips, though their roots are narrow; their leaves are somewhat flat and their capillaries form an irregular net. Each leaf is opened mainly in the direction of the cross section. In the arcade, the fetal arterial branches run vertically from the allantoic side to the chorionic side of the allanto-chorion, and disperse to the many capillaries returning to the allantoic surface. These capillaries form a network which connects with the fetal venous tributaries on the surface of the cotyledon. There are close relationships in the vascular system between the villi and arcades.

It is considered that the fetal arterial blood is sent into the villus through the axial artery to the top, and then flows in the capillaries which surround the axis. Then it returns to the axial vein in part, while the remainder flows to the root in the capillaries surrounding the axial vessels. The fetal blood in the surrounding capillaries flows to the crypt wall and drains to the arcade.

On the other hand, the branches of the maternal artery which penetrate into the cotyledon from the top of the pedicle show coiling and branching at the bottom of the cotyledon, and straight away reach the surface, running through the maternal septa, giving off few branches on the way. Near the surface the arteries turn to run along the surface of the maternal cotyledon and sometimes turn along the crypt wall to the bottom of the cotyledon. These arteries disperse gradually to the capillaries on the surface of the cotyledon and crypts on their way. These capillaries form a network and cover the papillate projections on the surface of the maternal cotyledon and crypt; they return to the bottom of the cotyledon. In the maternal cotyledon, these capillaries form a network with large polygonal meshes and connect with a venous tributary, either at the bottom of the cotyledon or in the upper or middle portions thereof.

It can be recognized, then, that the relationship of maternal and fetal blood streams is like that of the horse placenta; namely, the blood streams of the fetal and maternal sides in the cotyledon flow in opposite directions.

It has been discussed histologically, in respect to the placental barrier, whether the layer lining the maternal crypt originates from the maternal tissue or from fetal tissue. At any rate, there are six layers between the maternal

blood stream and the fetal blood stream: (1) endothelium of the maternal capillaries, (2) connective tissue of the crypt wall, (3) layer of epithelium lining the maternal crypt, (4) trophoblast of the villi, (5) thin embryonic connective tissue of the villi, and (6) endothelium of the fetal capillaries. It is, however, important that intraepithelial capillaries are recognized in the villus, as they are also in the pig's villi.

In the intercotyledonary area, the vascular systems of the fetal and maternal sides are different than in the cotyledon; they resemble those in the placenta of the pig. The areolae, which are formed on the surface of the allanto-chorion facing the uterine mucosa as small round projections, exist in the areas corresponding to the depressions of the uterine mucosa, into which the uterine glands open. The fetal capillaries are distributed immediately under the chorionic epithelium and they form a layer of capillary network along the chorionic surface, which is connected with the branches of fetal arteries and veins. This capillary net covers the surface of the areolae, and the areolae are connected with the venous tributaries at the bottoms of these areolae. Thus it can be estimated that the fetal blood in the superficial capillaries of the chorion is drained in part through these areolae to the veins, though the remainder is drained from all parts of the capillary net by the branch veins. The same state as in the chorion is recognized on the surface of the uterine mucosa. The maternal capillary net there is connected with the uterine arterial and venous branches everywhere, and the depressions in the area corresponding to the chorionic areolae are covered with the same capillary net. They connect with the uterine venous tributaries at their bottoms or sides. Then it can be surmised that the fetal and maternal blood streams in the intercotyledonary areas of both sides, which are sent into the capillary net everywhere through branch arteries, are drained partly from the surfaces of both sides by the tiny vein branches everywhere in the interareolar area, while the remainder of the blood is drained from the areolar portions to the venous tributaries after running through the superficial capillary net. It may also be considered that the two blood streams, which are flowing through the fetal and maternal capillaries, are moving in same direction in their contact surface.

In short, the placenta of the cow is subdivided in two parts, the cotyledons and the intercotyledonary areas; the blood systems in these two parts are different and show respectively peculiar vascular patterns. In the cotyledon, which is considered as a unit structure, the fetal vascular system shows resemblance to the fetal vascular system in the tufts of villi of the horse placenta. The maternal vascular system in the cow also shows resemblance to that in the maternal cotyledon of the horse placenta. The vascular systems in the two

sides of the intercotyledonary area show resemblance to the vascular systems in the pig placenta with respect to the existence of areolae. It can be said, then, that there are two different kinds of vascular systems in the placenta of the cow. Though the placenta of the cow is generally classified as a syndesmochorial placenta, and as a transitional type between the non-deciduate placenta and the deciduate placenta, like that of the sheep and goat, in HUXLEY's classification, it will be considered here that the placenta of the cow is a mixture of the horse and pig types, and that the maternal cotyledon corresponds to the small globes in the labyrinth of horse placenta. However, the distribution of fetal and maternal vessels in the placenta of the cow is not as regular as in the placenta of the horse.

D. RESULTS OF OBSERVATIONS ON THE PLACENTA OF THE SHEEP

The uterus of the sheep is bipartite, and it forms a cotyledonary placenta in pregnancy. It is said generally that the fertilized eggs appear in the uterine cavity about 3 days after ovulation (ASSHETON, 1906; DAVIES, 1952), and that the attachment takes place about 20 days after fertilization (ASSHETON, 1906; EWART, 1915; DAVIES, 1952; AUSTIN, 1959; HARVEY, 1959). ASSHETON (1906) observed the process of attachment between the fetal cotyledon and the maternal cotyledon in detail. TURNER (1875), FRAENKEL (1898), STRAHL and MARTIN (1908), BARCROFT and BARRON (1946), WIMSATT (1950), AMOROSO (1952) and others reported on the fully developed cotyledon. Concerning the intercotyledonary area, TURNER (1875) and ASSHETON (1906) simply described it, while WIMSATT (1950) observed it in considerable detail. As to the vascular pattern of the placenta, TURNER (1875) and BARCROFT and BARRON (1942, 1946) described only that in the cotyledon, and WIMSATT (1950) reported on only the fetal vascular system. The ends of the chorionic sac show necrosis and they are called "allantoic diverticulums" (JENKINSON, 1906, 1913). The freemartin in the sheep has been reported by LILLIE (1917), STORMONT, WEIR and LANE (1953) and others.

Studies of the vascular pattern in the sheep placenta are few like those for other species; therefore, the present author studied the fetal and maternal vascular systems in the sheep placenta with interesting results.

1. Macroscopic observations of the sheep placenta

The materials used in this study were limited to the period from 1.5 months to 3.5 months in fetal age. Though there were no full-term placentas used, those which were studied will be considered as fully developed placentas

because it is stated by ASSHETON (1906) and CLOETE (1939) that the cotyledons are in full development at about the 3-month stage in pregnancy.

The uterine arteries and veins on the broad ligaments give off many branches on the surface of the uterine horn at right angles to the uterine axis, and the ovarian veins on the right and left broad ligaments are anastomosed with large vessels. The branch arteries and veins on the surface of the uterine horn run close together and in parallel; these vessels give off branches to the base of the cotyledon.

On the surface of the endometrium, round and cup-shaped cotyledons, which are covered on the outer convex surface by the uterine mucosa, are arranged densely and longitudinally. The cotyledons situated in the area surrounding the transitional portion from the umbilical cord to the fetal sac are larger in size than those in the area near the ends of the fetal sac (Fig. 127). The placenta of the sheep is subdivided in two parts like the cow placenta: cotyledons and intercotyledonary area. In the intercotyledonary area, the wall of the uterine horn is comparatively thin and numerous small folds run transversely on the endometrium at right angles to the uterine horn. The cotyledons are covered by the uterine mucosa and they seem to be fixed by means of the large folds of uterine mucosa which pull the cotyledons from both sides.

The two umbilical arteries and the two umbilical veins are contained in the umbilical cord. These umbilical arteries and veins part right and left, respectively, after reaching the chorion, and each vessel follows along the mesometrial side of the uterine mucosa into the tip of one or the other uterine horn.

The fetal sac is fixed to the carunculae by the cotyledons. The sac can be pulled out from the uterine cavity by cutting the carunculae from the endometrium or by tearing off the cotyledons forcibly from the carunculae. Allantoic diverticulums, which show features different from those of the normal allanto-chorion, exist at the ends of the fetal membrane. Generally, the membrane of an allantoic diverticulum is somewhat brown and has no vascular distribution, while the allanto-chorion is colorless and semi-transparent. The cavities of the allantoic diverticulums and main body of the allanto-chorion are connected with each other; this state resembles that in the pig placenta. The amnion is attached to the chorion on one side of the fetus, while the other side faces towards the allantoic cavity freely, just as in the cow's fetal membrane.

The cotyledons are arranged mostly in 4 rows in the gravid horn, and the umbilical cord connects with the allanto-chorionic sac on the mesometrial side of the endometrium. There is no branch vessel which connects the two umbilical arteries as in the cow's umbilical cord. In most twin pregnancies, the fetal membranes in each horn are fused with the neighboring chorionic sac,

but clear anastomosis is not recognized. A non-vascular area, being a line of demarcation between the two fetal vascular distributions, is observed on the fetal membrane near the uterine body.

Generally, the fetal axial arteries and veins which extend longitudinally along the allanto-chorion give off many branches in parallel at right angles to the axial vessels and on both sides of the axial vessels; these branches reach to the cotyledons in the inner rows and elongate to the cotyledons in the outer rows. From these axial vessels and their primary branches, small branches are given off which are distributed in the intercotyledonary allanto-chorionic area. These small branches show anastomosis between the arterial and venous vessels. The axial vessels, also, give off branches radially to the end of the allanto-chorion. The tips of these branches are focused in the annular portions of the end of the allanto-chorion and show anastomosis between the arterial capillaries and the venous capillaries, similarly to the case on the pig placenta.

The cotyledons become deeply depressed in the upper portion and show a cup-shaped mound from the uterine wall. Branches of fetal arteries and veins enter this depression along the surface of a cotyledon and cover its inner surface forming a vascular net. From these branches, many tributaries are given off which radiate straight toward the outer wall of the cotyledon, showing a few branchings on the way (Fig. 128). The pattern of vascular distribution on the surface of the cotyledon, formed by the branches of the axial fetal vessels, is variable. In some cotyledons the branches of the axial vessels run near the edge of the depression, giving off a few branches into the depression, and reach to the next cotyledon in the outer row. In other cases the branches of the axial vessels enter directly into the depressions, running along the surface of the cotyledon and across the depression directly or in a tortuous U-shape, giving off branches on the inner surface of the cotyledon.

Areolae exist on the chorion, but in order to find them it is necessary to make close observation. They are scattered on the surface of the allanto-chorion as small whitish spots of elevated tissue, though the allanto-chorion of the interareolar area is transparent or semi-transparent. In some cases they are recognized as small round papillate projections.

2. Microscopic observations on the vascular pattren in the cotyledon of the sheep placenta

(a) Fetal vascular system

From the arteries and veins which are distributed on the inner surface of the cotyledon branches penetrate into the villi radially towards the outer wall of the cotyledon. Most villi show a few primary branchings at their main

stems. At the arcade area, the maternal tissues project into the main stems of the villi up to the inner surface of the cotyledon and face the fetal tissues (Fig. 129). The fetal arterial branches and venous tributaries which penetrate into the cotyledon radiate towards the outer wall, giving off lateral branchlets on their way along the branches of the villi. The fetal capillary net on the surface of villi is connected with these branchlets. The artery which runs through the central portion of a villus gradually approaches the surface, moving from the central portion as it nears the top of the villus; the top of this arterial vessel connects with the superficial capillary net before reaching the top of the villus, giving off lateral branchlets to the surface of villus on the way (Fig. 130). At the central portion of a cotyledon, the arterial vessel runs directly through the center of each villus, giving off the lateral branchlets to the surface of the villus. These fine branches are connected to the superficial capillary net (Fig. 131). Usually a single artery penetrates into the stem of the villus and is easily identified by its central position. With the subdivision of the primary stem of the villus to form branches, the artery also divides and usually sends a single trunk into each branch. The small arteries of the villi occasionally give off small lateral branches which join the capillary plexus, but each arterial vessel finally breaks up shortly below the tip of the villus into an interconnected series of capillary loops which extend the rest of the way into the tip of the villus (Figs. 132–134).

It can be surmised, then, that the fetal arterial blood which is sent into the villous artery reaches the tip of the villus and disperses into the capillary plexus on the surface of the villus; moreover, in many places of the villus the blood of an artery pours into the capillary plexus through its small lateral branches, and the blood in the capillary plexus flows back to the base of the villus along the surface of the villus. The same features as those of the villous arterial vascular system are also recognized in the fetal venous vascular system of the villus.

In neoprene latex cast specimens, the fetal vessels in the cotyledon are arranged radially, exhibiting a pin-cushion form on the whole, which gives a soft feeling like fully-developed dandelion fuzz. The tip and side surface of each villus is covered with a dense capillary plexus which forms a network. The tip of a villus becomes flat, whereas the primary stem is roughly cylindrical. It is noticeable that the venules, which run in parallel with the central artery of a villus, are connected throughout their length with the superficial capillary plexus by numerous small lateral branchlets (Fig. 135).

In cross section of the central part of a cotyledon, the stems of the villi are irregularly cylindrical; maternal septa forming a large net intervene between

these villi (Figs. 136–137). In the central portion of the cross section of the stem of a villus, the single large artery runs directly; the several venules are situated peripherally, immediately under the superficial capillary plexus which entirely covers the surface of a villus. However, in cross section, the tip of a villus becomes flat or elliptic and the central artery is not recognized. The vascular system in this portion of a villus is constructed only of capillaries which are arranged in a layer, generally (Fig. 138).

The superficial capillary plexus is joined with the capillary plexuses of neighboring villi at the arcade, and connects with the venous tributaries at the base of the villi.

(b) Maternal vascular system

The arteries, which penetrate spirally in the base of the cotyledon, run straight toward the inner surface as radii from a curved base (Fig. 139), giving off few branches on the way. Most arteries which approach the inner surface of the cotyledon disperse abruptly upward or sideward (Figs. 139–142), and these capillaries extend towards the base of the cotyledon, forming a dense network. Some arteries which run up straight to near the surface return to the base of the cotyledon and gradually disperse to the capillary net. In a few cases the arteries break indistincly into the area of the placental hematomata in the arcade.

In the perpendicular section of the central cotyledonary portion, the maternal capillary distribution in the maternal septa is recognized partly as a layer of capillary net in the area which intervenes in the longitudinal maternal septa, and partly as one or two dotted lines running along through the septa (Figs. 143–144). Further it is recognized that the fetal portions are cylindrically surrounded by the maternal septa and that they are subdivided in many small crypts towards the outer wall of the cotyledon. In sections which are cut obliquely through the cylindrical crypts of the cotyledon, the crypts are shown as irregular elliptic areas covered by a cylindrical surface constructed of the maternal capillary net, and large maternal arteries are included in the maternal septa (Fig. 145). In a cross section of the cotyledon, the fetal tissues of villi are somewhat transparent in comparison with the maternal septa; most sections of villi are circular or elliptical. The maternal septa form a net with large meshes and large maternal arteries run longitudinally in the septa. The maternal capillaries are distributed around the outer surface of the villi. The capillaries form two layers of capillary net on both sides of the septa, but in the narrow septa they form only one layer of capillary net (Fig. 146). Near the outer wall of the cotyledon the crypts are subdivided gradually. In some specimens, round

areas without any capillaries are recognized in the capillary net of the maternal septa. It is considered that the villi are branched in these places; the crypts are subdivided according to the branching of villi (Fig. 147). These maternal capillary nets are gathered irregularly to the small veins near the base of the cotyledon (Fig. 148).

In the neoprene latex cast specimens, it is clear that the maternal capillary net forms a concave area (Figs. 149–151), and that round or elliptical holes are situated on the capillary net. The maternal arteries run directly along the back side of this capillary net; arteries are connected with the capillary net by small branches (Fig. 151). The capillaries are gathered to the venous branches at the bottom of the cotyledon.

3. Microscopic observations on the vascular pattern in the intercotyledonary area of the sheep placenta

(a) Maternal vascular system on the surface of the uterine mucosa

The mouths of the uterine glands open on the surface of the endometrium and they can be recognized macroscopically as shallow circular depressions (Fig. 152). The capillary plexus which forms a fine network of anastomotic capillaries covers the surface of the endometrium, and the uterine venous tributaries are connected with this capillary net at the glandular depressions. It is considered, from these facts, that the maternal blood in the superficial capillaries drains to the venous tributaries partly at these glandular depressions (Fig. 153). In a perpendicular section, it is also clear that the small arterial and venous branches connect irregularly with the superficial capillary net. This vascular relationship is recognized clearly by observing the superficial layer of endometrium from its back side.

These aspects are very similar to the vascular pattern in the pig's endometrium. It is believed that many small local circulations exist on the surface of the uterine mucosa.

(b) Fetal vascular system on the surface of the allanto-chorion

The capillaries of the surface of the allanto-chorion in general form a fine meshed plexus of anastomotic vessels (Fig. 154), a capillary net which is connected irregularly with the numerous arterial and venous branches. This net also covers the surface of areolae (Fig. 155) and is connected with the venous tributaries at the bottoms of each areola (Fig. 156). This vascular system is similar to that of the surface of the uterine mucosa.

4. Histological observatio ns of the sheep placenta

The fetal cotyledons consist of numerous villi, which collectively form

a ball-like mass, occupying the concavity of the maternal cotyledon. Each villus consists of a main stem, which gives off branches of three orders (Fig. 157) and is composed of a core of richly vascular mesoderm which is made up of loose, gelatinous WHARTON's jelly. The villous tissue is clearly differentiated from the maternal tissue of a septum by the weak stainability of the fetal connective tissue. A large artery runs up to the top of a villus through its central portion; the artery gives off branches in the central portions of each branch of a villus. The veins run longitudinally along the inner surface of a villus. The villi become narrow with the branching and their tips are interlocked with the maternal tissue in a complicated manner. The branches of arteries and veins also become slender as they approach the tops of each branch of the villi, and the arteries which run through the central portion of each villus come near to the surface of a villus at its tip. The top of the maternal septum faces the fetal arcade, intervening between the cavities of hematomata.

In a cross section of the cotyledon, the villi are recognized as many circular areas in the central portion; they are subdivided into many narrow areas at the circumferential portion of the cotyledon (Fig. 158). This means that the tips of villi are not only cut obliquely, but also themselves become flat. Generally, the maternal septum is very thin at the central portion, and it become gradually thicker as it nears the outer wall of the cotyledon; but it becomes thin again at the circumferential portion of the cotyledon. An artery is situated in the center of each round villous area, and sometimes two arteries are recognized in the villus, indicating that the villus branches at that position. In the maternal septa, maternal arterial vessels are sometimes seen. Several venous vessels are recognized along the inner surface of a villus (Fig. 159).

The maternal septum which exists between the villi, loses its epithelium in some portions, and sometimes the maternal vessels are exposed on the surface of a septum (Fig. 160). In other parts the septum is covered intermittently with cubical or squamous epithelial cells which have pyknotic nuclei or form a syncytium (Fig. 161). In some areas many degenerated cells, red blood cells, binucleate giant cells and syncytium-like masses of various sizes intervene between the villi and the septa. The villus is covered with cubical epithelial cells on the surface; many mononucleate and binucleate giant cells are scattered in the epithelium. Generally, the villus capillaries, which are distributed on the surface, lie immediately under the epithelium, but sometimes they enter into the epithelium (Fig. 162). The degeneration of the epithelial cells on the maternal septum in the sheep is more remarkable than in the cow, and most of the epithelium disappears. The maternal capillaries which are distributed in the septum have comparatively thick vascular walls at the upper portion of

the septum, but they are thin at the lower portion. This means that the maternal arteries which are running up through the septa to their tops disperse to the arterial capillaries at the upper portions of the septa, and the arterial capillaries transform gradually to the venous capillaries, reducing the thickness of the vascular walls at the lower parts of the septa.

In the arcade, much bleeding occurs in the cavities between the fetal and maternal tissue (Figs. 163–164), single villous epithelium transforms into pseudo-stratified or stratified epithelium, and the arrangement of epithelial cells is irregular because the cytoplasms are vacuolated; giant cells intervene between the epithelial cells, and the maternal blood cells are mingled with the fetal arcade epithelium. The fetal capillaries are distributed immediately beneath the epithelium.

In the intercotyledonary area the uterine epithelium has largely disappeared, and the remaining uterine epithelium is single cubical or columnar, while degenerating epithelial cells are also recognized. Many maternal capillaries are distributed in the *lamina propria* of the uterine wall beneath the epithelium (Fig. 165).

The arrangement of the chorionic epithelial cells is irregular and the epithelium is pseudo-stratified or stratified. In the areolae, the epithelium shows the same features as the chorionic epithelium. The giant cells mingle with the epithelial cells and many fetal capillaries are distributed immediately beneath the epithelium (Fig. 166).

5. Summary of observations on the placenta of the sheep

TURNER (1875), BARCROFT and BARRON (1942, 1946), and WIMSATT (1950) have observed the vascular system in the placenta of the sheep. TURNER (1875) stated only that the umbilical vessels ramified within the villi and formed networks of capillaries; he drew a semi-diagrammatic figure of the maternal vascular system in the cotyledon. But according to the present author's observation, TURNER's figure is erroneous. BARCROFT and BARRON (1942, 1946) made detailed observations upon the form and relationships of the maternal and fetal vessels in the cotyledon. WIMSATT (1950) modified their observations and observed the areolae, but he did not mention the maternal vascular system at all. In the present study, the author has supplemented the above investigators' results and clarified the structure of the fetal and maternal vascular system in the placenta of the sheep.

The results of this observation on the sheep placenta may be summarized as follows: The branches of the umbilical artery and vein, which enter into the depression on the surface of a cotyledon, cover the inner surface of the

cotyledon and become finely divided towards the outer wall of the cotyledon. In most villi, the fetal arterial branches run through the central portion and give off a few small branches to the branches of a villus; their pathways are very straight. The capillaries extend in the epithelium and immediately beneath the epithelium of a villus; they form a network which covers the villus. The axial arterial branch to the villus gives off many small lateral branchlets on the way, which connect with the superficial capillary plexus. The terminus of the axial artery also connects with the superficial capillary net before reaching the top of the villus. Then the fetal arterial blood, which enters into the villus, disperses into the superficial capillary plexus, not only near the tip of the villus, but also over almost the entire surface of the villus; and the blood in the superficial capillaries back to the root of the villus through the capillary net. The superficial capillary plexus is joined with the capillary plexuses of the other villi at the arcade and connects with the veins at the base of the villi. But another route exists to drain the fetal blood in the superficial capillary plexus. Several venules are situated surrounding the central artery and immediately beneath the superficial capillary plexus. These little veins reach nearly to the top of a villus and they connect with the superficial capillary plexus on their way by means of many small lateral branches. It is believed that the exchange efficiency in the placenta is of high degree, because the fetal blood in the superficial capillary plexus flows partly to the base of the villus while the remainder drains into the small lateral branches of venules. Fresh blood is supplied by the many small lateral branches of the axial artery to every part of the surface of the villus.

The maternal arteries and veins which are distributed to the uterine mucosa give off branches to the bases of the cotyledons. The arteries which penetrate spirally in the base of a cotyledon run straight towards the inner surface as radii from the curved base, giving off few branches on the way. Most arteries which approach the inner surface of the cotyledon divide abruptly into many capillaries upwards or sidewards. These capillaries which form the network extend towards the base of a cotyledon, surrounding each villus cylindrically. The capillaries are gathered to the vein at the base of the cotyledon. Some arteries which run up close to the inner surface of the cotyledon make a U-turn and gradually disperse to the capillary plexus. In a few cases the arteries break indistinctly into the area of placental hematomata in the arcade. Therefore, the fetal and maternal blood streams on the contact surface in both sides of the tissues flow in opposite directions.

In the histological observations, the villous capillary plexus is seen to be distributed in the epithelium and immediately beneath the epithelium. The

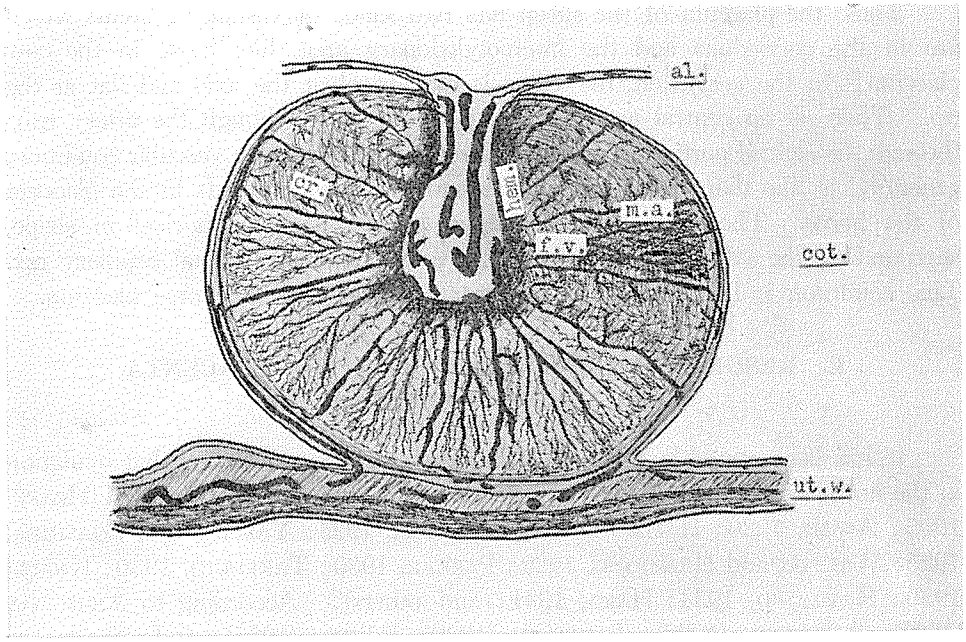

Diagram 5. Vascular pattern of the cotyledon in the sheep placenta.
cot.—cotyledon, al.—allanto-chorion, cr.—crypt, ut. w.—uterine wall, f. v.—fetal vessel, m. a.—maternal arterial vessel, hem.—hematomata.

epithelium which covers the maternal septa is widely degenerated, and in some places it has disappeared.

A diagram of the vascular system in the cotyledon is shown above.

The vascular pattern in the intercotyledonary area resembles that of the cow's intercotyledonary area. Areolae are found situated on the area of the allanto-chorion corresponding to the depressions of uterine glandular mouths. The tributaries of the uterine and umbilical veins reach to these areas. The superficial capillary nets on the surface of interareolar areas of the chorion and endometrium are connected irregularly with the numerous arterial and venous branches of the fetal and maternal vessels; they also cover the surface of the areolae or the depressions of glandular mouths. This state of the vascular system is like that in the pig placenta. It can be supposed that the fetal blood on the surface of the allanto-chorion and the maternal blood on the surface of the endometrium are drained from the areolae and their corresponding areas. It is also believed that there are many local circulations on the surface of the chorion and endometrium, and that their streams on the contact surfaces in both sides move in the same direction.

Thus, the placenta of the sheep has two kinds of vascular systems which are in the cotyledons and the intercotyledonary area, like those in the cow placenta. In the cotyledon, the villus is cylindrical at the axis and flat at the tip. There is no central artery at the tip of a villus, though the artery runs through the central portion of the axis of the villus. But this vascular condition, generally, is like that of the vascular system in the villous tuft in the placenta of the horse. The crypt of a cotyledon is irregularly cylindrical in shape, surrounding the villus. The villus is covered by the maternal capillary net. This condition is like that in the maternal cotyledon of the horse placenta.

E. RESULTS OF OBSERVATIONS ON THE PLACENTA OF THE RABBIT

It has been stated by many investigators since BARRY (1839) that ovulation in the normal estrous rabbit takes place about ten hours after copulation (HEAPE, 1905; ASAMI, 1920; HAMMOND and MARSHALL 1925; YAMANE and EGASHIRA, 1925; WALTON and HAMMOND, 1929; PARKER, 1930; TAKEUCHI, 1930; KNAUS, 1930; HAMMOND, 1934; HARA, 1941; and others). According to ASSHETON (1895), ANDERSEN (1927), TAKEUCHI (1930), BÖVING (1956), and others, the fertilized eggs appear in the uterine cavity about four days after copulation. Though the fertilized eggs become attached on the uterine mucosa, the attachment does not take place until about 8 days after copulation (MINOT, 1889, 1890; ASSHETON, 1895; WATANABE, 1918; KATŌ, 1927; TSUKAGUCHI and KATŌ, 1927; YAMAGUCHI, 1929; IWANE, 1935; ALLEN, 1949; BRAMBELL, HEMMINGS and HENDERSON, 1951; AMOROSO, 1952 and others). The placenta is formed completely by about 15 days after copulation, according to YAMAGUCHI (1929) and ALLEN (1949); but about 11 days after copulation according to the observations of YŌDA (1930), and IWANE (1935).

Concerning placentation in the rabbit, histological studies have been made during several decades by many investigators, because the placenta of the rabbit is very much like that of the human (MINOT, 1889, 1890; MAXIMOW, 1926; 1898, 1900; CHIPMAN, 1903; WATANABE, 1918; YOKOYAMA, 1925; MOSSMAN, TSUKAGUCHI and KATŌ, 1927; YAMAGUCHI, 1929; YŌDA, 1930; ŌHASHI and IWANE, 1935; IWANE, 1935; ALLEN, 1949; AMOROSO, 1952, and others).

The uterine mucosa of the non-pregnant mature rabbit consists of three pairs of symmetrical longitudinal folds which were named as follows by MINOT (1980): the placental folds, the peri-placental folds and the ob-placental folds. These three sets of folds show different changes during pregnancy; the chorio-allantoic placenta is formed in the placental folds. According to AMOROSO's

description (1952), the fully developed placenta of the rabbit is of the hemo-endothelial type, but it actually passes through stages in its development. The tissues separating fetal and maternal blood in the placenta are epitheliochorial in the 8th day of pregnancy, syndesmochorial in the 9th day, haemochorical in the 10–12th day, haemomesothelial in the 17th day, and haemoendothelial from the 22nd day to the termination of pregnancy.

Many giant cells are seen in the ob-placental folds (MINOT, 1889; CHIPMAN, 1903; HAMMOND, 1917; SANSOM, 1927; YAMAGUCHI, 1929; and others); syncytial cells are recognized in the placenta surrounding the uterine blood spaces in the intervillous area (MAXIMOW, 1900; CHIPMAN, 1903; WATANABE, 1918; TSUKAGUCHI and KATŌ, 1927; and others); multinucleate decidual cells also appear in the placenta (CHIPMAN, 1903; SANSOM, 1927; YAMAGUCHI, 1929; ŌHASHI and IWANE, 1935; IWANE, 1935; and others). The origin of all of these cells has been discussed variously.

Many histochemical studies of the placenta have been made by CHIPMAN (1903), LOVELAND, MAURER and SNYDER (1931), WISLOCKI, DEANE and DEMPSEY (1946) and others.

Concerning the course of the blood which flows in the rabbit placenta, DUVAL (1890) has already described the circulation of maternal blood from the fetal extremity towards the maternal extremity of a lobule; it was clarified by many other investigators that the maternal blood circulates in an ectodermal trophoblast of fetal origin. But a systematic investigation of the maternal and fetal vascular systems in the rabbit placenta has been made only by MOSSMAN, in 1926. ANDŌ and YAMASHITA (1952) reported on the distribution of the minute blood vessels of the normal and pregnant rabbit's uterus.

Although many detailed studies have been made on the rabbit placenta, there have been few published investigations concerning the vascular system in the rabbit placenta. As the present author had already observed the vascular patterns in the placenta of the horse, pig, cow and sheep, a comparative observation was undertaken with the rabbit placenta, using the same methods as described previously.

1. Macroscopic observations on the placenta of the rabbit

The placenta of the rabbit is discoidal; it is formed in the placental folds of the uterine mucosa. The fetus always faces the side of the body ventral to the placenta, but the direction of the head is not always constant. Uterine arteries and veins on the broad ligament branch radially to the uterine horns at the central portions of each side. The branches give off smaller branches before reaching the uterine horns, and small branches are distributed on both

sides of the surface of the uterine horns, running vertically to the horns. At the central portion on the surface of the uterine horn, a venous vessel runs longitudinally along each side of the surface and anastomoses with the venous vessels which are distributed vertically on the surface; arterial vessels on the uterine surface clearly show irregular anastomoses.

The fetus is connected with the placenta by two umbilical arteries and an umbilical vein. The yolk-sac splanchnopleur is connected by the yolk-sac stalk with the vitelline vessels. The amnion closely covers the fetus and is attached to the surface of the placenta. The yolk-sac splanchnopleur covers the outer surface of the amnion and connects with the bilaminar omphalopleur which is attached to the base of the placenta. The yolk-sac stalk forms a junction with the amnion and yolk-sac splanchnopleur at the portion behind the shoulder of the embryo. The vitelline vessels radiate from this juncture over the surface of the *area vasculosa*.. The *sinus terminalis* can be seen cut across on each side of the placenta, marked by the tag which is all that remains of the bilaminar omphalopleur (Figs. 167–168). The yolk-sac splanchnopleur is generally transparent in the form of a smooth membrane; while the bilaminar omphalopleur is a somewhat whitish, opaque, and rough membrane.

Sometimes, a sac-like, semi-transparent projection is recognized on the surface of the placenta; its origin is obscure, but the present author did not observe this material in detail because it was considered that the projection has no direct relationship with the vascular system of the placenta.

Moreover, the author found small vessels which run along on the bilaminar omphalopleur and connect the vitelline vessels with the fetal veins on the placenta (Figs. 169–170). These small vessels were recognized in all of six specimen placentas which were examined. In general, these vessels run across the narrow portion of the bilaminar omphalopleur at the side of the placenta and reach to the base of the placenta. The number of these vessels is not constant but there are several. They are projected from the vitelline vessels vertically to the *sinus terminalis* and their origins are not uniform; sometimes from the vitelline artery and sometimes from the vitelline vein.

Concerning the vitelline vascular system, a layer of capillary net is formed on the entire surface of the yolk-sac splanchnopleur. The fetal vitelline artery and vein which are enclosed in the yolk-sac stalk are very small. They start from the fetal navel, immediately branching from the large umbilical cord and bending upwards together on the left side of fetus along the amnion; there they connect with the yolk-sac splanchnopleur at the back side of the fetus and radiate on the yolk-sac splanchnopleur. The artery, having reached this point running through the yolk-sac stalk, elongates on the opposite side, the

right side of fetus, and splits right and left at the edge of the yolk-sac splanchnopleur to form most of the *sinus terminalis* running along the edge. At the same time the vein of the yolk-sac stalk elongates in the opposite direction to the artery and forms part of the *sinus terminalis* or disperses to the capillaries on the yolk-sac splanchnopleur. From these axial arterial and venous vessels on the yolk-sac splanchnopleur, many branches are given off to spread on the yolk-sac splanchnopleur. But this state is a general tendency and the direction of the axial artery and vain are not always in a line.

