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Comparative Histology, Histochemistry, and Ultrastructure of Rathke's Glands in Hatchlings of Two Species of North American Box Turtles (*Terrapene carolina* and *Terrapene ornata*)

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ABSTRACT. – **We examined the histology, histochemistry, and ultrastructure of Rathke's glands in hatchlings of the three-toed box turtle, *Terrapene carolina triunguis*, and the desert box turtle, *Terrapene ornata luteola*. Both species possess one pair (axillary) of Rathke's glands, which are similar anatomically and histochemically to one another. Each gland is composed of a single, highly vascularized secretory lobule, which is surrounded by a thick sheath of striated muscle. Two types of large secretory vacuoles characterize most of the holocrine cells produced by a relatively thin glandular secretory epithelium. Analysis of our results suggests that the chief secretory material of the smaller dark-staining type 1 secretory vacuole appears to be a glycoprotein complex. The larger, mostly translucent type 2 secretory vacuole contains multilayered and variously sized lamellar bodies, whose structural design is reminiscent of an epidermal lipid delivery system in vertebrates. The functional role of Rathke's glands in *Terrapene* and in other turtles remains unclear at the present time.**

KEY WORDS. – **Reptilia; Testudines; Emydidae; *Terrapene carolina triunguis*; *Terrapene ornata luteola***

Thirteen of the 14 living chelonian families have species that possess exocrine integumentary glands known as Rathke's glands (Waagen 1972; Ehrenfeld and Ehrenfeld 1973; Solomon 1984; Plummer and Trauth 2009). These musk or scent glands, which number from 1 to 5 pairs, exude a sometimes malodorous secretion through external pores and are named based upon the general location of the orifices (axillary and inguinal) and/or the proximity of the orifices to scutes (inframarginal). Rathke's glands consist of one or more lobules encased within a striated muscle tunic and whose secretory epithelium liberates spherical holocrine cells (Ehrenfeld and Ehrenfeld 1973; Solomon 1984; Plummer and Trauth 2009). The secretions released by these cells are primarily proteins and, to a lesser extent, lipids, as well as various acids (Seifert et al. 1994; Weldon et al. 2008). Lamellar bodies also may be present within the secretory vacuoles of these cells (Plummer and Trauth 2009). Little is known about the function of Rathke's gland secretions as well as their comparative anatomy among chelonians, despite our increasing knowledge about their glandular chemistry (Weldon et al. 2008). Moreover, few detailed studies have focused on the Rathke's glands in hatchling turtles (Stromsten 1917; Zangerl 1941; Weldon and Tanner 1990; Weldon et al. 1990; Rostal et al. 1991).

Rathke's glands are known to occur in both adults and hatchlings of several species of North American box turtles (Waagen 1972; Patton et al. 2004). When handled, hatchlings of the eastern box turtle, *Terrapene carolina carolina*, the three-toed box turtle, *Terrapene carolina triunguis*, and the desert box turtle, *Terrapene ornata luteola*, may produce a musky odor (Neill 1948; Norris and Zweifel 1950; Patton et al. 2004; Gangloff and Nash 2010). Our objectives in the present study were to investigate the comparative histology, histochemistry, and ultrastructure of Rathke's glands in hatchlings of *T. c. triunguis* and *T. o. luteola*. Our comparative approach helps clarify structural morphologies between these closely related species and supports the notion that Rathke's glands are homologous among all chelonians (Ehrenfeld and Ehrenfeld 1973).

METHODS

We examined Rathke's glands in 15 newly hatched *T. c. triunguis* and 3 hatchling *T. o. luteola*. Specimens were secured from an outdoor enclosed facility on the campus of Harding University in Searcy, White County, Arkansas. Hatchling turtles were mailed by one of us (M.V.P.) to the laboratory at Arkansas State University for processing, where they were measured (carapace and plastron lengths), euthanized with an intrapleuroperitoneal injection of sodium pentobarbital, photographed, and dissected. Carapace lengths of hatchling *T. c. triunguis* and *T. o. luteola* ranged from 27–31 mm and 38–40 mm, respectively.

