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A Revision of the Geology and Paleontology of the Bijou Hills, South Dakota

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INTRODUCTION

The two Bijou Hills adjacent to the Missouri River in south-central South Dakota were the site of Hayden's early fossil vertebrate collections and are the type locality for four of Leidy's generic taxa: *Leptarctus primus*, *Merycodus necatus*, *Hippodon speciosus*, and *Merychippus insignis*. The present report is the result of an investigation of these hills and the fauna obtained from them. In 1934 the senior author relocated the two hills from Hayden's original description and on six subsequent visits prospected and studied in detail the fossiliferous deposits. The exact geographic location of these hills and the stratigraphic description of the Tertiary sediments are presented here. A new formation, the Fort Randall, has been named. A type locality has been designated for the sediments called the "Rosebud Beds" by Gidley (Matthew and Gidley, 1904).

Literature on fossil mammals is replete with inadequate type specimens and undefined type localities, but seldom has one locality and one "fauna" shared in so many vicissitudes. The type specimens nearly defy either definitions or diagnosis; the type of *Merycodus necatus*, a partial ramus, is lost; the type of *Leptarctus primus* is one premolar; the type of *Hippodon speciosus* is a lower cheek tooth; the type of *Merychippus insignis* is a maxillary fragment with two milk premolars; Hayden (1857,

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p. 157) mistakenly included the name "*Hipparion occidentale*" in the fauna. The type of *H. occidentale* consisted of five upper molars and is not from the Bijou Hills. Moreover, the exact locality from which it came forever will be uncertain (see below, p. 18).

The types and referred examples of the Bijou Hills genera have been thoroughly studied as befits their long tenure in North American paleontological literature. We have established a neotype for the lost type of *Merycodus necatus*. The types of *Leptarctus primus* and *Hippodon speciosus* are figured and discussed. *Hippodon speciosus* is here considered a *nomen dubium*. The two milk teeth representing the type specimen of *Merychippus insignis* have been matched closely to an immature dentition and complete skulls from the Lower Snake Creek deposits of western Nebraska.

Two sets of deposits are well exposed at the Bijou Hills (see fig. 1B, C). A lower set (Fort Randall, new formation) is the deposit from which the neotype and paratype of *Merycodus necatus* were collected. It is probable that the lost type of *M. necatus* and the types of *Leptarctus primus* and *Merychippus insignis* were also collected from the Fort Randall Formation. The higher set, or the undifferentiated Valentine-Ash Hollow equivalents, have yielded fragments of horse teeth and a proboscidean tusk. The type of *Hippodon speciosus* might have been derived from either the Fort Randall or the undifferentiated Valentine-Ash Hollow deposits.

The Addendum by Mr. Stout is presented in its entirety, except for the legends and references which have been incorporated in the main body of the paper. Whereas Stout's rodent identifications are accepted unreservedly, the geologic usages and temporal correlations he employs do not, in all cases, agree with ours.

ACKNOWLEDGMENTS

The late Mr. Childs Frick not only provided the means for the collection and documentation of the specimens mentioned in this paper, but he also guided the basic research on them. The many trips to the Bijou Hills were made by the senior author at the request of Mr. Frick who long had realized the need for better documentation of Leidy's early types. Some of the trips were fruitless, and none was really successful in terms of quantity or quality of collections. The few small exposures on the Bijou Hills have produced only partial or fragmentary specimens numbering fewer than 40 in the Frick Collection. Our indebtedness to Mr. Childs Frick for this support and for much more is here acknowledged.

We are grateful to the members in the Frick Laboratory who have, by their interest and assistance, helped to bring this paper to publication. Dr. Malcolm C. McKenna, Dr. Richard H. Tedford, and Mr. Ted

Galusha have critically read and given valuable suggestions. Mr. Raymond J. Gooris has prepared the figures. Dr. Richard Estes has furnished the identification of the turtle fragments from the Bijou Hills. We thank Dr. Horace G. Richards of the Academy of Natural Sciences of Philadelphia for his assistance and generosity in making the Bijou Hills type specimens in his collection available for study and casting.

The following abbreviations are used:

A.M.N.H., the American Museum of Natural History, Department of Vertebrate Paleontology

A.N.S.P., Academy of Natural Sciences of Philadelphia

F.A.M., Frick American Mammals, the American Museum of Natural History

U.S.N.M., United States National Museum of the Smithsonian Institution

HISTORY OF THE BIJOU HILLS

The exact location of the two Bijou Hills of Hayden has been forgotten in the twentieth century because of their inaccessibility by automobile, but in Hayden's time the hills were prominent landmarks for all voyagers who traveled up the Missouri River by boat or along the river. The outcrops on the hills are clearly visible from the river (figs. 1A, 2). In a grass-covered country such outcrops would have attracted the attention of Hayden, and he did make several trips to them. The first was with F. B. Meek in 1853. The second was in the autumn of 1855. In 1856 Hayden accompanied Lieutenant G. K. Warren, a United States Army Topographical Engineer, who commanded a reconnoitering expedition through Nebraska and the Dakota territory. The trip, by steamboat up the Missouri, was halted when a heavy spring flood grounded the boat on a sand bar at Cedar Island.¹ Some members of the expedition set out on foot for the 130-mile march to Fort Pierre. This line of march, which passed between the two main Bijou Hills and their eastern extension, is shown on Warren's military map of Nebraska and Dakota in 1855-1856 (Warren, 1858). The hills were relocated in 1934 from this map and Hayden's (1857b, p. 156) description which was as follows: "These Hills are of considerable interest, as forming an intermediate link uniting Bijou Hills to the main body of the Bad Lands. The two upper beds [G and H of section, p. 153] of the vertical section are represented at this locality. The last outlier of this deposit is seen at Bijou Hills on the opposite side of the Missouri River in lat.

¹ Cedar Island is not shown on a present-day map, for it lies under the waters of Fort Randall Reservoir. Cedar Island was about 15 miles west of the town of Lake Andes, South Dakota.

43½°. These are a group of isolated hills towering high above the surrounding country and forming prominent land marks for the voyager. The two highest hills border upon the river and are from four to six hundred feet in height. Farther into the interior are two other hills, the first about two miles long, and the second about eight miles, ranging in a nearly east and west course, sloping gently down toward the Coteau de Prairie. In the summer of 1853 I ascended one of the hills nearest the river in company with my friend Mr. Meek, and, from a denuded portion near the summit, we obtained several fragments of jaws and teeth belonging to two new species of mammals, which have been described by Dr. Leidy as *Hipparion speciosum* and *Merycadus* [*sic*] *necatus*. In the autumn of 1856 I discovered on the denuded summits of the same hills *Hipparion occidentalis*¹ and two new genera, *Leptarctus primus*, an animal allied to the raccoon, and *Merychippus insignis*, a remarkable new genus of ruminant horse.”

The town of Bijou Hills, founded in 1877, is situated inland about 8 miles east of Hayden's two Bijou Hills bordering the river. This eastern extension of the hills has been considered by some authors as the locality where Hayden obtained the fossils later described by Leidy (Stevenson, 1958, p. 137; Green, 1958, p. 140). A narrow range called the Iona Hills extends west of the Missouri and a little south for about 50 miles to the Red Hill Buttes near Carter, South Dakota. Hayden was also aware of this westward extension (1857b, p. 156).

There were no legal land surveys in Hayden's time, and even now the two hills present a difficult geographic description. The difficulty arises because of a peculiar combination of three different survey corrections (see fig. 1A): (1) The hills lie astride a township line; (2) there is an exceptionally large jog correction in the ranges; (3) the hills are in two different counties, yet border the Missouri River. Although these differences seem to separate the two hills widely, the bench marks on their summits are only 7200 feet apart.

“THE BIJOU QUARTZITE”²

Hayden (1857a, map and profile; 1857b, p. 157) was the first to recog-

¹ This was neither the type of, nor was it referable to, *Hipparion occidentale*. Leidy (1869, p. 282) corrected the error. Hayden actually collected the type of *Hipparion occidentale* in 1855 at some unknown point along the White River.

² So far as we can determine Agnew (1958, p. 129) was the first to use the term “Bijou quartzite.” Apparently Agnew did not intend this as a formal name, for he used the term interchangeably with “quartzitic sandstone,” “green quartzite,” and “greenish siliceous quartzite.”

nize and describe the lithology of the two Tertiary beds present on the Bijou Hills, thus: “. . . The two upper beds of the vertical section are represented at this locality. The last outlier of this deposit is seen at Bijou Hills on the opposite side of the Missouri River in lat. $43\frac{1}{2}^{\circ}$. . . The two highest hills border upon the river and are from four to six hundred feet in height. . . The summits . . . are capped with a bed of bluish-gray compact rock, quite variable in its character. Sometimes it is very fine, not unlike a metamorphic rock; again it is composed of an aggregation of particles of granular quartz, interspersed with a few small water-worn pebbles; then a coarse grained somewhat friable sandstone.” On Hayden’s geologic chart (1857b, p. 153) Bed H (upper) contains what was later named the “Bijou quartzite.”¹ The generalized section Hayden gave described the deposits on the hills as we have figured them in detail (fig. 1B, C).

The hard orthoquartzite layers hold up and form a ledge on a prominent range of hills only a few miles wide which extend in an east-west direction for at least 50 miles. The north and south Bijou Hills are only a portion of the east end of the range. Most of the range is capped by the characteristic Pliocene quartzitic layers, the so-called “Bijou Quartzite.” The quartzitic layers, or zones, commonly vary in thickness from 1 foot to 4 feet on the range called the “Iona Hills” extending westward toward Carter, South Dakota.

Beds containing the “Bijou Quartzite” have been mapped as “Bijou Formation” on several areal geology quadrangles of the South Dakota Geological Survey (table 1). Stevenson and Carlson (1950; see table 1 of the present paper) were the first of several geologists to map the “Bijou Formation.” In 1954 Stevenson (p. 86) formally named the Bijou Formation and stated, “Because of the changing lithologic character of this formation, no type section has been chosen, instead a typical section is presented.” Stevenson made no mention of the Bijou facies in this article. By 1958, as table 1 shows, the consensus among some geologists was that Stevenson’s formation was only a facies.

In 1958 Stevenson revised the “Bijou Formation” and selected a type locality, but, through an error of typography, omitted the real-estate section number as follows, “. . . 5 miles north of Academy, South Dakota, in the Bijou Hills (SW $\frac{1}{4}$, SE $\frac{1}{4}$ Sec. [?] T. 101 N., R. 69 W.)” The critical square mile represented in the omitted section number left the type lo-

¹ Hayden’s geologic and faunal charts of 1869 are not in complete agreement with his earlier ones, for, as his knowledge of western deposits enlarged, he altered his early concepts.

TABLE 1
 CHRONOLOGY OF THE TERMS "BIJOU FORMATION" AND "BIJOU FACIES" AS USED ON
 AREAL GEOLOGY MAPS OF THE SOUTH DAKOTA GEOLOGICAL SURVEY^a

Quadrangle	Author or Geologist	Date of Survey	Date Published	Bijou Formation	Bijou Facies	Valentine Formation	Ash Hollow Formation
Wakpala	Baldwin, Glass	1949	[1950] ^b	?	—	—	—
Bonesteel	Stevenson, Carlson	1950	1950	x	—	—	—
Lucas	Baker, Carlson	1949	1951	x	—	—	—
Dixon	Baker	1949	1951	x	—	—	—
Lake Andes	Stevenson, Carlson	1950	1951	x	—	—	—
Mahto	Baldwin	1950	1951	?	—	—	—
Iona	Baldwin, Baker	1948	1952	x	—	—	—
Herrick	Baker and others	1949–1950	1952	x	—	—	—
Gregory	Stevenson	1956–1957	1958	—	x	x	x
Wewela	Collins	1957	1958	—	x	x	x
KeyaPaha	Schoon, Sevon	1957	1958	—	x	x	x
Witten	Schoon	1957	[1958] ^b	—	x	x	x
Dallas	Stevenson	1957–1958	1959	x ^c	x ^d	x	x
Okreck	Sevon, Sevon	1958	1959	—	x	x	x
Winner	Collins	1957	1960	—	x	x	x

^a These maps were obtained from the South Dakota Geological Survey, Vermillion, South Dakota.

^b No date of publication on the maps. The dates 1950 and 1958 were given in *Publications of the South Dakota Geological Survey*, University of South Dakota, Vermillion, South Dakota, 1965.

^c The term "Bijou Formation" appears on the legend of the map.

^d The term "Bijou Facies" appears in the geology text on the back of the map.

cality still unfixed within the township. Stevenson's redefinition of the "Bijou Formation" was slanted heavily toward a facies concept: "One of the basic ideas therefore, regarding facies is that they are strata characterized by definite and easily distinguished lithology. Formations are also characterized by diagnostic lithologies, therefore, the Bijou facies can also be considered as a formation.

"Diagnostic lithologic properties which characterize the Bijou as a formation, a facies, and an easily mappable unit, is the nearly homogeneous [*sic*] composition, siliceous cement, greenish color and resistance to erosion. These properties quickly distinguish the Bijou facies from the other strata of the Mio-Pliocene stratigraphic unit of which it is a part."

It is our contention that the "Bijou Quartzite," or facies, is not a formation but a post-depositional cementation of certain sand beds that may, and does, occur throughout several different lithic units or formations of the Tertiary and is not confined to any of them. A similar but unrelated condition exists in the area of the Spanish Diggings south of Manville, Niobrara County, Wyoming, but there the rocks are known locally as the "Spanish Diggings quartzite."

Agnew (1958, p. 131) stated, ". . . the Bijou quartzite has been mapped in Brule, Charles Mix, and Gregory Counties, South Dakota . . . in Holt and Boyd Counties, Nebraska . . . occurs throughout an east-west extent of at least 150 miles." Agnew and Tychsen (1965, p. 44) chose to designate these silicified sands as the "Bijou Quartzite Facies." This is a good descriptive field term for a secondary rock condition, but it should never be used as a formal stratigraphic term.

Green (1958, p. 142) advised that, ". . . the term 'Bijou formation' either be dropped or its usage be held in abeyance until accurate stratigraphic collecting of fossil remains can be made." We are in agreement with Green, for the distinction of a rock unit is based on sediments which must be recognized before the fauna contained therein may be compared on a biostratigraphic basis with faunas of other rock units.

Stevenson (1954, p. 89) gave a faunal list¹ with his initial description of the "Bijou Formation" but gave no lithic allocation for his specimens. Green (1958, p. 142) stated: "A faunal list from scattered localities of specimens alleged to have come from the 'Bijou Formation' . . . is now understood to be a mixed collection of Lower Pliocene specimens and

¹For the sake of taxonomic stability the misspelled generic and specific names in Stevenson's lists are corrected: *Nannhippus* should be *Nannippus*; *Hippoclan* should be *Hippodon*; *Procamelus* cf. *P. calcaneus* may have been *P. calcaneum*; *Ustachoerus* should be *Ustatochoerus*; *moclicus* should be *modicus*; *Rhinoceras* is *rhinoceros*; *Mustels* is *mustelid*.

