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The Anatomy of the Mammary Gland of Cattle

Fetal Development

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TABLE OF CONTENTS

PREFACE

Considering the magnitude of the industry built upon the products of the mammary gland of the dairy cow, there still is a surprising dearth of organized information relating to the anatomy of the udder of the dairy cow and the physiology of the process of milk secretion.

Many of the most elemental facts concerning the structure of the udder are not known to students of dairy husbandry. The neglect of the study of the anatomy of the udder was recently pointed out by a dairy bacteriologist interested in obtaining information in regard to a certain phase of the question. He noted that there had been no published study of the anatomy of the mammary gland in an American agricultural experiment station bulletin since 1900.

In order to fully appreciate and understand the functional activity of the mature udder it is fundamental that there be an understanding of the mode by which these structures arise during intrauterine growth and their progressive growth and development during the period from birth to puberty, and especially during pregnancy.

These studies are especially fundamental in connection with studies concerned with the causes of the growth of the mammary gland and the initiation of milk secretion. Only with detailed pictures of the normal gland structure during various stages of development can the results of experimental work be measured.

The present bulletin is the second one by Dr. C. W. Turner of this department dealing with the various phases of the development of the udder. Missouri Agricultural Experiment Station Research Bulletin 140 was the first one of the series.

A. C. Ragsdale,
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ABSTRACT

Continuing a study of the udder development of the bovine embryo and fetus, the differentiation of the primary sprout into the cistern of the gland and teat was described. The secondary sprouts soon begin to form. Upon the canalization of these sprouts, the primary milk ducts leading into the cistern of the gland develop. The duct system of the gland at birth is confined to a small area around the cistern of the gland. The development of the morphology of the udder and the histologic structures of which the udder is composed are then described.

ACKNOWLEDGMENT

The writer wishes to acknowledge his indebtedness to Mr. Leon V. Waughtal, assistant photographer of the Missouri Agricultural Experiment Station, for his technical skill in preparing the microphotographs included in this bulletin.

The Anatomy of the Mammary Gland of Cattle

II FETAL DEVELOPMENT

CHARLES W. TURNER

In the previous study of this series (Turner 1930) the embryonic development of the bovine mammary gland was traced from its earliest appearance as the mammary line in a 1.7 cm. embryo until the primary sprout had begun to canalize in about 20 cm. embryos.

This study indicated that the mammary lines quite definitely mark the location of future normal and accessory glands and account for their orderly linear arrangement.

The proliferation of the Malpighian layer at points along the mammary line determines the maximum number of individual glands in the complex. These centers of proliferation, which gradually change from lens shaped into ovoid or cuboidal structures, are called mammary buds.

From the proximal end of the mammary bud an invagination called the primary sprout begins to grow into the center of the teat. This sprout begins to invaginate at about the 12 cm. stage in the female and reaches its maximum development at the 16 cm. stage. Secondary sprouts then begin to form.

The purpose of the present study is to trace the development of these structures in the bovine fetus until birth. This consists essentially in the transformation of the primary sprout into the cistern of the teat and gland with secondary sprouts developing into the chief milk ducts of the udder.

TABLE 1.—RELATION BETWEEN LENGTH AND AGE OF BOVINE FETUS

Hammond 1927		Zschokke 1920		Missouri	
Month (4 weeks) of pregnancy	Fetal length in cm. from forehead to base of tail	Days	Length (cm.)	Days	Length crown rump cm.
1	0.8	73	11.0	---	----
2	5.4	88	14.7	---	----
3	13.3	91	13.7	---	----
4	24.5	98	15.0	---	----
5	39.0	105	20.0	108	21.6
6	51.0	---	----	123	25.0
7	68.0	---	----	132	34.0
8	80.0	---	----	239	74.5 83.5 (twins)
9	----	---	----	253	87.5 (twins)

Material and Technique

The fetuses for the present study were collected at an abattoir by the writer during the summer of 1927.* The measurements were immediately taken consisting of the length from the crown or poll (the anterior extension of the top line) to the rump; and from the withers to the hoof. (See Fig. 2). The mammary glands were then removed and immediately fixed in Bouin's Fluid. Further details in regard to the histological technique employed are given in the first report.

As stated in the previous study, the ages of the fetuses were not known. In this study it is necessary, therefore, to describe the develop-

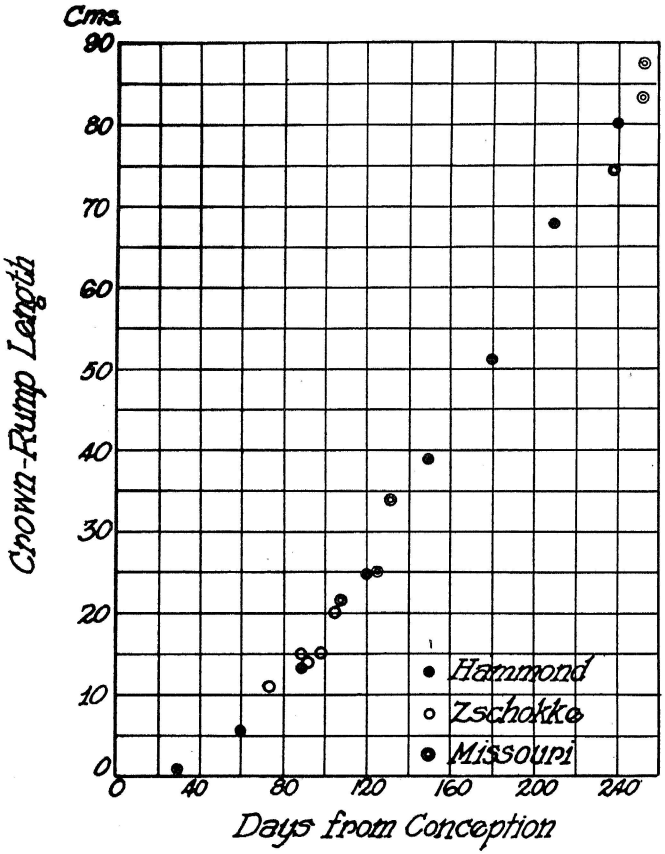

Fig. 1.—Interuterine growth of cattle as measured by crown-rump length. As the ages of the embryos and fetuses were not known, it is necessary to describe the development of the mammary glands in terms of growth in crown-rump length. The figure presents graphically the available data showing the length of a number of fetuses of known age.

*My thanks are due the Oscar Mayer Packing Company, Madison, Wisconsin, for their cooperation in facilitating the collection of the embryos, and to Dr. L. J. Cole, for placing the laboratory of the department of genetics, University of Wisconsin, at the writer's disposal in connection with the fixation of the specimens.

ment of the mammary glands in terms of growth in crown (poll)-rump length. From the data of Zschokke (1920), Hammond (1927), and a few specimens collected from the dairy herd of the Missouri Agricultural Experiment Station, a close estimate of the ages can be made. These data are presented in Fig. 1.

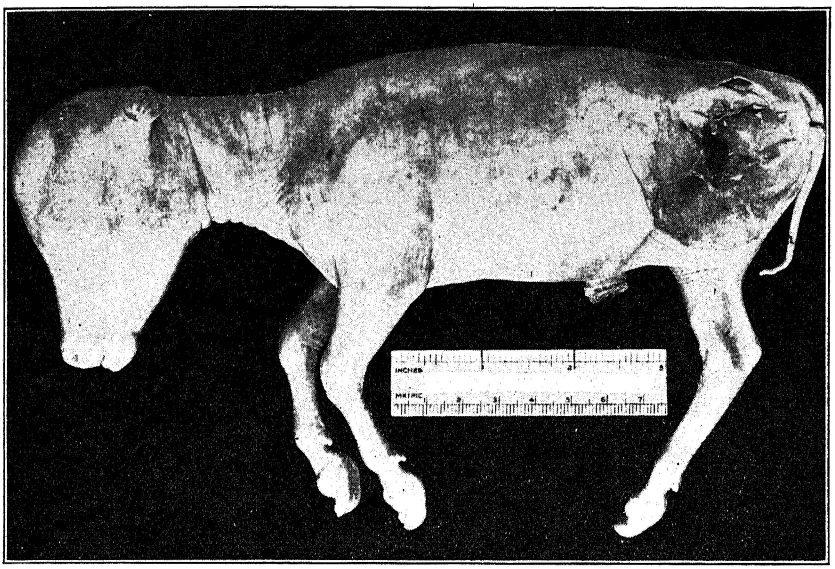

Fig. 2.—The development of a 21.6 cm. (108 days from conception) bovine fetus is shown. This measurement includes the length from the crown or poll (the anterior extension of the top line) to the rump. A second measurement (13.5 cm.) from the withers to the hoof was also taken. It will be noted that the form of the udder is well outlined at this time.

A description of the fetuses available for study is presented in Table 2. In addition to the measurements, the sex, weight of the udder, and teat number are included.