One of us (S.E.T.) extracted the axillary Rathke's glands from hatchling specimens and then fixed them in either 10% neutral buffered formalin (for paraffin sectioning) for 48 hrs or in a 2% glutaraldehyde solution buffered with 0.1 M sodium cacodylate at a pH of 7.2 (for plastic sectioning) for 2 hrs. For postfixation, 1% osmium tetroxide, buffered as above, for 2 hrs, was used. Routine

histologic techniques were used to prepare tissues for light microscopy (LM); paraffin embedding followed the methods of Presnell and Schreibman (1997). Glands were dehydrated in a graded series of increasing ethanol solutions (50%–100%), cleared with xylene, and then infiltrated and embedded in paraffin wax. Paraffin-tissue blocks were trimmed, serially sectioned into ribbons 8 μm in thickness by using a rotary microtome, and affixed to microscope slides by using Haupt's adhesive while floating on a 2% neutral buffered formalin solution.

Alternating sets of 5 slides were treated with the following histologic stains: 1) hematoxylin and eosin for general cytology; 2) Pollak trichrome stain (Pollak) for connective tissues and mucins; 3) bromphenol blue stain for proteins; 4) the periodic–acid Schiff (PAS) procedure (counterstained with fast green) for neutral carbohydrates, mucopolysaccharides, and other carbohydrate-protein substances; and 5) Alcian blue 8GX (AB) for primarily carboxylated glycosaminoglycans.

For LM of plastic-embedded tissues, we followed the methods of Bozzola and Russell (1992). After fixation, the tissues were dehydrated in a graded series of increasing ethanol solutions (70%–100%), placed in a 50%–50% acetone–plastic mixture for overnight infiltration, and then embedded in Mollenhauer's Epon-Araldite no. 2 (Dawes 1988). For thick sectioning (approximately 1 μm in thickness) and staining, we used glass knives on an LKB Ultrotome (type 4801A) with Ladd multiple stain, respectively. For photomicroscopy, we used a Nikon Eclipse 600 epifluorescent LM with a Nikon DXM 1200C digital camera (Nikon Instruments Inc, Melville, NY). A Konica Minolta Maxxum 7D digital single lens reflex camera fitted with a ProMaster AF Macro lens was also used to photograph macroscopic images of turtles and glandular tissues.

For scanning electron microscopy (SEM), we dehydrated glandular tissues in a graded series of increasing ethanol solutions (70%–100%), followed by fluid exchange to 100% ethanol. A Samdri-780 critical point drier (Tousimis Research Corporation, Rockville, MD) was used (31°C, 1072 psi, ventilation rate approximately 100 psi/min) to remove excess ethanol. Tissue samples were then mounted on 25.4-mm aluminum SEM specimen mounts and coated with gold by using a Cressington 108 sputter coater (Cressington Scientific Instruments Ltd, Watford, UK). Tissues were analyzed both qualitatively and quantitatively with a Vega TS 5136XM digital SEM (Tescan USA Inc, Cranberry Township, PA) at 19.5 kV.

Plastic-embedded samples prepared for LM also were used for transmission electron microscopy (TEM). Tissue blocks were sectioned on a glass or diamond knife. Sections were picked up with 200-mesh copper grids, stained with uranyl acetate (3% aqueous) and lead citrate for 40 min each. Grids were examined with a JEOL 100 CX-II TEM (JEOL USA, Inc, St Louis, MO) at 60 kV (55 μA). Positive digital images were generated by scanning developed TEM negatives by using an Epson Perfection 4990 scanner (Epson America, Inc, Long Beach, CA). We generally followed Ehrenfeld and Ehrenfeld (1973), Solomon (1984), and Plummer and Trauth (2009) for the descriptive terminology of Rathke's glands.

