Externally Secreting Glands of Freshwater and Sea Turtles

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The axillary and inguinal glands of the sea turtle *Chelonia mydas*, and the freshwater turtle *Sternotherus odoratus*, were studied using light microscopic and histochemical techniques. These externally secreting glands are remarkably similar in the two species. They consist of holocrine lobules surrounded by a thick capsule of striated muscle. Within each lobule large cells arise from an epithelial layer and produce droplets of a secretion product. The secretion material in both species contains a PAS-positive, protein-rich, non-acidic substance. In *S. odoratus*, additional cells, elaborating droplets of free lipid, are present. We propose that these glands in turtles be named "Rathke's glands," after their discoverer.

It is likely that Rathke's glands are homologous structures within the order Testudines. Their secretion product probably functions as a defensive substance to ward off predators; however, other functions in intraspecies communication cannot be ruled out.

MANY turtle species have large inguinal and axillary glands which are externally secreting. These glands have received little attention, and in no case has their morphology been described adequately, or has their function been studied.

Integumental glands are found in all four orders of reptiles (Gabe and St. Girons, 1965; Gadow, 1923; Quay, 1972). Glands of the Crocodilia are located under the skin of the back, below the second row of scales from the midline, and also in the throat region (Reese, 1920, 1921); those of lizards are subfemoral or preanal (Gabe and St. Girons, 1965; Cole, 1966), and those of snakes are nucho-dorsal (Smith, 1938) and anal. These glands have mostly been described as holocrine (Gabe and St. Girons, 1965; Quay, 1972), but some workers have given descriptions of a tubular morphology (Cole, 1966). Inguinal and axillary glands are common among turtles, having been reported in all families except the Testudinidae (Loveridge and Williams, 1957; Gadow, 1923; Deraniyagala, 1939; von Eggeling, 1931; Peters, 1848). The glands were first described by Rathke (1848) just prior to the comparative study by Peters (1848). Since then, their development has been studied (Stromsten, 1917; Zangerl, 1941), and the location of the gland pores has been used as a taxonomic character (Deraniyagala, 1939). We suggest that the inguinal and axillary glands in turtles be called Rathke's glands.

With the current interest in chemical-mediated communication in aquatic vertebrates (Sebeok, 1968), the study of the structure and function of Rathke's glands assumes a new significance. In this paper, we compare glands from two distantly related turtles, the green sea turtle (*Chelonia mydas* Linnaeus) and the musk turtle (*Sternotherus odoratus* Latreille). In the case of *C. mydas*, behavior provides no obvious indication of gland function; in the case of *S. odoratus*, a defensive function is presumed in view of its habit of secreting malodorous musk whenever handled. We have studied these glands to

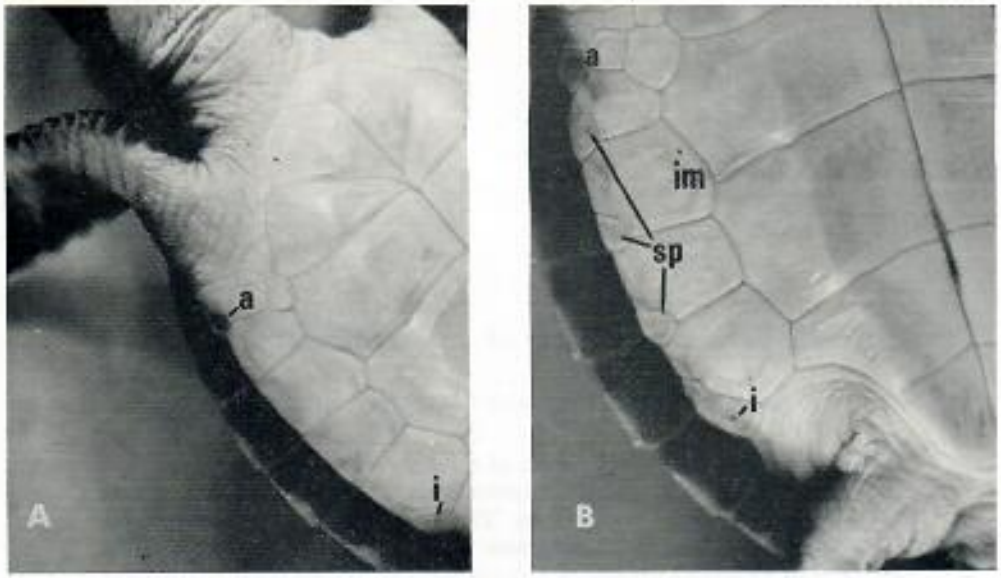

Fig. 1. Location of pores on plastron of *Chelonia mydas*. A. Turtle with pores in axillary (a) and inguinal (i) scutes. B. Turtle with supernumerary pores (sp) in scutes derived from inframarginal scutes (im).

determine whether their morphology and histochemistry are consistent with a function in intra or interspecies communication.

