AN ABSTRACT OF THE THESIS OF

LINDA SUZANNE GIBSON for the MASTER OF ARTS
(Name) (Degree)

in ZOOLOGY presented on March 10, 1969
(Major) (Date)

Title: SEASONAL VARIATIONS IN THE INTEGUMENTAL HISTOLOGY OF THE NEWT, TARICHA GRANULOSA (SKILTON)

Redacted for privacy

Abstract approved: _____
Ernst J. Dornfeld

The integumental histology of Taricha granulosa (Skilton) has been investigated with special attention being given to the seasonal variations associated with terrestrial and aquatic habitats.

The epidermis consists of a stratified squamous epithelium, four to seven cell layers thick, with one to two layers being cornified. The dermis is composed of two layers. The outer stratum spongiosum contains chromatophores, capillaries, smooth muscle cells, fibroblasts and skin glands. The inner stratum compactum is composed of horizontal bundles of collagenous fibers. The granular and mucous glands are simple alveolar glands possessing an intercalary region and a duct. The alveolar wall of the granular gland is comprised of a columnar epithelium, muscle layer, and connective tissue sheath. The mucous gland alveolar wall consists of two layers, a cuboidal to columnar epithelium and a connective

tissue sheath.

The roughness of the terrestrial skin is due to two types of tubercles. Major tubercles are caused by thickening of the epidermis over a dermal papilla, while minor tubercles are merely thickenings of the epidermis.

The aquatic epidermis is less cornified than that of the terrestrial. It also shows a slight increase in height, which is particularly evident in the tail. The swelling of the body and the enlarged tail of the male in the aquatic stage are caused by an edema of the stratum spongiosum. This stage also shows an increase in subepidermal capillaries and an increase in the activity of the mucous glands. Both aquatic and terrestrial animals have granular glands of equal secretory activity.

The aquatic phase possesses fewer glands per unit area of skin due to the increase in the size of the dermis. Terrestrial newts have the smallest granular glands and aquatic newts the largest, though there is a strong overlap of granular gland volume in the two stages. The aquatic phase has the largest mucous glands.

Seasonal Variations in the Integumental Histology of the Newt, Taricha granulosa (Skilton)

by

Linda Suzanne Gibson

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Arts

June 1969

APPROVED:

Redacted for privacy

Professor of Zoology
in charge of major

Redacted for privacy

Chairman of the Department of Zoology

Redacted for privacy

Dean of Graduate School

Date thesis is presented

Typed by Gwendolyn Hansen for Linda Suzanne Gibson

ACKNOWLEDGMENTS

I wish to acknowledge the assistance and support of Dr. Ernst J. Dornfeld, under whose direction this study was performed. I also express special appreciation to Dr. Ronald Altig, Edmund Brodie, Jr. and Jeffery Briggs for advice and aid in obtaining specimens, and to Flash Gibson for help with preparation of the figures.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

SEASONAL VARIATIONS IN THE INTEGUMENTAL HISTOLOGY OF THE NEWT, TARICHA GRANULOSA (SKILTON)

INTRODUCTION

The extensive literature on the integumental histology of amphibians has been well reviewed by Dawson (1920) in his detailed study of Necturus maculosus (Rafinesque). Since Dawson's work, investigations of amphibian integument have been principally concerned with the skin glands. General descriptions of these glands include those of McManus (1937) on Desmognathus fuscus (Rafinesque) and Noble and Noble (1944) on Rana pipiens Linnaeus. The development of the cutaneous glands in several amphibia was first studied by Ancel in 1902. More recently Helff and Stark (1941) and Bovbjerg (1964) discussed the development of skin glands in R. pipiens. Changes that occur in the nuclei of the granular glands during the secretory cycle have been studied by Dawson (1937) and Sacerdote (1956).

Many terrestrial amphibians enter water to breed or hibernate. This seasonal change in habitat is associated with morphological and histological changes in the skin, but the literature on the subject is limited. Tronchet (1952) carried out a brief histochemical study of the seasonal changes in the granular glands of Bufo vulgaris Laurenti. The seasonal changes in the epidermis of Bufo bufo gargarizans (Cantor) have been examined by Kun (1959). Gramentiskii (1964)

studied the seasonal changes in the skin glands of the grass frog, Rana temporaria Linnaeus. Aoto (1950) examined the causes of the swelling of the skin in the breeding (aquatic) male in Hynobius.

In the present study on the Rough-skinned Newt, Taricha granulosa (Skilton), the histology of the integument is investigated with particular references to the seasonal changes associated with terrestrial and aquatic habitats.

MATERIALS AND METHODS

Terrestrial specimens of the Rough-skinned Newt, Taricha granulosa (Skilton), were collected by digging under rocks and logs around ponds on Coffin Butte north of Corvallis, Oregon. Aquatic specimens were collected by dip netting in the ponds. The freshly collected newts were killed by decapitation after ether anesthesia. Anesthesia prevented extreme contraction of the body muscles which made removal of the skin very difficult. Pieces of skin, measuring about one square centimeter, were removed from the dorsal surface of the tail at its proximal end, from the dorsum of the trunk, from the flank, and from the abdomen.

For histological fixation Bouin's solution was used, although some specimens were fixed in Zenker's fluid or Zenker's without acetic acid. The tissue was embedded in both paraffin (sectioned at 10μ) and celloidin (sectioned at 20μ and 25μ). Stains employed were hematoxylin-eosin or allochrome (Schiff's reagent, Weigert's hematoxylin, picric acid, and aniline blue). The allochrome method differentiates mucus.

Measurements were made by use of a linear-scale ocular micrometer. Glands were counted and measured from serial sections.

