THE ANATOMY OF THE STRUCTURES INVOLVED IN THE ERECTION-DILUTION MECHANISM IN THE MALE DOMESTIC FOWL

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ABSTRACT

THE ANATOMY OF THE STRUCTURES INVOLVED
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IN THE MALE DOMESTIC FOWL

By

Carl Edward Knight

The mechanism of erection and semen dilution in the male chicken differs from that in mammals. In the mammal turgidity of the penis during sexual stimulation is due to engorgement of cavernous tissue with blood. In contrast, the phallus of the domestic chicken during sexual stimulation becomes engorged with a blood filtrate. Various accessory glands, such as the seminal vesicles, prostrate, bulbourethral glands of the mammal produce fluids which dilute the semen as it passes through the ductus deferens and urethra. The chicken does not possess any homologous glands. The same blood filtrate that engorges the phallus during erection is discharged during ejaculation into the seminal groove where it dilutes the semen ejected from the ejaculatory papillae.

A thorough anatomical description of the structures related specifically to the erection-dilution apparatus in the male chicken was found to be lacking. Because of the economic importance of reproduction in the chicken, an anatomical investigation into this mechanism was initiated.

The seminal fluid, which produces the turgidity in the phallus and plica lymphatica (lymphfold) during sexual excitation and serves as a diluent for semen was found to originate in two corpi paracloacales

vascularis. These vascularized bodies were covered laterally by the m. sphincter cloacae and m. contractor cloacae and medially by the wall of the urodeum (middle chamber of the cloaca). The bodies consisted of numerous glomi (capillary tufts) formed by branches of the a. pudenda interna, a. phalli, and a. pudenda terminalis and drained by branches of corresponding veins. Endothelial lined collecting lymph channels in juxtaposition to the capillaries formed an elaborate network of lymph channels which coursed from the corpus paracloacalis vascularis to the phallus and plica lymphatica.

The n. pudendus internus arose directly from the plexus pudendus and innervated the corpus paracloacalis vascularis, phallus and plica lymphatica. The distribution of the nerve fibers strongly suggested that both sympathetic and parasympathetic nerve fibers were involved in erection and ejaculation.

The corpus paracloacalis vascularis gave a positive test for acid and alkaline phosphatase. There was no noticeable difference in phosphatase activity between the corpus paracloacalis vascularis taken from ejaculated and non-ejaculated birds. This indicated that the blood filtrate crossed the capillary wall into the collecting lymph channel by simple diffusion during sexual stimulation.

Blood found in the seminal fluid, when the massage technique for semen collection (Burrows and Quinn, 1935) was used, originated from hemorrhages in the plica uroproctodeum (uroproctodeal fold) and was not a normal component of seminal fluid.

Terminology was recommended to refer to anatomical structures comprising the erection-dilution mechanism. These terms were primarily

based on older anatomical works according to the recommendations of Nomina Anatomica (1956; 1968).

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INTRODUCTION

The mechanism of erection and semen dilution in the male chicken differs from that in mammals. In the mammal turgidity of the penis during sexual stimulation is due to the engorgement of cavernous tissue with blood. In contrast, the phallus of the domestic chicken during sexual stimulation becomes engorged with a blood filtrate. Various accessory glands, such as the seminal vesicles, prostrate, and bulbourethral glands in the mammal produce fluids which dilute the semen as it passes through the ductus deferens and urethra. The chicken possesses no homologous glands. The same blood filtrate that engorges the phallus during erection is discharged through the epithelium of the plica lymphatica into the seminal groove during ejaculation. Here it dilutes the semen from the ejaculatory papillae.

I was unable to find a thorough anatomical description of the structures related specifically to the erection-dilution apparatus in the male chicken. Because of the economic importance of reproduction in the chicken, an anatomical investigation into this mechanism was initiated.

In 1967 a portion of the work was completed and published as a thesis (Knight, 1967). The major emphasis was on the cloaca and the cloacal musculature and their relationship to the phallus, plica lymphatica and corpus paracloacalis vascularis. The arterial, venous, lymphatic and nervous systems were mentioned but not described in detail.

The present work was undertaken to complete the anatomy of the structures involved in the erection-dilution mechanism in the domestic chicken and deals primarily with the distribution of the arterial, venous, lymphatic and nervous elements to the phallus, plica lymphatica and corpus paracloacalis vascularis.

In addition to the anatomical considerations two supplemental experiments were undertaken to support the hypothesis that the diluting fluid is produced in the corpus paracloacalis vascularis and that whole blood is not a normal constituent of the diluting fluid.

REVIEW OF LITERATURE

I. Major Arteries

The first description of the arterial supply to the corpus paracloacalis vascularis was by Barkow (1829). Included in his work was a description of the arterial supply to the cloaca in the chicken (Gallus gallus) and duck (Anser boschas).

In his work, Barkow (1829) referred to the aorta caudal to the aa. ischiadicae as the a. sacra media. The a. sacra media gave rise to the a. coccygeus communis and the paired aa. hypogastricae (Table I). The a. hypogastrica sinistra and dextra continued caudally as the a. pudenda interna and entered into the "corpora cavernosa" (Table III).

In its course the a. pudenda interna gave rise to a branch which coursed beside the ureter to supply the skin of the dorsal wall of the coprodeum. Barkow (1829) did not name this vessel. After giving off this branch, the a. pudenda interna coursed ventrally and caudally to the side of the cloaca where it divided into two branches. These branches, located closely beside one another, anastomosed at the caudal end of the cloaca with the branches of the opposite side. He considered this to be an indication of the "corpora cavernosa."

Barkow (1829) described a branch arising from the a. pudenda interna which supplied the cloacal bursa but did not name it.

Lereboullet (1851) described in the chicken an artery which arose from the aorta and accompanied the ductus deferens to supply the

TABLE I

ARTERIES

Barkow, 1829	1. a. sacra media a. a. coccygeus communis b. aa. hypogastricae 1. a. pudenda interna
Lereboullet, 1851	No terms
Eckhard, 1876	No terms
Gadow and Selenka, 1891	1. Aorta a. a. coccygea media b. a. pudenda communis 1. a. haemorrhoidalis infirma 2. a. pudenda externa 3. a. profunda penis
Müller, 1908	1. a. sacramedia a. a. coccygeus media b. a. pudenda communis 1. a. pudenda externa 2. a. pudenda interna
du Toit, 1913	1. a. sacralis media a. a. coccygea media b. a. pudenda communis 1. a. pudenda externa 2. a. pudenda interna

TABLE I (cont'd.)

Sapy, 1941	1. Aorta a. None b. a. pudenda interna 1. parietal ramus 2. visceral ramus
Nishiyama, 1955	Terminology followed Liebe, 1914
Bhaduri, Bievas and Das, 1957	Caudal Artery to Cloaca
Lake, 1957a; 1957b	Terminology followed Nishiyama, 1955
Westpahl, 1961	1. Aorta a. a. pudenda interna 1. ramus muscularis 2. ramus intestinalis
Nishida, 1964	1. a. sacralis media a. a. coccygea media b. a. pudenda communis 1. a. pudenda externa 2. a. pudenda interna 1. a. ureto-deferentiales posterior
Knight, 1967	1. a. sacralis media a. a. coccygeus media b. a. pudenda communis 1. a. hemorrhoidales 2. a. pudenda externa 3. a. pudenda interna

TABLE I (cont'd.)

Knight, 1970 (recommended)	1. a. sacralis media
	a. a. coccygeus media
	b. a. pudenda communis
	1. a. hemorrhoidales
	2. a. pudenda externa
	a. ramus uretodeferentiales posterior
	3. a. pudenda interna
	a. a. uretodeferentiales posterior
	b. a. coprodealis
	c. a. proctodealis
	d. a. uroproctodealis
	e. a. phalli
	f. a. pudenda terminalis

cloacal wall and "corps spongieux de l'urethre" (Table III). Lereboullet (1851) did not discuss the course of the vessel up to the spongy body although he did have an excellent illustration of the major vessels in this area of the chicken.

Eckhard (1876), a physiologist, dealt with the physiology of the corpus paracloacalis vascularis but did not discuss the arterial supply to the structure. He mentioned that strong rami emerged from the body which in turn had smaller branches.

In their classical anatomical work on birds Gadow and Selenka (1891) described the aorta as giving rise to the a. pudenda communis. They did not mention the a. sacra media in their description. They found that the right or left a. pudenda communis gave rise to the a. mesenterica inferior and further caudally the a. pudenda communis gave rise to the a. haemorrhoidales infirma which supplied the cloacal bursa, and the end of the cloaca.

According to Gadow and Selenka (1891) the a. pudenda communis divided in the duck into two branches, the a. pudenda externa, which supplied the m. ischiococcygeus and anus and the a. profunda penis, which ran close to the ductus deferens and ureter to enter the cloaca, phallus and their muscles. The a. pudenda externa corresponds to the a. pudenda externa described by Müller (1908) and the a. profunda penis corresponds to the a. pudenda interna. The illustration that Gadow and Selenka (1891) presented of the vascular supply to the caudal area did not include the course of these vessels.

Müller (1908) referred to the continuation of the aorta caudal to the large aa. ischiadicae as the a. sacromedia. The terms he employed for the three branches of the a. sacramedia were the a. pudenda

communis dextra, a. pudenda communis sinistra, and a. coccygea media (Table I).

Müller (1908) reported that the a. pudenda communis ran caudally and divided into the a. pudenda externa and a. pudenda interna. The a. pudenda externa supplied the m. ischiococcygeus and m. pubococcygeus. The a. pudenda interna passed medial to the ureter and lateral to the ductus deferens and reached the hollow body of the "corpus cavernosa."[1] The vessel continued into the protruding part of the phallus to provide it with blood.

Du Toit (1913) described the arterial supply to the caudal musculature in the chicken. He reported that the a. pudenda communis arose from the a. sacralis media at the level of the fifth sacrocaudal vertebra. He stated also that the a. pudenda interna and externa arose from the a. pudenda communis. He mentioned briefly the a. pudenda interna and reported that it coursed to the cloaca. The distribution of the a. pudenda externa to the caudal musculature was described in detail.

Liebe (1914) reported that in the duck the a. pudenda interna, after originating from the a. pudenda communis, coursed with the ureter. In its course it gave off numerous nutrient rami to the ductus deferens and ureter. He observed, as did Barkow (1844), a thickening of the a. pudenda interna about 1.5 cm in length just before the development of the "rete."

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[1]Müller (1908) included in this term both the hollow chamber and "Tannenberg'schen Körper" whereas Barkow (1829) included in the term "corpus cavernosa" only "Tannenberg'schen Körper."

Liebe (1914) observed that the a. pudenda interna pierced the "lymphbildungsraum" to the left and right on the side facing the cloaca. Here it formed an "arterial rete" with many fine branches connecting with one another.

He reported that the a. pudenda interna emerged from the "lymphbildungsraum" and proceeded to the distal part of the phallus. The branch, passing to the sides of the groove of the phallus, gave off numerous rami. These rami passed through the main part of the phallus to terminate in its walls.

Mauger (1941) reported that the blood supply to the cloaca in the chicken was mainly from the internal iliac arteries, but did not discuss the vascular supply further. In his entire paper he listed an abstract as his only reference.

Sapy (1941), in his study of the vascular system of the domestic chicken, mentioned the a. pudenda interna stating that it was paired and arose from the aorta. Sapy (1941) did not refer to the aorta caudal to the a. ischiadica as the a. sacra mediana. The a. pudenda interna corresponded to the a. pudenda communis described by Müller (1908), du Toit (1913) and Liebe (1914). The visceral and parietal branches which arose from the a. pudenda interna corresponded to the a. pudenda interna and a. pudenda externa as described by du Toit (1913) and pointed out by Knight (1967).

Sapy (1941) stated that the visceral branch supplied the cloacal bursa (Bursa of Fabricius), cloaca and the papilla, or phallus of swimming birds. The parietal branch supplied the tail musculature. Sapy (1941) did not refer to the corpus paracloacalis vascularis.

Nishiyama (1955) did not discuss the arterial supply in any depth and mentioned only that the a. pudenda interna was present and supplied the "vascular body" (Table III).

Bhaduri, Bievas and Das (1957) mentioned a caudal artery to the cloaca in the pigeon but did not elaborate on its distribution.

Lake (1957a; 1957b) referred only to the a. pudenda interna and did not elaborate on the vascular supply to the area.

Westpahl (1961) described the circulation in the pelvic area. He reported that in the cock the ramus intestinalis followed close to the ureter and spermatic duct and the ramus muscularis supplied the pelvic musculature (Table I).

Nishida (1964) discussed the blood vascular system of the male reproductive organs. He presented the most detailed and accurate illustrations of the major vessels supplying these structures. He reported that the cloacal region was supplied by branches of the a. pudenda interna, particularly the "vascular body." Nishida (1964) felt that this supported Nishiyama's theory on the production of lymph. (Nishiyama's theory will be discussed later.) He did not present observations on the structure of the "vascular body." In a table he compared the terms related to the vascular system employed by Neugebauer (1876), du Toit (1914) and Kaupp (1918).

Knight (1967) used the terminology of du Toit (1913) which corresponded to that used by Müller (1908), Liebe (1914), Nishiyama (1955) and Nishida (1964). Knight (1967) reported that the a. pudenda interna arose from the a. pudenda communis and proceeded caudally adjacent to the ureter, ductus deferens, n. pudenda interna and v. pudenda interna.

Anterior to the "vascular body" (Table III), two branches originated which supplied the rectum and coprodeum. The a. pudenda interna branched on the medial surface of the "vascular body." The dorsal branch continued on to supply the phallus and other reproductive structures of the proctodeum; the ventral branch crossed the vascular body and continued on to supply the area ventral to the cloaca.

II. Major Veins

The classical study of Neugebauer (1845) is the most extensive published on the venous system of birds and is the standard on which most researchers base their work on the venous system (Table II). For example, Gadow and Selenka (1891) followed Neugebauer (1845) and reproduced some of his illustrations of the avian venous system.

Neugebauer's (1845) description of the venous system of the cloacal area was not extensive. He described the drainage of the phallus and the "corpus cavernosum" (Table III) by the v. pudenda. In the duck, both sides of the groove of the phallus were provided with a small venous branch which followed the spiral twisting of the organ. The vessels entered the "hollow chamber" containing the "corpus cavernosum." It was joined here by an unnamed branch which drained the posterior, superior part of the "hollow chamber." The v. pudenda extended into the pelvic cavity from the "corpus cavernosum." It followed the ureter and accompanying artery and joined the common trunk of the v. cutanea caudae inferior and v. cutanea pubica. This trunk, along with the v. muscularis caudae inferior, formed the v. hypogastrica.

TABLE II

VEINS

Neugebauer 1845

I. *Arcus hypogastricus*

A. *v. hypogastrica* (s. *v. iliaca interna pars caudalis*)

1. *v. coccygeus*

2. *v. pudenda*

a. *v. penis*

b. *ramus e parte posteriore cavi cavernosi*

3. common trunk of

a. *v. cutanea caudae inferiori*

b. *v. cutanea pubica*

4. *v. muscularis caudae inferior*

Gadow and Selenka 1891

Same as Neugebauer (1845)

Müller 1908

Same as Neugebauer (1845)

du Toit 1913

I. *Arcus hypogastricus*

A. *v. coccygeus*

1. *v. pudenda communis*

a. *v. pudenda interna*

b. *v. pudenda externa*

1. *v. cutanea caudae*

2. *v. muscularis caudae*

Liebe 1914

Same as Neugebauer (1845)

Kaupp 1918

Same as Neugebauer (1845)

TABLE II (cont'd.)

Nishida 1964	I. *Arcus hypogastricus* A. *v. hypogastricus* 1. *v. coccygeus* 2. *v. pudenda communis* a. *v. pudenda interna* b. *v. pudenda externa*
Knight 1967	Same as du Toit (1913)
Knight 1970 (recommended)	I. *Arcus hypogastricus* A. *v. pudenda communis* 1. *v. coccygeus* 2. *v. pudenda interna* a. *v. phalli* b. *v. pudenda terminalis* c. *v. coprodealis* d. *v. proctodealis* e. *v. uroproctodealis* 3. *v. pudenda externa* a. *v. cutanea caudae* b. *v. muscularis caudae*

In his illustration of the chicken Neugebauer (1845) did not show the origin of the v. hypogastrica. He did show that within the pelvic cavity, the v. hypogastrica was different in the chicken than in the drake. In the chicken the v. coccygeus communis emptied into the v. hypogastrica whereas in the drake the corresponding vessel emptied into the arcus hypogastricus.

Eckhard (1876) did not discuss the venous drainage of "Tannenberg'schen Körper" (Table III).

Gadow and Selenka's (1891) description of the veins was similar to that of Neugebauer (1845). Müller (1908) based his description of veins on the work of Neugebauer (1845). He described the v. hypogastrica pars posterior in the drake as arising out of the same four veins as did Neugebauer (1845). Of these veins he discussed only the v. pudenda.

The v. pudenda, Müller (1908) reported, originated from the medial side wall of the cloaca and ran parallel to the ureter. The vein joined the v. caudalis inferior and v. cutanea pubica to form the v. hypogastrica. The "corpus cavernosum" (Table III) and phallus were drained by the v. pudenda.

Du Toit (1913) discussed the veins related to the musculature of the caudal region. He employed several new terms using the rationale that the same names should be used for artery, vein and nerve if they parallel each other and have the same distribution. Thus, he employed the terms v. pudenda communis, v. pudenda interna and v. pudenda externa to refer to those vessels accompanying the arteries having the corresponding names.

Du Toit (1913) reported that the v. pudenda externa accompanied the a. pudenda externa and returned blood from the skin, muscles, and

part of the cloaca. The v. pudenda interna joined the v. pudenda externa and formed the v. pudenda communis. The v. pudenda communis coursed cranially and joined, on the ventral side of the last synsacrocaudal vertebra, the v. coccygea. The v. coccygea continued cranially to end in the arcus hypogastricus. In their course they anastomosed with one another. Du Toit (1913) traced the circulation to the musculature of the caudal area and did not go into the terminal distribution of the v. pudenda interna. Neugebauer (1845) included in the term v. hypogastrica, the v. pudenda communis (du Toit, 1913) and that portion of the v. coccygeus cranial to the union of the v. pudenda communis with the v. coccygeus. The term v. pudenda (Neugebauer, 1845) corresponded to the term v. pudenda interna (du Toit, 1913). The term v. pudenda externa (du Toit, 1913) included the common trunk of v. caudalis inferior and v. cutanea caudalis inferior (Neugebauer, 1845) and the caudal continuation of the v. cutanea pubica. The terms v. cutanea caudalis inferior and v. muscularis caudae were employed by both Neugebauer (1845) and du Toit (1913).

Liebe (1914) summarized the venous system in the duck stating that the v. pudenda originated in the phallus on both sides of the sulcus and passed through the "Der lymphbildungsraum" (center of lymph formation) beside the a. pudenda interna. It is surprising that he did not give the corresponding name to the vein as well as the artery. Liebe (1914) reported that the v. pudenda followed the course of the ureter forward. The v. muscularis caudae inferior drained the ventral caudal muscles and emptied into the v. pudenda. The v. pudenda followed the ureter and finally merged into the arcus hypogastrica. the vv. coccygeae also discharged into the arcus hypogastricus. The v. coccygea

were well developed in the duck; according to Liebe (1914) these veins were related to the dorsal lymph heart which provided a second route by which lymph flowed away from the "gefässreiche Körper" (Table III). Kaupp's (1918) description followed the work of Gadow and Selenka (1891).

