DENTAL CARIES IN MAMMALS AS RELATED TO DIET AND TOOTH CROWN STRUCTURE

by

Harry H. Negley, III

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SIGNED: Harry H. Negley, III

APPROVAL BY THESIS DIRECTOR

This thesis has been approved on the date shown below:

E Lendell Cockrum — 13 august 1960

E. LENDELL COCKRUM
Associate Professor of Zoology

Date

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ABSTRACT

Although dental caries in mammals have been investigated using laboratory animals, few studies have been made concerning their incidence and distribution in wild mammals. Laboratory investigations have revealed three important factors influencing dental caries: influence of salivary gland secretions; dietary history; and genetic strains.

Feral mammals show great variation in their diet. Diets are influenced by the interaction of many factors including the morphology of the mammal, its distribution, age, sex, and individual food preferences. Basically three major categories of diet types are recognized: herbivorous (eat plants, grasses, etc.); carnivorous (eat meat); and omnivorous (eat a combination of the other two).

In mammals the majority of dental caries occur in the molar teeth. Structurally six basic types of mammalian molar teeth are recognized: tubercular, sectorial, bunodont, selenodont, lophodont, and myrmecophagous.

In this study I examined the teeth of 3,243 wild-taken mammals, representing nine different orders and thirty-eight different families and found only nineteen specimens with caries. In other words only 0.58% of the individuals examined had dental caries. All nineteen of the individuals with caries were members of the Order Carnivora and seventeen of them were members of the Family Ursidae (bears). The other two carious mammals were in the closely related Family Procyonidae (raccoons and allies) and were coatimundis (Nasua).

The type tooth crown structure does not appear to be related to cause or prevention of dental caries but is merely a modification for best chewing the food of the basic diet. The low incidence of dental caries in wild mammals appears to be the result of several factors: (1) Many are so short-lived that caries do not have an opportunity to develop and (2) in those that are medium to long-lived, diet appears to be more important than tooth structure. The food preferences of an animal may have a genetic basis or may result from learning from the parent. Through either one of these processes, and possibly both, a mammal becomes either caries resistant or caries susceptible.

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INTRODUCTION

This study was undertaken to determine the relationship between the incidence of dental caries in feral (wild) mammals living in natural conditions and their diets and/or the structure of their teeth.

Dental caries have plagued man since the time of his remote ancestors. The history of the need for and the development of modern dental techniques has been recounted many times and need not be repeated here. The Index to Dental Literature (published by the American Dental Association) and Rothstein (1958) will furnish additional references for those interested in this subject.

In recent years the cause of dental caries has been the subject of much investigation. Many of these investigations have been carried out using laboratory mammals as experimental subjects. Mammals used include the Syrian hamster (Cricetus auratus), Norway rats (Rattus norvegicus), and cotton rats (Sigmodon hispidus). These animals have been used for dental research for three reasons: their availability; the fact that their molar teeth have growth patterns similar to those in man; and finally, under certain conditions, carious lesions are formed which resemble those found in man (Sognnaes:1955).

Although the present study is restricted to a survey of the incidence of caries in feral mammals, three aspects of the laboratory experiments appear to bear on the interpretation of this study. These are: effect of diet; effect of saliva; and genetic studies.

General conclusions reached concerning the effect of diet on dental caries include that caries susceptibility appears to depend upon the dietary history of the animals during the period of tooth development. In rats fed by stomach tubes, thus eliminating food from coming into contact with the oral cavity, no caries were produced. This seems to indicate that certain food substrates are necessary in the oral cavity in order for caries to be produced. There are also indications that caries production depends upon the form in which sugar is ingested and the age at which the animals are first introduced to this dietary component (Sognnaes: 1955).

Removal of the salivary glands greatly increases dental caries. This must indicate conversely that salivary secretions are of benefit in the prevention of dental caries (Sognnaes: 1955). An examination of hamsters showed that in animals free of caries, pH readings of the saliva ranged from 6.9 to 9.9. In fifteen carious lesions, the saliva tested gave mean readings of pH 6.5 in contrast to mean values of pH 8.0 obtained on sound surfaces of the same teeth (Johansen and Keys in Sognnaes: 1955).

The question of whether or not there is an inheritance factor in the development of caries has been investigated in the albino rats (Rattus). Through phenotypic selection, progeny testing, and intensive inbreeding, two strains of rats were produced. One was highly susceptible to caries and the other was highly resistant to caries. The results showed that the average number of days required to produce the first carious cavity in a lower molar tooth for the strain of susceptible rats decreased from 57 days for the second generation to 35 days for the twenty-fifth

generation. The average caries time for the resistant strain of rats increased from 116 days for the second generation to 505 days for the seventeenth generation (Hunt, Hoppert, and Rosen in Sognnaes: 1955). However, the target through which genetic factors act on tooth decay has not been established (Sognnaes: 1955).

A survey of the literature reveals that few studies have been made concerning caries in feral populations of mammals. This study consists of (1) a literature survey of the diets of the various mammals in their native habitat; (2) a consideration (from an examination of the pertinent literature and from an examination of the pertinent features) of the factors influencing the diet of mammals and (3) an examination of the teeth of specimens of wild-taken mammals. The specimens examined include members of all of the living orders of the Class Mammalia with the exception of the Primates, Cetaceans, and Sirens.

The specimens examined in this study are in the Museum, Department of Zoology, University of Arizona, Tucson, and the American Museum of Natural History, New York City. The classification used is that found in Simpson's The Principles of Classification and a Classification of Mammals (1945).

I would like to express my sincere thanks and appreciation to my major professor E. Lendell Cockrum, Associate Professor of Zoology, University of Arizona, Tucson, for his beneficial assistance in the preparation of this manuscript and to Professors W. H. Brown and A. R. Mead for their many kind suggestions. I would also like to thank Dr. Richard G. Van Gelder, Chairman of the Department of Mammals, the American Museum of Natural History, New York City, for allowing me to examine specimens in the mammal collection of that museum.

DIETS

The diet of mammals varies greatly. A number of interacting factors including the morphological structure of the mammal, the geographical and ecological distribution of the species and of the food materials, and the individual mammal's food preferences, influence the diet of any given individual. Cockrum (1960) has summarized the major characteristics of the living orders and families and forms the basis of the following generalizations.

Several different morphological features such as type of locomotion, structure of teeth, and structure of the stomach influence the food gathering possibilities of a mammal.