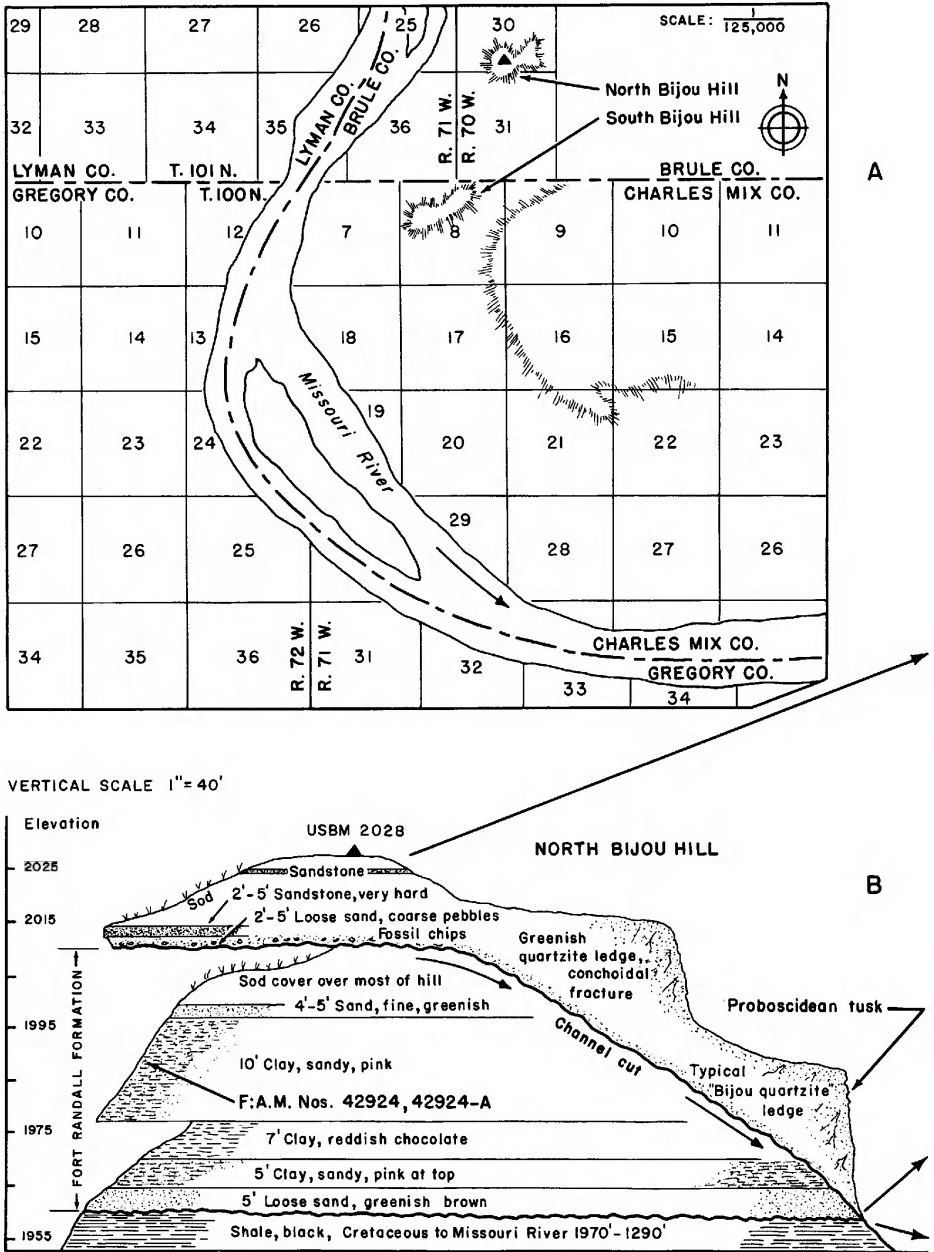
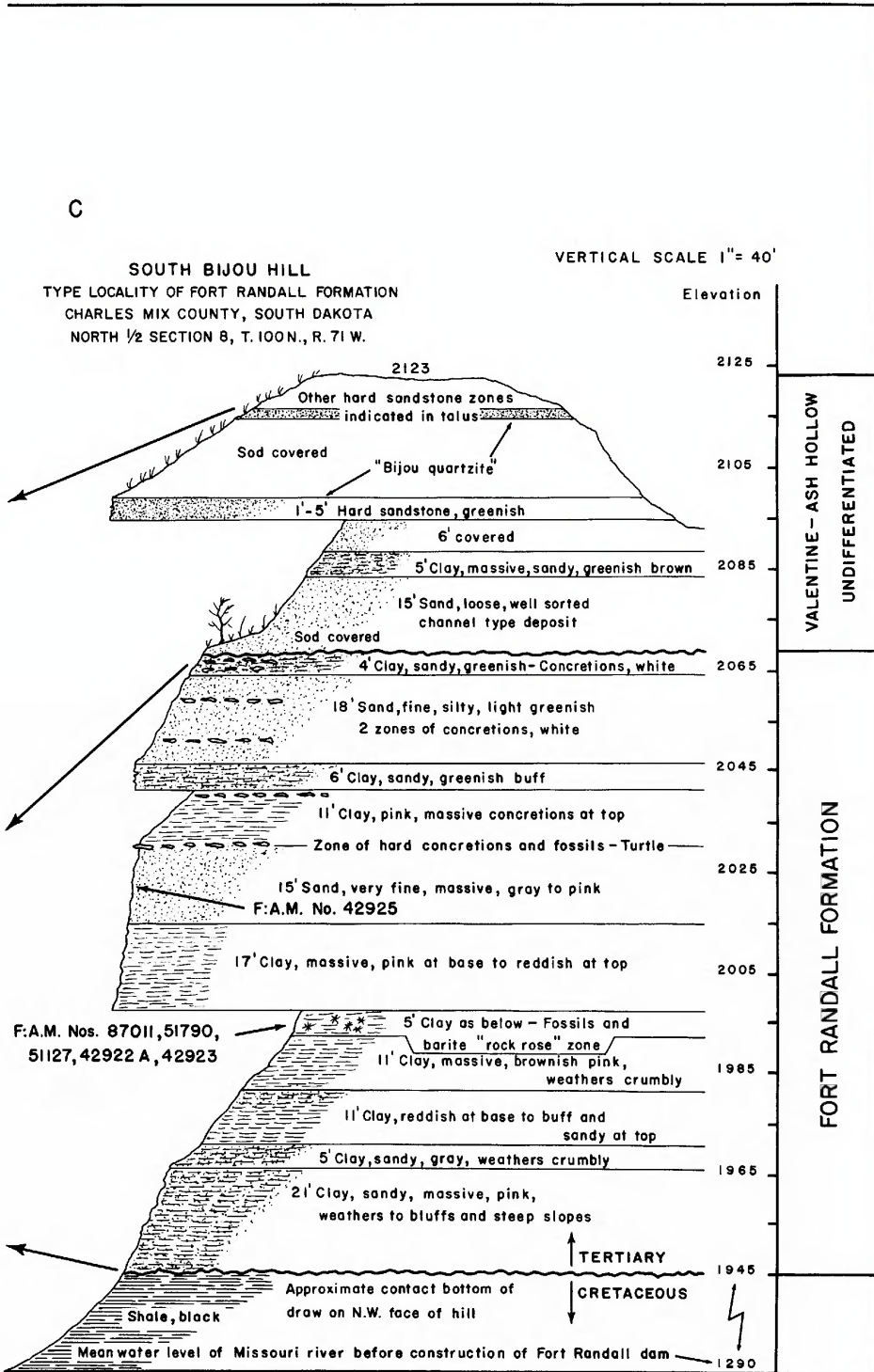


FIG. 1 (THIS PAGE AND OPPOSITE PAGE). A. Map of the north and south Bijou Hills from segments of the Dixon, Iona, and Lucas quadrangles of the South Dakota Geological Survey. B. Section of north Bijou Hill. C. Section of south Bijou Hill, the type locality for the Fort Randall Formation, new name.



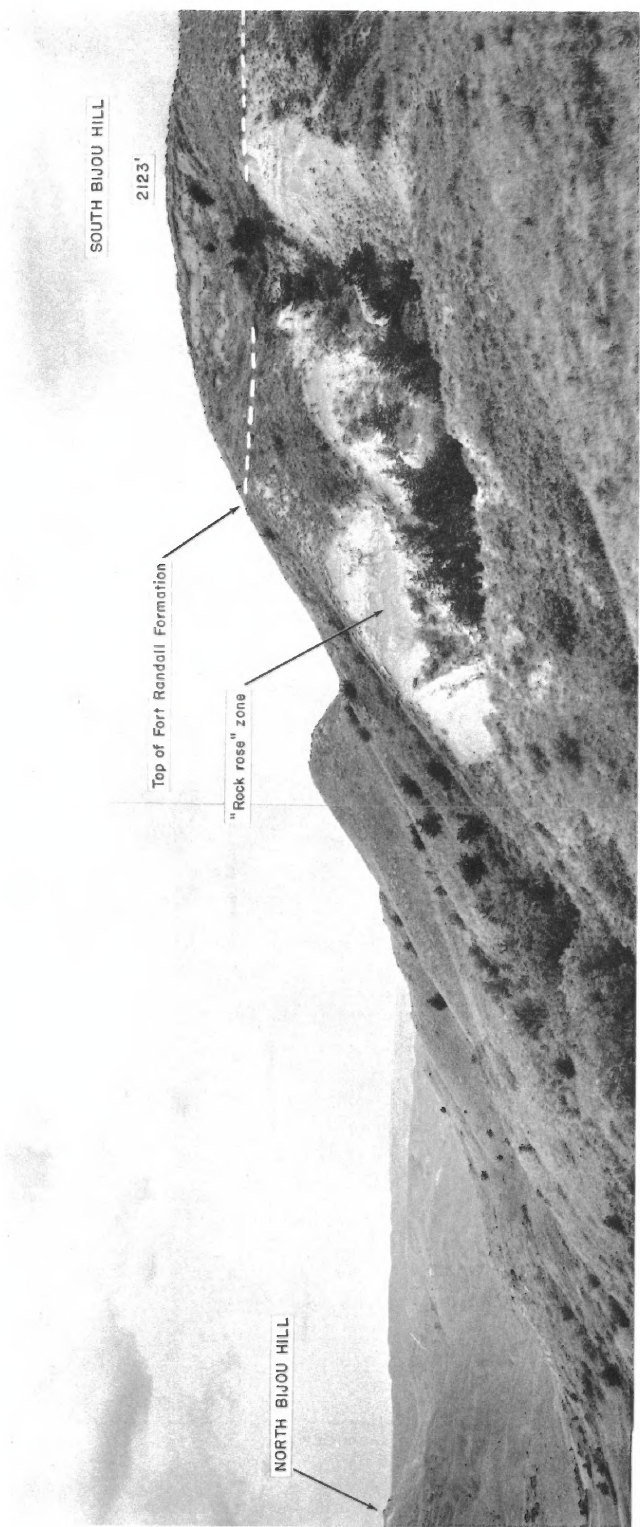


FIG. 2. Photograph of exposures on the northwest face of the south Bijou Hill, looking eastward from the Missouri River side. The north Bijou Hill is on the far left. The "rock rose" zone is indicated by an arrow.

some Upper Miocene forms . . . That some of these, in South Dakota at least, are clearly Lower Pliocene deposits is indicated by the presence of *Ustatochoerus medius* (Leidy) from one of the quartzite beds. The specimen referred to was collected by Stevenson. He informs the writer that it was found in place.”

The locality 5 miles north of Academy, South Dakota, cited by Stevenson (1958, p. 137) carries the usual sequence of rocks and lithology observed in the Upper Valentine and Lower Ash Hollow formations of north-central Nebraska and south-central South Dakota. This locality is also the eastern extension of the Bijou Hills, as pointed out above in the present paper. The sediments exposed north of Academy, however, are not to be confused with the older Fort Randall Formation exposed on the more westerly south and north Bijou Hills bordering the Missouri River.

STRATIGRAPHY

TERTIARY SYSTEM

FORT RANDALL FORMATION,¹ NEW

TYPE SECTION: The type section is on the south Bijou Hill in the northwest corner of Charles Mix County, South Dakota, in the N. 1/2, sect. 8, T. 100 N., R. 71 W. (fig. 1A, C). When viewed from the river, the slowly eroding exposures near the summit on the northwest face of the hill make a prominent landmark (see fig. 2). The major outcrops are in one small, cedar-covered wash which has a 5-foot zone of scattered barite crystals, or “rock roses,” at an elevation of 1995 feet. The details of the lithology of the Fort Randall Formation are described on the type section (fig. 1C).

DISCUSSION: Several writers² have observed two sets of Tertiary beds in the Bijou Hills. We are naming the lower part (fig. 1C, 1945 to 2067 feet) the Fort Randall Formation, here considered a new and previously unnamed set of Tertiary sediments.

The known thickness of the Fort Randall Formation varies from 60 to 120 feet and represents a cyclic type of deposition of siltstones and clays and a secondary deposition of barite crystals in one distinctive zone (“rock rose” zone on the section). The Fort Randall is uncon-

¹ Named for old Fort Randall and the Fort Randall Reservoir on the Missouri River.

² The following have indicated that either two beds or two faunal units were present: Hayden (1857b, p. 153), Agnew (1958, p. 129), Stevenson (1958, pp. 135, 137), Green (1958, p. 142).

formably overlain by undifferentiated sediments approximately equivalent to the Valentine-Ash Hollow formations and rests unconformably on the Cretaceous below. The Fort Randall Formation is, in reality, a limited remnant of a former set of deposits of unknown areal extent. The erosional hiatus between the Fort Randall and the Cretaceous indicates an immense gap in time. The fauna from the Fort Randall suggests that the erosional hiatus between the overlying undifferentiated beds and the Fort Randall Formation represents a span of time partially equivalent to that between the Lower Snake Creek beds and the Lower Valentine Formation of Nebraska.

The lower part of the Valentine Formation as exposed in the drainages of northern Brown and Cherry counties in north-central Nebraska is composed of massive, loose, sandy deposits of well-sorted channel sand with very little clay content, very different in grain size from the fine sandy silts and clays of the Fort Randall Formation. The 15-foot bed of sand at the 2067–2082 level (fig. 1C), above the Fort Randall Formation, is more like that of the upper part of the Valentine Formation in texture and appearance.

The fauna of the south Bijou Hill is extremely limited. From the Fort Randall Formation, shell fragments of cf. *Chrysemys* (painted turtle) and cf. *Geochelone* were obtained. From the “rock rose” zone of the Fort Randall, the following were collected: lagomorph calcaneum; *Eucastor* cf. *curtus* teeth; *Peromyscus* (*Copemys*) sp. ramus; *Merychippus* sp. maxilla fragment with P⁴–M²; *Merycodus necatus* neotype and paratype, a partial ramus and associated horn core; and from the talus of the “rock rose” zone, a skull condyle of a rhinoceros and a peccary-like canine.

A superficial examination of the color and texture of the Fort Randall sediments suggests that they might be correlated with the Rosebud Formation as defined by Gidley (*in* Matthew and Gidley, 1904, pp. 245–246). Gidley did not designate a type section but stated, “The lower formation above mentioned, for which we propose the local term *Rosebud Beds*, is best exposed along the Little White River and in the *vicinity of the Rosebud Agency*.” [Italics ours.] In the interest of nomenclatural stability, we select as the type section of the Rosebud Formation the only set of exposures mentioned by Gidley that can be locally identified. These exposures are in the vicinity of the Rosebud Agency buildings on both sides of Rosebud Creek in the E. 1/2, sect. 34, and the W. 1/2, sect. 35, T. 38 N., R. 30 W., Todd County, South Dakota, where some 100 feet or more of pink sandy sediments are exposed below overlying Pliocene deposits.

The north Bijou Hill is in the center of the S. 1/2, sect. 30, T. 101 N., R. 70 W., in the southwest corner of Brule County, South Dakota.

The bench mark on the top of this hill has an elevation stamped on it of 2028¹ feet, to which we have tied our stratigraphic section (fig. 1B).

The fauna from the north Bijou Hill is even smaller than that from the south hill. In the Fort Randall Formation, a partial skull of *Mylagaulus* sp. was collected 27 feet above the base (fig. 1B). Thirty-five feet above the base of the Fort Randall a worn upper molar of *Merychippus* sp. was collected; from the talus a calcaneum of *Ustatochoerus* sp., near *U. medius* in size, was obtained.