Methods

Eight immature green turtles of both sexes were used in this study; these were hatched from eggs collected at Tortuguero, Costa Rica. Two adult female and four adult male *S. odoratus* were collected at Pomona, New York. The axillary and inguinal glands from all turtles were excised and prepared for light microscopy by overnight fixation in San Felice's fixative (Humason, 1962) or in 10% neutral buffered formalin, followed by dehydration in t-butanol and embedding in paraffin. The weight of each turtle and the wet weights of the glands were recorded.

Histological and histochemical properties were determined by use of the following stains: 1) General histology. hematoxylin and eosin, Mallory's connective tissue stain; 2) Proteins. ninhydrin-Schiff, naphthol yellow S; 3) Carbohydrates. periodic acid-Schiff (PAS), PAS after acetylation and after saliva, methylene blue extinction, alcian blue-PAS, metachromasy with sulfation, colloidal iron-PAS, toluidine blue (Montagna, et al., 1951); 4) Lipids. Sudan Black B (all of above in Thompson, 1966 and Barka and Anderson, 1963). In addition, one-micron sections stained with Richardson's stain (Richardson, et al., 1960) were taken from material fixed in Karnovsky's fixative (Karnovsky, 1965) and 2% osmium tetroxide, and embedded in Epon.

A single axillary gland from a three-month-old ridley turtle, *Lepidochelys olivacea* Eschscholtz, from Surinam, which had been stored in cacodylate-buffered 2% glutaraldehyde for a year, was available for histological study. This material was not suitable for histochemical analysis; however, slides stained with hematoxylin and eosin were examined for histological organization.

Results

Chelonia mydas.—Rathke's glands are located along the angle formed by the carapace and plastron, and are outside the peritoneum. The anterior glands are largest and lie below the 4th and 5th marginal scutes; each empties by means of a duct that runs through the plastral axillary scute (Fig. 1A). The glands are tightly applied to the plastron directly internal to the duct opening (Fig. 2). A small gland lies just anterior to each main axillary gland and empties through a separate pore in a scute anterior to the axillary. Smaller posterior (inguinal) glands lie below

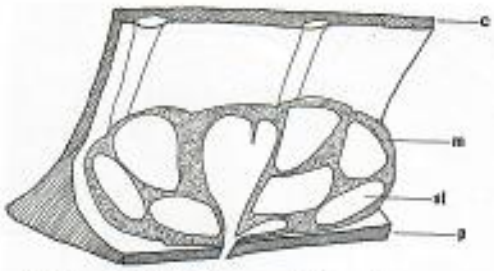

Fig. 2. Diagram of an axillary gland from *Chelonia mydas*. The gland is shown dissected to illustrate the relative positions of the secretory lobules (sl), muscle sheath (m), and carapace (c) and plastron (p).

the eighth and ninth marginals and empty through ducts in these scutes. All glands are morphologically and histologically identical. The duct aperture for each gland appears on the external surface as a slit-like opening. It is never closed by a plug or membrane and it is lined by simple epithelium. Occasional individuals possess supernumerary auxiliary glands and scutes along the junction of the carapace and plastron (Fig. 1B). These are histologically identical to the main glands, about 3 mm in diameter, and void through ducts in the inframarginal scutes. These glands are variable in number, ranging on each side from zero to four (the number of infra-marginal scutes on each side), and there is never more than one gland per scute. Their ductile openings may be contained in small extra scutes derived from the inframarginals. The secretion is white, and has a faint odor when released from the excised gland.

The glands are large; in a six-month-old turtle (carapace 15 cm long) an anterior gland may measure more than 1.5 cm long by 5 mm wide, and weigh 0.5 gm. The four glands of this turtle together ranged from 0.5 to 0.7 percent of the body weight. Variations observed in the entire sample did not seem correlated with age or sex. Weight

