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Stanley E. Trauth
Arkansas State University, strauth@astate.edu

Michael V. Plummer
Harding University

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Cover Page Footnote

We greatly appreciate students at Harding University and R. G. Neal for their field assistance in collecting turtles. We thank G. R. Zug for his constructive comments on an early draft of the manuscript. We also thank the Arkansas Game and Fish Commission for authorizing scientific collection permit numbers (020520182 and 022620199) for 2018 and 2019 to SET.

Distal Excurrent Ducts and Penile Morphology of the Urogenital System in the Mississippi Mud Turtle, *Kinosternon subrubrum hippocrepis* (Chelonia: Kinosternidae)

S.E. Trauth[1*] and M.V. Plummer[2]

[1]*Department of Biological Sciences, Arkansas State University (Emeritus), State University, AR 72467*
[2]*Department of Biology, Harding University (Emeritus), Searcy, AR 72149*

*Correspondence: strauth@astate.edu

Running Title: Distal Excurrent Ducts and Penile Morphology in the Mud Turtle

Abstract

We examined the distal excurrent ductal morphology and penile anatomy of the urogenital system in the Mississippi Mud Turtle, *Kinosternon subrubrum hippocrepis*, from a small sample of individuals collected in Arkansas in order to provide additional information regarding turtle urogenital anatomy. Specifically, we focused on the basic anatomy and histology of distal excurrent ducts (ductus deferens and ureter), associated structures (urogenital papillae), and penile histology in this kinosternid turtle. In addition, we provide an overview of the gross urogenital anatomy in this turtle, given that little detailed information exists on this topic in the chelonian literature.

Introduction

Recent descriptions and illustrations of the male squamate urogenital system have added much clarity to the basic functional morphology as interpreted through histological and ultrastructural studies of this anatomical region (e.g., Trauth and Sever 2011; Rheubert *et al*. 2015; Pewhom and Srakaew 2018; Trauth 2018, 2020). On the other hand, even the most general gross morphological illustrations of the male turtle urogenital system (MTUGS), which includes the testes, kidneys, penis, and associated excurrent ducts, have been largely neglected in most turtle species. For instance, the gross anatomy of the MTUGS is usually depicted in the form of schematic diagrams in comparative vertebrate anatomy textbooks (e.g., Kardong 2015) and in laboratory dissection guides (e.g., Ashley 1962). As a whole, macroscopic illustrations or actual anatomical displays through the use of photomicrographs encompassing the entire MTUGS appear infrequently in books on turtle reproductive biology (e.g., Kuchling 1999) and in the general literature (Fox 1977). Traditionally, the primary research regarding the MTUGS has focused on elucidating the male sexual cycle through examination of testicular histology (for review of sexual cycle literature, see Miller and Dinkelacker 2008) and by reporting on either kidney microanatomy (Solomon 1985) or macroanatomy (Thigpen *et al*. 2020). Other MTUGS studies have centered specifically on penile morphology (Gerecke 1932; Abe 1956; Seshadri 1956; Majupuria 1959; Zug 1966; Kelly 2002, 2004) or on extra-testicular excurrent ducts, specifically the proximal efferent ductules (Waqas *et al*. 2015). Very few microscopic studies have examined the histology of the distal excurrent ducts (i.e., the ductuli deferentia and the ureters) of the urogenital region, a distinct portion of the ducts which lies between the anteriormost structures (testes, epididymides and kidneys) and the posteriormost structure, the penis, that when unerect, lies along the ventral surface of the cloaca (Nicholson and Risley 1940; Zug 1966; Blüm 1986). Herein, we refer to this specific anatomical segment of excurrent ducts as the distal excurrent ductal region (DEDR).

In the present study, we histologically examined the DEDR and penile anatomy of the Mississippi Mud Turtle—MMT (*Kinosternon subrubrum hippocrepis*). This species is a small, semi-aquatic kinosternid turtle commonly found within mostly lowland habitats throughout much of Arkansas (Trauth *et al.* 2004; Powell *et al.* 2016). In addition, we provide gross morphological features of the entire MTUGS for the first time in this turtle family.

Materials and Methods

We collected 3 adult male specimens of the MMT from Arkansas. Each turtle was humanely sacrificed with an intra-pleuroperitoneal injection of dilute sodium pentobarbital in accordance with IACUC protocol guidelines at Harding University. We measured the standard carapace length (SCL) in each

turtle and permanently assigned each a museum number (Arkansas State University Museum of Zoology [ASUMZ]: ASUMZ 33828 [SCL = 89 mm] and 33830 [SCL = 79 mm], captured 9 May 2018 from White County; ASUMZ 34058 [SCL = 76 mm], captured 9 June 2019 from Lonoke County). Specimens are deposited in the herpetological collection in the Arkansas Center for Biodiversity Collections at Arkansas State University.