UNDIFFERENTIATED VALENTINE-ASH HOLLOW FORMATION

The upper deposits on the south Bijou Hill (above 2067 feet, fig. 1C) are approximately equivalent to the Valentine-Ash Hollow formations undifferentiated. A broken P², referable to "*Hipparion*" inasmuch as it has an isolated protocone, was collected from the upper deposits 31 feet above the contact with the Fort Randall Formation.

The exposures on the north hill are fewer and are not so large as those on the south hill. We discovered on the north hill a loose sandy channel deposit with coarse pebbles and fossil chips that can be allocated to the distinctly Pliocene phase of deposition. A prominent hard outcrop of the silicified quartz sandstone (orthoquartzite) is exposed on the southeast side of the hill. One of these outcrops contained portions of a proboscidean tusk which were left in the rock.² The quartzitic sand is part of the channel deposit that extends westward to Carter, South Dakota. The capping deposits are unconformable upon the earlier Fort Randall Formation and have at least 50 feet of erosional relief, as illustrated on the section (fig. 1B). This relief may also be interpreted as large blocks of quartzite which have moved down the hill as a result of gravity slump or soil creep. There are no distinct bedding planes at this place to allow for an exact interpretation.

In the upper deposits from a channel of loose sand above the erosional contact of the Fort Randall Formation, we collected a first phalanx of *Longirostromeryx* or of a merycodont. From the so-called "Bijou Quartzite" in the upper deposits we obtained a fragment of a proboscidean tusk.³

¹ See United States Geological Survey Iona Quadrangle, South Dakota, 15-minute series (topographic), scale 1:62,500, edition of 1940, which gives 2037 feet. We do not know the reason for this inconsistency. We simply note it.

² To date we have not found proboscidean remains in the Fort Randall Formation. We have never found proboscidean bones in the Lower Snake Creek deposits of Sioux County, Nebraska, though they are very common in the Valentine Formation.

³ Green (1958, p. 140) gave the location of the Bijou Hills as "Sec. 27, T. 101 N., R. 70 W., Brule County, South Dakota." This is the eastern extension of the Bijou Hills described by Hayden (1857b, p. 157) and not the source of Hayden's fauna (see p. 4).

SYSTEMATICS

CLASS MAMMALIA

ORDER CARNIVORA

SUBORDER FISSIPEDA

FAMILY MUSTELIDAE

SUBFAMILY LEPTARCTINAE

LEPTARCTUS LEIDY, 1857TYPE SPECIES: *Leptarctus primus* Leidy, 1857.TYPE: Left P⁴, A.N.S.P. No. 11293 (fig. 3).

LOCALITY: It is not known whether the type was collected on the south or the north Bijou Hill. The exact stratigraphic unit is also unknown.

DESCRIPTION: The type of *Leptarctus primus*, a P⁴, has characters which Leidy (1857a, p. 311), believed were similar to those of P⁴ of a *coati-mundi*; therefore *Leptarctus* was placed in the family Procyonidae which Bonaparte established in 1850. The P⁴ compared well with the corresponding tooth in a complete fossil skull described by Matthew (1924, p. 146), who referred *Leptarctus* to the Mustelidae on the basis of characters revealed in the more complete specimens. Matthew's revised diagnosis (1924, pp. 139-140) was based on two "neotypes,"¹ even though the type was in the Academy of Natural Sciences of Philadelphia. One of the "neotypes" (A.M.N.H. No. 18241) was a skull collected by Albert Thomson in the lower part of the Lower Snake Creek deposits in Sioux County, Nebraska. A photograph taken by Thomson² of this spot shows that it is the same as the Frick Laboratory Trojan Quarry. The ramus (A.M.N.H. No. 18240) is from Thomson's Quarry "B." In this case, Thomson's photograph shows that Quarry "B" is in a slightly higher zone, which directly overlies the Trojan Quarry, and is synonymous with the Frick Laboratory Far Surface Quarry.

The P⁴, as Matthew observed, has certain characters that are similar to those of the procyonids, especially the well-developed hypocone. It should be noted, however, that the protocone is also prominent and

¹ Matthew followed Osborn (1918, p. 35) whose usage of neotype was expressed as, "The specimen chosen in a subsequent paper by the original or another author as referable to the same species and amplifying the characters of the type by affording fuller material for description." Matthew's "neotypes" (A.M.N.H. No. 18241, a skull, and A.M.N.H. No. 18240, a jaw) are here considered referred specimens of *Leptarctus primus*.

² Albert Thomson personally gave a collection of labeled photographs of the Sioux County area to the senior author.

about one-fourth larger than the hypocone. The parastyle is a well-developed production of the anterior buccal cingulum. We have verified Leidy's and Matthew's measurements of the type of *Leptarctus primus*, which are as follows: anteroposterior length of crown, 7.4 mm.; width of crown, 6.3 mm.; crown height, 5.2 mm.

DISCUSSION: In 1869 Leidy supplemented his original description of the type of *Leptarctus primus* with figures (Leidy, 1869, pl. 1, figs. 15, 16). Matthew observed (1924, p. 139) that the figure of the type P⁴ was inaccurate. In reality the figure of the occlusal view is accurate, but it had been placed on the plate in such a way that the hypocone appears to be

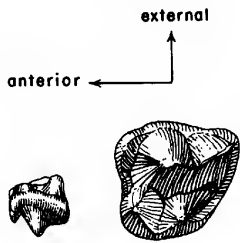


FIG. 3. *Leptarctus primus*, type, left P⁴, A.N.S.P. No. 11293, drawn from cast. Left: Lateral buccal view. $\times 1$. Right: Occlusal view. $\times 2$.

the protocone. The figure was rotated 90 degrees, completely misorientating it in relation to all the other figures. The type of *Leptarctus primus* is refigured in this paper (fig. 3).

Leidy's type of *Leptarctus primus* cannot be assigned to any particular late Miocene-early Pliocene temporal unit on the basis of stratigraphically controlled specimens in the Frick Collection. Specimens that are referable to *L. primus* are found in deposits ranging from the Lower Snake Creek into the Upper Valentine Formation, but below the Burge Member in north-central Nebraska.

ORDER PERISSODACTYLA
 SUBORDER HIPPIOMORPHA
 FAMILY EQUIDAE
 SUBFAMILY EQUINAE
HIPPODON LEIDY, 1854

TYPE SPECIES: *Hippodon speciosus* Leidy, 1854.

TYPE: Right M₁ or M₂, A.M.N.H. No. 465 (fig. 4).

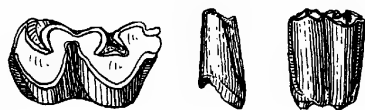
LOCALITY: Although it cannot be proved, the type may have come from the south Bijou Hill, only because it has more and larger outcrops than the north hill. Meek and Hayden, in the summer of 1853, made the collection for Prof. James Hall of Albany, New York. The Hall Collec-

tion was later transferred to the American Museum of Natural History.

STRATIGRAPHIC UNIT: Unknown, but the type may have been derived from the upper beds. The fossilization of the type of *H. speciosus* does not resemble that of specimens which we have collected from the Fort Randall Formation.

DESCRIPTION: (See fig. 4). The type of *Hippodon speciosus* (A.M.N.H. No. 465) is a partially worn molar, nearly free of cement, of a mesodont equid. Leidy (1854a, p. 90) observed that, "It appears to have had an envelope of crusta petrosa as in the horse, though nearly all removed in the specimen." It is possible that some earlier worker removed the cement, for a vestige still remains on the internal part of the postflexid. On the buccal side the enamel surface is finely crenulate. On the lingual side the enamel surface is smooth. The anteroflexid is shallow and does not extend to the base of the tooth. The postflexid is deeper than the anteroflexid and extends nearly to the base. The ectoflexid (between the proto-

FIG. 4. *Hippodon speciosus*, type, M_1 (or M_2), reversed, A.M.N.H. No. 465; from the Bijou Hills. *Left*: Occlusal view. $\times 1$. *Center*: Anterior view. $\times \frac{1}{2}$. *Right*: Buccal view. $\times \frac{1}{2}$.



conid and the hypoconid) is deep and separates the metaconid-metastylid column almost to the base. The anterocingulum is transversely wide at the base and extends obliquely upward, narrowing at the crown, whereas the hypoconulid is not so transversely wide at the base and extends more directly up to the crown. A distinct posthypoconid groove extends half-way down the crown to the base, and a distinct postentoconid groove extends from the crown half of the length of the tooth. The combination of the two grooves sets the hypoconulid off as a distinct entity on the posterior side of the tooth. The following measurements were made of the type (A.M.N.H. No. 465): length of crown (paralophid to hypoconulid), 18.4 mm.; width of crown (protoconid to metaconid), 8.4 mm.; greatest length at base of tooth, 14.6 mm.; greatest width at base, 10.7 mm.; greatest height of tooth, which is worn (metaconid to base of protoconid), 23.0 mm.

DISCUSSION: The first North American equid genus to be named was *Hippodon*, but unfortunately the single lower molar that is the holotype of the type species, *Hippodon speciosus*, has characters that are generally common to several equids. Leidy (1856, p. 311) indicated that he, too, was puzzled by the relationships of *Hippodon* when he transferred it to *Hipparion*, thus: *Hipparion (Hippodon) speciosum*. Later Leidy (1869, p. 282) referred certain specimens to *Hipparion speciosum* that Hayden had col-

lected in the Bijou Hills in the autumn of 1856, and these were the specimens that Hayden (1857b, p. 157) had misidentified as "*Hipparion occidentale*." Leidy (1869, pp. 320-321) specifically retained, however, the identity of the name *Hippodon speciosus* for the type in text and plate (pl. 19, fig. 23).

Gidley (1907, p. 877) could not find the type and assumed that, since it was a lower molar, ". . . [it] would probably show no distinguishing characters, even if located." He cited both the genus and species as indeterminate. Osborn (1918, p. 129) reproduced Leidy's 1869 figure of the type, but followed Gidley by citing *Hippodon speciosus* as "Gen. et sp. indet." and then placed it as ". . . intermediate between a small *Merychippus* and a small *Protohippus*."

The genus *Hippodon* is based on a nominal species and as such is nomenclaturally valid. Quinn (1955, pp. 13-17) went one step farther and treated *Hippodon* as a diagnostically useful genus. He gave a detailed description of the type of *Hippodon speciosus* and referred a low-crowned upper dentition from Texas and Florida to it. In so doing, he inferred diagnostic characters for the type which could be seen only in the referred examples. The characters limited to the type of *Hippodon speciosus* may be associated with *Parahippus*, *Merychippus*, *Desmatippus*, and other groups. The single molar may be matched in several disparate groups of equids.

We contend that it is not in the interest of nomenclatural stability to resurrect *Hippodon*. We prefer to leave it as a monotypic genus, *nomen dubium*, with a single species standing for its type [Stoll and others, 1961, Articles 42 (b) and 45 (b)]. Because the type species of *Hippodon* occurred in the same area as that of *Merychippus*, there is the possibility, which we cannot prove, that the two genera are synonymous, and that *Merychippus* is a junior synonym.

Hipparion occidentale Leidy, 1856

DISCUSSION: The species *Hipparion occidentale* was based on a syntypic series of "five superior and one inferior molar teeth" (Leidy, 1856, p. 59). Leidy (1869, p. 281) acted as his own reviser and fixed the type when he stated: "The teeth consist of four upper molars of the right and one of the left side, and are represented in figures 1-5, plate XVIII. They were accompanied by a fragment of a last upper molar and a lower molar, apparently of another equine animal." We interpret this as a valid revision not subject to change by Gidley (1907, p. 877) who designated a right P², P³, M², and a left P³ as the type.

There would never have been a question but that the Little White River was the type locality for *Hipparion occidentale* if Hayden (1857b, p. 157) had not written: "In the autumn of 1856 I discovered on the denuded summits of the same hills [Bijou] *Hipparion occidentalis* . . . These remains have all been described by Dr. Leidy in the Proceedings of the Philadelphia Academy." It is evident that Hayden could not have collected the type of *H. occidentale* some six or eight months after Leidy had described it. Hayden misidentified these specimens, a fact that is clearly shown by Leidy's statement (1869, p. 282): "Shortly after the discovery of the teeth of *Hipparion occidentale* on White River, Dr. Hayden obtained several specimens of equine molars at Bijou Hills, situated east of the Missouri River, below the outlet of the White River. In a notice of these fossils in the Proceedings of the Academy for 1856, page 311, they were referred to a species under the name of *Hipparion speciosum*." Note that Leidy, in his 1856 publication, had used "*Hipparion (Hippodon) speciosum*."

MERYCHIPPUS LEIDY, 1857

TYPE SPECIES: *Merychippus insignis* Leidy, 1857.

TYPE: *Merychippus insignis* is based on a fragment of a right maxilla with dP²⁻³, A.N.S.P. No. 11276 (fig. 5A, B; measurements are given in table 2).

LOCALITY: Collected by F. V. Hayden in 1856 from the Bijou Hills, South Dakota.

STRATIGRAPHIC UNIT: The fossilization of the type is similar to that of the neotype of *Merycodus necatus* from the Fort Randall Formation, but no positive allocation of level can be made.

KNOWN LITHIC, GEOGRAPHIC, AND TEMPORAL OCCURRENCE OF SPECIES: From the Fort Randall Formation, Bijou Hills, South Dakota, late Miocene or very early Pliocene; from the Lower Snake Creek beds¹ in Sioux County, Nebraska, late Miocene; Pawnee Buttes area in north-eastern Colorado, late Miocene; Trinity River Quarry, 7 miles north, 40° east, of the town of Coldspring, San Jacinto County, Texas, late Miocene.

STATEMENT: The holotype of *Merychippus insignis* has long been an enigma, because it is fragmentary and immature, and the over-all characters of the two upper milk teeth are similar to those of many immature equids in the late Tertiary. A detailed study reveals additional characters, however, which restrict *M. insignis* to one taxon in the late

¹ *Merychippus insignis* has not been observed in the Sheep Creek beds as defined by Matthew and Cook (1909).

Miocene. We did not discover a match for the holotype at the type locality in the Bijou Hills, but we did obtain a mature partial maxilla with left P^4-M^2 , F:A.M. No. 87011 (fig. 6A, B), an isolated M^1 , and another badly worn molar from the Fort Randall Formation, which are referable to *Merychippus insignis*. The fossilization of the type seems to match that of other specimens collected from the Fort Randall Formation. Future collecting from this locality may produce a more complete immature match for the holotype collected by Hayden.

Failing to find adequate topotypic material, we concentrated on matching the type specimen with examples from an approximate temporal unit. We were confronted with two, and possibly three, sets of deposits at the type locality, any one of which might have been the source of the type. The large, stratigraphically controlled Valentine-Ash Hollow collections in the Frick Laboratory have not produced an immature example that can be matched exactly with the type of *Merychippus insignis*.

The type can be nearly duplicated in the fauna of one quarry in late Miocene deposits in western Nebraska. A series of specimens ranging from immaturity to old age was found in the fauna of Echo Quarry in the Lower Snake Creek channel deposits of Sioux County, Nebraska. These specimens demonstrate the skull and upper dental characters of *Merychippus insignis*.¹

The Echo Quarry deposits in Sioux County extend for about a quarter of a mile along the bottom of an east-west trending draw, known in the Frick Collection field records as "Antelope Draw." The exact location is in the SE. $\frac{1}{4}$, sect. 33, and the SW. $\frac{1}{4}$, sect. 34, T. 26 N., R. 55 W., Sioux County, Nebraska. The Echo Quarry fauna belongs to the Lower Snake Creek biostratigraphic unit. We consider the Lower Snake Creek beds of Matthew (1924) as an independent temporal and faunal unit lithologically distinct from the Sheep Creek Formation of Matthew and Cook (1909). By 1918 Matthew had profited from the research (then unpublished) of Dr. J. C. Merriam on the later Tertiary mammalian faunas of the Pacific coast. These data added largely to the correlation studies of the faunas of the Plains. Matthew (1918, p. 184) stated that Merriam's studies ". . . afforded evidence strongly suggesting that the Snake Creek fauna might in fact be a composite and not all of the same age." However, in his revised faunal list of the Snake Creek (1918, April, pp. 185-188), Matthew made no faunal distinctions. Osborn (1918, June,

¹ Although there are lower dentitions from Echo Quarry that we suspect might be referable to *M. insignis*, we are not presenting the diagnosis of the lower jaws, because of the lack of articulated upper and lower dentitions.