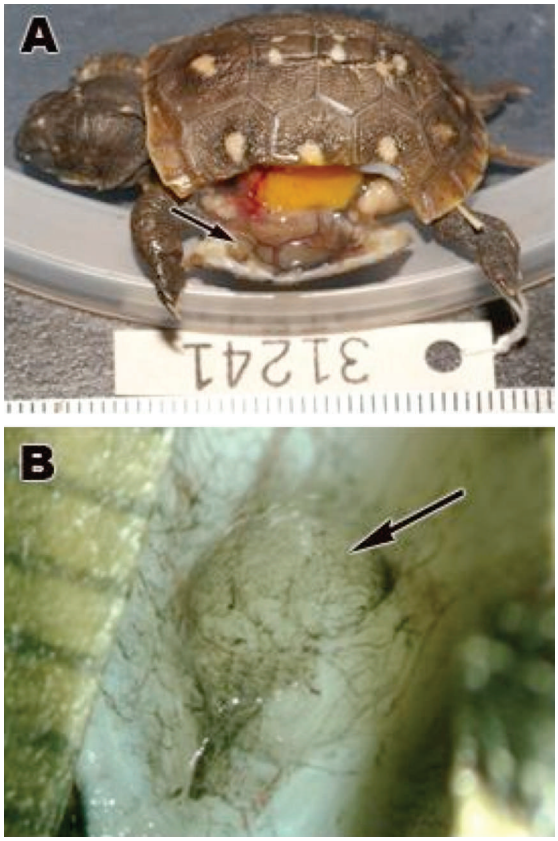

Figure 1. Rathke's glands in hatchling *Terrapene carolina triunguis* (A) and *Terrapene ornata luteola* (B). A. The arrow points to the axillary gland; metric scale (in mm) at bottom of image. B. The arrow points to an axillary gland surrounded by adipose tissue; metric scale (in mm) at left of image.

RESULTS

Gross Morphology. — One pair of Rathke's glands, namely the axillary glands, is found in hatchling *T. c. triunguis* and *T. o. luteola*. Upon necropsy, as shown in Fig. 1, the axillary gland (3.5–4.0 mm in length) of *T. c. triunguis* lies conspicuously adjacent to marginal bones; however, its anatomic location can be best described externally as lying dorsolaterally beneath the third and fourth marginal scutes at their junction with the first costal scute. The anatomic position of the axillary gland (2.5–3.0 mm in length) in the *T. o. luteola* is similar to that described for the *T. c. triunguis*, except that the glands are located beneath marginal scutes four and five at their junction with costal scutes one and two. In both species, all glands reside retropleuroperitoneally beneath a lightly pigmented parietal pleuroperitoneum.

Light Microscopy. — The internal anatomy of axillary glands in *T. c. triunguis* and *T. o. luteola* is

