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The Causes of the Growth and Function of the Udder of Cattle

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The Causes of the Growth and Function of the Udder of Cattle

C. W. Turner

Nature has long hidden the process by which the mammary glands (called the udder in cattle) are prepared during pregnancy to begin to secrete milk abundantly immediately following calving or parturition. Yet the life of all mammals (milk producing animals) depends upon the success of this process, as the young would die if the mother or foster mother were not prepared for this important function.

In the case of most mammals, it is sufficient for the mother to be capable of secreting milk for her own young, but with dairy cattle this function has been developed so that the surplus milk has made possible the development of the dairy industry which furnishes, in a variety of forms, unexcelled food for human nutrition.

Primarily because of the importance of knowledge concerning dairy husbandry and milk production, great interest has developed during recent years in the causes of the growth of the mammary gland and the stimulation of milk secretion. At the same time the results of the studies in this field are of interest to breeders of all types of live stock. As much of the advance in the field of clinical medicine is based upon animal experimentation, the results of the studies of milk secretion in animals will lay the foundation for the study of this problem of human physiology.

It is well known that the growth of the udder in heifers and the renewal of milk secretion in older cows are related to the process of reproduction. During the period of pregnancy, with the growth of the embryo or fetus in the uterus, there is rapid growth of the secretory tissue of the udder, accompanied at the approach of calving time by the initiation of milk secretion. Since early times, man has speculated about the regulation and control of the mammary glands and of milk secretion in relation to the reproductive process. (Fig. 1).

Before 1895 it was commonly thought that there must be a direct nervous connection between the uterus and the mammary glands. It was soon shown that the normal nervous connections could be severed in pregnant animals and the mammary glands would still continue to grow and secrete milk after parturition. Further, the mammary glands of the experimental animals could be removed and grafted into other parts of the body successfully with subsequent growth and secretion.

These experiments led to the belief that the mammary glands, in common with certain other organs of the body, were stimulated by some substance flowing in the blood stream. With progress in the study of this problem, small structures were found scattered over the body, whose function it was to secrete such substance.

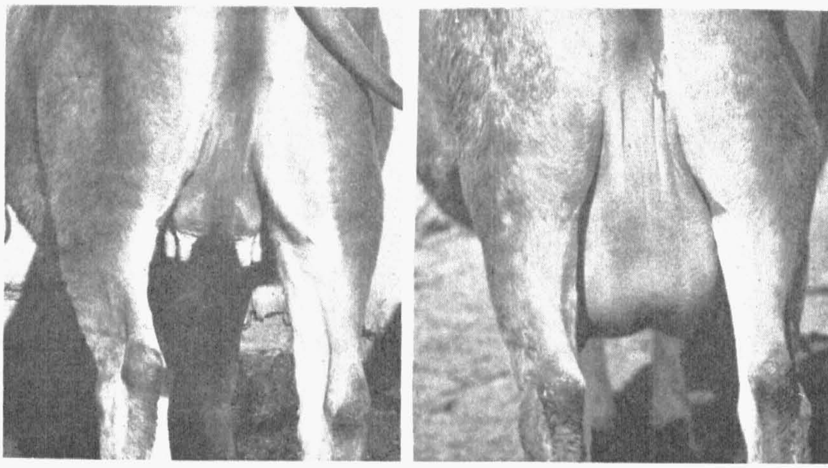

Fig. 1.—External change in the udder of a heifer during the first pregnancy. Dairymen have long speculated on the cause of the growth of the udder during pregnancy and the preparation for milk secretion at calving time. As the result of recent research, it is now possible to describe the hormones which play an important role in the change of the udder seen above.

As these structures did not have ducts into which they poured their secretion, they were called *ductless or endocrine glands* and the products were called *hormones or internal secretions* (Fig. 2). Within recent years a large number of hormones has been discovered, some of which have come into widespread use for the replacement of deficiencies in the body. Of these insulin from the pancreas and thyroxin from the thyroid gland are probably the most widely known. Research concerned with the nature of these substances indicate that the hormones are definite chemical compounds having the ability to stimulate activity of the cells of certain organs of the body even in very minute dilutions in the blood.

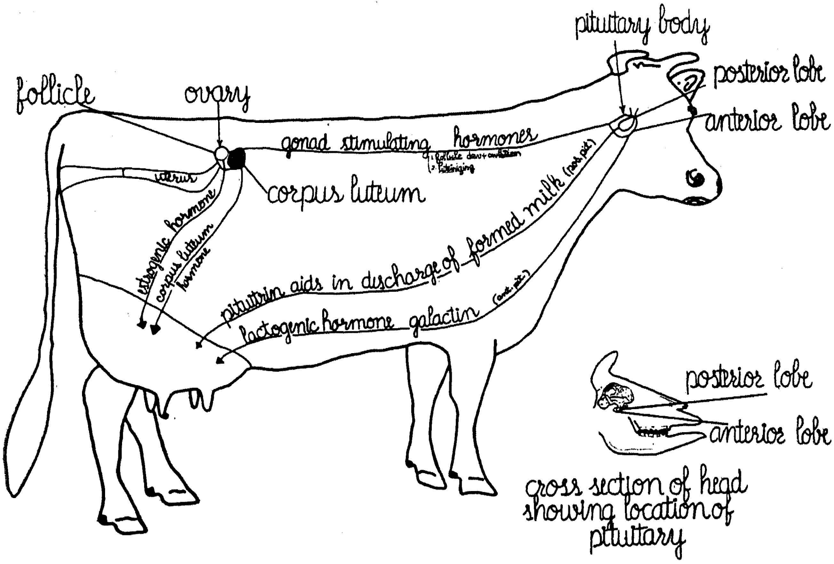

Fig. 2.—Location of the various glands of internal secretion which secrete hormones influencing the mammary gland.