TABLE 2.—MEASUREMENTS OF BOVINE FETUSES

Breed of Dam	Crown Rump Length	Height at Withers	Sex	Udder Weight	Teat Number	Record Number
	cm.	*cm.*		*gms.*		
Hereford	26.0	14.0	Male	----	3	37
Shorthorn	28.5	17.5	Male	----	4	53
Shorthorn	29.5	17.5	Female	3.7	4 + 2 RL	39
Holstein	29.5	18.0	Male	----	4	101
Blue Holstein	30.0	16.0	Female	6.1	4	88
Shorthorn	31.0	20.0	Female	7.3	4 + 2 RL	45
Shorthorn	31.5	24.0	Male	----	4	51
Shorthorn	32.0	19.0	Female	5.3	4	40
Shorthorn	32.0	20.5	Male	----	4 + 1 R	17

TABLE 2.—MEASUREMENTS OF BOVINE FETUSES (CONTINUED)

Breed of Dam	Crown Rump Length	Height at Withers	Sex	Udder Weight	Teat Number	Record Number
Hereford	34.0	19.0	Female	7.5	4 + 2 RL	38
Holstein	34.0	19.0	Male	----	4	556
Holstein	35.5	23.0	Female	9.8	4	28
Angus	36.0	21.0	Female	8.1	4	42
	36.0	20.0	Female	6.7	4	64
Red and White	36.0	22.5	Male	----	4	72
Red and White	36.5	21.5	Male	----	4	15
Hereford	37.0	25.0	Male	----	4	36
Holstein	37.5	22.5	Male	----	4	59
Hereford	37.5	24.0	Male	----	4	35
	38.5	25.0	Male	----	4	56
Shorthorn	39.0	27.0	Female	11.6	4 + 1 R	54
Red	40.0	25.0	Female	11.5	4	27
Angus	40.5	25.0	Male	----	4 + 1 R	46
Red	41.0	28.5	Female	29.8	4 + 2 RL	76
Holstein	43.0	27.5	Female	13.6	4 + 2 RL	92
Holstein	45.5	28.0	Male	----	4	26
Red and White	46.5	30.0	Female	15.3	4	9
Holstein	47.0	30.0	Male	----	4	83
Red	48.0	30.0	Female	13.1	4 + 2 RL	3
Holstein	48.0	31.5	Male	----	4 + 1 R	20
Holstein	48.0	33.0	Male	----	4	14
Holstein	49.0	35.0	Male	----	4	97
Shorthorn	50.5	35.0	Female	21.7	4 + 1 L	55
Holstein	51.0	36.0	Female	36.3	4 + 1 L	70
Holstein	52.0	34.0	Male	----	4	2
Red and White	52.5	34.0	Male	----	4	16
Hereford	53.0	37.0	Male	----	4	41
Holstein	55.0	36.0	Male	----	4	66
Holstein	55.0	37.5	Male	----	4	57
Red and White	56.0	36.0	Male	----	4	6
Red and White	57.5	38.0	Male	----	4	33
Holstein	59.5	41.0	Female	24.4	4 + 2 RL	65
Holstein	60.0	41.5	Female	25.6	4	25
Holstein	62.5	43.0	Male	----	4 + 2 RL	24
Hereford	64.0	40.0	Female	33.2	4 + 1 L	48
Jersey	64.0	49.0	Female	----	4	157
Red	68.0	47.0	Male	----	4	29
Brown and White	68.0	46.0	Male	----	4	10a
Red and White	68.5	51.0	Female	31.3	4 + 2 RL	32
Shorthorn	69.0	50.0	Female	65.7	4 + 2 RL	69
Holstein	70.0	46.0	Male	----	4	60
Brown and White	70.0	47.0	Male	----	4	10b
Holstein	70.0	48.5	Female	34.5	4 + 1 R	84
Red and White	73.0	57.0	Female	28.5	4 + 1 L	23
Holstein	74.0	61.0	Male	----	4	546U.M.
Holstein	77.0	56.0	Male	----	4	85
Brindle	82.0	73.0	Female	74.6	4 + 1 R	68
Shorthorn-Holstein	84.0	65.0	Male	----	4	71

Comparative Embryology of the Mammary Gland

In connection with this study a rather careful review of the literature concerned with the description of the development of the mammary glands in many mammals has been made. It was intended to review

these extremely interesting studies as part of this bulletin. In the course of preparation of this section so much information was found scattered in many inaccessible journals, and dissertations principally in German and French that it seemed worthwhile to prepare a more extensive comparative study of the development of the mammary gland than would be suitable to include as a part of this bulletin. For this reason there will be included in the present bulletin references only to other studies of the development of the bovine mammary gland, while in another publication the comparative developmental anatomy of the mammary glands of other placental animals will be reviewed.

OBSERVATIONS

The Canalization of the Primary Sprout

The canalization of the solid core of cells forming the primary sprout was first observed in a 19 cm. fetus. At this time the central cells at the proximal end of the primary sprout begin to separate forming a lumen. The canalization at this stage does not appear to be due to the disintegration of the cells but rather to the widening of the circumference of the sprout resulting in the formation of a lumen. The canalization of the primary sprout begins at the proximal end and gradually proceeds toward the distal end.

In cross section the sprout appears relatively free of cells in an area in the central part which gradually enlarges as the fetus develops. In some fetuses the canalized sprout appears to contain a fluid while in others the space is empty. The inner surface of the sprout, in many cases, appears smooth and the cells regularly arranged. The wall of the sprout is composed of approximately three layers of cells. However, at the upper end of the sprout where the cistern of the gland is beginning to form, the rows of cells lining the cavity increase and the surface is irregular.

The canalization of the primary sprout in the male fetus was not observed. In a 21 cm. fetus the lumen of the primary sprout was already developed.

In order to trace the further development of the primary sprout and the structures derived therefrom, it is necessary to describe the histology of the corresponding parts in the mature udder.

At the point of entrance to the mature teats, the residue of the mammary bud is observed as a slight funnel shaped depression. The duct at the lower end of the teat is called the streakcanal. It is lined by a many layered pavement epithelium. Above the streakcanal the cavity enlarges into the cistern of the teat. This cavity is lined with a two

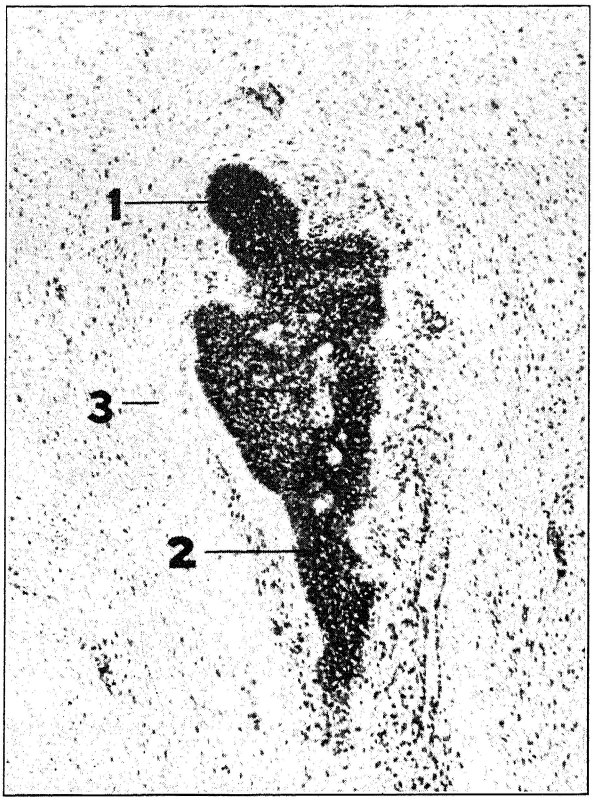

Fig. 3.—The formation of secondary sprouts in a 19 cm. female embryo. Canalization of the primary sprout has begun. The secondary sprouts are composed of solid cores of cells histologically similar to the primary sprout. 1. Secondary sprout. 2. Primary sprout. 3. Mesenchyme tissue.

layered epithelium. Above the cistern of the teat a constriction very frequently is observed which widens out into the cistern of the gland. The cistern of the gland is also lined with a two layered epithelium.

As will be noted in the following discussion, the streakcanal, the cistern of the teat, and the cistern of the gland are formed as a result of the canalization of the primary sprout.

The Residue of the Mammary Bud

The mammary bud is opened by the growth of the teat. The cells of the bud become cornified and appear similar to the epidermal layer of the skin. The bud comes to assume, in longitudinal section, the

Fig. 4.—Three secondary sprouts are observed in this 23 cm. embryo. The canalization of the primary sprout to form the cistern of the gland has progressed considerably. 1. Secondary sprout. 2. Cistern of the gland.

appearance of a cone composed of cornified cells at the apex of the teat. This condition remains almost the same throughout fetal development.

With the canalization of the primary sprout, the lumen may extend into the mammary bud residue but the outer layers of the cornified cells still appear to remain intact in many cases.

The mammary bud eventually forms the tiny crater-like formation which is still frequently observable in the mature teat. It is covered

by the external skin and plays no part in the formation of the internal structures of the teat.

The Formation of the Cistern of the Gland

In the 23 cm. fetus, the canalization of the cistern of the gland had progressed considerable toward the proximal end of the sprout. The cistern form was quite distinct. The cavity did not appear to arise as a result of the degeneration of the cells lining the sprout because they did not show signs of cornification. They were uniformly deep staining cells. Rather, it is believed that the cells lining the cistern continue to spread out pushing back the mesenchyme cells in all directions to form the cistern cavity.

The cistern of the gland is well outlined in the 29.5 cm. fetus. At this stage the cells lining the cavity consist of two or three rows. The cistern appears free of fluid, yet the appearance in cross sections is such as to give one the impression that it was extended with fluid.

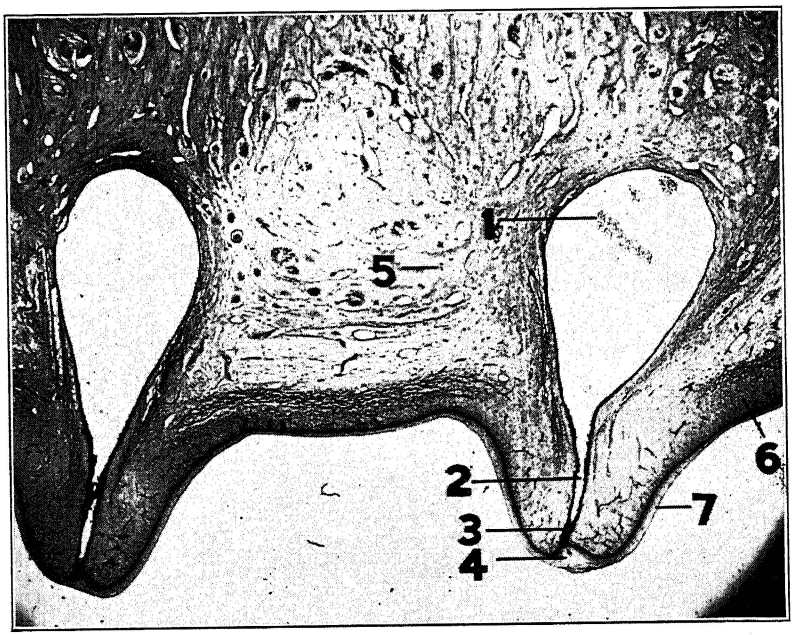

Fig. 5.—The formation of the cistern of the gland is complete in the udder of this 29.5 cm. fetus. The canalization of the entire sprout to form the cistern of the teat and streakcanal is shown. 1. Cistern of gland. 2. Cistern of teat. 3. Streakcanal. 4. Residue of mammary bud. 5. Mesenchyme tissue. 6. Dermis. 7. Epidermis.

