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THE ENDOCRINE GLANDS AND EVOLUTION, NO. 3:
OS CEMENTUM, HYPSONDONTY, AND DIET

BY
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THE ENDOCRINE GLANDS AND EVOLUTION, NO. 3:
OS CEMENTUM, HYSODONTY, AND DIET

BY
THEODORE E. WHITE

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INTRODUCTION

POSSESSION of hypsodont teeth and the presence of a heavy coat of cement on the crowns of the teeth of horses is a standard textbook example of adaptation to a specialized diet—grasses. These characters are not unique in horses but are shared by a number of groups, both living and extinct: the mylagaulids, beavers, microtine rodents, guinea pigs, toxodonts, warthogs, bovids, and elephants, to mention a few. Superficially at least, the diets of these animals appear to be unlike. Moreover, the increased growth of the crowns of the teeth was initiated in the various

groups at different times throughout the Cenozoic, as was also the deposition of cement on the crowns of the teeth. Since several groups appear to have developed the same general tooth form on different diets, the purpose of this study is to examine the occurrence of hypsodonty and cement in the light of the quantity, form, and availability of the various minerals, particularly calcium and phosphorus, in the natural foods of these groups. Any possible role which the endocrine glands may play will also be considered.

Since the discussion of the morphology, embryology, and histology of human teeth in any standard textbook of human anatomy will serve to explain these features for the teeth of mammals as a whole, these subjects will not be considered here. Cement is deposited on the roots and around the base of the crown of the tooth by the cement-depositing cells of the tooth sac. This tissue develops into the alveolar periosteum of the adult and is continuous with that of the gum. Cement is present on the roots and the base of the crowns of the teeth of all mammals and the absolute amount increases with the age of the individual, at least until full maturity. It possesses both lacunae and canaliculi and, if present in sufficient quantity, also Haversian systems (Robinson, 1917, p. 1123), and its chemical composition does not differ from that of the bone of the individual. Neither the cement nor the dentine are inert concretions, but are vascular structures and are subject to the same mineralogical changes which occur in the bone (Shohl, 1939, pp. 145-341).

The absolute amount of cement deposited on the teeth appears to be correlated with the necessity of utilizing the excesses of calcium and phosphorus (above normal physiological needs) that are retained by the individual in order to keep the electrolytes of these minerals at the proper concentration and balance in the body fluids (White, 1949). Biochemists have demonstrated from feeding experiments on infants and laboratory animals that the amount of calcium and phosphorus retained is a fairly constant percentage of the intake, depending on age, physiology, and so forth, for only when the intake is excessively high or excessively low is there any alteration of the percentage retained for any given age (Shohl, 1939, p. 351). According to Shohl, calcium and phosphorus are as readily retained when taken as soluble salts as when taken as compounds of natural food stuffs (p. 329), but the percentage has been increased experimentally by the administration of vitamin D (p. 350) and of estradiol (p. 115).

The ultimate source of vitamin D in herbivorous mammals is sunshine. By exposure to direct sunlight the provitamin D, which is contained in the skin and sebaceous secretions of mammals, is activated and absorbed.

Absorption has been demonstrated by the successful treatment of rickets by rubbing cod liver oil on the skin (Maynard, 1937, p. 203). Moreover, activation of the provitamin D may take place although the body may not be directly exposed to sunlight. The shadow on sunny days and "skyshine" from the northern sky on bright days may be one-half to two-thirds as potent as direct sunlight (Maynard, 1937, p. 203). From studies on animal nutrition, vitamin D appears to exist in the natural foodstuffs of herbivorous mammals only in very minute quantities. Growing crops, including pasture grass, and seeds and their by-products, are practically devoid of it. During the sun-curing of roughages, however, vitamin D is formed by the action of radiant energy upon ergosterol, or some other provitamin, and the principal source of the antirachitic factor in the winter rations of farm animals is thus provided (Maynard, 1937, p. 200).

The relation of the sex hormones to mineral metabolism, especially in regard to calcium and phosphorus, has attracted considerable attention within recent years. Although experimental data are very limited, the female hormones seem to be the more important. Estradiol is the most active one of these and, among its several functions, it appears to be specific for stimulating the ossification of bone. It also furthers the proliferation of the osteoblasts and aids in maintaining the calcium-phosphorus ratio at the proper balance (Shohl, 1939, p. 115).

ABSORPTION OF MINERALS BY PLANTS

Before proceeding to the specific role played by each mineral in plants and animals, it is desirable to consider some of the general aspects of the absorption of mineral salts from the soil by plants as reported by Meyer and Anderson, 1939, pp. 403-406). Minerals available to plants occur as diffusible ions in the soil solution and as ions adsorbed on the surface of the clay micelles. In either state they can be absorbed by the roots. The micelles of colloidal clay are almost invariably negatively charged and the cations commonly associated with the clay particles of natural soils are Ca^{++} , Mg^{++} , K^+ , Na^+ , and H^+ . Under certain conditions the cations of one mineral can be displaced from the micelles by those of another mineral—a phenomenon called "base exchange" or "cation exchange." Such exchanges take place very rapidly and are reversible. This fact has found practical application with certain soils in that one mineral is made available to the plant by adding another mineral as fertilizer. The replaceability of any cation is dependent on the soil conditions, its concentration in the soil, and so on. In neutral or slightly alkaline soils Ca^{++} is the principal replaceable cation, the H^+ ion for acid soils, and Na^+ for alkali soils. Of the anions, PO_4^{--} is retained by the soil in appreciable quantities, while the others

(Cl^- , SO_4^{--} , NO_3^- , and HCO_3^-) leach out rather rapidly. The discovery of cation exchange has necessitated a revision of the older concept of soil-mineral absorption relationship. Roots not only can absorb the freely diffusible ions in the soil solution, but they can also liberate cations adsorbed on clay micelles and these, in turn, can be utilized by the plant. In general, it appears that the cations which enter plants come largely from the outer layer of the clay micelles, whereas the anions come largely from the soil solution, according to Meyer and Anderson (1939, p. 406). Although not known with certainty whether electrolytes penetrate into cells as molecules, or as ions, actually it is of little consequence as far as this study is concerned.

A vast amount of experimental data has been collected on the absorption of minerals by plants under controlled environmental conditions. Existing relationships have been found to result from the interaction of multiple variables and very few generalizations are possible. One phase of this work has an important bearing on this problem. It deals with the intake of minerals in relation to water transpired. It was once the popular concept that the mineral content of plants was proportional to the amount of water transpired, but it now seems well established that the solutes enter a plant independently of the intake of water and that there is no connection between the amount of water transpired and the amount of ash in the plant (Miller, 1938, pp. 238-39). If this is true, plants growing in a semiarid climate can normally be expected to be as rich in minerals as those of the same species growing in a humid climate. Absorption and accumulation of minerals by plants appear to be dependent on nearly the same set of factors, as discussed below.

Plants not only absorb such quantities of each mineral as they need, but often take up mineral salts from the soil far in excess of the quantities utilized by the cells (Meyer and Anderson, 1939, p. 403). Addition to the soil, therefore, of a compound which can be used by the plant often results in an increased intake of that substance, but usually not in proportion to the amount of that substance in the soil. The absorption and retention of ions by the roots are dependent on a number of factors within the plants themselves. For example, a close correlation that exists between the accumulation of ions by plant cells and their rate of respiration has been shown in diverse plant tissues. The conditions necessary for rapid rate of accumulation of ions are these: (1) an adequate supply of oxygen, (2) a suitable temperature, and (3) a supply of sugars or easily hydrolyzable polysaccharides within the cells (Meyer and Anderson, 1939, p. 410). It is generally assumed that energy is expended by the plant in the absorption of ions, because the ions move into the cell in opposition to a concentration gradient. Likewise, if the cell membrane remains permeable to them, the

retention of ions requires a continuous expenditure of energy. In a number of aquatic algae the concentration of ions in the cell sap is many times that of the medium in which they live. Furthermore, conductivity measurements indicate that most (probably 90 per cent) of the inorganic elements of the cell sap of these algae are present in the ionic state; they are not tied up in some nondissociated form (Meyer and Anderson, 1939, p. 408).

Storing of salts at appreciable rates appears confined largely, if not entirely, to those tissues which have not lost the power of cell division. There is some evidence that the meristematic cells possess the most marked capacity for this and that, with the decrease in proportion of growing cells in any tissue, its capacity for the accumulation of electrolytes diminishes, even though conditions remain favorable (Meyer and Anderson, 1939, p. 410). Most annual crop plants accumulate all of the minerals needed by the time of blooming, and in most instances the greater portion are acquired during the early stages of growth (Miller, 1938, pp. 369-73). Plants do not take up mineral salts in the same amount or proportion however. They exhibit a wide range in this respect, depending on the species, age, distribution of roots, physical and chemical nature of the soil, availability of elements in the soil, and general climatic conditions. Different species, even different varieties of the same species, when grown on the same soil, will accumulate mineral salts in widely different proportions and amounts (Miller, 1938, pp. 284, 287). Plant kinds typically low in calcium and phosphorus remain low even when grown on soil rich in these elements; those that are high remain high when grown on soil poor in them. Some species appear to have an affinity for a particular mineral, such as the grasses for silica and the legumes for calcium (Miller, 1938, p. 307). Several attempts have been made to give a physiological explanation for this "selective absorption" but as yet none seem to meet all of the requirements.

The amount of a mineral accumulated by any part of the plant at any given stage of growth is dependent not only on the factors mentioned above, but also on the utilization and translocation of the mineral within the plant. When the activities of the cell have slowed down markedly, some minerals, such as potassium, disappear from that cell (Meyer and Anderson, 1939, p. 423), whereas others, such as calcium and silica, usually remain. Unless the mineral is used in an organic compound, most of it is present in the living cell as an electrolyte or as a water-soluble salt (Meyer and Anderson, 1939, p. 415; Miller, 1938, pp. 220, 290, 307) and not as a stable inorganic compound. This is essential in order that the mineral can perform its physiological role within the cell or become translocated to another part of the plant. Consequently, and with few exceptions, most if not all of the minerals in growing annuals or in the growing parts

of perennials are readily available to herbivorous mammals. Moreover, such minerals are not abrasive.

Distribution of the various elements in the plant parts varies to some extent with the stage of growth. That in barley will serve as an example for the grasses. Total ash increases up to the time of the milk stage of the grain; total phosphorus up to harvest time, highest in the leaves before heading and in the stems at heading time; total calcium highest in the leaves at heading time and in the stems during the milk stage; total potassium up to the milk stage, highest in the leaves before heading, and total nitrogen up to harvest time, highest in the leaves before heading and in the stems at heading time (Miller, 1938, p. 293).

Data on the mineral content of the leaves and stems of the dicotyledons are confined largely to cultivated crops and the weeds which infest the fields. As far as the diet of wild browsing animals is concerned these plants are negligible. Information on trees and shrubs for the different species, seasons, growth periods, and soil conditions is limited to a few hardwoods and fruit trees, but most of the mineral content of the leaves appears to have been accumulated by the time they have completed their growth (Miller, 1938, p. 373). Thereafter, those minerals which are readily translocated move out of the leaf into the stems and roots prior to leaf fall, those which are not remain in the leaf (Meyer and Anderson, 1939, p. 498). Thus, the small twigs which furnish the winter browse of deer will be as high in mineral content as were the leaves in summer.

Principally owing to the variation in physiology of the species within a group, reliable generalizations concerning the mineral content of the major groups of plants are difficult to arrive at and many exceptions can be found. A few will be brought out in the consideration of the role of the several minerals in plants and mammals. While, in general, the dicotyledons store most minerals, except silica, in greater quantities than do the grasses, this does not always hold true. Harper, *et al.* (1934, p. 39) found that Bermuda grass (*Cynodon dactylon*) at the seed stage had a much greater calcium content than the native weeds growing on the same soil. In view of the data on the absorption and accumulation of minerals by plants that have been cited, it is evident that with regard to the paleoecology of herbivorous mammals, an evaluation of the probable mineral content, character, and nature of the soil of a given area during a given time unit is of prime importance.

MINERAL METABOLISM BY PLANTS AND MAMMALS

Inasfar as the data are available, the role of the various minerals in plants and mammals will be treated in the following order:

Plants: (a) Total amount (per cent of dry weight); (b) location of greatest amount; (c) translocation; (d) solubility; (e) utilization and function; and (f) relation to other minerals.

Mammals: (a) Total amount; (b) location; (c) digestion and excretion; (d) utilization and function; (e) relationship to endocrine glands; and (f) relationship to other minerals.

Phosphorus

Plants.—The total amount of phosphorus varies from 0.2 to 0.8 per cent of the total dry weight (Miller, 1938, p. 301) due largely to the availability of this element in the soil rather than to the specific characteristics of the major group to which the plant belongs. Plants growing in an adequate supply of phosphorus show a steady increase in amount from the bottom to the top of the stem, but plants grown in a medium deficient in phosphorus have a nearly uniform amount in all parts except the rapidly growing tips, which are highest. Phosphorus appears to be readily redistributed from the older to the younger tissues, and in the mature plant usually more than 50 per cent is contained in the seeds and fruits (Meyer and Anderson, 1939, p. 421; Miller, 1938, p. 302). Only a small portion of the element in growing plants is tied up in insoluble compounds. The amount of water-soluble phosphorus varies from 60 to 80 per cent of the total in growing plants (Miller, p. 301) and, hence, is readily available to herbivorous mammals.

Phosphorus is an essential ingredient of a number of organic compounds in the plant; of these the phospholipids are the most common and one or more are found in practically every living cell (Miller, p. 304). It is also an essential ingredient of nucleic acid; when it is absent, no nuclear division occurs and meristematic activity is greatly diminished. The element also appears to act as a catalyst in the reduction of nitrates and the oxidation of glucose, it often enters into combination with the nitrogen and may act as a catalyst in converting starches to water-soluble carbohydrates (Miller, pp. 304–06; Meyer and Anderson, p. 421).

One of the phosphorus compounds, phytin, which is found only in plants, may have an important bearing on matters of this study. Phytin is an acid calcium-magnesium salt of inosite phosphoric acid. The amount in an individual plant varies with the species and age but is always greatest in the seeds; available data indicate that 50 per cent or more of the total phosphorus of seeds, especially of cereals, is tied up in this compound (Miller, p. 302; Maynard, 1937, p. 132). Phytin is very low or absent in plants till after pollination (Miller, p. 304).

