THE GUBERNACULUM TESTIS OF THE PIG (*SUS SCROPHA*)

By K. M. BACKHOUSE and H. BUTLER

Charing Cross Hospital Medical School, London, and Kitchener School of Medicine, University of Khartoum, Sudan

John Hunter (1762) first described the structure, which he named the gubernaculum testis, 'a substance which runs down from the lower end of the testis to the scrotum.' He considered it to be 'vascular and fibrous, and covered by the fibres of the cremaster or musculus testis which is placed immediately behind the peritoneum; this is not easily ascertained in the human subject, but it is very evident in other mammals, more especially in those whose testicles remain in the cavity of the abdomen after the animal is full grown.'

Since Hunter, the gubernaculum has been described repeatedly. In general the earlier authors, Paletta (1777), Wrisberg (1779), Vicq d'Azyr (1780), Martin (1780) and Brugnoni (1785) described a peritoneal covered structure, extending from the caudal pole of the testis to the scrotal floor, containing fibrous and/or muscular tissues, yet being soft and jelly-like. In the course of time the jelly-like nature of the gubernaculum testis became ignored and it is currently described as a fibro-muscular cord or band (Hamilton, Boyd & Mossman, 1952; Patten, 1948). Confusion was caused by Seiler's (1817) studies on a variety of adult mammals, each having its own peculiarities of testicular anatomy and physiology, because he uncritically applied facts derived from these studies to the gubernaculum testis of the human foetus. Inaccurate observations on adult rodents (particularly the *Sciuridae*) led him to believe that the function of the cremaster muscle is to pull the testis from the abdominal cavity into the scrotum: hence he assumed that the 'inverted cremaster' of the human foetus behaved in a like manner.

Seiler's views received support from Curling (1841) who described a layer of well developed striped muscle fibres surrounding the main bulk of the soft transparent and gelatinous gubernaculum. He believed that this muscle layer, with its various distal attachments, is gradually everted during testicular descent and persists as the cremaster muscle.

However, by that date the views of Cloquet (1817) and Carus (1827) had gained currency, viz. that the cremaster muscle is formed mechanically by the passage of the testis through the abodominal wall; indeed this idea that the testis or its associated gubernaculum burrowed its way through the layers of the abdominal wall dragging them with it to form the coverings of the cord and testis is still to be found in current textbooks (Keith, 1948).

The statement made by Curling that 'the testicle, therefore, does not pass directly and abruptly into a pouch prepared to receive it, but carries the peritonaeum with it...' is at variance with the findings made in the present study in the pig in which the processus vaginalis does in fact invade the gubernacular tissue in advance of the testis.

Lockwood (1887–88) attempted to equate the positions of the distal terminations of the human gubernaculum testis with those sites commonly occupied by an ectopic testis. He admitted that he could not find all the 'tails' of the gubernaculum testis which he postulated in the foetus, but insisted that they must exist because of the various sites of occurrence of ectopia testis and the presence of a fibrous band tethering such a testis to its abnormal site. Lockwood ignored the jelly-like consistency of the gubernaculum testis and referred to it as a fibro-muscular cord or band.

In view of the discrepancies in the accounts of the gubernaculum it was decided to make a thorough investigation of its development and structure in pig embryos and foetuses. This animal was chosen for these reasons: (1) it was possible to obtain abundant material during the critical period of testicular descent; (2) the gubernaculum testis is large; (3) there is precocious development of the processus vaginalis, and the cremaster muscle consists only of a single lateral fasciculus, thus greatly facilitating morphological analysis.

MATERIALS AND METHODS

Over 100 specimens of pig embryos and foetuses ranging in size from 6 mm. to 350 mm. crown-rump (C.R.) length were examined macroscopically and histologically. Many dissections of unfixed specimens of the larger foetuses were made within 2–3 hours of the mother's death. Comparable stages in the sheep (*Ovis aries*) were also examined.

OBSERVATIONS

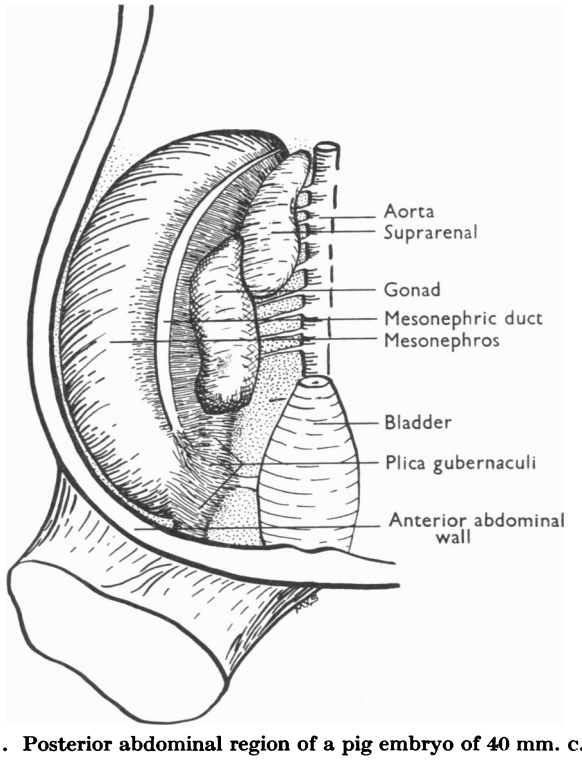
1. *Embryos of* 20–30 *mm.* C.R. *length*

A prominent feature of early pig embryos is the very large mesonephros whose caudal pole is in contact with the inguinal region of the anterior abdominal wall. The gonad develops at the cranial end of the mesonephros and the size of the latter organ appears to delay the formation of that part of the gubernaculum testis which extends from the gonad to the anterior abdominal wall. A strip of cuboidal coelomic epithelium overlying a thin layer of undifferentiated mesenchyme, the precursor of the gubernaculum testis within the abdomen, extends from the gonad, across the mesonephros and umbilical artery, to the inguinal region. This mesenchyme is continuous with a core of mesenchyme which demarcates the future inguinal canal within the differentiating abdominal wall muscles and which, in turn, is continuous externally with the mesenchyme in the genital swellings. Thus the precursor of the gubernaculum testis is a continuous strip of mesenchyme extending from the caudal pole of the gonad to the interior of the genital swelling. As yet, its abdominal part does not form a prominent intra-abdominal ridge.

