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V. E. Sokolov's English translation of his comprehensive survey of mammalian skin structure, a revised and updated version of the original Russian edition (Moscow: Nauka, 1974), makes available a unique achievement in comparative morphology and evolutionary biology. Based on the existing literature and on the author's own describes the macro- and microstructure of the skin of all orders and most genera of mammals. The work is divided into three sections. Section I considers the structure of the different parts of mammal skin. Treated in detail are the epidermis, the dermis, subcutaneous fat tissue, the blood supply, skin innervation, skin glands, and hair. Section II details the comparative morphology of the skin of different mammalian orders. Arranged taxonomically, it provides a systematic evolutionary characterization of the skin of mammal species and occasionally of families.

The third section of the volume examines the adaptive properties of mammal skin for life under the earth, in the water, in the air, on land, and in desert conditions. Season-determined adaptations are also treated in detail, and important new evidence is given on the role of the skin in chemical communication. Section III should be of particular interest to evolutionists, bringing the data of the first two sections to bear on the central theme of evolutionary biology.

TABLE 19

SCIURIDAE: SKIN MEASUREMENTS (μ)

	Skin	Epidermis	Stratum corneum	Dermis	Papillary layer	Reticular layer
Sciurus vulgaris						
Withers						
(1)	952	17	6	935	605	330
(2)	556	39	17	517	165	352
(3)	678	18	6	660	495	165
Breast						
(1)	792	22	6	770	220	550
(2)	550	22	6	528	418	110
(3)	902	22	10	880	605	275
Sciurus persicus						
Withers						
(1)	592	19	6	473	143	330
(2)	1,183	28	11	1,155	220	935
(3)	999	22	6	977	187	790
Breast						
(1)	666	28	11	638	528	110
(2)	853	28	14	825	165	660
Funambulus palmarum						
Withers						
(1)	650	45	24	605	110	495
(2)	727	45	20	682	132	550
Breast						
(1)	518	34	23	484	440	44
(2)	694	39	22	655	165	490
Tomeutes lacroides						
Withers	892	67	28	825	330	495
Breast	655	50	18	605	220	385
Atlantoxerus getulus						
Withers	968	–*	–*	968	88	880
Breast	898	28	14	870	100	770
Spermophilopsis leptodactylus						
Withers						
(1)	850	50	5	800	200	600
(2)	860	25	8	835	260	575
Marmota bobac						
Withers						
(1)	1,010	55	22	955	715	240
(2)	1,810	50	17	1,760	1,760	absent
(3)	2,160	50	17	2,110	1,450	660
Breast						
(1)	1,145	45	17	1,100	880	220
(2)	1,348	28	6	1,320	770	550
(3)	1,385	45	17	1,340	990	350

TABLE 19—*continued*

	Skin	Epidermis	Stratum corneum	Dermis	Papillary layer	Reticular layer
Marmota caudata						
(1)	1,630	90	23	880	550	330
(2)	1,466	36	*	1,430	770	660
Breast						
(1)*	832	62	28	550	440	110
Citellus undulatus stramineus						
Withers						
(1)	672	67	28	605	275	330
(2)	473	45	18	428	308	120
Breast						
(2)	658	28	8	630	330	300
C. u. leucostictus						
Withers						
(1)	457	39	17	418	187	231
(2)	540	45	17	495	275	220
Breast						
(2)	645	40	18	605	275	330

*The thickness of the subcutaneous fat tissue is indicated.

The pile hairs are similar to the guard hairs, but have a more pronounced granna. The fur hairs have no granna. The pile hairs are 13.1 mm long, 104μ thick, 90% medulla; the fur hairs (no medulla) (first order) 10 mm and 21μ; (second order) 9.4 mm and 16μ.

The hairs grow in tufts and groups (Lavrov and Naumov, 1934). In winter on the sacrum are groups of one central pile and ten fur hairs, in two lots of five (sometimes three or six) on either side of the pile hair. On the belly, the number of hairs in a group ranges from six to twelve. In summer the largest tufts on the sacrum have nine hairs; most have seven. The largest tufts on the belly have five, more often two or three.

