

19. DEVELOPMENT OF THE MALE UROGENITAL SINUS/VESTIBULE/URETHRA

Introduction:

In the first 4-6 weeks of development, the *cloacal fold surrounds the cloacal depression*. In the floor of the depression is the bilaminar *cloacal membrane*, which has an of external layer of ectoderm of the body wall, and an internal layer of endoderm of the cloaca, with no intervening mesoderm.

The cloaca is the terminal U-shaped segment of the hindgut.

The *urorectal septum* (URS), is a coronal septum that divides the cloaca into dorsal *anorectum* and ventral *primitive urogenital sinus* (UGS).

The *perineal plates* are lateral plates of mesoderm, covered by epithelium (ectoderm). The perineal plates merge in the in the midline, and divide the *cloacal fold, cloacal depression, and cloacal membrane* into posterior and anterior parts. The posterior part forms the *anal fold, the anal pit, and anal membrane*. The anterior part forms the *urogenital fold, the urogenital groove, and the urogenital membrane*.

Meanwhile, the *sinus bulb/Müllerian eminence*, inserts in the posterior wall of the *primitive urogenital sinus* (UGS). The sinus bulb/*Müllerian eminence* divides the primitive UGS into the *vesicourethral canal* above, and the *definitive UGS* below.

In males, the *sinus bulb* develops at the *upper border of the membranous urethra*. The *upper border of the sinus bulb* divides the primitive UGS, into the (tubular) vesicourethral canal above, and the (tubular) definitive UGS/vesibule below.

Vesicourethral canal:

In males: The upper third of the vesicourethral canal forms the *allantoic diverticulum or urachus, (median umbilical ligament)*, the middle third will expand to form the *urinary bladder*, and lower third will form the *prostatic urethra, and membranous urethra*.

Developmentally, the *membranous urethra belongs to the vesicourethral canal*. However, the membranous urethra functions as the pelvic part of the definitive UGS/vesibule/urethra.

The (tubular) vesicourethral canal is continuous with the (tubular) definitive UGS/vesibule.

The tubular UGS (distal to the membranous urethra), *extends on the ventral aspect* of the *genital swelling*. When this occurs the UGS assumes the shape of an inverted *funnel, flattened from side to side*. The funnel shaped UGS, is destined to form the *male vestibule/urethra* (bulbar urethra, penile urethra, and fossa navicularis). The UGS remains *closed* by the *intact urogenital membrane*.

In females, the *Müllerian eminence* develops at the *lower border of the membranous urethra*, then tilts backwards, to complete its development, *posterior to the membranous urethra*. The *lower border* of the Müllerian eminence divides the primitive UGS, into the (tubular) vesicourethral canal above (bladder, glandular urethra, and membranous urethra), and the (tubular) definitive UGS/vesibule (posterior, middle and anterior sections of the vestibule), below.

The definitive UGS/vesibule remains *closed below* by the *intact urogenital membrane*. Hower, it does extend forwards under the genital/phallic swelling (future anterior section of the vestibule).

In females: the upper third of the vesicourethral canal forms the *allantoic diverticulum or urachus*, (*median umbilical ligament*), the middle third will expand to form the *urinary bladder*, and lower third will form the *glandular urethra, and membranous urethra*.

The genital swelling: (m).

The genital swelling in the male or anlage of the phallus or penis, forms a prominent elevation in the genital area, as an extension of the perineum. It consists of the genital tubercle (mesoderm), covered on its dorsal and lateral aspects by the genital fold (ectoderm).

In cross section, the genital swelling has the shape of a half dome, with a core of mesoderm (genital tubercle), and a covering of ectoderm (genital fold). The ventral surface of the genital swelling presents the elliptical urogenital fold, which surrounds the urogenital groove. The intact urogenital membrane, lines the floor of the urogenital groove.

The genital tubercle:

The genital tubercle (mesoderm) contains the forwards continuation of the cavernous bodies in the perineum.

The genital fold:

The genital fold (ectoderm) covers the dorsal and lateral surfaces of the genital tubercle. The genital fold is destined to form the skin (ectoderm) of the penis and glans penis.

Cavernous bodies:

Cavernous bodies are composed of spongy tissue with large vascular spaces, that fill with blood during erection.