Mammals.—Of the total phosphorus in the body, about 80 per cent is

found in the skeleton, 10 per cent in the muscle, and 1 per cent in the nervous tissue (Shohl, 1939, p. 178). The remainder is in the blood, liver, and intestinal tract but, except in the case of blood, the amount is highly variable depending on such factors as the diet, time since feeding, age, physiology, and health of the individual. As in plants phosphorus is an essential ingredient of every living cell, entering into such compounds as phospholipids, nucleoproteins and phosphoproteins, and many others. Much of the organic phosphorus of food is converted during digestion to orthophosphate (Shohl, p. 188) and both inorganic and organic are absorbed by the intestine. It is probable that there is some resynthesis in the intestinal mucosa. The inorganic phosphorus is either quickly utilized, stored, or excreted, for its concentration in the body fluids normally varies within very narrow limits (Shohl, p. 143). In the digestive tract it is closely associated with calcium and a rough balance between them must be maintained in the diet, because a large excess of either results in the formation of insoluble tricalcium phosphate which cannot be absorbed (Maynard, 1937, p. 123). Large intakes of iron, aluminum, and magnesium also interfere with phosphorus absorption by forming insoluble phosphates. Phosphorus is excreted principally in the feces by the Herbivora and principally in the urine by the Carnivora. Its excretion is about equally divided between the two channels in man (Maynard, p. 124). Inorganic phosphorus in the urine makes up 92 to 96 per cent of the total of the element present and that in the feces about 50 per cent.

Phytin is practically indigestible by white rats and children (Maynard, p. 132; Shohl, 1939, p. 188). Since nearly half of the rodents of the world are classed as seed eaters, a grouping which includes the laboratory rat, it raises the question of whether the inability of these laboratory rats to digest phytin-phosphorus may not be connected with albinism. Here, there is a distinct need for biochemical data on other seed-eating rodents. The available data on adult man indicates that 25 to 50 per cent of the phytin of foods is excreted unchanged (Maynard, p. 133) and no reliable information on the utilization of this compound by domestic animals is available.

Since 80 per cent of the total phosphorus of the body is associated with calcium in the formation of bones and teeth, its role there will be discussed under that mineral. Calcium is the only mineral with which the metabolism of phosphorus is associated and both are greatly affected by the activities of the thyroid and parathyroid glands, as well as the quantitative production of some sex hormones, especially estradiol. These relationships will be considered under calcium.

Calcium

Plants.—The total calcium in the plant varies with the species and the environment. As a rule dicotyledons have a high percentage and monocotyledons (grasses) have a low percentage (Miller, 1938, p. 307). Since it is not readily redistributed in the plant (Meyer and Anderson, 1939, p. 421), the oldest living portions have the greatest amount; the leaves contain the most and the seeds the least (Miller, p. 307). Though more calcium than phosphorus in the plant is tied up in an insoluble form, even so a considerable portion (40 to 60 per cent) is soluble in water, and hence readily available to herbivorous mammals.

While not clearly demonstrated that it enters into more than one organic compound in the plant, calcium plays a number of important physiologic roles. It counteracts the deleterious effects of an excess of magnesium in the soil and also serves to neutralize acids within the cell of which oxalic acid is present in greatest quantity (Miller, pp. 308–09). The high per cent in spinach is not available because of the high oxalic acid content (Maynard, p. 133) and is little utilized if at all (Shohl, 1939, p. 348). The content of calcium and nitrogen in plants shows a close relationship. Because nitrogen is an essential ingredient of proteins, the more nitrogen is present the more proteins are produced, which, in turn, results in a greater production of acids due to the increased metabolism and a greater amount of calcium needed (Miller, p. 309). Calcium pectate is one of the compounds of the middle cell wall; it appears to be necessary for the retention of absorbed ions by the plant cell (Miller, p. 310) and to control the permeability of cell membranes—in the absence of calcium plants lose minerals by osmosis from the roots. Calcium prevents the degeneration of the protoplasts of the meristematic cells of the root tips and favors the translocation of carbohydrates and proteins away from the cells where they are manufactured (Miller, pp. 311–12); these move out of the cell very slowly if at all in the absence of calcium. Other than nitrogen calcium does not seem to have a close association with any other mineral in the plant. It is partly but not entirely replaceable by magnesium and sodium.

Mammals.—Approximately 99 per cent of the calcium in the body is found in the bones and the teeth (Maynard, 1937, p. 119). The remaining 1 per cent is distributed throughout the soft tissues, principally in the liver, intestines, and blood. The literature on calcium metabolism (nearly half of that on mineral metabolism) is concerned chiefly with this small fraction. The serum calcium (Shohl, 1939, pp. 110, 134, 274–310, 343, 348), the calcium-phosphorus balance in the body fluids, the amount excreted,

and the anion-cation relationships of the body can vary only within very narrow limits without deleterious results, and many investigators have sought the causes of and remedies for the maladies owing to an imbalance in the above factors. Since the results of these studies have been excellently summarized in the source material, they will not be repeated here.

Formerly it was assumed that the minerals in the feces represented the unabsorbed portions (Shohl, p. 336); the present concept is that most of those ingested, especially calcium and phosphorus, are assimilated but later broken down and excreted through the large intestine or kidneys. It is true, however, that both calcium and magnesium unite with fatty acids and phosphorus in the intestine to form soaps and phosphates which can be absorbed only with difficulty or not at all (Maynard, p. 123). The liver appears to be the chief temporary reservoir for the calcium which is assimilated and later excreted, principally into the blood (Shohl, p. 70), but the skeleton is the main storehouse of calcium in the body. The latter source is drawn upon as need arises (Shohl, pp. 140-41; Maynard, p. 124) by lactating mammals (Shohl, pp. 344-45) and, also conceivably, by laying hens and by cervids during the ossification of the antlers. If the skeleton is drawn on for any period of time to make up dietary deficiencies of either calcium or phosphorus, however, rickets result. So far as known the available data indicate that there is little or no mobilization of the calcium and phosphorus from the skeleton during pregnancy if the intake is adequate to meet the physiological needs. Studies on pregnant women show that the retention is sufficiently increased beyond the mother's physiological needs to meet the demands of the foetus and allow for additional storage (Shohl, p. 343). This is thought to be one of the effects of estradiol, a female sex hormone which is produced principally by the placenta during pregnancy.

Calcium metabolism (and also that of phosphorus) is closely related to secretion of the thyroid and parathyroid glands and at least one of the female sex hormones, estradiol, seems involved. Greater activity of the thyroid increases the excretion of calcium, principally through the large intestine and may result in osteoporosis (Shohl, p. 343; Grollman, 1947, p. 175). However, there is no evidence of any specific catabolic effects on the calcium deposits, if the diet is adequate. The inference is that the defective teeth and delayed ossification of the skeleton in hypothyroidism is more likely an effect of the lower metabolic rate rather than due to dietary deficiency.

The chief function of the parathyroid hormone appears to be to maintain the serum calcium at the proper level and the calcium-phosphorus balance at the proper ratio (Shohl, p. 110). In low-calcium rickets the

activity of the gland increases and calcium is mobilized from the skeleton. This overactivity of the parathyroid gland is the result and not the cause of rickets, though it does aggravate the symptoms. The administration of the parathyroid hormone to normal laboratory animals demonstrates that large doses exert an osteoclastic effect and induce stunting of growth and resorption of bone; moderate doses cause softening of the bone with a disappearance of the trabeculae and an increase of the osteoclasts; and small doses have an osteoblastic effect and produce hard and sclerotic bone (Grollman, p. 258-59).

The possible relationship of the estrogens (female sex hormones) to the metabolism of calcium and phosphorus has attracted attention only within the last few years. Our knowledge is as yet imperfect but is sufficient to show that there is a positive connection. Mice given estradiol show a great proliferation of the osteoblasts and increased density of the bone; chickens a rise in the serum calcium; and new-born rats given daily doses for 8-10 days show an increase in number and size of the centers of ossification in the wrist and ankle (Shohl, p. 115). Long continued administration of large doses may cause obliteration of the bone marrow and its replacement by bone with resulting anemia (Grollman, p. 520).

Estrogens are produced by both sexes, the difference being only in quantity, and are present in the urine of both children and adults. The amount in the urine of the human male is about one-third that of the nonpregnant female (Grollman, p. 516). The exact origin of estrogen in the male is unknown, but part of it is thought to come from the food, for, on an estrogen-free diet, the amount excreted is reduced, and the remainder may be an incidental catabolite of tissues like the testicle, which in the stallion contains estrogenic substances in very high concentration (Grollman, p. 516). In view of the role played by the estrogens in calcium-phosphorus retention, one may theorize that the male cervids produce estrogens in large quantities during the growth and ossification of the antlers. In forms like the elk and moose the amount of calcium and phosphorus to be mobilized must equal one-third to one-half of the skeleton.

The heavy coat of cement on the milk teeth of the Late Tertiary and Recent horses may be the result of the action of estrogens. In most mammals estrogens are present in the urine in fairly high amounts during pregnancy. In the mare excretion of estrogens in the urine reaches its maximum at the end of the second or third month of pregnancy, after which it continues to decline to a lower level until term. It is reasonable to assume, then, that this is not due to a decrease in production, but to an increase in the utilization of the hormones by the foetus and possibly also

by the mother. If this is true, one may set a geologic date (the Lower Pliocene) for a specific change in the physiology of the Equidae.

In one of the oreodonts (*Cyclopidius*) the milk teeth have a much heavier coat of cement than the permanent teeth. In most herbivorous mammals the milk teeth erupt a few days after birth and, consequently, the estrogens produced by the placenta would still be available during their formation. After birth, with the rich source of estrogens cut off, there would be a corresponding drop in the calcium-phosphorus retention and a decrease in the amount of cement on the teeth. Hence, it would appear that, after birth, *Cyclopidius* was unable to make the necessary glandular adjustment which the Pliocene and later *Equidae* did.

Many are familiar with the unpleasant effect which wild onions and ragweeds have on cow's milk and this poses the question to what extent can the hormones produced by the mother be passed on to the offspring in the milk. Although I have been unable to find any data specifically bearing directly on this subject, experiments so far indicate that a healthy mammary gland is a very effective barrier against the passage of foreign substance in harmful quantities. Heavy metals (mercury and arsenic), volatile organic compounds (alcohol, ether, and chloroform), aspirin, and alkaloids (morphine, atropine, and quinine) do not pass into the milk in toxic quantities, although certain essential oils, such as those present in onions, may pass into the milk, giving it an unpleasant odor or taste or even rendering it toxic. Without specific data to the contrary, there is no reason to assume that hormones produced by the mother are transmitted to the offspring in the milk. In his summary of the results of the past ten years of research by many workers on the content in milk of mothers rendered severely hyperthyroid, Blaxter (1952, pp. 239, 246) concluded that if thyroxine is present at all it was in such minute quantities that it was negligible.

Magnesium

Plants.—Magnesium is present in plants, usually in somewhat less amounts than calcium and is most abundant in the seeds and leaves (Miller, 1938, p. 313). Translocation from older to younger organs takes place quite readily (Meyer and Anderson, 1939, p. 422) and there is a higher percentage in rapidly developing tissues (Miller, p. 315). Magnesium appears to enter into very few stable compounds in the plant. In alfalfa 85 per cent is soluble in water (Miller, p. 290) and readily available to herbivorous mammals. As with calcium and phosphorus, the total amount varies with the species and environment. Most grasses are low and legumes high (Miller, p. 313); in fact, most dicotyledons run higher than grasses.

Since chlorophyll contains magnesium as an essential constituent, a disturbance in its formation occurs when this element is lacking (Miller, p. 313). Plants differ markedly in their response to a deficiency of magnesium in the soil, but the nature of this response does not correlate with particular groups of plants. Magnesium apparently serves as a carrier of phosphorus as it is most abundant in the tips of stems and roots, where phosphorus is actively utilized (Miller, p. 314). It also appears to be essential to the formation of vegetable oils, but the role is obscure; in magnesium-deficient solutions oil formation is greatly retarded or completely inhibited (Miller, p. 315). Magnesium shows no close relation to any other mineral in the plant, but to a small extent it may be replaced by calcium.

Mammals.—In all the cells and fluids of the body magnesium occurs in comparatively large amounts. Chief deposits are in the bones and muscles but its role in the latter is unknown (Shohl, 1939, p. 162). The element is closely allied to calcium but cannot replace it. Magnesium forms an integral part of the complex bone salt. For the species that have been examined, the magnesium content of the bone ash varies within very narrow limits, 0.5 to 0.7 per cent (Shohl, p. 162). The red cells of the blood contain more magnesium than the serum. Many controversial claims have been made concerning its function in the blood but none seems to fit all cases. The absorption and excretion of magnesium parallels that of calcium and like calcium, it forms insoluble soaps in the intestine with fatty acids (Shohl, p. 165). A large proportion of the excreted magnesium, about 60 per cent, is in the feces, most of it as unabsorbed material. Except in acid indigestion, the amount excreted by the kidneys appears to be more constant than that excreted by the large intestine (Shohl, p. 165). With high intakes, the amount in the feces increases, but that in the urine remains fairly stable.

Because there is no storage depot as with calcium and phosphorus, retention of magnesium in the body is related to the immediate needs of the individual. In man, it is higher in children than in adults, but in both the amount is very irregular; retention may be low on high intakes or high on low intakes, depending on needs of the individual at the time (Shohl, p. 167). Very little is known about the function of magnesium in the body. It is essential; a prolonged low-magnesium diet results in tetanic convulsions and death (Shohl, p. 164). A continued high intake causes diarrhea, loss of appetite, and eventually death. High intakes also appear to lower the calcium-phosphorus retention. A high magnesium, low calcium-phosphorus diet induces rickets in young and growing animals. This may be due in part to the formation of insoluble magnesium phosphates in the

intestinal tract (Maynard, 1937, p. 123) with an accompanying increase in the excretion of calcium in the feces. Normally, magnesium metabolism shows very little or no response to the activities of the endocrine glands or to the vitamin intake; it is only after drastic measures like parathyroidectomy that any changes are noticeable (Shohl, pp. 162, 166).

Potassium

Plants.—The total amount of potassium in a plant depends on its availability in the soil, the environment, and the plant species. While some plants can absorb potassium in any form from the soil, others cannot (Miller, 1938, p. 316). All meristematic tissues are rich in this element, especially growing tips of stems and roots, root hairs, pollen tubes, and the cambium layer of trees. Potassium is readily translocated from the older to the younger tissues; dying leaves are almost devoid of it (Miller, p. 316). It apparently does not enter into any organic compounds in the plant and practically all (99 per cent) of it can be removed by washing (Miller, p. 317).

