THE DORSAL HOLOCRINE SKIN GLAND OF THE KANGAROO RAT (DIPODOMYS)[1]

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EIGHT FIGURES

INTRODUCTION

The dorsal, holocrine, skin gland of the kangaroo rat (*Dipodomys*) is an area of modified and enlarged sebaceous gland units in the mid-dorsal skin over the arch of the back. It has been found in all examined species of the genus and its gross seasonal and sexual variations in size and secretory activity, differing from species to species, have been described (Quay, '53). The present report describes the microscopic structure and composition of the gland, as it appears in the species *agilis, spectabilis, merriami, ordi, deserti,* and *panamintinus.* The taxonomic arrangement follows that of Setzer ('49).

MATERIAL AND METHODS

The specimens studied and their data are listed in table 1. The techniques used may for convenience be divided into histological and histochemical categories and are as follows.

Histological techniques

(1) Ehrlich's acid hematoxylin and eosin; (2) Heidenhain's iron hematoxylin (Bensley and Bensley, '38) without counterstain; (3) Taenzer-Unna acid orcein method for

[1] I wish to thank W. H. Burt and E. T. Hooper of the Museum of Zoology for facilities and for the opportunity of examining specimens in their care, and Robert Smith for aiding in the collection of specimens.

TABLE 1

List of specimens and their data

SPECIMEN NUMBER [1]	SPECIES	SEX	DATE OF COLLECTION	LOCALITY	FIXATION FLUID	TIME	PARAFFIN (P) OR FROZEN (F) SECTIONS	TECHNIQUES PERFORMED
D 364	D. merriami	♂	Aug. 2, '48	Brewster Co., Tex.	FA [2]	2 yrs.	P	1.
D 295	D. merriami	♂	July 3, '48	Brewster Co., Tex.	FA	2½ yrs.	P	1.
D 514	D. merriami	♂	Sept. 27, '48	Brewster Co., Tex.	FA	2 yrs.	P	1.
UM 56110	D. merriami	♂	June 21, '24	San Bernardino Co., Cal.	FA	26 yrs.	P	1.
UM 61690a	D. merriami	♀	Apr. 18, '30	Pima Co., Ariz.	FA	20 yrs.	P	1.
UM 61691a	D. merriami	♂	Apr. 8, '30	Pima Co., Ariz.	FA	20 yrs.	P	1.
UM 56111	D. merriami	♂	June 21, '24	San Bernardino Co., Cal.	FA	26 yrs.	P	1.
UM 93543	D. agilis	♀	May 14, '48	San Diego Co., Cal.	FA	2 yrs.	P	1.
UM 81238	D. panamintinus	♀	July 27, '38	Mono Co., Cal.	FA	12 yrs.	P	1.
UM 87033	D. spectabilis	♂	Apr. 14, '41	Cochise Co., Ariz.	FA	10 yrs.	P	2,3,4,5,6.
UM 87032	D. spectabilis	♀	Apr. 16, '41	Cochise Co., Ariz.	FA	10 yrs.	P	2,3,4,5,7.
D 27	D. merriami	♂	Mar. 19, '47	Brewster Co., Tex.	FA	4½ yrs.	P	2,3,4,5,6.
D 39	D. merriami	♂	Apr. 14, '47	Brewster Co., Tex.	FA	4 yrs.	P	5.
D 139	D. merriami	♂	Apr. 23, '48	Brewster Co., Tex.	FA	3 yrs.	P	5.
3-C-192	D. merriami	♂	July 8, '51	Inyo Co., Cal.	Bouin's	5 wks.	P	2,3,5,6.
D 357	D. merriami	♀	Aug. 1, '48	Brewster Co., Tex.	FA	3 yrs.	P	2,5.
UM 76148	D. ordi	♂	June 14, '36	Woods Co., Okla.	FA	15 yrs.	P	2,5.
UM 76150	D. ordi	♀	June 14, '36	Woods Co., Okla.	FA	15 yrs.	P	2,3,4,5,6.
3-C-284	D. ordi	♀	July 21, '51	Harney Co., Ore.	Bouin's	3 wks.	P	2,3,5,6.
UM 81460	D. ordi	♂	Oct. 11, '38	Otero Co., N. Mex.	FA	12 yrs.	P	2,3,4,5,6.
3-C-188	D. deserti	♂	July 8, '51	Inyo Co., Cal.	Bouin's	5 wks.	P	2,3,4,5,6.
3-C-193	D. deserti	♀	July 8, '51	Inyo Co., Cal.	Bouin's	5 wks.	P	2,3,5,6.
3-C-201	D. merriami	♂	July 8, '51	Inyo Co., Cal.	10% NBF [3]	5 wks.	F	8,11,12,13,14,15,16,18.
3-C-285	D. ordi	♂	July 22, '51	Harney Co., Ore.	10% NBF	3 wks.	F	8,9,10,11,12,13,14,15,16,18.
3-C-189	D. deserti	♂	July 8, '51	Inyo Co., Cal.	10% NBF	5 wks.	F	8,9,11,12,13,14,15,16,18.
3-C-195	D. deserti	♂	July 8, '51	Inyo Co., Cal.	10% NBF	8 mos.	F	17.

