

Resumen por el autor, Alden B. Dawson.

La topografía de la cloaca del macho de *Necturus* en relación con las glándulas cloacales.

El orificio externo de la cloaca del macho de *Necturus* es una hendidura longitudinal franjeada por dos labios poco desarrollados los cuales en su extremo caudal llevan un par de papilas blandas. Los labios están más modificados a consecuencia de la presencia de numerosas fisuras transversas. En posición inmediatamente dorsal al orificio cloacal está la cámara cloacal o vestíbulo que se continúa cranialmente en el tubo cloacal. El piso de este último tiene forma de artesa honda, con la mucosa surcada por crestas delgadas y paralelas las cuales se interrumpen caudalmente convergiendo en las papilas altas y delgadas presentes a los lados de la cámara cloacal. El techo está modificado también por la presencia de un surco medio profundo y a cada lado del tubo cloacal, entre esta depresión dorsal y la ventral, existen dos surcos longitudinales.

La cavidad cloacal está por completo rodeada por masas de glándulas tubulares largas y tortuosas. La gran masa media ventral se conoce con el nombre de glándula cloacal. Sus túbulos se abren en las cimas de las crestas paralelas y en los ápices de las papilas delgadas internas. Dos masas de túbulos, las glándulas abdominales pares, están situadas ventrolateralmente a la cámara cloacal y sus túbulos desembocan en la superficie media de las papilas externas pares. Dorsalmente existe una masa glandular media, la glándula media. Esta glándula presenta por lo menos cuatro diferenciaciones, que se distinguen histológicamente por el carácter del epitelio que tapiza sus túbulos. Existe una pequeña masa media cranial, una masa media caudal muy grande y dos masas laterales. Todos los túbulos de la masa de la glándula pélvica se abren en el techo del tubo cloacal. El autor considera un método posible de formación de un espermátóforo.

THE CLOACA AND CLOACAL GLANDS OF THE MALE NECTURUS

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THREE PLATES (SIXTEEN FIGURES)

INTRODUCTION

At present the mating habits of *Necturus* are not definitely known. Strong circumstantial evidence indicates (Kingsbury, '95) that fertilization is accomplished by the deposition of spermatophores and the reception of the spermatozoa which are borne upon the summits of the deposited spermatophores into the cloaca of the female. The time and the exact manner of insemination are not known. An abundance of spermatozoa was found by Kingsbury ('95) in the spermathecae of six females which he examined during the late fall and winter. Females examined by the writer in October and March were found also to have large numbers of sperms in their spermathecae. According to Smith ('11), fertilized eggs are deposited chiefly during May and June.

Although our information on the time and manner of fertilization is still incomplete, it seems highly probable that spermatophores are produced by the male *Necturus*. The matrix of the spermatophores is probably a product of the cloacal wall acting in conjunction with the surrounding masses of tubular glands. The degree of glandular activity in this region should furnish therefore some clue as to the probable time of spermatophore deposition. With this in mind, a study of the cloaca was undertaken. Owing, however, to the complexity of the internal configuration of the cloaca, the complicated relations of the cloacal wall to the tubules of the surrounding gland masses, and the many varying types of tubules encountered, the comparative study of the glandular activity at different times of the year had

to be postponed until the limits of the different masses of glands had been definitely determined. Accordingly, the present report deals primarily with the various masses of tubular glands in their relation to one another and to the topography of the cloaca. In a later communication it is planned to describe the variations which occur in the glands during the different seasons of the year and to follow the changes undergone by the several types of cells during the production of secretion.

Only adult males were used in this study. The material was dissected out and fixed in either formalin, Zenker's fluid, or Bouin's fluid. Serial sections, transverse and longitudinal, were made of the entire cloacal mass, including the cloaca proper and the surrounding glands. The tissue was stained with haematoxylin and eosin, Van Gieson's picro-acid fuchsin and Mallory's stain for connective tissue.

LITERATURE

We are indebted to Heidenhain ('90) for the first detailed and accurate description of the cloaca of a male urodele. He described three kinds of cloacal glands in the male Triton, the so-called cloacal gland, the pelvic gland, and the abdominal gland. Before this but two types of glands were recognized. Zur Mühlen ('93), who worked on Triton, Salamandra, and Siredon, confirmed in the main the findings of Heidenhain. Kingsbury ('95), in the course of an extended study of the cloacas of female *Diemyctylus*, *Plethodon*, *Desmognathus*, *Amblystoma*, and *Necturus*, discussed, incidentally for purposes of comparison, the structure of the cloacas and the adjacent glands of the males of these different genera. In *Necturus*, Kingsbury did not make a sufficiently careful study of the glands to enable him to determine whether the abdominal gland is present.