2. *Embryos of* 30–50 *mm.* C.R. *length*

The mesonephros has grown in size but not so much as the body wall, and the caudal pole of the mesonephros moves away from the inguinal region of the anterior abdominal wall. The testis, still situated well cranialwards on the mesonephros, now possesses a well-defined mesorchium. The mesenchymatous continuum, linking the gonad with the scrotal pouch through the anterior abdominal wall musculature, exhibits marked growth, particularly in the abdomen. Within the abdomen the

gubernaculum testis now forms a well-defined ridge, the *plica gubernaculi* (the so-called ligamentum inguinale of Klaatsch, 1890), projecting into the abdominal cavity and carried on a mesentery. Cranially the plica gubernaculi merges with the mesorchium at the caudal pole of the testis and is also continuous with the mesenchyme surrounding the mesonephric duct (Text-fig. 1). Thus a part of the mesonephric duct is contained within the gubernaculum. The plica gubernaculi then crosses the caudal pole of the mesonephros and the umbilical artery to reach the inguinal region. That part of the plica gubernaculi overlying the mesonephros is less prominent than that



Text-fig. 1. Posterior abdominal region of a pig embryo of 40 mm. C.R. length showing the gubernaculum testis within the abdomen.

between the caudal pole of the mesonephros and the anterior abdominal wall. The processus vaginalis commences to form around the junction of the plica gubernaculi and the gubernacular mesenchyme in the site of the future inguinal canal, as an evagination of the coelomic cavity into the gubernacular mesenchyme of the abdominal wall. This evagination only extends around three sides of the column, leaving a mesentery in continuity with that of the already formed plica gubernaculi which therefore appears to enter the anterior abdominal wall beneath a prominent peritoneal covered lip. At the point of invasion, the coelomic cells are cuboidal and mitotic figures may be seen.

In a 38 mm. C.R. length embryo (Pl. 1, fig. 1), the plica gubernaculi between the lower pole of the mesonephros and the blind tip of the processus vaginalis is approximately 0·2 mm. long of which 0·1 mm. lies within the processus vaginalis: in an

embryo of 45 mm. C.R. length the equivalent distances are now 0·6 mm. and 0·15 mm. respectively (Pl. 1, fig. 2).

That part of the gubernaculum testis within the inguinal canal is a mass of relatively dense mesenchyme into which the processus vaginalis grows. It is separated from the well-differentiated abdominal wall muscles by a small amount of looser mesenchyme. As yet, the processus vaginalis has only penetrated for about one-fifth of the total length of the inguinal canal. Beyond the processus vaginalis, the solid mass of mesenchyme is continuous, through the external inguinal ring, with subcutaneous mesenchyme between the abdominal and thigh muscles. Here the gubernaculum testis is less well defined since the subcutaneous tissues have not yet differentiated but it can be identified as a strand of relatively dense mesenchyme surrounded by looser tissue. This strand is, in turn, continuous with a globular mass of relatively dense mesenchyme which forms the central core of the developing scrotum (Pl. 1, fig. 3).

From about 40 mm. C.R. length onwards, the cremaster muscle fibres are apparent and differentiate from the gubernacular mesenchyme contained within the inguinal canal. Initially, this short fasciculus of fibres is entirely contained within the inguinal canal and neither its proximal nor distal attachments are apparent (Pl. 1, fig. 2).

3. *Embryos of* 50–100 *mm.* C.R. *length*

During this period involution occurs in the caudal pole of the mesonephros which underlies the cranial part of the plica gubernaculi and this is associated with an increase in size of the cranial part of the gubernacular ridge. In an 83 mm. C.R. length foetus, the portion of the plica gubernaculi between the testis and the caudal pole of the mesonephros is 2 mm. long and the portion caudal to the mesonephros, where the distal half lies within the processus vaginalis, is 2 mm. long (Pl. 1, fig. 4). Thus the length of the plica gubernaculi from the testis to the internal ring is 3 mm., and a further 1 mm. to the blind tip of the processus vaginalis.

The processus vaginalis continues to extend further into the inguinal canal but does not yet emerge from the external inguinal ring. The lip at the entrance to the processus vaginalis now forms the long valve-like flap found in the adult animal. The mesenchyme of that part of the plica gubernaculi situated within the processus vaginalis has a more densely staining ground substance than the rest of the gubernaculum. The cremaster muscle has increased in size and its origin from the inguinal ligament, lateral to the external ring, is now apparent. The muscle is confined to the inguinal canal, and no fibres run cephalically towards the testis.

Beyond the blind tip of the processus vaginalis the inguinal canal contains a solid mass of mesenchyme which is continuous, through a strand of mesenchyme in the groin, with the intra-scrotal part of the gubernaculum testis. The gubernacular mesenchyme of the groin and scrotum becomes more clearly delineated as a result of the differentiation of the surrounding tissues. The subcutaneous mesenchyme of the scrotum and lower abdominal wall contains numerous irregular spaces lined by flattened cells and containing an acidophilic coagulum, the superficial lymphatic plexus. Interlacing strands of fibrous tissue are also being laid down in the subcutaneous mesenchyme. The central core of gubernacular mesenchyme, however, remains unchanged.

