

The Skin of Nonhuman Primates

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SYNOPSIS. What distinguishes man from all other primates is his archaic hair cover. Nearly all the details that make his skin unique are traceable to this single fact. In various degrees, all nonhuman primates have a good pelage, which is characterized by some morphological and physiological similarities but often differs even between closely related species. It can be thick or thin, short or long, woolly or shaggy, dense or sparse, and it assumes many varied colors. All primates have dermatoglyphics on their friction surfaces; they are also present on the volar surface of the tail of some New World monkeys and on the knuckle pads of chimpanzees and gorillas. The epidermis is uniformly thin and has little undersculpture. Every species of primate has epidermal and dermal melanocytes which are often relatively distinct from all others. Eccrine sweat glands are found on the friction surfaces of all species, but only the true prehensile-tailed New World monkeys and Old World monkeys and apes have them also in the hairy skin. Although chimpanzees and gorillas have more eccrine than apocrine glands in their bodies, in neither do the sweat glands respond to heat stimulation as they do in man. All primates have numerous apocrine glands in the hairy skin, but only man, the chimpanzee, and gorilla have an axillary organ. The Order Primates is large and heterogeneous; most species have some common cutaneous features but the details in each are so distinct as to preclude generalizations.

INTRODUCTION

Some years ago it occurred to me that the extraordinary differences between the skin of man and that of other mammals could be logically explained by a systematic study of the skin of selected nonhuman primates. Although this approach expanded my own knowledge of cutaneous structure and function, it failed to explain the unique feature of man's skin — its almost complete nakedness. Since it is this single factor that constitutes the chief difference between human skin and the skin of other mammals, we are left with the major objective of our study still unattained (Montagna, 1971).

However, these studies did reveal the remarkable differences in the skin of even closely related species of primates and showed that generalities can be made only

with great caution, if at all. Hence even today, despite many publications, the field of cutaneous research is still largely unexplored. The main purpose of this report is to call attention to some of the information we have gathered and, perhaps more importantly, to some of the numerous problems that await investigation. To maintain some order and simplicity, we have discussed each of the cutaneous items under broad headings.

GROSS APPEARANCE

The 200-odd species of nonhuman primate range in size from mouse lemurs, pigmy marmosets, and dwarf galagos, which weigh less than one hundred grams, to gorillas, which attain relatively gigantic proportions and sometimes weigh more than 500 pounds. In this heterogeneous group, short- and long-haired animals display striking differences in the density and color of their hair. Some prosimians and New World monkeys have dense, woolly pelages

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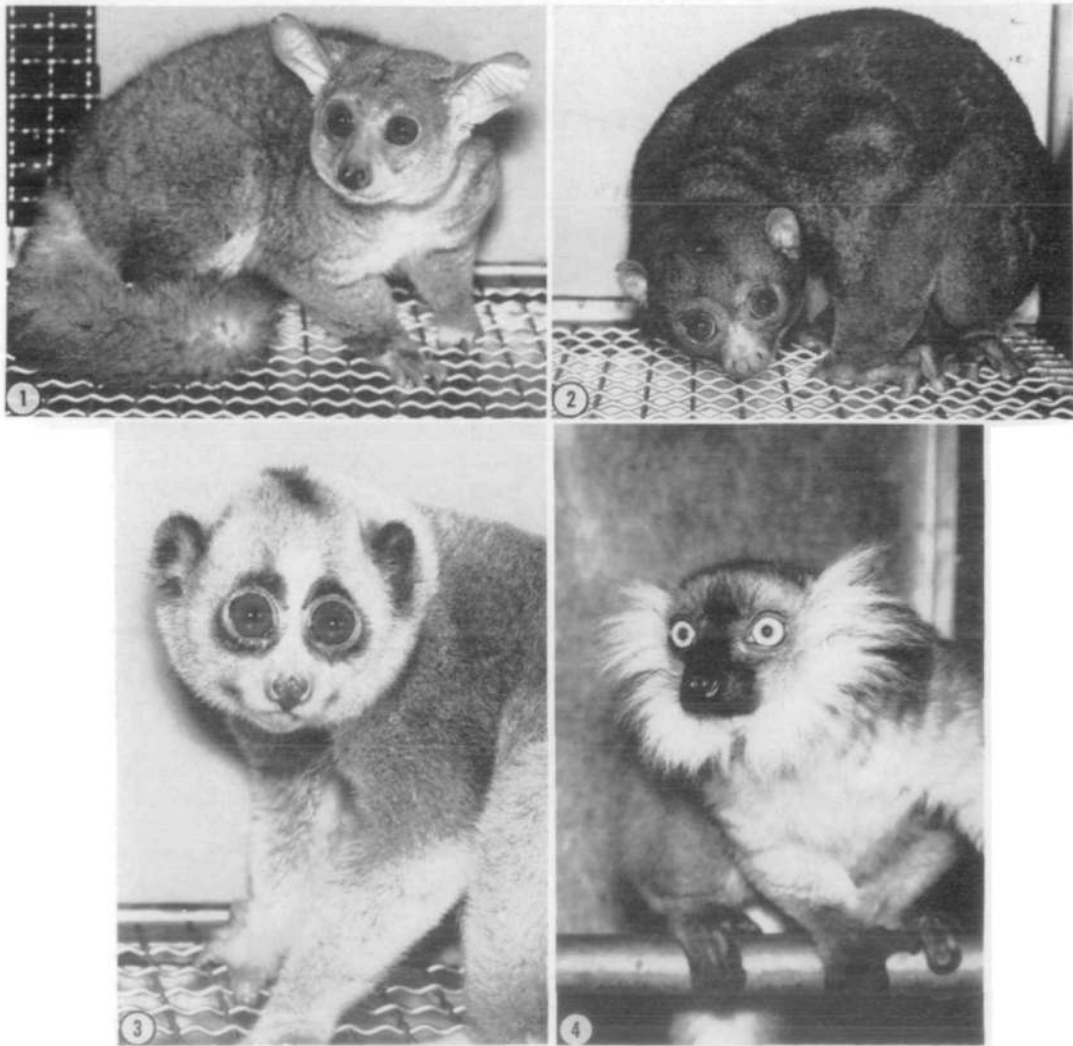


FIG. 1. A greater bushbaby (*Galago crassicaudatus*), a prosimian with a dense fur of almost uniform quality.

FIG. 2. A potto (*Perodicticus potto*), also with a dense, almost woolly fur, interspersed with long, coarse hairs.

FIG. 3. A slow loris (*Nycticebus coucang*), with a fur similar to that of the potto.

