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Measurement of the linear dynamics of the descent of the bovine fetal testis

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Abstract

Measurements were made on 86 male bovine fetuses collected from abattoirs in the vicinity of Sydney, Australia. The fetal body length was used to calculate the approximate day of gestational age (DGA); most fetuses were between 60 and 150 DGA. The distances from the caudal pole of the kidney (metanephros) to, respectively, the tip of the scrotum, the distal end of the testis and the internal ring of the inguinal canal were measured, as well as the dimensions of the testis and gubernaculum testis. Distances of (1) testis to inguinal canal, (2) inguinal canal to scrotum, (3) testis to scrotum and (4) gubernaculum to scrotum were calculated from these measurements, which were made on both left and right sides. The total length of the gubernaculum testis increased during transabdominal passage and during transinguinal passage of the testis. Furthermore, the gubernaculum appeared to maintain the testis at a relatively fixed distance from the scrotum during transabdominal passage so that the inguinal canal appeared to move towards the testis. The greatest distance between the testis and the tip of the scrotum was found during the transinguinal passage of the testis and was 2.8 cm for the left testis and 2.3 cm for the right. When located within the scrotum, each testis was still 1.6–1.7 cm from the tip of the scrotum, so the distance to be traversed was only 0.6–1.2 cm. Following passage of the testis through the inguinal canal, the gubernaculum became shorter and its distal tip was displaced toward the distal end of the scrotum. Traction by the gubernaculum could account for the final transposition of the testis from the external inguinal ring to the scrotum. Other factors involved in displacement of the testis include differential growth patterns as well as increases in the dimensions of the testis itself.

Key words growth; gubernaculum; inguinal; scrotum; testis.

Introduction

The translocation (descent, *descensus*) of the testis from the medial aspect of the mesonephros, across the abdomen, through the inguinal canal to be lodged within the scrotum is an impressive embryonic event. It has been studied in most species of scrotal mammals, but there is no general consensus about how it happens. Since John Hunter first described the *gubernaculum testis* (Hunter, 1762), different opinions have been offered about the mechanisms involved in testicular translocation (Heyns & Hutson, 1995).

Although Bramann (1884) and Hadziselimovic (1983) proposed a role for the epididymis in testicular descent and although androgens have an important influence on the process, most authors consider that the gubernaculum testis plays a major role in guiding the testis into the scrotum. Both size and composition of the gubernaculum change during the descent process. Several authors have followed the concept, which was suggested by Weber (1847) and put on a firm basis by the detailed studies of Lockwood (1888), that the mechanism of translocation of the testis in the human fetus involves a combination of traction exerted on the testis by the gubernaculum and differential growth of the pelvis (e.g. Blechschmidt, 1955, 1960; Youssef & Raslan, 1971). Hart (1909, 1910) also came to this

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conclusion based on studies of marsupial and human fetuses. Backhouse (1964) compared the gubernaculum in pig and human and mentioned the histological features of the bovine gubernaculum. Heyns (1987) and Hutson et al. (1997) gave a comprehensive description of changes in the position and nature of the gubernaculum in human fetuses, and Heyns & De Klerk (1985), Fentener van Vlissingen et al. (1989) and Heyns et al. (1990) studied composition of the gubernaculum in pig fetuses.

During a study of some features of the bovine uterus, the opportunity was presented to examine this process in specimens containing male fetuses of various gestational ages. The process in bovine fetuses does not appear to have been studied extensively possibly because failure of translocation is uncommon in cattle. However, Gier & Marion (1970) have presented dissections and diagrams of the pelvic region of the bovine fetus and Hullinger & Wensing (1985) have described testicular descent in a survey of 30 fetuses.

Materials and methods

Uteri of pregnant cows were collected from abattoirs located in the vicinity of Sydney, NSW. These cows were from a number of dairy breeds, mainly Friesian, but there were also some Australian Illawarra Shorthorn, Guernsey and Ayrshire, as well as a small number of beef breeds.

The uteri were opened on the day of receipt and a total of 86 male fetuses were collected for measurement. The age of all fetuses was in the range *c.* 50–210 days of gestational age (DGA), with the majority being between 60 and 150 DGA. The average duration of pregnancy in cattle is about 285 days.

The fetus was removed from the uterus and placed on its side with the vertebral column in a straight line and head at an angle of approximately 45° to the line of the vertebral column. The fetal body length (FBL) was measured from the middle of the frontal area (crown) of the skull in a straight line to the posterior aspect of the ischial tuberosity. The approximate fetal age was calculated from figures relating the FBL to DGA, published by Maneely (1952) and Arthur et al. (1989). These authors indicated that the breed of cow had little influence on the rate of linear development of the craniovertebral axis during the first and second trimesters of pregnancy. The abdomen of the fetus was opened and the gastrointestinal tract removed to allow access to, and measurement of, remaining structures within the abdominopelvic cavity.