Most mammals have ambulatory or walking locomotion. They are able to obtain food by browsing or grazing. Some have adaptations which enable them to move among the limbs of trees, that is, arboreal locomotion. These mammals can not only feed on the ground food sources but can also feed on food which is available in trees such as fruit, nuts, leaves, and similar items. Fossorial or underground locomotion, such as found in the moles (Talpidae), enables some to feed on subterrestrial food such as roots and buried insect larvae and pupae. Aquatic locomotion limits the mammals diet to aquztic forms of life. This is the case with the whales (Cetacea) and the seals (Pinnipedia). Their entire life is spent in the water, thus they must obtain all of their food from this source. The bats, Chiroptera, have aerial locomotion and their diet is composed largely of flying insects which they pick out of the air while

in flight.

The structure of the mammal's teeth and mouth is another important morphological characteristic. The spiny "anteater" has no teeth but it does possess an elongated snout which it passes over the ground and a sticky tongue which it can extend and pick up ants. The banded anteater, Family Myrmecobiidae, has teeth but it also has a cylindrical, extensible tongue which it uses to pick up ants, insects, and termites. The fruit-eating bats, Pteropodidae, have teeth with blunt cusps and an elongated snout enabling them to be better adapted for a frugivorous and nectivorous diet while most other bats have teeth with sharp cusps for chewing their insectivorous diet. The whalebone whales, suborder Mysticeti, have rudimentary teeth in embryonic life and these teeth are replaced by baleen in the adults. Baleen is a cornified epithelial structure which develops from papillae of the mucous membrane along the maxillary dental arch. It hangs from the palate in thin plates and is set close together with the bases parallel to each other. These whales obtain food by opening their mouths and allowing the food and water to enter the oral cavity. The water is then forced out of the mouth using the baleen as a strainer and the food is retained and swallowed. There is no mastication of food. The grass-eating mammals show adaptations in their tooth crown structure. The teeth are hypsodont or high crowned, allowing for much wear. This is especially noticeable in the cud-chewing ruminants.

The structure of the stomach in various mammals varies. At one extreme are the ruminants which have either a three or four chambered stomach and after swallowing their food it is regurgitated and the mammal rechews this food or cud. The digestive tract and especially the caecum

are greatly lengthened and enlarged, thus permitting greater digestive enzyme activity and bacterial decomposition of the grasses making up their food. Perhaps at the other extreme are the vampire bats, Desmodontidae, in which the stomach is a slender caecum-like structure and the intestine is extremely reduced in length and complexity. After a meal of blood the stomach becomes quite distended. Since its diet is chiefly blood and no solid food, as is evidenced by its liquid excreta (Hall and Kelson: 1958), little digestive action is necessary to convert the food into basic nutritional units for absorption into the blood stream.

Geographic distribution obviously affects the diet of mammals. Some mammals have a wide geographical range while others are extremely limited in their distribution. This range is not stable; rather as a result of the interaction of many environmental factors such as climate and population pressure, (Cockrum: 1960), it is continually expanding and contracting. It is equally obvious that the available foods in these areas are variable. For example a species such as the mountain lion (Felis concolor) whose geographic distribution extends from the northern cold regions to the tropics has a wide range of diet. In the north its prey is an entirely different assemblage of rodents, lagomorphs, and other mammals than those which occur in the tropics. Such animals, with a wide range of acceptable food species are known as euryphagous. In contrast is the koala (Phascolarctos) of Australia which only feeds on the leaves and shoots of a few species of eucalyptus trees. Such animals are stenophagous.

The type of environment normally inhabited by a species of mammal makes up its ecological range. This ecological distribution is an important factor in mammalian diets. The obvious animal environments are salt water, fresh water, and land. The land has many subdivisions

such as grasslands, desert, forests, and plains. Various food sources are found in each of these. Therefore the mammal's diet is limited to the type of food available in its own ecological range.

The relative abundance of food affects a mammal's diet. Mammals who eat the same type of food year round have trouble maintaining their diet in arctic and temperate regions as a result of seasonal variations in food sources. For this reason some mammals such as the insectivorous bats and the ground squirrels which feed on green vegetation hibernate during the winter when food is not available and become active only during the spring and summer when food is in abundance. Mammals who do not hibernate find it necessary to migrate to other areas during seasons when their chief diet is not available. Mammals which eat the year round show seasonal variations in their diet. Their diet is determined by the type of food available at a given time such as is the case with the red fox (Vulpes fulva) which is primarily carnivorous in winter and eats insects and plants in other seasons (Scott and Symons: 1958).

The individual animal has food preferences. These preferences are illustrated quite clearly by the age of the animal. Following birth the young mammal's diet consists of milk supplied by its mother. As it grows older it follows the food patterns of its parents and finally in old age it depends frequently upon eating carrion left by the other animals. It it believed that there may be variations in the diet which might be correlated with the sex of the animal but no specific references to studies of this nature have been found.

In spite of the large number of variables influencing diets, most mammals can be readily classified according to the type of foods they eat.

A mammal may eat only vegetation such as plants, seeds, fruits, etc. In this case it is classified as being herbivorous. If the mammal eats meat only it is carnivorous. Mammals which eat practically anything are omnivorous. The herbivores and carnivores are further sub-divided depending upon the specific type of food which they eat. Some of the more common categories of diets are shown in Figure 1.

The following is an attempt to correlate diets to the taxonomic classification of mammals, an undertaking that has not been wholly successful since many orders of mammals are extremely widespread and diverse, both in morphology and in food preferences. In such orders examples of specific mammals and their diets are given.

Order Monotremata - Egg-laying mammals. There are only two families found in this order, Ornithorhynchidae and Tachyglossidae. The duckbilled platypus (Ornithorhynchus) has a diet of aquatic insects, small crustaceans, and worms. The spiny "anteaters" (Tachyglossus and Zaglossus) have a diet of insects, ants, termites, and worms. (Henderson and Craig: 1932).