TABLE 3
 SKULL MEASUREMENTS (IN MILLIMETERS) OF *Merychippus insignis*
 (The measurements are orthogonal projections.)

	F:A.M. No. 87000 ♂ (W4) ^a	F:A.M. No. 87001 ♂ (W6)	F:A.M. No. 87002 ♂ (W6)	F:A.M. No. 87003 ♂ (W6+)	F:A.M. No. 87004 ♀ (W7-)	F:A.M. No. 87005 ♂ (W7x6)
MEDIAN						
Foramen magnum to incisive border (basilar)	—	286.0	—	300.0	—	292.0
Occiput to anterior incisive border (vertex)	312.0	333.0	—	352.0	(332.0) ^b	(338.0)
Postorbit to anterior incisive border (facial)	205.0	222.0	229.0	236.0	218.0	219.0
Postorbit to postocciput (cranial)	108.0	114.0	—	116.0	—	(118.0)
Occipital crest to tip of nasals (median)	—	(312.0)	—	320.0	(299.0)	(321.0)
Occipital crest to naso-premaxillary notch	271.0	291.0	—	291.0	(271.0)	(292.0)
Occipital crest to naso-frontal suture	153.0	170.0	—	172.0	(147.0)	(172.0)
Anterior of foramen magnum to vomer	—	66.0	—	82.0	—	83.0
Anterior of foramen magnum to postpalatine border	—	146.0	—	158.0	—	152.0
Anterior of foramen magnum to posterior of M ³	—	99.0	—	114.0	—	111.0
Anterior of foramen magnum to posterior of P ⁴	—	153.0	—	174.0	—	161.0
Anterior of foramen magnum to anterior of P ²	—	216.0	—	235.0	—	221.0
Anterior of foramen magnum to postpalatine fissure	—	233.0	—	246.0	—	232.0
Anterior of P ² to incisive border	70.0	70.0	69.0	69.0	71.0	70.0
Diastema, posterior of I ³ to anterior of P ²	50.0	49.0	48.0	52.0	51.0	51.0
WIDTH						
I ³ to I ³ (width of muzzle at alveolar border)	36.0	42.0	40.0	43.0	40.0	39.0
Narrowest part of rostrum on palatal side	23.0	28.0	26.0	28.0	21.0	25.0
Anterior nares, widest point on premaxilla	33.0	41.0	40.0	41.0	37.3	41.0
Anterior orbital width at narrowest point	(71.0)	87.0	(86.0)	86.0	76.5	84.0
Postorbital width, widest point	(116.0)	114.0	(124.0)	114.0	109.0	116.0
Zygomatic arch, greatest transverse width	(116.0)	118.0	(130.0)	129.0	114.0	124.0
Cranium, narrowest postorbital width	(62.0)	61.0	(58.0)	56.0	52.0	53.0
Cranium, widest part on squamosal	73.0	75.0	78.0	70.0	73.0	70.0

^a See table 2, footnote c.

^b Measurements enclosed in parentheses are approximate.

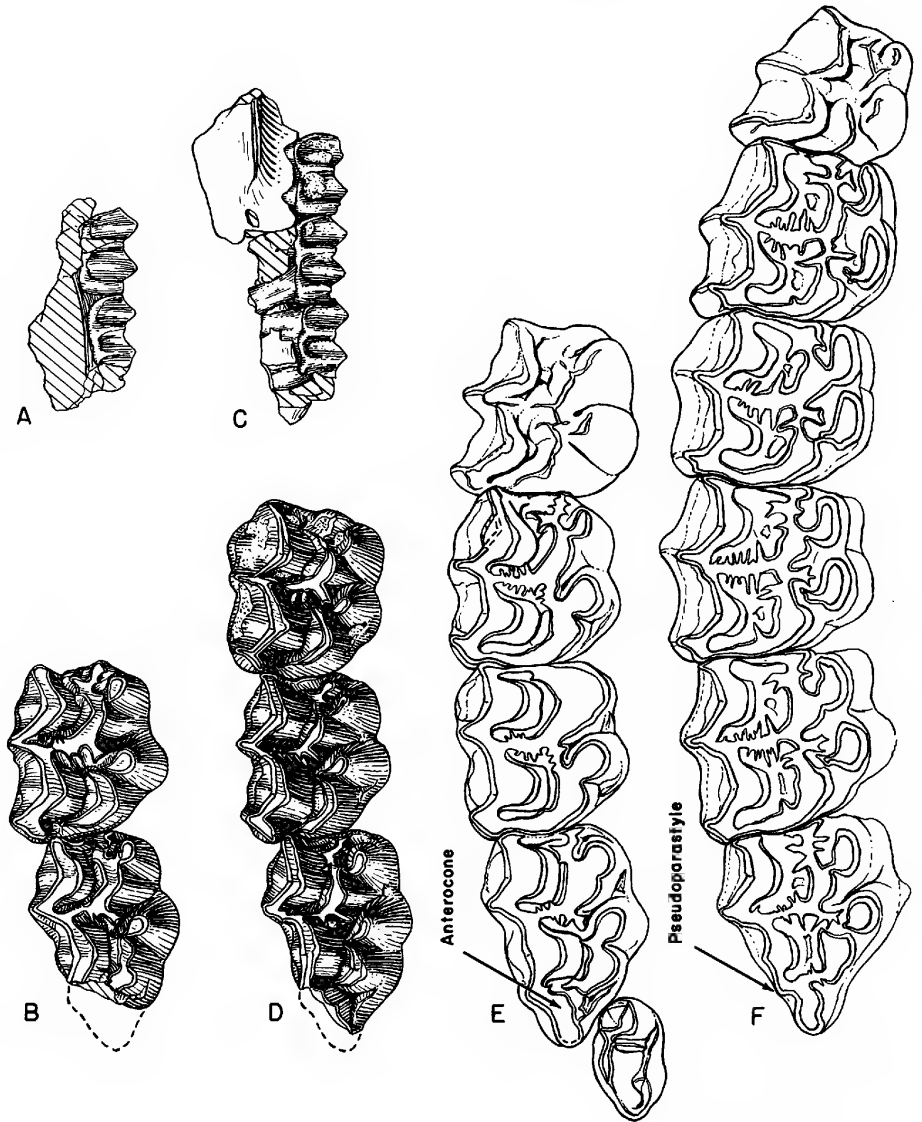


FIG. 5. *Merychippus insignis*. A, B. Type, dP^{2-3} , reversed, A.N.S.P. No. 11276; from the Bijou Hills. A. Lateral buccal view. $\times \frac{1}{2}$. B. Occlusal view, drawn from cast. $\times 1$. C, D. DP^{2-4} , reversed, F:A.M. No. 87006; from Echo Quarry, Sioux County, Nebraska. C. Lateral buccal view. $\times \frac{1}{2}$. D. Occlusal view. Note cement on dP^4 . $\times 1$. E. Left dP^{1-4} and M^1 , occlusal view, F:A.M. No. 87000; from Echo Quarry, Sioux County, Nebraska. Arrow at anterocone, new name. $\times 1$. F. P^2-M^3 , reversed, occlusal view, F:A.M. No. 87002; from Echo Quarry, Sioux County, Nebraska. Arrow at pseudoparastyle, new name. $\times 1$.

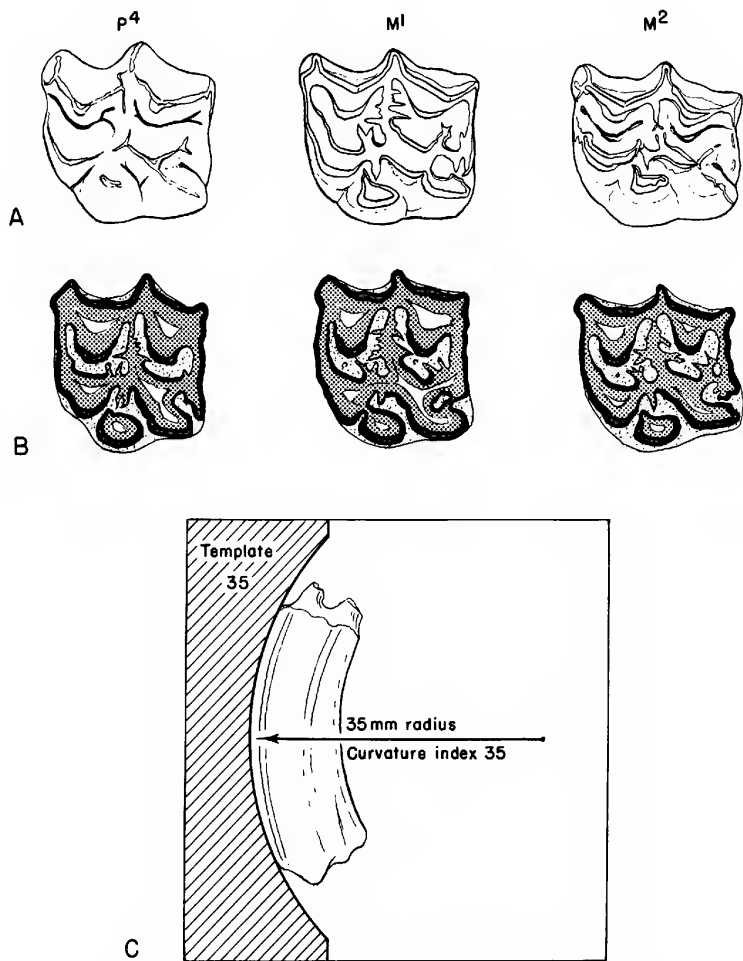


FIG. 6. A, B. *Merychippus insignis*, P⁴-M², reversed, F:A.M. No. 87011; from the Fort Randall Formation, south Bijou Hill (fig. 1C). A. Occlusal view. $\times 1$. B. Sectioned 10 mm. below crown. $\times 1$. C. Diagram for method of determining the index of curvature of upper dentition of the Equidae.

pp. 23, 28) pointed out that the Snake Creek beds contained at least two faunal levels of upper Miocene and lower Pliocene age and a third from "Upper Pocket Levels" which yielded the type of *Pliohippus leidyani*. In 1924 (pp. 64-68) Matthew gave a faunal list in which the Lower Snake Creek, the Upper Snake Creek, and the Sheep Creek appeared as distinct faunal units for the first time.

Matthew and Cook (1909, p. 386, fig. 11) listed four upper dentitions which they considered matched the type of *Merichippus insignis* "fairly well" and also exhibited the mature characters. The immature specimens

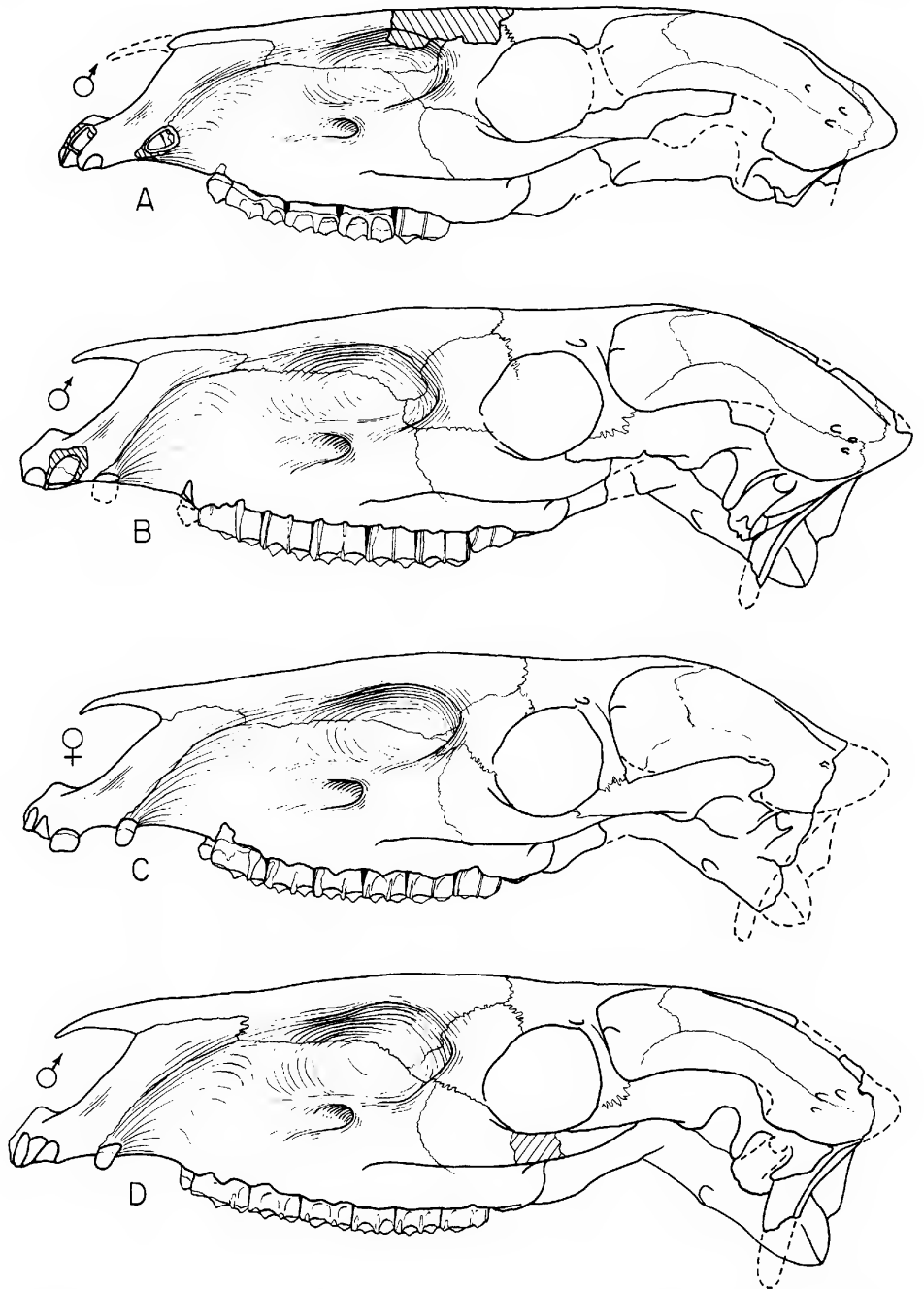


FIG. 7. Lateral views of *Merychippus insignis* from Echo Quarry, Lower Snake Creek beds, Sioux County, Nebraska. A. F:A.M. No. 87000. B. F:A.M. No. 87001. C. F:A.M. No. 87004. D. F:A.M. No. 87005. All approximately $\times \frac{1}{3}$.