FIG. 4. A female black lemur (*Lemur macaco*) (only the male is black) has a mixture of woolly underhairs, longer terminal hair, and sparsely distributed long coarse ones.

that contrast with the coarse, sometimes sparse hair of many Old World monkeys and chimpanzees. Orangs have long shaggy hair (Figs. 1-6). The color varies even more: from white, gray, and bluish to yellow, green, brown-gold, red, and black. Skin, too, varies from the intensely pigmented covering of the Black Celebes Ape (really a macaque) (Fig. 6) to the unpig-

mented skin of the other macaques. Macaques, baboons, mangabeys, and chimpanzees have prominent sex skin, which in the females visibly records the ovarian functions (Fig. 7). Some animals have huge fields of assorted glands with which they mark their environment: the large inguinal glands of some marmosets, the brachial glands of ring-tailed lemurs, the

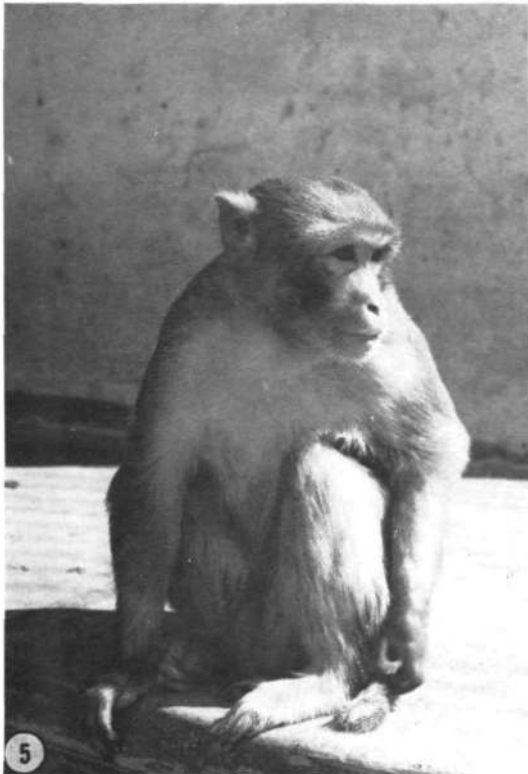


FIG. 5. A rhesus monkey (*Macaca mulatta*), with a pelage of mostly fine and coarse terminal hairs, with fairly dense underhair. These animals have many pigment variations in their fur. Some have a golden to white color, but most are dark brown



above and white below.

FIG. 6. Male Celebes ape (*Cynopithecus niger*), with a rich pelage of both coarse and fine terminal hairs and dense, woolly underhair.

perineal glands of many prosimians and simian primates (Montagna and Ellis, 1959, 1960; Montagna et al., 1961a,b; Yasuda et al., 1961; Montagna and Yun, 1962a,b). In pottos the neural spines of the last two or three cervical vertebrae, which protrude beyond the surface of the body, are covered with very thin skin like gloves over fingers (Montagna and Yun, 1962c). Except for marsupials, only primates have dermatoglyphics on the volar surfaces of the pes and manus (Cummins, 1971). Primates also have dermatoglyphics on all friction surfaces, including the underside of the tail of the true prehensile-tailed New World monkeys and on the knuckle pads of the three middle digits of chimpanzees and gorillas (Ellis and Montagna, 1962; Montagna and Yun, 1963). The latter two rest the front weight of

their body on their knuckles as they walk. Old World monkeys have tough, naked ischial callosities. The idiosyncrasies and generalities of primate skin are almost limitless; its unique characteristic is its lack of uniformity.

THE EPIDERMIS AND ITS INQUILINE CELLS

In nonhuman primates, as in all mammals almost without exception, there is an inverse relation between the thickness of the epidermis and the abundance of hair cover. Over the body that is usually well protected by hair, the epidermis, particularly the malpighian layer, is relatively thin, with a scarcely visible granular layer. On the face, however, where the hair is sparse or lacking, the epidermis is invariably much thicker. Moreover, in skin cov-

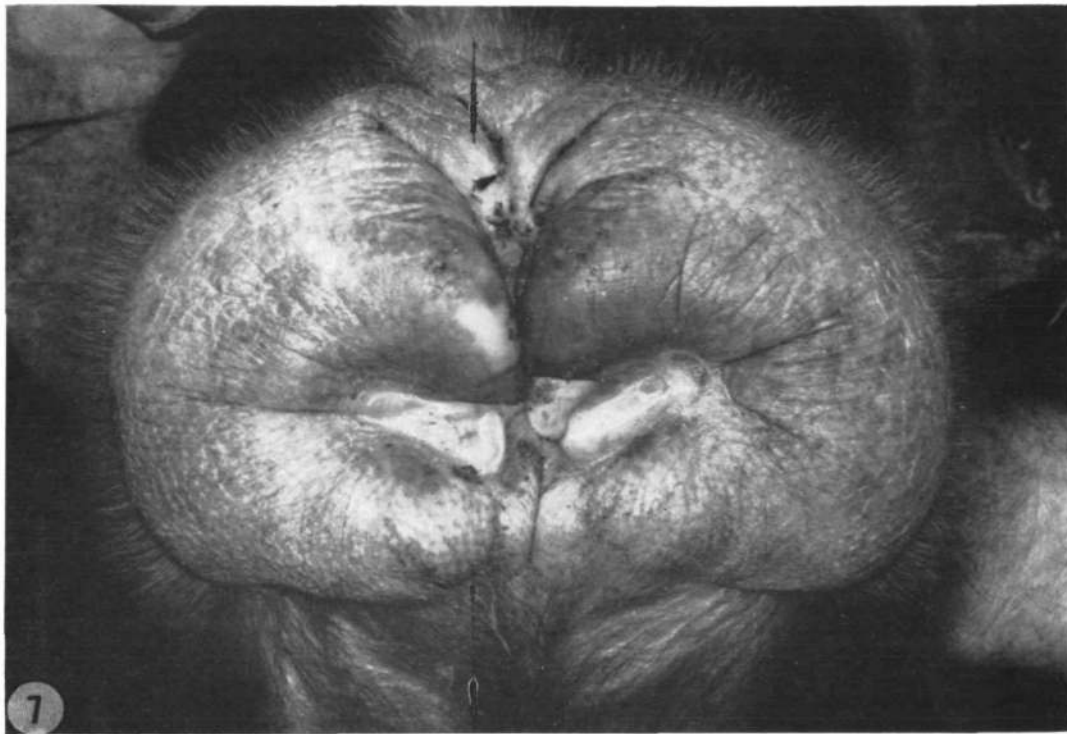


FIG. 7. The swollen buttocks (sex skin) of a female pigtail macaque (*Macaca nemestrina*). The many wrinkles on the surface indicate that the animal has recently ovulated. Before ovulation the skin is tumescent and free of wrinkles.

ered with hair, the dermoepidermal junction, seen best in split preparations (Montagna, 1971), shows a relatively flat underside, some ridging in scantily haired skin, and characteristic intricate patterns in glabrous skin (Fig. 8, 9). Thus, there is nothing singular about the epidermis of nonhuman primates; it is like that of most other mammals.