OBSERVATIONS

Taricha granulosa inhabits a wooded terrestrial environment during the summer months but breeds in temporary ponds and streams during the winter and spring. As fall rains start in September, the males migrate to water. The females do not begin migration until December or January and breeding takes place between January and July. When breeding is completed, the animals return to forested land. This change in habitat is associated with characteristic modifications of the integument. In the aquatic stage, the skin is smooth and swollen in contrast to a rough and firm texture in the terrestrial period (Figure 1, 2). In the male the aquatic phase is also characterized by development of a broad tail adapted to swimming.

Epidermis

The epidermis is composed of a stratified squamous epithelium four to seven cell layers deep. The cytoplasm of the epithelial cells contains pigment granules between the nucleus and the outer cell membrane, and chromatophores are present between the epithelial cells. The ventral surface of the newt contains no pigmentation.

The epidermis of terrestrial animals differs from the aquatic in possessing an additional layer of cornified cells (Table 1). Terrestrial newts also possess numerous epidermal tubercles

Figures 1, 3), while the aquatic epidermis is generally smooth (Figures 2, 12). Tubercles are elevated areas of the epidermis and are of two types: major tubercles, produced by a thickening of the epidermis overlying a dermal papilla, and minor tubercles consisting only of a thickened epidermis (Figure 3). The aquatic epidermis also shows a tendency to be uniformly thicker, especially on the tail (Table 1).

Lateral line organs are present in the tail of both terrestrial and aquatic animals (Figure 7). These consist of isolated sensoria embedded in the epidermis. A single organ is open to the surface via an epidermal pit and consists of a rounded mass of epidermal supporting cells surrounding a core of sensory cells. The base of the organ extends into the dermis, but is bounded by a basement membrane.

Dermis

The dermis consists of two layers, an outer stratum spongiosum and an inner stratum compactum (Figure 3). The stratum compactum usually lies next to the body musculature, but a subcutis may separate it from the latter. It is composed of horizontal bundles of dense irregular collagenous fibers. This layer is missing in the tail. The stratum spongiosum is composed of loosely joined bundles of collagenous and elastic fibers. It contains capillaries, fibroblasts,

chromatophores, and scattered smooth muscle cells. Skin glands are embedded in this layer. Chromatophores occur immediately under the epidermis and may surround the glands. The separation of the dermis into two parts can be strikingly demonstrated by the allochrome stain in which the stratum spongiosum is blue and the stratum compactum is yellowish.

Dermal height varies with seasonal change in habitat (Table 1). The stratum spongiosum becomes swollen (edematous) and less dense in the aquatic stage. The aquatic dermis also contains a greater number of subepidermal capillaries.

Granular Glands

The granular glands are simple alveolar glands which are found in the dermis throughout the body. They are normally spherical, but may become of irregular shape due to pressure of body musculature or neighboring glands. The glands are composed of three parts: alveolus, intercalary region, and duct.

The alveolus of the granular gland is made up of three layers. Innermost is the glandular epithelium, which consists of high, secretory columnar cells (Figures 4, 8). As the gland ages, the cell boundaries break down, leaving a secretion-filled sack. The basically-positioned nuclei of these cells are very large, due to their polyploidy (Truong and Dornfeld, 1955). They are initially spherical,

but become elongated or dome-shaped with increasing ploidy. The cells may also be binucleate. After the cell boundaries disappear the nuclei become displaced within the alveolus and can be extruded with the secretion. Surrounding the glandular epithelium is a thin layer of smooth muscle (Figures 4, 11). The muscle fibers run longitudinally over the body of the gland and end in the intercalary region. This muscle layer is most readily seen in glands that are not distended with secretion (Figure 14). Exteriorly the alveolus possesses a connective tissue sheath (Figure 4) which is continuous with the fibers making up the stratum spongiosum.

The intercalary region, or collar, is composed of a group of epithelial cells, two to three layers thick, which are radially arranged around the base of the duct (Figures 5, 8). It marks the transition from duct to alveolus.

The duct, which runs perpendicularly through the epidermis to the skin surface, is straight and cylindrical. It opens on the surface through a specialized stoma cell, the pore being intracellular. Surrounding the stoma cell are several crescent-shaped funnel cells which serve as replacements for the stoma cell after molting (Esterly, 1904) (Figure 6).

Granular glands show several stages of development and activity in an individual animal. The mature glands are the most numerous. These are large and are filled with acidophilic secretion. Cell

boundaries are usually broken down, but may persist in the basal part of the gland. The secretion appears granular or alveolar. The alveolar appearance, usually in the upper portion of the alveolus, is probably a fixation artifact and is dependent on the age of the secretion (Dawson, 1920) (Figures 4, 8, 15). The mature glands usually have a mucoid replacement gland located below the intercalary region (Figure 16). It can range from a bud of cells to a luminated alveolus.

Exhausted glands are small and spherical or irregularly-shaped. The nuclei are usually large and darkly staining. The glands contain debris which may represent secretion and/or cell membrane remnants. In some cases a cuboidal replacement epithelium is visible around the body of the gland (Figure 12). In others a mucoid gland appears to be growing into the space of the degenerating granular gland (Figure 13).

Immature granular glands have a high columnar epithelium. The nuclei are small, spherical, and are basically located. There are few secretion granules in the cytoplasm (Figure 14).

The study of the seasonal variations in the glands was limited to the tail region, as it undergoes the greatest morphological change in the migration from a terrestrial to an aquatic environment. The histological features, the volumes, and the numbers of glands per unit area of skin were compared.

With regard to histological structure, there were no discernible differences in the granular glands of terrestrial and aquatic animals. Both have glands of equal secretory activity.