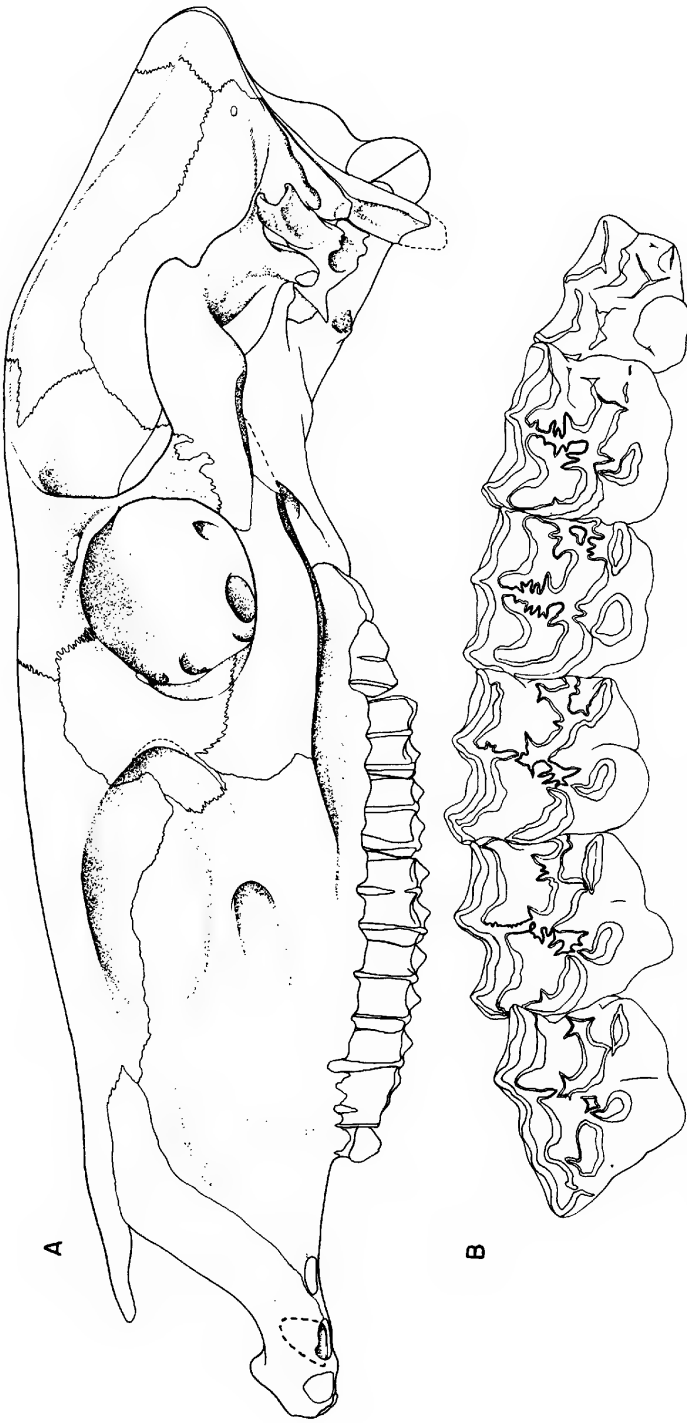


FIG. 8. *Merychippus insignis*, F:A.M. No. 87001; from Echo Quarry, Lower Snake Creek beds, Sioux County, Nebraska.
A. Lateral view. $\times \frac{1}{2}$. B. Occlusal view of upper dentition. $\times 1$.

(A.M.N.H. Nos. 14010 and 14014) do not match the type of *M. insignis*. The mature examples (A.M.N.H. Nos. 14003 and 14001) do not agree with our series of skulls which range from immature (duplicating the type) to adult individuals. Matthew (1924, p. 159) referred the bulk of the equids from the Lower Snake Creek faunal level to *Merychippus paniensis*. Two skulls were figured (fig. 47, A.M.N.H. No. 18297; fig. 48, A.M.N.H. No. 18299) as typical of *M. paniensis*, but these do not agree in dental pattern with Cope's lectotype of *M. paniensis*, A.M.N.H. No. 8249 (*vide* Gidley, 1907, p. 890). The partial female skull, A.M.N.H. No. 18299, figured by Matthew (1924, fig. 48) is here considered a good example of mature *Merychippus insignis*.

Examples from youth to old age, male and female, of *M. insignis* are presented in this paper (figs. 5, 7) to illustrate the uniformity of dental and facial morphology. These specimens indicate that the morphology of the preorbital fossae is as genetically fixed as that of the dentition. Within one quarry sample of a specific population the preorbital fossae do not exhibit wide ranges of individual variation because of sex or age, but are part of a set of morphological characters that remain constant with the dentition. The lateral views (fig. 7) of a colt, a young male, a young female, and an old male show the general outlines of the skulls of *Merychippus insignis*. Nearly uncrushed skulls were selected in order to show consistency in measurements, placement of preorbital fossae, crown height of cheek teeth, and so on. As noted in table 2, it is not possible to give the crown height of the entire dental series of one individual.

In table 2 the order of tooth eruption and wear of *M. insignis* may be compared with that of modern *Equus* (Sisson and Grossman, 1953, p. 405). We believe that the dental development of *M. insignis* proceeded at approximately the same rate as that of living *Equus*. The optimum dental pattern is developed shortly before the third molar is fully worn, after which the dental pattern changes rapidly on the preceding teeth (see fig. 5F). The normal life span of *Merychippus* is presumed to have been in direct ratio to the crown height of the cheek teeth. Since *Merychippus* was mesodont, its life span would presumably have been shorter than that of *Equus*, which is hypsodont.

IMMATURE UPPER DENTITION OF *Merychippus insignis*

Table 2 and figure 5 supplement this description. The holotype, A.N.S.P. No. 11276 (fig. 5A, B), consisting of dP²⁻³, was compared with immature dentitions from Echo Quarry: F:A.M. No. 87006 (fig. 5C, D), a right maxilla with dP²⁻⁴ very slightly less worn than the type; F:A.M.

No. 87009, a right maxilla with dP^{2-4} ; and F:A.M. No. 87010, a left maxilla with dP^{2-4} . All nearly duplicate the wear of the holotype. F:A.M. No. 87000 (figs. 5E, 7A) is an immature partial skull lacking the deciduous incisors. The left maxilla of the skull is complete, with deciduous premolars about to be shed, M^1 , and the unerupted germ of M^2 . This skull (F:A.M. No. 87000) serves as a link between the deciduous dentition exhibited in the holotype and referred immature examples and the mature dentition of *M. insignis*.

The milk premolars of the holotype (A.N.S.P. No. 11276) and the referred examples, F:A.M. Nos. 87006, 87009, and 87010, are in an early stage of wear with well-defined crown patterns. The dP^{2-4} of F:A.M. No. 87000 show a slightly advanced stage of wear. The referred examples all have the anterocone,¹ new name, preserved, which is broken off in the type. The deciduous premolars are low-crowned, with the ectoloph and the hypostylar region of dP^4 usually coated lightly with cement. Occasionally there are traces of cement on dP^3 and, more rarely, on dP^2 . The milk teeth of the holotype are devoid of cement. On the buccal side of the milk premolars there is an ectocingulum which is confluent with the mesostyle and metastyle. There are fairly prominent anterior and posterior ribs. On the lingual side there is usually an incipient style or slight swelling around the base of the enamel anterior to the protocone or at the base of the medivallum. This may or may not be present.

dP^2 : The mesostyle is prominent, but the metastyle is weakly defined. A crescent-shaped protoloph with one small pliprefossette is united to the anterior portion of the base of the paracone and to the posterior part of the protocone near the crown of the tooth. Posteriorly the protoloph has a slight elongation which might be interpreted as an antero-crochet, but this does not unite with the metaloph. The protocone is round, placed antero-internally to the mesostyle, and is united to the posterior part of the protoloph by an enamel isthmus or pliprotocone. The metaloph unites to the ectoloph on the posterior part of the paracone, anterior to the mesostyle, and has a distinct crochet, suggesting a pliacaballin. This crochet bifurcates lingually into the medivallum and internally into the prefossette toward the most posterior extension of the protoloph. On the anterior side the metaloph has two small enamel plicae entering the prefossette between the crochet and ectoloph. On the posterior side there is a cluster of three small enamel plicae extending

¹ The anterocone (fig. 5E) is a conelike structure developed on the dP^2 of equids between the true parastyle and the paracone.

into the postfossette near the junction of the metaloph and ectoloph. Posteriorly the metaloph is united to the hypocone slightly below the crown and is confluent with the hypoconule or hypoloph, or with both. The metaloph is united to the internal posterior base of the metacone. There is one small plihypoloph extending into the postfossette. The hypostyle is small, distinct, and united anteriorly to the metaloph. It is developed from the cingulum on the posterior median side of the tooth. Anteriorly the hypostyle unites with the metaloph and forms the internal wall of the hypoconal groove which extends to the base of the tooth. There is a weak cingulum extending from the crown of the hypostyle to the base of the hypoconal groove. One small plication extends from the hypostyle into the hypoconal groove.

dP³: The parastyle is prominent and overlaps dP²; the mesostyle is also prominent, and the metastyle is distinct but small. A crescent-shaped protoloph with one very small plica on the antero-internal side is united to the internal portion of the parastyle and posteriorly to the protocone near the crown of the tooth. The posterior part of the protoloph extends slightly beyond its junction with the protocone but differs from dP² in that no plication is developed.

The crown pattern of the protocone is tear-shaped, lingually rounded, and narrows toward its junction with the protoloph. There is a marked preprotoconal groove. The metaloph is crescentic, confluent with the hypoloph, and is united to the ectoloph slightly anterior to the mesostyle. It is also united to the posterior part of the paracone. On the anterior side a prominent crochet bifurcates the medivallum; the lingual fork produces a small plicaballin, and the buccal fork tends toward a union with the posterior part of the protoloph. There are two prominent internal plicae extending into the pefossette, the lingual plica extending toward the posterior extension of the protoloph and the more buccal one into the pefossette. On the posterior side the metaloph has a cluster of three small plicae extending into the postfossette toward the metacone at its junction with the ectoloph. Posteriorly the metaloph is united to the hypocone slightly below the crown of the tooth. The metaloph is confluent with the hypoconule or hypoloph, or both, the hypoloph extending posteriorly and externally to unite with the midposterior wall of the tooth. There is one small plihypoloph extending forward into the postfossette. The hypostyle is small but distinct and unites anteriorly to the metaloph. It is situated on the posterior side of the tooth. The anterior extension of the hypostyle and its junction with the metaloph form the internal wall of the hypoconal groove which extends to the base of the tooth. There is a distinct lingual cingulum extending from

the crown of the hypostyle to the base of the hypocone. Two plihypo-styles are present in the hypoconal groove.

MATURE UPPER DENTITION OF *Merychippus insignis*

There are 47 mature dental examples of *M. insignis* from Echo Quarry. The following description is supplemented by figures 5F and 8B in which the ultimate in dental complexity for this species is expressed in the occlusal patterns of F:A.M. Nos. 87001 and 87002. The dental formula of *Merychippus insignis* is I^{1-3} , C, dP^1 , P^2-M^3 . In the Equidae we have never observed a replacement for the first premolar that erupts with the milk dentition. Therefore, we refer to this tooth as dP^1 in order to distinguish it from the permanent premolars. In *Merychippus insignis* the dP^1 is double-rooted. In later equids the dP^1 is single-rooted, peglike, and frequently absent. The mature cheek teeth of *Merychippus* are mesodont, moderately curved (table 2, footnote e; fig. 6C), and cement-covered, except the centers of the fossettes which are not, in every case, completely filled.

There are no examples of I^{1-2} from Echo Quarry, but I^3 has a thin layer of cement in the bottom of the cups. Canines, which are heavy in males and smaller and lighter in females, are covered with enamel caps. Cement covers the external surfaces of P^2-M^3 but does not invariably fill the postprotoconal valley and the hypoconal groove in P^3-M^2 . Cement partially fills the fossettes. Deciduous premolars two and three are usually cement-free.

The greatest degree of dental complexity is observed on the occlusal pattern just before the M^3 comes into wear (fig. 5F). After the M^3 is in wear, the occlusal pattern of the cheek teeth becomes increasingly simplified as the result of attrition. The numerous plications that develop at right angles to the plane of the metaloph are leaflike outfoldings which change rapidly as the tooth wears.

The parastyle of P^2 is centrally placed and elongate, with a small pseudoparastyle, new name¹ (fig. 5F), posterior to it. The parastyles of P^{3-4} are large and overlap the metastyles of the preceding teeth. On the molars the parastyles are not so large and do not overlap the preceding metastyles as much as in the premolars. The mesostyles of the premolars are heavier than those of the molars. There is a prominent anterior rib, and a weak posterior external rib on P^2 . The external ribs of P^3-M^3 are all weak.

¹ Pseudoparastyle refers to a fold that develops on the ectoloph posterior to the parastyle and anterior to the paracone.

On P^2 the protoloph unites with the ectoloph posterior to the parastyle. Toward the base of P^2 , the protoloph is united to the true parastyle by a lingual cingulum that produces a small parastylar fossette. On P^3-M^3 the protoloph is united to the parastyle. The pliprotoloph is weakly developed on the crown of the premolars, is seldom observed on the molars, and disappears altogether toward the base of the tooth. There is a weak pliprotoconule on P^2 which becomes increasingly stronger on P^3-M^3 . The protoloph tends to remain separate from the metaloph on P^2 , but on P^3-M^3 the protoloph is united to the metaloph by plicae that originate from a crochet.

Early in wear the protocones of P^2-M^3 are free, narrow, and elongate, with prominent plicae on the antero-internal borders. Later in wear these plicae unite the protocone to the protoloph. This is in antithesis to the type of *Merychippus paniensis* which has a rounded protocone with no pliprotoconal folds. In *M. insignis* the occlusal pattern of the protocone becomes rounded with wear. There is a shallow protoconal cleft. In P^2-M^2 the protocones and hypocones are subequal, and in M^3 the hypocone is reduced. The protocones are either slightly anterior to, or opposite, the mesostyle, with the long axis nearly parallel to the antero-posterior length of the tooth. The protocones tend to be more posteriorly situated on the molars than on the premolars. There is a well-defined preprotoconal groove, and a deep postprotoconal valley.

The hypocones are united to the metaloph and are long and narrow on the crown but are oval-shaped or round toward the base. The axis of the hypocone is nearly parallel with the anteroposterior length of the tooth and is at right angles or oblique to the axis of the metaloph. There is a weak prehypoconal fold, and there is a deep posthypoconal groove which closes near the base of the tooth, producing a hypoconal fossette observed only on a well-worn tooth. On P^2-M^2 prominent lingualplihypostyles extend into the hypoconal groove and disappear toward the base.

The main portion of the metaloph is anterior to the hypocone and, on the crown, unites with the ectoloph near the mesostyle by a junction with a medicrista. With wear the medicrista becomes confluent with the metaloph. In early wear the borders of the fossettes are moderately complex. There is a well-developed plihypoloph into the postfossette, and in some specimens there is a very small shallow hypolophal fossette internal to the hypoconal groove (fig. 8B, M^1 of F:A.M. No. 87001). A caballin fold is produced by a crochet that develops from the metaloph. In the premolars it is bifurcate. In the molars the caballin fold is usually single.

MATURE SKULL OF *Merychippus insignis*

There are five mature skulls of *M. insignis* from Echo Quarry: F:A.M. Nos. 87001 (figs. 7B, 8), 87002, 87003, and 87005 (fig. 7D), males; and F:A.M. No. 87004 (fig. 7C), a female. The measurements of these five mature skulls and those of one immature skull (F:A.M. No. 87000) are given in table 3. The over-all length of the skulls of *M. insignis* ranges from 312 mm. to 352 mm., and the basilar length, from 286 mm. to 300 mm. The females exhibit a smaller canine than the males; otherwise no sexual dimorphism, such as variations in the size, shape, and position of the preorbital fossae, has been observed.

DORSAL AND LATERAL VIEWS OF SKULL: The muzzle is medium-sized in proportion to the skull. Anteriorly the nasals extend forward beyond the canines and overhang a comparatively small nasal opening. A deepening of the anterior part of the maxilla (buccinator fossa) extends back, but does not unite with the preorbital fossa. The nasal process of the premaxilla is broad, ending above posterior P² or anterior P³, and joins the nasal and the maxilla in a well-defined suture.