4. *Foetuses of* 100–160 *mm.* C.R. *length*

During this period the gubernaculum testis attains its completed form prior to testicular descent which normally occurs in foetuses of 190–200 mm. C.R. length. The mesonephros has now completed its involution leaving only its characteristic small remnants. As a result of this, the plica gubernaculi remains as a simple mesenchymatous column, carried on a mesentery continuous with the mesorchium and extending from the caudal pole of the testis to the distal end of the processus vaginalis. The testis and epididymis are carried on the apex of this column and that portion of the mesonephric duct embedded in it becomes convoluted to form the cauda epididymis. The portion of the gubernaculum testis distal to the external inguinal ring becomes much thicker, thus allowing the processus vaginalis to continue growing caudalwards towards the scrotum, within its substance. The processus vaginalis extends to emerge from the external inguinal ring at 110–120 mm. C.R. foetal length and it now becomes apparent that the cremaster muscle extends only so far distalwards as the processus vaginalis. The cremaster muscle differentiates along the line of attachment of the mesentery of the plica gubernaculi within the processus vaginalis and those two structures grow distally at the same rate.

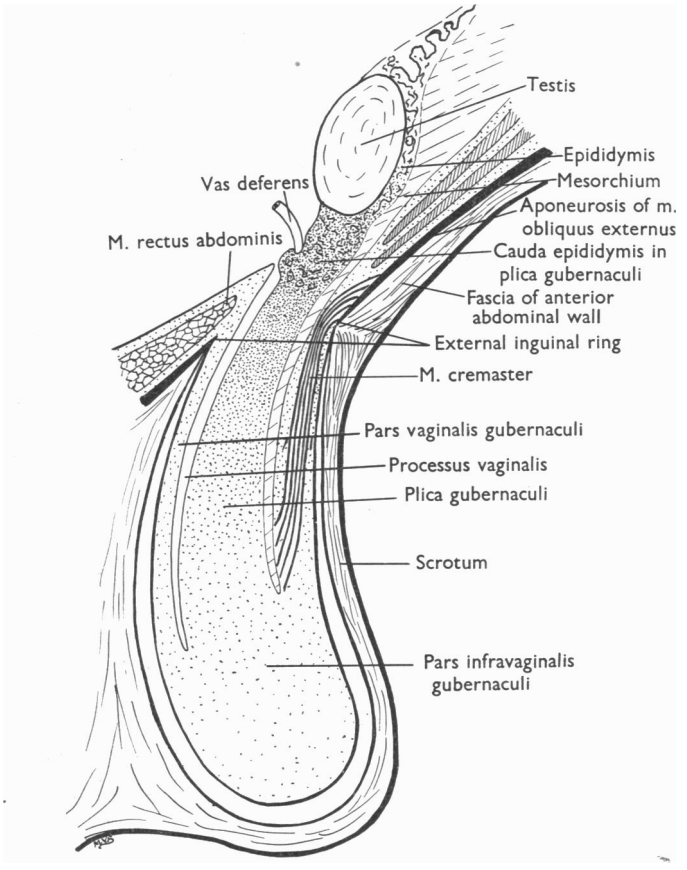
With the exception of the peritoneum and of the striated muscle fibres of the cremaster, the simple mesenchymatous nature of the gubernaculum testis is retained even though changes occur in the surrounding abdominal wall and scrotal mesenchyme. In the inguinal canal, the gubernacular mesenchyme is continuous with the mesenchyme and differentiating connective tissue surrounding the abdominal wall muscles, and in this tissue the cremaster muscle runs distalwards from its inguinal origin into the gubernaculum testis. Distal to the external inguinal ring the superficial fasciae of the abdominal and scrotal walls become differentiated and form a connective tissue pocket containing undifferentiated gubernacular mesenchyme. Concurrently with this superficial tissue differentiation, a split occurs around the enclosed gubernacular mesenchyme, and extends, distally, around the floor of the scrotum and, proximally, to the external inguinal ring. The gubernaculum testis thus comes to lie free in the scrotum and if, from 140–150 mm. C.R. foetal length onwards the scrotum be opened, an elongated pyriform mass can be lifted out. This mass, however, remains attached to the tissues surrounding the inguinal canal. (Pl. 1, fig. 5; Text-fig. 2).

In the fresh state the gubernacular tissue is pink and has a soft semi-fluid consistency: after formalin fixation it is semi-opaque and gelatinous. It closely resembles Wharton's jelly of the umbilical cord.

The definitive gubernaculum testis

It is now convenient to consider the gubernaculum testis as a whole and to name its constituent parts (Text-figs. 2, 3). The gubernaculum testis is an elongated pyriform mass of mesenchyme extending from the caudal pole of the testis to the scrotal floor. Its abdominal part is a mesenchymatous column suspended on a mesentery, continuous cranially with the mesorchium, and containing the cauda epididymis. Distally, it continues as a mesenchymatous mass which extends through the inguinal canal and fills the scrotal sac; the processus vaginalis and cremaster

muscle grow into this mass. As the processus vaginalis grows into the inguinal and scrotal parts of the gubernaculum, so does the abdominal gubernacular column extend within this mass to the distal extremity of the processus vaginalis. The term *gubernaculum testis* (Hunteri) refers to the whole mass of mesenchyme extending from the testis to the floor of the scrotum and in which the processus vaginalis and cremaster muscle develop. The gubernaculum testis can, however, be subdivided into:



Text-fig. 2. Schematic representation of the gubernaculum testis shortly before testicular descent, showing its component parts and also its relationship with the surrounding structures.