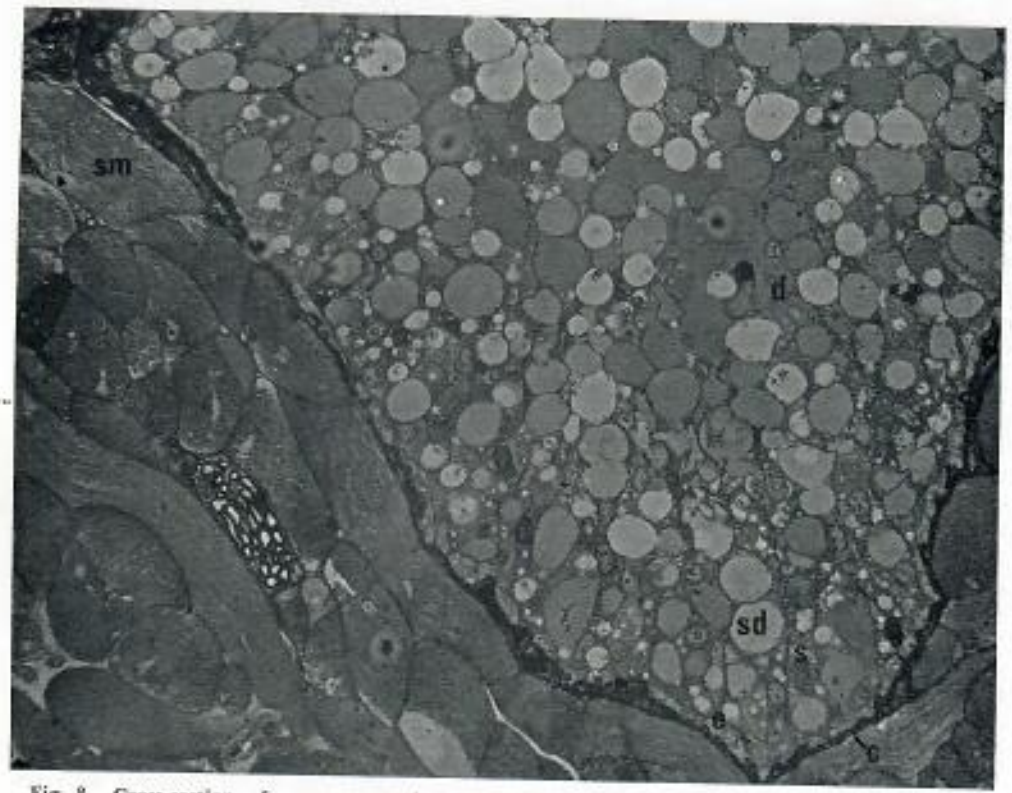

Fig. 3. Cross-section of a representative lobule from a *Chelonia mydas* gland. sm, striated muscle; e, epithelial cell; s, secretory cell; sd, secretion droplet; c, connective tissue; d, degenerated cells. Richardson's stain. (693 ×)

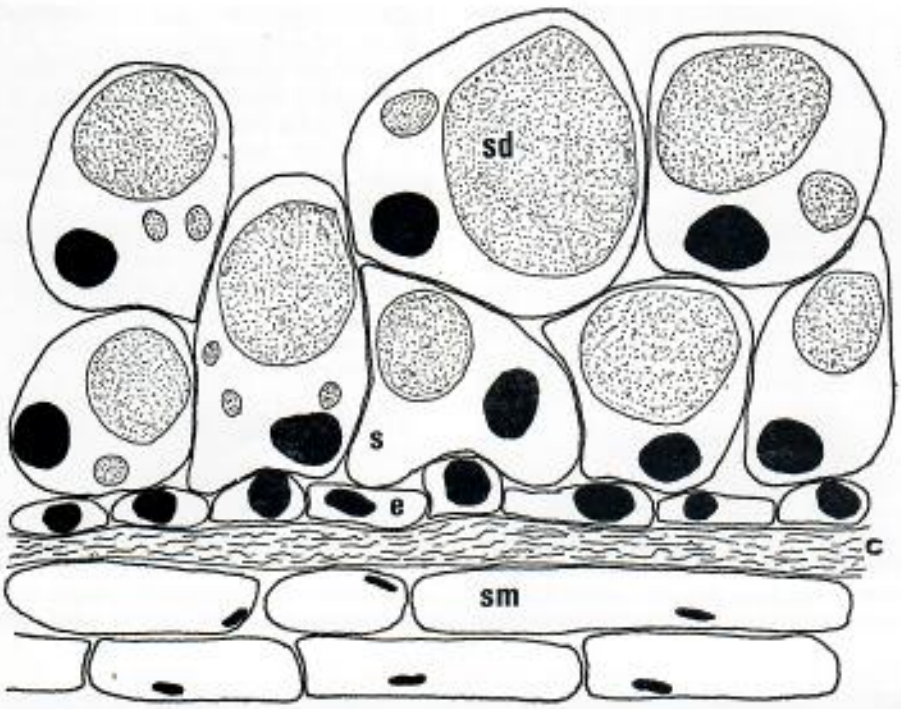

Fig. 4. Diagram of cell types in a Rathke's gland from *Chelonia mydas*. Labels as in Fig. 3.

variation was probably the result of both natural variance in gland size and loss of secretion material during dissection. The anterior glands were largest, ranging from two to five times the weight of the posterior glands.