The preorbital fossa is separated from the orbit by a preorbital bar which averages 16 mm. wide and involves the lacrimal, nasal, and maxillary bones. The fossa is oval-shaped and high on the face, ending anteriorly above P³ where it is separated from the buccinator fossa by a gently rounded ridge. The mid-superior border is sharp, and the posterior border is sharp and deeply rounded, whereas the inferior portion slopes into the maxilla with no defined border. There is no malar fossa, but there is a slight depression on the malar bone for the attachment of the levator labii superioris proprius muscle. The infraorbital foramen opens above the posterior half of P⁴, outside the preorbital fossa, and moderately low on the face. The opening is round, with a deeply defined sulcus fading out below the anterior portion of the preorbital fossa.

Well-rounded orbits sit about 15 mm. below the plane of the frontals immediately posterior to the midportion of the skull. The orbits are closed by a broad, well-developed, supraorbital process which unites strongly with the zygomatic process of the temporal bone. A large, completely closed supraorbital foramen is placed medianly on the supraorbital process. On the anterior internal part of the orbit there is a deep, well-defined fossa for the lacrimal sac. External to and slightly above this fossa there is a distinct lacrimal duct leading forward and opening internally into the nasal cavity. This duct leads forward and down behind the preorbital fossa.

A prominent, well-rounded, facial crest begins abruptly above post P⁴

or mid M^1 and, in confluence with the zygomatic process of the malar bone, forms a heavy crest which is, in no case, dorsoventrally compressed as in examples of *Pliohippus*. The malar bone is anteriorly expanded and forms the lower anterior third of the orbit. The zygomatic process of the temporal bone is fairly light and well separated from the cranium and ends just ahead of the auditory meatus.

The frontal bones are flat, without any indication of a dome as in *Griphippus*, and curve sharply downward to the low-placed orbits. The naso-maxillary and the naso-lacrimal sutures are in the superior and posterior portions of the preorbital fossa. The naso-frontal suture ends over the anterior half of the orbit and forms a distinct V at the mid-line. The parieto-frontal suture is about 23.0 mm. anterior to a sharply defined, moderately high, parietal crest. The parietal region is rounded and, at the maximum transverse width, is about equal to the width of the skull at the posterior borders of the preorbital fossae. Posteriorly the parietal crest unites with a moderately extended, narrow, nuchal crest which unites laterally with well-defined temporal crests. The paramastoid processes are at a 15-degree angle to the long axis of the skull, are wide posteriorly, with a broad lateral aspect, but are thin and narrow anteriorly.

VENTRAL VIEW OF THE SKULL: The incisive border forms a broad U. The palatine surface is concave, deepest at the posterior part of the palatine processes. A small foramen incisivum opens about 10 mm. behind the median line between the first incisors. Large palatine fissures open at the anterior end of the palatine processes and extend as far forward as the foramen incisivum and as far back as opposite the middle part of the canine. In *Equus* the palatine fissures are long, narrow slits, much narrower than in *Merychippus*.

The posterior nares are widest opposite M^2 in adult skulls and are widest opposite M^1 in immature specimens. In modern horses the posterior nares are widest opposite M^3 and post M^3 . The palatine foramen opens anteriorly opposite the anterior part of M^2 , whereas in modern horses the foramen is opposite M^3 .

The basilar part of the occipital and the body of the sphenoid are broad and heavy, with well-developed basilar tubercles. In the available specimens the vomer is not well preserved but appears light and may extend back as far as the alar canal of the pterygoid process.

The occipital condyles are moderate in size and roundness and have shallow, wide condyloid fossae; in *Equus* these condyloid fossae are deeply concave. The auditory bullae are moderately inflated, with deep hyoidal pits and grooves on the lateral external sides of the bullae which end at

the base of the auditory meatus. The canal of the meatus extends upward and back, opening posteriorly with a slight outward flare. The temporal canal is placed far back on the temporal fossa and opens posteriorly toward the wall of the auditory meatus.

ORDER ARTIODACTYLA

SUBORDER RUMINANTIA

FAMILY ANTILOCAPRIDAE

SUBFAMILY MERYCODONTINAE

MERYCODUS LEIDY, 1854

TYPE SPECIES: *Merycodus necatus* Leidy, 1854.

TYPE: Lost, a ramal fragment with P_4 - M_1 ; collected by Hayden and Meek in 1853 from the Bijou Hills, South Dakota.

NEOTYPE: F:A.M. No. 51790 (fig. 9B; table 4), a right partial ramus with dP_4 (P_4 germ)- M_3 ; dP_4 , P_4 germ, and M_3 are broken; M_{1-2} are damaged, but the crown height of both can be measured. (See horn core, F:A.M. No. 51127, probably the same individual.)

PARATYPE¹: F:A.M. No. 51127 (fig. 10A). A left incomplete horn with burr; both prongs are broken. (See partial ramus, F:A.M. No. 51790, probably the same individual.)

LOCALITY: The neotype and paratype of *Merycodus necatus* came from the south Bijou Hill in the extreme northwest corner of Charles Mix County, South Dakota, in the NW. $\frac{1}{4}$, sect. 8, T. 100 N., R. 71 W.; collected by Morris F. Skinner and party in May, 1937.

STRATIGRAPHIC UNIT: F:A.M. Nos. 51790 and 51127 came from a 5-foot zone of brownish pink clay that carries scattered barite crystals or "rock roses." These beds are part of a unit that has been named the Fort Randall Formation (this paper, p. 11) and are of late Miocene age,

¹ In the case of the horn core (F:A.M. No. 51127), we use the term "paratype" with some hesitation, because, although the neotype has all the status of a holotype (Stoll and others, 1961, Article 75), there is no term in the Code to designate a paratype for a neotype, such as "neoparatype." The neotype (F:A.M. No. 51790) and the paratype (F:A.M. No. 51127) were found by the senior author within 6 inches of each other. There is good reason to believe that the jaw and the horn core belonged to one individual. Because the supposition cannot be proved, they are treated as a syntypic series, in which the jaw becomes a neotype and the horn core a paratype, or a "neoparatype," a term that we do not wish to introduce. [See also Stoll and others, 1961, Article 73 (c) and Recommendation 73D.] The present diagnosis is based on both the neotype and the paratype and adds considerably to the concept of the genus.

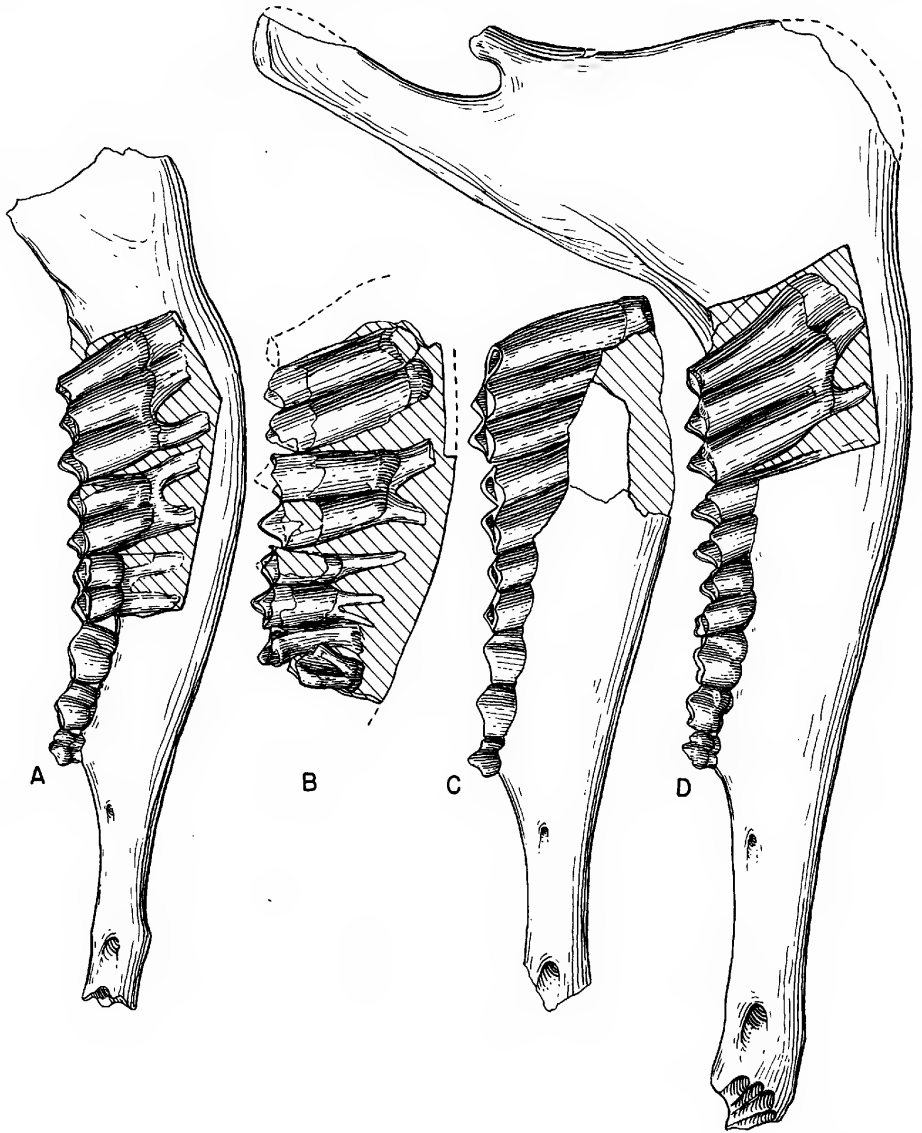


FIG. 9. Lateral buccal views. A. *Merycodus sabulonis*, type, reversed, A.M.N.H. No. 14109; from 23 miles south of Agate, Sioux County, Nebraska. B. *Merycodus necatus*, neotype, reversed, F:A.M. No. 51790; from south Bijou Hill (fig. 1C). C. *Cosoryx furcatus*, reversed (after Leidy, 1869, pl. 14, fig. 9); from Niobrara River, Nebraska. D. *Cosoryx furcatus*, F:A.M. No. 51024 (cf. fig. 10E, one individual); from June Quarry, Burge Member of the Valentine Formation, Brown County, Nebraska. All $\times 1$.

post Lower Snake Creek and pre-Lower Valentine (fig. 1C at 1995 feet above mean sea level).

HISTORY: Leidy's type of *Merycodus necatus* from the Bijou Hills has an involved history. The type was never figured and disappeared after 1918. Nevertheless, the concept, based on this lost ramus, of a group of primitive, antelope-like creatures has been carried through the writings of most subsequent authors. Even though the characters of the type species were in doubt, the genus *Merycodus* was selected by Matthew (1909, p. 115) as the type genus for the subfamily Merycodontinae. Frick (1937, p. 371) made two divisions of the Antilocapridae—Merycodontini and Antilocapriini. The division was intermediate between the family and subfamily. Frick's "-ini" ending for the division is not in accordance with the recommendation in the 1961 International Code (Stoll and others, 1961, Article 29A). If the type had been figured in 1854, Leidy's genus and species *Merycodus necatus* would now have fulfilled the requirements of a nominal taxon, but his failure to do so and the subsequent loss of the type left the genus and species indeterminate.

Matthew (1918, p. 219) stated, "The type of *M. necatus* is from the Bijou Hills and is in the American Museum but, in absence of topotypes, it affords no good specific characters except size." Matthew gave no catalogue number for the specimen. Frick (1937, p. 314) wrote that the whereabouts of the specimen was unknown and stated in a footnote, "The statement of Matthew (1918, p. 219) that the type is in the American Museum collection appears to be incorrect as the specimen has never been entered in the Museum catalogue." As of 1966 we have not found the specimen in the American Museum of Natural History collection or in that of the Academy of Natural Sciences of Philadelphia. The specimen is not recorded in either collection.

Henshaw (1939, p. 26) stated: "It is important to recognize that the species, being intangible, is not lost, and hence the genus *Merycodus* cannot be discarded. The only loss is the type specimen for the species. To rectify this, a neotype, providing that more material can be obtained at Bijou Hill, or a neoholotype from another locality should be set up. It is the contention of the present writer that the material described by Leidy in 1869 fulfills just such a category." Although Henshaw suggested that the material described by Leidy be considered a neoholotype, he did not formally designate it as such. Moreover, the ramus figured by Leidy (1869, pl. 14, figs. 9, 10) from the Niobrara does not have the qualifications for a neotype because it was not derived from the type locality. The specimens figured in the present report (*M. necatus* neotype and paratype) fulfill the requirements as set forth by the 1961 International Code (Stoll and others, 1961, Article 75C).

DESCRIPTION: Concerning the lost type of *Merycodus necatus*, Leidy

TABLE 4
MEASUREMENTS (IN MILLIMETERS) OF THE LOWER TEETH OF *Merycodus* AND *Cosoryx*

	<i>M. sabulonis</i> Referred F.A.M. No. 51691	<i>M. sabulonis</i> Type A.M.N.H. No. 14109	<i>M. necatus</i> Neotype F.A.M. No. 51790	<i>M. necatus</i> Type No Number	<i>Cosoryx furcatus</i> Referred F.A.M. No. 51405
Wear ^a	(W)	(W1)	(I)		(W)
Anteroposterior length					
P ₂	—	4.2	—	—	4.4
P ₃	—	6.3	—	—	6.1
P ₄	—	7.2	—	8.0	7.2
M ₁ on crown	8.0	7.4	9.8	8.0	9.5
M ₁ at base	7.2	6.7	7.2	—	7.8
M ₂ on crown	9.5	9.3	11.0	—	12.0
M ₂ at base	8.5	7.8	8.3	—	8.8
M ₃ on crown	12.5	12.5	—	—	15.9
M ₃ at base	13.0	12.0	—	—	15.0

^aWear, from Skinner (1942, p. 189); I, milk premolars present; W, M₁ retaining anterior fossette; W₁, anterior fossette worn away.

(1854a, p. 90), stated: “. . . Fragment of a lower jaw, containing a last premolar and the first true molar of a small ruminant allied to the Musk. The last premolar on the triturating surface presents a series of five folds projecting inwardly. Its measurement antero-posteriorly is 8 mm. The inner side of the true molar is nearly as plain as in those of *Poebrotherium*. Its measurement antero-posteriorly is also 8 mm.” The last premolar of the lost type of *M. necatus*, as Leidy described it, was unworn, because the five folds on the crown surface disappear with wear. The neotype, F:A.M. No. 51790 (fig. 9B), has an unerupted broken P_4

TABLE 5
COMPARISON OF LENGTH AND HEIGHT OF M_3

	Length of First Two Lobes ^a of M_3	Crown Height of M_3	Percentages
<i>Merycodus sabulonis</i>			
Referred, F:A.M. No. 51691	9.3	12.2	76%
Type, A.M.N.H. No. 14109	8.8	11 ^b	80%
<i>Merycodus necatus</i>			
Neotype, F:A.M. No. 51790	9.8	12.0	55%
Type (no number)	—	—	—
<i>Cosoryx furcatus</i>			
Referred, F:A.M. No. 51405	10.3	21.7	47%

^a The third lobe is missing from *M. necatus* neotype (F:A.M. No. 51790).

^b Estimated, because of wear.

and is therefore less mature than the lost type. Comparisons with Leidy's description of his lost type are limited to the M_1 .

The measurements of the neotype of *M. necatus* bracket the measurements of the lost type. Leidy gave the anteroposterior length of M_1 of the type as 8 mm. In the neotype the M_1 is 9.5 mm. long on the crown and 7 mm. long at the base; the lingual surface is smooth, as Leidy described his type. The crown wear of the lost type is unknown. However, Leidy's anteroposterior measurement of M_1 indicates that it was within the size range of the M_1 of the neotype. The M_2 of the neotype is broken, but enough is present to show that it was high-crowned and had a well-developed median external ridge between the protoconid and hypoconid. The first two lobes of the M_3 are unworn, revealing the degree of hypsodonty; the third lobe of M_3 is missing.