[1] "D" specimens were collected by H. A. Denyes and deposited in the Mus. Zool., Univ. Mich. "UM" specimens are in the collection of the Mus. Zool., Univ. Mich. "3-C" specimens are in the author's collection.

[2] "FA" = fixation probably 10% formalin, preservation 70% ethanol; time refers to combined times of fixation and preservation.

[3] 10% NBF = 10% neutral formalin buffered with sodium phosphates to pH 7.0 (Lillie, '48: 26).

elastic fibers with azure A counterstain (Lillie, '48); (4) Foot method for silver impregnation of reticulum (Bensley and Bensley, '38) with hematoxylin and eosin or azure A counterstain; (5) Heidenhain's modification of Mallory's connective tissue stain (Azan) (Bensley and Bensley, '38); and (6) buffered azure eosinate method (Lillie, '48: 83).

Histochemical techniques

(7) Romieu reaction for tryptophane in proteins (Glick, '49); (8) Berg ninhydrin test for α-amino acid groups (Glick, '49); (9) Mallory's iodine reaction for amyloid as amended by Lillie ('48) and with a preliminary wash in 1% acetic acid; (10) Masson's section method (Lillie, '48) for demonstrating the argentaffin reaction; (11)) 2,4-dinitrophenlhydrazine reaction (Lillie, '48); (12) Nile blue A after 10% NBF fixation and using saturated and 1% saturated solutions of Nile blue A (otherwise as in Cain, '47); (13) Sudan black (Lillie, '48); (14) Oil red O (Lillie, '48); (15) Oil blue N (Lillie, '48); (16) Windaus digitonin reaction (Lillie, '48); (17) Baker's acid hematein test ('46, '47) with and without previous pyridine extraction; (18) polarized, ultraviolet and visible light.

DEVELOPMENT AND MORPHOLOGY

The sebaceous glands budding from hair follicles in the dorsal gland area enlarge when the dorsal gland is becoming active. At the center of the dorsal gland area are the sebaceous glands of greatest development. At the periphery are those of least development, showing the transition from unmodified to modified glands (plate 1:3). In most species each group of 6 to 7 hair follicles and associated unmodified sebaceous glands is replaced by one greatly enlarged sebaceous gland (plate 1:3). The enlarged gland units are at first ovoid and slightly lobulated. In all species except *spectabilis* the continued enlargement of the gland acini occurs primarily by proliferation from the basal cells along the bottom of the gland, imparting a high conical shape to the

gland unit and limiting the lobulation to its base (plate 1: 2, 3). In these species the lobules are short and pressed together, so that the interlobular septa are very thin. In the species *spectabilis,* the exception, the enlargement of the gland units occurs by proliferation from the basal cells on all sides of the sebaceous parenchyma and by buds from the sides of the ducts. The result is a complex of lobes and lobules radiating in all directions from a central duct or ducts. The lobules are frequently long and are usually not pressed together (fig. 1).

In all species except *spectabilis* the basal cells at the bottom of the gland unit proliferate to form a hard pillar of secretion which extends intact through the neck of the gland and out to the surface (plate 1: 2, 7). In *spectabilis* the secretion breaks down within the duct to form a soft oily material (fig. 1). In the examination of dried skins of *Dipodomys* for dorsal glands (Quay, '53) the hard pillars of secretion were seen in all species except *spectabilis.* In this species the dorsal gland was detectable as an area of excessively oily and matted fur (see Vorhies and Taylor, '22: 6).