- a) *Crura of the corpora cavernosa of the penis, join to form the bicavernosal body of the penis.*
- b) *Corpus spongiosum of the bulbar urethra, is continuous with the corpus spongiosum of the penile urethra, and continuous with the dorsal plate of fossa navicularis which generates the glans penis.*

Corpora cavernosa penis:

The crura of the corpora cavernosa develop medial to the ischiopubic rami of the pelvis and continue forwards in the genital swelling as a bicavernosal body, which end in the glans penis.

Corpus spongiosum penis:

The bulbs of the vestibule develop on either side of the bulbar urethra, and continue forwards in the genital swelling, as the bulbs of the penile urethra. The bulbs develop into the corpus spongiosum of the bulbar urethra and penile urethra. Distal to the penile urethra, the corpus spongiosum is reduced to form the dorsal plate of fossa navicularis.

The perineum and its forward extension, the ventral surface of the genital swelling, presents the urogenital groove, urogenital fold, urogenital membrane

The urogenital groove:

The urogenital groove is an elongated, narrow elliptical depression, flattened from side to side, (anterior to the circular anal pit).

The urogenital fold:

The urogenital groove is surrounded by the elliptical urogenital fold.

The urogenital groove and urogenital fold:

The urogenital groove, surrounded by the urogenital fold, is divided into a *posterior* or *perineal section*, and an *anterior* or *phallic section*.

In the perineum, the urogenital fold (ectoderm), reflects on the medial borders of the scrotal folds.

In the phallus the urogenital fold (ectoderm), reflects on the lower border of the genital fold (ectoderm). The genital fold is destined to form the skin of the penis and glans penis.

The urogenital membrane:

The floor of the urogenital groove is formed by the urogenital membrane.

The urogenital membrane is a bilaminar membrane of endoderm and ectoderm, with no intervening mesoderm.

The external layer (ectoderm) reflects on the medial borders of the urogenital fold.

The inner layer of endoderm is continuous with mucosa (endoderm) that lines the funnel shaped UGS/vestibule.

Disintegration of the urogenital membrane:

The urogenital membrane disintegrates around 7 weeks of development.

Results of breakup of the urogenital membrane:

- a) mucosa (endoderm) of the UGS/vestibule, meets epithelium (ectoderm) of the inner border of the urogenital fold at *Hart's line*.
- b) the definitive urogenital sinus (UGS) becomes *the vestibule/urethra*, and the urogenital fold becomes the *vestibular/urethral fold*.

MALE VESTIBULE: ANATOMICAL SEGMENTS.

Pelvic segment: membranous urethra

Perineal segment: bulbar urethra

Phallic segment: penile urethra, fossa navicularis.

Development of the membranous urethra:

The vesicourethral canal is divided into three parts. The *upper third* of the vesicourethral canal forms the allantoic diverticulum or urachus (median umbilical ligament), the *middle third* expands to form the urinary bladder and the *lower third* forms the prostatic urethra and membranous urethra.

Membranous urethra is the distal segment of the vesicourethral canal and functions as the pelvic segment of male vestibule/urethra.

Sinus bulb/Müllerian eminence:

Sinus bulb/Müllerian eminence (future colliculus seminalis) develops at the *upper border* of the *membranous urethral segment* of the vesicourethral canal and projects into the prostatic urethral segment of the vesicourethral canal

Colliculus seminalis at cystourethroscopy:

The colliculus seminalis arises from the membranous urethra. The origin of the colliculus seminalis from the membranous urethra, is readily apparent at cystourethroscopy. The convex upper border of the colliculus seminalis is seamlessly continuous with the upper border of the membranous urethra. The colliculus seminalis is merged with the posterior wall of the membranous urethra.

The mesonephric/Wolffian ducts:

The *mesonephric/Wolffian ducts* (future ejaculatory ducts), leave the anterior wall of the fused paramesonephric (Müllerian) ducts, and enter the base of the prostate and descend in the prostatic urethra. At the distal end of the prostatic urethra, the mesonephric ducts run through the sinus tubercle, *anterolateral to a column of mesoderm (future vagina masculinus)*. The *mesonephric ducts (ejaculatory ducts)* open on the sinus tubercle, (anterior to the future ostium of vagina masculinus).