Nishiyama (1955) did not discuss the venous drainage in detail. He did mention that the "vascular body" (Table III) was drained by the v. pudenda. He based his anatomical description on the work of Liebe (1914). Lake (1957a; 1957b) did not discuss the veins.

Nishida (1964) presented a detailed illustration of the venous return from the cloaca. The v. pudenda communis drained into the v. hypogastrica. The v. hypogastrica was formed by the v. pudenda externa and v. pudenda interna. The v. uretodeferentiales posterior emptied into the v. pudenda interna. Nishida (1964) did not include in his description of the venous system cranial to the v. pudenda communis the formation of the v. hypogastrica. His labels, however, indicate that he considered the vessel between the arcus hypogastricus and the junction of the v. pudenda communis and the v. coccygea as the v. hypogastrica. This contrasted with both Neugebauer (1845) and du Toit (1913). As pointed out, Neugebauer (1845) in his term v. hypogastrica included a portion of the v. pudenda communis. Du Toit (1913) did not employ the term v. hypogastrica caudal to the arcus hypogastrica.

III. Corpus Paracloacalis Vascularis

Barkow (1829) described the "corpora cavernosa" (Table III) in the male chicken. He reported that the "corpora cavernosa" was found lateral to the middle division (urodeum) of the cloaca above the ductus

TABLE III

Corpus paracloacalis vascularis

1.	Barkow 1829	corpora cavernosa
2.	Neugebauer 1845	corpus cavernosum
3.	Lereboullet 1851	corps spongieux de l'urethre (spongy body of the urethra)
4.	Eckhard 1876	Tannenberg'schen Körper (Tannenberg's body)
5.	Gadow and Selenka 1891	none
6.	Müller 1908	Tannenberg'schen Körper (Tannenberg's body)
7.	Liebe 1914	"gefässreiche Körper" (vessel rich body)
8.	Nishiyama 1955	vascular body
9.	Nishida 1964	vascular body
10.	Lake and El Jack 1966	vascular body
11.	Lucas and Stettenheim 1965	corpus paracloacalis
12.	Knight 1967	vascular body
13.	Knight 1970 (recommended)	corpus paracloacalis vascularis

deferens and its papilla. The "corpora cavernosa" (Table III) as stated by Barkow (1829) consisted of fine arterial branches which originated from the a. pudenda interna. Barkow (1829) found the "corpora cavernosa" to be poorly developed in the capon.

Lereboullet (1851) described the "corps spongieux de l'urethre" (Table III) as a lentiform, rounded structure, 7 mm in length and 3 or 4 mm in width lying between the wall of the cloaca and the constrictor muscle of the vestibule at the level of the ejaculatory papilla.

Lereboullet (1851) stated the "corps spongieux de l'urethre" was composed of numerous, tightly intertwined blood vessels which arose from the artery accompanying the ductus deferens. The author was describing the same vessel as reported by Barkow (1829), namely the a. pudenda interna. Lereboullet (1851) found that these intertwining vessels were encased in a connective tissue capsule.

Lereboullet (1851) indicated that he disagreed with Barkow (1844) regarding the course of the vessels within the "corps spongieux de l'urethre." Barkow (1844) illustrated the body in the cock as being filled with parallel wavy vessels. Lereboullet (1851) instead found that the vessels were interlacing.

In Lereboullet's (1851) illustration of the circulatory system of the male genitalia of the chicken, there was included the "corps spongieux de l'urethre." The "corps spongieux de l'urethre" was shown as an encapsulated structure having a cavity packed with blood. The interlacing vessels were found coursing within the chamber. From the comparison he made with the mammalian corpus spongiosum and his illustration which shows the organ filled with blood, it appears that

he considered the organ to function similar to the erectile tissue found in mammals.

In his study of erectile tissue, Legros (1868) briefly referred to the "eminence" as containing dilated capillaries arranged in a net. It appears from his description that he was rather surprised to find that the communicating branches connecting the dilations in the net were narrower than the dilations themselves. He found this condition to exist not only in the chicken but in birds having a larger, more well-developed phallus such as the duck. Perhaps he expected some type of tissue similar to that found in the comb of the chicken, snood of the turkey or penis of the mammal where there is some enlargement of the small vessels into an "erectile tissue" which can become engorged with blood. Since he did not see any "erectile" tissue in the "eminence," this may have lead him to conclude that these "rudiments of the penis" (phallus) did not play an important role in copulation, at least not more than the clitoris in female mammals.

Eckhard (1876) referred to the vessels composing "Tannenberg'schen Körper" (Table III) as "vessel conglomerates." He did not elaborate further on the arterial structure within this body.

Müller (1908) described in detail the anatomy of the "kavernösen Körper" of the duck, (Table III). The "kavernösen Körper" was half-moon shaped and was located adjacent to the cloaca opposite the level of the "Genitalpapillen" (genital papillae). A synonym for the term genital papillae would be ejaculatory papillae. Genital papillae as used by Müller (1908) did not refer to the phallus.

Müller (1908) found that the cloacal sphincter covered the "kavernösen Körper." A fine connective tissue layer covering the

"cavernous body" was continuous with the perimysium of the cloacal sphincter. "Tannenberg'schen Körper" (Table III) did not have a covering of connective tissue but instead was attached at its cranial end to the inner cranial wall of the "kavernösen Körper" surrounded by the lymph within the "kavernösen Körper." Müller (1908) reported also that "Tannenberg'schen Körper" (Table III) consisted of vessels which had a ball-shaped arrangement; this had the appearance of a rete. These vessels arose from branches of the arteria pudenda interna. He recognized that the arterial system was the major component of the "Tannenberg'schen Körper," the veins were few in comparison. He did not observe any erectile tissue within the body.

Müller employed the term "Tannenberg'schen Körper" when referring to the structure which Tannenberg (1789, after Müller, 1908) and Barkow (1829) called "corpora cavernosa." He refuted the use of the latter term because he did not find cavernous structures similar to those found in the mammalian penis. He used the term "kavernösen Körper" to include both "Tannenberg'schen Körper" and the surrounding lymph chamber.

The nerve fibers in Tannenberg's body were found by Müller (1908) to be nonmyelinated and associated with arteries within the body. These nerve fibers continued to the terminal vessels which are devoid of muscles. Müller (1908) stated that no ganglia were present within Tannenberg's body.

Liebe (1914) described the "gefässreiche Körper" (Table III) of the duck as a reddish brown structure located inside the "Lymph-bildungsraum," along the outer wall adjacent to the cloaca. It occupied about one-third of the space within the chamber. The "gefässreiche

Körper" consisted of a fine arterial plexus derived from the a. pudenda interna after it had entered the "lymphbildungsraum." He observed in the "gefässreiche Körper" numerous transverse branches which arose from the a. pudenda interna and entered the body where they ramified. Liebe (1914) reported that the transition of arteries into veins occurs through simple capillaries. Here he was attempting to indicate the absence of "erectile" tissue.

Liebe (1914) observed that the a. pudenda interna passed along the side of the "gefässreiche Körper" facing the urodeum and was reduced considerably after supplying branches to the "gefässreiche Körper."

Liebe (1914) did not discuss the histology of the "gefässreiche Körper" in detail but relied on the work of Müller (1908).

Nishiyama (1955) identified the a. pudendalis interna (s. a. pudenda interna) as the vessel that vascularized the "vascular body" (Table III). The "vascular body" contained lymph producing tissue and numerous capillaries. He observed large blood vessels within the trabeculae. He found lymph channels within the "vascular body"; these had both peripheral and central distribution. The peripheral lymph channels, according to Nishiyama (1955) corresponded to the "lymph-bildungsraum" described by Liebe (1914).

According to Nishiyama (1955), the blood and lymph vessels continued to the base of the lymphfold (s. plica lymphatica) and phallus. The lymph channels passed into the phallus and right and left lymph folds (s. plicae lymphaticae) whereas the blood vessels involved in the production of lymph did not.

Nishiyama and Ogawa (1961) in their review of the publications of Lake (1956; 1957a; and 1957b) pointed out that Lake, in attempting

to describe the "vascular body," had described the fold between urodeum and proctodeum (uroproctodeal fold) as identical with the "vascular body." Nishiyama (1955) and previous authors clearly identified the "vascular body" as external to the cloaca. Lake (1966) modified his first concept of the location of the "vascular body" to agree with that presented by Nishiyama (1955).

Lake (1957a) discussed possible structural similarities between the plica uroproctodealis and the bulbourethral glands of man.

Knight (1967) reported that the "vascular body" (Table III) consisted of a bundle of capillaries that received their blood supply from branches of the a. pudenda interna; these capillaries were drained by branches of the v. pudenda interna. The capillaries had a tortuous course. Knight (1967) also reported that lymph channels were in close proximity to the blood capillaries. These lymph channels connected larger collecting lymph channels which in turn lead to the phallus and lymph fold.

IV. Nerves

Eckhard (1876) first demonstrated that nerves were involved in the control of erection of the phallus in the duck and the goose (Table IV). The phallus became erect when he electrically stimulated nerves lying in the mesorectum, adjacent to the rectum. Eckhard did not describe the origin of the nerves he stimulated.

Marage (1889) described the sympathetic nerves of the chicken but did not include a description of their relationship to the corpus paracloacalis vascularis (Table III) or to the cloaca. Gadow and Selenka (1891) discussed briefly the plexus pudendus and the

TABLE IV

NERVES

Eckhard 1876	nn. errigentes
Müller 1908	A. Plexus ischiadicus B. Lumbar Plexus 1. Nervus pudendus externa
du Toit 1913	A. Plexus ischiadicus B. Plexus pudendus 1. n. pudenda externa a. n. pudenda interna
Liebe 1914	A. Plexus cruralis (syn. lumbalis) B. Plexus ischiadicus C. Plexus pudendus 1. nn. errigentes
Hsieh 1957	A. Aortic plexus B. Anterior renal plexus C. Hypogastric plexus D. Plexus pudendus E. Pelvic plexus F. Cloacal plexus a. pudendal nerve b. pelvic splanchnic nerve G. Intestinal nerve of Remak
Knight 1970 (recommended)	A. Plexus ischiadicus B. Plexus pudendus a. n. pudenda externa b. n. pudenda interna 1. n. phalli 2. n. pudenda terminalis a. ganglion paracloacalis

distribution of its branches to the musculature of the tail, cloaca and to the skin surrounding the vent.

Müller (1908) described primarily the nerves to the musculature of the pelvic region and tail. He reported that the "n. spermaticus internus" coursed with the "funiculus spermaticus" but he did not describe the origin or termination of this nerve.

Müller (1908) stated that vasomotor and lymph secretion fibers from the sympathetic nerves regulated "Tannenberg's body."

Du Toit (1913) described the origin of the spinal nerves of the plexus pudendus. He found that the plexus pudendus was formed by sacral nerves 31-35 and in some instances a ramus from spinal nerve 30.

Du Toit (1913) reported that the n. pudendus externus was formed by spinal nerves 31 and 32. In some specimens he observed a small branch from the ventral root of the 30th spinal nerve. The n. pudenda interna originated from the middle of the n. pudenda externa and innervated the cloaca and the sexual organs. Du Toit (1913) did not discuss further the distribution of the n. pudenda interna.

Liebe (1914) reported that a plexus cruralis (s. lumbalis), plexus ischiadicus and plexus pudendus were present in the pelvic cavity. He stated that the plexus cruralis (s. lumbalis) did not supply the cloaca; the plexus ischiadicus gave rise to a small nerve which supplied the m. sphincter cloacae; and the plexus pudendus innervated the muscles of the tail, the cloaca, and the skin surrounding the vent. Liebe (1914) did not discuss these plexuses further, referring the reader to the work of Müller (1908).

Liebe (1914) described the sympathetic nerves of the duck in more detail than did Müller (1908). He observed that the sympathetic

trunk ramified at the origin of the a. pudendus communis and formed a dense network around the a. pudenda, ductus deferens and ureter. He reported that in the lower third of the sympathetic trunk 3 or 4 nerves formed a sympathetic nerve plexus. The n. errigentes originated from this plexus and passed caudally below the a. mesenterica posterior to innervate the "gefässreiche Körper" and the phallus. He found the nerve fibers in the phallus difficult to observe because they were small and blended readily with the small connective tissue fibers. The drawing Liebe (1914) presented to illustrate the nerve supply was inadequate to explain the distribution of the nerves he had described in the text.

Kaupp (1918) reported that the plexus pudendus was formed from the spinal nerves of the plexus ischiadicus. These spinal nerves were deeply imbedded in the kidney. His description of the distribution of the branches from the plexus pudendus was the same as that reported by Liebe (1914) and Gadow and Selenka (1891).

Mauger (1941) stated that the nerve supply to the cloaca originated from the "pelvic plexus" and the sacral and coccygeal nerves, but did not elaborate further on the formation of the "pelvic plexus" or the distribution of these nerves.

Hsieh (1951) also discussed the autonomic nerves of the pelvic region and their branches. This included the following plexuses and associated nerves: pudendal plexus, pudendal nerve, pelvic splanchnic nerve, a plexus in the area of the deferent duct, hypogastric plexus, a posterior mesenteric plexus, pelvic plexus, cloacal plexus and the intestinal nerve of Remak.

Hsieh found 13 sympathetic ganglia and 14 lumbosacral nerves in the lumbosacral region. The 7th and 8th ganglia were fused and accounted for the discrepancy between the number of ganglia and the number of spinal nerves. The ganglia were linked by interganglionic cords. These cords were single except for those between the last two ganglia. He found the sacral artery to pass between this double cord. He reported that the lumbosacral automonic nerves arising from the ganglia were particularly small.

The ventral rami of the 9th, 10th, 11th, 12th, and 13th lumbosacral nerves and a branch from ventral ramus of the 8th formed the lumbosacral plexus (Hsieh, 1951). These rami correspond with spinal nerves 31-35 as reported by du Toit (1913). The "pelvic splanchnic nerve" and the "pudendal nerve" originated from the plexus pudendus Hsieh stated that the "pudendal nerve" arose from the 8th, 9th, and 10th lumbosacral spinal nerves and passed backward on the dorsal wall of the pelvic cavity to supply the m. coccygeus, m. dilator ani, m. sphincter ani externus, m. levator ani and the skin around the cloaca. According to Hsieh (1951), the pudendal nerve distributed only somatic nerve fibers and his description of the "pudendal nerve" corresponded with du Toit's (1913) description of the n. pudenda externa.

Hsieh (1951) reported that the "pelvic splanchnic nerve" was formed by parasympathetic fibers from the 8th, 9th, 10th, 11th, and 12th lumbosacral nerves. The nerve followed the hypogastric artery (s. a. pudenda communis, Knight, 1967) and then the "middle haemorrhoidal artery" to the cloaca. The "pelvic splanchnic" nerve gave off collateral branches to the "plexus in the ligament of the deferent duct" and to the "cloacal plexus" in the wall of the cloaca. The "pelvic

splanchnic nerve" continued as a slender terminal branch around the cloacal opening. He considered this nerve to be homologous to the dorsal nerve of the penis in mammals, and his description of the "pelvic splanchnic" nerve corresponded to du Toit's description of the n. pudenda interna.

Hsieh (1951) further described the "plexus in the area of the deferent duct" as extending from the "testicular nerve plexus" cranially, to the "pelvic nerve plexus" and "cloacal nerve plexuses" caudally. The "plexus in the area of the deferent duct" was formed by sympathetic fibers from the "hypogastric plexus" and parasympathetic nerve fibers from the "pelvic splanchnic nerve."

The "hypogastric plexus" was shown to lie between the 9th-13th lumbosacral vertebrae, lateral to the aorta (Hsieh, 1951). He stated that the "hypogastric plexus" extended along both right and left "hypogastric arteries" (s. a. pudenda communis -- Knight, 1967) on the dorsal wall of the pelvic cavity. The "hypogastric plexus" was formed from sympathetic nerves arising from the 6th-12th or the fused 7th and 8th-12th lumbosacral ganglia of both right and left sympathetic trunks.

Hsieh (1951) reported that the nerves, which originated from the "hypogastric plexus" lying along the aorta lead to the "posterior mesenteric plexus" while those arising along the "hypogastric artery" (s. a. pudenda communis) lead to the "pelvic plexus."

Hsieh (1951) reported that the "posterior mesenteric plexus" was a caudal continuation of the "hypogastric" and "pelvic plexuses." In the upper part of the mesorectum the "posterior mesenteric plexus" followed the "posterior mesenteric artery" (s. a. mesenterica caudalis)

cranially. In the portion of the mesorectum the nerves passed to the "intestinal nerve of Remak."

Hsieh (1951) pointed out that the "hypogastric" and "posterior mesenteric plexuses" were situated between the "aortic plexus" cranially and the "pelvic plexus" caudally.

The "pelvic plexus" as described by Hsieh (1951) is composed of the rectal part of the "intestinal nerve of Remak" which receives branches from the "posterior mesenteric plexus," the "hypogastric plexus" and the "pelvic splanchnic nerve." He reported that "pelvic plexuses" were paired, located side by side on the dorsal aspect of the rectum between the two layers of the mesorectum. They were separated from the "cloacal plexuses" by the left and right suspensory muscles of the rectum.

Hsieh (1951) also reported that the "cloacal plexus" on each side of the cloaca had several ganglia. The cell bodies were located in the retroperitoneal region around the anus (vent). The "cloacal plexus" was formed mainly by the "pelvic splanchnic" nerve. Fibers arising from the "cloacal plexus" supplied the distal part of the ureter and deferent ducts, the cloacal bursa and sphincter muscle of the cloaca. The "cloacal plexus" was connected with the "pelvic plexuses" by communicating branches which pierced through or ran behind the suspensor muscle of the rectum. The anastomoses were so few that he questioned whether sympathetic fibers from the "pelvic plexus" were active in the "cloacal plexus" and the structures it supplied.

Hsieh (1951) found the "intestinal nerve of Remak" to be a ganglionated trunk which arose as a slender trunk" from the anterior mesenteric, aortic, posterior mesenteric and hypogastric plexuses" and

gave off branches to the jejunum, ilium and large intestine. It appears that the "intestinal nerve of Remak" described by Hsieh corresponds to the nn. errigentes which Liebe (1914) illustrated in his drawing of the phallus of the duck.

Hsieh (1951) pointed out that almost all nerves arising from the previously named plexuses that were destined to supply the intestine passed through the "intestinal nerve of Remak." Hsieh's work was the most complete work on anatomy of the nervous system related to the cloacal area. In place of "intestinal nerve of Remak," Hammond and Yntema (1947) used the term "Remak's ganglion"; Yntema and Hammond (1954) used the term "nerve of Remak" or "enteric ganglion."

Biswal (1954) found parasympathetic ganglion cells in the vagina of the female White Plymouth Rock. They were single or in groups of 2 or 3, on the peritoneal side of the spirally arranged longitudinal and circular muscular layers. He did not discuss the nerves in the male.

Yasuda (1961) described the nerves of the lumbar region. In his illustration he pictured the spinal nerves forming the pudendal plexus but did not discuss its formation or the distribution of its branches.

Neither Nishiyama (1955) nor Lake (1957a; 1957b; and 1966) described the nerve supply to the corpus paracloacalis vascularis.

Portman and Stingelin (1961) reported that the sympathetic system formed two chains which joined in a terminal unpaired ganglion in the cloacal region. Their review was extremely brief. Portman and Stingelin (1961) used Imhof's (1905) illustration to show the plexuses of the lumbosacral part of the spinal cord. This illustration revealed the location of the plexus cruralis, plexus ischiadicus and the plexus pudendus.

