A HISTOLOGICAL AND HISTOCHEMICAL SURVEY OF THE SKIN OF NEW WORLD MONKEYS (ORDER PRIMATES, INFRAORDER PLATYRRHINI), WITH EMPHASIS UPON THE FAMILY CALLITHRICIDAE: ITS TAXONOMIC AND PHYLOGENETIC SIGNIFICANCE.

by

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A THESIS
Presented to the Department of Anatomy
and the Graduate Division of the University of Oregon Medical School
in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy

December, 1968

APPROVED:

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(Chairman, Graduate Council)

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ACKNOWLEDGMENTS

For encouragement, counsel, assistance, and enlightenment, I am indebted to the following hominoids: K. Adachi, K. Aiasawa, F. Allegra, B. Angel, T. Arao, L. Archer, R. L. Bacon, F. Baden, M. Barss, D. Cramer, R. L. Dobson, E. H. Dolnick, E. Durrow, J. Egozcue, F. L. Fields, D. M. Ford, F. Giacometti, L. Giacometti, T. Grand, P. Guinn, F. Hagamenas, A. Hall, P. Healy, P. Hershkovitz, D. Higgins, J. Holte, F. Hu, F. Hulse, M. J. C. Im, J. Ito, H. Kirkpatrick, Y. Kitano, A. Knezevic, H. Lawler, I. MacDonald, H. Machida, D. McLean, W. Montagna, B. Murdock, M. Partlow, A. C. Perkins, E. M. Perkins, Sr., S. F. Perkins, C. Pommerane, N. A. Roman, W. Roupp, J. A. Saysette, N. Schultz, E. B. Scott, F. S. Shininger, A. A. Smith, I. Takashima, C. Taylor, A. Tooyoka, F. Uhlman, H. Uno, A. J. Warren, V. Wells, S. Yamasawa, J. S. Yun, and my wife and son.

This work is dedicated to my mentor, December, 1968.

Edwin Morrill Perkins, Jr.

INTRODUCTION

I. General Background.

The work presented in this thesis represents a union between primatology and the histological-histochemical microanatomy of skin.

Primate skin is not a new subject. Indeed, a large number of publications, which are fragmentary in scope, appear in the older literature. Most are concerned with pigmentation, hair texture, coat coloration, dermatoglyphics, hair patterns, or glandular concentrations. Notwithstanding histological materials of dubious quality, limited knowledge of skin structure, and primitive technological methodology, most authors of these early studies managed to make significant contributions to our understanding of the skin of primates.[1]

The first comprehensive study of the skin of a primate to employ modern methods of histology and histochemistry appeared less than a decade ago (Montagna and Ellis, 1959). In this publication, the senior author expressed the view that systematic comparative studies of skin in members of a family or order may turn up different modifications of cutaneous structures and thus provide information on phylogenetic relationships. Therefore, in identifying the many adaptations in the skin of primates, it was hoped that emphasis on basic underlying patterns would be a valuable point of reference to students of evolution, systematics, comparative physiology, experimental biology, and dermatology.

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[1]Many of these original investigators will be acknowleged at that place in the Discussion where their work is most apropos to the findings presented in this survey.

II. Statement of Problem.

As the cutaneous systems of an increasing number of prosimians and Old World monkeys (catarrhines) were subsequently examined and the properties cataloged, this aim was partially realized. Many experimental models were brought to light and general phylogenetic trends began to develop. However, a conspicuous vacuum existed within the hierarchy of primate subjects to be studied, namely the New World monkeys (platyrrhines).

Although New World monkeys represent approximately 30% of all primate genera and 34% of all primate species,[1] the integument of only 1 genus and species had been examined in detail (Hanson and Montagna, 1962) prior to the initiation of the present survey in 1966. It therefore became apparent that a thorough survey of New World monkeys was imperative in order to more fully understand the overall phylogeny of the Order Primates and, more specifically, to elucidate the phylogenetic stature of the colorful New World inhabitants. This, then, is the aim of the present work.

Before proceeding, however, it is necessary to introduce 2 general topics: 1) obstacles surrounding the study of New World monkeys, and 2) systematic definitions and a review of the primates.

III. Obstacles Surrounding the Study of New World Monkeys.

The New World monkeys are an interesting experiment in evolution; they constitute a large, highly divergent complex that has

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[1]These statistics are based upon a comprehensive list prepared by Buettner-Janusch (1963).

undergone an adaptive radiation in isolation. Because numerous subgroups successfully adapted to their respective arboreal niches, New World monkeys represent one of the most varied of all primate infraorders; this fact is supported by systematic biologists who recognize as many as 5 to 7 subfamilies within the complex.

To date, some 20 genera and subgenera, 76 species, and 176 subspecies have been described. To add to this confused state, many taxonomic nomina are accompanied by incorrectly applied synonyms, homonyms, and a variety of colloquialisms. It is regrettable that subtleties in color variation between individuals of a given subspecies, or unrecorded pelage variances in immature and aged individuals, were once considered sufficient characters for the designation of a new species or subspecies. Only the total aggregate of an organism's behavior, distribution, ecology, genetics, and morphology can determine its classification and nomenclature. Far too much emphasis was placed upon taxonomy; far too little effort was expended on biology. Consequently, a lucid study of the evolution of New World monkeys has always been bogged down by a quagmire of taxonomic confusion.

There are other obstacles to the study of New World monkeys, e.g., the physical barrier. Much of the tropical rain forest remains impenetrable, and vast regions of the Amazon basin await exploration. Geographical delineation of species-complexes is difficult, at best; rivers shift, natives are vague, and many traders are unreliable.

Animal dealers are dependent upon traders, who in turn are dependent upon natives. The native Indian who comes to a trading post has, in all liklihood, become aware of the supply and demand

concept. He has learned to be selective in an economic sense. The monkeys in his dugout represent bartering power for food staples and supplies. As a rule, he brings only those monkeys that are in demand, i.e., animals that are widely used in large numbers by research. He is not inclined to reveal their locale of capture, lest some enterprising competitor usurp his favorite collecting haunts. Hence, uncommon species and precise locale data are rarely obtained.

Other deterrents to the accumulation of sufficient material for a thorough survey of the New World monkeys include international friction, internal political strife, and conservation. At present, the Brazilian government has imposed total restriction upon the exportation of 2 genera endemic to its country, namely, the woolly spider monkey (Brachyteles) and golden lion-tamarins (Leontideus).

Should an investigator receive living specimens that are in relatively good health, one impediment remains: the correct identity of the animals. The accurate classification of a New World monkey is less simple than it would seem; there are numerous taxonomic pitfalls.

Carelessly used article adjectives are misleading. Many an investigator has doubtlessly been informed that the diminutive ceboid upon which his experiment is based is the white-faced tamarin (Saguinus). In actuality, the animal is a white-faced tamarin, 1 of 26 recognized species and subspecies. Similarly, the tufted-eared marmoset (Callithrix) is not necessarily the nominotypic species;

it is, however, a species of the 10 listed under that genus.

Taxonomic confusion also exists as a direct result of the usage of colloquial terminology; this is illustrated by the following example: squirrel monkeys (Saimiri) in no way resemble squirrels, but an investigator who orders squirrel monkeys from an animal dealer may receive Indo-Malayan tree shrews (Tupaia). Such a mistake is not altogether implausible, because tree shrews do resemble squirrels; as a matter of fact, local natives make no distinction, calling both tupai (Eimerl and DeVore, 1965).[1]

If the investigator, cited above, actually receives squirrel monkeys, he is confronted with an arduous taxonomic task: at present, the genus Saimiri contains 5 species and 15 subspecies. Therefore, unless the investigator consults the literature for original descriptions--granting that his particular animals have been named and described--he stands a good chance of misidentifying them. But the prose of original descriptions contains highly technical terminology and therefore, should the investigator harbor any doubts, he must finally confirm his tentative identification by conferring with a taxonomist. Unfortunately, there are too few qualified taxonomists; of these, it is the author's opinion that 1 only is eminently qualified to classify New World monkeys.[2]

The author has dwelled on this discussion because a conscientious approach to the accurate determination of primate species

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[1]In 1963, precisely the same misunderstanding took place at the Oregon Regional Primate Research Center (pers. comm., A. J. Warren).

[2]Dr. Philip Hershkovitz, Chicago Field Museum of Natural History.

is of prime importance (Hershkovitz, 1965). Montagna has shown that histological and histochemical studies of skin in 2 species of Galago reveal very great differences; such differences are of the magnitude one would expect between more distantly related animals (Buettner-Janusch, 1963). Because subhuman primates vary so much from one species to another--each possessing its own unique cutaneous characteristics--the correct generic determination of an experimental primate subject, alone, is inadequate. The proper identity of the species must be ascertained, and it must be done so systematically. The practice of simply assuming a species designation is both inept and unfounded. One wonders how many valid experimental results have been published, based upon subhuman primates whose taxonomic determinations were invalid!

IV. Systematic Definitions and a Review of the Primates.

In the preceding section, terms such as primate, family, prosimian, infraorder, platyrrhine, subfamily, and ceboid were used. What are their meanings and in what way are these various ranks and categories related? In order to establish a fundamental working knowledge of primates and gain a better perspective of the systematic framework of the Order Primates (Linnaeus 1758), it is the purpose of this section to explain, define, and restrict such taxonomic ranks and nomenclatorial terms.

Nearly one century ago, Mivart (1873) set down what may still be the best general description of a primate; this classic definition

is quoted from Hill (1953):

> "Unguiculate, claviculate placental mammals, with orbits encircled by bone; three kinds of teeth, at least at one time of life; brain always with a posterior lobe and calcarine fissure; the innermost digit of at least one pair of extremities opposable; hallux with a flat nail or none; a well-developed caecum; penis pendulous; testes scrotal; always two pectoral mammae."

Although other mammalian orders are also characterized by some of these features, the possession of a total complement of such anatomical characteristics is unique only to Primates.[1]

The Primates are 1 of 18 extant orders of true placental (subclass Eutheria) mammals. They do not occupy the paramount position in this mammalian schema, however, but are placed much lower in the list between the bats (order Chiroptera) and armidillos, sloths, and anteaters (order Edentata). Although primates are the most generalized existing mammals, and although they possess relatively large cerebral hemispheres, they have not developed far in the hierarchy of specialization (Montagna, 1963). It is generally held that the moles, shrews, and hedgehogs (order Insectivora) are their closest living relatives.

Unlike cosmopolitan man, subhuman primates are largely restricted in distribution to the tropical regions of Central and South America, Africa, Madagascar, Asia, and the East Indian Archipelago

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[1]The tree shrews (superfamily Tupaioidea) are the sole exception; although they are not characterized by a fully-developed grasping hand with an opposable thumb, paleontological studies tend to favor their inclusion within the Primate order (Simpson, 1962).

(Sumatra, Borneo, Celebes, Malay States, and Philippines), i.e., between the latitudes 40° N. and 35° S. Throughout this range occur some 60 genera and 225 living species, which vary greatly in size, appearance, locomotion, habitat, and behavior.

A gorilla (Gorilla) may weigh 700 pounds; a mouse lemur (Microcebus) may weigh only 50 grams (Buettner-Janusch, 1966). Some, like a tree shrew (Tupaia), are rodent-like in appearance; others, like a chimpanzee (Pan), are hominoid. Some macaques (Macaca) dwell at sea level; langurs (Presbytis) have been observed at 12,000 foot elevations in the Himalayas. Some, like the African bushbabies (Galago), are nocturnal; others, like the capuchins (Cebus), are diurnal. Some, like the slow loris (Loris), are indolent; others, like the marmosets (Callithrix), are extremely active. Primates may be herbivorous, omnivorous, or carnivorous. Most are arboreal; a few, like the baboons (Papio), are primarily terrestrial. Some primates crawl quadrupedally, others leap, and still others walk or run bipedally.

How is this highly variable group of individuals classified; in what manner is the Order Primates categorized?

The ensuing discussion of the Primates is largely a condensation of the following works: Booth, 1955; Buettner-Janusch, 1963, 1966; Clark, 1962; Eimerl and DeVore, 1965; Elliot, 1913; Fiedler, 1956; Fooden, 1963; Goeldi, 1907; Hershkovitz, 1949, 1955, 1958, 1959, 1963, 1966; Hill, 1953, 1955, 1957, 1960, 1962; Lyon, 1913; Miller, 1933; Napier and Napier, 1967; Pocock, 1907, 1918, 1920, 1925, 1934; Regan, 1930; Reman, 1961; Sanderson, 1957; Schwartz, 1928; Simpson, 1945, 1962; Walker, 1964; Washburn, 1944.

Primates are divided into 2 large suborders: the prosimians (Prosimii, Illiger 1811 = Strepsirhini, E. Geoffroy 1812) and anthropoids (Anthropoidea, Mivart 1864 = Pithecoidea, Pocock, 1918). Each of these divisions is subdivided into 4 monophyletic taxa, according to Simpson (1962) and Buettner-Janusch (1963, 1966).

Prosimians arose some 60 million years ago. Early German naturalists called them half-monkeys (Halbaffen); this term is fitting because the Prosimii are considered intermediate in development between the Insectivora and Anthropoidea. This point is illustrated by the first monophyletic prosimian taxon, the tree shrews (infraorder Tupaiiformes = family Tupaiidae).

Tree shrews are the most primitive living primates. They occur throughout southeastern Asia where, because of their small size, pointed muzzles, bushy tails, and energetic activity, they are likened to squirrels. Their dental formula is unique among the Primates: $\frac{2.1.3.3.}{3.1.3.3.}$. Although members of this taxonomic group possess some anatomical traits that are characteristic of an insectivore, most resemble a primate; they particularly resemble those 9 primate genera that comprise the second monophyletic taxon, the lemurs (infraorder Lemuriformes = superfamily Lemuroidea).

All 21 living species of lemur are restricted in distribution to the island of Madagascar. Like the New World monkeys, they are an excellent study of adaptive radiation in isolation. The group is highly diversified, containing adult individuals that vary from several

inches in length (Microcebus), to the 4-foot-tall indris (Indri). Also included in this group is the peculiar aye-aye (Daubentonia). The dental formula of the lemurs, excepting Lepilemur, is the same as that of the Lorisiformes: $\frac{2.1.3.3.}{2.1.3.3.}$.

The infraorder Lorisiformes constitutes the third monophyletic, prosimian taxon. Its members are arboreal and nocturnal. Structural limb modifications are the principal basis for their subdivision into 2 groups: the lorises (family Lorisidae = subfamily Lorisinae) and galagos (subfamily Galaginae). The lorises, whose limbs are equal or subequal in length, are deliberate, slow-moving, hand-over-hand climbers. Their tails and external ears are small and inconspicuous. The Lorisinae are composed of 4 monotypic genera: the potto (Perodicticus), angwantibo (Arctocebus), slender loris (Loris), and slow loris (Nycticebus). The former 2 genera are African; the latter occur in southern India and Ceylon, and southeast Asia, respectively. By contrast, the Galaginae are characterized by greatly elongated pelvic limbs that enable them to move by saltation, i.e., kangaroo-like leaping and jumping. Commonly called galagos or bushbabies, the Galaginae possess large, conspicuous external ears and long, bushy tails. All inhabit Africa.

The infraorder Tarsiiformes (= family Tarsiidae), the fourth monophyletic prosimian taxon, consists of a single genus, Tarsius. Once distributed over most of the Northern Hemisphere, tarsiers are now restricted exclusively to islands in the East Indian Archipelago. Crepuscular and nocturnal tree-dwellers that feed upon insects and lizards, they are distinguished by enormous eyes, large ears, long

tails, and highly-developed hindlimbs; the latter enable them to execute frog-like leaps of great distance with amazing accuracy and agility. Their dental formula is unlike that of other primates: $\frac{2.1.3.3.}{1.1.3.3.}$. Recent analysis of orbital structure in Tarsius indicates that members of the genus should no longer be considered lineal relatives of the anthropoids; rather, they are considered to be living Eocene relicts that managed to avoid extinction (Buettner-Janusch, 1966).

A synoptic list of those Prosimii, to which references have been or will be made, is presented in Table 1; like Tables 2-4, it is based largely upon the works of Simpson (1945) and Buettner-Janusch (1963). The list is by no means complete. It should be considered an aid, only, to the understanding of taxonomic status within the suborder Prosimii.

The second and larger primate suborder is the Anthropoidea; it is composed of some 35 genera and 140 species. The marmosets, monkeys, macaques, baboons, langurs, gibbons, chimpanzee, orangutan, gorilla, and man are all included in this highly variable group. Its members are usually subdivided by 1 of 3 categorical methods: the designation and recognition of 2 infraorders, 3 superfamilies, or 4 monophyletic, anthropoid taxa. Each method has its advantages and limitations.

The anthropoids may be classically divided into 2 infraorders: Platyrrhini and Catarrhini. These divisions are credited to E. Geoffroy St. Hilaire (1812) and Hemprich (1820), both of whom employed the term platyrrhine to describe the "broad-nosed" New World monkeys

(superfamily Ceboidea) whose nostrils are separated by wide nasal septa, and the term catarrhine to described the "downward, narrow-nosed" Old World monkeys (superfamily Cercopithecoidea) and great apes (superfamily Hominoidea) whose narrow nasal septa permit the nostrils to be closer together, comma-shaped, and inferiorly directed. Although some platyrrhines are descriptively catarrhines (Pocock, 1925), the platyrrhine-catarrhine infraordinal system is still preferred by some authorities. For example, Hershkovitz (pers. comm.) states that the use of "Ceboidea" is disturbing. As proposed, and employed, the name implies that New World monkeys (Ceboidea), Old World monkeys (Cercopithecoidea), and hominoids (Hominoidea) diverged from a common monkey-like ancestor, suborder Anthropoidea. Because the New and Old World monkeys almost certainly evolved independently from different lemuroid ancestors, he prefers to use Platyrrhini and Catarrhini as suborders, each derived from a prosimian.

Simpson (1945) abandoned the classic, infraordinal system and proposed that anthropoids be considered 3, not 2, well-marked subdivisions: the superfamilies Ceboidea, Cercopithecoidea, and Hominoidea. He objected to the cercopithecoids and hominoids being treated as one (Catarrhini)—as implied by the classic arrangement—stating that all 3 may be of equal antiquity.

Simpson's revised monophyletic taxa (1962) were but a slight departure from his original (1945) view. He chose to divide the latter taxon (superfamily Hominoidea) into 2 families: Pongidae and Hominidae. Hence, 4 monophyletic, anthropoid taxa are generally

recognized at present: superfamily Ceboidea, superfamily Cercopithecoidea, family Pongidae, and family Hominidae. They will be discussed in this order.[1]

The superfamily Ceboidea (Simpson 1931) is the only group of monkeys that inhabits Central and South America. All ceboids are adapted to an arboreal existence; they dwell throughout the tropical forests of the state of San Luis Potosi in Mexico (23° N.) southward to Argentina (27° S.) and are particularly abundant in the Amazon Basin. All but 1 genus (Aotus) are diurnal. The intergeneric variation in size of adult members is considerable; the pigmy marmoset (Callithrix [=Cebuella]) may weigh only 90 grams, whereas a howler monkey (Alouatta) may approach 9 kilograms. Four genera of New World monkeys are unique among the Primates in that they possess a true prehensile tail; this highly specialized structure, sometimes called a fifth-hand, subserves the functions of grasping,

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[1]Particular emphasis will be placed upon a review of the New World monkeys (superfamily Ceboidea = infraorder Platyrrhini) because the major portion of the thesis is concerned with this taxonomic group. The historical, ecological, and behavioral background of each of the New World species employed in this survey will be discussed in the present Introduction. However, in order to restrain a potentially voluminous work and keep it within reasonable limits, the author has chosen only to describe the histological and histochemical details of the skin of the following species of Callithricidae under Results: Callimico goeldii, Callithrix argentata, Callithrix pygmaea, Saguinus fuscicollis illigeri, and Saguinus oedipus. Consequently, the significant cutaneous characteristics of the following species of Ceboidea will be confined to the Discussion: Cebus albifrons, Sairimi sciureus, Alouatta caraya, Ateles geoffroyi, Lagothrix lagothricha, Aotus trivirgatus, Callicebus moloch, Callicebus torquatus, Pithecia monachus, and Cacajao rubicundus.

maintaining equilibrium, tactile sensation, and locomotion. Aside from the superfamily's geographical distinction, the majority of its members are also characterized by their relatively platyrrhine, laterally-directed nostrils and an imperfectly opposable pollex.

The New World monkeys[1] (superfamily Ceboidea) are currently divided into 2 families: the Cebidae and Callithricidae.[2] The family Cebidae (Swainson 1835) is distinguished from the family Callithricidae by its dental formula: $\frac{2.1.3.3.}{2.1.3.3.}$. Unlike callithricids, the cebids are generally larger, possess flattened or curved nails on all digits, and usually produce a single offspring. The family is presently subdivided into 6 subfamilies and 12 genera; the order in which these categories will be discussed corresponds to the systematic outline presented in a synoptic list of the Cebidae (Table 2).

The subfamily Cebinae (Mivart 1865) is among the most widely exported group of American monkeys. Its members are diurnal, long-tailed cebids that have relatively oval heads, prognathous faces, and vertically implanted incisors. The subfamily is divided into 2 major groups: the capuchins (Cebus) and squirrel monkeys (Saimiri). Both genera are widely distributed in the Americas and are sympatric throughout a large portion of this territory (Map 1).

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[1]As defined by Buettner-Janusch (1966), a monkey is any quadrupedal primate other than a prosimian or hominoid. Although the term is more frequently associated with New World primates, it is equally applicable to the nonprosimian, nonhominoid primate inhabitants of the Old World.

[2]Simpson (1962) suggests that the family status assigned these 2 groups may only exaggerate the difference between 2 such closely related families.

The genus Cebus (Erxleben 1777) is generally divided into 2 groups: those with, and those without headtufts. Its members (capuchins) are so phenotypically varied that the precise number of species has long been a matter of conjecture. The capuchins occupy a discontinuous range from Honduras to Paraguay, including Venezuela, Colombia, the Guianas, Amazon Basin, Bolivia, southern Brazil, Argentina, and the island of Trinidad (Map 1). In their native habitat of dense tropical forest, the omnivorous capuchins chatter and frolic in troops of 20-30 individuals. Capuchins are known to attain a weight of 4 kilograms and a longevity of 30 years (Walker, 1964). Members of the genus Cebus are singularly peculiar in that they possess a completely haired prehensile tail.[1] Because they often carry this tail with the tip in a coiled position, capuchins are sometimes referred to as "ring-tailed monkeys." This term is unfortunate and should be restricted to the descriptively appropriate prosimian lemur, (L. catta). Cebus albifrons (Fig. 7), the white-browed capuchin, was originally described by Humboldt in 1811 from the banks of the Rio Orinoco on the Venezuelan-Colombian border. Like the other species of capuchin--C. apella, C. capucinus, and C. nigrivittatus--it is colloquially referred to as "organ grinder's monkey." All capuchins adapt to captivity, are tractable, display facial expressiveness, and have considerable dexterity. They sometimes employ the latter talent to catch objects in the air, pick locks, and unfasten chains (Hill, 1960).

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[1]Whereas the prehensile tails of all Alouattinae and Atelinae are characterized by ventral, glabrous friction surfaces, those of Cebus are hairy. In this respect, the capuchins occupy a unique position in the Order.

The squirrel monkeys, genus Saimiri (Voigt 1831), represent the other major division of the subfamily Cebinae. Unlike the capuchins, their long thick tails are not prehensile; they are used only for support and balance. Squirrel monkeys inhabit the dense, vine-entwisted forest that borders river banks in the Amazon valley and the Guianas. They are also widely distributed between Costa Rica and Bolivia (Map 1). Perhaps the most common and prolific type of monkey in the Americas, they have been reported in flocks numbering several hundred. The small-faced, brightly colored squirrel monkeys subsist on a diet of flowers, fruits, nuts, and insects. They weigh approximately 1 kilogram and have a life span of 15-20 years. The common squirrel monkey, Saimiri sciureus (Linnaeus 1758), is probably the best-known and most widely used species (Fig. 8).

The subfamily Alouattinae (Elliot 1904) consists of 1 genus, Alouatta (Lacépède 1799) and 6 species. Its members are the largest of the New World monkeys; adults may weigh as much as 9 kilograms (Walker, 1964). They are characterized by a prominent beard, long silky hair, and a large prehensile tail that is glabrous on the distal one-third of its venter. A sloping symphysis menti and deep expanded jaws, which embrace an inflated hyoid, give them a goitrous appearance. An abnormal cranial form lends a forbidding expression to their face (Fig. 9). The genus is widespread in the forested American tropics, ranging from Veracruz, Mexico to Bolivia, Ecuador, Brazil, Paraguay, and Trinidad (Map 2). Much of our knowledge of the behavior of this genus we owe to Carpenter (1934). The inflated hyoid apparatus is used to vocalize and the reportedly "insufferable"

sounds produced by these animals are the basis for their colloquial name, howler monkey. They are at home in the uppermost stratum of the rain forest canopy, and seldom descend to the ground. They are pronograde and travel in troops of 4-40. They adhere to territorial rights and concertize regularly at dawn and dusk. The howler monkey is reported to be a vegetarian in its natural habitat.[1] Females are more prevalent than males by a ratio of 7♀♀:2♂♂; they are also the dominating sex. The Carayanese howler monkey (Fig. 9) is the species that will be referred to in this study: Alouatta caraya (Humboldt 1812).

The subfamily Atelinae (Miller 1924) has features somewhat intermediate between the Cebinae and Alouattinae; its members possess true prehensile tails but lack abnormal cranial form and specialized mandibulohyolaryngeal apparatus. The Atelinae are subdivided into 3 genera: Ateles, Brachyteles, and Lagothrix.

The genus Ateles (E. Geoffroy 1806) ranges from southern Mexico to central Bolivia and the Mato Grosso of Brazil (Map 3). Its 4 recognized species are all characterized by a slender build, small head, prominent muzzle, disproportionately long arms that are more elongated than the legs, and a tail that is half again the length of the head and body. This overall, arachnoid-like appearance is denoted by their common name, spider monkey. Many forms have a black face and white eye rings; their pelage is attractively colored, but lacks underfur. The female has a pendulous clitoris that is

[1]In this respect, it resembles the Old World leaf-eaters, i.e., the indrisoid lemurs, langurs, and colobus monkeys.

equal in length to that of the male penis. Individuals may weigh as much as 7 kilograms. Spider monkeys are frugivorous and travel in bands of 10-40. Because different bands occupied the same territory at different times of day, Carpenter (1935) concluded that territory is defined by time as well as by space. Spider monkeys are more graceful and have developed a more erect or orthograde mode of locomotion than any other New World monkey. They use their long prehensile tails for swinging, suspending their weight, and picking up objects. Because their thumbs are absent--although a corresponding metacarpal bone is present--spider monkeys use their hands as hooks. In so doing, they are excellent brachiators.[1] The golden spider monkey, Ateles geoffroyi (Kuhl 1820), is one of the more commonly used species (Fig. 10).

The genus Brachyteles (Spix 1823) is the least known of all New World primate genera. It contains only 1 species, arachnoides (Spix 1823). Woolly spider monkeys, as the name implies, are intermediate in morphology between Ateles and Lagothrix. The genus Brachyteles is a geographical isolate, which is confined to the mountains of southeastern Brazil from Bahia to São Paulo (Map 3). Like the genus Ateles, woolly spider monkeys are distinguished by long slender limbs and a true prehensile tail; their thumbs are vestigial or absent. They are reported to be frugivorous and are thought to be gregarious.

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[1]Brachiation may be defined as movement that is accomplished by swinging arm-over-arm along a horizontal support (Buettner-Janusch, 1966). The brachiating ability of spider monkeys parallels that of the southeast Asian gibbons.

The genus Lagothrix (E. Geoffroy 1812) is composed of 2 species of woolly monkey. Although the genus is geographically confined (Map 3) to the northwestern corner of South America--Colombia, Ecuador, Peru, and Brazil--it is ecologically less restricted, ranging from sea level to 9,000 foot elevations (Buettner-Janusch, 1966). Unlike the 2 preceding genera, woolly monkeys have round massive heads and heavy bodies; the vernacular name "barrigudos" refers to their prominent bellies. An ample growth of underfur contributes to the woolly appearance of their short thick pelage, hence the derivation of their common name. Notwithstanding the neckless, muscular appearance of a weight lifter, the relatively large size, and the formidable canines, woolly monkeys are more tractable as pets than most primates and are noted for their mild demeanor. They travel in bands of 15-50 individuals and subsist on a diet of fruits and leaves. The species of Lagothrix employed in this survey is lagothricha (Humboldt 1811); it is commonly called Humboldt's woolly monkey (Fig. 11).

The subfamily Aotinae (Elliot 1913) is composed of 2 small, strigiform-like cebid genera that are characterized by orthognathous faces and large eyes. The first of these genera, Aotus (Humboldt 1811) = Aotes (Humboldt 1811), has the distinction of being the only nocturnal primate genus in the New World. Only 1 species (Fig. 12) is assigned to this genus, namely, trivirgatus (Humboldt 1811). All described races of owl monkey may be distinguished from other cebids by their greatly enlarged, forwardly directed orbits, which encroach upon the cheeks, with a resulting shallowness of the maxillae (Hill 1960). Owl monkeys rarely exceed a weight of 1 kilogram;

they have long banded tails, dense, soft fur, and a throat sac, which may be inflated to impart a resonant quality to the voice. Owl monkeys, or night monkeys as they are sometimes called, are locally distributed throughout northern South America; they are most numerous in the Amazon and Orinoco basins (Map 4). They travel at night in small family bands, searching for fruits, insects, small birds, and bats. Pets of this genus are reported to have lived in captivity for 20 years (Walker, 1964).

The genus Callicebus (Thomas 1903) is locally distributed over a large area of South America (Map 4). Its 35-40 varieties, commonly called titi monkeys, have been reduced to 3 distinct species by Hershkovitz (1963). Titi monkeys inhabit the upper limits of the forest canopy, where they are omnivorous and live in small family groups. Their large eyes led early explorers to assume that titis were nocturnal; it has since been established that they are diurnal and crepuscular, only. Unlike Aotus, their pelage is long and silky; in other respects, however, their form and behavior largely resemble that of an owl monkey. Two species of titi monkey, described by Hoffmannsegg in 1807, are employed in the present study: C. moloch, the devil titi and C. torquatus, the necklaced titi.

Members of the subfamily Pitheciinae (Mivart 1865) are distinguished from other cebids by the following anatomical traits: moderate to large bodies, clothed with long, coarse hairs; noses more distinctly platyrrhine than any other subfamily; shafts of ribs more expanded than any other primate; manual digits I and II divergent from III, IV, and V; and elongated, upper and lower incisors

sloping forward and separated from canines by wide diastemata (Hill, 1960). The 3 generic groups of Pitheciinae may also be distinguished from other cebids, and from each other, by the following cephalic pelage traits: hair parted down the middle or bouffant-styled (Pithecia); juveniles fully haired, adults alopecic (Cacajao); and monk-styled haircut with chin hairs forming a prominent goatee (Chiropotes). Sakiwinkis, uacaris, and bearded sakis, respectively, are all restricted in range to that portion of Ecuador, Peru, the Guianas, Colombia, and Brazil that constitutes the Amazon basin. (Map 5).

The genus Pithecia (Desmarest 1804) contains 2 species. Both are completely arboreal and travel in social groups of 5–10 members. Sakiwinkis are omnivorous; they are reported to tear small mammals and birds apart with their hands, before eating them (Walker, 1964). Contrary to the ferocious disposition connoted by this habit, sakiwinkis are very gentle. The silvered (hairy) sakiwinkis (P. monachus, E. Geoffory 1812) that the author has observed assume a characteristic, melancholy or doleful expression (Fig. 13). When carefully handled, they are alert, gentle, and utter soft, high-pitched twitterings that appear to be deliberately articulated through carefully pursed lips. If disturbed from a somnolent state, however, they emit harsh, crescendo squawks that are quite unlike the sounds one would expect from a monkey that is seldom larger than 1.5 kilograms.

The genus Cacajao (Lesson 1840) contains the bizarre uacaris (uakaris). They have the distinction of being the only short-tailed American monkeys, their tails being less than one-third their combined

head and body length. There are 3 species of uacari; each is characterized by a sparsely haired scalp and pinkish face. All are timid, slow moving vegetarians. They travel in small bands and inhabit the higher trees that grow along river banks. The best-known species is C. rubicundus (I. Geoffroy & Deville 1848). Commonly called the red uacari, it has 2 striking external characteristics: a pinkish-red face, forehead, and ears, and "baldness" of the forehead and anterior scalp (Fig. 14). An inhabitant of the north Amazon basin, this unique primate appears to have a severely "sunburned" head protruding from an apparently large body that is clothed in a full-length "bear skin suit." Its countenance conveys an expression of pathos and its disheveled attire consists of very long, sparsely distributed, reddish-brown hairs. Stripped of its pelage, the skin is pallid, its body deceptively slender, and its long, gangly limbs terminate in disproportionately large hands and feet.

The genus Chiropotes (Lesson 1840) contains 3 species; its members are all distinguished by bearded faces and the presence of a medium hair whorl on the tip--not the proximal region--of the tail (Buettner-Janusch, 1966). Bearded sakis, as they are commonly called, occur in groups of 6 or less individuals. They dwell along rivers in the tropical rain forest and are omnivorous. Their call has been described as a modulated whistle (Walker, 1964). Little else is known about the behavior of this elusive cebid genus.

The subfamily Callimiconinae (Thomas 1913) contains a single monotypic genus. Species authorship is attributed to Thomas (1904), who described a specimen made available by Dr. E. A. Goeldi, director

of the Goeldi Museum at Pará. Ribeiro (1912), who recognized features intermediate between those of Callicebus and Mico, designated Thomas's Midas goeldii as a new genus, Callimico, with which Thomas agreed. Thus, the animal is currently named Callimico goeldii.

Information about C. goeldii is sketchy. Its type locality is not known, and little is known about its distribution in the upper Amazon of Peru and Brazil (Map 4). It is said to travel in bands of 20–30 individuals in the middle stratum of the forest, but there are no other descriptions of its behavior in a natural environment. Ribeiro (1940) and Sanderson (1957), however, made some observations on captive animals.

Among the New World subhuman primates, Callimico goeldii has been assigned its own distinct family, placed in 2 large subfamilies, and given at least 5 generic names—all within 64 years.

Two major structural characteristics place Callimico in an intermediate position between the Cebidae and Callithricidae (=Hapalidae). Because of its dental formula, Thomas (1913) considered Goeldi's "monkey" a subfamily of the Cebidae whereas Pocock (1920, 1925) contended that the more significant taxonomic characteristic of claw-like nails on all digits but the hallux placed Goeldi's "marmoset" as a distinct subfamily of the Hapalidae. Judging by the characteristic dentition, Elliot (1913), Weber (1924), and Simpson (1945), concurring with Thomas, treated Callimico as a subfamily of the Cebidae. Gregory (1920) and Jones (1929), however, stressing the importance of cheiridia, reaffirmed Pocock's classification. Thomas later (1928) reversed his original opinion and concluded that Callimico was a primitive hapalid, not a

cebid. Dollman (1933) took an extreme position and elevated Callimico to the rank of family, "Callimiconidae," between the Cebidae and the Hapalidae. Hill (1957) adopted this classification, but in the preface to his volume stated: "I now believe that Callimico is a tamarin, doubtless a primitive one, and that systematically it should form no more than a subfamily, Callimiconinae, of the Hapalidae." A comprehensive account of the structural bases for the taxonomic confusion surrounding C. goeldii has been published as a monograph (Hill, 1959). To compound the problem, authors as current as Buettner-Janusch (1966) list the subfamily Callimiconinae under the family Cebidae.[1]

The external features of Goeldi's marmoset resemble those of a large tamarin; the larger male in the present study (Fig. 15) weighed 510 grams. Goeldi's marmosets have a soft, glossy, jet-black pelage that contrasts sharply with chestnut-colored irises. The characteristic hair growth is described by Hill (1957):

> "A kind of domed pompadour adornment is formed by erect hairs arising from the supraciliary region and covering the crown as far back as the occiput; from thence arises a second cape-like growth or mane draping the neck and shoulders but also

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[1]The author suggests that the combined histological and histochemical properties of a given cutaneous system are reliable taxonomic criteria which, added to dentition, cheiridia, skeletal details, myology, arthrology, splanchnology, and other structural characters classically employed by systematic zoologists, should give a fuller understanding of an animal's position. It is one of the aims of the present study to record the integumentary characteristics of Callimico and compare them with 9 genera of Cebidae and 2 genera (6 subgenera) of Callithricidae; hopefully, such a contribution will augment our structural knowledge of C. goeldii and thereby facilitate the correct appraisal of its long-disputed taxonomic status.

> providing antrorse hairs like a couple of ostrich feathers over the crown. The upper parts are clothed with fine, black, silky hairs like that of a plucked, good quality, dressed fur-seal, but longer. Over the base of the tail the elongated hairs of the rump fall like another mane, but ending in a neat curve rather than a fringe."

The locomotor traits are similar to those of the tamarins, marmosets, and pinchés. The animal does not run, it darts; it does not jump, it leaps or springs with speed and agility. During brief pauses, it assumes the crouching position characteristic of callithricids. Its behavior also resembles that of the tamarin-marmoset-pinché group: it grimaces when distressed; its nervous jerky head movements are always accompanied by an alert gaze; it typically emits a loud, open-mouthed, screaming chatter. Characteristically, it grasps a vertical tree limb quadrupedally in order to hide in a crouching position, furtively peeking from behind alternate sides of the branch and foliage.

The histological and histochemical, integumentary characteristics of this genus, like those of the following callithricid genera, will be described in detail under Observations.

It is surprising that so much of the family Callithricidae (Thomas 1903) escaped the notice of earlier cutaneous biologists, since the marmoset-tamarin-pinché complex is one of the more diversified in the Order Primates. Periauricular corollas, red splotchy faces, naked pink faces, blue spotted ears, bald heads, moustaches, golden manes, piebald pelage, blue eyes, and diminutive proportions are only a few examples of the great variety to be found in this group.

The Callithricidae are distinguished from the Cebidae by their unique dental formula, $\frac{2.1.3.2.}{2.1.3.2.}$, and the presence of pointed falcate nails that terminate on all digits except the hallux, which has a flat nail. All members of the family are small; adult weights vary between 70 and 1,000 grams. Callithricid faces are naked or sparsely haired, pelage is soft, dense, and often silky, and the very long, nonprehensile tails are frequently characterized by annular bands. All marmosets, tamarins, and pinchés are excitable, and panic easily. Their movements are typically quick and jerky; their voices are high-pitched, staccato notes and trills, bird-like in quality. Unlike cebids, members of the Callithricidae usually produce twins or triplets; the male characteristically assists the female at birth, receiving, washing, and carrying the offspring on its back. Callithricids are widely distributed in the tropical forests of Panama and South America (Map. 6).

The family Callithricidae is currently divided into 3 recognized genera: Callithrix, Saguinus, and Leontideus. The first of these genera is separated from the latter according to the morphology of the lower canines: the genus Callithrix has lower canines that are equal in length to the contiguous incisors (incisiform canines), whereas the genera Saguinus and Leontideus possess lower canines that are much longer than the adjoining incisors (caniniform canines). Hence, marmosets are sometimes called "short-tusked" and tamarins and pinchés, "long-tusked."

Before proceeding to each of these 3 genera, it should be emphasized that Saguinus (Hoffmannsegg 1807) is the oldest valid

generic name for all callithricids referred to as tamarins (Hershkovitz, 1958, 1966). Thus Tamarin (Gray 1870), Tamarinus (Trouessart 1899), Marikina (Lesson 1840), and Oedipomidas (Reichenbach 1862) are presently treated as synonyms or subgenera of Saguinus. Similarly, Hapale (Illiger 1811), Mico (Lesson 1840), and Cebuella (Gray 1866) have been considered synonyms or subgenera of Callithrix (Erxleben 1777) since Simpson's classification in 1945.

The term Leontocebus (lion-like monkey) is somewhat disturbing to a nontaxonomist. Briefly, its background is as follows: the tamarins were at one time given the generic name Tamarin (Gray 1870); this taxon was replaced by Leontocebus (Wagner 1839) in 1956. At the same time, the golden lion-tamarins--now without a generic taxon--came to be designated Leontideus (Cabrera 1956). In 1958, however, it was pointed out that Saguinus antedates Leontocebus and thus the latter taxon comes to final rest as a synonym of its successor, Leontideus.

It is not the author's intention to belabor taxonomic intricacies and nomenclatorial legalities; it is hoped, however, that the reader be aware of such revisions. A synoptic list (Table 3) is presented as a reference to which the reader may refer when reviewing the following genera and species of the family Callithricidae; the accompanying distribution map (Map 6) subserves the same purpose.

The genus Callithrix (Erxleben 1777) inhabits the tropical and subtropical forests of Brazil and Bolivia (Map 6). All of its members are arboreal except the silver marmoset, Callithrix (=Mico) argentata. The latter species is unique among all callithricids in that it sometimes

leaves the forest to inhabit the tall grasses of the Mato Grosso. Most marmosets (genus Callithrix) are adorned with cephalic plumes and ear tufts. They are the smallest genus of the Callithricidae, weighing 90-450 grams. Marmosets travel in groups of 3-12, are omnivorous, and attain a life span of 10 years in the wild (Walker, 1964). A running and hopping type of locomotion is characteristic of the genus. Three species of Callithrix have been examined in the present survey: C. (=Cebuella) pygmaea, C. (=Mico) argentata, and C. (=Hapale) humeralifer; they will be described in this order.

The pigmy marmoset, designated Cebuella by Gray in 1866, is the smallest extant anthropoid (Hill, 1957). Its total body weight may be only 90 grams, and the overall body length as short as 160 mm. (Elliot, 1913). Spix, in 1823, first described this diminutive, mongoloid-eyed callithricid from the forested regions near Tapatinga, whence it ranges along the Solimões and Uacyali rivers of Brazil, Ecuador, and northern Peru (Map 6). These arboreal animals utter occasional, high-pitched twitterings as they dart about the forest canopy. Their entire pelage is thick, silky, and "salt and pepper" in coloration. They have a long bushy tail and large ears that are inconspicuous because of a neck and facial ruff. Pigmy marmosets are naturally timid, choosing to retreat behind foliage or tree limbs until imminent danger has abated. In captivity, however, they display a ferocious appearance that coincides with a fierce and aggressive demeanor (Fig. 18).

The silver marmoset, Callithrix (=Mico) argentata, was originally described by Linnaeus in 1771 from Pará, Brazil. The species complex,

which is composed of several geographically isolated races, is distributed along the right bank of the Rio Amazonas, southward to the Mato Grosso (Map 6).

Colloquially referred to as the silvery, or black-tailed marmoset (Fig. 17), this raucous callithricid travels in groups of a dozen or less individuals and subsists on a diet of insects and vegetables. The silver marmoset is capable of extraordinary leaps; when threatened but prevented from leaping to safety, grotesque grimaces not only register its dismay but also befit the audibly strident vocalizations and aggressive behavior that ensue.

The silver marmoset's external characteristics have been summarized by Hill (1957): "bare face of rubicund hue; naked ears of same color; pelage almost uniformly glistening silvery white; fine, silky hairs; tail black, sometimes brownish, contrasting strongly with body color." In addition to these external characters, the males possess a conspicuous, silver-white scrotum that is chromatically offset by a frame of crimson-colored integument, comparable in intensity to that of the characteristic, manikin face and elf-like ears. (Fig. 17).

Whereas 2 of the formerly recognized callithricid genera (Cebuella, Gray 1866, and Mico, Lesson 1840) were monotypic, the third (Hapale, Illiger 1811) was assigned 10 species. The white-shouldered marmoset, Callithrix (=Hapale) humeralifer, is included in this latter group. Callithrix humeralifer (E. Geoffroy 1812) is distributed along the left bank of the lower Rio Tapajóz, in Pará, Brazil (Map 6). It too possesses the typical, high-strung, clamorous, and

irritable callithricid temperament (Fig. 16). Its principal diagnostic features are described by Hershkovitz (1966): "long, thick, silky, silvery to silvery-buff tufts covering the inner and outer surfaces of the pinna, silvery or grizzled forequarters, black dorsum flecked with white, dark hindlimbs and annulated tail." Members of the Callithrix (=Hapale) group are keyed according to the arrangement and color of their aural adornments (members with ears hidden in a corolla or tuft but with external [medial] aspect of pinna naked = C. jacchus group; members whose ears contain intrinsic tufts [both surfaces of pinna completely covered with long, decorative hairs] = C. humeralifer group); however, some confusion exists regarding the correct identification of humeralifer because Hill (1957, p. 286) included it under the category, "intrinsic black tufts." As Hershkovitz (1966) states: "The only foundation for describing the ear tufts of this species as black appears to be a two-century accumulation of soot on the Paris [type] specimen."[1]

The genus Saguinus (Hoffmannsegg 1807) contains the tamarins and pinchés. Members of this genus inhabit the open woods and forests of Panama and northwestern South America (Map 6). They are larger than the marmosets, weighing between 225 and 900 grams. Tamarins and pinchés are omnivorous; some are reported to have lived 15 years

[1]Because histochemically prepared tissues were not available, a study of the skin of this callithricid cannot be considered complete. Therefore, rather than incompletely belabor its cutaneous characteristics in the Results, pertinent histological findings, alone, will be mentioned under the Discussion.

(Walker, 1964). The genus may be subdivided into 4 general groups, each corresponding to a formerly recognized genus; the black-faced tamarins, white-faced tamarins, bald tamarins, and pinchés.