Order Marsupalia - Pouched mammals. In this order there is great variation as to diet among the various species. Members of the Family Caenolestidae feed mainly on insects while the Dasyuridae are carnivorous feeding on meat, blood, and insects. Some members of the Family Macropodidae are herbivorous, others are insectivorous. The kangaroo (Macropus) is herbivorous (Bourliere: 1956). The marsupial mole (Notoryctes) of the Family Notoryctidae eats insects, insect larvae, and earthworms. Bandicoots of the Family Peramelidae are mostly carnivorous but a few are herbivorous. The members of the Family

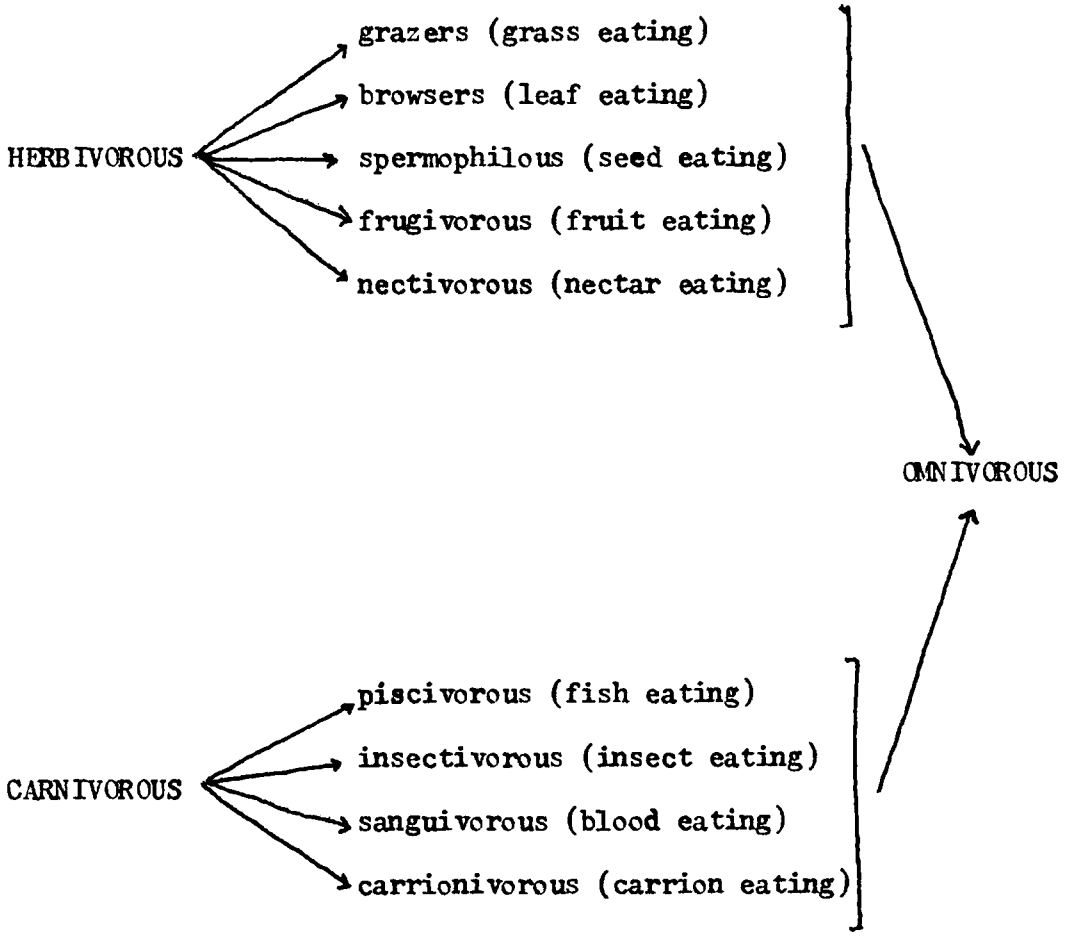


Fig. 1. The classification of mammalian diets.

Phalangeridae have diets which range from insects and insect larvae to nectar, honey, flowers, leaves, and fruits. One interesting member of this family, the koala bear (Phascolarctos cinereus cinereus), eats only the leaves of eucalyptus trees of the species Eucalyptus punctata, E. microcorys, E. melliodora, and E. rostrata (Bourliere:1956). The Family Didelphidae is a good example of the large variation of diets found in any one group of mammals. The common opossum of eastern United States (Didelphis marsupalis) is variously classified as an insectivore, an herbivore, and an omnivore. Latham (1950) for example states that this mammal eats mostly insects with some vegetable matter while Scott and Symons (1958) thought that it is chiefly herbivorous. Anthony and McSpadden (1917) list the diet of the opossum as omnivorous, consisting of birds and eggs, mice, frogs, fish, insects, and fruits. The diet probably varies according to the region which Didelphis inhabits and the season during which the observations on food habits were made. Hall and Kelson (1958) in referring to the Family Didelphidae in North America claim that some of the family is insectivorous while others are carnivorous and that all are probably to some extent omnivorous.

Order Insectivora - Insectivores. From the ordinal name one might assume that all members of this order are insectivorous. Such, however, is not the case although some are strictly insectivorous. Members of the Family Chrysochloridae eat earthworms, caterpillars, grubs and beetles while members of the Family Erinaceidae have substantially the same diet with the addition of rats, mice, snakes, frogs, roots, and eggs. The Macroscelididae are insectivorous while the Potamogalidae are mainly piscivorous, feeding on small fish and some crustaceans. The Solenodontidae are omnivorous, feeding on a variety of insects, small reptiles, birds, and

fruit. The Soricidae, or shrews, have a diet which includes insects, annelids, mollusks, centipedes, millipedes, sowbugs, arachnids, vegetables, small vertebrates, and inorganic matter (Hamilton: 1930). More specifically, the shorttail shrew (Blarina brevicauda) eats insects and meadow mice as does the least shrew (Cryptotis parva) (Anthony: 1917). Miller (1930) observed that in captivity the dusky shrew (Sorex obscurus) ate grasshoppers, stink bugs, earthworms, and watermelon rind.

The Talpidae, or moles, have a diet which includes earthworms, insect larvae, small amphibia and reptiles, aquatic insects, small crustaceans and fish. Hisaw (1923) noted that moles (Scalopus) are predominantly carnivorous having a diet consisting mainly of earthworms, white grubs, and adult insects, but also including corn, ripe tomatoes, Irish potatoes, and apples. Townsend's mole (Scapanus townsendii) in its native habitat has been observed to eat earthworms, insect larvae and pupae, centipedes, slugs, mature insects, and vegetables. In captivity it ate meat instead of vegetables and this meat consisted of earthworms, ground beef, chicken, veal, liver, and pork (Wight: 1928).

Order Dermoptera - Flying lemur. In this order there is but one living family, Cynocephalidae, and a single genus, Cynocephalus or flying lemur. It has a diet of fruit and leaves.

