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NEW NORTH AMERICAN ERINACEINE HEDGEHOGS (MAMMALIA: INSECTIVORA)

By

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Modern hedgehogs, members of the subfamily Erinaceinae, first appeared in the fossil record of Asia and Europe approximately 35 million years ago during the Oligocene. Today the subfamily continues to thrive on those two continents as well as Africa, where they are known to have occurred first 20 million years ago near the beginning of the Miocene.

Although now extinct in North America, members of the subfamily first appeared on that continent approximately 23 million years ago near the beginning of the Miocene. At that time, three erinaceine species, belonging to as many different genera, made their appearance in the fossil record. Two of the species are closely related to forms known in Oligocene deposits of Asia and Europe and hence, apparently immigrated into North America shortly after their appearance there in the fossil record. No known erinaceids in the pre-Miocene fossil record of either the Eastern or Western Hemisphere are closely related to the third species. Therefore the question of whether this third species is a newly arrived immigrant into North America or a descendant from an Oligocene endemic form remains unresolved.

The Erinaceinae persisted in North America until the latter part of the Miocene about 10 million years ago. During the interval of their presence on that continent, only one additional erinaceine

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genus and species appeared after the initial, nearly simultaneous appearance of the three forms that marked the beginning of the episode. Otherwise, the group did not undergo any noticeable change in North America other than the extinction of its members.

Previously, the North American history of the Erinaceinae had been documented by the description of fewer than two dozen specimens of which less than half were correctly recognized as erinaceines. In an attempt to further elucidate the history of the Erinaceinae, this report will describe a similar number of new North American erinaceine specimens and review those previously mentioned ones which are referred to the same taxa.

ACKNOWLEDGMENTS

For the loan of specimens we are deeply indebted to Mr. Morris F. Skinner and Dr. Malcolm C. McKenna, Department of Vertebrate Paleontology, and Dr. Sydney Anderson, Department of Mammalogy, American Museum of Natural History; Dr. Larry D. Martin, Museum of Natural History, University of Kansas; Dr. Robert W. Wilson, Museum of Geology, South Dakota School of Mines and Technology; Dr. Peter Robinson, University of Colorado Museum; Dr. Robert W. Fields, Department of Geology, University of Montana; the late Dr. Claude W. Hibbard, Museum of Paleontology, University of Michigan; and Dr. Elwyn L. Simons, Peabody Museum of Natural History, Yale University. We also thank Drs. Craig C. Black, Malcolm C. McKenna, and Larry D. Martin for criticizing the manuscript and making several suggestions for improvement.

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METHODS AND ABBREVIATIONS

The primary geochronologic units employed in this report are the North American and European Land-Mammal Ages. Also given are the approximate epoch and radiometric age equivalents based on data summarized in Berggren (1971) and Van Couvering (1972).

Figure 1 illustrates the method employed for making measurements of teeth discussed in this report, and figure 11 illustrates how angular measurements of lower jaws were taken.

Museum abbreviations used with catalogue numbers are as follows:

AMNH	Department of Vertebrate Paleontology, American Museum of Natural History
AMNH (M)	Department of Mammalogy, American Museum of Natural History
F:AM	Frick American Mammals, Department of Vertebrate Paleontology, American Museum of Natural History
KU	Museum of Natural History, University of Kansas
MPUM	Department of Geology, University of Montana
SDSM	South Dakota School of Mines and Technology
UCM	University of Colorado Museum
UMMP	Museum of Paleontology, University of Michigan
YPM	Yale Peabody Museum

HISTORICAL RESUMÉ

Established by Koerner in 1940, *Parvericius montanus* was the first erinaceine species to be recognized and named in North America. The new species was based on a single specimen, consisting of a maxillary fragment with M^{1-3} and the buccal regions of P^3-4 , from the Miocene Deep River Formation of Meagher County, Montana. Koerner regarded the species as an erinaceine and considered it to be more closely related to *Erinaceus* than to any other member of that subfamily, devoting the generic diagnosis to an enumeration

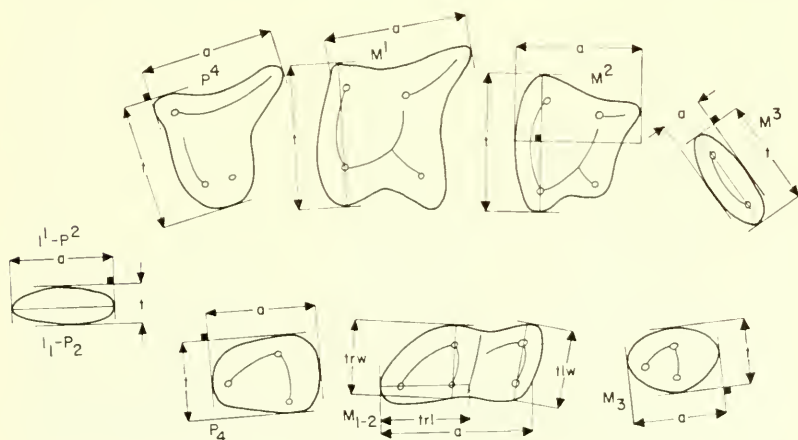


FIG. 1. Occlusal view of erinaceine dentition showing points between which tooth measurements were taken. Abbreviations: a , anteroposterior diameter; t , transverse diameter; $tl w$, talonid width; $tr l$, trigonid length; $tr w$, trigonid width. For I^1-P^4 , M^3 , I_1-P_4 , and M_3 , the transverse diameter, t , is defined as the greatest distance from the buccal to the lingual borders of the tooth measured perpendicular to the anteroposterior diameter, a , but not necessarily on a single line. For M^2 , the anteroposterior diameter, a , is defined as the greatest distance from the anterior to the posterior borders of the tooth measured perpendicular to the transverse diameter, t , but not necessarily on a single line.

of eleven differences he considered significant between the two (Koerner, 1940:841).

Although Butler (1948:490) suggested that *Parvericius* might belong to the tribe Erinaceini (subfamily Erinaceinae), he tentatively placed it in the Brachyericiini (subfamily Neurogymnurinae) in his classification of the Erinaceidae (1948:488). Butler (loc. cit.) regarded the M^1 as more transverse and the M^3 more reduced in *Parvericius montanus* than in *Amphechinus edwardsi*. Examination of Koerner's illustration of the upper dentition of *P. montanus* (see also Fig. 12a, this paper) and Hürzeler's of *A. edwardsi* reveals that the M^3 transverse width is equal to the distance from the buccal edge of the M^2 opposite the metacone to the buccal side of the hypocone on both specimens (Koerner, 1940:Pl. 1, Fig. 1a; Hürzeler, 1944: Fig. 4). Direct examination of the type of *P. montanus* (YPM 13956) confirms this relationship in that specimen. In the same way, the anteroposterior dimensions of the M^3 on the two specimens appear to be proportionally the same, and morphologically the two teeth are quite similar. Therefore, it cannot be said generally that *P. montanus* has a more reduced M^3 than is found on *A. edwardsi*.

In 1960, R. W. Wilson identified an isolated lower molar from the Hemingfordian lower Pawnee Creek Formation of northeastern Colorado as an M_2 of *Metechinus marslandensis*. This specimen now appears to be an M_1 of either *Parvericius* or *Stenoechinus*, new genus.

Friant (1961) placed *Parvericius* in her broadly defined Erinaceinae.

Van Valen (1967:273) synonymized *Parvericius* with *Amphechinus* for three reasons. At the time, Van Valen regarded it likely that material referred to *Metechinus marslandensis* was the otherwise unknown lower dentition of *Parvericius montanus*. On this basis, he assumed that *Parvericius* was similar to *Amphechinus* in possessing an enlarged lower incisor. Subsequently, however, the material referred to *M. marslandensis* has been shown to be the lower dentition of *Brachyerix macrotis*, an erinaceid quite unlike *P. montanus* (Rich and Rich, 1971:12-13). Secondly, Van Valen thought that both *Metechinus* (a genus he thought to have been derived from *Parvericius*) and *Amphechinus* had foreshortened skulls. However, comparison of figures of the skulls of *Amphechinus* and other erinaceines such as *Erinaceus*, reveals that the skull of *Amphechinus* is as elongated, if not more so, than those of other members of the Erinaceinae (cf. Viret, 1938: Fig. 1). Finally, Van Valen regarded the teeth of *Amphechinus* and *Parvericius* as quite similar. Although the available teeth of *Parvericius* do resemble those of *Amphechinus*, they show equally strong resemblances to other known erinaceines.

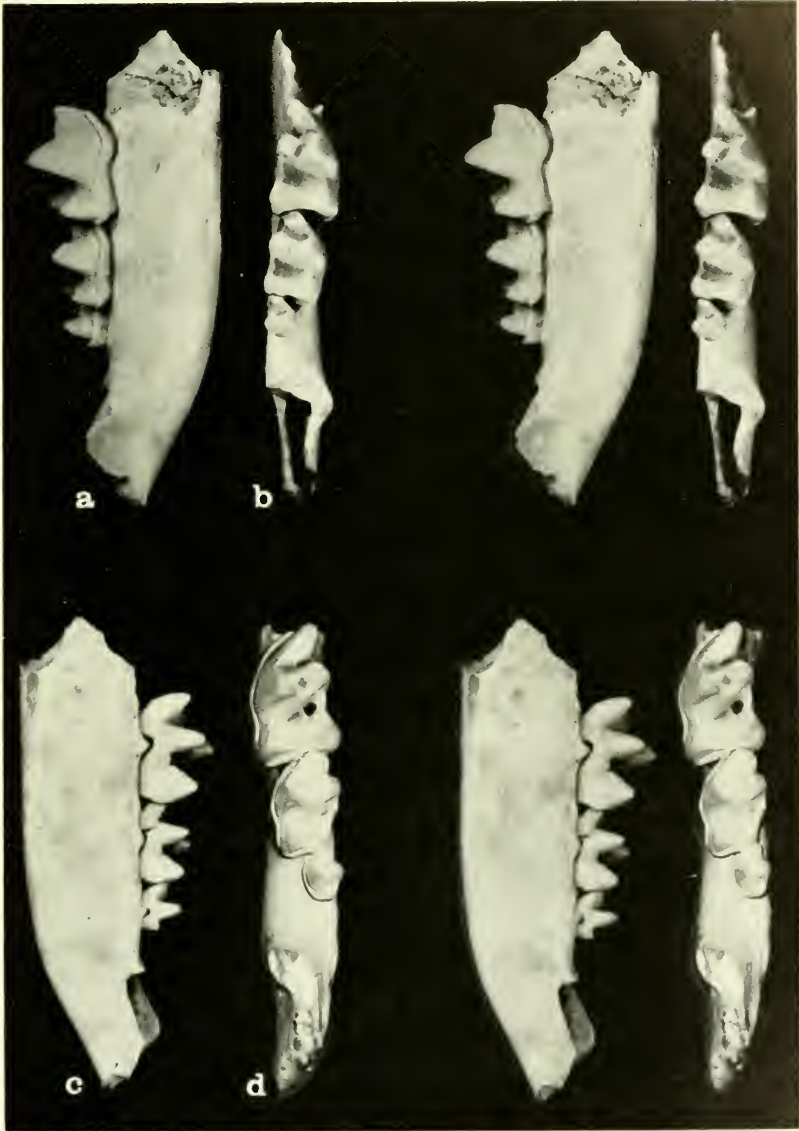


FIG. 2. *Stenoechinus tantalus*, n. gen. and n. sp. A. Lateral view; B. Occlusal view; C. Lingual view of holotype, KU 18001, right mandible, from the late Arikareean, upper Cabbage Patch beds, Tavenner Ranch locality 2 (KU-Mt-21), NW $\frac{1}{4}$, NW $\frac{1}{4}$, SW $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 11, T 8 N, R 10 W, Powell Co., Montana (= locality 1, Wood and Konizeski, 1965:462). D. Occlusal view of KU 18406, left mandible, from the medial Arikareean, middle Cabbage Patch beds, Cabbage Patch locality 13 (KU-Mt-46), CSW $\frac{1}{4}$, SE $\frac{1}{4}$, sec. 1, T 10 N, R 12 W, Granite Co., Montana (= MV6547, Rasmussen, 1969:132). $\times 6$.

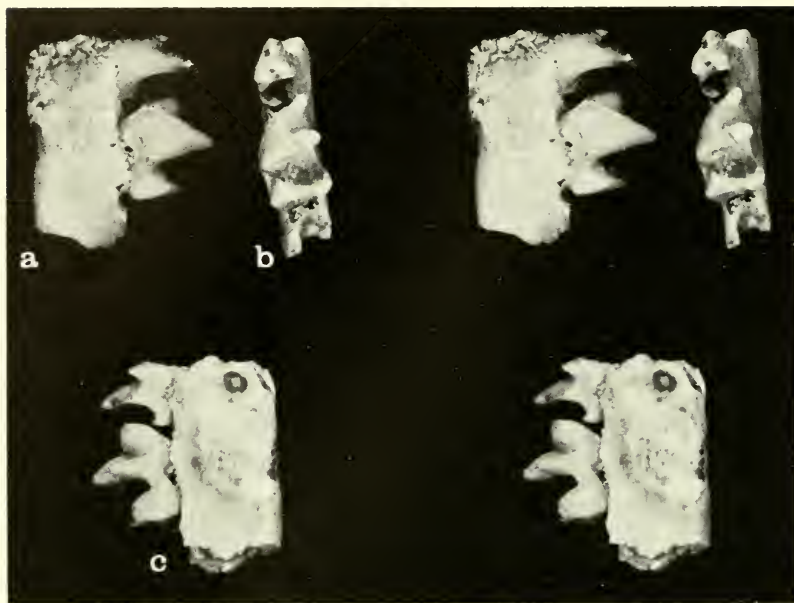


FIG. 3. *Stenoechinus tantalus*, n. gen. and n. sp., KU 18002, left mandible. A. Lateral view. B. Occlusal view. C. Lingual view. From the late Arikareean, upper Cabbage Patch beds, Tavenner Ranch locality 2 (KU-Mt-21), NW $\frac{1}{4}$, NW $\frac{1}{4}$, SW $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 11, T 8 N, R 10 W, Powell Co., Montana (= locality 1, Wood and Konizeski, 1965:462). $\times 6$.

Mandibles of *Parvericius montanus* described here for the first time support the placement of this species in a genus other than *Amphelchinus*. Although the two genera share the elongate I_1 that has so impressed previous workers, this new material demonstrates that the M_1 trigonid of *Parvericius* is anteroposteriorly compressed rather than being anteroposteriorly expanded as in *Amphelchinus*. Although but a single difference, in a group as highly uniform as the Erinaccinae, we consider it of generic significance.

Palaeoerinaceus minimus Bohlin (1942) was described first from Taben-buluk, Kansu, China; recently, additional material from Nareen Bulak, Mongolia, has been assigned tentatively to that species by Sulimski (1970) under the designation *Amphelchinus (Palaeoerinaceus)* cf. *minimus*. Both localities have yielded faunas regarded as somewhat younger than that from the Hsanda Gol Formation of Mongolia and medial or late Oligocene in age (Mellett, 1968:9; Sulimski, 1970:69). Although *P. minimus* apparently has the enlarged I_1 characteristic of all members of *Amphelchinus*, the M_1 trigonid is not anteroposteriorly expanded; therefore, this species is transferred to *Parvericius* with which it agrees in both characters. Furthermore, the few mandibles of *Parvericius minimus*

can be distinguished from the few of *Parvericius montanus* only by the greater depth of the latter, a difference probably due to ontogenetic stage of development. Therefore, *P. minimus* is regarded here as a junior synonym of *P. montanus*.