THE ESTROGENIC HORMONE

As early as 1906 Lane-Claypon and Starling in England tried to determine the source of the hormones stimulating the growth of the mammary gland. Their trials with watery extracts of placenta, fetuses, and ovaries were not successful due to insufficient amounts of the hormones present in their extracts. A number of other investigators tried to stimulate mammary gland growth

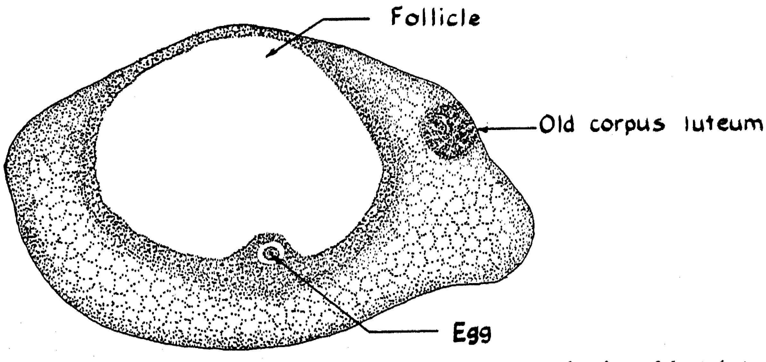

Fig. 3.—A cross section of the ovary (gonad) of the cow at the time of heat (estrum) showing a large follicle filled with fluid containing the estrogenic hormone. Attached to the wall of the follicle is an ovum or egg. In about 24 to 36 hours after estrum, the follicle ruptures, allowing the follicular fluid to flow out, carrying the egg into the Fallopian or egg tube. After the discharge of the egg and fluid from the ovarian follicle, a blood clot at first fills the cavity. (See Fig. 15 for subsequent changes.)

with various extracts in the years following with but little success.

The first marked success in stimulating the growth of the mammary glands followed the discovery of Doctors Edgar Allen and E. A. Doisy, two Missouri investigators, that the follicular fluid of the ovary (called the gonad) contained the hormone which caused animals to come "into heat" or into estrum (Fig. 3). They also devised a rapid biological test for the detection of this estrus-producing hormone, using castrated female rats. Many names have been given to this ovarian hormone, including the female sex, estrus-producing, estrogenic, estrin, theelin, folliculin, etc. The writer will refer to this hormone as the *estrogenic hormone.*

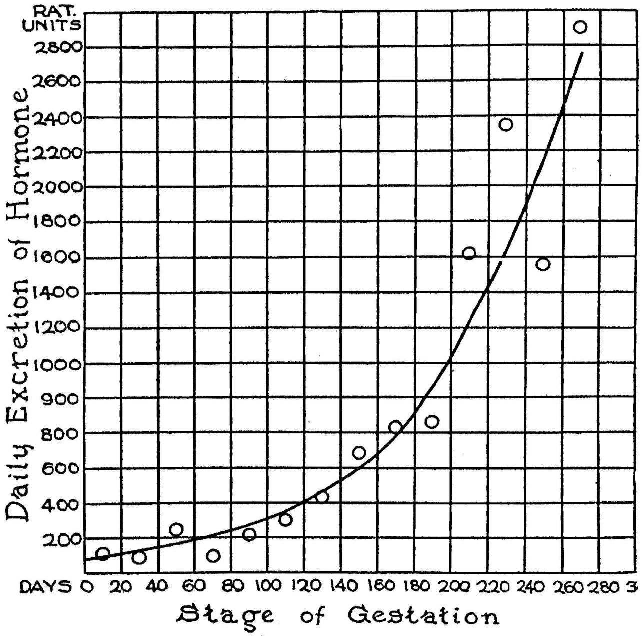

Fig. 4.—The average rate of passage of the estrogenic hormone into the urine. The same group of cows was used throughout the experiment. After parturition the rate of excretion drops very rapidly so that within a few days the hormone is no longer excreted.

The estrogenic hormone is secreted by the cells of the ovary into the follicular fluid. It then passes into the blood stream and is eventually excreted by the body into the urine. In animals "in heat" the hormone has been found in the ovary, blood, and urine. When animals become pregnant the amount of this hormone excreted in the urine increases gradually until parturition (Fig. 4).

It is also found in the blood, and in the placenta or "after birth" as well as in the amniotic fluid in which the fetus floats during pregnancy. Whether the placenta secretes the hormone or only stores it is still an open question.