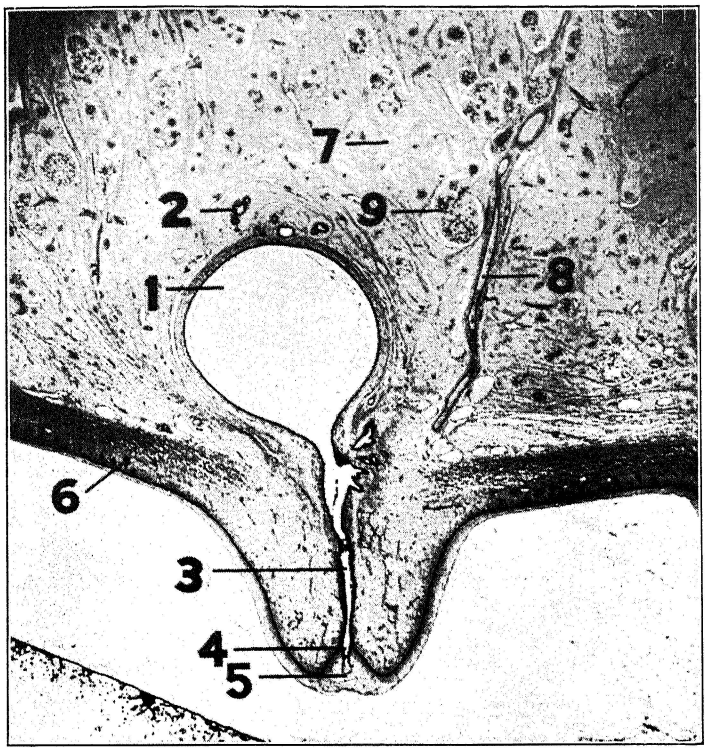

Fig. 6.—The cistern of the gland and teat are easily distinguished in this 32.0 cm. female fetus. Secondary sprouts are noted above the gland cistern and also at the side of the teat cistern. The latter may form accessory glands. The teat is free of hair. 1. Cistern of gland. 2. Secondary sprout. 3. Cistern of teat. 4. Streakcanal. 5. Residue of mammary bud. 6. Hair buds. 7. Mesenchyme tissue. 8. Blood vessel. 9. Cell whorls.

In a 30 cm. fetus (No. 88) a peculiar condition was observed in the stage of development of the front and rear gland. The cistern of the gland above the front teat was well developed whereas the primary sprout of the rear teat extended to the base of the udder. The sprout had canalized and a number of secondary sprouts were beginning to form. No cistern of the gland was present. Whether it would have formed later is not known. It might be noted that the writer has observed such a condition in a mature udder. The cistern consisted of a cavity about the size of a lead pencil with large ducts extending into the gland tissue.

In the male the relation between the cistern of the gland and of the teat is rather confusing because in many cases the upper part of the cistern which would be considered the cistern of the gland may be in

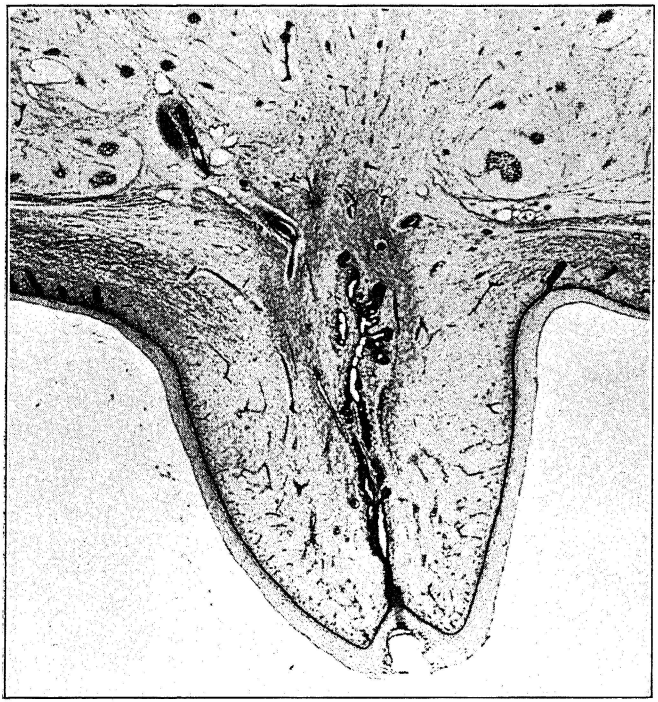

Fig. 7.—A peculiar type of development of the primary sprout is illustrated. The sprout extended only to the base of the udder. Secondary sprouts, however, were already beginning to form. (Fetus No. 88)

whole or in large part within the teat. In a few instances a very large cistern which would, in the case of the female, develop in the udder proper, here expands downward giving the appearance of a large teat cistern.

In other cases, it appears as though the primary sprout does not grow beyond the base of the teat. Upon canalizing, the cistern remained entirely confined to the teat. Thus in a 21 cm. male (Fig. 8) the latter type of development is observed. The so-called cistern of the gland has already formed to a considerable extent. Canalization extends to the distal end of the teat but has not broken the cornified layers above the residue of the mammary bud.

The Formation of the Cistern of the Teat

With the progressive canalization of the primary sprout there is formed a lumen of variable width in the teat. In female fetuses of about the 30 cm. stage the demarcation of the cistern of the teat becomes evi-

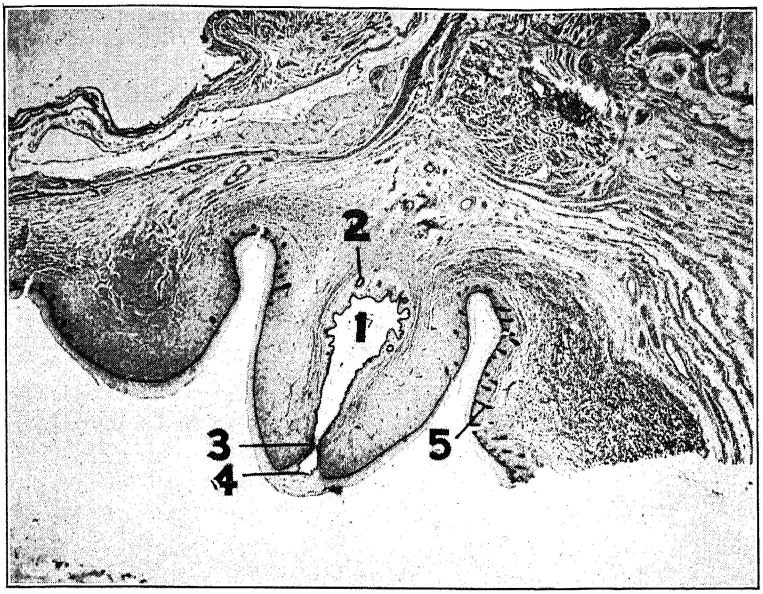

Fig. 8.—The entire cistern system is confined to the teat in this 21 cm. male fetus. Several secondary sprouts are observed. The anlage of the hair follicles are noted at the base of teat. 1. Cistern. 2. Secondary sprouts. 3. Streakcanal. 4. Residue of mammary bud. 5. Hair buds.

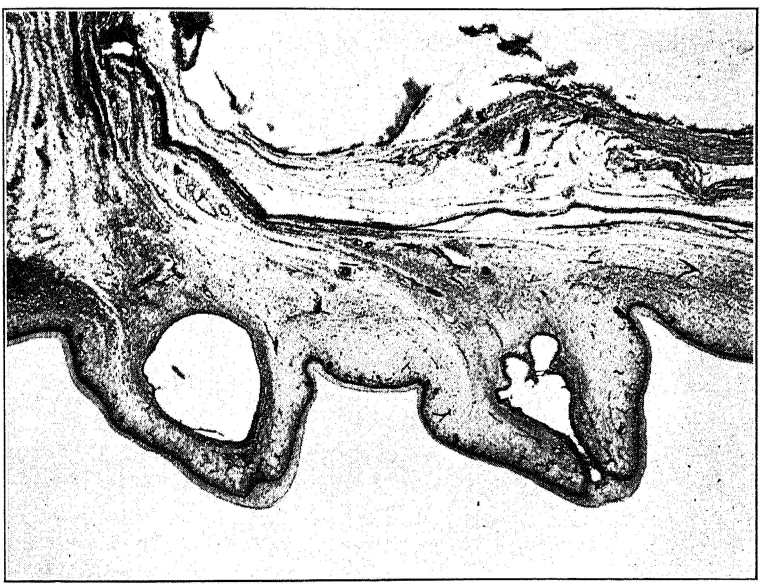

Fig. 9.—The cistern system in this 29.5 cm. male fetus is confined to the teat. The secondary sprouts are large in the anterior gland.

dent. At this time it could be called more correctly a canal as it does not widen out to any extent. Rather, the entire length of the teat is narrow. Only at the entrance to the teat where the streakcanal will later form is there a perceptible narrowing of the lumen. Here also the epithelial lining of the cistern consists of 2 to 3 layers.

The cistern of the teat in the male fetus is rather irregular in form and position due to the downward displacement of the cistern of the gland. When the cistern of the gland is large usually the cistern of the teat is very short if distinguishable at all. On the other hand, in some cases the male gland is quite similar in appearance to the female.

The Formation of the Streak canal

As noted above, the canalization of the primary sprout proceeds from the proximal (upper) end and proceeds toward the tip of the teat. Thus the last structure to open is the entrance to the teat. The part of the primary sprout which always remains rather constricted is called the streakcanal. At first it is histologically similar to the rest of the primary sprout. However, upon the differentiation of the cistern of the teat and gland into a two or three layered epithelium, the extent of the streakcanal becomes apparent due to the continuation of a many layered pavement epithelium similar to that of the skin covering the teat.