Order Chiroptera - Bats. Although the majority of bats are strictly insectivorous, one finds some species which are strictly carnivorous and others which are somewhat omnivorous. The Desmodontidae or vampire bats are sanguivorous or blood feeders. The Molossidae are insectivorous and the mastiff bat (Molossus = Eumops) is known to be a strict insectivore (Anthony: 1917). The Family Noctilionidae has a diet

which includes insects, fish, aquatic insects, and shrimp. One species of Noctilio has been observed to eat mole-crickets, ants, spiders, beetles, cockroaches, and insect eggs (Goodwin: 1928) and Noctilio leporinus has been observed to eat fish (Bourliere: 1956).

The Family Nycteridae is insectivorous while the Peteropodidae are mainly frugivorous (soft fruits and fruit juices) but some are nectivorous. Eonycteris and Megaloglossus of this family have both been observed to have a diet of nectar and pollen (Bourliere: 1956). The Vespertilionidae are chiefly insectivorous. Antrozous pallidus, the pallid bat, has been shown to have a diet of Jerusalem crickets, scorpions, beetles, and grasshoppers (Hatt: 1923). Myotis is insectivorous (Anthony: 1917) and in captivity Myotis lucifugus, the little brown myotis, ate moths and a few flies (Pittman: 1924). The small-footed myotis, Myotis subulatus, eats Diptera, spiders, scarabacoid beetles, and cuckoo-flies (Seton: 1922). The eastern pipistrel, Pipistrellus subflavus, has been observed to eat Diptera and Coleoptera (Hamilton: 1930). The genera Lasiurus and Eptesicus are all insectivorous (Anthony: 1917). Myotis vivesi (= Pizonyx) is piscivorous (Bourliere: 1956).

The Phyllostomatidae include species which are strictly insectivorous, some which are omnivorous in that they feed on both insects and fruits; still others which are strictly frugivorous and, finally, a small group which are nectivorous. The genera Choeronycteris, Glossophaga, and Lonchophylla are all nectivorous (Bourliere: 1956); the genus Macrotus is insectivorous (Anthony: 1917); and Huey (1925) recorded Macrotus californicus, the California leaf-nose bat, as feeding on grasshoppers, moths, harvest flies, and beetles.

Order Edentata - Sloths, anteaters, and armadillos. Three living families are included in this order. Myrmecophagidae, or anteaters, lack teeth and the three genera of this family Cyclopes, Myrmecophaga, and Tamandua have a diet of arthropods (Bourliere: 1956). The Daspodidae, or armadillos, include the well known nine-banded armadillo (Dasypus novemcintus). In a study of its diet it was found to eat insects, arthropods, snails, slugs, frogs, earthworms, toads, salamanders, eggs, reptiles, and plant life such as fleshy fruits, seeds, mushrooms, blueberries, dewberries, longleaf pine seeds, white bay fruits, muscadine grapes, and black persimmon (Fitch, Goodrum, and Newman: 1952). The Bradypodidae, or sloths, include the three-toed sloth (Bradypus tridactylus) which is herbivorous and eats the leaves, buds, and young shoots of Cecropia palmata (mulberry family) and Spondias lutea (hog plum tree) (Bourliere: 1956).

Order Lagomorpha - Hares and rabbits. There are two families in this order, the Ochotonidae (pikas) and the Leporidae (hares and rabbits). All members of the order are herbivorous (Hall and Kelson: 1958). The pikas (Ochotona) consume green plants, leaves of shrubs, and grasses and often dry and store such foods as hay. The hares and rabbits all feed primarily on green vegetation of a variety of species.

Order Rodentia - Rodents. The Order Rodentia is the largest of the mammalian orders both in number of species and in the number of individuals. Resultantly it is not surprising to find great variations in the diets of the various members of the order. While most rodents are herbivorous, feeding on a wide variety of grasses, bark, leaves, fruits, berries, roots, seeds, and nuts, some are omnivorous and others are almost entirely insectivorous. In the following discussion families are grouped in three suborders: Sciuromorpha, Myomorpha, and Hystricomorpha.

Suborder Sciuromorpha. The mountain "beaver" (Aplodontia rufa) of the Family Aplodontidae is strictly herbivorous. It consumes leaves, ferns, and other vegetation (Anthony: 1917).

The squirrels (Sciuridae) are generally herbivorous. The red-squirrel (Tamiasciurus) has been observed to eat fungi (Bourliere: 1956) and the eastern gray squirrel (Sciurus carolinensis), the Arizona gray squirrel (S. arizonensis), the tassel-eared squirrel (S. aberti), and the eastern fox squirrel (S. niger) all consume seeds, nuts, and other green vegetation. Chipmunks (Tamias and Eutamias) feed chiefly on nuts, seeds, and acorns. The prairie dogs (Cynomys) eat grasses, roots, and other vegetation (Anthony: 1917).

The pocket gophers (Geomyidae) are strictly herbivorous. Geomys and Thomomys are strict vegetarians (Anthony: 1917) and Aldous (1951) found Stellaria tubers, dandelion roots, Erythronium and Claytonia bulbs in underground storage spaces of the northern pocket gopher (Thomomys talpoides).

The beaver (Castoridae) has a diet of bark, twigs, roots, and aquatic plants.

The Heteromyidae have a diet primarily of seeds and some green vegetation. The pocket mouse (Perognathus) and kangaroo rat (Dipodomys) are strict vegetarians eating seeds, grain, and other vegetable matter. (Anthony: 1917).

Suborder Myomorpha. The cricetid rodents (Cricetidae) include a large number of genera and species. Selected examples follow: The tree phenacomys (Phenacomys longicaudus) has a diet of needles and bark of the young shoots of Douglas firs and Gerbillus gerbillus has a diet of seeds (Bourliere: 1956).

The woodrat (Neotoma), the cotton rat (Sigmodon), the rice rat (Oryzomys), the harvest mouse (Reithrodontomys), and the white-footed or deer mouse (Peromyscus) are all herbivorous and have a diet of seeds, grain, and green vegetation (Anthony: 1917). The grasshopper mouse (Onychomys) is omnivorous, feeding on insects, beetles, scorpions, grasshoppers, and occasionally seeds and other vegetation. The meadow mouse (Microtus) is also omnivorous but prefers grass, grain, and other green vegetation (Anthony: 1917). The boreal redback vole (Cleithrionomys gapperi) is omnivorous, consuming seeds, berries, roots, the bark of trees and shrubs, as well as insects. The muskrat (Ondatra zibethicus) has a diet of vegetation, clams, fish, and insects (Anthony: 1917).

