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COMPARATIVE STUDIES ON GONAD DEVELOPMENT IN THE RAT, THE PIG AND IN CATTLE⁽¹⁾

J. D. THOMSON

INTRODUCTION

The relatively clear and simple developmental pattern of the frog gonad (Witschi 1914, 1924, 1929) makes it a good basic type with which to compare the sex glands of higher vertebrates.

The frog gonad, before sex differentiation, consists of a germinal epithelium (cortex) containing germ cells and follicle cells, of a mesenchyme-filled primary gonad cavity (this mesenchyme later forming the primary albuginea), and of a series of rete cords (of mesonephric blastema origin) entering through the hilum and projecting into the primary gonad cavity. The rete cords constitute the primitive medulla. Testis differentiation occurs when all of the germ cells, each one with its follicle cell, move from the germinal epithelium into the medulla. The germinal epithelium becomes thin and devoid of germ cells. It remains separated from the medulla by the primary albuginea. The germ cells divide and together with the follicle cells form the contents of the seminal tubules: spermatogonia and Sertoli cells. The rete cells give rise to interstitial cells and the walls of the seminal tubules. The retetubule meshwork connects with the seminal tubules by tubuli recti, and with the mesonephric tubules by vasa efferentia. Tubuli and vasa are parts of the rete apparatus. In gonads differentiating into ovaries, germ cells and follicle cells remain in the germinal epithelium, which thickens to form the ovarian cortex. A cavity appearing in the distal part of the rete becomes the secondary gonad cavity. During the maturation process follicle cells form an envelope of granulosa cells around each ovocyte. The part of the rete applied to the follicles nearest to the gonad cavity forms the theca externa. Mesenchyme around the follicles give rise to the theca interna.

The origin and development of the elements of the sex glands of higher vertebrates, especially mammals, are not as clear as in amphibia. The different elements to be considered and studied in

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regard to their origin are: germ cells, germinal epithelium, cortex, medulla, seminal tubules, Sertoli and granulosa cells, thecae interna and externa, testis interstitials, rete apparatus, vasa efferentia, epididymis, vas deferens and oviduct.

There are still two principal schools of thought concerning the origin of the germ cells. Germ cells may arise from somatic cells of the germinal epithelium, or from cells segregated early in development and bearing certain diagnostic characteristics. Adherents of the first view (Simkins 1923, Hargitt 1925, 1926, Goldsmith 1932) have not satisfactorily proven that somatic cells of the germinal epithelium can and do transform into germ cells; while many of those holding the second view (Rauh 1929, Rubaschkin 1910, 1912) have demonstrated that germ cells migrate from extra-gonadal sources and become definitive germ cells. Some workers (Bookhout 1937, Kates 1937) hold a compromise view that germ cells move into the gonad from extragonadal sites but degenerate and do not give rise to definitive germ cells. Regarding the vast controversial literature, we refer to the discussions of Heys (1931), Risley (1933) and Willier (1939).

The germinal epithelium is a layer of splanchnic mesoderm lying between the coelomic angle and the place of attachment of the intermediate mesoderm to the splanchnic plate; germ cells come to lie in and beneath it. Risley (1933) in the musk turtle and Witschi (1935) and Stanley and Witschi (1940) in birds, have described how the germ cells which first lie laterally distributed in the endoderm (turtle) or in the splanchnic mesodermal plates (birds) are brought into the midline by movements of the splanchnic mesoderm during the formation of gut and dorsal mesentery. Later they move into cortex, tunica albuginea and medulla of the primordial gonads.

All investigators agree that the ovarian cortex differentiates from the germinal epithelium. While some workers hold that seminal tubules of testes and medullary cords of ovaries of higher vertebrates originate from germ and somatic cells proliferated inward from the germinal epithelium, others (Blocker 1933, Witschi 1935, in birds; and Felix 1912 in man) have described seminal tubules and medullary cords as arising in situ from germinal and somatic cells lying in the medulla. The findings of Witschi and Blocker bring the mode of formation of seminal tubules and medullary cords of birds into line with observations on amphibia, with this difference: in the frog all germ cells at first lie in the

germinal epithelium, and then, in the male, migrate into the medulla; whereas in other amphibia (*Ambystoma tigrinum*, Gilbert 1940) and in the birds (Blocker, Witschi, op. cit.) germ cells are already present in both cortex and medulla in indifferent stages.

As stated above, Sertoli cells of the frog testis are follicle cells of epithelial origin which accompany the germ cells when they move into the medulla. Opinions concerning the origin of mammalian Sertoli cells are many, but clear demonstrations of origin and source of these elements are lacking. Likewise, opinions differ as to the origin of granulosa cells in the mammalian ovary. It was shown by Witschi (1914) that in the embryonic frog ovary, each ovogonium is accompanied by a follicle cell of epithelial origin, and the granulosa layer of the follicles arises by the division of these cells. Kingsbury (1939) has recently reported that in the embryonic cat ovary, the granulosa layer of the primary follicle is of cortical origin, is one cell thick, and is bounded peripherally by a membrane, within which granulosa cells multiply. Pincus and Enzmann (1937) state that in the rabbit, the initial follicular layer arises from "spindle-shaped elements" and that these follicle cells increase in number to form the granulosa. Okamoto (1928) asserts that the initial granulosa layer of the dog ovary is derived from cortical somatic cells, but increases in thickness by the addition of mesenchyme cells.

It has been demonstrated in the frog ovary that the theca interna of the ovarian follicle is derived from mesenchyme, and the theca externa from the rete ovarii. In mammals, it has been shown that the theca externa arises from gonadal mesenchyme, while the origin of the theca interna is not clear. The internal theca cells (ovarian interstitials) of the cat have been said to arise from transformed mesenchymal cells (Kingsbury 1939, p. 310), but this has not, we think, been sufficiently substantiated. The question of origin and function of ovarian interstitials has been discussed by Stieve (1933), Corner (1938) and Kingsbury (1939).

According to recent reviews (Moore 1926, Rasmussen 1928, Maximow and Bloom 1938) most of the evidence indicates that testicular interstitials are transformed gonadal mesenchyme cells. However, Witschi (1939, p. 149) suggests that testicular interstitials "most probably derive from the rete cords which themselves originate from the mesonephric blastema."

The gonadal rete of the frog has been shown by Witschi (1914) to arise from accumulations of cells of mesonephric blastema origin between mesonephric tubules and seminal tubules; they form

the rete network, tubuli recti and vasa efferentia in the testis, and the theca externa of ovarian follicles. There is no agreement as to the source of the rete in mammals. Opinions concerning this point fall into two groups. The rete is said to arise from the mesonephros (outgrowths from mesonephric tubules or renal corpuscles, or aggregations of mesonephric blastema cells), or from ingrowths from the coelomic epithelium. For recent reviews of literature on the origin and development of the gonadal rete see Wilson (1926), Bovy (1928) and Risley (1933).