Two striking examples of the extraordinary variations in the degree of epidermal pigmentation are the Celebes Ape, whose epidermis is normally heavily laden with large dendritic melanotic melanocytes and with keratinocytes replete with melanin granules, and the rhesus monkey, which has at best a few scattered small melanocytes and keratinocytes that rarely contain melanin granules. These few examples of the different biological properties of melanocytes should whet the appetites of melanocyte biologists who have long ignored non-human primates.

Among the prosimians, the epidermis of Greater Bushbabies (*Galago crassicaudatus*) is deeply pigmented during the last fetal weeks and at birth (Yun and Montagna, 1965). It remains pigmented for two weeks (Fig. 10) and then, when the animals are about a month old, the pigmentary system gives up (Yun and Montagna, 1965). Later the melanocytes can be reactivated with irritating agents and with chronic exposures to UV light. The rhesus epidermis has active melanocytes during the second half of fetal life, beginning at about 90 days (average gestation period, about 175 days); by term only a rare melanocyte can be found and in later postnatal life some active melanocytes can be seen only on the scalp and face. Chronic exposure to UV light induces a steady rise in melanotic, dopa-positive melanocytes up to about 30 days (Montagna, 1966), after which, despite continued irradiation, the melanocytes begin to regress and by two

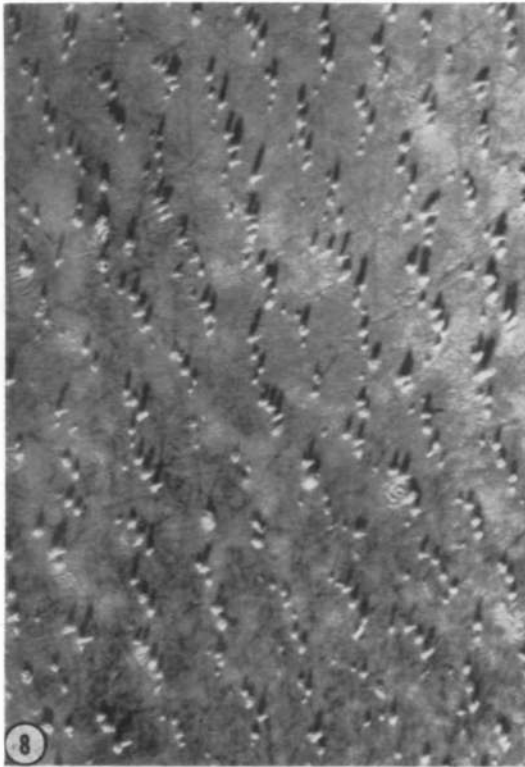


FIG. 8. The underside of the hairy skin of a rhesus monkey (*Macaca mulatta*), showing the typical pattern of smooth dermal-epidermal junction in hairy skin.