Table 5 gives the crown height and the ratio of the height to the length of the first two lobes of M_3 in the neotype of *M. necatus* as com-

pared with those of *Merycodus sabulonis*¹ (fig. 9A) and *Cosoryx furcatus*, referred (fig. 9C, D). The crown height of the M_3 in the neotype of *Merycodus necatus* is intermediate between that of *Merycodus sabulonis* from the Lower Snake Creek beds of Sioux County, Nebraska, and that of *Cosoryx furcatus*, referred, from the Burge Member of the Valentine Formation in Brown and Cherry counties, Nebraska.

Matthew and Cook (1909, p. 411, fig. 24) based *Merycodus necatus sabulonis* on a ramus (A.M.N.H. No. 14109) and referred a series of lower jaws to the subspecies from the "Pliocene deposits" of Sioux County, Nebraska. In this publication Matthew and Cook considered the channel deposits of the area as the Snake Creek beds, not realizing that there was a temporal difference. However, Matthew (1924, p. 68) recorded *Merycodus necatus* in a faunal list as occurring in the Sheep Creek and the Lower Snake Creek deposits but not from the Upper Snake Creek beds. Subsequent Frick collections of *Merycodus sabulonis*, referred, from both Sheep Creek and Lower Snake Creek beds, verify Matthew's 1924 corrected allocation.

A comparison between the neotype of *Merycodus necatus* and the type of *M. sabulonis* must take into account the difference in dental wear. *Merycodus sabulonis* has well-worn dentition; the dentition of *M. necatus* neotype is approaching maturity. If the differences in age be allowed for, the type of *M. sabulonis* has smaller, less hypsodont molars and a relatively larger P_4 than the incomplete P_4 in the dental series of *M. necatus* neotype, very possibly the result of temporal differences. Gregory (1942, pp. 405-406) also correlated dental changes with time.

The paratype of *Merycodus necatus*, F:A.M. No. 51127, is a small horn with a relatively short, straight shaft (fig. 10A). The burr is centrally placed, and the prongs are long relative to the length of the shaft. Although a portion of each prong is missing, the prongs appear subequal. A comparison of the paratype of *M. necatus* with the type and referred horns and skulls of *Cosoryx furcatus* (fig. 10D-F), shows that the horn of *M. necatus* is smaller, the shaft is much shorter, with prongs proportionately longer relative to the length of the shaft, and the burr is more centrally situated and comparatively higher than in *Cosoryx furcatus* (fig. 10F). The referred specimens of *Cosoryx furcatus* (fig. 10E, F) are from June Quarry, Brown County, Nebraska. The stratigraphic relationship and lithology of this quarry are typical of the Burge Member of the Valentine Formation. The size and variation of the horn cores shown

¹*Cosoryx (Subparacosoryx) savoronis* Frick, 1937 = *Merycodus sabulonis* Matthew and Cook, 1909. See synonymy, page 41.

in figure 10E and F illustrate the range of individual variation in a large population sample from a single faunal deposit.

Comparison of the paratype of *M. necatus* (fig. 10A) with Frick's type of "*Cosoryx* (*Subparacosoryx*) *savaronis*," A.M.N.H. No. 17339 (fig. 11B) [= *Merycodus sabulonis*], reveals that the horn shaft of *M. necatus* is shorter and the prongs longer. In both *M. necatus* and *M. sabulonis*, the burr is centrally placed on the shaft and is relatively higher than that in *Cosoryx furcatus* and *Meryceros warreni* (Leidy, 1858), Frick, 1937. There is, however, a great deal of variation in the length of the shaft and prongs in specimens referred to *M. sabulonis* Matthew and Cook. A referred *M. sabulonis* horn, F:A.M. No. 51259 (fig. 11A), from New Surface Quarry, East Sinclair Draw, in the Lower Snake Creek deposits, is an extreme variant of the species and differs from that of *Merycodus necatus* in having a much longer shaft and reduced prongs in comparison to shaft length. This referred specimen of *Merycodus sabulonis* is distinctively different from the type of *Cosoryx furcatus* and referred remains from the Burge Member of the Valentine Formation, the probable source of Leidy's type of *C. furcatus*. On the basis of the new horn evidence, the paratype of *M. necatus* is more comparable to the horns referred to the Lower Snake Creek *M. sabulonis* population and morphologically distinct from *Cosoryx furcatus*.

In the types of *Meryceros warreni*, U.S.N.M. No. 149 (fig. 10C), and *Meryceros nenzelensis*, the horns are larger and the horn shafts are heavier and more laterally compressed than in the paratype of *Merycodus necatus*. The type of *Meryceros* (*Submeryceros*) *crucianus*, F:A.M. No. 31495 (fig. 10B), is a small horn in which the prongs emerge from the fork at a more acute angle than in the paratype of *M. necatus*. In *M. (S.) crucianus* the burrs are developed separately at the base of each prong instead of on the main shaft as in *Merycodus necatus* and all other observed merycodont horns.

Merycodus sabulonis Matthew and Cook, 1909

Merycodus necatus sabulonis MATTHEW AND COOK, 1909, p. 411, fig. 24. The type is a ramus, A.M.N.H. No. 14109.

Merycodus necatus Leidy; referred: MATTHEW, 1918, p. 219, fig. 18. The referred skull is A.M.N.H. No. 17339; later selected by Frick, 1937, as the holotype of *Cosoryx* (*Subparacosoryx*) *savaronis*.

Merycodus necatus sabulonis Matthew and Cook: MATTHEW, 1924, p. 200.

Cosoryx (*Paracosoryx*) *sabulonis* (Matthew and Cook): FRICK, 1937, p. 353, fig. 44. The type is a ramus, A.M.N.H. No. 14109.

Cosoryx (*Subparacosoryx*) *savaronis* FRICK, 1937, p. 353, figs. 28, 28A.

DISCUSSION: Frick (1937, p. 353) described "*Cosoryx* (*Subparacosoryx*) *savaronis*" and designated it the subgenotypic species. The type is a partial

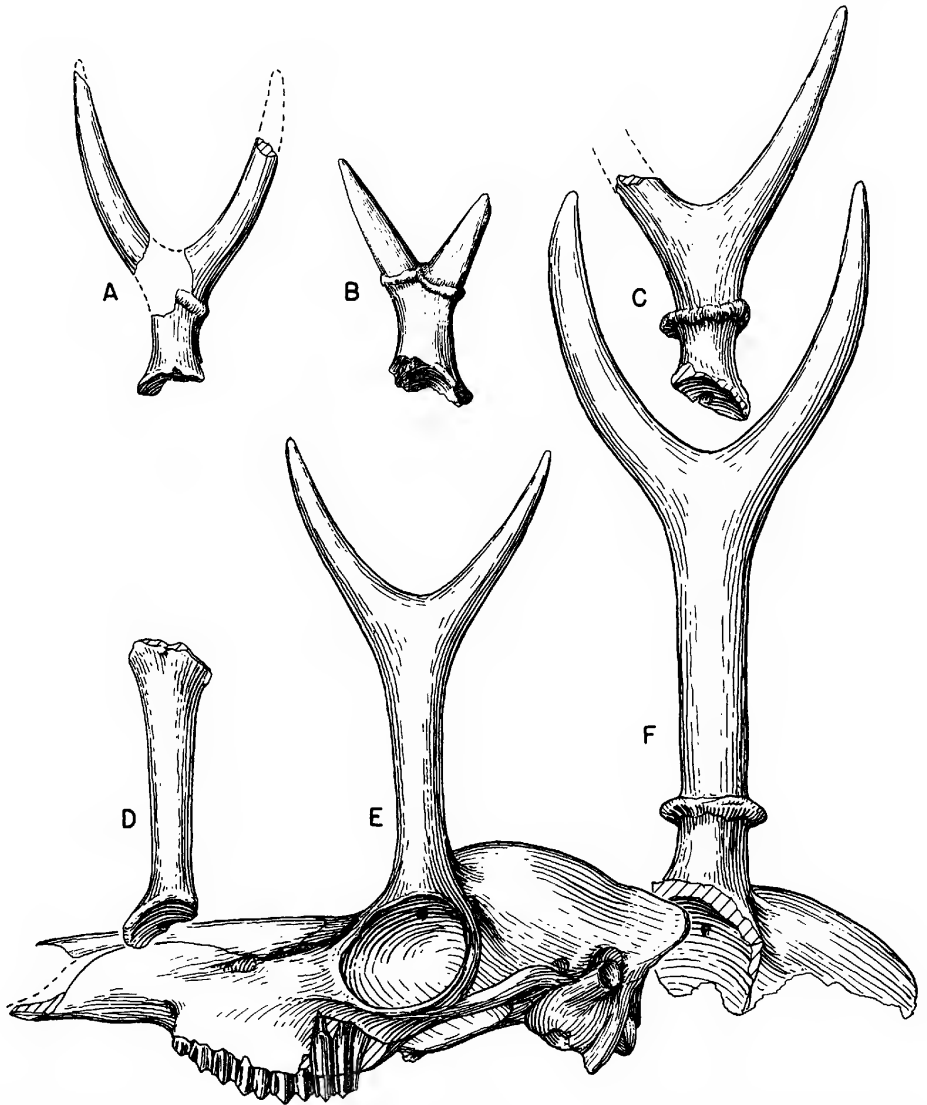


FIG. 10. Lateral views. A. *Merycodus necatus*, paratype, F:A.M. No. 51127; from south Bijou Hill (fig. 10C). B. *Meryceros (Submeryceros) crucianus*, type, F:A.M. No. 31495 (after Frick, 1937, fig. 35); from Santa Cruz, New Mexico. C. *Meryceros warreni*, type, U.S.N.M. No. 149, from cast, reversed; from Niobrara River, Nebraska. D. *Cosoryx furcatus*, type, U.S.N.M. No. 148, from cast; from Niobrara River, Nebraska. E, F. *Cosoryx furcatus*; from June Quarry, Brown County, Nebraska. E. F:A.M. No. 51024 (cf. fig. 9D, one individual). F. F:A.M. No. 51081, reversed. All $\times \frac{1}{2}$.

skull (A.M.N.H. No. 17339, fig. 11B). On the same page Frick transferred *Merycodus necatus sabulonis* Matthew and Cook (1909) to *Cosoryx*

(*Paracosoryx*). Concerning the change, Frick (1937, p. 353) stated, "It seems necessary, pending the securing of more satisfactory evidence, to hold the possibly equivalent crania from the general area in a separate species, *S. savaronis*." Through an error, Frick (1937, p. 353) included figure 18 from Matthew (1918), which was the type of his new species, "*C. (S.) savaronis*," in the synonymy of the referred material of "*Cosoryx (Paracosoryx) sabulonis*."

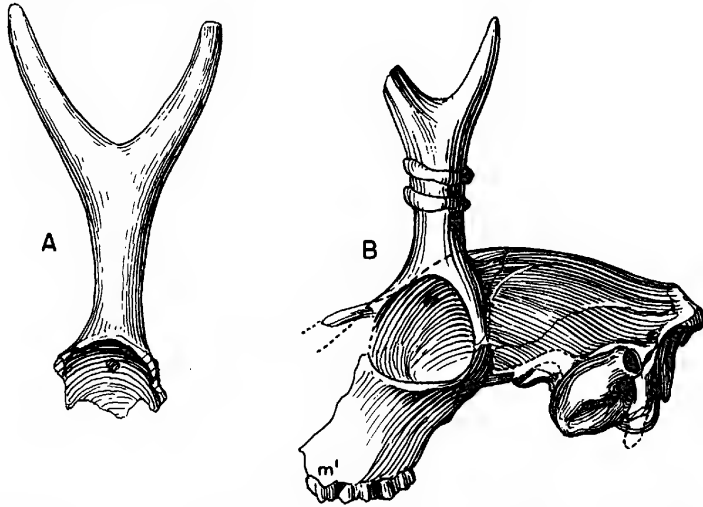


FIG. 11. Lateral views of *Merycodus sabulonis*. A. F:A.M. No. 51259; from New Surface Quarry, Sioux County, Nebraska. B. A.M.N.H. No. 17339 (after Frick, 1937, fig. 28A); Lower Snake Creek beds, Sioux County, Nebraska. Both $\times \frac{1}{2}$.

The subgenotypic species, *Cosoryx (Paracosoryx) wilsoni*, based on a partial skull, is from the Sheep Creek deposits in Sioux County, Nebraska. The dentitions of *Merycodus sabulonis* from the Lower Snake Creek deposits are smaller and lower-crowned than dentitions referred to *Cosoryx (Paracosoryx) wilsoni*. Unpublished stratigraphic studies by Skinner reveal that Long Quarry, the type locality of *C. (P.) wilsoni*, is in the lower part of the Sheep Creek deposits and therefore earlier than the Lower Snake Creek deposits from which *Merycodus sabulonis* came. The type ramus and referred dentitions of *M. sabulonis* occurred in faunal association with crania, horns, and dentitions of "*Cosoryx (Subparacosoryx) savaronis*" Frick, 1937, and appear to be the same species. On this basis, the species "*C. (Subparacosoryx) savaronis*," based on a partial skull (see fig. 11B), is here considered a synonym of *Merycodus sabulonis*. The type of *M. sabulonis* (fig. 9A) is a ramus, A.M.N.H. No. 14109.

The neotype of *Merycodus necatus*, which is a ramal fragment (F:A.M.

No. 51790), and the paratype, which is a horn core (F:A.M. No. 51127), were found in such close association that the two are almost certainly one individual. Leidy's description of the type ramus (now lost) gave no diagnostic characters, but gave measurements that can be duplicated in almost any of the Merycodontinae. The neotype (F:A.M. No. 51790) is from the type locality and approximates the measurements given by Leidy for the lost type (table 4). The associated horn core adds characters to the genotypic species, *M. necatus*, which have been heretofore unknown. It is presumed that Leidy's lost type of *M. necatus* came from the lower beds of the Fort Randall Formation where we obtained the neotype and paratype (see above, p. 4).

Frick (1937, pp. 271, 276, 292, 345) was unable to establish objective characters for *Merycodus* as a genus but did not drop the name, as witnessed by his use of the division Merycodontini for all included genera.

Frick (1937, p. 334) commented, "The genus *Cosoryx* . . . may prove to be synonymous with *Merycodus* Leidy, should it ever be possible to definitely determine the latter." However, the relatively short-shafted horn cited in this report as the paratype of *M. necatus* (F:A.M. No. 51127) is notably different from the taller and more slender-shafted incomplete horn (U.S.N.M. No. 148), the type of *Cosoryx furcatus* Leidy, genotypic species (fig. 10D).

Henshaw (1939, p. 26) contended that the ramus from the Niobrara, which Leidy figured as *Cosoryx furcatus* referred (this paper, fig. 9C), should be set up as a neoholotype of *Merycodus necatus*. However, Leidy's figures (1869, pl. 14, figs. 9, 10) show that the molars are larger and taller-crowned than those of the neotype (F:A.M. No. 51790) from the Bijou Hills. The taller-crowned molars and reduced premolars are comparable to dentitions referred to *Cosoryx furcatus* which is the dominantly occurring merycodont from the Burge Member of the Valentine Formation along the Niobrara River.

Gregory (1942, p. 407) predicated: ". . . *M. necatus* is known only from teeth, and is not positively associated with any horn pattern. There is some evidence, moreover, that '*Cervus*' *warreni* may be a synonym of *M. necatus*, and represents the horn pattern of that species. In the Niobrara River fauna only '*C.*' *warreni* horns occur, and this fauna appears to be the same as that at Bijou Hills, from which the type of *Merycodus* was obtained." There are observable differences in the horn cores that tend to refute Gregory's statement. The type of *Meryceros warreni* from the Niobrara River differs from the paratype of *Merycodus necatus* from the Bijou Hills in that *M. warreni* is larger and has a heavier, laterally more compressed shaft (see fig. 10C).