The epididymis, it is generally agreed, is formed from mesonephric tubules that persist after extensive mesonephric degeneration. It serves as a storage place for the sperm and connects with the vas deferens (wolffian duct). In females, some mesonephric tubules persist in rudimentary form as the epöphoron. The wolffian ducts disappear more or less completely.

The oviducts are structures which, in males and females alike, arise from the coelomic epithelium, lateral to the wolffian ducts. In females they persist while in males they degenerate.

The present study consists of a reinvestigation of the origin of the various elements of the sex glands in rat, pig and cattle, and of a comparison of the gonad development in these three forms with that occurring in amphibians.

I wish to express my gratitude to Professor Emil Witschi for suggesting this problem and for his helpful advice and criticism during the progress of the investigation.

MATERIALS AND METHODS

The rat material was obtained from a colony of Wistar rats. Pig and cattle embryos were collected on the killing floors of the Cedar Rapids, Iowa, branch of the Wilson Packing Co. The author wishes to thank the Wilson Co. for its cooperation and courtesy in making the specimens available.

Measurements of crown-rump lengths of pig and cattle embryos were made on fresh material immediately after removal from the uteri. Gonads of smaller specimens were sectioned serially, while only a portion of the larger gonads were sectioned. Routine fixing, embedding and staining methods were employed, and need not be described.

All drawings were made with the aid of a camera lucida.

OBSERVATIONS

Rat

Primordial germ cells in the 10 day embryo lie in the thin flat endoderm, ventral to the intermediate mesoderm and the paired dorsal aortae (plate I, fig. 1; table I). The endoderm forms a closed gut at 11 days, and primordial germ cells are contained in its walls (see plate I, fig. 2; table I) from which they move, and are found at 11½ days in the mesenchyme between gut and splanchnic plate, and in the splanchnic plate (plate I, fig. 3; table I). The splanchnic mesodermal plates between the medially located coelomic angles and the junctures of nephrotomes and mesodermal plates now constitute the germinal epithelium. Between 11½ and 12 days most of the germ cells are found in the germinal epithelium and a few in the medulla (table I). For the first time, each germ cell in the splanchnic plate at 11½ days has its own follicle cell, which must have been acquired in traversing the splanchnic plate, since germ cells in gut and mesenchyme do not have them.

At 11 days, solid wolffian ducts lie lateral to and separate from the nephrotomes (plate I, fig. 2). Between 11½ and 12 days the remaining intermediate mesoderm breaks up into a mesonephric blastema, which is concentrated between the wolffian ducts (now with lumina) and the root of the dorsal mesentery (plate I, fig. 4). By the 13th day the lateral portion of the blastema differentiates into mesonephric tubules with lumina, while other portions extend dorsomedially to form the rudiments of the adrenal cortex. At 13½ days vasa efferentia project from cephalic segments of the rete blastema toward the mesonephric tubules (plate I, fig. 5).

As shown in table I, the number of germ cells in the thin germinal epithelium at 13 days is about the same as at 12 days, while there has been an enormous increase in the number of germ cells in the medulla. Few or no germ cells remain in the dorsal mesentery at 13½ days, and the number in the germinal epithelium has decreased, while more are found in the medulla (table I). In all three places, germ cells still retain one follicle cell each.

Sex can be diagnosed by the 14th day on the basis of germ cell counts. One 14 day specimen showed 63 germ cells (8% of the total) in the germinal epithelium and 753 (92% of the total) in the medulla. Another 14 day specimen had 16 (2%) in the germinal epithelium and 834 (98%) in the medulla; while a third had no germ cells in the germinal epithelium and 732 (100%) in the medulla (table I). Evidently depletion of the cortex signifies

a testicular trend of differentiation. Almost every germ cell lying in medulla or cortex of more distinctly female specimens is seen to have a follicle cell closely applied to its surface. (Sections in which germ cells do not show attached follicle cells are undoubtedly cut at angles which do not show the follicle cells.) In 14 day males, follicle cells have fallen away from most of the germ cells. This is another indication of sex differentiation. Morphological evidence of sex differentiation becomes more obvious at 14½ days when, in males, stroma cells move from medial and lateral sides of the hilum toward the crest of the gonad to form the primary albuginea, separating, now broadly, the cortex from the medulla. At 15 days the tunica is thick and vascular, and the germinal epithelium has become quite thin. A few germ cells (still with attached follicle cells) remain in the tunica in the cephalic part of the gonads. Otherwise all of the germ cells lie in the medulla (table I).

Seminal tubules, at sex differentiation, are formed by partitioning of the medulla by mesenchyme (plate I, fig. 6). In them the follicle cells have lost their close connection with the spermatogonia and are scattered throughout the tubules.

The ovaries likewise appear clearly differentiated at 15 days. They consist of a greatly thickened cortex, and a medulla, the two separated by a very thin tunica (plate I, figs. 7 and 8). Nearly equal numbers of germ cells lie in medulla and cortex (table I). The ovogonia in the cortex, tunica and medulla still retain their individual follicle cells.

Adrenal cortical rudiments have separated completely from the mesonephric blastema at 14 days, and sympathetic ganglia cells are moving ventrally toward the cortical blastema to form the adrenal medulla.

Interstitial cells appear in the testis at sex differentiation. The rete blastema at the hilum of the 16 day embryonic testis is diffuse where it joins the intertubular tissue. This suggests the possibility of the blastemal origin of the interstitials.

At the 15th day the rete ovarii and rete testis are morphologically alike; and in both sexes vasa efferentia connect with mesonephric tubules.

The müllerian ducts are first seen at 14 days as grooves in the cephalic part of the urogenital ridges, ventrolateral to the wolfian ducts. At 15 days the müllerian ducts have sunken in from

the surface and have become solid strands of cells, caudad of the open ostia.

The following descriptions are of ovarian changes only, since changes occurring in the testis after sex differentiation are less drastic than those in the ovary, and may be followed in table II.

About the 18th day of embryonic life the cortex becomes divided by mesenchyme into small masses consisting of germ and follicle cells. In the deeper layers of the cortex the germ cells begin to undergo prematuration changes. As a result, ovocytes (synaptene stage) are more conspicuous in this inner zone (plate I, fig. 9). By 20 days most or all of the germ cells of the cortex have become ovocytes, i.e., are in prematuration stages (plate I, fig. 10).