As the amount of sebaceous tissue increases in the dorsal gland area, the skin becomes thicker. In *merriami* the unmodified skin with inactive hair follicles adjacent to the dorsal gland area is .20–.30 mm in thickness. In the center of the most active dorsal gland areas the skin thickness is 1.30 mm. This increase is primarily in the dermis. The undesquamated layer of the epidermis is 4–7 μ thick in unmodified areas and increases to 70 μ in the center of active dorsal gland areas in *merriami.*

The more densely packed the sebaceous tissue in the dorsal gland area, the fewer the hair follicles. What few hair follicles are visible may or may not be active. Usually when one of the dorsal gland area hair follicles is active in hair formation, nearly all are; however, none of the follicles lying outside the dorsal gland area may be active. Or when the follicles in the unmodified skin outside the dorsal gland area are active, none of those within the area are so. Thus

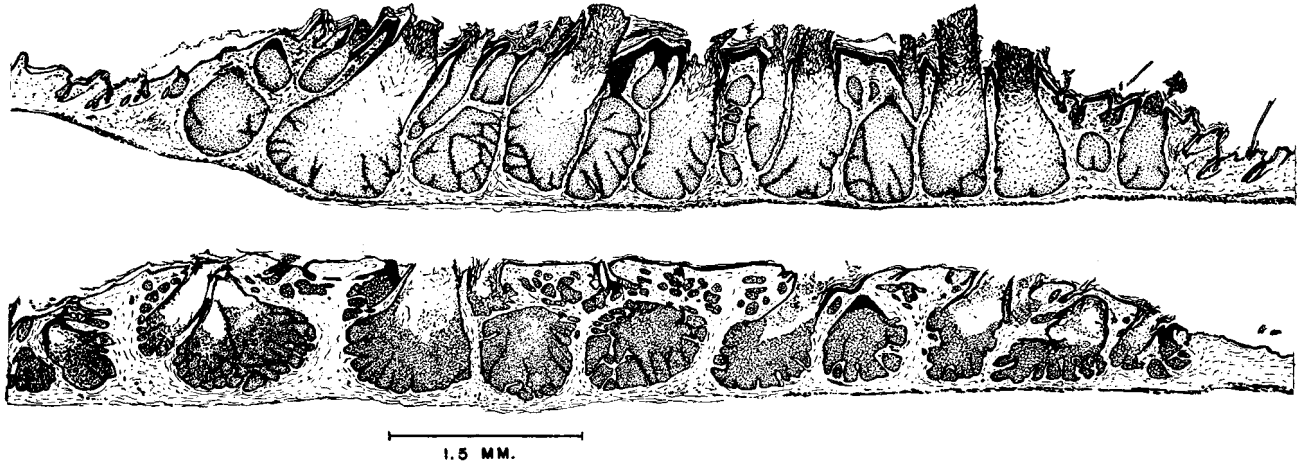

Fig. 1 Comparative histological structure of the dorsal gland.

Above. Parasagittal section of the gland of *D. merriami* ♂, UM 61691a, April 8, Pima Co., Arizona. The structure shown here is in general typical of that in most species.

Below. Parasagittal section of the gland of *D. spectabilis* ♂, UM 87033, April 14, Cochise Co., Arizona. The structure shown here is unique to this species.

the activity of the hair follicles within the glandular area is frequently out of phase with the activity of the follicles in the surrounding unmodified areas. This was apparent in the dried skins examined (Quay, '53) as well as in histological preparations.

The only sexual differences noted in the histology of the gland area are quantitative ones which require statistically significant samples for adequate description. These are not yet available.

HISTOLOGY

Parenchyma

The ducts of the glands are composed of stratified squamous epithelium which is continuous with that of the epidermis. In both the upper part of the gland necks and in the epidermis of the dorsal gland area the granular layer is distinct and continuous, and the cornified layer is thick. In the epidermis outside the glandular area the granular cells are exceedingly rare and the cornified layer is thin; the single or double layer of cuboidal basal cells is the primary one seen. Deeper within the necks of the gland units of the dorsal gland area the granular and cornified zones become thinner and finally are lacking and the basal cells become squamous and overlapping. In this region there may be 4 to 5 cell layers, composed of squamous cells, the superficial ones paler than the basal ones below. Deeper yet, the duct epithelium is reduced to a single layer of squamous cells continuous with the basal cells of the sebaceous acini. In glands that have been actively secreting for a longer time, as shown by higher pillars of secretion, the stratified and thicker type of duct epithelium extends farther toward the base of the gland.