The Family Muridae is also a large complex group. More familiar examples follow: The Norway rat (Rattus norvegicus) might well be termed a scavenger in that it eats birds, rodents, lizards, insects, spiders, garbage, seeds, vegetables, and fruits (Bourliere: 1956).

The jumping mice (Zapus) of the family Zapodidae are strictly herbivorous (Anthony: 1917). The Anomaluridae are said to feed on fruit and nuts while the Gliridae have a diet including hazel nuts, eggs, insects, young birds, fruit, seeds, and other vegetable matter.

Suborder Hystricomorpha. This suborder includes the procupine (Erethizon dorsatum) of the Family Erethizontidae which feeds on the bark and twigs of trees. The diets of other hystricomorph rodents, which are mainly South American in distribution, are not at all well known but presumably consist primarily of various vegetable substances.

Order Carnivora - Carnivores. The diet of most members of this order is just as the ordinal name implies, carnivorous. As usual, of

course, there are exceptions, some of which will be noted in the following accounts.

In the dog family (Canidae) the coyote (Canis latrans) has been observed to eat birds, mammals, fish, and fruits (Dixon: 1925). More specifically this diet consists of mice, hares, frogs, snakes, sheep, deer, and ground squirrels (Anthony: 1917). The red fox (Vulpes fulva) is primarily carnivorous in winter and eats insects and plants in other seasons (Scott and Symons: 1958). Latham (1950) lists its diet as including mammals, birds, fishes, insects, apples, grapes, strawberries, blueberries, cherries, sasparilla, grass, wheat, and oats. The gray wolf (Canis lupis), gray fox (Urocyon cinereoargenteus), and kit fox (Vulpes velox) are all meat eaters (Anthony: 1917). Chrysocyon brachyurus, the maned "wolf" of South America has a diet of fruits, small birds, and small armadillos (Miller: 1930).

The bears (Ursidae) are mainly omnivorous. The polar bear (Thalarctos) consumes seals, fish, and other mammals while the Alaska brown bear (Ursus middendorffi) eats salmon and vegetation (Anthony: 1917). The grizzly bear (Ursus horribilis) is omnivorous and feeds on roots, reed grass, horsetail, berries, ground squirrels, birds and eggs, fish and frogs, ants and ant larvae, and it is especially fond of honey and honey bees (Anthony: 1917).

The Procyonidae consist of the raccoons and their relatives. The raccoon (Procyon) is extremely omnivorous, feeding on vegetables, fruits, and meats (Latham: 1950). More specifically its diet includes wild fruits and berries, shell fish, fish, small mammals, reptiles, and birds (Howell: 1921). The ring-tailed cat (Bassariscus astutus) has a diet of small

mammals, birds and eggs (Anthony: 1917). One interesting member of this family is the giant panda (Ailuropoda melanolurea) of Asia. Its diet consists entirely of bamboo shoots (Bourliere: 1956).

The Mustelidae which includes the skunks, weasels, and otters, includes some species that are strictly carnivorous while others are relatively omnivorous. The striped skunk (Mephitis mephitis) and the spotted skunk (Spilogale) have similar diets that consist of small mammals, birds, insects, crayfish, frogs, and snakes (Anthony: 1917). The weasels, mink, and ferret (Mustela) are usually strictly carnivorous but some species are herbivorous at times (Latham: 1950). The black-footed ferret (Mustela nigripes), longtail weasel (Mustela frenata), least weasel (Mustela rixosa), and short-tail weasel (Mustela erminea) are strictly carnivorous (Anthony: 1917) as is the mink (Mustela vison) (Latham: 1950). The river otter (Lutra canadensis) is largely piscivorous (Anthony: 1917) and the European otter (Lutra lutra) has a diet that includes eels, trout, minnows, crayfish, frogs, snails, earthworms, rats, and aquatic birds (Bourliere: 1956). The badger (Taxidea) consumes small mammals and is strictly carnivorous. The wolverine (Gulo luscus) is an omnivorous scavenger (Bailey: 1926). The marten (Martes americana) is known to eat mice, squirrels, rabbits, birds, and sometimes berries, insects, and vegetables (Bailey: 1926). The fisher (Martes pennati) has essentially the same diet (Anthony: 1917).

The cats (Family Felidae) are primarily carnivorous, feeding on live animals that they capture by stalking. The mountain lion (Felis concolor) is carnivorous (Dixon: 1925) as is the ocelot (Felis pardalis), the lynx (Lynx canadensis), the bobcat (Lynx rufus) (Anthony: 1917),

and Felis ramsayi (Miller: 1930).

The Hyaenidae contains carrion feeders such as Crocuta crocuta, the spotted hyaena (Bourliere: 1956).

Order Tubulidentata - Aardvark. This order contains a single living family, Orycteropodidae, with but a single living species, the aardvark (Orycteropus afer). It has a diet strictly composed of arthropods, mainly ants and termites (Bourliere: 1956).

Order Proboscidea - Elephants. This order also contains a single living family, Elephantidae, with but two living species, the African elephant (Loxodonta) and the Indian elephant (Elephas). Both feed on foliage, twigs, grasses, and roots.

Order Perissodactyle - Odd-toed ungulates. This order contains the horses (Equidae), tapirs (Tapiridae), and the rhinocerisis (Rhinocerotidae). All members of this order are basically herbivorous.

Order Artiodactyla - Even-toed ungulates. The deer family (Cervidae) is nourished exclusively on herbaceous plants and foliage (Bourliere: 1956). The elk (Corvus canadensis), mule deer (Odocoileus hemionus), moose (Alces americana), and caribou (Rangifer) all have a diet of grasses, twigs, shrubs, and other foliage (Anthony: 1917).

The Family Bovidae is strictly herbivorous (Bourliere: 1956). The bison (Bison bison), musk-ox (Ovibos moschatus), the mountain sheep (Ovis), and mountain goat (Oreamos) have a diet of grasses and herbaceous plants (Anthony: 1917).

Members of the pig family (Suidae) are rooters. They consume herbs, roots, grubs, and fungi. The Family Tayassuidae includes the

peccary or javelina (Tayassu angulatus). This mammal eats roots, acorns and miscellaneous vegetation (Anthony: 1917).