Despite the removal of *Parvericius montanus* from *Amphechinus*, the latter genus still is known in North America because *Palaeoerinaeus horncloudi* J. R. Macdonald (1970) from the early Arikareean Monroe Creek Formation of South Dakota may be assigned to *Amphechinus* following Butler's action synonymizing the two genera (Butler, 1948:473). J. R. Macdonald (1970:21) distinguished *A. horncloudi* from other species of the genus by the talonid having a greater width than the trigonid on P_4 and the shorter trigonid on M_1 . However, the latter character does not appear valid when figures of other species of *Amphechinus* are compared to the type specimen of *A. horncloudi*. (For example, compare figures of the following species of *Amphechinus*: 1) *A. horncloudi*, Macdonald, 1970: Fig. 5; this paper: Fig. 9; 2) *A. edwardsi*, Hürzeler, 1944: Fig. 13; 3) *A. intermedius*, Viret, 1938: Fig. 9; and 4) *A. arvernensis*, Viret, 1929: Pl. 28, Fig. 1b.) Relative to either the width of the trigonid or the length of the tooth, the anteroposterior length of the M_1 trigonid is as great or greater on *A. horncloudi* as on any other species in the genus.

From the same lithic unit and general area that yielded the type specimen of *Amphechinus horncloudi*, L. J. Macdonald (1972) recently has reported the presence of additional specimens of that species (under the name *Metechinus marslandensis*) together with specimens of *Parvericius montanus*.

SYSTEMATIC ACCOUNTS

Class MAMMALIA Linnaeus, 1758

Order INSECTIVORA Illiger, 1811

Superfamily ERINACEOIDEA Fischer von Waldheim, 1817

Family ERINACEIDAE Fischer von Waldheim, 1817

Subfamily ERINACEINAE Fischer von Waldheim, 1817

Stenoechinus new genus

Type Species.—*Stenoechinus tantalus* new species.

Known Distribution.—Late Arikareean (22.5-21 my, early Miocene), North America.

Diagnosis.—Distinguished from *Aethechinus*, *Amphechinus*, *Atelerix*, *Dimylechinus*, *Erinaceus*, *Gymnurechinus*, *Hemiechinus*, *Mioechinus*, *Paraechinus*, *Parvericius*, and *Postpalerinaceus* by the greater width of the M^1 relative to its length; from *Amphechinus*, *Dimylechinus*, *Mioechinus*, *Palaeoscaptor*, and *Postpalerinaceus* by an anteroposteriorly compressed M_1 trigonid; from *Aethechinus*, *Amphechinus*, *Atelerix*, *Erinaceus*, *Hemiechinus*, *Mioechinus*, *Para-*



FIG. 4. *Stenoechinus tantalus*, n. gen. and n. sp., occlusal view. A. KU 18359, right M^1 . B. KU 18098, right M^2 . Same locality as in figure 3. $\times 12$.

echinus, *Parvericius*, and *Postpalerinaceus* by the presence of a prominent postcingulum on M_3 ; from *Palaeosaptor* by a talonid on M_3 reduced to a prominent postcingulum; and from *Dimylechinus* by presence of M_3 .

Etymology.—*Stenos*, Greek, meaning narrow, referring to the proportions of the M^1 , M^2 , M_1 trigonid, and M_3 talonid; *echinos*, Greek, meaning hedgehog.

Stenoechinus tantalus new species

Figures 2-4

Holotype.—KU 18001, right mandible fragment with M_{1-3} , lacking ascending ramus and horizontal ramus anterior to M_1 except for the medial wall of the horizontal ramus that has traces of four alveoli immediately anterior to M_1 .

Type Locality and Stratigraphic Position.—Upper Cabbage Patch beds, Taverner Ranch locality 2 (KU-Mt-21), NW $\frac{1}{4}$, NW $\frac{1}{4}$, SW $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 11, T 8 N, R 10 W, Powell Co., Montana (= Locality no. 1, Wood and Konizeski, 1965:462).

Diagnosis.—Only known species of genus.

Etymology.—*Tantalos*, Greek, mythological character symbolic of eternal torment.

Referred Material.—KU 18002, left mandible fragment with P_4 , M_1 , and that part of the mandible immediately below these two teeth. KU 18003, right mandible fragment with M_2 , alveolus for M_3 , and lacking horizontal ramus anterior to M_2 , ascending ramus, and angle. KU 18004, isolated left M_1 . KU 18098, isolated right M^2 , heavily worn. KU 18342, edentulous left mandible fragment with alveoli for M_{2-3} , and lacking horizontal ramus anterior to M_2 alveoli, ascending ramus, and angle. KU 18354, isolated right M_1 . KU 18356, left mandible fragment with M_1 and alveoli for M_{2-3} , lacking horizontal ramus anterior to M_1 and all of mandible behind M_3 alveolus. KU 18359, isolated right M^1 . KU 18404, isolated right M_1 trigonid. All the material referred to in this paragraph was collected at the same locality as the type specimen.

KU 18406, left mandible fragment with M_{1-3} , lacking ascending ramus and horizontal ramus anterior to M_1 . Found in the middle Cabbage Patch beds, Cabbage Patch locality 13 (KU-Mt-46), CSW $\frac{1}{4}$, SE $\frac{1}{4}$, sec. 1, T 10 N, R 12 W, Granite Co., Montana (= MV6547, Rasmussen, 1969:132).

TABLE 1. Measurements (mm) of the Upper Dentition of *Stenoechinus tantalus* and *Palaeoscaptor acridens*

	<i>S. tantalus</i> KU 18098	<i>S. tantalus</i> KU 18359	<i>P. acridens</i> AMNH 22080
M^1 anteroposterior diameter	1.7	2.2
M^1 , transverse diameter	2.2	2.6
M^2 , anteroposterior diameter	1.2	1.6
M^2 , transverse diameter	1.9	2.2

Lower Dentition.—(Figs. 2 and 3) Only indirect data are available to give an indication of the dental condition anterior to P_4 . In transverse section, the horizontal ramus of KU 18001 has a medial and a lateral layer of compact bone with a space in between. On the internal side of the medial wall of this specimen, immediately anterior to the M_1 , are preserved traces of the partitions between the next four anterior alveoli (Fig. 2a). The most posterior of these alveoli were occupied by the roots of P_4 (Fig. 3a, c). Although the forward wall of the most anterior alveolus preserved is absent, enough of that alveolus is preserved to indicate that it probably had a significantly greater anteroposterior diameter than the one immediately behind. A similar size relationship exists between the same alveoli on a specimen of another small erinaceine, *Palaeoscaptor* cf. *acridens* (AMNH 22082). On that mandible, the more posterior of these two alveoli was occupied by the rear root of P_3 and the more anteroposteriorly elongated anterior alveolus was occupied by the forward root of P_3 and the single root of P_2 (Fig. 5). If there was a bony partition between the forward root of P_3 and the root of P_2 , it has been lost without a trace on both KU 18001 and AMNH 22082 and must have been much thinner than the other alveolar walls, for these two roots are quite close to one another on AMNH 22082.

The most anterior alveolar wall preserved on the medial wall of the mandible of KU 18001 extends nearly to its ventral border. In erinaceids such as *Amphiechinus?* *rectus* (AMNH 22084), which have an enlarged I_1 root alveolus extending posteriorly to the region immediately in front of the anterior root of P_4 , the alveolar borders of the C_1 - P_3 may be traced on the internal side of the medial wall of the ramus from the dorsal lip of their respective alveoli only halfway to the ventral border of the mandible. At that point, the alveolar walls of C_1 - P_3 are cut off by the alveolar wall of I_1 because

TABLE 2. Measurements (mm) of P₁-M₃ of *Stenocephalus tantalus* and *Palaeoscaptor acridens*

	<i>S. tantalus</i>						<i>P. acridens</i>		
	KU 18001	KU 18002	KU 18003	KU 18004	KU 18354	KU 18356	KU 18404	KU 18406	AMNH 22080
P ₄ , anteroposterior diameter	---	1.5	---	---	---	---	---	---	2.0
P ₄ , transverse diameter	---	0.9	---	---	---	---	---	---	1.0
M ₁ , anteroposterior diameter	2.2	2.1	---	2.0	2.1	2.0	---	2.5	2.7
M ₁ , trigonid length	1.2	1.1	---	1.1	1.1	1.1	1.2	1.4	1.6
M ₁ , trigonid width	1.5	1.3	---	1.2	1.3	1.1	1.2	1.6	1.5
M ₁ , talonid width	1.6	1.3	---	1.3	1.4	1.1	---	1.7	1.6
M ₂ , anteroposterior diameter	1.8	---	1.8	---	---	---	---	---	1.9
M ₂ , trigonid length	0.9	---	1.0	---	---	---	---	1.1	1.1
M ₂ , trigonid width	1.3	---	1.3	---	---	---	---	1.4	1.4
M ₂ , talonid width	1.2	---	1.3	---	---	---	---	---	1.2
M ₃ , anteroposterior diameter	1.0	---	---	---	---	---	---	1.1	---
M ₃ , trigonid width	0.7	---	---	---	---	---	---	0.8	---

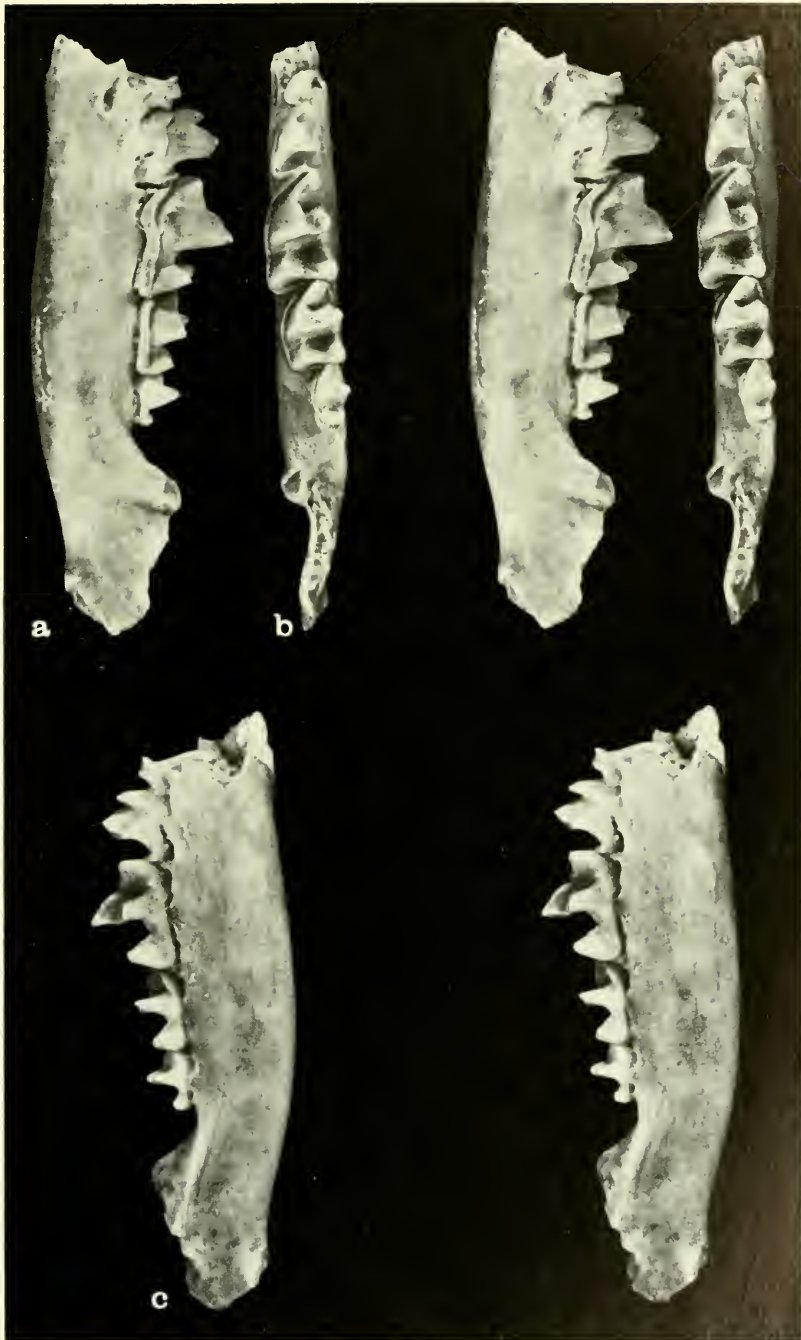


FIG. 5. *Palaeosaptor* cf. *acridens*, AMNH 22082, left mandible. A. Lateral view. B. Occlusal view. From the medial Oligocene, Hsanda Gol Formation, Tsagan Nor Basin, Mongolia. $\times 6$.

the root of I_1 passed medial to the roots of C_1 - P_3 . Hence, the root of I_1 in *Stenoechinus tantalus* did not extend as far posteriorly and was probably closer in relative size to the more reduced I_1 found in the living *Erinaceus europaeus*.

P_4 .—Tallest cusp on the tooth, the slender protoconid is half again as high as the paraconid above the base of the enamel, the height of the protoconid being one and one-fourth times the length of the tooth. On the single specimen in which the protoconid is preserved (KU 18002), the lingual third of that cusp has been lost; thus, the casual observer might believe that the metaconid is placed well away from the protoconid base, whereas the bases of the two cusps are actually quite close together. The paraconid is only slightly lower than the metaconid and is situated on the midline of the tooth at its anterior edge; the cusp lies so far forward that its base projects forward beyond the anterior root of the tooth. Along the rear margin of the tooth is a well developed posterior cingulum that dips steeply ventrobuccally. Continuous with this posterior cingulum is a weak buccal cingulum that is developed along the entire length of the tooth.

M_1 .—The length of the trigonid is slightly more than half that of the tooth. The trigonid is slightly shorter than wide; the protoconid is the tallest of the trigonid cusps and has the greatest basal dimensions. Intermediate in height, the metaconid is anterolingual to the protoconid; the two cusps are linked by a protolophid that has an acute V-shaped profile in posterior view. The paralophid links the protoconid with the paraconid, the lowest cusp on the trigonid. In lateral view the paralophid has a V-shaped profile; the angle between the two segments of the V is obtuse but close to a right angle. The lingual segment of the paralophid is nearly horizontal. The paraconid lies at the anterolingual corner of the tooth. In lingual view, the paraconid axis is either vertical and parallel to the metaconid axis, or anterodorsally inclined and forms an angle as great as 30 degrees with respect to the metaconid axis.

Width of the talonid is equal to, or slightly greater than that of the trigonid, with the entoconid and hypoconid at the extreme posterior corners of the tooth. The entoconid is the taller of the talonid cusps and is intermediate between the paraconid and metaconid in height. The entoconid is posterior to the metaconid and the hypoconid lies slightly more labial than the protoconid. In anterior view, the buccal margin of both the protoconid and hypoconid are buccally convex. Extending anteriorly from the hypoconid, the cristid obliqua abuts against the posterior wall of the trigonid at a point slightly buccal to the tip of the protoconid. A low entocristid closes the talonid basin lingually. A well developed but narrow cingulum extends along the entire buccal side of the tooth from a point below the paraconid to the base of the hypoconid where it passes into the posterior cingulum; the latter is directed dorsomedially.

ally so that it terminates lingually, midway between the hypoconid and entoconid just below the crest of the posteristid. In the region of transition between the buccal and posterior cingula, adjacent to the hypoconid base, these narrow cingula are even narrower.

No specimen is available with the alveoli of this double-rooted tooth exposed.

M_2 .—Because this tooth is quite similar to M_1 in general morphology, a detailed description is unnecessary, but a few points of difference are noted.

In length and width, this tooth is about four-fifths as large as the M_1 . No distinct paraconid is present; the paralophid terminates lingually without any noticeable swelling. The protoconid and metaconid are equal in height.

The entoconid is only slightly lower in height than the metaconid and markedly taller than the lingual region of the paralophid where the paraconid would be expected if developed. Despite the fact that the talonid is slightly narrower, not equal to, or slightly wider than the trigonid, the hypoconid position is still somewhat more buccal than that of the protoconid. The buccal cingulum is developed as extensively as on the M_1 , and terminates anteriorly at the forward edge of the prevallid.

Although the alveoli of this double-rooted tooth are equivalent in width, the posterior alveolus is nearly circular and about twice as long anteroposteriorly as the elliptical anterior alveolus.