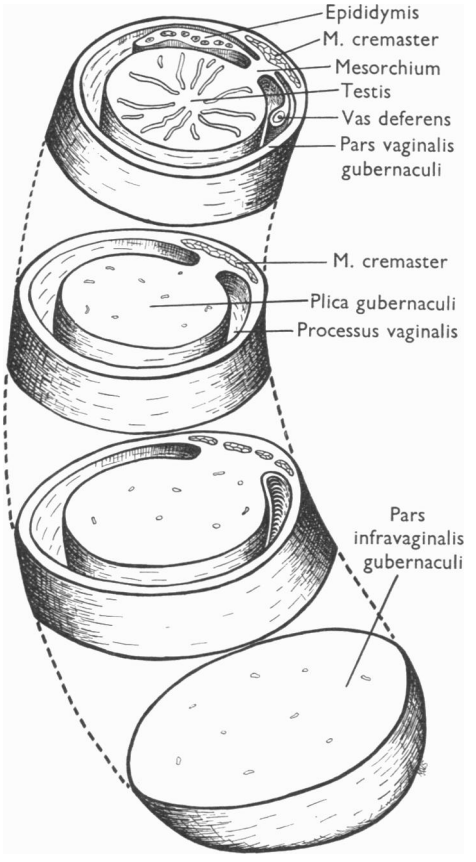
(i) *The plica gubernaculi* (*Seiler*), the intra-coelomic column of mesenchyme extending from the caudal pole of the testis to the distal extremity of the processus vaginalis.

(ii) *The pars vaginalis gubernaculi*, the thin layer of mesenchyme separated off by, and surrounding, the processus vaginalis. This layer is continuous with the plica gubernaculi through the root of the latter's mesentery. Distally it merges with

(iii) *The pars infravaginalis gubernaculi*, the solid mass of gubernacular mesenchyme distal to the processus vaginalis and into which the processus vaginalis and cremaster muscle grow as development continues.

Gubernacular changes attendant upon testicular descent

In the period immediately prior to testicular descent there are changes in the gubernaculum but its basic structure is not materially affected. The processus vaginalis and cremaster muscle continue their downward growth and by the time of testicular descent through the inguinal canal they have extended some two-thirds of the distance from the internal inguinal ring to the scrotal extremity of the gubernaculum. Other changes primarily affect the ground substance in various



Text-fig. 3. Schematic sectional representation of the gubernaculum testis, removed from the scrotum shortly after testicular descent.

parts of the gubernaculum. The distal portion of the gubernaculum testis has contained, from quite early in its development, a considerable amount of semi-fluid ground substance and this has formed the bulk of the swelling in the scrotal region. As the time of testicular descent approaches the amount of ground substance increases making the distal end of the gubernaculum larger and more globular, so dilating the scrotum. Externally, the scrotum has a bluish translucency compared with the surrounding tissues. As the ground substance increases the gubernaculum testis ceases to grow in length but, being fixed by the pars vaginalis in the inguinal

canal and free in the scrotum, increase in size of the surrounding tissues leads to a withdrawal of the gubernacular tip from the scrotal floor. This withdrawal may amount to as much as 5·0 mm. in the pig.

Initially, the increase in ground substance is limited to the pars infravaginalis gubernaculi so that only the scrotum is dilated. As the foetus approaches 190 mm. C.R. length the increases in ground substance and cessation of growth in length of the gubernaculum testis gradually extends proximalwards into the plica gubernaculi. Prior to this phase in development, the plica gubernaculi has remained relatively thin, especially in the inguinal canal and immediately subjacent to the testis. Here the cellular density has been high and the amount of ground substance small compared with the more distal parts of the gubernaculum. As the increase in ground substance extends proximalwards, the pars infravaginalis et plica gubernaculi become swollen. This increase gradually extends proximally, first dilating the scrotum and then the channel of testicular descent, the inguinal canal being affected last of all. Thus the testis comes to form the apex of an elongated cone of swollen mesenchyme which holds the pathway along which the testis will descend.

The pars vaginalis gubernaculi does not undergo this general cessation of growth and increase in ground substance but continues to grow along with the surrounding body wall, and so carries the plica gubernaculi and the gubernacular tip distalwards. Thus the combination of distal growth of the pars vaginalis gubernaculi and the conical form of the plica gubernaculi carries the testis, situated on the apex of the plica gubernaculi, through the inguinal canal into the groin. While these changes are taking place in the gubernaculum, there is concurrently rapid growth of the vas deferens and testicular vessels to allow the testis to move.

Following the passage of the testis through the inguinal canal further changes take place in the gubernaculum. The processus vaginalis and the cremaster muscle continue to grow towards the scrotal floor and, as a result, the pars infravaginalis gubernaculi virtually disappears, *thus leaving only the plica et pars vaginalis gubernaculi.*

The plica gubernaculi does not actively shorten; its mesenchyme becomes involved by further growth of the cauda epididymis which eventually reaches the distal extremity of the gubernaculum. (Pl. 1, figs. 5, 6) The cauda epididymis thus approaches the scrotal floor.

Further testicular descent is brought about by lengthening of the scrotum, the pars vaginalis gubernaculi, the vas deferens and the testicular vessels. The testis does not approach the scrotal floor but both it and the scrotal floor move further away from the external inguinal ring. The mesenchyme of the plica gubernaculi becomes converted into the connective tissue of the cauda epididymis. The pars vaginalis gubernaculi which surrounds the processus vaginalis and contains the cremaster muscle becomes converted into the fascial covering of the testis and spermatic cord (Pl. 1, fig. 7) (the internal and external spermatic fasciae of man).

DISCUSSION

The major concept arising from this study is that of the mesenchymatous nature of the gubernaculum testis, a histological feature which persists in the plica gubernaculi so long as the structure remains as a recognizable entity. The gubernaculum testis can thus be defined as a band of mesenchyme extending *in the developing animal* from

the caudal pole of the testis to the region of the future scrotum: it delineates the pathway along which the testis will migrate. As it is partly intra- and partly extra-abdominal, the intra-abdominal and extra-abdominal portions are often considered separately from a developmental point of view: certain authors have even described three developmentally fused portions to the structure, intra-abdominal, intramural and scrotal, with further subdivisions of the intra-abdominal portion (Felix, 1912; Moscowitz, 1936). Such complicated descriptions of the gubernaculum testis are considered however to be unnecessary and only in part true. A continuous band of mesenchyme exists in the track of the gubernaculum in the very early embryo, but only becomes a recognizable entity with the differentiation of the surrounding body wall structures, which thus delineate, in particular, the extra-abdominal portion of the gubernaculum lying in the inguinal canal and scrotal areas. Differences in cellular density can be seen within the inguinal canal and scrotum at different developmental stages, but these differences are related to the activity of the tissues and not to separate developmental entities. It is thus inaccurate to divide the extra abdominal portion of the gubernaculum into developmental intramural and scrotal entities, though these terms may be useful if limited to regional description.