TOOTH CROWN STRUCTURE

Mammals show great variation in the form of the crowns of their teeth. In general terms the teeth are divisible into four major types, based on the location in the jaw and on the form and function of the individual teeth. Anteriorly are the incisors, followed by the canines, premolars and molars. Primitively there are three incisors in each half of the jaw, both above and below. These teeth normally are nipping in function. Posterior to the incisors are the canines. Primitively there is one canine in each half of the jaw, both above and below. These teeth always have a simple conical crown and are long teeth used for piercing and holding of food. The premolars are located posteriorly to the canines. Primitively there are four premolars in each half of the upper and lower jaws. These teeth are used for shearing, cutting, and slicing. The most posterior teeth are the molars. Primitively there are three molars above and below in each half of the jaw. These teeth are crushing and grinding teeth.

Caries occur most frequently in the molar teeth. This is probably due to the fact that the molars are primarily crushing and grinding teeth as opposed to the nipping and shearing function of the incisors and canine teeth. For this reason in this study observation for dental caries was restricted to the molars.

There are six basic types of molar crown patterns found in mammals. These six types are classified according to the arrangement of the cusps or tubercles located on the occlusal surface of the tooth and as to whether

the crown of the tooth is hypsodont (high crowned) or brachyodont (low crowned). Hypsodont or high crowned teeth are found in the kinds of mammals that feed on a diet of vegetation (grasses, leaves, and woody shoots) wherein there is much wear on the tooth. These six basic types, tubercular, sectorial, bunodont, selenodont, lophodont, and myrmecophagous are described in more detail as follows.

Tubercular. - The tubercular molar crown pattern is the most primitive. It is believed that the other five types of molar crown patterns are modifications of this one. It is brachyodont and has three simple cusps. This type of tooth is modified for a diet of insects and is primarily a crushing and cutting type tooth. It is found in shrews (Soricidae) and some primitive carnivores.

Sectorial. - This type of molar crown pattern is a modification of the tubercular type. It is used for cutting and shearing. The cheek teeth of cats (Felidae) are of the sectorial pattern.

Bunodont. - The bunodont tooth is the third type of molar crown pattern and is also a modification of the tubercular type. It is usually brachyodont, quadrate in shape, and has low, rounded cusps. It is associated with an omnivorous diet. The bunodont type pattern is found in the cheek teeth of pigs (Suidae) and javelina (Tayassuidae) and in man (Homo sapiens).

Selenodont. - A modification of the bunodont type molar crown pattern is the selenodont tooth. It is characterized by having cusps which are worn down and converted into a series of crescents. This type may be brachyodont as in the deer (Cervidae) or it may be hypsodont as found in the cow (Bovidae). This type of molar crown pattern is adapted for an herbivorous diet.

Lophodont. - A second modification of the bunodont type molar crown pattern is the lophodont pattern. In this type the cusps are fused into transverse lophs or ridges with intervening valleys. It is also adapted for an herbivorous diet. In the tapir (Tapirus) it is brachyodont and in the elephant (Elephantidae) it is hypsodont.

Myrmecophagous. - This is the final basic type of molar crown pattern. It is a degeneration of the tubercular type and is found in sloths (Bradypodidae) and armadillos (Dasypus). The teeth of this type are simple peg-like structures lacking an enamel covering.

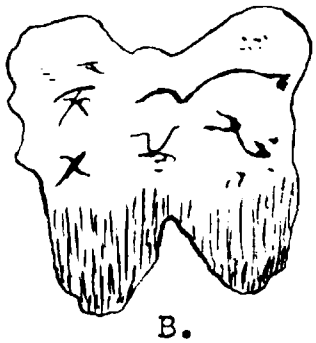
These six basic types of molar crown patterns are diagrammed in Figure 2. Their relationship as to their modification from the tubercular type is shown in Figure 3. Certain intermediate stages of modification are present in the molar crown pattern of mammals. These types are tuberculo-sectorial, buno-selenodont, and buno-lophodont (Cockrum:1955).

Tuberculo-sectorial. - This first type is found in dogs and coyotes (Canis) and is intermediate between the tubercular and sectorial types.

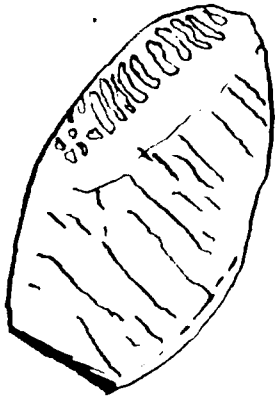
Buno-selenodont. - The buno-selenodont pattern consists of a molar tooth which has bunodont outer cusps and selenodont inner cusps. The extinct Anthrocotherium, a pig-like Artiodactyla, exhibited this type of tooth crown structure.

Buno-lophodont. - In this type of molar crown pattern the outer cusps are bunodont and the inner cusps lophodont. The extinct mastodon (Mastodon tapiroides) had this type of molar crown pattern.

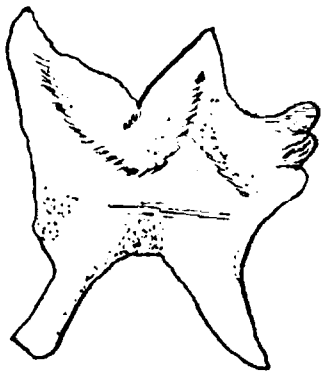
A.



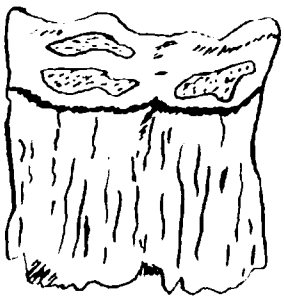
B.



C.



D.



E.

F.

Fig. 2. The six basic types of molar crown patterns.