M_3 .—This double-rooted tooth is markedly different than the more anterior molars; it lacks a well developed talonid, having only a wide postcingulum. The trigonid is anteroposteriorly expanded to the extent that it is slightly longer than wide. Of the two well developed trigonid cusps, the protoconid is the taller and has greater basal dimensions. Its base and that of the lower, smaller metaconid are in close juxtaposition; thus, the protolophid between the two cusps is short. A small, obtuse, V-shaped notch is present near the middle of the protolophid when viewed from the rear. The lingual end of the paralophid lacks a swelling marking the presence of the paraconid. As in the more anterior molars, the paralophid in lateral view has a V-shaped profile; the two limbs of the V meet at nearly right angles with the lingual segment nearly horizontal. A well-developed, continuous, and narrow basal cingulum is present along the buccal margin of the tooth; the basal cingulum passes into a much wider postcingulum that lies along the entire posterior side of the trigonid. This postcingulum is widest midway between the protoconid and metaconid, and tapers to minima at both the lingual and buccal margins of the tooth.

The M_3 is double-rooted in the holotype (KU 18001), but in two other specimens (KU 18003 and KU 18356) where alveoli of this tooth are known, only a single, anteroposteriorly elongated root is indicated; thus, suggesting the condition of the root of M_3 may vary

from specimen to specimen. On one of these specimens where the alveolus is exposed, a single elongated root is preserved just below the alveolar lip (KU 18356).

Mandible.—(Figs. 2 and 3) The preserved fragments of the mandible indicate that it is slightly deeper below M_1 than M_3 . Between those two areas, the ventral border is nearly straight, but behind the M_3 the ventral border curves sharply upward. The posterior border of the mental foramen is preserved on KU 18002 adjacent to the anterior root of P_1 , midway between the dorsal and ventral margins of the mandible. Beneath the M_1 of KU 18001 there is a slight ridge on the buccal side of the mandible near its ventral border. Presumably, this is the lateral border of the diastemic fossa. No diastema are developed between P_2 and M_3 .

Upper Dentition.—Two isolated upper molars from Tavenner Ranch locality 2 probably represent the otherwise unknown M^1 and M^2 of *Stenoechinus tantalus* (KU 18359 and KU 18098, respectively). The relative dimensions of these two upper molars are similar to those of the homologous teeth on a specimen of *Palaeosaptor acridens* from the Hsanda Gol Formation of Mongolia in which the left jaw was found in occlusion with the skull (AMNH

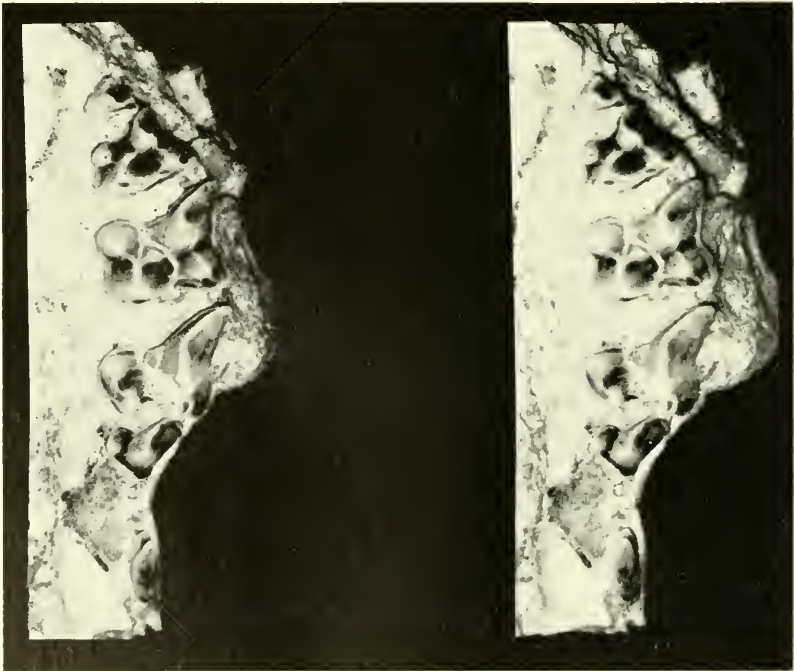


FIG. 6. *Palaeosaptor acridens*, AMNH 22080, partial skull, occlusal view of right upper dentition. From the medial Oligocene, Hsanda Gol Formation, Tsagan Nor Basin, Mongolia. $\times 6$.

22080), (Table 1). In addition, when the dimensions of the upper and lower teeth on this specimen of *P. acridens* are compared, the ratios are found to be similar to those between the lower teeth of *S. tatalus* and these two upper molars (compare Tables 1 and 2). In morphology, the M^1 is similar to that of *P. acridens* (compare Figs. 4a and 6). Extensive wear during life all but obliterated the cusps and trigon basin on the M^2 ; however, enough remains to show that in outline this tooth is similar to the M^2 of *P. acridens*. A further reason for associating these upper molars with the lowers in the type specimen of *S. tatalus* is that no other erinaceid is known from Tavenner Ranch locality 2 except the much larger *Amphelchinus horncloudi*.

M^1 .—(Fig. 4a) The length of this tooth is about three-fourths its width. Of the four principal cusps on the tooth, the metacone is the tallest, its height being slightly more than half the length of the tooth. The protocone and paracone are equal to one another in height and both are equal to the metacone in basal dimensions. Lowest of the four principal cusps and smallest in basal dimensions is the hypocone. The protocone is slightly forward of a point directly lingual to the paracone; the hypocone is lingual to the metacone. A line passing through the paracone and metacone is parallel to one drawn through the protocone and hypocone. The parastylar spur is directed anteriorly away from the main body of the tooth; the metastylar spur is directed posterobuccally. In occlusal view, the lingual, buccal, and posterior borders of the tooth are markedly concave, whereas the anterior border is broadly convex. Close to the convex anterior border are the preprotoecrista and preprotoconule crista which grade imperceptibly into one another, because no paraconule is developed. This crest extends from the anterobuccal side of the protocone to the vicinity of the anterior side of the paracone base from which it is separated by a shallow notch. In anterior view, this tooth has a profile reminiscent of an inverted, broad, truncated letter V; the margins are formed by the steeply sloping sides of the two cusps and the horizontal midsection is formed by the crest between them. The postprotoecrista is directed posterobuccally from the protocone. This crista divides at a point lingual to the anterior edge of the metacone; one branch extends posterolingually to the hypocone and the other extends buccally to the metacone. No trace of a metaconule is present. Developed along the anterior edge of the tooth, the narrow precingulum curves apically at its buccal end, there joining the anterior terminus of the short paracrista. The posterior terminus of the paracrista is at the base of the paracone. A short centreecrista links the bases of the paracone and metacone. From the metacone, the metacrista extends in a buccal and slightly posterior direction along the posterior edge of the metastylar spur for a distance approximately equal to one-fourth the length of the tooth. Along the buccal margin of the

tooth between the paracone and metacone is an extremely weak ectocingulum. Three roots are developed on this tooth—one above the paracone-paracrista region; a second over the metacone-metacrista region; and the third lingual root over the protocone-hypocone region. The anterior and posterior borders of the third lingual root converge toward its dorsal tip in contrast to other erinaceines in which the borders are parallel.

M².—(Fig. 4b) In basic outline, the tooth is a right triangle in which the hypotenuse represents the anterior margin. The narrow parastylar spur projects buccally and slightly anteriorly away from the main body of the tooth. The metastylar spur projects posteriorly and the base of the hypocone forms a third spur that projects posterolingually away from the main body of the tooth. A narrow ectocingulum lies buccal to the paracone; as it passes posteriorly, buccal to the metacone, the ectocingulum narrows. A short metacingulum is developed behind the metacone. A precingulum is developed along the anterior side of the tooth. The precingulum extends from the buccal region of the protocone base to a point slightly lingual to the paracone where a prominent wear facet on the parastylar spur has obliterated it. Three roots are developed on this tooth—one above the paracone-paracrista region, a second above the metacone-metacrista region, and a third over the protocone.

Comparisons.—*Stenoechinus tantalus* differs from *Palaeoscaptor acridens* found in the medial Oligocene of Mongolia in five important characters: *M₃* talonid reduced to a prominent postcingulum; *M₁* trigonid less anteroposteriorly expanded; *P₄* paraconid markedly lower than the protoconid; *P₄* protoconid height less than tooth length; and *I₁* root not extending as far posteriorly. Sulimski (1970: 63) characterized *Palaeoscaptor* as having a more reduced *I₁* than *Amphelchinus* (= *Palaeoerinaceus* of Sulimski's usage).¹ However, examination of an X-ray photograph of the only known mandible of *P. acridens* containing an *I₁* (AMNH 22080) shows that both the

¹ Following Butler (1948), Sulimski (1970:63) placed *Palaeoerinaceus* Filhol (1879) and *Palaeoscaptor* Matthew and Granger (1924) in *Amphelchinus* Aymard (1850). In addition, he formally divided *Amphelchinus* into two subgenera: *Palaeoerinaceus* and *Palaeoscaptor*. The basis for this division was the relative size of the *I₁* and single-rooted and reduced talonid condition of the *M₃*. Although a re-examination of specimens of *Palaeoscaptor* in the American Museum of Natural History which were unavailable to Sulimski indicates that all species included by him in *Amphelchinus* shared an enlarged *I₁*, the second criterion, condition of the *M₃*, continues to appear valid. By this valid criterion, the type species of *Amphelchinus*, *A. arverneusis*, clearly belongs in the subgenus *Palaeoerinaceus* for the *M₃* is single-rooted and possesses a reduced talonid. According to article 44(a) of the International Code of Zoological Nomenclature (Stoll *et al.*, 1961), if a genus is divided into subgenera, the subgenus containing the type species must be placed in a subgenus with the same name as the genus. For this reason, the name for the subgenus *Palaeoerinaceus* should be changed to *Amphelchinus*.

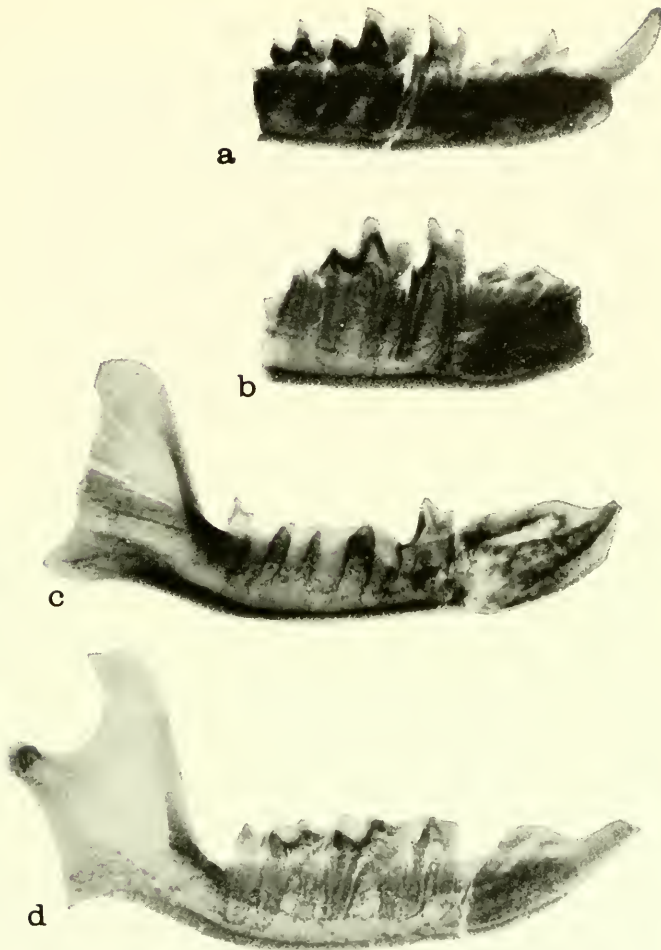


FIG. 7. X-rays of mandibles in lateral view. A. *Palaeosceptor acridens*, AMNH 22080, reversed left mandible, from the medial Oligocene, Hsanda Gol Formation, Tsagan Nor Basin, Mongolia. $\times 4$. B. *Amphexchinus horncloudi*, SDSM 62113, type, right mandible, from the Arikareean, Monroe Creek Formation, T 39 N, R 42 W, Shannon Co., South Dakota. $\times 3$. C. *Amphexchinus horncloudi*, KU 18162, right mandible, from the medial Arikareean, middle Cabbage Patch beds, Cabbage Patch locality 3 (KU-Mt-11), SE $\frac{1}{4}$, NE $\frac{1}{4}$, SE $\frac{1}{4}$, SE $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 7, T 10 N, R 11 W, Powell Co., Montana (= MV6617, Rasmussen, 1969:140). $\times 3$. D. *Parvericius montanus*, UMMP V56569, reversed left mandible, from the late Barstovian, Egelhoff Quarry, from an unnamed lithic unit beneath the Valentine Formation and overlying the Rosebud Formation, SW corner of NE $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 29, T 33 N, R 23 W, Keya Paha Co., Nebraska. $\times 4$. X-rays taken by Dr. Howard K. Bloomfield, DDS.

crown and root are as extensively developed in that species as in the various species of *Amphechinus* (compare figures 7a and 7b, this paper and Hürzeler, 1944: Fig. 7). Except for the features mentioned above, the molars of *S. tantalus* and *P. acridens* are quite similar in morphology, relative proportions, and size.

The species of *Amphechinus* from the Oligocene and Miocene of Europe, Asia, Africa, and North America differ from *Stenocheinus tantalus* by having an anteroposteriorly expanded trigonid on M_1 . Together with *Parvericius montanus*, the species of *Amphechinus* differ further in having an enlarged I_1 with a root that extends posteriorly to the region immediately anterior to the forward root of P_4 ; P_4 paraconid nearly as tall as the protoconid; P_4 protoconid height subequal to the tooth length; complete absence of a talonid on M_3 ; and M^1 and M^2 more expanded anteroposteriorly.

The species of *Gymnurechinus* from the Miocene of East Africa described by Butler (1956, 1969) are approximately twice as large

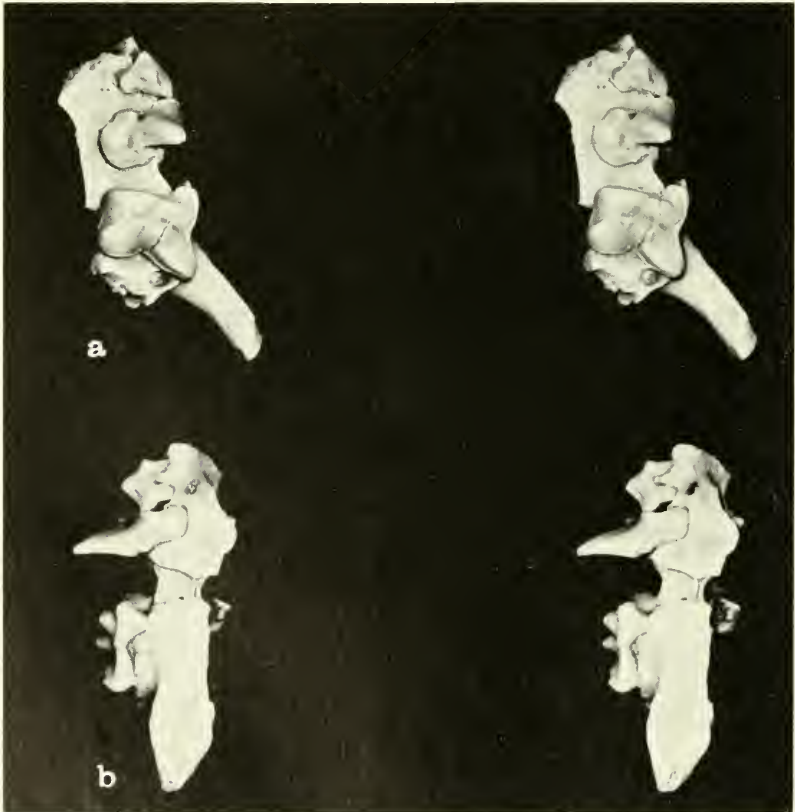


FIG. 8. *Amphechinus horncloudi*, KU 18097, left maxilla fragment. A. Occlusal view. B. Lateral view. From same locality as in figure 3. $\times 3$.

