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Distal Urogenital Anatomy of Male Prairie Racerunners, *Aspidoscelis sexlineatus viridis* (Reptilia: Sauria: Teiidae)

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Cover Page Footnote

I thank the Arkansas Game and Fish Commission for authorizing scientific collection permits for me for the past 45+ yr. Also, I dedicate this paper to David M. Sever (1948-2019), a longtime friend, colleague and the most productive and articulate histo-herpetologist of all time.

Distal Urogenital Anatomy of Male Prairie Racerunners, *Aspidoscelis sexlineatus viridis* (Reptilia: Sauria: Teiidae)

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Running Title: Distal Urogenital Anatomy in Male *Aspidoscelis sexlineatus viridis*

Abstract

I examined histologically the distal urogenital anatomy in male Prairie Racerunners (*Aspidoscelis sexlineatus viridis*) from a small seasonal sample of individuals collected in Arkansas in order to provide additional information regarding squamate urogenital anatomy. Specifically, I focused on the basic anatomy and positioning of posterior ducts and associated structures in this teiid lizard. The anatomical structures included the ductus deferens, ampulla ductus deferens, ampulla urogenital papilla (Aup), ureter, inner core tissue mass, urodaeum, and the urogenital papilla. The two Aup, which are small complimentary blind pouches representing the terminal repositories for products released by urogenital ducts, are striking anatomical features of the distal urogenital anatomy in this lizard. Interestingly, the Aup, which are characteristic anatomical structures present in very few additional lizard species (e.g., in some members of families Gerrhosauridae, Gymnophthalmidae, and Varanidae) are also present in colubrid snakes and not in crotalid snakes.

Introduction

Interest in the reproductive anatomy of reptiles has increased in recent years and has revealed new information on squamate (lizards and snakes) urogenital systems. Major investigations specifically involving distal urogenital structures, which are supplemented with literature summaries, include Trauth and Sever (2011), Rheubert *et al.* (2015), Pewhom and Srakaew (2018), and Trauth (2018).

Early macroscopic descriptions and illustrations of distal urogenital morphologies in male squamates provided valuable resources for today's anatomical studies. The pioneer works by Martin Saint Ange (1854), Brooks (1906), and Volsøe (1944) laid the groundwork for more rigorous histological studies as reported by Gabe and Saint Girons (1965) and Fox

(1977). The above studies, as a whole, reported on various aspects of male urogenital anatomy, and more recent studies into this anatomical region described several new caudal micro-anatomical structures (Gribbins and Rheubert, 2011; Trauth and Sever, 2011; Rheubert *et al.*, 2015). One of these anatomical structures, the ampulla urogenital papilla, was named by Trauth and Sever (2011) in North American male colubrid snakes and was also referenced in Siegel *et al.* (2011). Although these paired structures were originally illustrated by Martin Saint Ange (1854), Trauth and Sever (2011) described them in histological detail. These two complementary blind pouches reside in the anterior extent of the cloacal cavity. The pouches represent the terminal repositories of products released from the urogenital tracts. Brooks (1906) referred to these pouches as seminal vesicles in the Texas Spotted Whiptail (*Aspidoscelis gularis*), whereas Rheubert *et al.* (2015) more thoroughly examined these paired pouches histologically in this species.

The family Teiidae is a relatively large, New World assemblage of small-to-large lizards containing over 130 species (Vitt and Caldwell, 2014). One species of teiid lizard, the Prairie Racerunner (*Aspidoscelis sexlineatus viridis*), is widespread from the high plains fringing the Rocky Mountains eastward and southward to the eastern coast of the United States (Powell *et al.*, 2016); this species is commonly found in Arkansas (Trauth and McAllister 1996; Trauth 1980; Trauth 1983; Trauth *et al.*, 2004). Rheubert *et al.* (2015) briefly described aspects of the male urogenital anatomy in the Prairie Racerunner and included comments regarding reproductive macro-anatomy and scanning electron micrographs of its urogenital papilla.

In the present study, I provide a more intensive examination of the distal urogenital anatomy of male Prairie Racerunners using seasonal histology. I also discuss these anatomical findings by comparing them with those published on the Texas Spotted Whiptail reported as in Rheubert *et al.* (2015) and on colubrid snakes as reported by Trauth and Sever (2011).