EXTERNAL APPEARANCE OF THE CLOACA

The external opening of the cloaca of the male *Necturus* is simply a longitudinal slit bordered by two inconspicuous lips which, at their caudal ends, give rise to a pair of low rounded papillae (fig. 1, *ext.p.*). The lips are modified further by

numerous transverse fissures and, immediately caudad to the paired external papillae, there is a distinct transverse crescentic groove. A ventral enlargement extending laterally along the cloacal slit and cranially toward the region of the pelvic girdle marks the extent of the large cloacal gland.

INTERNAL TOPOGRAPHY OF THE CLOACAL CAVITY

For purposes of description, the cavity of the cloaca may be considered as consisting of two portions, an enlarged caudal chamber or vestibule opening ventrally to the exterior by way of the cloacal slit and a narrower cephalic, tubular portion connecting the cloacal chamber with the rectum (figs. 4, 5, *cl.ch.*, *cl.t.*).

The internal configuration of the cloaca is decidedly complex, but in an undistended condition the cavity exhibits a very definite and constant form. The various depressions, folds, papillae, etc., which go to produce the complicated pattern of the cavity serve therefore as landmarks of the different regions into which the tubular glands discharge their secretion.

Before entering upon the more detailed description of the several regions of the cloaca, brief mention will be made of the most conspicuous modifications of the cloacal wall. The ventral side of the cloacal tube has the form of a deep, narrow trough, the mucosa of which is thrown into high, thin ridges (figs. 4, 5, 12, 13, 14, *v.tr.*, *v.r.*). Caudally, in the region of the cloacal chamber, the ventral ridges are interrupted and merge into tall, slender papillae (figs. 4, 5, 15, *int.pp.*). Dorsally the cloacal tube contains a deep median groove (figs. 4, 5, 13, 14, *md.gr.*) and on its sides between the dorsal groove and the ventral trough are two well-defined longitudinal furrows (fig. 13, *lt.fur.*).

The cephalic end of the cloacal tube presents the simplest condition, and the transition from rectum to cloaca occurs without any very evident change in structure. The urogenital ducts open dorsolaterally into the extreme cephalic end of the tube. They terminate separately in a pair of prominent papillae which project ventrally from the bottoms of two pit-like depressions (figs. 4, 5, 7, *ug.p.*). The urinary bladder opens

medially into the ventral side of the cloaca, almost opposite the more dorsal urogenital papillae (figs. 4, 5, 8, *ur.bl.o.*).

Caudad to the orifice of the urinary bladder a prominent longitudinal fold projects from the midventral wall, and on either side of it other smaller irregular folds can be distinguished (fig. 5, *mv.f.*, *v.f.*). The main fold continues caudally for a short distance as a single fold, but soon becomes doubled and is eventually broken up into the thin ridges which cover the walls of the ventral trough (figs. 5, 9, 10, *v.tr.*, *v.r.*). Laterally the wall of the cloacal tube is also modified by two low folds which extend, on either side, from the regions of the urogenital papillae caudally to the cephalic ends of the longitudinal lateral furrows, with whose dorsal walls they merge (figs. 4, 9, *lt.f.*). Furthermore, when the cavity of the cloaca is laid open by a longitudinal ventral incision so that the dorsal portion of the cloacal tube is exposed, the lateral folds, with the aid of the median dorsal groove and lateral furrows, are seen to mark off a Y-shaped area, the stem of which extends cephalad toward the region of the urogenital papillae (fig. 4, *Y*).

Another striking feature of the cephalic portion of the cloacal tube is the presence of large numbers of melanophores in the underlying connective tissue. No other portion of the cloacal cavity exhibits a like pigmentation, although a few scattered melanophores can occasionally be seen in other regions.

The ventral trough, longitudinal lateral folds, and median dorsal groove already referred to, are found in the more caudal portion of the cloacal tube. The ridges of the ventral trough are relatively high and thin. They run almost parallel, but diverge slightly as they approach the cloacal chamber. The number of ridges present is quite constant, the average being thirty-two, although thirty-four ridges can occasionally be counted (figs. 13, 14, *v.r.*). The longitudinal lateral furrows and median dorsal groove do not exhibit any conspicuous modifications and, gradually growing shallower as they pass caudally, are eventually obliterated in the region of the cloacal chamber.

The cloacal chamber itself is relatively simple in form, two rather deep ventrolateral recesses being the only modifications of interest in this study (figs. 4, 5, 15, *vl.rec.*). The long, slender papillae, found on the floor and ventral portions of the walls of the chamber, are also present in the ventrolateral recesses. The papillae in the recesses, however, are usually short. Both the internal papillae and the ventral ridges are highly vascular, being permeated by blood channels of considerable size.