At the 21st day the cortex consists of irregular egg-cords, radiating peripherally from the inner edge of the cortex. In most of the egg-cords, follicle cells are arranged in a single layer around each ovocyte, the stroma is growing into the cords, cutting them up into smaller groups of ovocytes and primary follicles. One day later (at birth) primary follicles are scattered all along the inner edge of the cortex (plate II, fig. 11) and by 5 days postpartum fragmentation of the egg cords into primary follicles is practically complete (plate II, fig. 12). At 10 days postpartum some of the follicles show antrum formation (plate II, fig. 13).

At 10 days postpartum strands of large cells grow from the epoöphoron toward the periphery of the ovary and apparently scatter between the primary follicles near the surface. These cells are probably forerunners of the theca interna cells (plate II, fig. 15). Part of the rete blastema in the hilum forms the rete ovarii.

Principal changes undergone by testis and ovary after sex differentiation may be followed in table II.

Pig

In the youngest embryos studied (6 mm.) mesonephroi are well-developed, while germinal ridges consist merely of strips of cuboidal epithelium on the medial surfaces of the mesonephroi, and of a thin medulla located between the thickened epithelium and the medial walls of the renal corpuscles. Germ cells are found in germinal epithelium and medulla, and also embedded in the mesenchyme of the root of the dorsal mesentery (plate II, fig. 16). Counts of germ cells in one specimen showed, in 50 consecutive sections, 4 (11%) in the dorsal mesentery, 24 (65%) in the ger-

minal epithelium and 9 (24%) in the medulla (table I). In slightly older embryos (8 to 12 mm.) no germ cells are found in the dorsal mesentery (table I); otherwise the germ cell ratios remain about the same. In most cases each germ cell has an individual follicle cell closely applied to its surface.

Increase in gonad volume begins at 13 to 15 mm. The germinal epithelium remains thin and the medulla is divided into irregular masses by fine fibers (plate II, fig. 17). There has been a great increase in the number of germ cells in the medulla (table I). Just dorsal to the root of the mesentery lie the paired adrenal cortex primordia which are still continuous with the gonadal rete cords.

Sex differentiation occurs in 20 to 25 mm. embryos. In testes the germinal epithelium becomes very thin and devoid of germ cells. In the thick vascular tunica albuginea many germ cells may still be found. The seminal tubules are small and form a network (plate II, fig. 18a). In 20 to 25 mm. females, 8% of the germ cells are in the cortex and 92% in the medulla; while in males of the same stage, all of the germ cells lie in the albuginea or within the medulla. In the ovary at sex differentiation the germinal epithelium becomes rapidly thicker and the primary tunica is less sharply defined than in the testis (plate II, fig. 20a).

At this stage, other derivatives of the mesonephric blastema become more evident. Adreno-cortical primordia separate from the parent blastema, and in the cephalic part of the gonad ridge, cord-like vasa efferentia reach from the rete blastema toward the renal corpuscles. At the level of the rete, especially at the hilum, large round cells occur between the seminal tubules which may represent young stages of interstitial cells. (This is essentially as described in Ancel and Bouin, 1903.) From this time on, interstitial cells increase in number.

In the testes at 35 to 38 mm. (plate II, fig. 19a) a higher percentage of the medullary germ cells are without follicle cells, indicating that in the testis, follicle cells leave the germ cells to form Sertoli elements. In ovaries of the same age (plate II, fig. 21a) germ cells are found in both germinal epithelium and medulla. A high percentage of the cortical and medullary germ cells retain individual follicle cells.

Further development of the ovarian cortex is shown in plate II, fig. 22 and plate III, figs. 23 to 25.

Between 120 and 150 mm., just prior to the segregation of the primary follicles from egg cords, ovarian follicle cells divide and

become arranged in a single layer around each germ cell to form the granulosa layer.

Development of testis and ovary from sex differentiation to birth may be followed in table III.

Cattle

The genital ridge at the 6 mm. stage is relatively poorly developed: the germinal epithelium is thin and the medulla is sparse and loose (plate III, fig. 26). At 9 mm. the germinal ridges consist of strips of thickened epithelium on the ventromedial surfaces of the mesonephroi, underlain by shallow and densely packed medullae (plate III, fig. 27). The same proportion of germ cells is seen at 9 mm. as at 6 mm., in the dorsal mesentery, germinal epithelium and medulla (table I).

The enlarging gonads bulge into the coelom at 11½ mm. The germinal epithelium thickens, then begins to thin out at 16 and 20 mm. The dense medulla fills the core of the germinal ridge, and at 16 mm. becomes divided into cell masses by fine fibers of stromal origin (plate III, fig. 29). At 20 mm. the medulla is separated from the germinal epithelium by a cellular and fibrous tunica albuginea. At 11½ mm., 61% of the germ cells are found in the germinal epithelium and 39% in the medulla; none are left in the dorsal mesentery (table I). The gonads continue to increase in size and according to germ cell counts at 13 mm., some of the germ cells seem to shift from the germinal epithelium to the medulla (42% in the germinal epithelium, 58% in the medulla; table I). At 16 mm. a further shift of germ cells has occurred from the germinal epithelium to the medulla (11% in the germinal epithelium and 89% in the medulla; see table I).

At 20 mm. the corticoadrenal primordia have separated from the gonad medulla.

Sex differentiation begins at about the 25-30 mm. stage. In testes the germinal epithelium is very thin and sterile and is separated from the seminal tubules by a thick fibrous tunica albuginea which contains germ cells, while the ovary, smaller than the testis, retains a thicker germinal epithelium and has a less fibrous tunica, both structures containing germ cells. In testes shortly after sex differentiation, few germ cells (5%) remain in the germinal epithelium while 95% are found in the medulla. Large numbers are also found in the tunica. In ovaries at the same period there are found somewhat more germ cells in the

germinal epithelium than in the medulla (57% in the germinal epithelium, 43% in the medulla; table I). The majority of the germ cells of the testes do not retain individual follicle cells, while in the ovaries most of the cortical and medullary germ cells retain them.

In the testis after sex differentiation, rete testis cells diffuse into the areas between the seminal tubules, and may give rise to large blastemic cells found between the seminal tubules—the precursors of the interstitial cells. The rete at 35 mm. is in the form of solid cords of cells and is connected through vasa efferentia to degenerating renal corpuscles and to mesonephric tubules. The remaining mesonephric tubules constitute the epididymis. In 60 mm. embryos the rete cells are beginning to form the rete cords.

After sex differentiation, changes undergone by the ovaries are more striking than those occurring in the testes. The cortex is divided into egg cords by the ingrowth of stroma of the primary tunica. Beginning at 110 mm., germ cells at the inner edge of the cortex begin to undergo prematuration changes. This zone of prematuration thickens at the expense of the outer ovogonial zone (plate III, fig. 31).