The exact role of potassium in plants is obscure but it appears to be chiefly regulatory or catalytic (Meyer and Anderson, 1939, p. 423). Its presence is deemed necessary for normal maintenance of the following processes: (1) Synthesis of simple sugars and starches; (2) translocation of carbohydrates; (3) reduction of nitrates; (4) synthesis of proteins; (5) formation of oils; and (6) normal cell division. It also acts as a catalyst or condensing agent, accelerates the action of enzymes, and promotes the general health of the plant (Miller, pp. 318–22). An inverse correlation between potassium and calcium, magnesium, and phosphorus is believed to exist, for plants grown on potassium-deficient soil show an increased absorption of the other three elements (Miller, p. 323). Potassium can to a certain extent, but not entirely, be replaced by sodium (Miller, p. 316).

Mammals.—Potassium is distributed chiefly in cells, throughout the body. The red corpuscles and the muscle cells contain the greatest amounts. In the blood, the ratio of potassium in the red cells to that in the serum is about 34 to 1 (Shohl, 1939, p. 122). Since potassium occurs principally as an ion in both plants and animals, its absorption by the intestine presents no dietary problem for either herbivores or carnivores. It is excreted for the most part by the kidney and sweat glands (Maynard, 1937, p. 141), but a small amount is eliminated by the large intestine. Cellular potassium is associated with cellular phosphorus and, hence, is thought to balance some of the complex phosphate anions (Shohl, p. 122). Muscle cells lose potassium during activity, but potassium feeding restores it. The percent-

age of potassium in the blood serum is remarkably constant and ingestion of large amounts by mouth does not raise it (Shohl, p. 122).

There appears some connection between potassium and the adrenal cortex, but what it is, is not well understood. Addison's disease, which involves a disturbance of the adrenal glands, is accompanied by an increase of the element in the serum; after adrenalectomy there is an increase in the muscle cells but not in the liver or brain (Shohl, p. 123). Ingestion of potassium bicarbonate or potassium salts of organic acids not only acts as a diuretic but increases neuromuscular irritability (Shohl, pp. 122-23). The latter reaction has been thought to inhibit the adrenal cortex and stimulate the thyroid (Goldzieher, 1939, p. 14).

Sodium appears to be the only mineral which shows a close relationship to potassium; the Na/K ratio remains relatively constant, depending on the age of the animal. The kidney seems able to adjust to a moderate excess of either mineral within a short time. Because in adrenal cortical insufficiency the Na/K ratio is easily altered by the intake, it is thought that the adrenal cortex is also involved in maintaining the proper balance (Shohl, pp. 123-25; Maynard, pp. 141-42).

Sulphur

Plants.—The total amount of sulphur in the plant varies greatly according to the species of plant; in comparison with the phosphorus content, the cereals contain two-thirds as much sulphur, the legumes an equal amount, and such crops as turnips and cabbage two to three times as much (Miller, p. 324). Sulphur is fairly evenly distributed throughout the plant and occurs in proteins and volatile oils and as sulphates. In an apple tree its distribution (from greatest amount to least) is in the leaves, spurs, young bark, and old bark, respectively. The sulphates represent the "luxury absorption" of this element and may equal 65 per cent of the total sulphur (Miller, 1938, p. 324). The mineral appears to be readily translocated from older to younger tissues (Meyer and Anderson, 1939, p. 420). As much as 65 per cent of that found in certain plants is in the form of soluble sulphates (Miller, p. 324) and, hence, readily available to herbivorous mammals.

Sulphur functions as building material for proteins and other constituents of the plant (Miller, p. 325). In addition, it favors root development, formation of chlorophyll, development of root nodules in legumes, and reduction of nitrates and oxidation of sugars, and may stimulate seed production (Miller, pp. 326-27).

Sulphur does not appear to be closely associated with any other mineral in the plant.

Mammals.—Every cell of the body contains sulphur, mainly in the proteins; small amounts of inorganic sulphate occur in the blood and tissues. Sulphur also unites with the carbohydrates and the lipids (Shohl, 1939, p. 192). Of the total in the body, the muscle contains about one-half and the skeleton and skin about one-eighth each (Shohl, p. 196). Sufficient intake of sulphur is provided if the protein supply is adequate. The element is excreted by both the kidney and the large intestine, but the percentage for each varies with the diet (Shohl, pp. 198–201). Its metabolism does not appear to be specifically affected by the activities of any of the endocrine glands. Sulphur is related to nitrogen and phosphorus only in the formation of proteins.

Iron

Plants.—Iron occurs in green plants in very minute quantities but is necessary for their normal growth and development. It is uniformly distributed throughout the plant body, mostly in combination (Miller, 1938, pp. 328, 334), but very little is in a form that is readily soluble in water. The element is completely immobile in the plant; none is translocated from older to younger tissues (p. 334). Iron is essential for the synthesis of the chlorophyll molecule, although forming no part of it (Miller, p. 328). Moreover, it is thought to act as a catalyst or oxygen-carrier in oxidation-reduction processes in living plant cells (Meyer and Anderson, 1939, p. 423). Iron is not associated with any other mineral in the plant nor is it replaceable by any element.

Mammals.—Iron is an essential constituent of all the living cells of the vertebrate body. The carrying of oxygen to the tissues by the hemoglobin of the blood is its most important function. Iron is constant in the chromatin material of the nucleus and in the cytoplasm of nonnucleated cells (Shohl, 1939, p. 205). Of the 4.5 gm. of iron calculated to be in the body of a 70 kg. man, 2.9 gm. are in the blood, 1.5 gm. in the muscle, and the remainder as small amounts in the liver, spleen, and other tissues (Shohl, p. 208).

Probably the simple salts of iron are absorbed in the form of ferrous iron. Acid no doubt renders iron soluble in the stomach, but this is not easy to demonstrate experimentally (Shohl, p. 209). Iron is excreted principally by way of the large intestine. While iron salts injected intravenously lead to increased excretion of iron in the feces, there is practically no change in the amount in the urine (Shohl, p. 212). The metabolism of iron does not appear to be specifically related to the activities of any of the endocrine glands. Iron is intimately associated with copper, which serves as a catalyst in the synthesis of hemoglobin (Shohl, p. 215).

Silicon

Plants.—Silicon is almost universal in plants but the amount varies greatly for different plants and for different parts of the same plant. It is especially abundant in the aerial parts in *Equisetum*, the Gramineae, and the bark of trees. Whereas it composes 70 per cent of the ash in *Equisetum*, it is only 9.5 per cent of the ash of the stems and leaves of alfalfa. Deposits of silica are greater in tropical plants than in those of temperate zones. As a result of higher soil temperatures there, silicic acid is dissolved and taken into the plant with the water of transpiration; this, together with the leaching of other minerals by the frequent rains, accounts for the low nutritive qualities of tropical grasses. (Miller, 1938, p. 335.) I have been unable to find any data on the translocation of silica within the plant.

No specific physiological role for silicon within the plant has been established, but a number of general effects influencing the health of the plant have been attributed to it. Silicon is deposited principally in the epidermis of the leaves of grasses and, to a certain extent, in the epidermis of the stems. This fact is considered to make them more resistant to rusts, certain mildews, and to suffer less from attacks of plant lice. Numerous experiments suggest a relationship between silicon and phosphorus metabolism within the plant (Miller, pp. 336–38; Meyer and Anderson, 1939, p. 426). In plots which were low in phosphorus, the application of soluble silicates to the soil was followed by a marked increase in grain production but only a small increase in straw. This has been taken to indicate that silica may unlock phosphorus from the relatively quiescent parts of the plant and enable it to be transferred to regions where assimilation and growth are active; also, it is thought that colloidal silica may facilitate the uptake of phosphorus from the more insoluble mineral phosphates (Miller, p. 338).

Mammals.—All animal tissues contain silicon but in varying amounts (Maynard, 1937, p. 155); the kidneys and pancreas have the most and the brain the least. Recent determinations assess the silicon in the blood as equal to 16 mg./100cc. (Shohl, 1939, p. 245). In the dairy cow most of the ingested element is excreted by way of the large intestine, but in nearly all cases, there is some storage, frequently as much as 3 to 5 gm. daily (Maynard, p. 156). It is thought to contribute to the elasticity of the skin (Shohl, p. 245). A physiological role for the silica in the body has not been demonstrated and its presence there is generally regarded as an accumulation resulting from its universal occurrence in foods, particularly of vegetable origin; workers at Cornell have reared various species of Herbivora to maturity on synthetic diets of purified food materials, nutrients certainly very low in silica (Maynard, p. 156).

The metabolism of silicon is not known to be related to the activities of any of the endocrine glands nor is it associated with any other chemical element.

Micronutrients

Plants.—Boron, manganese, copper, zinc, and molybdenum have been classed as micronutrients of plants (Arnon, 1951, pp. 320–24; Miller, 1938, pp. 340–52, 362–63; Meyer and Anderson, 1939, pp. 424–25). Although amply demonstrated (by growing plants in controlled media) that these elements are essential to normal plant growth, their exact physiological role is yet unknown. If any of them are present, however, in other than extremely dilute solutions, they are toxic to plants.

Mammals.—Boron has been reported as present in the animal body. There is no proof that it has any function (Maynard, 1937, p. 164).

Manganese is present in all animal tissues, with the greatest amount in the liver and appreciable amounts in the pancreas, kidneys, sex glands, skin, muscle, and bones. It appears to be absorbed readily from natural foods and normally the supply is considered adequate. On high intakes a considerable quantity is stored in the liver and other glandular organs. The principal path of excretion is the large intestine. A requisite amount of manganese in the body is essential for normal reproduction and lactation, but exactly how it performs its function is not known, perhaps through its effect on the anterior lobes of the pituitary and the gonads. Whether manganese, along with iron and copper, has a role in the synthesis of hemoglobin is not yet proved (Maynard, p. 154; Shohl, p. 244).

Copper occurs in all tissues of the body with the largest amounts in the liver, spleen, and kidneys. Appreciable quantities are in the brain, milk, and blood, with most of that in the blood in the corpuscles. The element is readily absorbed from natural foods as well as from soluble salts; excessive intakes may cause cirrhosis of the liver. Copper is essential to the synthesis of hemoglobin and its action is specific. Salts of copper are active in biological oxidation-reduction systems and probably catalyze many reactions. Copper does not appear to be related to the activities of any of the endocrine glands nor to be closely associated with any other element except iron (Shohl, pp. 238–39, 242).

Zinc occurs in all tissues of the body with the greatest amounts in the hair and bone. It is in appreciable amounts in the liver, kidney, muscle, and spleen. The availability of zinc in natural foods would not be a dietary problem and most of the intake is excreted by the large intestine. However, the physiological function of zinc is unknown; that it may be essential is indicated by the death of mice on a zinc-free diet. (Shohl, p. 246.)

Molybdenum is not essential for animal nutrition.

Sodium

Plants.—Although not considered essential to plants, sodium is very generally distributed in their tissues, with the amounts varying greatly according to the species and environment. The highest concentration in cultivated plants appears to be in the organs of greatest physiological activity. Sodium is present in the cell sap as sodium chloride and, hence, is readily soluble in cold water. Although it does not appear to have a specific role in plant physiology, sodium is believed to be beneficial: (1) It appears to be a conserver of potassium; (2) to replace potassium to a limited extent as a plant nutrient; (3) when applied to soil deficient in available potassium, to liberate a certain amount of potassium and make it usable by the plant; and (4) to act, in certain specific cases, as an antidote against certain toxic salts in the medium. (Miller, 1938, p. 361; Meyer and Anderson, 1939, p. 425.) Aside from potassium, sodium does not have any close relationship with any mineral.

Mammals.—The body contains about 0.2 per cent sodium; this occurs principally in the extracellular fluids and makes up 93 per cent of the bases in the blood serum (Maynard, 1937, p. 410). Sodium is almost completely ionized and is largely associated with Cl^- and HCO_3^- ; small quantities also occur in muscle cells, in the skeleton, and in cartilage (Shohl, 1939, p. 121). Soluble salts of sodium are readily absorbed and circulate throughout the system. In the healthy body sodium is not stored; any excess intake is readily excreted. The kidneys and sweat glands are the principal paths of excretion (Maynard, p. 140).

Some correlation appears to exist between the activity of the adrenal cortex and sodium (and accompanying Cl^-) retention, or rather sodium and Cl^- reclamation. This relationship seems only to find its expression in cases of adrenal insufficiency or in adrenalectomized animals, because the administration of excessive doses of the adrenal hormone to normal animals had no effect on the animal's physiology (Grollman, 1947, p. 397). Adrenal insufficiency is attended by functional disturbances of the kidney. Normally, a considerable quantity of the water, sodium, and chloride excreted by the glomerulus is reabsorbed by the renal tubules (Grollman, p. 394). In the malfunction of the kidney accompanying adrenal insufficiency, water, sodium, and chloride are not reabsorbed in the tubules, but potassium, magnesium, and urea diffuse back into the blood (Grollman, p. 394), producing an excess potassium balance in the body fluids. In Addison's disease the excess potassium balance has an opposite effect to that in normal animals; it produces great lassitude and weakness (Shohl, p. 123).

Chlorine

Plants.—With the exception of conifers, chlorine occurs in practically all plants and, as far as is known, it is present in the form of chlorides dissolved in the cell sap. It usually increases in amount from the roots to the leaves. The responses of plants to the quantity of chlorides in the soil or a nutrient solution are so extremely variable that no generalizations can be drawn. Some plants show deleterious effects of a deficiency of chlorine, while others show the same effects from an excess. Since it is virtually impossible to rear a plant in an absolutely chlorine-free medium—artificial or otherwise—the question of whether it is essential or not will probably remain unanswered (Miller, 1938, pp. 352–56; Meyer and Anderson, 1939, p. 426). Chlorine is associated with both sodium and potassium in the plant and also in the soil.

Mammals.—Chlorine comprises about 0.12 per cent of the body of the adult and occurs principally as chlorides in the extracellular fluids. It is found in those tissues which contain the most interstitial water, that is, the skin, subcutaneous tissue, blood, muscle, and bone. Ingested chloride is rapidly absorbed from the intestine and deposited temporarily in the skin and interstitial spaces. The kidneys and sweat glands are the principal paths of excretion. Chlorine is so intimately associated with sodium that it is difficult to separate the two. Na^+ and Cl^- are the chief factors in the maintenance of the osmotic pressure of the extracellular fluids, since the cellular water is in osmotic equilibrium with the extracellular. Cl^- is the principal anion in the body fluids and under certain conditions can be excreted independently of the sodium. It plays a negligible part within the tissue cells, but the red blood cells may contain up to 55 per cent as much chlorine as the plasma. (Shohl, 1939, pp. 125–27).

