THE NATURE AND CAUSE OF THE PHYSIOLOGICAL DESCENT OF THE TESTES.

By D. BERRY HART, M.D., etc., *Lecturer on Midwifery, Surgeons' Hall, Edinburgh; Hon. Fellow, American Gynæcological Society; Carnegie Research Fellow.*

PART II.—DESCENT IN MAN.

IV. THE DESCENT OF THE TESTES IN THE HUMAN FŒTUS.

WE are not yet in a position to explain descent thoroughly, but with a distinct approach to this. The first naked-eye and comparative work was done after Haller by John Hunter in his well-known paper published in 1786. Since that time, papers on the subject have been sparse in Great Britain, with the exception of those by Cooper (1830), Cleland (1856), Owen (1868), and Lockwood (1888). Thus in the literature summarised by Frankl in his paper in 1900, 121 references are given, but of these only three are British (Cooper, Owen, Cleland); and Lockwood, the most recent, is not quoted.

On the other hand, research has been abundant in Germany, less so in France, and important papers have been written by Bramann (1884), Frankl (1895–1900), Katz (1882), Klaatsch (1890), Nagel (1891), Weil (1884), Weber (1886), and by others.

While one recognises in Hunter's paper *leonem ex ungue*, a large amount of comparative and microscopic work has been done abroad since his work, and very little if any has crept into our text-books and teaching. The reasons for this are that in the first place the idea that the abdominal wall was unbroken until, at the earliest, the 3rd month, and that at or about the 7th month the testes were drawn into the inguinal canal and scrotum by the gubernaculum, deriving their coverings during this progress, was held by many as a sufficiently exact account of the matter, although in several of our text-books the description of a preformed canal is mentioned so far as its peritoneal and even its muscular elements are concerned.

Then, again, an evident inaccuracy is present in all British and American text-books and most foreign ones, viz., the description of the testes as lying at first extraperitoneally in the abdomen and passing down into the scrotum extraperitoneally, either by muscular traction purely, or by the aid of mutual unequal growth of inguinal canal and gubernaculum, so that after the obliteration of the processus vaginalis we find a peritoneal covering to the testes (tunica serosa) and a peritoneal lining to the scrotum (tunica vaginalis). This mechanism is described in order to give a peritoneal covering to the testis. I need not criticise these statements in detail, but may shortly say that: (1) The testes in the abdomen of the fœtus are not covered by peritoneum, but by germ-epithelium. (2) The testes are not extra-peritoneal in the abdomen after the Wolffian bodies have involuted, but have a distinct mesentery, in the main developed from the diminished Wolffian structures. (3) In the scrotum the testes are not covered by peritoneum. If they were, the peritoneum would strip off as it does from a tumour such as the epoophoritic (par-ovarian) developing in the broad ligament. (4) The testes in the scrotum are really covered with involuting germ epithelium as the ovary is (Frankl, Hoffmann). (5) However the human testes get into the scrotum, their route is *viâ* the processus vaginalis, into the tunica vaginalis, and then the processus becomes obliterated. John Hunter says this distinctly. I came to this conclusion during the study of

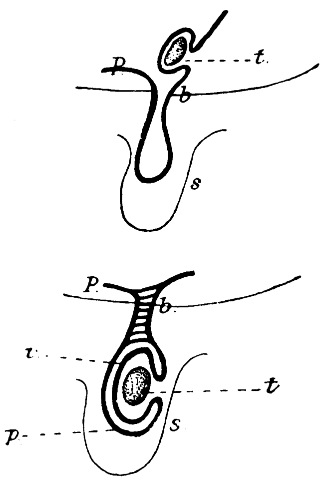

Fig. 20.—To show usual View of Descent and its Errors. (Frankl.)

t, testes; *P*, peritoneum; *b*, proc. vag. open; *S*, scrotum. The lower *b* shows obliterated proc. vag.

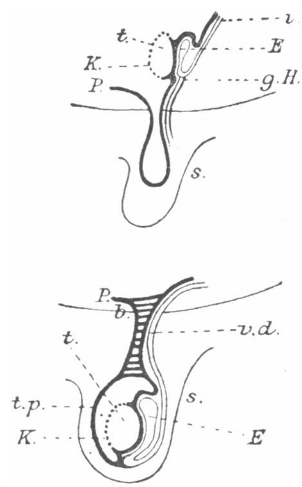

Fig. 21 —To show more exact View of Descent. (Frankl.)

v.d., vas. def.; *t*, testes covered with germ-epithelium; *E*, epididymis; *P*, peritoneum; *s*, scrotum.

my specimens, and was beginning to verify some points, but found it unnecessary to do so, on noting in the course of reading, that Frankl in 1895 showed clearly that "the testis has a peritoneal envelope (the tunica vaginalis), but not a peritoneal covering."

He points out, too, that Hoffmann (in the Quain-Hoffmann *Anatomie*, Erlangen, 1870) drew attention to this fact and showed the similarity of the testicular outer covering to the ovarian one.

Frankl's paper is of great interest. He shows that the testis, like the ovary, is not extraperitoneal, but covered by germ-epithelium. The fœtal testis in the scrotum is covered by low columnar epithelium—a contrast to the squamous endothelium of the adjacent parietal layer. He shows that the descent of the testes must occur through the processus vaginalis, and that then only the epididymis and inner wall of the scrotum are covered by peritoneum; the testes' outer covering is, as already said, involuting germ epithelium. There is, indeed, an evident naked-eye boundary between testes and epididymis, corresponding to the well-known white line of Farre in the ovary. This makes the explanation of the descent very much easier.

We may now consider the question of how the testes descend in the human embryo. I base this account on my own specimens and on the facts given by Bramann, Weil, Eberth, Lockwood, Klaatsch, and Frankl. The papers of these observers are of the greatest value. In Wiedersheim's work the description, so far as it goes, is excellent and suggestive.

We may consider descent of the testes in man under the following heads:—

(*a*) The development of the testes in relation to the Wolffian bodies in the early embryo (about 4th week).
(*b*) The development of the preformed inguinal canal.
(*c*) The abdominal changes in position of the testes.
(*d*) The passage of the testes into the inguinal canal and scrotum.

(*a*) *The Development of the Testes in relation to the Wolffian Bodies.*

I need not go into detail on this point, but only mention facts relevant to the inquiry. Details of this early development are well given by Lockwood and in all text-books of embryology. The testes develop on the inner aspect of the Wolffian bodies, have a short mesorchium, and are recognisable as such to the naked eye by the 5th week. When the Wolffian bodies atrophy, usually about the 2nd month, this primary mesorchium of the testes is amplified by the Wolffian mesentery, and we thus get a secondary mesorchium. At this time (2nd to 3rd month) the testes lie in the abdominal cavity.