With respect to average gland volumes (mature glands, only, considered), no statistically significant difference was found between terrestrial and aquatic newts (Table 2); the volumes were strongly overlapping. However, the smallest granular glands were restricted to terrestrial individuals, while the largest occurred in the aquatic form.

The number of granular glands per unit area of skin was calculated to determine if there is a seasonal change in this respect (Table 2). A decrease in the number of glands was noted in the aquatic stage. This is probably due to the increase of the size of the dermis which reduces the number of glands per unit area.

Mucous Glands

Mucous glands are smaller than granular glands. They are simple alveolar glands and are spherical or oval in shape. Mucous glands, like granular glands, are composed of an alveolus, intercalary region, and duct.

The alveolar wall possesses only two layers, the glandular epithelium and a connective tissue sheath. The epithelium consists of a single layer of cuboidal to columnar cells which surrounds a

lumen into which the secretion is discharged (Figures 9, 10, 14). The nuclei are oval, basically situated and lightly staining. The cells are capable of continuous secretion, in contrast to the granular gland cells whose secretory activity is followed by degeneration. The mucous secretion appears in diffuse granular form within the cytoplasm and in the glandular lumen. Muscle nuclei were seen in the intercalary region, but were not observed around the alveolar wall. The duct and intercalary regions of the mucous glands resemble those of granular glands. In senescent mucous glands, cytolysis may be observed and the entire alveolus shows a diffuse positive stain reaction for mucus (Figure 17).

Terrestrial and aquatic animals show histological differences in their mucous glands. Mucous glands in the terrestrial stage possess a low epithelium and a large lumen. This lumen is not infrequently empty, indicating that the cells are relatively inactive (Figure 14). In the aquatic stage, the epithelium may be higher and the lumen always contains secretion (Figure 9). Occasionally there are glands with a high columnar epithelium and a very small, secretion-filled lumen (Figure 10). The aquatic stage is therefore one of active mucus secretion. Aquatic mucous glands are also larger than terrestrial ones (Table 2). The difference in the number of mucous glands per unit area between terrestrial and aquatic

animals (less in the latter) can be attributed to the change in the size of the dermis, as in granular glands.

DISCUSSION

Although the integumental histology of T. granulosa is similar to that of other amphibia, especially urodeles, there are some differences that are worth noting.

Epidermis

The epidermis of T. granulosa is similar to that of other terrestrial amphibia, but unlike that of Necturus and a few other aquatic urodeles. The latter have retained the larval characteristics of a cuticular border and cells of Leydig.

Dermis

Dawson (1920) distinguished three dermal layers in Necturus: an inner compact, an intermediate spongy, and an outer compact layer. The latter, which is thin, replaces a basement membrane. However, recent electron microscope studies (Singer and Andrews, 1951; Pillai, 1962; Voute, 1963) have demonstrated the presence of an amorphous basement membrane in both urodeles and anurans. This is in agreement with my interpretation that the dermis of T. granulosa is two-layered.

Esterly, in his study of Plethodon oregonensis (1904), and Dawson (1920), in his work on Necturus, note that the perpendicular

collagenous fibers pass from the inner compact layer of the dermis to the spongy layer and serve to support the glands. In T. granulosa the collagenous fibers of the stratum compactum show only horizontal alignment.

Granular Glands

Granular glands in various amphibia are somewhat specialized. The very large glands in the tail of Plethodon oregonensis have evolved with the ability of the animal to shed its tail when disturbed (Esterly, 1904). Ambystoma gracile Baird also has concentrations of very large glands in the tail, in the parotoid gland and in the costal folds. The placement of these glands is correlated with the defensive postures of the animal (Brodie and Gibson, 1969). The glandular ducts of both these urodeles possess constrictor and dilator muscles. In addition, Ambystoma has a large muscle mass around the neck of the gland. The granular glands of T. granulosa, Necturus, and many other amphibia do not show these characteristics.

Mucous Glands

Most early investigators reported that muscle fibers do not surround mucous glands. Noble and Noble (1944) found it difficult to identify muscle around the mucous glands of R. pipiens. However, Voute (1963) in an electron microscope study, described myoepithelial

cells in this position. In T. granulosa, nuclei of muscle cells were identified in the intercalary region of the mucous glands, but fibers could not be identified around the alveolus.

Seasonal Variations

The integument of T. granulosa shows striking morphological change as the newt moves from a terrestrial to an aquatic environment.

In the terrestrial state the roughness of the skin is due to papillary elevations, or tubercles, which are conspicuous on the surface. In the aquatic stage both major and minor tubercles are absent, resulting in a smooth integument.

The terrestrial epidermis is more highly cornified than that of the aquatic, which aids in preventing desiccation of the animal. Kun (1959) also found an increase in the amount of cornification in the epidermis of terrestrial forms of Bufo bufo gargarizans. In the tail of terrestrial newts, the height of the epidermis is less than that of the aquatic. This difference in height is due to a change in cell size, not in cell number. The data do not show a significant difference in epidermal height in the other body areas, although there is a tendency for the overall height to be slightly greater in the aquatic stage. Kun, however, found that the aquatic epidermis is thinner, a modification that facilitates cutaneous respiration. Aquatic T. granulosa has an

increased number of capillaries below the epidermis which shows that cutaneous respiration indeed prevails. The reason for the tendency toward increase rather than decrease in the height of the aquatic epidermis is unclear.

The conspicuous swelling of the skin in the aquatic stage, and the formation of the enlarged tail in males, is due to an edema of the dermis, specifically the stratum spongiosum. Leydig (1892) also found the dermis in breeding males of Rana fusca Schneider and Triturus cristatus Laurenti to undergo swelling by water absorption. However, Aoto (1950) reported that in the breeding male Hynobius, the swelling of the skin is due to a distention of the subcutaneous connective tissue, not of the dermis.