The gland consists of a series of secretory lobules embedded in a thick capsule of striated muscle (Figs. 2, 3). Each lobule is further partitioned by connective tissue invaginations. Lobules empty directly into ducts in the central portion of the ventral surface, but there is no tubule system to convey the secretory product to the duct. A thin connective tissue sheath completely surrounds each lobule and contains a moderate number of blood vessels. Surrounding this sheath are bundles of muscle fibers, oriented in all planes around each lobule.

The secretory unit, encased in muscle and connective tissue, is constructed of two types of cells, epithelial and secretory (Figs. 3, 4, 5). Lying internal to the connective tissue is a single layer of epithelial cells with a well developed basal lamina. These cells average 6 μ wide and 10 μ long, and contain large nuclei. They do not form a continuous sheet on the connective tissue, and in a few regions, the differentiated secretory cells can be seen lying on the basal lamina between two epithelial cells or extending to the basal lamina through a narrow space between two epithelial cells.

The epithelial cells have a small amount of cytoplasm which is slightly basophilic, gives light background staining in the PAS reaction (which is eliminated by acetylation), and contains no demonstrable acid mucopolysaccharides or lipid other than phospholipid. The tests for protein also gave light background staining.

Secretory cells producing large secretion droplets form the bulk of the cellular portion of the lobule (Figs. 3 and 4 are representative of lobule morphology). They are large, averaging 36 μ long by 14 μ wide. There are several strata of cells, and near the lobule center the cells undergo degeneration. The cytoplasm of the secretory cells stains deeply for basic dyes and appears granular (Fig. 4). The cytoplasm of each cell surrounds vacuolated areas and secretion droplets of various sizes, including at least one large droplet averaging 9 μ in diameter

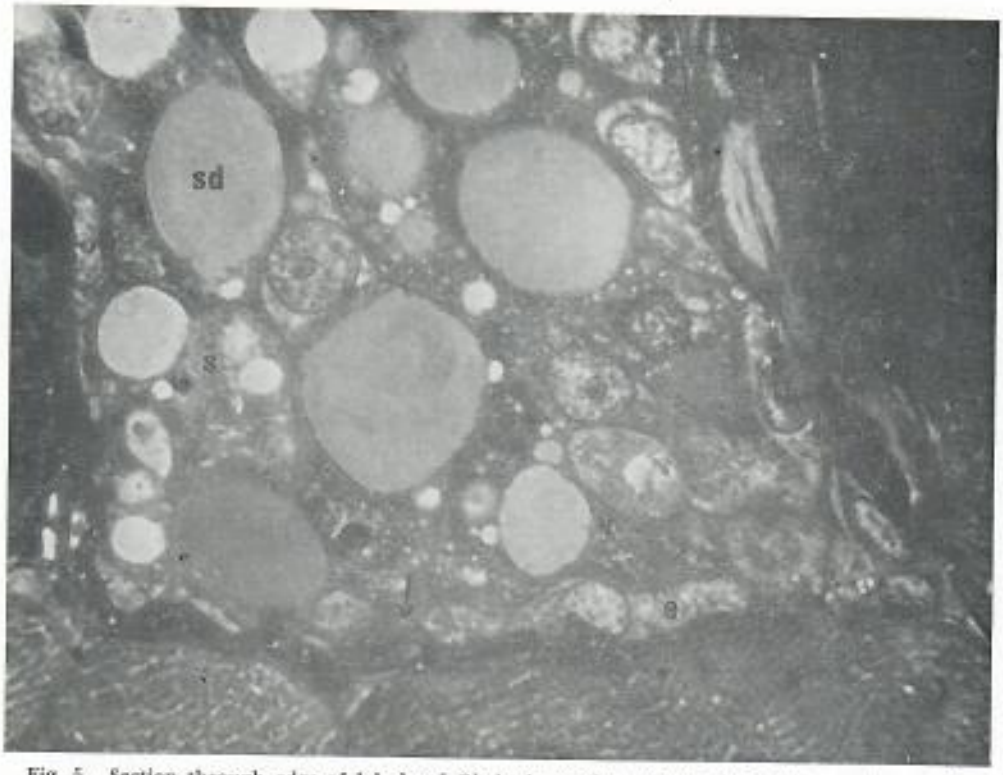

Fig. 5. Section through edge of lobule of *Chelonia mydas*. Arrow indicates secretory cell on basal lamina. v, vacuolated areas; other labels as in Fig. 3. Richardson's stain. (2700 ×).