The paramesonephric ducts/Müllerian ducts:

The *fused segments of the paramesonephric ducts/Müllerian ducts* (potential uterus and cervix) descend behind the middle segment (future bladder) of the vesicourethral canal, posterior to the mesonephric ducts. The *conical end of the fused mesonephric ducts inserts in the upper end of the cylinder of mesoderm in the sinus bulb*, (future vagina masculinus), but *does not enter the sinus bulb*.

The *fused paramesonephric ducts disappear* due to Müllerian inhibiting factor (MIF), secreted by the Sertoli cells of the embryonic testes.

The vagina masculinus:

The *vagina masculinus* develops by cavitation of the *cylinder of mesoderm* in the sinus tubercle, postero-inferior to the mesonephric (ejaculatory) ducts.

The *lower end of the vagina masculinus is closed by a bilaminar membrane*.

The *upper layer of the bilaminar membrane is epithelium (supported by a thin layer of mesoderm)*, derived from mesoderm lining of the vagina masculinus.

The *lower layer of the bilaminar membranes is epithelium*, (supported by a thin layer of mesoderm), derived from endoderm lining the UGS/vestibule.

A perforation develops in the bilaminar membrane, to form the *ostium of the vagina masculinus*. The remaining *ring of the bilaminar membrane* forms the diaphanous, *hymen of the vagina masculinus*.

The sinus bulb becomes the colliculus seminalis:

The distal ends of the mesonephric/ejaculatory ducts enter the *sinus bulb*, *run anterolateral to the vagina masculinus and open superolateral to the introitus of the vagina masculinus*. The *sinus bulb is now the colliculus seminalis*.

Membranous urethra functions as the pelvic segment of male vestibule/urethra:

a) Membranous urethra receives urine from the urinary tract.

When the bladder contracts, expelled urine, passes through the open bladder neck, prostatic urethra, and membranous urethra. Urine then passes through the penile urethra, and fossa navicularis and exits the body through the external urethral meatus.

b) Membranous urethra receives semen from the reproductive tract.

In the phase of emission, spermatozoa transported by the vas deferens, and fluid expelled from the seminal vesicles, pass through the ejaculatory ducts, which open on the colliculus seminalis, in the lower end of the *prostatic urethra*. Prostatic fluid (from the prostate glands), is added to the fluid from the ejaculatory ducts. Reflex contraction of the prostate (against the closed bladder neck), expels the seminal fluid *through the membranous urethra*, into the bulbar urethra.

In the *ejaculatory phase*, contractions of the bulbospongiosus muscles (against the closed membranous urethra), propel the seminal fluid through the vestibule/urethra.

Sphincters of the urethra (m): Lissosphincter, rhabdosphincter

In development the *omega* shaped *lissosphincter* (involuntary smooth muscle sphincter), forms around the *prostatic urethra within the prostate*. In the posterior midline, (behind the prostatic urethra), the lissosphincter inserts in a *connective tissue raphe*. In adult males, the lissosphincter is incorporated in the capsule of the prostate. At the bladder neck, the lissosphincter blends with the inner circular layer smooth muscle of the detrusor. Except during the passage of urine, and emission of semen, the *lissosphincter, is in a constant state of contraction*.

In the membranous urethra, the *omega* shaped *rhabdosphincter* (voluntary striated muscle), develops around the *omega* shaped *lissosphincter*. The *posterior borders both sphincters*, insert in a posterior midline *connective tissue raphe*. The lower border of the rhabdosphincter, is attached to the superior surface of the (inferior) perineal membrane. Some striated muscle fibers from the membranous urethra, fan out on the capsule on the anterior aspect of the prostate. The *lissosphincter and rhabdosphincter of the membranous urethra, form the distal sphincteric complex (DSC)*. The fetal arrangement persists in the adult.

Development of the perineal part of the vestibule/urethra:

The membranous urethra pierces the (inferior) perineal membrane, then runs through the upper surface of the bulb of the corpus spongiosum and joins the *bulbar urethra*.

Development of the bulbar urethra:

The *bulbar urethra* is formed by *postero-anterior ventral folding and midline fusion* of the vestibule/urethra, in the perineum, proximal to the suspensory ligament of the penis. Concomitantly, *postero-anterior and midline fusion*, of the *vestibular/urethral folds*, ventral to the bulbar urethra, forms the *bulbar raphe*. The *bulbar raphe is separated from the floor of the bulbar vestibule/urethra*, by a layer of mesoderm.