The placenta of the rabbit is dark brown and discoidal, and divided into two cotyledons by an intercotyledonary groove. The surface of each cotyledon is rough, covered with small gentle projections, and the branches of the umbilical arteries and vein are distributed on the placenta. There is a tendency for the two umbilical arteries to be distributed on each cotyledon separately, but the distribution of each artery on the placenta is not always bounded by the intercotyledonary groove (Fig. 171–172). It is clear from the observations of the back side of the fetal placenta in the neoprene latex cast specimens that the fetal placenta is formed of a thick vascular layer and that it covers the maternal placenta like an umbrella (Figs. 173–174). It is also recognized that the fetal capillaries form many tufts. The maternal capillaries show the same features as the fetal capillaries on the surface of the fetal placenta. The branches of the maternal arteries reach to the surface of the placenta through the fetal placenta, and run transversely on its surface. Generally, the maternal arteries which are distributed on the surface of placenta give off many branches which show anastomoses on the surface of the placenta; they give off numerous capillary tufts around the vessels (Fig. 176). But on the back side of the fetal placenta, the large maternal veins are situated on the central portion of the placenta. The maternal capillaries in the fetal placenta are gathered to the venous tributaries. Those capillaries resemble a coral which has many branches (Fig. 175). The branches of the uterine arteries become narrow temporarily and show coiling when they penetrate into the maternal placenta from the uterine wall. Arterial branches which enter into the maternal placenta become thick and run up directly nearly to the surface of the fetal placenta. (Fig. 177).

These relationships of the maternal arteries and veins are shown in the next diagrammatic figure.

The arteries of the mesometrium enter into the uterine wall to part right and left therein, and immediately after that branches are given off from the uterine wall into the maternal placenta. These branches reach the fetal placenta directly at its central portion, or at the intercotyledonary groove. On the other hand, the veins of the mesometrium part right and left in the uterine wall and,

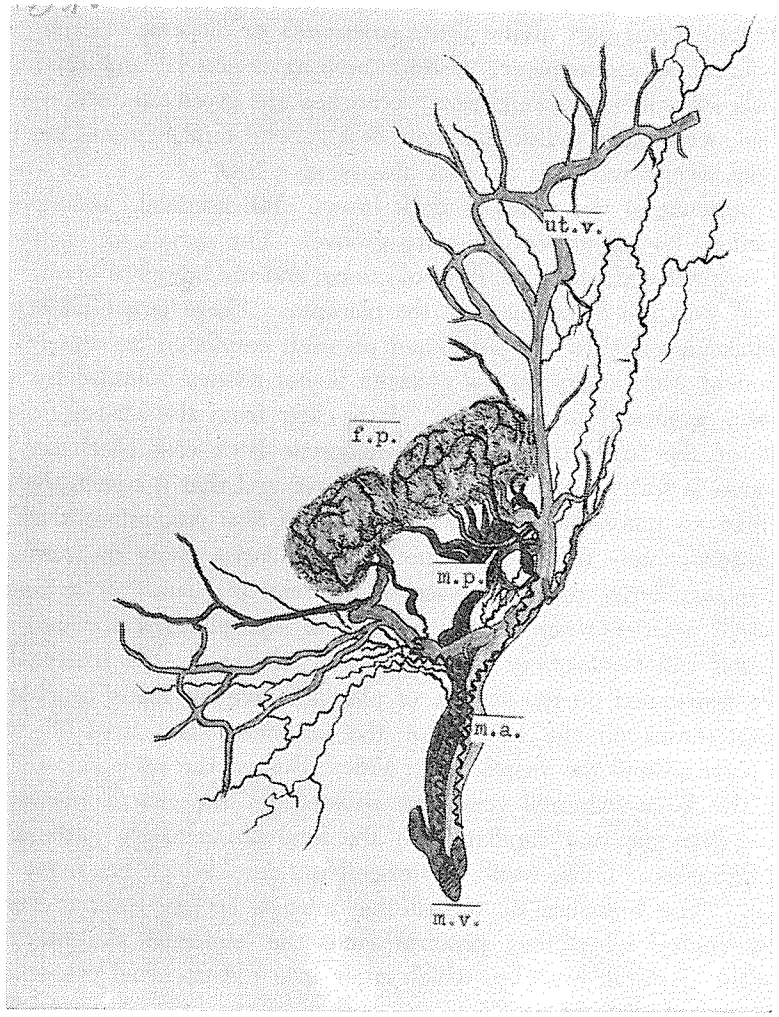

Diagram 6. Maternal vascular system in the rabbit placenta.

m. a.—maternal arterial vessel, m. v.—maternal venous vessel, ut. v.—maternal vessels in the uterine wall, f. p.—fetal placenta, m. p.—maternal placenta.

immediately after turning, enter into the maternal placenta; or sometimes enter the maternal placenta directly without dividing. The number of vessels which penetrate into the maternal placenta from the uterine wall is shown in the next table.

TABLE 6. The number of vessels which penetrate into the maternal placenta from the uterine wall.

Placentas	No. of arteries	No. of veins
1	4	2
2	8	1
3	6	2
4	8	3
5	9	4
6	12	4
7	11	6
8	10	3
Average	8.5	3.1

The figures of this table are based on the neoprene latex cast specimens. Althouth the number of vessels seems rather large, and although there are no apprehensions that the neoprene latex does not sufficiently penetrate into every vessel, the number of vessels is not as high as in MOSSMAN's diagram (1926).

2. Microscopic observations on the vascular pattern in the rabbit placenta

(a) Maternal vascular system

The surface of the rabbit placenta is formed of many irregular, small, convex surface which are the upper parts of the lobes. The branches of the uterine arteries run up to the surface of the fetal placenta, and their features are like those of the venous vessels, at a glance, since their walls are very thin (Fig. 178). These arterial vessels are distributed on the surface of the cotyledon, running along the shallow grooves formed by the small convex surfaces; the arterial vessels give off very short branches and tufts of capillaries independently on the surface of each lobe on both sides of the vessels. In some cases the tufts of arterial capillaries appear only from one edge of a lobe and run in parallel to the opposite side (Fig. 179). It is also recognized that the uterine venous capillaries show the same features as the arterial capillaries on the surface of the lobe. However, large venous vessels never appear on the surface of the placenta. The tufts of venous capillaries appear radially on the convex

surface of the lobe from the opposite side to the side of the appearance of the arterial capillaries. Naturally a connection between the arterial capillaries and the venous capillaries is seen (Fig. 180). Generally, the arterial capillaries are very small in diameter, but they become gradually larger and turn into the venous capillaries. The arrangement of each capillary is very beautiful at a glance, since the capillaries are clearly running in parallel on the convex surface from one edge to the other. However, it is known that the capillaries form a network by means of numerous complicated anastomoses between individual capillaries (Figs. 180–181).

In vertical section, the uterine venous vessels reach to the fetal placenta, showing the tree-like branching through the maternal placenta, and connect with the maternal capillaries in each lobe of the fetal placenta. The lobes are arranged in a row in most parts of the fetal placenta, but in some places they overlap one another. At the upper portion of each lobe, a large vessel which is maternal and arterial is always situated; this vessel gives off numerous capillaries radially in the lobe (Figs. 182–183). These capillaries run towards the maternal placenta through each lobe either directly or curving gradually. They gather gradually to the lower part of a lobe and connect with the venous tributaries. In short, the venous uterine vessel which enters the maternal placenta from the uterine wall runs directly up to the upper portion of the maternal placenta, receiving many branches and tributaries from the fetal placenta simultaneously, and splits into numerous capillaries which are connected with the arterial capillaries in each lobe (Fig. 184). The maternal capillaries in the lobe form a network by complicated anastomoses with each other, though they extend in a constant direction on the whole (Fig. 185). In a cross section of a tuft of capillaries, the capillaries are recognized as numerous scattered spots (Fig. 186).

These observations were made on transparent specimens injected with neoprene latex solution or with India ink diluted with saline solution (Figs. 187–189).

(b) Fetal vascular system

The features of the fetal vascular distribution on the surface of the placenta are very similar to those of the maternal vascular distribution (Figs. 190–191).

In vertical sections, it is recognized that the venous tributaries which penetrate into the placenta from the surface reach to the upper portion of each lobe and disperse to many capillaries in the lobe; the branches of the venous tributaries, also, elongate to other lobes. In general, a round or irregular space which is the maternal arterial vessel is situated at the upper portion of each

lobe. The fetal venous tributaries reach to the surrounding area of this maternal arterial vessel, and from this point many fetal capillaries are given off abruptly and radially in the lobe (Fig. 192). The fetal capillaries run towards the bottom of each lobe directly or curving gradually. In other words, the fetal arterial blood is focused into the fetal venous vessel at the upper portion of the lobe from the bottom or side portions. Such a fetal capillary tuft in each lobe is connected with the fetal arterial branchlets at the bottom of the lobe, which run along beneath the bottom of each lobe, showing a slow curve. The fetal capillaries in a lobe, that is to say, are gathered at the bottom of the lobe and connect with the fetal arterial vessels (Figs. 193–195). These fetal arterial branchlets under the lobes connect with the other arterial branches of similar construction and position (Figs. 196–197), and they are connected with the fetal arterial tributaries which penetrate vertically into the fetal placenta from the surface into the cotyledon, running among the lobes (Fig. 198). It is clear in Figures 199 and 200 that the small branch arteries which are situated under the bottom or at the side of lobes give off branches into the lobe. This vascular relationship is very clear in the neoprene latex cast specimens, also. The fetal arterial vessels penetrate into the inner portion of the placenta while the fetal venous tributaries connect directly with the capillary tufts on the surface of the placenta (Fig. 201). Each capillary tuft in the lobe is surrounded by fetal arterial branchlets at the side and bottom of each lobe, and their tributaries and fine branches are connected each other under the fetal placenta (Figs. 202–204). At the back side of the fetal placenta, as seen in the neoprene latex cast specimens, many irregularly-arranged, semicircular vessels project inward. They are connected to each other by means of their branches. It can be considered, then, that a vascular layer with fetal arterial tributaries and branches is formed immediately beneath the fetal placenta, and that this layer is different from the labyrinth in the fetal placenta with respect to vascular structure (Figs. 205–206). The fetal capillaries in the lobe form a network, just as the maternal capillaries do (Fig. 207).

On the basis of the above observations, the fetal vascular system in the rabbit placenta may be summarized as follows: The branches of the umbilical artery, which are distributed on the surface of a cotyledon, give off fine arterial vessels vertically into the cotyledon, mainly from the shallow depressions which are formed by the small convex surfaces on the cotyledon. These fiine vessels reach to the bottoms of each lobe, running between the lobes and curving along the bottom of each lobe. These vessels give off the very fine arteries at the back side of the fetal placenta, and the fine arteries connect with each other; they split up into smaller branches and capillaries at the bottom or side of each

lobe. The capillaries, which form a complicated network, run up to the upper portion of the lobe where they are gathered into the venous tributaries.

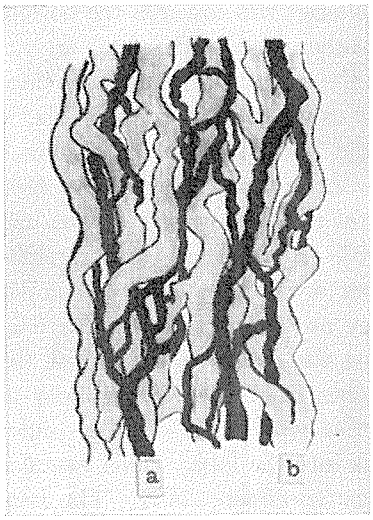

Diagram 7. Capillaries in the labyrinth.
a—fetal capillary,
b—maternal capillary.

(c) Relationship of the maternal and fetal vascular systems in the placental labyrinth

Observations on the fetal and maternal vascular systems have been described; it was necessary to study the relationship of the vascular systems in the fetal and maternal sides when they are observed simultaneously. Therefore, specimens injected with different colored latex solutions in the fetal and maternal vessels, respectively, were used for this purpose. Unfortunately, in most specimens the capillaries in the labyrinth burst and the two colored latex solutions mingled. The following diagram of the maternal and fetal capillaries in the labyrinth was drawn because it is hard to distinguish the two colored latexes in photographs. Each set of capillaries, fetal and maternal, forms a network, and those networks are interlocked with each other.

3. Microscopic observations on the vitelline vascular system on the yolk-sac splanchnopleur

The vascular system on the yolk-sac splanchnopleur will be described only briefly in this section, because it has already been partially described in another section. The axial vitelline artery and vein radiate on the yolk-sac splanchnopleur at the junction of the yolk-sac stalk with the yolk-sac splanchnopleur. The branches of the artery and vein show a tendency to run in parallel with each other near the junction (Fig. 208). But they separate on the way and become uniformly distributed in a layer on the yolk-sac splanchnopleur. The capillary net formed on the yolk-sac splanchnopleur is connected with the fine branches of the vitelline artery and vein; branches of the arterial vessels are generally narrow and smooth in comparison with the branch venous vessels (Fig. 209).

4. Histological observations of the rabbit placenta

Histological studies on the rabbit placenta have been made since many years

ago, and many reports have been published. In the present study the author tried to clarify the relationship between the vascular system in the cotyledon and the histological structure. Cytological details of the placenta are neglected.

The rabbit placenta can be distinguished into three parts histologically: the fetal placenta, the intermediate zone, and the maternal placenta (Fig. 210). The fetal placenta is almost entirely constructed of fetal tissue, both fetal and maternal circulations exist in it, and a labyrinth is formed in it. At the upper portions of each lobe in the fetal placenta are large maternal arterial blood vessels, and surrounding the maternal vessels are seen small fetal blood vessels which are venous. Capillaries join these vessels; they are arranged longitudinally, more or less in parallel, in the lobe. Those capillaries disappear in the intermediate zone in which the fetal and maternal tissues are mingled with each other. Many blood sinuses appear in the maternal placenta, which is constructed principally of degenerated maternal tissues. The depth of the intermediate zone is variable; it is considered that this is due to the difference between sections which are cut in different directions, or between the different parts of each lobe. The branches of the fetal artery which penetrate vertically into the cotyledon (Fig. 211) reach to the bottom of each lobe and give off capillaries in each lobe (Fig. 212). Generally, the maternal blood vessels are situated at the top of the lobes and the fetal venous blood vessels lie around them. The former emit maternal arterial blood into the labyrinth and the latter drain the fetal venous blood from it (Fig. 213). The walls of the maternal arterial blood vessels are comparatively thin; the endothelium is constructed of swollen cuboidal cells in most cases. The walls of the fetal venous vessels are also thin and have clear endothelial cells, generally. The fetal arterial blood vessels have thick walls and complete endothelium in most cases, but the endothelial cells are swollen in some cases. The branches of the fetal arterial vessels which penetrate into the fetal placenta run between the lobes as far as the intermediate zone. Small arterial vessels which have thick walls and clear endothelium are recognized often in the fetal connective tissue of this zone (Fig. 214). It is concluded from these histological observations, and microscopic and macroscopic observations of the neoprene latex cast specimens, that a vascular layer of fetal arterial vessels is formed in the intermediate zone of the rabbit placenta.

In the labyrinth of the rabbit placenta, the histological structure of the twenty-three-day placenta (Fig. 216) shows remarkable differences from the twenty-eight-day placenta (Fig. 215). Specifically, the trophoblast is predominant in the former and the fetal blood streams can be easily distinguished from the maternal blood stream. However, in the latter the trophoblast has almost disappeared and it is hard to distinguish whether the blood streams are fetal or

maternal, as the two blood streams are generally bounded only by the endothelium. It is considered that this relationship of the two blood streams is much more intimate than in fhe placenta of the horse, pig, cow or sheep.

In the intermediate zone, capillary structures such as seen in the labyrinth are not recognized. Trophoblast and polynuclear giant cells are predominant, and a large blood sinus, which is surrounded by the trophoblast, appears (Fig. 217). These blood sinuses are connected with the capillaries in the labyrinth and with the maternal veins in the maternal placenta. In this zone, as described above, small fetal arterial vessels exist also (Fig. 218).

In the maternal placenta, most cells are degenerated and there is no mixing of the fetal tissue (Fig. 219).

It is considered from the above observations that the branches of the fetal arterial vessels penetrate into the cotyledon and reach as far as the intermediate zone, after running among the lobes. There they connect with each other through their branches, forming a vascular layer which is situated beneath the labyrinth. The tips of the vessels turn up and penetrate into each lobe. Then it is reasonable that in the intermediate zone of the rabbit placenta the fetal trophoblast and mesenchyme predominate, that the number of vessels is not much more than in the labyrinth, and that mixing of fetal tissue and maternal tissue occurs.

5. Summary of the observations of the rabbit placenta

The placenta of the rabbit is always formed at the mesometrial side of the gestation sac. It has a discoidal shape and is divided in two cotyledons by the intercotyledonary groove, which usually runs longitudinally in parallel with the uterine axis. The placenta is dark brown and the surface of it is rough, with the many small convex protuberances. The two umbilical arteries and an umbilical vein are distributed on the surface. The branches of these vessels run along the shallow groove of the surface, and the branches of the fetal vein connect directly with the capillary tufts on the surface, while the branches of the fetal artery give off branchlets vertically into the placenta.

In a vertical section of the placenta, three portions are distinguished: the fetal placenta, which is constructed mainly of the fetal tissues and has circulations of both the fetus and the mother; the intermediate zone, which is situated between the fetal placenta and the maternal placenta and is constructed of mingled fetal and maternal tissues; and the maternal placenta, which is constructed of degenerated maternal tissues. The fetal placenta is subdivided into many lobes which are round, elliptical, or heart-shaped, and which possess independent vascular systems.

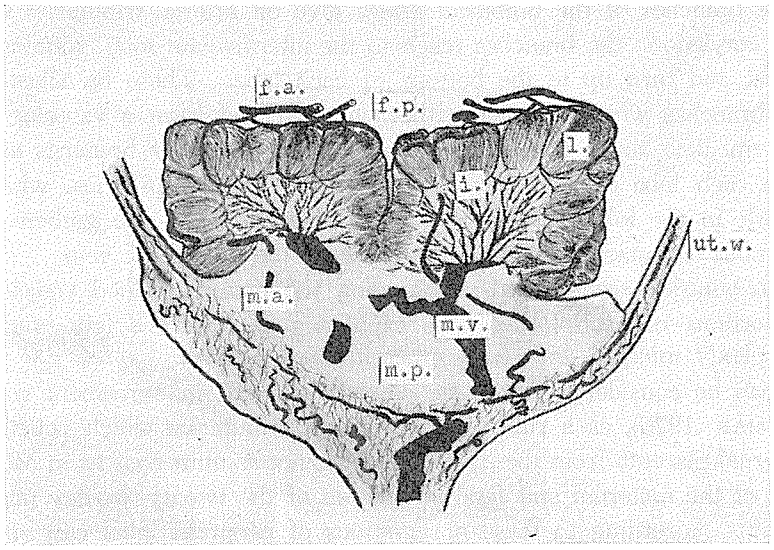

Diagram 8. Vascular pattern of the rabbit placenta.
Bilaminar omphalopleur and amion are removed. ut. w.—uterine wall, f. p.—fetal placenta, i.—intermediate zone, m. p.—maternal placenta, l.—-lobe, f. a.—fetal arterial vessel, m. a.—maternal arterial vessel, m. v.—maternal venous vessel.

A diagram of the vascular system in the placenta is drawn above on the basis of the above observations.

The branches of uterine arteries penetrate into the maternal placenta from the mesometrial side of the uterine wall, showing as a coiling of narrow vessels temporarily; they become large vessels in the maternal placenta and extend to the surface of the fetal placenta, running directly among the lobes or turning under the fetal placenta to the side of the cotyledon or to the intercotyledonary groove. These branches of the maternal arteries run transversely on the surface of the placenta and are distributed thereon, showing anastomoses with each other. These branches seem, at a glance, to be venous vessels, because they have thin walls and are expanded. But these branches give off, abruptly, a tuft of capillaries radially in each lobe; the capillaries are arranged longitudinally, more or less in parallel in each lobe. They are connected with the blood sinus in the maternal placenta, gradually joining with each other on the way through the intermediate zone. The blood sinus which is made up of venous vessels is connected with the mesometrial uterine vein running through the maternal placenta. The capillaries in each lobe form a network by anastomoses with each other.

The branches of the umbilical artery give off arterial tributaries vertically into the cotyledon; the branches reach to the intermediate zone, running among the lobes, and turn up to the bottom of each lobe. These branches give off smaller branches which connect with each other and form a vascular layer in this intermediate zone; and they split up into still smaller branches and capillaries in each lobe at its bottom or side. The fetal capillaries, which form a network in the lobe, run up to the upper portion and are gathered in the fetal venous tributaries which connect with the umbilical vein. The fetal venous tributaries are situated surrounding the maternal blood vessels at the upper portions of each lobe. The capillaries of both the fetus and mother are complexly mingled with each other in the labyrinth.

It can be considered that these observations are in agreement with those of MOSSMAN (1926), as a rule. However, the tributaries which penetrate into the maternal placenta from the uterine wall are not as numerous as in MOSSMAN's diagram of the maternal and fetal circulation of the twenty-two-day placenta of the rabbit. According to these observations of neoprene latex cast specimens, the number of maternal arterial vessels which penetrate into the maternal placenta from the uterine wall is 8.5, on the average, while the numer of maternal venous vessels is about 3.

MOSSMAN (1926) stated that in the twenty-two-day placenta the umbilical arterial branches, while still fairly large, penetrate into the fetal placenta nearly as far as the deepest growths of the trophoblast into the maternal tissue; and that in the twenty-eight-day placenta the umbilical arteries spread out upon the surface, then penetrate the placenta as fairly large branches, and at about the depth of the outer or deeper ends of the lobes they become horizontal to the surface again; and give off many branches back towards the surface. The present author considers that the intermediate zone of the placenta is a vascular layer of fetal arterial vessels which make a U-shaped curve and connect with each other through their branches at the portion beneath the fetal placenta.

The outer fetal membrane is a yolk-sac splanchnopleur which is connected with the bilaminar omphalopleur. The *sinus terminalis* runs along the edge of the yolk-sac splanchnopleur. The bilaminar omphalopleur connects with the placenta at its base. A layer of capillary network is formed on the entire surface of the yolk-sac splanchnopleur, and many anastomoses occur between arterial capillaries and venous capillaries. Small vessels are recognizable which run on the bilaminar omphalopleur and connect the vitelline vessels with the fetal venous vessels on the placenta.

Concerning exchange in the placenta, its structure seems to be very effective for placental transmission. The capillaries of the fetal and maternal sides are

intertwined closely with each other, and the maternl and fetal blood of the tubes and capillaries of the labyrinth flow in opposite directions—the maternal blood from the fetal surface of the placenta towards the uterus, the fetal blood from the uterine side towards the fetal side. This relationship in the directions of the fetal and maternal blood streams is the same, as a rule, in the placenta of the horse and in the cotyledon of the cow and sheep. However, in these animals the attachment between fetal and maternal tissue in the placenta or cotyledon involves face-to-face position of the tissues, and attachment of the capillary nets of the two sides clearly occurs. It can be considered that the active surface of the capillary net is only one side of the net and the other surface does not act so effectively as the other in the exchange between fetus and mother. But in the labyrinth of the rabbit placenta, the capillary nets of the fetus and mother are arranged irregularly and they are intertwined complexly with each other. It can be considered that the attachment of the vessels of the fetus and mother occurs between individual capillaries, not in the capillary net; the functional capillary area in placental transmission is expanded to include the entire capillary surface.

On the other hand, the labyrinth of the rabbit placenta is constructed of many lobes which have the fetal and maternal blood streams flowing in opposite direction. This vascular pattern is like that in the cotyledon of the placenta of the horse, cow and sheep.

V. DISCUSSION

Very few systematic studies have been published concerning the course of the fetal and maternal blood streams in the placentas of farm animals. In the following paragraphs, the author will compare critically the reported results of observations by earlier workers with his own observations.

First, concerning the vascular pattern of the horse placenta, there is only the simple description by TURNER (1875). He wrote as follows: "Though in the mare the villi seem to the naked eye to be closely set over the surface of the chorion, yet when examined with low powers of the microscope they are seen to be arranged in brush-like clusters or tufts. The tufts are like minute fetal cotyledons and the villi in each tuft are filamentous in shape and contain a loop of capillary blood-vessels. While, the surface of the uterine mucosa of a mare is subdivided into multitudes of irregular polygonal areas by slender ridges, which anastomosed with each other so as to have a reticulated appearance. And each area was seen to be subdivided into multitudes of crypts, which passed deeply into the mucosa. The arteries and veins of the mucosa

occupied the ridges, and broke up into small branches which ended in a compact capillary plexus situated in the walls of the crypts, the artery in each ridge giving off branches to the crypt-areas between which that ridge was situated. The filiform villi of the tufts of the chorion were so closely fitted into the uterine crypts."

These items are in agreement with the author's observations, but TURNE's description is too simple to include the vascular pattern of the horse placenta. He did not discuss the relationship of the vascular systems between the villi and the uterine mucosa. The present author observed the vascular systems of the villi and the uterine mucosa in detail and could clearly distinguish the relationship between the villi and the uterine mucosa.

Concerning the vascular pattern of the pig placenta, there is also only a description by TURNER (1875). He recognized the numerous slightly elevated circular spots, areolae, over the surface of the chorion. According to his observations, each spot was observed under the microscope to have a minute central depression surrounded by villi, which were the terminal villi of a group of ridges, and it was seen that the villous ridges were arranged on the chorion with special reference to these spots. The ridges and villi were seen to be very vascular, but the vascular distribution was slight in the spot. Examination of the maternal placenta in the gravid uterus showed that the free surface of the mucosa presented an undulating appearance, owing to numerous shallow furrows and fossae separated by intervening ridgelets. Opening on the surface of the mucosa, the openings being marked by shallow depressions distinct from the furrows, were the mouths of the uterine glands, and each gland-orifice was surrounded by a smooth portion of the mucosa. The ridges and the walls of the crypts were seen to contain a compact capillary flexus, while the smooth spots possessed a feeble vascularity, so that they appeared as distinct white spots, surrounded by highly vascular ridges. Moreover, he gave diagrams of the vascular distribution on the surface of the allanto-chorion and uterine mucosa.

However, TURNER (1875) did not described the state of the vascular distribution in detail, and said nothing concerning the direction of the blood streams in the placenta. The present author studied the vascular systems of the chorion and on the surface of the uterine mucosa in detail, and could judge that there are numerous small, limited fetal and maternal circulations which gather to the areolae or to the mouths of the uterine glands, and which flow simultaneously in parallel and in same direction.

Concerning the vascular pattern of the cow placenta, TURNER (1875) also observed only the cotyledon. According to his observation, the fetal cotyledons

were situated on umbrella-shaped maternal cotyledons, and numerous villi occupied the pits. The stems of the villi were comparatively large, and studded with multitudes of minute tufts, which, arising obliquely or almost at right angles to the main stem, entered and occupied the crypts. The minute villi forming these tufts were so slender and filiform that each terminal offshoot contained only a single capillary loop. The connective tissue in the maternal cotyledon was highly vascular, the maternal capillaries forming a compact network in it. These results of TURNER's observations are in agreement with the present author's observations, but his observations were very limited. KRONACH (1927) drew a diagram of the vascular system in the villus, but his figure shows only a simple model. HILLIGER (1958) observed the vascular systems of the uterus and maternal cotyledon macroscopically, but the finer vascular structure of the cotyledon and of the uterine mucosa remained obscure.

From the observations cited above, it was considered there is no hitherto published detailed observation concerning the vascular pattern of the cow placenta. Therefore, the present author undertook observations of the vascular systems of the cotyledon and intercotyledonary area, and was able to gain clear information regarding both the fetal and maternal vascular systems and the directions of each blood stream.

Concerning the vascular pattern of the sheep placenta, there are some detailed descriptions presented by TURNER (1875), BARCROFT and BARRON (1942, 1946), and WIMSATT (1950). TURNER (1875) stated that the cotyledons were highly vascular, and some of the arteries in the sub-cotyledonary connective tissue were corkscrew-like; in the deeper part of the cotyledon itself he found tortuous vessels. Most of the vessels within the cotyledon passed vertically towards the surface, lying in the connective-tissue walls of the pits, dichotomous as a rule, prior to forming a compact maternal capillary plexus—not dilating into maternal blood-sinuses. The fetal cotyledons, consisting of numerous villi, occupied the concavity of the maternal cotyledon. The umbilical vessels ramified within the villi and formed network of capillaries. These items barely outline the vascular system in the cotyledon. TURNER's description concerning the maternal vessels in the cotyledon is apparently incorrect, because the present author found that the maternal arterial vessels which penetrate into the cotyledon from the uterine wall run up directly towards the inner surface of the cotyledon through the maternal septa as fairly large vessels, giving off a few branches on the way; they break up abruptly into many capillaries at their tops, which form a network and return towards the base of the cotyledon. BARCROFT and BARRON (1942, 1946) described the fetal and maternal vascular systems in the cotyledon in detail. WIMSATT (1950) observed the vascular system of the fetal

villi and the chorion microscopically. The author's results derived from the present study are in accord with the results of the above workers, and moreover supply new information about the vascular system in the placenta.

Concerning the vascular system of the rabbit placenta, there is only MOSSMAN's report (1926), which describes the results of systematic observation. His results are in general agreement with those of the present author.

Next, the relationship between the structure of the vascular system in the placenta and placental functions is considered. It is well known that a larger quantity of blood flows in the pregnant uterus than in the non-pregnant uterus, and active exchange with the fetal blood occurs. BARCROFT and ROTHSCHILD (1932) studied the volume of blood in the uterus of the rabbit during pregnancy and recognized that, although the genital organs contain less than 2 c.c. of blood during the resting condition, they become appreciably more vascular from the fifth or sixth day onwards; about half-way through pregnancy they contain about 10 c.c. of blood, and by the twentieth day the embryos weigh only about 5 g. and the generative tract of the mother contains about 15 c.c. of blood. The maximum quantity of blood, about 30 c.c., seems to be found at about twenty-eight to twenty-nine days, after which the quantity falls rapidly before parturition. Moreover, it was shown by BARCROFT, HERKEL and HILL (1933) that the blood in the pregnant rabbit uterus becomes appreciably concentrated in its passage through the uterus, and the oxygen used by the pregnant uterus and its contents is less than 0.1 c.c. per minute up to the eighteenth day; within the next two days it undergoes a tenfold increase, corresponding to fetal growth, and after that time the oxygen used increases much more slowly and at a rate proportionately less than the growth of the embryos. BARCROFT and KENNEDY (1939) studied the distribution of blood between the fetus and the placenta in sheep. According to their observation, the placental cotyledons reach their maximum weight about half way through pregnancy, when the fetus is only about the size of a large rat (200 g.); at 100 days about half of the total volume of the blood is in the fetus and half in the placenta (including the umbilical cord); at 120 days about one-third is in the placenta; at 140 days a quarter to one-fifth is in the placenta. The absolute amount of blood in the placenta remains nearly constant during the last third of pregnancy, they stated.

It may easily be estimated, then, that most of the placental transmission will occur by means of these fetal and maternal blood streams, and that the contact of these blood streams will be intimate and effective. However, very complicated mechanisms take part in the placental transmission, not simply diffusion. For example, PAGE, GLENDENING, MARGOLIS, and HARPER (1957) infused the natural and unnatural optical isomers of histidine into maternal

veins for variable periods of time prior to delivery, and found that the unnatural D-histidine required three or four hours to approach equilibrium, whereas the natural L-histidine approached equilibrium within a matter of minutes; they considered that both molecules cross the placenta by a process of simple diffusion but that the natural isomer is transferred more rapidly by an additional active transport mechanism. WIDDAS (1951, 1952) showed the inability of simple diffusion to account for quantitative and qualitative circumstances associated with placental glucose transfer in the sheep. Further, according to DAVIES (1955), simple diffusion is inadequate to account for the placental transmission of glucose and fructose in the rabbit, and an active process must be invoked, the nature of which remains unknown. HUGETT, WARREN and WARREN (1951) studied the origin of the blood fructose of the fetal sheep and recognized that the placenta is permeable to glucose in both directions, but only from the mother to the fetus in the case of fructose; and that while possibly some glucose may pass across the placenta by a process of physical diffusion, there is, in addition, a chemical system within the placenta into which the glucose (whether maternal or fetal) enters with induced formation of fructose. PLASS and MATTHEW (1925) experimented on transmission in the human placenta, and concluded that the amino-acid content is uniformly higher in the normal fetal whole blood and plasma than in the maternal; and the total non-protein nitrogen is likewise always in higher concentration in the fetal whole blood and plasma. HOSKINS and SNYDER (1928) stated that the calcium content of fetal blood serum of the dog is about 1 to 2 mg. percent higher than in the maternal serum. NEEDHAM (1931) examined the relative concentrations of the different foodstuffs in the blood of the mother and fetus, and found that a substance may have a higher concentration in the maternal than in the fetal blood (*e.g.*, glucose in man), while a different material (*e.g.*, amino acids in man) may be higher in the fetal than in the maternal blood; and occasionally, as with sodium, both maternal and fetal concentration are the same. The data of CHRISTENSEN and STREICHER (1948) show that amino acids in the fetal plasma are about 5 times as great in the guinea pig, 1.5 to 2 times in the rabbit, 1.7 to 1.8 times in man. LOGOTHETOPOULOS and SCOTT (1955, 1956) demonstrated, using iodine-131, that the inorganic iodide level in the guinea pig, rabbit and rat is higher in the fetal than in the maternal plasma. HALL and MYANT (1956) also studied the passage of ^{131}I-labelled thyroxine from mother to fetus in the pregnant rabbit by measuring the fetal/maternal serum concentration ratio after injection of radiothyroxine into the mother. They showed that the concentration of radioiodide in the serum of the fetus exceeded that in the mother when radioiodide was injected into the mother after the 17th day of pregnancy.

Moreover, the transmission of bacteria or red blood cells between the fetal and maternal blood is recognized under certain circumstances (TAKEUCHI, 1919; SMITH, 1919; NAKAGAWA, 1934; IWATA and KAWASHIMA, 1955; YAMAMOTO, 1955, 1958; SANGER and COLE, 1955; KIHARA, 1956; ONO, 1957; PAGE, 1957; TANAKA, 1958; SHINOBE, 1958; TAJIMA, 1958; and others); however, the mechanism of the transmission is quite obscure.

On the other hand, concerning the directions of blood movement in the maternal and fetal capillaries of the placenta, it is postulated that the two blood streams flow either in the same direction or in opposite directions. MOSSMAN (1926) explained the gas exchange efficiency between the maternal and the fetal vessels of a placenta of the labyrinthine type with a diagram, and used the nomenclature "type I" when the two blood streams flow in the same direction and "type II" when the two blood streams flow in opposite directions. It was assumed in his scheme that the placental membrane is a simple, two-way permeable structure, that the gas-carrying capacities of the two blood streams are equal, that their volume and rate of flow are also equal, and that the length of the adjacent vessels is sufficient to allow practically complete equilibrium to be reached. If the oxygen and carbon dioxide figures are as follows in type I —$O=4$ and $CO_2=8$ in maternal artery, and $O=2$, $CO_2=10$ in fetal artery— the values change to $O=3$, $CO_2=9$ in both fetal and maternal veins. If, in type II, $O=4$ and $CO_2=8$ in maternal artery, and $O=2$, $CO_2=10$ in fetal artery, the values become $O=2$, $CO_2=10$ in maternal vein and $O=4$, $CO_2=8$ in fetal vein. MOSSMAN further stated that the rabbit placenta is type II, while the existence of type I has never been shown. NOER (1946) also studied the effect of flow direction on placental transmission, using an artificial placenta which was a rigid tube, consisting of plastic tubing ripped open lengthwise and tapped with take-off vessels, and constructed with the thinnest cellophane cemented to it between the two sides. He concluded that the opposite direction of flow in the maternal and fetal sides of the placental membrane is physiologically more efficient than flow in the same direction.