The black-faced tamarins, Saguinus (=Tamarin, Gray 1870), are aptly described by their common name. The pelage of members of this species-group is generally black over the entire body; one species, however, has red-orange paws and is appropriately called the red-handed tamarin, Saguinus (=Tamarin) midas, Linnaeus 1758.

By contrast, the white-faced tamarins, Saguinus (=Tamarinus), Trouessart 1899), are characterized by predominantly white faces and muzzles. The group is composed of approximately a dozen recognized species; one of these is the red-mantled tamarin, Saguinus (=Tamarinus) fuscicollis illigeri, Pucheran 1845. It is perhaps the best-known and most representative member of the white-faced tamarin species-group (Fig. 19). It is an arboreal, omnivorous callithricid whose distribution (Map 6) occurs along the Colombian bank of the Rio Solimões, the Rio Napo of northern Peru, and the Rio Pastaza of eastern Ecuador (Hill, 1957). Its pelage is described by Hill (1957):

> "Distinguished chiefly from all the species so far described in having the mantle and shoulders some shade of red, chestnut or purplish-brown instead of black, but the bases of individual hairs black, the terminal halves being tawny or reddish, with sometimes a blackish tip. The brighter shade extends along the limbs to the wrists, but the hands, feet and tail (except base) are black. Lower back marbled, in strong contrast to mantle; the hairs are black, strongly zoned with ochraceous distally. Sides of rump, thighs and legs reddish, but lighter

than mantle. Under-parts dark liver-brown speckled with black; separated from dorsal saddle by brownish-red line. White hairs on forehead between eyes, also on face below eyes and on both lips; circumbuccal zone leaving nostrils free."

Like other tamarins and all callithricids, it has a typically flat and scowling face, to describe which the French used the word marmouset, signifying "manikin" or "grotesque image." Members of the Saguinus (=Tamarinus) species-group lack cilia on the palpebral border of the upper eyelids; their external ears are inconspicuous; and all have large fields of sebaceous glands, mingled with apocrine glands on the posterior abdominal wall. Tamarins are said to have an even temperament (making them fashionable pets of the affluent in Shakespeare's time); actually, all of them are nervous, chirpy and exceedingly neurotic little creatures.

The bald tamarins, Saguinus (=Marikina, Lesson 1840), are represented by 2 species. They are limited in distribution to an area north of the Amazon, between the Rio Parú and Rio Negro of Brazil (Map 6), and are distinguished from all other tamarins by their relatively large size, "hairless" faces, and naked ears. One of the species, Saguinus (=Marikina) bicolor, Spix 1823, is striking in that the above features are further accentuated by a body whose anterior half is clothed in white hairs, and whose posterior half is clothed in black hairs. The animal is appropriately called the pied or piebald tamarin.

The pinchés, Saguinus (=Oedipomidas, Reichenbach 1862), like the bald tamarins, comprise 2 species. The first of these, Saguinus (=Oedipomidas) oedipus, was described by Linnaeus in 1758. Its type locality has been restricted to the lower Rio Sinú, department of Bolivar, Colombia (Hershkovitz, 1949). This attractive pinché (Fig. 20) inhabits wooded areas along the northern coast of Colombia between the gulf of Darien and the Rio San Jorge. To the west, in the Colombian Choco and Panama, it is replaced by its allied species, spixi, the only callithricid to enter Central America (Map 6).

S. oedipus was called "le pinché" by the French naturalist Buffon, who later bestowed a living specimen on the celebrated Madame Pompadour (Hill, 1957). It is widely known as the cottontop pinché or cotton-head tamarin. These colloquial terms stem from the conspicuous cephalic crown of long white hairs that contrasts strongly with the black face and dark dorsum (Fig. 20). The pelage has been described by Hill (1957):

> "Face glabrous, black; the glabrous area extending from chin to forehead and, on either side, as a wedge-shaped area as far back on the crown as the ears; cheeks and ears similar. Sparsely planted short, white hairs occur on chin, lips, and along a line from the nasal bridge to the angle of the gape. Other tracts of white hairs (i) across forehead, narrowing rapidly laterally, (ii) in line with preceding, but separated by a gap between outer canthus and masseteric region, (iii) a small tuft on tragus. Center of crown and nape adorned with long white plumes, covering a wedge-shaped

> area with apex, anteriorly, long posterior hairs flowing like a mane over interscapular region. Dorsal surface of body dark brown (varying from fuscous to drab) grizzled with buff; rump and lateral surface of thighs like back, but more uniform, often with tendency to ferruginous or hazel, the tips of the hairs greyish. Entire underparts, arms, shanks, and dorsum of manus and pes white, yellowish-white or pale ochraceous. Tail, proximal one-fourth to one-third burnt sienna to Mars orange, distally paler and mixed with dark brown or black; the terminal half, dark brown or black."

Cottontop pinchés have a bird-like vocabulary. They live in troops of 3 to 12 and thrive on a diet of fruits and insects. They have the typical callithricid temperament: when distressed or angered, the cephalic crest becomes erect; alternate external ear muscles relax and contract causing the ears to elevate and depress asynchronously, gliding back and forth like the antennae of a cockroach; frequent, high-pitched, irritatingly loud chatters are emitted; body weight is nervously shifted from forelimbs to hindlimbs; the eyes assume an intent, ominous stare; the formidable canines are displayed; and finally, as Hill (1957) aptly admonishes, "Biting the aggressor is the usual response in fear or anger, the sharp teeth being capable of inflicting a penetrating wound in the human skin."

The third and final genus of the family Callithricidae consists of 3 species of golden lion-tamarins. Members of the genus Leontideus,

Cabrera 1956 (=Leontocebus, Wagner 1839) are restricted in distribution to the forests of eastern Brazil (Map 6). The lion-tamarins have the habitus of a medium-sized tamarin, ranging in weight between 200 and 600 grams. However, their long silky hairs contribute to a distinctive mane that encircles the head and shoulders, much like that of a lion; hence, their generic and common names. Lion-tamarins are also distinguished from other callithricids by the presence of a web of skin that proximally connects manual digits III and IV. All 3 species of Leontideus are quite striking: they are characterized by variable amounts of golden, silky hair that is admixed with black or rusty red pelage. One species, Leontideus rosalia (Linnaeus 1766), is predominantly golden in color and possesses bright blue eyes. Members of the genus are reported to live 15 years (Walker, 1964).

The superfamily Cercopithecoidea, Simpson 1931 (= family Cercopithecidae, Gray 1821) is the second of 4 monophyletic anthropoid taxa. It is a large and complex group, which contains some 14 genera and 61 species, i.e., 25 and 30% of all primate genera and species, respectively. Cercopithecoids are found on Gibraltar, from North Africa to the Cape of Good Hope, in the Arabian peninsula, from southern Asia to the Himalayas, and throughout Indonesia, the Philippines, Formosa, and the islands of Japan; hence, they are commonly called Old World monkeys. All are quadrupedal catarrhines, whose pelvic limbs are longer than their pectoral limbs. They are characterized by the following dental formula: $\frac{2.1.2.3.}{2.1.2.3.}$. The hands and feet of all Old World monkeys are adapted for fine control and

precision grasping. Thumbs (excluding the Colobinae) and large toes are opposable. Most Old World monkeys are diurnal. Their muzzles are elongate or rounded; tails are nonprehensile. Old World monkeys are generally divided into 2 subfamilies: the Cercopithecinae and the Colobinae (Table 4).

The subfamily Cercopithecinae (Blanford 1888) is both African and Asian. Its members are omnivorous, possess paired herniations of the buccal mucosa (cheek pouches), and have simple, sac-like stomachs. All possess 5 digits on the pes and manus. Most are distinguished by the presence of moderate to large, naked callosities that overlie the ischial tuberosities or "seat pads." The Cercopithecinae may be subdivided into 3 groups: the baboons and macaques, the mangabeys, and the guenons.

Baboons, genus Papio (Müller 1773) and macaques, genus Macaca (Lacépède 1799) are the principal terrestrial members of the subfamily Cercopithecinae. Baboons occur throughout Africa, south of the Sahara Desert; they are also found on the Arabian peninsula. Macaques occur in Morocco, Algeria, and Gibraltar (the Barbary ape, Macaca sylvana), and are widely distributed in India, Pakistan, southeast Asia, China, and Japan. Because the occurrence of fertile hybrids is common, the 2 groups may eventually be treated as 1 genus (Buettner-Janusch, 1966). Baboons and macaques are both sexually dimorphic: males are noted for their elongated, tusk-like, upper canines; females are conspicuous because of their gluteal, cephalic, or sternal sex skin, which characteristically becomes bright red and engorged during estrus. Although most baboons and macaques

are terrestrial during their daytime activities, they retire to the trees during sleeping hours. All are highly social animals, whose troop makeup is strongly influenced by a dominance hierarchy. The rhesus monkey (Macaca mulatta), held sacred by the Hindus, is the most common and widely used of the macaques; probably the best-known of the baboons is the sacred Anubis or Hamadryas baboon (Papio anubis/hamadryas), of ancient Egyptian fame.

The other 2 cercopithecine groups are comprised of the mangabeys, genus Cercocebus (E. Geoffroy 1812) and guenons, genus Cercopithecus (Brünnich 1772). Both genera are largely arboreal, exclusively African, and often sympatric. The mangabeys inhabit the wet forests of equatorial Africa, from French Guinea and Liberia eastward to Kenya and Uganda. Unlike the guenons, they are longer, taller, and more slender; they have large cheek pouches, pale upper eyelids, and the male buttock pads are fused. The guenons are widely distributed throughout Africa; they range between Gambia and Abyssinia in the north, southward to the Cape. Like the mangabeys, they travel in troops and are characterized by very long tails; unlike the mangabeys, they inhabit a variety of habitats, including dense forest, bush, scrub, and savannah. The vervet or green monkey (Cercopithecus aethiops) is the most widely distributed and best-known of the guenons.

The subfamily Colobinae (Elliot 1913) occurs both in Africa and Asia. All of its members are vegetarian. They lack cheek pouches and ischial callosities, but possess highly specialized, sacculated stomachs that are adapted to handle the bulkage of their leafy diet. The Colobinae do not possess a fully-developed, opposable thumb;

this digit is absent or vestigial, the other 4 are elongated. Their hands, therefore, are particularly well suited for brachiation. Colobus (Illiger 1811) is the only genus to occur in Africa, ranging between Senegal, Ethiopia, and Angola. Its members are the most arboreal of all African cercopithecoids. Commonly called guerezas or colobus monkeys, these strikingly-marked brachiators inhabit heavy forests, where they occur in structured troops. The Asian members of the subfamily are known as leaf monkeys or langurs. They comprise 5 genera, the largest of which is Presbytis (Eschscholz 1821). Langurs range over a wide area of Asia that varies in elevation between sea level and the snow-covered Himalayas. They occur in Ceylon, India, southern China, Tibet, Assam, and Indonesia. One genus (Nasalis) occurs in the mangrove swamps of Borneo; it is characterized by a prominent, protuberant nose and is called the proboscis monkey. Another genus, the snub-nosed langur (Simias), is isolated on the Mentawi Islands, off the west coast of Sumatra. The latter 2 locales are shared by these Colobinae with their hominoid relatives, the Pongidae.

The superfamily Hominoidea (Simpson 1931) is composed of 6 genera and 12 species. It contains both of the remaining, monophyletic anthropoid taxa: the families Pongidae and Hominidae (Table 4).

The family Pongidae (Elliot 1913) contains what are generally conceded to be the closest living relatives of man. Apes are tailless, gregarious, catarrhines. Their ears and faces are naked, their arms are longer than their legs, their pollex is short, their hallux is opposable, and their skulls are longer anteroposteriorly than they

are broad. Apes are quadrupeds capable of bipedal locomotion. Their dental formula is: $\frac{2.1.2.3.}{2.1.2.3.}$. They convey food to the mouth with their hands. They are characterized by acute vision and hearing. All are anatomically capable of brachiation. The ape family contains 2 subfamilies: the gibbons (Hylobatinae) and the great apes (Ponginae).

Members of the subfamily Hylobatinae (Gill 1872) inhabit the rain forests of Java, Borneo, Sumatra and the Mentawi Islands, the Malay States, Assam, Burma, Thailand, and Indo-China. Unlike great apes and man, the gibbons possess greatly elongated arms, slender bodies, long canines, and buttock pads.[1] The subfamily is composed of 2 genera: Hylobates (Illiger 1811) and Symphalangus (Gloger 1841); the latter genus contains the siamang gibbon from the Malay States and Borneo. Unlike Hylobates, the siamang possesses a naked throat sac and a cutaneous, interconnecting webbing between pedal digits II and III. All gibbons, as the generic name Hylobates implies, are "tree dwellers." They are considered to be the most agile and graceful of all arboreal mammals. Their hands are used as hooks while brachiating; their movement is flowing and seemingly effortless. Gibbons are omnivores. Their vocalization is described as a "hooting" sound (Carpenter, 1940). Gibbons are bipedal on the ground; they raise and extend their arms for balance when walking or running in the orthograde position.

The subfamily Ponginae (Allen 1925) contains 3 genera: Pongo, Pan, and Gorilla. Each genus contains 1 species. Together, they

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[1]Gibbons are the only members of the family Pongidae that do not build nests or sleeping platforms; they are also the only genera of Pongidae in which buttock pads are present on all individuals.

constitute the prognathous, man-like, great apes. Terrestrially, great apes move as semierect, quadrupeds. Although the major portion of their weight is borne by the posterior limbs, they casually rest the weight of the anterior body on the second phalanges of their half-flexed fingers. The dorsum of each of these phalanges is differentiated into a thickened, glabrous friction surface, commonly called a "knuckle pad." Although their anatomy affords great apes the freedom of shoulder movement necessary to effectively brachiate, only the orangutan swings hand-over-hand with any frequency. The orangutan, Pongo (Lacépède 1799), is confined to Sumatra and Borneo. It possesses special cheek pads, has air sacs for vocal resonance, and is a vegetarian. The chimpanzee, Pan (Oken 1816), inhabits the tropical rain forest of Africa. Like the orangutan, it builds nests in trees for sleeping; like the gibbon, it is omnivorous; unlike all other Pongidae, however, it is the only ape reported to use tools, commonly. The placid, retiring gorillas, Gorilla (I. Geoffroy 1852), reside in the forests of equatorial Africa. These massive vegetarians occur in 2 forms: the lowland gorilla of coastal west Africa and the mountain gorilla of central Africa (vic. Lakes Tanganyika and Albert). Gorillas and chimpanzees are reported to have a longevity of 40-50 years. Extensive field studies on the habits, behavior, and social structure of orangutans, chimpanzees, and gorillas have been carried out by B. Harrisson (1962), J. M. Goodall (1962, 1964), and G. B. Schaller (1961, 1963, 1964), respectively. It would be redundant to further pursue a discussion of the great apes, in light of these excellent accounts. Prior to reports of this quality, however, no group of subhuman primates had been more

maligned by anthropomorphic man than this, the Pongidae.

Although the family Hominidae (Gray 1825) contains but a single genus and species, Homo sapiens (Linnaeus 1758), it is the most widely distributed, largest in terms of sheer numbers, and probably the most successful of all primate families to expoit its own evolutionary niche (Buettner-Janusch, 1963).

We are indebted to this family for what little we understand about the Order Primates. We might understand more, were the family not, in part, characterized by disagreement, emotionalism, and lack of objectivity. As Simpson (1945) puts it:

> "The primates are inevitably the most interesting of mammals to an egocentric species that belongs to this order. No other mammals have been studied in such detail, yet from a taxonomic point of view this cannot be considered the best-known order, and there is perhaps less agreement as to its classification than for most other orders. The peculiar fascination of the primates and their publicity value have almost taken the order out of the hands of sober and conservative mammalogists and have kept, and do keep, its taxonomy in a turmoil. Moreover, even mammalogists who might be entirely conservative in dealing, say, with rats are likely to lose a sense of perspective when they come to the primates, and many studies of this order are covertly or overtly emotional."

MATERIALS AND METHODS

I. Acquisition of Material.

All monkeys utilized in this study were prepared for skin excision by the intravenous injection of Sernylan® (3 mg./kg. body weight).[1] The external characteristics of the following species and sexes were observed and recorded, prior to their exsanguination and subsequent prosection: white-browed capuchins (Cebus albifrons), 9♂♂2♀♀; common squirrel monkeys (Saimiri sciureus), 2♀♀; golden spider monkey (Ateles geoffroyi), 1♂; woolly monkeys (Lagothrix lagothricha), 2♂♂; owl monkeys (Aotus trivirgatus), 1♂1♀; devil titi (Callicebus moloch), 1♂; necklaced titi (Callicebus torquatus), 1♂; silvered sakiwinkis (Pithecia monachus), 1♂1♀; red uacaris (Cacajao rubicundus), 2♂♂1♀; Goeldi's marmosets (Callimico goeldii), 2♂♂1♀; white-shouldered marmoset (Callithrix humeralifer), 1♂; silver marmosets (Callithrix argentata), 2♂♂; pigmy marmosets (Callithrix pygmaea), 9♂♂; red-mantled tamarins (Saguinus fuscicollis illigeri), 4♂♂1♀; and cottontop pinchés (Saguinus oedipus), 1♂1♀. Hair was then clipped and whole-thickness samples of the skin, including the tela subcutanea, were removed from those body regions listed in Table 5. The excised skin specimens were properly oriented on aluminum foil, identified according to body region, and bisected.

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[1]Phencyclidine hydrochloride, Parke, Davis & Co., Detroit, Mich.

II. Processing of Tissues.

A. Histological Procedures.

Half of each biopsy was fixed 24 hours in Zenker-formol according to Helly.[1] Fixed tissues were then placed in running tap water (24 hours), 0.2% iodine in dioxane (3 hours), three changes of dioxane (12 hours each), toluene (3 hours), and "Paraplast" tissue embedding medium[2] (overnight) in a 57° C. paraffin oven.[3]

Specimens were embedded in paraffin blocks and cut at 7 micra on a Spencer microtome.[4] The resultant paraffin ribbons were then floated onto precleaned, prelabeled microscope slides[5] with the aid of an electric tissue float.[6] These slides, which had been pretreated with "Tissue-Tac" slide adhesive,[7] were then placed on a 47° C. slide warmer[8] for 4 hours, after which they were placed in microscope

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[1]To prepare 100 ml. of stock solution, add 5 gm. mercuric chloride, 2.5 gm. potassium dichromate, and 1 gm. sodium sulfate to 100 ml. of distilled water; just before using, add 5 ml. concentrated (37%) formaldehyde to 95 ml. of stock solution.

[2]Cat. No. 48667, Van Waters, & Rogers, Inc., Los Angeles, Calif.

[3]Model No. B-1-P, Electrical Heat Control Apparatus Co., Newark, N. J.

[4]Model No. 820, American Optical Co., Buffalo, N. Y.

[5]Cat. No. 2951, Erie Scientific, Buffalo, N. Y.

[6]Model No. 375, Lipshaw Mfg. Co., Detroit, Mich.

[7]Cat. No. M-7645, Dade Reagent, Inc., Miami, Fla.

[8]Cat. No. 26000, Chicago Surgical & Electrical Co., Div. of Lab-Line Instruments, Inc., Chicago, Ill.

slide boxes[1] and stored in a 37° C. incubating oven[2] until required.

All paraffin sections were deparaffinized in two changes of xylene (5 minutes each), placed in three changes of absolute alcohol (5 minutes each), hydrated through 95% alcohol to 0.5% iodine in 80% alcohol (5 minutes), further hydrated through the lower grades of alcohol to distilled water, placed in 5% sodium thiosulfate (5 minutes), washed in tap water (5 minutes), and placed in distilled water prior to performing the following histologic staining procedures: Harris' hematoxylin and eosin (Lillie, 1965); toluidine blue, buffered to pH 4.5 (Montagna, Chase and Melaragno, 1951); the periodic acid-Schiff method (Montagna, Chase and Lobitz, 1953); Gallego's iron fuchsin (Conn, Darrow and Emmel, 1962); orcein-hematoxylin in iodized ferric chloride (Roman, Perkins, Perkins and Dolnick, 1967); Fontana-Masson ammoniacal silver (Lillie, 1965); and an acid mucopolysaccharide technique (Reinhart and Abul-Haj, 1951).

Fresh tissues were also treated with the osmium iodide method of Mishima and Miller-Milinska (1961) for the demonstration of junctional amelanotic melanocytes and high-level dendritic cells.[3]

Additional tissues were stained with luxol fast blue-cresyl violet (Klüver and Barrera, 1953), Heidenhain's iron hematoxylin (Lillie, 1965), and Altmann's aniline acid fuchsin-methyl green

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[1]Cat. No. M-6285, Scientific Products, Div. of American Hospital Supply Corp., Evanston, Ill.

[2]"Narco" Model No. 320, National Appliance Co., Portland, Ore.

[3]This and each of the preceding histological staining techniques is described in the Appendix.

(Lillie, 1965); others were prepared according to the gold chloride technique for the demonstration of Langerhans cells (Gairns, 1930) and the silver impregnation method for peripheral nerve endings (Winkelmann, 1955; Winkelmann and Schmidt, 1957).

B. Histochemical Procedures.

The other half of each biopsy, which had been stored in liquid nitrogen at -70° C. while the paraffin material was being recorded and placed in fixative, was cut at -20° C. in an International-Harris cryostat.[1] Tissue sections (40, 80, and 100 micra thick) were placed on chilled, prelabeled microscope slides; the latter had been pre-coated with "Tissue-Tac" and were allowed to equilibrate to the temperature of the cryostat before being used. When the desired number of tissue sections had been placed on a microscope slide, the slide was carefully removed from the cryostat and the technician's finger was placed beneath the tissue sections, on the under surface of the slide. In several seconds, the frozen tissue sections melted and the slides were returned to the cryostat, where they were stored in small slide boxes[2] until required.

Such unfixed, frozen section preparations were used to study the following enzymes: phosphorylase (Takeuchi and Kuriaki, 1955; Smith, Perkins and Machida, 1966); succinic dehydrogenase, (Farber and Louviere, 1956); cytochrome oxidase (Burstone, 1959, 1960); and monamine oxidase (Glenner, Burtner and Brown, 1957).

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[1]Model No. CTD, International Equipment Co., Needham Heights, Mass.

[2]Cat. No. A-1604B, Clay-Adams, Inc., New York, N. Y.

Other frozen sections, fixed 4 hours in chilled 10% formalin, were used for the demonstration of the following enzymes: acid phosphatase (Burton, 1954); alpha-naphthol esterase (Gomori, 1952); alkaline phosphatase (Gomori, 1952); and acetyl- and butyrylcholinesterase (Koelle and Friedenwald, 1949; Montagna and Ellis, 1957).[1]

III. Criteria for Interpretation.

Certain criteria had to be established and/or defined prior to the recording and subsequent interpretation of histological and histochemical observations.

Proportionate dimensions are expressed either 1) relative to comparable adnexa of other body regions or 2) in relation to other structures. Included in the former category are the length of the sebaceous duct, sizes of the sebaceous gland and arrector pili muscle, and extent of the thin or thick epidermis, papillary body, and reticularis dermis. Sweat gland proportions are depicted in terms of the latter category; i.e., the overall length of the gland and its duct are stated as a function of the level at which the apocrine or eccrine glomeruli rest in relation to the mid-dermis, lower reticular layer, or tela subcutanea. The narrow or wide diameters of secretory coils and excretory ducts are expressed as their proportion to one another; i.e., the respective ratio of secretory and excretory ducts may be 1:1 in eccrine glands of hairy skin, whereas it may be 4:1 in eccrine glands of friction surfaces.

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[1]Each of the above histochemical methods is described in the Appendix.

By way of clarification, the term "friction surface" denotes a weight-bearing body region that is subject to excessive abrasion (friction). It is characterized by an absence of hair and sebaceous glands and the presence of a greatly thickened epidermis. Examples include the palm and fingerballs of the ventral manus, sole and toe pads of the ventral pes, knuckle pads, and ischial callosities.

When used, the term "general body surface" refers to that major portion of body skin that is both hirsute and unspecialized, in contrast to those regions that are either glabrous or exhibit a high degree of specialization. Examples of "general body surface" include the neck, back, chest, belly, forelimbs and hindlimbs. Examples of specialized regions include friction surfaces of the pes, manus and prehensile tail, ischial callosities, eyelids, lips, nose, ears, axilla, ventral wrist, circumanal area, external genitalia, and fields of glandular aggregation, e.g., the gular region, sternum, posterior abdomen, brachium, and/or antebrachium.

The criteria for 1) the gradation of melanotic pigmentation and 2) the classification of hair follicle groupings are those devised in two earlier studies, respectively (Machida and Perkins, 1967; Perkins, Smith and Ford, In Press).

Briefly, melanotic epidermal pigment (Fig. 21) is hypothetically graded from a stratum basale with occasional melanocytes (0) to an epidermis so heavily pigmented that copious numbers of melanin granules appear in the stratum corneum (+3). Similarly, dermal pigment (Fig. 22) varies from a dermis with occasional melanocytes in both papillary and reticular layers (+1) to a dermis with abundant

melanotic pigment cells at all levels (+3). Melanocytes may occasionally course along superficial blood vessels and/or deeper, myelinated nerves; at times they are localized inter- or perifollicularly. Hair follicles (Fig. 23) are classified as those devoid of visible melanotic melanocytes (0), those in which melanotic pigment is present about the outer root sheath at the level of the pilary canal (+1), and those in which melanotic pigmentation extends down the outer sheath to the level of the hair bulb (+2); rarely, melanocytes may specifically encircle hair follicle nerve end-organs. Sebaceous glands (Fig. 24) may be categorized as those that are destitute of melanocytes (0) to those in which ductal and peripheral acinar melanocytes are profuse and sebum is melanotic (+3). Generally, most sweat glands do not possess visible melanocytes (Fig. 25); when they do, (+1) indicates ductal pigmentation and (+2) signifies the presence of melanotic melanocytes about secretory coils.

The 8 basic classifications of hair follicle arrangement (Fig. 26) are defined as follows: 1) Randomly Arranged Individual Follicles are so distributed that they lack any apparent, specific direction and therefore do not constitute a discernible pattern; 2) Paired Follicles are sets of hair follicles that may occasionally be accompanied by individual follicles or triads; 3) Imperfect Lines are comparable to independent perfect lines except that linear orientation is less organized, and as a consequence, 1 or 2 follicles in each unit are displaced from an otherwise straight line; 4) Independent Perfect Lines consist of 3 or more follicles so related to one another that

a straight or smooth, curved line may be drawn through each of their respective axes (unlike the next example, independent perfect lines do not contribute to larger units, although they are generally parallel; 5) Sets of Perfect Lines consist of repeating subunits of 3 or more follicles whose individual linear arrangements are such that each contributes to a larger row or wave of comparably oriented follicles (hair follicles sharing the same pilary canal were considered as one follicle); 6) Elongated Clusters constitute noncircular clusters of linearly disposed follicles that, nevertheless, cannot qualify as lines; 7) Independent Circular Clusters are simply circular clusters of hair follicles that are independently scattered (they are neither constituents of a larger unit nor are they markedly elongated); 8) Sets of Circular Clusters consist of large assemblages that are composed of smaller, subunit groups. Like each of the other specific categories, the designated major unit of hair follicles (unlike the individual follicles) is separated from contiguous units by appreciable amounts of dermal connective tissue.

The interpretation of histochemical procedures employed in this study is solely dependent upon the localization and intensity of color formation. Therefore, the quantitative assessment of enzyme reactivity is necessarily expressed by such oversimplified terms as absent (0), weak (+), moderate (++), and strong (+++). Unlike the alkaline phosphatase and cholinesterase techniques, which may be used to demonstrate blood vessels and nerves, respectively, the other histochemical methods are used primarily for the appraisal of tissue viability and work-energy production; they are also useful

adjuvants in the acquisition of characteristic enzyme signatures and the accumulation of pure data.

The normal anatomy of skin and its appendages may be referred to in Montagna (1962). Such a review under Materials and Methods would be redundant in light of the following Results (Observations).

IV. Microscopy and Photomicrography.

Microscopic observation was conducted on a Carl Zeiss GFL standard microscope equipped with 1, 2.5, 10, 40, and 100-power Neoflaur objectives, Kpl 8x eyepieces, and a 39-25-24 type transformer.[1]

Photomicrographs were taken on a Carl Zeiss Ultraphot II camera microscope[2] using 4 x 5 inch Panatomic-X film.[3]

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[1]Scientific Supply Co., Div. Van Waters & Rogers, Inc., Los Angeles, Calif.

[2]Brinkmann Instruments, Great Neck, N. Y.

[3]Eastman Kodak Co., Rochester, N. Y.

RESULTS

I. Callimico goeldii (Thomas 1904); Goeldi's marmoset.

A. Gross Observations.

A description of the pelage was given in the Introduction. The following regions of cutaneous specialization are present on the venter of both sexes:

(1) Ulnar Vibrissae (Fig. 27) are composed of 5 to 6 sinus hair follicles on the ventral ulnar aspect of the wrist, a relatively glabrous area peripherally populated by many thin, more lightly pigmented hairs. Each large black vibrissa arises from a shallow depression that is surrounded by a circumscribed, opalescent elevation about 0.5 mm. in diameter. The fields of sinus hairs on each wrist are approximately 2 x 4 mm., and the most distal vibrissa in each field is 4 to 8 mm. proximal to the glabrous, hypothenar friction surface.

(2) The Gular Field (Fig. 28), 4 x 6 mm., occupies an interramal position and tapers in an anteroposterior plane. Surrounded by hirsute skin, this kite-shaped, pebbly-appearing region is easily visualized because it is covered by vellus hairs only.

(3) The Manubrial Tuft (Figs. 30 and 31), approximately 10 mm. long, is better developed in the male. Composed of a triangular mat of long, coarse encrusted hairs, it tapers posteriorly, and its cephalic margin is situated 6 to 8 mm. below the sternal notch.

(4) The Sternal Field (Figs. 30 and 31) lies over the corpus sterni. In the male, it is 5 mm. wide and extends 60 mm. from the

the manubrial tuft to the xiphoid process; in the female, it is comparably wide but only half as long. The surface is relatively hairless, pustular in appearance, brown to ochraceous, and oily textured.

(5) The Genitopubic Field (Figs. 30 and 31) commences caudal to the linea alba at the symphysis pubis. In the male, it extends over the mons pubis for a distance of 15 mm. until it integrates with the scrotum. Like the sternal field, it is pustular, relatively hairless, and greasy. In the female, a comparable field rests over the mons pubis; it bifurcates and extends posteriorly to the frenulum, lateral to the rima pudendi. In both sexes, some of these glands accompany the dorsal raphe and partially surround the anal orifice.

B. Histological and Histochemical Observations.

The Epidermis

Over the general body surface, the epidermis is only 1 or 2 cells thick. In the gular and ulnar regions, it is 3 to 4 cell layers deep, whereas the mucous membranes of the lips, nose, and anogenital region are composed of 4 to 10 cell layers. The mucosa of the inner margin of the lower lip is invaginated to form a prominent longitudinal sulcus. The volar friction surfaces of the pes and manus attain a thickness of 10 to 25 cells with a distinct stratum granulosum and well-developed undersculpturing.

The modified skin of the gular area is characterized by a series of minute, undulating papillae-like surface folds (Fig. 28); the epidermis of this specialized area and of the interscapular and lumbar back is devoid of melanotic melanocytes. The author, like

Hill (1959), noted a diminution of pigment in the form of irregular, pink patches over the thenar eminence and proximal interphalangeal joints of the palms. All other body regions, however, contain numerous epidermal melanocytes (Fig. 35), even the buccal and labial mucosae.

Histochemical properties are listed in Table 6.

The Dermis

Only the modified friction surfaces possess thick, serrated basement membranes, dense papillary layers, highly-developed elastic networks, and perpendicularly oriented collagenous fibers interlaced with large numbers of collagen bundles aligned parallel to the skin surface. Scattered perivascular mast cells occur in all body regions, most commonly in anogenital skin. Bipolar, melanotic melanocytes, present throughout the dermis of the general body surface, tend to concentrate in cephalic body regions where they characteristically reside in the upper dermal levels (Fig. 35).

Capillaries, whose endothelia are reactive for alkaline phosphatase, form well-developed arcades beneath all volar friction surfaces and mucous membranes. All organized nerve endings contain cholinesterase: Meissner corpuscles, papillary nerve end-organs in unpigmented areas of the palm (Fig. 33), and mucocutaneous end-organs in the nose and lips are more reactive for butyryl- than for acetylcholinesterase; anogenital corpuscles, however, are equally reactive for both. In addition, Meissner corpuscles exhibit cytochrome oxidase and alpha-naphthol esterase activities and contain a PAS-positive, diastase-resistant substance.

Free subepidermal nerve fibers, which contain more butyryl- than acetylcholinesterase, are common in the gular area, manubrial tuft, sternal field, tail, lips, nose, and anogenital skin. In the gular region, these nerves form delicate, branching fibers just beneath the epidermis that covers the apex of each denticle (Fig. 29).

The Hair Follicle

Hairs grow in linear perfect sets of 3 to 5 follicles over the general body surface, including the cheek. One apocrine gland accompanies each hair follicle in the manubrial, sternal, and anogenital glandular fields; elsewhere, one gland accompanies each hair grouping. Sinus hairs are present in the upper and lower lips, perialar region, and ventral ulnar wrist.

In the scalp, eyebrow, cheek, manubrial tuft, back, tail, and thigh, the terminal portion of the hairshaft becomes increasingly thick and melanotic distally (Fig. 34); some hairs subdivide into several smaller, terminal fila (Figs. 30 and 36). Arrectores pilorum muscles are most developed in the distal tail. Melanotic melanocytes descend along the connective tissue sheath to the level of the hair bulge. In other respects, the anatomy of the hair follicle is similar to that described for the red-mantled tamarin.

Moderate amounts of glycogen and phosphorylase are present in the outer root sheath of active follicles and in the epithelial sac of quiscent follicles. Hairs are generously supplied by alkaline phosphatase-positive capillaries and cholinesterase-reactive nerve end-organs (Fig. 35). Other histochemical properties are cited in Table 6.

The Sebaceous Glands

One or 2 uni- or bilobular sebaceous glands, small to medium-sized, accompany each hair follicle throughout most body regions; larger, multiacinar glands reside in the lips, nose and cheek. All glands have a short duct that empties into a pilary canal. Acini are surrounded by occasional alkaline phosphatase-positive capillaries and are invested by few cholinesterase-reactive nerves. Their histochemical properties are given in Table 6.

The large multilobular sebaceous glands of the manubrial tuft, sternal field, genitopubic area, and circumanal skin are histologically and histochemically different from those of other body regions (Figs. 30 and 31). Most glands in the sternal, genitopubic, and circumanal areas are associated with vellus hairs. All have somewhat longer, larger excretory ducts that empty into pilary canals, which are often distended with PAS-positive, diastase-resistant sebum. Occasionally, the terminal portion of an ampulliform excretory duct contains abundant glycogen. The peripheral acini, unlike those of the general body surface, are characterized by intense cytochrome oxidase, monoamine oxidase, phosphorylase (Fig. 32), acid phosphatase, and alkaline phosphatase (Fig. 36) activities. The glands, particularly those of the sternal field and genital skin, are surrounded by abundant capillaries whose endothelia are reactive for alkaline phosphatase. Large numbers of acetyl- and butyrylcholinesterase-containing nerves supply only the manubrial and sternal sebaceous glands of the male and the meibomian glands of both sexes.

The Apocrine Glands

One small to medium-sized gland, whose excretory duct opens at the skin surface adjacent to a pilary orifice, is associated with each hair follicle grouping in all general body regions. These glands have a paucity of alkaline phosphatase-positive capillaries and cholinesterase-reactive nerves. Their histological details are similar to those of the red-mantled tamarin; histochemical properties are indicated in Table 6.

Secretory coils in the manubrial tuft, sternal field, mons pubis, genital skin, and circumanal area are larger in diameter than those in other body regions (Figs. 30 and 36). In all but one of these glandular fields (mons pubis), the glands are concentrated in a ratio of 1:1 with hair follicles. However, only in the manubrial tuft do secretory coils occupy an area larger than that of the admixed sebaceous glands. Thus, of the 5 ventral glandular fields, only one is predominantly apocrine.

Several histological and histochemical traits are peculiar to the large type of apocrine gland found in these admixed, sebaceous-apocrine concentrations. Excretory ducts are rich in phosphorylase (Fig. 32) and their terminal portions are often dilated; secretory lumina contain large, PAS-positive, diastase-resistant casts; secretory epithelium is intensely reactive for alkaline phosphatase (Fig. 36); glomerate portions are generously provided with alkaline phosphatase-positive capillaries; and secretory coils in the manubrial tuft of the male are invested by a profusion of acetyl- and butyrylcholinesterase-containing nerves. The glomeruli of those of

the female, as well as those of other glandular fields in both sexes, are accompanied by moderate numbers of cholinesterase-containing nerves.

The Eccrine Glands

Confined to the ventral friction surfaces of the pes and manus, glomeruli rest in the tela subcutanea and consist of one-third excretory duct and two-thirds secretory coil; each secretory coil is about 3 times the diameter of neighboring excretory ducts.

Both coiled and straight portions of the two-cuboidal cell-layered excretory duct are surrounded by dendritic, melanotic melanocytes; the intraepidermal segment ascends to the skin surface as a weak, right-handed coil. Although the coiled excretory duct contains abundant glycogen, it is unreactive for phosphorylase; the straight portion of the duct contains neither substance.

Secretory epithelium is composed of clear and dark cells whose structure is similar to that of the red-mantled tamarin; neither cell type contains glycogen. Only the dark cells contain a PAS-positive, diastase-resistant material that stains metachromatically with toluidine blue (cf. Formissano and Lobitz, 1957). Secretory coils are surrounded by many alkaline phosphatase-positive capillaries and numerous nerves strongly reactive for acetyl- but weakly reactive for butyrylcholinesterase. Other histochemical properties are recorded in Table 6.

II. Callithrix [=Cebuella] pygmaea (Gray 1866); pigmy marmoset.

A. Gross Observations.

The pelage is predominantly salt-and-pepper in coloration. The author quotes a description of the following external characteristics from Hill (1957):

> "Head rounded and clothed with longish, backwardly directed hairs; ears, though relatively large, completely hidden by the long backwardly directed hairs of the cheeks, giving the face a rounded appearance; face also relatively hairy, only a small area round nose and lips and circumocular regions relatively naked and pallid. Palpebral fissures rather slanting, giving mongoloid aspect to face, facial vibrissae consisting of short black hairs on muzzle along a curved line extending from above nose to angle of gape; a few on chin and some longer supraorbital hairs, the latter sometimes reduced to a single pair; face otherwise clothed more densely than in any other hapalid [callithricid] genus. Eyelashes on upper and lower eyelids."

In addition to these characteristics, the following specialized regions are also observed: 1) sinus hairs, grouped on the ulnar aspect of the ventral wrists; 2) greasy, sparsely haired, glandular-appearing fields, over the manubrium sterni and mons pubis; and 3) convoluted scrotal skin that is distinctly mottled black and white.

B. Histological and Histochemical Observations.

The Epidermis

In most of the body regions the epidermis has a stratum malpighii that is only 1 or 2 cells thick; however, it is 3 to 5 cells deep in the lip, nose, and ulnar region and 5 to 15 cells in the ventral pes and manus. Markedly ridged dermoepidermal junctions and continuous, 1 or 2-cell-thick strata granulosa are prominent in the lip and glabrous friction surfaces.

Moderate numbers of epidermal melanocytes and melanin granules occur in the strata basale and spinosum of the head, dorsal trunk, and dorsal extremity areas (Fig. 37). The scalp is most heavily pigmented; numerous melanin granules are present in all epidermal layers. By contrast, practically no melanotic melanocytes are found in the gular region, chest, belly, ventral tail, wrist, palms, or soles.

Large aggregations of epidermal and dermal pigmented cells are noted in those areas of the scrotum where the invaginated epidermis is thrown into ridges; elsewhere the thin, flat epidermis and underlying dermis are devoid of melanotic pigmented cells (Figs. 43 and 44).

Thick, serrated, PAS-reactive basement membranes are prominent beneath the epidermis of the friction surfaces. Glycogen occurs only around the intraepidermal portion of the eccrine sweat gland ducts.

In all body regions, moderate concentrations of succinic dehydrogenase, cytochrome oxidase, and alpha-naphthol esterase are

distributed throughout the lower stratum malpighii; slight reactivity for monoamine oxidase and phosphorylase is perceptible in the stratum basale and lower malpighian layer, respectively; all epidermal layers are intensely reactive for acid phosphatase (Table 7).

The Dermis

Only in the friction surfaces is there a very thin papillary layer with scant numbers of fine collagenous and elastic fibers; elsewhere, papillary bodies are indistinct.

Coarse collagen bundles are alternately oriented to the surface of the epidermis in the reticularis dermis of the eyelid, lip, scrotum, and friction surfaces; elsewhere, the reticular layer is thin, and less dense bundles of collagen are mostly oriented parallel to the epidermal surface. Elastic fibers are numerous everywhere. There are many PAS-positive, metachromatic mast cells, and scattered aggregations of melanotic melanocytes in the upper reticularis dermis. In any given body region, the quantity of dermal melanocytes varies proportionally with the amount of coincident, epidermal pigmentation.

There is a paucity of dermal vasculature; few adnexa are supplied by capillaries whose endothelia are reactive for alkaline phosphatase. Subepidermal capillary arcades are distinct only in the friction surfaces and mucous membranes of the lip, nose, and external genitalia.

There are very few cholinesterase-reactive, subepidermal nerve fibers. All organized nerve endings--i.e., Meissner corpuscles and Vater-Paccini corpuscles in the friction surfaces and mucocutaneous end-organs in the lips, nose, and external genitalia--are reactive for acetyl- and butyrylcholinesterase. (Table 7).

The Hair Follicle

Hair follicles grow in linear perfect sets of 3 over the general body surface. They occur singly on the face (eyebrow, cheek, eyelids, lips, nose, and gular region), ulnar area, and external genitalia. One apocrine gland usually accompanies each hair grouping and each follicle has 1 or 2 sebaceous glands. Sinus hair follicles reside in the lips, nose, and ulnar region (Fig. 45). Arrectores pilorum muscles, well-developed in all body regions except the face and external genitalia, are largest in the distal tail (Fig. 38).

Glycogen occurs in moderate concentrations in the outer root sheath of active follicles and epithelial sac of quiescent follicles. The dermal papillae of active follicles are alkaline phosphatase-rich, and PAS-positive, but diastase-resistant; they are not metachromatic when stained with toluidine blue. Hair follicles have moderate monoamine oxidase and alpha-naphthol esterase activity, but intense cytochrome oxidase, succinic dehydrogenase, phosphorylase, and acid phosphatase activity (Table 7).

Few hair follicles are invested with alkaline phosphatase-reactive blood vessels. Nerve end-organs are faintly reactive for acetylcholinesterase in the eyebrow, scalp, eyelids, lips, and external genitalia. They are moderately reactive for alkaline phosphatase in the face (eyebrow, cheek, ear, eyelids, lips, nose and gular area), proximal and distal tail, and external genitalia (Fig. 39).

The Sebaceous Glands

Sebaceous glands are small over the general body surface;

1 or 2 are associated with each hair follicle. Large, multiacinar glands occur in the eyelids, lips, nose, gular area, suprapubic region (Fig. 40), and external genitalia. Only the ducts of the meibomian glands open at the epidermal surface; all other sebaceous glands empty at the base of their respective pilary canals. Although the ducts of most small glands are short and narrow, many in the scalp, gular area, sternal region, back, and tail are distended with sebum and are subsequently larger. Those of the large, multilobular glands of the suprapubic region characteristically empty into stout, ampulliform pilary canals. All sebaceous glands are free of melanotic melanocytes and contain neither glycogen nor phosphorylase.

Moderate to strong succinic dehydrogenase, cytochrome oxidase, monoamine oxidase, alpha-naphthol esterase, and acid phosphatase activity is present in all sebaceous glands; no acinar reactivity for cholinesterase or alkaline phosphatase is present (Table 7). Alkaline phosphatase-positive capillaries and acetyl- and butyrylcholinesterase-reactive nerves invest only the larger glands of the eyelids, lips, and external genitalia.

The Apocrine Glands

Apocrine glands occur in all hairy body regions except the eyebrow, scalp, and back. Each excretory duct opens at the skin surface, adjacent to its respective pilary orifice; in the suprapubic region, an occasional gland opens to the surface independent of hair follicles. Moderate aggregations of large glands occur over the manubrium sterni and suprapubic areas (Figs. 40 and 42). All glands rest in the deeper dermis or tela subcutanea; they are composed of a cuboidal

or columnar epithelium that contains a PAS-positive, diastase-resistant material. Although luminal casts are also PAS-positive and diastase-resistant, they are not metachromatic when stained with toluidine blue.

The glands exhibit the following enzyme activities: succinic dehydrogenase and cytochrome oxidase, strong; monoamine oxidase, strong only in the inguinal region and external genitalia; acid phosphatase and alpha-naphthol esterase, weak; and phosphorylase, moderate in ductal portions only (Table 7). Secretory coils are moderately supplied by blood vessels whose endothelia are reactive for alkaline phosphatase; however, neither luminal borders nor myoepithelial cells contain discernible amounts of this enzyme. Only secretory coils in the external genitalia are invested by nerves rich in butyrylcholinesterase. Elsewhere, cholinesterase-reactive nerves cannot be demonstrated around the glands.