THE WALL OF THE CLOACA

The wall of the cloaca, especially in its cephalic portion, closely resembles that of the rectum. Mucous and muscular layers are readily recognized (figs. 7, 8). No serous coat, however, is present, but the outermost layer consists of areolar tissue which blends with the connective tissue of the adjacent structures. The presence of large numbers of long tubular glands, which surround and open into the cloacal cavity, has resulted in a great thickening and extensive modification of practically the entire cloacal wall and of the three coats comprising it, but the tunica muscularis has suffered the greatest displacement.

a. The tubular glands

The grouping of great numbers of tubular glands in the cloacal wall has resulted in the production of a large glandular mass about the cloaca, which, for the lack of a better term, will be designated as the cloacal gland mass. This mass lies caudad to the pelvic girdle and occupies a large median ventral area. It is enclosed in a connective-tissue sheath which apparently is a modified portion of the median ventral septum which more caudally separates the hypaxial muscles of the tail (fig. 3, *m.v.s.*).

The dorsal portion of the mass extends close to the trunk-tail vertebrae and laterally is bounded in part by the unmodified trunk-tail myotomes and in part by three pairs of slender caudal muscles (mm. ischiocaudalis, caudalifemoralis, and caudalipuboischiotibialis, Wilder, '12) which are attached to the posterior appendicular skeleton (fig. 2). Cranially, the dorsal gland mass extends to the posterior ends of the mesonephroi and to the caudal

margin of the pelvic girdle. Dorsocaudally, the common sheaths of the three pairs of caudal muscles and the unmodified median ventral septum limit the mass.

The ventral portion of the gland mass is continued into the loose subcutaneous connective tissue, extending laterally beyond the median area bounded by the hypaxial muscles and, cephalically, to cover the surface of the caudal portion of the pelvic girdle.

In the cloacal mass of the urodeles studied (Heidenhain, '90; Zur Mühlen, '93; Kingsbury, '95) at least three distinct types of tubule have been recognized. They are arranged in definite groups and are known as the cloacal, pelvic, and abdominal glands, respectively. In *Necturus* both the cloacal and pelvic glands are greatly developed. The homolog of the abdominal gland can also be recognized, but it is relatively small and separated into two compact lateral masses (figs. 2, 3, 16, *abd.gl.*).

The cloacal-gland tubules form the large median ventral portion of the cloacal mass (figs. 11 to 15, *cl.gl.*). The tubules are long and straight. They extend in a cranial direction and end blindly. The mouths of the tubules open both on the summits of the thin ridges covering the ventral trough of the cloacal tube, and on the tips of the slender internal papillae which fringe the cloacal chamber. On the ridges the tubules terminate in low conical elevations which are arranged longitudinally to form two parallel rows. The terminal elevations which compose these double rows on each ridge are not placed opposite to each other, but have a regular alternating arrangement. The tubules which are connected with the internal papillae also exhibit a regular arrangement, usually two and occasionally three opening together at the tip of each papilla.

The large group of tubules comprising the dorsal portion of the cloacal mass has been designated as the pelvic gland. They are sharply separated from the ventral cloacal tubules by two lateral connective-tissue septa (fig. 2, *c.t.s.*). The pelvic-gland tubules, in contrast with the relatively straight cloacal tubules, are distinctly convoluted. They extend dorsocranially,

do not branch, and end blindly. In fresh material they appear opaque, while tubules of the cloacal gland usually appear clear. The difference in appearance is due to the different character of the secretion in their lumina.

All of the tubules of the pelvic gland open into the dorsal portion of the cloacal tube. They are arranged in four groups: a small cephalic medial group of short tubules (fig. 10, *plv.gl.*"); further caudad, two symmetrical, lateral groups of somewhat longer tubules (figs. 11, 12, *plv.gl.*'''), and a very large median caudal group of long, greatly convoluted tubules (figs. 11, 12, 13, 14, *plv.gl.*'). The caudal portion constitutes the greater part of the pelvic gland. The tubules which form the lateral differentiations of the pelvic gland are comparatively few in number. They are distributed cephalocaudally on either side of the cloacal tube and lie close to the lateral septa (*c.t.s.*) which separate the main mass of the pelvic gland from the more ventral cloacal gland.