Materials and Methods

I examined the distal urogenital anatomy of adult male Prairie Racerunners currently retained in my personal collection of these lizards (SET tag numbers with date of collection are below); each, however, has been reassigned a permanent museum tag (Arkansas State University Museum of Herpetology—ASUMZ 32724, 12 June 2013; 34075 [SET 975, 6 October 1974]; 34076 [SET 1583, 12 April 1975]; 34078 [SET 2756, 9 June 1978]; 34080 [SET 1662, 3 May 1975]; 34081 [SET 1227, 23 December 1974]; 34082 [SET 1515, 5 April 1975], and 34090 [SET 1213, 21 December 1974]). All lizards, except ASUMZ 32724, 34076, 34078, and 34080 were excavated from hibernation burrows. Specimens will be permanently housed in the herpetological collection in the Arkansas Center for Biodiversity Collections at Arkansas State University. Most of the lizards were collected in Arkansas in 1974 and 1975 during a multi-year study of the species (Trauth 1980). All 8 specimens were euthanized with an intra-pleuroperitoneal injection of sodium pentobarbital following current IACUC protocol guidelines; the urogenital organs from 7 lizards were then fixed using abdominal injections of 10% formalin. The specimens were eventually preserved in 70% ethanol.

I removed segments of distal urogenital anatomy (approximately 5 mm in length; see Fig. 1) and placed the tissues temporarily into vials of 70% ethanol. Then, I followed standard histological procedures to prepare tissues for light microscopy following the paraffin embedding techniques described in Presnell and Schreibman (1997) and Trauth (2018). Briefly, these steps included tissue dehydration in ethanol solutions (70 to 100%), clearing in 100% xylene, infiltration overnight in a paraffin oven (56°C), embedding in paraffin using plastic molds (tissue positioned in a cranial-to-caudal axis), sectioning with a rotary microtome into 8 or 10 μ m serial strips (affixed onto glass microscope slides coated with Haupt's adhesive prior to floating strips in 2% formalin 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 microscope slides with Permount® (Fisher Scientific Products).

For slide photomicroscopy, I used a Leica MC 120 HD camera atop a Leica DM 2000 LED compound light microscope. For macrophotography, I used a Canon T4i digital single lens reflex camera fitted with

a 50 mm macro lens.

All descriptions of urogenital structures follow the terminology found in Trauth and Sever (2011),

Figure 1. Macroscopic view of the urogenital system of a recently sacrificed reproductively active *Aspidoscelis sexlineatus viridis* (ASUMZ 32724) as adapted with modifications from Rheubert *et al.* (2015). Graphic box delimits region where tissues were histologically examined and represents the distal urogenital complex. Lt, left testis; Lk, left kidney; Rt, right testis; Rk, right kidney; Rde, right ductus epididymis; Rdd, right ductus deferens; Ugp, urogenital papilla. Scale bar at upper left = 5 mm.

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Rheubert *et al.* (2015), and Trauth (2018). Microscope slides are currently in my possession and will be deposited in the herpetological collection in the Arkansas Center for Biodiversity Collections.

Results

Gross morphology

A gross morphological aspect of the urogenital anatomy (ventral view) of a reproductively active male is shown in Figure 1, and a brief description of the structural morphology is provided here. The paired testes appear yellow in color with the right testis lying more cranial compared to the left. Each testis is flanked laterally by a highly looped ductal complex, the ductus epididymis and other efferent ductules. The ductus deferens extends caudally from this ductal complex. The ductus deferens lies along the ventromedial surface of the primary lobe of each kidney. The ductus deferens also continues as a slightly looped duct on both sides as each enters the distal urogenital complex (graphic box in Fig. 1). Not seen in Figure 1 are the ureters, which lie dorsomedial to the ductus deferens. A urinary bladder is absent in this species.

Light microscopy

The highly looped, posterior segment of each ductus deferens (Pdd in Fig. 2) resides immediately anterior to the ampulla ductus deferens (Add) of the distal urogenital complex. It is lined with a low simple columnar epithelium and is packed with sperm (Sp) in this lizard collected on 9 June 1978. Each Pdd becomes abruptly constricted caudally into a narrow, straight duct, the Add. The ductal epithelium is now lined with pseudostratified columnar epithelium. The ampulla urogenital papilla (Aup) is also revealed as a conspicuous lateral sac on either side of the midline in Figure 2. Not seen in Figure 2 are the ureters (Ur), which lie dorsomedial to the Pdd and Add.