In most respects the sebaceous cells of the *Dipodomys* dorsal gland units are similar to those of unmodified sebaceous glands in this and other rodents. However, they are distinguished in histological preparations by two features: (1) the presence of a very large vesicle within each

cell, and (2) resistant cell walls and intercellular material which tend to hold the secretion mass together in a column. These two features are most highly developed in *D. deserti* (plate 1: 7, 8). The tall pillars of sebaceous cells described in the flank gland of the water rat (Vrtis, '30) resemble the secretion pillars in the *Dipodomys* dorsal gland, but differ from them in the fact that they are composed of immature cells rather than highly modified dead cells. Similarly there is some resemblance between the tall cell columns in the femoral organ of Lacerta (Tolg, '05) and those in the *Dipodomys* dorsal gland.

Stroma

A diffuse network of delicate elastic fibers permeates the dermis, even into the interlobular septa of the glands. In the upper third of the dermis between glands the elastic fibers are enlarged and more numerous, especially in the glandular areas of greater activity and depth. In this region many elastic fibers may be followed into the crevices between the basal epithelial cells of epidermis and gland necks. In the tips of the dermal partitions in *D. deserti* the elastic fibers are very densely woven and are circularly arranged around the necks of individual glands. In most specimens elastic fibers are abundant between and beneath the muscle fibers of the subjacent panniculus dorsalis (of Howell, '32).

The Foot silver impregnation blackens delicate fibers which delimit the glands and the sides of the interlobular septa. Elsewhere such fibers are diffusely scattered, as also are the thicker fibers of collagenous type.

Mast cells are found throughout the dermis between the glands. They are especially abundant in the upper part of the dermis where they are associated with abundant small blood vessels. A few mast cells occur in the interlobular septa of the glands.

In sections treated with lipid colorants, dermal fat cells are shown to be practically nonexistent in the active dorsal

TABLE 2

Results of histochemical studies

Included here are some tests of unknown or dubious specificity, but which are of comparative interest since they have been repeatedly used in describing the composition of certain sebaceous glands of other mammals

TEST	SPECIFICITY	RESULTS
Romieu reaction	Tryptophane in proteins	Negative: in dors. gl. acini.
Berg ninhydrin	A-amino acid groups	Positive: (deep violet) sides of upper part of most dors. gl. secretion pillars.
Mallory's iodine reaction (emended by Lillie, '48)	Amyloid	Negative: (upper part of hair shafts and sides and tops of dors. gl. secretion pillars — yellow).
Argentaffin reaction	Reducing substances (Gomori, '52)	Black bodies (0.2–0.5 μ diam.) between and on the surface of small vesicles and vacuoles in basal cells of dors. gl. acini — present also in untreated frozen sections.
2,4-dinitro-phenylhydrazine (no controls)	Aldehydes or keto groups (Danielli, '53)	Positive: (bright yellow) sebum at surface and sides of secretion pillar and intervesicular material of upper part of pillar; intermediate sebaceous cells have very pale yellow droplets and intervesicular material; basal cells clear.
Nile blue A A. 5 min. with 1% sat. sol. B. 15 min. with sat. sol.	Lipids colored pink = "neutral"; those colored blue contain "acidic" lipids; intermed. colors = mixtures. (Cain, '47, '48, '50; Gomori, '52)	A. In dors. gl. acini: 1. Basal zone blue; 2. Degenerating sebaceous cells increasingly paler blue; 3. Vesicular area of secretion pillar very pale blue or clear; 4. Exposed sebum (except in *deserti)* mixed pink and purple. (Unmodified sebaceous glands similar, but lack zone 3.) B. In dors. gl. acini: 1. Small cells of extreme base with small and sparse pink droplets with purple or blank granule adhering to one side, and with clear cytoplasmic background; 2. Larger cells with slightly larger and more abundant pink droplets and larger purple or dark blue masses adhering to their sides, against pale blue cytoplasmic background; 3. Cells with small clear vesicles on whose sides are larger purple masses and hemispheroidal caps, which may have a pinkish cast — against blue cytoplasmic background; 4. Larger cells with larger and fewer clear vesicles — against dark blue cytoplasmic background containing large purple masses; 5. Large cells with large coalescing clear vesicles capped with purple or pink masses which blend into the dark blue cytoplasm; 6. Large cells each nearly filled by a large clear vesicle with pink or purple covering; 7. Apical sebum dark and irregular with black and purple masses in dark blue matrix. (On the basis of the results with Sudan black, the blue cytoplasm in 2, 3, and 4 is not lipid.)
Sudan black A. Unextracted B. Ether (15 hrs., room temp.) extraction before staining	Liquid lipids (Cain, '50)	A. 4 zones in dors. gl. acini: 1. Basal cells with minute, solitary, black droplets and black hemispheroidal caps on small, clear vesicles; 2. Intermediate cells with larger and more numerous black globules and caps; 3. Central cells, each with a single large clear vesicle capped with black (plate 1: 6), and with a pale gray layer separating adjacent cells; 4. Black sebum. (Unmodified sebaceous glands of adjacent skin differ in that the small clear vesicles present in zone 1 do not enlarge noticeably,