In winter there are 4,436 fur and 528 other hairs per 1 cm^2 on the middle of the back, and 3,548 fur and 4,300 others on the middle of the belly. The figures for summer are 1,032, 868, 344, and 276.

S. leptodactylus has much hair on the front soles, even more on the hind soles, and a hair lining on the edge of the front and hind toes and the outer edge of the foot.

Marmota bobac

Material. Skin from withers and breast (table 19) from three specimens taken in the Starobelsk Steppes, Ukraine, June.

The hair is growing. The stratum malpighii of the body epidermis is three to four cells deep. There are large melanocytes in the basal layer of the epidermis. The hind sole epidermis attains great thickness, 750 to 880μ; the stratum granulosum, which is two to three cells deep, is well expressed; the stratum corneum and the stratum lucidum are 455 to 605μ. The alveoli on the inner side are rather far apart, 210 to 275μ deep; the stratum basale is pigmented.

Owing to the pelage growth on the body, the reticular layer of specimen (2) is absent (the hair bulbs adhere directly to the subcutaneous fat tissue); the reticular layer of specimen (1) is thinner than the papillary. Only specimen (3) has equal dermal layers. The dermal collagen fiber bundles are mostly horizontal and form a dense plexus.

Elastin fibers are few. Under the subcutaneous fat tissue, next to the subcutaneous muscles, is a horizontal bundle of elastin fibers. In the reticular layer, specimens (1) and (3), groups of fat cells extend down from the hair bulbs to the subcutaneous fat tissue. The subcutaneous fat tissue, well developed in the withers skin, is 0.88, 0.66, and 0.66 mm thick, respectively, in specimens (1), (2), and (3), with only rare bundles of collagen fibers. The fat cells in the subcutaneous tissue are 55 x 110; 77 x 121 in (1), and 34 x 56; 28 x 56 in (3). The sebaceous glands are oval or round, and small (28 x 56; 56 x 84), one behind each hair.

In the corners of the mouth, a specific gland 2.2 mm long, 0.4 mm thick, is formed of sebaceous glands reaching 243 x 373μ (Skurat, 1972). The

Fig. 62. *Marmota bobac*. Complex of sweat glands: *a*, corner of mouth.

ducts are connected with the hair bursae, opening into the mouth cavity. There is a complex of tubular glands under the hair bulbs (fig. 62), with individual segments of 0.33 x 0.36, 0.26 x 0.84 in size. The anal glands form three pouches on the dorsal and lateral sides of the orifice (Schaffer, 1940; Ortman, 1960; Skurat, 1972). The duct of the central pouch leads to the gland cavity, which is 10 mm long and 10 mm at the basal cross-section. The lateral pouches are smaller. Their walls are made up of glandular tissue 0.67 mm thick formed by alveolar glands. Under the sebaceous gland layer are a few large tubular glands with glomi reaching 0.67 x 1.79 mm. A similar structure is found in the anal glands of *Marmota marmota* (Kratochvil, 1968). In the hind sole dermis, large glomi of eccrine sweat glands (119 x 309, 224 x 717μ) lie surrounded by fat cells. The diameter of the glandular secretion cavities ranges from 45 to 65μ. Well-developed arrectores pilorum muscles are 33 to 55μ thick.

Marmota caudata

Material. Skin from withers, breast (table 19), and hind sole of two-year-old male (1) taken in Western Tien-Shan, August 19, and adult female (2) taken in Central Pamir, June 18.