The Secondary Sprouts

The primary sprouts in cattle reaches its greatest extension as a solid core of cells at about the 16 cm. stage in the female. At this time the growing end divides into several *secondary* sprouts which begin further growth into the mesenchyme tissue. Instead of continuing to grow upward, these sprouts begin to grow at an angle as compared with the direction of growth of the primary sprout.

In some cases the proximal end of the primary sprout forms an irregular enlargement and begins to canalize just as the secondary sprouts begin to form. They are composed of solid cores of cells histologically similar in every way to the primary sprout.

The secondary sprouts are the anlagen of the duct system of the udder. These sprouts later divide into tertiary sprouts, etc. However, the extent of their fetal development is relatively very slight.

The canalization of the secondary sprouts follow the growth of the sprouts. Soon the ducts are lined by two celled epithelium characteristic of the cistern and ducts.

While some further growth and even tertiary sprouts may develop before birth, it may be said that the extent of the duct system in relation to the size of the udder is very limited. The ducts are confined to a small area around the cistern of the gland.

Huss (1873) observed the budding of the primary sprout in a 22 cm. female fetus. Five secondary sprouts were observed, arranged in part above and in part side by side, thus giving the primary sprout the appearance of a small cluster-like gland.

In a 19.5 cm. fetus Rein (1882) describes the formation of new sprouts from the lower end of the anlage (primary sprout). Klaatsch (1884) observed at least five sprouts coming from the primary sprout in a 19 cm. embryo.

Profé (1899) observed secondary sprouts in a 20 cm. female fetus. Zschokke (1919) noted that the proximal end of the primary sprout in a 21.5 cm. fetus was thickened but had not divided into secondary sprouts. However, in a 26.3 cm. fetus the primary sprout had divided into three secondary sprouts. In a 29.0 cm. fetus 15 to 20 secondary sprouts were observed which had already become canalized.

Under the title of the development of the milk ducts in cattle, Wicki (1926) reports a study of the growth of the secondary sprouts in a series of six fetuses (25.5 cm., 25.5 cm., 37.0 cm., 39.0 cm., 46.0 cm., and 104 cm.) as well as three calves between 8 and 21 days of age. A summary of his observations follow:

> This milk duct anlage (secondary sprout) gradually canalizes from the cistern outward rather than like the primary sprout. The secondary sprouts give off individual tertiary sprouts along their course and especially toward their ends which run in all directions.
>
> The milk ducts branch from the cistern of the gland at angles of 90 to 120 degrees, but most frequently at an angle of about 95 degrees. The angle increases gradually but continuously toward the proximal end, but no tree-like ramification could be observed.
>
> From the beginning, the milk ducts are arranged asymmetrically. This asymmetry constantly becomes more evident in the course of development. The largest and longest milk ducts run laterally in the front glands and caudally in the rear glands.

Accessory Glands in the Cistern Wall

Wicki (1926) observed the formation of the accessory glands in the cistern wall described by Riederer (1903) in the mature gland. They form in niches in the cistern wall. In some cases the sprouts begin to form above the anlage of the streakcanal; however, more frequently they appear at the base of the teat. They have a short fine main duct and have a tendency to ramify in a plane parallel to the cistern. Such a structure was observed in the wall of a 32 cm. fetus. (Fig. 6.)

The Morphology of the Udder

The development of the form of the udder in cattle appears to begin at a very early period. Even as early as in the 12 to 20 cm. female

embryos, distinct differences in shapes of the udders are observed. In some cases the sections indicate the development of an udder carried well forward and backward (No. 12) whereas in others a short, deep udder is present. (No. 21).

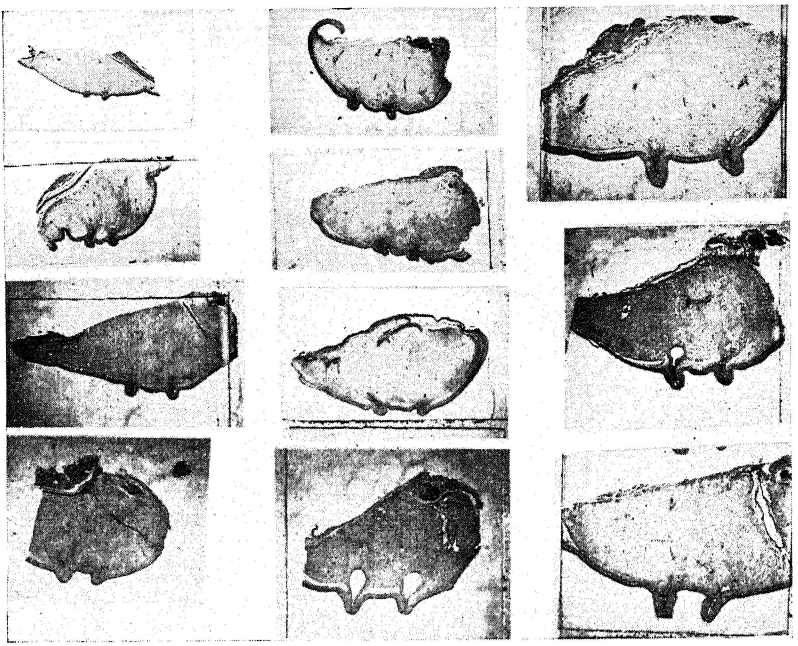

Fig. 10.—The form of the udder in cattle is outlined at a very early age. The above sections indicate the diversity of form appearing at various stages of growth. It should be noted especially that the future gland structure is still limited to a small area above the teats. The embryos included are of the following sizes. 12.3, 16.0, 19.0, 19.3, 19.5, 21.0, 23.5, 29.5, 35.5, 36.0 and 40.0 cm. in length.

The precocious development of the udder is especially remarkable due to the fact at this time the primary and secondary sprouts are confined to a very limited region above each teat. It would appear from this that the udder is laid out in its essential form much in advance of the growth of the gland and connective tissue which will eventually fill the udder. Such being the case, it seems obvious that the development of the form of the udder is not related to the development of the secretory activity of the gland within the udder. It is probable, however, that the size of the udder will be regulated by the extent of the gland developed. If the gland is stimulated to great development, the udder will increase in size to accommodate the greater amount of tissue. This is observed in the normal development of the udder during recurring pregnancy.

The male fetus is entirely lacking in udder development. The teats are located either anterior to or upon the scrotal sac. As a consequence the deep underlying mesenchyme tissue pad into which the primary and secondary sprouts develop is absent and the gland anlage is restricted to an area much less than that observed in the female.

Differentiation of the Skin

The outer covering of the early embryo consisted of a deeply staining layer of cuboidal cells (Malpighian layer) resting upon a distinct basement membrane. Underlying this layer are found the spindle shaped embryonic mesenchyme cells. A superficial layer called the periderm or epitrichium consisting of a single layer of flattened cells soon form. The epitrichium persists for a time but is shed with the growth of the hair.

The differentiation of the epidermis of the skin begins to appear at about the 8 cm. stage when the epidermal layers begin to cornify. The

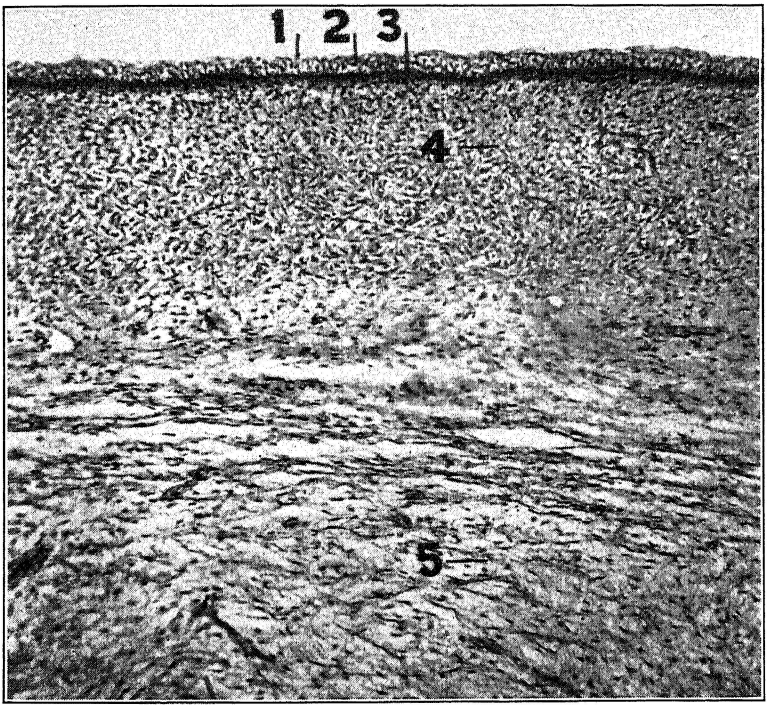

Fig. 11.—The differentiation of the mesenchyme tissue into a distinct dermis or corium below the deeply staining Malpighian layer is observed in this 12.3 cm. embryo. The epidermis is composed of the Malpighian layer, several intermediate cell layers, and a single layer of flattened cells called the periderm or epitrichium. 1. Periderm or epitrichium. 2. Cornified layer of epidermis. 3. Malpighian layer of epidermis. 4. Dermis or corium. 5. Mesenchyme tissue.

Malpighian layer is the active germial layer and as growth proceeds, the cells are displaced toward the surface and quickly undergo progressive cornification. By the time the primary sprout begins to invaginate, the epidermis has increased to 4 or 6 layers of which the outer are entirely cornified.

The differentiation of the dermis or corium of the skin is somewhat slower. In the 12 cm. embryo there is observed a slight condensation of the mesenchyme cells anterior to the teats whereas posterior to the teats the cells of the fetal udder were more or less uniform. The differentiation had become quite marked in the 16 cm. stage. Here the dermis was composed of deeply staining condensed mesenchyme cells of uniform thickness following the contour of the epidermis. The mesenchyme cells below the dermis were quite diffused with the spindle shaped cells gradually forming threads extending perpendicular to the base of the udder.