One of us (SET) removed the entire urogenital system from each turtle, photographed the gross anatomy, and then placed tissues into 10% neutral buffered formalin (NBF) in preparation for histological examination. Following fixation, the tissues were temporarily placed into vials of 70% ethanol and were readied for light microscopy following the paraffin embedding techniques outlined in Presnell and Schreibman (1997). In brief, the histological steps included dehydrating tissue in increasing ethanol solutions (70 to 100%), clearing in 100% xylene, infiltrating in paraffin overnight in a paraffin oven (56°C), embedding in paraffin using plastic molds (tissues positioned to yield either transverse or longitudinal sections), sectioning with a rotary microtome into 10 µm serial strips (affixed onto glass microscope slides coated with Haupt's adhesive prior to floating strips in 2% NBF on a slide warmer), and staining using either hematoxylin/eosin (H&E) to reveal general cytology or Pollak trichrome stain (Pollak) for the enhancement of connective tissues and muscle. Cover slips were then adhered to the microscope slides with Permount© (Fisher Scientific Products).

For histosection photomicroscopy, SET used a Leica MC 120 HD camera atop a Leica DM 2000 LED compound light microscope. For macrophotography, SET used a Canon T4i digital single lens reflex camera fitted with a 50 mm macro lens. Most descriptions of urogenital structures follow the terminology found in Zug (1966), Blüm (1986), Kuchling (1999), and Trauth (2018, 2020). Microscope slides are currently housed in the Trauth Histo-herpetology Laboratory in Morrilton, Arkansas.

Results

Gross Urogenital System Morphology

The gross anatomy of the urogenital system (ventral aspect) of a reproductively active male MMT is shown in Figure 1, and we provide here a brief description of the structural morphology. The paired, ellipsoidal-shaped testes are positioned ventromedial to the paired kidneys and appear a light tawny brown in color. The kidneys are deep brown, exhibit superficial convolutions, and extend cranially and caudally away from the testes. Each highly looped and tightly bound epididymis lies ventrolateral to each testis and projects a silvery-white sheen due to the presence of sperm and seminal fluids within the ductus epididymis. Short paired excurrent ducts (ductus deferens and the ureter) lead caudally away from the testes and kidneys. These ducts appear superficially together (Fig. 1; see also excurrent duct configurations in Figs. 4 – 6) as they lie ventral to the supportive dorsal musculature and connective tissues within the urogenital complex. (Both excurrent ducts descend deeply to connect with the urogenital sinus near the anterior extension [coprodeum] of the cloaca; see Figs. 2 and 3 for gross anatomical positioning of ducts.) The urinary bladder attaches ventrally to the urogenital sinus. A greatly expanded and darkly pigmented penis terminates as the

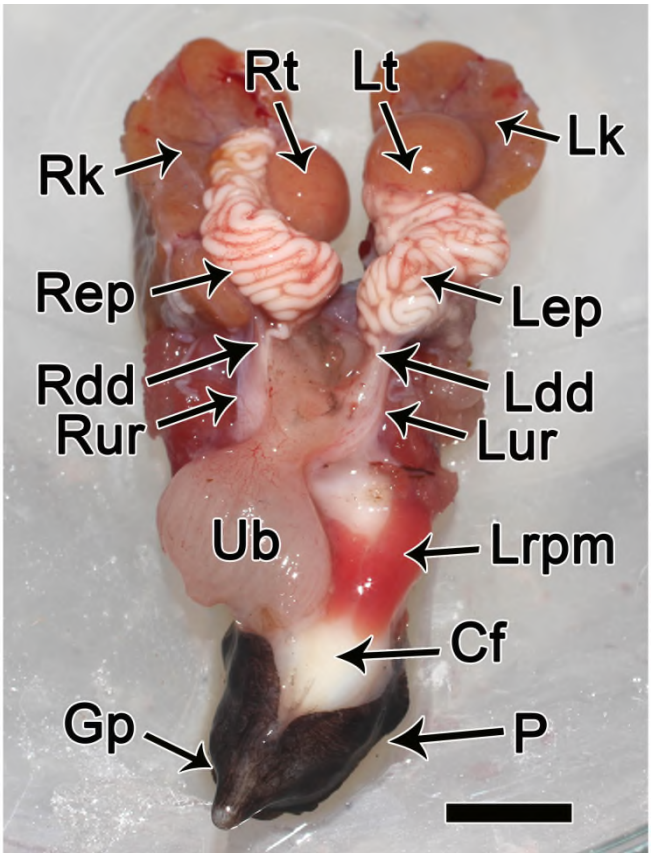

Figure 1. Ventral aspect of the urogenital system of a recently sacrificed, reproductively active MMT (ASUMZ 33828). Cf, corpus fibrosum; Gp, glans penis; Ldd, left ductus deferens; Lep, left epididymis; Lk, left kidney; Lrpm, left retractor penis muscle; Lt, left testis; Lur, left ureter; P, penis; Rdd, right ductus deferens; Rep, right epididymis; Rk, right kidney; Rt, right testis; Rur, right ureter; Ub, urinary bladder. Scale bar = 5 mm.

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narrow-projecting glans penis (Fig. 1). Retractor penis muscles attach to the ventrolateral surfaces of the corpus fibrosum of the penis (see Figs. 8 and 9 for penile structural anatomy).