The intra-abdominal portion of the gubernaculum develops in a manner different from the extra-abdominal portion but it need not be considered as a separate entity. In early stages (20 mm. C.R. length) the plica gubernaculi is slight, being only a thin band of undifferentiated mesenchyme underlying a primitive coelomic epithelium, but later this band forms a true ridge, the plica gubernaculi (ligamentum inguinale of Klaatsch). A continuous mesenchymatous band nevertheless runs from the testis to the scrotum even before the formation of the true ridge. The plica gubernaculi does not arise in the pig by the fusion of a plica inguinalis with a crista inguinalis as was postulated by Felix to be the case in man, but by a simple thickening along the length of the mesenchymatous band. In the pig, however, the close proximity of the mesonephros to the anterior abdominal wall which exists at the time of these changes would make the process scheme postulated by Felix unnecessary, whereas in man the gubernaculum testis must leave the mesonephros and pursue a course around the pelvic floor to reach the anterior abdominal wall.

The essentially continuous nature of the gubernaculum testis is emphasized by the gradual distal extension of the plica gubernaculi beyond the inner aspect of the anterior abdominal wall; by the growth of the processus vaginalis the plica gubernaculi eventually extends so far distalwards as the floor of the scrotum, but with no intrinsic change in the tissue within the plica and the pars infravaginalis gubernaculi. The described mode of extension of the processus vaginalis, by active coelomic epithelial invasion of the gubernacular mesenchyme, is at variance with the mode of extension of the lesser sac of peritoneum into the mesenchyme around the foregut as described by Kanagasuntheram (1957). He denied an active epithelial invasion and maintained that clefts formed in the mesenchyme, the clefts coalescing with each other and with the coloemic cavity. Such cleft formation has not been seen distal to the extending processus vaginalis.

The fact that the processus vaginalis forms well prior to testicular descent and has extended far into the scrotum before this event, gives no support to the thesis put forward by Curling and by Moscowitz among others, that the descending testis

'drags' the peritoneum with it to form the processus vaginalis. For such a thesis to be acceptable, the formation of the processus vaginalis must be closely linked both in time and extent with testicular descent. In man, a reasonably close linkage exists between these events, so that such a mode of formation of the processus vaginalis is perhaps not unreasonable, but in the pig the two processes are so widely separated in both time and extent that no direct mechanical linkage can possibly be entertained. The presence of actively growing primitive type coelomic epithelial cells at the point of extension of the processus vaginalis into the gubernaculum testis, whilst elsewhere the coelomic epithelial cells are of a specialized flattened form points to a simple invasion process taking place. Such an active coelomic invasion of the gubernacular mesenchyme offers a rational explanation of the mode of extension of the peritoneal cavity to form the processus vaginalis in the male and, also, the formation of the canal of Nuck in the female which was quite outside the range of the Curling-Moscowitz theory.

Just as the formation of the processus vaginalis is less intimately linked with the actual descent of the testis in the pig than man, so also is the development of the cremaster muscle. In man the medial and lateral cremaster muscles are initially formed quite early in embryonic development but do not extend beyond the inguinal canal until shortly before the testis descends. In the pig, however, as the processus vaginalis extends distalwards so the cremaster muscle differentiates *within the gubernacular mesenchyme* along the root of the mesentery of the plica gubernaculi but in the pars vaginalis gubernaculi. It develops as a single lateral bundle extending only so far distalwards as the processus vaginalis, the two developing both spatially and temporally in unison and well in advance of testicular descent. Such developmental features amply illustrate that the cremaster muscle, in the pig at least, does not consist of muscle fibres dragged off the abdominal wall by the descending testis as was postulated by Cloquet, Carus and Moscowitz. Furthermore, the early distally directed differentiation of the muscle towards the scrotum in the pig does not permit consideration of an 'inverted' cremaster muscle running from an inguinal origin to the abdominal testis and capable of hauling the testis down into the scrotum as Seiler, Curling, Lockwood and many other authors have postulated as taking place in man and certain other mammals. If the cremaster muscle were to contract in a pig foetus, the testis would be elevated on its plica gubernaculi rather than descend, an action comparable with that of the adult cremaster muscle.

The mesenchymatous nature of the gubernaculum testis has been described in part by previous authors, but details of its complete separation from the scrotal wall have been neglected. It is unlikely that this separation has not been seen, probably having been dismissed as an artefact, a distal attachment being essential if the traditional contractile role is assigned to the gubernaculum testis. That the separation is not an artefact is quite obvious from histological study. The gubernaculum testis is initially continuous with the remaining mesenchyme of the scrotum and of the abdominal wall, but when this differentiates the gubernaculum testis becomes distinct as a mesenchymatous structure and a separation zone forms. This zone remains as loose tissue so long as the gubernaculum remains small, but, with distal expansion due to changes in the ground substance, so forming a globular mass within the scrotal swelling, separation of the gubernaculum testis from the scrotal wall

becomes complete. A factor involved in the separation process is the differentiation of the scrotal wall, which does not change shape directly with the changes occurring in the gubernaculum.