Knight (1967) reviewed briefly the articles by Liebe (1914), du Toit (1913), and Hsieh (1951), but did not discuss the anatomy of the nervous system of the reproductive mechanism.

Lucas and Stettenheim (in press) depicted the pudendal nerve in the Single Comb White Leghorn chicken as reviewing branches from spinal nerves 31 through 35 -- a total of five nerves. In their review of literature they reported that Buckholz (1960) observed three spinal nerves contributing to the pudendal nerve and that Yasuda (1961) observed four spinal nerves.

V. Lymphatics

The lymphatic system of the domestic chicken was not considered in detail by early anatomists. Dransfield (1944) felt the major reason for the scarcity of work was due to the small size of the vessels which could be used for injection and the absence of lymphatic glands.

Eckhard (1876) was the first investigator to relate the lymphatic system to the erection of the phallus. He reported that lymph flowed from "Tannenberg'schen Körper" to the phallus of the duck during sexual stimulation. After stimulation the lymph drained from "Tannenberg'schen Körper" in the lymph vessels leading away from the cloaca.

Müller (1908) discussed the lymphatic system of the duck in considerable detail. However, his description was primarily concerned with lymphatic vessels lying cranial to "Tannenberg'schen Körper" rather than the lymphatic vessels within the body (Table V).

Müller (1908) reported that lymph drained from "Tannenberg'schen Körper" of the duck back into the venous system by two routes. The

TABLE V

LYMPHATICS

Müller 1908	1. Plexus cruciatus (s. ductus thoracici lumbales and their cross and oblique connections -- Baum, 1830).
Liebe 1914	1. Ductus thoracicus dextra 2. Plexus cruciatus
Baum 1930	1. Ductus thoracicus thoracicalis 2. Ductus thoracicus lumbalis (s. cisterna chyli of mammals) a. vasa lymphacea lumbalia
Dransfield 1944	1. thoracic ducts 2. aortic lymph vessels a. common pudendal lymph vessel b. middle sacral lymph vessel
Knight 1970 (recommended)	1. Ductus lymphaticus thoracicalis 2. Ductus lymphaticus lumbalis a. vas lymphaticus pudendus communis 1. vas lymphaticus pudendus internus 2. vas lymphaticus pudendus externus

first route was through small lymph vessels to the "plexus cruciatus,"[1] which in turn drained to the "ductus thoracicus." The other route was through vessels leading to a "dorsalen Lymphsäcken" which emptied directly into the v. coccygea superior. Müller (1908) reported the presence of valves in this lymph sac which prevented retrograde flow of lymph back into the large collecting lymph vessels. Müller (1908) stated that these two routes allowed for the rapid drainage of the phallus and "Tannenberg'schen Körper" after erection.

Baum (1930) presented the first major work related specifically to the lymphatic system of the domestic fowl. He described two ductus thoracici in the fowl but found so many variations in their structure that he was unable to establish a set pattern of their distribution. He subdivided each "ductus thoracici" into two parts, a "pars thoracicalis" and a "pars lumbalis." The "pars thoracicalis" was limited to that portion of the paired ducts which laid in the thorax. The ducts coursed on each side of the "aortica thoracica" and emptied into their respective v. cava cranialis. He limited the "pars lumbalis," which he correlated with the cisterna chyli in mammals, to that portion of the duct from the cranial end of the kidney or adrenals to the level of the aa. ischiadicae.

Baum (1930) reported that the "ductus thoracicus lumbalis" were formed by the union of the "vasa lymphacea lumbalia" with the lymphatic vessels accompanying the aa. ischiadicae. He described numerous

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[1] Panizza (1830) according to Baum (1930) employed this term to refer to cross and oblique communicating vessels between the two "ductus thoracici pars lumbalis." Baum (1930) stated that these connections were numerous and very thin and formed a course network but they did not constitute a plexus.

anastomoses between the paired "ductus thoracicus lumbalis." At the cranial end of the kidney the "ductus thoracicus lumbalis" continued as the "ductus thoracicus thoracicalis."

The "vasa lymphacea lumbalia" were formed by the union of the lymphatic vessels draining the cloaca with the lymphatic vessels draining the pelvic region. The "vasa lymphacea lumbalia" coursed on the ventral side of the os lumbosacrale and emptied into the cisterna chyli (s. pars lumbalis).

The most substantial contribution to the study of the lymphatic system of the domestic fowl was presented by Dransfield (1944). Included in his work was an excellent review of the older literature on the lymphatic system. According to Dransfield (1944) most of the work on birds, prior to the work of Baum (1930), was done by Owen (1846, 1866) and Chauveau (1873).

Dransfield (1944) divided his review of the literature of the lymphatic system into three sections: 1) lymph hearts; 2) lymph glands; and 3) lymphatic vessels.

1) Lymph hearts: The lymph hearts were dilations of lymphatic vessels. These vessels possessed a covering of striated muscle in their most advanced state of development. He reviewed the works of the following authors [Stannius (1832, 1843); Owen (1866); Panizza (1830); Huxley (1871); Chauveau (1873); Budge (1881); Sala (1900); Apostoleano (No date); Gadow and Selenka (1891); Gegenbaur (1901); Müller (1908); Wiederheim (1909); Gourin (1911); Fürther (1913); Kaupp (1918); Ward and Gallagher (1923); Ellenburger and Baum (1926); Josifoff (1930); and Schaffer (1929)] who had described lymph hearts.

Dransfield summarized the work of the above authors related to lymph hearts by stating that

> it seems to be generally agreed that pelvic lymph hearts, lying in the angle between the pelvis and the caudal region, are present in the Cursores and in certain aquatic birds in adult life. They appear in all birds in embryonic life, but disappear at the time of hatching in the more highly developed birds. In the domestic fowl, they are definitely visible in the embryo chick, but disappear at the time of hatching, although they have been observed 30-35 days after hatching in some subjects.

2) Lymph glands: Dransfield (1944) found that Jolly (1909a, 1909b, 1909c, 1910) provided the first authoritative statements on the presence of lymph glands in birds. Jolly (1909a, 1909b, 1909c, 1910) examined 30 species of birds and found lymph glands present only in a few species of anatides. As reviewed by Dransfield, Retterer (1912) and Fürther (1913) reported the presence of lymph glands in the duck. He also stated that Josifoff (1930), Fürther (1913) and Seifried (1927) did not find lymph glands in the hen, although Bradley (1938) and Sission (1936) were reported to have stated that lymph glands were present in the domestic fowl. Jolly (1910) and Baum (1930) also reported that lymph glands were absent in the chicken. Dransfield (1944) concluded after comparing the work of these authors that no lymph glands were present in the fowl.

3) Lymph vessels: Dransfield (1944) found the descriptions of the lymphatic system of the fowl prior to the work of Baum (1930) to be rather superficial.

He stated that earlier investigators [Lauth (1824), Owen (1846 and 1866), Chauveau (1873), Kaupp (1918), Ward and Gallagher (1923), Ellenburger and Baum (1926)] described the thoracic ducts as entering the jugular veins whereas Barthels (1909), and Awtgeratoff (1928), in

contrast, stated that the thoracic ducts emptied into the "anterior vena cava." Gadow and Selenka (1891) and Baum (1930) also stated that the thoracic ducts emptied into the "anterior vena cava." Dransfield (1944) did not present a detailed summary of the earlier works related to the lymphatic vessels, other than the ductus thoracici.

Dransfield's (1944) own findings were similar to those reported by Baum (1930). He observed that the lymphatic trunk coursing along the a. pudenda communis was formed by branches draining the rectum and cloaca (s. ductus thoracici pars lumbalis, Baum, 1930). This trunk was joined by the lymphatic trunk coursing with the middle sacral artery to form the common trunk (s. ductus thoracici pars lumbalis, Baum, 1930) which followed the aorta to the thorax. After the vessels had entered the thorax he referred to the lymphatic ducts as the ductus thoracici (s. ductus thoracici pars thoracales, Baum, 1930).

Dransfield (1944) found that the lymphatics followed closely the course of blood vessels; often two or three lymphatic vessels accompanied a single artery or vein. Valves in the lymphatic vessels were rather weak but efficient enough to prevent retrograde flow. At the junction of lymphatic trunks with the venous system the valves consisted of two small cusps.

Dransfield's findings revealed that no lymph hearts or lymph glands were present in the chicken, thus supporting the work of Baum (1930). Plexuses of the lymphatics appeared to take the place of the glands but these were comparatively rare in the domestic fowl. When two or more lymphatics were running on a common course, they often united with one another by successive transverse or oblique anastomosing branches, but these anastomoses could not be called plexuses.

Dransfield (1944) disagreed with the terminology of Baum (1930). He related each lymphatic vessel to the corresponding artery or vein which it paralleled rather than establishing terminology, which he considered artificial such as "ductus thoracici pars lumbalis." He limited the term thoracic duct to include that portion of the lymphatic trunk which is in the thorax. The thoracic duct terminated in the v. cava superior.

Nishiyama (1955) injected gelatin into the "round folds" of the phallus and observed the filling of the lymph folds, "vascular bodies" and the lymphatic vessels coursing with the a. pudendalis interna. He concluded that these structures all belonged to the lymphatic system. He did not discuss the lymphatic vessels cranial to the "vascular bodies."

Lake (1957a), quoting Nishiyama (1955) only mentioned a connection between the lymph folds, "vascular bodies" and the lymph channels, but gave no additional anatomical details.

VI. Erection Mechanism

Eckhard (1876) was the first to describe accurately the erection mechanism in the duck. His interest in this subject stemmed from his anatomical findings of the distribution of arteries to the phallus; they were contrary to those reported by Müller (1836). Eckhard (1876) consistently observed that upon injection, the "cavernous tissue" in the phallus did not fill with the injection material.

Eckhard (1876) therefore conducted several rather simple but conclusive experiments. He first stimulated the nerve lying close to the rectum (s. intestinal nerve of Remak) and observed the cavity

(lymphbildungsraum -- Liebe, 1914) surrounding the "corpora cavernosa" to fill with a clear yellowish fluid and simultaneously observed the phallus to become erect and evert through the vent. This was the first evidence that lymph or a lymph-like fluid was involved in erection. He attempted this same experiment in young animals but was not able to produce the same results. His results were supported by the anatomical findings of Barkow (1829) and later Nishiyama (1955) who reported that the "vascular body" was poorly developed in young birds.

Eckhard (1876) then determined where the fluid was produced. He isolated the "Tannenberg'schen Körper" (Table III) and cut off the end of the structure. After hemorrhaging had ceased, he stimulated the bird as previously described and observed the fluid emerging from the cut edge. The fluid initially gushed out from the base of the body and then oozed from the cut surface. When contraction of the surrounding skeletal musculature occurred the fluid spurted from the cut edge. No blood was observed in the fluid. He collected 8-10 cc of this fluid in 2-3 minutes. Prolonged stimulation resulted in the body becoming colder and lighter in color. During the stimulation he did not observe the "Tannenberg'schen Körper" to swell significantly.

His third experiment was to determine if this fluid was found in the erected phallus. He pierced the phallus with a capillary tube and collected the fluid directly from the phallus and found no evidence of hemoglobin in this fluid.

The remaining problem was to determine how the fluid drained from the phallus after erection. Eckhard (1876) injected the lymph chamber surrounding "Tannenberg'schen Körper." The injection material filled lymph vessels along the ureter, as well as the lymph channels of

the phallus. The material drained cephalicly into the abdominal and then thoracic lymph ducts. He established the continuity through lymphatic vessels between the phallus, and "Tannenberg'schen Körper."

Gadow and Selenka (1891) unfortunately did not consider the work of Eckhard (1876). They described the erection of the phallus as a filling of cavernous vessels with blood. The groove of the phallus in the duck during erection formed a trough by the closing together of the dorsal border of the groove along the length of the phallus. They did not discuss the production of lymph nor relate it to the erection process.

Müller (1908) dealt almost entirely with the anatomical aspects of the corpus paracloacalis vascularis. His findings supplemented the work of Eckhard (1876).

Liebe (1914) summarized the work of Eckhard (1876) and reported that lymph, originated from the "arterial vascular coil" in the "gefässreiche Körper" and flowed to the phallus causing the phallus to swell. The trabeculae supported the lymph cavities and regulated the lymph pressure within the phallus.

Nishiyama (1955) was the first to report that "lymph" was involved in the erection of the phallus in the chicken. In addition he reported that this same fluid was also a semen diluter. Nishiyama (1955) and Nishiyama and Ogawa (1961) were primarily interested in the production of the diluting fluid. They conducted several experiments to demonstrate the origin and release of this fluid.

Nishiyama and Ogawa (1961) sexually stimulated the bird using the method of Serebrovskii and Sokolovskaja (1934).[1] This resulted in erection of the phallus and a copious outflow of transparent fluid from the lymph fold. They then tied off the a. pudenda interna and excised the "vascular bodies" of the cock. No evidence of erection or transparent fluid production was found when the bird was stimulated postoperatively. This they considered as supportive evidence for the hypothesis that erection was caused by the inflow of lymph. In their technique however, they removed the a. pudenda interna and v. pudenda interna along with the "vascular body." By removing the a. pudenda interna, Nishiyama and Ogawa (1961) negated their experiment because the blood supply to the phallus as well as the "vascular body" was removed so that no erection would result whether the phallus was composed of erectile tissue similar to that of mammals or lymph channels as found in birds.

Other experiments however, supported the initial hypothesis that transparent fluid was responsible for erection and the production of a diluting fluid. Nishiyama and Ogawa (1961) isolated the "vascular body," stimulated the bird and directly observed the production of transparent fluid. Nishiyama (1955) described in some detail the route of flow of the lymph during erection. His findings in the chicken were similar to those found in the duck by Liebe (1914).

Lake (1955, 1957a, and 1957b) described erection in the chicken as an engorgement of the phallus with blood. He reported that the

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[1] Serebrovskii's, A. S. and I. I. Sokolovskaja's (1934) technique: one pole was applied to the skin of the sacral region and the other placed in a basin of water into which the beak was emersed. 80 volts, 40 milliamphers for two seconds were given at 15 second intervals.

transparent fluid was produced only by forcible compression of the engorged copulatory organ in collecting semen. Lake (1957a, 1957b) did not present any evidence to support his concept of blood filling the copulatory organ. In 1966, based on the work of Nishiyama and Ogawa (1961), Lake and El Jack (1966) agreed that lymph was involved in erection. They still considered blood to be involved in erection of some of the tissues but did not identify the tissues to which they were referring.

VII. Supplemental Experiment

Phosphatase activity in the Corpus Paracloacalis Vascularis

Pearse (1961) reported that hydrolytic enzymes were known to break down phosphate esters and could be divided into mono, di and triphosphatases. The phosphomonoesterases hydrolyzed a wide variety of organic phosphates. There are no known histochemical tests for the detection of phosphokinase or transphosphorylase and the interpretation of alkaline or acid phosphatase as a manifestation of phosphate transfer is speculative.

Pearse (1961) was of the opinion that the histochemistry of the phosphatases was significant if the assumption was made that high phosphatase activity indicated increased phosphate transfer rather than hydrolysis of phosphate esters.

Based on the above assumption the three histochemical tests, azo dye test for acid phosphatase, Burstone's method for acid phosphatase and Burstone's method for alkaline phosphatase were selected to determine the presence of phosphatase.

The principle behind the three tests was that phosphate esters such as Napthol AS-BI ® or Napthol AS-MX ® can be used as substrates for nonspecific phosphatases. If the phosphate was hydrolyzed by the phosphatases, the phosphate group would react with a salt, such as Red Violet LB, present in the medium and will give a colored reaction which could be observed in the tissue.

OBJECTIVES

1. To locate the structures of the erection-dilution mechanism, anatomically, in relation to the cloaca, cloacal musculature, and to describe their arterial, venous, lymphatic, and nervous supply.

2. To establish standard terminology for these structures.

3. To re-introduce some of the more classical German and French works related to the anatomy of the structures involved in the erection-dilution apparatus.

4. To determine, anatomically, how the mechanism functions to cause erection of the phallus and the production of a diluent of semen.

MATERIALS AND METHODS

Approximately 100 specimens which included White Plymouth Rock, White Leghorn, Cornish and Araucana males were used in this study. The White Plymouth Rock was used as the reference animal and the other specimens were used for comparison. The White Plymouth Rocks were selected because their large size made a detailed study of parts easier than in breeds of smaller size. Initially turkeys were considered because they are larger than the chicken; however, the corpus paracloacalis vascularis was found to be approximately the same size. No advantage was found over the chicken to justify the added cost involved in obtaining and maintaining turkeys.

The arteries supplying the corpus paracloacalis vascularis, phallus and plica lymphatica were injected with red latex. Euthanasia of birds, prior to injection, was accomplished by an overdose of sodium phenobarbitol injected into the vena basilica of the wing. Heparin (4 mg/cc/kg of body weight; 1 gm = 160,000 units) was injected prior to euthanasia. The heparin did not result in any noticeable advantage in the filling of the arteries, if the injection mass was introduced immediately after euthanasia.

Preparation of the bird was as follows: The skin overlying the abdomen and breast was deflected and the legs forced dorsally until the head of the femur was sublated from the acetabulum. The large aa. ischiadicae and vv. iliacae were isolated from the musculature of the

leg and incised, which allowed the blood to drain from the vessels. This minimized the amount of blood in the vessels of the body cavity, and prevented excessive amounts of blood from filling the pelvic cavity when cut during cannulation of the vessels. The sternum was removed and the viscera displaced to reveal the bifurcation of the aorta into the aa. ischiadicae. The aa. ischiadicae were ligated approximately 0.5 inches lateral to the bifurcation of the aorta to prevent the flow of the injection mass into the caudal appendages. A ligature was placed around the aorta dorsal to the bifurcation but not tightened. The aorta cranial to the ligature was incised and a cannula inserted.

A plastic syringe was used to inject red latex. About 12 cc of red latex gave satisfactory results. The arteries of the pelvic region supplied by branches of the a. sacra mediana were filled; this included vessels of the corpus paracloacalis vascularis, plica lymphatica and phallus. More complex procedures were tried initially but were found to give, at best, similar results.

Microphil (a microvascular injection mass from Canton Bio-Medical Products, Swarthmore, Pennsylvania) also was used as an injection mass. The birds were prepared for injection as described above. Microphil has a small particle size and readily passes from the arterial to the venous system through capillary beds. This has the disadvantage of having the arterial and venous system injected with the same colored material. In order to obtain better differentiation between arteries and veins, microphil was injected into the vessels followed by latex. The latex forced the microphil into the capillaries and the venous system. The latex, having a much larger particle size, did not pass

through the capillaries. The specimens prepared in this manner provided good differentiation of the two systems.

The veins which supply the phallus, plica lymphatica and corpus paracloacalis vascularis were difficult to inject with latex. Other larger veins of the caudal part of the bird's body, namely those to the musculature, were more easily filled and the smaller vv. pudendae internae were by-passed or partially filled.

The same techniques employed for the injection of the arterial system were used to prepare the bird for venous injection. In this case, the vv. ilicae were ligated rather than the aa. ischiadicae. Initial injections made into the v. mesenterica inferior did not fill vessels draining the corpus paracloacalis vascularis. Subsequently, the cannula was inserted into the v. mesenterica inferior and guided through the arcus hypogastricus into either the v. pudenda communis dextra or v. pudenda communis sinistra. The corresponding v. pudenda externa was ligated. Injection of the latex gave satisfactory results and these specimens were used in conjunction with the latex-microphil injected specimens.