Table 1 Translocation of testis from kidney to scrotum (in cm)

FBL group (mean)	*n*	K–S (SD)	K–IC (SD)	K–T (SD)	G (SD)	T l × w (SD)
Left						
5.0–9.9	10	1.3	0.5	0.0	0.6	0.4 × 0.2
(8.2)		(0.2)	(0.1)		(0.2)	(0.1) (0.1)
10.0–12.9	9	1.7	0.5	0.2	0.9	0.5 × 0.3
(11.8)		(0.2)	(0.1)	(0.1)	(0.1)	(0.1) (0.1)
13.0–19.9	19	2.6	0.7	0.5	1.5	0.7 × 0.3
(16.6)		(0.5)	(0.2)	(0.3)	(0.2)	(0.1) (0.1)
20.0–24.9	17	4.1	1.2	1.4	1.9	0.9 × 0.5
(22.7)		(0.5)	(0.3)	(0.5)	(0.3)	(0.2) (0.1)
25.0–34.9	18	5.7	1.4	3.5	1.6	1.2 × 0.6
(28.5)		(1.0)	(0.5)	(1.1)	(0.2)	(0.1) (0.1)
35.0–50.0	10	9.9	2.7	8.4	1.4	1.7 × 0.8
(41.8)		(2.0)	(0.5)	(2.1)	(0.2)	(0.3) (0.2)
65.0	1	16.3	5.2	5.9	1.4	–
Right						
5.0–9.9	10	1.3	0.5	0.0	0.6	
(8.2)		(0.3)	(1.3)		(0.2)	
10.0–12.9	9	2.0	0.8	0.3	1.0	
(11.8)		(0.3)	(0.2)	(0.2)	(0.2)	
13.0–19.9	19	3.2	1.2	0.9	1.6	
(16.6)		(0.6)	(0.3)	(0.5)	(0.2)	
20.0–24.9	17	5.1	2.0	2.9	1.7	
(22.7)		(0.6)	(0.4)	(0.8)	(0.4)	
25.0–34.9	18	6.9	2.4	5.1	1.5	
(28.5)		(1.3)	(0.6)	(1.2)	(0.2)	
35.0–50.0	10	11.7	4.3	10.0	1.4	
(41.8)		(2.2)	(0.4)	(2.2)	(0.1)	
65.0	1	18.2	6.8	17.2	1.3	

n, number of observations; SD, standard deviation; K–S, kidney to scrotum distance; K–IC, kidney to inguinal canal distance; K–T, kidney to testis distance; G, length of gubernaculum; T (l × w), testis (length × width).

Using Vernier callipers, the following distances (Table 1) were measured to the nearest millimetre on the left and right sides separately: (1) posterior aspect of the kidney to the distal tip of the scrotum, (2) posterior aspect of the kidney to the distal end of the testis and (3) posterior aspect of the kidney to the internal inguinal ring. Macroscopically, the gubernaculum of the testis is club-shaped, consisting of the gubernacular cord (plica gubernaculi) attached at the testis and a distal rounded end (pars infravaginalis gubernaculi) near the scrotum. The portion of the gubernacular cord that lies within the inguinal canal and within the inferior extension of the abdominopelvic cavity, known as the vaginal process (processus vaginalis), is described as its vaginal part (pars vaginalis gubernaculi). The inguinal

Table 2 Derived distances in translocation of testis from kidney to scrotum (cm)

FBL (mean)	n	T–IC (SD)	IC–S (SD)	T–S (SD)	G–S (SD)
Left					
5–9.9 (8.2)	10	0.5 (0.1)	0.8 (0.2)	1.3 (0.2)	0.7 (0.1)
10–12.9 (11.8)	9	0.3 (0.2)	1.2 (0.2)	1.5 (0.2)	0.6 (0.2)
13–19.9 (16.6)	19	0.2 (0.2)	1.9 (0.4)	2.1 (0.3)	0.6 (0.2)
20–24.9 (22.7)	17	*	3.0 (0.4)	2.8 (0.3)	0.9 (0.2)
25–34.9 (28.5)	18	*	4.3 (0.8)	2.2 (0.4)	0.6 (0.3)
35–50 (41.8)	10	*	7.3 (1.7)	1.6 (0.3)	0.2 (0.2)
Right					
5–9.9 (8.2)	10	0.5 (0.1)	0.8 (0.2)	1.4 (0.3)	0.7 (0.1)
10–12.9 (11.8)	9	0.4 (0.2)	1.2 (0.2)	1.7 (0.2)	0.7 (0.2)
13–19.9 (16.6)	19	0.3 (0.3)	2.0 (0.4)	2.3 (0.3)	0.8 (0.2)
20–24.9 (22.7)	17	*	3.1 (0.5)	2.2 (0.5)	0.5 (0.4)
25–34.9 (28.5)	18	*	4.6 (0.9)	1.7 (0.2)	0.2 (0.2)
35–50 (41.8)	10	*	7.3 (2.0)	1.6 (0.3)	0.3 (0.2)