Light Microscopy

DEDR.—The positioning of the DEDR in relation to the other anatomical structures of the MTUGS is revealed by examining 2 longitudinal histosections of the tissue complex (Figs. 2 and 3). In Figure 2, a dorsal slice shows the coprodeum of the cloaca nestled between the more anterior testes and kidneys and the dorsal musculature of the carapace; the epididymis as well as the DEDR are not visible in this image. However, in Figure 3, which depicts a deeper and more ventral histosection in comparison to Figure 2 and represents an anatomical section at the level of the epididymis, one pair of excurrent ducts is now evident as small, oblong, transverse slits on the left side of the tissue complex (Fig. 3). The interior lining of the coprodeum exhibits a highly-folded epithelium; this anatomical feature is visible inside the relatively thick muscularis externa layer that surrounds the coprodeum and is shown in Figures 4 – 7.

The entire DEDR is best illustrated through a composite series of cranial-to-caudal, transverse histosections (Figs. 4 – 6) beginning at a point of attachment between each ureter and its respective kidney (Fig. 4A). At this juncture, each ductus deferens is transitioning from a coiled ductus epididymidis into a straight duct lying medial to each ureter. In a more caudal section (Fig. 4B), each ureter has become detached from its respective kidney and is now incorporated into a rapidly expanding smooth muscle/connective tissue mass along with its ipsilateral ductus deferens. Eventually, the ductus deferens and ureter move together more medially to lie in close proximity to the anteriormost region of the coprodeum (Figs. 4C; 7A) prior to its transition to become the urodeum (Fig. 6B) of the cloaca. The coprodeum remains characterized by a relatively thick muscularis externa (Figs. 4C; 6B; 7).

As the urogenital sinus appears ventral to the coprodeum (Fig. 5A), each pair of excurrent ducts are now firmly positioned ventromedial to the coprodeum. The ducts also lie embedded in a smooth muscle/connective tissue mass that incorporates them but also includes the coprodeum and the urogenital sinus. Also, as observed within the coprodeum, the urogenital sinus characteristically possesses some folding of the epithelial lining. With the appearance of the urogenital papillae along the lateral surfaces of the urogenital sinus (Fig. 5B), the excurrent ducts begin to lose their outer muscular walls, flatten, and extend toward the tip of each papilla. Each ureter now lies dorsal to each ductus deferens. The ductus deferens and ureter then empty their contents independently into the urogenital sinus through 2 distinct urogenital orifices (Figs. 5C; 6A); the ductus deferens opens cranially, and the ureter opens caudally.

The urogenital sinus begins to narrow into a butterfly-shaped cavity in a region just posterior to the orifices of the urogenital papillae (Fig. 6B). Small, papilla-like structures can be seen projecting from its dorsal wall and, to a lesser extent, from its ventral epithelial lining. Also, a thinning of the muscularis externa of the coprodeum has occurred. A slightly more posterior section reveals the merging of the urogenital sinus with the urodeum (Fig. 6C). At this point the muscular wall of the coprodeum has lost most of its structural integrity and has expanded ventrally to cojoin with the thin bands of muscle and loose connective tissue surrounding the urogenital sinus; the

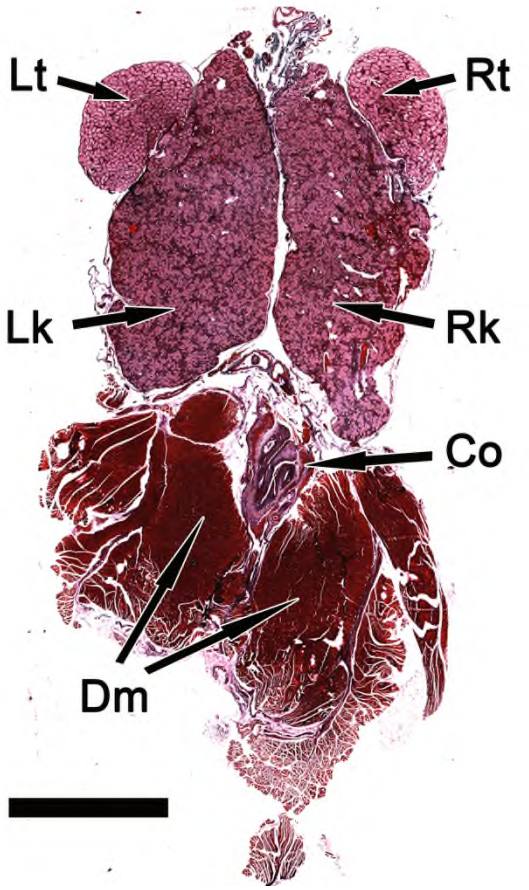

Figure 2. Photomicrograph of a longitudinal dorsal section through the urogenital structures of a reproductively active male MMT (ASUMZ 34058). See text for explanation of structures. Co, coprodeum; Dm, dorsal musculature; other abbreviations same as in Fig. 1. Scale bar= 5 mm. Pollak.

combined cavity is now referred to as the urodeum of the cloaca.