A. Tubercular

B. Bunodont

C. Lophodont

D. Sectorial

E. Selenodont

F. Myrmecophagous

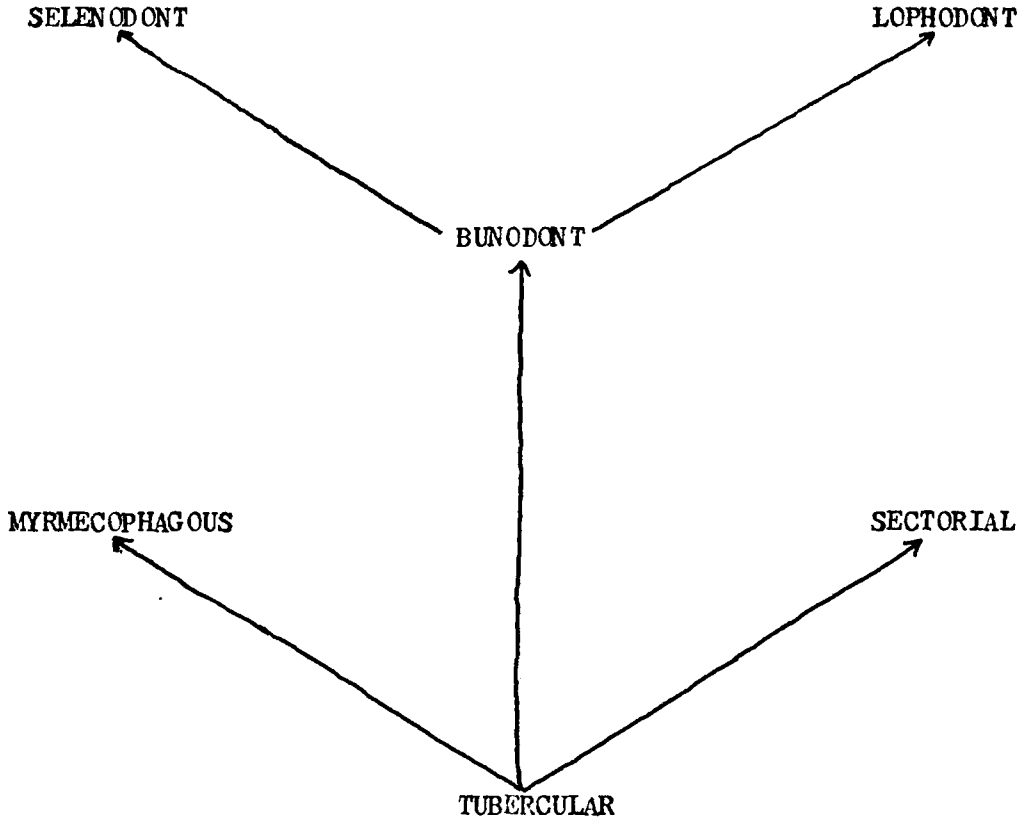


Fig. 3. The six basic molar crown patterns and their pattern of modification from the primitive tubercular type.

SPECIMENS EXAMINED

The following is a list of the specimens examined in this study together with an indication of the dental caries noted. The specimens are arranged by orders and, within the given order, by family and species.

Order Marsupalia - Marsupials. Ten specimens were examined, none of which contained caries. Family Didelphidae: Didelphis, 6; Family Peramelidae: Perameles, 1; Family Phascolomidae: Phascolomis, 1; Family Macropodinae: Protemmodon, 1; Potorous, 1.

Order Insectivora - Insectivores. A total of 43 specimens were examined; no dental caries were found. Family Soricidae: Sorex, 16; Blarina, 3; Cryptotis, 2; Notiosorex, 9; Family Talpidae: Neurotrichis, 1; Scapanus, 5; Scalopus, 5; Parascalops, 1; Condylura, 1.

Order Chrioptera - Bats. A total of 631 specimens were examined; no dental caries were found. One genus of fruit-eating bat, Glossophaga, showed several specimens with dark colored teeth but it is my opinion that the teeth were not carious. Family Pteropidae: Pteropus, 1; Family Emballonuridae: Emballonura, 1; Saccopteryx, 2; Family Phyllostomatidae: Chilonycteris, 9; Pteronotus, 27; Mormoops, 14; Macrotus, 100; Glossophaga, 24; Artibeus, 13; Choeronycteris, 11; Leptonycteris, 33; Family Desmodontidae: Desmodus, 4; Family Natalidae: Natalus, 20; Family Vespertilionidae: Myotis, 129; Lasionycteris, 19; Pipistrellus, 30; Eptesicus, 50; Lasiurus, 22; Plecotus, 28; Antrozous, 40; Family Molossidae: Tadarida, 30; Eumops, 24.

Order Edentata - Edentates. 5 specimens were examined and no

dental caries were found. Family Dasypodidae: Dasypus, 5.

Order Lagomorpha - Hares, rabbits, and pikas. A total of 170 specimens were examined; no caries were found. Family Ochotonidae: Ochotona, 20; Family Leporidae: Lepus, 50; Romerolagus, 10; Sylvilagus, 70; Oryctolagus, 10; Brachylagus, 10.

Order Rodentia - Rodents. A total of 1,351 specimens were examined and no dental caries were found. Family Aplodontidae: Aplodontia, 2; Family Sciuridae: Sciurus, 58; Tamiasciurus, 10; Marmota, 1; Cynomys, 4; Citellus, 118; Eutamias, 33; Glaucomys, 2; Family Geomyidae: Thomomys, 105; Family Heteromyidae: Perognathus, 150; Dipodomys, 200; Family Castoridae: Castor, 3; Family Cricetidae: Reithrodontomys, 25; Peromyscus, 200; Baiomys, 1; Onychomys, 100; Sigmodon, 55; Neotoma, 200; Cricetus, 4; Clethrionomys, 4; Ondatra, 2; Microtus, 38; Family Muridae: Rattus, 5; Mus, 20; Family Zapodidae; Zapus, 3; Napaeozapus, 2; Family Caviidae: Cavia, 3; Family Erethizontidae: Erethizon, 3.

Order Carnivora - Carnivores. 997 specimens were examined and 19 of these had carious lesions. This is approximately 1.9% of the total. 17 bears had dental caries out of a total of 125 examined. Of these 17 carious bears, 3 were Selenarctes, 11 were Ursus, and 3 were Euarctos. The other two carious carnivores were two specimens of Nasua narica narica. Family Canidae: Canis, 70; Alopex, 20; Vulpes, 20; Urocyon, 20; Dusicyon, 5; Chrysocyon, 3; Nyctereutes, 10; Speothos, 5; Cuon, 15; Lycaon, 15; Family Ursidae: Selenarctos, 7; Ursus, 64; Euarctos, 33; Thalarctos, 21; Family Procyonidae: Bassariscus, 27; Procyon, 30; Nasua, 100; Potos, 12; Bassaricyon, 5; Ailurus, 1; Family Mustelidae: Mustela, 20; Martes, 18; Charronia, 4; Galera, 7; Grison, 2; Zorilla, 2; Poecilogale,

2; Gulo, 4; Mellivora, 2; Meles, 8; Arctonyx, 1; Taxidea, 12; Helictis, 5; Mephitis, 110; Spilogale, 60; Conepatus, 94; Lutra, 10; Aonyx, 10; Enhydra, 10; Family Viverridae: Poiana, 2; Genetta, 18; Viverricula, 7; Viverra, 10; Civettictis, 5; Nandinia, 6; Arctogalidia, 2; Paradoxurus, 2; Paguma, 3; Arctitictis, 4; Cynogale, 1; Galidia, 1; Herpestes, 10; Atilax, 2; Mungos, 2; Crossarchus, 4; Family Hyaenidae: Crocuta, 20; Family Felidae: Felis, 24; Panthera, 10.