(*b*) *The Development of the Preformed Inguinal Canal.*

The material for determining this point is not great in the human male fœtus, but we have microscopic (serial sections in the main, by Weil, Klaatsch, and Frankl) as well as serial sections of two human female embryos (5th and 6th to 7th week) in my possession. If we summarise these as to sex and age, they are as follows:—

Male.—In a 14·5 mm. embryo (Frankl, measurement from head to breech) approximately 25 to 28 days, the caudal end of the Wolffian body and that of the Wolffian duct are placed at the abdominal wall: no inguinal fold, *i.e.* gubernaculum, is present.

In a 16 mm. embryo (28 days) the same conditions are present.

In a 28·5 mm. embryo (5th to 6th week) we have a marked change (fig. 22). There is not only an inguinal fold but a beginning processus vaginalis. The inguinal fold has begun to penetrate, and a peritoneal dimple has formed. The transverse and internal oblique muscles are distinctly seen, but are, as yet, not beginning to penetrate, with the peritoneum and gubernaculum, as a wedge, through the abdominal wall. Into the base of the inguinal fold a few striated muscle fibres have radiated. The aponeurosis of the external oblique is also shown unbroken.

In a 4 cm. and 4·8 cm. embryo (3rd month) the peritoneal dimple was no deeper.

In an 8 cm. embryo (3rd month), Frankl figures the gubernaculum passing through the abdominal wall and presenting in the main the appear-

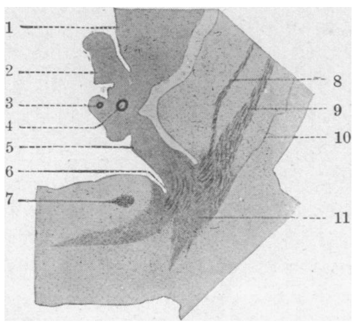

FIG. 22.—Trans. section through the body-wall, proc vaginalis, inguinal fold, and sexual gland of a male embryo, 28·5 mm. head-breech diameter. The mass of cells at 11 is traversed by muscular fibres.

1, Wolffian body; 2, testis; 3, duct of Miller; 4, Wolffian duct; 5, inguinal fold; 6, p.v. peritonei; 7, m.r. abdominis; 8, m. trans. abd.; 9, m. obl. uterus; 10, aponeurosis m. obl. extern.; 11, mass of cells. (Frankl and Eberth.)

ance I found in the *Macropus ruficollis* specimens (figs. 11 to 13). He divides the developing gubernaculum into three portions: an abdominal portion, a vaginal portion (in the peritoneal dimple), and an infravaginal portion below the level of the peritoneal dimple. It is into the last only that striated muscle radiates from below, the analogue of the conus inguinalis (*v.* V., section on Phylogeny), and forms really what has been described as the ascending fibres of the cremaster.[1]

Klaatsch, in an 8 cm. embryo, figures these ascending fibres as well marked, and indeed as forming by an inversion of the gubernaculum into the peritoneal cavity a structure quite comparable with the conus inguinalis of rodents; and in fact in the 17 cm. embryo he figures the processus vaginalis as obliterated (shown in 8 cm., 11 cm., 15 cm., and

[1] This division of the gubernaculum comes up specially under the changes at the 7th month.

17 cm. (4th month) fœtuses). He would thus make the processus vaginalis be present as an inversion of this conus in the 17 cm. embryo. Frankl criticises this, and indeed it is evident that the peritoneal dimple or fossette is formed in 25 mm. embryos by, or along with, the passage of the gubernaculum through the abdominal wall.

As the sections of the Frankl 8 cm. embryo are followed down, we see how the processus is formed by the penetration of the double crescentic peritoneal folds, and finally at the lowest sections we come on the end of the developing gubernaculum, uncovered by peritoneum, and with the cremaster on all its aspects but the lowest. At or about this time (10 cm. embryo) the gubernaculum increases in size, mainly by growth of its connective tissue elements, and at this period, too, the external abdominal ring has formed.

In the 12 cm. embryo (4th month) the gubernaculum is deeper and the testis is at the internal abdominal ring.

In the 19 cm. embryo (5th month) the gubernaculum thickens and lengthens, and the testis rises a little from the internal ring—a real ascensus.

In the 23 cm. embryo (5th month) the processus vaginalis is deeper, and in the neighbourhood of the pars vaginalis of the gubernaculum there is striated muscle, and more of it in the infravaginal portion. This thickening of the gubernaculum may dilate the processus vaginalis, but probably there is a combined growth of the two.

At the end of the 5th month and beginning of the 6th, the aponeurosis of the external oblique and the cremaster fascia are everted along with the gubernaculum, which is now at the entrance to the scrotum. The gubernaculum is shorter, and striated muscle fibres (vertical and circular) are present in the infravaginal portion.

It must be noted that the ages of the embryos given are based on measurements, are difficult to give exactly, and are therefore only approximate.

There is thus complete evidence that in the human embryo, prior to the passage of the testes through the abdominal wall, there is a preformed inguinal canal, due to a passage of the peritoneum, gubernaculum, and transverse and oblique muscles, to the outer side of the rectus, forwards and inwards towards the scrotum.—It happens as in the marsupial embryo, with the difference that the gubernaculum contains scrotal, not abdominal unstriped fibres, and that the marsupial scrotum is suprapubic and not perineal as in man. None of Frankl's or Klaatsch's drawings show lymphatics, but this is probably merely an omission. I found them in relation to the developing round ligament, as I shall explain in a subsequent paper.

(c) *The Abdominal Changes in Position of the Testes.*

These have been given with great accuracy and clearness, so far as dissection can go, by Bramann, who examined forty specimens, and his results may be briefly summarised as follows :—

In a specimen *at the end of the 2nd or beginning of the 3rd month*, the testes 3 mm. × 1·3 mm. were about 1 mm. from the internal abdominal ring. Behind them lay the epididymis : the vas deferens ran in a horizontal direction to the bladder. From the point where the vas deferens issues from the epididymis, or, as Frankl puts it, at the junction of the globus minor and vas, the gubernaculum, 1 mm. long and ·5 mm. broad, passed to the internal ring, where there was a shallow peritoneal depression—the beginning of the processus vaginalis.