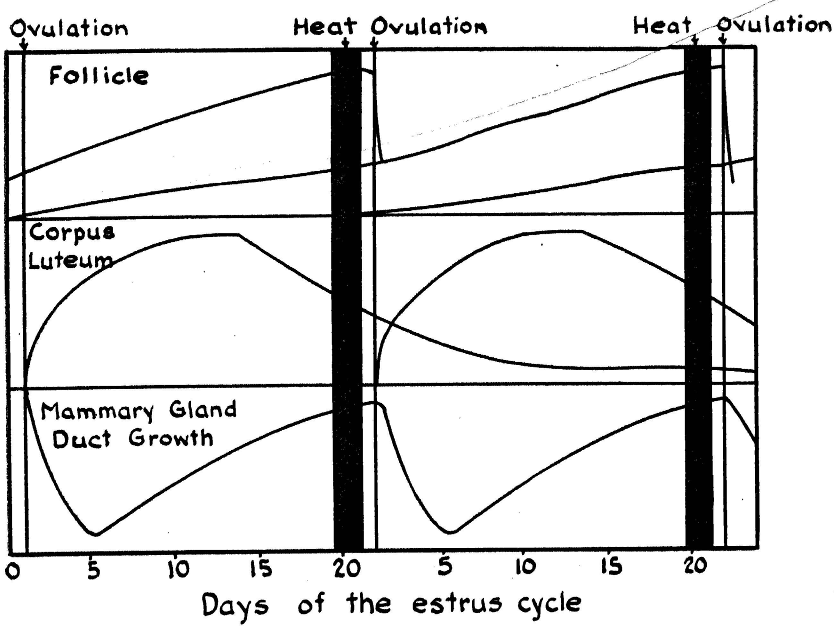

Fig. 5.—The relation of the growth of the ovarian follicle and corpus luteum to that of the mammary gland duct system. It will be noted that duct growth and follicle growth go together due to the estrogenic hormone stimulating duct growth. The corpus luteum hormone does not stimulate lobule-alveolar development during the recurring estrus cycles, only during pregnancy when its influence is long continued is it effective.

The estrogenic hormone stimulates a wave of growth of the accessory genital organs of the female, especially of the epithelial cells lining the vagina and uterus. It also stimulates the mating reaction of an animal "in heat" (Fig. 5).

THE RELATION OF THE ESTROGENIC HORMONE TO THE MAMMARY GLAND

With the isolation of the estrogenic hormone and its availability in large amounts, it became possible to determine its effect upon the mammary gland. Because of the cost of the hormone, small experimental animals have been used in the work. The results are so consistent in the various species which have been used that there is little question but that the same results would be obtained with cattle and other large domestic animals and man.

Examination of the udder of dairy calves before reaching sexual maturity (the first estrum) reveals four very rudimentary mammary glands, each consisting of a small teat and milk cistern. The ducts leading out from the cistern are small and short with few branches (Fig. 6). After reaching sexual maturity the duct sys-

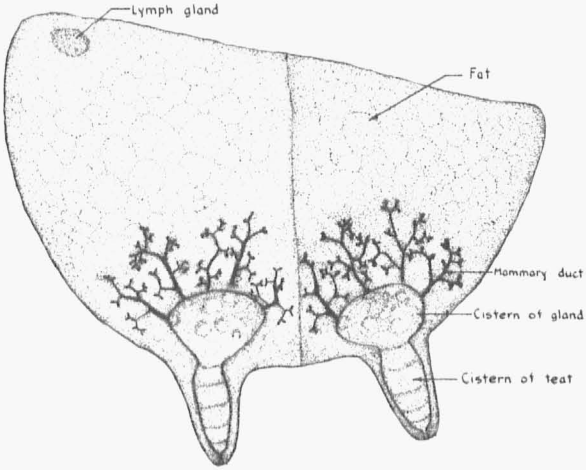

Fig. 6.—Diagram of a cross section of the udder of a heifer before reaching sexual maturity. At this stage the glands consist of a small teat and milk cistern. The ducts leading out from the cistern are small and short with few branches.

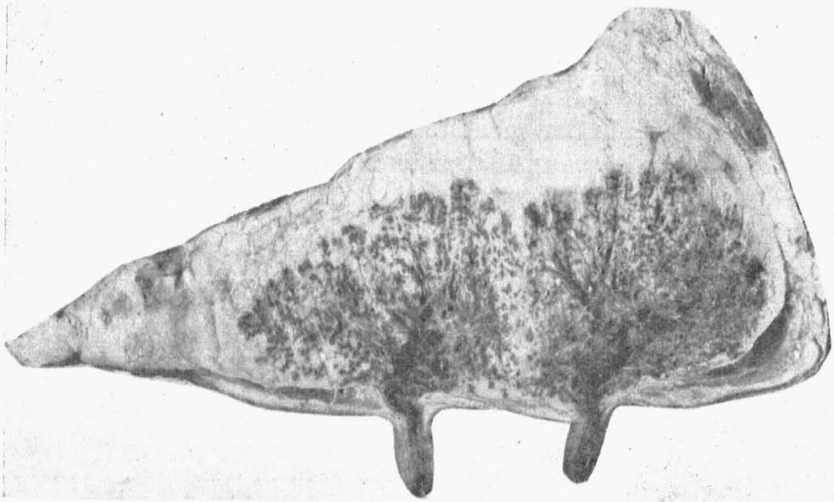

Fig. 7.—Cross section of the udder of an un-bred heifer showing the development of the duct system after a number of heat periods. Note the fatty pad of tissue into which the ducts extend. It will be seen that the front and rear glands are separate structures which eventually come to lie very close together.

tem begins to grow and branch out into the fatty pad of tissue at the time composing the udder. With each successive "heat period" further growth of the duct system occurs (Fig. 7). If the heifers are not bred or do not conceive, the duct system eventually becomes quite extensive, but never in any way comparable to the extent of growth observed at the end of pregnancy (Fig. 8). If such heifers are milked they will usually secrete a small amount of fluid in the ducts but again the amount is in no way comparable to that of a heifer at calving time.