The hair of neither animal is growing, but the skin is rather thick. The

stratum corneum of the epidermis is compact, the well-pronounced stratum granulosum is one to two cells deep. The female's epidermis is pigmented, and the hind sole epidermis is thick (0.60 to 1.10 mm). The stratum granulosum is two to three cells deep; the stratum corneum is well developed (440μ); the inner surface of the epidermis is alveolar. The alveoli are from 110 to 440μ high; the epidermis is lightly pigmented. In the dermis of the body skin horizontal bundles of collagen fibers predominate. Their plexus is rather loose. The elastin fibers, few in number, lie horizontally in the upper and middle papillary layers. In specimen (2) are small groups of fat cells (28 x 56; 39 x 56μ) in the lower reticular layer and near the hair bulbs. Only specimen (1) has fat cells in the subcutaneous tissue, which is 660μ on the withers, and 220μ on the breast. The sebaceous glands are small (28 x 78; 39 x 50μ), one at each hair. Sole glands are made up of large eccrine sweat gland glomi (diameter of the secretion section, 45 to 50μ). Arrector pili muscles are thin (22 to 44μ). The withers hairs divide into guard, pile (three order) are slightly wavy, the second and third orders are curly (seven to eight waves). The fur hairs are of uniform thickness the whole length. Guard hairs are 44.2 mm long, 137μ thick, medulla 87.3%; pile hairs (first order) 38.6 mm, 80μ, and 73.5%; (second order) 33.2 mm, 52μ, and 52.0%; and (third order) 30.1 mm, 46μ, and 58.7%; fur hairs are 11.8 mm, 18μ and 55.6%. The hairs grow in tufts, one guard hair in the middle with eleven to eighteen other hairs at the sides. There are 250 guard and 3,083 other hairs per 1 cm^2.

Citellus undulatus stramineus

Material. Skin from withers, breast (table 20), and hind sole of two specimens taken in Jungar Ala-Tau, June.

The hairs are in the earliest stage of growth. The stratum malpighii is two to four cells deep. The epidermis is strongly pigmented in the withers and lightly in the skin of the breast. The hind sole has a thick (330μ) epidermis; the stratum granulosum is two to three cell rows deep; the stratum lucidum is well expressed; the stratum lucidum and stratum corneum are 132μ thick; the inner surface of the epidermis is alveolar, the alveoli being 110μ high; there is no pigment in the epidermis. In the dermis of the body skin, horizontal bundles of collagen fibers predominate and form rather a compact plexus. In the upper papillary layer they run in several directions. In the middle of the withers reticular layer are one to two layers of fat cells (56 x 60; 50 x 67μ). The sebaceous glands are small (22 x 56; 34 x 56μ), ball-shaped or oval, one at each tuft, two at each guard hair. The specific glands

ously these poikilothermic bats do not need pelage with good insulation properties or a powerful source of heat radiation in the flying membrane. Indeed, their pelage is short and without medulla (the medulla is recorded only in *Megadermatidae* and *Rhinopomatidae,* Benedicts, 1957). However, in some circumstances (as during rapid flight) bats employ the pelage as insulation to protect their inner organs from excessive cooling. For this reason the abdominal surface, which is more exposed to head winds, has denser pelage than the dorsal surface. When taking off, the bat produces heat by sharp movement (Young, 1963). The pelage helps it to accumulate heat. In most of the bats, the fur hairs have peculiar cuticle cells with lateral protuberances that make for better cohesion.

SKIN ADAPTATION IN BURROWING MAMMALS

Burrowing mammals are halfway between terrestrial and subterranean mammals. Their skins are thicker dorsally or on their sides. The epidermis has a developed stratum corneum. The dermis of shallow burrowers is usuture. This prevents congealment during hibernation, when the body temperature drops down to 1 to 3°C. This character derives from a high content of unsaturated acids in the fat, of which the high iodine count is indicative. The physical and chemical properties of fat in hibernating mammals (e.g., bear and badger) with organ systems that keep going normally, resemble those of the fats of mammals active in winter (Goosen, 1941; Kuznetsov, 1962):

Hibernating mammal	Iodine count	Congealing t°C
Sable	57.0	28-30
Fitch	65.7	18
Bear	73.1	21
Badger	70.0	22
Marmot	170.9	—
Tawny ground squirrel	109.6	0
Little suslik	110.2	2-0

Most shallow burrowers have short, loose, rather coarse pelts. Wintering in warm burrows (warm even in northern latitudes) requires a pelage resistant to the wear of rubbing against burrow walls. Other shallow burrowers

have warm pelts because they spend much time on the surface. The fur hairs of many rodents are abundant and thin, with a sizable air-carrying medulla of not less than 47% and often as much as 80%. Thus, rodents carry insulation both as a layer between the fur hairs and in the hairs themselves. The guard and pile hair medulla is also well developed, providing better insulation than, for instance, carnivores would have, but the hairs of the burrowers are not as hard wearing. Most rodents have guard hairs with a long, thin medulla-free tip. This is absent in squirrels, mice, and a few species in other families. These thin but durable tips protect the fur and pile hairs. The differentiation of the pelage is pronounced in rodents. Their hairs grow in tufts and form groups, with arrectores pilorum muscles in the skin.