The epithelial lining of the ductus deferens reveals morphological variation along its pathway from the epididymis to the urogenital papilla. Initially, the duct exhibits a thin epithelial layer of low columnar cells but as it approaches the urogenital papilla, the lining changes to an irregular pseudostratified columnar epithelium (Fig. 7C). Its smooth muscular wall (Figs. 4C; 6B), however, remains intact, being dominated by a relatively thick outer circular band of smooth muscle compared to a much thinner inner longitudinal band. Both layers remain unchanged until entering the base of the urogenital papilla (Fig. 7B, C). By comparison, the epithelial lining of the ureter contains a transitional epithelium throughout its entire length (Fig. 7A, B).

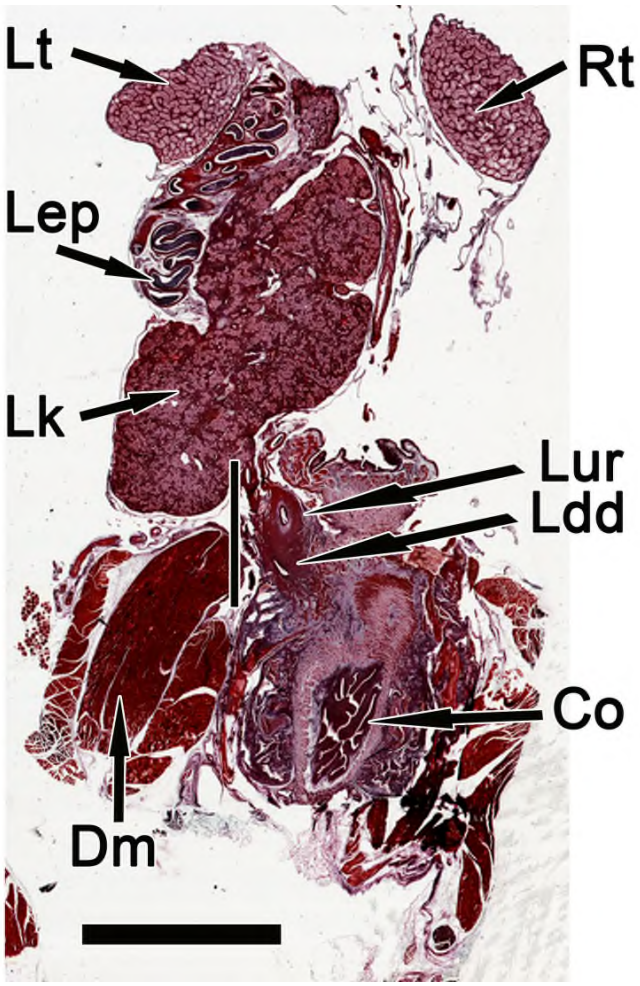

Figure 3. Photomicrograph of a longitudinal dorsal section of ASUMZ 34058 (Fig. 2) showing the emergence of the DEDR (area delineated by the vertical bar) anterior to the coprodeum. Notice the extensive internal foldings of the coprodeal lining. The left ureter (Lur) and the left ductus deferens (Ldd) are wrapped in a smooth muscle/connective tissue sheath. Abbreviations same as in Figure 1. Scale bar = 5 mm, Pollak.

Its muscular wall contains a much-reduced muscularis band compared to that of the ductus deferens.

The structural wall of the coprodeum (Fig. 7) remains pronounced as this cavity accompanies the 2 excurrent ducts posteriorly toward the urogenital sinus. The columnar epithelial lining of the coprodeum has numerous goblet cells along its entirety, and a well-defined muscularis externa comprised of longitudinal and circular bands of smooth muscle is evident. These bands mostly disappear during its transition to become the urodeum (Fig. 6C).

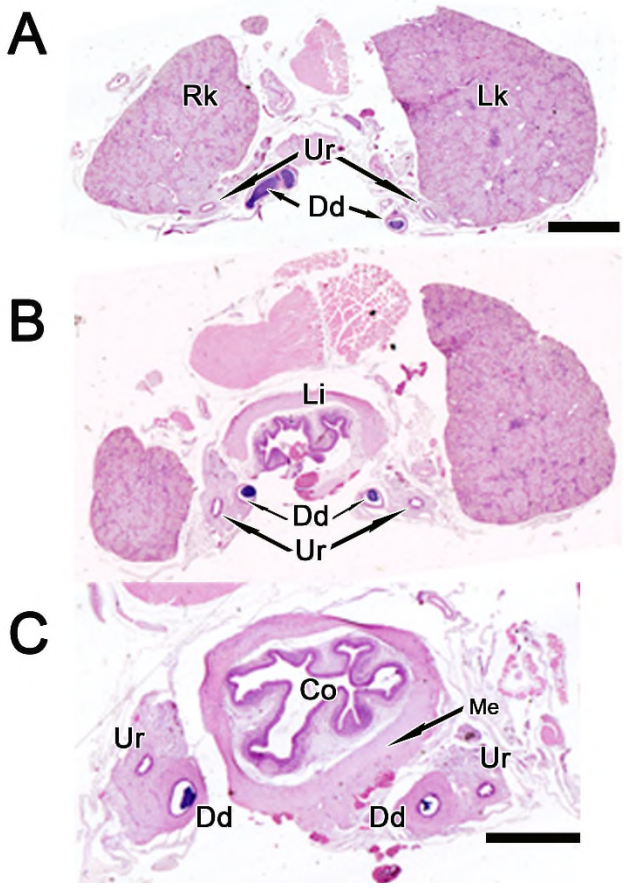

Figure 4. Photomicrographs of transverse sections showing the positioning of the distal excurrent ducts of ASUMZ 33830 in relation to the coprodeum (Co). See text for further explanation of ducts and structures. Li, large intestine; Me, muscularis externa. Abbreviations same as in previous figures. Scale bars= 1 mm; H&E.