n, number of observations; SD, standard deviation; T–IC, testis to inguinal canal; IC–S, inguinal canal to scrotum; T–S, testis to scrotum; G–S, gubernaculum to scrotum; *, testis through inguinal canal.

canal was opened along the ventral margin of the processus vaginalis and the enclosed section of the plica gubernaculi was exposed. The total length of each gubernaculum, from its attachment to the testis to its distal rounded end, was then measured, along with the length and maximum diameter of the testis. The subcomponents of the gubernaculum and the length of the processus vaginalis were not measured. In the early stages of the study it was observed that the sizes of the left and right testis did not differ significantly so only one testis, usually the left, was measured. The other distances (derived distances, Table 2) were calculated from these figures.

Changes in the position of the metanephros during development relative to the crown and the scrotum were examined by making comparisons of the ratios of the FBL to the distance between the caudal end of the kidney to the scrotum. The FBL (distance between crown and ischial tuberosity) is similar to the distance between the crown and distal end of the scrotum. Therefore, the FBL minus the distance between the caudal end of the developing kidney and the scrotum represents approximately the distance between the crown and the caudal end of the kidney. The method of ranked normal deviates (rankits) was used to test for a normal distribution of the small number of values (Sokal & Rohlf, 1996) and Student's *t*-test was used to test the significance of differences between mean values.

Results

It was possible to follow the early development of the testis, inguinal region and gubernaculum in a few very early fetuses. At FBL 3 cm (*c.* 42 DGA), with the fetus lying on its back and the kidneys and inguinal region exposed, the gonad was located in the middle of the long mesonephros, on its medial aspect. The mesonephric duct was lateral to the mesonephros and passed toward the urachus. A fine fold of peritoneum was identified extending from the duct toward the area of the future inguinal canal. At FBL 4.8 cm (about 56 DGA), the mesonephros had begun to regress and the developing metanephros (termed kidney hereafter) was identified on its anteromedial aspect. The testis was located on the caudomedial aspect of the mesonephros and kidney. A gubernaculum, 0.3 cm long, was attached to the mesonephric duct, approximately 0.3 cm distal to the caudal pole of the testis; the gubernaculum extended toward the vicinity of the inguinal canal.

In an embryo 5.8 cm FBL, a band originating at the caudal end of the mesonephros and passing toward the inguinal area was seen to be connected to a club-shaped gubernaculum, which extended further into the inguinal area. At 8.8 cm FBL, the entrance to the inguinal canal was identified, with a peritoneal pouch (processus vaginalis) extending approximately 0.3 cm into the canal. This pouch enclosed a small gubernaculum that was 0.6 cm long and estimated to be 0.15 cm wide. At FBL 10.8 cm, just prior to when the testis separates from the kidney, an inguinal canal of depth 0.3–0.4 cm contained a gubernaculum of total length 0.9 cm. During its transabdominal migration, the testis was enclosed in the same peritoneal fold that also enclosed the gubernaculum.

For further analysis of testicular translocation, all measurements were grouped according to six FBL