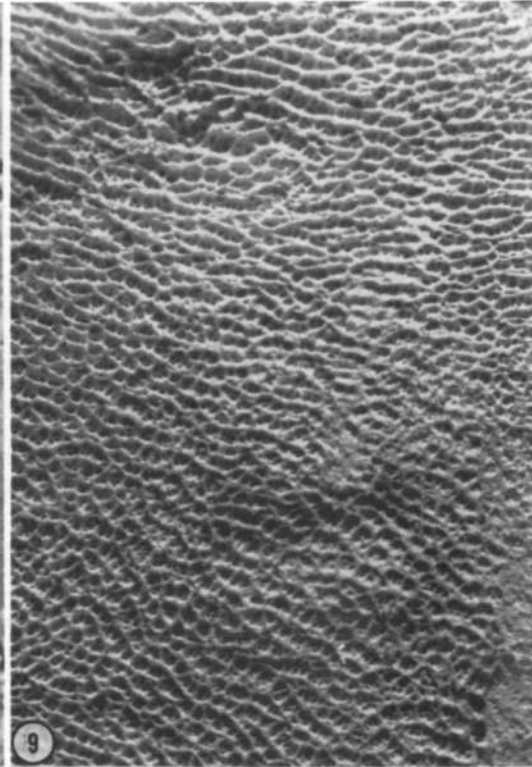


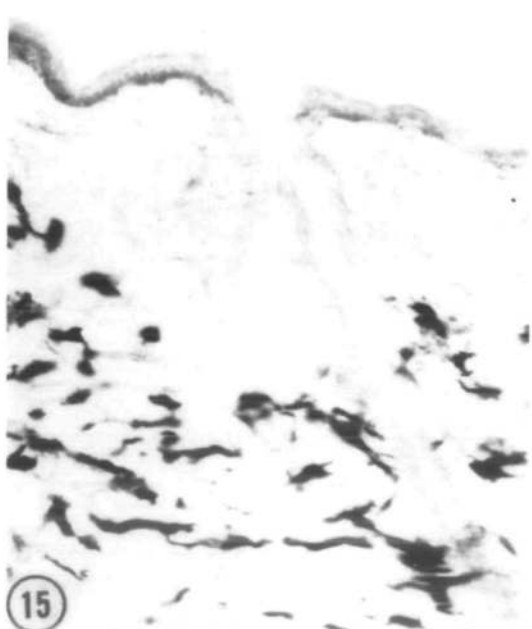
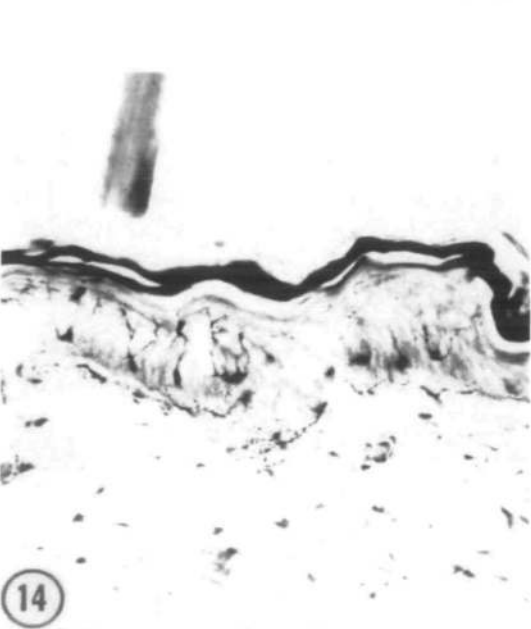
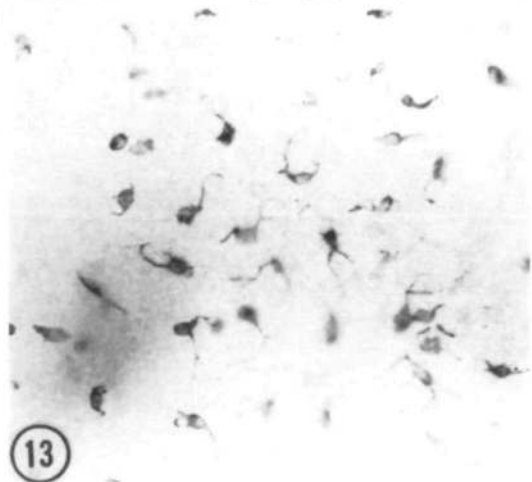
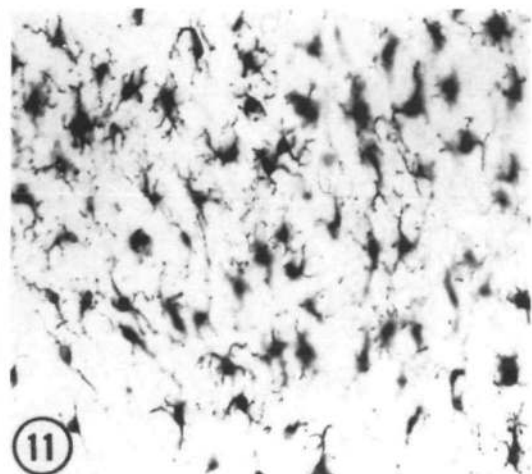
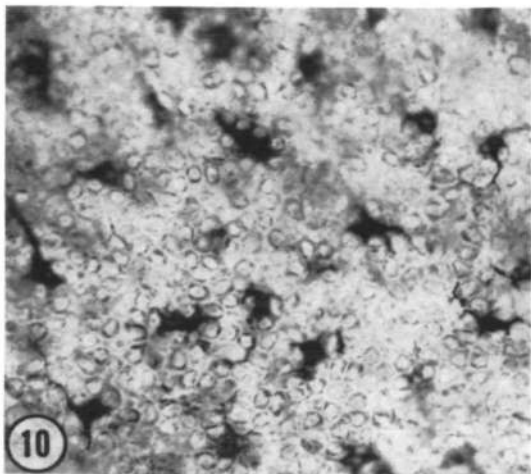
FIG. 9. The highly sculptured surface of the glabrous ischial callosities of the same animal as in Figure 8.

months are no longer active (Figs. 11, 12, 13). Even during the height of melanization at 30 days, however, most of the melanin granules stay within the blunted dendrites and are rarely found inside the keratinocytes. In contrast, a close relative, the Celebes Ape (*Cynopithecus niger*) is born with a white skin that first becomes bluish and by three months turns black. Some chimpanzees have white skin, others black. No one has systematically studied this phenomenon.

These and other examples of the different behavior of melanocytes in primate skin must be genetically controlled as they are in other mammals (Quevedo et al., 1967). However, much remains to be done on pigmentation in nonhuman primates before such isolated observations can be synthesized into an opus of information.

Another but different resident of the epi-

dermis, the Langerhans cell was the object of intense interest a few years ago. According to fairly convincing evidence, these cells, though grossly similar to melanocytes, are distinct and, for that matter, appear not to have derived from the neural crest. We have found them in all nonhuman primates (Fig. 14), varying from animal to animal in size, shape, and histochemical properties. The only uniformity we have found is in the epidermis of all species of African Lorisidae, where the large, high-level branched cells are all reactive for alkaline phosphatase (Montagna and Ellis, 1960; Montagna and Yun, 1962a; Kechijian, 1965). In other prosimians and most simian primates, they are not. Interest in these cells has now subsided, mostly because of our inability to determine their function. A distinct line of self-duplicating cells (Giacometti, 1967,



1969), their biological significance remains completely unknown.

Assertions or denials of the presence of intraepidermal nerve fibers must for the most part be discounted until the contradictory results arising from technical problems on the one hand and differences in topography, age, and sex on the other are resolved. Unfortunately, most of these factors are ignored by investigators. We have often found nerve fibers inside the epidermis of skin of the face, rhinarium, eyelids, and genitalia in most young primates but not in older ones.

THE STROMA (DERMIS)

This section will be singularly brief because of the limitations of space and time. Unlike the epidermis, which is almost similar in most primates, the dermis shows many family, genus, and even species differences. The two layers, the pars papillaris on the surface and pars reticularis below it, are generally well differentiated in most primates. Prosimians have a very thin papillary dermis, simian primates a thicker and more vascular one. This is to be expected since the differentiation of a papillary dermis is directly related to the complexity of the underside of the epidermis. In other words, a papillary dermis is most conspicuous in sparsely haired and particularly in glabrous areas. The reticularis dermis is composed of layers of fibers, which in some prosimians, but not in simian primates, are orthogonally arranged. As in all other mammals, the thickness varies from place to place. The dermis of the chimpanzee is most like that of man (Montagna and Yun, 1963).

FIG. 10. A split skin preparation of the epidermis of a newborn greater bushbaby (*Galago crassicaudatus*) showing the distribution of dopa-positive melanocytes. After two or three weeks, most of the melanocytes are amelanotic. Ca. 500X.

FIG. 11. Dopa positive melanocytes in the epidermis of a rhesus monkey (*Macaca mulatta*) after exposure for 21 days to UV light. Split skin preparation treated with dopa. Ca. 500X.

FIG. 12. Dopa positivity in these melanocytes has greatly decreased after 60 daily irradiations with

UV light. Note that the melanocytes are much smaller than those in Figure 11. 500X.

Whereas the skin of the great apes and that of some of the simian primates have variable amounts of elastic fibers, in no animals, regardless of age, sex, or locality, have we found the abundance of elastic tissue characteristic of human skin. This is to be expected: since the major function of elastic fibers is to anchor the epidermis, the greater the number of hair follicles in a skin area, the fewer the elastic fibers. In general, numerous elastic fibers are present around the bulge of hair follicles, where they attach the arrector muscles, and around sweat glands, where they form a delicate network or exoskeleton (Montagna and Giacometti, 1969). Very fine fibers rise up to the epidermis especially in glabrous or sparsely haired areas.