The Eccrine Glands

These glands are confined to the friction surfaces of the pes and manus. Most of the glomerate portion, consisting of approximately equal parts of secretory coil and excretory duct, rests in the tela subcutanea. The ratio of secretory coil

diameter to that of excretory duct is nearly 3:1. The simple secretory epithelium is composed of dark and clear cells. The less numerous dark cells have dense oval neclei, and are displaced toward the lumen. They have the following properties: they are not metachromatic when stained with toluidine blue; they possess moderate amounts of glycogen; and when so treated, both acid mucopolysaccharides and argyrophilic granules may be observed in their nuclear karyoplasm (Fig. 41). Clear cells, on the other hand, possess spherical, finely-stippled nuclei, and faintly acidophil cytoplasm but no glycogen. Secretory coils are surrounded by a thick hyaline basement membrane, the inner layer of which is PAS-positive, but diastase-resistant. Excretory ducts, consisting of 2 layers of cuboidal epithelium, contain glycogen in their basal layer. The ducts form weak, right-handed coils as they ascend through the epidermal ridges.

The following intensities of enzyme activity are demonstrable in the eccrine glands of the pigmy marmoset: succinic dehydrogenase, cytochrome oxidase and phosphorylase, strong; monoamine oxidase, acid phosphatase and alpha-naphthol esterase, weak; and alkaline phosphatase, weak except the strongly reactive

intercellular canaliculi (Table 7). Secretory coils are well vascularized by alkaline phosphatase-reactive capillaries and generously enwrapped by nerves rich in acetylcholinesterase.

III. Callithrix [=Mico] argentata (Linnaeus 1771); silver marmoset.

A. Gross Observations.

The silvery-white pelage, black tail, opaque scrotum, and naked, red face and ears have been described in the Introduction. Not mentioned, however, are the following specialized body regions, each characterized by the presence of vibrissal hairs: the eyebrow, cheek, and ventral wrist.

Hill (1957) states that sinus hair follicles occur on the muzzle, upper lip, chin, and nose but specifies "none over orbits or on the genal region." However, in this study each animal possessed sinus hairs on both the eyebrow and cheek. In addition, this author also detected 2 or 3 sinus hairs on each of the circumscribed ulnar elevations, 4 mm. in diameter, located on the ventral ulnar aspect of each wrist. Notwithstanding these ommissions, Hill accurately

described and illustrated a specialized, sparsely haired gular area that is distinguished by "a single, long interramal vibrissa arising from a papilla in some specimens. Interramal region with thin, modified skin sharply demarcated from that covering rami by abrupt change in thickness. Modified area slightly depressed, of triangular outline, limited posteriorly by swellings caused by submandibular salivary glands; marked anteriorly by longitudinal parallel sulci cutis, but posteriorly by small papillae (non-glandular)." Such a modified region was demonstrated on both males in this study.

B. Histological and Histochemical Observations.

The Epidermis

The epidermis of the silver marmoset is thin. The skin of the facial disc (eyelids, periorbital area, muzzle, haired lips, and interramal field), external ears, and anogenital zone is composed of a single epidermal cell layer. The occurrence of melanotic melanocytes in such regions is very rare, as it is throughout the 2 or 3 cell-layered epidermis of the general body surface. A few basal melanocytes are encountered only in the 25-cell-deep mucous membranes, the somewhat thicker volar friction surfaces, and the palpebral margin of the eyelids.

Two body regions are characterized by distinctive surface modifications. The thin interramal skin, which is anterior to the submandibular salivary glands, is covered with numerous minute papillae whose epidermis is 2 to 3 cell layers thick, unlike the contiguous, monolayered, interpapillary epidermis. The dorsal surface of the corpus penis contains well-developed, keratinized spines whose

hollow apices are proximally directed (Fig. 37). The thickened epidermis of such modified surface areas, like that of the mucous membranes and volar friction surfaces, contains variable amounts of intracellularly dispersed glycogen.

The epidermis contains rich amounts of acid phosphatase in the lower stratum corneum and alpha-naphthol esterase in the stratum malpighii. Moderate concentrations of cytochrome oxidase are present in the malpighian layer of most body regions, but succinic dehydrogenase and monoamine oxidase activities are moderate to weak. The epidermis is unreactive for phosphorylase and alkaline phosphatase. The intensities of the various enzymes are summarized in Table 8.

The Dermis

The dermis is moderately dense over the dorsum, chest, belly, axilla, tail, and scrotum. It is best developed in the ventral friction surfaces of the pes and manus, where a definitive papillary body and laminated, alternately perpendicular and parallel collagen bundles constitute the bulk of this supportive layer. The dermis of the facial disc, external ear, and anogenital skin is sometimes no thicker than the overlying epidermis. Its thin collagen bundles, elastic fibers, fibrocytes, and mast cells appear to be compressed between the epidermis and an enormous subcutaneous bed of yellow adipose tissue. Though less extensive, the yellow fat of the scalp characteristically ascends to interdigitate with columns of connective tissue that encircle descending hair follicles. A less extensive panniculus adiposus also occurs throughout other body regions but,

unlike that of the scalp, is horizontally delineated by a more dense reticularis dermis.

Perivascular, metachromatic mast cells are scattered throughout the dermis of all body regions. Melanotic melanocytes occur rarely beneath the mucous membrane of the upper lip and palpebral border of the eyelid; they are observed in no other region. The dermis of the silver marmoset contains a moderate population of elastic fibers; in the friction surfaces, a prominent layer of coarse fibers is horizontally aligned at the dermal-adipose interface (Fig. 58). Subepidermal capillary loops arch beneath the undulating contours of the volar and mucosal epidermal undersurfaces. The adnexa of hirsute body areas are accompanied by numerous blood vessels whose endothelia are reactive for alkaline phosphatase.

The skin is richly innervated by cholinesterase-reactive subepidermal nerve fibers and organized nerve endings.

Meissner corpuscles are arranged in rows that border the epidermal ridges of the volar friction surfaces (Fig. 49); they are reactive for alpha-naphthol esterase and the cholinesterases. Cholinesterase-reactive nerve fibers interconnect the Meissner corpuscle with its neighbors and its associated papillary nerve end-organ (Figs. 50 and 51). The latter structure is a disc-shaped plaque that forms a cap over the base of its respective epidermal ridge (crista limitans). The papillary nerve end-organs are more strongly reactive for pseudocholinesterase than specific cholinesterase. They are not observed at the base of the intermediate type of epidermal ridge (crista intermedia). Single nerve fibers emerge from the papillary nerve

end-organs to join afferent fibers from Meissner corpuscles, thus contributing to large myelinated nerves (Figs. 50 and 52).

Mucocutaneous end-organs containing both acetyl- and butyryl-cholinesterase are plentiful in the lips, nose, anus, and glans penis.

On the dorsum of the corpus penis, digitating cholinesterase-positive nerve endings rest beneath hollow keratinized spines (Fig. 48). A nerve fiber is occasionally observed entering the conical-shaped cavity, appearing to terminate distally in an acute loop--much as a stamen emerges from the everted corolla of a fuchsia blossom (Fig. 48). Alkaline phosphatase-reactive capillary loops accompany such intraspicular nerves (Fig. 46).

The Hair Follicle

Hairs are arranged as linear perfect sets of 3 to 5 follicles over the general body surface, including the cheek (Fig. 59). Active and quiescent follicles frequently occur in the same grouping; some hairs open independently to the surface, others share a common pilary canal. The number of apocrine sweat glands associated with each hair grouping varies considerably from region to region; one gland usually occurs with each hair follicle group. Sinus hair follicles are present on the temple, eyebrow, upper and lower lips, nose, gular area, and ulnar eminence. Large populations of terminal guard hairs dwell only in the proximal and distal tail. Unlike hairs of other body regions, the lower half of each caudal guard hair is bent along the panniculus adiposus, the hair bulb and cortex are heavily pigmented (contrasting strongly with the amelanotic epidermal and dermal

elements), and the associated arrector pili muscle is large. Arrectores pilorum muscles are not present in the eyebrow, eyelids, lips, nose, external ears, axilla, perianal region, or scrotum. The general structure of active and quiescent hair follicles is similar to that of the red-mantled tamarin.

Two types of dendritic cells are observed on the hair follicles: melanocytes and alkaline phosphatase-positive cells. The spider-like, melanotic melanocytes are composed of small perikarya and long filiform dendrites. Oddly, they occur rarely in dorsal surface areas such as the back and tail. They are distributed around the hair bulge of active and quiescent follicles, and are argyrophilic and osmiophilic. By contrast, the stellate-shaped alkaline phosphatase-positive cells are amelanotic. Their perikarya are large but their dendrites are short and stout (Figs. 56 and 57). Their occurrence is common but their distribution is strictly limited to the active and quiescent hair follicles of the ulnar gland and all cephalic regions (scalp, brow, eyelids, lips, ear, nose, cheek, and gular area). These alkaline phosphatase-positive cells encircle the hair follicle around its lower half; occasionally their distribution coincides with that of the hair follicle nerve end-organ (Fig. 60). Although readily demonstrated by the alkaline phosphatase method, they are neither argyrophilic, aurophilic, nor osmiophilic. The characteristics of both cell types are summarized in Table 9.

Copious quantities of glycogen and phosphorylase occur in the lower two-thirds of the outer root sheath of active follicles and epithelial sac of resting follicles. Succinic dehydrogenase and monoamine

oxidase are intensely reactive in the keratogenous zone and matrix of active follicles. Alkaline phosphatase activity is limited to the dermal papillae (Figs. 56 and 60). Other enzymes are also normally distributed in the hair follicles of the silver marmoset and their reactivities are listed in Table 8.

An intimate neuropilary relationship exists in all hirsute skin, particularly in the scalp, eyebrow, cheek, chest, belly, back, and tail (Figs. 52-55). Many hairs have an extensive plexus of cholinesterase-positive nerve fibers and nerve endings. Large, tortuous nerves twist and spiral to the level of the arrector pili muscle, where they terminate; others accompany the muscle, sending branches to the hair follicle nerve end-organ. Organized nerve endings, in the form of terminal boutons or large plaques, reside beneath the overlying epidermis, particularly about the pilary orifice. The largest subepidermal nerve end-organ is always located on the obtuse-angled side of the hair follicle. Peripheral secondary boutons are frequently situated near the origin of the arrector pili muscle. Delicate fibers, which emerge from the organized subepidermal nerve endings, descend along the pilosebaceous apparatus and merge into large trunks at the level of the hair bulge. All compoments of this nerve network contain both acetyl- and butyrylcholinesterase.

Hair follicles are invested by a rich supply of alkaline phosphatase-reactive capillaries. A capillary plexus frequently resides beneath the somewhat thickened epidermis that occurs over the obtuse-angled side of the follicle (Fig. 55). The position of this vascular plexus coincides with that of the characteristically enlarged, subepidermal nerve plaque.

Acetyl- and butyrylcholinesterase-reactive hair follicle nerve end-organs appear in all body regions; their numbers are somewhat reduced in the back and tail. The arrectores pilorum muscles contain much more acetyl- than butyrylcholinesterase.

The Sebaceous Glands

Sebaceous glands vary in size from the miniscular glands of the tail to the enormous, "clusters of grapes" type in the scrotum (Fig. 61). Generally, 1 or 2 small unilobular sebaceous glands occur in each pilosebaceous unit; their medium-length ducts join the hair follicle at the base of its pilary canal. Large, multiacinar glands are prominent in the lips, ear, nose, and anogenital skin; their short, distended collecting ducts also empty into the pilary canal. Only meibomian glands are independent of hair follicles. None of the sebaceous glands has melanotic melanocytes. Acinar cells contain neither glycogen nor phosphorylase; sebaceous ducts in the chest, belly, posterior abdomen, and scrotum contain small amounts of these substances, however.

Traces of succinic dehydrogenase are contained in the undifferentiated peripheral acini. Monoamine oxidase activity is mild: that of cytochrome oxidase and alpha-naphthol esterase is strong. The intensity of alpha-naphthol esterase appears to be inversely proportional to the size of the sebaceous gland. The peripheral, undifferentiated acinar cells are mildly reactive for alkaline phosphatase in the medium-sized sebaceous glands of the scalp, eyebrow, and lip (Fig. 60); moderate to intense reactivity is present in the larger glands of the face and anogenital skin (Fig. 61). The enzyme activities of the sebaceous glands are recorded in Table 8.

Alkaline phosphatase-positive capillaries invest most sebaceous acini; they predominate around the meibomian gland. Only meibomian glands are surrounded by numerous cholinesterase-reactive nerve fibers; such nerves contain more acetyl- than butyrylcholinesterase.

The Apocrine Glands

Apocrine glands are throughout the hairy skin associated with hair follicles; their long excretory ducts empty into the pilary orifice or at the skin surface immediately adjacent to the pilary orifice (Fig. 60). The glands are very small on the scalp; one medium-sized gland occurs with every 2 to 3 hair groupings in the face. In the thigh, belly, gular area, tail, and back, 1 small gland accompanies each hair follicle group (Fig. 59). Unlike the small- and medium-sized glands, large glands occur with a frequency of 2 to 3 with each follicle grouping in the chest, and 1 or 2 in the circumanal region. On the ulnar eminence, axilla, posterior abdomen, and scrotum, large glands occur in a ratio of 1 gland per hair follicle.

The secretory coils of all glands are composed either of irregular columnar epithelium with a brush border or of flattened cuboidal cells. PAS-positive, diastase-resistant supranuclear cytoplasmic granules are prominent in the columnar epithelium of small- and medium-sized glands; metachromatic luminal casts are common in large secretory coils whose epithelium is cuboidal. Both the secretory segments and the two-layered cuboidal excretory ducts are devoid of melanotic melanocytes.

The secretory coils exhibit the following enzyme activities: acid phosphatase and monoamine oxidase, mild; alpha-naphthol esterase and succinic dehydrogenase, moderate; cytochrome oxidase, intense.

A weak phosphorylase reactivity occurs in the terminal excretory ducts of the chest and belly only. Moderate amounts of alkaline phosphatase are present in the cuticular borders and luminal debris of larger glands. Variances in enzymatic activity are indicated in Table 8.

A rich plexus of alkaline phosphatase-reactive capillaries encircles the glomerate portion of each apocrine gland; the excretory duct is seldom accompanied by such capillaries. The apocrine glands are not invested by nerves reactive for the cholinesterases.

The Eccrine Glands

Eccrine glands are confined to the ventral friction surfaces of the pes and manus; they are more common in the digital pads than in the palmar and plantar surfaces. The glomerate portion of the gland rests in the tela subcutanea and consists of three-fourths secretory coil and one-fourth coiled excretory duct. The diameter of the secretory segment is 3 times that of the excretory duct. The long, two-layered cuboidal excretory duct passes linearly through the dermis and penetrates the epidermis as a weak, right-handed coil.

Secretory coils are composed of differentiated clear and dark cells. The former possess spherical, slightly acidophil nuclei; the latter are characteristically displaced toward the lumen and contain dense, oval, basophilic nuclei. Most secretory coils contain no glycogen. However, some coils are sporadically reactive throughout all secretory cells; other coils demonstrate glycogen localization in the clear cells only. By contrast, the basal cells of the amelanotic excretory duct always contain glycogen.

Secretory epithelia contain large amounts of succinic dehydrogenase, cytochrome oxidase, and alpha-naphthol esterase; alpha-naphthol esterase is notably more reactive in the glomeruli of the palm and sole than in the digital pads. The distribution of phosphorylase is identical to that of glycogen. Acid phosphatase, alkaline phosphatase, and monoamine oxidase are weakly localized in the secretory coils only. A summary of these histochemical properties is presented in Table 8.

Eccrine glands are poorly supplied by alkaline phosphatase-positive capillaries. Secretory coils are surrounded by numerous acetyl- and a few butyrylcholinesterase-containing nerve fibers.

IV. Saguinus [=Tamarinus] fuscicollis illigeri (Pucheran 1845); red-mantled tamarin.

A. Gross Observations.

The pelage of adult animals has been described in the Introduction. Each adult animal is additionally characterized by the following 4, specialized cutaneous structures:

(1) The Sternal Gland (Fig. 63) is a nodular, palpable aggregate of glands that is better developed in males. It is approximately 4 mm. in diameter and is situated above the manubrium sterni. Hairs in this region are encrusted by a reddish-brown, greasy substance.

(2) The Suprapubic Gland (Fig. 62) is a slightly elevated, elongated, glandular field that is 10 mm. wide. It is situated in the midline of the posterior abdomen, extending approximately 6 mm. superior to the mons pubis; it is better developed and more extensive in the

female. The ferruginous hair over this region is greasy and matted. On gross inspection, this area contains a massive, cream-colored field of loculated glands filled with a thick, semi-fluid, fatty substance.

(3) The Radial Papillae (Fig. 65) are a series of verrucae-like papules, 0.5 mm. in diameter, which arch from a point distal to the ulnar gland in a linear, radial fashion for a distance of 1.5-2.0 cm.

(4) The Ulnar Eminence (Fig. 66) is a circumscribed, vibrissae-bearing swelling, 2 mm. in diameter, which occurs on the hypothenar aspect of each ventral wrist.

B. Histological and Histochemical Observations.

The Epidermis

The epidermis of the hairy skin has a stratum malpighii only 1 to 2 cells thick. On the tail, external genitalia, and suprapubic region, the malpighian layer may be 2 to 5 cells deep. The dermo-epidermal junction, normally flat, is occasionally ridged in these areas, and is deeply ridged in all glabrous friction surfaces where the stratum malpighii is 5 to 15 cell-thick. A prominent and continuous stratum granulosum is found only in the friction surfaces.

Melanotic epidermal melanocytes and melanin granules are dispersed throughout the stratum basale and stratum spinosum of all regions studied. The greatest concentrations of melanin granules occur in the friction surfaces, the pinna and external auditory meatus of the ear, and the external genitalia. Branching dendritic melanocytes are seen clearly in the epidermis of the back and scalp (Fig. 68).

A serrated, PAS-reactive basement membrane is conspicuous beneath the epidermis of all friction surfaces. Glycogen is confined to the

intraepidermal portion of eccrine sweat gland ducts; it also occurs sporadically in the upper levels of the spinous layer of the tail, and in the radial papillae.

The cells in the basal and lower spinous layers everywhere have moderate concentrations of succinic dehydrogenase, cytochrome oxidase and alpha-naphthol esterase. A mild reaction for monoamine oxidase is limited to the stratum basale. Phosphorylase is characteristically weak in the lower malpighian layer; acid phosphatase is confined to the upper stratum spinosum (Table 10).

The Dermis

In the lips, external genitalia, and friction surfaces, a dense papillary layer contains superficial, PAS-positive reticular fibers, collagenous fibers oriented parallel to the thick PAS-positive basement membrane, and scattered elastic fibers insinuated into the columns of connective tissue that grow perpendicular to the dermoepidermal junction. Over the general body surface, the papillary layer is poorly defined.

In the reticularis dermis are dense, coarse, and branching collagen bundles. In the lips, friction surfaces, and eyelids these are alternately oriented to the surface of the epidermis; they are oriented parallel to the surface only in the back, scalp, chest, belly, and tail. Elastic fibers are most numerous in the friction surfaces. Mast cells, which are PAS-positive and stain metachromatically, are common in the areolar tissue and particularly around sweat glands and blood vessels. Dermal melanocytes are present everywhere except in the chest. The tip of the tail, external genitalia, scalp, eyelid, eyebrow, lip, and ear have

the most intense population of dermal melanocytes. Dendritic melanocytes occur at random in the dermis, as well as around the outer root sheath of hair follicles, the excretory ducts of sweat glands, and the peripheral acini of sebaceous glands.

The dermis is poorly supplied by capillaries whose endothelium is reactive for alkaline phosphatase; such capillaries, however, are common around hair follicles, sweat glands, and sebaceous glands. Subepidermal capillary arcades are distinct only in the friction surfaces and mucous membranes of the lips and external genitalia.

There are very few cholinesterase-reactive subepidermal nerve fibers. Simple terminal nerve endings are encountered in the suprapubic area and in the ulnar region. Small arteries and arterioles are surrounded by cholinesterase-reactive nerve fibers. Large, myelinated nerve trunks, deep in the reticularis dermis, are numerous in the external genitalia, eyelids, suprapubic region, and sternal gland. No encapsulated end-organs are found in those areas that have a poorly-developed papillary layer. In all friction surfaces, between the rete ridges of the epidermis, are found Meissner corpuscles and their emergent nerve fibers (Fig. 69); deep in the tela subcutanea are the Vater-Paccini corpuscles. In the digits there are fewer but larger Meissner corpuscles than in the palms or soles. Mucocutaneous end-organs are found beneath the glabrous surface of the lips, and in the external genitalia. All organized nerve endings are acetyl- and butyrylcholinesterase-reactive. Meissner corpuscles also contain PAS-positive, diastase-resistant material, alpha-naphthol esterase, and cytochrome oxidase activity.

The Hair Follicle

Hairs grow in linear perfect sets of 3 to 5 follicles (Fig. 77). They occur singly in the lip, eyebrow, eyelid, ulnar eminence, and suprapubic region. Active and quiescent follicles are occasionally found in the same groups. One to 2 sebaceous glands open into the base of the pilary canal of each follicle. One apocrine gland usually accompanies each hair follicle group; its duct terminates adjacent to one of the pilary orifices (Fig. 71). All hair follicles are narrow and long. Sinus hair follicles occur in the lips, cheek, and ulnar eminence. Sinus hairs are surrounded by cavernous sinuses; 2 small sebaceous glands empty into the base of each pilary canal (Fig. 66).

Most of the active (anagen) hair follicles extend approximately one-third their length into the panniculus adiposus. The bulge is about half-way up the follicle. The arrectores pilorum muscles are better developed in the cheek, scalp, back, and tail; in the tail the muscles are larger in the distal than in the proximal part. The keratogenous zone is nearly one-fifth the total length of the follicle. Most hairs have a large, septulated medulla, and a thin cortex, both containing some melanin granules. Melanotic, dendritic melanocytes frequently descend to the pilary canal, outer root sheath (Fig. 70), and upper bulb; the hair bulge is heavily pigmented (Fig. 76). Moderate concentrations of glycogen occur about the middle one-third of the outer root sheath; lesser amounts are found about the remaining outer root sheath, medulla, and cuticle cells of the cortex. The inner root sheath contains no glycogen. The dermal papilla and inner layer of the vitreous membrane are PAS-positive, but diastase-resistant. The long, narrow dermal papilla is the only structure that stains metachromatically

with toluidine blue.

Quiescent follicles are less than one-half the length of active ones. A 1- to 2-cell-thick epithelial sac is fashioned about a long, clavate club hair. Between the epithelial sac and club hair is a capsule that corresponds to the inner root sheath of active follicles. Eccentric to this capsule is a short hair germ to the base of which is attached the small, hemispherical dermal papilla. A 1-cell-thick hyalin membrane is interposed between the epithelial sac and connective tissue sheath. A few pigment cells are seen about the hair germ and epithelial capsule. None of the elements in quiescent follicles is metachromatic when stained with toluidine blue. Glycogen is concentrated in the epithelial sac.

Active hair follicles contain moderate concentrations of phosphorylase in the lower one-half of the outer root sheath but none in the upper one-half. A moderate amount of enzyme also occurs randomly in the epithelial sacs of quiescent follicles. Active follicles are rich in both succinic dehydrogenase and monoamine oxidase in the upper bulb, matrix, and keratogenous zone of the outer root sheath. Cytochrome oxidase is most pronounced in the pilary canal and the matrix of active follicles; mild reactivity occurs in the pilary canal and epithelial capsule of quiescent follicles. Alpha-naphthol esterase intensity is strong in the bulb and the lower one-third of the outer root sheath of active follicles; it is mild in the inner root sheath, at the base of the pilary canal, but weak in the matrix. In quiescent follicles, granules in the cells of the base of the hair club show strong alpha-naphthol esterase concentration. Comparable reactivity is also evident

in the capsule and epithelial sac. In all follicles, the intensity of alkaline phosphatase reaction is inversely proportional to the size of the dermal papilla in which it is present. The connective tissue plate at the base of the papilla is also moderately reactive. Acid phosphatase is very weak in all follicles; the keratogenous zone and inner root sheath of the lower pilary canal show minimal activity (Table 10).

The arrectores pilorum muscles abound in alpha-naphthol esterase, succinic dehydrogenase, and cytochrome oxidase. Some are very reactive for phosphorylase but others are not. Mild reactions occur for monoamine oxidase. Most arrectores pilorum muscles contain moderate amounts of acetyl- and butyrylcholinesterase.

A moderate plexus of capillaries, with an alkaline phosphatase-reactive endothelium, surrounds the lower one-third of active follicles. Above this level, the vessels run along the arrector pili muscle, encircle the accompanying sebaceous glands and then align themselves, in reduced numbers, parallel to the upper follicle, where they sometimes anastomose with transverse subepidermal capillaries. In quiescent follicles, only a few capillaries are entwined around the lower portion. The dermal papillae of larger follicles are invested by few capillaries.

Acetyl- and butyrylcholinesterase-containing nerve fibers, which ascend from larger trunks in the reticularis dermis and hypodermal fat, loosely encompass the lower portion of the follicle, sebaceous glands, and arrector pili muscle. Most hair follicles, and particularly larger ones, have a cholinesterase-reactive hair follicle end-organ that surrounds the pilary canal just below the entrance of the sebaceous

glands. It consists of an internal palisade of fibers, oriented parallel to the shaft of the hair; occasionally, these fibers terminate as end-feet. External to this palisade is a horizontal, circularly-arranged collar of fibers (Fig. 64).

The Sebaceous Glands

Small over the general body surface, the sebaceous glands have 1 or 2 unilobular acini whose short ducts empty at the base of the pilary canal. Sebaceous glands are large on the lips, eyelids, and external genitalia. Those of the lips have 2 to 6 multilobular acini that empty into the base of the pilary canal via short ducts. Most of the sebaceous glands of the eyelid are alike, although those of the lower palpebral cilia have a long duct that empties at the pilary orifice. The bilaterally racemose meibomian glands are long and narrow. The sebaceous glands of the external genitalia are very large, multilobular structures whose numerous short ducts empty from all sides into a dilated, ampulliform pilary canal (Fig. 72).

A few dendritic melanocytes may be found between the peripheral differentiating acinar cells in the scalp, eyebrow, ear, and cheek. The outer peripheral differentiating cells of the glands in the lips and eyelids are occasionally laden with glycogen. The sebum usually contains a PAS-positive and diastase-resistant substance.

Many sebaceous glands have mild phosphorylase activity. Reactive granules are most pronounced at the periphery of the acini in the lips and eyelid (Fig. 74). The peripheral acinar cells of all sebaceous glands are moderately reactive for succinic dehydrogenase, cytochrome oxidase, and monoamine oxidase. Alkaline phosphatase is present

only in the peripheral cells of the larger glands of the lip and eyelid (Fig. 75). Acid phosphatase and alpha-naphthol esterase activities are moderate in all glands (Table 10).

The large sebaceous glands have a rich supply of capillaries around them with an endothelium reactive for alkaline phosphatase. Acetyl- and butyrylcholinesterase-reactive nerves are wound about the sebaceous glands of the eyebrow, lips, ulnar eminence, tail, sternal gland, external genitalia, and eyelids.

The Suprapubic Gland

Histological inspection of the suprapubic region reveals a field that is composed of aggregates of gigantic, multilobular sebaceous glands. Some of them have numerous, short and narrow ducts that empty into large, central collecting ducts (Fig. 62). Bullous ducts, about equal in size to an entire gland, often open independently to the skin surface. These large ducts are lined by thin, squamous epithelium. Both the locules of individual glands and distended collecting ducts are separated by a thin connective tissue stroma, composed of delicate elastic and collagenous fibers. The squamous cells that line the central ducts are intensely basophilic but not metachromatic. The sebum and cellular debris are PAS-positive, diastase-resistant. The cells along the cuticular border of the collecting ducts, as well as some differentiating acinar cells, contain appreciable amounts of glycogen and phosphorylase.

In the periphery, and to a lesser extent in the center, all glands are strongly reactive for alpha-naphthol esterase, monoamine oxidase, succinic dehydrogenase, and cytochrome oxidase; alkaline phosphatase

and acid phosphatase activity is slight. Individual sebaceous acini are encompassed by alkaline phosphatase-positive capillaries. Alkaline phosphatase-reactive luminal casts are often encountered.

Delicate connective tissue septa, which accommodate other blood vessels and wisps of acetyl- and butyrylcholinesterase-reactive nerve fibers, are insinuated between the glands and ducts.

The Apocrine Glands

Apocrine glands, numerous over the entire hairy surface, are large in the lips, eyelids, ulnar eminence, tail tip, external genitalia, and suprapubic region. They are most plentiful in the external genitalia, scalp, and tail, and least numerous in the back. Except for the lips and ulnar region, where 1 gland is associated with each sinus hair, and the eyebrow and suprapubis, where some glands open to the surface independent of hair follicles, there is about 1 gland to every 3 follicles.

The coiled secretory portion of the glands rests deep within the reticularis dermis and tela subcutanea. An abrupt transition in diameter marks the junction of the narrow straight duct and the secretory coil (Fig. 78). The ducts are about one-fifth the diameter of the secretory coil. Those ducts associated with hair follicles are aligned parallel to the pilary canal and empty at, or are contiguous to, the pilary orifices (Fig. 71). In the tip of the tail, suprapubic region, and external genitalia, each duct possesses a terminal, ampulliform dilatation.

The ducts are composed of 2 layers of cuboidal epithelial cells; those lining the lumen are flattened. Basophilia, intense in both cell layers, is absent at the luminal border.

The secretory coil consists of a single layer of uneven, columnar epithelial cells, only some of which possess a terminal cuticular margin. The cells rest upon a thin layer of myoepithelium and a thick, hyaline basement membrane. When stained with toluidine blue, only the cytoplasmic granules of the basal portion of the secretory cells show basophilia. The debris in the glands of the ears and eyelids stains a strong metachromatic color. The inner layer of the basement membrane, some secretory cells, supranuclear cytoplasmic granules, and all luminal casts are PAS-positive and diastase-resistant. The cytoplasm of the secretory cells contains small osmiophilic granules.

Some apocrine secretory tubules in the ulnar area and external genitalia of both sexes are encircled by melanotic, dendritic melanocytes (Fig. 79).

A reaction for phosphorylase is confined to the cells of the excretory duct (Fig. 78); secretory cells are seldom reactive. Succinic dehydrogenase reactivity in the secretory coil equals or exceeds that of the excretory duct. Cytochrome oxidase activity, although slight in the ductal cells, is very strong in the secretory segment. The secretory coil is also very reactive for monoamine oxidase; the ducts contain minimal amounts of this enzyme. There is no acid phosphatase reaction. Moderate alpha-naphthol esterase activity occurs only in the supranuclear area of the secretory cells. An alkaline phosphatase reaction is absent from the ducts but moderate to strong in the secretory coils; it is concentrated along the luminal border of smaller glands, and in the base of the columnar and myoepithelial cells of larger glands.

The secretory coils have a generous supply of alkaline phosphatase-reactive blood vessels around them. The large apocrine glands of the lips and external genitalia are surrounded by moderate numbers of nerve fibers that are rich in both acetyl- and butyrylcholinesterase (Table 10).

The Sternal Gland

Microscopically, the sternal gland is composed of a concentration of large apocrine glands, situated deep in the reticularis dermis (Fig. 63). The other morphological features of these glands are similar to those of the large apocrine glands of the rest of the body.

Unlike the glands over the rest of the body, however, the lumina of the sternal apocrine glands seldom contain PAS-positive, diastase-resistant casts. The secretory cells contain very fine granules that stain with the colloidal iron technique (Mowry, 1958). The cells of the excretory ducts are more reactive for phosphorylase than are those elsewhere in the body (Fig. 78). The distribution of most other enzymes is similar to that found in the other large apocrine glands, although the activity is somewhat stronger (Fig. 73).

The secretory coils are surrounded by a rich plexus of capillaries and moderate numbers of cholinesterase-reactive nerve fibers.

The Eccrine Glands

Eccrine sweat glands are confined to the volar surfaces of the pes and manus. The convoluted, glomerate segment of these glands rests in the superficial tela subcutanea and consists of two-thirds secretory segment and one-third duct. The diameter of the secretory tubules is approximately 3 times that of the long, straight excretory duct. The intraepidermal helical segment of the duct outlines a right-handed coil.

Secretory coils are composed of 2 types of cells. The small, dark, PAS-negative cells have a bullous terminal portion and are crowded toward the lumen. They have dense, oval nuclei and a granular cytoplasm, which is intensely basophilic and occasionally metachromatic. The larger cells, devoid of basophilic granules, rest upon a thin layer of myoepithelial cells. A thick, hyalin basement membrane surrounds only the secretory segment. These large, clear cells possess spherical, finely-stippled nuclei; they do not contain glycogen. The casts in the lumina of the secretory tubules and excretory ducts are PAS-positive, diastase-resistant. The inner layer of the basement membrane, adjacent to the myoepithelial cells, is PAS-positive, diastase-resistant. The outer hyaline layer is PAS-negative.

The excretory ducts are composed of 2 layers of cuboidal epithelial cells. The basal layer of cells contains moderate amounts of glycogen. Occasional melanotic pigment granules are seen around this layer of the excretory duct.

Except for slight activity in the basal cells of the coiled excretory ducts, the glands are unreactive for phosphorylase. Cytochrome oxidase and succinic dehydrogenase are concentrated in the secretory segment; the duct has practically no reactivity. The reactivity is very strong in the clear cells and slight in the dark cells. Monoamine oxidase is weak in both duct and secretory tubules. Acid phosphatase reactivity is weak. Alpha-naphthol esterase activity is very marked in the cuticle of the secretory cells and gradually diminishes in the basal part. The excretory duct has a mild concentration of alpha-naphthol esterase. Alkaline phosphatase activity is intense only in myoepithelial cells

and infranuclear portions of clear cells.

Secretory coils are surrounded by rich plexuses of alkaline phosphatase-positive blood vessels and cholinesterase-reactive nerve fibers. The nerve fibers are noticeably more reactive for acetylcholinesterase than for butyrylcholinesterase.

V. Saguinus [=Oedipomidas] oedipus (Linnaeus 1758); cottontop pinché.

A. Gross Observations.

Several external characteristics, besides those presented in the Introduction, deserve to be mentioned: namely, the occurrence and distribution of sinus hair follicles; the absence of detectable glandular concentrations over the sternum; and the presence of well-defined, suprapubic glandular fields.

Large black vibrissae, conspicuously longer than the hairs with which they are intermingled, are found on the eyebrows, lips, and cheeks. Others arise from an elevated area on the ventral ulnar surface of the wrist. This specialized cutaneous region, 4 mm. in diameter, represents the ulnar eminence.

Contiguous with the labia pudendi and anterior part of the scrotum is an area of deeply pigmented, relatively hairless skin that extends anteriorly as paired pubic ridges; the ridges or "cushions" are separated bilaterally by a slight depression. The few hairs that populate this area are of the vellus type. More extensive in the female, the modified skin of the suprapubic region extends 25 mm. anterior to the ventral commissure; it is 16 mm. at its greatest width (Fig. 81).

In the male, the suprapubic skin becomes indefinitely demarcated only 10 mm. anterior to the mons, at a point caudad to the inguinal testes (Fig. 80).

B. Histological and Histochemical Observations.

The Epidermis

The thin epidermis of the general body surface is composed of 2 to 3 cell layers. On the proximal and distal parts of the tail it consists of 4 to 7 cell layers. The epidermis that covers the ulnar eminence is 5 to 7 cell layers thick. The mucous membrane of the nose, anogenital skin, and lips varies from 8 to 20 cells; the mucosa is invaginated at the inner margin of the lower lip, forming a prominent longitudinal sulcus (Fig. 85). Epidermal thickness culminates in the volar friction surfaces where the malpighian layer is often 30 cells deep; prominent undersculpturing, thick basement membranes, and well-defined strata granulosa occur only in such regions.

The epidermis is heavily pigmented everywhere (Fig. 86) except the chest, belly, axilla, and ventral friction surfaces (Fig. 84). The labial mucosa gradually loses melanotic pigment as it approaches the gingiva (Fig. 85). Glycogen is occasionally observed in the upper stratum spinosum of mucous membranes. It is absent from the volar friction surfaces; the intraepidermal portions of eccrine excretory ducts contain only a PAS-positive, diastase-resistant substance.

Except in the friction surfaces and mucous membranes, phosphorylase activity is absent in the epidermis. Succinic dehydrogenase and

monoamine oxidase reactivities are somewhat weak. The enzymatic properties of the epidermis are outlined in Table II.

The Dermis

The relatively thick dermis contains a well-defined papillary body in the lips, tail, anogenital area, and ventral friction surfaces of the pes and manus. Large plicated bundles of collagen comprise the bulk of the thick reticular layer; intermingled with this dense collagenous meshwork are a few metachromatic mast cells, large bipolar melanocytes, and coarse elastic fibers. Although they are present in all body regions, perivascular mast cells are most common in the face and external genitalia. Spindle-shaped melanotic melanocytes (Fig. 86) reside in the papillary body and higher levels of the reticularis dermis of all skin except the chest, belly, axilla, and volar friction surfaces.

Extensive and well-developed subepidermal capillary arcades are found beneath all friction surfaces and mucous membranes. Throughout the dermis of the hairy skin is a profusion of capillaries, whose endothelia are reactive for alkaline phosphatase.

All free subepidermal nerve endings, mucocutaneous end-organs, and Meissner corpuscles are cholinesterase-positive; however, cephalically distributed nerve fibers and end-organs contain more acetyl- than butyrylcholinesterase, whereas those throughout the remainder of the body are equally reactive for specific and pseudocholinesterase. Mucocutaneous end-organs are also alpha-naphthol esterase positive.

The Hair Follicle

Groups of 3 to 5 hair follicles are arranged in linear perfect sets; hairs occur singly on the muzzle. Over the general body surface,

1 apocrine gland is associated with each hair grouping. Sinus hair follicles appear in the eyebrow, lips, perialar region, and cheek; several large sinus hairs are also found on the ventral ulnar aspect of the wrist (Fig. 82). Anagen and telogen follicles often occur in a mutual hair grouping; occasionally 2 hairs share the same pilary canal. Pigmented hairs are laden with melanin (Fig. 86): active follicles bear numerous melanocytes along the length of their outer root sheath, and around the hair bulge, upper bulb, and dermal papilla; quiescent follicles sustain large numbers of melanocytes about the pilary canal, and in the epithelial sac, hair germ, and dermal papilla. The white hairs of the cephalic crest contrast sharply with contiguous hairs in the parietal scalp; the former are large terminal follicles that are totally devoid of pigment, whereas the latter are smaller anagen follicles abundantly pigmented (Fig. 87). Arrectores pilorum muscles are present in all body regions except the facial disc (eyebrow, eyelids, lips, and perialar area), external ears, anogenital skin, and suprapubic region; they are largest in the tail. The skin of the suprapubis is populated by vellus hairs only.

The outer root sheath of active follicles contains large concentrations of glycogen and phosphorylase; however, the epithelial sac of quiescent hairs contains neither glycogen nor phosphorylase. Succinic dehydrogenase, cytochrome oxidase, and monoamine oxidase activities are moderate. Alkaline phosphatase is restricted to the dermal papilla and connective tissue plate to which it is attached. Other enzyme activities are listed in Table II.

Hair follicles are generously supplied with alkaline phosphatase-positive capillaries. Nerve fibers and arrectores pilorum muscles are acetylcholinesterase-reactive. Hair follicle nerve end-organs are equally reactive for acetyl- and butyrylcholinesterase. (Fig. 86).

The Sebaceous Glands

Two small unilobular sebaceous glands are associated with each hair follicle in the scalp, thigh, and axilla; one occurs with every hair in the back, tail, chest, and belly. One or 2 medium-sized, multilobular sebaceous glands accompany each hair follicle in the facial regions. The short excretory ducts of the smaller glands empty into narrow pilary canals. Large multiacinar glands are prominent in the lips, external ears, perialar skin, and anogenital area; the acini of all empty into common collecting ducts and ampulliform pilary canals.

The dichotomously glandular suprapubic region, which is more extensive and better developed in the female (Figs. 81 and 83), consists of gigantic sebaceous glands that are subdivided into hundreds of small acini. The acini fuse proximally with distended collecting ducts that empty into the bullous pilary canal of each diminutive vellus follicle. Large apocrine secretory coils are admixed with the sebaceous components of each sebaceous-apocrine unit but empty independently at the skin surface adjacent to the pilary orifice.

In pigmented body regions, melanotic melanocytes cling to the excretory ducts of all sebaceous glands; occasionally these dendritic cells also venture out onto the surface of a sebaceous acinus (Fig. 86). Except those of the suprapubic region, none of the sebaceous glands

contain glycogen and phosphorylase. Cytochrome oxidase activity is intense (Fig. 88). Succinic dehydrogenase and monoamine oxidase reactivities are moderate or weak. The various properties of the sebaceous glands are summarized in Table II.

Many alkaline phosphatase-positive capillaries surround the sebaceous glands. This rich vascularization is outstanding in the suprapubic gland (Fig. 83). The sebaceous glands are also invested by numerous nerves that are strongly reactive for acetyl- and weakly reactive for butyrylcholinesterase.

The Apocrine Glands

One medium-sized apocrine gland accompanies each hair grouping in the skin of the general body surface. One to 2 medium or large apocrine glands occur with each grouping of hairs in the chest. Large apocrine glands are present in a 1:1 ratio with hair follicles in the anogenital skin, axilla, and suprapubic gland. The excretory ducts of all glands open to the skin surface, adjacent to the pilary orifice.

Secretory coils are composed of irregular columnar or flattened cuboidal epithelium. Although glycogen is not found in the apocrine glands, PAS-positive, diastase-resistant supranuclear cytoplasmic granules are prevalent in the secretory cells. Luminal casts contain a PAS-positive, diastase-resistant substance that is metachromatic when stained with toluidine blue. Excretory ducts are composed of 2 layers of cuboidal epithelium; each is heavily pigmented around its terminal portion (Fig. 86).

Enzyme reactivities are given in Table II. The notable diminishment of cytochrome oxidase (Fig. 88) and moncamine oxidase activities in the large apocrine secretory coils of the suprapubic gland and external genitalia is surprising; apocrine glands in all other body regions contain intense or moderate concentrations of these enzymes. Alpha-naphthol esterase content is diminished in all apocrine secretory segments. All luminal borders are strongly reactive for alkaline phosphatase (Fig. 83). Capillaries, which surround the secretory segments, are alkaline phosphatase-positive. Cholinesterase-containing nerves cannot be demonstrated.

The Eccrine Glands

Eccrine sweat glands are present only in the ventral friction surfaces of the pes and manus. The glomerate portion of each gland rests in the tela subcutanea and consists of two-thirds secretory coil and one-third coiled excretory duct. Secretory segments are 3 times the diameter of the coiled excretory duct. The relatively short, straight portion of the excretory duct passes through the epidermal ridge but does not commence to spiral as a weak right-handed coil until it has attained the higher levels of the stratum malpighii.

Secretory coils are composed of clear cells and dark cells, surrounded by myoepithelial cells, around which is a moderately thick basement membrane. Luminal casts do not stain metachromatically. The straight excretory ducts contain very few melanotic melanocytes. Glycogen is completely absent from the eccrine sweat gland unit and only the coiled portion of the excretory duct contains intense amounts of a PAS-positive, diastase-resistant material. Similarly, only the

coiled excretory duct demonstrates phosphorylase reactivity (Fig. 84). Monoamine oxidase activity is weak. Other enzymatic concentrations are presented in Table II.

The eccrine glomeruli are surrounded by numerous capillaries with an endothelium reactive for alkaline phosphatase. Nerve fibers that encompass the secretory coils are intensely reactive for acetyl- but very weakly reactive for butyrylcholinesterase.

DISCUSSION

I. Introductory Remarks.

At this point, a variety of questions might be asked: e.g., can systematic comparative studies of skin actually turn up different modifications? If so, do basic underlying patterns occur that would be valuable points of reference to students of evolution, systematics, comparative physiology, experimental biology, and dermatology? More specifically, if general phylogenetic trends do develop, which ones contribute to a better understanding of the phylogenetic stature of New World monkeys? Is such a study as this also an adjuvant to one's overall comprehension of phylogeny within the Order Primates? Is the author justified in suggesting that the combined histological and histochemical properties of a given cutaneous system are every bit as reliable criteria to the accurate assessment of an animal's taxonomy and phylogeny as are those structural characters, classically employed by systematic zoologists: i.e., dentition, cheiridia, skeletal details, myology, arthrology, and splanchnology? If they are, how can a myriad of disconnected cutaneous traits, such as that presented in the preceding Results, be organized into a meaningful schema? What experimental models have been brought to light and what is their significance? On what basis, if any, can the extent of parallel development between primate superfamilies or infraorders be considered evidence of close biological affinity? Can the morphological traits of the skin of New World monkeys be considered intermediate between the Prosimii

and the Cercopithecoidea and Hominoidea? Lastly, wherein do the preceding findings substantiate or reject the currently accepted concepts of taxonomy and the evolutionary lineage of primate groups?

