REPRODUCTION IN THE BASKING SHARK, *CETORHINUS MAXIMUS* (GUNNER)

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[Plates 10 to 20]

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In the male part of the ductus deferens is an ampulla nearly two metres in length, containing numerous transverse septa each with a central opening. In pockets between the septa spermatozoa are formed into spermatophores up to about 3 cm. in diameter, each with a core of sperm and a firm translucent cortex. They float in a clear fluid, and about four gallons of them are transferred to the female.

In the female the right ovary alone is functional; it contains at least six million ova 0·5 mm. or more in diameter, most of which degenerate and are replaced by bodies resembling corpora lutea.

The yolky eggs must be ripe at a diameter of about 5 mm., for the diameter of the anterior end of the oviduct, which has inelastic fibrous walls, is too narrow for anything larger to pass. The uterus, about 1 m. in length, is lined throughout its greater part with trophonemata up to 1·0 cm. long.

The structure of the ovary would suggest that *Cetorhinus* is oviparous, but that of the uterus clearly shows that it is viviparous (or ovo-viviparous). There are no modern records of pregnancies, although the sex ratio in the commercial catch is thirty or forty females to one male. Sexual maturity is not reached until at least the third year of age. Females are impregnated in surface inshore waters during early summer, but pregnant females evidently migrate elsewhere, either horizontally or vertically or both, and do not reappear until after parturition.

Introduction

It is remarkable that the anatomy and biology of a fish so large, conspicuous and common as the Basking shark should be practically unknown, especially in view of the fact that it is the subject of a commercial fishery in the British islands and consequently is not inaccessible to naturalists. The modern literature contains reports on the general anatomy of this fish by only four persons, Home (1809, 1813) who examined two adult males, de Blainville (1811) who examined one, Pavesi (1874, 1878) who examined two immature males, and Carazzi (1904, 1905) who examined an immature female. There are numerous observations on the occurrence of the species in various parts of the world, and some authors have described the whalebone-like gill-rakers, but our knowledge, such as it is, of the general anatomy depends entirely upon the work of the four named above; Owen (1866) obtained his information from the work of Home, and adapted some of his figures.

An invitation from Major Gavin Maxwell to Dr H. W. Parker and the present writer to visit his shark-fishing station and factory on the Isle of Soay off the coast of Skye in the early summer of 1947 was therefore very welcome and accepted with much pleasure. The second half of May was spent in Soay, examining and dissecting sharks, and at sea in the hunting craft. A large amount of information was collected and much material fixed and preserved for subsequent examination. The results here presented contain all the information gathered on the subject of reproduction in the Basking shark and are offered, incomplete as they are, as a foundation for further research. Observations on other points in the anatomy and natural history of this fish will, it is hoped, be prepared for publication in due course.

Practically nothing has been recorded hitherto of the reproductive processes in the Basking shark. The observations reported in this paper are based upon an examination of ten fish, four males and six females. Many of the details of the reproductive organs in both sexes are peculiar and, as far as present knowledge goes, unique; the physiological state of these structures throws some light on the breeding activities of the fish. In this paper a systematic account is given first of the macroscopic anatomy and then of the microscopic anatomy and histology of the urinogenital structures. This is followed by a discussion of the findings in comparison with the facts recorded in the literature about other elasmobranch fishes, and by some tentative conclusions on the breeding and life history of the species.

Basking sharks reach a great size, being exceeded in bulk by only one other fish, the Whale shark (*Rhineodon*) of tropical seas. The maximum length, measured in a straight line, is about 29 ft., and the weight about 4 tons. They are not easy subjects for dissection, the size and weight of the individual organs making handling difficult; and woe betide the

anatomist who inadvertently punctures the stomach and releases perhaps the better part of a ton of semi-digested plankton over his dissection. The machinery used in dismembering sharks at the factory was an invaluable aid to the work.

Macroscopic anatomy

1. *The male*

Testes and epigonal organ

The testes lie far forward in the abdominal cavity, one at each side of the anterior end of the stomach (figure 1). They are supported by stout mesorchia taking their origin from the dorsal wall of the cavity on each side of and close to the origin of the mesogastrium. Each

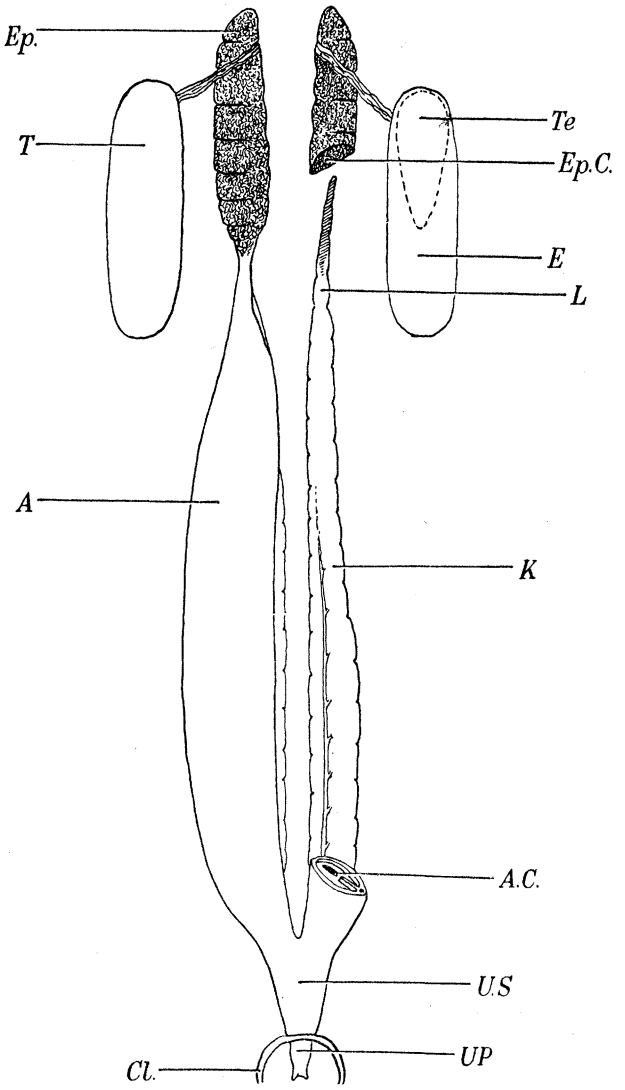

Figure 1. General view of the internal reproductive organs in the male. Most of the ampulla on the right side of the drawing has been removed to expose the kidney. *A*, ampulla ductus deferentis; *AC*, cut end of ampulla; *Cl*, cut wall of cloaca; *E*, epigonal organ; *Ep*, epididymis; *EpC*, cut end of epididymis; *K*, kidney; *L*, Leydig's gland; *T*, testis and epigonal organ; *Te*, position of testis tissue defined by dotted line; *UP*, urinogenital papilla; *US*, urinogenital sinus.

testis is combined with its corresponding epigonal organ to form a single compact body cylindrical in shape with rounded ends. In shark no. 1, a rather small but sexually active adult measuring 6·9 m. from the tip of the snout to the caudal notch, these bodies had a total length of 70 cm. and a diameter of 20 cm.; their weight was 17·5 lb. each. Of this total length the testicular part of the body occupied the anterior 37 cm., the posterior 33 cm. consisting of epigonal tissue alone. The anterior part does not consist entirely of the testis, for the epigonal tissue completely encloses the organ forming a cortex about 0·5 to 1·0 cm. thick outside it. Caudal to the anterior end of the composite body the testis diminishes in diameter and tapers towards its caudal end, where it lies towards the ventral surface of the organ. Since the organ is roughly cylindrical, the thickness of the epigonal cortex correspondingly increases caudally as the diameter of the testis decreases. The mesorchia thus support the combined testes and epigonal organs, the peritoneum forming a single tunica enclosing each composite body.

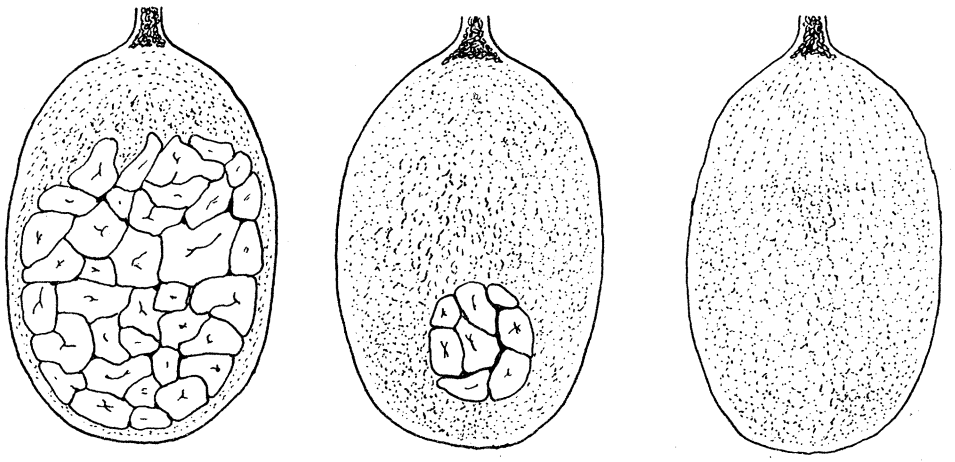

FIGURE 2. Transverse sections of the testis and epigonal organ. (*a*) Near the cranial pole; *b*, intermediate; *c*, near the caudal pole. The testis lobes are seen in *a* and *b* but not in *c*. At the upper edges of the drawings the mesorchia with their contained pampiniform vessels are seen.

The testis tissue is divided up into a number of irregular lobes about 1·0 to 1·5 cm. or more in diameter, each lobe being subdivided into lobules by fine trabeculae radiating towards the circumference from a more or less centrally placed spot. The lobes are closely packed together so that each is moulded by contact with its neighbours (figure 2). The epigonal tissue is dark red in general colour, mottled and speckled with lighter and darker tints. The darker mottlings produce a vague pattern which suggests an indistinct division of the tissue into roughly circular lobes in the ventral half of the organ, and into strands radiating from the attachment of the mesorchium in the dorsal half. The consistency of the tissue is soft and pulpy and tears under its own weight if lifted after the peritoneal tunica is divided or removed. There is no macroscopic appearance of any supporting strands of fibrous or connective tissue within the pulpy mass.

Epididymis

A little posterior to the anterior end of the testis-epigonal organs the vasa efferentia leave them and pass within the mesorchium to the head of the epididymis. The latter is thrown

into a mass of complex convolutions to form a compact body with a cerebriform surface. The shape of this is semi-cylindrical with rounded ends, the flattened surface lying in apposition to the dorsal abdominal wall and the rounded surface being covered with peritoneum and facing the abdominal cavity. The lateral edge is interrupted by six or seven notches from which trabeculae of fibrous and connective tissue extend transversely across the organ, becoming less distinct as they approach the medial edge which is entire. The trabeculae thus cut the body up into a number of lobes distinctly separated from each other in the lateral part but confluent in the medial part. The lobes are tightly packed with the convoluted tubes of the ductuli and ductus epididymidis, the latter of which is 2 to 3 mm. in diameter in the cranial part and increases gradually to attain a diameter of 5 to 7 mm. in the caudal part, where it becomes the ductus deferens; it is embedded in a supporting mass of loose connective tissue. The length of the organ in shark no. 1 was 69 cm., its width 14 cm. and its dorso-ventral thickness in its middle line from 7 to 10 cm. The anterior end of the organ lies about 30 cm. cranial to the level of the cranial end of the testis-epigonal organ.

Ductus deferens and ampulla

The posterior end of the epididymis is constricted, and caudal to this the ductus deferens becomes progressively expanded to form the enormous ampulla ductus deferentis which joins the urinogenital sinus close to the cloaca. In shark no. 1 the ampulla was 1·8 m. long and 25 cm. in its greatest diameter, which lay about one-third of the total length from the caudal end. From this point the diameter decreases very gradually towards both ends, the extreme cranial diameter being less than the caudal one. Where the ampullae of the two sides join the urinogenital sinus at their caudal ends their medial borders coalesce for a few centimetres proximal to the junction with the sinus.

The interior of the ampulla is lined with transverse folds, each in the form of a circular diaphragm or septum with an eccentric aperture, so that the effective lumen of the ampulla is reduced to less than half of the external diameter of the organ (figure 3). A longitudinal ridge runs along the lateral side of the interior of the ampulla; at the cranial end it is low and inconspicuous, but more caudally it projects into the lumen for a distance equal to the width of the diaphragmatic folds so that its summit is level with the circumference of the effective lumen. At the cranial end of the ampulla the transverse folds are thin and membranous, but they become stouter more caudally where the longitudinal ridge reaches the effective lumen. In this part the height of the longitudinal ridge is about 10 cm., the diameter of the effective lumen about 6 cm., and the width of the septum opposite the lumen about 3 cm. A deep pocket is thus formed between each pair of septa where they meet the sides of the longitudinal ridge. The circumferential parts of each septum near the attachment to the wall of the ampulla are stout, from 5 to 10 mm. in thickness, and the thickness of the longitudinal ridge is about the same. More centrally the septa become thinner and are split into three or four component laminae which are thin and membranous like the folds of the cranial part of the ampulla. The spaces between the laminae do not extend to the bases of the septa at the attachment to the wall of the ampulla but stop short so that the laminae are only about 2 cm. in width. The width of the laminae is greatest opposite the longitudinal ridge and decreases gradually as the ridge is approached.

In consequence, the pockets between the laminae are very much shallower at their junction with the ridge than the pockets between adjacent main septa. The wall of the interior of the ampulla and the surfaces of the main transverse septa are covered with low villi, larger on the longitudinal ridge and adjacent parts, smaller on the opposite side. On the laminae

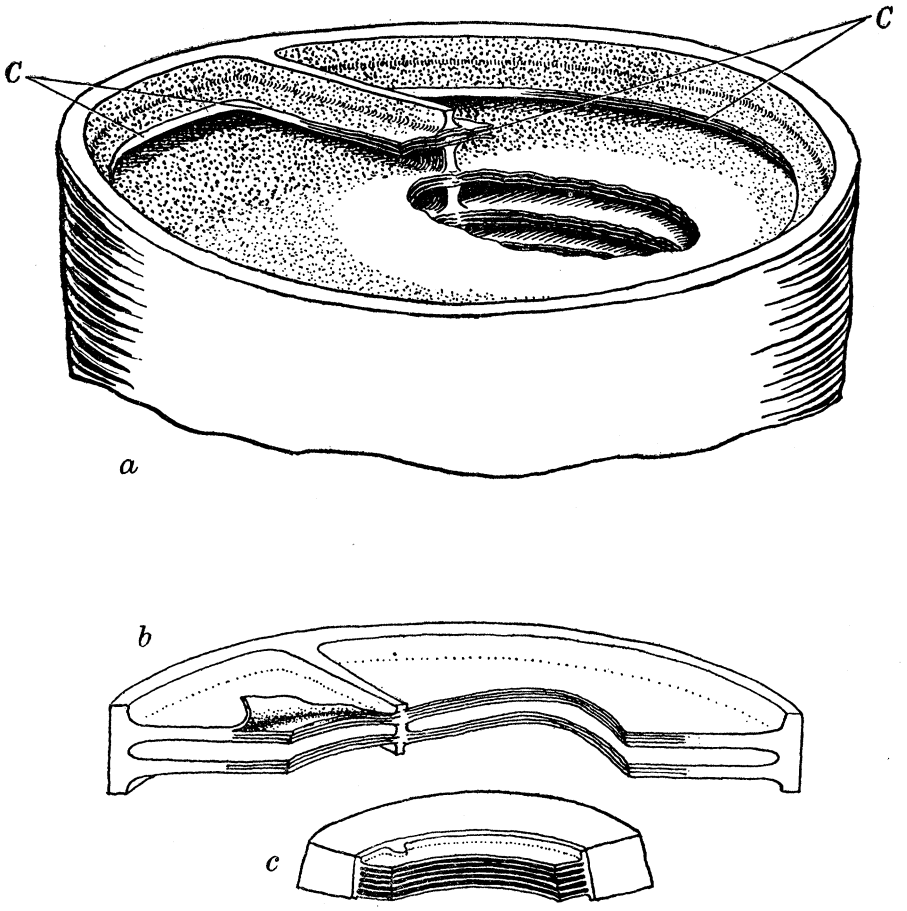

FIGURE 3. *a*. A portion of the ampulla ductus deferentis at about the middle of its length. The uppermost septum has been removed leaving a cut edge, *C*. The longitudinal ridge joins successive septa, and the edges of the septa surrounding the lumen are split into several component laminae. The density of the stippling represents the relative density of the small villi. *b*. A portion of the ampulla ductus deferentis bearing two adjacent septa, cut open longitudinally and opened out. The cut edges at right and left were originally continuous with each other. The upper lamina on the left has been raised to display the character of the border. *c*. A portion of the cranial end of the ampulla ductus deferentis with thick walls and thin membranous septa. The longitudinal ridge is much reduced in this part of the ampulla.

the villi are so small that they are not visible macroscopically, and on the membranous folds of the cranial part of the ampulla the villi are likewise too small to be visible to the naked eye. The wall of the ampulla is rather less than 1 cm. in thickness throughout the greater part of its length, but at the cranial end, where the folds are small and membranous, the thickness of the wall is much greater, being 2·5 to 3 cm. The external diameter of this end of the ampulla is therefore much greater in proportion to the diameter of the lumen than it is more caudally.

Spermatophores

On opening the ampulla the narrow proximal part with thin membranous septa is seen to be filled with the opaque white spermatic fluid entering from the coiled part of the ductus deferens (figure 4). The contents of the remainder of the ampulla are, however, very different, for it is completely filled with rounded lumps of firm hyaline material floating in a comparatively small quantity of clear fluid. The lumps are small in size, a few millimetres in diameter, in the proximal part of the ampulla, but very much larger, up to 2·5 to 3·0 cm.

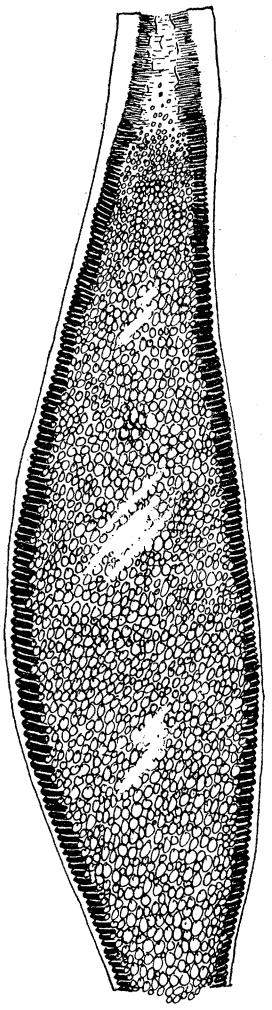

FIGURE 4. The ampulla ductus deferentis of the right side split open by longitudinal incision of its ventral surface, showing the transverse septa and the content of spermatophores. At the anterior end the walls are thick, the septa are small and membranous, and the fluid contents have not yet been formed into spermatophores.

or more in diameter in the greater part of the organ (figure 5). Most of these bodies consist of a cortex of translucent hyaline material surrounding a central mass up to 1·0 cm. in diameter of opaque, white sperm. A few of them contain no central mass but consist entirely of the hyaline matter, and conversely, scattered among the fully formed bodies, there is a small number of rounded aggregations of sperm without the hyaline cortex; some of these are equal in size to the fully formed bodies and contain small masses of the hyaline

material embedded in them. The sperm entering the ampulla is evidently aggregated into small rounded masses which are semi-solid in consistency when compared with the fluid received from the coiled part of the ductus deferens, and thereafter the hyaline cortex is secreted round them to form these very peculiar spermatophores. The formation of the larger hyaline lumps appears to take place in the pockets formed by the junction of the transverse septa with the longitudinal thickened ridge. The identity of the substance forming the cortex has not yet been established; it appears to be a protein, but it does not give a positive reaction to tests for mucin. The quantity of spermatophores present in each ampulla was estimated at about five or six gallons.

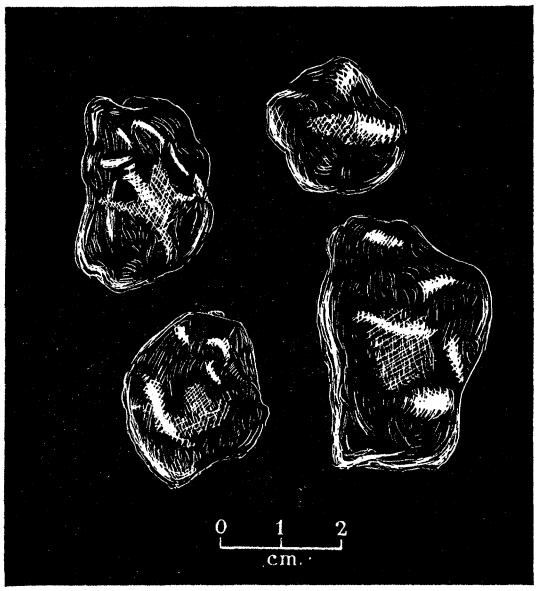

FIGURE 5. Spermatophores.

Kidneys and interrenal bodies

The kidneys lie on the posterior abdominal wall on each side of the aorta and dorsal to the whole of each ampulla and the distal ends of the coiled mass of the epididymis. Their length in shark no. 1 was 2·08 m., the narrow anterior part distinguished as Leydig's gland being 39 cm. in length. The opisthonephric duct lies medial to the mid line of the kidney on its ventral surface. Between the posterior parts of the kidneys the unpaired interrenal body of flattened oval section, 2 to 3 cm. wide and about 1 cm. thick, extends forward from their caudal ends for a distance of about 1·4 m., its anterior end lying about 50 cm. posterior to the origin of the anterior mesenteric artery. At the level of the cloaca the renal portal vein abruptly breaks up into a great number of small vessels which enter the kidney tissue, and at almost the same level the posterior cardinal sinus arises as suddenly by the coalescence of many tributaries. Just before reaching the level of the posterior edge of the dorsal fin the sinus divides into paired posterior cardinal sinuses. These vessels lie between and slightly ventral to the kidneys; at the level of the axilla the posterior cardinal sinuses have diverged so that they lie ventral to the medial parts of the kidneys. Throughout the course of the aorta on the dorsal wall of the abdominal cavity an immense number of small vessels are given off in addition to the main trunks and segmental arteries. These form a reteform

spongy mass behind the kidneys, surround the posterior cardinal sinuses and the interrenal body, and extend as a layer about 1 cm. thick between the folds of peritoneum supporting the gonads and epigonal organs. This spongy arterial tissue does not surround the aorta, whose walls are not unusually stout. The walls of the anterior mesenteric artery, however, are most peculiarly thickened, the lumen of the vessel being about 1 cm. in diameter surrounded by walls about 2 cm. thick composed of fibrous and elastic tissue. The unpaired part of the posterior cardinal sinus which lies dorsal to the interrenal body has its internal surface thickly scattered with small excrescences, pedunculated lobes and strands of tissue (figure 6) forming a mass resembling fungal hyphae projecting into the lumen. Similar tissue lies outside the sinus, between it and the interrenal body and the kidneys; it consists of sympathetic ganglia and suprarenal tissue.

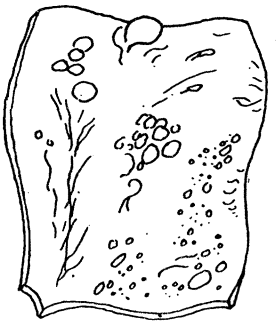

FIGURE 6. Part of the interior of the wall of the posterior cardinal sinus showing lobes and pedunculated masses of sympathetic ganglia. The surface shown is that which bounded the lumen before the vessel was opened. Natural size.

Urinogenital sinus and cloaca

The urinogenital sinus is a chamber about 25 cm. in length and the same in width at its anterior end, but it tapers towards its posterior end (figure 7). On each side of the middle line at the anterior end lie the openings of the ampullae ductus deferentis, and a few centimetres lateral to these there is a further pair of rather smaller openings. These lead to diverticula which run longitudinally in the wall of each ampulla immediately below the longitudinal thickened ridge, between it and the external surface of the ampulla. These diverticula appear to be the homologues of the sperm-sacs of other elasmobranchs. They are 2 to 3 cm. in diameter and 40 cm. in length; they are entirely confined to the thickness of the walls of the ampullae and do not appear as separate organs in the abdominal cavity. Posterior to the openings of the ampullae the opisthonephric ducts join the urinogenital sinus near the mid-line on the dorsal side. Behind their openings the sinus becomes narrowed and passes through the posterior abdominal wall to communicate with the dorsal part of the cloaca through the urinogenital papilla, a soft-walled tube projecting into the cloaca with a free part about 10 cm. in length. It is slightly flattened dorso-ventrally and tapers towards its free end, just before which it expands to form a funnel-shaped orifice. Its distal part is covered with low rounded papillae.

The rectum opens into the cloaca ventral to the urinogenital papilla, and the openings of the abdominal pores lie just without the cloacal border on each side between the bases of the claspers. The pores are narrow canals, 4 cm. in diameter at their abdominal orifices,

which lie on the ventral side of the posterior end of the abdominal cavity. The canals rapidly decrease in diameter to 1 cm., and run through the pelvic tissues for a distance of 15 cm. to reach the external surface. Here they are continued within flaccid tubular papillae about 5 cm. long, at the summits of which their external orifices are situated.

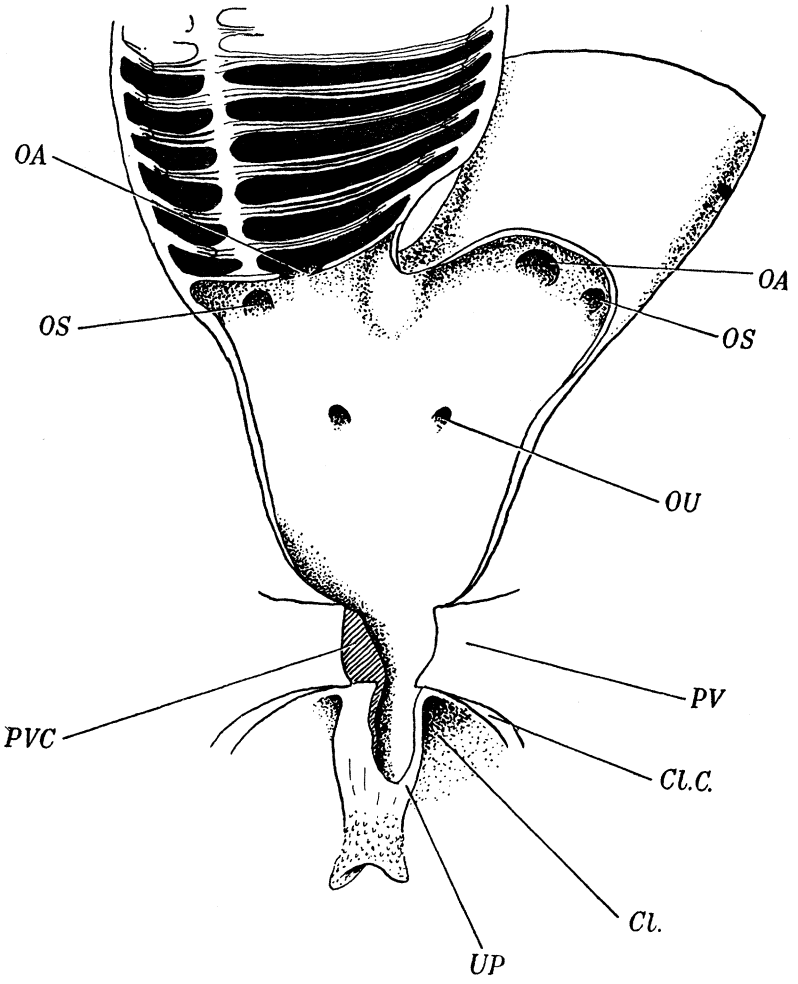

FIGURE 7. The urinogenital sinus seen from the ventral side, most of the ventral wall having been removed. The ampulla ductus deferentis of the right side has been opened longitudinally and spread out. *Cl*, cloaca; *ClC*, cut edge of cloaca; *OA*, orifice of the ampulla; *OS*, orifice of the sperm sac; *OU*, orifice of the opisthonephric duct; *PV*, ventral pelvic cartilage; *PVC*, cut surface of ventral pelvic cartilage; *UP*, urinogenital papilla, part of the ventral wall of which has been removed to show the lumen.

Siphons

The siphons lie on each side of the mid-line in the antero-lateral abdominal wall. Each is an elongated sac, in shark no. 1, 1·36 m. in total length, the anterior ends lying 60 cm. posterior to the base of the pectoral fin. The width of the greater part of the siphon is about 30 cm., but at the anterior end it increases to 50 cm.; when cut open longitudinally the width between the two cut edges at the middle of its length is 66 cm. The siphon forms a potential cavity with the external and internal surfaces in close apposition. From the posterior end a duct about 5 cm. in diameter leads to the base of the groove formed by the

scroll of the clasper. The lining of the siphon is a smooth white mucous membrane; the wall of the external surface is thinly muscular and membranous, and that of the internal surface more strongly muscular and about 1 cm. thick. On the medial border of the internal surface a large vessel runs forward with a winding course, branching repeatedly proximally.

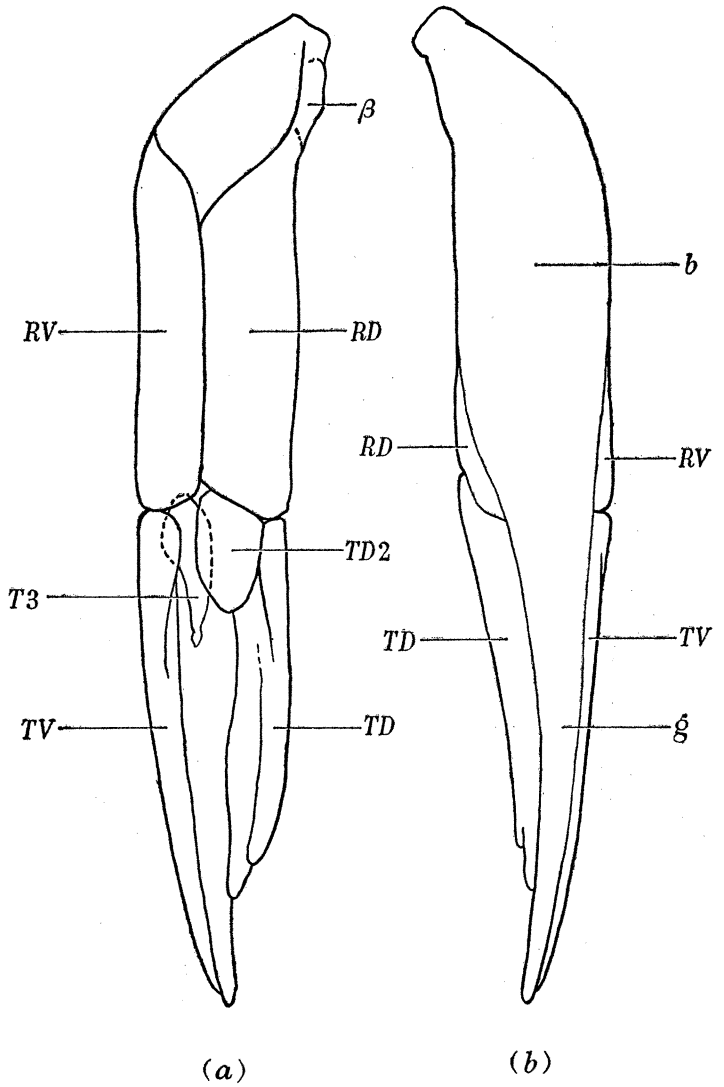

FIGURE 8. Skeleton of the clasper of the right side (*a*) dorsal, (*b*) ventral surface. *b*, appendix stem; *β*, beta cartilage; *g*, end-style; *RD*, dorsal marginal cartilage; *RV*, ventral marginal cartilage; *T*3, third terminal piece (claw); *TD*, dorsal terminal piece; *TD*2, subsidiary dorsal terminal piece; *TV*, ventral terminal piece.

Clasper

In the skeleton of the clasper (figure 8) the main cartilage, or appendix-stem of Jungersen (1899), whose terminology is adopted here, forms the chief support of the organ; its proximal half is wide, but its distal half tapers to a point and constitutes the 'end style'. Fused to its base on the medial side is the small beta cartilage or dorsal stem-piece. Firmly united to the lateral and medial edges respectively of the appendix-stem are the ventral and dorsal marginal cartilages which form the sides of the clasper groove, and by wrapping

over it in scroll form convert it functionally into a tube. The appendix-stem with the two marginal cartilages forms a single functional unit, and the three together are conveniently referred to as the axial cartilage. Terminal pieces tapering to points are united to each side of the end-style, the ventral terminal piece to its lateral edge and the dorsal terminal piece to its medial edge. The proximal ends of these terminal pieces are firmly joined to the distal

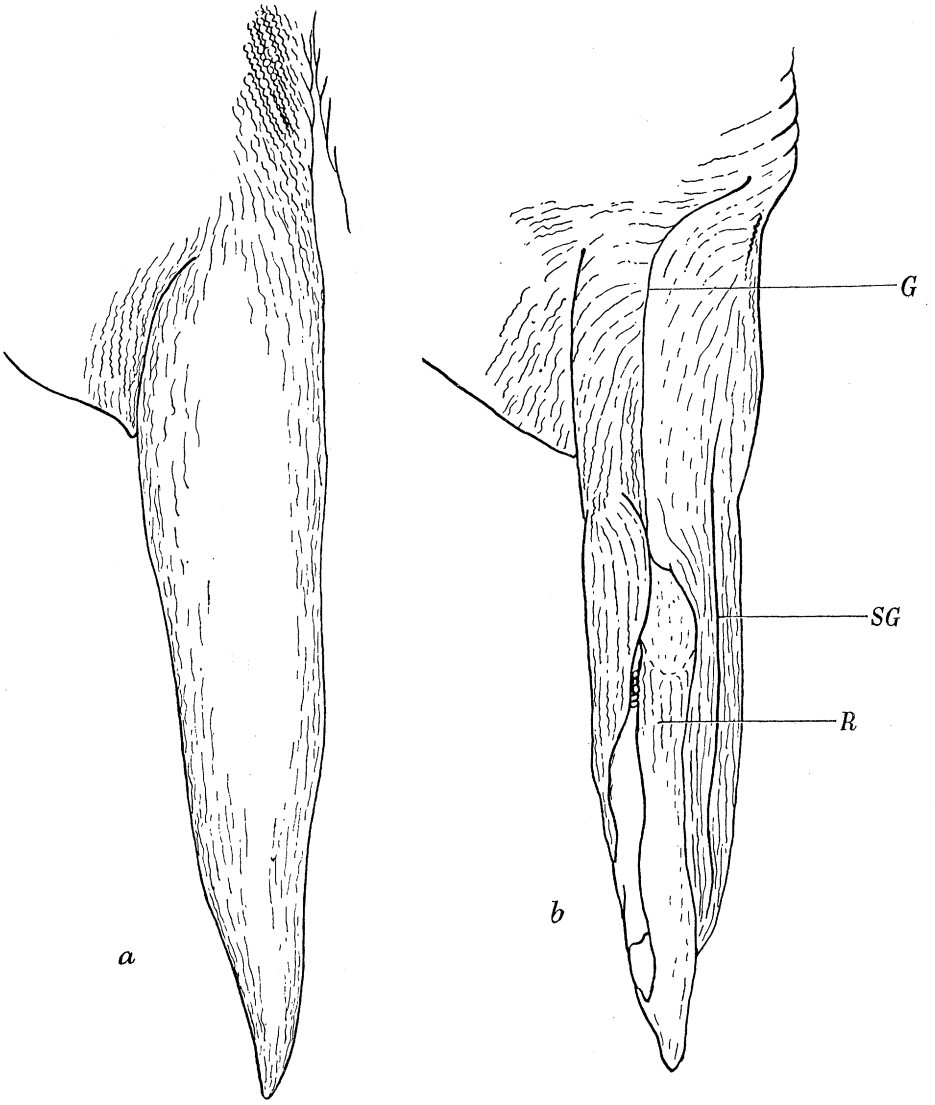

FIGURE 9. *a*. Clasper of the right side, ventral surface. Note corrugations and longitudinal ridges of the surface, and the tendency for the ridges to break up into rows of papillae near the cloaca. *b*. Clasper of the left side, dorsal surface. *G*, clasper groove; *R*, rhipidion; *SG*, second subsidiary groove.

ends of the ventral and dorsal marginal cartilages respectively. The surface of the dorsal terminal piece facing the clasper groove bears a longitudinal furrow, deepest distally and becoming shallower proximally to fade out distal to the base of the terminal piece. The distal end of this furrow notches the edge of the terminal piece, separating off a small subterminal point. The dorsal and ventral terminal pieces form the sides of the distal half of the clasper groove, but they do not roof it by enclosing it in scroll fashion. A second

dorsal terminal piece, smaller than the first, articulates firmly with the distal end of the dorsal marginal cartilage and the proximal part of the free edge of the dorsal terminal piece; it extends the roof of the clasper groove distally beyond the ends of the marginal cartilages. A third terminal piece is movably articulated with the distal end of the ventral marginal cartilage and the appendix-stem at their point of fusion and lies within the clasper groove; it bears a sharp point which projects through the integument. The axial cartilage is hard, tough and partly calcified; only the appendix-stem consists of hyaline cartilage, the marginal cartilages being white fibro-cartilage. Apart from the musculature, the investment of the skeleton consists of dense white fibrous tissue. The skeleton of the clasper thus consists of eight cartilages, the appendix-stem (*b*), to which is fused the beta cartilage, and whose pointed end forms the end style (*g*); dorsal (*Rd*) and ventral (*Rv*) marginal cartilages; three main terminal pieces, the dorsal (*Td*) and ventral (*Tv*) and third (*T*3) terminal pieces, the last being the claw or spur; and a subsidiary dorsal terminal piece (*Td*2).

The intact claspers (figure 9) taper from base to tip and have the shape of elongated cones flattened on one side. The medial surfaces of the claspers are normally in contact with each other, and join together at their proximal ends to form the anterior limit of the cloaca which opens between their bases. The lateral surfaces of the claspers are shorter than the medial ones and fuse with the pelvic fins caudal to the level of fusion of the medial surfaces. The lateral surface curves inwards slightly immediately before its fusion with the fin, so that the width of the base is a little less than the width more distally. The total length of the clasper in shark no. 1 was 1·090 m. from the anterior end of the cloaca to the tip along the medial surface, and 0·940 m. along the lateral edge. Its greatest diameter, a little more than one-quarter of the distance from base to tip, was 17 cm. The lateral, ventral and medial surfaces of the claspers are rounded, the dorsal surface, normally in contact with the ventral surface of the body, is flattened. The skin of the claspers is raised into a series of irregular longitudinal corrugations which diminish in size towards the tip. The colour of the organ is the same dark tint, almost black, as the general surface of the body, but at the base of the medial surface it becomes white at the margins of the cloaca, a narrow transitional region of grey spots intervening. At the sides and in front of the cloaca the longitudinal corrugations are more pronounced, reaching a depth of 0·5 cm. or more. There is also a tendency for the corrugations in this region to be broken up into rows of bead-like papillae by sulci crossing them transversely.

The claspers take the usual form of a longitudinal scroll, the edges of the groove overlapping on the dorso-medial surface (figures 9*b* and 15). The groove starts near the medial edge of the base of the clasper at the side of the cloaca and runs obliquely outwards and backwards for a short distance until it reaches the middle line of the dorsal surface. It then curves and follows a course approximately parallel to the long axis of the clasper to the tip, but slightly lateral to the mid-line, the lateral margin overlapping the medial one. At about the middle of its length a subsidiary groove is given off obliquely from the medial side of the main one to curve caudally and run parallel to it so that a narrow longitudinal lobe, the rhipidion of Leigh-Sharpe (1920), is defined. Medial to this last groove on the dorsal surface there is another subsidiary groove which is not connected with the others. It runs longitudinally, becoming shallower until it fades out at each end about 20 cm. from base and tip respectively. At about the middle of its length, opposite the bifurcation

of the main groove, it communicates with a blind pocket which lies underneath the skin and runs proximally for a short distance. This pocket appears to be homologous with the cul-de-sac described as the 'pseudosiphon' in *Galeus vulgaris* and some other elasmobranch fishes by Leigh-Sharpe (1921), but, being merely a fold of the skin with no glandular or muscular structures associated with it, a name implying a special function for it seems scarcely warranted (figures 10*b* and 11, *SG.*).

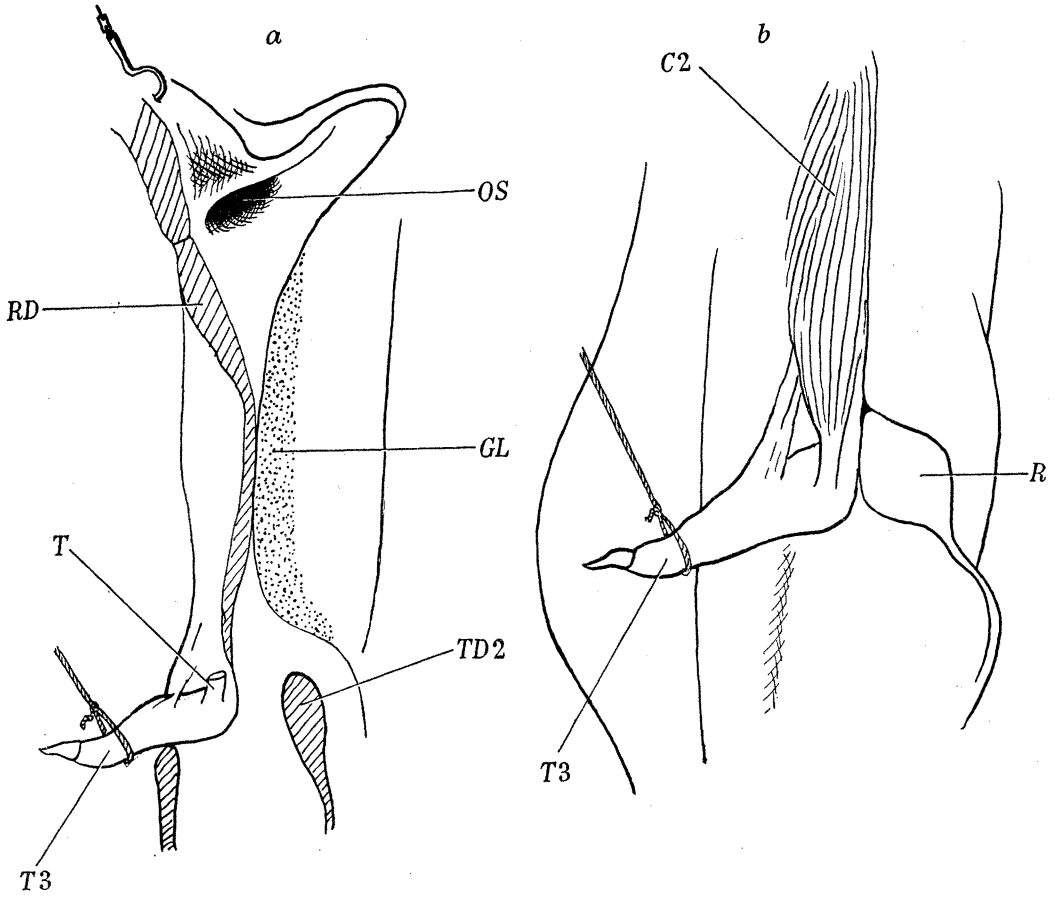

FIGURE 10. *a.* Proximal part of the clasper of the left side dissected. The fascia and muscles have been removed, as has a part of the edge of the dorsal marginal cartilage and of the dorsal and ventral terminal pieces. The tissues at the anterior end of the clasper groove are reflected cranially. *GL*, the stippled area shows the approximate extent of the clasper gland on the inside of the ventral marginal cartilage facing the lumen of the groove; *OS*, opening of the siphon tube; *RD*, cut edge of the dorsal marginal cartilage; *T*, cut tendon of m. compressor inserting on the base of the claw-cartilage; *T*3, claw-cartilage; *TD*2, cut surface of base of secondary dorsal terminal piece. *b.* Middle part of the clasper of the left side dissected to show the claw-cartilage and its muscle. *C*2, the part of m. compressor inserted by a tendon on to the claw-cartilage; its action is to extend the cartilage; *R*, base of the rhipidion; *T*3, cartilage with claw.

The scroll-shaped cartilages of the clasper enclose the main groove so closely in its proximal half that the fleshy margins can be separated only slightly; in the distal half the support of the cartilages is less complete, and the fleshy parts of the scroll can be successively unfolded to disclose its structure. Dissection of the proximal half shows that the siphon tube joins the clasper groove on the antero-lateral border of its oblique part (figures 10*a*,

OS and 14*a*, *ST*), and that the walls of the groove, from the junction of the siphon tube to the bifurcation at the proximal end of the rhipidion, are lined with a thick glandular layer, whereas the more distal part of the groove is lined with a thin white mucous membrane. The glandular layer varies from 1 cm. to about 2 cm. thick and is extremely soft (figure 15, ii, iii and iv); in the sharks examined it was in a high state of activity, and great

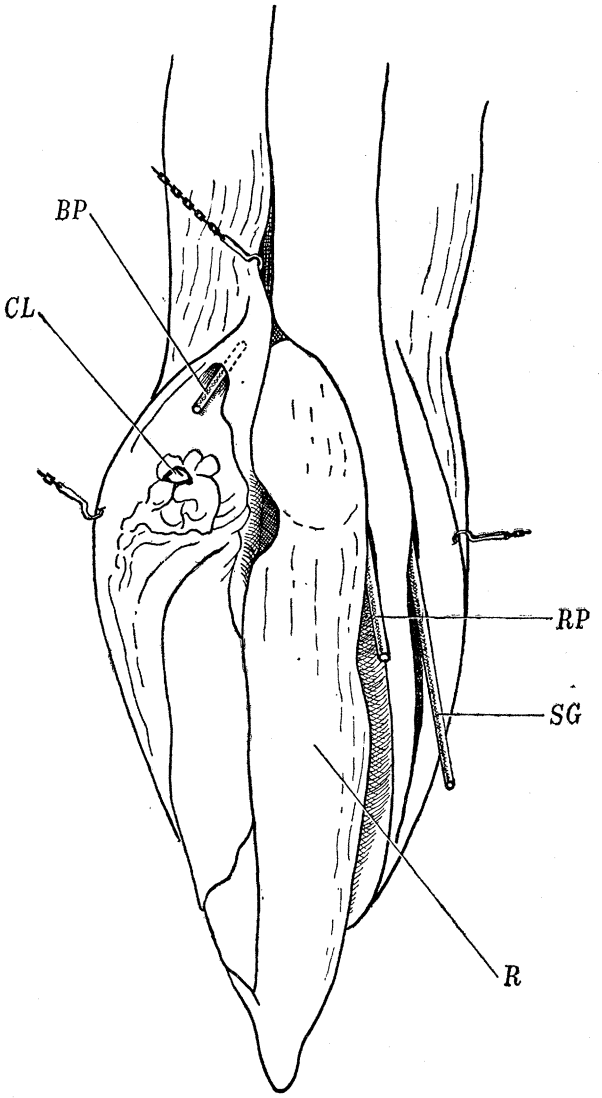

FIGURE 11. Distal half of the clasper of the left side, the edges of the component scrolls drawn aside. *BP*, small blind pocket; *CL*, claw; *R*, rhipidion; *RP*, probe inserted in blind-pocket medial to the rhipidion in the first subsidiary groove; *SG*, probe inserted into blind pocket of the second subsidiary groove.

quantities of an opaque white slimy secretion oozed from it and ran from the distal end of the clasper groove when the fish were hauled out of the water. This secretion was at first mistaken for the spermatic fluid until further examination revealed its true nature.

A small proximal part of the rhipidion is marked off from the main distal part by a notch on its lateral border; this part is firmly supported by cartilage (*Td*2) so that it cannot be displaced, whereas the distal part can be folded back from its normal position as part of the roof of the groove. The minor groove given off from the main one and defining the

medial border of the rhipidion is shallow where it borders the rigid proximal part of the rhipidion but immediately becomes much deeper distal to the level of the notch. At the point where it becomes deeper it gives off a diverticulum which extends proximally for a short distance to end as a blind pocket (figure 11, *RP*).

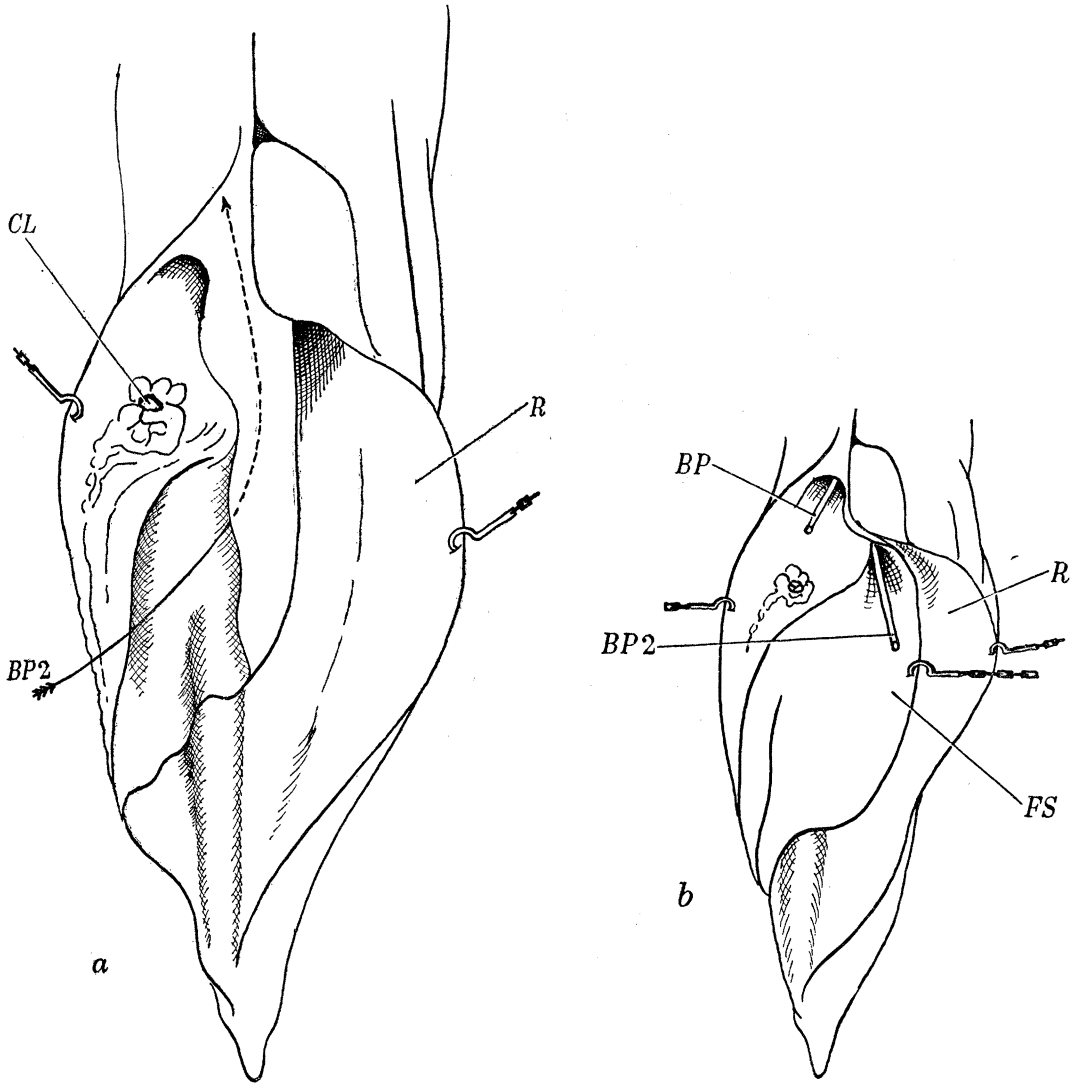

FIGURE 12. *a*. Distal half of the clasper of the left side, the rhipidion and lateral scrolls drawn aside. *CL*, claw; *BP*2, blind pocket enclosed by fleshy scroll, the dotted part of the arrow showing its extent; *R*, inner surface of rhipidion. *b*. The same, with the fleshy scroll unrolled medially. *FS*, fleshy scroll. *BP*, probe inserted into small blind pocket; *BP*2, probe inserted into pocket enclosed by fleshy scroll; *R*, inner surface of rhipidion.

When the outer margin of the groove opposite the rhipidion is folded back (figure 11) a pocket is seen on the inner surface of the lifted flap from which projects a stout curved claw lying opposite the notch on the lateral border of the rhipidion. The margins of the pocket are surrounded by a number of low puckered lobes covered with a white mucous membrane, and can be retracted to expose the terminal 2·5 to 3·0 cm. of the claw (figure 11, *CL*). The claw is set upon the summit of a partly calcified cartilage which articulates with the axial cartilage. It can be flexed so that the claw projects from the groove with its long

axis at right angles to that of the groove; it is thus directed dorso-laterally. The exposable part of the claw is covered with very hard chondro-dentine. In two of the sharks examined the claw of one clasper appeared to have been damaged, for in place of the conical tooth-like ending there was an irregular knob of calcareous substance resembling bone, constricted at its base by a circular groove giving it a fungiform shape. Proximal to the claw there is a small blind pocket opposite the fixed part of the rhipidion (figures 11 and 12*b*, *BP*).

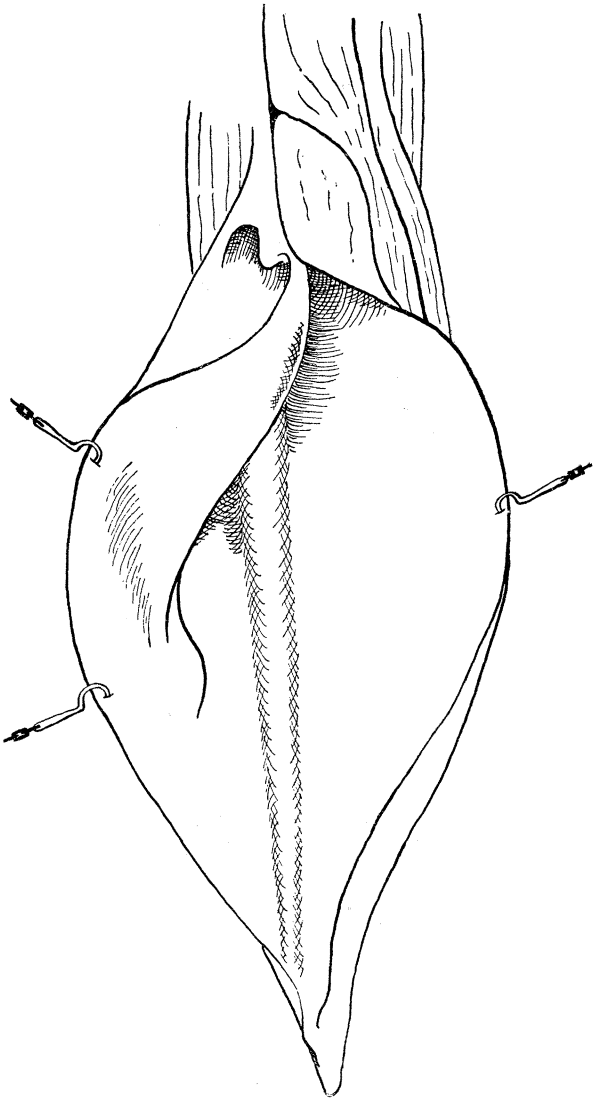

FIGURE 13. Distal half of the clasper of the left side with all scrolls drawn aside to show the clasper groove. The rhipidion has been drawn to the right of the figure, and the fleshy scroll to the left until it covers and hides the claw. The ridge within the clasper groove is produced by the supporting end-style.

When the distal part of the rhipidion is folded back medially (figure 12*a*) the lumen of the distal end of the main groove is partly exposed, but is not visible in its entirety because it is roofed by another fleshy scroll. This originates from the lateral wall of the groove medial to the pocket containing the claw as a thin fleshy sheet which descends towards the bottom of the groove close to its lateral edge. It is then reflected upon itself so that its free edge lies near its point of origin and parallel to the long axis of the clasper. The distal end of this

scroll is free, but the proximal end fuses with the deep surface of the flap covering the claw; as it does so its edge is curved at its extreme proximal end so that a small blind pocket extending proximally for a few centimetres beneath the skin is formed (figure 12*b*, *BP*). When the last-described scroll is displaced laterally (figure 13) the distal part of the main groove is completely exposed and is seen to reach the exterior just short of the apex of the clasper on its lateral edge.