Penile anatomy.—The penis of the MMT consists of a proximal shaft and a distal glans penis. The shaft contains of 2 types of erectile tissue: the ventral corpus fibrosum and the dorsal surface layer, the corpus spongiosum (Fig. 8). Anteriorly, these 2 tissue components appear as a circumferential layer surrounding a cavernous interior comprised mostly of

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blood vessels and loose connective tissue (Fig. 8A); however, the two are clearly separate entities (see diagonal line in Fig. 8D), posteriorly, prior to the glans.

The corpus fibrosum consists of a thick, dense plate of connective tissue that provides the primary support for the penis. Proximally, the corpus fibrosum rises as a broad, slightly curved structure (Fig. 8A), but more distally a superficial partitioning of it into a bi-lobed mass occurs as the anterior medial sinus of the seminal groove penetrates deeply into the plate (Fig. 8B – F). However, at the proximal region of the glans (Fig. 8G, H), these 2 masses unite to form a much

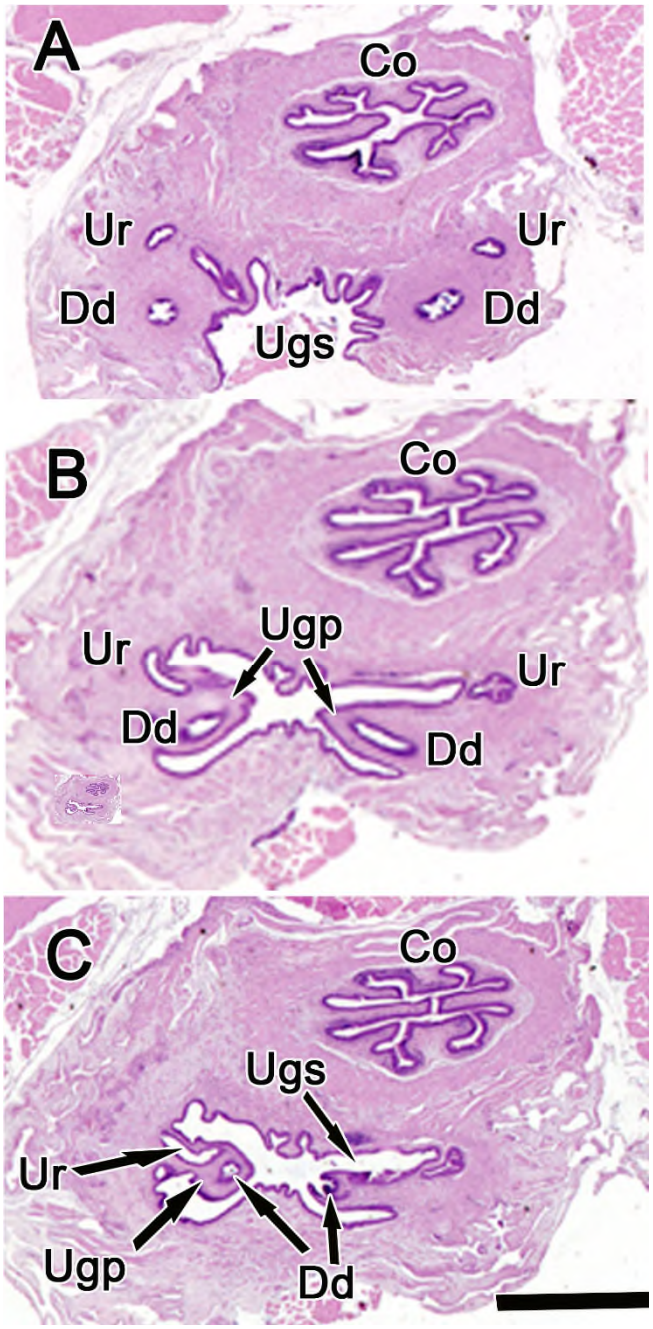

Figure 5. Continuation of Figure 4. Photomicrographs showing the positioning of the coprodeum in relation to the urogenital sinus and excurrent ducts. See text for further explanation of ducts. Ugp, urogenital papilla. Abbreviations as in previous figures. Scale bar = 1 mm for A – C, H&E.