Consequent upon these changes and the cessation of growth of the plica gubernaculi relative to the surrounding structures, the gubernacular tip becomes withdrawn from the scrotal floor. It must be emphasized however that this withdrawal, of up to 5 mm., is much more marked in the pig, which has a perineal scrotum, than in the sheep or man in which the scrotum is dependent. Due to the perineal position of the pig scrotum, the gubernaculum testis is falciform, whereas that of the sheep or man is more nearly straight. Increase in thickness of the pig gubernaculum around its curve tends to carry the distal portion of the gubernaculum forwards out of the perineal scrotum. The gubernaculum testis of sheep or man is only affected by differential growth between itself and the surrounding tissues and only rises some 1–2 mm. from the scrotal floor.

Some shortening of the combined plica et pars infravaginalis gubernaculi is obviously essential if the testis is to pass into the scrotum, although no active contractile shortening occurs, for the inguinal canal and scrotum are completely filled by the gubernaculum testis, leaving no room for the testis. Shortening however is shown to be a relative factor due to a cessation of growth in these parts of the gubernaculum, while the surrounding tissues (including the pars vaginalis gubernaculi) continue to grow. Thus with relative gubernacular shortening there will be progressive retraction of the gubernacular tip from the floor of the scrotum if the testis does not descend. However, lengthening of the pars vaginalis gubernaculi will permit the gubernacular tip to remain close to the floor of the scrotum and the testis to descend. This movement is facilitated by the plica gubernaculi taking on a conical form, surmounted by the testis, and dilating the scrotum and, in particular, the inguinal canal. Such a mechanical arrangement permits the gubernaculum testis and the testis to slide distalwards to fill the space in the scrotum created by the cessation of gubernacular growth.

The movement of the testis through the inguinal canal is rapid, for although many foetuses were examined about the time of testicular descent, in only one specimen could the testis be considered in transit. In this specimen the testis could not be pushed onwards through the inguinal canal, the vas deferens being too short to permit further testicular descent. It is suggested that, in view of the rapidity of testicular descent, some motivating force such as increased intra-abdominal pressure due to intra-uterine respiratory movements, may initiate passage of the testis through the inguinal canal once the canal has been dilated by the gubernaculum testis. It is submitted, however, that such a motivating force is of little significance, for the mechanical arrangement of the gubernacular apparatus described is sufficient to precipitate testicular descent.

Clearly, this testicular translation must be preceded by sufficient growth in length of the vas deferens and testicular vessels. The vas deferens is initially too short to permit testicular descent, and in the single case of arrested descent described herein, the limiting factor was the length of the vas deferens. The growth in length of the vas deferens and in particular of the cauda epididymis is appreciable from the time of testicular descent until birth. The gubernaculum testis forms a ready medium

into which the cauda epididymis can expand. This expansion of the epididymis stimulates testicular descent, but mensuration shows no actual shortening of the distance between the lower pole of the testis and the distal extremity of the processus vaginalis or the floor of the scrotum, once the testis has passed through the inguinal canal. Thus, once the testis has passed through the inguinal canal no absolute testicular descent takes place, though relative to the animal as a whole such a descent is obvious. The final stages are thus brought about, not by an intrinsic function of the plica gubernaculi but by simple lengthening of the pars vaginalis gubernaculi and of the vas deferens and testicular vessels, associated with lengthening of the distance between the external inguinal ring and the floor of the scrotum. Under normal conditions the gubernaculum testis does not remain as a well-organized residual band as is often asserted but changes into the connective tissues in the neighbourhood of the testis. The thin sheath of mesenchyme which remains from the partes vaginalis et infravaginalis gubernaculi, and which surrounds the processus vaginalis and its contents, becomes the fascial coverings of the testis and cord. In the pig, this covering is not readily divisible into three layers as it is in man. The cremaster muscle of the pig is a single fasciculus representing only the lateral cremaster muscle. Hence, instead of medial and lateral cremasteric fibres interdigitating around the testis and cord, with deep and superficial fascial covering layers as in man, a single fasciculus runs distalwards along the line of the mesorchium, with the vessels and vas deferens. Except along this line the spermatic fascia is simple and not split into internal and external layers by the cremaster muscle. As in man (Backhouse & Butler, 1955) the external spermatic fascia develops only a *fascial* continuity with the margins of the external ring after the development of the processus vaginalis, and after the testis has descended and is not formed by 'dragging down' the external oblique aponeurosis. Fibrous tissue forms in the pars vaginalis gubernaculi and becomes joined proximally with the external inguinal ring.

Testicular descent may be divided into three phases; two of these are slow processes dependent upon the relative growth of various organs and are connected by a rapid propulsion of the testis through the inguinal canal.

1. When the testis first develops in the abdomen, it is separated from the future internal inguinal ring by the large mesonephros. As a result of testicular growth and mesonephric degeneration the caudal pole of the testis comes to lie very close to the internal inguinal ring.

2. In foetuses of 190–200 mm. C.R. length, the testis passes through the inguinal canal to a position high in the groin just outside the external inguinal ring, facilitated by changes in the gubernaculum testis and growth in length of the vas deferens and testicular vessels. The available evidence suggests that this passage is very rapid and it is possible that the motivating force may be intra-uterine respiratory movement, though dilatation of the inguinal canal by the gubernaculum testis is the main factor involved.

3. Final descent is partly apparent and partly real. The apparent further descent is brought about by the caudal expansion of the cauda epididymis into the plica gubernaculi to approach the scrotal floor. Any real descent is a result of growth in length of the scrotum, the vas deferens and testicular vessels and the pars vaginalis gubernaculi (including the cremaster muscle).

SUMMARY

The gubernaculum testis is described in the domestic pig (*Sus scropha*) from its first appearance in the early embryo until eventual change to the adult form. Its three component parts are named and defined. It is a simple mesenchymatous structure, around which the body wall muscles and fasciae differentiate, and into which the processus vaginalis grows and the cremaster muscle differentiates. No muscular tissue, which could bring about testicular descent, extends from the distal end of the gubernaculum to the abdominal testis. Towards the time of testicular descent, the distal end of the gubernaculum testis comes to lie free in the scrotum and the gubernacular ground substance is greatly increased in amount; the scrotum and inguinal canal thus become dilated in advance of testicular descent. Passage of the testis through the inguinal canal is rapid and is preceded by lengthening of the vas deferens and testicular vessels. This movement represents the only true descent of the testis. Further descent to the floor of the scrotum is due to lengthening of the structures of the testicular cord and their coverings and the invasion of the distal portion of the gubernaculum by the growing cauda epididymis. After testicular descent the remains of the gubernaculum testis are converted into the fascial coverings of the testis and cord and the connective tissue around the cauda epididymis.