15 hrs., 57°C.) extraction before staining		ules in zones 1–3 in both gland types; 2. Black lining on vesicle walls in zone 3 of dors. gl. acini (plate 1: 8). C. All black-staining materials removed except vesicle linings in zone 3.
Oil red O and Oil blue N A, B, C as for Sudan black	Neutral lipids (Pearse, '53)	Similar to results with Sudan black except: less sudanophilia in basal cells, and particularly no granulation either with or without previous ether extraction — in both dors. gl. and unmodified glands.
Acid hematein A. Unextracted B. Previous pyridine ext.	Phospholipids (Cain, '50)	A. Darkly colored: 1. Fine black cytoplasmic granules in both dors. gl. and unmodified seb. gl. acini; these granules are smaller and more diffuse in zones 1 and 2 (Sudan black) than are the Sudan black granules in the same zones, and in zone 3 they are about the same; 2. Amorphous black material, first apparent and most concentrated around the granules in dors. gl. acini zone 3, and lines the vesicles in zone 4; 3. Gray sebum in unmodified seb. gl. B. Reduction of color in granules and vesicle linings above.
Digitonin	Most 3-beta hydroxy sterols (Fieser and Fieser, '49; Deuel, '51; Gomori, '52)	Negative (no birefringent digitonide crystals).
Color (untreated frozen sections)	Lipid oxidation products (?)	Oldest, most exposed sebum in dors. gl. acini frequently pale yellowish-brown with yellow and brown inclusions.
Birefringence (untreated frozen sections)	Ambiguous (Lison, '36; Cain, '50; Gomori, '52)	*D. deserti* dors. gl. acini: 1. Irregular birefringent objects at surface of secretion pillars. 2. Lining of vesicles in gland neck region, when viewed intact each appears as a huge spherocrystal with maltese cross. 3. Small, irregular birefringent objects in more central cells. *D. merriami* dors. gl. acini: 1. As in *deserti* 1. above. (Unmodified seb. gl.: sebum and degenerating cells irregularly birefringent.) *D. ordi* dors. gl. acini: 1. Many objects of brilliant birefringence in sebum at gl. mouth. 2. Many small ellipsoids and rods in neck and most central cells are brilliantly birefringent. 3. Small spherocrystal with maltese cross in intermediate cells. (In all three species dors. gl. basal cells are isotropic; compare: Montagna et al., '46, '47, '48a, b, '49a, b, c.)
Fluorescence (untreated frozen sections)	Lipid oxidation products (?) (Gomori, '52; Pearse, '53)	Vesicular area of sebum and secretion pillar fluoresces: 1. Pale green to white, in *D. deserti.* 2. Pale greenish yellow, in *D. merriami.* 3. Pale yellowish brown, in *D. ordi.* (Compare: Montagna et al., '46, '47, '48a, b, '49a, b, c.)

gland areas, but are abundant in the lower levels of the dermis in the adjacent unmodified skin.

Large and highly branched dermal melanophores are abundant and are nearly restricted to the upper part of the dermal partitions between the necks of dorsal gland units.

Histochemistry

The results of the histochemical studies of the dorsal gland acini are presented in table 2. The correlations and interpretations of the results are included in the following discussion.