The different groups of pelvic tubules are not distinctly separated from one another in any portion of the gland, but are distinguished by the character of their glandular epithelium. Owing to the great variety of secretory phases exhibited by the different tubules, it is not always easy to determine with certainty whether the tubules under consideration are of an entirely different character or are merely different phases of activity of the same kind of tubule. It is with some hesitation, therefore, that I have distinguished a median cephalic group, since cephalad to the main mass of the caudal division of the pelvic gland the tubules of its lateral differentiations approach the middorsal line, and in serial sections are seen to be intermingled with the more caudal tubules of the cephalic group. However, so far as my histological study has progressed at this time, there appears to be good evidence that the tubules of the groups under discussion, although intermingled where they come in contact, possess secreting cells of two distinct types. The tubules of the median caudal division, on the other hand, can be readily recognized at all times.

All pelvic tubules terminate in low papillae. At the bases of these papillae shallow circular depressions are usually observed recalling the structure of the circumvallate papillae of the tongue. In some regions papillae are indistinct and only barely recognizable. The tubules of the large median caudal division, for the most part, open upon the walls of the median dorsal groove (figs. 13, 14, 15). The more cranial tubules of the lateral pelvic differentiations open on the dorsal walls of the so-called longitudinal furrows (figs. 12, 13), while the most caudal ones are found to open upon a middorsal region, the caudal end of the stem of the Y-shaped area previously described (figs. 11, 12). The short tubules of the median cephalic group terminate on the middorsal region which forms the cranial portion of the stem of the Y-shaped area (fig. 10).

In comparison with the cloacal and pelvic glands, the abdominal gland in *Necturus* appears almost vestigial. It is divided into two masses which lie near the caudal end of the cloacal orifice and dorsolaterally to the paired external papillae (figs. 2, 3, *abd.gl.*). The tubules which compose this gland are short and greatly convoluted and possess a characteristic epithelium which distinguishes them definitely from the other tubules of the cloacal mass (fig. 16). They open mainly on the medial surfaces of the external papillae, but a few are also found to open along the inner margins of the cloacal lips.

b. Muscular layers and dorsal ganglion

The muscular coat consists of two layers of smooth muscle which, in the extreme cephalic portion of the cloacal tube, are sharply differentiated into an inner circular and an outer longitudinal layer (figs. 7, 8). Further caudad, however, this definite arrangement is more or less disturbed by the presence of a large, dorsal, ganglionated plexus and the numerous tubular glands.

The dorsal ganglion represents a local enlargement of a portion of the sympathetic nervous system, being apparently a caudal continuation of the myenteric plexus of the intestinal tube (figs. 9, 10). From the ganglion small bundles of nerve fibers pass caudally to the various cloacal glands.

Heidenhain ('90) observed a like mass of nerve tissue occupying a somewhat similar position in the male Triton and, according to him, it is found only in the males. He was in doubt as to the function of the ganglion, but interpreted it as being a terminal enlargement of the ganglionated plexus associated with the kidneys, and suggested that it might be a portion of the adrenal system which is more or less diffuse in urodeles. "Wo hin diese Ganglienmassen zu rechnen sind (Nebenniere?), ist mir unbekannt" (p. 190). In some specimens of *Necturus* I have found scattered cells which exhibit a specific affinity for chromium.

The tubular glands extend deep into the cloacal wall, of which, as has been already stated, they form the most conspicuous part. In the dorsal portion of the wall the tubules of the pelvic gland obliterate the sharp differentiation of the muscularis into two layers, and the muscle fibers are irregularly arranged and interwoven, forming with the intermingled connective tissue a dense fibromuscular stroma in which the secreting tubules are imbedded. Some of the muscle cells of the stroma, however, are arranged circularly about the numerous tubules to form delicate muscular tunics.

The tubules of the cloacal gland, on the other hand, while as large and closely packed as those of the pelvic gland, do not produce such a decided rearrangement of muscle fibers, so that, in the ventral portion of the cloacal wall, a circular as well as a longitudinal layer can usually be distinguished. The tubules pierce only the circular muscle layer and are imbedded in a fibromuscular stroma similar to that described for the pelvic gland. Each tubule is also surrounded by a delicate layer of circularly arranged muscle cells. The ventral portion of the longitudinal coat of muscle fibers is not invaded by the cloacal tubules, but persists as a compact layer, arranged as a flat sheet to cover the ventral or external surface of the cloacal gland (figs. 11, 12, 13, 14). In the region of the cloacal chamber the definite arrangement of the smooth muscle into layers is gradually lost and the fibers are mingled with the connective tissue of the cloacal wall.

c. Epithelium of cloaca

The epithelium lining the cloaca of the male *Necturus* is not simple in any region. In the cephalic portion it is two-layered, consisting of a superficial columnar or cuboidal layer and a deep somewhat flattened replacing layer. In certain areas the outer layer of cells is ciliated; in others, the outer cells are of the tall mucous type, and in still others, they are unmodified. More caudad the number of cell layers is gradually increased until at the margins of the cloacal aperture a stratified epithelium similar to that of the external surface of the body is found. No Leydig cells, however, are present within the cloaca, although they occur in considerable numbers in the epidermis a short distance from the cloacal orifice.