We wish to express our thanks to Prof. A. J. E. Cave and Prof. W. J. Hamilton for much helpful criticism and advice during this work, and also, with Dr T. W. A. Glenister, for allowing us the use of certain of their sectioned material; to Messrs A. E. Westwood and K. W. Iles for their photography and to Miss M. V. Stokes for the drawings.

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EXPLANATION OF PLATES

PLATE 1

Fig. 1. Section of a 38 mm. C.R. length pig embryo showing the gubernaculum testis in the region of the inguinal canal and showing the plica gubernaculi extending from the surface of the mesonephros to the anterior abdominal wall, the distal 0·1 mm. being within the processus vaginalis.

Fig. 2. Section of a 45 mm. C.R. length pig foetus showing the plica gubernaculi extending from the large mesonephros into the gubernaculum of the inguinal canal region. The processus vaginalis extends some 0·2 mm. into this gubernacular mesenchyme and the early differentiating M. cremaster can also be seen.

PLATE 2

Fig. 3. Section of a 45 mm. C.R. length pig foetus showing the mesenchyme of the scrotal region. The gubernacular mesenchyme can only be recognized at this stage as a slightly denser region.

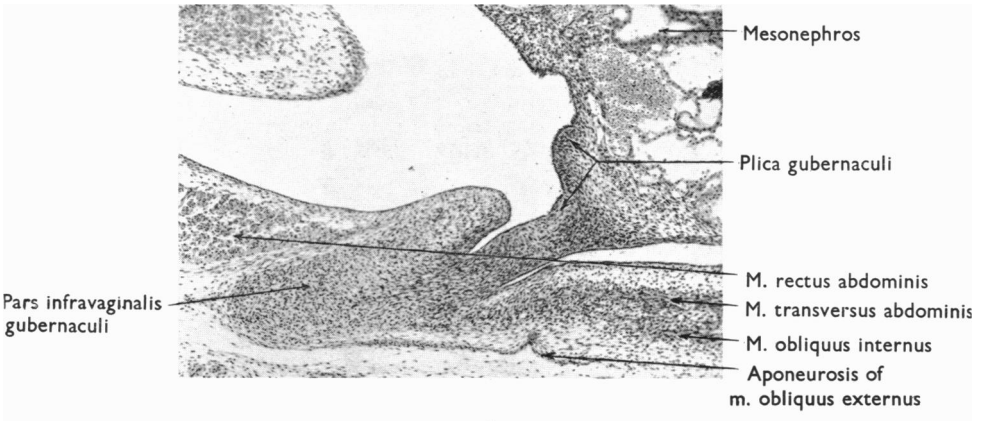
Fig. 4. Section of the inguinal region of an 85 mm. C.R. length pig foetus showing the gubernacular mesenchyme containing the cremaster muscle and the processus vaginalis.

PLATE 3

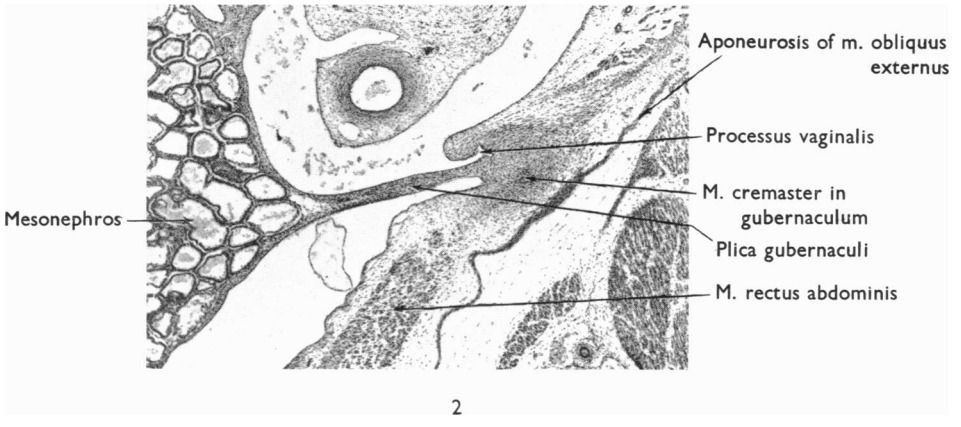
Fig. 5. The sectioned testis and gubernaculum testis of a 165 mm. C.R. length sheep foetus; the structures have been divided around the inguinal region but the distal portion has merely been lifted from the scrotal sac.

Fig. 6. Section of testis and gubernaculum testis of a 310 mm. C.R. length pig foetus. The testis has descended into the scrotum and marked growth of the cauda epididymis within plica gubernaculi can be seen.

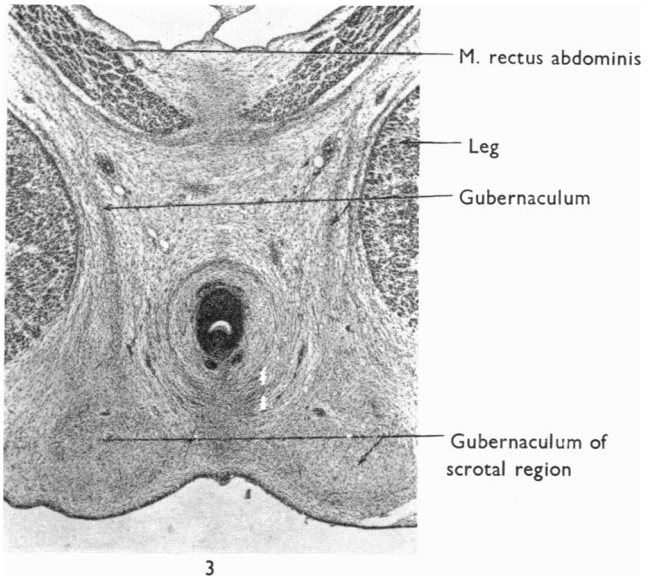
Fig. 7. Transverse section through the gubernaculum testis of a 290 mm. pig foetus showing the plica gubernaculi and the now well-differentiated pars vaginalis gubernaculi, containing the M. cremaster.