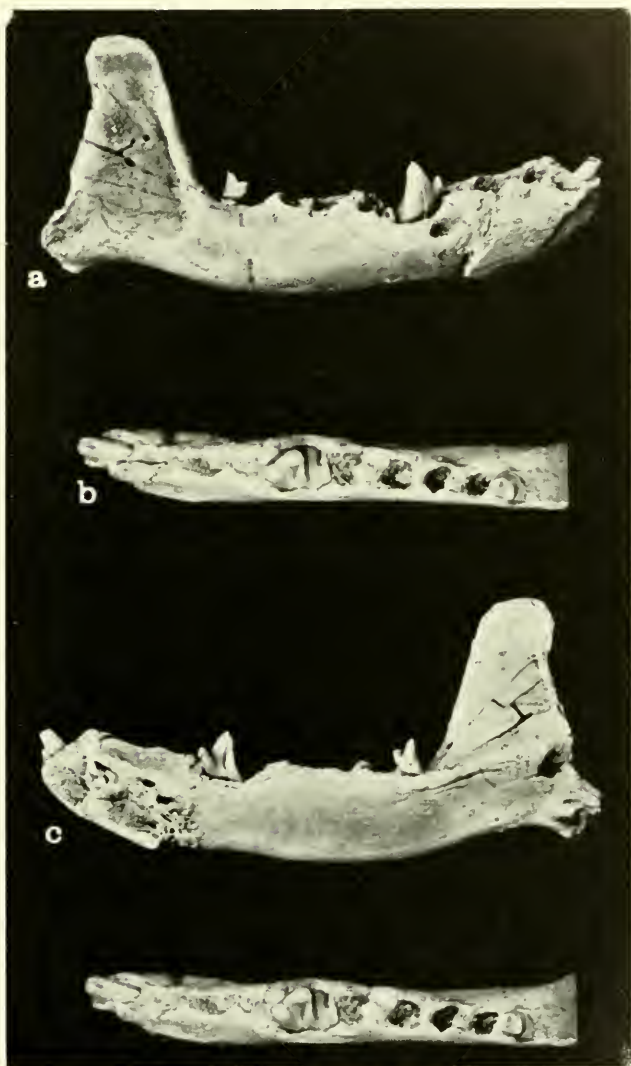


FIG. 9. *Amphiechinus horncloudi*, KU 18162, right mandible. A. Lateral view. B. Occlusal view. C. Lingual view. From the medial Arikarean, middle Cabbage Patch beds, Cabbage Patch locality 3 (KU-Mt-11), SE $\frac{1}{4}$, NE $\frac{1}{4}$, SE $\frac{1}{4}$, SE $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 7, T 10 N, R 11 W, Powell Co., Montana (= MV6617, Rasmussen, 1969:140). $\times 3$.

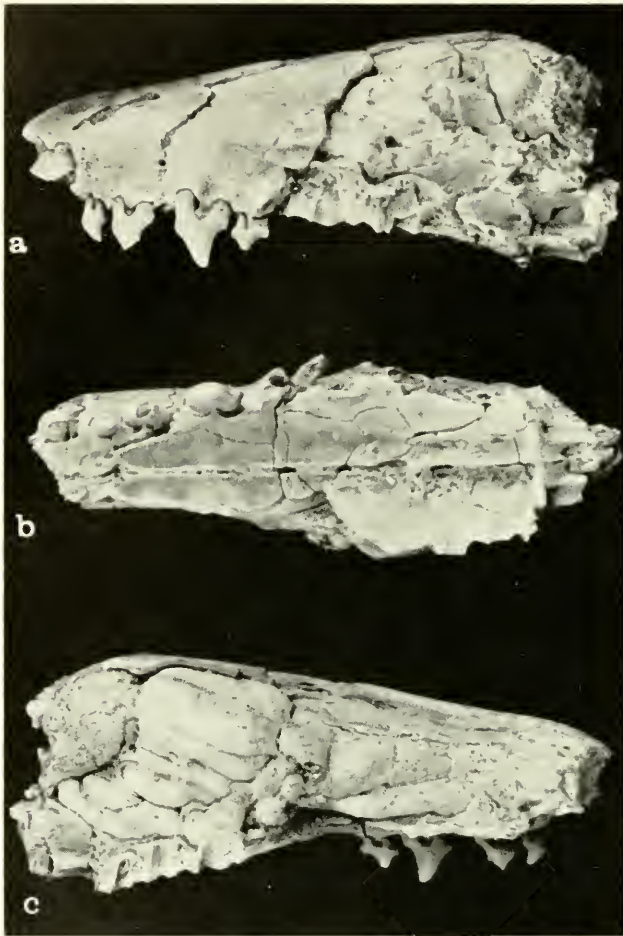


FIG. 10. *Amphiechinus hornclouidi*, KU 18163, skull fragment. A. Left lateral view. B. Palatal view. C. Right lateral view. From the medial Arikareean, middle Cabbage Patch beds, Cabbage Patch locality 2 (KU-Mt-9), SE $\frac{1}{4}$, NW $\frac{1}{4}$, SW $\frac{1}{4}$, SE $\frac{1}{4}$, sec. 1, T 10 N, R 12 W, Granite Co., Montana (= MV6504-5, Rasmussen, 1969:131-132). $\times 3$.

as *Stenoechinus tantalus*. In addition, the African species differ in that the paraconid is large and nearly as tall as the protoconid on P_4 ; and the M^1 and M^2 are expanded more anteroposteriorly.

The anteroposteriorly expanded condition of the lower molar trigonids indicates that *Stenoechinus tantalus* is too advanced or derived to be considered a member of the Adapisoricidae as Van Valen (1967) constituted that group. Among late Mesozoic and early Tertiary insectivores including the adapisoricids, the lower

molar trigonid is characteristically anteroposteriorly compressed as compared with the condition commonly observed among several geologically younger groups of insectivores; e.g. Erinaceidae, Talpidae, and Soricidae.

Within the Erinaceidae, *Stenoechinus tantalus* is more closely allied with the Erinaceinae than Galericinae due to the reduction of the talonid on M_3 to a prominent postcingulum, a condition rarely encountered among other insectivores and hence considered derived. However, if *S. tantalus* is assigned correctly to the Erinaceinae, it is the most primitive member of that subfamily because its P_4 paraconid lacks the prominence that is the unique derived character state which distinguishes every other member of the subfamily from all other insectivores.

If *Stenoechinus tantalus* is the most primitive known member of the Erinaceinae, the known forms most closely related to that species' immediate ancestors are presumably members of the Adapi-soricidae. Found in Europe, Asia, and North America, this family ranges temporally from Paleocene to Oligocene. For this reason, it is not possible to select between the hypotheses that the stock that gave rise to *S. tantalus* was part of the general Arikareean invasion of North America or that the lineage had a prior Oligocene history in North America.

Amphechinus Aymard 1850

Type Species.—*Amphechinus arvernensis* (deBlainville 1838).

Known Distribution.—Stampian?—Vindobonian (?35—14 my, early? Oligocene—medial Miocene), Europe; Aquitanian—Vallesian (20—11 my, early to late Miocene), Africa; 32—31 my (medial Oligocene), Asia; medial Arikareean—medial Barstovian (23—14 my, early to medial Miocene), North America.

Diagnosis.—Distinguished from *Palaeoscaptor* by absence of a metacone on M^3 ; from *Palaeoscaptor* and *Stenoechinus* by the greater length of the M^1 relative to its width; from *Aethechinus*, *Atelerix*, *Erinaceus*, *Gymnurechinus*, *Hemiechinus*, *Mioechinus*, *Paraechinus*, *Postpalerinaceus*, and *Stenoechinus* by presence of an enlarged I_1 ; from *Aethechinus*, *Atelerix*, *Erinaceus*, *Gymnurechinus*, *Hemiechinus*, *Paraechinus*, *Parvericius*, and *Stenoechinus* by an anteroposteriorly elongated trigonid on M_1 ; from *Gymnurechinus*, *Palaeoscaptor*, and *Stenoechinus* by absence of a talonid or postcingulum on M_3 ; and from *Dimylechinus* by presence of M_3 and M^3 .

***Amphechinus horncloudi* (J. R. Macdonald, 1970)**

New Combination

Figures 7b-c, 8-10

Palaeoerinaeus horncloudi J. R. Macdonald 1970:20.

Holotype.—SDSM 62113, fragment of right mandible with P_2 - M_1 , damaged C_1 , roots of I_{1-2} , and anterior root of M_2 .

Type Locality and Stratigraphic Position.—Collected from the Monroe Creek Formation in T 39 N, R 42 W, Shannon Co., South Dakota (SDSM V6229; more precise locality information is on file at the South Dakota School of Mines and Technology, Museum of Geology).

Diagnosis.—Distinguished from other species of *Amphechinus* by the talonid being greater in width than the trigonid on P_4 .

Referred Material.—KU 18097, left maxilla fragment with P^3 , P^4 (except metacrista), M^1 and anterior alveoli of M^2 . KU 18405, right P^4 fragment. From the upper Cabbage Patch beds, Tavenner Ranch locality 2 (KU-Mt-21), NW $\frac{1}{4}$, NW $\frac{1}{4}$, SW $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 11, T 8 N, R 10 W, Powell Co., Montana (= locality 1, Wood and Konizeski, 1965:462).

KU 18162, right mandible with partially erupted I_1 , P_4 , fully erupted M_3 , alveoli for I_2 , C_1 , P_2 , and M_{1-2} , missing region posterior to base of angle. Found in the middle Cabbage Patch beds, Cabbage Patch locality 3 (KU-Mt-11), SE $\frac{1}{4}$, NE $\frac{1}{4}$, SE $\frac{1}{4}$, SE $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 7, T 10 N, R 11 W, Powell Co., Montana (= MV6617, Rasmussen, 1969:140).

KU 18163, anterior half of skull with broken right I^1 ; complete right I^2 - P^2 ; missing lateral part of left palate and lateral part of

TABLE 3. Measurements (mm) of the Upper Dentition of
Amphechinus horncloudi

	KU 18097	KU 18163
I^2 , anteroposterior diameter	1.1
I^2 , transverse diameter	0.9
I^3 , anteroposterior diameter	2.0
I^3 , transverse diameter	1.1
C^1 , anteroposterior diameter	2.6
C^1 , transverse diameter	1.2
P^2 , anteroposterior diameter	1.7
P^2 , transverse diameter	0.9
P^3 , anteroposterior diameter	2.1
P^3 , transverse diameter	1.7
P^4 , anteroposterior diameter	3.5 ^a
P^4 , transverse diameter	3.3
M^2 , anteroposterior diameter	3.4
M^2 , transverse diameter	3.7

^a Posterior limit of tooth estimated by assuming contact with parastylar spur on M^1 .

TABLE 4. Measurements (mm) of the Lower Dentition of
Amphechinus horncloudi

	type, SDSM 62113	KU 18162
Mandible depth below M ₁ anterior root ...	4.0	3.3
Mandible depth below M ₂ posterior root		3.9
P ₄ , anteroposterior diameter	2.5	2.7
P ₄ , transverse diameter	2.0	1.9
M ₃ , trigonid length		1.1
M ₃ , trigonid width		0.9

right palate behind P₂; casts of olfactory bulbs, chambers for ethmo-turbinals, and left maxillary sinus exposed. Found in the middle Cabbage Patch beds, Cabbage Patch locality 2 (KU-Mt-9), SE $\frac{1}{4}$, NW $\frac{1}{4}$, SW $\frac{1}{4}$, SE $\frac{1}{4}$, sec. 1, T 10 N, R 12 W, Granite Co., Montana (= MV6504-5, Rasmussen, 1969:131-132).

Lower Dentition.—(Fig. 9) *I*₁.—Near the tip of this tooth, its cross section is crudely circular with noticeable flattening on the medial and anterior sides. The crown is anterodorsally inclined.

*I*₂, *C*₁.—In dorsal view, the outline of the single alveolus for each of these teeth is an oval with the broad end posterior and the major axis directed anteroposteriorly. The maximum length and width of the alveolus for *I*₂ are 1.0 and 0.5 mm respectively; similar dimensions for *C*₁ are 1.6 and 0.9 mm. Both alveoli are anterodorsally inclined.

*P*₂.—The single alveolus for this tooth is too damaged to allow meaningful statements concerning its outline or dimensions. It seems to have been about the size of the alveolus for *I*₂.

*P*₄.—Of the trigonid cusps, the protoconid is tallest and largest in basal dimensions. The paraconid is anteromedial to the protoconid, from which it is separated by a distinct notch. In height, the paraconid is equal to the metaconid, but in basal dimensions, the paraconid is much larger. The protolophid is directed lingually from the posteromedial corner of the protoconid. At the site of the metaconid at the lingual end of this lophid, there is no swelling to mark the presence of the cusp. The talonid is a narrow ridge along the posterior border of the tooth with its highest point behind the protoconid. The maximum transverse diameter of this tooth occurs in the talonid region.

*M*₁.—The forward alveolus for this double-rooted tooth is trapezoidal in outline; the base of the trapezoid is formed by the medial wall of the alveolus. The maximum anteroposterior measurement of this alveolus is 1.3 mm and the maximum mediolateral measurement is 1.1 mm. The shape of this alveolus may not accurately reflect the condition that would be found in a fully mature individual, because the unerupted P₄ talonid forms the anterior border, and no bony partition is preserved between the tooth and alveolus. The posterior

alveolus is roughly rectangular in outline; the anterioposterior length is 1.2 mm and the mediolateral width is 1.3 mm. The bony partition between the forward and rear alveoli displays the paired bony ridges common in erinaceids.

M_2 .—In outline, the two alveoli for this tooth are crudely circular except in the area of the bony partition which separates them from one another; here they are straight or actually concave in the case of the anterior alveolus. Their diameters are approximately 1.0 mm. As on the M_1 , the bony partition between the two alveoli has bony ridges.

M_3 .—The prevallid is expanded anteriorly, the length of the trigonid being about 10 percent greater than the width. No distinct paraconid is developed at the anterior end of the paralophid; this region is markedly lower than the posterior area. Along the rear of the trigonid is a tall protolophid. At the lingual and buccal ends of this crest there are slight swellings that represent the metaconid and the slightly taller protoconid, respectively. No talonid is developed, but a narrow postcingulum is present that is continuous with a buccal cingulum that extends to the anterior extremity of the tooth.

Upper Dentition.—(Figs. 8 and 10) I^1 .—The single root of this mediolaterally flattened tooth passes posteriorly above the roots of the succeeding incisors and terminates near the premaxilla-maxilla suture. Although broken off at the base of the crown, this tooth is clearly much larger than the posterior incisors.

I^2 - C^1 .—Morphologically, these three teeth are quite similar, but there is a marked progressive increase in size posteriorly. In outline, each tooth is crudely elliptical with the major axis directed antero-posteriorly. I^3 and C^1 are double-rooted but I^2 has only one root; however on the buccal side of the I^2 root there is a clear division into anterior and posterior lobes. On the crown of all three teeth there is a single, tall cusp, the height of which is nearly equal to or slightly greater than the length of the respective teeth. The anterior edge of this cusp dips posteroventrally and the posterior edge is nearly vertical. The tip of the cusp is ventral to the posterior root on the I^3 and C^1 and to the posterior lobe on the single root on the I^2 . Extending posteriorly from the base of the cusp along the midline of each tooth is a short crest which slopes posterodorsally.

P^2 .—Two roots are present on this small tooth. As on I^2 - C^1 , the outline of the tooth is crudely elliptical and there is a single, prominent cusp, but its height is only two-thirds the length of the tooth. Moreover, the tip of the cusp is further forward than on I^2 - C^1 for it is ventral to the anterior root. The posterior edge of the cusp dips anteroventrally. Extending anteriorly from the base of the cusp is a short crest on a precingulum which projects forward of the anterior root. Extending posteriorly from the base of the cusp is a second, much longer crest that terminates at a small

cuspsule on a cingulum which projects posteriorly beyond the rear root.