Development of the corpus spongiosum of the bulbar urethra:

The *corpus spongiosum of the bulbar urethra*, develops from the *vestibular/urethral bulbs*. The *vestibular bulbs, develop as* longitudinal bodies of cavernous erectile tissue, along the sides of the bulbar vestibule/urethra.

The vestibular bulbs will form the cylindrical corpus spongiosum of the membranous urethra, and penile urethra. Distal to the penile urethra, the corpus spongiosum is reduced to the dorsal plate of fossa navicularis.

The vestibular bulbs *fuse dorsally and ventrally* to form an adherent cylinder of spongy tissue around the bulbar urethra, called the *corpus spongiosum of the bulbar urethra*. The *vestibular bulbs unite posterior to the bulbar urethra*.

The posterior end of the joined vestibular bodies, expands to form the *bulb of the corpus spongiosum*.

The *superior surfaces* of the vestibular bodies adhere to the inferior surface of the (inferior) perineal membrane.

The *inferior/ventral surface* of the corpus spongiosum, and bulb of the corpus spongiosum, presents a *shallow groove*. From the ventral groove, a *sagittal septum*, extends to the floor the

bulbar urethra, and divides the corpus spongiosum into two *hemispheres*. The septum is thicker posteriorly and thin and incomplete, anteriorly.

Corpus cavernosum of the bulbar urethra, forms the middle part of the *root of the phallus*. The other two parts of the root of the penis, are the *crura of the corpora cavernosa*.

Development of the scrotum and scrotal septum:

The scrotal folds destined to form scrotal sacs and the scrotal septum, develop in the pelvic part of the perineum, posterior to the genital swelling or phallic part of the perineum.

(The suspensory ligament of the penis marks the level where the pelvic parts of the perineum, join the phallic parts of the perineum).

The *scrotal folds* develop, lateral to the segments of the vestibular/urethral folds, on either side of the bulbar urethral segment of the vestibule. The *lateral borders of the vestibular/urethral folds* reflect on the medial borders of the scrotal folds.

In the pelvic part of the perineum, development proceeds as follows:

- a) Ventral folding and postero-anterior fusion, of the vestibule, forms the *bulbar urethra*.
- b) Postero-anterior midline fusion of the vestibular/urethral folds forms the *bulbar raphe*.
- c) Postero-anterior midline fusion of the medial aspects of the scrotal folds (mesoderm), forms the *sagittal scrotal septum*.

The bulbar raphe becomes the scrotal raphe:

The *bulbar urethra* becomes enclosed in the *corpus spongiosum* with a *median sulcus*.

The *corpus spongiosum* is covered by the *bulbospongiosus muscle*, with a *median raphe*.

The *scrotal septum* joins the *bulbar raphe* to the *median raphe* of the *bulbospongiosus muscle*.

The *scrotal sacs* lie on either side of the *bulbar raphe*.

The *scrotal septum* (fused medial surfaces of the scrotal folds) joins the upper borders of the bulbar raphe (fused vestibular/ urethral folds), to the *tendinous raphe of the bulbospongiosus muscle*. Since the *scrotal septum*, distances, the bulbar raphe from the bulbar urethra, the *bulbar raphe* can be called the *scrotal raphe*.

Development of the bulbourethral (Cowper's) glands:

The ducts of the *bulbourethral glands* emerge from the floor of the bulbar urethra on each side of the midline. The ducts run posteriorly, below the floor of the bulbar urethra. Under the influence of testosterone, each duct proliferates in the bulb, to form lobules of tubuloalveolar glands. The small bulbourethral glands become embedded in the expanded bulb of the corpus spongiosum.

Anatomy of the bulbourethral glands:

The bulbourethral glands are a pair of pea sized glands embedded in the bulb of the corpus spongiosum of the bulbar urethra. The glands lie on either side of the midline, in the superficial perineal pouch, below the (inferior) perineal membrane.