The following discussion will attempt to answer these questions, first by examining the cutaneous characteristics of individual callithricids, and secondly by pursuing the significance of phylogenetic trends within the superfamily Ceboidea and the Order Primates.[1]

The initial discussion of callithricid traits will not be presented according to the systematic order of the family Callithricidae, as it was in the Results; rather, it will reflect the sequential availability of material, thus adhering to the order in which each of the 6 callithricid species was examined. In so doing, the author hopes that the reader will be able to follow the various chronological discussions, noting the development of trends, the ebb and flow of speculation, and the formulation of more concrete evidence--in other words, the acquisition of knowledge about the skin of primates, its metamorphosis, and emergence as a phylogenetic philosophy. Inherent in such an approach is the fact that comparative discussions of individual species will be somewhat repetitious; however, they are necessarily so because individual species share certain cutaneous traits with other, widely diversified members of the Order--hence, the presence of underlying patterns and development of trends. The following

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[1]Although the author's familiarity with the skin of 9 of the 11 genera of the Cebidae lends some support to his views, the ensuing discussion of phylogenetic trends would carry little weight and be literally impossible to substantiate were it not for 1) the combined effort of colleagues who worked with the author on these cebid studies, and 2) the numerous skin surveys carried out by Montagna and his associates, prior to and during the author's initiation into the skin of primates.

discussions, therefore, are repetitive only when they serve to emphasize those cutaneous characteristics that might shed light upon the phylogeny of the New World monkeys. These traits will then be summarized; the monophyletic primate taxa will be cutaneously characterized; and the Discussion will be concluded by a general critique of that position in the Order Primates, assigned to the New World monkeys.

II. An Appraisal of Cutaneous Characteristics in Members of the Family Callithricidae.

A. Saguinus [=Tamarinus] fuscicollis illigeri.

This being the first detailed study of the skin of a member of the family Callithricidae, it seems profitable to compare and contrast its characteristic features with those of other primate families that have been studied. It is apparent that the skin of this callithricid shares characteristics with both the Prosimii and the Cercopithecoidea.

The red-mantled tamarin has a moderately pigmented epidermis, similar to that of the black lemur (Montagna, Yasuda and Ellis, 1961) and Spix's pinché. The metachromatic substance in the stratum corneum, around the pilary orifices of the sternal region, is probably induced by acid mucopolysaccharides secreted by the apocrine glands.

The relative abundance of elastin in the dermis of the red-mantled tamarin may have some phylogenetic significance; only some primates have numerous elastic fibers in their dermis; among these are the rhesus monkey (Montagna, Yun and Machida, 1964), stump-tailed macaque (Montagna, Machida and Perkins, 1966), and Sykes' monkey (Machida, Perkins and Montagna, 1964). As in most of the other primates studied,

dermal vasculature is generally scant except for the superficial arcades of capillaries in the friction surfaces and mucous membranes. Organized cutaneous end-organs consist of cholinesterase-reactive Meissner corpuscles and mucocutaneous end-organs such as those found in other primates. There were no mammalian end-organs (Winkelmann, 1959, 1960), such as those found in some of the lorisoids. The presence of single melanocytes in the papillary layer and scattered aggregations of them in the upper reticularis dermis is a characteristic that this animal shares only with the other genera of the family Callithricidae. The skin of the callithricids, then, is somewhat unique in that it contains both epidermal and dermal melanotic melanocytes.

The grouping of hair follicles into 3 and 4 is unlike the situation in the Prosimii, and similar to that of the higher primates such as the macaques, mangabeys, baboons, gibbons, chimpanzee, and gorilla. In spite of this similarity, there is 1 apocrine gland with each hair group, as in the Prosimii. Unlike either the Prosimii or higher primates, however, the hair follicles of the red-mantled tamarin are arranged in linear perfect sets. The occurrence of hairs in groups of 3 on the muzzle is peculiar; hair follicles grow singly on the muzzle of other primates, studied thus far. The presence of melanotic melanocytes on the pilary canal and hair bulge is shared with howler monkeys, spider monkeys, woolly monkeys, Celebes apes, gibbons (Parakkal, Montagnà and Ellis, 1962), and the great apes (Ellis and Montagna, 1962; Montagna and Yun, 1963). The presence of sinus hairs on the ventral ulnar surface of the wrist is shared with some of the lemurs. The hair follicles of the red-mantled tamarin, unlike the prosimians,

have well-developed arrectores pilorum muscles.

The sebaceous glands are relatively free of melanocytes except along their ducts, as in the case of some Cercopithecidae, Hylobatidae, and Pongidae. Unlike those of most prosimians, the large sebaceous glands are surrounded by cholinesterase-reactive nerve fibers (cf. Montagna and Ellis, 1959). These animals have assemblages of gigantic, multiacinar sebaceous glands, collectively referred to as the peringuinal or perigenital glands (Pocock, 1920; Wislocki, 1930). They are composed of numerous locules whose ducts empty into respective, ampulliform pilary canals. Their general structure is somewhat analogous to that of the brachial gland of the ring-tailed lemur (Montagna and Yun, 1962), and they are probably social, or marking glands.

All prosimians (except the tree shrews), tarsiers, and some ceboids have only apocrine glands in the hairy skin. Most apocrine ducts open at the surface of the skin, adjacent to the pilary orifices (Schiefferdecker, 1922; Steiner, 1926; Yasuda, Kaga, Goto, Kashimura, Furusawa and Kobayashi, 1957). The presence of acetyl- and butyryl-cholinesterase-reactive nerve fibers around the larger glands of the lips and external genitalia is common among the Anthropoidea. The outstanding feature of the apocrine glands of the red-mantled tamarin is the presence of melanotic, dendritic melanocytes situated around the secretory coils in the external genitalia and ulnar gland. Melanocytes in the apocrine glands have been found heretofore only in the domestic pig (Montagna and Yun, 1964).

The aggregations of apocrine glands in the suprasternal region are reminiscent of similar gatherings in the owl monkey (Hill, Appleyard

and Auber, 1959; Hanson and Montagna, 1962), spider monkey (Wislocki, 1930; Schwarz, 1937), and orangutan (Wislocki and Schultz, 1925). Comparable aggregates of glands in other primates are the brachial organs of the slender loris (Montagna and Ellis, 1960) and slow loris (Montagna, Yasuda and Ellis, 1961) and the inguinal glands of the potto (Montagna and Ellis, 1959). The secretion of these glands probably has some relevance to recognition between members of a group (Hill, et al., 1959). In the higher primates, large concentrations of apocrine glands may be found in the circumanal region, anterior chest, and axilla.

True eccrine sweat glands are found only in the volar surfaces of the palms and soles of the red-mantled tamarin. This limited distribution resembles that in the owl monkey and all prosimians except the tree shrew (Montagna, Yun, Silver and Quevedo, 1962). Whereas in most other animals the eccrine glands are rich in glycogen and phosphorylase activity, in Saguinus fuscicollis illigeri these reactions are weak, resembling those of Nycticebus and Loris. This condition resembles that of apocrine glands; perhaps this is indicative of a more primitive type of eccrine gland. As in other primates, the glands of the red-mantled tamarin are surrounded by acetyl- and butyrylcholinesterase-reactive nerve fibers.

B. Callithrix [=Cebuella] pygmaea.

The skin of the pigmy marmoset has several species specific peculiarities, as well as some common to the other members of the family Callithricidae; it also shares cutaneous characteristics with the Prosimii and Anthropoidea.

The presence of moderate amounts of epidermal pigment on the dorsal skin is similar to that observed in the black lemur and red-mantled tamarin; however, pigmentation is suppressed in such areas as the ventral tail, chest, gular region, and friction surfaces. The pigmented mottling of the scrotum is reminiscent of that noted in the Lorisidae and Galagidae (Montagna and Yun, 1962). The presence of scattered melanocytes in the papillary body of friction surfaces and piebald aggregations in the upper reticularis dermis (although less pronounced in ventral body regions) is comparable to that observed in the white-shouldered marmoset and the tamarins and pinchés (Machida and Perkins, 1967). Thus far, this occurrence and distribution of epidermal and dermal melanocytes appears to be a distinguishing characteristic of members of the family Callithricidae.

Like the red-mantled tamarin, rhesus monkey, stump-tailed macaque (Montagna, Machida and Perkins, 1966), and Sykes' monkey, the pigmy marmoset possesses abundant dermal elastin. Hair follicles grow in linear perfect sets of 3 or 4, similar to those of the red-mantled tamarin. The occurrence of 1 apocrine gland per hair follicle group is similar to the situation in many Prosimii; the presence of sinus hairs on the ventral ulnar wrist of the pigmy marmoset, like the white-shouldered marmoset (Fig. 89), is comparable to that previously observed in the red-mantled tamarin. However, unlike those of the red-mantled tamarin, neither pilary canals nor hair bulges are heavily pigmented and radial papillae are not discernible. The pigmy marmoset has well-developed arrectores pilorum muscles, as do most Anthropoidea. Alkaline phosphatase-positive hair follicle nerve end-organs are more prevalent

in the pigmy marmoset than those formerly observed in the potto, lesser bushbaby (Yasuka, Aoki and Montagna, 1961), or woolly monkey (Machida and Perkins, 1966).

As in other Anthropoidea, the larger sebaceous glands are surrounded by cholinesterase-reactive nerves. A suprapubic aggregation of large, multiacinar sebaceous glands resembles the suprapubic gland of the red-mantled tamarin.

Like the white-shouldered marmoset, the scalp and back of the pigmy marmoset contain few or no apocrine glands. Elsewhere, however, apocrine glands occur throughout the hairy skin. The widespread distribution of apocrine glands throughout the haired general body surface parallels that situation noted in the Lemuridae, Lorisidae, Galagidae, some Callithricidae, and most Cebidae. It will be recalled that eccrine glands do occur together with apocrine glands in the brow and pubic regions of the red-mantled tamarin. Unlike those of the red-mantled tamarin, the apocrine secretory coils of the pigmy marmoset are devoid of melanotic melanocytes; they are invested by butyrylcholinesterase-rich nerves in the external genitalia only. A concentration of large apocrine glands in the sternal region of the pigmy marmoset corresponds to those groupings that comprise the brachial glands of the slow and slender lorises, the inguinal glands of the potto, and the sternal localizations of the red-mantled tamarin, owl monkey (Hanson and Montagna, 1962), spider monkey, and orangutan.

The limitation of eccrine gland distribution to the volar surfaces of the pes and manus is comparable to that of all Prosimii except the tree shrew, many Cebidae, the red-mantled tamarin, and the white-shouldered

marmoset. Unlike those of the red-mantled tamarin but like those of the angwantibo (Montagna, Machida and Perkins, 1966), owl monkey, and white-shouldered marmoset, the dark cells contain glycogen; unlike those of the red-mantled tamarin and owl monkey but like those of the angwantibo and white-shouldered marmoset, the clear cells contain none. In addition, both argyrophilic granules and an acid mucopolysaccharide substance--previously observed in the squirrel monkey (Machida, Perkins and Hu, 1966)--occur in the karyoplasm of the dark cell nuclei. Eccrine secretory coils are surrounded by specific cholinesterase-containing nerves; this phenomenon was previously observed in the tree shrew, slow loris, squirrel, golden spider (Perkins and Machida, 1967), and woolly monkeys. These findings would suggest that pigmy and white-shouldered marmosets, like the red-mantled tamarin, possess somewhat primitive sweat glands.

C. Saguinus [=Oedipomidas] oedipus.

A moderate pigmentation of the epidermis concomitant with occasional spindle-shaped melanocytes in the upper dermis is characteristic of most Callithricidae; for example, this trait is shared by the red-mantled tamarin, pigmy marmoset, and white-shouldered marmoset. However, among all callithricids studied, the following pigmentary peculiarities are unique to the pinché: 1) the epidermis is so deeply pigmented that the stratum corneum is laden with melanin granules, and 2) the dermis does not merely contain scattered melanocytes in the papillary body and upper reticular layer: many body regions contain large bipolar melanocytes throughout the entire upper one-half or three-fourths of the dermis. Of all primate pigmentary systems histologically examined

to date, that of the cottontop pinché resembles most closely the Anubis baboon (Montagna and Yun, 1962). Melanotic melanocytes are less common in the ventral body regions of all primates studied; the paucity of epidermal and dermal melanocytes in the chest, belly, and axilla of the pinché corresponds to this general tendency.

Diminished epidermal monoamine oxidase activity is an enzyme signature that is common to a variety of New World monkeys: the owl monkey, white-browed capuchin (Perkins and Ford, in press), pigmy marmoset, and red-mantled tamarin.

All Callithricidae, studied to date, have hair follicles arranged in linear perfect sets. The distribution of melanotic melanocytes on hair follicles and sebaceous glands is like that of the red-mantled tamarin. The presence of glycogen and phosphorylase in the epithelial sac of quiescent follicles is characteristic of man and primates but unlike all other mammals studied (Montagna, 1963); the unusually weak glycogen and phosphorylase activities in the pinché's quiescent hairs are therefore somewhat puzzling.

An elevated cluster of sinus hairs occurs on the ventral wrists of lemurs (Montagna and Yun, 1963) and each of the following callithricids: the cottontop pinché, red-mantled tamarin, white-shouldered marmoset, and pigmy marmoset. Histologically, such localizations are composed of several large sinus hair follicles and medium-sized apocrine glands. The apocrine glands are associated in a 1:1 ratio with the vibrissae; although moderately large, they are often better developed in other body regions, e.g., the sternal and suprapubic aggregations. Cholinesterase and alkaline phosphatase preparations do not reveal subepidermal nerve

end-organs or specialized capillary plexuses; only the sinus hairs exhibit a vascular complex and profusion of nerves. The term "ulnar gland" may be unfortunate if one were to base the probable function of the ulnar specialization on morphological evidence. Sherrington (1950) has stated: "We must now become literate enough to read function out of design, for anatomy is the theater in which physiology takes place." The anatomy of the ulnar "gland" indicates that it is less glandular than tactile. The ulnar eminences, however, may subserve a secondary glandular "marking" function that is mediated through the associated apocrine glands. Perhaps it would be more accurate to refer to these typical callithricid modifications as ulnar "tufts" or "eminences."

The suprapubic glands or "pubic cushions" of the cottontop pinché were overlooked by Pocock (1920); it is possible that he based his observations on male animals only. Three years earlier, deBeaux had observed and described variations in the turgescence of the pubic "cushions" that were apparently related to seasonal sexual fluctuations (Hill, 1957). The structure of the suprapubic glands was not accurately described for another 2 decades; Wislocki (1936) finally wrote: "Sexual skin provided with glands of sebaceous type overlying a stratum of tubular glands." Homologous glandular concentrations were previously observed in the red-mantled tamarin and pigmy marmoset. Their function is probably one of sexual attraction (they are much better developed in the female); a secondary function may be that of territorial marking.

One or 2 apocrine glands occur with each hair follicle grouping in the chest. Again, the tendency to concentrate in the vicinity of

the sternum is observed. Comparable concentrations of apocrine glands have been reported in the chest of the following New World monkeys: the golden spider monkey, white-browed capuchin, and red uacari (Perkins, Arao and Uno, In Press); true sternal aggregations—composed of gigantic apocrine glands that dwarf each of their respective follicles—have been found in the red-mantled tamarin and pigmy marmoset.

The terminal portion of apocrine excretory ducts is heavily pigmented in only 3 other species of primates: the golden spider monkey, howler monkey (Machida and Giacometti, 1968), and Philippine tarsier (Montagna and Machida, 1966; Arao and Perkins, In Press). The apocrine glands of the cottontop pinché are not surrounded by cholinesterase-reactive nerves.

Eccrine glands reside in the volar friction surfaces only. This restricted distribution is characteristic of all New World primates except the true prehensile-tailed monkeys (Alouattinae and Atelinae). The total absence or only sporadic presence of glycogen and phosphorylase in eccrine sweat glands is a histochemical trait that is thus far unique to species of the primate family Callithricidae (marmosets, tamarins, and pinchés).

D. Callithrix [=Mico] argentata.

Several cutaneous modifications and specializations in the skin of the silver marmoset set it apart from other primates; others exemplify characteristically primitive and advanced traits common to many primates. The assortment of integumental components in the silver marmoset would serve as experimental models for the exploration of numerous morphological

and physiological unknowns.

The skin of this callithricid is very thin. The 1 to 2 cell-layered epidermis, poorly defined papillary body, and meager reticular layer overlie an extensive field of subcutaneous fat. Like that of the lorisoids, the general body surface is free of epidermal and dermal melanotic melanocytes. The diminishment of epidermal monoamine oxidase activity appears to be a characteristic enzyme signature that is shared by certain ceboids: the owl monkey, white-browed capuchin, pigmy marmoset, and red-mantled tamarin. The interramal papillae of the gular region parallel the radial papillae of the red-mantled tamarin; both occur exclusively in a specialized cutaneous region where they are linearly or curvilinearly disposed relative to an intimate aggregate of large sinus hairs. It is possible that such structures subserve a sensory function, although nerve fibers were not observed in the papillae of either species.

The presence of keratinized spines on the corpus penis is found in such a varied assortment of primates as the common marmoset, white-shouldered marmoset (Figs. 90 and 91), squirrel monkey, spider monkey, vervet, rhesus macaque, Celebes ape, Anubis baboon, lutong, and others (Wislocki, 1936; Hill, 1958). As Hill (1958) states: "A specialization of the epithelium of the glans, or of the pars intrapraeputialis of the corpus, or both, is the tendency for local keratinization giving rise to horny papillae (e.g., in langurs), spicules (e.g., in the chimpanzee) or even quite large recurved hooks (e.g., in Galagidae and Indriidae)." Comparable keratinized spines were histologically

demonstrated on the glans penis of the howler monkey and stump-tailed macaque (Machida and Giacometti, 1967).

The profusion of subepidermal and periadnexal, alkaline phosphatase-reactive blood capillaries in the silver marmoset--unlike the relative avascularity of prosimians and scanty supply of many ceboids--approximates the cutaneous vasculature of the cercopithecoids and hominoids. But it is not a honeycombing of subepidermal venous sinuses, like that illustrated in the sex skin of the macaques (Perkins, Arao and Dolnick, 1968) and cephalic skin of the uacari, that imparts the crimson color to the face, external ears, and anogenital region of the silver marmoset; rather, it is the combination of an exceedingly thin epidermis and dermis, which is amelanotic and sparsely haired, that rests upon a copious bed of blood vessels and subcutaneous fat.

Machida, Giacometti and Allegra (1967) described the papillary nerve end-organ in the skin of subhuman primates: "Five of 49 species of primates studied--the mangabey (Cercocebus atys), stump-tail macaque (Macaca speciosa), tarsier (Tarsius syrichta), squirrel monkey (Saimiri sciureus), and silvered sakiwinki (Pithecia monachus)--have butyryl-cholinesterase-rich nerve end-organs at the base of the epidermal ridges in the fingerball." The red uacari and 2 species of capuchins were listed among the primates that did not possess these Merkel's disk-like end-organs. In addition to the white-crowned mangabey (Machida, Perkins, Montagna and Giacometti, 1965), stump-tailed macaque, Philippine tarsier, squirrel monkey, sakiwinki (Perkins and Ford, In Prep.), and present study, papillary nerve end-organs have also been described and illustrated in the red uacari and white-browed capuchin. In all

of these species, such nerve end-organs contain not only intense reactivity for butyrylcholinesterase but also moderate reactivity for acetylcholinesterase; they are confined not to the fingerball but to all volar friction surfaces. The possibility that papillary nerve end-organs have previously escaped detection because they were masked by the accumulation of melanin warrants more detailed investigation.

One of the outstanding features of the skin of the silver marmoset is an extensive neurovascular plexus that accompanies the hair follicle in all hirsute body regions. Particularly well-defined in the scalp, eyebrow, cheek, chest, belly, back and tail, such plexuses consist of the following components: 1) numerous afferent and efferent nerve fibers, 2) a hair follicle nerve end-organ, 3) one to 3 flat, organized subepidermal nerve endings, 4) a somewhat thickened epidermis adjacent to the pilary orifice on the obtuse-angled side of the hair follicle, and 5) a vascular plexus that shares the tissue immediately subjacent to the epidermal thickening with the largest of the subepidermal neural end-plates. The latter 3 components are identical to those described by previous authors (Pinkus, 1904; Tamponi, 1939) and constitute the Haarscheibe of Pinkus. Unlike the tylotrich follicle (Straile, 1960; In Press), the tactile follicle complex of the silver marmoset lacks an annular component (smooth muscle-like band of cells, annulus, vascular capillary ring, annular nerve, and annular sheath). Of all the subhuman primate integuments studied, that of the silver marmoset contains the most frequently occurring and histologically distinct Haarscheibe.

Several aspects of hair distribution and arrangement are frequently encountered in the skin of the Callithricidae: linear perfect sets of hairs are characteristic of the family; the grouping of hair follicles on the cheek recalls similar observations made in the red-mantled tamarin and white-shouldered marmoset--genal hairs grow singly in other primates that have been studied; an abundance of the cephalically located sinus hairs is shared by all Callithricidae; and the ulnar vibrissae are a distinctive feature that the silver marmoset, red-mantled tamarin, pigmy marmoset, white-shouldered marmoset, and cottontop pinché share only with the prosimian lemurs.

Another outstanding feature of the skin of the silver marmoset is the localization of alkaline phosphatase-reactive cells on the outer root sheath and epithelial sac of active and quiescent hair follicles. These amelanotic, stout, stellate cells are confined to the cephalic and ulnar body regions. They cannot be demonstrated with the routine ammoniacal silver, osmium iodide, or gold chloride techniques; histochemically, they resemble those cells that were formerly thought to be unique to the African Lorisidae (Machida, Perkins and Giacometti, 1966). The role of these cells awaits investigation. If the alkaline phosphatase-positive cells of the silver marmoset are comparable in lineage to those of the prosimian lorisines (cf. Kechijian, 1965), the knowledge of their presence in anthropoid skin may shed light on their phylogeny and function.

The peripheral acini of larger sebaceous glands contain moderate amounts of alkaline phosphatase, like those of the red-mantled tamarin, woolly, golden spider, and squirrel monkeys. The unusual opacity of the

scrotum can be attributed to a widespread field of huge, multilobular sebaceous glands that reside beneath the thin, unpigmented epidermal surface.

Apocrine glands are distributed throughout the hairy skin of the silver marmoset; one gland is associated with each hair grouping over the general body surface. Notable variations of this ratio occur, however. The glands are relatively scarce on the head but occur in a 2-3:1 ratio with hair groupings on the chest. This sternal concentration of apocrine glands parallels 1) similar localizations in some of the New World tamarins, marmosets, capuchins, the owl monkey (Perkins, In Prep.), uacari, and titis (Perkins and Ford, In Prep.) and 2) the intermixed apocrine-eccrine sternal aggregations in some of the Old World macaques, baboons, and the Sykes' monkey. In the silver marmoset, the presence of 1 large apocrine gland with each hair follicle in the suprapubic skin is comparable to the inguinal gland of the relatively primitive potto; on the other hand, the ratio in the axilla resembles that of the gorilla and man (Montagna, 1964).

Eccrine sweat glands are confined to the volar friction surfaces of the silver marmoset, unlike all hominoids and cercopithecoids but like all ceboids (except the subfamilies Alouattinae and Atelinae), lorisoids, and lemuroids. The sporadic localization of glycogen and phosphorylase in the secretory segments of eccrine glomeruli is similar to that observed in the red uacari. The peculiar distribution of these glycolytic components remains inexplicable.

E. Callimico goeldii.

The results of the preceding histological and histochemical examination of the various aspects of the skin of C. goeldii concur with Thomas's conclusion (1913) that "On the basis of preserved skin, there is nothing sufficiently striking to distinguish this animal from a marmoset [Callithricidae]." However, several distinct cutaneous aspects do distinguish it from the family Cebidae.

Most hairy regions are characterized by an epidermis heavily laden with melanin and a dermis whose upper levels contain scattered numbers of melanotic melanocytes. This distinctive trait is shared with only 6 of 56 species of subhuman primates: the white-shouldered marmoset, pigmy marmoset, red-handed tamarin and Spix's pinché (Machida and Perkins, 1967), red-mantled tamarin, and cottontop pinché. Each of these species belongs to the family Callithricidae; the other 50 represent most prosimian families as well as tarsioids, other ceboids, cercopithecoids, and hominoids.

Except for the Philippine tarsier and silvered sakiwinki, only Goeldi's marmoset and all species of Callithricidae have a unique hair follicle grouping in the form of linear perfect sets. By contrast, the groupings of the Cebidae are generally in independent perfect lines; those of prosimians, in circular clusters; and those of the cercopithecoids and subhuman hominoids, in independent perfect or imperfect lines.

Delicate, subepidermal, cholinesterase-positive nerve fibers in the gular papillae of Goeldi's marmoset lend support to the possibility

that comparable papillae in the silver marmoset and red-mantled tamarin are tactile or sensory in function.

Although single tufts of sinus hairs occur on the flexor surface of the forearm of lemurs (Sutton, 1887; Pocock, 1918; Hill, 1953), circumscribed aggregations of sinus hair follicles per se are characteristically restricted to the ventral ulnar wrist of the tarsier (Arao and Perkins, In Press), Goeldi's marmoset, and all callithricids.

Basing their classification upon the gross morphology of the glandular sternal fields, Epple and Lorenz (1967) placed Aotus, Callimico, and 6 callithricid subgenera into 1 category and 9 genera of the family Cebidae into 6 other categories. The arrangement of the sternal gland of a tamarin, marmoset, or pinché is distinctive; that of Callimico has each of the 3 typical components described by Epple and Lorenz and is indistinguishable from the callithricid-type marking gland. Similarly, the anogenitopubic glandular field of Callimico most closely resembles that of a callithricid.

The eccrine sweat glands of Callimico, like those of all Cebidae (except the prehensile-tailed monkeys) and all Callithricidae, are confined to the volar friction surfaces. The secretory epithelium of C. goeldii, unlike that of all Cebidae, contains no glycogen; in this respect, Goeldi's marmoset resembles only the red-mantled tamarin and cottontop pinché of the callithricid genus, Saguinus.

Pocock's original (1920) suggestion that Callimico be treated as a subfamily of the Callithricidae (=Hapalidae) is substantiated by the foregoing cutaneous traits and by a recent karyological survey (Egozcue, Perkins and Hagemenas, In Press): "From a chromosomal point

of view, C. goeldii is more related to Saguinus and consequently to Callithrix and Leontideus than to any other ceboid studied."

III. Phylogenetic Trends in the Skin of the Superfamily Ceboidea.

Although available materials were sufficient to constitute the nucleus of our knowledge about the skin of New World monkeys, they were not adequate enough to comprise its other organelles, cytoplasm, or external limiting membrane. Consequently, notwithstanding the author's awareness of the dangers inherent in generalization, many of the following cutaneous traits and trends must be treated in terms of generality.

By way of introduction, some of the major diagnostic skin characteristics of each of the 8 monophyletic taxa have been itemized in Table 14. Much of this data was obtained in earlier studies by other authors; however, it is presented here in order that the reader be able to more fully appreciate the distinctive combination of cutaneous traits that denotes each taxon. A careful examination of skin characteristics--such as the abundance of apocrine glands, the degree of epidermal and dermal development, the distribution of eccrine sweat glands, and the type of hair follicle grouping--reveals that the 8 taxa may generally be reduced to 4 distantly related taxa, on the basis of their common integumental traits: the Prosimii, Ceboidea, Cercopithecoidea, and Hominoidea. It will also be noted that the superfamily Ceboidea contains a highly variable number of cutaneous traits, many of which its members share with other non-ceboid taxa. For example, most subhuman monophyletic taxa can be characterized by 1 type of

hair grouping configuration; the Ceboidea contain at least 5. Generally, each member in the other taxa is pigmented like all other members in its taxon; it may contain variable numbers of melanocytes in either its dermis or epidermis, or it may contain none at all. In the Ceboidea, however, melanocytes are almost always present and occur in any combination; small or large numbers may reside in the epidermis, the dermis, or both layers (Tables 13 and 14).

Can an orderly relationship be formulated by a cutaneous study of such a variable taxon as the New World monkeys? Would a subdivision of the Ceboidea into smaller groups with the subsequent assessment of their cutaneous properties be useful? Would such findings substantiate or negate current taxonomic practices and phylogenetic concepts? In other words, can a cutaneous survey be a valid and useful tool to such ends? The following discussion of cutaneous traits within the genera, subfamilies, and families of the Ceboidea provides affirmative answers to each of these questions.

The synonymic reductions of the genera [Hapale], [Mico], and [Cebuella] to Callithrix by Simpson (1945) and [Tamarin], [Tamarinus], and [Oedipomidas] to Saguinus by Hershkovitz (1958)[1] are substantiated by an appraisal of the cutaneous characteristics of these respective taxa (Table 12). Within limits, their degrees of homology are proportional to their degrees of affinity. A comparison of the following cutaneous data also indicates that the genera Callithrix and Saguinus

[1]Hershkovitz also placed [Marikina] under the genus Saguinus and treated Leontideus as the third callithricid genus. Examples of neither taxon were available for inclusion in the present survey, however.

are quite distinct. Members of the genus Callithrix are characterized by widespread but relatively inconspicuous sternal glands; admixed suprapubic glands, predominantly apocrine in type; slight or moderate epidermal, dermal, and adnexal pigmentaion; commonly occurring penile spines; sebaceous glands that lack glycogen and phosphorylase; eccrine secretory epithelium that contains moderate phosphorylase activity, and glycogen (when present) that concentrates in the dark cells. By contrast, members of the genus Saguinus possess well-developed, prominent sternal glands; admixed suprapubic glands that are predominantly sebaceous in type; intensely pigmented skin and appendages; an absence of penile spines; large sebaceous glands that contain both glycogen and phosphorylase in their peripheral acini; and eccrine secretory epithelium, which contains neither phosphorylase nor glycogen.

Another outcome of this study is the more detailed appraisal of that position assigned the taxonomically long-disputed Callimico goeldii. By cutaneous definition, it must be considered a member of the family Callithricidae, not the family Cebidae (Table 13); more specifically, it most closely resembles the genus Saguinus (Table 12). The cutaneous traits of Goeldi's marmoset are so influential that the author has taken the liberty to place it in the family Callithricidae—in this, a cutaneous study. Certainly the cheiridia and recent karyological evidence support this action but the cebid-like skull and dentition cannot be ignored. At best, C. goeldii should be designated incertae sedis; it should not, however, be considered a member of the family Cebidae, as is the present practice.

It will be recalled that Simpson (1962) suggested that the subdivision of New World monkeys into 2 closely related families may only exaggerate their differences. The findings of this study suggest that Swainson (1835) and Thomas (1903) would have been even more sure of their familial designations (Cebidae and Callithricidae, respectively) had they been aware of the dissimilar cutaneous qualities possessed by the cebids and callithricids (Table 13).

The skin of the marmosets, tamarins, and pinchés (family Callithricidae) may be distinguished from that of the Cebidae and all other primates by the following cutaneous characteristics:[1] abundant epidermal melanin, concomitant with scattered melanocytes in upper dermal levels; diminished epidermal monoamine oxidase activity [Pithecia]; grouped hairs often present on cheeks [Pithecia]; eccrine glands confined to friction surfaces (except Saguinus fuscicollis) and apocrine glands common throughout entire hairy skin, but often quantitatively diminished or totally absent on dorsum [Pithecia]; eccrine clear cells always, and dark cells frequently devoid of glycogen; grouped sinus hairs on ventral ulnar wrist [Tarsius and Lemur]; "tactile" papillae often present in specialized regions; prominent sebaceous-apocrine suprapubic glands [Perodicticus]; extensive or well-developed apocrine sternal glands [Tarsius and Aotus]; and hair follicles arranged in linear perfect sets [Pithecia and Tarsius].

A comparison of cutaneous traits also affords perspective regarding hierarchy within the family Callithricidae. For example, the

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[1]Occasionally, non-callithricid or non-ceboid genera may share some of these characteristics; such genera are then indicated in brackets.

absence of glycogen and phosphorylase in sebaceous glands, absence of dorsal sweat glands, confinement of eccrine glands to volar friction surfaces, thinner epidermis and more poorly-developed dermis, occurrence of alkaline phosphatase-positive cells, scant adnexal blood supply, and paucity of elastic fibers are all cutaneous traits that characterize the genus Callithrix as the least advanced of the callithricid genera.

The study of cutaneous properties also permits a comparable characterization and appraisal of each of the 5 subfamilies of the Cebidae. Because the cebid integuments were not described in detail, however, it would be inept to expound upon their peculiarities; instead, their outstanding characteristics have been listed in Table 13, where they may be compared with those of other cebids and also the callithricids. Suffice it to say that, within the family Cebidae, the cutaneous characters of any 1 genus in a given subfamily more closely resemble those of another genus in that subfamily than they do genera of other subfamilies. For example, the hair follicle groupings of Saimiri and Cebus (subfamily Cebinae) are both in the form of independent perfect lines, whereas those of Aotus and Callicebus (subfamily Aotinae) are both arranged in circular clusters. Similarly, Ateles and Lagothrix (subfamily Atelinae) both possess glabrous prehensile tails; Cacajao and Pithecia (subfamily Pitheciinae) are both distinguished by poorly differentiated eccrine sweat glands. At this point it should be noted that the subfamilies Aotinae and, to a lesser extent, Pitheciinae--on the basis of their integumental characteristics--are certainly the most primitive of the Cebidae; in many ways, their cutaneous signatures

more closely resemble the family Callithricidae than they do other subfamilies of Cebidae.

It would therefore be tempting to fashion the following evolutionary schemata: North American prosimian ancestors invaded South America, giving rise to the Aotinae. From the Aotinae arose the Callithricidae and Pitheciinae. The family Callithricidae, which closely resembled the Callithrix grade of organization, progressed to the Saguinus, Leontideus, and Callimico groups; the subfamily Pitheciinae served as the common ancestral form for the remaining Cebidae, i.e., Cebinae, Atelinae, and Alouattinae. A second possibility is that the Pitheciinae, having arisen from the Aotinae, produced 2 divergent lineages: on the one hand, the Callithricidae (including Callimico)—their archetype being Pithecia, on the other, the Cebinae, Atelinae, and Alouattinae--their archetype being Cacajao. The latter scheme is particularly attractive in light of what may well be the single most reliable and constant cutaneous characteristic: the configuration of hair follicle groupings.

Modern prosimians (superfamilies Lemuroidea and Lorisoidea) are all characterized by circular, clustered hair follicle groupings (Perkins et al., In Press). So too are the Aotinae, which are generally believed to be descended from North American prosimian ancestors during the Eocene. The subfamily Pitheciinae contains 3 extant genera: Pithecia, Chiropotes, and Cacajao. Pithecia (the proposed progenitor of the Callithricidae), like the marmosets, tamarins, and pinchés, possesses linear perfect sets of hair follicles; Cacajao (the proposed progenitor of the Cebinae, Atelinae, and Alouattinae), like the squirrel

monkeys, capuchins, and howler monkeys, possesses hair follicles arranged in independent perfect lines.

The Atelinae do not adhere to this categorization, however: the genus Ateles possesses imperfect lines of hairs, whereas Lagothrix is distinguished by circular clusters of follicles. The former occurrence might be a mutation of the type that was independently acquired but more successful within the Cercopithecoidea and Pongidae. Linear imperfect hair follicle configurations characterize many members in the latter monophyletic taxa; in each of these cases, the trait appears to be a product of convergence. Because single characters can sometimes return to an ancestral condition and lost characters can be regained, the occurrence of circular clustered hairs in Lagothrix may also be explained away, based upon the principle of irreversibility, i.e., Dollo's law.

Of course, all of this is purely hypothetical and serves only to demonstrate to what extremes phylogenetic speculation may be carried. Homology and parallelism can be employed to reinforce or negate many phylogenetic proposals, and the latter may be as widely varied as the objective--or even subjective--characteristics upon which they are based. A positive quantitative correlation exists, concerning the quality of phylogenetic speculation: the more numerous and definable the characters, the more nearly valid the phylogenetic proposal.

Morphological parallelism sometimes occurs as a result of coincident convergence and homology. Arboreal brachiation is such an example; it can be very misleading. One who attempts to prove intimate affinity by equating such parallelism between the Ceboidea and Cercopithecoidea,

for example, is best recommended to an ophthalmologist because the single character or, at best, few characters upon which he is focusing would indicate that he is afflicted by tunnel vision. Should his optics be corrected, he would surely be able to view a wide variety of morphological, genetical, embryological, physiological, geographical, and ecological data--all of which, when taken into consideration, would serve as a warning sign to the precarious detour that he was on.

Because morphological data are the principal basis for the study of phylogeny and because palaeontology is one of the better bases for the phylogenetic interpretation of that morphology, palaeontological primate evidence will now be briefly discussed. The author trusts the subject matter will attest to the agreement that exists between modern theories of primate lineage and the preceding cutaneous findings.

Fossil evidence indicates that the early Tertiary prosimians radiated in the Paleocene, some 60 million years ago. The resulting prosimian forms became more highly diversified during the Eocene; some inhabited Madagascar, others ventured from North America into the tropics, and still others remained in the Old World. During the late Oligocene or early Miocene (25-35 million years ago), 4 distinct groups underwent adaptive radiation: the modern prosimians, including the Malagasy isolate; New World monkeys; Old World monkeys; apes and man (Simpson, 1949).

Prosimians, on the whole, are considered more primitive than other primates and are known to have originated first. Older prosimian forms include the tree shrews, bushbabies, lorises, and pottos; more recent forms include the lemurs of Madagascar and the tarsiers. Speaking

in very broad terms, the 3 remaining groups might generally be considered suitable for a hierarchal classification, which would be based upon their relative degrees of primitivity: e.g., because the Ceboidea retain 2 more premolars, they are "more primitive" than the Cercopithecoidea; the Cercopithecoidea, however, are less intelligent and still possess tails; therefore, they are "more primitive" than the Hominoidea. This type of reasoning--e.g., considering the morphological traits of New World monkeys to be between Prosimii and the Cercopithecoidea and Hominoidea--is, in a strict sense, full of pitfalls because the 3 groups did not arise one from another; rather, each originated separately, at an equivalent time in the Miocene radiation.

Of the 3 primate groups, fossil evidence is most wanting in the New World monkeys. Only 3 main Tertiary forms have been discovered: Homunculus (Ameghino 1891), Neosaimiri (Stirton 1951), and Cebupithecia (Stirton and Savage 1951). Each was unearthed in Colombia and dates to the late Oligocene or Miocene. Other than this evidence, which substantiates the fact that typically structured ceboids were in South America during this time, little is known about the history of the Ceboidea. It is presumed that their varied and successful divergence occurred exclusively in moist rain forests of South America, which climatically discourage the processes of fossilization. Hence, a clear view of the phylogeny of the New World monkeys has been obscured by an ever condensing tropical mist.

It has not been the purpose of this study to unravel the mystery of primate phylogeny, let alone ceboid phylogeny; but it is hoped that the additional morphological evidence presented herein will serve to better enhance the professional taxonomist's vista.

SUMMARY AND CONCLUSIONS

Because the results of this study have been presented and summarized in table-form, and their significance has already been considered and interpreted, the reader is referred to Tables 12-14 and the Discussion, respectively.

One may draw the following conclusions from this systematic comparative survey: (1) the results define a previously unestablished baseline regarding the normal histology and histochemistry of the skin of most genera and many species of New World monkeys; (2) because the New World species employed in this study represent those that are most commonly used in research, and because the abnormal cannot be interpreted without an appreciation of the normal, the results of this study are important and are now available to those investigators who are or will be engaged in experimental skin studies; (3) many previously unknown or unreported cutaneous modifications have been brought to light; (4) the present study substantiates the fact that intrageneric and intraspecific subtleties in cutaneous variation do exist in primate integument; (5) it has been demonstrated that single or multiple cutaneous traits enable the characterization and accurate identification of most levels of taxa within the hierarchy of the Order Primates; (6) some traits negate recent taxonomic practice, e.g., the position of Callimico goeldii; (7) many basic underlying cutaneous patterns exist that tend to confirm the currently accepted concepts of taxonomy and phylogeny; (8) the skin of the New World monkeys reflects their

history of adaptive radiation in isolation and suggests that the designation of 2 distinct families is warranted; and (9) the author has demonstrated that the combined histological and histochemical properties of a given cutaneous system are every bit as reliable criteria to the accurate assessment of a primate's taxonomy and phylogeny as are those other characters, classically employed by systematic zoologists (e.g., dentition, cheiridia, skeletal details, arthrology, myology, and splanchnology).

The preceding survey of cutaneous characteristics in the Callithricidae and Cebidae is far from complete. Cutaneous information regarding 2 of the 15 presently recognized genera of New World monkeys (Brachyteles and Leontideus) is totally lacking. However, even if these genera had been available, our knowledge would still have been fragmentary. Although certain underlying patterns lend a given species to a broader systematic classification, the total complement of its cutaneous traits serves only to set it apart from all other primates assigned a higher-ranking taxon. If more species had been available, the resulting study would have been more thorough, and its discussion more compendious. The present study, however, is a beginning. Much unexplored cutaneous territory lies ahead.

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TABLES

Table 1. Synoptic list of the prosimians.

Order PRIMATES (Linnaeus 1758)

Suborder PROSIMII (Illiger 1811)

Infraorder TUPAIIFORMES (Buettner-Janusch 1966)
Superfamily TUPAIOIDEA (Dobson 1882)
Family TUPAIIDAE (Mivart 1868)
Subfamily TUPAIINAE (Lyon 1913)
Tupaia (Raffles 1822)
glis (Diard 1820).....Common tree shrew

Infraorder LEMURIFORMES (Gregory 1915) [restricted]
Superfamily LEMUROIDEA (Mivart 1864)
Family LEMURIDAE (Gray 1821)
Subfamily LEMURINAE (Mivart 1864)
Lemur (Linnaeus 1758)
catta (Linnaeus 1758).....Ring-tailed lemur
macaco (Linnaeus 1766).....Black lemur
mongoz (Linnaeus 1766).....Mongoose lemur
Lepilemur (I. Geoffroy 1851).....Sportive lemur
Subfamily CHEIROGALEINAE (Gregory 1915)
Microcebus (I. Geoffroy 1828).....Mouse lemur
Family INDRIIDAE (Burnett 1828)
Indri (E. Geoffroy & Cuvier 1795).....Indris
Superfamily DAUBENTONIOIDEA (Gill 1872)
Family DAUBENTONIIDAE (Gray 1870)
Daubentonia (E. Geoffroy 1795).....Aye-Aye

Infraorder LORISIFORMES (Gregory 1915)
Family LORISIDAE (Gregory 1915)
Subfamily LORISINAE (Flower & Lydekker 1891)
Loris (E. Geoffroy 1796).....Slender loris
tardigradus (Linnaeus 1758)
Arctocebus (Gray 1863).....Angwantibo
calabarensis (J. A. Smith 1860)
Nycticebus (E. Geoffroy 1812).....Slow loris
coucang (Boddaert 1785)
Perodicticus (Bennett 1831).....Potto
potto (P. L. S. Müller 1766)
Subfamily GALAGINAE (Mivart 1864)
Galago (E. Geoffroy 1812).....Galago
crassicaudatus (E. Geoffroy 1812)...Great bushbaby
senegalensis (E. Geoffroy 1796)....Lesser bushbaby
demidovii (Fischer 1808).....Pigmy bushbaby

Infraorder TARSIIFORMES (Gregory 1915)
Family TARSIIDAE (Gill 1872)
Tarsius (Starr 1780)
syrichta (Linnaeus 1758).....Philippine tarsier

Table 2. Synoptic list of the New World cebids (superfamily Ceboidea).

Order PRIMATES (Linnaeus 1758)

Suborder ANTHROPOIDEA (Mivart 1864)

Infraorder PLATYRRHINI (Hemprich 1820)

Superfamily CEBOIDEA (Simpson 1931)

Family CEBIDAE (Swainson 1835)

Subfamily CEBINAE (Mivart 1865)

- Cebus (Erxleben 1777).....Capuchin monkey
  - albifrons (Humboldt 1811).....White-browed capuchin
  - apella (Linnaeus 1758).....Black-capped capuchin
  - capucinus (Linnaeus 1758).....White-throated capuchin
- Saimiri (Voigt 1831).....Squirrel monkey
  - sciureus (Linnaeus 1758).....Common squirrel monkey

Subfamily ALOUATTINAE (Elliot 1904)

- Alouatta (Lacépède 1799).....Howler monkey
  - caraya (Humboldt 1812).....Carayanese howler monkey

Subfamily ATELINAE (Miller 1924)

- Ateles (E. Geoffroy 1806).....Spider monkey
  - geoffroyi (Kuhl 1820).....Golden spider monkey
- Brachyteles (Spix 1823).....Woolly spider monkey
  - arachnoides (E. Geoffroy 1806)
- Lagothrix (E. Geoffroy 1812).....Woolly monkey
  - lagothricha (Humboldt 1811).....Humboldt's woolly monkey

Subfamily AOTINAE (Elliot 1913)

- Aotus (Humboldt 1811).....Douroucouli, owl monkey
  - trivirgatus (Humboldt 1811).....Three-banded night monkey
- Callicebus (Thomas 1903).....Titi monkey
  - moloch (Hoffmannsegg 1807).....Devil titi
  - torquatus (Hoffmannsegg 1807).....Necklaced titi

Subfamily PITHECIINAE (Mivart 1864)

- Pithecia (Desmarest 1804).....Sakiwinki
  - monachus (E. Geoffroy 1812).....Hairy sakiwinki
- Cacajao (Lesson 1840).....Uacari
  - rubicundus (I. Geoffroy & Deville 1848).....Red uacari
- Chiropotes (Lesson 1840).....Bearded saki

Subfamily CALLIMICONINAE (Thomas 1913)

- Callimico (Ribeiro 1911)
  - goeldii (Thomas 1904).....Goeldi's "marmoset"

Table 3. Synoptic list of the New World callithricids (superfamily Ceboidea).