The lymphatics were injected with latex by inserting a 20-gauge needle into the phallus, para lateralis and directly injecting the latex. The latex filled the lymph channels back to the corpus paracloacalis vascularis and the lymph vessels coursing cephalicly along the ureter. In some specimens, the arterial system was injected with red latex, the venous system with blue latex and the lymphatic system with yellow latex and provided a good demonstration of the relationship of the three vascular systems to one another in the corpus paracloacalis vascularis.

The nerves to the corpus paracloacalis vascularis, phallus and plica lymphatica were dissected in fresh and embalmed specimens. The nerves were small and had to be dissected with the aid of a dissecting microscope. The fine nerve rami blended readily with the surrounding connecting tissue.

In studying nerves, specimens that had the arterial system injected were superior to non-injected specimens because the smaller nerves were not confused with the smaller vessels. Embalmed birds were more satisfactory for dissection than fresh specimens because the larger nerves appeared to have a slight orange tint in contrast with the surrounding connective tissue. The formula for the embalming fluid was obtained from the South Carolina Medical School through Dr. Daris Swindler (Appendix I).

Prior to study, some specimens were decalcified in 10% nitric acid for 16 hours. The softening of osseous tissue provided some advantage in dissecting the nerves passing through the spinal column.

The nerve fibers within the corpus paracloacalis vascularis, plicae lymphaticae and phallus were so delicate that it required histological sections to determine their course. The tissues were stained using the chloral hydrate silver method (Nonidez, 1939) as published by Humason (1967). Satisfactory results were obtained (Appendix II).

To support further the concept that turgidity of the erected phallus is a result of a blood filtrate, two supplemental experiments were undertaken. The first experiment was concerned with phosphatase activity in the corpus paracloacalis vascularis, the second experiment

was conducted to determine the origin of blood found in the seminal fluid.

In determining the presence of phosphatase activity three histochemical tests were selected (Pearse, 1961). Two tested the acid phosphatase activity and one the alkaline phosphatase activity. In addition, these tests were employed to determine any difference in phosphatase activity in the corpus paracloacalis vascularis of ejaculated and non-ejaculated birds. The tests used were the standard coupling azo dye technique for acid phosphatase (Pearse, 1961), Burstone's method (Pearse, 1961) for acid phosphatase and Burstone's method (Pearse, 1961) for alkaline phosphatase.

Eight sexually mature cocks were divided into two groups: four non-ejaculated and four ejaculated. The latter were ejaculated according to the method of Burrows and Quinn (1935). Cocks of both groups were killed by cervical dislocation and the corpus paracloacalis vascularis removed immediately after death. Total lapsed time was about 5 minutes. All tissues were frozen with acetone and dry ice except for tissues from one ejaculated and one non-ejaculated bird which were frozen with Cryokwik (International Equipment Company). Cryokwik is a compound which provides for rapid freezing of tissues.

Sections 8 microns thick were cut at -19° F. on an International Cryostat and recovered on coverslips. The sections were placed in their respective staining jars. After staining, all sections were mounted on slides in glycerine jelly. Tissue sections of the corpus paracloacalis vascularis taken from both ejaculated and non-ejaculated birds were stained simultaneously for each test (Appendix III).

Azo Dye Test for Acid Phosphatase

A preliminary test was conducted using tissue of the corpus paracloacalis vascularis from a non-ejaculated bird. A positive test for acid phosphatase was observed in the tissue after 10 minutes of incubation. The most satisfactory staining time, however, was found to be 1 hour. At the end of this period a strong positive acid phosphatase reaction was observed. More extended incubation periods resulted in overstaining.

After the incubation period was determined, three males of the ejaculated and three of the non-ejaculated group were killed and the tissues removed, sectioned, and placed in the incubation medium for 1 hour.

Burstone's Method for Acid Phosphatase

A preliminary test was undertaken to determine the proper incubation period and to ascertain if this test would confirm the findings of the azo dye method. It was found that the incubation period for acid phosphatase activity was 6 hours. At 2 hours a reaction could be observed which progressively increased up to 8 hours. Six hours, however, gave satisfactory results and was used as the incubation period time.

Tissue sections of the corpus paracloacalis vascularis from the three ejaculated and three non-ejaculated males used in the azo-dye experiment were subsequently incubated for 6 hours and examined.

Burstone's Method for Alkaline Phosphatase

From a preliminary test it was determined that a minimum incubating period of 2 hours gave a positive reaction for alkaline phosphatase. Tissue sections from the corpus paracloacalis vascularis of

the ejaculated and non-ejaculated males used in the acid phosphatase experiment were also used in this experiment. The tissue sections were incubated for 2 hours and evaluated microscopically.

The second supplemental experiment was to determine if blood was a normal component of seminal fluid. In this experiment five male chickens were repeatedly ejaculated using the massage technique until blood appeared in the seminal fluid. Three other birds were ejaculated only once using the same technique. The birds were necropsied and the cloaca was examined for the presence of hemorrhages.

RESULTS

I. Arteries

The a. sacralis mediana originates from the aorta in the midline and is approximately 3 cm. long (Figure 1). Caudal to the posterior lobe of the kidney the a. sacralis mediana bifurcates, forming the a. pudenda communis dextra and a. pudenda communis sinistra. The a. pudenda communis proceeds caudolaterally from its origin, passing dorsal to the ductus deferens and ureter. Lateral to the ductus deferens, the a. pudenda communis divides into the a. pudenda interna and a. pudenda externa.

The a. pudenda externa supplies the musculature in the caudal part of the body and is not associated with the phallus, plica lymphatica, and corpus paracloacalis vascularis. The latter three structures are involved in the erection-dilution mechanism of the fowl.

From its origin the a. pudenda interna proceeds first caudomedially and then proceeds caudally with the ductus deferens, ureter, v. pudenda interna, n. pudendus internus and vas lymphaticus pudendus internus. The a. pudenda interna lies dorsal to the ureter and ductus deferens but ventral to the v. pudenda interna.

The ductus deferens and ureter course dorsolaterally to the coprodeum until they near the plica urocoprodealis. At this level the ureter continues its caudal course turning slightly ventral as it passes lateral to the plica urocoprodealis. Here it penetrates the

wall of the urodeum and opens on the dorsolateral surface of the chamber. The ductus deferens courses further ventrally before crossing lateral to the plica urocoprodealis. It then penetrates the urodeal wall and terminates in the ejaculatory papilla which projects out from the ventrolateral wall of the urodeum.

The a. pudenda interna continues further caudally than the ductus deferens and ureter. At the level of the plica urocoprodealis, the a. pudenda interna courses sharply ventrocaudad, almost at a 90° angle, passing between the m. contractor cloacae and the wall of the urodeum. Ventrocaudal to the ductus deferens the a. pudenda interna approaches the corpus paracloacalis vascularis.

Immediately cranial to the corpus paracloacalis vascularis the a. pudenda interna gives off the a. phalli and continues as the a. pudenda terminalis. The a. phalli supplies the dorsal part of the corpus paracloacalis vascularis, plica lymphatica and phallus. The a. pudenda terminalis supplies the ventral portion of the corpus paracloacalis vascularis and the ventral lip of the cloaca, including the ventral portion of the m. sphincter cloacae and the area ventral to the vent.

The a. pudenda interna, before dividing into the a. pudenda terminalis and a. phalli, gives off three major branches to the cloaca. The first branch is the a. coprodealis (Figures 1 and 2). It arises from the a. pudenda interna at the more caudal end of the coprodeum. The a. coprodealis courses from its origin about 5 mm, before dividing into two branches. The smaller of the two branches, namely, the more dorsal branch, supplies the cloacal bursa and a portion of the dorsal lip of the cloaca. In adult birds the cloacal bursa has atrophied

forming a small mass of bursal tissue located ventral and cranial to the m. contractor cloacae and the mucosa lining the dorsal wall of the coprodeum. In some specimens this dorsal branch was found to arise directly from the a. pudenda interna in close proximity to the a. coprodealis.

The larger ventral ramus of the a. coprodealis courses caudomedially over the ureter to the lateral wall of the coprodeum. It penetrates the muscularis externa of the coprodeum and ramifies in the submucosa. In the submucosa its branches extend as far caudally as the plica urocoprodealis; ventrally they follow the contour of the coprodeum to the midline; cranially they extend to the opening of the rectum into the coprodeum; and dorsally they anastomose with branches from the dorsal ramus.

Small rami from the dorsal and ventral branches of the a. coprodealis course to the mucosa where they form dense capillary beds. The mucosal surface in specimens injected with red latex has a bright red appearance indicating the abundance of vessels near the surface.

The a. coprodealis gives rise to a small vessel to the ductus deferens and ureter. This vessel bifurcates before reaching the ureter sending one ramus to supply the medial surface and the other to the lateral surface of the ureter and ductus deferens. The a. proctodealis is the second major artery arising from the a. pudenda interna (Figure 3). The a. proctodealis originates caudal to the a. coprodealis and lateral to the ductus deferens at the level of the plica urocoprodealis. The a. proctodealis passes lateral to the plica urocoprodealis and plica uroproctodealis, following the contour of the m. contractor cloacae and m. sphincter cloacae, to the cranial boundry

of the proctodeum. The proctodeum extends further laterally than the smaller urodeum. The a. proctodealis therefore by-passes the urodeum and courses directly to the proctodeum where it supplies the dorso-cranial wall.

In addition to its major supply to the dorsolateral wall of the proctodeum, the a. proctodealis gives off a small nutrient ramus to the ureter and a small ramus to the dorsal wall of the urodeum. The latter ramus supplies the dorsal part of the plica urocoprodealis and plica uroproctodealis. Another branch of the a. proctodealis supplies the cranial portion of the cloacal bursal duct and the m. contractor cloacae.

The third major branch of the a. pudenda interna is the a. uroproctodealis. The a. uroproctodealis originates from the a. pudenda interna close to the cranial end of the corpus paracloacalis vascularis (Figure 3). It also may arise from the a. phalli close to the bifurcation of the a. pudenda interna into the a. phalli and a. pudenda terminalis.

The a. uroproctodealis courses dorsally from its origin until it reaches the level of the dorsal extent of the urodeum, dorsal to the m. levator cloacae. Here the artery divides into a cranial and caudal branch. The cranial branch, ramus urodealis, enters the connective tissue of the plica uroproctodealis and then courses ventrally to supply the lateral and ventral surface of the urodeum including the ejaculatory papillae. The caudal branch, ramus proctodealis lateralis, courses over the dorsal surface of the m. levator cloacae to supply the lateral wall of the proctodeum, dorsal to the plica lymphatica. Its branches anastomose with branches from the more cranial lying a. proctodealis which supplies the dorsal wall of the proctodeum.

As previously mentioned, the a. pudenda interna located at the cranial end of the corpus paracloacalis vascularis branches to form the a. phalli and a. pudenda terminalis. The primary rami of the a. phalli supply the dorsal portion of the corpus paracloacalis vascularis and those of the a. pudenda terminalis, the ventral portion. In one specimen the corpus paracloacalis vascularis was 7 mm in length with seven primary rami originating from the a. phalli. The a. pudenda terminalis gave rise to five primary rami over a distance of 3.5 mm. The a. pudenda terminalis has a shorter course over the surface of the corpus paracloacalis vascularis than has the a. phalli and accounts for the fewer number of rami. The arborization of primary rami is readily observed in transversely cut specimens of the corpus paracloacalis vascularis whose vessels have been injected with latex. The primary rami lie at right angles to the major vessels. A few of these primary rami traverse the corpus paracloacalis vascularis, penetrating the connective tissue capsule to supply the m. contractor cloacae and m. sphincter cloacae which lie lateral to the corpus paracloacalis vascularis. These nutrient rami, after leaving the capsule, are similar in structure to other muscular nutrient rami.

The primary rami give rise to secondary rami (Figure 6). The secondary rami are small vessels which have an irregular course. They are more prevalent at the periphery of the corpus paracloacalis vascularis. The small tertiary rami arise from the secondary rami and form the capillary tufts. In one specimen a secondary ramus 1.5 mm long gave rise to six tertiary rami each of which formed a capillary tuft. In some cases more than one tertiary ramus is found to supply a single capillary tuft. The origins of the two tertiary rami that

supply a single capillary tuft are not always from the same secondary ramus.

Tertiary rami vary in length with some being rather short, almost non-existent before breaking up into the capillary tuft and some have a longer, more tortuous course.

Dissection of the connective tissue capsule and surface lymph channels of a corpus paracloacalis vascularis whose arterial system is injected with latex, reveals the densely packed capillary tufts. The capillary tuft has a definite rounded to oblong shape and varies in length from .5 mm to .75 mm. At a magnification of 9x the capillary tufts appear as tiny loose balls interconnected by vessels that resemble small, winding threads. In addition the large primary rami that penetrate through the capsule are readily seen. Microphile-injected specimens have an arrangement of capillary tufts similar to those injected with latex. The vessels were not as distended as they were when injected. Therefore the individual capillaries were readily distinguishable.

In fresh specimens the individuality of the capillary tufts could not be ascertained. Aggregations of capillary tufts usually appear as small bundles of reddish tissue surrounded by trabeculae.

A transverse cut through the corpus paracloacalis vascularis of a non-injected specimen reveals that the reddish tissue as observed beneath the capsule dominates the internal parts of the body. A transverse cut of the corpus paracloacalis vascularis of a specimen injected with latex reveals that the reddish tissue observed in the fresh specimen is composed of densely-packed tufts (Figure 12).

The capillary tufts arise from the ramifications of tertiary arteries. These ramifications are few, ranging from 3-7. These rami subdivide forming an elaborate capillary network, the capillary tuft. There is some anastomosing of one part of a capillary tuft with that of another but the majority of the tufts are separate.

The a. phalli after giving off the primary rami supplying the corpus paracloacalis vascularis continues medially to supply the plica lymphatica, phallus and dorsal part of the ventral cloacal lip including a portion of the enclosed m. sphincter cloacae and plica proctodealis (Figure 4).

At the caudal border of the corpus paracloacalis vascularis the a. phalli parallels the medial surface of the m. levator cloacae. The m. levator cloacae at this level is coursing medially to insert at the base of the phallus.

The a. phalli is relatively short (Figures 3 and 4). In one bird it was 1.5 cm in length from its origin at the a. pudenda interna to its termination in the phallus-pars medialis.

Passing over the corpus paracloacalis vascularis the a. phalli continues to give rise to additional branches which extend medially as far as the plica lymphatica. The a. phalli continues on medially to supply the plica lymphatica and the phallus.

The a. phalli terminates in the phallus-pars medialis. At the base of the pars medialis it sends rami into the connective tissue core. These branches transverse the connective tissue core giving off extremely delicate rami to the connective tissue and the trabeculae of the phallus (Figure 4). The vessels reaching the dermis of the phallus

form a capillary layer which gives the dermis a deep red color in red latex injected specimens. The core of the phallus through which the branches of the a. phalli pass is not filled when the arterial or venous system is injected.

The arterial supply to the plica lymphatica arises from the a. phalli. One or two small branches enter the plica lymphatica. Coursing through the fold, they give off few small rami that supply the connective tissue trabeculae; the core appears white in cross section. The vessels ramify in the mucosa of the plica lymphatica forming capillary nets and give the surface of the structure a red color in red latex-injected specimens. A similar arrangement is found in the phallus-pars lateralis. If blood replaced the latex, it would have the red coloration as found in the structure of a living bird. The phallus-pars medialis does not have the density of capillaries in the dermis as the pars lateralis and appears more white.

The a. pudenda terminalis continues ventromedial to the corpus paracloacalis vascularis and supplies the lower lip of the cloaca including the ventral portion of the m. sphincter cloacae and the area ventral to the cloacal opening. It does not send rami to the phallus or plica lymphatica.

II. Veins

The venous system related to the corpus paracloacalis vascularis, plica lymphatica, and phallus closely parallels the arterial supply (Figure 1).

Like the arteries, the veins draining from the cloaca are paired caudal to the arcus hypogastricus. The description of the following vessels applies to both the right and left sides.

The arcus hypogastricus is a large transverse vein which connects the right and left vv. hypogastricae (Figure 1) at the caudal end of the kidney, ventral to the a. sacra mediana. The unpaired v. mesenterica caudalis empties in the middle of the arcus hypogastricus. The v. pudenda communis which drains the pelvic region, empties into the arcus hypogastricus. The v. coccygeus empties into the v. pudenda communis caudal to the bifurcation of the a. sacra mediana into the aa. pudendae communis.

The v. pudenda communis is formed by the anastomoses of the v. pudenda interna and v. pudenda externa. The v. pudenda externa drains the musculature of the tail and pelvic region and has been described at length by du Toit (1913). The v. pudenda externa is not involved in the erection-dilution mechanism and will not be considered further.

The v. pudenda interna originates from the union of the v. phalli and the v. pudenda terminalis on the medial surface of the corpus paracloacalis vascularis. The v. pudenda interna closely parallels the a. pudenda interna. The v. coprodealis, v. proctodealis and v. uro-proctodealis empty into the v. pudenda interna. In addition the v. pudenda interna receives rami from the ureter and ductus deferens which are referred to as the vv. uretodeferentiales posterior.

The v. uroproctodealis empties into the v. pudenda interna immediately cranial to the corpus paracloacalis vascularis (Figure 2). The v. uroproctodealis closely parallels the a. uroproctodealis. The

v. uroproctodealis is formed by two major branches, one draining the lateral wall of the proctodeum, the other draining the ventral portion of the urodeum. The ramus draining the proctodeum arises from the capillaries in the mucosa. It proceeds cranioventrally, passing lateral to the plica uroproctodealis and receives some small branches from the m. levator cloacae. The vessel is joined by the ramus draining the ventral wall of the urodeum and its ejaculatory papillae, forming the common trunk of the v. uroproctodealis.

The large v. proctodealis originates from the capillary beds of the mucosa on the dorsal surface of the proctodeum and proceeds ventrocranially passing lateral to the plica urocoprodeum and ductus deferens. The v. uroproctodealis receives branches from the cloacal bursal duct, the m. contractor cloacae, m. sphincter cloacae, m. levator cloacae, and a branch from the dorsal part of the plica uroproctodealis. The v. uroproctodealis empties into the v. pudenda interna cranial to the v. uroproctodealis (Figure 3).

The branches of the v. coprodealis parallel the branches of the corresponding a. coprodealis (Figures 1 and 3). Its branches arise in the wall of the coprodeum with a long branch originating in the caudal portion and a short branch originating in the cranial portion. Vessels from the ureter and ductus deferens join into the longer of the two rami.

Small rami from the cloacal bursa may enter the v. coprodealis or course directly to the v. pudenda interna. These latter branches arise in the bursal remnant. In older birds, these vessels are relatively small due to the atrophy of the cloacal bursa.

The v. phalli drains the phallus, plica lymphatica, ventral lip of the cloaca and the dorsal portion of the corpus paracloacalis vascularis (Figure 3). The v. phalli originates from the anastomosis of perpendicular running rami from the dermis of the phallus and submucosa of the plica lymphatica. These perpendicular vessels are small, few in number, and parallel the arterial rami arising from the a. phalli. Into these small perpendicular veins drain extremely delicate vessels from the trabeculae supporting the phallus and plica lymphatica.

The v. phalli courses laterally and follows the inner contour of the m. sphincter cloacae, the m. levator cloaca and the ventral portion of the plica proctodealis.

The v. phalli, reaching the caudal end of the corpus paracloacalis vascularis, leaves its association with the m. sphincter cloacae and proceeds across the medial surface of the corpus paracloacalis vascularis, just beneath the connective tissue capsule.

The v. pudenda terminalis parallels the a. pudenda terminalis. It drains the ventral lip, a small area ventral to the lip, and the m. sphincter cloacae. The vein then passes across the medial surface of the corpus paracloacalis vascularis to enter the v. pudenda interna.