Follicle cells are arranged in one layer around each germ cell to form a granulosa layer. By 150 mm. a few primary follicles have appeared at the inner edge of the prematuration zone (plate III, fig. 32). By 520 mm. the cortex has been extensively invaded by connective tissue, and contains many degenerated primary follicles, besides a few normal primary follicles and sterile cords of cells (plate III, fig. 34). Follicles begin to grow again just before birth (900 mm.) (plate III, fig. 36), and a few atretic follicles are found at this time.

DISCUSSION

In vertebrates more primitive than amphibia (e.g. cyclostomes), sex glands consist of germ cells and germinal epithelia without mesonephric components (medulla, rete, vasa efferentia). The latter becomes added in some fishes, the amphibia and all higher forms.

Germ cells, in frogs, pass from the gut roof endoderm into the germinal epithelium (each germ cell receiving one follicle cell en route, Witschi 1914) and then, in males at sex differentiation, into the medulla. In the ovarian medulla, in the frog, no germ cells are received at any time (Witschi 1929); while in *Ambystoma tigrinum* (Gilbert 1940), reptiles (Allen 1906; Risley 1933), birds (Hoffmann 1892, Blocker 1933, Witschi 1935, and others)

and in mammals (Vannemann 1917, Bookhout 1933, Rubaschkin 1910, 1912, Rauh 1929, and present investigation) both medulla and cortex of indifferent gonads contain germ cells.

Hargitt (1925, 1926, 1930) and Goldsmith (1932) state that, in the rat, extragonadal germ cells are not found, and that germinal epithelium somatic cells give rise to definitive germ cells. Hargitt apparently later modified his original stand, since two of his students, Bookhout (1937) and Kates (1937) state that in guinea pig embryos germ cells of extragonadal origin and some that arise from germinal epithelium cells are present in the gonads simultaneously. It is claimed that the former all degenerate. The author of the present paper has been unable to find evidence of transformation of somatic into germ cells.

In the rats differentiation of mesonephric tubules, adrenal cortical primordia and gonad rete blastema from mesonephric blastema all occur within a very short period of time, while in pigs and in cattle mesonephroi are differentiated from the blastema (earlier in pigs than in cattle) some time before the gonads arise.

At first sterile, the splanchnic mesoderm becomes a germinal epithelium when the germ cells enter it. At the time when the germ cells are first found in the germinal epithelium, the distribution of germ cells in 12 day rats is: 75% in the germinal epithelium, 24.9% in the medulla, including the albuginea, and 0.1% in the dorsal mesentery; in 6 mm. pigs: 65% in the germinal epithelium, 24% in the medulla and 11% in the dorsal mesentery; and in 6 mm. cattle: 46% in the germinal epithelium, 23% in the medulla and 31% in the dorsal mesentery.

Contrary to many earlier interpretations, the medulla does not arise as a "first proliferation", nor the cortex as a "second proliferation" from the germinal epithelium. In the testis the germinal epithelium thickens during early stages, then becomes thin. At sex differentiation, all of the germ cells in male rats, and most of the germ cells in male pigs and cattle move inward from the germinal epithelium. (In pigs and cattle some germ cells are caught in the tunica albuginea). These migrating germ cells (plus their follicle cells) move inward singly, not as cords. In ovaries the germinal epithelium thickens en masse to form the cortex, and only secondarily becomes divided into "egg cords" by growth of stroma of the primary tunica toward the surface of the gonad. Ovarian medullary cords in rats persist for a very short time, while in pigs and cattle they remain for a longer period, becoming more fragmented as development progresses. In 190 mm. fe-

male pigs and 100 mm. cattle, medullary germ cells begin to exhibit degenerative changes.

In males the formation of seminal tubules in situ from the medulla is similar in all three species. At first solid, the testicular medulla is divided into seminal tubules by the ingrowth of stroma. At birth, seminal tubules of all three animals look essentially alike. The individual tubules containing germ cells in central and peripheral positions, and Sertoli cells along the periphery.

In females, cortical transformations are alike in all three species. Germ cell maturation proceeds in a wave from the depth of the cortex toward the periphery. In the ovaries of rats at birth, primary follicles are just beginning to be cut off the inner edges of the egg cords, and have not yet begun to enlarge; in pigs at birth primary follicles are beginning to enlarge, but not all of the egg cords have entirely become divided into primary follicles; toward the periphery there remain egg cords containing oocytes in the synaptene stage; in cattle, the ovary is more advanced at birth: some of the follicles are of considerable size and have large antra; follicular atresia is in progress.

The stage of development reached in the rat ovary at birth corresponds to stages attained in 150 mm. pig embryos and 150 to 200 mm. cattle embryos.

The origin and early development of the follicle cells is the same in rats, pigs and cattle. They arise from coelomic mesoderm. Counts of germ cells bearing individual follicle cells suggest that, in females, the germ cells retain their follicle cells which later multiply and form the granulosa layers of the primary follicles. In males, soon after sex differentiation the follicle cells fall away from the germ cells and become attached to the connective tissue of the seminal tubule walls to form Sertoli cells. This remarkable behavior of the follicle cells is a relatively recent sex characteristic; in amphibians the follicle cells remain directly associated with the germ cells until a late stage of spermiogenesis (Witschi 1924).

The rete testis and rete ovarii arise during sex differentiation in rats, pigs and cattle from the rete blastema, which in itself is a mesonephric derivative. From the rete blastema vasa efferentia grow out toward, and later connect with, the mesonephric tubules in rats, and with both mesonephric tubules and degenerating renal corpuscles in pigs and cattle. In testes of all three species, rete tubules form by the arrangement of rete blastema cells into cords which later acquire lumina, and remain near the hilum in rats, or penetrate into the center of the testis in pigs and cattle.

In all three forms tubuli recti grow from the rete and connect to the central ends of the seminal tubules.

The rete ovarii of rats, pigs and cattle consists of tubules in the hilum of the gland, and persist even in the adult. Some loose peripheral cells of the rete become scattered and their fate could not be ascertained.

The rete ovarii in the ovary of rats, 10 days postpartum, is seen to give off large cells which surround the primary follicles; these cells probably later form the theca interna of ovarian follicles. This was not observed in pigs and cattle, although such large cells were seen to be present. Kingsbury (1939), on the basis of his work on the cat, states that most of the evidence points to the theca arising by transformation of gonadal mesenchyme, but such transformations were not observed in the three forms studied here.

The origin of the testis interstitials was not clearly made out in the forms studied, but there were indications that cells of the rete testis are continuous with more cuboidal cells lying between the seminal tubules. Recent reviews state that testis interstitials most likely arise from gonadal mesenchyme. As in the case of theca interna cells, such transformations were not seen in the material at hand. It is necessary to emphasize that mesonephric blastema cells are scattered through the medulla and may be the source of many cell types usually attributed to mesenchyme.