Order PRIMATES (Linnaeus 1758)

Suborder ANTHROPOIDEA (Mivart 1864)

Infraorder PLATYRRHINI (Hemprich 1820)

Superfamily CEBOIDEA (Simpson 1931)

Family CALLITHRICIDAE (Thomas 1903)

- *Callithrix* (Erxleben 1777).....Marmosets
  - [=*Hapale*] (Illiger 1811).....Tufted-eared marmoset
    - *humeralifer* (E. Geoffroy 1812).White-shouldered marmoset
    - *jacchus* (Linnaeus 1758).....Common marmoset
  - [=*Mico*] (Lesson 1840).....Naked-eared marmoset
    - *argentata* (Linnaeus 1771).....Silver marmoset
  - [=*Cebuella*] (Gray 1866).....Pigmy marmoset
    - *pygmaea* (Spix 1823)
- *Saguinus* (Hoffmannsegg 1807)
  - [=*Tamarin*] (Gray 1870).....Black-faced tamarin
    - *midas* (Linnaeus 1758).....Red-handed tamarin
  - [=*Tamarinus*] (Trouessart 1899).....White-faced tamarin
    - *fuscicollis* (Spix 1823)
      - *illigeri* (Pucheran 1845).....Red-mantled tamarin
  - [=*Marikina*] (Lesson 1840).....Bald tamarins
  - [=*Oedipomidas*] (Reichenbach 1862).....Pinchés
    - *oedipus* (Linnaeus 1758).....Cottontop pinché
    - *spixi* (Reichenbach 1862).....Spix's pinché
- *Leontideus* (Cabrera 1956).....Golden lion-tamarins
  - [=*Leontocebus*] (Wagner 1839)

Table 4. Synoptic list of the Old World monkeys (superfamily Cercopithecoida), family Pongidae, and family Hominidae.

Order PRIMATES (Linnaeus 1758)

Suborder ANTHROPOIDEA (Mivart 1864)

Infraorder CATTARRHINI (Hemprich 1820)

Superfamily CERCOPITHECOIDEA (Simpson 1931)
Family CERCOPITHECIDAE (Gray 1821)
Subfamily CERCOPITHECINAE (Blanford 1888)
Cercopithecus (Brünnich 1772).....Guenon
aethiops (Linnaeus 1758).....Green monkey
mitis (Wold 1822).....Sykes' monkey
Cercocebus (E. Geoffroy 1812).....Mangabey
torquatus (Kerr 1792).....White-collared mangabey
atys (Booth 1956).....White-crowned mangabey
Macaca (Lacépède 1799).....Macaque
mulatta (Zimmerman 1780).....Rhesus macaque
nemestrina (Linnaeus 1766).....Pig-tailed macaque
speciosa (Cuvier 1825).....Stump-tailed macaque
Papio (Müller 1773).....Baboon
doguera (Pucheran 1856).....Dog-faced baboon
anubis (Fischer 1829).....Anubis baboon

Subfamily COLOBINAE (Elliot 1913)
Colobus (Illiger 1811).....Colobus monkey, guereza
Nasalis (E. Geoffroy 1812).....Proboscis monkey
Presbytis (Eschscholz 1821).....Langur, leaf monkey
cristatus (Raffles 1821).....Silvered leaf monkey
pyrrhus (Horsfield 1823).....Lutong

Superfamily HOMINOIDEA (Simpson 1921)

Family PONGIDAE (Elliot 1913)
Subfamily PONGINAE (Allen 1925)
Pongo (Lacépède 1799).....Orangutan
Pan (Oken 1816).....Chimpanzee
Gorilla (I. Geoffroy 1852).....Gorilla
Subfamily HYLOBATINAE (Gill 1872)
Hylobates (Illiger 1811).....Gibbon
hoolock (Harlan 1834).....White-browed gibbon

Family HOMINIDAE (Gray 1825)
Homo (Linnaeus 1758).....Man

Table 5. Body regions from which skin samples were routinely removed.

- Scalp
  - Forehead
  - Frontal
  - Temporal
  - Parietal
  - Occipital
- Face
  - Eyebrow (supraorbital)
  - Eyelids (upper & lower)
  - Lips (upper & lower)
  - External ear (pinna)
  - Nose (perialar)
  - Cheek (malar; genal)
  - Chin (mentum)
- Neck
  - Dorsal (cervical)
  - Ventral
    - Gular (interramal)*
- Back
  - Interscapular
  - Lumbar
- Tail
  - Hairy
    - Proximal (dorsal & ventral)
      - Subcaudal*
    - Distal (dorsal & ventral)
  - Glabrous prehensile*
    - Proximal (dorsal & ventral)*
    - Distal (dorsal & ventral)*
- Venter
  - Axilla
  - Chest
    - Manubrial (peristernal)*
  - Belly
    - Epigastric*
  - Posterior abdomen
    - Suprapubic (periinguinal)*
- Extremities
  - Thigh (lateral)
  - Ventral wrist
    - Radial papillae*
    - Ulnar gland*
  - Friction surfaces
    - Pes (sole & toe pads)
    - Manus (palm & fingerballs)
- Anogenital
  - Circumanal
  - External genitalia
    - (penis & scrotum)
    - (clitoris & labia pudendi)

*Asterisk denotes specialized region present only in certain species.

Table 6

Histochemical properties of the skin of Goeldi's marmoset.

	Epidermis	Dermis	Hair follicle	Sebaceous gland	Apocrine gland	Eccrine gland
Glycogen	- to +*	---	++ to +++	-	- to +*	- to +
Succinic dehydrogenase	+ to +++*	---	++	+ to ++	++ to +++	+++
Cytochrome oxidase	++	---	++	+++	+++	+++
Monoamine oxidase	+ to ++	---	++	+++	+ to +++*	+ to ++
Phosphorylase	-	---	+ to +++*	- to +++*	- to +*	++ to +++
Acid phosphatase	+ to +++*	---	++ to +++	++ to +++	+ to +++*	- to +
Alpha-naphthol esterase	+++	---	+++	+++	+ to +++*	+++
Alkaline phosphatase	-	---	- to +*	- to +++*	+ to +++*	-
Alkaline phosphatase in blood vessels	---	+++	+++	+ to +++*	+ to +++*	++
Acetylcholinesterase in nerves	---	++	++	+	+ to +++*	+++
Butyrylcholinesterase in nerves	---	+++	+++	++	+ to +++*	+

* Regional differences; -, negative; +, weak; ++, moderate; +++, strong; ---, not applicable.

Table 7

Histochemical properties of the skin of the pigmy marmoset

	Epidermis	Dermis	Hair follicle	Sebaceous gland	Apocrine gland	Eccrine gland
Glycogen	- to +*	---	++	-	-	++
Succinic dehydrogenase	++ to +++	---	+++	++	+++	+++
Cytochrome oxidase	++ to +++	---	+++	+++	+++	+++
Monoamine oxidase	+ to ++	---	++	++ to +++	+ to +++*	+
Phosphorylase	- to +	---	+++	-	- to +*	+++
Acid phosphatase	+++	---	+++	++ to +++	+	+
Alpha-naphthol esterase	++ to +++	---	+ to +++*	++	+	+
Alkaline phosphatase	-	---	++	-	-	- to +
Alkaline phosphatase in blood vessels	---	+ to +++*	+	- to ++*	++	+++
Acetylcholinesterase in nerves	---	+ to ++*	+	- to +*	-	+++
Butyrylcholinesterase in nerves	---	+ to ++*	-	- to ++*	- to ++*	-

* Regional differences; -, negative; +, weak; ++, moderate; +++, strong; ---, not applicable.

Table 8

Histochemical properties of the skin of the silver marmoset.

	Epidermis	Dermis	Hair follicle	Sebaceous gland	Apocrine gland	Eccrine gland
Glycogen	- to +	---	+++	-	-	- to +++
Succinic dehydrogenase	+ to ++*	---	+++	- to +	++ to +++	+++
Cytochrome oxidase	++	---	++	+++	+++	+++
Monoamine oxidase	+ to ++*	---	+++	+ to ++	+ to ++*	+
Phosphorylase	-	---	+++	-	-	- to +++
Acid phosphatase	+++	---	++ to +++	+ to ++	+ to ++*	+
Alpha-naphthol esterase	+++	---	++	+++	++	+ to +++
Alkaline phosphatase	-	---	+	+ to +++*	+ to ++*	+
Alkaline phosphatase in blood vessels	---	+ to +++*	+++	+++	+++	+
Acetylcholinesterase in nerves	---	+++	+ to +++*	- to ++*	-	+++
Butyrylcholinesterase in nerves	---	++	+ to +++*	- to ++*	-	+

* Regional differences; -, negative; +, weak; ++, moderate; +++, strong; ---, not applicable.

Table 9

Comparison of the two types of dendritic cells on the outer root sheath and epithelial sac of active and quiescent hairs in the silver marmoset.

	Melanotic Melanocytes	Alkaline Phosphatase Cells
General appearance	spider-like	stellate-shaped
Perikaryon	small	large
Dendrites	long, filiform	short, stout
Frequency of occurrence	rare	common
Body region distribution	dorsal	cephalic and ulnar
Location		
Anatomical landmark	at hair bulge	at or below level of hair follicle nerve end-organ
Relative to follicle	lateral to hair	encircle hair
Melanotic	+	-
Alkaline phosphatase-reactive	-	+
Argyrophilic	+	-
Osmiophilic	+	-
Aurophilic	-	-

Table 10

Histochemical properties of the skin of the red-mantled tamarin.

	Epidermis	Dermis	Hair follicle	Sebaceous gland	Apocrine gland	Eccrine gland
Glycogen	- to +*	---	++ to +++	- to ++*	-	- to +*
Succinic dehydrogenase	++ to +++	---	++ to +++	++ to +++	++ to +++	+++
Cytochrome oxidase	++ to +++	---	++ to +++	++ to +++	+ to +++*	+++
Monoamine oxidase	+ to ++*	---	++ to +++	++ to +++	+ to +++*	+
Phosphorylase	- to +	---	++	- to ++*	-	- to +*
Acid phosphatase	+ to +++*	---	- to +	- to ++*	-	- to +
Alpha-naphthol esterase	++ to +++	---	++ to +++	++ to +++*	+ to ++	+++
Alkaline phosphatase	-	---	+	- to ++*	++ to +++	+++
Alkaline phosphatase in blood vessels	---	++	++ to +++*	+ to +++*	+++	+++
Acetylcholinesterase in nerves	---	+++	+++	- to ++*	- to +++*	+++
Butyrylcholinesterase in nerves	---	++ to +++	++ to +++*	- to ++*	- to +++*	+

* Regional differences; -, negative; +, weak; ++, moderate; +++, strong; ---, not applicable.

Table 11

Histochemical properties of the skin of the cotton pinché.

	Epidermis	Dermis	Hair follicle	Sebaceous gland	Apocrine gland	Eccrine gland
Glycogen	- to +*	---	- to +++*	- to +*	-	-
Succinic dehydrogenase	++	---	++	+ to ++	++ to +++	+++
Cytochrome oxidase	++ to +++	---	++	+++	+ to +++*	+++
Monoamine oxidase	+ to ++	---	+ to ++	+ to ++	+ to +++*	+
Phosphorylase	- to +*	---	- to +++*	- to ++*	-	- to +++
Acid phosphatase	+ to +++*	---	++ to +++	++	+	-
Alpha-naphthol esterase	++ to +++	---	++ to +++	+++	+	+++
Alkaline phosphatase	-	---	+	-	+++	-
Alkaline phosphatase in blood vessels	---	+++	+++	+++	+++	+++
Acetylcholinesterase in nerves	---	+++	+++	+++	-	+++
Butyrylcholinesterase in nerves	---	++ to +++*	+	- to +	-	- to +

* Regional differences; -, negative; +, weak; ++, moderate; +++, strong; ---, not applicable.

Table 12. Comparative Cutaneous Characteristics of the Callithricidae.[1]

	C. pygmaea	C. humeralifer	C. argentata	S. fuscicollis	S. oedipus	C. goeldii
Amount of epidermal pigment	++	++	-	+++	+++	+++
Alkaline phosphatase cells	-	-	+	-	-	-
Penile spines present	-	+	+	-	-	-
"Tactile" papillae present	-	-	+	+	-	+
Amount of dermal pigment	+	+	-	+	++	+
Hair grouping [2]	LPS	LPS	LPS	LPS	LPS	LPS
Hairs grouped on cheek	-	+	+	+	-	+
Pigmented hair follicles	-	+	-	++	++	++
Ulnar vibrissae present	+	+	+	+	+	+
Glycogen and phosphorylase in sebaceous glands	-	-	-	+	+	+
Suprapubic gland[2]	S	A	A	S	S	S=A
Sternal gland development	±	±	±	+	+	+
Few apocrine glands dorsally	+	+	-	±	-	±
Pigmented apocrine glomeruli	-	-	-	+	±	-
Eccrine glands.....						
confined to friction surfaces	+	+	+	±	+	+
phosphorylase activity	+++	?	++	-	-	++
glycogen in clear cells	-	-	±	-	-	++
glycogen in dark cells	+	+	-	-	-	-

[1] The marmosets, tamarins, and pinchés are arranged according to their generic taxa: Callithrix to the left; Saguinus in the center; Callimico to the right.

[2] LPS, linear perfect sets; S, predominantly sebaceous; A, predominantly apocrine.

Table 13. Comparative Cutaneous Characteristics of the Ceboidea.[1]

	Callithrix	Saguinus	Callimico	Aotinae	Pitheciinae	Atelinae	Alouattinae	Cebinae
Prehensile tail, haired	-	-	-	-	-	-	-	+
Prehensile tail, glabrous	-	-	-	-	-	+	+	-
Epidermal MAO activity	+	+	+	++	+++	+++	+++	++
Epidermal thickness	-	-	-	-	-	+	+	-
Epidermal melanin	++	+++	+++	-	+	+++	+++	-
Dermal melanin	+	+	+	+	++	-	-	++
Well-developed dermis	-	-	-	-	-	+	+	-
"Tactile" papillae	±	±	±	-	-	-	-	-
Hair groupings[2]	LPS	LPS	LPS	CCI / CE	LPS / LPI	LI / CCI	LPI	LPI
Hairs grouped on cheek	+	+	+	-	±	-	-	-
Ulnar vibrissae	+	+	+	-	-	-	-	-
Suprapubic glands	+	+	+	-	-	-	-	-
Few apocrine glands dorsally	+++	+	+	-	+	-	-	±
Eccrine glands.....								
confined to friction surfaces	+	±	+	+	+	-	-	+
phosphorylase activity	++	-	++	+++	++	+++	+++	++
glycogen in clear cells	-	-	-	+	±	+	+	+
glycogen in dark cells	+	-	-	+	±	-	+	+

[1]The New World monkeys are arranged with the family Callithricidae to the left (generic taxa) and the family Cebidae to the right (subfamilial taxa).

[2]LPS, linear perfect sets; CCI, independent circular clusters; CE, elongated clusters; LPI, independent perfect lines; LI, imperfect lines.

Table 14. Comparative Cutaneous Characteristics of the Order Primates.[1]

	Tupaiiformes	Lemuriformes	Lorisiformes	Tarsiiformes	Ceboidea	Cercopithecoidea	Pongidae	Hominidae
Glabrous specializations[2]	-	-	-	-	PT	IC	-	-
Epidermal thickness	-	-	-	-	+	++	+++	+++
Alkaline phosphatase cells	-	-	+	-	±	-	-	-
Epidermal melanin	+	++	-	-	±±±	-	+++	+++
Dermal melanin	-	-	-	-	±±±	++	-	-
Adnexal blood supply	-	-	-	-	±	±	+	+++
Defined papillary body	-	-	-	-	-	±	+	++
Abundant elastic fibers	-	-	-	-	±	±	+	++
Hair groupings[2]	Rows	CCI	CCS	LPS	~	LPI	LI	~
Number of hairs per group	~	<24	<20	<9	~	< 7	< 5	~
Sinus hairs present	+	+	+	+	+	+	+	-
Ulnar vibrissae	-	+	-	+	+	-	-	-
Arrector pili muscles occur	+	-	±	-	+	+	+	+
Admixed suprapubic glands	-	-	±	-	+	-	-	-
Sebaceous gland size	-	++	-	-	±	+	+	+++
Numerous apocrine glands	+	++	++	++	+	±	-	-
Apocrine ducts open at[2]	PC	SS	SS	SS	PO	PO	PO	PC
Sternal apocrine glands	-	-	-	+	+	-	±	-
Axillary organ	-	-	-	-	-	±	+	++
Eccrine glands.....								
confined to volar surfaces	-	+	+	+	±	-	-	-
throughout hairy skin	+	-	-	-	±	+	++	+++
ratio to apocrine glands	E<A	-	-	-	E<A	E≤A	E≥A	E>A
differentiated secretory cells	-	-	±	-	±	+	+	+
phosphorylase and glycogen	+	+	±	+	±	+	+	+

[1]The 8 monophyletic taxa are arranged with the suborder Prosimii to the left (infraordinal taxa) and the suborder Anthropoidea to the right (superfamilial and familial taxa).

[2]PT, prehensile tails; IC, ischial callosities; CCI, independent circular clusters; CCS, circular clustered sets; LPS, linear perfect sets; LPI, independent perfect lines; LI, imperfect lines; PC, pilary canal; SS, skin surface; PO, pilary orifice.

MAPS & ILLUSTRATIONS

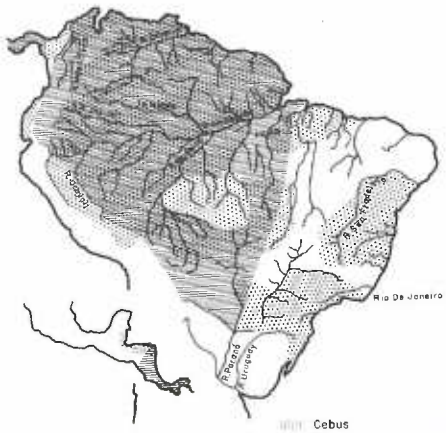
Map 1.
Distribution of
the Cebinae.

Map 2.
Distribution of
the Alouattinae.

Map 3.
Distribution of
the Atelinae.

Map 4.
Distribution of
the Aotinae
and Callimico.

Map 5.
Distribution of
the Pitheciinae.



Cebus
Saimiri

1

Alouatta

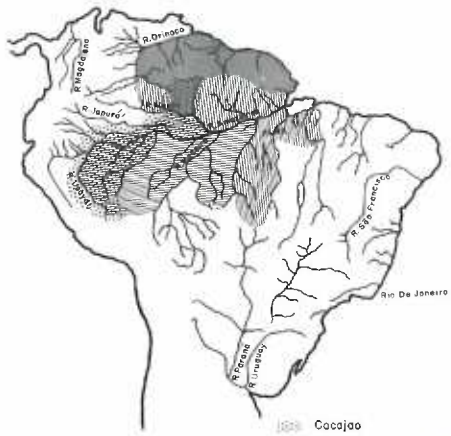
2

Ateles
Brachyteles
Lagothrix

3

Aotes
Callicebus
xxx Callimico

4

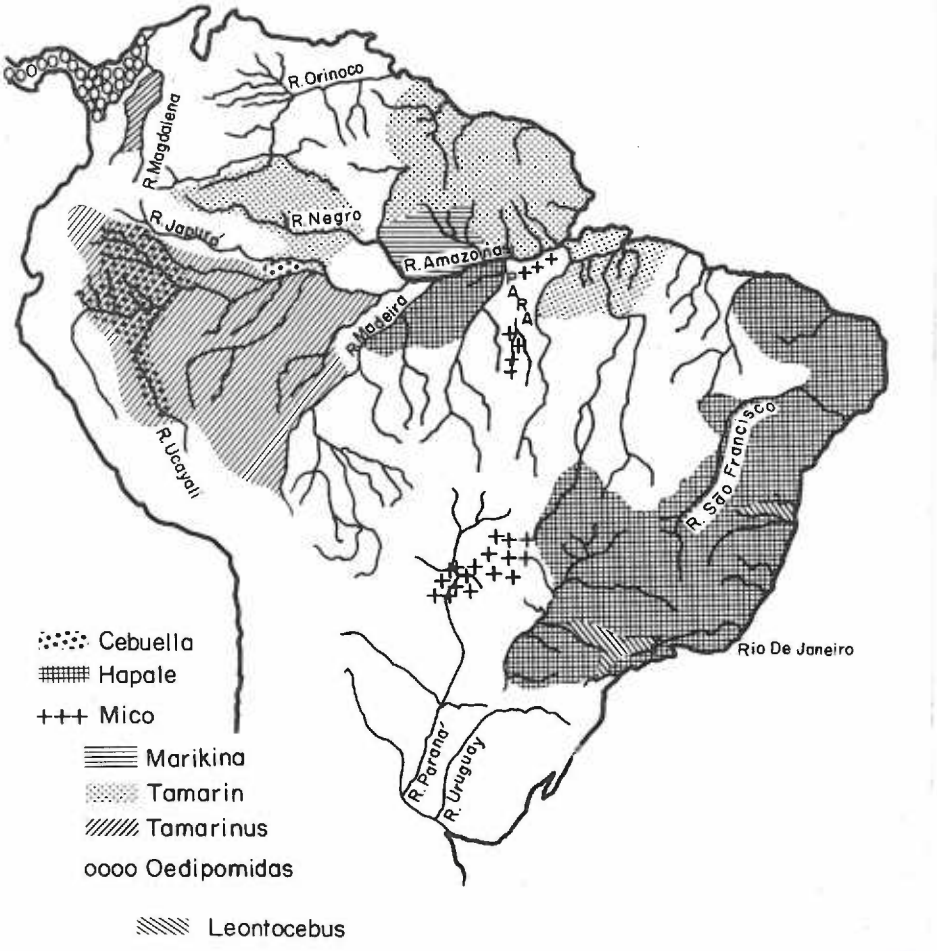


Cacajao
Pithecia
Chiropotes

5

Map 6.

Distribution of the 3 generic groups of the family Callithricidae: *Callithrix* (=*Cebuella*, =*Hapale*, =*Mico*); *Saguinus* (=*Marikina*, =*Tamarin*, =*Tamarinus*, =*Oedipomidas*); *Leontideus* (=*Leontocebus*).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R. Magdalena
R. Negro
R. Japurá
R. Amazonas
R. Madeira
R. Ucayali
R. São Francisco
Rio De Janeiro
R. Paraná
R. Uruguay
Cebuella
Hapale
Mico
Marikina
Tamarin
Tamarinus
oooo Oedipomidas
Leontocebus

Fig. 7.
Adult white-browed capuchin
(*Cebus albifrons*).

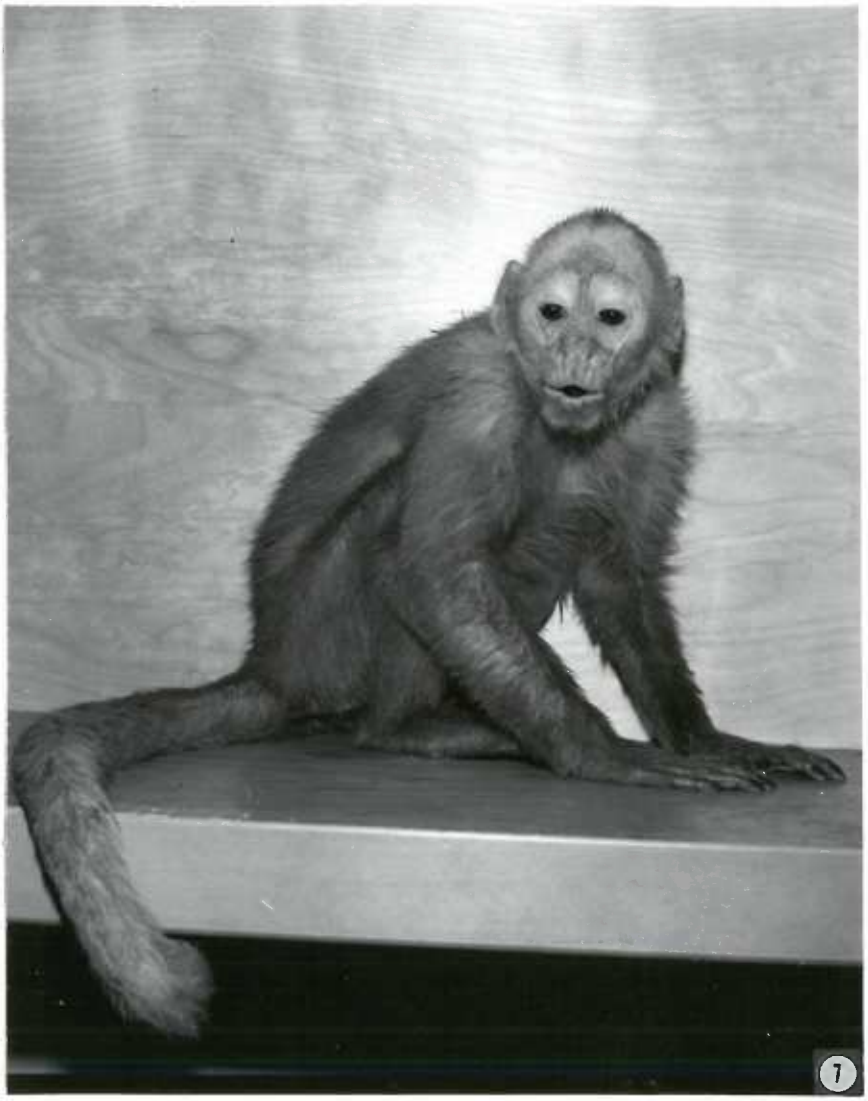
7

Fig. 8.
Adult squirrel monkey
(*Saimiri sciureus*).

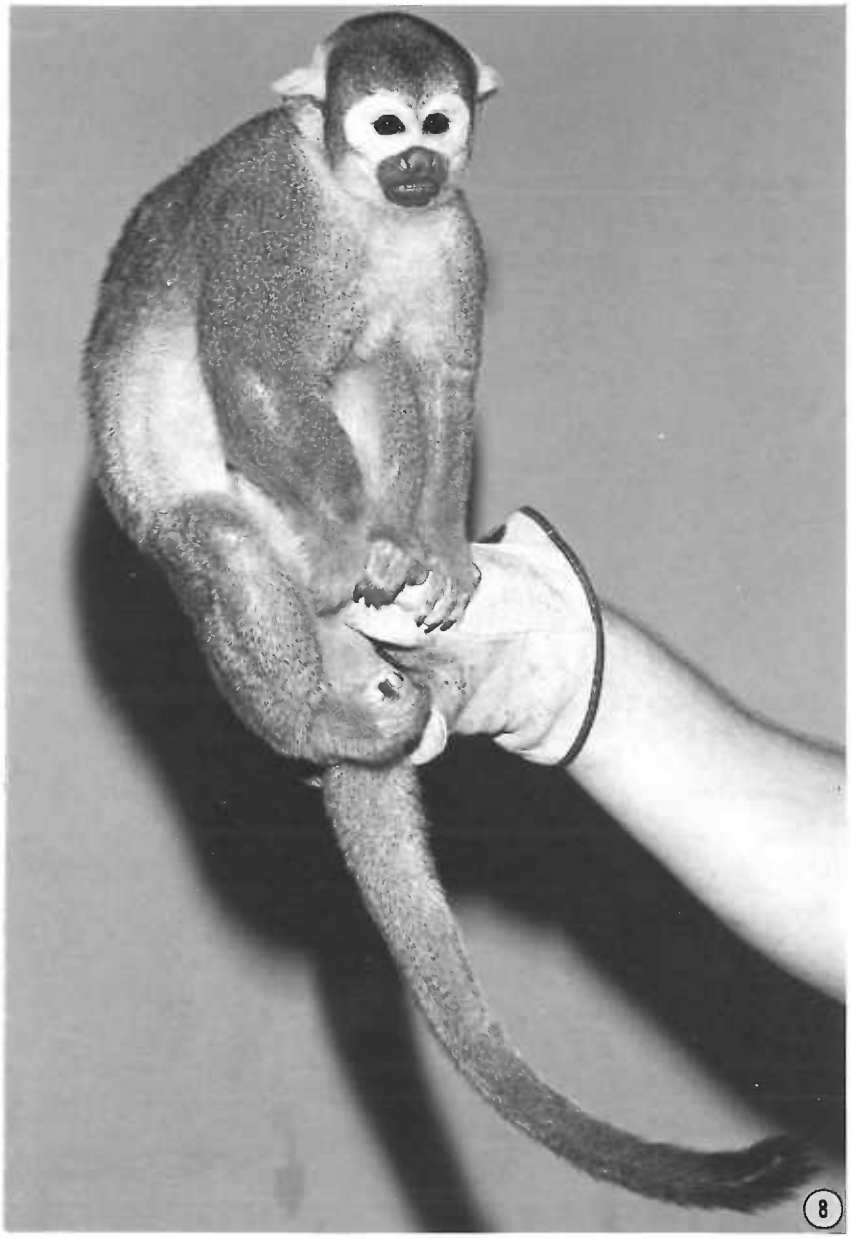
8

Fig. 9.
Adult howler monkey
(*Alouatta caraya*).

Fig. 10.
Adult golden spider monkey
(*Ateles geoffroyi*).


10

Fig. 11.
Adult woolly monkey
(Lagothrix lagothricha).

Fig. 12.
Adult owl monkey
(Aotus trivirgatus).

12

Fig. 13.
Adult silvered sakiwinki
(Pithecia monachus).

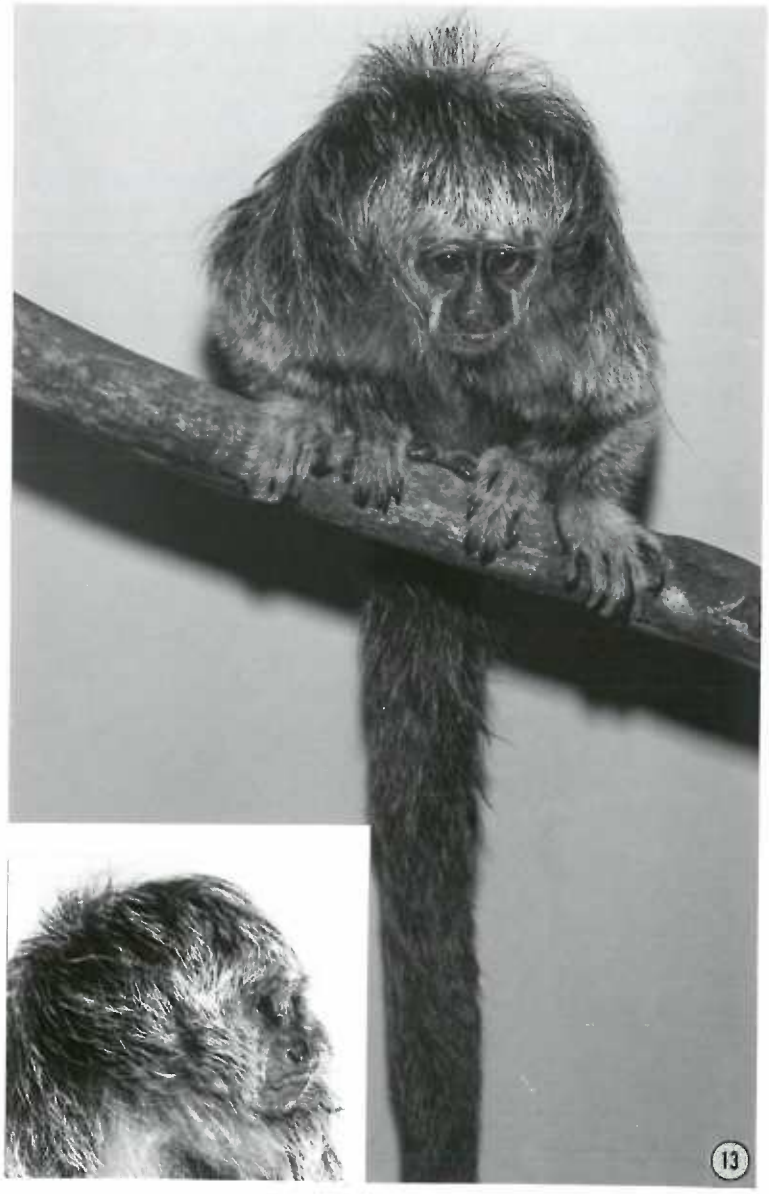

Fig. 14.
Adult red uacari;
inset depicts profile of juvenile.
(Cacajao rubicundus).

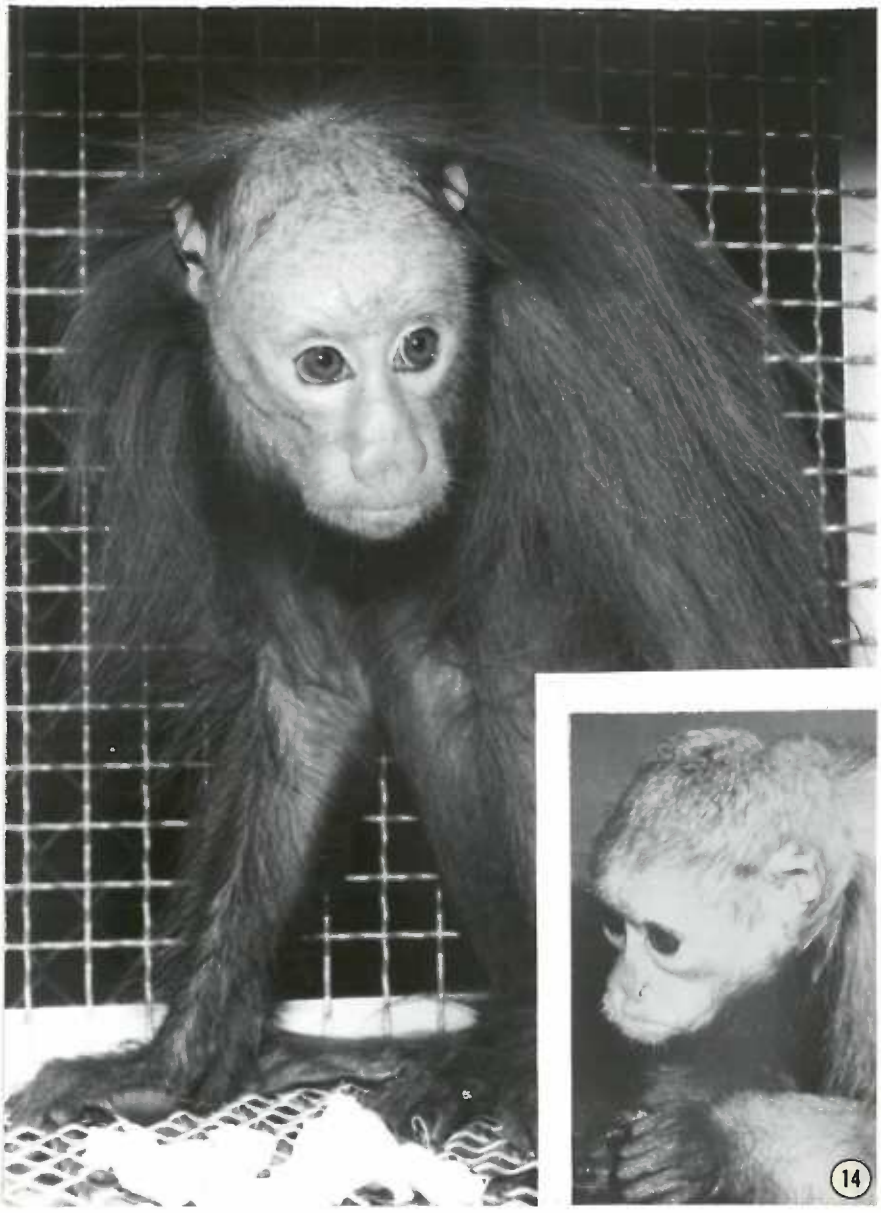
14

Fig. 15.
Adult Goeldi's marmoset
(Callimico goeldii).

15

Fig. 16.

Adult white-shouldered marmoset
(Callithrix [=Hapale] humeralifer).

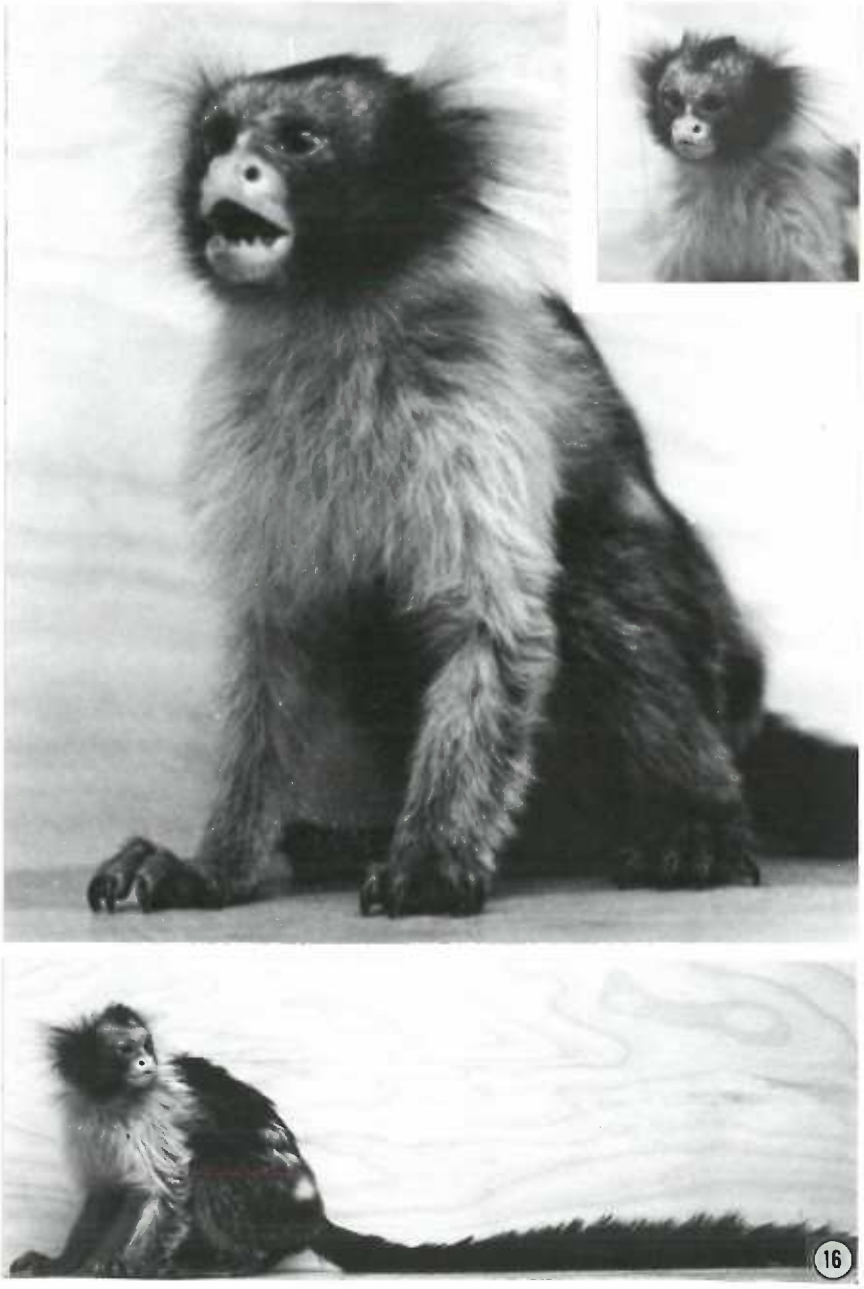

Fig. 17.
Adult silver marmoset
(*Callithrix* [=*Mico*] *argentata*).

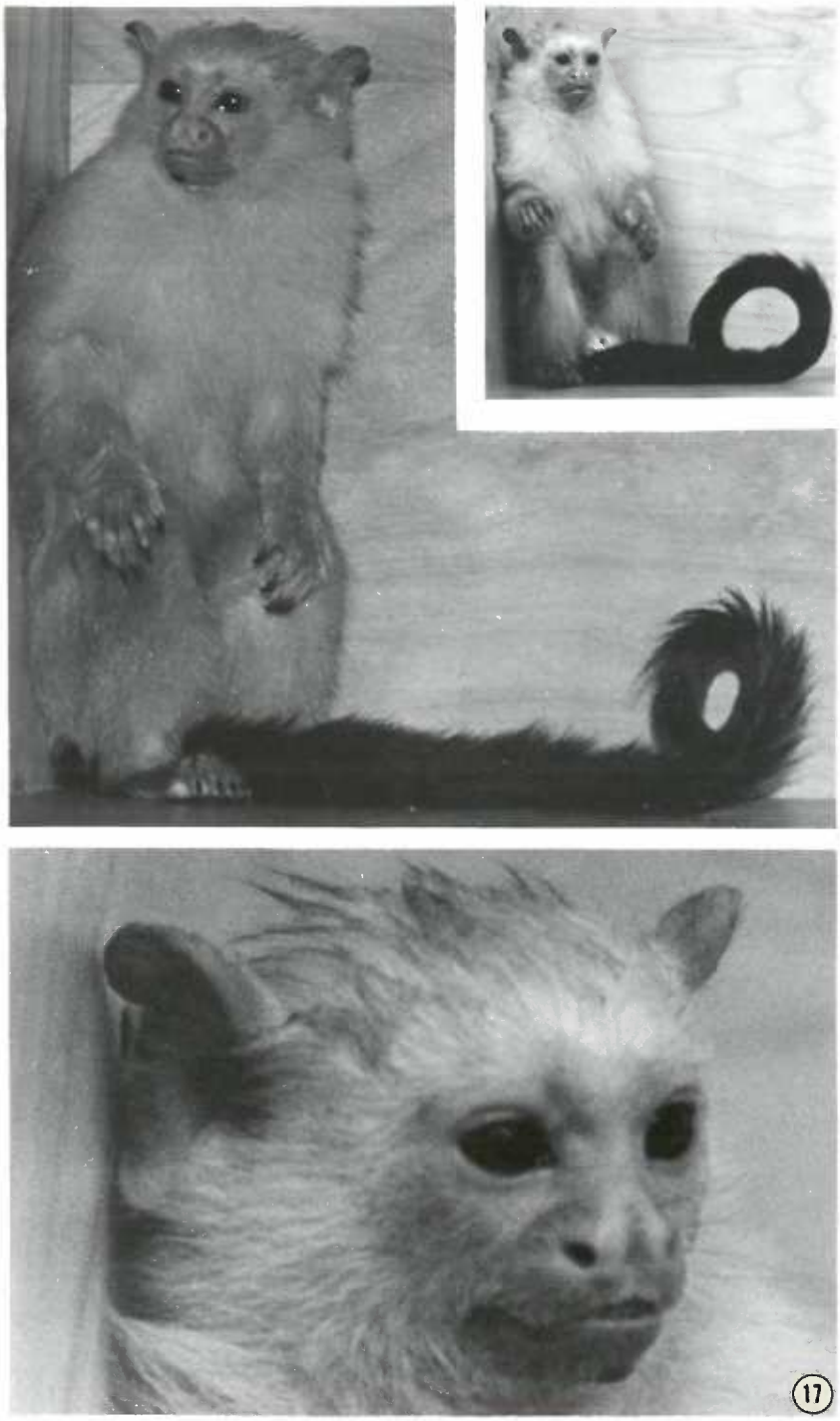

Fig. 18.
Adult pigmy marmoset
(*Callithrix* [=*Cebuella*] *pygmaea*).

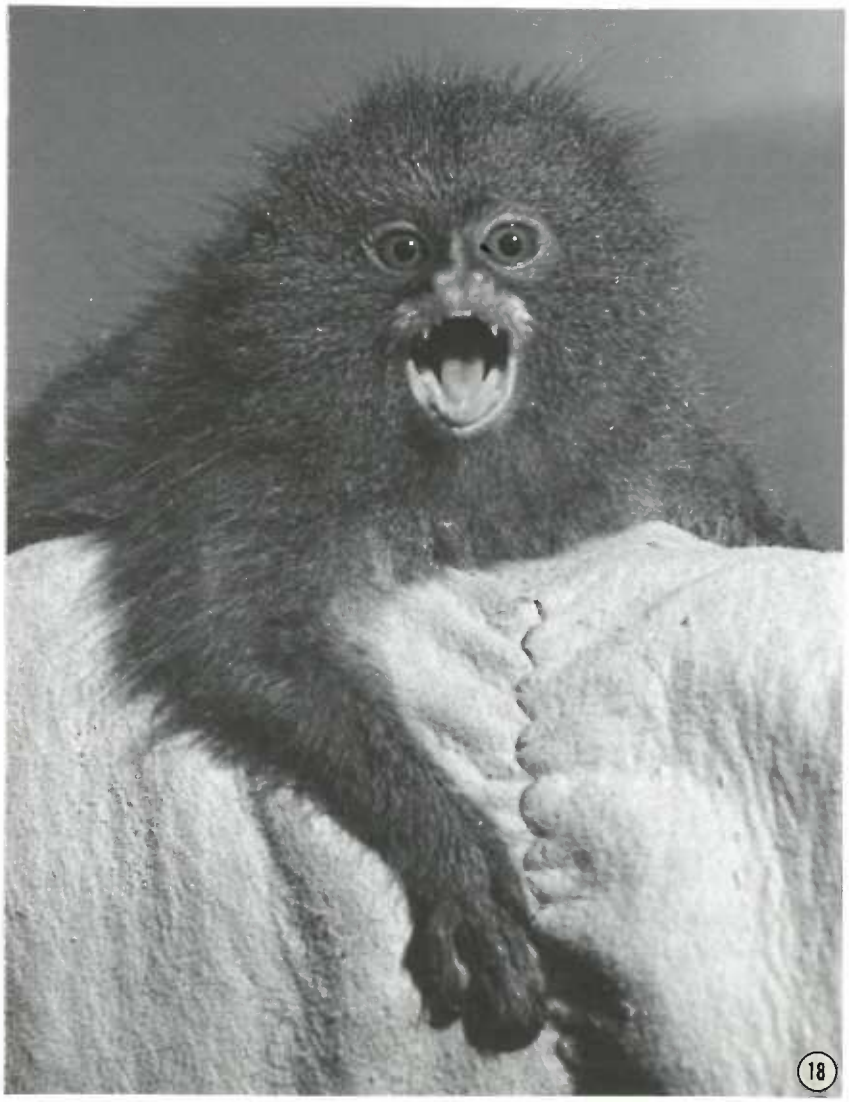
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Fig. 19.