*P*³.—In occlusal view, the straight buccal border of the tooth is directed anteromedially; the anterior and posterior borders are concave, and the lingual border is convex. The prominent meta-crista extends posterobuccally from the paracone along the midline of the well developed metastylar spur to the posterior tip of that structure. The protocone is somewhat less than half the height of the paracone, and anteromedial to it. Behind the protocone is a flat surface that dips posterodorsally. This surface lacks any trace of a hypocone. A narrow cingulum extends along the anterior side of the base of the paracone. Three roots are developed on this tooth, one above the protocone, another over the paracone, and a third over the metacrista.

*P*⁴.—This tooth is several times larger than the preceding *P*³. The height of the paracone, the tallest and most prominent cusp on the tooth, is subequal to the tooth length. The metastylar spur projects posteriorly and somewhat laterally away from the buccal side of the main body of the tooth; thus, the main body of the tooth is more anteroposteriorly elongated buccally than lingually. One-third the height of the paracone, the protocone is located lingual and slightly anterior to that cusp, as in modern hedgehogs. The hypocone is equal in basal dimensions to the protocone but lower. Linking these two cusps is a low crest. A similar crest extends anterolaterally from the protocone to the base of the paracone. On the anteromedial side of the hypocone base are two cuspsules. Posterior to the hypocone is a small planar surface that dips steeply anteroventrally. Along the posterior and medial edges of this surface is a weak cingulum. Although no distinct parastyle is present, a prominent parastylar spur is developed on the anterior side of the base of the paracone. Along the margin of the parastylar spur is a distinct cingulum. Three roots are developed on this tooth, one about the protocone-hypocone, a second above the metacrista, and the third above the paracone-parastylar spur.

*M*¹.—Although this tooth is slightly shorter anteroposteriorly than the *P*⁴, it is markedly broader. The paracone and metacone are subequal in height, their heights being about one-half the length of the tooth. The paracone is anterobuccal to the metacone. Third tallest cusp on the tooth, the protocone is lingual and slightly anterior to the paracone. Posterolingual to the protocone is the lowest of the four principal cusps, the hypocone. Unlike modern erinaceines, the protocone and paracone are no closer to one another than the hypocone and metacone. Because no protoconule is developed, the preprotocrista and preprotoconule crista grade imperceptibly into one another. Linking the protocone and paracone, this loph extends along the anterior border of the tooth and in anterior view has a broad U-shaped profile. The postprotocrista

and postmetaconule crista grade imperceptibly into one another because no metaconule is present. They form a loph which extends posterobuccally from the protocone and gradually turns so that it is convex posteromedially and directed mediolaterally at its termination near the base of the metacone. This loph lacks any connection with the hypocone, for not even a weak crest is developed between them. A weak paracrista linking the paracone and precingulum is developed on the small parastylar spur, which, despite its name, lacks any trace of a distinct parastyle. From the metacone, the metacrista extends posterobuccally for a distance equal to two-fifths the tooth length, and terminates in a weak metastyle. Except for the posterior tip of the metastylar spur, the entire margin of the tooth is bounded by a weak cingulum. In occlusal view, the anterior and medial borders are nearly straight and the buccal and posterior borders, concave. The metastylar spur forms a prominent projection posterobuccally away from the body of the tooth while the parastylar spur is a much weaker anterior projection. Three roots are developed—one above the paracone-paracrista region, a second above the metacone-metacrista region, and a third above the protocone-hypocone region.

*M*².—The circular alveolus above the paracone-parastylar region is approximately 0.8 mm in diameter. Posteromedial to this alveolus is the alveolus above the metacone-metastyle region and medially is the one above the protocone-hypocone region. Only the anterior part of the rims of these latter two alveoli are preserved. Judging from the placement of the three alveoli, the angle formed by the buccal edge of this tooth with that of the *M*¹ appears to have been about 135°, and the width of this tooth was slightly less than that of the *M*¹.

Face.—As is typical of erinaceids, the nasals are long and narrow, their posterior ends contacting the frontals. Due to extensive damage on the specimen available, it is not clear how far forward the nasals extended relative to the premaxilla or if there was direct contact between the frontal and premaxilla. The maxilla-premaxilla suture begins ventrally between the *C*¹ and *I*³ and forms an irregular arc that curves upward and backward. The supraorbital crest and the region posterior to it are not preserved.

Palate.—Most of the palate is formed by the maxilla, the premaxilla contributing only in the area immediately adjacent to the upper incisors. The anterior border of the maxilla extends as far forward as the anterior side of the *I*². The palatine fissure is developed on the maxilla-premaxilla suture close to the midline of the palate. The palate extends for a short distance behind the transverse crest, as in the Erinaceinae. Because the lateral margin of the palate has been destroyed in the region of the transverse crest on all

TABLE 5. Degree of Elongation of Palate (mm)

Taxa	Specimen number or literature source	A Distance from anterior edge of maxilla to transverse crest	B Width of palate at P ²	Degree of elongation of palate: A/B
<i>Amphelichinus hornclouidi</i>	KU 18163 Fig. 4 in Hürzeler (1944)	20.0	8.3 ^a	2.41
<i>Amphelichinus edwardsi</i>	Fig. 7 in Viret (1938)	19.0	8.7 ^a	2.30
<i>Amphelichinus edwardsi</i>	Fig. 16 in Butler (1956)	18.0	7.5	2.40
<i>Amphelichinus ruingensis</i>	AMNH(M) 42562	16.0	6.7	2.39
<i>Erinaceus europaeus</i>	AMNH(M) 160470	29.4	15.0	1.96
<i>Erinaceus europaeus</i>	AMNH(M) 149412	26.7	13.4	1.99
<i>Atelerix albiventris</i>	AMNH(M) 187230 ^b	24.6	13.0	1.89
<i>Paraechinus hypomelas</i>	AMNH(M) 166942	18.2	9.9	1.84
		22.6	12.3	1.84

^a Width of left half of palate doubled.^b Immature.

specimens available, the presence or nature of posterior palatine foramina in that crest cannot be determined.

A slight groove is developed on either side of the midline at the anterior end of the palatine; it extends posteriorly to a small foramen. Presumably this groove is homologous to the similar one found in galericines, in which the palatine nerve and artery lie. Midway between the aforementioned foramen and the transverse crest is a smaller palatine foramen. The bones of the palate are as thick and solid as those of the living galericines. No vacuities typical of the modern erinaceines are present in the palate.

Although the snout is more elongate than in living erinaceines, the molars are more posterior relative to the zygomatic arch. The elongation is reflected in the high length-to-width ratio of the palate (Table 5). On KU 18163 this ratio is 2.41, on species of *Amph-echinus edwardsi* it is from 2.30 to 2.40, and in a sample of recent erinaceines it ranges from 1.84 to 1.99. The location of the base of the zygomatic arch, mainly opposite the M^1 , is indicative of the degree of posterior displacement of the molars; however, a small segment of the base lies opposite the M^2 . In most modern erinaceines the base of the arch is equally developed above both molars.

Mandible.—(Fig. 9) The mental foramen lies below the anterior root of P_4 . A wide groove extends anterodorsally from the mental foramen and terminates below the partition between the alveoli for P_2 and C_1 . In the region beneath P_2 - M_2 , the mandible depth is nearly uniform. Moving away from this region in either direction, the depth gradually decreases.

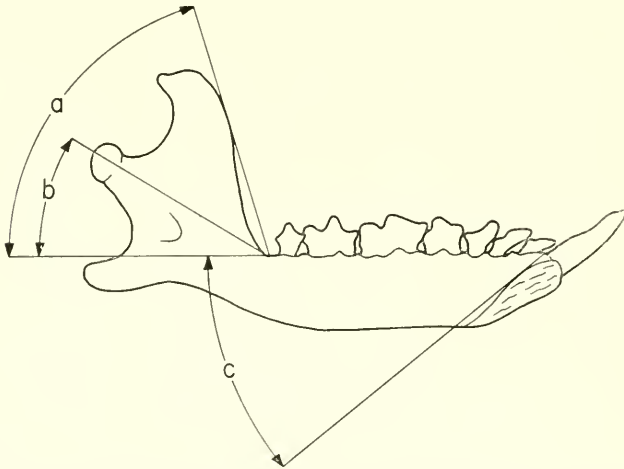


FIG. 11. Method of measuring the elevation of the anterior edge of the ascending ramus ($\angle a$), elevation of the condyle ($\angle b$), and inclination of the dorsal border of the midline symphysis ($\angle c$) on the lower jaw.

Extending forward from beneath P_2 , the unfused symphysis occupies the ventral three-quarters of the mandibular surface. The dorsal border of the symphysis is convex dorsally and roughly parallel to the ventral border, dipping posteriorly at an angle of 25° ($\angle c$ in Fig. 11).

The ascending ramus lies slightly labial to the midline of the mandible. Due to damage sustained by the only mandible available, the anteroposterior length of the ascending ramus, precise position of the condyle, and extent of the angle cannot be determined. The straight anterior border of the ascending ramus is posteriorly inclined at an angle of 76° ($\angle a$ in Fig. 11). This angle is the same as Butler's (1948:469-470) "elevation of anterior edge of coronoid process." Contact between the dorsal and anterior edges of the ascending ramus is at a gently rounded corner. A strong lateral flange on the leading edge of the ascending ramus forms the anterior margin of the masseteric fossa. There is a ridge near the base and on the medial side of the ascending ramus. It extends posterodorsally from the anterior edge of the ascending ramus, passes immediately above the mandibular foramen (which is level with the tooth row), and continues a short distance further before being abruptly cut off by the damage described above. Because ridges similar to this are directed at the condyle on complete erinaceine mandibles, it appears that the condyle was quite low, with an angle of elevation ($\angle b$ in Fig. 11) of about 15° . This angle is the same as the "elevation of the condyle" as defined by Butler (*loc. cit.*). On the medial side of the angle can be seen the most anterior part of the inflected ridge which is directly below the mandibular foramen.

Comparisons.—Each of the three specimens from Montana identified as *Amphechinus horncloudi* are from different localities and stratigraphic positions in the Cabbage Patch beds. All are of the proper size to be parts of the unknown dentition, jaw, or skull of *Amphechinus horncloudi* originally described from South Dakota. However, with the exception of KU 18162, there is no reason other than geographic proximity to regard these specimens as conspecific with *A. horncloudi* rather than the slightly larger *Amphechinus edwardsi* of Europe or slightly smaller *Amphechinus rusingensis* of Africa. See Butler (1956: Tables 4 and 7) and Hürzeler (1944:461) for measurements of the dentitions of these two species.

KU 18097, a maxilla fragment with P^3 - M^1 , is similar to the species of *Amphechinus* in the proportions of the upper molars. Molars of modern erinaceines, *Gymnurechinus*, *Mioechinus*, and *Postpalerinaceus* are all more anteroposteriorly elongate. *Palaeoscaptor* and *Stenoechinus* have much smaller molars.

KU 18162, a mandible with I_1 , P_4 , and M_3 is similar to other species of *Amphechinus* and unlike other erinaceines except *Palaeoscaptor* and *Gymnurechinus*. The P_4 is similar to that of the type of



FIG. 12. *Parvericinus montanus*. A. YPM 13956, type, right maxilla fragment, occlusal view, from Arikareean or Hemingfordian, Deep River beds, sec. 3, T 10 N, R 5 E, Meagher Co., Montana. $\times 6$. B. UMMP V61033, right P⁴, occlusal view, from late Barstovian, Egelhoff Quarry, from an unnamed lithic unit beneath the Valentine Formation and overlying the Rosebud Formation, SW corner of NE $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 29, T 33 N, R 23 W, Keya Paha Co., Nebraska. $\times 12$. C. UMMP V61026, right M¹, occlusal view, same locality as B. $\times 12$.

Amphexinus horncloudi (SDSM 62113) and unlike any other known species of the genus in that the maximum transverse diameter is in the talonid region, not further forward across the trigonid.

KU 18163, a partial skull with P¹-P², resembles *Amphexinus edwardsi* and *Amphexinus rusingensis* in the presence of an en-

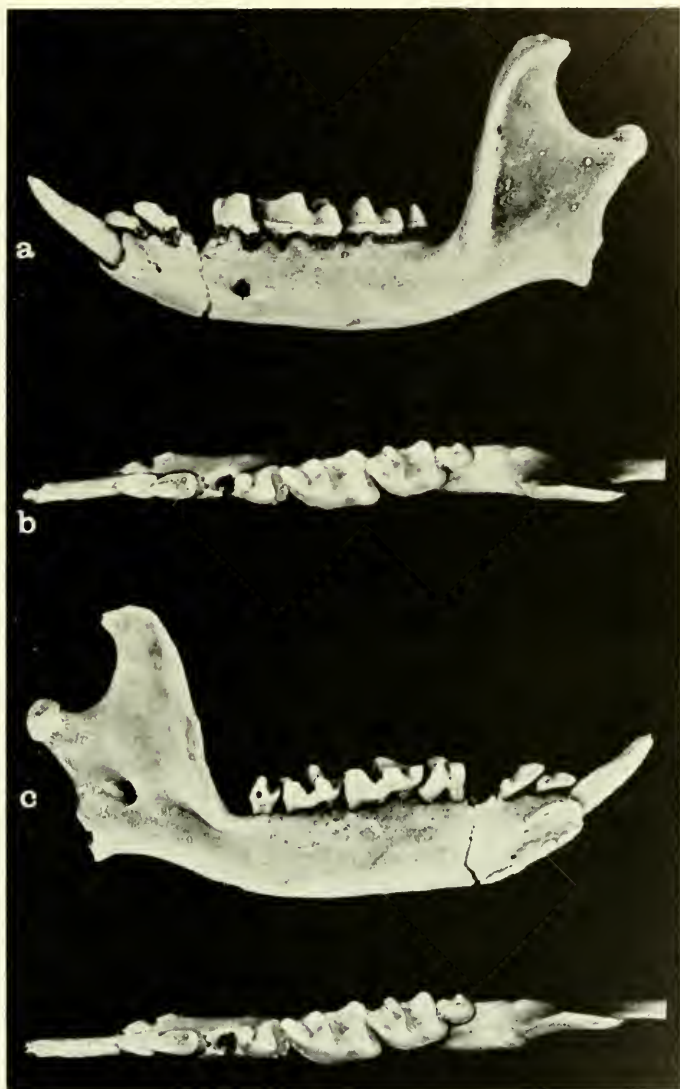


FIG. 13. *Parvericius montanus*, UMMP V56569, left mandible. A. Lateral view. B. Occlusal view. C. Lingual view. From the late Barstovian, Egelhoff Quarry, from an unnamed lithic unit beneath the Valentine Formation and overlying the Rosebud Formation, SW corner of NE $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 29, T 33N, R 23 W, Keya Paha Co., Nebraska. $\times 4.5$.

larged P^1 . Among the other genera of Erinaceinae, only the much smaller *Palaeosceptor* is known to possess as enlarged an P^1 (Trofimov, 1960:38 and Fig. 1).

Parvericius Koerner 1940

Type Species.—*Parvericius montanus* Koerner 1940.

Known Distribution.—?32—?31 my (medial? Oligocene) Asia; medial Arikareean—late Barstovian (23—12.5 my, early to medial Miocene), North America.

Diagnosis.—Distinguished from *Palaeosceptor* and *Stenoechinus* by the greater length of the M^1 relative to its width; from *Palaeosceptor* by absence of a metacone on M^3 ; from all other erinaceines except *Palaeosceptor* and *Amphechinus* by the presence of an enlarged I_1 ; from *Stenoechinus* by a prominent paraconid taller than the metaconid on P_4 ; from *Amphechinus*, *Dimylechinus*, *Mioechinus*, *Palaeosceptor*, and *Postpalerinaceus* by the anteroposteriorly compressed M_1 trigonid; from *Gymnurechinus*, *Palaeosceptor*, and *Stenoechinus* by absence of a talonid or postcingulum on M_3 ; and from *Dimylechinus* by presence of M_3 and M^3 .