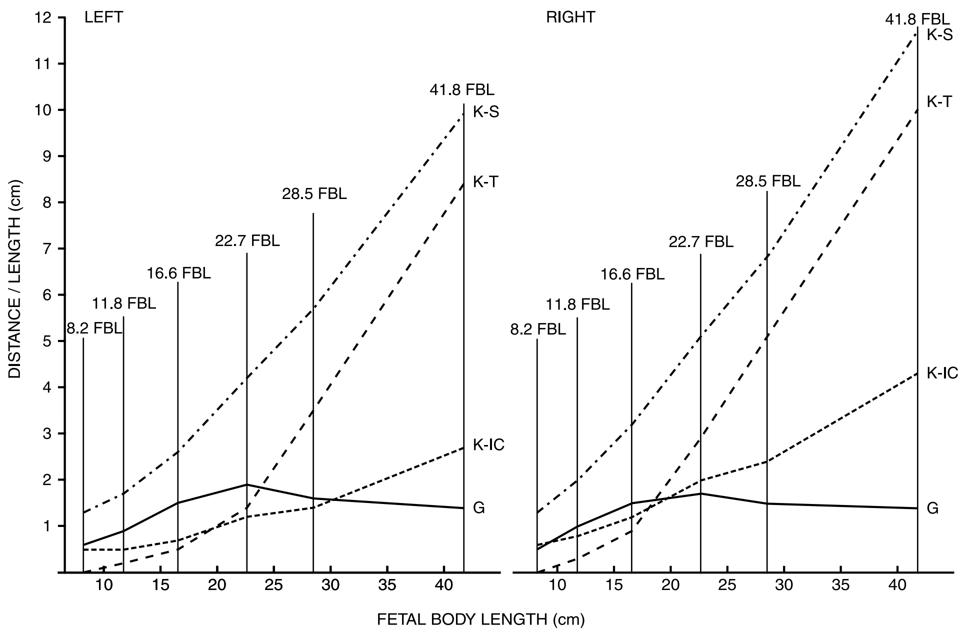

Fig. 1 Changes in the distances between kidney and scrotum (K–S), kidney and testis (K–T) and kidney to inguinal canal (K–IC), and in the length of the gubernaculum (G) during translocation of the testis.

ranges defining significant developmental stages. These groups and their main characteristics are as follows: Group I, FBL 5–9.9 cm (mean 8.2 cm), *c.* 65 DGA, prior to separation between the kidney and testis; Group II, FBL 10–12.9 cm (mean 11.8 cm), *c.* 75 DGA, early stages of separation of testis from kidney; Group III, FBL 13–19.9 cm (mean 16.6 cm), *c.* 90 DGA, abdominal translocation of testis to the inguinal canal; Group IV, FBL 20–24.9 cm (mean 22.7 cm), *c.* 95 DGA, transit of testis through the inguinal canal; Group V, FBL 25–34.9 cm (mean 28.5 cm), *c.* 120 DGA, transit of testis from the inguinal canal into the neck of the scrotum; Group VI, FBL 35–50 cm (mean 41.8 cm), *c.* 160 DGA, testis located within the scrotum.

Figure 1 shows the changes during fetal growth in the distances for kidney–scrotum (K–S), kidney–inguinal canal (K–IC), kidney–testis (K–T), and the length of the gubernaculum (G) for the left and right sides. The graph for kidney–testis crosses the graph for kidney–inguinal canal for the left side at FBL 20–21 cm, and at FBL 18–19 cm for the right, indicating that at these stages of development the testis is passing through the internal inguinal ring.

The gubernaculum testis

During translocation, the gubernaculum testis was of a soft, gelatinous consistency and had a club shape, with its widest diameter toward the distal end. Distal to the internal ring of the inguinal canal, the gubernacular cord lay within the processus vaginalis. There was no appreciable adhesion between the gubernaculum and the surrounding tissues within the inguinal canal and the scrotum at any stage during translocation. When the testis had passed through the inguinal canal, the mesenchyme between the end of the gubernaculum and body of the scrotum became distinctly fluid.

At FBL 8–10 cm, the gubernaculum was attached to the vas deferens approximately 0.3–0.4 cm distal to the caudal end of the testis. In specimens of FBL *c.* 17 cm, the distance between the point of attachment to the vas deferens and the testis had decreased to approximately 0.1 cm. By this stage, the vas deferens had become coiled to form the tail of the epididymis, the coiled segment apparently including part of the vas between the attachment to the gubernaculum and the distal end of the testis.

The dimensions of the gubernaculum at a number of stages during development are summarized in Tables 1 and 3 and plotted in Fig. 2. The gubernaculum enlarged gradually while the testis was in the process of translocation from the kidney to the inguinal canal. On the left side, when the testis was within the inguinal canal, the gubernaculum was significantly longer than immediately before the testis entered the canal. When the testis had passed through the external ring, the