Fur insulation may differ even in closely related burrowing mammal species. The midday gerbil is an example, with several subspecies whose pelage differs markedly in morphology, such as *M. m. meridianus* Pall. and *M. m. nogaiorum* Hept. (Kalabukhov, 1955, 1957, 1958, 1959, 1950; Kalabukhov and Pryakhin, 1954; Kalabukhov, Mokrievich, and Petrosyan, 1959; Kalabukhov and Kazakevich, 1963). Midday gerbils living on the West Volga bank (*M. m. nogaiorum*) have much in common with northern and mountain mammals living in colder climates. Investigation of the hair of these two gerbil subspecies confirms the previously published data on other organ systems. *M. m. nogaiorum* has more abundant fur than *M. m. meridianus* (the former has 35,916 hairs per 1 cm^2 in winter; the latter has 30,874). The relationship remains much the same in summer (*M. m. nogaiorum* 27,999; *M. m. meridianus* 21,966). No essential differences are found in length, thickness, or medulla.

Those mammals that need to lose a lot of heat by radiation usually have short, sparse hair. The long-clawed ground squirrel is perhaps the most vivid example. In winter, when he needs good insulation (he is active through the winter in Kara Kum, staying in his burrow only for a few days when the temperature is very low) (Sokolov, 1959*a;* Sapozhenkov and Sokolov, 1960), his pelage includes guard, pile, and two orders of fur hairs. The pelage is very dense and the hairs are thick. The guard and pile hairs have a highly developed medulla. These factors combine to give good winter thermoinsulation.

Unlike all other desert animals, the ground squirrel is not nocturnal in the summer, so he faces very high temperatures. It is essential for this animal to ensure rapid losses of excess heat, so his summer pelage is much shorter (down to half or a quarter the length) and very sparse. The hairs themselves are of completely different shape. They are very flat, broad hairs with a thin club and with no medulla. They are not divided into categories, though there are three size orders. The medulla in all these hairs is well developed. This short, sparse pelage allows for easy heat loss from the skin surface. When feeding in the sun, the ground squirrel retires to its burrow for a while or takes shelter in the shade of saxaul trees. Presently it comes back into

the open and resumes feeding. A very curious cooling technique has been observed in a young *S. leptodactylus.* After being out in the sun it runs into the shadow of saxaul trees, shovels away the hot surface sand, and lies on its belly in the hole (Sokolov and Naumova, 1962). After a while, the animal runs out into the sun again.

Most shallow burrowers have coarse pelage on the ventral side, where the skin is barely covered by fur. The direction of the tips is pronounced because the animals move head first in the burrow. Many shallow burrowers have a peculiar topography of the pelage: the longest hairs are on the sides of the body, and the tail is not very fluffy.

Burrowers that hibernate molt only once a year. Some species of burrowers have adaptations for passive defense, such as spines and armor. Despite apparent similarity, spiny animals vary not only in skin structure but also in spine structure. Spine structure differs even in *Erinaceidae* and *Tenrecidae,* which belong to the same order. In the spine, medulla cells have very thick septa. These form peculiar beams that strengthen the spine. This is absent in the more primitive spine of the tenrec, whose strength depends on a thickened cortical layer. *Echidnidae* raises his spines differently from *Erinaceidae, Tenrecidae,* and *Hystricidae.* The spiny anteater has no arrectores pilorum muscles, though bundles of cross-striated muscles rise high into the skin. The spines are raised by contracting these muscles. *Tenrecidae, Erinaceidae,* and *Hystricidae* have powerful arrectores pilorum muscles at the spines, which usually consist of several sections.