The present author has demonstrated the placental vascular patterns in the horse, pig, cow, sheep and rabbit, and discussed the directions of the fetal and maternal blood flows in these placentas. From his observations, placentas or parts of placentas are classified into two types: namely, one type comprising the parts of the placenta which show opposite direction of flow on the maternal and fetal sides, and another type in which parts of the placenta show uniform direction of flow. If these two types are designated as the "opposite type" and the "parallel type", respectively, the former includes the placenta of the horse, the cotyledons of the cow and sheep, and the placenta of the rabbit;

the latter includes the placenta of the pig and the intercotyledonary areas of the cow and sheep.

Generally, when one speaks of the placenta he has in mind a fairly complex and special structure which is formed by fusion of the chorion with the uterine wall, such as in the human and rodent; and considers that the placenta which does not show such a clear fusion of the chorion with the uterine wall is in a primitive stage of evolution. However, now-a-days it is known that such fusion between the chorion and the uterine wall occurs to some extent in the intercotyledonary area, and that the gas or nutrient exchange between fetus and mother occurs in this area partly. It is considered from the definitions of FLYNN (1923), GROSSER (1933) and MOSSMAN (1937), that these intercotyledonary areas of the cow and sheep have to be treated as parts of the placenta. According to the author's observations, the relationship between the chorion and the uterine wall in the intercotyledonary areas of the cow and sheep is the same as in the placenta of the pig. The latter is classified as an apposed placenta, and shows only close apposition of the fetal and maternal tissues. Their contact surface in the pig placenta is smooth at first, but gradually becomes rough; the villi form on the chorion, and the crypts form on the surface of the uterine mucosa. At the same time, many areolae exist on the entire surface of the chorion, exposing the mouths of uterine glands on the uterine mucosa, and areolae absorb the so-called uterine milk. Concerning the vascular distribution in the pig placenta, the superficial capillary net of the allanto-chorion elongates and enters into the areolae radially; these capillaries connect with the tributaries of a fetal vein at these areolar areas, while the numerous branches of fetal arteries and veins are connected irregularly with the superficial capillary net of the allanto-chorion in the interareolar area. It is considered that although numerous irregular, small, local circulations occur on the surface of the allanto-chorion, there are also many larger circulations in which the fetal blood in the superficial capillary net runs transversely along the secondary folds of the allanto-chorion and drains into the tributaries of the fetal vein at the areolar areas; they exist on the surface of the allanto-chorion. The circulations on the surface of the uterine mucosa also exhibit the same condition. Then the blood flows of the fetal and maternal side are in the same direction, and the placenta can be classified as belonging to the parallel type. Concerning exchange in the placenta, there is a tendency for the density of any substance concerned in placental transmission to be kept constant, because the fetal and maternal blood streams in the superficial capillary nets on the allanto-chorion and uterine mucosa are supplied with fresh blood by numerous small branches of the artery throughout the intercotyledonary area, while the blood

leaves from the surface in part by numerous small veins throughout, and the remainder is drained at the areolar areas. These conditions are seen on the uterine side, too. Therefore, it is considered that the efficiency of the placental transmission is kept always high, and the efficiency of diffusion does not diminish because the density concerned with the placental transmission does not attain equilibrium.

In the intercotyledonary area of the chorion of the cow and sheep, the areolae also exist, facing the mouth of each uterine gland. The areolar areas of the chorion and the areas of the uterine mucosa corresponding to the areolae are connected by tributaries of the fetal and maternal veins, respectively. The superficial capillary nets of both sides are connected irregularly with numerous branches of the fetal and maternal arteries and veins. This distribution pattern of blood vessels is entirely the same as the vascular pattern in the placenta of the pig. Accordingly, the blood flows of the intercotyledonary area in the cow and sheep are classified as "parallel type."

The placenta of the horse is commonly classified as "diffuse epitheliochorial type", like that of the pig. However, they are quite different, not only in respect to the histological observations but also in the observations of the vascular distribution; the structure of the placenta of the horse is like that of the cotyledon of the cow or sheep rather than like the placenta of the pig. Accordingly, the present author calls the vascular distribution of the horse placenta "the cotyledonary vascular tuft." The main difference in the vascular system between the villus of the horse placenta and the villus of the pig placenta is the existence of the central arterial vessels in the horse's villus; such a blood vessel is never recognized in the villus of the pig placenta. Concerning the relationship between the maternal and fetal blood streams at the contact surface of the two sides of the tissue layers of the horse placenta, the maternal blood flows in the direction from the fetal surface of the uterine mucosa towards the outer surface of the uterus, while the fetal blood flows in the direction from the uterine side towards the fetal side. The two flows of blood are in opposite directions, so the placenta of the horse is classified as "opposite type." The central artery of a villus in the horse placenta gives off many small lateral branches which join the capillary net. This vascular pattern seems to be more able to facilitate placental transmission. It is certain that the diffusion occurs at high speed at first, but it becomes gradually slower according to the progress of the diffusion. Concerning the absorptive ability of the fetal blood in the superficial capillaries of the villus in the horse placenta, it is considered that the fetal blood which flows on the surface of the villus from top to base receives transmitted substances from the maternal blood and increases their concentration gradually, but the concentration

does not become very high because the fetal blood is supplied with fresh blood everywhere on the surface of villus by the many small lateral branchlets of the central artery. This mechanism keeps the absorptive process highly efficient.

Such a vascular relationship exists in the cotyledons of the cow and sheep; the morphological features of the cotyledon of these animals are, also, very simular to those of the placenta of the horse.

In the rabbit, the placenta is discoidal, and the vascular system has been assigned importance only in this portion. Recently, it has become clear that antibodies do not cross the allanto-chorionic placenta, and transmission of antibodies from mother to fetus is performed from the uterine wall to the vitelline vessels *via* the uterine cavity. It can be said that the yolk-sac splanchnopleur plays an important part in the transmission, like the intercotyledonary areas in the cow and sheep. However, an area corresponding to the areola in other animals is never recognized on the rabbit yolk-sac splanchnopleur; the vascular system on the yolk-sac splanchnopleur shows a special feature. It is not usually held that the vascular system on the yolk-sac splanchnopleur corresponds to the vascular system on the surface of the uterine mucosa. This idea was confirmed by the papers of ANDŌ and YAMASHITA (1952 a, b,) which discussed the distributions of the minute blood vessels of the normal and pregnant rabbit's uterus. The author considers, from the above reasoning, that the vascular system in the rabbit placenta is limited to the discoidal allanto-chorionic placenta. In this portion the maternal and fetal blood streams flow in opposite directions, so the placenta of the rabbit is classified as "opposite type."

To summarize, the author categorized the placentas into three types according to vascular pattern:

1. Placenta of parallel type: The maternal and fetal blood streams flow in the same direction in the whole placenta (pig).

2. Placenta of opposite type: The maternal and fetal blood streams flow in opposite directions in the whole placenta (horse and rabbit).

3. Placenta of mixed type: In some parts of the placenta, such as the cotyledon, the two blood streams flow in opposite directions; while in the other parts, such as the intercotyledonary area, the two blood streams flow in the same direction (cow and sheep).

That is to say, the present author recognized the existence of maternal and fetal blood streams which flow in the same direction in the placenta, a phenomenon which has never previously been described.

The GROSSER classification of placental types, based on intimacy of relation of chorion with endometrium, is used commonly, with some modification. However, the intraepithelial capillaries of the villus in the cotyledons of the cow and

sheep also exist in the placenta of the pig, and the epithelial cells which cover the surface of the maternal septa of the cotyledons of the cow and sheep show more or less degeneration in most portions; in some portions they show desquamation. Moreover, the origin of these epithelial cells covering the maternal septa in the sheep's cotyledon is obscure. In the fully developed rabbit placenta, it is not decided whether the trophoblast in the labyrinth exists until termination of pregnancy or not. As mentioned above, even the structure of the placenta is not clear in many points. However, this classification of GROSSER has been recognized as a very logical one in many researches concerning the placental transmission of carbon dioxide gas, sodium, antibodies and other substances (RATNER, JACKSON and GRUEHL, 1927 a, b; SCHNEIDER and SZÁTHMARY, 1938; FLEXNER and GELLHORN, 1942; YOUNG, 1952). Recently, many questions have been raised regarding such explanation of the placental transfer and GROSSER's classification, itself. For example, concerning the placental transfer of antibodies, which is often cited as strong support for rationality of the GROSSER classification, in the rabbit's allanto-chorionic placenta the antibodies do not pass from mother to fetus, but rather are transferred by a route from the uterine wall to the vitelline membrane *via* the uterine cavity. It is known that such exchange between mother and fetus occurs also in the intercotyledonary area, in part. Further, the decidual cells which were not recognized in the horse placenta in former times are actually found in the endometrial cups during pregnancy. In respect to these problems, the classification of the placenta is in an entirely unsettled question, and it is considered that the morphological and functional classifications of the placenta need reconsideration.

Additional reconsideration is needed with respect to the vascular pattern of the placenta. Though the egg yolk of the birds is large in amount, and is a main source of fetal nutrition, the mammalian egg is meiolecithal and there is usually little development of the yolk-sac. In respect to this point, it is considered that the rabbit is more like birds, because the yolk-sac portion in the rabbit placenta is developed remarkably, has a distribution of vitelline vessels, and contributes to the transmission of diffused substances from the uterine wall to the fetus. It can be said, in view of these considerations, that the rabbit placenta is quite different from the human placenta, in which the yolk-sac is degenerated; in other words, the rabbit placenta is more primitive.

In the pig placenta, the development of the areola is remarkable, while the yolk-sac is degenerated. It may be considered that the role of the yolk-sac in absorption of nutrients is partially assumed by the areola, which absorbs uterine milk. This pattern of nutrient exchange in the placenta is considered by the present author to belong to a transitional type between oviparous and viviparous.

Though special structures corresponding to the areolae of the pig placenta are recognized in the intercotyledonary areas of the cew and sheep, in the horse placenta such a special structure is not to be seen at all. It can be considered that the placenta of the horse represents complete development to the hemotrophic type, getting rid of the role of uterine milk in the nutritional pattern, as in the pig, and that the placentas of the cow and sheep are situated in a middle position between those of the horse and pig.

As mentioned above, the placenta of the pig is the most simple and primitive among these five animals in regard to the vascular pattern. In the placentas of the horse, cow, sheep and rabbit, the basal elements in the structure are the villi or the tufts of villi, despite the remarkable difference in general features of the placentas. In the rabbit placenta, the tufts of villi are gathered only in the discoidal portion; while in the cow's and sheep's placenta, the tufts of villi are gathered in many so-called cotyledons, and in the horse placenta the villi are not gathered, but are scattered independently over the entire surface of the chorion.

Concerning the relationship between the areola and villus, there is a tendency for remarkable development of the tufts of villi, and accordingly the existence of the areola becomes unclear. That is to say, the tufts of villi in the cow and sheep are formed in cotyledons, but such villi in cotyledonary placentas scatter over the entire surface of the allanto-chorion to form a diffuse placenta, such as the pig placenta, and at the same time the complete areolae appear. Such areolae are not present in the horse placenta, and each tuft of villi appears independently.

In the rabbit placenta, each tuft of villi forms a lobe independently, as in the horse placenta, and each lobe is gathered in the fetal placenta. At the same time, the yolk-sac remains, showing a cystic character. It cannot be recognized that the rabbit placenta is included in the same group with the human's discoidal placenta, which has a trace of yolk-sac.

Concerning the vascular pattern of the villus, in the horse it shows an orderly construction, while in the cow and sheep it shows only a vascular loop at the tip of each villus. But in the rabbit, formation of villi is not clear. In the pig placenta, the villi are continuous and transversal along the fold; each villus shows only a club-like projection. The blood streams of the fetal and maternal sides in the pig placenta flow differently from those in the well-developed hemotrophic placenta, as in the rabbit and horse placentas.

On the basis of the above considerations, except the consideration as to GROSSER's classification and its meaning, the author concludes from his observations of the vascular pattern in the horse, pig, cow, sheep and rabbit, that

the rabbit placenta shows a special development while a primitive character remains in part. Of the other four species, the pig placenta is the most primitive, while the horse placenta is the highest in development, though it is like the pig placenta at a glance; the other two are at a lower developmental level than the horse placenta.

VI. CONCLUSIONS

1. Pregnant uteri of the horse, pig, cow, sheep and rabbit were collected. The vascular pattern of the placenta in these animals was studied mainly with neoprene latex solution which was injected into the umbilical vessels or uterine vessels, or by means of histological methods.

2. The placenta of the horse is classified as the diffuse epitheliochorial type. Numerous tufts of villi are formed over the entire surface of the chorion. They are interlocked with the crypts of the uterine mucosa. The tufts of villi show tree-like shape in general. One fetal arterial tributary usually penetrates into the axis of each tuft of villi, giving off branches radially through the center of each villus. The small central arterial capillary reaches to the top of each villus and connects with the superficial capillary net. Each central arterial capillary also gives off many lateral branchlets which connect with the surface capillary net. These nets which cover each villus are connected with each other at the root of each villus and they are gathered in the several venous tributaries which surround the axial arterial capillary at the axis of each villus. The venous tributaries in turn connect with the chorionic vein gathering the neighboring venous tributaries.

On the other hand, on the surface of the uterine labyrinth the maternal superficial capillaries form numerous small globes of the compact capillary plexus which are arranged in a row and surround each tuft of villi. The branches of the uterine artery run up to the surface of the uterine mucosa among the globes and disperse radially along the ridges of the surface to the top of each globe; they connect with the capillary net of the globe. A globe of the capillary plexus is connected with the venous tributary at its bottom. Inside of the globe there are formed many cylindrical crypts which are fitted to the villi. The maternal septum contains the capillary net.

3. The placenta of the pig is an apposed placenta; specifically, on the surface of the chorion primary and secondary folds are formed and fitted to the folds of the uterine mucosa. The fully developed villus shows a club-like shape and is covered with a superficial capillary net which continues along the surface of the chorionic folds. This capillary net is irregularly connected with

numerous arterial and venous branches in the interareolar area. This fact indicates the existence of numerous small, limited, local circulations. Many areolae are scattered on the chorion, and venous tributaries are distributed in these portions. The superficial capillaries surrounding the areola elongate and extend into the areola radially; these vessels connect with the venous tributaries. This fact, also, shows the existence of other larger local circulations in which the fetal blood in the superficial capillary net is drained in portions of each areola. The maternal vascular system on the surface of the uterine mucosa is in the same condition as on the fetal side. Thus the vascular pattern of the pig placenta is quite different from that in the horse placenta; it is appropriate to call it a "diffuse placenta", because the vascular system on the chorion of the pig is continuous and extends over the whole surface of the chorion, while the vascular system of the horse placenta is formed of many independent vascular globes which can be called cotyledonary vascular tufts.

4. The placental area of the cow is subdivided into two parts, the cotyledons and the intercotyledonary area. Concerning the vascular system of the villus, the axial artery penetrates into the villus, running directly through the villus to the top, giving off a few main branches on the way. Many small branches, which are given off from the axial artery, make small loops in leaf-like shape, surrounding the axis radially, and return to the venous tributaries in the axis or connect with the other capillaries. On the other hand, the branches of the maternal arteries which penetrate into the cotyledon from the top of the pedicle run straight through the maternal septa, and after arrival near the surface of the cotyledon they turn along the surface, and sometimes return along the surface of the crypts to the bottom of the cotyledon. These arterial branches disperse gradually to the capillaries on the surfaces of the cotyledon and crypts. The capillaries form a network and run along the walls of crypts and reach the bottom of the cotyledon. In the maternal cotyledon, these capillaries form a network with large polygonal meshes and connect with the venous tributaries at the bottom of the cotyledon, or sometimes in its upper or middle portions. Then the tops of the villi thrust into the maternal spongy capillary plexus of the cotyledon. In the intercotyledonary area, areolae exist in the area corresponding to the mouths of the uterine glands, and the vascular systems in the fetal and maternal sides are in the same condition as in the pig placenta.

5. In the placenta of the sheep, the placental area is subdivided into two parts as in the cow, the cotyledons and intercotyledonary area. The villi are cylindrical in most portions, while their tips become flat. The fetal arterial branches penetrate into the villus, run through its central portion to the top,

and give off a few small branches to the main branches of the villus. These axial arteries give off many small lateral branches on the way and the small branches connect with the superficial capillary net. The tip of the axial artery also connects with the superficial capillary net before reaching the top of the villus. The superficial capillary net is connected with the venous tributaries at the arcade or already in the villus. In the cotyledon the maternal arteries, which penetrate into the cotyledon, run straight toward the inner surface as radii from the curved base of the cotyledon, and give off many capillaries near the inner surface of the cotyledon. These capillaries form the network which surrounds each villus as a cylinder, and run reversely to the outside; they are gathered to the venous tributaries at the bottom of cotyledon. The structure of the cotyledon is more like that in the horse placenta than in the cow cotyledon. In the intercotyledonary area, areolae exist on the allanto-chorion. The vascular pattern on the surface of the allanto-chorion and uterine mucosa is like that in the cow.

6. The placenta of the rabbit is discoidal; the outer fetal membrane is a yolk-sac splanchnopleur. Thus the allanto-chorionic placenta in the rabbit is limited to the extent of the discoidal placenta. Contact of the fetal and maternal blood streams occur in the fetal portion and the intermediate zone in the placenta. The branches of the uterine arteries penetrate into the maternal placenta and reach to the surface of the fetal placenta. These maternal arterial tributaries are distributed on the surface of the placenta and anastomose with each other. From these tributaries many tufts of capillaries are given off in each lobe. The capillaries form a network and connect with the blood sinuses in the maternal placenta, which are maternal venous vessels. On the other hand, the branches of the umbilical artery give off small branches into the cotyledon, and they reach directly to the intermediate zone running among the lobes, and turn up to the bottom of each lobe. These smaller branches give off still smaller branches which connect with each other and form a rough vascular layer in the intermediate zone; they split up into smaller branches and capillaries in each lobe at its bottom or side. These capillaries form a network in the lobe, and are gathered into the fetal venous tributaries at the upper portions in each lobe.

7. In the pig placenta and in the intercotyledonary area of the cow and sheep placenta, the areolae lie opposite to the mouths of the uterine glands on the uterine mucosa. The fetal and maternal bloods in the superficial capillaries in both sides are drained together from these areolar portions. The blood streams in both sides flow in the same direction and are classified as the "parallel type." On the other hand, in the placenta of the horse and rabbit, and in the

cotyledons of the cow and sheep, the fetal and maternal blood streams flow in opposite directions, so these blood streams are classified as "opposite type." The present author has classified the placentas into three types by the combination of two different types of blood streams:

1. Placenta of "parallel type": The maternal and fetal blood streams flow the same direction in the whole placenta (pig).
2. Placenta of "opposite type": The maternal and fetal blood streams flow in opposite directions in the whole placenta (horse and rabbit).
3. Placenta of "mixed type": In some parts of the placenta, such as the cotyledon, the two blood streams flow in opposite directions; while in the other parts, such as the intercotyledonary area, the two blood streams flow in the same direction (cow and sheep).

8. From the observations of the histological structures and vascular systems in the placentas of the horse, pig, cow, sheep and rabbit, it is considered by the author that the rabbit placenta shows special development, while its primitive character remains in part. Among the other four, the pig placenta is most primitive, while the horse placenta is the highest type, though it resembles the pig placenta macroscopically; the other two are in a lower level than the horse placenta.

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Explanation of Plates

PLATE I.

(The placenta of the horse)

Fig. 1. (Horse 11). Fetus, amnion and allanto-chorion in the pregnant uterus. Formalin solution was injected directly into the allantoic cavity.

Fig. 2. (Horse 42). Fetus and fetal membrane which were taken from the uterus.

PLATE II.

(The placenta of the horse)

Fig. 3. (Horse 36). Blood vascular distribution on the allantoic side of the allanto-chorion.

Fig. 4. (Horse 48). Blood vessels of the tufts of villi. Transparent specimen. × 40.

Fig. 5. (Horse 31). Tufts of villi on the surface of the allanto-chorion. Latex cast specimen. × 40.

Fig. 6. (Horse 2). Blood vascular distribution on the allantoic side of the allanto-chorion. Latex cast specimen. × 20.

Fig. 7. (Horse 45). Sideview of the tufts of villi. Latex cast specimen. × 40.

PLATE III.

(The placenta of the horse)

Fig. 8. (Horse 36). Capillaries of the villi. Latex cast specimen. × 100.

Fig. 9. (Horse 31). Capillaries of the villi. Latex cast specimen. × 100.

Fig. 10. (Horse 37). Capillaries at the tips of villi. × 400.

Fig. 11. (Horse 36). Capillaries at the tip of a villus. × 400.

Fig. 12. (Horse 36). Central arterial vessel in the tip of a villus. × 400.

Fig. 13. (Horse 36). Central arterial vessel in the tips of villi. × 400.

PLATE IV.

(The placenta of the horse)

Fig. 14. (Horse 28). Fetal vascular distribution of the villi in the uterine crypts. × 40.

Fig. 15. (Horse 28). Same as Fig. 14. × 40.

Fig. 16. (Horse 28). Same as Fig. 14. × 40.
Fig. 17. (Horse 28). Longitudinal section of the villi in the uterine crypts. × 100.
Fig. 18. (Horse 28). Cross section of the villi in the uterine crypts. × 100.
Fig. 19. (Horse 48). Surface of the uterine mucosa. Groups of crypts are seen. × 40.

PLATE V.

(The placenta of the horse)

Fig. 20. (Horse 48). Surface of the uterine mucosa. × 40.
Fig. 21. (Horse 48). Surface of the uterine mucosa. This specimen was illuminated from the back side of the uterine mucosa. × 100.
Fig. 22. (Horse 47). Surface of the uterine mucosa. Capillary network. × 100.
Fig. 23 and Fig. 24. (Horse 27). Vascular layer on the surface of the uterine mucosa. Many globes of compact capillary plexus are seen. Latex cast specimen. × 20.
Fig. 25. (Horse 29). Upper surface of the globes of compact capillary plexus. Latex cast specimen. × 50.

PLATE VI.

(The placenta of the horse)

Fig. 26. (Horse 43). Back side of the globes. Latex cast specimen. × 20.
Fig. 27. (Horse 29). Back side of the globes. Latex cast specimen. × 100.
Fig. 28. (Horse 43). Back side of the globes. Latex cast specimen. × 100.
Fig. 29. (Horse 29). Inner structure of a globe in sideview. Latex cast specimen. × 20.
Figs. 30, 31 and 32. (Horse 48). Maternal capillary net of the septa in a globe. These photographs are of same specimen, but the focus of the microscope was changed. Transparent specimen. × 100.

PLATE VII.

(The placenta of the horse)

Fig. 33. (Horse 48). Vertical section of the uterine mucosa. Transparent specimen. a—maternal artery. × 100.
Fig. 34. (Horse 43). Vertical section of the uterine mucosa. Transparent specimen. a—materinal artery, v—maternal vein. × 40.
Fig. 35. (Horse 48). Vertical section of the uterine mucosa. Upper portion of a globe. Transparent specimen. a—maternal artery. × 100.

Fig. 36. (Horse 48). Vertical section of the uterine mucosa. Bottom of a globe. v—maternal vein. × 100.

Fig. 37. (Horse 47). Vertical section of the horse placenta. H. -E. stain. 15 μ thick. × 40.

Fig. 38. (Horse 35). Vertical section of the uterine muosa. u—duct of the uterine gland. H. -E. stain. 10 μ thick × 80.

Fig. 39. (Horse 35). Vertical section of the uterine mucosa. a—maternal artery. H. -E. stain. 5 μ thick. × 80.

PLATE VIII.

(The placenta of the horse)

Figs. 40 and 41. (Horse 47). Longitudinal section of the placental labyrinth. H. -E. stain. 10 μ thick. × 400.

Fig. 42. (Horse 18). Cross section of the placental labyrinth. H. -E. stain. 5 μ thick. × 400.

Fig. 43. (Horse 47). Cross section of the placental labyrinth. H. -E. stain. 5 μ thick. × 800.

Fig. 44. (Horse 47). Bottom of the cotyledon. Cross section of the placental labyrinth. H. -E. stain. 5 μ thick. × 200.

PLATE IX.

(The placenta of the pig)

Fig. 45. (Pig 30). Pregnant uterus.

Fig. 46. (Pig 33 and 32). Fetus and fetal membrane.

Fig. 47. (Pig 18). Allantoic side of the allanto-chorionic fetal membrane. Areolae are rendered recognizable as white spots.

PLATE X.

(The placenta of the pig)

Fig. 48. (Pig 12). Surface of the allanto-chorion. An areola is situated in the central portion of this picture. × 20.

Fig. 49. (Pig 12). Vascular distribution of the allanto-chorion. Latex cast specimen. × 40.

Fig. 50. (Pig 18). Vascular distribution on the surface of the allanto-chorion. Latex cast specimen. × 40.

Figs. 51 and 52. (Pig 4). Numerous villi are arranged on the surface of the allanto-chorion (chorionic side). × 40.

Fig. 53. (Pig 4). Tops of the villi. × 100.
Figs. 54 and 55. (Pig. 4). Sideview of the villi. × 40.

PLATE XI.

(The placenta of the pig)

Fig. 56. (Pig 15). Sideview of the villi. Transparent specimen. × 100.
Fig. 57. (Pig 18). Capillaries on the surface of the villus. Latex cast specimen. × 400.
Fig. 58. (Pig 15). Cross section of the villi. Transparent specimen. × 40.
Fig. 59. (Pig 19). Areola. × 40.
Fig. 60. (Pig 19). Capillaries of the secondary folds extend into the areola. × 40.
Fig. 61. (Pig 18). Capillaries of the areola. × 80.
Fig. 62. (Pig 19). Vertical section of an areola. × 40.

PLATE XII.

(The placenta of the pig)

Fig. 63. (Pig 19). Vertical section of the areola. × 40.
Fig. 64. (Pig 19). Allantoic side of the allanto-chorion. Branch of vein is connected with the bottom of an areola. v—fetal vein. × 20.
Fig. 65. (Pig 20). An irregular areola is situated in the central portion of this picture and two regular areolae in the upper portion. × 20.
Fig. 66. (Pig 19). Surface of the uterine mucosa. × 40.
Fig. 67. (Pig 25). Vascular distribution on the surface of the uterine mucosa. Latex cast specimen. × 40.
Fig. 68. (Pig 6). Cross section of the fold of the uterine mucosa. × 40.
Fig. 69. (Pig 20). Longitudinal section of the uterine mucosa. Transparent specimen. × 100.

PLATE XIII.

(The placenta of the pig)

Fig. 70. (Pig 12). Capillary distribution on the surface of uterine mucosa. Latex cast specimen. × 100.
Fig. 71. (Pig 2). Vascular distribution on the surface of the uterine mucosa. This photograph is taken from the back side of it. × 40.
Fig. 72. (Pig 19). Same as Fig 71. × 40.

Fig. 73. (Pig 12). Same as Fig. 71. × 40.

Figs. 74 and 75. (Pig 19). Surface of the uterine mucosa. Area corresponding to the areola. × 40.

Fig. 76. (Pig 12). Area corresponding to the areola. Latex cast specimen. × 40.

PLATE XIV.

(The placenta of the pig)

Fig. 77. (Pig 6). Cross section of the uterine fold. a—area corresponding to the areola. × 40.

Fig. 78. (Pig 12). Vascular distribution on the surface of the uterine mucosa. This photograph was taken from the back side. Central portion of this photograph is area corresponding to the areola. a—maternal artery, v—maternal vein. × 40.

Fig. 79. (Pig 4). Vascular distribution of the pig placenta. Villi are interlocked with the maternal folds. × 40.

Fig. 80. (Pig 21). The fetal membrane is attached to the uterine mucosa. No secondary fold is formed. H.-E. stain. 5 μ thick. × 200.

Fig. 81. (Pig 5). The fetal membrane is attached to the uterine mucosa. The secondary folds are formed. H.-E. stain. 5 μ thick. × 200.

Fig. 82. (Pig 15). Fetal membrane and uterine mucosa. H.-E. stain. 20 μ thick. × 40.

PLATE XV.

(The placenta of the pig)

Fig. 83. (Pig 15). Epithelia of the villi and uterine mucosa. Intraepithelial capillaries are seen in the villous epithelium. H.-E. stain. 5 μ thick. × 800.

Fig. 84. (Pig 15). Intraepithelial capillaries in the villus. H.-E. stain. 5 μ thick. × 800.

Fig. 85. (Pig 15). Cross section of an areolar. f—fetal membrane, u—uterine mucosa. H.-E. stain. 5 μ thick. × 80.

Fig. 86. (Pig 15). Cross section of an areola. H.-E. stain. 5 μ thick. × 200.

PLATE XVI.

(The placenta of the cow)

Fig. 87. (Cow 8). Cotyledons and fetal vessels which are distributed on the surface of cotyledons. u—fetal vessels in the umibilical cord.

Fig. 88. (Cow 42). Vascular distribution of the fetal cotyledons. Latex cast

specimens. Right—surface of the fetal cotyledon (allantoic side), left-villi which are inserted into the crypts of the maternal cotyledon.

Fig. 89. (Cow 41). Vascular distribution of the maternal cotyledons. Latex cast specimens.

PLATE XVII.

(The placenta of the cow)

Fig. 90. (Cow 42). Vertical section of a cotyledon.

Fig. 91. (Cow 22). Fetal vascular distribution on the surface of the cotyledon.

Fig. 92. (Cow 13). Fetal vascular system in the cotyledon. × 40.

Fig. 93. (Cow 44). Vascular distribution of the villi. Latex cast specimen. × 40.

PLATE XVIII.

(The placenta of the cow)

Fig. 94. (Cow 44). Vascular distribution in the tip of the villus. Latex cast specimen. × 100.

Fig. 95. (Cow 13). Fetal vessels in the cotyledon. Transparent specimen. × 40.

Fig. 96. (Cow 13). Fetal capillaries in the tip of a villus in a cotyledon. Transparent specimen. × 100.

PLATE XIX.

(The placenta of the cow)

Fig. 97. (Cow 13). Fetal vascular distribution in the cotyledon. Transparent specimen. m—maternal vessel. × 100.

Fig. 98. (Cow 13). Fetal vessels in a cross section of the cotyledon. Transparent specimen. × 40.

Fig. 99. (Cow 8). Cross section of the cotyledon. Transparent specimen. × 40.

Figs. 100 and 101. (Cow 13). Fetal vessels in the arcade. Transparent specimen. × 40.

PLATE XX.

(The placenta of the cow)

Fig. 102. (Cow 20). Maternal vascular distribution in the maternal cotyledon. Transparent specimen. × 40.

Fig. 103. (Cow 14). Maternal capillaries on the surface of the maternal cotyledon. Transparent specimen. × 40.

Fig. 104. (Cow 41). Maternal vessels in the cotyledon. Latex cast specimen. × 20.

PLATE XXI.

(The placenta of the cow)

Fig. 105. (Cow 20). Maternal vessels at the bottom of the cotyledon. Transparent specimen. × 40.

Fig. 106. (Cow 41). Maternal vessels in the cotyledon. Latex cast specimen. v—maternal vein. × 40.

Fig. 107. (Cow 14). Maternal vessels in a cross section of the cotyledon. Transparent specimen. × 40.

Fig. 108. (Cow 22). Fetal and maternal capillaries in the cotyledon. f—fetal tissue, m—maternal tissue. Transparent specimen. × 100.

Fig. 109. (Cow 20). Capillary net on the allanto-chorion (inter-areolar area). a—fetal artery. × 40.

Fig. 110. (Cow 14). Vertical section of the allanto-chorion. Inter-areolar area. × 40.

Fig. 111. (Cow 8). Surface of an areola. × 40.

PLATE XXII.

(The placenta of the cow)

Fig. 112. (Cow 8). Vertical section of the areola. × 40.

Fig. 113. (Cow 14). Vascular distribution on the allanto-chorion. a—areola, v—fetal vein. × 40.

Fig. 114. (Cow 8). Surface of the uterine mucosa. Depressions are correspond to the areolar area of the allanto-chorion. × 40.

Fig. 115. (Cow 20). Vascular distribution on the surface of the uterine mucosa. This specimen was illuminated from the back side. × 40.

Fig. 116. (Cow 2). Capillaries on the surface of the uterine mucosa. × 100.

Fig. 117. (Cow 20). Vertical section of the uterine mucosa. Area corresponding to the inter-areolar area of the allanto-chorion. × 40.

Fig. 118. (Cow 14). Vertical section of the uterine mucosa. Area corresponding to the areola of the allanto-chorion. × 40.

PLATE XXIII.

(The placenta of the cow)

Fig. 119. (Cow 51). Vertical section of the cotyledon. v—villus, m—maternal septum. H.-E. stain. 5 μ thick. × 40.

Fig. 120. (Cow 26). Vertical section of the cotyledon. Bottom of the cotyledon. H.-E. stain. 15 μ thick. × 40.

Fig. 121. (Cow 44). Cross section of the cotyledon. H.-E. stain. 15 μ thick. × 40.

PLATE XXIV.

(The placenta of the cow)

Fig. 122. (Cow 26). Vertical section of the cotyledon. f—fetal tissue, m—maternal tissue. H.-E. stain. 15 μ thick. × 200.

Figs. 123 and 124. (Cow 26). Epithelial cells of the villi and the maternal septa. Intraepithelial capillaries of the villi are seen. H.-E. stain. 5 μ thick. × 800.

Fig. 125. (Cow 25). Epithelium of the allanto-chorion. H.-E. stain. 10 μ thick. × 200.

Fig. 126. (Cow 25). Vertical section of an areola. H.-E. stain. 10 μ thick. × 40.

PLATE XXV.

(The placenta of the sheep)

Fig. 127. (Sheep 30). Fetuses and pregnant uterus.

Fig. 128. (Sheep 27). Vertical sections of the cotyledons.

Fig. 129. (Sheep 18). Fetal vessels at the arcade area. × 40.

Fig. 130. (Sheep 33). Fetal vessels at the tips of villi. × 40.

Fig. 131. (Sheep 29). Fetal vessels in the cotyledon. a—fetal arterial vessel. × 40.

PLATE XXVI.

(The placenta of the sheep)

Fig. 132. (Sheep 29). Vascular distribution at the tip of a villus. × 100.

Fig. 133. (Sheep 29). Vascular distribution of the villi. Latex cast specimen. × 40.

Fig. 134. (Sheep 29). Vascular distribution at the tips of the villi. × 100.

Fig. 135. (Sheep 29). Vascular distribution of the villi. a—fetal artery, v—fetal vein. × 40.

