Charles D. and Mary Vaux Walcott
Research Fund

THE TILLODONTIA: AN EARLY TERTIARY ORDER OF MAMMALS

(WITH 16 PLATES)

BY

C. LEWIS GAZIN

Curator, Division of Vertebrate Paleontology
United States National Museum

(PUBLICATION 4109)

Charles D. and Mary Vaux Walcott
Research Fund

THE TILLODONTIA: AN EARLY TERTIARY ORDER OF MAMMALS

(With 16 Plates)

BY

C. LEWIS GAZIN

Curator, Division of Vertebrate Paleontology
United States National Museum

CONTENTS

ILLUSTRATIONS

PLATES

(All plates following page 110)

FIGURES

THE TILLODONTIA: AN EARLY TERTIARY ORDER OF MAMMALS

By C. LEWIS GAZIN

Curator, Division of Vertebrate Paleontology
United States National Museum

(WITH 16 PLATES)

INTRODUCTION

The Tillodontia is an order of mammals comprising a relatively small number of forms, distinctive in character, obscure in origin, and of seemingly short duration in geologic time. The oldest of these known are Clark Fork or upper Paleocene in age, and no forms in the earlier stages of the Paleocene can be surely identified as ancestral. These creatures were relatively abundant, as represented in collections, but showed little diversity of form in the lower Eocene. By middle Eocene time they became tremendously larger and somewhat more diversified, but exceedingly rare. They apparently evolved very rapidly during lower and middle Eocene time and then became extinct in North America. It would seem, however, that representatives of the order persisted somewhat later in Asia.

As may be expected, the combination of characters distinctive of the order is not so emphasized in the lower Eocene and Paleocene *Esthonyx* as it is in the Bridger *Trogosus* and *Tillodon*. The principal characteristics include in part the enlarged rodentlike incisors in the upper and lower jaws and the basically arctocyonid or almost *Pantolambda*-like construction of the cheek teeth. The tillodont cheek teeth are further characterized by a peculiarly emphasized brachydont-hypsodont condition in which the buccal side of the lower teeth and the lingual side of the upper teeth have become arcuately columnar while their opposite portions remained decidedly cuspate with prominent styles.

In addition to the suggested affinity with an arctocyonid-pantodont ancestry there are also points of resemblance to insectivores, condylarths, primates, and taeniodonts. All of which indicates derivation

from an early mammalian stock of rather generalized structure. Individually, the characters of *Esthonyx,* or potentialities of these characters, can be found in various Paleocene forms, but collectively no one form or group satisfactorily meets all the requirements. The diversification found in the Insectivora might appear to encompass the requirements and may well have given rise to the tillodonts. On the other hand, skeletal similarities, particularly in the feet, as well as in the teeth, lead me to favor a relationship, though remote in time, with the pantodonts, which in turn seem related (or at least show a resemblance) to some of the arctocyonid creodonts.

ACKNOWLEDGMENTS

Investigation of the tillodonts was originally undertaken as a part of a more general study of the middle Eocene mammalian fauna of the Bridger formation. Consideration of the antecedents of the Bridger tillodonts, however, indicated a need for review and revision of the lower Eocene representatives of the order as well. As a consequence the study was expanded to include all known forms of this obscure but compact order. Review of *Esthonyx* material was early planned by Dr. Walter Granger as a further contribution to the "Revision of the Lower Eocene Wasatch and Wind River Faunas," a series of researches carried on by Matthew and Granger but not quite completed. Of Granger's investigation of the tillodonts, however, little remains beyond notes and memoranda on specimen labels and on some of the drawings prepared for his study.

The present study is based on materials from the "Wasatch" of Wyoming and New Mexico, from the Huerfano of Colorado and from the Bridger of Wyoming in the collections of the U. S. National Museum and the American Museum of Natural History. The Clark Fork and lowermost Gray Bull materials are for the most part in the collections of the American Museum and Princeton University. The Bridger materials studied include, in addition, those of Yale University, the Academy of Natural Sciences of Philadelphia, and Walker Museum of the University of Chicago. The lower Eocene materials from the Plateau Valley "Wasatch" are in the collections of the Chicago Museum of Natural History.

I am indebted to Dr. George Gaylord Simpson for permitting me to study the tillodont materials in the American Museum, particularly the beautiful skull herein described as the new species *Trogosus grangeri,* and in turning over to me for use in this publication the many drawings of *Esthonyx* and *Trogosus* material which had been

prepared for Dr. Granger's studies. I am also indebted to Dr. Joseph T. Gregory and Dr. Carl O. Dunbar of Peabody Museum at Yale University for making available for this study the well-preserved skull which Marsh described as *Tillotherium fodiens,* and other Bridger tillodont types and referred specimens. Acknowledgment is due Dr. Charles M. B. Cadwalader, Dr. B. F. Howell, and Miss M. Dorothy Reed, of the Academy of Natural Sciences of Philadelphia, for arranging the loan of the important Leidy types. The Plateau Valley *Esthonyx* specimens in the Chicago Museum and a Bridger *Trogosus* specimen at Walker Museum were loaned through the courtesy of Bryan Patterson and E. C. Olson. The Clark Fork and Gray Bull specimens at Princeton University were made available by Dr. Glenn L. Jepsen. *Trogosus* material from the Eocene of British Columbia in the National Museum of Canada was sent to me for study by Dr. L. S. Russell.

All the wash drawings comprising the plates of this paper, and most of the text figures, were made by William D. Crockett, artist for the division of vertebrate paleontology in the U. S. National Museum. Text figures 2, 3, 5, 7, 9, 10, 11, and 34 were furnished me through the kindness of the American Museum of Natural History, most of which were prepared for Granger's study.

HISTORY OF INVESTIGATION

Since the era of Leidy, Cope, and Marsh, the tillodonts have been one of the most neglected groups of mammals. Except for Simpson's (1937) study of the Clark Fork materials, little has been added during the past 50 years to our knowledge of the peculiar forms comprising this order.

The early history of investigation concerning the discovery and description of various tillodont materials involved the independent studies of Leidy and Marsh of the middle Eocene or Bridger forms, and Cope's contributions to our understanding of the "Wasatch" fauna. Leidy's descriptions for the most part preceded those of Marsh and, remarkably enough, no contest for generic and specific names of tillodonts took place between Cope and Marsh, although later polemics developed regarding ordinal relations.

The first tillodont discovered was named *Anchippodus riparius* by Leidy (1868) from a lower cheek tooth (figs. 14 and 17 of this paper) found in Eocene deposits exposed along Shark River in Monmouth County, N. J. The specimen was collected by Dr. Knieskern and given to Conrad, who in turn presented it to the Academy of Natural Sci-

ences of Philadelphia. During the latter part of the summer of 1870, Marsh secured a tillodont lower tooth (fig. 18 of this paper) which he erroneously described as representing a new species of *Palaeosyops*. The specimen, named *"P." minor,* was found in the Grizzly Buttes, not far from Fort Bridger. Marsh's description was published in the July 1871 issue of the American Journal of Science and Arts (p. 36), but his separates, with separate pagination and different type arrangement, bear the date June 21, 1871, with the signature in Marsh's handwriting. This date becomes important when it is realized that the species *Trogosus castoridens,* described by Leidy in the May 1871 Proceedings of the Academy of Natural Sciences, had an actual publication date of July 11 of that year. If Marsh's statement is to be relied on, *"P." minor* is the earliest species name for Bridger tillodonts. The lower jaw of *Trogosus castoridens,* collected by Dr. J. Van A. Carter, was also found in Grizzly Buttes, about 11 miles from Fort Bridger. A little-worn lower incisor (fig. 13 of this paper), also found by Dr. Carter near Fort Bridger, was sent to Leidy in the summer of 1871, and was described in November of that year as *Trogosus vetulus.*

The true affinities of *"P." minor* were not recognized until some time later when Leidy had occasion to see the tooth. His conclusions then of the relationship between *"P." minor, Trogosus castoridens,* and *Anchippodus riparius* were brought out in a short note in 1872 (b).

It was not until 1873 that upper teeth of tillodonts were known. In June of that year Marsh (p. 485) described a fragmentary upper jaw portion (fig. 15 of this paper), not associated with lower teeth, to which he gave the name *Tillotherium hyracoides.* No precise locality data were given but a specimen label having the designation *"Tillotherium hyracoides* type" in Marsh's handwriting also carries the information "Grainger Station." The Bridger beds exposed around Granger are considered as Bridger "B," although upper Bridger is exposed in the higher cliff sections several miles to the south. Comparison between this material and earlier-described jaws could not be made, but Marsh noted the possibility of *Tillotherium's* being generically identical to *Anchippodus* (or *Trogosus*). In the spring of 1874 Marsh (p. 533) named a second species of *Tillotherium, T. latidens,* on a relatively large, isolated second upper molar (fig. 16 of this paper), which he misidentified as the last molar. The specimen is described as coming "from the same geologic horizon" as *T. hyracoides,* but this may have no greater significance than implying some part of the Bridger beds. Unfortunately, and as is well known, Marsh

was very cautious in giving out information about localities where his fossils were found.

The discovery of associated skull and lower jaw material (pls. 14-16 of this paper), together with other parts of the skeleton, was announced in 1875 (b) when Marsh published a brief description of *Tillotherium fodiens*. The specimen was described as coming from the "*Dinoceras* beds," which would place it in the upper part of the Bridger. However, several field labels associated with the skeletal fragments belonging to the skull, and identified by the same catalog number as the skull, carry the information "Millersville." This place, no longer designated on maps of the area, has been demonstrated from various independent sources to have been near the confluence of Smith's and Black's Forks, hence in Bridger "B." *Trogosus castoridens* and "*P.*" *minor* are from the lower Bridger exposed at Grizzly Buttes. The *T. fodiens* material was more fully described in 1876 but in all no statement appears as to its distinctness from the genotype, *T. hyracoides,* or from *T. latidens.* Moreover, no certain evidence can be gleaned from the literature as to the horizons of the Bridger the latter two may represent.

Cope's contributions to the literature on tillodonts began in 1874 with his descriptions of the new materials which he collected while with the Wheeler Survey in New Mexico. These include the types of *Esthonyx bisulcatus* (fig. 1 of this paper), *E. burmeisterii, E. acer,* and *E. miticulus* from the so-called "Wasatch" beds which Simpson has named the San Jose. The latter form, however, has since been shown to represent a different group of mammals. In 1880 he described *Esthonyx spatularius* (fig. 4 of this paper) as coming from the Wind River beds, and in 1881 described *Esthonyx acutidens* (fig. 6 of this paper) from the same formation, restating the description of *E. spatularius* as though it belonged to the same fauna. However, in 1884 (a) *E. spatularius* was attributed to the Big Horn Basin, and under the discussion of this form evidence is brought out in the present paper demonstrating a Gray Bull origin.

During the above history of discovery and later, it is interesting to follow the development of Cope's systematics, particularly as it applies to the tillodonts. He at first (1869, 1873) regarded the middle Eocene forms as perissodactyls, but at the time of his description of the New Mexican lower Eocene material (1874) it seems evident, though not clearly stated, that he regarded *Esthonyx,* as well as *Ectoganus,* as representing the Toxodontia, an opinion not long held. The following year (1875, p. 23), in further comments on the Eocene of New Mexico, he noted the resemblance between *Esthonyx* and *Pelycodus*

and considered the lower molars as not unlike those in *Ectoganus,* the latter being known then only from deciduous teeth. Cope (1876a) came to recognize Marsh's Tillodontia, as a suborder, Tillodonta, for the middle Eocene *Anchippodus,* but included in it the taeniodont *Ectoganus.* The history of Cope's investigations of the various tillodonts was closely tied to his study of the taeniodonts, which he considered as closely allied. His reasons for believing in this relationship were based on a misinterpretation of dental homologies. The evidence used in identifying the various teeth in these forms, including the caniniform teeth, was in turn derived from his observations on *Esthonyx.* Strangely enough, he never regarded *Esthonyx* as a tillodont, but placed it in the Insectivora because of its resemblance to the hedgehog, *Erinaceus.*

Cope's classification of these forms in 1876 (a, p. 447-448) was an arrangement which included the "Tillodonta" and Creodonta as suborders of the Insectivora, and in the same year (1876b) he proposed the Taeniodonta as an additional suborder for *Ectoganus* and *Calamodon.* However, upon later discoveries of Paleocene mammals, he placed *Conoryctes* and *Psittacotherium* in the Tillodontia. By 1877 the major elements of Cope's classification were more or less crystallized, and in his monograph on the New Mexico collections he proposed the order Bunotheria to include the suborders Creodonta, Mesodonta, Insectivora, Tillodonta, and Taeniodonta. The Tillodonta were characterized as before by scalpriform incisors, growing from persistent pulp, and distinguished from the Taeniodonta which were described as having incisors truncate. Cope also called attention to the similarity of the tillodont dentition to that of insectivores, but justified the separation on the basis of the incisors, a gap diminished by the genus *Esthonyx.* *Esthonyx* was retained in the Insectivora but later discovery of the forefoot of this form, demonstrating a separate scaphoid and lunar, caused Cope to regard the relationships to *Erinaceus* as more remote. Hence, in 1884 (b, p. 351), grouping *Esthonyx* with the leptictids, he placed it in the Creodonta. Separate family rank in the Creodonta, the Esthonychidae, however, was proposed in 1889 (b, p. 876).

Little more was added by Cope to our knowledge of the tillodonts and later references to members of this order were essentially reiterations and defenses of his arrangement and interpretation of the relationships of the various parts of the "Bunotheria." It may be further noted that Cope regarded the tillotheres (including *Psittacotherium*) as standing in ancestral relationship to the rodents, a conclusion un-

tenable with our present understanding of the morphology and chronology of the forms concerned.

Contemporary opinion, while largely dependent on Cope's original investigations, often disagreed with his conclusions in biological interpretation, and we find Osborn, Wortman, and others following Marsh in considering *Esthonyx* as tillodont in affinities. Wortman (1897) was the first to straighten out the confusion between the genera of tillodonts and taeniodonts, and although his conclusions with regard to edentate relationships of the taeniodonts are not in agreement with most later investigators, he laid the foundation for the orders as now recognized. His studies of these forms were published within a month of Cope's death, and in the same year (1897) Osborn described *"Tillotherium"* remains from Huerfano beds of Colorado, earlier reported by R. C. Hills.

Since Cope's death the literature of vertebrate paleontology shows a dearth of references to the tillodonts, with very few contributions to our knowledge of this order. References for the most part are citations in faunal lists or reiterations in textbooks of the descriptions and conclusions of the earlier investigations, although in several instances independent conclusions as to relationships were advanced. A. S. Woodward, for example, in his textbook on vertebrate paleontology (1898, p. 374) placed the tillodonts in the Rodentia. Weber (1904, p. 513, and 1928, p. 168) was not in agreement with such an arrangement and retained the order Tillodontia, and Gregory, in "The Orders of Mammals" (1910, p. 292), strongly supported Weber in criticism of such an implied relationship, enumerating and commenting on the many morphological criteria against suggested rodent affinities. In Zittel's textbook (1923, p. 450), Schlosser followed Cope's earlier thinking in retaining the tillodonts in the order Insectivora, as did Abel (1914, p. 52; 1919, p. 728) in his textbook treatment. Winge (1923, p. 133) went even further and included the taeniodonts there as well.

The first report involving original investigation of new materials, the results of later field explorations, in what might be termed a second era of paleontological exploration and researches was in the form of an abstract by Granger in 1918. In this he told briefly of the finding of a nearly perfect skull and jaws of a tillodont in the Huerfano beds of Colorado, description of which is a part of the present paper. Summarizing his unpublished study, he concluded that the form represented was near *Trogosus* and that the age of the uppermost Huerfano was slightly older than lower Bridger.

The principal contribution to our understanding of the previously known tillodont materials outside of North America is P. Teilhard de Chardin's (1922, vol. 11, p. 63) revision of esthonychid materials discovered in the lower Eocene of France. In his study of the fauna from d'Epernay he redescribed Lemoine's *Plesiesthonyx munieri* and referred it to *Esthonyx*. At the same time he recognized that *Platychoerops* (=*Miolophus*) is not to be distinguished from *Plesiadapis*, removing it from consideration with regard to *Esthonyx*, once a "bone of contention" between Cope and Lydekker.

The most recent tillodont studies include Russell's description in 1935 of the *Trogosus* tooth from Eocene beds of British Columbia, extending the known range of the middle Eocene forms, and Simpson's description of the Clark Fork specimens and analyses of the Paleocene and lower Eocene representatives of the order in 1937. The occurrence of *Esthonyx* in the Paleocene was first reported by Sinclair and Granger (1912) in beds below the Knight (Gray Bull) to the southwest of McCulloch Peak and on Big and Little Sand Coulee in the Big Horn Basin. Simpson's treatment of the Clark Fork material is the first systematic study of *Esthonyx* since Cope and includes, in addition to a description of the new species recognized in the Clark Fork (and Sand Coulee), a statistical analysis of the Gray Bull materials for comparative purposes. In addition to these studies, Young (1937, p. 434) has described the form *Adapidium* from the early Tertiary of Yuanchü, which he considered tentatively as a primate. It almost certainly represents a tillodont, close in size to *Esthonyx*, but exhibiting a dental pattern strikingly like *Trogosus*.

GEOGRAPHIC AND GEOLOGIC OCCURRENCE

Our knowledge of the geographic distribution of extinct forms of life is necessarily incomplete, obviously limited to a consideration of the distribution of fossil-bearing rocks of the proper age. It seems likely that *Esthonyx* was widely distributed in the Northern Hemisphere during lower Eocene time, as collections representative of the land faunas of that age in this country almost invariably include remains of *Esthonyx*, and in addition to its recognition in the lower Eocene of France, a closely related esthonychid, as noted above, seems present in the early Tertiary of China. In this country its occurrence is recorded in beds of Wasatchian age from Wyoming to New Mexico and in the late Paleocene of Wyoming. During middle Eocene time, however, distribution of tillodonts, so far as known, is limited to North America, with their remains occurring in New Jersey and British Columbia, as well as Wyoming and Colorado.

The recorded range of the tillodonts in geologic time is astonishingly brief, one of the shortest, for an order of mammals, but at the same time witnessing what appears to be one of the most rapidly evolving mammalian phyla. *Esthonyx* first appears in the Clark Fork or uppermost Paleocene, represented by at least three species and associated with a fauna of definitely lower Eocene affinities. These species appear to be carried over into the Sand Coulee beds at the base of the Eocene, but only one or two forms seem represented in the Gray Bull and in the San Jose of New Mexico. Ascending to the Wind River horizons, we find evidence of possibly two species in the Lysite, and probably only the large *E. acutidens* in the Lost Cabin member, which might conceivably have given rise to the middle Eocene forms.

It has long been held that *Trogosus* did not first appear until Bridger time; however, more recent evidence has come to light, from more than one source, demonstrating the presence of trogosine remains in the Cathedral Bluff tongue of later Wasatchian time, to the northwest of the Red Desert in Wyoming, and in typical exposure of this tongue to the south. Nevertheless, an appreciable interval of time is represented by the gap between Lost Cabin and lower Bridger stages, which may be partially filled by the upper beds of the Huerfano. The hiatus between fossiliferous zones of the Huerfano may not be so great. The Bridgerian horizon in the Huerfano, though relatively barren, has yielded a surprisingly large proportion of tillodont remains, including two of the four known skulls and a good number of isolated fragments. This stage appears from other faunal evidence to be slightly older than Bridger B, although tillodonts recognized are in all probability *Trogosus,* originally described from the lower Bridger. Tillodonts are exceedingly rare in the Bridger and it seems evident that their numbers were waning from a maximum in the Huerfano stage to about middle Bridger time, when it is presumed that they became extinct in North America. It seems likely from all evidence at hand, including the observations of several seasons in the Bridger, that tillodonts are limited to the lower horizons of the Bridger. Their most advanced stage, so far as known, is admirably exhibited by the skull and skeletal portions of the type of *Tillodon fodiens*.

ENVIRONMENT

The environmental conditions under which the tillodonts lived and thrived are among the best documented for any portion of geologic time. The associated faunas, except for the interval between Wind River and Bridger ages, have been the subject of numerous investi-

gations, and although addition, revision, and much more precise data will be forthcoming from future exploration and studies, the Wasatchian and Bridgerian faunas are comparatively well known. The tillodonts first appear slightly in advance of the majority of modern mammalian lines of descent, associated with late survivors of typical Paleocene groups. Almost all the Clark Fork genera are of archaic forms otherwise peculiar to the Eocene. During the second recorded stage of tillodonts, their association was with the first appearances and early development of forms belonging to Perissodactyla and Artiodactyla, and the early development of rodents. A variety of primates and insectivores was also present, but their recorded ancestry began much earlier. The lower Eocene was further characterized by a flourishing of such archaic groups as the creodonts, condylarths, and pantodonts.

With regard to the floristic and climatic environment of the tillodonts, we are permitted an unusually vivid picture by the remarkable mass of information that has been accumulated on the Green River formation. Although deposition of a significant part of the Green River lake beds took place during the interval of time between Wind River and Bridger proper, it is known that the lacustrine deposits interfingered with beds of Wind River age below (Gazin, 1952) and with Bridger above. In the work of Sears and Bradley (1924) and Bradley (1926) the nature of the relation between the lacustrine and older fluviatile deposits is clearly demonstrated. A relatively important and extensive segment of Wasatchian material, the Cathedral Bluffs tongue, is included between the main body of Green River and the Tipton tongue below, in the marginal areas of the basin. Above, the transition to Bridger, as I have observed, is not abrupt, and tongues of Green River are not uncommon interfingering with the Bridger facies. Moreover, considering a section southeastward across the Bridger Basin, the lower members of the Bridger are replaced by Green River facies in this direction, so that eventually only upper Bridger is found to rest on Green River beds. This retreat of the lake was in the direction presumably of its outlet, around the east end of the Uinta Mountains.

From the above evidence, it is reasonable to assume that the environmental conditions brought to light by the paleontology, paleobotany, and limnology of the Green River beds are applicable to portions of the Knight and Bridger and to the intervening period which part of the Green River represents, and during which the tillodonts undoubtedly flourished.

For comprehensive and detailed studies of the Green River we are indebted to W. H. Bradley and R. W. Brown, of the U. S. Geological Survey. Revealing conclusions as to the climate and environment have resulted from Bradley's analysis of the varves, together with the microfauna and microflora, and studies of the shore phases of the formation. In Bradley's summary (1929, p. 87)—

A climate is postulated which was characterized by cool, moist winters and relatively long, warm summers. Presumably the temperature fluctuated rather widely from a mean annual temperature that was of the order of 65° F. The rainfall varied with the seasons and probably also fluctuated rather widely from a mean annual precipitation between 30 and 43 inches.

Bradley further concludes (p. 89)—

. . . that the mountain ranges and high divides that form the rim of the Gosiute drainage basin were probably somewhat higher with respect to the floor of the basin during Eocene time than at present. The floor of the basin, however, in common with the general level of that part of the continent, was probably less than 1000 feet above sea level.

R. W. Brown, in a study of the Green River flora (1929, p. 281) envisions—

. . . a broad, low-lying warm inland region, with shallow ponds, lakes, and marshes, fed by slow streams, which meandered through muddy and sandy swamps as they flowed out of the distant cooler foothills and surrounding mountains. In these waters or in the adjacent open marshes grew *Sparganium, Cyperus, Arundo, Juncus, Equisetum,* and no doubt *Potomogeton, Alisma,* and other plants whose remains have not yet been found or identified. On the sandy or muddy flats farther back grew palms, *Acrostichum, Aneimia, Ficus, Sophora,* and other Leguminosae, together with such lianes as *Dalbergia* and *Cucurbita.* These were succeeded gradually on drier ground by *Oreodaphne, Zizyphus, Planera, Ternstroemia, Maytenus, Cinnamomum, Lomatia, Banksia, Myrica, Cassia, Mimosites, Sapindus, Celastrus, Euonymus, Pimelea, Thouinia, Rhus, Taxodium* (if *Taxites* is interpreted as that), and such lianes as *Banisteria, Cissus,* and the fern *Lygodium.* Along the streams and adjacent meadows higher in the foothills flourished willows, poplars, *Aralia, Ilex,* Apocynaceae, *Clethra, Sambucus, Juglans, Hicoria, Liquidambar, Potentilla, Betula, Alsinites, Acer, Quercus, Fraxinus,* species of *Rhus, Ailanthus,* and the vine *Parthenocissus.* Oaks and maples finally gave way to forests of pine and spruce at higher altitudes.

Of such an environment as I have conjured up for the Green River flora there is perhaps no exact duplicate on the earth today, but the climatic conditions of the southeastern Gulf States plus those of parts of the Great Valley of California would, it seems to me, roughly approximate those of the Green River Lake area.

Studies by both Bradley and Brown have shown that climatic conditions during Green River time were highly variable, and that although the climate was essentially warm temperate, the amount of moisture varied widely, with repeated droughts, during which there were great fluctuations of the level of the lakes.

Eventually, during later Green River time, the fluviatile phase, encroaching from the north and west over the former lake bottoms, restricted the lake area, and finally, probably accompanying diastrophic change, Green River deposition ended and only Bridger facies persisted.

CLASSIFICATION

The order Tillodontia is retained to include the compact and closely related groups of animals ranging, so far as known, from *Esthonyx* to *Tillodon*. The ordinal usage here is not in the original sense, as defined by Marsh, which included the Stylinodontidae, but as revised by Wortman (1897), and recognized by Simpson (1945). Recognition of ordinal status for this very small group of genera seems entirely justified by the unique combination of characters exhibited by the contained elements; moreover, reference of these forms to any other order of mammals would promote more confusion than simplification.

The family names which have been proposed for the tillodonts are Anchippodontidae, Tillotheriidae, and Esthonychidae. However, it seems likely that but one family is represented, as maintained by Simpson (1945), although Hay (1930) went so far as to use all three names, and others have used Esthonychidae in combination with one or the other names for the middle Eocene genera. The earliest name proposed is Gill's Anchippodontidae and this also is based on the first named genus. Simpson suppressed Anchippodontidae as of doubtful validity in favor of Marsh's Tillotheriidae. Marsh, however, recognized the possibility of the names being synonymous. Actually, Tillotheriidae, on the basis of the present studies, cannot be defended, inasmuch as the genus *"Tillotherium"* is based on a genotype, *T. hyracoides,* which exhibits no characters generically separable from *Trogosus* (or for that matter *Anchippodus*). However, there is precedent for retaining a family name, not necessarily the oldest, which may be considered as more representative of the known forms. Cope's name Esthonychidae is selected as the remaining family name that can be regarded as stable.

The taxonomic situation that exists among the latter tillodonts is, as intimated above, unusually complex for so small a group of forms, not simplified by the relatively small amount of material involved. The few remarkably good specimens extant indicate that more than one genus should be recognized, but the original genotypes themselves are based on fragmentary materials which for the most part exhibit characters scarcely of generic value. *Anchippodus riparius,* the earliest name, was based on an isolated lower tooth from New Jersey. While

a careful examination of the specimen convinces me that the form represented is a tillodont and not to be confused with any other group of mammals, the material is not adequate to determine generic relations with Bridger material.

The earliest named genus based on a Bridger species is *Trogosus.* The genotype, *T. castoridens,* was described on an incomplete lower jaw which, fortunately, exhibits characters permitting comparisons on a generic level. The earliest named species, however, from the same horizon and locality, is *"Palaeosyops" minor,* which has for a type an isolated lower molar, but such comparisons as may be made are not sufficiently conclusive to identify the species with one, and only one, of two recognized Bridger forms of *Trogosus.*

Our understanding of the genus *Tillotherium* was derived almost entirely from Marsh's description of the magnificent skull he secured from the Bridger and named *Tillotherium fodiens.* At that time no reference was made to the genotype *Tillotherium hyracoides,* based on a fragmentary upper dentition, presumably from the lower Bridger. The latter specimen presents no information regarding the characteristics later attributed to *Tillotherium,* and its distinction from *Trogosus* cannot be upheld. Also, more complete material in the American Museum from the lower Bridger, but possibly from higher levels in Bridger "B" than *Trogosus castoridens,* so closely resembles the *T. hyracoides* type as to be surely conspecific. The information presented by this better material further supports reference of this species to *Trogosus.*

The tillodont genera and species recognized in this paper, and the horizons in which they are found, are presented below.

ESTHONYCHIDAE

ESTHONYCHINAE

Esthonyx

E. *grangeri* Simpson .... Clark Fork and lower Gray Bull.
E. *latidens* Simpson .... Clark Fork and lower Gray Bull(?).
E. *spatularius* Cope .... Lower Gray Bull and Clark Fork.
E. *bisulcatus* Cope .... San Jose, Gray Bull, and Lysite.
E. *acutidens* Cope .... Lost Cabin, upper Knight, and Lysite.
E. *munieri* (Lemoine) .... d'Epernay, France.

Incertae sedis

Adapidium

A. *huanghoense* Young............ Yuanchü, China.

Trogosinae

Trogosus

T. hillsii, new species.............Huerfano B.
T. grangeri, new species...........Huerfano B.
T. castoridens Leidy..............Bridger B.
T. hyracoides (Marsh) ....Bridger B.
T.? latidens (Marsh)............Bridger B and Cathedral Bluff tongue.

Tillodon, new genus

T. fodiens (Marsh)..............Bridger B.

Anchippodus

A. riparius Leidy................Shark River, New Jersey.

SYSTEMATIC REVISION OF THE TILLODONTIA

Family ESTHONYCHIDAE Cope, 1883

Anchippodontidae Gill, 1872, is clearly the oldest tillodont family name and based on the first named genus. However, Esthonychidae is here used because it is based on the more-representative and better-known genus *Esthonyx* as permitted under both the Stricklandian and International Codes.

The characters for the family are essentially those distinguishing tillodonts from other orders of mammals. The dental formula for the known forms is $I^2_{3\text{-}1\,?}$, C^1_1, P^3_3, M^3_3. The second incisors above and below are progressively enlarged and may be rooted (*Esthonyx*) or have grown from persistent pulp (*Trogosus* and *Tillodon*). The third incisor above became progressively enlarged but remained rooted, whereas the first and third lower incisors became relatively reduced, as in *Trogosus* (although I_1 would appear to have become rootless), or were lost, as evident in *Tillodon*. The canines are prominent, but overshadowed by the incisors in the more advanced genera. The premolars increase in complexity from second to fourth, the former being simple and single- or double-rooted, whereas the latter is nearly molariform above and below.

The upper molars are characterized by a large protocone with a slightly lower but widely flaring hypoconal crest. Anterior cingulum moderate to absent. Buccal margin of upper molars may exhibit a wide shelflike cingulum. Particularly characteristic of the upper cheek teeth is the prominence of the parastyle and metastyle, although on M^3 the metastyle is weak or absent. The lower molars and P_4 show an elevated, U-shaped trigonid with a lingually placed paraconid. The

Stages	Horizons	WYOMING			COLORADO		NEW MEXICO
		Big Horn Basin	Wind River Basin	Washakie, Bridger, and Fossil Basins	Plateau Valley	Huerfano Basin	San Juan Basin
Bridgerian	Bridger "B"			*Tillodon fodiens*, *Trogosus? latidens*, *T. hyracoides*, *T. castoridens*			
Bridgerian	Huerfano "B"					*Trogosus grangeri*, *T. hillsii*	
Wasatchian	Cathedral Bluff Tongue			*T.? latidens*, *E. sp.*			
Wasatchian	Lost Cabin	*E. bisulcatus*	*E. acutidens*	*E. cf. acutidens* (U. Knight)	*E. cf. acutidens*	*E. sp.* (Huerfano "A")	*E. bisulcatus* (San Jose)
Wasatchian	Lysite	*E. bisulcatus*	*E. cf. acutidens*, *E. bisulcatus*	*E. sp.* (Knight)	*E. bisulcatus*		
Wasatchian	Gray Bull	*E. bisulcatus*					
Wasatchian	Sand Coulee	*E. grangeri*, *E. bisulcatus*, *E. spatularius*					
Clarkforkian	Clark Fork	*E. grangeri*, *E. latidens*, *E. spatularius*					

talonid is basined, lower than the trigonid, except in advanced wear, and in the first two molars the occlusal area is nearly equal to or slightly larger than that of the trigonid. The talonid in P_4 may be relatively small but in M_3 it is elongate, nearly or quite bilobed, and exhibits a prominent hypoconulid. Particularly characteristic of lower molars of the tillodonts is the presence of a metastylid, a small cuspule about midway vertically on the posterior slope of the metaconid. Moreover, the enamel of the cheek teeth has a vertical distribution which is much greater on the buccal wall of the lower series and perhaps somewhat greater on the lingual wall of the upper series. Eruption of the lower cheek teeth appears to have been more rapid on the outer side so that the teeth may have actually rotated on an antero-posterior axis during wear, which has certainly taken place at a differential rate between the two sides. In advanced wear the small amount of enamel remaining may become about equal on the two sides of the tooth. There is less evidence for such a rotation in the upper dentition, although the most marked attrition took place in the talon area.

Subfamily ESTHONYCHINAE Zittel and Schlosser, 1911

The subfamily Esthonychinae includes tillodonts having relatively large, rooted second incisors above and below. In these teeth the enamel on the anterior surface is limited to an elongate crown portion. Moreover, the second premolars (first of the series) above and below are two-rooted. So far as known, the Esthonychinae includes only *Esthonyx,* and possibly *Adapidium.*

Recognition of subfamilies among so small a group of genera seems unnecessary, and in the present arrangement may not follow the best interpretation of the meaning of subfamilies, i. e., as phylogenetic lines within a family. There appears, nevertheless, to be some overlap or a partial parallel arrangement of the subfamilies in the Cathedral Bluff stage of Wind River time. The separation here proposed is based essentially on significant structural differences, thought by some to be of family rank, in which the middle Eocene forms representing more than one group are allied to one another in a way which distinguishes them from the characteristic lower Eocene and upper Paleocene genus. *Adapidium,* if this form is correctly regarded as a tillodont, may represent survival into post-Bridger time in Asia of an esthonychid, possibly an esthonychine, since free communication of faunas between the two continents does not appear to have taken place during the middle Eocene, in which case a parallel arrangement of subfamilies would be further emphasized.

Genus ESTHONYX Cope, 1874

Synonym.—Plesiesthonyx Lemoine, 1891.

Type.—Esthonyx bisulcatus Cope.

Generic characters.—In addition to the rooted character of the second incisors observed as characterizing the subfamily, these teeth are more nearly oval in cross section at the alveolar border. The canines of *Esthonyx* are observed to be relatively large and the anterior cheek teeth less reduced, with P_4 having a better-developed talonid than in the Trogosinae. The upper molars have a shelflike external cingulum and a distinct cingulum on the anterior margin of the talon in P^4 to M^3. Moreover, no evidence is seen for the cuspule or enamel flexure observed in the center of the median basin in the upper molars of *Trogosus*.

ESTHONYX BISULCATUS Cope, 1874

Text figures 1-3, 34

Synonyms.—Esthonyx burmeisterii Cope, 1874; *Esthonyx acer* Cope, 1874.

Type.—Left lower jaw with the three molars, P_3, and two associated incisors, U.S.N.M. No. 1103.
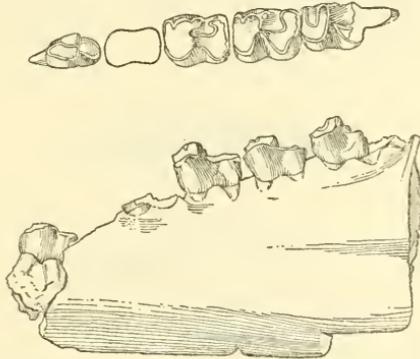
FIG. 1.—*Esthonyx bisulcatus* Cope: Left ramus of mandible (U.S.N.M. No. 1103), type specimen, occlusal and lateral views, × 1. San Jose lower Eocene, New Mexico.