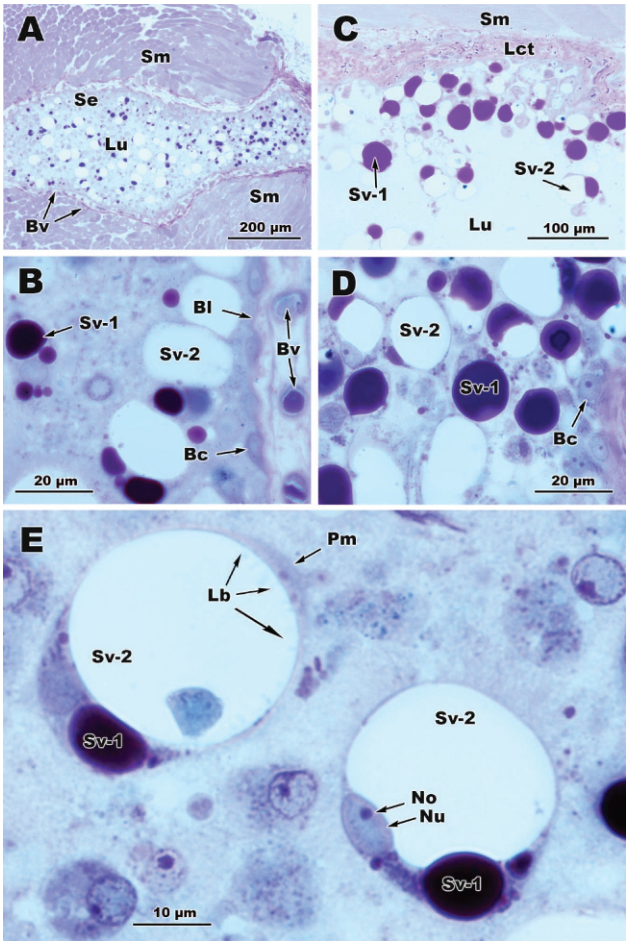

Figure 2. Light micrographs of axillary glands in hatchling *Terrapene carolina triunguis* (A, B, and E) and *Terrapene ornata luteola* (C and D). A. Section showing gland lumen (Lu) filled with holocrine cells that contain smaller, dark-staining, type 1 secretory vacuoles and larger, lipid droplets (clear spheres) characteristic of type 2 secretory vacuoles. The secretory vacuoles are interspersed within secretory cell/cellular debris matrix. A repetitive series of blood vessels (Bv) surrounds the secretory epithelium. Se, secretory epithelium; Sm, striated muscle. B. Magnification of (A) (between 2 arrows above Bv), showing the basal lamina (Bl) of the secretory epithelium (at the right) and the enlargement of several holocrine cells. Bc, basal cell nucleus; Sv-1, type 1 secretory vacuole; Sv-2, type 2 secretory vacuole. C. Axillary gland, showing expansive lumen mostly devoid of secretory material. Holocrine cells appear clustered along the secretory epithelium. Lct, loose connective tissue. D. Magnification of (C), revealing large type 1 secretory vacuoles along the secretory epithelium. E. Lumen of axillary gland, showing 2 holocrine cells that contain large type 2 secretory vacuoles. Lb, lamellar body; No, nucleolus; Nu, nucleus; Pm, plasma membrane. A–E, Ladd multiple stain.

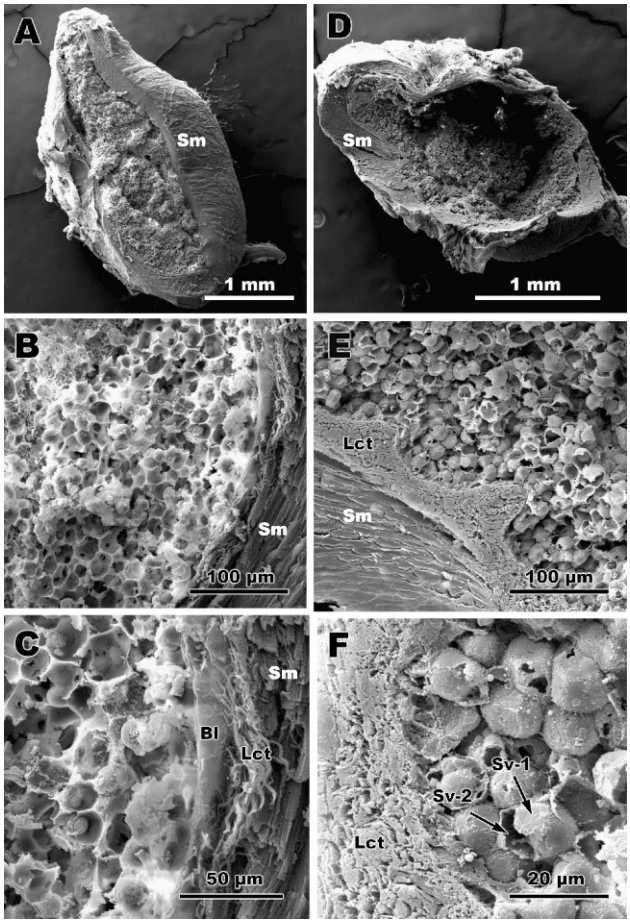

Figure 3. Scanning electron micrographs of Rathke's glands in hatchling *Terrapene carolina triunguis* (A–C) and *Terrapene ornata luteola* (D–F). A. Longitudinal, midsection of axillary gland filled with holocrine cells and cellular materials. B. Magnification of (A), revealing honeycomb appearance of holocrine cells within lumen. C. Magnification of (B), revealing the basal lamina of the secretory epithelium. D. Axillary gland with partially filled lumen. E. Magnification of (D), showing a relatively thick layer of loose connective tissue. Most holocrine cells within lumen maintain their individual integrity. F. Magnification of (E), revealing developing holocrine cells with type 1 and type 2 secretory vacuoles. Abbreviations are the same as in Fig. 2, unless otherwise stated.

mostly similar in both species. Each axillary gland is composed of a single lobule, which possesses a secretory epithelium that rests upon a thin basal lamina (Figs. 2B and 3C). A thin-to-moderately thick layer of loose connective tissue is contiguous with the basal lamina (Fig. 2D). A repetitious series of mostly evenly spaced, minute capillaries was observed immediately external to the basal lamina in the axillary gland of *T. c. triunguis* (Fig. 2A–B). In general, the secretory epithelium is composed of a thin, basal, generative cell layer, which produces roughly spheroid-shaped holocrine cells (Fig. 2B–E). These epithelial cells proliferate outward into an expansive lumen (Fig. 2C). The external wall of each gland is made of a relatively thick muscular tunic (Figs. 2A, 3, and 4). At some point after their release from the apical region of the secretory epithelial cell surface, secretory cells lose their structural integrity and degenerate, exuding their cellular contents into the glandular lumen. This flocculent cellular debris becomes the material that is eventually passed into a duct that leads to the exterior. We did not investigate these ducts or their pathways during the present study.