DISCUSSION

Cytological constituents and their changes

Granules in the dorsal gland acinar cells are probably the first visible structures related to secretion formation in these cells. The granules are difficult to remove with solvents; only xylene-glacial acteic acid mixture was completely successful in this regard. However, at least the outer covering of the granules contains lipid and is apparently acidic. In the more central cells particularly, this acidic lipid material contains phospholipids. Similar granules have been described by Montagna et al. ('48a, b; '49a, b, c) using similar techniques on the sebaceous glands of other genera and Orders. Granular mitochondria in sebaceous cells studied by other workers with different techniques have a similar appearance and position (Nicolas, Regaud and Favre, '12; Ludford, '25) and recent knowledge of mitochondrial structure and composition (Bourne, '51) is in harmony with this tentative correlation.

Associated with the granules are: (1) "neutral" lipid droplets or globules, and (2) "acidic" lipid caps or coverings. The granules lie on the surface of the neutral droplets and are embedded in the acidic caps. In older or more central acinar cells the size of the two lipid structures increases until they finally fuse. The "neutral" lipid droplets are so-called

because of their pink color after Nile blue treatment. Similar pink droplets stained in this manner have been reported in the sebaceous glands of other mammals by Montagna et al. ('47; '48a, b; '49a, b, c). The "acidic" lipid caps or coverings are so-called because of their dark blue color after Nile blue treatment, resulting probably from the presence of fatty acids. They bear a close positional and structural similarity to structures designated as Golgi apparatus in the Meibomian gland of the cat (Bowen, '26) and in the sebaceous glands of the mouse (*Mus*) (Ludford, '25); however, there is some doubt concerning the true nature of the material designated as Golgi material in these two investigations (Bowen, '29: 503).

Within and at one side of each "neutral" lipid droplet a clear vesicle develops. It enlarges concurrently with the enlargement of the droplet and the "acidic" covering of the droplet. The vesicles within each cell fuse until finally there is but one within each cell. The content of the vesicles, aqueous or gaseous, is unknown and enigmatic, especially so since the excretion of waste materials by the kangaroo rat presents unique physiological problems (see Schmidt-Nielsen and Schmidt-Nielsen, '52).

As the "neutral" and "acidic" lipid materials become mixed in the central cells of the dorsal gland acini, the granules become the centers of phospholipid formation. The phospholipid is then mixed with the other lipid materials and with them lines the vesicles of the pillar of secretion.

SUMMARY

The dorsal, holocrine, skin gland, a mid-dorsal area of enlarged and modified sebaceous glands was studied in 26 kangaroo rat (*Dipodomys*) specimens (species: *agilis, spectabilis, merriami, ordi, deserti, panamintinus*). Glandular area epidermis and dermis are thickened; elastic fibers, mast cells, capillaries, and melanophores are particularly abundant in the dermal partitions between gland units.

Observations on tests for tryptophane and α-amino acid groups in proteins, amyloid, argentaffin reaction, 2,4-dinitrophenylhydrazine reaction, "neutral" and "acidic" (Nile blue) lipids, 3-β hydroxy sterols, phospholipids, color, birefringence, and fluorescence are presented. Sebaceous cell lipids are first apparent in relation to granules which: (1) are thinly covered with phospholipid, (2) adhere to "neutral" lipid droplets, and (3) lie in "acidic" (fatty acid) caps over the droplets. Within each droplet, a clear vesicle develops. In maturation, the "neutral" droplets, "acidic" coverings, and clear vesicles enlarge and fuse until finally within each cell there is one large, clear vesicle covered with mixed lipids. Within this lipid material α-amino acid groups, aldehydes or keto groups, and phospholipids are demonstrable. This phospholipid is first formed and is most concentrated around the granules which persist in the mixed lipid material. Resistant cell membranes cause the sebum to be excreted as a pillar, except in *spectabilis*. The size and characteristic features of the gland are best developed in *deserti*.

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PLATE 1

EXPLANATION OF FIGURES

2 Parasagittal section of a typical gland unit with secretion pillar. Hematoxylin and eosin. *D. merriami* ♂, UM 6169la. × 41.

3 Tangential section of dorsal skin, showing transition from groups of hair follicles in unmodified skin to enlarged sebaceous glands in the dorsal gland area. Hematoxylin and eosin. *D. merriami* ♂, D 364. ×41.