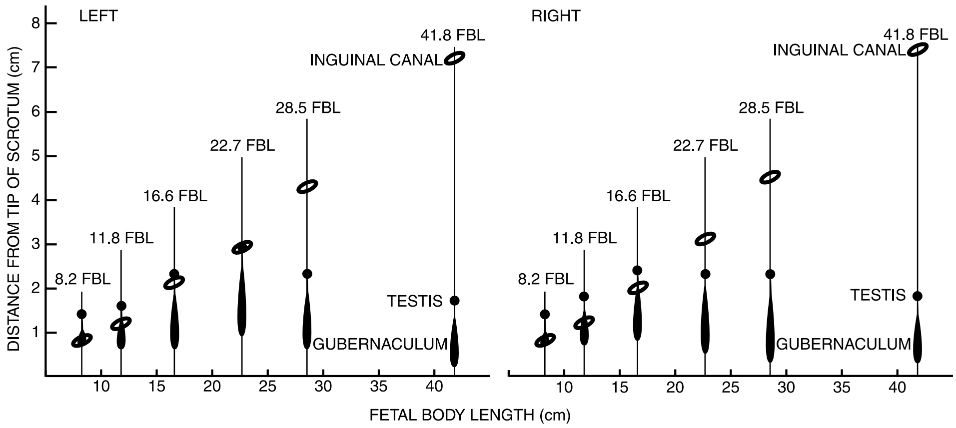

Fig. 2 The relative positions of the testis (T) and gubernaculum (G) during translocation of the testis, and their positions relative to the inguinal canal (IC) and to the distal tip of the scrotum (abscissa).

Table 3 Length of gubernaculum before, during and after passage of testis through inguinal canal

	Before passage	During passage	After passage
Left			
n	16	7	14
Mean FBL (cm)	19.4	23.0	26.7
Length G (cm)	1.7	2.0*	1.6
(SD)	(0.2)	(0.2)	(0.2)
Right			
n	11	2	15
Mean FBL (cm)	19.5	21.5	24.8
Length G (cm)	1.8	1.9	1.6
(SD)	(0.3)		(0.2)

n, number of observations; G, gubernaculum. Before passage: immediately before entry into canal with testis at or within 0.3 cm of inguinal canal. During passage: testis within inguinal canal. After passage: immediately after exit of testis from canal, but with distal edge of testis within 1.5 cm of inguinal canal.
*$P < 0.01$ by unpaired *t*-test compared with both before passage and after passage through the inguinal canal.

gubernaculum became significantly shorter compared with its length when the testis lay within the canal. The difference in the length of the left gubernaculum before and after transit of the testis through the inguinal canal was not significant. For the right gubernaculum, there were insufficient specimens that had a testis within the inguinal canal to make statistical comparisons between gubernacular length before transit, in the canal or after transit. However, the length of the gubernaculum just before and just after transit did not differ statistically. The data suggest that the gubernaculum continues to lengthen until the testis passes through the canal. In a specimen of 65 cm (210 DGA), the length of the gubernaculum was approximately 1.4 cm.

The testis

The testis in fetuses of FBL 3–6 cm was situated on the medial side and in the middle of the length of the mesonephros. For fetuses longer than FBL 10 cm, the testis was located on the lateral and posterior aspect of the kidney. It increased in size from 0.4×0.2 cm (length $\times$ breadth) at FBL 8 cm to 0.9×0.5 cm at FBL 22–23 cm when passing through the inguinal canal. By FBL 41 cm, it was in the scrotum and measured 1.7×0.8 cm (Table 1). The rate of increase in size was almost linear during this period.

Kidney to scrotum distance

On both the left and the right sides, the kidney to scrotum distance increased almost linearly from 1.3 cm at FBL 8.2 cm to 9.9–11.7 cm at FBL 41.8 cm (Fig. 1).

Kidney to testis distance

Up to the stage at which the testis entered the inguinal canal, the kidney to testis distance increased more slowly than the kidney to scrotum distance. After passage through the canal, the rate of growth increased in a linear fashion, to approach the gradient for kidney to scrotum. By FBL 28.4 cm, the growth line lay almost parallel to that of the kidney to scrotum distance (Fig. 1).

Kidney to inguinal canal distance

Between FBL 8.2 cm and 41.8 cm, an almost linear growth of kidney to inguinal canal distance occurred. This rate of growth was slower than that for the kidney to scrotum and kidney to testis distances (Fig. 1).

Testis to scrotum distance

In the younger specimens (FBL 5.8–10 cm), the distance from the distal end of the testis to the tip of the scrotum was approximately 1.3 and 1.4 cm on the left and right side, respectively (Table 2). From the time the testis separated from the kidney until when it came close to or lay within the inguinal canal, this distance increased to about 2.8 cm (left) and 2.3 cm (right; see Fig. 2). When the testis had passed through the canal, the distance decreased to 2.2 cm on both sides. Thereafter, the distance from the distal end of the testis to the tip of the scrotum decreased gradually to 0.5–0.6 cm at FBL 41.8 cm. However, in a single specimen of FBL 65 cm, the testis to scrotum distance was 1.3 cm on the left and 2 cm on the right.