It is interesting to note that both *Tenrecidae* and *Echidnidae* have a dense network of cross-striated muscles in the inner layers of the skin. The long, relatively heavy spines must have roots, which are also long and reach deep into the skin, so that the skin of all spined animals is thick. For instance, in *Echinosorex gymnurus,* which has no spines, the withers skin is only 0.4 mm, while *Erinaceidae* is 2.0 to 3.1 mm. *Echidnidae*'s skin is still thicker at 6.3 mm. The porcupine's skin reaches 15.7 mm (the thickest of all rodent skins under investigation). The epidermis and stratum corneum are thicker because of the sparse pelage. In *Echinosorex gummarus,* which has rather a dense pelage, the withers epidermis is only 9μ and the stratum corneum is 5μ, whereas the hedgehog's epidermis reaches 196μ and the stratum corneum 185μ. In the porcupine, the epidermis and stratum corneum are the thickest of all rodents at 330 and 296μ. The spines on the porcupine's tail (gobetlike) and in the middle of the tenrec's back (a bulge at the base), are most diverse. Both send acoustic signals (Gould and Eisenberg, 1966).

The skin of many shallow burrowers shields the body from the harmful effects of sun-rays while the animals stay on the surface. Hair being removed, skin permeability increases many times in all the animals in question except *Spermophilopsis leptodactylus.* A certain role in skin permeability is played by its thickness, specifically the thickness of epidermis and stratum corneum. Among other functions, skin pigment protects the organism

against long-wave rays in the sun spectrum (even if only partially). In all the mammals under investigation, the body skin pigment (excluding the pigment in the bulbs of the growing hair) is noted in some *Rodentia, Artio-* and *Perissodactyla, Hyracoidea,* and *Insectivora.*

Among rodents, the skin of *Spermatophilopsis leptodactylus,* ground squirrel, *C. pygmaeus, C. suslicus, C. undulatus, Marmota caudata, M. bobac,* and *H. indica hirsutricostris* is pigmented. *S. leptodactylus* differ biologically from other desert rodents in that they are active even in the hottest summer daytime hours. Since the pelage of *S. leptodactylus* is sparse in summer, this animal needs extra protection against the sun. This demand is met by intensive skin pigmentation. The number of melanocytes in the skin of *S. leptodactylus* is considerably higher than in other rodents. There are large numbers of pigment cells in the epidermis, mostly in the stratum basale. Sometimes small groups of melanocytes occur in the outer dermis. Individual variations are recorded in the intensity of pigmentation, but no seasonal variations are recorded. The skin of a young *S. leptodactylus* (three months) is more strongly pigmented than the adult's.

Like *S. leptodactylus,* the ground squirrel is active in the daytime. This appears to be the reason for strongly pigmented skin. The pattern of pigment distribution is the same as in *S. leptodactylus. Sciurus vulgaris* has no skin pigment. *S. vulgaris* lives in the forest, always in the shade, and needs no extra protection from the sun. So skin pigmentation is not common to all the members of *Sciuridae* (pigment is also absent in *Sciurus palmarum* and *Callosciurus locroides*). *S. anomalus* lives in much sunnier areas than *S. vulgaris* and has a slightly pigmented epidermis. *S. leptodactylus, C. pygmaeus, C. suslicus, M. caudata,* and *M. bobac* have pigment cells in their skin, though many fewer than in *S. leptodactylus* and *Atlantoxerus getulus;* they are mostly found in the stratum basale. In summer, susliks and marmots tend to be active in the cool hours of morning and evening, staying in their burrows in the middle of the day, so they are little affected by the sun. *Rhombomys opimus* is also active only in early morning and evening hours in the summer. All have only light skin pigmentation. It is noteworthy, however, that their pigment distribution pattern is peculiar. Large melanocytes are found in the dermis but not in the epidermis. The pattern may depend on the systematic status of the animal. In this investigation, none of the other nocturnal mammals or rodents that live out of the sun have pigment in the skin.