At the end of the 3rd month or beginning of the 4th, the testes lay lower and at the region of the internal abdominal ring. The testes were 4 mm. × 2 mm. in a 14 to 15 weeks' embryo, and close on the internal ring, with an inguinal fold ½ mm. long. The mesorchium was longer, and allowed mobility to the testis.

After this, the testes ascend somewhat, owing to the increase in length and thickness of the developing gubernaculum—its length and breadth at this period (13th to 16th week) being about 1 to 3 mm. by ½ to 1 mm. (average in seven specimens).

At the end of the 4th or beginning of the 5th month, the testes are larger (5½ mm. × 3½ mm.), the mesorchium is longer, and the upper portion of the epididymis has a mesepididymis (mesorchiagogos of Seiler). The gubernaculum measures 3 to 2 mm. in length. By dissection, from without, in the region of the external abdominal ring, and removal of skin, superficial fascia and aponeurosis of external oblique, one can see white fibres issuing from the external ring, and these pass to the external oblique aponeurosis.

Up to the *end of the 6th month* the gubernaculum seems to have attained its highest development, its length being from 3 to 8 mm., and its breadth, a little below the testes, 2 to 4 mm. The processus vaginalis is about 3 to 3½ mm. deep, and its entrance admits a fine sound.

At the *beginning of the 7th month* the real descensus begins. The testes, which were 5 to 8 mm. from the internal ring, now approach it, and the inguinal fold is shorter, the processus vaginalis deeper, so that a sound can be passed to the aponeurosis of the external oblique. The testes, as the age of the fœtus increases, still descend, and now pass to near the internal ring, and the processus vaginalis now projects from the external ring, covered by the external aponeurosis, a hollow cylindrical structure 6 mm. × 4 mm.

If the aponeurosis and peritoneum be incised we now come on the peritoneal sac, and can see, on the posterior wall, the gubernaculum about 12 mm. long, projecting into the sac-lumen for about 1½ mm. without a mesentery, and reaching from the epididymis (where the globus minor meets the vas deferens, according to Bramann and Frankl) to the base of the inguinal canal.

In the 7½ *month* the testes are now in the inguinal canal, the gubernaculum shorter; and when they pass the external ring, the peritoneal sac is covered by the unpenetrated aponeurosis of the external oblique, and the fibres of the internal oblique and transversalis. The lower end of the peritoneal sac is attached to the fascia superficialis, and not united to it by

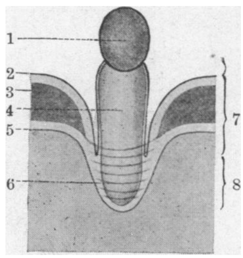

FIG 23.—Position of testes to ligt. inguinal and proc. vaginalis in a 7th month fœtus.

1, testis; 2, peritoneum; 3, muscles; 4, ligt. ing. (gubernaculum); 5, ext. obliq.; 6, cremaster; 7, vaginal part of G.; 8, infravaginal part of G. (Frankl and Eberth.)

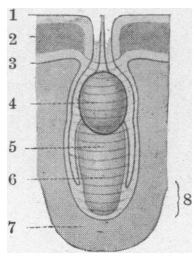

FIG. 24.—Deepening of proc. vag. and approach to base of scrotum: 8th month fœtus.

1, peritoneum; 2, muscles; 3, external oblique; 4, testis; 5, gubernaculum; 6, cremaster; 7, scrotum; 8, vaginal portion of G. (Frankl and Eberth.)

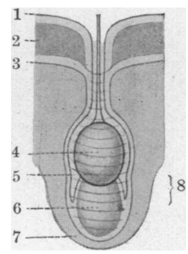

FIG. 25.—Shortening of vaginal part of gubernaculum in 8th month fœtus.

1, peritoneum; 2, muscles; 3, abd. ext.; 4, testis; 5, cremaster; 6, gubernaculum; 7, scrotum; 8, vaginal portion of G. (Frankl and Eberth.)

a rudiment of the gubernaculum. The fibres of the gubernaculum blend with the tissue of the processus. This is also what I have found in the marsupial embryo when the testis is in the inguinal canal. In fact the gubernaculum then spreads out as a thin layer between peritoneum and cremaster (fig. 16). The testes at last pass into the scrotum.

The changes beginning about this last stage have been well worked out by Frankl and Eberth. I have already spoken of the division of the gubernaculum into three parts by Frankl, and must now consider it according to his description in the 7th month fœtus. He gives three useful diagrams on this point.

In the first (fig. 23) the right testis is at the internal ring, and we see the abdominal part, vaginal part, and infravaginal part of the gubernaculum. The testis and gubernaculum show marks of contact with the small intestine, On the left side the testis was much deeper, the lowest third of the gubernaculum being in the processus vaginalis.

In a third specimen at the 7th month, the testis has passed the inguinal canal, is partly in the scrotum, the processus vaginalis has begun to involute, and both the vaginal and infravaginal portions of the gubernaculum are shorter (figs. 24 and 25). Frankl's diagrams give the descent somewhat earlier than other observers.

Eberth gives an excellent figure of the relations at this time. Similar conditions may be found at the 8th month and in the newly born (fig. 27).

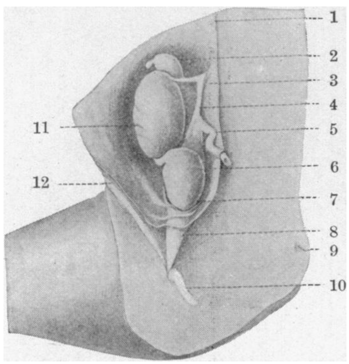

FIG. 26.—Male fœtus (11 cm. h.-b.), sagittal mesial section. (1½.)

1, peritoneum; 2, epididymis; 3, mesepididymis; 4, blood-vessels in mesepididymis; 5, ductus deferens; 6, inguinal fold; 7, entrance to proc. vaginalis; 8, inguinal ligament; 9, os coccygis; 10, symphysis; 11, testis; 12, body-wall. (Eberth.)

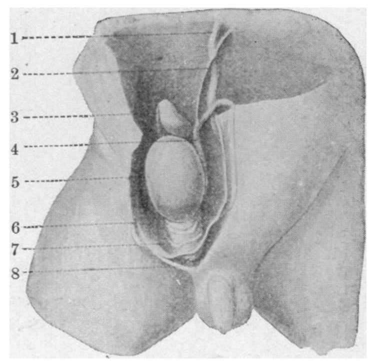

FIG. 27.—Male fœtus before birth. (1.)