Mesonephros
Plica gubernaculi
M. rectus abdominis
M. transversus abdominis
M. obliquus internus
Aponeurosis of
m. obliquus externus
Pars infravaginalis
gubernaculi

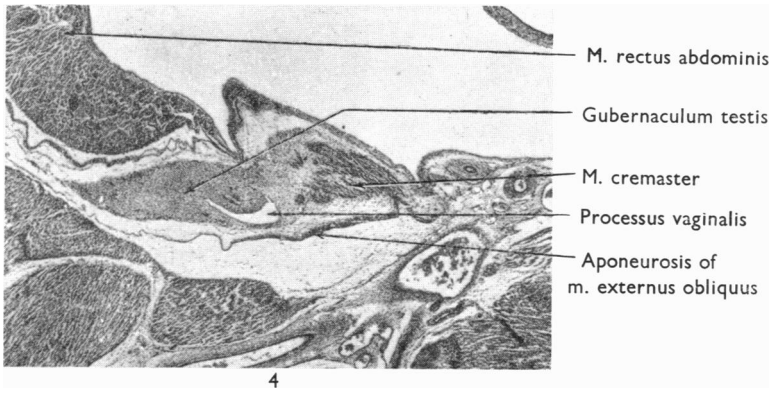
1


Aponeurosis of m. obliquus
externus
Processus vaginalis
M. cremaster in
gubernaculum
Plica gubernaculi
M. rectus abdominis
Mesonephros

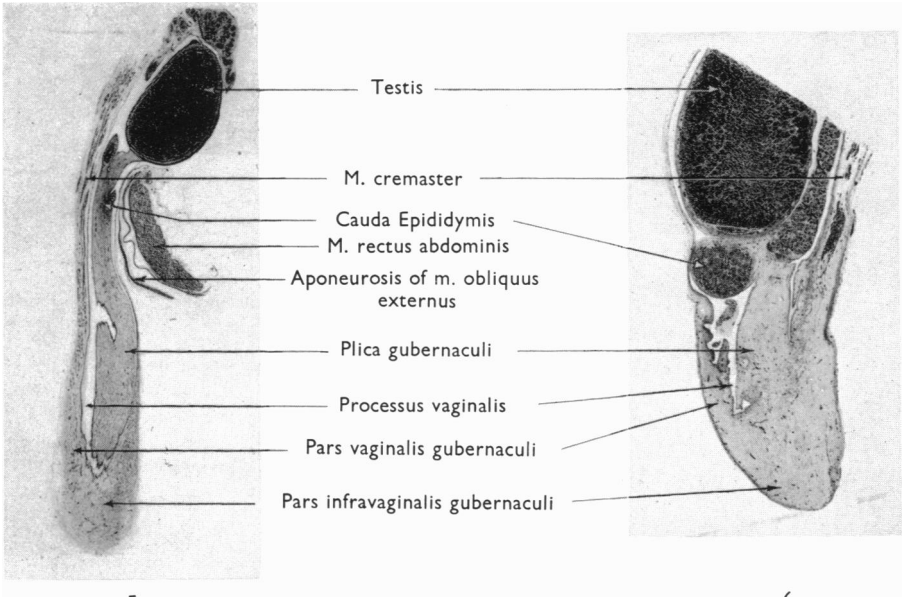
2


M. rectus abdominis
Leg
Gubernaculum
Gubernaculum of
scrotal region

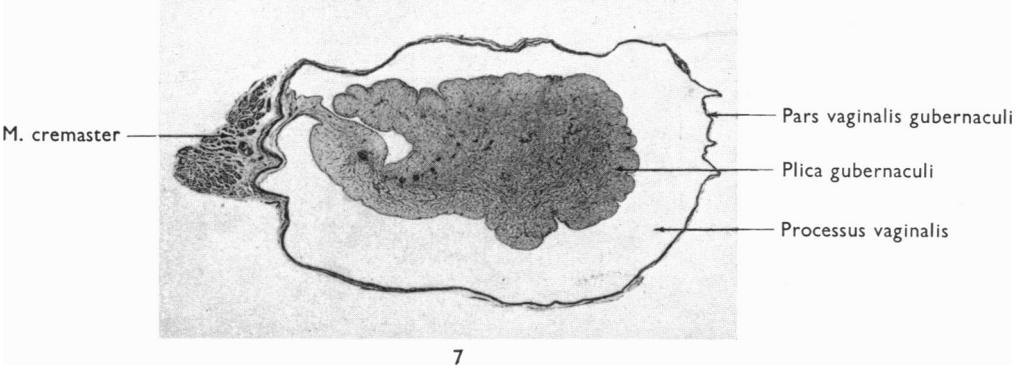
3


M. rectus abdominis
Gubernaculum testis
M. cremaster
Processus vaginalis
Aponeurosis of
m. externus obliquus

4


Testis
M. cremaster
Cauda Epididymis
M. rectus abdominis
Aponeurosis of m. obliquus externus
Plica gubernaculi
Processus vaginalis
Pars vaginalis gubernaculi
Pars infravaginalis gubernaculi

5 6


M. cremaster
Pars vaginalis gubernaculi
Plica gubernaculi
Processus vaginalis

7