and ranging up to 19 μ. Secretory cells are of similar size and shape throughout the lobule; cells more distal from the epithelial layer have a slightly decreased amount of cytoplasm and an increased number of droplets. Lobules are often seen with three or four layers of secretory cells and an empty lumen; it is probable that this represents a postsecretory condition. The cytoplasm of these cells has the same staining characteristics as the epithelial cells, but stains more intensely. All PAS-positive staining was abolished by acetylation but not by saliva, and it was restored by treatment with 0.1 N KOH. Methylene blue staining began at pH 3.6 in the cytoplasm. Protein was present in larger amounts than in the epithelial cells. No lipid or acid mucopolysaccharide was detected.

The secretion droplets stained similarly; they contained a mucoprotein with no acidic groups demonstrable by the techniques we used. They stained with methylene blue at pH 4.6. Differences in staining intensity were attributed to partial elution of the droplet material during fixation, but no qualitative differences were found.

In the center of each lobule beyond the layers of secretory cells lies a mass of discrete globules of secretion product surrounded by bits of cytoplasm, membranes, and nuclei (see Fig. 3). Pyknotic nuclei are often seen, but some nuclei retain an open-faced appearance. An acellular matrix surrounds the nuclei and free droplets.

Sternotherus odoratus.—Gland morphology in this turtle is remarkably similar to that of the green turtle. Glands beneath the anterior and posterior edges of the plastral bridges, void secretory products through the axillary or inguinal pores. The four glands comprise approximately 0.1% of the body weight. They are histologically identical and similar in size. Each gland is composed of a single, large unit about 1 mm in diameter and 4 to 5 mm long, which is encircled by a sheath of striated muscle with a thin layer of connective tissue between the secretory portion and the muscle (Fig. 6). The lumen of the gland

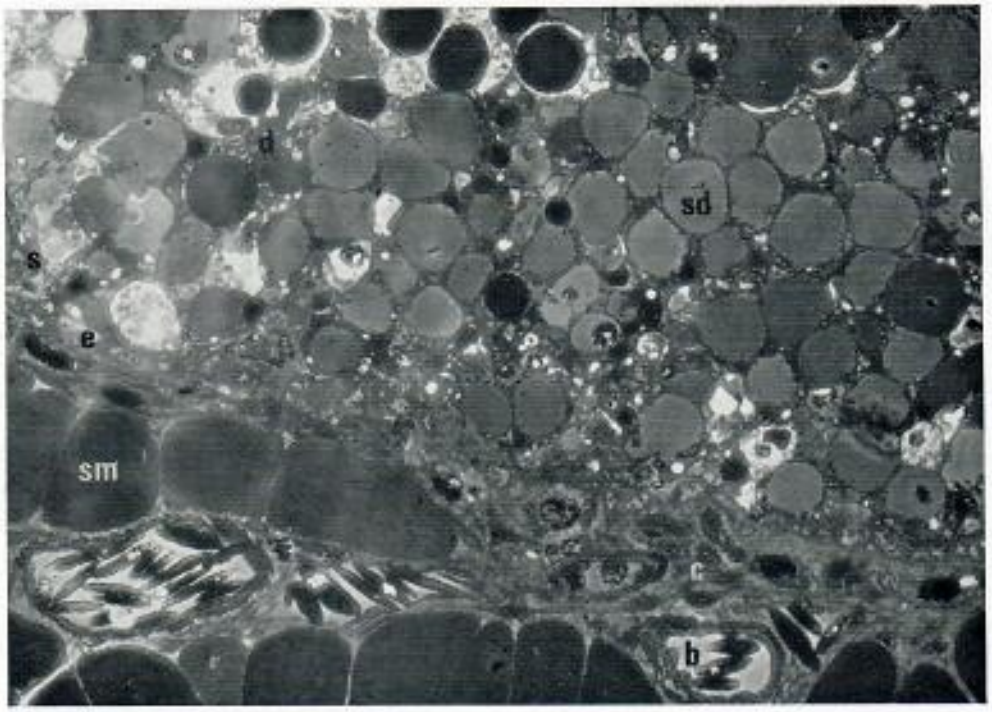

Fig. 6. Cross-section of representative gland of *Sternotherus odoratus*. b, blood vessel; other labels as in Fig. 3. Richardson's stain. (900 ×).

narrows to form a duct at the midpoint of the gland, on the ventral surface. The secretion material is yellow, and has a disagreeable odor.