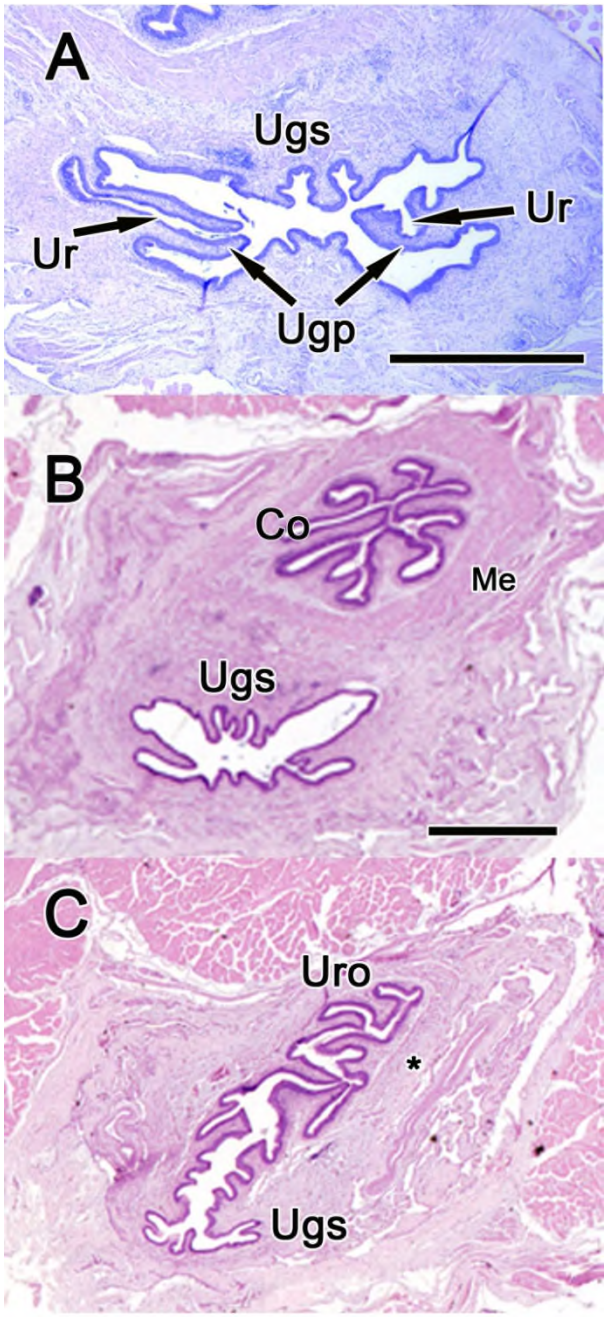

Figure 6. Continuation of Figure 5. Photomicrograph in A shows urogenital sinus just posterior to orifices of the ductus deferens (Fig. 5C). B. Remnants of the urogenital papillae remain in urogenital sinus caudally from urinary orifices. C. Merging of the urogenital sinus with the urodeum (Uro) of the cloaca. Asterisk in C demarks a thinning of the muscularis externa (Me, as seen in B). See test for further explanation of structures. Abbreviations as in previous figures. Scale bar = 1 mm for A; scale bar in B = 1 mm for B and C; H&E.

reduced, oval-shaped, rod-like structure (Fig. 8H). Paired retractor penis muscles shown in Figure 1 attach to the ventrolateral surfaces of the corpus fibrosum (Fig. 8B – F). The corpus fibrosum extends distally beyond the glans and ends in a point (Fig. 1).

The corpus spongiosum arises as a highly vascularized connective tissue layer that is anteriorly bisected dorsally by the seminal groove (Fig. 8). The seminal groove superficially separates the corpus spongiosum into 2 seminal ridges (Fig. 8A – D); however, a medial connection between the 2 ridges is present (see arrow in Fig. 8B). The corpus spongiosum also gives rise to the entire glans penis as it rests atop the corpus fibrosum. The seminal groove extends from the urethral opening (not shown here) along the proximal wall of the urogenital sinus and posteriorly into the glans.

There are paired surface depressions (sinuses) associated with the seminal groove. They lie atop each seminal ridge (Fig. 8E, F). In addition, a single sinus, the anterior medial sinus of the seminal groove (Fig. 8B – D), extends anteriorly and medially beneath the corpus spongiosum.

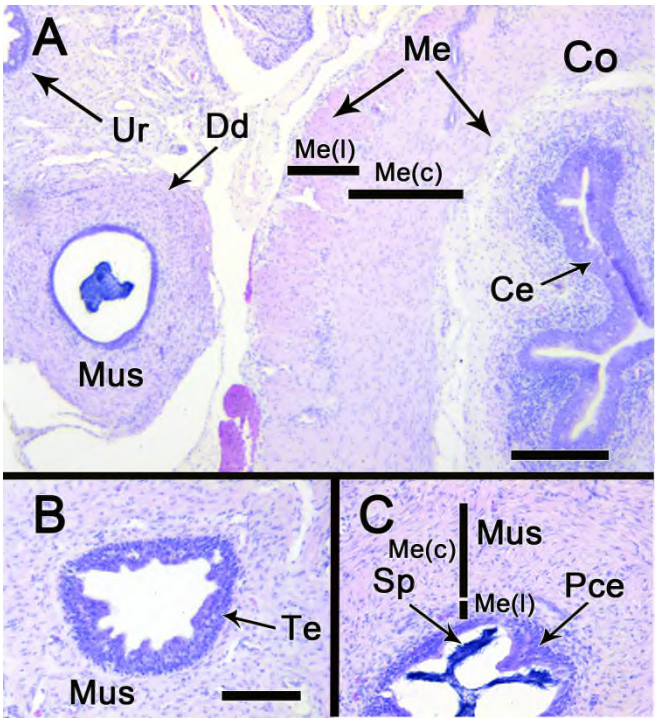

Figure 7. Photomicrographs of epithelial linings and wall structure of the excurrent ducts and coprodeum. Me(c) and Me(l) represent circular and longitudinal smooth muscle bundles of the muscularis externa. Ce, columnar epithelium; Mus, muscularis; Pce, pseudostratified columnar epithelium; Sp, spermatozoa. See text for further explanation of structures. Abbreviations as in previous figures. Scale bar in A = 250 µm; in B – C, 100 µm. H&E.