According to the unpublished diary of Warren, and that of Snowden, Warren's cartographer, the expedition that collected the type of *Meryceros warreni* passed the mouth of the Snake River on October 22, 1857. The night of October 22-23, the Warren-Hayden expedition camped 8 miles below the mouth of the Snake River on the Niobrara. On the following day, October 23, the party crossed the Minnecheduza Creek and ascended the canyons north of the present town of Valentine, Nebraska. They camped for the night on a high bluff on the north side of the Niobrara River approximately 1½ miles northeast of the site of the present Fort Niobrara buildings.¹ There are exposures of the Lower Valentine Formation throughout this area, and it is possible that the type of *Meryceros warreni* could have been found at this time. The type horn of *Meryceros warreni* is characteristic of horns from the Lower Valentine Formation, whereas the paratype of *Merycodus necatus* more closely resembles *Merycodus sabulonis* from the Lower Snake Creek deposits of Sioux County, Nebraska, which occurred earlier.

CONCLUSIONS

A revision of faunal names and geologic terms, such as the present paper attempts by supplying factual data, is rewarding only when it appears that a step forward has been made and that something useful has been added for future studies. McKenna's statement (1965, p. 17), "The use of the written word to denote various aspects of nature demands that concepts be disciplined by facts and that these facts be readily accessible to any investigator," is particularly applicable to a revision of this nature. For every long-known group of fossil animals, a revision of some sort should be made in order to establish a firm foundation for an evolutionary concept. In this paper, we have placed Leidy's fauna from the Bijou Hills where we believe it belongs in time and have supplied a stratigraphic framework. A long and cloudy history has been built around Leidy's types, and either we have diagnosed these so that the characters they exhibit are identified with more complete material, or we have left them in the category of *nomina dubia* (i.e., *Hippodon speciosus*).

We believe that a step forward has been taken by the introduction of a new formation in the Bijou Hills area. It would serve little purpose to name a new geologic formation if it did not represent deposits and time missing from the record elsewhere. The deposits of the Fort Randall Formation (new) have yielded a fauna which, in part, represents the

¹ Fort Niobrara was not established until 1880. The town of Valentine, Nebraska, was not in existence in 1857.

hiatus between the Lower Snake Creek and the Lower Valentine formations. Certain other rocks in this region, which have been variously mapped as "Bijou Formation" and "Bijou facies," are here considered as representing neither a formation nor a facies but rather a sedimentary condition.

We have designated a type set of rocks in the type locality for the Rosebud Formation in order to stabilize the nomenclature for this lithic unit. There is still no published description of the Rosebud Formation, and it is beyond the scope of this paper to supply one.

In the case of *Merychippus insignis*, we have duplicated as nearly as possible the fragmentary holotype and associated it with an extensive population sample from the Lower Snake Creek deposits of western Nebraska. The morphological characters of the type taxon are here re-defined and enlarged upon.

In the case of *Merycodus necatus*, the neotype (a ramal fragment) was found in such close association with the paratype (an incomplete horn) that the two are believed to represent one individual. The paratype, therefore, enables us to give, for the genus *Merycodus*, diagnostic horn characters which have been heretofore unknown. These characters, taken with all the known temporal aspects of the Bijou Hills fauna, show that *Merycodus* is morphologically distinct from *Cosoryx*.

The stratigraphic nomenclature of the Miocene of western Nebraska has been summarized by McKenna (1965, fig. 1). McKenna clearly stated the need for more precise studies and adequate definitions of the sediments from which faunas have been obtained. For the past 30 years at least, Frick Laboratory parties have been accumulating factual data about the sequence of sediments in the Great Plains and their contained faunas.

ADDENDUM: RODENT IDENTIFICATIONS

BY THOMPSON M. STOUT¹

Among the many interesting specimens collected by Morris F. Skinner and associates from the Bijou Hills are teeth of several rodents, listed below. Of these, only the beaver and mylagaulid seem presently useful for correlation purposes. The beaver teeth, of which one is illustrated (fig. 12A), compare best with specimens from the highest-known level of the "Lower Snake Creek" (Hemingford Group) sediments of western

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Nebraska, the highest unit in the Great Plains Miocene in Nebraska usage.¹ The mylagaulid teeth seem also to relate best to specimens from this same "Lower Snake Creek" horizon.

FAMILY CASTORIDAE

"*Eucastor*" cf. *curtus* (Matthew and Cook)

Dipoides curtus MATTHEW AND COOK, 1909, p. 381, fig. 9 [= "*Dipoides brevis*" Matthew and Cook, a *nomen nudum* in the faunal list of this same paper, p. 364; type, A.M.N.H. No. 13871]. MATTHEW, 1918, p. 186; 1924, pp. 66, 74.

Monosaulax curtis [*sic*] (Matthew and Cook): STIRTON, 1935, pp. 420-421, figs. 74-75, chart 2.

SPECIMENS: Three cheek teeth (F:A.M. Nos. 42922A-42922C), apparently of different individuals: left P₄ (fig. 12A), right P⁴, and left M³.

LOCALITY AND LEVEL: South Bijou Hill (F:A.M. Prospect No. 55), Charles Mix County, South Dakota, at "Rosestone level"; collected by Morris F. Skinner and associates, 1950.

DENTAL MEASUREMENTS: P₄, wear surface, length, 4.4 mm.; width (anterior), 2.9; width (posterior), 3.8; external crown height, 7.6; external groove height, 5.75; central internal groove height, 0.8; other two internal grooves worn out to form enamel lakes in pattern; moderate mature wear. P⁴, wear surface, length, 3.7; width (anterior), 3.75; width (posterior), 3.7; internal crown height not measured; internal groove height, 4.1; anterior external groove height, 0.2; other two external grooves worn out to form enamel lakes in pattern; moderate mature wear. M³, wear surface, length 2.9; width (anterior), 3.0; width (posterior), 2.6; internal crown height, 5.0; internal groove height, 1.9; the three external grooves worn out to form enamel lakes in pattern; moderate mature wear.

COMPARISONS: A specimen from the highest level of the "Lower Snake Creek" (Mill Quarry of the Frick Laboratory), in the "Sheep Creek-Snake Creek collecting area," Sioux County, Nebraska, compares favorably (fig. 12C), except for a slight difference in the stage of wear: it is a mandible with both incisors (broken), both right and left P₄-M₃

¹The present writer considers the Hemingford Group to be of late Miocene age, with the Marsland an approximate early Vindobonian (Helvetian) correlative, the principal or restricted part of the Sheep Creek equivalent to the lower part of the late Vindobonian (Tortonian), and the "Lower Snake Creek" equal to that part of the French Miocene usually termed late Vindobonian and in central Europe late Vindobonian to (or) Sarmatian. The evidence from the fossil beavers for these correlations, together with a report on recently completed European studies, will be presented in full elsewhere.

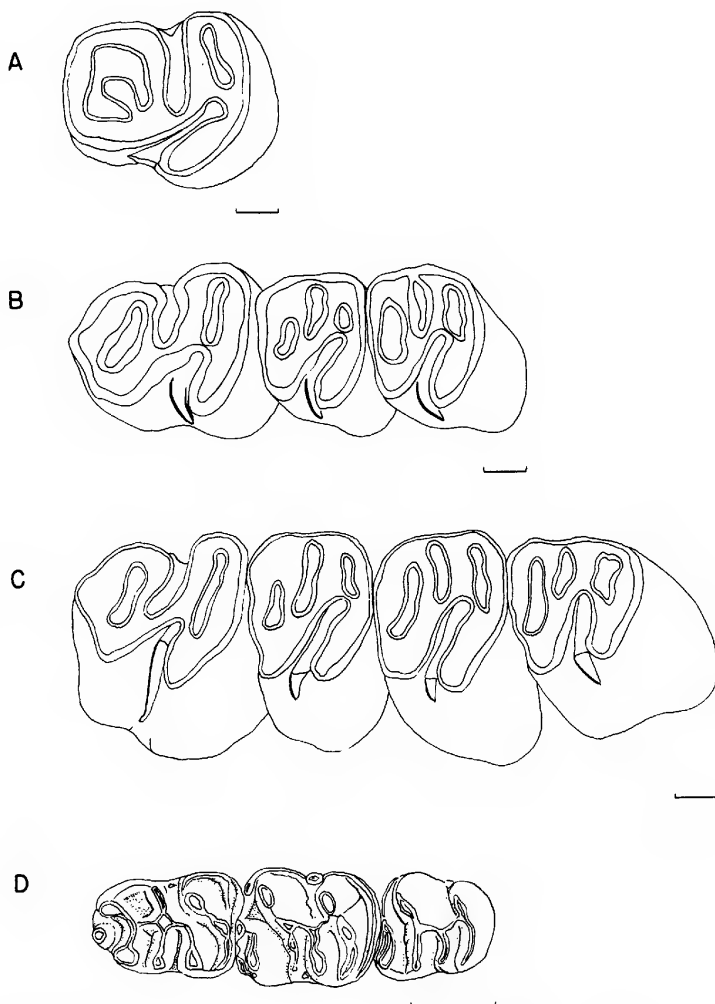


FIG. 12. Comparison of beaver specimens, and a cricetine dentition. A. "*Eucastor*" cf. *curtus* (Matthew and Cook), left P_4 , F:A.M. No. 42922A; from the south Bijou Hill (fig. 1C). $\times 5$. B. "*Eucastor*" *curtus* (Matthew and Cook), holotype, right P_4-M_2 , reversed, A.M.N.H. No. 13871; from the "Lower Snake Creek," Sioux County, Nebraska. $\times 5$. C. "*Eucastor*" cf. *curtus* (Matthew and Cook), left P_4-M_3 , F:A.M. No. 42926; from the "Lower Snake Creek," Sioux County, Nebraska. $\times 5$. D. *Peromyscus* (*Copemys*) sp., right M_{1-3} , F:A.M. No. 42923; from the south Bijou Hill (fig. 1C). $\times 10$. Each bar equals 1 mm.

(F:A.M. No. 42926), of which the left ramus is illustrated.¹ Further comparison with the holotype of this species (fig. 12B), a right ramus with

¹ This "Lower Snake Creek" specimen was also collected by Morris F. Skinner and associates.

P₄-M₂, alveolus of M₃ (A.M.N.H. No. 13871), probably from a somewhat older level of the "Lower Snake Creek" of the same collecting area, Sioux County, Nebraska,¹ emphasizes the smaller size of the type. A new subspecific name may be necessary eventually to accommodate the Mill Quarry and Bijou Hills specimens.

DISCUSSION: This species cannot now be assigned to "*Monosaulax*," following Stirton (1935, pp. 420-421), because this genus proves to be invalid and a synonym of *Eucastor*, with their type species apparently conspecific also. Since the Bijou Hills teeth and the abundant materials from the "Lower Snake Creek" here under consideration presumably belong in the lineage ancestral to the Pliocene *Eucastor*, this generic allocation is employed here but in quotation marks ("*Eucastor*").

FAMILY MYLAGAULIDAE

Mylagaulus sp.

SPECIMEN: Skull fragment, chiefly basicranium, with left P⁴, and mandibular fragments with right incisor (broken), left and right P₄, together with some fragments of the appendicular skeleton; all taken as pertaining to a single individual (F:A.M. No. 42924).

LOCALITY AND LEVEL: "From the extreme north Bijou Hill, near the Missouri River, in Brule County, South Dakota" (F:A.M. Prospect No. 55), in the "Pink deposits," referred to in the 1949 field geologic section²; collected by Morris F. Skinner and associates.

DENTAL MEASUREMENTS: Left and right P₄, wear surfaces, lengths, 10.4 and 10.5 mm.; widths (anterior), 6.8 and 6.6; widths (posterior), 7.45 and 6.8; external crown heights, 13.3 and 15.5, the former approximate; early mature wear, with crown cementum. P⁴, wear surface, length, 11.3;

¹ The holotype was collected by the American Museum of Natural History Expedition of 1908, from the "Snake Cr'k Beds, 23 mi. S. of Agate, Nebr." After careful investigation of the field records and long familiarity with the collecting history of this area, Morris F. Skinner (personal communication) has determined that the "1908 or Old Workings" are probably the same as the "Princeton Locality 1000-C" and as the site worked by the Frick Laboratory and called "West Surface Quarry." In any case, specimens from the "West Sinclair Draw" in Sioux County, and the truly remarkable series collected by Ted Galusha at the "Observation Quarry" in Dawes County, Nebraska (all in the Frick Collection), can be matched almost identically with the holotype. The typical horizon is therefore also "Lower Snake Creek."

² [F:A.M. No. 42924 was collected at an elevation of 1987 feet, 27 feet above the base of the Fort Randall Formation (fig. 1B)].—SKINNER.

width (anterior), 7.1; width (posterior), 8.0; internal crown height, 13.4; early mature wear, with crown cementum.

COMPARISONS: As remarked above, the Bijou Hills specimen of mylagaulid also compares favorably with specimens from the "Lower Snake Creek."

DISCUSSION: This is the largest of the three mylagaulids of the "Lower Snake Creek," for which a new generic name and possibly a new specific name may be necessary. The first mylagaulid specimens to receive names were loose cheek teeth. Later, generic weight was given to the presence or absence of horned processes on the nasals, together with the relative heights of the horns, if present. Since it is now evident that the presence or absence of horns is a sex-linked character, a reinvestigation of all available materials was undertaken and is now nearing completion, parallel to a revision of the beavers.

FAMILY MURIDAE

SUBFAMILY CRICETINAE

Peromyscus (Copenys) sp.

SPECIMEN: Fragment of right ramus (F:A.M. No. 42923), with M_{1-3} (fig. 12D).

LOCALITY AND LEVEL: South Bijou Hill (F:A.M. Prospect No. 55), Charles Mix County, South Dakota, at "Rosestone level"; collected by Morris F. Skinner and associates, 1950.

DENTAL MEASUREMENTS: M_{1-3} , total crown length at base, 4.8 mm. M_1 , total crown length, 1.7; total width (anterior), 1.1; total width (posterior), 1.25. M_2 , total crown length, 1.65; total width (anterior), 1.4; total width (posterior), 1.35. M_3 , total crown length, 1.35; total width (anterior), 1.2; total width (posterior), 1.05.

COMPARISONS: A study of probably topotype specimens of *Peromyscus (Copenys) loxodon* (Cope), collected in New Mexico for the Frick Laboratory by Ted Galusha, reveals apparent minor differences from the Bijou Hills specimen. A specimen from the Pliocene of Cherry County, Nebraska, collected by Morris F. Skinner, is also available, and it likewise differs only slightly. More study, but also additional specimens, will be necessary before this problem of significant differences can be settled.

DISCUSSION: The affinities of the New Mexico materials with *Peromyscus* seem evident, but the subgeneric name of *Copenys* Wood (1936) is tentatively retained. A recent discussion by Clark, Dawson, and Wood (1964) must be given careful study.

INDETERMINATE

SPECIMENS: Two small rodent incisors, F:A.M. No. 42924A (fig. 1B), found associated with the above-listed mylagaulid specimen from the Bijou Hills; also a matrix block, F:A.M. No. 42925 (fig. 1C), still embedded in plaster, with a mass of broken bones, presently undetermined.

LOCALITY AND LEVEL: The incisors were associated with the mylagaulid (see under *Mylagaulus* sp., above). The block (a "concentration of rodent bones") is from the south Bijou Hill (F:A.M. Prospect No. 55), Charles Mix County, South Dakota, in the "Zone above the Rock Roses"; collected by Morris F. Skinner and associates, 1949.

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