PLATE XXVII.

(The placenta of the sheep)

Fig. 136. (Sheep 29). Fetal vessels in the cross section of a cotyledon. × 40.
Fig. 137. (Sheep 29). Fetal vessels in the cross section of a cotyledon. × 100.
Fig. 138. (Sheep 27). Fetal vessels of the tips of the villi in the cross section of a cotyledon. × 40.
Fig. 139. (Sheep 9). Maternal vessels in a cotyledon. Vertical section of the cotyledon. × 40.

PLATE XXVIII.

(The placenta of the sheep)

Fig. 140. (Sheep 9). Maternal vessels in the vertical section of the cotyledon. Transparent specimen. a—maternal artery, h—placental hematomata. × 40.
Fig. 141. (Sheep 9). Maternal vessels in the cotyledon. Transparent specimen. a—maternal artery. × 40.
Fig. 142. (Sheep 11). Maternal vessels in the cotyledon. Latex cast specimen. × 40.

PLATE XXIX.

(The placenta of the sheep)

Fig. 143. (Sheep 34). Vertical section of the cotyledon. Maternal capillaries are seen in the maternal septa. × 40.
Fig. 144. (Sheep 24). Maternal capillaries in the cotyledon. Mixed solution of sodium alginate, indigo carmine and Prussian blue was injected into vessels. × 40.
Fig. 145. (Sheep 34). Maternal capillaries in the cotyledon. Cylindrical crypts of the cotyledon were cut obliquely. × 40.
Fig. 146. (Sheep 34). Cross section of the cotyledon. f—fetal tissue, m—maternal tissue. × 40.
Fig. 147. (Sheep 7). Maternal vessels in the cotyledon. The base of the cotyledon. Transparent specimen. × 40.

PLATE XXX.

(The placenta of the sheep)

Fig. 148. (Sheep 12). Maternal vessels near the base of the cotyledon. Transparent specimen. × 40.

Figs. 149 and 150. (Sheep 28). Maternal capillary net in the cotyledon. These photographs were taken from the villous side. Latex cast specimen. × 40.

Fig. 151. (Sheep 28). Maternal capillary net in the cotyledon. This photograph was taken from the inner side of the septum. Latex cast specimen. × 40.

Fig. 152. (Sheep 27). Surface of the uterine mucosa. × 40.

Fig. 153. (Sheep 34). Vascular distribution on the surface of the uterine mucosa. This specimen was illuminated from the back side. a—maternal artery, v—maternal vein. × 40.

PLATE XXXI.

(The placenta of the sheep)

Fig. 154. (Sheep 29). Fetal vascular distribution on the allanto-chorion. × 40.

Fig. 155. (Sheep 29). Fetal vascular distribution on the allanto-chorion. Areolae are seen. × 40.

Fig. 156. (Sheep 29). Areola. v—fetal vein. × 40.

Fig. 157. (Sheep 35). Vertical section of the cotyledon. H.-E. stain. 5 μ thick. × 40.

PLATE XXXII.

(The placenta of the sheep)

Fig. 158. (Sheep 23). Cross section of the cotyledon. H.-E. stain. 10 μ thick. × 40.

Fig. 159. (Sheep 33). Cross section of the cotyledon. m—maternal septum, f—fetal tissue. H.-E. stain. 5 μ thick. × 200.

Fig. 160. (Sheep 17). Vertical section of the cotyledon. m—maternal septum. H.-E. stain. 5 μ thick. × 200.

Fig. 161. (Sheep 35). Epithelial cells of the villi and the maternal septa. H.-E. Stain. 5 μ thick. × 200.

PLATE XXXIII.

(The placenta of the sheep)

Fig. 162. (Sheep 17). Intraepithelial capillaries of the villus. H.-E. stain. 5 μ thick. × 800.

Fig. 163. (Sheep 35). Fetal epithelium in the arcade. H.-E. stain. 5 μ thick. × 200.

Fig. 164. (Sheep 6). Fetal epithelial cells in the arcade. H.-E. stain. 5 μ thick. × 800.

Fig. 165. (Sheep 27). Uterine mucosa in the intercotyledonary area. H.-E. stain. 5 μ thick. × 800.

Fig. 166. (Sheep 27). Vertical section of an areola. H.-E. stain. 5 μ thick. × 200.

PLATE XXXIV.

(The placenta of the rabbit)

Fig. 167. (Rabbit 17). Fetus, placenta and fetal membrane. Distribution of the vitelline vessels on the yolk-sac splanchnopleur. Right side of the fetus.

Fig. 168. (Rabbit 17). This fetus is the same as in Fig. 167. Left side of the fetus.

Fig. 169. (Rabbit 17). Fetus, amnion, placenta and yolk-sac splanchnopleur. The yolk-sac splanchnopleur is stripped.

PLATE XXXV.

(The placenta of the rabbit)

Fig. 170. (Rabbit 17). Placenta, bilaminar omphalopleur and yolk-sac splanchnopleur.

Figs. 171 and 172. (Rabbit 17). Vascular distribution on the fetal placenta. Two umbilical arteries were injected with different colored latex solutions. Latex cast specimen.

Figs. 173 and 174. (Rabbit 17). Same specimens as in Figs. 171 and 172. Back side of the fetal placenta.

Fig. 175. (Rabbit 11). Maternal vascular distribution in the placenta. Maternal placental vessels were injected with the latex solution *via* the maternal veins. Back side of the placenta. Latex cast specimen.

Fig. 176. (Rabbit 15). Maternal vascular distribution in the placenta. Latex cast

specimen.

Fig. 177. (Rabbit 15). Same specimen as in Fig. 176. Sideview of the placenta.

PLATE XXXVI.

(The placenta of the rabbit)

Fig. 178. (Rabbit 15). Maternal vascular distribution on the surface of the placenta. × 40.

Fig. 179. (Rabbit 15). Maternal capillaries on the surface of the placenta. × 40.

Fig. 180. (Rabbit 16). Maternal capillaries on the surface of the placenta. × 100.

Fig. 181. (Rabbit 15). Maternal capillaries on the surface of the placenta. × 40.

Fig. 182. (Rabbit 16). Vertical section of the placenta. Maternal vessels in the fetal placenta. × 40.

Fig. 183. (Rabbit 15). Maternal vessels in the lobes of the fetal placenta. × 40.

PLATE XXXVII.

(The placenta of the rabbit)

Fig. 184. (Rabbit 16). Vertical section of the placenta. Maternal venous vessels in the placenta. × 40.

Fig. 185. (Rabbit 15). Vertical section of the fetal placenta. Maternal capillaries in the labyrinth. × 100.

Fig. 186. (Rabbit 15). Cross section of a tuft of maternal capillaries in the fetal placenta. × 40.

Fig. 187. (Rabbit 3). Vertical section of the fetal placenta. India ink was injected into the maternal vessels. × 40.

Fig. 188. (Rabbit 3). Vertical section of the placenta. India ink was injected into the maternal vessels. Bottom of the lobes and upper portion of the maternal placenta. × 40.

Fig. 189. (Rabbit 3). Vertical section of the fetal placenta. India ink was injected into the maternal vessels. Maternal capillaries in a lobe. × 100.

PLATE XXXVIII.

(The placenta of the rabbit)

Figs. 190 and 191. (Rabbit 13). Fetal vascular distribution on the surface of the placenta. × 40.

Fig. 192. (Rabbit 17). Vertical section of the fetal placenta. Fetal capillaries in

the fetal placenta. v—fetal vein. × 40.

Figs. 193 and 194. (Rabbit 6). Vertical section of the fetal placenta. Fetal vascular distribution in a lobe. a—fetal artery, v—fetal vein. × 40.

PLATE XXXIX.

(The placenta of the rabbit)

Fig. 195. (Rabbit 12). Vertical section of the fetal placenta. Fetal vascular distribution in a lobe. v—fetal vein. × 40.

Figs. 196 and 197. (Rabbit 17). Vertical section of the placenta. Transparent specimen. a—fetal arterial vessels beneath the bottom of each lobe. × 40.

Fig. 198. (Rabbit 12). Vertical section of the placenta. Fetal vascular distribution in the placenta. Transparent specimen. a—fetal arterial vessel. × 40.

PLATE XL.

(The placenta of the rabbit)

Fig. 199. (Rabbit 13). Fetal vascular distribution in the fetal placenta. Transparent specimen. × 40.

Fig. 200. (Rabbit 17). Fetal capillaries which penetrate into a lobe. Transparent specimen. a-fetal artery. × 100.

Fig. 201. (Rabbit 17). Fetal vascular distribution on the surface of the placenta. Latex cast specimen. × 20.

Figs. 202, 203 and 204. (Rabbit 17). Sideview of the tufts of the fetal vessels in the lobes. Latex cast specimen. × 20.

PLATE XLI.

(The placenta of the rabbit)

Figs. 205 and 206. (Rabbit 17). Fetal vessels at the back side of the fetal placenta. Latex cast specimen. × 20.

Fig. 207. (Rabbit 17). Fetal capillary net in the labyrinth. Latex cast specimen. × 200.

Figs. 208 and 209. (Rabbit 17). Vitelline vessels on the yolk-sac splanchnopleur. a—arterial vessel, v—venous vessel. × 50.

Fig. 211. (Rabbit 14). Vertical section of the fetal placenta. a—fetal arterial vessel. H.-E. stain. 10 μ thick. × 40.

PLATE XLII.

(The placenta of the rabbit)

Fig. 210. (Rabbit 17). Vertical section of the placenta. f—fetal placenta, i—intermediate zone, m—maternal placenta. H.-E. stain. 5 μ thick. × 40.

Fig. 212. (Rabbit 14). Vertical section of the fetal placenta. a—maternal arterial vessel. H.-E. stain. 5 μ thick. × 100.

Fig. 213. (Rabbit 14). Vertical section of the fetal placenta. m—maternal arterial vessel, f—fetal venous vessel. H.-E. stain. 5 μ thick. × 100.

PLATE XLIII.

(The placenta of the rabbit)

Fig. 214. (Rabbit 14). Intermediate zone. H.-E. stain. 5 μ thick. × 800.

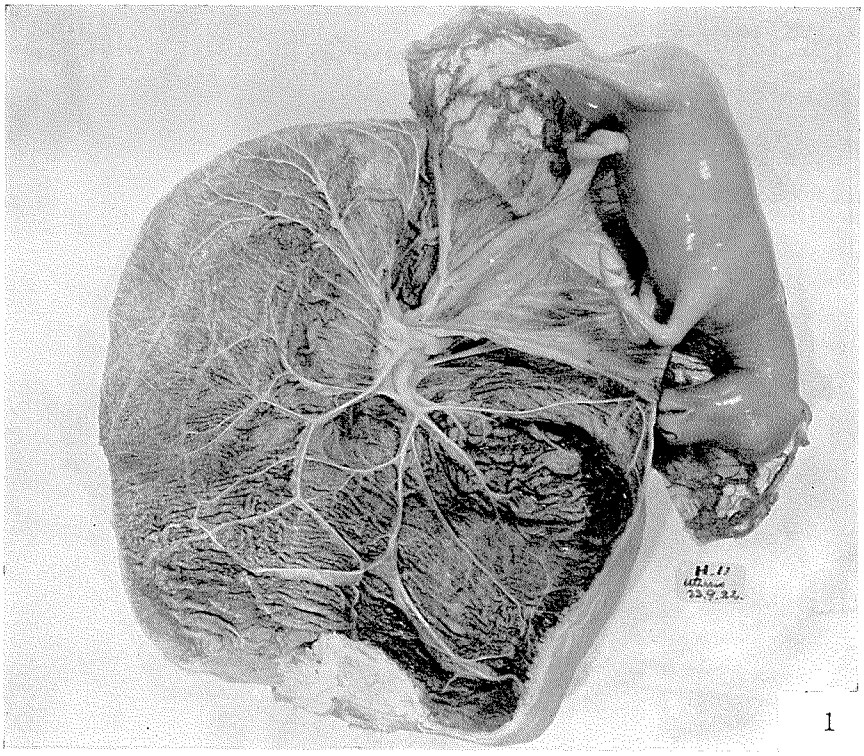
Fig. 215. (Rabbit 17). Labyrinth. Twenty-eight-day placenta. H.-E. stain. 5 μ thick. × 800.

Fig. 216. (Rabbit 14). Labyrinth. Twenty-three-day placenta. H.-E. stain. 5 μ thick. × 800.

Fig. 217. (Rabbit 14). Intermediate zone. H.-E. stain. 5 μ thick. × 800.

Fig. 218. (Rabbit 14). Intermediate zone. Fetal arterial vessel is seen. H.-E. stain. 5 μ thick. × 400.

Fig. 219. (Rabbit 17). Maternal placenta. H.-E. stain. 5 μ thick. × 100.



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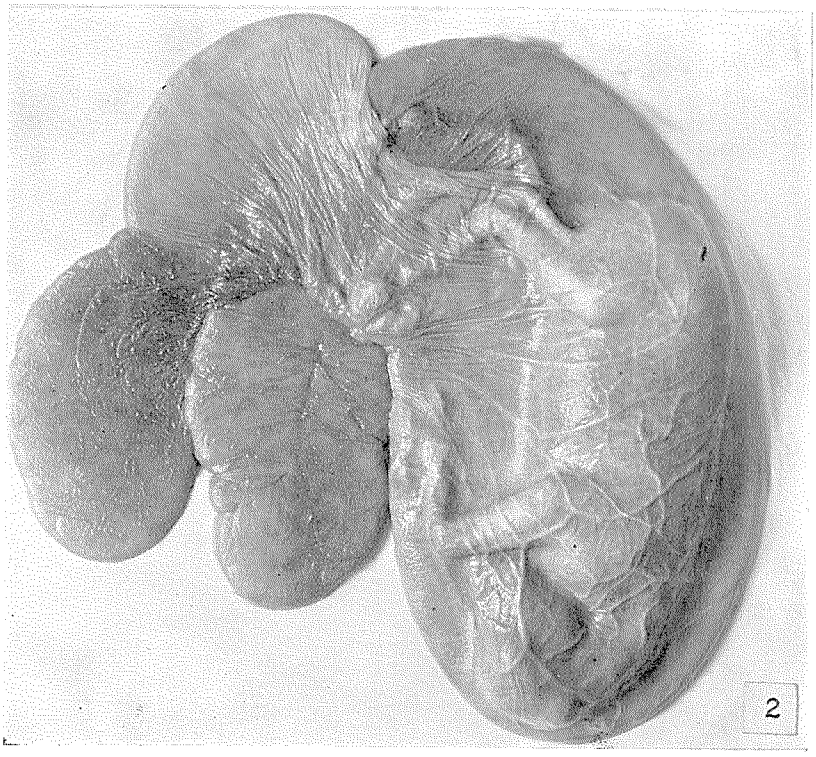