For most of its length, the Add is a circular-to-oblong linear duct within the distal urogenital complex and is uniformly lined with either a short or tall pseudostratified columnar epithelium depending upon the season (Fig. 3). Closely associated with each Add is a ureter (Ur), which exhibits a transitional epithelium, also known as the urothelium. In addition, depending upon the season, the Add is encompassed by thin-to-relatively thick layers of smooth muscle, the muscularis (Fig. 3). As both Add and Ur extend caudally, each duct becomes displaced slightly to lie in a more medial position (Figs. 4A – C; 6A – E). Near

the cloacal region and more specifically, the urodaeum (Uro), these ducts independently dump their contents into each Aup, which becomes apparent as progressively enlarging pouches lateral to the Add and Ur (Figs. 4 – 7).

Figure 2. Light micrograph of a bilateral longitudinal section through the urogenital structures of a reproductively active *Aspidoscelis sexlineatus viridis* (ASUMZ 34078) collected on 9 June 1978. The ampulla ductus deferens (Add) is a narrow, constricted duct compared to the expansive, highly looped posterior portion of the ductus deferens (Pdd), which is packed with sperm (Sp). Both ampullae urogenital papillae (Aup) are clearly visible in this image. Scale bar = 2 mm at upper left. H&E, 10 μ m.

Seasonal differences between the urothelial lining of the Ur and the pseudostratified columnar epithelium of the Add are revealed in Figures 3A and 4. In the inactive lizard (Fig. 3A), the urothelium is thin, irregular, and much reduced in height, whereas in the active lizard (Fig. 3B), the urothelium is much thicker and relatively unpleated. In comparison, the epithelial

thickness of the Add is basically similar (in both Fig. 3A, B); however, the muscularis layer (M) in the wall of the Add in the inactive lizard is thin, whereas it is much thicker in the active lizard.

Figure 3. Seasonal variation in the Ur and Add in the anterior region of the distal urogenital complex in *Aspidoscelis sexlineatus viridis* as revealed by transverse sections. A. ASUMZ 34075 collected on 6 October 1974. B. ASUMZ 34076 collected on 12 April 1975. Aup, ampulla urogenital papilla; M, muscularis. See text for explanation of ductal morphology. Scale bar = 200 μ m for A and B. A, Pollak, 8 μ m; B, H&E, 10 μ m.

The expansion of each Aup is characterized by a circumferential movement of these pouches (Figs. 4 – 7). Both Aup increase in length and diameter as they completely surround the inner core of connective and muscular tissues (hereafter called the inner core tissue mass, ICTM) supporting the paired Add and Ur. I observed that the positioning of the Ur varied among the lizards examined. For example, in Figures 4 and 5, the Ur elongates as each moves to take a dorsal

position above the Add (Figs. 4E, 5A) within the ICTM. (See Fig. 7 for a more complete explanation of the ICTM complex.) The left Ur elongates (Fig. 4F) in a ventral direction and opens into the left Aup. Each Add is now embedded in the ICTM at a point ventral to the Ur. The left Add (Fig 4E) exhibits a ventral expansion reminiscent of the left Ur as viewed in Figure 4F. The urogenital papilla (Ugp), shown in Figure 5A, begins to appear approximately 20 μ m posterior to Figure 4F. The Aup extend ventrally into the tip of the Ugp. Both pouches will eventually open into the Uro. These orifices of the Aup are shown in Figures 5B and 7B.

Figure 4. Light micrographs of the distal urogenital anatomy in an inactive *Aspidoscelis sexlineatus viridis* (ASUMZ 34075) as revealed by a cranial-to-caudal series of transverse sections. A. Section through the anterior region of the urogenital complex at the level of the Add and the Ur. B. Section showing movement ventrally by the Ur and medially by each Add as they near the urodaeum (Uro). C. Section showing all structures in B, but revealing more of the Uro. D. Section showing the ventral elongation of the Ur. E. Section revealing the Aup lateral to the Add. F. Section showing the expansion of the Aup and the orifice of the left Ur (arrow) opening into the Aup. K, kidney. Scale bar = 500 μ m for A – F; Pollak, 8 μ m.

The relationship between the distal urogenital complex and the alimentary tract is shown in Figures 6 and 7. At the anteriormost level of this complex (Fig.