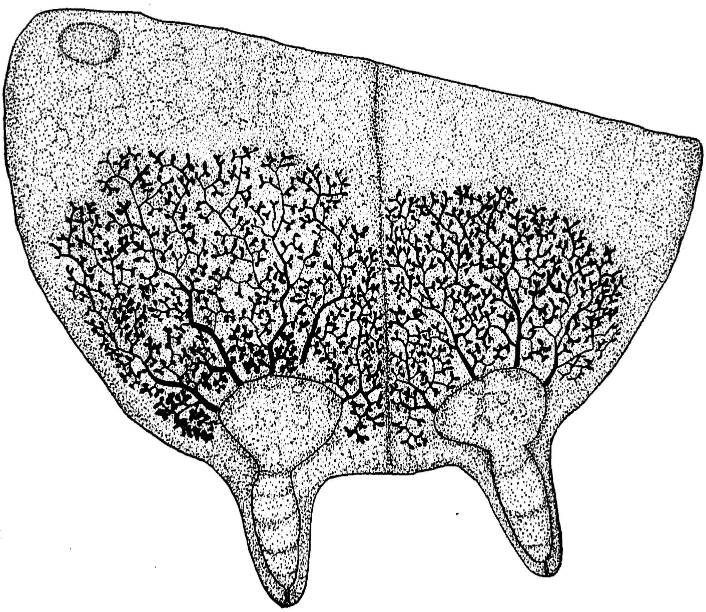

Fig. 8.—Diagram of a cross section of the udder of a heifer after many "heat periods". The duct system shows extensive development but the lobule-alveolar system is not stimulated to growth.

The injection of the estrogenic hormone into female animals before the mammary duct system has developed or in males where the duct system usually fails to develop, has been found to stimulate extensive growth of the duct system comparable with the mammary glands developed in similar species of mammals after a succession of estrus cycles. These experimental studies are believed to indicate that the estrogenic hormone not only stimulates the growth of the vagina and uterus and produces the mating reaction at each successive heat period (estrus) but causes also the cyclic growth of the duct system of the mammary gland. The duct system at this stage of growth may be likened to the trunk and large branches of a leafless tree (Fig. 9).

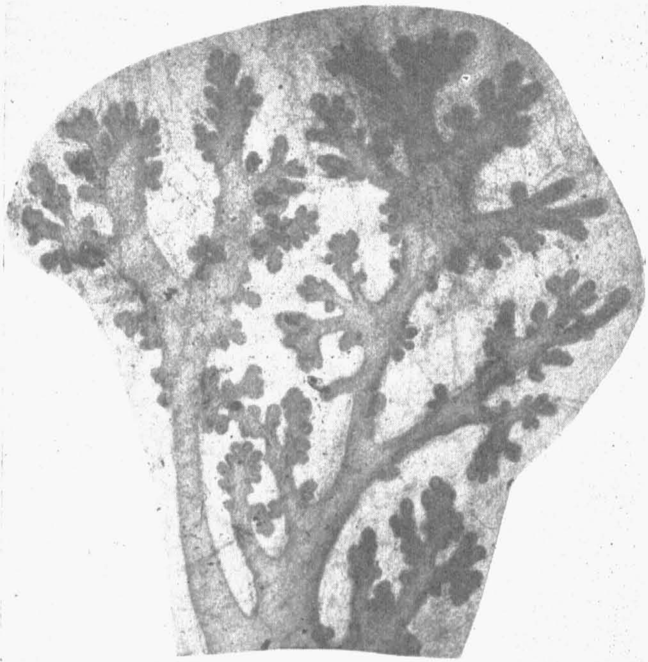

Fig. 9.—After the duct system of the mammary gland has been stimulated to extensive growth by the estrogenic hormone of the ovary, it may be likened to the trunk and large branches of a leafless tree.

GROWTH OF THE MAMMARY GLANDS DURING PREGNANCY

The udder in heifers before they are bred for the first time consists of a small cistern in each quarter with a more or less extensive duct system depending upon the age and the number of previous estrus cycles. Following breeding and conception, there is rapid growth and extension of the duct system to all parts of the udder. Numerous side branches also form from which tiny cellular end-buds called alveoli eventually develop. These alveoli are at first solid but later open up and enlarge due to the secretion of milk into the central cavity (Fig. 10).

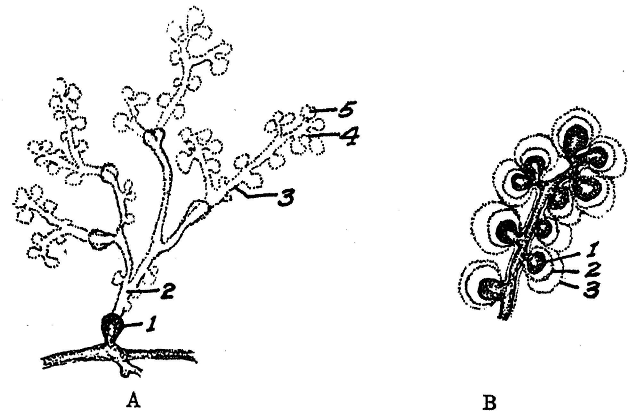

Fig. 10.—A. Drawing showing the formation of the lobule-alveolar system. 1. The first stage consists of a bud-like outgrowth on the wall of the duct. 2. The bud grows into a duct and divides with the formation of several branches (3). 4. These ducts branch further to form tiny cellular end-buds called alveoli (5). B. Drawing showing the gradual enlargement of the alveoli during the latter part of pregnancy with the gradual initiation of milk secretion and its discharge into the lumina of the alveoli.