While gonad development in amphibians and mammals follows essentially the same course, there exist some minor, but very characteristic differences: (a) Ovogonial mitoses and synaptic stages of ovocyte maturation are observed throughout the whole life in amphibians, but only prenatally in the rat, pig and cattle. (b) The theca interna of mammalian ovaries corresponds to the theca externa of the frog. (c) The participation of the medullary cords in the formation of the follicular theca is less obvious in mammals than in amphibians. (d) The follicle cells fall away from the spermatogonia and become sustentacular cells soon after sex differentiation in the mammalian embryo; the same transformation occurs at a much later stage in amphibians.

SUMMARY

Comparative studies were made on gonad development in rats, pigs and cattle.

Primordial germ cells of the early rat embryo first lie in the endoderm, then, when the gut forms, in the gut walls. Cell counts at various stages prove that the germ cells move from gut endoderm to the dorsal mesentery (where each germ cell acquires one follicle cell), and into both medulla and germinal epithelium (the base of the latter being the splanchnic mesoderm between the root of the dorsal mesentery and the place of attachment of the nephrotomes). In the youngest cattle and pig embryos available, most of the germ and follicle cells were found in medulla and germinal epithelium of the sex glands, and a few still in the dorsal mesentery.

In the rat, nephrotomes give rise to the wolffian ducts. The remainder becomes mesonephric blastema, out of which arise mesonephric tubules, adrenal cortex and gonad medulla.

Germ cell counts indicate that, in males before and at sex differentiation, most of the germ cells move from the germinal epithelium into the medulla, each one retaining its follicle cell; in females, such migration, if it occurs at all, is much less extensive, and germ cells in the germinal epithelium become ova. In males, germ cells remaining in the periphery are trapped in the primary tunica albuginea, and apparently degenerate.

In the three investigated species, the germinal epithelium in males thickens in early stages, and later becomes thin. In females it thickens to form the cortex. The medulla plus its germ cells is divided by stroma into seminal tubules in males and medullary cords in females. In females the medullary cords fragment and the germ cells undergo degeneration and finally disappear.

In males, individual follicle cells leave their attachment to the germ cells. Germ cells later lie attached to the walls of the seminal tubules where they multiply, mature and become ripe spermatozoa. In females, cortical germ cells retain their follicle cells, which later form the granulosa layer. Egg cords are formed by the cutting up of the cortex by stroma; primary follicles are cut off the inner ends of these cords after the germ cells have undergone prematuration changes in a centrifugal wave.

The rete differentiates from a portion of the mesonephric blastema and in both sexes the vasa efferentia grow out from the rete

and connect with the mesonephric tubules. (The latter constitute the epididymis in the male, the epoöphoron in the female). In males the tubuli recti arise as growths from the rete toward the seminal tubules.

Müllerian and wolffian ducts are found temporarily in both sexes. In the male the müllerian ducts persist and the wolffian ducts disappear.

Theca interna cells (at least in the rat ovary) may arise from cells derived from the mesonephric blastema and surround the primary follicles.

In males, interstitial cell origin was not clearly ascertained, but evidence favors the mesonephric blastema as the source.

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EXPLANATION OF PLATES

ABBREVIATIONS

AD — Adrenal cortex	MC — Mesenchyme
AT — Atretic follicle	MD — Müllerian duct
C — Ovarian cortex	MT — Mesonephric tubule
DA — Dorsal aorta	N — Nephrotome
DF — Degenerated follicle	OC — Ovocyte
DG — Degenerated glomerulus	OG — Ovogonium
DM — Dorsal mesentery	PF — Primary follicle
E — Endoderm	R — Rete
EC — Egg cord	S — Spermatocyte
EP — Epoöphoron	SC — Sertoli cell
G — Gut	SPL — Splanchnic mesoderm
GC — Primordial germ cell	ST — Seminal tubule
GE — Germinal epithelium	SZ — Spermatozoön
GF — Growing follicle	TAI — Primary tunica albuginea
I — Interstitials	TAII — Secondary tunica albuginea
M — Medulla	TI — Theca interna
MB — Mesonephric blastema	VE — Vasa efferentia
W — Wolffian duct	

PLATE I

Rat embryos. X170.

Fig. 1. 10 days. Primordial germ cells in endoderm.

Fig. 2. 11 days. Germ cells in gut wall. Wolffian ducts solid. Nephrotomes separated from somites.

Fig. 3. 11½ days. Germ cells moving from gut into germinal epithelium.

Fig. 4. 12 days. Nephrotome diffuse (mesonephric blastema). Germ cells in germinal epithelium. Mesonephric tubules forming from blastema. Wolffian ducts with lumina.

Fig. 5. 13½ days. Vasa efferentia growing from rete toward mesonephric tubules.

Fig. 6. 15 days. Testis. Tunica albuginea formed. Medulla dividing into seminal tubules. Vasa efferentia clearer. Solid Müllerian ducts.

Fig. 7. 15 days. Ovary. Tunica albuginea very thin.

Fig. 8. 16 days. Ovary. Primary tunica albuginea. Müllerian ducts with lumina.

Fig. 9. 18 days. Ovary. Egg tubes forming from cortex.

Fig. 10. 20 days. Ovary. All cortical germ cells ovocytes. Secondary tunica albuginea.