Parvericius montanus Koerner 1940

Figures 7d, 12-15

Parvericius montanus Koerner 1940:841.

Palaeoerinaceus minimus Bohlin 1942:23.

Amphechinus (*Palaeoerinaceus*) cf. *minimus* Sulimski 1970:64.

Holotype.—YPM 19356, right maxilla fragment with P^3 - M^3 complete except for lingual halves of P^{3-4} .

Type Locality and Stratigraphic Position.—Collected from the Deep River beds in sec. 3, T 10 N, R 5 E, Meagher Co., Montana.

Diagnosis.—Only known species of genus.

Referred Material.—MPUM 1551, right mandible with highly worn P_4 - M_3 , tip of I_1 root, fragment of C_1 , P_3 alveolus, horizontal ramus complete from C_1 to base of leading edge of the ascending ramus. Found in the middle Cabbage Patch beds, Bert Creek locality 2 (MV6504-2), NW $\frac{1}{4}$, NE $\frac{1}{4}$, SW $\frac{1}{4}$, SE $\frac{1}{4}$, sec. 1, T 10 N, R 12 W, Granite Co., Montana (Rasmussen, 1969:131-132).

UCM 29507, isolated left M_1 . Found in the Split Rock Formation, SW $\frac{1}{4}$, NW $\frac{1}{4}$, sec. 36, T 29 N, R 90 W, Fremont Co., Wyoming.

UCM 29853, isolated right M_1 . UCM 29955, left mandible with M_{1-3} , posterior half of rear alveolus of P_4 , horizontal ramus complete from rear alveolus of P_4 to base of leading edge of ascending ramus. Found in the Split Rock Formation, NE $\frac{1}{4}$, NE $\frac{1}{4}$, NW $\frac{1}{4}$, sec. 36, T 29 N, R 90 W, Fremont Co., Wyoming.

F:AM 76704, complete left mandible, edentulous except for P_4 . UMMP V56569, left mandible lacking only P_2 and the angle. UMMP V57331, left mandible fragment lacking the region pos-

terior to the alveolus for the forward root of M_2 with I_1 , C_1 , P_4 and alveoli for I_2 , P_3 , M_1 and anterior alveolus for M_2 . UMMP V61029, isolated left M_1 (this specimen appears to have been etched by acid). UMMP V61031, isolated right M_2 . UMMP V61027, isolated right M_2 . UMMP V61033, isolated left P^4 . UMMP V61034, isolated right M^1 . UMMP V61026, isolated left M^1 . Found at Egelhoff Quarry in the SW corner of NE $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 29, T 33 N, R 23 W, Keya Paha Co., Nebraska, in an unnamed lithic unit that unconformably overlies the Rosebud Formation and is unconformably overlain by the Valentine Formation.

UMMP V61022, isolated left M_1 . Found at Norden Bridge Quarry in the SE $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 33, T 33 N, R 23 W, Brown Co., Nebraska, in the same lithic unit as Egelhoff Quarry described in the previous paragraph.

Upper Dentition.—(Fig. 12) P^3 .—Only the buccal half of this tooth is preserved on the single specimen available. The paracone is the largest and tallest cusp preserved on the tooth. The anterior side of the paracone is straight and the posterior side, concave. Wear has blunted the tip of the paracone, but, when unworn, the apical height of this cusp was probably no more than two-thirds the crown length. Directed posteriorly from the metacone, the metaerista abruptly turns in a buccal direction at the posterior border of the tooth, but no metastyle or other cuspules are developed there. On the anterior side of the paracone base there is a narrow precingulum with a weak paraerista which extends ventrally

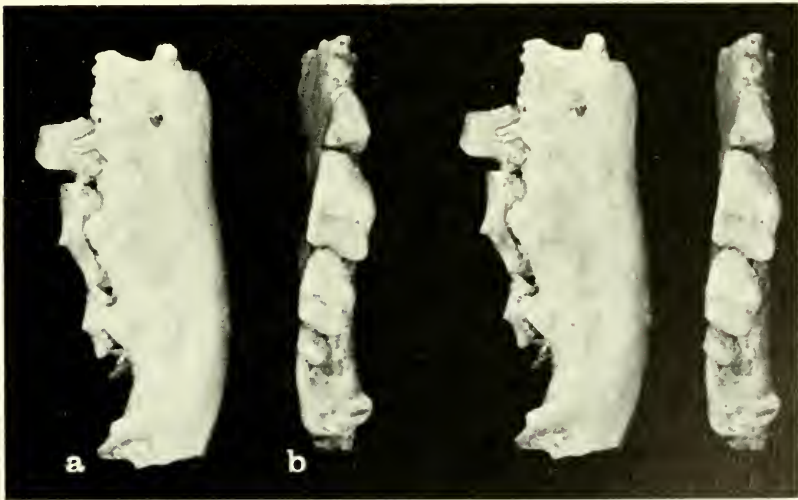


FIG. 14. *Parvericius montanus*, MPUM 1551, right mandible. A. Lateral view. B. Occlusal view. From the medial Arikareean, middle Cabbage Patch beds, Bert Creek locality 2 (MV6504-2), NW $\frac{1}{4}$, NE $\frac{1}{4}$, SW $\frac{1}{4}$, SE $\frac{1}{4}$, sec. 1, T 10 N, R 12 W, Granite Co., Montana (Rasmussen, 1969:131-132). $\times 6$.

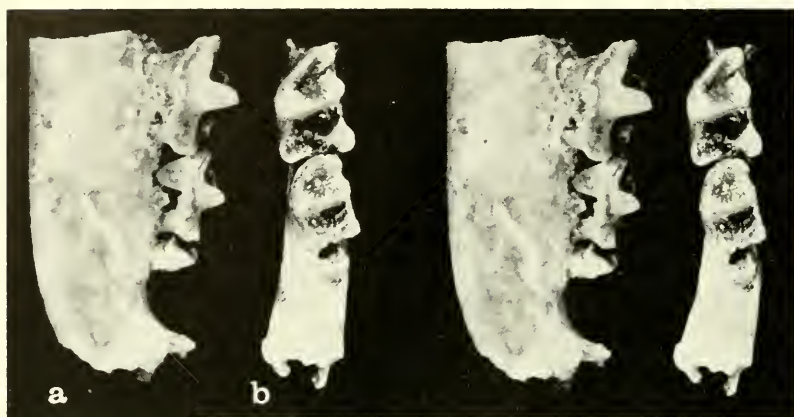


FIG. 15. *Parvercicus montanus*, UCM 29955, left mandible. A. Lateral view. B. Occlusal view. From the Hemingfordian, Split Rock Formation, NW $\frac{1}{4}$, sec. 36, T 29 N, R 90 W, Fremont Co., Wyoming. $\times 6$.

from the cingulum toward, but not reaching, the apex of the cusp. Examination of the broken surface where the lingual half of the tooth broke away suggests that it was markedly shorter anteroposteriorly than the buccal half; thus, the metastylar spur projected away from the body of the tooth as on the P^4 . On the buccal side of the tooth along the base of the paracone is a weakly developed cingulum. Two prominent roots are preserved, one above the parastylar region, the other over the metacrista. If a third root were present above the missing lingual region of the tooth, all trace of it has been lost.

P^4 .—This tooth is several times larger than the preceding P^3 . The height of the paracone, tallest cusp on the tooth, is about five-sixths of the tooth length. Two-fifths the height of the paracone, the protocone is lingual and slightly anterior to the cusp, as in living hedgehogs. Equally as large in basal dimensions, the hypocone is

TABLE 6. Measurements (mm) of the Upper Dentition of *Parvercicus montanus*

	YPM 13956 type	UMMP V61033	UMMP V61026	UMMP V61034
P^3 , anteroposterior diameter	1.1	---	---	---
P^4 , anteroposterior diameter	2.1	2.2	---	---
P^4 , transverse diameter	---	2.2	---	---
M^1 , anteroposterior diameter	2.1	---	2.0	2.2
M^1 , transverse diameter	2.5	---	2.4	2.6
M^2 , anteroposterior diameter	1.6	---	---	---
M^2 , transverse diameter	1.8	---	---	---
M^3 , anteroposterior diameter	0.4	---	---	---
M^3 , transverse diameter	1.1	---	---	---

lower than the protocone and posterolingual to it. Although these two lingual cusps are linked together by a low crest, neither cusp is joined to the buccal structure of the tooth by a crest. Between the hypocone and the base of the metastylar spur is a planar surface that slopes posterodorsally. A small parastyle is present on the well-developed precingulum anterior to the base of the paracone. Although no paracrista is present, the prominent metacrista is directed posterobuccally away from the paracone and terminates posteriorly without a distinct metastyle. Likewise, the metastylar spur projects posterobuccally away from the body of the tooth so that its lingual half is narrower anteroposteriorly than the buccal half. Continuous with the precingulum is a weaker cingulum along the buccal side of the tooth. The three roots of the tooth lie above the protocone and hypocone, paracone, and metacrista, respectively; all are subequal in length and diameter.

*M*¹.—Largest tooth in the skull, the *M*¹ is somewhat broader but subequal in length to the *P*¹. The height of the paracone, third tallest and third largest of the four principal cusps, is half the length of the tooth. The paracone is anterior to the metacone and their bases are confluent. Subequal in height and basal dimensions, the metacone and protocone are the tallest and largest of the four principal cusps. The anterior side of the metacone is steep; the posterior side is more gently dipping. The protocone is lingual and slightly anterior to the paracone. The hypocone is the lowest and smallest of the four principal cusps. The hypocone and metacone are as close to one another as the protocone and paracone. Linking the anterobuccal corner of the protocone and the anterolingual corner of the paracone are the well-developed preprotocrista and preprotoconule crista which grade imperceptibly into each other in the absence of a paraconule. In anterior view this loph has a broad, inverted V-shaped profile. The postprotocrista is directed posterobuccally from the protocone. This crista divides at a point lingual to the anterior edge of the metacone; one branch extends posterolingually to the hypocone whereas the other, the postmetaconule crista, extends buccally to the metacone. No metaconule is developed on this tooth. A short paracrista crosses the precingulum and terminates against the base of the paracone at the anterobuccal corner of the tooth. No parastyle is present. The metacrista extends posterobuccally from the metacone for a distance equal to one-half the tooth length. A cingulum is developed along the entire margin of the tooth except at the posterior tip of the metastylar spur. In outline the tooth is approximately square, with prominent excavations on the posterior and lingual side. A well-developed metastylar spur projects posterobuccally away from the body of the tooth, and a much smaller parastylar spur projects anteriorly. Three roots are present—one above the paracone-paracrista region, a second

TABLE 7. Measurements (mm) of the lower dentition of *Parvicitus montanus*

	MPUM 1551	UCM 29507	UCM 29853	UCM 29955	UMMP V56569
P ₄ , anteroposterior diameter	1.2	---	---	---	1.5
P ₄ , transverse diameter	0.9	---	---	---	1.2
M ₁ , anteroposterior diameter	1.9	2.4	2.2	2.2	2.5
M ₁ , trigonid length	1.1	1.2	1.2	1.2	1.3
M ₁ , trigonid width	1.3	1.3	1.6	1.4	1.6
M ₁ , talonid width	1.3	1.5	1.7	1.5	1.8
M ₂ , anteroposterior diameter	1.5	---	---	1.7	2.0
M ₂ , trigonid length	0.9	---	---	0.9	1.0
M ₂ , trigonid width	1.2	---	---	1.2	1.5
M ₂ , talonid width	1.0	---	---	1.2	1.4
M ₃ , anteroposterior diameter	0.7	---	---	0.7	1.0
M ₃ , trigonid width	0.6	---	---	0.6	0.8

TABLE 7. (continued)

	UMMP V57331	UMNIP V61031	UMNIP V61029	UMMIP V61027	F:AM 76704	UMNIP V61022
P ₄ , anteroposterior diameter	1.4	---	---	---	1.5	---
P ₄ , transverse diameter	1.1	---	---	---	1.0	---
M ₁ , anteroposterior diameter	---	---	2.5	---	---	2.5
M ₁ , trigonid length	---	---	1.5	---	---	1.3
M ₁ , trigonid width	---	---	1.4	---	---	1.5
M ₁ , talonid width	---	---	1.6	---	---	1.6
M ₂ , anteroposterior diameter	---	1.8	---	2.0	---	---
M ₂ , trigonid length	---	1.0	---	1.0	---	---
M ₂ , trigonid width	---	1.4	---	1.5	---	---
M ₂ , talonid width	---	1.2	---	1.4	---	---
M ₃ , anteroposterior diameter	---	---	---	---	---	---
M ₃ , trigonid width	---	---	---	---	---	---

above the metacone-metacrista region, and a third above the protocone-hypocone region.

M².—Although smaller, the *M²* is basically similar to the *M¹*. The protocone and paracone are subequal in height and basal dimensions, being the tallest and largest of the four principal cusps. The lingual region of the *M²* is the same as the *M¹*; however, the buccal region, particularly the posterobuccal area, is different. The metacone has shifted position so that it is posterolingual to the paracone, not posterior. The metastylar spur projects posteriorly, not posterobuccally, and is reduced. The buccal border of the tooth is not subparallel to the midline of the skull, but is directed posteromedially. Similarly, the parastylar spur has shifted so that it projects anterobuccally rather than anteriorly. Narrow cingula are developed on all sides except the lingual. Only the two buccal roots of the tooth can be observed; relative to structures on the crown, their positions are the same as on the *M¹*.

M³.—This tooth is basically a mediolaterally elongated blade with a protocone at the lingual end and an equally large and tall paracone at the buccal end; the two cusps are joined together by a short, straight crest. A weak precingulum is developed along the anterior margin of this tooth. Two roots are developed on this tooth—one above the protocone and a second over the paracone.

Lower Dentition.—(Figs. 13-15) *I₁*.—In morphology and size, this tooth is quite distinct from the incisor behind (*I₂*). It is elongated, extends forward, and curves slightly upward from the anterior end of the mandible for a distance about equal to the *I₂-P₃* length, or 3.7 mm on the least worn specimen (UMMP V56569). Posteriorly, the root extends beneath and medial to the roots of *I₂-P₃* to terminate just in front of the anterior root of *P₄*. In cross-section at the alveolar border, the tooth is a slightly distorted, dorsoventrally elongated oval with the blunt end dorsal and the medial side straight rather than curved. The tooth is mediolaterally compressed so that its dorsoventral diameter is about half again as great as its mediolateral diameter. At its alveolar border, the tooth is nearly as wide and deep as the mandible itself. Further posterior, beneath the canine, the dorsoventral diameter of the tooth is equal to about half the height of the mandible.

I₂.—This tooth and the somewhat larger canine behind are more similar in form to one another than either is to the *I₁*. Presumably, the same could be said for the *P₂*, although the tooth is known only by its alveolus in this species. The single root of the *I₂* dips posteriorly at a shallow angle. Overlapping the *I₁* ahead, the crown of the *I₂* projects forward from the root. Along the midline is a low crest with two prominent swellings. The anterior swelling lies slightly forward of the midpoint of the tooth and is the protoconid; the second swelling lies at the posterior margin of the short talonid. The length of the tooth is about twice the width.

C₁.—In addition to its somewhat larger size, the *C₁* differs from the *I₂* primarily in the relative sizes of protoconid and talonid cusp, which are slightly taller relative to the length and width of the tooth.

P₂.—This tooth is known in this species only by its single alveolus. The *P₂* was probably similar in size and morphology to the *I₂*, because the alveoli of the two teeth are of similar dimensions; in other erinaceines, they are similar in morphology. The posterior dip of the *P₂* alveolus is steeper than in *I₂* or *C₁*.