Dorsally, in the region of the paired urogenital papillae, a small ciliated area is found. More cephalad, toward the rectum, the epithelium is non-ciliated and of the mucous type. Caudad, on the portions of the dorsal wall through which the pelvic tubules open, i.e., on the Y-shaped area, the median dorsal groove and the dorsal walls of the lateral furrows, the superficial cells, for the most part, are unmodified, resembling in their staining reactions the cells which in other areas possess cilia. Locally, however, groups of tall clear cells, typically mucous in appearance, are found. It seems possible, therefore, that the unmodified cells may be young or rejuvenating mucous cells.

Ventrally, in the region of the orifice of the urinary bladder, the cloacal wall is covered by a mucous epithelium, but more caudad ciliated cells are found, chiefly along the summits of the longitudinal folds. Also scattered patches of ciliated epithelium link up the ventral ciliated portions with the dorsal ciliated area. The high, thin ridges of the ventral trough are for the most part covered with a two-layered ciliated epithelium, but the conical elevations, on which the cloacal tubules terminate, have a mucous epithelium. The transition from one type of epithelium to the other is abrupt.

The slender internal papillae, through which the cloacal tubules open, with the exceptions of small areas at their bases, do

not have a ciliated epithelium. The more cephalic papillae are covered by a two-layered mucous epithelium, while those nearer the external aperture have a stratified epithelium of three to four layers similar to that covering the unmodified wall of the cloacal chamber and the cloacal lips.

DISCUSSION

In *Necturus*, spermatozoa are regularly found within the cloaca of the female. The transfer of spermatozoa from the body of the male to that of the female is supposedly accomplished by means of spermatophores. In *Cryptobranchus*, however, fertilization is external and the sperms are expelled into the water without the formation of spermatophores (Smith, '07). In *Diemyctylus* (Jordan, '01) and *Amblystoma* (Wright and Allen, '09) spermatophores are deposited and the female by her own activity must ensure the entrance of the spermatozoa into her cloaca. In the Tritons and in *Desmognathus* (Wilder, '13) the transfer of the spermatophore is accomplished by a venter to venter copulation.

Just what rôle the greatly developed cloacal glands of the male *Necturus* play in the mingling of the sexual products it is difficult to say. The success of the spermatophore method depends largely on the proximity of the female. In some urodeles specialized integumental glands are believed to attract the opposite sex. No such glands have been found in the integument of *Necturus* (Dawson, '20). Some of the cloacal glands, accordingly, may perform this function. The abdominal glands, on account of their superficial position, would not apparently enter into the spermatophore formation. They may, therefore, liberate chemicals which diffuse through the water and attract the female or, if the spermatophores are transferred directly to the female by a venter to venter copulation, these glands, together with the external papillae on whose median surfaces they open, may assist in overcoming the difficulties involved in sperm transfer in the water, the external papillae forming a kind of intromittent organ.

The configuration of the cavity of the cloaca, the arrangement of the glands and the positions of the ciliated areas make the theory of spermatophore formation in *Necturus* seem plausible and tend to stimulate speculation. The mucous secretion of the cloacal gland when liberated into the ventral trough would be gradually moved caudally by the cilia on the ridges and would eventually collect in the cloacal chamber and the ventrolateral recesses projecting from it. In this position the mass of mucous material would probably be increased by additional secretion from the cloacal tubules which terminate on the internal papillae. Dorsolaterally in the cloacal tube, the ripe sperm would be expelled from the urogenital ducts and the median dorsal ciliated area would carry them back until they became mingled, first, with the secretion of the median cephalic portion of the pelvic gland and later with the secretions of the lateral and caudal portions of this same gland. By this time the sperms would be in the dorsal groove and far enough caudad to be caught up by the moving mass of mucous secretion which is propelled caudad by the cilia of the ventral ridges. In this manner a spermatophore, having as a base a mass of mucous secretion and bearing on its dorsal surface spermatozoa mingled with secretion from the pelvic gland tubules, might be formed. The final solution of this problem must await direct observation in the field.