Some animals have isolated patches of melanin-containing cells in the dermis. Rhesus monkeys, for example, have piebald skin (Montagna et al., 1964) with blue patches interspersed with pink. The blue areas have cells laden with melanin deep in the reticularis dermis, but no pigment anywhere else (Fig. 15). These cells are not dopa positive and probably are melanophores; at any rate, melanin production does not continue after the animal has attained full size. In some animals, like the spider monkey (*Ateles geoffroyi*), the dermis has so much pigment throughout that it looks like a melanoma. But dermal pigment occurs normally in most primates. It may be densely scattered throughout, as in some New World forms, isolated in dense areas, as just described in rhesus monkeys, loosely scattered as in most simian primates, or located perivascularly and perineurally, as in the scalp and face of chimpanzees (Montagna and Yun,

UV light. Note that the melanocytes are much smaller than those in Figure 11. 500X.

FIG. 13. Whole skin of the animal in Figure 11, to show dopa positive melanocytes. Ca. 500X.

FIG. 14. Langerhans cells in the epidermis of a rhesus monkey. Paraffin section treated with Cairn's gold chloride technique. Ca. 500X.

FIG. 15. Dermal melanocytes or melanophores in the skin of a rhesus monkey (*Macaca mulatta*). Ca. 100X.

1963).

Another peculiarity of the dermis is the sex skin of many Old World monkeys, which is most conspicuous in some macaques, baboons, and mangabeys. Female Celebes apes and pig-tailed macaques develop huge, disc-like red buttocks at ovulation (Fig. 7). The dermis in these areas is spongy and resembles cavernous tissue. The spongy nature is due to large venous sinuses that become engorged and to an intrafibrous accumulation of mucopolysaccharides, which abound in hyaluronic acid (Bentley, 1970). Some macaques (e.g., *M. speciosa*) have facial skin that is identical with sex skin, usually more elaborate in males than in females (Montagna et al., 1966). The redness on the face of rhesus monkeys, for example, is entirely due to venous blood in this cavernous-like tissue.

THE PELAGE

Like nearly all the other cutaneous appendages of nonhuman primates, the hairs of the various species differ in almost every conceivable way. In prosimians, they grow in islands of different sizes, each containing hairs of various lengths and diameter. In other primates, they grow in various patterns, which have been described by Perkins et al. (1969). An intriguing fact is that all nonhuman primates have vibrissae, longer and better developed in nocturnal than in diurnal species (Van Horn, 1970). Hair density and size are usually correlated: they are most dense in prosimians and some New World species, whose hairs are fine and woolly, and coarse and sparse in many Old World forms. All the animals we have studied have variable amounts of fine underhair or wool hair.

As mentioned earlier, the range of hair color is wide, even in closely related species. Contrast, for example, the black pelage of Celebes apes with the golden hair of rhesus monkeys. Hair can be one color in some species, banded in others. In rhesus monkeys, the same hair bulb contains melanocytes that produce dark

brown, orange, or pale yellow melanin. The hairs in the white bands of the tail of ring-tailed lemurs appear to be white (Montagna and Yun, 1962*b*), even though the medulla contains black melanin and the bulb has a number of large melanocytes. In brief, to do justice to nonhuman primate hair, one would have to describe each species in detail.

Hair growth cycles are peculiar to individual species, although most animals shed some hairs constantly in a diffuse or mosaic pattern. Since most observations have been made on captive animals, we must be prepared for surprises. It is well known, for example, that house dogs shed constantly whereas those kept mostly outdoors shed synchronously in the fall and spring. One predictable shedding pattern is that of post-partum female macaques, which become nearly naked two months after delivery.

We cannot leave hair growth without a brief allusion to baldness. Far from being an idiosyncrasy of man, baldness is also found among several nonhuman primates (Montagna and Uno, 1968*a,b*). Most adult chimpanzees, for example, regardless of sex show various degrees of baldness and all adult oranges have a naked forehead. Adult New World uakaris (*Cacajao rubicundus*) have very short hair over the entire skull. Japanese macaques occasionally show bald spots on the forehead, and all stump-tailed macaques after adolescence develop relatively bald foreheads, more extensive in males than in females (Fig. 16). The latter animals are excellent model systems for studies in baldness since alopecia develops in response to androgenic stimulation. Readers interested in a more detailed discussion of this phenomenon are referred to Uno et al. (1967, 1968, 1969), Allegra et al. (1970), and Takashima et al. (1970, 1971).

We have observed, but cannot account for, a curious phenomenon in gibbons and siamangs, which, unlike man and all other nonhuman primates, have hair follicles on the dorsum of the last phalanges of the digits.

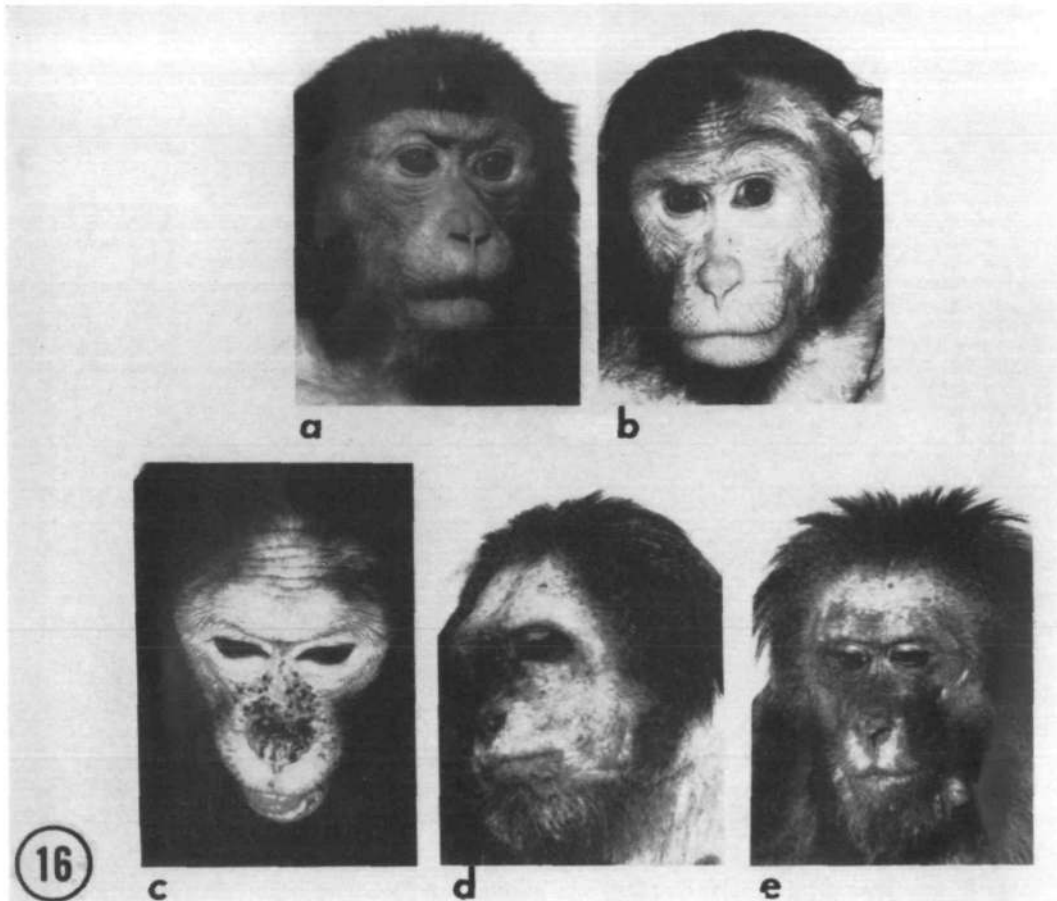


FIG. 16. The progressive development of baldness in stump-tailed macaques (*Macaca speciosa*): (a) an adolescent animal with heavy fur down to the brows; (b) the same animal after being treated with testosterone propionate for 3 months; (c)

same animal treated with testosterone propionate for 8 months; (d) normal adult male; (e) a front view of an adult male showing the extent of its alopecia.