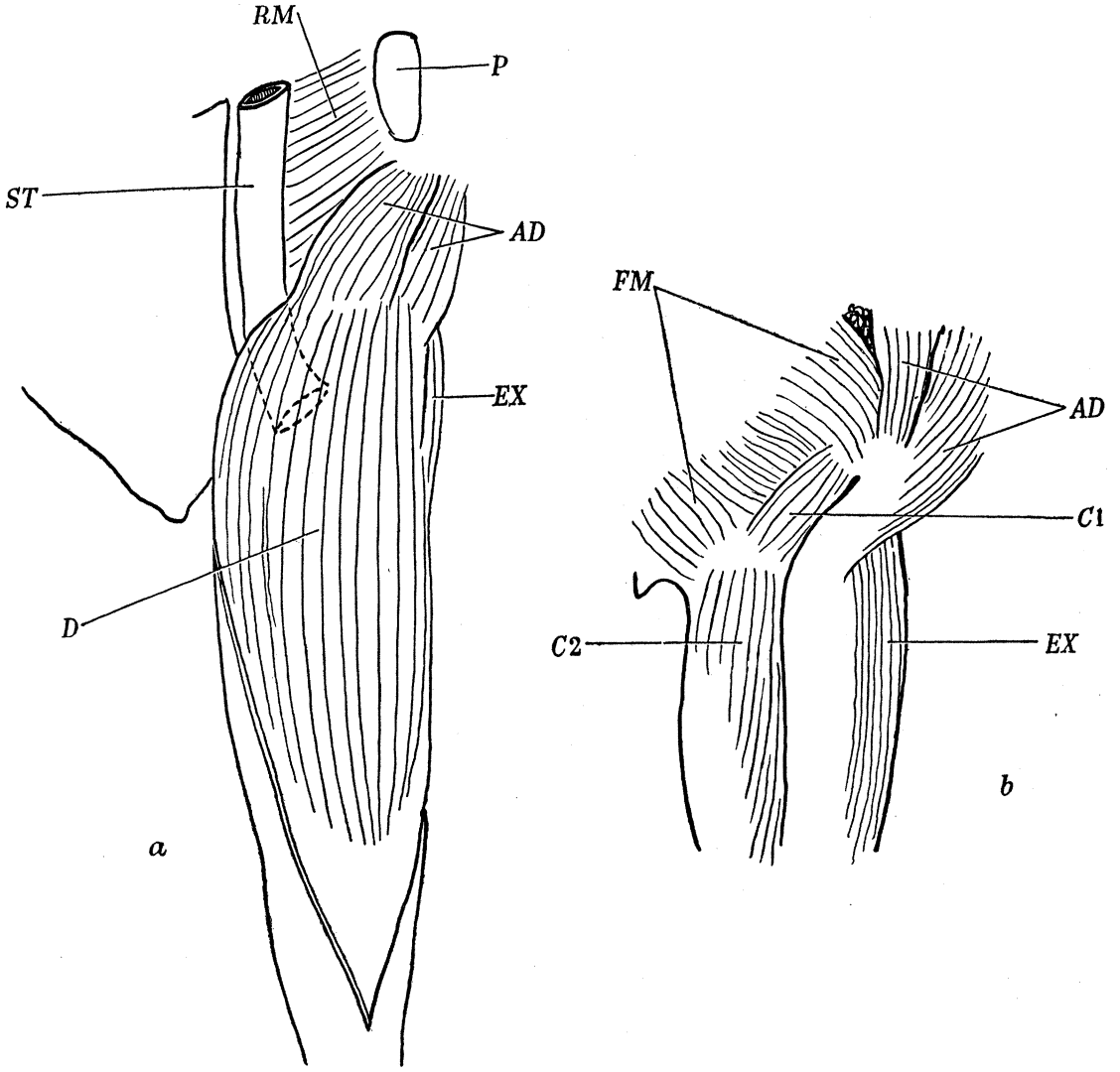

FIGURE 14. *a*. The musculature of the ventral side of the clasper. *AD*, m. adductor; *D*, m. dilatator; *EX*, m. extensor; *P*, cut surface of pelvic cartilage; *RM*, ray muscle of the pelvic fin; *ST*, siphon tube. *b*. The musculature of the dorsal side of the clasper. *AD*, mm. adductores; *C*1, first part of m. compressor covering the opening of the siphon tube; *C*2, the second part of m. compressor, some of its fibres inserting on the ventral marginal cartilage, and some by a tendon on the base of the claw; *EX*, m. extensor; *FM*, muscles of the pelvic fin.

Beneath the superficial fascia of the ventral side of the clasper lies the large dilatator muscle which originates from the distal end of the basipterygium and is inserted on the ventral surface of the proximal half of the axial cartilage and the aponeurosis investing the clasper (figure 14*a*). On the medial side of this muscle lies the extensor muscle which

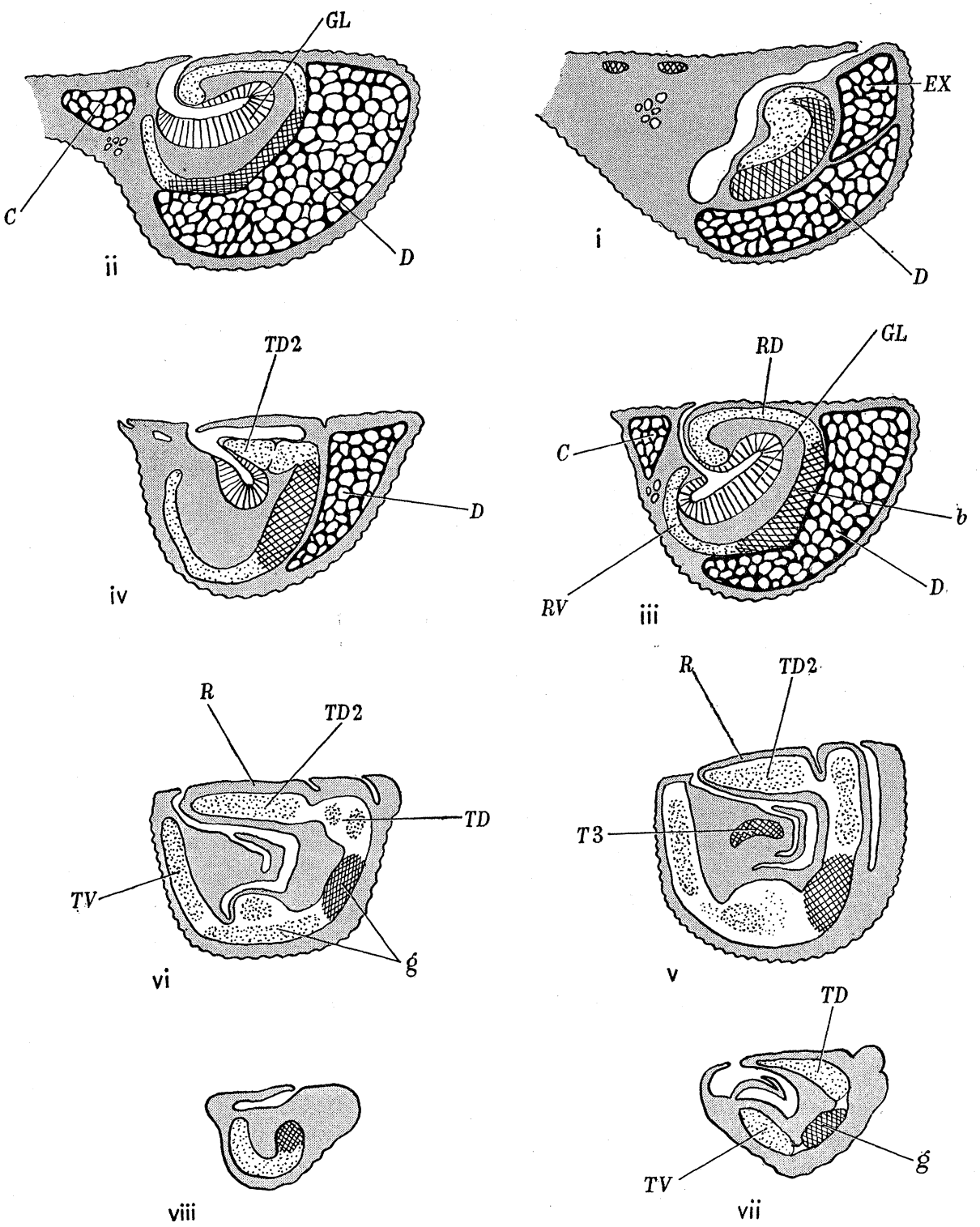

FIGURE 15. Transverse sections of the clasper, (i) the most proximal, (viii) the most distal. Hyaline cartilage cross-hatched; fibro-cartilage stippled; the gland cross-lined. *b*, appendix-stem; *C*, m. compressor; *D*, m. dilatator; *EX*, m. extensor; *g*, end-style; *GL*, clasper gland; *R*, rhipidion; *RD*, dorsal marginal cartilage; *RV*, ventral marginal cartilage; *T*3, third terminal piece (claw); *TD*, dorsal terminal piece; *TD*2, secondary dorsal terminal piece; *TV*, ventral terminal piece.

inserts on to the medial side of the axial cartilage and sends some slips to the fibrous fascia on the medial wall of the blind pocket lying parallel and medial to the rhipidion. Medial to the origin of the dilatator muscle a smaller adductor muscle arises from the basipterygium and runs obliquely to insert on the base of the axial cartilage, dorsal to the belly of the dilatator muscle and medial to the first, oblique, part of the main groove. The compressor muscle forms the muscular investment of the siphon; one part of it is modified to form a small oblique muscle lying superficial to the junction of the siphon tube with the clasper groove (figure 14*a*, *C*1). Another part forms a lateral bundle lying alongside the clasper groove, some of its fibres inserting on the ventral marginal cartilage but most of them being inserted by a tendon into the base of the hinged style (*T*3) which terminates in the claw (figures 10*b* and 14*b*, *C*2). It acts as an extensor for the style; that is, it returns the style to the normal from the erect position. This action was confirmed by traction on the muscle in fresh material; no separate muscle capable of erecting the style was found, though several claspers were dissected in search of one. The articulation of the style with the axial cartilage is surrounded by a fibrous capsule, the wall of which is thickened on the lateral edge to form a ligamentous band.

2. *The female*

Ovary and epigonal organ

The ovary of the right side only is present, that of the left either being absent or so rudimentary that no trace of it could be found. The organs are, however, so large and heavy that handling them is difficult, and an unsuccessful search for rudimentary structures does not necessarily mean that they are not present (figure 16). The right ovary is a large soft organ of elongated oval shape suspended by a short mesovarium attached to the dorsal wall of the abdominal cavity on the right of the mesogastrium (figure 17). It lies at the anterior end of the cavity on the right side of the stomach, its anterior pole level with the junction of oesophagus and stomach. It is invested in a fibrous coat on the surface of which thickened bundles of fibres form a criss-cross pattern in all directions. Apart from the irregularity produced by these fibre bundles the surface is smooth and shining, showing no projections caused by follicles or ova. The latter do not dehisce from the outer surface but are discharged into an internal cavity. On the right side of the ovary, towards the anterior pole and near the dorsal surface where the mesovarium joins it, there is a pocket which communicates with the internal cavity, the opening of the pocket being directed dorsally. The fibrous bundles of the surface of the ovary are continued into the pocket, especially on its medial side (figure 18). The pocket is not more than about 12 to 15 cm. wide and deep, its cavity beyond this depth breaking up into a very large number of tubular branches which ramify by progressively smaller twigs through all parts of the organ. On cutting into the ovary its structure is revealed as a very loose stroma filled with an immense number of small ova bound together mainly by the ramifying tubular twigs which lead eventually to the exterior through the pocket. The ovary measures about 50 cm. in length, the posterior third in some specimens tending to be demarcated as a separate lobe by a transverse sulcus on the ventral surface. The epigonal organ lies posterior and slightly dorsal to the ovary, being suspended from the dorsal abdominal wall by a backward extension of the mesovarium. Its length is some 60 cm. and its diameter 20 cm.; its anterior end overlaps the

posterior third of the ovary. If a posterior lobe of the latter is differentiated it projects freely beneath the anterior end of the epigonal organ. The anterior end of the epigonal organ is fused with the tissue of the ovary so that the line of demarcation between the two

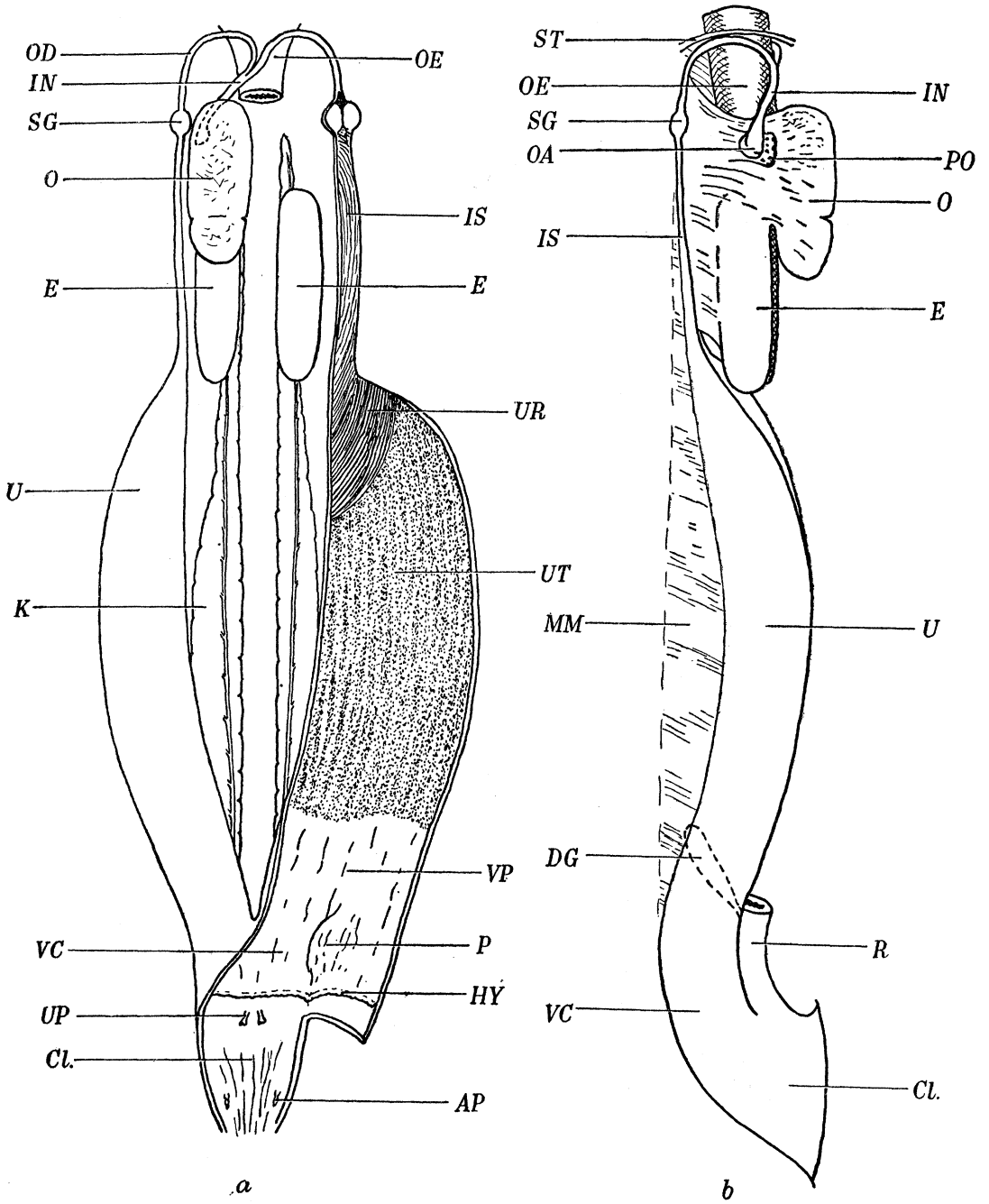

FIGURE 16. General view of the female reproductive tract, *a*, from the ventral surface, the oviduct on the right of the figure opened longitudinally; *b*, lateral view from the right side. *AP*, abdominal pores; *Cl*, cloaca; *DG*, digitiform gland; *E*, epigonal organ; *HY*, hymen; *IN*, unpaired oviduct; *IS*, isthmus; *K*, kidney; *MM*, mesometrium; *O*, ovary; *OA*, ostium abdominale; *OD*, paired oviduct; *OE*, oesophagus; *P*, pad in lateral wall of common vagina; *PO*, pocket in right side of ovary; *R*, rectum; *SG*, nidamentary gland; *ST*, septum transversum; *U*, uterus; *UP*, urinary papilla; *UR*, uterus lined with folds; *UT*, uterus lined with trophonemata; *VC*, common vagina; *VP*, paired vagina of the left side.

is not sharp. In the corresponding position on the other side of the mesogastrium the left epigonal organ of similar size and shape is suspended by its own double fold of peritoneum, but there is no ovary fused with its anterior end. The weights of the epigonal organ and of

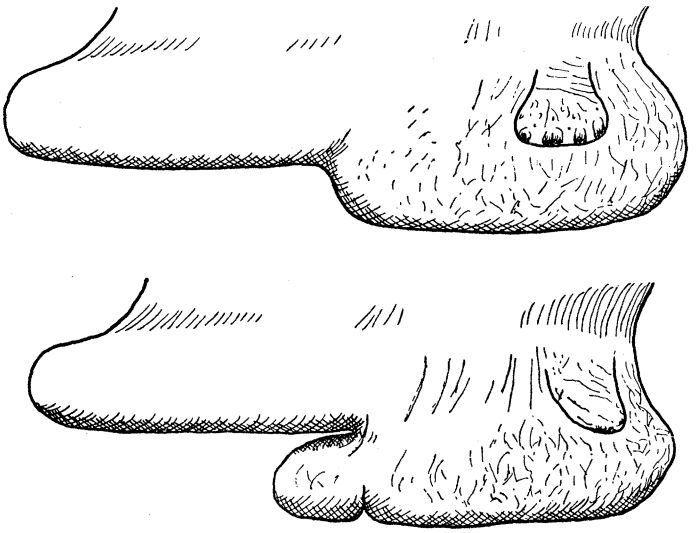

FIGURE 17. Right ovary and epigonal organ supported by the mesovarium seen from the right side. In the lower specimen the posterior part of the ovary is partly separated as a distinct lobe. In both specimens the pocket on the right side leading to the interior is visible.

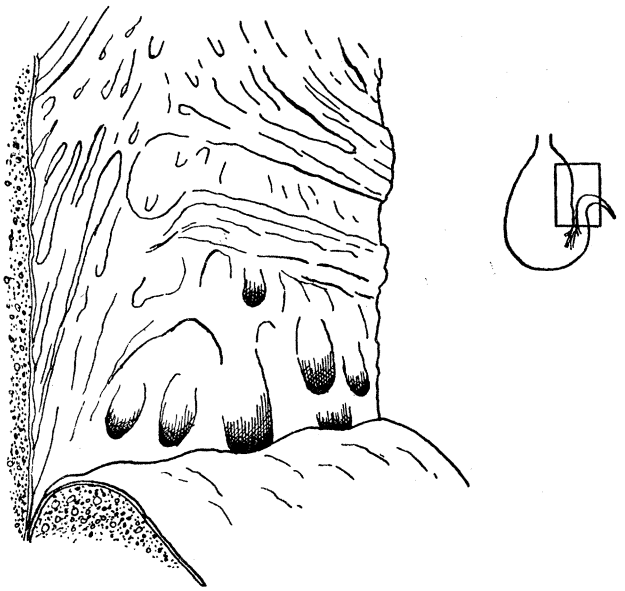

FIGURE 18. A slice of the ovary cut through the pocket, and the outer wall of the latter folded down outwards. The insert shows a transverse section of the ovary, and the square indicates the portion shown in the drawing. Note the ovarian substance showing large numbers of ovarian follicles, the fibrous bundles on the medial wall of the pocket, and the openings of the internal tubular branches.

the ovary in six fish are shown in table 1, which shows that the weight of the epigonal organ is about 0·6 of that of the ovary. The tissues of the ovary and epigonal organ are very soft and pulpy; the structures tear under their own weight if an attempt is made to lift them after the investing peritoneal layers have been divided. The ovary is filled with innumerable

minute ova among which are scattered a smaller number of larger ones in various stages of growth. The larger ova are spherical, up to about 4 or 5 mm. in diameter, pale yellowish white in colour and semi-translucent. Distributed among the ova is a number, which varies from fish to fish, of other bodies that may be designated corpora lutea. These are conspicuous among the ova because in contrast with them they are quite opaque. They are lenticular in shape, not spherical, and lighter in colour than the larger ova. The largest measured were 4 mm. in diameter, and many much smaller ones are present among the ovarian tissue. Reasons are given below (p. 283) for regarding the larger ones as the products of ovulation and the smaller as those of atresia. The general appearance of the interior of the ovary is similar to the roe of a teleostean fish and quite unlike the typical elasmobranch ovary in which the small ova are inconspicuous and are completely overshadowed by a small number of large ones.

TABLE 1. WEIGHTS OF EPIGONAL ORGAN AND OVARY (LB.)

shark no.	epigonal organ	ovary
3	12·25	21·5
5	14·5	13·25
6	11·25	17·5
7	11·5	21
8	14	26
9	14	27

Ostium abdominale and oviduct

The ova when discharged from the ovary pass out through the pocket and are taken up by the ostium abdominale formed by the fused proximal ends of the oviducts. This lies on the ventral surface of the anterior end of the right lobe of the liver (figure 19), its dorsal

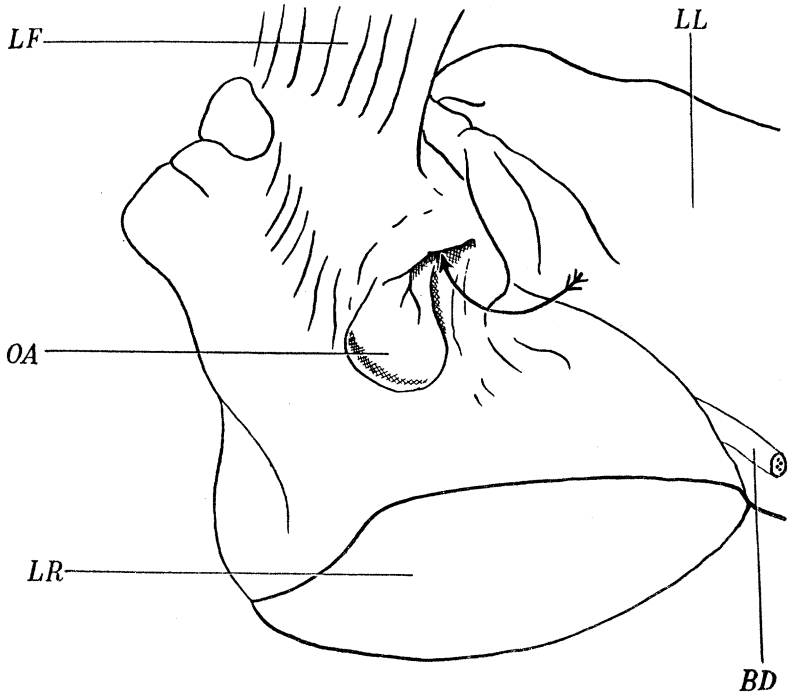

FIGURE 19. The anterior end of the liver seen from the ventral side to show the ostium abdominale, indicated by the arrow. *BD*, bile duct; *LF*, falciform ligament; *LL*, left lobe of the liver; *LR*, cut surface of the right lobe of the liver; *OA*, lobed edge of the ostium abdominale.

surface in contact with the liver and its ventral surface covered with a thin layer of liver tissue; the fused tubes are thus in effect embedded in the liver close to its ventral surface. The ostium is rather vaguely defined but is guarded by a rounded lobe on the right dorso-lateral edge. From the ostium a single tube runs forward for about 22 cm. dorsal to the attachment of the falciform portion of the suspensory ligament of the liver; its diameter at the ostium is 6 or 7 cm. but it rapidly narrows anteriorly, to the point where the oviducts become separate. These tubes run forward side by side for a further 15 cm. diverging from each other towards the anterior end of this course. The lumen of each tube is very small, not more than 2 to 3 mm. in diameter for the first 8 cm. from the junction, but it increases gradually in the following 10 cm. The wall of the narrow part is fibrous and inelastic, so that the lumen cannot be dilated even by considerable internal pressure. Dorsal to the anterior attachment of the falciform ligament to the septum transversum the oviducts diverge (figure 20), passing lateral to the hepatic veins, and are directed laterally on the

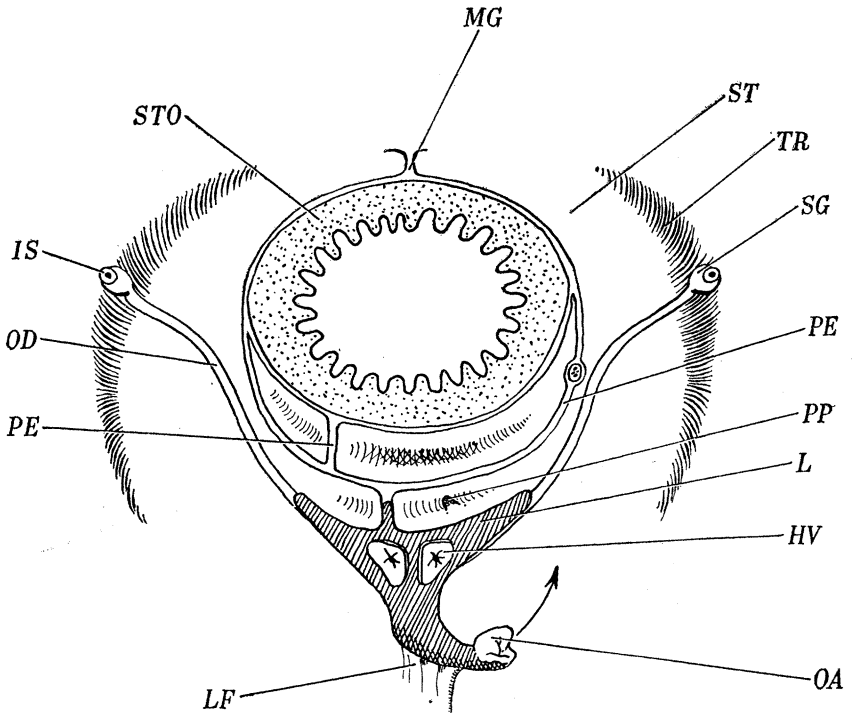

FIGURE 20. Diagrammatic view of the anterior end of the abdominal cavity of the female, seen from behind to show the relations of the oviducts. *HV*, hepatic vein; *IS*, cut proximal end of isthmus; *L*, cut surface of liver; *LF*, falciform ligament; *MG*, mesogastrium; *OA*, ostium abdominale, the arrow pointing towards the direction from which it has been displaced; *OD*, paired oviduct; *PE*, attachments of peritoneal laminae which form parts of the mesenteries; *PP*, pericardio-peritoneal canal; *SG*, nidamentary gland; *ST*, septum transversum; *STO*, transversely divided anterior end of the stomach; *TR*, curved edge of the septum transversum fusing with the parietal wall.

surface of the septum transversum immediately ventral to the attachments of the right and left parts of the suspensory ligament of the liver. The abdominal opening of the pericardio-peritoneal canal, about 1 cm. in diameter, lies a few centimetres dorsal to the right oviduct shortly after it reaches the septum transversum. The posterior surface of the septum transversum arches round caudally to fuse with the parietal wall of the abdominal cavity, the

exact point of fusion being indefinite. The oviducts run on this curved surface for a distance of 30 to 40 cm. lying under the peritoneum so that there is no mesosalpynx. The mucous membrane lining them is raised into closely spaced longitudinal ridges each 2 to 3 mm. in height. They then join the nidamentary glands which form the first part of the oviducts lying definitely on the parietal wall of the abdominal cavity.

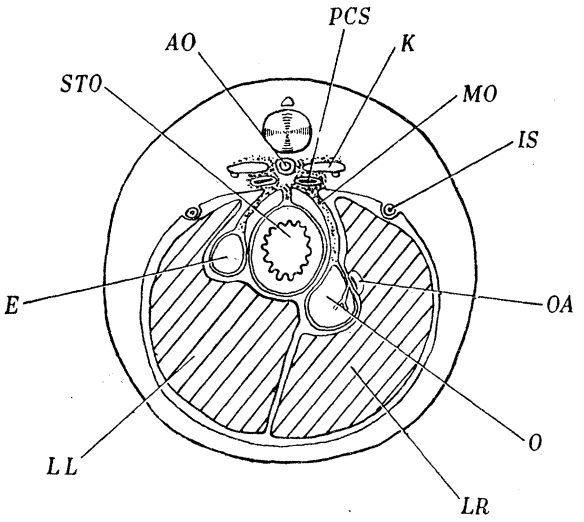

FIGURE 21. Diagrammatic cross-section across the body of a female Basking shark to show the relations of the viscera. *AO*, aorta; *E*, epigonal organ; *IS*, isthmus; *K*, kidney; *LL*, left lobe of the liver; *LR*, right lobe of the liver; *MO*, mesovarium; *O*, ovary; *OA*, ostium abdominale; *PCS*, posterior cardial sinus (paired at this level); *STO*, anterior end of the stomach.

Nidamentary gland and isthmus

Each nidamentary gland is a dorso-ventrally flattened oval swelling of the oviduct about 8 cm. long and 5·5 cm. wide with thickened glandular walls (figure 16). Internally the glandular part is thickest, about 1·5 to 2·0 cm. in depth, on the antimesometrial side; on the mesometrial side it is so reduced in thickness that a longitudinal sulcus, most marked posteriorly and decreasing anteriorly, divides it. The glandular tissue increases gradually in thickness from the anterior end and projects as a valve-like ridge into the succeeding part of the oviduct at its posterior end where a deep transverse groove forms the dividing line. The posterior edge of the gland does not follow the circumference of the lumen of the oviduct but extends farther in a posterior direction on the antimesometrial side than on the meseometrial. The margin thus curves anteriorly from both sides to meet the sulcus on the mesometrial side in a deep forwardly directed notch. Posterior to the nidamentary gland the oviduct runs straight back caudally for a distance of 75 to 85 cm. and has a diameter of 3 to 4 cm.; this portion is the isthmus. In the posterior three-quarters of this part of its course it gradually leaves the abdominal wall and is suspended by a mesoviduct of increasing depth towards its posterior end. The mucous membrane lining this part of the duct is thrown into obliquely longitudinal folds.

Uterus and vagina

At the posterior end of the isthmus the oviduct suddenly increases in width to measure about 20 to 30 cm. transversely, forming an elongated uterus some 1·2 to 1·4 m. in length

suspended from the dorsal abdominal wall by a mesometrium which decreases in width posteriorly (figure 16). The peritoneal laminae of the mesometrium are separated by a space about 1 cm. wide which is entirely filled with a mass of reteform blood vessels of small diameter. In consequence the mesometrium, like the mesovarium, presents a dense spongy appearance when cut across. The mucosa lining the uterus consists of two parts. In the first part it is thrown into deep overlapping folds some 1 to 2 cm. deep lying close to each other like the pages of a book. The folds are arranged obliquely and run in an antero-ventral to postero-dorsal direction, and where the isthmus joins the uterus they are continuous with the folds in that part. The area covered by these folds is more or less triangular

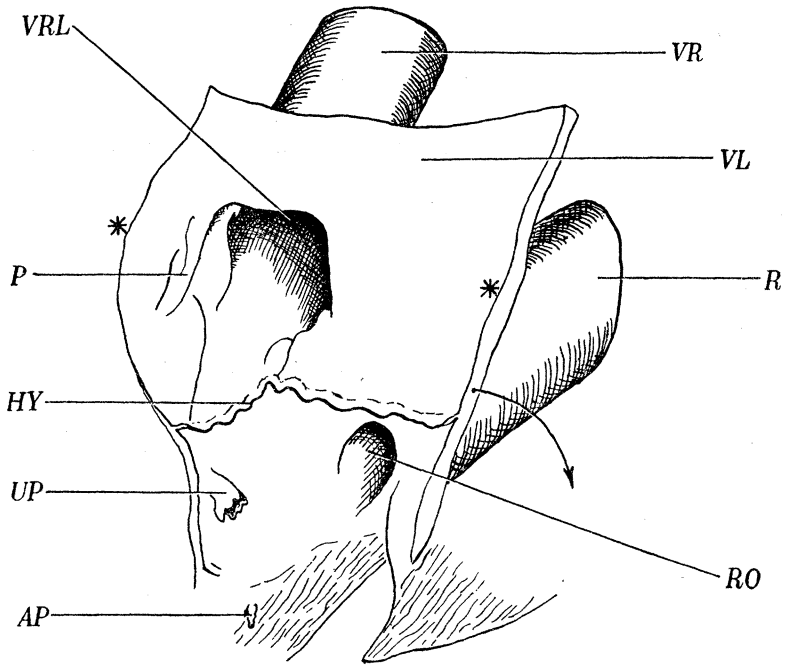

FIGURE 22. Cloaca, common vagina, and left-paired vagina opened and seen from the left side. The stars mark points which were in apposition before the incision was made; the arrow shows the direction in which the cut edge from which it springs has been displaced. *AP*, abdominal pore; *HY*, hymen; *P*, pad in the wall of the common vagina; *R*, rectum; *RO*, orifice of rectum; *UP*, urinary papilla; *VL*, inner surface of left paired vagina; *VR*, right paired vagina; *VRL*, lumen of right paired vagina. The part between the level of the stars and the hymen is the common vagina.

and lies on the mesometrial side of the organ. On this side the area of folds covers the proximal 40 cm. of the uterus, but on the antimesometrial side it extends for rather less than 10 cm. from the junction with the isthmus. The line joining the posterior ends of these limits follow a curved oblique course parallel to the direction of the page-like folds. The rest of the endometrium is closely covered with innumerable trophonemata, processes which resemble villi and vary in length between individual fish, the longest measured being about 1 cm. in length and the shortest about 0·5 cm. The length of the trophonemata varies too in the different parts of the same uterus, but no definite areas of different length were identified, though the trophonemata tended to be longer in the distal than in the proximal part. In most of the female fish examined there was a considerable number of small clear

fluid-filled vesicles with membranous envelopes scattered among the trophonemata. They were from 2 to 4 mm. in diameter and were embedded with their exposed surfaces about level with the summits of the trophonemata. The mucous membrane with its trophonemata is raised into low longitudinal ridges up to 2·0 cm. in height spaced 2·0 to 3·0 cm. from each other.

At the posterior end of the uterus the trophonemata cease abruptly at the junction with the vagina, which is lined with a smooth white mucous membrane raised into broad rounded folds of little height. Each vagina is about 35 cm. long from the distal end of the uterus to its junction with the vagina of the opposite side to form a common passage (figure 22). The diameter of the separate vaginae is about 30 cm., that of the common vagina about 40 cm. The length of the common vagina is about 25 cm., and its distal end is demarcated by the hymen, a circular transverse fold 1 to 2 cm. in height with a darkly pigmented border entirely surrounding the lumen. The lateral walls of the common vagina consist of thick

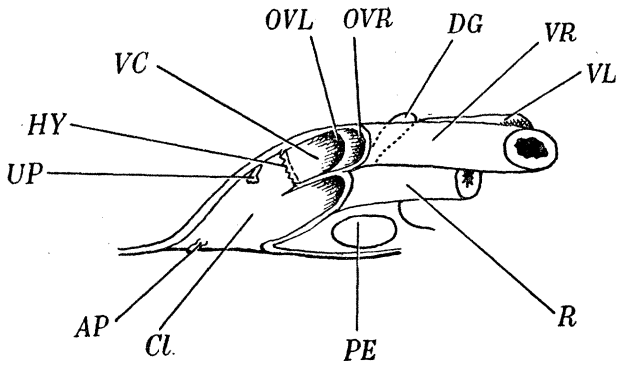

FIGURE 23. The posterior end of the abdominal cavity seen from the right side to show the relations of the viscera. *AP*, abdominal pore; *Cl*, cloaca; *HY*, hymen; *OVL*, orifice of the left paired vagina; *OVR*, orifice of the right paired vagina; *PE*, cut surface of the pelvic cartilage; *R*, rectum; *VC*, common vagina; *VL*, left paired vagina; *VR*, right paired vagina; *UP*, urinary papilla.

pads of fibrous tissue beneath the mucous membrane. In all the female fish examined these pads were covered with scars derived from the lacerations caused by the claw on the clasper of the male. The hymen separates the common vagina from the cloaca, into the anterior side of which the rectum opens immediately ventral to the vaginal orifice (figure 23). The rectal gland lies between the two separate vaginae immediately cranial to their junction. The urinary papillae open into the dorsal side of the cloaca a little caudal to the hymen; they are funnel-shaped tubes about 5 cm. long and 2 cm. in diameter with irregularly lobate free edges. On the lateral walls of the cloaca the external openings of the abdominal pores lie at the summits of tubular papillae as in the male. The kidney extends from the extreme posterior end of the abdominal cavity caudal to the level of the cloaca almost as far forwards as the septum transversum, its anterior pole lying just caudal to the level of the nidamentary gland. The urinary duct lies towards the lateral edge of the kidney in its anterior part, and gradually crosses the kidney as it runs back so that it lies on the medial edge a little anterior to the level of the cloaca.

The arrangement of the interrenal body, renal portal vein, posterior cardinal sinuses and reteform arterial spongy tissue is similar to that in the male.

Microscopic anatomy

Histological methods

Material for histological examination was fixed and preserved in Bouin's fluid. Some of the larger specimens from which histological material was later taken were fixed in 10% formalin and preserved in 5%. Most of the specimens were embedded in paraffin and cut at a standard thickness of 10 μ. The stains used were the triple stains of Mallory and Masson, the latter being the most generally useful, and Heidenhain's haematoxylin counterstained with Biebrich scarlet. Leishmann's stain was used to differentiate the lympho-myeloid tissue of the epigonal organ. Tissues in which a demonstration of the presence or absence of lipoids was sought were cut by the freezing technique and stained with Sudan black.

1. *The male*

Testis and spermatogenesis

The testis is divided from the epigonal organ by a thin layer of connective tissue through which are scattered a number of coiled tubules similar in general appearance to, though smaller than, vasa efferentia. Similar tubules ramify also among the tissue on each side of the connective tissue tunica of the testis, to a small extent on the epigonal side of the boundary and more plentifully on the side of the testis. Each consists of a rather thick coat of connective tissue lined by a single layer of tall columnar ciliated cells, many of the small but definite lumina being empty. The full course of these tubules was not traced, but it is probable that those within the testis and connective tissue tunica are part of the rete testis, and those within the epigonal organ are vasa efferentia.

Each lobe of the testis is subdivided into lobules separated from each other by thin connective tissue trabeculae, and each lobule consists of many closely packed ampullae. In transverse section each lobe is roughly circular and each lobule wedge-shaped, the apices of the wedges meeting at the centre of the lobe. At this central point the space between the apices of the lobules is filled with solid connective tissue which does not, contrary to the impression given by a first macroscopic inspection, contain any duct. Scattered among the central connective tissue mass are many capillary vessels and small aggregations of lymphoid tissue. Lying among the connective tissue also are numerous nests of cells which extend from an approximately central point and become larger as they enter the apices of the lobules. Each nest is surrounded by a very thin coating of flattened investing cells enclosing a larger central cell. The nuclei of the central cells are very large and the chromatin is broken up into small scattered fragments. As the nests enter the lobules they increase in diameter and the central cells become increased in number but decreased in size, presumably by division. These inner cells are arranged peripherally, forming solid strands which shortly become ampullae by the appearance of central lumina. The least mature parts of the lobules are thus at the centres of the lobes, and the contents of the ampullae filling the lobules become progressively riper nearer the periphery of the lobes. Only in the parts of the ampullae at the outer edges of the lobes, that is, at the bases of the wedge-shaped lobules, are fully formed spermatozoa to be found. The testis canaliculi therefore leave the lobules at their outer edges and not, as at first sight would appear, at the centres of the lobes. They soon join the coiled rete testis and vasa efferentia which lie embedded in connective tissue filling the spaces between the rounded corners of the bases

of adjacent lobules and the investing connective tissue sheath of the lobe. The vasa efferentia are from 112 to 200 μ in diameter, and each is lined with a single layer of tall columnar ciliated cells, the large lumina being filled with a mass of spermatozoa.

The central cells of the nests at the apices of the lobules are 20 to 25 μ in diameter, and since the nests consist at first of single cells surrounded by a very thin investment they have practically the same diameter (*PA*, figure 25, plate 10). Just within the apex of a lobule the nests become multicellular and then have a diameter of about 30μ. The cells here are smaller than the single cells from which, presumably, they are derived (*LA*, figure 25, plate 10). In the next stage the cells are differentiated into two kinds, outer cells with dark-staining nuclei surrounded by a considerable quantity of cytoplasm, and inner cells with larger and paler nuclei but much less cytoplasm. The ampullae now acquire lumina and measure from 45μ in diameter upwards (figure 26, plate 10). Although the nuclei of the inner cells are less chromophil these cells in stained sections form a darker zone surrounding the lumen because, having much less cytoplasm, their nuclei appear very much more crowded. The number of layers of outer cells increases up to four or more, so that the lumen remains small although the diameter of the ampullae increases greatly (figure 28, plate 10). When the ampulla is almost entirely filled with outer cells the remaining inner cells can be seen scattered among them, apparently in process of migrating through the mass to the periphery of the ampulla (figure 29, plate 10) where they come to rest, having completely changed their place and being now outermost in position. The number of originally outer cells appears to be increased both by division of the inner ones (figure 27, plate 10) and subdivision of the outer ones thereby produced. The originally inner cells are thus spermatogonia, and the originally outer ones are spermatocytes, those derived from the spermatogonia being primary spermatocytes and those derived from the latter being secondary spermatocytes. The spermatogonia after their migration to the periphery become Sertoli cells, and the number of spermatocytes continues to increase by division until the maximum diameter of the ampulla is attained, some 250 to 300μ (figure 30, plate 10). All the cells in each ampulla are in approximately the same stage of activity, and after the migration of the spermatogonia-Sertoli cells and the further increase in the number of spermatocytes, the latter divide almost simultaneously into spermatids (figures 31 and 32, plate 11). These have very much smaller nuclei in which the chromatin is more concentrated. The spermatids gather towards the periphery of the ampulla and are aggregated into clumps arranged radially round the lumen (figure 32, plate 11). The nuclei of the spermatids next become elongated (figure 33, plate 11) and then extremely attenuated (figure 34, plate 11) to form the heads of the spermatozoa. These are arranged in radial bunches corresponding with the former arrangement of the spermatids in clumps, the apices of the heads in each bunch being attached to the periphery of the ampulla between the Sertoli cells (figure 35, plate 11). At this stage the tails are in course of development and the bases of the heads begin to assume a spiral form (figure 35). The spiral arrangement passes along the head from the base to the apex and at the same time the spermatozoa withdraw a little from the periphery of the ampullae, and each bunch now depends from the Sertoli cell rather than from one of the spaces intervening between them (figure 36, plate 11). It is noticeable that the heads tend to be arranged not at random but with the turns of the spirals on adjacent spermatozoa coinciding with each other; the middle pieces

remain straight and are not spirally twisted. The tails are now well developed and sweep round the lumen of the ampulla in a whorl whose centre coincides with that of the lumen.

In the next stage the heads of each bunch of spermatozoa approach each other so that they lie much more closely approximated side by side (figure 37, plate 12), until finally each bunch forms a dense mass in which the individual heads cannot be distinguished from each other. The apices of the heads become more closely packed together than the bases so that each bunch takes on a conical shape, the turns of the spirals of all the heads in each bunch coinciding so that a compact body is formed (figure 38, plate 12). The middle pieces are closely bunched together and are now separated from the heads by an intermediate zone which stains less intensely. The intermediate zones of the spermatozoa in each bunch do not closely approximate but appear to be repelled from each other. At this stage the Sertoli cells have enlarged so that they extend farther into the lumina of the ampullae, and their nuclei lie between the adjacent bunches of heads. The bunches become very compact before they are released, so that in the final stage the lumina of the ampullae appear comparatively empty owing to the great concentration of the heads of the spermatozoa into dense bunches (figure 38, plate 12). Many of these bunches pass unaltered through the epididymis and ductus deferens to the ampulla of the ductus deferens, where they are incorporated into the spermatophores. The cores of the spermatophores contain great numbers of these closely bunched spermatozoa lying among more scattered ones, though even when the bunches become broken up the individual spermatozoa are not generally released but remain aggregated in smaller clumps (figure 39, plate 12).

The heads of the spermatozoa measure about 40μ in length and 0·4 to 0·5μ in diameter, and are thrown into seven to eight spiral turns. Each bundle contains from fifty to sixty ripe spermatozoa. When the bunches of spermatozoa leave the ampulla the outer part of some of the Sertoli cells is seen to contain a body rather smaller than the nucleus and staining less intensely than it though more intensely than the cytoplasm. These bodies were not recognized in the ampullae before the spermatozoa had started to leave them, probably because the bunches of spermatozoa obscured them. The empty ampullae shrink considerably in size, the cytoplasm of the Sertoli cells diminishing greatly in amount and the bodies just mentioned being no longer visible. The later stages of the involution of the ampullae were not observed.

Each lobule of the testis is surrounded by a thin coating of connective tissue which is continuous with the thicker investment of the lobe at the periphery and with the interlobular mass at the centre of the lobe. It sends off delicate strands which penetrate into the lobule and form the thin connective tissue sheaths of the ampullae and contribute to the filling of the interstices between them. Capillaries are numerous throughout the connective tissue and are most plentiful around the ampullae in the later stages of spermatogenesis, the parts of the lobule in early stages of activity being noticeably less vascular. Interstitial tissue occurs in the form of strands and lobules of cells ramifying between the ampullae, the cells in the strands tending to be grouped circumferentially. In some places the peripheral parts of the testis lobules contain considerable quantities of tissue, indistinguishable from interstitial cells, external to the ampullae. The interstitial tissue is compact in those parts of the lobules where spermatogenesis is in its earlier stages but is very much looser between the riper ampullae.

Epididymis and ductus deferens

The coiled tubes forming the epididymis, the numerous ductuli epididymidis about 2 mm. in diameter and the single ductus epididymidis formed by their junction and measuring as much as 7 mm. in diameter at its caudal end, consist of a compact layer of connective tissue lined by tall columnar pseudo-stratified epithelium from 50 to 60μ in height (figure 40, plate 12). The epithelium contains two sorts of cells: columnar cells with nuclei near their bases and the outer parts of the cells tapering towards the surface but not reaching it; and ciliated cells wedged between the former so that their bases are narrow but their wider outer ends are in contact with those of adjacent cells. The whole of the epithelial surface lining the lumen of the tube is thus entirely covered with cilia. The nuclei of the ciliated cells are at about the middle of their height, so that the epithelium appears filled with rather irregularly placed nuclei in the basal two-thirds of the cells. The compact connective tissue sheath of the tube merges gradually with the much looser connective tissue containing small vessels which separates adjacent coils of the tubes. In the lower part of the epididymis where the diameter is comparatively great the epithelium is similar and is raised into widely separated folds (figure 41, plate 12). These at first appear as very low ridges but soon increase in height to 1·0 to 1·5 mm. and then consist of two thicknesses of epithelium placed back to back supported by a very thin lamina of connective tissue continuous with that surrounding the tube (figure 42, plate 12). The lamina is so thin that the capillaries coursing through it cause appreciable bulges where they occur.

At the upper end of the ductus deferens, before it has expanded into the ampulla, the ridges are greatly increased in height so that they reach almost right across the lumen (figure 43, plate 13). They are here much stouter, the epithelium being supported by a blade of connective tissue about 100μ thick, the epithelium itself being nearly as thick.

Ampulla ductus deferentis

The epithelium of the whole of the ampulla of the ductus deferens is of the same general character. In the upper part where the transverse septa are thin and membranous it is 75 to 80μ in height (figures 44 and 45, plate 13); farther down it increases to 100, 150 and finally to 200μ or slightly more in thickness on the stout parts of the septa near the lateral wall of the ampulla. In the lower part of the ampulla it is raised into closely set villi, each supported by a central core of connective tissue (figure 46, plate 13). On the central membranous parts of the septa the villi are about 300μ in height; on the stouter peripheral parts they reach a height of nearly 600μ. The epithelium is tall and cylindrical, the surface being thickly ciliated. The ciliated cells have elongated oval nuclei situated at about the middle of the cells so that the superficial part of the epithelium consists of clear cytoplasm, the walls of the ciliated cells abutting against each other in this part (figure 47, plate 13). At about the level of the nuclei the ciliated cells taper towards the basement membrane so that spaces are left which are filled by other cells. These have rounded oval nuclei which are not set at the same level in all the cells; the basal half of the epithelium thus appears to be filled with an irregularly arranged mass of nuclei. Between the outer clear parts of the ciliated cells fine vertical canaliculi run from the surface down to the inner cells which are secretory. In some sections drops of secretion can be seen protruding from the mouths of the canaliculi; they are connected to strands of secretion filling the canaliculi and running deep between the

lower parts of the ciliated cells to the secretory cells below (figure 48, plate 13). This secretion is undoubtedly the matter which forms the cortex of the spermatophores. Near the basement membrane occasional polyhedral plasma cells are present, scattered here and there among the bases of the other cells. The epithelium is carried on laminae of very loose connective tissue which is similar to that of the adiacent wall of the ampulla. On this wall it gradually becomes denser on passing outwards and merges with the very dense fibrous connective tissue of the outer layers.

Kidney, Leydig's gland and interrenal body

The anterior part of the kidney which is in contact with the epididymis is non-excretory and is modified to form Leydig's gland (figure 49, plate 14). It consists of a mass of convoluted tubules embedded in a comparatively small amount of connective tissue, the tubules opening eventually into the ductus deferens; there are no glomeruli in this part of the kidney. The tubules range in diameter from 150 to 300μ, and are lined with a very tall columnar secretory epithelium up to about 100μ in height. The nuclei of most of the cells are oval and lie at their bases, but in parts of the tubules some of the cells have very narrow elongated nuclei near the surface. The epithelium is ciliated in most of the tubules, but in their distal parts tne cilia appear to be absent in some places. The most distal parts of the tubules are 300μ in diameter and are lined with a low ciliated epithelium about 20μ high, consisting of not more than two layers of cubical to polyhedral cells, the greater part of whose volume is filled by the nuclei. Because the epithelium of these terminal parts is so much lower the lumina are much larger than those of the secretory parts. These parts of the tubules are evidently no more than ducts; their epithelium is surrounded by a very much more compact layer of connective tissue than that forming the matrix in which the secretory parts of the tubules are embedded. In fixed material many parts of the tubules contain a coagulum.

In contrast with Leydig's gland the posterior urinary part of the kidney consists of typical mesonephric tissue (figure 50, plate 14). The glomeruli and tubules are embedded in a well-vascularized connective tissue matrix, the glomeruli measuring from 220 to 400μ in diameter, and the tubules from 80 to 200μ. The latter are lined with an epithelium consisting of a single layer of cubical or low columnar cells with central nuclei and with a brush border on their free edges.

The interrenal tissue presents the characteristic appearance of adrenal cortex, consisting of groups of cells divided into columns and rounded masses by thin septa of connective tissue. Stouter trabeculae delimit larger areas of the gland, which is not conspicuously vascularized, although capillaries are fairly numerous throughout its substance. The cells are polyhedral and contain rather large round to oval nuclei; the cytoplasm is very heavily loaded with droplets of lipoid material, as shown by their strong staining reaction with Sudan black.

The excrescences and pedunculated lobes of tissue attached to the interior surface of the posterior cardinal sinus and projecting into its lumen consist of connective tissue, containing numerous lymphocytes and some erythrocytes, enclosing ganglionic masses of nerve cells. Each of these cells has a nucleated sheath and many of them are large, being up to 70μ in diameter (figure 52, plate 14). Some of them contain numerous granules

which stain intensely with haematoxylin, others have homogeneous contents which show an equal affinity for this stain; in the smaller cells the granules are fewer but much larger.

Epigonal organ

The epigonal organ consists of a mass of lymphoid tissue and erythrocytes. The peritoneal capsule consists of a layer of connective tissue about 100μ thick, the deeper parts of which contain large quantities of fibrous tissue. The capsule does not give off trabeculae penetrating deep into the lymphoid tissue; at most there is an occasional wisp extending a very short distance among the cells of the interior. There is, however, a very small amount of connective tissue, which can be demonstrated by appropriate staining, scattered throughout the main mass of cells. A moderate amount of connective tissue, too, accompanies such vessels as wander through the mass. Immediately in contact with the capsule there is a thin cortical zone not more than 50μ thick. This is composed of small polyhedral cells whose nuclei have much less, and whose cytoplasm has much more, affinity for haematoxylin than is shown in the cells of the lymphoid tissue. The whole of the medulla of the organ is nearly homogeneous, the only differentiation being that here and there patches occur from which erythrocytes are absent, so that in stained sections they appear lighter than the surrounding tissue. Some blood vessels ramify through the mass, but they are comparatively small and few. The general character of the tissue in the medulla of the organ is essentially lympho-myeloid, and in it the following different kinds of cells are numerous while other kinds occur less plentifully (figure 53, plate 14): (1) Small lymphocyte-like cells 3 to 5μ in diameter. These are strongly basophil, and occur not only scattered throughout the medulla but also aggregated into numerous islands distributed in all parts of the mass and containing practically no other type of cell. These islands have the appearance of lymphocyte germ centres (figure 54, plate 14). (2) Larger basophil cells about 9μ in diameter, with large nuclei. These are comparatively few in number and occur singly scattered among the other types. (3) Neutrophil cells very similar to the last in general appearance, but the cytoplasm showing rather weak affinity for both acid and basic dyes. (4) Medium-sized oxyphil cells about 8μ in diameter, with very large nuclei filling much of the cell volume. The nuclei are more or less centrally situated. (5) Very large oxyphil cells 10 to 12μ in diameter, the nuclei smaller than in the medium-sized oxyphils and usually placed near the edge of the cell. (6) Elongated oval oxyphil cells about $17 \times 6\mu$ with rather small and dense oval nuclei situated approximately centrally in the cell. (7) Erythrocytes, similar to the last, but up to $20 \times 10\mu$, and with distinct cell membranes, the nuclei oval, rather dense, and central in position.

The neutrophil cells (3) and the medium-sized oxyphil cells (4) form the greater part of the medulla, the larger oxyphils (5) being slightly less in number. The neutrophils give the appearance of being intermediate stages in the transformation of the larger basophils into the medium oxyphils; and the elongated oval oxyphils (6) similarly appear to be intermediate stages between the large oxyphils (5) and erythrocytes; cells of categories (5) and (6) would thus be normoblasts. Erythrocytes occur both scattered singly and, more frequently, in elongated sinuses in which they are arranged with their long axes parallel to each other. Though definite vessels are present in many places, no endothelium can be

identified bounding these elongated sinuses of erythrocytes. No difference was detected in the histological structure of the epigonal organ in the two sexes.

Siphon

The siphon is lined with a layer of epithelium about 180μ thick (figure 51, plate 14). The greater part of it, the inner 145μ, consists of closely packed polyhedral cells with rounded oval nuclei. The nuclei are most crowded at the base of this layer and become more widely spaced as the superficial part is approached through an increase in the amount of cytoplasm surrounding them. The nuclei themselves increase in size and become paler in staining reaction in the outer layers. External to the thick inner layer of epithelium there is a thinner superficial one about 35μ thick lining the lumen of the siphon. At the junction of the two layers there is an abrupt change in the character of the cells. Passing from within outwards, the large pale nuclei of the cells suddenly become small, flattened and pycnotic. The cells themselves become strongly flattened and arranged parallel to the surface, forming a thin layer not more than 10μ thick. Superficial again to this layer the cells are greatly swollen and have clear contents and degenerate or no nuclei. It would appear thus that the secretion released from the surface of the epithelium lining the lumen of the siphon is derived from the breakdown of the superficial cells and the release of their transformed contents. Beneath the epithelium there is a stratum of connective tissue containing large numbers of unstriped muscle fibres and small vessels; this layer is about 600μ in thickness. Outside this layer lie the striped-muscle bundles of the m. compressor.

Clasper gland

The clasper gland consists of a solid mass of cells, and the secretion is produced by the breaking up and detachment of the cells directly from the surface so that there are no ducts nor any tubular structure. The basal layer of the epithelium is set upon a stratum of connective tissue and unstriped muscle fibres, which is raised into small conical papillae projecting into the cell mass of the gland for a distance of about 0·75 mm. From the summits of the papillae extremely fine strands of connective tissue stretch to the free surface through the cell mass (figure 55, plate 15). The basal layer of the epithelium consists of a stratum three to four cells deep of small polyhedral cells; it covers the surface of the papillae and at their summits forms a solid strand of similar cells running towards the free surface, the connective tissue extending outwards from the summits of the papillae forming part of the core of each strand (figure 56, plate 15). Thus in sections parallel to the surface of the gland the cell mass is seen to contain scattered throughout its substance a number of these strands cut transversely. The cores of the strands contain a little connective tissue and a few capillaries and small vessels embedded in a matrix of lymphoid tissue, the connective tissue forming an extremely thin sheath round the latter. Outside the connective tissue lies the layer of epithelium consisting of polyhedral cells from four to eight cells thick. These cells are about 10μ in diameter and their nuclei fill a large part of their volume. At the surface of the layer the epithelial cells undergo a sudden change, the nuclei becoming shrunken and pycnotic while the cell volume is enormously increased so that the cell diameter reaches 40 or 50μ. The main cell mass consists of these swollen cells filled with clear contents and the remains of a nucleus, the cells being separated from each other by

extremely tenuous cell walls. The process of swelling and nuclear degeneration must take place with great rapidity because very few cells are seen in transitional stages; for the greater part the swollen cells abut directly against the basal layer and only occasional intermediate cells are seen (figure 57, plate 15). At the free surface the cell walls tend to become indefinite and the cells both break away and break down, the contents in fixed material showing an irregular vacuolated appearance (figure 58, plate 15). The cell contents, after coagulation by the action of fixatives, cause the cell mass near the free surface to break up under the action of the knife in sectioning, into strands arranged vertically to the free edge.

2. *The female*

Ovary and oogenesis

The ovary contains very little stroma, its main bulk being made up of follicles in various stages of development, corpora lutea, and blood vessels. These structures are very loosely bound together by small amounts of connective tissue, so that the tissue within the main investing tunica is very fragile. Through every part of the organ extend fine ramifications of the passages which, joining together to form larger and larger trunks, eventually open on to the surface of the ovary in the pocket on the right side (figure 59, plate 15). The passages are lined with a low columnar to cubical epithelium, the cells having large ovoid nuclei nearer their free ends than their bases. The epithelium is lowest in the finer subdivisions of the passages, taller in the larger trunks where it is ciliated and contains some goblet cells scattered among the taller ciliated cells. The smaller follicles always lie close beneath the epithelium; the larger ones, though one point on their circumference is never far distant, are separated from it by a narrow layer of stroma consisting of very loose connective tissue with numerous small blood vessels.