Gubernaculum to scrotum distance

The distance between the tip of the gubernaculum and scrotum at different stages is summarized in Table 2 and plotted in Fig. 2; these data show that the end of the gubernaculum remains within 1 cm of the scrotum. The gubernaculum–scrotum distance was greatest (0.9 cm on left; 0.8 cm on right) up until the testis entered the inguinal canal. By FBL 41.8 cm, the gubernaculum to scrotum distance decreased to 0.2 cm and 0.3 cm on the left and right, respectively.

Relative position of the kidneys

Between the stage when the kidney and the testis separate (after FBL 10 cm) and the stage when the testis enters the inguinal canal (FBL 17–23 cm), the relative distance between the left kidney and the crown [(crown–kidney)/FBL × 100] decreased by 3.5%, from 85.5% to 82%. Similarly, the relative distance from the crown to the right kidney decreased from approximately 84% to 79%, or by approximately 5%. Comparing fetuses of FBL 10 cm and 18–21 cm, these reductions in the relative distances of the kidneys to the crown were *c.* 0.7 cm on the left side and *c.* 0.9–1 cm on the right side.

Discussion

It was not possible to ascertain the precise gestational age of the specimens used in this study, but the figures published by Maneely (1952) and Arthur et al. (1989) indicate that the distance from fetal crown to ischial tuberosity gives a reasonable estimate, particularly during the earlier stages of pregnancy. These figures also indicate that, in fetuses of similar gestational ages, there can be an appreciable discrepancy in FBL.

In an adult bull, the distance between the kidney and the scrotum is well in excess of 1 m. However, during development, the displacement of a fetal testis is a very small fraction of this distance. There are many factors believed to be involved in testicular translocation, including differential growth rates, the function of androgens, the role of the gubernaculum, the growth of the testis and the nature of the attachment of the testis to the gubernaculum.

Much of the recent literature has concentrated on the activity of androgens (Hosie et al. 1999) and the role of the gubernaculum. Heyns (1987), in a study of human fetuses, found that while the testis was within the abdomen, the gubernaculum was firmly attached to the region of the inguinal canal. Once the testis was through the inguinal canal, the end of the gubernaculum was no longer firmly attached to any structure and it did not extend to the bottom of the scrotum. The length of the intra-abdominal gubernaculum and its wet mass increased prior to descent. Heyns & De Klerk (1985) found similar changes in the gubernaculum of pig fetuses during descent. Using pig fetuses, Fentener van Vlissingen et al. (1989) described the cellular, hyaluronic acid, collagen and glycosaminoglycan content of the gubernaculum during descent. All these constituents increased during the transabdominal phase of displacement. Cell numbers and collagen content remained static during descent from the external ring of the canal into the scrotum. Similar results were also reported by Heyns et al. (1990).

In a review of the structure of the human inguinal canal and gubernaculum, Husmann & Levy (1995) proposed that the gubernaculum initially dilates the inguinal canal and, with accompanying intra-abdominal pressure, applies traction to the testis to introduce it into, and pass it through, the inguinal canal. Lam et al. (1998) showed that the gubernaculum of rats was not in close proximity to the scrotum at any stage of descent and that, during the early stages of development, the testis appeared to be held close to the inguinal canal by the gubernaculum, which was wedged through it. In a study of 30 bovine fetuses at various stages of testicular descent, Hullinger & Wensing (1985) proposed that the swelling of the gubernaculum dilated the inguinal ring and enlarged the inguinal canal.

Although the relative positioning of the kidneys during development is of interest in the present study, it appears to have no influence on testicular translocation. Furthermore, such positioning might give a false impression of the distance to be covered during the process of translocation. Part of the increase in the kidney to testis distance could be due to the relative decrease between kidney and crown during development. This increase might also be due to different growth rates with a relative diminution in size of the kidneys compared with neighbouring structures, or due to both of these factors. In young fetuses, the mesonephros and early developing metanephros are very large structures compared with the size of other organs. Between FBL 10 cm and FBL 18–22 cm (the stage at which the testis is at the inguinal canal), there was an increase of 2.4–2.5 cm in the distance between the kidneys and scrotum. Of this total distance of 2.4–2.5 cm, the relatively forward positioning of the kidneys amounted to approximately 0.7 cm on the left and 0.9–1 cm on the right.

To comprehend the mechanism of testicular translocation, it is necessary to focus attention on the distance between the testis and its target, the scrotum. The gubernaculum testis plays an important role and the inguinal canal appears to be an obstacle. A notable feature in translocation is that the maximum distance between the testis and the scrotum is 2.8 cm on the left and 2.3 cm on the right, when the testis is passing through the inguinal canal. When about to separate from the kidney, the testis is only 1.3–1.4 cm from the scrotum (Table 2). Thus, between separation of the testis from the kidney and its entry into the inguinal canal, the testis–scrotum distance appears to increase with overall growth although several factors are acting to diminish it.