Terrestrial T. granulosa are very dry to the touch. In contrast, aquatic individuals are always slimy, a result of the increased activity of the mucous glands. Gramenitskii (1964) similarly found a rise in the activity of large mucous glands in the aquatic stage of Rana temporaria. The increased activity of the glands is probably an aid to cutaneous respiration (Parakkal and Matoltsky, 1964).

The granular gland secretion of T. granulosa is extremely toxic (Brodie, 1967). The glands thus have a protective function. It is reasonable to assume that the need for protection is equally great in both environments. Examination of the granular glands shows that there is no difference in the secretory activity of the two stages.

Gramenitskii (1964) found that granular glands show a decrease in activity in the aquatic stage of R. temporaria; such frogs, however, are in hibernation.

SUMMARY

1. The integumental histology of Taricha granulosa (Skilton) has been investigated with special attention being given to the seasonal variations associated with terrestrial and aquatic habitats.

2. Skin from the dorsal tail, dorsal trunk, flank, and abdomen was fixed in Bouin's or Zenker's fixative. The tissue was embedded in paraffin or celloidin and stained with hematoxylin-eosin or allochrome.

3. The epidermis consists of a stratified squamous epithelium, four to seven cell layers thick. Terrestrial animals have two layers of cornified cells, while aquatics have just one.

Lateral line organs are present in both terrestrial and aquatic animals.

The dermis is composed of two layers. The outer stratum spongiosum is constructed of loose irregularly-aligned bundles of collagenous and elastic fibers. It contains fibroblasts, smooth muscle cells, capillaries, chromatophores, and the skin glands. The stratum spongiosum becomes edematous in the aquatic stage. The stratum compactum, which adjoins the body musculature or an intervening subcutis, consists of horizontally aligned collagenous fibers. It is absent in the tail.

4. The skin glands comprise large acidophilic granular glands and small basophilic mucous glands. Both types are of simple alveolar pattern, with an intercalary region and a duct.

The alveolar wall of the granular gland is composed of three layers: a glandular epithelium of columnar cells which degenerate upon elaboration of the secretion, a thin surrounding layer of smooth muscle whose fibers run longitudinally over the gland wall, and a connective tissue sheath whose fibers are continuous with those of the stratum spongiosum. The intercalary region of the granular gland is composed of a group of epithelial cells, two to three layers thick, which are radially arranged around the base of the duct. The straight duct passes through the epidermis and opens on the surface through a specialized stoma cell. Exhausted granular glands are small, with large and darkly staining nuclei; they possess either a mucoid replacement gland or a replacement epithelium. Immature granular glands possess a columnar epithelium with little granular secretion.

The alveolar wall of the mucous glands is two-layered: an inner glandular epithelium of cuboidal to columnar cells, and an outer connective tissue sheath. The intercalary region and the duct of the mucous glands are similar to those of the granular glands; muscle fibers are present in the intercalary region.

5. The roughness of the terrestrial skin is produced by two types of tubercles: major tubercles with a thickened epidermis overlying dermal papillae, and minor tubercles consisting of only thickenings of the epidermis. These are absent in the aquatic stage, leaving the skin smooth.

The aquatic stage is characterized by an increase in subepidermal capillaries, by reduced cornification of the epidermis, and by more active mucous glands. Granular glands show equal secretory activity in both terrestrial and aquatic newts. Because of the dermal edema, the aquatic phase shows fewer glands of both types per unit area of skin. Terrestrial newts have the smallest granular glands and aquatic newts the largest, though there is a strong overlap of granular gland volume. The aquatic phase has the largest mucous glands.

Table 1. Comparison of epidermis and dermis in terrestrial and aquatic animals.

	Terrestrial Phase				Aquatic Phase			
	Dorsal Tail	Dorsum	Flank	Abdomen	Dorsal Tail	Dorsum	Flank	Abdomen
Number of Epidermal Cell Layers	5-7 (2 corn.)	5-6 (2 corn.)	4-6 (2 corn.)	5-6 (2 corn.)	6-7 (1 corn.)	4-7 (1 corn.)	4-6 (1 corn.)	5-7 (1 corn.)
Average Height of Epidermis	.05mm	.04mm	.05mm	.06mm	.09mm	.07mm	.06mm	.08mm
Average Height of Dermis	.11mm	.17mm	.21mm	.17mm	.44mm	.31mm	.35mm	.26mm

Table 2. Comparison of volumes of glands and numbers of glands per unit area in terrestrial and aquatic tails.

	Terrestrial	Aquatic
Average granular gland volume and range (10 glands)	$.00885mm^3$ $.00083mm^3$-$.02643mm^3$	$.03122mm^3$ $.00536mm^3$-$.06125mm^3$
Average mucous gland volume and range (10 glands)	$.00065mm^3$ $.00038mm^3$-$.00088mm^3$	$.00111mm^3$ $.00058mm^3$-$.00150mm^3$
Number of granular glands	$29/mm^2$	$22/mm^2$
Number of mucous glands	$9/mm^2$	$5/mm^2$

PLATE 1

Figure 1. Terrestrial Taricha granulosa male. (1X)

Figure 2. Aquatic Taricha granulosa male. (1X)