The *thin excretory ducts*, about 2.5cm in length, run between the floor the bulbar urethra and the bulb of the corpus spongiosum and the floor of the bulbar urethra. The ducts open in the floor of the bulbar urethra, by tiny circular openings, on either side of the midline. The bulbourethral glands receive both parasympathetic and sympathetic innervation. Parasympathetic nerves cause mucus production, and

sympathetic nerves cause contraction of the myoepithelial cells that drive secretions of the alveoli, through the bulbourethral ducts, into the bulbar urethra.

The bulbourethral glands lubricate the vestibule (bulbar urethra, penile urethra, and fossa navicularis), in the arousal phase or sexual activity, and contribute 5% of the volume of the ejaculate.

Development of the bicavernosal body of the penis:

The crura of the corpora cavernosa leave their attachments to the medial everted edges of the ischiopubic rami, acquire a dense coat of mesoderm (tunica albuginea) and converge towards the midline. The coats of tunica albuginea on the medial aspects of the *corpora cavernosa*, fuse in the midline at the level of the arcuate ligament of the pubic symphysis, to form the *bicavernosal body*. At the level of the *arcuate ligament* of the pubic symphysis, the *corpus spongiosum* of the *bulbar urethra*, acquires a thick coat of mesoderm (tunica albuginea), and adheres to the ventral groove of the bicavernosal body of the penis. Distal to the level of the *suspensory ligament of the penis*, the bulbar urethra and corpus spongiosum of the bulbar urethra, becomes the *penile urethra and corpus spongiosum of the penile urethra*.

Development of the phallic part of the male vestibule/urethra:

Forward growth of the *genital swelling* extends the perineal part of the male vestibule/urethra, *distal to the suspensory ligament of the penis* to forms the phallic segments of the male vestibule/urethra (penile urethra and fossa navicularis).

Development of the penile urethra:

The *penile urethra* develops in the phallus, between the suspensory ligament of the penis and fossa navicularis.

a) *postero-anterior folding and ventral midline fusion* of the vestibule/urethra (endoderm) and

b) forward extension of *postero-anterior folding and ventral and dorsal fusion of the bulbs of the vestibule*, forms *corpus spongiosum that envelops the penile urethra*. between the suspensory ligament of the penis and the fossa navicularis.

c) the penile urethra lies in the groove on the ventral aspect of the bicavernosal body.

Concomitant, postero-anterior fusion of the *vestibular/urethral folds*, forms the *penile raphe*, ventral to the penile vestibule/urethra

Development of the prepuce:

Near the distal end of the penile urethra, the *genital fold and penile raphe*, form a double layered fold (the frenulum), that grows distally to cover the coronal sulcus and developing glans penis. The (penile) raphe on the outer and inner layers of the prepuce, is termed the *preputial raphe*.

The coronal sulcus:

The coronal sulcus refers to the part of the genital fold, that surrounds the segment of the bicavernosal body, and penile urethra, between the recess of the prepuce and the corona of the glans penis. The diameter of the coronal sulcus is the same as the diameter of the phallus behind the sulcus. The coronal sulcus appears as a sulcus, due to its location behind the prominent corona of the wings of the glans penis. The lateral and ventral borders of the corona of the glans penis, curve forwards and medially, creating a V-shaped extension of the coronal sulcus on either side of the ventral midline.

The distal end of the penile urethra lies in the V-shaped extension of the coronal sulcus, in the groove (of tunica albuginea), ventral to the bicavernosal body of the penis. The V-shaped extension of the coronal sulcus is divided in the midline by the frenulum of the coronal sulcus. The genital fold that covers the coronal sulcus reflects on the lateral surfaces of the frenulum (of the coronal sulcus).

Development of the frenulum:

The *frenulum* is formed by *postero-anterior fusion of the vestibular/urethral folds* to form a *quadrilaminar membrane* in the coronal sulcus and its forward V-shaped extension, between the corona of the wings of the glans penis. The lateral surfaces of the frenulum, reflect on the genital fold covering the coronal sulcus.

The *frenulum* is *barely separated* from the floor of the *penile urethra*, by a small amount of mesenchyme. At the *distal end of the frenulum*, at the apex of the V-shaped extension of the coronal sulcus, between the corona of the wings of the glans penis, the penile urethra joins the *fossa navicularis*.

In the *recess* between the *prepuce* and the coronal sulcus, the frenulum is attached to the inner surface of the prepuce. The *free anterior border of the frenulum* connects the inner end of the *preputial raphe*, to the posterior end of the *navicular raphe*.