One of the most singular characteristics of human hair follicles, large and small, is a well-structured sensory nerve end-organ around the upper part, between the bulge and the ingress of the sebaceous duct in the follicular infundibulum (Fig. 17). We have never found hair follicles that lack such a sensory mechanism and the large numerous nerves along its entire length (Montagna and Giacometti, 1969). Human follicles, therefore, are sensory mechanisms of the highest degree, but not so those of nonhuman primates. Despite the fairly elaborate nerve network and much simplified end-organ seen in many follicles, numerous others, particularly in

those forms, like prosimians, that have dense, woolly hair, have only a few nerves around them. In the Lorisidae, for example, whose hair tends to grow in islands of different sizes, only some of the stouter follicles are well-innervated.

The follicles on the facial disc and in the anogenital areas are more richly innervated. However, all nonhuman primates have numerous vibrissae follicles around the mouth, many of which are so small that they just barely fit within this category (Van Horn, 1970). Thus, when man lost the protection of a hair coat, the diminutive follicles became more important in the total cutaneous sensory mechanism. Par-

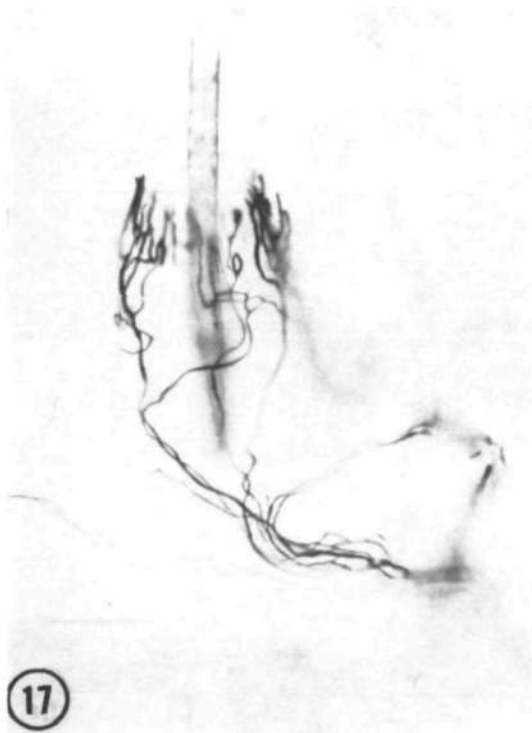


FIG. 17. The sensory end organ around a vellous follicle from a human auricula. Treated with Winkelmann's silver chloride. 125 \times .



FIG. 18. Sebaceous glands from the skin of a black lemur (*Lemur macaco*). Both glands are separated from hair follicles and reach the surface by way of a long duct which is usually coiled. 50 \times .

enthetically, without a doubt, man has the most exquisitely sensory skin of all animals and thus is better aware of his environment; furthermore, his entire skin has become a "sex skin."

SEBACEOUS GLANDS

We are faced again with so many species differences that we have to resort to a few striking examples. To begin with, one of the characteristics of human skin is the apparently useless abundance of sebaceous glands. Among the nonhuman primates we have studied, only the lemurs have as many sebaceous glands as man. Recent studies with the electron microscope (Bell, personal communication) indicate that the ultrastructure of the glands of lemurs most resemble that of man. But lemur glands have many peculiarities. In the fetus and newborn, they are attached to hair

follicles but soon separate and open independently to the surface through long, often corkscrewed, thin ducts (Yun and Montagna, 1964) (Fig. 18). Most of the glands have gigantic melanotic melanocytes at their periphery, and differentiating sebaceous glands usually contain some pigment granules (Fig. 19).

In most primates, glands are more numerous on the facial disc and the anogenital areas. In many species, the scrotum is covered with an oily substance that has a strong odor (Fig. 20). Aggregates of glands or gigantic single glands are found in marmosets and tamarins (Perkins, 1966), lemurs (Fig. 21) (Montagna et al., 1961*b*), lorises (Montagna and Ellis, 1960), and others. Although very little is known about the function of these and all other sebaceous glands, sebum, even in man, has a distinct odor and is probably the principal source of pheromones.

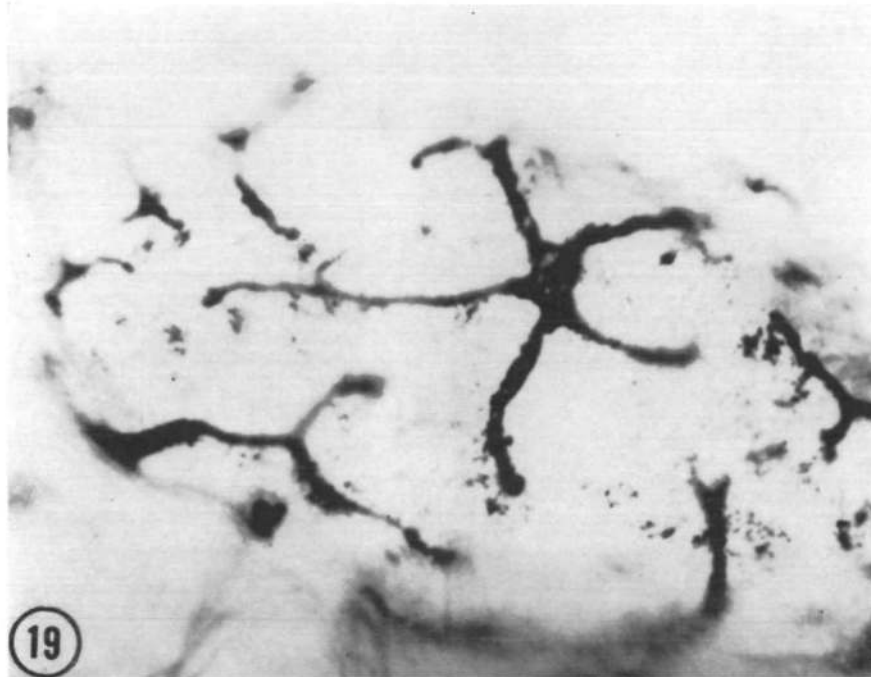


FIG. 19. Very large melanocytes around the sebaceous glands of a mongoz lemur (*Lemur mongoz*). Ca. 250 \times .