Early writers attempted to homologize the cloacal glands of urodeles with the prostate and bulbo-urethral glands of the higher mammals. Any such homology has been denied by Heidenhain ('90) and Kingsbury ('95). In attempting to discover homologies it seems unwise to begin with what are obviously specializations of some more simple arrangement, and the prostate and bulbo-urethral glands doubtless represent such specialization. A more primitive condition is seen in both monotremes and marsupials, in which urethral glands, tubular glands occurring in the wall of the urogenital canal, are abundant. In monotremes there is a common cloaca with a primitive penis projecting slightly from its ventral wall. From this simple organ it is believed the typical penis of mammals has been derived and it is also regarded as homologous with the intromittent organ of

turtles and crocodiles which develops from the ventral wall of the cloaca. The cloaca of urodeles is doubtless homologous with the cloaca of both reptiles and mammals, and from the ventral portion of this the special organ of copulation has been evolved. The cloacal glands of urodeles and the urethral glands of monotremes and marsupials perform the same function, i.e., furnish a fluid or semifluid vehicle for the spermatozoa, but this similarity of function is not sufficient to establish the homology, since we have many instances of similar structures performing the same function in different groups of vertebrates, but they are not homologous. However, even if the homology between the cloacal glands of urodeles and the urethral glands of lower mammals cannot be established, it is at least interesting to note that in such widely separated groups of vertebrates the same type of gland has been evolved in a similar position to serve apparently similar needs.

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DESCRIPTION OF PLATES

ABBREVIATIONS

<i>abd.gl.</i> , abdominal gland	<i>m. capit.</i> , muscle caudalipuboischio-
<i>c. mu.</i> , circular muscle layer	tibialis, impression of
<i>cl. ap.</i> , cloacal aperture	<i>masc.</i> , muscle ischiocaudalis, im-
<i>cl. ch.</i> , cloacal chamber	pression of
<i>cl. gl.</i> , cloacal gland	<i>pl.gl.'</i> pelvic gland, median caudal
<i>cl.gl.a.</i> , cloacal gland, area of	division
<i>cl.lp.</i> , cloacal lip	<i>pl.gl.''</i> , pelvic gland, median cranial
<i>cl.lp.f.</i> , cloacal lip, fissures of	division
<i>cl. t.</i> , cloacal tube	<i>pl.gl.'''</i> , pelvic gland, lateral division
<i>c.t.s.</i> , connective-tissue septum	<i>p.</i> , peritoneum
<i>d.g.</i> , dorsal ganglion	<i>rectum</i> , rectum
<i>ext.p.</i> , external papilla	<i>t.c.gr.</i> , transverse crescentic groove
<i>int.pp.</i> , internal papillae	<i>ug.d.</i> , urogenital duct
<i>lt.f.</i> , lateral fold	<i>ug.p.</i> , urogenital papilla
<i>lt.fur.</i> , lateral furrow	<i>ur.bl.</i> , urinary bladder
<i>l.mu.</i> , longitudinal muscle layer	<i>ur.bl.cav.</i> , urinary bladder, cavity of
<i>md.gr.</i> , median dorsal groove	<i>ur.bl.o.</i> , urinary bladder, orifice of
<i>md.g.w.</i> , median dorsal groove, wall of	<i>ur.t.</i> , urinary tubules
<i>mv.f.</i> , median ventral fold	<i>vl.rec.</i> , ventrolateral recess
<i>mv.s.</i> , median ventral septum	<i>v.f.</i> , secondary ventral folds
<i>mes.</i> , mesonephros	<i>v.r.</i> , ventral ridges
<i>m.cf.</i> , muscle caudalifemoralis, im-	<i>v.tr.</i> , ventral trough
pression of	Y, Y-shaped area

PLATE 1

EXPLANATION OF FIGURES

- 1 Ventral view of the pelvic region of a male *Necturus*, showing the superficial topography of the cloaca. Drawn from a live animal in May.
- 2 Lateral view of the entire gland mass. Dissected from a specimen which had been hardened in alcohol.
- 3 Dorsal view of the entire gland mass. Dissected from a specimen which had been hardened in alcohol.
- 4 Dorsal view of the cloacal cavity. The cloaca was slit longitudinally, slightly to one side of the midventral line, and laid open. The cloacal gland is completely divided. Dissected from a specimen which had been hardened in alcohol.
- 5 Ventral view of the cloacal cavity, laid open by a longitudinal incision along the middorsal line. Pelvic gland is completely divided. Dissected from a specimen which had been hardened in alcohol.