Horizon and locality.—"Wasatch" or San Jose of New Mexico, Eocene of the divide between Chama and San Juan Rivers.

Specific characters.—A species of comparatively small size, but showing much individual variation. $P^{\underline{2}}_{\underline{2}}$ evidently two-rooted. Cusps of teeth moderately acute, with parastyle, metastyle, and external cingulum on upper molars and P^4 prominent. Hypocone well developed.

Discussion.—The species *Esthonyx bisulcatus,* the genotype, is represented by a very considerable number of specimens, including material from the Wasatchian of the Big Horn Basin and from the Plateau Valley of Colorado, as well as the San Juan Basin in New Mexico. Its range in geologic time extends presumably through the
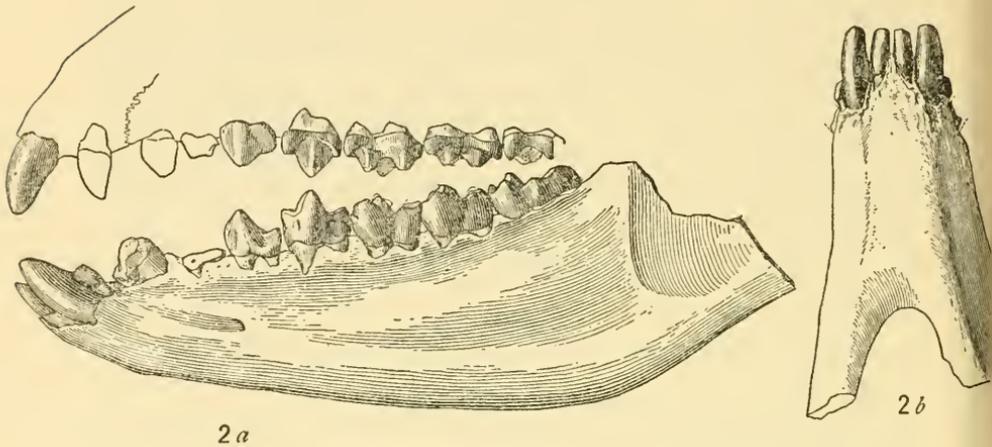
FIG. 2.—*Esthonyx bisulcatus* Cope: *a,* Left upper dentition (P³ drawn from right side) and lower jaw (drawing reversed from right side), lateral view; *b,* symphysial portion of lower jaw, inferior view (A.M. No. 4275), × 1. Gray Bull lower Eocene, Wyoming.
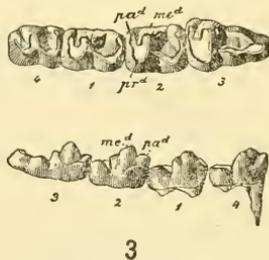
FIG. 3.—*Esthonyx bisulcatus* Cope: Lower dentition (A.M. No. 4276), occlusal and lingual views, × 1. Gray Bull lower Eocene, Wyoming.

fossiliferous horizons of the Almagre and Largo of New Mexico, and from the Sand Coulee through the Gray Bull to the Lysite of Wyoming and the Lysite equivalent in Colorado.

The types of *Esthonyx burmeisterii* and *Esthonyx acer* from New Mexico, described by Cope (1874) along with *E. bisulcatus,* do not appear to be significantly different from *E. bisulcatus* and are retained in synonymy.

Simpson (1937, p. 6) has discussed the homogeneity of the Gray Bull collections and presented data showing that on the basis of size of teeth there would be no justification for recognizing more than one species in the material so allocated. The results from a larger sample, based on M_1 as well as M_2, and including materials in both the U. S. National Museum and the American Museum are given below. Moreover, comparison is made with the limited sample known from the San Jose beds in New Mexico.

GRAY BULL COLLECTIONS

	Number	Observed range	Mean	Standard deviation	Coefficient of variation
Length of M_1........	60	7.0–9.3	8.01 ± .06	.43 ± .04	5.3 ± 0.5
Length of M_2........	62	7.3–9.1	8.30 ± .05	.42 ± .04	5.1 ± 0.5

The frequency distribution in .3-mm. groups is as follows:

M_1		M_2	
7.0–7.2:	2	7.3–7.5:	4
7.3–7.5:	6	7.6–7.8:	5
7.6–7.8:	14	7.9–8.1:	11
7.9–8.1:	16	8.2–8.4:	22
8.2–8.4:	15	8.5–8.7:	10
8.5–8.7:	4	8.8–9.0:	8
8.8–9.0:	1	9.1–9.3:	2
9.1–9.3:	2		

SAN JOSE COLLECTIONS

	Number	Observed range	Mean	Standard deviation	Coefficient of variation
Length of M_1........	9	7.0–8.0	7.47 ± .11	.33 ± .08	4.5 ± 1.1
Length of M_2........	6	7.1–8.4	7.72 ± .17	.41 ± .12	5.4 ± 1.6

The frequency distribution in .3-mm. groups is as follows:

M_1		M_2	
7.0–7.2:	3	7.1–7.3:	1
7.3–7.5:	3	7.4–7.6:	2
7.6–7.8:	1	7.7–7.9:	1
7.9–8.1:	2	8.0–8.2:	1
		8.3–8.5:	1

COMPARISON OF GRAY BULL AND SAN JOSE M_1

	N	M	σ_m	σ^2_m
Gray Bull	60	8.01	.055	.003025
San Jose	9	7.47	.111	.012321

From these data the difference in means between the Gray Bull and San Jose first molars is .54 and the standard error,[1] σ_d, is .148, giving $d/\sigma_d = 3.65$.

COMPARISON OF GRAY BULL AND SAN JOSE M_2

	N	M	σ_m	σ^2_m
Gray Bull	62	8.30	.053	.002809
San Jose	6	7.72	.169	.028561

The difference in mean above is .58 and the standard error is calculated to be 0.178, giving $d/\sigma_d = 3.25$.

In the calculations for both M_1 and M_2 it is seen that the difference in means is between three and four times the standard error. This would appear to be "significant." However, it should be noted that N instead of N-1 was used in the calculations of the smaller as well as the larger sample. Interestingly enough the range of the larger Gray Bull sample includes the limits of the smaller San Jose sample, and one wonders if the difference in means would change much with a more satisfactory sample of San Jose material. The Gray Bull and San Jose materials may well represent different species, as suggested

MEASUREMENTS IN MILLIMETERS OF *Esthonyx bisulcatus* SPECIMENS

	U.S.N.M. No. 20113 Gray Bull	A.M. No. 4275 Gray Bull	A.M. No. 15111 Gray Bull
Upper dentition:			
I^2, greatest diameter at alveolus...............	6.3	7.0	...
I^3, greatest diameter at alveolus...............	5.7	...	...
C, greatest diameter...........................	6.3	...	...
P^2, anteroposterior diameter....................	5.2	...	...
P^2, transverse diameter........................	3.3	...	...
P^3, anteroposterior diameter....................	...	8.7	7.8
P^3, transverse diameter........................	...	7.4	7.5
P^4, anteroposterior diameter, externally.........	...	7.7	7.5
P^4, transverse diameter, anteriorly..............	...	10.0	10.0
M^1, anteroposterior diameter, externally........	7.8	8.0	8.2
M^1, transverse diameter, anteriorly.............	...	11.8	11.4
M^2, anteroposterior diameter, externally.........	8.5	8.7	8.4
M^2, transverse diameter, anteriorly.............	...	13.8	12.3
M^3, anteroposterior diameter, perpendicular to anterior face	6.5	7.5a	7.3
M^3, transverse diameter, anteriorly.............	...	13.5a	12.3

[1] Calculated from the formula:

$$\sigma_d = \sqrt{\frac{N_1}{N_2}\sigma^2_{m_1} + \frac{N_2}{N_1}\sigma^2_{m_2}}$$

(See Simpson and Roe: Quantitative Zoology, p. 192, 1939.)

Lower dentition:[2]	A.M. No. 16764 San Jose	U.S.N.M. No. 30113 Gray Bull	A.M. No. 4275 Gray Bull
I_1, greatest diameter at alveolus	3.5	...	3.5
I_2, greatest diameter at alveolus	5.8	5.8	6.0
I_3, greatest diameter of crown	...	...	2.4
C, greatest diameter at alveolus	5.6	5.2	6.0
P_2, anteroposterior diameter	3.8	4.4	...
P_2, transverse diameter	2.8	2.9	...

	U.S.N.M. No. 1103 Type	U.S.N.M. No. 1104 Type of E. acer	A.M. No. 16764 San Jose	A.M. No. 4275 Gray Bull	A.M. No. 15111 Gray Bull
P_3, anteroposterior diameter	6.8	...	5.5	6.8	6.9
P_3, transverse diameter	4.3	...	3.8	4.5	4.2
P_4, anteroposterior diameter	...	7.4	7.5	8.8	8.0
M_1, anteroposterior diameter	8.0	7.7	7.2	8.4a	8.3
M_2, anteroposterior diameter	8.4	7.7	7.7	8.6	8.1
M_3, anteroposterior diameter	11.0a	10.6	9.6	11.5	10.0
M_3, anteroposterior diameter	[3]10.4				

a, approximate.

by the above comparison; however, I see no way as yet of distinguishing one from the other, except statistically, and as Simpson has intimated, the difference may be only racial. It is also noteworthy that the type of *Esthonyx bisulcatus* is the largest of the San Jose specimens that I have examined and is very near the mean for the Gray Bull sample.

ESTHONYX SPATULARIUS Cope, 1880

Text figures 4-5

Type.—Eight separate teeth, including M_3 and questionably associated incisors, canines, premolar, and a molar fragment, A.M. No. 4809.

Horizon and locality.—Gray Bull, presumably the lower part, in the Big Horn Basin, Wyo.

Specific characters.—Distinctly small. Trigonid of M_3 relatively short anteroposteriorly. Validity of species in doubt.

Discussion.—Although Simpson (1937) has shown by analysis that the specimen which is the type of *E. spatularius* falls within the size range for *E. bisulcatus,* near its lower limits, he has suggested that it

---

[2] Because of the peculiar form and eruption of tillodont lower molariform teeth, their transverse diameters cannot be given with any meaning.

[3] U.S.N.M. No. 1105, type of *Esthonyx burmeisterii.*

may represent a distinct species for which the type is not near its mean. In consideration of certain specimens which he mentioned as coming from Sand Coulee and Clark Fork horizons, and which seem to be distinct from *E. bisulcatus,* but cannot be logically distinguished from *E. spatularius,* we are faced with the following alternatives: allocating all to *E. bisulcatus,* which appears to be an unlikely arrangement; naming a new species on one of the geologically older and perhaps more typical specimens, with *E. spatularius* in synonymy with *E. bisulcatus,* though certainly within the size range of the new named form; or retaining *E. spatularius* as the name for these distinctly small individuals of *Esthonyx,* appreciating that the *E. spatularius* type may
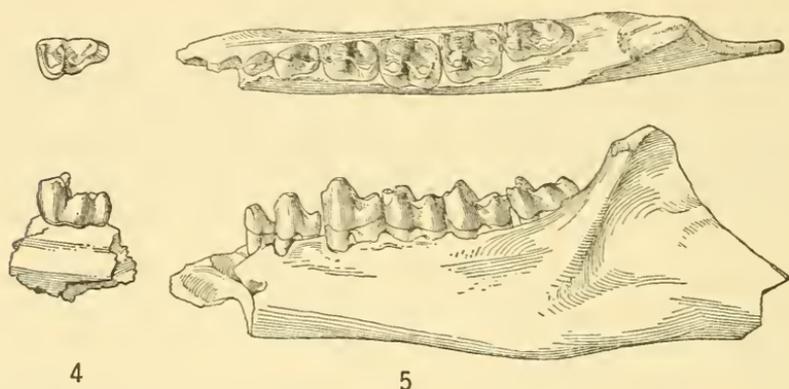
Fig. 4.—*Esthonyx spatularius* Cope: Portion of left ramus of mandible with M₃ (A.M. No. 4809), type specimen, occlusal and lateral views, × 1. Sand Coulee or lower Gray Bull lower Eocene, Wyoming.

Fig. 5.—*Esthonyx* cf. *spatularius* Cope: Left ramus of mandible (A.M. No. 16065), occlusal and lateral views, × 1. Clark Fork upper Paleocene, Wyoming.

not be near the mean. As a tentative measure, until such time as a more adequate representation of Clark Fork and Sand Coulee populations are at hand to verify or indicate a more satisfactory conclusion, I propose to retain *E. spatularius.* Such a tentative solution has in its favor the evidence outlined below, demonstrating a Gray Bull, and a highly probable lower Gray Bull or Sand Coulee, origin for the *E. spatularius* type.

Further investigation of the probable locality from which Wortman obtained the type of *E. spatularius* has demonstrated beyond reasonable doubt that the specimen is not from the Wind River basin as Cope first announced. In the original description (1880, p. 908) Cope stated, "The following species have been received from Mr. Wortman from beds of the Wind River group subsequent to the publication of

my last notice of his discoveries." There follows his description of *Esthonyx spatularius, Didymictis leptomylus,* and *Hyopsodus speirianus.* Subsequently, Matthew (1915, p. 314), in his discussion of *H. speirianus,* made the following observations, which because of their importance in fixing the *E. spatularius* locality are quoted:

> The type (*Haplomylus speirianus*) was originally described with other fossils as from the Wind River basin, but in 1885 the locality was definitely stated as Bighorn Valley. In cataloguing the Cope Collection in 1896 I referred this discrepancy to the collector, Dr. Wortman, who informed me that although most of his collections of 1880 came from the Wind River Valley and of 1881 from the Bighorn Basin, he did obtain a few specimens in 1880 from the Bighorn which were at first wrongly supposed by Professor Cope to have come from the Wind River Valley, the error being subsequently corrected. I cite these circumstances, because later collecting indicates that this genus is wholly limited to the lower part of the Wasatch, and is a valuable horizon-indicator (leitfossil). This is equally true of *Didymictis leptomylus,* described in the same notice as *H. speirianus,* as from the Wind River.

Matthew did not mention the first of the three species, *E. spatularius,* described in the same notice, and what appears to be a lapsus calami in Cope's "Tertiary Vertebrata," in which *E. spatularius* is cited as coming from the "Basin of the Big Horn River," is the emendation referred to by Wortman (in Matthew). This was applied in the "Tertiary Vertebrata" to each of the three forms included in the 1880 notice cited above. Cope also included the correct information on his specimen label for *E. spatularius,* although Matthew does not appear to have followed up on this with regard to his new specimen label after his discussion with Wortman.

Speculating from here, it seems probable that Wortman obtained the three specimens from about the same locality and horizon, inasmuch as a collector of Wortman's experience would, in these beds, have obtained much more material had he at that time extended his examination over any appreciable area. Two of the species Matthew has shown are lower Gray Bull, and such an assignment for *E. spatularius* is entirely compatible, and can be maintained by much the same evidence.

Among the specimens tentatively embraced by the name *E. spatularius* are the lower jaw (fig. 5 of this paper), A.M. No. 16065, from the Clark Fork beds, which Simpson figured as *Esthonyx ?bisulcatus* (1937, fig. 1); three Sand Coulee specimens, including A.M. Nos. 16144 and 16873; and a few fragmentary, unnumbered Gray Bull specimens in the collections of the American Museum. There is, moreover, a single, decidedly small specimen in the U.S.N.M. New Mexico collections, No. 17156, consisting of a jaw fragment with M_3

which has the same dimensions as the type of *E. spatularius*. Its dimensions are approximately 18 to 20 percent less than for the *E. bisulcatus* type, whereas the types of the invalid species *E. acer* and *E. burmeisterii* are roughly 4 percent and 8 to 10 percent smaller, respectively. However, the small size of No. 17156 is even less significant in the New Mexico collections than the proportions of the type of *E. spatularius* are in the Gray Bull population, inasmuch as mean for the New Mexico material is somewhat lower.

The Clark Fork specimen included in the above tentative assignment, and to a certain extent the type, exhibit an almost intangible condition, more distinctive in the large *E. grangeri* from the same beds, i. e., a somewhat inflated or more circular appearance of the cusps than in Gray Bull materials, a condition, of course, not reflected in the statistical analyses of tooth lengths. This probably represents a more primitive condition of *Esthonyx,* indicating a more bunodont, less crescentic tooth pattern in the ancestry. Possibly further collecting will demonstrate that the Clark Fork specimen represents a distinctive species. It should be noted, however, that the third molars in A.M. No. 16065 and the type of *E. spatularius* are much more alike than the drawings (figs. 4 and 5, made by different artists) would seem to indicate.

MEASUREMENTS IN MILLIMETERS OF *Esthonyx spatularius* SPECIMENS

	A.M. No. 4809	A.M. No. 16065
	Type	Clark Fork
P_2, anteroposterior diameter	...	4.2
P_2, transverse diameter	...	2.5
P_3, anteroposterior diameter	5.3	6.0
P_3, transverse diameter	3.7	4.1
P_4, anteroposterior diameter	...	7.4a
M_1, anteroposterior diameter	...	7.8
M_2, anteroposterior diameter	...	7.8
M_3, anteroposterior diameter	8.8	9.4

a, approximate.

ESTHONYX ACUTIDENS Cope, 1881

Text figures 6-8

Type.—Left M_2 and M_3, A.M. No. 4807.

Horizon and locality.—Wind River formation, Wind River Basin, Wyo.

Specific characters.—Size distinctly larger than *E. bisulcatus*. Rostrum more elongate and upper incisors relatively larger; P^2 and (in

some specimens) P_2 single-rooted, and P_4 more molariform. Parastyle on P^4-M^3 and metastyle on P^3-M^2 well developed, with cingulum extending outward and forward from the metastyle widely flaring. Cingulum on anterior surface of talon reduced. Upper molars transversely broad. Lower molars elongate, and bases relatively broad as compared to width at occlusal surface. Talonid of M_3 comparatively elongate.

Discussion.—The type (fig. 6) and referred upper dentition (A.M. No. 4808, fig. 7 of this paper) of *E. acutidens* described by Cope do not have accurate locality data other than Wind River Basin. It seems likely, however, that these are from the Lost Cabin horizon. Sinclair and Granger (1911, p. 104), in naming the Lost Cabin beds, noted that the *Lambdotherium* zone had previously been synonymous with Wind
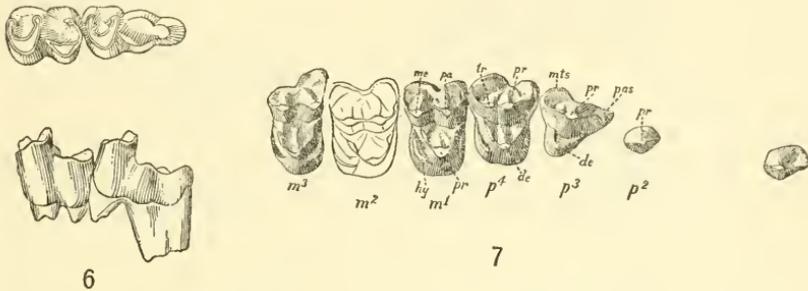
Fig. 6.—*Esthonyx acutidens* Cope: Left M_2 and M_3 (A.M. No. 4807), type specimen, occlusal and lateral views, $\times$ 1. Lost Cabin lower Eocene, Wyoming.
Fig. 7.—*Esthonyx acutidens* Cope: Right upper dentition (A.M. No. 4808), occlusal view, $\times$ 1. Lost Cabin lower Eocene, Wyoming.

River. However this may be, only *E. acutidens* has been certainly recorded from the Lost Cabin beds, and material known from Lysite localities may include both *E. bisulcatus* and *E. acutidens*.

Among the more significant specimens of *E. acutidens,* in addition to the two collected by Wortman and originally described by Cope, are the greater part of a lower dentition, A.M. No. 14738, collected by George Olson on Alkali Creek (Lost Cabin) ; skull fragments and part of the upper dentition which have been incorporated into a generalized skull restoration, together with some vertebrae and limb portions, A.M. No. 14735, collected by Walter Granger on Alkali Creek ; and a rostral portion of a large skull (fig. 8) including representation of all the upper teeth except the third upper incisor (or canine?), U.S.N.M. No. 18202, collected by Harry Tourtelot, of the U. S. Geological Survey, in beds identified by him as Lost Cabin in age. *Esthonyx* material collected by Patterson from the Plateau Valley beds in Colorado in-

cludes a lower jaw portion with a single molar from the Lost Cabin
equivalent and two lower molars from beds intermediate to the Lysite
and Lost Cabin equivalents which correspond rather closely to the
type of *E. acutidens.*

The specimen of *Esthonyx acutidens* collected by Tourtelot in the
Wind River Basin was discovered in about section 12 of T. 39 N.,
R. 94 W., not far from, and a little lower than, material of *Eotitanops.*
According to Tourtelot,[4] the Lost Cabin beds here are nearly horizontal
and the Lysite is not exposed, having gone underground about 15 or
20 miles to the east. This specimen of *E. acutidens* is distinctly large
for the species and decidedly advanced among Wasatchian esthony-
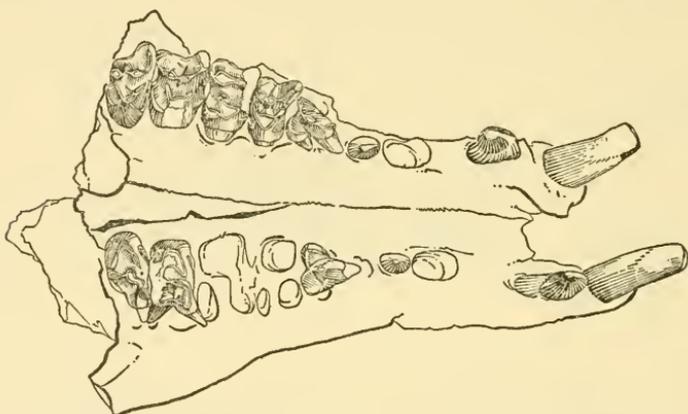
Fig. 8.—*Esthonyx acutidens* Cope: Rostral portion of skull (U.S.N.M. No.
18202), ventral view, $\times \frac{2}{3}$. Lost Cabin lower Eocene, Wyoming. (The loose
teeth drawn in the position of I³ may be canines.)

chids. It is the only Wind River specimen so far found exhibiting the
anterior portion of the rostrum.

The rostral portion, as exhibited by U.S.N.M. No. 18202, is dis-
tinctly enlarged anteriorly, approaching in appearance the equivalent
portion of a skull of *Trogosus hyracoides.* The anterior incisors are
robust, but rooted, with the enamel limited to the crown portion. I²
has a nearly triangular cross section with the posterior surface of the
tooth much worn so that no enamel remains. Also, the anterior surface
of the tooth is slightly beveled by attrition so that a small patch of
enamel has been removed adjacent to the cutting edge.

The alveoli for I³ and canines are both large and of about the same
diameter. A marked diastema is present between these teeth, but fol-
lowing the canine the diminutive, single-rooted second premolar and

---

[4] Personal communication.

remaining cheek teeth are in close sequence. The cheek teeth in U.S.N.M. No. 18202 are appreciably larger than in the American Museum specimens Nos. 4808 and 14735, but probably not beyond the range of the species.

A pair of loose teeth associated with the Lost Cabin rostrum, U.S.N.M. No. 18202, are uncertainly identified as the canines, but may possibly be the third or posterior upper incisors as depicted in figure 8. These are large but vertically short-crowned, with very robust and decidedly curved root portions. Wear has taken place only along the anterior slope of the crest and on the apex. The crowns of these teeth resemble in form a canine belonging to A.M. No. 4808 of *E. acutidens,* but are distinctly larger—larger even than the canine of *Trogosus hyracoides* (U.S.N.M. No. 17886). The third upper incisor in A.M. No. 4808, like *E. bisulcatus,* is long-crowned, not sharply curved, and has the enamel distributed well down the outer side, lower than in the questioned teeth of the Tourtelot specimen. Also in A.M. No. 4808, as in *E. bisulcatus,* both the posterior and anterolingual margins of the crown portion of the tooth are characterized by a relatively sharp longitudinal rib, between which, on the posterolingual wall of the tooth, the enamel recedes toward the apex of the tooth. The characteristics of I^3 in A.M. No. 4808 strongly suggest that the isolated teeth in U.S.N.M. No. 18202 are canines. On the other hand, the latter strikingly resemble much larger, loose teeth interpreted as third incisors of *Tillodon,* and to some extent I^3 in *Trogosus hyracoides,* although here I^3 appears more hypsodont.

MEASUREMENTS IN MILLIMETERS OF *Esthonyx acutidens* SPECIMENS

Upper dentition:	U.S.N.M. No. 18202	A.M. No. 4808	A.M. No. 14735
I^2, greatest diameter, at alveolus	9.5	...	...
C, greatest diameter	8.4	...	...
P^2, anteroposterior diameter	5.8	5.5	...
P^2, transverse diameter	3.6	3.6	...
P^3, anteroposterior diameter	9.5	9.8	8.5
P^3, transverse diameter	9.5	8.8	7.9
P^4, anteroposterior diameter, externally	9.0a	8.8	9.4
P^4, transverse diameter, anteriorly	13.7	11.4	11.3
M^1, anteroposterior diameter, externally	10.0a	8.6	8.6
M^1, transverse diameter, anteriorly	14.0a	13.5a	12.5
M^2, anteroposterior diameter, externally	11.0a	...	9.2
M^2, transverse diameter, anteriorly	17.0a	...	14.5
M^3, anteroposterior diameter, perpendicular to anterior face	8.5	...	...
M^3, transverse diameter, anteriorly	16.2	...	...

Lower dentition:	A.M. No. 4807	A.M. No. 14738
P$_2$, anteroposterior diameter........................ ...		6.7
P$_3$, transverse diameter........................... ...		4.2
P$_4$, anteroposterior diameter........................ ...		8.8
M$_1$, anteroposterior diameter........................ ...		8.9
M$_2$, anteroposterior diameter........................	9.4	9.3
M$_3$, anteroposterior diameter........................	13.0	12.3

a, approximate.

ESTHONYX GRANGERI Simpson, 1937

Text figures 9, 10

Type.—Left lower jaw with P$_4$-M$_3$, A.M. No. 16067.

Horizon and locality.—Clark Fork or Sand Coulee, at head of Big Sand Coulee, Clark's Fork Basin, Wyo.
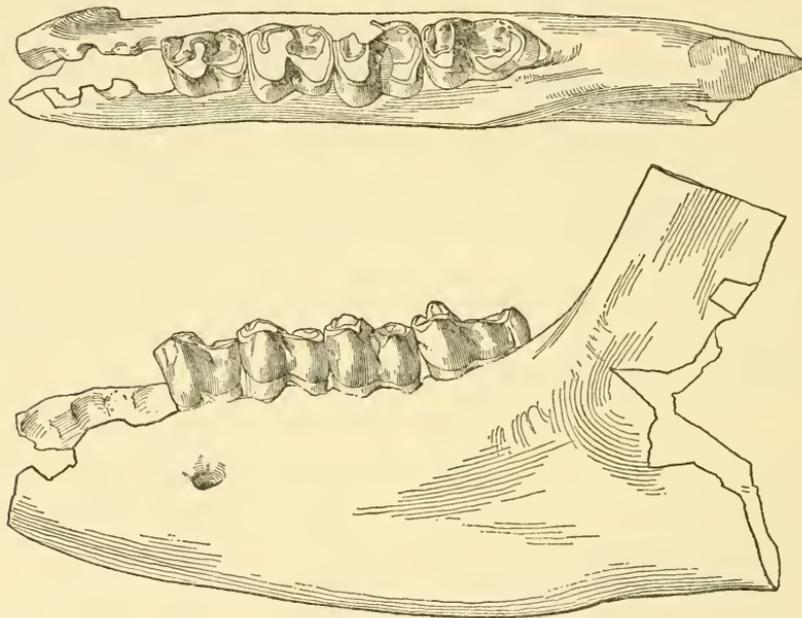
Fig. 9.—*Esthonyx grangeri* Simpson: Left ramus of mandible (A.M. No. 16067), type specimen, occlusal and lateral views, ×1. Clark Fork upper Paleocene or Sand Coulee lower Eocene, Wyoming. (After Simpson, 1937.)

Specific characters.—Significantly larger than *Esthonyx bisulcatus,* but approached in size by individuals of *E. acutidens* and *E. latidens.* Characterized in part by inflated appearance of tooth cusps, and by the less striking development of styles and cingula of the upper cheek teeth. P^4 shows an advanced degree of separation of the metacone (or tritocone), but with hypocone (or tetartocone) undeveloped. Molarization of P$_4$ well advanced.

Discussion.—This particularly large species of *Esthonyx* is known only from the Clark Fork and Sand Coulee horizons, unless it is represented by a Princeton Gray Bull specimen (No. 14727, see fig. 21), and so far as we know, did not give rise to any of the later species. The diversification of species in these, the earliest horizons for known tillodonts, approaches that in the Bridger, whereas in most of Wasatchian time a single or possibly two species were known to be extant in any one horizon.

E. grangeri, though large, exhibits structural characters which may be regarded as primitive, and not evident in *E. bisulcatus.* Although the extent to which the premolars have become molarized is comparable (except for the lack of development of the hypocone in P^4), the
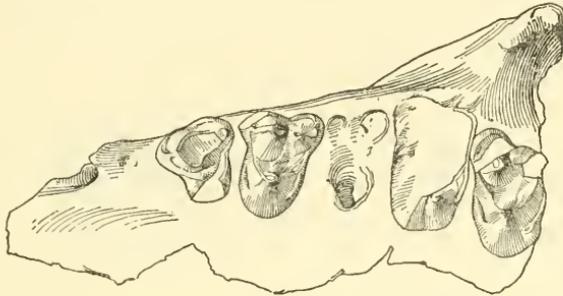
Fig. 10.—*Esthonyx grangeri* Simpson: Left maxilla (A.M. No. 16123), occlusal view, $\times$ 1. Clark Fork upper Paleocene. (After Simpson, 1937.)

more inflated or bunodont appearance of the cusps, together with the less flaring development of the styles and cingula on the outer walls of the upper teeth, suggest a less advanced condition than in *E. bisulcatus.* This is indicated in the lower dentition by the lack of development of the metastylid, the less marked hypsodonty of the outer lobes, as well as by the cusp inflation, the latter effecting somewhat shallower, distinctly less concave basins. These characteristics may be shared in certain respects by *E. latidens,* and by the Clark Fork specimen referred to *E. spatularius.*

MEASUREMENTS IN MILLIMETERS OF *Esthonyx grangeri* SPECIMENS

Upper dentition:	A.M. No. 16123
P^3, anteroposterior diameter	10.5*a*
P^4, anteroposterior diameter	10.4*a*
P^4, transverse diameter	13.5*a*
M^3, anteroposterior diameter, perpendicular to anterior face	9.3
M^3, transverse diameter, anteriorly	16.7*a*

Lower dentition:	A.M. No. 16067 Type	A.M. No. 15858
I₂, greatest transverse diameter	... ...	10.0
P₃, anteroposterior diameter	... ...	8.8
P₃, transverse diameter across talonid	... ...	7.2
P₄, anteroposterior diameter	10.7	11.4
M₁, anteroposterior diameter	11.0	11.0
M₂, anteroposterior diameter	11.0	...
M₃, anteroposterior diameter	15.1	13.6

a, approximate.

ESTHONYX LATIDENS Simpson, 1937

Text figure 11

Type.—Left maxilla with Dp^3-M^1, right maxilla with Dp^4, left ramus with Dp_3-M_1, also upper incisors in premaxillary portions of both sides, A.M. No. 16066.
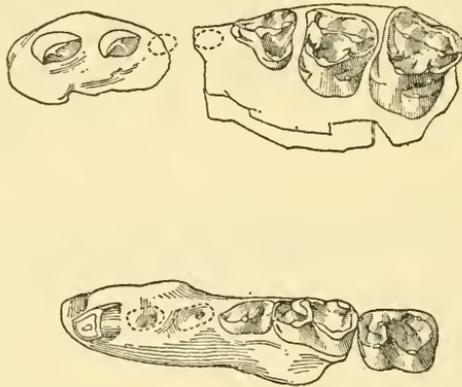
Fig. 11.—*Esthonyx latidens* Simpson: Left maxilla with I^2, I^3, Dp^3, Dp^4 and M^1; and left ramus of mandible with I_2, Dp_3, Dp_4, and M_1 (A.M. No. 16066); type specimen, occlusal views, × 1. Clark Fork upper Paleocene, Wyoming. (After Simpson, 1937.)

Horizon and locality.—Clark Fork beds, 3 miles east of Pat O'Hara Creek, Clark's Fork Basin, Wyo.

Specific characters.—Intermediate in size between *E. grangeri* and *E. bisulcatus*. Characterized principally by the low width-to-length ratio of M^1.

Discussion.—Little can be added to Simpson's definition of *E. latidens*. Only the first upper molar of the permanent dentition is preserved in the type, the remaining two teeth representing the deciduous series. Dp^3 can scarcely be distinguished from a Dp^3 in *E. bisulcatus* (A.M. No. 15113) and the Dp^4's are similar, although in the *E. bi-*

sulcatus specimen the hypocone base has an almost periptychid appearance. M_1 of *E. latidens* is markedly narrow, transversely, as compared to its anteroposterior length. The cusps are stout and the hypocone and external cingulum are both relatively strong, but not so flaring as is characteristic of *E. bisulcatus.* The external cingulum, moreover, is continuous around the paracone and metacone, joining the protoconule and metaconule rather more noticeably than in *E. bisulcatus,* with a less prominent union of the parastyle and metastyle crests with their associated primary cusps. The talonid and its basin in the lower molar of the type of *E. latidens* could scarcely be distinguished from that in an unworn M_1 of *E. bisulcatus,* but in the trigonid the cusps are emphasized at the expense of a well-formed crest.

MEASUREMENTS IN MILLIMETERS OF TYPE SPECIMEN OF *Esthonyx latidens,*
A.M. NO. 16066

Upper dentition:

Dp^3, anteroposterior diameter	8.5
Dp^3, transverse diameter	7.3
Dp^4, anteroposterior diameter, externally	10.5a
Dp^4, transverse diameter, posteriorly	10.7a
M^1, anteroposterior diameter, externally	10.6
M^1, transverse diameter	12.6

Lower dentition:

Dp_3, anteroposterior diameter	7.2
Dp_3, transverse diameter	4.5
Dp_4, anteroposterior diameter	10.8
M_1, anteroposterior diameter	10.4

a, approximate.

ESTHONYX MUNIERI (Lemoine), 1889

Type.—Right M_3, Lemoine collection in Museum of Paris.

Horizon and locality.—Sparnacian or Cuisian (Agéien), lower Eocene in the vicinity of d'Epernay, France.

Specific characters.—Size of M_3 close to that of *Esthonyx bisulcatus,* but described as having a lower or secondary parastylid. No mention is made of a metastylid, but a slight development of this cusp seems evident in Teilhard de Chardin's illustration (1922, pl. 3, fig. 19a). The occlusal view (1922, pl. 3, fig. 19) also shows a relatively brief third lobe for this tooth.

Description.—The third lower molar, selected as the type, is one of the two teeth which Teilhard de Chardin retained in the species *E. (Plesiesthonyx) munieri* from out of the four described by Lemoine. The two upper teeth in Lemoine's collection he referred to

Phenacodus. The other lower tooth, a P_4, was regarded as perhaps showing a relationship to *Esthonyx.*

Teilhard's description of the two lower teeth follows:

M_3 (long. = 10) très caractéristique: trigone bien plus haut que le talon; paraconide très distinct, mais fortement rapproché du métaconide, et relié au protoconide par une crête qui forme, à l'angle antéro-externe du trigone, un coude prononcé (caractère de Chiromyidé); parastylide fort, ayant au-dessous de lui un deuxième parastylide secondaire; talon creux; troisième lobe simple, bien marqué, et légèrement retroussé postérieurement.