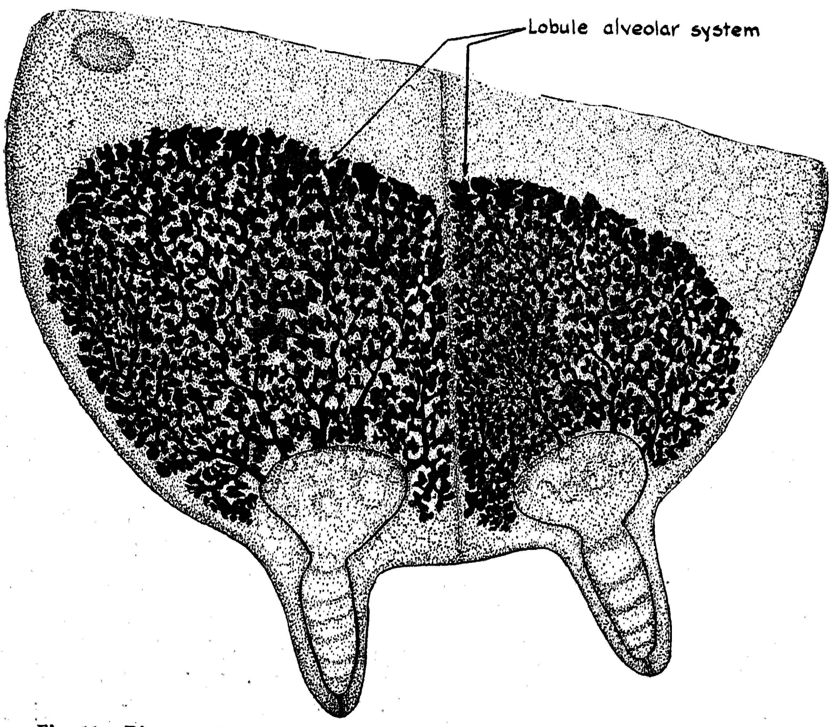

Fig. 11.—Diagram of a cross section of the udder of a heifer at about the fifth month or the middle of pregnancy. From the ducts shown in Fig. 8 the lobule-alveolar system has grown, due to the combined stimulus of the estrogenic and corporin hormones.

The growth of the gland during pregnancy may be compared to the leafing out of a tree in which the leaves represent the alveoli and the branches the connecting ducts. A somewhat better comparison would be to consider the alveoli as grapes and the ducts, the branching stems. A group of alveoli corresponding to a bunch of grapes is called a lobule, and a group of lobules is called a lobe. These various divisions of the gland tissue are surrounded and supported by bands of connective tissue (Fig. 11).

Observations in heifers indicate that the growth of the entire lobule-alveolar system is complete at about the fifth month or roughly during the first half of pregnancy (Fig. 12). During the

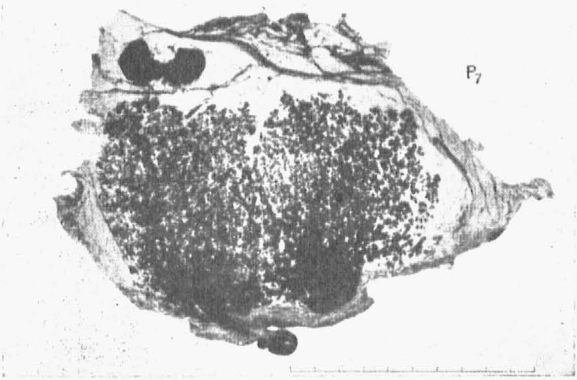

Fig. 12.—Cross section of the udder of a heifer pregnant six months. At this stage of development, the growth of the lobule-alveolar system is complete. Note the pad of fat still visible in the upper part of the udder. (From Hammond.)

second half of pregnancy, the tiny epithelial cells bordering the alveoli of the lobules gradually enlarge and begin to secrete a fluid into the central cavity or lumina of the alveoli, thus gradually causing the enlargement of the alveoli to many times their former size (Fig. 13 and 14).

Because of the rapid enlargement of the udder during the second half of pregnancy, it has been commonly thought that the greatest growth takes place during the latter part of pregnancy. As indicated above, nothing could be further from the truth. The actual growth of the gland takes place during the first half of pregnancy, whereas the enlargement of the udder during the second half is due to the gradual accumulation of the products of secretion which are not usully removed until after calving time.