P₁.—This tooth is markedly larger than the three immediately anterior to it. The protoconid is most prominent of the cusps; its height is nearly as great as the length of the tooth. Anteromedial to the protoconid is the lower paraconid, a well-developed cusp. In lateral view the paralophid linking the two cusps has a deep, acute V-shaped profile. The protolophid is directed medially from the protoconid and has a slight swelling on the lingual end, but no distinct metaconid. Along the buccal border of the tooth is a weak cingulum. This cingulum passes into the narrow talonid which is developed for the full width of the trigonid.

On no specimen were the alveoli of this double-rooted tooth visible.

M₁.—The length of the trigonid is four-fifths its width and approximately equal to half the length of the tooth. Lowest of the trigonid cusps, the paraconid is anterior to the metaconid; the bases of the two cusps are separated by a deep cleft. The protoconid is posterobuccal to the paraconid; the two cusps are linked by a paralophid. In lateral view, the paralophid has a V-shaped profile that is acute but nearly a right angle, whereas in occlusal view, the paralophid is somewhat buccally convex. The protoconid is the tallest cusp on the tooth and has the greatest basal dimensions. On the least worn specimen (UCM 29553), the height of the protoconid is equal to 85 percent of the tooth length. The protolophid joins the metaconid and protoconid; when viewed posteriorly, it has an acute, V-shaped profile. The metaconid is intermediate in height between the protoconid and paraconid.

Ten percent wider than the trigonid, the talonid has only two cusps, one in each posterior corner. The entoconid is the taller of these two cusps and is intermediate in height between the metaconid and paraconid. The entoconid is directly posterior to the metaconid and the hypoconid is slightly more buccally placed than the protoconid. In anterior view, the buccal margin of the protoconid is nearly straight and that of the hypoconid, convex. Between the entoconid and that part of the posterior wall of the trigonid beneath the apex of the metaconid is a low entocristid which encloses the talonid basin lingually. Directed anteriorly and slightly lingually from the hypoconid, the cristid obliqua abuts against the postvallid immediately behind the protoconid. A continuous, well-

developed, narrow cingulum extends along the entire buccal side of the tooth. At the base of the hypoconid, the buccal cingulum passes into the posterior cingulum which is directed dorsomedially so that it terminates lingually midway between the hypoconid and entoconid just below the crest of the posteristid. In the region of transition between the buccal and posterior cingula, these narrow cingula are even narrower.

The partition between the alveoli of this double-rooted tooth has twinned vertical ridges characteristic of erinaceids. On the posterior wall of the rear alveolus is a single vertical ridge. The anterior alveolus is nearly circular with the posterior side slightly flattened. Its diameter is approximately 0.7 mm. The larger, posterior alveolus is roughly rectangular with an anteroposterior length of 0.8 mm and width of 0.9 mm.

M_2 .—Although the M_2 is only four-fifths as large as the M_1 , in other respects the teeth are quite similar. Therefore, only differences between these teeth will be noted in the following two paragraphs.

The trigonid length is only two-thirds as great as its width. The paraconid is not developed as a distinct cusp but rather is a small swelling at the anterolingual end of the paralophid. The anterolingual quarter of the protolophid is at an abrupt angle with respect to the remainder of that crest, being oriented mediolaterally rather than anterolingually.

The entoconid is more buccally placed on the tooth than the metaconid. When viewed anteriorly, the buccal margin of the protoconid is buccally convex. No buccal cingulum is developed on the most anterior quarter of the prevallid.

M_3 .—This tooth differs from the two anterior molars in several ways: markedly smaller size; complete absence of a talonid; more anteroposteriorly expanded trigonid, its length being one-fourth greater than its width; and a single anteroposteriorly elongated root that may be weakly bifurcated. Only two distinct cusps are present on the trigonid—the protoconid and metaconid. The protoconid is taller and somewhat larger in basal dimensions than the metaconid; the bases of the two cusps are so close to one another that only a narrow notch separates them. No swelling is present at the lingual end of the paralophid to mark the presence of a distinct paraconid. Only the worn base of the paralophid remains on the best available specimen of this tooth. A well-developed, continuous, narrow basal cingulum is present along the buccal margin of the tooth, but no cingulum is present along the posterior side of the trigonid.

Oval in outline, the single alveolus of this tooth departs slightly from the vertical so as to dip posteriorly. The length of the oval is 0.9 mm and the width, 0.5 mm.

Mandible.—(Figs. 13-15) Circular in outline, the mental foramen lies below the middle of P_4 , midway between the dorsal and

ventral borders of the ramus. Beneath P_3 - M_2 , the mandible is of a uniform depth; it gradually decreases in depth posteriorly and abruptly anteriorly. The angle of the jaw protrudes ventrally and posteriorly away from the body of the mandible and is slightly inflected. The unfused midline symphysis of the mandible extends posteriorly to a point beneath the C_1 - P_3 juncture. The dorsal boundary of the symphysis dips posteriorly at an angle of 25° with respect to the dorsal edge of the mandible ($\angle c$ in Fig. 11). Beneath I_1 , the symphysis covers the entire medial surface of the mandible; posteriorly it covers a progressively decreasing amount. Parallel and adjacent to the ventral margin of the midline symphysis is a faint depression which opens posteriorly and may have been the site for the insertion of the geniohyoideus muscle.

The ascending ramus lies slightly labial to the midline of the mandible. Its anteroposterior width, measured from the condyle, is twice the maximum depth of the jaw. The anterior border of the ascending ramus departs slightly from the vertical and dips an-

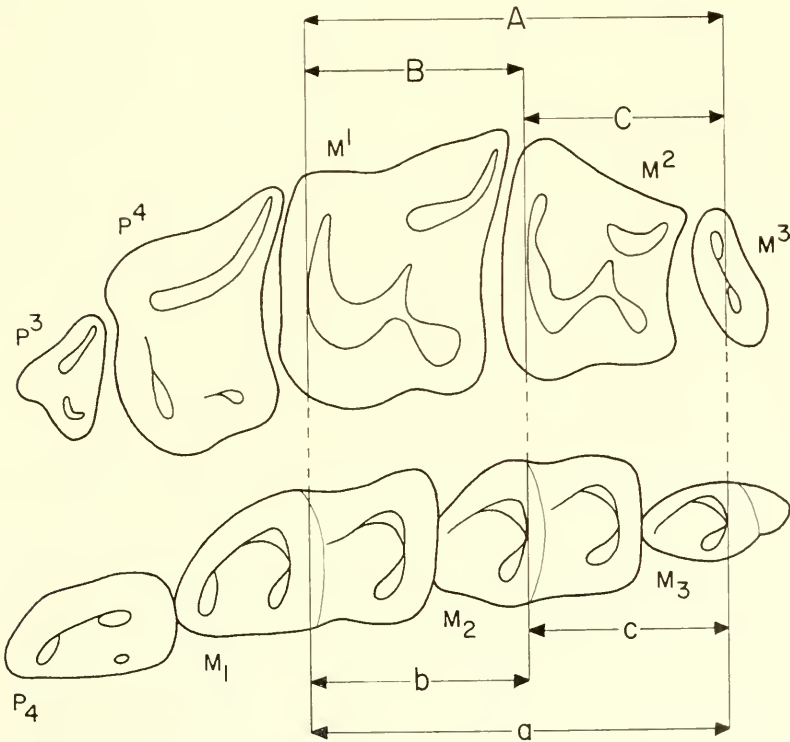


FIG. 16. Method of measuring distances between occluding surfaces. Corresponding measurements on the upper and lower teeth are indicated by the same letter of the alphabet, capital letters for the upper teeth and small letters for similar measurements on the lower teeth.

teriorly; the angle of elevation ($\angle a$ in Fig. 11) is 80° . Near its dorsal end, the anterior edge curves slightly posteriorly and dorsally and passes smoothly into the convex dorsal edge of the ascending ramus. On the leading edge of the ascending ramus, there is a sharp lateral flange that forms the anterior margin of the masseteric fossa. The prominence of this flange decreases dorsally. There is a ridge on the medial side of the ascending ramus. Beginning in the anteroventral corner of the ascending ramus immediately behind the tooth row, the ridge extends posterodorsally for a distance less than one-fourth the width of the ascending ramus. To the rear, the ridge terminates somewhat anterior to the mandibular foramen; between that point and the condyle, there is no ridge developed on the medial side of the mandible. The mandibular foramen is midway between the anterior and posterior borders of the ascending ramus and level with the tooth row. The condyle is well above the level of the tooth row, the angle of elevation ($\angle b$ in Fig. 11) being about 35° . In posterior view, the margin of the mandible has a knife-edge thinness except immediately below the condyle. The posterior border of the ascending ramus curves anterodorsally from the condyle and meets the dorsal edge of the ascending ramus at a sharp angle.

Comparisons.—In a living erinaceine such as *Erinaceus europaeus*, the distances between adjacent occlusal surfaces of the upper dentition are found to be close to those of the corresponding occlusal surfaces of the lower dentition. For example, the distance from the prevallum of M^1 to that of M^2 is nearly the same as that from the postvallid of M_1 to that of M_2 . Because the prevallum of M^1 is adjacent to the postvallid of M_1 when the two teeth are in occlusion and likewise, the prevallum of M^2 is adjacent to the postvallid of M_2 in the same circumstances; this result is hardly surprising. See figure 16 for a diagrammatic explanation and table 8 for a set of measurements in a sample of five recent specimens of *E. europaeus*.

If the distances between the prevalla of the upper molars of *Parvericinus montanus* (YPM 13956, Fig. 12a) are compared to the

TABLE 8. Measurements (mm) of the distances between occlusal planes in *Erinaceus europaeus* (See Fig. 16 and text for explanation)

	AMNH(M) 34820	AMNH(M) 34821	AMNH(M) 149412	AMNH(M) 160470	AMNH(M) 164391
A	8.9	9.2	8.4	9.1	8.8
a	8.7	9.1	8.6	8.6	8.6
B	4.6	4.9	4.4	4.6	4.5
b	4.6	4.8	4.7	4.6	4.5
C	4.3	4.3	4.0	4.5	4.3
c	4.1	4.3	3.9	4.0	4.1

TABLE 9. Measurements (mm) of the distances between occlusal planes in *Palaeoscaptor*, *Parvericius*, and *Stenoecichnus* (See Fig. 16 and text for explanation)

	<i>Palaeoscaptor</i> <i>acridens</i> AMNH 22080	<i>Parvericius</i> <i>montanus</i> type, YPM 13956	<i>Parvericius</i> <i>montanus</i> UCM 29955	<i>Parvericius</i> <i>montanus</i> UNMP V56569	<i>Stenoecichnus</i> <i>tantalus</i> type, KU 18001
A	3.9	3.2			
a			3.5	4.0	3.4
B	2.2	1.8			
b	2.1		2.0	2.1	1.9
C	1.7	1.4			
c	1.5	1.9	1.5

distances between the postvallids of the mandible fragment presumed to be that of *P. montanus* from the Split Rock Formation (UCM 29955, Fig. 5), the corresponding measurements are found to be similar to the degree found between individuals of *Erinaceus europaeus* of slightly different size (compare Tables 8 and 9). In addition, these upper and lower dentitions have been modified in the characteristic erinaceine pattern; M^3 reduced to a straight blade between the protocone and paracone; M_3 diminished to a trigonid lacking a talonid. These specializations of the most posterior upper and lower molars are functionally correlated with one another and are not known to occur singly.

On the basis of the above evidence only, it could be postulated that the mandibles of *Stenoechinus tantalus* were the previously unknown lower jaws of *Parvericius montanus*. The distances between the corresponding occlusal surfaces are nearly the same (Table 9); and, although the M_3 of *S. tantalus* does have a wide postcingulum, it conceivably did occlude with an M^3 similar to that on *P. montanus*. However, the M^1 and M^2 referred to *S. tantalus* (found at the same locality as the majority of known lower dentitions of that species) appears to be quite unlike those of *P. montanus*; thus, the possibility of taxonomic synonymy seems improbable. The material from Egelhoff Quarry further supports the assignment of the lower dentitions, here inferred to belong to *P. montanus*, with the upper dentition on which the species is based. At that locality only one form of small erinaceine tooth is known for each position of the dental series represented, suggesting that all such teeth belong to a single species. The isolated P^4 and two M^1 's from Egelhoff Quarry are quite similar to those of the type of *P. montanus*, whereas the lower teeth from there are 10 percent larger than those of the Split Rock mandible.

Dentitionally, specimens of *Parvericius montanus* from Tabenbuluk (originally described as *Palaeoerinaceus minimus* Bohlin, 1942), and from Nareen Bulak (originally described by Sulimski, 1970, as *Amphechinus (Palaeoerinaceus) cf. minimus*), are similar to specimens of *P. montanus* from North America. On the basis of dimensions of the teeth, this Asian material is most similar to older, smaller Arikareean and Hemingfordian North American specimens of *P. montanus*. There is a marked difference in the depth of the mandible; the North American specimens are about half again as deep as the Asiatic ones (Bohlin, 1942: Fig. 3d, d', Plate 1, Fig. 4; Sulimski, 1970: Fig. 2d-f; Plate 19, Figs. 5-7). Besides *P. minimus*, Bohlin described another species in 1942 from Taben-buluk, *Palaeoerinaceus kansuensis* Bohlin (1942). This species is based on an incomplete edentulous mandible fragment. The mandibular depth is closer to the North American *P. montanus* than *P. minimus*, being only one-fifth larger. Furthermore, based on the alveoli, the

molars appear to have been about as large as the later, larger Barstovian North American specimens of *P. montanus*.

Comparisons with *Stenoechinus tantalus* were made on p. 18.

Direct comparison of the type and referred specimen of *Amphiechinus horncloudi* (SDSM 62113, and 6278; J. R. Macdonald, 1970: Fig. 5) together with the descriptions and figures of *Amphiechinus edwardsi* in Viret (1938: Figs. 4, 8, and Plate I, Fig. 2) and Hürzeler (1944: Figs. 7, 10, 13) and of *Amphiechinus arvernensis* in Viret (1929: Plate 28, Figs. 1-2), reveals two significant differences between these three species and *Parvericius montanus*. The corresponding dimensions of the teeth are only about one-half to three-fifths as large, and the trigonid of M_1 is anteroposteriorly compressed on *Parvericius montanus*.

Erinaceinae genus and species *indet.*

Figure 17

Material.—KU 18396, isolated right M^2 . Found in the middle Cabbage Patch beds, Cabbage Patch locality 4 (KU-Mt-12), SW $\frac{1}{4}$, SE $\frac{1}{4}$, SW $\frac{1}{4}$, SE $\frac{1}{4}$, sec. 1, T 10 N, R 12 W, Granite Co., Montana (= MV6504-4, Rasmussen, 1969:131-132).

M².—(Fig. 17) Length of the tooth is only two-thirds the width (length = 1.5 mm, width = 2.4 mm). Few signs of wear mark the surface of the tooth. Tallest of the four principal cusps, the paracone is anterobuccal to the metacone and their bases are confluent. Second tallest of the cusps, the metacone has more gently sloping anterior and posterior sides than the paracone. Nearly equal in height to the metacone, the protocone is approximately lingual to the paracone. The base of the protocone projects medially beyond the body of the tooth. Posterolingual to the protocone is the lowest of the four principal cusps, the hypocone. The base of the hypocone projects posterolingually away from the body of the tooth. The hypocone and metacone are nearly as far apart as the protocone



FIG. 17. Erinaceinae, genus and species *indet.*, KU 18396, right M^2 , occlusal view. From the medial Arikarean, middle Cabbage Patch beds, Cabbage Patch locality 4 (KU-Mt-12), SW $\frac{1}{4}$, SE $\frac{1}{4}$, SW $\frac{1}{4}$, SE $\frac{1}{4}$, sec. 1, T 10 N, R 12 W, Granite Co., Montana (= MV6504-4, Rasmussen, 1969:131-132). $\times 15$.

and paracone. Linking the anterobuccal corner of the protocone and the paracrista are the well-developed preproto-crista and preprotoconule crista which grade imperceptibly into one another, in the absence of a paraconule. In anterior view, this loph has a broad inverted V-shaped profile. The postproto-crista is directed posterobuccally from the protocone and terminates posteriorly lingual to the metacone. A short crest is directed from the posterior tip of the postproto-crista posterolingually toward the hypocone. However, the length of the crest is only about one-third of that necessary to link the postproto-crista to the hypocone; therefore, the cusp is isolated. A similar gap exists between the postproto-crista and the metacone because the postmetaconule crista extends buccally from the cusp but does not reach the crest. No metaconule is developed on this tooth. Along the straight anterior margin is a well-developed precingulum that buccally becomes progressively wider and curves ventrally until it merges with the paracrista buccal to the paracone. Together the precingulum and paracrista extend further buccally to the margin of the prominent parastylar spur. No distinct parastyle is developed. From the metacone, the metacrista extends posterobuccally for about two-thirds of its length and then turns to an anterobuccal direction to terminate finally without development of a distinct metastyle. A well-developed ectocingulum is present between the paracrista and metacrista. Along the posterior margin of the base of the metacone is a similarly well-developed postcingulum.