1, ureter; 2, mesorchium; 3, epididymis; 4, d. deferens; 5, testis; 6, p. v. peritonei; 7, pars vaginalis, lig.-genito-ing.; 8, pars infravag. lig.-genito-ing. (Eberth.)

Increased growth of the processus vaginalis and shortening of the involuting gubernaculum, are the conspicuous features in the 7th to 8th month.

(*d*) *The Passage of the Testes into the Inguinal Canal and Scrotum.*

It may now be asked what are the causes of descent of the human testicle, and the approximate explanation is as follows:—

The disappearance in great part of the Wolffian body, and the guidance as a rudder, but not as a tractor, of the inguinal fold (gubernaculum at this stage), determine the position of the testes near the internal abdominal ring at or about the 3rd month (fig. 26).

The subsequent hypertrophy of the developing gubernaculum and its appearance in the peritoneal cavity as a thickened projection analogous to the conus inguinalis, if we follow Klaatsch's specimens of this period, cause a temporary ascent of the testicle. The hypertrophy with increased projection into the peritoneal cavity is a fact, whatever view as to its analogy to the conus in rodents we adopt, and has the result of causing the testis to lie higher. It may also have a dilating effect on the processus vaginalis; but as I have already said, there is more probably a combined growth of gubernaculum and processus.

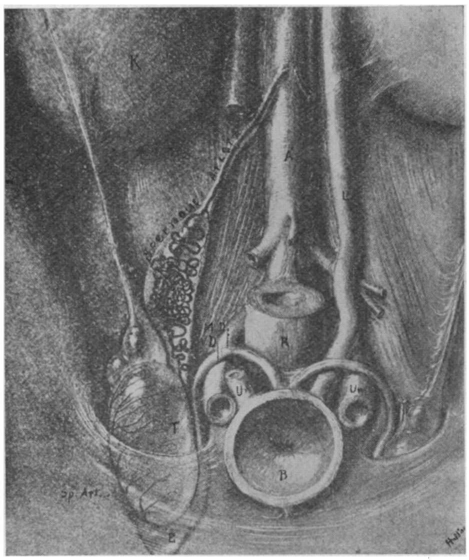

FIG. 28.— A transparent preparation of the right testis of an embryo pig, 210 mm. in length × 6.

Left testis nearly in inguinal canal; right testis, T, just entered; K, right kidney; A, dorsal aorta; E, epididymus; U, ureter; R, rectum; M.D., W.D., Müllerian and Wolffian ducts; U.A., umbilical artery. (Eben. C. Hill.)

The next stage (6th month to 8th month) is probably an increase in the capacity and length of the processus vaginalis, so that it expands and grows up, as it were, over the testis, enclosing it in the inguinal canal (fig. 28).

Owen has suggestive remarks on the presence of the more or less complete ovarian peritoneal capsule of the ovaries found in many mammals. "In the white bear (*Ursus maritimus*) the ovaries are completely enclosed in a reflected capsule of the peritoneal membrane, *like the testes in the tunica vaginalis*: a small opening, however, leads into the ovarian capsule at the part next the horn of the uterus" (*op. cit.*, § 99). This is an interesting comparison, as the ovarian capsule probably grows up round the ovary as I have described the inguinal canal enclosing the testis.

In the meantime the unstriped muscle gubernacular fibres with the striped muscle at its apex, and the peritoneum are developing into the solid scrotum, thus forming a cavity in it, lined with peritoneum. At this stage a shrinking of the gubernacular fibres takes place, and this is one factor (with probably some play allowed to the testis by the secondary mesorchium or mesepididymis of Frankl) in determining its ultimate position in the scrotum.

It will be seen, therefore, that in explaining the passage of the testis into the inguinal canal, a growth and development of the canal and of the gubernaculum, and not an actual descent of the testis, is considered the great factor. This is well demonstrated in the marsupial specimens, as well as in those of Klaatsch and Frankl.

I have said little of gubernacular traction. The penetrating power of the unstriped muscle of the gubernaculum is of importance, but it develops in the canal, beneath the peritoneal ridge derived from the inguinal fold, *i.e.*, is in the main sessile and not effective for exerting downward traction. It is not attached directly or even indirectly to the testis, as the upper attachment of the caudal ligament is to the epididymis and not to the testis. Bramann, however, says it is attached at the 4th month.

The striped muscle in connection with the gubernaculum ultimately forms the external cremaster. It does not favour descent by any means: indeed any action, if it really occurred in fœtal life, would cause ascent of the testicle, as it does in adult life. The external cremasteric fibres passing into the lower part of the gubernaculum form the ascending cremasteric fibres, and are analogous to the conus inguinalis of rodents.[1] The internal cremaster is unstriped muscle round the vas and vessels, and in the tunica vaginalis propria.

Thus while the cremaster fibres advance at first at the apex of the penetrating gubernaculum, their function is in relation to the adult cord and testis.

Minor factors may help descensus. Thus Eberth mentions intestinal pressure, and Bramann considers the distended sigmoid had some influence in depressing the left testis. Increased inclination of the pelvis has been considered to have an influence by altering the direction of the inguinal fold favourably for traction. The lengthening of the cremaster has been supposed to exert traction, but all these, if not wrong, are insignificant, so that Eberth is right in his contention, "Vielmehr scheinen aktive und complizierte Wachstumsvorgänge bei der Verlagerung des Hodens die Hauptrolle zu spielen."

I agree with this, and would minimise even the ultimate shrinking traction urged by Frankl, were it not for its apparent action in ectopia testis.

[1] Lockwood in his work rightly says that "the ascending cremaster of the human embryo is so trivial that perhaps it ought to be looked on as a mere survival of a muscle which in some of the lower animals is more active and better developed" (*op. cit.*, p. 108). Klaatsch's work on the conus inguinalis confirms this.

V. The Phylogeny of the Parts concerned in Descent of the Testes and of Descent Itself.

The phylogeny of an organ or developing process in a plant or animal is the history of its occurrence and development in some division of the animal kingdom, usually in the phylum or class of the animal or vegetable world to which it belongs. We are specially concerned just now with the phylogeny of the anatomical structures or organs involved in testicular descent in mammals, and with the phylogeny of the process itself. Up to this point we have been considering their ontogeny, *i.e.* their development in special animals or species. From the fact that we have, in this question of descent of the testes, to consider the organs and descent in the various species of the mammalia so far as known, as well as the embryology in many of them, the problem is a most fascinating one, and will repay careful consideration.