Adult red-mantled tamarin

(Saguinus [=Tamarinus] fuscicollis illigeri).


19

Fig. 20.
Adult cottontop pinché
(Saguinus [=Oedipomidas] oedipus).

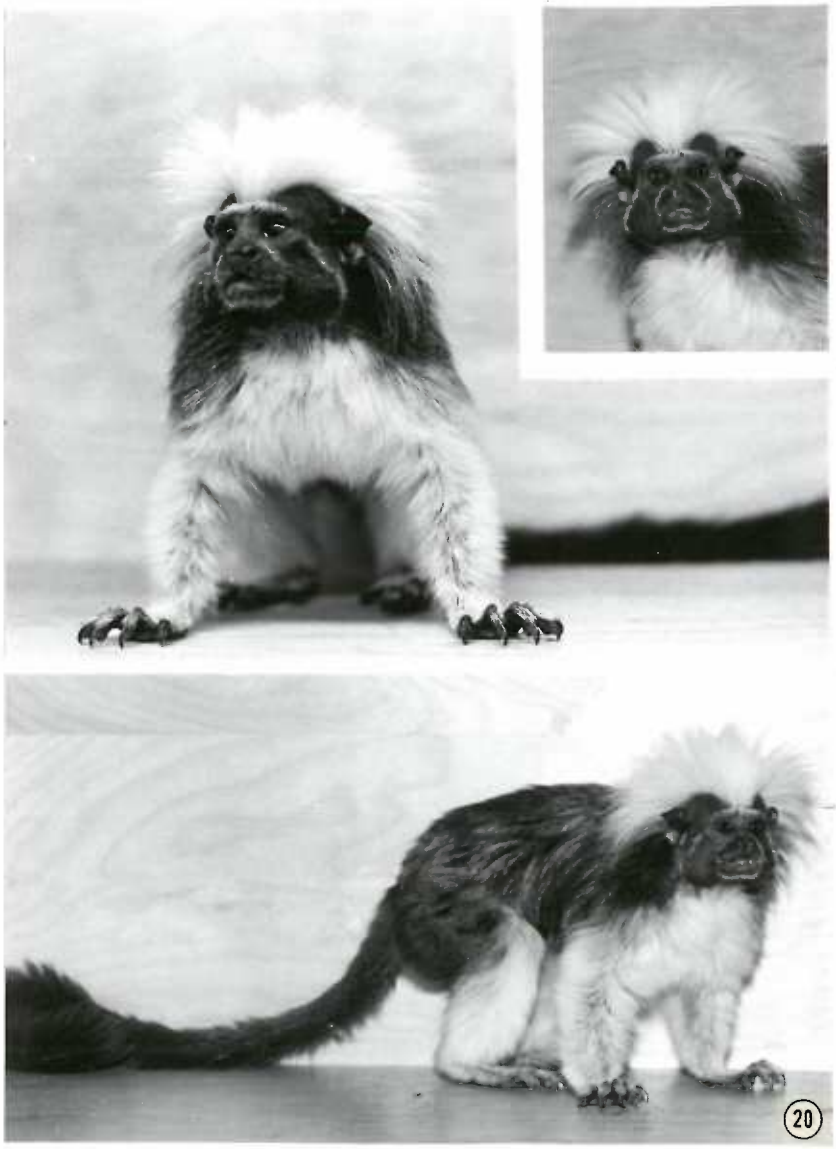
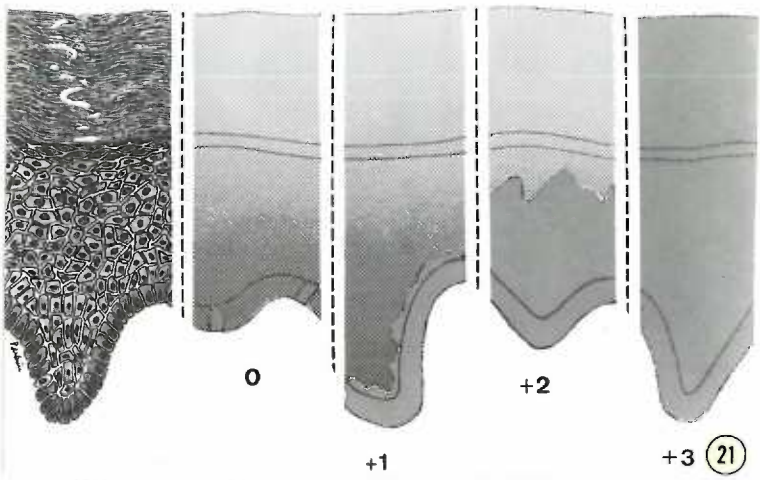


Fig. 21.
Distribution and gradation
of epidermal pigmentation.

Fig. 22.
Distribution and gradation
of dermal melanocytes.

Fig. 23.
Distribution and gradation
of hair follicle melanocytes.



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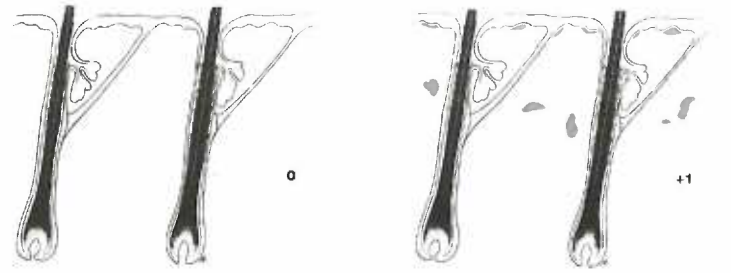

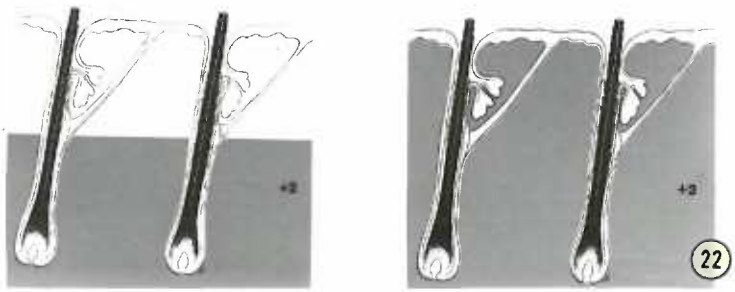

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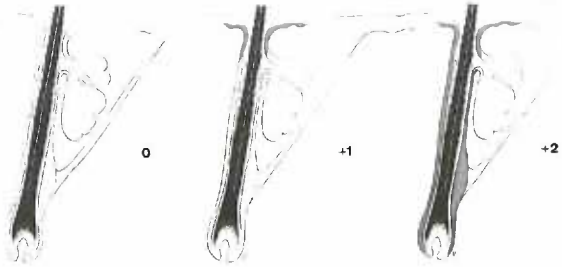
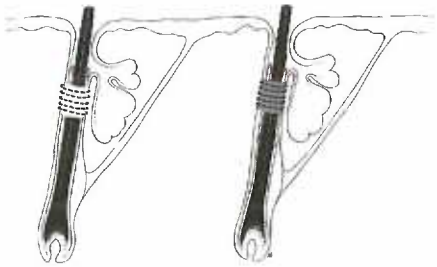


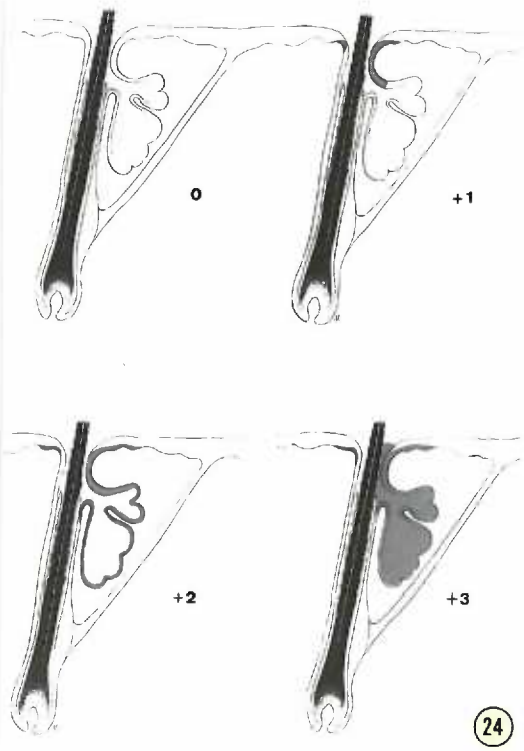


23

Fig. 24.
Distribution and gradation
of sebaceous gland pigmentation.

Fig. 25.
Disposition and gradation of
melanocytes about eccrine (above)
and apocrine (below) sweat glands.

Fig. 26
Schema of hair
follicle groupings.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+1
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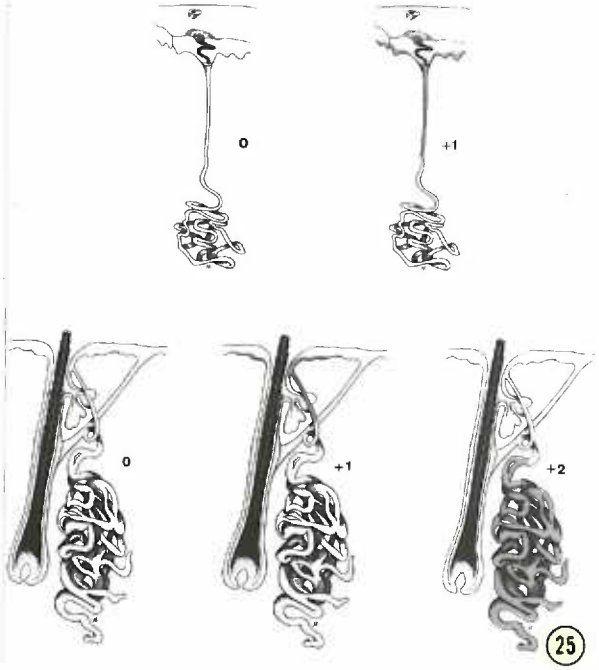
+3

24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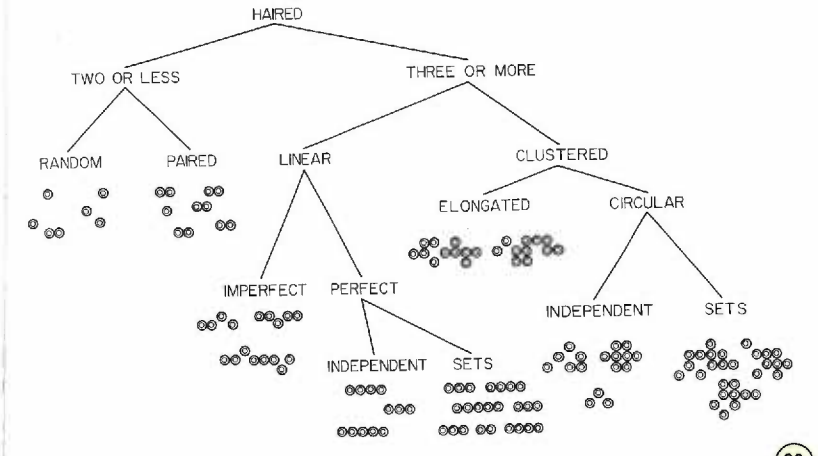

HAIRED
TWO OR LESS
THREE OR MORE
RANDOM
PAIRED
LINEAR
CLUSTERED
ELONGATED
CIRCULAR
IMPERFECT
PERFECT
INDEPENDENT
SETS
INDEPENDENT
SETS

26

Goeldi's marmoset (Callimico goeldii).

Fig. 27.

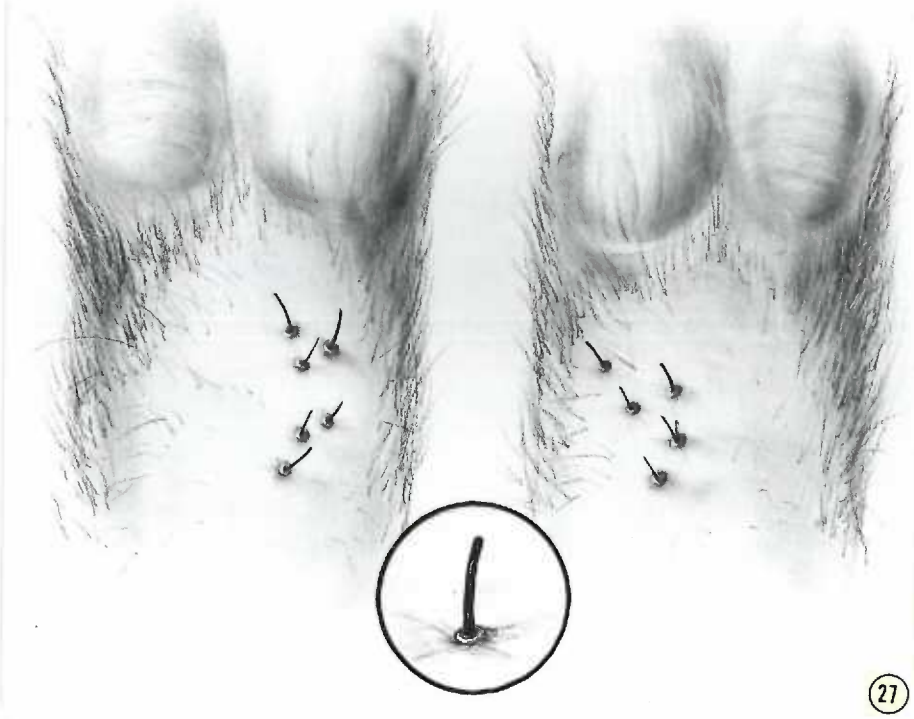
Artist's sketch of the arrangement of sinus hairs on the ventral ulnar aspect of each wrist; inset depicts large vibrissa arising from a shallow depression that is surrounded by a circumscribed elevation, 0.5 mm. in diameter.

Fig. 28.

Skin of modified, amelanotic gular region characterized by papillae-like surface folds and thickened epidermis. Alkaline phosphatase. ca. X 40.

Fig. 29.

Arrow denctes delicate, subepidermal, butyrylcholinesterase-positive nerve fiber in apex of one of the denticle-like surface modifications of the gular region. ca. X 170.



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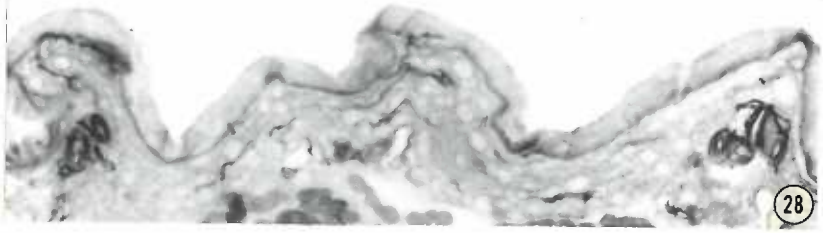

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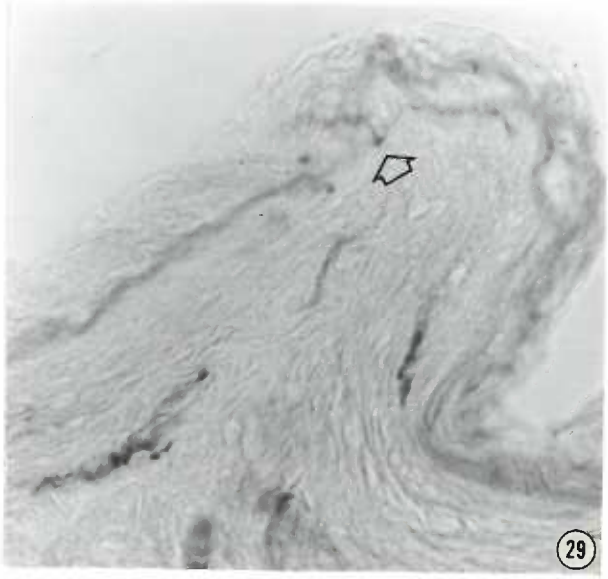


29

Fig. 30.

Glandular areas on the venter of the male:

A) Manubrial tuft;

B) Sternal field;

C) Belly;

D) Pubic region;

E) Scrotum.

Corresponding histologic preparations are treated for the demonstration of cytochrome oxidase. ca. X 25.

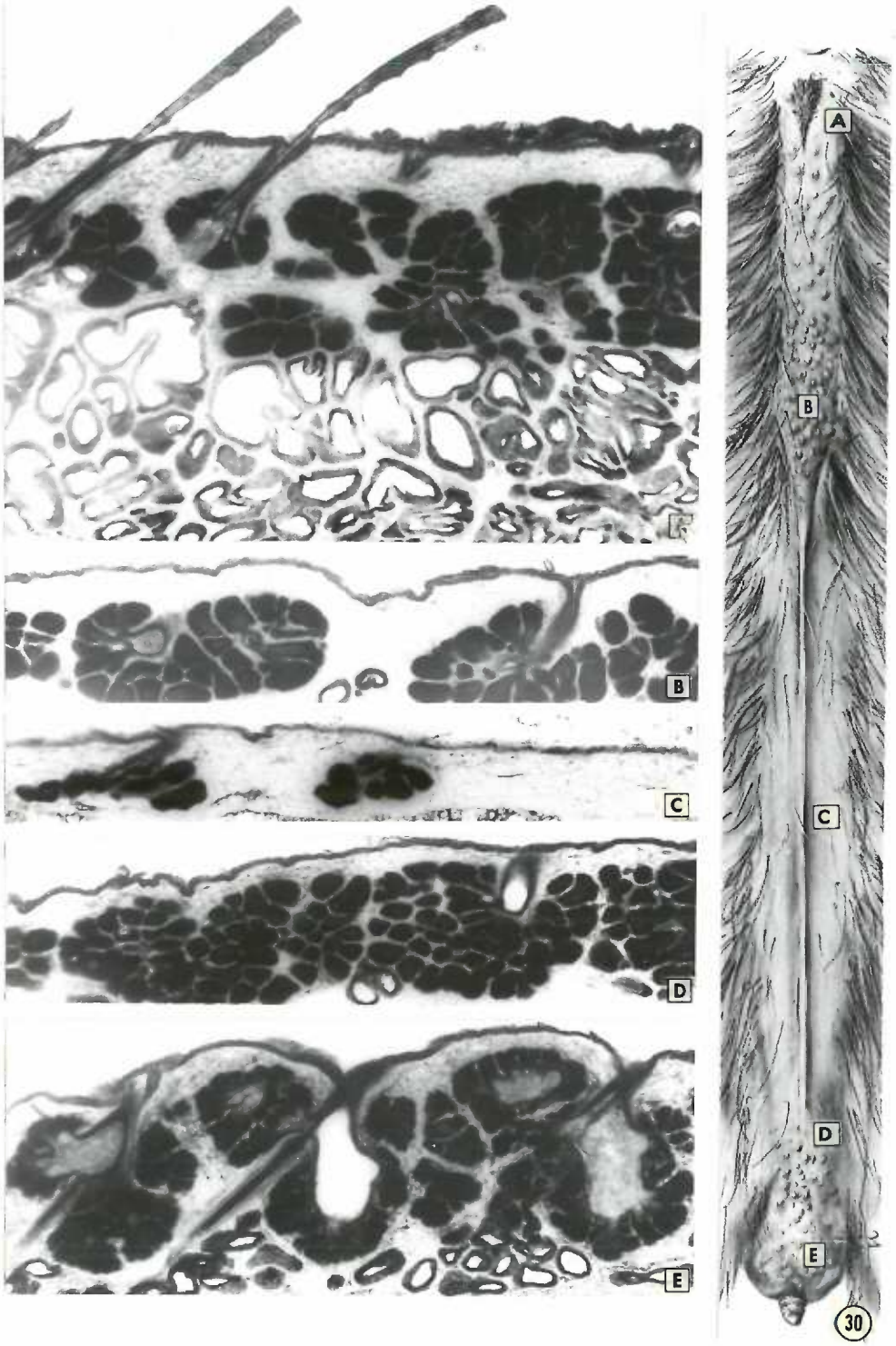

A
B
C
D
E
30

Fig. 31.

Glandular areas on the venter of the female:

A) Manubrial tuft;

B) Sternal field;

C) Belly;

D) Pubic region;

E) Labia pudendi.

Corresponding histologic preparations are treated for the demonstration of cytochrome oxidase. ca. X 25.

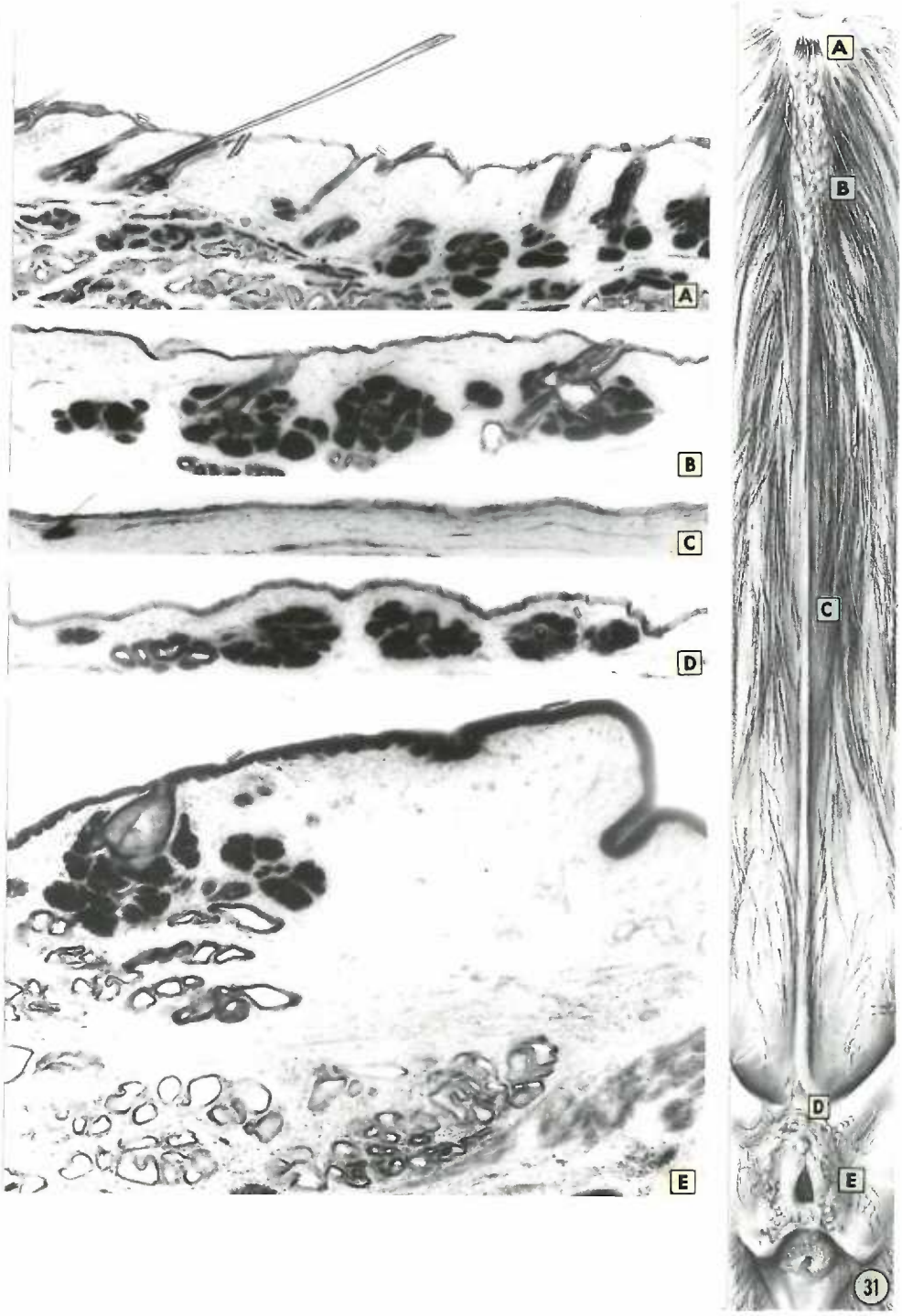
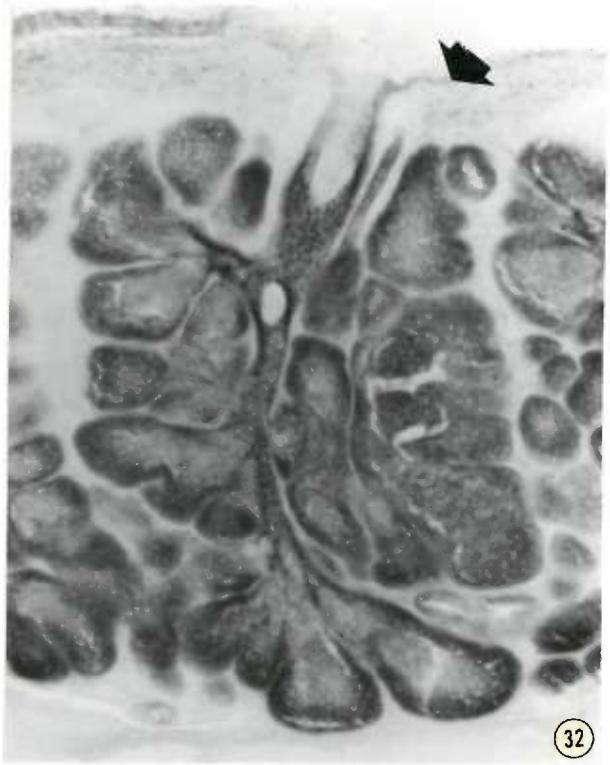

A
B
C
D
E
A
B
C
D
E
31

Fig. 32.

Intense phosphorylase activity in acini of large, multi-lobular sebaceous gland in the male sternal tuft. Arrow indicates phosphorylase-reactive apocrine excretory duct. ca. X 60.

Fig. 33.

Meissner corpuscles and papillary nerve end-organs (arrows) in amelanotic area of palmar friction surface. Note the normally pigmented epidermal ridge on left. Butyrylcholinesterase. ca. X 60.



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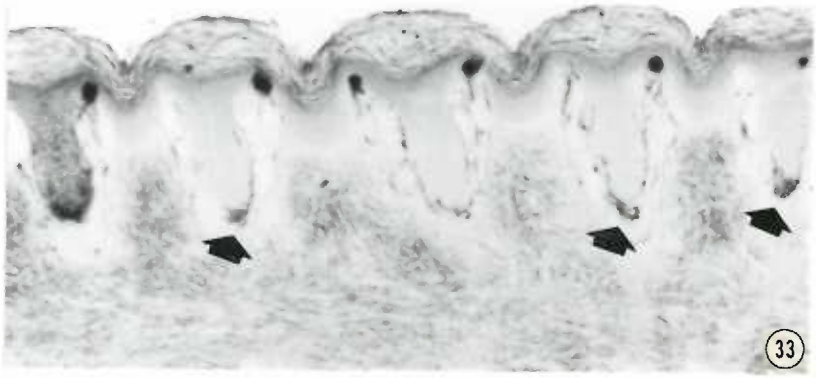


33

Fig. 34.

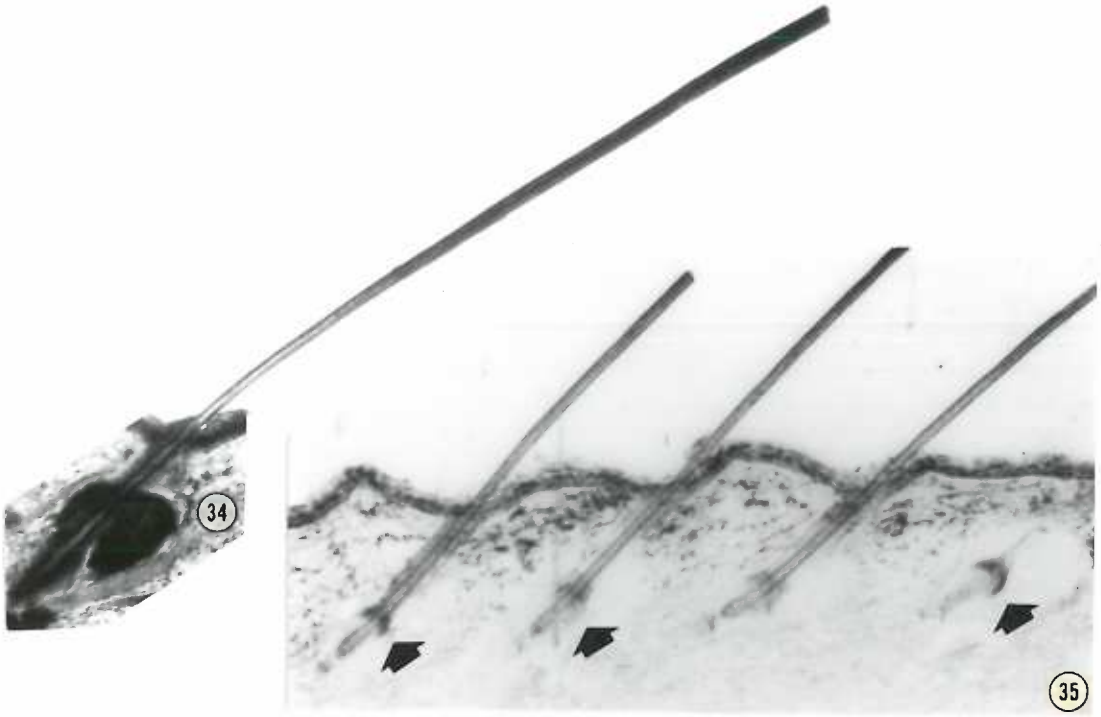
Hair follicle from the frontal scalp, demonstrating distal thickening and accumulation of melanin in terminal shaft. Cytochrome oxidase. ca. X 60.

Fig. 35.

Heavily pigmented epidermis and scattered aggregates of upper level, dermal melanocytes in the parietal scalp. Arrows denote hair follicle nerve end-organs.
Butyrylcholinesterase. ca. X 60.

Fig. 36.

Alkaline phosphatase preparation of male manubrial tuft. Note subdivision of hair into several small fila and intense enzymatic activity in peripheral sebaceous acini and apocrine secretory coils. ca. X 25.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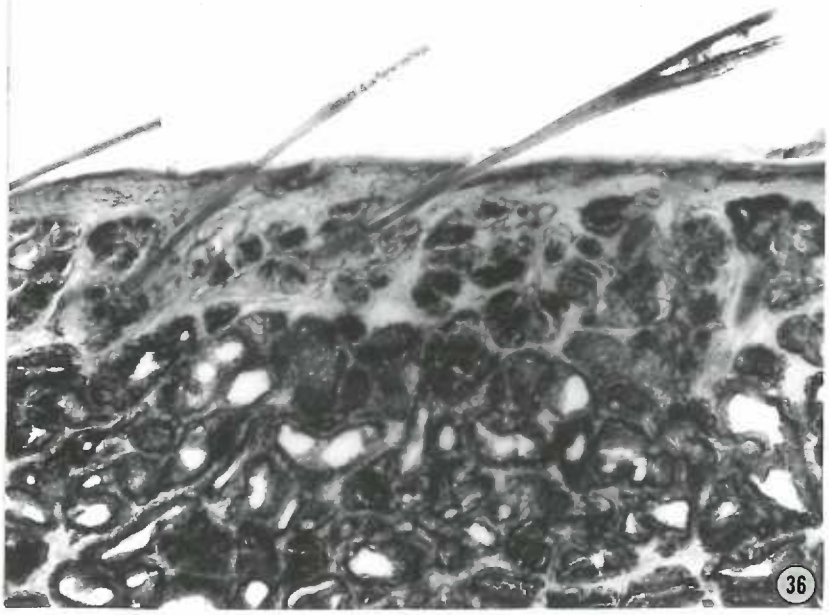

36

Pigmy marmoset (Callithrix [=Cebuella] pygmaea).

Fig. 37.

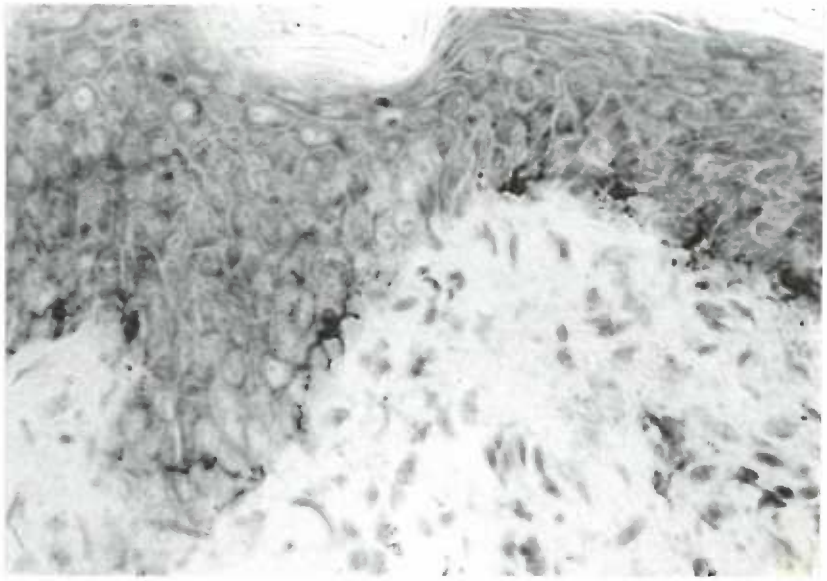
Dendritic, melanotic melanocytes in basal layer of epidermis of nose.
Toluidine blue preparation. ca. X 475.

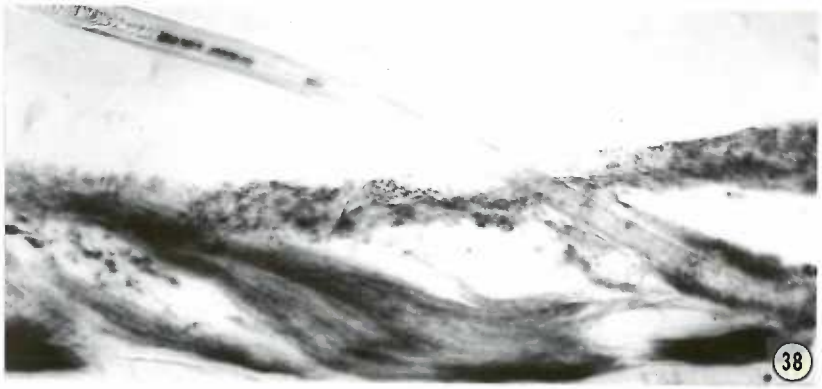
Fig. 38.

Large arrector pili muscle of hair follicle in distal tail.
Phosphorylase. ca. X 100.

Fig. 39.

Alkaline phosphatase-reactive hair follicle nerve end-organ in external genitalia.
ca. X 220.





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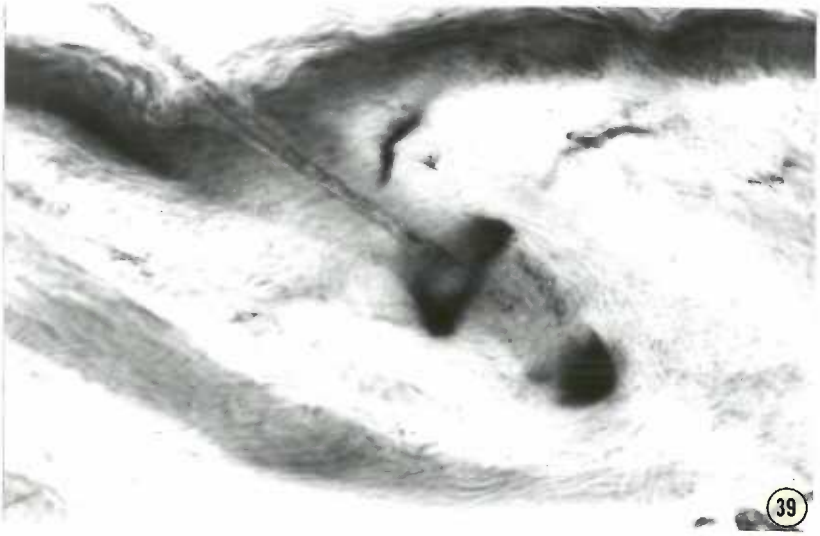


39

Fig. 40.

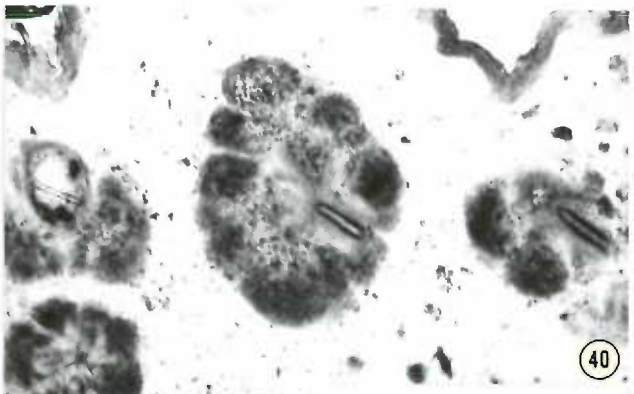
Large sebaceous glands and apocrine secretory coils in suprapubic region.
Monoamine oxidase. ca. X 60.

Fig. 41.

Argyrophilic granules in nuclear karyoplasm of dark cells from eccrine secretory coil of fingerball.
Fontana's silver method. ca. X 625.

Fig. 42.

Gigantic apocrine sweat glands in sternal region. Cytochrome oxidase. ca. X 60.



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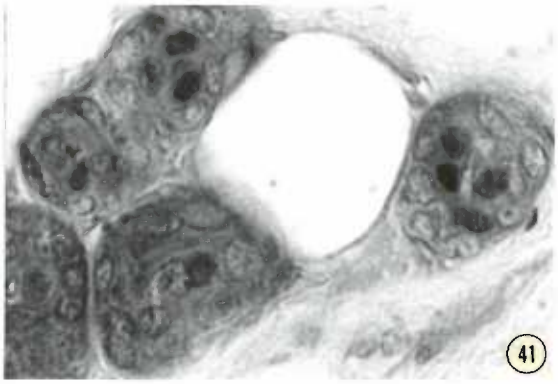

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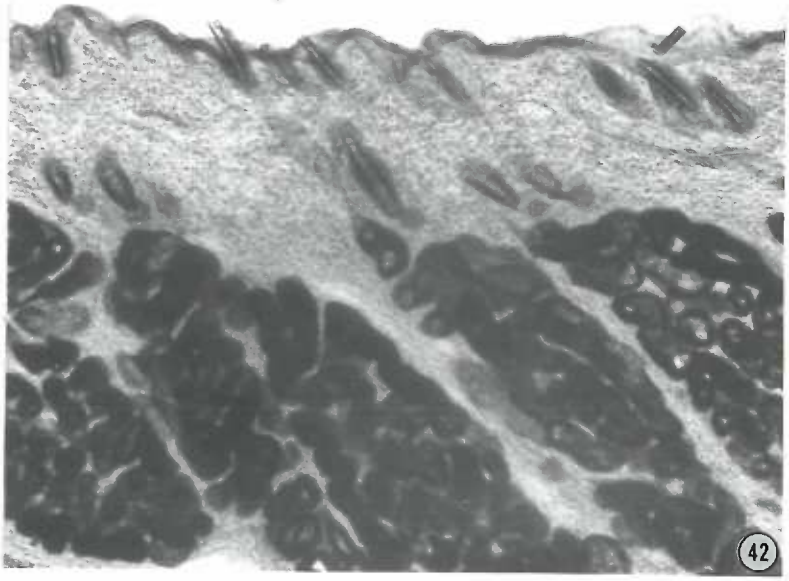


42

Fig. 43.

Epidermal and dermal melanocytes restricted to invaginated skin of scrotum. Note regional variance in contour and thickness of epidermis. Toluidine blue. ca. X 60.

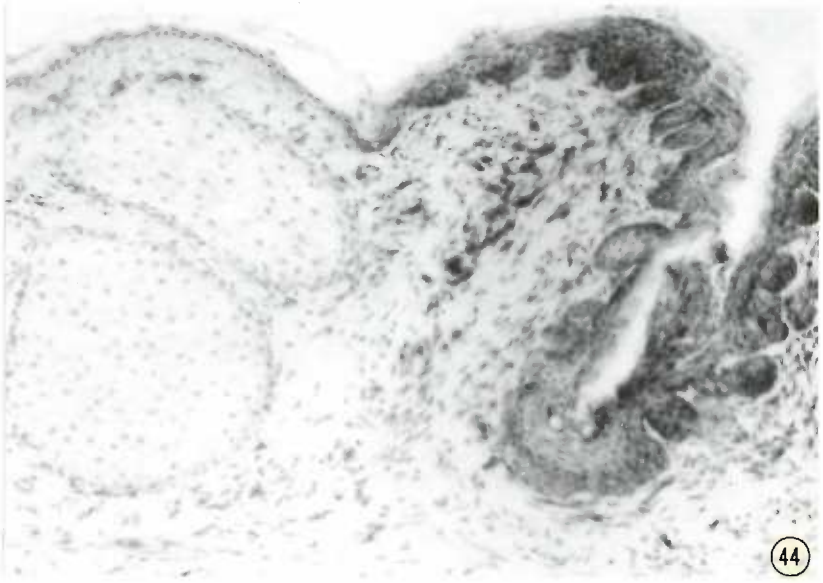
Fig. 44.

Same as Figure 43. ca. X 130.

Fig. 45.

Prominent sinus hair follicles localized on ventral ulnar aspect of wrist. Cytochrome oxidase. ca. X 40.

43



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45

Silver marmoset (Callithrix [=Mico] argentata).

Fig. 46.

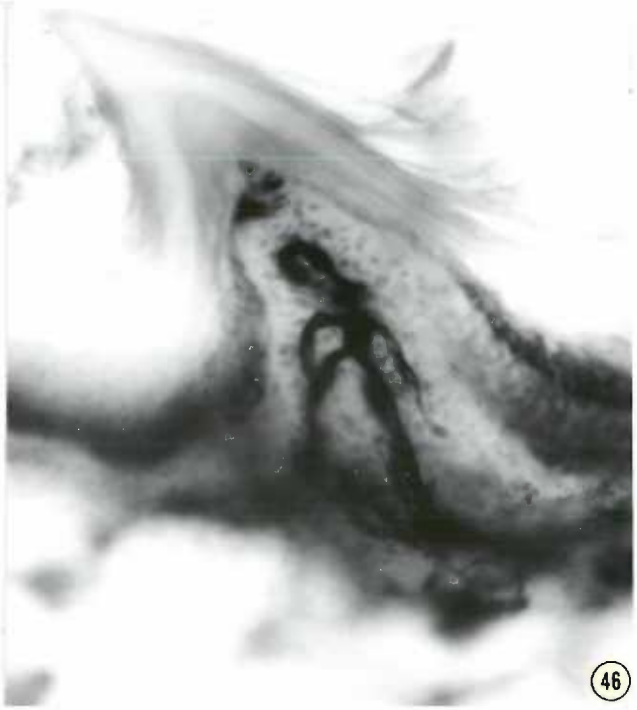
Alkaline phosphatase-positive, branching capillary loops in a hollow, keratinized spine of the corpus penis. ca. X 375.

Fig. 47.

Dorsum of corpus penis displaying numerous, proximally directed penile spines. Alkaline phosphatase. ca. X 45.

Fig. 48.

Acetylcholinesterase-reactive organized nerve endings, with finger-like processes, beneath a penile spine. A terminal nerve fiber is seen in the cavity. ca. X 250.



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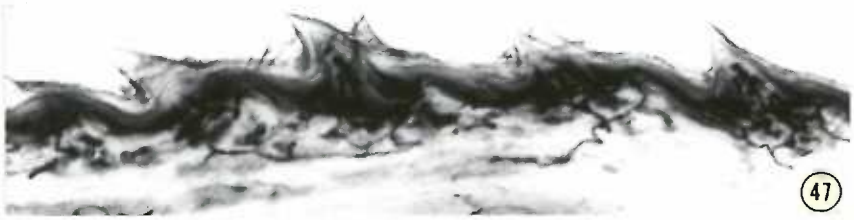

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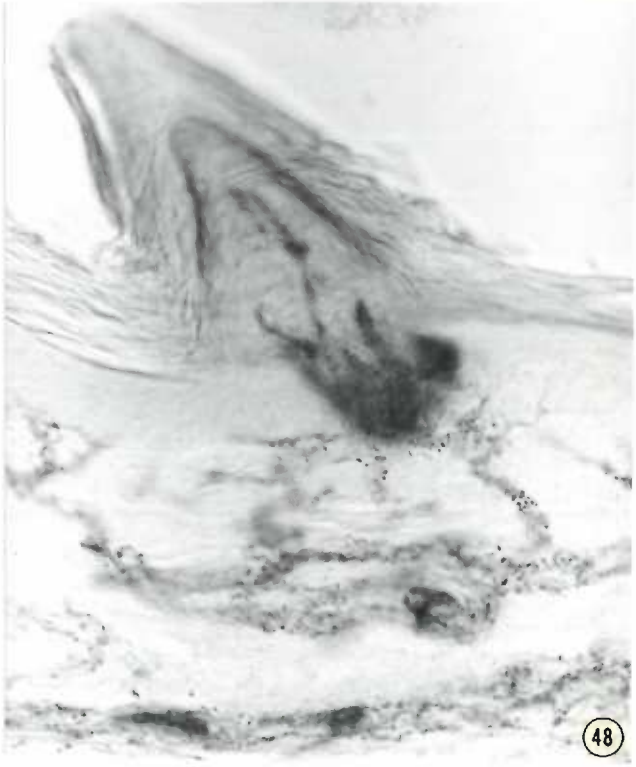


48

Fig. 49.