No attempt will be made here to give an exhaustive cytological account of the development of the follicle, but a brief sketch of the main changes which occur during the growth of the ovum will not be out of place. Follicles containing ova in which the deposition of yolk has started are very numerous, but those in the earlier stages of development are very few. The smallest follicles are about 80μ in diameter and consist of a number of similar polyhedral cells packed closely together and surrounded by a theca formed by a very thin layer of connective tissue, one cell thick, the cells and their nuclei being strongly flattened (*P*, figure 60, plate 15). In the next recognizable stage one of the cells has become considerably larger than the others, measuring up to 70μ in diameter; it has taken up a more or less central position in the follicle, now 150 to 200μ in diameter, and is definitely recognizable as the oocyte (*E*, figure 60, plate 15). The outer cells of the follicle lose their boundaries so that the contents of the follicle surrounding the oocyte are syncitia (*L*, figure 60, plate 15). Immediately surrounding the oocyte is a closely packed ring of cells about 15μ deep, with little or no cytoplasm and prominent nuclei, separated from the oocyte by a clear structureless vitelline membrane about 2 to 3μ thick. The outer cells filling the rest of the follicle are few in number but large in size; their cytoplasm is finely granular and the nuclei of the larger ones have disintegrated. In the smaller ones which have not swollen so greatly the nuclei are still recognizable, and there is a discontinuity at the limit of their cytoplasm although no cell boundary remains (figure 61, plate 16). The theca of the follicle is formed by a single layer of very thin connective tissue.

When the oocyte has reached a diameter of 85μ the clear vitelline membrane has almost disappeared, and the surrounding nuclei are no longer arranged in a columnar manner but are more rounded and form a narrow ring round the oocyte (figure 62, plate 16). The outer follicle cells have completely degenerated and the remains of their nuclei have disappeared, leaving the greater part of the follicle filled with a homogeneous mass of granular protoplasm. The theca still consists of a single layer of extremely flattened cells. Within the oocyte the nucleus is changing to form the germinal vesicle; it is bounded by a fine membrane and contains a very finely granular plasma. The cytoplasm of the oocyte is likewise finely granular and differs little in appearance from the plasma within the nuclear membrane. With further growth of the ovum the surrounding layer of nuclei becomes attenuated so that they are no longer in contact with each other but are spaced out round the circumference (figure 62, plate 16); further additional connective tissue cells become arranged concentrically round the follicle outside the original theca of extremely flattened cells. Thereafter the ovum increasingly fills the follicle, while the granular material surrounding the ovum gradually disappears. The expanding ovum pushes its surrounding layer of nuclei outwards until they finally come into contact with the theca and thenceforward form the follicular epithelium (figures 63 and 64, plate 16). During this process of expansion the outer granular material appears to be transferred through the vitelline membrane which has become extremely tenuous, and to be laid down as yolk surrounding the original cytoplasm and its original yolk material which stains less darkly and so can be distinguished from the former. Before this stage of growth is complete and while there is yet some of the outer granular mass present outside the epithelium surrounding the expanding ovum a fine clear vitelline membrane reappears between the ovum and its surrounding layer of nuclei, in the position where the much more prominent membrane was present in an earlier stage.

During these stages the nucleus undergoes a striking change. A sharply marked nuclear membrane appears and the chromatin is concentrated centrally in a vaguely defined mass, the rest of the space within the membrane being filled with a finely granular plasma. The chromatin then breaks up into a number of fine strands which are scattered through the nucleus and one or more nucleoli appear. In later stages the chromatin is no longer visible within the nucleus, now the germinal vesicle, and the number of nucleoli increases up to a dozen or more, most of them lying close together at one side of the vesicle immediately beneath the bounding membrane (figure 65, plate 16). These changes are not constant in their time of occurrence, being complete in some follicles only when the follicular epithelium is about to make entire contact with the follicular wall, whereas in others the germinal vesicle is fully formed while the future follicular epithelium is still entirely surrounded by the swollen outer cells.

The ovum and follicle are now about 300μ in diameter, and the further changes leading up to the discharge of the follicle are mainly those of size. As growth continues the yolk in many but not all follicles is distinguishable into an inner and an outer zone, the inner surrounding the terminal vesicle and being very sharply differentiated from the outer by some strains, particularly by Masson's triple stain (figure 65, plate 16). The sharpness of differentiation, however, decreases greatly in the largest follicles. The follicular epithelium at first forms a layer of cubical cells one cell thick, but in later stages it increases to two or three

cells in thickness (figure 66, plate 16). A well-marked vitelline membrane lies within this, but in the largest follicles it is again reduced to a thickness of about 2μ. Within the vitelline membrane a thin zona radiata can be traced in some follicles, but it is not recognizable in the largest (figure 67, plate 17). The zona radiata consists of fine protoplasmic strands extending from the follicular epithelium through the vitelline membrane; their function is to transfer yolk material to the ovum. The theca is increased in thickness, forming a layer up to four or five cells thick. Between the theca and the follicular epithelium an extremely fine basal membrane can be traced in the largest follicles.

Corpora lutea

The ovary contains many small corpora lutea, but fewer large ones, the two sizes differing greatly in structure. The large corpora lutea, up to 4 or 5 mm. in diameter, consist of a mass of large cells with small rounded nuclei, the cell volumes appearing practically empty in paraffin sections (figure 68, plate 17). In the largest corpora lutea these cells form a peripheral zone surrounding a central cavity which is filled with loose cells, many lymphocytes, and much cellular debris. The surrounding theca is a thin sheath of much-flattened cells, two or three cells in thickness. In frozen sections stained with Sudan black the contents of these cells stain intensely, showing that they are lipoid in nature and are dissolved out during the preparation of paraffin sections. The outer zone is plentifully invaded by blood vessels. These large corpora lutea gradually diminish in size, the central cavity becoming obliterated and the outer cells forming a loosely united mass as the cells undergo degeneration (figure 69, plate 17). It is suggested that the corpora lutea of this type are formed in the empty follicles left after the discharge of the ova at ovulation, and that those of the other, smaller, type are the result of the atresia of follicles which have reached a diameter of about 1·0 mm.

In the second type of corpus luteum the central cavity is a small space filled with loose coagulum and bounded by a clear structureless membrane much resembling the vitelline membrane in general appearance but folded upon itself as it follows the irregularities of the lining of the cavity (figure 70, plate 17). Most of the cells of the body are vacuolated, but at the periphery there are clumps of cells without vacuoles, and these increase in size and number while the central cells decrease, the latter apparently undergoing a process of degeneration. It is suggested that the clear membranous lining of the cavity represents the remains of the vitelline membrane. The result of this process is such that when the corpus luteum has shrunk to a mean diameter of 500 to 600μ the main bulk of it consists of a compact outer zone of polyhedral cells filled with cytoplasm, and without vacuoles, surrounding a small central cavity containing a little coagulum and lined with a wrinkled structureless membrane, the cellular zone being richly vascularized (figure 71, plate 17). When the corpora lutea have reached this stage they appear to persist for a long time without further change, for these structures are very common throughout the ovary, and no bodies which might be interpreted as stages in their degeneration or resorption were found (figure 72, plate 17).

Oviduct

The lobed edge of the abdominal ostium of the oviduct consists of a thick pad of moderately vascularized connective tissue. The surface is thrown into a number of minute

furrows, wider at their bases than at the surface so that the edges overhang their lumina. The general surface of the lobes between the furrows is covered with a stratified epithelium several cells thick which becomes cubical and then columnar at the edges of the furrows. Within the furrows the epithelium is tall and columnar; it is two to three cells deep, the cells not arranged in layers, the outer ends of the basal cells being wedged between the inner ends of the superficial ones. The first part of the oviduct proximal to its division into right and left components is flattened, its dorsal and ventral walls being in contact. The lumen measures about 8 mm. in width and 1 mm. transversely (figure 78, plate 18). The outer fibrous connective tissue coat containing some unstriped-muscle fibres is 2 to 3 mm. in thickness, and the inner surface of the tube is thrown into about thirty longitudinal ridges which fill most of the lumen. The majority of these are simple, but a few of them bear subsidiary ridges so that they appear forked in transverse section; they measure up to about 1·5 mm. in height and 150μ in width. They consist of connective tissue containing numerous small vessels, and are coated with a tall columnar ciliated epithelium about 60μ thick. Rather less than the outer quarter of the epithelium is clear, the rest being occupied by the nuclei which lie at several levels but are not segregated into layers. The basal cells do not reach the surface and appear to be of a secretory nature; they are polyhedral in shape and contain rounded nuclei. After bifurcation into right and left parts the oviduct becomes more robust, roughly circular in section, and no longer dorso-ventrally collapsed. The lumen measures from 2·0 to 4·0 mm. or a trifle more in diameter, and the dense fibrous connective tissue wall is up to 5·0 mm. in thickness (figure 73, plate 18). The inner surface is raised into twenty-five to thirty high ridges which converge towards the centre of the lumen and almost completely fill it. The ridges are up to 2·0 mm. in height and up to 350μ in width; they consist of well-vascularized connective tissue covered with tall columnar epithelium up to 70μ in thickness. As in the proximal part of the tube, the outer part of the epithelium is clear and the oval nuclei lie in an irregular deeper zone; many smaller cells with rounded nuclei lie at the bases of the tall ciliated cells (figure 74, plate 18).

Nidamentary gland

The nidamentary gland is enclosed in an outer coat of fibrous connective tissue continuous with that of the upper oviduct and the isthmus. The inner glandular part is from 10 to 15 mm. in thickness and consists of a mass of closely packed tubular glands (figure 75, plate 18). The bases of the glands abut directly on the connective tissue coat and are so closely packed that only the most tenuous strands of connective tissue, given off by the outer coat, penetrate between them. The glands are 100 to 110μ in diameter and run more or less at right angles to the connective tissue base for a distance of about 4·0 mm. At this level they alter their direction, and curving towards the distal end of the gland they reach the surface by an oblique course, opening into the main lumen facing distally at an acute angle. Where they complete their change of direction the spaces between them are invaded by connective tissue, and the nearer they approach the surface the greater is the amount of connective tissue separating them from each other. Near the surface this tissue is so great in amount that the glands no longer present the appearance of being separated from each other by it; the organ here appears to consist of a mass of connective tissue with

widely spaced glandular tubules embedded in it. The epithelium of the glands is ciliated throughout, as is that covering the surface which bounds the lumen of the organ as a whole. The outer parts of the epithelial cells are clear and the nuclei are arranged irregularly in a deeper zone. The nuclei of the ciliated cells are oval; between the bases of the ciliated cells lie many cells of irregular shape with rounded nuclei. The tall ciliated cells in the deeper parts of the glands are arranged with their long axes obliquely set with respect to the long axis of the gland tubule, so that the free ends of the cells face towards the mouths of the glands. After the gland tubules have changed direction the axes of the epithelial cells are more nearly at right angles to the lumina and finally become completely so at the mouths. At the bases of the glands the epithelium is about 30μ in height, and the diameters of the lumina are the same or a trifle greater (figure 76, plate 18). In the more superficial parts, where the tubules are separated by large amounts of connective tissue, the thickness of the epithelium is increased to 40 or 45μ. In the distal millimetre or two of their course, where they are separated from each other by comparatively large amounts of connective tissue, the glands are slightly coiled before opening into the main lumen through rather funnel-shaped mouths (figure 77, plate 18). The increased amount of connective tissue surrounding the tubules in the more superficial part of the nidamentary gland produces the characteristic plano-convex lenticular shape of the glandular area which forms the cushion-like pad seen when the gland is opened by longitudinal incision. No trace of secretion was seen in any of the gland tubules.

Isthmus

The obliquely longitudinal ridges of the interior of the isthmus are low and wide at the proximal end but become higher and narrower distally (figure 79, plate 19). In the proximal part they are covered with a tall columnar epithelium 40 to 50μ high. The surface is ciliated and the nuclei of the ciliated cells are oval; between the ciliated cells lie a number of narrow columnar cells with very elongated dense nuclei. At the base of the epithelium, and occasionally in the outer clear stratum external to the nuclei, there are scattered rounded cells with small dark-staining nuclei (figure 80, plate 19). Epithelium of this nature covers most of the folds, but on the summits of some of them there is a different arrangement of cells. Here the epithelium is irregularly stratified, about 50μ thick, the outermost layer of about 15μ consisting of more or less cubical cells with dark-staining nuclei. Below this lies a layer two to three cells deep of polyhedral cells with large pale nuclei; among the larger cells are packed numerous smaller cells with little cytoplasm and small dark nuclei. Scattered throughout this epithelium are numerous vacuoles up to 40μ in diameter, much like goblet cells in appearance. They appear to be formed, however, from one or more polyhedral cells the contents of which have swollen greatly, destroying the nucleus and compressing the surrounding cells which become flattened and form an investing layer round each vacuole. These epithelia abut directly against the homogeneous fibrous connective tissue wall of the isthmus. In the more distal parts of the isthmus there is a differentiated layer underlying the epithelium consisting of a zone about 60μ thick, of crowded polyhedral cells with large nuclei and little collagenous material. This zone is sharply marked off from the epithelium but merges gradually with the deeper connective tissue. The epithelium is in general similar to that in the proximal parts, but it is not

ciliated. It is columnar, 50μ or more in height, the oval nuclei lying at about the middle of the cells. At the extreme base of the epithelium there is a layer of polyhedral cells with large pale rounded nuclei, and between them and the level of the nuclei of the columnar cells there are many smaller scattered polyhedral cells with darker-staining nuclei. Many of these are in the process of vacuolar degeneration, the contents becoming clear and swollen and the nuclei becoming dense and shrunken.

Uterus

Where the isthmus joins the uterus the ridges of the former are continuous with those of the latter. In the uterus, however, the ridges are very much higher, forming parallel folds like the pages of a book (figure 81, plate 19). The inner parts of the folds consist of a lamina of connective tissue arising from the fibrous and muscular wall of the uterus and projecting into the lumen; it is heavily vascularized, containing tortuous vessels running from the base to the free edge. Minor ridges and projections are present on the sides of the main ridges; the larger of these are supported by projections from the connective tissue core of the main ridge, but the smaller ones are not. A subepithelial layer of polyhedral cells is present as in the isthmus, and enlargements of it form the entire core of the smaller projections from the main ridge when there is no connective tissue extension into them. The epithelium is columnar but not ciliated, the large oval nuclei lying close to the free edge so that no conspicuous clear border is left superficially. Scattered polyhedral cells lie at the base of the epithelium deep to the zone of nuclei and a few vacuolated cells are present at wide intervals (figure 82, plate 19).

The trophonemata which line the greater part of the uterus are produced as modifications of longitudinal ridges and do not arise individually from the mucosa. The mucosa is raised into ridges that are broken up by transverse incisions into more or less separate lappets on the summits of which the filiform trophonemata are produced by further incisions of the edge (figure 83, plate 19). The ridges and trophonemata consist of narrow laminae of richly vascularized connective tissue covered with an epithelium (figure 84, plate 19). The trophonemata differ in length to some extent in different parts of the same uterus, but the greatest differences are found between the uteri of different fish and are probably correlated with various stages in the sexual cycle.

In fishes with short trophonemata the epithelium covering the ridges and trophonemata is undergoing rapid proliferation so that a solid mass of cells entirely fills the spaces between these structures, which are in effect embedded in the mass with sometimes not even their distal ends freely projecting from the surface (figure 85, plate 20). The ridges are supported by strands of connective tissue given off from the submucosa and extending throughout the ridges and to the tips of the trophonemata, but the strands become very tenuous distal to their origin, so that both ridges and trophonemata measure only 50 to 120 μ in transverse thickness for the greater part of their height. The outer surface of each ridge and trophonema is highly vascularized, small vessels and capillaries following tortuous courses so close to the surface that they rise above it for a distance of half their diameters (figure 86, plate 20). The basal stratum of the epithelium consists of a single layer of polyhedral cells with large pale staining oval nuclei up to about 8μ in longest diameter, the nuclei filling almost the entire cell volume. Outside the basal layer the cells are very much larger, up to

25 to 30μ in diameter, the nuclei of those near the basal layer being as large as those in that layer. Farther from the base the nuclei are smaller, eventually becoming shrunken and pycnotic. The cell walls remain distinct, surrounding a comparatively large amount of clear cytoplasm. Cells of this type form the greater part of the cellular mass in which the ridges and trophonemata are embedded, and appear to be derived from the division of the cells of the basal layer (figure 86, plate 20). Scattered among the large cells is a number of smaller ones with small round nuclei, about 6μ in diameter, which stain very much more darkly than the large nuclei of the larger cells.

In the fishes with long trophonemata both the ridges and the trophonemata are very much stouter and are not embedded in the cellular mass characteristic of those with short trophonemata. The connective tissue strands extending into the bases of the ridges are more robust, and the amount of connective tissue even at the free ends of the trophonemata is so great that the transverse thickness of the latter is 220μ or slightly more. The vascularization differs, for, in addition to some capillaries, small vessels up to 50μ in diameter follow extremely tortuous courses to the extreme tips of the trophonemata. The epithelium of the trophonemata and the distal parts of the ridges consists of a single layer of flattened cells, their nuclei not conspicuously larger than those of the underlying connective tissue (figure 84, plate 19). At the bases of the ridges the epithelial cells become much larger, polyhedral, and have large light-staining nuclei so that they are similar to the epithelial cells described in the last paragraph. They here form a basal layer outside which there is a cellular mass filling all the space between adjacent ridges, the cells being large and similar to those described above. The uteri with long trophonemata thus differ from those with short ones chiefly in the robustness of the trophonemata and the absence of the cellular mass between them except at the extreme bases of the ridges.

In the uteri with short trophonemata, but not in those with long ones, many small vesicles are present embedded in the intervening cellular mass. They are filled with a clear fluid, and occur scattered singly or in groups of some numbers (figure 87, plate 20). In the earlier stages of their development they are solid masses of cells similar to those forming the mass between the trophonemata. Their formation always starts within a trophonema (figure 88, plate 20) and appears to be brought about by one of the cells of the basal layer of the epithelium wandering into the connective tissue of the trophonema and there dividing to form a small aggregation of cells which becomes invested by a thin layer of connective tissue (figure 89, plate 20). As cell division goes on, the cell aggregate increases in size, and when a diameter of about 150μ is reached a cavity appears at the centre (*V*1, figure 89, plate 20). During growth to this stage the surrounding connective tissue forms a thin but definite theca, the cells being elongated and arranged parallel to the circumference. The inner cell aggregate becomes differentiated into a basal layer immediately within the theca, with large pale-staining nuclei which nearly completely fill the cell volumes, and an inner zone of very large clear cells with degenerating nuclei (*V*2, figure 89, plate 20). The inner cells thus exactly resemble those of the cell mass between the trophonemata, even to the presence in the interstices between the large cells of smaller cells with small dark-staining nuclei. The cavity is bounded by cells the walls of which have broken down, the contained fluid being almost certainly derived from the products of degeneration of the cells. It is interesting to note that in some places the cells of the mass between the trophone-

mata show a similar tendency to degenerate so that the trophonemata are partly separated from each other.

In their later stages the vesicles increase to several millimetres in diameter; they are then entirely filled with fluid and the cellular content has completely degenerated; after fixation and sectioning the contents consist of a coagulum with small scattered masses of cell debris derived from the former epithelium. The epithelium has disappeared as a continuous layer and the boundary is formed by the theca of connective tissue, several cells thick, with isolated epithelial cells scattered at wide intervals.

Discussion

1. *The male*

Testis and epididymis

The almost complete enclosure of the testis within the epigonal organ appears not to have been recorded in other elasmobranchs. The two organs may be entirely separate as in *Scyliorhinus* or *Scoliodon* (Thillayampalam 1928), but more frequently the testis is embedded in part of the epigonal tissue so that some of it appears upon the surface, as, for example, in *Raia clavata*. In *Cetorhinus* the epigonal and testis tissues are so closely united that the older observers failed to distinguish them as separate entities. De Blainville (1811) recognized the lobes of testis tissue, but appeared to consider that they were connected with 'filaments' ramifying through the epigonal tissue; he believed that the 'filaments' became veins near the surface and joined the reteform vessels lying between the laminae of the mesorchium. Home (1809) described as 'testis' the combined organs, but later stated that the 'epididymis nearly surrounds the testicle', evidently considering the epigonal organ, or possibly the reteform vessels, to be the epididymis. He designated as 'vas deferens' the upper coiled part of the ductus deferens, but in a later paper (Home 1813), dealing with a fish in which the testes had been destroyed before he examined it, he referred to this structure as 'epididymis' and described its macroscopic character accurately. The testis in *Cetorhinus*, though a large organ absolutely, is relatively small in comparison with the size of the testis of many of the smaller elasmobranchs. The weight of one epigonal organ and testis together in shark no. 1 was 17·5 lb., so that 10 lb. would be a very generous allowance for the weight of the testicular tissue alone. One may be quite certain therefore, that the total weight of the two testes was not more than 20 lb. If the weight of the shark were no more than 3 tons (they reach 4) the weight of the testes was thus 1/334 of the total weight at the most conservative estimate. This may be compared with *Sciliorhinus canicula*, where in a specimen of total weight 1500 g. the weight of the two testes together was 25 g., a proportion of 1/60 of the total weight. The testis differs too, in shape from that in most sharks, where it is elongate and triangular in transverse section. There is no noticeable asymmetry between the testes of the two sides, nor any tendency to fusion between the posterior ends of the testes of opposite sides; indeed, such fusion would be impossible in this species, for the testes are so short that their posterior ends do not reach the posterior border of the anterior mesentery and consequently cannot come into direct apposition.

The earliest studies of spermatogenesis in elasmobranchs are those of Hallmann (1840) and Lallemand (1841), but it was in the voluminous work of Semper (1875) that most of the essentials of the process were first given as a connected account in considerable detail.

Spermatogenesis in *Cetorhinus* for the greater part agrees fairly closely with the process in the species which he examined, *Sciliorhinus* and several of the Raiidae. He was unable to trace the fate of the spermatogonia, and although he said that the Sertoli cells appear at about the time that the spermatogonia disappear he did not realize that they are the same, and suggested that the Sertoli cells might be derived from the outermost layer of spermatocytes. Herrmann (1881), working on *Sciliorhinus stellaris*, confirmed most of the details, but he too was unable to decide the origin of the Sertoli cells. Swaen & Masquelin (1883), working with the same species, believed that the original outer follicle cells formed the ring of cells lining the cavity of the ampulla, but 'were forced to admit' that some of them migrate to the periphery of the ampulla in the later stages of spermatogenesis, and suggested that the remainder atrophy; Jensen (1883) also thought that migration occurs in some of the Raiidae. Sabatier (1896) had no doubt that the central cells (the spermatogonia) give rise to the spermatocytes, but he denied the migration of spermatogonia to form the Sertoli cells, and in an earlier paper (Sabatier 1895) had stated that the Sertoli cells are formed from very fine nuclei in the basement membrane of the ampulla. Moore (1894), who was studying the chromosomes during meiosis, incidentally mentioned the migration of the spermatogonia to become the Sertoli cells, but he gave no figure of the process. He found that in *Sciliorhinus* the 'foot cells' migrate 'with a singular amoeboid movement' from the central cavity and arrange themselves on the boundary membrane, assuming a 'normal foot-cell character'. Stephan (1902*b*), also working on *Sciliorhinus*, found that at first the spermatogonia lie internal to the spermatocytes, but that after three or four rows of the latter have been formed the spermatogonia are irregularly mixed with them. This irregular mixing is undoubtedly a stage in the migration of the spermatogonia to the periphery, but Stephan appears not to have appreciated this, for he referred to Moore (1894) as suggesting that migration takes place but stated that he himself 'cannot affirm the contrary with certainty', and added that many of the spermatogonia degenerate. He stated that the Sertoli cells start to increase in size when the spermatocytes go into synapsis, and that the spermatids aggregate into bunches corresponding in number with that of the Sertoli cells, a finding which agrees completely with the process now found in *Cetorhinus*.

Semper (1875) found that in *Sciliorhinus*, when the spermatozoa reach the stage in which all the heads are bunched together and lie to one side of the nucleus of the Sertoli cell to which each bundle is attached, each Sertoli cell contains a discrete body in addition to the nucleus. The bodies lie at the level of the caudal ends of the sperm heads and, according to Semper, those in consecutive cells form a very regular zone; he was unable to offer any suggestion as to their meaning. Herrmann (1881) found similar bodies in the Sertoli cells of *Squatina*, but he expressed no opinion as to their nature. Swaen & Masquelin (1883) stated that the bodies are formed from the nuclei of the Sertoli cells and that they fuse with them again after the spermatozoa have left the ampulla. Sabatier (1896) agreed that they are formed by the division of the Sertoli nuclei but denied that there is afterwards any fusion. The present study of *Cetorhinus* adds little on this point, for no trace of any such bodies could be recognized in the Sertoli cells until after the spermatozoa had left the ampullae.

During the final transformation of the spermatid into a spermatozoon the head-piece becomes elongate and then spiral, the spiral character appearing first at the posterior end

and extending gradually to the anterior end. Retzius (1902, 1909) studied the spiral nature of the head of the spermatozoon in several species of elasmobranchs and found that it is caused by a filament or thickening of the envelope which follows a spiral course from end to end of the head. Stephan (1903) found a fusiform body in the transforming elasmobranch spermatid, and traced it to a position alongside the future middle piece; he suggested that this body later becomes the spiral filament. The number of spiral turns differs according to species; in *Cetorhinus* it is seven to eight. La Valette St George (1878) found nine to ten in *Galeus canis* and five in *Raia clavata.*

There are several points of interest in the aggregation of the spermatozoa into clumps before they are released from the ampullae when ripening is complete. The spermatids arrange themselves in bunches, each bunch in relation to a Sertoli cell; Sertoli (1878) applied the name 'spermatogemme' to such aggregations, a term which is not now in general use. Swaen & Masquelin (1883) erroneously thought that each clump of spermatids is surrounded by an incomplete envelope formed from what they termed the follicle cells, the cells now shown to be spermatogonia.

In *Cetorhinus* when the heads elongate they lie parallel to each other; the spiral shape then appears at the posterior ends of the heads, and by the time that it has reached the anterior ends the heads are arranged so that the spirals of every head in each clump coincide and all are in phase. This correspondence of phase allows the heads to become very closely approximated in the final stages of maturation. The heads appear to be strongly attracted to each other, but the attraction is not of equal strength along the whole length of the heads, being strongest at the anterior and weakest at the posterior end, and showing a gradient between the two. As a consequence the clumps of heads take on a conical shape, coming to a point distally. The succeeding intermediate pieces, however, appear to be strongly repelled from each other so that they form a more or less spherical cage at the bases of the heads, between the latter and the elongated middle pieces. In *Cetorhinus* the middle pieces are separated from the heads by faintly staining intermediate pieces of about equal length; the middle pieces themselves do not stain very strongly.

Herrmann (1881) pointed out that Semper (1875) failed to recognize the middle piece of the selachian spermatozoon. Suzuki (1898) stated that the middle piece is derived from the proximal centrosome of the spermatid, and the minute terminal body from the distal one, but Moore (1895) thought that the middle piece consists of a mass composed of the 'nebenkern', archoplasm, and the intracellular part of the flagellum, and that the terminal body is derived from a swelling on the cell membrane where the flagellum originally passed out and which 'remains as a little bead at the hinder end of the Mittelstuck'.

In *Cetorhinus* the middle pieces appear to be strongly attracted to each other so that they are closely approximated in each clump, producing a well-marked proximal boundary to the cage formed by the intermediate pieces. The tails of the spermatozoa in each clump are closely approximated throughout the greater part of their length, except for a small distance immediately succeeding to the middle pieces. Here they appear to be repelled from each other so that they form a second cage much smaller, however, than that formed by the intermediate pieces. Such an arrangement of the spermatozoon does not appear to have been recorded in any other elasmobranch. It would be rash to suggest possible causes of this peculiar arrangement of the spermatozoa, with different parts in different degrees of

approximation, but it may be permissible to emphasize that the appearances give a strong impression of mutual attraction or repulsion between different parts of adjacent spermatozoa in each clump.

The testicular ampullae in their earliest stages of formation bear a striking resemblance to young ovarian follicles, a single large cell being enclosed in a sheath formed from a few flattened ones. This arrangement is derived, as noted by Sabatier (1895), from nests of cells in which one enlarges and becomes the 'ovule' surrounded by the others. Indeed, several authors, for example, Semper (1875) and Herrmann (1881), speak of this original cell as the 'egg-cell', 'ovum' or 'male ovule', and Moore (1894) went so far as to say that the immature gonads in 'the future male *Scyllium* are conspicuously hermaphroditic', and suggested that he was unable to find any reference to this fact in the literature because 'as the testes grow older the hermaphroditic character dies out'. It would appear to be more appropriate to regard the young stage merely as sexually undifferentiated until good grounds are brought forward for attributing the characters of both sexes to the immature gonad.

The Sertoli cells are large, but this character is masked by the presence of the spermatozoa, so that it is not until the ampullae are discharged that it is fully revealed. Shortly after the loss of the spermatozoa the ampullae shrink in size and the Sertoli cells begin to degenerate. The cytoplasm decreases in amount and the secondary bodies of unknown function disappear, but the nuclei remain prominent for some time. Thereafter the ampullae are probably gradually resorbed as stated by Sabatier (1895). Stephan (1902*a*), however, stated that after the spermatozoa have been discharged the Sertoli cells increase by amitosis, phagocytose the debris, and fill the ampulla completely. It is true that they fill the ampulla, but this is because the wall of the ampulla shrinks round them and obliterates the lumen by crowding them together; Stephan goes rather too far in comparing the ampulla at this stage to a corpus luteum. He was not the first to do so, for Semper (1875) had made a similar comparison and Sabatier (1896) had mentioned that this opinion was 'not unchallengeable'; Van den Broek (1932) misunderstood part of Semper's description and so gave an incorrect account of the involution of the ampulla. Stephan stated further that after this stage some of the ampullae degenerate to form lymphomyeloid tissue, implying that part at least of the epigonal organ is thus derived, and that others reach a stage in which they resemble primitive follicles again. These opinions have not been confirmed by other authors.

Ampulla ductus deferentis and spermatophores

The ampulla of the ductus deferens, which is often incorrectly termed the 'vesicula seminalis', varies considerably in comparative size among the elasmobranchs, but is short and fusiform in many species. The mucous membrane of the interior is thrown into a number of transverse folds of greater or less complexity whereby the surface area of the lumen is greatly increased; according to van den Broek (1932) this condition is found generally in all male selachii. The relative size and complication of the internal structure of the ampullae in *Cetorhinus* appear to be unsurpassed in any elasmobranch yet recorded. Both Home (1809, 1813) and de Blainville (1811) note the large size of the ampulla and the presence within it of the transverse folds which they liken to valvulae conniventes. But de Blainville says they are placed 'in pairs back to back forming a double series of pretty

deep cells'; he had evidently examined the interior of the ampulla only after the wall of the organ had been divided longitudinally, so that the pockets on each side of the longitudinal ridge between successive septa were displayed (cf. figure 7). It is very easy to fall into this misconception, and considerable study of the parts is necessary to appreciate the true nature of the relationships; he does not mention the subsidiary laminae at the free edges of the septa. Home (1813) suggests that the fluid within the ampulla is secreted from the surface of the 'valvulae', a guess which approaches the truth. He noted that the ampulla contains a 'substance like starch broken down into small rounded portions, mixed with thinner fluid'; de Blainville describes the contents as 'curds of greater or lesser size of an albuminous appearance' containing cores of the seminal fluid such as he found in the upper part of the ductus deferens.

Examination of the present material suggests that the formation of the spermatophores takes place thus: the spermatozoa pass into the upper coiled part of the ductus deferens where they are mixed with the secretion of the epithelium and with that received from the tubules of Leydig's gland, the anterior non-urinary part of the kidney. The resulting fluid passes into the anterior end of the ampulla where it becomes aggregated into small globules, perhaps by the action of cilia, in the region of the thin septa. These aggregations then pass into the pockets between the stouter more posterior septa and the longitudinal ridge in the lower part of the ampulla and are there caused to rotate by the action of the ciliated epithelium. At the same time the deeper glandular cells of the epithelium secrete a fluid which becomes the jelly, and this is laid down in concentric layers as a cortex round the core of spermatozoa when the aggregation is rotated in the pocket. The fluid in which the spermatophores float is probably also secreted from some part of the ampullary epithelium; it may react upon the fluid forming the cortex of the spermatophores causing it to coagulate after it has been laid down. On the other hand, the coagulant may be already present in the cortical fluid when it is secreted and the coagulating process may be slow, so that there is time for the layers of the cortex to be laid down and moulded to shape before it sets. The occurrence of occasional blank spermatophores shows that the coagulation is not caused by anything derived from the spermatozoa or the upper part of the ductus deferens; the blanks evidently are formed round cores consisting of small masses of coagulated secretion which have failed to adhere to a spermatophore. The opposite condition, aggregations of sperm without a cortex of gelatinous material, is evidently brought about by the core of spermatozoa travelling along the central lumen of the ampulla without being diverted into one of the pockets between the septa.

The comparatively small diverticulum arising from the posterior end of the ampulla and running cranially for a short distance closely applied to the ampullary wall beneath the peritoneum is evidently the homologue of the 'sperm sac' which is present as a comparatively large and distinct structure in many elasmobranchs. According to van den Broek (1932) it ranges in shape from short and rounded in *Trygon* to long and narrow in *Scilliorhinus*. This, rather than the ampulla, would more appropriately bear the name of vesicula seminalis. Home (1809, 1813) does not notice this structure, but de Blainville (1811) describes it and points out that it is a true seminal vesicle 'into which the semen must reflux from the deferent canal'. He does not, however, state whether he found any contents inside it; in the subjects of the present study contents were not present, nor was the diameter

of the lumen such as to suggest that the fully formed spermatophores would be likely to enter it. On the other hand, de Blainville states that in the fish which he examined the orifice was at least as large as that of the ampulla into which he was able to introduce his fist; but the tissues of his specimen may have become softened by incipient decay, for it had been transported by waggon from Dieppe to Paris.

The production of spermatophores in the male *Cetorhinus* is, as far as our present knowledge goes, unique among the elasmobranchs. But in view of the structure of the ampulla of the ductus deferens where they are formed, it would appear to be desirable to examine with care the contents of the ampullae in other species. The ampulla is certainly comparatively large in *Cetorhinus*, and its internal structure may be rather more complicated than in some other species, but its general morphology does not appear to differ fundamentally from that in other species where, as van den Broek (1932) says, transverse folds of the mucous membrane of the interior are generally found. It is probable that similar structures serve similar functions, and some sort of aggregation of the spermatozoa may well be found to occur in the ampullae of the ductus deferens in some other elasmobranchs. It may be suggested that as a consequence of the sperm being enclosed in spermatophores, there will be less likelihood of loss of sperm by leakage into the water when it passes from the cloaca to the groove of the clasper during copulation, if, in fact, the clasper groove is the route by which it is transferred. Conservation may well be an important matter because so large a quantity, amounting to several gallons, of spermatophores is transferred.

Kidney

The upper part of the kidney is modified as Leydig's gland in the male, but in the female, though urinary in function, it is much less developed than the lower part and a number of its segments are atrophied in the adult. Leydig's gland has completely lost its urinary function, any Malpighian corpuscles that may have been present in early life having atrophied in the adult, and is purely an accessory genital gland. It appears to secrete the greater part of the fluid in which the spermatozoa are suspended when they reach the ampulla of the ductus deferens. As pointed out in the section discussing the ampulla of the ductus deferens the secretion of Leydig's gland appears to play no part in the coagulation of the ampullary secretion to form the cortex of the spermatophores; indeed, a small quantity of it is probably enclosed with the spermatozoa at the centre of each of those bodies.

Interrenal and suprarenal bodies

The interrenal body is similar in form to that in other pleurotrematous Euselachii as described by several authors (Vincent 1897; Giacomini 1898; Grynfeltt 1903; Diamare 1905; Pittoti 1937, 1938) being unpaired and elongated. Though unpaired in the adult, it is derived, according to van Wijhe (1889), from paired rudiments arranged metamerically along the whole length of the mesonephros, but Poll (1905), while admitting the possibility of a metameric origin, did not regard the matter as proved. Ramalho (1921) and Pittoti (1938) both report the presence of lipoid material in the cells of the interrenal body of other elasmobranchs, as now found in *Cetorhinus*. Fancello (1937) found a characteristic modification of the interrenal body at the onset of sexual maturity in female oviparous elasmo-

branchs, the glandular lobules becoming larger and more distinct from each other, the cells enlarging and containing more cytoplasm and larger nuclei. But Ranzi (1936) found that in female viviparous elasmobranchs the cells of the interrenal body are smaller during gestation, though the general size of the organ is larger; changes of this nature may be expected to occur in *Cetorhinus*. The experimental work of Beidl (1910), Kisch (1928) and Dittus (1937) shows that the interrenal body is the homologue, functionally as well as anatomically, of the adrenal cortex of the higher vertebrates.

The suprarenal tissue of elasmobranchs is usually gathered into numerous distinct bodies arranged metamerically along the whole length of the abdominal cavity in close relation with the segmental arteries. In *Cetorhinus* this arrangement was not obvious, but the circumstances of the field work did not favour fine dissection, and it would be unsafe to insist upon this point. As shown by Young (1933) the sympathetic ganglia of the kidney region of elasmobranchs always lie in close relationship with the suprarenals, and in *Cetorhinus* the two structures appear to be very intimately intermingled. The irregular masses lying inside the posterior cardinal sinus appear to consist of sympathetic nervous tissue that has invaginated the wall of the sinus into the lumen of the vessel. The histological details of the suprarenals are similar to those in other elasmobranchs as described by Diamare (1902), Grynfeltt (1903), Fancello (1937) and Pittoti (1937).

Epigonal organ

The epigonal organ was mentioned as the 'milt-like part of the testis' by Monro (1785), Cuvier (1805) and Davy (1839), but was first described as a separate organ by Müller (1842); it has been noticed by a number of subsequent authors but overlooked by more. Semper (1875) studied this organ in some detail and pointed out that it varies greatly in size from species to species. He also mentioned some species from which he said that it is wholly lacking, a statement in which he was mistaken and in which he was corrected by Redeke (1898). In most sharks the epigonal organ lies between the caudal pole of the gonad and the digitiform gland, and may actually extend from the one to the other in those species where it is large; in the rays it is short, broad and closely applied to the caudal pole of the gonad which may appear to be embedded in it. The close relationship of the epigonal organ to the gonad in many species has misled some authors into regarding the former as the stroma of the latter, and even van den Broek (1932) said that it consists entirely of a stroma very rich in cells like the stroma of the sex gland. All authors who have examined the histology of the epigonal organ emphasize its lymphoid character. Leydig (1852) suggested that destruction of blood corpuscles takes place in it, but Semper (1875) took the opposite view, saying that there could be no mistake about his observation that true blood corpuscles are formed in it, but he surprisingly added that this is 'the only interpretation that can be made, but I can only put it forward as an hypothesis'. Policard (1902) concluded that the organ is leucocytopoietic only, stating definitely that it appears to have no erythrocytopoietic role, although he described its tissue as lymphomyeloid. Drzewina (1905) did not mention the presence of erythrocytes in the epigonal organ of young *Raia clavata*, and spoke of the organ as the 'lymphoid tissue of the testis'. She concluded that this tissue, like the lymphoid tissue found elsewhere in the body of elasmobranchs, is concerned with the formation both of lymphocytes and of granular leucocytes, and claimed to have traced the

transformation of the former into the latter. However, Phisalix (1885) recorded that the spleen of elasmobranchs produces both red and white blood cells. Although the first of these three authors denied an erythrocytopoietic function to the epigonal organ, and the second did not refer to such a function, the histology of the organ in *Raia clavata* differs in no essential from that of *Cetorhinus*, and the formation of erythrocytes was traced in preparations made for comparison in the present study. There can be no doubt that the epigonal organ in *Cetorhinus* and in *Raia* is a centre for the formation of erythrocytes as well as leucocytes; it is not within the scope of the present paper to enter into the details of the formation of these cells, but the writer would commend to haematologists the epigonal organ of the elasmobranchs as possibly a profitable and certainly a most interesting subject of investigation.

Clasper and siphon

The clasper of the adult *Cetorhinus* has never been described; Home (1809, 1813) and de Blainville (1811) gave some incomplete notes upon it, Pavesi (1878) gave some details of the partly developed organ in an immature fish, and Jungersen (1899) investigated the skeleton of it in dried material removed from a stuffed specimen. In spite of the unsatisfactory nature of Jungersen's material his description of the cartilages is very nearly correct and agrees closely with the conditions found in the fresh specimens dissected in the present study. His chief omission was due to his failure to find the rather small second dorsal terminal piece (*Td*2), but he was aware that this cartilage was probably present in the intact clasper and mentions that he thought it was probably similar to the corresponding piece in *Lamna*. It is, in fact, considerably smaller proportionally than in that species, but its articulation with the distal end of the dorsal marginal cartilage and the free edge of the proximal part of the dorsal terminal piece is homologous.

Several authors have studied the comparative anatomy of the skeleton of the clasper in the elasmobranchs, and have gone into considerable detail in naming the various cartilages and finding their homologies in different species. The work of Gegenbaur (1870), Petri (1878) and Davidoff (1879) was reviewed and much extended by Jungersen (1898, 1899), whose monograph of 1899 forms an admirable treatise on the subject; it may be questioned whether the elaboration of Jungersen's work by Huber (1901) is any real improvement. Leigh-Sharpe (1920, 1921, 1922) described the external clasper form of a number of species, but unfortunately he did not relate his observations to the supporting skeletal parts or the muscles, nor did he consider these when proposing new names for the cutaneous and other lobes which give the external form much complexity in some species. One only of his terms has been adopted in the present study, viz. rhipidion, for the conspicuous dermal flap in whose base the cartilage *Td*2 forms a stiffening; Leigh-Sharpe himself uses this name for structures which are not homologous, for instance, in dogfish and rays.

In *Cetorhinus* the skeleton is comparatively simple in the number and arrangement of its component cartilages. Similarly, its musculature is much less complicated than in many species, the compressor muscle in the clasper being small, and the muscles being surprisingly limited for so large an appendage. The compressor muscle, or at least that part of it which appears in the clasper, is small, and the extensor is much reduced in comparison with its development in many species where it is often large and divisible into two parts, the flexor

exterior and interior of Huber (1901) and Daniel (1922). The largest muscle is the dilatator, whose action, together with that of the adductor, is to erect the clasper, bringing it forward so that it is directed cranially beneath the abdomen. At the same time, by the traction of the muscle on the fascia of the appendage, the distal end of the clasper groove is caused to open, and the tissue surrounding the neck of the style being drawn in a proximal direction the style is erected (flexed) and the claw caused to protrude from its pocket. A similar action occurs in *Lamna* according to Dunlop (1892).

The action of the compressor muscle is opposite to that of the dilatator, and actively returns the style to its normal position (extends it); but when the action of the dilatator ceases the parts at the distal end of the clasper return to their normal position mainly by the elasticity of the tissue. Jungersen (1898) cleared up the misconceptions which had confused an understanding of that part of the compressor muscle surrounding the siphon. He pointed out that the muscles of the clasper are specialized parts of the dorsal and ventral radial muscles of the pelvic fin, and that the siphon is to be regarded as an inpushing of the integument, taking with it an enclosing sheath of muscle. Thus the muscle surrounding the whole of the siphon, even when its anterior end extends nearly as far forward as the pectoral fin, as in *Cetorhinus*, is in origin part of the musculature of the pelvic fin.

The function and mode of action of the siphons remain very obscure. Agassiz (1858) suggested that the siphons are reservoirs for spermatozoa, an entirely erroneous opinion, for spermatozoa have never been reliably reported as found there. Jungersen (1899) pointed out that the records of Schneider (1883) and of Redeke (1898) are doubtful, and that if sperm were really present in the single instance which each of these authors adduced they were probably introduced by accident. Leigh-Sharpe (1920) stated that in sharks the siphons are normally filled with sea water, an assertion which is scarcely correct, for the siphons are normally empty and collapsed with their internal and external walls in contact so that the lumen is potential only. He suggested that during copulation the sea water contents are expressed in order to force the spermatozoa into the vagina of the female. He said that sperm is constantly dribbling from the cloaca of the male and that some of it reaches the clasper groove, but he implied that the sea water directed from the siphon tube would draw the sperm into the groove on the principle of the air spray-gun rather than by acting as a propellant charge. It appears to the present writer that, if something of this sort occurs, the water most probably acts as a propellant, for if the other alternative were correct the sperm would be diluted with the water. That no such dilution occurs in *Cetorhinus* is shown by the female which had recently been inseminated, and which contained a compact mass of spermatophores that showed no signs of any dilution. It must be confessed that it is difficult to understand how the siphons could be filled with sea water, for there appear to be no muscular arrangements by which this might be accomplished; the siphons are normally only potential spaces and are compressed between the skin and the abdominal wall. Once they were filled, of course, the compressor muscles would have no difficulty in forcibly expelling their contents.

Jungersen (1899), in discussing the function of the claspers, pointed out that some authors have suggested that both claspers are inserted together thus forming a duct between their opposed inner surfaces, and that others have thought that they act as dilators for the intromission of the urinogenital papilla; but the only direct evidence is that of Bolau (1881),

who observed that in *Sciliorhinus* only one clasper is inserted, the photograph published by Schensky (1914) showing no details. The condition of the scars and lacerations found in the female *Cetorhinus* show that in this species too, only one clasper is used at a time. The distance of the scars from the cloacal opening also shows that the tip of the clasper must reach quite to the anterior end of the common vagina, and consequently one may be practically certain that it is through the clasper groove that the spermatophores are introduced.

Jungersen (1899) states his inability to understand how the sperm finds its way from the cloaca into the clasper groove, but it is evident from the observations of Friedmann (1935) on *Raia* and of Leigh-Sharpe (1920) on *Sciliorhinus* that the proximal opening into the clasper groove is brought into close apposition with the cloaca during erection, and the latter author was able to satisfy himself by experiments on dead fish that the sperm actually pass into the groove. Nevertheless, it is not easy to understand how the spermatophores of *Cetorhinus* pass into the groove, for the lips of its proximal end are in close apposition. It may be suggested that the contraction of the small oblique portion of the compressor muscle may cause a puckering of the tissues in this region with a consequent dilation of the end of the groove. It is evident that something of this sort must occur in order to make sufficient space for the comparatively large spermatophores to pass, and it is possible that a similar dilation occurs in other species in which the spermatozoa are suspended in a seminal fluid.

Although the epithelial lining of the siphons is glandular in character the amount of secretion present is not great. A similar epithelium from which secretion is produced by degeneration of the cells themselves has been found in the siphons of *Squalus acanthias* by Petri (1878), but here, in addition, many more goblet cells were present than in *Cetorhinus*. In rays the siphon sacs are very much reduced in extent and are completely filled with a large compound tubular gland which discharges into the sac through numerous papillae. The gland is enclosed by a modification of the part of the compressor muscle which surrounds the siphon, and upon suitable stimulation its contraction discharges the semi-viscous secretion in large quantity and forces it down the siphon tube to the clasper groove. The gland, though undoubtedly a derivative of the siphon epithelium, is very different in type from the glandular epithelium lining the syphons of *Cetorhinus*; it is tubular, and the cells lining the tubes are seen in sections of the gland to be filled with granules of secretion which are released into the lumina of the tubes and thence discharged through the surface papillae. Neither can the gland within the scroll of the clasper groove of *Cetorhinus* be homologous with the siphon gland of the rays, for its secretion, like that of the siphon itself, is produced by the actual breakdown of the cells, and it has no tubular structure. It is probable that the function of the secretion of this gland is merely that of a lubricant; reasons are given in the section dealing with the breeding of *Cetorhinus* for supposing that it has neither a solvent action upon the spermatophores nor an activating action on the spermatozoa. There appears to be no description in the literature of any similar clasper gland in any elasmobranch beyond a brief mention by Davy (1839); de Blainville (1811) very nearly found it, for he records that he found the clasper groove filled with a large quantity of matter 'exactly similar to that filling the upper part' of the ductus deferens, thereby making the same mistake that the present writer made on a first superficial

examination of the clasper. De Blainville, thinking this secretion to be the sperm, claimed that the theory of Bloch (1801) postulating that the myxipterygium is literally a clasper was thereby refuted, a correct conclusion reached from false premises.

2. *The female*

Ovary

The ovary is conspicuously different from that in any other elasmobranch as far as can be ascertained from a careful search of the literature. The germinal epithelium has been invaginated so that the ovary is in effect a hollow organ, although it does not at first sight appear as such, for the internal hollow is broken up into innumerable fine tubules. The tubules join to form progressively larger tubes which finally open to the surface in the pocket, on the right side. The hollow of the interior is thus a direct extension of the peritoneal cavity and is not comparable with the sac-like structure of the ovary in, for example, *Scyliorhinus* or the anuran Amphibia. In other elasmobranchs the germinal epithelium covers the outer surface of the ovary, and ripe follicles burst through this surface to discharge their ova into the peritoneal cavity.

The immense number of follicles and small ova found in *Cetorhinus* is unusual; calculation shows that the ovary contains at least six million ova measuring 0·5 mm. or more in diameter, a number similar to that present in the ovaries of many oviparous teleostean fish. Ova as small as 0·5 mm. in diameter already contain a considerable proportion of yolk, but the largest yolky eggs found were not more than 5·0 mm. in diameter. It is probable that this is the maximum size attained by the ova before discharge from the ovary, for it appears to be impossible for anything larger to pass through the finer ramifications of the internal cavity. The correctness of this conclusion is confirmed by the fact that the lumen in the infundibular part of the oviduct is not greater than 2·0 to 3·0 mm. in diameter, so that an egg even of the small size mentioned would undergo considerable distortion in passing through it. The wall of this part of the oviduct is thick, fibrous and inelastic, so that unless great changes take place in it at the period of ovulation the eggs almost certainly cannot be larger when discharged.

The formation of the follicles from nests of cells is in general similar to the process in other elasmobranchs, as described by Balfour (1878*b*) and Ludwig (1875), but the formation of vitelline material in the follicle cells during early stages and its transfer to the ovum do not appear to have been described in other species. When all this material has been transferred so that the follicle cells form a comparatively thin layer of epithelium the component cells are all of much the same size, as in *Scyliorhinus*, and do not show the great differences in size characteristic of the younger follicles in the rays. Retzius (1912) showed that in the later stages of vitellogenesis fine protoplasmic strands extend from some of the cells of the follicular epithelium through the vitelline membrane to the yolk, and presumably add material to it. These occur in *Cetorhinus* and form the zona radiata visible in some follicles. Schultz (1875) and Schmidt (1898), in addition to Balfour (1878*b*), have studied the vitelline membrane of the elasmobranch ovum, and in particular the second named has traced the differences in different species.

The formation of corpora lutea, or bodies resembling them, after the discharge of the ova, is known in a number of elasmobranchs, especially in some of the rays (Giacomini

1896; Samuel 1943), and it is not surprising to find similar structures in *Cetorhinus*. But in this genus the majority of these bodies must be formed by atresia for they are very numerous, and if, as is suggested below, *Cetorhinus* is viviparous, only a minute proportion of the millions of small ova present in the ovary can possibly give rise to embryos and the remainder must necessarily perish. The larger corpora lutea, which are less numerous in the ovary and are approximately equal in size to the largest follicles, appear to be derived from discharged follicles. On the other hand, it is possible that they also are formed by atresia of the larger follicles, for no other signs of pregnancy were found in any of the fish examined, although the ovaries of them all contained these large corpora lutea. If the larger corpora lutea are formed by atresia of ripe follicles, the absence of any visible remains of the vitelline membrane in them would be consistent with the extremely tenuous nature of the membrane in the larger follicles. Nevertheless, in the opinion of the present writer, these large corpora lutea are probably those of ovulation. Even in the smaller corpora lutea there is an important change in the composition of the vitelline membrane, for while the follicles are intact it shows no affinity for Sudan black, whereas when the ovum has become degenerate it takes up this stain very intensely. These bodies are undoubtedly homologous with the corpora lutea of higher vertebrates, for they are produced by the proliferation of the follicular epithelium, but there is no evidence to show whether they function in a similar manner. It would be interesting to know if they reach a larger size in pregnant fish where any secretion they may produce might be expected to be concerned with the maintenance of pregnancy; it is certain that their presence in large numbers has no inhibiting effect on the maturation of follicles in the ovaries of non-pregnant fish. Although the degree of development of the trophonemata in the uterus was unequal in different fish there was no obvious difference in the amount of luteal tissue present in the different ovaries.

Oviduct, nidamentary gland and uterus

In most elasmobranchs, as far as is recorded, the ostium abdominale of the oviducts lies ventral to the oesophagus immediately posterior to the septum transversum and at some distance from the ovary, the discharged ova being swept into it by ciliary action. Though both oviducts usually share a single ostium they are not fused together except on the dorsal sides of their proximal ends. In *Cetorhinus*, however, the proximal parts of the oviducts are fused together to form a single tube which is shallowly embedded in the ventral surface of the liver so that the ostium is carried in a caudal direction to lie in very close apposition with the pocket on the right side of the ovary into which the internal ovarian cavity opens. In correlation with the great size of all the organs in this fish the falciform part of the suspensory ligament of the liver is strongly developed, and the unpaired part of the oviducts lies in close relationship with this ligament, occupying in fact a position corresponding to the ciliated bridge connecting the two liver lobes and along which, according to Metten (1939), the ova pass from the anterior end of the ovary to the ostium in *Sciliorhinus*. The ostium is closely applied to the ovarian pocket so that the ova can pass directly from the one to the other without the necessity of being swept by cilia through any part of the peritoneal cavity. A somewhat similar apposition of the ostium abdominale to the ovary has been described by Widakowitch (1908) in *Torpedo ocellata*. The fact that the diameter of the infundibular part of the oviduct is smaller than the ripe ova has already been

mentioned; it is obvious that the ova must be considerably distorted while passing through this portion, though they will have no difficulty in passing into the ostium which is comparatively very large. In most elasmobranchs the ostium is very small, although it becomes wider in the breeding season. According to Redeke (1898) it is never so wide that the ova can pass undistorted, and they are strongly compressed during their passage through it.

The nidamentary gland is small in *Cetorhinus* compared with that in oviparous elasmobranchs. No trace of any secretion of shell material was found, but since no eggs were found in the oviducts that does not necessarily imply that no shell is formed. Gerbe (1872), Henneguy (1893), Borcea (1904) and Widakowich (1905) were able to distinguish two parts of the gland in oviparous forms, one secreting the albumen and the other the cornified shell. In *Cetorhinus* the gland appears to be homogeneous and no division is obvious, nor does its microscopic structure suggest that it may have more than one function. All the alveoli of the gland in *Cetorhinus* are unbranched and simple though rather elongated. Gerbe (1872) found that in the rays the glands of the albumen-secreting part were straight and often dichotomous; he added that the albumen is not deposited in concentric layers round the egg, but in an unstratified mass. The structure of the gland in *Cetorhinus* is such as to suggest that its function is solely that of secreting albumen; if any shell is produced it is unlikely to be more than a membranous sac, as in *Acanthias*. There is another, non-secretory, function which the shell gland may serve, though no evidence was found to confirm this. In *Sciliorhinus* Metten (1939) found that the shell-secreting part of the gland serves as a receptaculum seminis, and that many spermatozoa are to be found within the tubular glands at all times of the year. In this species the egg is fertilized when it passes through the gland, the spermatozoa being released with the shell material. Although some of the fish examined in the present investigation had recently copulated, no traces of any such storage of sperm were found; but here again the negative evidence does not prove that storage does not occur.

In the oviparous elasmobranchs the wall of the uterus serves only to transmit the egg and is smooth and covered with flattened epithelium. In the viviparous forms, as in *Cetorhinus*, the wall bears numerous villus-like appendages. In their simplest form, as in *Acanthias* (Brinkmann 1903; Widakowitch 1907; Blaizot 1908, 1909), they appear as rounded lobes on the summits of longitudinal ridges of the mucosa, and in certain stages of pregnancy they are considerably elongated and some of them may branch into two terminal lobules. In their most complicated form, as in some of the rays (Alcock 1890, 1892; Wood-Mason & Alcock 1891, 1892; Brinkmann 1903), they appear as long flattened strap-shaped appendages which have a microscopic structure of considerable complexity. Wood-Mason & Alcock proposed the name 'trophonemata' for these structures in order to distinguish them from the villi of the intestine which have an absorptive function, a name which has been generally adopted. The trophonemata of *Cetorhinus* are intermediate in character between the two extremes; they lie in rows, thus showing their derivation from longitudinal ridges of the mucosa, but their free ends are so crowded and branched that this arrangement is not obvious at first sight and can only be demonstrated by dissection of the surface of the mucosa. As in the more complicated trophonemata of some of the rays, in those of *Cetorhinus* there is a central core of connective tissue containing arteries, veins and capillary plexuses, the whole covered by a secretory epithelium, but there is no development of definite shallow

tubular glands on their surfaces. There is, however, great proliferation of the epithelial cells, which become distended with secretion and release it by becoming detached and disintegrating. It is probable that the secretion thus produced serves an embryotrophic function, as does the secretion in other viviparous forms. There is some indication of a similar proliferation of the epithelium between the bases of the trophonemata in *Trygon* (Brinkmann 1903) and in *Acanthias* (Widakowitch 1907). So great is the proliferation in *Cetorhinus* that a compact mass of cells is formed in which the bases of the trophonemata are solidly embedded, and which in many places in some specimens extends quite to their free ends.