P_4 fortement molarisée: paraconide transverse et tranchant; métaconide peu détaché du protoconide; talon circulaire, creux, à bords coupants; émail plissé sur la face extérieure du trigone. La forme générale de la dent rappelle, en un peu plus court, P_4 de *Phenacodus.*

The rugosity of the outer wall of trigonid of P_4 seems unusual, and may be exaggerated in Lemoine's figures (1891, pl. 10, figs. 32s and 32i).

The upper molar, formerly included with material of *Propachynolophus gaudreyi,* which Teilhard referred tentatively to *Esthonyx munieri,* appears to be incomplete externally, or did not have the characteristic external styles and shelflike cingulum. Moreover, the anterior cingular crest, or "ectocone" seems relatively better developed and more nearly comparable to the hypoconal ridge than observed in "Wasatch" *Esthonyx.*

Subfamily uncertain

Genus ADAPIDIUM Young, 1937

Type.—*Adapidium huanghoense* Young.

Generic characters.—Not distinguished by Young from those of the species, but lowness of paraconid and distinctly lingual junction of hypoconid crest with trigonid may be significant.

ADAPIDIUM HUANGHOENSE Young, 1937

Type.—Portion of right ramus of mandible with M_2 and M_3, Y. Y. Lee's collection, Cenozoic Research Laboratory, Geological Survey of China.

Horizon and locality.—Upper Eocene? Basin in the Yuanchü-Mienchih border along the Huangho, China. (Locality F. 12 of Lee.)

Specific characters.—Species of large size compared with those of *Esthonyx,* considerably smaller than forms of *Trogosus.* Length of lower molars equivalent to those in *E. grangeri,* but more hypsodont and slender, and lower jaw shallower.

Discussion.—It is an interesting fact that those characters to which Young (1937) has called attention in distinguishing *Adapidium* from

Adapis are indicative of the Tillodontia. In size the form does not differ greatly from *Esthonyx grangeri,* but the tooth pattern is more suggestive of *Trogosus.* The external hypsodonty of the lower teeth as compared with the more brachydont appearance of the lingual wall is characteristic of all the tillodonts, but becomes increasingly distinctive in the later forms. The same may be said of the degree to which the selenodont pattern is developed. The position at which the talonid crest joins the trigonid in *Adapidium,* that is, between the metaconid and metastylid, is distinctly like *Trogosus.* In *Esthonyx* this junction is at a more median position on the posterior wall of the trigonid. An interesting condition described in *Adapidium* is the union by a transverse crest of the hypoconid and entoconid across the talonid of M_3, more completely defining a third lobe carrying the hypoconulid. This development has been observed in a more advanced stage, in which the transverse crest divides the basin, in various relatively unworn third lower molars of *Trogosus* from the Huerfano B horizon, and with a tendency in this direction in certain, though not all, Bridger last lower molars. In *Esthonyx* the talonid may be constricted immediately anterior to the hypoconulid, but the hypoconulid is less distinctly set off and in no case does the basin appear divided. The lingual profile of M_3 shown by Young (1937, fig. 16) is strikingly like that seen in certain Huerfano B specimens.

There is no information on the extent to which the incisors of *Adapidium* may have been developed, hence its subfamily reference cannot be made. Its occurrence in deposits believed to be younger than Bridger suggests survival of a stage of development approximately equivalent to that intermediate between Lost Cabin and Huerfano B, or to represent independent and parallel development in Asia from an earlier Eocene stage when Wasatchian forms are known to have migrated more freely between the eastern and western hemispheres, and *Esthonyx* is known to have been present in the Sparnacian or Cuisian of France.

Trogosinae, new subfamily

The subfamily Trogosinae is proposed for the tillodonts having enlarged, rootless second incisors above and below. In these forms the enamel on the anterior face of the second incisors is not limited to the crown portion and these teeth grow from persistent pulp. Moreover, the second premolars (first of the series) above and below are single-rooted. As presently arranged, the Trogosinae includes the middle Eocene forms *Trogosus, Tillodon,* and presumably *Anchippodus.*

Genus ANCHIPPODUS [5] Leidy, 1868

Type.—Anchippodus riparius Leidy.

Generic characters.—Not determinable from the known material representing the genotype.

ANCHIPPODUS RIPARIUS Leidy, 1868

Text figures 14, 17

Type.—Left lower molar, presumably M_2, A.N.S. No. 10338.

Horizon and locality.—Middle (?) Eocene, Shark River, Monmouth County, N. J.

Specific characters.—Large tillodont with lower molars equaling in size those of *T. fodiens* from the Bridger formation.

Description.—The type and only known specimen representing this, the first described tillodont, is an isolated lower molar believed to be M_2. It is clearly tillodont, beyond reasonable doubt, exhibiting the characteristics of a tillodont lower molar. The tooth is moderately well worn but preserves the metastylid. The trigonid is elevated with respect to the talonid and both exhibit the nearly equal U-shaped occlusal surfaces, slightly compressed buccally in the stage of wear presented. The enamel is distributed well down the outer surface of the tooth to a point well below the maximum width of the strongly convex columns. Lingually, the enamel is limited downward to a level immediately below the opening to the talonid basin, a condition duplicated in Bridger tillodont teeth.

Discussion.—Geographically, the Shark River and the Bridger formations are widely separated, and outside of the tillodont evidence little information is available on the relative stratigraphic position of the two deposits. Moreover, more than one genus of Bridger tillodonts is recognized, and these are currently distinguished by characters not clearly provided by the material of *Anchippodus riparius,* so that for taxonomic purposes we are compelled to disregard this form, at least until such time as diagnostic material is forthcoming from the New Jersey deposits.

MEASUREMENTS IN MILLIMETERS OF TYPE SPECIMEN OF *Anchippodus riparius,* A.N.S. NO. 10338

Lower molar, anteroposterior diameter................................... 20.9
Lower molar, greatest width of trigonid perpendicular to lingual wall..... 17.1*a*
Lower molar, greatest width of talonid perpendicular to lingual wall...... 15.1*a*

a, approximate.

---

[5] In this, and certain taxonomic headings to follow, names which must be disregarded will not appear in boldface type.

Genus **TROGOSUS** Leidy, 1871

Synonym.—Tillotherium Marsh, 1873.

Type.—Trogosus castoridens Leidy.

Generic characters.—Skull relatively short or of moderate length. Lachrymal foramen located midway on orbital rim. Rostrum short among tillodonts, with canine set off by slight or no diastemata, to somewhat longer with diastemata of moderate length. Molar teeth above with high acute cusps and relatively open external folds. Greatest width of cheek teeth in M^3. I_1 and I_3 present. Lower teeth anterior to P_3 closely spaced or crowded with a short or no diastema between P_2 and P_3. Lower molars high-crowned with external columns distinctly convex in a transverse vertical plane, but dorsally not so sharply convergent with the inner wall as in *Tillodon.*

TROGOSUS MINOR (Marsh), 1871

Text figure 18

Type.—Right lower molar, M_2, Y.P.M. No. 11083.

Horizon and locality.—Bridger B, Grizzly Buttes, Bridger Basin, Uinta County, Wyo.

Specific characters.—Moderate-sized tillodont, otherwise indeterminate.

Discussion.—This is the earliest specific name applied to Bridger tillodont material, first referred by Marsh to *Palaeosyops.* Leidy (1872b) recognized its true relationships and regarded his *T. castoridens* as a synonym under *Anchippodus minor.* The material, however, is inadequate as the species cannot be defined. No one of the species of *Trogosus* can be exclusively restricted to it as the specimen can be matched in material of *Trogosus hyracoides* as well as in *Trogosus castoridens.* In consequence, the name *T. minor* must necessarily be disregarded, unless it can be demonstrated that *T. hyracoides* and *T. castoridens* are dimorphs of the same species, possibly male and female, or simply variants, in which case *Trogosus* minor as the earliest name might be defended as valid.

MEASUREMENTS IN MILLIMETERS OF TYPE SPECIMEN OF *Trogosus minor*,
Y.P.M. NO. 11083

Lower molar, anteroposterior diameter...................................... 21.0
Lower molar, transverse diameter of trigonid perpendicular to inner wall.. 17.0*a*
Lower molar, transverse diameter of talonid perpendicular to inner wall... 16.0*a*

a, approximate.

TROGOSUS CASTORIDENS Leidy, 1871

Text figure 12

Type.—The anterior portion of the right and left rami of the mandible, including the large incisors, M_2, a part of M_1, and the root or alveolar representations of other teeth, A.N.S., Philadelphia, No. 10337.

Horizon and locality.—Bridger B, Grizzly Buttes, Bridger Basin, Uinta County, Wyo.

Specific characters.—Small among middle Eocene tillodonts with a relatively short skull indicated. Anterior extremity of lower jaw noticeably shallow. Cheek teeth of moderate size and those anterior to P_4 in the lower jaw decidedly crowded.

Discussion.—The jaw which Leidy described as the type of *Trogosus castoridens* is evidently from a relatively small and short-faced form. The masseteric fossa extends forward beneath M_3 and the posterior portion of this tooth is actually embedded in the base of the anterior face of the ascending ramus. Alveoli are present for I_1 and for C, P_2 and P_3, and the latter three teeth may have been of relatively small size. Alveoli for I_3 are not preserved, and indeed this tooth may have been crowded out; however, both rami of the mandible are here broken down to a depth perhaps below that for the root of I_3.

MEASUREMENTS IN MILLIMETERS OF TYPE SPECIMEN OF *Trogosus castoridens,*
A.N.S. NO. 10337

Length of symphysis	70.5
Depth of jaw, internally below point between M_2 and M_3	46.0
Thickness of jaw beneath M_2	21.5
Posterior margin of alveolus for I_2 to anterior margin of alveolus for P_3, estimated	19.0
Length of tooth series P_4 to M_3, inclusive, at alveolar border	79.5
Length of molars, M_1 to M_3, inclusive, at alveoli	65.5
I_2, anteroposterior diameter of exposed portion	13.0
M_3, anteroposterior diameter at occlusal surface	20.0
M_2, transverse diameter of trigonid perpendicular to inner wall	17.5*a*
M_2, transverse diameter of talonid perpendicular to inner wall	15.5*a*

a, approximate.

TROGOSUS? VETULUS Leidy, 1871

Text figure 13

Type.—The erupted portion of a right lower I_2, possibly deciduous, A.N.S., Philadelphia, No. 10336.

Horizon and locality.—Bridger B, vicinity of Fort Bridger, Bridger Basin, Uinta County, Wyo.

Specific characters.—Described by Leidy as being a species of smaller size than *T. castoridens.*

13

14

12 a

12 b
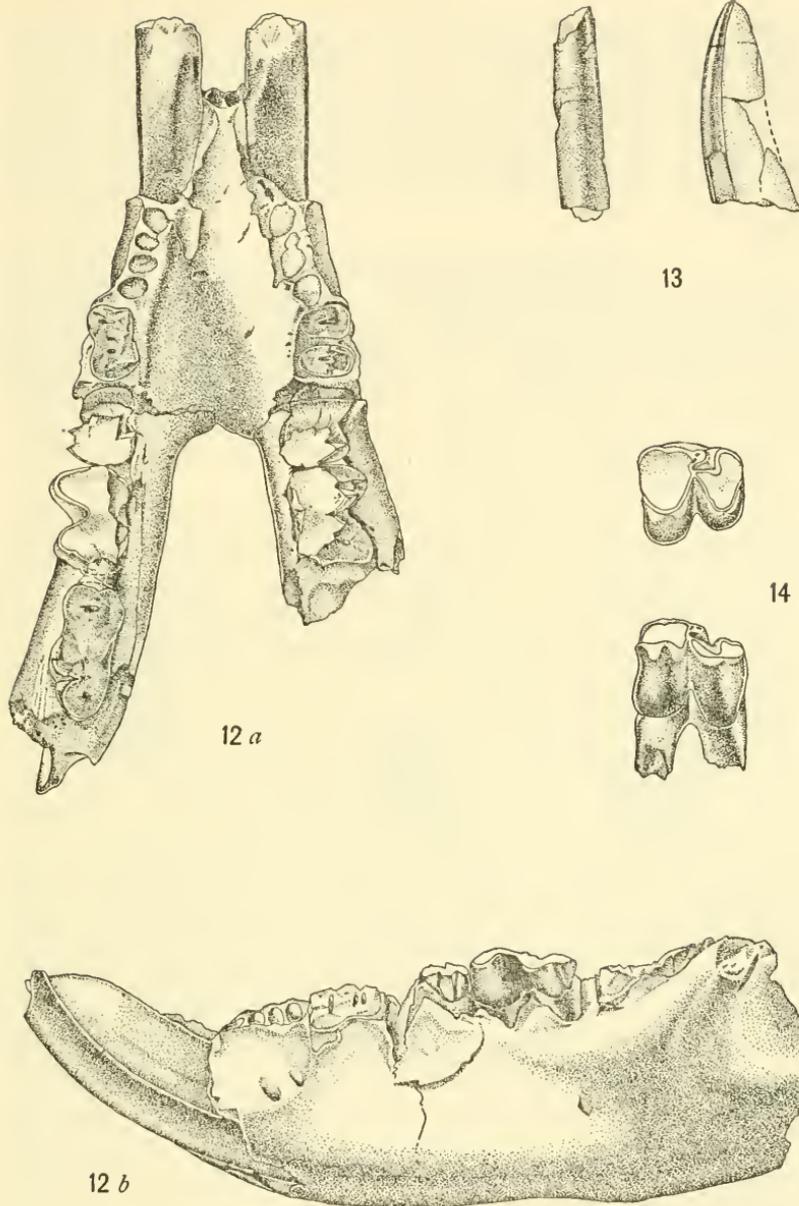
FIG. 12.—*Trogosus castoridens* Leidy: Portions of both rami of mandible (A.N.S. No. 10337), type specimen; *a*, occlusal view; *b*, lateral view of left ramus; × ⅔. Bridger (B) middle Eocene, Wyoming.

FIG. 13.—*Trogosus? vetulus* Leidy: Portion of I₂ (A.N.S. No. 10336), type specimen, anterior and medial views, × ⅔. Bridger (B) middle Eocene, Wyoming.

FIG. 14.—*Anchippodus riparius* Leidy: Left M₂? (A.N.S. No. 10338), type specimen, occlusal and lateral views, × ⅔. Shark River Eocene, New Jersey.

Discussion.—The diameter of the incisor in Bridger tillodonts changes noticeably with increased age and wear. The type of *T.? vetulus* is presumed to represent a youthful individual with the incisors but little worn, or perhaps of the deciduous series. Except for size, which is a function of age, no characters are exhibited which would distinguish it from *T. castoridens,* or any of the other Bridger tillodonts.

TROGOSUS HYRACOIDES (Marsh), 1873

Plates 1-4; text figures 15, 30, 31 (part), 32, 33, 37 (part), and 38e and g

Type.—Right maxillary and premaxillary portions, including M^1 to M^3, parts of I^2 and P^4, and incomplete alveolar representations of I^2 to P^3 (?) ; Y.P.M. No. 11084.

Horizon and locality.—Bridger B, "Grainger Station," Bridger Basin, Sweetwater County, Wyo.

Specific characters.—A tillodont of larger size and with a relatively longer rostrum than in *Trogosus castoridens.* Upper teeth between I^3 and P^3 well spaced. I_1 very long and slender, but possibly rooted, with enamel on anterior surface as in I_2. Molar teeth comparable in size to those in *T. castoridens.* Talonid basin of M_3 open between second and third lobes, with little or no division, and hypoconulid closely joined with entoconid.

Discussion.—In addition to fragmentary material in the Marsh collection, constituting the type, there is a specimen in the collections of the American Museum, No. 18982, having upper molars so nearly like those in the type that they must surely represent the same species. The American Museum specimen consists of an incomplete rostral portion of a skull and lower jaws, together with limb fragments including the greater part of a forefoot, and was collected by Olsen in 1922 along Middle Cottonwood Creek in about the middle of horizon "B." Although the preserved teeth in this specimen retain their natural shape and something of their relative positions in the jaws, the bony portions have much disintegrated, and except for a small portion of the right premaxilla, little can be ascertained as to the character of the specimen between $I\frac{2}{2}$ and the molars. However, it is interesting to note that the first lower incisors are preserved in place between the large second incisors.

A skull and lower jaws (pls. 1-4), exhibiting a beautifully preserved dentition, together with a radius (fig. 30) and a complete fore foot (figs. 32, 33), in the collection of the U. S. National Museum, No. 17886, are also referred to *Trogosus hyracoides.* The specimen was found by G. F. Sternberg while with the 1947 Smithsonian Insti-

tution expedition, in the Bridger "B" horizon near the top of a west-
ward-facing escarpment about a mile and a half due south of Church
Buttes. The skull belonging to this individual is moderately large and
comparatively slender, with the rostrum elongate and the anterior teeth
above well spaced, while those below are uncrowded. However, the

15

16

17

18
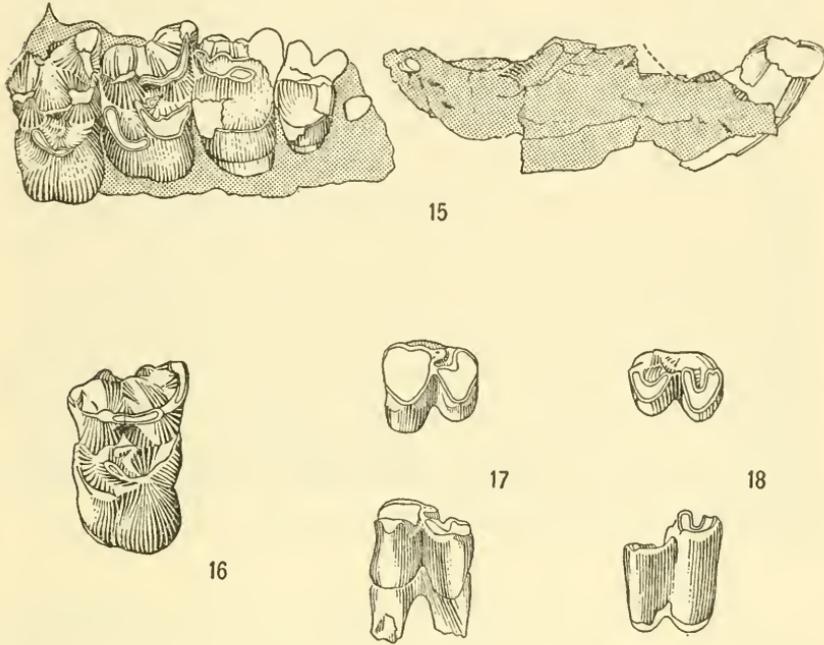
FIG. 15.—*Trogosus hyracoides* (Marsh): Portions of right maxilla and pre-
maxilla with I^2 and P^4 to M^3, incl. (Y.P.M. No. 11084), type specimen, occlusal
view, $\times \frac{2}{3}$. Bridger middle Eocene, Wyoming.
FIG. 16.—*Trogosus? latidens* (Marsh): Right M^2 (Y.P.M. No. 11085), type
specimen, occlusal view, $\times \frac{2}{3}$. Bridger middle Eocene, Wyoming.
FIG. 17.—*Anchippodus riparius* Leidy: Left M_2? (A.N.S. No. 10338), type
specimen, occlusal and lateral views, $\times \frac{2}{3}$. Shark River Eocene, New Jersey.
FIG. 18.—*Trogosus minor* (Marsh): Right M_2? (Y.P.M. No. 11083), type
specimen, occlusal and lateral views, $\times \frac{2}{3}$. Bridger (B) middle Eocene,
Wyoming.

upper molars are slightly smaller than in the type or than in A.M.
No. 18982. The lower jaw is longer and deeper, and the anterior teeth
much less crowded than in Leidy's type of *Trogosus castoridens*.

Trogosus hyracoides was described by Marsh as the type of the
genus *Tillotherium*. The characterization was made on the basis of
an upper dentition, and at that time comparison with Leidy's *Trogosus
castoridens* was not feasible, inasmuch as upper and lower tillodont

teeth had not been found associated. Nevertheless, Marsh suspected their generic identity, as noted in his discussions, but later (1875b, p. 241), in naming the skull and jaws of *T. fodiens,* he called attention to differences from the *Trogosus castoridens* jaw. These differences served to distinguish *T. fodiens* but not the genotype, *T. hyracoides,* which was subsequently ignored. Careful examination of the type of *T. hyracoides,* aided by associated skull and jaw material described above, has failed to reveal differences between *T. hyracoides* and *T. castoridens* of more than species value.

It is suspected, however, as has been mentioned under discussion of the type of *T. minor,* that the differences between *T. hyracoides* and *T. castoridens* may be dimorphic and not taxonomic. The possibility of such an interpretation was brought to mind by the parallel differences between these two Bridger species and the two Huerfano types. The differences amount to the recognition of a long-faced and a short-faced form in both horizons. As to whether such a difference might logically be attributed to a dimorphic state is debatable, and with scarcely more than one truly diagnostic specimen representing each of the forms involved the possibility lacks the force of demonstration, and indeed may be impossible to demonstrate, so that the differences are here retained as taxonomic.

MEASUREMENTS IN MILLIMETERS OF *Trogosus hyracoides* SPECIMENS

	U.S.N.M. No. 17886
Skull:	
Length from anterior margin of premaxillae to posterior surface of postglenoid process	272.0
Distance from posterior margin of alveolus for I^2 to posterior surface of postglenoid process	253.0
Distance from posterior margin of alveolus for I^2 to posterior margin of palate at narial aperture	137.0
Distance from posterior margin of alveolus for I_2 to anterior margin of orbit at lachrymal foramen	97.0
Distance between lachrymal foramen and posterior surface of postglenoid process	157.0
Length of nasals	122.0
Greatest width of rostrum above canines	58.7
Width across postorbital processes	79.0
Width of palate between second molars	36.0*a*
Depth of rostrum posterior to canine	53.0*a*

	Y.P.M. No. 11084 Type	A.M. No. 18982	U.S.N.M. No. 17886
Upper dentition:			
Length of upper dentition I^2-M^3, incl......	...	...	163.0
Distance between I^2 and P^2 at alveoli......	59.5a	...	50.0
Length of P^3 to M^3, incl...................	...	...	83.1R to 85.6L
Length of molars, externally.............	60.0a	63.0a	56.1R to 57.6L
I^2, greatest diameter at alveolus...........	...	20.0	20.0
I^3, greatest diameter at alveolus...........	...	...	12.0
C, anteroposterior diameter of crown......	...	...	8.0
C, transverse diameter....................	...	...	5.5
P^2, anteroposterior diameter...............	...	...	7.3
P^2, transverse diameter....................	...	...	4.9
P^3, anteroposterior diameter, externally....	...	...	16.6
P^3, transverse diameter perpendicular to buccal surface	...	...	15.8
P^4, anteroposterior diameter, externally....	...	...	15.1
P^4, transverse diameter, anteriorly........	...	...	22.5
M^1, anteroposterior diameter, externally...	...	18.0a	16.8
M^1, transverse diameter, anteriorly........	...	...	23.5
M^2, anteroposterior diameter, externally...	23.0	23.0	21.3
M^2, transverse diameter, anteriorly........	35.0	33.5	29.7
M^3, anteroposterior diameter, perpendicular to anterior face......................	21.5	20.0	20.3
M^3, transverse diameter, anteriorly........	38.0a	36.0	35.5R to 33.5L

Lower jaw:

Length from posterior margin of alveolus for I_2 to posterior surface of condyle..	...	...	21.7a
Length from posterior margin of alveolus for I_2 to posterior margin of angle....	...	...	21.6a
Length of symphysis.....................	...	...	75.0a
Depth of jaw internally beneath point between M_2 and M_3....................	...	...	55.0a
Distance between top of coronoid process and bottom of angle.................	...	...	136.0
Thickness of jaw beneath M_2.............	...	...	23.5

Lower dentition:

Cutting edge of I_2 to posterior margin of M_3.......	...	148.0
Posterior margin of alveolus of I_2 to anterior margin of alveolus for P_3.............................	...	27.3
P_3 to M_3, inclusive...............................	...	92.0a
M_1 to M_3, inclusive...............................	...	66.6a

	A.M. No. 18982	U.S.N.M. No. 17886
I₂, greatest diameter at alveolus..................	20.0a	20.0
I₃, greatest diameter of crown....................	...	4.5
C, anteroposterior diameter of crown..............	...	7.1
C, transverse diameter...........................	...	5.6
P₃, anteroposterior diameter......................	...	11.5
P₃, transverse diameter across talonid............	...	8.5
P₄, anteroposterior diameter......................	15.8	15.6
M₁, anteroposterior diameter at occlusal surface....	17.2a	16.8
M₂, anteroposterior diameter at occlusal surface....	21.0	18.7
M₃, anteroposterior diameter......................	33.0a	28.2

Limb and foot material:

Greatest length of radius.........................	...	152.0
Greatest diameter of proximal extremity of radius..	...	28.5
Transverse diameter of distal extremity of radius...	...	33.5
Greatest length of 1st metacarpal..................	36.0	34.3
Greatest diameter of proximal extremity of 1st metacarpal	18.0	17.0
Greatest length of 2d metacarpal..................	...	43.5
Transverse diameter of proximal extremity of 2d metacarpal	13.3	12.5
Greatest length of 3rd metacarpal.................	53.0	48.6
Transverse diameter of proximal extremity of 3rd metacarpal	12.0	11.5
Greatest length of 4th metacarpal.................	...	43.7
Transverse diameter of proximal extremity of 4th metacarpal	...	12.3
Greatest length of 5th metacarpal.................	...	8.5
Transverse diameter of proximal extremity of 5th metacarpal	...	17.2
Length of proximal phalanx of 3d digit...........	25.1	24.9
Length of medial phalanx of 3d digit.............	20.3	18.5
Greatest length of distal phalanx of 3d digit........	...	35.0a
Length of astragalus proximodistally..............	36.0a	...
Greatest width of astragalus......................	40.2	...

a, approximate.

TROGOSUS? LATIDENS (Marsh), 1874

Text figure 16

Type.—Right second upper molar, Y.P.M. No. 11085.

Horizon and locality.—Bridger formation, Bridger Basin, Wyo.

Specific characters.—Undeterminable except for very large size. No other characters of specific significance are evident.

Discussion.—The above isolated tooth is the type of the second species which Marsh described as *Tillotherium.* The principal characters which were attributed to *T. latidens* resulted from a misconception of the position of the tooth in the dental series. He regarded it as a third molar, whereas it must surely be a second, as determined by the development of the metastyle and hypoconal crest. The external cingular cusps are distinctive but not unique, as these have been noted in a less-developed condition in certain other specimens.

This species is retained as distinct from *Trogosus hyracoides* because of the remarkably large size of the teeth. The possibility of its representing *Tillodon* rather than *Trogosus* has not been overlooked but the crown of the type tooth is distinctly less brachydont than the corresponding tooth in *T. fodiens,* although the external folds of the tooth approach the sharpness seen in the latter.

A second specimen referred to this species is an isolated M³ obtained by a Princeton University party in the Cathedral Bluffs tongue exposed in the Washakie Basin. It corresponds exceptionally well with the type, considering the difference in position in the cheek-tooth series.

Portions of both rami of a mandible with M_1, M_2, and most of M_3 in the left, but only M_2 in the right ramus, in the collections of the National Museum of Canada may represent *Trogosus? latidens.* This specimen, like that earlier described by Russell (1935) as possibly representing *Trogosus minor,* was found in a coal mine at Princeton, British Columbia, in beds determined as the Princeton group. It certainly contains the largest tillodont lower teeth known, a size entirely appropriate for *T. ? latidens;* however, the lingual and buccal surfaces of the teeth appear to converge dorsally somewhat more rapidly than, for example, in *Trogosus hyracoides,* suggestive rather of *Tillodon fodiens.* The Canadian specimen is much too large to be referred to *Tillodon fodiens* and in the absence of associated upper and lower teeth is retained tentatively and questionably in *T. ? latidens.*

MEASUREMENTS IN MILLIMETERS OF *Trogosus? latidens* SPECIMENS

M² (type, Y.P.M. No. 11085), anteroposterior diameter, externally, perpendicular to anterior face.. 26.2
M² (type, Y.P.M. No. 11085), transverse diameter, anteriorly............. 41.5
M³ (U.S.N.M. No. 18480, cast of P.U. specimen), anteroposterior diameter, externally, perpendicular to anterior face............................ 23.4
M³ (U.S.N.M. No. 18480, cast of P.U. specimen), transverse diameter, anteriorly 39.8
M_1 (N.M.C. No. 8709), anteroposterior diameter......................... 20.5
M_2 (N.M.C. No. 8709), anteroposterior diameter......................... 26.3

TROGOSUS GRANGERI, new species

Plates 5-8; text figures 22, 23, 25-28

Type.—Skull, lower jaws, atlas, several dorsal and lumbar verte-brae, scapulae, limb fragments, and a forefoot; A.M.N.H. No. 17008.

Horizon and locality.—Huerfano B, Huerfano-Muddy divide, 3 miles west of Gardner, Huerfano Basin, Colo.

Specific characters.—Skull of moderate size and relatively broad. Frontal region decidedly broad and prominently arched in longitudinal profile. Palate broad and zygomae widely arched. Cranium and basi-cranial region noticeably short. Jaws deep. Anterior cheek teeth well developed above and below, but second incisors comparatively slender (probably due to advanced wear) and molars anteroposteriorly short in type. Canine well spaced from I^3 and P^2 in upper jaw and un-crowded in lower jaw, with a short diastema between P_2 and P_3.

Discussion.—The breadth of the skull of *T. grangeri* is particularly noticeable in comparison with the National Museum skull referred to *T. hyracoides,* although the rostral lengths are about equal. Its short-ness is emphasized in comparison with the type of *T. fodiens.* The shortness and relative breadth of the basicranial region posterior to the pterygoids is also noticeable when viewed with the skull of *T. fodiens.*

An interesting detail noted in various dentitions of Huerfano speci-mens in which the teeth are not too well worn is the appearance of the talonid of M_3. Unlike the few Bridger specimens exhibiting a suffi-ciently unworn M_3, the entoconid is separated from the posterior crest and strongly united with the hypoconid crest, dividing the talonid basin in two, with the posterior basin open lingually through a sharp, though deep, notch. Due to wear or incompleteness, it is not known whether this is characteristic of *T. grangeri* or of *T. hillsii,* but possibly of both.

The material comprising the type of *Trogosus grangeri* was col-lected by Dr. Walter Granger of the American Museum of Natural History in 1916 from the upper Huerfano beds in the Huerfano basin of Colorado. It includes the third skull of a middle Eocene tillodont to be found, which, except for the teeth, is clearly the most nearly perfect extant.

MEASUREMENTS IN MILLIMETERS OF TYPE SPECIMEN OF *Trogosus grangeri*,
A.M. NO. 17008

Skull:

Length from anterior margin of I^2 at alveolus to crest of supra-
occipital 309.0
Length from anterior margin of I^2 at alveolus to posterior surface of
occipital condyle 281.0
Distance from posterior margin of alveolus for I^2 to posterior surface
of postglenoid process.................................... 245.0
Distance from posterior margin of alveolus for I^2 to posterior margin
of palate at narial opening............................... 133.0
Distance from posterior margin of alveolus for I^2 to anterior margin
of orbit at lachrymal foramen............................. 102.0
Distance from anterior margin of orbit at lachrymal foramen to
posterior surface of postglenoid process................. 147.0
Length of nasals.. 108.0
Greatest width of rostrum above canines................... 62.0
Width across postorbital processes........................ 103.0
Width of cranium at postorbital constriction.............. 58.3
Width across zygomae...................................... 215.0a
Width across occiput...................................... 121.0
Width of palate between second molars..................... 47.0a
Depth of rostrum posterior to canines..................... 60.0
Height of occiput above lower margin of condyles.......... 98.0a

Upper dentition:

Anterior margin of I^2 at alveolus to posterior margin of M^3......... 151.0
Posterior margin of I^2 at alveolus to anterior margin of alveolus
for P^2 .... 55.0
P^3-M^3 at alveoli...................................... 85.0
M^1-M^3 at alveoli...................................... 49.5
I^2, greatest diameter at alveolus....................... 19.0
I^3, greatest diameter................................... 12.6
P^4, anteroposterior diameter, externally................ 14.9
P^4, transverse diameter................................. 21.1
M^1, anteroposterior diameter, externally................ 17.0
M^1, transverse diameter, anteriorly..................... 23.5a
M^3, anteroposterior diameter, perpendicular to anterior face.......... 18.0
M^3, transverse diameter, anteriorly..................... 32.3

Lower jaw:

Length from posterior margin of alveolus for I_2 to posterior surface
of condyle 230.0
Length from posterior margin of alveolus for I_2 to posterior margin
of angle 228.0
Length of symphysis....................................... 76.8
Depth of jaw beneath point between M_2 and M_3, internally.......... 58.0
Distance from top of coronoid process to bottom of angle............ 138.0
Thickness of jaw beneath M_2............................. 22.5

Lower dentition:

Cutting edge of I_2 to posterior margin of M_3 .... 146.0
Posterior margin of alveolus for I_2 to anterior margin of alveolus
    for P_3 .... 34.0
P_3 to M_3, inclusive at alveoli 89.0
M_1 to M_3, inclusive 61.8
I_2, greatest diameter at alveolus 18.5
P_3, anteroposterior diameter 12.0
P_3, transverse diameter across talonid 8.2
P_4, anteroposterior diameter 15.2
M_1, anteroposterior diameter at occlusal surface 15.0
M_2, anteroposterior diameter at occlusal surface 18.5
M_3, anteroposterior diameter 28.5

Other skeletal portions:

Greatest width of atlas 98.8
Width across articular surfaces of atlas for condyles of skull 50.5
Width across articular surfaces of atlas for axis 47.0
Length of clavicle 102.0
Length of scapula from anterior margin of glenoid surface to supra-
    scapular border 175.0
Anteroposterior diameter of glenoid surface 38.5
Transverse diameter of glenoid surface 27.0a
Greatest diameter of proximal extremity of radius 28.8
Transverse diameter of distal extremity of radius, perpendicular to
    axis of shaft 31.5a
Greatest diameter of proximal extremity of first metacarpal, perpen-
    dicular to shaft 18.2
Greatest length of second metacarpal 42.4
Transverse diameter of proximal extremity of second metacarpal 11.3
Greatest length of third metacarpal 47.2
Transverse diameter of proximal extremity of third metacarpal 10.5
Greatest length of fourth metacarpal 44.3
Transverse diameter of proximal extremity of fourth metacarpal 12.4
Greatest length of fifth metacarpal 40.2
Transverse diameter of proximal extremity of fifth metacarpal 16.0a
Transverse diameter of proximal extremity of fibula, perpendicular to
    axis of shaft 21.0

a, approximate.

TROGOSUS HILLSII, new species

Plates 9-12; text figures 29(part), 31(part), 35(part)

Type.—Skull and jaws, U.S.N.M. No. 17157.

Horizon and locality.—Huerfano B, Huerfano Basin, Colo.

Specific characters.—Skull smaller and much shallower than that of *T. grangeri.* Rostrum short and cranium relatively elongate. Frontal region narrow and very little arched. Palate broad and zygomae widely expanded. Diastemata separating canine from I^3 and P^2 very

short and lower anterior cheek teeth crowded. Molars distinctly larger and slightly more brachydont than in *T. grangeri*.

Discussion.—The type of *T. hillsii* was collected about 1885 by R. C. Hills and J. Milligan in the upper Huerfano beds of Colorado. The material was sent to Marsh for study in 1889, and in 1899 the collection was given by Hills to the National Museum. The crowns of the teeth are missing from the skull and jaws, but casts of P^3, M^2, and M^3 were obtained from impressions in the accompanying matrix. Associated limb fragments included the proximal and distal extremities of humeri and femora, proximal portions of ulnae and a tibia, the distal end of a radius and an ilium; representing two (or more) individuals of about the same size.