Secretory cells of all axillary glands are characterized by the presence of 2 different types of secretory vacuoles: type 1 and type 2 (Fig. 2B–E). Type 1 secretory vacuoles are generally smaller than type 2 and appear singularly as

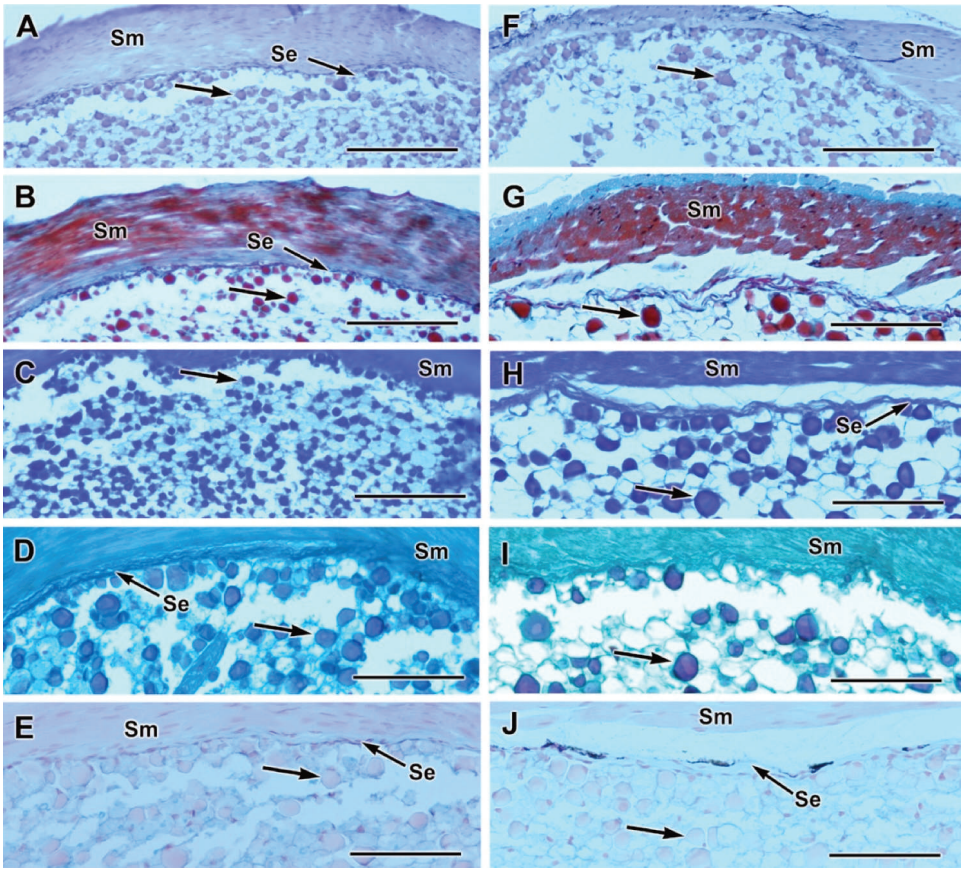

Figure 4. Histochemical staining properties of axillary glands in hatchling *Terrapene carolina triunguis* (A–E) and *Terrapene ornata luteola* (F–J). All sections are cross sections through the gland wall and lumen; A and F, hematoxylin and eosin stain; B and G, Pollak stain; C and H, bromphenol blue stain; D and I, periodic–acid Schiff stain; E and J, Alcian blue 8GX stain. All arrows point to type 1 secretory vacuoles. Scale bars in A, B, C, and F equal 200 µm; scale bars in D, E, G, and H equal 100 µm. Abbreviations are the same as in Fig. 2, unless otherwise stated.

a dark-staining sphere (or oval) or occur as small aggregated clusters. Their matrix is not removed during tissue preparation. In contrast, type 2 secretory vacuoles are quite large, nearly circular when fully distended, and generally appear mostly devoid of material. Type 2 secretory vacuoles contain lipoidal material that is normally referred to as lipid droplets. Soluble lipids of these lipid droplets are removed from these vacuoles during histologic preparation; however, lipoidal membrane-bound structures (Figs. 2E, 5, and 6) are also found within type 2 secretory vacuoles (see details in ''Transmission Electron Microscopy'' section) and remain intact during treatment with solvents during tissue preparation.