Development of the fossa navicularis (glanular urethra):

The *fossa navicularis* or *glanular urethra*, is the terminal segment of the vestibule/urethra. It is formed by *postero-anterior ventral midline fusion of the mucosa (endoderm) of the vestibule/urethra*, within the developing *wings of the glans penis*.

The *roof of corpus spongiosum* of the penile urethra, is prolonged as a *dorsal plate* which is adherent to the roof of fossa navicularis.

Tunica albuginea on the dorsal surface of the dorsal plate, adheres to the groove (of tunica albuginea) of the conical end of the bicavernosal body of the phallus. The bicavernosal body, dorsal plate of fossa navicularis and fossa navicularis become enwrapped by the wings of the glans penis.

Development of the navicular raphe:

The quadrilinear *navicular raphe* develops (in concert with development of fossa navicularis), by *postero-anterior fusion of the vestibular/urethral folds*. The navicular raphe is barely separated from the floor of fossa navicularis, by a minute amount of mesenchyme.

The dorsal end of the *anterior free border of the frenulum*, joins the *posterior end of the navicular raphe*.

The lateral borders of the quadrilinear navicular raphe, reflect on the ventral borders of the genital fold, over the glans penis.

Meanwhile, the unfused distal ends of the vestibular/urethral folds have tilted dorsally, to align with the opening of fossa navicularis to form the labia of the glans penis. The lateral borders (ectoderm) of the labia of the glans penis, reflects on the anterior border of the genital fold (over the wings of the glans penis, and the outer border of the dorsal commissure of the vestibular/urethral fold, reflects on the anterior curved border of the genital fold.

The *anterior/distal end of the quadrilinear navicular raphe* splits, to join the ventral ends of the *labia of the glans penis* (unfused distal ends of the vestibular/urethral folds).

Development of the glans penis:

The glans penis develops from the dorsal plate of the fossa navicularis.

Dorsal plate of fossa navicularis:

At the distal end of the penile urethra, the *corpus spongiosum* of the penile urethra, is reduced to a *dorsal plate over the roof of the fossa navicularis*. The (tunica albuginea on the) dorsal surface of the dorsal plate, adheres to the groove of the tunica albuginea, on the ventral aspect of the bicavernosal body of the penis. The *dorsal plate ends just distal to the conical tip of the bicavernosal body of the penis*.

The *anterior end, and lateral borders of the dorsal plate, generate a layer of spongy tissue that flows between the genital fold and the bicavernosal body of the penis, to form the body of the glans penis (cap, roof, and wings)*.

- a) Spongy tissue from the *distal end* of the dorsal plate of the fossa navicularis, flows under the genital fold, and over the conical end of the bicavernosal body, to form the *cap of the glans penis*.
- b) Spongy tissue from the *lateral borders* of the dorsal plate of the fossa navicularis, flows under the genital fold and over the dorsal and lateral aspects of the bicavernosal body, to form the *roof of the glans penis*.
- c) Spongy tissue generated by the *inferior surfaces of the lateral borders* of the dorsal plate of fossa navicularis, forms the *wings of the glans penis*. The outer surfaces of the wings of the glans penis attaches to the genital fold, which covers the wings of the glans penis, as the wings grow ventrally. The wings of the glans penis, covered by the genital fold, grows ventrally, draping over the (mucosal) lateral walls of the fossa navicularis. The wings, covered by the genital fold, envelop the lateral walls, and floor (except in the midline), of the fossa navicularis.

Concurrently, the *vestibular/urethral folds* fuse in the midline to form the quadrilinear *navicular raphe*.

The ventral midline of fossa navicularis

- a) the *lateral borders* of the quadrilinear *navicular raphe*, reflect on the *genital fold*, covering the wings of the glans penis.
- b) the *navicular raphe* is barely separated from the *floor of fossa navicularis*, by a (thin) linear *strip of mesenchyme*.
- c) the *ventral borders of the wings of the glans penis* are separated in the midline by contact with the strip of mesenchyme, between the navicular raphe and the floor of fossa navicularis.

The corona of the glans penis:

The *prominent rounded border* of spongy tissue at the base of the glans penis is termed the *corona of the glans penis*.