The lower jaw belonging to the skull of *T. hillsii* exhibits a shortness nearly comparable to that in the type of *T. castoridens,* with the masseteric fossa extending well forward and the posterior portion of M_3 arising from the base of the anterior face of the ascending ramus. However, the anterior extremity of the jaw is not so shallow and the teeth are noticeably larger. The skull is, in nearly all respects, shorter, shallower, and broader than U.S.N.M. No. 17886 referred to *T. hyracoides*.

The type of *T. hillsii* is much shallower and has a shorter rostrum than the type of *T. grangeri,* but the length of cranial portion of the skull from the last molar to the condyles is about equal. Nevertheless, the basicranial region, posterior to the pterygoids, is a little narrower and longer than in the *T. grangeri* skull. Notwithstanding the apparently significant differences noted between the two skulls from the Huerfano beds, differences which seem almost of generic magnitude, there is a curious resemblance of one to the other not shared with the Bridger skulls. The points of similarity include the widely expanded zygomae, the almost identical position and appearance of the lachrymal foramen, and the presence of prominent longitudinal swellings located dorsolaterally on each of the parietals, above the cerebral hemispheres. These resemblances may not be significant other than indicating a closer relationship than with the Bridger forms, but should their meaning be interpreted as indicating specific identity, then the marked differences in relative proportions throughout the skulls could only be accounted for by a surprising degree of individual variation, or again a dimorphism which one hesitates to advance with so few specimens at hand. It should be noted that in many groups of animals where sexual dimorphism is very marked, that the differences between the two forms are often in an order of magnitude that would likely be attributed to generic separation were dimorphism not known to exist.

MEASUREMENTS IN MILLIMETERS OF TYPE SPECIMEN OF *Trogosus hillsii*,
U.S.N.M. NO. 17157

Skull:

Distance from posterior margin of alveolus of I^3 to posterior surface
of occipital condyles...................................... 233.0
Distance from anterior margin of orbit at lachrymal foramen to poste-
rior surface of postglenoid process........................... 142.0*a*
Width across postorbital processes............................... 89.8
Width of cranium at postorbital constriction...................... 46.1
Width across zygomae, estimated................................ 180.0
Width of palate between second molars........................... 36.5
Depth of rostrum posterior to canines........................... 52.0*a*

Upper dentition:

P^3 to M^3, inclusive, at alveoli................................... 83.8
M^1 to M^3, inclusive, at alveoli................................... 52.5
P^4, anteroposterior diameter.................................... 15.2*a*
M^2, anteroposterior diameter, externally.......................... 23.0*a*
M^2, transverse diameter, anteriorly............................... 33.0*a*
M^3, anteroposterior diameter, perpendicular to anterior face......... 17.5*a*
M^3, transverse diameter, anteriorly............................... 35.0*a*

Lower jaw:

Length of symphysis... 68.0
Depth of jaw internally beneath point between M_2 and M_3.......... 52.0
Thickness of jaw beneath M_2................................... 23.0

Lower dentition:

Posterior margin of alveolus for I_2 to posterior margin of alveolus
for M_3 .... 114.0*a*
Posterior margin of alveolus for I_2 to anterior margin of alveolus
for P_3 .... 24.0*a*
P_3 to M_3, inclusive, at alveoli................................... 89.5
M_1 to M_3, inclusive, at alveoli................................... 66.0

a, approximate.

TILLODON, new genus [6]

Type.—*Tillotherium fodiens* Marsh.

Generic characters.—Skull elongate through both cranial and rostral
portions. Lachrymal foramen well forward of orbital rim. I_3 and

---

[6] It is a regrettable circumstance that *Tillotherium* cannot be defended as a
valid genus, as this name has become fixed in the literature and associated with
the only complete skull material hitherto described. Moreover, it was adopted
as representing the best known material for the family name Tillotheriidae.
There appears, nevertheless, reasonable evidence for recognizing a second genus
of tillodonts in the Bridger, based on the species *T. fodiens* Marsh, and in order
to preserve a part of the original name structure to which the ordinal name was
related, *Tillodon* is proposed.

apparently I_1 absent. Marked diastemata separating upper canine from I^3 and P^3. Lower canine and P_2 spaced and well separated from P_3. Upper and lower cheek teeth distinctly brachydont, with cusps of upper teeth obtuse, and outer walls of lower teeth very sloping or markedly convergent upward toward inner wall. Folds between external styles of upper cheek teeth compressed. Greatest width of cheek teeth across M^2.

TILLODON FODIENS (Marsh), 1875

Plates 13-16; text figures 19, 20, 24, 37 (part), and 38d, h, and i

Type.—Skull, lower jaws, and some fragmentary remains of other portions of the skeleton, Y.P.M. No. 11087.

Horizon and locality.—Bridger B, Millersville, Bridger Basin, Uinta County, Wyo.
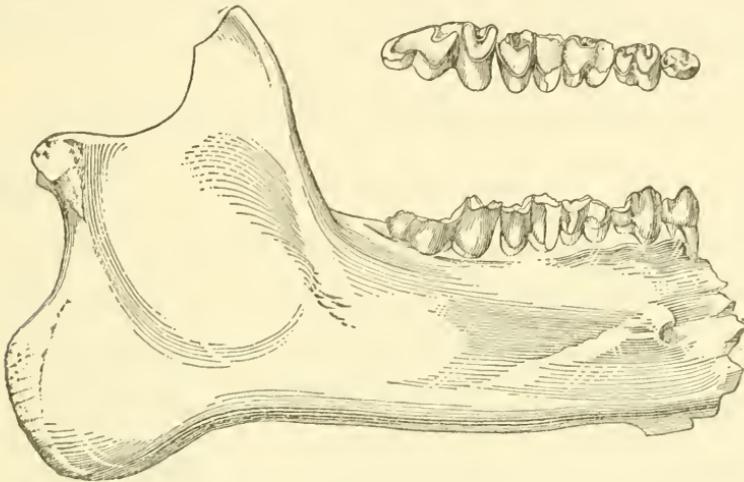
FIG. 19.—Cf. *Tillodon fodiens* (Marsh), new genus: Right ramus of mandible (U.S.N.M. No. 18164), occlusal and lateral views, $\times \frac{2}{3}$. Bridger (B) middle Eocene, Wyoming.

Specific characters.—Skull massive and elongate, broad through frontals and rostrum. Basicranial area broad and elongate. Lower jaws thick and deep. Teeth moderately large. Other specific characters not distinguished from generic.

Discussion.—The type of *Tillodon fodiens* includes the first complete skull and jaws found, and is the first material to have given an adequate conception of the tillodonts. It demonstrated the relationship between the types of teeth seen in the skull and jaws, the two having never before been found associated.

A lower jaw (fig. 19), U.S.N.M. No. 18164, with rather large, well-preserved teeth from P_3-M_3, is referred to this species. The specimen

was found by the writer in beds considered to be low in Bridger B, a little over 2 miles south of Church Buttes and not far from Black's Fork. The anterior extremity of the jaw, forward of P_3, is missing, but the preserved portion is very deep and elongate and the posterior termination of the symphysis is well forward. The teeth are very broad at the base, but markedly convergent or tapering upward. The specimen compares favorably with the type except in being less thickened transversely beneath the cheek teeth and having a little longer tooth row.

Some associated and relatively unworn upper teeth in the National Museum collection, No. 17158, including second and third incisors and P^3-M^1, are referred to *T. fodiens*. These teeth were found by the writer in 1941 about 24 miles southeast of Granger, in beds regarded as well up in Bridger B. They are of a size comparable to those in the type, and M^1 illustrates particularly well the highly brachydont character attributed to *Tillodon fodiens* molars.

MEASUREMENTS IN MILLIMETERS OF *Tillodon fodiens* SPECIMENS

	Y.P.M. No. 11087
Skull :	Type
Length from posterior margin of alveolus for I^2 to posterior surface of condyles	310.0*a*
Distance from posterior margin of alveolus for I^2 to posterior surface of postglenoid process..	288.0*a*
Distance from posterior margin of alveolus for I^2 to posterior margin of palate at narial opening....................................	170.0*a*
Distance from posterior margin of alveolus for I^2 to anterior margin of orbital rim at lachrymal foramen...........................	120.0*a*
Distance from anterior margin of orbital rim at lachrymal foramen to posterior surface of postglenoid process.......................	170.0*a*
Length of nasals...	140.0*a*
Width of rostrum above canines..................................	80.0*a*
Width across postorbital processes...............................	130.0*a*
Width of cranium at postorbital constriction......................	70.0*a*
Width of palate between second molars............................	51.0
Depth of rostrum posterior to canines............................	58.0*a*

	U.S.N.M. No. 17158	
Upper dentition :		
Posterior margin of alveolus for I^2 to posterior margin of M^3.................................	...	160.0*a*
Distance between I^2 and P^2 at alveoli..............	...	61.0*a*
P^3 to M^3, inclusive, at alveoli.....................	...	86.5
M^1 to M^3, inclusive, at alveoli.....................	...	58.5
I^2, greatest diameter.............................	21.5	...

	U.S.N.M. No. 17158	Y.P.M. No. 11087
I^3, greatest diameter.............................	13.5	...
P^3, anteroposterior diameter, externally at occlusal surface	...	16.8
P^3, transverse diameter, perpendicular to outer wall.	17.0a	17.0a
P^4, anteroposterior diameter, externally...........	15.0	14.0
P^4, transverse diameter............................	23.5	24.5
M^1, anteroposterior diameter, externally..........	21.3	18.0
M^1, transverse diameter, anteriorly................	31.5	39.3
M^2, anteroposterior diameter, externally..........	...	23.0
M^2, transverse diameter, anteriorly................	...	35.5
M^3, anteroposterior diameter, perpendicular to anterior face	...	18.2
M^3, transverse diameter, anteriorly................	...	34.5

	U.S.N.M. No. 18164	
Lower jaw:		
Length from posterior margin of alveolus for I^2 to posterior surface of condyle..................	...	248.0
Length of symphysis.............................	...	91.0
Depth of jaw internally beneath a point between M_2 and M_3	63.5	66.0
Distance from top of coronoid process to bottom of angle	165.0a	...
Thickness of jaw beneath M_2.....................	24.5	28.0

Lower dentition:		
Posterior margin of alveolus for I_2 to posterior margin of M_3.............................	...	135.0a
Posterior margin of alveolus for I_2 to anterior margin of alveolus for P_3........................	...	38.0
P_3 to M_3, inclusive.............................	100.5	93.0a
M_1 to M_3, inclusive.............................	73.7	70.0
P_3, anteroposterior diameter......................	12.5	11.7
P_3, transverse diameter...........................	9.5	9.1
P_4, anteroposterior diameter......................	16.3	13.5
M_1, anteroposterior diameter at occlusal surface....	16.5	16.7
M_2, anteroposterior diameter at occlusal surface....	21.8	20.0
M_3, anteroposterior diameter......................	37.7	32.3

Other skeletal portions:		
Width of third cervical vertebra across transverse process	56.0a	...
Distance across postzygapophyses of third cervical vertebra	45.0a	...
Length of centrum of third cervical vertebra along upper surface	22.8	...
Greatest diameter of proximal extremity of humerus, perpendicular to axis of shaft.................	56.5	...

	U.S.N.M. No. 18164	Y.P.M. No. 11087
Transverse diameter of proximal extremity of humerus across tuberosities.....................	55.5	...
Greatest width of distal extremity of ulna..........	...	29.5
Greatest length of first metacarpal................	...	39.3
Greatest diameter of proximal extremity of first metacarpal	...	21.5
Greatest length of second metacarpal..............	...	46.8
Transverse width of proximal extremity of second metacarpal	...	15.4
Greatest width of proximal extremity of fibula......	...	30.8
Greatest length of calcaneum.....................	...	74.2
Transverse width dorsally of proximal extremity of third metatarsal	...	12.0
Transverse width dorsally of proximal extremity of fourth metatarsal	...	13.5

a, approximate.

THE TILLODONT SKELETON

SKULL

In a discussion of the tillodont skull one is limited largely to the end products, *Trogosus* and *Tillodon* of the middle Eocene, as the earlier form, *Esthonyx,* though known by more numerous remains, is actually far less well represented so far as quality or completeness of the material is concerned. The Wasatchian materials are for the most part more poorly preserved, often crushed, distorted, and have a mineral encrustation that can be satisfactorily removed with only the most painstaking preparation. Of the fragmentary skull portions known, other than maxillae, two fair, but exasperatingly incomplete specimens are known from the Wind River stage. A few, much-encrusted skull fragments, among the many dentitions, are included in lower Wasatchian or Gray Bull materials, and the Clark Fork has furnished only maxillae and lower jaws.

The tillodont skull possesses an archaic appearance, shared by many of the Eocene and Paleocene mammals, but is unusual in its modification of the rostral portion accompanying the tremendous enlargement of the second incisors. In its gross form the rostrum is elongate, somewhat tapering, slightly to markedly concave above, and anteriorly resembling that of a hedgehog on a much larger scale. The ventral surface is broad, particularly in the posterior portion, across the large, relatively brachydont molar teeth, and is moderately concave between the tooth rows. The frontal area is especially broad, and dorsally more or less inflated, giving the skull, particularly that of *T. grangeri* (pl.

6), a "high brow" appearance. The orbits are low and widely separated, and the zygomae well expanded. The postorbital processes are
weak but the temporal crests well defined, though less prominently in
the *T. hillsii* skull (pl. 9), forming the anterodorsal extent of the deep
temporal fossae. The sagittal crest, developed to varying amounts
anteriorly, has a pronounced saddle about midway of its length, over
the narrow brain case, and rises to considerable prominence posteriorly
as it joins the heavy lambdoidal crests. Ventrally, the pterygoids
project prominently and the basicranial area posterior to these is very
short and broad. The occipital area, as observed in *T. grangeri,* has
an outline that is almost semicircular, though slightly acute dorsally,
and viewed from the sides is nearly vertical in the lower part, but the
dorsal half curves backward toward the inion (pl. 6).

In greater detail, the rostrum of the tillodont skull exhibits a number
of features which should be brought out, in addition to the peculiar
dental specialization characterizing the order. Beginning with the dorsal surface, the nasals are very elongate, extending well back between
the frontals. Forward, the sides of the nasals are nearly parallel or
somewhat converging, but posteriorly these bones widen markedly,
with the greatest width between the maxillofrontal sutures. Posteriorly, the nasals may terminate in a broad V-shaped wedge between
the frontals, as in *T. fodiens* (pl. 13), or form a broad, nearly rectangular reentrant as in *T. grangeri* (pl. 5) or *T. hillsii* (pl. 9). The
skull referred to *T. hyracoides* (pl. 1) shows an intermediate form,
with a noticeable pit at the apex, probably due to an injury.

The premaxilla occupies an unusually large proportion of the lateral
and dorsolateral surface of the snout. In its surface expression, this
bone extends posteriorly to a point about even with a position intermediate between the infraorbital foramen and the orbit. The premaxillo-
maxillary suture extends from its posterior limit obliquely across the
face to a midposition between the third incisor and the canine, resulting in a surface distribution for the premaxilla which is approximated,
but not quite reached, in the living hedgehog, *Erinaceus.* Between I^3
and C the suture is deflected to the canine alveolus (not as shown in
Marsh's illustration, 1876, pl. 9) and then extends abruptly forward,
passing close to I^3, to the anterior palatine foramen. The premaxilla
is prominently flexed over the unerupted portion of I^2 which extends
through this bone and terminates posteriorly in the maxilla at a position
slightly above and inward from the anterior opening of the infraorbital
foramen. Anteriorly, the premaxillae join in a pair of backward-
directed wings, partially or completely separating the anterior palatine
foramina, and producing a wide palatal notch opening forward between

the large incisors. The anterior portion of the nasal cavity, as noted in the *T. hyracoides* skull, shows a nearly lemniscate outline in a vertical section, in which prominent ridges on the mesial walls of the premaxillae, presumably for attachment of the maxilloturbinals, partially constrict the nasal passage into upper and lower chambers. These may correspond to the middle and inferior meatuses of the nose. The superior meatuses are defined by the arcuate form of the inferior surface of the nasals as seen from in front. In the *T. hillsii* skull the nasal section observed is more posterior in position, showing a less pronounced horizontal stricture, and in which the outline of the section is somewhat more bell-shaped, with the nasal fossae partially separated by the sutural ridge of the maxillae, and possibly by a part of the vomer.

In a ventral aspect of the rostrum it has been observed that the maxillae widen very greatly from the position of P^2 backward; however, with the increase in size of the cheek teeth posteriorly, the effective width of the palate between the lingual margins of the teeth increases but little from the incisors back. The anterior margin of the maxillae and the anterior palatine foramina are far forward on the palatal surface, in a position median to the third incisors, almost as far forward as in *Erinaceus*.[7]

Weak posterior palatine foramina appear in the customary position at or near the suture between the maxillae and palatines, but a nonsymmetrical scattering of such foramina occur forward of this position, and a pair of much-better-developed foramina, with well-defined forward continuing grooves are to be found median to the third premolars in three of the skulls, and opposite the second premolars in *T. fodiens* (pl. 15).

The nasal wing of the maxilla makes but a short contact with the nasal bone and is excluded from participation in the anterior margin of the orbit by the lachrymal and jugal bones, except in the *T. hyracoides* skull where the edge of the maxilla forms a part of the rim. The anterior opening of the infraorbital canal is above a point between P^3 and P^4. Posteriorly its opening into the orbital fossa is very large and bounded above by the lachrymal and below by the orbital plate of the maxilla. The ascending plate of the palatine does not appear to take part in the foramen. The orbital plate of the maxilla is a broad shelflike structure of considerable extent, and a conspicuous feature of the tillodont skull when viewed from above and behind.

---

[7] In making comparisons with the European hedgehog, it should be borne in mind that the highly specialized incisors are probably not homologous in the two forms. This tooth is I^1 in the hedgehog.

The lachrymal bone is well developed and prominently exposed on the outer surface of the rostrum anterior to the orbital rim in all but the *T. hyracoides* (pl. 2) skull, and there the development is similar but the most prominent crest of the orbital margin has a more forward position. The lachrymal foramen in *T. fodiens* (pl. 14) is well forward and completely out of the orbital fossa. In the two Huerfano skulls the foramen is situated about midway fore and aft on the broad convexity of the orbital rim and surmounted by a distinct lachrymal process. In the *T. hyracoides* skull the foramen is located in a depressed portion of the rim, neither anterior nor completely posterior to it, but facing well outward.

The frontal segment of the skull is broadly expanded and markedly convex dorsally between the subdued but widely separated postorbital processes. The frontals are deeply notched anteriorly by an invasion of the nasals but their posterior margin or suture extends rather uniformly across the skull just posterior to forward extent of the sagittal crest in all the skulls except that of *T. grangeri*. In the latter the anterodorsal margins of the temporal fossae unite to form the sagittal crest on the adjacent portion of the parietal. The orbital and temporal portions of the lateral plate of the frontal are indistinctly divided but the temporal portion would appear to be much the larger, as a result of the marked surface extent of the lachrymal in the orbital fossa. The lower portion of the lateral plate is bounded posteriorly by the alisphenoid and above this by the parietal. Below, the lateral plate of the frontal is bounded by the orbitosphenoid, palatine, and possibly by a small segment of the orbital plate of the maxilla forward.

Posterior to the coronal suture the parietals are anteroposteriorly elongate to near the lambdoidal crest and envelope the sides of the brain case over its most constricted part, terminating below at the alisphenoid, and at the squamosal posteroventrally. The sagittal crest is relatively subdued anteriorly, concave in profile, and high and rugged posteriorly as it rises to join the lambdoidal crest at the inion. The parietals are deeply excavated posteriorly on either side of the sagittal crest, and with the adjacent squamosals here show several large asymmetrically placed vascular foramina (Edinger, 1933, p. 271).

The squamosal exhibits a semicircular or fan-shaped temporal portion and a sturdy zygomatic process. The latter arises from the posteroventral portion of the temporal plate and carries a broad glenoid surface for articulation of the lower jaw. The glenoid surface extends well out onto the zygoma and has its long axis anterolateral rather than strictly transverse. The rather prominent postglenoid process is limited to the posteromedial extent of the surface, although a prominence at

the posterolateral extremity of the broad lateral portion of the surface gives further support to the condyle of the jaw. About midway between the inner and outer extremities the glenoid surface may be somewhat constricted fore and aft. Outward and forward from the strong support to the glenoid surface the zygomatic process tapers rapidly and extends superior to the slender, less sturdy jugal.

The separate elements of the occiput cannot be clearly distinguished and the presence or absence of an interparietal cannot be determined, as coosification has obliterated sutures in those specimens having this portion preserved.

Although the cranial portion of the tillodont skull is moderately long and decidedly slender, the most striking characteristic in the ventral aspect, particularly in *Trogosus,* is the extremely short basicranial area posterior to the axis of jaw articulation. The outstanding lambdoidal crests in *Trogosus grangeri* extend downward, below their union with the superior crest of the zygomatic arches, to a prominent anteroposteriorly compressed process lateral to each of the condyles. In *Tillodon* this process is more bulbous. Its identity or composition is not certainly determined but it would appear to involve both the mastoid and exoccipitals and may well have a covering from the squamosal on its forward surface, forming the posterior wall of the audital canal, although this has not been clearly determined. The channel for the audital tube, between this process and the postglenoid process, is narrow but deeply impressed, with the postglenoid process close to the occipitomastoid process and almost as posterior in position as the occipital condyles.

The basioccipital in *Trogosus* is relatively short, though less so in *Tillodon,* and broad, but the proportions of the basisphenoid cannot be clearly determined in the material at hand. The alisphenoid is well developed and extends forward and upward occupying a significant portion of the lateral surface of the cranium. The orbitosphenoid is less distinctly outlined but appears to be restricted to a relatively small area anterior to the sphenoidal fissure. The ascending plate of the palatine also appears restricted forward to a slender wedge between frontal and maxilla. Posteriorly, the suture between the palatine and alisphenoid is indistinct. The pterygoids project prominently downward from the well-developed lamellae laterally bounding the posterior narial passage. The ventral aperture of the passage ends forward between the third molars. The posterior margin of the hamular process rises abruptly to join the crest of the pterygoid plate of the alisphenoid, which is slightly offset lateral to the pterygoid. The crest then con-

tinues backward, upward, and then outward to the squamosal where, subdued, it reaches the inner margin of the glenoid surface.

The foramina of the basal portion of the cranium are decidedly more simple than in most modern mammals. Considerably posterior to the infraorbital canal, within the ascending plate of the palatine, and completely behind the orbital plate of the maxilla is the large posterior opening of the palatine foramen, including also the sphenopalatine foramen as indicated by the partition evident in the *Trogosus hyracoides* skull. The large sphenoidal fissure is deeply recessed below the more constricted portion of the cranium and is apparently the common aperture for the second, third, fourth, and sixth nerves, as well as both the first and second divisions of the fifth or trigeminal. There is no foramen rotundum and the optic foramen does not appear to be separate externally, although Marsh (1876), in discussing the endocranial cast of *T. fodiens* noted that, "the exit for the optic nerve is quite large." If the optic foramen is separate from the sphenoidal fissure internally, as the cast surely indicates, they evidently became confluent at the external aperture as shown by the absence of a separate optic foramen, externally, in the *T. grangeri* specimen. There is also evidence, in a broken section through this part of the skull of *T. hillsii,* of a separation posteriorly of the optic foramen, if these elements are correctly identified. A small foramen well forward of the sphenoidal fissure and somewhat above the posterior palatine foramen, which earlier I tentatively regarded as for the optic nerve, so far as I can determine is actually located at the suture between the frontal and orbitosphenoid, hence it is in all probability the ethmoidal foramen. In addition to the above-enumerated nerves, the opening of the sphenoidal fissure apparently also transmitted the external carotid. The presence of an alisphenoid canal is clearly evident in the *Trogosus hyracoides* and *Tillodon fodiens* skulls, less so in the *Trogosus grangeri* skull. In the type of *T. fodiens* the covering of the canal has been destroyed so that the smooth channel can be followed from its separation from the sphenoidal fissure to a low saddlelike separation from the foramen ovale. The foramen ovale is of good size and normal in position immediately above and lateral to the outward sweeping crest of the alisphenoid, but well separated from the glenoid articular surface.

In the absence of an osseous bulla the basicranial foramina in the auditory region are uncovered ventrally and for the most part enter the cranial cavity anterior and posterior to the petrosal through or near the open positions of the foramen lacerum medium and foramen lacerum posterius. The internal carotid entered the skull along a broad,

well-marked sulcus between the basisphenoid and the pterygoid plate of the alisphenoid, then through the aperture anterior to the petrosal. Lateral to this, and extending upward from the medial margin of the glenoid surface, is an open sulcus on the squamosal apparently for the venous system which would exit through the postglenoid foramen. This canal becomes covered anterior to the petrosal, where it separates from the opening for the internal carotid and enters the squamosal. Posterior to the petrosal is a large, posteriorly well-rounded aperture, the position of the foramen lacerum posterius, for the ninth, tenth, and eleventh nerves. Lateral to this the bone, presumably the mastoid, is notched, evidently for the facial nerve which would enter the periotic immediately above and anterolateral to the posterior lacerate foramen. Posteromedial to the posterior lacerate foramen, and about midway to the condyle, is a large, circular hypoglossal or condylar foramen.

The petrosal or petrous portion of the periotic, an element of very considerable interest in mammalian anatomy, is unfortunately missing or badly damaged in the four skulls at hand, so that little other than its small size and anteromedial elongation can be ascertained.

<center>ENDOCRANIAL CAST</center>

The endocranial cast of *Tillodon fodiens* made for Marsh appears to be rather poorly prepared, and Marsh's illustration (1876, fig. 1) of it is much reduced and rather generalized. It was figured in greater detail by Edinger (1929, fig. 119b, c), whose drawings are here reproduced (fig. 20a, c) with the addition of a ventral view (fig. 20b). Marsh's description (p. 250) of the cast is very brief, consisting essentially of a statement of relative development of the cerebellum, cerebrum, and olfactory lobes, and the relative size of the whole. Edinger's discussion (pp. 148-149) is brief but with a number of

<center>EXPLANATION OF FIGURE 20</center>

1. Olfactory lobes (incomplete).
2. Commissure of II or optic nerve.
3. Contents of sphenoidal fissure.
4. Pyriform lobe?
5. Cerebrum.
6. Position of hypophysis.
7. Third branch of V or trigeminal nerve.
8. Pons?
9. Position of median lacerate foramen.
10. Commissure of VII and VIII or facial and auditory nerves.
11. Fossa for petrosal.
12. Flocculus?
13. Crest of cerebellum.
14. Position of posterior lacerate foramen.
15. Medulla oblongata.
16. Commissure of XII or hypoglossal nerve.
17. Position of venus canal.
18. Foramen magnum.
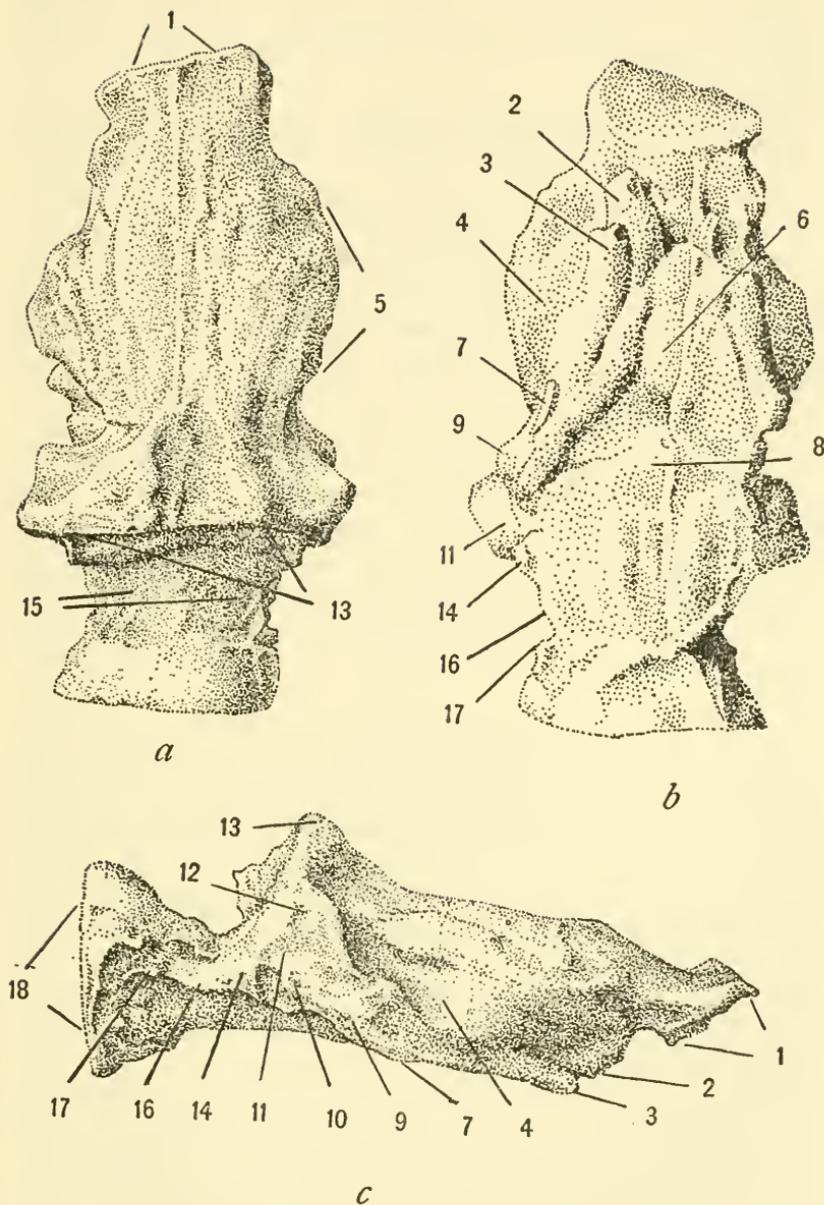
Fig. 20.—*Tillodon fodiens* (Marsh), new genus: Endocranial cast (Y.P.M. No. 11087), from type specimen; *a,* dorsal view; *b,* ventral view; *c,* right lateral view; approximately $\times \frac{4}{5}$. (*a* and *c* after Edinger, 1929; *b,* drawn by Mrs. Sally Lee.) For explanation see opposite page.

pertinent comments regarding its form. She was, however, handi-
capped in her discussion by not having the skull at hand. The form
is there regarded as insectivore, and comparison is made with the
hedgehog.

The cast, extrapolating for the probable size of the olfactory lobes,
is about 30 to 33 percent of the length of the skull. The rhinencepha-
lon is incompletely represented, although Marsh has shown the olfac-
tory lobes in his drawing. The skull was broken and somewhat re-
stored at this point so that it is likely that the form of the lobes was
not preserved. As noted by Edinger, the cerebrum is slender and flat-
tened; however, the latter should not be too emphasized as the cranial
portion of the skull has been somewhat flattened by crushing, most
noticeably on the left side. The sculpturing on the dorsal surface of
the cerebral portion was noted to be indistinct, and is evidently compli-
cated by marks of the preparator's tools, as well as by crushing. Such
sulci and gyri as may have existed are obscured; moreover, it is more
than likely that this group was lissencephalic. Fissura on the left
side in the dorsal view tempt interpretation as the sylvian sulcus and
the rhinal fissure, but this is the more-crushed side, and on the right
the fissura rhinalis may be indicated lower, beneath(?) the widest
point, with the pyriform lobe visible only in the lateral and ventral
views.

The cerebellum is noticeably shortened anteroposteriorly, but, as
noted by both Marsh and Edinger, it is high and wide, more so than
the cerebrum. It does not exhibit a median lobe or vermis but is pe-
culiarly depressed medially, immediately anterior to the transverse
crest. There is no indication on the cast, as noted by Marsh, of a
tentorial crest (of the skull), concomitantly the mesencephalon is not
exposed dorsally. However, the cerebrum and cerebellum are sepa-
rated laterally by a deep invagination anterior to the flocculus.

The medulla oblongata is broad and somewhat flattened, in part
through crushing. Much of the dorsoventral expansion of the cast
shown posteriorly is outside the foramen magnum.

Detailed features in the lateral view, concealed from above by a
large lobe of the widely expanded crest of the cerebellum, apparently
the flocculus, include a fossa for the petrosal and a median swell or
commissure for the seventh and eighth or facial and auditory nerves,
with protuberances representing the dorsomedial openings of the
median and posterior lacerate foramina, ventral to the fore and aft
extremities of the fossa. Forward, the inferior profile of the cast
shows approximately the position at which the nerves carried by the
sphenoidal fissure leave the cranium, and the separate, large, and

closely adjacent commissure of the optic nerve. Posteriorly, on the lateral margin of the medulla oblongata, the position at which the hypoglossal emerges is indistinct, as the foramen had not been prepared prior to casting. This is followed by an incomplete lateral protuberance near the posterior margin of the cast that is the filling of an opening of a venous canal in the occipital just within the foramen magnum.

In the ventral view, in addition to the forward positions of the representation of the optic nerve and the contents of the sphenoidal fissure, there is beneath a position just posterior to the midpoint of the cerebrum a subdued but elongate-oval prominence interpreted as the position of the hypophysis. Posterior to this a depression is followed by a somewhat irregular, wide, raised area, presumably the pons, just ahead of the anteroposteriorly elongate lobes of the medulla oblongata. On the right side (left of the illustration), anteroventral to the filling of the internal opening of the foramen lacerum medium, is a protuberance representing the commissure of the third branch of the trigeminal. Also in the lateral view, the indication of the hypoglossal and the vein leaving the exoccipital can be seen posterior to the foramen lacerum posterius, on the lateral margin of the right side of the medulla oblongata.

MANDIBLE

In a description of the tillodont lower jaw, unlike the skull, there is available for study much *Esthonyx* material, in addition to the few, though better-preserved, *Trogosus* and *Tillodon* specimens. The principal change in outline of the jaw that has taken place between *Esthonyx* and *Trogosus* has been a marked deepening of the ramus beneath the posterior premolars and first molar, so that the inferior border is more nearly parallel to the occlusal surface of the tooth row as far forward as P_3. In the much smaller *Esthonyx* (fig. 2a), the inferior margin converges rapidly with the tooth row from a point beneath M_3 to the incisors. The anterior cheek teeth are relatively much reduced in *Trogosus* and *Tillodon,* and the depth of the jaw falls away rapidly anterior to P_3 (pl. 2).

The symphysis of the jaws in both the lower and middle Eocene forms is strong and elongate. In *Esthonyx* (fig. 2b) this extends posteriorly from between the incisors, and with increasing depth, to a position between and below about the contact of the third and fourth premolars. In the middle Eocene forms (pls. 4, 8, 12, and 16), the symphysis extends back to a point beneath M_1 and in some instances

almost or quite to below the anterior margin of M_2, accommodating the basal portion of the enlarged incisors. It is interesting to note that, in this respect, the Bridger tillodont jaws appear most advanced in that they are fused farther back than those from the Huerfano beds. Likewise, the *Esthonyx* material from the Clark Fork is least advanced and the two rami may not always be well fused.

The mental foramina on the anterior portion of the outer surface of the jaw in both the esthonychinae and trogosinae are remarkably variable and may consist of from one large to four or five smaller openings of irregular arrangement, often differing on the two rami of the same individual. When more than one opening is seen, these may be in part above one another or scattered from beneath P_2 to P_4. When single or closely grouped, the usual position is nearly under P_3.