The glans penis is a highly folded structure consisting of 2 types of pleats. The largest fold, the plica externa, forms the lateral and distal borders of the glans (Figs. 8H; 9). Anterior sinuses of the glans penetrate anteriorly within the enlarged proximal bases of each plica externa (Figs. 8H; 9A) and then increase in size within the paired proximal portions of plica externa. These anterior sinuses terminate as a smaller fold, the plica media, arises (Fig. 9A, B) along the medial surface of the plica externa. The plica media forms a pair of papilla-like folds on each side of the seminal groove and also has a distal fold, the distomedial triangular fold. The seminal groove enters the glans singly (Fig. 9A, B) and then trifurcates with 2 branches leading into each lateral fold of the plica externa (see triple arrow set in Fig. 9C) and a medial third branch that leads distally onto the distomedial triangular fold near the termination of the glans (Fig. 9D). The posterior sinuses of the seminal groove occupy the distal cavities of the plica externa.

Discussion

As pointed out earlier, morphological descriptions of the MTUGS are not available for most turtle species and even fewer microscopic studies on turtles have examined the histology of the distal excurrent ducts. Thus, comparing our results with those of other turtle species is not possible. Instead, we will compare our results with those from several microscopic studies on squamates.

The intricate terminal anatomy of the DEDR in the MMT differs markedly to the comparable anatomical region for these ducts found in male squamate reptiles. For example, colubrine snakes possess a single common chamber, the ampulla urogenital papilla (AUP), in which the ductus deferens and ureter dump their reproductive materials and nitrogenous wastes, respectively, directly into before these materials exit from the AUP into the cloaca through urogenital papillae (Trauth and Sever 2011). On the other hand, crotaline snakes lack an AUP, but possess an expanded distal segment of the ureter, the ampulla ureter (AUR), which receives reproductive components from the ductus deferens. All urogenital products are then dumped into the urodeum of the cloaca from the AUR through urogenital papillae (Trauth and Sever 2011). No similar terminal modifications of this excurrent duct system were observed in the MMT.

Considerable variability exists in the structural morphology related to the release pathways of urogenital products in male lizards (Fox 1977). An

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AUP is present in only a few lizard families (e.g., in Gerrhosauridae, Gymnophthalmidae, Teiidae, and Varanidae). In addition, some lizard species, such as skinks (family Scincidae), possess excurrent ducts that unite prior to the orifice of the urogenital papilla (Rheubert *et al.* 2015; Trauth 2018, 2020). This type of adjoining of the excurrent ducts cranial to the urogenital papilla was not observed in the MMT. Instead, the seminal materials from the ductus deferens exit the urogenital papilla anteriorly through a separate terminal orifice. The ureter then follows, dumping its contents through a urinary orifice found posterior to the genital orifice of the urogenital papilla (Figs.5C; 6A). The position of these ducts differs from their anatomical counterparts described by Nicholson and Risley (1940) in Blanding's Turtle, *Emys blandingii*, and by Ashley (1962) in the Red-eared Slider, *Trachemys scripta elegans*, in which the urinary orifice lies in an anterior position. However, as is the case with these 2 turtle species, total separation of excurrent duct orifices is present on the urogenital papilla of the MMT. Because of this papillary configuration, some authors have referred to the reproductive papilla as the genital papilla as mentioned by Nicholson and Risley (1940) and Ashley (1962). That papillary designation would not apply to the MMT.