Both the v. phalli and v. pudenda terminalis lie superficial and slightly ventral to the corresponding artery as they proceed over the corpus paracloacalis vascularis (Figure 5).

The corpus paracloacalis vascularis cut transversely shows that the veins within this organ collect blood from capillary tufts and drain toward the periphery of the corpus paracloacalis vascularis where they form larger vessels which enter the v. phalli, v. pudenda

terminalis or v. pudenda interna. The large primary venous rami, in general, do not appear to parallel the primary arterial rami and are most prominent at the periphery of the corpus paracloacalis vascularis.

Using similar terminology as used for the arteries, the term "tertiary vein" of the corpus paracloacalis vascularis is defined as those veins which directly drain a capillary tuft (Figure 6). A primary ramus is a vein which originates in the corpus paracloacalis vascularis and drains into the v. phalli, the v. pudenda terminalis, or the v. pudenda interna. Secondary rami are defined as those branches draining into the primary rami and which do not connect directly with capillary tufts.

The tertiary rami are usually very short. In some instances a distinct tertiary vein is all but absent. The secondary venous rami do not have a tortuous course as observed in the secondary arterial rami. They arise from the tertiary rami and course more directly to the larger primary rami. Each secondary ramus must drain several capillary tufts as it proceeds to the primary ramus. The arterial supply dominates the central core of the corpus paracloacalis vascularis while the periphery is associated with the venous return.

Latex injected into the arterial system fills the primary, secondary, tertiary rami and the capillary tuft. Injection of the venous system results in the primary, secondary and tertiary venous vessels being injected but not penetrating to any great extent into the capillary tufts.

A few branches receive venous blood from the laterally lying m. contractor cloacae, m. sphincter cloacae and penetrate the capsule of the corpus paracloacalis vascularis and join either the v. phalli

or the v. pudenda terminalis. Upon entering the corpus paracloacalis vascularis these veins receive many secondary rami.

III. Nerves

The nervous system and its relationship to the phallus, plica lymphatica and corpus paracloacalis vascularis have not been investigated thoroughly in the domestic fowl. Modern investigators who have discussed the anatomy of the erection-dilution mechanism did not discuss the nerve supply to these structures (Portman, 1951; Nishiyama, 1955; Lake, 1957a; 1957b; and Knight, 1967). In addition, they have not considered earlier anatomical findings related to these structures in the duck and goose (Eckhard, 1876; Müller, 1908; and Liebe, 1914).

The plexus ischiadicus is the largest plexus of the pelvic region, giving rise to the large n. ischiadicus (s. sciaticus) to the leg. For the most part the plexus ischiadicus does not give rise to branches that innervate the cloacal area but does provide a reference point for determining the origin of the more caudal plexuses.

The plexus ischiadicus is composed primarily of five large spinal nerves. These correspond to spinal nerves 25-30 which du Toit (1913) and Lucas and Stettenheim (In press) described. The a. ischiadica lies ventral to spinal nerve 30 and approximates the caudal extent of the plexus. In some specimens a short, small ramus from spinal nerve 31 contributes to the formation of the plexus.

The portion of the sympathetic trunk associated with the plexus ischiadicus lies close to the vertebral column affixed to the ventral surface of the spinal nerves. Here it is difficult to detach the sympathetic trunk and their ganglion from the ventral rami of the

spinal nerves. Delicate rami from the sympathetic trunk pass medially; they follow the contour of the vertebral column and combine with rami from the opposite side to form a delicate nerve plexus on the ventral surface of the column.

The plexus pudendus lies caudal to the plexis ischiadicus. The n. pudendus internus arises from this plexus and innervates the structures involved in the erection-dilution mechanism -- the phallus, plica lymphatica and corpus paracloacalis vascularis. In addition the branches of the n. pudendus internus innervate the ureter, ductus deferens, and the musculature of the pelvic region.

The ventral rami of the spinal nerves composing this plexus pudendus are considerably smaller than those of the plexus ischiadicus. The spinal nerves forming the plexus ischiadicus are oriented at right angles to the vertebral column whereas spinal nerves of the plexus pudendus parallels the vertebral column.

The plexus pudendus varies in the number of spinal nerves comprising the plexus and in the manner in which they anastomose and branch. The largest and often the most cranial ramus of the plexus pudendus is the ventral ramus of spinal nerve 31. It emerges from its vertebral foramen caudal to the large transverse process of the 30th caudal vertebra. This large transverse process provides a landmark for locating the 31st nerve as transverse processes immediately cranial to the 30th transverse process are markedly smaller and are associated with the large spinal nerves of the plexus ischiadicus. Another landmark for orienting the 31st spinal nerve is the a. ischiadica which lies ventral and slightly cranial to the emergence of the 31st spinal nerve.

The 31st spinal nerve emerging from the vertebral foramen proceeds directly caudally, bending slightly ventral as it proceeds over the transverse process of caudal vertebra 31. Caudally, it becomes closely associated with the ventral ramus of spinal nerve 32 but does not anastomose with the latter ramus until it reaches the level of the 34th vertebra.

A thin, small branch from the ventral ramus of spinal nerve 30 contributes to the formation of the plexus pudendus in many specimens. From its origin this branch courses ventrocaudally passing over the large transverse process of vertebra 30. Continuing caudally on the lateral surface of the vertebral column, it comes to lie close to nerve 31 and finally anastomoses with spinal nerve 31 in the region of the 33rd and 34th vertebra. When present, the ramus from spinal nerve 30 is the most ventral ramus of the spinal nerves forming the plexus pudendus.

In some specimens, usually not in those possessing the ramus from spinal nerve 30, a short, rather large ramus, the n. bigeminus, arise from spinal nerve 31 and courses cranially over the large transverse process of caudal vertebra 30. It anastomoses with the large ventral ramus of spinal nerve 30 and contributes to the formation of the plexus ischiadicus.

The 31st sympathetic ganglion lies ventral to the vertebral foramen close to the point of emergence of the ventral ramus of spinal nerve 31. In these specimens, short rami communicantes connect the sympathetic ganglia to the ventral ramus of spinal nerve 31.

The ventral ramus of spinal nerve 32 has a similar course pattern to that of 31. Emerging from the vertebral foramen, it courses

caudoventral over the transverse process of the 32nd caudal vertebrae. It continues caudally on the lateral side of the vertebral column dorsal to spinal nerve 31.

The ventral ramus of spinal nerve 32 is the second largest nerve branch of the plexus pudendus. It, along with spinal nerve 31, forms the major part of the ventral trunk of the plexus pudendus.

The sympathetic ganglion associated with spinal nerve 32 lies close to the point of emergence of the ventral ramus from the vertebral foramen. The sympathetic trunk lies medial to spinal nerve 31.

The 32nd sympathetic ganglion is connected dorsally to the ventral ramus of spinal nerve 32 by short rami communicantes. Small delicate branches course ventrally from the surface of the ganglion. Because of their delicate nature, they are difficult to trace.

The sympathetic trunk leaves the 32nd ganglion and courses caudoventral over the transverse process of caudal vertebra 32. It takes a dorsal course caudal to the process, passing medial to spinal nerves 31 and 32 and connects to the 33rd sympathetic ganglion. The 33rd ganglion lies ventral to spinal nerve 33.

The ventral ramus of spinal nerve 33 emerges from the vertebral foramen and courses ventrocaudally. The ventral ramus of spinal nerve 33 is smaller than 31 or 32 and due to the more dorsally located vertebral foramen the nerve does not parallel rami 31 and 32 initially, but takes a course at a slight angle to these nerves. At the level preceeding the 34th caudal vertebra the 33rd nerve becomes closely associated with nerves 31 and 32.

The 33rd sympathetic ganglion is smaller than those of 31 and 32. Long rami communicantes connect the ganglion to the spinal nerve. The

sympathetic trunk courses over transverse process 33 and joins the 34th sympathetic ganglion on the ventral surface of the transverse process of caudal vertebra 34.

The ventral ramus of the 34th spinal nerve emerges from the vertebral foramen and courses caudoventrally. It has a more ventral origin than spinal nerve 33. The 34th transverse process is flatter, allowing the nerve to course almost directly caudally after emerging from the foramen. It becomes associated with the other nerves of the plexus caudal to the 34th transverse process.

The 34th sympathetic ganglion lies on the 34th transverse process and is connected by small rami communicantes to the 34th spinal nerve as it courses over the process. Numerous branches course from the surface of this ganglion.

Spinal nerve 35 is the smallest of the spinal nerves of the pudendal plexus. It courses caudally and becomes associated with spinal nerve 34.

The anastomosis of five or six spinal nerves to form the plexus pudendus is quite variable, particularly between the more caudal of the spinal nerves. Spinal nerves 30, 31 and 32 are closely associated with one another and form the ventral trunk of the plexus pudendus. Spinal nerves 33, 34, and 35 form the dorsal trunk. There is an anastomosis between the dorsal and ventral trunks.

In one specimen, a short ramus from the dorsal surface of the ventral trunk anastomosed with spinal nerve 33 to form a small nerve branch which was joined by spinal nerve 34 to form the dorsal trunk. Spinal nerve 35 in this specimen did not join the dorsal trunk (Figure 7a). In another specimen spinal nerve 32 bifurcated prior to

anastomosing with spinal nerve 31 (Figure 7b) with one ramus joining with spinal nerve 31 to form the ventral trunk and the other ramus joining with spinal nerve 33 to form the dorsal trunk. Approximately 1 cm caudal to the bifurcation of spinal nerve 32, a short connecting ramus joined together the dorsal and ventral trunks.

The n. pudendus internus arises directly from the ventral trunk. There is no n. pudendus communis present. The n. pudendus externus is the caudal continuation of the ventral trunk after giving off the n. pudendus internus. The n. pudendus internus is rather small in comparison to the large n. pudendus externus. The n. pudendus internus courses caudoventral from its origin, crossing over the ventral surface of the a. pudenda communis cranial to the bifurcation of the vessel into the a. pudenda interna and a. pudenda externa. The n. pudendus internus continues caudally on the medial surface of the a. pudenda communis to the bifurcation of the vessel where it becomes closely associated with the a. pudenda interna. Caudal to the bifurcation of the a. pudenda communis, the n. pudendus internus is joined by a second ramus from the plexus pudendus, more specifically from the dorsal trunk composed of spinal nerves 33 and 34. The branch from the dorsal trunk courses mediocaudally passing dorsal to the a. pudenda externa, and anastomoses with the paralleling n. pudendus internus, lying adjacent to the a. pudenda interna.

The n. pudendus internus, after receiving the second branch, gives rise to the n. uretodeferentialis posterior. This nerve ramus parallels the corresponding a. uretodeferentialis posterior as it courses to the ureter and ductus deferens.

Paralleling the a. pudenda interna, the n. pudendus internus gives off a small branch, the n. coprodealis, which follows the artery and vein of the same name. In addition, there are numerous delicate nerve rami arising from the n. pudendus internus which innervate the cloacal wall. These rami anastomose with one another and with delicate ganglia associated with them. Many of these rami terminate in the large intestinal nerve of Remak. The intestinal nerve of Remak is a long ganglionated nerve chain lying in the mesentary associated with the digestive tract.

Further caudad arose a nerve, the n. proctodealis which paralleled the a. proctodealis and which coursed to the intestinal nerve of Remak.

Near the origin of the a. uroproctodealis, the n. phalli gives rise to the n. uroproctodealis, which innervates the area of the ejaculatory papilla, the wall of the urodeum and the caudal wall of the coprodeum. It is a delicate nerve and was difficult to follow.

The n. pudendus internus proceeds caudally along with the a. pudenda interna and v. pudenda interna. Cranial to the corpus paracloacalis vascularis the n. pudendus internus gives rise to the n. phalli and continues caudally as n. pudendus terminalis (Figure 8).

The n. pudendus terminalis lies on the medial surface of the corpus paracloacalis vascularis and is medial to the a. pudenda terminalis and v. pudenda terminalis. In its course, small rami arise which course medially to innervate the cloacal wall. However, the main trunk courses ventrally. At the ventral border close to the medial end of the corpus paracloacalis vascularis lies a large ganglion, ganglion paracloacalis. From the surface of the ganglia arise branches which go to the ventral and lateral walls of the proctodeum, the m. sphincter

cloacae and the integument of the ventral lip as well as the corpus paracloacalis vascularis.

The n. phalli courses ventrally from its origin across the medial surface of the corpus paracloacalis vascularis medial to the a. phalli and v. phalli.

The n. phalli and its branches are considerably more variable in their distribution than the corresponding vessels. Anastomoses are present on the medial surface of the corpus paracloacalis vascularis among branches of the n. phalli as well as those of the n. pudendus terminalis (Figure 8).

Caudal to the corpus paracloacalis vascularis, the n. phalli innervates the phallus, plica lymphatica, m. sphincter cloacae and skin of the ventral lip.

As the n. phalli and n. pudendus terminalis course over the corpus paracloacalis vascularis they give off delicate rami which penetrate into the structure. These rami are so small and delicate that they must be examined histologically.

The nerves within the corpus paracloacalis vascularis are closely associated with the blood vessels. The larger nerves are found in the connective tissue stroma surrounding the larger vessels. Their branches can be traced to the capillary tufts where they pass through the spaces between capillaries (Figure 9). They have free nerve endings, similar to those generally found in blood vessels.

Knight (1967) found avian lamellar corpuscles (Herbst corpuscles) in the ventral lip and the proctodeal fold. None were found in the phallus, plica lymphatica or corpus paracloacalis vascularis.

In the phallus and plica lymphatica, nerve fibers with free nerve endings are associated with vessels of the phallus and plica lymphatica.

IV. Lymphatics

The lymphatics of the phallus, plica lymphatica and corpus paracloacalis vascularis are readily traced in injected specimens. Within these structures the lymphatic system consists of a complex network of lymphatic channels rather than distinct lymphatic vessels; thus, there are no lymphatic vessels which correspond to the a. phalli or a. pudenda terminalis.

Excision of the m. contractor cloacae, m. sphincter cloacae and the connective tissue capsule overlying the corpus paracloacalis vascularis reveals the large collecting lymph channels lying on the surface of corpus paracloacalis vascularis (Figure 10). At the cranial end of the corpus paracloacalis vascularis three or four small lymph vessels originate from these large collecting lymph channels, (Figure 11). These small lymph vessels anastomose with one another to form the vas lymphaticus pudendus internus. The vas lymphaticus pudendus internus is composed generally of two vessels which lie lateral to the a. pudenda interna and v. pudenda interna. There are interconnecting lymphatic rami which lie on the lateral surface of a. pudenda interna and v. pudenda interna. The lymphatic vessels weave as they proceed cranially and lack the straight, more tubular arrangement of the arteries.

Distinct valves are present in the vas lymphaticus pudendus internus and in the connecting vessels. The valves are numerous and oriented in the vessels to prevent retrograde flow, (Figure 11).

The large lymph channels on the surface of the corpus paracloacalis vascularis have an irregular pattern and are interconnected with one another (Figure 11). These collecting channels have a tiered arrangement consisting of 3 to 4 layers of interconnecting lymph channels which lie at different depths below the capsule. Supportive connective tissue fills the spaces between the channels.

In triple-injected specimens the arteries and veins pass between the collecting channels to supply the overlying muscles. These are the only arterial or venous vessels observed on the surface of the corpus paracloacalis vascularis.

At the caudal end of the corpus paracloacalis vascularis the collecting lymph channels continue dorsomedially coming to lie between the m. sphincter cloacae and the wall of the proctodeum. They ultimately terminate in the plica lymphatica and phallus. The small lymph channels drain into the large collecting lymph channels lying on the surface of the corpus paracloacalis vascularis from within the structure. These lymph channels originate from around the capillary tuft and are easily filled with an injection mass; the injection mass does not pass into the capillary tuft. The lymphatic channels draining the capillary tufts are interconnected and drain to the large lymph channels at the surface of the corpus paracloacalis vascularis. As they course peripherally, the lymphatic channels become larger. A transverse cut through the corpus paracloacalis vascularis injected with latex reveals the drainage pattern to the periphery, (Figure 12).

A parasagittal cut reveals the interconnections of the lymph channels coursing craniocaudally. A frontal section through the corpus paracloacalis vascularis reveals the interconnection of the lymphatic channels around and between the capillary tufts.

The lymphatic collecting channels supplying the phallus and plica lymphatica are a direct continuation of the lymph channels from the corpus paracloacalis vascularis. As the channels course dorsomedially to the phallus and plica lymphatica they initially surround the vascular tissue extending from the caudal end of the corpus paracloacalis vascularis. Reaching the level of the plica lymphatica the vascular tissue terminates but the channels continue into the phallus and plica lymphatica.

The lymphatic channels occupy a narrow area as they course dorsomedially between the wall of the proctodeum and the skeletal musculature of the m. sphincter cloacae. The m. levator cloacae crosses the dorsal surface of the lymph channels medial to the major portion of the corpus paracloacalis vascularis and lateral to the phallus and plica lymphatica.

Figure 9 illustrates the corpus paracloacalis vascularis and the channels connecting the phallus and plica lymphatica. The drawing was made from a specimen whose arterial, venous and lymphatic systems were injected with latex.

The folds (usually 2 or 3) of the plicae lymphaticae are quite prominent in the erected state. Within each of the folds lie numerous lymph channels. A sagittal section through the plica lymphatica reveals the netlike arrangement of the lymph channels within the core of the structure covered by the mucosa and submucosa. The lymphatic channels injected with latex did not penetrate into the mucosa or submucosa. In

the plica lymphatica the connective tissue trabeculae supports the structure and separates the lymph channels. As the lymph channels course toward the surface, small distinct channels can be observed.

The phallus-pars lateralis or pars medialis also contains numerous lymph channels within the tissue. The major branches from the a. phalli and v. phalli lie in the connective tissue between the lymphatic channels of the core of the phallus. The lymph channels course to a level immediately below the dermis. The lymph channels of the phallus-pars medialis freely interconnect with the channels of the pars lateralis.

V. Corpus Paracloacalis Vascularis

The corpus paracloacalis vascularis is a small, oblong shaped structure which lies medial to the m. sphincter cloacae and m. contractor cloacae; and lateral to the urodeum at the level of the ejaculatory papillae (Figures 2 and 3).

The m. sphincter cloacae covers the caudal third of the corpus paracloacalis vascularis and the channels leading to the plica lymphatica and phallus. The m. contractor cloacae covers the cranial two-thirds of the corpus paracloacalis vascularis. The perimysium of these muscles and the connective tissue capsule surrounding the corpus paracloacalis vascularis are inseparable laterally. The capsule of the corpus paracloacalis vascularis is inseparable from the fibrosa of the urodeum on the medial surface of the body. The ventral surface of the corpus paracloacalis vascularis is covered with peritoneum from the wall of the pelvic cavity as it reflects onto the surface of the cloaca. Here the

peritoneum becomes attached to the connective tissue capsule of the corpus paracloacalis vascularis.

Excision of the corpus paracloacalis vascularis reveals that the lateral surface is oval and covered with a delicate connective tissue which is interrupted only by the nutrient rami which penetrate the capsule to supply the overlying m. sphincter cloacae and m. contractor cloacae.

The medial surface of the corpus paracloacalis vascularis is flatter than the lateral surface. The major vessels lie on the medial surface beneath the capsule.

The corpus paracloacalis vascularis can be divided into a cortex and medulla. The cortical area corresponds to the area just below the capsule which contains the densely packed capillary tufts. The medulla corresponds to the area in which the primary and secondary rami lie.