The coronoid, condylar, and angular portions of the *Esthonyx* jaws are poorly represented and for the most part no significant details can be obtained. There is, however, a remarkable pair of lower jaws (fig. 21) of an unusually large esthonychid in the Princeton collections from the Gray Bull horizon showing most of the angle, the condyle, and part of the coronoid process. The anterior portion of the masseteric fossa is observed in many specimens and this depression is seen to be well defined in the Gray Bull material, with a prominent crest anterodorsal to the fossa. The anterior margin of the fossa is rather indistinct in *E. grangeri,* whereas, in the middle Eocene material the fossa is deeply excavated and the marginal crest high and rugged. These jaws show evidence of powerful muscles having insertions in the area of the masseteric fossa, particularly the *masseter lateralis,* with its well-defined attachment area for the posterior branch, and the prominent muscle scar around the broadly expanded angle for the anterior branch. The evidence for a strongly developed *masseter lateralis anterius* is to be correlated with the obvious development of gnawing incisors.

The Princeton specimen (No. 14727), particularly large for *E. bisulcatus* and possibly a late survival of *E. grangeri* or *E. latidens,* shows a truly tremendous posterior ramal portion. The ridge at the forward margin of the area for insertion of the *masseter lateralis anterius* is directed forward and upward from near the lower posterior margin of the angle and is remarkably high and rugged. The development of this crest exceeds considerably that observed in middle Eocene materials indicating an exceedingly strong development of the anterior branch of the *masseter lateralis,* associated, nevertheless, with the rooted, esthonychine type, rather than the persistent growing trogosine type of incisors.

The ascending ramus of the middle Eocene jaws shows some small differences between *Trogosus* and *Tillodon*. In *Tillodon* the masseteric fossa extends farther upward, well into the coronoid, and the notch between the coronoid process and the condyle is more widely open. The coronoid appears more truncate and does not curve backward so noticeably as in *Trogosus*. In *Esthonyx,* as evidenced by the Princeton specimen, the condyle is not widely separated from the coronoid, the posterior margin of the latter rising from immediately in front of the condyle, if reliance is to be placed on this specimen as it has been restored.

The articular portion of the condyle as observed in the Trogosinae and in the Princeton *Esthonyx* specimen is largely confined to the
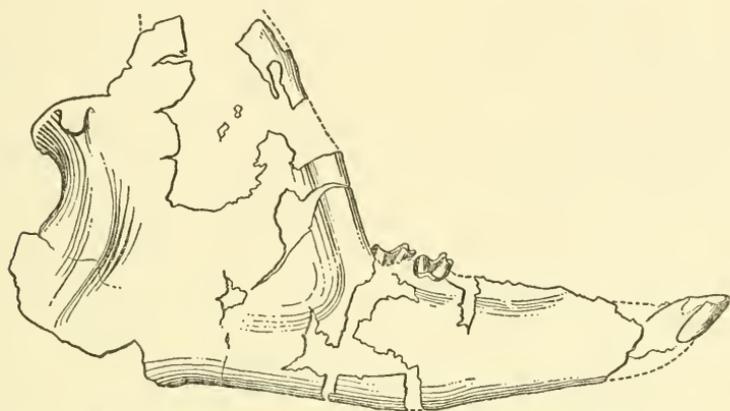
FIG. 21.—*Esthonyx,* species: Right ramus of mandible (P.U. No. 14727), lateral view, × ½. Gray Bull lower Eocene, Wyoming.

dorsal surface, suggesting considerable fore and aft motion of the jaw as in gnawing and grinding. This is further reflected in the glenoid surface of the squamosal, which, though quite unlike that in rodents, permits considerable forward motion of the jaw, limited backward, however, by a postglenoid process.

A significant detail observed on the inner face of the lower jaws of *Trogosus* and *Tillodon* is the rather conspicuous sulcus mylohyoideus for the mylohyoid artery and nerve. It was double or consisting of parallel grooves in most specimens examined, extending downward and forward from adjacent to the opening of the mandibular or inferior dental foramen, for a little over 4 cms., to an indefinite point just above the position on the lower margin of the jaw determined by the anterior extent of the angle, about even with the anterior margin of the scar determined by insertion of the *pterygoid internus.* The

sulcus mylohyoideus is stated by Zittel to be especially characteristic of the marsupials; however, it is not uncommon in certain placental groups. It was not definable in carnivores examined, but can be detected in various perissodactyls and artiodactyls, and is prominent in man.

<div style="text-align:center">DENTITION</div>

Characteristics of the teeth in tillodonts are briefly outlined, as defining the family, in the systematic portion of this paper. The following description is a more detailed study and includes a discussion of the evolution of the teeth within the order.

Both lower and middle Eocene forms have their upper incisors reduced to two, with the loss, apparently, of I^1. The second incisor is the most strikingly modified of any of the tillodont teeth. In *Esthonyx* (fig. 2a) this tooth is large, but little more so than I^3. The root is long, only slightly curved and without enamel. Its cross section at about the alveolar opening is a distorted oval, with the posteromedial expansion effecting an approach toward triangular. The crown portion is nearly triangular, scalpriform at the apex and apparently covered with enamel in the unworn state. The posteromedial and posteroexternal angles of the crown are compressed and in early wear the posterior surface shows a slight longitudinal bulge. With wear the enamel is first removed from this bulge and later it is removed, rodentlike, from the entire posterior surface. Enamel is preserved around the medial surface and higher on the broader anterolateral surface, but in advanced wear it is removed part way up the anterior angle, broadening, but somewhat blunting, the cutting edge.

In *Trogosus* I^2 has become relatively much enlarged (see plates). It is long, sharply curved, and evidently grew from persistent pulp. In cross section, which increased markedly in size with growth and eruption during earlier life, it was more decidedly triangular than the root portion in *Esthonyx*. Its anterolateral surface is broadly convex and the shorter medial or anteromedial surface is nearly flat to slightly concave or broadly grooved. The posterointernal and posteroexternal angles are rounded and the intervening posterior surface is rather distinctly concave, more so than the medial surface. Enamel was developed around the anterior portion of the tooth, extending much farther posteriorly on the anterolateral surface than on the medial. As in *Esthonyx,* wear is rodentlike on the posterior surface with a transversely convex cutting edge of enamel.

The third upper incisor has not been observed complete in a premaxilla of *Esthonyx,* unless the loose teeth shown in this position in

figure 8 are actually incisors and not from the canine alveoli, but broken portions and alveoli of other specimens show I³ to have been only a little smaller than I². It is a little shorter and more nearly oval in cross section at the alveolar margin. The basal portion of the crown shows a compressed anteromedial and posterior longitudinal margin with a broad and strong bulge between the margins posteromedially. In *Trogosus* also, I³ is relatively large. In the skull of *T. hyracoides* (pls. 2 and 3) it is seen to be strongly curved and probably rooted. It is nearly oval in cross section and enamel covers only the lateral and anterior wall in the stage of wear observed. Wear has truncated the tooth bluntly with the bevel rising forward, resulting from articulation forward with I₂.

The canines in the tillodonts, unlike the second incisors, show progressive reduction. The upper canine in Gray Bull *Esthonyx* has a diameter not greatly different in size from that of I² but is scarcely caniniform in the conventional sense and has a crown rather like that of the somewhat smaller P², single-cusped and posteriorly broad. It does, however, have a single heavy root. In Lost Cabin *Esthonyx* the upper canine is still relatively large, much larger than P², but has lost in relative importance to the incisors. In *Trogosus* (pl. 3) the canine has a simple, transversely compressed but blunt conical crown, scarcely greater in diameter than the root, and nearly as small as P².

P² in *Esthonyx* (figs. 7 and 8) is a simple, single-cusped, two-rooted tooth, transversely compressed along the anterior margin, but less so posteriorly. In *Trogosus* (pl. 3) the tooth is small and peglike with a somewhat flattened, blunt conical crown, about the same diameter as its single root.

In contrast with P², the third and fourth upper premolars are large and functional teeth in the tillodonts. Both of these have prominent talons, which in P³ in *Esthonyx* (figs. 7 and 8) is anteroposteriorly narrow, but has a well-developed deuterocone. In P⁴ the deuterocone extends prominent crests anteroexternally and posteroexternally toward the external angles of the tooth and may in some individuals, particularly in the Lost Cabin stage, exhibit a small tetartocone or hypocone at the internal extremity of the posterior cingulum. The primary cusp of P³ is single, but in P⁴ a separate tritocone is exhibited. The parastyle on P³ is generally but weakly developed and not expanded buccally as in P⁴; however, the metastyle is similarly developed in the two teeth. P³ lacks a distinct external cingulum on the forward part of the tooth. In *Trogosus* (pl. 3) P³ and P⁴ are surprisingly like those in *Esthonyx,* except for their much greater size; however, the deuterocone of both P³ and P⁴ may be relatively longer

anteroposteriorly and more crested, and in P^4 the tritocone and tetartocone perhaps relatively weaker, although the external styles appear to be more powerfully developed.

The upper molars in tillodonts (figs. 7 and 8; pls. 3, 7, 11, and 15) are characterized by widely sweeping hypoconal crests, which in some material of *Esthonyx* (figs. 10 and 11) appears to be more nearly a cusp. In *Trogosus* the hypoconal crest may sweep higher on the protocone. The basin between the three primary cusps in *Esthonyx* is relatively unadorned, but in *Trogosus* this basin is characterized by a distinctive enamel loop, having in the unworn type tooth of *T. latidens* (fig. 16) somewhat the form of a question mark with its lower point rising as a low ridge medially on the external wall of the protocone. In the external half of the molars the paracone and metacone in Gray Bull *Esthonyx* are moderately prominent, although they appear to be transversely compressed in some material, and exhibit, lateral to each, a wide shelflike cingulum rising to an outstanding style at the anterior and posterior angles of the tooth. The parastyle, the more prominent of the two, increases somewhat from M^1 to M^3, whereas the metastyle crest is, of course, together with the hypocone, very greatly reduced on M^3. In *Trogosus* the paracone and metacone show a rather heavier lateral buttress extending to the base at the expense of the cingulum which has lost its shelflike appearance. The anterointernal cingulum of *Esthonyx* is also much reduced or lost in *Trogosus*. The metastyle and particularly the parastyle are well developed in *Trogosus*.

In the lower jaw the incisors are three in number, except in *Tillodon*, and in *Esthonyx* I_1 is only a little smaller than I_2. The first two lower incisors in *Esthonyx* (fig. 2a, b) are long and but gently curved. Their root portion in cross section is nearly oval with the long axis fore and aft. The posterior portion is more compressed transversely, and enamel extends well down on the forward surface of the root. The crown of I_1 has not been observed, but that of I_2 is much like that of I^2 except that it is smaller, narrower, and the posterior part is compressed transversely and posteriorly extended.

In *Trogosus* the discrepancy in size between I_1 and I_2 is tremendous. I_1 is scarcely or but little larger than in *Esthonyx* whereas I_2 has become several times larger than in the earlier genus. I_1 has become very elongate, however, and, like I_2, may have had persistent growth. In cross section it appears to have been a transversely flattened oval with a possible increase in the anteroposterior diameter in depth. The cross section of I_2 has changed from a near oval in *Esthonyx,* transversely attenuated posteriorly, to an almost lemniscate outline in some individ-

uals of *Trogosus,* with the anterior lobe the larger. Enamel is limited to the anterior portion in both I_1 and I_2, and in I_2 it extends somewhat farther back on the lateral than on the medial wall. The diameter of the cross section of the *Trogosus* I_2 increased distinctly with growth and eruption in earlier life, although this process seems to have reversed in more aged individuals with some shrinkage in diameter, a more rounded lateral wall, and disappearance of enamel, to judge by isolated incisors from Huerfano "B" beds. This might appear to discredit growth from persistent pulp; however, there is no doubt but that the incisor was in a process of growth during earlier wear, probably throughout life, and that at no time was the incisor complete.

I_3 is very small in both *Esthonyx* (fig. 2a, b) and *Trogosus* (pls. 2 and 4), and apparently lost in *Tillodon* (pl. 16). In the material of *Esthonyx* in which this tooth is preserved, the crown is much less elongate longitudinally and, in the stage of wear presented, enamel is shown only as a small patch on the anterolateral wall, forming the cutting edge. In *Trogosus* this tooth has become peglike with a slightly oblong cross section. In the particular specimen in which this tooth is observed, enamel was preserved around the lateral and anterior surface, apparently in a stage of wear in which only the basal portion of the crown remains.

The lower canine in *Esthonyx* (fig. 2a) is even larger and would appear to be functionally more important than I_2. The crown portion of this tooth is strikingly like that of I_2 in form, but the root portion is not compressed posteriorly. It is rather distinctly procumbent, almost as much so as the incisors, and closely follows the reduced I_3. Its functional significance is almost lost in *Trogosus* (pls. 2 and 4) and it has become almost peglike, little larger than I_3, to which it is closely appressed, and with it decidedly procumbent. In the specimen in which this tooth is preserved, wear has reduced the crown so that the enamel is not complete around the medial and posterior surface.

P_2 is simple, but more nearly oval in outline in *Esthonyx,* and in all instances observed the tooth is set with its anterior root noticeably external to the posterior, with its long diameter often about 45° from the alignment of the cheek-tooth series. The second lower premolar is not in place in any of the *Trogosus* jaws at hand and it has not been recognized in loose teeth; however, it is clearly single-rooted and of relatively small size, as shown by its alveolus.

P_3 is relatively simple in *Esthonyx* (figs. 1, 2a, and 5) with a moderately high single-cusped anterior portion, but with a basined talonid. No evidence of a paraconid or metaconid was observed in any of the

material at hand, and in the talonid, which is variable in size, only the externally placed hypoconid is distinct on the crest which bounds it. P_4 (figs. 2a, 3, 5, and 9), however, is almost completely molariform. Its distinction from the molars lies in the relatively longer trigonid, with the paraconid widely separated from the metaconid, and the smaller talonid. It also lacks the metastylid characteristic of the molars. In *Trogosus* (pls. 2, 4, 6, and 8) these two premolars have become more globular in appearance, and in both the talonid is relatively much reduced. The trigonid of P_3 in some of the middle Eocene specimens may show evidence of a weak paraconid and metaconid, or, rather, somewhat compressed lingual ridges on the protoconid in these positions, and in P_4 the paraconid is relatively not so widely separated from the metaconid.

Characteristic of the tillodont lower molars (figs. 1-5, 9, 12, 14, 17-19; pls. 4, 7, and 16) is the U-shaped crested trigonid and talonid, in which the trigonid is more elevated, and in *Esthonyx* anteroposteriorly more compressed. The paraconid is lingual in position and the anterior and posterior transverse crests of the trigonid are nearly parallel. The metastylid part way down the posterior margin of the metaconid seems invariably present. The crest of the talonid is not joined directly with the metastylid in *Esthonyx* but originates below the posterior crest of the trigonid about midway on the posterior surface. The crest is continuous to the entoconid, with the hypoconid, hypoconulid, and entoconid distinct, but is separated by a deep notch from the metastylid posteriorly. In *Trogosus* the crest forward from the hypoconid originates closer to the metastylid and may appear to join it directly in some teeth with only a slight groove between, which, of course, would be obliterated by wear. Although most of the *Trogosus* teeth examined are rather worn, the individual cusps forming the crest of the talonid would appear to have lost much of their identity, except in M_3. In the last lower molar of both *Esthonyx* and *Trogosus* the talonid is distinctly bilobed, but the development of the last lobe or hypoconulid portion appears rather variable both as to its posterior extent and width. A peculiarity noted in the systematic description of the Huerfano "B" materials of *Trogosus* is the more complete division of the talonid basin of M_3 in specimens from that horizon. A feature also noted in a foregoing section, but characterizing the tillodonts as an order, is the discrepancy in the height of inner and outer walls of the lower molars, and perhaps to a lesser extent the upper molars. Viewed from the lingual side the lower molars and posterior lower premolars appear brachydont as well as cuspate, but externally they are strikingly hypsodont and columnar. This is least

noticeable in Paleocene and Sand Coulee materials, but is climacteric in the Bridger. Wear shows that these teeth must erupt with rotation along an axis parallel to the tooth row.

Very few specimens having milk teeth are known of *Esthonyx* and so far none has been observed of *Trogosus*. Deciduous premolars of *Esthonyx latidens* (fig. 11) were figured by Simpson (1937, fig. 4) and a few juvenile specimens of Gray Bull *E. bisulcatus* are extant. Dp^3 in the Gray Bull material has a talon rather like P^3, but the parastyle seems better developed with a slightly better-developed external cingulum, and the primary cusp is weakly twinned. Dp^4 is structurally much like M^1, except that it is relatively narrower transversely and in some specimens the hypoconal portion projects inward more at the base of the crown. In the lower series Dp_3 does not differ greatly from P_3, except for compressed ridges down the paraconid and metaconid section of the protoconid, observed in *E. grangeri*. The talonid portion of Dp_3 in *E. grangeri* cannot be observed, owing to hematite matrix. Dp_4 in *E. bisulcatus* as well as *E. grangeri* is seen to be very elongate both in the trigonid and talonid portions. The paraconid is well forward of the metaconid as in P_4, but the talonid basin is larger and more elongate as in M_1.

HYOID ARCH

Right and left portions of elements believed to be the stylohyal and epihyal (fig. 22) are included among the materials of the *Trogosus*
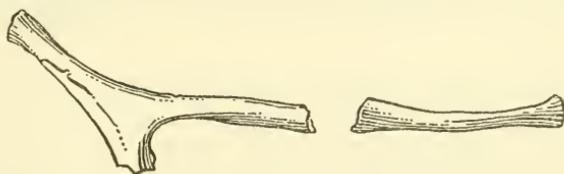
FIG. 22.—*Trogosus grangeri,* new species: Stylohyal and possibly epihyal (A.M. No. 17008), type specimen, outer view, $\times \frac{2}{3}$. Huerfano (B) middle Eocene, Colorado.

grangeri type. If properly identified and oriented the stylohyal exhibits a prominent bifurcation with a much flattened bladelike process extending downward, separating from the body or shaft well below the proximal extremity which would be joined by cartilaginous material to a small process adjacent to the notch for the facial nerve in the basicranium. The element thought to be the epihyal is elongate and only slightly flattened, but is otherwise without significant features.

VERTEBRAE

No complete series of tillodont vertebrae are known; however, the general features can be ascertained from segments of the column belonging to different individuals. The atlas, 6 dorsals, and 14 caudals are preserved in the skeletal remains composing the type of *Trogosus grangeri,* A.M. No. 17008. A third cervical is associated with a jaw, U.S.N.M. No. 18164, referred to *Tillodon fodiens* and the fourth cervical to first dorsal, inclusive, are in the material, U.S.N.M. No. 17886, belonging with the Bridger *Trogosus hyracoides* skull. Lumbars are represented only in *Esthonyx* material. There are, however, several fragmentary vertebrae, mostly centra, associated with the skull of *Tillodon fodiens,* Y.P.M. No. 11087.
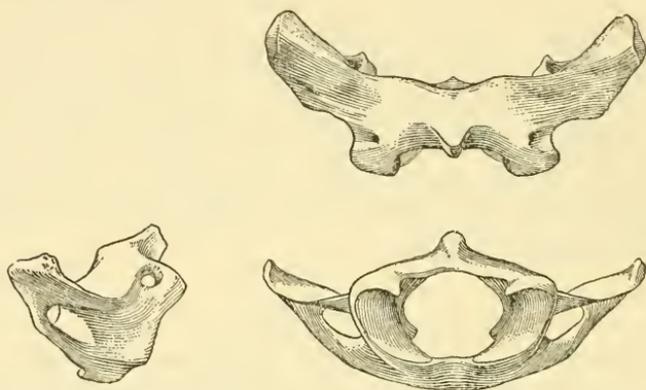
FIG. 23.—*Trogosus grangeri,* new species: Atlas vertebra (A.M. No. 17008), type specimen, dorsal, lateral, and anterior views, × ½. Huerfano (B) middle Eocene, Colorado.

The tillodont cervical vertebrae are characterized by their shortness and noticeable breadth. The processes are strong and the zygapophyses carry relatively large articular surfaces. The atlas (fig. 23) vertebra in *Trogosus grangeri* is remarkably short but exhibits narrow, widely extended transverse processes which sweep backward and upward. The transverse processes are penetrated fore and aft by a strikingly large vertebrarterial canal. The anterior surfaces for articulation with the condyles of the skull are deep and recurved above. Above and posterior to each of the surfaces for the condyles a moderate-size foramen for the first spinal nerve perforates the arch transversely. A rather pronounced process in the position of the spine is developed on the dorsal surface at its forward margin. The large posterior articular surfaces for the axis are gently concave and encroach medially upon the opening of the arch.

The superior surface of an incomplete atlas associated with *Esthonyx* material, A.M. No. 4276, was figured by Cope (1884a, pl. 24c, fig. 3). This atlas is anteroposteriorly shortened as in *Trogosus,* but the specimen is much damaged and the transverse processes are missing, so that detailed comparison is not feasible. It was noted, however, that the foramen for the first spinal nerve has its outer opening more posterior in position.

The axis vertebra is included among the materials, A.M. No. 17011, of *Trogosus* from the Huerfano. The vertebra is very short and its anterior surface shows a large odontoid process and articular surfaces for the atlas. The posterior surface of the centrum is incomplete but in an *Esthonyx* specimen, figured by Cope (1884a, pl. 24c, fig. 4), it
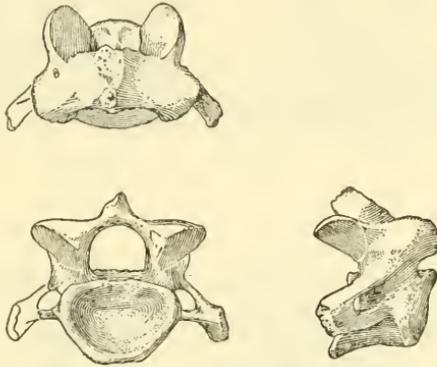
Fig. 24.—Cf. *Tillodon fodiens* (Marsh), new genus: Third cervical vertebra (U.S.N.M. No. 18164), dorsal, posterior, and lateral views, × ½. Bridger (B) middle Eocene, Wyoming.

it seen to have a marked upward and forward slope. The arch is very high in contrast with its shortness, and the superior margin of the spine apparently slopes sharply downward and forward. High on the posterior margin of the arch the large postzygapophyses face downward, outward, and somewhat posteriorly. The transverse processes directed backward and outward from immediately behind the surfaces for articulation with the atlas do not appear to be so well developed as in the atlas and third cervical vertebra (fig. 24). The vertebrarterial canal is obscured by matrix.

The remaining cervicals of *Trogosus,* however, have short, broad centra and sturdy arches. The transverse processes are narrow, backward sweeping and, except for the seventh, have good-sized vertebrarterial canals. The zygapophyses are widely expanded for the nearly circular articular surfaces.

The dorsal series in *Trogosus* is known by but six vertebrae (fig. 25). Four of these are marked as having been found in articulation. The centra are noticeably narrower than in the cervical series and become deeper and more elongate posteriorly. The arches exhibit spines moderately short and slender, which in the forward part of the series of four are directed strongly backward. Posteriorly the spines are shorter and expanded fore and aft. The articular surfaces of the zygapophyses are, of course, much smaller than in the cervical series, and in the fourth of the articulated four, the change from nearly horizontal
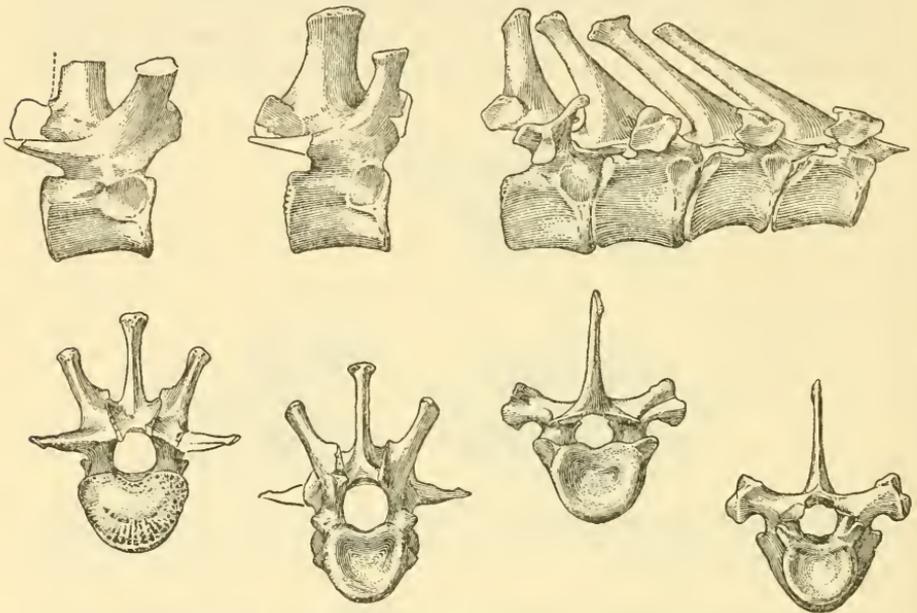
FIG. 25.—*Trogosus grangeri,* new species: Dorsal vertebrae (A.M. No. 17008), type specimen; above, lateral view; below, posterior and anterior views of second vertebra from left and second vertebra from right, respectively, of the series shown above; × ½. Huerfano (B) middle Eocene, Colorado.

to nearly vertical takes place. Also at this point the metapophyses and anapophyses appear slender and elongate, and this may well be the last vertebra to have an articular facet for the tubercle of the rib. The above transition in modern *Canis* and *Felis* is at about the tenth dorsal, suggesting that the four vertebrae preserved are well back in the series. Posteriorly in *Trogosus* the metapophyses and anapophyses are decidedly prominent, the metapophyses rising nearly as strongly as the spine.

Lumbar vertebrae of *Trogosus* are not known but those of *Esthonyx,* if correctly associated, show these vertebrae to be decidedly

elongate, and with the centra dorsoventrally somewhat flattened. The transverse processes are slender, flattened, and strike forward from the upper portion of the centrum. The anterior zygapophyses face medially and are strongly concave. The spine between them is transversely compressed and rises forward over about the anterior half of the length of the vertebra. The lower surface of the centrum is transversely compressed to form a slight keel, but without significant development of a hypapophysis.

A series of 14 caudal vertebrae (fig. 26), apparently in articulation and probably incomplete at both ends, belong to the *Trogosus grangeri* skeleton. These are broad and robust, showing that *Trogosus* had a long and heavy tail. Those preserved increase in length from the first
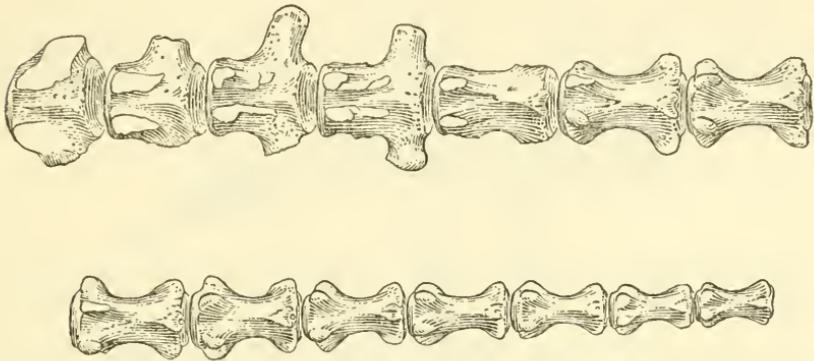
FIG. 26.—*Trogosus grangeri*, new species: Caudal vertebrae (A.M. No. 17008), type specimen, dorsal view, $\times \frac{1}{2}$. Huerfano (B) middle Eocene, Colorado.

to the sixth and then shorten again posteriorly. None shows the neural arch complete but it may have originally bridged the neural spine in the first three or four of those present. The first four or five show prominent transverse processes extending laterally from just below the midsection of the posterior portion of the centrum. Posteriorly they are much reduced and the anterior pair becomes equally important. The fifth of the series is the first to show a separate prominent process serially continuous with the pedicles for the postzygapophyses. This is in the form of an arch with a very small longitudinal foramen. In the tenth vertebra this foramen also becomes uncovered dorsally. On the under surface, beginning with about the third or fourth, a pair of anteriorly placed hypapophyses appear, and posteriorly become developed equivalent to the anterior transverse processes and metapophyses. No haemapophyses or chevron-bones were associated with the above described caudal vertebrae.

RIBS

A portion of the rib basket is included with the material belonging to the type of *Trogosus grangeri*. The series is not sufficiently complete to note detailed changes with position; however, the ribs are well rounded for the most part, becoming flattened only near the extremities. The tubercle and head are about equally developed and show but little difference in spacing through much of the series. The point at which articulation with the transverse process is lost cannot be determined. No sternal ribs are recognized in the collections nor are any portions of the sternum at hand.

CLAVICLE

The clavicle (fig. 27) belonging to *Trogosus grangeri* is elongate and only a little smaller in diameter than an average rib. The sternal extremity is expanded and markedly cupped for its union with the

FIG. 27.—*Trogosus grangeri*, new species: Left clavicle (A.M. No. 17008), type specimen, anterior view, × ⅔. Huerfano (B) middle Eocene, Colorado.

presternum. In its double-curved sweep toward the scapula the distal portion becomes flattened for a broad but not sharply defined contact with the acromion.

SCAPULA

The *Trogosus* scapula, as exemplified by *T. grangeri* (fig. 28), is very broad proximally, giving the bone a nearly quadrangular rather than triangular appearance, with the spine running diagonally from the anterosuperior angle to the posteroinferior portion. The prescapular fossa is thus broad near the glenoid extremity and becomes very narrow though deeply pocketed near the suprascapular border. Conversely, the postscapular fossa is very wide superiorly and narrow below with the glenoid border converging sharply with the spine. The spine itself rises very high with its crest deflected posteriorly in the lower part, presenting an increasingly broad lateral surface toward the acromion. The tip of the acromion projects downward and forward slightly beyond the glenoid cavity but is not bifurcate. The glenoid cavity is a nearly oval-shaped concavity, transversely somewhat restricted forward. The coracoid portion is set off medially from the

anterior extremity of the glenoid surface and, although fused to the scapula, it is separated from the glenoid surface rather distinctively by a deep notch or groove. The subscapular fossa shows no important
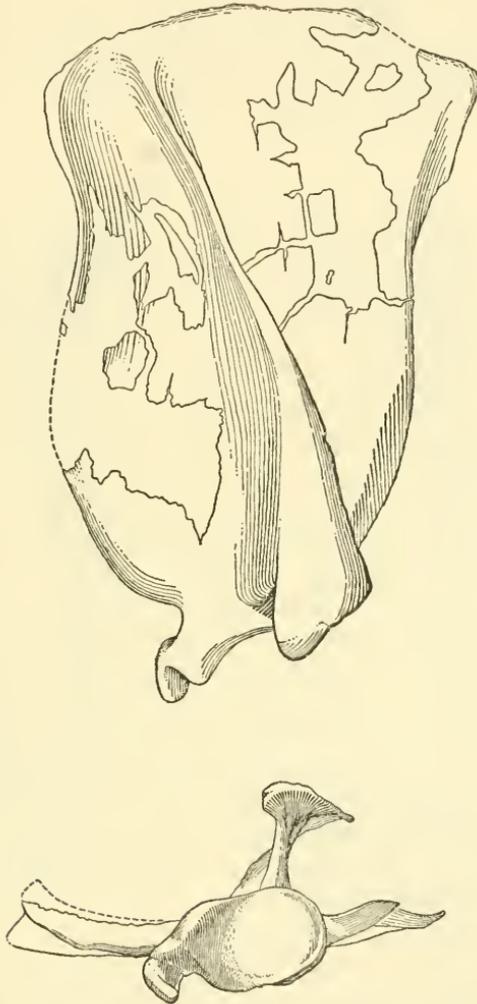

FIG. 28.—*Trogosus grangeri,* new species: Left scapula (A.M. No. 17008), type specimen, lateral and distal views, × ½. Huerfano (B) middle Eocene, Colorado.

details, other than a ridgelike extension downward on its surface of the superior portion of the posterior border, with a strong flange or flexure of the lower part of the posterior border, posterior to the ridge.

The scapula of *Trogosus* is rather unlike that of any other animal to which it might be compared. It does not particularly resemble any

carnivores with which it was compared, and is decidedly different from the scapula of *Stylinodon mirus*. The anterior border expands near the lower extremity somewhat as in *Phenacodus* but no other special resemblances were noted with Cope's figure (1884a, pl. 57c). Among the larger modern insectivores neither *Erinaceus* nor *Solenodon* shows an expansion of the lower part of the prescapular fossa and in these the postscapular border is approximately parallel to the spine. Also, the acromion is strongly bifurcate.

HUMERUS

Several incomplete humeri are known belonging to individuals of *Trogosus,* mostly from the Huerfano "B" horizon, and one of a Gray Bull *Esthonyx*. There is, however, a nearly complete humerus belonging with *Trogosus* material bearing A.M. No. 17011 (fig. 29) from the Huerfano. These have a distinctly insectivore-like appearance, rather like that in *Erinaceus* and *Solenodon*. This is most noticeable in the proximal extremity with the head set back more nearly in the line of the shaft than in, for example, the carnivores, and with the tuberosities closely contained. The lesser tuberosity is a broadly rounded protrusion for insertion of the *subscapularis* and projects but little beyond the anteromedial margin of the head. The greater tuberosity is large and prominent, extending very little if any above the head and not flaring forward as in so many carnivores. The greater tuberosity is somewhat as in *Erinaceus,* but with a better-developed bicipital groove and no aperture into the head from between the tuberosities. In *Solenodon* the anterior portion of the greater tuberosity curves inward markedly toward the lesser tuberosity. The outer and posterior surface of the greater tuberosity in *Trogosus* is markedly scarred, apparently for the *teres minor* which would originate on the prominent flange of the lower part of the posterior border of the scapula.

On the shaft of the humerus the deltoid ridge is very outstanding and projects distally below the middle of the bone. The proximal part of this ridge may be weak or subdued where it joins the greater tuberosity, as indicated in various fragmentary humeri of *Trogosus* and *Esthonyx,* but is noticeably outstanding at this point in the complete humerus belonging to A.M. No. 17011. Distally in the latter specimen it becomes very rugged in the vicinity of the insertion of the *deltoid*. The prominence of this abducting muscle is also attested to by the outstanding posterolateral margin of the spine and its acromion on the scapula where a portion of this muscle originates. The deltoid ridge
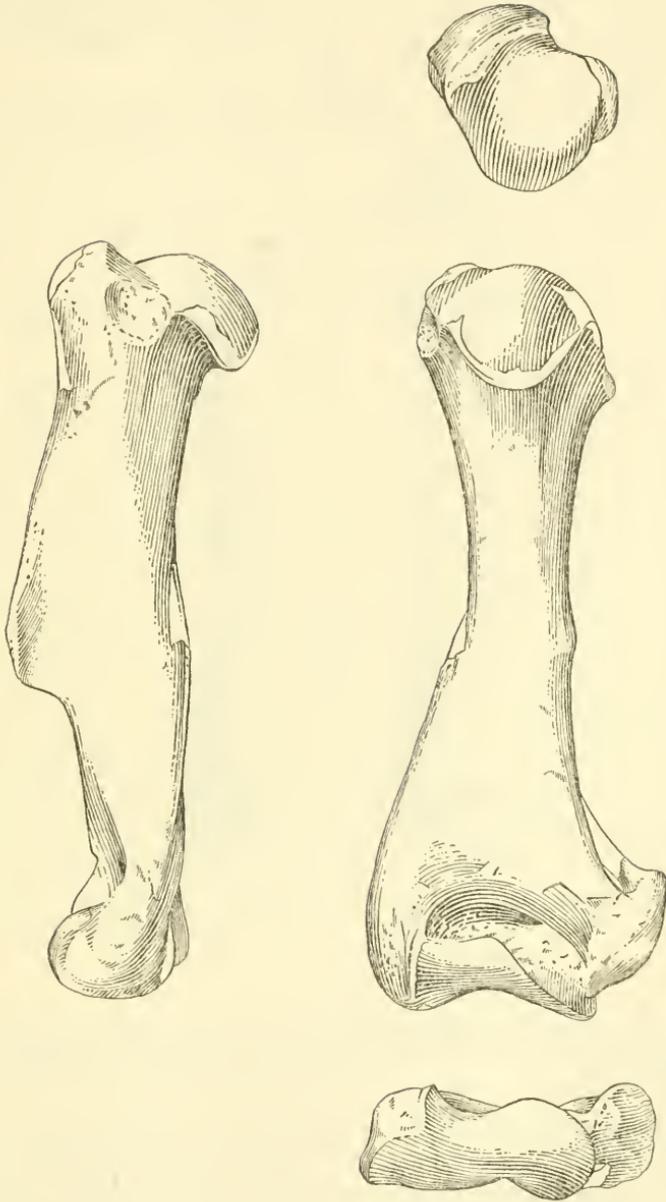
FIG. 29.—*Trogosus*, species: Left humerus (A.M. No. 17011, restored proximally from specimen associated with U.S.N.M. No. 17157), proximal, lateral, posterior, and distal views, × ½. Huerfano (B) middle Eocene, Colorado.

is comparatively weak in *Erinaceus* and though strong in *Solenodon* would appear to be differently constructed, presenting a broad surface posterolaterally between crests running from the anterior as well as the posterior extremities of the greater tuberosity.