The formation of vesicles by the breakdown of some of the swollen epithelial cells below the surface so that cavities are formed has not been recorded elsewhere. Once the cavity has been formed it enlarges by the further breakdown of the surrounding cells, which degenerate in a manner similar to those on the free surface of the mucosa. The fluid contents accumulate until the vesicle appears on the surface of the uterine cavity, where, presumably, it finally ruptures to discharge its contents into the lumen. If the product is similar in nature to that from the rest of the epithelium it, too, would be expected to serve a trophic function, but it is possible that it may serve another purpose.

When the female receives the mass of spermatophores from the male some process must occur by which the spermatozoa are released from the thick and solid cortex which encloses them. It appears possible that the fluid in the vesicles may be released when the spermatophores are received and that it may have a softening action upon the cortex. Certainly some such action, however it may be produced, takes place; for in one of the fish examined which had very recently copulated and in which there were several gallons of spermatophores present in the uterus and vagina, the softening process had already started. The spermatophores filled the common and paired vaginae, and extended up into the uteri well into the region of the trophonemata. The lower part of the mass consisted of unchanged spermatophores, but the upper part, in the uteri, was gelatinous, sticky and stringy, the separate identity of the spermatophores being lost, and the farthest conical end of the mass degenerating into a slimy jelly. The surface of the mass in contact with the walls of the paired vaginae was also becoming gelatinous. The trophonemata in the uterus of this fish were luxuriantly developed and there was much vascular congestion. A consideration of these conditions shows that it is improbable that the softening of the spermatophores is caused by any secretion from the male, for instance, from the clasper glands, for the softening would be expected to occur evenly throughout the mass, since any such male secretion would be more or less evenly distributed through it.

In the lower part of the oviduct the thick fibrous pads forming the lateral walls of the common vagina are of interest. Their function is to provide anchorage for the claw on the clasper of the male, and they have every appearance of being an intrinsic part of the vagina, and not of having been produced as a sort of scar tissue in response to the laceration caused by the claw. Scars and lacerations were present in this position in all the female fish examined, but, though large, they were not such as to give the impression that the pads are a consequential production. At the posterior end of the common vagina the circular hymen is low and even, and is much too small to provide any effective closure of the passage. It appears very improbable that it is punctured by the myxipterygium of the male as was suggested by Widakowitch (1908) for *Torpedo* and Friedman (1935) for the skates.

3. *Breeding cycle*

The reproductive cycle of *Cetorhinus* is undoubtedly correlated with the seasonal migrations of the fish. Basking sharks appear in considerable numbers off the west coast of the British Isles from the Scillies to the Orkneys during April, and remain among inshore waters throughout the summer. They are most numerous during May and June, after which their numbers decrease, although they are usually sufficiently numerous to make commercial fishing profitable until September. They are said to be seen regularly off the Norwegian coast in May and June, and also to be quite common in the Pacific off the coast of British Columbia, where there is a similar spring inshore movement. Nothing is known of where the sharks may go when they leave the coasts, nor whether their migration is horizontal or vertical, or both. The fish appear at all points along the coast at about the same time and there is not a shred of good evidence to indicate any migration from south to north, or in the reverse direction later in the season, although such migrations are often spoken of, for example, by Darling (1947), as though they were ascertained fact. The account given by this author is based upon the results of the 1946 fishing season, when the weather was very bad and unsuitable for hunting or basking, during most of July and August. In the 1947 season the weather was better and hunting was successful throughout the summer. Basking sharks are captured commercially by harpooning them as they swim at the surface with the dorsal fin exposed; they are rarely caught in the fishing gear commonly employed in European seas. It is therefore only when they are basking that their presence becomes known, and since they bask only when the weather conditions are suitable it is possible for large numbers to be present some depth below the surface and yet for them to be entirely overlooked. A calm sea and bright sunny weather give the optimum conditions for seeing the fish. Although large numbers of *Cetorhinus* are seen close inshore during the summer they are by no means entirely absent in the winter; in fact, the earliest attempts at a scientific description of the anatomy of this fish were made with sharks captured in the English Channel in November and December (Home 1809, 1813; de Blainville 1811). A male fish 28 ft. 10 in. long was stranded off Shanklin Chine, Isle of Wight, in February 1875, and its skin was purchased by the British Museum (Hadfield 1875); a recent record is of four Basking sharks seen off the Argyllshire coast near Cambletown on December 18 (Anon. 1948).

The sex ratio of the fish in the commercial catch is peculiar, females being very much more plentiful than males. There is no reason to suppose that the commercial catch is not a random sample of the fish basking at the surface, but it does not follow that this is a random sample of the total population, indeed, it is practically certain that it is not. No exact records are available of the numbers of the sexes in the catches at the commercial fishing stations, but an estimate has been made (Watkins 1948)* that one male is captured for every thirty or forty females. It is all the more surprising then to find that all the four fish examined by Home (1809, 1813) and de Blainville (1811) which had been captured during the winter were males, and to find that de Blainville says 'up to the present no one has ever seen a female individual...'. This remark is not quite correct for Pennant (1769) had alluded to one, though he gave no description of it; but it is possible that these records

* A. T. Watkins, Scottish West Coast Fisheries, Ltd. (private communication).

may point to some sort of seasonal segregation of the sexes. It may be recalled that in some elasmobranchs, for example, in *Squalus scanthias*, the shoals in which the fishes occur usually consist entirely of individuals belonging to one and the same sex. It is possible that shoals of this composition are those of sexually immature fish, but the point does not appear to have been definitely decided.

It is probable that the basking habit of *Cetorhinus* is in some way connected with the breeding season. All the adult fish examined in the field during the course of the present study were in breeding condition and showed signs of having recently copulated. One of the females contained a large quantity of spermatophores, and though none of the others contained visible sperm they all bore recent and unhealed lacerations on the pad-like lateral walls of the common vagina, lacerations produced by the claw on the clasper of the male during copulation. In addition, both males and females carried abrasions of the skin in the neighbourhood of the cloaca, minor injuries which one can only suppose were produced by contact with the roughly denticulated skin of a partner during pairing. There are no records to show how long the breeding season may last, but the present observations show that it is in full swing during the second half of May off the west coast of Scotland. In many elasmobranchs breeding takes place at any time of the year and there is no restricted season. This may be true also of *Cetorhinus*, for de Blainville (1811) remarks that the males, caught in the winter months, which he and Home had dissected 'have always been found to have the organs of generation engorged with seminal fluid....'

Very little has been added to our knowledge of the pairing of elasmobranchs since Bolau (1881) made his observations on the copulation of *Sciliorhinus* and showed that the male entwined his body round that of the female in a very unexpected manner. It is probable that similar contortions accompany pairing in other elasmobranchs, and that the dorsal spines present in some species then function literally as claspers, but it is less likely that much entwining occurs with the rather rigid body of *Cetorhinus*. While hunting sharks in the Minch off Barra in June 1947 the writer was able to observe at very close range a group of sharks that were behaving in a peculiar manner. When basking the sharks usually follow a more or less straight course, cruising slowly along with the dorsal fin and the tip of the tail projecting above the surface of the sea, the mouth widely open and the gills expanded by the water flowing through them. But the fish in this group, which numbered three or perhaps four, were swimming rather more rapidly than usual and were following each other closely in a circular course of narrow radius. One or another sank completely beneath the surface at short intervals, making it difficult to be sure of the exact number of fish present; not more than three fins appeared above the surface at any one moment. The writer gained the impression that this performance was a preliminary to pairing; it certainly was widely different from the usual basking, but further observation was unfortunately cut short by the necessity of harpooning a fish before the opportunity to do so was lost. It can, however, be definitely stated that in *Cetorhinus* one clasper only is inserted at a time into the vagina of the female. In the present series of fish, no. 3 had healed scars on both sides of the common vagina, and a fresh laceration on the right side; no. 5 had a recently healed laceration on the right side; no. 7 had a fresh unhealed laceration and two older wounds in which scar tissue was beginning to be formed on the left side; and no. 9, the female which contained the mass of spermatophores, had on the right side a single very fresh and

still open laceration 25 cm. in length and about 1·0 cm. in maximum depth. These findings prove that both claspers are not used simultaneously.

Cetorhinus exhibits the paradox of having an ovary containing immense numbers of small yolky eggs, and a uterus thickly lined with trophonemata—a condition which cannot conceivably serve any other function than producing viviparous young. The writer believes that the species is viviparous, but there is very little evidence beyond that of morphology to support this view. Graham Kerr (1919) mentioned that *Cetorhinus* is viviparous, but it is not clear upon what evidence his observation is based; Pennant (1769) said, 'They are viviparous, a young one about a foot in length being found in the belly of a fish of this kind'. But this appears not to be his personal observation, for he made his statement in general terms and then immediately gave the measurements of one that he 'found dead on the shore of Loch Ranza in the Isle of Arran'. Carazzi (1904) examined an immature female Basking shark 3·37 m. long from the Mediterranean, and because he could find no nidamentary gland he concluded that the species is 'probably viviparous'. These three statements appear to be the only ones in the literature upon the subject. The writer was informed by one of the fishermen engaged in hunting sharks that he remembered, some years ago, that a female shark was opened which contained a young one about 6 ft. long; but his recollection of the particulars was not clear. The proprietors of the two Scottish shark fisheries have never seen female fish which contained recognizable embryos. By analogy with all other elasmobranchs, viviparous or oviparous, in which the ripe egg is known, it might be suggested that all the fish examined in the present study contained only immature ova, for the typical elasmobranch egg is large and yolky. Even in the Greenland shark, *Somniosus microcephalus*, which for long was thought to lay minute eggs, Jungersen (1899) has shown that the ripe ovum is as large as a goose egg.* It is improbable that only unripe eggs were present in the fishes examined, for evidence has already been given to show that they had recently copulated, and the contents of the ovary in the female which had only just done so were indistinguishable from those of the other females.

It is obvious from the particulars set out above that if *Cetorhinus* is viviparous the females must desist from basking at the surface as soon as pregnancy starts, or at least before any embryo reaches a recognizable size. There is no evidence to show whether they depart from inshore waters or whether they merely descend to a depth where they are inaccessible to hunting. Wherever they go they do not return to the surface near the coast until after the birth of the young and until the onset of the next breeding cycle. There is, of course, no information about the length of the gestation period, but if it bears any close resemblance to that in other viviparous elasmobranchs, for example, *Squalus acanthias*, where it lasts about 22 months (Hisaw & Abramowitz 1939), there is little probability that breeding can recur every year. In the literature there is only one record of the occurrence of a Basking shark less than 6 ft. long, that of Day (1880–4), who noted one $5\frac{1}{2}$ ft. long taken in July.

* As a result of a misinterpretation of observations made in dissecting an immature female *Somniosus*, Turner (1873) announced that there are no oviducts in this species and suggested that minute eggs are discharged through the abdominal pores and that fertilization is external. Five years later, after making further dissections in which he found the oviducts, he corrected these mistakes (Turner 1878) and repeated his correction later (Turner 1885); but, notwithstanding, these errors have been copied and repeated many times by other authors, even by Felix (1906) and even to the present day (Budker 1947). The large yolky eggs of *Somniosus* are fertilized internally as are the eggs of all other elasmobranchs.

Watkins (1948) states that in the shark fishery based at Carradale, Argyllshire, a young one of less than 6 ft. in length has never been seen. The statement, unreliable as it may be, received quite independently from a fisherman that the length of a foetus in a pregnant fish was about 6 ft., does agree with this; and it appears probable that sharks about 6 ft. long are the young of the year. So too would be the fish 9 ft. long recorded by Day (1880–4) from Mounts Bay in June 1870, the one 10 ft. 1 in. long mentioned by Cornish (1885) from the same locality at the end of July 1885, and the one 3·25 m. long noted by Pavesi (1878) from Savona in June 1877. In August 1948 an immature fish about 15 ft. long was examined on the north coast of Skye, and the conclusion seems justified that this fish was in its second

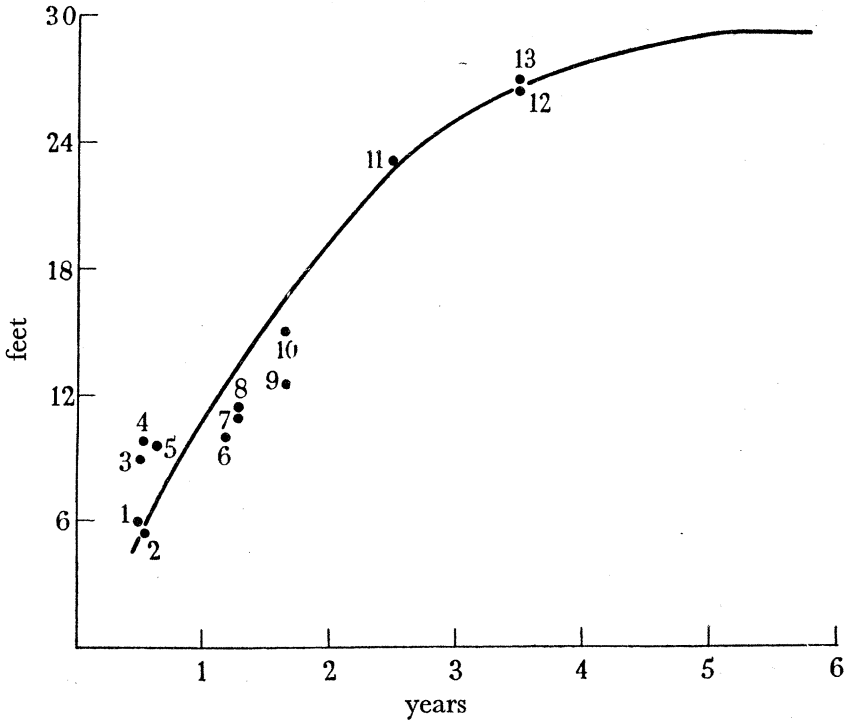

FIGURE 24. Suggested growth curve of the Basking shark. Overall lengths plotted against years of life. The part beyond 4 years obtained by extrapolation. 2, 3, Day (1880–4); 4, Pavesi (1878); 5, Cornish (1885); 6, Pavesi (1874); 7, Gervais (1876); 8, Carazzi (1904); 9, Platt (1937); 10, Skye.

year. A slightly younger age would be assigned to the female fish 3·37 m. (11 ft.) long examined by Carazzi (1904) in Sardinia (May); this fish contained 'very small ovaries' [epigonal organs?] which showed no macroscopic traces of ova. The fishes described by Pavesi (1874) as 2·95 m. long in April, by Gervais (1876) as 3·65 m. long in the same month, and by Platt (1937) as 12 ft. 7½ in. long in August, would similarly be yearlings. This classification would imply a fast but not unreasonable rate of growth. Whether this growth rate would continue and bring the fish to the length at which sexual maturity is attained by the following year is uncertain, but if these values are plotted against a time scale as in figure 24 a plausible growth curve is produced. Point 11 plotted on this curve is derived from the length of a fish measured at Soay in June 1947; this was a male 6·22 m. in length which was just approaching sexual maturity, for though the testis was showing incipient activity the ampullae of the ductus deferentia were rather small, completely empty of spermatophores and showed no signs of having contained any. Point 12 is derived from the

average length of three fully adult male fish in vigorous sexual activity measured at the same place and time, the average length from the tip of the snout to the base of the caudal emargination being $7{\cdot}12 \pm 0{\cdot}16$ m. Point 13 is derived from the corresponding measurement in five females, the value being $7{\cdot}24 \pm 0{\cdot}116$ m., and indicating that the females tend to be slightly larger than the males, a common sexual dimorphism in elasmobranchs. In order to make the last three points comparable with the preceding ones, which are overall length, it is necessary to add about 1 m. to the figures, and this has been done in the graph. Extrapolation from this curve shows the attainment of the maximum length of 29 ft. towards the end of the fifth year. In the absence of adequate data this curve is presented in the most tentative manner as a possible representation of the true course of events. It should be noted that it would be possible to fit a curve of much less slope to the points for the first two years, but this would necessitate moving the points for the third and fourth years one year to the right. The curve shown therefore represents the least possible time for the attainment of maturity.

From a consideration of the particulars recorded above it may be concluded that most of the fish which approach the western coasts in summer and are seen basking at the surface are non-pregnant females in at least their third year of life, that their presence inshore is connected with the behaviour-pattern associated with breeding, and that when they have become pregnant they withdraw, not to reappear until a subsequent season, after the young have been born.

Summary

Practically nothing has hitherto been known of the reproductive anatomy and physiology of the Basking shark, no work having been published on the subject since the first incomplete reports over 130 years ago.

The testes are embedded in the anterior ends of the epigonal organs which form an investing cortex round them. The testes are divided into lobes, and these into lobules which contain many ampullae. Testis tubules lead the spermatozoa from the ampullae to the vasa efferentia, whence they pass through the ductuli and ductus epididymidis to the enormous ampulla ductus deferentis, where they are incorporated in spermatophores.

The ampulla ductus deferentis contains numerous transverse septa, each with an eccentric perforation; successive perforations form the lumen of the organ as a whole. Spermatic fluid enters the ampulla ductus deferentis and becomes broken up into small aggregations which pass into the pockets between the septa. Here they are rotated by ciliary action while the secretion from the deeper epithelial cells is laid down round them in concentric layers. The spermatophores are up to 2·0 to 3·0 cm. or more in diameter and consist of a translucent hyaline cortex surrounding an opaque core of spermatozoa. Several gallons of spermatophores are present in each ampulla.

The skeleton of the clasper is comparatively simple in structure, the cartilages being few in number and forming a scroll proximally and a groove distally. There is a movable style towards the distal end, armed with a sharp claw. The musculature of the clasper is reduced, the dilatator muscle being the largest. The inner surface of the clasper groove within the scroll is covered with a thick layer of glandular tissue whose secretion is produced by the swelling, degeneration and detachment of the superficial cells.

The siphons are long and wide sacs lying between the skin and the body wall on the ventro-lateral surface of the abdomen. They are connected by the siphon tubes with the bases of the clasper grooves and are invested by a thin sheet of muscle, part of m. compressor, derived from the pelvic fin. The thick epithelium lining the siphons produces a secretion by the swelling, degeneration and detachment of the superficial cells. Nothing was found in the siphons beyond a small quantity of mucoid secretion. The siphon is probably used in some way not understood for introducing the spermatophores into the female by way of the clasper groove, but the spermatophores do not enter the siphon sacs.

The epigonal organ in both sexes is alike and consists of a mass of lymphomyeloid tissue. Its function is haematopoietic, and it produces lymphocytes, leucocytes and erythrocytes.

The ovary of the right side alone is developed; it is large and enclosed in a fibrous tunica. It consists mainly of a mass of small follicles loosely held together by a small amount of connective tissue, and is penetrated everywhere by the ramifications of a system of branching tubes which derive ultimately from a pocket on the right side of the outer surface of the ovary. The ova are discharged from the follicles when they are not more than 5·0 mm. in diameter and pass through the ramifying tubes to reach the exterior through the pocket. The epithelium of the discharged follicle proliferates to form a corpus luteum, the cells of which contain large quantities of lipoid material. Most of the ova, however, are not discharged but degenerate within the follicles, forming atretic corpora lutea. Great numbers of corpora lutea atretica are present in the ovary. In an average ovary there are at least six million ova 0·5 mm. or more in diameter, a size at which there is a considerable amount of yolk already present. The ovary is thus unlike that of other elasmobranchs in which there are usually a few large ova, and in general appearance is more like that of an oviparous teleost. This is remarkable in view of the fact that *Cetorhinus* is almost certainly viviparous.

The unpaired infundibular part of the oviducts opens at the ostium abdominale and lies shallowly embedded in the liver adjacent to the attachment of the falciform ligament. It follows a course such that the ostium abdominale is brought directly opposite, and into contact with, the pocket on the right side of the ovary. Ova thus pass from the ovary at once into the oviduct and do not wander in the peritoneal cavity. The paired oviducts are applied to the posterior surface of the septum transversum and pass to the parietal wall of the abdomen where they join the nidamentary glands. Their lumina are very narrow, not more than 2·0 to 3·0 mm. in diameter, and their walls are thick and inelastic so that it is impossible for an object larger than an ovum about 5·0 mm. in diameter to pass through them, and even an ovum of this size must undergo considerable distortion.

The nidamentary gland is comparatively small and shows no subdivision into albumen and shell-secreting parts; no stored spermatozoa were found in it. An elongated narrow isthmus leads from the nidamentary gland to the enormous uterus. The greater part of the uterus is lined by innumerable villus-like trophonemata. These are based upon low longitudinal ridges and may be regarded as strap-like prolongations of their free edges. Each trophonema is supported by a central core of connective tissue and is richly vascularized; no separate glands are present upon it but the epithelial cells increase greatly in number, and become swollen with secretion, perhaps trophic in function, which they release by

becoming detached and disintegrating. In many places the proliferation of epithelial cells is so great that a solid mass of swollen cells, in which the trophonemata are partly or wholly buried, results. Numerous vesicles up to 4·0 or 5·0 mm. in diameter and containing a clear fluid may be present in the solid cell-mass. It is possible that their secretion may have a solvent action on the cortex of the spermatophores.

The lateral walls of the common vagina bear thick pads of dense fibrous tissue; in adult fish these pads bear scars or lacerations caused by the claw on the clasper of the male. The incidence of the lacerations shows that one clasper only is inserted at a time. A small but distinct hymen marks the lower limit of the common vagina.

The majority of the sharks seen basking at the surface of the inshore waters of the west coasts are non-pregnant females, and pairing certainly takes place during the late spring and early summer; it may possibly also take place at other times of the year. The basking habit, however, is probably in some way connected with the sexual behaviour-pattern, as is the annual appearance of the fish near the coast. *Cetorhinus* shows the paradox of having an ovary containing a vast number of small ova and a large uterus thickly lined with trophonemata, the first suggesting that reproduction is by spawning as in teleost fish but the second showing that it is undoubtedly viviparous. There is no record of a female fish containing recognizable embryos ever having been examined in modern times. It is evident therefore, that the female fish, after being inseminated and before any embryo is recognizable, must refrain from basking, and either swim nearer the bottom or leave inshore waters, or both.

No young Basking shark less than about 6 ft. in length has ever been recorded, and it may therefore be provisionally assumed that sharks of this length are the young of the year. A consideration of the lengths of immature sharks and of the months in which they have been recorded leads to the tentative conclusion that sexual maturity is not attained until at least the third year of life or perhaps the fourth, when the fish have reached an overall length of about 23 ft. Thereafter growth continues for another two years until the maximum overall length of about 29 ft. is attained.

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Description of plates 10 to 20

Plate 10

Figures 25 to 30, all same scale.

Figure 25. Transverse section of a testis lobe at the apices of the lobules. *IL*, interlobular tissue separating the apices; *LA*, ampulla lined with a single layer of cells all alike; no lumen; *PA*, ampulla in an early stage of development, containing a single central cell surrounded by a thin theca.

Figure 26. Transverse section of a testis lobule showing the ampullae; lumina are present and are surrounded by a single layer of spermatogonia (*G*) outside which lies a single layer of spermatocytes (*C*). *T*, a testis tubule in oblique transverse section.

Figure 27. Transverse section of an ampulla showing an outer layer of spermatocytes surrounding an inner layer of spermatogonia which are dividing to form a second layer of spermatocytes. *T*, a testis tubule in longitudinal section.

Figure 28. Transverse section of an ampulla containing several layers of spermatocytes; the spermatogonia lining the lumen are beginning to sink among the spermatocytes.

Figure 29. Transverse section of an ampulla showing the spermatogonia (*G*) migrating from a position lining the lumen to one immediately inside the outer wall. The three spermatogonia indicated on the left show stages in the migration.

Figure 30. Transverse section of an ampulla showing the increased content of secondary spermatocytes. The spermatogonia have completed their migration and have taken up their final positions next to the wall of the ampulla; they are now Sertoli cells (*S*).

Plate 11

Figures 31 to 36 all same scale.

Figure 31. Transverse section of an ampulla. The secondary spermatocytes are dividing to form spermatids. Division is complete in the upper right-hand part.

Figure 32. Transverse section of an ampulla, showing the spermatids grouped in clumps round the periphery.

Figure 33. Transverse section of an ampulla, showing the spermatids beginning to elongate to form the heads of the spermatozoa.

FIGURE 34. Transverse section of an ampulla, showing transformation of spermatids into spermatozoa; the clumps are becoming more distinct.

FIGURE 35. Transverse section of an ampulla, the heads and tails of the spermatozoa now being visible. The ends of the clumps are attached to the wall of the ampulla between the large Sertoli cells. The spiral shape is beginning to appear at the bases of the heads.

FIGURE 36. Transverse section of an ampulla, showing the clumps of spermatozoa withdrawing a little from the wall of the ampulla and becoming attached to the free ends of the Sertoli cells. The whole of each head is now spiral, and the spirals of adjacent heads are becoming arranged in phase with each other.

PLATE 12

FIGURE 37. Transverse section of an ampulla, showing the clumps of spermatozoa becoming closely aggregated.

FIGURE 38. Transverse section of an ampulla, showing the final arrangement of the spermatozoa. The clumps again lie between the Sertoli cells, and the tails lie free in the lumen. The apices of the clumps are closely aggregated, the bases less closely; the intermediate pieces (*I*) are separated, and the middle pieces (*M*) closely aggregated.

FIGURE 39. Transverse section of the core of a spermatophore recovered from the vagina of a female, showing that many clumps of spermatozoa remain intact until the spermatophore disintegrates in the female.

FIGURE 40. Transverse section of the ductus epididymidis, showing the pseudo-stratified epithelium and the loose connective tissue between adjacent loops.

FIGURE 41. Transverse section of the lower part of the ductus epididymidis, showing the epithelium raised into widely separated folds.

FIGURE 42. Transverse section of two of the folds in the lower part of the ductus epididymidis, showing that they consist of two layers of epithelium separated by an extremely thin layer of connective tissue.

PLATE 13

FIGURE 43. Longitudinal section of the upper part of the ductus deferens, showing the high internal folds covered with tall columnar epithelium.

FIGURE 44. Transverse section of one of the thinner septa from the anterior end of the ampulla ductus deferentis, showing the supporting connective tissue and the surface raised into numerous small villi.

FIGURE 45. The same, showing the pseudo-stratified epithelium with tall columnar ciliated cells.

FIGURE 46. Transverse section of one of the thick septa from the lower part of the ampulla ductus deferentis, showing the stout supporting layer of connective tissue and the surface raised into numerous villi.

FIGURE 47. Pseudo-stratified epithelium from the tip of a villus on one of the stout septa of the ampulla ductus deferentis, showing the nuclei at different levels and the tall columnar ciliated cells.

FIGURE 48. The same, more highly magnified, showing the pear-shaped drops of secretion (*S*) protruding on the surface among the cilia, and the canaliculi (*C*) penetrating between the ciliated cells to the deeper secretory ones. The outer ends only of the epithelial cells are shown.

PLATE 14

FIGURE 49. Transverse section of part of Leydig's gland. The small secretory tubules lie to the left, the large ducts to the right; there are no glomeruli.

FIGURE 50. Transverse section of part of the kidney. The tubules are in general smaller than those in Leydig's gland, and their epithelium is not so thick and glandular. Two glomeruli are seen at *G*.

FIGURE 51. Transverse section of the lining of the siphon. *B*, basal layer of the epithelium with closely packed nuclei at the base and more widely spaced ones superficially; *S*, transition layer of flattened cells with pycnotic nuclei; *D*, superficial layer of swollen cells with degenerate nuclei.

FIGURE 52. Transverse section of one of the irregular masses projecting into the lumen of the posterior cardinal sinus. *G*, ganglion cells; *L*, lumen of the posterior cardinal sinus; *W*, wall of the vessel.

FIGURE 53. Section through part of the epigonal organ. *B*, basophil cell; *E*, elongated oval oxyphil cells; *L*, lymphocytes; *O*, large oxyphil cell; *S*, medium oxyphil cell.

FIGURE 54. Section through part of the epigonal organ, showing a lymphocyte germ centre, the area containing many small nuclei at the centre of the photograph.

PLATE 15

FIGURE 55. Vertical section through the base of the clasper gland. *C*, supporting connective tissue raised into small papillae; *S*, fine strands of connective tissue arising from the papillae and extending towards the free surface through the solid mass of cells.

FIGURE 56. Horizontal section through the clasper gland, showing the strands of connective tissue (*C*) running towards the surface.

FIGURE 57. The same showing the connective tissue with some lymphoid tissue and a few vessels at the centre of a strand, and the surrounding epithelium proliferating to form the swollen cells with shrunken nuclei that make up the bulk of the gland.

FIGURE 58. Vertical section of the free edge of the clasper gland. The free edge lies to the left, and shows the secretion being formed by the degeneration and detachment of the cells. The cells of the gland are swollen with contained secretion, and the nuclei are minute and degenerate.

FIGURE 59. Section through part of the ovary, showing numerous follicles in course of development. *CL*, corpora lutea; *L*, lumina of the tubes ramifying throughout the substance of the ovary and leading to the exterior through the pocket.

FIGURE 60. Section of the ovary showing young follicles. *P*, follicle in the earliest stage containing a number of polyhedral cells packed closely together; *E*, a follicle in which one of the cells has become the central definitive oocyte; *L*, a larger oocyte surrounded by a vitelline membrane and a layer of epithelium. Some of the epithelial cells are swollen with yolk material and separate the oocyte and epithelium from the wall of the follicle.

PLATE 16

FIGURE 61. Section of a young follicle, in which swollen cells (*S*) surround the oocyte and epithelium. *E*, epithelium; *V*, vitelline membrane. Some of the nuclei and parts of the cell boundaries of the outer yolk-laden cells are still visible.

FIGURE 62. Section of ovary, showing two follicles (left and right) in which the material from the outer cells is being transferred to the oocyte. The nuclei lie centrally, surrounded by cytoplasm containing yolk material. The vitelline membrane is now thinner and is surrounded by an attenuated layer of epithelium; the yolk material of the outer cells is now confluent.

FIGURE 63. Section of an older follicle, in which the transfer of the yolk material through the epithelium has proceeded so far that the epithelium is in contact with the follicular wall over more than half the circumference.

FIGURE 64. Section of an older follicle. The transfer of yolk material is now nearly complete and the epithelium consists of more than a single layer of cells in most parts. The germinal vesicle is visible and the cytoplasm of the ovum is filled with yolk.

FIGURE 65. Section of a large follicle. The ovum has shrunk away from the follicle wall during fixation, taking with it the epithelium (*E*) which is closely applied to the thick vitelline membrane (*V*). The germinal vesicle (*G*) contains a group of nucleoli, and the staining reactions of the inner and outer zones of the yolk differ.

FIGURE 66. Section of part of a follicle wall. The ovum has shrunk away from the follicular wall, the separation being at the interface epithelium-vitelline membrane. *E*, the epithelium containing more than a single layer of cells; *T*, the theca.

PLATE 17

FIGURE 67. Section of part of an advanced follicle. The ovum has shrunk away from the follicular wall taking the epithelium with it. Part of the theca appears at the top right-hand corner; the germinal vesicle lies at the bottom left-hand corner. *E*, multilayered epithelium; *V*, vitelline membrane; *Z*, zona radiata.

FIGURE 68. Section through a young corpus luteum of ovulation. The cavity, filled with loose cells and debris, lies eccentrically to the right of the follicle; the main mass of the cells of the corpus luteum lies to the left.

FIGURE 69. Section through an old corpus luteum of ovulation. The central cavity is almost obliterated and the body is filled with loose cells among which some small vessels wander.

FIGURE 70. Section of an atretic corpus luteum. The large cavity is surrounded by the wrinkled and dark-staining vitelline membrane within which lie the remains of the degenerate ovum. At the bottom centre the epithelium is proliferating and invading the cavity pushing the vitelline membrane before it.

FIGURE 71. Section of an older atretic corpus luteum. The remains of the ovum have almost disappeared from the central cavity which is still bounded by the reduced remnant of the vitelline membrane. The epithelium has proliferated so as to fill the greater part of the body, and there is considerable invasion by vessels (the darkest parts).

FIGURE 72. Sections of an old atretic corpus luteum. The central cavity is nearly lost and the remnant of the vitelline membrane is becoming tenuous. The body consists of a nearly solid mass of proliferated epithelial cells and small blood vessels.

PLATE 18

FIGURE 73. Transverse section of the paired oviduct between the bifurcation and the nidamentary gland, showing the lumen nearly filled with longitudinal ridges, and the thick inelastic outer coat.

FIGURE 74. Transverse section of the summit of one of the ridges of the oviduct shown in figure 73, showing the epithelium with basal polyhedral cells and outer columnar ciliated ones.

FIGURE 75. Vertical section through the nidamentary gland. The base, abutting on the muscular wall, lies to the left and the mouths of the glands, opening into the main lumen, at the right.

FIGURE 76. Vertical section of the base of the nidamentary gland. The bases of the tubular glands which are closely packed and parallel to each other lie to the left against the muscular wall.

FIGURE 77. Vertical section of the nidamentary gland, showing the mouths of the glands opening into the lumen. The main lumen lies at the top, and the spiral shape of the distal ends of the gland tubules is shown on the right. The amount of connective tissue between gland tubules is much greater at this level than at the base.

FIGURE 78. Transverse section of the unpaired oviduct before its bifurcation, showing the high longitudinal folds lining the lumen.

PLATE 19

FIGURE 79. Transverse section of the proximal part of the isthmus, showing the low wide longitudinal ridges covered by tall columnar epithelium.

FIGURE 80. Section of the columnar ciliated epithelium of the proximal part of the isthmus, showing the dark-staining elongate nuclei.

FIGURE 81. Transverse section of one of the tall ridges of the proximal part of the uterus (one of the 'pages' of the 'book'), showing the minor ridges of the surface.

FIGURE 82. Transverse section of the surface of the ridge shown in figure 81. The epithelium is not ciliated, and the oval nuclei lie near the surface so that a clear sub-surface zone is not present.

FIGURE 83. Vertical section of part of the uterus with trophonemata. The muscular wall lies to the right, and the trophonemata project into the uterine lumen towards the left.

FIGURE 84. Vertical sections through two trophonemata. *C*, connective tissue strands of the core; *V*1, tortuous vessels running longitudinally inside the core; *V*, tortuous vessels outside the core.

PLATE 20

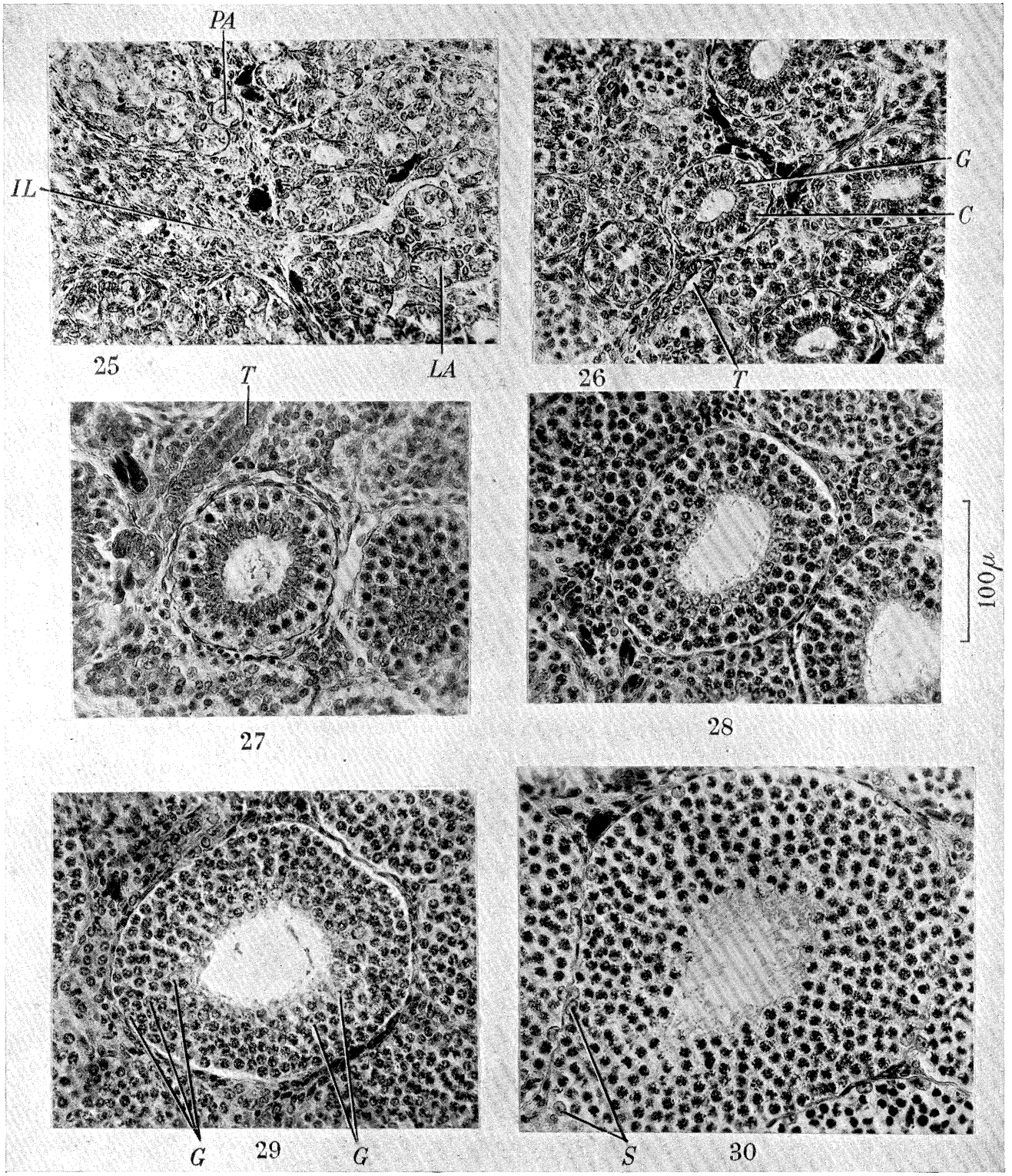
FIGURE 85. Vertical section through the wall of the uterus showing the trophonemata embedded in a mass of proliferated epithelial cells. The muscular wall lies below, the uterine lumen at the top.

FIGURE 86. Vertical section through a part of the uterus similar to that shown in figure 85. The base lies to the right, the uterine lumen to the left. The epithelial masses have shrunk away from the trophonemata which are seen as narrow strands with tortuous vessels coursing along their surfaces. The deep layers of the epithelium, adjoining the shrinkage cavities, are compact, the more superficial ones, at the centres of the epithelial masses, are swollen.

FIGURE 87. Horizontal section through part of the uterus where the trophonemata are embedded in epithelial cells, showing numerous vesicles, some lined with a layer of epithelial cells and some containing a coagulum.

FIGURE 88. Vertical section through part of the uterus, showing trophonemata, epithelial cell masses, and a vesicle in course of formation. *V*, vesicle. *C*, connective tissue strand of the trophonema from which the vesicle arises.

FIGURE 89. Horizontal section through part of the cell mass and trophonemata, showing the earliest stages in the formation of vesicles. *V*, a vesicle consisting of a few cells surrounded by a very thin layer of connective tissue; no lumen; *V*1, a larger vesicle in which the cells are swollen, and the degeneration of one cell has produced the first beginning of the lumen; *V*2, a young vesicle with connective tissue sheath, swollen internal cells, and a lumen produced by the degeneration of some of the latter.



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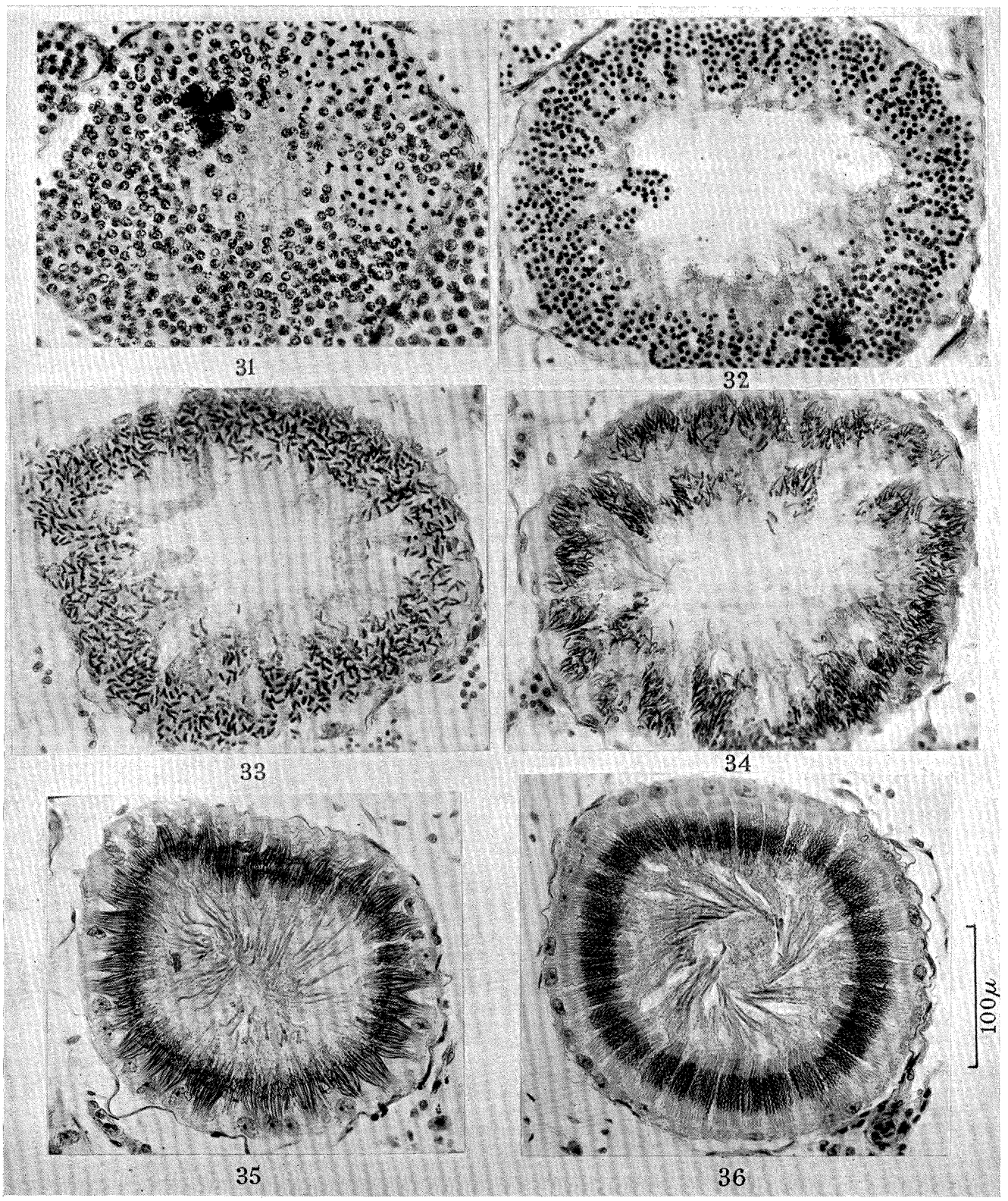
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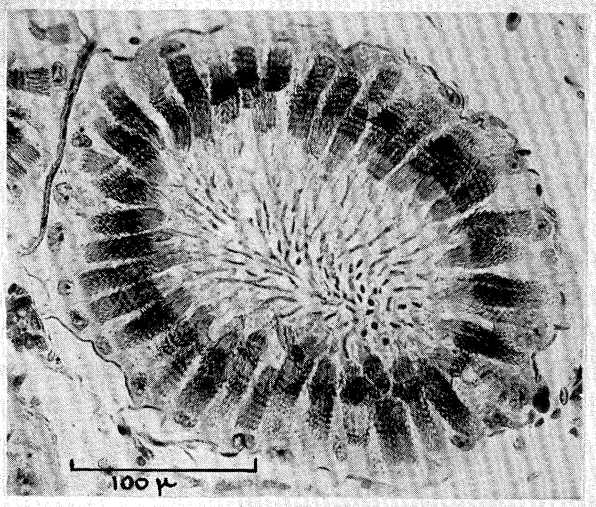

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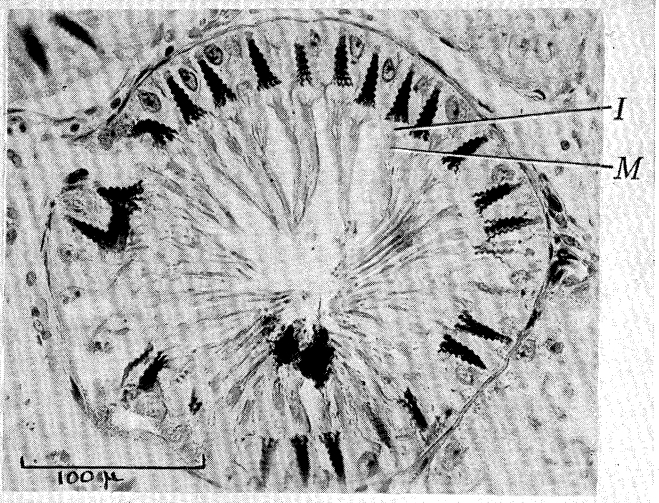

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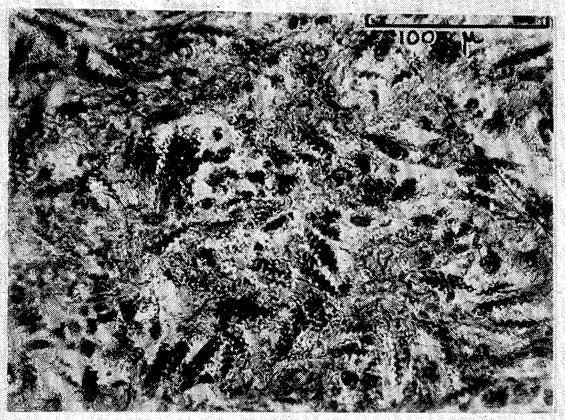

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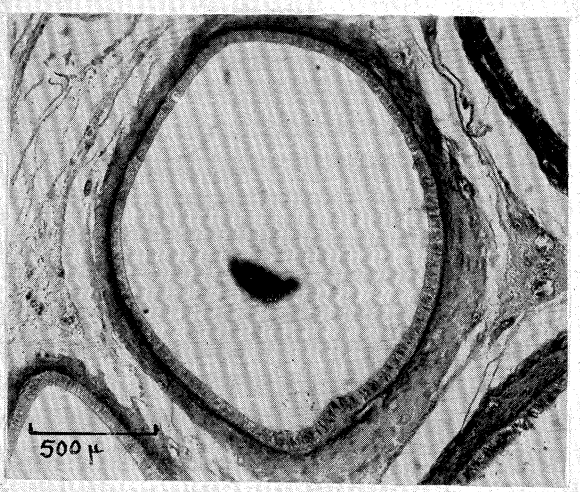

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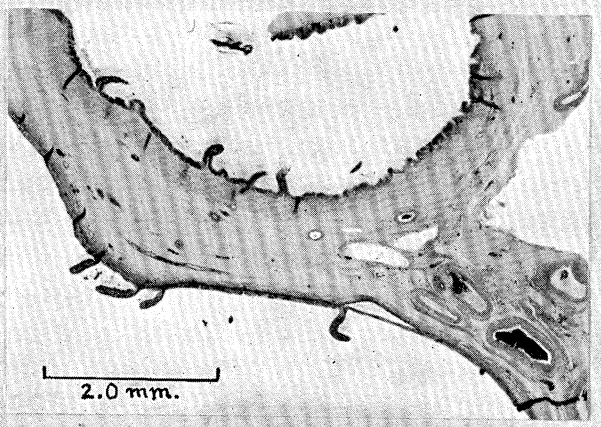

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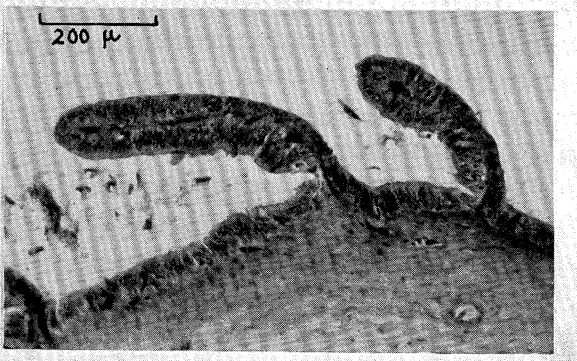

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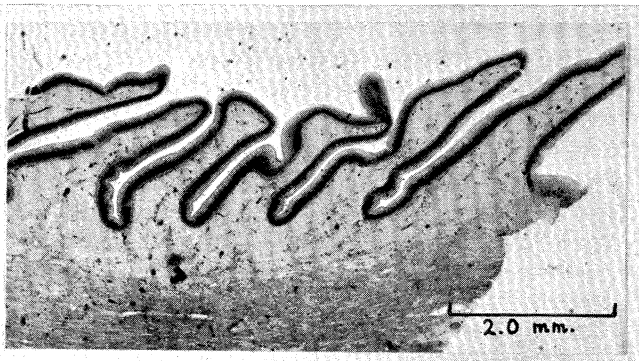

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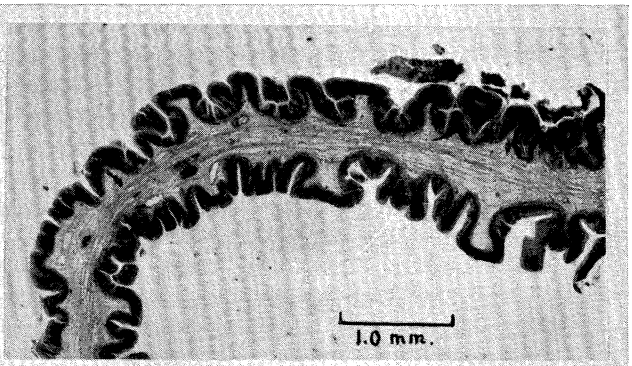

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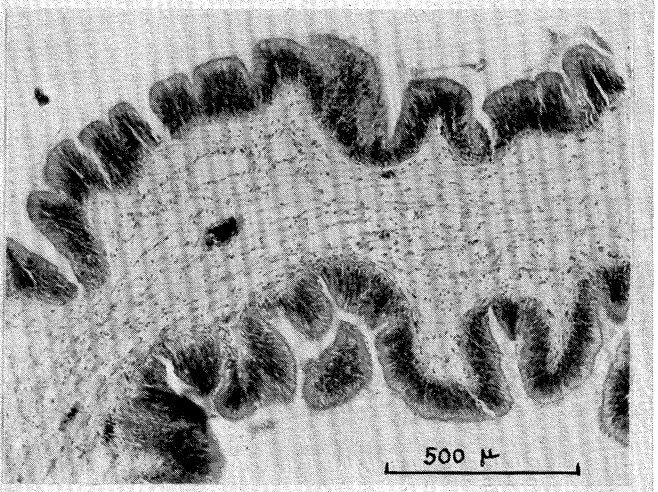

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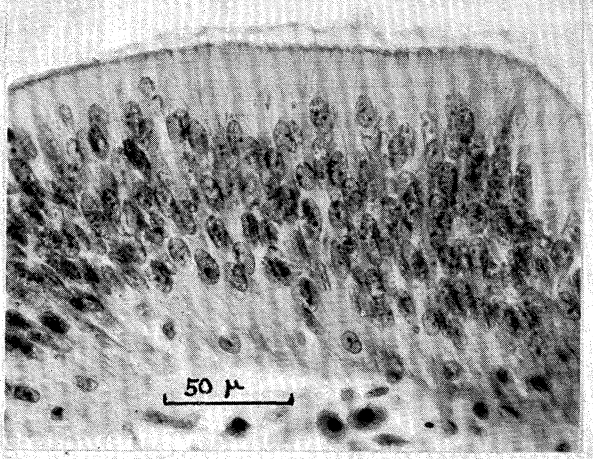

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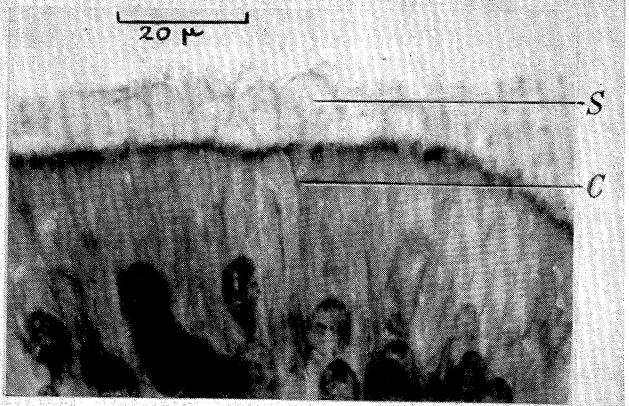