While it is not definitely established that chlorine has any relation to the activities of the endocrine glands, it is intimately associated with sodium and its retention (or reclamation) is decreased in adrenal cortical insufficiency. Sodium is the only mineral with which chlorine is known to be associated.

Iodine

Plants.—Higher plants absorb iodine more or less proportionately to the amount in the medium in which they are growing. Iodine occurs in both the organic and inorganic forms in plants, but the ratio of one to the other is extremely variable even in those of the same species. The addition of iodine to the medium as a fertilizer, produces improvement in certain plants, has no effect on some, and is decidedly toxic to others even in very dilute solutions (1.2 p.p.m.). (Miller, 1938, p. 365.) As yet no specific

function of this element within the plant has been demonstrated. Iodine is not known to be associated with any other mineral in the plant.

Mammals.—In man, the total iodine content of the adult body may be roughly estimated as about 20 mg., of which half is in the thyroid and the remainder in the rest of the body. Iodine is absorbed from the intestinal tract, regardless of the form administered, probably as iodides and thus circulates in the blood. The requisite amount is extracted from the blood and the excess is quickly carried around the body, distributed to the various fluids and eliminated, principally by way of the kidneys and the sweat glands.

The only known function of iodine in the body is as an essential ingredient of thyroxin—the product of the thyroid gland. This gland is unique in its ability to extract iodine from the blood. Balance studies indicate that nearly all of the iodine liberated by the normal breakdown of thyroxin is retained by the body and reclaimed by the thyroid (Shohl, 1939, pp. 225–27). The thyroid is the only endocrine gland to which iodine metabolism is related, and the disorders of the thyroid due to iodine deficiency are well known. As far as is known, iodine is not associated with any other mineral in the body.

Plant Hormones

Many workers have investigated the properties and physiological action of the growth-stimulating substances secreted by the growing tips of grasses and the buds of dicotyledons. Since such minute quantities of these substances have such profound effects, they are, by definition, hormones and have been given the name “auxins.” The results of these researches have been collated by two very able men in this field, Went and Thimann (1937) and are summarized below.

Auxins are present not only in the coleoptile tips of grasses, buds, leaves, and root tips, but also are generally distributed in certain tissues of the body of vertebrates and many invertebrates, especially in the liver and kidneys of vertebrates. Mammalian urine is particularly rich in auxins and provides the principal source of these substances for experimental purposes. A large percentage of the auxins in the urine is derived from the food and from the action of intestinal bacteria. The source of the remainder is unknown, whether it is an animal secretion or an incidental catabolite of the liver or kidneys.

Addition of auxins to animal-tissue cultures has no effect on their growth; the culture medium itself, however, is relatively rich in auxins. The auxin content of the incubating-hen egg increases up to the 14th day and is contained principally in the embryo. After the 14th day the auxin

content decreases. This certainly suggests that the auxins may affect embryonic growth in the early stages, but the evidence is not conclusive. No physiological function for auxins has been demonstrated in animals nor has a lack of function been proven. If auxins have a physiological function in animals, the situation may parallel that of the hormone of the adrenal cortex in that there is a minimum requirement and excesses above this minimum have no noticeable effect.

APPEARANCE OF HYPHODONTY IN TIME

The correlation between grazing habit and hypsodont teeth in horses and the browsing habit and brachyodont teeth in deer are established examples of adaptation. Both have been used repeatedly to explain the tooth condition and food habits of many groups of herbivorous mammals. At this point in the discussion, however, it is desirable to briefly review the initiation of hypsodonty in the various groups of mammals, both living and extinct, together with the geologic date of its appearance in the latter, and the time required for full development. The date of initial deposition of cement on the crown, how long it takes to form a heavy coat, if one develops, and whether or not it is accompanied by increased complexity of enamel pattern, as well as the food of living representatives of each group will be considered for each group and are also presented in tabular form (Table I). Data have been taken from the more comprehensive works dealing with faunas or the revisions of groups. Any minor errors in geological dates that may have been introduced are no greater than those which result from the inadequacies of the paleontological record, and presumably, will not invalidate the thesis.

Whether a tooth is hypsodont or not is determined by comparison with other members of the same group (subfamily, family, or suborder), I have refrained from the use of such terms as "subhypsodont" or "subbrachyodont." Furthermore, not all members of a group listed are hypsodont; some groups, such as the Suidae, may have only two hypsodont members. It is not my intention to propose a classification of hypsodonty but only to state the criteria which I have used in this study. For tooth proportions, I selected *Mesohippus* as a typical brachyodont, herbivorous mammal and measured the second upper molar, in a specimen which showed only a slight amount of wear. The dimensions are as follows: height of paracone, 9 mm.; length of ectoloph, 10 mm.; and width across protocone, 15 mm. Thus, the brachyodont upper molar is a tooth which is as high as it is long and two-thirds as high as it is broad. As I interpret it, a tooth as high as it is broad marks the initiation of hypsodonty, and a tooth twice as high

as it is broad the fully hypsodont. This latter proportion, however, is eventually greatly exceeded in most hypsodont forms.

Insofar as are available data relating to the groups of mammals are presented in the following order (see Table I): (1) Initiation of hypsodonty; (2) accomplishment of hypsodonty; (3) time at which cheek teeth become rootless; (4) initial deposition of cement on crown of teeth; (5) earliest deposition of a heavy coat of cement; (6) distribution of enamel; and (7) food of living members of the group.

Taeniodonta.—In this extinct group hypsodonty was initiated in the middle Paleocene (Torrejonian) in *Psittacotherium* and was fully accomplished by the beginning of the upper Paleocene in *Lampadophorus*. The cheek teeth were rootless at the end of the lower Eocene (Wasatchian) in *Stylinodon* (see Patterson, 1949, p. 249). The deposition of cement paralleled the development of hypsodonty in time, but it never became a heavy coat comparable to that of the horses or elephants. The cheek teeth remained simple and the cusps of the crown were soon obliterated by wear. On the upper molars the enamel extended farther on the inner side than on the outer, whereas on the lower molars it extended farther on the outer. The food is unknown.

Megalonychoidea.—Hypsodonty was fully accomplished when this group is first encountered in the lower Oligocene, in *Octodontotherium* and *Orphodon*, of South America. Early members, whose family affinities are uncertain, are known only from isolated teeth that are devoid of enamel and were, presumably, rootless. In the earliest recorded forms the teeth consist of simple dentine pegs encased in a thin layer of cement. Although the whole group is extinct, the dung of later members was found in caves in the southwestern United States. It showed that *Ephedra* (Gnetaceae) was the principal food plant in that area. (Laudermilk and Munz, 1938.)

Bradypodoidea.—No fossil forms are certainly referable to this group. The teeth of the living forms are rootless and devoid of enamel; they are simple dentine pegs with a thin coat of cement. The animals subsist entirely on leaves, buds, and small twigs.

Dasydodoidea.—Hypsodonty was fully accomplished and the cheek teeth were rootless by the time the group (*Utaetus*) was first encountered in the lower Eocene (Casaomyoran) of South America. Eocene members have a thin layer of enamel on the inner and outer sides of the teeth but this coating has disappeared from the teeth of the later forms. In all known forms the teeth are simple dentine pegs. Living armadillos appear to feed upon arthropods (Fitch, Goodrum, and Newman, 1952, p. 29), but

TABLE I
GEOLOGICAL APPEARANCE OF HYPSONDONTY IN MAMMALIAN GROUPS

Group	Initiation of Hypsodonty	Accomplishment of Hypsodonty	Cheek Teeth become Rootless	Initial Deposition of Cement
Taeniodonta*	Middle Paleocene	Upper Paleocene	Lower Eocene	Upper Paleocene
Megalonychoidea*	?	?	Lower Oligocene
Bradypodoidea	?	?	?
Dasydopoidea	?	By Lower Eocene	Lower Eocene
Glyptodontoidea*	?	By Upper Oligocene	Upper Oligocene
Leporidae	?	Upper Paleocene	Lower Oligocene	Lower Oligocene
Aplodontidae	Lower Miocene	Lower Miocene	Middle Miocene
Mylagaulidae*	?	Lower Miocene	Middle Miocene
Geomyiidae	?	Lower Miocene	Upper Pliocene
Heteromyidae	Lower Miocene	Middle Miocene
Castoridae				
Castorinae	Upper Oligocene	Lower Miocene	Middle Miocene
Castoroidinae*	Upper Oligocene	Lower Miocene	Middle Pliocene	Middle Miocene
Cricetidae				
Microtinae	?	Middle Pliocene	Lower Pleistocene	Upper Pliocene
Hystricidae	Lower Pliocene	Middle Pliocene
Cavioidae	Lower Oligocene	Upper Oligocene	Lower Miocene	?
Toxodonta*	Lower Oligocene	Upper Oligocene	Middle Pliocene	?
Typotheria*	Lower Eocene	?	Lower Oligocene	?
Hegetotheria*	?	?	Lower Oligocene
Elephantidae	Upper Pliocene	Lower Pleistocene	Upper Pliocene
Equidae	Lower Miocene	Middle Miocene	Middle Oligocene
Suidae	Middle Pliocene	Upper Pliocene	Middle Pliocene
Merycoidodontidae				
Leptaucheninae* ...	?	Upper Oligocene
Camelidae	Lower Miocene	Middle Miocene	Middle Oligocene
Hyperttragulidae				
Hypisodontini*	?	Lower Oligocene	Lower Oligocene
Cervidae	Middle Miocene	By Upper Pliocene	Middle Miocene
Antilocapridae	?	Lower Pliocene
Giraffidae				
Sivatheriinae	?	Upper Pliocene
Bovidae	Upper Miocene	Lower Pliocene	?

* Group extinct.

TABLE I (Cont.)

Earliest Heavy Coat of Cement	Distribution of Enamel			Food	Type of Hypsodonty
	Coronal Pattern to Base of Tooth	Coronal Pattern Soon Obliterated by Wear	Reduced or Absent		
.....	..	X	X	Unknown	Root
.....	..	X	X	Inferred from dung	Root
.....	..	X	X	Leaves, buds, and twigs	Root
.....	..	X	X	Arachnida, amphibia, lizards	Root
.....	X	Unknown	Root
Middle Oligocene	..	X	..	Grass, leaves, buds, bark, etc.	Root
.....	..	X	..	Grass, leaves, buds, bark, etc.	Tooth-base
.....	X	Unknown	Cusp
.....	..	X	X	Roots, some stems and leaves	Root
.....	..	X	X	Seeds, some young grass	Root
.....	X	Bark, leaves, buds, twigs, etc.	Cusp
.....	X	Unknown	Cusp
Lower Pleistocene	X	Seeds, leaves, stems and roots of grasses; also insects, etc.	Cusp
.....	X	Green vegetation and tubers	Cusp
Lower Miocene	X	X	X	Green vegetation, seeds	Cusp
Upper Oligocene	X	Unknown	Cusp
Lower Oligocene	..	X	..	Unknown	Tooth-base
.....	..	X	..	Unknown	Tooth-base
Lower Pleistocene	X	Leaves and young branches of trees	Cusp
Lower Miocene	X	Grass	Cusp
Upper Pliocene	X	Green vegetation, fruit, etc.	Cusp
.....	..	X	..	Unknown	Tooth-base
.....	X	X	..	Grass	Tooth-base
.....	..	X	..	Unknown	Tooth-base
.....	X	Browse and grass	Cusp
.....	..	X	..	Browse and grass	Tooth-base
.....	X	Unknown	Cusp
Lower Pleistocene	X	Grass and browse	Cusp

this diet is occasionally supplemented by amphibians, small reptiles, bird eggs, and some plant material.

Glyptodontoidea.—In this extinct group the teeth were fully hypsodont and rootless in the dentitions recovered from the upper Oligocene. The teeth are bilobed dentine pegs without any trace of enamel. The food of members is unknown.

Leporidae.—The hypsodont condition was accomplished in the lower teeth by the time this group was first encountered in *Eurymylus* from the upper Paleocene (Gashoto formation) of Mongolia (Wood, 1942, p. 3). Rootlessness was well established by the lower Oligocene in *Palaeolagus*. Cement was initially deposited on the crowns of the teeth in the lower Oligocene but in much greater amount by the middle Oligocene. Since the coronal cusps are low and soon obliterated by wear, the tooth consists of a single or double column of dentine encased in enamel. According to Cahalane (1947, p. 621), it is easier to enumerate the plants which rabbits do not eat than to list those which make up their diet. In general, they eat grasses, sedges, leaves and buds of trees and shrubs, and in winter the bark of young trees or brush.

Aplodontiidae.—Hypsodonty was initiated in this group in the lower Oligocene, in *Pipestoneomys* (Donahoe, 1956, p. 264). In the lower Miocene of the John Day beds of Oregon representatives of three genera, *Haplomys*, *Allomys*, and *Meniscomys*, have been recovered which show morphological stages that took place in the development of hypsodonty in this group. In another genus, *Liodontia* of the late middle Miocene Virgin Valley formation, the cheek teeth are rootless; cement on the crowns is very thin or absent; and the enamel valleys are very shallow and soon obliterated by wear so that the tooth soon became a simple dentine peg encased in enamel. The food of *Aplodontia* consists of almost any kind of green grass, clover, herbs, and leaves and twigs of shrubs and trees (Cahalane, 1947, p. 554).

Mylagaulidae (communication from C. W. Hibbard).—At the time of the appearance of this family in the lower Miocene of North America the teeth are hypsodont, high-crowned, and rooted (McGrew, 1941, p. 19). There is a definite increase in hypsodonty of the cheek teeth during middle and upper Miocene. P_4 becomes enlarged and the base closes off during adult life. M_1 and M_2 are single rooted in *Mesogaulus* (Cook and Gregory, 1941, p. 551; Dorr, 1952, p. 326). There is still an increase in hypsodonty of the teeth during the lower and middle Pliocene especially in the lower and upper fourth premolar. By late middle Pliocene the fourth premolar has become so large that it has displaced both the upper and lower second molars. The first molar is greatly reduced. Enamel extends to the base

of the fourth premolar in Pliocene forms. So far as known, the fourth premolar closes off at the base in old adult life. A small amount of cement is present on *Mesogaulus* in the middle and upper Miocene. There is a slight increase through the Pliocene with the increased hypsodont condition. Since this group is extinct the food is unknown.