I purpose therefore to state the main facts bearing on the phylogeny of our subject. Some repetition is unfortunately unavoidable, especially as some of the structures, for instance the gubernaculum and cremaster, are joined with one another anatomically and functionally.

The organs concerned are the *scrotum*, *gubernaculum*, *cremaster*, and *inguinal canal*, and we shall consider these first, and then the *process of descent* itself.

The *scrotum* is a temporary or permanent pouch or sac for the testes. In the former instance, in certain mammals, at the rutting period, the testes pass back into the abdominal cavity, to re-enter the scrotum after the rutting period is over; in the latter case in other mammals they remain permanently in the scrotum when once they have passed in. In some of the latter, the processus vaginalis may be closed or open.

In the *monotremata* we start from "bed-rock," inasmuch as in these, the lowest of known mammals, there are none of the structures present whose phylogeny we are considering; they appear at first sight to come into the existing mammalian species *per saltum*, first in the marsupials, but the significance and accuracy of this requires to be carefully scrutinised. In the *marsupials* the scrotum is, in its position and development, the analogue and also the homologue of the female mammary pouch. In some males, apparent rudimentary mammary skin folds remain, but these are merely the folds after the scrotum has separated from its epidermic bed. The development of the mammary pouch in the female is by a passage backwards and outwards of the deep and superficial layers of the epidermis into the subjacent connective tissue; the connective tissue beneath the epidermis is not snared in. In the development of the marsupial scrotum the deep layer of the epidermis passes back and in and snares in the connective tissue which forms the site of the future interior of the scrotal sac. The amount of superficial epidermis passing in is slight, but its ultimate desquamation frees the scrotum, superficially embedded at first as it is in the epidermis, and allows of its pendulous character. In most marsupials the mammary pouch has its opening above for obvious reasons, but in one at least, Katz figures the aperture as opening below with a sphincteric muscular arrangement of evident utility. This position of the aperture is of importance as showing an intermediate stage relative to the openings of the mammary pouch and its analogue. In regard to the muscular arrangement of the mammary pouch, the round ligaments act, according to Cunningham, as a compressor mammæ, while the sphincter is developed from the subcutaneous unstriped muscle.

The mammary pouch, then, may have a caudal or cephalic aperture, but the scrotum, its analogue and homologue, has its aperture cephalic and communicates up to its later stages with the peritoneal cavity (open processus vaginalis), has the testis ultimately in it, and then usually becomes shut off from the peritoneal cavity by the closure of its processus vaginalis. In *rodents and insectivora* the scrotum is a shallow pouch in the abdominal wall in the region of the inguinal teats, the cremaster sac or pouch. When the testes are in the abdomen in the adult, the transversales and internal oblique muscles project into the inguinal fold, thus forming a conical projecting eminence in the peritoneal cavity—the inguinal cone (conus inguinalis) of Klaatsch, who first drew attention to it. The nature and functions of this "conus" will be considered presently.

In *rats* the scrotum is lower down, towards the perineum, and finally in higher mammals it becomes the pendulous, sac-like scrotum.

The following summary gives the scrotal conditions known to us in the chief species of the mammalia. For convenience, I add in this summary the main facts as to position of testes, the gubernaculum, and the cremaster. The conditions, however, vary very much; there is no gradual gradation but an undulating one, and we must therefore conclude that variation is still going on in regard to these organs and to their descent.

Scrotal Conditions and those as to Gubernaculum and Cremaster in the Chief Orders of Mammalia (mainly from Frankl).

Monotremata.—Testes abdominal; no scrotum; no inguinal fold; no cremaster. Echidna shows ligamentum testis joined to vas deferens.

Marsupialia.—Suprapubic scrotum with processus vaginalis closed; mesorchium broad and four-angled; inguinal fold well developed.

Edentata.—Testes abdominal; position of testes really varies; may be primary abdominal, subintegumental, or secondary abdominal; no scrotum; no inguinal fold; cremaster has transverse and internal oblique fibres; no conus; in *Dasypus sexcinctus*, inguinal fold marked and runs to equivalent of processus vaginalis, ending in its fundus; in *Dasypus novemcinctus*, short conical cremaster sac from internal and transverse below aponeurosis of external oblique.

Cetacea.—Testes primary abdominal and no inguinal fold.

Proboscidea.—Testes abdominal.

Rodentia.—Testes in scrotal pouch, but return to abdomen at "rutting"; cremaster from transverse and internal oblique, and forms "conus inguinalis."

Insectivora.—Much as in rodentia; have conus inguinalis, but not always; testes in some, abdominal, and no descent; in others, abdominal, and return to scrotum after rutting.

Chiroptera.—Testes return; conus present; cremaster from transverse and internal oblique.

Pinnipedia.—Testes extra-abdominal, subintegumental in inguinal canal; shallow cremaster sac from transverse and internal oblique; no scrotum; no return of testes; in *Phoca Vitulina.*

Carnivora.—Show beginning involution of processus; cremaster from transversus.

Artiodactyla.—Processus vaginalis narrow; cremaster from internal oblique.

Perissodactyla.—More primitive conditions; processus vaginalis wide open; traces of inguinal ligament even in adults; cremaster from internal oblique and well marked.

Prosimiæ.—(Lemurs) Processus vaginalis narrow; cremaster from internal oblique and transversus (mainly).

Primates.—Conditions very varied (*v.* Frankl, pp. 186–187), from simple to complex.

The facts are too varied to give any definite results, but some points are interesting.

The *monotremes* show the most rudimentary conditions. The *marsupials*, however, approach man in having definite scrotum, usually closed processus vaginalis, well-marked gubernaculum, very definite descent of testes in embryo, with a preformed inguinal canal.

Their scrotum shows clearly the most primitive type of scrotum, being evidently mammary in its nature and suprapubic in position. Its cremaster is derived from the transverse and internal oblique muscles as in man, and its fasciæ are much the same. Its gubernaculum, however, is not the specialised scrotal fibres of man, but consists of well-marked abdominal fibres which are normally rudimentary in man. The transition from monotreme conditions to marsupial ones is thus extraordinary.

We may put down, abdominal testes; absence of, or rudimentary scrotum; open processus vaginalis; return of testes to abdomen at "rutting," all as characteristic of a low position in mammalia; while permanent scrotum, especially if perineal; closed processus vaginalis, are all evidence of a high position. Exceptions, however, are plentiful, and in the *edentates* and *primates* we find almost all forms.