Histochemical Staining Properties. — The effects of histochemical staining on type 1 and type 2 secretory vacuoles of secretory epithelial cells of axillary glands in both species of box turtles are shown in Fig. 4. Tissues of both species were similar in their staining reactions. For example, when treated with Pollak, type 1 secretory vacuoles appeared highly acidophilic, which indicated a strong positive reaction, whereas type 2 secretory vacuoles showed no affinity for Pollak (Fig. 4B, G). When treated with bromphenol blue, the contents of type 1 secretory vacuoles appeared purple (a positive reaction for protein), whereas only the cellular membranes of type 2 secretory vacuoles were picked up by the stain (Fig. 4C, H). When using PAS, type 1 secretory vacuoles showed a mild-to-strong positive reaction by appearing mildly acidophilic, as indicated by a purple appearance. However, type 2 secretory vacuoles showed no affinity for PAS stain (Fig. 4D, I). We also observed that type 1 secretory vacuoles appeared mildly acidophilic and not blue, which would have indicated a positive reaction for mucosubstances with AB stain. Type 2 secretory vacuoles failed to show any staining reaction to AB (Fig. 4E, J).

Scanning Electron Microscopy. — We examined the secretory epithelial cells of axillary glands in both species of box turtles by using SEM. The internal structure of axillary glands is shown in Fig. 3. We observed several noticeable structural design differences between the 2 species. One of these was evident in the framework pattern of the secretory vacuoles within the lumina. For example, a honeycomb configuration, which results from a lack of maintaining plasma membrane integrity, was exhibited by the type 2 secretory vacuoles in *T. c. triunguis* (Fig. 3B–C), whereas this structural design was not nearly as pronounced in *T. o. luteola* (Fig. 3E–F). In both species, however, type 1 secretory vacuoles maintain

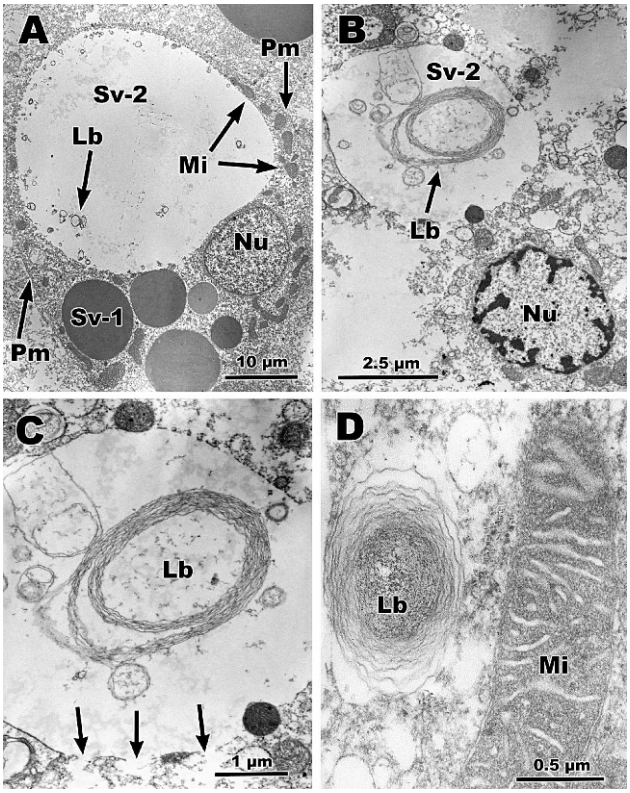

Figure 5. Transmission electron micrographs of Rathke's glands in hatchling *Terrapene carolina triunguis*. A. Holocrine cell of axillary gland showing type 1 and type 2 secretory vacuoles. Lamellar bodies are scattered along the inner surface of the type 2 secretory vacuole. B. Apoptotic cell, revealing one large and several small lamellar bodies. C. Magnification of (B). The arrows point to openings in the membrane-bound vacuole. D. Minute lamellar body adjacent to a mitochondrion (Mi). Abbreviations the same as in Fig. 2, unless otherwise stated.