PLATE 1

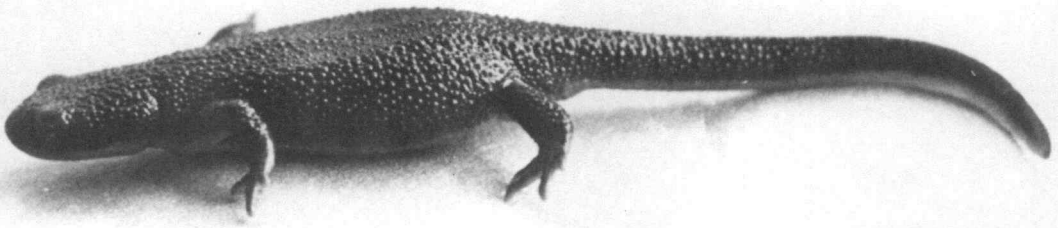

FIGURE 1

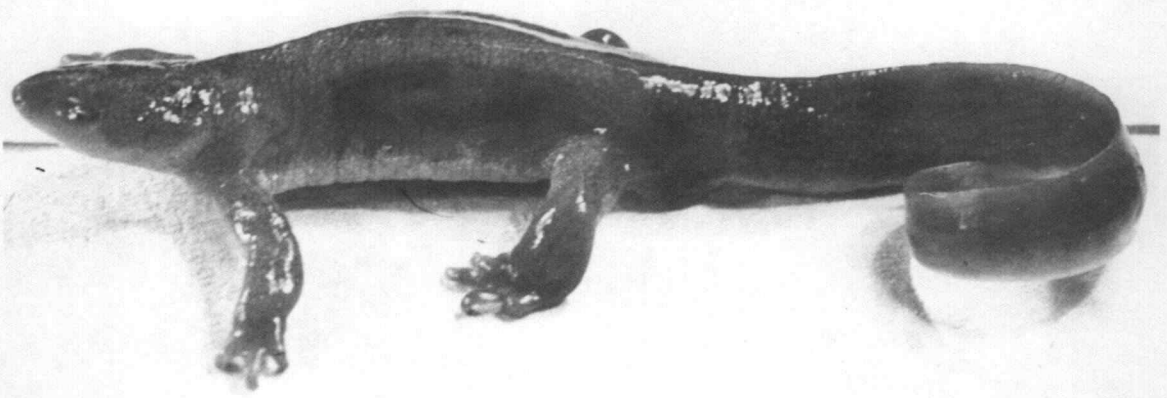

FIGURE 2

PLATE 2

Figure 3. Terrestrial integument. a. epidermis b. stratum spongiosum c. stratum compactum d. body musculature e. granular gland. Note major tubercle which is a combination of a and b and minor tubercles, located above e. (170X)

Figure 4. Mature granular gland. a. muscle fiber nucleus b. alveolar secretion c. granular secretion in glandular epithelial cell d. connective tissue sheath. Note that cell boundaries still persist. (163X)

Figure 5. Cross section of granular gland through intercalary region. Note radial arrangement of cells. (230X)

Figure 6. Surface view of epidermis showing stoma cell and funnel cells. a. nucleus of funnel cell b. pore of duct within stoma cell. (1670X)