Surface-sectioned acetylcholinesterase preparation of finger-ball. Meissner corpuscles are aligned in rows that border the alternately wide and narrow epidermal ridges. The tissue has been cut in such a way that the plane of sectioning passes through the upper malpighian layer of the crista limitans and the stratum corneum, superior to the crista intermedia.

Inset is a longitudinal section of comparably treated finger-ball that has been placed so that the orientation corresponds to that of the larger photomicrograph. ca. X 145.

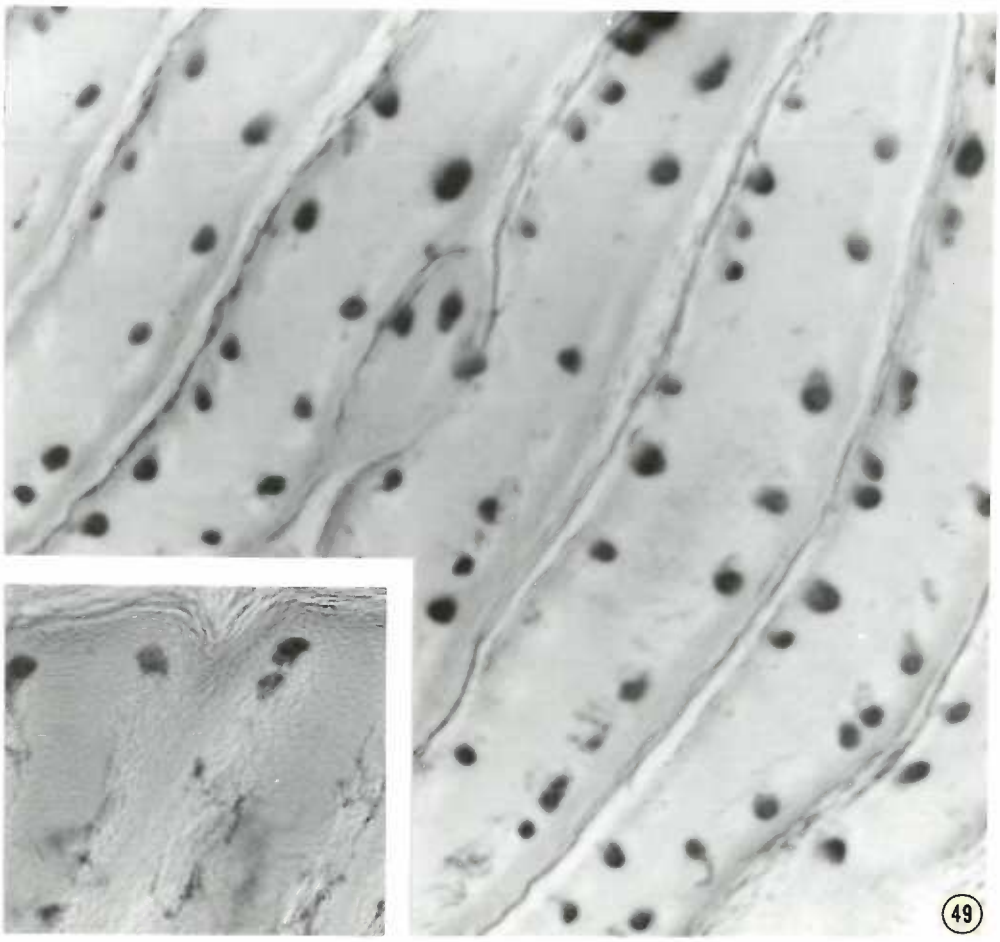

49

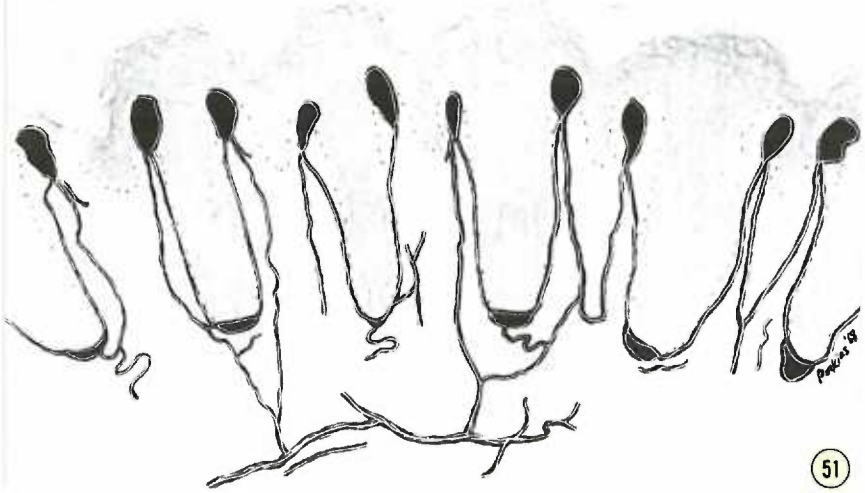
Fig. 50.

Meissner corpuscles, papillary nerve end-organs, and their interconnecting nerve fibers in the fingerball. Butyrylcholinesterase. ca. X 110.

Fig. 51.

Diagrammatic outline of Figure 50.

50



51

Fig. 52.

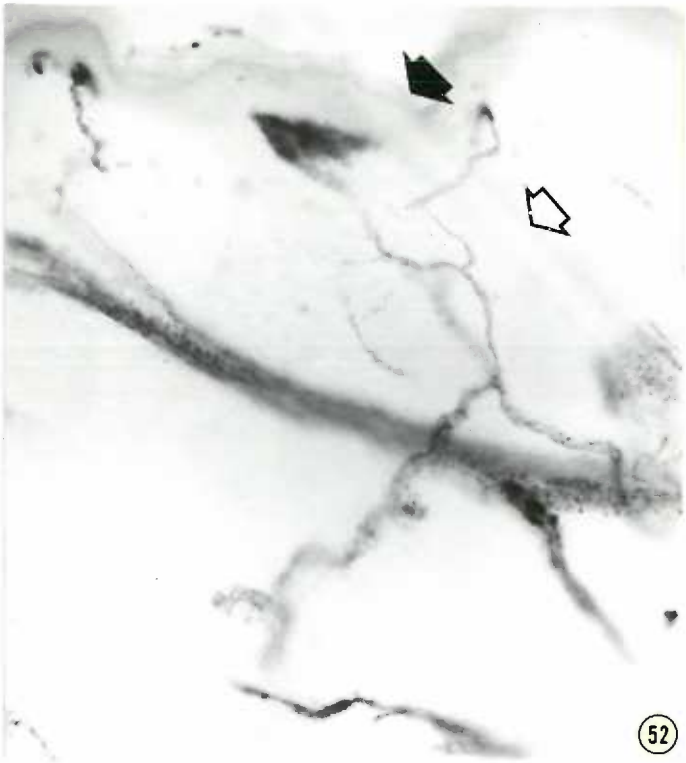
Acetylcholinesterase-reactive components of the Haarscheibe of Pinkus and related structures in the frontal scalp:

1) thickened epidermal plaque;
2) large subepidermal nerve end-plate;
3) secondary nerve boutons;
4) hair follicle nerve end-organ;
5) arrector pili muscle;
6) neuromuscular synapse;
7) hair bulge;

pilary orifice (solid arrow); and
hair shaft (open arrow). ca. X 130.

Fig. 53.

Diagrammatic sketch of Figure 52. The hair follicle and sebaceous glands have been included to facilitate structural relationships.



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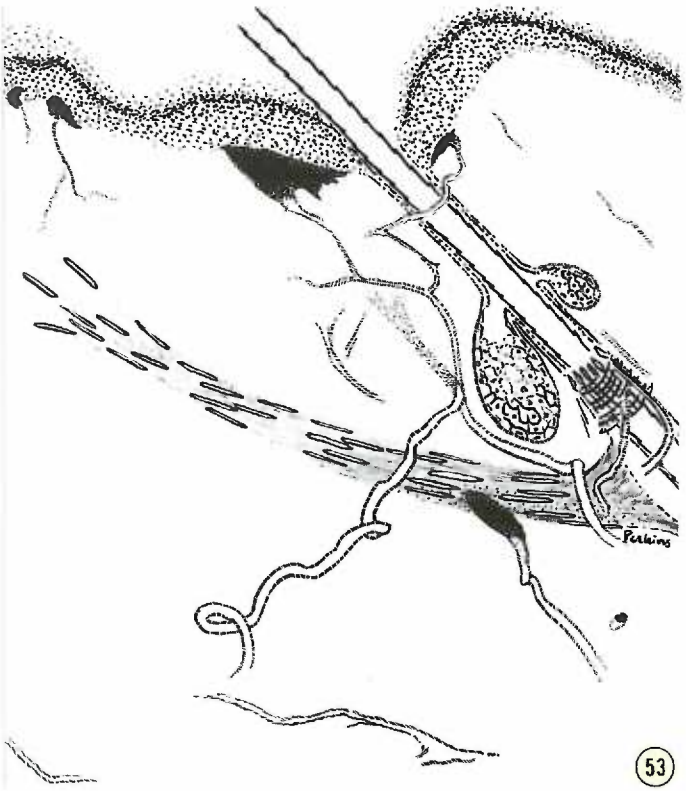


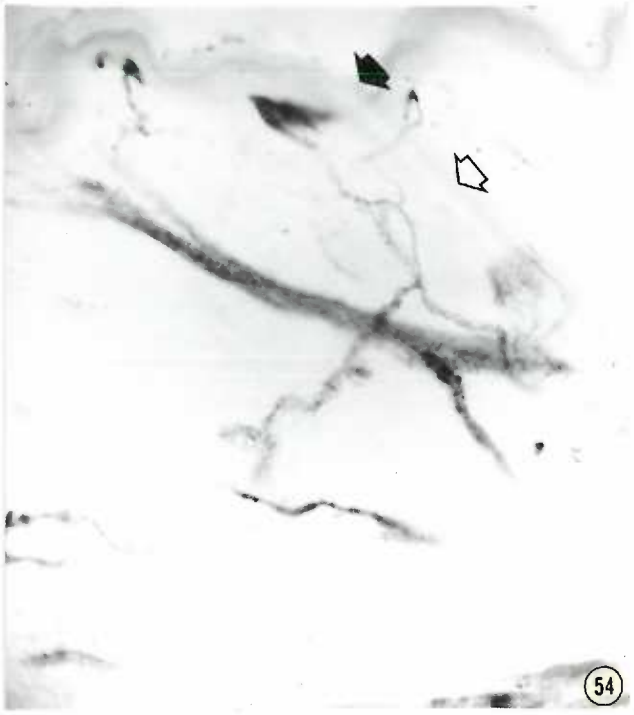
53

Fig. 54.

Same as Figure 52. Pilary orifice (solid arrow) and hair shaft (open arrow). Acetylcholinesterase. ca. X 100. Compare with Figure 55.

Fig. 55.

Hair follicle from frontal scalp (same region as Figure 54). Arrow denotes the vascular capillary plexus beneath the thickened epidermal plaque. ca. X 100.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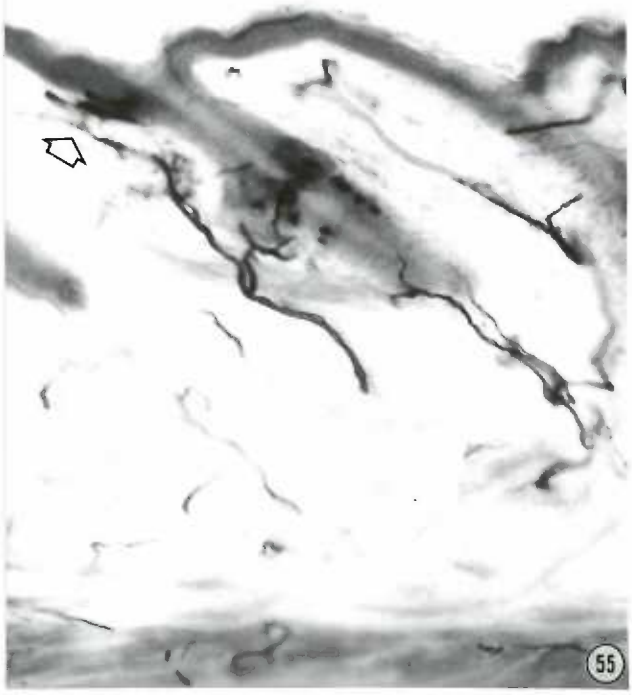
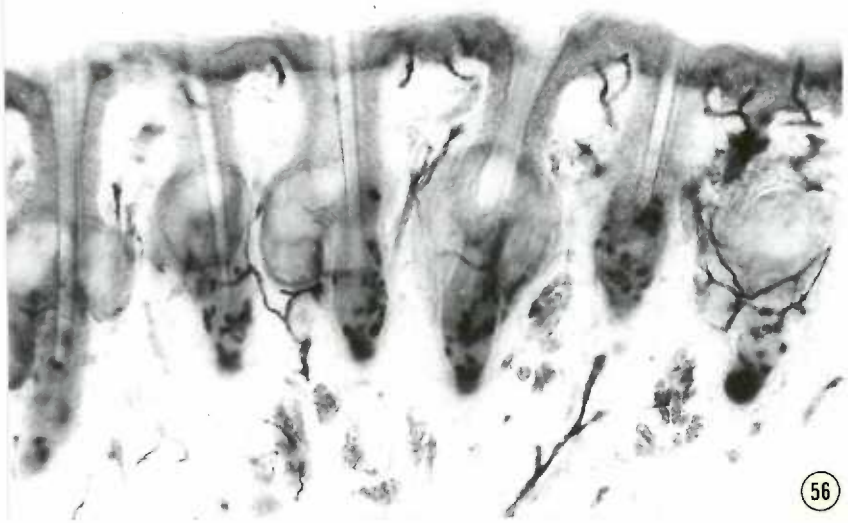

55

Fig. 56.

Numerous alkaline phosphatase-positive cells encompassing resting follicles in perialar skin. Also note enzyme reactivity in dermal papillae. ca. X 100.

Fig. 57.

Abundant alkaline phosphatase-positive cells encircling the epithelial sac of a quiescent hair in the temporal scalp. ca. X 170.



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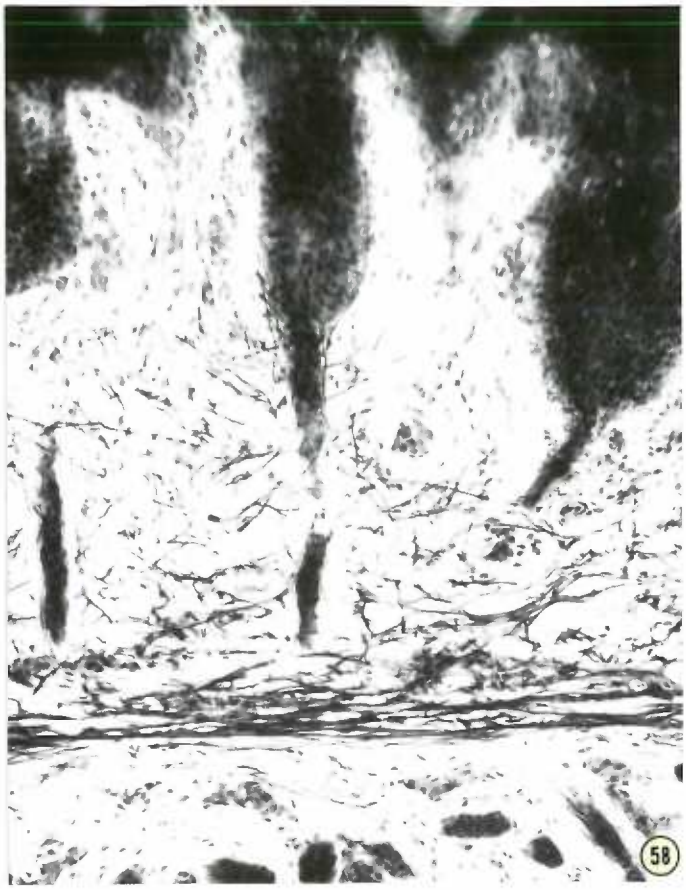
57

Fig. 58.

Section from toepad demonstrating fine elastic fibers, which are oriented perpendicular to skin surface in the upper dermis, and large, coarse, horizontally-oriented elastic fibers that demarcate the dermal-subcutaneous interface. A few coiled portions of eccrine excretory ducts are seen in the upper levels of the panniculus adiposus. A. O. V. ca. X 150.

Fig. 59.

Linear perfect sets of hair follicles in the distal tail. Hairs grow in groups of 3 to 5. One apocrine gland (arrows indicate apocrine excretory ducts) is associated with each hair group. A. O. V. ca. X 40.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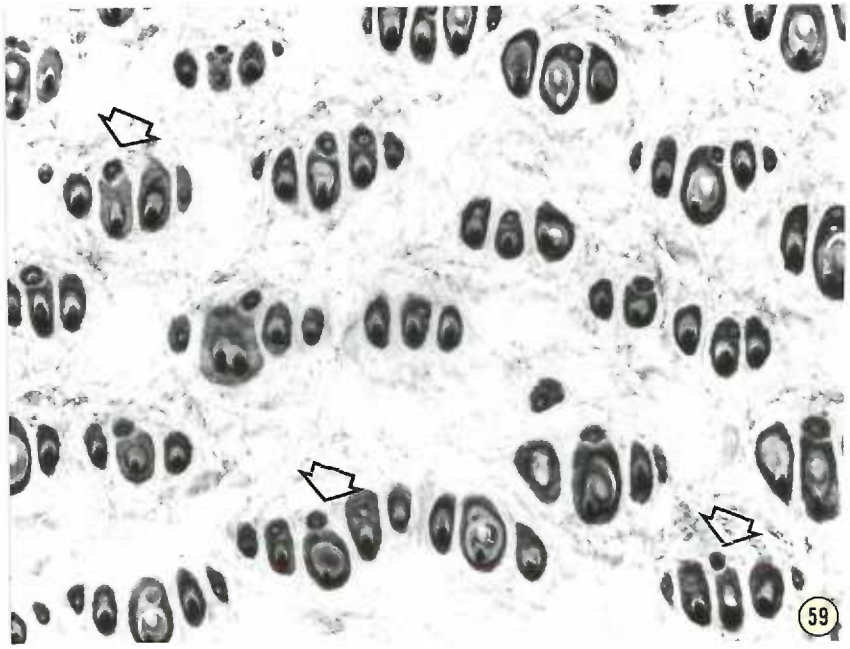
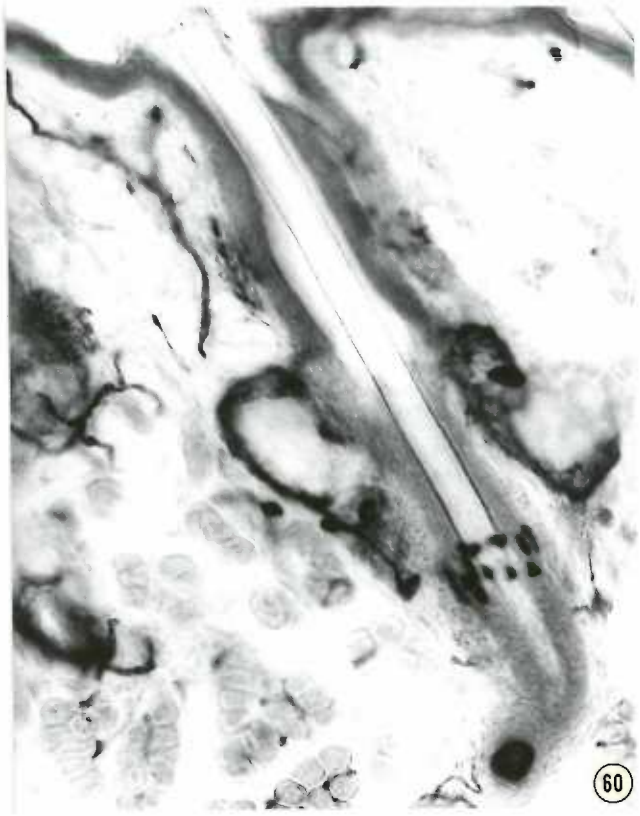

59

Fig. 60.

Pilosebaceous unit from lower lip. Note alkaline phosphatase-positive cells encircling hair follicle at level of the hair follicle nerve end-organ, alkaline phosphatase reactivity in peripheral sebaceous acini and dermal papilla, and excretory duct of apocrine sweat gland emptying at pilary orifice (arrow). ca. X 150.

Fig. 61.

Large sebaceous gland in scrotum. The numerous acini, which resemble clusters of grapes, contain moderate to intense alkaline phosphatase reactivity in the peripheries. ca. X 100.



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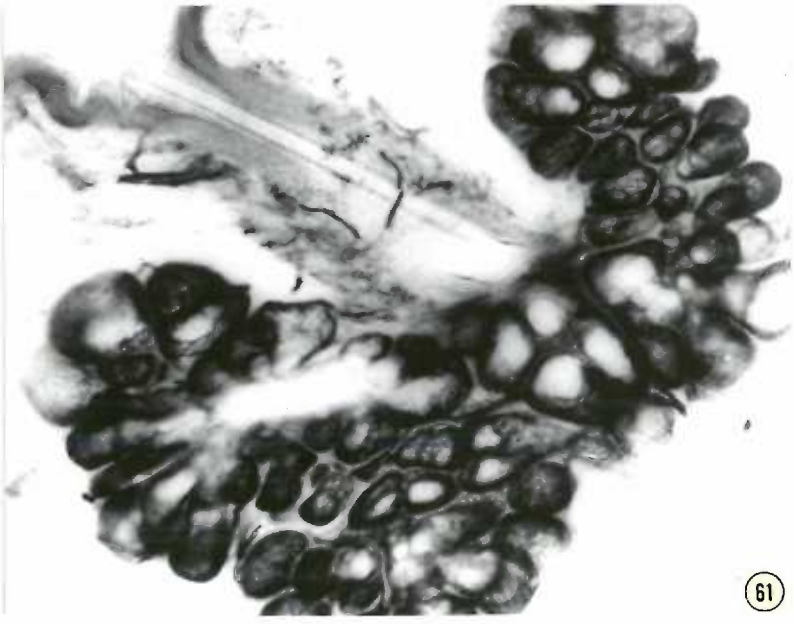


61

Red-mantled tamarin (Saguinus [=Tamarinus] fuscicollis illigeri).

Fig. 62.

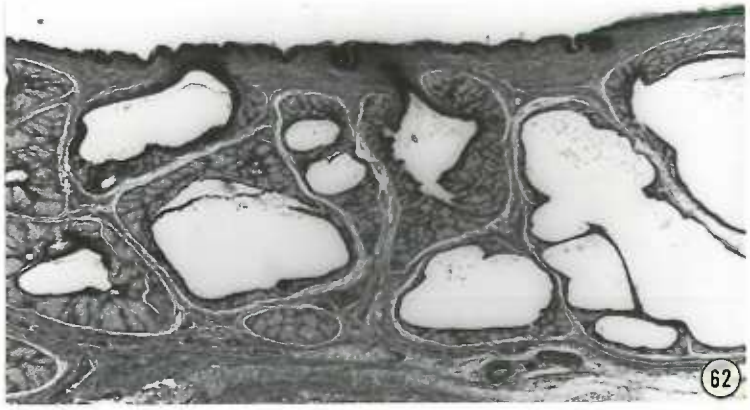
Periinguinal gland stained with Gallego's iron fuchsin. Note distended pilary canal in center and bullous collecting ducts. ca. X 20.

Fig. 63.

Alkaline phosphatase reactivity in large apocrine secretory tubules of sternal gland. ca. X 20.

Fig. 64.

Three butyrylcholinesterase-reactive hair follicle end-organs in lip. Plane of focus is such that both circular, external collar of nerve fibers about central follicle and horizontal, internal palisade arrangements about flanking follicles can be observed. ca. X 150.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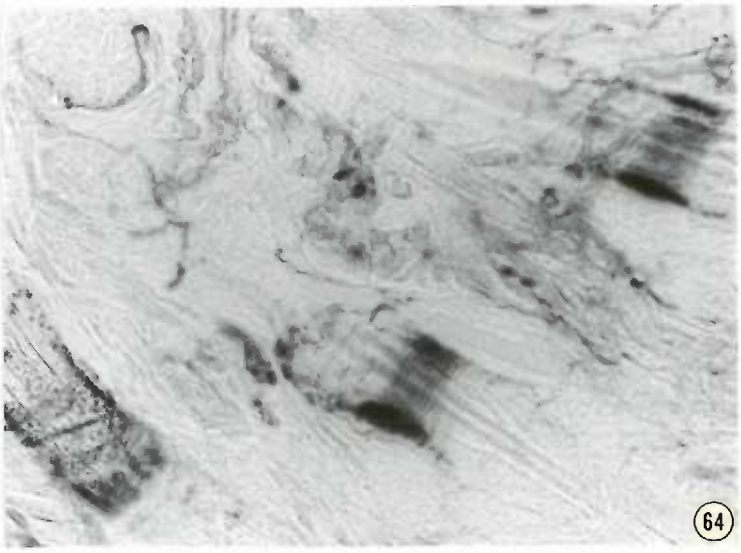
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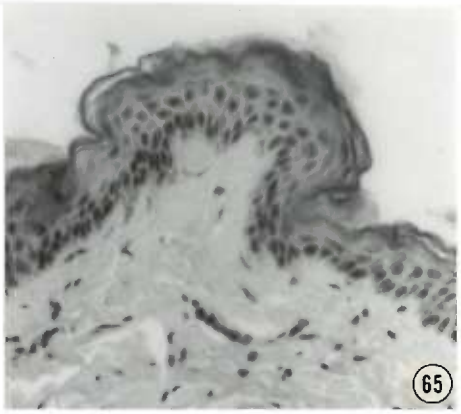
Fig. 65.

Radial papilla treated with hematoxylin and eosin. ca. X 190.

Fig. 66.

Ulnar eminence prepared with Gallego's iron fuchsin. Note large sinus hair follicles and small bilateral sebaceous glands. ca. X 40.



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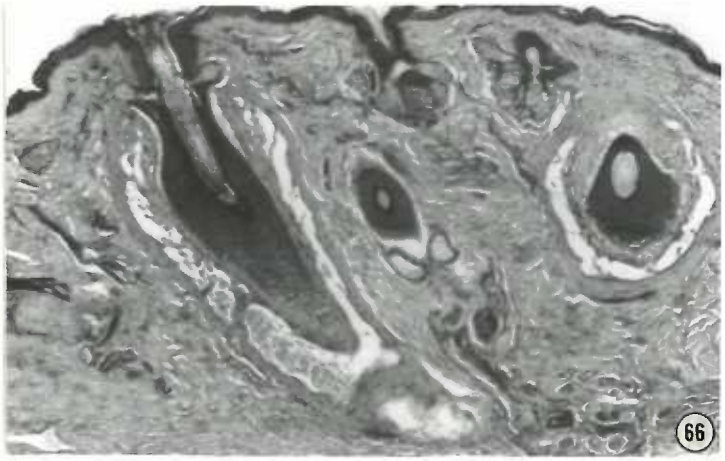


66

Fig. 67.

Elastic fibers anchoring distal attachment of arrector pili muscle in lip.

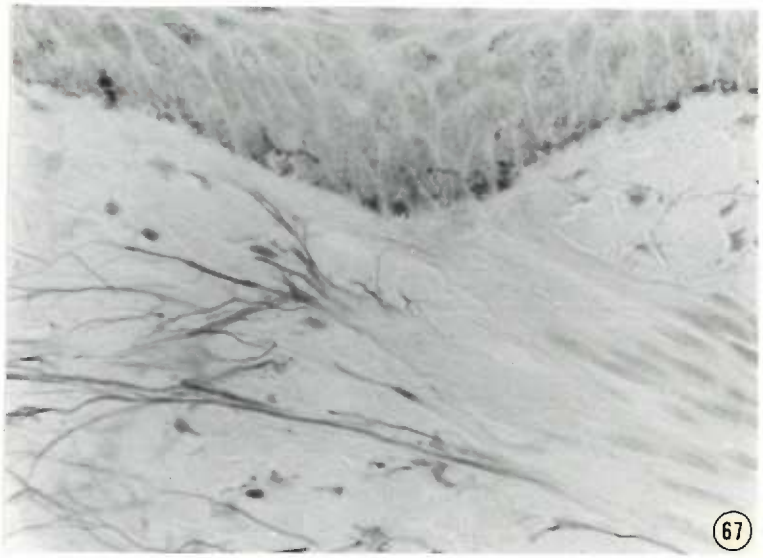
Roman's acid orcein-Giemsa preparation. ca. X 475.

Fig. 68.

Epidermal dendritic melanocytes in scalp (arrow) demonstrated by Mishima and Miller-Milinska's osmic acid - sodium iodide method. ca. X 400.

Fig. 69.

Acetylcholinesterase preparation of palm demonstrating reactivity of Meissner's corpuscles and their emergent nerve fibers. ca. X 100.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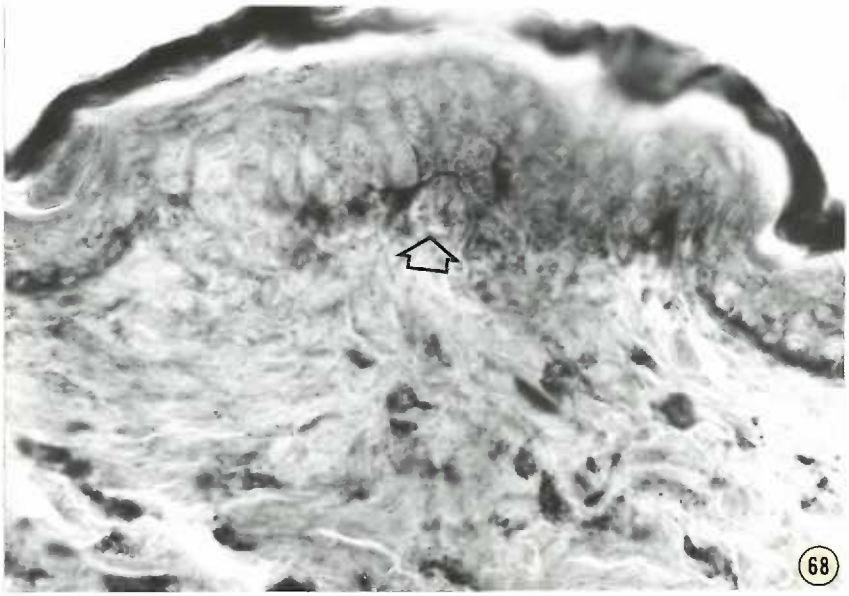
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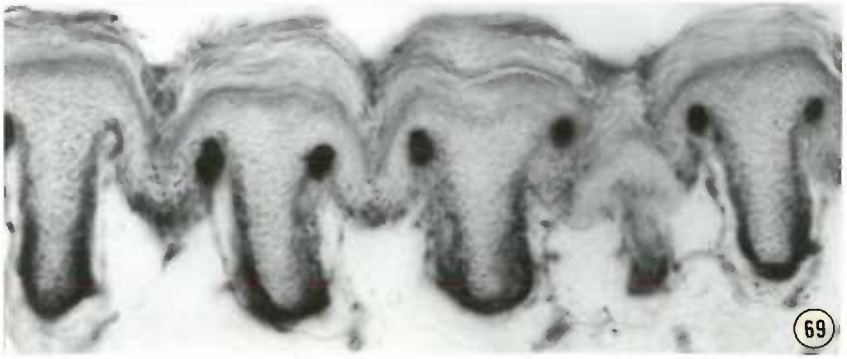
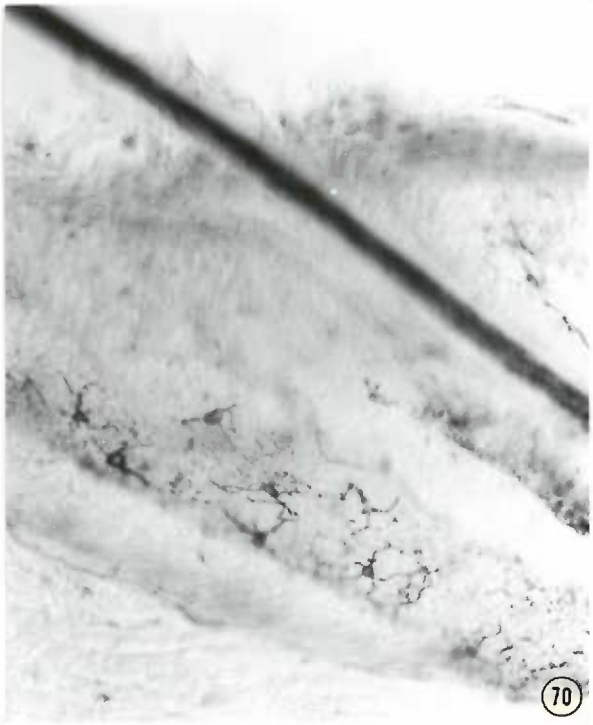

69

Fig. 70.

Melanotic, dendritic melanocytes on outer root sheath of pilary canal of hair follicle in proximal tail.
Acetylcholinesterase. ca. X 200.

Fig. 71.

Apocrine duct (arrow) coursing along pilary canal of proximal tail and terminating adjacent to pilary orifice. P. A. S. ca. X 200.



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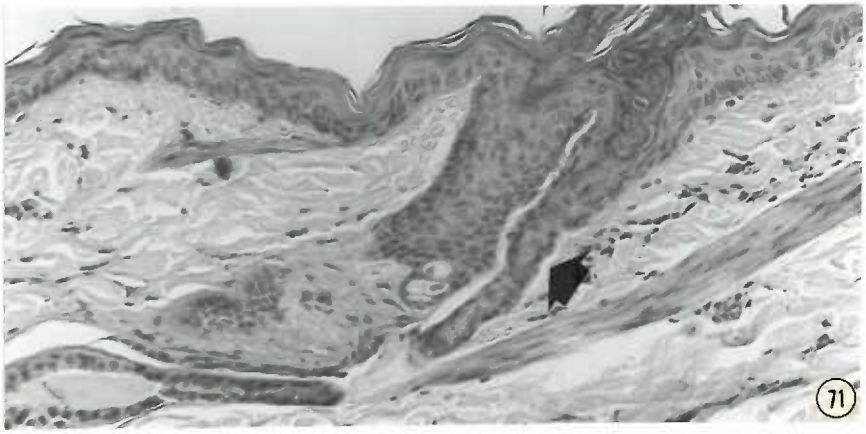


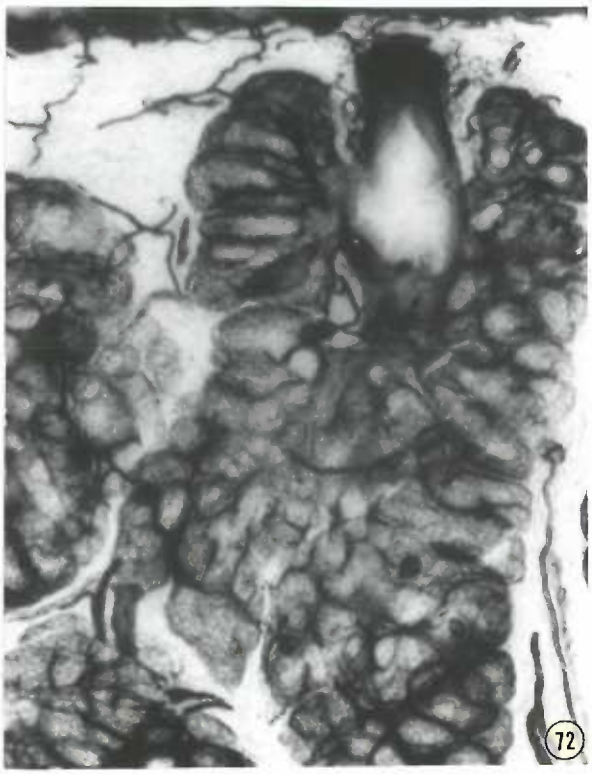
71

Fig. 72.

Gigantic sebaceous gland of external genitalia, demonstrating alkaline phosphatase reactivity. Note ampulliform pilary canal. ca. X 60.

Fig. 73.

Intense reactivity for succinic dehydrogenase in large apocrine secretory coils of sternal gland. ca. X 40.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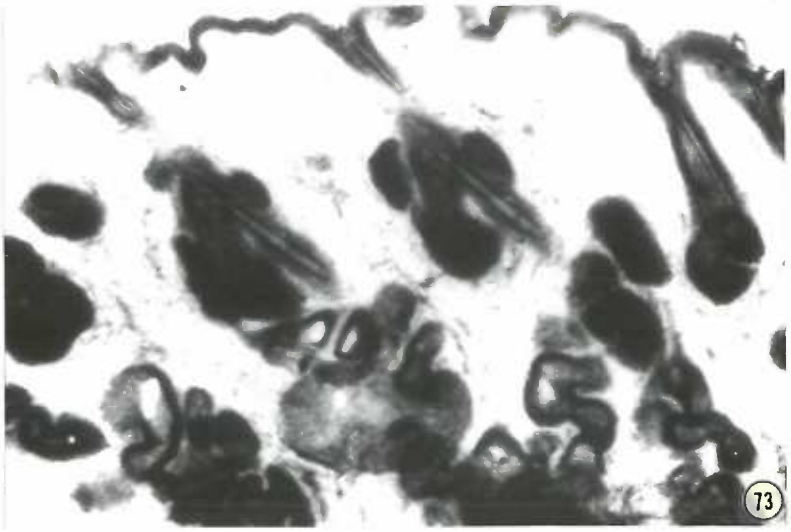

73

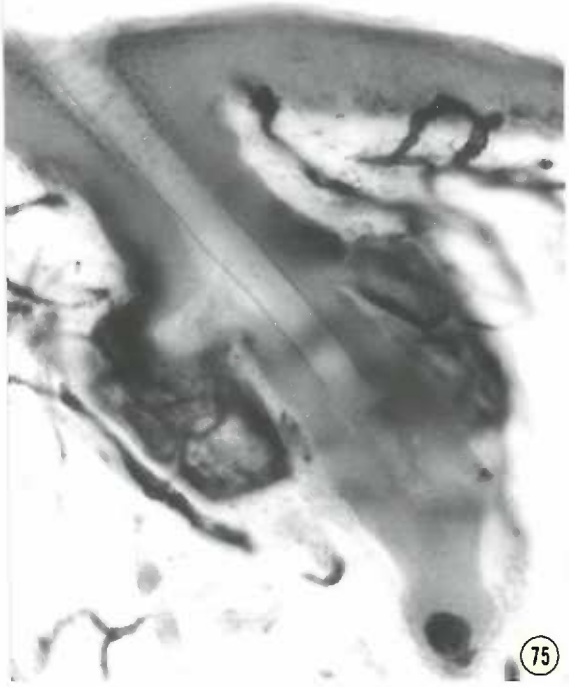
Fig. 74.

Phosphorylase reactive granules in peripheral acini of sebaceous glands in lip. ca. X 200.

Fig. 75

Alkaline phosphatase reactivity in peripheral acini of sebaceous glands in lip. ca. X 150.

74



75

Fig. 76.

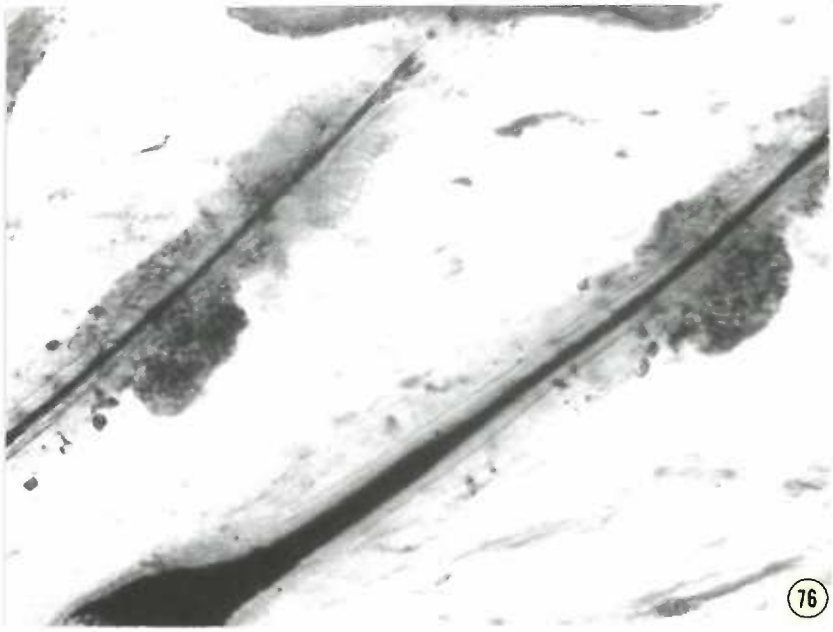
Heavily pigmented hair bulges in scalp.

S. D. H. ca. X 170.

Fig. 77.

Linear perfect sets of 3 to 5 follicles in the scalp.

S. D. H. ca. X 35.



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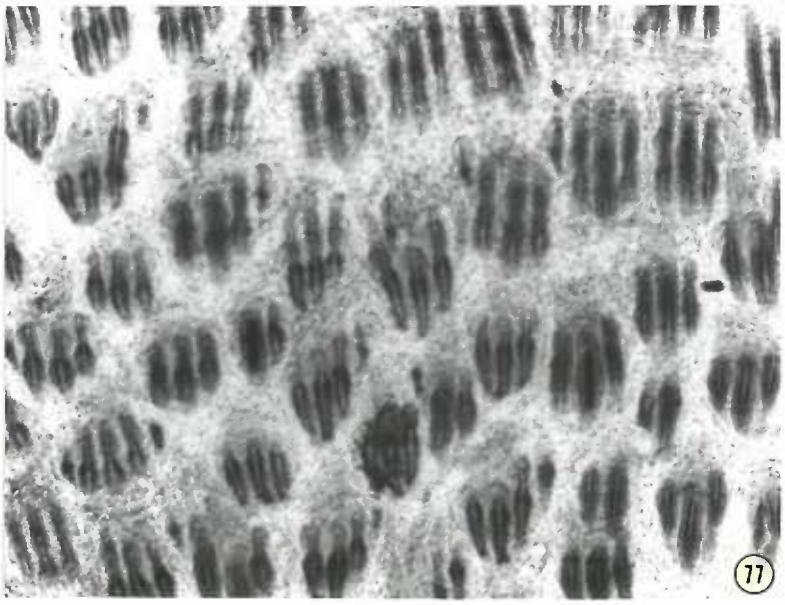


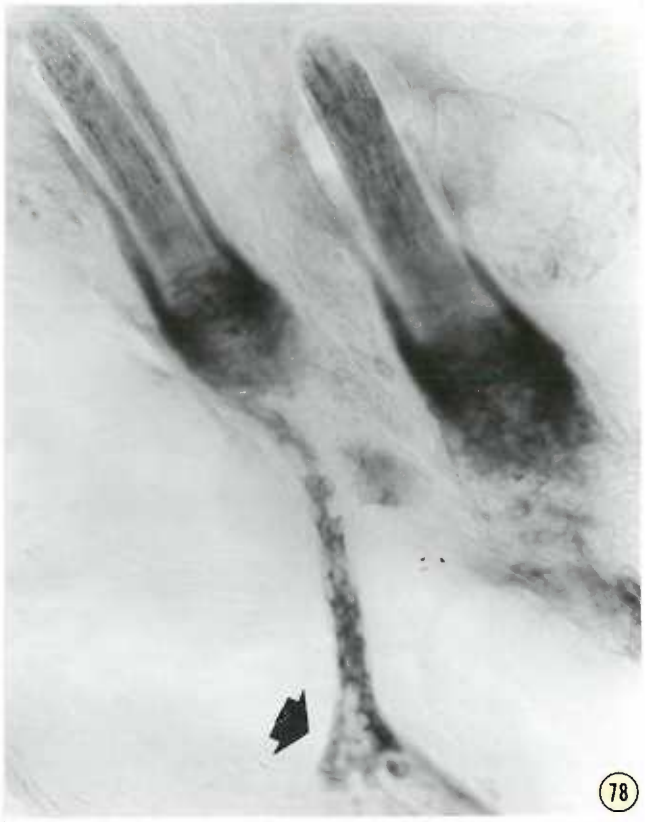
77

Fig. 78.

Phosphorylase in apocrine excretory duct of sternal region. Note absence of reactivity in secretory segment and abrupt transition in diameter (arrow) between excretory and secretory portions. ca. X 250.

Fig. 79.

Acetylcholinesterase preparation depicting numerous melanotic dendritic melanocytes circumventing apocrine secretory tubules in the external genitalia. ca. X 180.