The secretory portion of the gland is composed of three cell types; there are small epithelial cells and large secretory cells elaborating large droplets of non-lipid material, as in *C. mydas*, but unlike *C. mydas*, there are cells containing many small lipid droplets (Fig. 7). The epithelial cells lie on a basal lamina over the connective tissue. They are about 15 μ long with large nuclei. The cells are similar to those in *C. mydas* in paucity of cytoplasm, light background staining for protein and PAS-positive carbohydrate, and absence of staining for lipid or acid mucopolysaccharide.

The secretory cells are large with finely granular, uniform cytoplasm surrounding circular nuclei about 6.5 μ in diameter and large droplets averaging 14 μ in diameter (Fig. 8). Small droplets are dispersed throughout the cytoplasm. Like the secretory cells in *C. mydas*, the secretory cytoplasm in *S. odoratus* differs from the epithelial cells only in that it stains more deeply for the same components. The secretion droplet material from these cells occupies the bulk of the secretion mass; it is PAS-positive, stains deeply for protein with ninhydrin and naphthol yellow S, contains no demonstrable acidic groups, and has a pH of about 5.3 (as determined with methylene blue staining). Toward the center of the gland the secretory cells degenerate, leaving nuclei interspersed with droplets, which remain discrete.

The lipid containing cells are scattered among the epithelial and secretory cells and the free droplets of the secretory lobule; in addition, they are found among the encircling muscle fibers and connective tissue (Figs. 7, 8). Lipid cells are about 14 μ in diameter and contain numerous sudanophilic droplets surrounding a small nucleus. They appear yellow when not stained, which probably accounts for the color of the secretion material.

Although the pattern of gland morphology in these two turtle species is similar, there are some differences in details. *S. odoratus* does not have the auxiliary glands observed

in some *C. mydas*. The green turtle's glands are proportionally larger (0.5%–0.7% of the body weight), and composed of several lobules, each similar to the single unit of *S. odoratus*. Both epithelial and secretory cells are less basophilic in *C. mydas* than in *S. odoratus*. Finally, no lipid-containing cells are found anywhere in *C. mydas* and the secretion material is not colored.

Lepidochelys olivacea.—A gland from *L. olivacea* reveals a similar histological structure (Fig. 9). Several large holocrine lobules are embedded in bundles of striated muscle; these are lined by an epithelial layer of small cells and contain large secretory cells elaborating large droplets of secretion material. Invaginations of connective tissue divide each lobule into compartments which empty into a large central cavity. The bulk of each lobule is filled with discrete droplets, pyknotic nuclei, and other cell debris. The droplets are of comparable size to those in the green turtle.

Discussion

The axillary and inguinal glands of both *C. mydas* and *S. odoratus* are large exocrine glands specialized for the production and rapid extrusion of a carbohydrate-protein substance. The glands of both species have a similar morphology and histochemistry. A germinal epithelium, consisting of cells with large nuclei and little cytoplasm, probably gives rise to the secretory cells. These cells develop large amounts of cytoplasm which is strongly basophilic, a characteristic of cells containing large amounts of rough endoplasmic reticulum. They have vacuolated areas that probably represent well developed Golgi complexes, and have numerous small and large droplets of secretion product. This morphology is similar to that described for glands producing and secreting a "packaged" product (e.g. Brandes et al., 1965; Ito and Winchester, 1963). In the center of each lobule cells commonly degenerate leaving little cytoplasm, nuclei that are often pyknotic, and intact secretion droplets. This morphology suggests strongly that the glands are holocrine as are most of the integumental glands in reptiles (Quay, 1972). In addition to the positive morphologic evidence, we found no evidence suggesting the presence of ductile systems typical of merocrine glands. The morphological progression from epithelial cells through secretory cells in contact with the basal lamina, to more median layers of cells and finally to cell debris and secretion droplets in the lumen suggests that the glands function by differentiation of epithelial cells, production and accumulation of secretion product, and finally breakdown of the cells.