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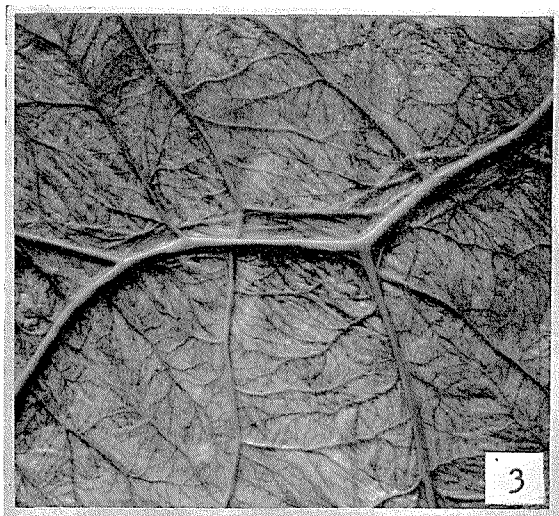
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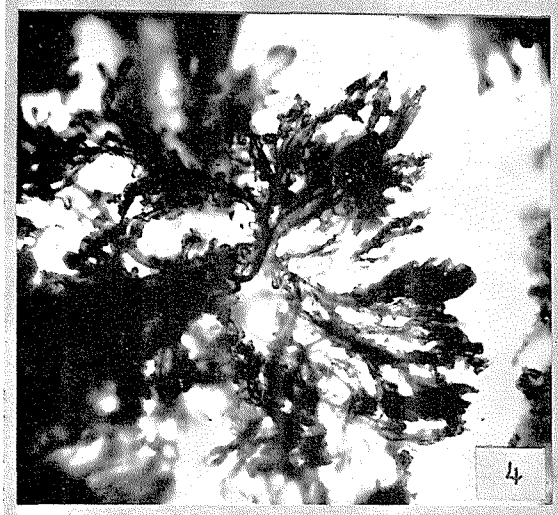
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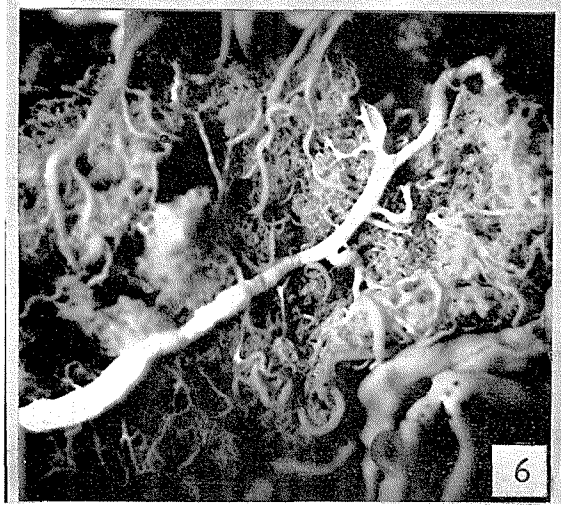
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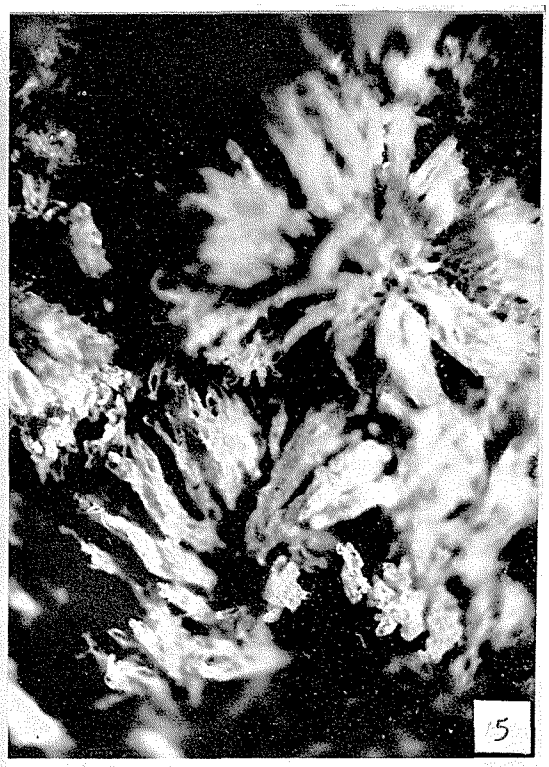
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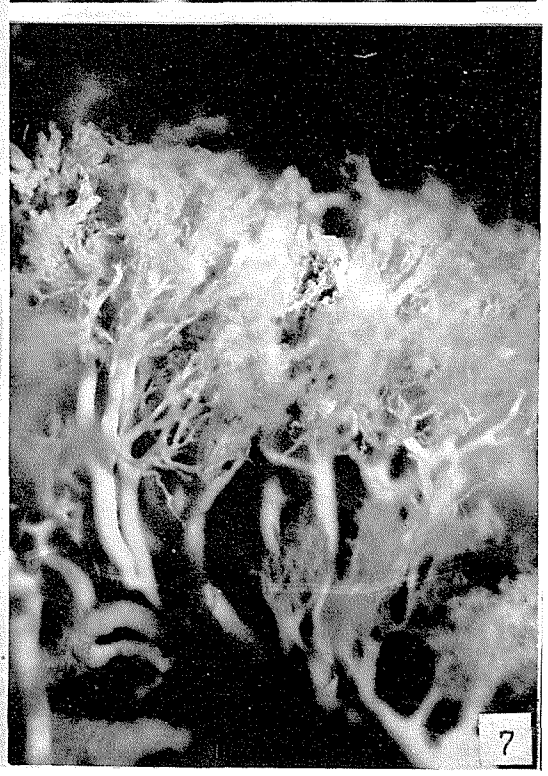
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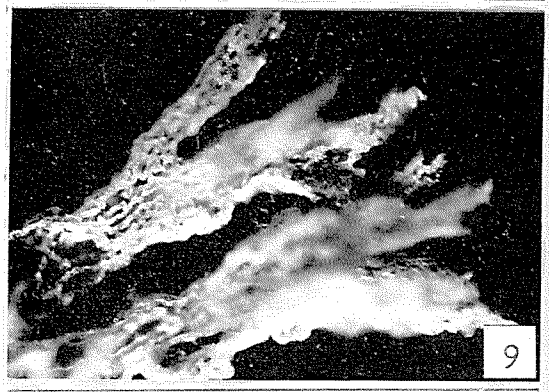
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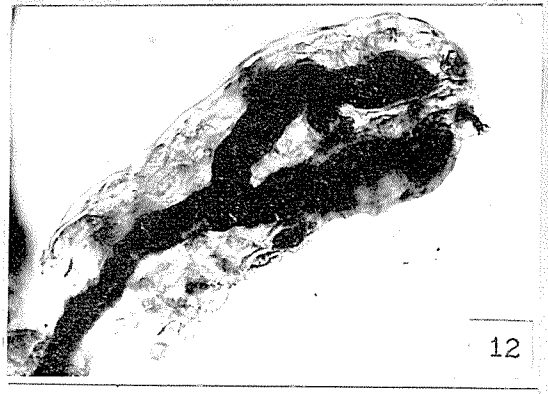
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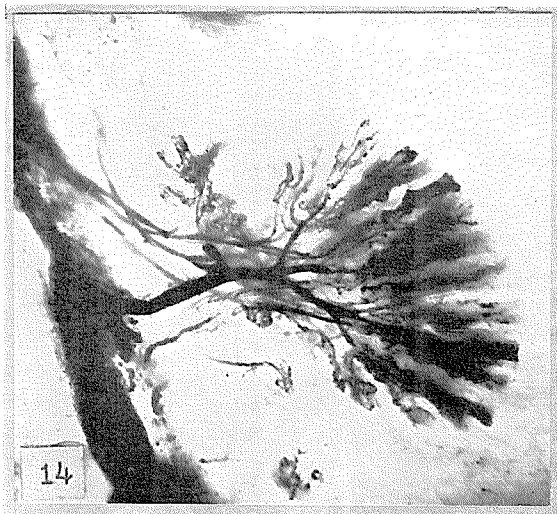
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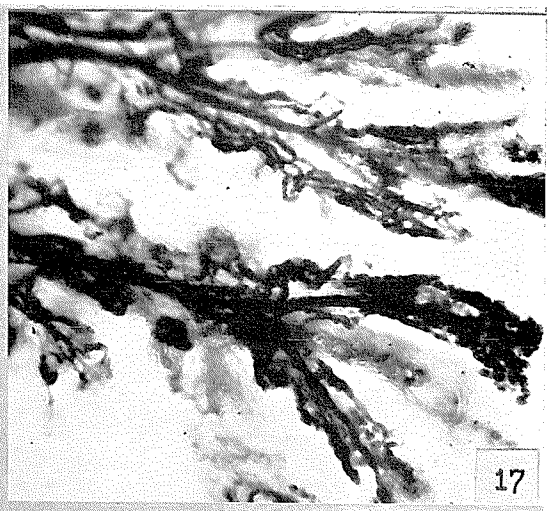
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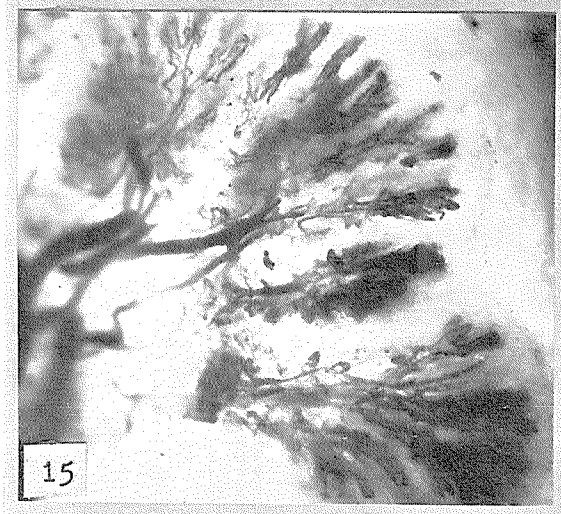
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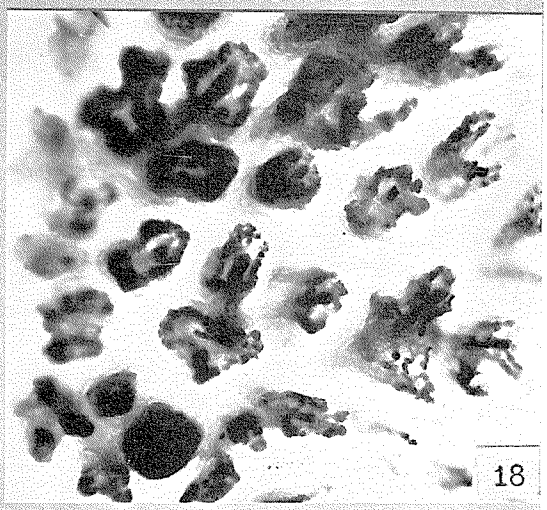
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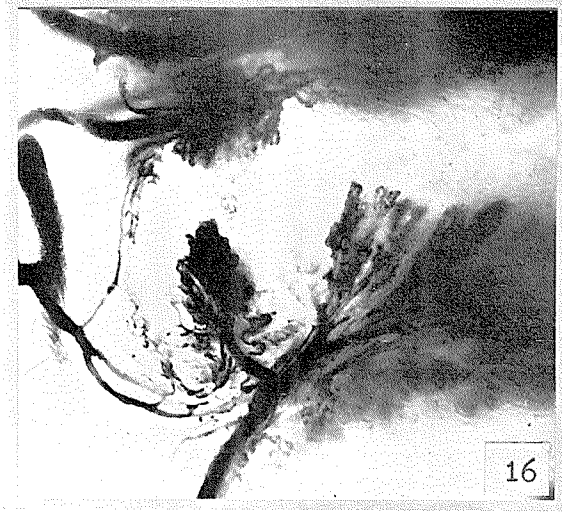
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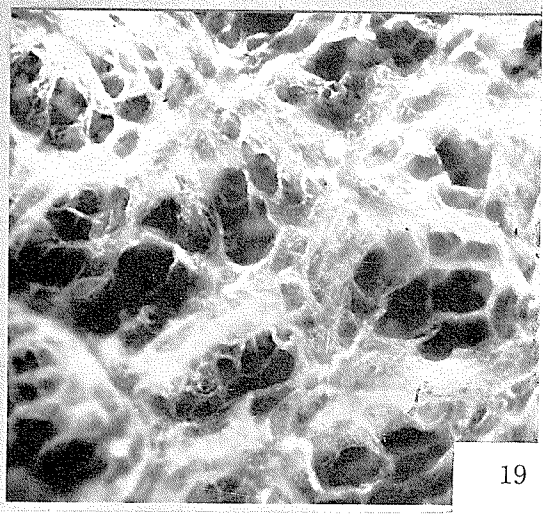
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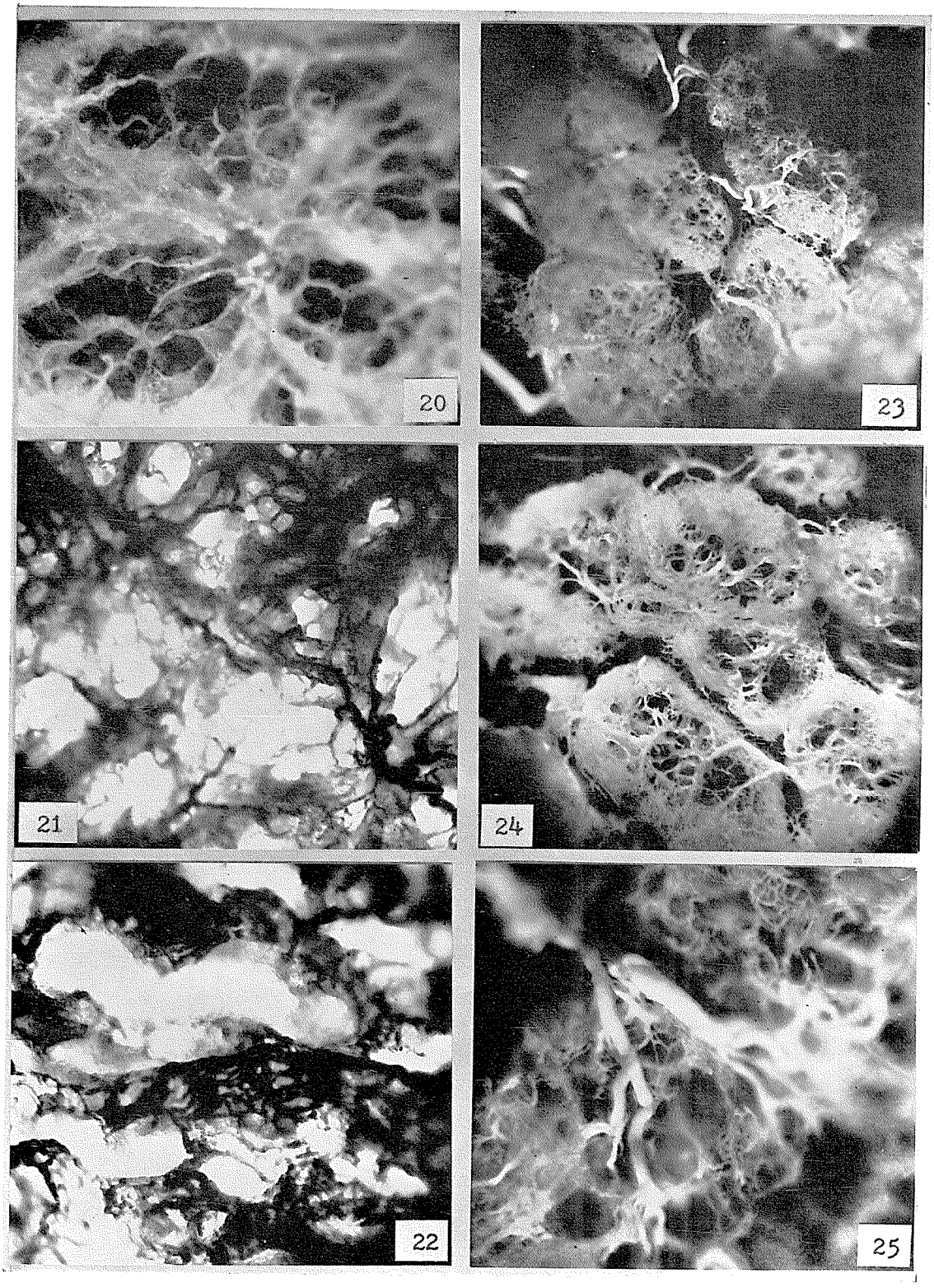
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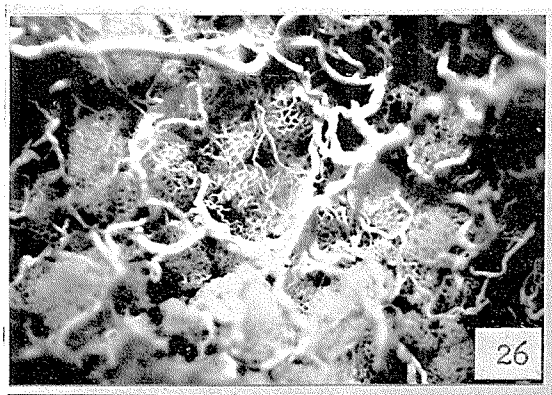
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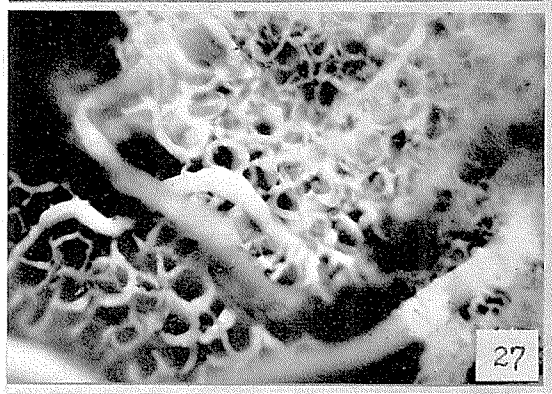
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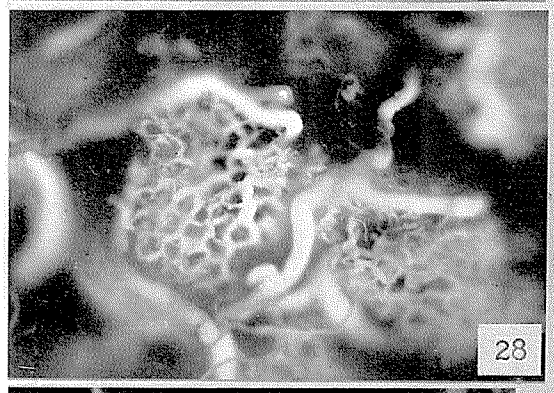
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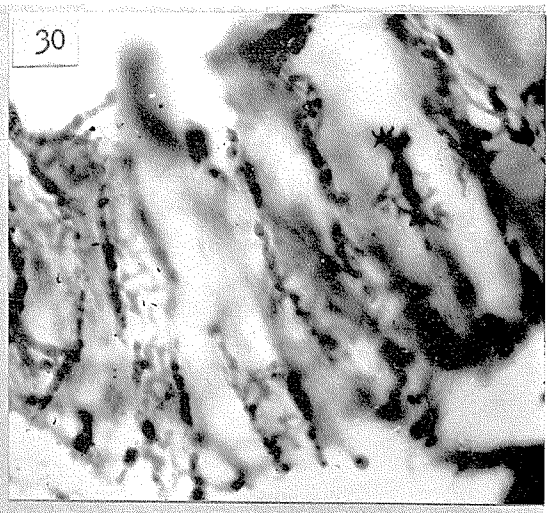
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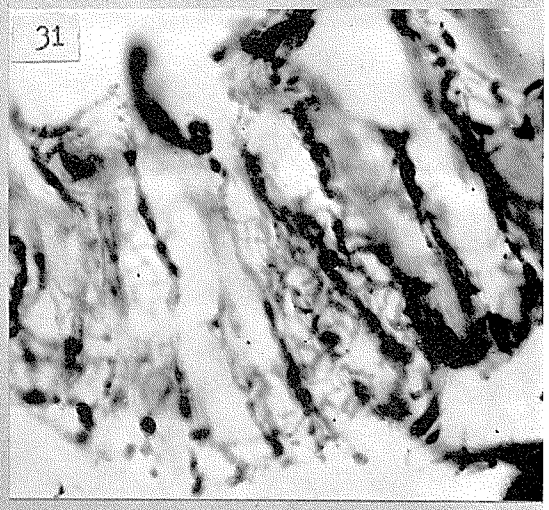
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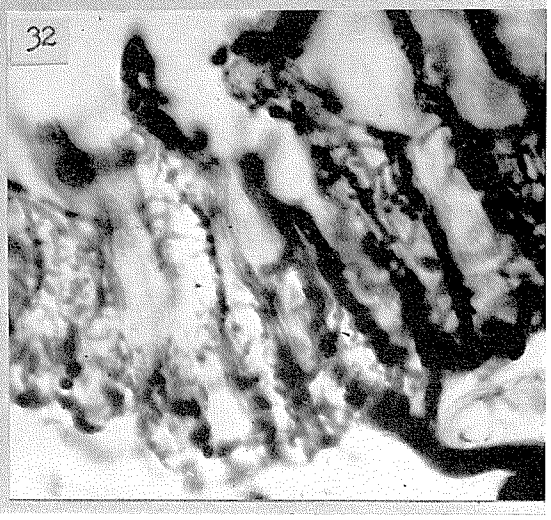
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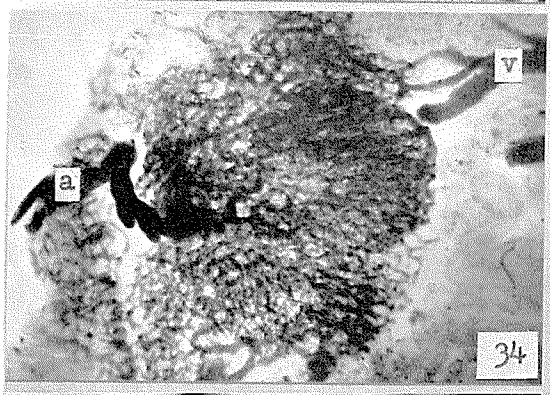
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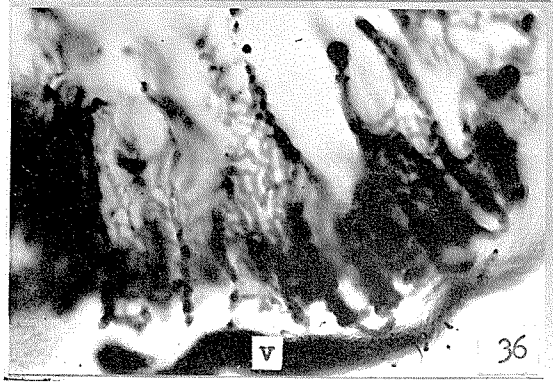
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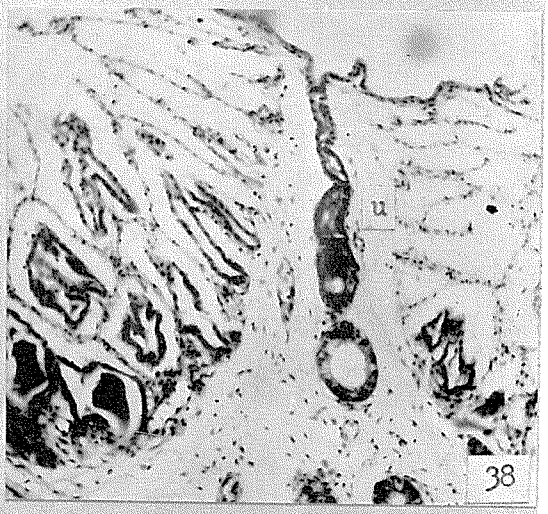
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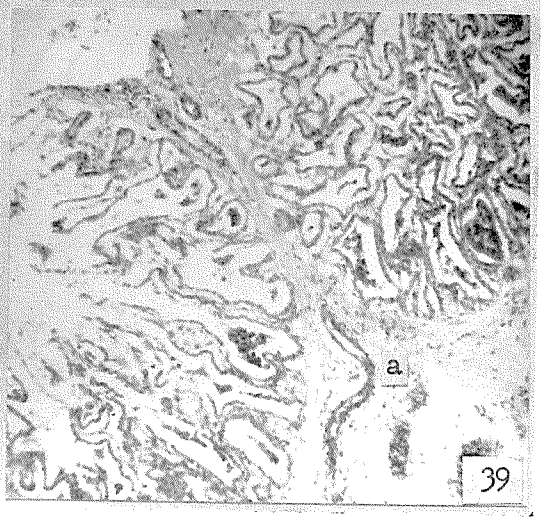
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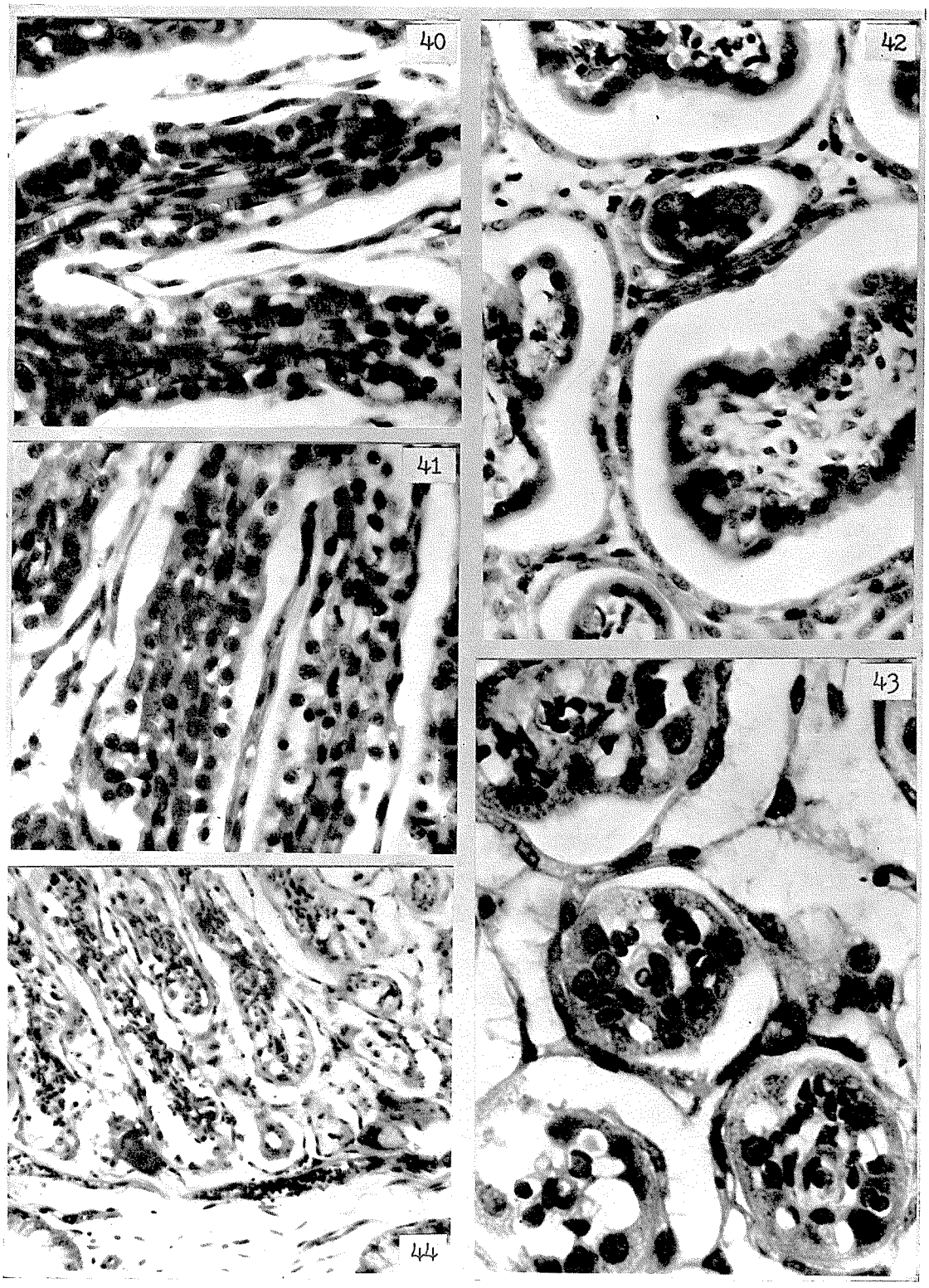
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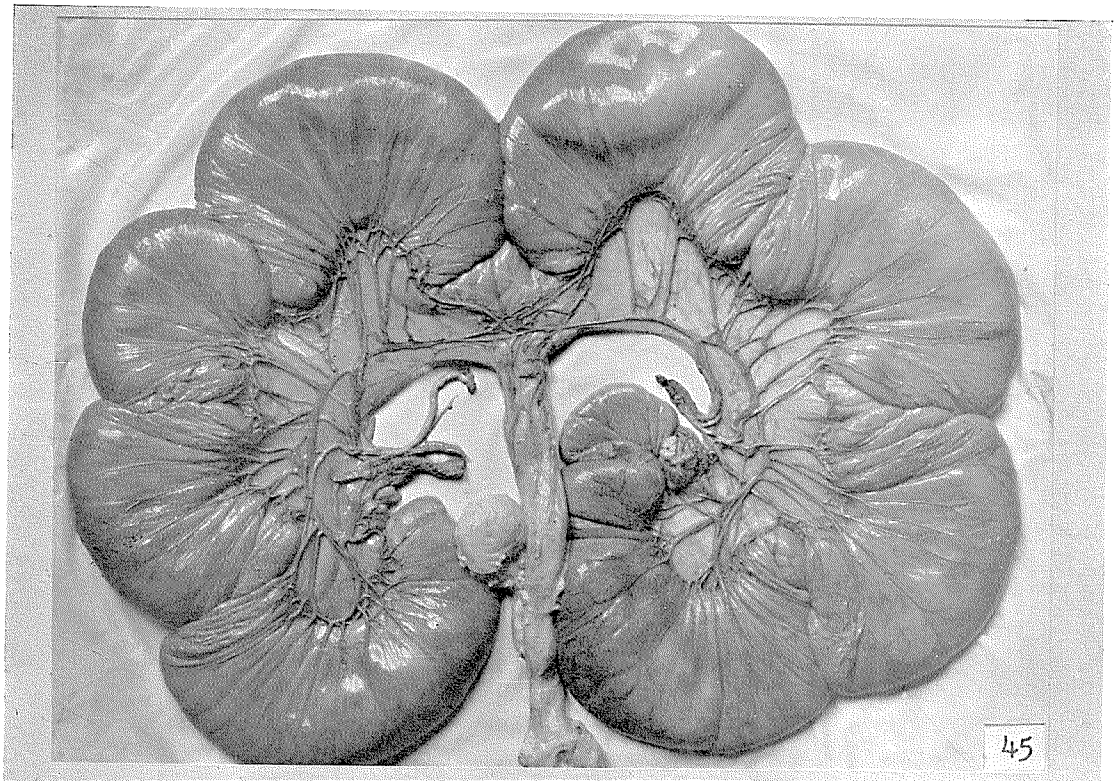
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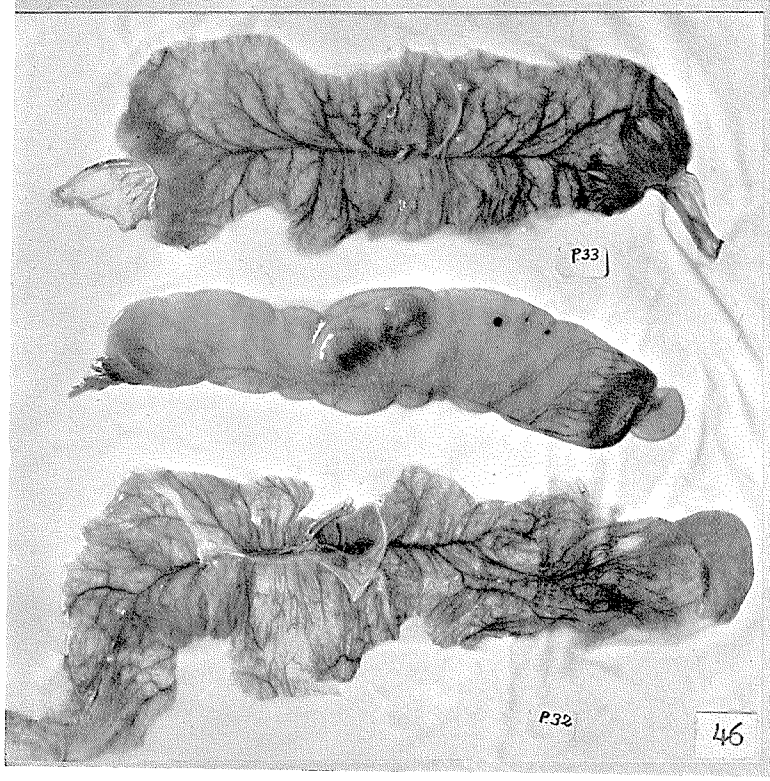
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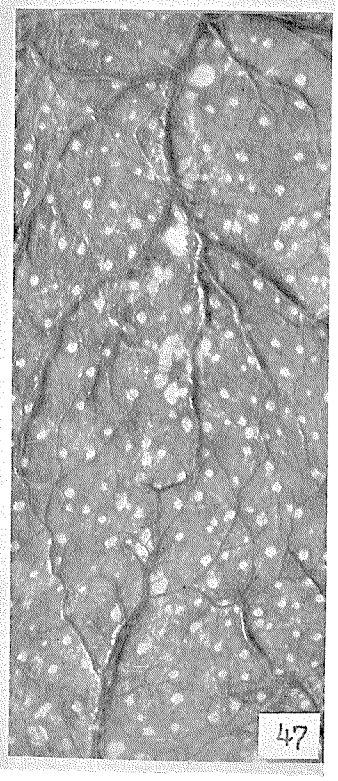
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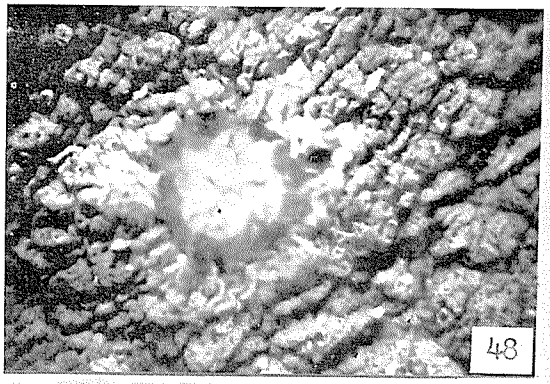
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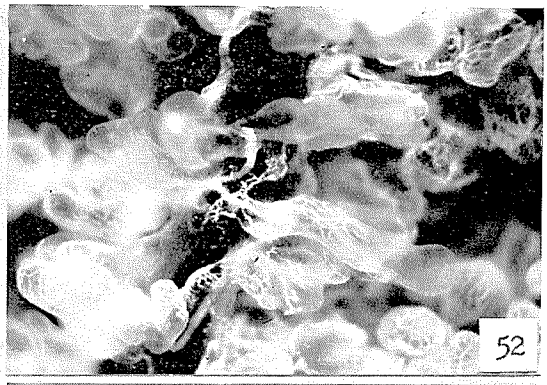
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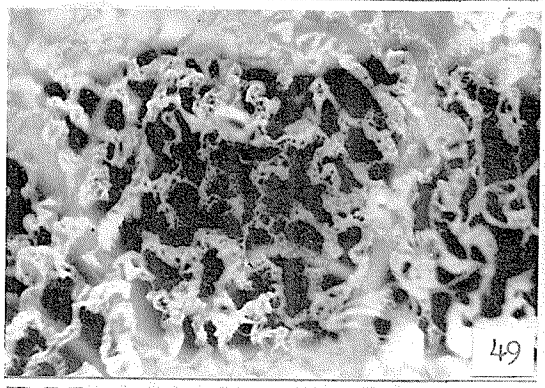
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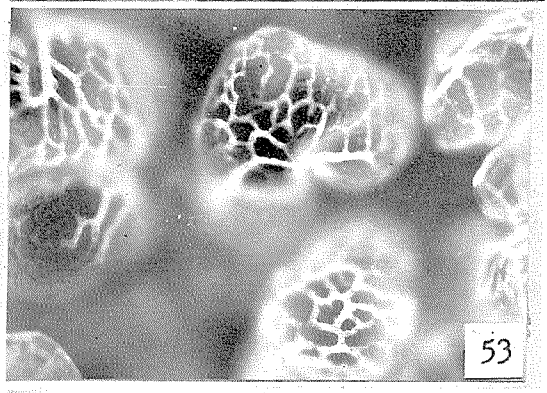
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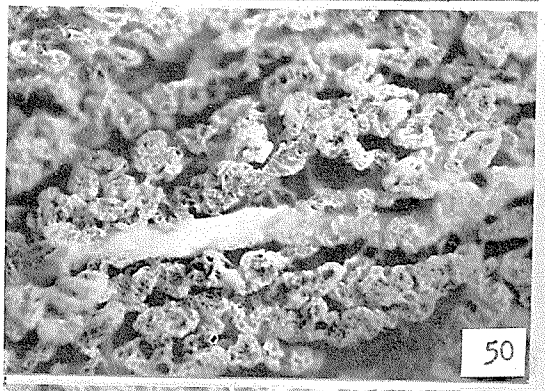
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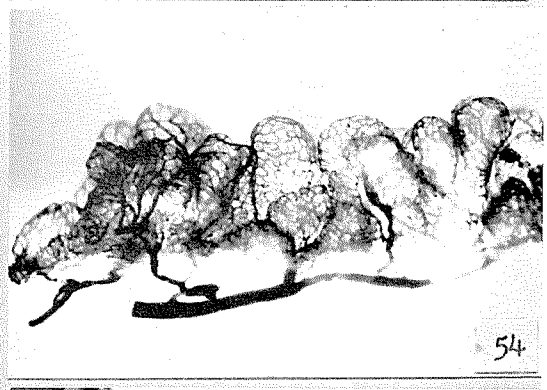
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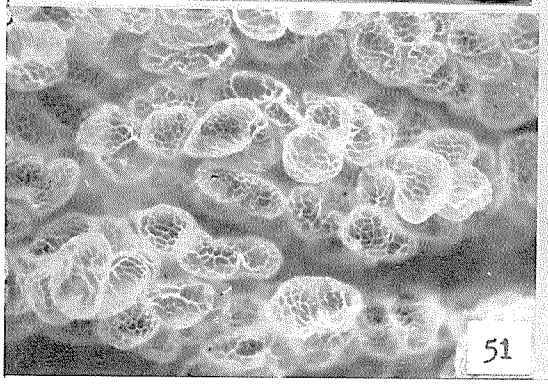
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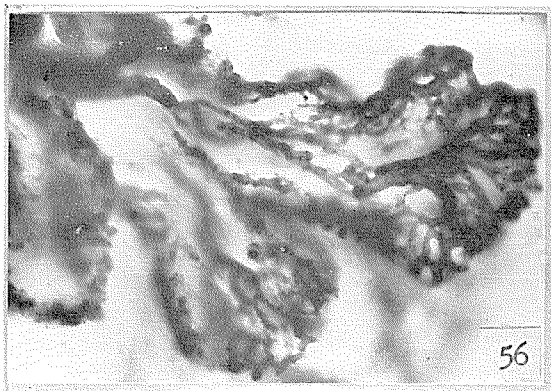
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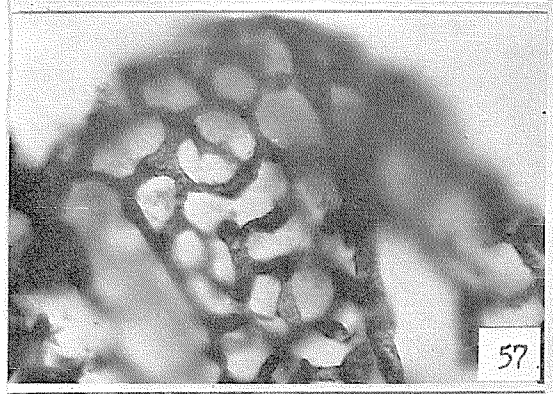
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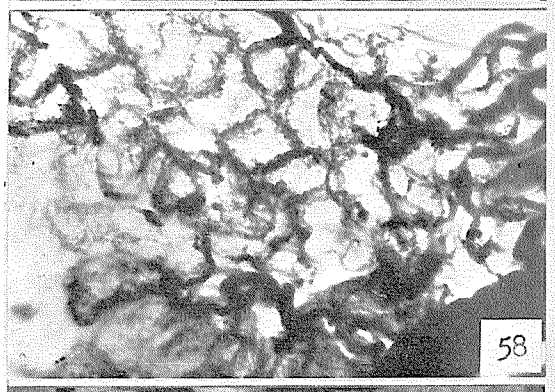
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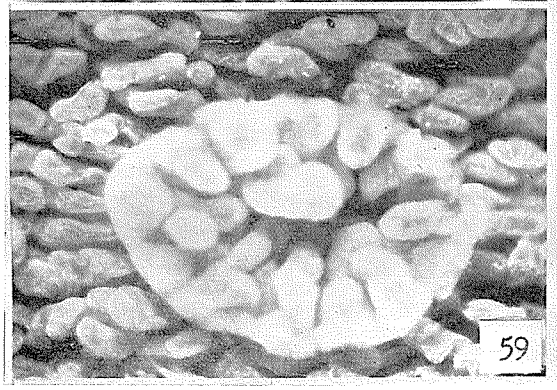
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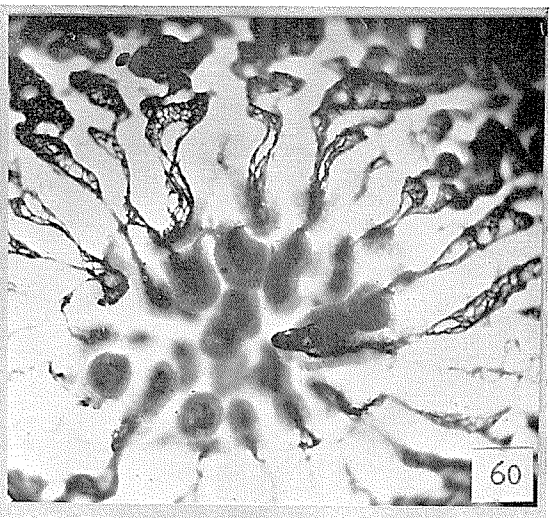
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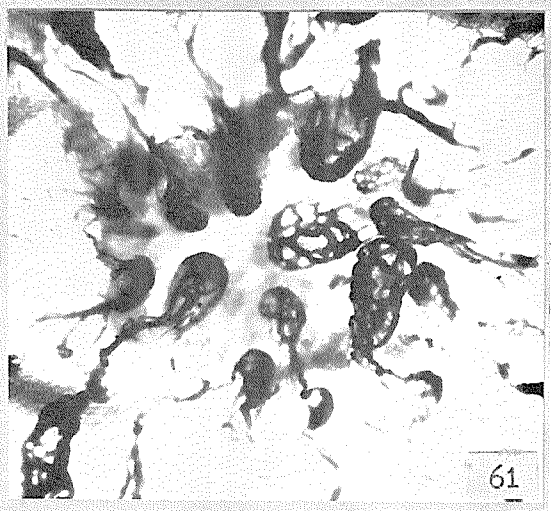
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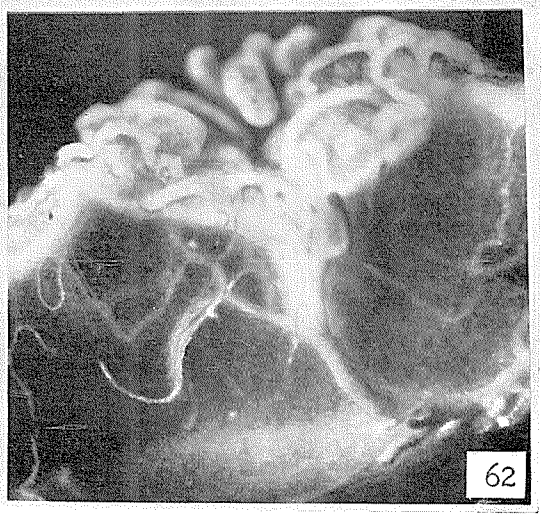
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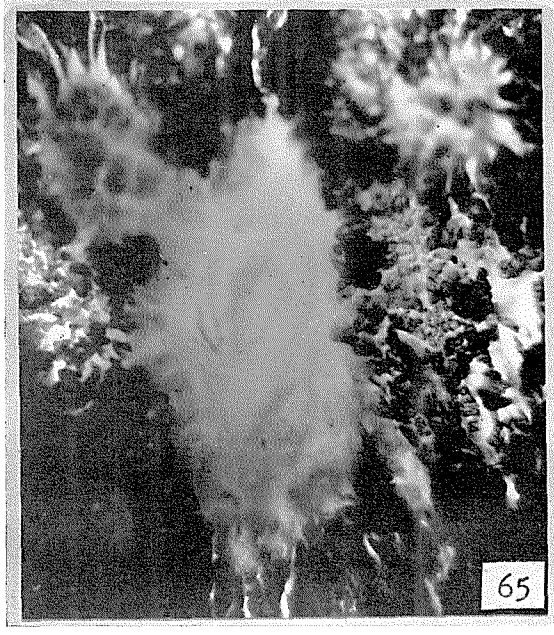
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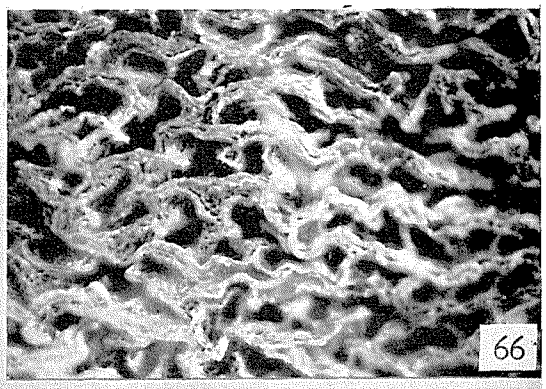
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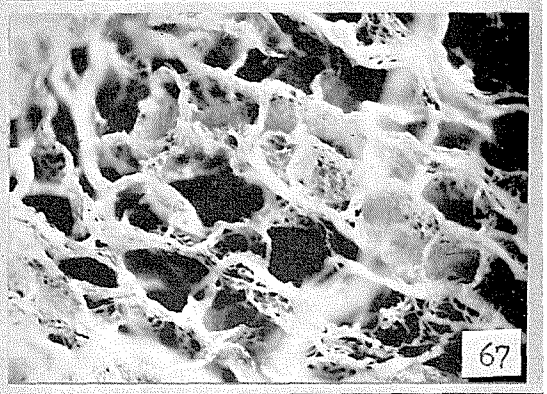
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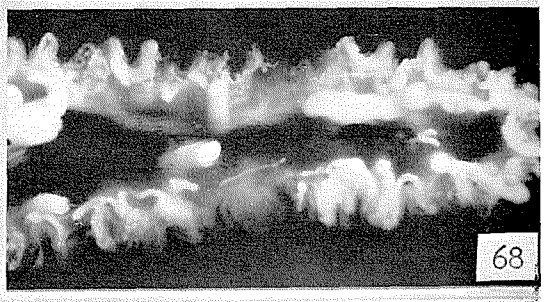
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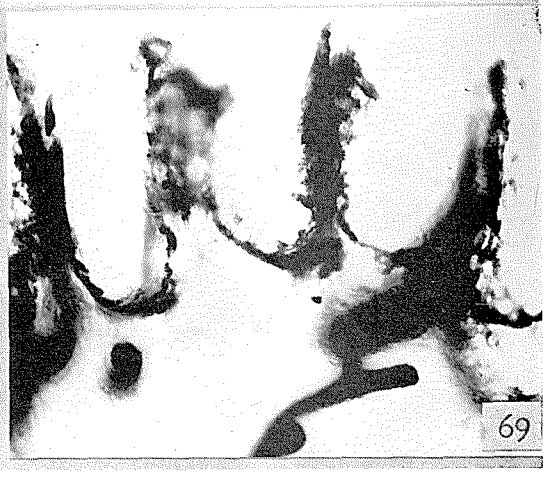
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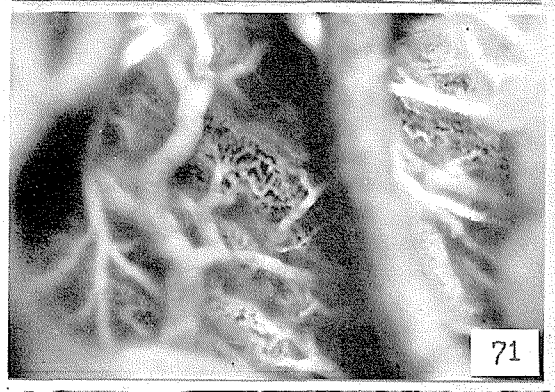
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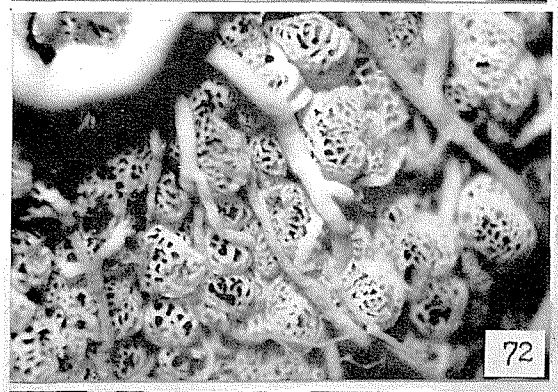
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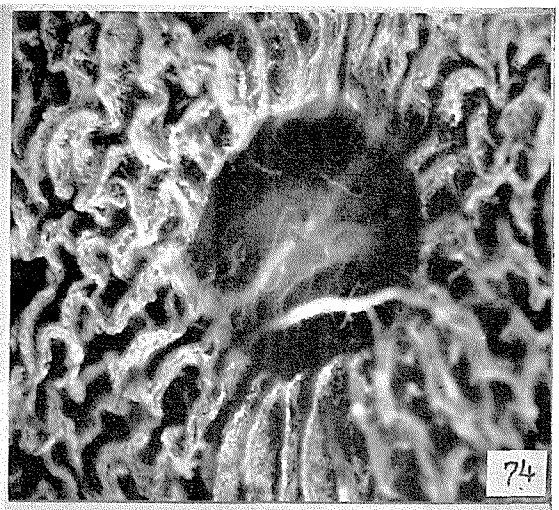
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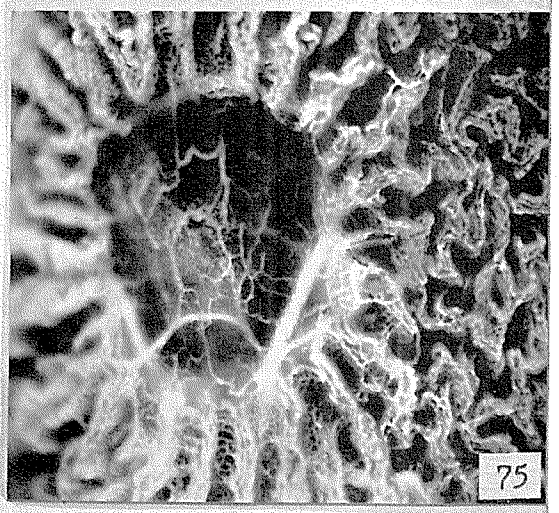
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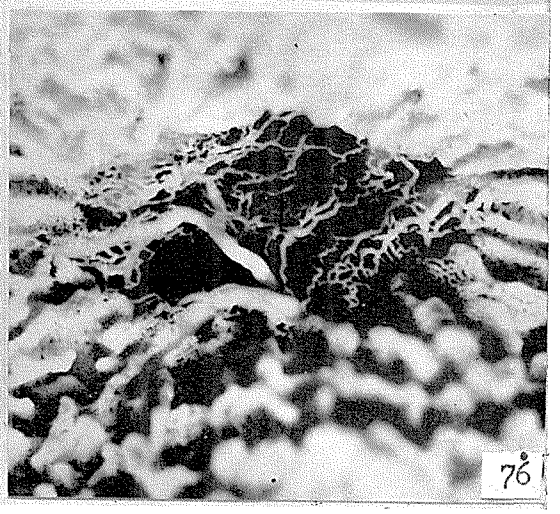
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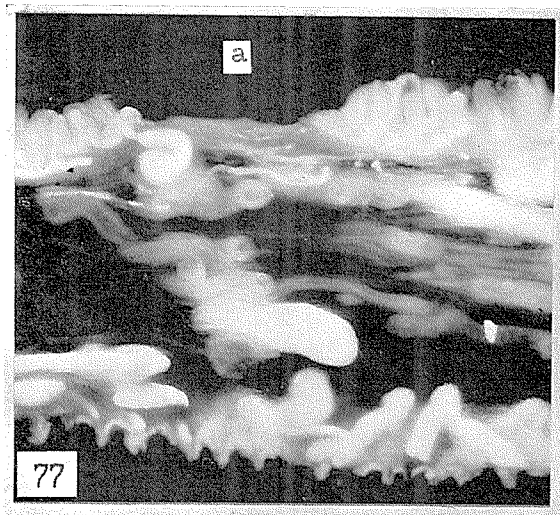
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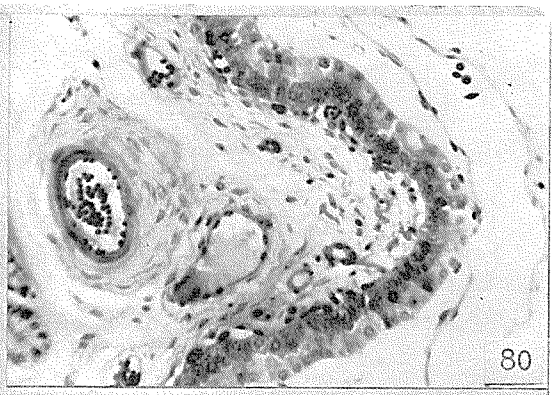
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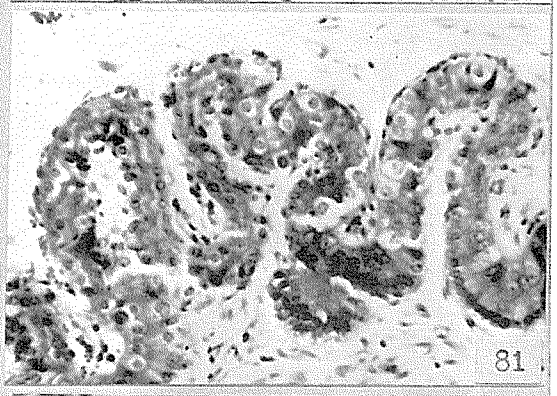
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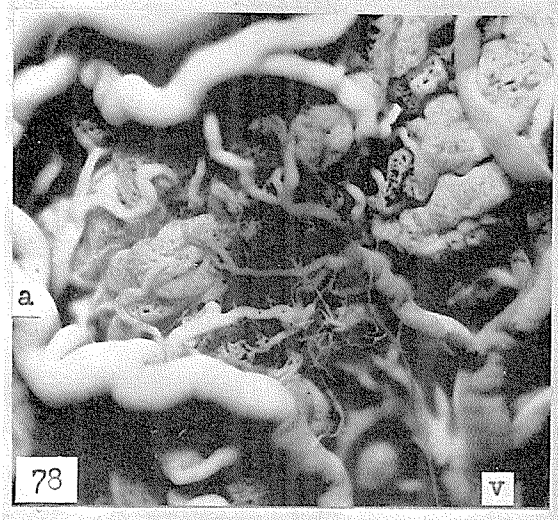
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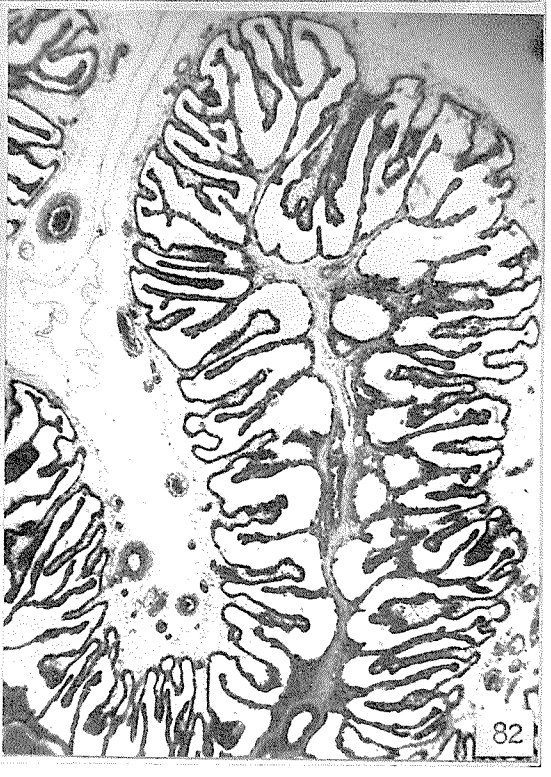
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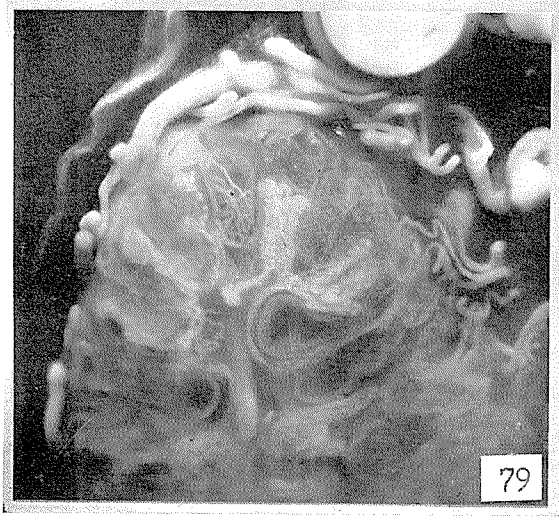
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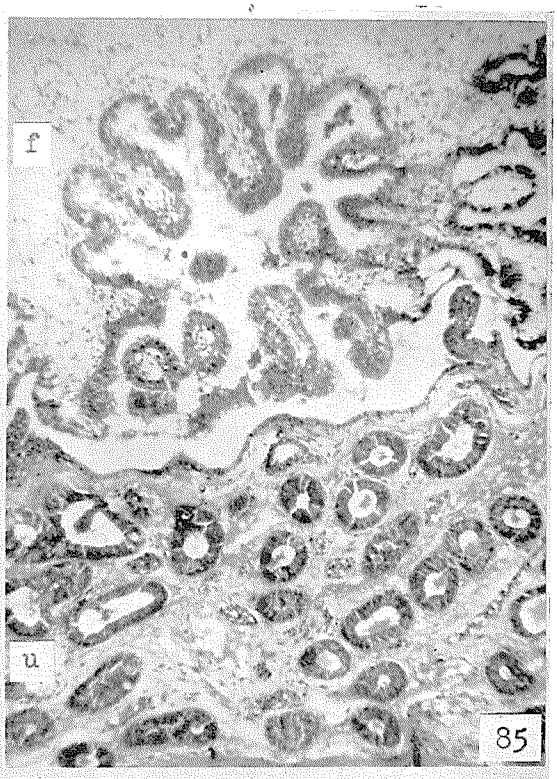
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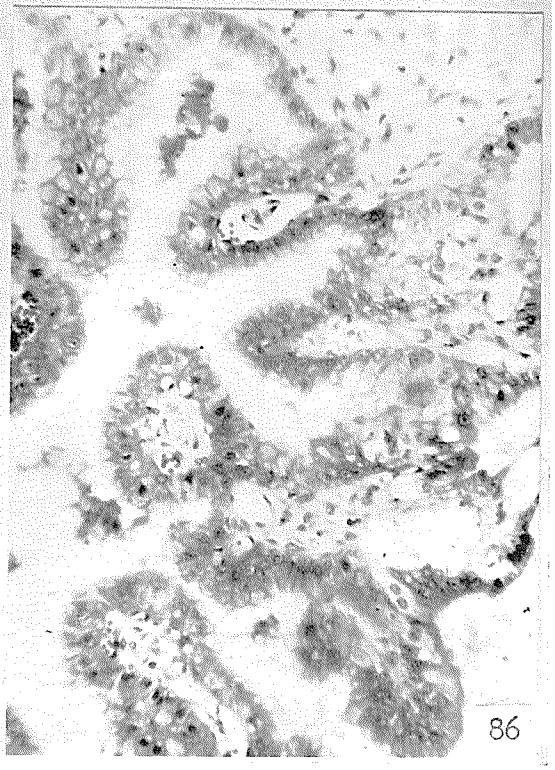
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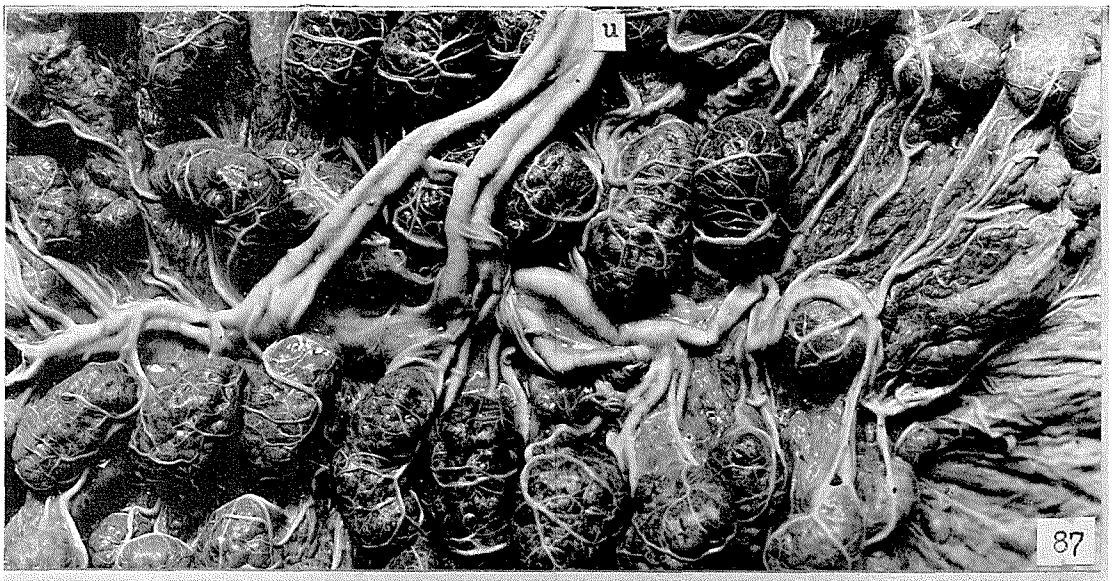
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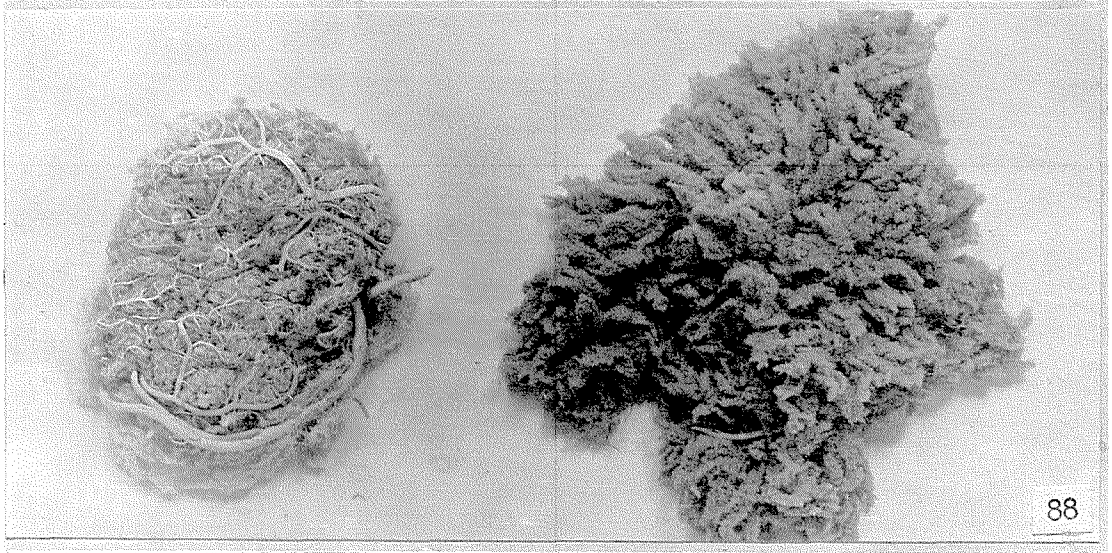
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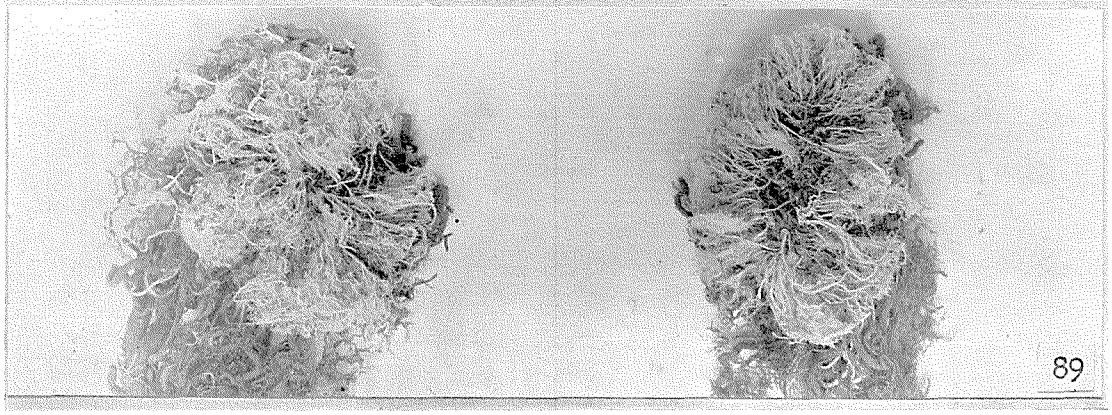
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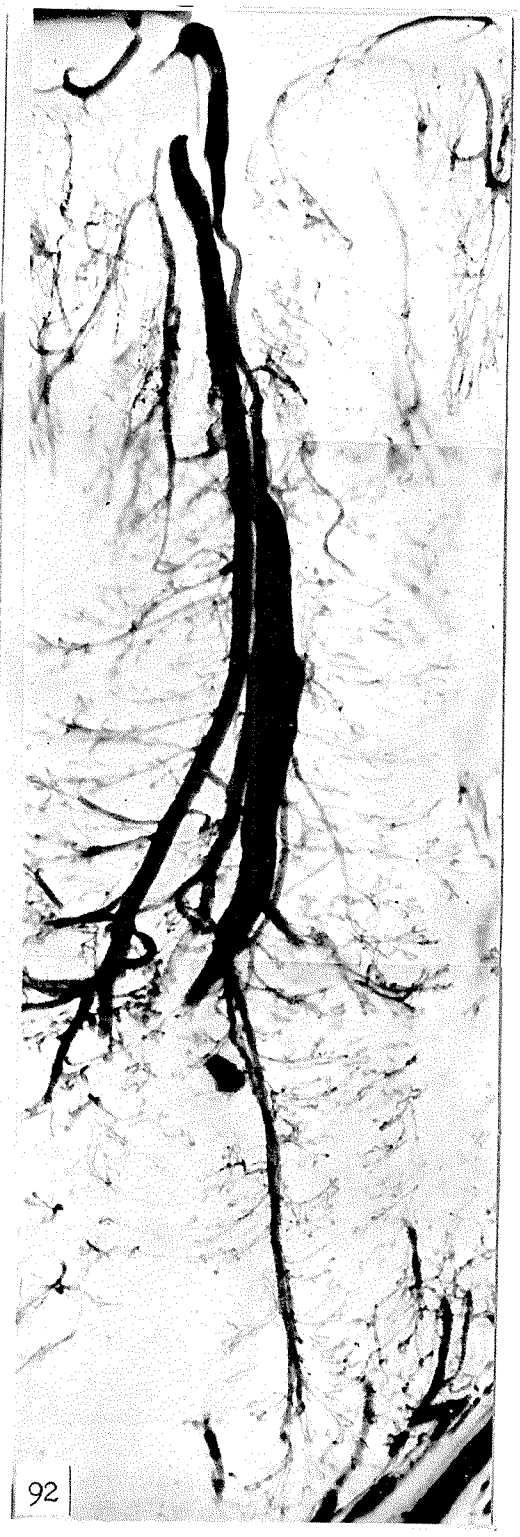