PLATE 2

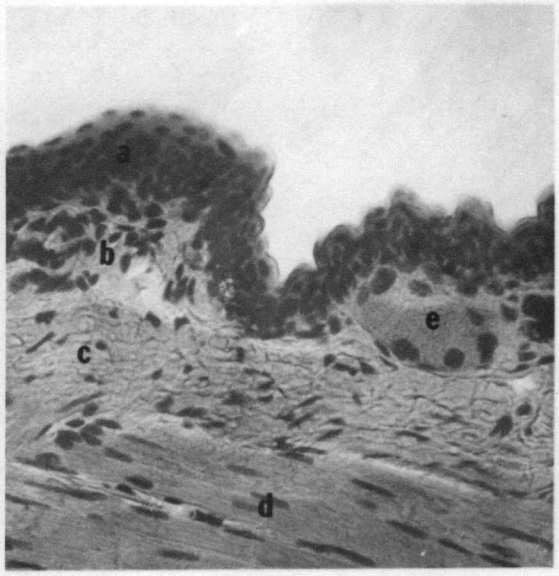

FIGURE 3

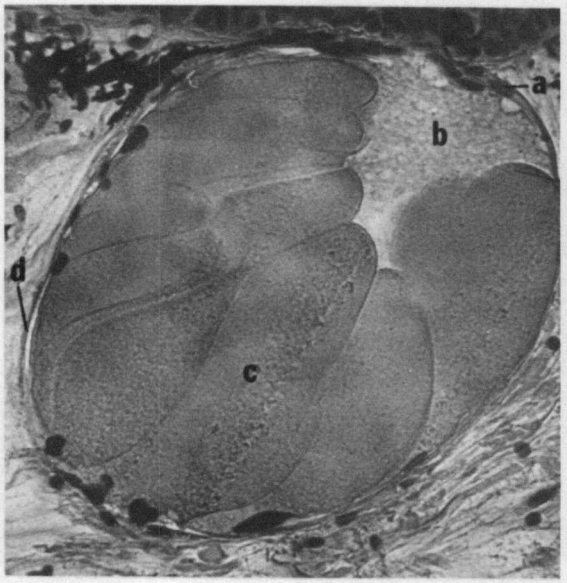

FIGURE 4

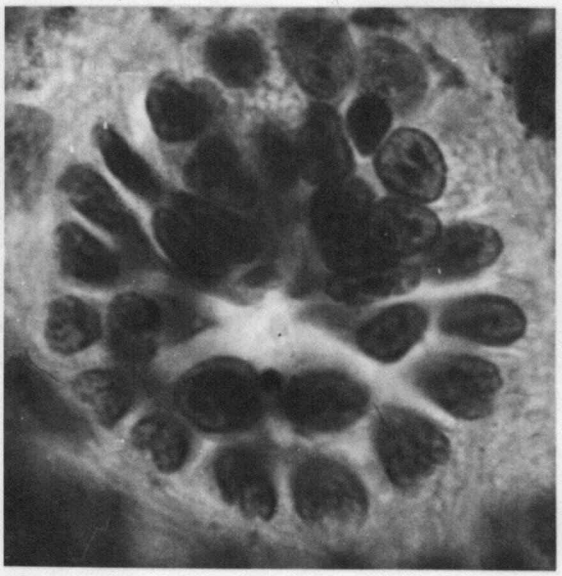

FIGURE 5

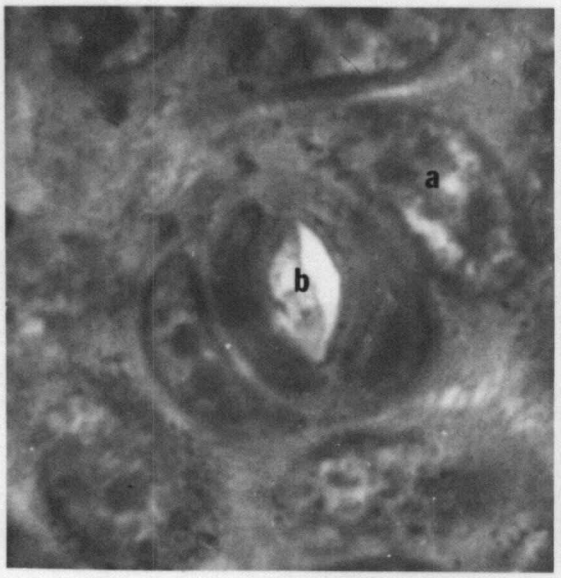

FIGURE 6

PLATE 3

Figure 7. Lateral line organ. Note the surrounding mass of supporting cells and the inner sensory cells. (177X)

Figure 8. Mature granular gland. a. intercalary region b. subepidermal capillary. Note alveolar and granular secretion. (180X)

Figure 9. Mucous gland. a. chromatophore b. lumen of mucous gland filled with diffuse granular secretion. Note cuboidal glandular epithelium with basically located nuclei, and intercalary region at base of duct. (190X)

Figure 10. Aquatic mucous gland with high columnar epithelium. (190X)

PLATE 3

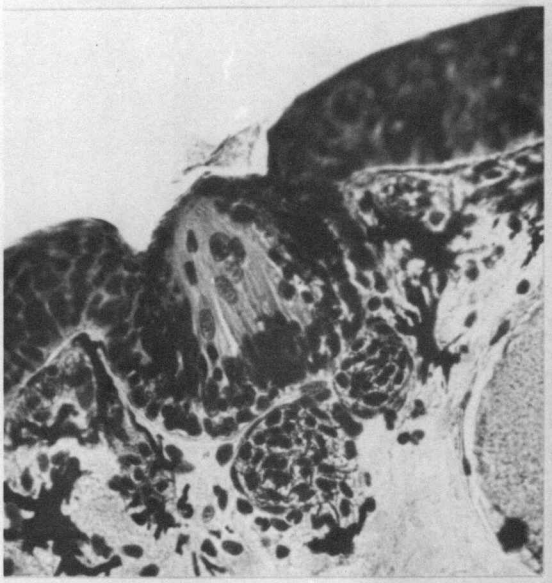

FIGURE 7

FIGURE 8

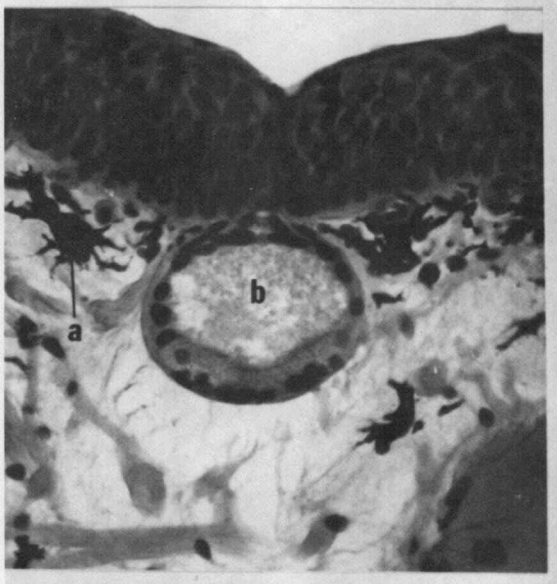

FIGURE 9

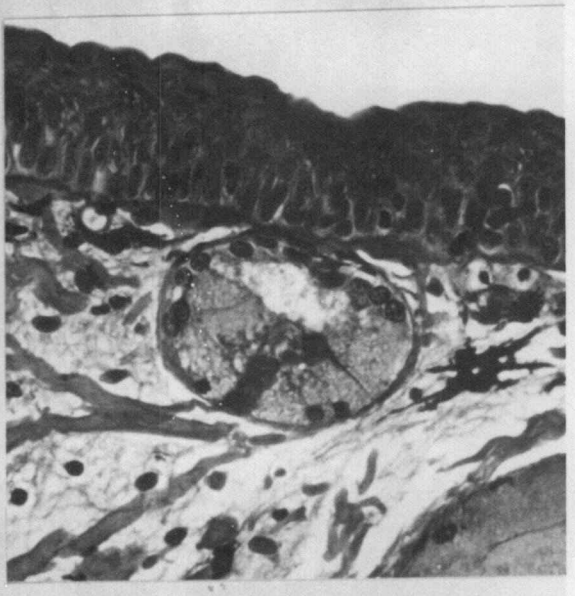

FIGURE 10

PLATE 4

Figure 11. Tangential section of granular gland showing muscle fibers. a. muscle nuclei. Note that all muscle nuclei run longitudinally. (830X)