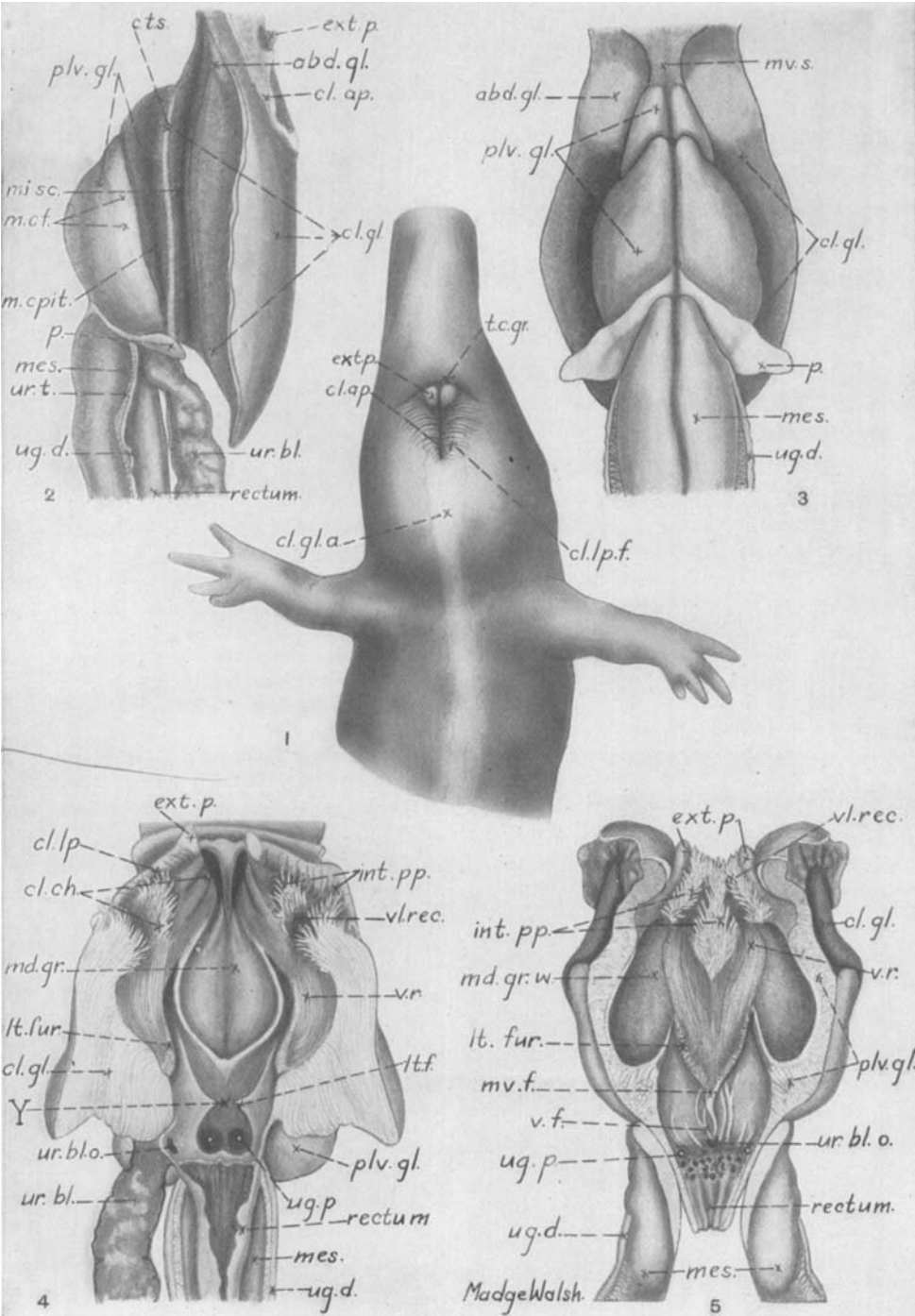


PLATE 2

EXPLANATION OF FIGURES

6 An outline sketch of figure 5, showing the position and plane of section of the sections represented in figures 7 to 17. The number at the end of each line corresponds with the number of the plate figure representing that level.

7 Transverse section cutting the cloaca at the level of the urogenital papillae.

8 Transverse section cutting the cloaca at the level of the orifice of the urinary bladder.

9 Transverse section of cloaca cutting the caudal end of the mesonephros and passing through the dorsal ganglion in the region of its greatest extent.

10 Transverse section of the cloaca, showing the tubules of the cranial differentiation of a pelvic gland.

11 Transverse section of cloaca through the cranial ends of the lateral furrows and ventral trough, showing the tubules of the lateral differentiations of the pelvic gland.