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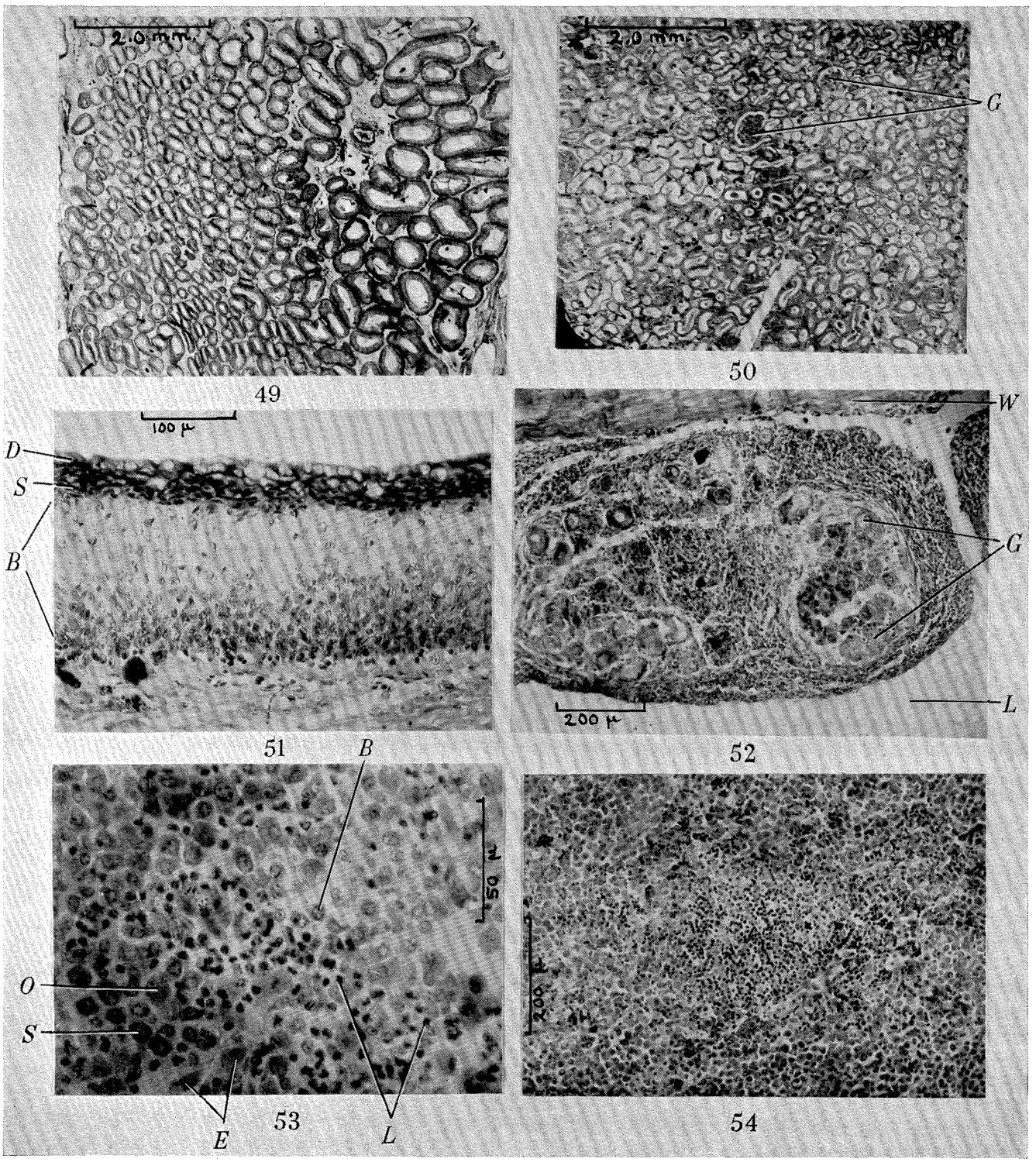
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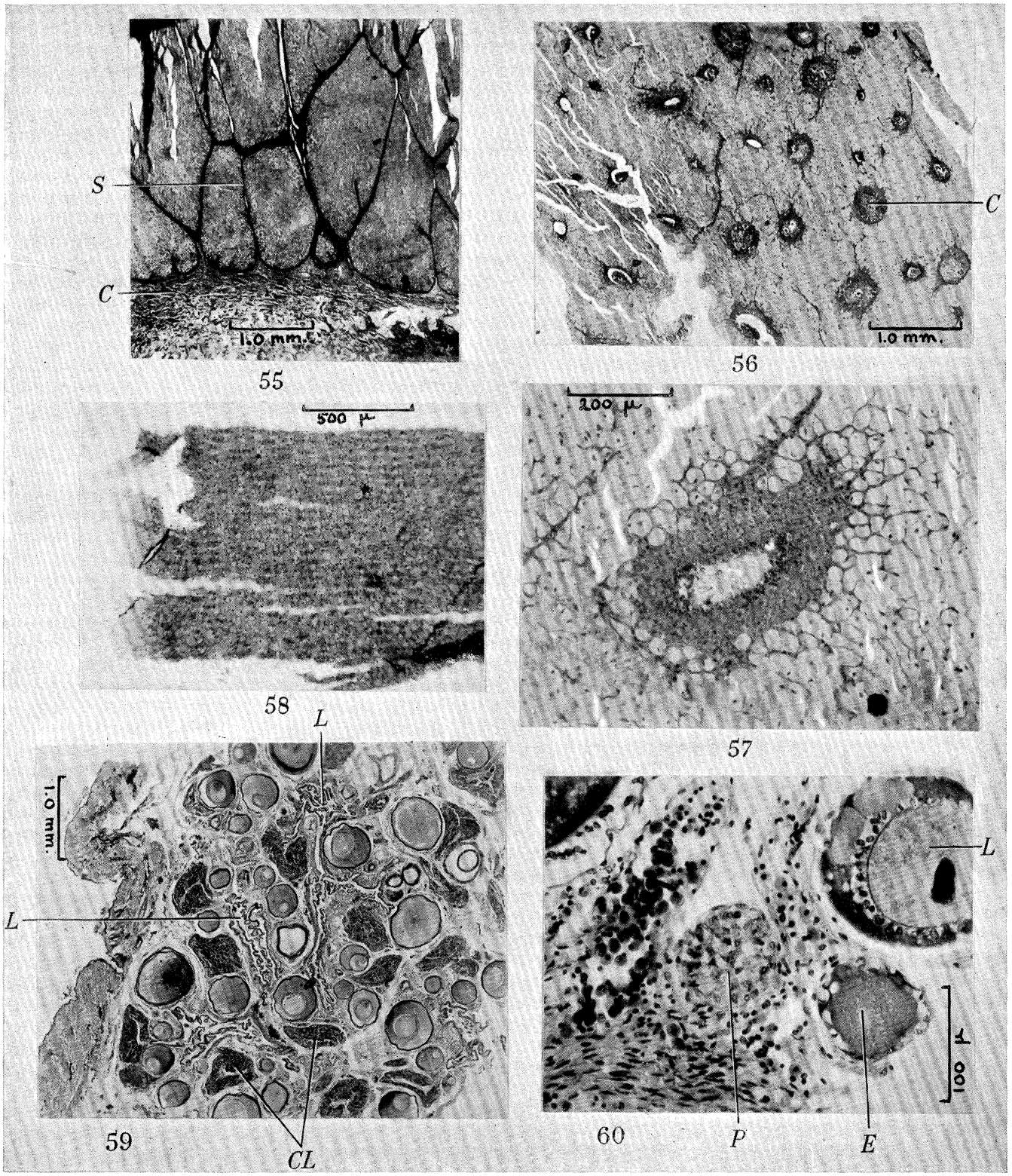
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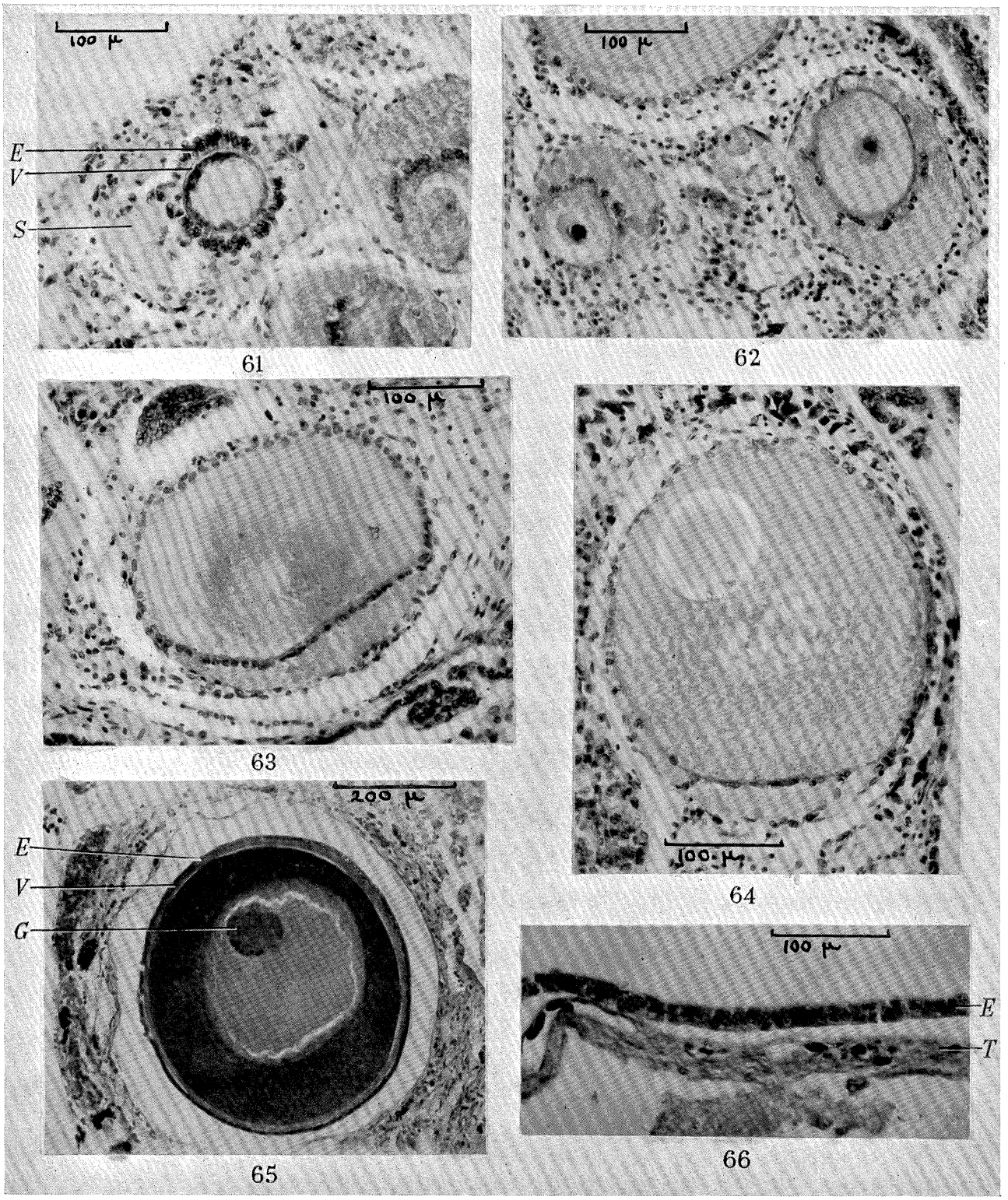
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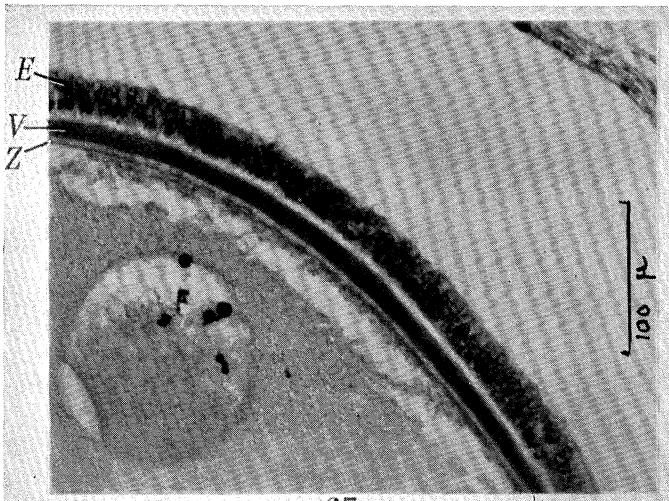

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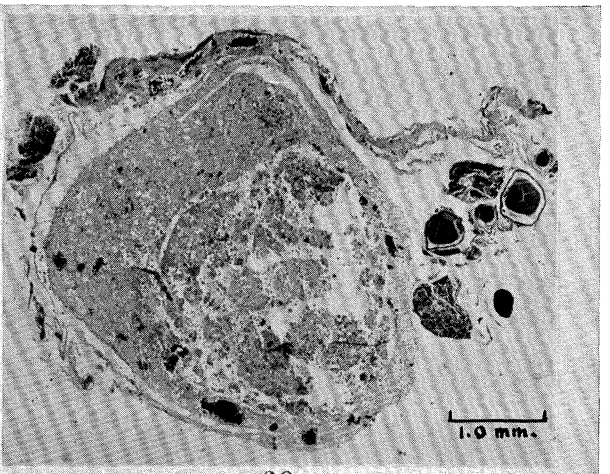

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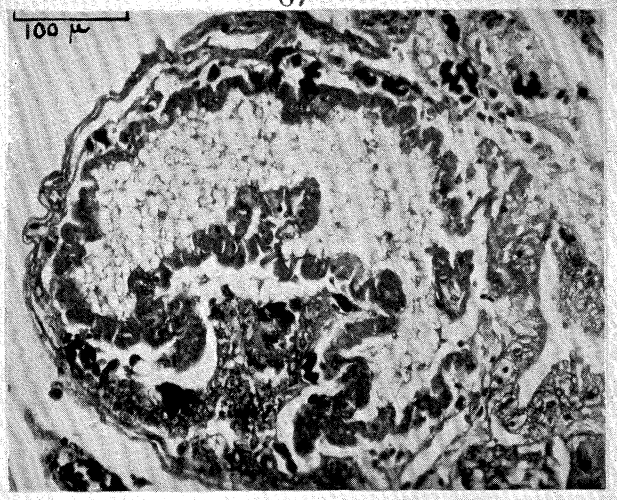

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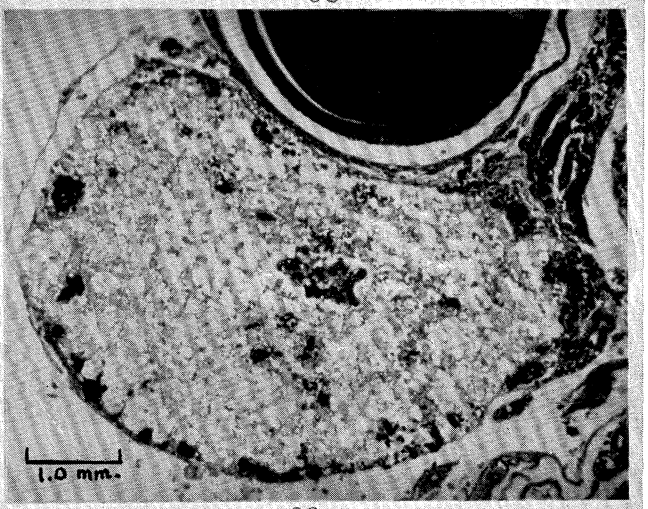

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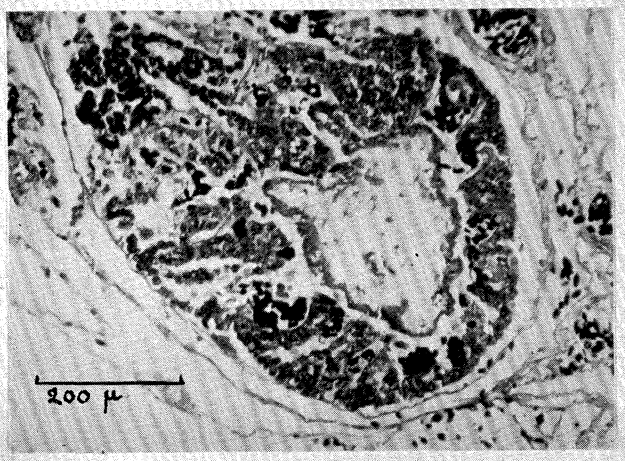

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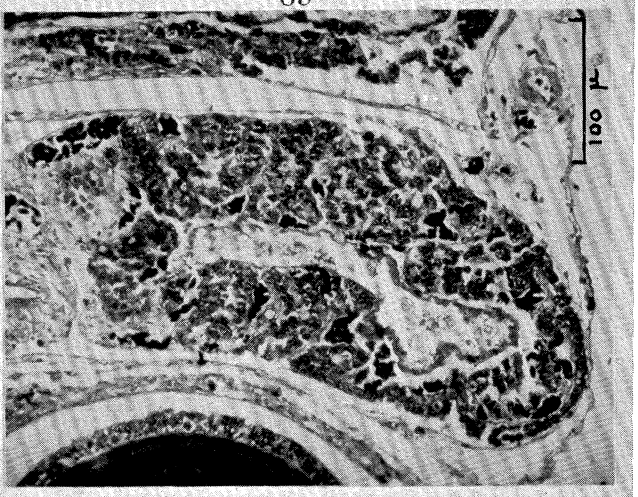

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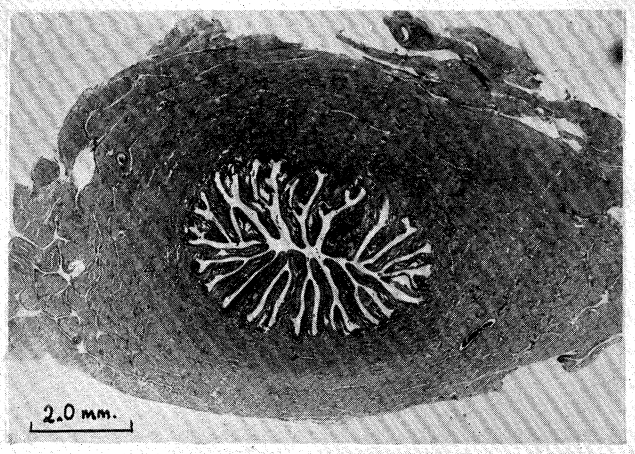

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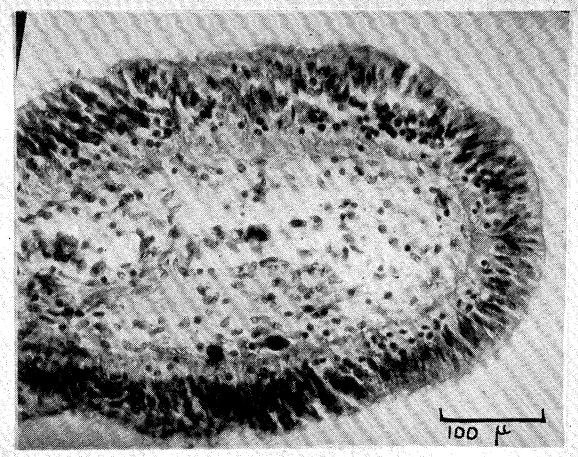

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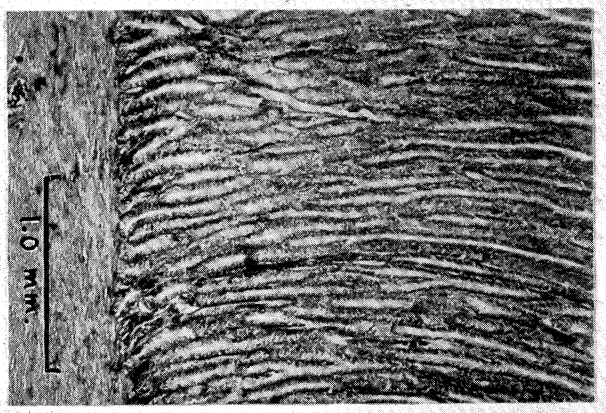

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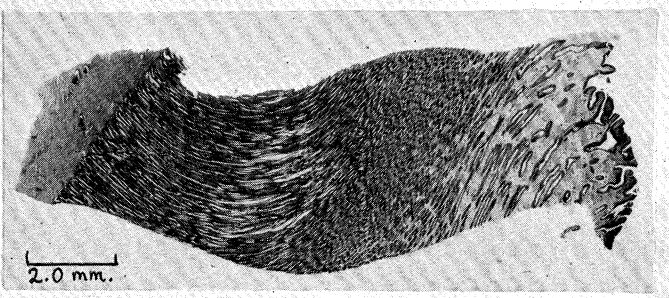

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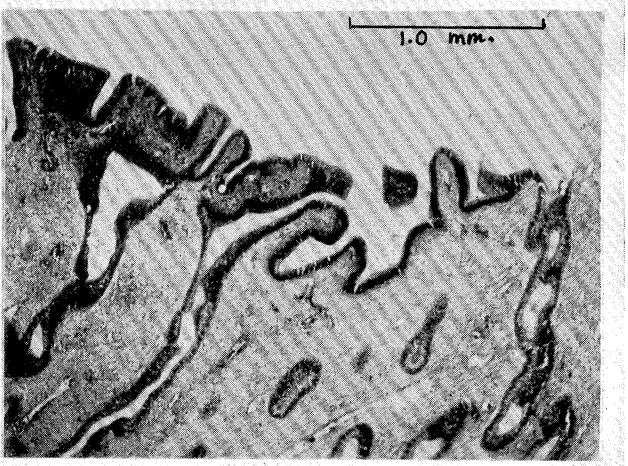

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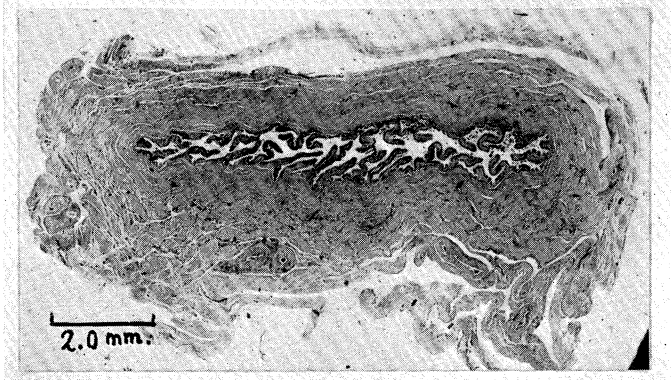

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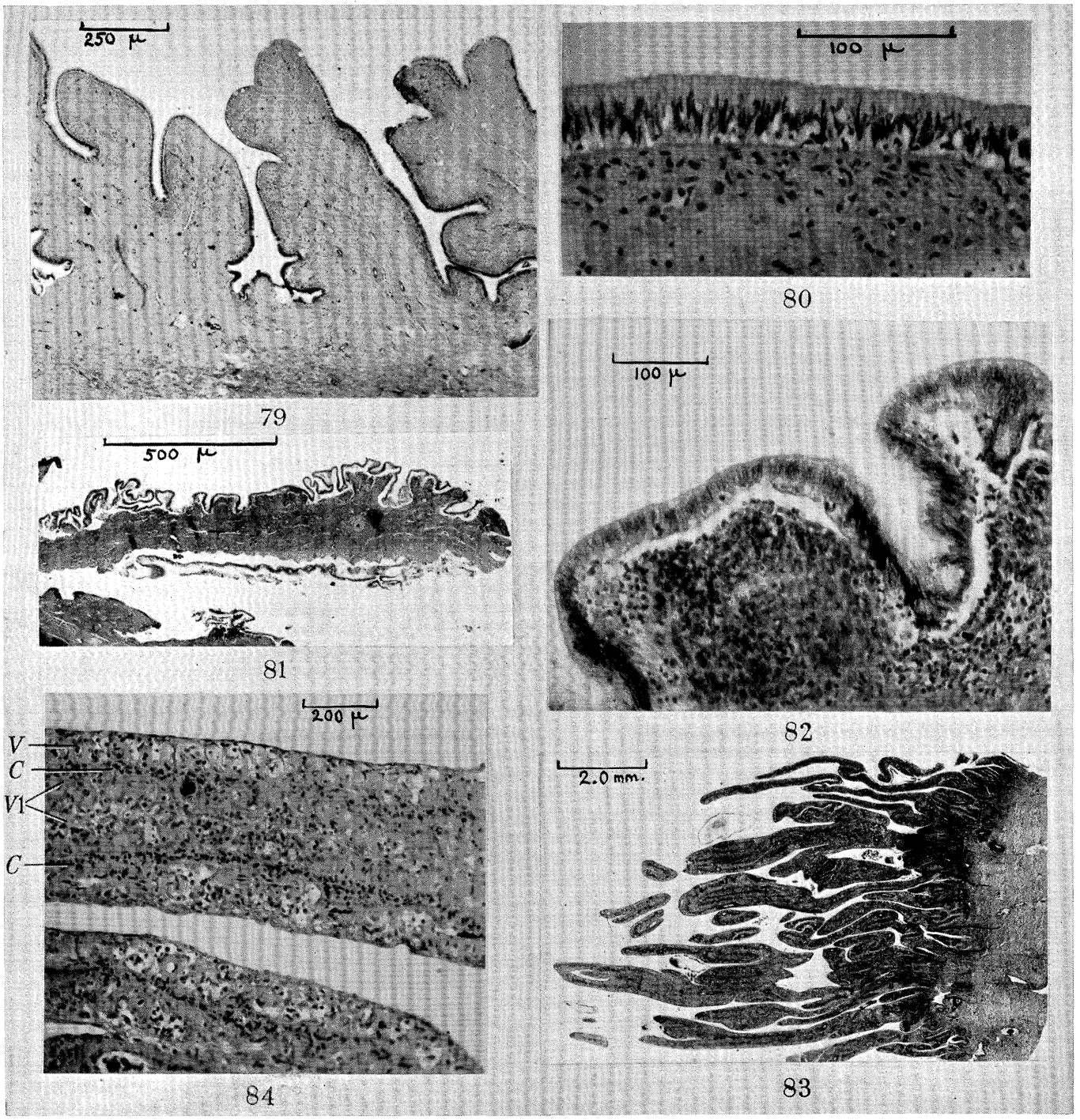
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V
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V1
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84
2.0 mm.
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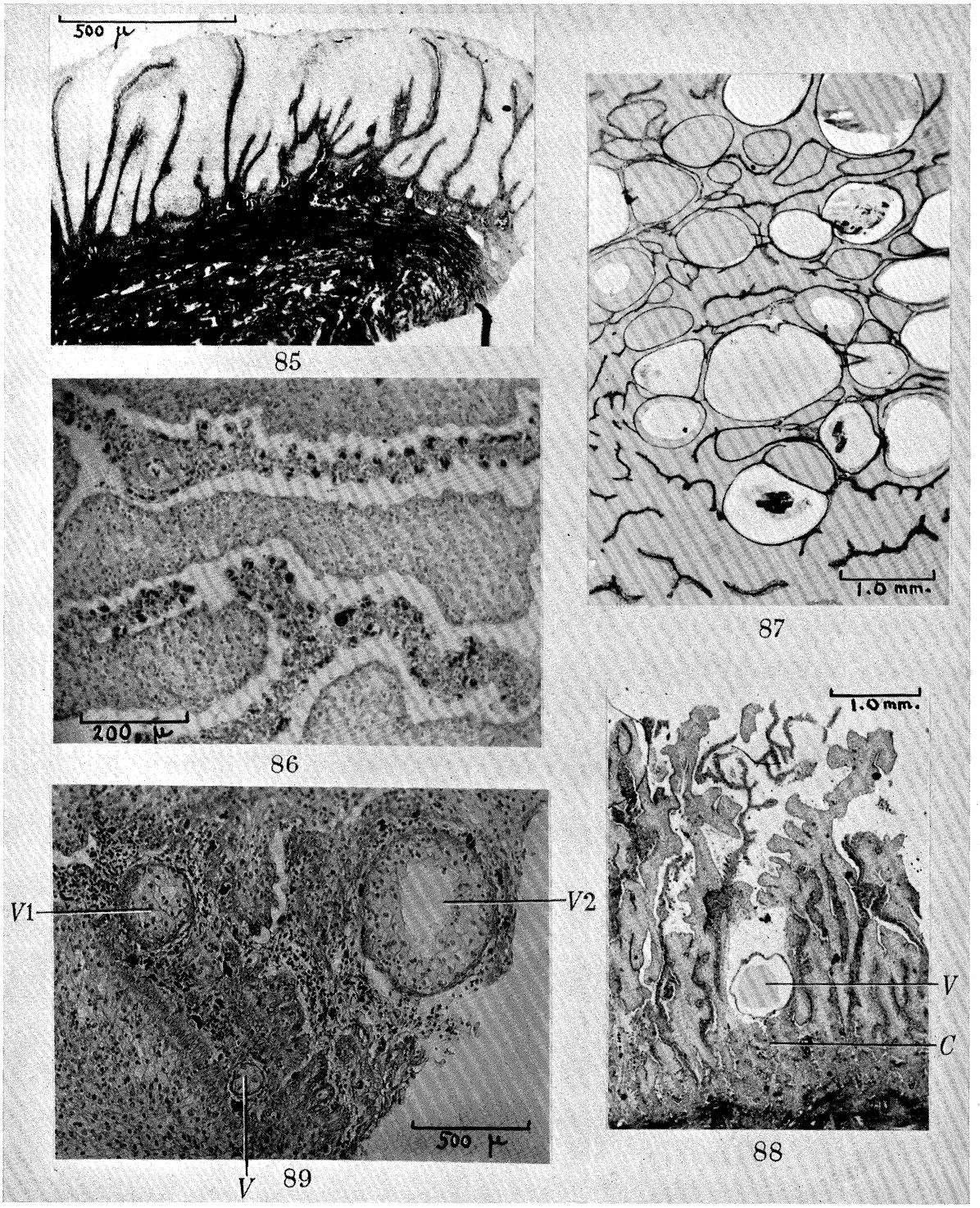
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V1
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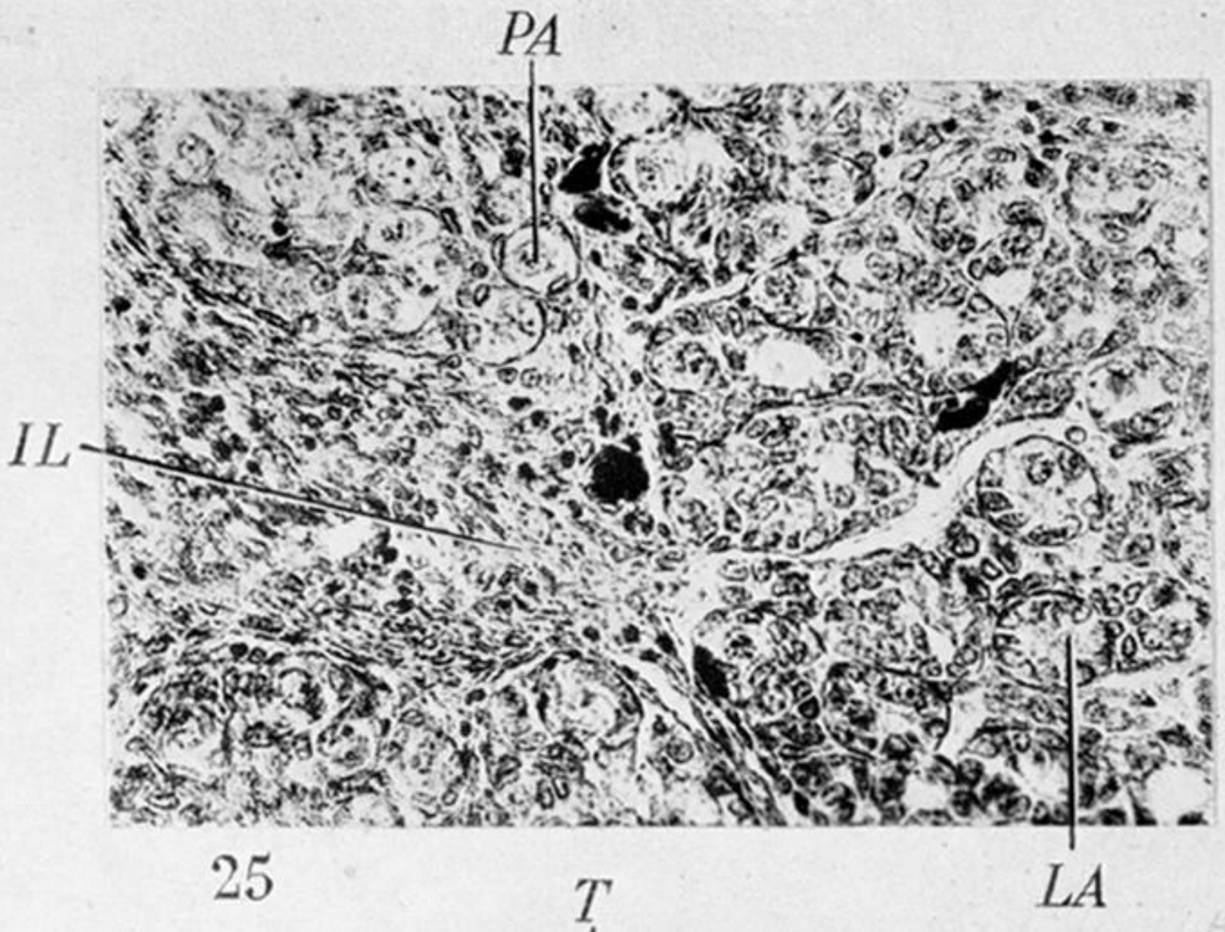

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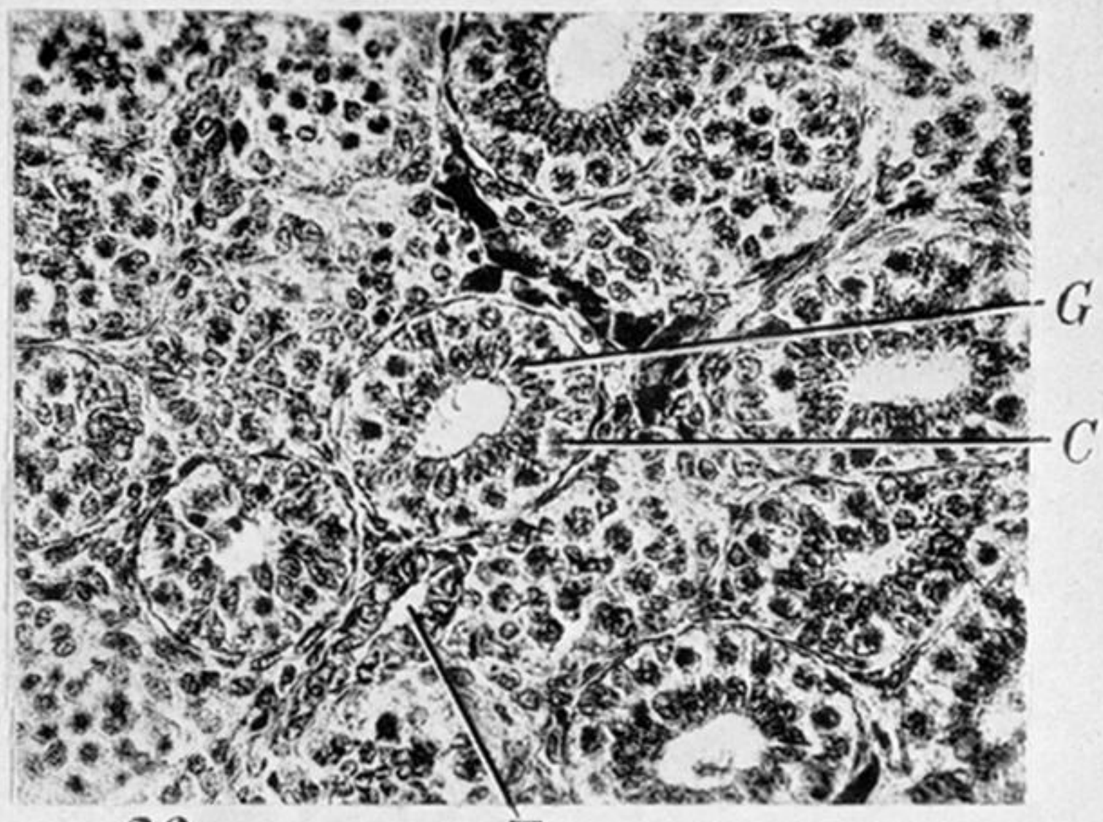

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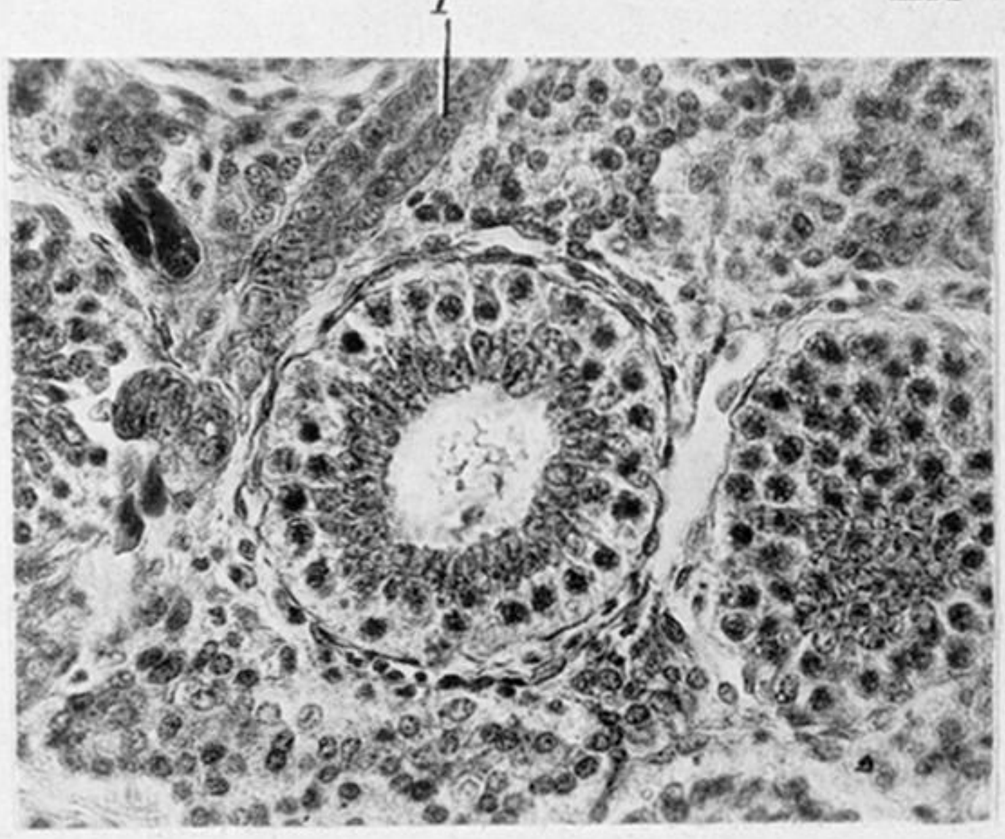

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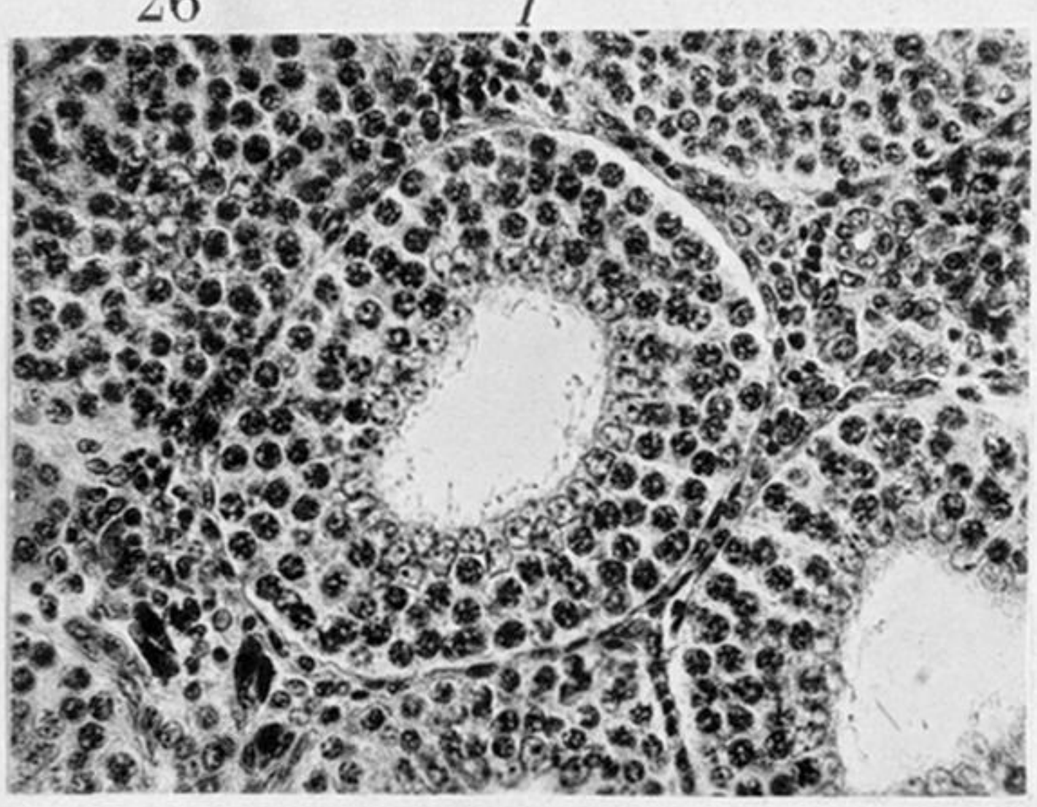

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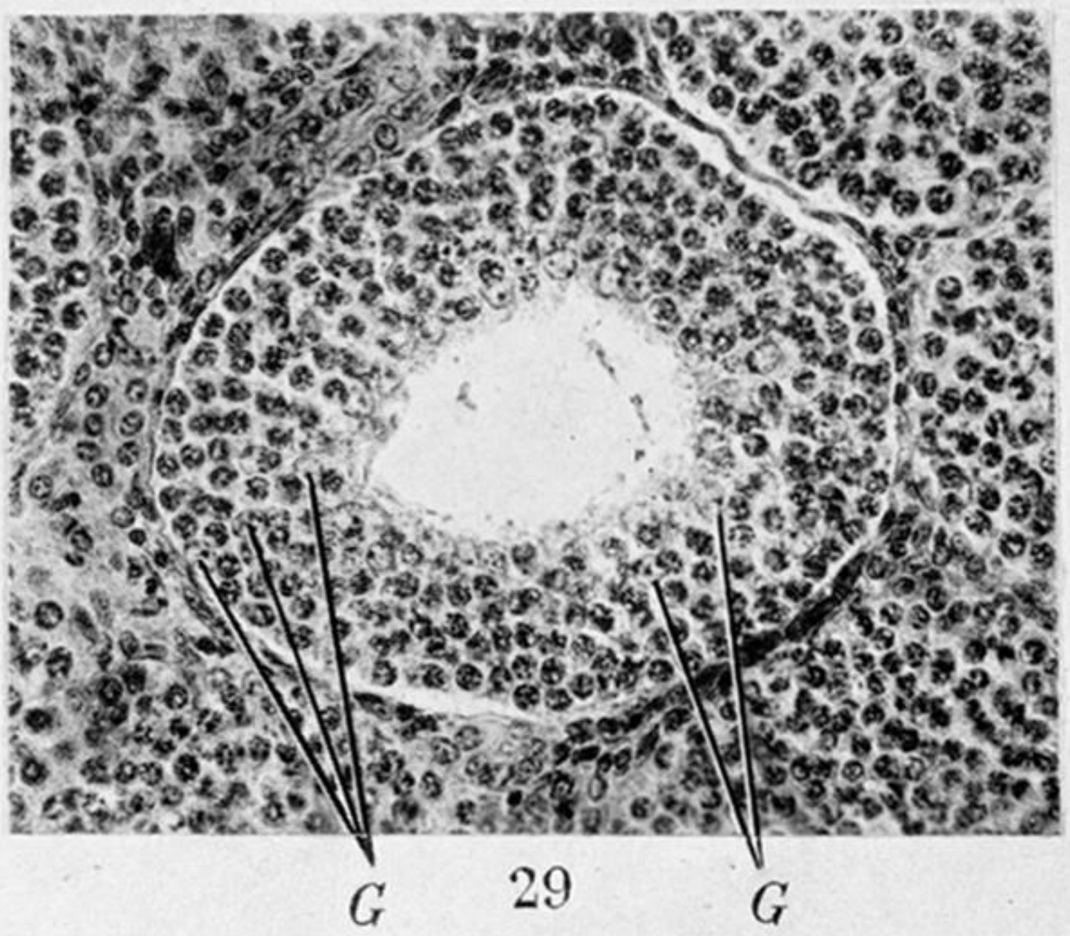
100 μ



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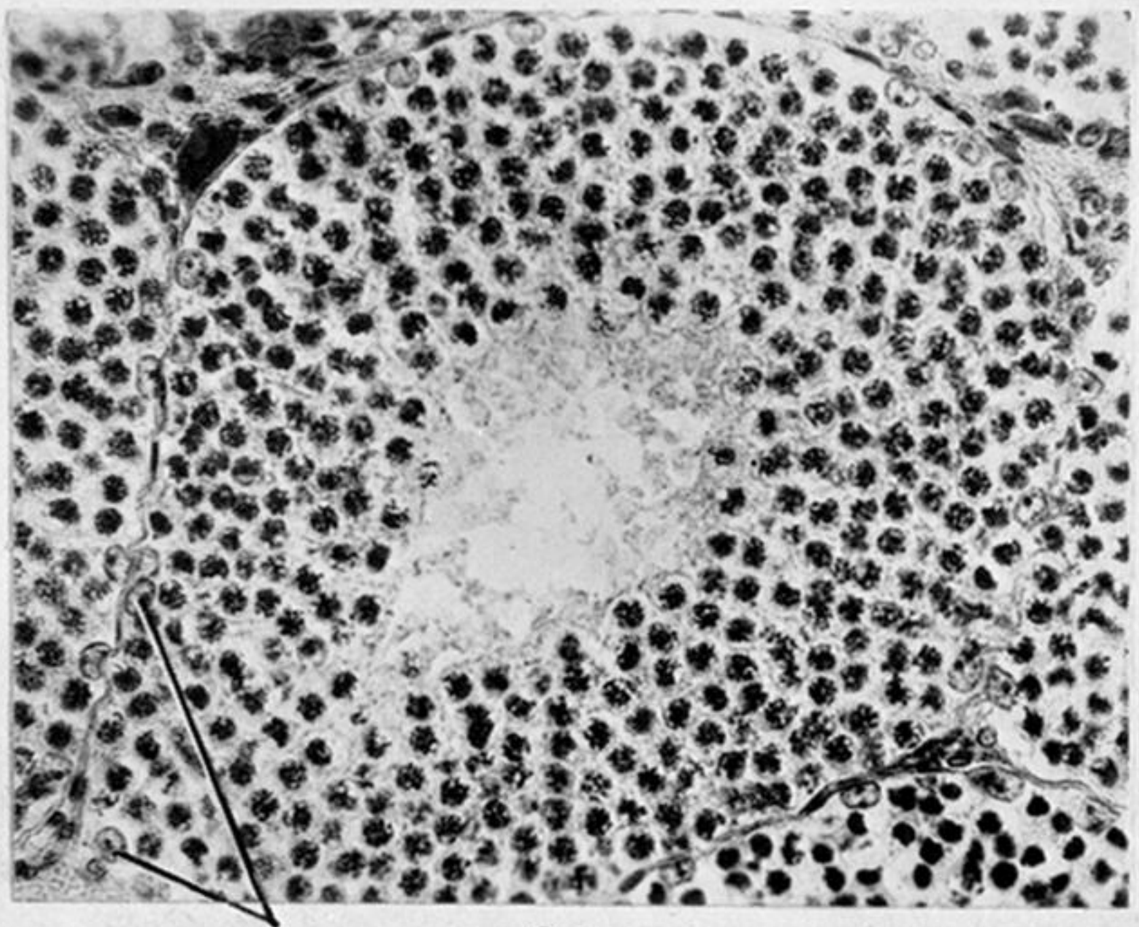


30

PLATE 10

Figures 25 to 30, all same scale.

FIGURE 25. Transverse section of a testis lobe at the apices of the lobules. *IL*, interlobular tissue separating the apices; *LA*, ampulla lined with a single layer of cells all alike; no lumen; *PA*, ampulla in an early stage of development, containing a single central cell surrounded by a thin theca.

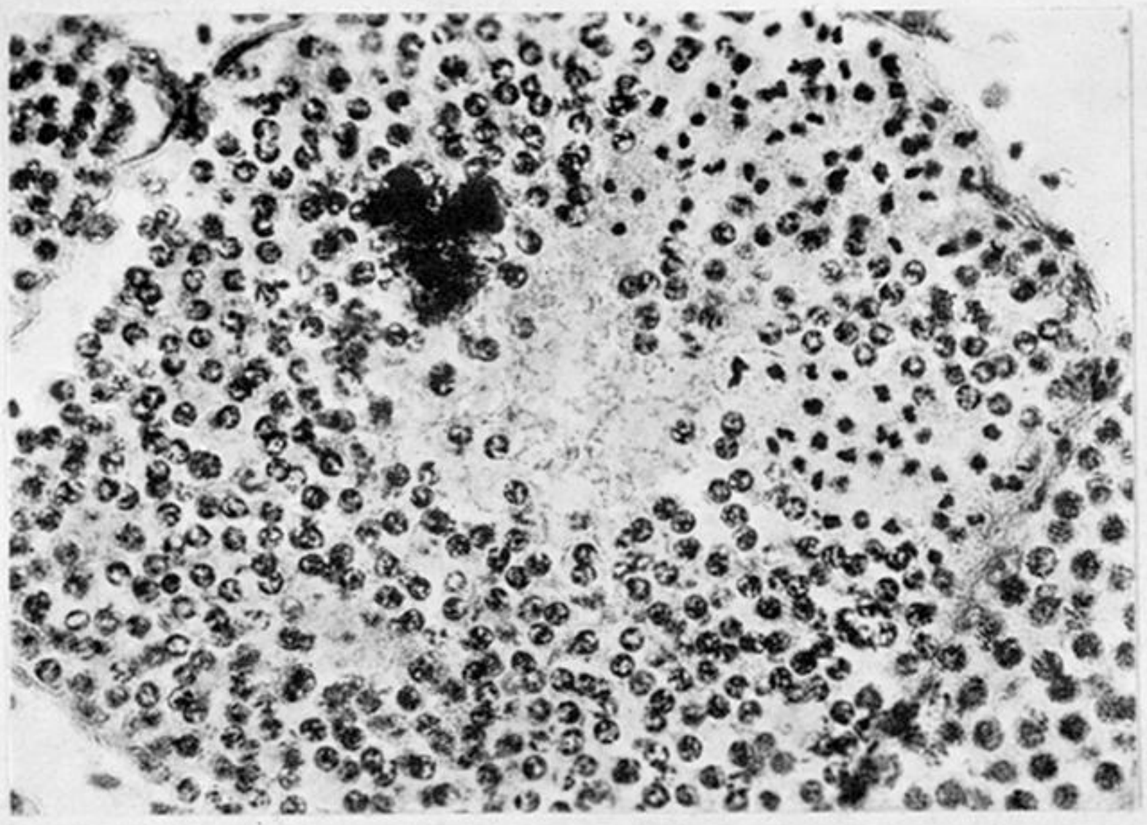
FIGURE 26. Transverse section of a testis lobule showing the ampullae; lumina are present and are surrounded by a single layer of spermatogonia (*G*) outside which lies a single layer of spermatocytes (*C*). *T*, a testis tubule in oblique transverse section.

FIGURE 27. Transverse section of an ampulla showing an outer layer of spermatocytes surrounding an inner layer of spermatogonia which are dividing to form a second layer of spermatocytes. *T*, a testis tubule in longitudinal section.

FIGURE 28. Transverse section of an ampulla containing several layers of spermatocytes; the spermatogonia lining the lumen are beginning to sink among the spermatocytes.

FIGURE 29. Transverse section of an ampulla showing the spermatogonia (*G*) migrating from a position lining the lumen to one immediately inside the outer wall. The three spermatogonia indicated on the left show stages in the migration.

FIGURE 30. Transverse section of an ampulla showing the increased content of secondary spermatocytes. The spermatogonia have completed their migration and have taken up their final positions next to the wall of the ampulla; they are now Sertoli cells (*S*).



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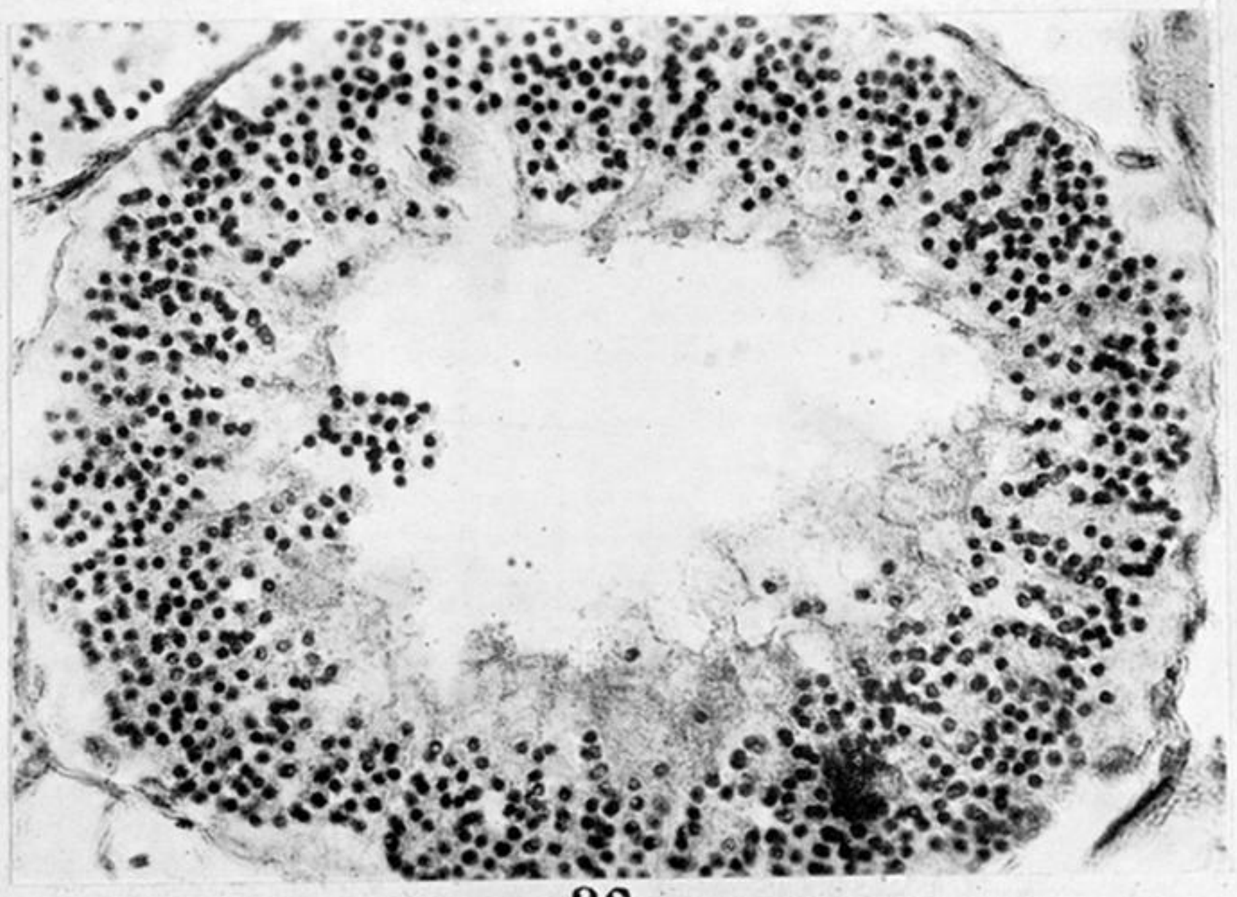

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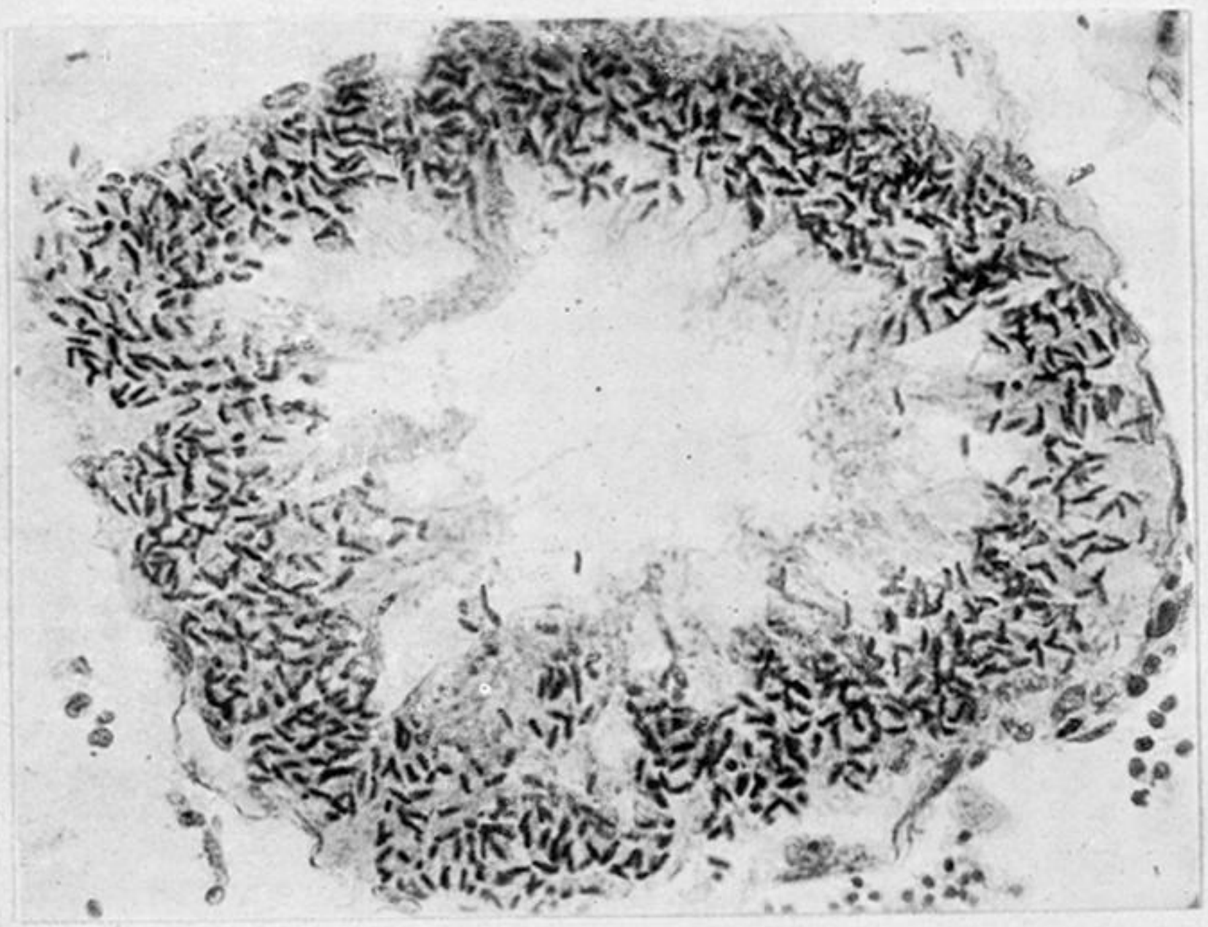

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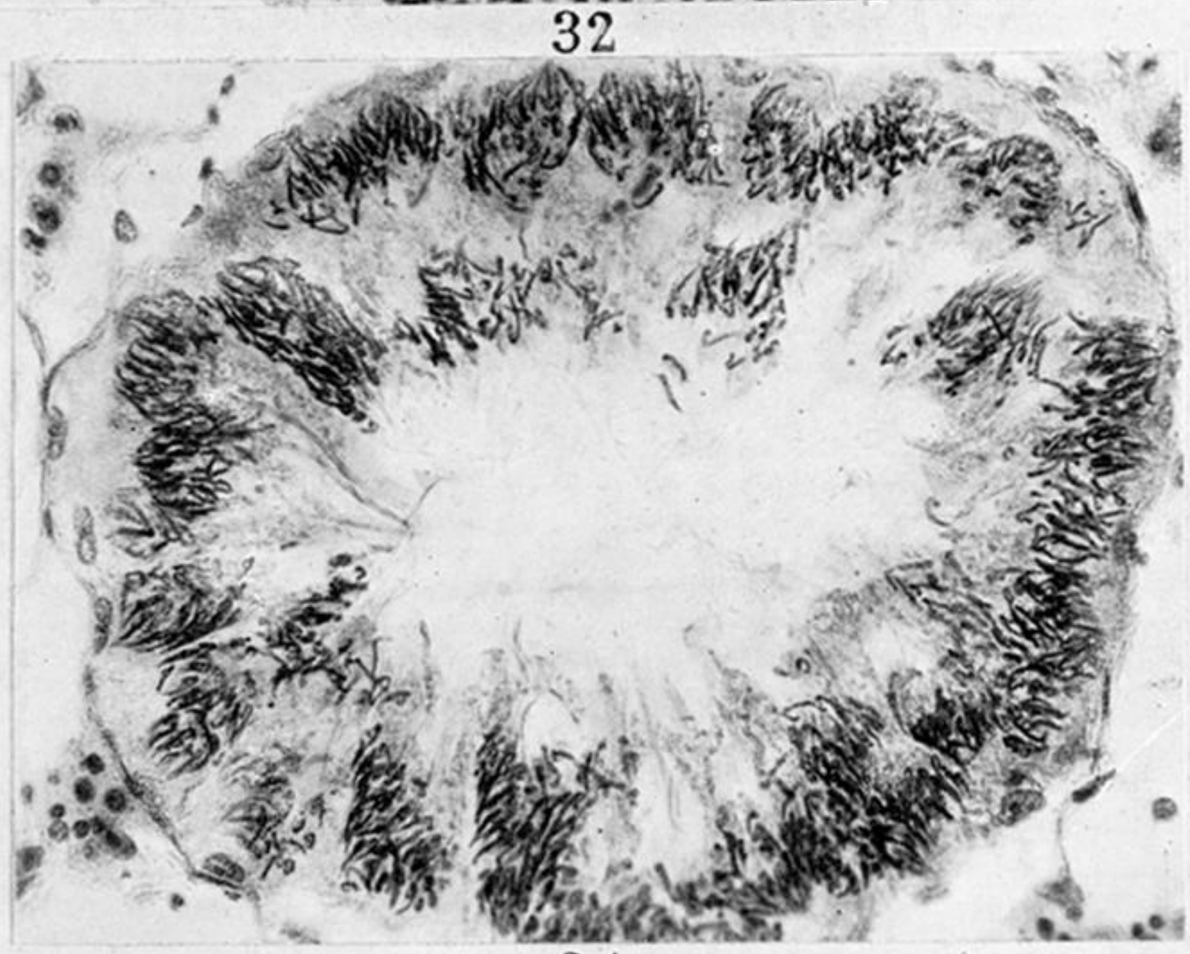

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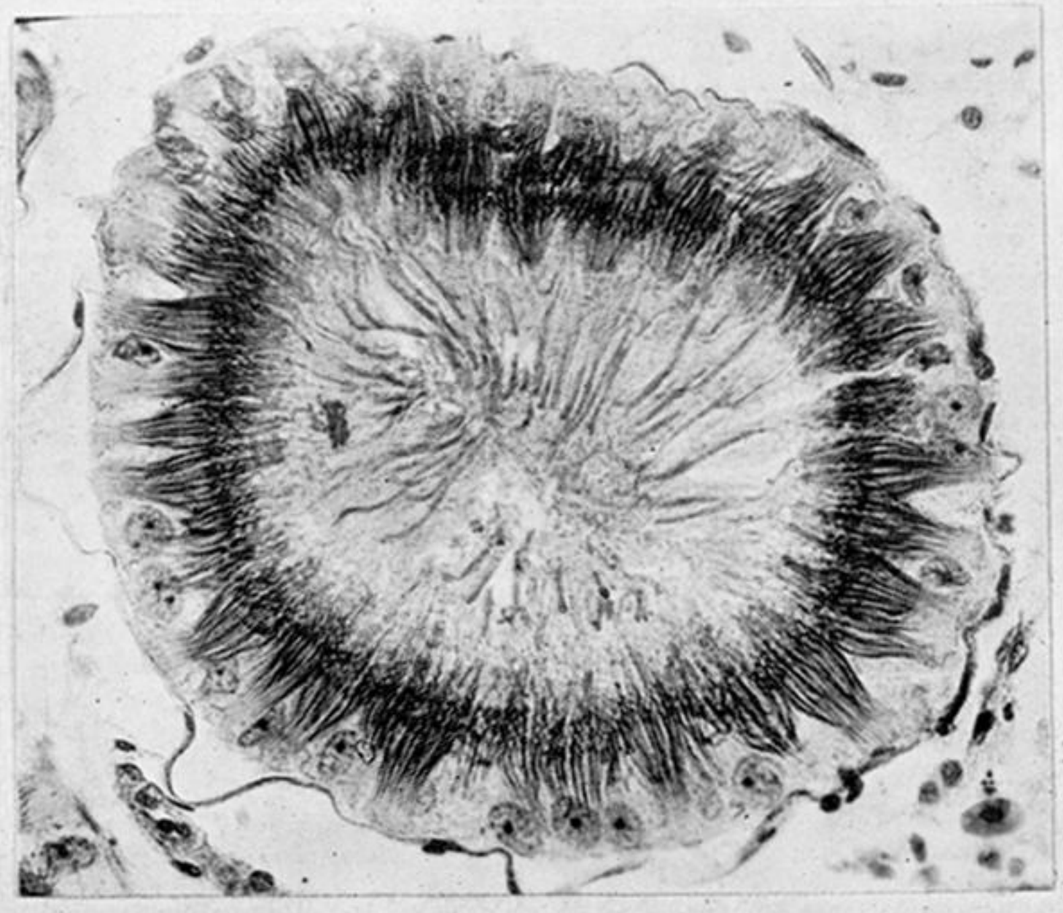

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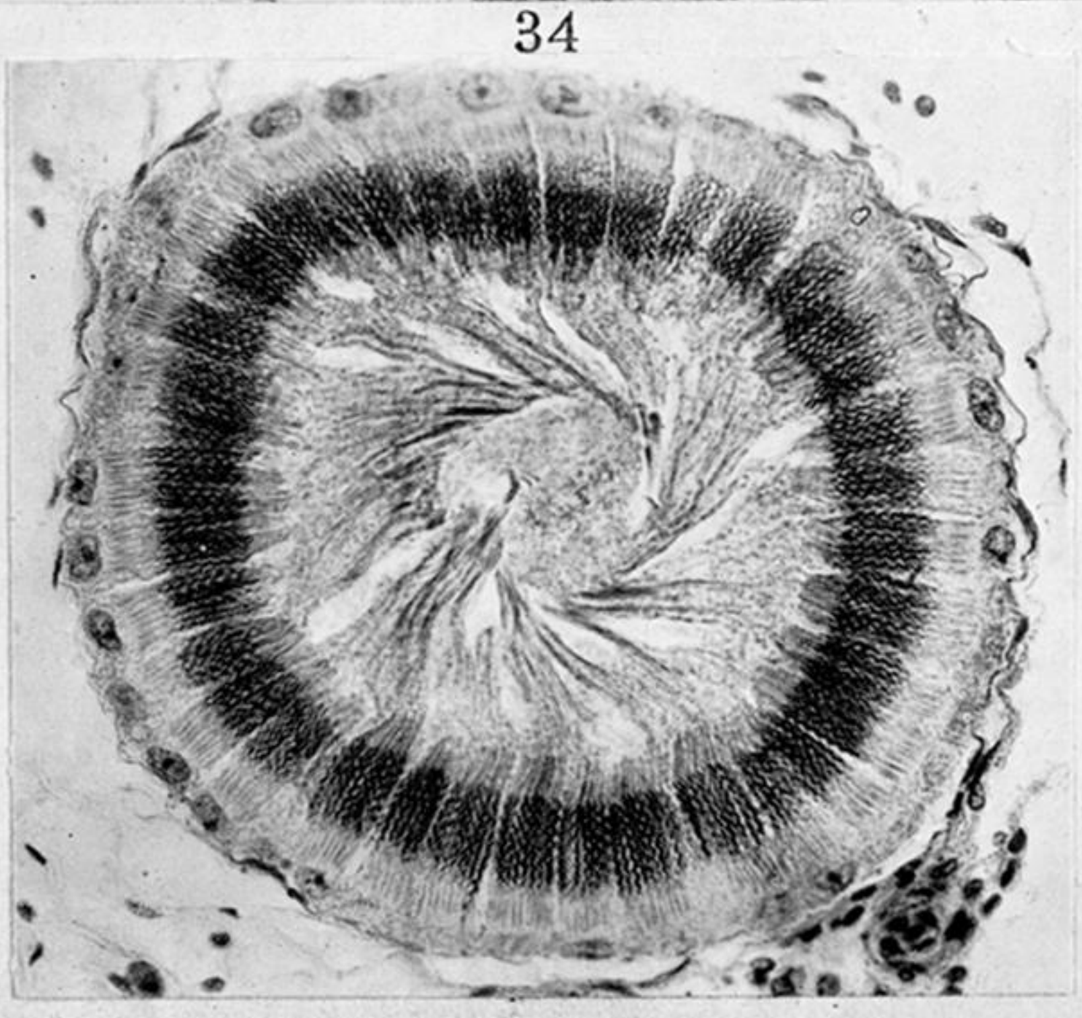


36

100μ

PLATE 11

Figures 31 to 36 all same scale.