Primitive or comparatively primitive conditions are found in *Monotremes*, *Edentata*, *Proboscidea*, *Cetacea*, *Rodents*, *Insectivora*, *Chiroptera*, *Pinnipedia*, *Carnivora*; while in the *Artiodactyla*, *Perissodactyla*, *Carnivora*, *Prosimiæ*, *Marsupialia*, and *Primates* the arrangements are more advanced and finally culminate in the most advanced type as found in man.

Klaatsch has shown that in many mammals the site of the future scrotum is marked out by a certain area of skin, the area scroti, evident both by its naked-eye and microscopic character. The hairy covering is less marked; the small hairs arise from projections due to elevations of the cutis which possess a thin epidermic covering. Its most characteristic microscopic structure is a layer of unstriped muscle, ceasing abruptly at the edge of the "area." In the middle line the "areæ scroti" coalesce. The full phylogeny and nature of the scrotum will be best taken up after the gubernaculum and cremaster and conus have been considered.

The Gubernaculum, Cremaster, and Conus Inguinalis.—I need not recapitulate the facts as to the gubernaculum, but merely point out the constancy of its type in all mammals above monotremes. Thus its lower end is always in a mammary area, its upper at the Wolffian duct. It is not connected directly or indirectly with the testes. Its origin and insertion, in constant relation to primitive structures, viz, the mammary area and Wolffian duct, explain its almost uniform structure and relations in all species. In all, it acts as the active agent, with peritoneum and cremaster, in preforming the inguinal canal.

The *cremaster* is quite constant in all mammals above monotremes, and is derived, in almost all mammals, from the internal oblique and transversalis muscles. In front of it, as it passes in with the peritoneum and gubernaculum, lies the aponeurosis of the external oblique. Occasionally only one muscle forms the cremaster. In the marsupials the pyramidalis is well developed, but takes no part in the cremaster, as the gubernaculum skirts its outer edge, as it does that of the rectus. The great function of the cremaster is in the adult, as I have already stated, and it takes no part in causing the descent of the testes. It grows down with the inguinal fold, but how far, actively or passively, is difficult to say.

Conus inguinalis.—This is an important modification of the cremaster and gubernaculum found in rodents and insectivora, and first described by Klaatsch. I have found what appears to be its representative in marsupials, but in them it plays no part in changing the position of the testes. In rodents it can be seen as a cone projecting into the abdomen from the scrotal site, and it consists of fibres from the internal oblique and transverse muscles, passing into the inguinal fold. When the testes are in the scrotal inguinal pouch, the "conus" runs from the inguinal fold to the base of the scrotum. The muscular fibres must have grown into the fold (Wiedersheim). They do not draw the testes into the scrotal pouch, as the direction of their fibres prevents this; nor can they draw it out. It would be absurd to consider them as drawing the testes at one time into the abdomen and at another time into the scrotum. Probably the best idea is to consider the cremaster fibres of the conus as first growing up into the inguinal fold to form the conus. Then they grow into the scrotum after rutting. Thus, at rutting, the conus develops or grows into the inguinal fold and by its shrinkage or involution after rutting, and by accommodation, the testes resume their scrotal position. This is the most probable and consistent explanation in the present state of our knowledge, but serial sections at the various stages would be needed to confirm or reject it.

Klaatsch figures a conus in the human embryo, and Eberth does so too.

Thus the cremaster has its share in the function of developing the inguinal canal and the cavity of the scrotum, and ultimately, in man for instance, forms a muscular incomplete covering to the cord and testes. It is a valuable supporting constituent in a pendulous organ, and has a probable function in preventing dilatation of vessels in the cord and testes. Its action under voluntary impulses in man is known and is well figured by Wiedersheim, but in the descent of the testes into the preformed inguinal canal it has not as yet been shown to play any direct part.

Statement as to Nature of Relations of Scrotum, Gubernaculum, and Cremaster.—In man the scrotum develops partly in the perineal region and partly above this, and the question now arises: Is this region and that of the labia majora in the female related phylogenetically to the suprapubic region of the marsupial or to the inguinal in rodents where the scrota respectively develop? If so, it would enable us to make the consistent statement that *the gubernaculum and round ligament, and with them for a certain distance the peritoneum and cremaster, are developed in relation to a mammary region in all mammals,* thus extending the striking generalisation first made by Klaatsch in his suggestive paper. Developmentally the labia majora and scrotum are due to an extension downwards and backwards from an area contiguous to and blending with the inguinal region. We have seen that the developing gubernaculum abuts on the abdominal wall at this point before it begins to penetrate, and thus the scrotal or labial skin is practically a pendulous extension of the inguinal.

The nerve and vascular supply to the scrotum bear this out. The upper part of the scrotum is supplied by nerves and blood-vessels common to the inguinal region. Cooper states that "(1) a branch of a lumbar scrotal nerve . . . . divides into numerous branches which supply the skin of the groin, scrotum, and skin of the root of the penis; (2) the external spermatic nerve . . . . is distributed to the cremaster and the cellular tissue of the scrotum . . . . sends a branch to the skin of the groin . . . . The perineal nerve supplies the lower part of the scrotum."

A striking confirmation of this generalisation would be an abnormal teat or mamma on the scrotum or labium majus. I ventured to predict to a scientific friend that this would be found, and finally came on a reference to a mamma on the labium majus in Bateson's invaluable work on *Materials for the Study of Variation* (p. 187), where he quotes Harting, *Ueber einen Fall von Mamma accessoria*, the mammary structure of the gland being verified microscopically. I have said that Klaatsch has drawn attention to the fact that the gubernaculum and round ligament end in a mammary area, and I have confirmed and extended this. This would lead one to the conclusion by Klaatsch that the changes in the mamma induced by pregnancy are analogous to the changes in the conus inguinalis of the resting and rutting male. One might indeed look back, as Klaatsch suggests, to a primitive period when the young were suckled by both parents, and that then the differentiation took place which ended in the predominance of the mammary function in the female, with a round ligament equivalent to the developing gubernaculum only, and a rudimentary inguinal canal; while in the male the mammary function became rudimentary, and the gubernaculum initiated the changes in the abdominal wall, which not only gave the inguinal canal, but also the descent of the testes. This, however, is very speculative. I agree with Klaatsch in his views as to the mammary area insertion of the gubernaculum, but he has not pushed his most interesting theory far enough.