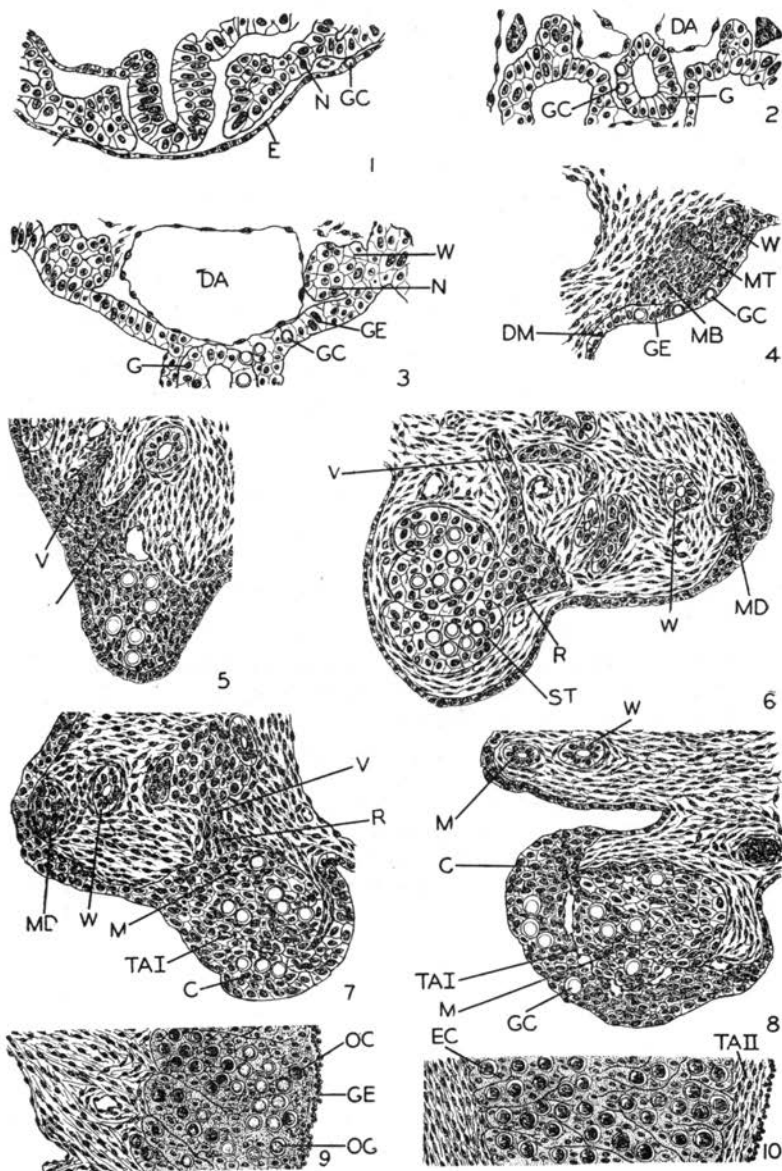


PLATE II

Figs. 11-15, postpartum rats, X170. Figs. 16-22, pig embryos; all X170, except figs. 18, 19, 20 and 21 (diagrammatic.)

Fig. 11. Newborn female. Primary follicles appearing at inner edge of cortex.

Fig. 12. 5 days postpartum. Female. Increased number of primary follicles.

Fig. 13. 10 days postpartum female. Growing follicles, one with small antrum. Primary follicles and ovogonia in secondary tunica albuginea.

Fig. 14. 29 days postpartum female. Enlarged follicles with thick theca interna. One atretic follicle shown.

Fig. 15. 10 days postpartum female. Theca interna cells moving toward primary follicles.

Fig. 16. 8-10 mm. pig embryo. Germinal epithelium and medulla with germ cells.

Fig. 17. 15-20 mm. pig embryo.

Fig. 18. 20-25 mm. male embryo. Testis at sex differentiation.

Fig. 18a. Same. Part outlined in fig. 18, enlarged.

Fig. 19. 35-38 mm. male embryo.

Fig. 19a. Same. Part outlined in fig. 19, enlarged.

Fig. 20. 20-25 mm. female embryo.

Fig. 20a. Same. Part outlined in fig. 20, enlarged.

Fig. 21. 35-38 mm. female embryo.

Fig. 21a. Same. Part outlined in fig. 21, enlarged.

Fig. 22. 50 mm. female embryo. Part of ovary, showing cortex and medulla.

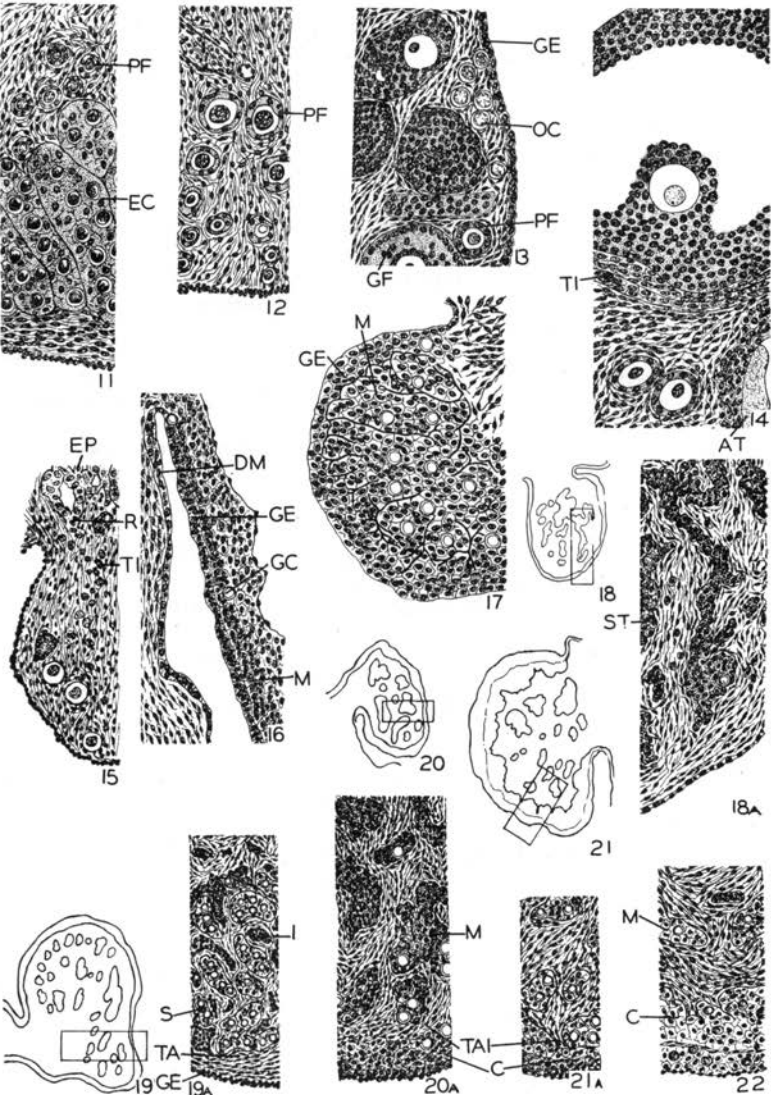


PLATE III

Figs. 23-25, pig embryos, X170. Figs. 26-36, cattle embryos, X170, except fig. 35 (X70), and fig. 36 (X731).

Fig. 23. 90 mm. female. Egg cords beginning to form from cortex.

Fig. 24. 150 mm. female. Egg cords further differentiated. Few primary follicles at inner edge of cortex.

Fig. 25. 220 mm. female. Showing one follicle beginning to grow. Egg cords reduced in size.

Fig. 26. 6 mm. cattle embryo. Germ cells in mesentery and in medulla under thin germinal epithelium.

Fig. 27. 9 mm. cattle embryo. Germinal epithelium thickened.

Fig. 28. 13 mm. cattle embryo.

Fig. 29. 16 mm. cattle embryo. Medulla cut up by stroma. Thin germinal epithelium.