FIGURE 31. Transverse section of an ampulla. The secondary spermatocytes are dividing to form spermatids. Division is complete in the upper right-hand part.

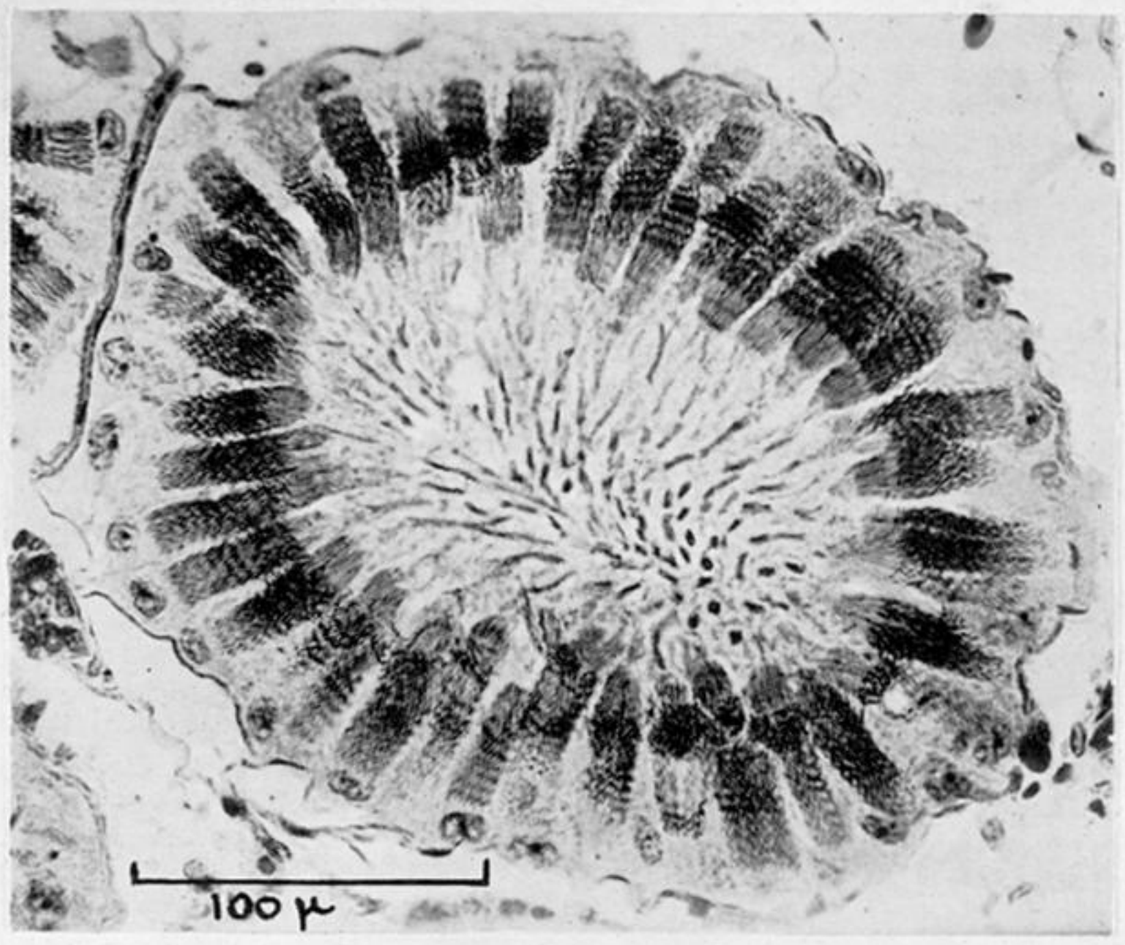
FIGURE 32. Transverse section of an ampulla, showing the spermatids grouped in clumps round the periphery.

FIGURE 33. Transverse section of an ampulla, showing the spermatids beginning to elongate to form the heads of the spermatozoa.

FIGURE 34. Transverse section of an ampulla, showing transformation of spermatids into spermatozoa; the clumps are becoming more distinct.

FIGURE 35. Transverse section of an ampulla, the heads and tails of the spermatozoa now being visible. The ends of the clumps are attached to the wall of the ampulla between the large Sertoli cells. The spiral shape is beginning to appear at the bases of the heads.

FIGURE 36. Transverse section of an ampulla, showing the clumps of spermatozoa withdrawing a little from the wall of the ampulla and becoming attached to the free ends of the Sertoli cells. The whole of each head is now spiral, and the spirals of adjacent heads are becoming arranged in phase with each other.



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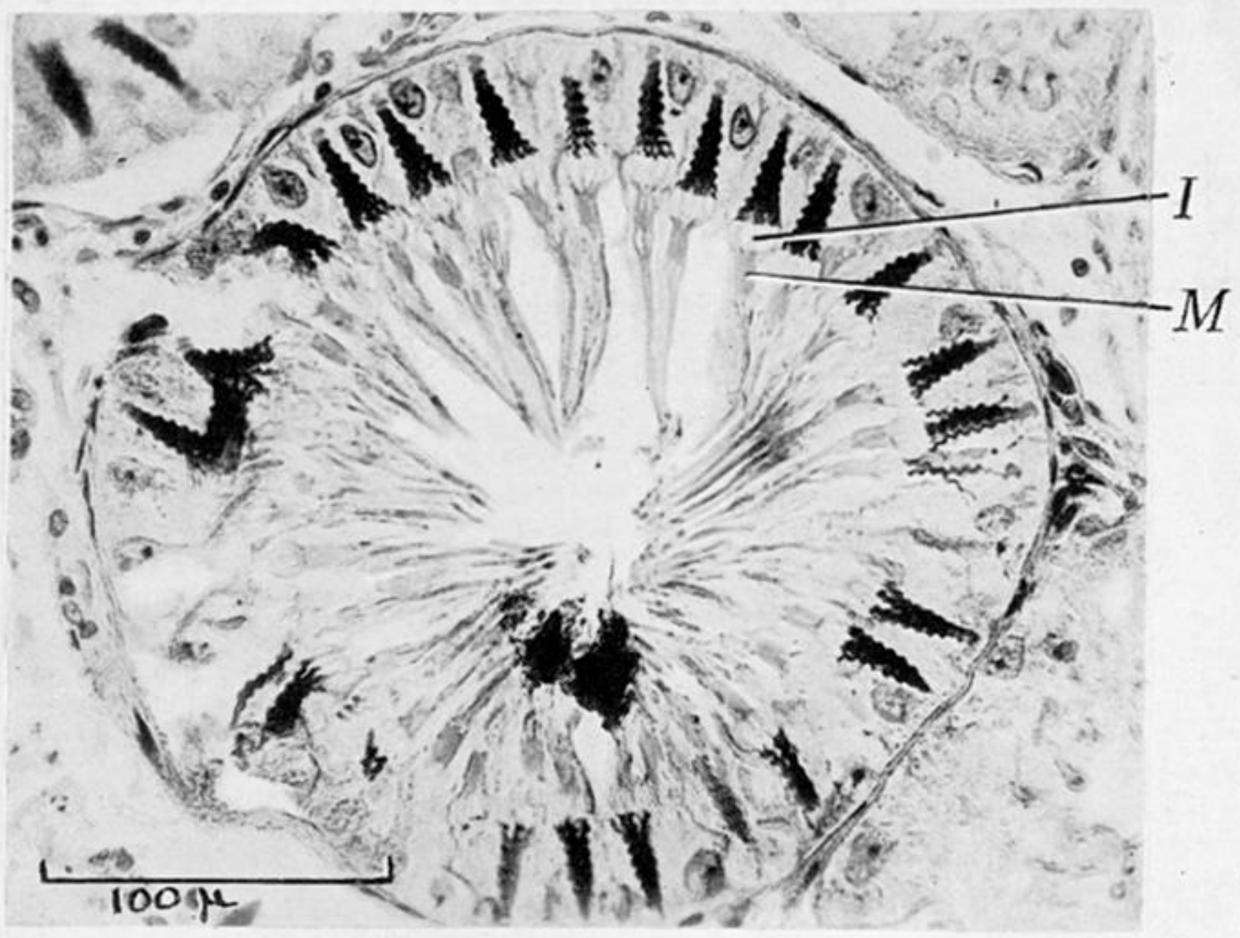

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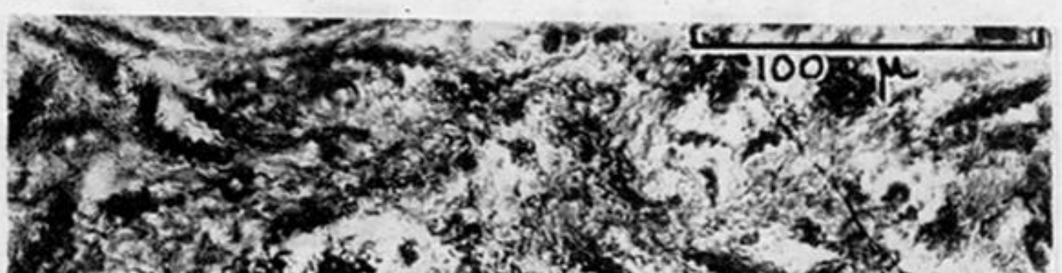

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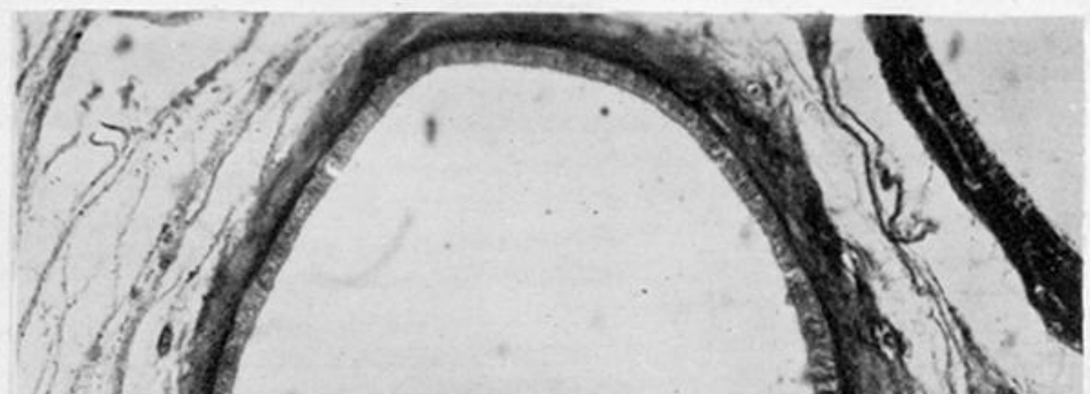

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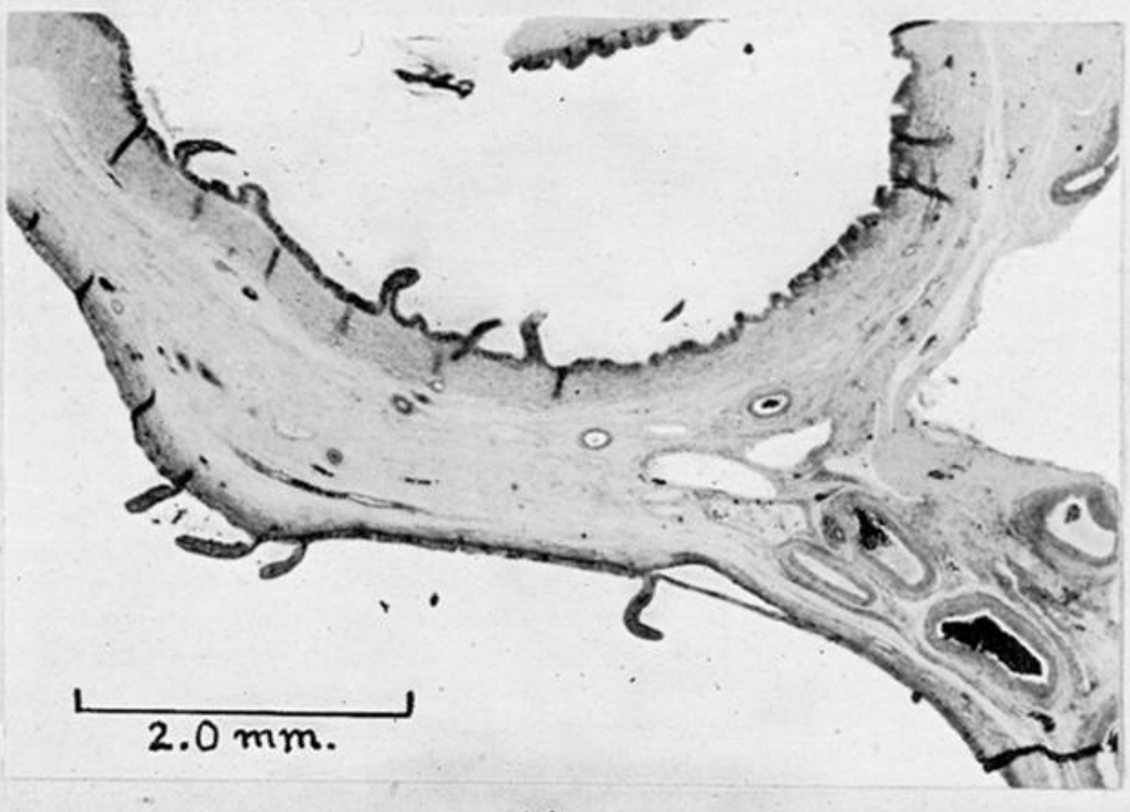

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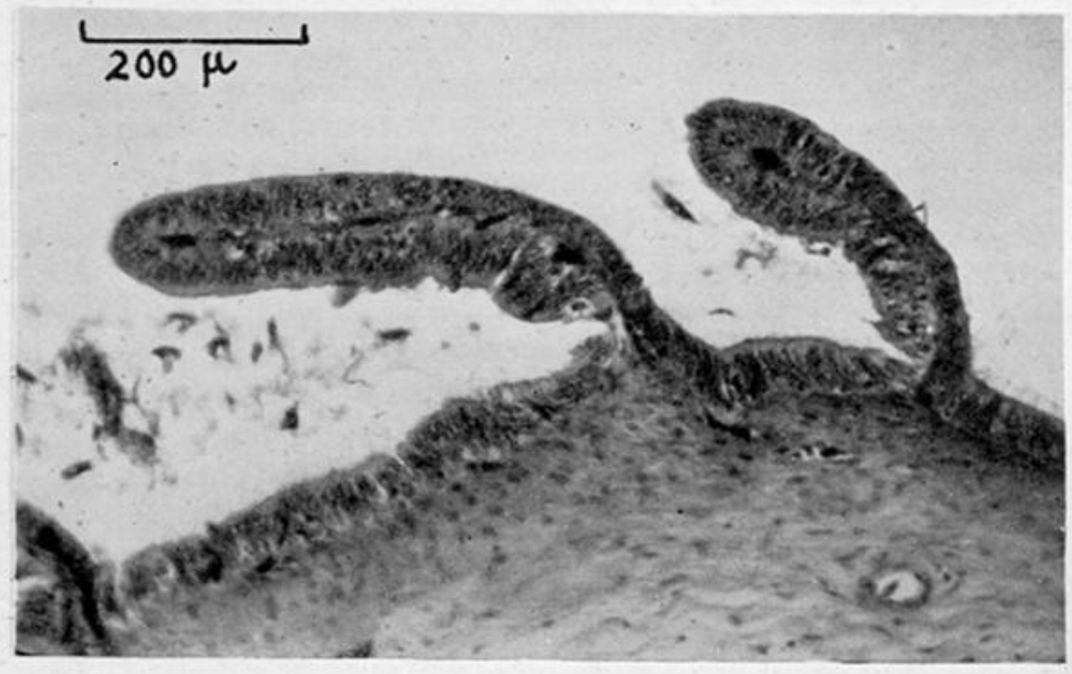

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PLATE 12

FIGURE 37. Transverse section of an ampulla, showing the clumps of spermatozoa becoming closely aggregated.

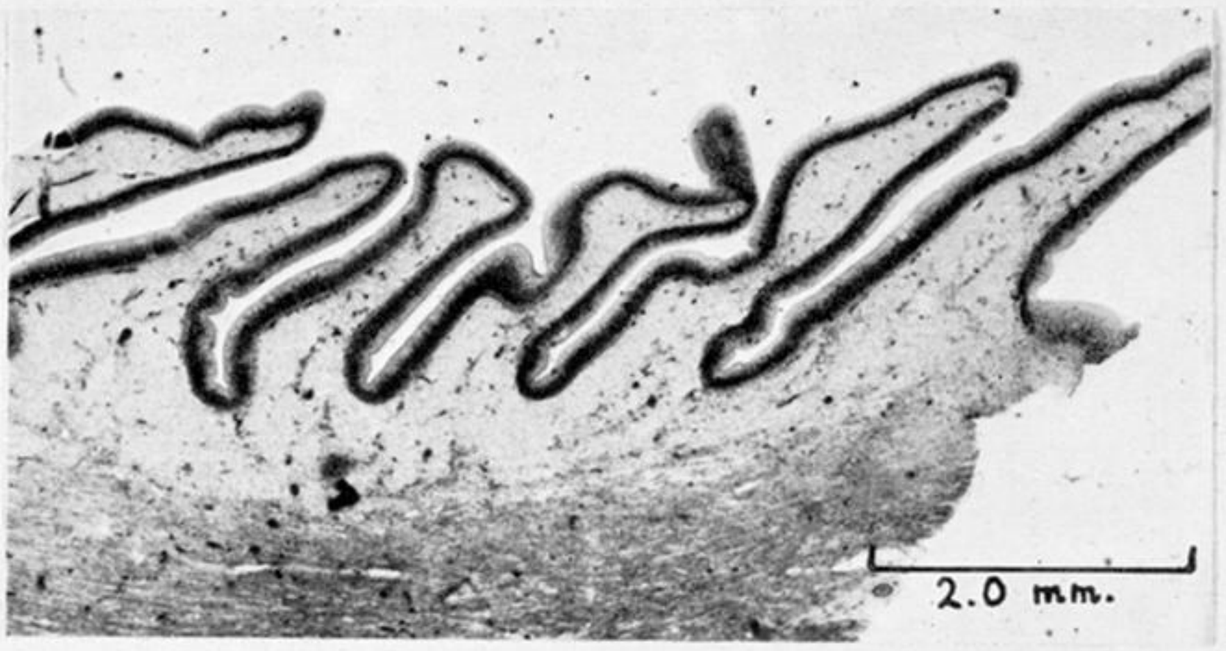
FIGURE 38. Transverse section of an ampulla, showing the final arrangement of the spermatozoa. The clumps again lie between the Sertoli cells, and the tails lie free in the lumen. The apices of the clumps are closely aggregated, the bases less closely; the intermediate pieces (*I*) are separated, and the middle pieces (*M*) closely aggregated.

FIGURE 39. Transverse section of the core of a spermatophore recovered from the vagina of a female, showing that many clumps of spermatozoa remain intact until the spermatophore disintegrates in the female.

FIGURE 40. Transverse section of the ductus epididymidis, showing the pseudo-stratified epithelium and the loose connective tissue between adjacent loops.

FIGURE 41. Transverse section of the lower part of the ductus epididymidis, showing the epithelium raised into widely separated folds.

FIGURE 42. Transverse section of two of the folds in the lower part of the ductus epididymidis, showing that they consist of two layers of epithelium separated by an extremely thin layer of connective tissue.



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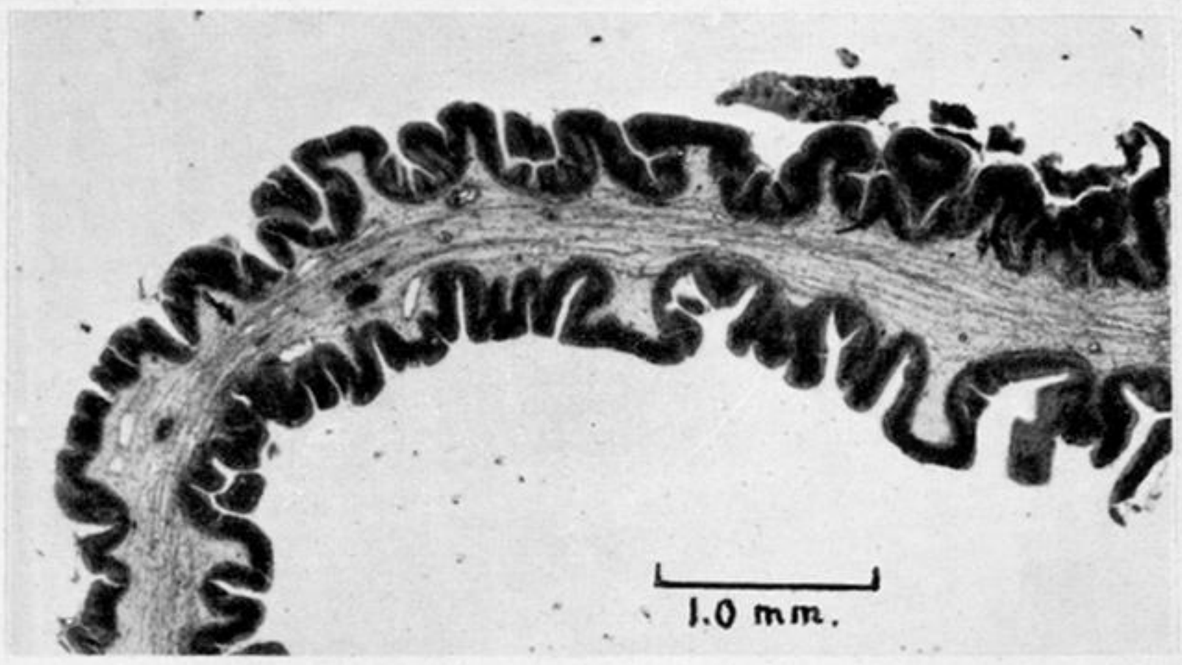

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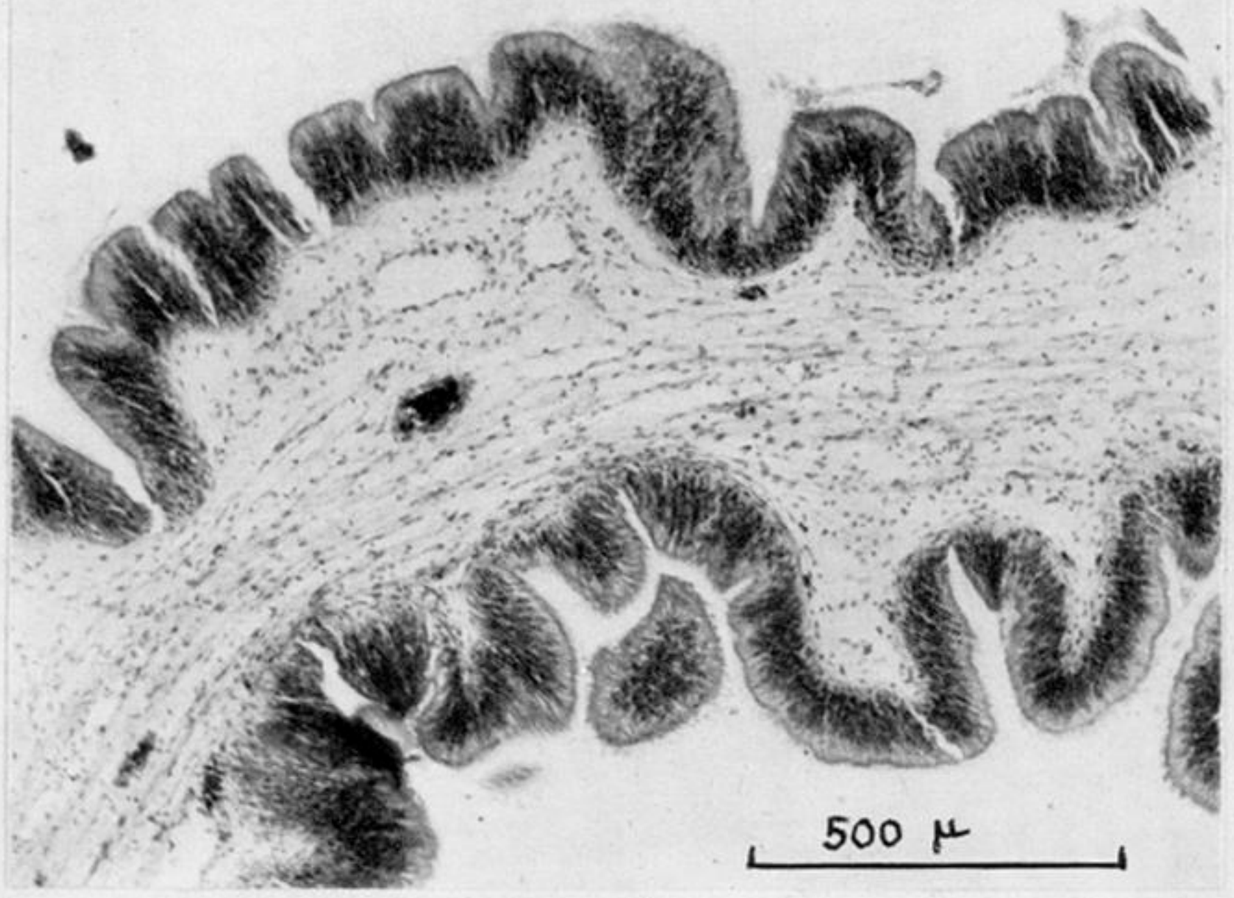

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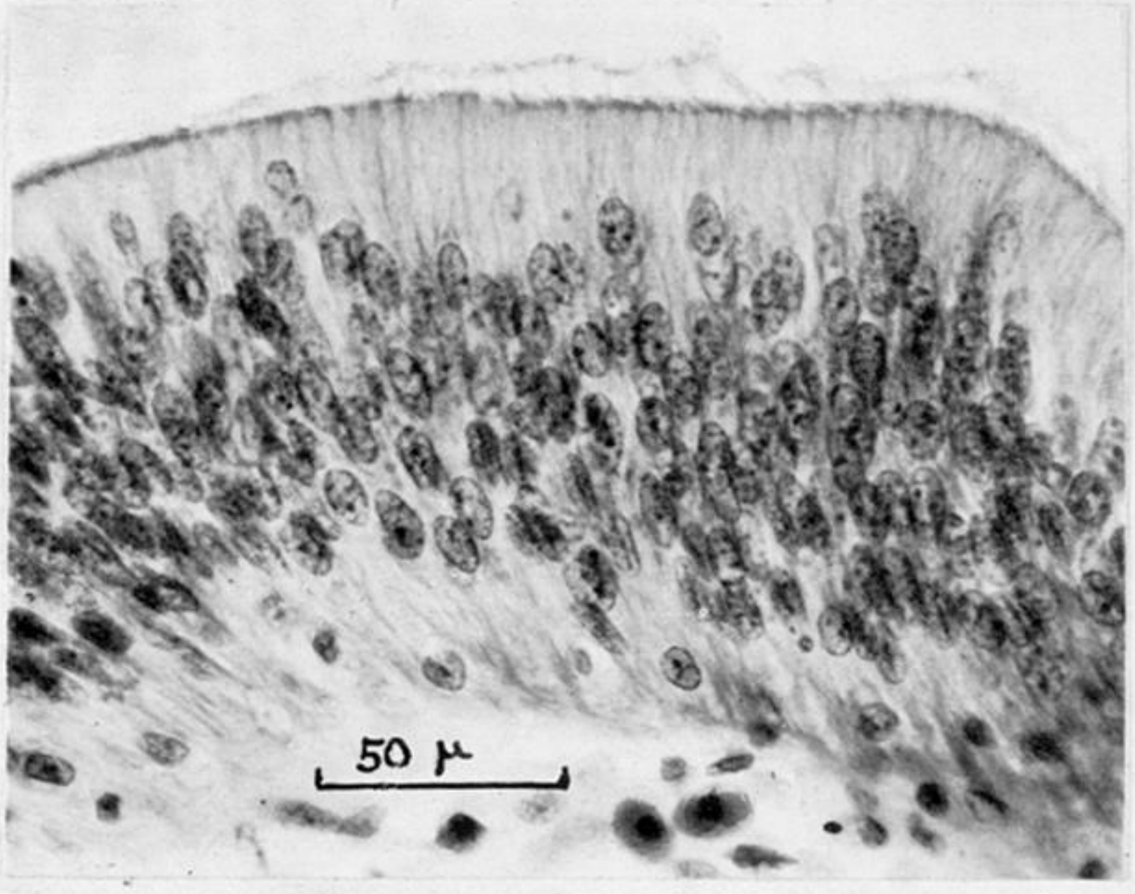

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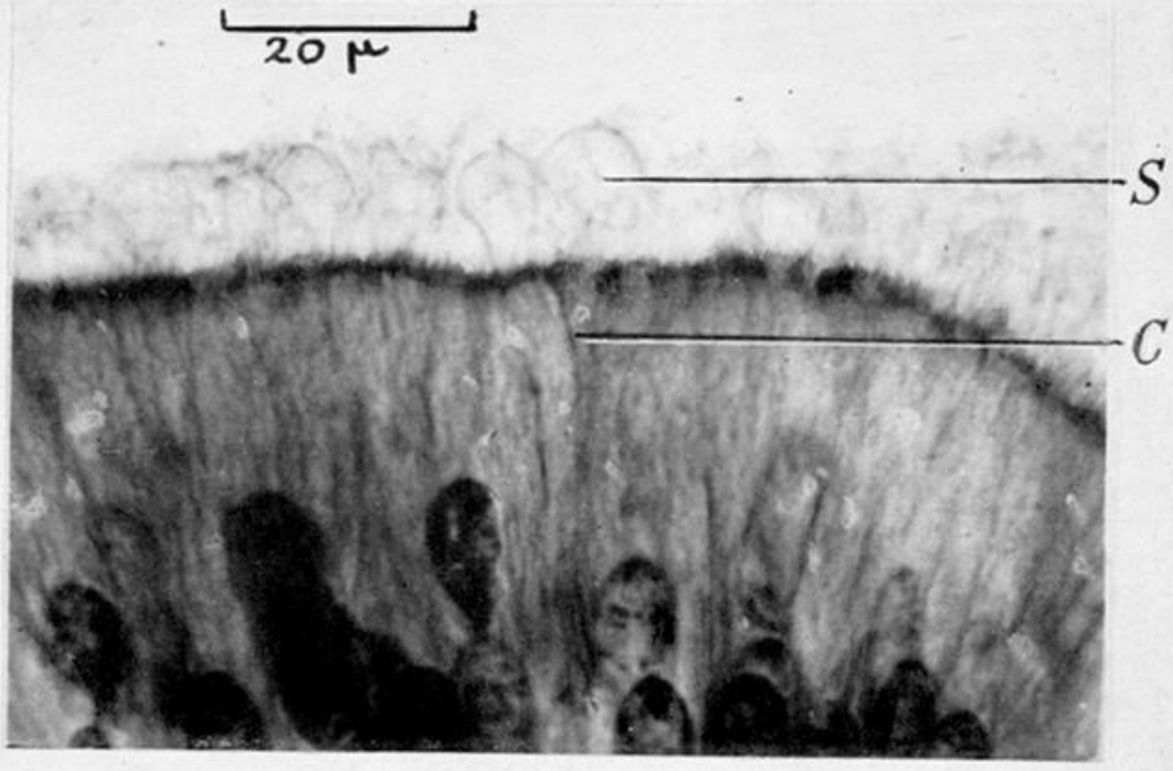

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PLATE 13

FIGURE 43. Longitudinal section of the upper part of the ductus deferens, showing the high internal folds covered with tall columnar epithelium.

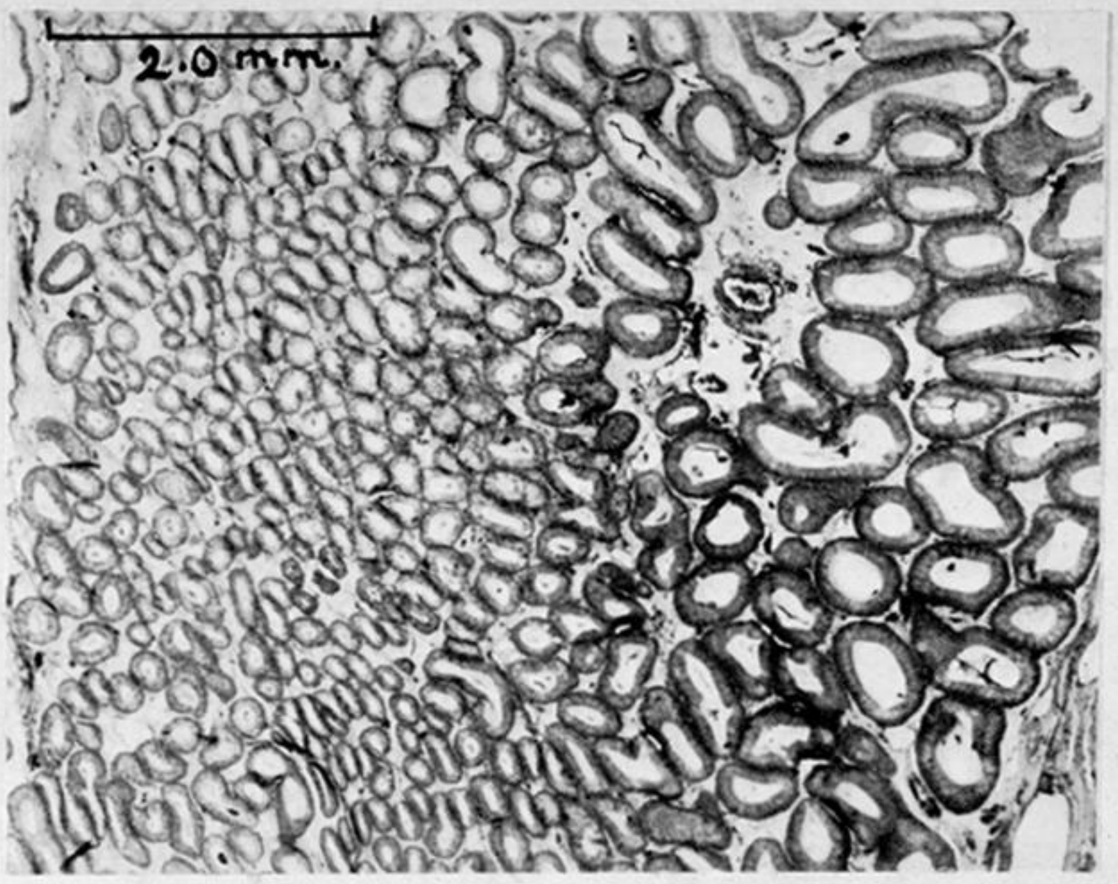
FIGURE 44. Transverse section of one of the thinner septa from the anterior end of the ampulla ductus deferentis, showing the supporting connective tissue and the surface raised into numerous small villi.

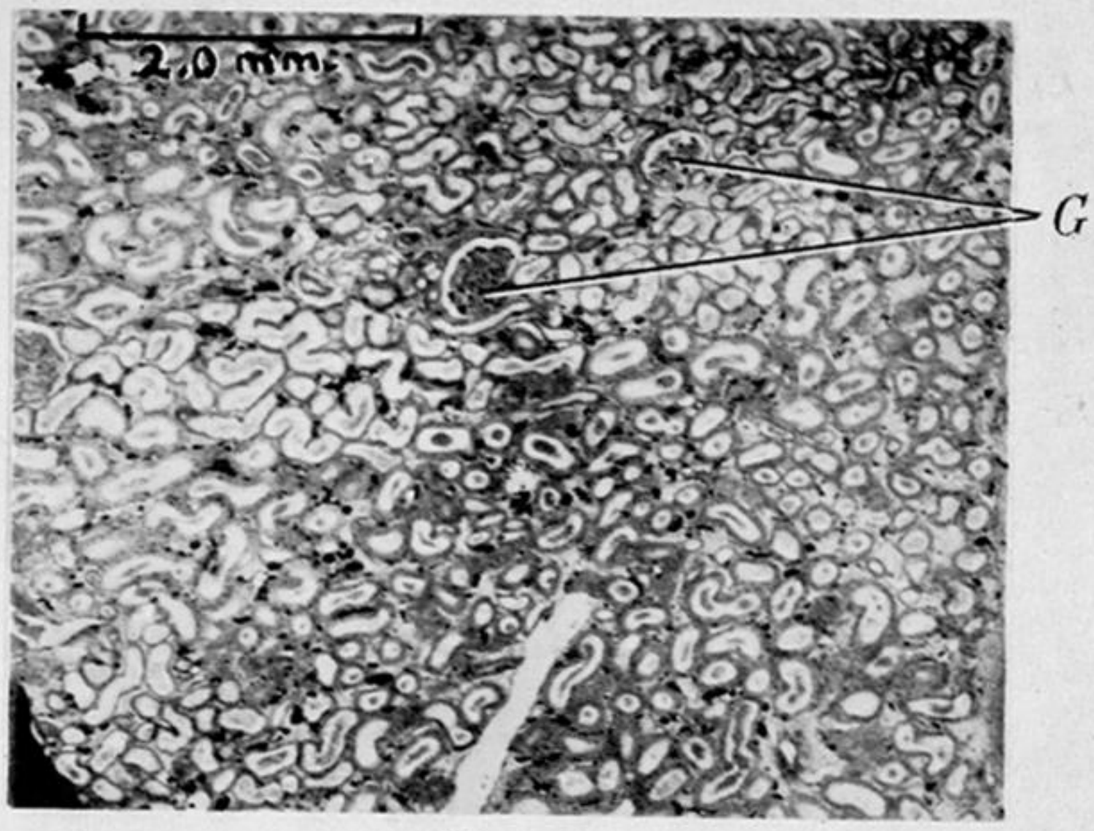
FIGURE 45. The same, showing the pseudo-stratified epithelium with tall columnar ciliated cells.

FIGURE 46. Transverse section of one of the thick septa from the lower part of the ampulla ductus deferentis, showing the stout supporting layer of connective tissue and the surface raised into numerous villi.

FIGURE 47. Pseudo-stratified epithelium from the tip of a villus on one of the stout septa of the ampulla ductus deferentis, showing the nuclei at different levels and the tall columnar ciliated cells.

FIGURE 48. The same, more highly magnified, showing the pear-shaped drops of secretion (*S*) protruding on the surface among the cilia, and the canaliculi (*C*) penetrating between the ciliated cells to the deeper secretory ones. The outer ends only of the epithelial cells are shown.





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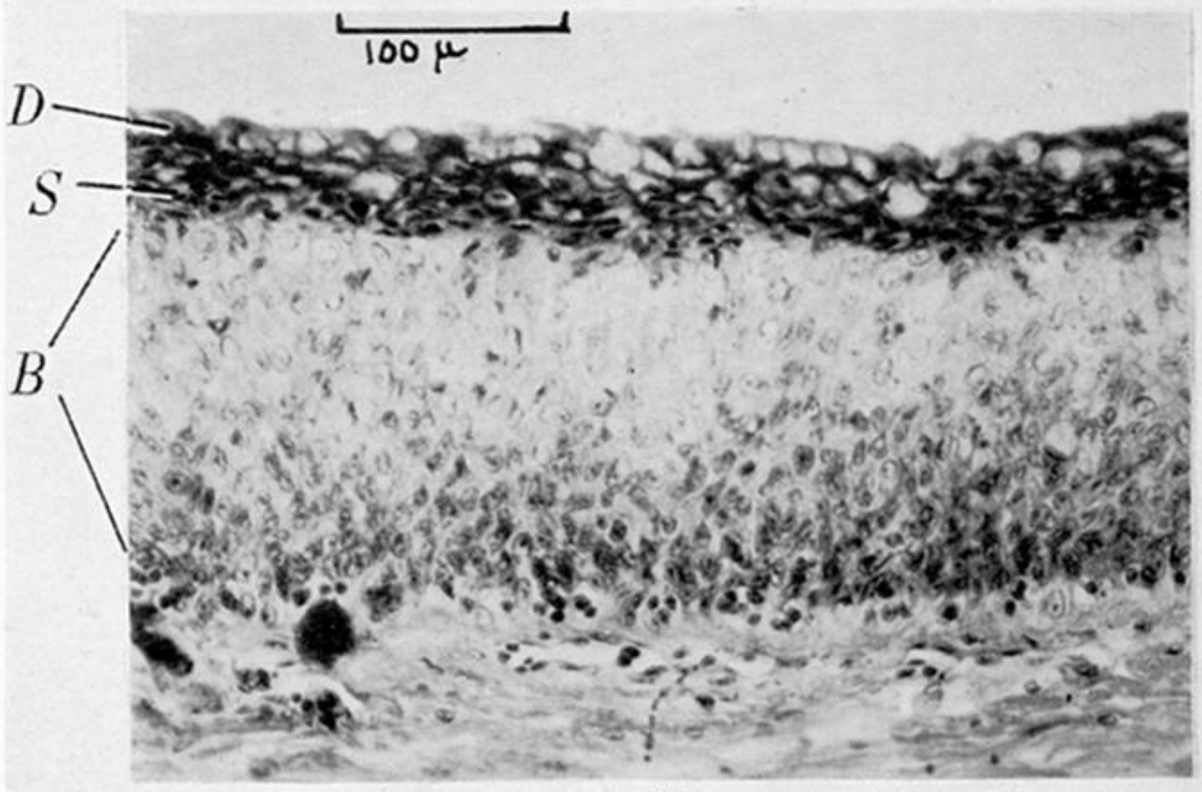

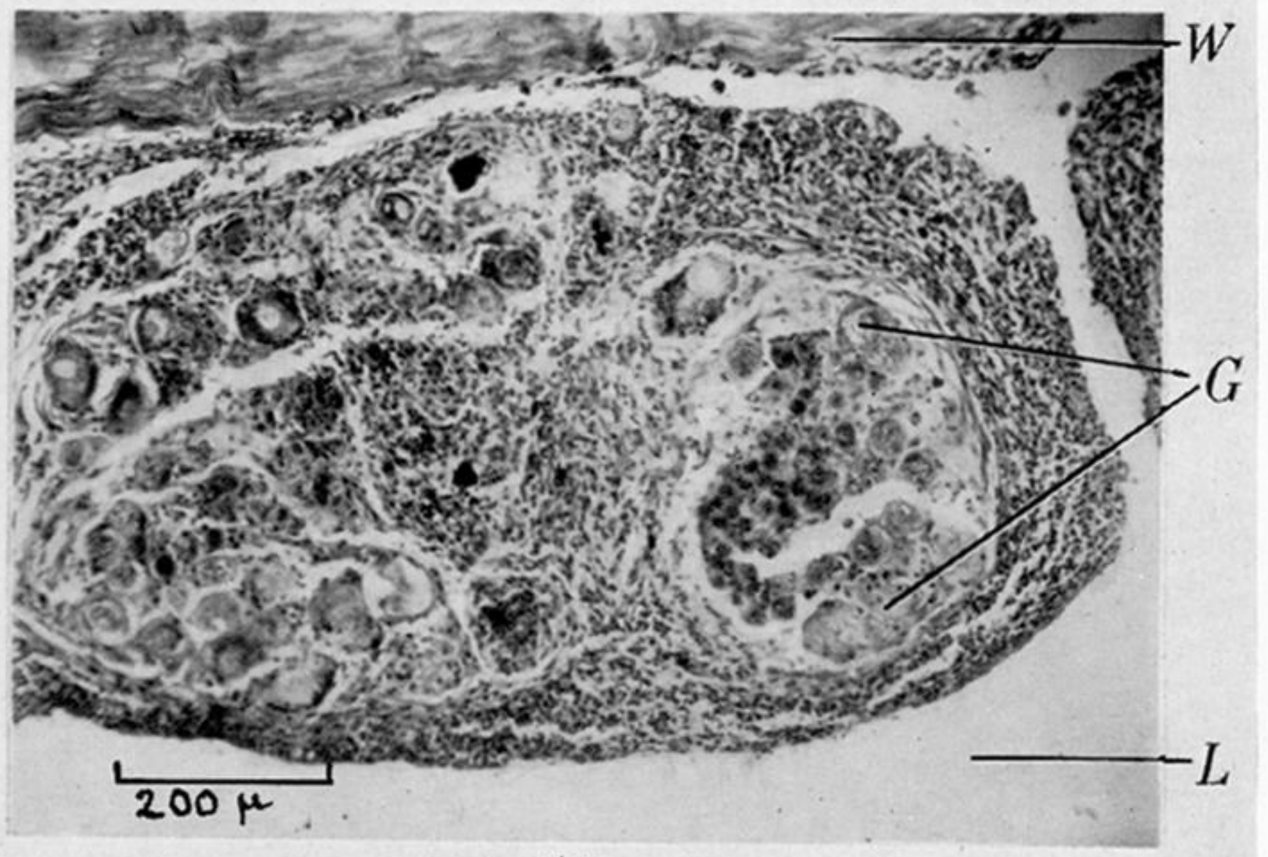

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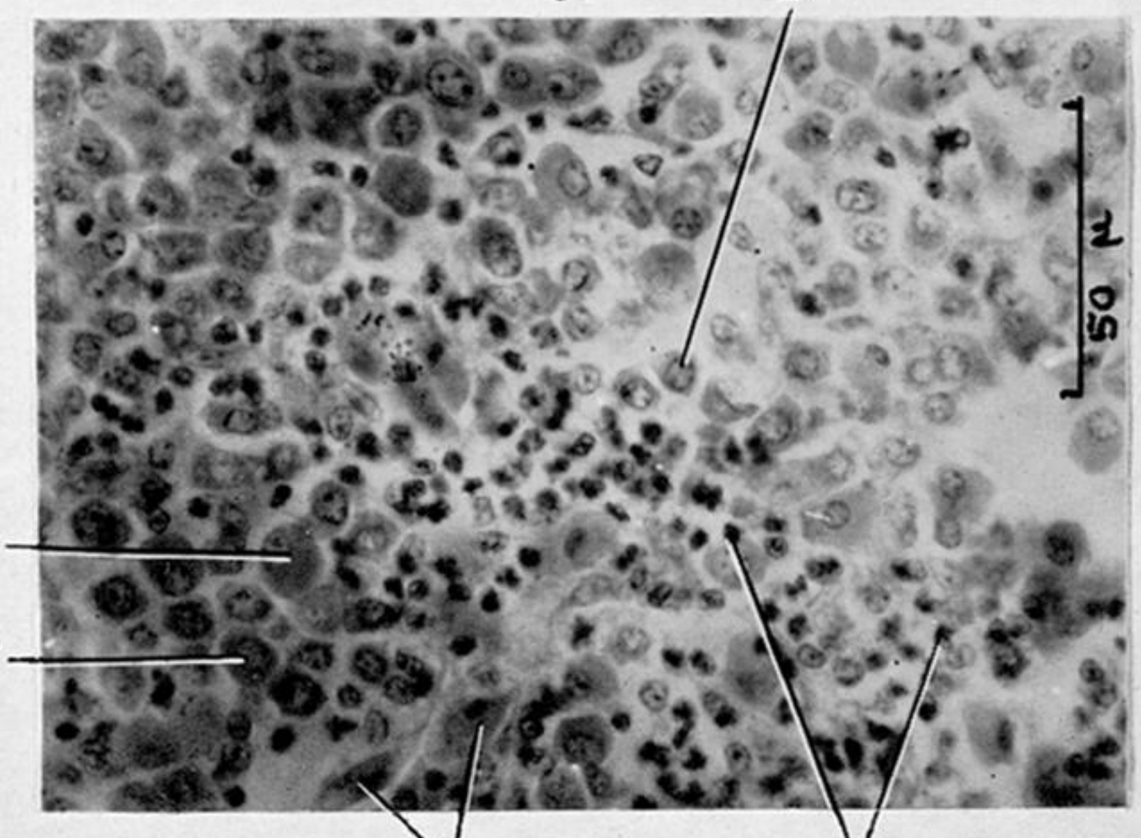

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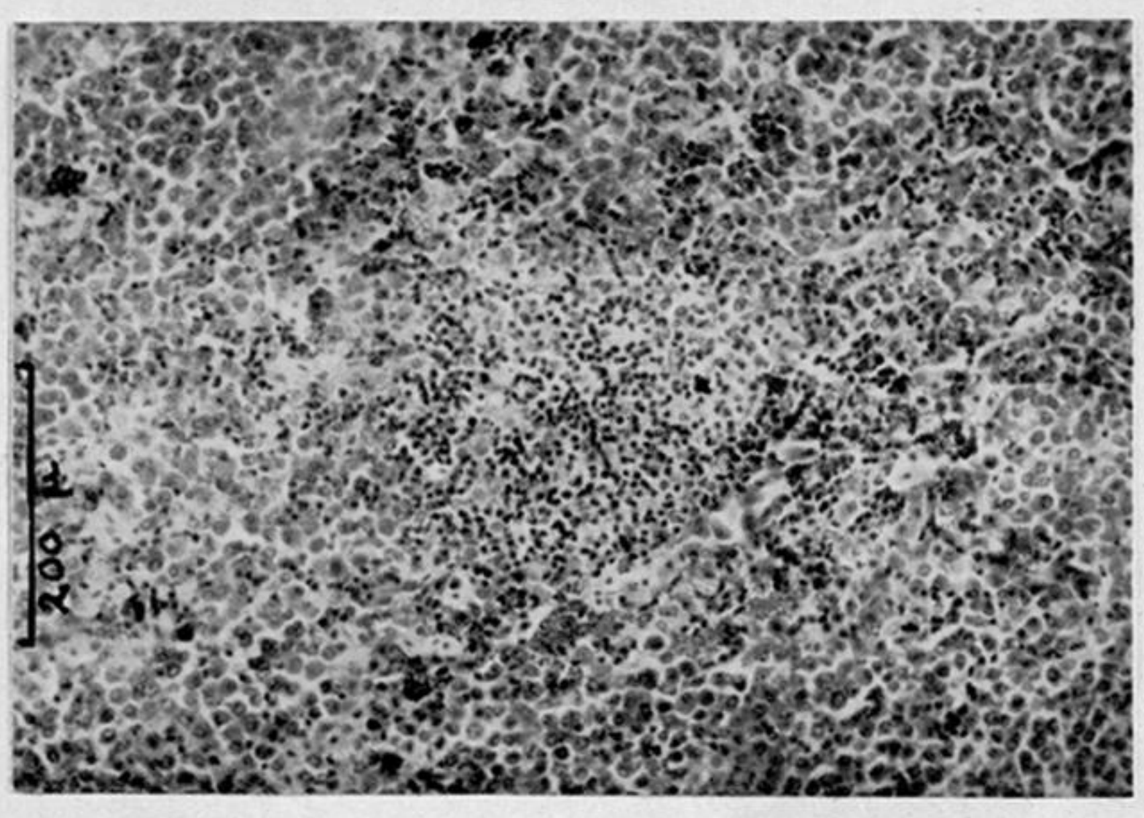

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PLATE 14

FIGURE 49. Transverse section of part of Leydig's gland. The small secretory tubules lie to the left, the large ducts to the right; there are no glomeruli.