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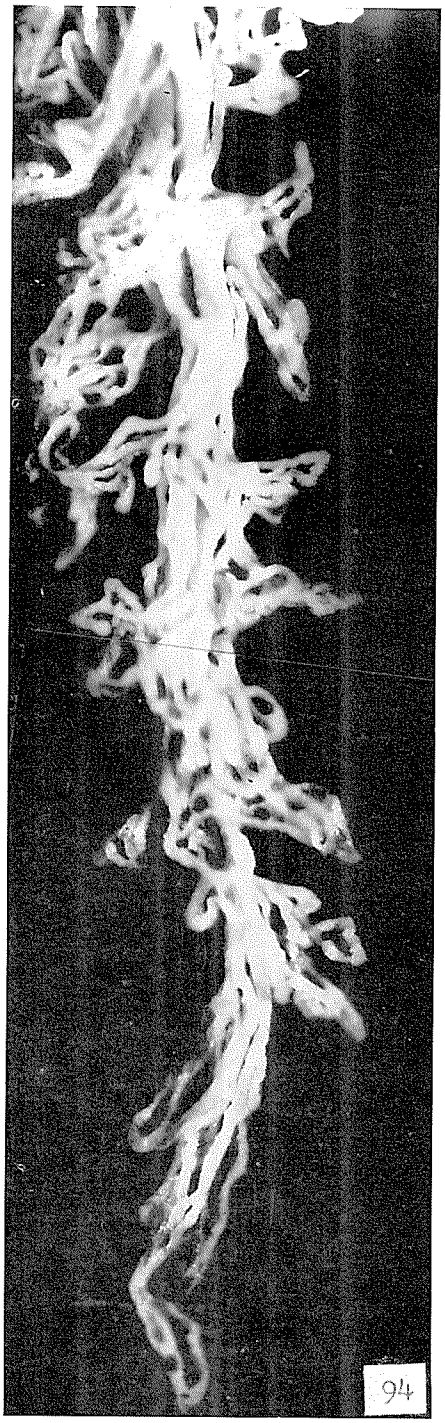
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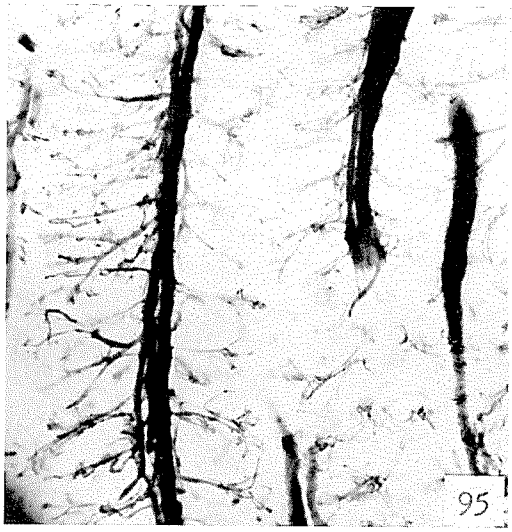
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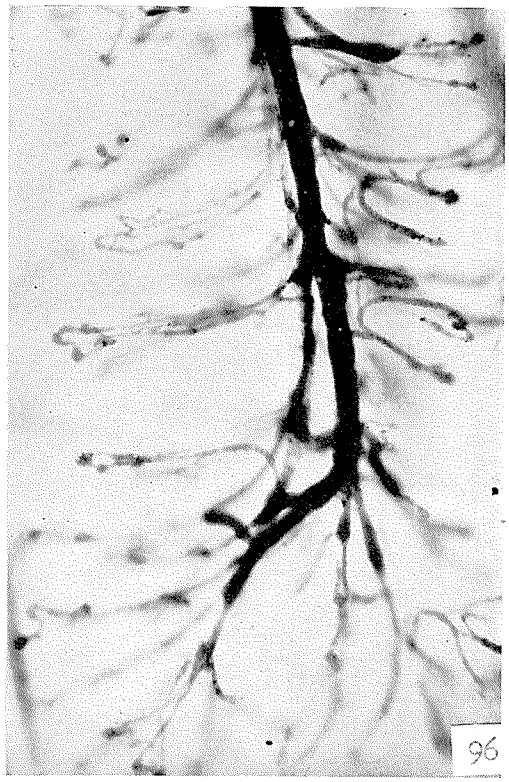
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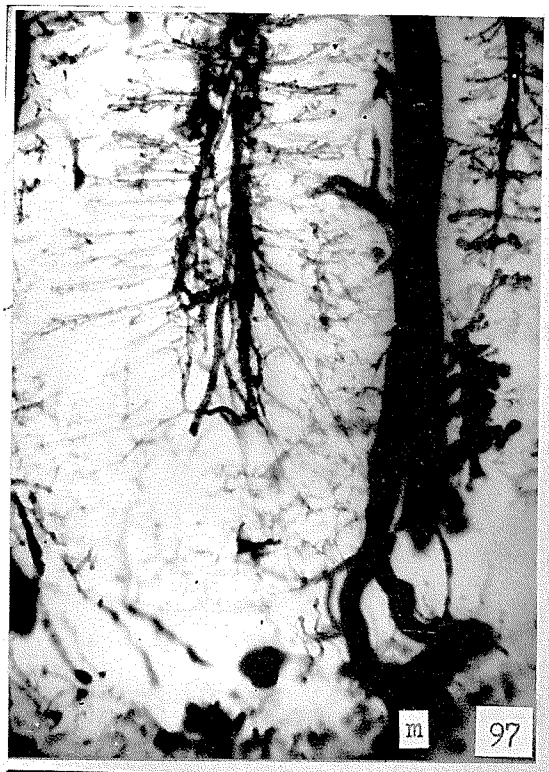
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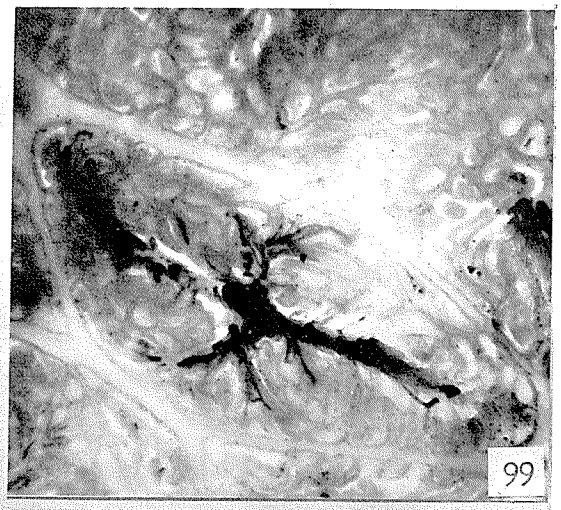
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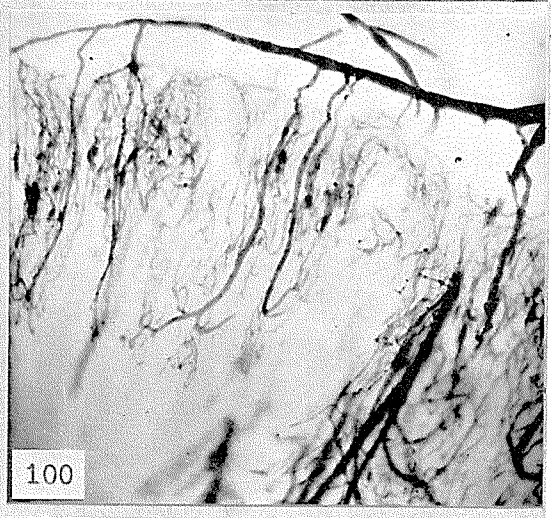
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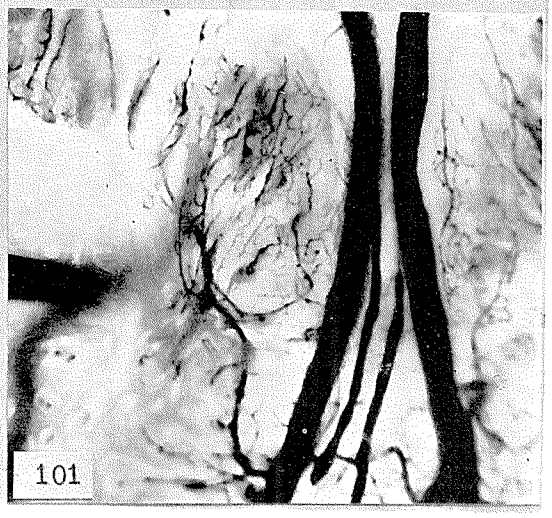
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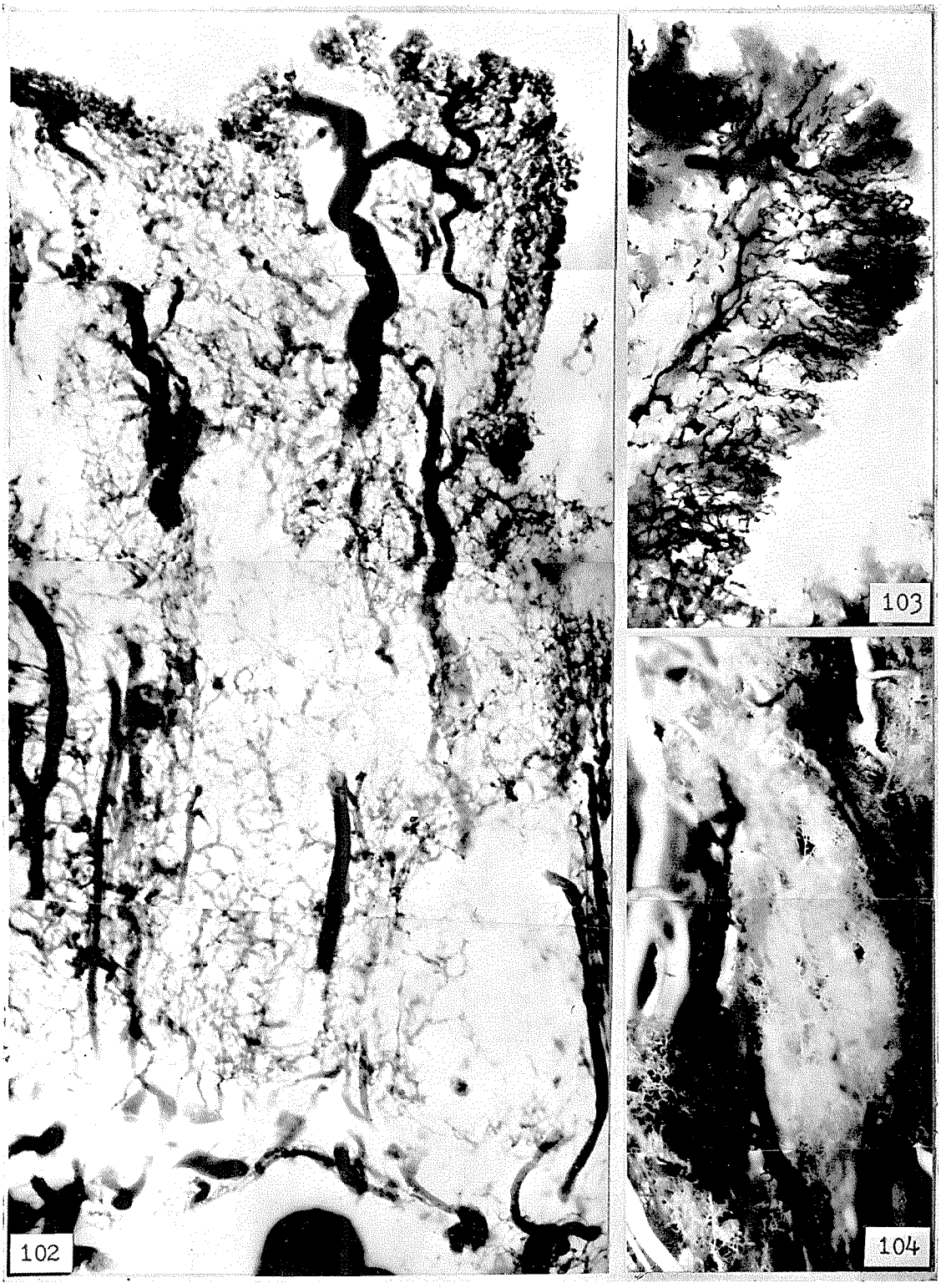
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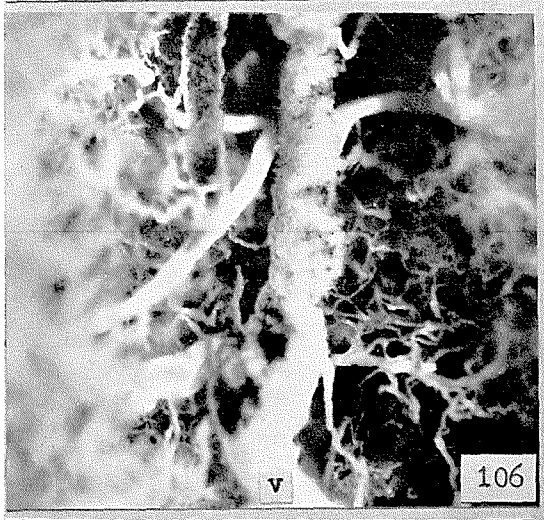
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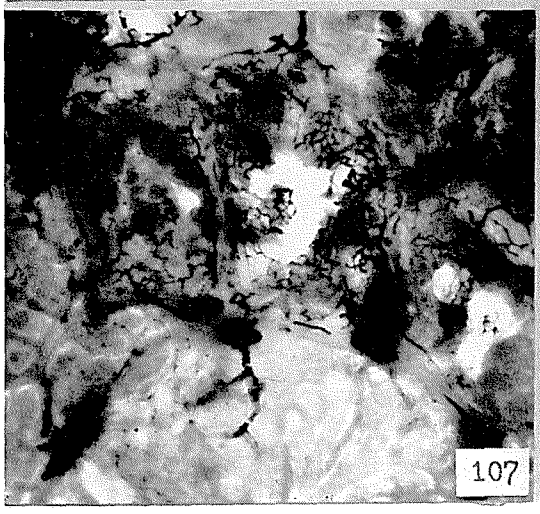
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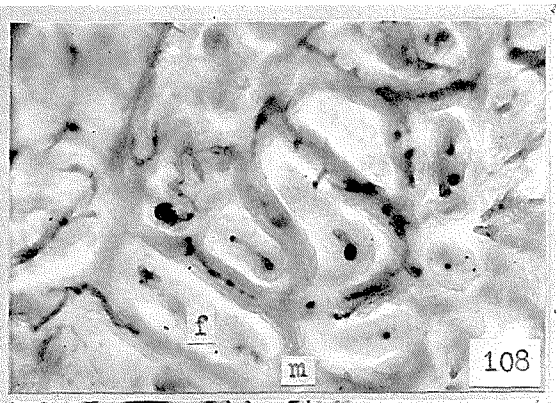
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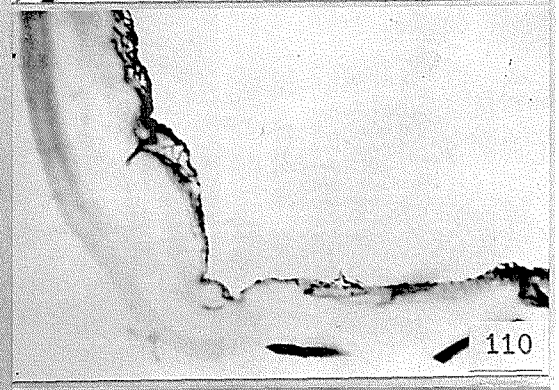
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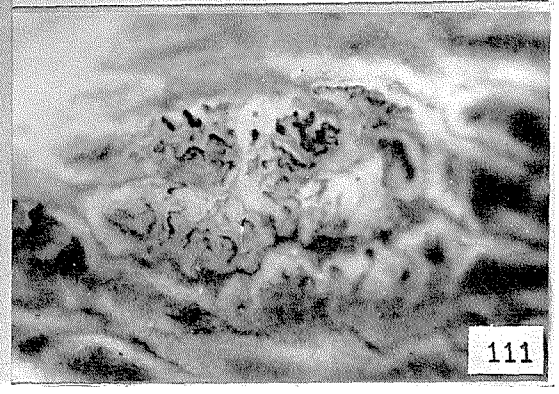
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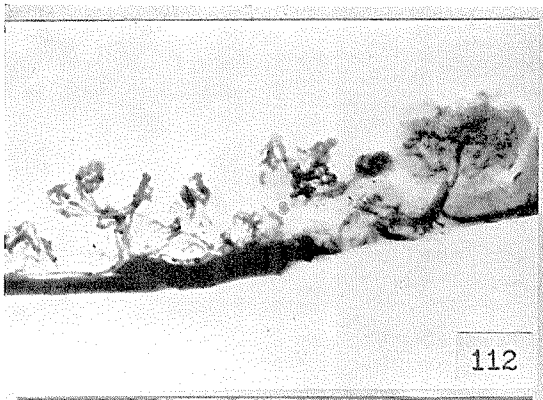

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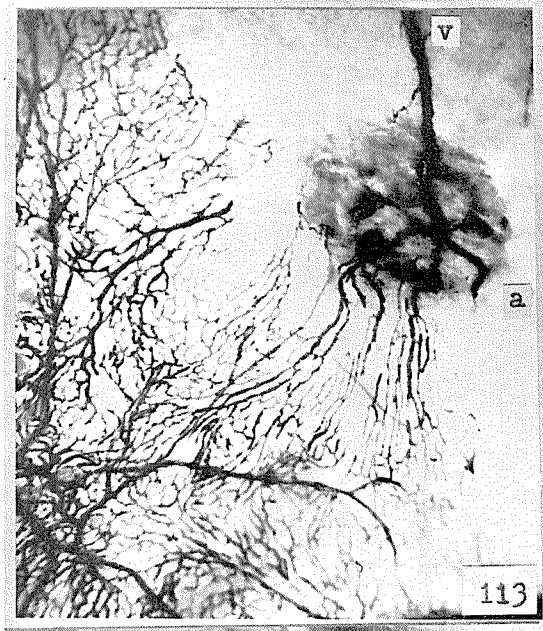

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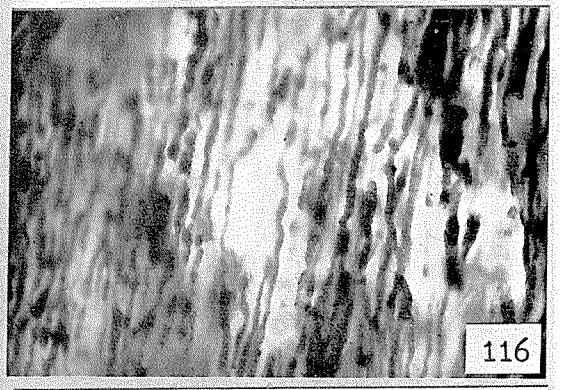

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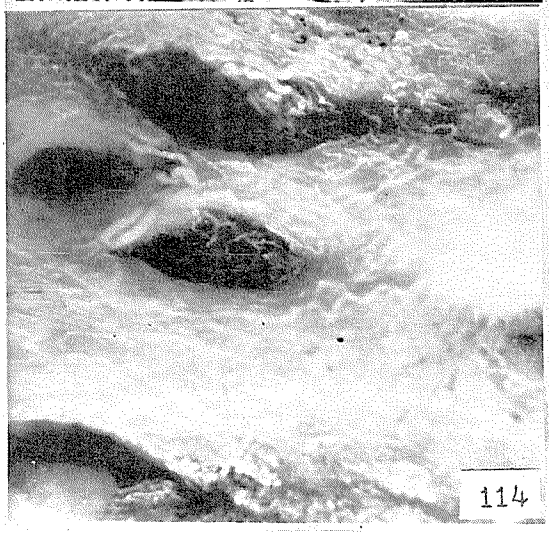

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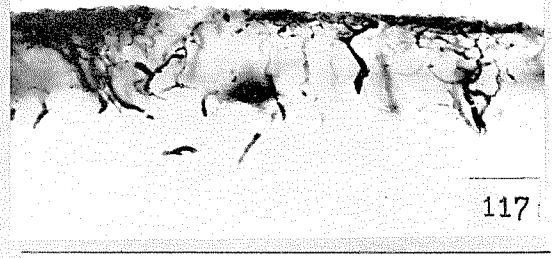