On the distal part of the shaft the supinator ridge is prominently
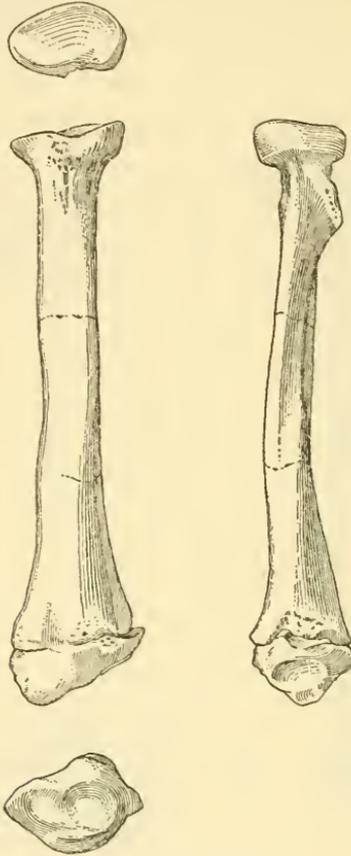
Fig. 30.—*Trogosus hyracoides* (Marsh) : Left radius (U.S.N.M. No. 17886), proximal, anterior, lateral, and distal views, × ½. Bridger (B) middle Eocene, Wyoming.

developed and extends farther proximally than in *Solenodon*. It is comparatively weak in *Erinaceus*. Medially, the distal extremity is much expanded and exhibits a large entepicondylar foramen, about as in *Solenodon*. In *Erinaceus* the inner condyle is relatively reduced and there is no entepicondylar foramen. The distal extremity of the *Trogosus* humerus is a little like that in *Patriofelis,* which is of comparable size, but is transversely broader with a wider articular surface. Also,

the supinator ridge extends rather smoothly upward a greater distance
on the shaft and apparently is not flexed posteriorly so markedly as
in the creodont.

RADIUS

A complete radius (fig. 30) was associated with the skull and other
material of *Trogosus hyracoides*. Incomplete radii were also found
associated with materials of *Trogosus hillsii* and *Tillodon fodiens*.
The shaft of the *Trogosus* radius is slender proximally, with a much
expanded extremity for articulation with the humerus above and the
ulna posteriorly. Just below the proximal expansion, on the posterior
surface of the shaft, the tuberosity for the biceps is prominent and
rugged. Distally the shaft increases in diameter and the interosseous
crest extends prominently along the posterolateral margin. Immedi-
ately lateral to the crest proximally, the shaft is longitudinally scarred,
possibly for extensor and abductor muscles which would normally
originate on this side of the interosseous membrane. Distally, the
anterior surface of the radius shows medially only a broad, shallow
groove for the radial extensors and externally a less well-defined de-
pression for the digital extensors. The distal extremity of the radius is
much enlarged and extends distally a greater distance in its antero-
medial portion. Its articular surface for the lunar is a nearly circular,
gentle concavity extending more flattened mediodistally over the
scaphoid. On the posteromedial margin there is a small, slightly con-
cave, transverse facet for the ulna.

As might be expected, the portion of a radius included in the *Tillo-
don fodiens* material is rather distinctly more robust, particularly in
the anteroposterior depth of the shaft and, laterally, of the distal
extremity. The distal articulation between the radius and ulna would
appear to be much broader.

ULNA

No complete ulna is extant among the known tillodont materials;
however, from the greater part of a shaft and a separate olecranon
portion associated with the skull of *T. hillsii,* together with a distal
portion from *Tillodon fodiens* and a distal epiphysis belonging to
Trogosus hyracoides, a composite picture (fig. 31) can be obtained.
Among the materials of *Esthonyx* only an olecranon portion was
observed.

The *Trogosus* olecranon is elongate, robust, and transversely much
expanded at the proximal extremity, giving good leverage and a large
area for the insertion of the triceps. The medial surface of the bulbous

extremity is deeply cleft, noticeable also in *Esthonyx*. The sigmoid notch or cavity is widely flaring distomedially and laterally the lesser sigmoid cavity exhibits two well-separated surfaces for the head of the radius. Below the sigmoid cavity the shaft is transversely com-
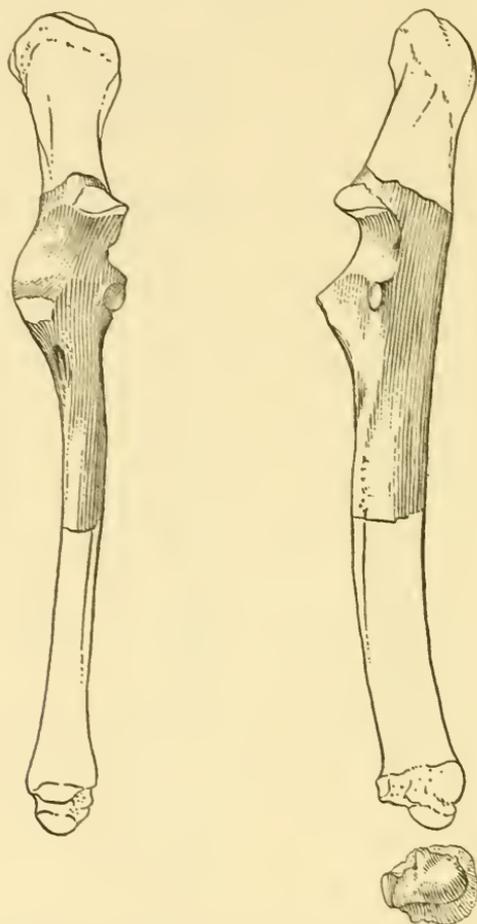

Fig. 31.—*Trogosus*, species: Left ulna (associated with U.S.N.M. No. 17157, type of *Trogosus hillsii*, new species; olecranon restored from second specimen associated with type of *T. hillsii*; distal extremity restored from U.S.N.M. No. 17886 of *Trogosus hyracoides*), anterior, lateral, and distal views, × ½. Huerfano (B) and Bridger (B) middle Eocene, Colorado and Wyoming.

pressed in *Trogosus* with a prominent interosseous crest as in the radius. The distal extremity shows a convex facet on the forward and medial margin for the radius, and a small saddle-shaped surface between that and the styloid process, which, together with the styloid process, articulates with the cuneiform. The posterior portion of the styloid process articulates also with the pisiform.

In *Tillodon fodiens* the distal portion of the shaft represented is considerably more robust, less flattened, and the large styloid process extends relatively farther distally.

MANUS

The tillodont forefoot is rather well represented among specimens from the middle Eocene. The type of *Trogosus grangeri* includes
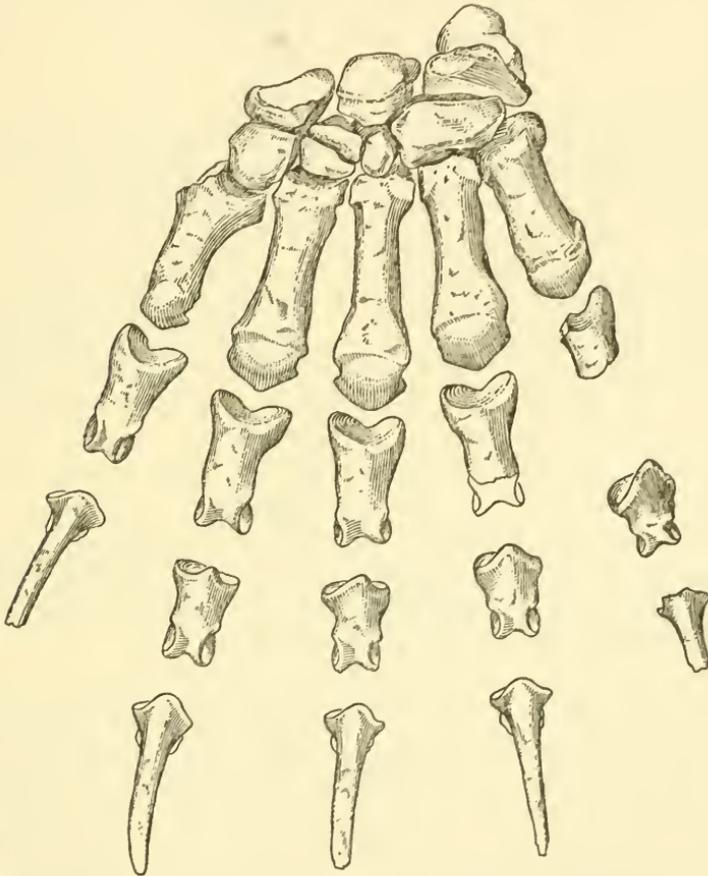

Fig. 32.—*Trogosus hyracoides* (Marsh): Left manus (U.S.N.M. No. 17886), dorsal view, × ⅔. Bridger (B) middle Eocene, Wyoming.

several phalanges as well as metacarpals and a few carpals, and a second *Trogosus* specimen from the Huerfano, A.M. No. 2692, includes several elements of the manus, principally phalangeal. A specimen regarded as representing *Trogosus hyracoides*, A.M. No. 18982, from the Bridger, includes most of the left manus, and there are portions of the forefoot in the material belonging to the type of *Tillodon fodiens*. The most nearly complete foot (figs. 32 and 33), lacking only

the distal portions of two phalanges, is that associated with the skull of *Trogosus hyracoides,* U.S.N.M. No. 17886. Much of the opposite or right forefoot of the same individual is present also. From the lower Eocene the proximal portion of a manus (fig. 34), including the carpals and proximal portions of the metacarpals in articulation, is associated with jaw material of a Gray Bull *Esthonyx,* A.M. No. 4276 (Cope, 1884a, pl. 24c, figs. 8, 8a, 8b; 1884b, fig. 24b). Caution must be exercised, however, with respect to this manus as a certain admixture of skeletal materials under this number was noted, part of which may be creodont.

The tillodont forefoot appears to be a generalized primitive structure in which the scaphoid, lunar, and centrale are all separate and the five unguiculate digits show nearly equivalent development. As noted by Gregory (1910, p. 445) for the *Esthonyx* specimen, the trapezium is relatively large and the lunar rests about equally on the centrale, magnum, and unciform. He considered the *Esthonyx* carpus as suggestive of the creodont type; however, I see no special resemblance to that group in *Trogosus,* other than a similar primitive arrangement noted in several groups of early mammals, and the hind foot is rather less suggestive of creodonts. The carpus shows a basic arrangement which may be compared favorably to that in the periptychids and in *Pantolambda,* although the details of the individual elements would probably show many differences. The phalanges are, of course, markedly different. It is interesting to note that among insectivora the modern *Erinaceus* has the scaphoid, lunar, and centrale fused, whereas in *Solenodon* they are separate. The tillodont carpus does not otherwise particularly resemble that in *Solenodon.*

Scaphoid.—In dorsal view the *Trogosus* scaphoid (fig. 33a) would appear to be a triangular wedge with proximal surface for articulation with the radius converging forward and medially toward the distal surface for the trapezium. Proximally the surface for the radius is dorsopalmad convex and transversely very slightly concave, and has a quadrilateral outline with its shortest side medial. The lateral side of the scaphoid is much higher than the medial, proximodistally, and although it fits snugly with the lunar it shows only a very small facet, adjacent to the proximopalmar extremity of the facet for the radius, for articulation with the lunar. Along the distal margin of the external surface, the scaphoid exhibits a slender facet for the centrale. Distally the scaphoid shows a large and nearly rectangular facet, slightly concave dorsally and convex palmad, for the trapezium. The palmar surface and the palmar portion of the medial surface of the scaphoid pro-

ject prominently to form a deep, transversely elongate, and smoothly
rounded process presumably having a ligamentous attachment.

The scaphoid of the *Esthonyx* specimen (fig. 34) would appear to
be much like that in *Trogosus* except that it is relatively wider trans-
versely, and the proximal articular surface for the radius is relatively
wider and more convex dorsopalmad.
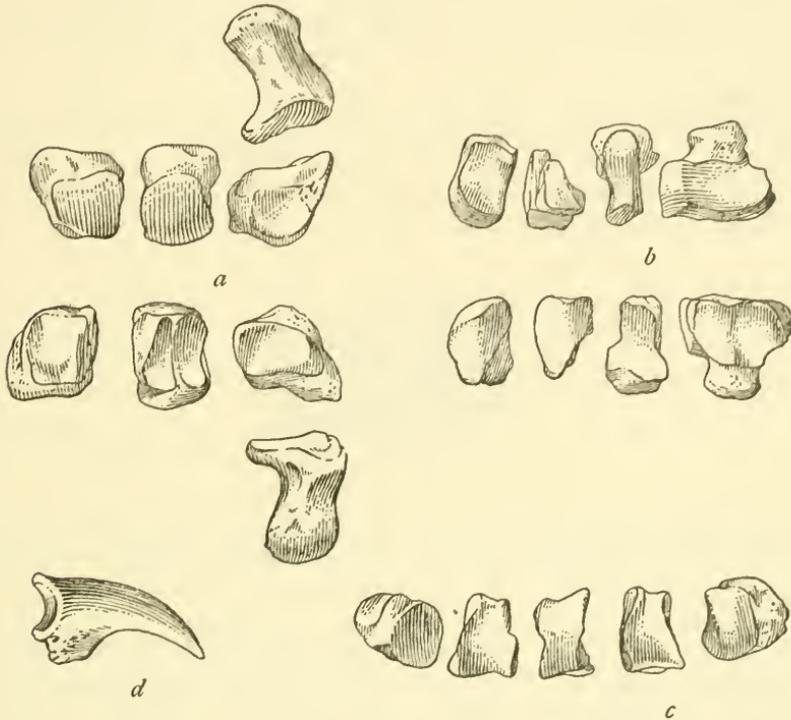
Fig. 33.—*Trogosus hyracoides* (Marsh) : Left carpals, metacarpals, and distal
phalanx (U.S.N.M. No. 17886) ; *a*, proximal (above) and distal (below) views
of scaphoid, lunar, cuneiform, and pisiform; *b*, proximal (above) and distal
(below) views of trapezium, trapezoid, centrale (proximal only), magnum, and
unciform; *c*, proximal view of metacarpals I to V; *d*, medial view of distal
phalanx of 2d digit; × ⅔. Bridger (B) middle Eocene, Wyoming.

Lunar.—The lunar of *Trogosus* is less wedgelike, as seen dorsally
(fig. 33a), and more nearly rectangular, as seen in proximal and distal
views, than the scaphoid. Its surface for articulation with the radius
covers the dorsal two-thirds to three-quarters of the proximal surface
(about half in the dorsopalmad elongate lunar of *Tillodon*) and is con-
vex transversely as well as in a dorsopalmar direction. The lateral and
medial surfaces are without facets for the cuneiform and scaphoid.
Distally, the lunar shows three subequal dorsopalmad elongate surfaces

for the centrale, magnum, and unciform. The distomedially-facing facet for the centrale is more flattened than the others, broad dorsally, but pinches out toward the palmar extremity. The central facet for the magnum is narrow dorsally, widens in a palmar direction, and is distinctly concave both dorsopalmad and transversely. The distolaterally-facing facet for the unciform is broad dorsally, narrows slightly toward the palmar margin, and is concave only in the dorsopalmar direction. As in the scaphoid, the palmar portion of this bone is much expanded or inflated, evidently also supporting a ligamentous attachment.

The lunar belonging to the foot of the *Esthonyx* specimen is likewise very like that in *Trogosus,* but more arcuate as seen from the side, with a more convex dorsopalmar profile for the proximal surface and a more concave profile for the distal surface.
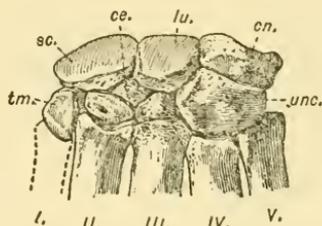
Fig. 34.—Cf. *Esthonyx bisulcatus* Cope: Left manus (associated with A.M. No. 4276), dorsal view (cuneiform drawn upside down), × 1½. Gray Bull lower Eocene, Wyoming.

Cuneiform.—The *Trogosus* cuneiform is roughly triangular viewed proximally (fig. 33a), and has a broad anterior surface that sweeps widely around the lateral side to the palmar extremity. The facet for the ulna is slightly concave and nearly circular, truncated toward the palmar margin by the transversely elongate facet for the pisiform. A single facet for the unciform covers most of the distal surface, with the exception of a very small facet for the fifth metacarpal at its lateral extremity. The medial portion of the unciform facet has a greater dorsopalmar extent and is slightly concave, whereas the more constricted lateral portion is convex. Medially this bone is moderately deep, dorsoventrally, and shows no facet for articulation with the lunar. Laterally it tapers nearly to a point at its palmar extremity. The palmar portion does not show the expansion noted in the scaphoid and lunar, this area being surmounted by the pisiform.

The *Esthonyx* cuneiform lacks the tip of the bone at the palmar extremity of the lateral portion, but otherwise resembles that in *Tro-*

gosus. In detail, however, the facet for the ulna is more elongate transversely and that for the pisiform more generally concave. Also, the distal surface for the unciform shows somewhat more flexure. It should be noted, moreover, that this bone in figure 34 was drawn upside down.

Pisiform.—The pisiform (fig. 33a) is large and sturdy as represented in the *Trogosus* material. The head is well expanded and transversely oval-shaped, offering a substantial area for insertion of a part of the *flexor carpi ulnaris*. The forward extremity is widely extended medially and has transversely broad articular surfaces for the ulna and cuneiform. The proximal facet for the ulna is transversely concave, wide at its lateral extremity and tapering medially. The distal of the two surfaces is likewise broad laterally and narrower medially, but is more nearly flat.

The pisiform is not represented in the *Esthonyx* specimen, but on the other hand it is included in the type material of *Tillodon fodiens*. The *Tillodon* pisiform is strikingly larger, particularly in the diameter of the extremities, also the facet for the ulna would appear to be larger relative to that for the cuneiform. The length of the pisiform, however, though actually a little longer than that in the *Trogosus* specimen, is relatively shorter.

Centrale.—The centrale (fig. 33b) is the smallest of the carpal elements although it presents dorsally a surface as large as, or perhaps larger than, that of the magnum. It is a thin tabular bone, nearly triangular in the outline of its proximal surface for articulation with the lunar. Along its medial edge it articulates with the scaphoid and laterally with the magnum. Its surface for the magnum is slightly concave and extended laterally along a part of the distal margin, so that the distal surface for the trapezoid is somewhat larger and more nearly trapeziform than the proximal.

Little can be said of the *Esthonyx* centrale other than that as exposed in the articulated manus (fig. 34) it appears distinct and rectangular in outline dorsally. It is noticeably less flattened, proximodistally, than in *Trogosus*.

Trapezium.—The trapezium is by no means the smallest bone in the *Trogosus* carpus. It presents a comparatively broad and deep face dorsally (fig. 32), but is much reduced in the palmar aspect. The proximal articular facet (fig. 33b) for the scaphoid covers almost the entire proximal surface and except for the rounded dorsomedial portion would be nearly rectangular. In a dorsopalmar profile the dorsal portion of the proximal surface is gently convex and the palmar portion concave. Moreover, the proximal surface is noticeably deflected

distally in its palmar-medial portion. The distal surface for the first metacarpal is approximately triangular in outline with the smallest angle directed palmad. The surface is concave fore and aft, convex from side to side, and in general inclined decidedly proximad in a palmar-medial direction, so that the proximal and distal facets almost meet at the palmar extremity of the medial margin. The lateral surface of the trapezium shows an elongate facet extending the length of the proximal margin for articulation with the trapezoid, and at the dorsal and palmar extremities it is extended distally for articulation with the second metacarpal. The more palmar of these two facets for the second metacarpal is deflected sharply medial so that the trapezium slightly overrides the metacarpal.

So far as can be determined in the manus (fig. 34) with the *Esthonyx* material, the trapezium is relatively wider transversely across the dorsal surface, in comparison with its proximodistal extent, than in *Trogosus,* and may not be relatively so deep in a dorsopalmar direction. Also, so far as exposed, the proximal and distal surfaces are only convex.

Trapezoid.—The *Trogosus* trapezoid is a little larger than the centrale and more distinctly wedgelike with its thin edge directed laterally. Its proximal surface (fig. 33b) articulates with the centrale and is deeply notched at the palmar-lateral portion of its margin. The compressed lateral margin of the trapezoid may make a line contact with the magnum but is largely eliminated from this articulation by the centrale. Medially, the rectangular face of the trapezoid articulates with the trapezium, and along the slightly rounded angle between the proximal and medial surfaces it makes a line contact with the scaphoid. The distal surface of the trapezoid is convex from side to side and covers the proximal extremity of the second metacarpal, except where the latter has a small facet at the palmar extremity of the medial margin for the trapezium.

Only the dorsal surface of this bone can be seen in the articulated Gray Bull manus but it is almost identical in outline to that of *Trogosus.*

Magnum.—The magnum (fig. 33b) is beyond doubt the most peculiarly shaped bone in the *Trogosus* manus. It has something of the form of a narrow-soled shoe, inverted and with the toe directed dorsally and distally. It presents an irregularly oval face dorsally, and proximally it rises keel-like toward the "heel" beneath the lunar. The sides of the elongate proximal portion articulate medially with the centrale and laterally with the unciform. The very large knoblike distopalmar portion articulates on its medial side with a facet on the

lateral side of the proximal extremity of the second metacarpal. The saddle-shaped distal surface of the magnum is widely expanded in its palmar portion and its articulation there extends somewhat beyond the third metacarpal onto the second. The bulbous palmar expansion of this bone is evidently for ligamentous attachment.

In *Esthonyx* the magnum would appear likewise to be of limited dorsal exposure and to rise high and keel-like in a proximopalmar direction beneath the lunar.

Unciform.—The tillodont unciform (fig. 33b) is a very large segment of the manus, rivaling the pisiform in size. Its form resembles somewhat that of a hammer head with the large bulbous palmar projection corresponding to the direction of the handle. The dorsal exposure of the bone (fig. 32) is broad and deep, with two liplike prominences lapping dorsally over the median portions of the heads of the fourth and fifth metacarpals. The proximal articular portion of the unciform is deep and very broad transversely. It consists of two principal parts, a wide segment for articulation with the cuneiform and a transversely, much narrower, and somewhat medially turned segment for the lunar. The surface for the cuneiform is convex medially but the lateral portion is transversely concave, sloping distally toward the palmar-lateral margin. Medially, and at about a 90° angle with the surface for the lunar, the unciform articulates with the magnum, and somewhat lower with the lateral side of a proximally directed lip of the third metacarpal. Distally the surface is concave in a dorsopalmar direction and the medial portion is slightly convex transversely, corresponding to the transverse concavity in the head of the fourth metacarpal. The lateral portion of the distal surface articulates with the fifth metacarpal and at the palmar extremity of the lateral margin comes to a thin edge with the proximal surface for the cuneiform, permitting contact between the cuneiform and fifth metacarpal. The palmar projection is much like that of the magnum and about equally developed, evidently also for ligamentous attachment.

An unciform is also included in the type material of *Tillodon fodiens,* which is appreciably larger than that in the *Trogosus* manus. It appears also to be relatively a little deeper medially and to have a relatively broader surface for the lunar. Distally the surface for the fourth metacarpal and that for the third and for the magnum grade into one another more smoothly, and the surface for the fifth metacarpal extends more palmad onto the relatively less-produced palmar process.

The unciform in the *Esthonyx* material (fig. 34) is relatively deeper proximodistally than in *Trogosus,* and like the magnum shows a rela-

tively broad palmar process. The proximal and distal surfaces of the unciform converge laterally, but may not permit contact between the fifth metacarpal and cuneiform as it does in both *Trogosus* and *Tillodon*.

Metacarpals.—The *Trogosus* metacarpals (fig. 32) are moderately short and sturdy, increasing in length from the first to the third and decreasing again to the fifth. The first and fifth, however, show no appreciable tendency toward reduction from a fully functional pentadactyl foot. The transverse profile across the dorsal surface of the articulated metacarpals is but gently curved and the divergence between the metacarpals is moderate with perhaps somewhat greater divergence between the first and second, although this appears compensated, at least in part, by the curvature of the first metacarpal. The proximal extremity of the first metacarpal is set distinctly distal to that of the second metacarpal, whereas the second and third are even. The fourth and fifth together are located slightly distal to the proximal extremity of the third. The dorsal surface of each in longitudinal profile shows but slight deviation from a straight line. The palmar surfaces, however, are strongly concave longitudinally, with both the extremities much expanded in a palmar direction. The distal extremities, in articulation with the proximal phalanges, are smoothly convex dorsally in all, and strongly keeled on the palmar surface. Also the distal extremities, at the widest points, are more expanded transversely than the proximal extremities, except in the first and fifth.

Considering the metacarpals in more detail, the first (fig. 33c) is seen to have a broadly expanded proximal extremity with the broad and transversely concave facet for the trapezium tilted decidedly distolateral, directing the metacarpal distally rather than medially from the trapezium. There is no facet, however, for articulation between the first and second metacarpals. Medially the proximal portion of the first is expanded and noticeably roughened. The distal articular surface is relatively narrow transversely, and is twisted slightly with respect to the proximal extremity, so that the phalanges are oriented similarly to those of the other digits.

The second metacarpal has its proximal articulating surface (fig. 33c) almost perpendicular to the long axis of the bone, and although this surface shows practically no dorsopalmar convexity, it is somewhat concave transversely. The dorsal portion is broad with the lateral margin projecting proximally more than the medial, but the palmar portion is narrower and has facets on either side inclined slightly away from the principal facet for the trapezoid. The medial of these is for an overlap of the trapezium which also articulates with a small facet

at the dorsal extremity of the medial surface of the second metacarpal, and the lateral is for the expanded side of the magnum. The medial surface of the second metacarpal does not articulate with the first, but the lateral surface has a small oval facet at the dorsoproximal angle for the third metacarpal.

A scarred process for the *extensor carpi radialis longior* is prominently displayed about a third of the way distally on the medial side of the dorsal surface of the second metacarpal, and for the *extensor carpi radialis brevior* in about the same position on the third metacarpal of *Trogosus grangeri*. These processes are relatively more proximal, and that on the second metacarpal is more centrally placed on the dorsal surface in A.M. No. 18982 of *Trogosus hyracoides*. In U.S.N.M. No. 17886 of *T. hyracoides* the processes are scarcely evident.

The nearly rectangular surface for the magnum on the third metacarpal (fig. 33c) is decidedly convex in its dorsopalmar profile, and slightly concave transversely near the dorsal margin, but tilted so that the lateral margin is extended noticeably more proximad than the medial. The medial side of the third metacarpal articulates with the second metacarpal only at its dorsoproximal angle. The lateral side, however, articulates with the fourth throughout the dorsopalmar extent of the head. The facet for the fourth metacarpal is strongly arcuate, as determined by the convexity of the surface for the magnum, and exhibits a marked dorsopalmar concavity. The upturned lip of the lateral margin of the surface for the magnum permits articulation for a short distance along its outer surface with the unciform, proximal to that for the fourth metacarpal.

The proximal extremity of the fourth metacarpal (fig. 33c) is broad dorsally, but somewhat narrower in its palmar portion. The proximal surface for the unciform is gently concave transversely, and the dorsopalmar profile convex, although the convexity is distinctly less than that of the surface for the magnum on the third metacarpal. The medial surface shows an arcuate facet for the third metacarpal throughout the dorsopalmar portion of this surface, and facing more nearly proximal is a small lenticular facet for the transversely expanded palmar portion of the magnum, noticeably constricting the palmar portion of the facet for the unciform. This facet for the magnum is less well defined in the *T. grangeri* foot than in the U.S.N.M. foot of *T. hyracoides*. Laterally, the proximal extremity of the fourth metacarpal is markedly excavated, with an arcuate facet for the fifth metacarpal, resembling that on the lateral side of the third, but under-

cut dorsally so that the fourth metacarpal rides over a small knoblike prominence on the medial side of the fifth.

The proximal extremity of the fifth metacarpal (fig. 33c) is widely expanded transversely, with the strongly convex articular surface confined to the medial half of the head. The very large lateral expansion of the head probably includes the insertion for the tendon of the *extensor carpi ulnaris*. Transversely, the facet for the unciform is of uniform width and has a straight to slightly convex profile. At its palmar-lateral extremity it articulates with the cuneiform, when the metacarpal is extended, as a slight flexure of the proximal surface at this point would so indicate. The crescentic medial facet for the fourth metacarpal is proximodistally wide and its dorsal portion is extended medially and distally to occupy the concavity of the opposing surface on the fourth metacarpal.

The few metacarpals found associated with the type material of *Tillodon fodiens* are essentially similar to those in *Trogosus;* however, the extremities, particularly the proximal, are noticeably enlarged, although the length of each is only a little greater than in *Trogosus*.

Of the metacarpals in the manus considered to be *Esthonyx,* only the proximal portions of the second to the fifth are preserved. The heads of those are obscured in articulation with the carpus and partly by matrix so that no significant details are evident. It is noted, however, that the shafts of the metacarpals extend from the proximal extremities in uniform and full width, not so noticeably constricted a short distance from the head as in *Trogosus*. In all probability the Esthonyx metacarpals were relatively longer than in *Trogosus*.

Phalanges.—The proximal and intermediate phalanges (fig. 32) are, like the metacarpals, moderately short and sturdy. The articulations are developed to permit extensive flexure as in clawing, digging, or grasping. Moreover, the distal phalanges are transversely compressed, markedly curved, uncleft, birdlike claws.

The proximal extremities of the proximal phalanges are deeply cupped and much expanded, both transversely and in dorsopalmar depth. The palmar margin of the cup is deeply notched to accommodate the keel of the metacarpal. Moreover, the wings to either side of the notch are roundly faceted above for contact with the elongate sesamoids articulating with the palmar surface of the distal extremity in each metacarpal.

The distal extremity of the proximal phalanges is distinctly narrower and shallower than that proximally, and the distal articular surface is a well-rounded trochlea with the median groove deeply im-

pressed. In the first digit the distal articular surface is appreciably narrower than in the others, articulating directly with the claw.

The intermediate phalanges are progressively narrower than those proximally and between two-thirds and three-quarters as long. Their proximal surface is deeply concave and divided. The ridge between the concavities meets the dorsal margin in a lip for extensor muscles, which projects well up on the dorsal surface of the trochlea articulating with it. The distal surface, articulating with the distal phalanx or claw, is narrower than that of the proximal phalanx, but distinctly deeper in a dorsopalmar direction, with the expansion dorsal to the shaft as well as palmar. Moreover, the condyles of the distal trochlea are more nearly parallel, affecting a more perfect pulley than on the proximal phalanx.

The proximal extremity of each of the claws is transversely expanded to cover the lobes of the distal articular surface of the intermediate phalanx, and much recurved in a dorsopalmar plane. The claw is transversely very flattened, longitudinally curved (fig. 33d), and distally pointed. Also, as noted above, it shows no evidence of a median cleft or fissure distally. On the palmar margin near the proximal surface there is a broad, rugged process for the tendon of the *flexor profundus digitorum*. Between this rugosity and the palmar margin of the articular surface on either side is a small nutrient foramen penetrating the bony claw.

PELVIS

Of the pelvic girdle in *Trogosus* only the ilium is known; however, a portion of an innominate bone associated with *Esthonyx*, A.M. No. 4276, from the Gray Bull, includes the acetabulum and adjacent parts of the ilium and ischium. The *Trogosus* ilium, found associated with the *T. hillsii* material, is strikingly trihedral in form in its posterior portion, recalling the Rodentia. However, a relationship to this order is not implied, inasmuch as a three-sided ilium with the iliac surface rather well developed would appear to be a primitive mammalian condition, noted in monotremes, didelphid marsupials, and certain insectivores, creodonts, and edentates as well. The form in *Trogosus* may be compared to that in *Solenodon* or limnocyonid creodonts, but with important differences from both.

The sacral surface is relatively narrow posteriorly where it makes a nearly 90° angle with the iliac surface at the pubic border; however, it becomes wider forward and more nearly confluent with the iliac surface toward the suprailiac border. The gluteal surface is much the

widest; it is gently concave forward and makes a very acute angle with the iliac surface at the acetabular border, more acute than in *Solenodon,* almost as in *Castor.* Toward the acetabulum the acetabular border exhibits a rather rugged longitudinal prominence for the *rectus* muscle of the leg.

Of the three innominate portions associated with *Esthonyx,* A.M. No. 4272, one may be *Esthonyx,* the other two (one of which was figured by Cope, 1884a, pl. 24c, figs. 10, 10a; 1884b, fig. 24c) are surely creodont. The particular fragment regarded as *Esthonyx* exhibits, as in *Trogosus,* an acute acetabular border between the gluteal and iliac surfaces, but the sacral surface is relatively wider posteriorly and the iliac surface narrower. The iliac surface is turned more nearly inward than, for example, in *Solenodon* and some of the creodonts, with a tendency toward confluence with the sacral surface forward. This would appear to be a tillodont peculiarity.

<div align="center">FEMUR</div>

Remains of six or more femora of *Trogosus* are known, two of these, Y.P.M. No. 11088 (fig. 35) and A.M. No. 17011, from the Bridger and Huerfano, respectively, are nearly or quite complete though showing evidence of limited crushing and distortion. There are in addition several femoral portions associated with the *T. hillsii* skull, but representing more than one individual.