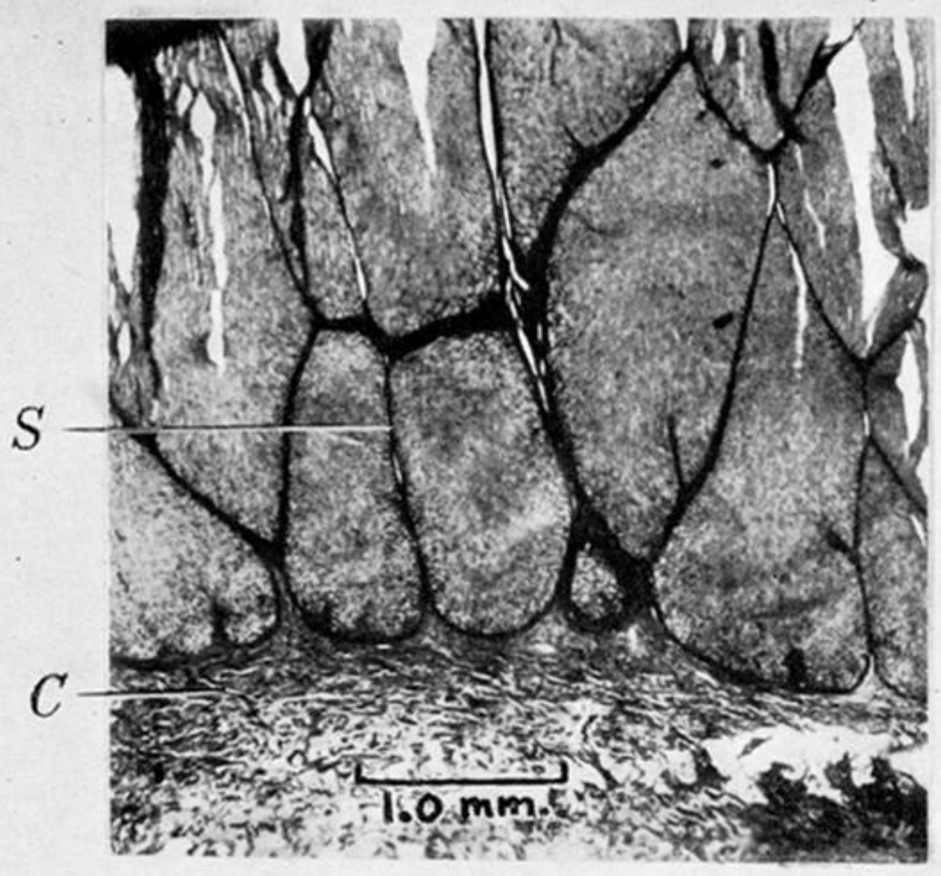
FIGURE 50. Transverse section of part of the kidney. The tubules are in general smaller than those in Leydig's gland, and their epithelium is not so thick and glandular. Two glomeruli are seen at *G*.

FIGURE 51. Transverse section of the lining of the siphon. *B*, basal layer of the epithelium with closely packed nuclei at the base and more widely spaced ones superficially; *S*, transition layer of flattened cells with pycnotic nuclei; *D*, superficial layer of swollen cells with degenerate nuclei.

FIGURE 52. Transverse section of one of the irregular masses projecting into the lumen of the posterior cardinal sinus. *G*, ganglion cells; *L*, lumen of the posterior cardinal sinus; *W*, wall of the vessel.

FIGURE 53. Section through part of the epigonal organ. *B*, basophil cell; *E*, elongated oval oxyphil cells; *L*, lymphocytes; *O*, large oxyphil cell; *S*, medium oxyphil cell.

FIGURE 54. Section through part of the epigonal organ, showing a lymphocyte germ centre, the area containing many small nuclei at the centre of the photograph.



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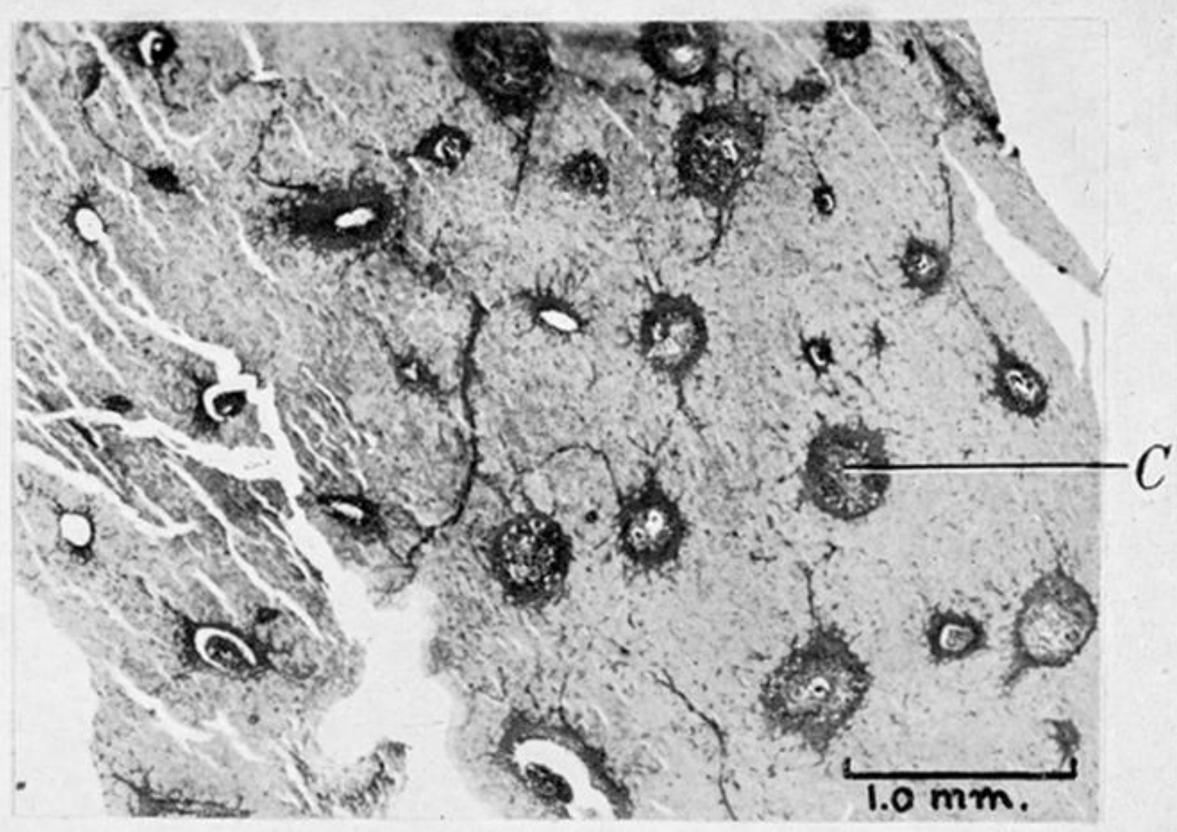

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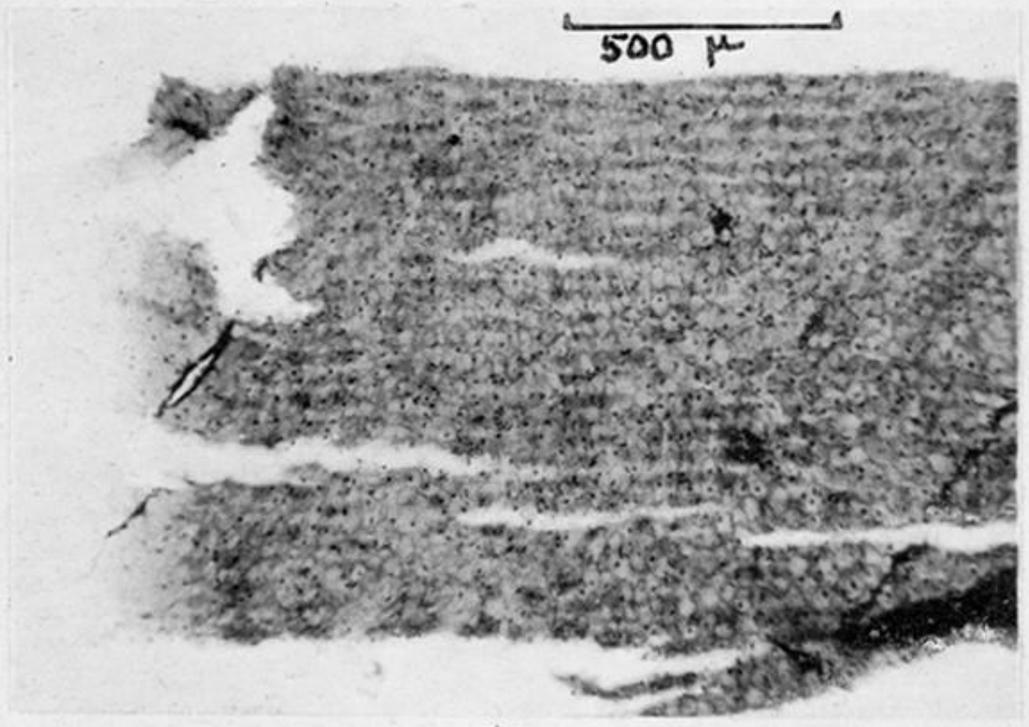

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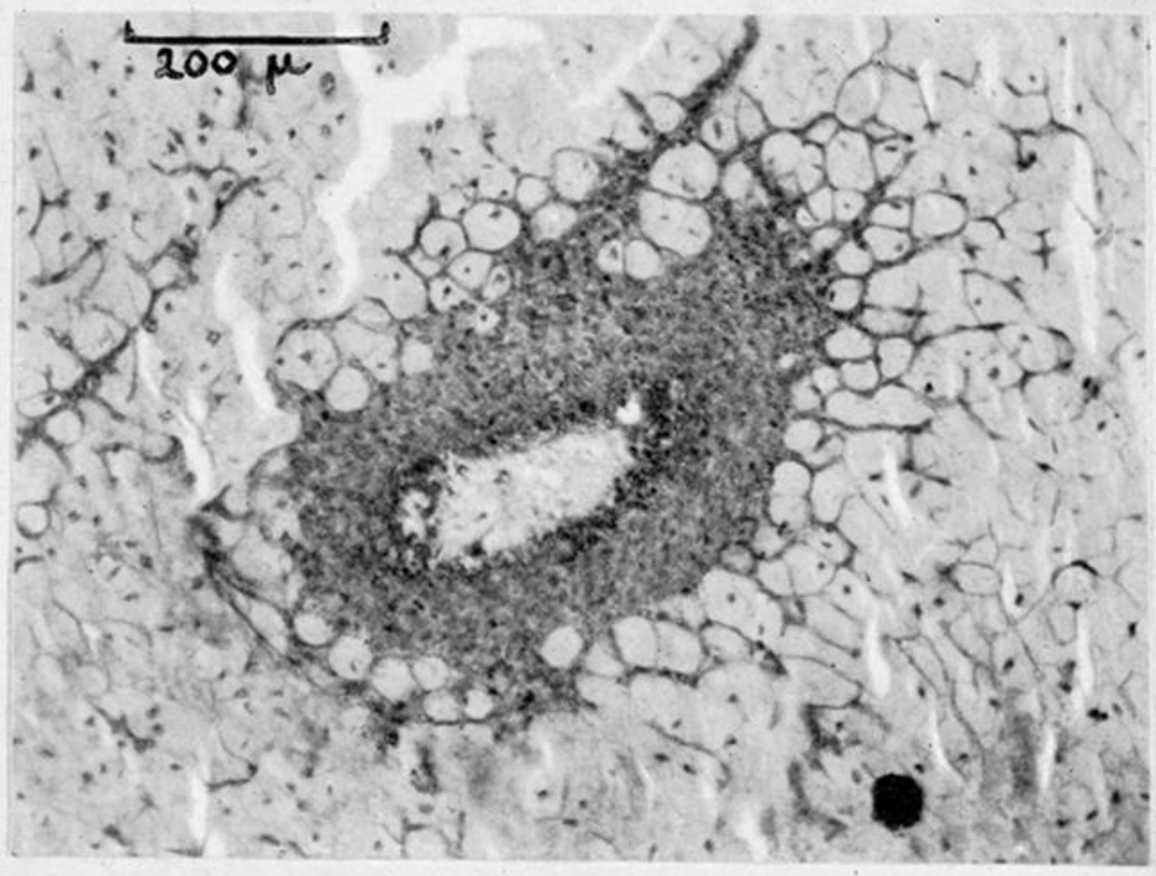

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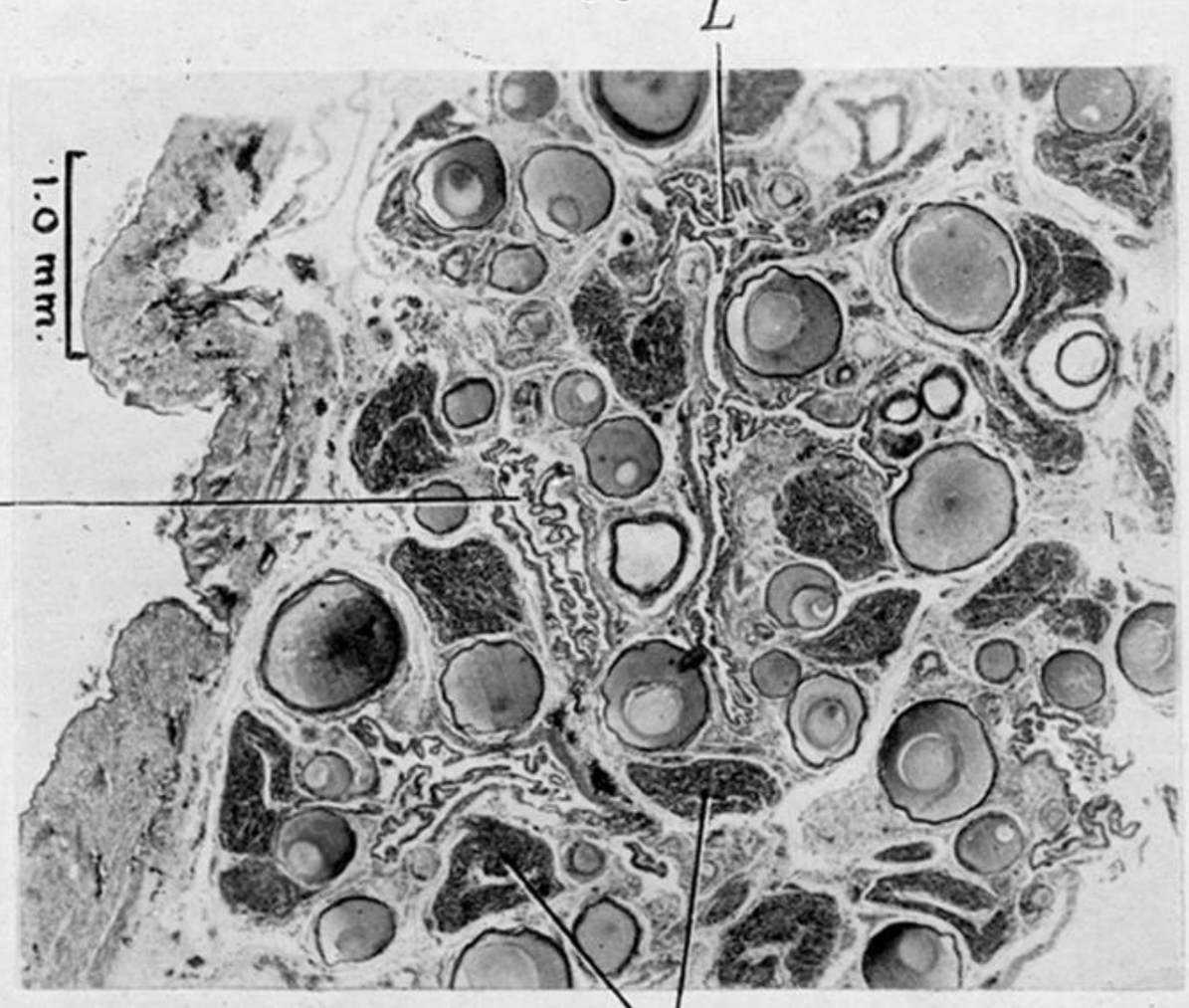

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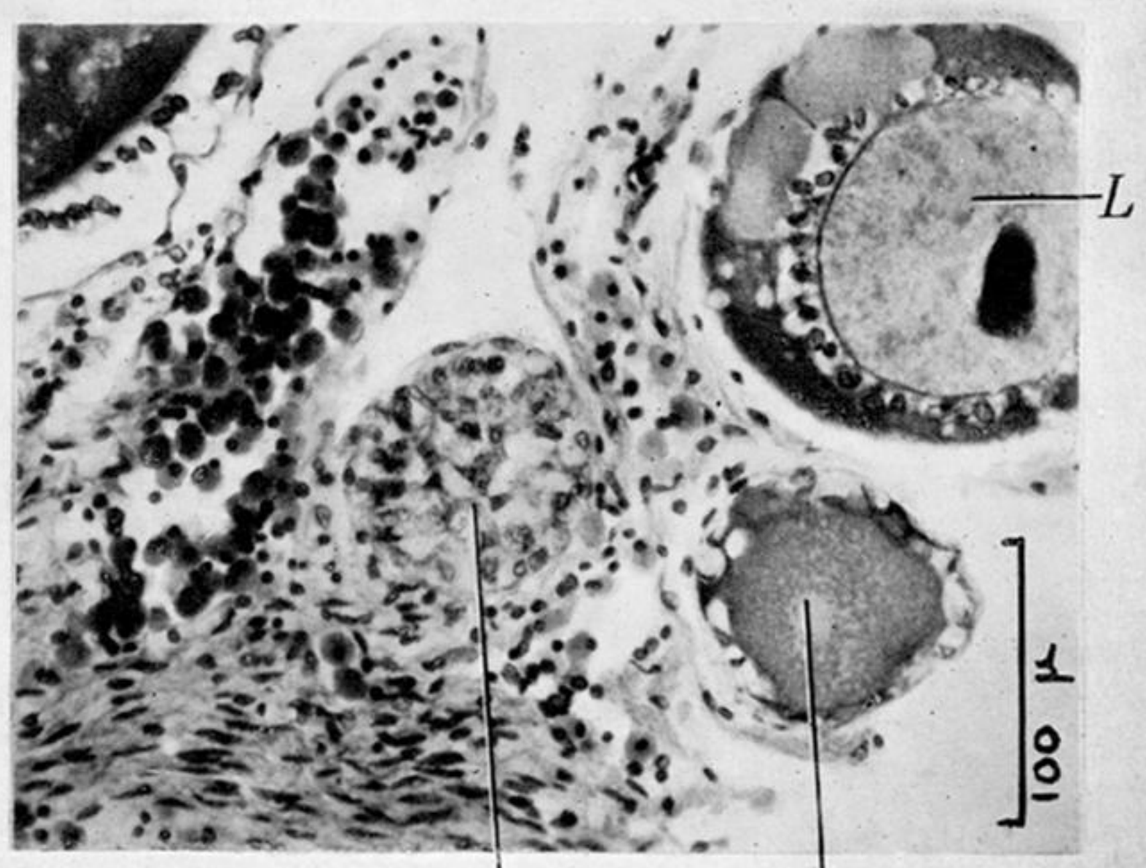

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P

E

L

Plate 15

Figure 55. Vertical section through the base of the clasper gland. *C*, supporting connective tissue raised into small papillae; *S*, fine strands of connective tissue arising from the papillae and extending towards the free surface through the solid mass of cells.

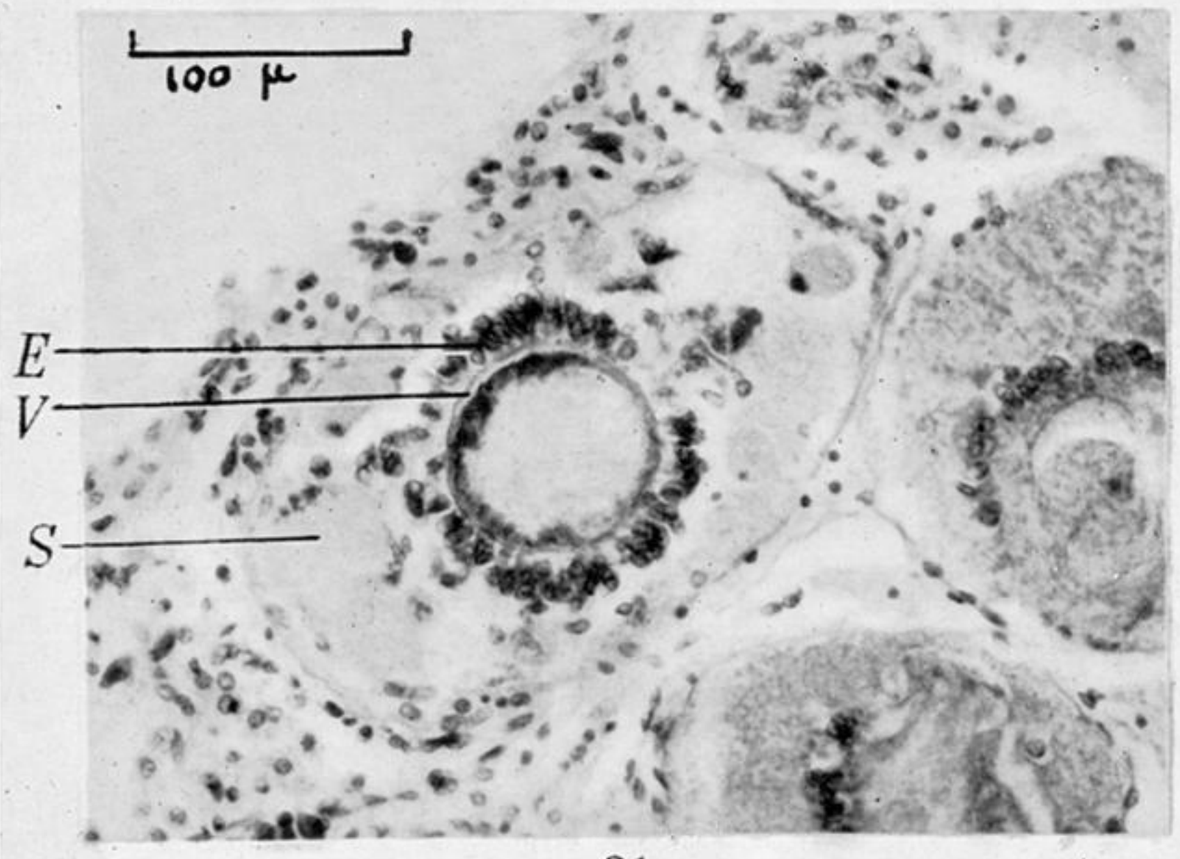
Figure 56. Horizontal section through the clasper gland, showing the strands of connective tissue (*C*) running towards the surface.

Figure 57. The same showing the connective tissue with some lymphoid tissue and a few vessels at the centre of a strand, and the surrounding epithelium proliferating to form the swollen cells with shrunken nuclei that make up the bulk of the gland.

Figure 58. Vertical section of the free edge of the clasper gland. The free edge lies to the left, and shows the secretion being formed by the degeneration and detachment of the cells. The cells of the gland are swollen with contained secretion, and the nuclei are minute and degenerate.

Figure 59. Section through part of the ovary, showing numerous follicles in course of development. *CL*, corpora lutea; *L*, lumina of the tubes ramifying throughout the substance of the ovary and leading to the exterior through the pocket.

Figure 60. Section of the ovary showing young follicles. *P*, follicle in the earliest stage containing a number of polyhedral cells packed closely together; *E*, a follicle in which one of the cells has become the central definitive oocyte; *L*, a larger oocyte surrounded by a vitelline membrane and a layer of epithelium. Some of the epithelial cells are swollen with yolk material and separate the oocyte and epithelium from the wall of the follicle.



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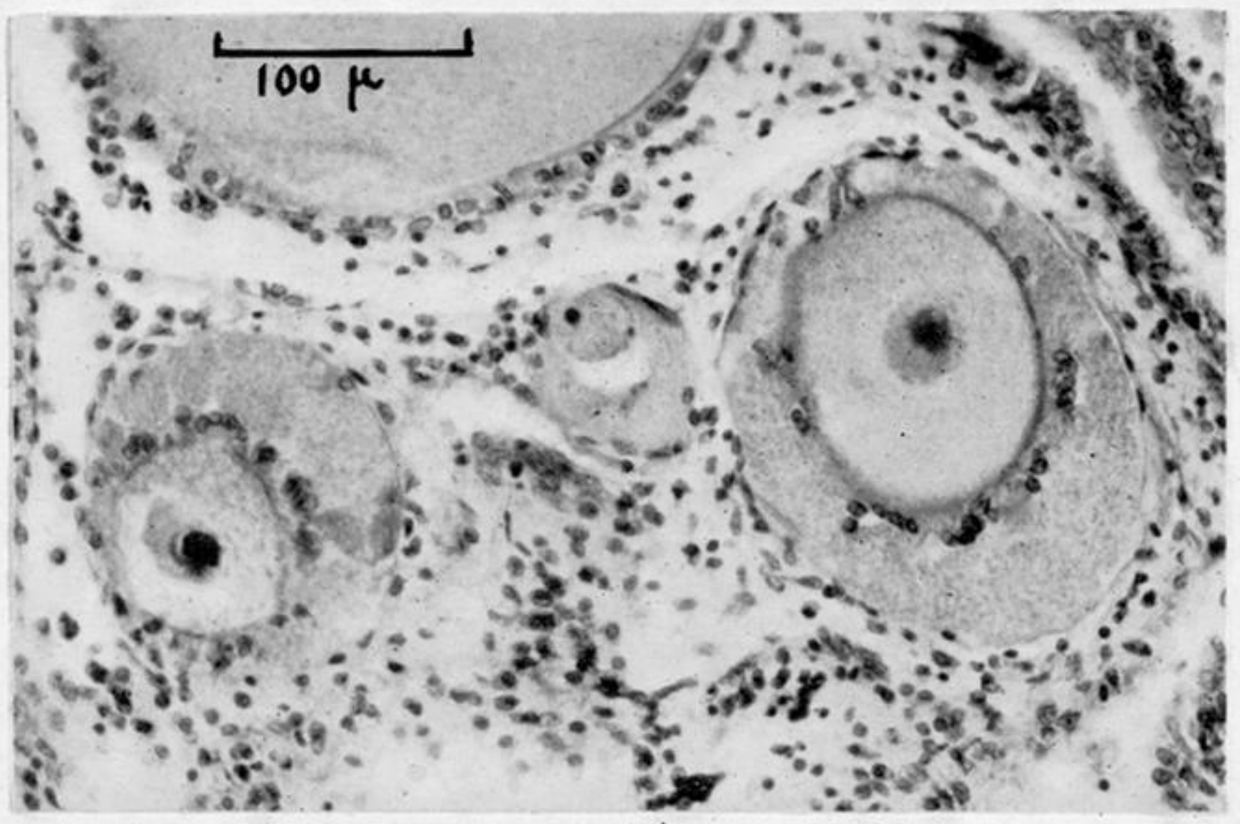

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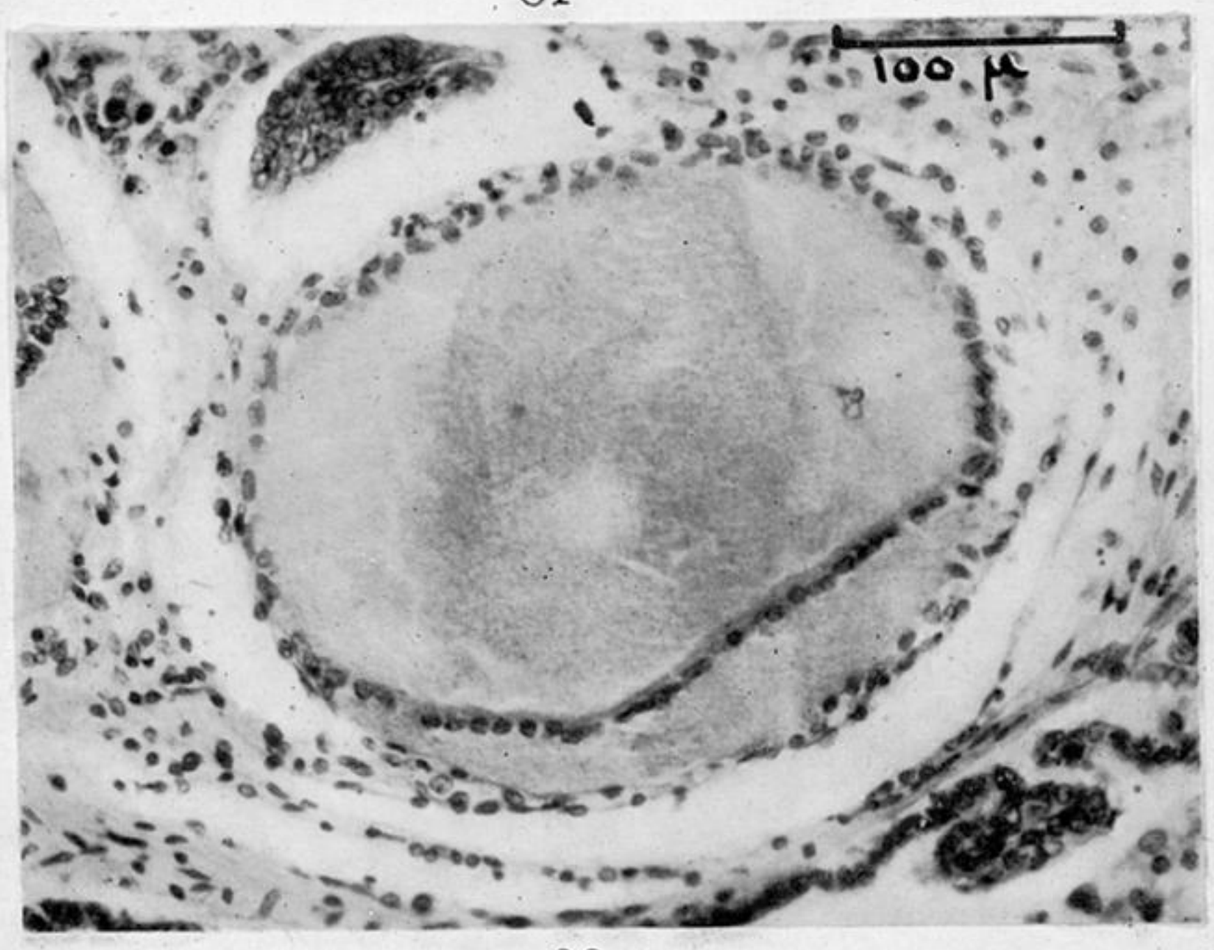

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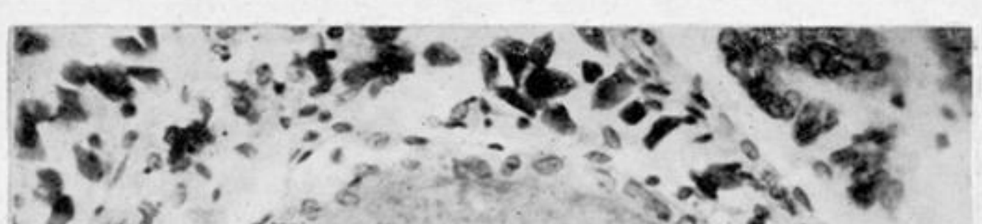

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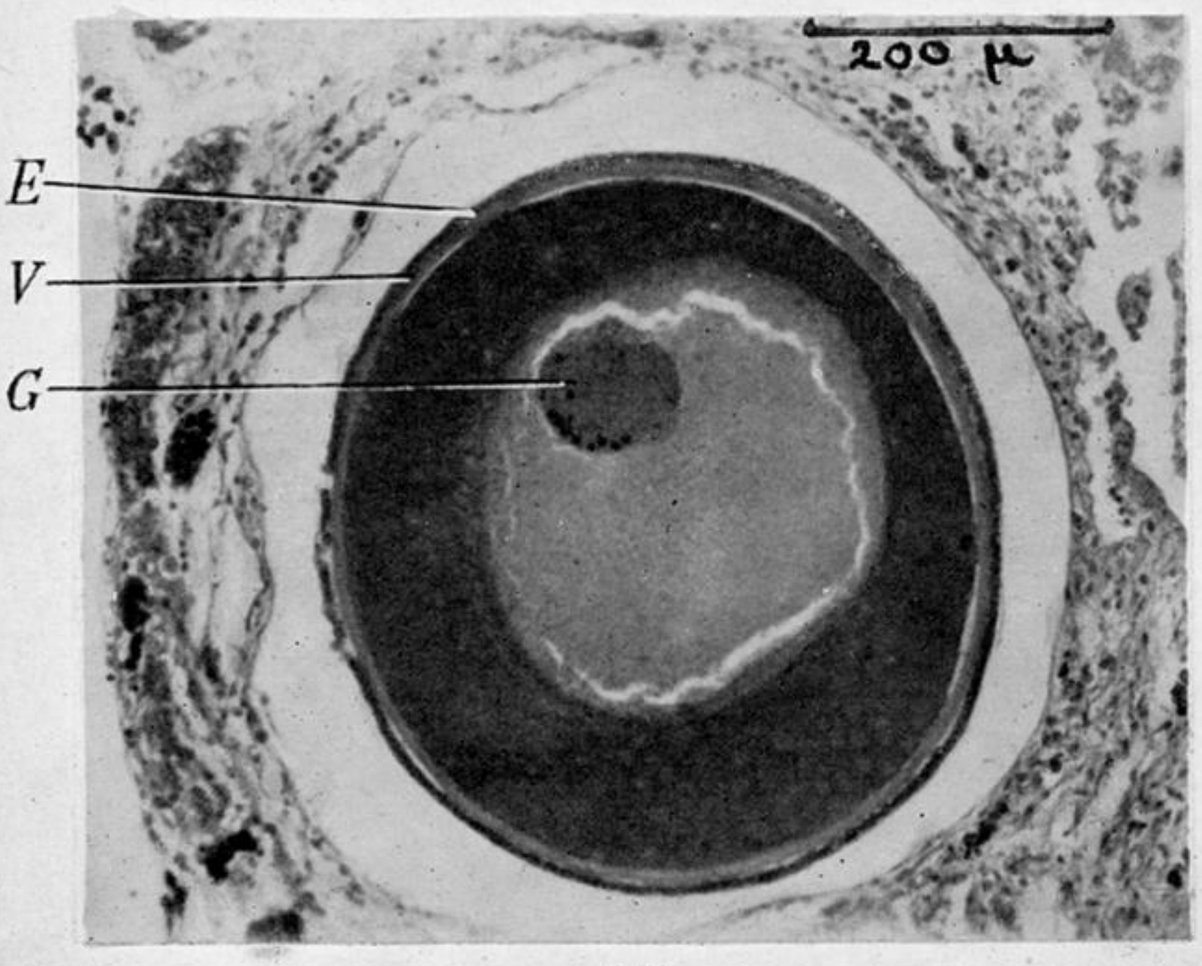

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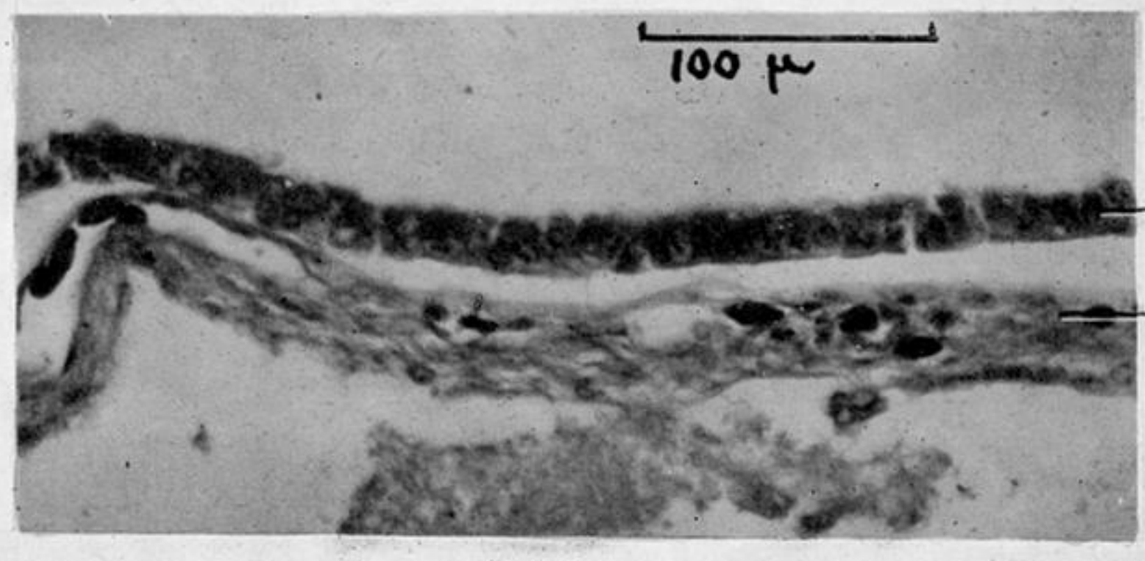

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Plate 16

Figure 61. Section of a young follicle, in which swollen cells (*S*) surround the oocyte and epithelium. *E*, epithelium; *V*, vitelline membrane. Some of the nuclei and parts of the cell boundaries of the outer yolk-laden cells are still visible.

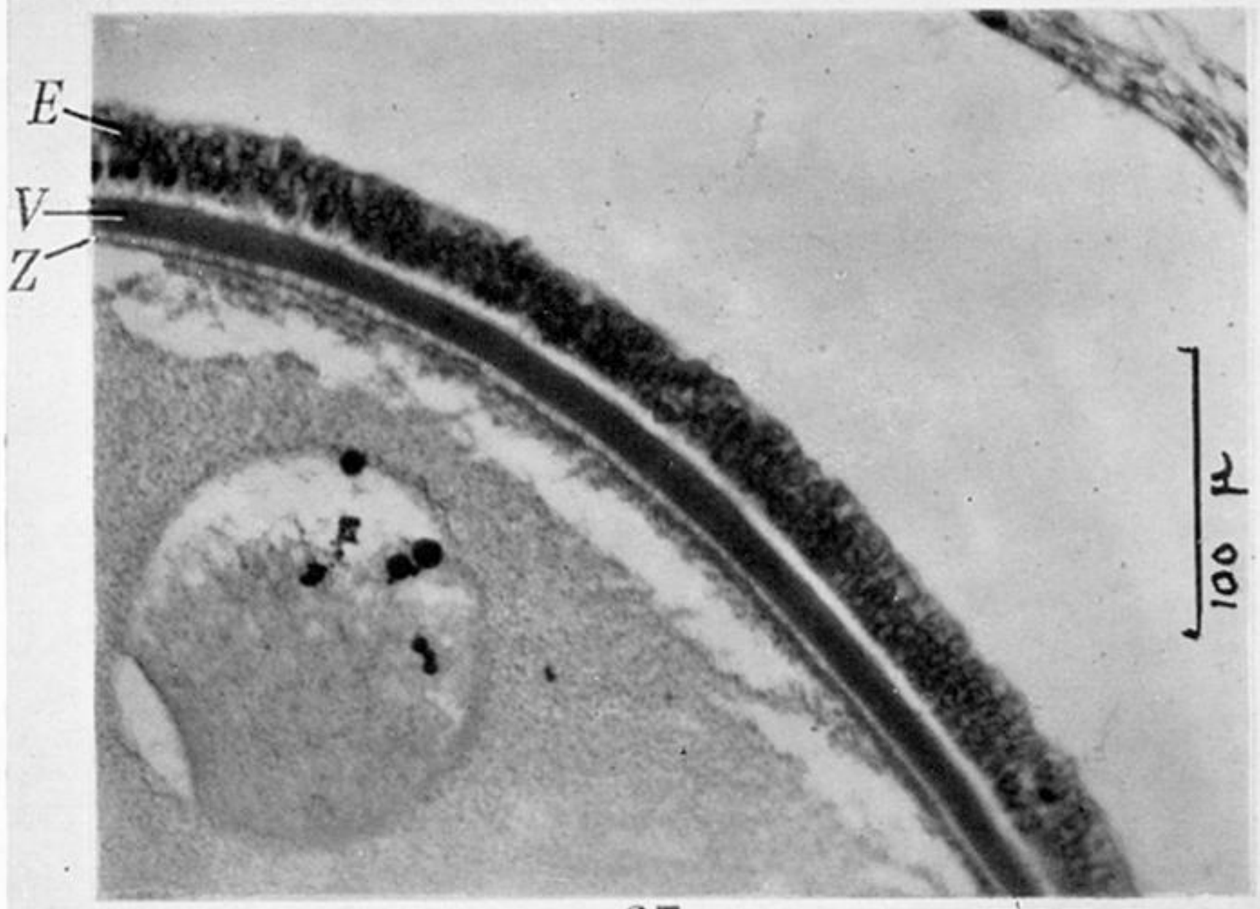
Figure 62. Section of ovary, showing two follicles (left and right) in which the material from the outer cells is being transferred to the oocyte. The nuclei lie centrally, surrounded by cytoplasm containing yolk material. The vitelline membrane is now thinner and is surrounded by an attenuated layer of epithelium; the yolk material of the outer cells is now confluent.

Figure 63. Section of an older follicle, in which the transfer of the yolk material through the epithelium has proceeded so far that the epithelium is in contact with the follicular wall over more than half the circumference.

Figure 64. Section of an older follicle. The transfer of yolk material is now nearly complete and the epithelium consists of more than a single layer of cells in most parts. The germinal vesicle is visible and the cytoplasm of the ovum is filled with yolk.

Figure 65. Section of a large follicle. The ovum has shrunk away from the follicle wall during fixation, taking with it the epithelium (*E*) which is closely applied to the thick vitelline membrane (*V*). The germinal vesicle (*G*) contains a group of nucleoli, and the staining reactions of the inner and outer zones of the yolk differ.

Figure 66. Section of part of a follicle wall. The ovum has shrunk away from the follicular wall, the separation being at the interface epithelium-vitelline membrane. *E*, the epithelium containing more than a single layer of cells; *T*, the theca.



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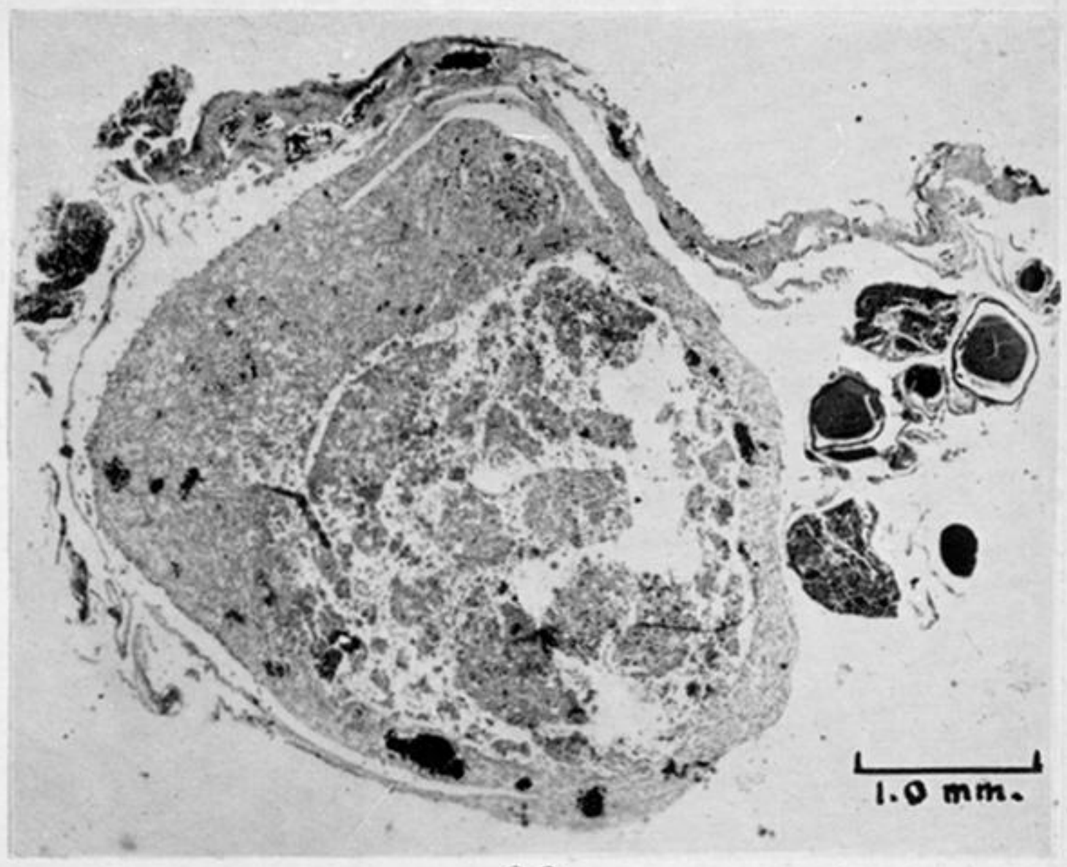

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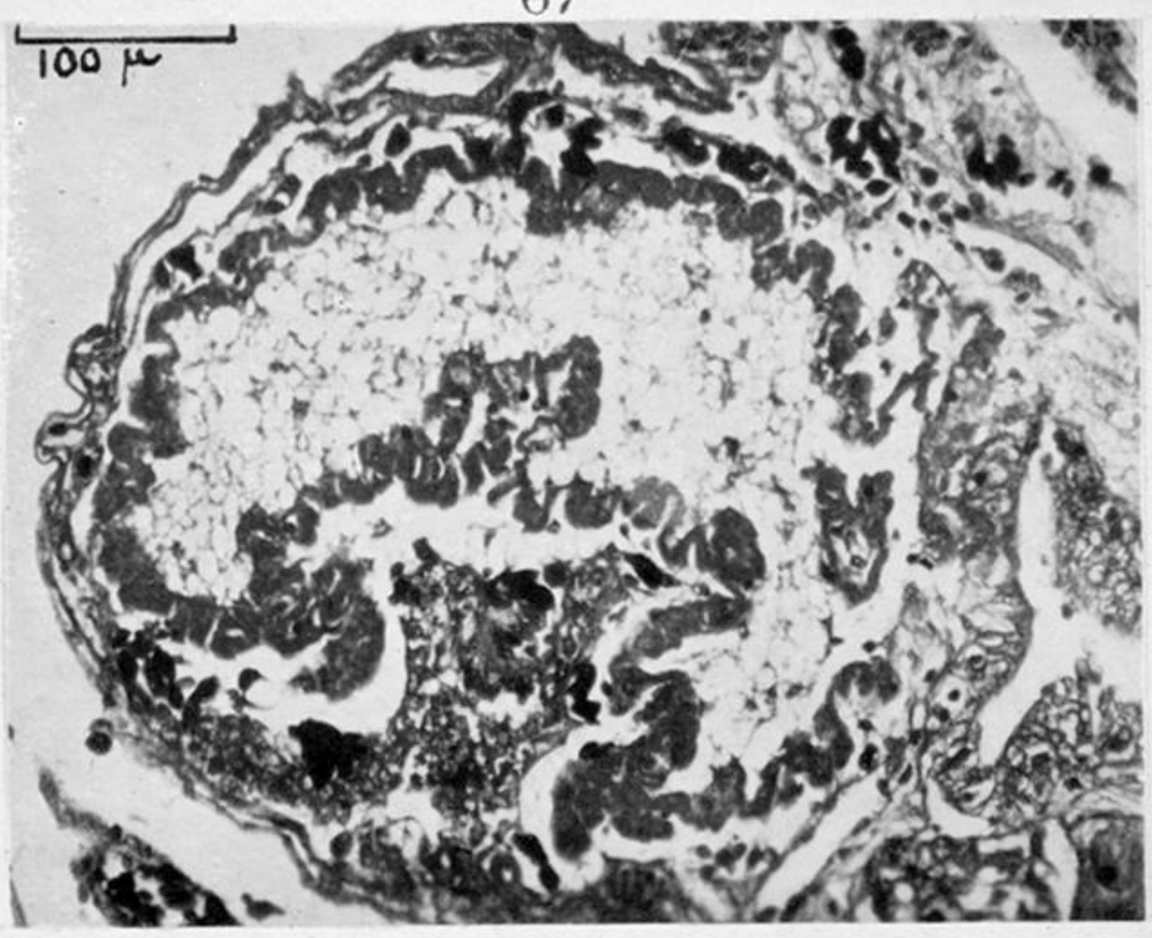

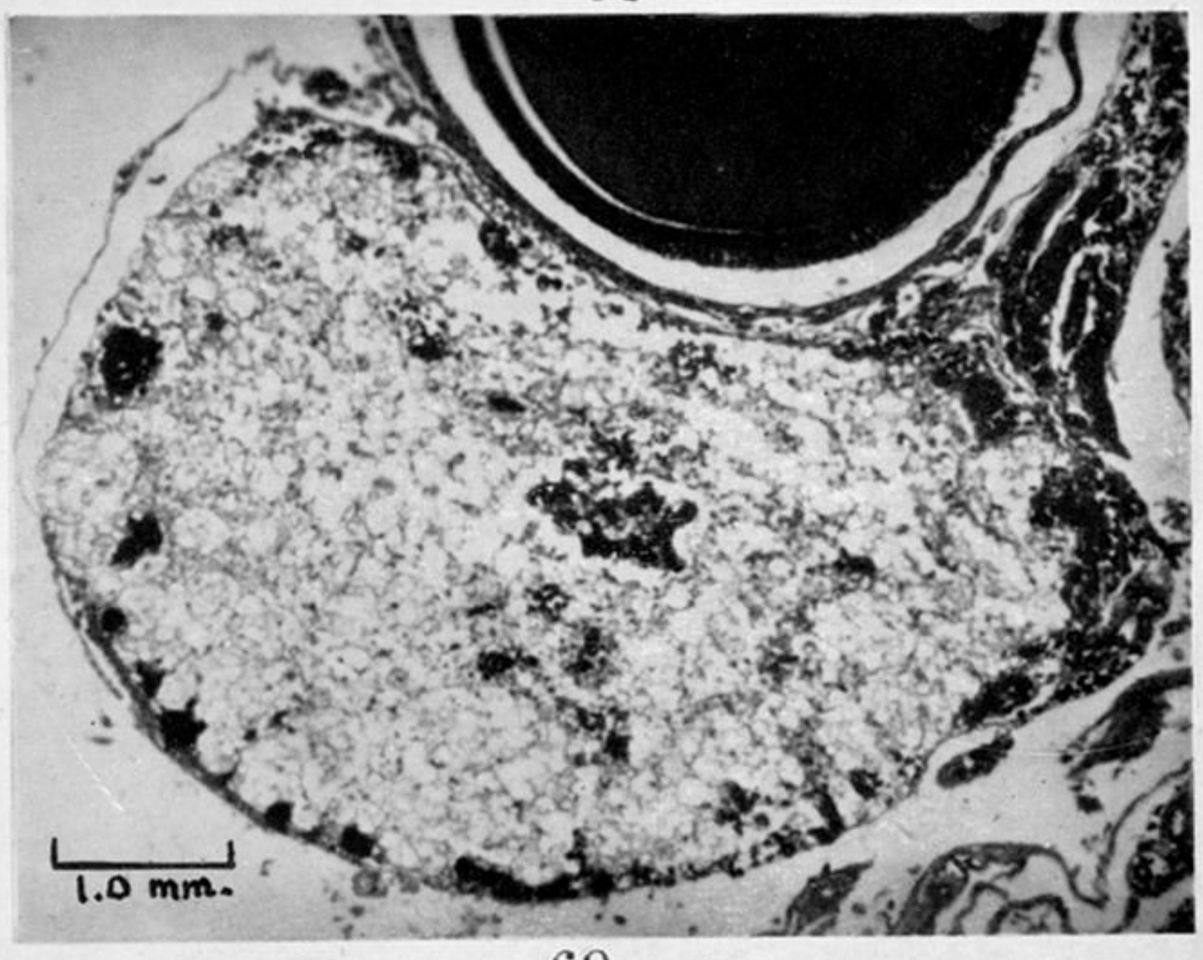

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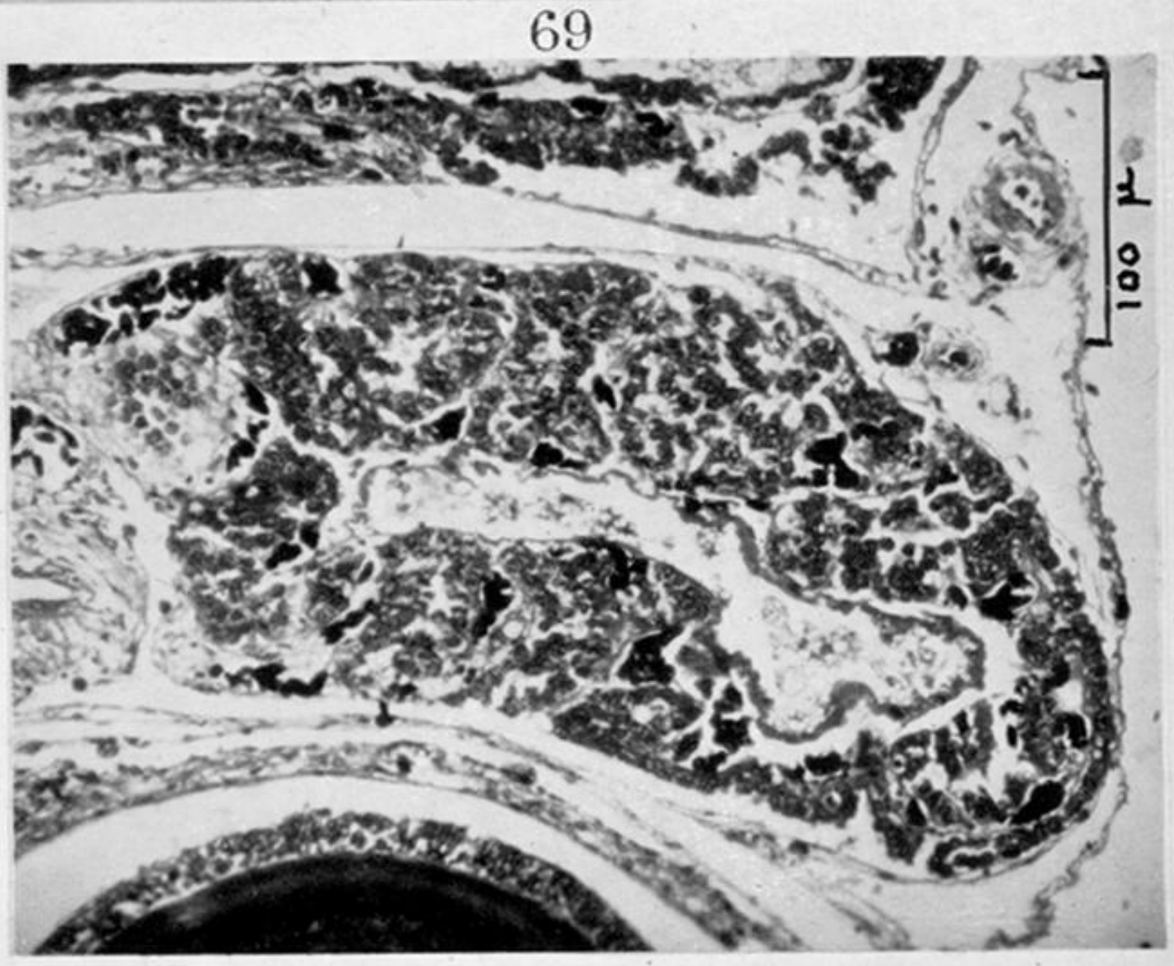

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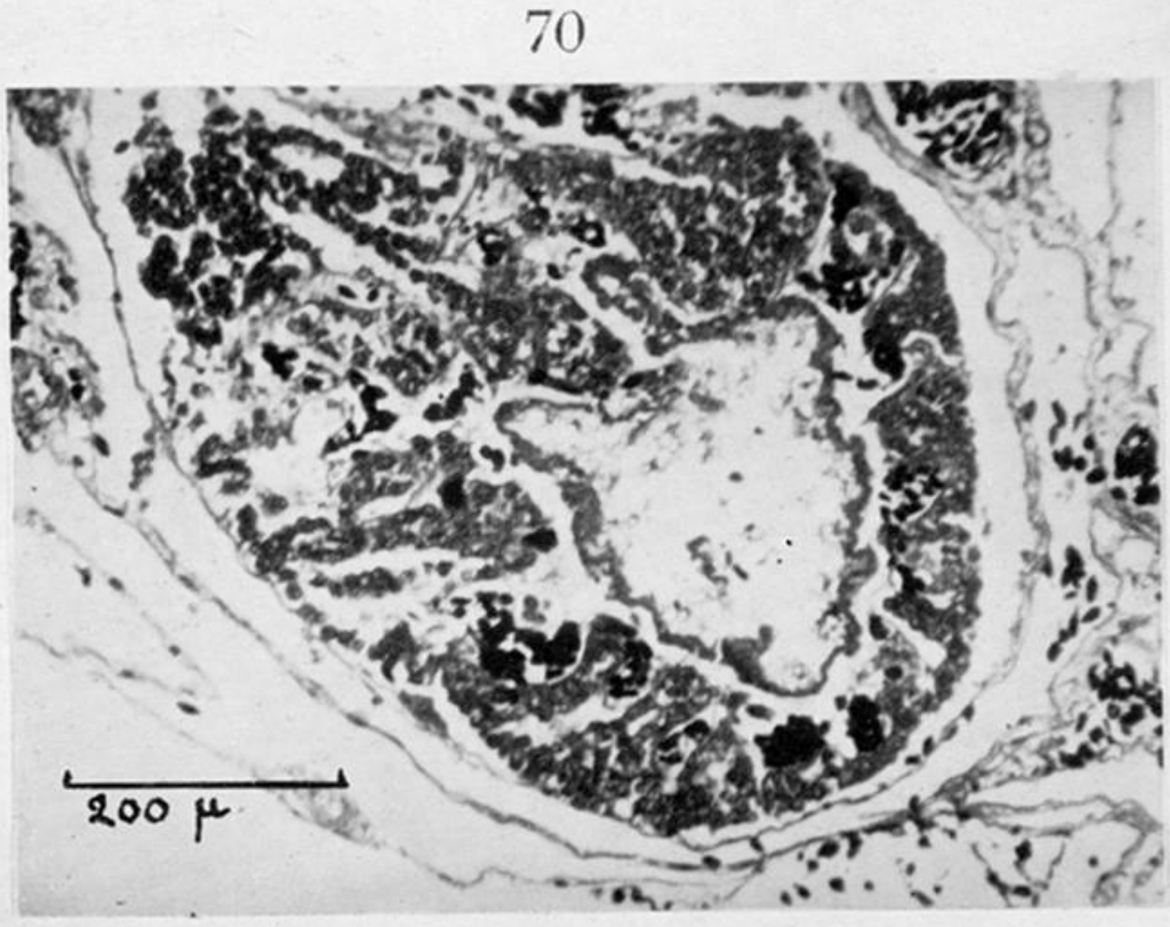

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PLATE 17

FIGURE 67. Section of part of an advanced follicle. The ovum has shrunk away from the follicular wall taking the epithelium with it. Part of the theca appears at the top right-hand corner; the germinal vesicle lies at the bottom left-hand corner. *E*, multilayered epithelium; *V*, vitelline membrane; *Z*, zona radiata.