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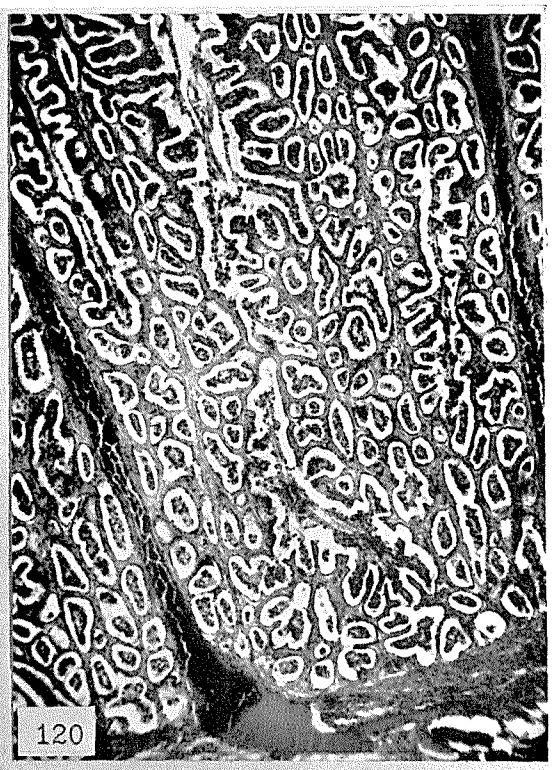
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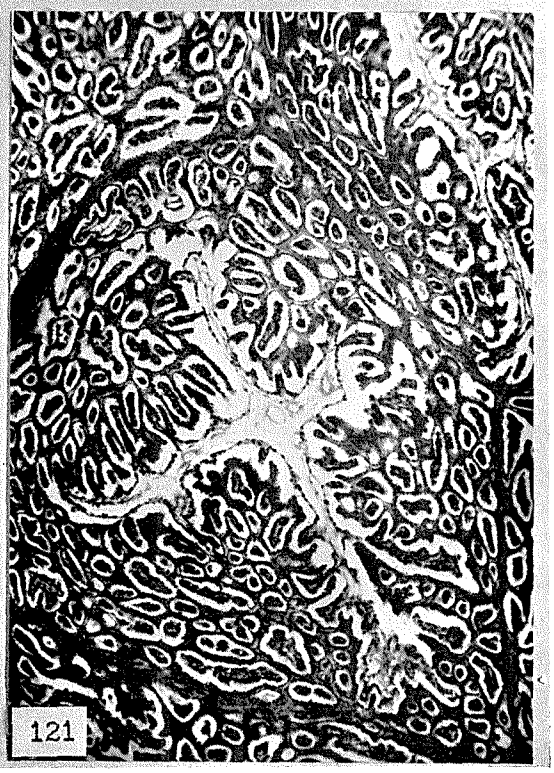
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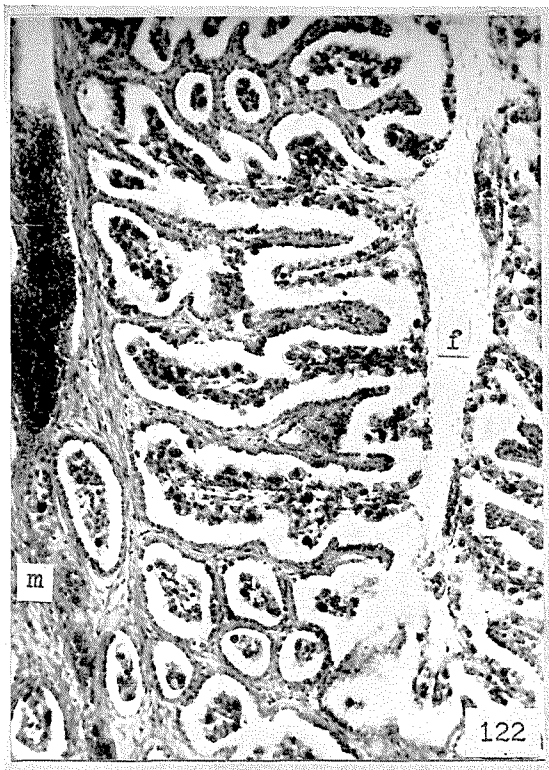

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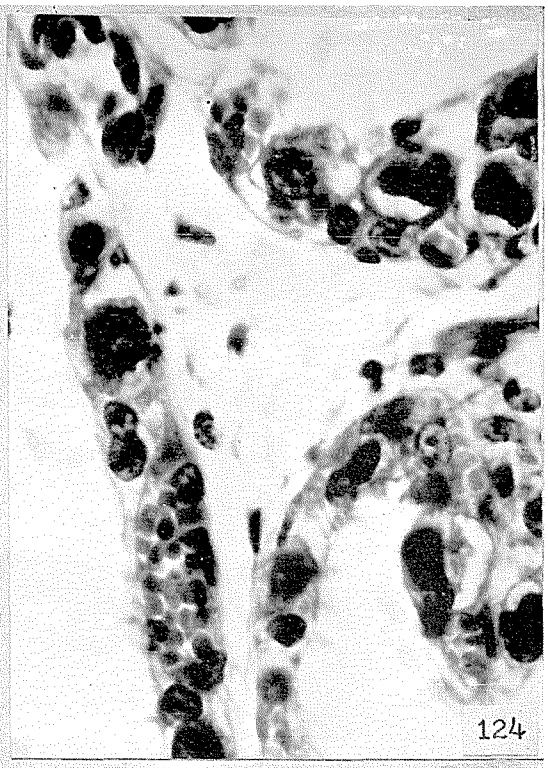
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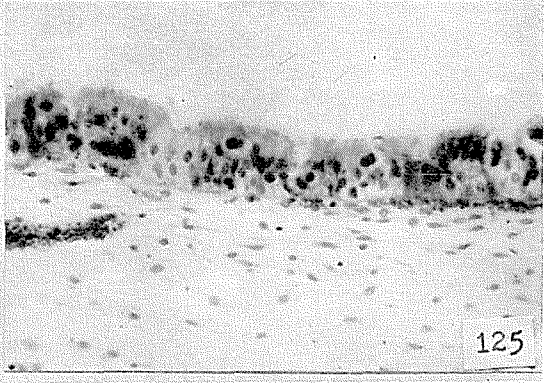
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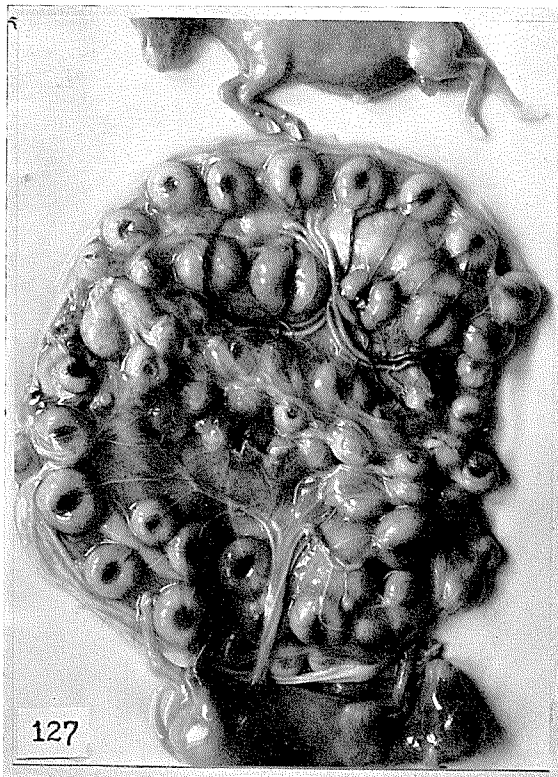
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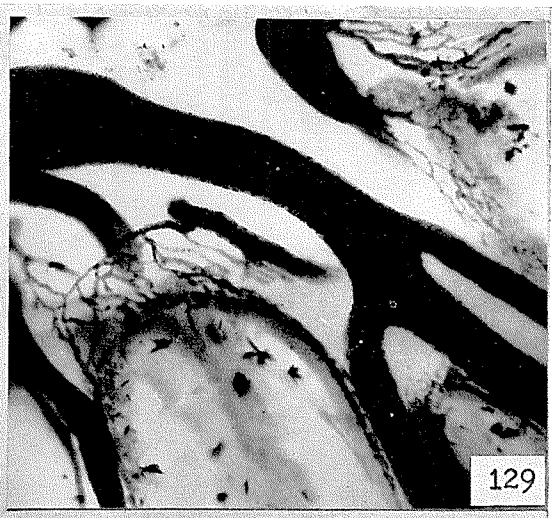
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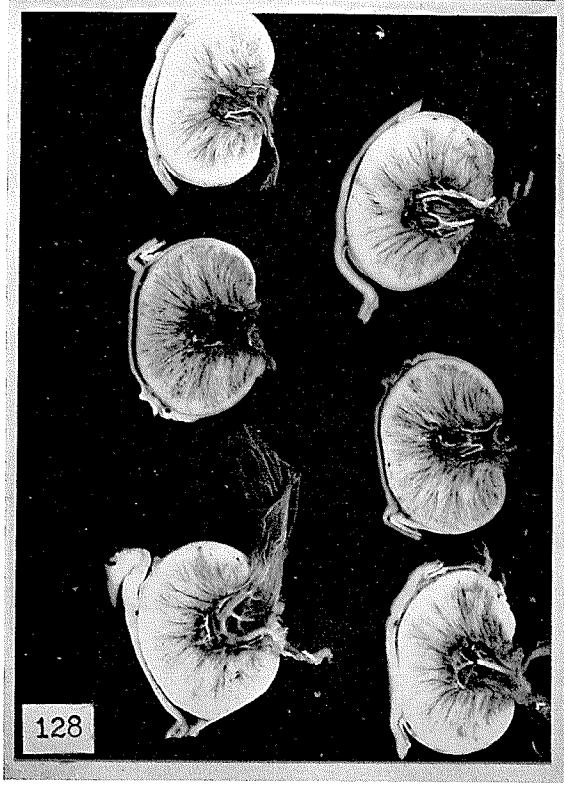
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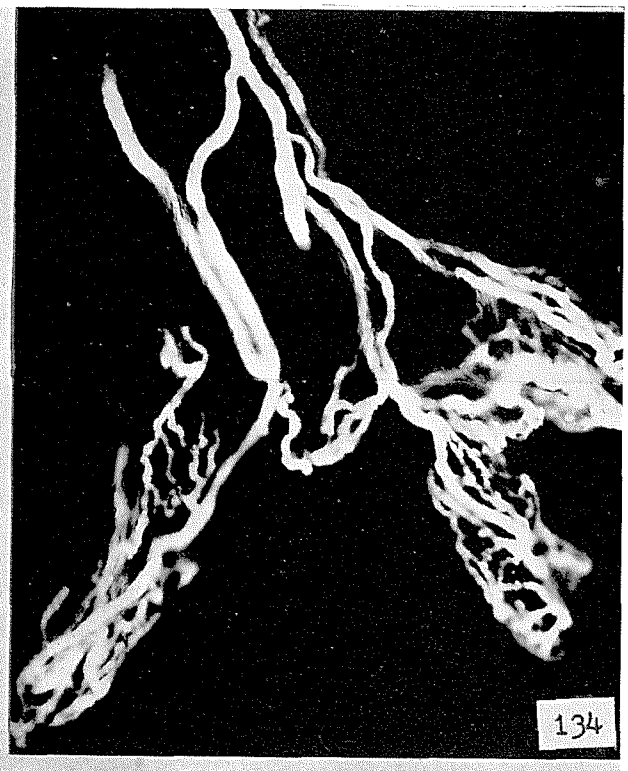
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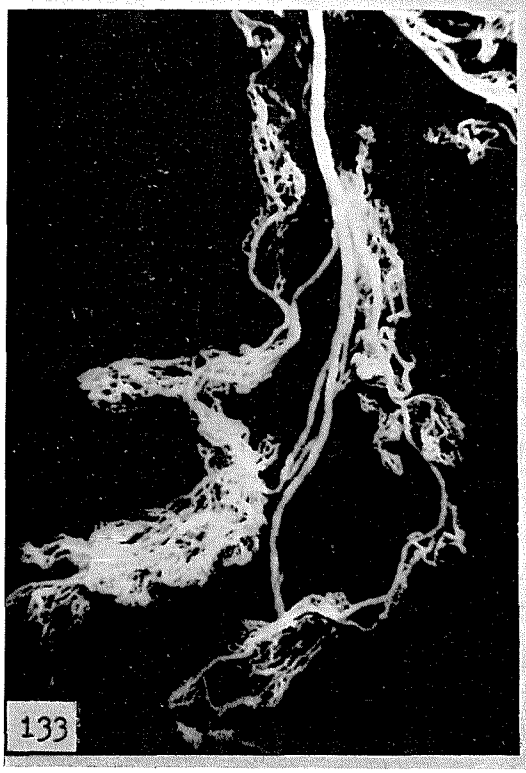
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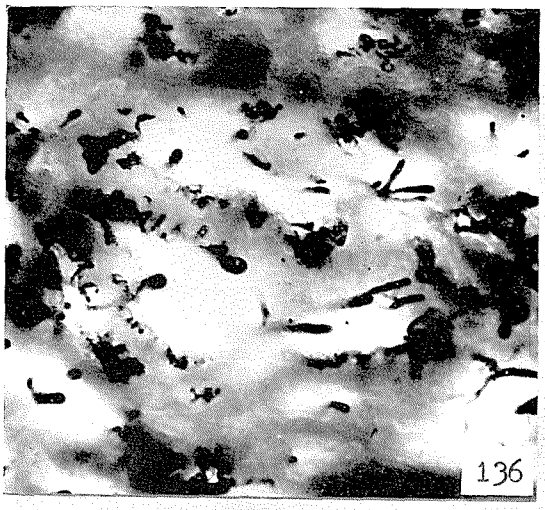
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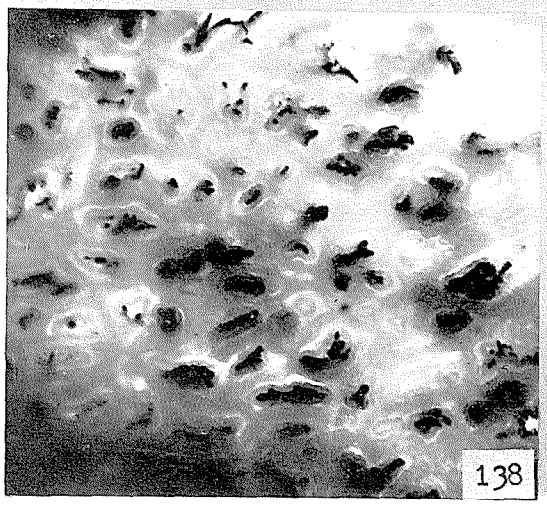
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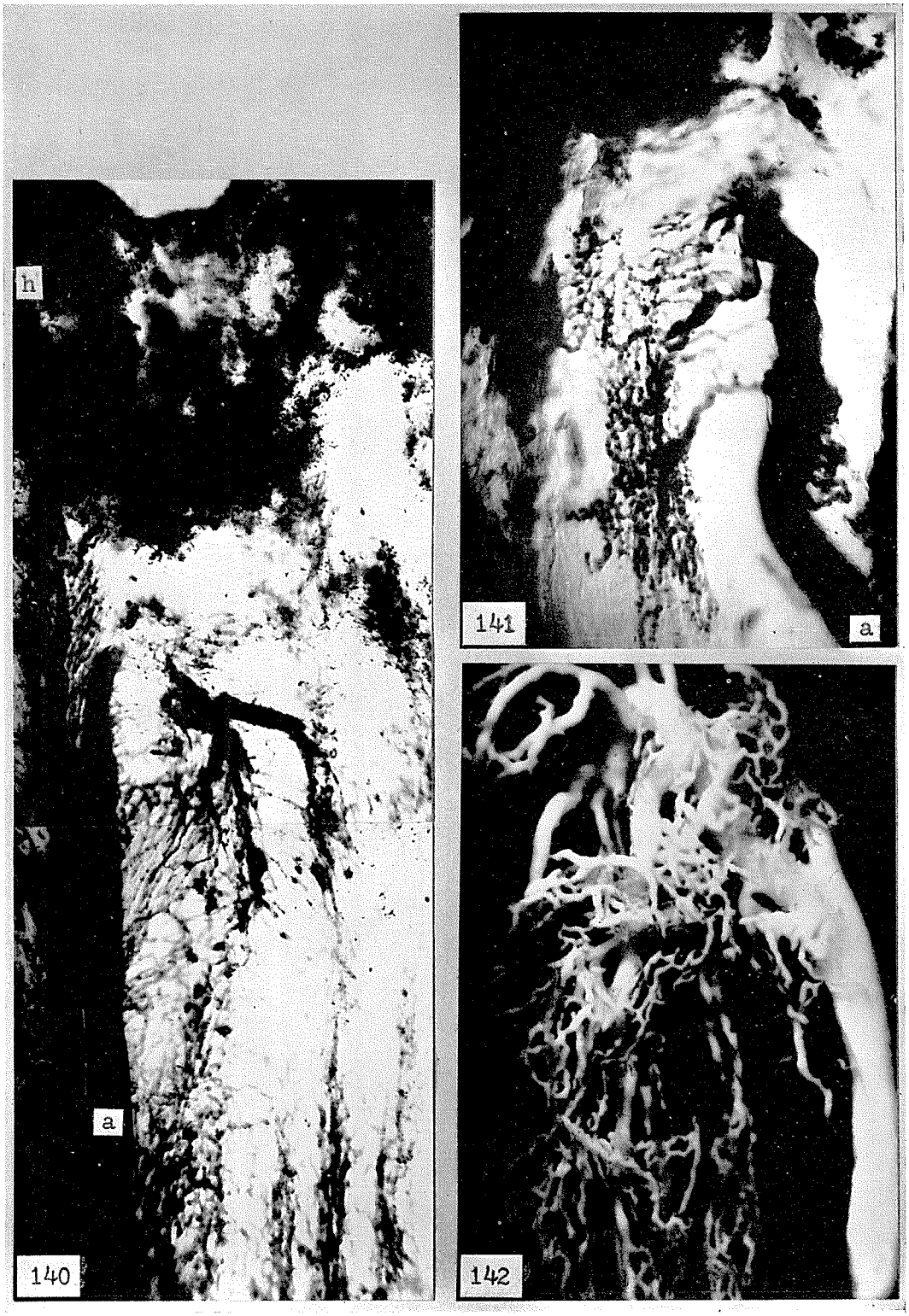
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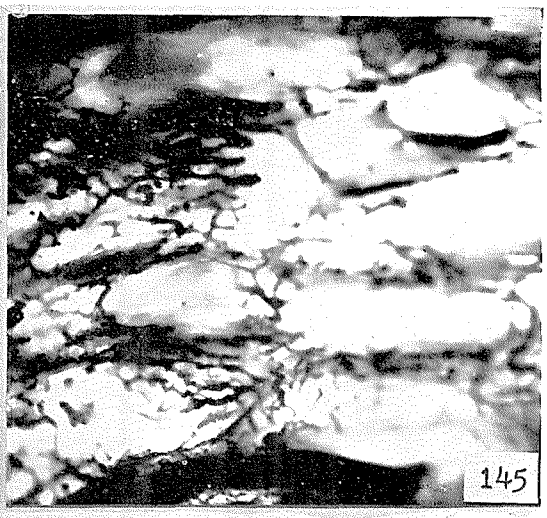
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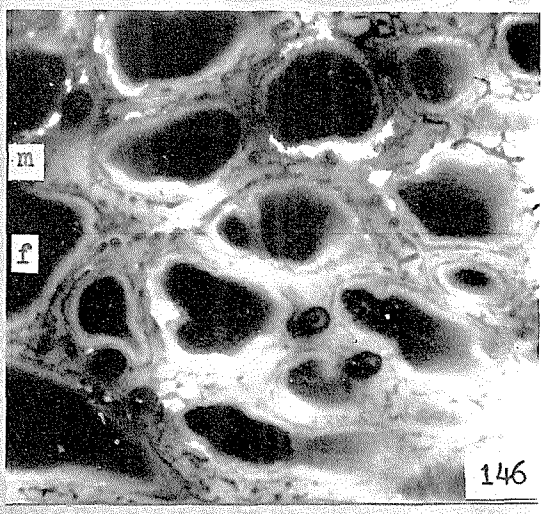
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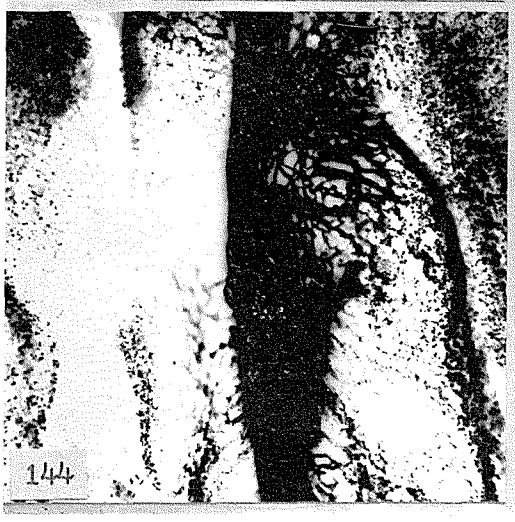
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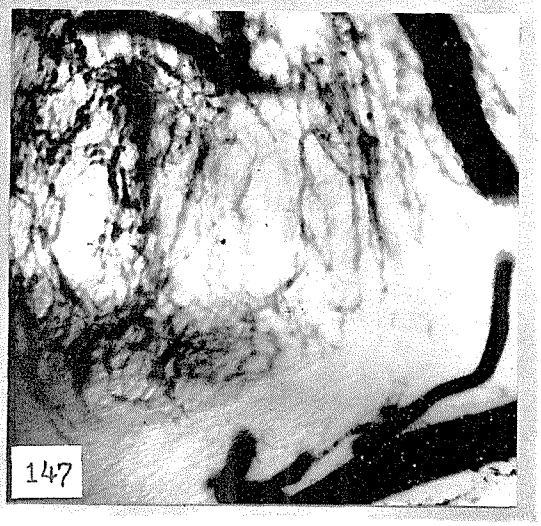
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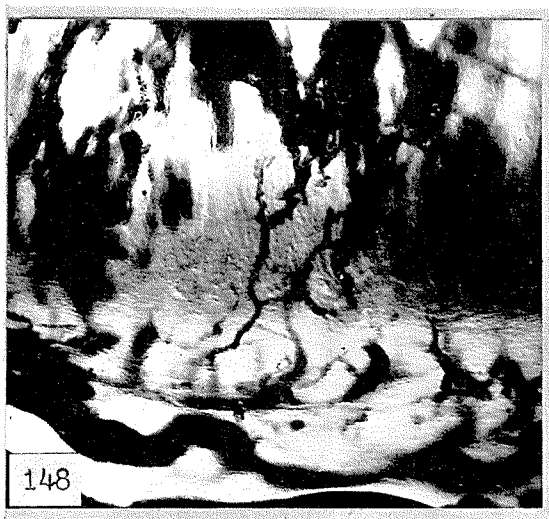
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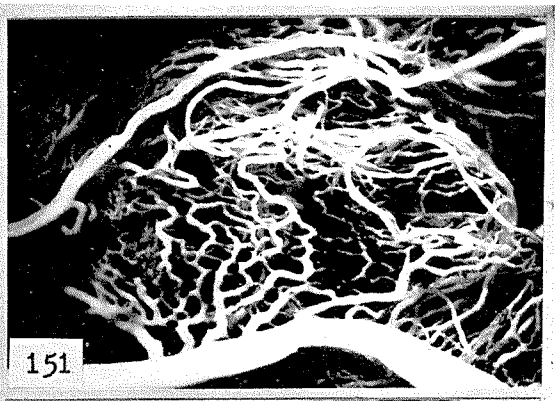
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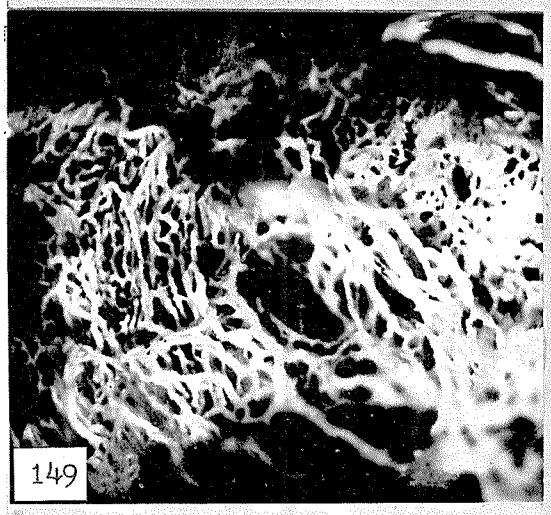
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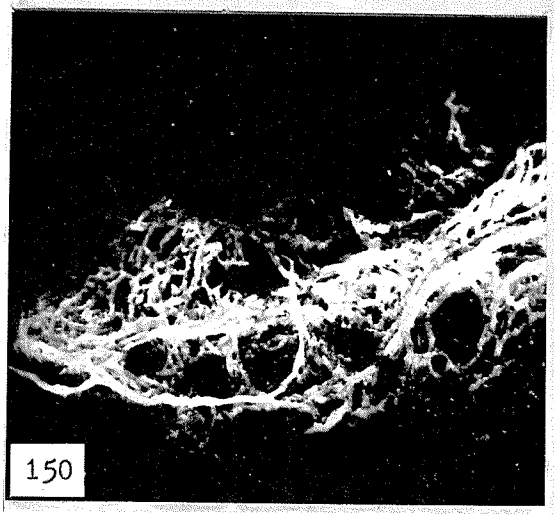
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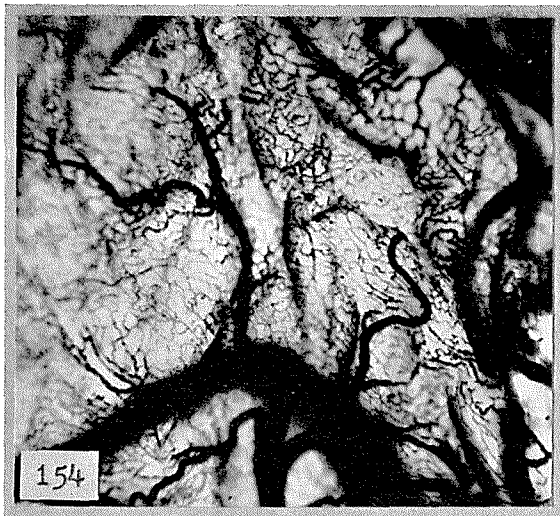
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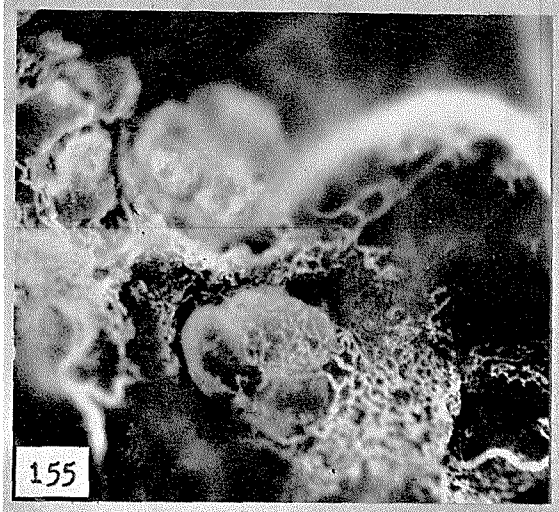
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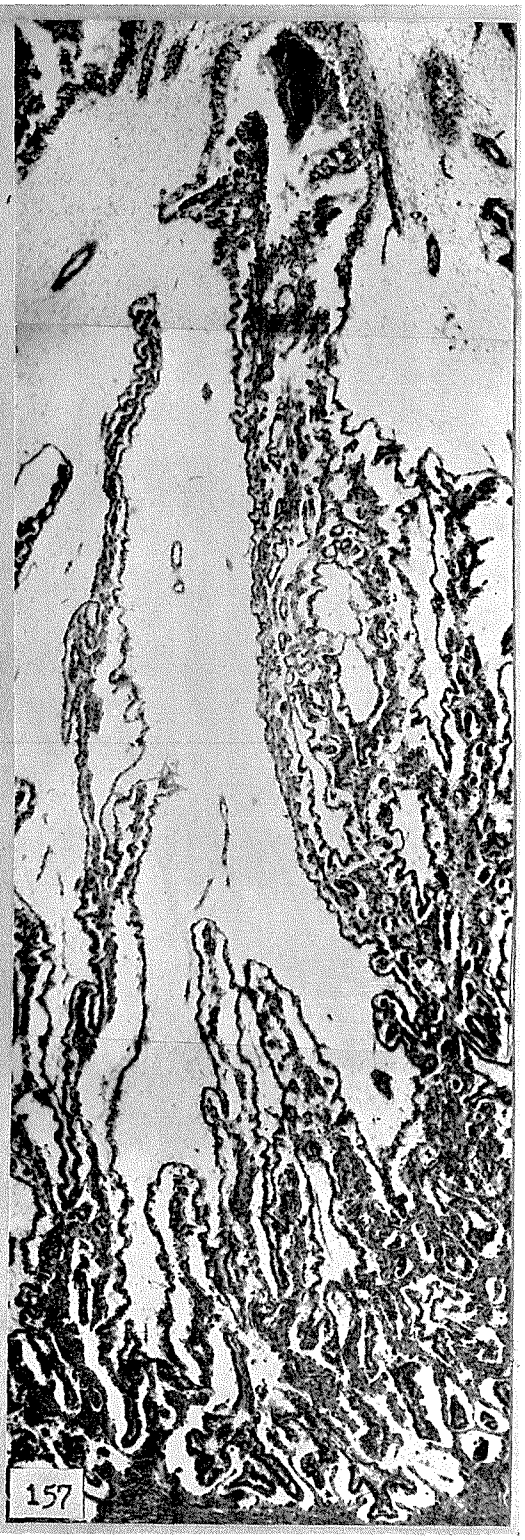
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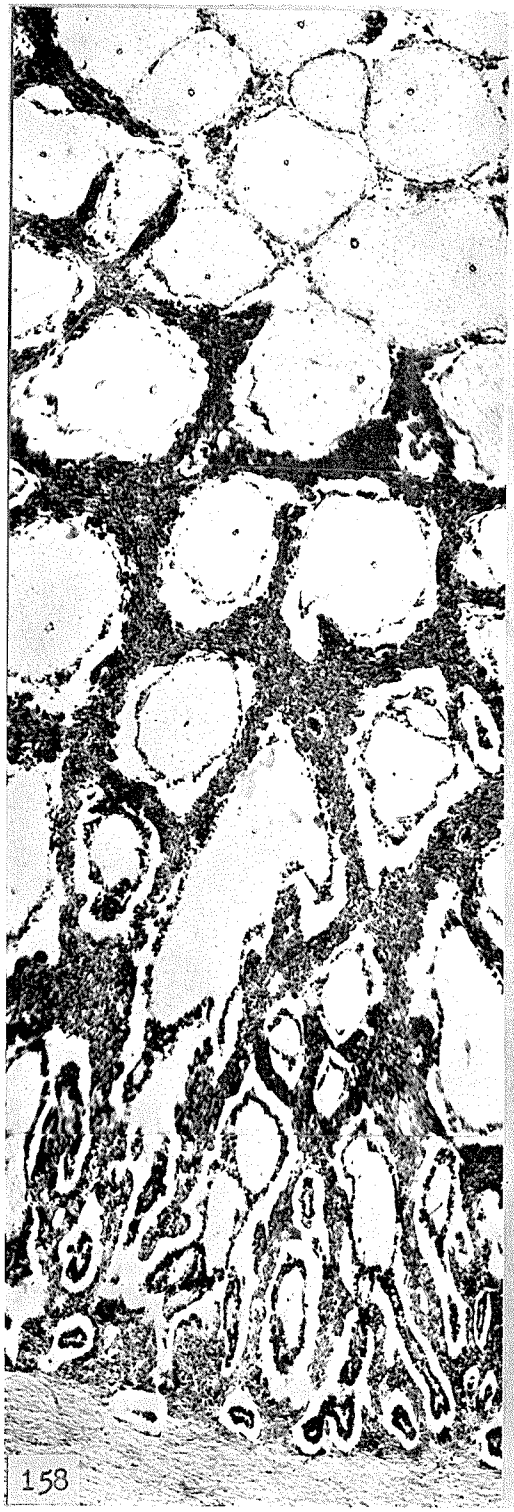
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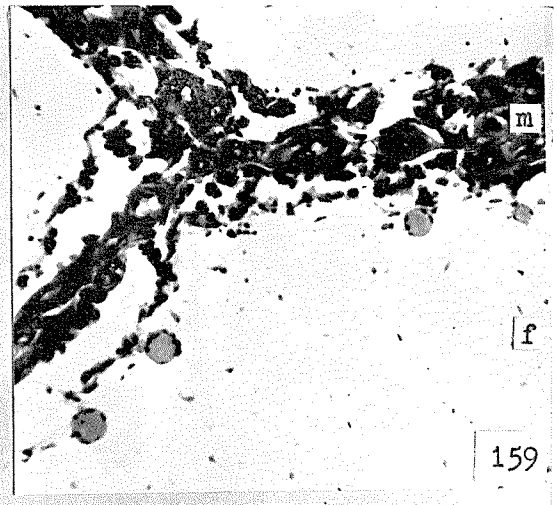
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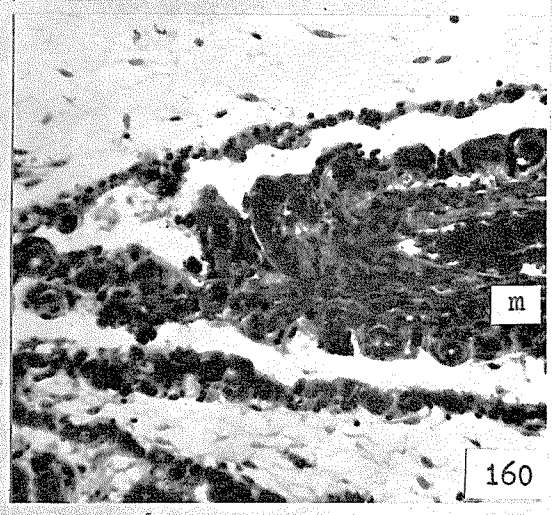
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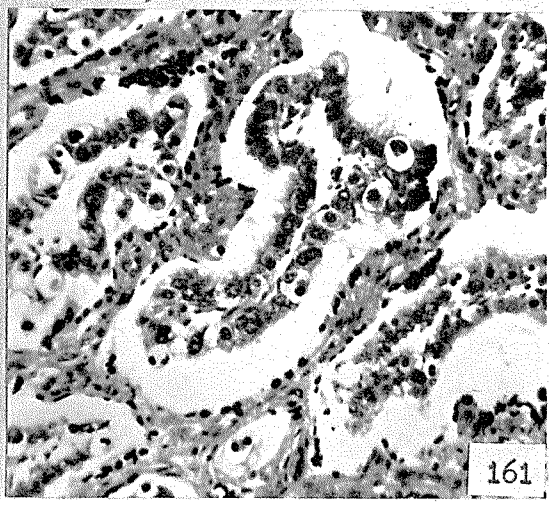
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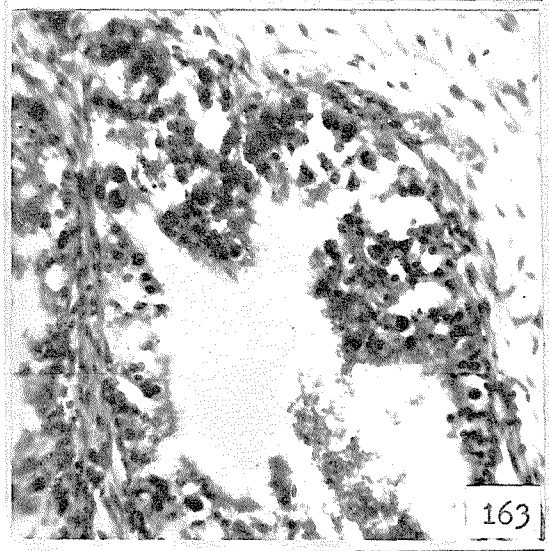
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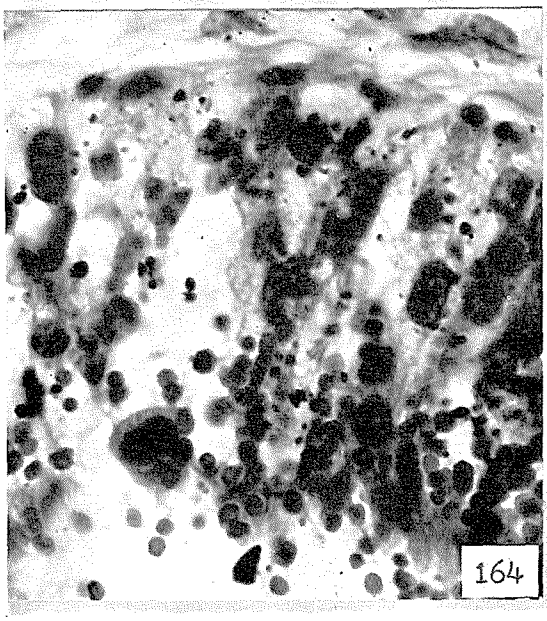
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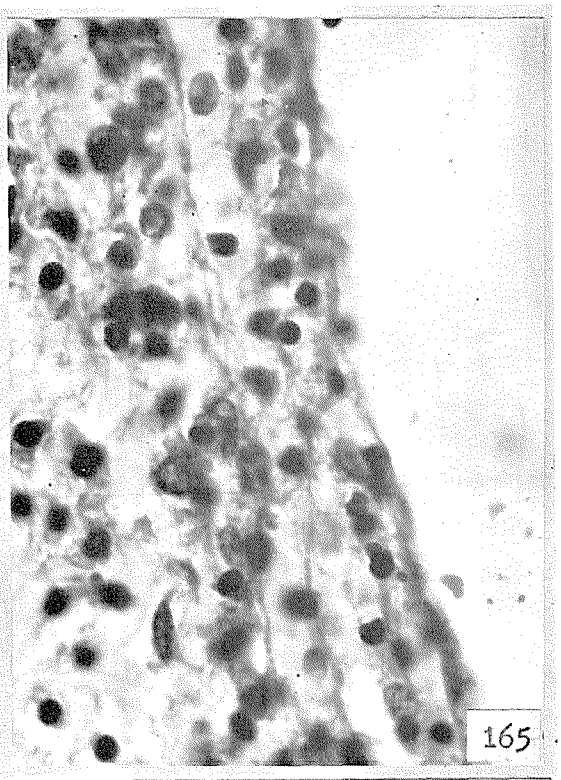
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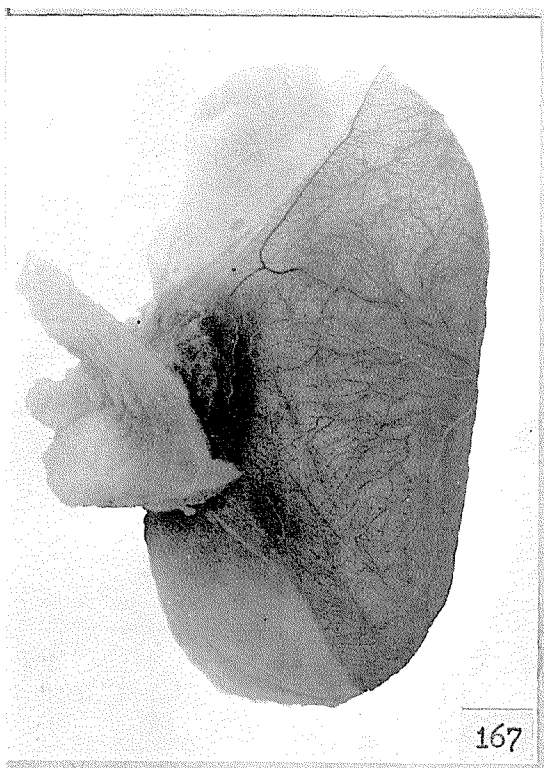