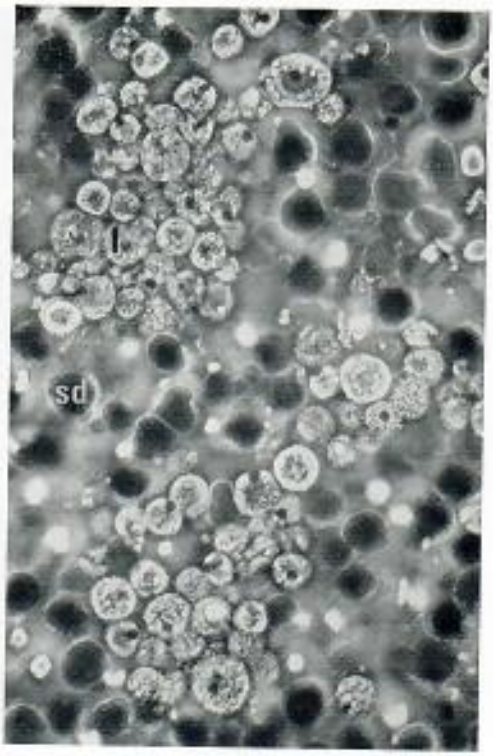

Fig. 7. Lipid droplets in center of *Sternotherus odoratus* gland. l, lipid; sd, secretion droplet. Mallory's stain. (645 ×).

Histochemical tests indicate that the secretion product in both turtle species includes a protein moiety and a carbohydrate moiety. Most PAS-positive substances are known to be protein-carbohydrate complexes (Barka and Anderson, 1963). The consistent results of the various tests for acid mucopolysaccharides indicate that sulfate esters are definitely not present in the carbohydrate fraction and that other acidic groups such as carboxyl groups or sialic acid residues are unlikely as regularly occurring constituents. According to Leppi (1968), this indicates that the product may be a glycoprotein, with a carbohydrate moiety comprising less than 4% of the total molecule, which is composed of

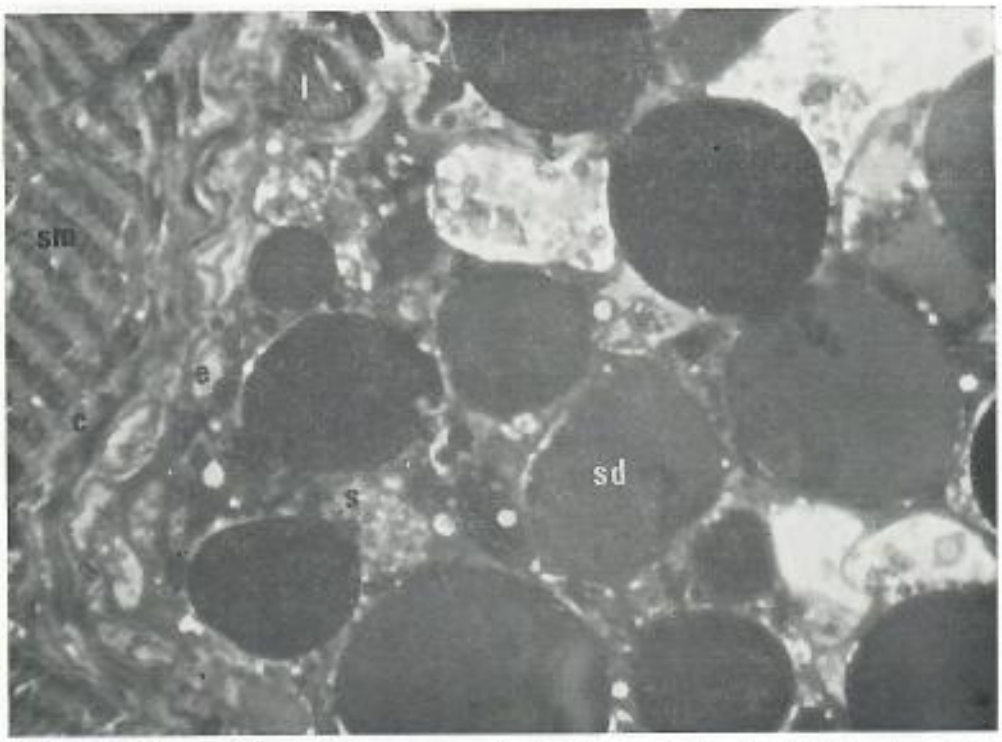

Fig. 8. Cell types in *Sternotherus odoratus* gland. Labels as in Figs. 3, 7. Richardson's stain. (3000 ×).

a short chain of varying residues. A mucoprotein, on the other hand, would be expected to have sulfate esters in the long-chain carbohydrate comprising more than 4% of the total molecule. Although the secretion product stained uniformly in all our tests, we cannot rule out the possibility of undetected components without further biochemical analysis. No reptilian integumentary gland has previously been described that produces mucoproteins (Quay, 1972), although PAS-positive protein-rich materials have been found in other reptiles (Gabe and St. Girons, 1965).