- a) The *vertical part* of the corona, is formed by the proximal border of the roof section of the glans penis.
- b) The *curved part* of the corona is formed by the proximal borders of *wing sections of the glans penis*. The wing sections of the corona, curve forwards and medially towards the midline. The *V-shaped gap* of the wing sections of the corona borders the forwards extensions of the coronal sulcus.

The horizontal *ventral borders of the wings of the glans penis*, are separated in the midline by line of mesenchyme, between the navicular raphe, and the floor of the fossa navicularis.

Glans clitoris: (f).

In females, the *pars intermedia* of the *roof anterior section of the vestibule*, is analogous to the dorsal plate of fossa navicularis. Just as the dorsal plate of fossa navicularis, generates the cap and roof of the glans penis in the male, so *pars intermedia* generates the *cap and roof of the glans clitoris* in the female.

In male development, the dorsal plate of fossa navicularis, generates *wings of the glans penis*.

In female development the *pars intermedia* does not generate wings of the glans clitoris.

The vestibular/labial folds (f).

The vestibular/labial folds remain unfused below the *anterior section of the vestibule*. The vestibular/ labial folds unite distally in the anterior commissure of the vestibular/labial folds.

The *outer borders of the vestibular/labial folds/frenulum* (ectoderm), reflect on the ventral borders of the dorsal hood of the glans clitoris, and ventral border of the genital fold over the roof and cap of the glans clitoris.

The *outer border of the anterior commissure* of the vestibular/labial folds (ectoderm), reflects on the genital fold covering the (ventral end of the) crescentic cap of the glans clitoris.

The *inner borders of the vestibular/labial folds*, (ectoderm), meet the lateral borders of the flat mucosal roof (endoderm), of the anterior section of the vestibule of the fossa navicularis, at Hart's line.

The *inner border of the anterior commissure of the vestibular/labial folds* (ectoderm), meets the distal/anterior border of the mucosal roof (endoderm), of the anterior section of the vestibule, at Hart's line.

Megameatus with intact prepuce (m).

In the male, arrested development at the stage, of folding and ventral fusion of a) the penile urethra in the coronal sulcus, and b) the glanular urethra (fossa navicularis), is accompanied by failure to form the frenulum and navicular raphe. c) the roof and cap of the glans penis, are generated normally by the dorsal plate of the open glanular urethra, however, the wings of the glans penis are not generated by the dorsal plate over the glanular urethra.

The result is the genital fold (over the coronal sulcus and roof and cap of the glans penis, meets the unfused vestibular/urethral folds alongside a wide urethral groove or megameatus.

The megameatus is formed by a) the open penile urethra in the coronal sulcus, and b) the open glanular urethra (fossa navicularis).

Wings of the glans fail to develop (from the ventral surface of the lateral borders of the dorsal plate) and the *vestibular/urethral folds remain unfused*. The result is that the *genital fold* over the roof and cap of the glans penis, reflects on the *lateral borders of the unfused vestibular/urethral folds* ventral to the distal end of the *penile urethra* in the coronal sulcus and *unfused vestibular/urethral folds* ventral to the *glanular urethra/fossa navicularis*.

The *inner borders of the unfused vestibular/urethral folds*, (ectoderm), ventral to the *penile urethra* in the coronal sulcus, (*potential frenulum*), meet the *lateral borders of the flat mucosal roof* (endoderm), of the open penile urethra, *ventral to the roof of the corpus spongiosum* of the penile urethra, (ventral to the bicavernosal body and overlying genital fold of the coronal sulcus).

The *inner borders of the unfused vestibular/urethral folds* (ectoderm), ventral to the glanular urethra/ fossa navicularis, (*potential navicular raphe*), meet the lateral borders of the flat mucosal roof of the open glanular urethra/fossa navicularis, *ventral to the dorsal plate* of the glanular urethra/fossa navicularis (ventral to the bicavernosal body and overlying roof and cap of the glans penis, covered by the genital fold).

The unfused vestibular/urethral folds unite distally in the anterior commissure (of the vestibular/urethral folds), ventral to the distal end of the dorsal plate of the glanular urethra/fossa navicularis.