Fig. 30. 36 mm. female cattle embryo. Thick cortex. Wide secondary tunica albuginea. Medulla still large, solid.

Fig. 31. 110 mm. female cattle embryo. Many cortical germ cells in synaptene stage.

Fig. 32. 150 mm. female cattle embryo. Thin inner zone of primary follicles.

Fig. 33. 320 mm. female cattle embryo. Few small bundles of synaptene oocytes remaining.

Fig. 34. 520 mm. female cattle embryo. Few degenerated primary follicles at inner edge of cortex. Enlarged primary follicles.

Fig. 35. 53 mm. male cattle embryo. Rete strands attached to degenerated renal corpuscles and mesonephric tubules.

Fig. 36. 900 mm. female cattle embryo. Cortex full of connective tissue. Primary follicle shown. Very thin germinal epithelium.

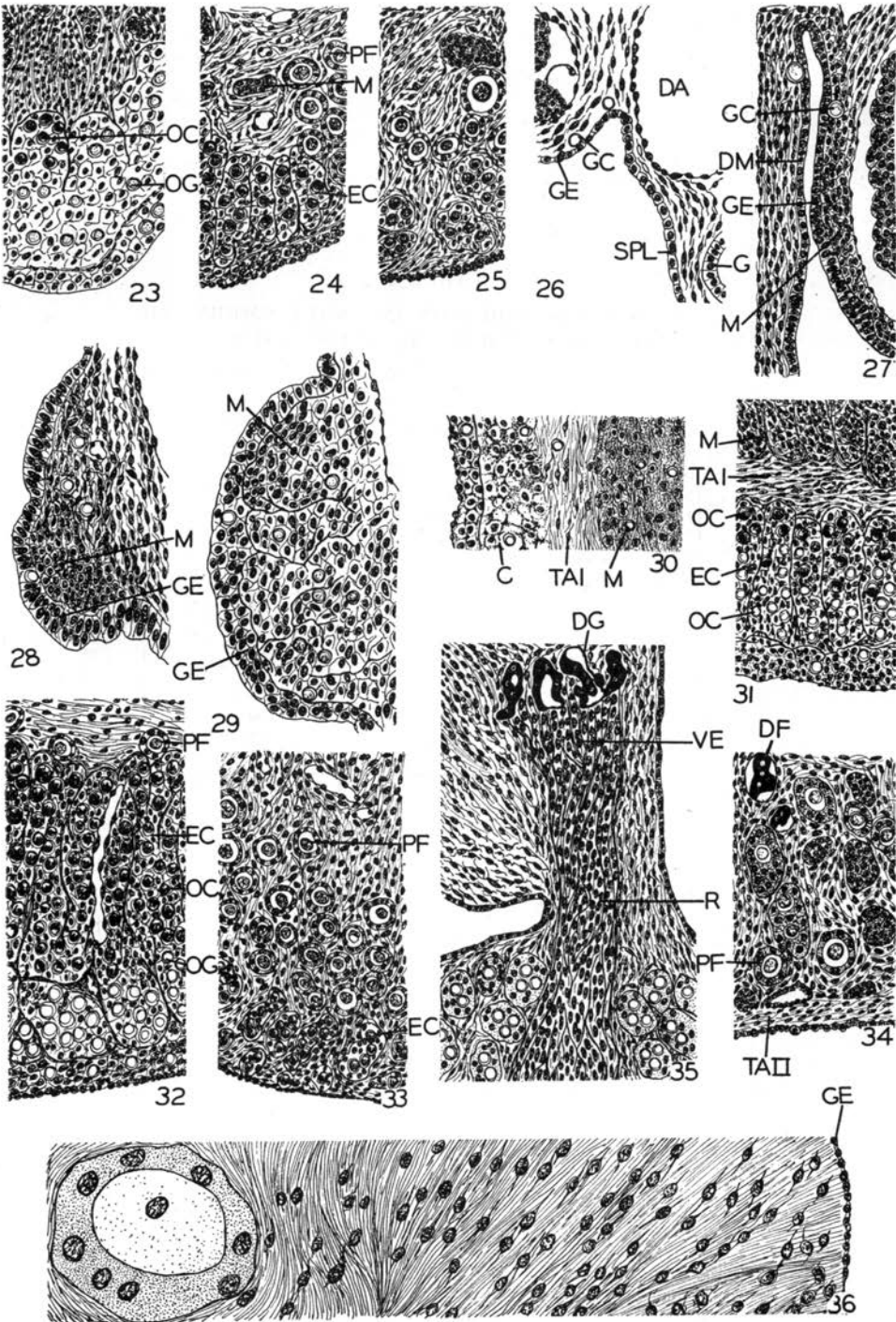


TABLE I
GERM CELL DISTRIBUTION IN EARLY EMBRYONIC
GONADS OF RAT, PIG AND CATTLE

Animal	Age (da.)	Sex	C.-R. length (mm.)	No. of germ cells in 50 consecutive sections							
				Gut end.	%	D. Mes.	%	Cortex	%	Med.	%
Rats	10	---	1.3	18	100	---	---	---	---	---	---
	11 (a)	---	4.0	63	100	---	---	---	---	---	---
	11 (b)	---		16	100	---	---	---	---	---	---
	11½	---	3.3	26	42	36	58	---	---	---	---
	12	---	4.2	---	---	8	0.1	66	75	14	24.9
	13 (b)	---	6.4	---	---	---	---	50	22	174	78
	13 (A'')	---		---	---	7	2	87	25	255	73
	13½ (1)	---	7.2	---	---	---	---	36	9	358	91
	13½ (2)	---		---	---	10	3	47	12	325	85
	14 (b)	---	8.3	---	---	---	---	63	8	753	92
	14 (d)	---		---	---	---	---	16	2	834	98
	14 (c)	---		---	---	---	---	---	---	732	100
	15 (a)	♀	11.0	---	---	---	---	680	50	679	50
	15	♀		---	---	---	---	920	55	747	45
	15	♂		---	---	---	---	---	---	all	100
Pigs			6	---	---	4	11	24	65	9	24
			8-12 (1)	---	---	---	---	31	60	21	40
			8-12 (2)	---	---	---	---	38	58	27	42
			13-15	---	---	---	---	61	18	273	82
			15-18 (1)	---	---	---	---	69	21	258	79
			15-18 (2)	---	---	---	---	42	11	321	89
		♂	20-25	---	---	---	---	47	8	506	92
Cattle			6	---	---	5	31	10	46	7	23
			9	---	---	18	37	20	42	11	21
			11½	---	---	---	---	17	61	11	39
			13	---	---	---	---	21	42	29	58
			16	---	---	---	---	17	11	140	89
		♀	28	---	---	---	---	154	57	114	43
		♂	30	---	---	---	---	16	5	390	95