Some interesting features are noted in the pattern of body pigmentation of *Spermatophilopsis leptodactylus.* On back and sides, the skin is pigmented with equal intensity. The scrotum skin is highly pigmented. Melanocytes are distributed through the whole thickness of the epidermis to the stratum corneum but are more numerous in the inner epidermal layers, where they form a continuous black background. The scrotum skin proves to be more impermeable to light than the body skin, where the sparse pelage

TABLE 131

AMPHIBIAN AND LAND MAMMALS: COMPARISON OF WITHERS HAIR

Species	Granna to pile section axes ratio	Number of wavelike curves		Thickness of medulla in pile granna as % of granna thickness
		Pile	Fur	
Ornithorhynchus anatinus	1 : 6	absent	7-9	16
Tachyglossus sp.	1 : 3	1.5-2	absent	absent
Chironectes minimus	1 : 3	10	14	57
Galemys pyrenaicus	1 : 3.6	4	9	absent
Desmana moschata	1 : 4	5-6	14	absent
Talpa europaea	1 : 1.5	3	3	65-73
Neomys fodiens	1 : 2	3	2-3	57-60
Sorex araneus	1 : 2	1-1.5	1-2	70
Marmota caudata	1 : 2.5	absent	5	72
Ondatra zibethica	1 : 2.6	same	7	57
Arvicola terrestris	1 : 2	same	8	42
Microtus arvalis	1 : 3	same	3-5	82
Mustela lutreola	1 : 2	3-5	7	46
Martes foina	1 : 1.7	absent	6	58
Castor fiber	1 : 2.3	absent	7	46

and 14,000 on the breast; the shrew has 40,000 and 22,000; *D. moschata* has 22,000 and 37,000; *Ondatra zibethica* has 11,000 and 12,000; the otter has 35,000 and 51,000; *Ornithorhynchus paradoxus* has 57,000 on the breast; and *Chironectes minimus* has 39,000 on the back. It is noteworthy that, unlike the terrestrial mammal, the amphibian belly is protected from overcooling by long, dense fur. The density of hair differs much less from north to south in amphibians than in terrestrial forms, for water temperatures are much less varied in different latitudes.

All these properties (a sharp category division, long, flattened pile hairs with little or no medulla in the granna, and very dense fur) are associated with the need for the pelage to carry an air layer while the animal is swimming. Wide, flat grannas or pile hairs bend over and cover the fur hairs parallel to the body, forming a tile pattern under the water's surface tension, retaining air in the fur (Gudkova-Aksenova, 1951; Sokolov, 1961; Belkovich, 1962). The air layer appears to be present even in migrating fur seals that have spent several months at sea. This peculiar external cover in amphibian mammals (a combination of air and pelage) probably has

renewed systematically as the odor left by the male disappears rapidly. At 60°C with no wind, gerbils stop perceiving odor after two hours (Sokolov, Isaev et al., 1977). The male does not mark the entire area but only those areas near inhabited and visited burrows and near permanent paths (Sokolov, 1977). The marking rate increases greatly if an alien individual appears in the colony area or if an alien male odor is introduced. Some rodents, such as the long-clawed ground squirrel (*Spermophilopsis leptodactylus*) mark their territory with fecal hillocks evidently lubricated with anal gland secretion. Marmots, such as *Marmota flaviventris* (Armitage, 1974, 1976), *M. marmota* (Koenig, 1957; Münch, 1958), *M. olympus* (Barash, 1973), *M. broweri* (Rausch and Rausch, 1971), use buccal gland secretion for marking territory.

Territorial marking is characteristic of many carnivores. Urination and defecation are commonly employed, but specific skin gland secretion appears also to be involved. In the weasel (*Mustela nivalis*) in captivity, three types of marking of the area or of objects are observed (1) rubbing against the object or substrate with the anal region; (2) rubbing with inguinal region of the belly; (3) leaving of feces (Rozhnov, 1975). The first and third types of marking involve anal glands, the second involves skin, inguinal, and abdominal glands (Neal, 1948). In the wild, the weasel uses the abdominal gland secretion to mark definite sites.