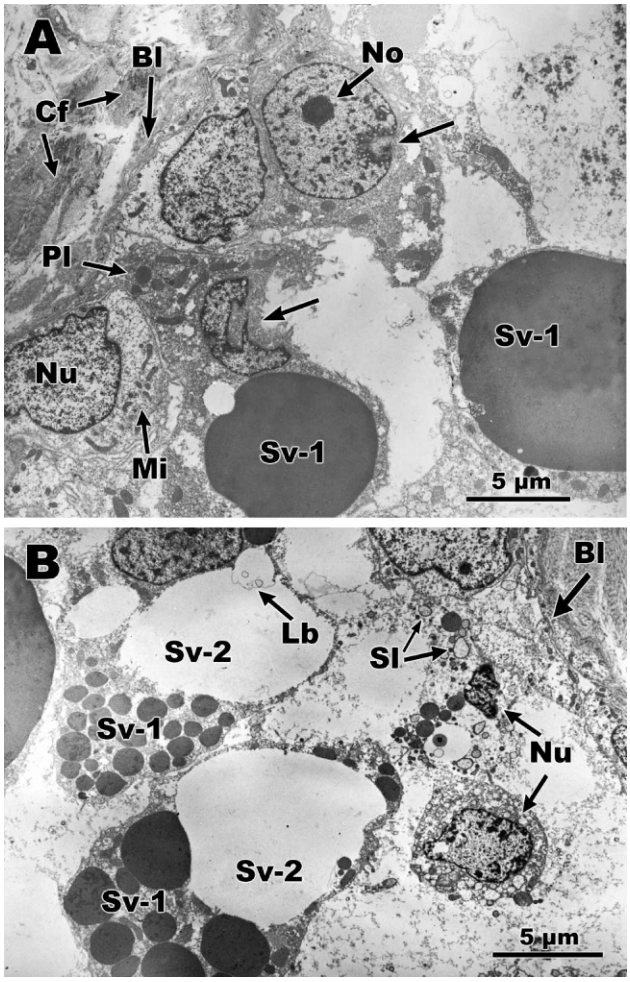

Figure 6. Transmission electron micrographs of the secretory epithelium of Rathke's glands in hatchling *Terrapene ornata luteola*. A. Section through an axillary gland showing large type 1 secretory vacuoles. The free arrows point to pyknotic nuclei of holocrine cells. Cf, collagen fibrils; Pl, primary lysosome. B. Section of an axillary gland revealing large type 2 secretory vacuoles and nuclei of apoptotic cells. Sl, secondary lysosome. Abbreviations the same as in Fig. 2, unless otherwise stated.

their structural identity and shape. Another difference was observed in the irregular thickness of the connective tissue sheath that immediately surrounds the glandular lumen. In *T. o. luteola*, a repetitive folding of the loose connective tissue into cup-shaped indentations was evident (Fig. 3E); this condition was not observed in *T. c. triunguis*.

Transmission Electron Microscopy. — We observed similar ultrastructural features of secretory epithelial cells in axillary glands between *T. c. triunguis* (Fig. 5) and *T. o. luteola* (Fig. 6). Primary cytologic components of a typical mature secretory cell (Fig. 5A) include a single or small cluster of type 1 secretory vacuoles situated in a polar-opposite position to a single, large type 2 secretory vacuole. Circular-to-oblong lamellar bodies were observed scattered along the inner membrane surface of the type 2 secretory vacuole (faintly apparent in vacuoles shown in Fig. 2E). These minute, membrane-bound, lipoidal entities also are found residing within the luminal interior of deteriorating vacuoles (Fig. 5B–C). Conspicuous mitochondria appear within narrow cytoplasmic spaces flanking this large vacuole. A uniform chromatin fills the secretory cell nucleus. Upon cell death and fragmentation, the cytoplasm of secretory cells becomes highly vacuolated due to destructive lysosomal activity. In addition, the nucleus has shrunk, and its heterochromatin has become radially dispersed (Fig. 5B). Lamellar bodies of varying shapes and sizes can be seen inside the vestige of a type 2 secretory vacuole (Fig. 5B–C). Some individual lamellar bodies may exhibit numerous membranes that surround an electron-dense core region (Fig. 5D).