The capillary tufts are surrounded by endothelial lined lymphatic vessels. The relationship of the capillary tuft to the collecting lymph channel can be compared to a ball pressed onto the surface of a partially inflated balloon. The part of the balloon next to the ball would compare to the endothelial lining on the surface of the capillary tuft. The space inside the balloon would correspond to the lumen of the collecting duct and the outer wall not contacting the ball would correspond to the outer wall of the collecting duct.

The lymphatic collecting channels are found interconnecting between and around the tufts and with the large collecting lymphatic channels. They also extend into the medulla, (Figure 12).

The medulla contains, in addition to the major vessels and nerves, some supportive connective tissue, and is primarily associated with the larger vessels and nerves.

At the caudal end of the corpus paracloacalis vascularis the vascular-lymphatic tissue is drawn out into a narrow neck with the vascular tissue becoming progressively reduced as it continues caudomedially. The a. and v. phalli lies dorsal to the vascular tissue and is surrounded by the lymph channels. At the levels of the plica lymphatica the vascular tissue terminates with the lymph channels continuing up into the plica lymphatica and phallus.

VI. Phosphatase Activity

The Standard Coupling Azo-Dye Technique for Acid Phosphatase

The corpus paracloacalis vascularis of both non-ejaculated and ejaculated birds demonstrated acid phosphatase activity. There were no noticeable differences between the two groups of birds.

Small to medium maroon granules were found in the endothelial cells of the lymph channels. Granules were present in the supportive connective tissue but did not appear as heavily infiltrated as the endothelial cells. The walls of the larger blood vessels contained some granules. The blood vessel walls appeared yellowish in color with a few maroon granules. This was more noticeable in vessels cut longitudinally.

The azo dye technique gave a rapid test for determining the presence of acid phosphatase activity.

Burstone's Method for Acid Phosphatase

The Burstone method for acid phosphatase demonstrated numerous granules in the tissue sections of both ejaculated and non-ejaculated birds. These granules imparted to the tissue a pinkish color. Under microscopic examination at 10x, the granules appeared purplish on a tannish-white background. At higher magnification, 43x, very prominent granules were located in the endothelial cells and connective tissue. They were as numerous as those in the azo dye test for acid phosphatase. Again, there was no difference between the ejaculated and non-ejaculated birds.

Burstone's Method for Alkaline Phosphatase

The alkaline phosphatase determination also was found to be positive. The granules, however, were not observed in the endothelial or connective tissue cells. They were located in the red blood cells within the capillaries of the corpus paracloacalis vascularis. Again, no noticeable increase in staining was found to occur between the ejaculated and non-ejaculated birds. From this experiment it was determined that both the acid and alkaline phosphatase were present in the corpus paracloacalis vascularis of the domestic chicken. There were no distinguishable differences between the corpus paracloacalis vascularis of ejaculated and non-ejaculated birds.

VII. Blood as a Component of the Seminal Fluid

Birds ejaculated only once by the massage technique were found at necropsy to have no petechial hemmorrhages in the wall of the urodeum. Petechial hemmorrhages were found in the wall of the plica uroproctodealis of birds in which blood had been observed in the ejaculate.

TERMINOLOGY

Establishing terminology that can be correlated with structures in other species within a class and between classes is a difficult problem. The problem is magnified by anatomists or others who do not examine the literature and who sometimes introduce new terminology without justification.

In 1950 the International Anatomical Nomenclature Committee (I.A.N.C.) was established to recommend nomenclature that would be internationally acceptable.

The Recommendations for establishing terminology were set forth by the I.A.N.C. Below is a brief resume of their recommendations from the second edition, Nomina Anatomica (1956):

(a) each structure should be designated by one term only.

(b) every term in the official list be in Latin. (It is also recommended that in scientific publications official Latin terms should always be employed -- more especially in the titles of such publications).

(c) each term should be short and simple.

(d) each term should have some information or descriptive value.

(e) structures closely related topographically shall have similar names.

(f) differentiating adjectives shall be arranged as opposites.

(g) eponyms shall not be used in the Official Nomenclature of gross and microscopic anatomy.

The third edition (1968) adds the following:

(a) all diphthongs should be eliminated.

(b) all hyphens between vowels in the middle of words should be eliminated. Other unnecessary hyphens should also be eliminated.

The following terminology of the arteries, veins, nerves and lymphatics related to the erection-dilution mechanism is presented. New terms are introduced only when it is necessary to fulfill the established rules set forth by the I.A.N.C.

The terminology for the main arterial and venous supply to the cloaca over the years has been based primarily on the work of Neugebauer (1845), Gadow and Selenka (1891), Müller (1908), du Toit (1913), Liebe (1914), and more recently Nishida (1964), and Knight (1967). From their works the following terms are recommended: a. sacralis mediana, a. and v. pudenda communis, a. and v. pudenda interna, a. and v. pudenda externa, a. and v. uretodeferentialis posterior and v. coccygeus. These terms meet the recommendations of I.A.N.C. and are derived from the terms employed by the previous authors.

The terms recommended to refer to the arterial system related to the cloaca offered little difficulty in definition whereas the venous system presented some problems. The terms employed by Neugebauer (1845) for the venous system have been extensively used. In attempting to alter his terminology, adequate justification is required. It is my feeling that several terms, based principally on the work of du Toit (1913) and supported in general by Nishida (1964), more clearly define the course of the vessels and meet the requirements of the I.A.N.C.

The term "v. hypogastrica" as employed by Neugebauer (1845) is too inclusive and should be further delineated. Du Toit (1913) did

not use the term "hypogastrica" to refer to vessels caudal to arcus hypogastrica; rather, he employed the term "pudenda." Du Toit's (1913) term is recommended because it more closely associates the vessels with the urogenital system and caudal end of the body in contrast to the term "hypogastrica" which is more related to the stomach. Du Toit (1913) subsequently divided the term into a common pudendal trunk which was composed of an internal and external pudendal branch, thus delimiting the vessel while maintaining a continuity between the main trunk and its branches.

My findings reveal that the v. coccygeus in the chicken empties into the v. pudenda communis rather than directly into the arcus hypogastricus. This agrees with Neugebauer (1845). Du Toit (1913) conversely considered the v. pudenda communis to empty into the v. coccygeus. Nishida (1964) illustrated the v. pudenda communis and the v. coccygeus as forming a common trunk which he labeled v. hypogastrica. The v. hypogastrica emptied into the arcus hypogastricus. Nishida's (1964) terminology would at first seem the most satisfactory, because it incorporates the terms of both Neugebauer (1845) and du Toit (1913). However, Nishida's subdivisions break down when referring to other species of birds such as the duck in which the v. coccygeus empties as a separate branch into the v. pudenda communis. Then there is no common trunk, thus no corresponding v. hypogastrica. It is my belief that it would be best to do away with the term "hypogastrica" in referring to vessels caudal to the arcus hypogastricus to minimize confusion. The basic decision now lies as to whether the v. coccygeus empties into the v. pudenda communis (s. v. hypogastrica) as reported by Neugebauer

(1845) or the v. pudenda communis empties into v. coccygeus as reported by du Toit (1913).

Since the v. pudenda communis is the larger of the two vessels, the v. coccygeus is considered to drain into the v. pudenda interna. These terms can also be employed in describing the vessels in the duck. Here the v. pudenda communis and v. coccygeus empty independently into the arcus hypogastricus.

In addition to these terms, new terms for various rami have been introduced to refer to branches of the a. and v. pudenda interna. These branches were consistently present in the chicken and warrant further differentiation.

The first terms recommended are a. phalli and v. phalli. These vessels supply the phallus, plica lymphatica, corpus paracloacalis vascularis and a portion of the plica proctodealis. The term "penis" is not employed to describe this branch in order to minimize the association of the avian structure with the well-developed intromittent organ in the mammal. The use of the term "phallus" is also an attempt to disassociate the internal structure of blood-filled cavernous tissue associated with the term "penis" from a lymph-filled erectile tissue found in the avian phallus. It is realized that "phallus" is the Greek term and "penis" the Latin term for copulatory organ. The term phallus, however, is not as intimately associated with such a distinct type of organ as the term penis.

The ventral branch of the a. pudenda interna and v. pudenda interna is termed a. and v. pudenda terminalis. This term is recommended as it meets the recommendations of Nomina Anatomica (1968). The term

has informative value by indicating that it is the terminal branch of the pudendal vessels.

The term pudenda terminalis does not indicate the structures relationship to the corpus paracloacalis vascularis but because of its distribution to other structures in this area it is felt that a more general term would be more appropriate than limiting it strictly to the corpus paracloacalis vascularis. Applying the latter rationale when defining the terms "a. phalli" and "v. phalli" would necessitate calling this artery and vein a dorsal branch of the corpus paracloacalis vascularis. The recommended terms therefore are a. phalli and v. phalli and a. pudenda terminalis and v. pudenda terminalis.

The term glomus can be used to refer to the capillary tuft, between the afferent tertiary artery and the efferent tertiary vein. Glomus is a Latin term meaning a ball (Stedman, 1961) and defined as: "(1) a small globular body; (2) a highly organized anastomosis between a small artery and a small vein." This term would apply to the capillary tuft of the corpus paracloacalis vascularis as it consists of a highly organized arterial anastomosis which is drained by a small vein.

The a. and v. pudenda interna give off three major vessels to the cloaca. The a. and v. coprodealis supplies the coprodeum, ureter, ductus deferens and plica lymphatica. The term meets the recommendations of Nomina Anatomica and is employed because its major distribution is to the coprodeum.

The a. proctodealis and v. proctodealis supply the ureter, urodeum, cloacal bursa and laterodorsal wall of the proctodeum. This term meets the requirements of Nomina Anatomica and is employed because its major distribution is to the lateral wall of the proctodeum.

The third artery, the a. uroproctodealis, arises from either the a. pudenda interna or the a. phalli and mainly supplies the ventral part of the urodeum and the lateral wall of the proctodeum. The term meets the recommendations of Nomina Anatomica.

The terminology employed for the nerves accompanying the a. uroproctodealis, a. proctodealis and a. coprodealis is more difficult. The nerve that accompanies the a. pudenda interna and v. pudenda interna is termed "n. pudendus internus" which arises from the plexus pudendus. There is no n. pudendus communis. There is a large n. pudendus externus arising from the plexus pudendus which innervates to the musculature of the pelvic region and tail.

The n. pudendus internus coursing caudally gives off a small n. coprodealis, n. proctodealis, and n. uroproctodeus. These names are the same as used for the arteries and veins that supply the same organs. The n. pudendus internus, like the arteries and veins, forms the n. phalli and the n. pudenda terminalis. The main roots of the nerves course to their respective structures. However, unlike the arteries there are considerable anastomoses on the surface of the corpus paracloacalis vascularis, and the separate identity of the two branches is not as apparent.

The ganglion located on the ventrocaudal surface of the corpus paracloacalis vascularis associated with the n. pudenda terminalis is termed ganglion paracloacalis to show its relation to the cloaca. It is specifically referred to because it is a large ganglion and found consistently next to the corpus paracloacalis vascularis.

The terminology recommended by du Toit (1913) is followed in this work to refer to the pudendal plexus. His terms are the most

satisfactory of the authors reviewed. Thus the plexus is composed of spinal nerves 30, 31, 32, 33, 34, and 35 with 30 being variable. This eliminates overlapping of numbers. Further study needs to be made before recommending a new term to refer to the intestinal nerve of Remak. Certainly the present term does not meet the standards set forth by Nomina Anatomica as it employs an eponym.

The lymphatic system has not had satisfactory terminology applied to the vessels. Table V presents the major vessels draining the reproductive structures. The literature reveals that Dransfield (1944) does not agree with the terminology of Baum (1930), particularly concerning the term ductus thoracici lumbalis. Since there is no "thorax" in the lumbar region, he considers the term artificial. He suggests referring to the vessels according to the arteries with which they correspond. Using his recommendation, I suggest the following terms: vas lymphaticus pudendus communis, vas lymphaticus pudendus internus, and vas lymphaticus pudendus externus. There are no distinct lymphatic vessels caudal to the corpus paracloacalis vascularis; therefore, there are no corresponding lymphatic vessels to the a. pudenda terminalis and v. pudenda terminalis or a. phalli and v. phalli.

The term thoracic duct is so ingrained in the literature that it does not seem feasible to attempt to change the name. In addition it does meet the recommendations of all but recommendation (e); structures closely related topographically shall have similar names. I recommend the term ductus lymphaticus thoracicus. This, in addition to locating the structure, indicates the system it is associated with. Since the major lymphatic duct in the thorax was named according to the region in which it lies, it seems logical to use the same rationale

to name the duct in the lumbar region. Therefore, I recommend the term ductus lymphaticus lumbalis which is a caudal continuation of the ductus lymphaticus thoracicus.

The term corpus paracloacalis vascularis is recommended to refer to the reproductive structure containing the capillary tufts. The earlier term "corpora cavernosa" (Barkow, 1829) is a misleading term as it indicates that the tissue is composed of vascular tissue similar to that found in the penis of mammals. As pointed out this is not the case. Spongy body of the urethra (Lereboullet, 1851) is not an acceptable term for the same reason. The term "Tannenberg'schen Körper" (Eckhard, 1876); Müller, 1908) does not meet the recommendations of the I.A.N.C. that each term should be in Latin, eponyms should not be used, and each term should have informative value. The term "gefässreiche Körper" (Liebe, 1914) and "vascular body" (Nishiyama, 1955) are not Latin terms. Lucas and Stettenheim (1965) recommended the term "glomus paracloacalis." There is some question whether it is a true glomus, but the term does locate the structure in the body of the bird. The term corpus paracloacalis vascularis is recommended. The term locates the structure in relation to the cloaca, presents it in Latin, and indicates its vascularity. Thus, the preferable features of the terms recommended by Lucas and Stettenheim's (1965) and Nishiyama (1955) (after Liebe, 1914) are combined.

DISCUSSION

The anatomy of the previously described structures refutes the concept put forth by Lake (1957) that "erection is brought about by engorgement with blood." Injection of the arterial and venous system reveals that there are no cavernous veins in the phallus of the chicken corresponding to those found in erectile tissue of the penis in mammals. The a. phalli gives rise only to nutrient rami in the phallus and plica lymphatica. The data strongly support the work of Nishiyama (1955) who reported that "in the cock, erection of (the) phallus is caused by means of flowing in of the lymph or a similar fluid; this fluid is generated from the tissue of the vascular body by sexual excitement and flows into the lymph sinuses of the phallus." Thus Nishiyama (1955) realized that the corpus paracloacalis vascularis was a highly vascular structure which produced the lymph fluid. He did not, however, elucidate where the fluid originated within the corpus paracloacalis vascularis. My findings related to the anatomical structure of the corpus paracloacalis vascularis strongly suggest that the fluid originates from the densely packed capillary tufts.

The a. phalli and a. pudenda terminalis and their branches have two major roles, one of providing nutrients to the tissue and one involved in the production of the blood filtrate. In the sexually unstimulated chicken the vessels supplying the corpus paracloacalis vascularis originate at right angles to the a. phalli and a. pudenda

terminalis. This arrangement offers resistance to flow and would allow blood to by-pass the capillary tufts in the corpus paracloacalis vascularis and supply the phallus, plica lymphatica and the musculature and integument of the cloaca.

The secondary, tertiary rami and capillary tufts offer considerable resistance to flow due to their small diameter, thus only small amounts of blood flow through these vessels from the primary rami during periods when the bird is not sexually stimulated.

We can hypothesize that in the sexually unstimulated chicken the arterioles, of the corpus paracloacalis vascularis are under neural control and are constricted, offering resistance to the flow of blood through the capillary beds (Figure 13). Only a small filtration gradient would exist between the capillary wall and the collecting lymph channel. This would allow some filtration across the capillary wall. The lymph fluid would drain into the collecting lymph channels to the vas lymphaticus pudendus internus draining the corpus paracloacalis vascularis. The presence of valves within the lymph vessels in the vas lymphaticus pudendus internus probably prevents retrograde flow. The contraction of the cloacal musculature during the birds daily activity would provide enough movement to force the small amount of fluid into the vas lymphaticus pudendus internus.

During sexual stimulation there is some change in the flow pattern within the corpus paracloacalis vascularis which allows a blood filtrate to be produced (Figure 14). If we hypothesize that during sexual stimulation there is a vasodilation of the arterioles and an increase in arterial pressure to the glomus, the filtration gradient in the capillary tuft would increase tremendously.

As pointed out the corpus paracloacalis vascularis is composed primarily of arteries. The veins on the other hand occupy a rather small portion. If the venules draining the capillary tuft do not dilate or if they constrict there would be even further elevation of the pressure within the capillary tuft. Even if the veins do dilate, they do not appear to be capable of dissipating the increase in pressure.

The collecting channels surrounding the capillary tuft offer little resistance to the flow of the blood filtrate across the capillary wall. Thus a large filtration gradient is established and filterable blood components pass through the capillary wall and into the collecting lymph channels.

As the flow of the blood filtrate continues the lymph channels leading to the phallus and plica lymphatica begin to fill. This continues until erection occurs with the erected phallus and plica lymphatica forming the seminal groove.

As the lymph channels become more and more distended with the blood filtrate, the filtration gradient across the capillary wall is reduced. At the point where erection is complete the filtration gradient would approach zero. There would be some drainage into the vas lymphaticus pudendus internus and perhaps some of the fluid may pass between the columnar epithelial cells of the plica lymphatica into the proctodeum. The trabeculae within the phallus and plica lymphatica would act to prevent any excessive distention of these structures.

The pressure within the lymphatic channels during sexual stimulation is not sufficient to cause the fluid to flow through the epithelial surface of the plica lymphatica in any quantity. The resistance of the columnar epithelium to the passage of the fluid is perhaps as great or

greater than that produced by the inflowing blood in the capillaries. Contraction of the musculature during ejaculation would result in increased pressure exerted on the corpus paracloacalis vascularis and the lymph channels. Since the lymph cannot flow cranially as the vasa lymphaticae pudendae internae are working at maximum capacity during the erection phase, the fluid is forced out between the columnar epithelium of the plica lymphatica. The fluid cannot go through the surface of the phallus as it is covered by stratified squamous epithelium. This erection followed by dilution of the semen during copulation is accomplished.

Erection of the phallus and plica lymphatica is quite rapid due to the production of the lymph by the corpus paracloacalis vascularis. Eckhard (1876) reported collecting 8-10 cc of lymph fluid from the corpus paracloacalis vascularis of the duck in 2-3 minutes. The chicken, with a smaller copulatory organ, would require approximately 1 cc - 2 cc of lymph to fill the lymphatic channels in the phallus, plicae lymphaticae and corpi paracloacalis vascularis. An additional .5 - .75 cc of fluid would be added to semen as a diluent. Thus, a maximum 2.75 cc of fluid would be required for erection of the phallus and dilution of semen. This amount of fluid is far below the production capacity of the corpus paracloacalis vascularis.

The ability of the corpus paracloacalis vascularis to produce proportionately large quantities of fluid results in the rather rapid erection of the phallus and plica lymphatica. This rapid filling of the lymph channels supports the hypothesis that the "shut-off" mechanism for the production of lymph fluid for erection-dilution is a result of a decrease in the filtration gradient across the capillary

wall. Isolation of the corpus paracloacalis vascularis allows the body function at capacity, with no resistance being exerted by back pressure from the fluid in the phallus and plica lymphatica to "shut-off" the production of the lymph fluid. This would account for the large amount of fluid collected by Eckhard (1876).