Other *Mustelidae* rub against the substrate with the anal region, specifically in the course of rut. These include the ermine (*Mustela erminea*), the Siberian weasel (*Musela sibirica*), the Siberian polecat (*Mustela eversmanni*) (Zverev, 1931), (*Mustela altaica*) (Zlobin, Shiryaev, 1975), and the mink (*Mustela vison*) (Ktitorov, 1950). A tame *Mustela eversmanni* female rubs against all the objects in the room new to it with its underbelly (Il'enko and Zagorodnyaya, 1977). The sable (*Martes zibellina*) rubs against the soil with its belly or inguinal region (Manteifel, 1934; Raevsky, 1947). The American marten (*Martes americana*) marks the area with inguinal gland secretions (Herman and Fuller, 1974). The wolverine (*Gulo gulo*) uses the highly odorous secretion of the perianal gland for marking the area and prey (Weddle, 1968). The wolverine will push the snow away from the object being marked and will rub against the object with the anal region; Pullianen and Ovaskainen (1975) report a wolverine leaving twenty-six marks over 7.5 km. The badger (*Meles meles*) in captivity, after sniffing at new objects, will touch them with its tail base (the site of the caudal gland) (Pod'yapolsky, 1933; Eibl-Eibesfeldt, 1950). Among all *Mustelidae,* feces and urine appear also to be involved in marking.

Territorial marking is common among most ungulates. Males of the Siberian roe (*Capreolus capreolus pygargus*) mark small trees and shrubs in their territories, decorticating them with the horns or rubbing against them with the frontal portion of the head, cheek, and neck (Sokolov, Danilkin, 1975, 1977) (fig. 207). Specific skin glands have not been found in these

possibly the odor of fleeing from danger) is evidently produced by the caudal glands of some deer (*Cervus nippon*). In danger, *C. nippon* flees, tail up. This tail posture is regarded as a visual signal, opening a white field on the posterior portions of the thighs. As noted earlier, a large part of the tail incorporates tubular gland tissue situated over and under the vertebrae. When the deer is running fast, a head wind blows over its raised tail. From the tail surface, specifically from the lower, hairless portion, secretion evaporates, creating an odorous air used as a cue by other deer. This is of particular importance in the thicket where the visual cue may be ineffective. In the damans (*Procavia* and *Heteroxyrax*), during anxiety the hairs surrounding the dorsal gland are raised to open the glandular field, the secretion evaporation being evidently augmented. In the suslik (*Citellus*), the anal gland sacs bulge when the animal is gripped. In the maral (*Cervus elaphus sibiricus*), during fright or pain the orbital glands are wide open.

Some carnivores use the anal gland secretion for protection from enemies. Polecats (*Mustela eversmanni, Mustela putorius*) produce malodorous and pungent secretions from the anal glands during danger. The same is done by *Viverra, Viverricula,* and *Herpestes.* The anal glands of some *Viverridae* and skunks (*Mephitis* and *Spilogale*) are most developed and specialized for protection (Blackman, 1911; Bourliere, 1954; Dücker, 1965; Wynne-Edwards, 1962; Goethe, 1964). Skunks can spray the pungent anal gland secretion for considerable distances (4 to 5 meters), directing it at the enemy. It is suggested that the duck-billed platypus utilizes a gland located at the limbs to produce venomous secretion during fights for territory and female (Calaby, 1968).

The specific skin gland secretion can be involved in aggressive behavior. The significance of odors in the agonistic behavior of mountain goats (*Oreamnos americanus*), musk-oxen (*Ovibos moschatus*), blacktailed deer (*Odocoileus hemionus*) (Geist, 1964), and a number of rodents (Ropartz, 1977; Fass and Stevens, 1977). In agonistic behavior, the yellow-bellied marmot (*Marmota flaviventris*) uses its anal glands (Armitage, 1974). Marking is an essential component of aggressive behavior in *Mesocricetus auratus* (Dieterlen, 1959; Johnston, 1975*a*), guinea pigs (*Cavia porcellus*), and some other rodents (Kunkel and Kunkel, 1964). It is part of agonistic behavior in the wild rabbit; males give up fighting to dig, immediately marking the dug-up earth and other objects within reach of the chin gland. Production of fecal pellets lubricated with the anal gland secretion is also frequently observed at intervals throughout fighting. Raising of the posterior portion of the body and wagging the tail by rabbit males during fights indicates that the odor of inguinal and anal glands bears aggressive significance. Between strength demonstrations or fights, the aggressive behavior of *Capreolus capreolus* males, in particular, may include marking small trees and shrubs with the secretions of head and neck.

Olfactory signals are of great significance for breeding. However, because