Let us apply it to the marsupials. In the male we have a scrotum topographically and developmentally equivalent to the mammary pouch; it contains the testes. In the female we have a mammary pouch with the round ligament, the analogue of the gubernaculum, ending in it, in relation to the mammary gland. One usually looks on the mammary pouch as only a pouch for the mamma, and for the young marsupial. To make it exactly equivalent to the male scrotal arrangement, it should, however, contain the ovary. It does not; but if we go back to the monotreme echidna, we find, as Haacke has shown, that it carries its egg—the product of the ovary—in a pouch developed for it at the time, a pouch large enough to hold almost completely a gold watch. *The mammary pouch therefore is primitively the egg or ovarian-product pouch just as the scrotum is the testicular pouch.* Thus in all mammals above monotremes the developing gubernaculum joins the lower end of the primitive Wolffian body to an area of skin which is primitively an ovarian-product or testicular pouch—a mammary area; and when it loses the fœtus-carrying functions (as it does in all above marsupials) retains in the female the mammary function, and in the male the testicular pouch function. The development of the inguinal fold and cremaster thus begins primitively in rodents in Klaatsch's inguinal cone, and develops to the more perfect gubernaculum of higher mammals. The active agent in the gubernaculum is the unstriped muscle; thus the peritoneum only forms a shallow processus in the female processus; it is the unstriped muscle that mainly forms the round ligament and preforms the inguinal canal.

The Inguinal Canal.—On this one can be brief, as much of its phylogeny is involved in the previous sections. There is no inguinal canal in the monotremes. It may be a shallow pouch (rodents, insectivora); a deeper canal, with its processus narrow or closed; a well-formed canal in the embryo, with closed processus (marsupials, carnivora, primates, man). Its line of evolution is thus, increase of depth in abdominal wall (its direction varying according to the position of the scrotum), and closure of processus. Its highest development is thus in man, but it is high, as already noted, in marsupials. The position of the inguinal fossa or canal, as the case may be, is determined by two factors: the direction of radiation of the gubernaculum fibres and the area of spread of a developing lymphatic centre. This is best seen in the marsupial embryo, but probably holds good for others.

Descent of the Testes.—There is no descent in monotremes, edentates, cetacea, or proboscidea. The first beginning is in rodents and insectivora, and there the descent is temporary and periodic after rutting. As we pass up the mammalian scale the descent becomes more marked, penetrating the abdominal wall and into a scrotum, inguinal, suprapubic, or perineal. While we use the term "descent" it must be noted that this is most marked in the abdominal phases; afterwards, when the testes are in the inguinal canal, the testes are relatively stationary, and growth of the inguinal canal is the active factor; descent again asserts itself if the testes reach the perineal scrotum; but if the scrotum is suprapubic, this last stage is really an ascent. We thus must always use the inevitable term "descent" with these reservations.

The Relation of Descent of the Testes to Haeckel's Law and to Mammalian Classification.—Haeckel's law (or rather the Müller-Haeckel law) is briefly stated as follows[1]:—Ontogeny repeats and condenses phylogeny in whole or in part—the development of the organs and their functions in man repeats and condenses in time and stages the parts of various organ-

[1] See Weismann's *Theory of Evolution*, vol. ii. p. 160; and also *Darwin's Life*, where Darwin claims this law.

ontogenies and their functions necessary to complete the ontogeny of the whole organism. In some stages, indeed, it gives what may appear an irrelevant reminiscence of its lower mammalian origin, as in the ascending cremaster fibres and temporary ascent of the testes.

This is a great generalisation, and is completely vindicated when we consider testicular descent in man. We cannot but accept this law, which points most probably to the continuity of the germ plasma as being at the root of the phylogenetic repetition in ontogeny. Let us consider the phylogeny of testicular descent. There is no descent in monotremes, in some edentates, in cetacea, and in proboscidea. The testes lie in a shallow inguinal pouch in rodents, and during rutting are abdominal from change in the "conus inguinalis," their cremaster: they are suprapubic in marsupials; perineal, and usually in a pendulous scrotum, in higher mammals.

The "ontogeny" of the process in man repeats in a few months of fœtal life (2nd to 8th) all these stages in the long phylogeny of the lower mammals. The testes are in the human male fœtus abdominal in the 2nd month (as in monotremes) at the peritoneal fossette, and afterwards a little higher in the 3rd to 4th month (as in the rutting of rodents); in the inguinal canal, *i.e.* subintegumental, at the 5th to 6th month, as in the rodents after rutting; and finally, perineal and scrotal at the 8th to 9th month.

In man the gubernacular fibres are scrotal, but in the pubic and perineal and inguinal rudimentary fibres we see a phylogenetic reminiscence of these conditions in marsupials and rodents. Those who believe in active gubernacular fibres in man as causing descent, regard these rudimentary fibres as aiding mechanically, like guy-ropes, the scrotal ones; but that the sessile or attached unstriped muscle of the gubernaculum can act "dynamically," *i.e.* cause transition, is erroneous; the true interpretation of the rudimentary fibres in man is seen in this, that they are an illustration of Haeckel's law.

In the development of our knowledge of testicular descent, indeed, it was really by a reversal of Haeckel's law that progress was made, *i.e.* the conditions in the lower mammals, a long-spun-out history, as it were, of what occurs in man, explained in the hands of the great early investigators —Hunter, Owen, Seiler—the more rapid and condensed stages in man— Haeckel's law was worked backwards by them.

But Haeckel's law can be used to bring back lost history, and supply stages in phylogeny we have lost; just as in his great periodic law as to the chemical elements, Mendeleëf rightly predicted that chemical elements would be discovered with certain definite atomic weights, and in approximate places in his scale, to complete the series.

Let us apply Haeckel's law to its logical extent. The monotremes and marsupials are lowest in the mammalian scale, and yet the marsupial has a development of inguinal canal, and a condition after descent in many respects resembling the human male, and higher than that in rodentia, for example. So far, therefore, as the conditions we are discussing go, we cannot adopt a linear mammalian classification. Mammals must be classified in several lines radiating from an ancestor more primitively developed than the monotreme. If then we wish to speculate as to this ancestor, we must consider early ontogenetic stages of the region in which the descent process takes place, *i.e.* the rump end of human embryos. Such stages are to be found in the human embryo as shown by Keibel, when the entodermal cloaca[1] is formed, the urogenital ducts opening into a common closed chamber. Here the cloaca is closed in front by the cloacal membrane devoid of the mesoblast which afterwards develops. The yielding of this membrane gives the distressing "ectopia vesicæ" of the human adult, but this yielding and patency of the cloacal membrane may have been normal in some predecessor of the monotremes. The egg may have been incubated in the upper part of the entodermal cloaca, which lay beneath the region in which the abdominal egg-pouch afterwards developed. From such an hypothetical ancestor the mammals may have developed, and the subsequent grouping may be arranged as follows:—

After the hypothetical mammalian ancestor, the first group would include the monotremes and marsupials. Between these, however, there is, in their testes arrangement, a tremendous gap, one being testiconda, the other having a well-formed scrotum, a closed-off processus vaginalis, and a descensus only differing from that of man in having a suprapubic scrotum (the analogue and homologue of the mammary pouch), and a gubernaculum, the fully developed abdominal fibres of which are rudimentary in man. This gap must either have been gradually filled with slowly evolved and now extinct members of the marsupials, or we may hold that the inguinal fold came into mammals *per saltum*, in a way analogous to the "Mutation" theory of de Vries as to the origin of species. The existence of intermediate forms of testicular position and descent as in the higher mammals, as in rodents, however, negatives this.