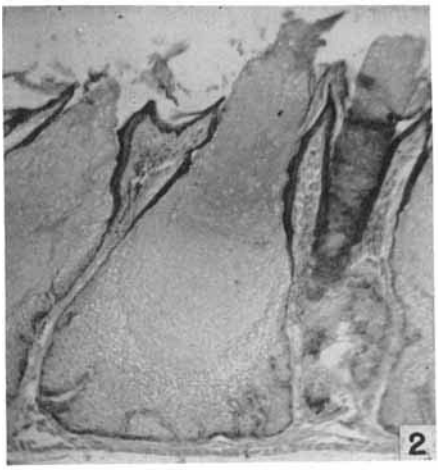
4 Parasagittal section of typical dorsal gland units, showing the distribution of lipids. Sudan black. *D. ordi* ♂, 3–C–285. × 64.

5 Parasagittal section of dorsal skin from epidermis (above) to panniculus (below), showing size and relations of unmodified sebaceous glands colored for lipids. Sudan black. *D. merriami* ♂, 3–C–201. × 88.

6 Basal cells (below) and maturing cells (above) from the base of a dorsal gland acinus colored for lipids and showing the formation of lipid-covered vesicles. Sudan black. *D. deserti* ♂, 3–C–189. × 272.

7 Parasagittal section of typical dorsal gland units after 15 hour ether extraction and 5 min. Sudan black coloring. *D. deserti* ♂, 3–C–189. × 34.

8 Enlarged cells from near the base of the gland unit shown at right in figure 6, showing amorphous and granular phospholipid around the vesicles. *D. deserti* ♂, 3–C–189. × 800.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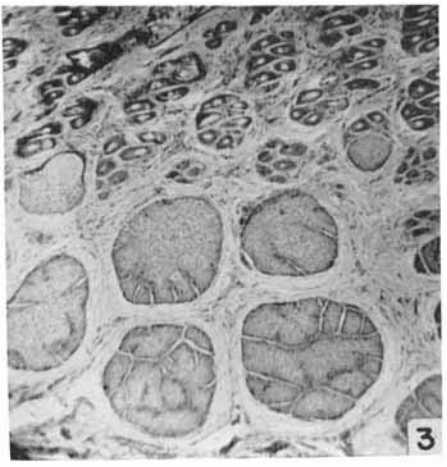
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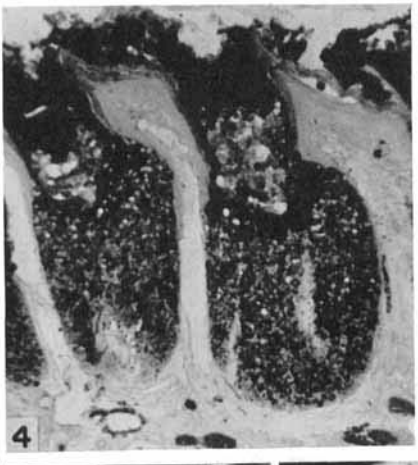
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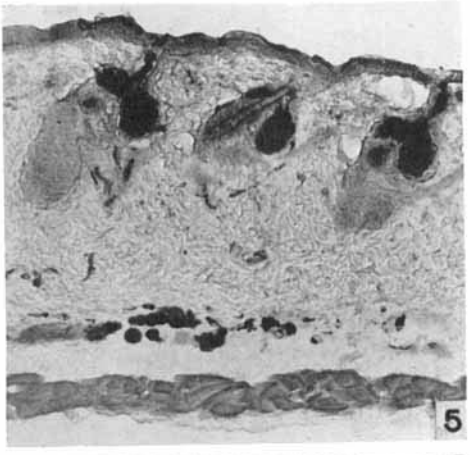
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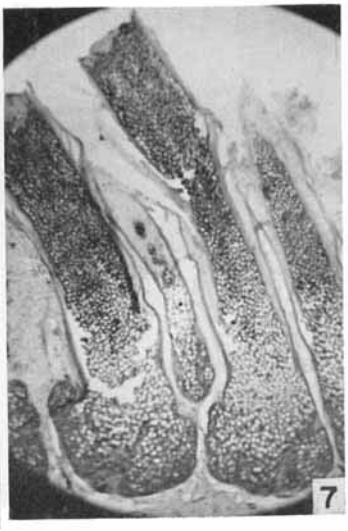
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