TABLE II
DEVELOPMENT OF RAT GONADS

Age (da.)	C.-R. L. (mm.)	Sex	No.	Mesonephroi and Ducts	Germ Cells	Germinal Epithelium (Cortex)	Medulla	Follicle & Sertoli Cells	Rete	Interstitials
11	1.4	---	1	W.d.	In gut	Thin	---	---	---	---
11½	3.3	---	1		In gut & d. mes.			---	---	---
12	4.2	---	1	Tubules	In d. mes., g ep., medulla		Loose blastema. G.c.	---	---	---
13	6.4	---	2		In g. ep. & med.			On g.c. in g. ep. & med.	---	---
13½		---	5	Post. tub. degen.			Blastema concentrated		V. eff.	---
14	8.3	♂	2	W.d. & M.d.	Few in g. ep.					---
14		♀	1	As in ♂	Many in g. ep.					---
15	11.0	♂	3		In sem. tub.	Thin	Sem. tub.			---
15		♀	4		In cortex	Thick				---
16	13.0	♂	5	Lumina in M.d. & W.d.	Thruout sem. tub.			At periph. of s.tub.		Present
16		♀	1	As in ♂						---
18	19.7	♂	2	Epid. M.d. degen.					V. eff. connect to epid.	Large masses
18		♀	2	Large M.d.	Premat. stages	Divided	Reduced		V. eff. connect to epoö.	---
19	22.5	♂	2	W.d. only						---
19		♀	1	M.d. only			---			---
Newb.	40.0	♂	1		At periph. of sem. tub.					---
Newb.		♀	2		Primary foll.					---
5 d.pp.	45.0	♀	1		Mostly prim. foll.			Foll. cells form		---
10 d.pp.	75.0	♀	1		Most foll. with antra		---			---
16 d.pp.	80.0	♂	1		Spermatocytes					---
29 d.pp.		♂	1				Lumina in sem. tub.			---
29 d.pp.		♀	1		Some atretic foll.		---			---
36 d.pp.		♂	1		Spermatids					---
51 d.pp.		♂	1		Spermatozoa					---

ABBREVIATIONS

abund.—abundant
corp.—corpuscle
cort.—cortex
degen.—degenerated
devel.—developed
d.mes., dors. mes., dors. mesent.
—dorsal mesentery
epid.—epididymis
epoö.—epoö.phoron

foll. c.—follicle cell
g. c.—germ cell
g. ep.—germinal epithelium
irreg.—irregular
med.—medulla
M.d.—müllerian duct
periph.—periphery
premat.—prematuration
prim.—primary

sem. tub., s. tub., s. t., sem. t.
—seminal tubule
Sert. c.—Sertoli cell
Tub. recti—tubuli recti
T. alb. II—secondary tunica albuginea
V. eff.—vasa efferentia
W.d.—Wolffian duct

TABLE III
DEVELOPMENT OF PIG GONADS

C.-R. L. (mm.)	Sex	No.	Mesonephroi & Ducts	Germ cells	Germinal Epithelium (Cortex)	Medulla	Follicle & Sertoli Cells	Rete	Inter- stitials
6	---	1	W. d.	In g. ep., dors. mesent. & med.	Thin. Cu- boidal.	Dense. G.c.	Foll. c. on g.c.	---	---
13-15	---	6			Thin. Col- umnar.	Divided			---
20-25	♂	5	W.d. & M.d.	In med.	Very thin	Irreg.		V. eff.	Scatter- ed.
20-25	♀	3	As in ♂		Thicker than ♂	As in ♂		---	---
35-38	♂	6		In walls & center of sem. tub.		Sem. tub. regular.	Sert. c. scatter- ed.	Rete & fibers	Abund.
35-38	♀	2		In cortex & med.		Fragment- ed.			
62-68	♂	2	Degen. begins	Most at periph. of sem. tub.			Sert. c. at per- iph. of sem. tub.	V. eff. con- nects to epid.	Strands & masses
62-68	♀				Irregular				---
85-95	♂	4							Large masses
85-95	♀	4		Few premat. g.c. deep in cortex		Scattered. T. alb. II			---
120-140	♂	10	Epididymis					Tub. recti. connect to s. tub.	
120-140	♀	4		Thick zone of premat. stages					---
150 150	♂ ♀	1 2		Prim. foll. at inner edge cortex. Thick premat. zone			1 layered granu- losa.	Lumina	---
190 190	♂ ♀	1 1	M.d. convol- uted	Most at periph. of sem. tub. Foll. zone thicker.		Reduced further			
250	♂	1					1 layer of Sert. c. at periph. of sem. tub.		
260	♀	2	M.d. large	Few degen. prim. foll. at central edge of cortex					---

TABLE IV
DEVELOPMENT OF CATTLE GONADS

C.-R. I. (mm.)	Sex	No.	Mesonephroi & Ducts	Germ Cells	Germinal Epithelium (Cortex)	Medulla	Follicle & Sertoli Cells	Rete	Inter- stitials
6	---	1		In dors. mesent., g. ep., & med.	Cuboidal	G. c. & foll. cells.	One foll. c. per g. c.	---	---
9	---	2	Well devel. mesoneph.		Columnar			---	---
11½	---	2		In g. ep. & medulla	Thicker			---	---
16	---	1		More in medulla		Divided		---	---
25	♂	3	M.d. & W.d.	In med. & g. ep.	Very thin	Sem. tub.			Between s. tub.
28	♀	1	Like ♂ 25 mm.	Like 25 mm. ♂	Thicker than ♂			---	---
30	♂	1	Degen. begins					---	---
36	♂	1					Few foll. c. on g. c.		---
45	♀	2			Thicker			---	---
53	♂	1	Epid. M.d. small, solid	Throughout s. t.	Thin. No g. c.	Sem. tub. well- devel.	Thruout sem. t.	V. eff. con- nects to renal corp. & tub.	
60	♂	2	No M.d.					Cords	Strands & masses
110	♂	2	W.d. only			G. c. at per- iph. of sem. tub.	Sert. c. at per- iph. of sem. t.		
110	♀	2	M.d. only	Thin premat. zone at inner edge of cortex.		Fragmented			---
140	♂	2						Tub. recti connect to s.tub.	
150	♀	3		Few prim. foll. at inner edge cort. Thick premat. zone.				Lumina	---
220	♀	3		Thick zone prim. foll.		Few small clumps.	One layer granu- losa.		---
320	♀	1		Prim. foll. zone thicker				Large	---
520	♀	1		Most pr. foll. degen.	G. ep. thin sterile	---			---
900	♂	1				Solid s. t.			Large masses
900	♀	1		Few foll. with antra					