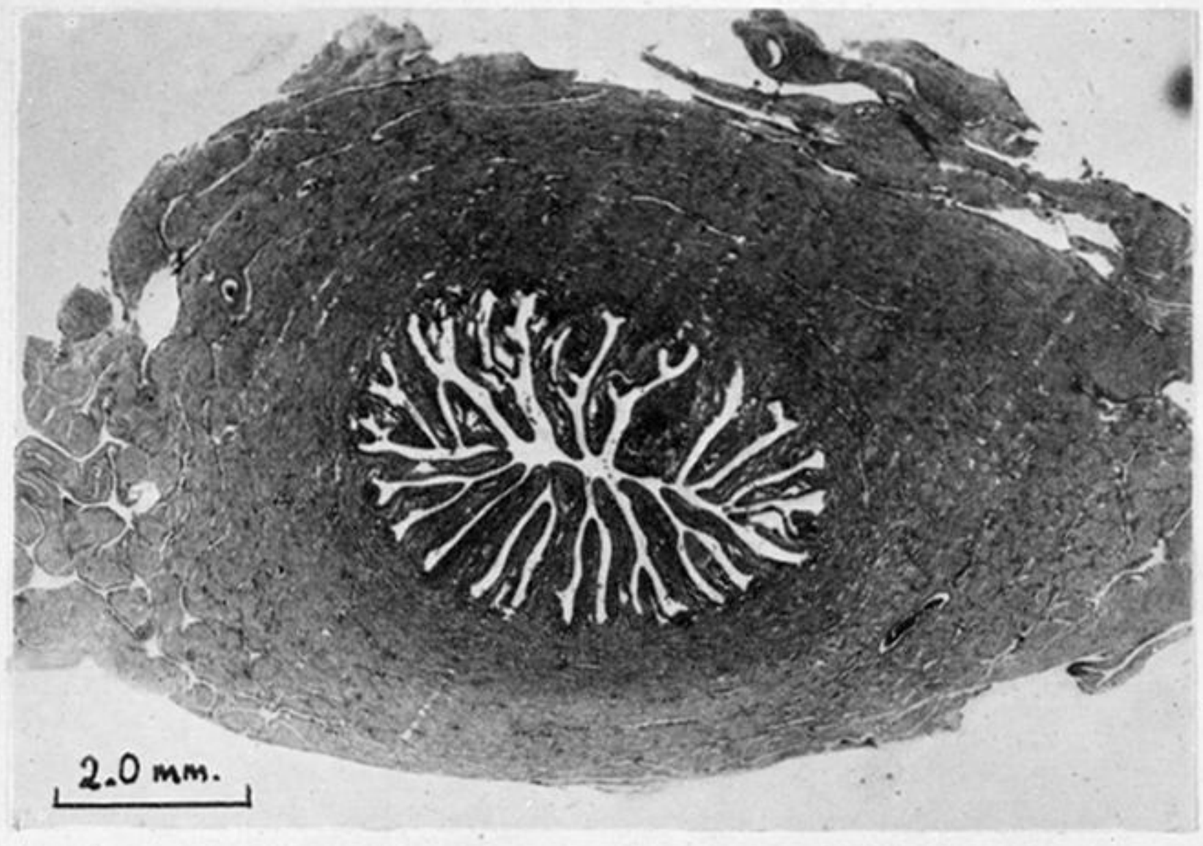
FIGURE 68. Section through a young corpus luteum of ovulation. The cavity, filled with loose cells and debris, lies eccentrically to the right of the follicle; the main mass of the cells of the corpus luteum lies to the left.

FIGURE 69. Section through an old corpus luteum of ovulation. The central cavity is almost obliterated and the body is filled with loose cells among which some small vessels wander.

FIGURE 70. Section of an atretic corpus luteum. The large cavity is surrounded by the wrinkled and dark-staining vitelline membrane within which lie the remains of the degenerate ovum. At the bottom centre the epithelium is proliferating and invading the cavity pushing the vitelline membrane before it.

FIGURE 71. Section of an older atretic corpus luteum. The remains of the ovum have almost disappeared from the central cavity which is still bounded by the reduced remnant of the vitelline membrane. The epithelium has proliferated so as to fill the greater part of the body, and there is considerable invasion by vessels (the darkest parts).

FIGURE 72. Sections of an old atretic corpus luteum. The central cavity is nearly lost and the remnant of the vitelline membrane is becoming tenuous. The body consists of a nearly solid mass of proliferated epithelial cells and small blood vessels.



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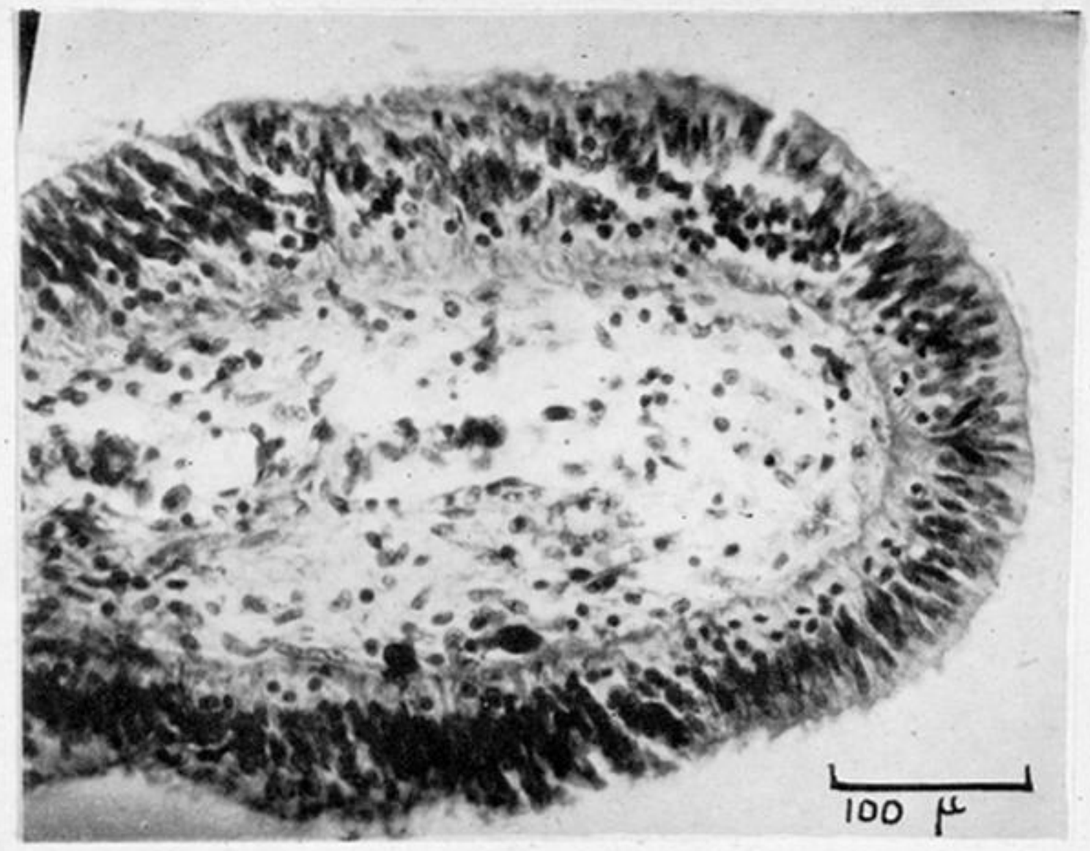

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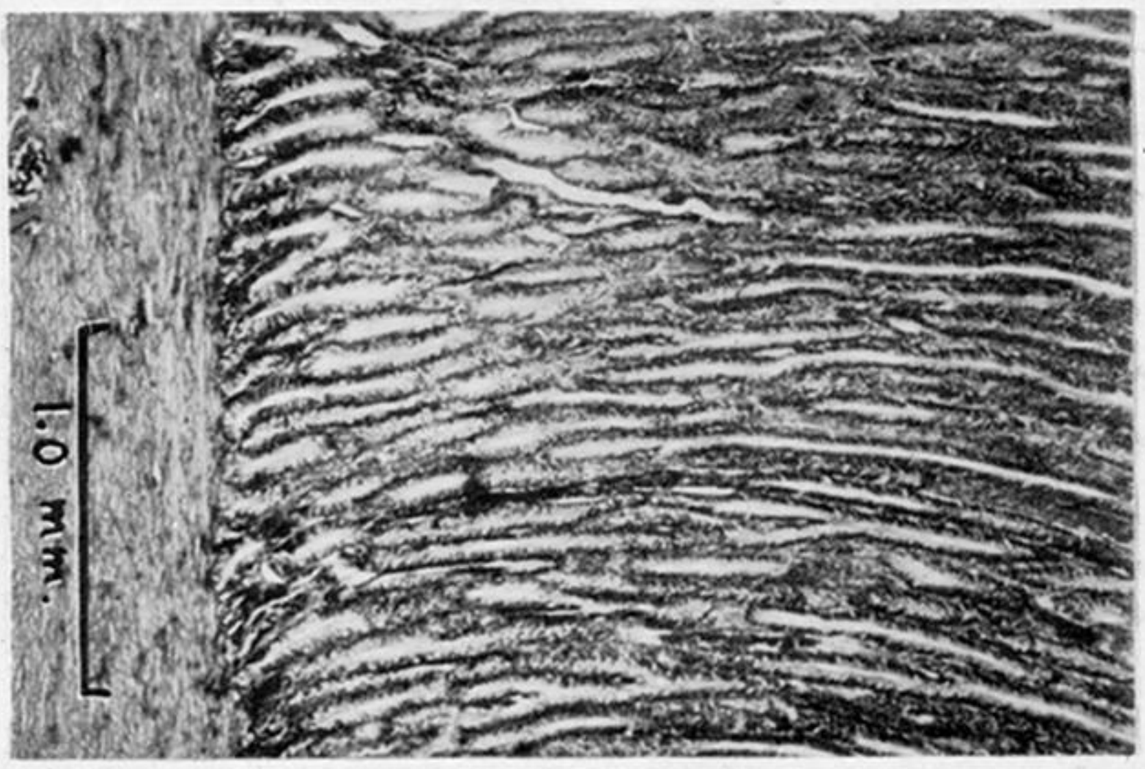

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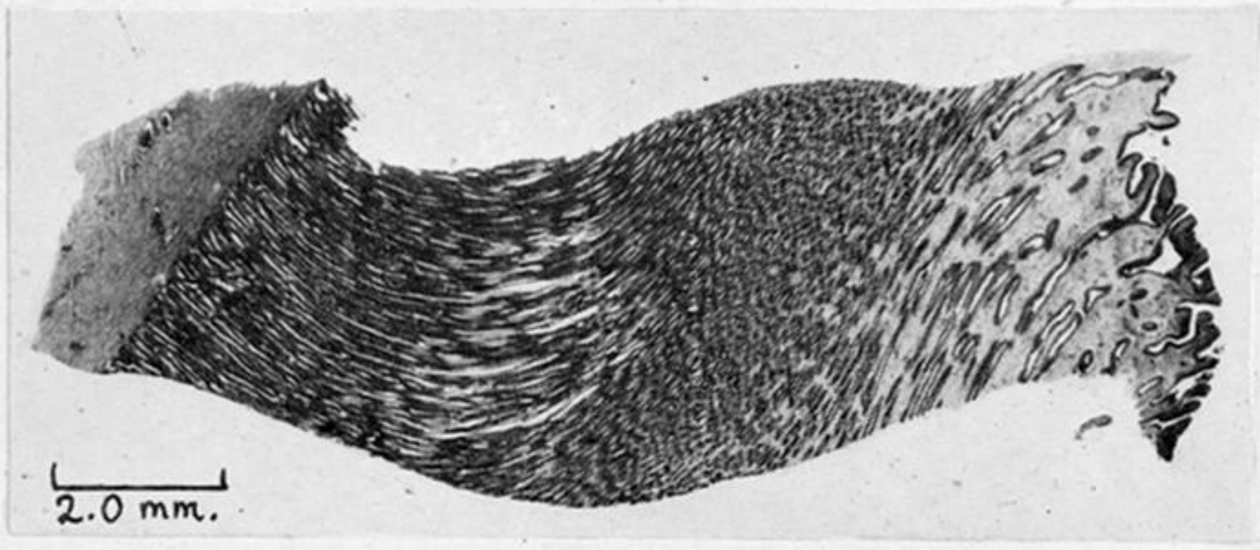

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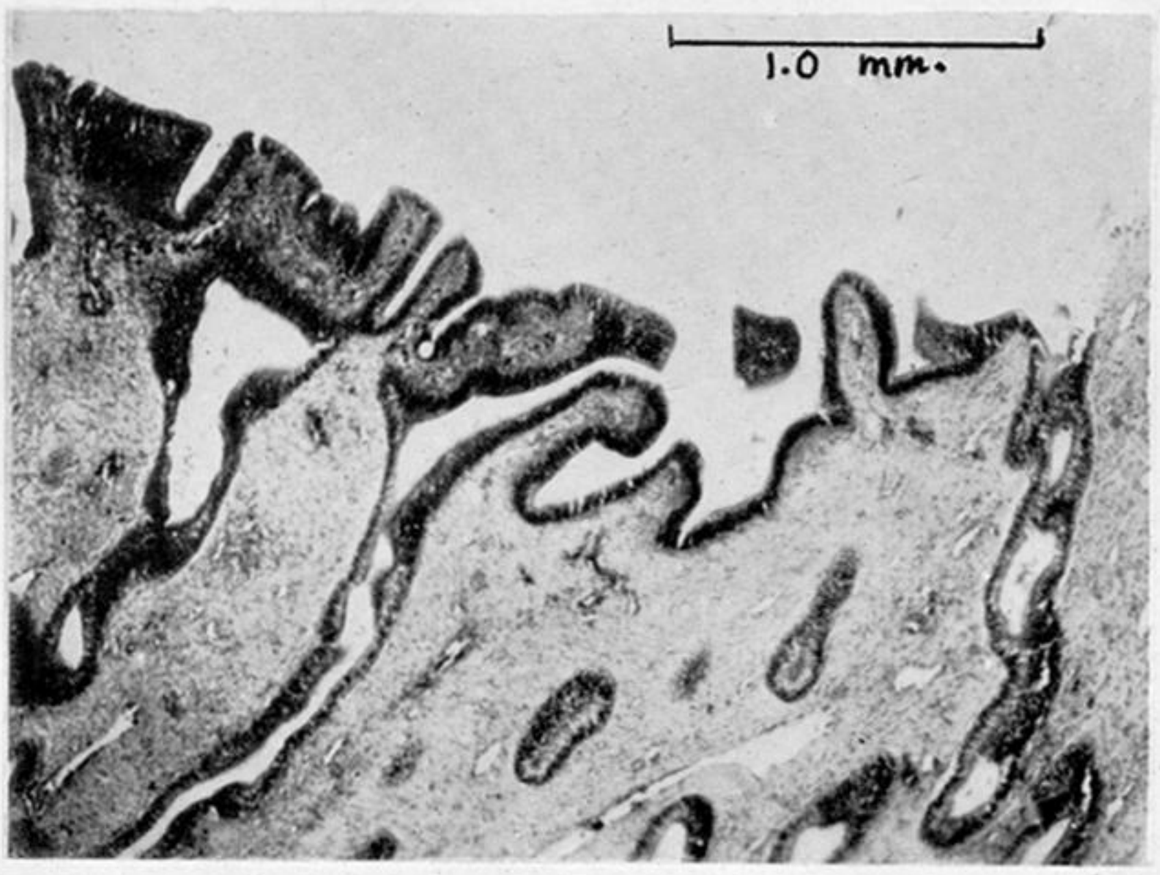

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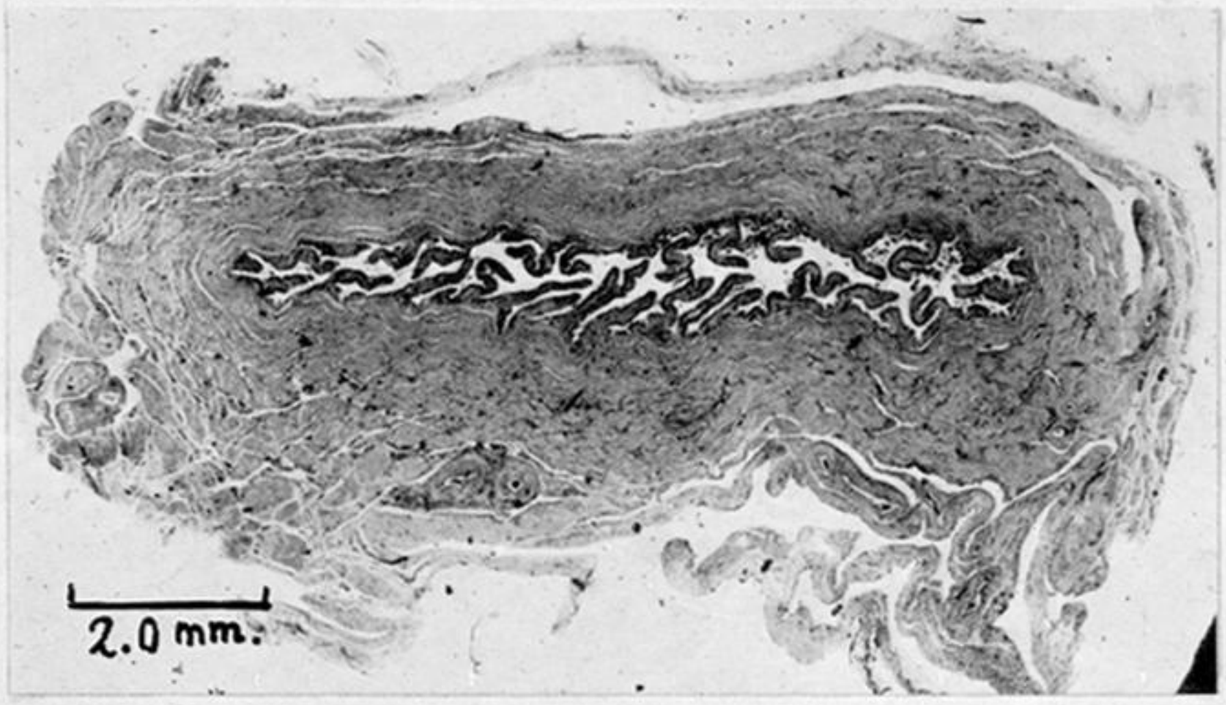

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Plate 18

Figure 73. Transverse section of the paired oviduct between the bifurcation and the nidamentary gland, showing the lumen nearly filled with longitudinal ridges, and the thick inelastic outer coat.

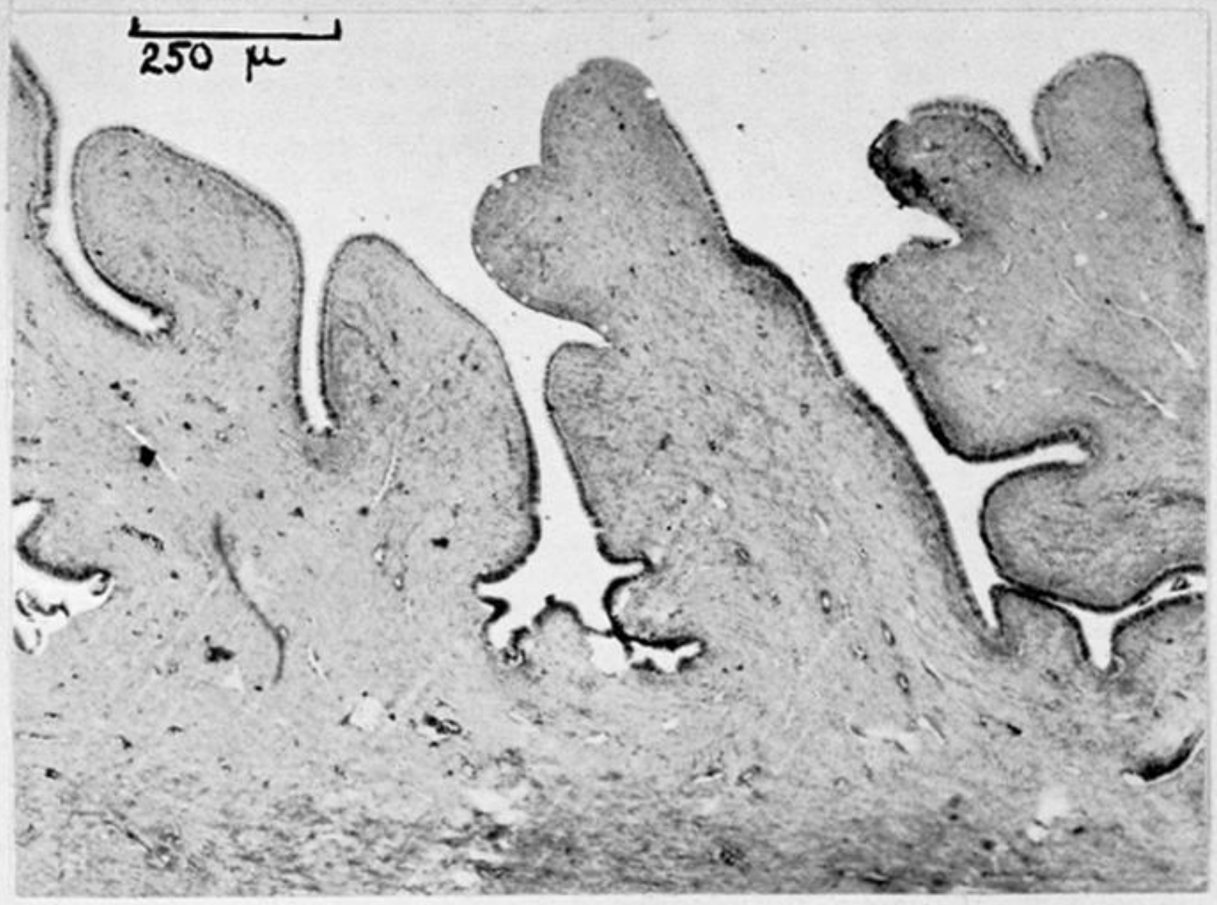
Figure 74. Transverse section of the summit of one of the ridges of the oviduct shown in figure 73, showing the epithelium with basal polyhedral cells and outer columnar ciliated ones.

Figure 75. Vertical section through the nidamentary gland. The base, abutting on the muscular wall, lies to the left and the mouths of the glands, opening into the main lumen, at the right.

Figure 76. Vertical section of the base of the nidamentary gland. The bases of the tubular glands which are closely packed and parallel to each other lie to the left against the muscular wall.

Figure 77. Vertical section of the nidamentary gland, showing the mouths of the glands opening into the lumen. The main lumen lies at the top, and the spiral shape of the distal ends of the gland tubules is shown on the right. The amount of connective tissue between gland tubules is much greater at this level than at the base.

Figure 78. Transverse section of the unpaired oviduct before its bifurcation, showing the high longitudinal folds lining the lumen.



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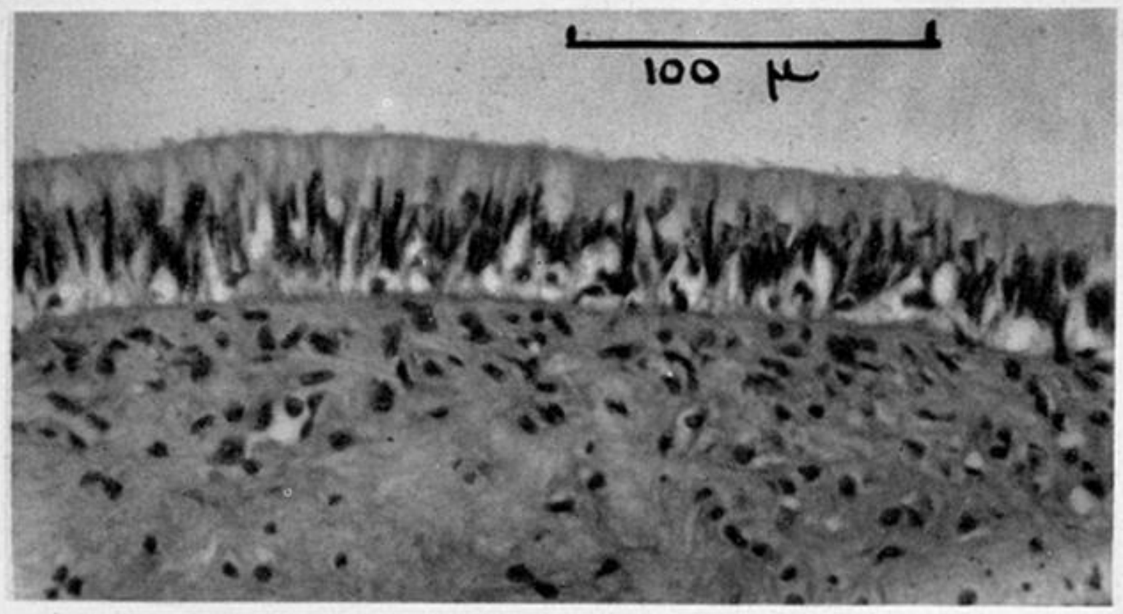

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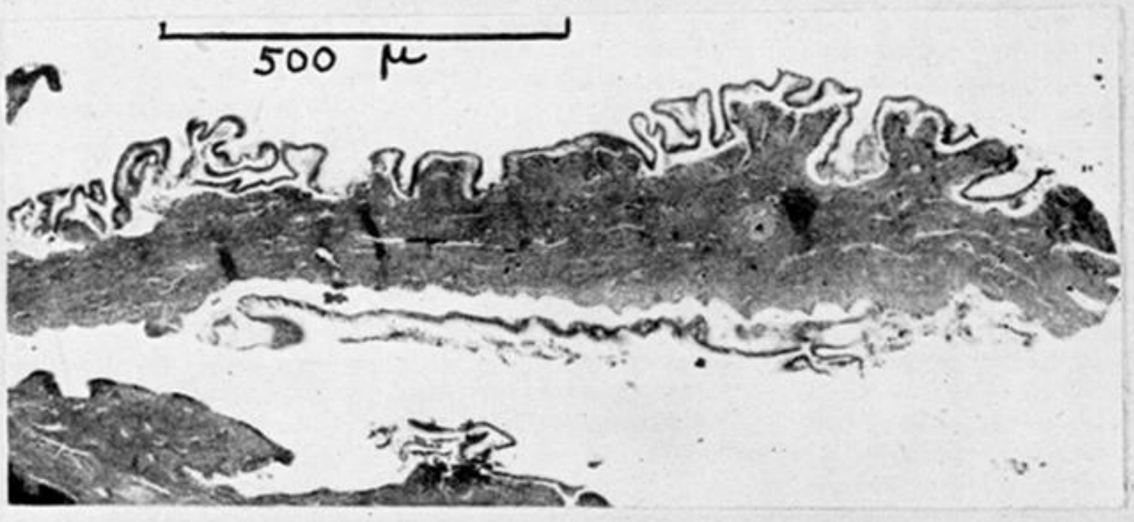

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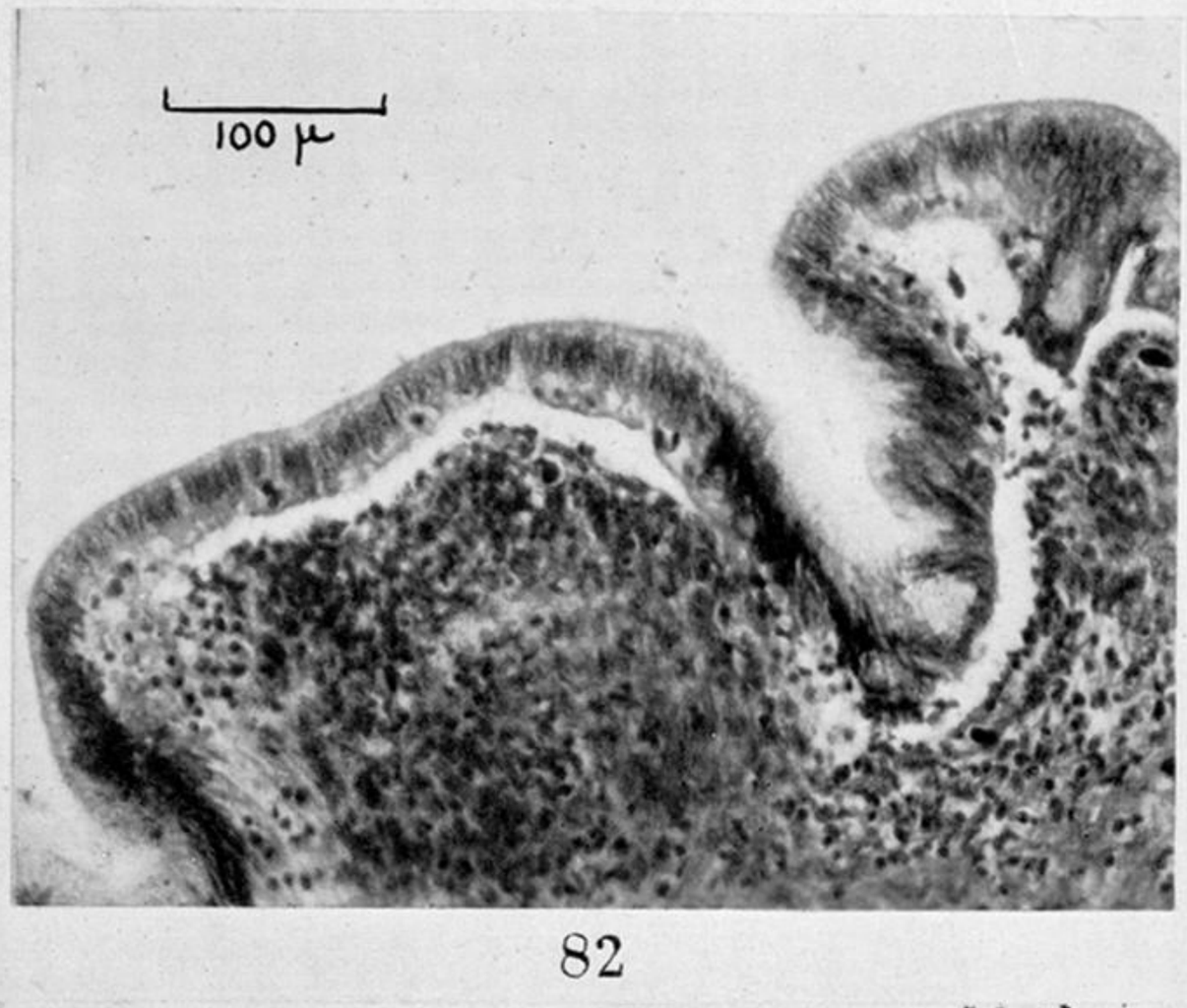

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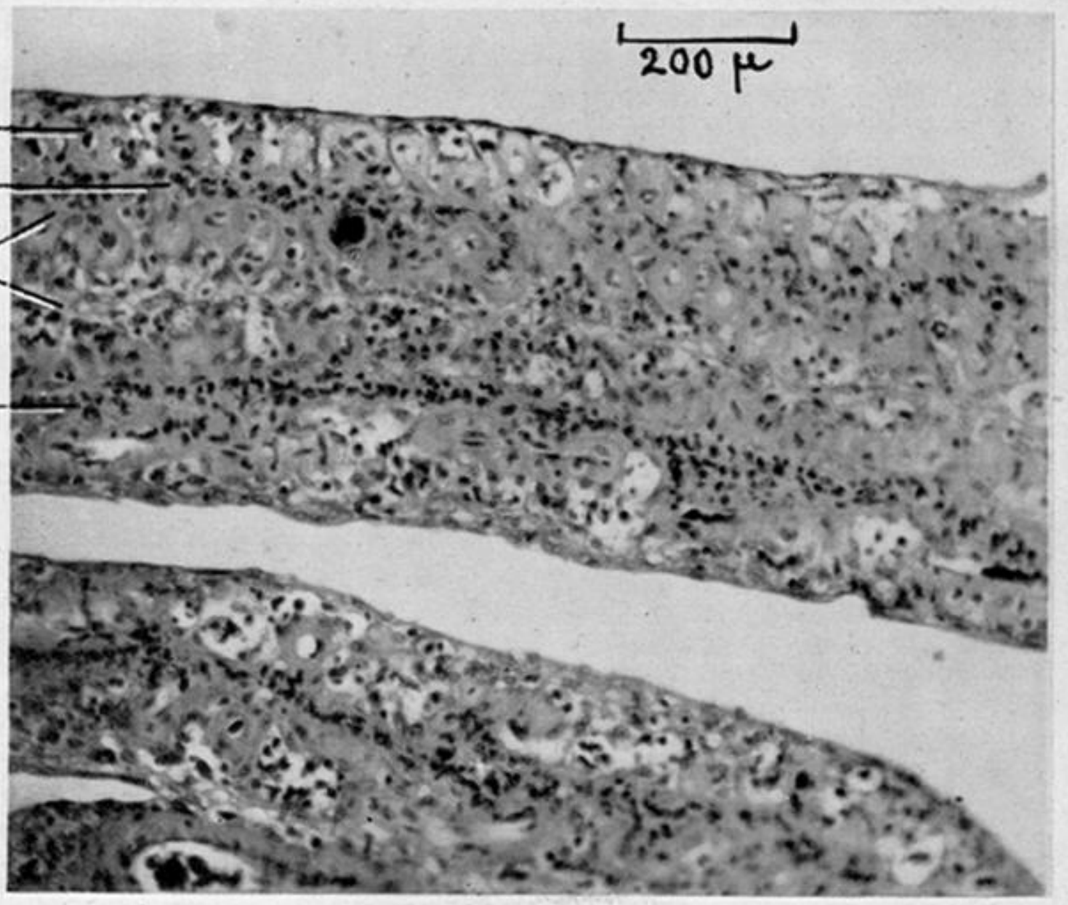

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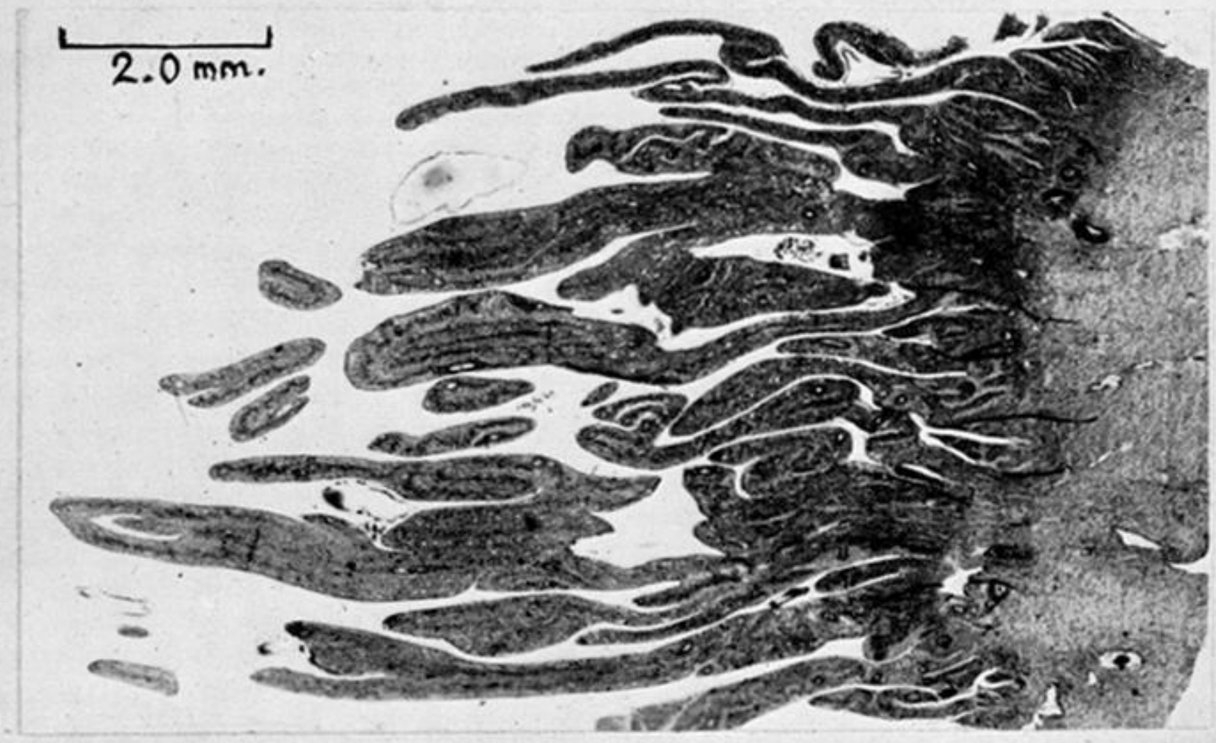

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PLATE 19

FIGURE 79. Transverse section of the proximal part of the isthmus, showing the low wide longitudinal ridges covered by tall columnar epithelium.

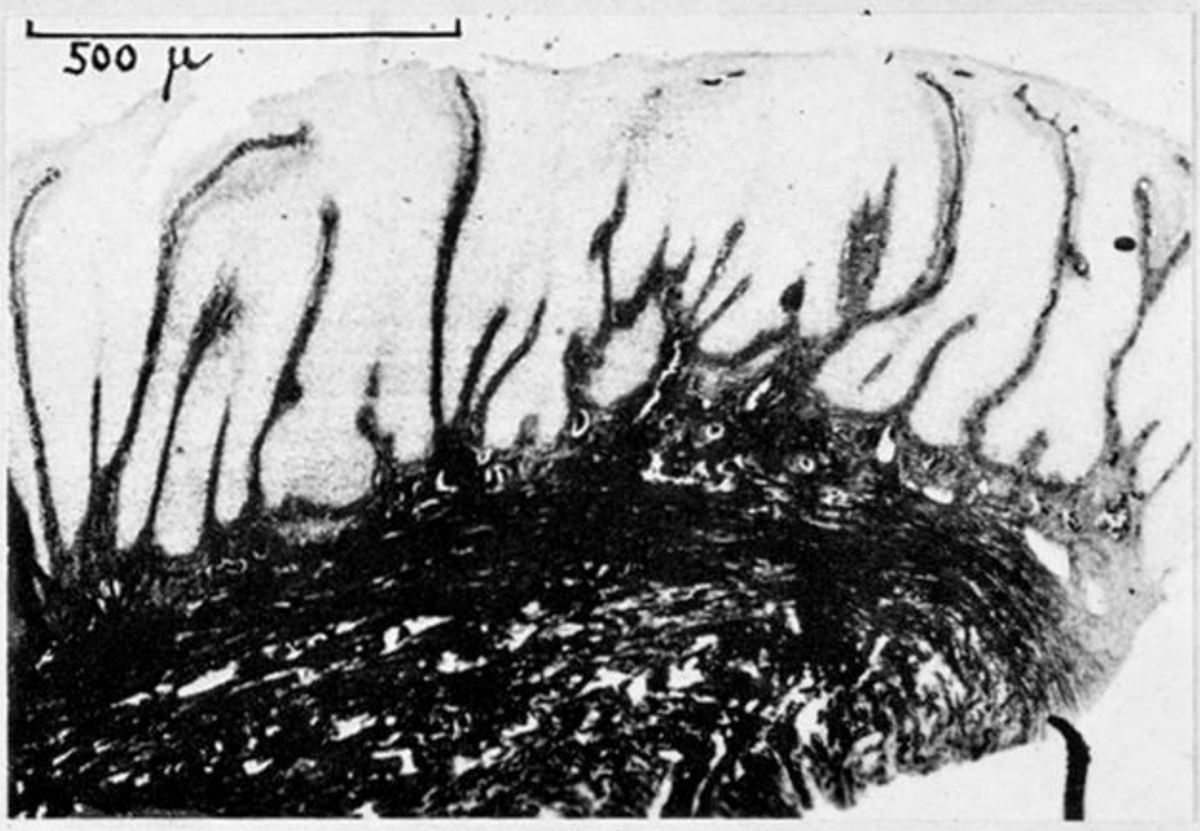
FIGURE 80. Section of the columnar ciliated epithelium of the proximal part of the isthmus, showing the dark-staining elongate nuclei.

FIGURE 81. Transverse section of one of the tall ridges of the proximal part of the uterus (one of the 'pages' of the 'book'), showing the minor ridges of the surface.

FIGURE 82. Transverse section of the surface of the ridge shown in figure 81. The epithelium is not ciliated, and the oval nuclei lie near the surface so that a clear sub-surface zone is not present.

FIGURE 83. Vertical section of part of the uterus with trophonemata. The muscular wall lies to the right, and the trophonemata project into the uterine lumen towards the left.

FIGURE 84. Vertical sections through two trophonemata. *C*, connective tissue strands of the core; *V*1, tortuous vessels running longitudinally inside the core; *V*, tortuous vessels outside the core.



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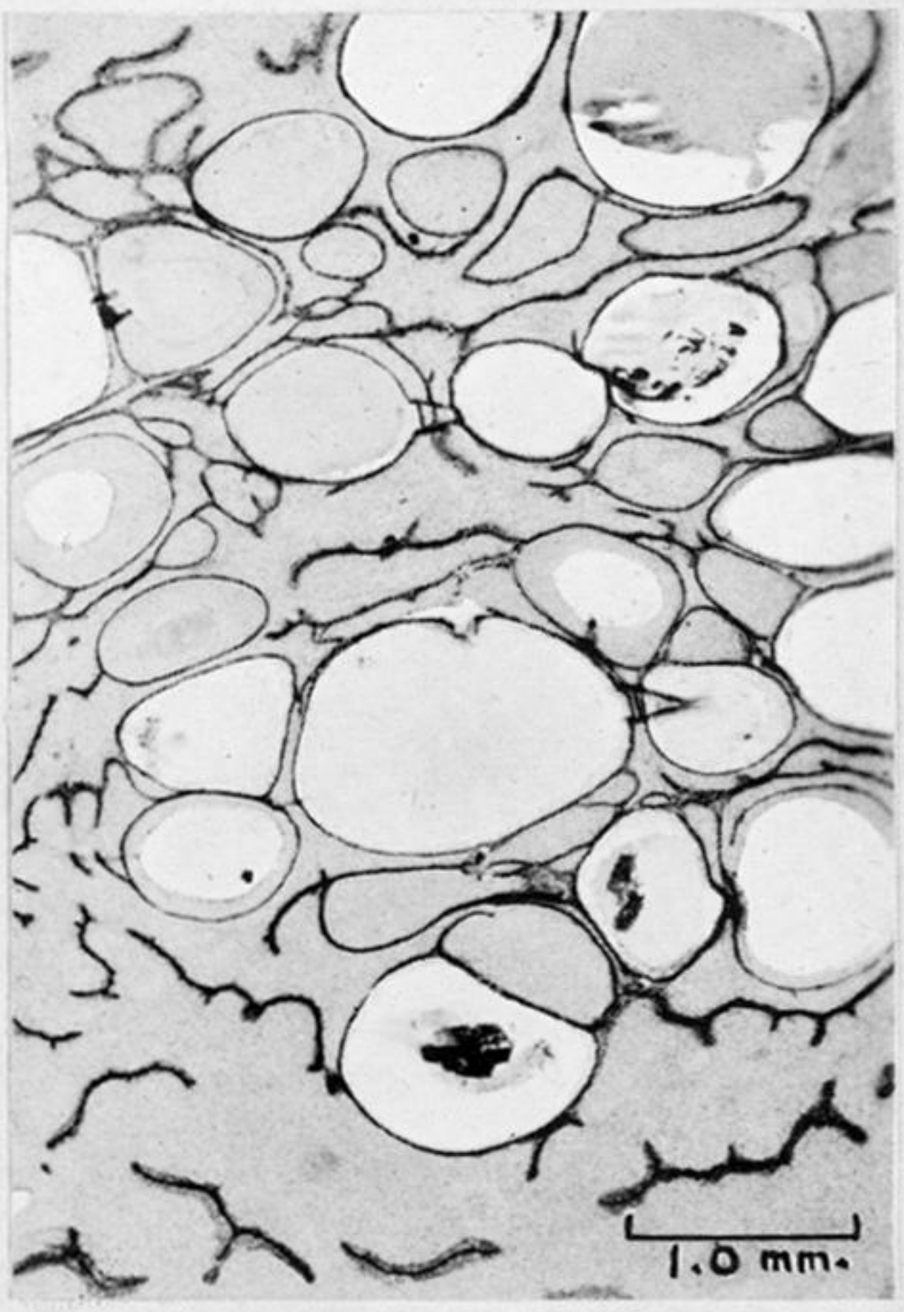

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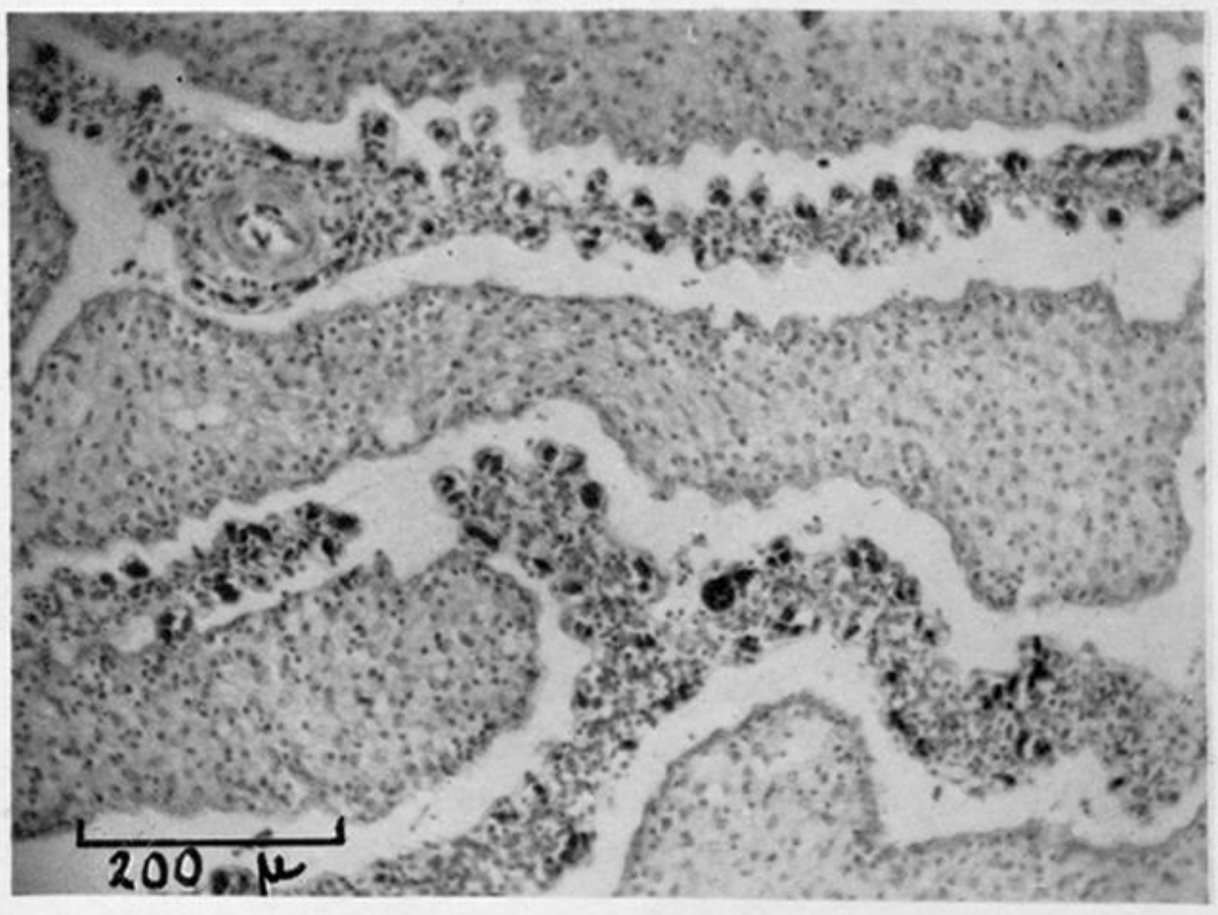

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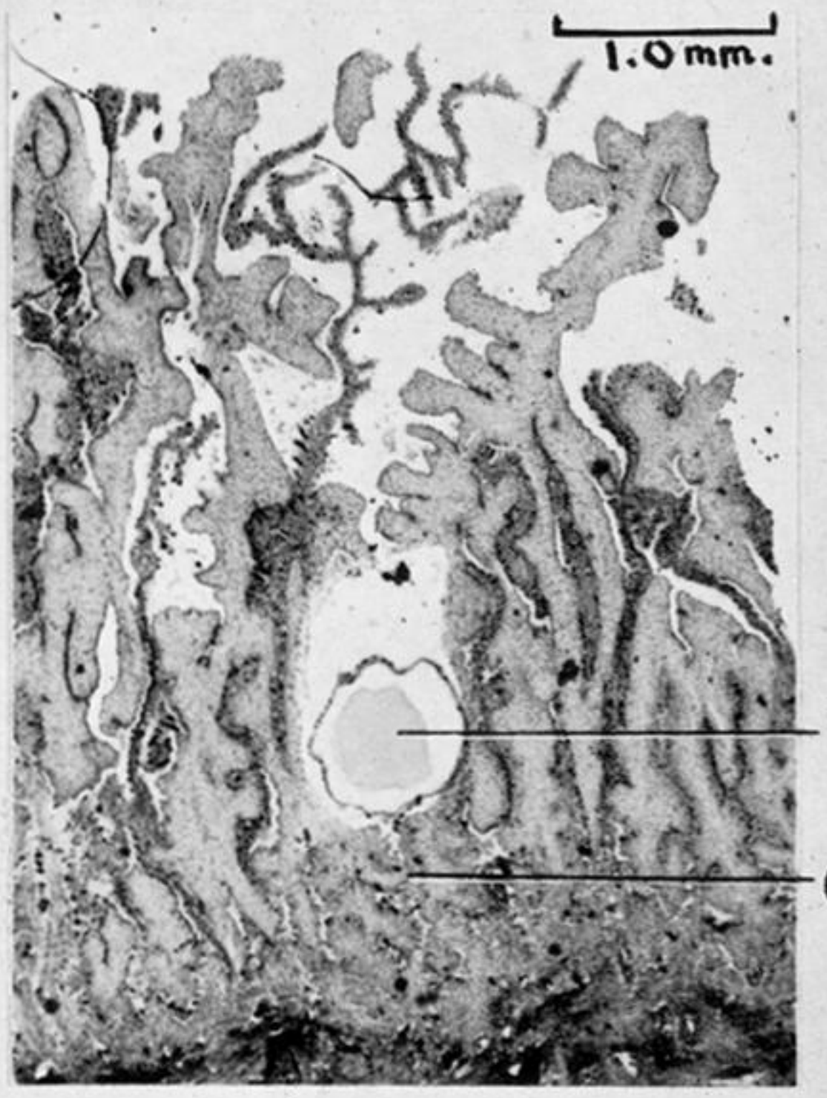

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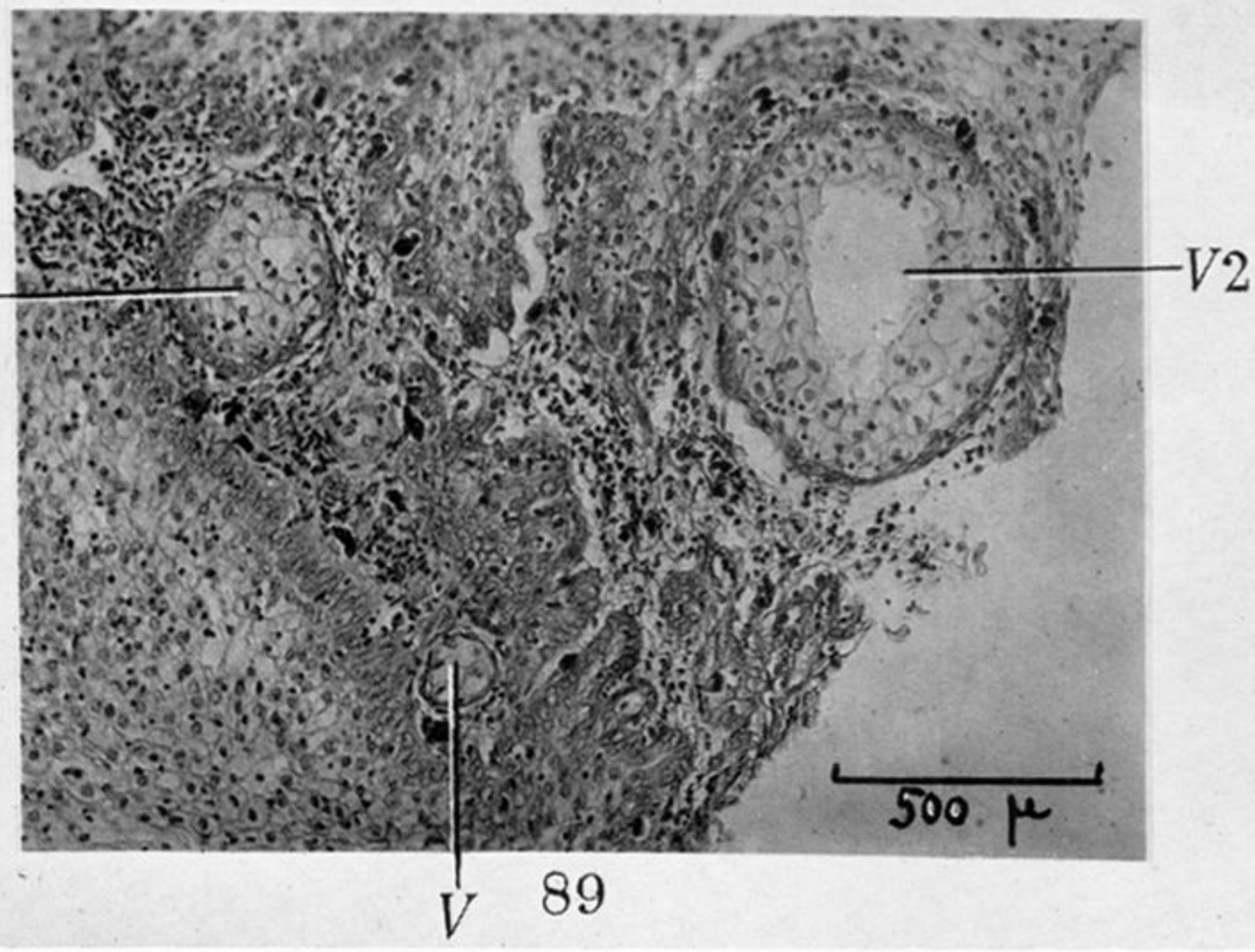

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PLATE 20

FIGURE 85. Vertical section through the wall of the uterus showing the trophonemata embedded in a mass of proliferated epithelial cells. The muscular wall lies below, the uterine lumen at the top.

FIGURE 86. Vertical section through a part of the uterus similar to that shown in figure 85. The base lies to the right, the uterine lumen to the left. The epithelial masses have shrunk away from the trophonemata which are seen as narrow strands with tortuous vessels coursing along their surfaces. The deep layers of the epithelium, adjoining the shrinkage cavities, are compact, the more superficial ones, at the centres of the epithelial masses, are swollen.

FIGURE 87. Horizontal section through part of the uterus where the trophonemata are embedded in epithelial cells, showing numerous vesicles, some lined with a layer of epithelial cells and some containing a coagulum.

FIGURE 88. Vertical section through part of the uterus, showing trophonemata, epithelial cell masses, and a vesicle in course of formation. *V*, vesicle. *C*, connective tissue strand of the trophonema from which the vesicle arises.

FIGURE 89. Horizontal section through part of the cell mass and trophonemata, showing the earliest stages in the formation of vesicles. *V*, a vesicle consisting of a few cells surrounded by a very thin layer of connective tissue; no lumen; *V*1, a larger vesicle in which the cells are swollen, and the degeneration of one cell has produced the first beginning of the lumen; *V*2, a young vesicle with connective tissue sheath, swollen internal cells, and a lumen produced by the degeneration of some of the latter.