The next diverging group would hold the edentata, sirenia, cetacea, proboscidea, and hyracoidea; then would come a parallel group of rodents, insectivora, and chiroptera; next the ungulata and carnivoræ, and finally the lemurs, anthropoids, and primates. Intermediate forms exist in the edentata, lemurs, and anthropoids, so that the groups are not sharply differentiated.

[1] This is better termed "penultimate gut," *pars penultima* of the primitive gut: the "tail gut" is then *pars ultima*.

I merely throw out the arrangement of classification according to the position of testes and the evolution of their descensus as a suggestion, and one that must be modified greatly as our knowledge increases.

My final conclusion is that the testis, appendix testis, and prostatic utricle, Wolffian body and its duct, the gubernaculum, the mamma, the external genitals, form an associated anatomical unit, the male urogenital and mammary unit—for shortness, the male genital unit; and in the same way, the ovary, epoophoron, Wolffian body and its duct, the round ligament, the mamma, the external genitals, are the female urogenital unit - for shortness, the female genital unit.

This is an important and convenient condensation of the relation of these organs, and in a future paper on Mendelian action on differentiated sex I go on to analyse the nature and significance of these units as to this question.

I may, however, sum up descensus testiculorum in terms of the male unit. The essence of the process is this:—The testis is united to a mammary area, at first by the testicular caudal ligament and the inguinal fold or gubernaculum, afterwards by the involuting caudal ligament and developing gubernaculum. The developing gubernaculum, with the aid of the cremaster and peritoneum, forms a pit or fossa for the testis in the rodentia: a more complete canal or more or less pendulous scrotum in higher mammals. By subsequent disproportionate growth of canal and testes, and finally (according to Frankl) by the involution and shrinkage of the gubernaculum, the testes in man become lodged permanently in the scrotum. I need not bring in intermediate stages in this summary. The progression in mammals is thus primary testiconda, secondary testiconda; finally, more or less of a descent of testes into a closed sac. The gubernaculum site of origin is primarily a Wolffian duct area and only indirectly, by means of the caudal ligament, testicular; the insertion always mammary.

What the reason of testicular descent is I do not know, but the gubernaculum always penetrates to a mammary area, and this area, in the human male, is finally a scrotal or labial one, and the formula of the progressive change in the relations of the testes, commonly called "descent" in all mammals, is this: *the gubernaculum always develops towards, and ends in, a mammary area, suprapubic, inguinal, perineal, scrotal. The testis appears to follow its guide—its canal-former—the gubernaculum, and the gubernaculum in marsupials certainly passes through the substance and skirts the edge of a developing lymphatic area.*

As the heading of this paper I have given three quotations from John Hunter's works.

The second one shows plainly that Hunter held that the testis came through the processus vaginalis.

In the first quotation we see Hunter laying the foundation of the subject of testicular position and descent. The gubernaculum, the term which has rightly become permanent in anatomy, he never uses in the sense of a "tractor," but always of a "rudder"—its true meaning. Here again, Hunter's teaching has been for long discarded, with disaster to accuracy and clear comprehension, and the gubernaculum has been credited with powers that the examination of serial sections shows to be illusory.

Hunter held the only possible view at that time as to the testis-covering, viz., that it was a peritoneal one in the abdomen and scrotum.

The last quotation is a remarkable one, and shows Hunter's unique powers as an unprejudiced observer. We see in the record of this fact, shadowed forth the modern view that the scrotum is equivalent to a mammary area, towards which the gubernaculum develops and the testis passes; and so we may fitly and finally say that in the investigation of this great anatomical and physiological question there is one observer who was at the beginning and is still in the van—John Hunter.

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Not only did Frankl clearly show the points as to the testicular covering detailed in my paper, but he quotes Hoffmann in the Hoffmann-Quain *Anatomie*, Erlangen, 1870, as saying, "Allein auch an der vordere Abtheilung des Hodens fehlt der Peritonealuberzüg, indem dieser nur mit einem schmalen Saum auf die hintere Abtheilung der Hodens in der Umgebung des Nebenhodens sich erstreckt, fast genau so wie Waldeyer das Verhalten des Peritoneums zum Eierstock beschrieben hat. Der grossere theil des Hodens ist frei vom Bauchfell." This was written thirty-nine years ago. *Beiträge zur Lehre vom Descensus testiculorum. Sitzbericht der K. akademie der Wissenschaften*, Wien, 1900, Bd. cix. Hft. i. A most valuable monograph in the comparative anatomy of Descensus.

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As this rare case is in a somewhat inaccessible form, I give a short résumé of it. The patient was under the care of Drs Dietz and Heydenrich at Nürnberg. She was 30 years of age, and had observed this labial tumour for several years. During the suckling of her infant a milky fluid oozed from an ulcerated surface. The whole tumour was about the size of a large goose-egg, and had a special isolated palpable part the size of a walnut. The mass was pediculated, the pedicle being about 1 cm. long. It was easily removed. Macroscopic examination showed mammary structure, and a flattened-out teat with small openings was found. The fluid had fat globules. Without giving further detail, it may be said that the evidence of its mammary nature was absolutely complete.

His statistics are interesting. In 63 cases of accessory mamma he found 55 in women, 11 in men. In the women, 29 had one accessory mamma, 25 had two, and 3 had one. Of the 29, one was mammary, three in the groin, one on the back, one on the thigh, two above the navel, one on the axillary line, two in the axilla, eighteen on the breast.

Such cases are not uncommon. I have in my museum drawings of two specimens of double nipple and a cast of the axillary mammary or milk secretory condition to which Champneys has drawn attention.

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This represents the chief literature consulted. It is, however, fully given by Frankl and Klaatsch.