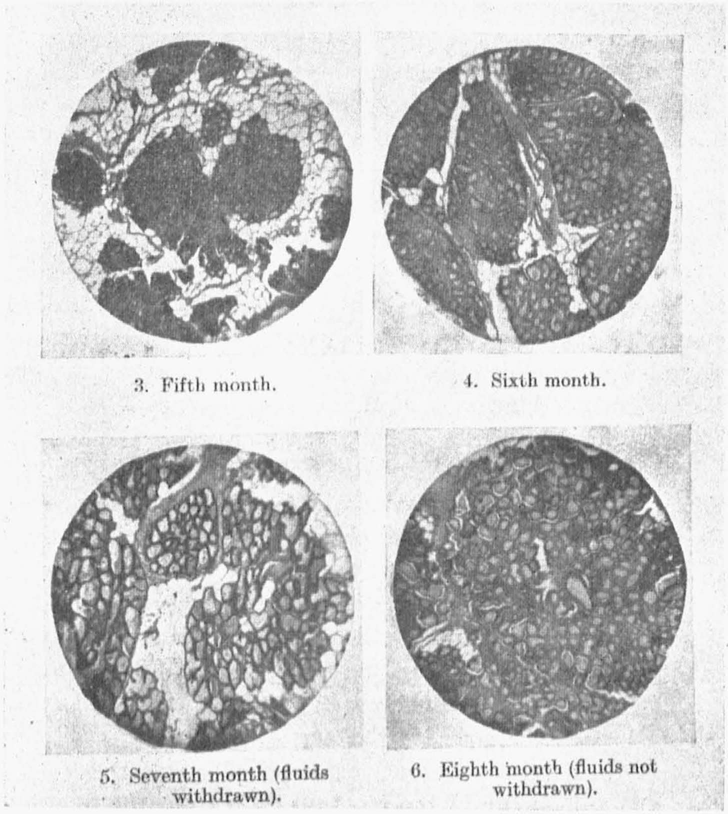

Fig. 13.—The gradual initiation of secretion in the alveoli of the mammary gland during the last part of pregnancy. During the first half of pregnancy, the growth of the ducts and alveoli occurs. Then the cells bordering the alveoli gradually begin to secrete a fluid into the central cavity or lumina, thus causing a gradual enlargement of the alveoli as noted above. (From Hammond.)

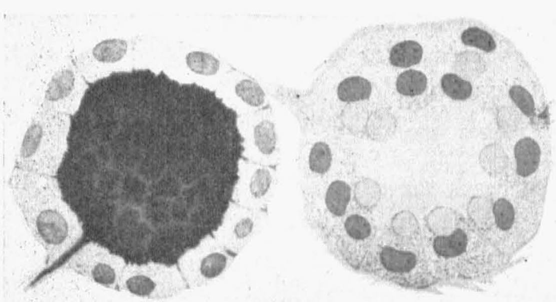

Fig. 14.—Diagram of an alveolus fully developed but not secreting milk. As milk secretion is initiated, the small cells gradually enlarge with milk, then discharge the products into the central cavity or lumina. (From Rubeli.)

THE HORMONES STIMULATING LOBULE-ALVEOLAR GROWTH

The estrogenic hormone was observed to stimulate the extensive growth of the duct system characteristic of the glands in unbred heifers, but failed to stimulate the growth of the alveoli which normally develop during pregnancy, even on long continued treatment. It appeared that another hormone was necessary to stimulate lobule-alveolar growth.

As the ovary is the seat of production of the estrogenic hormone, let us note the changes that occur in this structure during pregnancy to determine if some part of the ovary may not secrete a second hormone which would be effective in carrying the growth of the mammary gland to completion.

If the ovary of a heifer is examined just before the appearance of heat, there will be noted a large follicle filled with fluid. As already noted this fluid contains the estrogenic hormone which passes into the blood and causes the appearance of heat or estrum. At this time the cow will accept the male and may be bred. Attached to the wall of the follicle is an ovum or egg. In about 24 to 36 hours after estrum, the follicle ruptures, allowing the follicular fluid to flow out carrying the egg into the Fallopian or egg tube. The egg passes down this tube into the uterus. If the animal is bred, the sperm meets the egg either in the egg tube or uterus and fertilization takes place.

After the discharge of the egg and fluid from the ovarian follicle, a blood clot at first fills the cavity. Soon there is a rapid growth of large cells containing a deep yellow or orange pigment, and these cells completely fill the cavity. This structure is called the *corpus luteum* or *yellow body* (Fig. 15). If the heifer is not bred, the corpus luteum soon declines in size and a new follicle containing the estrogenic hormone begins to develop in order to stimulate the next heat period about 21 days later. If the animal conceives, the corpus luteum remains during the entire period of pregnancy and further estrus cycles are inhibited.

For many years the corpus luteum was believed to secrete a hormone which acted upon the uterus preparing it for the implantation of the fertilized egg. It was not until 1928-29, however, that methods were discovered by Dr. F. L. Hisaw in Wisconsin and Dr. G. W. Corner and W. M. Allen in New York for obtaining this hormone from the corpora lutea in concentrated form. The hormone has been called *corporin, progestin* or *lutein.*

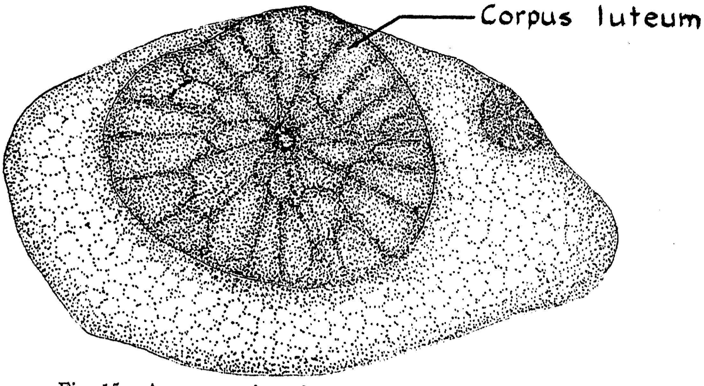

Fig. 15.—A cross section of the ovary of the cow typical of the condition about 10 days after the previous heat period or during pregnancy. The follicle shown in Fig. 3 has been completely filled by the rapid growth of large cells containing a deep yellow or orange pigment. This structure is called the corpus luteum or yellow body. It is the seat of production of a hormone called *corporin,* which in conjunction with the estrogenic hormone, stimulates the growth of the lobule-alveolar system during the first half of pregnancy.