Apoptosis appears to be aphasic in both species, and apoptotic cells may reside adjacent to basal cells (Fig. 6A) along the basal lamina. Large type 1 and type 2 secretory vacuoles may also be present in secretory cells that reside in close proximity to basal cells of the secretory epithelium (Fig. 6). Pyknotic nuclei in varying stages of degeneration are evident in secretory cells adjacent to basal cells (Fig. 6A). Primary lysosomes were seen in the supranuclear region of these cells. Conspic-

uous secondary lysosomes were apparent in some apoptotic cells that release their cellular contents immediately adjacent to basal cells (Fig. 6B).

DISCUSSION

Rathke's glands of relatively few nonmarine turtles have been studied anatomically or histologically in any detail; however, a number of common morphologic and histologic features occur among those species. For example, the glands of *Sternotherus odoratus* (Ehrenfeld and Ehrenfeld 1973), *Apalone mutica* and *Apalone spinifera* (Plummer and Trauth 2009), *Kinosternon subrubrum* (Webb 2010), and *T. carolina* and *T. ornata* (present study) are composed of either a single lobule or, in most cases, multiple lobules, which exhibit a relatively thick layer of loose connective tissue immediately surrounding the secretory epithelium. All are also encased in a tunic of striated muscle, and all receive a rich supply of blood from capillaries that lie in close proximity to the basal lamina of the secretory epithelium. Despite these structural similarities, hatchling box turtles possess glands with holocrine cells that more closely resemble those of *Apalone* and *Kinosternon* than to those of *Sternotherus*. Although all of these species possess at least 2 types of epithelial cells (basal and secretory), *S. odoratus* differs from the others by possessing a third cell, best described as a holocrine cell that contains a number of small lipoid droplets. These lipoid cells are concentrated within the center of the glandular lumen.

We identified both numerous small as well as solitary large type 1 secretory vacuoles in box turtles, and these secretory vacuoles also were present in *Apalone* (Plummer and Trauth 2009) and in *Kinosternon* (Webb 2010). The secretory material of type 1 secretory vacuoles was putatively identified as a glycoprotein complex in *Sternotherus* by Ehrenheld and Ehrenheld (1973) based upon PAS+ staining results. The carbohydrate component of the glycoprotein comprised less than 4% of the total molecule in *Sternotherus*. We found similar staining results in the holocrine cells of box turtles as did Webb (2010) for *Kinosternon*.

Type 2 secretory vacuoles of box turtles were generally large open spheres devoid of material, except for multilayered lamellar bodies. These lamellar bodies are similar to those in softshell turtles, although the lamellar membranes, for the most part, were more densely compacted and more numerous in both species of *Apalone* (Plummer and Trauth 2009). Lamellar bodies may play a role in lipid transfer (Ehrenheld and Ehrenheld 1973), but their function remains unknown in Rathke's glands.

The presence of Rathke's glands is likely the basal condition for turtles (Waagen 1972; Weldon and Gaffney 1998) and is known to occur in every family except the terrestrial testudinids (Waagen 1972; Ehrenfeld and Ehrenfeld 1973). The presence of axillary Rathke's glands has been previously documented by dissection in *T. carolina* and *T. ornata* (Legler 1960; Waagen 1972). However, Waagen (1972) found Rathke's glands in only 3 of 16 *Terrapene* that he dissected. Based on low detection rates of musky odors by humans in more than 1400 hatchling *T. carolina* and *T. ornata*, Norris and Zweifel (1950), Patton et al. (2004), and Gangloff and Nash (2010) concluded that either few juveniles possess Rathke's glands or gland function quickly decreases after birth. We found axillary Rathke's glands to be clearly present in each of 17 *T. carolina* and 3 *T. ornata* necropsied during our study. Noting that absence of odors does not confirm the absence of glands, we suggest that *T. carolina* and *T. ornata* hatchlings typically have Rathke's glands but are often reluctant to musk when handled. Legler (1960) stated that, ''Strong odors were produced by nearly all small juveniles [*T. ornata*] until they became accustomed to being handled.''

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