Figure 12. Exhausted granular gland with a. replacement epithelium. Note the large displaced nuclei within the glandular lumen. Some secretion is also visible. Note also the smoothness of the aquatic epidermis and the diffuseness of the stratum spongiosum (compare with Figure 3). (190X)

Figure 13. Exhausted granular gland with mucoid replacement gland. a. replacement gland b. granular gland. Note displaced granular nuclei with debris in gland lumen. (190X)

Figure 14. Immature granular gland. a. muscle fiber and nucleus. Note columnar epithelial cells with basically located nuclei. Cells contain few secretion granules. To the left is a terrestrial mucous gland. Note absence of secretion in lumen. (163X)

PLATE 4

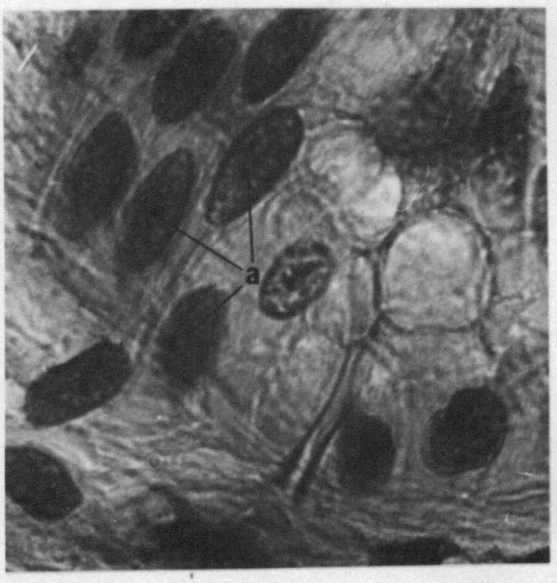

FIGURE 11

FIGURE 12

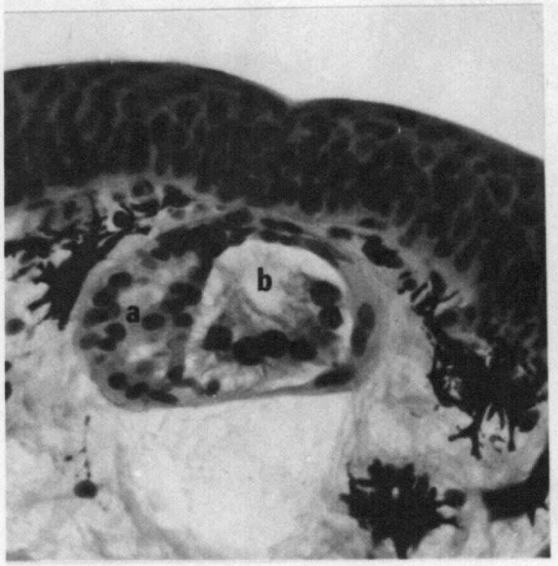

FIGURE 13

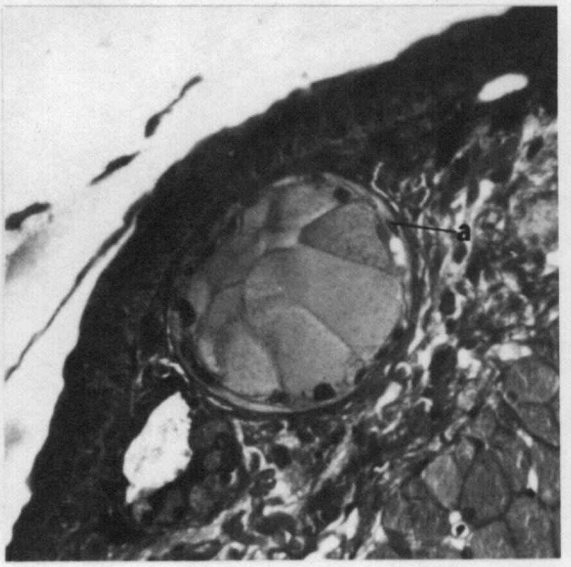

FIGURE 14

PLATE 5

Figure 15. Mature granular gland. a. granular secretion b. alveolar secretion. Note absence of cell boundaries. Intercalary region is visible at base of duct. (150X)

Figure 16. Cross section of granular gland showing mucoid replacement gland (a). (250X)

Figure 17. Senescent mucous gland. Note absence of cell boundaries and displaced nuclei. (190X)