The nervous system is involved in the erection-dilution mechanism. This was determined by Eckhard (1876) when he stimulated the nerve to the corpus paracloacalis vascularis. The presence of the n. pudendus internus coursing with the artery and vein and dividing to innervate the phallus and plica lymphatica and the presence of the ganglion paracloacalis anatomically supports the physiological findings regarding nervous involvement in the erection-dilution mechanism. In addition, the nerves histologically are associated with the vessels and have free nerve endings in the corpus paracloacalis vascularis indicating that they are involved in vasodilation.

If we relate these findings to the mammal, and this is strictly a hypothesis, the erection-dilution mechanism would appear to be under autonomic control. If we assume that erection is under sympathetic control as is the case of mammals, and ejaculation is under parasympathetic control, we can hypothesize that tonic stimuli from the sympathetic system causes vasodilation of the arteries resulting in increased filtration gradient in the capillary tuft. The parasympathetics, as in mammals, would produce rhythmatic stimuli resulting in contraction of the musculature in forcing the fluid through the columnar epithelium of the plica lymphatica. The presence of the large ganglion paracloacalis at the base of the corpus vascularis paracloacalis indicates that the parasympathetics do play a role in erection-dilution. The sympathetic

ganglia associated with the spinal nerves would also indicate sympathetic involvement. In addition, the observation that there is an erection phase followed by an ejaculation phase during copulation supports the comparison of the control of erection-ejaculation between birds and mammals.

No increase in acid phosphatase nor alkaline phosphatase during ejaculation would indicate simple diffusion across the capillary wall, rather than active transport. This is in keeping with the concept that there is a rapid movement of fluid across the capillary wall caused by a pressure gradient. Since erection and ejaculation can occur rapidly it is thought that active transport of the fluid would require too much time and energy to move this large volume of fluid.

The histochemistry conducted by Lake (1957) on the "vascular body" later referred to as "vascular tissue" was actually done on the plica uroproctodealis of the cloaca and cannot be compared to the corpus paracloacalis vascularis.

Lake (1957) observed the presence of blood in the blood filtrate of the bird after multiple ejaculations, giving the fluid a red tinge. The same phenomena was observed in these experiments. Upon necropsy, we found that the blood did indeed come from the plica uroproctodealis which had several petecheal hemorrhages in its wall. Lake (1957a) assumed this blood was, in some instances, part of the diluting fluid. In all probability what he had observed was blood from the ruptured vessels in the plica uroproctodealis. This perhaps led him to the conclusion that the plica uroproctodealis was the corpus paracloacalis vascularis. The mucosal lining of the entire cloaca is highly vascular and extreme pressure exerted on these structures such as that often

applied in the massage method for collection of semen (Burrows and Quinn, 1935) will result in ruptured vessels. It therefore appears that Lake's (1957a) assumption that blood is a constituent of the normal seminal fluid is invalid.

As in the case with most investigations, new areas of interest are uncovered which warrant further study. This investigation is no exception. From this work new approaches to several systems have been opened; for example, the study of the lymphatic system. Dransfield (1944) mentioned that one of the major problems in studying lymphatics of the birds is the absence of lymph nodes for injection. The phallus provides a route for filling lymphatic vessels. Also injecting the phallus with a compound flow rates through the lymphatic system can be determined. In addition the ability of a compound to pass through a capillary bed can also be determined. This can be accomplished by injection of the material into the arterial or venous system followed by collection and subsequent analysis of the seminal fluid. We now have located and described a capillary bed close to the surface that can be isolated for study with little damage necessary to the bird.

The corpus paracloacalis vascularis is under hormonal control (Nishiyama, 1955) and further hormone studies would be of interest. Perhaps a larger or smaller corpus paracloacalis vascularis would have an influence on fertility. This could have considerable economic value.

Further study on the sympathetic and parasympathetic system and its effect on the erection-dilution mechanism in the bird is needed. The location of the nerves as outlined herein can be utilized to make

transections of the nerves to determine their influence on the erection-dilution mechanism.

Another interesting and economically feasible consideration is the influence the diluting fluid has on frozen semen. The preparation of the diluting fluid can be readily controlled and may remove one of the stumbling blocks in frozen semen preservation.

SUMMARY

The anatomy of the phallus, plica lymphatica and corpus paracloacalis vascularis, the structures involved in the erection-dilution mechanism of the chicken, have been described. Branches of the a. phalli and a. pudenda terminalis supply these structures which in turn were drained by the accompanying veins. In the corpus paracloacalis vascularis branches of a. phalli and a. pudenda terminalis give rise to capillary tufts (glomi). The phallus and plica lymphatica were supplied by the a. phalli. Cavernous tissue corresponding to the erectile tissue of the mammalian penis was not found in the phallus, plica lymphatica or corpus paracloacalis vascularis.

A network of lymph channels originating from around the capillary tuft connected the phallus, plica lymphatica and corpus paracloacalis vascularis. The vas lymphaticus pudendus internus originated from the collecting lymph channels at the cranial end of the corpus paracloacalis vascularis.

The n. phalli and n. pudenda terminalis, branches of the n. pudendus internus, innervated the corpus paracloacalis vascularis. Both sympathetic and parasympathetic nerves were associated with the corpus paracloacalis vascularis. The phallus and plica lymphatica were innervated by the n. phalli.

The n. pudendus internus originated directly from the plexus pudendus. No common pudendal nerve was found.

The anatomy of the structures involved in the erection-dilution mechanism of the domestic fowl suggests strongly that the fluid which provides for the turgidity of the phallus during erection originates from the glomi found in the corpus paracloacalis vascularis and courses through the lymph channels to the phallus and plica lymphatica.

The excess fluid after erection drains into the vas lymphaticus pudendus internus and ultimately back into the general circulation. The erection-dilution mechanism appears to be controlled by the autonomic nervous system.

The corpus paracloacalis vascularis was found to give a positive test for both acid and alkaline phosphatase. No difference between the phosphatase activity in the corpus paracloacalis vascularis of ejaculated and non-ejaculated birds were observed. This result suggests that the fluid crosses the wall of the capillary tuft into the collecting channel by simple diffusion.

Petechial hemorrhages found in the plica uroproctodealis in birds where blood appeared in the ejaculate were caused by excessive pressure when using the massage method of Burrows and Quinn (1935). Blood was not a normal component of seminal fluid.

Terminology has been recommended to refer to anatomical structures which comprise the erection-dilution mechanism. These terms are based on older anatomical works and follow the recommendations of Nomina Anatomica (1965; 1968).

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APPENDICES

APPENDIX I

EMBALMING FLUID

5443 grams KNO_3

3175 grams borax

2268 grams boric acid

327 ml. thymol

118 ml. menthol

30 ml. salicylic acid

30 ml. oil of wintergreen

3000 ml. formalin

189.5 liters H_2O

To each 7.6 liters of solution add 100 cc. cresol and 500 cc. ethylene glycol.

APPENDIX II

CHLORAL HYDRATE SILVER METHOD (NONIDEZ, 1939)B

Fixation: 24 hours or longer (up to 3 days):

Chloral hydrate	25.0 g
50% ethyl alcohol	100.0 ml

Procedure:

1. Wipe off excess fixative and put blocks in:

95% ethyl alcohol	60.0 ml
ammonia, concentrated	4 drops

   Leave for 24 hours, but change at least once, particularly if blocks are large or contain a large amount of fat.

2. Rinse in distilled water: 5 minutes.

3. Place in 2% aqueous silver nitrate (2 g/100 ml water) in dark cupboard or box, 37-40° C: 5-6 days. Replace silver solution after 2 days, or as soon as it becomes brownish in color.

4. Rinse in distilled water: 2-3 minutes.

5. Reduce for 24 hours in:

pyrogallol	2.5-3.0 g
formalin	80 ml
distilled water	100.0 ml

6. Wash in several changes of distilled water: 2-3 hours.

7. Transfer to 50% alcohol, change twice over a period of 24 hours.

8. Dehydrate, clear and embed.

9. Section, mount on slides, deparaffinize, clear and cover.

Results:

Nerve fibers and endings--brown to black.

APPENDIX III

TEST FOR PHOSPHATASE

Standard Coupling Azo Dye
Technique for Acid Phosphatase

Ten mg. of N-Naphthyl phosphate was dissolved in 10 ml of Walpole's Buffer (pH 5.2). To this mixture was added 7.5 mg of polyvinyl pyrralidone and 20 mg. of Fast Garnet GBC salt. The solution was shaken well and filtered over the sections.

Burstone's Method for Alkaline Phosphatase

Ten mg. of Napthol AS-MX® Phosphate was dissolved in 0.25 ml. of dimethyl sulfoxide. To this was added 5 ml of 0.2 M Tris buffer (pH 8.3) and 30 mg. of Red Violet L.B. salt (5-benzamido-4-chloro-o-toluidine).

Burstone's Method for Acid Phosphatase

All the steps were the same except Napthol AS-BI® phosphate was used as the substrate and the buffer was 0.2 M Acetate buffer with a pH of 5.2. Six drops of 10% MnCl were then added with 30 mg. of Fast Violet LB® salt.

FIGURES

Figure 1. Ventral view of the arterial, venous, lymphatic and nervous supply to the corpus paracloacalis vascularis.

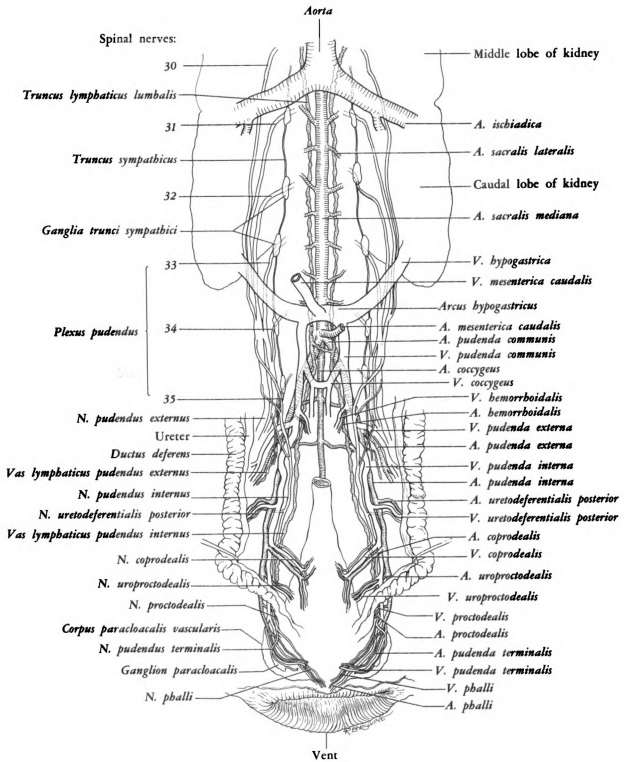

Aorta
Spinal nerves:
30
Truncus lymphaticus lumbalis
31
Truncus sympathicus
32
Ganglia trunci sympathici
33
Plexus pudendus
34
35
N. pudendus externus
Ureter
Ductus deferens
Vas lymphaticus pudendus externus
N. pudendus internus
N. uretodeferentialis posterior
Vas lymphaticus pudendus internus
N. coprodealis
N. uroproctodealis
N. proctodealis
Corpus paracloacalis vascularis
N. pudendus terminalis
Ganglion paracloacalis
N. phalli
Middle lobe of kidney
A. ischiadica
A. sacralis lateralis
Caudal lobe of kidney
A. sacralis mediana
V. hypogastrica
V. mesenterica caudalis
Arcus hypogastricus
A. mesenterica caudalis
A. pudenda communis
V. pudenda communis
A. coccygeus
V. coccygeus
V. hemorrhoidalis
A. hemorrhoidalis
V. pudenda externa
A. pudenda externa
V. pudenda interna
A. pudenda interna
A. uretodeferentialis posterior
V. uretodeferentialis posterior
A. coprodealis
V. coprodealis
A. uroproctodealis
V. uroproctodealis
V. proctodealis
A. proctodealis
A. pudenda terminalis
V. pudenda terminalis
V. phalli
A. phalli
Vent

Figure 2. Lateral view of the musculature related to the corpus paracloacalis vascularis. A section of the m. sphincter cloacae, m. contractor cloacae, m. transversus cloacae, m. dilator cloacae and the wall of the proctodeum has been removed.

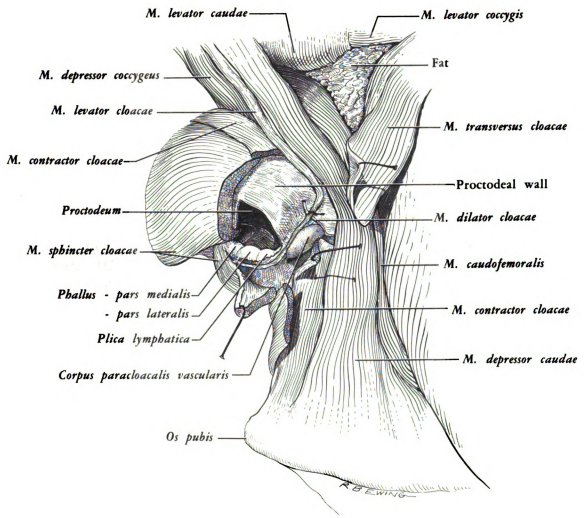

M. levator caudae
M. levator coccygis
Fat
M. depressor coccygeus
M. levator cloacae
M. transversus cloacae
M. contractor cloacae
Proctodeal wall
Proctodeum
M. dilator cloacae
M. sphincter cloacae
M. caudofemoralis
Phallus - pars medialis
- pars lateralis
M. contractor cloacae
Plica lymphatica
M. depressor caudae
Corpus paracloacalis vascularis
Os pubis

Figure 3. Medial view of the vascular and nervous supply to the corpus paracloacalis vascularis. The cloaca was cut in the mid-sagital plane. Incisions were made cranial, caudal and ventral to the urodeum. The urodeum was then displaced dorsally to reveal the arterial, venous, lymphatic and nervous supply to the corpus paracloacalis vascularis. The coprodeum was dissected free from the cloacal musculature and displaced ventrally. An incision was also made at the cranial base of the phallus and plica lymphatica and the floor of the proctodeum was removed to reveal the vascular and nervous supply to the phallus.

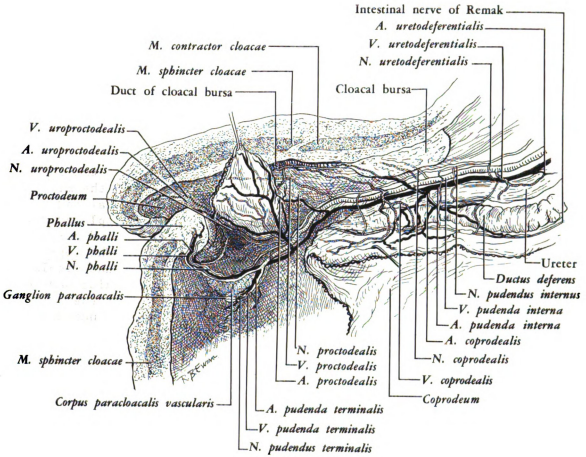

Intestinal nerve of Remak
A. uretodeferentialis
V. uretodeferentialis
N. uretodeferentialis
M. contractor cloacae
M. sphincter cloacae
Duct of cloacal bursa
Cloacal bursa
V. uroproctodealis
A. uroproctodealis
N. uroproctodealis
Proctodeum
Phallus
A. phalli
V. phalli
N. phalli
Ganglion paracloacalis
M. sphincter cloacae
Corpus paracloacalis vascularis
Ureter
Ductus deferens
N. pudendus internus
V. pudenda interna
A. pudenda interna
A. coprodealis
N. coprodealis
V. coprodealis
Coprodeum
N. proctodealis
V. proctodealis
A. proctodealis
A. pudenda terminalis
V. pudenda terminalis
N. pudendus terminalis

Figure 4. Medial view of the vascular supply to the corpus paracloacalis vascularis.

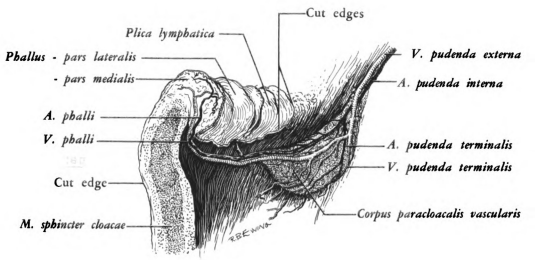

Cut edges
Plica lymphatica
Phallus - pars lateralis
- pars medialis
A. phalli
V. phalli
Cut edge
M. sphincter cloacae
V. pudenda externa
A. pudenda interna
A. pudenda terminalis
V. pudenda terminalis
Corpus paracloacalis vascularis

Figure 5. Detailed illustration of medial surface of the corpus paracloacalis vascularis illustrating the vascular supply. The major portion of the connective tissue capsule has been removed.

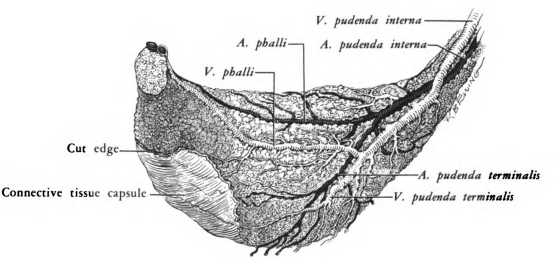

V. pudenda interna
A. phalli
A. pudenda interna
V. phalli
Cut edge
A. pudenda terminalis
Connective tissue capsule
V. pudenda terminalis

Figure 6. Diagram of the arterial supply and venous drainage of the glomi found in the corpus paracloacalis vascularis.