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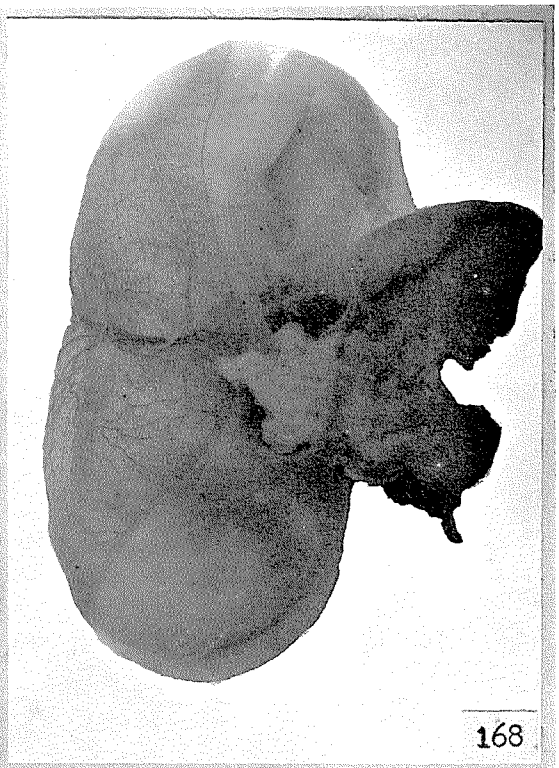

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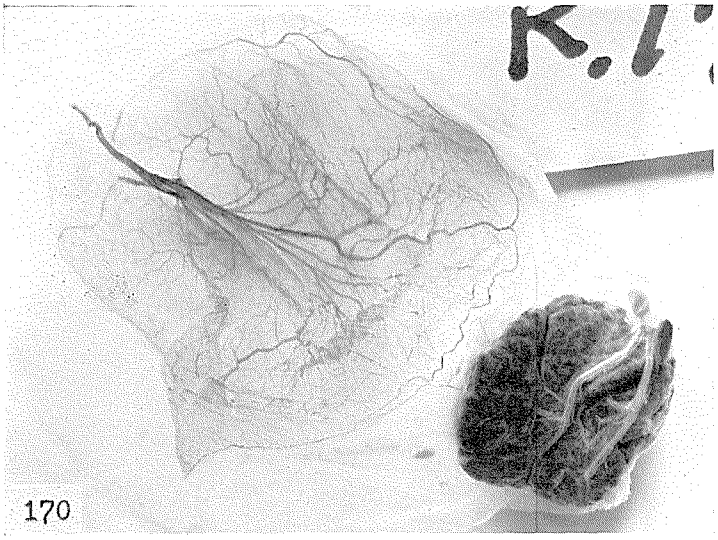
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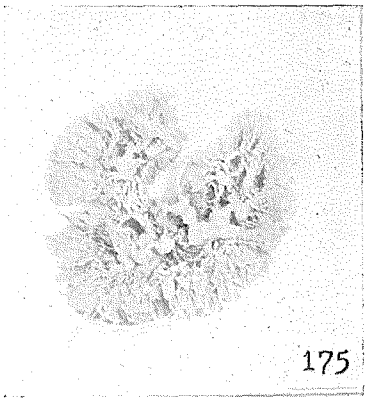
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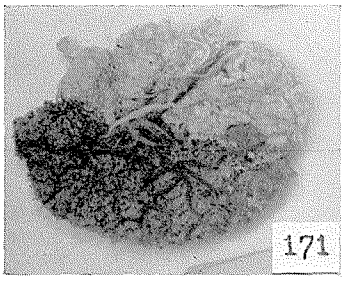
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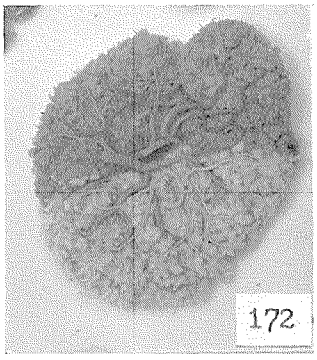
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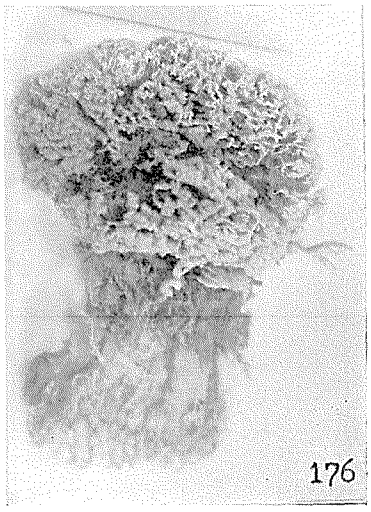
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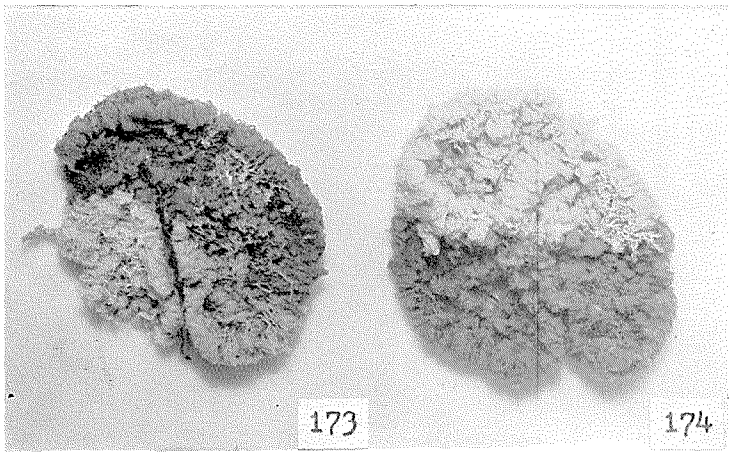
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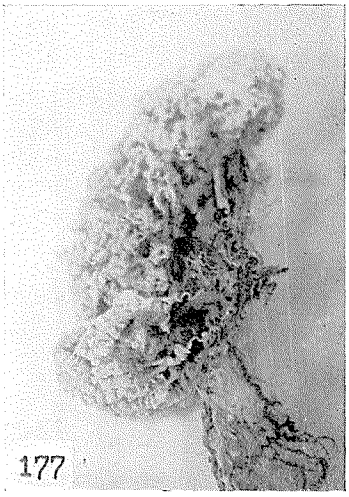
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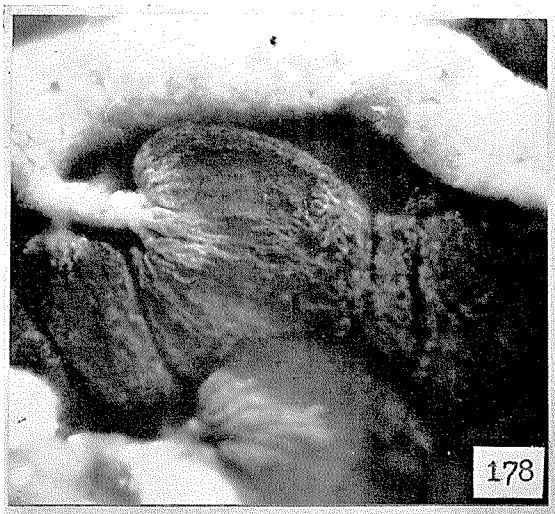
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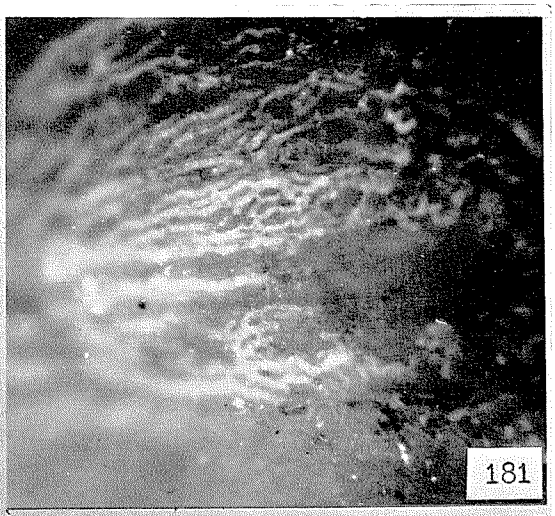
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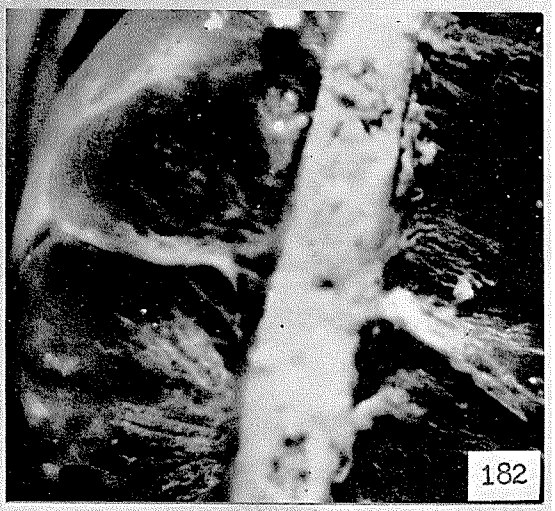
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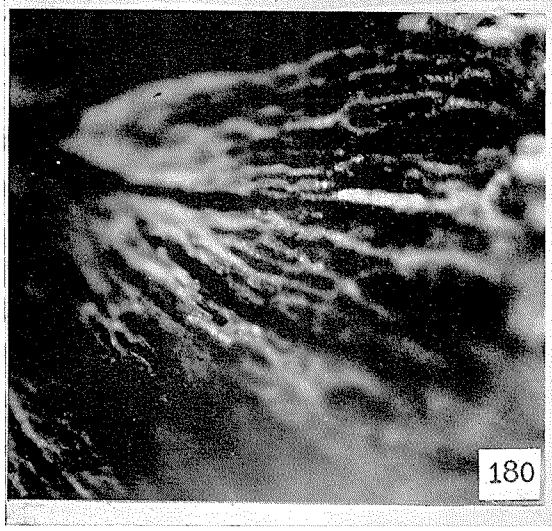
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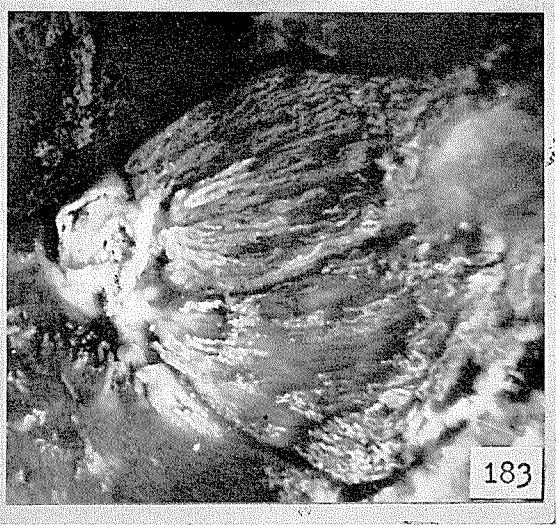
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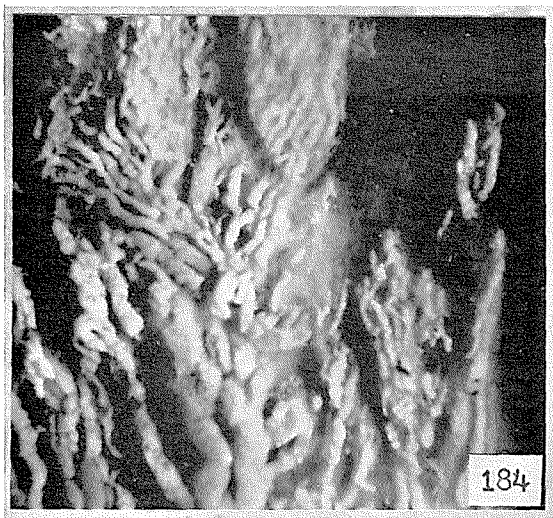
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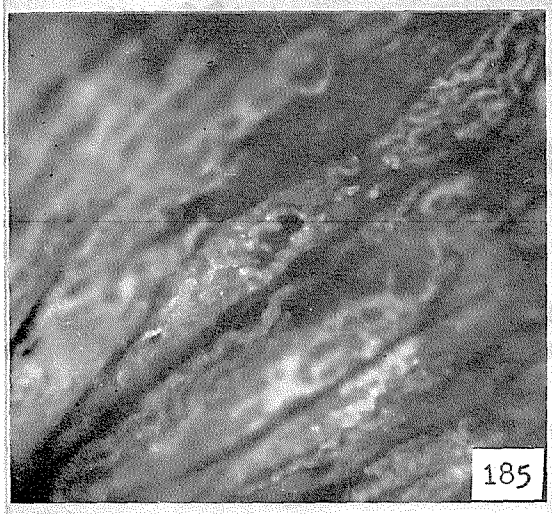
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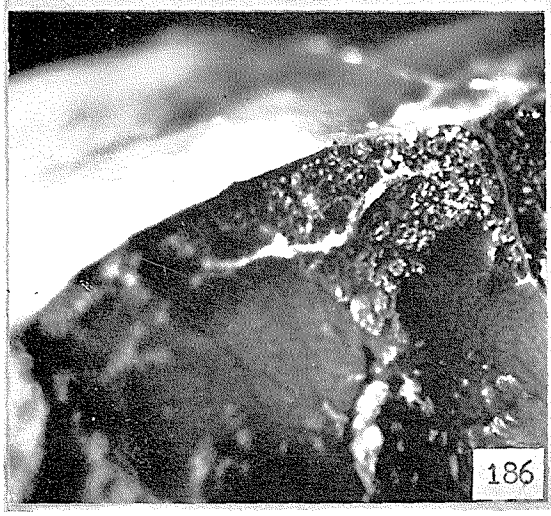
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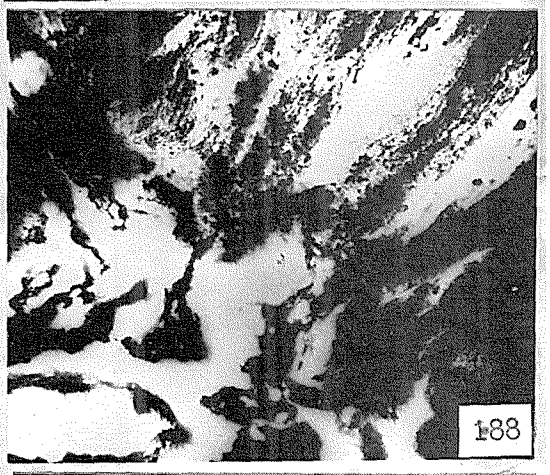
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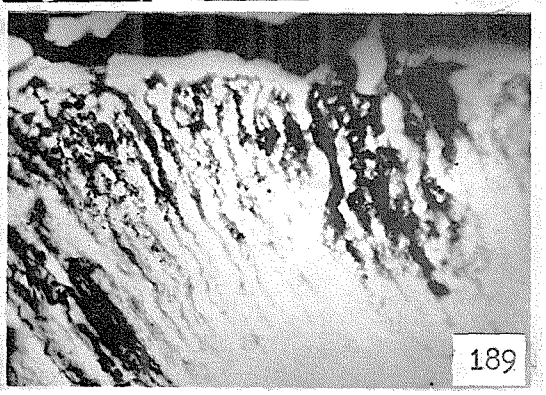
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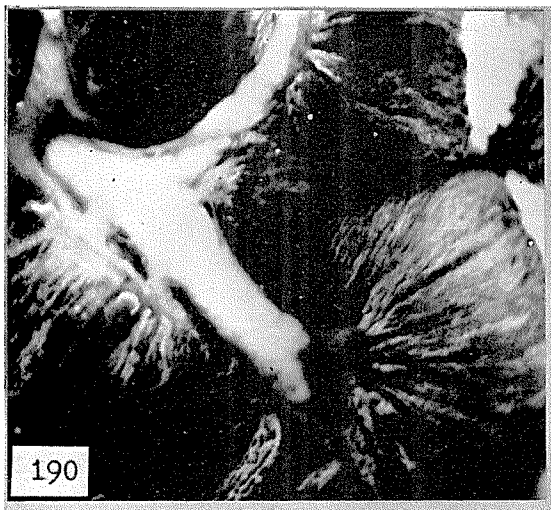
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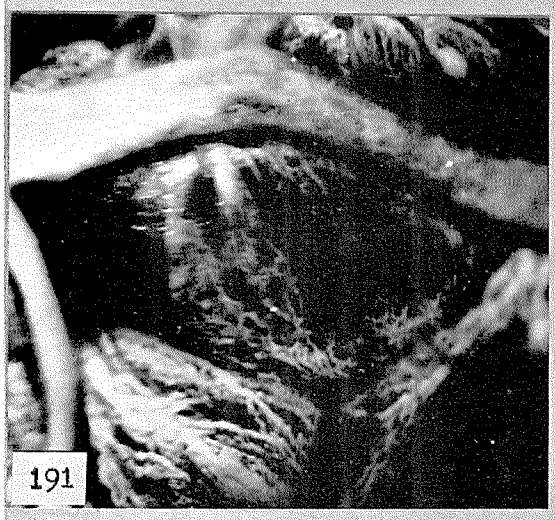
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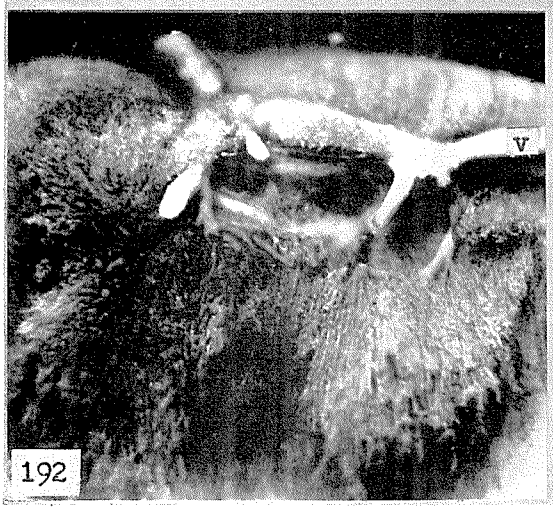
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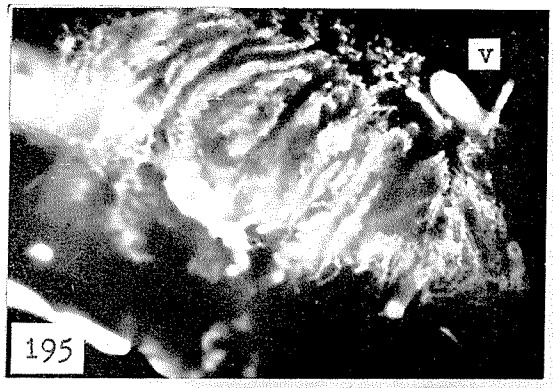
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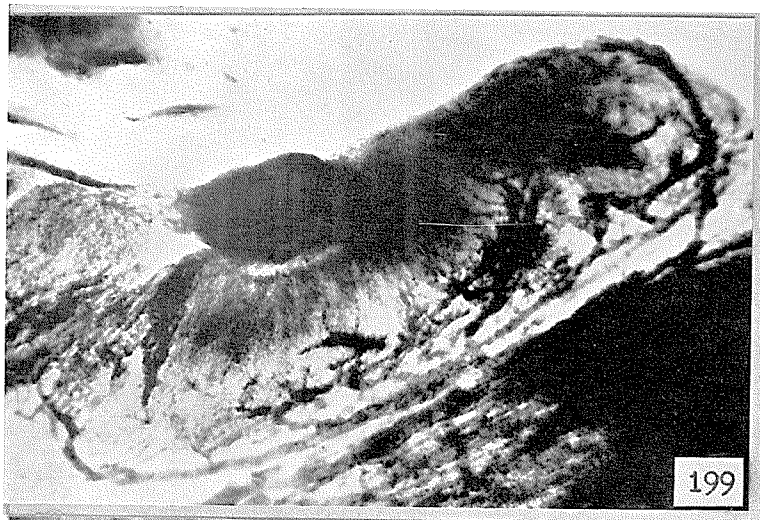
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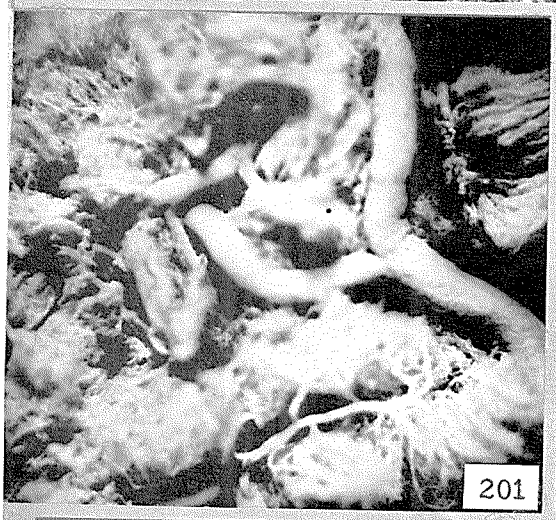
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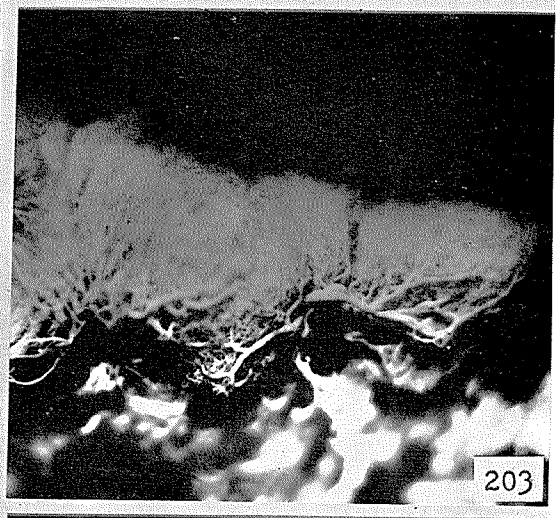
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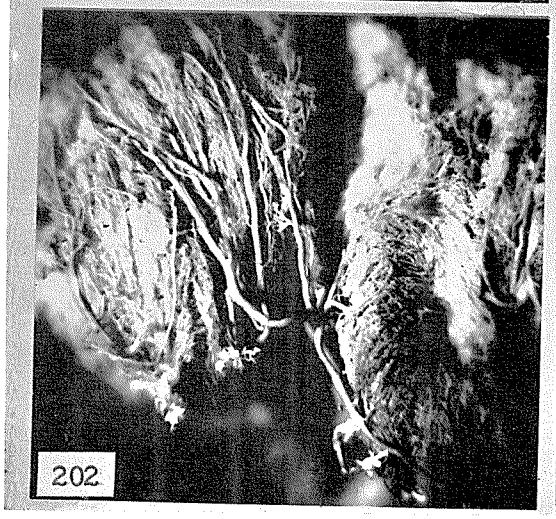
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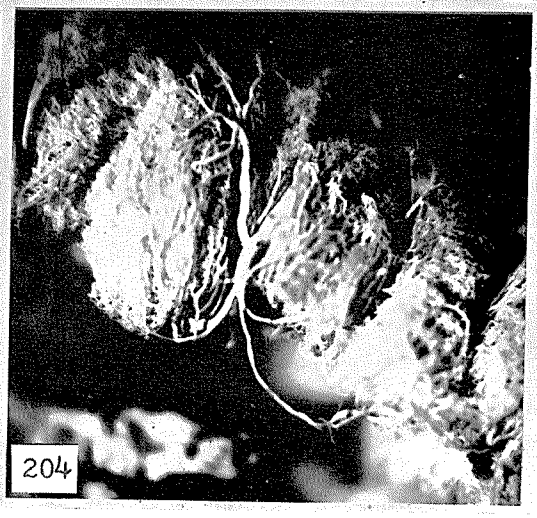
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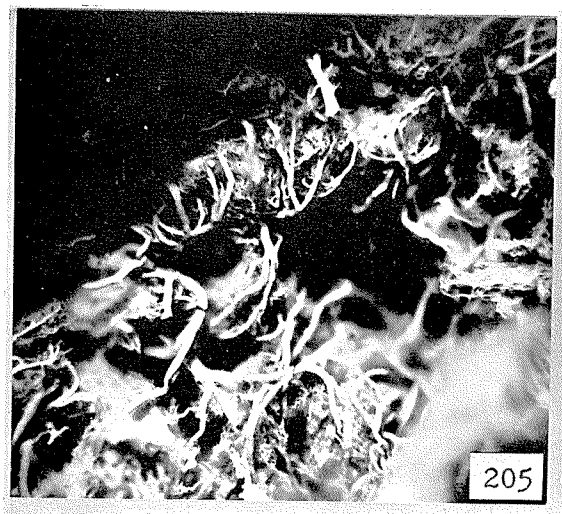
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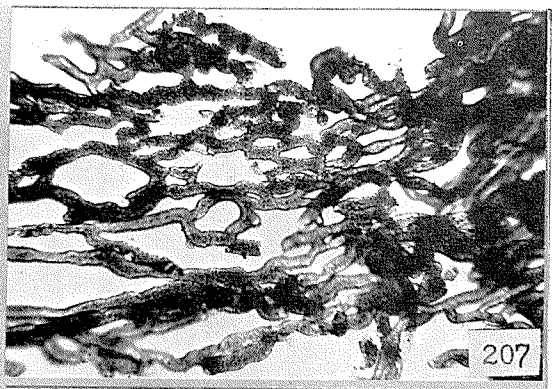
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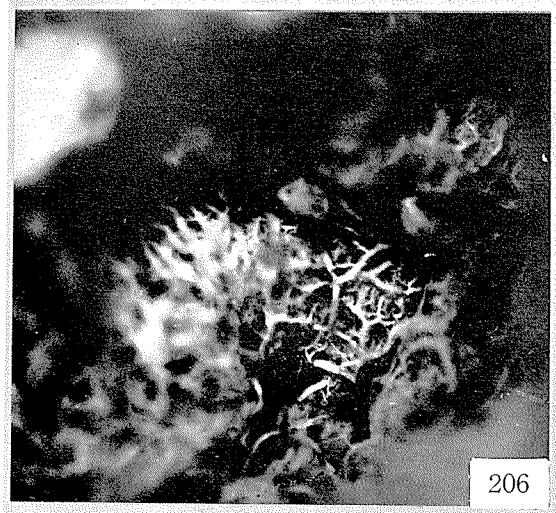
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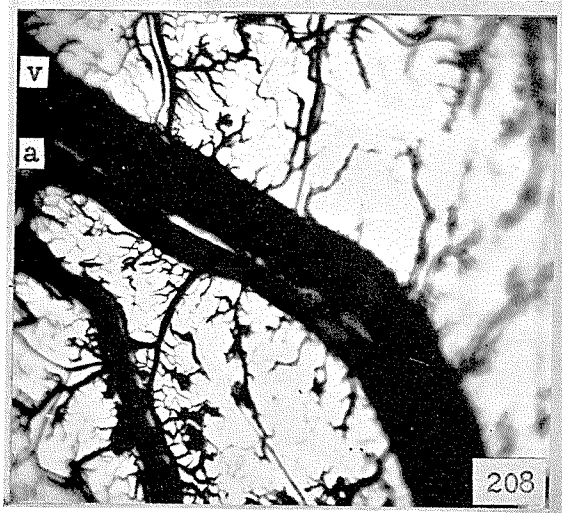
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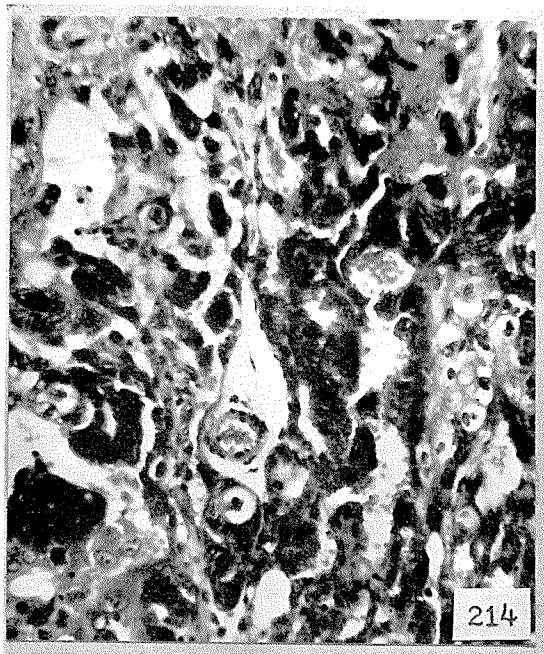
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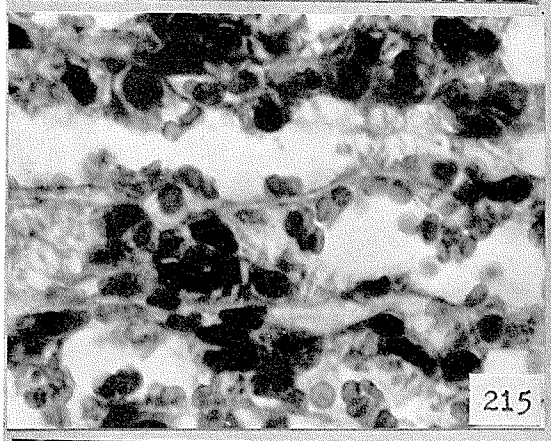
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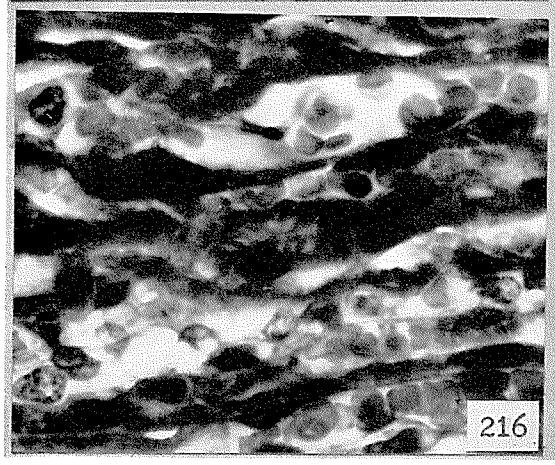
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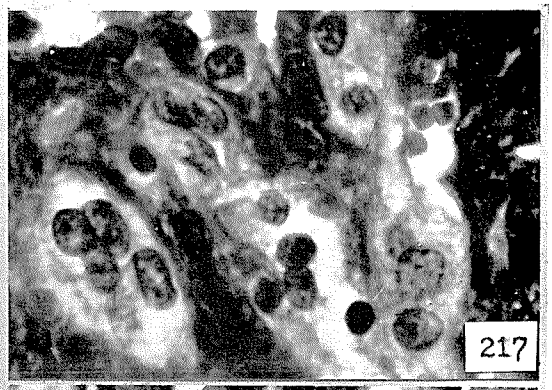
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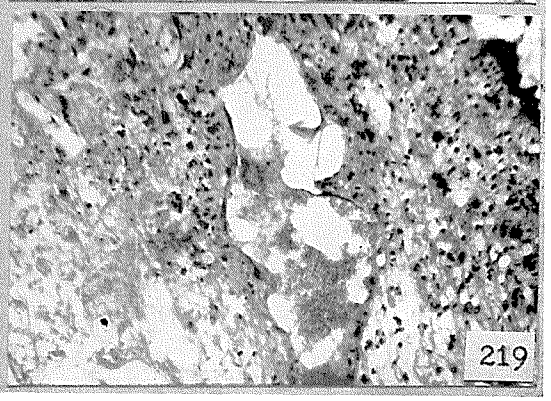
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