Geomyidae.—A series of the subfamily Entoptychinae from the lower Miocene (John Day beds) shows several stages from the beginning of hypsodonty to rootless cheek teeth. In the contemporary Geomyinae (only form known, *Dikkomys*) the teeth are hypsodont but rooted. The Geomyinae are poorly represented as fossils before the late Pliocene; forms with rootless cheek teeth are known from the Rexroad fauna of southwestern Kansas (Hibbard, 1950, pp. 138–39). The coronal cusps are soon obliterated by wear, leaving the tooth a double or single column of dentine. The enamel remains thick on the anterior and posterior sides, but is quite thin on the inner and outer sides, from which it soon disappears as the tooth is worn. Living species feed principally on the roots of whatever plants they encounter in their burrows (Aldous, 1951, p. 87).

Heteromyidae.—The paleontological record leaves much to be desired. Of the subfamily Perognathinae, the genus *Mookomys* shows tendencies toward hypsodonty. *Perognathus*, from the upper Cuyama beds, is definitely hypsodont at least in comparison with *Mookomys*, and the lower Pliocene and later members are distinctly so. All members of the Dipodominae are hypsodont when first encountered in the lower and upper Pliocene. Of the Heteromyinae, one species of *Proheteromys* (*P. magnus*) appears to be tending toward hypsodonty (Wood, 1935, p. 166) and *Peridiomys* of the middle Miocene is definitely hypsodont as are all later members. In none of the heteromyids do the cheek teeth become rootless. A very old specimen of *Dipodomys deserti deserti* Stephens (USNM Division of Mammals, No. 60264) has the roots coalesced and closed off as in the beaver. The crowns of the teeth are without cement. In the Dipodominae the coronal cusps are soon obliterated by wear, leaving a simple dentine column encased in enamel which is very thin on the sides. In the Heteromyinae the cusps are high and persist for considerable time before they are obliterated by wear. The Perognathinae (pocket mice) have an intermediate development of cusps. All species in this family live almost entirely on seeds, but most will eat considerable grass when it is young and tender (Cahalane, 1947, p. 446).

Castoridae (by T. M. Stout).—"The oldest beaver specimens at present admitted as such are from the Lower Oligocene. Eight subfamilies are now recognized, of which only one (Castorinae) survives in North America and Eurasia. Progressive hypsodonty occurs in the cheek-teeth of each

subfamily, and the living beavers exemplify a true hypsodont condition with cement. The complete progression series is in six stages: (1) sub-brachyodont; (2) brachyodont; (3) advanced brachyodont; (4) sub-hypsodont; (5) hypsodont; and (6) super-hypsodont (ever growing, rootless).

"Probably all four of the ancestral subfamilies passed through stages 1-3 in the Oligocene and Early Miocene, but in one, stage 3 is the earliest known. From this fourth subfamily there were derived four additional subfamilies, each of which attained stage 5 by the time of differentiation (beginning of Pliocene). Thus, at least an approach to a true hypsodont condition (stage 5) was accomplished by all of the beavers in the interval Late Miocene-Medial Pliocene, with the date of the initiation of hypsodonty in a more general sense probably to be considered as in about the Late Oligocene for the four main lineages.

"Only three of the subfamilies attained stage 6, the super-hypsodont or rootless condition. The ancestors of the Giant Beavers achieved this stage abruptly in the Medial Pliocene (upper part Ash Hollow fm. and equivalents), but the third lineage was more conservative, delaying the rootless condition until the Medial Pleistocene.

"Two subfamilies, one (Trogontheriinae) being restricted to Eurasia, never developed cementum on the cheek-teeth, but all of the other fossil beavers initiated cementum almost abruptly in the Late Miocene. The deposition of cementum became increasingly more prominent in the interval Early Pliocene-Early Pleistocene. At this later date the deposition of cementum became essentially stabilized, and the enamel margin began to give way at several points to expose the dentine of each cheek-tooth of the Giant Beavers. With the exception of these 'giants,' the cheek-teeth of the fossil beavers have the same complete enamel jackets about the dentine that one observes in the teeth of the living beavers, the enamel being infolded along the marginal grooves progressively and less evident over the cuspal summits in the later forms.

"The food of the living beavers is probably almost limited to willow and poplar bark in the winters, being supplemented in the summers with grass, leaves, berries, or roots (Nasset, 1953; Warren, 1927). The role of the 'cardiac gland' and of the caecal round-worms in digesting the large quantities of cellulose is still imperfectly understood (Nasset, 1953)."

Cricetidae, subfamily Microtinae (communication from C. W. Hibbard).—The Microtini group is first known from the middle Pliocene and at that time had hypsodont teeth (Wilson, 1937, p. 9); example, *Gomiodontomys* from the Rome fauna of Oregon. There is an increase in hypsodonty during the Pliocene with the roots developing later in the life of

the individuals. The North American specimens of the genera *Ogmodontomys* Hibbard and *Pliophenacomys* Hibbard, recovered from the upper Pliocene, and *Cosomys* Wilson, from the early Pleistocene, have not contained cement. The upper Pliocene genus, *Mimomys* Forsyth Major, of Europe is found in most cases without cement; a few specimens possess a small amount (Hinton, 1926, p. 362). Ever-growing teeth appear in some of the Microtini during late Nebraskan time or early Aftonian. The group is extremely variable. All Recent genera possessing ever-growing teeth had appeared by Kansas time. These forms possess well-developed cement. In contrast, *Phenacomys* has hypsodont teeth with well-developed roots and no cement. Food consists chiefly of grasses.

The Lemmini group is first known from the early Pleistocene (Nebraskan) and possessed at that time ever-growing teeth with cement (Wilson, 1933, p. 124; *Synaptomys*). Food consists of green grasses and *Equisetum*.

According to Cahalane (1947, p. 515), *Microtus* feeds on the seed heads, leaves, tender stems, and roots of grasses; also, grains of all kinds, tubers, bulbs, bark, buds, carrion, insects, crayfish, and snails. Occasionally, it kills its own kind to satisfy its craving for concentrated proteins.

Hystricidae.—In this group hypsodonty was initiated in *Sivacanthion* in the lower Pliocene (Chinji zone) of the Siwalik Hills, Punjab, India. There is a gap in the record for the middle Pliocene but the hypsodont condition was very advanced in *Hystrix* in the upper Pliocene (Dhok Pathan). The cheek teeth never became rootless. In living members the cement is very thin or absent and the height of the cusps are materially increased but conceivably might be obliterated by wear in old individuals. The contemporary forms feed on green vegetation and tubers (Flower and Lydekker, 1891, p. 487).

Cavioidea.—In the cavioids hypsodonty was initiated in the lower Oligocene (Deseadean) in Patagonia and was fully accomplished by upper Oligocene (middle Oligocene deposits are as yet unknown in Patagonia). In some forms the cheek teeth are rootless by the lower Miocene (Santacrucian). Certain forms had the valleys filled with cement by lower Miocene. The earliest known members have two cross lophs on both the upper and lower teeth. In some later ones these lophs become multiplied several times so that with wear a number of transverse lamellae of enamel appear. The food consists principally of green vegetation.

Toxodonta.—Hypsodonty was initiated in the lower Oligocene and was accomplished by the upper Oligocene in this group. In *Toxodon* the cheek teeth are rootless when the genus is first known in the Pliocene. One family, Notohippidae, had developed a heavy coat of cement on the

cheek teeth by the upper Oligocene. The enamel valleys extend to the base of the tooth. The group is extinct and the food is unknown.

Typotheria.—In this group, while hypsodonty appears to have been initiated in the lower Eocene, there is a gap in the record up to the lower Oligocene. At that time the cheek teeth are rootless and in some members had acquired a heavy coat of cement. The coronal pattern, if any, was soon obliterated by wear, leaving the tooth as a double column of dentine encased in enamel and cement. The group is extinct and the food is unknown.

Hegetotheria.—Members of this extinct group had acquired rootless cheek teeth without cement by the lower Oligocene. The coronal enamel pattern is soon obliterated by wear, so that the teeth consist of a single dentine column encased in enamel. The food is unknown.

Elephantidae.—In this group hypsodonty was initiated in *Stegodon* in the upper Pliocene (Dhok Pathan) and was fully accomplished in *Elephas* by the beginning of the Pleistocene (Pinjor). The teeth never became rootless. The development of hypsodonty was accompanied by the deposition of cement in ever-increasing quantities on the crowns and an increase in number and a decrease in size of the cross lophs on the cheek teeth. Anteroposterior dimension of the tooth also became greater. The food of wild elephants consists chiefly of the leaves and young branches of forest trees (Flower and Lydekker, 1891, p. 423).

Equidae.—In the horses hypsodonty started in the early lower Miocene (*Hippodon leonensis*) and is regarded as fully accomplished by the middle Miocene (*Merychippus primus*), even though the crowns of the teeth have continued to add height up to the present time. The cheek teeth never become rootless. Occasional specimens of *Meshippus* from the middle Oligocene have a thin film of calcareous material on the labial surface and at times in the valleys of one or two of the upper molars, but this does not become a uniformly heavy coat until the lower Miocene (*Hippodon leonensis*). In *Meshippus* calcareous material appears to be deposited in specific areas according to a definite pattern. Histological sections, however, do not reveal any bony structure. Enamel valleys extend to the base of the tooth and the pattern on the triturating surface becomes more complex as the crown becomes higher. Grass is the principal food of wild horses.

Suidae.—Even though the Suidae are cited as standard examples of mammals with bunodont, brachyodont teeth adapted to an omnivorous diet, actually the hypsodont condition developed in two distinct but closely related groups. One group (*Hyosus—Sivahyus—Hippohyus*) became extinct in the lower Pleistocene, but the other (*Sus comes—Sus*

falconeri—Phacochoerus) has a living representative in South Africa. While the fossil record does not reveal the start of hypsodonty in the latter line, it was fully accomplished in *Sus falconeri* of the lower Pleistocene. The teeth never become rootless, and deposition of cement on the crowns is contemporaneous with the progression of hypsodonty. The enamel pattern, which is made more complex by the multiplication of the cones and conules, appears, as in the horses, to antedate the initiation of hypsodonty. The diet of *Phacochoerus* consists largely of grass, supplemented with berries, fruit, and other vegetable matter when available (Roberts, 1951, p. 268).

Merycoidodontidae, subfamily Leptaucheniinae.—The genus *Leptauchenia* Leidy had attained an advanced hypsodont condition when it was first encountered in the upper Oligocene. The cheek teeth never became rootless. Some forms possess a thin coat of cement on the crowns. The enamel valleys are soon obliterated by wear, leaving the tooth a double column of dentine encased in enamel. This group is extinct and the food unknown.

Camelidae.—Hypsodonty was initiated in the camels in the lower Miocene in *Protomeryx* and was fully accomplished by the middle Miocene in *Protolabis*. The teeth never became rootless. A thin coat of cement is present on the crowns of some forms but it never constitutes a heavy coat. Persistence of the enamel lakes in the teeth is extremely variable; in some forms (*Camelops*) it continues well toward the base of the tooth but in others (*Rakomylus*) it is soon obliterated by wear. The enamel pattern remains fairly constant throughout the group. The only undomesticated member of this group subsists largely on grass.

Hypertragulidae, tribe Hypisodontini.—These diminutive artiodactyls were already fully hypsodont when first encountered in the lower Oligocene. The cheek teeth are rooted. Some specimens show a thin film of cement on the lower cheek teeth. The enamel valleys are soon obliterated by wear, leaving the tooth a double column of dentine encased in enamel. This is an extinct group and the food is unknown.

Cervidae.—In this group hypsodonty was initiated in *Micromeryx* in the middle Miocene (Sansan). The paleontological record of the Cervidae is very inadequate, but those known from upper Miocene and lower Pliocene show little advance over *Micromeryx*. Two forms (*Cervus simplicidens* and *C. triplidens*) of the upper Pliocene (Dhok Pathan), and living members of the Rusine group of *Cervus* and of *Axis*, are definitely hypsodont. None of the cervids, however, have attained the degree of hypsodonty characteristic of the bovids. The teeth are always rooted. Some specimens of *Blastomeryx* from the middle Miocene of the Plains

of the United States have a thin coat of cement on the outer surface of the molars but no specimen has a heavy coat. Theoretically, the small amount of cement may be regarded as the result of the annual production of antlers, because the first "spike antler" utilizes eight to ten times as much calcium and phosphorus as would be required for one heavy coat of cement on the teeth. The enamel valleys extend to the base of the tooth and the enamel pattern has remained relatively constant. While the Cervidae are the standard example of browsing mammals with brachyodont teeth, the group include a number of grazers; for example, *Muntiacus* (Flower and Lydekker, 1891, p. 317), *Odocoileus hemionus* (Calahane, 1947, p. 37), and *Cervus canadensis* (Cahalane, p. 21; Murie, 1951, pp. 196-99). Indeed, most cervids graze extensively in the spring when grass is fresh and green. The most notable exception to this is *Alce*. The moose's long legs and short neck make grazing in the manner of horses and bovids impossible, yet even in it the teeth approach a hypsodont condition.

Antilocapridae.—Hypsodonty was well advanced by the time members of this group (*Cosoryx* and *Meryceros*) were first encountered in the lower Pliocene. The teeth are always rooted. Very little or no cement is deposited on the crowns. The enamel valleys are soon obliterated by wear, leaving the tooth a double column of dentine encased in enamel. Living members depend principally on browsing, but will graze exclusively when grasses are tender and green (Cahalane, 1947, p. 68).

Giraffidae, subfamily Sivatheriinae.—This is the only subfamily of the Giraffidae that attained hypsodonty, and in about the same degree as the hypsodont cervids. The teeth of members of this subfamily were moderately high-crowned when first encountered in the upper Pliocene (Dhok Pathan); increase in height in later forms is negligible. There is no cement on the crowns. The enamel valleys extend to the base of the teeth. Members of the subfamily are extinct and their food is unknown.

Bovidae.—In the bovids hypsodonty was initiated in *Oioceros?* in the upper Miocene (Tung Gur) and was fully accomplished, except in one subfamily, the Tragelaphinae, by the lower Pliocene (Pontian). The cheek teeth are always rooted. The data on the fossil members furnishes no clue to the time of appearance of cement on the crowns; in the living the amount varies from a rather heavy coat (*Bos* and *Bison*) to practically none (*Ovis*). The enamel valleys extend to the base of the tooth; there is very little subsequent elaboration of the enamel pattern on the triturating surface. Although most of the living members are grazers, the group also includes some browsers which are hypsodont. Probably, the best known example of the latter is the domestic goat, which is used extensively for clearing brush in certain sections of the United States.