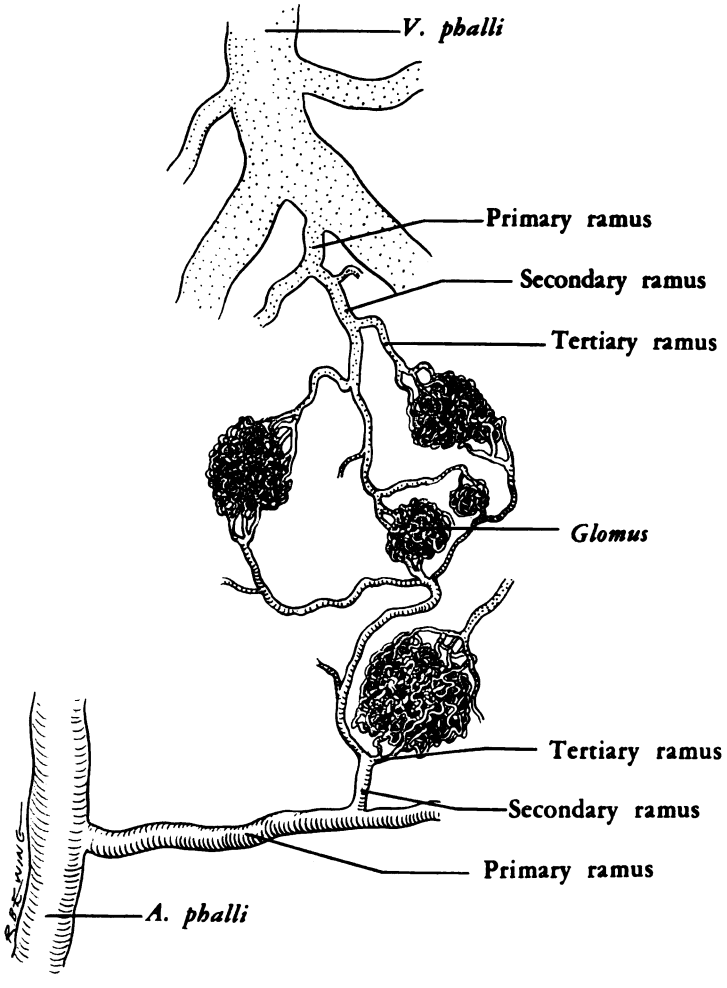
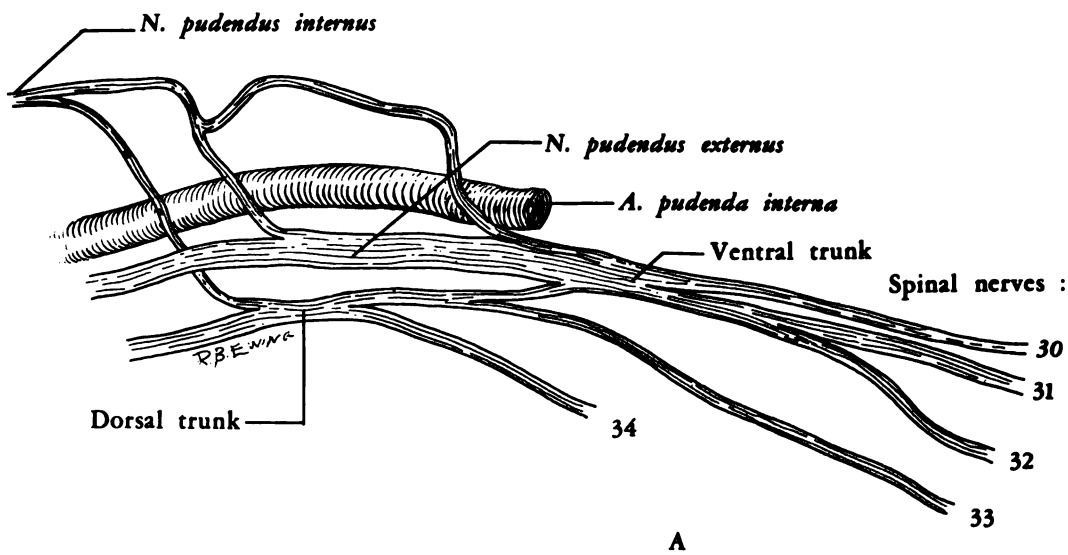
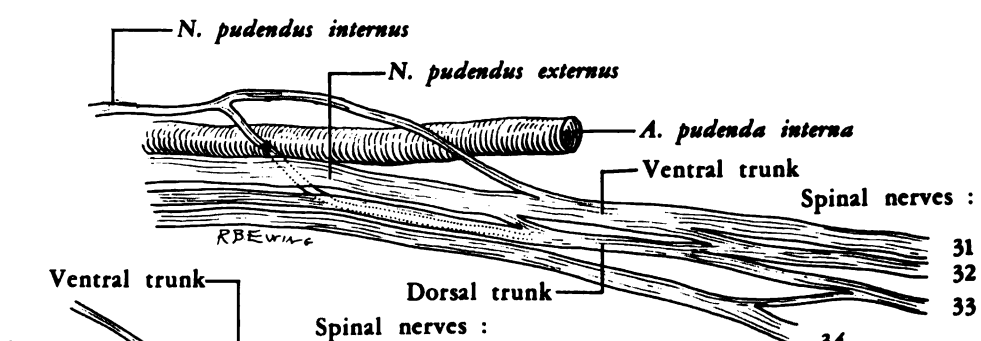

V. phalli
Primary ramus
Secondary ramus
Tertiary ramus
Glomus
Tertiary ramus
Secondary ramus
Primary ramus
A. phalli

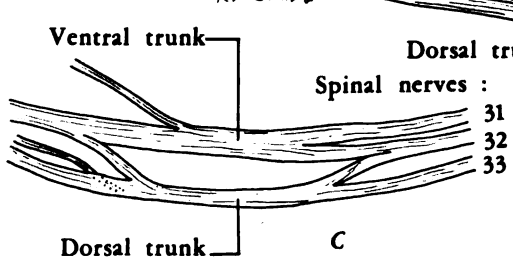
Figure 7. Diagram of variations found in the formation of the plexus pudendus.
A. Spinal nerve 30 is included in formation of the plexus.
B. Spinal nerve 30 is not included in formation of the plexus.
C. More dissected view of dorsal and ventral trunks of the plexus pudendus.


N. pudendus internus
N. pudendus externus
A. pudenda interna
Ventral trunk
Spinal nerves :
30
31
32
33
34
Dorsal trunk
RBEWING

A


N. pudendus internus
N. pudendus externus
A. pudenda interna
Ventral trunk
Spinal nerves :
31
32
33
34
Dorsal trunk
RBEWING

B


Ventral trunk
Spinal nerves :
31
32
33
Dorsal trunk

C

Figure 8. Medial view of the corpus paracloacalis vascularis illustrating the nerve supply.

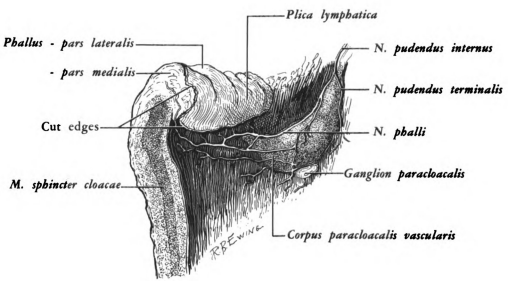

Plica lymphatica
Phallus - pars lateralis
- pars medialis
Cut edges
M. sphincter cloacae
N. pudendus internus
N. pudendus terminalis
N. phalli
Ganglion paracloacalis
Corpus paracloacalis vascularis
R.R.E.WING

Figure 9. Relationship of nerve fibers to endothelial cells within the corpus paracloacalis vascularis.

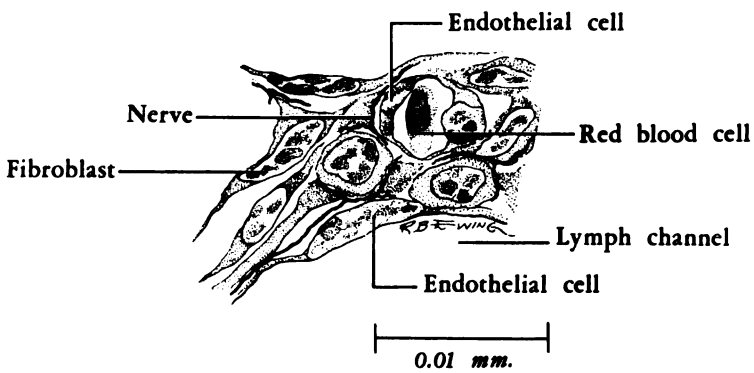

Endothelial cell
Nerve
Red blood cell
Fibroblast
Lymph channel
Endothelial cell
0.01 mm.

Figure 10. **Lateral view of the corpus paracloacalis vascularis and the collecting lymph vessels.**

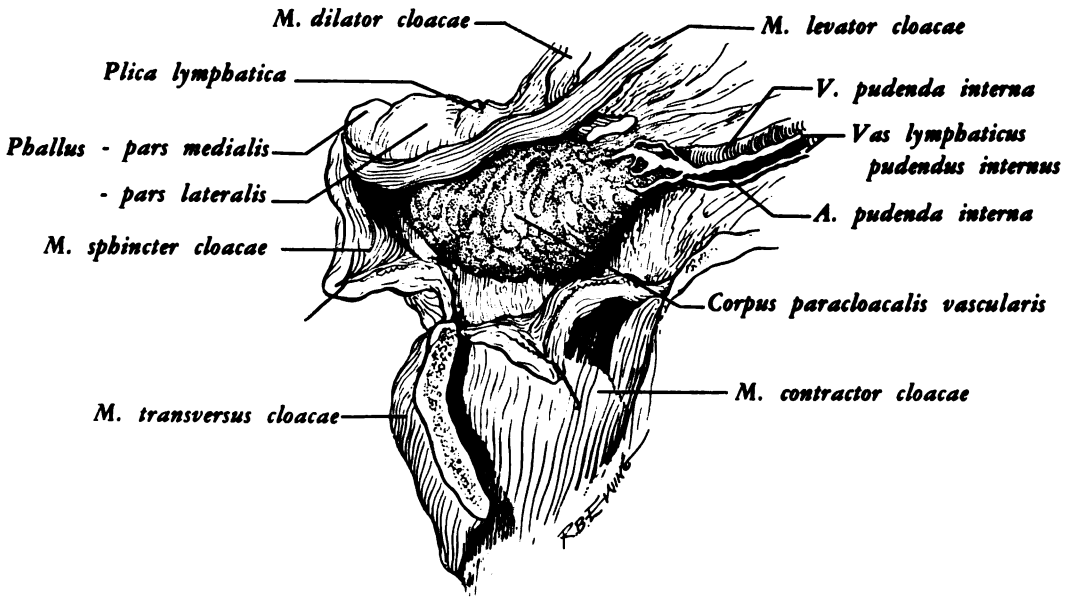

M. dilator cloacae
M. levator cloacae
Plica lymphatica
V. pudenda interna
Vas lymphaticus pudendus internus
Phallus - pars medialis
- pars lateralis
A. pudenda interna
M. sphincter cloacae
Corpus paracloacalis vascularis
M. contractor cloacae
M. transversus cloacae

Figure 11. Lateral view of the lymphatic vessels draining the corpus paracloacalis vascularis.

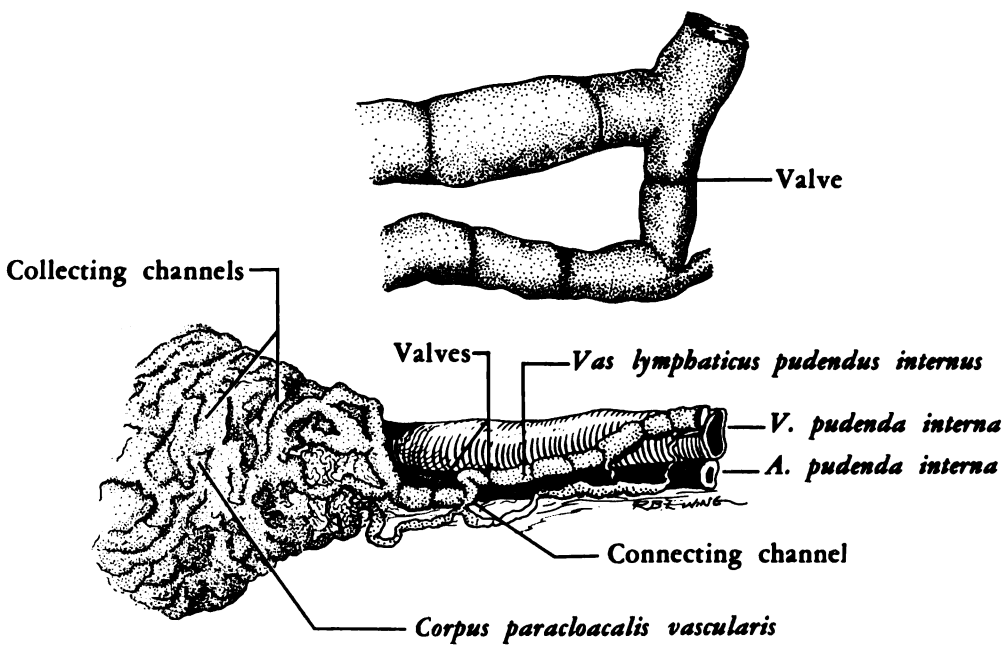

Valve
Collecting channels
Valves
Vas lymphaticus pudendus internus
V. pudenda interna
A. pudenda interna
Connecting channel
Corpus paracloacalis vascularis

Figure 12. Three dimensional drawing of corpus paracloacalis vascularis revealing the pattern of lymph channels within the structure.

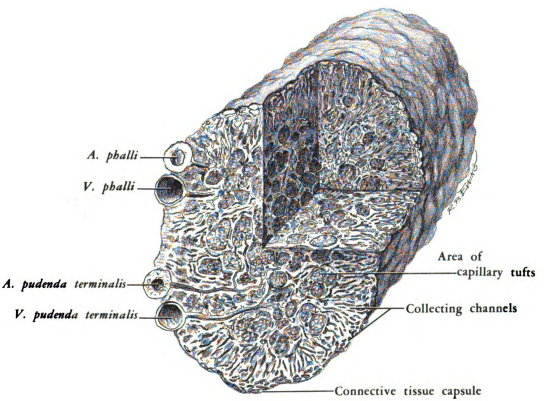

A. phalli
V. phalli
A. pudenda terminalis
V. pudenda terminalis
Area of capillary tufts
Collecting channels
Connective tissue capsule

Figure 13. Hypothetical schema of the production of lymph in a sexually unstimulated chicken.

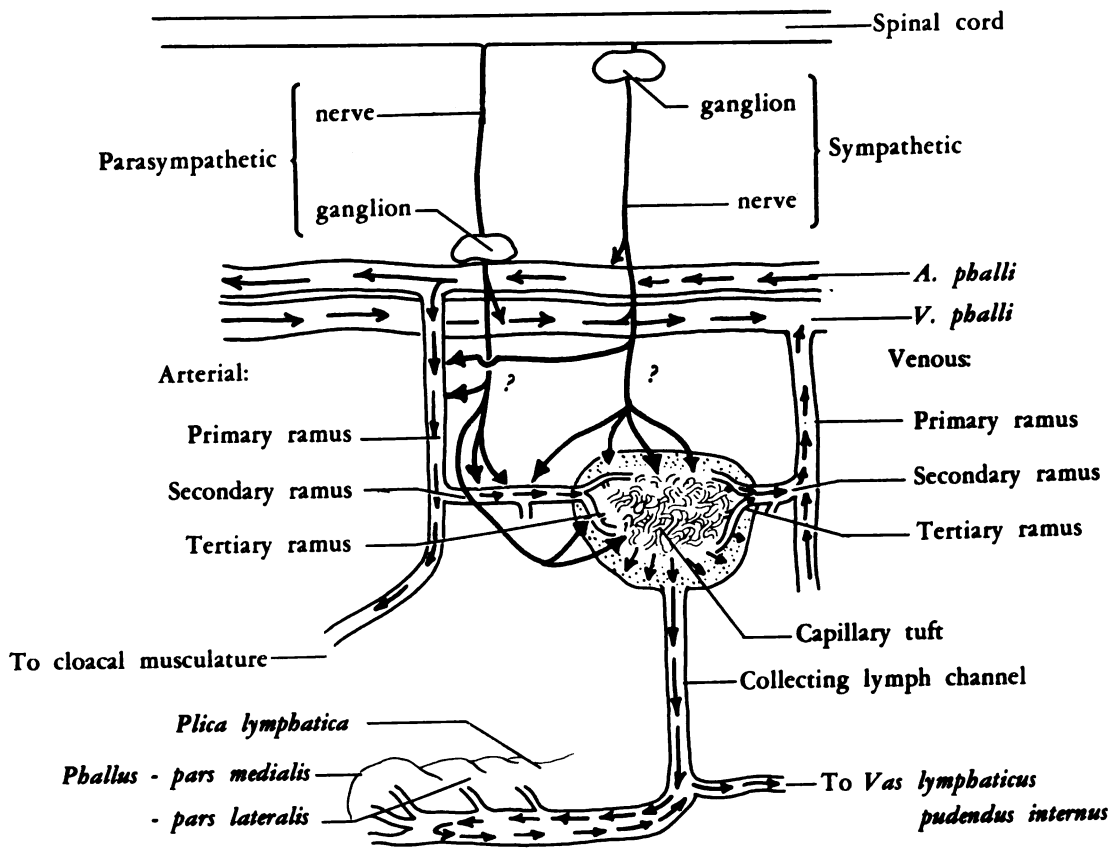
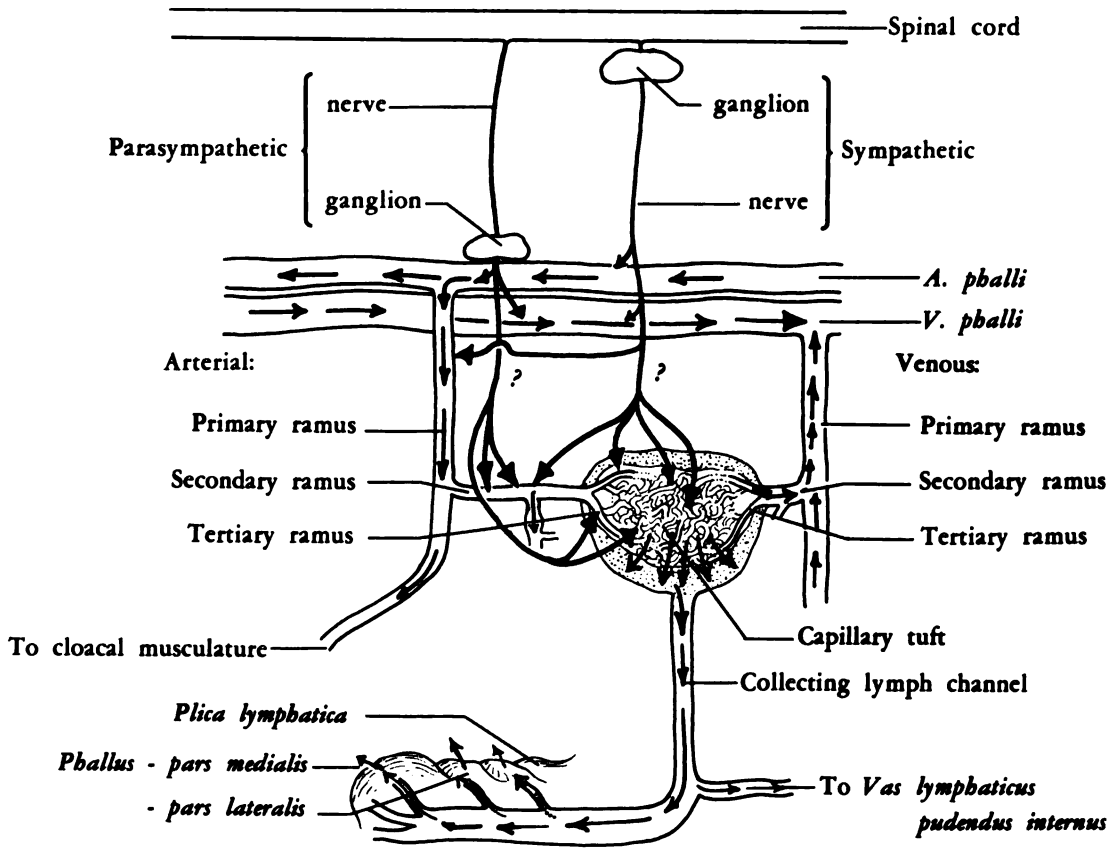

Spinal cord
nerve
ganglion
Parasympathetic
Sympathetic
ganglion
nerve
A. phalli
V. phalli
Arterial:
Venous:
?
?
Primary ramus
Secondary ramus
Tertiary ramus
Primary ramus
Secondary ramus
Tertiary ramus
Capillary tuft
To cloacal musculature
Collecting lymph channel
Plica lymphatica
Phallus - pars medialis
- pars lateralis
To Vas lymphaticus pudendus internus

Figure 14. Hypothetical schema of the production of lymph in a sexually stimulated chicken.


Spinal cord
Parasympathetic
nerve
ganglion
ganglion
nerve
Sympathetic
A. phalli
V. phalli
Arterial:
Venous:
?
?
Primary ramus
Secondary ramus
Tertiary ramus
Primary ramus
Secondary ramus
Tertiary ramus
To cloacal musculature
Capillary tuft
Collecting lymph channel
Plica lymphatica
Phallus - pars medialis
- pars lateralis
To Vas lymphaticus pudendus internus