With the growth of hair the dermis gradually separates into a deep layer in which coarse fiber bundles interlace to form a connective tissue network and a superficial layer in which finer bundles of connective

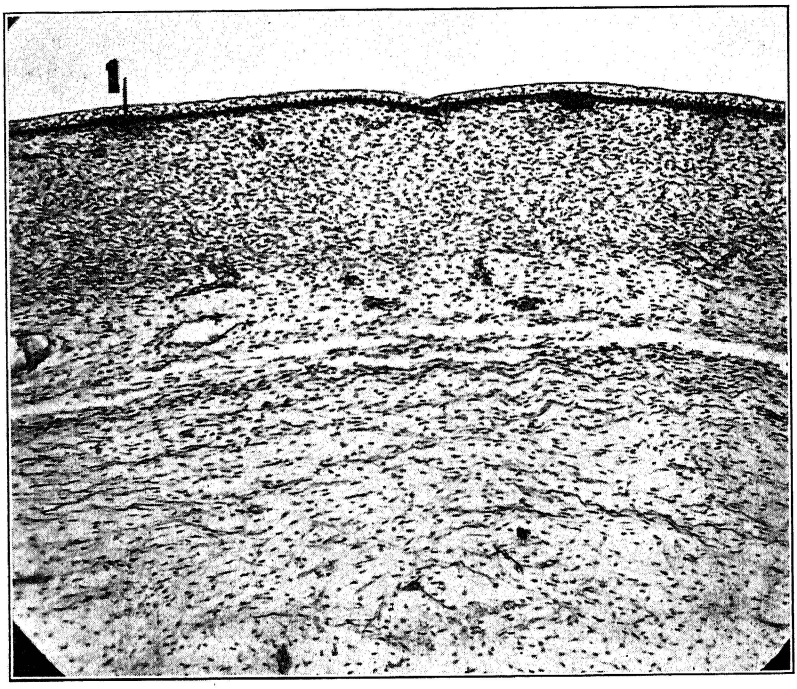

Fig. 12.—The anlage of the hair buds are forming in the Malpighian layer of this 16 cm. embryo. The condensation of the mesenchyme cells to form the dermis continues. 1. Hair bud.

tissue form a network. In the fully developed skin this layer forms the papillary layer composed of conical elevations of the dermis. The papillae, however, were not present in the fetuses examined.

Capillary blood vessels extend through the dermis up to the Malpighian layer of the epidermis.

In a 24 cm. fetus Huss (1873) noted the complete separation of the cutis (epidermis) from the subcutaneous (dermis) connective tissue. The latter contained a great wealth of fat into which the secondary sprouts grew.

Development of Hair in the Skin of the Udder and Teats

The anlage of the hair bud forms as an invagination of the ectoderm in the 13.7 cm. embryo. In this respect it is similar to the mammary gland. The hair bud gradually forms a solid core of cells as it continues its ingrowth into the dermal layer of the skin. The ingrowth takes an oblique rather than a perpendicular course.

A sex difference was noted in regard to the presence of hair in relation to the teat. In the female fetus the hair follicles are very numerous in the dermis of the udder skin but were not observed in the skin of the

Fig. 13.—The hair buds have invaginated into the dermis to a considerable extent in this 23.5 cm. fetus. The extent of the dermal layer is clearly outlined.

teat, being entirely free of hair up to the base of the teat. In the male fetus, however, the hair is frequently present on the upper half of the teat as well.

These observations differ from those of some of the early workers. Huss (1878) for example states that rudiments of the hair appeared not only around the teat, but also on the teat itself up to the tip in a 24 cm. female. In a 46 cm. fetus the teats were observed to be entirely hairless. Rein (1881) observed that the hair buds form at the time the secondary sprouts begin to develop (20 cm.). At this time they always occur some distance from the teat; later, however, hair was observed up to the tip of the teat. In an embryo 18 cm. long Klaatsch (1884) observed the appearance of the hair rudiments. They were almost entirely absent on the surface of the teat; however, in older animals he claims to have observed them there also.

Fig. 14.—The hair rudiments have continued their growth to form the bulbus stage in this 48 cm. fetus. The superficial and deep layers of the dermis may be observed.

Profé (1899) observed that the first hair buds begin to form in embryos 14 to 16 cm. long. Zschokke (1919) confirmed the observations of Rein that the hair development is initiated at the same time that the secondary sprouts appear. On the other hand, hair buds were never found on the teat itself. Hammond (1927) observed hair buds in the general skin surface of a 24.5 cm. fetus but the epithelium of the nipple was quite free.

Changes in the Mesenchyme Tissue

In the early embryos the entire udder structure is composed of mesenchyme tissue below the Malpighian layer. This embryonic tissue is made up of loosely connected spindle shaped cells. As noted in the preceding section the dermis or corium of the skin gradually differentiates from this tissue.

The mesenchyme cells, which have begun to differentiate into white fibrous tissue at this stage (8-12 cm.) show a tendency to congregate

Fig. 15.—The formation of connective tissue cell whorls are illustrated. The compact aggregation of cells in the center with few cells further out is characteristic of these structures in the early stages of development. (Embryo 16 cm. long)

in the form of threads or bundles and gradually take positions perpendicular to the base of the udder.

The blood vessels are difficult to follow in the sections but they were observed to pass downward from the base of the udder and to ramify throughout the tissue.

In embryos between 12 and 13 cm. long, near the base of the udder (attachment to the abdomen) the connective tissue cells are observed to begin to form a series of whorls composed at this time of an aggregation of cells in the center with circularly disposed cells further toward the outside of the whorl. Some of these whorls are rather small and compact, others are large.

With further development a second and third irregular row of whorls form. Soon throughout the entire tissue dense aggregations of cells appear as the anlage of other whorls. Wicki (1926) is of the opinion that these aggregations of cells are made up of leucocytes. Our observations are not in confórmation with this opinion. While there may be a few

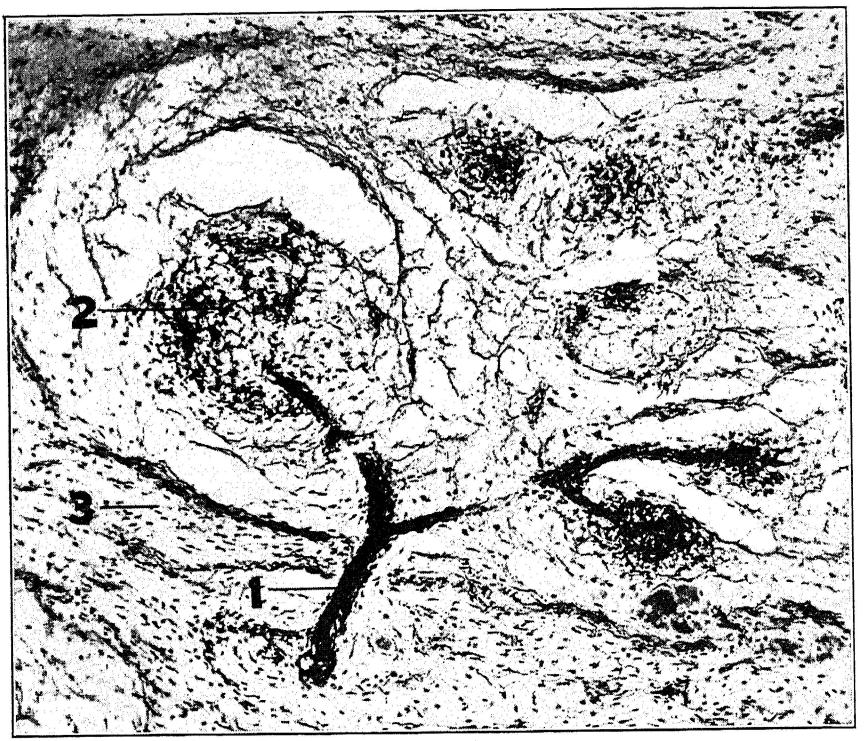

Fig. 16.—The vascularization of these aggregations of connective tissue cells soon becomes noticeable. The adipose nature of the tissue also becomes apparent. (Fetus 29.5 cm. long) 1. Blood vessel. 2. Cell whorls (Capillary network) 3. Mesenchyme tissue.

lymphocytes present, the whorls of cells are composed essentially of connective tissue cells some of which differentiate further into adipose tissue.

The central cells of these aggregations gradually indicate their adipose nature by storing fat in the cytoplasm. As the fat droplets were not fixed with osmic acid, they appear as large empty spherical cells. In many cases the tufts of cells are separated by fibrous connective tissue, while in some cases a number of tufts are associated together with the fibrous connective tissue cells surrounding the group. In a 60 cm. fetus the development of the adipose tissue had become very extensive throughout the udder tissue above and around the cistern and duct system. The formation of the fat pad or cushion at this time appears to be complete.

Fig. 17.—The gradual storage of fat in these cells is indicated by the spherical adipose cells. The capillary connections can be observed. (Fetus 36 cm. long) 1. Blood vessel. 2. Fat cells. 3. Mesenchyme tissue (Connective tissue).

Rein (1881) was first to note the differentiation of the mesenchyme tissue of the udder in the bovine fetus. In a 19.5 cm. female he saw the characteristic arrangement of connective tissue cells in groups, which

on cross-section showed round globules indicating the presence of fat in the cells. In a female 39 cm. long the fat lobules were already completely developed.

It is further reported by Rein that the adipose tissue increases rapidly in circumference and becomes a definite fat cushion, which is divided into individual sections by scattered connective tissue septa. The fat cushion develops toward the cistern and milk ducts (secondary sprouts) until the latter are separated from the fat cushion only by a connective tissue septum.