Characteristic of the *Trogosus* femur is its sturdy, almost straight shaft with no appreciable curvature fore and aft. The proximal extremity is broad with a prominent greater trochanter well separated from the head. At its outer margin the greater trochanter is directed posteriorly over a deep and longitudinally elongate digital fossa with the intertrochanteric crest not continuous with the lesser trochanter. Beneath the head the lesser trochanter is prominent and extends flange-like a noticeable distance along the posteromedial margin of the shaft. A third trochanter is present well over a third of the way down the lateral margin of the shaft. It is longitudinally extended and almost as much expanded as the lesser trochanter, apparently more so than the third trochanter in larger creodonts. The lesser and third trochanter are relatively more elongate, extending more distally than in *Solenodon.* The prominence of the lateral trochanters is in keeping with the relative importance of the gluteal surface of the ilium in the expected development of the gluteal muscles for extension of the femur, such as in running and other motions of the hind limb. The rather unusually expanded lesser trochanter would suggest a powerful *psoas magnus* which acts in flexing the hip.
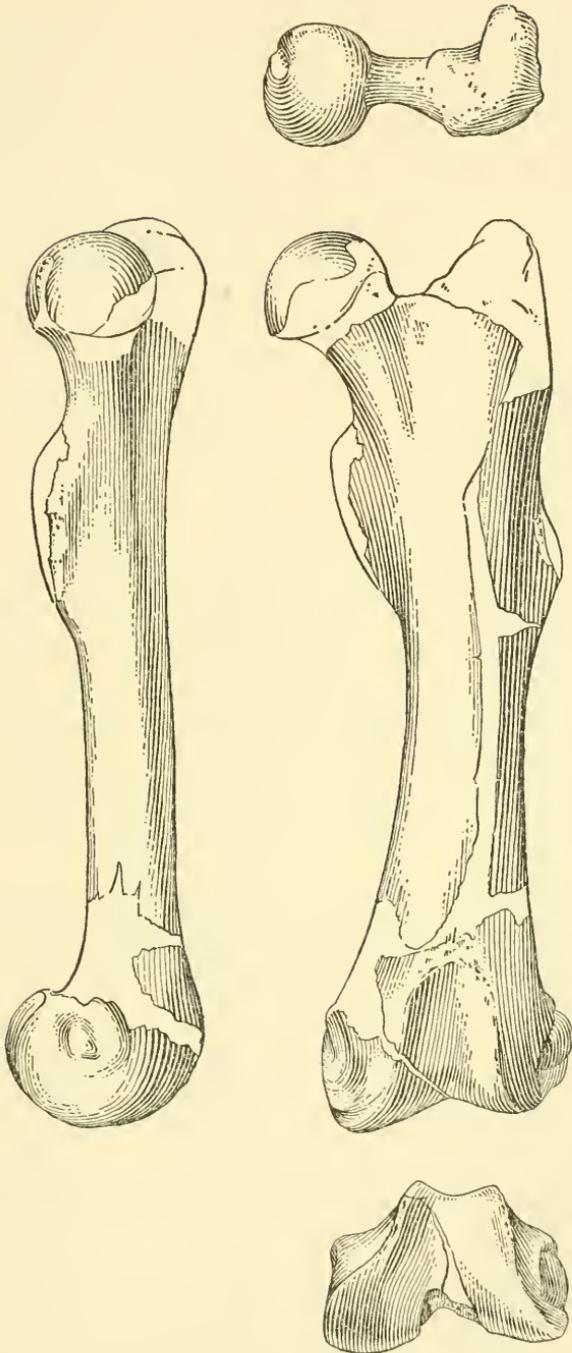
FIG. 35.—Cf. *Trogosus,* species: Left femur (Y.P.M. No. 11088, restored from A.M. No. 17011 and material associated with type of *T. hillsii,* U.S.N.M. No. 17157), proximal, medial, anterior, and distal views, × ½. Bridger and Huerfano (B) middle Eocene, Wyoming and Colorado.

The distal portion of the femur would appear to be characterized by its fore and aft shortness, in which the condyles do not project posteriorly so markedly as observed, for example, in various carnivores. The medial condyle, as customary, extends posteriorly somewhat more than the lateral condyle. The patellar surface extends broadly well up the anterior surface of the bone.

The femur of a Gray Bull *Esthonyx* in its proximal portion is much like that of *Trogosus*. It shows the same relative transverse width and the longitudinally elongate digital fossa. The distal portion of a femur of another individual, believed associated with teeth of a Clark Fork *Esthonyx,* may be somewhat crushed but appears rather narrow transversely across the condyles and across the patellar surface, as well as anteroposteriorly deep, as in certain creodonts. There is no certainty, however, that this fragment of a femur is *Esthonyx.*

TIBIA

A complete tillodont tibia is not known; however, there are at least 10 tibiae represented by proximal or distal extremities, or both. These are included among materials representing *Esthonyx* as well as *Trogosus* and *Tillodon.* In one individual of *Trogosus,* Y.P.M. No. 11088 (fig. 36), the entire shaft of a fibula is preserved, associated with the proximal and distal extremities of the tibia from the same side, making it possible to determine closely the length of the latter bone. Undoubtedly the most striking feature of the tibia is its shortness. Its length is but two-thirds that of the femur, measured in the same individual.

The tibia of *Trogosus* has strong, rugged articular portions and the proximal extremity is markedly excavated posterolaterally beneath the lateral condyle. The articular surface of the medial condyle is the larger of the two and slightly concave, whereas the lateral articular surface would appear to be slightly higher, smaller, and more convex. The shaft, though strong, is somewhat flattened anteromedial-posterolaterally and rounded distally. The cnemial crest is rugged and broad proximally but rapidly loses its ruggedness distally as it blends smoothly with the shaft. The distal extremity of the tibia exhibits an anteroposteriorly deep and medially expanded internal malleolus, projecting bluntly downward below the internal surface for the astragalus. On its posterior surface the internal malleolus shows a prominent groove apparently for both the *tibialis posticus* and *flexor longus digitorum.* The articular surface for the astragalus is composed of two shallow concavities, the outer of which is somewhat more flattened

and abbreviated, and is bounded high externally by the lower margin
of the small, posteroexternally-facing facet for the fibula.

The fragments of tibiae representing *Tillodon fodiens* do not appear
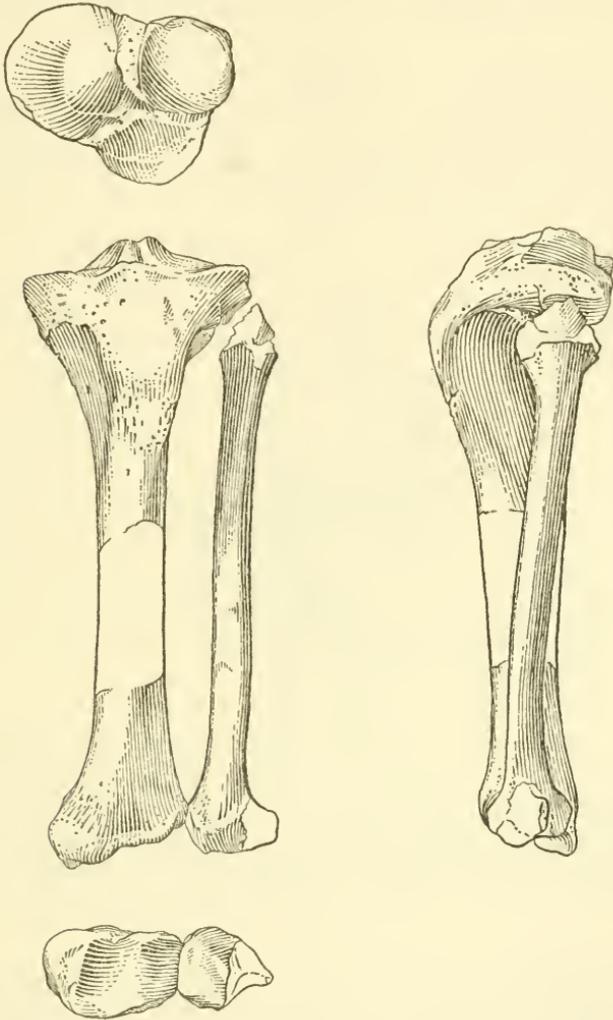
FIG. 36.—Cf. *Trogosus,* species: Left tibia and fibula (Y.P.M. No. 11088),
proximal, anterior, lateral, and distal views, × ½. Bridger middle Eocene,
Wyoming.

to differ significantly from those of *Trogosus* other than being of a
little greater size. The proximal extremity is deeper through the
cnemial crest and the distal extremity is a little heavier throughout.
The *Esthonyx* tibia, if correctly associated, would appear to be rela-
tively longer and more slender, with the external condyle of the

proximal extremity supported below by a more prominent, though compressed, ridge extending upward from the posterolateral wall of the shaft. The internal malleolus is less expanded medially and the external portion is slightly more compressed anteroposteriorly.

FIBULA

The fibula belonging to Y.P.M. No. 11088 (fig. 36) of *Trogosus* is nearly complete, though damaged somewhat at the proximal extremity where contact is made with lower surface of the external condyle of the tibia, and the posterolateral flange on the external malleolus is missing. The proximal extremity, as seen in A.M. No. 17008 of *Trogosus grangeri,* has a nearly horizontal, slightly concave articulating surface on an abruptly expanded head, the forward margin of which is proximodistally much compressed. The anteromedial margin of the shaft shows a thinly compressed interosseous crest only on the proximal portion. The greater part of the shaft is nearly circular but distally, as seen in Y.P.M. No. 11088 and more prominently in A.M. No. 2692, a crest is developed on the external margin which expands abruptly posterolaterally from the external malleolus. The wide notch posterior to this flattened process carries the tendon of the *peroneus brevis.* The distal articular surface for the outer wall of the astragalus is large and inclined at an angle of about 45° with the long axis of the fibula. At its medial upper limit the surface is joined by the small marginal facet for the tibia.

A proximal portion of a fibula, found associated with Gray Bull *Esthonyx,* A.M. No. 4276, is relatively more flattened transversely than in *Trogosus,* but shows a compressed and low interosseous crest for approximately three centimeters down the median surface. This fibula was figured by Cope (1884a, pl. 24c, figs. 9, 9a) but he was uncertain as to whether the bone represented was a fibula or the radius.

PES

Representation of the tillodont hind foot is very scant, and in only one specimen of *Trogosus,* Y.P.M. No. 11088 (figs. 37(part) and 38c), are there as many as three elements which can be articulated: the astragalus, calcaneum, and cuboid. In U.S.N.M. No. 17886 of *Trogosus hyracoides,* the cuboid and ectocuneiform (figs. 37(part) and 38e) are preserved and in the material associated with *Trogosus hillsii* incomplete calcanea and a partial astragalus are included. Certain other specimens include single elements of the hind foot. Associated with the type of *Tillodon fodiens* are an incomplete calcaneum, cuboid,

mesocuneiform (figs. 37 (part) and 38d), and the proximal extremities
of the third and fourth metatarsals (figs. 37 (part) and 38h and i).
Calcanea and astragali are included in materials associated with jaws
or teeth of *Esthonyx,* but the identity of these is uncertain.

The composite hind foot here illustrated (fig. 37) is made up of
elements from four different individuals, representing two genera.
The navicular, cuneiforms, and metatarsals are poorly matched to the
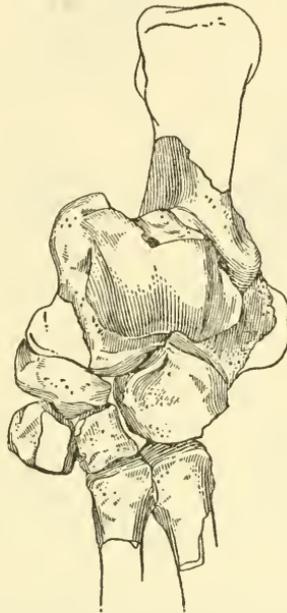
FIG. 37.—*Trogosus,* and *Tillodon,* new genus: Composite left pes (astragalus,
calcaneum, and cuboid, Y.P.M. No. 11086) of Cf. *Trogosus;* navicular, Y.P.M.
No. 11086 of Cf. *Trogosus;* left external cuneiform, U.S.N.M. No. 17886 (re-
versed in error) of *Trogosus hyracoides;* and middle cuneiform and metatarsals
III and IV (metacarpals reversed from right side) of *Tillodon fodiens,* new
genus (internal cuneiform and 1st, 2d, and 5th digits not represented), dorsal
view, × ⅔. Bridger middle Eocene, Wyoming.

remaining elements in size so that distortion as to direction and relative
position is inevitable. The composite does, however, show the general
arrangement of the elements and, in particular, suggests marked diver-
gence of the medial digits.

The tillodont tarsus does not particularly resemble that in either
insectivores or creodonts. It does, however, show a resemblance to
the structure seen in such forms as *Periptychus* and *Pantolambda,* as
Matthew (1937) has illustrated their pes. These Paleocene genera
are currently regarded as representing the orders Condylarthra and

Pantodonta, respectively, although Matthew regarded them as belonging to the same order, the Taligrada. His description of the "taligrade" astragalus corresponds well with that in *Trogosus*. It should be noted, however, that *Trogosus* is not subungulate but distinctly unguiculate.

*Astragalus.*—The astragalus of *Trogosus* is in general flattened,
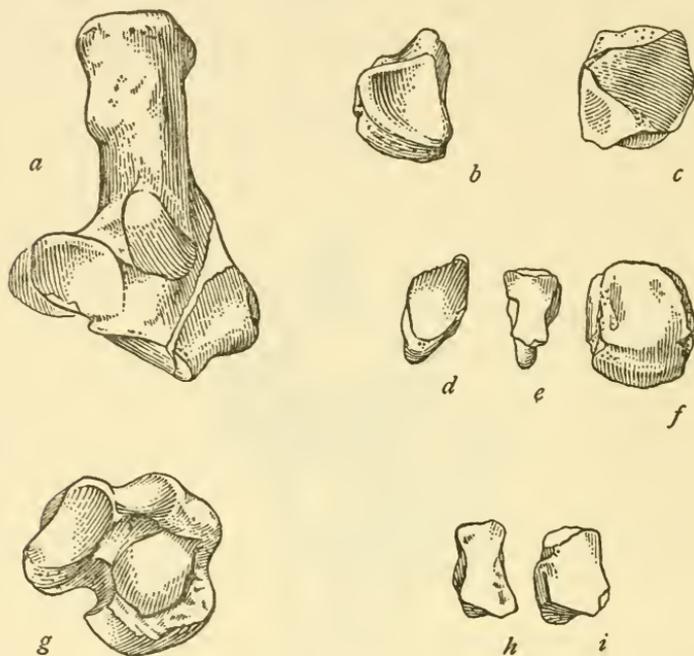
Fig. 38.—*Trogosus,* and *Tillodon,* new genus: Tarsals and metatarsals; *a, Trogosus,* species, left calcaneum (A.M. No. 17011), dorsal view; *b,* Cf. *Trogosus,* species, left navicular (Y.P.M. No. 11086), proximal view; *c,* Cf. *Trogosus,* species, left cuboid (Y.P.M. No. 11088), proximal view; *d, Tillodon fodiens,* new genus, right middle cuneiform (Y.P.M. No. 11087), type specimen, distal view; *e, Trogosus hyracoides,* left (reversed in error) external cuneiform (U.S.N.M. No. 17886), distal view; *f,* Cf. *Trogosus,* species, left cuboid (Y.P.M. No. 11088), distal view; *g, Trogosus hyracoides,* left astragalus (A.M. No. 18982), plantar view; *h* and *i, Tillodon fodiens,* new genus, left (reversed from right side) 3d and 4th metatarsals (Y.P.M. No. 11087), type specimen, proximal view; × ⅘. *a,* Huerfano (B) middle Eocene, Colorado; *b-i,* Bridger middle Eocene, Wyoming.

short-necked, and with a transversely broad articular surface on the head. It is noticeably like that figured for *Periptychus* but in detail the articulation for the tibia is somewhat more trochlear in form, with the medial ridge approaching the head more closely than in *Periptychus*. The amount of rotation between the astragalus on the one hand and tibia and fibula on the other was decidedly limited, however, in comparison with modern carnivores and ungulates. In poste-

rior view the medial portion of the surface for the tibia extends rather more plantad than the outer half, and between these two portions, just dorsal to the groove for the tendon of the *flexor longus hallucis,* is a prominent astragalar foramen. Anteriorly, the articular surface on the head, though not complete in any specimen at hand, is transversely more broad than deep. A slight deflection of this surface posteriorly in its lateral part denotes the separation of the portion articulating with the cuboid from that which articulates with the navicular. The medial surface of the astragalus extends broadly inward in its plantar portion and shows a rather limited area of articulation above for the internal malleolus of the tibia. The external surface extends laterally in a more nearly conical form with its apex at the plantar margin. The external malleolus articulates broadly with this surface and at a nearly 90° angle from that for the tibia. In the plantar view (fig. 38g) the elongate-oval and decidedly concave ectal facet for the calcaneum is marginally placed with its long diameter anterolaterally directed. Somewhat medial to the center of the plantar surface, the less elongate, more nearly circular sustentacular facet is gently convex, anteroposteriorly, and may or may not extend completely to the portion of the anterior facet for the cuboid. Posteriorly, the sustentacular facet turns abruptly plantad beneath the median tubercle on the posterior extremity.

Calcaneum.—The calcaneum of *Trogosus* has an elongate heel which is somewhat flattened. The posterior extremity or tuberosity is enlarged and rounded, but showing a division into an upper and lower prominence, and near the extremity on the dorsomedial surface there is a rather large process. This process is missing on the lower Eocene calcanea and the shaft for the tuberosity is flattened more nearly transversely. The anterior portion of the *Trogosus* calcaneum (fig. 38a) has a relatively widely extended sustentacular process which projects noticeably inward and forward beyond the sustentacular facet, giving a large rugged surface for the attachment of ligaments and a part of the *tibialis posticus.* The sustentacular process shows a smooth groove below and posteriorly, extending toward the posterior margin of the ectal facet, for the *flexor hallucis longus.* The sustentacular facet for the astragalus is irregular in shape, slightly concave and extends forward to the facet for cuboid with which it makes a sharp angle. Posteriorly the sustentacular facet curves abruptly for a very short distance onto the posterior margin of the sustentacular process. The ectal facet is obliquely elongate, convex, and separated from the sustentacular facet by a deep and broad groove into which is attached the interosseous ligament to the astragalus. The outer surface of the calcaneum

exhibits a very prominent and widely extended peroneal process which is grooved longitudinally for the *peroneus longus*. Immediately dorsal to the peroneal process and close to the lateral margin of the ectal facet are two noticeable grooves, one of which may be for the *peroneus brevis* if this occupies a separate channel. The anterior extremity of the calcaneum has a large, slightly concave surface for the cuboid. The surface for the cuboid, rather than being perpendicular to the long axis of the heel, is decidedly oblique, with its long axis directed posteromedially toward the sustentacular process.

The calcanea presumed to be of *Esthonyx* are characterized by much less expanded sustentacular processes and apparently smaller peroneal processes. Moreover, the facet for the cuboid is more nearly transverse and is well separated from the sustentacular facet so that there is no continuity between the two as there is in *Trogosus*.

Navicular.—Only two tillodont naviculars are known: one, Y.P.M. No. 11086 from the Bridger, and the other included in material associated with *Esthonyx* teeth, obtained by Princeton University in Paleocene beds of the Big Horn Basin. The navicular belonging to Y.P.M. No. 11086 (fig. 38b), which is believed to represent *Trogosus,* but may possibly be *Tillodon,* is a much-flattened bone, slightly arcuate in outline, as viewed proximally, and exhibits a strong posteroexternal process. This process is undoubtedly for a part of the *tibialis posticus,* although in many widely divergent groups of mammals the process for this muscle is located on the medial side of the plantar surface. The proximal facet for the head of the astragalus is concave, and laterally, through a rather slender line of contact with the cuboid, it joins the distal external facet for the external cuneiform. The distal surface of the navicular is gently convex from side to side and the facets for articulation with the three cuneiforms are nearly confluent so that their limits between are not easily discerned, except near the dorsal and plantar margins. Medially, the facet for the entocuneiform turns inward rather markedly.

The navicular associated with *Esthonyx* material is relatively thicker proximodistally, has a deeper, cup-shaped proximal surface for the astragalus, and the distal surface is not so convex as in the Bridger specimen. Also, the facet for the entocuneiform is relatively very small.

Cuneiforms.—The internal cuneiform was not found or recognized in any of the tillodont materials examined; however, an incomplete mesocuneiform (fig. 38d) is apparently included in the type material of *Tillodon fodiens*. This element is a dorsoplantad elongate bone, transversely compressed in its posterior or plantar portion, so that

scarcely more than the process for a part of the *tibialis posticus* is exposed. The proximal and distal surfaces are both dorsoplantad elongate, gently concave surfaces for the navicular and second metatarsal, respectively. Articulation with the external cuneiform is indicated by a facet along the proximal margin of the lateral surface.

The external cuneiform (fig. 38e) is included in the skeletal material, U.S.N.M. No. 17886, belonging with the skull of *Trogosus hyracoides.* As noted for the mesocuneiform, the ectocuneiform is an elongate bone very narrow at its plantar extremity. The process for a part of the *tibialis posticus* is high and more clearly set off from the lower portion, which is notched transversely for the *peroneus longus* tendon. Proximally, the surface for the navicular is joined by a narrow margin of articulating surface on both the medial and external surfaces, for the middle cuneiform and cuboid, respectively. The distal articulation is L-shaped, or almost T-shaped, for the proximal extremity of the third metatarsal. The distal surface is distinctly notched externally and but slightly so internally, dividing the facets on the distal portion of the lateral and medial surfaces into dorsal and plantar portions.

Cuboid.—The tillodont cuboid (fig. 38c, f) is scarcely cubical in form, as a result of the very oblique angle in which the calcaneum articulates with it. The dorsal face is large and nearly pentagonal in outline. The proximal surface of the cuboid has a gablelike crest separating the concave facet for the astragalus from the larger convex and proximolateral surface for the calcaneum. Externally, the facet for the calcaneum almost meets the distal surface, leaving only a slender gap between. Medially, the facet for the navicular is a narrow dorsoplantar band adjacent to that for the astragalus but joined smoothly below by the facet for the ectocuneiform, which does not quite reach the distal surface. Distally, on the medial surface, small dorsal and plantar facets, adjacent to the distal surface of the cuboid, articulate with the distal margin of the external face of the ectocuneiform. The plantar surface of the cuboid is more nearly triangular, characterized at its broad distal portion by a rugged, transversely broad process or tuberosity, apparently for attachment of the ligament to the calcaneum. On the distal surface of the cuboid, between the broad, gently concave surface for the fourth and fifth metatarsals and the lower margin of the enlarged posterior tuberosity, is a smooth, well-defined transverse groove for the tendon of the *peroneus longus.*

Metatarsals.—The only metatarsals that can be identified and recognized as to position are the proximal portions of the third and fourth (figs. 37 and 38h and i) belonging to *Tillodon fodiens,* and possibly

a second in material associated with the skull of *Trogosus hyracoides*. There are other metatarsals in the *Trogosus* specimen but these are mostly distal portions and not certainly determined as to position.

The tillodont metatarsals are clearly more slender and in all probability longer than the metacarpals. The second metatarsal (not illustrated), whose proximal portion is preserved, exhibits only the dorsal portion of the articulating surface for the mesocuneiform. This surface is relatively flat and inclined slightly toward the medial side. No facets for articulation show on the medial side, but a single small facet is preserved, proximodorsally, on the lateral side. I cannot determine from the material at hand whether this small facet articulated externally with the lower margin of the ectocuneiform or with the third metatarsal. The absence of an equivalent facet on the *Tillodon* third metatarsal suggests that the second may well have had articulation with the outer cuneiform.

The proximal extremity of the third metatarsal has a slightly convex articular surface for the external cuneiform which is inclined distally to the dorsal and medial sides. The surface is approximately quadrilateral but transversely constricted across its middle portion. There do not appear to be articular facets on the somewhat roughened medial surface of the extremity, but the lateral surface shows two well-defined facets for the fourth metatarsal. The plantar and more proximal of the two is plane and triangular in outline, whereas the larger, more dorsal surface, also triangular, is noticeably concave, partially enveloping its counterpart on the fourth metatarsal.

The proximal extremity of the fourth metatarsal lacks the plantar portion, but it is sufficiently complete to determine its correct position in the series. As in the third, the proximal articular surface, which in this case articulates with the cuboid, is gently convex and inclined distally toward the dorsal and lateral sides. On the medial side is shown the convex, proximodistally elongate facet for the concavity on the third, but the more plantar facet is broken away. The external surface shows an arcuate, concave facet entirely across the preserved portion adjacent to the cuboid facet.

Phalanges.—None of the preserved phalanges belonging to the hind foot of the *Trogosus* specimen, U.S.N.M. No. 17886, are determined as to digit represented, but these elements, presumably in contrast to the metatarsals, are clearly shorter than in the forefoot and, moreover, the proximal phalanges appear somewhat more compressed dorsoventrally.

RELATIONSHIPS OF ORDER AND CONCLUSIONS

One might expect, after having examined nearly all the known tillodont material and made extensive comparisons with various forms in other orders, to have arrived at well-founded conclusions regarding the origin and affinities of the group, but this is not the case. Resemblances of one kind or another were noted to several of the orders of mammals represented in the early Tertiary. Some would appear to be fundamental in nature and surely significant, but the best that can be said of these in most such cases is that their significance is basic or fundamental to perhaps several early groups of mammals. Other characters, largely adaptive in significance, are strikingly like those in representatives of other orders but can be regarded only as samples of parallelism, or perhaps convergence.

Perhaps the most misleading resemblance is to the remarkable development of the anterior teeth in the Taeniodonta. This early led to their being included in the same order; however, the specialization was reached independently in different geologic periods and, still more noteworthy, the principal teeth involved in the two groups are not homologous. The anteroposteriorly shortened basicranial area, known only in the latest stage of tillodonts, is unlike the elongate basicranial area observed in Paleocene taeniodonts, and the rostral portion, though robust, is relatively attenuated in comparison with the shortened and anteriorly deepened taeniodont snout. There is no particular resemblance between upper molar teeth in the earlier forms of each group; however, the conoryctid-type lower molars with their somewhat higher trigonid and hypsodont outer walls approximate the esthonychid type, although the structure of the talonid is distinctly different. Moreover, the foot structures in the two groups, though in part largely adaptive in importance, have early evolved in entirely different directions.

The rodentlike incisors of the later tillodonts led A. S. Woodward to regard them as rodents, and indeed the teeth so modified may well be homologous, although there is no proof for this. However, as Weber and Gregory have shown, there is no justification for this assignment and the fossil record itself shows the development of rodentlike incisors to be obviously a case of convergence. The peculiar trihedral ilium of the tillodonts might be regarded as rodentlike, but I regard this as basically primitive among mammals, noted in monotremes, didelphid marsupials, and certain insectivores, pantodonts, creodonts, and edentates as well.

Insectivore resemblance is probably in a large measure due to the almost "prototypal" character of this order with respect to several groups of mammals, and also undoubtedly to the very wide range of

characters represented by the various families. Cope regarded *Esthonyx,* though not the later tillodonts, as an insectivore, this because of certain resemblances to *Erinaceus.* It should be noted, however, as has been mentioned in a foregoing section, that the enlarged upper incisor in the two may not be homologous. It is I^1 in *Erinaceus.* Moreover, the basicranial region in *Erinaceus* bears little or no resemblance to that of the tillodonts. There are, of course, many points of similarity between tillodonts and insectivores, and likewise between tillodonts and creodonts, but whether the correspondence is closer to one or to the other or whether, as Gregory (1910, p. 293) has postulated, derivation was from an earlier insectivore-creodont stock is not clearly evident.

A general structure of the tillodont teeth somewhat resembling those of the primate *Pelycodus* was observed by Cope, and what I believe to be an even greater similarity was observed in comparison with arctocyonid teeth of the chriacine type, i.e., *Chriacus* and *Deltatherium.* On the other hand, much may be said in favor of the *Pantolambda* type of dentition. I do not mean to imply a derivation of *Esthonyx* teeth from *Pantolambda* itself, but feel there is a basic cheek-tooth pattern suggesting relationships through a pre-Torrejonian ancestry (possibly within the Arctocyonidae?). *Pantolambda* has already become too specialized with distinctly crescentic cusps in both the upper and lower teeth. The stylar development of the upper cheek teeth, except for the presence of a small mesostyle, is comparable to that in *Trogosus;* however, *Pantolambda* lacks the sweeping hypoconal ridge seen in both *Trogosus* and *Esthonyx.* The correspondence of the lower molars to those of *Trogosus* is rather striking, even to the metastylid; however, the external walls are distinctly less hypsodont and more compressed anteroposteriorly. Much of the resemblance is undoubtedly due to parallelism, evolving at different geologic times, but possibly from basically similar patterns. The anterior teeth, of course, are quite different in their relative development, but this is a later modification in the tillodont line, but weakly shown in *Esthonyx,* so probably not significant in earlier Paleocene time.

The basicranial region of *Pantolambda* is not preserved or exposed in the American Museum specimens figured by Matthew (1937) so that many of the more conservative skull characters are not evident; however, comparison is permitted with other skeletal portions and many points of resemblance noted. The gross form of most limb elements is largely adaptive in significance. Modification in one way or another to methods of locomotion and food getting and similar habits will be correlated with similar-appearing structures. Nevertheless,

there is much to be said for the basic character of the shapes, arrangement, and relative proportions of the elements of the carpus and tarsus. In consideration of these, I am much impressed by the striking similarity noted between the tillodonts and *Pantolambda* in both the carpus and tarsus, in spite of the quite different modification of the distal portions of the feet, with Pantolambda decidedly more ungulate. I do not know what foot structure *Deltatherium* or *Chriacus* may have possessed. It is likely that the manus would be similar, but I suspect that the more creodont tarsus would prevail. The tillodont tarsus, as has been noted in its description, is most like that in *Pantolambda* and *Periptychus*, or of a taligrade type according to Matthew's arrangement of the orders.

So much for the supposed earlier history of the order. During Eocene time it has been generally assumed, and I know of no evidence against it, that *Trogosus* and *Tillodon* were derived from *Esthonyx;* however, the species from which they were derived is not clearly evident. It may well have been from *E. acutidens,* but in that case there appears to have been a remarkable transition, apparently in Green River time, not all recorded in the Wyoming and Colorado fluviatile equivalents. One is tempted to postulate derivation of the middle Eocene forms from some larger and earlier *Esthonyx,* such as *E. grangeri,* with the absent intervening stages not recorded in the Rocky Mountain region. On the other hand, *E. grangeri* itself has no particular characteristics to recommend it, other than its size, and possibly the less-developed state of the posterior lobe of P_4, as the upper teeth of this species are less likely looking than those of *E. acutidens.* The situation with regard to *Trogosus* and *Tillodon* would, however, not appear to be unique; perhaps no more so than that with regard to the immediate ancestry of such genera as *Hyrachyus* and *Palaeosyops.*

REFERENCES

ABEL, OTHENIO.

    1914. Die vorzeitlichen Säugetiere, pp. i-v, 1-309 (52-53), figs. 1-250 (26). Jena.

    1919. Die Stämme der Wirbeltiere, pp. i-xviii, 1-914 (728), figs. 1-669. Berlin and Leipzig.

BRADLEY, WILMOT H.

    1926. Shore phases of the Green River formation in northern Sweetwater County, Wyo. U. S. Geol. Surv. Prof. Pap. 140-D, pp. 121-131, figs. 7-8, pls. 58-62.

    1929. The varves and climate of the Green River epoch. U. S. Geol. Surv. Prof. Pap. 158-E, pp. 87-110, figs. 14-15, pls. 11-14.

    1931. Origin and microfossils of the oil shale of the Green River formation of Colorado and Utah. U. S. Geol. Surv. Prof. Pap. 168, pp. i-vi, 1-58, figs. 1-3, pls. 1-28.

Brown, Roland W.

1929. Additions to the floras of the Green River formation. U. S. Geol. Surv. Prof. Pap. 154-J, pp. 279-293, 7 pls.

1934. The recognizable species of the Green River flora. U. S. Geol. Surv. Prof. Pap. 185-C, pp. 45-77, pls. 8-15.

Chardin, P. Teilhard de.

1922. Les mammifères de l'Éocène inférieur Français et leurs gisements. Ann. de Pal., vol. 10, pp. 171-176; vol. 11, pp. 1-108 (55-56), figs. 1-42 (30), pls. 1-8 (3, figs. 18, 19, 26).

Cope, Edward D.

1869. Synopsis of extinct Mammalia of New Jersey. Appendix C, Geology of New Jersey, pp. 739-742 (740).

1873a. On the extinct Vertebrata of the Eocene of Wyoming, observed by the expedition of 1872, with notes on the geology. 6th Ann. Rep. U. S. Geol. Surv. Terr., pp. 545-649 (605), pls. 1-6.

1873b. On the short-footed Ungulata of the Eocene of Wyoming. Proc. Amer. Philos. Soc., vol. 13, pp. 38-74 (42-43), pls. 1-4.

1873c. On the flat-clawed Carnivora of the Eocene of Wyoming. Proc. Amer. Philos. Soc., vol. 13, pp. 198-209 (208-209), 2 pls.

1874. Report upon vertebrate fossils discovered in New Mexico, with description of new species. Geogr. Expl. and Surv. West of 100th Meridian, Appendix FF, Ann. Rep. Chief of Engineers for 1874, pp. 1-18 (6-8).

1875. Systematic catalogue of Vertebrata of the Eocene of New Mexico, collected in 1874. Geogr. Expl. and Surv. West of 100th Meridian, pp. 1-37 (24).

1876a. On the supposed Carnivora of the Eocene of the Rocky Mountains. Proc. Acad. Nat. Sci. Philadelphia, vol. 27 (1875), pp. 444-449 (447-448).

1876b. On the Taeniodonta, a new group of Eocene Mammalia. Proc. Acad. Nat. Sci. Philadelphia, vol. 28, p. 39.

1877. Report upon the extinct Vertebrata obtained in New Mexico by parties of the expedition of 1874. Rep. U. S. Geogr. Surv. West of 100th Meridian, vol. 4, Paleontology, pt. 2, pp. 1-370 (83-85, 153-157), pls. 22-83 (40, figs. 26-33).

1880. The northern Wasatch fauna. Amer. Nat., vol. 14, pp. 908-909.

1881. On the Vertebrata of the Wind River Eocene beds of Wyoming. Bull. U. S. Geol. and Geogr. Surv. Terr., vol. 6, art. 8, pp. 183-202 (185-186).

1882. Contributions to the history of the Vertebrata of the lower Eocene of Wyoming and New Mexico, made during 1881. Proc. Amer. Philos. Soc., vol. 20, pp. 139-197 (146-148), 1 fig. (Also Paleont. Bull. No. 34.)

1883. On the mutual relations of the bunotherian Mammalia. Proc. Acad. Nat. Sci. Philadelphia, pp. 77-83.

1884a. The Vertebrata of the Tertiary formation of the West. Book 1, Rep. U. S. Geol. Surv. Terr., vol. 3, pp. i-xxxiv, 1-1009 (185-188, 194-195, 197-198, 202-211), figs. 1-38, pls. 1-75a (pl. 24a, figs. 17-25, pl. 24c, figs. 1-10).

1884b. The Creodonta. Amer. Nat., vol. 18, pp. 255-267, 344-353, 478-485 (351, 479-480), figs. 1-30 (23-24).

1885a. Mr. Lydekker on *Esthonyx*. Geol. Mag., n. s., decade 3, vol. 2, pp. 526-527.

1885b. Polemics in Paleontology. Amer. Nat., vol. 19, pp. 1207-1208 (1208).

1887. The origin of the fittest. Essays on Evolution, pp. i-xix, 1-467 (343), 81 figs., 5 pls. New York.

1888a. The mechanical causes of the origin of the dentition of the Rodentia. Amer. Nat., vol. 22, pp. 3-13 (4), figs. 1-9.

1888b. The vertebrate fauna of the Puerco epoch. Amer. Nat., vol. 22, pp. 161-163 (163).

1888c. Lydekker's catalogue of fossil Mammalia in the British Museum, Part V. Amer. Nat., vol. 22, pp. 164-165.

1889a. The mechanical causes of the development of the hard parts of the Mammalia. Journ. Morph., vol. 3, pp. 137-288 (144, 146, 220-221, 261-263), figs. 1-93 (48), pls. 9-14.

1889b. Synopsis of the families of Vertebrata. Amer. Nat., vol. 23, pp. 849-877 (876).

1891a. Flower and Lydekker's mammals. Amer. Nat., vol. 25, pp. 1116-1118 (1117).

1891b. Syllabus of lectures on geology and paleontology, pp. 1-90 (73), figs. 1-60. Philadelphia.

1893. Forsyth Major and Rose on the theory of dental evolution. Amer. Nat., vol. 27, pp. 1014-1016 (1015).

1898. Syllabus of lectures on the Vertebrata, pp. 1-135 (115), figs. 1-66 (revision of 1891b). Philadelphia.

EDINGER, TILLY.