The outer border of the anterior commissure (of the vestibular/urethral folds) reflects on the genital fold over the crescentic cap of the glans penis. the inner border of the anterior commissure, meets the distal end of the flat mucosal roof of the glanular urethra/fossa navicularis.

The fold of the *prepuce*, which originates posterior to the coronal sulcus, *develops normally*.

Development of the labia of the glans penis: external urethral meatus (m).

The labia of the glans penis are formed by the distal unfused ends of the vestibular/urethral folds, and the anterior commissure of the vestibular/urethral folds.

- a) The fossa navicularis develops by postero-anterior ventral midline fusion of the distal segment of the vestibule/urethra. At this stage the *ventral opening of the fossa navicularis* is lined up ventrally, with the unfused distal ends of the vestibular/urethral folds.
- b) Differential growth of the ventral and distal borders of the (developing) wings of the glans penis, pushes the proximal ends of the unfused vestibular/urethral folds (distal to the navicular raphe). This tilts the unfused vestibular/urethral folds dorsally, so they line up vertically with the vertical opening at the end of the tubular fossa navicularis.
- c) The unfused vestibular/urethral folds, align with the floor and lateral walls of the vertical opening at the end of the fossa navicularis. The anterior commissure of the vestibular/urethral folds, lines up with the roof of the vertical opening of the fossa navicularis.

The distal unfused ends of the vestibular/urethral folds have become the labia of the glans penis and the anterior commissure of the unfused vestibular/urethral folds has become the dorsal commissure of the labia of the glans penis.

The labia of the glans penis, and the dorsal commissure of the labia of the glans penis, form the external urethral meatus.

Reflections of the external urethral meatus:

The outer border of the fold of the dorsal commissure of the labia of the glans penis (ectoderm), reflects on the (ventral end of the) genital fold (ectoderm), covering the cap of the glans penis.

The outer borders of the folds of the labia of the glans penis (ectoderm), reflect on the (anterior border of the) genital fold (ectoderm), covering the wings of the glans penis.

The ventral ends of the labia of the glans penis, join the distal end of the quadrilinear navicular raphe.

Hart's line: (m).

Hart's line demarcates, the line of breakdown of the urogenital membrane, which separated the elliptical definitive urogenital sinus (endoderm), from the elliptical urogenital fold.

In male differentiation, the inner border of the fold of the dorsal commissure of the labia of the glans penis, and the inner borders of the labia of the glans penis (ectoderm), meets mucosa (endoderm) of the elliptical opening at the end of fossa navicularis, at Hart's line.

The extant opening of the vestibule/urethra to the exterior, is preserved at Hart's line.

Prior to postero-anterior ventral midline fusion of the elliptical ventral borders of the vestibule/ urethra, and postero-anterior fusion of the elliptical vestibular/urethral folds, there was a wide connection between the ventral border of the vestibule/urethra, and the inner layer of the vestibular/urethral folds, at the embryonic Hart's line. This is the arrangement in female development.

In male development, Hart's line moves distally due to:

- a) postero-anterior fusion of the vestibule/urethra to form the bulbar urethra, penile urethra and fossa navicularis.
- b) postero-anterior fusion of the vestibular/urethral folds, to form the scrotal/bulbar urethral

raphe, the penile (and preputial) raphe, and the navicular raphe.

c) the developing (ventral and anterior borders) of the wings of the glans penis, push the proximal end of the unfused vestibular/urethral folds distally.

As a result, the *unfused vestibular/urethral folds*, and *anterior commissure of the vestibular/urethral folds* become the *labia and dorsal commissure of the labia of the glans penis*, which are *aligned, with the elliptical distal end of the fossa navicularis*.

Mucosa at the end of fossa navicularis, (endoderm of the vestibule), meets epithelium of the inner layers of the labia, and dorsal commissure of the labia, (ectoderm of the vestibule/urethra) at Hart's line.

The extant opening of the vestibule/urethra is preserved at Hart's line.

Development of the outlet of the vestibule/urethra:

Dorsal tilt of the unfused *vestibular/labial folds*, results in the formation of the *labia and dorsal commissure of the labia* of the external urethral meatus, aligned with the opening of the fossa navicularis (vestibule/urethra).

The *outlet of the vestibule/urethra* is formed by epithelium (ectoderm), *lining the inner layers of the labia and dorsal commissure of the labia*, of the glans penis.

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