TYPES OF HYPHODONTY

This review of the mammalian groups which contain members with hypsodont teeth, shows that hypodonty developed many times during the Cenozoic and occurred in most of the larger categories of herbivorous mammals. While there appear to be as many types of the phenomenon as there are groups of herbivores, closer scrutiny materially reduces this number. In general, however, there are three principal types of hypsodont teeth, but an attempt to assign the various groups to a particular one of them has been far from satisfactory. Not only are there borderline cases (Camelidae, Antilocapridae, and Hystricidae), but also in one group at least (Leporidae), the upper teeth are of one type and the lower of another. The difficulty of classification is further increased not only by the inadequacies of the paleontological record but by the failure to report in the literature such data as are available. Although additional data may necessitate changes, I am presenting a tentative arrangement that is based on the three categories.

Type 1. *Cusp hypsodonty*.—An actual increase in the height of the cusps or crests above the base of the tooth, the enamel pattern usually showing only minor variations with wear, and teeth usually but not always (Microtinae and Castoroidinae) rooted characterize this type. To Type 1 are assigned the Mylagaulidae, Castoridae, Microtinae, Hystricidae, Caviioidea, Toxodonta, Elephantidae, Equidae, Suidae, Cervidae, and Bovidae.

Type 2. *Tooth-base hypsodonty*.—In this type, the principal growth of the tooth takes place between the base of the cusps and the top of the roots and the cusps or crests are usually low and soon obliterated by wear, leaving the tooth a single or double dentine column encased in enamel. To Type 2 I assign the Aplodontidae, Typotheria, Hegetotheria, Leptaucheniinae, Hypsodontini, Camelidae, and Antilocapridae. The teeth in the Camelidae and Antilocapridae are more or less intermediate between Types 1 and 2, but to erect a separate category for them would not solve the problem for the Camelidae, because some genera belong definitely in Type 1 and others just as certainly in Type 2.

Type 3. *Root hypsodonty*.—In this type the principal growth of the tooth takes place in the roots and may represent either a fusion of the roots, as in the taeniodonts, or a single main root as in the upper teeth of rabbits; the enamel-depositing organ may or may not persist or it may be limited to certain areas of the tooth, as in the heteromyids. To Type 3 I assign the Taeniodonta, Megalonychoidea, Bradypodoidea, Dasypodoidea, Glyptodontoidea, Leporidae, Geomyidae, and Heteromyidae. However, just

as much evidence for placing the Leporidae in Type 1 as in Type 3 exists, because in the lower teeth (in which hypsodonty was first initiated) the principal growth occurs in the trigonid and the talonid, whereas in the upper teeth (hypsodonty initiated later) the additional growth occurs in the median principal root. While the condition in the upper teeth of the prairie dog (*Cynomys*) appears analogous to that in the upper teeth of upper Eocene and some lower Oligocene rabbits (*Megalagus*), this requires further study.

APPEARANCE OF GRASSES IN TIME

Any consideration of hypsodonty in mammals is usually confined to that in the horses, though beaver and elephants have occasionally been mentioned. In these discussions one or both parts of the palimpsest axiom may be encountered. In effect this axiom says: (1) horses did not become hypsodont before the Miocene because, prior to that time, grasses were only a minor part of the flora and (2) the fact that grasses were only a minor part of the flora before then is proof that hypsodonty was not initiated earlier in the horses. Perhaps, this is an unassailable line of reasoning, but first one should examine what is actually known about fossil grasses.

Compared with other plant groups, only a few genera of the family *Gramineae* are known from the Tertiary deposits of North America and most of these are deposits younger than the Miocene. Less than half of the genera of grasses which make up the bulk of the forage on the extensive grasslands of North America are known from fossils. A list of fossil grasses from La Motte's (1952) catalogue of Cenozoic plants is included with geologic dates (Table II), together with one of the principal forage grasses native to North America taken from the 1948 Yearbook of the United States Department of Agriculture (Table III).

The importance of the forage grasses, both as native pasture and as cured roughage, needs no elaboration. They are typically upland grasses and require considerable sunshine, but most species appear to be unaffected by thin shade and some even to be improved by it. If the habitat of the living representatives is any indication in the past the forage grasses did not normally grow in locations where they would be buried and preserved as fossils. Furthermore, since the leaves, stems, and seeds are quite delicate, even if by chance they were buried in their natural surroundings, the leaching of ground water and the action of aerobic bacteria would soon remove all traces. Consequently, infrequency of these grasses in the early Tertiary sediments is no proof of their scarcity in the flora of that time.

TABLE II
GEOLOGICAL DISTRIBUTION OF GRASSES IN NORTH AMERICA

Epoch	Genus	Localities
Paleocene	<i>Arundo</i> (?)	Colorado, Alaska (?)
	<i>Phragmites</i>	Alaska (?), Montana, Grinnell Land, Greenland, Colorado, Iceland, Alberta, North Dakota
	<i>Poacites</i>	Greenland, Alaska (?)
Eocene	<i>Arundo</i>	Georgia, Alabama, Louisiana, Arkansas, Texas, Wyoming
	<i>Phragmites</i>	Wyoming, British Columbia, Utah, Louisiana
	<i>Poacites</i>	Wyoming, Kentucky, Louisiana, Tennessee, British Columbia
Oligocene	<i>Clementsella</i> *	Colorado
	<i>Poacites</i>	California
Miocene	<i>Arundo</i>	Switzerland
	<i>Berriochloa</i> *	Nebraska
	<i>Phragmites</i>	Oregon
	<i>Poacites</i>	California
	<i>Stipidium</i>	Nebraska, Colorado
Pliocene	<i>Berriochloa</i> *	Kansas, Colorado, Nebraska, Texas, Oklahoma
	<i>Echinochloa</i>	Nebraska
	<i>Nassella</i>	Kansas
	<i>Paleoeriocoma</i> *	Colorado
	<i>Panicum</i>	Kansas, Nebraska
	<i>Poacites</i>	California
	<i>Setaria</i>	Nebraska
Pleistocene	<i>Aristida</i>	Nevada
	<i>Arundinaria</i>	Alabama, Louisiana
	<i>Bromus</i>	Ontario
	<i>Festuca</i>	Ontario
	<i>Hilaria</i>	New Mexico
	<i>Oryzopsis</i>	Ontario
	<i>Paspalum</i>	Louisiana
	<i>Phragmites</i>	New York, Arizona

* Known only from fossils.

Another concept frequently encountered in the literature is that the whole of North America was well forested prior to the Miocene. Yet, if so, where are the fossil woods and leaves from the White River deposits of the Big Bad Lands? True, in some localities seeds of hackberry are common, but this is not a forest tree. Its habitat is the valleys of intermittent stream of the prairie region. The genus *Populus* has a wide geographical distribution throughout the North American Tertiary, yet it is not listed by LaMotte from the White River deposits. Should this be

TABLE III
PRINCIPAL FORAGE GRASSES OF NORTH AMERICA
List taken from the Yearbook of Agriculture, 1948.

Genus	Common Name	Native Distribution
<i>Agropyron</i>	Wheat Grass	Eurasia, North and South America
<i>Agrostis</i>	Bent Grass	North America
<i>Andropogon</i>	Bluestem	Warm temperate regions of world
<i>Axonopus</i>	Carpet Grass	Central America and West Indies
<i>Bouteloua</i>	Gramma Grass	Pole to pole in Western Hemisphere
<i>Bromus</i> *	Brome Grass	North Temperate Zone
<i>Buchloe</i>	Buffalo Grass	Great Plains
<i>Eragrostis</i>	Lovegrasses	Temperate regions of world
<i>Festuca</i> *	Fescue	Temperate or cool zones of world
<i>Oryzopsis</i> *	Indian Ricegrass	Western States
<i>Panicum</i> *	Panicgrasses	Warm regions of world
<i>Paspalum</i> *	Paspalum Grasses	Western Hemisphere
<i>Phalaris</i>	Canary Grass	World-wide
<i>Poa</i>	Bluegrass	Temperate and cool regions of world
<i>Setaria</i> *	Foxtail Millet	Northern Hemisphere
<i>Sporobolus</i>	Dropseeds	Southern Great Plains and Southwest
<i>Stipa</i> *	Needlegrass	Temperate Zones

*Representatives known as fossils in North America.

regarded as proof of the absence of poplar in this area or merely as proof that conditions were unsuited for its preservation? In view of the very small percentage of the total area of the North American continent which is represented by the early Tertiary deposits, as well as the above considerations, one need not assume that the grasses played a less important role in the flora of that time than they do now. If on purely negative evidence the bulk of the pasture grasses are to be excluded from the pre-Miocene flora, then by the same negative evidence they should be given a post-Pleistocene development.

HYPHODONTY AND ITS COINCIDENCES

Throughout the literature the supposed advantages of high-crowned over low-crowned teeth for grazing are usually stated in a way to invite the inference that the advantage provided the stimulus that caused the increased growth of the teeth. The coincidence of a structural feature and a feeding habit is thus mentioned as constituting a correlation. This may not be true. It is, therefore, desirable to reconsider the several correlations that have been assumed between food habits and hypsodont teeth. In most of the related literature, horses are used as the typical example and, because they are so widely mentioned, they are also used here.

Mechanical abrasion.—Many citations state that grass contains harsh abrasive silica which rapidly wears away the teeth and that grazing mammals developed hypsodont teeth as a response to this wear. It is inferred and occasionally stated (Stirton, 1935, p. 449) that the abrasion furnished the stimulus for the additional tooth growth. In laboratory mammals, man, and presumably other mammals, the cement and dentine are highly vascular structures and the dentine is enervated; the tiny canals for the blood vessels and nerve are closed off, however, by the odontoblasts a short distance ahead of the wear. If it were otherwise there would be considerable loss of blood and an exposure of the nerve that would discourage chewing. Thus, the triturating surface is, in reality, inert, it cannot possibly respond to a stimulus. In order to assign any hereditary influence to the amount of wear produced on the teeth, it is first necessary to find an answer to the question which Professor E. C. Case used to pose to each of his classes in vertebrate paleontology: "How can the mechanical abrasion of an inert concretion, which the triturating surface of a tooth is, have any effect on the germ-plasm?"

Pressure on tooth.—One suggestion is that the pressure of chewing on the worn surface of the tooth may have stimulated the deposition of more dentine to protect the nerve, thus postponing the closure of the roots (Stirton 1935, p. 449). But this overlooks the fact that the sides of the crown of hypsodont teeth and the sides of the roots of brachyodont teeth are so securely bound to the walls of the socket by the alveolar periosteum, that no pressure can be applied to the base of the tooth (Hinton, 1926, p. 102). If this were not true, the sharp edges of the unclosed roots or crown would sever both the nerve and blood vessels and development would cease, not only for the tooth involved but for all those anterior to it. Moreover, except for the very hypsodont forms like the horses and beaver, in those mammals which have rooted teeth, the enamel skeleton is very nearly filled with dentine when the tooth erupts and the roots have started to form. The roots develop fully and fill with dentine soon afterward. This

happens before the tooth receives any extensive wear not only in the carnivores and brachyodont herbivores but also in the hypsodont bovids. Stirton's suggestion, therefore, is untenable because operation of a pressure stimulus depends on a condition which never existed and could not possibly have existed without defeating itself.

Contamination of food by abrasives.—From the increasing sandiness of the continental Miocene and Pliocene deposits in North America Stirton inferred (1947, pp. 35–36) that the region of their occurrence was the center of dispersal and evolution for the Plains mammals, at least those of North America. He also pointed out that the sandy soil naturally present over these deposits would add contaminating grit to the vegetation through the action of wind and rain. This fails to take into consideration that the area of these deposits is a very small percentage of the total of North America and that there were vast stretches to the north, east, and south of them which could have, and probably did, support extensive grasslands on a very fertile soil derived from limestone and shale. The assumption that the latter were completely wooded throughout the Early Tertiary is not substantiated by finds of fossil plants or by the ecology of any region in the world which has a comparable physiography, latitude and climate. No geological structure justifies the assumption that the general physiography of the terrain between the Appalachian and Rocky mountains was radically different from what it is today. It would seem more logical to assume a wide region of rolling prairie with wooded stream valleys and grass-covered uplands than to postulate a continuous climax forest from the crest of the Appalachians westward to central Kansas and Nebraska. Certainly, the distribution of fossil Equidae in the Miocene and Pliocene indicates that suitable ecological "islands" were sufficiently close together to allow the horses to move up the Atlantic Coast as far as Chesapeake Bay. Absence of their remains in the Ohio Valley is rather the result of the lack of Miocene and Pliocene sediments in which they could have been preserved. Consequently, the center of the dispersal and evolution of the grazing mammals was not, necessarily, where the record is the most abundantly preserved and the sandy soil furnished the maximum contaminating grit in the food. Recent studies by J. H. Quinn (1955, pp. 65–68) on the horses of the Gulf Coastal Plain of Texas presents cogent evidence that the center of evolution and dispersal of the horses was in the southern United States and that the deposits on the High Plains are actually records of successive dispersals of advanced members of several lines of evolution. Certainly, if contaminating grit in the food were a factor contributing toward hypsodonty, then the pigs and peccaries, due to their habit of rooting for tubers, should have become hypsodont before the horses did!

Species survival.—The opinion that a hypsodont condition of the cheek teeth of horses was essential if the species was to survive on a diet of grass, because brachyodont teeth would wear away too fast for the animals to produce enough offspring to maintain the species has been expressed by Watson (1930, p. 90) and by Simpson (1951, pp. 131, 186). When the white man first saw the plains, elk (*Cervus canadensis*), mule deer, (*Odocoileus hemionus*), and the prairie dog (*Cynomys ludovicianus*) were very successfully maintaining themselves in competition with the hypsodont bison. All three are brachyodont and subsist almost entirely on grass. Here then are three brachyodont forms which were able to invade (the date is yet unknown) the habitat of the horse and bison in successful competition for the same food.

Stirton (1947, p. 40) theorized that hypsodont teeth were not the only determining factor in species survival because the difference in crown height between succeeding species of the same genus was too small to be advantageous. He also pointed out that *Nannippus*, very small but the most hypsodont of the horses, neither survived nor left any descendants.