Examination of the glandular tissue of *L. olivacea* suggests that large holocrine glands of similar morphology are found throughout the Cheloniidae. Similarities in the details of position, gross morphology and microscopic morphology among the turtles we examined indicates possibly a common mode of origin of these glands. In the suborder Cryptodira, only the Testudinidae are presumably without these glands; further investigation may yet reveal them. Other studies have mentioned the existence of similar exocrine glands in the Pleurodira (Rathke, 1848; Peters, 1848). Thus, it is possible that these are homologous structures within the order Testudines, although a more comprehensive study would be needed to substantiate this.

Possible gland function, in the light of the characteristics described above, and with respect to the natural history of turtles, is considered below:

1) Functions not involving communication: Excretion of material filtered from the blood seems unlikely; the moderate vascularization, the morphology of the epithelial cells, and the holocrine structure are unlike those characters in any gland known to perform this type of function [e.g. salt gland (Abel and Ellis, 1966), eccrine sweat gland, (Montagna, 1962)]. The mode of extrusion of the secretion material and the small number of duct openings also make it unlikely that the secretion material is a lubricant or other agent designed to remain on the shell. There are, no doubt, other non-communicatory

functions possible, but none have occurred to us that seem consistent with the specific morphology and histochemistry of the gland. Metabolic functions, however, are varied and cannot be excluded.

2) Functions involving intra-species communication: a) Courtship and mating. The occurrence of functional glands of constant relative size in embryos (Neill, 1948a), hatchlings, juveniles and adults of both sexes does not support the hypothesis that the glands are involved in reproductive behavior. However, the chasing behavior seen in some turtles during the mating season could involve a chemical cue, and the chemical diversity of glycoproteins could provide for specificity at the species level. b) Aggregation. Some turtles aggregate at mating and nesting time but most do not; Rathke's glands are widespread among the turtle that do not. Aquatic turtles may aggregate at basking sites, but there is no indication of social interaction at this time. Basking aggregations probably result from a limitation of the number of basking sites, and thus are not necessarily a result of communication. c) Alarm. Turtles are generally asocial organisms, and alarm reactions of the type frequently seen in some fish have not been observed. However, this role is consistent with the hypothesis that the thick, striated muscle capsule of the gland enables rapid emptying, so this function cannot be ruled out. d) Individual recognition. Although species and sex identification occur during mating, we have no evidence that turtles can recognize each other individually. e) Orientation. *C. mydas* and other marine species undertake long-range migrations between nesting beaches and feeding areas; olfaction has been suggested as a possible cue in orientation (Koch, Carr and Ehrenfeld, 1969). However, any substance deposited on the nesting beach (by hatchlings or nesting females) as a site marker would have to be both slightly soluble in seawater and capable of persisting until the following nesting season. It is difficult to conceive of a glycoprotein or related compound having these properties.

3) Functions involving inter-species communication: As indicated above, the function of Rathke's gland must be consistent with its widespread occurrence, with its presence in turtles of both sexes and all ages, with the generally solitary nature of turtle life, and with evidence of the capability of episodic, rapid secretion. A defensive role of the secretion against predators is consistent with these conditions. All turtles have predators. Mammals, birds, large reptiles, amphibians and fish prey on them; turtles of all ages are vulnerable in varying degrees. Adult green turtles, which cannot withdraw into their shells and which are occasionally attacked by sharks (Carr, pers. comm.), have holocrine glands (although the duct openings may disappear with age in some individuals). The box turtle (*Terrapene carolina*) produces an offensive odor when it is a semi-aquatic hatchling (Neill, 1948b) but it does not as a terrestrial, heavily armored adult. Indeed, many turtles that have glands produce a disagreeable odor when handled, although a direct connection between gland and odor has not been established in most cases.

Defense against predators seems the only function considered thus far which might be useful to all turtles possessing such glands.

Fig. 9. Cross-section of gland from *Lepidochelys olivacea*. Labels as in Fig. 3. Hematoxylin and eosin. (420 ×).

It is possible that in some turtle groups the function of the glands has been modified; the lipid-containing cells found in *S. odoratus* but not in *C. mydas* may support this notion. Although the evidence that suggests a primarily defensive role for Rathke's glands is now circumstantial, many of the hypotheses above are amenable to experimental test.

Acknowledgments

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