Male ringtail lemurs (*Lemur catta*) have two large sebaceous glands, one above each clavicle (Montagna and Yun, 1962b). All of the cells in these glands are multinucleated. The glands are shaped like craters and secrete a central plug of hardened, malodorous sebum containing interesting histochemical properties. The males, when excited, comb their tails with the spur and a curious gland on the anti-brachium, just proximal to the wrist, and routinely brush their brachial sebaceous gland with the inside of the forearm, presumably adding their secretion to the tail. We have also observed males marking objects with these glands, as well as with their perineum. The relationship of this marking to pheromones is obvious.

Recent studies of the sebaceous glands of assorted animals show unique patterns not found elsewhere. Under light microscopy, most sebaceous glands look so much alike that, except for gross structure, it is difficult to distinguish the glands of one primate from those of another. Bell (1970,

1971), however, has discovered genus and even species differences. For example, in several macaques, lysosomes have a complex crystalline architecture not seen in man or other primates (Fig. 22). Cytoplasmic membranes ~ 100 Å apart and intersecting planes form patterns unique to greater bushbabies (*G. crassicaudatus*). Other membranous configurations continuous with the agranular endoplasmic reticulum characterize the lesser bushbaby (*G. senegalensis*) (Fig. 23) and the pigtail macaque (*M. fascicularis*). Such samplings indicate how much work must be done before we can fully understand how structure relates to function.

OTHER CUTANEOUS GLANDS

Nonhuman primates have a large assortment of cutaneous glands. Although many of these are different enough to deserve special attention, for the sake of brevity, they are lumped together here as apocrine and eccrine.

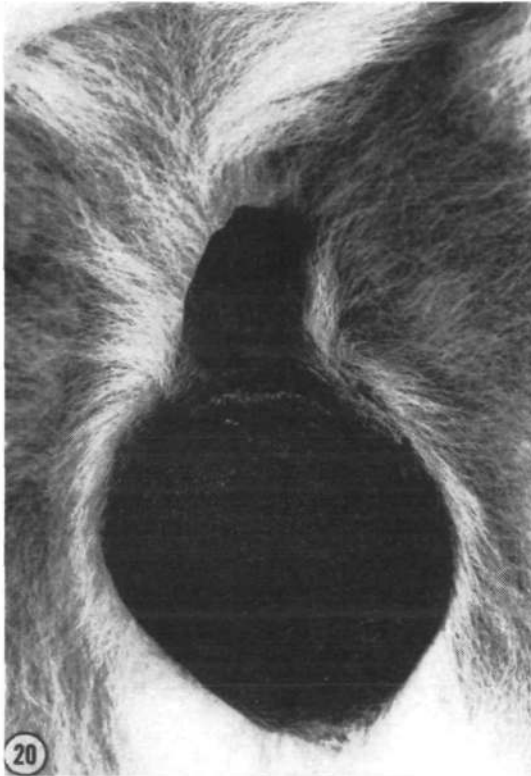


FIG. 20. The scrotum of *Lemur catta* is a solid field of large sebaceous glands. The pebbled surface is always covered with a thick layer of malodorous sebum.



FIG. 21. The orifice of the crater-like brachial gland of *Lemur catta* (present only in males), which secretes abundant lipoidal material.

Apocrine Glands

All primates have glands that can be included in this category. This does not mean that they are necessarily all alike; in fact, they are sometimes enormously different. Most, but not all, apocrine glands are in some way associated with hair follicles. The secretory segment has a wide diameter and is variously coiled (except that of the tarsier whose glands are ampulliform); the very narrow, long duct opens inside, alongside, or somewhere near a hair follicle. In the antibrachial organ of *L. catta*, the glands open onto a glabrous, friction surface similar to and continuous with the hypothenar eminence (Fig. 24) (Montagna and Yun, 1962b; Sisson and Fahrenbach, 1967). In the same animal, the ducts of apocrine glands wind their way through the spur of males and open on its

surface. The brachial glands of lorises (*L. tardigradus*; *Nycticebus coucang*) are gigantic and secrete a viscid substance on the surface of a sparsely haired area (Montagna and Ellis, 1960; Montagna et al., 1961a). Spider monkeys (*Ateles geoffroyi*), owl monkeys (*Aotus trivirgatus*), and orangs (*Pongo pygmaeus*) have an aggregate of sebaceous and apocrine glands just above the manubrium of the sternum where they form the sternal pit (Perkins and Machida, 1967; Hanson and Montagna, 1962). Female pottos have unusual-looking apocrine inguinal glands about the size and shape of a pea (Montagna and Yun, 1962c). Man, chimpanzees, and gorillas (Ellis and Montagna, 1962; Montagna and Yun, 1963) have large aggregates of apocrine, eccrine, and sebaceous glands in the axilla, called in complex the axillary organ. The list of various apocrine glands

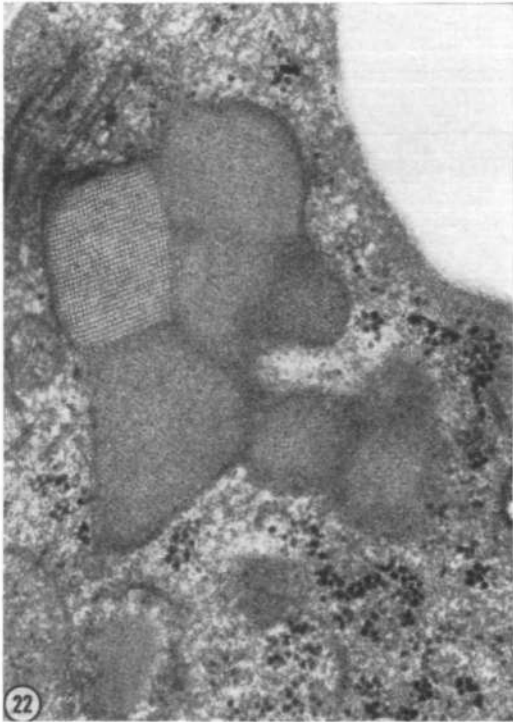


FIG. 22. A lysosome in a sebaceous cell of a stump-tail macaque. In macaques, but in no other genus, the lysosomes are characterized by crystalline patterns, which are demonstrated in this electron micrograph. The periodicity of the crystalline material is $\sim 80 \text{ \AA} \times 97,500$.

could go on indefinitely, but these will have to suffice. In addition to the clusters of glands just described, all primates have apocrine glands over nearly the entire hairy skin (Montagna, 1971).