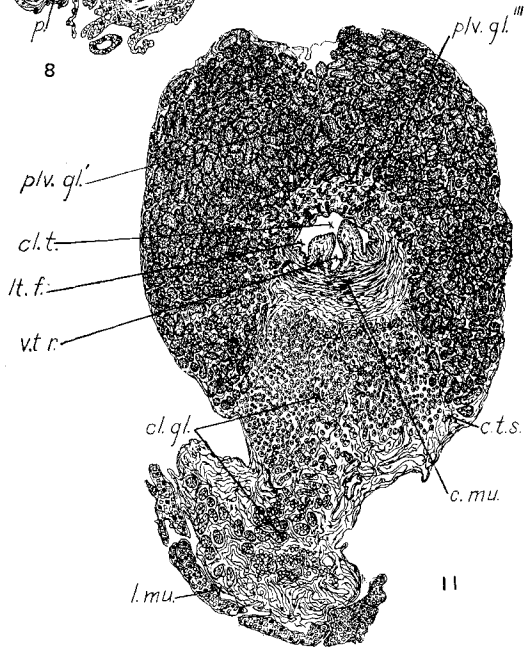
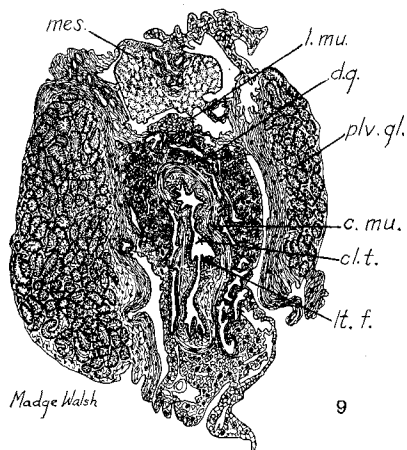
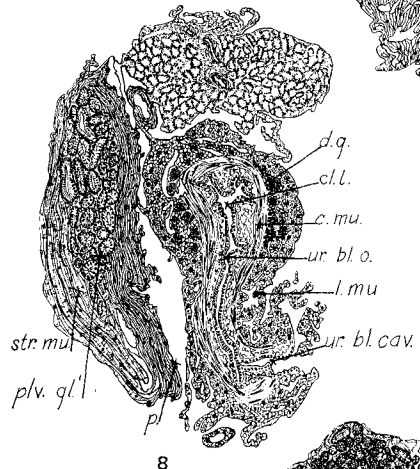
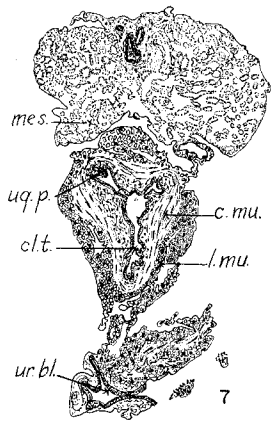
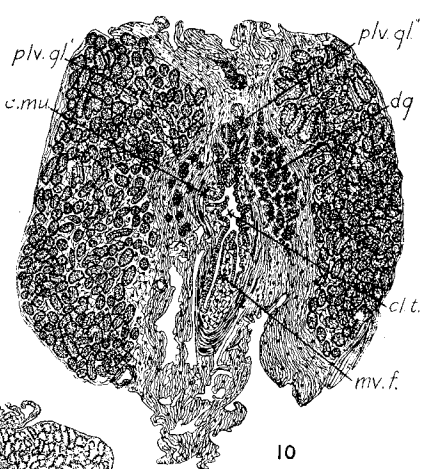
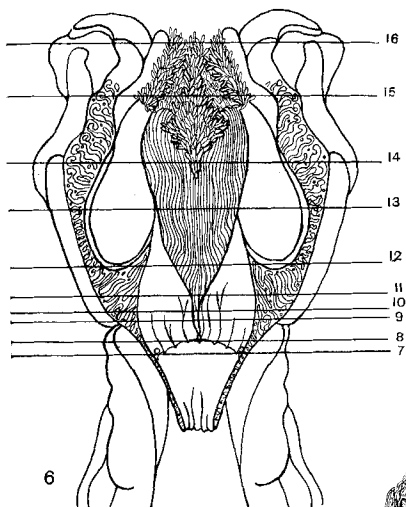


PLATE 3

EXPLANATION OF FIGURES

12 Transverse section of the cloaca immediately anterior to the cranial end of the median dorsal groove.

13 Transverse section of the cloaca showing the median dorsal groove, lateral furrows and ventral trough.

14 Transverse section through the cloaca caudal to the extent of the lateral furrows and immediately cranial to the chamber of the cloaca.

15 Transverse section of the cloacal chamber, showing the ventrolateral recesses.

16 Transverse section through the caudal end of the cloacal slit showing the paired masses of abdominal gland tubules.