More evidence on the theory that hypsodonty is essential to survival is presented in an exhibit in the American Museum of Natural History that was prepared under the direction of S. H. Chubb. This exhibit, of the development of the modern horse, shows that the last deciduous premolar (Dp_4^4) is replaced with a permanent tooth when the animal is four years old. Whether an animal is brachyodont or hypsodont, the permanent teeth last as long (usually twice as long) as the deciduous teeth. This would give a minimum age of eight years for the horses, five of which would be potentially reproductive, a span that would provide ample offspring for the species not only to maintain itself but to multiply and spread. Ethnographic data on the length of the period of fertility of the horses owned by the Indians, while very limited, is valuable, because their horses are believed to have received no more care than feral horses. The mares were seldom fertile beyond the age of twelve and the stallions seldom beyond the age of eight. This is a 65 per cent increase over the theoretical condition mentioned above, but if one concedes that the permanent teeth last twice as long as the deciduous teeth (usually true) there is no gain whatever. Consequently, the concept that hypsodont teeth are essential for species survival must be rejected because facts do not support it.

Size.—Watson (1930, p. 91) suggested that in the modern horse the hypsodont condition was an adaptation to be correlated with the increase in size over *Eohippus*. This concept was further elaborated by Simpson (1951, p. 181). In substance, the reasoning behind it is as follows: when

the linear dimensions of an animal are doubled, the bulk is cubed and this would accordingly cube the amount of feed required if the metabolic rate is to remain the same. But when the linear dimensions are doubled the area of the triturating surface of the teeth is increased only by the square and the animal, as a result, would have to eat twice as long to obtain the required amount of food and the teeth would receive twice the wear. If one follows this attractive line of reasoning to its logical conclusion, especially as applied to jaws and teeth, it will be seen that if the linear dimension is doubled, any given tooth will be twice as far from the hinge of the jaws, and if the jaws are opened to the same angle the distance between any two opposing teeth will be twice as great, thus accommodating a morsel of food twice as thick. Consequently, when the linear dimensions are doubled, the feeding capacity is cubed along with the bulk. I well remember as a boy on the farm that at noontime the 1600-pound work horses consumed their quota of oats and hay as quickly as did a 700-pound pony.

The data presented by J. H. Quinn (1955, p. 66) gives one good reason to believe that the diminutive horses, *Calippus* and *Nannippus*, developed from species of *Hippodon* through merychippine stages, with a negligible increase in size, rather than that they are dwarfed forms of pliohippine and hipparion stages as was formerly believed. *Nannippus* possessed the most fully hypsodont teeth of any of the horses, yet its increase in bulk over its ancestor *Hippodon* is negligible. In fact, any gain over *Miohippus* is more apparent than real, because of the difference in the length of the legs of the two, the actual amount probably does not exceed 15 per cent.

In this connection (size and hypsodonty) it is necessary to consider the anchitherine horses which, in North America, culminated in *Hypohippus* (with a bulk equal to that of *Hipparion*) and *Megahippus*, the largest of the horses. All of this group remained brachyodont, yet these horses continued to increase in bulk from the early Miocene up to the end of their record in the early Pliocene. Thus, an increase in the height of the crowns of the teeth cannot be a corollary of an increase in bulk. It has been argued, further, that the persistence of brachyodont teeth contributed largely to the extinction of the anchitheres because their teeth wore out too fast to maintain the species. Yet the large hipparions, the most hypsodont of the horses, failed to survive, whereas the tapir, rhinoceros, and hippopotamus, of equal or greater bulk than the horses and with as long a geologic history, remained brachyodont and survived. The only rhinoceros (*Elasmotherium*) to attain rootless cheek teeth and a complicated enamel pattern did not.

Thus, while it is true that many of the large herbivorous mammals are

hypsodont (horses, elephants, bovids, and camels), others of equal bulk (rhinoceros and hippopotamus) have brachyodont teeth. If one regards the sheep to be an example of a medium-sized mammal, the majority of the hypsodont mammals, both living and extinct, must be classed as small or tiny. The increase in proportions of the armadillos, rabbits, aplodontids, mylagaulids, heteromyids, geomyids, microtines, hegetotheres, and antilocaprids during their known history was negligible, as was that of the line from the brachyodont *Stegodon* to the hypsodont *Elephas*. Consequently, if hypsodonty has any correlation with bulk, it would seem, from the evidence above, to be associated with small rather than large size.

Actually, mammals of all sizes became hypsodont. A few increased their bulk as they became hypsodont, but the majority did not. The line of reasoning that size and hypsodonty are correlated must be rejected as a biological principle; it is neither applicable to the Mammalia as a whole nor to the group upon which it was based, the Equidae.

Deposition of cement.—About 50 per cent of the groups possess a partial or complete coat of cement on the teeth (see Table I). In the Leporidae, Castoridae, and Caviioidea the cement only fills the enamel valleys and does not constitute a uniform coating. In the Toxodonta and Typotheria, some members have a heavy coat of cement on the teeth, but other lack it entirely. In the hypsodont members Mylagaulidae, Elephantidae, Equidae, and Suidae there is a heavy deposit over the whole crown. In the Camelidae and Antilocapridae the cement is never more than a thin film. In the Bovidae the amount on the teeth is quite variable, not only as between genera but within a species. In hundreds of bison dentitions from archeological sites which I have examined, the amount varied from almost none to a coat 1.5 mm. thick.

Although cusp hypsodonty (Type 1) is characteristic of most of the groups with cement on the crowns of the teeth, tooth-base hypsodonty (Type 2) occurs in certain members of the Typotheria that have cement on the teeth. Thus, the presence of cement on the crowns cannot be correlated with any one type of hypsodonty, nor does it follow, as suggested by Simpson (1951, p. 188), that the coating must be heavy. In the camels and many bovids the coat is so thin that it cannot possibly have any adaptive value. Furthermore, in the hypsodont cervids and in the most hypsodont toxodonts, cement is absent.

The paleontological record is incomplete, but inasfar as present knowledge goes, the appearance of cement on the crowns does not seem to have any close relationship with the development of hypsodonty. In the horses, elephants, and pigs, cement slightly antedates the initiation of hypsodonty. It slightly postdates the start of hypsodonty in the rabbits, beavers,

mylagaulids, and cavioids, but is very much later in the bovids and microtine rodents. In many groups the cement on the crowns of the teeth is very thin or absent; it is not confined to the herbivores. For example, the mole (*Hesperoscalops*) from the Rexroad fauna, has the crowns of its teeth coated with cement (Hibbard, 1953, p. 22).

Hinton (1926, p. 353) has pointed out that, in the Microtini (*Miomomys*), the cemented teeth were mechanically better bound to their sockets by the alveolar periosteum than had been the noncemented teeth. In man the cement-depositing cells of the tooth sac develop into the alveolar periosteum of the erupted tooth. Also, these cells retain their old function of depositing tricalcium phosphate upon the tooth as well as assuming the new function of securely binding it to the walls of the socket. Moreover, the absolute amount of cement for any species increases with the age of the individual—at least, until full maturity. Since cement occurs at the base of the crown and on the roots of the teeth of all mammals, it is difficult to escape the conclusion that it has a specific function which is applicable to the class as a whole regardless of the amount deposited or whether the tooth is brachyodont or hypsodont.

If one takes into consideration its physical nature and development the tooth, in relation to the alveolar periosteum, is a "foreign body," inasmuch as it was initiated and completed by a set of cells, operating in a different area (perhaps only 0.5 mm. distant). Whereas under certain pathological conditions (local areas of inflammation) tissues attach themselves to foreign bodies (as may the intestines to the abdominal wall), normally this does not take place unless the tissue in question secretes a special "glue." Consequently, since the alveolar periosteum is related to the tooth in the same manner as fibrous connective tissue is to a foreign body, it cannot perform its function without secreting its own special type of "glue," which it does—the os cementum.

On theoretical grounds, at least, a layer of glue one molecule thick would be adequate for the alveolar periosteum to perform its function, but as the tooth grows up (or down) in the socket it is necessary for each fiber to shift its position on the tooth. Additional glue, therefore, will be necessary, because the fiber is attaching itself to a new surface. As a result hypsodont teeth should have a thin but discernible layer of cement on the crown, except possibly on the part exposed above the gum; at least this is true for those forms which I have examined. In certain bovids (*Bison* and *Bubalus*) the amount of cement on the crown appears to be correlated with age, because old individuals with well worn teeth usually have a heavy coat and the young a light one. In certain groups (Leporidae, Castoridae, Equidae, and Suidae) the cement-depositing cells at the rim

of the socket seem to be extremely active, because there is a very marked difference in the thickness of the coat of cement outside and within the socket. In the Elephantidae the difference in the thickness of the coat of cement within and outside the socket is discernible in some specimens but not in others, within the same genus.

Examination of a series of unerupted teeth of these (Leporidae, Castoridae,, Elephantidae, Equidae, and Suidae) revealed that the cement-depositing cells of the tooth sac, which are located at the rim of the socket and cover the crown of the tooth, become activated very soon after the enamel skeleton of the tooth is deposited. At this time the tooth sac would be molded to the irregularities of the enamel skeleton of the tooth and early activation of the cement-depositing cells would result in partially or wholly filling the valleys between the cusps or crests from the base of the tooth to the top of the crown. The mechanical advantage of the enamel valleys being filled with cement is obvious. No known biological principles, however, permit us to postulate that this advantage provided the stimulus for the early activation of this group of cement-depositing cells, nor can this phenomenon be correlated with any particular food habit. Also in these groups, as far as any single cheek tooth is concerned, there is a local area of this group of cells which responds very energetically to the stimulus for depositing tricalcium phosphate on the tooth, while the remainder of the cells only respond at a rate which is very little greater than that for other mammals. Eventually the fields of experimental embryology and endocrinology may supply the reason for this differential response to a stimulus within the same group of cells.

In conclusion, it appears that in mammalian dental physiology the os cementum performs the specific function of attaching the alveolar periosteum to the tooth, and that a thin coat performs this function equally as well as a heavy one.

Metabolic rate.—Except for forms with rootless cheek teeth, the period of growth for any particular tooth, whether brachyodont or hypsodont, involves an equal segment of the life of the animal, that is, it does not require any greater portion of the life of a bovid to grow a hypsodont molar than it does a suid to grow a brachyodont one. The difference in length results from the rate of growth, and the degree of hypsodonty of rooted teeth is a function of the rate of growth of the tooth. Hypsodont molars must then have a more rapid growth rate than brachyodont, in order to accomplish different results in the same time unit. The change from a brachyodont to a hypsodont molar in any group of mammals expresses an acceleration in rate of growth. Modification of growth rate necessitates a change in the stimulus, whatever its source, which initiates

and maintains the growth of the tooth until it reaches maturity. The extensive work of experimental embryology and endocrinology has shown that in stimuli of this sort the change is generally (except under some pathological conditions) quantitative rather than qualitative; the larger the stimulus (except it be excessive), the more rapid the growth.

For the animal as a whole, the rate of growth, the metabolic rate, and the activity of the thyroid are very closely related. In laboratory and domestic mammals (as well as in man), it has been found that the slow-growing and late-maturing individuals are subthyroid, and usually exhibit certain tooth defects and characteristic hair patterns. Although other factors may be involved, this naturally raises the question as to whether the hypsodont condition can be correlated with the metabolic rate, and, hence, by inference, with the activity of the thyroid. Without extensive laboratory tests, the most general criterion used to indicate the activity of thyroid is the energy with which an animal goes about its daily routine; the more energetic the animal the more active the thyroid. The castoroids, aplodontids, geomyids, and microtines are hypsodont; they are also active and energetic and, by inference, at least mildly hyperthyroid. On the other hand, the brachyodont sciurids and cricetines are equally energetic and are presumed to have an active thyroid. The cavioids, which embrace both brachyodont and hypsodont forms are in general extremely apathetic and, by inference, subthyroid. It is obvious that, within this single order, there is no correlation between the metabolic rate and hypsodont teeth.

Food.—Diet of extinct mammals can be determined from their tooth character only along the most general lines. By reconstructing the probable musculature, when the entire skeleton is known, the animal's physical capabilities can be determined with reasonable reliability. But, as pointed out by Watson (1930), to extend such implications too far can easily lead to serious error.

If the groups of hypsodont mammals listed in Table I are separated on the basis of food habits, the results are as follows: Unknown, 12 (Tae-niodonta, Megalonychoidea, Glyptodontoidea, Mylagaulidae, Entoptychinae, Castoroidinae, Toxodonta, Typotheria, Hegetotheria, Leptaucheninae, Hypisodonti, Sivatheriinae); insectivore, 1 (Dasypodoidea); seed eater, 1 (Heteromyidae); root eater, 1 (Geomyinae); grazers, 3 (Equidae, Bovidae, Camelidae); mixed grazing and browsing, 2 (Cervidae, Antilocapridae); browsers, 4 (Bradypodoidea, Aplodontidae, Castorinae, Elephantidae); and any green vegetation, 5 (Leporidae, Microtinae, Caviodea, Suidae, Hystricidae). On the basis of available data there is no justification to conclude that the change from brachyodont to hypsodont teeth

indicates a shift from browsing to grazing habit. Even if one should interpret the hypsodont cheek teeth of the Equidae, Camelidae, and Bovidae as a special adaptation to the grazing habit, to what adaptation can one assign the teeth of the other groups of living mammals with hypsodont teeth? In fact, since the height of crown and the complexity of enamel pattern is determined by the growth of soft tissues while the animal is on a milk diet, it is just as logical to postulate that hypsodonty is an adaptation to a milk diet as to any other one food habit. The only generalization which can be made is that most hypsodont mammals eat fresh green vegetation when obtainable.

These data also show that neither hypsodonty, nor the deposition of cement, nor a more complicated enamel pattern are to be correlated with any particular type of diet, because when the foods of the herbivores are broken down into their essential ingredients (proteins, carbohydrates, fats, mineral salts, and vitamins) the differences are very small. It is true that on the whole, the dicotyledons contain more calcium and phosphorus than grasses but they also contain much more magnesium, which combines with these two minerals and/or fatty acids to form insoluble soaps and phosphates in the intestines. Therefore, since the hypsodont condition developed one or more times with each food habit, the difference then lies not in the food but in the animals themselves, in the way they utilized the food. Sixty-seven percent of these groups of hypsodont mammals have one or more members with rootless (or persistently growing) cheek teeth and this character cannot be correlated with any particular food habit.