At the time of separation of the testis from the kidney, the attachment of the gubernaculum to the vas deferens was approximately 0.3–0.4 cm from the distal end of the testis. By FBL 17 cm, the part of the vas between the attachment of the gubernaculum and the testis had become coiled and condensed and the attachment was only *c.* 0.1 cm from the distal end of the testis and epididymis. This factor would reduce the distance between testis and inguinal canal (and scrotum) by about 0.2–0.3 cm. The testis also increased in length from about 0.5 cm to 0.9 cm during the period between separation from the kidney and entry into the inguinal canals and, if this growth were evenly spatially distributed, the testis–scrotum distance would be reduced by a further 0.2 cm. When the testis was within the scrotum at FBL 41.8 cm, the testis–scrotum distance was still approximately 1.6 cm. This means that, between FBL 22.7 and 41.8 cm, the actual distance that the testis moved toward the scrotum was only approximately 0.6–1.2 cm. During this same period, the gubernaculum became 0.3–0.5 cm shorter and if this shortening exerted traction on the testis, it would bring it closer to the margin of the scrotum. Furthermore, during translocation, the length of the testis increased from 0.9 cm at FBL 22.7 cm to 1.7 cm at FBL 41.8 cm. Thus, about 0.3–0.4 cm of the testis–scrotum distance would be taken up by this growth. These last two factors together could account for 0.6–0.9 cm of the total displacement of 0.7–1.2 cm that occurs during this period.

Throughout testicular translocation, the gubernaculum retained its club shape and had a soft, gelatinous consistency. There was no detectable adhesion between any part of the gubernaculum and the surrounding tissues of the inguinal canal, parietal layer of the processus vaginalis or scrotum at any stage during testicular transit.

The measurements involving the gubernaculum give some insight into its possible function. In the very early stages of testicular translocation (FBL 8–10 cm), the end of the gubernaculum was about 0.1–0.3 cm within the inguinal canal and 0.7 cm from the scrotum (Fig. 2). The right testis separated from the right kidney earlier than the left and it entered the canal before the left testis. The right kidney was situated more anteriorly than the left. At this stage, the ends of the right and left gubernaculum were approximately 1.3–1.4 cm distal to the inguinal canal and both were located at the same distance from the scrotum (0.6–0.7 cm). These data are compatible with the concept that during transabdominal transposition, the gubernaculum acts as an anchor, holding the testis at a relatively fixed distance from the scrotum, acting initially on the right testis that was situated more anteriorly than the left. When the testis was at the internal ring or was just passing through the inguinal canal, the end of the gubernaculum was at its greatest distance (0.8–0.9 cm) from the end of the scrotum, suggesting that the gubernaculum was under tension during this stage.

After the testis had passed through the canal and the gubernaculum was shorter, the mesenchyme between it and the body of the scrotum became distinctly fluid, which might indicate an interaction between the tissues of these adjacent structures. This change in texture could facilitate movement of the gubernaculum toward the scrotum through transmission of intra-abdominal pressure via the processus vaginalis. After this stage, the end of the gubernaculum was only 0.2–0.5 cm from the margin of the scrotum. These figures indicate that, during transabdominal translocation of the testis, the gubernaculum remained at a short and relatively static distance from the scrotum; the approximation of the gubernaculum to the scrotum only occurred after the testis had passed through the canal.

Transabdominal and transinguinal passage of the testis does not appear to be due to differential growth or to tension from shortening of the gubernaculum. Between the time that the testis separated from the kidney (FBL 10–11 cm) to become adjacent to the inguinal ring (FBL 19.4 cm; Table 3), the length of gubernaculum and the FBL had both approximately doubled (Table 1). During testicular transit through the canal, the length of the gubernaculum continued to increase, becoming shorter only after inguinal passage was complete between FBL 20 and 25 cm. After transinguinal passage, the final transposition of the testis to the scrotum could be due to tension from shortening of the gubernaculum together with intra-abdominal pressure exerted through the processus vaginalis. At the last stages examined (mean FBL 41.8 cm) and in one specimen of FBL 65 cm, the length of the gubernaculum was approximately 1.4 cm. In ungulates, Backhouse (1964) also reported a decrease in length of the gubernaculum but commented that such a decrease was accompanied by an increase in thickness. Thus it remains possible that the volume of the gubernaculum is not changing during the period of testicular translocation through the canal.