6A), a collecting duct (Cd) extends ventrally from the posterior lobe of the left kidney and leads into the left Ur. Both Ur and Add are situated dorsal to the large intestine (In). As the arms of the Uro move lateral to the Add (Fig. 6B), the In can be seen constricting to become a much narrower passageway, termed the anterior sphincter of the coprodaeum (Sph), which marks the terminal point of the In (Fig. 6C). Just caudal to this juncture, the Uro spreads both laterally and ventrally to encompass the emerging ICTM (Fig. 6D, E). The ICTM is characterized by a central-located pair of striated muscle masses (see Figs. 6 – 8). The appearance of the pouches of the Aup (Fig. 6D) and their further enlargement (Fig. 6F) displace the lateral arms of the Uro which had previously surrounded the ICTM. Eventually, the Aup elongate further to become narrow passageways within the Ugp (Figs. 5A, 7B). These passageways eventually open into the Uro of the cloaca.

A comparison of the epithelial linings of the Ur, Add, and Aup is shown in Figure 8. The lining of the Aup, not mentioned previously, appears as a low columnar epithelium.

Discussion

The primary morphological structures associated with the distal urogenital system in *Aspidoscelis sexlineatus viridis* are as follows: 1) ductus deferens, 2) ureter, 3) urodaeum, 4) inner core tissue mass, and 5) the urogenital papilla. The following discussion pertains to these anatomical structures by separately comparing each with what has been published about them in the most recent literature.

Ductus deferens

Pewhom and Srakaew (2018) mentioned two segments of the ductus deferens in the Butterfly Lizard (*Leiolepis ocellata*): a ductal portion and an ampullary portion. The ductal portion is further subdivided into the proximal and distal ductal regions based on the type of epithelium present. The posterior segment of the ductus deferens in *Aspidoscelis sexlineatus viridis* (i.e., the Pdd in Fig. 2) equates closely to the distal ductal portion mentioned in *L. ocellata* based on epithelial type, which these authors describe as simple cuboidal. In contrast, this epithelium in *A. s. viridis* more closely resembles a low simple columnar epithelium. Also, Pewhom and Srakaew (2018) defined the ampulla ductus deferens as the straight terminal segment of the testicular ducts; however, they did not thoroughly examine the Add within the distal

Figure 5. Light micrographs comparing the urogenital papilla (Ugp) of an inactive and an active *Aspidoscelis sexlineatus viridis*. A. Section through the Ugp of an inactive lizard (ASUMZ 34075). Arrow points to thin epithelial lining of the Aup. B. Section through the Ugp of an active lizard (ASUMZ 34076). Arrows point to thick folded epithelial lining of the Aup. Abbreviations the same as in previous figures. Scale bar = 200 μ m for A and B. A, Pollak, 8 μ m; B, H&E, 10 μ m.

urogenital complex as described herein. Consequently, no comparison with the Add of *A. s. viridis* is available for that region. Although *L. ocellata* does possess a deeply folded modification of the ampullary portion of the ductus deferens, a structure termed the ampulla ductus deferentis (Akbarsha *et al.* 2005), *A. s. viridis* does not possess this modification of the Add.

Rheubert *et al.* (2015) found the ampulla ductus deferentis in 5 lizard species (i.e., in one scincid-*Scincella lateralis* and 4 phrynosomatids-*Cophosaurus*

texanus, *Holbrookia propinqua*, *Phrynosoma cornutum*, and *Sceloporus consobrinus*), and Trauth (2018) also found an ampulla ductus deferentis in

Figure 6. Light micrographs of the distal urogenital complex in *Aspidoscelis sexlineatus viridis* (ASUMZ 34090) as revealed by a cranial-to-caudal series of transverse sections. A. Section through the complex at the level of the Add and the Ur. A collecting duct (Cd) from the kidney is merging with the right Ur. B. Section showing movement ventrally by the Ur and medially by the Add as they near the region of the Uro. C. Section showing all structures in B, but revealing enlargement of the anterior arms as well as the ventral extension of the Uro. D. Section showing the elongation of the Ur and the first appearance of the Aup dorsolateral to the Ur. E. Section revealing the complete isolation of the inner core tissue mass (ICTM as labeled in F) by the Uro; striated muscle masses (Mu) are prominent. The Aup begin to increase in size lying dorsolateral to the Ur. F. Section showing the greatly expanded Aup surrounding the lateral protuberances of the ICTM containing the Ur and Add. The merging of the Uro with the coprodaeum (asterisk). Scale bar = 500 µm for A – F. Sph, anterior sphincter of the coprodaeum. Abbreviations as in previous figures; Pollak, 8 µm.