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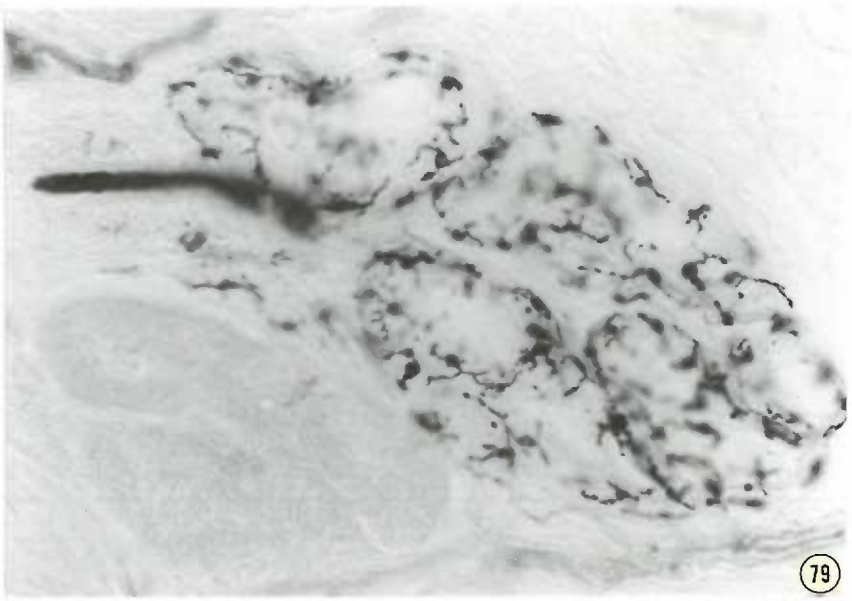


79

Cottontop pinché (Saguinus [=Oedipomidas] oedipus).

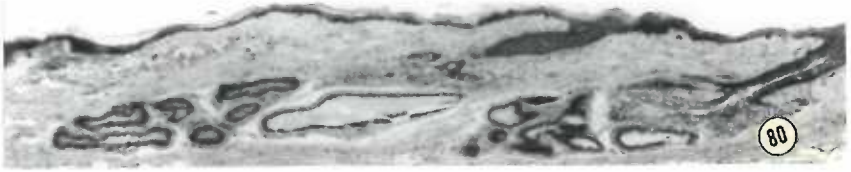
Location and histology of suprapubic glandular fields.

Fig. 80.

Large sebaceous and apocrine glands in the thin, sparsely haired posterior abdominal skin of a male pinché. Hematoxylin and eosin. ca. X 45.

Fig. 81.

Gigantic multiacinar sebaceous glands and apocrine secretory coils beneath the moderately thickened epidermis of the female suprapubic "cushion." Each sebaceous-apocrine unit is associated with one vellus hair, whose pilary canal is often distended.
Hematoxylin and eosin. (Same magnification as Figure 80).



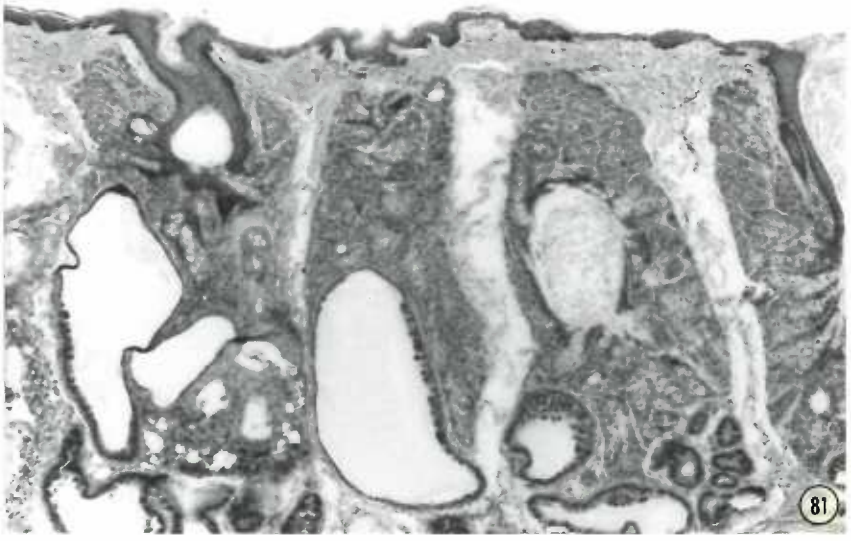
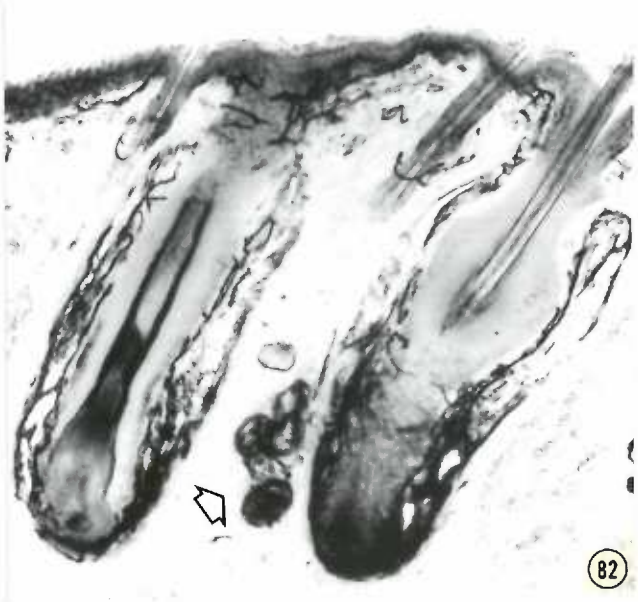


Fig. 82.

Alkaline phosphatase preparation of two large sinus hairs in the ulnar tuft. The vibrissae dwarf the normal-sized hairs of the region. Note large apocrine secretory coils (arrow). ca. X 60.

Fig. 83.

Profusion of blood capillaries investing sebaceous acini and apocrine secretory segments in the suprapubic gland of a female pinché. Alkaline phosphatase. ca. X 60.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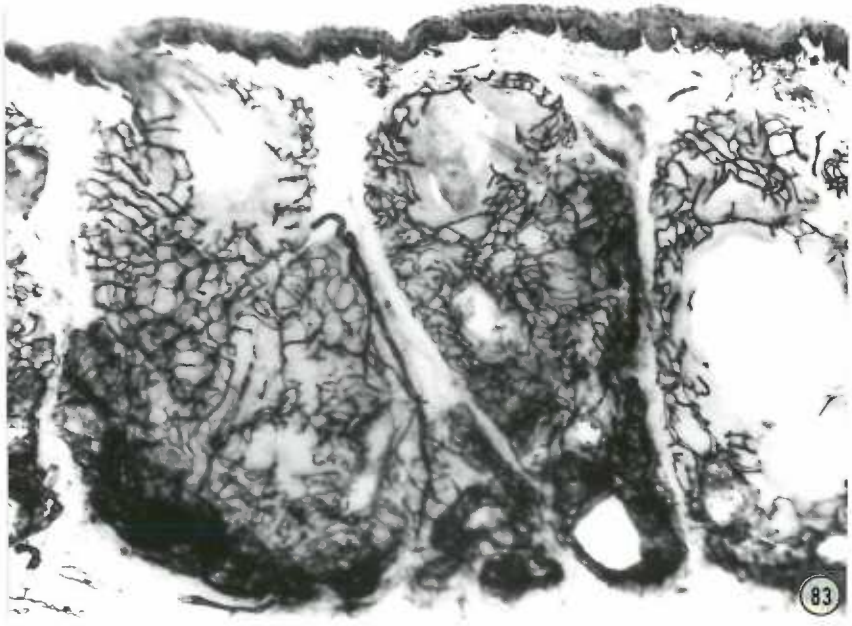
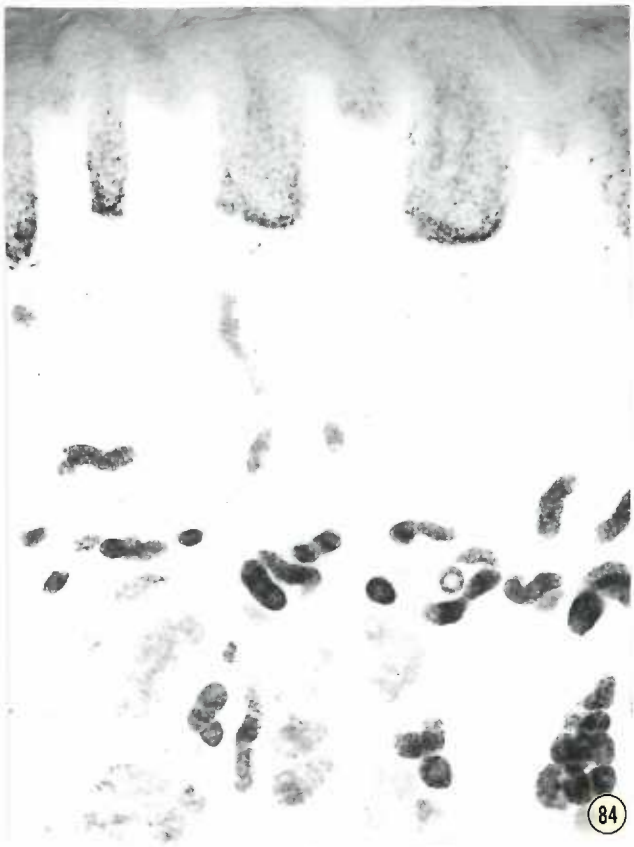

83

Fig. 84.

Section of fingerball processed for the demonstration of phosphorylase activity in eccrine sweat glands. Enzyme concentrations occur only in the coiled excretory ducts. Observe the general diminishment of epidermal and dermal melanocytes. ca. X 100.

Fig. 85.

Alkaline phosphatase-positive capillaries investing pilo-sebaceous units along the cutaneous border of the lower lip; others loop beneath the epithelium of the mucosal margin. The mucosa is folded upon itself distal to the mucocutaneous junction, forming a sulcus. Note that the inner surface of the muccus membrane is devoid of melanotic pigment. ca. X 30.



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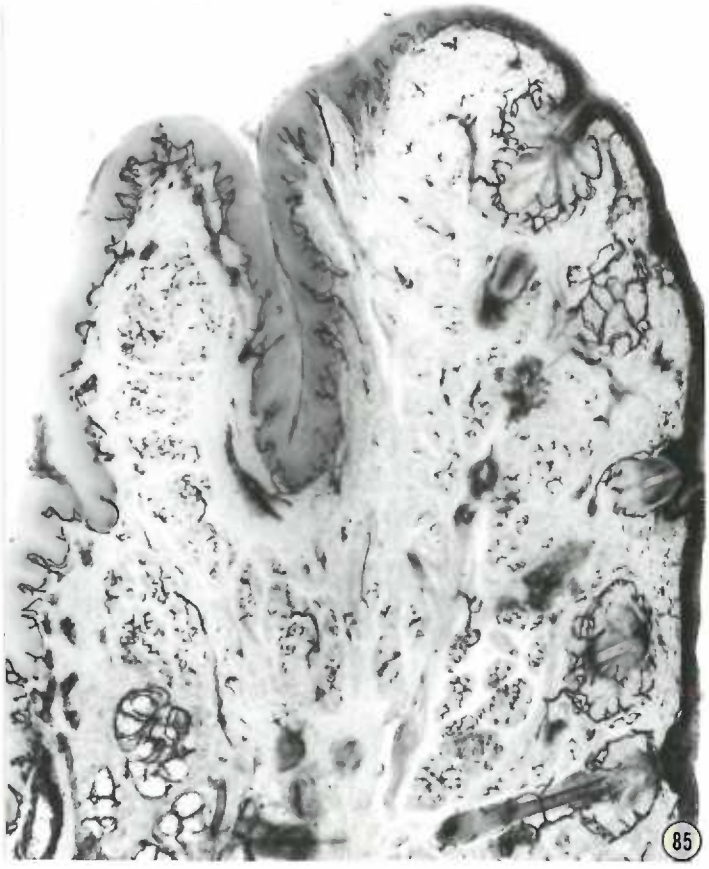


85

Fig. 86.

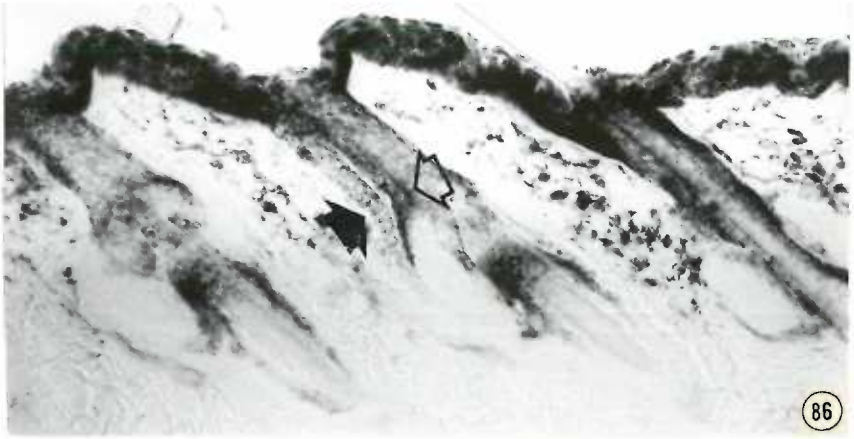
Distribution of melanotic melanocytes in the frontal scalp. Note heavily pigmented epidermis, abundant spindle-shaped dermal melanocytes, intense pigmentation of hair follicles, melanocytes about sebaceous ducts and peripheral acini (open arrow), and pigmented terminal portion of an apocrine excretory duct (solid arrow).
Butyrylcholinesterase. ca. X 100.

Fig. 87.

Scalp hair follicles in the occipital-parietal transition zone. Large amelanotic bulb typifies follicles of the occipital crest and smaller, melanotic hair bulb represents the short black hairs of the contiguous parietal region. Even the smaller follicle is large compared with characteristic follicles in the frontal scalp (Fig. 86).
Butyrylcholinesterase. ca. X 130.

Fig. 88.

Cytochrome oxidase preparation of female suprapubic region, illustrating disparity in enzyme activity; sebaceous glands contain large amounts of the enzyme but most apocrine coils are weakly reactive. ca. X 50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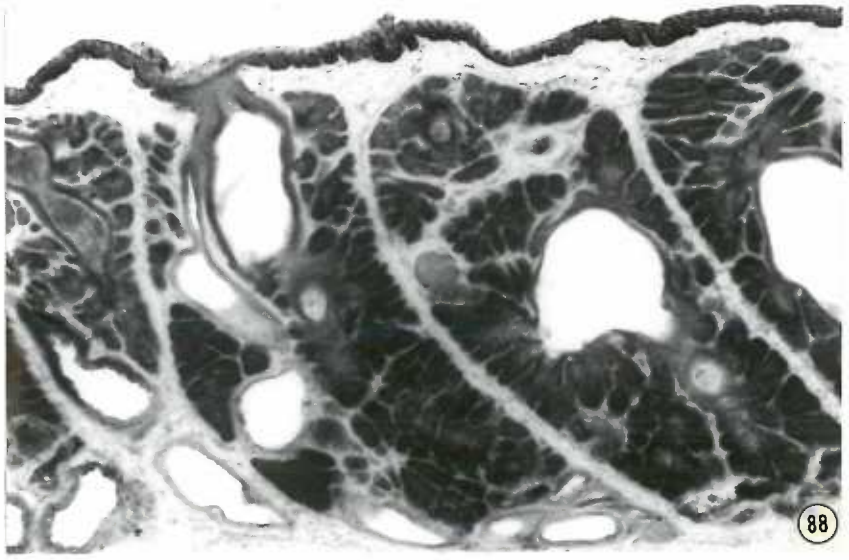

88

White-shouldered marmoset (Callithrix [=Hapale] humeralifer).

Fig. 89.

Transmitted and incident light microphotograph of ulnar vibrissae. Note large blood sinuses, and relatively glabrous, unpigmented, circumscribed field around sinus hairs. ca. X 25.

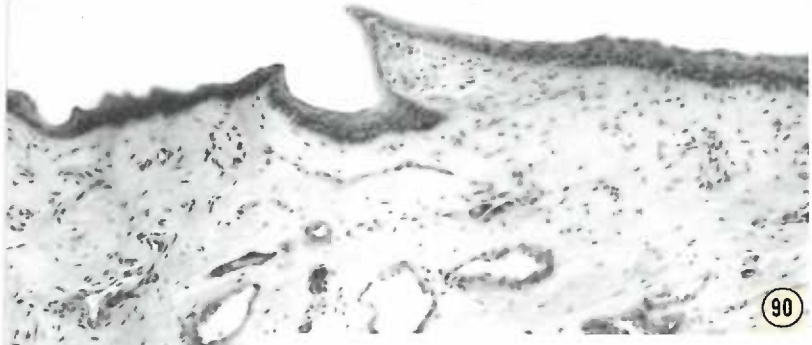
Fig. 90.

Proximally-directed spine overlying spongy dermis of the corpus penis.
P. A. S. ca. X 110.

Fig. 91.

Same as Figure 90. ca. X 450.


89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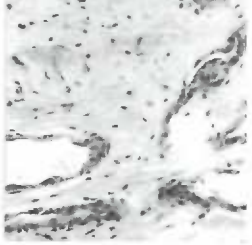

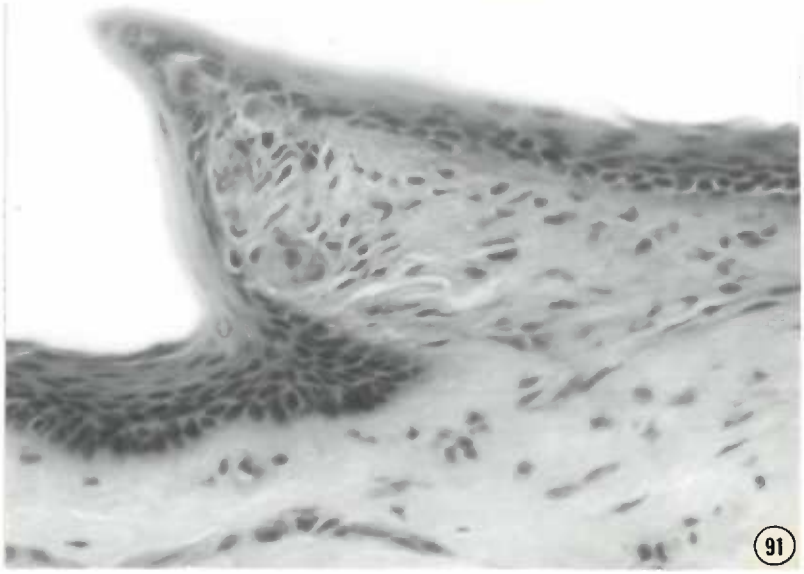
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APPENDIX

I. HISTOLOGICAL STAINS.

A. Harris' Hematoxylin and Eosin (Lillie, 1965).

Procedure:

1. Place paraffin sections in two changes xylene.....5 min. each
2. Rinse in absolute alcohol.
3. Two changes absolute alcohol.....5 min. each
4. Two changes 95% alcohol.....4 min. each
5. 80% alcohol.....3 min.
6. 0.5% iodine in 80% alcohol.....5 min.
7. Rinse in two changes 70% alcohol.
8. Rinse in 60%, 50%, and 30% alcohol.
9. Rinse in distilled water.
10. Place in 5% sodium thiosulfate.....5 min.
11. Wash in running tap water.....5 min.
12. Place in distilled water.....5 min.
13. Stain in hematoxylin solution.....5 min.
14. Rinse in acid water.[1]
15. Wash in running tap water.....5 min.
16. Dip in sat. solution of lithium carbonate.
17. Rinse in distilled water.
18. Dehydrate in 30%, 50%, and 60% alcohol.....2 min. each.
19. Dehydrate in 70% and 80% alcohol.....3 min. each
20. Dehydrate in 95% alcohol.....5 min.
21. Dip in 0.25% solution eosin Y[2] in 95% alcohol.
22. Rinse in two changes 95% alcohol.
23. Dehydrate in three changes absolute alcohol.....5 min. each
24. Clear in three changes xylene.....5 min. each
25. Use No. 1 coverslips[3] and mount in Permount®.[4]

Reaction:
- Nuclei.....blue
- Cartilage.....dark blue
- Calcium Deposits.....dark blue
- Cytoplasm.....pink
- Muscle.....pink
- Mucin.....often light blue
- Keratohyalin.....often dark blue

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[1](4 drops 1N HCl in 100 ml. distilled water).

[2]Roboz Surgical Instrument Co., Washington, D. C.

[3]Cat. No. M-6075, Scientific Products, Div. of American Hospital Supply Corp., Evanston, Ill.

[4]Cat. No. 12-568, Fisher Scientific Co., Fair Lawn, N. J.

Preparation: 1) Hematoxylin Solution –
Dissolve 1 gm. hematoxylin (Roboz) in 10 ml. absolute alcohol. Using heat, dissolve 20 gm. potassium aluminum sulfate [$AlK(SO_4)_2 \cdot 12H_2O$] in 200 ml. distilled water. Add hematoxylin-alcohol and bring to rapid boil. CAUTION: turn off flame and carefully add 0.5 gm. mercuric oxide. Plunge container immediately into ice water, cool, and filter into stock bottle.

B. Toluidine Blue (Montagna, Chase and Melaragno, 1951).

Procedure:

1. Bring deparaffinized sections down to distilled water.
2. Place in toluidine blue solution (pH 4.5).....15 min.
3. Rinse in distilled water.
4. Place tissue sections in tert-butyl alcohol.....5 min.
5. Repeat with fresh tert-butyl alcohol.....5 min.
6. Cover sections with absolute alcohol.....5 min.
7. Cover sections with toluene.....5 min.
8. Cover with fresh toluene.....5 min.
9. Repeat.....5 min.
10. Mount in Permount®.

Reaction: Acid Mucopolysaccharides..metachromatic
Other Tissue Elements.....light blue

Preparation: 1) McIlvaine Buffer –
0.1M Citric Acid (to 25 ml. 25% methanol add 1.1 gm. citric acid)
0.2M Sodium Phosphate (to 0.71 gm. dibasic sodium phosphate – Na_2HPO_4 anhyd. – add 25 ml. 25% methanol)

2) Toluidine Blue Solution –
To 23 ml. 0.1M citric acid and 17 ml. 0.2M sodium phosphate add 1000 ml. distilled water. Mix and pour off 40 ml. To remaining 1000 ml. add 500 mg. o-toluidine blue (Roboz). Mix and store in refrigerator. Check pH before use.

C. Periodic Acid-Schiff (Montagna, Chase and Lobitz, 1953).

Procedure:

1. Deparaffinize control slides and bring down to distilled water.
2. Incubate control slides in diastase solution at 37° C.....15 min.
3. Wash control slides in running tap water.....30 min.
4. At this time deparaffinize all PAS slides, hydrating to distilled water.
5. Combine ALL slides in freshly prepared 0.5% periodic acid at 37° C.....15 min.
6. Place in two changes distilled water.....3 min. each
7. Place in dilute Schiff reagent.....30 min.
8. Place in 10% potassium metabisulfite.....4 min.
9. Repeat.....4 min.
10. Wash in running tap water.....5 min.
11. Place in distilled water.....3 min.
12. Stain in Harris' hematoxylin (filter before use).....1/2 min.
13. Rinse in acid water (5 ml. 1N HCl in 100 ml. distilled water).
14. Dip in lithium carbonate until blue
15. Wash in running tap water.....5 min.
16. Place in distilled water, dehydrate through alcohols, and clear in xylene.
17. Mount in Permount®.

Reaction: Polysaccharides (glycogen, starch, cellulose); Muco- and Glycoproteins (Reticulin, collagen); Unsaturated Lipids and Phospholipids; Glycolipids; and Neutral Mucopolysaccharides.....rose to red-violet
Nuclei.....blue

Preparation: 1) Diastase Solution -
To 1 gm. sodium chloride, 0.163 gm. dibasic sodium phosphate (Na_2HPO_4 anhyd.), and 0.1 gm. monobasic sodium phosphate ($NaH_2PO_4.H_2O$) add 125 ml. distilled water. Pour off 25 ml. and to remaining 100 ml. add 1 gm. malt diastase.[1]

2) Schiff Reagent -
To 100 ml. boiling distilled water add 1 gm. basic fuchsin[2] and stir. Cool to 50° C. and filter. Add 20 ml. 1N HCl and cool to 25° C. Add 1 gm. potassium metabisulfite ($K_2S_2O_5$ anhyd.) and keep in dark several days. After sulfurous

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[1]Nutritional Biochemicals Corp., Cleveland, Ohio

[2]National Aniline Div., Allied Chemical & Dye Corp., New York, N. Y.

acid has decolorized as much of fuchsin as it will, add one spatula decolorizing carbon, mix, and filter. Store in dark bottle in refrigerator, protected by layer of xylene.

3) Dilute Schiff Reagent -
To 60 ml. conc. Schiff reagent add 240 ml. 10% potassium metabisulfite.

D. Gallego's Iron Fuchsin (Conn, Darrow and Emmel, 1962).

Procedure:

1. Bring deparaffinized sections down to distilled water.
2. Stain in Weigert's iron hematoxylin solution.....6 min.
3. Wash in running tap water.....1 min.
4. Place sections in mordant.....30 sec.
5. Rinse in distilled water.
6. Stain in fresh working solution of carbol-fuchsin.....2 min.
7. Rinse in distilled water
8. Return sections to mordant.....2 min.
9. Rinse in distilled water.
10. Stain in aniline blue - picric acid solution.....1 min.
11. Rinse in 0.1% acetic acid.
12. Dehydrate and clear in several changes of acetone, acetone-xylene, and xylene.
13. Mount in Permount®.

Reaction:
Nuclei.....gray to black
Mucus.....blue-violet
Muscle.....green to orange-yellow
Cartilage.....purple to violet
Cytoplasm.....olive to brown
Collagen and Reticulum.....deep blue
Calcium.....reddish to purplish-brown
Mast Cell Granules.....deep red
Elastic Fibers.....purple to red

Preparation:
1) Weigert's Iron Hematoxylin -
Soln. A (to 2 gm. hematoxyline [Roboz] add 200 ml. 95% alcohol)
Soln. B (to 190 ml. distilled water add 2 ml. conc. HCl and 8 ml. 29.1% ferric chloride)
Working Solution (mix equal parts of Soln. A and Soln. B)

2) Mordant -
To 200 ml. distilled water add 1.5 ml. conc. nitric acid, 1 ml. conc. formaldehyde, and 1.5 ml. 29.1% ferric chloride.

3) Carbol-Fuchsin -
Soln. A (to 8 gm. basic fuchsin [Allied] add 16 ml. phenol, 40 ml. 95% alcohol, and 200 ml. distilled water)

Soln. B (to 200 ml. distilled water add 0.4 ml. conc. glacial acetic acid)
Working Solution (mix 7 ml. Soln. A. and 100 ml. Soln. B)

4) Aniline Blue - Picric Acid -
To 0.2 gm. aniline blue (Allied) add 200 ml. sat. aq. picric acid.

E. Orcein-Hematoxylin in Iodized Ferric Chloride (Roman, Perkins, Perkins and Dolnick, 1967).

Procedure:

1. Bring deparaffinized sections down to water and back up to 70% alcohol.
2. Stain in orcein-hematoxylin solution.....2 hrs.
3. Rinse in distilled water until excess stain is removed.
4. Differentiate in 1.2% ferric chloride (observe every 5 sec.)
5. Wash in running tap water.....5 min.
6. Agitate in 0.01% HCl in 70% alcohol.....1 min.
7. Rinse briefly in 70% alcohol and place in distilled water.....2 min.
8. Counterstain in 0.25% aq. metanil yellow.....10 sec.
9. Dehydrate in absolute alcohol, clear in xylene, and mount in Permount®.

Reaction: Coarse and Fine Elastic Fibers.....intense purple
Nuclei.....violet
Other Tissue Elements.....yellow

Preparation: 1) Acid Orcein -
Dissolve 0.25 gm. orcein (Roboz) in 125 ml. 70% alcohol. Add 1 ml. conc. HCl and filter.

2) Hematoxylin -
Dissolve 2 gm. hematoxylin (Roboz) in 40 ml. absolute alcohol and filter.

3) Orcein-Hematoxylin Staining Solution -
Add ingredients in order listed: orcein, 0.2% in 70% alcohol (125 ml.); hematoxylin, 5% in absolute alcohol (40 ml.); ferric chloride, 6% aq. (25 ml.); and iodine, 1% in 2% aq. potassium iodide (25 ml.). Prepare fresh each time and filter before use.

4) 0.25% Metanil Yellow -
To 200 ml. distilled water add 0.5 gm. metanil yellow[1] and 1 ml. 1% acetic acid.

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[1]Hartman-Leddon Co., Philadelphia, Pa.

F. Fontana-Masson Ammoniacal Silver (Lillie, 1965).

Procedure:

1. Bring deparaffinized sections down to distilled water.
2. Immerse in silver nitrate solution at 56° C.....1 hr.
3. Rinse in distilled water.
4. Immerse in 0.2% gold chloride solution.....10 min.
5. Rinse in distilled water.
6. Place in 5% aq. sodium thiosulfate.....5 min.
7. Rinse in distilled water.
8. Dip in 0.25% eosin Y (Roboz) in 95% alcohol.
9. Rinse in 95% alcohol, dehydrate in absolute alcohol, and clear in xylene.
10. Mount in Permount®.

Reaction: Melanin Granules.....black
Other Tissue Elements.....pink

Preparation: 1) Silver Nitrate Solution -
Dissolve 10 gm. silver nitrate in 100 ml. distilled water. To 95 ml. this solution add conc. ammonium hydroxide until precipitate disappears. Add, drop by drop, enough of remaining silver nitrate solution to cause slight turbidity. Allow to stand overnight. Prior to using, dilute each 25 ml. of silver nitrate stock solution with 75 ml. of distilled water. Filter before use.

G. Acid Mucopolysaccharide Technique (Reinhart and Abul-Haj, 1951).

Procedure:

1. Bring deparaffinized sections down to water and back up to 70% alcohol.
2. Place in 3% glacial acetic acid.....5 min.
3. Stain in acid-colloidal complex iron solution.....10 min.
4. Wash in distilled water until sections are colorless.
5. Immerse in ferrocyanide-hydrochloric acid solution...10 min.
6. Rinse in two changes distilled water.
7. Stain in aluminum ammonium sulfate - cochineal solution.....15 min.
8. Wash in running tap water.....5 min.
9. Rinse in distilled water.....2 min.
10. Stain in picrofuchsin solution.....6 min.
11. Without washing, pass quickly to 95% alcohol and dehydrate in absolute alcohol.
12. Clear in xylene and mount in Permount®.

Reaction:
Nuclear Chromatin.....delicate brownish-gray
Collagen.....red
Mucopolysaccharides.....bright blue
Mucoproteins.....buff - orange
Fibrin.....buff - orange
Glycoproteins.....buff - orange
Cell Cytoplasm.....greenish-yellow to orange

Preparation: 1) Colloidal Iron -

To 333 ml. distilled water add 100 gm. ferric chloride and 133 ml. glycerin. Then add 33 ml. conc. ammonium hydroxide and mix until precipitate dissolves. Repeat addition of ammonium hydroxide using the following successive quantities: 16.6 ml., 10.0 ml., and 6.6 ml. The product of this reaction is a clear, deep red-brown colloidal solution of ammonium ferric glycerate.

This solution is then dialyzed as follows - for 5 min. soak a sausage bag (18" x 1 7/8") in distilled water. Tie off one end and add 533 ml. of solution. Tie off other end at the 18" mark, place in large beaker of distilled water and use magnetic stirrer.[1] This requires 8-10 changes over a 72 hour period. Solution will increase to approximately 1400 ml. and is quite stable.

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[1]Cat. No. 1250, Lab-Line Instruments, Inc., Chicago, Ill.

2) Acid-Colloidal Complex Iron Solution –
To 40 ml. colloidal iron solution add 10 ml. glacial acetic acid.

3) Ferrocyanide-Hydrochloric Acid Solution –
To 20 ml. 2% potassium ferrocyanide [$K_4Fe(CN)_6$] add 40 ml. 1% HCl.

4) Aluminum Ammonium Sulfate – Cochineal Solution –
To 450 ml. distilled water add 26 gm. aluminum ammonium sulfate [$AlNH_4(SO_4)_2.12H_2O$]. Dissolve by heating to 85° C. and add 30 gm. powdered cochineal.[1] Stir thoroughly. At 85° C. add 5 ml. conc. ammonium hydroxide SLOWLY and stir until precipitate dissolves. Now boil vigorously 35 minutes. Add 150 ml. distilled water, cool, filter, and add several phenol crystals.

5) Picrofuchsin Solution –
To 95 ml. sat. aq. picric acid add 6 ml. 1% acid fuchsin (Matheson).

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[1]Matheson Coleman & Bell, Div. of Matheson Co., Inc., Cincinnati, Ohio.

H. Osmium Iodide Method (Mishima and Miller-Milinska, 1961).

Procedure:

1. Trim away excess fat and cut whole-thickness pieces of skin 4 x 4 mm.
2. Immerse in 1:3 solution at room temperature.....overnight
3. Wash in running tap water.....5 min.
4. Dehydrate in 70% alcohol.....8 hrs.
5. Dehydrate through absolute alcohol, clear in toluene, and embed in paraffin.
6. Cut 15 micron tissue sections.
7. Deparaffinize in two changes xylene.....5 min. each
8. Mount in Permount®.

Reaction: Amelanotic Melanocytes, Melanotic Melanocytes, Langerhans Cells, Myelin Sheaths, and Lipids.....black

Preparation: 1) 1:3 Solution –
Mix 1 part 2% osmic acid and 3 parts 3% sodium iodide just before use.

II. HISTOCHEMICAL TECHNIQUES.

A. Phosphorylase (Takeuchi and Kuriaki, 1955; Smith, Perkins and Machida, 1966).

Procedure:

1. Incubate fresh frozen, 40 micron tissue sections in substrate at 37° C.....20 min.
2. Continue to incubate in substrate at room temperature.....15 min.
3. Agitate in 10% aq. Lugol's iodine solution until color develops.
4. Dehydrate in two changes absolute alcohol (to which 1 mg./ml. iodine is added).....5 min. each
5. Clear in two changes xylene (to which 1 mg./ml. iodine is added).....5 min. each
6. Mount in Histoclad [1] (to which 1 mg./ml. iodine is added).

Reaction: Glycogen.....henna
Amylose.....gray-violet

Preparation: 1) 0.1M Acetate Buffer (pH to 5.8) -
0.1M Acetic Acid (to 497 ml. distilled water add 3 ml. glacial acetic acid)
0.1M Sodium Acetate (to 6.8 gm. sodium acetate add 500 ml. distilled water)
Buffer (To 25 ml. 0.1M acetic acid add 475 ml. 0.1M sodium acetate) Adjust pH.

2) Substrate -
To 100 mg. glucose-1-phosphate[2], 20 mg. adenosine-5-phosphoric acid[3], and 10 mg. glycogen (Nutribio) add 30 ml. distilled water, 20 ml. 0.1M acetate buffer, 1 ml. insulin (1 ml. = 40 units)[4], and 10 ml. absolute alcohol.

3) Lugol's Iodine Solution -
To 2 gm. potassium iodide and 1 gm. iodine crystals add 1000 ml. distilled water.

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[1]Cat. No. A-1399, Clay-Adams Co., New York, N. Y.

[2]A grade cryst. dipotassium salt, dihydrate, Calbiochem, Los Angeles, Calif.

[3]Muscle adenylic acid, type II, Sigma Chemical Co., St. Louis, Mo.

[4]No. M-340, NPH Iletin , Eli Lilly & Co., Indianapolis, Ind.

B. Succinic Dehydrogenase (Farber and Louviere, 1956).

Procedure:

1. Incubate fresh frozen, 40 micron tissue sections in substrate at 37° C.....45 min.
2. Place directly into 10% formalin in refrigerator....overnight
3. Wash in distilled water.
4. Mount sections in Glycerol-Gelatin.[1]

Reaction: Sites of Enzyme Activity.....blue

Preparation: 1) 0.1M Phosphate Buffer (pH 7.4) – 0.1M Sodium Phosphate (to 7.2 gm. dibasic sodium phosphate – Na_2HPO_4 anhyd. – add 500 ml. distilled water). 0.1M Potassium Phosphate (to 2 gm. monobasic potassium phosphate – KH_2PO_4 anhyd. – add 150 ml. distilled water). Buffer (to 404 ml. 0.1M sodium phosphate add 96 ml. 0.1M potassium phosphate). Adjust pH.

2) Substrate – To 6 ml. 0.5M sodium succinate[3] add 20 ml. 0.1M phosphate buffer, 6 ml. 0.004M calcium chloride, 3 ml. freshly prepared 0.6M sodium bicarbonate, 10 ml. distilled water, 14 ml. 0.1% nitro blue tetrazolium[4], and 1 ml. 0.1% methylene blue.[5]

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[1]Stock No. GG–1 (Sigma).

[2]Cat. No. 36483, The Varniton Company, Burbank, Calif.

[3]Cat. No. S–413, Fisher Scientific Co., Fair Lawn, N. J.

[4]Grade III (Sigma).

[5]Methylthionine chloride, U. S. P. XII, Millinckrodt Chemical Works, New York N. Y.

C. Cytochrome Oxidase (Burstone, 1959, 1960).

Procedure:

1. Incubate fresh frozen, 40 micron tissue sections at room temperature.....1 hr.
2. Transfer to 10% cobalt acetate.....1 hr.
3. Wash in distilled water.
4. Transfer to 10% formalin in refrigerator.....overnight
5. Wash in distilled water.
6. Mount sections in Glycerol-Gelatin.

Reaction: Sites of Enzyme Activity.....blue

Preparation: 1) 0.2M Tris Buffer (pH 8.0) –
0.2M Tris[1] (to 12.1 gm. Tris add 500 ml. distilled water).
0.1M HCl (to 495.8 ml. distilled water add 4.2 ml. conc. HCl).
Buffer (to 250 ml. 0.2M Tris add 300 ml. 0.1M HCl and 450 ml. distilled water).
Adjust pH.

2) Substrate –
To 0.5 ml. absolute alcohol add 12 mg. p-amino-diphenylamine[2], 2 drops 8-amino-1,2,3,4-tetra-hydroquinoline[3], 35 ml. distilled water, and 15 ml. 0.2M Tris buffer. Just before substrate is used, add 20 mg. cytochrome C[4], shake, and filter in refrigerator.

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[1]2-amino-2-(hydroxymethyl)-1,3-propanediol, Eastman Organic Chemicals, Rochester, N. Y.

[2]N-phenyl-p-phenylene diamine (Sigma)

[3]Grade II (Sigma)

[4]Equine heart, salt free, type II (Sigma)

D. Monoamine Oxidase (Glenner, Burtner and Brown, 1957).

Procedure:

1. Incubate fresh frozen, 40 micron tissue sections at 37° C.....1 1/2 hrs.
2. Transfer directly to 10% formalin in refrigerator.....overnight
3. Wash in distilled water.
4. Mount sections in Glycerol-Gelatin.

Reaction: Sites of Enzyme Activity.....blue

Preparation: 1) 0.1M Phosphate Buffer (pH 7.6) -
0.1M Disodium Phosphate (to 7.2 gm. dibasic sodium phosphate - Na_2HPO_4 anhyd. - add 500 ml. distilled water).
0.1M Monosodium Phosphate (to 0.68 gm. monobasic sodium phosphate - $NaH_2PO_4.H_2O$ - add 100 ml. distilled water).
Buffer (to 435 ml. 0.1M disodium phosphate add 65 ml. 0.1M monosodium phosphate). Adjust pH.

2) Substrate -
To 150 mg. tryptamine hydrochloride[1] add 12 mg. sodium sulfate, 15 mg. nitro blue tetrazolium (Sigma), 15 ml. 0.1M phosphate buffer, and 45 ml. distilled water.

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[1][3-(2-aminoethyl)indole hydrochloride] cryst. (Sigma)

E. Acid Phosphatase (Burton, 1954).

Procedure:

1. Fix fresh frozen, 40 micron tissue sections in chilled 10% formalin in refrigerator.....4 hrs.
2. Rinse in cold distilled water.
3. Incubate fixed tissue sections in substrate, on ice.30 min.
4. Rinse in cold distilled water.
5. Place in 10% formalin in refrigerator.....overnight
6. Rinse in distilled water.
7. Mount sections in Glycerol-Gelatin.

Reaction: Sites of Enzyme Activity.....deep pink

Preparation: 1) 0.1M Acetate Buffer (pH 5.0) -
Soln. A (to 248.5 ml. distilled water add 1.5 ml. glacial acetic acid).
Soln. B (to 6.8 gm. sodium acetate add 500 ml. distilled water).
Buffer (mix 150 ml. Soln. A and 350 ml. Soln. B). Adjust pH.

2) Substrate -
To 10 mg. sodium alpha-naphthol acid phosphate[1] add 50 ml. 0.1M acetate buffer and 150 mg. naphthanil diazo blue B.[2] Filter in refrigerator.

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[1]Dajac Laboratories, Div. of Borden Chemical Co., Philadelphia, Pa.

[2]o-dianisidine (Dajac)

F. Alpha-Naphthol Esterase (Gomori, 1952).

Procedure:

1. Fix fresh frozen, 40 micron tissue sections in chilled 10% formalin in refrigerator.....4 hrs.
2. Rinse in cold distilled water.
3. Incubate fixed tissue sections in substrate, on ice.....15 min.
4. Rinse in cold distilled water.
5. Place in 10% formalin in refrigerator.....overnight
6. Rinse in distilled water.
7. Mount sections in Glycerol-Gelatin.

Reaction: Sites of Enzyme Activity.....red-brown

Preparation:
1) Stock Solution -
1% alpha-naphthol acetate[1] in 50% acetone.
2) 0.2M Disodium Phosphate -
To 2.8 gm. dibasic sodium phosphate - Na_2HPO_4 anhyd. - add 100 ml. distilled water.
3) Substrate -
Pipette 0.5 ml. refrigerated stock solution into 50 ml. distilled water. Add 2 ml. 0.2M disodium phosphate and 20 mg. naphthanil diazo blue B (Dajac). Mix and filter in refrigerator.

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[1]Cat. No. 2380 (Eastman)

G. Alkaline Phosphatase (Gomori, 1952).

Procedure:

1. Fix fresh frozen, 80 and 100 micron tissue sections in 10% formalin in refrigerator.....4 hrs.
2. Rinse in distilled water.....15 min.
3. Incubate in preheated 37° C. substrate.....1 hr.
4. Rinse in 2% calcium chloride.....3 min.
5. Rinse in distilled water.
6. Rinse in 2% cobalt chloride.....5 min.
7. Rinse in five changes distilled water.
8. Place in dilute ammonium sulfide (1 ml. conc./ 74 ml. distilled water).....30 sec.
9. Rinse in two changes distilled water.
10. Place in 10% formalin in refrigerator.....overnight
11. Rinse in distilled water.
12. Dehydrate through absolute alcohol, clear in xylene, and mount in Permount®.

Reaction: Sites of Enzyme Activity.....black

Preparation: 1) Substrate -
To 10 ml. 2% calcium chloride add 10 ml. 2% sodium glycerophosphate[1], 5 ml. 2% sodium barbital[2], 25 ml. distilled water, and 0.5 ml. 10% magnesium sulfate.

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[1]Cat. No. S-314 (Fisher).

[2]Cat. No. 3708 (Mallinckrodt).

H. Acetyl- and Butyrylcholinesterase (Koelle and Friedenwald, 1949).

Procedure:

1. Fix fresh frozen, 80 and 100 micron tissue sections in 10% formalin in refrigerator.....4 hrs.
2. Rinse in distilled water.....15 min.
3. Incubate in preheated 37° C. substrate.....4 hrs.
4. For controls....add 4 drops eserine per 10 ml. substrate.
5. Rinse in four changes of sat. sodium sulfate.
6. Place in dilute ammonium sulfide.....30 sec.
7. Rinse in two changes distilled water.
8. Place in 10% formalin in refrigerator.....overnight
9. Rinse in distilled water.
10. Dehydrate through absolute alcohol, clear in xylene, and mount in Permount®.

Reaction: Sites of Enzyme Activity.....dark brown

Preparation: 1) Stock Solution -
Place 68 gm. sodium sulfate ($Na_2SO_4 \cdot 10\ H_2O$) in graduated cylinder and add to 170 ml. with distilled water. Add 0.3 gm. copper sulfate ($CuSO_4 \cdot 5H_2O$), 0.375 gm. glycine[1], and 1 gm. magnesium chloride ($MgCl_2 \cdot 6H_2O$) to sat. 40% sodium sulfate solution and mix. Then mix 1.75 gm. maleic anhydride[2] and 30 ml. 4% aq. sodium hydroxide. Adjust pH to 5.2 and add to mixture.

2) Substrates -
ATCh (to 100 mg. acetylthiocholine iodide [Sigma] add 50 ml. stock solution).
BTCh (to 125 mg. butyrylthiocholine iodide [Sigma] add 50 ml. stock solution)

3) Eserine -
For a 5×10^{-3}M aq. solution, add 103.5 mg. eserine[3] to 50 ml. distilled water.

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[1]Aminoacetic acid, cryst. (Sigma).

[2]Cat. No. A-168 (Fisher).

[3]Physostigmine salicylate, Merck & Co., Inc., Rahway, N. J.