Taken together, the data suggest that, rather than the bovine testis migrating toward the scrotum during its passage across the abdomen and through the inguinal canal, the distal end of the gubernaculum remains at an essentially fixed distance from the scrotum, thereby holding the testis at a relatively fixed distance from the scrotum while the pelvis is enlarging. The final positioning of the testis within the scrotum could simply be the result of the bovine gubernaculum undergoing a shape change: widening and shortening, together with intra-abdominal pressure possibly being applied via the processus vaginalis, as suggested for other species (Weber, 1847; Hunter, 1926; Husmann & Levy, 1995).

Our interpretation of bovine testicular displacement is in agreement with previous quantitative studies in the human fetus that have taken account of the overall growth of the pelvis (Lockwood, 1888; Blechschmidt, 1955, 1960; Youssef & Raslan, 1971). Blechschmidt (1955) emphasized the importance of studying the spatiotemporal displacement of the testis from lateral and superior viewpoints, as well as from the conventional ventral aspect. He showed that the total arc of subcutaneous connective tissue between the testis and the fascia of the coccyx remained relatively constant while the fetus doubled in length from 15 to 31 cm and the testis moved to the scrotum. The pararectal arc of fetal connective tissue was subsequently named the testococcygeal ligament and the gubernaculum testis was identified as the most ventral segment of this whole ligament (Blechschmidt, 1960). Because the testococcygeal ligament is anchored in the fascia of the vertebral column and retains a constant length, the 'prime mover' for the displacement of the testis to the scrotum is the piston-like tridimensional growth of the cartilaginous pelvis. Nevertheless, a potential role for abdominal fluid pressure acting directly on a mobile testis (Weber, 1847; Hunter, 1926; Bergin et al. 1970) or acting indirectly via the processus vaginalis to increase the tension in the gubernaculum (Shrock, 1971; Johansen, 1988) cannot be excluded by anatomical studies.

Many authors have claimed that gubernacular traction cannot be involved in testicular descent because the gubernaculum has only a diffuse weak attachment to the skin of the scrotum (e.g. Hunter, 1926; Wyndham, 1942). However, Lockwood (1888) observed in the human fetus that the gubernaculum testis can have multiple and variable distal termination sites. Thus, a dorsally directed extension of the gubernaculum towards the vertebral column (i.e. as the testococcygeal ligament) has been frequently overlooked, perhaps because of the historical tendency to examine the descent of the testis only from a ventral perspective (e.g. Hullinger & Wensing, 1985; Wensing, 1986; Wartenberg, 1990).

It is convenient to summarize the process of bovine testicular translocation in three phases. The first phase is the passage of the testis from the kidney to the inguinal canal. The second phase is the transit of the testis through the inguinal canal and the third phase is the translocation from the external ring of the canal to the scrotum.

In the first phase, the transabdominal transit of the testis appears to be due to the testis being held at a relatively fixed distance from the scrotum. The end of the gubernaculum remained within 0.6–0.9 cm of the end of the scrotum. During this phase, the point of attachment of the gubernaculum to the vas deferens moved closer to the testis and the testis became longer. Rather than the testis 'migrating' toward the inguinal canal, the inguinal canal appears to be 'migrating' toward the testis – an appearance due to the global growth movements at the pelvic end of the fetus.

During the second phase – the transit of the testis through the inguinal canal – the length of the gubernaculum and the distance between the testis and scrotum were greatest. The bulk of the gubernaculum and the processus vaginalis appeared to have dilated the canal in preparation for the passage of the testis. Up to and during this stage, the gubernaculum increased in size at about the same rate as, or slightly faster than, the body of the fetus. The increase in body size together with the testis being held at a relatively fixed distance from the scrotum and intra-abdominal pressure could all contribute to the passage of the testis through the canal. The precise stage at which the gubernaculum began to diminish in length was not determined, but it appeared to take place soon after the testis passed through the canal. Shortening of the gubernaculum together with intra-abdominal pressure might be responsible for bringing the testis from the canal into the neck of the scrotum.

The third phase – the final positioning of the testis in the scrotum – can be accounted for by the combined effects of growth of the testis, shortening of the gubernaculum and displacement of the gubernaculum towards the margin of the scrotum. At the stage of passage through the inguinal ring, the distance between the testis and scrotum was at its greatest (2.3–2.8 cm). At the stage when the testis was located in the scrotum, this distance was 1.6–1.7 cm. Thus the actual distance to be traversed by the testis was only 0.6–1.2 cm. In addition to the shortening of the gubernaculum (0.3–0.5 cm) and its displacement toward the scrotum (0.2–0.7 cm), the length of the testis increased by 0.6 cm and this could account for 0.3 cm of the distance to be traversed.

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