1929. Die fossilen Gehirne. Ergebn. Anat. und Entw. (III, Abt. Zeitschr. ges. Anat.), vol. 28, pp. 1-249 (148-149), figs. 1-203.

1933. Die Foramina parietalia der Säugetiere. Zeitschr. Anat. und Entw. (1, Abt. Zeitschr. ges. Anat.), vol. 102, pts. 2 and 3, pp. 266-289 (271), figs. 1-28.

FLOWER, WILLIAM H.

1876. The extinct animals of North America. Proc. Roy. Inst. Great Britain, vol. 8, pp. 103-125 (122-124), figs. 1-3 (3).

FLOWER, WILLIAM H., and LYDEKKER, RICHARD.

1891. An introduction to the study of mammals, living and extinct, pp. i-xvi, 1-763 (441-442), figs. 1-357 (193). London.

GAZIN, C. LEWIS.

1952. The lower Eocene Knight formation of western Wyoming and its mammalian faunas. Smithsonian Misc. Coll., vol. 117, No. 18, pp. 1-82, 11 pls., 6 figs.

GRANGER, WALTER.

1918. New tillodont skull from the Huerfano Basin, Colorado (abstract). Proc. Paleont. Soc.-Bull. Geol. Soc. Amer., vol. 29, pt. 1, pp. 147-148.

GREGORY, WILLIAM K.

1910. The orders of mammals. Bull. Amer. Mus. Nat. Hist., vol. 27, pp. 1-524 (292-294, 445), figs. 1-32.

HAY, OLIVER P.
    1930. Second bibliography and catalogue of the fossil vertebrata of North
        America. Carnegie Inst. Washington Publ. 390, vol. 2, pp. i-xiv,
        1-1074 (853-856).

LEIDY, JOSEPH.
    1868. Notice of some remains of extinct pachyderms. Proc. Acad. Nat.
        Sci. Philadelphia, vol. 20, pp. 230-233 (232).
    1869. The extinct mammalian fauna of Dakota and Nebraska, with a
        synopsis of the mammalian remains of North America. Journ. Acad.
        Nat. Sci. Philadelphia, ser. 2, vol. 7, pp. 23-472 (403), pls. 1-30
        (30, figs. 45-46).
    1871a. Remains of extinct mammals from Wyoming. Proc. Acad. Nat.
        Sci. Philadelphia, vol. 23, pp. 113-116.
    1871b. Remarks on fossil vertebrates from Wyoming. Proc. Acad. Nat.
        Sci. Philadelphia, vol. 23, pp. 228-229 (229).
    1872a. On the fossil vertebrates of the early Tertiary formation of Wyo-
        ming. U. S. Geol. Surv. of Montana and portions of Adjacent
        Territories, 5th Ann. Rep. of Progress, pp. 353-372 (359-360).
    1872b. Remarks on some extinct mammals. Proc. Acad. Nat. Sci. Phila-
        delphia, vol. 24, pp. 37-38.
    1873. Contributions to the extinct vertebrate fauna of the western territories.
        Rep. U. S. Geol. Surv. Terr., vol. 1, pp. 1-358 (71-75, 328-329),
        pls. 1-37 (5, figs. 1-3; 6, fig. 43).

LEMOINE, VICTOR.
    1889. Considérations générales sur les vertébrés fossiles des environs de
        Reims et spécialement sur les mammifères de la faune Cernaysienne.
        C.-R. Congr. Internat. Zool., pp. 233-279 (237), figs. I-VIII (VII-9).
        Paris.
    1891. Étude d'ensemble sur les dents des mammifères fossiles des environs
        de Reims. Bull. Soc. Geol. France, ser. 3, vol. 19, pp. 263-290
        (276), pls. 10-11 (10, figs. 32n, 32s, 32i).

LYDEKKER, RICHARD.
    1885. Note on the generic identity of the genus *Esthonyx*, Cope, with *Platy-
        choerops*, Charlesworth (= *Miolophus*, Owen). Geol. Mag., n. s.,
        decade 3, vol. 2, pp. 360-361.

MARSH, OTHNIEL C.
    1871. Notice of some new fossil mammals from the Tertiary formation.
        Amer. Journ. Sci. and Arts, ser. 3, vol. 2, pp. 35-44 (36).
    1873. Notice of new Tertiary mammals (continued). Amer. Journ. Sci.
        and Arts, vol. 5, pp. 485-488 (485-486).
    1874. Notice of new Tertiary mammals. III. Amer. Journ. Sci. and Arts.,
        ser. 3, vol. 7, pp. 531-534 (533-534).
    1875a. New order of Eocene mammals. Amer. Journ. Sci. and Arts, vol. 9,
        p. 221.
    1875b. Notice of new Tertiary mammals. IV. Amer. Journ. Sci. and Arts,
        vol. 9, pp. 239-250 (241-242).
    1876. Principal characters of the Tillodontia, Part 1. Amer. Journ. Sci.
        and Arts, vol. 11, pp. 249-251, 1 fig., pls. 8-9.

MATTHEW, WILLIAM D.

1915. A revision of the lower Eocene Wasatch and Wind River faunas. Part II. Order Condylarthra, family Hyopsodontidae. Bull. Amer. Mus. Nat. Hist., vol. 34, pp. 311-328, figs. 1-10.

1937. Paleocene faunas of the San Juan basin, New Mexico. Trans. Amer. Philos. Soc., n. s., vol. 30, pp. i-viii, 1-510, figs. 1-85, pls. 1-65.

NICHOLSON, HENRY A., and LYDEKKER, RICHARD.

1889. A manual of paleontology. Vol. 2, pt. 3, Palaeozoology, Vertebrata, pp. i-xi, 889-1624 (1408-1410), figs. 813-1419. Edinburgh and London.

OSBORN, HENRY F.

1897. The Huerfano lake basin, southern Colorado, and its Wind River and Bridger fauna. Bull. Amer. Mus. Nat. Hist., vol. 9, art. 21, pp. 247-258 (249, 252, 254, 257).

1907. Evolution of mammalian molar teeth. Biological Studies and Addresses, vol. 1, pp. i-ix, 1-250 (151), figs. 1-215 (116). New York.

RUSSELL, LORIS S.

1935. A middle Eocene mammal from British Columbia. Amer. Journ. Sci., vol. 29, pp. 54-55, figs. 1-4.

SCOTT, WILLIAM B.

1937. A history of land mammals in the Western Hemisphere, pp. i-xiv, 1-786 (224, 229), figs. 1-420 (155). New York.

SEARS, JULIAN D., and BRADLEY, WILMOT H.

1924. Relations of the Wasatch and Green River formations in northwestern Colorado and southern Wyoming, with notes on the oil shales in the Green River formation. U. S. Geol. Surv. Prof. Pap. 132-F, pp. 93-107, fig. 9, pls. 24-25.

SIMPSON, GEORGE G.

1929. Tillodontia. Encycl. Brit., 14th ed., vol. 22, pp. 215-216, 1 fig.

1937. Notes on the Clark Fork, upper Paleocene, fauna. Amer. Mus. Nov. No. 954, pp. 1-24 (4-11), figs. 1-6 (1-4).

1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., vol. 85, pp. i-xvi, 1-350 (68).

SINCLAIR, WILLIAM J., and GRANGER, WALTER.

1911. Eocene and Oligocene of the Wind River and Bighorn Basins. Bull. Amer. Mus. Nat. Hist., vol. 30, pp. 83-117, figs. 1-4, pls. 4-11.

1912. Notes on the Tertiary deposits of the Bighorn Basin. Bull. Amer. Mus. Nat. Hist., vol. 31, art. 5, pp. 57-67 (60), figs. 1-2, pls. 5-6.

WEBER, MAX.

1928. Die Säugetiere. Vol. 2, Systematischer Teil, 2d ed., pp. i-xxiv, 1-898 (168-169), figs. 1-573 (96). (1st ed., 1904, pp. i-xi, 1-866 (513-514), figs. 1-567 (358).) Jena.

WINGE, HERLUF.

1923. Pattedyr-Slaegter. Vol. 1. Monotremata, Marsupialia, Insectivora, Chiroptera, Edentata, pp. i-viii, 1-360 (129-131). Copenhagen.

WOODWARD, ARTHUR S.

1898. Outlines of vertebrate paleontology for students of zoology, pp. i-xxiv, 1-470 (374-377), figs. 1-228 (212-213). Cambridge, England.

WORTMAN, JACOB L.

   1886. The comparative anatomy of the teeth of the Vertebrata. Reprinted
         from the American System of Dentistry, pp. 351-515 (425-428, 433-
   434), figs. 187-269 (207), pls. 1-6.
   1897. The Ganodonta and their relationship to the Edentata. Bull. Amer.
         Mus. Nat. Hist., vol. 9, art. 6, pp. 59-110 (61-63), figs. 1-36.

YOUNG, CHUNG-CHIEN.

   1937. An early Tertiary vertebrate fauna from Yuanchü. Bull. Geol. Surv.
         China, vol. 17, Nos. 3-4, pp. 413-438 (434-436), figs. 1-16 (16).

ZITTEL, KARL A. VON. (Edited by Broili and Schlosser.)

   1923. Grundzüge der Paläontologie (Paläozoologie), Pt. 2, Vertebrata, pp.
         1-v, 1-706 (450-451), figs. 1-800 (572-573). München and Berlin.
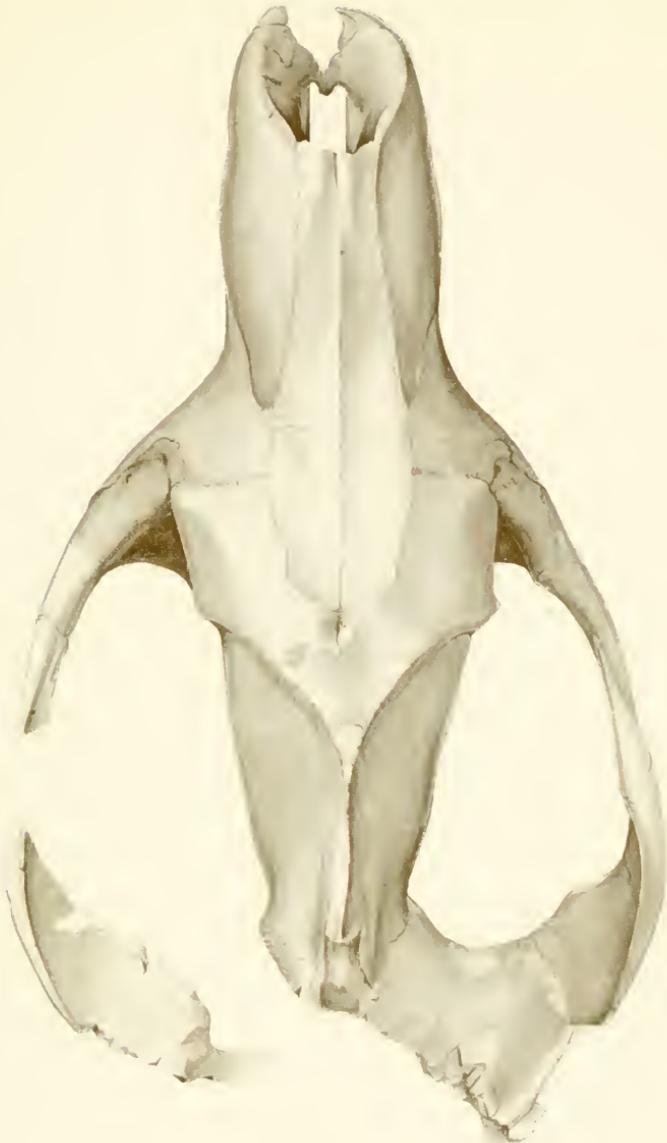
TILLODONT SKULL FROM THE BRIDGER MIDDLE EOCENE

Trogosus hyracoides (Marsh): Skull (U.S.N.M. No. 17886), dorsal view.
Approximately one-half natural size.
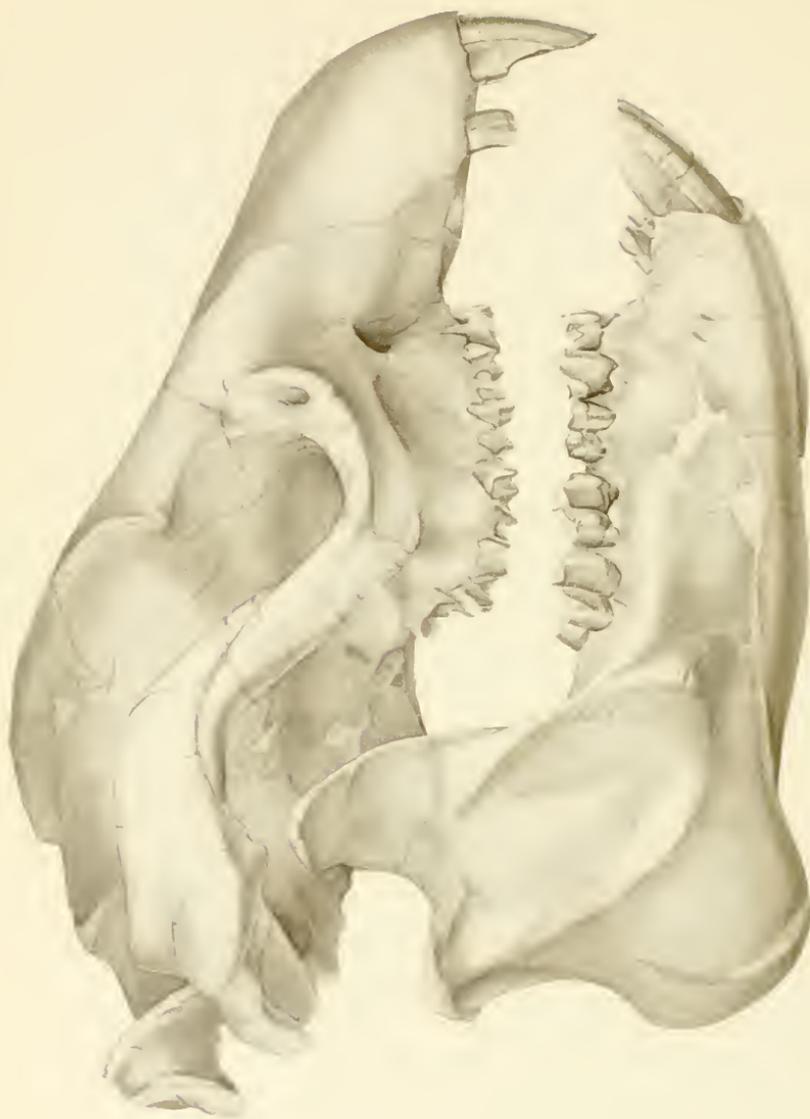
TILLODONT SKULL AND JAWS FROM THE BRIDGER MIDDLE EOCENE

Trogosus hyracoides (Marsh): Skull and mandible (U.S.N.M. No. 17886), lateral view. Approximately one-half natural size.
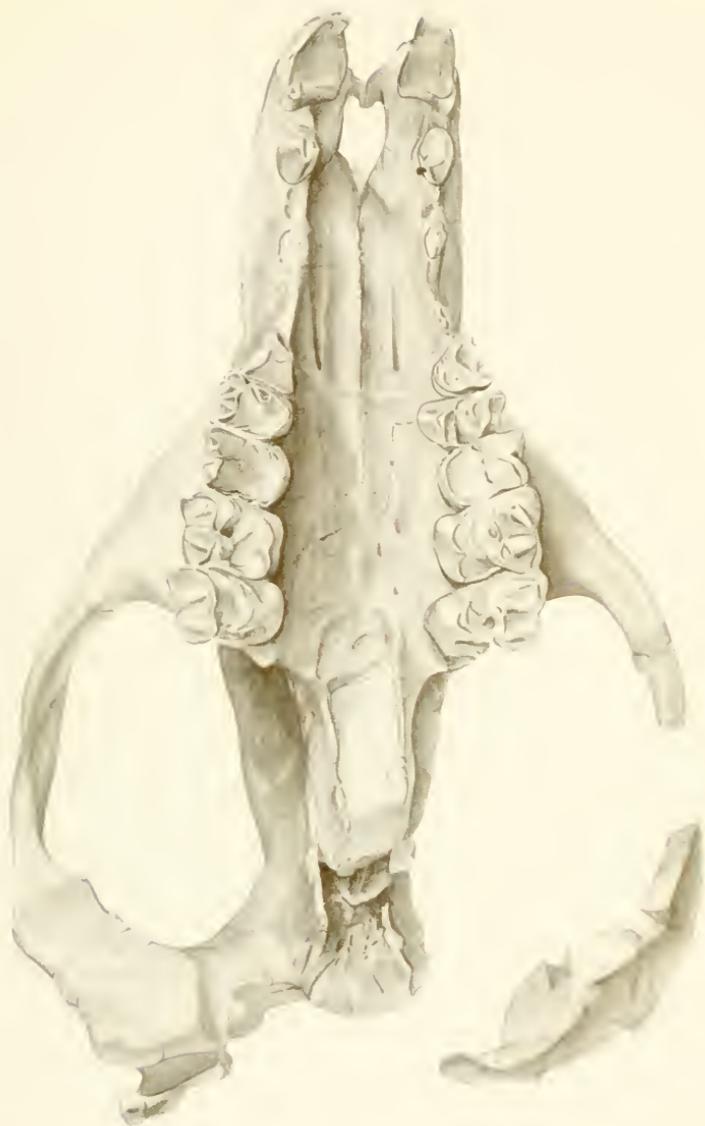
TILLODONT SKULL FROM THE BRIDGER MIDDLE EOCENE

Trogosus hyracoides (Marsh) : Skull (U.S.N.M. No. 17886), ventral view.
Approximately one-half natural size.

TILLODONT MANDIBLE FROM THE BRIDGER MIDDLE EOCENE

Trogosus hyracoides (Marsh) : Mandible (U.S.N.M. No. 17886), dorsal view
Approximately one-half natural size.

TILLODONT SKULL FROM THE HUERFANO MIDDLE EOCENE

Trogosus grangeri, new species: Skull (A.M. No. 17008), type specimen, dorsal view. Approximately one-half natural size.
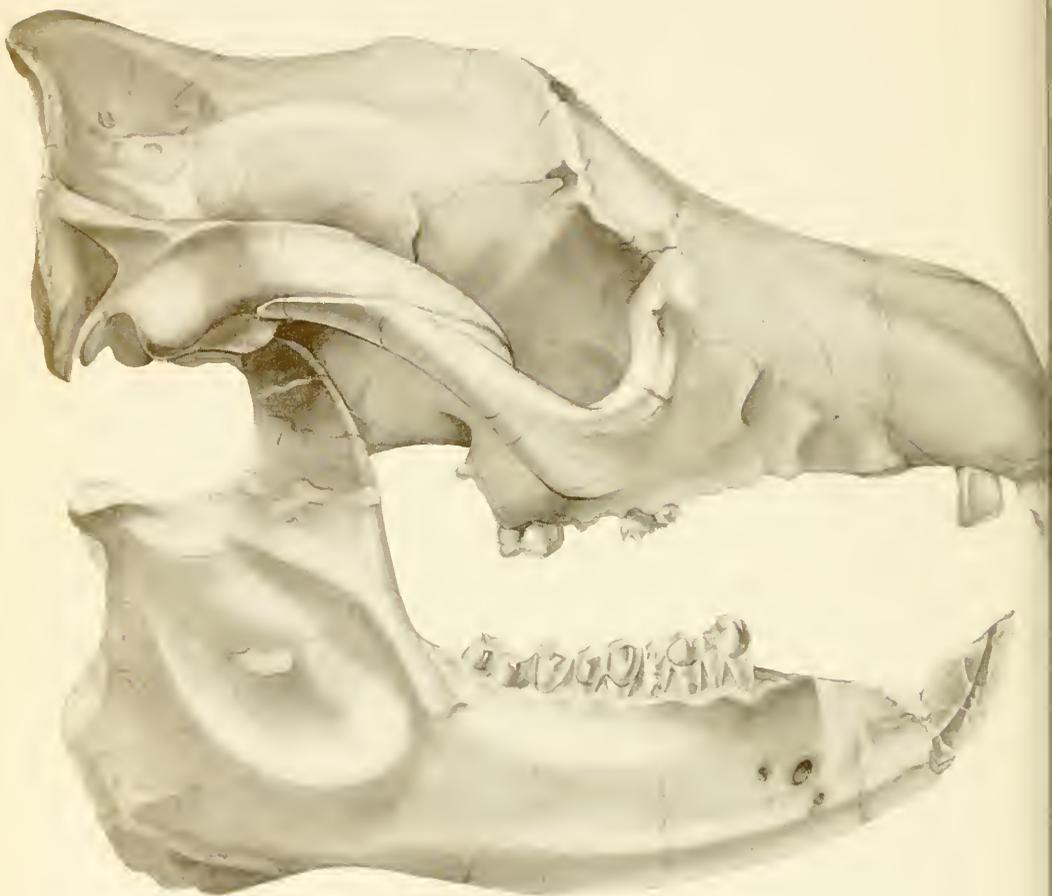
TILLODONT SKULL AND JAWS FROM THE HUERFANO MIDDLE EOCENE

Trogosus grangeri, new species: Skull and mandible (A.M. No. 17008), type specimen, lateral vie
Approximately one-half natural size.
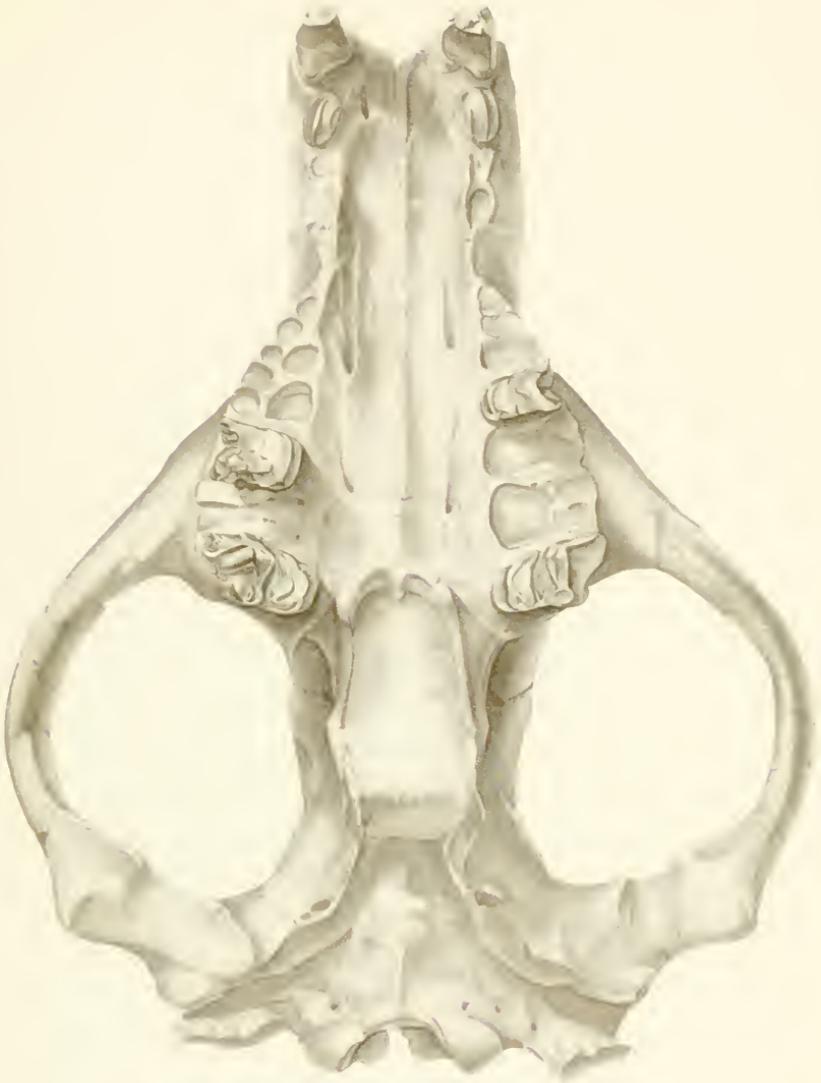
TILLODONT SKULL FROM THE HUERFANO MIDDLE EOCENE

Trogosus grangeri, new species: Skull (A.M. No. 17008), type specimen, ventral view. Approximately one-half natural size.

TILLODONT MANDIBLE FROM THE HUERFANO MIDDLE EOCENE

Trogosus grangeri, new species: Mandible (A.M. No. 17008), type specimen, dorsal view. Approximately one-half natural size.
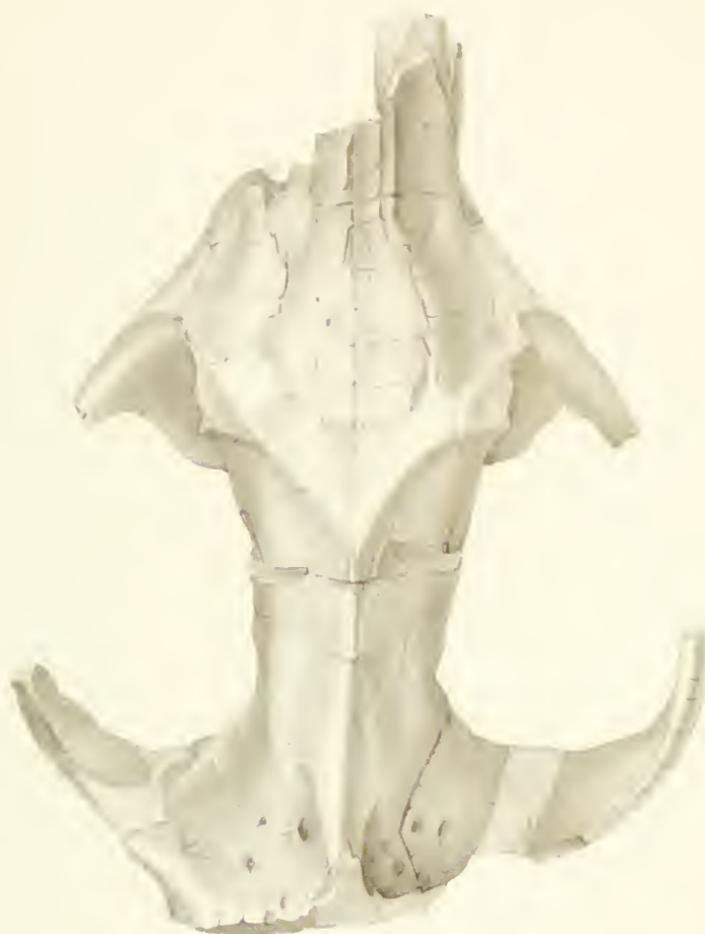
TILLODONT SKULL FROM THE HUERFANO MIDDLE EOCENE

Trogosus hillsii, new species: Skull (U.S.N.M. No. 17157), type specimen, dorsal view. Approximately one-half natural size.

TILLODONT SKULL AND JAWS FROM THE HUERFANO MIDDLE EOCENE

Trogosus hillsii, new species: Skull and mandible (U.S.N.M. No. 17157), type specimen, lateral view. Approximately one-half natural size.

TILLODONT SKULL FROM THE HUERFANO MIDDLE EOCENE

Trogosus hillsii, new species: Skull (U.S.N.M. No. 17157), type specimen, ventral view. Approximately one-half natural size.

TILLODONT MANDIBLE FROM THE HUERFANO MIDDLE EOCENE

Trogosus hillsii, new species: Mandible (U.S.N.M. No. 17157), type specimen, dorsal view. Approximately one-half natural size.

TILLODONT SKULL FROM THE BRIDGER MIDDLE EOCENE

Tillodon fodiens (Marsh), new genus: Skull (Y.P.M. No. 11087), type specimen, dorsal view. Approximately one-half natural size.
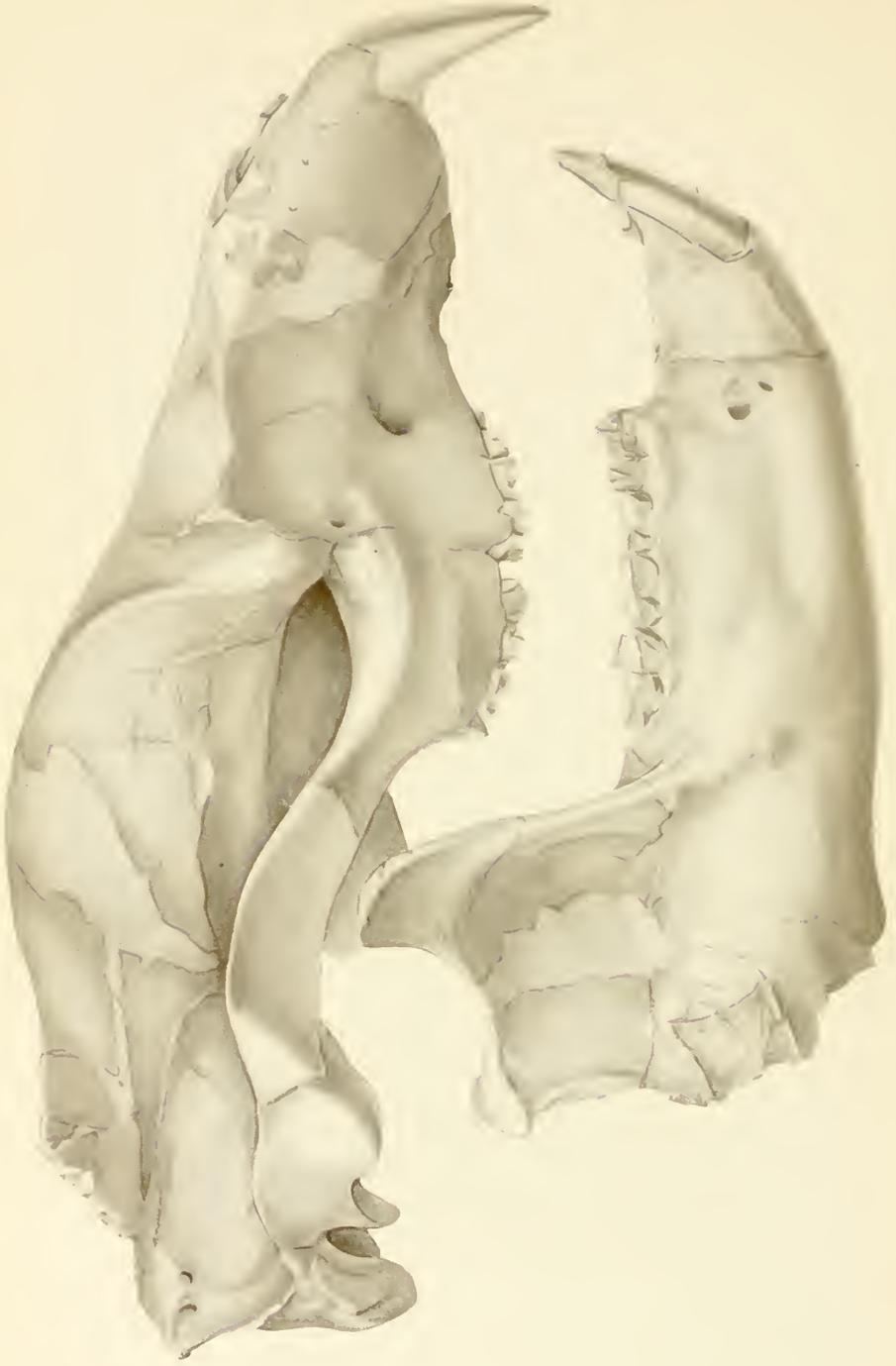
TILLODONT SKULL AND JAWS FROM THE BRIDGER MIDDLE EOCENE

Tillodon fodiens (Marsh), new genus: Skull and mandible (Y.P.M. No. 11087), type specimen, lateral view. Approximately one-half natural size.
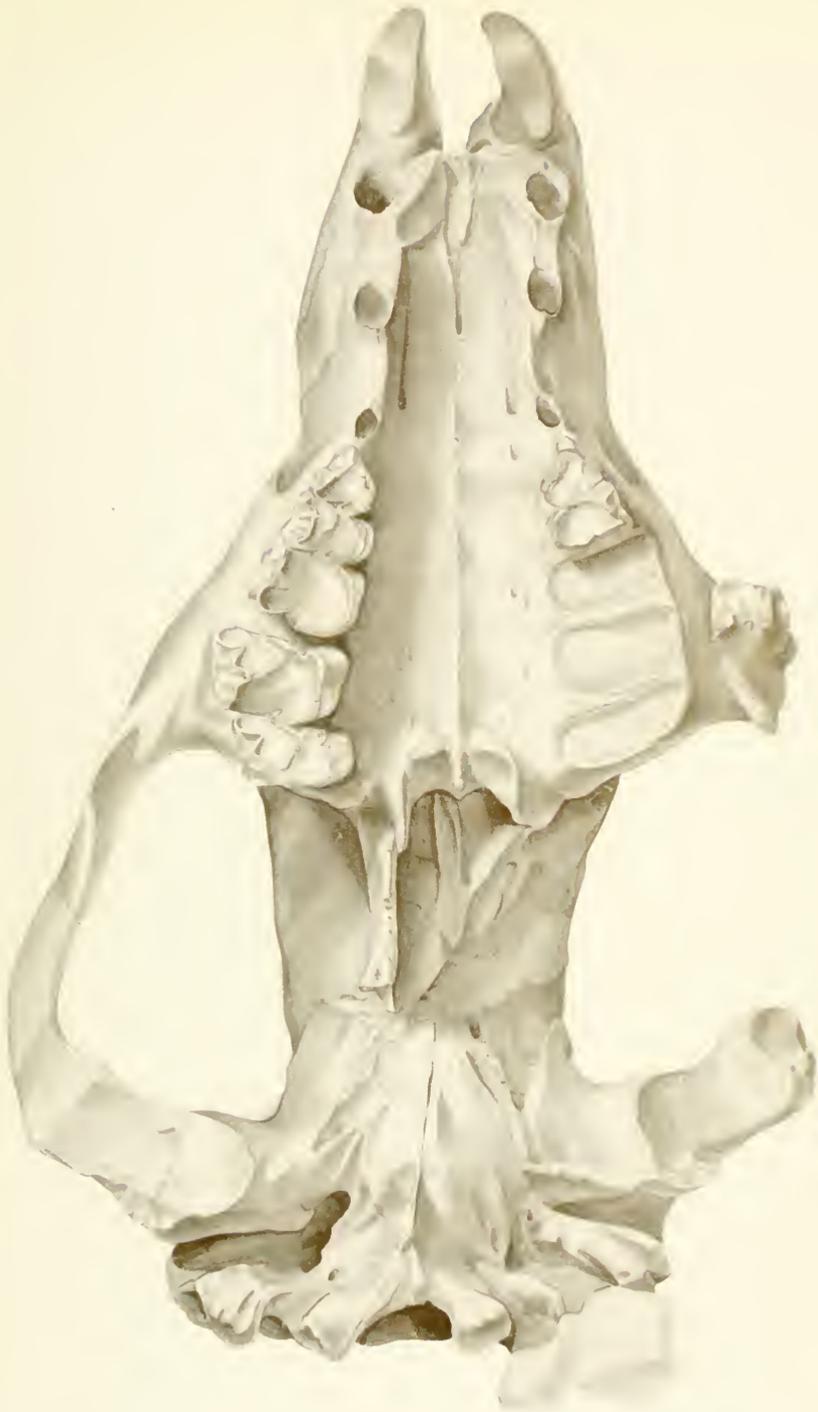
TILLODONT SKULL FROM THE BRIDGER MIDDLE EOCENE

Tillodon fodiens (Marsh), new genus: Skull (Y.P.M. No. 11087), type
specimen, ventral view. Approximately one-half natural size.

TILLODONT MANDIBLE FROM THE BRIDGER MIDDLE EOCENE

Tillodon fodiens (Marsh), new genus: Mandible (Y.P.M. No. 11087), type specimen, dorsal view. Approximately one-half natural size.