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another scincid, *Plestiodon anthracinus pluvialis*. Also, Rheubert *et al.* (2015) did not mention this modification in *Aspidoscelis gularis*. Trauth and Sever (2011) provided numerous light micrographs of the ampulla ductus deferentis in a number of North American colubrid snakes. Akbarsha *et al.* (2005) suggested that the ampulla ductus deferentis in some agamid lizards functions like seminal vesicles found in mammals.

Ureter

Rheubert *et al.* (2015) examined the Ur of 7 species of lizards. The urothelium of the Ur in *Aspidoscelis sexlineatus viridis*, as reported in the present study, is similar to the urothelia found in these other species. However, only one of these species examined (*Aspidoscelis gularis*) possesses an Aup, and, as expected, the pouch structure is very similar to that found in *A. s. viridis*. Consequently, the terminal release point of urinary products in most lizards differs structurally (i.e., materials go directly from the Add into a Ugp or directly into the Uro) compared to the situation found in teiid lizards.

Urodaeum

The morphology of the Uro in *Aspidoscelis sexlineatus viridis* differs slightly from that of *Aspidoscelis gularis* as illustrated by Rheubert *et al.* (2015). In *A. gularis*, the Uro advances beneath the ICTM as a pair of ventrolateral blind pockets. More caudally these two pockets eventually merge ventrally into a broad and somewhat flattened space, termed the anterior dorsal recess (Adr) of the Uro and remain ventral in position to the developing ICTM. In contrast, *A. s. viridis* exhibits a Uro with anterior lateral arms as well as a mid-ventral pouch. These three branches eventually merge and expand posteriorly to surround the ICTM (Fig. 6C – E). Consequently, the Uro of *A. s. viridis* has structural differences from the Adr of *A. gularis*. The Adr was first described in both colubrid and crotalid snakes as anterior projecting cavities of the Uro (Trauth and Sever, 2011).

The internal lining of the Uro in the two teiid lizards mentioned above shows some structural similarity to that found in scincid lizards as illustrated in Rheubert *et al.* (2015) and Trauth (2018). For example, in the skinks (*Plestiodon fasciatus*—former study and *Plestiodon anthracinus pluvialis*—latter study), the epithelium of the Adr is highly convoluted and contains numerous primary and secondary crypts. Electron microscopical analysis of these crypts revealed

in *P. fasciatus* an orderly arrangement of sperm clustered within these spaces. In *A. s. viridis*, dorsolateral crypts are evident (Figs. 4C, 5B, 6F, 7) and are lined with a bistratified columnar epithelium.

Inner core tissue mass

The tissues of the ICTM, a previously undefined region of the distal urogenital complex in lizards, support the Ur and Add as these ducts descend ventrally into their final anatomical positions within the distal urogenital complex. Centrally located inside this tissue mass in *Aspidoscelis sexlineatus viridis* are a bilateral pair of longitudinal skeletal muscle masses (Figs. 4, 6, 7). In *A. gularis*, the muscle core appears as a single mass comprised on multiple bands of skeletal muscle (Rheubert *et al.* 2015). Immediately surrounding this inner muscle core in both species, though, is an area of loose connective tissue and blood vessels. More lateral to this layer of loose connective tissue are tightly arranged bundles of dense irregular connective tissue and elastic fibers which support the ducts. The muscularis layer of the Add supports the Add within its position in the ICTM (Figs. 7 – 8). Near their termination, orifices of both the Ur and Add are projecting outward into each Aup from the ICTM and are supported by tissue prominences (Fig. 7), although these masses were not as apparent in specimen ASUMZ 34075 (Figs. 4, 5A). The muscular core of the ICTM undoubtedly helps maintain some stability in the final positioning of these distal ducts, although their precise function remains unclear.

Ampulla urogenital papilla

The first illustration of these pouches was provided by Martin Saint Ange (1854) as drawn from the reproductive anatomy of the Grass Snake (*Natrix natrix*), a European colubrid snake. Trauth and Sever (2011) named these pouches, noting their presence in North American colubrid snakes and their absence in North American crotalid snakes. These urogenital pouches are homologous to the ampullae uriniferous papillae of female colubrid snakes (Siegel *et al.* 2011).