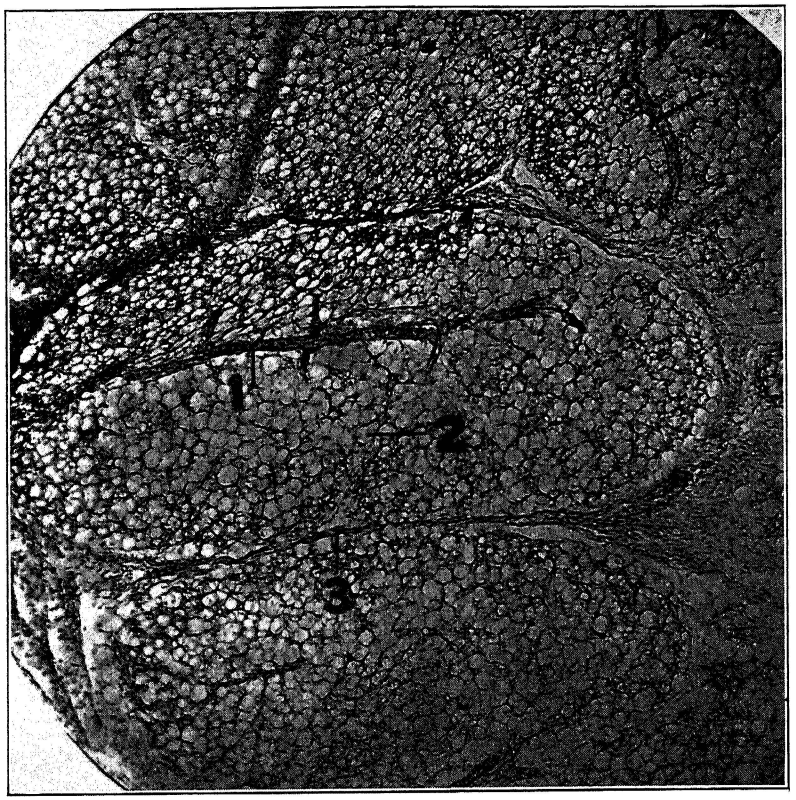

Fig. 18.—The larger part of the udder tissue is gradually transformed into adipose tissue. The aggregations of fat cells are surrounded by connective tissue septa. It is possible that the separation of the future gland into lobules is determined by these septa. (Fetus 60 cm. long) 1. Blood vessel. 2. Fat cells. 3. Connective tissue septum.

Wicki (1926) described in detail a peculiar coiled shaped capillary network containing numerous fat cells which developed in connection with the whorl of connective tissue cells previously described. In a 25.5

cm. fetus in which the mesenchyme tissue is still present groups or whorls of cells were observed composed of leucocytes. Wicki describes them as consisting of from 50 to 100 mononuclear leucocytes among which often erythrocytes and large double nuclear leucoplasts are located. To a few of these accumulation of cells fine capillaries can be traced. Simultaneously but separately, there occurs the transformation of embryonic tissue into adipose tissue.

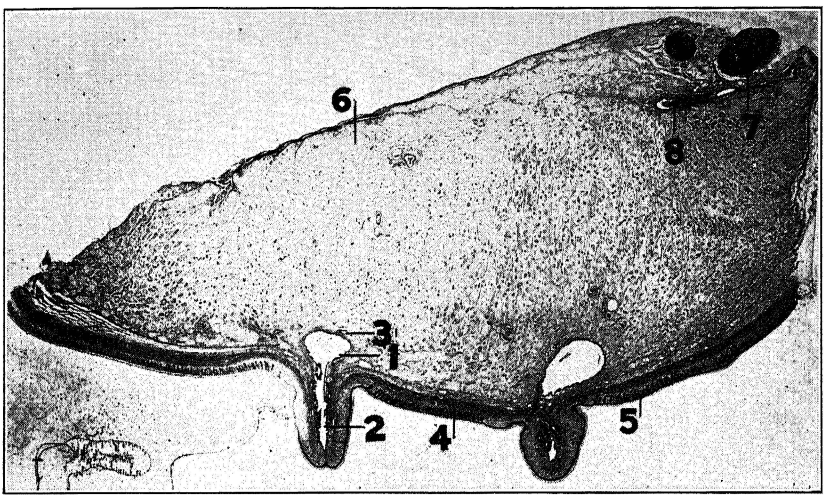

Fig. 19.—The development of the adipose structures is observed in this 48 cm. fetus. The greatest deposition of fat is noted in the upper parts of the udder. The region surrounding the cisterns is the last to become transformed. 1. Cistern of gland. 2. Cistern of teat. 3. Secondary sprouts (ducts). 4. Skin (epidermis and dermis). 5. Hair follicles. 6. Fat lobules. 7. Supramammary lymph gland. 8. Vein.

Structure of the Teat

The initial stages in the development of the teat were described in the previous report. At that time the teat was made up of mesenchyme tissue into which the primary sprout had begun to grow. The external covering was composed of a Malpighian layer with several further layers undergoing cornification.

The differentiation of the skin of the teat is similar to that already described except that the teat is free of hair and the dermis or corium is reduced to a thin layer. The epidermis covers the entire exterior of the teat including the streakcanal. Above the streakcanal, the many layered epithelium quickly changes over into a two layered cistern epithelium. Even in the oldest fetuses (84 cm.) neither the skin nor the streakcanal of the teat were underlain with papillary eminences described by Mankowski (1903) in the mature teat. However, these eminences

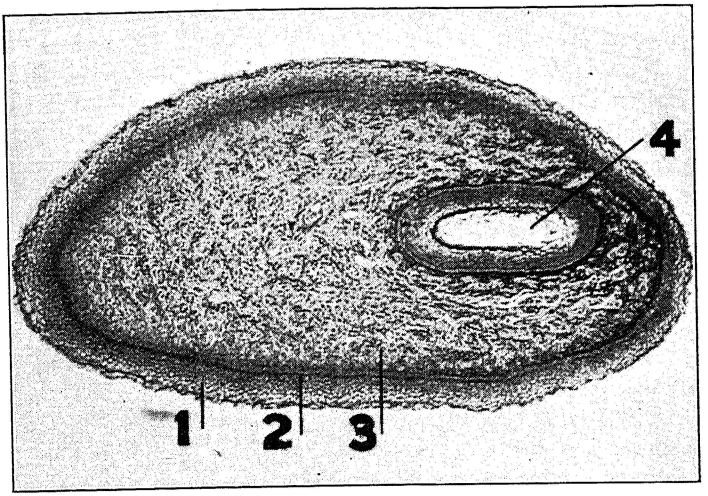

Fig. 20.—Cross section of the teat of a 70 cm. male fetus close to the tip end. It will be noted that the epidermis is composed of many layered pavement epithelium. The entrance to the streakcanal is similar in structure. Irregularly arranged connective fibers characterize the dermis. The absence of papillary eminences may be noted. 1. Epidermis. 2. Malpighian layer. 3. Dermis. 4. Residue of mammary bud.

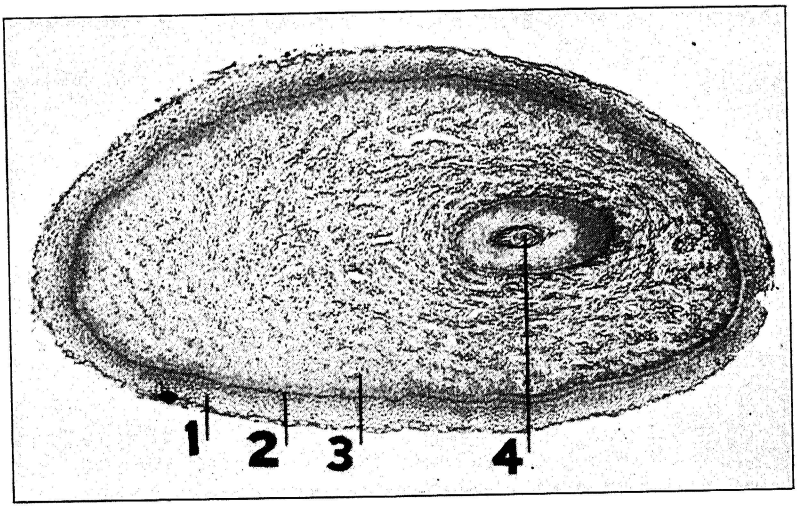

Fig. 21.—A cross section of the above described teat in the region of the streakcanal. A cornified plug is still present in the canal. Surrounding the canal elastic connective and possibly smooth muscle cells which will eventually form the sphincter muscle are present. In the middle zone of the teat a few blood vessels may be seen. 1. Epidermis. 2. Malpighian layer. 3. Dermis. 4. Streakcanal (unopen).

must develop shortly after as Zschokke (1920) noted their presence in 6-14 day old calves.

It will be noted in Figures 20 and 21 that cross section of the teat either below or in the region of the streakcanal show pavement epithelium not only outside of the teat but also in the central orifice, whereas above the streakcanal, the cistern is characterized by a two-cell-layered epithelium.

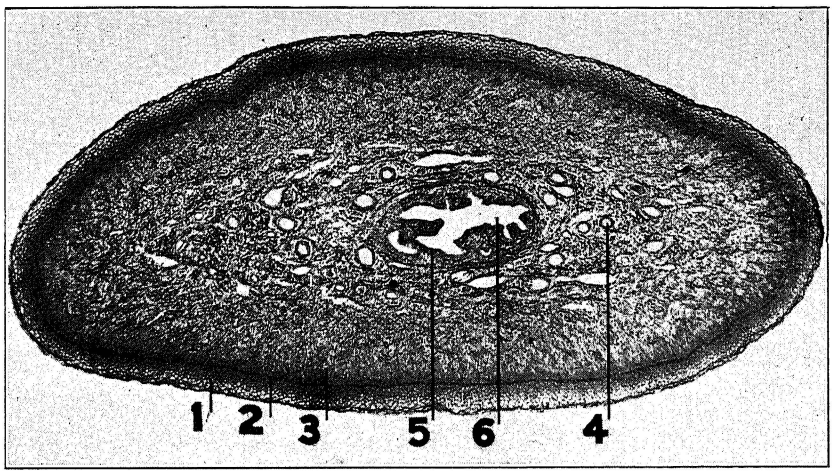

Fig. 22.—A cross section of the teat in the mid section. The irregular nature of the wall of the teat cistern may be observed. The development of the vascular zone of the teat is quite striking. The cistern is lined by a two layered epithelium. 1. Epidermis. 2. Malpighian layer. 3. Dermis. 4. Vascular zone. 5. Epithelial layer (not clear). 6. Cistern of teat.

The sphincter muscle surrounding the streakcanal has not become well developed. The elastic connective tissue fibers are circularly disposed but smooth muscle cells cannot be definitely identified.