Whereas most apocrine glands are morphologically similar, they differ from species to species. The secretory epithelium, always simple cuboidal or columnar, rests on a loosely dovetailed single-layered myoepithelium, which in turn is surrounded by a thick basement membrane. There are vast differences in innervation. Whereas the brachial glands of lorises are richly innervated, those over the rest of the body may or may not be (Montagna et al., 1961a). The axillary organs of chimpanzees and gorillas are very similar to those of man, despite some peculiarities of the latter. The axillae of other primates are not noteworthy; none have special

glands there. The axillary odor of man is almost identical with that of the two great apes. Although nearly always referred to as sweat glands, apocrine glands in primates have nothing to do with sweating; their secretion partially contributes to the characteristic odor of these animals.

Eccrine Sweat Glands

All primates have eccrine glands on the volar surfaces of the pes and manus, true prehensile-tailed New World monkeys have them on the specialized ventral surface of the tail, and gorillas and chimpanzees have them on the knuckle pads (Montagna, 1971). The glands in these areas are all somewhat similar in structure and function. In most prosimians the secretory coils are thick and the excretory ducts very narrow so that the glands grossly resemble

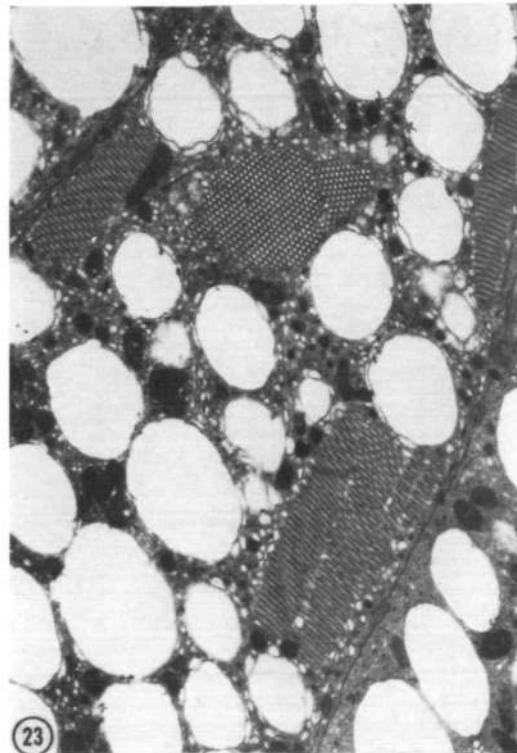


FIG. 23. Cytoplasmic membrane formations in sebaceous cells of *Galago crassicaudatus*. Such formations have been seen only in this species and can measure up to 8μ in length. The periodicity of the structures is $1000 \text{ \AA} \times 13,700$.



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FIG. 24. The antibrachial organ of a male *Lemur catta* covered with beads of secretion. Males usually mark certain territorial sites with this organ.

apocrine glands. In almost all other primates, they are not appreciably different from those of man. Structurally and biologically, they are similar to those of man and can be used effectively as models for the study of palmar (or solar) sweating (Smith and Dobson, 1966).

However, the glands in the hairy skin are different. None of the prosimians we have surveyed have eccrine glands over the general body surface; neither do the New World monkeys, except the true prehensile-tailed ones (woolly, spider, howler, and woolly-spider monkeys). In these animals, in fact, the ratio of eccrine to apocrine glands is about 1:1 (Perkins and Machida, 1967; Machida and Perkins, 1966). Eccrine sweat glands found in all Old World monkeys vary in number from species to species. There are fewer in the orang than in chimpanzees and gorillas. In the latter two, eccrine glands actually out-

number apocrine glands by two to one except in the axilla where they are on a 1:1 ratio as in man. The most surprising of our findings is eccrine sweat glands in the hairy skin of tree shrews (*Tupaia glis*) (Montagna et al., 1962).

In spite of minor detailed differences peculiar to each species, the glands are mostly alike whether in tree shrews or gorillas, and to a degree all resemble those of man. Those of gorillas and chimpanzees are almost identical with those of man in form and in cytological and cytochemical characteristics. Ellis (1960) has shown that even the ultrastructure of the eccrine glands of rhesus monkeys is similar to that of man. All glands, whether on friction surfaces or hairy skin, and regardless of species are surrounded by copious nerves, clearly demonstrable with techniques for cholinesterases. There are many species differences, however; hence some are best seen with techniques for acetylcholinesterase, others can be demonstrated only with those for butyrylcholinesterase. Thus, with the exceptions listed above, many primates are equipped with eccrine glands that are more or less alike.

One might surmise that, like man, these animals sweat in response to heat stimulation. However, with singular exceptions, if the glands secrete at all, the amount is so small that it cannot be recorded. Sometimes animals show beads of sweat on the facial disc when under deep anesthesia, but our efforts to induce thermal sweating have failed. We have also largely failed to induce sweating with sudorific drugs, either cholinomimetic or adrenomimetic. In the chimpanzee, very few, small sweat drops were recorded even after the administration of shockingly large doses of these drugs. Even less success was obtained in vervets (*Cercopithecus aethiops*) and rhesus monkeys (*M. mulatta*). Here, then, is a paradox that should suggest something about the evolution of these glands in man. Why do these glands not function when they seem to have all the equipment for doing so? The suggestion that they are a waning organ system cannot be support-

ed for two reasons: (1) they are not present in prosimians, and (2) they develop very late in gestation in man (Montagna, 1962) and in the few isolated species of other primates for which we have had fetal material. Parenthetically, apocrine glands in man also develop late and all over the body except the friction surfaces, but later in gestation they largely disappear. It appears, then, that eccrine glands are relatively new acquisitions in the hairy skin of primates and that only in man do they really serve the purpose of thermoregulation.

COMMENTS

The reader who may lament the lack of fluidity in this presentation is reminded again of the near impossibility of discussing the skin of this large and heterogeneous Order in general terms. Perhaps one of the reasons is the fragmentary nature of available information and the extremely meager physiological and pharmacological information. Only the study of eccrine sweat glands has demonstrated a trend that culminates in a complete differentiation of these glands in man. Granted that there are many detailed morphological, metabolic, and immunologic similarities between the skin of some primates and that of man; nevertheless, the total skin is always different because of the single fact that man's skin lacks the protection of a pelage. We have said nothing here about primate claws and nails because nothing has been added beyond the thoughtful analyses of Clark (1959). These efforts are mere beginnings and much spade work is ahead of us.

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