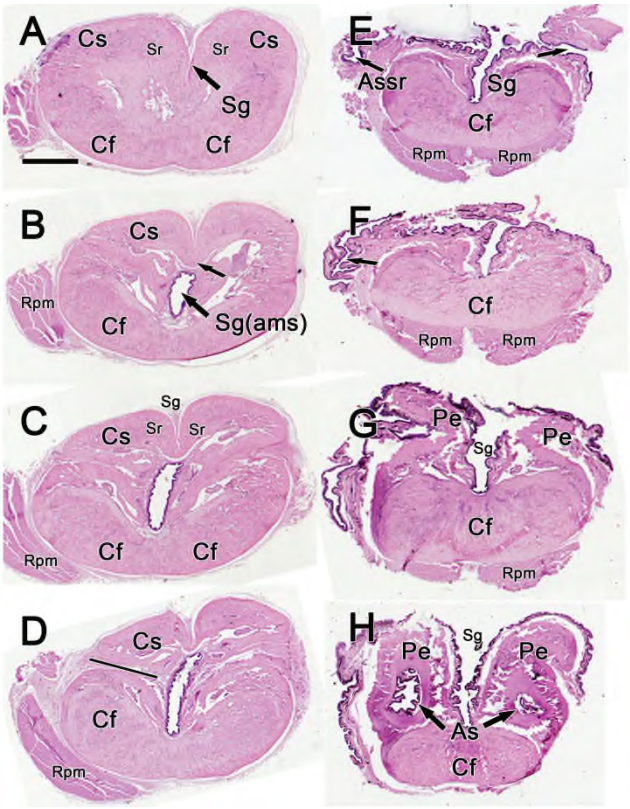

Figure 8. Photomicrographs of transverse sections of penile morphology in ASUMZ 33828. See text for explanation of structures. As, anterior sinus of the glans; Assr, anterior sinus of the seminal groove atop the seminal ridge; Cf, corpus fibrosum; Cs, corpus spongiosum; Pe, plica externa; Rpm, retractor penis muscle; Sg, seminal groove; Sg (ams), anterior medial sinus of the seminal groove; Sr, seminal ridge. Scale bar in A = 1 mm for A – H. H&E.

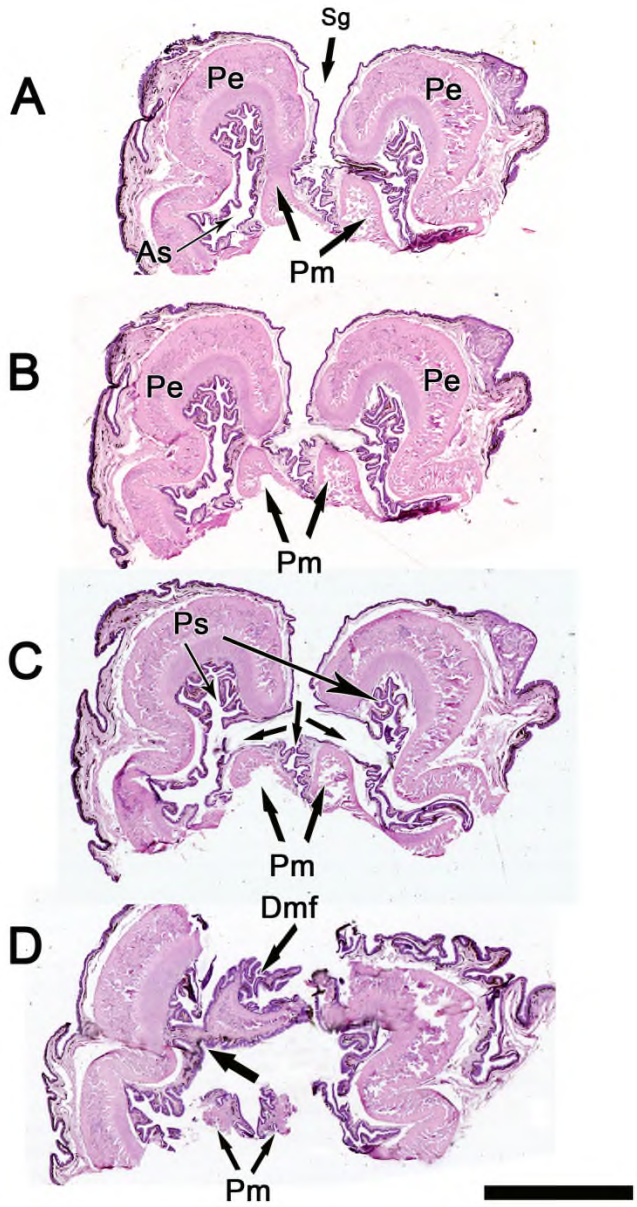

Figure 9. Continuation of Figure 8. Photomicrographs of penile morphology in the distal region of glans penis. Dmf, distomedial triangular fold of the plica media (Pm). Arrow in D points to attachment of the Dmf to the plica externa. See text for explanation of structures. Additional abbreviations as in Figure 8. Scale bar = 2 mm. H&E.

In his classic paper on penile morphology in cryptodiran turtles, Zug (1966) provided an in depth descriptive analysis of penile structure in 4 genera within the family Kinosternidae, including the genus

Kinosternon. Our histological observations on the penis in the MMT are in agreement with his findings, except that we noted the presence of a new sinus of the seminal groove, the anterior medial sinus.

In conclusion, we have demonstrated that a histological mode of discovery is an effective method for revealing anatomical relationships among distal urogenital ducts in the MMT. Moreover, we have shown that examining urogenital morphology can be a beneficial avenue of research for comparing differing urogenital anatomies among reptilian species. We recommend that future researchers on turtle urogenital morphology consider incorporating histological analyses into their research protocol.

Acknowledgments

We greatly appreciate students at Harding University and R. G. Neal for their field assistance in collecting turtles. We thank G. R. Zug for his constructive comments on an early draft of the manuscript. We also thank the Arkansas Game and Fish Commission for authorizing scientific collection permit numbers (020520182 and 022620199) for 2018 and 2019 to SET.

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