With the hormone, corporin, available from the corpus luteum, experiments were immediately initiated to determine its effect upon the mammary gland duct system. The duct system of experimental animals was stimulated to extensive growth by the injection of the estrogenic hormone. Then the estrogenic hormone was stopped and corporin was injected for a period. However, the hormone corporin was found to be ineffective in stimulating the growth of the gland typical of pregnancy. Due to the fact that the estrogenic hormone had been observed to be excreted in the urine of cattle in increasing amounts during pregnancy, it was decided to try the effect of the estrogenic hormone and corporin together. Following the injection of the two hormones for a period, the mammary glands of the experimental animals showed the growth of the lobule-alveolar system typical of the growth observed during the first half of pregnancy.

These experiments and observations are believed to indicate that the growth of the udder of heifers during the first pregnancy is stimulated by the simultaneous secretion of the estrogenic hormone by the ovary and possibly some other structure such as the placenta, and the secretion of corporin by the corpora lutea of pregnancy. However, long continued injection of these two hormones failed to stimulate the gradual initiation of milk secretion normally observed during the second half of pregnancy and after calving.

THE LACTOGENIC HORMONE

Located at the base of the brain is a tiny structure, no larger than a pea in cattle, called the hypophysis or pituitary gland (Fig. 2). It is divided into two parts, the anterior and posterior lobes. Recent study has shown it to be an exceedingly important gland of internal secretion. Recent research has demonstrated that the anterior lobe is the seat of production of several important hormones, including one which stimulates general body growth, and a second which stimulates the prepubertal or immature ovary (called the gonad stimulating hormone) to activity and thus brings on

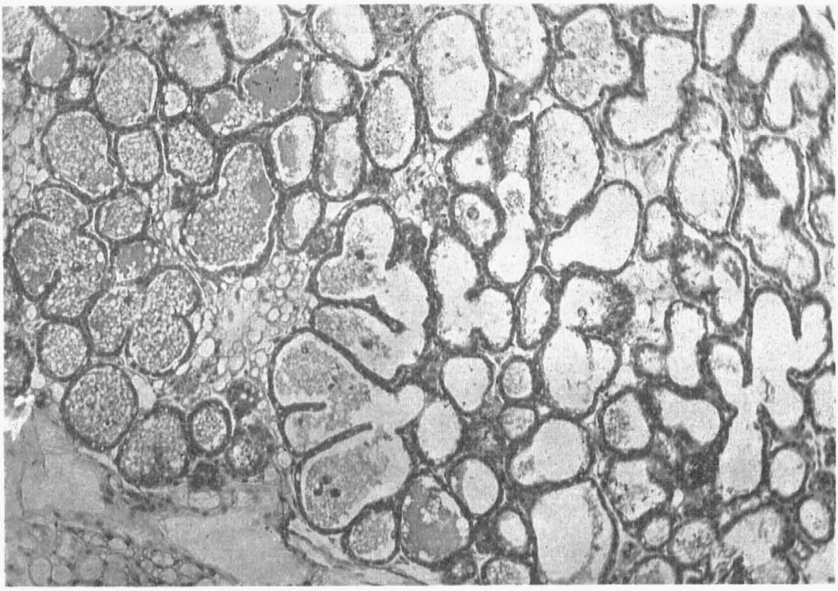

Fig. 16.—Cross section of a mammary gland in active secretion. The alveoli are greatly distended with milk.

indirectly the growth of the mammary duct system. By some investigators it is believed to secrete a hormone (called the luteinizing hormone) which stimulates the formation of the corpora lutea after ovulation and thus affects the growth of the lobule-alveolar system. Several other hormones, including a thyroid and an adrenal stimulating factor are being investigated at the present time.

In 1929 two investigators working in France, Drs. P. Stricker and F. Grüeter, noted that an extract of the anterior lobe of the pituitary would stimulate the initiation of milk secretion in the mammary glands of certain experimental animals if the glands were fully grown, i. e. with a well developed lobule-alveolar system. These observations have been fully confirmed and much progress made in isolating the active principle and in studying its mode of action in normal lactation. This lactogenic hormone has been called *galactin* or *prolactin.*

To demonstrate the effectiveness of the hormones in stimulating the growth of the mammary gland and the initiation of milk secretion, male animals have been injected with the estrogenic hormone to stimulate duct growth, then the estrogenic hormone and corporin injected to stimulate lobule-alveolar growth, and finally the lactogenic hormone injected to stimulate the glands to extensive lactation. The mammary glands at the end of the treatment were comparable with those of normal females after parturition (Fig. 16).

It seems clear from the above experiments that the hormones concerned in the control of milk secretion probably function in the sequence indicated, yet the story is not complete. In normal pregnancy, after the growth phase is completed the cells gradually begin to function and if abortion occurs milk secretion is quickly initiated. The question arises as to the mechanism which starts the lactation stimulus during the second half of pregnancy, yet holds in check the extensive secretion of milk until abortion or parturition occurs? In answer, two possibilities have been advanced. It is suggested that the estrogenic hormone which has been shown to be secreted in the urine of cattle in increasing amounts during the latter stages of pregnancy acts upon the anterior pituitary, holding in check the secretion of the lactogenic hormone. After parturition the amount of the estrogenic hormones quickly decreases, permitting the increased secretion of the lactogenic hormone and the gradual increase in the rate of milk secretion. The second possibility advanced is that the estrogenic hormone acts directly upon the secreting cells of the mammary gland checking the secretory activity of the cells. Experimental study has shown that the injection of the estrogenic hormone with the lactogenic hormone does depress the activity of the latter but does not disprove the first theory (Fig. 17).