The vascular zone is quite prominently developed in the mid section of the teat previous to birth. A prominent coronary vein was observed at the base of the teat in the transitional zone between the cistern of the teat and gland. The formation and nature of the epithelial lining of the cistern system has already been described.

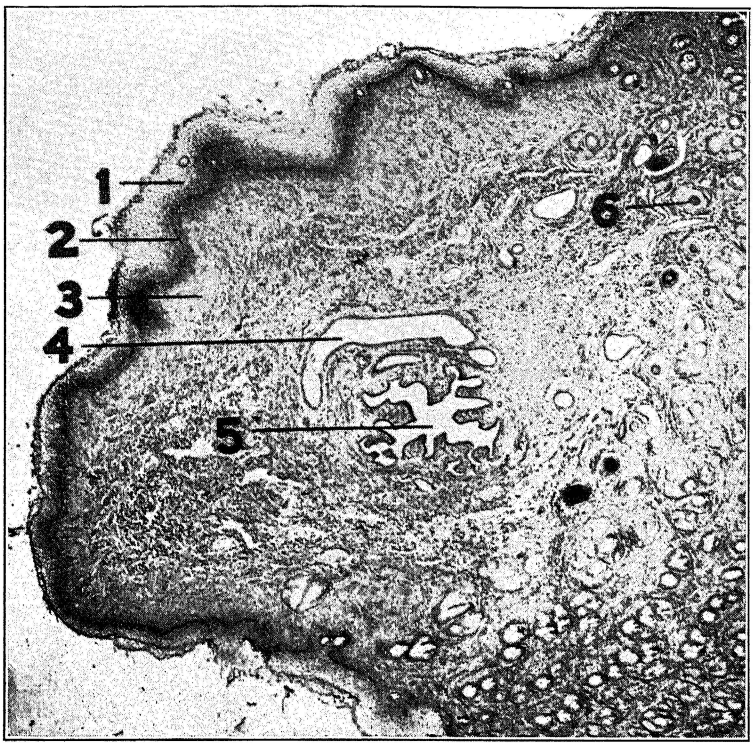

Fig. 23.—A section of the teat at the attachment to the udder. The presence of a large coronary vein partly surrounding the cistern is noted. The prominent vascular zone observed in the previous section no longer appears. 1. Epidermis. 2. Malpighian layer. 3. Dermis. 4. Coronary vein. 5. Teat cistern. 6. Hair follicles.

Supernumerary Teats

In addition to the four "normal" teats and mammary glands in cattle, there may be a variable number of additional teats, some of which are the orifice of small glands, others may be without glands, and yet others which may open into one of the normal glands.

Burckhard (1897) considered the supernumerary teat as abortive in structure. This would mean that the anlage of the gland of the supernumerary frequently was very weak and that after birth and during pregnancy the gland failed to develop.

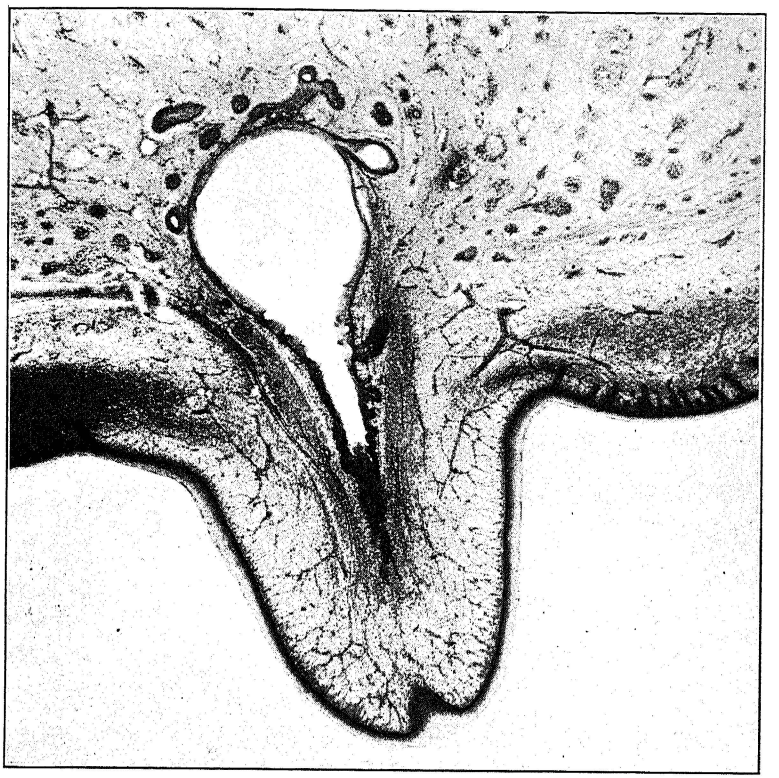

Fig. 24.—A section of a teat of a 34 cm. fetus showing the development of the vascular system at this stage.

From the standpoint of structure there is considerable variation in the extent of the development of the supernumerary teat. Burckhard found in some cases that the teat consisted of a conical elevation of the skin without teat canal or gland which he called a *pseudo-teat.* He considered this a case of hyperthelia or polythelia, the technical terms for a multiplicity of teats.

A second type consists of a small mammary gland with a small teat, streakcanal, cistern and gland anlage. This gland structure is called a *micro-gland*, and the teat a *micro-teat.* This condition is called *hypermastia* or *polymastia*, meaning a multiplicity of glands.

In the present study the structure of the supernumeraries have not received special attention.

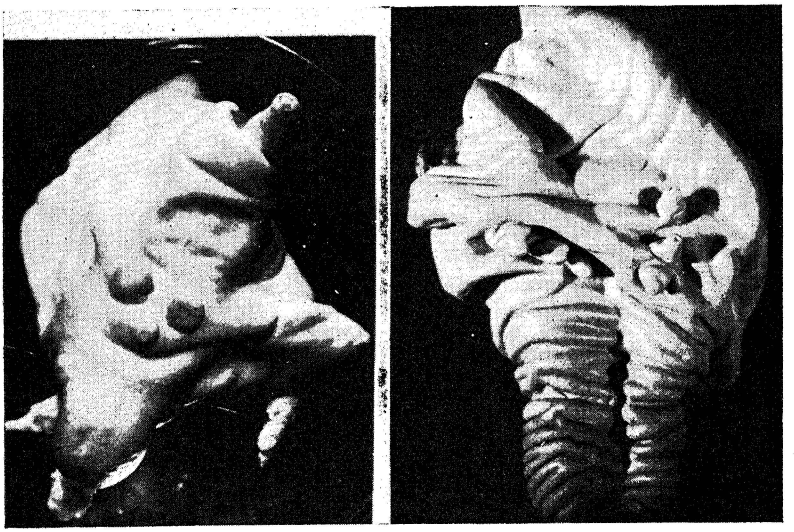

Fig. 25.—The minimum and maximum number of teats observed in the male bovine fetus are shown. The three-teated condition was present in the Hereford fetus No. 37 while six teats were observed in Holstein fetus No. 24.

Frequency of Supernumerary Teats

Of the 100 bovine embryos and fetuses examined, the sex of the five smallest embryos was not determined. Of the older animals 45 were found to be females and 50 were found to be males. However, five females and three males were so small that the teats could not be detected by gross inspection. One of these, a male embryo 2.5 cm. long upon section showed a structure which is believed to be the anlage of a supernumerary teat. (See Fig. 7 in Mo. Res. Bul. 140).

The 87 remaining embryos and fetuses are believed to have been of sufficient size to show the presence or absence of supernumerary teats by gross inspection. The frequency of the supernumerary teats is presented in Table 3. Of the 40 females examined, 10 had one extra teat, and 10 two extra teats making a total of 50 per cent with supernumerary teats.

One male fetus was observed with only three teats, 37 with four teats, 6 with five teats and one with six teats (or rudimentaries). Thus only about fifteen per cent of the males had more than four teats as compared to fifty per cent in the females.

TABLE 3.—THE FREQUENCY OF SUPERNUMERARY TEATS IN BOVINE FETUSES

With	Female		Male		Total	
	Frequency	Percentage	Frequency	Percentage	Frequency	Percentage
4 teats	20	50	39	83.0	59	67.8
1 supernumerary	10	25	6	12.7	16	18.4
2 supernumerary	10	25	1	2.1	11	12.6
3 only	--	--	1	2.1	1	1.1
Total	40		47		87	

Development of the Supramammary Lymph Gland

The supramammary lymph glands are the centers of the lymphatic system in the udder. They are located on the posterior dorsal surface of the udder in each half. They can be observed in the series of sections of the udders showing the variation in form

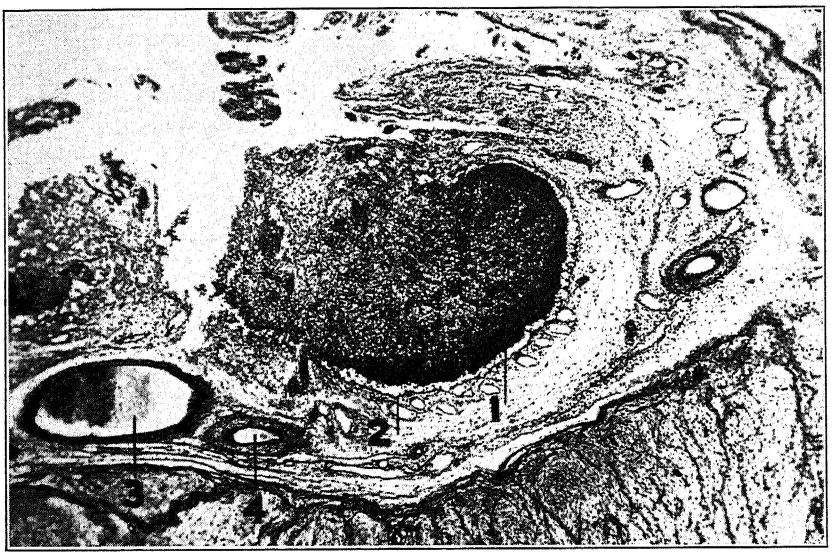

Fig. 26.—The structure of a supramammary lymph gland of a 16 cm. embryo is shown. The infiltration of lymphocytes into the lymph gland has begun. The capsule of connective tissue is forming. 1. Lymphoid tissue. 2. Capsule. 3. Vein. 4. Artery.