PLATE 5

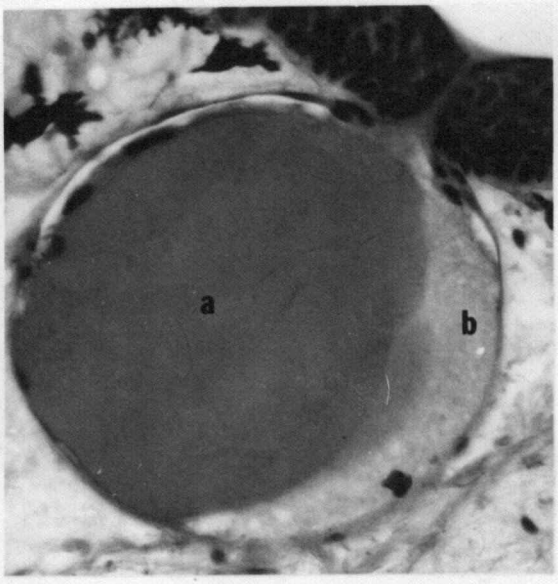

FIGURE 15

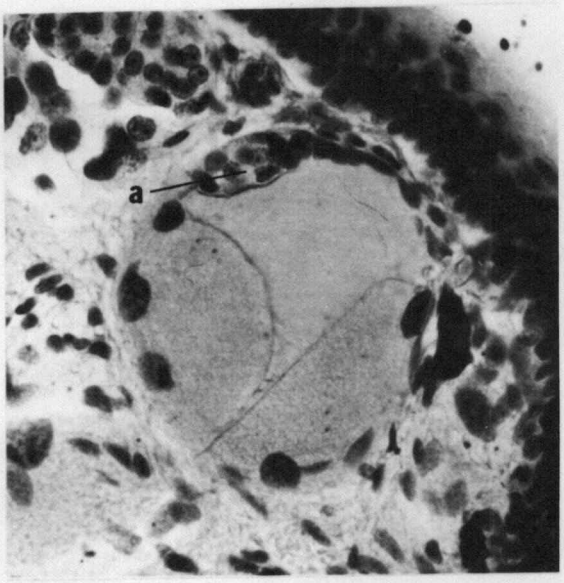

FIGURE 16

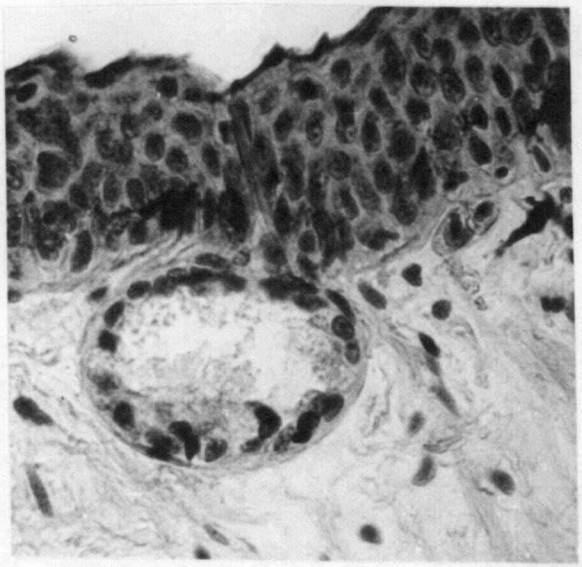

FIGURE 17

BIBLIOGRAPHY

Ancel, P. 1902. Étude du développement des glandes de la peau des Batraciens et en particulier de la Salamandre terrestre. Archives de Biologie 18:257-289.

Aoto, T. 1950. A remarkable swelling of male skin of a salamander (Hynobius) in the breeding season. Journal of the Faculty of Science (Hokkaido University), Ser. 6, 10:45-53.

Bovbjerg, Ann M. 1964. Development of the glands of the dermal plicae in Rana pipiens. Journal of Morphology 113:231-243.

Brodie, Edmund D., Jr. 1967. Inverstigations on the skin toxin of the adult Rough-skinned Newt, Taricha granulosa. Copeia, 1968, p. 307-313.

Brodie, Edmund D., Jr. and Linda S. Gibson. 1969. Defense behavior and related glandular concentrations of the north-western salamander, Ambystoma gracile. (Submitted to Copeia)

Dawson, Alden B. 1920. The integument of Necturus maculosus. Journal of Morphology 34:487-589.

Dawson, Alden B. 1937. Changes in the volume, form and internal architecture of the nuclei of the granular glands of the integument of the newt, Triturus viridenscens. Journal of Morphology 61:385-397.

Esterly, C. O. 1904. The structure and regeneration of the poison glands of Plethodon. University of California Publications in Zoology 1:227-268.

Gramenitskii, E. M. 1964. Seasonal cytochemical changes in the cutaneous glands of the grass frog (Rana temporaria). (Abstract) In: Problems of herpetology, ed. by Paul V. Terent'ev. 1964. Leningrad, University of Leningrad. (Microfilm) (In Russian)

Helff, O. M. and William Stark. 1941. Studies on amphibian metamorphosis. Journal of Morphology 68:303-327.

Kun, Skin Lian. 1959. Observations on the seasonal changes in the histological structure of the skin of the giant toad, (Bufo bufo gargarizans (Cantor). Acta Zoologica Sinica 11:313-330. (Abstracted in Biological Abstracts 35:no. 59050. 1960)

Leydig, F. 1892. Integument brünstiger Fische und Amphibien. Biologisches Centralblatt 12:205-221.

McManus, Mary Idolene. 1937. A cytological study of the skin glands of the dusky salamander. Journal of the Elisha Mitchell Scientific Society 53:101-111.

Noble, Glenn A. and Elmer R. Noble. 1944. On the histology of frog skin glands. Transactions of the American Microscopical Society 63:254-263.

Parakkal, Paul F. and A. Gedeon Matoltsy. 1964. A study of the fine structure of the epidermis of Rana pipiens. Journal of Cell Biology 20:85-94.

Pillai, P. Aiyappan. 1962. Electron microscopic studies on the epidermis of newt with an enquiry into the problem of induced neoplasia. Protoplasma 55:10-62.

Sacerdote, M. 1955. Nuovi dati sul ciclo secretorio e sulla struttura del nucleo nelle ghiandole granulose cutanee di Salamandra salamandra. Archivio Zoologico Italiano 40: 361-397. (Abstracted in Biological Abstracts 32:no. 30848. 1958)

Singer, Marcus and Jean S. Andrews. 1951. The adepidermal reticular network of the skin of the urodele, Triturus. Anatomical Record 109:346-347.

Tronchet, J. 1952. Etude des glandes à venin de Bufo vulgaris (Laur) en fonction de la saison. Bulletin de la Société Zoologique de France 77:241-242.

Truong, Simone Thi-hue and Ernst J. Dornfeld. 1955. Desoxyribosenuclei acid content in the nuclei of salamander somatic tissues. Biological Bulletin 108:242-251.

Voute, Cornelis L. 1963. An electron microscopic study of the skin of the frog (Rana pipiens). Journal of Ultrastructure Research 9:497-510.