Comparisons.—This specimen differs from the upper molars of all other erinaceids possessing a distinct metacrista in that the buccal third of that crest is directed anterobuccally rather than posterobuccally.

In general form, this tooth is quite similar to the M^2 of *Palaeoscaptor acridens* and *Parvericius montanus*, although it is about 10 to 15 percent larger in every dimension and possesses a more prominent parastylar spur. In contrast to *P. acridens*, the postproto-crista and postmetaconule crista are not parts of one continuous crest, but instead form two short crests quite distinct from one another. Unfortunately, the M^2 of the only specimen of *P. montanus* is too worn to discern the condition of these crests in that species.

The M^2 's of *Amphelchinus*, *Neurogymnurus*, *Mioechinus*, *Postpalerinaceus*, and the modern Erinaceinae are markedly longer relative to their respective widths and larger in size than this specimen. With the exception of *Postpalerinaceus* and some specimens of *Amphelchinus*, this group also differs from this isolated M^2 in that the base of the hypocone does not project away from the main body of the tooth.

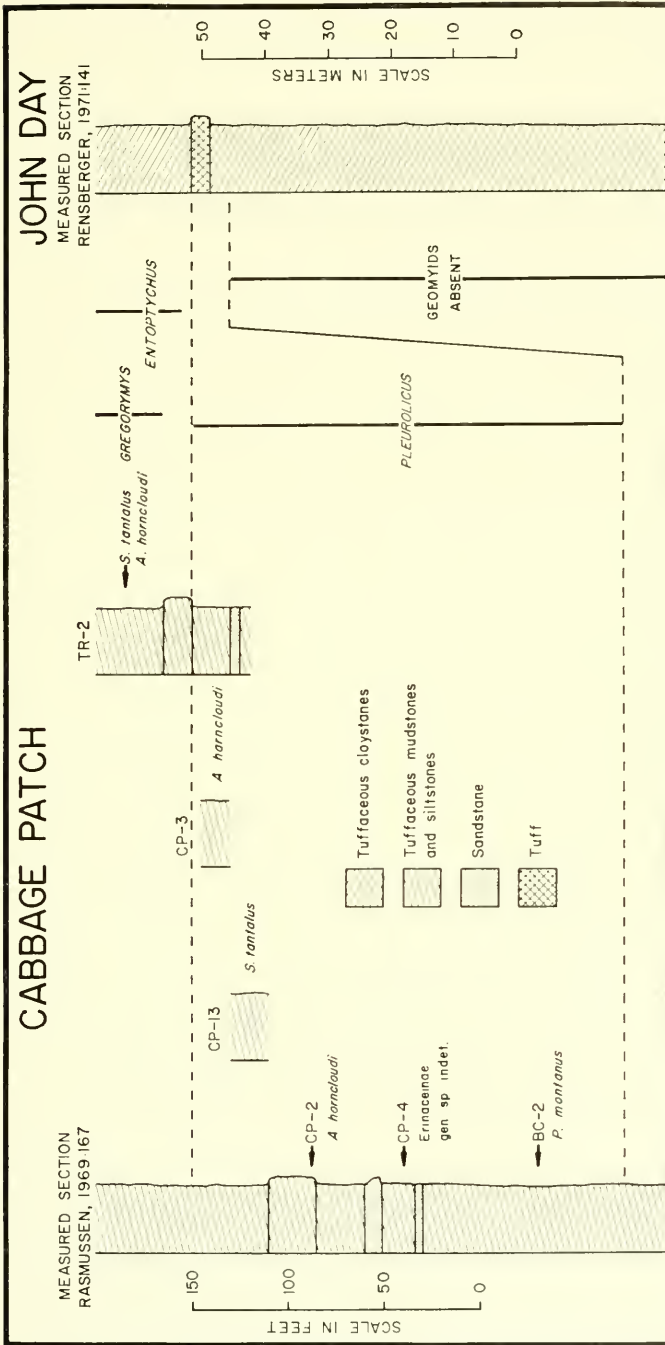


FIG. 18. Generalized stratigraphic sections of Cabbage Patch beds showing stratigraphic positions of hedgehogs from Montana discussed in this report. Correlation to a section measured in the John Day Formation is based on the highest and lowest occurrence of *Pleurolocus* and the lowest occurrence of *Gregorymys* (Cabbage Patch beds) and *Entoptychus* (John Day Formation).

STRATIGRAPHIC RELATIONSHIPS

Stratigraphic positions of the erinaceine insectivores discussed in this paper from Granite and Powell Counties, Montana, are illustrated in figure 18. Cabbage Patch beds shown in this figure range in age from medial to late Arikareean (late Oligocene and early Miocene), as based on correlations of the enclosed Cabbage Patch faunas to Arikareean faunas in the John Day of Oregon and Great Plains of South Dakota, Nebraska, and Wyoming. Cabbage Patch localities 2 (KU-Mt-9) and 4 (KU-Mt-12) and Bert Creek locality 2 (MV6504-2) occur within a single measured section. Cabbage Patch locality 13 (KU-Mt-46) occurs not far from this measured section and can be directly correlated into it. Because of poor exposures, erosional gaps, and distances up to several kilometers, correlation of Cabbage Patch locality 3 (KU-Mt-11) and Tavenner Ranch locality 2 (KU-Mt-21) to the measured section discussed above is difficult, but each can be approximately correlated using the stratigraphic position of the range zone of the gopher *Pleurolicus*. Thus, each locality is correlated by recording whether it occurs above, within, or below the *Pleurolicus* range zone. Likewise, an approximate correlation of this biostratigraphic zone can be made to the *Pleurolicus* range zone in the John Day Formation of Oregon (Rensberger, 1971:141, Fig. 69).

Ten of the eleven specimens of *Stenoechinus tantalus* occur at a single horizon and locality (Tavenner Ranch locality 2) in the upper Cabbage Patch beds above the *Pleurolicus* range zone. Although several rich fossil localities above and below this stratigraphic position of Tavenner Ranch locality 2 have been extensively searched and large bulk samples have been washed from some of them, only one other specimen of *Stenoechinus* has been found (at Cabbage Patch locality 13 which lies within the *Pleurolicus* range zone in the middle Cabbage Patch beds). Also occurring at Tavenner Ranch 2 is a partial maxillary (KU 18097) and partial isolated tooth (KU 18405) of *Amphelchimus horncloudi*. Other mammals found at this locality include *Nanodelphys*, *Peratherium*, *Domnina*, *Proscalops*, *Meniscornys*, *Niglarodon*, *Pacificulus*, *Leidyornys*, *Plesiosminthus*, *Gregoryornys*, *Mookornys*, *Paleocastor*, *Archaeolagus*, *Nothocyon*, *Leptomeryx*, and oreodonts, and will be reported on in a later paper by Rasmussen.

Two additional specimens of *Amphelchimus horncloudi* have been found within the *Pleurolicus* range zone in the middle Cabbage Patch beds (Fig. 18)—KU 18162 from Cabbage Patch locality 3, and KU 18163 from Cabbage Patch locality 2. Each was found associated with a fauna that is less varied but similar to that accompanying *A. horncloudi* at Tavenner Ranch locality 2, except that *Pleurolicus* is present and *Gregoryornys* is absent.

An upper second molar of a small erinaceine (KU 18346) was

found at Cabbage Patch locality 4 within the *Pleurolicus* range zone in the middle Cabbage Patch beds. Although more than one ton of matrix has been washed from this locality and several hundred specimens have been recovered, this is the sole record of a hedgehog in the fauna other than the genus *Ocajila*. Mammals from the locality include *Peratherium*, a mole, *Ocajila*, *Dommina*, *Allomys*, *Niglarodon*, *Pleurolicus*, *Mookomys*, a beaver, *Eutypomys*, *Archaeolagus*, an ochotonid, and *Diceratherium*.

A lower jaw of a small hedgehog (MPUM 1551) referred to *Parvericius montanus* was found in the middle Cabbage Patch beds in association with *Peratherium*, a beaver, *Pleurolicus*, and *Archaeolagus* at Bert Creek locality 2. The *Pleurolicus* specimens collected at this locality are among the most primitive in the Cabbage Patch beds, indicating this locality is near the base of the *Pleurolicus* range zone.

Several specimens of *Stenoechinus* have been found at Tavenner Ranch locality 2 in the Cabbage Patch beds and were not found at other localities stratigraphically above and below (except the single specimen from Cabbage Patch locality 13). Even at localities which were intensively sampled, the absence of *Stenoechinus* may be due to paleoecological differences among the various localities. The type locality of *Stenoechinus* (Tavenner Ranch locality 2) is uniquely rich in terrestrial gastropods, whereas all other localities where hedgehogs were found (including Cabbage Patch locality 13) have very numerous freshwater gastropods. The scarcity of freshwater gastropods and other aquatic organisms and the abundance of terrestrial animals at Tavenner Ranch locality 2 suggests that the area was relatively remote from aquatic environments during most of the episode of deposition of this particular bed. The sediment at Tavenner Ranch locality 2 is composed almost entirely of silt-sized glass shards with little clay and sand, and may have been partially wind-blown into the site of deposition. Root burrows are extremely common, indicating abundant vegetation. A grassy or wooded habitat in an area free from frequent flooding or standing water is indicated. Thus *Stenoechinus* may have lived in habitats which were drier than those indicated at the other localities where other types of hedgehogs have been found.

Two isolated lower molars and a mandibular fragment of *Parvericius montanus* were found in Fremont Co., east central Wyoming, in the upper porous sandstone sequence of the Split Rock Formation in association with mammals of the Split Rock local fauna considered to be of Hemingfordian age, medial Miocene (Love, 1961:24; Munthe and Lander, 1973:497). All these specimens were found at or near locality 11-V of Love (1970).

Two mandibles, three isolated lower teeth, and three isolated upper teeth of *Parvericius montanus* were found at Egelhoff Quarry in Keya Paha Co., north-central Nebraska, in an unnamed lithic

unit that unconformably overlies the Rosebud Formation and in turn is unconformably overlain by the Valentine Formation (R. H. Tedford, pers. com., 1972). In the same lithic unit and about 2 km southeast of Egelhoff Quarry, is the Norden Bridge Quarry in Brown Co., Nebraska, where an isolated M_1 of *P. montanus* was found. Both local faunas are regarded as Barstovian in age (C. W. Hibbard, pers. com., 1972).

The type of *Parvericius montanus* Koerner (1940), a maxilla fragment, was found in Meagher Co., central Montana, in the Deep River beds. Unfortunately, Koerner never published a complete faunal list for the Deep River beds. However, the oreodont material he collected and described (Koerner, 1940), together with his rodent and lagomorph specimens described by Black (1961), indicate that some parts of the unit (as Koerner conceived it) are of Arikareean age and other parts Hemingfordian. In other areas of North America, *Promerycochoerus* and *Paciculus* are known from Arikareean deposits while *Hypolagus* and *Monosaulax* are known from Hemingfordian or later deposits (Schultz and Falkenbach, 1949; Black, 1961; Dawson, 1958; R. W. Wilson, 1960).

CONCLUSIONS

In the Arikareean (latest Oligocene and earliest Miocene), a general faunal interchange of mammals, particularly small forms, took place between the Old World and North America after an extended interval of almost no interchange during the medial and late Oligocene (R. W. Wilson, 1968). It is at that time, and presumably as part of that episode of widespread interchange, that the North American history of the Erinaceinae appears to have begun with an invasion from Asia by at least two species. These are documented by the presence of two erinaceine species in Arikareean deposits of North America—*Amphexinus hornclouidi* and *Parvericius montanus*. Each species appears to be more closely related to known Oligocene species of Europe or Asia than to any other North American erinaceines. The Arikareean appearance of *Stenochinus tantalus* n. gen. and n. sp. in North America may be the result of yet another invasion immediately prior to the Arikareean. Or it is equally as likely that *S. tantalus* could represent the first record of a lineage endemic to North America through the Oligocene. Because no earlier species in either the Western or Eastern Hemisphere closely resembles *S. tantalus*, it is not possible at the present time to strongly support one alternative over the other. A poorly known species described here as "Erinaceinae, genus and species indet." may be congeneric with one of the three other species.

Largest of the North American erinaceine species, *Amphexinus hornclouidi* can be readily allied with the early Oligocene to early

Miocene European group *Amphexinus cayluxi*, *Amphexinus arvernensis*, and *Amphexinus edwardsi*. The three European species and *A. horncloudi* are all quite similar to one another in size and morphology; apparently little change took place in this group during the time of its existence.

Except for a somewhat deeper mandible, *Parvericius montanus* from North America is nearly identical to medial or late Oligocene east Asian specimens originally described by Bohlin (1942) as *Palaeoerinaceus minimus*. *Parvericius* would seem to be most similar and closely allied to *Amphexinus* among the known erinaceine genera but more primitive in the shorter length of the M^1 and M^2 relative to their respective widths and in the more anteroposteriorly compressed M_1 trigonid.

The M^2 described as "Erinaceinae, genus and species indet." appears to be yet another distinct species, because it is too large to be the M^2 of either *Parvericius montanus* or *Stenoechinus tantalus* and much too small to be the M^2 of *Amphexinus horncloudi*. In addition, it is distinguished from the M^2 of *Paleosaptor acridens* in having a more prominent parastylar spur, and the postprotocrista and postmetaconule crista developed as two distinct ridges rather than as one continuous ridge.

One of the three erinaceine genera described here has a post-Arikareean record in North America and a second one may. *Parvericius* survived until the late Barstovian; this genus has been found in the samples of that age collected at Egelhoff and Norden Bridge Quarries in north-central Nebraska. Rich will describe these specimens in a future paper. John Storer is describing three molar talonids of a large erinaceid of the proper size to be *Amphexinus*, collected at the medial Barstovian Kleinfelder Farm locality in southern Saskatchewan. Although none of the genera discussed here endured in North America after the Barstovian, the Erinaceinae were represented on this continent until at least Clarendonian time as attested by the presence of a single, isolated lower molar belonging to a member of this subfamily in the WaKeeney local fauna of Kansas (see R. L. Wilson, 1968: Fig. 12a-b).

SUMMARY

The history of the Erinaceinae in North America begins in the Arikareean (latest Oligocene and earliest Miocene) with the appearance of four species: *Amphexinus horncloudi*, *Parvericius montanus*, *Stenoechinus tantalus* n. gen. and n. sp., and Erinaceinae, genus and species indet. The first two species listed are more closely related to various species known from Oligocene deposits of Europe and Asia than to any North American ones; hence, at least two separate erinaceine groups appear to have invaded North America. Presumably these invasions took place immediately prior to the

first record of these species in North America and were part of an episode of renewed, widespread interchange of mammals between North America and the Old World that occurred at that time (R. W. Wilson, 1968). *Stenoechinus tantalus* is not closely related to any known earlier forms; therefore, the Arikareean record of this species may be either the first discovery of a lineage whose unknown Oligocene history was in North America, or the descendant of yet another group that invaded North America from Asia in the Arikareean. The fourth, poorly known species may have been derived from one of the stocks that gave rise to one of the first three mentioned species, or it may represent yet another lineage with an independent history extending well back into the Oligocene.

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