Another problem of great interest is the relation of the lactogenic hormone to the persistency of milk secretion. Is milk secretion once initiated maintained by the removal of milk at frequent intervals or is the lactogenic hormone required during the entire period to maintain lactation? Further, if it is required, is the variation in the amount of hormone secreted by cows the explanation of the variation in the persistency of lactation? Complete answers to these questions are not yet available. It has been demonstrated that if the pituitary is removed at any stage of lactation, the secretion of milk quickly stops. However, the pituitary

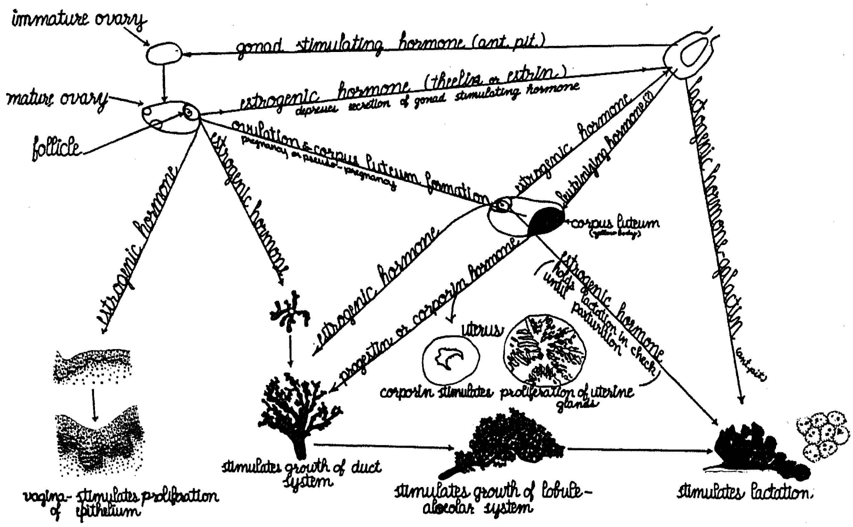

Fig. 17.—Sources of the hormones stimulating the mammary gland. In this diagram is presented the relation of the pituitary gland to the ovary and the effect of the hormones secreted by the ovary on the reproductive organs and the mammary gland. The daggers indicate the origin of the hormone and the changes induced in the structures affected. In each case the hormone is transported in the blood from its source to the ovary or mammary gland. It is interesting to note that up to the present time no hormone has been discovered which directly influences the gland in which it is secreted. Thus the cyclic changes in the ovary are induced by the action of the gonad stimulating hormone of the anterior pituitary. In turn the rate of secretion of the gonad stimulating hormone is depressed by the action of the estrogenic hormone acting upon the pituitary.

secretes so many important hormones that the cessation of lactation may be ascribed to other indirect effects. Recently, tests of the blood of pregnant and lactating cows showed the presence of the lactogenic hormone. It would appear that the hormone is secreted during lactation but whether it varies in amount during various stages of lactation and in various animals at the same stage of lactation still awaits determination.

THE CHANGES IN THE UDDER AS CATTLE "DRY UP"

The daily yield of milk increases for a time after calving, then gradually declines until the cow is "dry". The udders of cows in various stages of lactation have been examined to determine the changes taking place. It was found that in cows well advanced in lactation, there was an outer zone of the udder in which milk secretion was no longer taking place, while around the larger ducts there was an active zone still secreting as before. With the complete cessation of milk secretion, it has been noted in experimental animals that the lobule-alveolar system gradually degenerates, leaving only the cistern and duct system. When this occurs such animals cannot be brought back into lactation with the lactogenic hormone alone. The lobules must be regrown or only slight duct secretion will be induced.

These observations indicate that cows which have a considerable dry period between lactations must rebuild the lobule-alveolar structure during pregnancy as well as renew the stimulation to secretion.

PRACTICAL APPLICATIONS TO MILK PRODUCTION

The process by which the normal heifer or cow develops an udder capable of secreting milk after calving has been described. The method by which small experimental animals have been brought into lactation by means of the proper sequence in the injection of these hormones, leads us to believe that similar results could be obtained in stimulating the growth of the udder of heifers and the initiation of milk secretion. Unfortunately, it would require a very large amount of hormone and take considerable time to stimulate each phase of development. Thus it probably never will be feasible to bring unbred heifers into production by this method. In fact, the normal process of reproduction is the only method of maintaining a constant supply of heifers coming on to replace animals culled from the herd. It might be asked, of what practical value is this knowledge? While a few possibilities will be pointed out, the object of this bulletin is to place the available knowledge on this subject in the hands of dairymen who may see practical uses for the information and possibilities far beyond anything now considered.

It is hoped that investigations now in progress may suggest practical methods of bringing into lactation sterile cows which can no longer be brought into lactation in the normal manner. It is also possible that the rate of decline of lactation may be reduced or that lactation may be increased at intervals by the periodic injection of the lactogenic hormone. Will it be possible at some future time to supplement the amount of hormones normally secreted by cattle and thus insure the development of super dairy cattle, or will these studies point the way to methods of selecting and breeding dairy cows capable of secreting larger amounts of these various hormones? Only time will tell.

When it is considered that scarcely ten years has elapsed since the isolation of the estrogenic hormone and that all the knowledge concerning the relation of the hormones to milk secretion has been obtained during the intervening years, it is not too much to hope that many of the more practical phases of the problem will be solved within an equal period in the future.