Available silica.—Silica is present in considerable quantity in *Equisetum*, grasses, and the bark of trees, but only in *Equisetum* and in the harsh tropical and marsh grasses are excessive amounts deposited in the epidermis of the leaves and stems. A part of the total silica appears (1) to remain in the cell sap as an electrolyte of silicic acid or (2) to be bound up in organic compounds. In either form it would be readily assimilated by herbivores. Hence, grazing mammals and those which feed on bark would obtain far more silica than the browsers, since the leaves of trees are normally very low in silica. If one divides the groups according to food habit (as in the section on food), it will be seen that only a very small percentage of hypsodont mammals feed exclusively or principally on plants or plant parts (bark) which have a high content of available silica. Also, one exclusive bark eater (*Erethizon*) and one grass eater (*Cynomys*) have remained brachyodont. It is clear, therefore, that no correlation between the hypsodont condition and foods high in silica can be demonstrated.

Complexity of enamel pattern.—A more complex enamel pattern is

associated with the hypsodont condition in only 45 per cent of the groups with cusp hypsodonty, the Mylagaulidae, Cavoioidea, Elephantidae, Equidae and Suidae (see Table I). In all but the Cavoioidea the start of the more involved enamel pattern slightly antedates the initiation of hypsodonty. In the elephants and suids it is accomplished by the budding of minor cusps from the mesodermal papillae which form the principal cusps and by the growth of cusps on the posterior cingulum. Eventually the principal and additional cusps become subequal in size but only in the elephant *Stegodon* are they arranged in regular transverse rows on the crown of the tooth. In the Elephantidae and Suidae the complexity of pattern is an expression of the response on the mesoderm of the tooth bud to the heightened stimulus for growth (see Metabolic rate). The growth rate of the ectoderm increased sufficiently to give the tooth a uniform covering of enamel. In these two groups essentially the same result was accomplished in essentially the same manner, yet elephants are browsers and the wart hog *Phacochoerus* primarily a grazer.

In considering the enamel pattern of the teeth of the horses of the Florida Miocene (White, 1942, p. 47), I offered the explanation that there the complexity was a function of the rate of multiplication of the enamel-depositing cells between the principal cusps. A rapid rate would yield more enamel-depositing tissue than there was space between the principal cusps to accommodate it and the internal pressure thus created, by pushing against the principal cusps as buttresses, would cause the tissue to buckle or fold in one or more places and the resulting spaces to fill first with mesodermal tissue and later with dentine. In horses, then, the greater complexity is due to a greater response by the ectoderm rather than the mesoderm of the tooth bud to the increased stimulus for growth. This explanation also appears to be applicable to the enamel pattern in elasmotheres. While a more complex enamel pattern developed in the horses, it did not in the bovids or camels, yet all three groups subsist principally by grazing. The more complex enamel pattern is not, therefore, a corollary of the grazing habit.

In the other groups with cusp hypsodonty (Castoridae, Microtinae, Hystricidae, Toxodonta, Cervidae, Bovidae, and some members of the Camelidae), the growth of the mesoderm and of the ectoderm of the tooth bud proceeded at a uniform rate with respect to each other; there was only an increase in the height of the crown with negligible changes in the enamel pattern. These groups embrace grazers, browsers, and feeders on other green vegetation.

In groups with tooth-base hypsodonty there is no elaboration of the enamel pattern on the triturating surface of the tooth. The mesoderm and

ectoderm of the tooth bud respond uniformly with respect to each other to the increased stimulus for growth so that the tooth is always encased in enamel.

Of those groups with root hypsodonty, the Leporidae is the only one in which the mesoderm and ectoderm of the tooth bud respond to an equal rate to the increased stimulus for growth. In the Geomyidae and Heteromyidae there is a differential response in the enamel-depositing cells of each tooth, the result of which is that the enamel on the sides of the tooth becomes very thin or disappears with age. The early history of the groups without enamel on the teeth is either unknown (Megalonychoidea, Bradypodoidea, Glyptodontoidea) or very poorly known (Dasy-podoidea) yet the oldest species known all had rootless teeth with little or no enamel. Seemingly, in these groups the ectoderm of the tooth bud was entirely unable to respond to the increased stimulus for growth and, if any enamel was deposited on the crown of the tooth, it was soon obliterated by wear.

In general, therefore, a complex enamel pattern is found in some but not all of the groups with cusp hypsodonty. It is neither restricted to groups with a particular food habit nor is it a corollary of any special diet.

Illation.—This survey of hypsodonty and any possible correlations reveals that hypsodont cheek teeth developed one or more times in nearly every group of herbivorous mammals and that every food habit typical of herbivores supports one or more of the hypsodont groups. There are three principal types of hypsodont teeth, but none of them is restricted to mammals of any one preference. Thus, the field for speculation becomes extremely broad and any suggested explanation of the phenomenon must be applicable to all types, conditions, and degrees of hypsodonty.

Under the section on the metabolic rate I pointed out that the degree of hypsodonty is a function of the rate of growth of the tooth and that data from the fields of experimental embryology and endocrinology permit us to postulate a quantitative change (increase) in the stimulus which initiated and maintained the growth of the tooth till it reached its mature form. The time at which this change in stimulus took place explains not only the principal but the intermediate types of hypsodonty. If the quantitative change in the stimulus occurs while the coronal pattern is being determined by the growth of the mesodermal papillae, it results in cusp hypsodonty (Type 1); if it takes place after the coronal pattern has been determined, but before the roots start to form, it results in tooth-base hypsodonty (Type 2); and if while the roots are forming it results in root hypsodonty (Type 3).

Generally, if any of the cheek teeth are hypsodont, all of them are, but this is not universally true. The most notable exceptions are *Mylagaulus* and *Phacochoerus*. The latter has only a single hypsodont tooth ($M_{\frac{3}{3}}$) in each jaw. It is not known whether the other teeth fail to receive the increased stimulus or could not respond to it. In view of the rather large time overlap during tooth formation and the fact that all teeth of a single jaw are supplied from the same principal artery, it seems more probable that the other teeth were incapable of response. According to the evidence from experimental embryology, the interval during which tissues can react to the stimulus for extra rapid growth is very short, and if the stimulus is applied before or after the responsive period it has no effect. In *Phacochoerus*, it would appear then that the increased stimulus was applied for only a short period, too late for the teeth which preceded the hypsodont tooth.

Presumably, the continuous application of, and a corresponding response to, an increased stimulus would result in the continuous growth of the teeth, and this appears to be true of the incisors of rodents and lagomorphs as well as the cheek teeth of a number of groups. If this premise is acceptable, then the degree of hypsodonty is an expression not only of the duration of the application of the increased stimulus but also the duration of the ability to respond to the increased stimulus for rapid growth.

The deciduous teeth of nearly all mammals make most of their growth, and the enamel skeleton of the first molar is usually formed, during the last third of the prenatal life of the individual. Hence, it is natural to look again to experimental embryology for information concerning the nature of the stimulus which initiates and maintains the growth of teeth until they reach their mature form. The principle of unequal growth—that a tissue may lie dormant for a considerable period and then make a very rapid growth for a short time after which it diminishes to a rate in keeping with the rest of the organism—is a well known embryological phenomenon. It applies not only to teeth but to every organ in the body. The stimuli which initiate and maintain the growth of organs or tissues have been called "Directive Organizers." While their source or sources are as yet unknown, there is good reason to believe that they are chemical in nature and that only minute quantities are necessary to produce profound effects. If this is true, they are, by definition, hormones. Inasmuch as certain hormones occurring in vertebrates are universally distributed in the animal kingdom (three in *Paramecium*, Goldzieher, 1939, p. 32), it is not unlikely that some are produced at a very early stage in the development of the embryo. With the exception of those of the anterior lobe of the pituitary, the hormones secreted by the endocrine glands are largely those which produce

general physiological effects. Of the fourteen or more fractions identified from the anterior lobe of the pituitary (Goldzieher, p. 276) half or more are directed at a particular organ or gland. In view of the very early date of the formation of the brain and spinal chord and the late date of that of the teeth, the anterior lobe of the pituitary would certainly be sufficiently well developed to produce an odontotropic fraction. If it does, the degree of hypsodonty would, in addition to the factors mentioned above, be an expression of the quantitative production of such a fraction. That the anterior lobe of the pituitary secretes such an odontotropic fraction seems indicated by the retention of the deciduous teeth in experimental mammals following hypophysectomy (Grollman, 1947, p. 38).

RATES OF EVOLUTION OF HYPSONDONTY

Few statements regarding the rates of evolution in hypsodonty are applicable to the mammalian class as a whole. Yet two points stand out. There is a surprising uniformity among the groups in the geologic time interval between initiation and its accomplishment, but a much less uniform interval between the initiation of hypsodonty and the incidence of rootless cheek teeth.

Adequate data on the development of hypsodonty are available for only ten of the 28 groups considered here (35.7 per cent), that is, for somewhat more than one-third. The ten are Taeniodonta, Aplodontidae, Heteromyidae, Castorinae, Castoroidinae, Hystricidae, Elephantidae, Equidae, Suidae, Camelidae, and Bovidae. In the others either the date of the initiation of hypsodonty or the date of its accomplishment is unknown. Although generalizations based on such a small percentage of the total cannot be considered conclusive, yet in each of the cases in which the history is known the hypsodont condition developed at the uniform rate of approximately one-third of a geologic epoch. Hypsodonty was initiated from time to time between the upper Paleocene and upper Pliocene, and its development passed over epoch boundaries without seriously altering the picture. This is all the more interesting because the epochs of the Tertiary are not allotted the same number of years. In fact, some epochs (Eocene, 20,000,000 years) are estimated to be twice as long as others (Oligocene, 10,000,000) (Simpson, 1951, p. 102). If the deposits from which the specimens have been collected were zoned more carefully than they have been in the past, these relationships might be altered appreciably.

Because of lack of data on some groups, it is necessary to appraise the development of rootless cheek teeth under two sections. The first section takes into consideration the groups in which the history is known from the beginning of hypsodonty to the acquisition of rootless cheek teeth;

these are the Taeniodonta, Aplodontidae, and Castoroidinae. The second section deals with those groups which were fully hypsodont when first known but which later developed rootless cheek teeth; they are the Leporidae, Microtinae, and Geomyinae. This treatment leaves out the majority of the groups with rootless cheek teeth, either because their teeth were rootless when first encountered or because there is a gap in the geologic record which makes it impossible to be certain when hypsodonty was accomplished. These are the Megalonychoidea, Bradypodoidea, Dasypodoidea, Glyptodontoidea, Entoptychinae, Caviioidea, Toxodonta, Typotheria, and Hegetotheria.

Section 1: In the Taeniodonta, hypsodonty was initiated in late middle Paleocene and rootlessness was attained about the end of Wasatch time. Roughly calculated, this corresponds to a little less than one geologic epoch. In the Aplodontidae, the transition from low-crowned teeth to the rootless condition took place within the Miocene, or one geologic epoch. In the Castoroidinae, hypsodonty began in the upper Oligocene but the rootless condition was not accomplished until the middle Pliocene. Thus, it would appear that as the Tertiary progressed the rate of this phase of evolution was retarded. If the time was calculated in years, however, the rate might appear more uniform.

Section 2: In the Leporidae, the lower teeth were fully hypsodont when specimens were first encountered in the upper Paleocene and were rootless (lower teeth of *Palaeolagus*) in the lower Oligocene. According to the available data it required one and one-third geologic epochs to develop the rootless condition. The Microtinae were fully hypsodont in middle Pliocene and some genera had rootless cheek teeth by the earliest Pleistocene; in them the transition from the hypsodont condition to rootless cheek teeth appears to have required only two-thirds of a geologic epoch. The Geomyinae had rooted teeth in the lower Miocene but the rootless condition did not appear till the upper Pliocene (Rexroad); thus, it seems to have required two geologic epochs for them to develop rootless teeth.

On the basis of the data in Sections 1 and 2 no generalizations on the transition from hypsodont teeth to the rootless condition are possible for the class as a whole.

SUMMARY

The occurrence of hypsodont, or high-crowned, teeth in herbivorous mammals is usually correlated with the type and mineral content of the food. In many groups hypsodonty is accompanied by the deposition of cement on the crowns. These correlations are here examined in the light of the absorption and accumulation of minerals from the soil by plants, the

mineral metabolism of plants and mammals, and the activities of the endocrine glands.

Plants take up minerals from the soil far in excess of their physiological needs but not in the same amount or proportion. In this respect, they exhibit a wide range of variation, depending on the species of plant, its age, distribution of roots, physical nature of the soil, proportion and distribution of the elements in the soil, and the general climatic conditions. Fifty to 80 per cent of the mineral content of living plants is present in the cell sap as electrolytes or water-soluble salts and, in either case, is readily available to herbivorous mammals. Minerals in these states are not abrasive.

A brief review of hypsodonty in 28 groups of mammals, both living and extinct, is given in the text, together with the geologic date of its appearance, time required to develop, date of initial deposition of cement on the crown of the tooth and time required to develop a heavy coat (if one develops), whether or not the cusp pattern becomes more complex, and the food of living members of the groups. Hypsodonty arose many times throughout the Tertiary and appears to have been initiated in more groups during the Miocene than in any other epoch. High-crowned cheek teeth developed one or more times in nearly every group of herbivorous mammals; each kind of herbivorous food habit supports one or more of the 17 living groups with such teeth.

There are three principal types of hypsodont teeth depending on the part of the tooth involved in the additional growth. They are cusp hypsodonty, tooth-base hypsodonty, and root hypsodonty. Because of intermediate types the assignment of the larger groups of hypsodont mammals to these three categories is not entirely satisfactory. When more is known concerning the larger groups, it may be possible to satisfactorily categorize the subfamily or tribes.

Current explanations for hypsodonty have been critically examined and rejected because they were based on the observable data of one or two groups and were applicable neither to the class as a whole nor to the groups on which they were based. As pointed out, the basic biomechanical principle involved in the production of hypsodont teeth, at least during the early period of its development within a group, is that the degree of hypsodonty is a function of the rate of growth of the tooth. An increased rate of growth of the tooth is the result of an increase in the stimulus which initiates and maintains the growth of the tooth until it reaches maturity. All types, conditions, and degrees of hypsodonty are the result of the interaction of multiple variables, four of which are: the amount of increase, the time of increase, the duration of the increase, and the duration

of the response to the increased stimulus for growth. Although experimental biology has not yet isolated a specific stimulus for tooth growth, such a stimulus must, by process of elimination, be a "Directive Organizer," or hormone.

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