The study of the formation of the lymphatic system has not been attempted. In a 16 cm. fetus, the lymph gland was already quite well developed. The central mass of lymphoid tissue composed of a network of white fibers and deeply staining lymphocytes is clearly seen. Surrounding the gland is noted a peripheral lymph sinus and covering the the entire gland is a capsule of young connective tissue.

Further development of the lymph glands is noted in fetuses of 29.5 cm., 36 cm., and 48 cm. length. Accessory supramammary glands were observed in a number of cases.

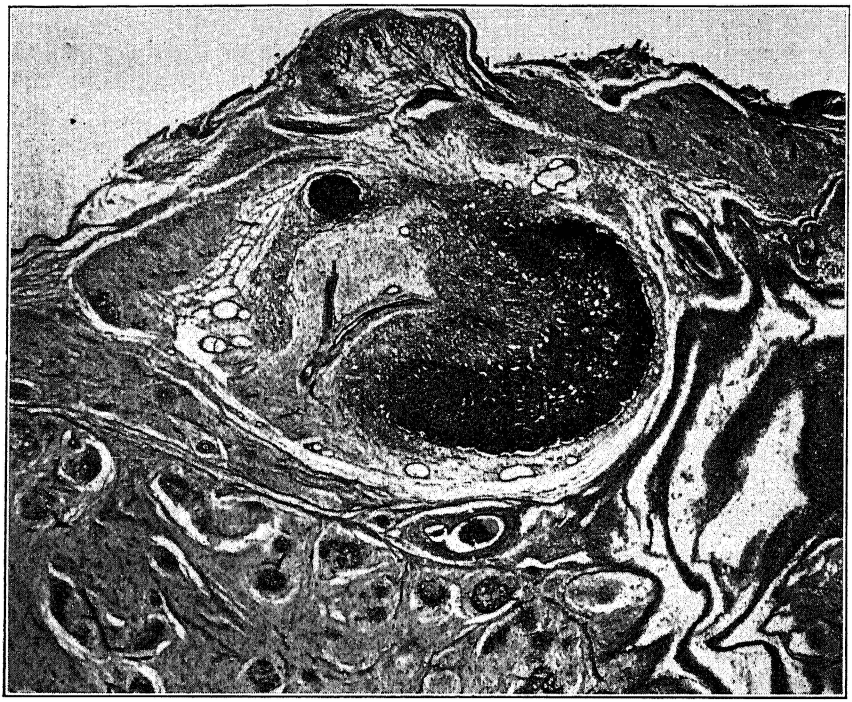

Fig. 27.—Further development of the supramammary lymph gland may be noted in this 29.5 cm. fetus. An accessory gland is forming.

Fig. 28.—Supramammary lymph gland of a 36 cm. fetus. The development of adipose tissue around the lymph gland can be noted.

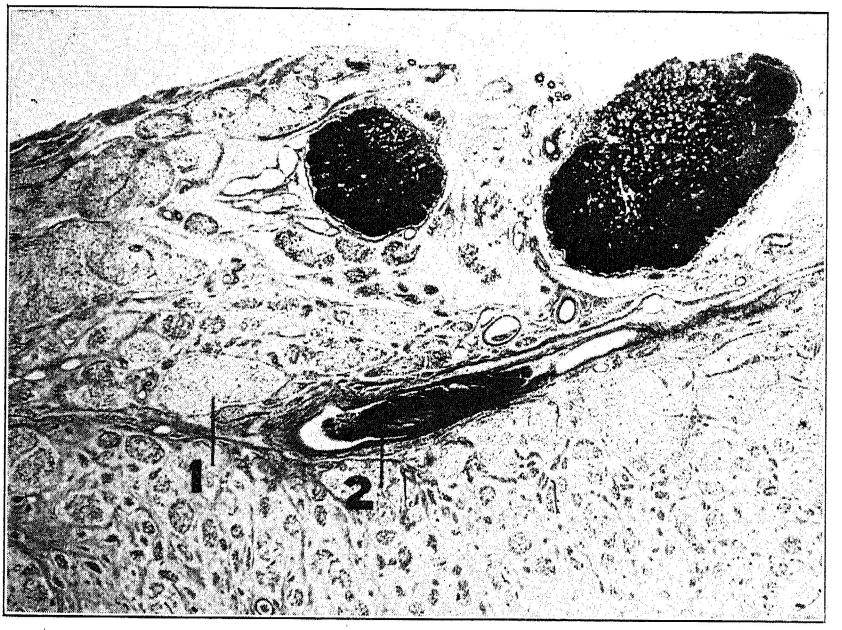

Fig. 29.—In this 48 cm. fetus the supramammary lymph gland has become entirely encapsulated. A well developed accessory gland is also shown. The development of the adipose tissue has continued in the region of the lymph gland. 1. Lobule of fatty tissue. 2. Vein.

The Union of the Glands

As observed in the early development of the mammary glands, there are four normal structures represented by the mammary buds which later develop into teats. Most of the glands were sectioned showing the fore and rear quarters of the half. In these sections it is apparent that the formation of the fore and rear glands are quite separate and distinct. Even at birth the ducts of the two quarters are widely separated. That this separation of the ducts and glands continues with the completion of the development of the udder during pregnancy has been

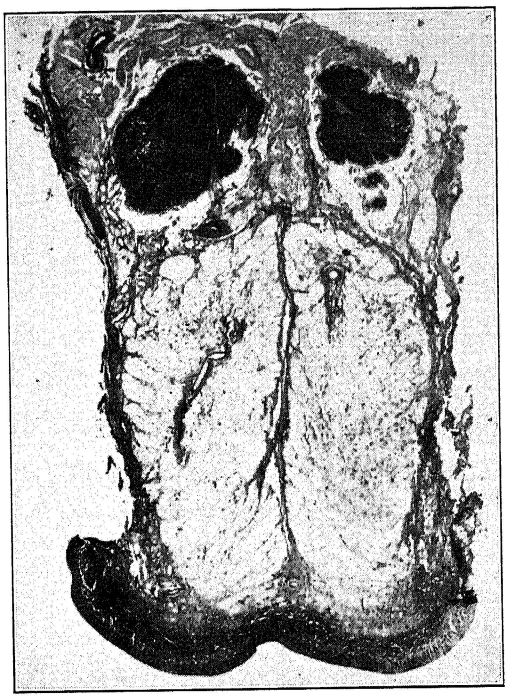

Fig. 30.—A cross section of the udder of a 59.5 cm. fetus The connective tissue capsule enveloping each half with a well defined median connective tissue septum may be seen. The large supramammary lymph glands are shown in relation to the udder.

demonstrated by the injection of dye into the quarters. The division of the front and rear quarter is a thin connective tissue septum.

Each half of the udder is enclosed in a connective tissue sack which unites medially to form the thick median septum. The development of the median septum has not been traced in the early udders. However, gross examination of the preserved udders indicates the early formation

of a definite membrane. By the time the fetus has reached the 60 cm. stage the median connective tissue septum is well developed.

The Bovine Udder at Birth

In closing the present study of the intrauterine growth of the bovine mammary gland and udder, it is of interest to describe the extent of mature development attained at the close of this epoch.

Considering first the extent of the growth of the actual secretory apparatus, it will be noted that the central collecting place for milk consisting of the cistern of the teat and gland has reached essentially mature form. Further changes in these structures consist largely in growth in size as maturity is reached.

The secondary sprouts at birth have made only slight development as compared to that which takes place during the recurring estrus cycles and pregnancy. Adjoining the cistern of the gland, these sprouts have canalized but at the growing ends of the sprouts solid cellular structures still persist. These ducts and growing sprouts are confined to a very limited area around the cistern of the gland. Extensive growth of the duct system followed by the proliferation of the secretory alveoli await the sexual maturity of the animal.

As far as the actual secretory apparatus is concerned, there is little difference in the extent of development in the male and female. It should be noted, however, that at times the cistern of the gland and teat of the male are not as well differentiated as in the female.

The non-glandular structures of the bovine udder at birth are rapidly approaching their mature form. One of the outstanding observations was the early development of the morphology of the udder. With slight exceptions, the skin and hair covering the udder appear as in the adult. The vascular and lymphatic systems are layed out essentially as in the mature udder. While the morphological development of the teat is practically complete some of the histologic elements such as the smooth muscle elements continued to develop.

The adipose and other connective tissues are well organized at birth. The development of the adipose tissue into a distinct fatty pad or cushion making up the larger part of the udder is very striking. The separation of the aggregation of adipose cells by distinct connective tissue septa may be the forerunner of the gland lobules. Only a careful study of the histogenesis of the gland lobules during pregnancy will definitely prove the relation of the gland lobule to the adipose tissue lobules of the udder at birth.

The apparent growth of the udder following birth and until conception occurs consists largely in the further deposition of fat and growth of other non-glandular structures.

SUMMARY AND CONCLUSION

1. In a previous study the early development of the bovine mammary gland was described. It was shown that two mammary buds develop from each mammary line, the early anlage of the future udder half. From the mammary buds, single primary sprouts invaginate each developing teat.

2. In the present study the canalization of the primary sprout forming the streakcanal, the cistern of the teat and the cistern of the gland is described.

3. From the upper end of the primary sprout which has begun to canalize, secondary sprouts begin to develop which upon canalization form the primary milk ducts entering the cistern of the gland.

4. It was observed that the morphology of the udder of the female develops at a very early stage whereas in the male udder, development is entirely lacking.

5. The differentiation of the skin from the embryonic tissue and the development of the hair buds is described.

6. The transition of the mesenchyme tissue constituting the larger part of the udder into pockets or lobules of adipose tissue surrounded by connective tissue septa is believed to give a clue as to the mode of formation of the future gland lobules.

7. The essential structures of the fetal teat at various levels are described.

8. The frequency of the supernumerary teats in the material available for study were tabulated. It was observed that the frequency of these structures in the female far surpassed those of the male.

9. Several stages in the development of the supramammary lymph glands are illustrated.

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