The Aup are striking features of the distal urogenital complex of *Aspidoscelis sexlineatus viridis* and represent a diagnostic feature found in teiid lizards (Figs. 2, 3B, 4 – 8); they are also illustrated in its close relative, *Aspidoscelis gularis* (Rheubert *et al.* 2015). These pouches receive sperm and urinary products and then immediately redirect all materials emanating from these distal urogenital ducts into the cloaca through the orifices of a urogenital papilla (Fig. 7A). A moderate degree of folding was observed within the lining of the

Figure 7. Continuation of Fig. 6. Formation and structure of the Ugp in *Aspidoscelis sexlineatus viridis*. A. The Ugp projects ventrally from the roof of the Uro. Both the Ur and the Add are held within fleshy masses projecting outward from medial surfaces of the ICTM. The ICTM exhibits a central pair of longitudinal masses of striated muscle (Mu) at its core that are surrounded by loose connective tissue. (See text for further explanation.) These muscle masses are present in Figs. 4; 6 – 8). B. The Ur and Add are adjoining the Aup, and urogenital orifices (Ugo) of the Ugp are present. The Ugp projects ventrally into the coprodaeum. Scale bar = 200 μ m for A and B; Pollak, 8 μ m.

Aup (e.g., Figs. 5B, 8A). The folding may allow for some expansion of these sacs upon the delivery of sperm. Another possible function could be temporary housing for sperm, as was observed in the Adr of *A. gularis*. At present, the function of these folds remains unclear. The internal lining of the Aup appears to be a low-to-bistratified columnar epithelium (Fig. 8).

Urogenital papilla

The termination release structure for all ductal materials in male squamates is the Ugp, which may be either a single medial structure or paired bilateral structures hanging from the dorsal wall of the urodaeum of the cloaca (Trauth and Sever, 2011; Rheubert *et al.*, 2015). A detailed description and illustration of a generalized Ugp morphology (and its surrounding tissues) was provided by Trauth and Sever

(2011). In addition, the highly variable external micro-anatomy of the Ugp in squamates is best viewed using scanning electron microscopy as depicted in Trauth and Sever (2011) for snakes and Rheubert *et al.* (2015) for lizards.

In *Aspidoscelis sexlineatus viridis*, the Ugp develops as a ventral extension of the ICTM (Fig. 7) and drops into a transitional space between the Uro and the coprodaeum. A thin tissue barrier separates the two Aup within the neck of the Ugp (Fig. 7B).

Only a single Ugp was present in the *A. s. viridis* examined in the present study. Variation does exist, however, with respect to Ugp structure in teiid lizards. Rheubert *et al.* (2015) showed SEM images of paired papillary mounds and paired Ugp in this species. The Ugp of other teiid lizards is found in Rheubert *et al.* (2015).

Distal Urogenital Anatomy in Male *Aspidoscelis sexlineatus viridis****Ampulla urogenital papilla in lizards and snakes***

There are 43 lizard families according to Vitt and Caldwell (2014), and I have histologically examined the distal urogenital complex in 35 species from 17 of these families. At present, only members of the Gerrhosauridae (1), Gymnophthalmidae (2), Teiidae

(5), and Varanidae (1) exhibit Aup. In snakes, all members of North American colubrid snakes possess Aup, whereas no North American crotalid snakes have them (Trauth and Sever 2011). Future research in other squamates may reveal interesting relationships expressed by the presence or absence of these pouches.

Figure 8. Light micrographs showing the urogenital epithelial types in *Aspidoscelis sexlineatus viridis* in an inactive lizard (ASUMZ 34090). A. Image of the Aup lying lateral to the Ur and Add. Arrows point to dorsal folding. B. Magnification of A. Urogenital epithelial linings: a—urothelium; b—low columnar epithelium; c—pseudostratified columnar epithelium. Mu = striated muscle mass of ICTM. Abbreviations the same as in previous figures. Scale bar = 200 μ m for A; 100 μ m for B. Pollak, 8 μ m.

Acknowledgments

I thank the Arkansas Game and Fish Commission for authorizing scientific collection permits for me for the past 35+ yr. Also, I dedicate this paper to the late Dr. D. M. Sever (1948-2019), a longtime friend, academic colleague and the most productive and articulate histo-herpetologist of all time.

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