Order Perissodactyla - Odd-toed ungulates. Three specimens were examined; no dental caries were found. Family Equidae: Equus, 3.

Order Artiodactyla - Even-toed ungulates. A total of 33 specimens were examined and no dental caries were found. Family Tayassuidae: Tayassu, 10; Family Cervidae: Cervus, 2; Odocoileus, 9; Mazama, 1; Family Antilocapridae: Antilocapra, 1; Family Bovidae: Bos, 4; Ovis, 6.

DISCUSSION

Of the total of 3,243 specimens of wild-taken mammals which were examined, only nineteen (0.58%) had dental caries. These findings are summarized in Table 1. Thus it is evident that dental caries are practically nonexistent in wild mammals. Suprisingly enough all nineteen that did have caries were in the Order Carnivora and seventeen of these were bears. Hall (1945) has previously reported on the occurrence of caries in bears. Table 2 shows Hall's findings and lists the findings in the present study for comparative purposes.

The other two specimens with caries were both coatimundis (Nasua narica narica), Family Procyonidae. A total of 100 specimens of Nasua were examined in the course of this study and only these two, both from Costa Rica, were found to have caries.

An extensive survey of the literature has revealed only one other intensive study of the incidence of caries in wild mammals. Hall (1940) reported that an examination of 3,401 wild-taken insectivores revealed no incidence of dental caries.

A study of the sea otter (Enhydra lutris) revealed that it has a high incidence of dental caries in its molar teeth. The molar teeth of this mammal are not characteristic of mustelids, but are bunodont in form. The northern sea otter has more caries than the southern species and it is believed that these carious lesions are due to the different molar tooth form and to diet (Murie and Scheffer: 1959). No caries were found in the ten specimens of Enhydra examined in this study.

	Present Study			Hall (1940)		
Order	No. Examined	No. With Caries	%	No. Examined	No. With Caries	%
Marsupalia	10	0	0	-	-	-
Insectivora	43	0	0	2,256	0	0
Chiroptera	631	0	0	-	-	-
Edentata	5	0	0	-	-	-
Lagomorpha	170	0	0	-	-	-
Rodentia	1,351	0	0	-	-	-
Carnivora	997	19	1.9	3,401*	0	0
Perissodactyla	3	0	0	-	-	-
Artiodactyla	33	0	0	-	-	-

* Other than bears

Table 1. Results of present study and of Hall's (1940).

	Hall (1945)			Present study		
	No. Examined	No. with Caries	%	No. Examined	No. with Caries	%
Euarctos	195	6	3.0	33	3	9.0
Ursus	165	3	1.8	64	11	17.0
Thalarctos	16	0	0.0	21	0	0.0
Selenarctos	-	-	-	7	3	43.0
TOTAL	376	9	2.4	125	17	13.6

Table 2. A comparison of dental caries in bears (Ursidae) between the report of Hall (1945) and the present study.

The question now arises as to why dental caries are apparently extremely uncommon in wild mammals in general and why they do occur with some frequency in bears. One factor that may play a very important role is the fact that the life expectancy of most mammals is extremely short. For example, Matthews (1952) reports that individual shrews (Family Insectivora) live about fourteen to sixteen months. The average life expectancy for many small rodents is from eighteen to twenty-two months. Thus it is probable that death often occurs before dental caries have had an opportunity to develop.

It does not appear to be likely that crown structure is an important consideration in predicting the presence or absence of dental caries. While it is true that both bears and man have molars of the bunodont type, that is, with low, rounded crowns, it is also true that certain types of molars are found in other groups (Suidae, Tayassuidae, and certain Rodentia) wherein dental caries are not found. Further, not all kinds of bears have dental caries.

There appears to be a much better correlation between the incidence of dental caries and diet. Bears are notoriously fond of honey and other sweets. The bears examined which had dental caries are ones which inhabited areas where honey is obtainable. The polar bear (Thalarctos) is strictly carnivorous and has no opportunity to eat honey and, as shown above, had no dental caries. From the moment of birth the young mammal begins to learn the food habits of its parents. As a result of this process, generation after generation of a specific mammal follows the same basic diet. If, as in the case of the bears, it learns to eat honey,

then it becomes susceptible to caries because it eats more foods that are rich in sugar than do other mammals. A notable exception to this appears to be the fruit and nectar-eating bats. Presumably their diet, ripe fruits of various types and nectar of flowers, is rich in sugars yet no caries were found in the 231 specimens examined (Glossophaga, Choeronycteris, Artibeus, and Leptonycteris). As stated before, several specimens of Glossophaga had dark colored teeth but I could find no evidence of dental caries.

The two specimens of coatimundis (Nasua narica) with dental caries are worthy of special note. First, the molar crown patterns of Nasua are best classified as bunodont, with low, rounded cusps. Secondly, only two of a total of 100 specimens examined contained caries, a relatively low incidence. Finally, the diet of the coatimundi is generally omnivorous consisting chiefly of fruits and berries (Hall and Kelson: 1958). Both of the specimens that had caries were taken in the same region of Costa Rica. Perhaps the Nasua population in this region has learned to feed on foods such as tropical fruits and berries that are much richer in sugar than are the foods usually eaten by this species.

Thus in summary it appears that the reason for the low incidence of dental caries in wild mammals is the result of several factors: (1) many are so short-lived that caries do not have an opportunity to develop and (2) in those that are medium to long-lived diet appears to be more important than tooth structure. Caries appear to be more the result of a diet high in sugars. The food preferences of an animal may have a genetic basis or may result from learning from the parents. The genetic

question has been experimented with in the laboratory satisfactorily but the key to this has not yet been discovered (Sognnaes: 1955).

When the final answer to dental carries has been found it will probably be a matter of basic diet and not tooth crown structure. Tooth crown structure seems to be merely a modification in mammals to aid them in chewing the food of their particular diet. Although many questions remain concerning the problem of diet and dental caries in wild animals, this study clearly indicates that those mammals which eat diets rich in carbohydrates are more susceptible to dental caries than those that do not.

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